The Carrion Beetles (Coleoptera: Silphidae) of Nebraska

Brett C. Ratcliffe

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Cover. An adult burying beetle, *Nicrophorus marginatus*, tending her larvae in a brood ball, which she has helped to fashion with her mate, from a dead field mouse. Painting by David Reiser.

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THE CARRION BEETLES (COLEOPTERA: SILPHIDAE) OF NEBRASKA

by

Brett C. Ratcliffe

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Abstract. *A faunal study of the carrion beetles (Coleoptera: Silphidae) of Nebraska is presented. An overview of the family and its two subfamilies is given as well as keys to the adults and, when known, the larvae. Each of the six genera and 18 species is reviewed. The treatment for each species consists of synonymy, a brief diagnosis, distribution in general, Nebraska locality records, temporal distribution, and remarks. The remarks include commentary on how to best distinguish the adults, references to the larval stages, and a discussion of biology and ecology.*

Distribution maps, showing Nebraska county records, are given for all the species. A habitus drawing for each species is provided along with line drawings of particular characters to supplement the taxonomic keys. An extensive bibliography and a glossary are also included.

INTRODUCTION

The Silphidae is a relatively small family of beetles, but interest in them has always been substantial because of the semi-social behavior displayed by species in the genus *Nicrophorus*. As currently defined, there are 13 genera and about 208 species found worldwide. North America has eight genera and 30 species. As a result of this study, silphids in the mid-continental state of Nebraska are now known to number six genera with 18 species (75% of the North American genera and 60% of the species). Those species are found in two subfamilies: the Silphinae with seven species and the Nicrophorinae with 11 species.

This study was begun in 1990 in order to produce an identification manual that could be used by professional entomologists, students, interested amateurs, and an increasingly large number of biologists and ecologists who are conducting surveys for the endangered American burying beetle, *Nicrophorus americanus* Olivier. The intent has been to include as much information as possible about each species as well as illustrations and keys for identification of both adults and larvae.

While other synoptic works have partially reviewed the North American fauna (*e.g.*, Anderson and Peck 1985), this study marks the first time that an in-depth review of the Silphidae of any state has been provided. Meserve (1936) compiled a checklist of Nebraska silphids, but otherwise nothing of a comprehensive nature has been written for the state.

METHODS

The results of this study were based on the examination and records of 29,719 specimens. Most of the specimens are housed in the Systematics Research Collections (Division of Entomology) of the University of Nebraska State Museum. These collections, now numbering nearly two million specimens, are recognized as one of the top 20 collections in North America (Anonymous 1971, Fischer et al. 1975). They represent over a century of collecting and data gathering in the prairie biome. Additional data were gathered from the collections at Hastings College, Chadron State College, University of Nebraska at Kearney, and the University of Nebraska's Cedar Point Biological Station in western Nebraska.

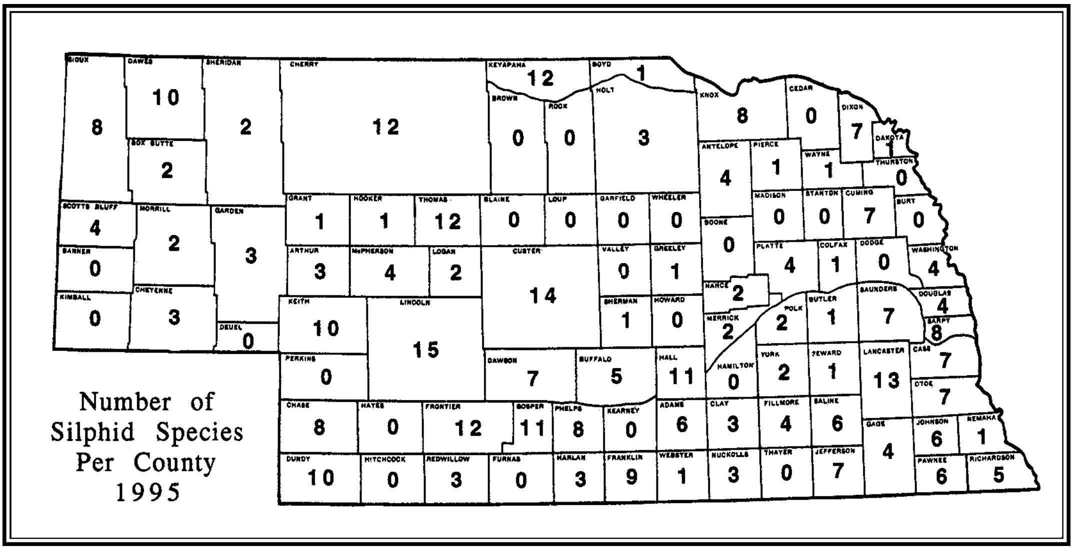


FIG. 1. Number of silphid species recorded from each Nebraska county. Counties with no records or few records are clearly in need of additional collecting.

Extensive collecting was conducted across the state by myself and others (see Acknowledgments). Collecting techniques consisted of baited pitfall traps, light traps, whole animal bait stations, and examination of road-killed animals. While this collecting effort has been substantial, there are still areas of Nebraska that remain poorly known entomologically. Figure 1, showing the number of silphid species recorded from each Nebraska county, will give a general idea of where additional collecting could be done. Some counties have never been sampled for silphids, which is, of course, very different than silphids not occurring there.

Conventional, artificial keys to all the silphids found in Nebraska are presented. I have attempted to use key characters that are consistently expressed, low in intrinsic variability, and easily observed with reasonable procedures (Figs. 2-3). The keys and descriptions are all accompanied by illustrations to aid the reader in correctly identifying specimens. The illustrations consist of line drawings and habitus drawings on pebble board. Dot maps showing county distributions are included to show where in the state beetles occur as exemplified by label data.

Each genus and species-level taxon is introduced with its chronological, nomenclatural history. An abbreviated, descriptive diagnosis for each species then follows. This consists of range of length (from tip of clypeus to apex of elytra) followed by distinguishing characteristics of the head, thorax, elytra, and legs.

Remarks on the overall distribution, and then the Nebraska distribution, are presented following the description. Fitzpatrick (1960) was the source for Nebraska place names. The locality data (accompanied by a reference to a map figure) is next and is followed by the temporal distribution, both rangewide and in Nebraska. The "Remarks" section is divided into distinguishing features of the adult, reference to larval descriptions, and life history and ecological information.

By necessity, some technical terms (largely those dealing with body structure) have been used. A brief glossary is provided in the back of this work for those unfamiliar with these words. Definitions used are primarily those of Torre-Bueno (1937). A total of 242 references have been referred to in this work.

NEBRASKA

Physical

Nebraska, one of the richest agricultural states in the nation, is located just north of the geographic center of the United States. Nebraska is found 40°-43° north of the equator and 95°25'-104° west of Greenwich. It occupies an area of 77,510 sq. miles (200,673 sq. km.) and extends 462 miles (743 km.) east to west and 205 miles (330 km.) north to south (USGS data). The lowest elevation is 825 ft. (251 m.) in Richardson County in the southeast. Elevation gradually rises to 5,340 ft. (1,623 m.) in Banner and Kimball counties in the west near the Wyoming line.

The chief rivers in the state are the Missouri (along the eastern border), Platte (its largest tributaries being the Loup and Elkhorn), Niobrara, Republican, and Big Blue. Surface drainage is generally from west to east. Aside from streams and rivers, Nebraska has about 2,500 lakes, marshes, and artificial reservoirs containing 15 acres or more of water. The largest lake in the state (26 miles in length) is located in Keith and Garden counties. Most of the natural lakes and marshes are in the Sand Hills where, counting bodies of standing water of all sizes, the number exceeds 3,000 (Jones 1964).

As is typical for all of the Great Plains, Nebraska's geologic formations consist of deep granite or granite-like rocks, sedimentary bedrock in the form of shale, mudstone, sandstone, and limestone, and unconsolidated sediments (mantle rock) shaped by glaciers, water, and wind. The mantlerock is primarily Pleistocene in age whereas the

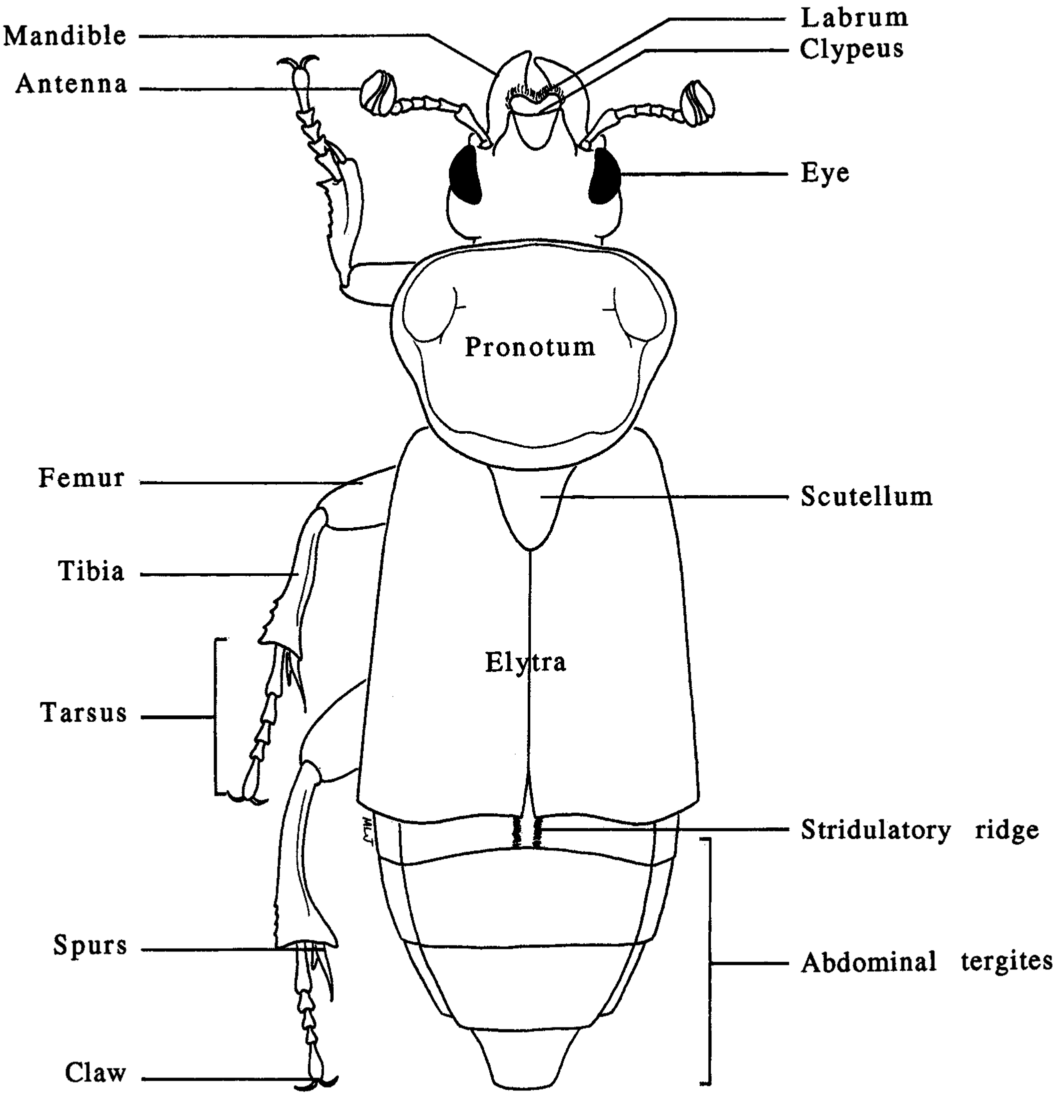


FIG. 2. Dorsal aspect of adult *Nicrophorus* species showing morphological features.

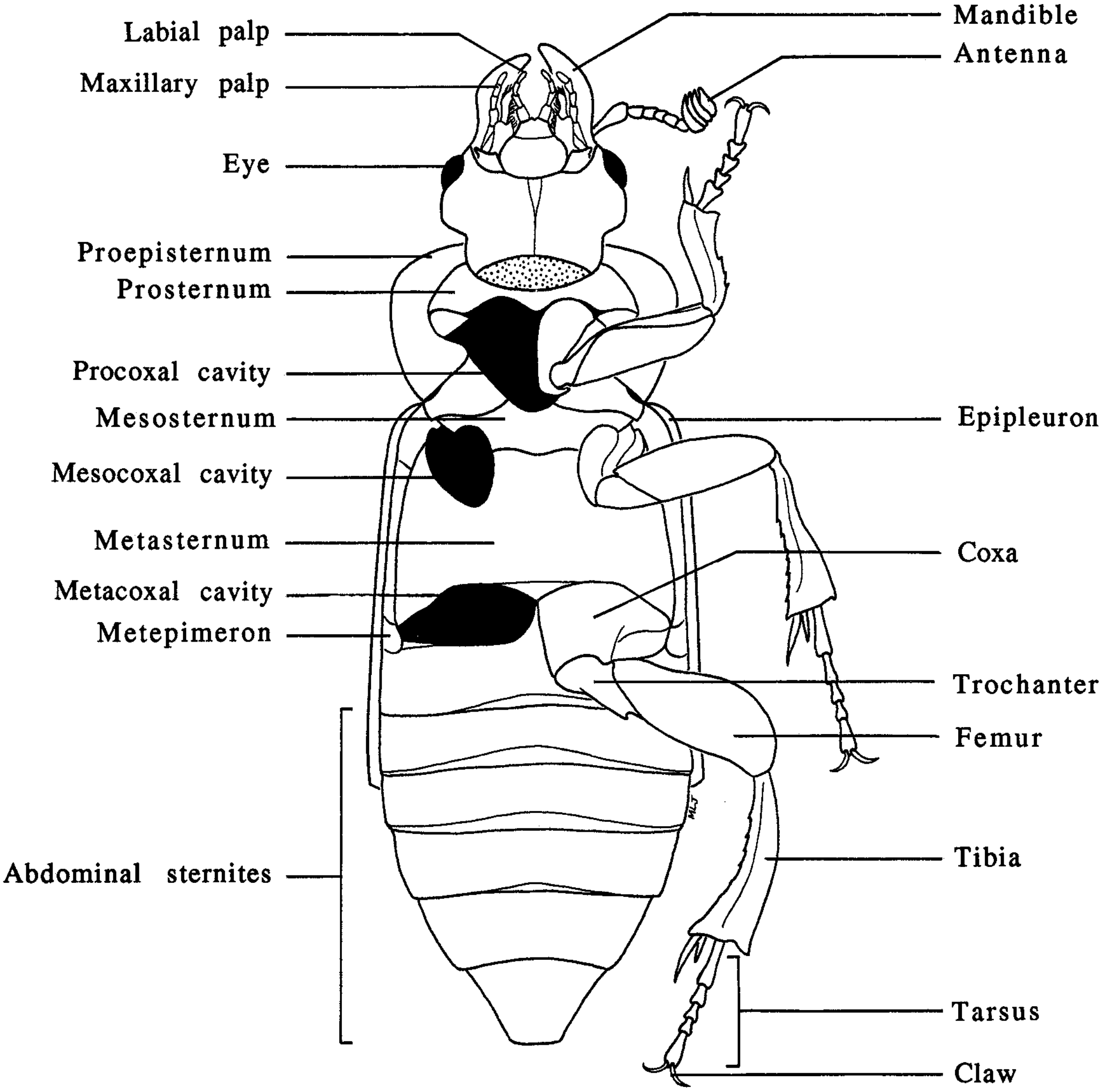


FIG. 3. Ventral aspect of adult *Nicrophorus* species showing morphological features.

bedrock ranges in age from the early Paleozoic to late Tertiary (Condra and Reed 1943). Three of the major soil divisions of North America are found in Nebraska in the form of six general soil associations. Three of these associations (brunizem, chernozem, and chestnut) are among the dark-colored soils that are found under prairie vegetation. The soils of Nebraska were described in detail by Elder (1969).

The Nebraska Sand Hills is a remarkable physiographic region covering approximately 19,300 square miles and stretching 265 miles across Nebraska and into South Dakota. It is the largest sand dune area in the Western Hemisphere and is one of the largest grass-stabilized dune regions in the world (Bleed and Flowerday 1989). The Sand Hills are, for the most part, a treeless landscape of grass-covered sand dunes in the western two-thirds of Nebraska. Wright (1970) suggested that the sand that formed these dunes was probably deposited by Pleistocene periglacial winds in an environment that was characterized by Smith (1965) as first a desert (with large, transverse dunes built by northerly winds) and later as an area of sparse vegetation (with longitudinal dunes superimposed on the older dunes by northwesterly winds). The origin of the sand was probably the poorly consolidated Tertiary sediments of southwestern South Dakota and eastern Wyoming or from alluvium derived from these rocks about 10,000 years ago (Watts and Wright 1966). Today, some dunes are as high as 400 feet and as long as 20 miles and have slopes as steep as 25% (Bleed and Flowerday 1989).

CLIMATE

The climate of the Great Plains is controlled largely by the rain shadow created by the Rocky Mountains as they intercept the easterly flow of moist Pacific air (Baker and Waln 1985). The plains are drier along the western edge near the rain shadow and become progressively moister to the east as air masses from the Gulf of Mexico play increasingly important roles in causing precipitation. Maximum precipitation in the Great Plains occurs in early summer (Fig. 4) due to the combined influences of moisture from the Gulf of Mexico and the penetration of modified Pacific air masses (Barry 1983).

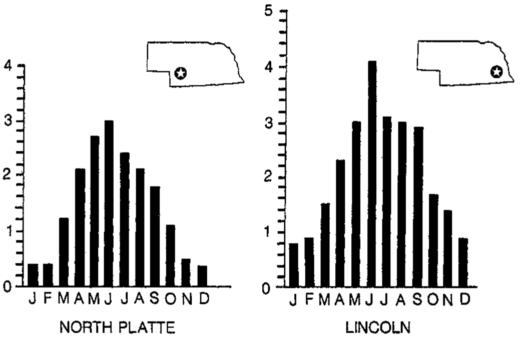


FIG. 4. Monthly precipitation for North Platte (Lincoln Co.) in the west and Lincoln (Lancaster Co.) in the east.

A major characteristic of subhumid to semiarid climates (such as are found in Nebraska) is the high year to year variability in precipitation (Barry 1983). From ecological and historical perspectives, drought is possibly the most significant climatic element of the Great Plains environment because it determines the carrying capacity of the region.

Nebraska has a continental, temperature zone climate characterized by hot summers, cold winters, moderate precipitation that is markedly seasonal or periodic, and occasional drastic changes in weather from day to day. It is often said in Nebraska, for example, that if you don't like the weather, then wait an hour because it will change significantly. Rapid changes in weather are influenced by invasions of warm moist air from the Gulf of Mexico; hot, dry air from the Southwest; cool, usually dry air from the northern Pacific ocean; or cold, dry air from interior Canada. Masses of air over Nebraska are generally associated with the eastward movement of high and low pressure systems (Jones 1964). Precipitation and temperature are inversely related during the summer, and this relationship is less pronounced in the spring and fall. Drought frequency is greater in the western part of the state, but there are more consecutive dry months in the east. Nebraska is subhumid in the east and gradually becomes semiarid in the west.

The mean annual precipitation in the southeast is 33 inches (838 mm), 23 inches (584 mm) in the northeast, and decreases to 15 inches (381 mm) in the west. Approximately three-fourths of this precipitation occurs between April and September and originates in warm, moist air from the Gulf of Mexico. However, much of the air moving north from the Gulf is deflected to the east by the eastward movement of air over the Rockies with the result that the easternmost part of the state receives more than twice as much precipitation as the drier westernmost part (Jones 1964).

The mean annual temperature in Nebraska is 49.3°F (27.4°C). The mean annual summer temperature is 72.7°F (40.4°C). The mean annual winter temperature is 25.3°F (14.1°C). Winter temperatures in the northern Great Plains are low and often associated with strong winds and occasional severe blizzards. The lowest temperature ever recorded was -47°F (-46.4°C) in February of 1899, and the highest temperature was 118°F (65.6°C) in July 1934. Figure 5 shows climatological information for the state.

The prevailing winds are predominantly from the north and northwest in winter and from the south from May to November. Spring winds are usually the strongest and most variable in direction. It is of interest to note that greater climatic variation exists west to east across Nebraska (462 miles) than from eastern Nebraska to the Atlantic coast (approximately 1,110 miles).

VEGETATION OF NEBRASKA

Although primarily a prairie state, Nebraska has many diverse habitats (Fig. 6) that range from eastern deciduous forests to short and tall grass prairies (actually six different grassland types), a large section of Sand Hills prairie (19,000 sq. mi.), and a small western component of Rocky Mountain forest.

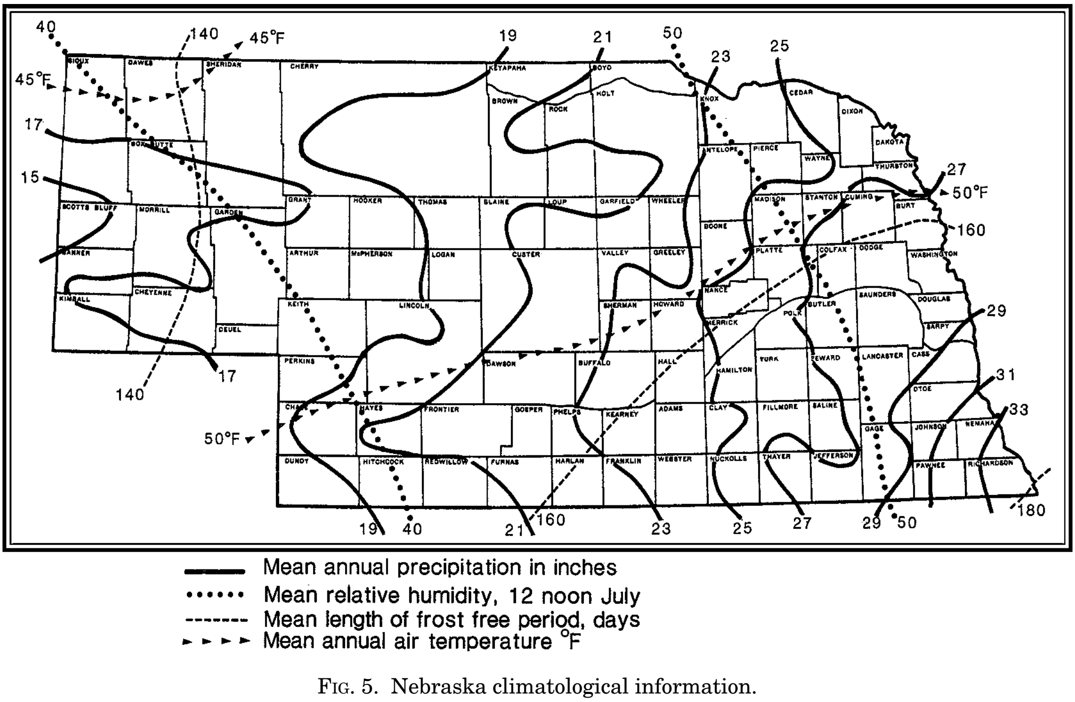


FIG. 5. Nebraska climatological information.

Weaver (1965) provided an excellent summary of the native vegetation of the state, and the distributions of all vascular plant species in the central grasslands were mapped in 1977 (Great Plains Flora Association 1977).

The vegetation in Nebraska has undergone considerable change since the pioneers first began settling here in the 1800s. Probably the three most significant changes are loss of many native prairies to agriculture, the introduction of trees in urban areas where once there were few, and the growth of woody vegetation in eastern Nebraska's gullies and draws. These changes in the flora have affected the fauna because vegetation is a limiting factor for animals both as food and shelter. In some cases, floristic changes have been mirrored by the loss of animals to a particular habitat while in others it has resulted in a net gain in diversity. The interplay between plant and animal distribution is dynamic, and the human factor has substantially changed this relationship.

The sense of living in a prairie environment or being in a prairie state has been largely lost because of the almost complete destruction of the original prairie by modern agriculture. This is especially true in eastern Nebraska where the once-dominant tallgrass prairie, stretching as far as one could see, has been eliminated by intense cultivation and urbanization. What follows is a very brief overview of Nebraska's several floristic associations.

Short and Tallgrass Prairie

The prairie is a land of waving grasses and broad-leaved forbs. Compositae and Leguminosae, along with the many grasses, are the dominant plant families found in the prairie. John Weaver, a noted Nebraska scholar of the prairie habitat, observed (1954) that the prairie appears almost monotonous in the general uniformity of its plant cover . . . but that it also has a special grandeur in its open expanses and in the abundance of its varicolored flowers. The dominance of perennial grasses, the paucity of shrubs, the absence of trees (except along rivers and streams), and a characteristic drought-enduring flora constitute its main features. Prairie is the name given to the vast expanse of grasslands in central North America. Similar grasslands in Eurasia are called "steppe" whereas in southern South America

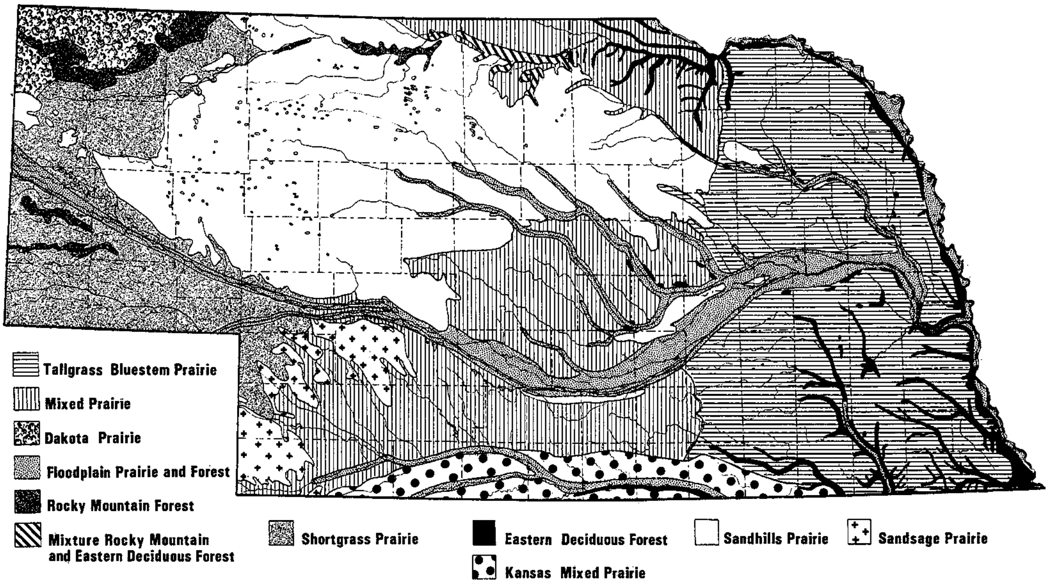


FIG. 6. Vegetation of Nebraska, *circa* 1850 (map modified from that by R. Kaul 1975).

they are referred to as "pampas," and in southern Africa they are known as "veld."

The dominant grasses of North American prairies change along an east-west gradient as precipitation changes. This can be seen clearly in the vegetation map of Nebraska (Fig. 6). The eastern fourth of the state is (or was) tallgrass prairie, (Fig. 7), so called because the grasses there may reach a height of seven feet during moist years. The principal grasses are big bluestem (*Andropogon gerardi* Vitman), switchgrass (*Panicum virgatum* L.), and Indian grass (*Sorghastrum avenaceum* Michaux). The western border of tallgrass prairie approximates the line of 23 inches of annual precipitation (Jones 1964).

Tallgrass prairie grades into mixed prairie (Fig. 8) where the dominant grasses are bluestems (*Andropogon* spp.), grama grasses (*Bouteloua* spp.), and buffalo grass (*Buchloe dactyloides* Nuttal). According to Weaver and Clements (1938), this association owes its name to the fact that its climax vegetation is composed of short and longer grasses in almost equal diversity. Jones (1964) observed that mixed prairie covers the largest area of any of the grassland associations in North America; it is *the* grassland of the Great Plains. Jones (citing Weaver and Clements) indicated the so-called shortgrass prairie of western Nebraska and adjacent regions was once considered a distinct grassland association, but was now known to represent only a "disclimax" of the mixed prairie that resulted primarily from overgrazing. There remains today no consensus of opinion as to whether this association is true shortgrass or "disclimax" mixed prairie. Based upon my own observations in western Nebraska, I prefer the designation of shortgrass prairie.

