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THE CARRION BEETLES (COLEOPTERA: SILPHIDAE) OF NEBRASKA

by

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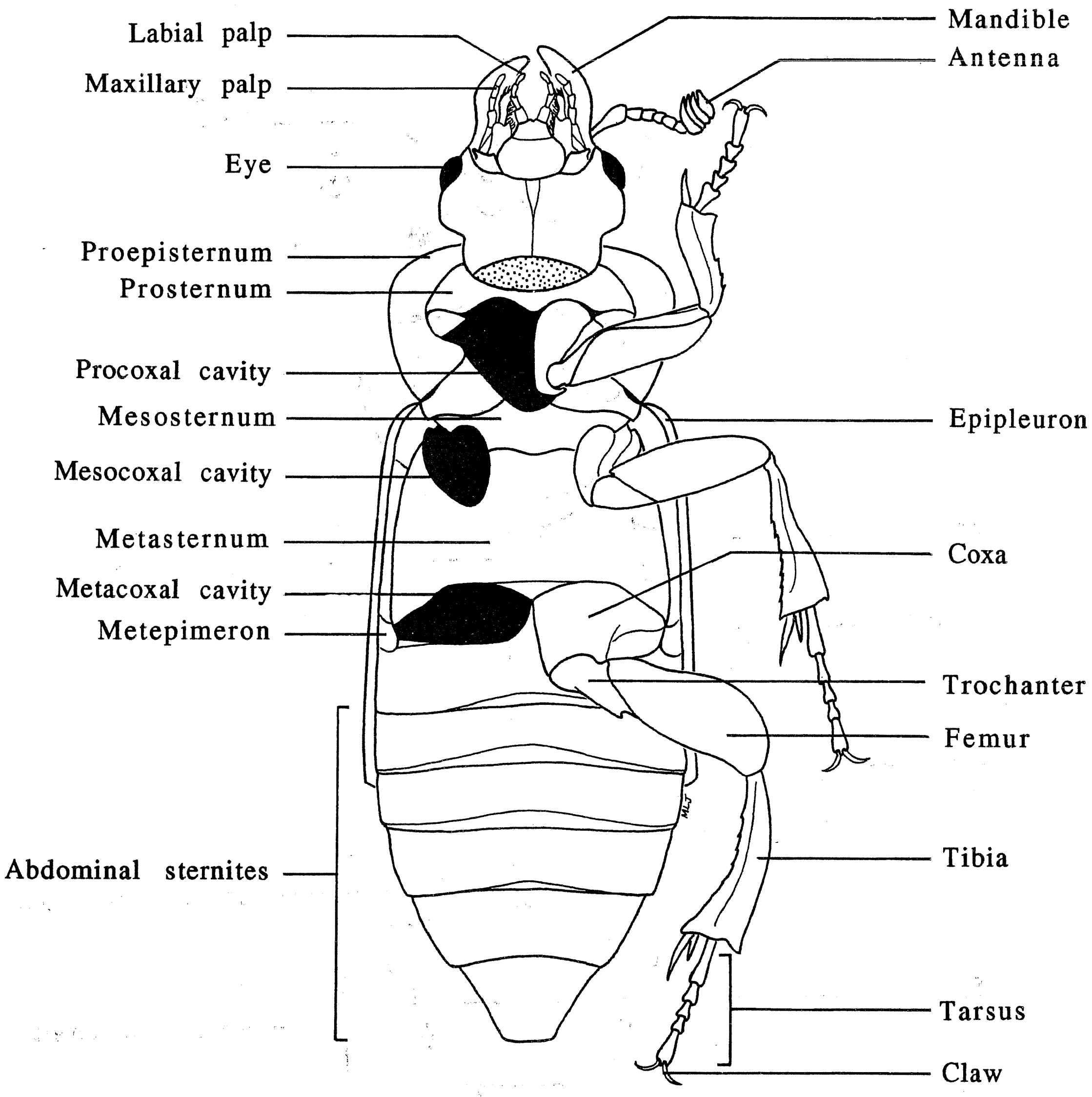


FIG. 3. Ventral aspect of adult *Nicrophorus* species showing morphological features.

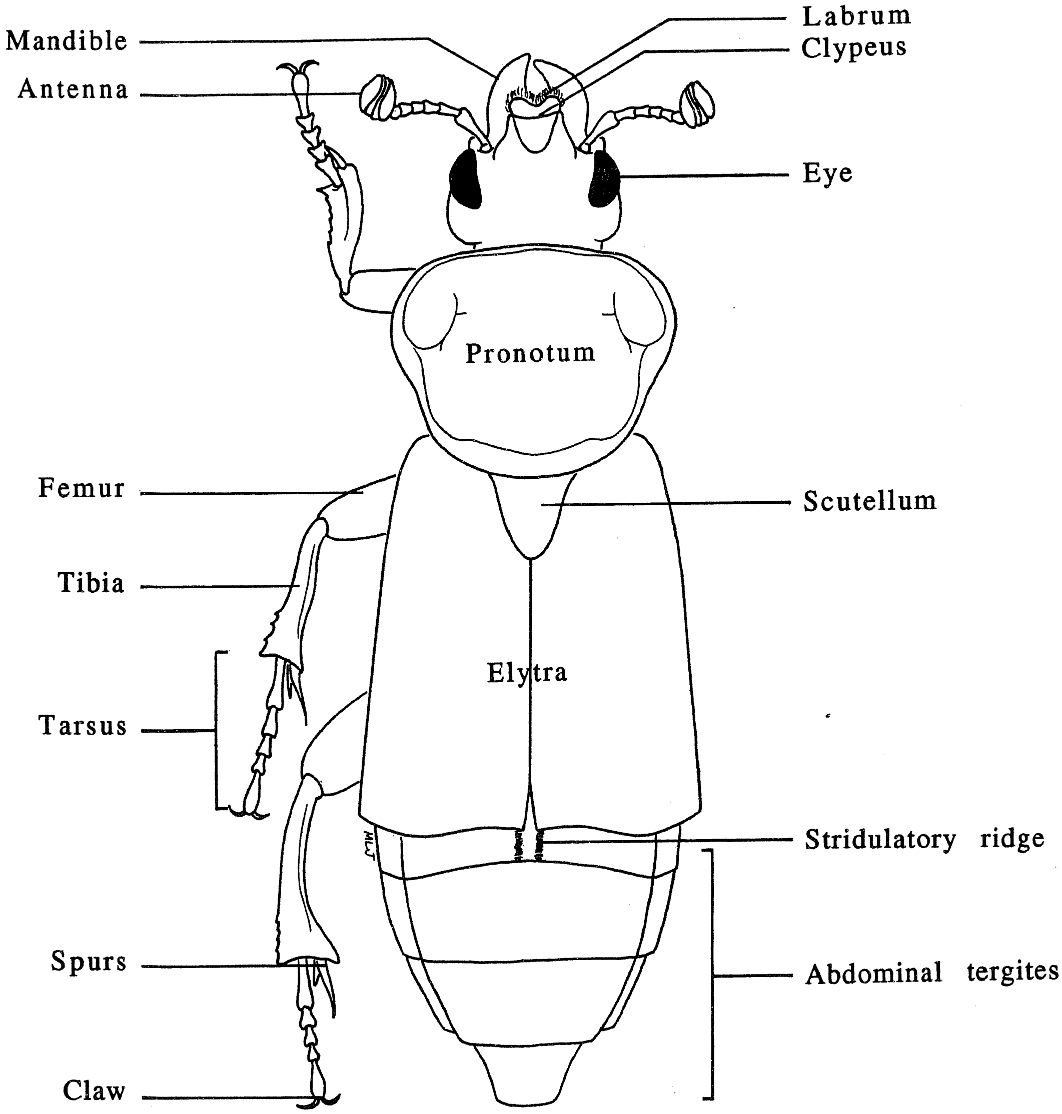


FIG. 2. Dorsal aspect of adult *Nicrophorus* species showing morphological features.

of north-central Nebraska. Ponderosa pine (*Pinus ponderosa* Lawson) and narrow-leaf cottonwood (*Populus angustifolia* James) are common Rocky Mountain trees that are found in this region of the state. Quaking aspen (*Populus tremuloides* Michaux) and western black birch (*Betula fontinalis* Sargent) also indicate the montane floral affinities of the Pine Ridge. These species probably occurred widely over much of the western part of the state in post-Wisconsin times, and the areas that remained when Europeans first reached western Nebraska were relics of this former widespread distribution (Jones 1964). The large influx of settlers since that time has altered considerably those remaining forest relics which, today, are disturbed remnants of the former plant associations.

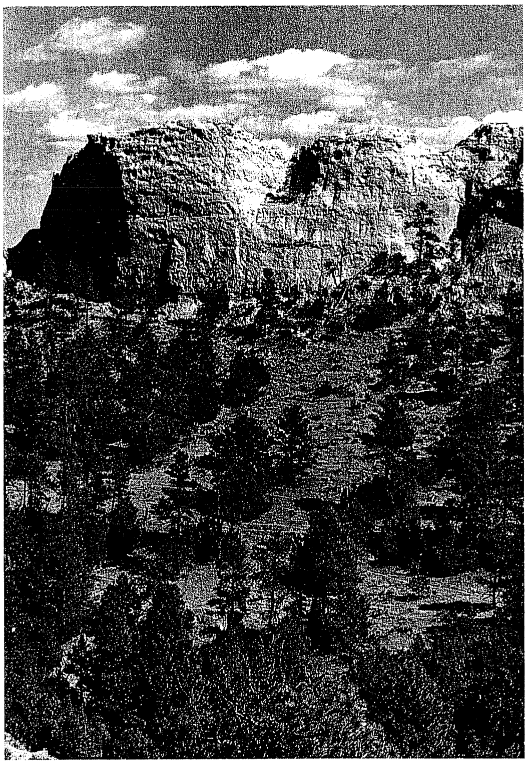


FIG. 14. Rocky Mountain forest near Chadron in Dawes Co. in northwestern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

THE SILPHIDAE

> *The spectacle of nature is always new, for she is always renewing the spectors. Life is her most exquisite invention, and death is her expert contrivance to get plenty of it.*
>
> — Goethe

Carrion beetles is the term applied, in a strict sense, to a single family of beetles, the Silphidae. Silphids are also generally referred to as burying beetles or sexton beetles because of the behavioral adaptations of *Nicrophorus* species to inter small vertebrates in the ground.

