A literature based key to the subfamily Nicrophorinae (Coleoptera: Silphidae) of Washington State

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Abstract

Within the family Silphidae or carrion beetles are the Nicrophorinae. Over the last century, classification of the Nicrophorinae has shifted back and forth (Ratcliff 1996), with publications of Hatch (1927,1940,1957) and Arnett (1944) giving tribal status to the taxon. Taxonomic revision however, has resulted in the division of Silphidae into two subfamilies (Anderson and Peck 1985; Peck and Miller 1982; Sikes et al. 2002; Hoback et al. 2005) based on observable morphological differences, but with most emphasis on behavioral characteristics within the more complex life cycle of the Nicrophorinae (Anderson and Peck 1985). The behavioral characteristics distinguishing the Nicrophorinae include the namesake “burying” behavior, bi-parental care, mate finding tactics, stridulation, and the interesting symbiotic relationship that exists between the beetles and phoretic mites.

Morphological Differences

All Silphids, including the Nicrophorinae, are fairly large beetles, ranging in size from 10 to 35 mm. Morphologically, the differences between the adults are not as pronounced as those between the larvae of the two subfamilies with Nicrophorus larvae appearing soft and “grub like” and characterized by extremely reduced sclerotization and quadrispinose abdominal tergites (Anderson and Peck 1985). Features distinguishing adult Nicrophorinae include variations in elytral coloration, antennal structure, and foretarsal segments (Anderson and Peck 1985; Ratcliff 1996), but mention should also be made of the stridulatory files located on the fifth abdominal tergite. These are used in communication or as a defense mechanism, addressed under behavioral differences (pp.7-8; Fig. D), and are not found in the Silphinae (Anderson and Peck 1985).

(Elytral Coloration)

Unlike the Silphinae, which are typically colored all brown or black, most adult Nicrophorinae are colored all black but distinguished with easily recognizable
bright orange markings on truncate elytra (Haggard 2006; Ratcliff 1996; Sikes 2005) which, in combination with other characteristics, aid in further separating species within the genus (Ratcliff 1996).

(Antennal Structure)
The antennal structure in the Nicrophorinae is eleven segmented and capitate, with the apical four segments forming a loose club and the second segment small and difficult to see (Ratcliff 1996). In Silphinae, the second antennal segment is large, and the antennae are gradually clavate from segments seven through eleven (Ratcliff 1996).

(Foretarsal Segments)
Males of most *Nicrophorus* species possess asymmetrical and laterally expanded foretarsal segments (Plate 4, illustration 44a) with females of the genus having segments with only slightly symmetrical and laterally expanded segments (Plate 4, illustration 44b). This adaptation, possibly acquired to aid the Nicrophorinae in the process of digging into soil in order to bury carrion, is not needed in Silphinae as they oviposit and feed on a carcass above ground.

Behavioral Differences
(Olfaction, “Burying” Behavior and Bi-parental Care)
Unique to the subfamily Nicrophorinae, is the characteristic “burying” behavior in which the beetles inter the carcass of a small animal (Fig. B, illustrations 69-74) to use as a source of food for their young (Hoback et al. 2005; Ratcliff 1996). The *Nicrophorus* beetles use olfaction, via sensitive chemosensors on the terminal segments of antennae, (Anderson and Peck 1985; Scott 1998) as they fly in search of small carrion to bury. Research by Petruska (as cited by Ratcliffe 1996) attests that sensilla on the Nicrophorinae antennae are so specialized that the beetles can find a dead mouse or other carcass within an hour of death and from as far away as two miles.
Even more remarkable is the demonstration of bi-parental care in rearing offspring (Hoback et al. 2005; Scott 1998), with cooperation throughout the entire process of caring for the young exemplifying the highest level of sociality attained in the Coleoptera (Ratcliff 1996). The bi-parental care (Fig B, illustrations 69-74) of Nicrophorinae commences as a conspecific pair of beetles unites and works together, excluding competitors, as they move and conceal a carcass that may weigh as much as 100-300 times more than the insects themselves (Eggert 1997; Peck 1982). By burying the carcass, the “Nicrophorus species are the only ones attempting to break the cycle of competition at a food source” (Ratcliffe 1996). Concealing the carcass underground and guarding to prevent its use by vertebrates, other insects and microbes, is a strategy that gives these beetles a competitive advantage for successful reproduction (Hoback et al. 2005; Ratcliffe 1996; Scott 1998).

