OFFPRINTS FROM SOIL BIOLOGY GUIDE
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Insecta: Coleoptera
Silphidae
and the Associated Families
Agyrtidae and Leiodidae

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The beetle superfamily Staphylinoidea contains some 10 families, of which the Ptiliidae, Staphylinidae, and Pselaphidae are covered in other chapters of this book. These families all share an intimate relationship with soil-associated habitats along with the families Silphidae, Agyrtidae, and Leiodidae: the subjects of this chapter. General keys to beetle families and a coverage of general beetle morphology can be found in introductory entomology texts such as Borror et al. (1976) or in general works on beetles such as Arnett (1963), Crowson (1967), Dillon and Dillon (1961), Jacques (1951), and Hatch (1953, 1957). Recent research efforts have reexamined evolutionary relationships between these groups and the classification followed here is that recently proposed by Lawrence (1982) and Lawrence and Newton (1982).

These three beetle families collectively spend most of their adult and larval lives in association with soil and its extensions; they usually function as scavengers and decomposers. Many occur in association with carrion, dung, decaying plant material, and fungi. They are important in ecosystems in promoting recycling of nutrients. A few specialized scavengers have become guests in nests of social insects, in burrows and nests of ground-dwelling vertebrates, as ectoparasites of some mammals, and as blind and wingless inhabitants of deep soil and caves.

Members of these families are often collected through general sampling of soil, litter, and decomposing organic matter. A program using pitfall traps baited with various materials (Newton and Peck 1975, Southwood

1966) can yield data on food and habitat preferences, seasonality, reproductive activity, and so on. To collect most genera in these families, one must concentrate on their special habitats and habits.

The Family Silphidae

These are the large carrion beetles. They are 10–35 mm long, often brightly colored, and are commonly found with the bodies of dead animals. They are most closely allied to the family Staphylinidae (Lawrence and Newton 1982) from which they may be separated by their clavate or capitate 10- or 11-segmented antennae with dense pubescence on at least segments 9–11, by their large and conical front coxae, and enlarged pronotum. The elytra often bear red or orange markings, and the tarsi are always five-segmented. The members of the family vary much in shape, from almost circular to elongate–oblong, and from flattened to strongly convex. The elytra vary from short and truncate (exposing last three dorsal abdominal segments), to apically rounded or acute.

In many species the adults and larvae feed on carrion and in at least some cases on fly larvae. Some seem to be more associated with decaying fungi or vegetable matter, and one genus is strictly phytophagus. In Eurasia some genera are predatory specialists on snails and caterpillars. In all cases, though, the silphids are intimately tied in the completion of their life cycle to ground and soil habitats.

The attractive red or orange and black *Nicrophorus* (Fig. 37.1) are called burying beetles because they can rapidly excavate the soil from under a dead mouse or other small animal until the body sinks into the ground. They exhibit a very interesting parental care, and the larvae are fed by a parent through regurgitation (work of Pukowski, abstracted by Balduf 1935). Stridulation may be used for inter- and intraspecific communication (Bredohl 1984, Niemitz 1972, Schumacher 1973). Verification of these biologies and a comparative-evolutionary study of *Nicrophorus* biology has not been made for North American species (see Milne and Milne 1944, 1976).

It is amazing that so little is known in North America about the general biology, ecology, and natural history of these large, attractive, and easy-to-collect beetles. Some studies have examined the entire community of carrion insects and the position of silphids in the process of faunal succession (Johnson 1975, Payne, 1965, Payne and King 1970, Reed 1958, Walker 1957). Many studies have looked at limited aspects of the biology of all or a few silphids in a limited geographic area (Shubeck 1969, Shubeck et al. 1977). Older literature indicates that various species have preferences for the carrion of certain classes of vertebrates, but there now seems to be little basis to believe that the beetles choose between the carrion of homiotherm or poikilotherm vertebrates (Shubeck 1976). Olfactory sensitivity is of primary importance in locating carrion. Early studies were concerned with locating the sense organs (Dethier 1947, and references) but modern electrophysiological studies have precisely identified the sense receptors and some of the specific decay compounds that activate them (Waldow 1973). The effect of wind in locating carrion is important (Shubeck 1968). Silphids have reduced interspecific competition by "dividing" their carrion resource in several ways. There are differences in the season in which a species is most active (Anderson 1982a), in their diel periodicities (Shubeck 1971), in the age of the carrion that they can use, and in habitat preferences (Anderson 1982a) (e.g., such as upland forests, swamp forests, open grassy or steppe habitats, and boreal versus warm temperature forests). But so little is yet known of their present-day ecologies that although they can be locally common as fossils in Pleistocene deposits, they are not yet useful indicators of paleoecological or paleoenvironmental conditions (Miller and Peck 1979). The size of the carrion resource may also be important in resource partitioning. The Silphinae seem to be abundant as adults and larvae on large carcasses as well as on small ones, but the Nicrophorinae seem to use only smaller carcasses for reproductive purposes.

The beetles may generally act to maintain ecosystem health and productivity by aiding the recycling of nutrient matter. While doing so they reduce the frequency of occurrence and suitability of carrion as a site of fly oviposition and maggot development. Their feeding activities may also destroy potential foci of infection of pathenogenic bacteria or parasitic worms. Rabies virus (but not anthrax bacteria) is inactivated in the gut of *Nicrophorus* (Sidor 1970), which also phoretically carry *Poecilochirus* and several other mites (Springett 1968, Wilson 1983) and several species of nonpathogenic nematodes as commensals (Theodorides 1950). Detailed studies of *Nicrophorus* ecology have been done only on species in Michigan (Wilson and Fudge 1984, Wilson and Knollenberg 1984, Wilson et al. 1984).

Systematics

Much of the existing literature is difficult to use in making determinations of North American silphids. Because of the widespread and growing interest in them and the lack of comprehensive keys, the following is provided, which should allow determination of all species in North America north of Mexico, based on a modern understanding of their systematics. It is modified from a manuscript key of world genera and North American species of Silphidae by Dr. R. B. Madge, Commonwealth Institute of Entomology, London. The generic placement of North American species of Silphinae is somewhat confused in the older literature. The silphine genera used in the following key are not the traditional ones for North America, but do bring the fauna into evolutionary perspective with the world fauna, and should help establish stability in nomenclature. Anderson and Peck (1985) present keys and distribution maps for Canadian and Alaskan spe-

cies. Distribution and bionomics of the U.S. species are summarized by Peck and Kaulbars (1988). Anderson (1982b) and Anderson and Peck (1985) give data on all known larvae. The fauna of Latin America is reviewed by Peck and Anderson (1985a) and phylogenetic relationships are proposed. A complete systematic catalog is that of Peck and Miller (1989).

Morphological Characters

Males usually have broadly expanded protarsal segments, while those of the female resemble the segments on the other legs. The outer and bent-under margins of the elytra are the epipleura (sing., epipleuron). The elytra may have one to three upraised ridges or costae (sing., costa). A raised area or callus may occur near the posterior end of the outermost costa. The elytral suture is where the two elytra meet at the midline. The elytra of *Nicrophorus* have broad and transverse red or yellow-orange bands called fasciae. Surface microsculpture and hairs may be difficult to see in worn, greasy, or dirty specimens (which should be cleansed in a warm detergent–ammonia solution).

ACKNOWLEDGMENTS

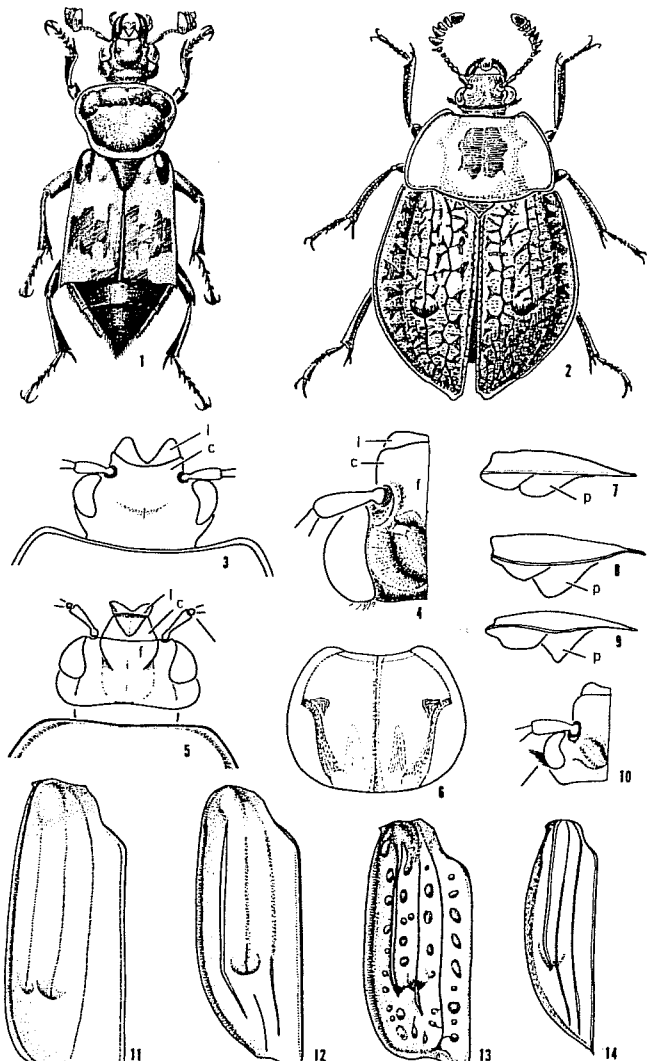
I thank Robert Anderson, J. M. Campbell, Ronald B. Madge, Scott E. Miller, Alfred F. Newton, Paul Shubeck, and Quentin D. Wheeler for sharing their research results and helping me to achieve an up-to-date understanding of the beetles covered in this chapter, and for checking part or all of the manuscript. Jarmila Kukalova-Peck lovingly prepared the illustrations. Field and laboratory research on soil and litter scavenging beetles has been supported by operating grants from the Natural Sciences and Engineering Research Council of Canada (NSERCC).