Silphids are relatively large beetles, ranging in size from 10 to 35 mm. The majority are usually a dull black or grey in color, but most species in the genus *Nicrophorus* have bright orange markings on the elytra that may serve as warning coloration.

Most silphids occur in north temperate regions, which is where they probably originated (Peck and Anderson 1985, in part). The majority of silphids are scavengers on carrion, and a few are found on dung or fungi, are phytophagous, or prey on fly larvae.

Carrion beetles are a conspicuous element of that vast host of scavengers that are responsible for breaking down and recycling back into the ecosystem the basic elements found inside of each organism. The decay process is an efficient and natural system whereby the raw materials of dead organisms are returned directly into the energy budgets of living organisms when they consume the dead ones.

Once an animal dies, its remains are ravenously set upon by a diverse array of food-seeking scavengers and predators that are attracted by the odors of decay. Assuming that vertebrate scavengers do not find and consume the remains first while they are still fresh, the remains will become a valuable food resource for a reasonably orderly progression of bacteria and fungi (the microconsumers) and insects (the macroconsumers) (Ratcliffe 1980). The progression of insects is fairly predictable because specific insects are attracted to a cadaver only after certain levels of decay have occurred. These stages of decay (and associated fauna) are influenced by season, weather, and the size and exposure of the remains. The net effect of this food partitioning is to reduce competition among the different guilds of insect scavengers by spacing them out through time and enabling increased use of a patchy, limited resource by more organisms. Arthropod succession at carrion has been thoroughly studied by Fuller (1934), Bornemissza (1957), Reed (1958), Payne (1965), and Early and Goff (1986), among others.

Many silphids are active at night, which may be a strategy to reduce competition from flies that are primarily diurnal. If flies do manage to lay eggs on a carcass, that carcass can become unfit for use by *Nicrophorus* species because the fly larvae consume nearly all of the fleshy remains that would otherwise be used by the beetles.

Nicrophorus species are renown for their habit of burying small vertebrate carcasses beneath the surface of the soil. Usually a male/female pair will process these remains to provision their developing larvae. The burial of the food source is important to these beetles and their young because it effectively removes the food from the arena of intense competition by maggots and other carrion-feeding insects. *Nicrophorus* species are unique among silphids because they are the only ones attempting to break the cycle of competition at a food source. At the same time, they provide their larvae with a safer underground environment that is relatively free from predators in which to develop.

Species in the Silphinae do not inter remains like *Nicrophorus* species. Instead, adults arrive at a carcass during the early to middle stages of decay (Payne 1965, Johnson 1974). Most seem to lay eggs just beneath the surface of the soil near the carcass, and the eggs hatch after four or five days (Anderson 1982c). The larvae then feed on the remains at the same time as all the other carrion-frequenting insects. The larvae pass through three instars, and they pupate in earthen cells beneath the soil. Details of the life history for most of these species remain poorly known. Young (1983) assembled an extensive bibliography on the biology of the Silphidae.

According to Lawrence and Newton (1982, 1995), the Silphidae, a once vaguely defined group, is now restricted to the larger carrion and burying beetles. The family is clearly monophyletic and related to the Staphylinidae. The Agyrtidae were formerly included in the Silphidae (*e.g.*, Arnett 1968, Madge 1980, Cho and Lee 1986) as were parts of the Leiodidae (*e.g.*, Hatch 1928), but these are now considered to be valid families unto themselves.

The Silphidae, then, consists of two subfamilies: the Silphinae and Nicrophorinae. Between them, there are 13 genera with about 208 species worldwide. North America has eight genera and 30 species, and in Nebraska there are six genera and 18 species.

Early synoptic treatments of the North American silphids were provided by LeConte (1853) and Horn (1880), both of whom recognized only the genera *Silpha* and *Nicrophorus*. Portevin (1926) split *Silpha* into many of the genera that we use today although there was not wide acceptance of these genera until the works of Miller and Peck (1979) and Anderson and Peck (1985) appeared.

Hatch (1927) and Arnett (1944) compiled relatively comprehensive works for the U.S. fauna, and they were among the first to actually use some character analysis. Portevin (1926) monographed the world fauna, and Hatch (1928) provided a checklist of the world fauna in the *Coleopterorum Catalogus* series. Peck and Anderson (1985) reviewed the taxonomy, phylogeny, and biogeography of the silphids of Latin America.

A preliminary checklist of the silphids of Nebraska was published by Meserve in 1936, and he recognized 15 species for the state. The silphids of other states have been listed or treated taxonomically by Fall and Cockerell (1907) for New Mexico, Blatchley (1910) for Indiana, Hatch and Rueter (1934) for Washington, Hatch (1957) for the Pacific Northwest, Lago and Miller (1983) for Mississippi, Lingafelter (1995) for Kansas, and Cuthrell and Rider (in press) for the Dakotas. Checklists of the North American fauna were prepared by Leng (1920), Blackwelder and Arnett (1974), and Peck and Miller (1993).

COLLECTING SILPHIDS

Carrion beetles are relatively easy to collect because they are so readily attracted to carcasses or bait that can be easily manipulated. The most obvious way of collecting these beetles is to find them at naturally-occurring carrion. In the earlier stages of the decay process, *Nicrophorus* species can be found beneath carcasses either feeding or preparing to bury the remains. If the carcass is slowly rolled over, *Nicrophorus* species can be collected with fingers or forceps as they run for cover. Species of silphines can be collected in much the same way from carcasses that are slightly older in the decay cycle.

Carcasses can also be deliberately placed in selected areas in order to attract or survey for silphids. Whole animal carcasses can often be obtained from pig, chicken, or turkey farms where there is always juvenile mortality. Frozen laboratory rats are also a more expensive option. These remains can be periodically checked for silphids in the same way as naturally-occurring carrion. With smaller carcasses that are likely to be buried by *Nicrophorus* species, an 18-inch length of dental floss can be tied to a rear leg. The dental floss remaining above the ground serves as a marker that can be followed down to the buried remains after several days. In this way, both the adults *and* larvae can be collected.

One of the most popular methods of collecting is the use of baited pitfall traps. In this method, a wide-mouth jar, can, bottle, or plastic bucket containing rotting meat as a bait is placed into the ground with the lip of the container level with the surface of the soil. Soil should be packed around the opening of the trap to enable an unobstructed approach by beetles walking to the trap. Silphids are attracted to the odor of the bait and fall into the container where they may be either live-trapped in a sand substrate or killed in a preservative solution such as ethylene glycol (diluted automobile anti-freeze) or soapy water. There are probably as many trap designs as there are people to invent them, but some do seem to be more successful than others in trapping beetles. Figure 15 shows a generalized schematic for a baited pitfall trap. The experience of the people working in my lab seems to indicate that traps with larger surface areas *tend* to have more beetles in them when the amount of bait remains the same. Similarly, traps with *more* bait attract more beetles even when the trap container size varies. Whole animal remains seem to attract more carrion beetles than when only parts (*e.g.*, beef liver, pieces of fish, or chicken gizzards) are used. As always, proper aging of bait (two to three days in warm weather) helps to ensure greater trapping success. Ripening of bait in a closed container will keep flies from ovipositing on the bait, thus making it unusable. The jar or

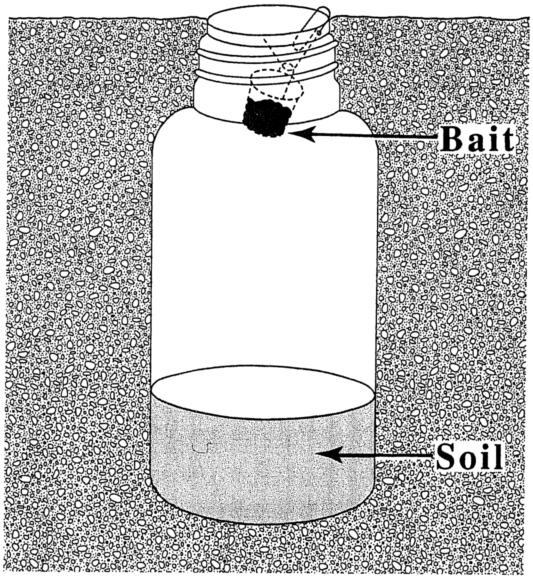


FIG. 15. Graphic representation of a baited pitfall trap.

container should not be tightly sealed in order to allow for the escape of gases that will be generated; otherwise, a nasty surprise could greet anyone opening the jar for the first time as the rotted bait explodes from the container. Ripened bait can then be suspended in one of several ways in the trap (as in Fig. 15) or placed in a small receptacle on the sandy bottom of a live trap (such as a small jar inside of a five-gallon bucket). Bait should always be wrapped or containerized to prevent beetles from actually coming into contact with it.

Placement of traps is also important. Traps placed in dense woods attract fewer beetles than those placed in more open woods, meadows, or prairies. This is probably because flying through dense undergrowth while searching for carrion is more difficult. Traps exposed to direct sun may attract fewer beetles if the bait inside the trap becomes dried out and mummified. A rain cover/sun shield should always be placed over pitfall traps so as to protect both the bait and trapped beetles from the elements. Traps should generally not be placed in areas so low that they might flood if it rains heavily. Traps should also not be placed near an ant nest because the ants may usurp the bait and deter beetles from approaching.

Vertebrate scavengers will often attempt to get at the bait in traps, thus disrupting any trapping program. Raccoons especially are tenacious in their efforts to get at rotting bait. A one-foot-square piece of one-inch mesh screen wire will prevent such scavenging if it is securely staked down above the opening of the pitfall trap. Even so, I have had very persistent scavengers dig entire traps out of the ground in order to eat the bait. Shubeck (1984b) designed an inexpensive carrion beetle trap that might inhibit such scavenging although it is more labor intensive for the initial construction and more cumbersome to transport, especially if a large number of them are being used.

When live-trapping (as for the endangered American burying beetle or to acquire other species alive for behavioral studies) great care must be taken to prevent beetle mortality in the trap resulting from flooding, overcrowding, or from heat stress. For nocturnal species, traps should be serviced daily and preferably in the morning before daytime high temperatures cause traps to become lethal. Pitfall traps should always be completely and securely covered or removed when they are no longer in use to prevent additional, unnecessary mortality to non-target beetles because additional beetles will fall into them, die, rot, and then attract more beetles.