Once buried, the beetle parents work the mass of food designated for their offspring into a compact ball, cleaning it of fur or feathers while adding secretions that retard bacterial and fungal growth (Acorn 2001; Dikeman 2009; Milne and Milne 1976). The female constructs a brood chamber near the carcass, and eggs are laid. Once the eggs hatch, both parents feed the larvae from regurgitated fluids with the brood care lasting throughout larval development (Milne and Milne 1944, 1976; Sikes 2005). This cooperative brood care (Fig. A) can be compared to behavior seen in birds with nestlings (Ratcliffe 1996) and is indeed rare and unique.
FEEDING OF LARVAE by a burying beetle of the species *N. vespillo* is shown on the basis of photographs made by the Polish naturalist Erna Pukowski. The parent beetle sips from the pool of fluid food in the top of the buried carcass and then transfers the material to one larva after another. The larvae rear up instinctively, much the way nestling birds do when feeding.

Fig. A.

Illustration from Scientific American Inc. (1976)
Illustrations from Scientific American, Inc. (1976)

Fig. B.
(Mate Finding Tactics)
Another characteristic distinguishing the Nicrophorinae from the Silphinae is also behavioral in nature. Mate finding behavior by a *Nicrophorus* male can result in flamboyant posturing should he arrive at a carcass with no female present. This "headstand wagg[e]" (Fig. C), or "sterzeln" position with hind legs extended and abdomen pointing up has been assumed to indicate the release of an attractant or pheromone to lure females to the site (Bartlett 1987; Eggert 1992; Ratcliff 1996).

![Image of a beetle](image)

Fig. C. "Headstand" or "sterzeln" position, from Behavioral Ecology, 1992. Vol. 3(3), cover illustration.

(Stridulating Behavior)
Distinctive and interesting within the Nicrophorinae is the phenomenon of stridulation. Adults in the genus *Nicrophorus* have a pair of stridulatory files on the fifth abdominal tergite (Fig. D), with Schumacher (as cited in Anderson and Peck 1985), finding the structure to be species specific. Audible to humans, sound is made when the files are rubbed on the apex of each elytron. The scraping sound or sawing noise is produced in situations of defense or stress, but also is exhibited during burial of a carcass, copulation and in the interaction between a female and her brood (Ratcliff 1996) and, according to Darwin, (as cited in Lane and Rothschild 1965) may have evolved as an intraspecific form of communication. Coupled with the aposematic elytral markings, the stridulations
are likely to aid the Nicrophorinae in warding off would be predators and competition over a highly valued source of food and resource for reproduction (Lane and Rothschild 1965).

Fig. D.

Illustrations from Scientific American, Inc. (1976)
The advanced brood care behavior of the Nicrophorinae makes them ideal carriers (Figs. E&F) for phoretic mites (Schwarz and Müller 1992). Studies by Springett (1968) show that the species of mites, *Poecilochirus necrophori* indicate a preference to only *Nicrophorus* beetles, using them for transport to a food source and a carefully guarded and tended crypt in which to reproduce. As they prefer to feed on fly larvae laid on the carcass before internment, they aid the *Nicrophorus* beetles in eliminating competition for the food resources intended for the beetle larvae (Schwarz and Müller 1992; Springett 1968).
Fig. F.
photo of *N. defodiens* with phoretic mites
American Camp National Park, San Juan Island, WA 98250
by Cyndi Brast (2010)
Species of Nicrophorinae in Washington State

Within Nicrophorinae, there are 15 species of the single representative genus, *Nicrophorus* Fabricius, which exist in North America, north of Mexico (Anderson and Peck 1986). Sampling records in the Pacific Northwest region were sparse, based largely on the research of Hatch (1927, 1940, 1957), until Anderson and Peck provided data from studies in Canada and Alaska, including portions of western coastal USA (Anderson and Peck 1986). Research records from these sources record six species of Nicrophorinae in Washington State, with four of the six species reported in data collected by the U.S. Department of Interior – National Park Service (LaBonte, 1998). These Nicrophorinae, all in the genera *Nicrophorus*, are *Nicrophorus defodians*, *N. guttula*, *N. hybridus*, *N. investigator*, *N. nigrita*, and *N. marginatus*.

