

THE NATURAL HISTORY OF *NECRODES*
SURINAMENSIS (FABR.) (COLEOPTERA: SILPHIDAE) ¹

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INTRODUCTION

There has been very little non-taxonomic research in the past dealing with *Necrodes surinamensis* (Fabr.). Clark (1895) and Davis (1915) briefly mentioned food habits, and Malkin (1953) presented an interesting survey of its distribution in western North America. Dorsey (1940) described in considerable detail the fourth instar larva; Hatch (1927) discussed elytral variations and food habits, and Arnett (1944, 1946) mentioned the female genitalia and several morphological variations.

Generic synonymies have not been avoided by most authors even though there was no substantial basis for confusion. The result has been that even today the beetle is variously alluded to as *Silpha*, *Protonecrodes* or *Necrodes*.

The life history, behavior and ecological relationships have not been established, and the accepted distribution was fragmentary and erroneous. The egg, first instar larva and pupa were undescribed (Dorsey, 1940) although Wickham (1895a) was apparently familiar with the pupa.

This study is an attempt to rectify some of these unknowns and determine, as much as possible, the natural history of *N. surinamensis*.

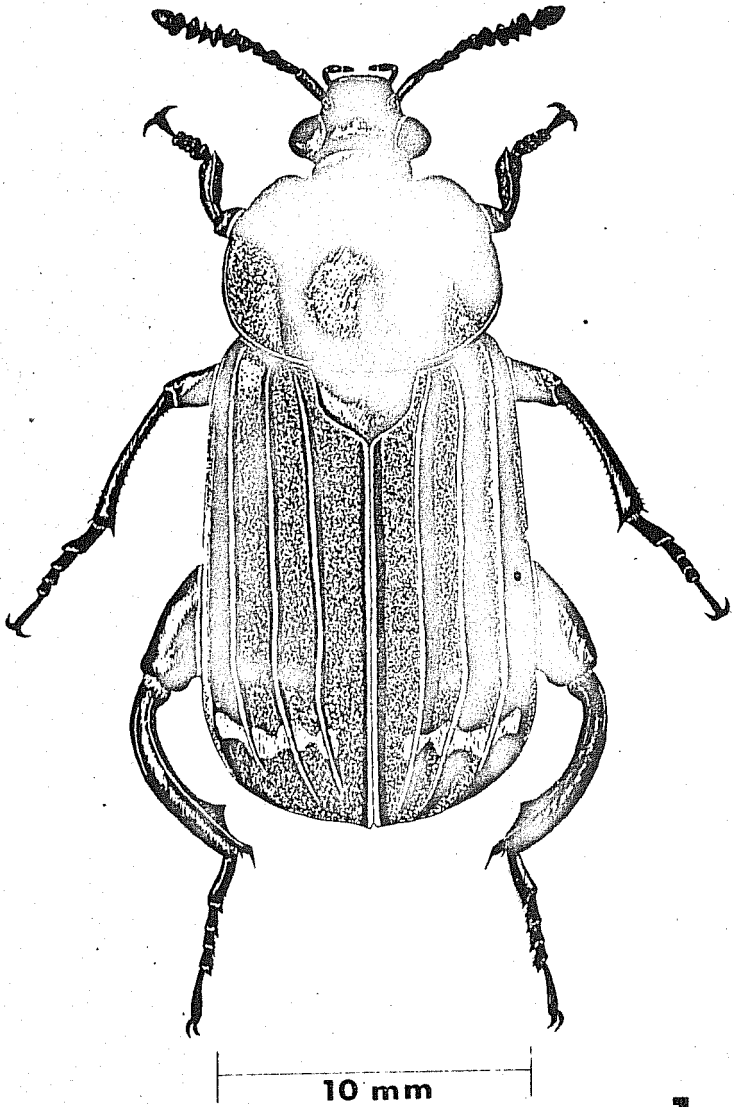
METHODS AND MATERIALS

The study area selected for this research was the vicinity around Lincoln, Nebraska. This region consists of rolling farm land, small wood lots and intermittent streams.

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Fig. 1. Dorsal aspect of adult male.

Two methods were employed to attract silphids: carrion and lights.

Animal carcasses placed in the field for observation were obtained from the local humane society; they consisted primarily of small to medium size dogs and cats. Carcasses set out in the field were positioned near gravel, county roads in areas where silphids were known to be common by previous collecting and where vehicular traffic was not extensive. Wild animals found dead near roads were also extensively utilized, usually being left where they lay. Mammal scavengers frequently disturbed field carcasses, but this usually did not cause problems unless a carcass was completely taken. A supply of frozen carcasses was maintained so that they might be available at any time.

Field carcasses were observed twice daily (AM and PM) in most instances for the duration of the decay cycle; occasionally they were observed more or less than that as circumstances warranted. Carcasses were inspected for approximately ten minutes to note any insect activity. They were then turned over so that the area beneath the carcass could be observed. Depending on the experiments in progress, larval or adult *N. surinamensis*, when encountered, were left on the carrion or brought into the laboratory for further study.

Outdoor screen cages with their floors sunken 30 cm into the ground were used in the hopes of approaching a level of "controlled" rearing in the field (Fig. 2). A carcass was placed in a cage, and carrion fauna was allowed entrance until active decay began. At this point varying numbers of *N. surinamensis* were placed within the cage which was then closed. This rearing method proved unfavorable as the normal decay sequence was impeded, and observation was difficult.

Successful laboratory rearings were accomplished by using a small piece of slightly decomposed carrion placed on 3 cm of fine, sterilized soil in a clear plastic shoe box (17 × 31 × 9 cm). Sterilized soil was used to alleviate the invariable occurrence of nematodes. Moist cotton was placed in each colony. Each plastic box, containing a number of *N. surinamensis*, was put in a glass topped rearing chamber (Fig. 3) where temperature was kept at 25 ± 1 C and relative humidity at 60%. A 12 hour

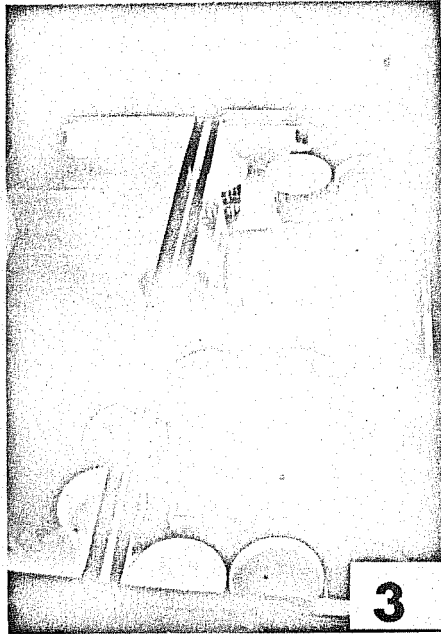
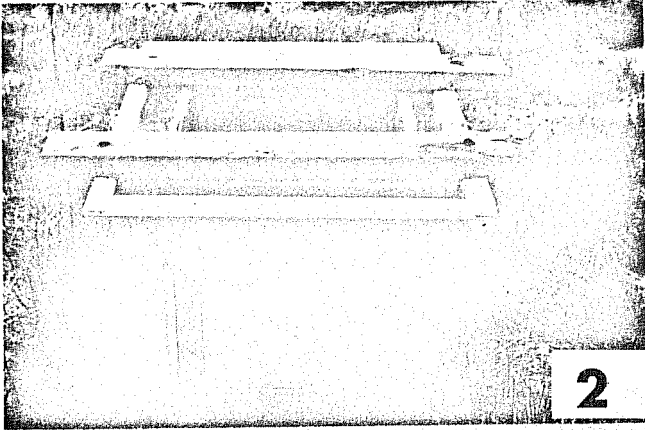


Fig. 2. Field rearing cage. Fig. 3. Chamber for laboratory rearing.

photoperiod was maintained by using two 15 watt cool white fluorescent lights positioned 15 cm above the rearing colonies. An exhaust fan was used in the chamber to carry away excessive odors that would have disturbed others working in the building.

Since observation of the larvae under natural field conditions was so difficult, $\frac{1}{2}$ -pint cylinder containers were employed for more isolated observation and rearing of larvae. From one to four larvae were placed in each carton which contained fine, sterilized soil to a depth of $6\frac{1}{2}$ cm. Moist cotton and a small piece of decomposing flesh were added. These larval rearing containers were provided with clear plastic covers to prevent escape and yet maintain the photoperiod and were placed in the main rearing chamber. Temperature within the cartons was the same as that of the rearing chamber, and humidity was, desirably, a little higher.

The second method used to obtain *N. surinamensis* was to collect them beneath mercury vapor lights in several selected areas. Light collecting was normally conducted from 10:00 to 11:00 PM nightly from May through September.

A red, 100 watt light was used to observe the behavior of laboratory beetles under simulated conditions of darkness beneath a carcass or at night. Viewing was conducted in a small dark-room and, under these circumstances, grooming, feeding and mating were seen more frequently than in a lighted observation condition. *N. surinamensis* always reacted in a strong, negative manner to a white, 100 watt light by frantically scurrying about and seeking cover. It was determined that the beetles were unable to detect (or tolerant of) the red light because they did not react at all when one was switched on. This procedure was duplicated numerous times with the same results to substantiate the conclusion.

Various authors (Fuller, 1934; Bornemissza, 1957; Payne, 1965) have presented different interpretations of the successive stages of decay of carrion. The scheme of Payne was adapted in this study as it best illustrated what was actually encountered in the field in this case. Payne's stages of decomposition are: fresh, bloated, active decay, advanced decay, dry and remains. The duration of each stage depends on the season, weather, size of carcass and activity of the carrion fauna.

Seasonal and geographic distribution was determined by field research and by taking the data from 3,424 specimens representing 59 institutional and private collections.

Measurements were obtained for eggs, larvae and pupae with the aid of a Leitz ocular micrometer.

Illustrations, except where noted, were made by the author.