KEY TO THE SUBFAMILIES OF ADULT SILPHIDAE IN NEBRASKA

1. Elytra with apices rounded, not truncate or shortened, usually exposing 1-2 segments (*Thanotophilus truncatus* has truncate elytra, but it is entirely black and has a gradually widening antennal club). Antenna with 11 distinct segments, gradually widening into club .... **Silphinae**

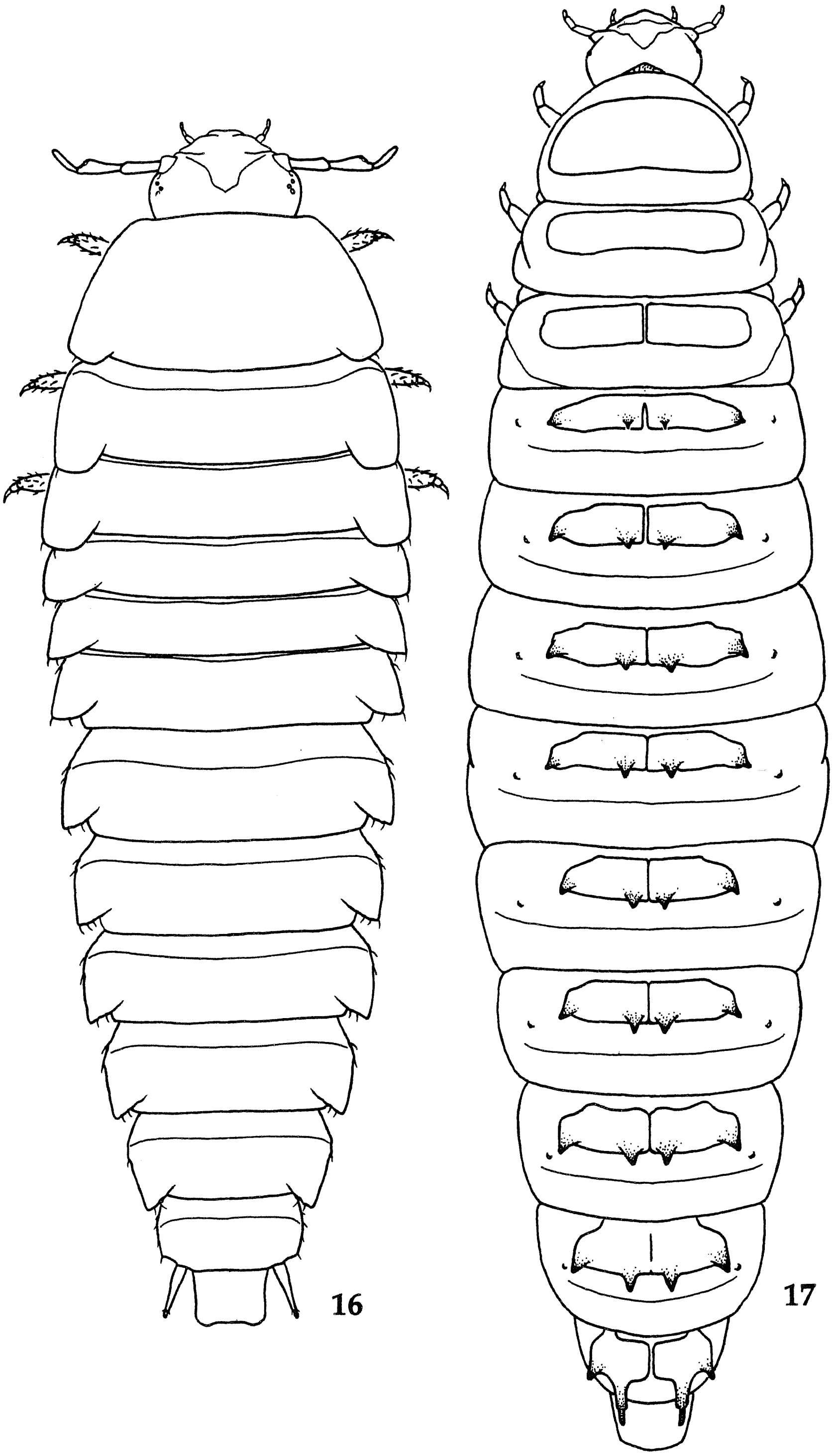
1′. Elytra with apices truncate, shortened, usually exposing 3-4 segments.Antenna apparently 10-segmented (actually 11-segmented but second small, nearly hidden in apex of first), last 4 segments widened into distinct, compact club ...... **Nicrophorinae**

KEY TO THE SUBFAMILIES OF THIRD INSTAR LARVAE OF SILPHIDAE IN NEBRASKA

(after Anderson and Peck 1985)

1. Tergites large, laterally produced, each usually with posterior angles attenuated (Fig. 16). Ventral surface with sternites large, sclerotized, and pigmented. Head on each side with 6 pigmented stemmata .... **Silphinae**

1′. Tergites small, those on abdomen each with 4 small spines (Fig. 17). Ventral surface soft, creamy white, lacking sclerotization. Head on each side with 1 unpigmented stemma .... **Nicrophorinae**



FIGS. 16-17. Body form of 16, a larval silphine, *Necrophila americana* and 17, a larval nicrophorine, *Nicrophorus investigator*.

SUBFAMILY SILPHINAE

The Silphinae is comprised of ten genera containing about 120 species (Hatch 1928, Lawrence and Newton 1995). They are worldwide in distribution with most of the species occurring in Eurasia and North America although there are two genera (*Diamesus* and *Ptomaphila*) with five species that reach Australia. In North America there are seven genera represented, and five of these genera (representing seven species) occur in Nebraska.

As with the Nicrophorinae, the status of the category Silphinae has shifted back and forth from tribe to subfamily depending on which specialist's views held sway at the time. The taxonomic category seems finally to have settled at the subfamily level following the works of Anderson and Peck (1985), Peck and Anderson (1985), and Lawrence and Newton (1995).

KEY TO THE GENERA AND SPECIES OF ADULT SILPHINAE IN NEBRASKA

(modified from Anderson and Peck 1985)

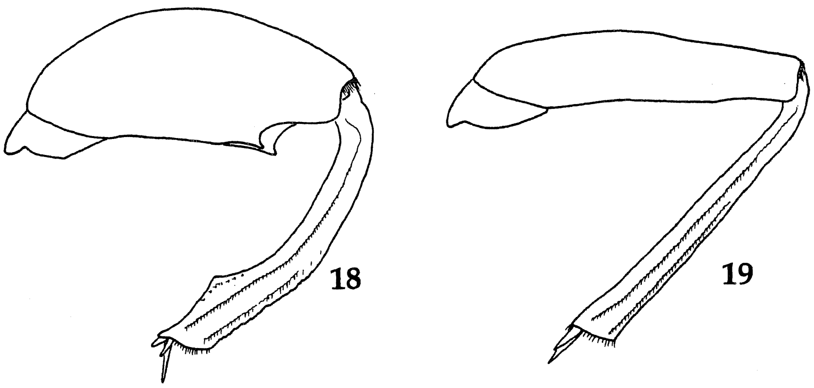
1. Pronotum black with yellow margins (Fig. 57). Elytra with reticulate sculpturing .... ***Necrophila***

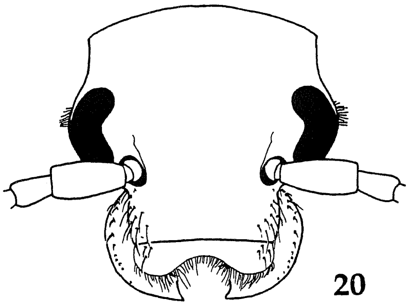
1′. Pronotum entirely black or black with reddish orange margins. Elytra with or without reticulate sculpturing 2

2. Eyes large (Fig. 49). Pronotum distinctly orbicular, widest at middle, basal angle broadly rounded. Male with metafemora enlarged and with tooth near apex (Fig. 18) .... ***Necrodes***

2′. Eyes small. Pronotum not orbicular, widest toward base, basal angles subangulate. Males with metafemora not enlarged or toothed 3

3. Head with distinct row of stout setae behind eyes (best seen in anterior view) (Fig. 20) 4





Figs. 18-19. Ventral view of left posterior femur and tibia of (18) male and (19) female *Necrodes surinamensis*. Fig. 20. Anterior view of head of *Oiceoptoma inaequale* showing row of stout setae behind eye.

Creek Reservoir, Red Willow Reservoir; GOSPER CO. (22): Lexington, Smithfield; HALL CO. (1): Alda; KEITH CO. (4): Cedar Point Biological Station; LANCASTER CO. (16): Lincoln; LINCOLN CO. (183): Box Elder Canyon, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; PHELPS CO. (5): Bertrand; RED WILLOW CO. (1): McCook.

Temporal Distribution. Rangewide: May to October (Peck and Kaulbars 1987). Nebraska: March (1), April (1), May (7), June (5), July (279), August (45), September (7), October (1).

Remarks. *Thanatophilus truncatus* may be readily distinguished by its dull black color, lack of costae or tubercles on the elytra, and truncate elytra. The truncate elytra *might* lead one to conclude that this species is a nicrophorine, but the gradually widening antennae will place it in the Silphinae. Among the Nebraska fauna, this beetle is unique in its appearance and is easily identified. A cautionary note: *T. truncatus* possesses setae behind the eye that might lead one to key it to *Oiceoptoma* species. In *Oiceoptoma*, however, there is normally a distinct *row* of long setae exactly on the posterior margin of the eye whereas in *T. truncatus* these setae are shorter, directed anteriorly, and are in a small but distinct field just behind the posterior margin of the eye.

The immature stages of this species remain undescribed.

Virtually nothing is known of the biology of this species. Peck and Kaulbars (1987) indicated it lives in such diverse habitats as grasslands, arid scrub desert, oak-pinyon-juniper woodlands, pine forests, and montane meadows. Lingafelter's (1995) study in Kansas showed this species had a strong preference for open meadows. In Nebraska, it has been collected in short grass prairie, sandhills, juniper canyonlands, deciduous gallery forests, and heavily disturbed tall grass prairie habitats. I have collected a specimen from dog feces in Arizona.

SUBFAMILY NICROPHORINAE

The Nicrophorinae contains the genera *Nicrophorus* (with about 85 species), *Ptomascopus* (three extant and one fossil species), and *Paleosilpha* (one fossil species) (Hatch 1927, 1928, Peck and Anderson 1985). The species of *Nicrophorus* are found throughout the Americas (including the first record from the Caribbean region, a new species from the Dominican Republic being described by Davidson and Rawlins; J. Rawlins, pers. comm., October 1995), Europe, and Asia. Most of the species are north temperate in distribution. They are not found in subsaharan Africa, Australia, or India.