Key to Subfamily Nicrophorinae

(Anderson and Peck 1985)

1. Elytra truncate, exposing 3 or 4 abdominal tergites, usually with red or orange maculations (frontispiece). Fifth abdominal segment with stridulatory files on dorsum (Plate 2, Fig. 24). Epistomal suture present (Plate 1, Fig. 1). Second antennal segment small, indistinct, hidden in tip of first antennal segment (Plate 2, Fig. 21)………………*Nicrophorinae*

Elytra usually not truncate, at most exposing 1 or 2 abdominal tergites. Fifth abdominal segment lacking stridulatory files. Epistomal suture absent (Plate 1, Fig. 2). Second antennal segment large, not hidden in tip of first antennal segment (Plate 2, Fig. 20)………………*Silphinae*
Subfamily Nicrophorinae
(Anderson and Peck 1985)

Genus Nicrophorus Fabricius

*Nicrophorus* Fabricius, 1775:71; Portevin 1926:181; Hatch 1928:126;
Madge 1980:357.

*Necrophorus* Thunberg, 1789:7.
*Necrophagus* Leach, 1815:88.
*Cyrtoscelis* Hope, 1840:149.
*Acanthopsilus* Portevin, 1914:223.
*Necrocharis* Portevin, 1923:141.
*Necroxenus* Semenov-Tian-Shanskij, 1926:46.
*Eunechrophorus* 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.
*Neonicrhoporus* Hatch, 1946:99

Key to species of adult *Nicrophorus* in North America

*Washington species noted in bold
(modified from Anderson and Peck 1985)

1. Pronotum without anterior transverse impression, lateral margins extremely narrow (Plate 4, Fig. 43). Elytral epipleuron narrow (Plate 6, Fig. 55).........................*N. carolinus* (Linnaeus)

Pronotum with anterior transverse impression, lateral margins not narrow (Plate 4, Figs. 39-42). Elytral epipleuron wide (Plate 5, Fig. 45).................................................................2

2(1). Frons and pronotal disc red. Tarsal empodium quadrisetose (Plate 3, Fig. 33)...........*N. americanus* Oliver

Frons and pronotal disc black. Tarsal empodium
bisetose (Plate 3, Fig. 34)……………………………………3

3(2). Pronotum with dense yellow pubescence……………………………………..N. tomentosus Weber
Pronotum glabrous, or with sparse hair on anterior
or lateral margins……………………………………………………..4

4(3). Posterior lobe of metepimeron (Plate 1, Fig. 5) with dense yellow pubescence; pronotum cordate (Plate 4, Fig. 42)………
……………………………………………………………………..5
Posterior lobe of metepimeron glabrous, or with dark hairs or only a few yellow hairs; pronotum variable (Plate 4, Figs. 39-41)……………………………………………………………7

5(4). Anterior face of procoxa with short hairs on basal
half…………………………..N. marginatus Fabricius
Anterior face of procoxa with long hairs on basal
half…………………………………………………………………….6

6(5). Penultimate antennal segment with outer edge deeply emarginated (Plate 3, Fig. 35); basal segment of antennal club black. Elytron with anterior black band reaching epipleural ridge but not crossing onto epipleuron (Plate 8, Figs. 71,72)……………………………………..N. Obscurus Kirby
Penultimate antennal segment with outer edge shallowly emarginated (Plate 3, Fig. 36); basal segment of antennal club black or orange; if orange, elytron with anterior black band crossing onto epipleuron (Plate 8, Fig. 65); if black, the elytral maculations reduced or absent (Plate 8, Figs. 67-69)……………………………………N. guttula Motschulsky