KEY TO SUBFAMILIES, GENERA, AND SPECIES OF U.S. AND CANADIAN SILPHIDAE†

1a Frontoclypeal suture absent (Figs. 37.3, 37.4); elytra usually tricostate and tips usually prolonged at suture; antennae distinctly 11-segmented (second segment about as long as third), gradually widening into club; gula strongly constricted medially (fifth abdominal tergum without a pair of stridulatory files); Subfamily **Silphinae** **2**

1b Frontoclypeal suture present (Fig. 37.5); elytra always smooth and truncate; antennae apparently 10-segmented (the second segment being very short and more or less hidden in the tip of the first, Fig. 37.5); last four segments abruptly widened into a distinctly swollen club; gula absent except for narrow triangular piece anteriorly (fifth abdominal tergum with a pair of midlongitudinal stridulatory files); Subfamily **Nicrophorinae**, Genus ***Nicrophorus*** Fabricius, 1775 (Fig. 37.1) **16**

† Key prepared by Ronald B. Madge and Stewart B. Peck.



Figs. 37.1–37.14. **1.** *Nicrophorus marginatus* female. **2.** *Necrophila americana* female. **3.** Head of *Aclypea bituberosa* (*c*, clypeus; *l*, labrum). **4.** Head of *Oxelytrum discicolle* (*c*, clypeus; *f*, frons; *l*, labrum). **5.** Head of *Nicrophorus marginatus*, symbols as in 4. **6.** Pronotum of *Necrodes surinamensis*. **7.** Lateral view of pronotum *Necrodes surinamensis* (*p*, pronotal postcoxal lobe). **8.** Lateral view pronotum *Thanatophilus trituberculatus*. **9.** Lateral view pronotum *Thanatophilus sagax*. **10.** Head *Oiceoptoma inaequale*. **11.** Elytron *Thanatophilus truncatus*. **12.** Elytron *Thanatophilus coloradensis*. **13.** Elytron *Thanatophilus lapponicus*. **14.** Elytron *Oxelytrum discicolle* female.

2a (1a) Postcoxal lobe of pronotum (seen in side view) short and broadly rounded (Fig. 37.7); moderate to large males (with expanded protarsi) with metafemora swollen and toothed toward apex; pronotum orbicular, widest toward middle (Fig. 37.6) . . . . . Genus ***Necrodes*** Leach, 1815

Our only species is ***N. surinamensis*** (Fabricius); widely distributed in the United States and southern Canada in farmland, prairie, and forests, often in great numbers. Ratcliffe (1972) has summarized the natural history.

2b Postcoxal lobe of pronotum well developed, usually angular (Figs. 37.8, 37.9); metafemora of males never toothed or swollen; pronotum usually widest toward base and not as markedly orbicular 3

3a (2b) Eyes very large (Fig. 37.4); underside of elytra with many longer hairs in region of posterior callus (raised tubercle) (careful positioning of the light is required to see them) . . . Genus ***Oxelytrum*** Gistel, 1848

Several species occur in the Neotropics, but only the most widespread, ***O. discicolle*** (Brullé) (Fig. 37.14), has crossed the Rio Grande into extreme southern Texas.

3b Eyes smaller, underside of elytra without longer hairs in region of posterior callus (at most with a fine tomentum of microsetae) 4

4a (3b) Head with a short row of prominently longer and more erect hairs on side just behind eyes (Figs. 37.2, 37.10) (styli of female genitalia with terminal setae extending along outer face, coxites curving down) 5

4b Head without a short row of prominently longer, more erect hairs just behind eyes (styli of female genitalia with terminal setae restricted to apex or curving around apex; coxites variable) 10

5a (4a) Elytral shoulders with small tooth (Fig. 37.19); posterior face of metafemora without carinae (female genitalia with styli small); Genus ***Oiceoptoma*** Leach, 1815 6

5b Elytral shoulders rounded; posterior face of metafemora with two carinae 8

6a (5a) Pronotum bicolored, with a black disk and broad orange margins; metatibiae in female abruptly enlarged on apical third . . . . . ***O. noveboracense*** (Forster)

Widespread in more northerly parts of eastern and north-central United States and southern Canada; most active in spring and early summer.

6b Pronotum entirely black; metatibiae in female not abruptly enlarged on apical third 7

7a (6b) Elytral epipleuron wide (i.e., on posterior half the upper oblique part is at least twice the width of the lower vertical part) (Fig. 37.17) . . . ***O. inaequale*** (Fabricius)

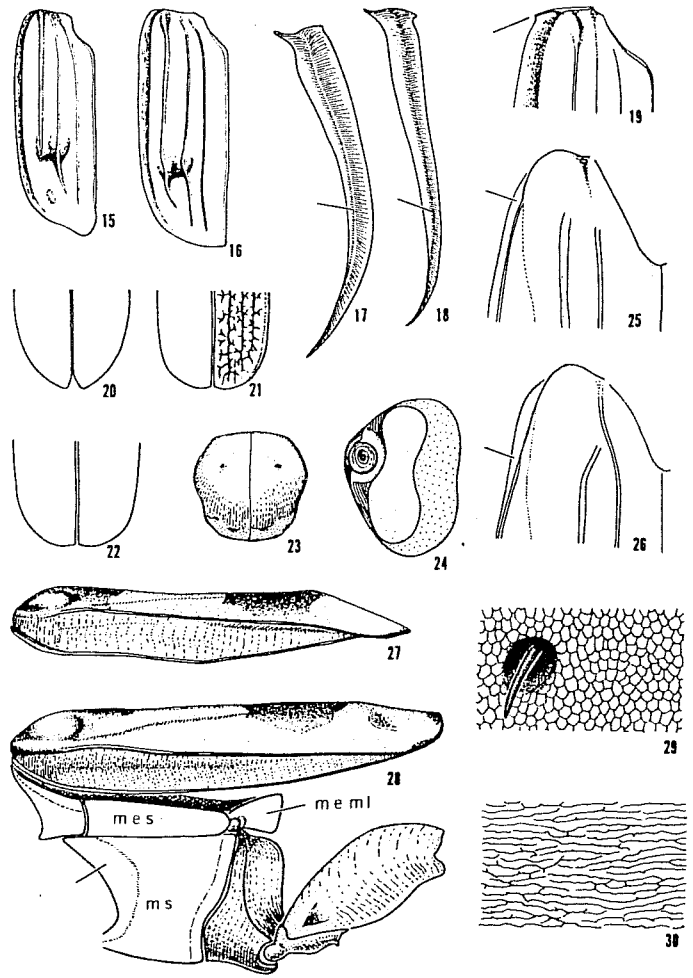
Widespread in eastern North America; active in spring and early summer.

7b Elytral epipleuron narrow (i.e., on posterior half the upper oblique part is subequal to lower vertical part) (Fig. 37.18). . . . . ***O. rugulosum*** (Portevin)

This has a poorly understood distribution in the southeastern United States from southern Indiana to Florida and Texas; previously confused with foregoing species.

8a (5b) Pronotum black, entirely covered with a simple dense punctuation; (female genitalic styli short); Genus ***Heterosilpha*** Portevin, 1926 . . . 9

8b Pronotum bicolored and with elongated punctures; (styli of female genitalia large, usually extending beyond apex of coxite) . . . . . Genus ***Necrophila*** Kirby and Spence, 1828



Figs. 37.15–37.30. 15. Elytron of *Thanatophilus trituberculatus*. **16.** Elytron of *Thanatophilus sagax*. **17.** Epipleuron of *Oiceoptoma inaequale*. **18.** Epipleuron of *Oiceoptoma rugulosum*. **19.** Elytral humeral angle *Oiceoptoma inaequale*. **20.** Elytral tip *Heterosilpha ramosa* female. **21.** Elytral tip *Heterosilpha ramosa* male. **22.** Elytral tip *Heterosilpha aenescens* male and female. **23.** Pronotum *Nicrophorus carolinus*. **24.** Interior face tenth antennal segment *Nicrophorus investigator*. **25.** Elytral humeral angle *Nicrophorus pustulatus*. **26.** Elytral humeral angle *Nicrophorus orbicollis*. **27.** Epipleuron *Nicrophorus investigator*. **28.** Elytral epipleuron and part of thorax *Nicrophorus hybridus* (*meml*, metepimeral lobe; *mes*, metepisternum; *ms*, metasternum with anterior bald patch). **29.** Isodiametric or granular microsculpture of elytral disk *Nicrophorus vespilloides*. **30.** Transverse meshwork or brick-wall microsculpture elytral disk *Nicrophorus orbicollis*.

North America's sole species, ***N. americana*** (Linnaeus) (Fig. 37.2) has distinctive yellow pronotal margins; commonly and widely distributed in eastern and central North America in open and forested habitats, active from spring to fall. It may mimic bumble bees (Fisher and Tuckerman 1986).

9a (8a) Males (eighth abdominal tergum with apex truncate or concave) with pro- and mesotarsal segments 1–4 broadly expanded, and elytral apex not drawn out (Fig. 37.21); females (eighth abdominal tergum with apex rounded) with elytra drawn out at apex (Fig. 37.20); male genitalia thicker and broader, parameres with apices thick and downcurved (Figs. 37.33, 37.34); elytra without metallic shininess. . . . . ***H. ramosa*** (Say)

Widespread in western and north-central North America. See Brewer and Bacon (1975) for biology.

9b Males with pro- and mesotarsal segments 1–4 not expanded; male genitalia more thin and slender, parameres with apices more narrow and straight (Figs. 37.31, 37.32); males and females with elytra not drawn out at apex; (Fig. 37.22); elytra often with metallic shininess ***H. aenescens*** (Casey)

Ranges from Baja California north to Oregon, west of the Sierra–Cascade mountains (Miller and Peck 1979).