Ptomascopus has three extant species in Asia and one fossil species (*P. aveyronensis* Flach) from the Oligocene of France (Hatch 1927). The monotypic *Paleosilpha fraasii* Flach is also known only from the Oligocene of France.

During most of the last century, the Nicrophorinae has shifted back and forth from tribe to subfamily status depending on the views of the particular specialist at the time. Both Hatch (1928) and Peck and Miller (1993), in their checklists of the world and North American faunas respectively, give tribal status to the taxon. Conversely, Anderson and Peck (1985), in their treatment of the Canadian and Alaskan fauna, Peck and Kaulbars (1987), in their distribution and bionomics of U.S. carrion beetles, Peck and Anderson (1985), in their treatment of the carrion beetles of Latin America, and Lawrence and Newton (1995), in their new classification of beetle families, use the subfamily level for the taxon. Subfamily status appears to be the current consensus.

Genus *NICROPHORUS*

Nicrophorus Fabricius 1775: 71.
Necrophorus Thunberg 1789: 7.
Necrophagus Leach 1815: 88.
Crytoscelis Hope 1840: 149.
Acanthopsilus Portevin 1914: 223.
Necrocharis Portevin 1923: 141.

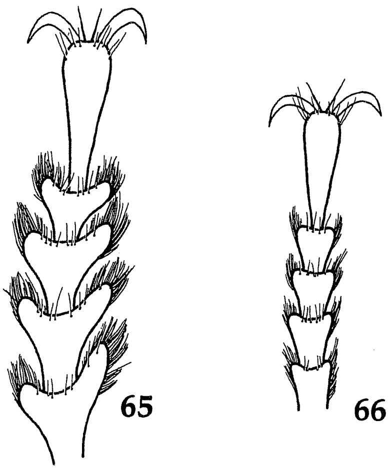
Necroxenus Semenov-Tian-Shanskij 1926: 46.
Eunecrophorus Semenov-Tian-Shanskij 1933: 152.
Necrocleptes Semenov-Tian-Shanskij 1933: 153.
Necrophorindus Semenov-Tian-Shanskij 1933: 153.
Necrophoriscus Semenov-Tian-Shanskij 1933: 152.
Nesonecrophorus Semenov-Tian-Shanskij 1933: 153.
Necropter Semenov-Tian-Shanskij 1933: 154.
Nesonecropter Semenov-Tian-Shanskij 1933: 154.
Stictonecropter Semenov-Tian-Shanskij 1933: 154.
Neonicrophorus Hatch 1946: 99.

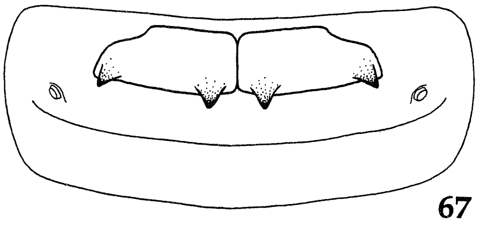
The genus *Nicrophorus* presently contains about 85 species distributed in Europe, Asia, North and South America (Hatch 1928, Peck and Anderson 1985). Most of the species occur in Europe and Asia. There are 15 species in the United States, and all but four of these occur in Nebraska (*N. defodiens* Mannerheim, *N. nigrita* Mannerheim, *N. sayi* Laporte, and *N. vespilloides* Herbst). *Nicrophorus defodiens* Mannerheim is found throughout much of South Dakota, and further sampling may indicate its presence in northern Nebraska.

While there is an abundance of literature on the taxonomy of the genus and the life histories of its species, there has been no modern, comprehensive treatment. The North American taxa were last reviewed by Anderson and Peck (1985). The most recent synoptic world catalog is that of Hatch (1928) while the latest North American catalog was provided by Peck and Miller (1993). Peck and Anderson (1985) conducted a preliminary phylogenetic analysis of the species groups of *Nicrophorus* as well as a general overview of biogeography.

In the past, the spelling of this genus name varied from *Nicrophorus* to *Necrophorus* and back again. Fabricius (1775) established the name *Nicrophorus*, and it was subsequently used in this form by himself in other publications, by Olivier (1790), and by other contemporaries. Thunberg (1789), however, used the spelling *Necrophorus*, and from that point confusion has reigned. Hatch (1932) first explored the spelling dilemma, but he did not conclude which name should be accepted. Herman (1964) provided a detailed history of these two names. He concluded that *Necrophorus* was an incorrect transliteration (hence, an unjustified emendation), and that the original spelling should be maintained.

The adults of nearly all of the species of *Nicrophorus* show parental care in rearing their young, and this has resulted in the life histories of several species becoming well studied, mostly by ecologists. For other species, however, very little is actually known of their life history or immature stages.





FIGS. 65-66. Foretarsus of (65) male and (66) female *Nicrophorus marginatus* showing dimorphism in tarsomeres. Also note bisetose empodium. Fig. 67. Abdominal tergite of larval *Nicrophorus investigator* showing 4 posterior spines.

Adults in the genus *Nicrophorus* are easily recognized because of the presence of truncate elytra that are usually marked with conspicuous orange or reddish bands or spots. The males of most species possess expanded segments of the foretarsus (Fig. 65) whereas in females the tarsi are only slightly expanded (Fig. 66). Bliss (1949) observed that some species of *Nicrophorus* show secondary sexual characters although there are no characters common to the entire genus.

Larvae of *Nicrophorus* species are distinctive because of the presence of quadrispinose abdominal tergites (Fig. 67) and reduced sclerotization. Anderson (1982b) described the larvae of ten Nearctic species of *Nicrophorus*.

NICROPHORINE BIOLOGY

Flying upwind against a gentle breeze, silvery moonlight reflecting dully from hardened wing covers held high over her body, orange-tipped antennae fully extended and quivering in the warm night airs, a female burying beetle searches for the odor of recent death. She is seeking the relatively fresh remains of a recently dead animal so that she and a prospective mate can quickly bury it and use it as a food source for themselves and their young.

It is a truism indeed that what passes for food to some is absolutely repulsive to others. This is due, in part, to culture, familiarity, and available food resources because, after all, various foods are composed of the same basic set of proteins, carbohydrates, fats, and sugars. Fortunately, burying beetles have no culture, and they dig in (literally) with a necessary haste that reflects a competitive principle of "better to eat quickly than to let the flies have it." Calliphorid flies are often the first to oviposit at carrion and, if the eggs are not detected and destroyed by *Nicrophorus* adults, the carcass may be consumed by developing fly larvae, causing the beetles to abandon the resource.

The majority of silphids are scavengers on dead animals, dung, and decaying plant materials, and some prey on snails. Although not all silphids bury carrion, the orange and black banded species in the genus *Nicrophorus* inter small, dead vertebrates in the ground, hence their common names of carrion or sexton beetles. There the beetles lay eggs and process the remains in order to provide a food source for their developing larvae.

SEARCHING BEHAVIOR

Burying beetles are found primarily in temperate regions of the world. They are rare or absent in the tropics because they are simply out-competed by more efficient carrion feeding ants and vultures. Most burying beetles are nocturnal, and they search widely for carrion. They are remarkably adept at detecting the odor of animals that have recently died. Using the organs of smell located on their antennae, they can find a dead mouse, for example, within an hour of death and from as far away as two miles (Petruska 1975)! Attesting to their extreme sensitivity in detecting odors is the fact that humans do not usually consider that there is *any* odor associated with remains within an hour of death. Customarily, however, beetles find a carcass after a day or two. Experiments conducted by Shubeck (1975a) demonstrated that vision did not play a role in searching behavior. Most searching behavior is guided by the sense of smell.

Dethier (1947) conducted olfaction experiments with several *Nicrophorus* species, *Oiceoptoma novaboracense*, and *Necrophila americana*. He concluded that the ability to perceive odors from a distance resided in the antennae while the end organs of the palpi detected odors from a short distance. He observed that beetles that had their antennae surgically removed could still locate carrion from short distances (30 inches); it was on this basis that Abbott (1927a-b, 1936) had previously and erroneously concluded that the antennae of *Nicrophorus orbicollis*, *N. tomentosus*, and *Oiceoptoma inaequale* were of little importance in orientation to odors.

Dethier concluded that the major difference between long range and short range odor perception probably involved thresholds of individual sensillae. These sensillae are sensitive to hydrogen sulfide and some cyclic carbon compounds (Waldow 1973) that are released as a carcass decays. The antennal lamellae (the apical three segments) possess several hundred sensillae whereas the remaining segments have few to none.

Shubeck (1968) conducted a large mark/recapture experiment using 460 individuals of *Oiceoptoma novaboracense* and 205 individuals of *N. tomentosus* and *N. orbicollis*. Only 2% of released *O. novaboracense* returned to carrion from a distance of 75 m, and only 28% returned when released 5 m from carrion. Rates of return were even lower for the *Nicrophorus* species. The return rate increased as the distance was reduced. Shubeck suggested that these species were not very efficient at locating carrion. Perhaps the "trauma" of capture or some environmental factors may have deleteriously influenced the return rate inasmuch as these insects rely on finding ephemeral patches of carrion for survival and breeding. In other words, the results of this study may not be indicative of the searching ability of silphids. In pitfall studies conducted by Wilson *et al.* (1984) in Michigan, 94% of pitfall traps baited with mice were discovered within 24 hr, and 95% of the discoverers were *Nicrophorus* species. These beetles seem to be abundant relative to their resources.

In studies conducted by Conley (1982) using *N. carolinus*, location of carcasses varied from 24-100 hours; when putrefying carrion was present, the location time was less than six hours. Locating efficiency ranged from 10-80% (mean=36%) of available carcasses. Of 37 carcasses colonized, 14 (38%) were occupied by single beetles, and 10 (27%) were occupied by two beetles.

Pukowski (1933) observed a colonization pattern in six European species of *Nicrophorus* in which male beetles locate carrion, produce pheromones to attract a female, and then the pair vigorously rebuffs all other beetles attempting to colonize the carcass. Milne and Milne (1944) found that first colonizers of *N. orbicollis* and *N. tomentosus* may be of either sex, that there was no advertisement by males, and that burial and brooding was often accomplished by several pairs of beetles. Conley's observations of *N. carolinus* concurred with those of the Milnes. Conversely, Wilson and Fudge (1984) reported that while several beetles may find and bury a carcass together, a single pair will eventually drive off the others and secure the carcass for themselves. Wilson and Knollenberg (1984) noted that success in finding carrion is influenced by many factors, including density of competing vertebrate scavengers, density of competing individuals of *Nicrophorus*, individual searching ability, reproductive condition, and temperature.