With declining rainfall, changing soil profiles, and increasing evaporation in the western half of Nebraska, mixed prairie is replaced by shortgrass prairie, sand hills prairie, and sandsage prairie. The shortgrass prairie (Fig. 9) is dominated by blue grama grass (*Bouteloua gracilis* Humboldt, Bonpland, and Kunth) and buffalo grass (*Buchleo dactyloides* Nuttal). Shortgrass prairie is found in much of Nebraska's western panhandle region.

FIG. 7. Tallgrass prairie remnant at Roe Sanctuary near Gibbon in Buffalo Co. in eastern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

FIG. 8. Mixed prairie in Sarpy Co. in eastern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

FIG. 9. Shortgrass prairie at Jail and Courthouse Rocks in Morrill Co. in western Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

FIG. 10. Sandsage prairie near Parks in Dundy Co. in southwestern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

FIG. 11. Sand Hills prairie at "Arapaho Prairie" in Arthur Co. in western Nebraska. Photo by the author.

Sandsage prairie (Fig. 10) is characterized by several species of sage (*Artemisia* spp.) as well as by sandreed grass (*Calamovilfa longifolia* Hooker) and bluestems (*Andropogon* spp.). This prairie type is found in the southwestern corner of Nebraska.

SAND HILLS PRAIRIE

The vegetation of the Sand Hills (Fig. 11) is surprisingly diverse. It is also unique. . . not because it consists of many unusual species, but because it is a mixture of so many different types of vegetation. It is a "borrowed" vegetation in that most plants probably moved into the area from elsewhere during and after retreat of the glaciers (Kaul 1989). Kaul noted that there is only one species of plant, Hayden's, or blowout penstemon (*Penstemon haydenii* S. Watson), that is endemic to the Nebraska Sand Hills. It is the only endemic plant in Nebraska and one of only a few endemics in the Great Plains.

Some of the most characteristic plants of the prairie region are bluestem grasses (*Andropogon* spp.), sandreed grass (*Calamovilfa longifolia* Hooker), needle grass (*Stipa* spp.), and yucca (*Yucca* spp.). The grass cover of the sand dunes comprising this area is fragile and susceptible to erosion. Excessive cultivation during the drought years of the 1930s caused erosion and some sand movement. Although the dunes are stabilized by plant cover today, local blowouts remain common. This region is one of the richest grazing areas in the United States.

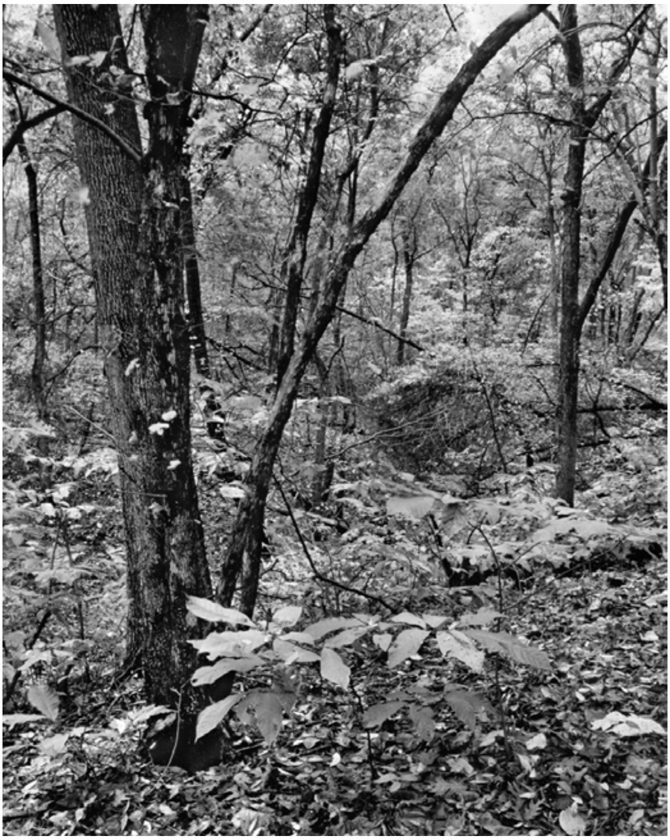


FIG. 12. Eastern deciduous forest adjacent to the Missouri River in Richardson Co. in southeastern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

Eastern Deciduous Forests

The majority of Nebraska's native trees entered the state (especially as they are represented in the Ohio Valley) following the Missouri River and its tributaries from the eastern forests (Pool 1929).

Nebraska's eastern deciduous, hardwood forests (Fig. 12) are largely restricted to the southeast corner of the state, the west bank of the Missouri River, and the Niobrara River in its eastern third. Within these riverine strips of forest, steep and undulating ridges contain dense upland forests dominated by the drought resistant bur oak (*Quercus macrocarpa* Michaux), shagbark hickory (*Carya ovata* [P. Miller]), and basswoods (*Tilia americana* L.). The deep ravines provide shelter from drying prairie winds and permit many species of broadleaf trees to survive. About 44 species of deciduous trees are native to southeastern Nebraska (Pool 1929). These hardwood forests extend west along rivers well out into the grasslands where they become impoverished in species (Kaul 1986). The eastern red cedar (*Juniperus virginiana* L.) is one of Nebraska's four native coniferous trees. It is found widely scattered over the eastern half of the state on dry, gravelly slopes and limestone ridges (Pool 1929).

Nebraska's numerous floodplains that border rivers are usually at least partially covered by trees (Fig. 13) such as cottonwood (*Populus deltoides* Marshall), willow (*Salix* spp.), ash (*Fraxinus pennsylvanica* Marshall), elm (*Ulmus americana* L.), box elder (*Acer negundo* L.), and sycamore (*Platanus occidentalis* L.) (Kaul 1986).

Rocky Mountain Forests

Elements of the coniferous, evergreen forests of the Rocky Mountains (Fig. 14) are also found in Nebraska's panhandle, primarily in the northwestern corner along the Pine Ridge escarpment. These forests extend eastward to approximately the 100th meridian on the north-facing slopes of the Niobrara River valley and its spring-fed tributaries. They meet the westward extensions of the eastern deciduous forests only in this region

Fig. 13. Seasonally dry riverbed with gallery forest along the Platte River in Hall Co. in central Nebraska. Photo by the author.

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.

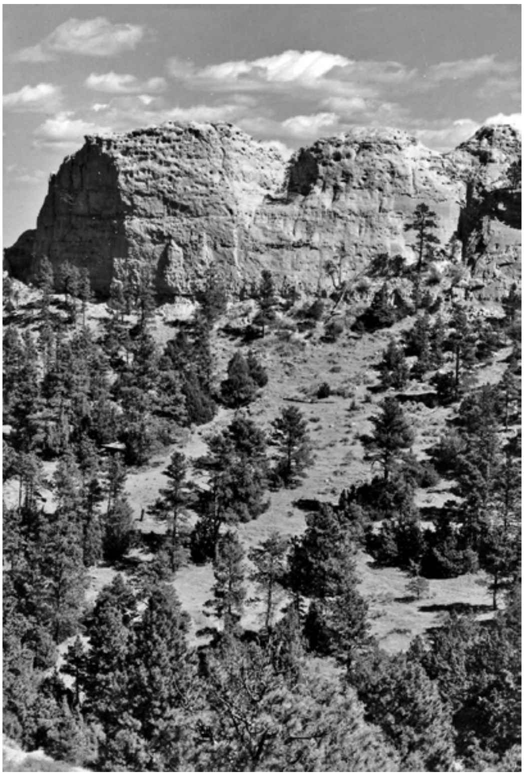


FIG. 14. Rocky Mountain forest near Chadron in Dawes Co. in northwestern Nebraska. Photo courtesy of NEBRASKAland Magazine/Nebraska Game and Parks Commission.

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 col-lecting 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 antifreeze) 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.

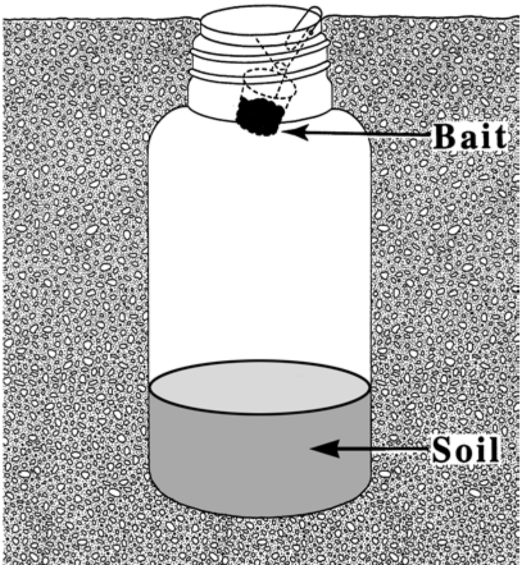


Fig. 15. Graphic representation of a baited pitfall trap.

The jar or 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**

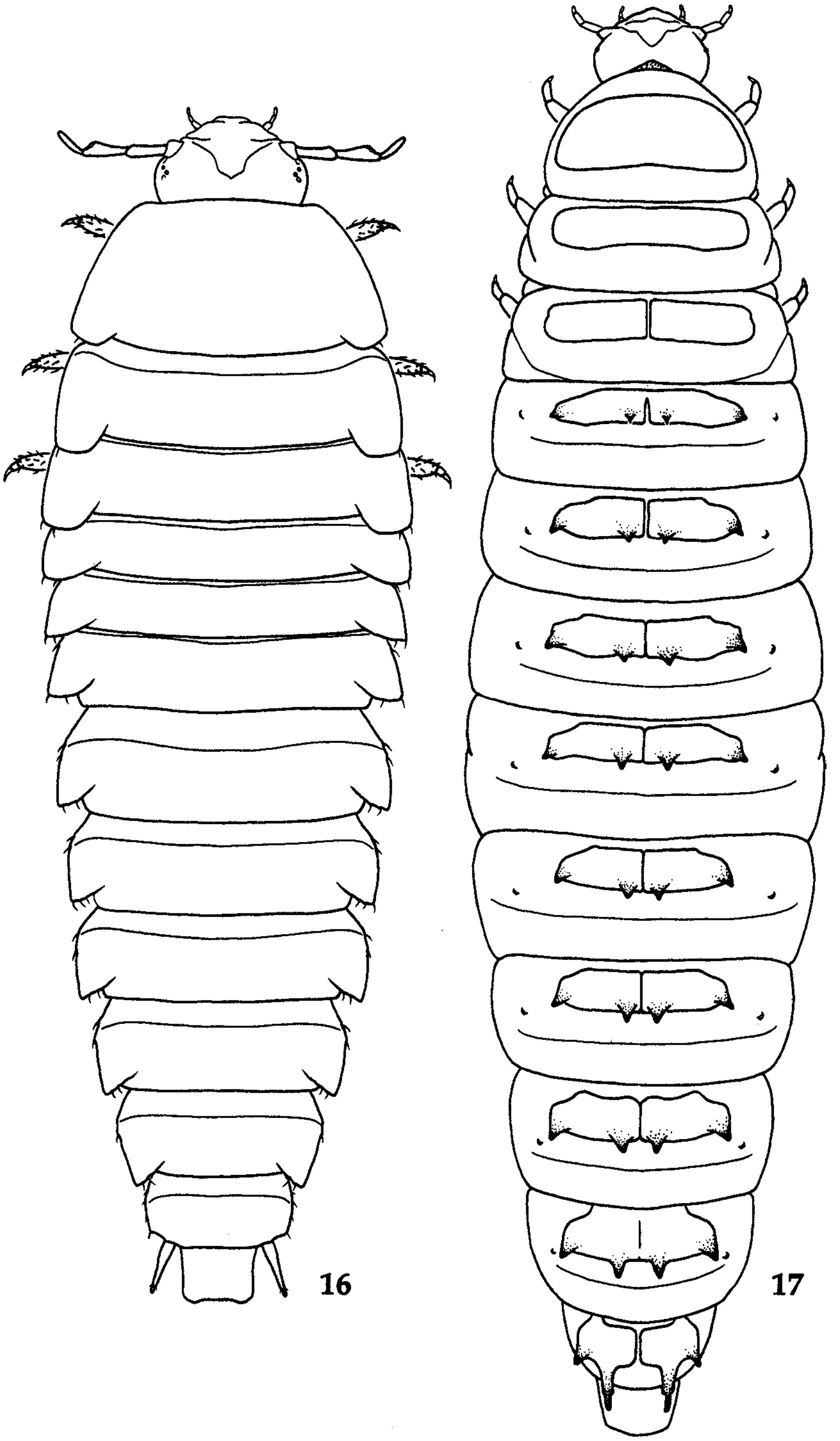
1'. Elytra with apices truncate, shortened, usually exposing 3-4 segments.Antenna apparently 10-segmented (actually 11-segmented but second small, nearly hidden in apex of first), last 4 segments widened into distinct, compact club . . . **Nicrophorinae**

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)

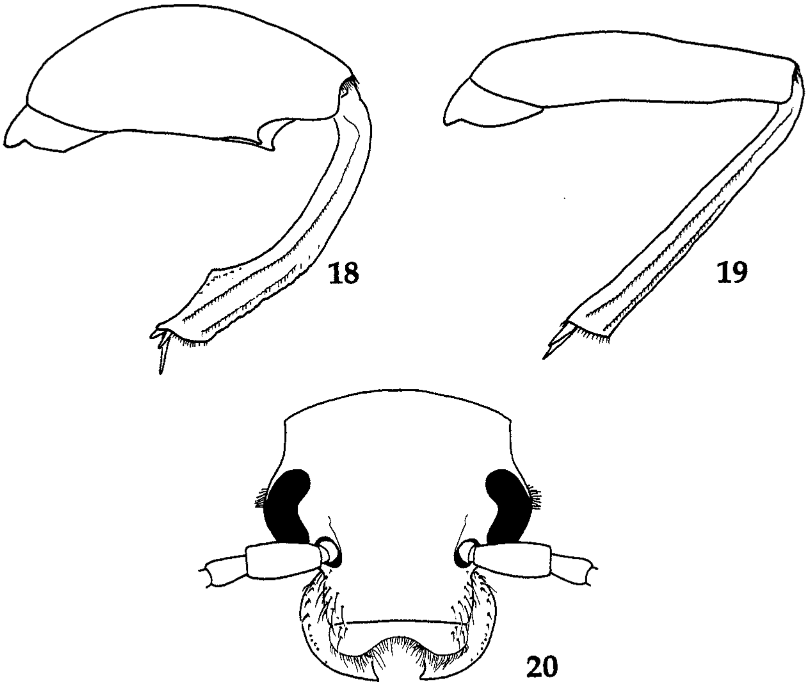
1\. Pronotum black with yellow margins (Fig. 57). Elytra with reticulate sculpturing . . . . ***Necrophila***

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

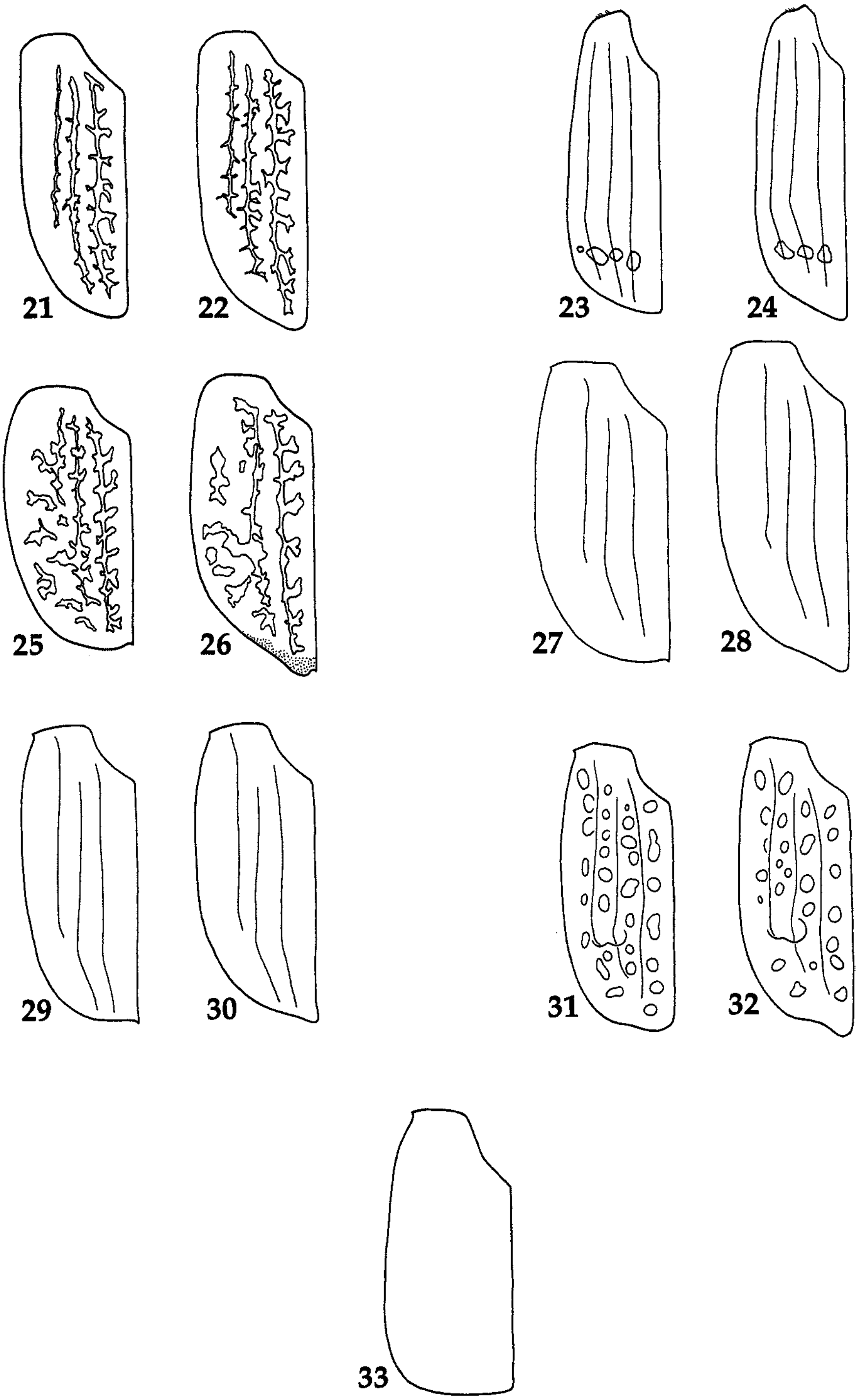
2\. Eyes large (Fig. 49). Pronotum distinctly orbicular, widest at middle, basal angle broadly rounded. Male with metafemora enlarged and with tooth near apex (Fig. 18) . . . . ***Necrodes***

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.



FIGS. 21-33. Left elytron of 21-22, *Heterosilpha ramosa*, male and female; 23-24, *Necrodes surinamensis*, male and female; 25-26, *Necrophila americana*, male and female; 27-28, *Oiceoptoma inaequale*, male and female; 29-30, *O. novaboracense*, male and female; 31-32, *Thanatophilus lapponicus*, male and female; 33, *T. truncatus* (either sex).

3'. Head may have short setae, but not with stout setae in a *distinct row* behind eye . . . 5

4. Humerus with small tooth (Figs. 27-30) or acute angle. Elytra without reticulate sculpturing . . . . ***Oiceoptoma***

A. Pronotum entirely black . . . . ***O. inaequale*** **(Fabr.)**

A'. Pronotum black with reddish orange margins. . . . ***O. novaboracense*** **(Forster)**

4'. Humerus rounded, lacking tooth. Elytra with reticulate sculpturing . . ***Heterosilpha***

5. Humerus with small tooth (Figs. 31-33). Labrum shallowly emarginate. Mesocoxae widely separated (by about width of mesocoxa) . . . . ***Thanatophilus***

A. Elytra smooth, lacking costae (Figs 33, 64) . . . . ***T. truncatus*** **(Say)**

A'. Elytra tuberculate, with costae (Figs. 31, 32, 62) . . . . ***T. lapponicus*** **(Herbst)**

5'. Humerus rounded. Labrum deeply emarginate. Mesocoxae narrowly separated (by about half or less width of mesocoxa) . . . . ***Aclypea***

KEY TO THE GENERA AND SPECIES OF THIRD INSTAR LARVAE OF SILPHINAE IN NEBRASKA

(modified from Anderson and Peck 1985)

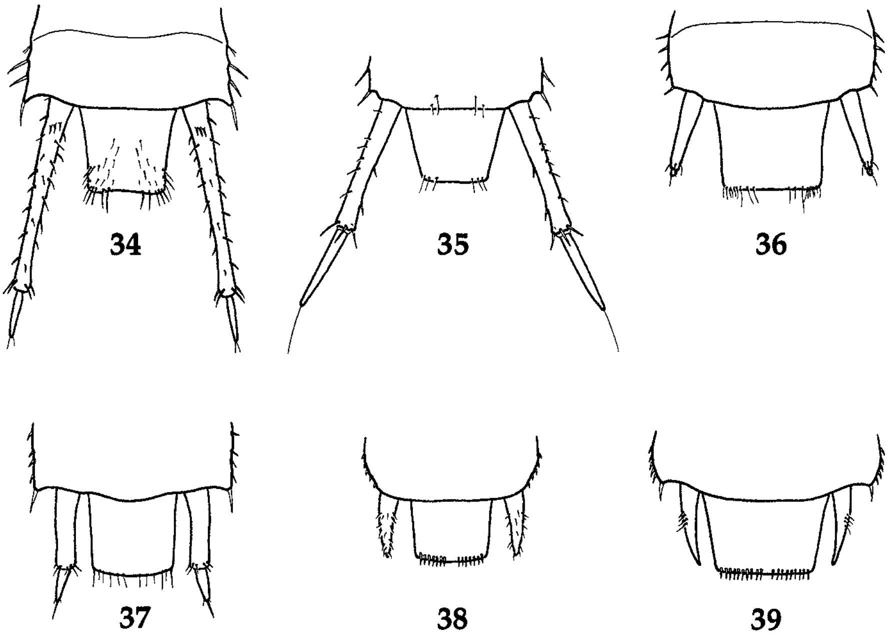
1. Urogomphi distinctly longer than 10th abdominal segment (by at least half their length) (Figs. 34-35). Sternum of 2nd abdominal segment with 3 large sclerites . . 2

1'. Urogomphi equal to or slightly longer than 10th abdominal segment (Figs. 36-39). Sternum of 2nd abdominal segment with 1 large sclerite 3

2. Basal segment of urogomphus up to twice as long as 10th abdominal segment (Fig. 35). Dorsal color dark brown to black . . . . ***Thanatophilus***

2'. Basal segment of urogomphus more than twice as long as 10th abdominal segment (Fig. 34). Dorsal color reddish brown . . . . ***Necrodes surinamensis*** **(Fabr.)**

3. Second segment of antenna with 1 large sensory cone (Fig. 40). Prothoracic tergite



FIGS. 34-39. Abdominal apex of larval silphine (dorsal view): 34, *Necrodes surinamensis*; 35, *Thanatophilus truncatus*; 36, *Necrophila americana*; 37, *Oiceoptoma novaboracense*; 38, *Aclypea bituberosa*; 39, *Heterosilpha ramosa* (Figs. 38-39 after Anderson and Peck 1985).

emarginate anteriorly at middle (Figs. 43-44). Dorsal color reddish brown . . . ***Oiceoptoma***

A. Prothoracic tergite deeply emargiate anteriorly (Fig. 43). Thoracic and abdominal tergites 1-8 with lateral margins pale, pale areas with small, dark, spots or oblique lines (Fig. 43) . . . . ***O. novaboracense* (Forster)**

A'. Prothoracic tergite shallowly emarginate anteriorly (Fig. 44). Meso- and metathoracic tergites as well as abdominal tergites 1-8 with pale areas limited to posterolateral angles (Fig. 44) . . . . ***O. inaequale* (Fabr.)**

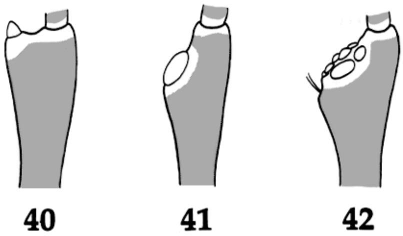
3'. Second segment of antenna with 1 or more plates on sensory area (Figs. 41-42). Prothoracic tergite not emarginate anteriorly (Fig. 45). Dorsal color dark brown 4

4. Second and third segments of antenna subequal in length. Urogomphi distinctly 2-segmented (Fig. 36) . . . . ***Necrophila americana* (L.)**

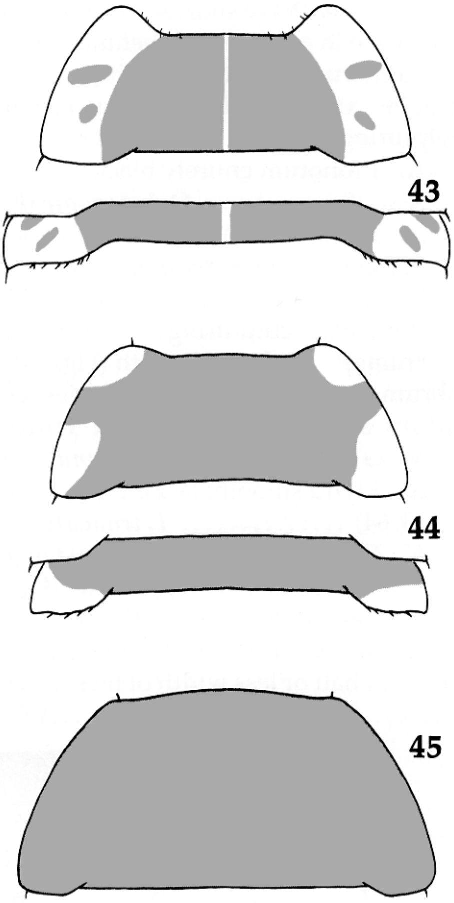
4'. Third segment of antenna distinctly longer than second segment. Urogomphi apparently with 1 segment (Figs. 38-39) . . 5

5. Second segment of antenna with 1 plate on sensory area (Fig. 41). Last segment of maxillary palpus about twice as long as wide . . . . ***Aclypea bituberosa* (LeConte)**

5'. Second segment of antenna with numerous plates (Fig. 42). Last segment of maxillary palpus about 3 times as long as wide . . . . . ***Heterosilpha ramosa* (Say)**



FIGS. 40-42. Second antennal segment of larval Silphinae: 40, *Oiceoptoma novaboracense*; 41, *Aclypea bituberosa*; 42, *Necrophila americana* or *Heterosilpha ramosa* (Fig. 41 after Anderson and Peck 1985).



FIGS. 43-45. Prothoracic and abdominal tergites of larvae of 43, *Oiceoptoma novaboracense*; 44, *O. inaequale*; 45, *Necrophila americana*.

Genus *ACLYPEA*

The genus *Aclypea* has about 22 species (Hatch 1928). They are Holarctic in distribution. Only two species are found in the United States.

Aclypea bituberosa (LeConte) (Fig. 46) is included in this work because there are some old references indicating its presence in Nebraska. This species does not occur in Nebraska. I believe that the earlier citations of its occurrence here were a result of misidentification where *Silpha opaca* (later thought to be *bituberosa*) was confused with *Oiceoptoma inaequale* or *Heterosilpha ramosa*.