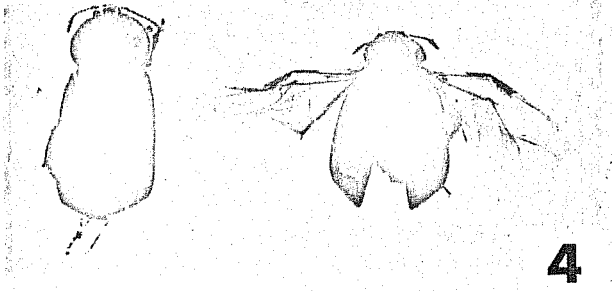
CLASSIFICATION

Johann C. Fabricius (1775) named and described *Necrodes surinamensis* but under the generic name *Silpha*. He designated two cotypes (Fig. 4), a male and a female, which are deposited in the Hunterian collection at the University of Glasgow. Locality data for the specimens is lacking as is typical for many Fabrician types, but notes by Fabricius and Olivier indicated Cayenne and Surinam in South America as habitats (Staig, 1931). Based on these notes and the name given to the insect, it might be reasonable to assume that the type-locality is what is now French Guiana or Surinam. Staig compared the types with modern examples in the British Museum (Natural History) in 1926 and found them to be conspecific (Crowson, *in litt.*).

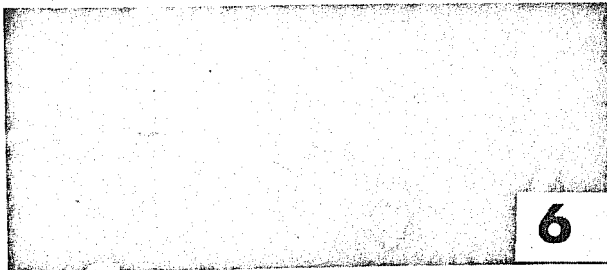
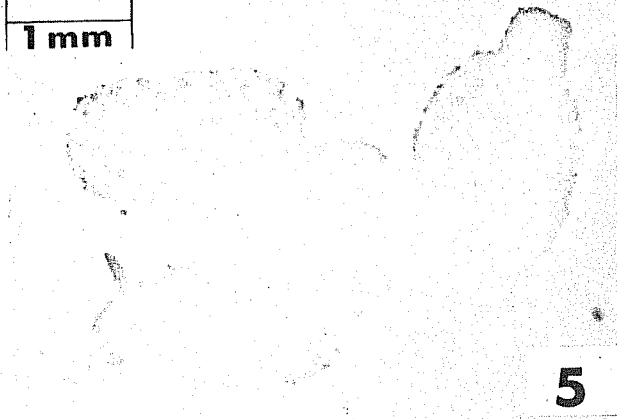
At one time Arnett (1944, 1946) preferred to call *N. surinamensis* a maculate form of the European *N. littoralis* (L.) because there were not enough valid characters to separate the two species. Arnett no longer holds with this earlier view but is of the opinion that *N. surinamensis* is a distinct species.

The genus *Necrodes* was proposed by Leach in 1815 with *N. littoralis* as the type-species; *N. surinamensis* was included in the new genus. Ever since that time, however, there has been considerable and needless confusion regarding the nomenclature of *N. surinamensis*. Many authors (Balduf, 1935; Dillon and Dillon, 1961; Jaques, 1951; Leng, 1920) apparently overlooked the new genus and continued to place the beetle in *Silpha*. Kirby (1837) was one of the first American entomologists to correctly

Fig. 4. Type specimens in the Hunterian Collection (courtesy R. A. Crowson, Glasgow University). Fig. 5. Eggs, two hours old. Fig. 6. Older eggs; egg on left is yellowish-brown while egg on right has changed to a cryptic, dark brown.



1 mm



apply Leach's new generic designation. But after Kirby, only Portevin (1922, 1926), Hatch (1927), Blackwelder (1944), and Arnett (1968) have correctly used the name *Necrodes surinamensis* in works of major taxonomic importance. Hopefully Arnett's listing of generic synonymies will have clarified the matter to the satisfaction of all.

Portevin (1922) split off the new genus *Protonecrodes* from *Necrodes*, and *N. surinamensis* was placed in the new genus. Hatch (1927) disagreed with Portevin's split and chose to consider *Protonecrodes* a subgenus of *Necrodes*. Hatch's position is more tenable because the characters used to erect the new genus (elytral angles and form of hind legs) do not seem to warrant such a split.

N. surinamensis had usually been included in the tribe Silphini, but Portevin (1926) included it in the new tribe Necrodini. Hatch (1927) favored the new tribal status for *Necrodes* as does this author, but Arnett (1968) preferred to keep it under the Silphini. It is recommended that the use of Necrodini be adopted because it more accurately reflects probable phyletic relationships within the Silphidae.

DESCRIPTION

EGG.—Eggs of *N. surinamensis* (Figs. 5, 6) are elongate, cylindrical, widest at the middle, and taper slightly at both ends which are bluntly rounded. Measurements of 11 eggs indicated the maximum length and width was 2.36 and 1.48 mm respectively; the minimum length and width was 1.53 and 1.05 mm respectively; the mean length and width was 1.96 and 1.27 mm respectively.

Texture of the chorion is smooth and unsculptured. Color of the egg when first deposited is cream white (Fig. 5) and remains this way for several hours. Color gradually changes to yellowish-brown and then to approximately the color of the soil on which it is resting (Fig. 6). Older eggs were occasionally seen to shrink slightly and become wrinkled.

LARVA.—Measurements were made of larvae in each instar and show a small distribution of values in each instar for the first two characters measured (Table 1). Total body length is a highly variable character and so less helpful when attempting to determine the instar of a larva.

The following description is compiled from Dorsey (1940):

Body (Figs. 7, 8, 9, 15, 16, 17, 18) campodeiform, wider than depth from dorsum to sternum in all body regions; entire length of dorsum

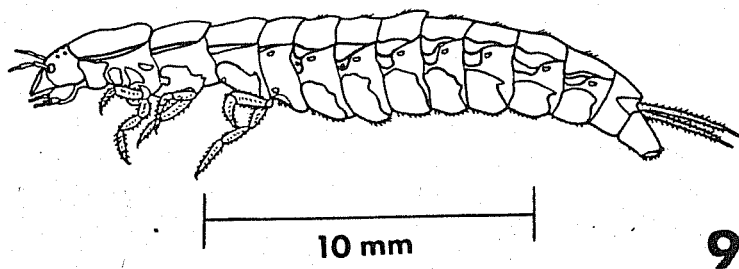
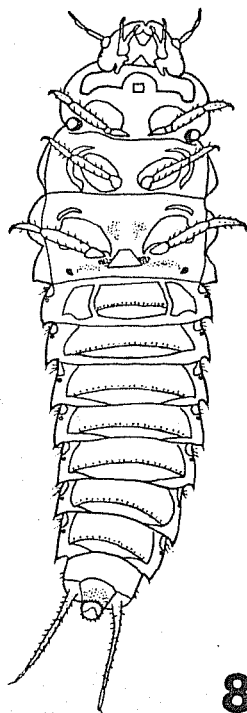
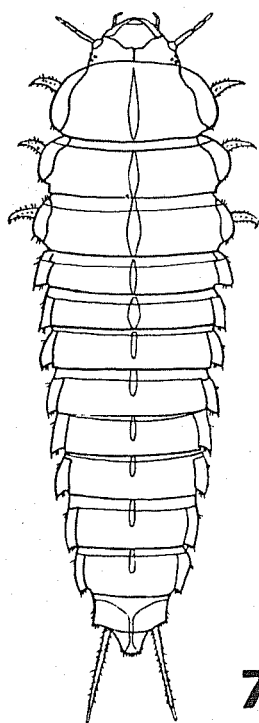
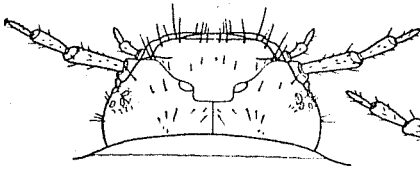


Fig. 7. Dorsal aspect of fourth instar larva. Fig. 8. Ventral aspect of fourth instar larva. Fig. 9. Lateral aspect of fourth instar larva.

marked with a narrow, shallow, central, longitudinal, light colored impression.

Head (Figs. 10, 11) broader than long. Epicranium tuberculate, sparsely furnished with scattered setae. Frons tuberculate, very sparsely setose; two strong setae borne in each frontal angle. Clypeus short and broad with two strong setae on each half near anterior margin, and two setae located centrally on anterior margin. Labrum directed sharply ventrad. Carinae not prominent. Dorsal occipital region furnished with two small, strong setae on each side. Antennae slightly longer than width of anterior margin of clypeus; first segment longest and widest of the three; second segment slightly longer than third; third subulate and less than one-half as wide as apex of second; second segment bears a sensory area which is a minute, very blunt cone; all three segments sparsely setose. Dorsal ocelli four in number, irregularly ovate, arranged around the periphery of a small, round, sclerotized mound; ventral ocelli two in number, ovate, located on lateral margin of ventral surface of the head. Mandible (Fig. 12) with broad, sub-triangular base tapering to posterior region of the strong and gradually tapering incisor lobe; apex bears two teeth which are acute and slightly serrate; mandible about as long as combined length of first and second antennal segments; a small seta at base of incisor lobe, adjacent to outer margin, on ventral surface; posterior, outer, lateral base of mandible, on dorsal surface, with one strong seta accompanied by several smaller ones. Clypeo-frontal suture distinctly defined only at lateral margins; clypeo-labral suture distinct. Labrum bilobed, sub-trapezoidal with anterior angles rounded; labral cleft furnished on each side with a small seta; a long, strong seta on each anterior labral margin, and one strong seta caudad and mesad of last mentioned seta. Maxillary palpiger closely connected with stipes; mala and stipes fused, stipes bearing two large setae anterior and one seta posterior to base of palpus; ventral surface of stipes furnished with one large seta caudad of palpus and adjacent to inner margin, and one mesad of base of palpus; several small setae scattered over remainder of surface; maxillary lobes free distally, fused proximally; maxillary palpus three-segmented, subequal and sparsely setose; third segment subulate and much narrower than other two. Galea with rounded, thickly-haired, brushlike tip; comb-like row of spines on lacinia consisting of nine spines. Cardo irregularly sub-triangular, marked centrally by a Y-shaped suture with arms of Y directed towards posterior margin; anterior lateral margin furnished with two small setae. Ligula

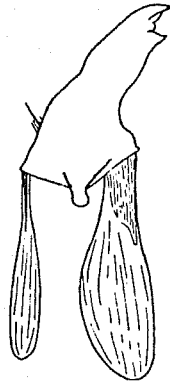
Fig. 10. Dorsal aspect of head of larva (from Dorsey, 1940; reprinted by permission). Fig. 11. Ventral aspect of head of larva (from Dorsey, 1940; reprinted by permission). Fig. 12. Ventral aspect of right mandible of larva (from Dorsey, 1940; reprinted by permission). Fig. 13. Dorsal aspect of labium of larva (from Dorsey, 1940; reprinted by permission). Fig. 14. Ventral aspect of labium of larva (from Dorsey, 1940; reprinted by permission).