7(4). Metatibia curved. Anterior black band of elytron not reaching epipleuron (Plate 5, Fig. 47)……………………………………N. sayi Laporte
Metatibia straight. Anterior black band of elytron usually reaching epipleuron (Plates 5 & 6, Figs. 45, 46, 51)…..
8(7). Elytral epipleuron unicolorous, black or orange………………9
Elytral epipleuron bicoloried, black and orange
(Plate 6, Figs. 49-51).................................................................13
9(8). Elytral epipleuron black...................................................10
Elytral epipleuron orange.......................................................12
10(9). Dorsal surface of elytron with long fine hairs. Epipleural
ridge short, reaching only to level of tip of scutellum
(Plate 5, Fig. 45)........................................................................
..........................................................................................N. orbicollis Say
Dorsal surface of elytron without long hairs.
Epipleural ridge long, reaching almost to level of base
of scutellum (Plate 5, Fig. 46).....................................................11
11(10). Elytron immaculate, entirely black. Metasternal pubescence
brown, long, dense.................................................................
.........................................................................................N. nigrita Mannerheim
Elytron maculate, with 1 small anterolateral spot and 2 small
posterior spots (Plate 5, Fig. 46). Metasternal pubescence
yellow brown, sparse..............................................................
.........................................................................................N. pustulatus Herschel
12(9). Metasternum with elongate bald patch immediately posterior
to each mesocoxa (Plate 1, Fig. 5). Elytron with continuous
multiple and irregular rows of stout, erect hairs around
shoulder to base of epipleural ridge (Plate 3, Fig. 37)...........
.........................................................................................N. hybridus Hatch & Angell
Metasternum without bald patches immediately posterior
to each mesocoxa. Elytron with continuous multiple and
irregular rows of hairs around shoulder but ending well
before base of epipleural ridge (Plate 3, Fig. 38); elytral
maculations often greatly reduced (Plate 7, Figs. 59-62)......................N. investigator Zetterstedt
13(8). Metasternal pubescence brown; apical three segments of antennal club red

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.................................................N. mexicanus Matthews*

*Distributed in the southwestern United States and Mexico

Metasternal pubescence yellow; apical three segments of antennal club black

.................................14

14(13). Base of elytral epipleuron orange, with prebasal black spot (Plate 6, Figs. 49-50). Upper and lower faces of ninth and 10th antennal segments each with patch of dense white hairs arranged in “figure eight” pattern...

.................................................N. vespilloides Herbst

Base of elytral epipleuron entirely black (Plate 6, Fig. 51). Upper and lower faces of ninth and 10th antennal segments without dense white hairs, though vestige of the “figure eight” pattern may be present..............

.................................................N. defodiens Mannerheim
Illustrations from Anderson and Peck (1985)

Plate 1.
Illustrations from Anderson and Peck (1985)

Plate 2.
Illustrations from Anderson and Peck (1985)

Plate 3.

Fig. 44. Tarsi of adult *Nicrophorus orbicollis* (dorsal view: a, male; b, female).

Illustrations from Anderson and Peck (1985)

Plate 4.
Illustrations from Anderson and Peck (1985)

Plate 5.
Illustrations from Anderson and Peck (1985)

Plate 6.
Illustrations from Anderson and Peck (1985)

Plate 7.

Illustrations from Anderson and Peck (1985)

Plate 8.
Species Descriptions
(Anderson and Peck 1985)

*Nicrophorus defodiens* Mannerheim

*Necrophorus defodiens* Mannerheim, 1846:513
*Necrophorus pollinctor* LeConte, 1854:19
*Necrophorus conversator* Walker, 1866:320
*Necrophorus plagiatus* Motschulsky, 1869:352
*Necrophorus defodiens binotatus* Portevin, 1926:236
*Necrophorus defodiens kadjakensis* Portevin, 1926:236
*Necrophorus defodiens mannerheimi* Portevin, 1926:236

![Photo](image)

Photo from Hanley and Cuthrell (2008)

**Diagnosis of adult** (from Anderson and Peck 1985). Pronotum quadrate, with wide lateral and basal margins (Plate 4, Fig. 40). Antennal club entirely black; vestige of the “figure eight” pattern of white hairs may be present. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibia straight. Elytron with pattern variable (Plate 6, Figs. 51-54). Smaller in size, 12-18 mm long.