In a report by Lawrence Bruner on the "Insect injuries in Nebraska during the summer of 1892," Bruner discusses *second hand* information from a Mr. Huxman that "*Silpha opaca*" was a pest of sugar beets at West Point. Huxman had told Bruner that he could not be mistaken about the identity of the insect because he had seen so many of them in Europe that he knew them on sight. I believe that Huxman had the very similar appearing *Oiceoptoma inaequale* or *Heterosilpha ramosa* (which does not occur in Europe) and not *Aclypea bituberosa*. In a 1916 letter from Myron Swenk (entomologist at the Nebraska Experiment Station) to R. Cooley, it is again mentioned that "*Silpha*" *bituberosa* was found in beet fields in Nebraska . . . but, it is important to note, Swenk obtained this information *from* Bruner (who, by extension, received it from Huxman). There are no actual specimens to support these claims. Cooley (1917), in a detailed report on the biology, distribution, and description of *Aclypea* (his *Silpha*) *bituberosa*, then erroneously concluded that there is "*positive* information of its occurrence in Nebraska."

Meserve (1936), in his list of Nebraska silphids, also mentioned a single, no-data

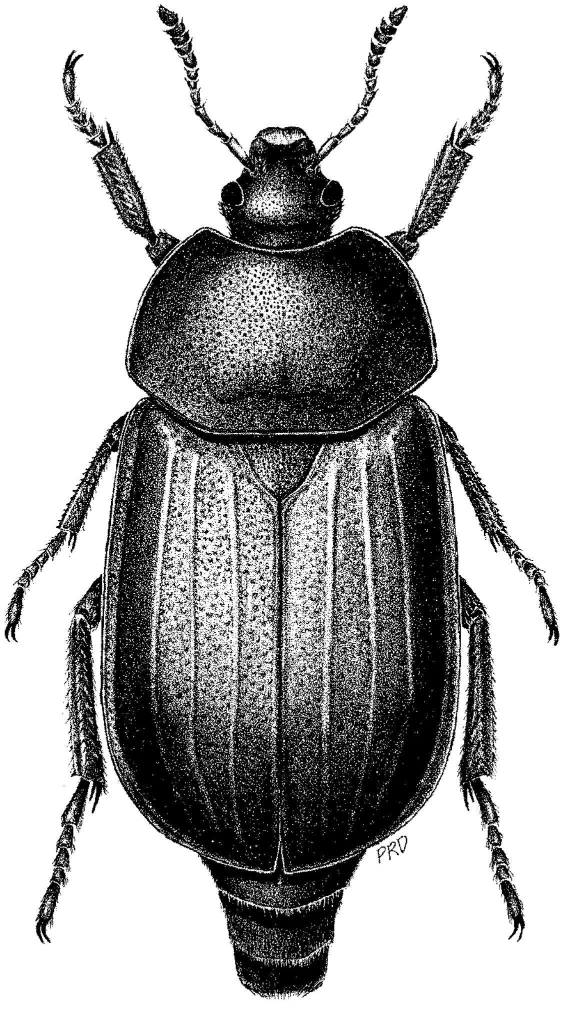


FIG. 46. *Aclypea bituberosa* (LeConte).

record of *Silpha opaca*, but, again, there is no voucher specimen. Anderson and Peck (1985) and Peck and Kaulbars (1987), using the information in Cooley (1917), included Nebraska in the distribution of this species. This species occurs just west of the Rocky Mountains in Wyoming, Montana, Utah, and Idaho.

According to Anderson and Peck (1984), both adults and larvae of *Aclypea bituberosa* are phytophagous and eat the leaves and shoots of native species of Solanaceae and Chenopodiaceae, introduced weeds, and at least 12 species of plants of agricultural or horticultural importance, including squash, pumpkin, spinach, wheat, beet, radish, rhubarb, potato, lettuce, cabbage, rapeseed, and turnip. Occasionally, this species has been considered a pest of some of these crops.

Genus *HETEROSILPHA*

Heterosilpha Portevin 1926: 83.

The genus *Heterosilpha* consists of two species that are both endemic to North America. *Heterosilpha aenescens* (Casey) occurs near the west coast from southern Oregon to northern Baja California in Mexico (Miller and Peck 1979, Peck and Anderson 1985) and *H. ramosa* (Say) is found in most of western North America from southern Canada to northern Mexico (Peck and Anderson 1985). Only the latter species is found in Nebraska.

Prior to Portevin's (1926) establishment of the genus *Heterosilpha*, these species were included in *Silpha*, a catch-all genus at the time. Arnett (1946) suggested that *aenescens* was a synonym of *ramosa*, but this has not been adopted by subsequent authors.

Species of *Heterosilpha* are unique among North American silphids because of the presence of three, branching costae on each elytron. Larvae are characterized by having the sensory area of the second antennal segment with numerous small plates (as in Fig. 42) and the urogomphi subequal to the tenth abdominal segment.

Heterosilpha ramosa **(Say)**

(Figs. 21-22, 39, 47-48)

Silpha ramosa Say 1823: 193.
Silpha cervaria Mannerheim 1843: 252.

Diagnosis. Length 11.2-16.7 mm. *Thorax*: Color entirely black. Surface finely, densely punctate. *Elytra*: Color black. Surface tricostate, costae with short, lateral branches. Males with apex rounder, females with apex slightly elongated and attenuated (Figs. 21-22). *Legs*: Males with tarsomeres 1-4 on first and second pair of legs laterally expanded and densely pubescent beneath; females with tarsomeres normal, not expanded.

Distribution. *Heterosilpha ramosa* is found west of a line from northeastern Minnesota to south-central New Mexico; it also occurs in southern Canada west of Lake Superior to British Columbia as well as in northern Baja, California (Anderson and Peck 1985, Peck and Kaulbars 1987). In Nebraska, this species is more abundant in the western half of the state with populations extending eastward as far as Grand Island. There are two old Lincoln records (pre-1920), but this species does not now occur in Lancaster Co.

Locality Records (Fig. 48). 78 Nebraska specimens examined or recorded.
CHERRY CO. (43): Hackberry Lake, Trout Lake, Valentine, Valentine Wildlife Refuge; CUSTER CO. (2): Anselmo, 17 mi. E. Anselmo; DAWES CO. (1): Pepper Creek; GARDEN CO. (4): Crescent Lake, Oshkosh; HALL CO. (2): Alda, Mormon Island Refuge; KEITH CO. (15): Cedar Point Biological Station; KEYA PAHA CO. (1): Mills; LINCOLN CO. (8): Box Elder Canyon, Moran Canyon, North Platte, Wellfleet; LOGAN CO. (1): No data; McPHERSON CO. (1): Sandhills Ag Lab; MORRILL CO. (3): No data; SCOTTS BLUFF CO. (1): Mitchell.

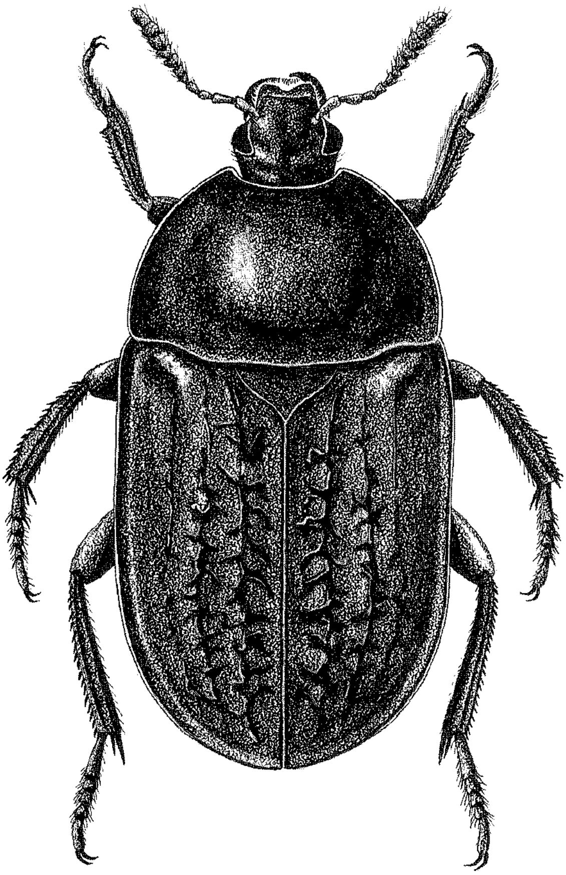


FIG. 47. *Heterosilpha ramosa* (Say).

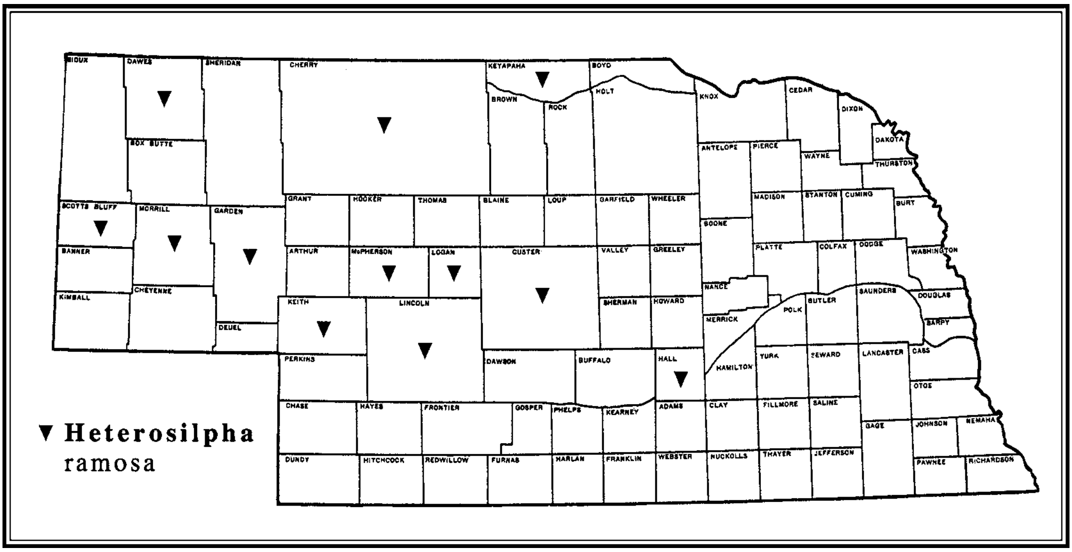


FIG. 48. Nebraska distribution of *Heterosilpha ramosa*.

Temporal Distribution. Rangewide: March to October (Peck and Kaulbars 1987). Nebraska: May (2), June (37), July (34), August (10), October (3).

Remarks. *Heterosilpha ramosa* is easily recognized because it is the only silphid in North America that is entirely black, with distinctly tricostate elytra, and with the costae branching and weakly shining against a dull black background.

The larval stage was described by Gissler (1880), Dorsey (1940), Brewer and Bacon (1975), and Anderson and Peck (1985).

Brewer and Bacon (1975) studied the natural history of this species in Colorado, and their observations are probably representative for Nebraska as well. Adults overwinter and become active the following spring when temperatures become warm. Eggs are laid in the soil around a carcass, and this stage typically lasts 5 days. The first instar takes 4-5 days, the second instar 5-6 days, the third instar 8-10 days, and the pupal stage 8-9 days. The period from egg to adult lasted about 30 days. There are two generations a year with adults of the first brood (in Nebraska) appearing in June and those of the second in late July and August.

Genus *NECRODES*

Necrodes Leach 1815: 88.
Asbolus Bergroth 1884: 229.
Protonecrodes Portevin 1922: 508.

The genus *Necrodes* contains five species (Hatch 1928) distributed in North America, Europe, and Asia. There is only one species in North America, and it is found throughout Nebraska. There is no modern taxonomic treatment of the genus, and the most recent world catalog is Hatch (1928).

Madge (1980) reported that Bergroth (1884) believed that the name *Asbolus* was validly published by Voet (1778) and proposed that it replace *Necrodes* Leach 1815. However, Voet's work was not consistently binomial and thus is not available for zoological nomenclature according to the Code. *Asbolus*, therefore, dates from Bergroth (1884) whose action can be regarded as the proposal of an unnecessary *nomen novum*.

While life history information is probably generally known for all of the species, only the North American *N. surinamensis* has been studied in detail (Ratcliffe 1972).

The genus *Necrodes* is easily recognized because of its large eyes, broadly orbicular pronotum, strongly tricostate elytra, and males with enlarged posterior femora. The larvae are distinctive because the basal segment of the urogomphus is more than twice as long as the tenth abdominal segment.

Necrodes surinamensis (Fabr.)

(Figs. 18-19, 23-24, 34, 49-56)

Silpha surinamensis Fabricius 1775: 72.
Protonecrodes surinamensis bizonatus Portevin 1926: 165.

Diagnosis. Length 12.0-24.0 mm. *Head*: Color black, widest across large eyes. Antenna 11-segmented, gradually clavate. Labrum broadly, shallowly emarginate. *Thorax*: Pronotum shining black, orbicular, widest near middle. Surface densely punctate, punctures small. *Elytra*: Color black, usually with subapical, transverse row of 1-5, small, reddish orange spots variously combined; occasionally with subbasal, transverse row of 1-3 spots; rarely immaculate. Surface strongly tricostate, with short costa at base between costae 2-3. Surface densely punctate, punctures moderately large. *Legs*: Foretarsi of males with segments 1-4 usually expanded, as wide as long; in females, segments a little longer than wide. Males with hind femora usually enlarged and with acute tooth on posterior edge; femora not enlarged or toothed in females (Figs. 18-19). Posterior tibia usually curved in males, straight in females.

Distribution. *Necrodes surinamensis* is broadly distributed in the eastern United States east of the Rocky Mountains and in certain areas of the Pacific Northwest, Montana, and Utah; it is also found in southern Canada from Newfoundland to British Columbia (Ratcliffe 1972). This species is distributed throughout Nebraska and seems to show a preference for wooded areas.

Locality Records (Fig. 50). 2,479 Nebraska specimens examined or recorded.
ADAMS CO. (10): No data; BOYD CO. (9): Spencer; BUFFALO CO. (2): Kearney; CASS CO. (7): Plattsmouth, South Bend, Union; CHASE CO. (1): Enders Reservoir; CHERRY CO. (5): Ft. Niobrara National Wildlife Refuge; CLAY CO. (1): No data; DAWSON CO. (350): No data; DOUGLAS CO. (6): Omaha; DUNDY CO. (1): S side Republican River E of Benkelman; FILLMORE CO. (5): Fairmont; FRANKLIN CO. (1): No data; FRONTIER CO. (46): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GAGE CO. (3): Beatrice; GOSPER CO. (338): Elwood Reservoir, Lexington, Smithfield; HALL CO. (21): Alda; HOLT CO. (1): O'Neill; JEFFERSON CO. (14): Fairbury; JOHNSON CO. (11): No data; KEYA PAHA CO. (16): Mills, Norden; KNOX CO. (18): Bazile Creek Wildlife Management Area; LANCASTER CO. (40): Hickman, Lincoln, Reller Prairie; LINCOLN CO. (49): Box Elder Canyon, Brady, Cottonwood Canyon, Moran Canyon, North Platte, Wellfleet; OTOE CO. (1,048): Nebraska City; PAWNEE CO. (11): No data; PHELPS CO. (28): Bertrand; PLATTE CO. (2): Columbus; RED WILLOW CO. (3): McCook; RICHARDSON CO. (2): Indian Cave State Park;

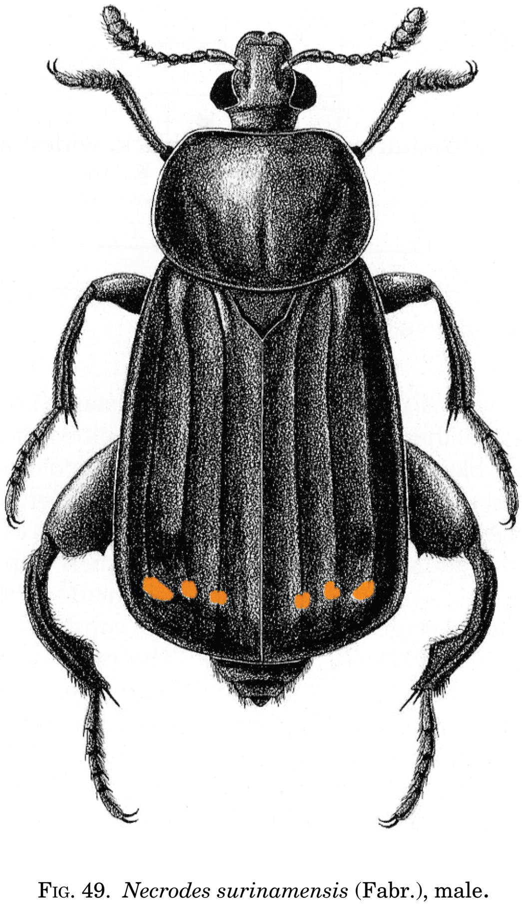


FIG. 49. *Necrodes surinamensis* (Fabr.), male.

SALINE CO. (1): Dewitt; SARPY CO. (5): Bellevue, Fontenelle Forest; SAUNDERS CO. (424): Ashland.

Temporal Distribution. Rangewide: January through December (Ratcliffe 1972). Nebraska: April (8), May (5), June (54), July (269), August (2,016), September (12), October (10), November (3). The large number for August is a result of a survey in Otoe County in 1995.

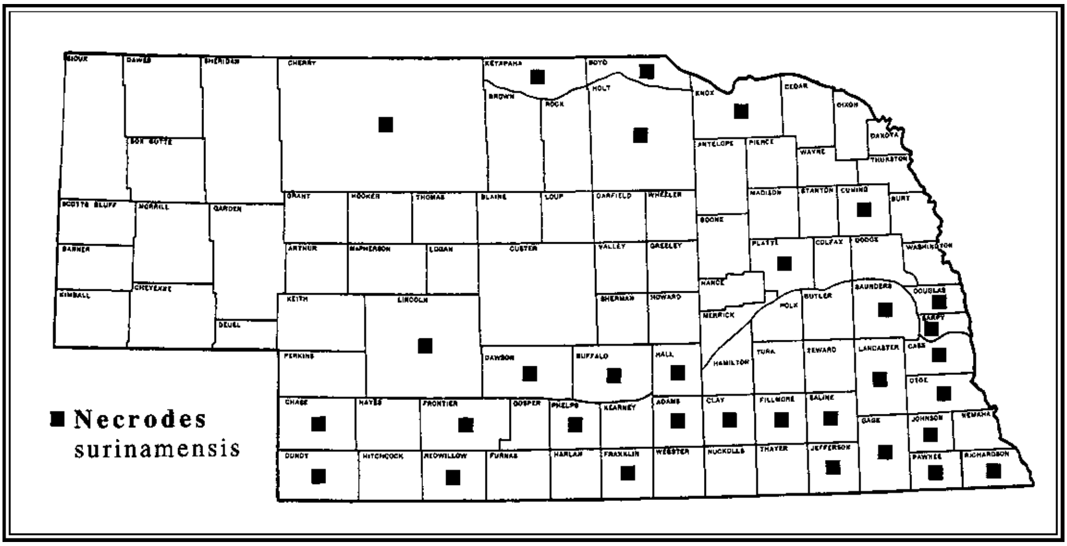
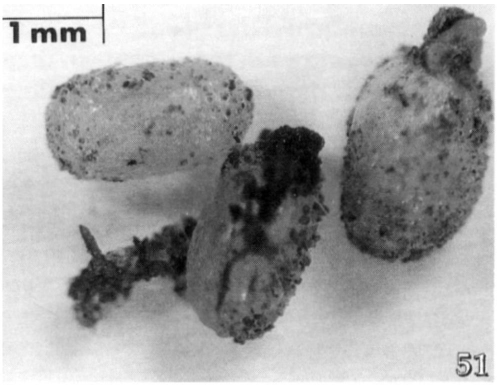


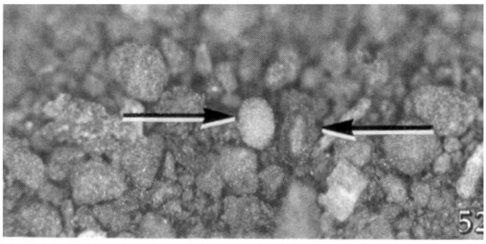
FIG. 50. Nebraska distribution of *Necrodes surinamensis*.

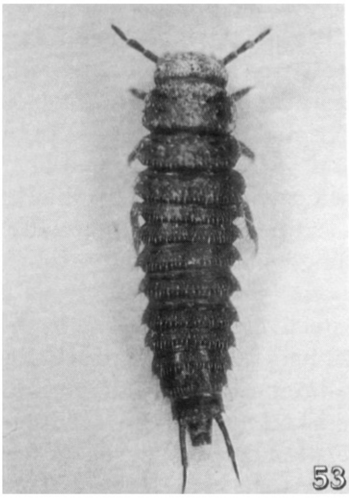
Remarks. *Necrodes surinamensis* is distinguished from other members of the Silphinae by its large eyes, completely black, orbicular pronotum, strongly tricostate elytra, and enlarged femora in the males. The variation in elytral spots is considerable and was documented by Ratcliffe (1972).

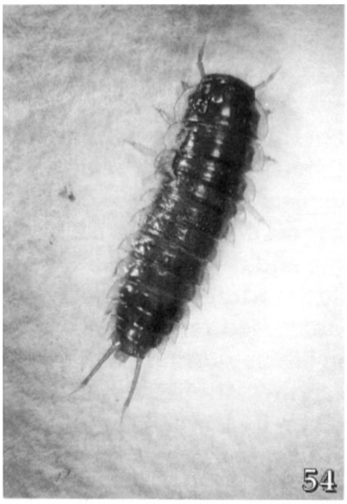
The egg, larval, and pupal stages were described in detail by Ratcliffe (1972).

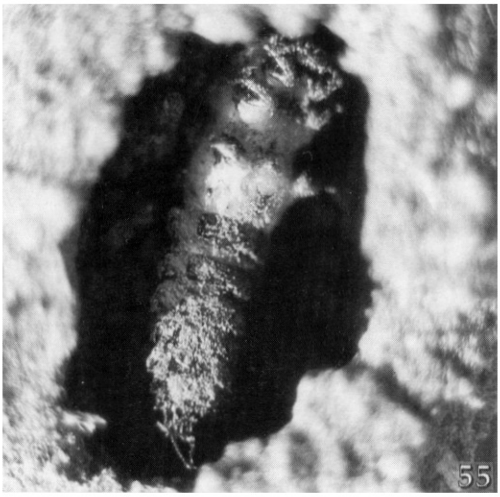
The life history of this species was studied in detail by Ratcliffe (1972), and a brief synopsis is provided here. After locating carrion, adults of *Necrodes surinamensis* feed actively on the dipterous larvae that are present. They mate during the one to seven days they are at the carcass. The females oviposit relatively large, cream colored eggs one at a time randomly on the soil near the carcass. The eggs (Figs. 51-52) gradually darken to resemble the soil on which they rest. Larvae of different instars are found on the same carcass because eggs are laid over a span of several days. Larvae normally hatch from the eggs in 2-4 days and immediately seek the shelter of the carcass to begin feeding. Under favorable conditions, first instar larvae (Fig. 53) molt in 1-2 days. Second instar larvae molt after 2-5 days. The third instar stage (Fig. 54) lasts 3-5 days and, as in all previous stages, may be greatly extended due to cold or wet weather or poor food supply. When ready to pupate the larvae wander a short distance from the carcass to form earthen pupal cells in the ground. Pupal cells made in laboratory rearing chambers were constructed 5 cm below the surface. The pupal cell is formed by sharp, convulsive thrashing of the abdomen that gradually forms an oval, hollow chamber with firmly packed walls (Fig. 55). After construction of the pupal cell, a period of quiescence follows lasting from 5-8 days. This is the pharate pupal stage, so called because the new pupa is developing inside the cuticle of the last instar. Ecdysis eventually occurs

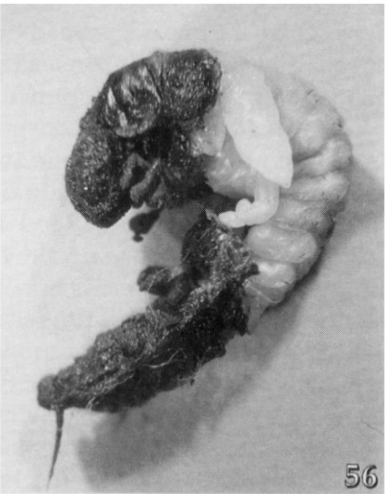












FIGS. 51-52. Eggs of *Necrodes surinamensis*: 51, eggs 2 hours old; 52, eggs one day old. Egg on right has turned a cryptic brown. Figs. 53-54. First and third instar, respectively, of *N. surinamensis*. Fig. 55. Ventral aspect of pharate pupa of *N. surinamensis* within its pupal chamber. Fig. 56. Final molt to pupal stage of *N. surinamensis*.

and exposes the cream-white pupa (Fig. 56). The length of the pupal period varies from 12-17 days. After emerging from the pupa, the adult becomes sclerotized in about 24 hours, after which it digs its way out of the subterranean cell. Adults overwinter beneath the soil or in areas that afford protection.

Adults feed primarily on fly larvae during the active decay stage of a carcass when maggots are usually abundant, but they will also consume carrion as well. Typically, an adult *N. surinamensis* seizes a maggot with its mandibles, restrains it with its forelegs placed on either side of the maggot, and raises its head to lift the struggling maggot off of the substrate and so prevent it from pulling away. After easily breaking the integument of the maggot with its mandibles, the beetle chews rapidly and extracts the soft body contents. Young (1985) observed that adults may, on occasion, consume noctuid moth larvae and dead insects.

While the adults are predators on maggots and may feed on carrion to a limited extent, the larvae normally feed on carrion upon which they are free living and, in addition, feed on fly larvae to a limited extent. During active decay of a carcass, larvae feed on decomposing flesh and semi-liquid putrefaction. When maggot feeding, a larvae seizes a maggot in the mid-region of the body with the mandibles while the forelegs assist in immobilizing the prey. After puncturing the cuticle, the soft contents are consumed.

Necrodes surinamensis is unique among silphids because it can eject anal fluid as a spray (rather than an ooze) (Reed 1958, Ratcliffe 1972, Eisner and Meinwald 1982). The abdominal tip, which projects beyond the posterior margins of the elytra, serves as a revolvable turret by which ejections are actually aimed (personal observation, Eisner and Meinwald 1982). Eisner and Meinwald noted that *N. surinamensis* is anomalous in that it expels its aimed, secretory discharges from the anus (admixed with enteric matter). Other beetles that spray (*i.e.*, Carabidae) also discharge from the tip of the abdomen, but the glands responsible for the spray are integumental and open *beside* the anus. According to Schildknecht and Weis (1962), the high concentration of ammonia in the spray is probably derived from decaying, ingested animal protein and may serve for defense.

Adults are nocturnal and are strongly attracted to lights at night. And it is for this reason that I have concerns for the future welfare of this species. During the mid-1970s when I conducted extensive research on the biology of *N. surinamensis*, this was an abundant species in the Lincoln, NE, area both at carrion and at lights. During the early 1990s, however, I have rarely seen this insect near the city at lights or at carrion, even in places where it used to be abundant. Artificial lighting may be a contributing factor because I believe that lights decrease populations of some nocturnally active insects. Insects are attracted to lights where they are congregated and easily preyed upon by vertebrate scavengers such as toads, opossums, and raccoons. Even if they are not eaten, they are effectively drawn away from their natural habitats and, instead of breeding, die from exposure on hot pavement or are run over by cars and trucks. I believe there is a direct correlation between the electrification of rural America and the decline of some nocturnal insects.

Genus *NECROPHILA*

Nerophila Kirby and Spence 1828: 509.
Necrobora Hope 1840: 151.
Necrotropha Gistel 1848: 121.
Eusilpha Semenov-Tian-Shanskij 1891: 299.
Calosilpha Portevin 1920: 396.
Deutosilpha Portevin 1920: 396.
Chrysosilpha Portevin 1921: 538.
Deuterosilpha (misspelling); in Hatch 1928: 112.

Necrophila is a genus consisting of about 20 species (Hatch 1928, Peck and Miller 1993). With the exception of *N. americana*, all species are found in Asia and India (Hatch 1928). *Necrophila americana* is the only species found in North America. It is broadly distributed throughout the eastern half of the United States and southern Canada.