10a (4b) Antennae placed closer to eye than to labrum; temples not swollen; labrum broadly and shallowly emarginate; mesocoxae widely separated; elytra flat at apex; eyes normal, comparatively large (female genitalia with coxites curving up); Genus ***Thanatophilus*** Leach, 1815 **11**

10b Antennae as close to, or closer to, labrum than to eye; temples swollen; labrum sharply and deeply emarginate (Fig. 37.3); mesocoxae more narrowly separated; elytra curved down near apex; eyes comparatively small; (female genitalia with coxites curving down); Genus ***Aclypea*** Reitter, 1884 . . . . . **15**

11a (10a) Elytra without costae (costae effaced), and abruptly truncate (Fig. 37.11) . . . . . ***T. truncatus*** (Say)

Southwestern United States in desert, scrub, and open forests.

11b Elytra with costae **12**

12a (11b) Elytra with tubercles between costae (Fig. 37.13). . . . . ***T. lapponicus*** (Herbst)

Throughout Alaska, Canada, northeastern United States, and the southwest to New Mexico, Arizona, and California; in forest, grassland, and arctic–alpine tundra habitats. Also occurring in Eurasia.

12b Elytra without tubercles between costae. **13**

13a (12b) Inner two elytral costae absent (effaced) except at apex (Fig. 37.12); eighth abdominal segment orange . . . . ***T. coloradensis*** (Wickham)

Only at treeline and above in arctic–alpine tundra in the Rocky Mountains from New Mexico to Alaska (Peck and Anderson 1982).

13b Elytra with three fully developed costae; eighth abdominal segment black **14**

14a (13b) Outer elytral costa extending beyond apical callus (Fig. 37.16); postcoxal lobe of pronotum pointed (Fig. 37.9); female with sutural apices of elytra not prolonged but similar to those of male (Fig. 37.16). . . . ***T. sagax*** (Mannherheim)

Pacific northwest, north-central states, central and northern Canada, and Alaska.

14b Outer elytral costae ending at apical callus (Fig. 37.15); postcoxal lobe of pronotum broadly rounded (Fig. 37.8); female with sutural apices of elytra prolonged (Fig. 37.15) . . . . . ***T. trituberculatus*** (Kirby)

Central and northern Canada and northern Alaska.

15a (10b) Pronotum with narrower anterior margin near middle; margin at anterior angle flatter; often with impunctate (smooth) spot on anterior third behind the eye (in addition to other spots near midline and along base) . . . . . ***A. opaca*** (Linnaeus)

A Eurasian species in the far north of Canada and Alaska (Anderson and Peck 1984).

15b Pronotum with wider anterior margin near middle; margin at anterior angle more upcurved; never with impunctate spot on anterior third behind eye (although other spots may be present) . . . . . ***A. bituberosa*** (LeConte)

Phytophagous on native **Chenopodiaceae** and various garden and crop plants like spinach and sugar beets. In western prairie and mountain states; Nebraska to California, north to Northwest Territories. Active in early spring. See Cooley (1917) and Anderson and Peck (1984) for biology.

16a (1b) Pronotum (Fig. 37.23) without an anterior transverse impression; with extremely narrow lateral margins; and with distinct punctures along base . . . . . ***N. carolinus*** (Linnaeus)

Widely distributed but most commonly found in the southeastern coastal plain northward to central plains states and adjacent Canada; usually in open (mesic to arid) habitats.

16b Pronotum (Fig. 37.1) with an anterior transverse impression, distinct at least at sides of disk; lateral margins not extremely narrow; base without distinct punctures **17**

17a (16b) Frons and pronotal disk red; abdominal sterna with setae along posterior margins much shorter on basal than on apical segments; tarsal empodium normally quadrisetose . . . . . ***N. americanus*** Olivier

This, our largest species, was formerly widely distributed in the eastern United States and into extreme southern Ontario (in heavily forested habitats?). The species has been only rarely taken in the past few decades and may be endangered or extinct over most of its former range (Anderson 1982c).

17b Frons and pronotal disk black; abdominal sterna with marginal setae (especially at middle) long on both basal and apical segments; tarsal empodium bisetose **18**

18a (17b) Pronotum covered with dense golden pubescence except for two small spots on disk; seventh abdominal tergum covered with dense semierect pubescence . . . . . ***N. tomentosus*** Weber

Widely distributed over eastern and central United States and southern Canada in both forested and open habitats. In behavior and appearance it seems to be a bumblebee mimic (Fisher and Tuckerman 1986).

18b Pronotum glabrous or with only sparse hairs anteriorly and on margins; seventh abdominal tergum with short, sparse, depressed hairs **19**

19a (18b) Posterior lobe of metepimeron (Fig. 37.28) with many long, golden hairs **20**

19b Posterior lobe of metepimeron with dark hairs or only a few short golden hairs, or glabrous **22**

20a (19a) Anterior face of procoxae with very long hairs on basal half; middle black band of elytra usually reaching the dorsal ridge of the epipleuron; inner face of metatibiae with a dense brush of hair. **21**

20b Anterior face of procoxae without very long hairs on basal half; middle black band of the elytra never reaching the dorsal ridge of the epipleuron; inner face of metatibiae with sparse hair . . . . . ***N. marginatus*** Fabricius

Widely distributed across the United States and southern Canada; in open grassland, old-field areas, desert scrub, and sagebrush steppe habitats.

21a (20a) Next-to-last antennal segment with outer edge usually deeply emarginate (Fig. 37.36); basal segment of antennal club black; anterior black elytral band reaching epipleural ridge but not significantly crossing onto epipleuron; posterior elytral fascia reaching dorsal ridge of epipleuron . . . . . ***N. obscurus*** Kirby

Distributed in prairies of central Canada and the United States.

21b Next-to-last antennal segment with outer edge usually only shallowly emarginate (Fig. 37.35); basal segment of antennal club red or black; *if* red, then anterior black elytral band crossing over epipleural ridge onto epipleuron; posterior elytral fascia may or may not reach dorsal epipleural ridge; *if* basal antennal segment black, then elytral markings very reduced or absent . . . . . ***N. gutula*** Motschulsky

This species is widespread across the western United States and adjacent southern Canada; in grassland, shrub, and open montane forest habitats; usually all black in the Pacific northwest except for reddish elytral shoulders; populations (to which the name ***N. hecate*** Bland has been applied) inland from the Pacific coast and in the Rocky Mountain states have normal to widely expanded fasciae. Geographic variation is discussed by Anderson and Peck (1986).

22a (19b) Metatibiae curved; basal black band of elytra not reaching the epipleuron . . . . . ***N. sayi*** Laporte

The species is widely distributed in the more temperate parts of eastern North America and northwest to Alberta; in forested habitats; usually active in very early spring.

22b Metatibiae straight; basal black band of elytra usually reaching the epipleuron **23**

23a (22b) Elytral disk with strong isodiametric microsculpture (appearing as equidimensional or granular units at magnification of about 100–150×) (Fig. 37.29) **24**

23b Elytral disk with microsculpture arranged in fine transverse lines or meshes (appearing as an irregular "brick-wall" pattern of units at magnification of about 100–150×) (Fig. 37.30) **27**

24a (23a) Metasternal pubescence brown; metepisternum (Fig. 37.28) with pubescence long and well developed; anterior margin of pronotum straight **25**

24b Metasternal pubescence golden; metepisternum with pubescence short and poorly developed; anterior margin of pronotum concave **26**

25a (24a) Elytral disk entirely black (very rarely with small red spots) . . . . . ***N. nigrita*** Mannerheim

The species is limited to a wide strip, in and west of the Sierra–Cascade mountain range, paralleling the Pacific, from southern British Columbia to southern California; usually in openly forested habitats.

25b Elytral disk distinctly bifasciate . . . . . ***N. mexicanus*** Matthews

Distributed in the southern Rocky Mountain states southward; in sparsely forested habitats.

26a (24b) Base of epipleuron orange with a postbasal black spot; both upper and lower faces of antennal segments 9 and 10 with a patch of dense white hairs arranged in a figure-eight pattern across base (Fig. 37.24) ***N. vespilloides*** Herbst

Distribution across northern United States and throughout Canada and Alaska; in forested habitats that are colder, and wetter (usually marshy, boggy, or swampy); also occurring in Eurasia; commonly confused with the following species.

26b Base of epipleuron all black, antennal segments 9 and 10 without a patch of dense white hairs (figure-eight pattern may be present as faint vestige only) . . . . . ***N. defodiens*** Mannerheim

Distribution in more northerly localities in the United States and across Canada, and in better drained or drier forests; from Alaska to central California in the west, and penetrating the southeast in the upper elevation forests of the Appalachian Mountains. Geographic variation is discussed by Anderson and Peck (1986).

27a (23b) Elytral epipleuron black **28**

27b Elytral epipleuron orange-red **29**

28a (27a) Dorsal ridge of epipleuron short, reaching anteriorly only to level of tip of scutellum (Fig. 37.26); elytra bifasciate . . . . . ***N. orbicollis*** Say

One of the most common species in forested habitats in eastern and central North America.

28b Dorsal ridge of epipleuron long, reaching anteriorly to level of basal third of scutellum (Fig. 37.25); elytra with only small posterior fascia ***N. pustulatus*** Herschel

Widely distributed in forested habitats in eastern North America and northwest to Alberta.

29a (27b) Metasternum with elongate bald patch just behind mesocoxae (Fig. 37.28); with continuous multiple and irregular rows of stout and erect hairs running from anterior face of elytral shoulder to base of epipleural ridge; elytral epipleuron narrow, the dorsal ridge usually straight or curving gently upward at posterior end (Fig. 37.28); moderate to large males with free apical process of metatrochanter strongly bent back. . . . . ***N. hybridus*** Hatch and Angel

Distributed in northern plains and Rocky Mountain states into adjacent Canada; in open and sparsely forested habitats.