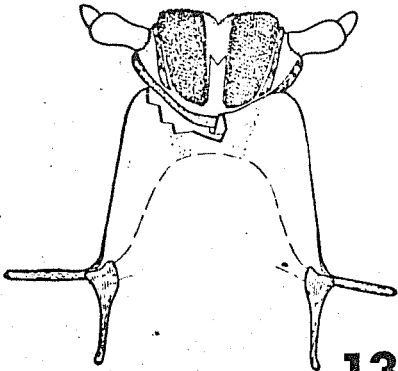
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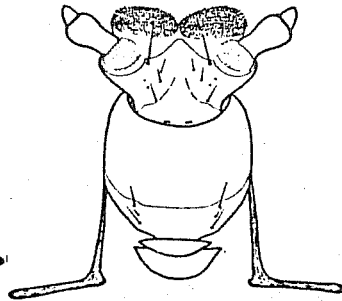
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bilobed. Glossa (Fig. 13) with anterior margin rounded and thickly furnished with very short hairs; dorsal surface fleshy and furnished with numerous longitudinal rows of very fine, strong setae; lateral margin supported by a narrow, elongate sclerome; cleft about one-third as deep as glossa. Mentum (Fig. 14) small; submentum trapezoidal with flaring base. Gula small. Labial palps two-segmented, extending beyond glossa; first segment clavate; second segment subulate and only two-fifths as long as first; both segments without setae. Epipharynx bilobed, with heavily sclerotized anterior and lateral margins furnished with rows of short, strong spines gradually diminishing in size laterad; posterior region of the heavily sclerotized lateral margin furnished with four short, strong spines; a short, rectangular spine lies on each side of epipharyngeal cleft; caudad and slightly laterad of rectangular spine lies an oval area densely covered with slender spinules more or less parallel with anterior epipharyngeal margin.

Spiracles annular; opening kidney-shaped, wide, directed laterad and slightly caudad; mesothoracic spiracle about two times the size of other spiracles; metathoracic spiracle greatly reduced in size and probably non-functional; abdominal spiracles on first to eighth segments inclusive, borne ventrally near lateral anterior angle of dorsal shield.

Tergum sparsely setose; anterior lateral angle of prothoracic shield rounded; anterior inner margin of prothoracic shield without prominent setae; posterior margin of dorsal shield with four to five strong setae; posterior lateral angle U-shaped. Mesothorax similar to other two, but only about six-tenths as long as prothorax.

Legs gradually increasing in length from first to third; furnished with numerous spine-like setae; coxa large, sub-pyriform, with a deep, longitudinal groove on outer face; trochanter small; femur about equal in length to coxa; tibia slightly shorter than femur; tarsungulus long, strong, with two small, lateral spines.

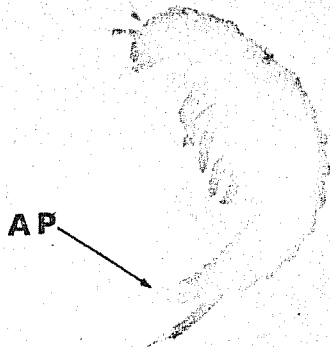
Sternal plate of prothorax orbicular, somewhat flattened anteriorly; prosternal sclerome triangular, apex directed laterad, with a contiguous plate lying laterad and caudad of it; episternal sclerome surrounding the anterior and lateral coxal margins; epimeron narrow, elongate, located adjacent to lateral coxal margin; basisternum soft, lighter in color and furnished with a small, central group of fine setae; sternal plate of first abdominal segment trapezoidal, accompanied on each side by a small, rounded sclerite near the lateral sternal margin.

Dorsal shield of abdomen sub-triangular, with anterior lateral angle rounded and furnished with two strong setae accompanied by several smaller ones; posterior angle acute, directed laterad and slightly caudad;

Fig. 15. Dorsal aspect of first instar larva. Note absence of laterally flared dorsal shields. Fig. 16. Lateral aspect of second instar larva. AP, anal processes. Fig. 17. Dorsal aspect of third instar larva. Fig. 18. Lateral aspect of fourth instar larva.



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lateral margin furnished with several strong setae accompanied by smaller ones. Ten abdominal segments tapering from first to last; tenth segment trapezoidal, with strong setae on posterior half, with anus in which is located the eversible anal processes (Fig. 16); tergum and sternum furnished with numerous rather strong setae; posterior margin of the sternum of each segment with a row of long setae; urogomphi borne sub-dorsally between ninth and tenth abdominal segments. Tenth abdominal segment about two-fifths as long as first segment of urogomphus; second segment of urogomphus about one-sixth the length of the first; first segment furnished with small, strong setae, the bluntly subulate second segment very sparsely setose.

Ventral shields on abdominal segments two to eight inclusive similar to those of dorsum; the lateral margins never extend beyond inner margin of spiracular peritreme; posterior margin furnished with a row of strong setae, surface sparsely setose.

PUPA. — Pupae (Figs. 23, 24) are elongate and exarate. Pupal size varies in accordance with the nutritional history of the larva. Table 1 indicates measurements obtained for three pupae.

Color of the pupa is cream white which gradually darkens as eclosion approaches. Sclerotization is light to moderate, the prothorax being the most sclerotized region of the body.

Head rotundate, somewhat compressed dorso-ventrally, glabrous and sharply bent beneath the prothorax so that the mouthparts are directed posteriorly. Eyes bulge prominently from the head; antennae project at a right angle from the head and lie against the ventral surface of the prothorax with their distal ends curving posteriorly. Labrum deeply emarginate, glabrous. Mandibles and maxillary palps are easily discernible.

Pronotum orbicular, transverse and bears small scattered spines, especially on the anterior portion of the disc and bordering the margins; four long setae project cephalad from the anterior margin of the pronotum. Scutellum of mesothorax triangular and partially covering metathorax; scutellum of metathorax broadly triangular. Elytra extend posteriorly to the second abdominal segment; wings extend posteriorly to the third abdominal segment; elytra and wings pressed close to body.

Fore- and mesofemora extend anteriorly at approximately 45° angles from the longitudinal axis of the body; metafemora project at nearly a right angle from the longitudinal axis of the body. Legs without setae.

Abdomen consists of nine, tapering, movable segments, the ninth ending with slightly incurved, stout urogomphi; each segment, except the first, bears a lateral rumule which terminates in a long, slender, recurved seta that is basically thickened and gradually tapers towards its distal end; each urogomphus possesses a similar terminal seta.

ADULT. — Adults (Fig. 1) are broadly oblong, depressed; length 12 to 24 mm, width at widest point 6 to 14 mm; color dull, glossy black.

Head (Figs. 25, 26) elongate, broadest across the eyes, densely punctate, slightly deflexed; occipital ridge prominent; constriction behind eyes strong.

TABLE 1.—Measurements for larvae in each instar and pupae in mm.

	Instar				Pupa	
	1	2	3	4		
Head width between ocelli	RANGE	0.9-1.0	1.0-1.1	1.4-1.5	1.7-2.0	1.4-2.0
	MEAN	0.9	1.1	1.5	1.9	1.6
Pronotum width at widest point	RANGE	1.8-1.9	1.7-2.1	2.9-3.2	3.8-4.8	5.0-6.5
	MEAN	1.9	1.8	3.1	4.4	5.5
Total body length	RANGE	5.5-6.0	7.0-8.0	8.5-25.2	17.6-25.0	18.5-25.2
	MEAN	5.7	7.3	14.4	21.3	22.5

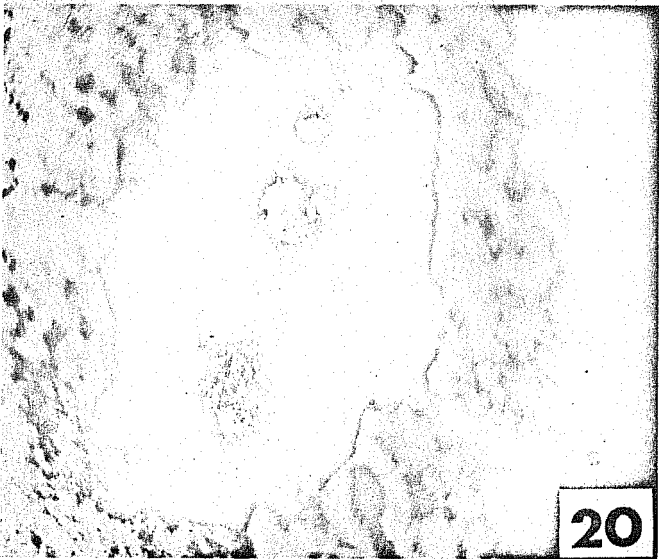
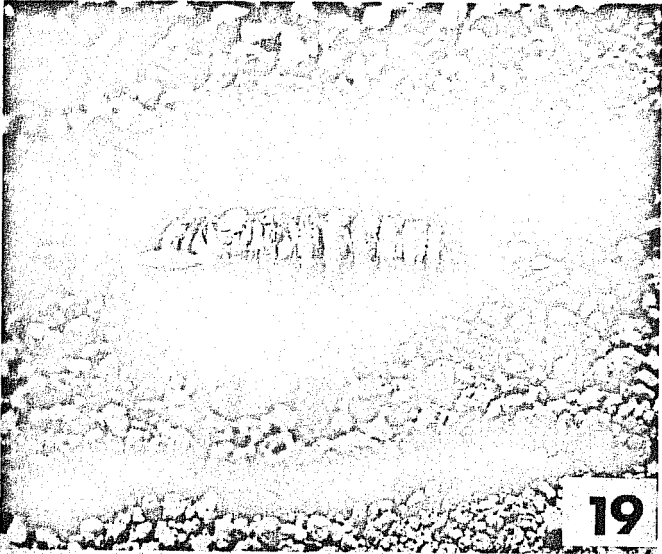


Fig. 19. Dorsal aspect of larva preparing to moult. Fig. 20. Ventral aspect of a pharate pupa within its pupal chamber.