Necrophila americana is the only North American silphid with a mostly yellow pronotum. That, in combination with its broadly oval body shape and reticulate elytral sculpturing will easily distinguish the only member of this genus in Nebraska. Anderson and Peck (1985) indicated the larvae are characterized by their black color, short two-segmented urogomphi, second sternite with a single sclerite, and the presence of numerous plates on the sensory area of the second antennal segment.

***Necrophila americana* (L.)**
(Figs. 25-26, 36, 41-42, 57-58)

Silpha americana Linnaeus 1758: 360.
Silpha peltata Catesby 1748: Plate 10, Fig. 7.
Oiceoptoma terminata Kirby 1837: 103.
Oiceoptoma affine Kirby 1837: 103.
Oiceoptoma canadense Kirby 1837: 104.

Diagnosis. Length 13.8-20.0 mm. *Thorax*: Color yellow, usually with a large, discal, black spot. Surface extremely finely punctate to rugopunctate, punctures and rugae longitudinal. *Elytra*: Color black, females with apical tips usually yellow or rarely all black. Surface tricostate (lateral costa occasionally indistinct), intervals confusedly tuberculate, tubercles irregular in shape and usually connected to costae. Apex in males rounded, slightly elongated in females (Figs. 25-26).

Distribution. *Necrophila americana* is found in the eastern half of the United States and southern Canada (Peck and Anderson 1985, Peck and Kaulbars 1987). This species occurs throughout Nebraska. While there are no records for the panhandle, they may also occur there.

Locality Records (Fig. 58). 3,562 Nebraska specimens examined or recorded.

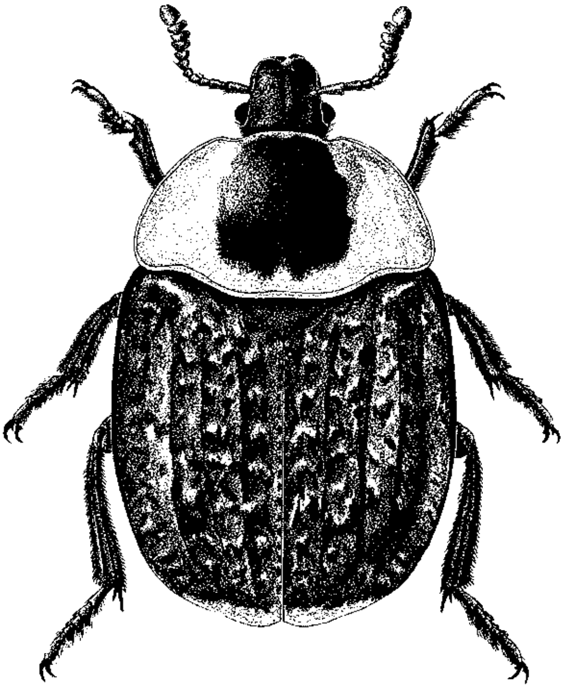


FIG. 57. *Necrophila americana* (L.), male.

ANTELOPE CO. (2): Neligh; CASS CO. (396): Plattsmouth; CHASE CO. (3): Enders Reservoir, Imperial; CHERRY CO. (27): Dewey Lake, North Loup River, Pelican Lake, Valentine; CUSTER CO. (94): Anselmo, Sargent; DIXON CO. (8): Aowa Creek; DOUGLAS CO. (1): Omaha; FRONTIER CO. (5): Farnam; GAGE CO. (2): Wolf-Wildcat Creek; HALL CO. (4): Alda; JOHNSON CO. (100): No data; KEITH CO. (19): Cedar Point Biological Station; KEYA PAHA CO. (88): Mills, Norden; KNOX CO. (755): Bazile Creek Wildlife Management Area; LINCOLN CO. (4): Box Elder Canyon, Brady, North Platte, Wellfleet; LOGAN CO. (1): No data; OTOE CO. (53): Nebraska City; PAWNEE CO. (105): No data; SALINE CO. (1): Swan Creek; SARPY CO. (6): Fontenelle Forest, Schramm Park; SAUNDERS CO. (3): Wahoo; SHERIDAN CO. (2): Gordon; THOMAS CO. (59): Halsey Forest; WASHINGTON CO. (5): Ft. Calhoun.

Temporal Distribution. Rangewide: March to September (Peck and Kaulbars 1987). Nebraska: May (59), June (252), July (282), August (1,080), September (4). The August numbers reflect a concerted trapping effort near Niobrara, NE, in 1994 and is not reflective of a true August peak in the population.

Remarks. *Necrophila americana* is distinctive because of the relatively large, broadly rounded, dorso-ventrally flattened body, and conspicuous, yellow pronotum. As in *Heterosilpha ramosa*, males have rounded elytral apices and females have the apices slightly prolonged (Figs. 25-26).

The larvae were described in detail by Dorsey (1940) and by Anderson and Peck (1985).

According to Anderson (1982c), adults overwinter and begin reproducing in late May through mid-July. Larvae were numerous during this time, but they appeared later than the larvae of other species. Anderson observed teneral adults in late July through August indicating the emergence of the first brood of larvae. These adults evidently overwintered (despite their relatively early emergence in the year), which suggests that there is only one generation a year. Development from egg to the adult stage took about 10-12 weeks. This is a diurnal species (personal observation, Shubeck 1971). Clark (1895) and Steele (1927) observed adults feeding on maggots at carrion. Dorsey (1940) observed both adults and larvae feeding on decaying flesh, usually near softer parts and excretions. However, the larvae fed principally

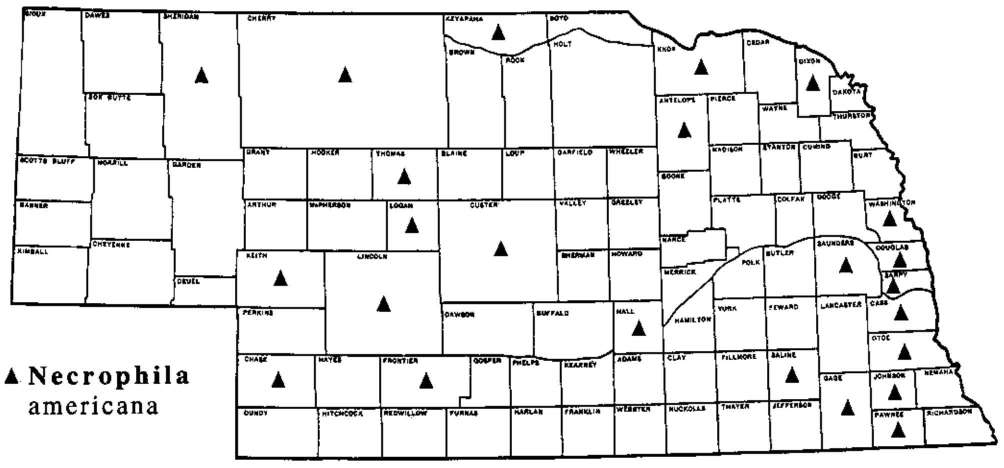


FIG. 58. Nebraska distribution of *Necrophila americana*.

on the dried remains of hide, sinew, and shreds of flesh that are left after the dipterous larvae have finished with the carcass. Trapping in Nebraska indicated this species shows a strong preference for marshy and forested areas, a result also observed by Lingafelter (1975) in Kansas.

Fisher and Tuckerman (1986) observed that *Psithyrus ashtoni* (Cresson), a cuckoo bumble bee, is mimicked by *N. americana*. Both model and mimic occur in the field-forest interface, have flight periods that coincide, share similar flight behavior, and have similar coloring and overall appearance when flying. *Necrophila americana* presumably acquires some protection from predation by mimicking a large, stinging bee.

Genus *OICEOPTOMA*

Oiceoptoma Leach 1815: 89.
Oeceoptoma Agassiz 1847: 256 (unjustified emendation).
Isosilpha Portevin 1920: 398.

Seven species are placed in the genus *Oiceoptoma* (Hatch 1928, Peck and Miller 1993). Three species occur in North America, and the remainder are found in Asia with one of those reaching Europe. Two species are found in Nebraska while the third North American species, *O. rugulosum* Portevin, is restricted to the southern United States.

North American species of the genus *Oiceoptoma* are characterized by having a head with a short row of long setae on the posterior margin of the eye (Fig. 20), small eyes, a pronotum that is widest at the base and entirely black or with a black disc and dull orange margins, and an elytral shoulder with a small tooth (Figs. 27-30). It should be noted that while *Thanatophilus truncatus* (Say) also has setae behind the eye, these setae are shorter, directed anteriorly, and are in a small field behind the posterior margin of the eye.

The larvae are characterized by having the urogomphi subequal in length to the tenth abdominal segment (Fig. 37) and the second segment of the antenna with a large sense cone (Fig. 40).

***Oiceoptoma inaequale* (Fabricius)**
(Figs. 20, 27-28, 44, 59-60)

Silpha inaequalis Fabricius 1781: 87.

Diagnosis. Length 8.6-14.4 mm. *Thorax*: Color black. Surface finely and densely punctate, with short, black setae. *Elytra*: Color black. Surface finely and densely punctate, tricostate. Apex rounded in males, attenuated in females (Figs. 27-28).

Distribution. *Oiceoptoma inaequale* occurs from southern Ontario and Quebec to Florida and extends west to Texas and the Dakotas (Anderson and Peck 1985, Peck and Kaulbars 1987). This species is found in Nebraska in approximately the eastern two-thirds of the state; there are no records for the panhandle or the southwest corner.

Locality Records (Fig. 60). 427 Nebraska specimens examined or recorded.
ANTELOPE CO. (3): Neligh; CASS CO. (4): Plattsmouth, South Bend; CHASE CO. (3): Enders Reservoir; CUMING CO. (3): West Point; CUSTER CO. (1): Anselmo; DAWES CO. (1): No data; DIXON CO. (2): Aowa Creek; DOUGLAS CO. (5): Omaha; DUNDY CO. (20): 1.5 mi. SW Max, Republican River E of Benkelman; FILLMORE CO. (1): Fairmont; FRANKLIN CO. (75): 5 mi. S Franklin; FRONTIER CO. (108): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GOSPER CO. (1): Lexington; HALL CO. (3): Alda; HARLAN CO. (8): Republican River S of Orleans; JEFFERSON CO. (67): Fairbury; LANCASTER CO. (63): Lincoln, Reller Prairie, Sprague; LINCOLN CO. (16): North Platte, 2 mi. S Sutherland, Wellfleet; NUCKOLLS CO. (14): No data; SARPY CO. (28): Bellevue, Schramm Park; THOMAS CO. (1): Halsey Forest.

Temporal Distribution. Rangewide: January to October (Peck and Kaulbars 1987).

Nebraska: April (21), May (57), June (206), July (139), August (3), September (1).

Remarks. The characters in the key and in the diagnosis will serve to separate this species from others. It is similar in appearance to *O. noveboracense* (Forster) but lacks the dull orange pronotal margin of that species. It also vaguely resembles *T. lapponicus* (Herbst) but lacks the distinctive elytral tubercles present in that species.

Dorsey (1940) described the larval stage in detail, and Anderson and Peck (1985) provided a diagnosis of the larva. The shallow emargination of the anterior margin of the prothoracic tergite (Fig. 44) will separate the larva of this species from that of *O. noveboracense*, which has the anterior margin of the prothoracic tergite deeply emarginate (Fig. 43).

Anderson and Peck (1985) suggested there is only one generation per year based on data from Howden (1950), Reed (1958), and Anderson (1982c). In Nebraska, oviposition probably occurs from late May to June. Goe (1919) observed oviposition in the soil, and the egg-laying period in one female lasted 36 days with an average of two eggs laid per day (range 1-7 eggs/day, total of 62 eggs). One pair of eggs hatched in six days. The length of the first stadium was ten days, the second stadium was four days, and the third about eight days. Adults emerged 17-20 days after the third instars entered the soil to pupate. Cole (1942) observed the eggs to hatch in about seven days and a larval duration of 20 days; pupation took 2-3 weeks. Overwintering was in the adult stage.

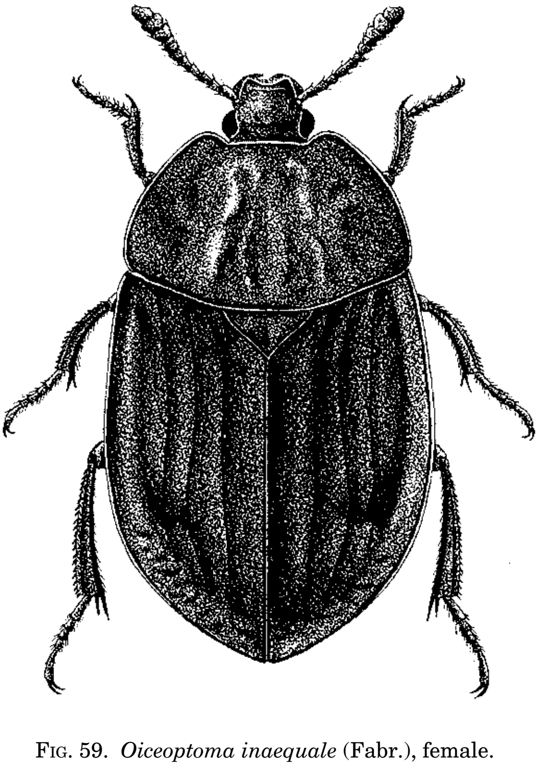


FIG. 59. *Oiceoptoma inaequale* (Fabr.), female.

Oiceoptoma inaequale is a diurnal species (personal observation, Shubeck 1971). Lampert (1977) observed that, during flight, the elytra are raised to the vertical and held together over the back like the wings of a resting butterfly. The ventral side of the

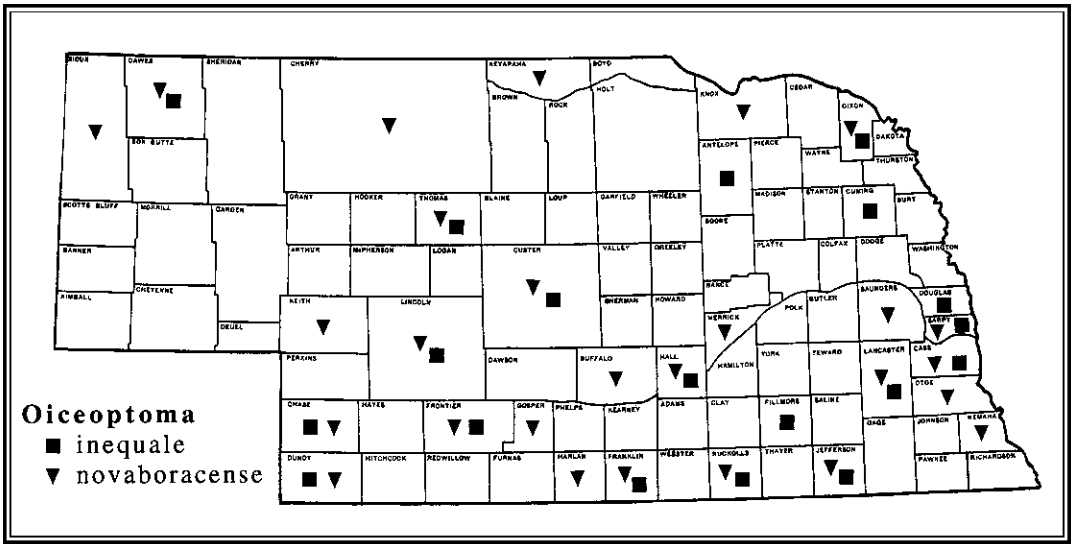


FIG. 60. Nebraska distribution of *Oiceoptoma inaequale* and *O. novaboracense*.

elytra are exposed and are a bright, metallic blue. He noted that, as the beetle flew, the vertically oriented elytra created the impression of a much larger insect because the ventral surfaces of the elytra flashed metallic blue as they reflected light. Upon landing and lowering the elytra, the large metallic beetle suddenly vanished leaving only a small, black one. This has also been observed in *T. lapponicus* (J. Bedick, pers. comm., September 1995). The adaptive value of this strategy is an abrupt "disappearance" from the search image of a potential predator.

This species is most commonly found throughout its range in areas of deciduous forest (Anderson and Peck 1985). Most of the records from eastern Nebraska are also from forested areas although specimens from west central Nebraska come from mostly prairie habitats. Results of a study by Shubeck (1984a) showed a slight preference for open areas while that of Lingafelter (1995) demonstrated a slight preference for forests. Although a broad zone of geographic overlap occurs between *O. inaequale* and *O. noveboracense*, one of the two species always seems to be locally rare or absent when both occur in the same area (Anderson and Peck 1985). Steele (1927) observed adults feeding on maggots at carrion.

Oiceoptoma noveboracense (Forster)

(Figs. 16, 29-30, 37, 40, 43, 60-61)

Silpha noveboracensis Forster 1771: 17.
Silpha marginalis Fabricius 1776: 215.
Oiceoptoma marginata Kirby 1837: 100.

Diagnosis. Length 10.0-13.5 mm. *Thorax*: Disc black with broad margins pale orange or tan. Surface finely and densely punctate, with several longitudinal, dense rows of short, tawny setae. *Elytra*: Color light brown (most common) to black. Surface finely and densely punctate, tricostate. Apex rounded in males, attenuate in females (Figs. 29-30).

Distribution. *Oiceoptoma noveboracense* is a widely distributed species in the eastern part of the United States (although it does not occur in Florida, Louisiana, and Texas). Its range extends west to Oklahoma, Kansas, Nebraska, and the Dakotas. There are only sporadic records for Wyoming and Montana. According toAnderson and Peck (1985) and Peck and Kaulbars (1987), it is recorded from the southern part of Canada and extends westward to Alberta. In Nebraska, this species is found statewide except for the southern portion of the panhandle as well as the southwestern corner.

Locality Records (Fig. 60). 327 Nebraska specimens examined or recorded.
BUFFALO CO. (3): Kearney; CASS CO. (7): Plattsmouth; CHASE CO. (9): Enders Reservoir; CHERRY CO. (6): Ft. Niobrara National Wildlife Refuge; CUSTER CO. (50): Anselmo, Sargent; DAWES CO. (28): Ash Creek, Chadron; DIXON CO. (18): Aowa Creek; DUNDY CO. (1): 1.5 mi. SW Max; FRANKLIN CO. (32): 5 mi. S Franklin; FRONTIER CO. (40): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GOSPER CO. (3): Lexington; HALL CO. (8): Grand Island; HARLAN CO. (6): Republican River S of Orleans; JEFFERSON CO. (15): No data; KEITH CO. (1): Cedar Point Biological Station; KEYA PAHA CO. (38): Mills, 5 mi. SW Norden; KNOX CO. (13): Bazile Creek; LANCASTER CO. (11): Lincoln; LINCOLN CO. (158): Box Elder Canyon, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; MERRICK CO. (3): No data; NEMAHA CO. (1): Auburn; NUCKOLLS CO. (1): No data; OTOE CO. (1): Nebraska City; SARPY CO. (15): Fontenelle Forest, Schramm Park; SAUNDERS CO. (4): Cedar Bluffs, Wahoo; SIOUX CO. (29): Ft. Robinson, Gilbert-Baker State Wayside Area, Monroe Canyon, Warbonnet Canyon; THOMAS CO. (36): Halsey Forest.

Temporal Distribution. Rangewide: February to October (Anderson and Peck 1985; Peck and Kaulbars 1987). Nebraska: March (1), April (13), May (32), June (66), July (211), August (172), September (1).

Remarks. *Oiceoptoma noveboracense* is a smaller silphid that may be readily identified because of its usually light brown color and distinctive dull orange color of the pronotal margins. Only *O. inaequale* (Fabr.) is similar, but it lacks the marginal coloration of the pronotum.

The larvae were described in detail by Dorsey (1940) and by Anderson and Peck (1985). The deep emargination of the anterior margin of the prothoracic tergite (Fig. 43)

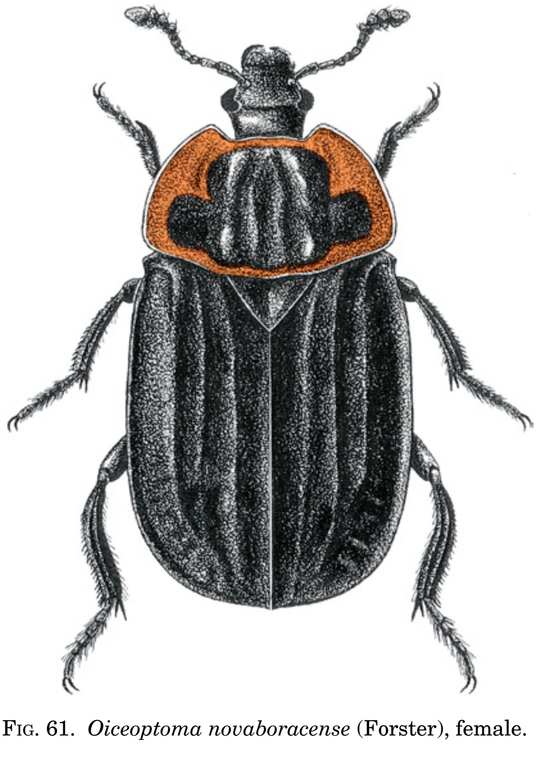


FIG. 61. *Oiceoptoma novaboracense* (Forster), female.

will distinguish the larva of this species from *O. inaequale*, which has the anterior margin of the prothoracic tergite shallowly emarginate (Fig. 44).

Adults of this species are diurnal (personal observation, Shubeck 1971), and the adults are reproductively active in the spring (Pirone 1974, Shubeck 1976, Anderson 1982c). Anderson and Peck (1985) noted that in more northerly localities, this species is the dominant early season silphine of forested areas. Shubeck (1975b) studied flight activity as influenced by temperature for *O. noveboracense*. He found that the normal temperature range of flight activity was 23° C to 30° C with a pronounced peak of activity at 25° C. Beetles did not fly if the temperature was above 30° C or below 23° C.

In the eastern part of its range, *O. noveboracense* is most commonly found in forested habitats (Shubeck 1984a, Lingafelter 1995), but in west central Nebraska it seems to be just as abundant in prairie habitats.

In Nebraska, there is probably one generation a year. According to Anderson and Peck (1985), mating and egg laying usually occur from about mid-April to late May. A female lays 8-10 eggs in the warm soil surrounding a carcass. Anderson and Peck noted that the egg stage lasted 5-6 days, the first instar 4-5 days, the second instar 7-8 days, and the third instar 10 days. Third instar larvae then pupated in the soil. The duration of the pupal stage was 2-3 weeks. New adults began to appear in July, and these individuals then overwintered.

Clark (1895) noted some feeding by adults on fly larvae at carrion.

Genus *THANATOPHILUS*

Thanatophilus Leach 1815: 89.
Pseudopelta Bergroth 1884: 229.
Philas Portevin 1903: 331.
Silphosoma Portevin 1903: 333.
Chalcosilpha Portevin 1926: 31.

The genus *Thanatophilus* contains 20 species and was last revised by Schawaller (1981). Interestingly, Schawaller did not include the North American *T. truncatus* in his revision. I do not know if this was an oversight or whether he purposefully excluded it from the genus . . . in which case I would have expected him to mention this in his revision. Five species are found in North America (Anderson and Peck 1985, Peck and Miller 1993) while the remaining species occur in Europe and Asia with two species in sub-Saharan Africa (Schawaller 1981). In Nebraska, there are two species.

Species of *Thanatophilus* are characterized by having widely separated mesocoxae, small eyes that lack a short row of long setae on the posterior margin of the eye, and elytra that lack costae or else have tubercles in the intervals. It should be noted that while *T. truncatus* has setae behind the eye, these setae are not in a distinct row (but in a small field), are directed forward, and are short.

Only two of the five North American species of larvae have been described (including only *T. lapponicus* from the Nebraska species). The larvae of these species are distinguished by the urogomphi being longer than the tenth abdominal segment (Fig. 35) and the presence of three large sclerites on the second sternite (Anderson and Peck 1985).

Thanatophilus lapponicus (Herbst)
(Figs. 31-32, 62-63)

Silpha lapponica Herbst 1793: 209.
Silpha caudata Say 1823: 192.
Silpha tuberculata Germar 1824: 81.
Silpha granigera Chevrolat 1834: 1.
Silpha californica Mannerheim 1843: 253.
Silpha sachalinica Kieseritzky 1909: 126.
Thanatophilus irregularis Portevin 1914: 221.
Thanatophilus lapponicus mulleri Portevin 1932: 58.

Diagnosis. Length 9.4-14.0 mm. *Head* and *Thorax*: Color black. Surface with dense, tawny setae. *Elytra*: Color black. Surface tricostate, densely setose, intervals each with a row of small tubercles. Apices in males rounded, females with apex attenuate (Figs. 31-32).

Distribution. *Thanatophilus lapponicus* ranges broadly throughout Canada and Alaska, across the northern United States from coast to coast, and south to southern California, Arizona, and New Mexico (Anderson and Peck 1985, Peck and Kaulbars 1987). It is also found in northern Europe and Asia (Hatch 1928, Schawaller 1981). In Nebraska, this species probably occurs statewide although it is more abundant in the north and west.

Locality Records (Fig. 63). 650 Nebraska specimens examined or recorded.
ADAMS CO. (2): No data; ARTHUR CO. (2): Arapaho Prairie; BUFFALO CO. (5): Kearney, Ravenna; CHERRY CO. (25): Dewey Lake, Valentine, Ft. Niobrara National Wildlife Refuge; CHEYENNE CO. (2): Dalton; CUMING CO. (1): West Point; CUSTER CO. (100): Anselmo, Milburn, Sargent; DAWES CO. (15): Chadron, Pine Ridge area; DAWSON CO. (3): Johnson Lake, Lexington; DIXON CO. (2): Concord; DUNDY CO. (6): Haigler, 1.5 mi. SW Max, Republican River E of Benkelman; FRANKLIN CO. (4): No data; FRONTIER CO. (71): Farnam, Medicine Creek Reservoir, Red Willow Reservoir;

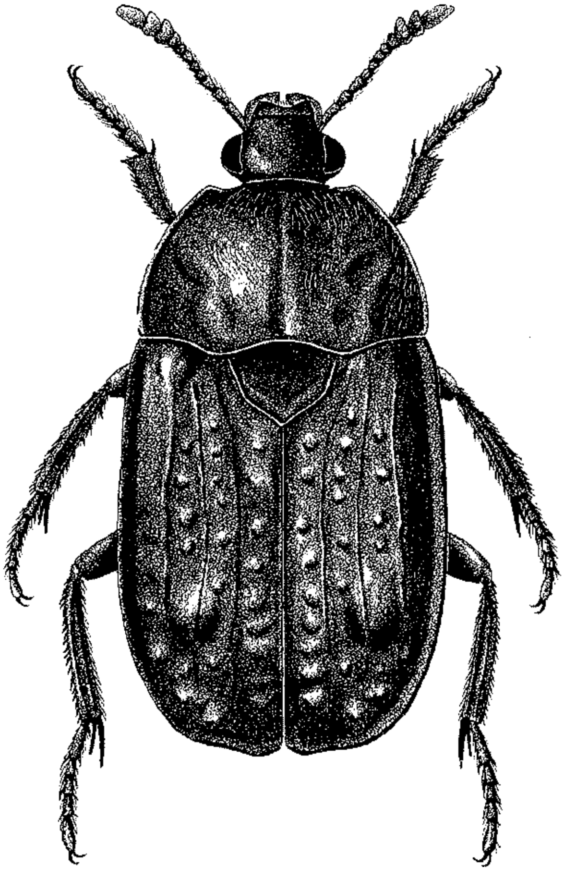


FIG. 62. *Thanatophilus lapponicus* (Herbst), male.