A male that is successful at locating a carcass emits a sex pheromone that serves to attract a sexually receptive female (Pukowski 1933, Eggert and Müller 1989b). Often climbing to a higher perch, the male assumes a "headstand" position with the head held down and the fully extended abdomen pointing upward (Fig. 68). This exposes the last abdominal segment from which the pheromone is released as the tip of the tip is moved up and down slightly in such a way that the intersegmental membranes can be seen (Eggert and Müller 1989b). This segment is supplied with a number of cuticular pores and lined with specialized epithelial gland cells (Eggert and Sakaluk 1995). Studies by Eggert (1992) showed that *Nicrophorus* males emit pheromones both when they have found a carcass and when they have not. It seems likely that females cannot always tell whether a male is emitting pheromones on or off a carcass until there is physical contact between the two (Eggert and Müller 1989a). What, then, is the benefit accruing to a female responding to a pheromone emitter without a carcass? Eggert suggested that the benefit obtained by the female is obtaining an adequate sperm supply for when she finds a carcass on which no mate is present.

A few field studies have shown that some *Nicrophorus* females can often raise their brood without a mate (Scott and Traniello 1990b, Eggert 1992). Under these circumstances, females depended on sperm transferred from a male during previous matings for fertilization of their eggs. Eggert (1992) demonstrated with *N. vespilloides* that sperm stored in a female's spermatheca started to become infertile three weeks after insemination, even when the female had not produced any eggs in the meantime. The reproductive period of the female is longer than that of the male and may last several months.

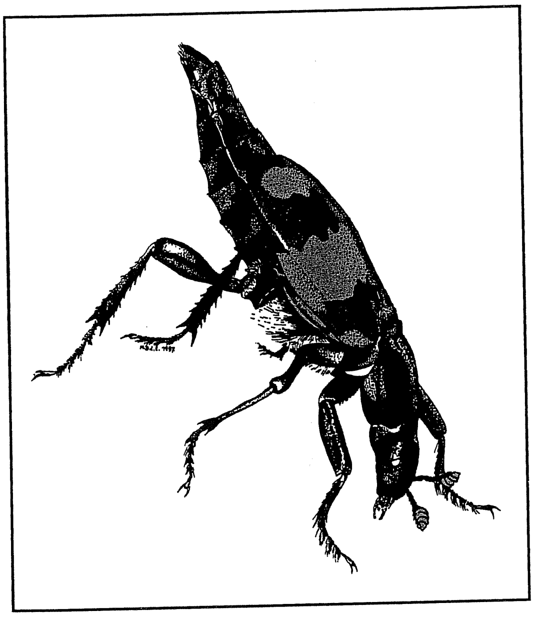


FIG. 68. Male *Nicrophorus* sp. emitting pheromone in typical "headstand" position. Illustration from cover of *Behavioral Ecology* 3(3), 1992. Used by permission of Oxford University Press.

BURIAL AND PREPARATION OF THE CARCASS

After arriving at a carcass, a male/female pair will first examine the body (Fig. 69) and assess its size by trying to move it. Adults make short trips to nearby terrain to find a suitable spot for burial (Scott and Traniello 1989). Less interest seems to be shown if the carcass is too large for burial although it can be an important food resource for the adults (Wilson and Knollenberg 1984). This may be because large carcasses are more difficult to transport or because a pair of beetles cannot bury it before the arrival of competitors, whether they be conspecifics, other *Nicrophorus* species, or flies (Trumbo 1990b, Eggert and Müller 1992). Smaller species, such as *N. tomentosus* and *N. defodiens*, bury carcasses just below the leaf litter while larger species take carcasses to greater depths beneath the soil (Pukowski 1933, Wilson and Knollenberg 1987).

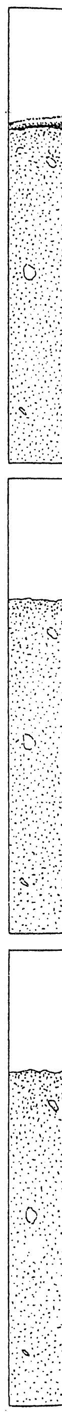
According to Muths (1991), *Nicrophorus* species were tested in the laboratory to determine if they discriminated between different substrates when burying a carcass. His results suggested beetles do discriminate, preferring substrates with higher "bulk" (*i.e.*, grass clippings) over those without. Factors other than those influencing the speed of concealment probably influence burial site selection. A stable, non-collapsing burial chamber to hold the carcass and provide a nursery for the larvae is important for successful reproduction (Pukowski 1933, Milne and Milne 1976). Muths indicated that discrimination may be explained mechanistically in terms of substrate qualities such as ease of excavation and suitability in the substrate for stable burial chamber construction. Alternatively, discrimination can be explained functionally in terms of response to competition, where immediate burial insures exclusive resource use. It is not clear which explanation is most appropriate. There may be a tradeoff; immediate burial in a less than optimum substrate may be the best choice in situations where competition is intense, but delayed burial may be a better strategy where competition is less intense and optimum substrate is available only some distance from the carcass.

If, after an exploration of the surrounding soil, the ground is found to be too hard for burial, the pair of beetles (working together) may move mouse-size remains three to four feet per hour for as much as three hours until a substrate soft enough for burial is found. It remains unknown how a pair of beetles can "agree" on a burial site or how they are able to keep the carcass moving uniformly in one direction. The soil at the burial site is loosened by "plowing" through it in much the same fashion as does a bulldozer (Fig. 70). Using its head, a beetle presses its head in and forces soil upward until it crumbles. Roots are forced aside or chewed through. Gradually, soil from beneath the carcass is displaced to each side, and the carcass settles into the ground and is buried by several inches of soil (Figs. 71-72). Milne and Milne (1944), working with *N. tomentosus*, observed burial chambers 6.5 cm long and 2.7 cm wide and deep. Burial is usually completed in five to eight hours although some beetles will continue for days if obstructions slow their work. Immediate, nocturnal burial is important to these beetles because this prevents flies from laying eggs on the remains. Although fly larvae can be eaten or killed by the adult beetles, the presence of numerous fly larvae would make the remains unsuitable for the beetles and their young. In smaller species of *Nicrophorus*, brood failures may be more common on large rather than smaller carcasses because of uncontrollable fly infestations (Trumbo and Fiore 1994).

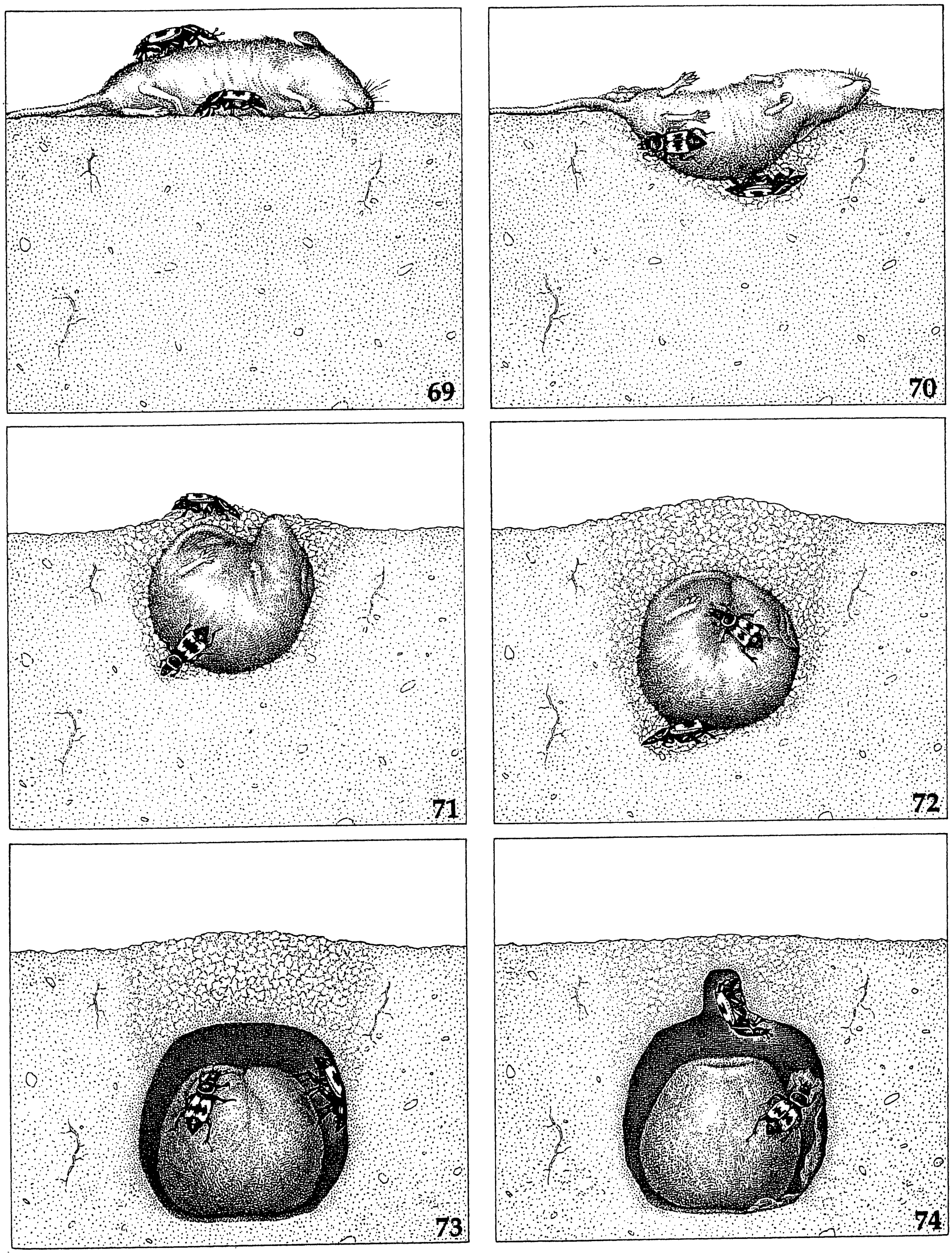
Scott and Traniello (1987), working with *N. tomentosus*, suggested that animals that require a patchy food source would be expected to make use of cues provided by that resource to trigger ovarian maturation. Newly eclosed females have previtellogenic ovaries that gradually develop to the resting stage in about three weeks (Wilson and Knollenberg 1984). These authors demonstrated that females at this stage were reproductively capable, and their ovaries matured rapidly (48 hr) when they were given a dead mouse to bury. Scott *et al.* (1987) demonstrated that the particular cue that brings about the physiological changes for ovarian development is the behavior of the female when she assesses, prepares, and attempts to bury a carcass. The location and burial of a suitable carcass is followed by vitellogenesis and rapid maturation. They noted that the mere presence of carrion was not sufficient in and of itself to trigger vitellogenesis nor were nutritional or feeding cues, presence of a male, or mating.