**Distribution** (from Anderson and Peck 1985). This species is widely distributed in Canada and Alaska. It is also found in the western coastal
and Rocky Mountain States, and in the north central and eastern states, south along the Appalachian Mountains to Tennessee and North Carolina.

**Natural history** (from Anderson and Peck 1985). *N. defodiens* is found primarily in the dry boreal forest throughout its range but also occurs in montane and coastal forests of British Columbia and the coastal states. Adults of *N. defodiens* conceal a carcass under debris or leaf litter instead of burying it. Adults are crepuscular throughout the range of the species.

**Geographic variation** (from Anderson and Peck 1985). Variation in elytral patterns of adults of *N. defodiens* is extensive (Plate 6, Figs. 51-54), with many forms represented in a single brood. Elytral patterns in western coastal areas may be more melanistic (Plate 6, Figs. 52-54) than inland and eastern coastal areas (Plate 6, Fig. 51), which may be due to a correlation between decreasing availability of solar radiation with increasing melanism.

*Nicrophorus guttula* Motschulsky

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

Photo from Hanley and Cuthrell (2008)
Diagnosis of adult (from Anderson and Peck 1985). Pronotum strongly cordate, with narrow lateral and wide basal margins (Plate 4, Fig. 42). Antennal club either orange or with the basal segment black and the apical three segments orange. Anterior face of procoxa with long hairs on basal half. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibia straight. Elytron with pattern variable (Plate 8, Figs. 65-69). Moderate in size, 14-20 mm long.

Distribution (from Anderson and Peck 1985). This species is widely distributed in the western United States. It is found in Canada in southern areas of British Columbia, Alberta, and Saskatchewan.

Natural history (from Anderson and Peck 1985). *N. guttala* inhabits dry forests, prairies, and deserts. Adults are diurnal and have been collected from human and coyote dung as well as at carrion. Specimen data indicate adults are active from May-September and overwintering probably occurs in the adult stage.

Geographic variation (from Anderson and Peck 1985). The adults of *N. guttala* display much diversity in elytral color pattern and in color of the antennal club (Plate 8, Figs. 65-69) with melanic forms (Plate 8, Figs. 67-69) occurring in southwestern coastal areas of the United States. The melanistic variation led to much misidentification and taxonomic inaccuracy in early species descriptions (Anderson and Peck 1986).

*Nicrophorus hybridus* Hatch & Angell

*Necrophorus hybridus* Hatch and Angell, 1925:216
Diagnosis of adult (from Anderson and Peck 1985). Subquadrate pronotum, with wide lateral and basal margins (Plate 4, Fig. 41). Apical three segments of antennal club orange, with basal segment black. Metasternum with dense, yellow pubescence, but with a bald spot behind each mesocoxa (Plate 1, Fig. 4); metepimeron glabrous. Hind tibia straight. Elytron with pattern as in Fig. 63, Plate 7. Moderate in size, 15-20 mm long.


Natural history (from Anderson and Peck 1985). *N. hybridus* inhabits prairies and dry inland valleys of the coastal provinces and states. The adults are reproductively active in summer and appear to be primarily diurnal. Overwintering occurs in the prepupal stage.

Geographic variation (from Anderson and Peck 1985). None noted.

**Nicrophorus investigator** Zetterstedt

*Necrophorus investigator* Zetterstedt, 1824:154.  
*Necrophorus maritimus* Escholtz in Guérin-Méneville, 1835:PL. 17.
\textit{Necrophorus melsheimeri} Kirby, 1837:97.
\textit{Necrophorus particeps} Fischer von Waldheim, 1844:139.
\textit{Necrophorus aleuticus} Gistel, 1848:190.
\textit{Necrophorus pollinctor} Mannerheim, 1853:169.
\textit{Necrophorus infodiens} Mannerheim, 1853:170.
\textit{Necrophorus confossor} LeConte, 1854:20.