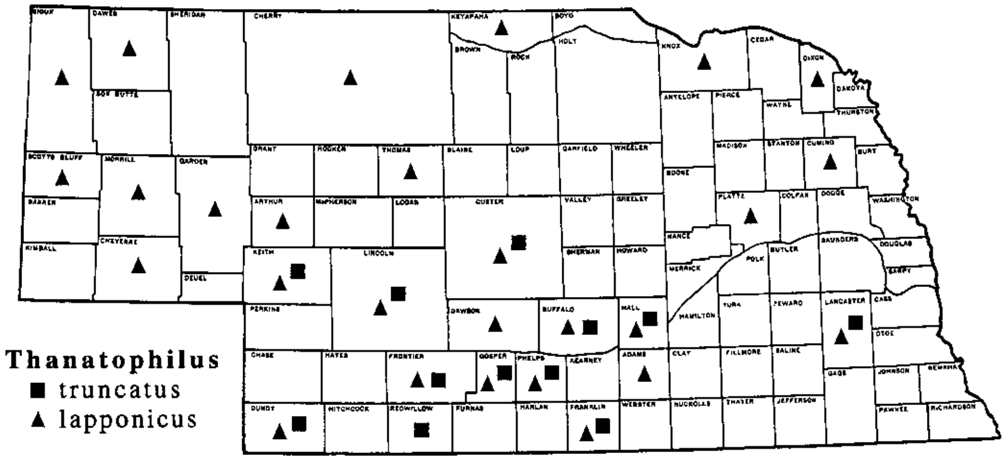


FIG. 63. Nebraska distribution of *Thanatophilus lapponicus* and *T. truncatus*.

GARDEN CO. (2): Crescent Lake; GOSPER CO. (36): Elwood Reservoir, Lexington, Smithfield; HALL CO. (12): Alda; KEITH CO. (7): Cedar Point Biological Station; KEYA PAHA CO. (8): Mills, Norden; KNOX CO. (8): Bazile Creek; LANCASTER CO. (5): Lincoln; LINCOLN CO. (235): Box Elder Canyon, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; MORRILL CO. (2): Bayard; PHELPS CO. (6): Bertrand; PLATTE CO. (3): No data; SCOTTS BLUFF CO. (27): Mitchell; SIOUX CO. (17): Crawford, Ft. Robinson, Gilbert-Baker State Wayside Area, Glen, Monroe Canyon, Warbonnet Canyon; THOMAS CO. (44): Halsey Forest.

Temporal Distribution. Rangewide: March to October (Peck and Kaulbars 1987). Nebraska: April (11), May (24), June (149), July (232), August (206), September (8), October (5).

Remarks. *Thanatophilus lapponicus* is readily identified because of the presence of a row of small tubercles on each of the elytral intervals (Figs. 31-32, 62); it is the only silphid in North America with this distinctive form of elytral sculpturing.

The larval stage was described by Dorsey (1940), and a brief synopsis was given by Anderson and Peck (1985). The larva of this species is characterized by a dark brown to black color on the dorsal surface, urogomphi that are about two times the length of the 10th abdominal segment, and antennae with a large sense cone on the second segment (as in Fig. 40).

Overwintering adults become reproductively active in late April and May in Nebraska. There are two generations a year in Nebraska; Anderson (1982c) reported two generations a year also in Ontario, Canada. Adults of the first generation appear in June and early July when they mate and lay eggs. Adults of the second generation appear in late July through September, and these are the overwintering adults. Anderson and Peck (1985) reported that individual females lay about ten eggs in the soil surrounding a carcass. The egg stage lasts 5-6 days, the first instar about 7 days, the second instar 8-10 days, and the third instar 10-12 days. Anderson and Peck did not observe pupae.

Anderson and Peck noted that *T. lapponicus* is a cold-adapted species that occurs at higher elevations in the western mountains of North America. It is often the only silphid present in some of these areas. *Thanatophilus lapponicus* shows a strong preference for open areas (Anderson 1982c).

Emetz (1975) reported that this species is sometimes injurious to furs, meats, and dried fish. Clark (1895) observed extensive predation on fly larvae by adult beetles.

***Thanatophilus truncatus* (Say)**

(Figs. 33, 63-64)

Silpha truncata Say 1823: 193.

Diagnosis. Length 10.5-15.9 mm. *Head* and *Thorax*: Color black. Surface with small, dense punctures, punctures with minute, black, adpressed setae. *Elytra*: Color black. Surface with small, dense punctures, costae or tubercles absent. Apices of elytra truncate, not attenuated, in both sexes (Fig. 33).

Distribution. *Thanatophilus truncatus* is found from Nebraska southwest to Kansas, Colorado, Texas, New Mexico, and Arizona (Peck and Kaulbars 1987). It occurs in much of Mexico also, ranging as far south as southcentral Mexico (Peck and Anderson 1985). In Nebraska, this species has been found as far east as Lincoln and as far north as Custer county.

Locality Records (Fig. 63). 346 Nebraska specimens examined or recorded.
BUFFALO CO. (2): Kearney; CUSTER CO. (5): Sargent; DUNDY CO. (5): Haigler, 1.5 mi. SW Max; FRANKLIN CO. (1): No data; FRONTIER CO. (101): Farnam, Medicine

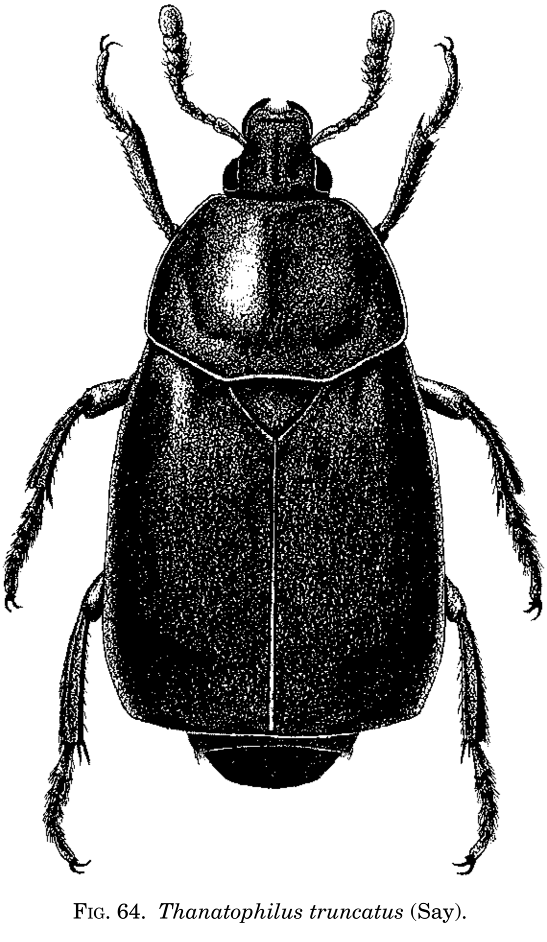


FIG. 64. *Thanatophilus truncatus* (Say).

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.

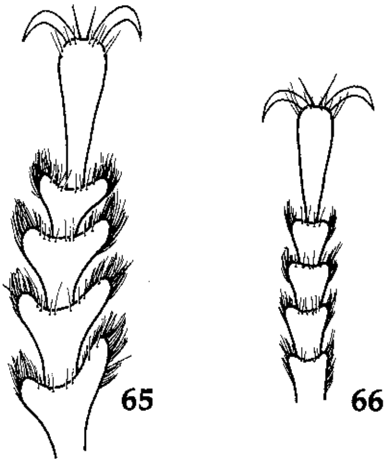
Necroxenus Semenov-Tian-Shanskij 1926: 46.
Eunecrophorus Semenov-Tian-Shanskij 1933: 152.
Necrocleptes Semenov-Tian-Shanskij 1933: 153.
Necrophorindus Semenov-Tian-Shanskij 1933: 153.
Necrophoriscus Semenov-Tian-Shanskij 1933: 152.
Nesonecrophorus Semenov-Tian-Shanskij 1933: 153.
Necropter Semenov-Tian-Shanskij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

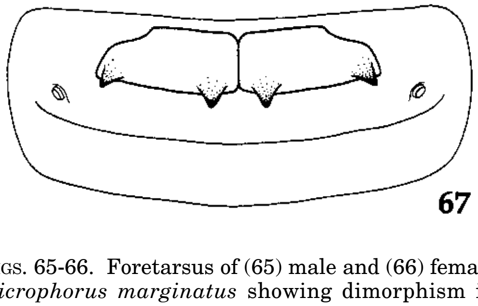
The genus *Nicrophorus* presently contains about 85 species distributed in Europe, Asia, North and South America (Hatch 1928, Peck and Anderson 1985). Most of the species occur in Europe and Asia. There are 15 species in the United States, and all but four of these occur in Nebraska (*N. defodiens* Mannerheim, *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.

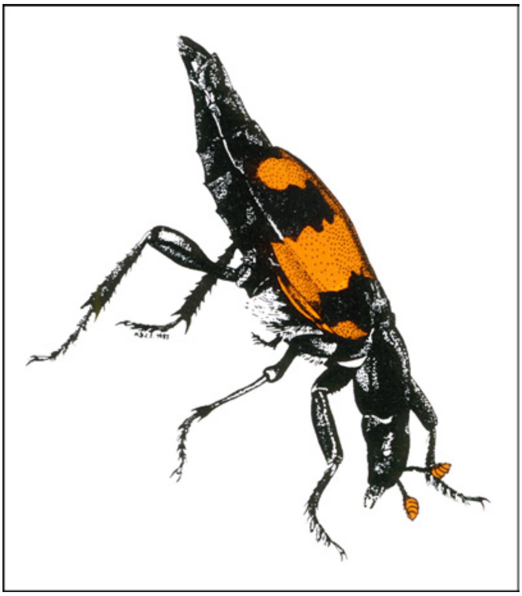


FIG. 68. Male *Nicrophorus* sp. emitting pheromone in typical "headstand" position. Illustration from cover of *Behavioral Ecology* 3(3), 1992. Used by permission of Oxford University Press.

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).

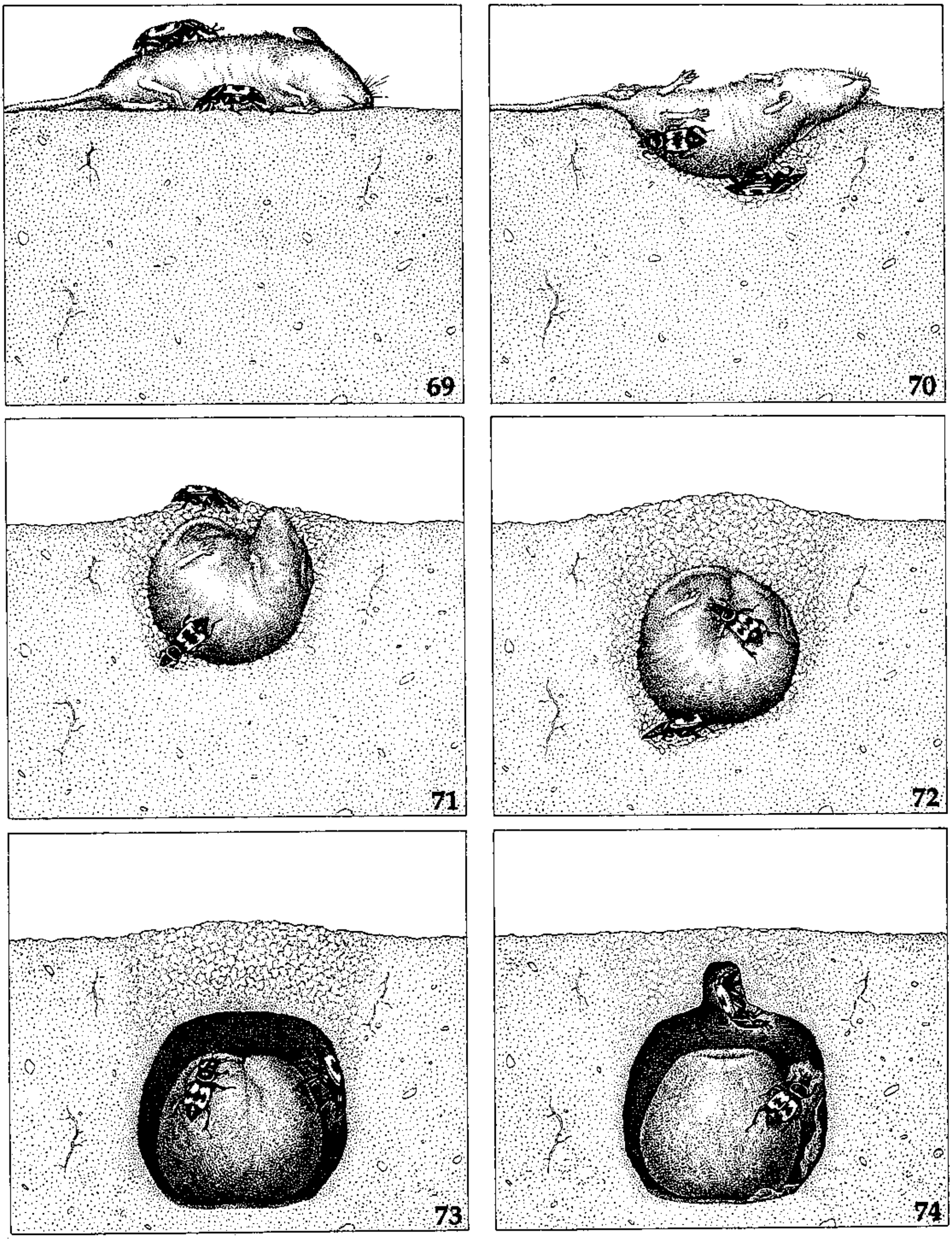
According to Muths (1991), *Nicrophorus* species were tested in the laboratory to determine if they discriminated between different substrates when burying a carcass. His results suggested beetles do discriminate, preferring substrates with higher "bulk" (*i.e.*, grass clippings) over those without. 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. 69-74. 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 regur-gitate 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 regur-gitation 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 by

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

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: Parasit-idae). 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 deuto-nymphs 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

5. Anterior face of procoxa with short setae on basal half, setae about half length of those on humerus . . . . . . ***marginatus* Fabr.**

5'. Anterior face of procoxa with long setae on basal half, setae as long or longer than those on humerus 6

6. Penultimate antennal segment with outer edge only moderately emarginate (Fig. 94); basal segment of antennal club black or orange; if club orange, elytron with anterior black band crossing onto epipleuron (Fig. 84); if club black, orange elytral maculations reduced or absent and epipleuron bicolored . . . . ***guttula* Motschulsky**

6'. Penultimate antennal segment with outer edge deeply and abruptly emarginate (Fig. 95); basal segment of antennal club black. Elytron with anterior black band reaching epipleural ridge but not crossing onto epipleuron (Fig. 89) . . ***obscurus* Kirby**

7. Elytral epipleuron unicolorous, black *or* orange 8

7'. Elytral epipleuron bicolored, black *and* orange (Fig. 88) . . ***mexicanus* Matthews**

8. Elytral epipleuron black 9

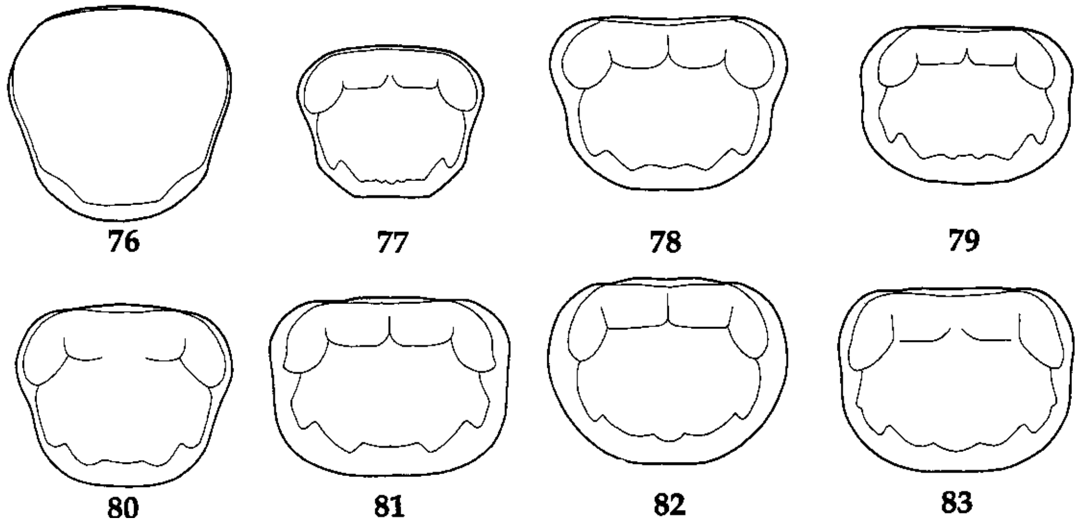
8'. Elytral epipleuron orange 10

9. Dorsal surface of elytra with long, fine, erect setae (Fig. 90). Epipleural ridge short, extending anteriorly only to level of apex of scutellum . . . . ***orbicollis* Say**

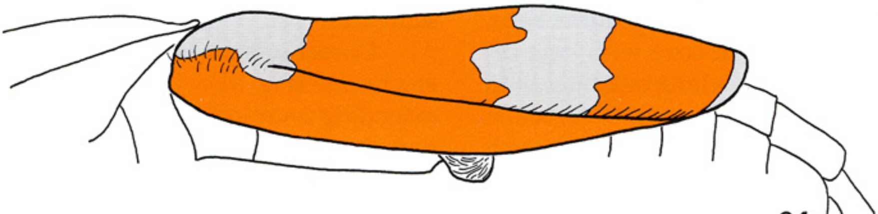
9'. Dorsal surface of elytra without long, erect setae (Fig. 91). Epipleural ridge long, extending anteriorly to near level of base of scutellum . . . . ***pustulatus* Herschel**

10. Humerus covered by field of small, stout setae that extend to base of epipleural ridge (Figs. 85, 92). Metasternum with crescent-shaped area immediately behind each mesocoxa that is glabrous or with sparse setae only. Posterior edge of metatrochanter of males with acute tooth projecting perpendicular (dorsally) from trochanter (Fig. 96). Females with small eyes, post-ocular bulge a little shorter than length of eye (Fig. 98) . . . . ***hybridus* Hatch & Angell**

10'. Humerus with small, stout setae but these ending well before base of epipleural ridge (Figs. 86, 93). Metasternum with long, dense setae immediately behind each mesocoxa. Posterior edge of metatrochanter of males with acute tooth re*curving* dorsally (Fig. 97). Females with large eyes, post-ocular bulge less than half length of eye (Fig. 99) . . . . ***investigator Zetterstedt***



FIGS. 76-83. Pronotum of 76, *Nicrophorus carolinus*; 77, *N. guttula*; 78, *N. hybridus*; 79, *N. investigator*; 80, *N. marginatus*; 81, *N. mexicanus*; 82, *N. orbicollis*; 83, *N. pustulatus*.



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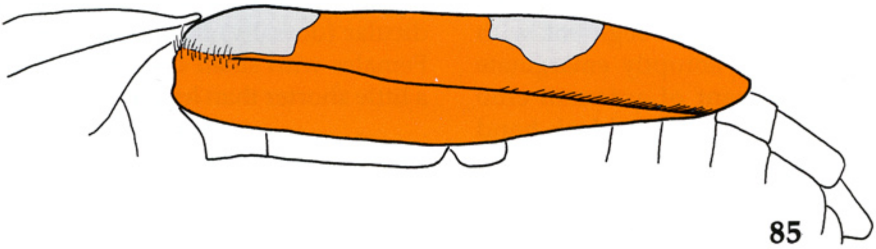

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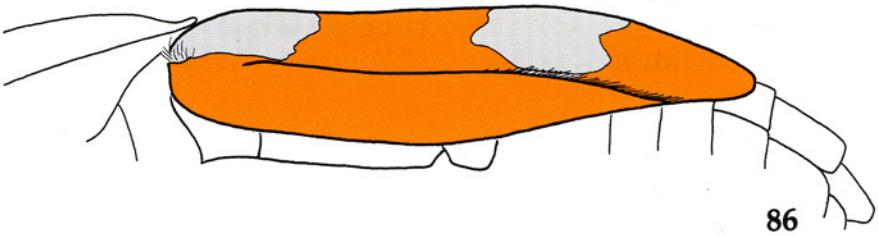

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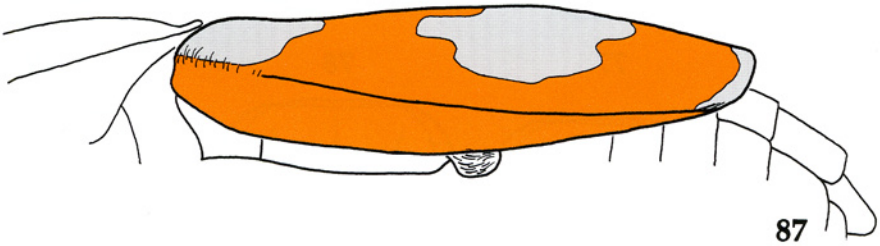

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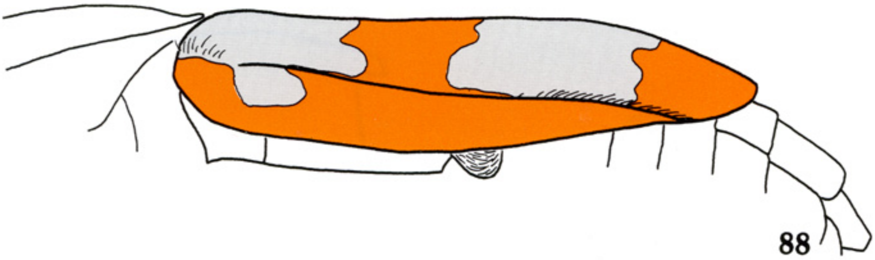
FIGS. 84-87. Lateral view of left side of elytra showing form and color of epipleuron and elytra, metepimeron, and humeral setae of 84, *Nicrophorus guttula*; 85, *N. hybridus*; 86, *N. investigator*; 87, *N. marginatus*.



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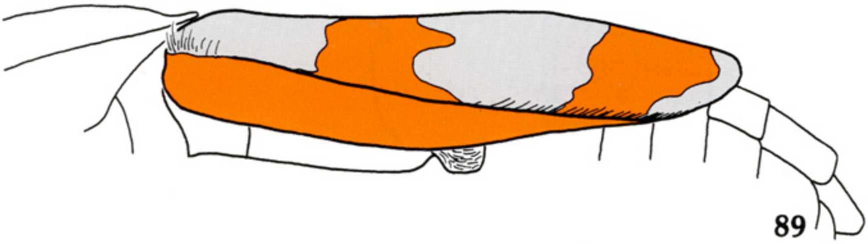

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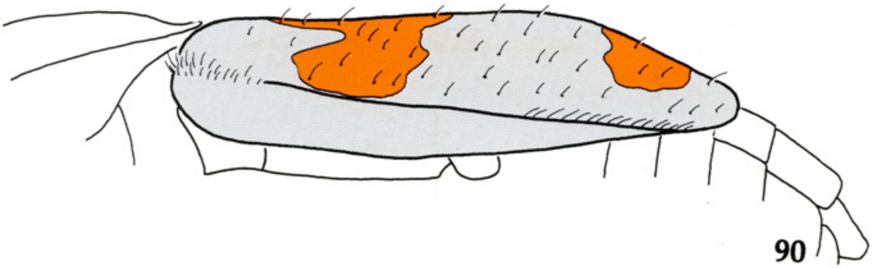

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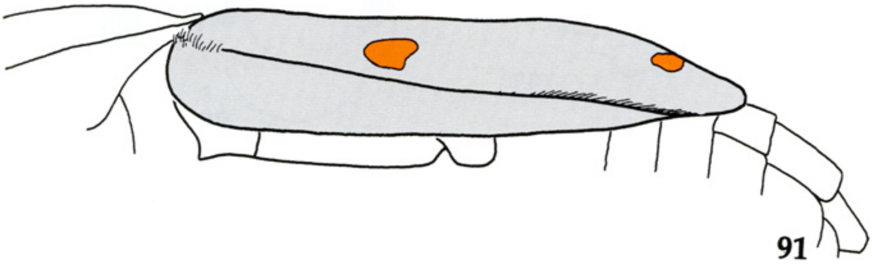
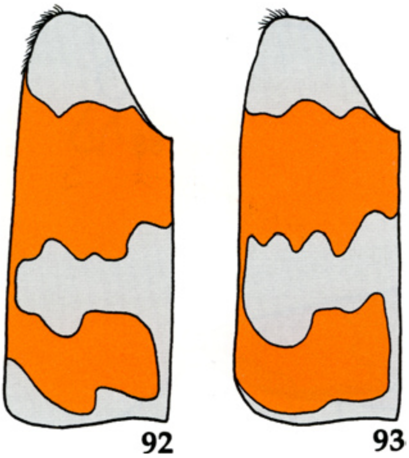
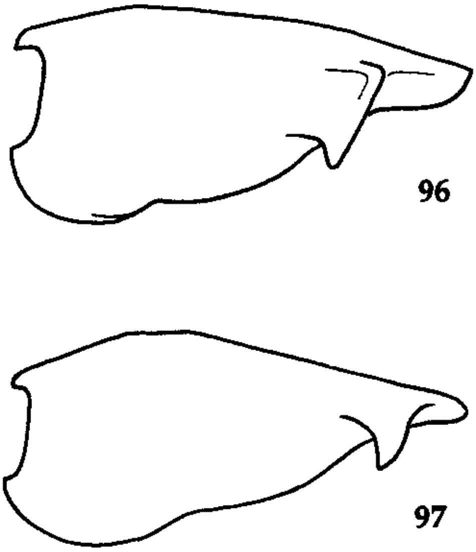


91

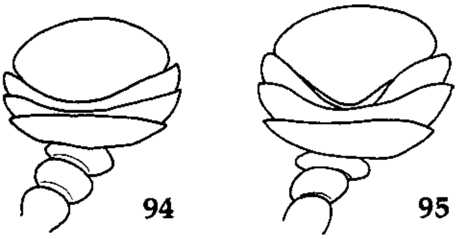
FIGS. 88-91. Lateral view of left side of elytra showing form and color of epipleuron and elytra, metepimeron, and humeral setae of 88, *Nicrophorus mexicanus*; 89, *N. obscurus*; 90, *N. orbicollis*; 91, *N. pustulatus*.



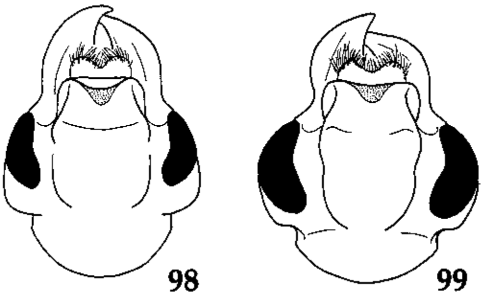
FIGS. 92-93. Left elytron of 92, *Nicrophorus hybridus* and 93, *N. investigator* showing length of row of setae on humerus.



FIGS. 96-97. Caudal view of metatrochanter of males of 96, *Nicrophorus hybridus* and 97, *N. investigator*. Note form of tooth.



FIGS. 94-95. Club of antenna of 94, *Nicrophorus guttula* and 95, *N. obscurus*. Note emargination of penultimate segment.



FIGS. 98-99. Dorsal view of head of 98, *Nicrophorus hybridus* female and 99, *N. investigator* female. Note size of post-ocular bulge. Males of both species are similar to Fig. 98.