After burial, the beetles use their large jaws to strip away fur or feathers and work the remaining mass into a compact ball (Fig. 73). They will then "inoculate" the remains with oral and anal secretions that preserve the carrion and modify the course of decomposition (Scott *et al.* 1987). The female usually constructs a short chamber above the carrion in which she lays 10-30 eggs (Fig. 74). Wilson and Fudge (1984) conducted lab experiments with *N. orbicollis*. They found that the number of eggs laid by females varied directly with the body size of the female and not with the size of the carcass. The smallest number of eggs laid was 22. The largest number of larvae that survived to pupation was 26 in a single brood. Nearly all females laid more eggs than would ultimately survive. When adults were experimentally removed prior to hatching of the eggs, many broods failed completely. Those that survived resulted in few larvae, and these were much smaller than when the adult was present. Hatching success was high, but a thick mold grew over the carcasses in most cases when the parents were absent. Müller *et al.* (1990), on the other hand, concluded that the number of eggs was positively correlated with carcass weight in the European *Nicrophorus vespilloides*, and that there was no correlation between female body size and clutch size as reported by Wilson and Fudge (1984).

Trumbo (1992) experimented with *N. orbicollis*, *N. tomentosus*, and *N. defodiens* and found that they can raise a maximum of 35-50 young. In contrast, *N. pustulatus* (a brood parasite) is unique among *Nicrophorus* species because it can raise nearly 200 young on larger carcasses. Trumbo observed further that *N. orbicollis* and *N. sayi* were extremely dependent on parental regurgitations, and that young failed to survive to the second instar if parents were removed. Young of *N.*



FIGS. 69
it slips
mouse
receive
Milne.



FIGS. 69-74. Burial of a mouse by a pair of *Nicrophorus* beetles. As the beetles remove soil from beneath the carcass, it slips downward and is ultimately covered by about 3 cm of soil. After burial, a chamber is made. The skin of the mouse is removed and the remains are fashioned into a ball. A shallow depression is made on top of the ball to receive liquified food that the adults regurgitate there. From *The Social Behavior of Burying Beetles* by L. and M. Milne. Copyright © 1976 by Scientific American, Inc. All rights reserved.

defodiens, *N. pustulatus*, and *N. tomentosus* survived without parental regurgitations.

Müller and Eggert (1989) determined that males of *Nicrophorus* species are able to achieve a high level of paternity (mean = 92%). The mechanism they employ is a repeat mating tactic, *i.e.*, the female is mated frequently shortly before and during oviposition. Repeated matings are essential for a high reliability of paternity since single copulations resulted in the fertilization of only a small number of the female's eggs.

PARENTAL CARE

After returning to the carcass, the female prepares a conical depression on the top of it (Fig. 74). Both parents regurgitate droplets of partly digested food into the depression. The fluid accumulates as food for the larvae that will hatch in a few days (cover figure). First instar larvae, as well as older larvae that have just molted, also approach any adult and press their mouth parts against the jaws or palps of the adult. This action stimulates regurgitation directly to the larva (Milne and Milne 1976). Although some species require parental regurgitation (at least initially), a few other species (including *N. tomentosus*) can develop normally without parental feeding (Trumbo 1992, Scott 1994b). Otherwise, growing larvae feed directly from the depression (Fig. 75) or pull fragments from the surface of the carrion ball.

The larvae receive parental care during the entire time they are feeding and growing. This is an extremely rare and highly developed behavior in insects, a condition normally found only in the social bees, wasps, ants, and termites. Both adults regurgitate food to begging larvae (Scott 1989), a behavior also seen in birds and their nestlings. The larvae grow very rapidly and are soon able to feed themselves. Parental regurgitation to larvae is reduced by the third day, and after the fourth day there is very little. It is probable that parents continue to facilitate feeding throughout larval development

FIG. 75. *Nicrophorus* larvae feeding within the prepared remains of a mouse. Photo by D. S. Wilson.

by preparing the feeding cavity of the carcass (Scott and Traniello 1990a). The oral secretions are very proteolytic (Wilson and Knollenburg 1987). In a study by Fetherston *et al.* (1994), both single males and single females regurgitated to larvae and maintained carrion more frequently than paired males and females. Their data suggested male and female burying beetles increase their brood-care behavior to compensate for loss of a mate. This study may represent the first demonstration of compensation for mate loss in an invertebrate.

Bartlett and Ashworth (1988) and Scott and Traniello (1990b) demonstrated that larval weight correlated negatively with larval numbers. Neither the duration of parental regurgitation per larva nor the duration of activity within the carrion had a significant effect on mean larval weight (Fetherston *et al.* 1990). Consequently, the number of larvae, rather than the duration of parental feeding per larva, was the critical factor that determined mean larval weight. The mechanisms that parents use to determine brood size are poorly understood (Trumbo 1990c). Sometimes, if the size of the brood is too large to be successfully reared on a small carcass, both adults will regulate brood size by selective infanticide of smaller larvae, usually during the first 24 hours after eclosion, so that the remaining young will have a sufficient food supply (Bartlett 1987, Trumbo 1990c). Trumbo and Fernandez (1995) examined the ability of male *N. orbicollis* to regulate brood size, and they also manipulated the mass and volume of carcasses to determine whether correlates of these factors were important as cues in the assessment of resource potential. They found that single males of *N. orbicollis* raise broods of similar number and mass as those raised by single females and pairs. The results of their mass and volume manipulations with carcasses indicated that burying beetles use volume-related cues (not mass) to assess resource potential. This study indicated that, in the absence of the female, males perform the additional task of brood size regulation. Direct and early culling of larvae in excess of the carrying capacity of the carcass is the most unusual feature of infanticide by *Nicrophorus* species and is a consequence of their particular biology (Bartlett 1987). Such intentional parental cannibalism is exceptional among invertebrates (Trumbo 1990c).

The effect of male presence, if he remains until larval development is complete, may be to decrease the number or weight of the larvae reared (Scott 1989, Scott and Gladstein 1993). Conversely, the male's presence greatly reduces the probability that the carcass will be taken over by a conspecific intruder and the brood killed (Scott 1990, Trumbo 1990b, 1991, Scott and Gladstein 1993). Scott and Gladstein (1993) noted that the cause of increased larval mortality (especially on small carcasses) when the male is present appears to be due to both decreased resources available to larvae and to infanticide. On small carcasses, the amount consumed by an adult male was equivalent to the amount of resources required for one larva. Fetherston *et al.* (1990), for example, observed females of *N. orbicollis* attempting to drive off males from carcasses of 25-30 g. Since the presence of the male may result in a decrease in total brood weight, and the female is subject to a lower cost than the male if the male deserts and is replaced by an intruder (Scott 1989), the female may prefer that the male leave the brood chamber earlier than the male would prefer to leave (Fetherston *et al.* 1990).

The adults continually tend the carcass, removing fungi and covering the carrion ball with a presumed antibacterial secretion. To my knowledge, research has not yet been conducted on this phenomenal ability to inoculate and alter the course of decomposition. On the other hand, Solter *et al.* (1989) examined the midgut, hindgut and associated hemolymph of *Nicrophorus tomentosus*, *Necrophila americana*, and *Oiceoptoma novaboracense*. They found 19 species of bacteria. In their study, six species of bacteria were also associated with the skin, an additional four with the respiratory system, and ten species with the gastrointestinal tract, all of humans.

In a similar study, Berdela *et al.* (1994) recovered 607 isolates consisting of 42 different strains of bacteria from *Nicrophorus tomentosus, N. orbicollis, Oiceoptoma novaboracense, O. inaequale, Necrophila americana,* and *Necrodes surinamensis.* Of these, 52.1% were gram negative bacteria, 21.1% were coagulose-negative staphylococci, 8.1% were obligately anaerobic bacteria, 7.6% were streptococci, 5.4% were *Bacillus* spp., 4.4% were *Aerococcus* spp., and less than 1% were coryneform bacteria. Many of these species are known opportunistic pathogens.

After about a week, the larvae have consumed all but the bones of the carcass and, at this time, one or both adults break out of the chamber and fly away. The young pupate in the nearby soil about two weeks after hatching and emerge as adults about a month later. Overwintering then occurs in the adult stage.

AGONISTIC BEHAVIOR

Suitable carcasses are scarce relative to the number of potential breeders (Wilson and Fudge 1984, Trumbo 1992), and beetles will accept a broad size range of carcasses (Trumbo and Eggert 1994). On a small carcass, fights reduce the resident population to a dominant male-female pair (Pukowski 1933, Wilson and Fudge 1984). Intrusions and takeovers appear to be a regular feature of the breeding system of *Nicrophorus* species (Trumbo 1990a).

Trumbo (1990a) observed that interactions between intruders and residents were agonistic, and infanticide occurred regularly as a consequence of a takeover. Intruders of both sexes generally kill larvae of the resident parents when they find them on the carcass. Once infanticide began, larvae were not killed all at once but opportunistically as the intruder inspected the carcass. Intruders pierced the integument of larvae with their mandibles and handled them for 3-72 seconds. Those held the longest were almost entirely consumed while those held for only a few seconds were dropped, immobilized but alive, and later consumed by the intruder or the resident. Milne and Milne (1944) saw that *N. orbicollis* became quite excited when expelling a competitor and stridulated audibly by rubbing the upper surface of the abdomen against the bottom surface of the elytra. The outcome of fights is largely determined by relative body size of the combatants (Pukowski 1933, Bartlett and Ashworth 1988, Otronen 1988). Scott's (1994a) study showed that male presence in *N. defodiens* is generally ineffective against larger, congeneric intruders. Competition with other beetles can be severe. Scott and Traniello (1990b) observed no significant differences between males and females in four species of *Nicrophorus* in the proportion of individuals suffering injury (loss of body parts) from competitive fights for carcasses.