29b Metasternum without an elongate bald patch just behind mesocoxae; multiple irregular rows of hairs on elytral shoulder, but ending well before the base of epipleural ridge; elytral epipleuron wide, the dorsal ridge usually curving down at posterior end (Fig. 37.27); moderate to large males with free apical process of metatrochanter not strongly curved back . . . . . ***N. investigator*** Zetterstedt

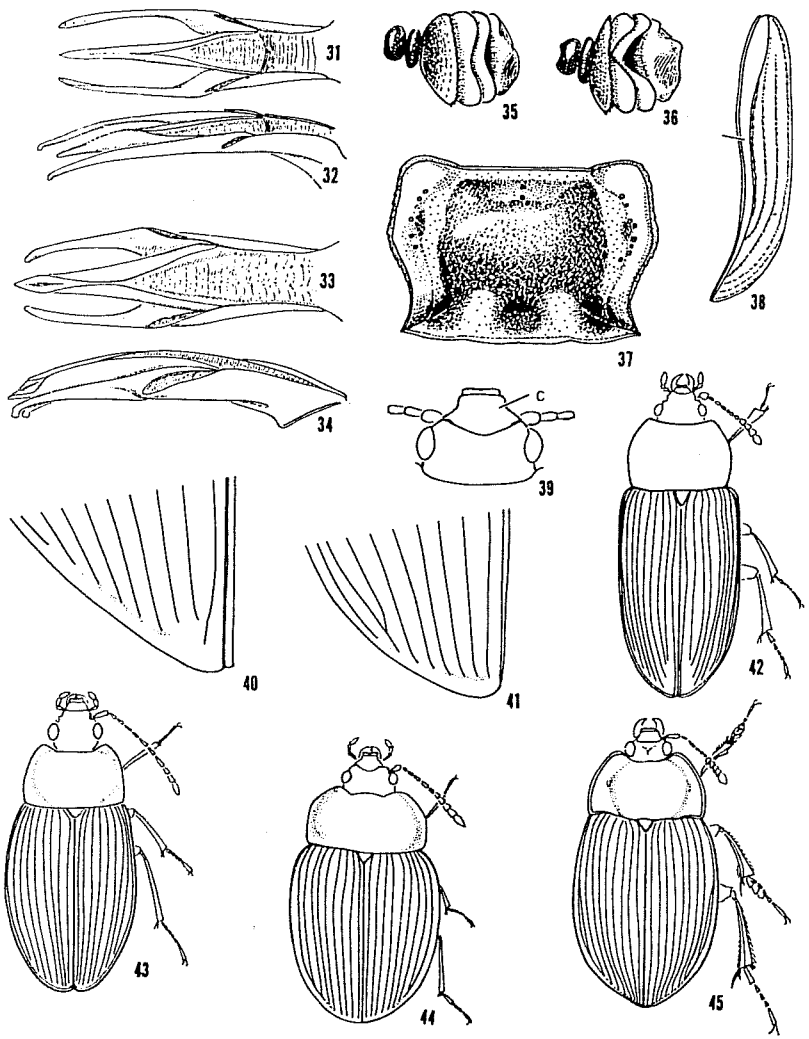
Widely distributed across Canada and southward along the Rockies to New Mexico; in forested habitats; also occurring in Eurasia. Geographic variation is discussed by Anderson and Peck (1986).

Family Agyrtidae

Members of this family have no common name. They have traditionally been included within the Silphidae, but recent study interprets them to have many adult and larval characters that separate them from the staphylinid-like silphids, and more closely allying them with the Leiodidae (Lawrence and Newton 1982). Very little is known of their general biology. They seem to be general scavengers and may frequently be baited with carrion. Their greatest diversity is in the Pacific Northwest, and only one species occurs in eastern North America. They are usually associated with litter and soil habitats, although most species of *Pteroloma* and *Apteroloma* seem connected with streamside or other cool, moist habitats in montane

areas and may be locally common on snowfields at night, feeding on dead insects.

The family is most easily separated from the Silphidae by the nontruncate elytra, which bear 9 (or 10) punctate striae (Figs. 37.42–37.45). The antennae are filiform or only gradually clavate, and there are five or six



Figs. 37.31–37.45. 31,32. Aedeagus of *Heterosilpha aenescens*. **33,34.** Aedeagus of *Heterosilpha ramosa* (after Miller and Peck). **35.** Antennal club *Nicrophorus gutula*. **36.** Antennal club *Nicrophorus obscurus*. **37.** Pronotum *Pteroloma nebrioides*. **38.** Epipleuron *Agyrtes longulus*. **39.** Head *Ipelates latus*. **40.** Elytral tip *Apteroloma caraboides*. **41.** Elytral tip *Apteroloma tahoecum*. **42.** *Agyrtes longulus*. **43.** *Apteroloma tenuicorne*. **44.** *Ipelates latus*. **45.** *Necrophilus hydrophiloides*.

visible abdominal sternites (always six in the Silphidae). Additional description, characters, or detailed distributions are given by Lawrence (1982) and Lawrence and Newton (1982), and Anderson and Peck (1985).

Key to Genera and Species of U.S. and Canadian Agyrtidae†

1a Dorsal ridge of elytral epipleuron (in side view) depressed behind shoulder (Fig. 37.38); last segment of maxillary palp swollen; Genus ***Agyrtes*** Frölich, 1799 2

1b Dorsal ridge of elytral epipleuron evenly curved from shoulder to apex; last segment of maxillary palp not inflated 3

2b (1a) Antennal club of four segments; posterior angles of pronotum sharp; elytral epipleuron glabrous; aedeagus in side view with pronounced bend . . . . . ***A. longulus*** (LeConte)
Fig. 37.42. From southern California to Alaska, inland to Idaho; seemingly most active in winter months; presumably a forest litter scavenger (Hatch 1957, Peck 1974b).

2b Antennal club of five segments; posterior angles of pronotum rounded; elytral epipleuron hairy; aedeagus in side view relatively straight . . . . . ***A. similis*** Fall
Limited to mountain forests in southern California; active in winter months; presumed scavenger (Peck 1974b).

3a (1b) Last five or six segments of antennae with uniform vestiture of microsetae (plus ring of long tactile setae); segments 1–5 or 6 with only a ring of tactile setae; tenth segment transverse; Genus ***Necrophilus*** Latreille, 1829. 4

3b Antennal segments evenly pubescent (in addition to tactile setae), the pubescence gradually becoming shorter and denser apically; tenth segment usually elongate 5

4a (3a) Winged; metasternum long; first abdominal spiracle large and eliptical ***N. hydrophiloides*** Guérin-Méneville
Fig. 37.45. In moist, forested sites from coastal southern California to southern Alaska; often carrion scavenger (Hatch 1957).

4b Wingless; metasternum short; first abdominal spiracle almost circular ***N. pettitii*** Horn
A deep litter and soil scavenger; from New York, Ontario, and Missouri south to Louisiana and northern Florida; most frequently found at high elevations in the southern Appalachians (Peck 1981a).

5a (3b) Posterior coxae distinctly separated; wingless; elytra completely without shoulders . . . . . Genus ***Lyrosoma*** Mannerheim, 1953
The only North American species is ***L. opacum*** Mannerheim, known from Alaskan coastal and island sites, where it feeds on decaying seaweed in and above the tidal zone (Hatch 1957).

5b Posterior coxae contiguous; winged or wingless; elytra with well-marked shoulders 6

6a (5b) Clypeus transversely "pentagonal" in shape (Figs. 37.39, 37.44); mandibles not toothed; preapical antennal segments with a sharp ridge around apex of each segment. . . . . Genus ***Ipelates*** Reitter, 1884
The only North American species is ***I. latus*** (Mannerheim) (Fig. 37.44); from northern California to Alaska and Alberta; a forest litter inhabitant, often under bark, and apparently feeding on fleshy fungi (Hatch 1957, Schwaller 1983).

† Prepared by Ronald B. Madge and Stewart B. Peck.

6b Clypeus rectangular or trapezoidal; mandibles toothed; preapical antennal segments without a sharp ridge around apex of each segment **7**

7a (6b) Pronotum with a strong depression in each posterior angle and at middle of base (Fig. 37.37); tibiae with a longitudinal dorsal ridge; frons usually with two pale "ocelli" or "eyespots"; protarsi of males scarcely widened; aedeagus with a single large paramere . . . . . Genus ***Pteroloma*** Gyllenhal, 1827

The only North American species is ***P. nebrioides*** Brown of the Rocky Mountains of British Columbia, Alberta, and Montana (Hatch 1957).

7b Pronotum without basal impressions; tibiae without a longitudinal dorsal ridge; protarsi of males strongly widened; aedeagus without parameres; Genus ***Apteroloma*** Hatch, 1927 . . . . . **8**

8a (7b) Elytral epipleuron without punctures **9**

8b Elytral epipleuron densely punctate along lower margin. **10**

9a (8a) Internal angle of elytral apex evenly rounded (Fig. 37.41); pronotum strongly transverse, base more than one and a half times the length along midline. . . . . ***A. tahoecum*** (Fall)

A scavenger of forest stream margins in the Sierra Nevada mountains of California and adjacent Oregon (Hatch 1957).

9b Internal angle of elytral apex sharp (often with broad tooth) (Fig. 37.40); pronotum only slightly transverse; base less than one and a third times the length along the midline . . . . . ***A. caraboides*** (Fall)

A rare scavenger from northern California to British Columbia and Idaho (Hatch 1957).

10a (8b) Posterior angles of pronotum obtusely angulate. . . . . ***A. arizonicum*** (Van Dyke)

A rare scavenger of mountain forest streamsides, from Arizona, New Mexico, and possibly mountains of west Texas; seemingly active in fall and winter.

10b Posterior angles of pronotum rounded (Fig. 37.43). . . . . ***A. tenuicorne*** (LeConte)

Often abundant in montane areas at streamsides or damp and wet habitats and at edges of (and at night upon) melting snowfields; from British Columbia and southern Alberta to California and Colorado (Hatch 1957).