KEY TO THE SPECIES OF THIRD INSTAR LARVAE OF *NICROPHORUS* IN NEBRASKA

(modified from Anderson 1982)

1. Abdominal segment 10 with venter unsclerotized at base. Abdominal segment 9 with sclerotization of sternite fragmented (Fig. 102) or else truncated at lateral margins (Figs. 100, 103) 2

1'. Abdominal segment 10 with venter sclerotized at its base. Abdominal segment 9 with sclerotization of the sternite entire, straight along posterior margin, arcuate and emarginate at middle along anterior margin (Fig. 101) 4

2. Abdominal segment 9 with sclerotization of sternite fragmented (Fig. 102) .... ***marginatus* Fabr.**

2'. Abdominal segment 9 with sclerotization of sternite entire and truncated along lateral margins (Figs. 100, 103) 3

3. Abdominal segment 3 with lateral and mid-dorsal spines equal in length (Fig. 103). Ligula without lateral lobes .... ***obscurus* Kirby**

3'. Abdominal segment 3 with mid-dorsal spines about 3 times length of lateral spines (Fig. 100). Ligula with small lateral lobes .. .. ***guttula* Motschulsky**

4. Abdominal segment 10 with y-shaped sclerite on venter in apical half, sclerite extending to bases of innermost pair of apical setae .... ***investigator* Zetterstedt**

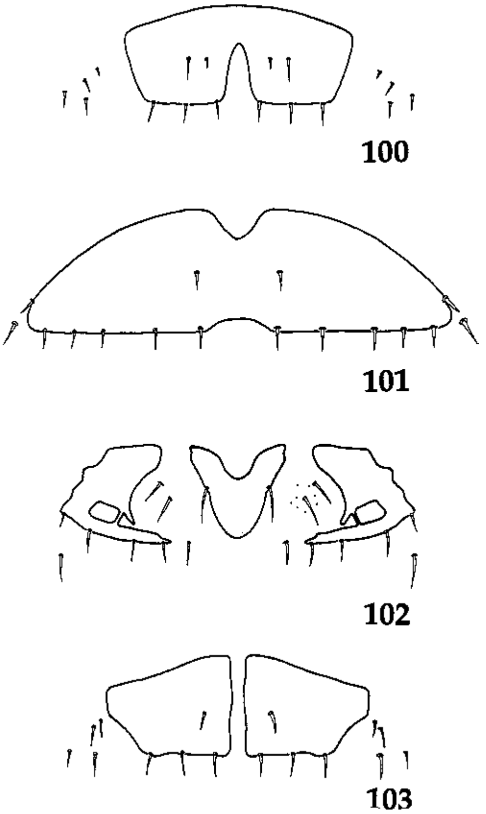
4'. Abdominal segment 10 not sclerotized on venter in apical half............... 5

5. Abdominal segment 1 with lateral and mid-dorsal spines equal in length. Dorsal spines at middle of segments 2-8 at least twice as long as lateral spines. Lateral spines of segments 1-8 short, not exceeding diameter of spiracle ..... ***tomentosus* Weber**

5'. Abdominal segments 1-3 with lateral spines slightly longer than or equal to mid-dorsal spines. Mid-dorsal spines of segments 4-8 at least twice as long as lateral spines. Lateral spines of segments 1-8 long, approximately twice diameter of spiracle on segments 6-8 6

6. Abdominal segment 9 with large lateral spines. Distance between the base of urogomphus and base of lateral spine subequal to length of lateral spine .... ***hybridus* Hatch & Angell**

6'. Abdominal segment 9 with minute lateral spines, appearing as small cones. Distance between base of urogomphus and base of lateral spine at least 4 times length of lateral spine .... ***orbicollis* Say**



FIGS. 100-103. Ventral view of ninth abdominal segment of larva of 100, *Nicrophorus guttula*; 101, *N. investigator*; 102, *N. marginatus*; 103, *N. obscurus* (after Anderson and Peck 1985).

***Nicrophorus americanus* Olivier**
(Figs. 104-107)

Nicrophorus americanus Olivier 1790: 6.
Nicrophorus virginicus Frölich 1792: 123.
Necrophorus grandis Fabricius 1801: 247.

Diagnosis. Length 20.0-35.0 mm. *Head*: Frons orange. Club of antenna orange. *Thorax*: Pronotum orbicular. Lateral and basal margins broad, black. Disc orange; anterior transverse impression distinct. Metasternum with dense, yellow pubescence. Metepim-eron with sparse, light brown setae. *Elytra*: Each elytron with two transverse, orange maculae, maculae not reaching suture. Epipleuron completely orange. *Legs*: Posterior tibia slightly curved. Tarsal empodium quadrisetose.

Distribution. *Nicrophorus americanus* was formerly distributed throughout 35 states and three Canadian provinces in temperate eastern North America from Nova Scotia to western Nebraska and from the upper peninsula of Michigan to Texas (U.S. Fish and Wildlife Service 1991). During this century, it has disappeared from over 90% of its historic range (Lomolino *et al*. 1995) (Fig. 105). It is now known from only five states: on Block Island off the southern coast of Rhode Island (Kozol 1989, 1991), eastern Oklahoma/western Arkansas (U.S. Fish and Wildlife Service 1991), the Sand Hills

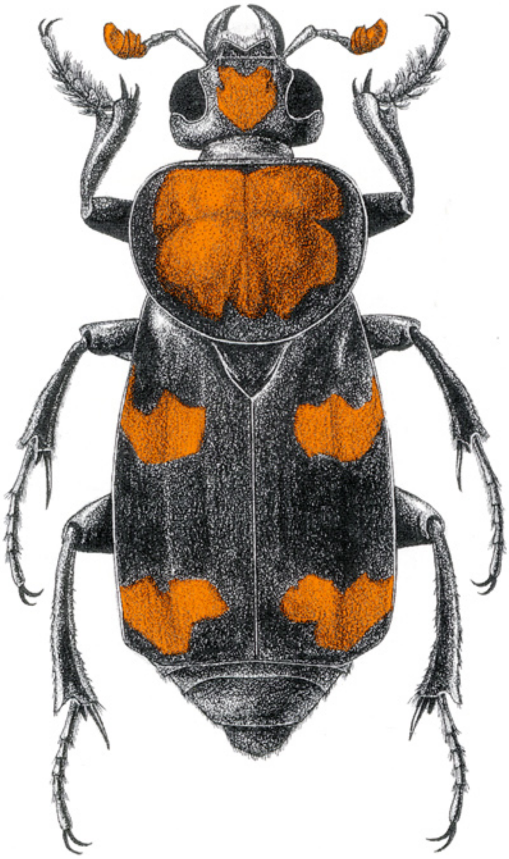


FIG. 104. *Nicrophorus americanus* Olivier.

in north-central Nebraska (Ratcliffe and Jameson 1992, Ratcliffe on-going studies), and, as of late 1995, southern South Dakota (Backlund and Marrone 1995).

Anderson (1982a) suggested that *N. americanus* was an obligate denizen of primary forest, and that the coincident decline of this species and the destruction of this habitat were linked. Anderson suggested that dependence on larger vertebrate carcasses for breeding may have restricted *N. americanus* to ecosystems with deeper soils, hence mature forests with deep, humic soils. Lomolino *et al.* (1995) tested this hypothesis and found it to be false; *N. americanus* exhibited the widest niche breadth of the four most common *Nicrophorus* species present in their studies with the Arkansas and Oklahoma silphids. They found that *N. americanus* was broadly distributed across habitats, and that there was no preference for forest or shrub cover. The extant populations on treeless Block Island in Rhode Island and in the grassland areas of Ft. Chaffee Military Reservation in Arkansas also do not support Anderson's idea nor do the records from relatively treeless west-central Nebraska and South Dakota. Creighton *et al.* (1993) reported beetles occur both in oak-hickory forests and in grasslands in Oklahoma; higher numbers were observed in grasslands than in bottomland forests (where, presumably, foraging flight is severely hampered by denser undergrowth). Considering the broad geographic range formerly occupied by the American burying beetle, it is unlikely that vegetation or soil type were historically limiting (U.S. Fish and Wildlife Service 1991). Today, the American burying beetle seems to be largely restricted to areas most undisturbed by human influence.

In Nebraska, the Sandhills is just such an area, and it is there that the beetles have been recently rediscovered. Gothenburg, Brady, North Platte, the Valentine National Wildlife Refuge, and Jamison are all locales in which beetles have been found during 1994 and 1995. Mark Peyton, Senior District

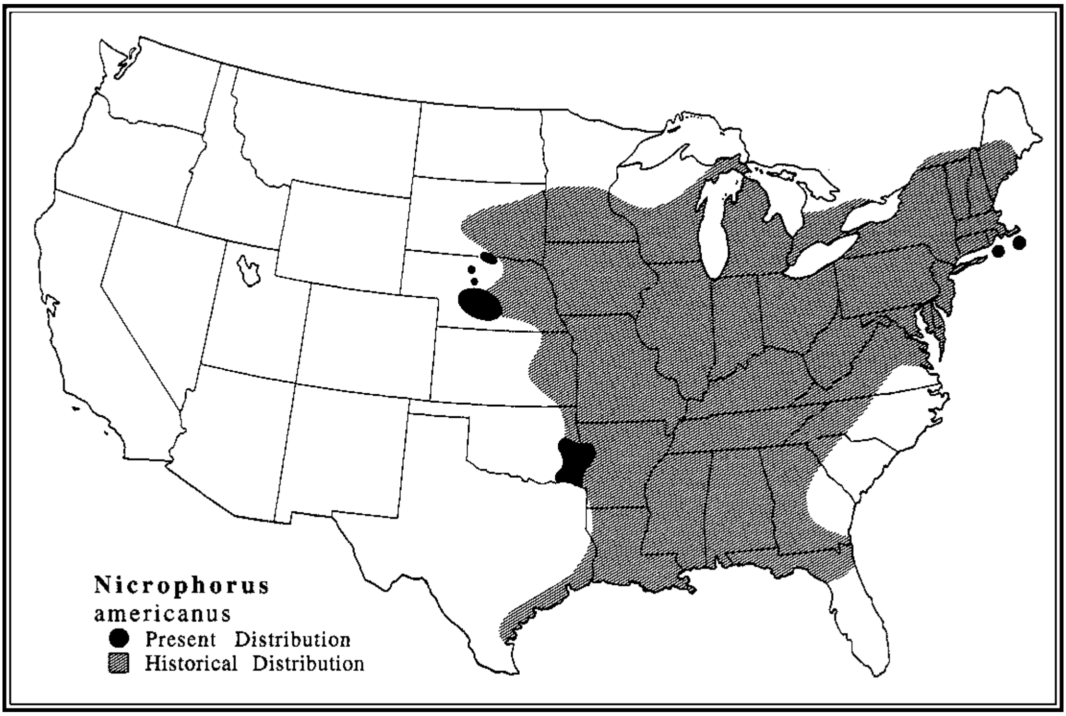


Fig. 105. Present and historical distribution of *Nicrophorus americanus*.

Biologist for the Central Nebraska Public Power and Irrigation District, made the first discovery of a substantial population near Gothenburg in 1994 when he collected 40 specimens (Peyton 1994). During the summer of 1995, Peyton and Jon Bedick (my research assistant who is conducting studies on the Gothenburg population of the American burying beetle) captured more than 300 specimens. Contrary to the earlier belief that the insects were associated with eastern deciduous woodlands, it now seems that carrion availability (appropriate size as well as numbers) is more important than the type of vegetation or soil structure. Habitats in Nebraska where these beetles have been recently found consist of grassland prairie, forest edge, and scrubland (Ratcliffe 1995).

Locality Records (Fig. 106). 332 Nebraska specimens examined or recorded.
ANTELOPE CO. (1): Neligh; CHERRY CO. (9): Valentine National Wildlife Refuge, 8 mi. N Valentine National Wildlife Refuge; CUSTER CO. (1): Milburn; DAWSON CO. (173): Darr Strip Wildlife Management Area, Gallagher Canyon, 6 mi. S Gothenburg , Midway Lake; FRONTIER CO. (2): 3 mi. S Farnam; GOSPER CO. (3): Elwood; KEYA PAHA CO. (4): Jamison, Mills; LANCASTER CO. (3): Lincoln; LINCOLN CO. (146): Box Elder Canyon, Brady, Cottonwood Canyon, 9 mi. S Cozad, Jeffries Canyon, Moran Canyon, Snell Canyon, Wellfleet, North Platte; THOMAS CO. (5): Halsey Forest.

Temporal Distribution. Rangewide: February to September (Peck and Kaulbars 1987). Nebraska: April (1), June (93), July (107), August (96), September (2), October (2). One specimen from the Valentine National Wildlife Refuge was taken on 29 October 1995. It was crawling in the grass, and the temperature was 42°F! Several inches of snow had fallen about two weeks earlier.

Remarks. The American burying beetle, *Nicrophorus americanus*, is the largest (up to 35 mm) carrion beetle in North America. It is easily distinguished from other orange banded species of *Nicrophorus* by its large size and by the *orange pronotal disc*. Males are easily distinguished by the large, orange rectangle on the clypeus whereas females have a small, orange triangle on the clypeus.

Although all the immature stages are known, none appear to have been formally described in the literature. My student, Jon Bedick, and I will be rectifying this by describing the larval stage in the future.

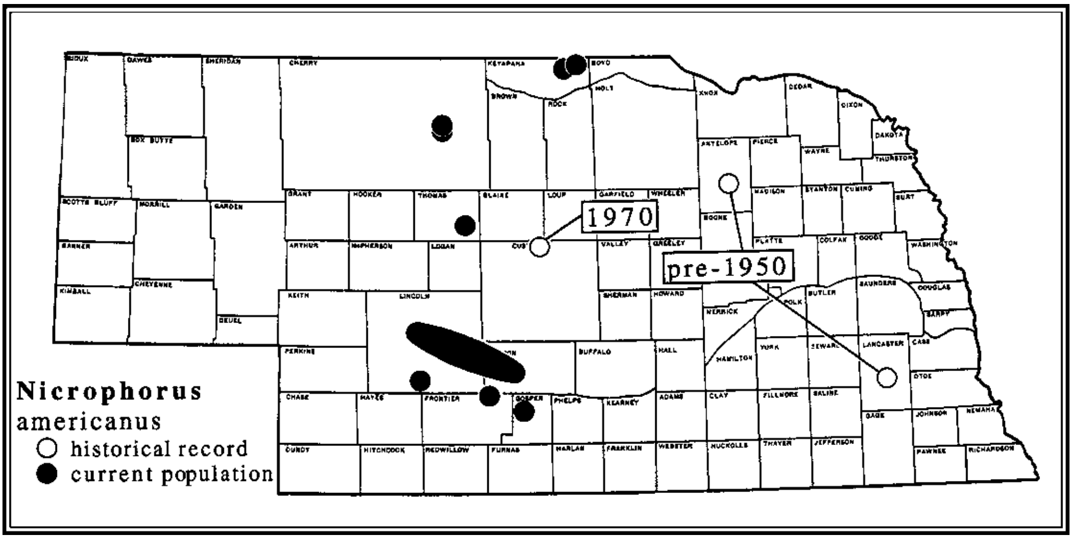


FIG. 106. Nebraska distribution of *Nicrophorus americanus*.

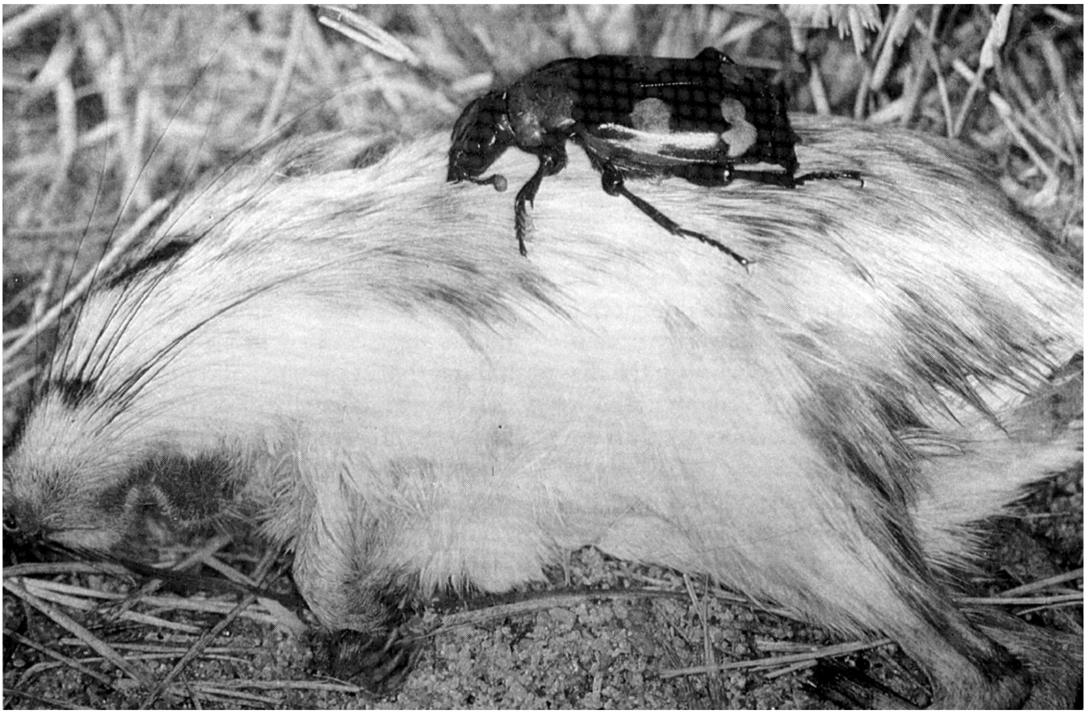


FIG. 107. Adult *Nicrophorus americanus* on a kangaroo rat in west central Nebraska. Photo by M. L. Jameson.

U.S. Fish and Wildlife Service (1991) gives the most complete information regarding the ecology of this species. Adults are active at night (Schweitzer and Master 1987, Peck and Kaulbars 1987), searching for carrion on which to feed and lay eggs; they are occasionally attracted to lights. These beetles seek out large carcasses (up to 300 g) of mostly birds and mammals, although carrion sources between 50 and 200 grams are apparently adequate for rearing their young (Fig. 107) (Schweitzer and Master 1987).

Nicrophorus americanus, like many other *Nicrophorus* species, provides parental care for its young. Kozol, Scott, and Traniello (1988) demonstrated that carrion was prepared by the parents for the larvae in a fashion similar to that described for other *Nicrophorus* species. *Nicrophorus americanus* may cooperate in burying carrion, but individuals of both sexes are capable of burying carrion alone. The carrion is buried, shaved of fur or feathers, rolled into a ball, and treated with anal and oral secretions that favorably alter the decay process. The female lays eggs in the soil near the carcass, and larvae hatch within a few days and move toward the carcass. The larvae are first fed regurgitated food by both the male and female parents. The larvae grow rapidly and are soon able to feed themselves. Approximately two weeks after burial of the carrion, the larvae complete their development and pupate in the soil nearby. Adults emerged from the pupal stage from 48 to 65 days later.

They observed further that, in laboratory studies, reproductive success (measured by total brood weight and by the number of tenerals eclosed) is significantly correlated with carcass size as has also been shown in laboratory broods of *N. orbicollis* (Wilson and Fudge 1984). The negative correlation between the number of adults reared per brood and their average weight suggested that *N. americanus* parents make a tradeoff between a larger number of small offspring or a smaller number of large offspring. The results of this tradeoff may depend on carcass size, prior reproductive history of the parents, and possibly a "prediction" of future reproductive opportunities for the offspring.

In the 1980s, entomologists documented the decreasing abundance of *N. americanus* across North America (Davis 1980, Anderson 1982a, Kozol *et al.* 1988). Since that time, beetles of this species have not been collected or sighted in the United States except for the known and widely separated populations previously mentioned. Because of the precipitous decline in the distribution of this species, it was included in the IUCN Invertebrate Red Book as an endangered species (Wells *et al.* 1983). It was proposed as an endangered species in the United States Federal Register in 1988 (Recce 1988) and was placed on the Endangered Species List on 14 August 1989.

Scott *et al.* (1987) noted that *Nicrophorus* species diversity is highest at northern latitudes, and it is likely that congeneric competition would be greatest where species diversity is highest. Kozol *et al.* (1988) observed that body size appears to be the most important determinant of success in competition for securing carrion; the largest individuals invariably displace smaller burying beetles. Because *N. americanus* are the largest carrion beetles in North America and even the smallest *N. americanus* overlap in size only slightly with the largest *N. orbicollis* and *N. marginatus*, it seems unlikely that *N. americanus* have been outcompeted by other *Nicrophorus* species. However, factors other than size that might affect the outcome of competition remain to be examined.

Kozol *et al.* (1994) studied genetic variation within and between two populations of *N. americanus, one* from Rhode Island (Block Island) and the other from Oklahoma and Arkansas. They used the polymerase chain reaction RAPD-PCR with single short primers to randomly amplify polymorphic DNA. Comparable low levels of genetic variation were observed in both the island and distantly removed mainland populations. These populations were not differentiated, and this suggested that no genetic isolation had yet occurred as a result of the relatively recent geographic isolation.

The prevailing theory explaining the disappearance of the American burying beetle involves habitat fragmentation. Fragmentation of large expanses of natural habitat changed the species composition and lowered the reproductive success of prey species required by the American burying beetle for optimum reproduction. Fragmentation also resulted in an increase in edge habitat that supported and increased the occurrence and density of vertebrate predators and scavengers such as crows, raccoons, foxes, opossums and skunks, all of which compete with burying beetles for available carrion. Fragmented habitats not only support fewer or lower densities of indigenous species that historically may have supported burying beetle populations, but there is also now a great deal more competition for those limited resources among the "new" predator/scavenger community.

Determining a single cause for the decline of the American burying beetle would simplify and facilitate its recovery. Unfortunately, the decline is probably the result of an interplay of several complex factors that may include (1) artificial lighting that decreases populations of nocturnally active insects, (2) changing sources of carrion because of habitat alteration, (3) isolation of preferred habitat because of land use changes, (4) increased edge effect harboring more vertebrate competitors for carrion and (5) the possibility of reduced reproduction because of some genetic characteristic of the species.

The U.S. Fish and Wildlife Service, in cooperation with the scientific community, has formulated a recovery plan that is now being implemented. Surveys at several places in the United States are being conducted to find remnant populations so they can be protected.

Beetles are being reintroduced in Massachusetts from a laboratory colony at Boston University, and other introductions are planned. Life history studies are being conducted in order to determine possible factors responsible for the decline of the species. Similarly, DNA studies are ongoing to ascertain what, if any, genetic differences exist among the known populations. Knowledge of those differences could be important for future breeding programs.

There is now an ongoing, unprecedented loss of species diversity throughout the world as well as a decline in the absolute numbers of organisms from the smallest microorganism to the largest mammal. The current loss of biota has several causes. One is the destruction, conversion, or degradation of entire ecosystems with the consequent loss of entire assemblages of species. Another is the accelerating loss of individual species within communities or ecosystems as a result of habitat disturbance, pollution, and overexploitation. Third and more subtle is the loss of genetic variability. Selective pressures such as habitat alteration, the presence of chemical toxins, or regional climate changes may eliminate some genetically distinct parts of the population yet not cause extinction of the entire species.

Why worry about one insect that most of us have never seen? The World Wildlife Fund perhaps said it best: "All that lives beneath Earth's fragile canopy is, in some elemental fashion, related. Is born, moves, feeds, reproduces, dies. Tiger and turtle dove; each tiny flower and homely frog; the running child, father to the man and, in ways as yet unknown, brother to the salamander. If mankind continues to allow whole species to perish, when does their peril also become ours?"

***Nicrophorus carolinus* (Linnaeus)**

(Figs. 76, 108-109)

Silpha carolina Linnaeus 1771: 530.
Necrophorus mediatus Fabricius 1801: 334.
Necrophorus mystacallis Angell 1912: 307.
Necrophorus carolinus scapulatus Portevin 1923: 142.
Necrophorus carolinus dolosus Portevin 1923: 307.

Diagnosis. Length 13.8-26.6 mm. *Head*: Club of antenna completely orange. *Thorax*: Pronotum cordate, with lateral margins very narrow; basal margin moderately wide; anterior, transverse impression lacking (Fig. 76). Metasternum with dense, yellow pubescence. Metepimeron glabrous. *Elytra*: Epipleuron extremely narrow. Each elytron with two transverse, orange maculae; maculae variably reduced, anterior macula often broken into two spots. *Legs*: Posterior tibia slightly curved.

Distribution. *Nicrophorus carolinus* occurs widely from the central United States south to Texas and Arizona, east along the Gulf Coastal Plain to Florida, and north along the Atlantic Coastal Plain to Virginia (Anderson and Peck 1985, Peck and Kaulbars 1987). In Nebraska, this species is known from the western half of the state. One specimen was collected in Lincoln in 1930, but no additional specimens have been taken since that time.

Locality Records (Fig. 109). 422 Nebraska specimens examined or recorded.
ARTHUR CO. (31): Arapaho Prairie; CHASE CO. (1): Imperial; CHERRY CO. (40): Bloomington, Dewey Lake, Ft. Niobrara National Wildlife Refuge; CUSTER CO. (16): Anselmo, Milburn; DAWES CO. (1): Marsland; DAWSON CO. (1): Gothenburg; DUNDY CO. (1): Haigler; FRONTIER CO. (1): Farnam; GARDEN CO. (1): Oshkosh; KEITH CO. (5): Cedar Point Biological Station; KEYA PAHA CO. (3): Mills, Norden; LANCASTER CO. (1): Lincoln; LINCOLN CO. (172): Box Elder Canyon, Brady, Cottonwood Canyon, Moran Canyon, Sutherland, Wellfleet; McPHERSON CO. (1): Sandhills Ag Lab; NANCE CO. (1): Genoa; SCOTTS BLUFF CO. (10): Mitchell; SHERIDAN CO. (2): Gordon; THOMAS CO. (134): Halsey Forest, Thedford.

Temporal Distribution. Rangewide: March to October (Peck and Kaulbars 1987). Nebraska: May (6), June (15), July (168), August (224), September (8), October (1).

Remarks. *Nicrophorus carolinus* is easily distinguished from all other North American species by the largely *unsculptured* pronotum (lacking a transverse, anterior impression and with very narrow explanate margins laterally) (Fig. 76). The elytral epipleuron is also narrow in comparison to other species of *Nicrophorus*. Anderson and Peck (1985) and Peck and Kaulbars (1987) noted that the elytral maculations are discontinuous and reduced in populations occurring in the north-central states, and nearly all the Nebraska material exhibits this trait.

The immature stages, while undoubtedly known, have not been described in the literature.

Anderson and Peck (1985), Peck and Kaulbars (1987), and Lingafelter (1995) remarked that *N. carolinus* occurs most frequently in areas with loose or sandy soils. The Nebraska specimens seem to corroborate this. Scott *et al*. (1987) found *N. carolinus* equally in fields and forests. Arnett (1946) described briefly how a dead snake was buried by these beetles, and Conley (1982) concluded that this species (at least in New

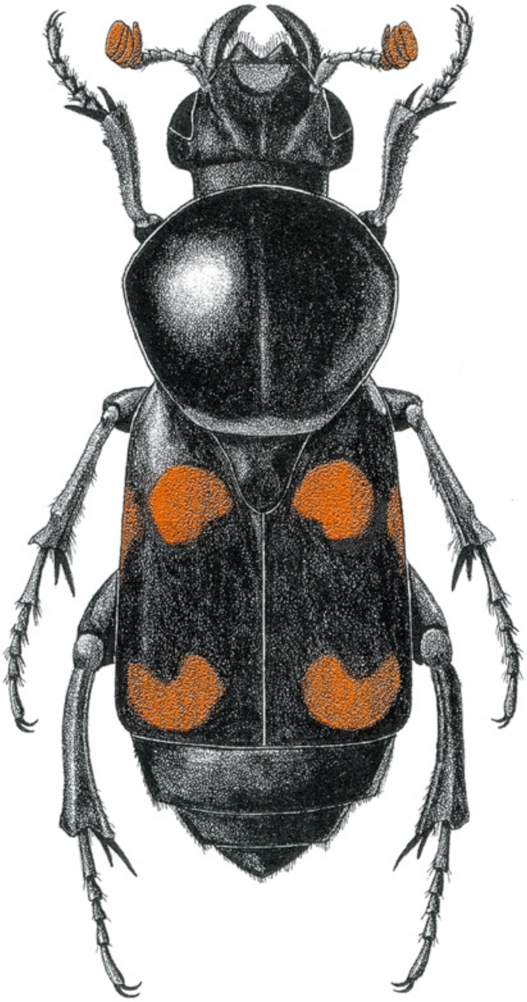


FIG. 108. *Nicrophorus carolinus* (L.).