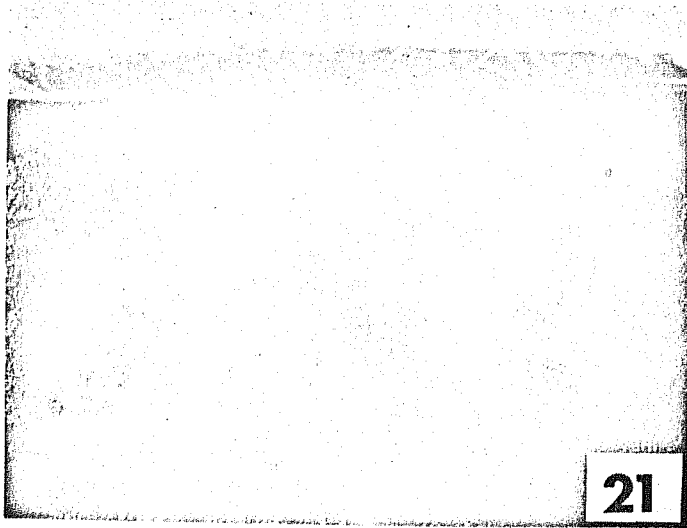


Fig. 21. Unearthed pupal cells. Fig. 22. Ecdysis of a pharate pupa.

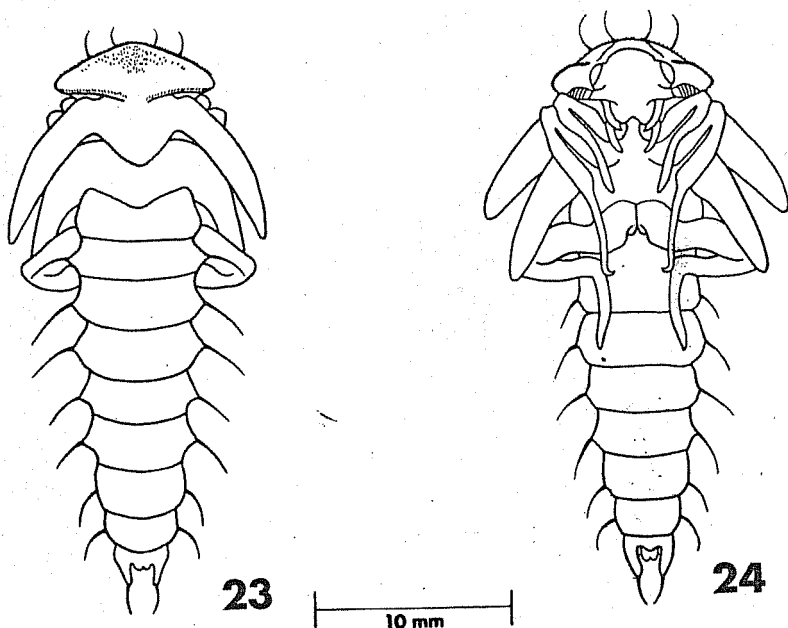
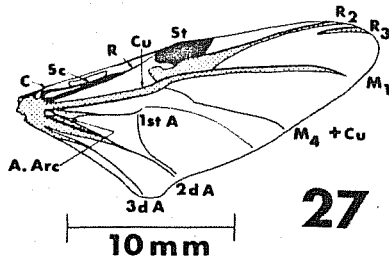
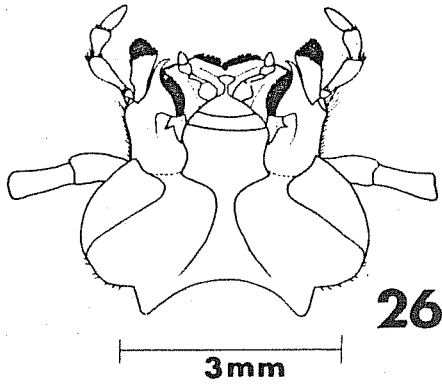
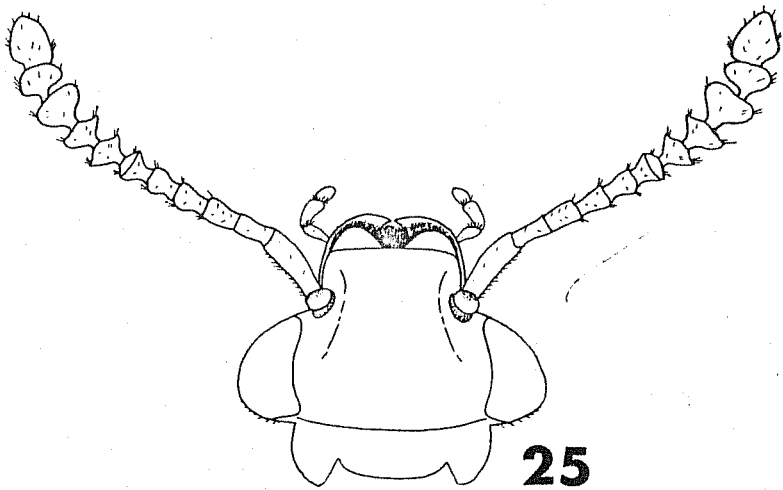


Fig. 23. Dorsal aspect of pupa. Fig. 24. Ventral aspect of pupa.

Eyes large, prominent, bulging laterally, oval, posteriorly truncate. Antennae 11-segmented, gradually clavate, inserted below the eyes; second segment as long as third, segments 9 to 11 grayish pruinose. Labrum small, distinct, broadly emarginate. Mandibles prominent, curved, apices acute. Maxillae with four-segmented palpi of moderate size, segments subequal. Labium with small, three-segmented palpi, segments subequal.

Thorax with pronotum much larger than head, as wide as base of elytra, orbicular, transverse, borders margined, shining black, densely punctate, more coarsely punctate near marginal posterior half; prothoracic spiracle exposed. Pro- and mesosternum small, metasternum large, pleural area explanate. Trochantin of foreleg distinct; forecoxae prominent, quadrate; hind femora of male (Fig. 28) usually enlarged; tibia slender, frequently curved in male, straight in female (Fig. 29), large apical spurs; tarsal formula 5-5-5, segments with tomentose pads ventrally; first four

Fig. 25. Dorsal aspect of adult head. Fig. 26. Ventral aspect of adult head. Fig. 27. Right wing; interpretation of veins based on Forbes (1922). C, costa; Sc, subcosta; R, radius; St, stigma; R₂, second branch of radius; R₃, third branch of radius; M₁, first branch of medius; M₄ + Cu, fourth branch of medius plus cubitus; 1st A, first anal; 2d A, second anal; 3d A, third anal; A. Arc., anal arculus.



segments of protarsi of male more strongly dilated than mesotarsi. Scutellum large and prominent.

Elytra not shortened, slightly wider posteriorly, surface punctate, tricostrate; tubercle behind middle between second and third costae, a short basal costa between second and third costae; apices sub-truncate in male and slightly arcuate in female; elytra occasionally immaculate, usually marked with a transverse, subapical row of one to five reddish-orange spots variously combined, occasionally with a sub-basal transverse row of one to three spots (Fig. 30). Wings (Fig. 27) with thickened stigma, anal area simple with no connection between second anal and third anal; anal arculus present.

Abdomen with five visible ventral segments, surface punctate. Male genitalia (Fig. 31) trilobed, median lobe large, lateral lobes prominent, basal-piece ring-shaped. Female genitalia (Fig. 32) with simple proctiger and simple paraprocts; valvifer simple and flattened; stylus apical, stout, broader at apex; coxite stout.

Males occasionally occur with entirely undeveloped femora or sub-truncate elytra and differ in no respect from the female except for the dilation of the protarsi.

DISTRIBUTION.

GEOGRAPHIC. — *N. surinamensis* has a relatively broad distribution. Portevin (1926) reported (incorrectly) that it occurred over all of North America. Blackwelder (1944) and Hatch (1928) delineated its distribution in South America with question marks. No effort was made in this study to plot the South American distribution, and only one specimen, a male, with the following data was obtained: Ucayali and Marañon Rivers, [PERU], South America, C. Sarkady collector. Arnett (1946) pointed out that few silphids are to be found in tropical lowlands because their food source, e.g., decaying animals, does not exist long enough in these areas for the beetles to complete their development. Carrion is either set upon by vultures, reduced by swarms of ants and flies or desiccated by the sun in a few hours. Apparently *N. surinamensis* may be limited to the medium highland areas of northern South America. Topographically, it would have encountered few difficulties in expanding throughout this region from Central America (?) as the northern Andes can be easily circumvented. It is probable that *N. surinamensis* invaded