The Family Leiodidae

The family Leiodidae is composed of small beetles, from 1 to 8 mm in length; usually of an ovoid shape; and usually with 11-segmented antennae with an interrupted five-segmented club, with segment 8 smaller than 7 and 9. Other antennal conditions occur but are less common. What are grouped here have been variously placed elsewhere under the names Catopidae, Cholevidae, Leptodiridae, Anisotomidae, Colonidae, Leptinidae, and Platypsyllidae. A consistent family feature (although difficult to observe) is the shared derived character of a usually nearly enclosed gutter ringing the antennal articulation on the dorsal face of segments 7, 9–10, or 8–10 or (in 10-segmented antennae) 7–9. These segments often have internal sensory vesicles opening into the gutter (Peck 1977a). Further characterization is given in Lawrence (1982) and Lawrence and Newton (1982). This section follows Newton's (1984) newly proposed higher classification within what now seems to be a monophyletic family.

The members of the family are for the most part scavengers; inhabiting decaying litter, leaves, fungi (see Newton 1984), moss and grass roots, and the subcortical region of dead trees. Some species live on carrion, may be attracted to dung, and occur in the nests of ants, in caves, and the burrows of ground-dwelling reptiles, birds, and mammals. The habits of the individual subfamilies are fairly diverse and are discussed separately below.

The Subfamily Leptininae

These are very dorsoventrally flattened, louselike beetles, 2–5 mm long, with eyes reduced or absent. They are called mammal nest beetles, and have been traditionally treated as a separate family. However, they have internal antennal vesicles on antennal segments 9 and 10, an advanced character for the leiodid assemblage, and represent a line of Cholevinae character for the leiodid assemblage, and represent a line of Cholevinae (Catopinae) that has become specialized for a life of ectoparasitism on small mammals. *Leptinus* is occasionally found in soil and leaf litter, but more frequently on various voles, moles, and shrews, and in their nests, and rarely, in old nests that have been occupied by bumblebees and *Vespula* wasps (Peck 1982). They may questionably be a guest in *Formica* ant nests.

The Subfamily Cholevinae

These have been variously placed under the names Catopidae and Leptodiridae, and Catopinae of the Leiodidae. Zwick (1979) has shown that the family group name Cholevinae has priority over Catopinae. These may be called the small carrion beetles. They are elongate–oval; pale brownish, to brown, to black; and 2–6 mm in length. They often have a pronotum and elytra with a finely granulate surface or with faint cross striations or strigae. Their eighth antennal segment is always shorter and smaller in diameter than the seventh and ninth segments. The tarsal formula is almost always 5–5–5. These fragile, rapidly running beetles are mostly found on vertebrate carrion, but may act as more general litter decomposers by feeding on the bodies of terrestrial arthropods and decaying plant material. Some are found most frequently on decomposing fungi, in caves on moist organic matter such as bat and cricket guano, and in the nests of ants, where they are probably scavengers. They may be collected in their special microhabitats, or by setting large or small dung and carrion baited pitfall traps (Newton and Peck 1975, Zwick 1979), and by sifting rotting leaves, forest litter, moss, and grass roots. Baited traps can be used to determine seasonality and habitat preferences of the species (Peck and Anderson 1985b).

The Subfamily Coloninae

Little is known of the biology and general natural history of this subfamily. All species are in the single genus *Colon*. The beetles have a characteristic facies that is easy to distinguish when once seen. The antennal club is

gradually formed from the last four to six segments. Contrasted with other members of the family, segment 8 is not smaller than 7 and 9. [See Hatch (1933, 1957) for more details.] The beetles are taken in forest litter, humus, and moss, and often near tree bases or stumps, where they and their larvae may be fungal feeders. The use of flight-intercept traps, or the sweeping of low vegetation in forest glades and clearings on still, warm, and humid evenings and afternoons, can occasionally take adults.

The Subfamily Catopocerinae

This group is endemic to North America. There is no common name. It is characterized by widely separated hind coxae, an elongate prosternum, and lack of internal vesicles on the antennal segments, which bear periarticular gutters. Two genera are known, of which both are eyeless and inhabitants of deep forest litter or caves. They may be general scavengers but association with subterranean fungi is known in some (Fogel and Peck 1975).

The Subfamily Leiodinae

These may be collectively called the round fungus beetles. They are generally convex, shiny, oval beetles, 1.5–7 mm in length and from pale yellow-brown to reddish brown to black in color. The antennal club and tarsal formula vary with the genus. Many species can contract the head and prothorax under the body, conceal their appendages, and roll into a ball. The beetles occur in decomposing vegetation and in and on the soil, in fungi, under bark, and in decaying wood and leaves, where they feed on fungi and slime molds. Different groups show different feeding preferences. The Leiodini and Hydnobiini seem to feed on subterranean fungi, while the Pseudoleiodini feed on soft fungi and are more generally saprophagous, and the Agathidiini seem to be specialists on the plasmodia and fruiting bodies of slime molds or Myxomycetes (Fogel and Peck 1975, Newton 1984, Russell 1979, Wheeler 1979a,b). The beetles may be caught by sifting and Berlese extraction from their microhabitats, or in flight in forests, or by sweeping as they rest on vegetation toward dusk, or in Malaise and "window" or "flight intercept" traps (Peck and Davies 1980, Chandler and Peck 1989). Higher classification in the group was previously unsatisfactory, and the keys here use recently proposed advances (Newton 1984).

KEY TO SUBFAMILIES, TRIBES, GENERA, AND SOME SPECIES OF U.S. AND CANADIAN LEIODIDAE

1a Head with occipital carina or elevated crest (Fig. 37.50) (this may be hard to see if head is tightly retracted against pronotum; the crest is weak in ***Platycholeus*** which has a tarsal formula of 5–5–5 in males and 4–5–5 in females) 2

1b Head without occipital carina or crest 14

2a (1a) Occipital crest overlapping pronotum when head is in repose; cervical sclerites absent; procoxal cavities internally open behind; body dorsoventrally flattened; eyes reduced or absent; Subfamily **Leptininae 3**

2b Occipital carina resting against front of pronotum when head is in repose; cervical sclerites present; procoxal cavities internally closed behind; body and eyes usually normal; Subfamily **Cholevinae 5**

3a (2a) Prosternum short and acute at apex, not extending between procoxae; length about 2 mm . . . . . Genus ***Leptinus*** (Müller, 1817)
Distributed over much of eastern North America and the Pacific northwest; with three described species (Fig. 37.46), most frequently found in nests and fur of mice, shrews, and moles and occasionally in litter (Peck 1982). Their biology is not well known, although it has been studied for ***L. testaceus*** of Europe (Buckle 1976, Ising 1969).

3b Prosternum produced posteriorly, extending beyond procoxae and appearing to separate them, *or* forming a broad flat plate, ending in a median lobe fringed with long setae 4

4a (3b) Prosternum produced posteriorly; separating the procoxae . . . . . Genus ***Leptinillus*** Horn, 1882
L. aplodontiae Ferris has a prosternum without apical setae; is 3.5 mm long; and is confined to the fur and nests of the mountain beaver ***Aplodontia rufa*** from California to Washington. ***L. validus*** (Horn) has a prosternum fringed with long, closely set setae extending to the mesosternum; is 4.5 mm long; and is confined to the lodges and fur of the beaver (***Castor canadensis***) throughout the host's range (see Parks and Barnes 1955, Wood 1965).

4b Prosternum forming a broad, flat plate, ending in a median lobe fringed with long setae . . . . . Genus ***Platypsyllus*** Ritsema, 1869
The highly modified and flea-appearing ***P. castoris*** Ritsema is a true ectoparasite of beavers (***Castor***) in North America and Eurasia (see Wood 1965, Janzen 1963).

5a (2b) Posterior coxae somewhat separated, tarsi all five-segmented except for female protarsi with four segments . . . . . Tribe **BATHYSCIINI,** Genus ***Platycholeus*** Horn, 1880
Two species, ***P. leptinoides*** Crotch and ***P. opacellus*** Fall are the only described North American representatives of this large and predominantly cavernicolous tribe of Eurasia. They occur in the Pacific northwest, in litter and under bark of logs and stumps, often with ants and termites (Hatch 1957).

5b Posterior coxae contiguous, all tarsi five-segmented 6

6a (5b) Elytra with setal bases arranged as transverse or oblique strigae . . . 7

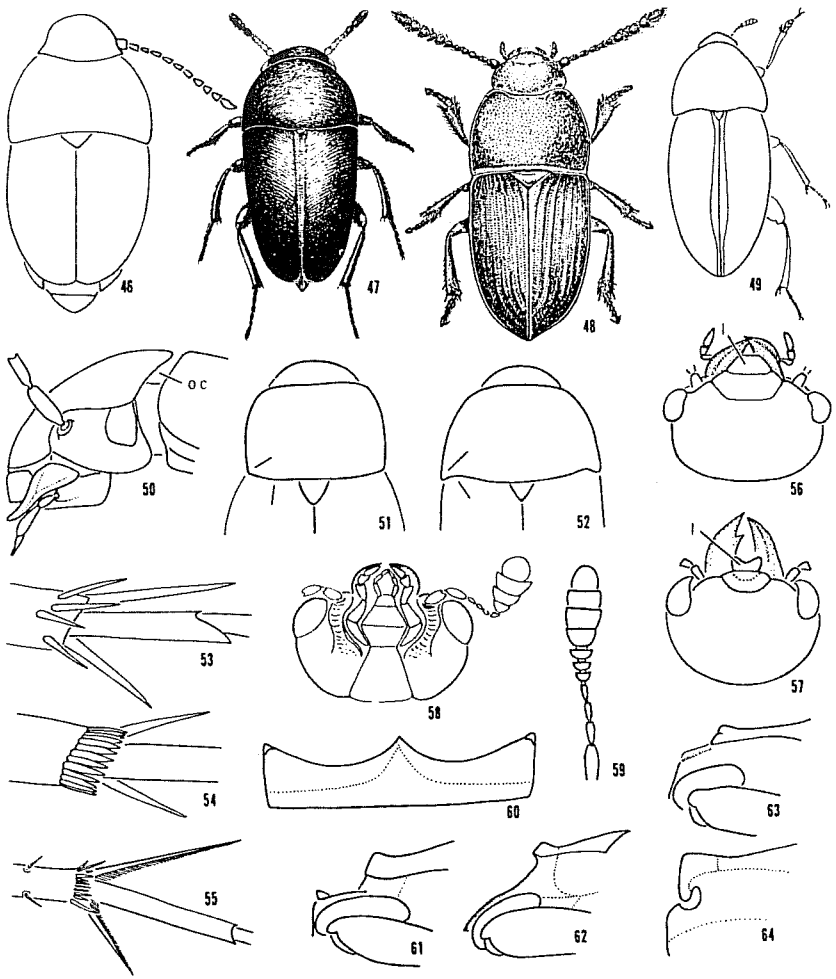
6b Elytra with granular surface of irregularly arranged setal bases; strigae absent; Tribe **Cholevini** 11

7a (6a) Hind margin of hind tibia with two inner long spines and an outer row or comb of short and equal spines only (Fig. 37.54); Tribe **Ptomaphagini** 8

7b Hind margin of hind tibia with two long inner spines (and perhaps a comb of equal spines), but more importantly, also with about four longer outer spines (Fig. 37.53); Tribe **Nemadini** 10

8a (7a) Form oval; with long and erect hairs as well as short recumbent hairs; mesosternal carina low, effaced, or absent; compact and modified for life as guests in ant nests . . . . . Genus ***Echinocoleus*** Horn, 1885
Three species are known as inhabitants of nests of ***Pogonomyrmex*** and ***Novomessor*** harvester ants in the western United States (Peck 1976).