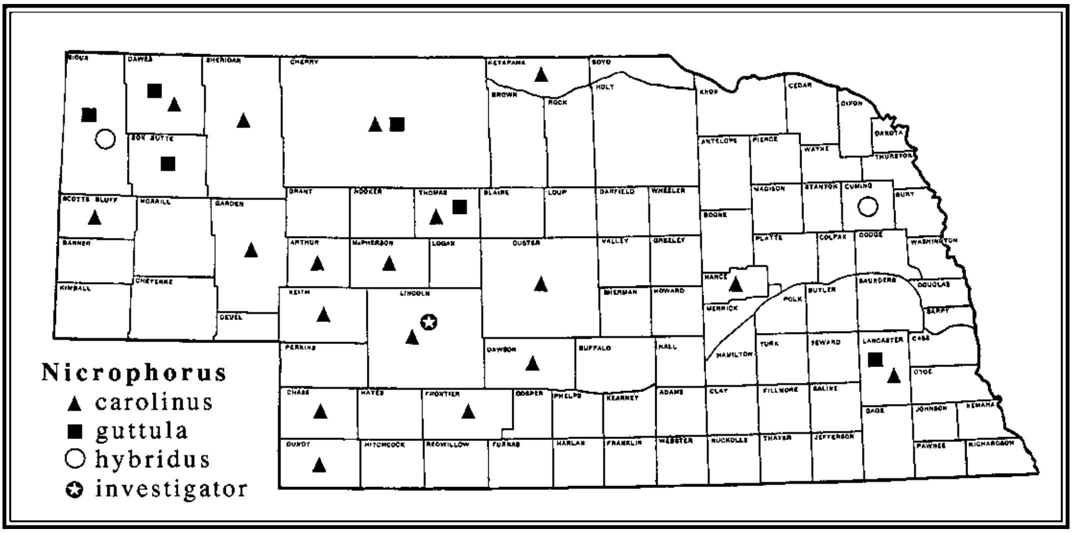


FIG. 109. Nebraska distribution of *Nicrophorus carolinus*, *N. guttula, N. hybridus, N. investigator*.

Mexico) had relatively low efficiency of carrion-locating behavior. I have collected this species commonly in western Nebraska using pitfall traps baited with fish. Otherwise, little is known of its biology.

***Nicrophorus guttula* Motschulsky**
(Figs. 77, 84, 94, 100, 109-110)

Necrophorus guttula Motschulsky 1845: 53.
Necrophorus hecate Bland 1865: 382.
Nicrophorus guttula punctostriatus Pierce 1949: 66.
Nicrophorus hecate immaculosus Hatch 1957: 15.

Diagnosis. Length 12.2-20.0 mm. *Head*: Club of antenna completely orange or with basal segment black or piceous; penultimate segment with outer edge emarginate (Fig. 94). *Thorax*: Pronotum cordate, with lateral margins narrow; basal margin wide; anterior, transverse impression deep, distinct (Fig. 77). Metasternum and metepimeron with dense, yellow pubescence. *Elytra*: Pattern variable; each elytron with two transverse, orange maculae, maculae frequently coalesced near center, anterior macula usually reaching suture, posterior macula not quite extending to suture; or, maculae reduced to two separate bands, or spots, or entirely absent. Epipleuron usually orange with anterior black band of elytra crossing onto it (Fig. 84); in specimens with predominantly black elytra, only extreme base of epipleuron orange, remainder black. *Legs*: Posterior tibia straight. Anterior face of procoxa with long setae on basal half.

Distribution. *Nicrophorus guttula* is widely distributed in the western half of the United States, southern British Columbia, Alberta, and Saskatchewan in Canada, and northern Baja California in Mexico (Anderson and Peck 1985, Peck and Kaulbars 1987). In Nebraska, this species is recorded from the west primarily, but there is a Lincoln record.

Locality Records (Fig. 109). 117 Nebraska specimens examined or recorded.
BOX BUTTE CO. (1): No data; CHERRY CO. (7): Ft. Niobrara National Wildlife Refuge; DAWES CO. (6): Chadron; LANCASTER CO. (1): Lincoln; SIOUX CO. (56): Gilbert Baker Wildlife Area, Glen, Monroe Canyon, Warbonnet Canyon; THOMAS CO. (46): Halsey Forest Reserve.

Temporal Distribution. Rangewide: May to September (Anderson and Peck 1985).

Nebraska: May (8), June (13), July (32), August (15).

Remarks. *Nicrophorus guttula* is similar to *N. obscurus* and is distinguished by the form of the third antennal segment (emarginate as opposed to the deeply emarginate segment of *N. obscurus*) (Figs. 94-95), the variable color of the first antennal segment (always black in *N. obscurus*), and the variably colored elytral epipleuron (always completely orange in *N. obscurus*). All but one of the Nebraska specimens have broad, orange elytral maculae. The single Lincoln specimen has completely black elytra, characteristic of southwestern coastal areas of the United States where melanistic forms occur. *Nicrophorus guttula* also resembles *N. marginatus* but is distinguished from it by the presence, in *N. guttula*, of long setae (as long or longer than those on humerus) on the anterior

FIG. 110. *Nicrophorus guttula* Motschulsky.

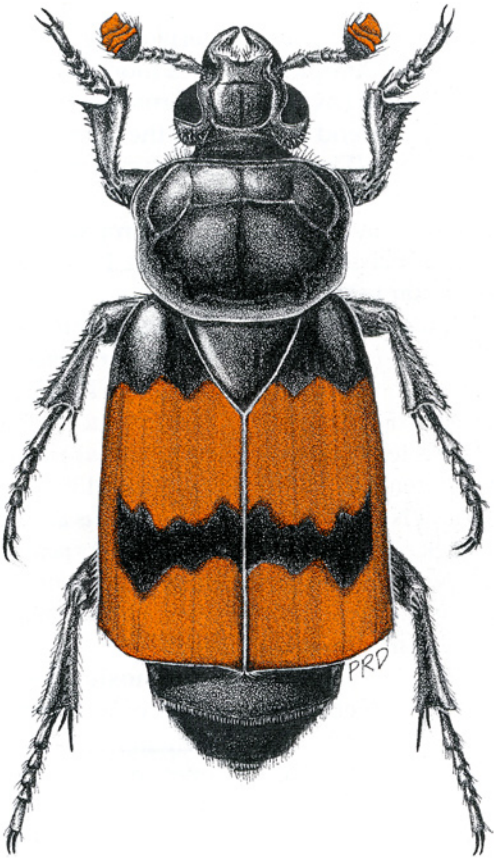


FIG. 111. *Nicrophorus hybridus* Hatch and Angell.

face of the procoxa in the basal half; *N. marginatus* has short setae (shorter than those on humerus).

The larval stage was described by Anderson (1982b), and a brief diagnosis was given by Anderson and Peck (1985).

According to Anderson and Peck (1985), this species exhibits a broad range of ecological tolerances and inhabits dry forests, prairies, and deserts. Adults are diurnal, and they have been collected at human and coyote dung as well as carrion. In our studies done in Nebraska, numerous specimens have been taken using pitfall traps baited with the flesh of mice, rats, and rhinoceros. Yes, rhinoceros.

***Nicrophorus hybridus* Hatch and Angell**

(Figs. 78, 85, 92, 96, 98, 109, 111)

Necrophorus hybridus Hatch and Angell 1925: 216.

Diagnosis. Length 13.8-20.5 mm. *Head*: Club of antenna with basal segment black, remaining three segments orange. Both sexes with small eyes; post-ocular bulge in female a little shorter than length of eye (Fig. 98). *Thorax*: Pronotum with lateral and basal margins wide; anterior transverse impression deep, distinct (Fig. 78). Metasternum with dense, yellow pubescence except for a crescent-shaped, sparsely setose or nearly glabrous area immediately behind margin of each mesocoxa. Metepimeron glabrous. *Elytra*: Each elytron with 2 broad, complete, transverse, orange bands. Humerus covered by field of short, stout setae that extend posteriorly to base of epipleural ridge (Figs. 85, 92). Epipleuron orange (Fig. 85). *Legs*: Anterior face of procoxa with sparse, minute setae on basal half. Posterior tibia straight. Posterior edge of metatrochanter with acute tooth projecting perpendicular from trochanter (Fig. 96).

Distribution. *Nicrophorus hybridus* ranges from the southern part of western Canada southward through the north-central United States to northern Arizona and New Mexico (Anderson and Peck 1985, Peck and Kaulbars 1987). In Nebraska, this species is known from the northern portion of the state only but may also occur in the panhandle.

Locality Records (Fig. 109). 3 Nebraska specimens examined.
CUMING CO. (2): West Point; SIOUX CO. (1): Warbonnet Canyon.

Temporal Distribution. Rangewide: June to September (Peck and Kaulbars 1987). Nebraska: No data.

Remarks. *Nicrophorus hybridus* is best identified by the combination of key characters, especially when trying to separate it from *N. investigator*. *Nicrophorus hybridus* is distinctive because of its broad elytral maculations, crescent-shaped region immediately behind each mesocoxa that is glabrous or sparsely setose, and stout humeral setae that extend to the base of the epipleural ridge. Both the males and females have small eyes. The posterior edge of the metatrochanter in the males has an acute tooth that projects perpendicular to the plane of the trochanter (Fig. 96). Contrast this with Fig. 97 for *N. investigator*.

The larval stage was described by Anderson (1982), and a diagnosis was given by Anderson and Peck (1985).

Little is known of the biology of this species. Peck and Kaulbars (1987) characterized their habitat as prairie, sage steppe, and montane meadow. Adults are probably diurnal and are reproductively active during the summer (Anderson and Peck 1985). Overwintering occurs in the prepupal stage.

Nicrophorus investigator **Zetterstedt**

(Figs. 17, 79, 86, 93, 97, 99, 101, 107, 110)

Necrophorus investigator Zetterstedt 1824: 154.
Necrophorus maritimus Guérin-Méneville 1835: Pl. 17, Fig. 8.
Necrophorus melsheimeri Kirby 1837: 97.
Necrophorus particeps Fischer von Waldheim 1844: 139.
Necrophorus aleuticus Gistel 1848: 190.
Necrophorus pollinctor Mannerheim 1853: 169.
Necrophorus infodiens Mannerheim 1853: 170.
Necrophorus confossor LeConte 1854: 20.

Diagnosis. Length 13.2-18.0 mm. *Head*: Club of antenna with basal segment black, remaining segments orange. Male with small eyes, post-ocular bulge subequal to length of eye. Female with large eyes, post-ocular bulge less than half length of eye (Fig. 99). *Thorax*: Pronotum subquadrate, with lateral and basal margins wide; anterior, transverse depression deep (Fig. 79). Metasternum with dense yellow pubescence, including area just posterior of each mesocoxa. Metepimeron glabrous. *Elytra*: Pattern variable; each elytron with two broad, transverse, orange bands; or anterior band reduced to one, two, or three spots. Epipleuron orange (Fig. 86). *Legs*: Anterior face of procoxa with minute setae on basal half. Posterior tibia straight. Posterior edge of metatrochanter of males with acute tooth *recurving* dorsally (Fig. 97).

Distribution. *Nicrophorus investigator* is widely distributed throughout Canada and Alaska and along the Rocky Mountains to New Mexico and Arizona. It is occasionally found in the northeastern United States. It is also broadly distributed in Europe and Asia (Anderson and Peck 1985, Peck and

Kaulbars 1987). In Nebraska, this species is known only from North Platte, and this locality represents a NEW STATE RECORD. These specimens were prepared by me from samples collected in a stand-alone light trap in 1966. Unfortunately, no specimens have been collected since 1966 even though recent trapping programs have been conducted both to the immediate east and west of North Platte.

Locality Records (Fig. 109). 2 Nebraska specimens examined.
LINCOLN CO. (2): North Platte.

Temporal Distribution. Rangewide: May to October (Peck and Kaulbars 1987). Nebraska: July (2).

Remarks. *Nicrophorus investigator* is most reliably identified by the combination of key characters, but especially by the length of the field of small setae on the humerus when differentiating it from *N. hybridus*. Although variation in elytral pattern is extensive (with darker forms occurring in the northwestern coastal populations), all the specimens from Nebraska, Wyoming, and Colorado have broad bands of orange on the elytra.

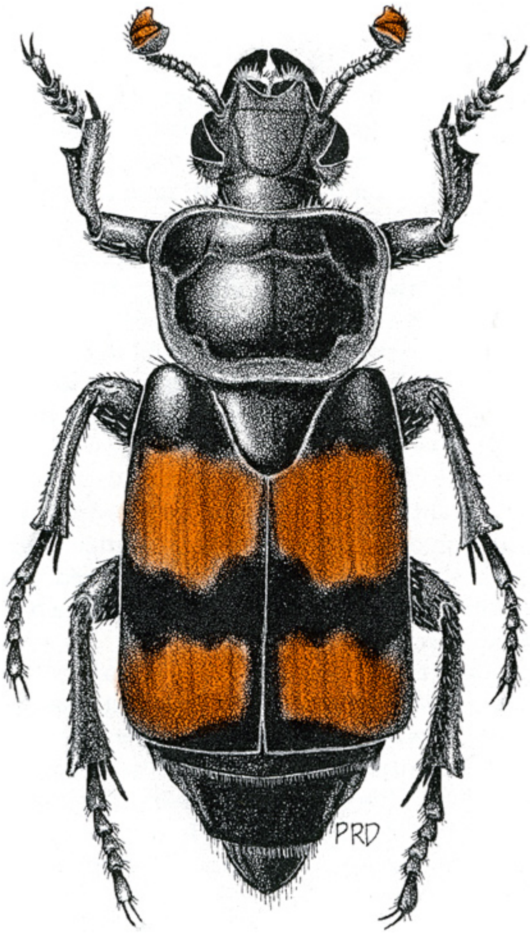


Fig. 112. *Nicrophorus investigator* Zetterstedt.

The larval stage was described by Anderson (1982) and a brief synopsis was given by Anderson and Peck (1985).

Most of the work on the biology of this species has been conducted by Katakura and Fukuda (1975) in Japan, Pukowski (1933) and Mroczkowski (1949) in Europe, and Smith and Heese (1995) in the United States. According to these authors, adults appear in June or July and begin reproductive activities. Their later emergence in the year is reflective of their more northerly distribution or at greater elevations where summer-like conditions are brief. Overwintering occurs in the prepupal stage.

Smith and Heese (1995), working at 2,900 m in the Colorado Rockies, found a distinct preference by these beetles for particular carcasses based on size. They rejected carcasses less than 16 g or larger than 55 g. The beetles apparently "weigh" carcasses to determine size by crawling under them and experimentally lifting them while on their backs beneath the carcass. Results from this study indicated that choice of a carcass of a certain minimum size had important fitness consequences because beetles that buried small carcasses did not raise any larvae, and average brood mass was larger on larger carcasses.

Smith and Heese (1995) also found that carcasses located in shady, hence cooler, habitats were not utilized as frequently as those in sunnier habitats. Larvae reared in shaded conditions developed more slowly. While this could cause negative fitness for the larvae (if they don't develop sufficiently before winter), these authors propose that slowed development may have negative effects on the total reproductive output of brood-tending parents by reducing the number of broods they can rear in a season. Hines and Smith (1995), as part of the same study, found that the average elytral length was significantly longer at higher elevations in the Rocky Mountains.

Lane and Rothschild (1965) reported that *N. investigator* is a very good visual and sound mimic of the bumblebees *Bombus lucorum* (L.). Beetles presumably acquire some degree of protection from predators by mimicking a large, stinging bee.

***Nicrophorus marginatus* Fabricius**

(Figs. 65-66, 80, 87, 102, 113-114)

Necrophorus marginatus Fabricius 1801: 334.
Necrophorus requiescator Gistel 1848: 190.
Necrophorus montezumae Matthews 1888: 92.
Necrophorus marginatus cordiger Portevin 1924: 84.
Nicrophorus guttula labreae Pierce 1949: 63.
Nicrophorus mckittricki Pierce 1949: 66.
Nicrophorus obtusiscutellum Pierce 1949: 67.
Nicrophorus investigator latifrons Pierce 1949: 67.

Diagnosis. Length 13.9-22.0 mm. *Head*: Club of antenna completely orange. *Thorax*: Pronotum subtrapezoidal, widest anteriorly, with lateral margins narrow; basal margin wide; anterior, transverse impression present, occasionally only weakly indicated (Fig. 80). Metasternum with dense, yellow pubescence. Metepimeron with dense, yellow pubescence. *Elytra*: Each elytron with two transverse, orange maculae, anterior orange macula nearly always reaching median suture while posterior macula does not, both maculae usually joined laterally; maculae rarely reduced to spots. Epipleuron completely orange (Fig. 87). *Legs*: Posterior tibia slightly curved. Anterior face of procoxa with short setae on basal half.

Distribution. *Nicrophorus marginatus* occurs throughout most of the United States (excluding Florida and northwestern Washington), across southern Canada, and into northern Mexico (Anderson and Peck 1985, Peck and Kaulbars 1987). It is the most widely distributed of the North American *Nicrophorus*. It is found across the entire state of Nebraska.

Locality Records (Fig. 114). 5,290 Nebraska specimens examined or recorded.

ADAMS CO. (30): No data; ARTHUR CO. (15): Arapaho Prairie; BOX BUTTE CO. (4): No data; BUFFALO CO. (6): Elm Creek, Kearney; BUTLER CO. (1): David City; CASS CO. (260): Plattsmouth; CHASE CO. (3): Enders Reservoir; CHERRY CO. (77): Dewey Lake, Sparks, Valentine, Ft. Niobrara National Wildlife Refuge; CHEYENNE CO. (1): Sidney; CLAY CO. (2): No data; CUMING CO. (1): West Point; CUSTER CO. (491): Anselmo, Milburn, Sargent; DAKOTA CO. (1): South Sioux City; DAWES CO. (9): Ash Creek, Chadron; DIXON CO. (5): Aowa Creek, Concord; DUNDY CO. (3): Haigler, Republican River east of Benkelman; FILLMORE CO. (1): Fairmont; FRANKLIN CO. (3): Bloomington; FRONTIER CO. (597): Curtis, Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GAGE CO. (1): Beatrice; GOSPER CO. (274): Elwood Reservoir, Gothenburg, Lexington, Smithfield; GREELEY CO. (2): Greeley; HALL CO. (54): Alda, Grand Island; JEFFERSON CO. (33): No data; JOHNSON CO. (4): No data; KEITH CO. (21): Cedar Point Biological Station; KEYA PAHA CO. (7): Mills, Norden; KNOX CO. (9): Bazile Creek Wildlife Management Area, Niobrara; LANCASTER CO. (38): Lincoln, Sprague; LINCOLN CO. (3,332): Box Elder Canyon, Brady, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; MERRICK CO. (1): Central City; NANCE CO. (6): Genoa; OTOE CO. (14): Nebraska City; PAWNEE CO. (5): No data; PHELPS CO. (231): Bertrand; PIERCE CO. (1): No data; POLK CO. (10): No data; RED WILLOW CO. (1): McCook; RICHARDSON CO. (1): Verdon; SALINE CO. (4): Swan Creek; SARPY CO. (1): Bellevue; SAUNDERS CO. (2): Wahoo; SCOTTS BLUFF CO. (43): Mitchell, Scottsbluff; SHERMAN CO. (1): Loup City; SIOUX CO. (59): Gilbert Baker

FIG. 113. *Nicrophorus marginatus* Fabr.

Wildlife Area; THOMAS CO. (60): Halsey Forest Reserve; WASHINGTON CO. (2): Ft. Calhoun; WEBSTER CO. (1): Red Cloud; YORK CO. (1): No data.

Temporal Distribution. Rangewide: February to October (Peck and Kaulbars 1987). Nebraska: April (5), May (11), June (230), July (1,944), August (2,221), September (296), October (270), November (3). The large numbers in July and August reflect, in part, a concerted trapping program in Lincoln County in 1995.

Remarks. *Nicrophorus marginatus* cannot be separated from *N. obscurus* and *N. guttula* based on overall appearance. It can be separated from these other two species because it has short setae (shorter than those on humerus) on the anterior face of the procoxa in the basal half; the two other species have long setae (as long or longer than those on humerus).

The larval stage was described by Anderson (1982b), and a brief larval diagnosis was given by Anderson and Peck (1985).

Adults become active in the spring when the weather is consistently warm; most adults become active in June in Nebraska. Reproduction occurs in June and July, and the new generation of adults appears in July and August. Overwintering is in the adult stage. According to Peck and Kaulbars (1987), most collections have been from open fields, montane meadows, prairies, and desert woodlands. This species is abundant in the grasslands of western Nebraska. Lomolino *et al.* (1995) and Lingafelter (1995) demonstrated that this species shows a strong preference for meadows or open, grassy areas.

This species is probably diurnal even though some specimens have been taken at lights. I and my students have taken *N. marginatus* in large numbers using baited pitfall traps. Clark (1895) observed extensive feeding by adults on fly larvae at carrion.

Nicrophorus mexicanus Matthews
(Figs. 81, 88, 114-115)

Necrophorus mexicanus Matthews 1888: 91.

Diagnosis. Length 14.0-20.8 mm. *Head*: Club of antenna with basal segment black, remaining segments orange. *Thorax*: Pronotum subquadrate, both anterior and posterior angles rounded. Lateral

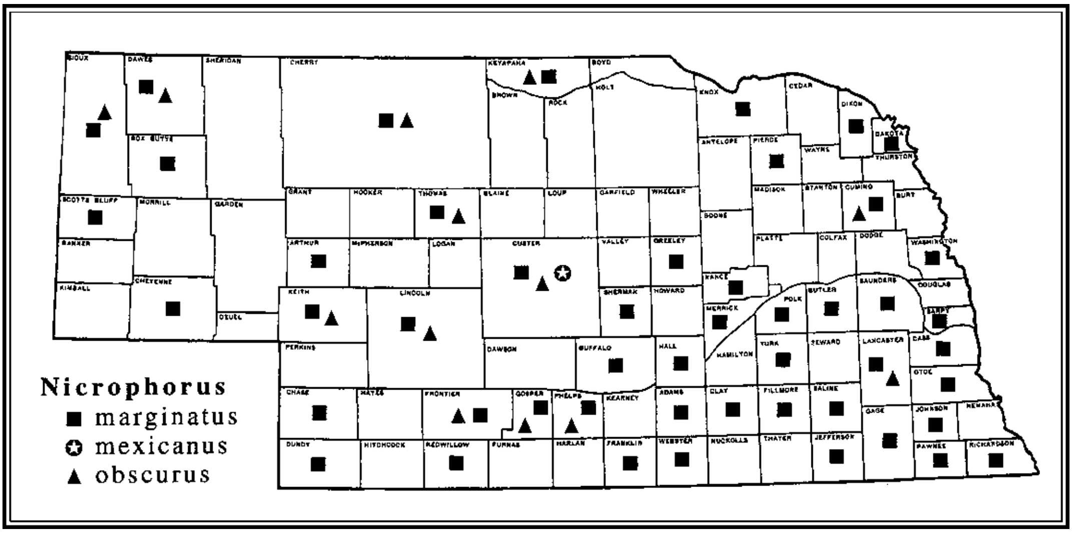


FIG. 114. Nebraska distribution of *Nicrophorus marginatus*, *N. mexicanus*, *N. obscurus*.

and basal margins wide; anterior transverse impression deep, distinct (Fig. 81). Metasternum with dense, dark brown pubescence. Metepim-eron with small, central patch of dark brown setae. *Elytra*: Each elytron with two transverse, orange maculae, anterior orange macula joined at suture, posterior macula long but not quite reaching suture. Epipleuron orange with anterior black band crossing onto it (Fig. 88). *Legs*: Posterior tibia straight. Anterior face of procoxa with minute setae on basal half.

Distribution. *Nicrophorus mexicanus* was formerly known from the southern Rocky Mountain states southward through Mexico to El Salvador (Peck and Kaulbars). The specimen listed below from central Nebraska represents a NEW STATE RECORD and represents a range extension from the closest known current collection localities in central Colorado.

Locality Records (Fig. 114). 1 Nebraska specimen examined.
CUSTER CO. (1): 17 mi. E. Anselmo.

Temporal Distribution. Rangewide (including Mexico): All months. United States: May to October (Peck and Kaulbars 1987). Nebraska: July (1).

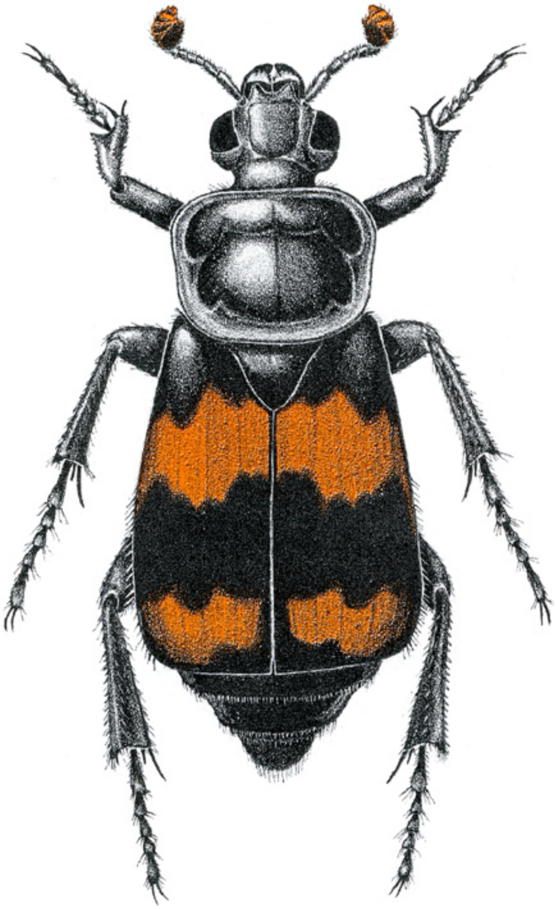


FIG. 115. *Nicrophorus mexicanus* Matthews.

Remarks. *Nicrophorus mexicanus* adults are most easily distinguished by the dark setae on the metepimeron, subquadrate pronotum, and bicolored epipleuron.

The larval stage has apparently not been described.

Peck and Anderson (1985) recorded this species from habitats ranging from semi-arid and open thorn scrub to moist, closed-canopy cloud forests. The Nebraska specimen was collected in a baited pitfall trap from an area of scrub vegetation in the floodplain of the Loup River.

***Nicrophorus obscurus* Kirby**

(Figs. 89, 95, 103, 114, 116)

Nicrophorus obscurus Kirby 1837: 97.
Necrophorus melsheimeri LeConte (not Kirby) 1853: 275.

Diagnosis. Length 13.1-24.0 mm. *Head*: Club of antenna with basal segment black, apical three segments orange; penultimate segment with outer edge deeply emarginate (Fig. 89). *Thorax*: Pronotum subtrapezoidal, widest anteriorly, with the lateral margins

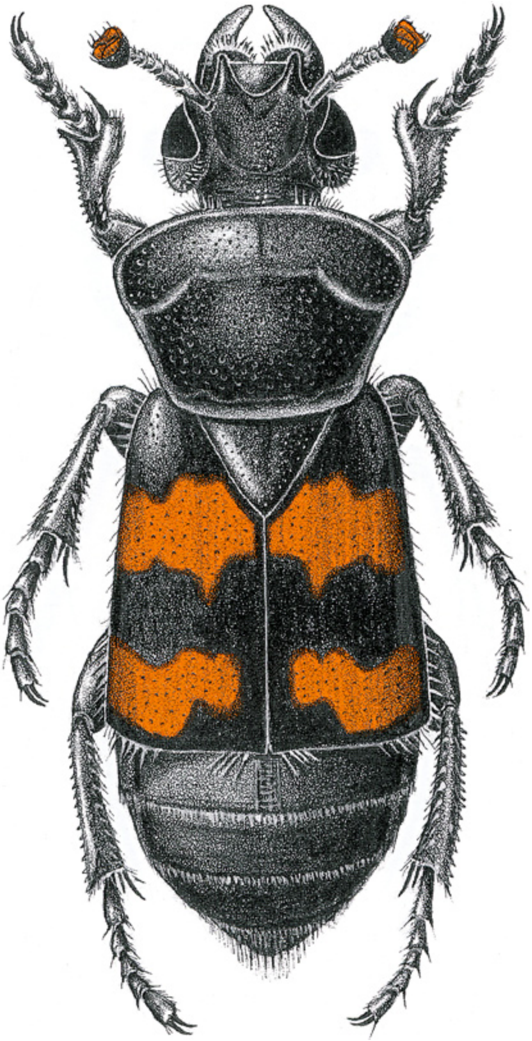


Fig. 116. *Nicrophorus obscurus* Kirby.

narrow; basal margin wide; anterior, transverse impression present (as in Fig. 80). Metasternum and metepimeron with dense, yellow pubescence. *Elytra*: Each elytron with two transverse, orange maculae, anterior orange macula nearly always reaching suture, posterior macula not quite extending to suture; surface with sparse, short, slender, decumbent, black setae. Epipleuron completely orange (Fig. 89) *Legs*: Posterior tibia slightly curved. Anterior face of procoxa with long setae on basal half.