Illustration from Ratcliff (1996)

**Diagnosis of adult** (from Anderson and Peck 1985). Quadrate pronotum, with wide lateral and basal margins (Plate 4, Fig. 40). Apical three segments of antennal club orange, with basal segment black. Dense yellow metasternal pubescence; metepimeron glabrous. Hind tibia straight. Variable elytra pattern (Plate 7, Figs. 57-62). Moderate in size, 13-18 mm long.

**Distribution** (from Anderson and Peck 1985). Widely distributed in Western United States as well as eastern U.S. Species also found throughout Canada and Alaska with distribution in Eastern Canada primarily in northern areas.

**Natural History** (from Anderson and Peck 1985). Limited to published data on Japanese and European species since virtually no publications have studied the natural history of this species in North America. Specimen sampling data in North America indicate that reproductively active adults of this species first appear in mid-June through early July. Research by Katakura and Fukuda (as cited by Anderson and Peck 1985) show adults of this species to be both nocturnal and diurnal in flight habits.
Geographic variation (from Anderson and Peck 1985). Much variation in elytral patterns of adults, with darker forms (Plate 7, Figs. 59-62) occurring along the northwest coastal areas of North America. The melanistic variation seems to correlate with the cooler and wetter climate conditions existing in this region. Typically only maculated forms (Plate 7, Figs. 57,58) are seen in southern coastal areas.

Nicrophorus marginatus Fabricius

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

Diagnosis of adult (from Anderson and Peck 1985). Strongly cordate pronotum, with narrow lateral margins, and wide basal margin (Plate 4, Fig. 42). Antennal club orange. Anterior face of procoxa with short hairs on basal half. Metasternal pubescence yellow and dense. Hind tibia slightly curved. Elytron pattern as in Fig. 70, Plate 8. Moderate in size, 15-22 mm long.
**Distribution** (from Anderson and Peck 1985; Ratcliff 1996). Widely distributed along western coastal U.S. but excluding northwestern Washington; ranging south into northern Mexico. Canadian distribution is found in Ontario and Quebec, southern areas of Manitoba, and west into British Columbia. *N. marginatus* is the most widely distributed North American species of *Nicrophorus*.

**Natural history** (from Anderson and Peck 1985; Ratcliff 1996). Adults of *Nicrophorus marginatus* are active beginning in Spring when the weather becomes consistently warm and reproduction occurs May-July with a new generation of adults appearing from July-Aug. This species has been collected from prairies, open fields, grasslands, desert woodlands, and montane meadows. It has not been determined whether adults are diurnal or nocturnal.

**Geographic variation** (from Anderson and Peck 1985). Arid areas of the southwestern United States show adult specimens of *Nicrophorus marginatus* with anterior and posterior orange maculations fused.

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**Nicrophorus nigrita** Mannerheim

*Necrophorus ruficornis* Motschulsky, 1869:352.
*Nicrophorus investigator* alpha Pierce, 1949:67.

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Photo by Gary McDonald (2009)
From BugGuide.Net
**Diagnosis of adult** (from Anderson and Peck 1985). Pronotum quadrate, with wide lateral and basal margins (Plate 4, Fig. 40). Apical three segments of antennal club orange with basal segment black. Metasternal pubescence dense, brown; metepimeron glabrous. Hind tibia straight. Elytron entirely black. Small in size, 13-18 mm long.

**Distribution** (from Anderson and Peck 1985). *N. nigrita* is widely distributed in the coastal areas of Washington, Oregon, and California. In Canada, found rarely in southwestern British Columbia and Vancouver Island.

**Natural history** (from Anderson and Peck 1985). *N. nigrita* has been found in coastal forests. Specimen data from California is indicative of adult activity in the cooler and wetter months of September to May.

**Geographic variation** (from Anderson and Peck 1985). None noted.
References


Arnett, R.H., Jr. 1944. A revision of the Nearctic Silphini and Nicrophorini based on female genitalia.


Ratcliff, B.C. 1996. The Carrion Beetles (Coleoptera: Silphidae) of