Müller *et al.* (1990) observed (in *N. vespilloides*) that females losing fights did not immediately abandon the carcass. Instead, they often stayed to lay their own eggs. In their lab experiments, some of the loser's larvae were cared for by the winner and survived to adulthood in 60% of the cases observed. These experiments showed a positive correlation between the parents duration of stay near the carcass and her chances of parasitizing the other female's brood. Müller and Eggert (1990) further observed that winning females did not discriminate against unrelated larvae if they arrived on the carcass within a window of time that corresponded with the oviposition period of the dominant female. *Nicrophorus vespilloides* females responded parentally only to larvae they encountered during a distinct and relatively short parental phase. Before or after that phase, larvae encountered were killed and eaten, irrespective of carrion availability. These authors believe that the time dependency of infanticidal behavior and parental care is an example of a simple "rule of thumb" (Dawkins 1979) that increases the probability that parental care is allocated to the parents' own offspring. Recognition of individuals by the parents is not involved and may not even occur.

Mite Relationships

Nicrophorus species have a mutualistic relationship with phoretic mites of the genus *Poecilochirus* (Mesostigmata: Parasitidae). Springett (1968) gave the following overview. Deutonymphs are carried by *Nicrophorus* adults to carrion where the mites leave the beetle and feed on fly eggs and small larvae. If the carcass is buried by the beetle, the feeding behavior of the mite (on fly eggs) helps to ensure successful breeding by the beetle. When the carcass is buried, both beetles and mites reproduce underground. When the *Nicrophorus* larvae pupate, the adult female beetle abandons the brood chamber, and large numbers of deutonymphs are carried by her to another carcass. The continuity of the association is maintained when the mite deutonymphs join the beetle larvae when they pupate or encounter other adult *Nicrophorus* at a carcass. The mites may not be completely dependent on *Nicrophorus* species for successful reproduction, and *Nicrophorus* species would be much less successful in competing with the larvae of *Calliphora* fly species without the mites. Brown and Wilson (1992) observed that *P. carabi* usually do not reproduce on large carcasses but wait until their *Nicrophorus* host has found a small carcass suitable for its own reproduction.

In more detailed observations of *Poecilochirus carabi* and *Nicrophorus vespilloides* in Europe, Schwarz and Müller (1992) observed the first deutonymphs of the new mite generation aggregated on the male beetle. The mites did not use sex-specific traits to discriminate between male and female beetles in the brood chamber but traits that are related to the behavior of the beetles. When the male beetle departed, it carried away nearly all the deutonymphs then present in the brood chamber. Deutonymphs that developed later congregated on the female beetle, which left the chamber several days after the male. Only those deutonymphs that missed the female's departure dispersed on the beetle larvae; this meant they had to wait in the pupal chambers until the beetles completed their development. On average, 86% of the deutonymphs left the brood chamber on the parent beetles.

Springett's (1968) laboratory experiments demonstrated that the presence of mites helps to enable successful reproduction of beetles whereas in cultures lacking mites (but with calliphorid eggs), the *Nicrophorus* adults were unsuccessful in rearing young. Calliphorid eggs hatched only when mites were absent because the mites were such avid predators of the fly eggs. Beetles could then utilize the carcass without the competition from fly larvae. Adult *Nicrophorus* do eat fly larvae but were never successful in killing all of them. Mites would also attack fly larvae but only those less than 5 mm. The presence of mites does not guarantee the absence of flies. In studies conducted by Scott and Traniello (1990b), 9.1% of carcasses buried (N=33) were lost to flies in June, 44.7% (N=38) were lost in July, and 66.7% (N=15) were lost to flies in August.

Deutonymphs stayed with the *Nicrophorus* larvae and remained active within the pupal cell throughout the pupal period (Springett 1968). During this time it was impossible for mites to free themselves from the pupal cell, and the beetles emerged as adults bearing the deutonymph mites. The deutonymphs are chemically attracted to burying beetles and prefer them to non-*Nicrophorus* species; they could not be induced to use other carrion beetles as hosts (Springett 1968, Korn 1983).

Beninger (1993) and Blackman and Evans (1994), working with *Nicrophorus vespilloides* in Europe, observed the mites *Poecilochirus carabi* G. and R. Canestrini and *P. davydovae* Hyatt attacking the eggs of their host burying beetles with a consequent reduction in brood size. Their studies indicate that mite predation on burying beetle eggs occurs, and that further studies are needed.

NEMATODE RELATIONSHIPS

Richter (1993) reported that *Rhabditis stammeri* (Völk), a carrion-dwelling nematode, is specifically associated with *Nicrophorus vespilloides*. Juveniles of the nematode use the adult beetle for transport to carrion where both adults and larvae of beetles become infected. Inside the beetle larvae, the juvenile nematodes are transported to the pupal chamber via the larval gut. After pupation, the juvenile nematodes are found in the pupal chamber at protected places such as the exuvium or beneath the wings of the pupa. After emergence from the pupa, the nematodes migrate to the gut and genitalia of the adult beetles. *Rhabditis stammeri* is also transmitted from one adult beetle to another during copulation. Infection by nematodes probably occurs in many other species of *Nicrophorus* as well, and is an area needing additional study.

STRIDULATION

All species of *Nicrophorus* have a stridulatory structure in both males and females (Fig. 2). Stridulation is used during burial of the carcass, copulation, and the interaction between the female and her brood (Niemitz 1972, Niemetz and Krampei 1972). Huerta *et al.* (1992) conducted lab experiments with *N. mexicanus* and found that a lack of stridulation in the female resulted in poor or no "bonding" between the female and her offspring, which negatively affected larval survival. Inhibition of stridulation in the male affected and sometimes precluded copulation. Lack of stridulation in both nest partners may affect the coordination of nest preparation (Halffter 1982, Huerta *et al.* 1992, Halffter *et al.* 1983).

PREDATION

Most ground-feeding insectivorous birds are probably familiar with burying beetles, and these beetles have been recorded as among the food items of several species, especially crows that routinely visit carrion. Jones (1932) conducted a number of experiments using *N. americanus*, *N. orbicollis*, and *N. pustulatus* to determine if a variety of insectivorous birds would be deterred by these aposematically colored beetles. Although he tested only seven specimens, none were eaten by the birds, while 42 out of 46 other beetles (representing seven species) of comparable size were eaten by seven species of birds during 93 feeding events. Jones concluded that birds do avoid these brightly colored beetles, at least when other food is available.

SOCIALITY

The activities of adult *Nicrophorus* species in rearing their young is the highest level of sociality attained in the Coleoptera (Wilson 1971, Wilson and Fudge 1984). On a large carcass, the mating system is variable. Larger carcasses can support greater numbers of larvae and support broods of greater total mass than smaller carcasses (Trumbo 1992). Consexual adults often tolerate each other and often feed each other's young in a quasisocial fashion (Scott and Traniello 1990a, Eggert and Müller 1992, Trumbo 1992, Scott and Williams 1993, Trumbo and Wilson 1993). According to Trumbo and Wilson (1993), females of smaller *Nicrophorus* (*N. defodiens*, *N. tomentosus*) species were much more likely to feed young cooperatively than females of, for example, *N. orbicollis*. They hypothesized that since adults cannot discriminate between related and unrelated young, they feed any larvae on the carcass to ensure adequate care for their own young. Larger carcasses were more difficult to exploit because: (a) they took longer to conceal beneath the leaf litter; (b) they were less likely to be rounded into brood balls; (c) they were more likely to be utilized by dipterans; and (d) they were occupied by greater numbers of congeners (Trumbo 1992).

Scott (1994b) suggested that competition with flies promotes communal breeding in *N. tomentosus*. She demonstrated that broods reared on small carcasses by foursomes were 32% larger than those reared by a pair, and that on larger carcasses they were 49% larger when the beetles were in competition with flies. Her study showed that subordinate males provided longer care on flyblown carcasses, which indicated there is a benefit gained when both males assist. In these cases, the subordinate remained a few days longer to help eliminate maggots and fly eggs. Scott indicated that the actual frequency of communal breeding in the field depends on the density of the beetle population as well as other factors because a carcass must be discovered by several consexual adults within 24 hours, or else the resulting late-arriving larvae will be killed by the resident adults.

A female can produce two broods in a short time in response to partial or total brood failure (Müller and Eggert 1987), an intruder male that destroys her initial brood (Trumbo 1987, Scott and Traniello 1990a), or completing a reproductive cycle and locating a second carcass (Scott and Traniello 1990b). In similar experiments, Müller (1987), Scott and Traniello (1990a), and Trumbo (1990c) found that the number and mean mass of larvae declined between the first and second reproductive events.

If a male fails to discover the carcass, a female can breed on her own using stored sperm (Bartlett 1988, Scott 1989, Trumbo 1990b). Females acquire sperm by copulating with males that emit pheromones in the absence of a carcass or by copulating with males on large carcasses where feeding only occurs (Müller and Eggert 1987, Eggert and Müller 1989a, Trumbo and Fiore 1991). Both males and females can breed more than once in a season (Bartlett and Ashworth 1988, Scott and Traniello 1990a).

Trumbo (1991) found in his studies of *N. orbicollis* that males investing time with their brood forfeit time spent searching for new breeding opportunities. Such costs imply that some benefits are derived from paternal care. On large carcasses, larvae raised by pairs were further along in development than broods raised by single females. Trumbo saw no differences on small carcasses. On large carcasses, the brood is vulnerable for a shorter period of time when the male is present. Trumbo concluded that at least one parent is needed throughout development to defend against predators, control microbial activity, and open new portions of the carcass to larval feeding. The major benefit, then, of male assistance lies in guarding against intraspecific competition after the carcass is buried. The presence of both parents dramatically reduced the probability that conspecifics will usurp the resource, replace either the male or female, kill the newly hatched brood, and produce a replacement clutch (Scott 1990).

Eggert and Sakaluk (1995) observed that the reproductive interests of the sexes often do not coincide, and that this fundamental conflict probably underlies a variety of sex-specific behavioral adaptations. Sexual conflict arises when a pair of beetles secures a carcass that can support more offspring than a single female can produce. They noted that in such a situation, any male attracting a second female sires more surviving offspring than he would by remaining monogamous whereas the female's reproductive success decreases if a rival female is attracted to the carcass. Their observations and those of Trumbo and Eggert (1994) demonstrated that monogamously paired males on large carcasses do attempt to attract additional females by means of pheromone emission whereas males on small carcasses do not. In a series of remarkable experiments, Trumbo and Eggert (1994) and Eggert and Sakaluk (1995) demonstrated that females physically interfered with male polygnous signaling using various behavioral tactics. These interference tactics included mounting, pushing him from a perch from which he emits pheromones, undercutting the male, or pinching his abdomen with her mandibles.