Distribution. *Nicrophorus obscurus* occurs from the southern Canadian prairie provinces into the north-central United States as far south as Nebraska and northern Colorado (Anderson and Peck 1985, Peck and Kaulbars 1987). Nebraska records indicate this species is found statewide.

Locality Records (Fig. 114). 382 Nebraska specimens examined or recorded.
CHERRY CO. (19): Ft. Niobrara National Wildlife Refuge; CUMING CO. (1): West Point; CUSTER CO. (5): Sargent; DAWES CO. (7): Pine Ridge area; FRONTIER CO. (42): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GOSPER CO. (10): Elwood Reservoir, Lexington, Smithfield; KEITH CO. (1): Cedar Point Biological Station; KEYA PAHA CO. (1): Carns; LANCASTER CO. (1): Lincoln; LINCOLN CO. (290): Box Elder Canyon, Cottonwood Canyon, Moran Canyon, Sutherland, Wellfleet; PHELPS CO. (1): Bertrand; SIOUX CO. (1): Harrison; THOMAS CO. (3): Halsey Forest Reserve.

Temporal Distribution. Rangewide: March to September (Peck and Kaulbars 1987). Nebraska: June (3), July (180), August (193), September (4), October (1).

Remarks. The deeply emarginate outer edge of the third antennal segment (Fig. 85) is particularly characteristic of this species. *Nicrophorus guttula* is similar in appearance, but has a simply emarginate third antennal segment (Fig. 84). *Nicrophorus obscurus* also closely resembles *N. marginatus* but is distinguished from it by the presence, in *N. obscurus*, of long setae on the anterior face of the procoxa in the basal half; *N. marginatus* has short setae.

The larval stage was described by Anderson (1982b), and a brief diagnosis was given by Anderson and Peck (1985).

Anderson and Peck (1982) observed that this is a diurnal prairie species, and that adults have been collected at carrion and human feces. I have taken this species in moderate numbers in western Nebraska using baited pitfall traps.

***Nicrophorus orbicollis* Say**

(Figs. 82, 90, 117-118)

Necrophorus orbicollis Say 1825: 177.
Necrophorus halli Kirby 1837: 98.
Necrophorus quadrisignatus Laporte 1840: 1.

Diagnosis. Length 14.8-23.0 mm. *Head*: Club of antenna with basal segment black, remaining segments orange. *Thorax*: Pronotum suborbicular, with lateral and basal margins broad; anterior, transverse impression deep, distinct (Fig. 82). Surface usually with setae along margins and in transverse impression laterally, these sometimes worn away. Metasternum with dense, light brown pubescence. Metepimeron with sparse, dark brown setae. *Elytra*: Elytra with long setae over entire surface, setae occasionally abraded away and present only along lateral margins (best seen in oblique lighting). Each elytron with an anterior, transverse, orange macula and a posterior, orange spot; markings not reaching suture. Epipleuron black; epipleural ridge extending anteriorly only to level of apex of scutellum (Fig. 90). *Legs*: Posterior tibia straight. Anterior face of procoxa with short setae on basal half.

Distribution. *Nicrophorus orbicollis* is widely distributed in the eastern half of North America to southeastern Saskatchewan to eastern Texas (Anderson and Peck 1985, Peck and Kaulbars 1987). This species occurs throughout Nebraska.

Locality Records (Fig. 118). 8,824 Nebraska specimens examined or recorded. ADAMS CO. (2): No data; ANTELOPE CO. (1): Clearwater; BUFFALO CO. (28): Gibbon, Kearney; CASS CO. (232): Plattsmouth, South Bend; CHASE CO. (44): Enders Reservoir; CHERRY CO. (98): Ft. Niobrara Wildlife Refuge; COLFAX CO. (1): No data; CUMING CO. (1): West Point; CUSTER CO. (301): Anselmo, Ansley, Milburn, Sargent; DAWES CO. (57): Ash Creek, Chadron; DAWSON CO. (26): Cozad, Gothenburg, Lexington; DIXON CO. (316): Aowa Creek; DUNDY CO. (30): 1.5 mi. SW Max, Republican River E of Benkelman; FRANKLIN CO. (83): Franklin; FRONTIER CO. (727): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GAGE CO. (38): Wolf-Wildcat Creek; GOSPER CO. (299): Elwood Reservoir, Gothenburg, Lexington, Smithfield; GRANT CO. (2): No data; HALL CO. (138): Alda,

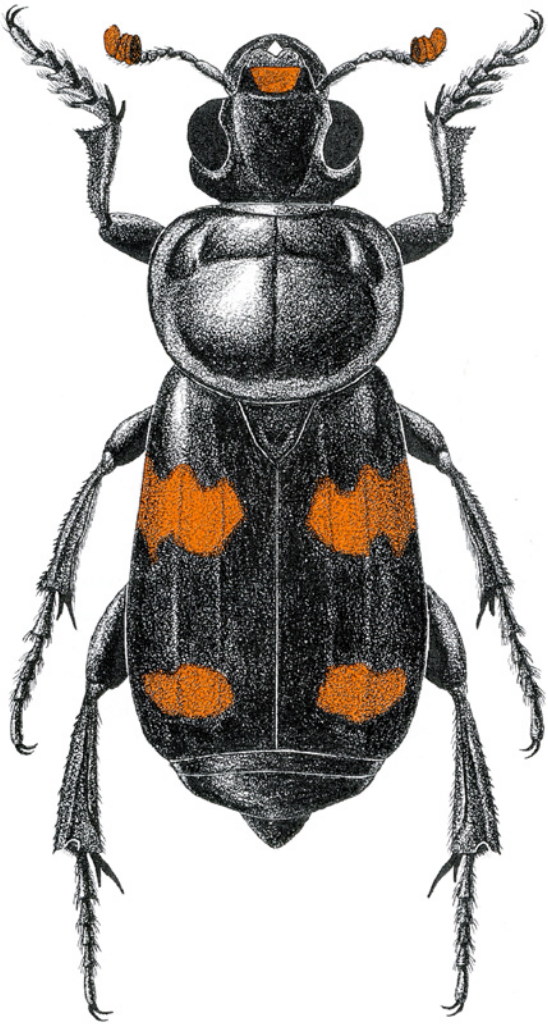


FIG. 117. *Nicrophorus orbicollis* Say.

Mormon Island; HARLAN CO. (17): Republican River S of Orleans; HOLT CO. (1): Spencer; HOOKER CO. (1): Mullen; JEFFERSON CO. (16): No data; JOHNSON CO. (75): No data; KEITH CO. (61): Cedar Point Biological Station; KEYA PAHA CO. (7): Mills, Norden; KNOX CO. (45): Bazile Creek Wildlife Management Area; LANCASTER CO. (64): Lincoln, Reller Prairie, Sprague; LINCOLN CO. (1,142): Brady, Box Elder Canyon, Cottonwood Canyon, Moran Canyon, North Platte, 2 mi. S Sutherland, Wellfleet; McPHERSON CO. (1): No data; NUCKOLLS CO. (1): No data; OTOE CO. (476): Nebraska City; PAWNEE CO. (706): No data; PHELPS CO. (27): Bertrand; PLATTE CO. (2): Columbus; RICHARDSON CO. (2): Indian Cave State Park; SALINE CO. (431): Swan Creek; SARPY CO. (612): Fontenelle Forest, Schramm Park; SAUNDERS CO. (680): Mead, Wahoo; SIOUX CO. (35): Gilbert Baker Wildlife area, Monroe Canyon; THOMAS CO. (165): Halsey Forest Reserve; WASHINGTON CO. (629): Ft. Calhoun.

Temporal Distribution. Rangewide: February to October (Peck and Kaulbars 1987). Nebraska: May (58), June (432), July (2,349), August (5,188), September (597), October (214).

Remarks. *Nicrophorus orbicollis* is the most abundant and commonly encountered species of *Nicrophorus* in the state. The long, elytral setae are diagnostic for this species, but they are occasionally abraided away and so caution should be used when identifying specimens. It most closely resembles *N. mexicanus*, but *N. mexicanus* has a bicolored epipleuron whereas *N. orbicollis* has a black epipleuron.

The larval stage was described by Anderson (1982), and a brief larval diagnosis was provided by Anderson and Peck (1985).

Shubeck (1984a, 1993) and Lomolino *et al.* (1995), in studies in New Jersey, Oklahoma and Arkansas, demonstrated that this species seems to show a preference for forested areas. Contrary to these studies, this species is found abundantly in the grasslands of western Nebraska as well as the forested areas of eastern Nebraska. Lingafelter (1995) observed a similar pattern in Kansas. *Nicrophorus orbicollis* is the most commonly collected species in eastern North America (Peck and Kaulbars 1987) and seems to be the most abundant species of *Nicrophorus* in Nebraska. Trumbo (1990d) reported that they are the dominant burying beetle on small carcasses in the woodlands of the eastern United States. Shubeck (1971) reported they are nocturnal and are often taken at light traps; this has been my experience also.

Adults overwinter and become active in the spring at which time reproduction takes place. *Nicrophorus orbicollis* is successful on a higher proportion of carcasses of all sizes and gains substantial benefits by excluding rivals; it rarely tolerates consexuals in the nest (Trumbo 1995). Generally, the male parent remains in the nest 5-12 days and the female parent for 10-15 days (Scott and Traniello 1990b, Trumbo 1991). In another study (under natural conditions in the field), Scott (1990) found that *N. orbicollis* males remained with the brood a mean of 9.5 days and females 17.2 days; however, 22% of the broods were reared by single females. In her experiments examining male assistance in guarding against conspecifics, 87% of the males and 93% of the females were still present after eight days; females normally remain with the brood longer than eight days post-burial. This long period of parental care represents a considerable investment for an animal with a reproductive span of two months or less, especially in view of the fact that both parents are foregoing additional reproductive success while they remain with their current brood. Larvae completed development about seven days after hatching and dispersed to pupate in the soil, emerging as adults about 30 days later (Scott and Traniello 1990b). Adults of the new generation are found in late July and early August in Nebraska. Wilson *et al.* (1984) suggested that *N. orbicollis* appear to enter *reproductive* diapause in late summer before temperatures become too cold to find carrion. This is an adaptation to season length since only individuals that have enough time to reach the adult stage can successfully overwinter.

Peck and Kaulbars (1987) noted that they have been taken on human and carnivore dung and on rotting fruits as well as on carrion. I and my students have taken them in large numbers in Nebraska in pitfall traps baited with rotting fish, beef liver, and chicken hearts and gizzards. Adults have been observed to feed on maggots (Clark 1895, Steele 1927).

Pronotum subquadrate, with lateral and basal margins wide; anterior, transverse impression distinct (Fig. 83). Metasternum with sparse, light brown pubescence. Metepim-eron glabrous. *Elytra*: Each elytron with a small to medium, orange spot on lateral edge at about middle and two small to medium-sized spots near apex; elytra lacking long, distinctive setae. Epipleuron entirely black; epipleural ridge extending anteriorly to near level of base of scutellum (Fig. 91). *Legs*: Posterior tibia straight. Anterior face of procoxa glabrous on basal half.

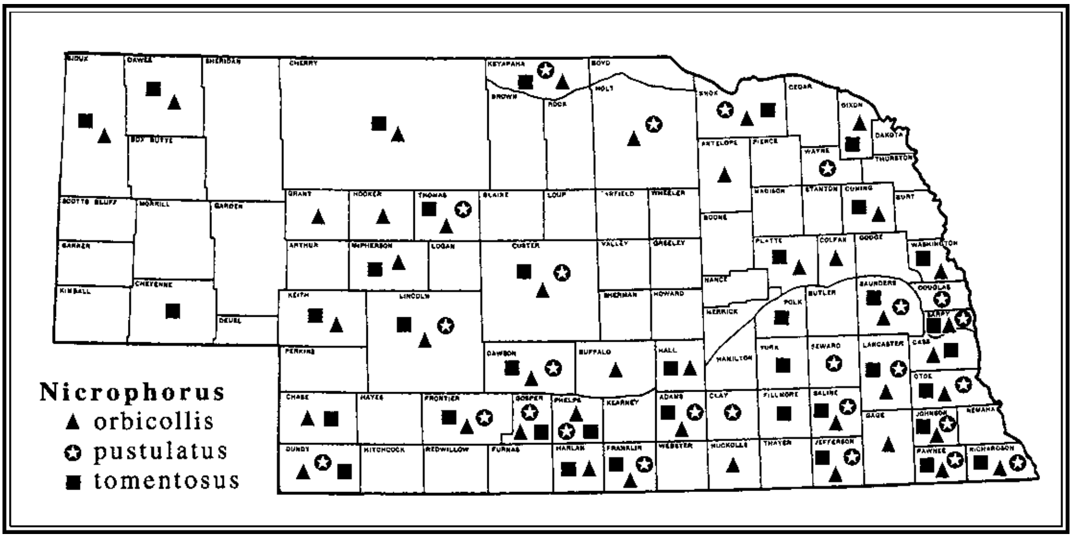


FIG. 118. Nebraska distribution of *Nicrophorus orbicollis*, *N. pustulatus, N. tomentosus*.

Nicrophorus pustulatus **Herschel**

(Figs. 83, 91, 118-119)

Necrophorus pustulatus Herschel 1807: 271.
Necrophorus bicolon Newman 1838: 385.
Necrophorus tardus Mannerheim 1853: 170.
Necrophorus marginatus fasciatus Portevin 1924: 86.
Necrophorus marginatus unicolor Portevin 1924: 86.

Diagnosis. Length 14.0-22.2 mm. *Head*: Club of antenna with basal segment black, remaining three segments orange. *Thorax*:

Distribution. *Nicrophorus pustulatus* is found from southern Canada east of the Rocky Mountains and in the eastern half of the United States from North Dakota to eastern Texas (Anderson and Peck 1985, Peck and Kaulbars 1987). This species is known from the eastern two-thirds of Nebraska; collecting records are lacking for the panhandle.

Locality Records (Fig. 118). 487 Nebraska specimens examined or recorded. The large number for Saunders County is the result of an intensive pitfall survey during the summer of 1995.

ADAMS CO. (2): No data; CLAY CO. (1): No data; CUSTER CO. (5): Anselmo, Milburn; DAWSON CO. (4): No data; DOUGLAS CO. (1): Omaha; DUNDY CO. (1): Republican River E of Benkelman; FRANKLIN CO. (3): Franklin; FRONTIER CO. (11): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GOSPER CO. (3): 4 mi. S. Gothenburg, Lexington; HALL CO. (13): Alda, Mormon Island; HOLT CO. (1): Spencer dam; JEFFERSON CO. (20): Fairbury; JOHNSON CO. (10): No data; KEYA PAHA CO. (19): Mills, Norden; KNOX CO. (1): Bazile Creek Wildlife Management Area; LANCASTER CO. (5): Lincoln, Sprague; LINCOLN CO. (47): Box Elder Canyon, Brady, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; OTOE CO. (1): No data; PAWNEE CO. (7): No data; PHELPS CO. (7): Bertrand; RICHARDSON CO. (11): Indian Cave State Park; SALINE CO. (8): Swan Creek; SARPY CO. (6): Bellevue; SAUNDERS CO. (295): Wahoo; SEWARD CO. (1): Garland; THOMAS CO. (4): Halsey Forest Reserve; WAYNE CO. (1): Wayne.

Temporal Distribution. Rangewide: March to October (Peck and Kaulbars 1987). Nebraska: April (1), May (3), June (42), July (39), August (402), September (3), October (3).

Remarks. *Nicrophorus pustulatus* is easily recognized by its primarily black color and the presence of small elytral spots rather than

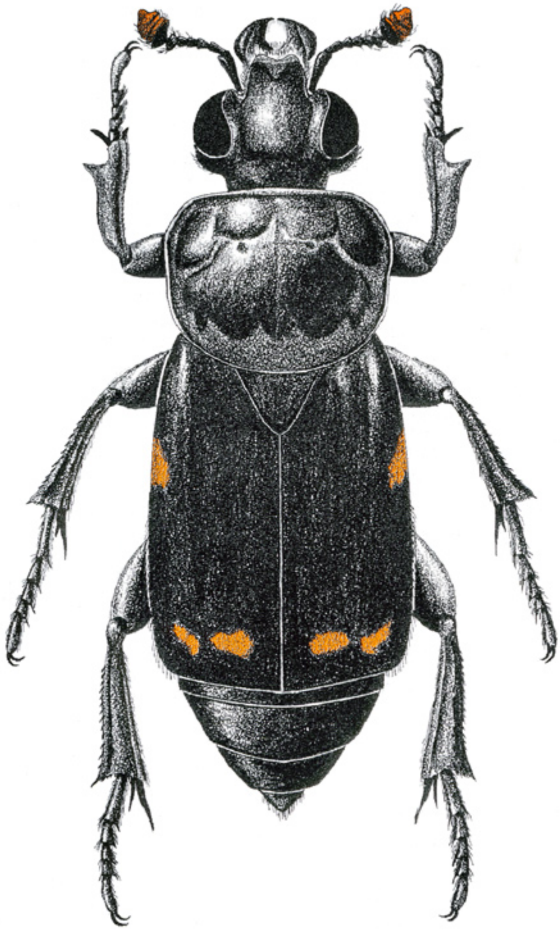


FIG. 119. *Nicrophorus pustulatus* Herschel.

transverse bands. Some specimens of *N. orbicollis* may also have small spots, but then they also possess elytral setae whereas *N. pustulatus* do not.

The larval stage remains undescribed.

Wilson and Knollenberg (1984) and Anderson and Peck (1985) observed that *N. pustulatus* is one of the rarer species of *Nicrophorus* and that it may, in fact, have a different natural history than other species as exemplified by its rarity in pitfall traps, absence from mice carcasses, and common occurrence at lights. Trumbo (1992) observed that *N. pustulatus* is a formidable brood parasite and produces the largest clutches (nearly 200 young) of any *Nicrophorus* species. They are routinely able to parasitize the broods of *N. orbicollis* but the reverse was never observed (Trumbo 1994). Adults are nocturnal. Adult activity, including reproduction, occurs in the spring, and teneral adults usually appear in mid to late summer. These adults probably overwinter (Peck and Kaulbars 1987). Anderson (1982) and Shubeck (1983) suggested this species has a strong preference for forested habitats while Lingafelter's (1995) study in Kansas showed a preference for the ecotone between forests and fields.

***Nicrophorus tomentosus* Weber**

(Figs. 118, 120)

Necrophorus tomentosus Weber 1801: 47.
Necrophorus velutinus Fabricius 1801: 334.
Necrophorus velutinus angustifasciatus Portevin 1925: 170.
Necrophorus velutinus aurigaster Portevin 1925: 170.

Diagnosis. Length 11.2-19.0 mm. *Head*: Club of antenna black, basal segment shining, remaining segments dull. *Thorax*: Pronotum subquadrate with lateral margins broad; basal margin wide; surface covered with dense, long, yellow setae. Metasternum with long, yellow setae, with a glabrous spot present posterior to each of the mesocoxae. Metepimeron with only a few yellow setae or glabrous. *Elytra*: Each elytron with two, transverse orange maculae, maculae usually reaching suture, occasionally connected laterally, occasionally coalesced on disc. *Legs*: Posterior tibia straight.

Distribution. *Nicrophorus tomentosus* is an abundant and widely distributed species. It occurs in nearly all of the United States (not the southern halves of Texas or Florida) and southern Canada east of the Rocky Mountains (Anderson and Peck 1985, Peck and Kaulbars 1987). In Nebraska, it is found throughout the state.

Locality Records (Fig. 118). 5,991 Nebraska specimens examined or recorded. ADAMS CO. (3): Hastings; CASS CO. (166): Plattsmouth; CHASE CO. (76): Enders Reservoir; CHERRY CO. (20): Valentine, Ft. Niobrara Wildlife Refuge; CHEYENNE CO. (4): Dalton, Gurly; CUMING CO. (3): West Point; CUSTER CO. (250): Anselmo, Milburn, Sargent; DAWES CO. (11): Ash Creek, Chadron; DAWSON CO. (2): 5 mi. S. Gothenburg; DIXON CO. (192): Aowa Creek; DUNDY CO. (27): 1.5 mi. SW Max, Republican River E of Benkelman; FILLMORE CO. (5): Fairmont; FRANKLIN CO. (19): Franklin; FRONTIER CO. (1,287): Farnam, Medicine Creek Reservoir, Red Willow Reservoir; GOSPER CO. (192): Elwood Reservoir, Lexington, Smithfield; HALL CO. (37): Alda; HARLAN CO. (6): Republican River S of Orleans; JEFFERSON CO. (36): No data; JOHNSON CO. (5): No data; KEITH CO. (10): Cedar Point Biological Station, Sand Creek at Hwy. 2; KEYA PAHA CO. (50): Carns, Mills, Norden; KNOX CO. (72): Bazile Creek Wildlife Mgmt. Area, Center; LANCASTER CO. (46): Lincoln, Reller Prairie, Sprague; LINCOLN CO. (2,719): Brady, Box Elder Canyon, Cottonwood Canyon, Moran Canyon, North Platte, Sutherland, Wellfleet; McPHERSON CO. (1): No data; OTOE CO. (26): No data; PAWNEE CO. (6): No data; PHELPS CO. (5): Bertrand; PLATTE CO. (1): Columbus; POLK CO. (10): No data; RICHARDSON CO. (1): Indian Cave State

Park; SALINE CO. (4): Swan Creek; SARPY CO. (28): Bellevue, Fontenelle Forest, Schramm Park; SAUNDERS CO. (597): Wahoo; SIOUX CO. (53): Gilbert Baker Wildlife area, Glen, Monroe Canyon; THOMAS CO. (64): Halsey Forest; WASHINGTON CO. (13): Ft. Calhoun; YORK CO. (10): No data.

Temporal Distribution. Rangewide: May to October (Peck and Kaulbars 1987). Nebraska: June (186), July (3,157), August (2,413), September (182), October (98). The high numbers for July and August reflect, in part, extensive trapping programs that were carried out in Frontier and Lincoln counties during the summer of 1995.

Remarks. *Nicrophorus tomentosus* is readily separated from all other silphids in North America by the presence of long, dense, yellow setae covering the pronotum.

The larval stage was described by Anderson (1982b), and a brief diagnosis was given by Anderson and Peck (1985).

According to Anderson and Peck (1985), this species is unlike other species of Nearctic *Nicrophorus* in that adults do not bury the carcass. Instead, they make only a shallow pit into which the carcass sinks. It is then covered with litter. After a period of feeding, mature larvae move into the surrounding soil where they spend the winter as a third instar, prepupal larva.

FIG. 120. *Nicrophorus tomentosus* Weber.

Pupation occurs the following spring, and adults emerge in June in Nebraska. Scott and Traniello (1990b) indicated they do not become reproductively active until August. Wilson *et al*. (1984) suggested that *N. tomentosus* does not reproduce immediately because of competition from larger species of *Nicrophorus*. Smaller, "subordinate" species, such as *N. tomentosus*, can persist by restricting themselves to activity periods when more dominant species are not abundant or by using resources for which interference is unprofitable for the more dominant (larger) species (Trumbo 1990b).

Adults are diurnal (personal observation, Shubeck 1971, Wilson *et al*. 1984). They greatly resemble bumble bees when flying, and Milne and Milne (1944) and Fisher and Tuckerman (1986) suggested they are Batesian mimics of bumble bees. Bumble bees are strictly diurnal, and one would expect that they are mimicked only by diurnal carrion beetles; this appears to be the case. Clark (1895) and Steele (1927) observed adults feeding on maggots at carrion.

Anderson (1982c), Lingafelter (1995), and Lomolino *et al*. (1995) observed that *N. tomentosus* is a habitat generalist with no preference for forests, shrubby areas, or open grasslands. Our experience in Nebraska corroborates these observations.

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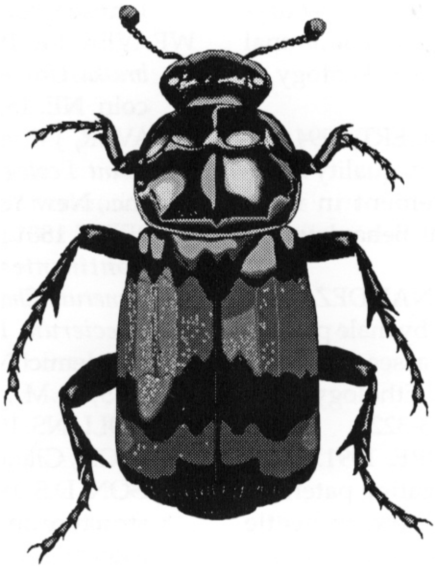

GLOSSARY

(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.

CHECKLIST OF NEBRASKA SILPHIDAE

Life List	**Subfamily Silphinae**
☐	*Heterosilpha ramosa* (Say)
☐	*Necrodes surinamensis* (Fabr.)
☐	*Necrophila americana* (L.)
☐	*Oiceoptoma inaequale* (Fabr.)
☐	*Oiceoptoma novaboracense* (Forster)
☐	*Thanatophilus lapponicus* (Herbst)
☐	*Thanatophilus truncatus* (Say)
	Subfamily Nicrophorinae
☐	*Nicrophorus americanus* Olivier
☐	*Nicrophorus carolinus* (L.)
☐	*Nicrophorus guttula* Motschulsky
☐	*Nicrophorus hybridus* Hatch and Angell
☐	*Nicrophorus investigator* Zetterstedt
☐	*Nicrophorus marginatus* Fabr.
☐	*Nicrophorus mexicanus* Matthews
☐	*Nicrophorus obscurus* Kirby
☐	*Nicrophorus orbicollis* Say
☐	*Nicrophorus pustulatus* Herschel
☐	*Nicrophorus tomentosus* Weber

ABOUT THE AUTHOR

Dr. Brett Ratcliffe is the Curator of the Division of Entomology and Professor at the University of Nebraska State Museum in Lincoln. He is a specialist in the taxonomy, biology, ecology, phylogeny, and biogeography of scarab beetles, especially those of the Neotropics. He studied silphids for his Master's degree, and he has maintained an interest in carrion beetles ever since. He is currently leading research programs in Nebraska to study the endangered American burying beetle (*Nicrophorus americanus*), which is now found in only five states, including Nebraska.

Dr. Ratcliffe has conducted extensive field research in Japan, North America, Mexico, Central America, South America, and South Africa. From 1976 to 1978, he was head of the systematics entomology research collections for the National Institute for Amazonian Research (INPA) in Manaus, Brazil. During the past five years, he has collaborated closely with the National Institute for Biodiversity (INBio) in Costa Rica, the University of Panama, and the Smithsonian's Tropical Research Institute in Panama to conduct biodiversity survey programs of the dynastine scarab beetles of those countries. He is the author of numerous scientific papers and popular articles about beetles as well as a book, *The Scarab Beetles of Nebraska*.