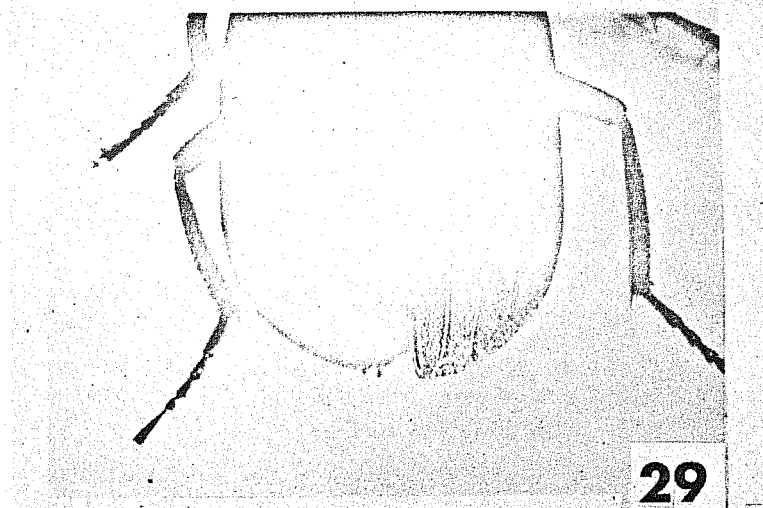
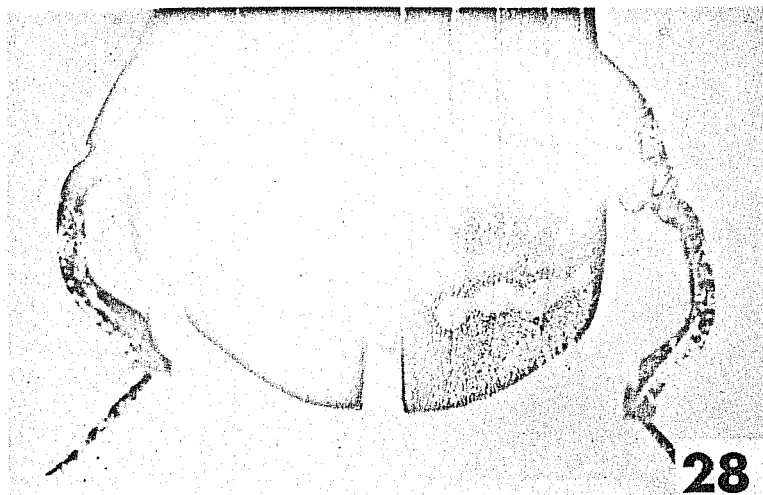
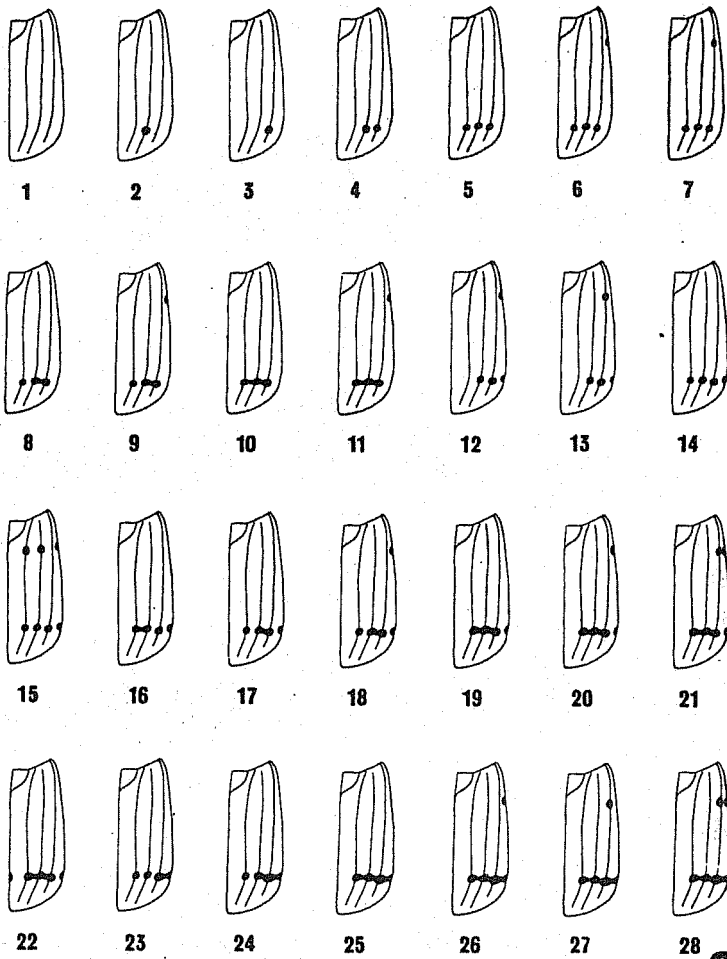


Fig. 28. Dorsal aspect of male showing greatly enlarged femurs and curved tibiae of hind legs. Fig. 29. Dorsal aspect of female showing unmodified hind legs.



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Fig. 30. Total variation known in elytral markings. Those specimens possessing a sub-basal row of spots were designated an aberration by Portevin (1926) and called *bizonatus*.

this area from North America because it would be unlikely for such a carrion-inhabiting insect to evolve in the predominantly inhospitable conditions of the tropics and then move northwards into more temperate regions. *N. surinamensis* is indigenous to

temperate North America and has secondarily occupied parts of South America.

Dr. Alfredo Barrera, Museo de Historia Natural de la Ciudad de Mexico, indicates (*in litt.*) that he is not aware of any Mexican records. Thorough, selected collecting would undoubtedly yield Mexican specimens, especially in light of the fact that there are Texas border records.

In the United States *N. surinamensis* is known from east of the Rocky Mountains and in certain areas of the Pacific Northwest, Montana and Utah (Blatchley, 1910; Brimley, 1938; Britton, 1920; Dury, 1902; Fattig, 1936; Hatch, 1928, 1933, 1957; Knudsen, 1959; Leng, 1920; Malkin, 1953; Meserve, 1936; Rauterberg, 1885; Wickham, 1895b). The arid and semi-arid conditions of the American Southwest and probably parts of Mexico prevent it from establishing there, and the Rocky Mountains provide a barrier preventing direct westward movement. Fig. 33 indicates distribution for the United States by county record. Extremely thorough collecting would probably provide records for all counties east of the 104th meridian on this map.

N. surinamensis has been taken throughout much of southern Canada (Carr, 1920; Chagnon, 1917) though much less so in Saskatchewan, Alberta and British Columbia. Kirby (1837) incorrectly stated that it occurred in all parts of Canada. Ronald Hooper, Saskatchewan Museum of Natural History, suggests (*in litt.*) that it is scarce in Saskatchewan. Fig. 34 indicates distribution for Canada by county and census division records.

Malkin (1953) took note of the isolated and sporadic records in the Pacific Northwest, Montana and Utah. He conjectured that the beetles may have been transported there by human agency or that they migrated from Alberta to the Northwest and then to Utah. Table 2 lists all the known collecting records for this region. *N. surinamensis* may have actively dispersed into these areas by skirting to the north of the Rockies and then proceeded southwards by the routes of least resistance, namely, large river valleys which, in many cases, are accompanied by transportation systems. Malkin stated that Pouce Coupe, British Columbia, is about 60 miles east of the Rockies. Elevations in this region often drop below 7000 ft. In the absence of direct experimental evidence, it is suggested that *N. surinamensis* may have moved

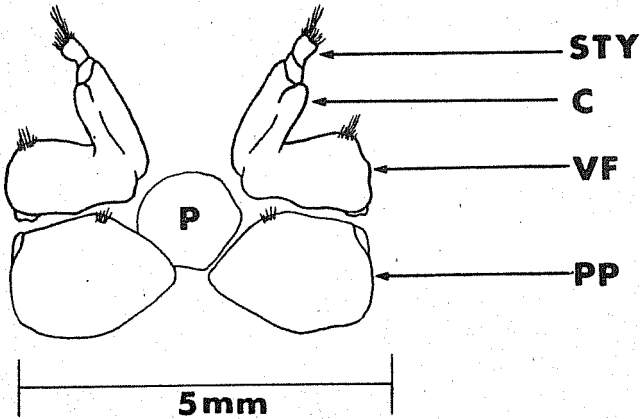
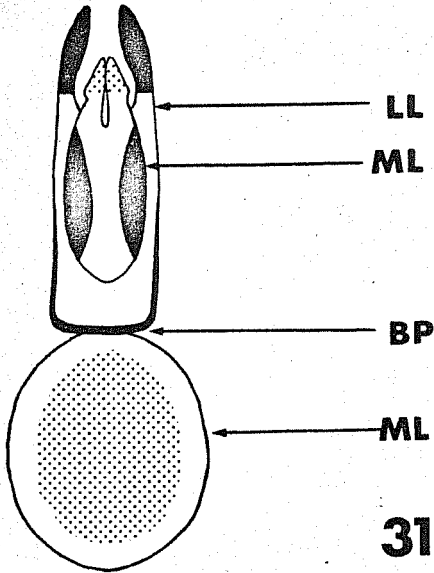


Fig. 31. Ventral aspect of male genitalia. LL, lateral lobe; ML, median lobe; BP, basal piece. Fig. 32. Female genitalia with all parts flattened

west through the Rockies by way of the Peace River and then south to the vicinity of Prince George by way of the Parsnip River and Crooked River valleys. The Fraser River provided a southward dispersal route to extreme northwest Washington where the Coast Ranges and the Cascade Range funneled the insects south to the Columbia River. Further southward movement along the Willamette River accounts for the Oregon records. Following the Columbia River east through the Cascades allows for the Yakima and Walla Walla county records in Washington.

The Snake River valley was then used to reach Spokane and Whitman counties in eastern Washington and Latah county in western Idaho. Following the Snake into southern Idaho opened the way into Utah where again movement was southward. Arid conditions in Utah may have presented some difficulties to dispersal.