8b Form elongate oval (Fig. 37.47); with short recumbent hairs only; mesosternal carina present and usually well developed; may live with ants but not as highly modified myrmecophile 9



Figs. 37.46–37.64. 46. *Leptinus americanus*. **47.** *Ptomaphagus consobrinus*. **48.** *Catopocerus appalachianus*. **49.** *Colon* sp. **50.** *Ptomaphagus shapardi* (*oc*, occipital carina). **51.** Pronotum *Catops* sp. **52.** Pronotum *Sciodrepoides* sp. **53.** Metatibial spurs *Dissochaetus* sp. **54.** Metatibial spurs *Ptomaphagus* sp. **55.** Metatibial spurs *Prionochaeta opaca*. **56.** Head *Agathidium* sp. **57.** Head *Hydnobius* sp. **58.** Head with antennal grooves *Apheloplastus egenus*. **59.** Antenna *Colon* sp. **60.** First visible abdominal segment *Aglyptinus laevis*. **61.** Mesosternum *Cyrtusa luggeri*. **62.** Mesosternum *Leiodes* sp. **63.** Mesosternum *Colenis impunctata*. **64.** Mesosternum *Cainosternum imbricatum* (from Wheeler, in litt.).

9a (8a) Size medium (2.6 mm) to smaller; flight wings absent; eyes reduced to poorly defined collection of about 20 pigmented facets; aedeagal tip more elaborately sculptured, broader, and more blunt . . . . . Genus ***Adelopsis*** Portevin, 1907

Sixteen species, all forest litter and soil inhabiting scavengers, are known from the southeastern United States (Peck 1978b).

9b Size medium (2.6 mm) to larger; flight wings usually present and eyes

usually normal (wings absent, and eyes smaller (Fig. 37.50) or reduced to unpigmented spot in most cavernicolous species); aedeagal tip simple, elongate and pointed . . . . . Genus ***Ptomaphagus*** Illiger, 1798

Twenty-five species are known from the United States and Canada (Peck 1973, 1978a), occupying a wide range of litter and soil habitats as scavengers, and extensions of these habitats such as ant nests and animal burrows. Eighteen additional species have become specialized for cave habitats in the southern United States (Peck 1973, 1984, 1986).

10a (7b) Basal segments of male (with expanded protarsi) midtarsi weakly dilated and spongy pubescent beneath; mesosternal carina more elevated and extending nearly to anterior margin of mesosternum. . . . Genus ***Nemadus*** Thomson, 1867

Ten species are described from North America, where they are scavengers in forest litter and sometimes in caves and animal burrows; some species seem restricted to ant nests (Hatch 1933, Jeannel 1936, Fall 1937).

10b Basal segments of male (with expanded protarsi) midtarsi not expanded; mesosternal carina feebly elevated, sometimes confined to region between mesocoxae . . . . Genus ***Dissochaetus*** Reitter, 1884

Three species occur as scavengers in forest litter, in ant nests and on carrion in eastern, central, and southwestern North America (Hatch 1933, Jeannel 1936).

11a (6b) Segments 1–10 of antennae bipectinate; with anterior projections, giving sawtoothed appearance. . . Genus ***Catoptrichus*** Murray, 1856

One species, ***C. frankenhauseri*** (Mannerheim), occurs in forest litter in the Pacific northwest; habits unknown, probably scavenger (Hatch 1933).

11b Antennae normal, not bipectinate **12**

12a (11b) Tibial spurs long, serate, longest metatibial spur as long as first metatarsal segment (Fig. 37.55); first mesotarsal segment not dilated in males. . . . . Genus ***Prionochaeta*** Horn, 1880

One species, ***P. opaca*** (Say) occurs in forest litter and some caves in eastern North America; common on carrion (Peck 1977b).

12b Tibial spurs not long and serate; much shorter than first tarsal segment; first mesotarsal segment dilated in males. **13**

13a (12b) Pronotum with base sinuate on either side just within the more or less distinctly rectangular posterior angles (Fig. 37.52) . . . . . Genus ***Sciodrepoides*** Hatch, 1933

Two subspecies of two Eurasian species, ***S. fumatus terminans*** (LeConte) and ***S. watsoni hornianus*** (Blanchard), are commonly found as scavengers in many forest and soil-related habitats across the forested parts of the northern half of the continent (Hatch 1933, Jeannel 1936).

13b Pronotum with base arcuate, the hind angles obtuse or more or less evidently rounded (Fig. 37.51) . . . . . Genus ***Catops*** Paykull, 1798

Ten described species occur in forest litter and related habitats across North America; carrion scavenger (Hatch 1933, Jeannel 1936, Peck, in preparation).

14a (1b) Antennae 11-segmented; club gradual, of four to six uninterrupted segments, segment 8 as large as segments 9–10 (Fig. 37.59) (and with periarticular gutter and internal vesicles); cervical sclerites absent; intersegmental membranes between abdominal sterna with brick-wall pattern of minute sclerites; female with four visible abdominal sterna . . . . . Subfamily **Coloninae,** Genus ***Colon*** Herbst, 1797

Some 35 species are known from litter habitats in North America. Their shape (Fig. 37.49) and antennal club is distinctive; males often with tooth on hind femora; biology and larvae unknown (Hatch 1933, 1957).

14b Antenna 10- or 11-segmented; club usually interrupted when 11-segmented (segment 8 usually smaller than segments 9 and 10 and without periarticular gutter or internal vesicles); cervical sclerites present; abdominal intersegmental membrane without minute sclerites; females with five or six visible abdominal sternites. **15**

15a (14b) Hind coxae separated by about a third their width; prosternum in front of coxae longer than coxal width; always with no eyes; Subfamily **Catopocerinae** 16

15b Hind coxae not separated; prosternum in front of coxae much shorter than coxal width; Subfamily **Leiodinae** 17

16a (15a) Appendages short, body ovoid and flattened, pronotum and elytra of similar widths (Fig. 37.48) . . . . . Tribe **CATOPOCERINI**, Genus ***Catopocerus*** Motschulsky, 1869

Fourteen species are named in this widespread North American genus of forest soil and deep litter (Hatch 1957, Peck 1974); scavengers or feeders on subterranean fungi (Fogel and Peck 1975).

16b Appendages conspicuously long, body elongate and rounder, pronotum much narrower than elytra . . . . . Tribe **GLACICAVICOLINI,** Genus ***Glacicavicola*** Westcott, 1968

The single species, ***G. bathyscioides*** Westcott, a highly evolved cave inhabitant, occurs as a scavenger in lava tube and limestone caves in Idaho and Wyoming (Peck 1974, 1981; Westcott 1968).

17a (15b) Labrum deeply emarginate apically (Fig. 37.57) (obscure in ***Cyrtusa*** and some ***Hydnobius***) 18

17b Labrum shallowly or not at all emarginate apically (Fig. 37.56) . . . 28

18a (17a) Tarsal formula 5–5–5; Tribe **HYDNOBIINI**. 19

18b Tarsal formula 5–5–4; Tribe **LEIODINI**. 20

19a (18a) Antennal club three-segmented, segment 7 as small as 8 . . . . . Genus ***Triarthron*** Maerkel, 1840

Two species known; from Pennsylvania to Oregon (Hatch 1957).

19b Antennal club five-segmented, segment 8 smaller than 7 . . . . . Genus ***Hydnobius*** Schmidt, 1847

Sixteen species, mostly western, but several with a general northern distribution; subterranean fungi feeders (Hatch 1957).

20a (18b) Head without antennal grooves beneath; body not contractile . . . 21

20b Head with antennal grooves beneath (Fig. 37.58); body sometimes contractile. 25

21a (20a) Mesosternum oblique (Fig. 37.62). 22

21b Mesosternum vertical between the coxae (Fig. 37.61) 23

22a (21a) Mesosternum with median longitudinal carina. . . . . Genus ***Leiodes*** Latreille, 1792

Some 29 generally distributed species known in North America; usually in forested habitats (Hatch 1957).

22b Mesosternum without median carina. . . . . Genus ***Ecarinosphaerula*** Hatch, 1929

The single species, ***E. ecarina*** Hatch, is known from British Columbia and Nevada (Hatch 1957).

23a (21b) Mesosternum with a median longitudinal carina 24

23b Mesosternum without median carina Genus ***Cyrtusa*** Erichson, 1842

The species ***C. luggeri*** Hatch is spread from Quebec and Michigan to British Columbia (Hatch 1957).

24a (23a) Antenna 10-segmented, club four-segmented . . . . . Genus ***Anogdus*** LeConte, 1866

Four species occur in the eastern United States and British Columbia (Hatch 1957).