Halffter (1991), among others, concluded that subsocial behavior in general is accompanied by a reduction in the number of offspring and that this is compensated for by a significant reduction in juvenile mortality. He observed that subsociality in *Nicrophorus* species was favored by several behavior patterns: (1) A reduction in the effort needed for both sexes to find one another. The characteristic discontinuity of carcass distribution in space and time favors the sexes meeting and cooperating at the food source; (2) The relative ease by which the sexes meet may simplify precopulatory mating behavior, thus reducing valuable energy expenditures; (3) The food needs to be manipulated by the parents before being ingested by the larvae. This includes transport, burial, processing, guarding, and tending the food. This is accomplished more efficiently by pairs of beetles; (4) The evolution of cooperative nesting and care of progeny generally favors pair bonding that is accompanied by chemical, acoustic, or tactile behaviors.

Of principal importance to these beetles and their young is the burial of the food resource because this effectively removes it from the arena of intense competition by maggots, other carrion-feeding insects, and even mammal scavengers. Carrion is an ephemeral, unpredictably encountered food source, and its "bonanza" nature is so valuable to the prospective parents that they bury it to keep it from being stolen. Burying beetles are unique among the silphids because they are the only ones that break the cycle of competition at the food source while, at the same time, providing their larvae with a considerably safer subterranean environment in which to develop that is relatively free from predators. Burying beetles exhibit one of the most advanced forms of parental care described among Coleoptera (Zeh and Smith 1985).

According to Scott and Traniello (1990a) the principal determinants of reproductive success for burying beetles are clear. There is a positive correlation between brood mass and carcass mass (Kozol *et al.* 1988, *N. americanus;* Wilson and Fudge 1984 and Scott and Traniello 1990b, *N. orbicollis;* and Robertson 1992, *N. orbicollis* and *N. pustulatus*). Beetles probably do not bury larger carcasses because they are too heavy to move or because a pair of beetles cannot bury it before the arrival of competitors, whether they be conspecifics, other *Nicrophorus* species, or flies (Eggert and Müller 1992). The size of the carcass is the most important factor influencing the total weight of the brood. Offspring size is increased by care from the primary parents throughout larval development by facilitation of feeding even though the presence of each parent may reduce the amount of food available to offspring (Scott 1989). The presence of the second parent reduces the probability that the carcass will be taken over by a competitor and the brood killed. Males almost always participate in defense and feeding of the brood (Bartlett 1988).

KEY TO THE SPECIES OF ADULT *NICROPHORUS* IN NEBRASKA

(modified from Anderson and Peck 1985)

1. Pronotum lacking anterior, transverse impression; lateral margins extremely narrowly explanate (Fig. 76) ..... ***carolinus* (L.)**

1′. Pronotum with anterior, transverse impression; lateral margins broadly explanate (Figs. 77-83) 2

2. Frons and pronotal disc red. Tarsal empodium quadrisetose .... ***americanus* Olivier**

2′. Frons and pronotal disc black. Tarsal empodium bisetose (Figs. 65-66) 3

3. Pronotum with dense yellow pubescence .... ***tomentosus* Weber**

3′. Pronotum glabrous or with sparse setae on anterior or lateral margins 4

4. Posterior angle of metepimeron with dense, yellow pubescence (Figs. 84, 87, 89) 5

4′. Posterior angle of metepimeron glabrous (Figs. 85, 86, 90, 91), or with dark setae (Fig. 88), or with only a few yellow setae 7

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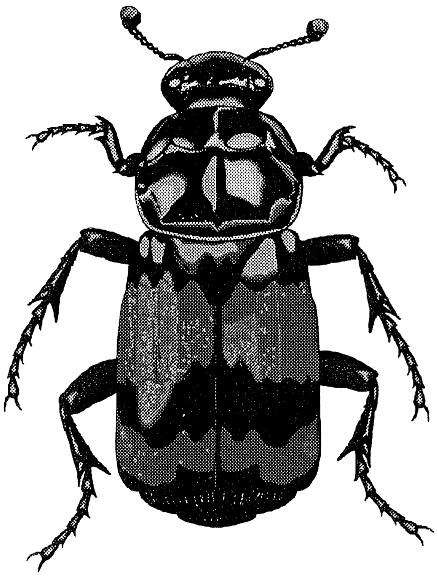

GLOSSARY

(modified from Torre-Bueno 1937)

Antenna (pl. **antennae**). The paired, segmented sensory organs borne on the head.

Anterior. Front or forward; opposite of posterior.

Aposematic. Conspicuous and warning of danger.

Base. On the thorax, that part nearest the abdomen; on the abdomen, that part nearest the thorax.

Carina. A longitudinal, narrow, raised ridge.

Club. The enlarged, distal segments of the antenna (Figs. 83-84).

Clypeus. That part of the head in front of the frons. In dorsal view of a silphid, that part of the head between the frons and labrum (Fig. 2).

Congeneric. Belonging to the same genus.

Conspecific. Belonging to the same species.

Cordate. Loosely, heart-shaped or triangular with the corners rounded.

Costa. Longitudinal, elevated ridges of the wing covers.

Coxa. Basal segment of the leg that articulates with the body (Fig. 3).

Diurnal. Active during the day.

Dorsal. The upper surface.

Elytron (pl. **elytra**). The anterior, chitinous wings of beetles that serve as covers to the folded flight wings (Figs. 2, 21-33).

Emarginate. Notched or with a rounded or obtuse section removed from a margin.

Empodium. The single pad-like or filiform median structure often present in the insect claw.

Epimeron. The posterior division of a thoracic pleuron, usually small (Fig. 3, 85-92).

Epipleuron. The deflexed portion of the lateral edge of the wing cover.

Exuvium. The cast skin of the larva after metamorphosis.

Femur. Usually the stoutest segment of the leg, articulated to the body by the trochanter and coxa and bearing the tibia at its distal end (Figs. 2-3).

Frons. The upper portion of the head capsule behind the clypeus and before the vertex.

Glabrous. Smooth, lacking setae.

Hemolymph. The blood of arthropods.

Hindgut. The posterior portion of the alimentary tract, between the midgut and the anus.

Humerus. The basal, exterior angle of the elytra; shoulder.

Impressed. Having shallow, depressed areas.

Instar. The form between molts in the larva, numbered to designate the various periods, e.g., the first instar is the stage between the egg and the first molt, etc.

Interval. The longitudinal space between striae or costae on the elytra.

Labrum. The upper lip that covers the base of the mandibles and forms the roof of the mouth (Fig. 2).

Lateral. Relating to the side.

Longitudinal. In the direction of the long axis.

Macula. A colored mark larger than a spot, of indeterminate shape.

Mandibles. The stout, tooth-like pair of jaws in chewing insects.

Margin. The more or less narrow part of a surface adjacent to the edge.

Median. Pertaining to the middle.

Meso. Greek prefix referring to the middle.

Meta. Greek prefix referring to posterior (generally third).

Metasternum. The ventral part of the metathorax. In silphids, generally the large plate extending from the middle to the posterior legs (Fig. 3).

Metepimeron. In *Nicrophorus* species, the small lobe behind and laterad of the metasternum (Figs. 3, 85-92).

Midgut. The middle portion of the alimentary tract.

Necrophagous. Feeding on dead or decaying matter.

Nocturnal. Active at night.

Ocellus (pl. **ocelli**). The simple eye in adult insects. See Stemma.

Orbicular. Round and flat.

Pheromone. A chemical that is secreted to the outside that causes a specific reaction in a receiving individual of the same species.

Phoretic. Referring to the relationship between different species where one is carried on the body of another.

Piceous. Pitchy black.

Pleuron. The lateral region of any segment of the insect body.

Posterior. Rear or rearward; opposite of anterior.

Posterolateral. Toward the rear and side.

Pro. Latin prefix meaning anterior or before.

Pronotum. The upper or dorsal surface of the thorax (prothorax) (Fig. 2).

Pubescence. Short, fine setae.

Punctate. With impressed points or punctures.

Puncture. A small impression on the hard surface of the body.

Pygidium. In dorsal view, the last segment usually left partially exposed by the elytra.

Ruga (pl. **rugae**). A wrinkle.

Rugose. Wrinkled.

Saprophagous. Feeding on dead or decaying vegetable matter.

Scape. The first or basal segment of the antenna.

Sclerite. Any piece of the insect body wall bordered by sutures.

Scutellum. The triangular piece between the bases of the elytra (Fig. 2).

Setigerous. Bearing setae.

Spur. A spine-like appendage, articulated or not, usually on the tibia (Fig. 2).

Stadium. The interval of time between the molts of the larva.

Stem. The segments of the antenna exclusive of the club.

Stemma (pl. **stemmata**). The simple eye of holometabolous larvae.

Sternite. The ventral part of a segment.

Stria (pl. **striae**). A longitudinal, depressed line or furrow, frequently with punctures, usually extending from the base to the apex of the elytra.

Stridulation. The sound produced by rubbing one surface or structure upon another.

Stridulatory Ridge. In *Nicrophorus* species, the short, subparallel, transversely grooved ridges on top of the third abdominal segment that are used in stridulation.

Sub. Latin prefix meaning almost or not quite.

Subequal. Similar but not quite equal in form, size or other characters.

Suture. The longitudinal line of juncture of the elytra.

Sympatric. Species or populations whose distributions overlap at least in part.

Tarsomere (pl. **tarsomeres**). One of the segments of the tarsus.

Tarsus (pl. **tarsi**). The foot; the jointed appendage attached to the apex of the tibia. The distal part of the insect leg consisting of (in silphids) five segments (Figs. 2-3).

Teneral. The condition of the adult shortly after emergence when it is not entirely hardened or fully colored.

Tergite. The dorsal part of a segment.

Thanatosis. The act of faking death.

Tibia (pl. **tibiae**). The fourth division of the leg, articulated at the proximal end to the femur and bearing the tarsus on the distal end (Figs. 2-3).

Transverse. Broader than long, or crossing the longitudinal axis at right angles.

Trochanter. The second segment of the insect leg between the coxa and the femur.

Truncate. Cut off squarely at the apex.

Tubercle. A small, conical bump.

Umbone. An elevated knob situated on the humerus or near the apical angles of the elytra, hence humeral umbone or apical umbone.

Urogomphi (sing. **urogomphus**). Elongated processes found on the terminal segments of certain larvae (Figs. 34-39).

Ventral. Pertaining to the under surface.

Vitellogenesis. Referring to yolk production in the egg.