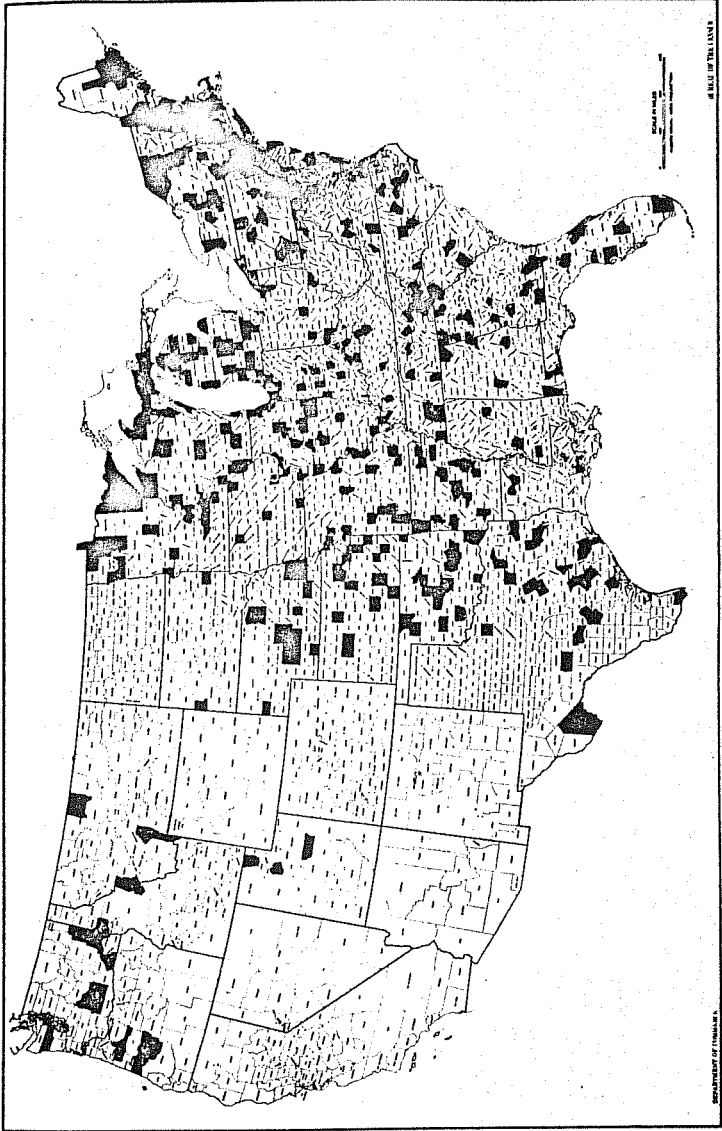
All the Montana records reflect direct southwestwards movement from the eastern part of its range. Gallatin county was reached by extending southwest along the Missouri and Gallatin Rivers, and establishment in Ravalli county was a southward extension by way of the Bitterroot River south of Missoula. These records do not indicate an eastward extension of the western population because the northern Rockies are a barrier here.

The earliest record for the region is 1946 at Eugene, Oregon. Hatch (1957; *in litt.*) is of the opinion that *N. surinamensis* was recently introduced and is rapidly becoming established. It is agreed that its presence is recent, and that it is establishing itself. However, the dispersal routes described above form a natural pathway, and the possibility remains that its occurrence in the Pacific Northwest is the result of a natural phenomenon, rapid though it may seem, and not an introduction by human agency. When natural pathways, such as river systems, are accompanied by human transportation routes, then past movements by active dispersal versus a modified biochore dispersal become extremely difficult to ascertain. At the present time the data are insufficient to determine how *N. surinamensis* arrived in western North America.

out (after Arnett, 1944). STY, stylus; C, coxite; VF, valvifer; PP, paraproct; P, proctiger.

TABLE 2. — Collecting records for *surinamensis* in the Pacific Northwest, Montana, Utah, etc.

DATA	DEPOSITORY
ALBERTA	
Edmonton, VI (Carr, 1920)	—
SASKATCHEWAN	
1, Neptune, X-6-49, M. Johnson coll.	U. Manitoba
2, Indian Head, VII-25-48, C. Brown coll.	"
4, Somme, V-13-64 and VII-68, R. Hooper coll.	R. Hooper
1, Fort Qu' Appelle, X-65, R. Hooper coll.	"
1, Livelong, IX-1928	Ent. Res. Instit., Ottawa
BRITISH COLUMBIA	
1, Oliver, VI-18-58	"
1, Nelson, VII-31-60	"
1, Woodcock, 1953	Mus. Comp. Zoo., Harvard
1, Pouce Coupe, VI-18-27, P. Vroom coll.	Calif. Acad. Sci.
WASHINGTON	
1, Colleege Place, V-4-49, G. Nelson coll.	U. Wash.
1, Pullman, V-11-58, C. Hagel coll.	Wash. St. U.
2, Cheney, IV-6-51	Ore. St. U.
4, Toppenish, VI-25-57, VII-17-57, VII- 6-56, VII-15	U. Wash.
OREGON	
1, Eugene, VII-46, B. Malkin coll.	"
1, Salem, 1955, P. Larsen coll. (Hatch, 1957)	—
IDAHO	
1, Moscow Mountain, V-5-49, W. Barr coll.	U. Idaho
MONTANA	
1, Hamilton, VIII-19-61	Ent. Res. Instit., Ottawa
1, Gallatin Co., V-5-51 series, Bozeman, V-17-40, R. Foote coll. & VI-1-24	Mont. St. U.
	"
UTAH	
1, Salt Lake City, XI-1-51 Jorgenson coll.	U. Utah
2, Dennison, 1951, Solander coll.	"
1, Logan, VIII-6-48, J. Judd coll.	Utah St. Ag. College
2, Green Canyon, V-51	"



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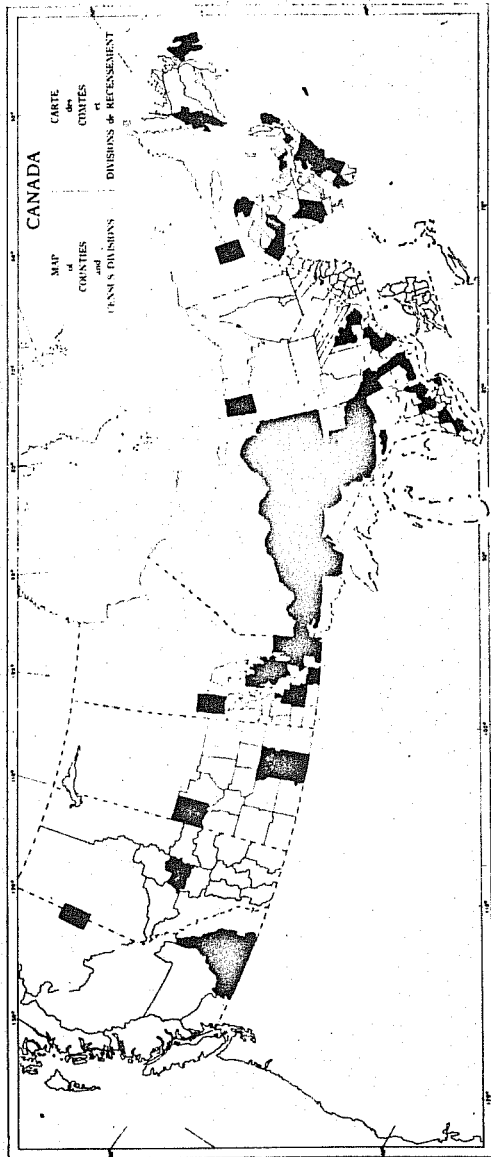
Fig. 33. United States distribution by county.

Because of its wide distribution, *N. surinamensis* is found in a variety of climates. A large portion of lowland South and Central America are tropical rainy with different local climates in the highlands and in the dry scrub and desert areas. The southeastern United States is humid mesothermal, and the Northeast and Canada are humid microthermal. Parts of the Great Plains are dry, while various local climates exist in the Northwest and adjoining mountain regions.

The northernmost occurrence of *N. surinamensis* approximates the northern boundary of the -20 to -10C January average temperature curve through Canada. Furthermore, *N. surinamensis* will probably not be found in areas of less than 37.5 cm average annual precipitation. The beetle is found in various habitats ranging from flat farmland and prairie to forests. Walker (1957) encountered it in great numbers in a maple-gum-oak forest indicating that foliage density does not serve to maintain any ecological separation which is interesting from the standpoint of food-search behavior as a forest habitat would conceivably interfere with random in-flight searching.

Collecting records indicate that populations in the eastern United States are far greater than in the Midwest, West or North; these records were not extensive enough to indicate population densities when the distribution was mapped.

SEASONAL. — There are no standard limitations for the seasonal occurrence of *N. surinamensis*. As soon as winter conditions (where applicable) ameliorate sufficiently, the overwintering adults emerge and become active; in the study area this was normally in the first two weeks in April. Since *N. surinamensis* is a homodynamic insect, a continuous sequence of overlapping generations occur as long as conditions are favorable. Obviously the termination of these conditions varies in different parts of its range depending on local climates. Beetles may remain active during the winter months in the southern parts of its distribution. In the study area, overwintering usually began before the first week of November. *N. surinamensis* has been collected in every month of the year.



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Fig. 34. Canadian distribution by county and census division.

FOOD RELATIONSHIPS

The food relationships of *N. surinamensis* have been so fragmentarily reported that they have remained in a state of confusion, and the literature contains nothing of substance in reference to larval foods. Bell (1873) reported *N. littoralis* (L.) adults feeding on fly maggots in England, and Clark (1895) was the first to report *N. surinamensis* feeding on maggots. Clark divided the carrion-feeding beetles into three divisions based on the character of their food: (1) those feeding on carrion entirely, (2) those feeding on maggots to a limited extent, and (3) those feeding on maggots exclusively. He placed *N. surinamensis* in the third division. Clark accurately pointed out that collectors generally had gone on the supposition that these beetles fed on the substances in which they were found. He was, however, inaccurate in limiting the beetle to a diet of maggots only. Champlain (1909) observed *N. surinamensis* feeding on maggots, and Davis (1915) reported adults consuming maggots and decaying



Fig. 35. Alert position of adult.

flesh. Hatch (1927) said that *N. surinamensis* adults were primarily predators on fly maggots, and that carrion may serve as a partial source of food; he kept imagos on a carrion diet for several weeks.

Reed (1958) was the first to report a larva consuming a maggot. Larvae or adults have never been recorded as feeding on maggots from any source other than carrion. Furthermore, the beetles have never been observed feeding on smaller insects while at lights, but there is need for further observation in this regard.

Nothing is known about the food-search behavior of *N. surinamensis*. It is probably carried out on the wing, but such aspects as the distances at which the odor of food is perceived, pattern of search flight, territory covered by a single beetle, altitude of flight and the duration of flight remain a mystery. The means by which the beetles detect carrion is also not known, and the specific olfactory receptors for detecting odors have not been located. It may even be possible that the beetles rely on senses other than olfaction for finding food.