24b Antenna 11-segmented, club five-segmented (segment 8 hidden by 7 and 9 when club is contracted) . . . Genus ***Neocyrtusa*** Brown, 1937

Eight species are known; widely distributed (Hatch 1957).

25a (20b) Antenna 11-segmented, club five-segmented. . . . . Genus ***Lionothus*** Brown, 1937

The genus is widespread in North America, but only the species ***L. ulkei*** Brown is recorded from the District of Columbia.

25b Antenna 10-segmented, club three- or four-segmented. 26

26a (25b) Middle and hind tibiae distinctly wider than anterior tibiae; middle and hind tarsi wide, compressed; intervals between elytral striae nearly smooth. 27

26b All tibiae relatively more slender and elongate; tarsi slender, cylindrical; elytral intervals with dense punctures, approaching size of strial punctures . . . . . Genus ***Caenocyrta*** Brown, 1937

The species ***C. picipennis*** (LeConte) is distributed from the District of Columbia to Quebec, to British Columbia (Hatch 1957).

27a (26a) Antennal club four-segmented (Fig. 37.58) . . . . . Genus ***Zeadolopus*** Broun, 1903

The species ***Z. egenus*** (LeConte) ranges from Quebec and Michigan to Georgia. Until recently, the genus was called ***Apheloplastus*** (Newton 1983).

27b Antennal club three-segmented . . . . Genus ***Isoplastus*** Horn, 1880

The species ***I. fossor*** ranges from Quebec and Michigan to the District of Columbia.

28a (17b) All tarsi three-segmented; abdominal sternum 3 (first visible) with transverse carina (Fig. 37.60) . . . . . Tribe **SCOTOCRYPTINI,** Genus ***Aglyptinus*** Cockerell, 1906

The only species in the United States and Canada is ***A. laevis*** (LeConte), in the east from Canada to Louisiana; usually associated with fungi.

28b All tarsi of at least four segments; abdominal sternum 3 (first visible) without transverse carina 29

29a (28b) Tarsal formula 5–4–4, segmentation not sexually dimorphic, elytra usually transversely striolate; male with enlarged (tenent) setae on protarsi only; tibiae without longitudinal carinae; Tribe **PSEUDOLEIODINI** 30

29b Tarsi sexually dimorphic in segmentation, 5–5–4 in male, 5–4–4 or 4–4–4 in female; elytra not transversely striolate; male tenent setae usually on pro- and mesotarsi; tibiae with longitudinal carinae; Tribe **AGATHIDIINI**. 31

30a (29a) Elytra without longitudinal rows of punctures; color pale (testaceous); mesosternal carina simple (Fig. 37.63) Genus ***Colenis*** Erichson, 1845

C. impunctata (LeConte) is the only North American species; in forests from eastern United States and Canada to British Columbia (Hatch 1957).

30b Elytra with longitudinal rows of punctures; color dark; mesosternal carina with transverse depression (Fig. 37.64) . . . . . Genus ***Cainosternum*** Notman, 1931

Only one known species, ***C. imbricatum*** Notman from New York (Wheeler 1984).

31a (29b) Eighth antennal segment distinctly narrower than seventh; antennal club five-segmented; head narrowed behind the eyes; body form convex to hemispherical, contractile. . . Genus ***Anisotoma*** Panzer, 1797

Fifteen species are known; generally distributed in forests over much of Canada and the United States; feeders on plasmodia and fruiting bodies of slime molds (Russell 1979, Wheeler 1979a).

31b Eighth antennal segment not (or slightly) narrower than seventh, antennal club abruptly three-segmented; head often broad behind eyes ("postocular tempora" well developed); body form variable, sometimes oblong–eliptical and subdepressed, sometimes hemispherical and highly contractile. 32

32a (31b) Elytra with nine complete, punctate striae; head narrowed behind eyes; body form oblong–eliptical, subdepressed; clypeus not emarginate. . . . . Genus ***Stetholiodes*** Fall, 1910

The only species, ***S. laticollis*** Fall, occurs in Indiana (Wheeler 1981).

32b Elytra with fewer than nine complete, punctate striae (or without striae); head often wide behind eyes; body form variable, often hemispherical and very contractile; clypeus contractile . . . . . Genus ***Agathidium*** Panzer, 1797

Forty-six species are known; widely distributed across the United States and Canada; usually in forested habitats and on slime molds (Hatch 1957, Russell 1979).

References

Anderson, R. S. 1982a. Resource partitioning in the carrion beetle (Coleoptera : Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Can. J. Zool.* 60:1314–1325. **1982b.** Burying beetle larvae: Nearctic *Nicrophorus* and Oriental *Ptomascopus morio* (Silphidae). *Syst. Entomol.* 7:249–264. **1982c.** On the decreasing abundance of *Nicrophorus americanus* Olivier (Coleoptera : Silphidae) in eastern North America. *Coleopt. Bull.* 36:362–365. **Anderson, R. S. and S. B. Peck. 1984.** Bionomics of Nearctic species of *Aclypea* Reitter: phytophagous "carrion" beetles (Coleoptera : Silphidae). *Pan-Pac. Entomol.* 60:248–255. **1985.** *The Insects and Arachnids of Canada.* 13. *The Carrion Beetles of Canada and Alaska (Coleoptera : Silphidae and Agyrtidae).* Publ. 1778. Agriculture Canada, Ottawa, Ontario, Canada. 121 pp. **1986.** Geographic patterns of colour variation in North American *Nicrophorus* burying beetles (Coleoptera : Silphidae). *J. Nat. Hist.* 20:283–297. **Arnett, R. H., Jr. 1963.** *The Beetles of the United States (A Manual for Identification).* Catholic University of America Press, Washington, D.C. 1112 pp. **Balduf, W. V. 1935.** *The Bionomics of Entomophagous Coleoptera.* John S. Swift Co., St. Louis, Mo. 220 pp. **Borror, D. J., D. M. DeLong and C. A. Triplehorn. 1976.** *An Introduction to the Study of Insects,* 4th ed. Holt, Rinehart, and Winston, New York. 852 pp. **Bredohl, R. 1984.** Zur Bioakustic mitteleuropäischer Totengräber (Coleoptera : Silphidae : *Necrophorus*). *Entomol. Gen.* 10:11–25. **Brewer, J. W. and T. R. Bacon. 1975.** Biology of the carrion beetle *Silpha ramosa* Say. *Ann. Entomol. Soc. Am.* 68:786–790. **Buckle, A. P. 1976.** Studies on the biology and distribution of *Leptinus testaceus* Müller within a community of mixed small mammal species. *Ecol. Entomol.* 1:1–6. **Chandler, D. and S. B. Peck. 1989.** Species richness and abundance of Leiodidae (Coleoptera) in an uncut and 40 year old forest in New Hampshire. *Can. J. Zool.* (in press). **Cooley, R. A. 1917.** The spinach carrion beetle. *J. Econ. Entomol.* 10:94–102. **Crowson, R. A. 1967.** *The Natural Classification of the Families of Coleoptera,* reprint ed. E. W. Classey, Faringdon, Oxfordshire, England. 214 pp. **Dethier, V. G. 1947.** The role of the antennae in the orientation of carrion beetles to odors. *J. N.Y. Entomol. Soc.* 65:285–293. **Dillon, E. S. and L. S. Dillon. 1961.** *A Manual of Common Beetles of Eastern North America.* Row, Peterson, Evanston, Ill. 884 pp. **Fall, H. C. 1937.** The North American species of *Nemadus,* with descriptions of new species (Coleoptera, Silphidae). *J. N.Y. Entomol. Soc.* 45:335–340. **Fisher, R. M. and R. D. Tuckerman. 1986.** Mimicry of bumble bees and cuckoo bumble bees by carrion beetles (Coleoptera : Silphidae). *J. Kans. Entomol. Soc.* 59:20–25. **Fogel, R. and S. B. Peck. 1975.** Ecological studies of hypogeous fungi. I. Coleoptera associated with sporocarps. *Mycologia* 67:741–747. **Hatch, M. H. 1933.** Studies on the Leptodiridae (Catopidae) with descriptions of new species. *J. N.Y. Entomol. Soc.* 41:187–239. **1953, 1957.** *The beetles of the Pacific Northwest.* I. *Introduction and Adephaga.* 340 pp. II. *Staphyliniformia.* 384 pp. Univ. Washington Publ. Biol. 16. University of Washington Press, Seattle, Wash. **Ising, E. 1969.** Zur Biologie des *Leptinus testaceus* Müller, 1817 (Insecta, Coleoptera). *Zool. Beitr.* 15:393–456. **Janzen, D. H. 1963.** Observations on populations of adult beaver-beetles, *Platypsyllus castoris* (Platypsyllidae : Coleoptera). *Pan-Pac. Entomol.* 39:215–228. **Jaques, H. E. 1951.** *How to Know the Beetles.* Wm. C. Brown, Dubuque, Iowa. 372 pp. **Jeannel, R. 1936.** Monographie des Catopidae. *Mem. Mus. Natl. Hist. Nat. (Paris) (N.S.),* Vol. 1. 433 pp. **Johnson, M. D. 1975.** Seasonal and microseral variations in the insect populations on carrion. *Amer. Midl. Nat.* 93(1):79–90. **Lawrence, J. F. 1982.** Coleoptera. Pp. 482–553 in S. P. Parker (ed.). *Synopsis and Classification of Living Organisms,* Vol. 2. McGraw-Hill, New York. **Lawrence, J. F. and A. F. Newton, Jr. 1982.** Evolution and classification of beetles. *Annu. Rev. Ecol. Syst.* 13:261–290. **Miller, S. E. and S. B. Peck. 1979.** Fossil carrion beetles of Pleistocene California asphalt deposits, with a synopsis of Holocene California Silphidae (Insecta : Coleoptera : Silphidae). *Trans. San Diego Soc. Nat. Hist.* 19:85–106. **Milne, L. J. and M. J. Milne. 1944.** Notes on the behavior of burying beetles (*Nicrophorus* spp.). *J. N.Y. Entomol. Soc.* 52:311–327. **Milne, J. J. and M. Milne. 1976.** The social behavior of burying beetles. *Sci. Am.* 235(2):84–89. **Newton, A. F., Jr. 1983.** New generic synonymies, new combinations, and distributional comments on Leiodini (Coleoptera : Leiodidae). *Coleopt. Bull.* 37:173–176. **1984.** Mycophagy in Staphylinoidea. Pp. 302–351 in Q. Wheeler and M. Blackwell (eds.). *Fungus–Insect Relationships; Perspectives in Ecology and Evolution.* Columbia University Press, New York. 514 pp. **Newton, A. and S. B. Peck. 1975.** Baited pitfall traps for beetles. *Coleopt. Bull.* 29:45–46. **Niemitz, O. 1972.** Bioakustische, verhaltensphysiologische und morphologische Untersuchungen an *Necrophorus vespillo* (Fab.). *Forma Functio* 5:209–230. **Parks, J. J. and J. W. Barnes. 1955.** Notes on the family Leptinidae including a new record of *Leptinillus validus* (Horn) in North America (Coleoptera). *Ann. Entomol. Soc. Am.* 48:417–421. **Payne, J. A. 1965.** A summer carrion study of the baby pig *Sus scrofa* L. *Ecology* 45(5):592–602. **Payne, J. A. and E. W. King. 1970.** Coleoptera associated with pig carrion. *Entomol. Monthly Mag.* 105(1969):224–232. **Peck, S. B. 1973.** A systematic revision and the evolutionary biology of the *Ptomaphagus (Adelops)* beetles of North America (Coleoptera : Leiodidae : Catopinae), with emphasis on cave-inhabiting species. *Bull. Mus. Comp. Zool. Harv. Univ.* 145:29–162. **1974a.** The eyeless *Catopocerus* beetles (Leiodidae) of eastern North America. *Psyche (Camb.)* 81:377–397. **1974b.** A review of the *Agyrtes* (Silphidae) of North America. *Psyche (Camb.)* 81:501–506. **1974c.** Biology of the Idaho lava tube beetle, *Glacicavicola. Bull. Natl. Speleol. Soc.* 36:1–3. **1976.** The myrmecophilous beetle genus *Echinocoleus* in the southwestern United States (Leiodidae, Catopinae). *Psyche (Camb.)* 83:51–62. **1977a.** An unusual sense receptor in internal antennal vesicles of *Ptomaphagus* (Coleoptera : Leiodidae). *Can. Entomol.* 109:81–86. **1977b.** A review of the distribution and biology of the small carrion beetle *Prionochaeta opaca* of North America (Coleoptera : Leiodidae : Catopinae). *Psyche (Camb.)* 83:299–307. **1978a.** New montane *Ptomaphagus* beetles from New Mexico and zoogeography of southwestern caves (Coleoptera : Leiodidae : Catopinae). *Southwest. Nat.* 23:227–238. **1978b.** Systematics and evolution of forest litter *Adelopsis* in the southern Appalachians (Coleoptera : Leiodidae : Catopinae). *Psyche (Camb.)* 85:355–382. **1981a.** Distribution and biology of flightless carrion beetle *Necrophilus pettitii* in eastern North America (Coleoptera : Silphidae). *Entomol. News* 92:181–185. **1981b.** The Idaho cave beetle *Glacicavicola* also occurs in Wyoming. *Coleopt. Bull.* 35:141–142. **1982.** A review of the ectoparasitic *Leptinus* beetles of North America (Coleoptera : Leptinidae). *Can. J. Zool.* 60:1517–1527. **1984.** The distribution and evolution of cavernicolous *Ptomaphagus* beetles in the southeastern United States (Coleoptera; Leiodidae; Cholevinae) with new species and records. *Can. J. Zool.* 62:730–740. **1986.** Evolution of adult morphology and life-history characters in cavernicolous *Ptomaphagus* beetles. *Evolution* 40:1021–1030. **Peck, S. B. and R. S. Anderson. 1982.** The distribution and biology of the alpine–tundra carrion beetle *Thanatophilus coloradensis* (Wickham) in North America (Coleoptera : Silphidae). *Coleopt. Bull.* 36:112–115. **1985a.** Taxonomy, phylogeny, and biogeography of the carrion beetles of Latin America (Coleoptera : Silphidae). *Quaest. Entomol.* 21:247–317. **1985b.** Seasonal activity and habitat associations of adult small carrion beetles in southern Ontario (Coleoptera, Leiodidae, Cholevinae). *Coleopt. Bull.* 39:347–353. **Peck, S. B. and A. E. Davies. 1980.** Collecting small beetles with large-area "window" traps. *Coleopt. Bull.* 34:237–239. **Peck, S. B. and M. M. Kaulbars. 1987.** A synopsis of the distribution and bionomics of the carrion beetles (Coleoptera : Silphidae) of the conterminous United States. *Proc. Entomol. Soc. Ont.* 118:47–81. **Peck, S. B. and S. E. Miller. 1989.** *A Catalog of the Coleoptera of North America, Family:* Silphidae. U.S. Dept. Agric. Handb. 529–28 (in press). **Ratcliffe, B. C. 1972.** The natural history of *Necrodes surinamensis* (Fabr.) (Coleoptera; Silphidae). *Trans. Am. Entomol. Soc. (Phila.)* 98:359–410. **Reed,**