Shubeck (1968), experimenting with *Silpha noveboracensis* (Forst.), found that there was a linear relationship in the distance at release and the rate of return to carrion when released at distances from 5 to 75 meters. He concluded this was apparently due to random wandering and not because of orientation to carrion odors. His experiments demonstrated a significant increase in ability to return to carrion below two meters, and the periphery of odor perception seemed to be about one meter from carrion when air movements were negligible. The distance of attraction was much less than what had generally been believed.

Unfortunately, Shubeck's paper was consulted too late in this study to make use of his observations. A release-recapture experiment was conducted but employed release distances of one-fourth, one-half and three-fourths of a mile in the four compass points from a centrally placed carcass. Careful checks of wind direction and velocity were kept but proved useless as the distances used for release were probably too great. No marked beetles were recaptured.

It would be hazardous to apply Shubeck's results to *N. surinamensis* without experimentation. But, considering the irregular

occurrence of carrion, it is reasonable to assume that the beetles engage in random in-flight searching for food.

When approaching carrion, *N. surinamensis* circles the carcass from one to several times and lands clumsily a few inches to a few feet away. After landing the beetles usually walk in a straight line to the carcass and immediately seek cover beneath or in it.

N. surinamensis adults feed primarily on fly maggots (Calliphoridae) during the active decay stage of a carcass when maggots are always in great abundance. Excretions and decomposing flesh are also consumed regularly but not as frequently as dipterous larvae. Beetles are commonly found on carcasses in early stages of dry decay after maggots have burrowed into the ground for pupation. During this time they may feed on the dried skin, muscle and connective tissue that remain or possibly on soft bodied insects such as dermestid larvae or not at all. Beetles in laboratory colonies, in general, did not eat carrion in the early stages of dry decay; adults placed on fresh carcasses in the laboratory fed on flesh only half-heartedly or to occasionally obtain moisture. In neither of the preceding instances were other insects present. Although primarily predators of maggots, *N. surinamensis* can subsist on flesh alone.

Under laboratory conditions it was noted that adult beetles would often move aside for maggots that had blindly run into them. This happened on numerous occasions, and it could reasonably be supposed that the beetles did not attack because they were not hungry at the time; however, beetles denied food for several days initially behaved in the same manner. The beetles were definitely aware of the maggots but were probably not being stimulated under the proper set of conditions, namely, those of a decaying carcass. The various sign stimuli associated with carrion were not present to activate the fixed action pattern of feeding on maggots. Under the artificial conditions of the laboratory it may have taken *N. surinamensis* longer to associate the maggots for what they actually were.

It was easily apparent that *N. surinamensis* adults were aware of maggots because a beetle would actually turn its head (as much as it was able) to follow the movement of a maggot. It was observed that, at distances of two inches, *N. surinamensis* would

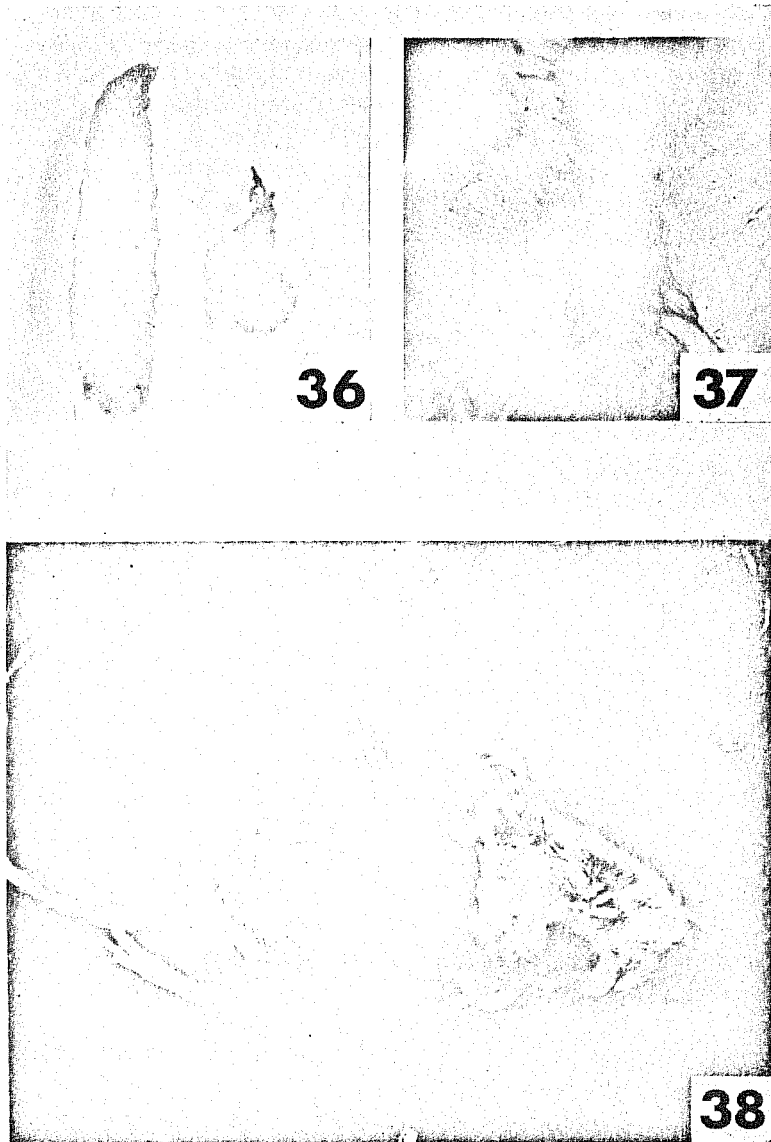


Fig. 36. Intact maggot contrasted with remains of maggot of comparable size showing extent of feeding by adult beetles. Fig. 37. Access slit cut through skin of carcass. Fig. 38. View of carcass illustrating results of fur-stripping behavior of adult beetles.

start, elevate its head, and extend its antennae as it recognized a maggot approaching (Fig. 35). As previously mentioned, beetles often moved aside when run into by a maggot; occasionally they would remain stationary when struck. In numerous instances beetles seized maggots, dropped them and repeated this sequence several times. In the presence of a single maggot, *N. surinamensis* pursued and snapped sporadically at the same individual for as long as ten minutes. When a number of maggots were present, beetles successively picked up and dropped several until one was ultimately eaten. Champlain (1909) and Reed (1958) also observed this picking up and dropping behavior which would finally end with a meal. Whether *N. surinamensis* is selecting for something in particular is unknown, but, based on this curious behavior, it would appear likely.

The fourth type of maggot response recorded for *N. surinamensis* was to directly attack a maggot on sight. Maggots were seized with the mandibles and restrained by the forelegs which were positioned on either side of the prey. In every instance noted, *N. surinamensis* raised or elevated its head as it grasped the struggling larva. This maneuver reduces the possibility of escape by the maggot as it is lifted above the substrate and so prevented from pulling away from its captor. After easily breaking the integument of the maggot, beetles chewed rapidly and extricated the soft contents. From the mid-region of the maggot body, chewing quickly and methodically proceeded forward to the head and then caudad to the end of the body. This kneading was repeated two or three times until nothing but an empty skin remained (Fig. 36). Duration of feeding on a single maggot ranged from between 5 to 40 minutes. Maggots were usually eaten under or immediately adjacent to the carcass or occasionally carried away into nearby shrubbery. Davis (1915) observed three *N. surinamensis* resting on low plants and feeding on maggots. He stated that the beetles usually did not climb on anything but sought some retreat on the ground or fed at the carcass.

Orientation of the beetles when feeding is of little importance except when it may afford some advantage to a still struggling meal. *N. surinamensis* were seen feeding in horizontal to head down vertical positions. When feeding is completed a short

period of inactivity may follow during which a variable amount of grooming is performed.

N. surinamensis practice intraspecific predation both as larvae and adults. Overcrowding and shortage of food are the major causes of cannibalism. In one field colony of 36 adults (maggots not present on carcass) fully eight-ninths of the beetles were killed or eaten by their companions. Individuals in a weakened state resulting from age, hunger or disease are more susceptible to predation.

Cannibalism in the larvae was very pronounced in laboratory colonies although crowding was kept from being a factor. In one instance, a particular larva attacked and killed every other larva with which it was placed; the presence of decaying flesh seemed to be ignored until after other larvae had been killed. Survival techniques may apparently tend to become exaggerated in some individuals.

When one larva engages another, the attacker continually attempts to seek out the soft underparts of the victim which, naturally enough, thrashes about wildly in an effort to dislodge its antagonist. The attacker, tightly curled over one end of its prey, normally subdues it in about ten minutes providing the resistance can be overcome. Feeding begins after the soft sternum of the prey is pierced.

Larvae and adults in all laboratory colonies were found to be extremely fond of moisture whether it was water soaked cotton, a water soaked carcass or water poured into a cage. Adults frequently gave preference to clustering around moist cotton rather than beneath carrion; this tendency was not as noticeable in the larvae although they would, on occasion, go to water soaked cotton and drink from it. Adult *N. surinamensis* actually drink water in droplet form and even from shallow puddles. Beetles were seen to imbibe large drops of water that beaded up on a plastic surface. The mandibles were placed in the drop and moved rapidly and regularly in a chewing motion while the water was sucked up. When drinking from a puddle, *N. surinamensis* walk into it and drink in the same fashion as from a droplet.

When larvae or adults feed on a fresh carcass, access slits (Fig. 37). are cut through the skin with the sharp mandibles so

that the soft flesh can be reached. Steele (1927) reported holes cut for this purpose by *Nicrophorus*. Feeding normally begins at the natural body openings if access slits are not cut. In the adult beetles, no concerted effort is made to consume the flesh of the carcass past the point of making slits.

Adults also frequently strip off the fur (Fig. 38), usually from the venter of a carcass, in what may be described as maggot searching behavior. Maggots are commonly found just under the fur in fresh mammal carcasses and, in actively seeking them out, the beetles tear away the fur which conceals them. Cutting away the body hair was pronounced in maggot-free laboratory colonies and less observable in field carcasses because the activities of maggots usually denuded the carcass rapidly anyway.

Larvae and adults are active during the day on carrion and remain active at night. The adults and possibly the larvae continue to feed on maggots nocturnally. Champlain (1909) also observed adults feeding on maggots at night.