H. B., Jr. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. *Am. Midl. Nat.* 59:213–245. **Russell, L. K. 1979.** Beetles associated with slime molds (Mycetozoa) in Oregon and California (Coleoptera : Leiodidae, Sphindidae, Lathridiidae). *Pan-Pac. Entomol.* 55:1–9. **Schwaller, W. 1983.** Die Arten der Gattung *Ipelates* (*sensu lato*) (Coleoptera : Silphidae : Agyrtinae). *Rev. Suisse Zool.* 90:101–110. **Schumacher, R. 1973.** Beitrag zur Kenntnis der Stridulationsapparate einheimischer *Necrophorus*-Arten (*Necrophorus humator* Ol., *Necrophorus investigator* Zetterst., *Necrophorus vespilloides* Herbst) (Insecta, Coleoptera). *Z. Morphol. Tiere* 75:65–75. **Shubeck, P. P. 1968.** Orientation of carrion beetles to carrion: random or non-random? *J. N.Y. Entomol. Soc.* 76:253–265. **1969.** Ecological studies of carrion beetles in Hutcheson Memorial Forest. *J. N.Y. Entomol. Soc.* 77:138–151. **1971.** Diel periodicities of certain carrion beetles (Coleoptera : Silphidae). *Coleopt. Bull.* 25:41–46. **1976.** Carrion beetle responses to poikilotherm and homoiotherm carrion (Coleoptera : Silphidae). *Entomol. News* 87:265–269. **Shubeck, P. P., N. M. Downie, R. L. Wenzel and S. B. Peck. 1977.** Species composition of carrion beetles in a mixed-oak forest. *W. L. Hutcheson Mem. For. Bull.* 4:12–17. **Sidor, C. 1970.** Resultati ispitivanja uloge insekata grobara (*Necrophorus vespillo* L.) u prenosenju besnila. *Mikrobiologija* (*Belgr.*) 7:131–138. **Southwood, T. R. E. 1966.** *Ecological Methods with Particular Reference to the Study of Insect Populations.* Methuen London. 391 pp. **Springett, B. P. 1968.** Aspects of the relationship between burying insects *Necrophorus* spp. and the mite, *Poecilochirus necrophori* Vitz. *J. Anim. Ecol.* 37:417–424. **Theodorides, J. 1950.** Notes diverse sur les *Necrophorus* (Coleoptera, Silphidae). *Bull. Inst. R. Sci. Nat. Belg.* 26: no. 52. 20 pp. **Waldow, U. 1973.** Elektrophysiologie eins neuen Aasgeruchrezeptors und seine Bedeutung für das Verhaltern des Totengräbers (*Necrophorus*). *J. Comp. Physiol.* 83:415–424. **Walker, T. J., Jr. 1957.** Ecological studies of the arthropods associated with certain decaying materials in four habitats. *Ecology* 38:262–276. **Westcott, R. L. 1968.** A new subfamily of blind beetle from Idaho ice caves with notes on its bionomics and evolution (Coleoptera : Leiodidae). *Contrib. Sci.* (*Los Ang.*) 141, 14 pp. **Wheeler, Q. D. 1979a.** Slime mold beetles of the genus *Anisotoma* (Leiodidae): classification and evolution. *Syst. Entomol.* 4:251–309. **1979b.** Revision and cladistics of the middle American genus *Creagrophorus* Matthews (Coleoptera : Leiodidae). *Quaest. Entomol.* 15:447–479. **1981.** Diagnosis and phylogenetic relationships of the monotypic genus *Stetholiodes* (Coleoptera : Leiodidae). *Ohio J. Sci.* 81:165–168. **1986.** Rediscovery and cladistic placement of the genus *Cainosternum* (Coleoptera : Leiodidae). *Ann. Entomol. Soc. Am.* 79:377–383. **Wilson, D. S. 1983.** The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. *Am. Nat.* 121:851–870. **Wilson, D. S. and J. Fudge. 1984.** Burying beetles: intraspecific interactions and reproductive success in the field. *Ecol. Entomol.* 9:195–203. **Wilson, D. S. and W. G. Knollenberg. 1984.** Food discrimination and ovarian development in burying beetles (Coleoptera : Silphidae: *Nicrophorus*). *Ann. Entomol. Soc. Am.* 77:165–170. **Wilson, D. S., W. G. Knollenberg and J. Fudge. 1984.** Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). *Ecol. Entomol.* 9:205–216. **Wood, D. M. 1965.** Studies on the beetles *Leptinillus validus* (Horn) and *Platypsyllus castoris* Ritsema (Coleoptera : Leptinidae) from beaver. *Proc. Entomol. Soc. Ont.* 95:33–63. **Zwick, P. 1979.** Contributions to the knowledge of Australian Cholevidae (Catopidae auct. : Coleoptera). *Aust. J. Zool. Suppl. Ser.* 70. 56 pp.