Payne (1965) noted that temperature during the bloated decay stage was slightly higher than the soil temperature. In active and advanced decay, carrion temperature was considerably higher than soil temperature and even higher than the surrounding air temperature. Payne stated that the activities of insects were more influenced by temperature than by any other environmental factor. *N. surinamensis* adults and immatures are also active on carrion during period of precipitation and do not appear disturbed by it.

While the adults are predators on maggots and, in addition, may feed on carrion to a limited extent, the larvae normally feed on carrion and, in addition, feed on maggots. During active decay the larvae feed on the decomposing flesh and semi-liquid putrefaction.

Larvae were occasionally seen feeding on maggots but never to that degree practiced by the adults. The relative size of the maggot is apparently not important because larvae were seen devouring maggots larger than themselves. Maggots are usually seized 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. In one instance a maggot was reduced to half its original size in four minutes by a foraging

larva; the remaining portion of the maggot was not eaten but discarded.

Individuals inhabiting carcasses in active decay are, on the whole, considerably more active than those inhabiting carcasses in dry decay. Some continually wander, perhaps in search of maggots, while others writhe in the putrefaction. The crowded conditions caused by the presence of numerous other carrion insects during this stage of decay may also provoke increased activity by *N. surinamensis* larvae. Larvae reared and isolated in groups of two in the laboratory were noticeably less active; laboratory conditions may have contributed to this state although this was not ascertained.

In the later stages of advanced decay and the early stages of dry decay larvae feed on skin, connective tissue and the shreds of remaining flesh by scraping and gnawing with their mandibles. They usually do not move around a great deal after finding a satisfactory place to feed. Larvae have been successfully reared in the laboratory to the adult stage in the absence of maggots which would indicate that maggots are not essential to the diet.

N. surinamensis larvae, like the adults, often feed in groups. Larvae were frequently seen feeding together with their heads in close proximity. Although adults tend to congregate in the skull or chest cavity of a carcass for sexual contacts and to feed in shelter, larval feeding tends to be in non-specific areas of a carcass: no particular use is made of the body cavities by the larvae. Larval communal feeding might be explained by the fact that a preferable portion of a carcass is conducive to feeding in a particular spot.

Larvae inhabiting old and extremely dry carcasses in the latter stages of dry decay would, when the infrequent occasion presented itself, migrate to a fresher carcass if it became available at a relatively close distance. In the instance observed, larvae were seen moving over a gravel road a distance of approximately 20 feet from an old to a new carcass. The sensory capabilities of *N. surinamensis* larvae are unknown but may be better than would be expected.

N. surinamensis did not show any marked preferences for various types of carrion such as amphibian, reptilian, avian or

mammalian. This in itself is not extremely significant as the adult beetles do not actively and extensively feed on the decomposing flesh. Whether or not these carcasses will support maggot populations is of more importance to the adults and may limit their occurrence to carcasses in those circumstances which will allow development of a maggot population.

Size and dermal character of the carcass are probably more salient aspects than type of flesh when considering whether a carcass will or will not be a food site for *N. surinamensis*. Howden (1950) stated that reptile carcasses are often void of carrion fauna because of their scales and shells. It should be added that most reptiles are elongated and present a much greater ratio of surface area than to volume; as a consequence they desiccate very rapidly and so become unsuitable feeding or breeding areas for most carrion insects. Bird and fish carcasses also desiccate with relative swiftness and do not normally support large populations of necrophagous insects. The usual carrion fauna, including *N. surinamensis*, can be found on these types of carcass but in a considerably compressed time sequence. Most amphibians, because of their small size and soft, moist skins, dry up rapidly and are not utilized extensively by carrion insects. It should be remembered that the microclimate in the vicinity of the carcass site can play a significant role in moderating or accelerating rate of desiccation, especially in those types of carcass most sensitive to moisture loss. Extensive documentation exists on the capacity of mammal carcasses to support carrion insects, and it is on these carcasses that *N. surinamensis* are most frequently encountered.

N. surinamensis has been found at the following types of carrion: lobster, fish, toad, snake, crow, chicken, pheasant, cow, horse, deer, rabbit, mouse, squirrel, dog, cat, raccoon, opossum, skunk, pig, porcupine and muskrat. In addition, there are reports of the beetle being found at sugar baits in Illinois and boring in "birch fungus" in Wisconsin.

Ronald R. Hooper reported (*in litt.*) specimens collected from the bottom of pails that had been used to feed milk to calves. He suggested that the beetles had come at night to feed on the accumulated remains of sour milk in the pails. An experiment was conducted to determine the desirability of small portions of

congealed, sour milk. When presented with this new food, beetles immediately began feeding on it with apparent relish and for a considerable length of time. How they were able to detect and locate residual amounts of souring milk in pails located inside of a barn is another question.

Laboratory specimens have also been observed to feed actively on peanut butter, lettuce and fresh hamburger. It is believed that the range of accepted foods demonstrated in the laboratory and recorded for collected specimens opens up new questions as to what the beetles may feed on in the wild when they are not at carrion or carrion is not available.

Inadequate nutrition can cause a prolonged larval period or an increased number of moults (Wigglesworth, 1950). Prolonged larval periods in *N. surinamensis* were observed, especially in laboratory colonies. In other instances, immature larvae did not moult, became inactive, refused food and eventually died. Payne (1965) noted that on many occasions larval silphids and staphylinids failed to complete their development because the carrion was dry and void of the dipterous larvae which were their prey. In the case of *N. surinamensis*, it has already been indicated that larvae survive well in the absence of maggots and can develop on carrion alone. However, a point can be reached when the remains of a carcass are so dry and hard as to impede development of the larvae.

Variation in the quantity of food available may also cause larvae to pupate early or late in their development and thus cause extensive variation in the body size of the adult insect. *N. surinamensis* seems to exemplify this as intraspecific size variation is considerable.

ENEMIES

N. surinamensis has a number of enemies, but apparently none pose a severe threat to any population of the beetle. It was observed that the larvae of *N. surinamensis* were often attacked and eaten by adults of *Staphylinus maxillosus* L. This staphylinid is normally found in conjunction with carrion where they feed primarily on the larvae of Diptera. Its predatism probably extends

to anything that falls within its grasp easily, including silphid larvae.

To better observe the predatory habits of *S. maxillosus* on *N. surinamensis*, individuals of both were confined together in the laboratory. After a lapse of just over a minute, the staphylinid attacked the larva. It mounted the dorsum of *N. surinamensis* and, facing in the same direction, attempted to reach the softer underparts by curling its head in front of and under the head of its prey. This was repeated several times. On occasion, *S. maxillosus* mounted facing in the opposite direction and, in so doing, curled the tip of its abdomen over the head of *N. surinamensis* in what appeared to be a holdfast movement. During the entire time while the rove beetle was maneuvering for a kill, the larva thrashed about wildly in a usually futile attempt at escape. *N. surinamensis* larvae are relatively quick and agile, but are no match for an adult *S. maxillosus*. Eventually the sternum of the larva was pierced by the mandibles, and most of the soft contents were consumed.

A similar experiment was conducted to ascertain whether *S. maxillosus* would attack adult *N. surinamensis*. After an elapsed period of two days there had been no observed encounter, and *N. surinamensis* remained unharmed. The size of the adult silphid may have been a deterrent to the rove beetle; however, Fichter (1948) observed *S. maxillosus* attacking trogids and members of its own species, beetles as large or larger than itself. The agility, speed and strength of an adult *N. surinamensis* are probably more instrumental in saving it from insect predators such as *S. maxillosus*.

In September, 1969, two *Staphylinus* sp. were found feeding on a third instar *N. surinamensis* beneath a dog carcass. Also feeding on the same larva were three histerids, *Euspilotus assimilis* Payk. It could not be determined whether the smaller staphylinids and histerids were able to subdue a healthy, larger larva or one that was in a weakened condition for some reason or another. Moulting can be a dangerous time for the larvae of *N. surinamensis* because they are temporarily incapacitated and highly vulnerable to predators such as staphylinids, histerids and other silphids. The larva in this case was not engaged in a moult.

Because the eggs of *N. surinamensis* are deposited randomly on the soil near a carcass, some are probably eaten by mites, histerids, ants and other insect predators which frequent carrion. Many eggs might also suffer mechanical damage if placed close to a carcass because of the movements of the numerous insects that are present.

It is likely that various soil insects occasionally discover pupal cells of *N. surinamensis*. Even if the pupa is not consumed by an insect intruder, the destruction of the integrity of the microclimate of the pupal chamber might be such as to cause the death of the pupa. In addition, burrowing mammals such as moles and shrews consume insect pupae when they discover them.

Adult beetles are frequently found at lights in the spring and summer, and a variety of frogs and toads can also be found at these lights during parts of the year feeding on insects. Two such amphibians were common at lights in the study area: the Rocky Mountain Toad, *Bufo woodhousii* (Gerard), and the Leopard Frog, *Rana pipiens* Shreber. Specimens of each were brought into the laboratory to determine whether they would accept *N. surinamensis* adults as food, which they subsequently did. Ingestion by frogs and toads at lights probably occurs infrequently because the number of *N. surinamensis* proportional to other insects at these lights is small.

Some reptiles may also include *N. surinamensis* in their diets. Reed (1958) reported that a carcass in a marsh area was visited by turtles. The gut contents of a Snapping Turtle, *Chelydra serpentina* (L.), contained, among other carrion insects, four silphid larvae; the gut contents of Box Turtles, *Terrapene carolina* (L.), contained larval and adult silphids. No mention is made of *N. surinamensis*, but these data do show that silphids are in a vulnerable position.

Mammals such as foxes, skunks and opossums forage for insects beneath lights, and *N. surinamensis* may fall prey to them. As was previously noted, test carcasses were often disturbed by nocturnal mammal scavengers. Although these animals were not searching directly for carrion insects, it is likely they would devour them on occasion, especially when these insects are right under their noses as it were.

Nothing is known in regards to the bacteria and viruses that may attack *N. surinamensis*. Similarly, internal parasites are unknown for the beetle. The digestive tracts of 30 adults were examined for parasites, but none were found. Laboratory colonies, especially those utilizing fish carcasses, often became infested with nematodes. These did not appear to harm *N. surinamensis* even though the beetles often became covered with them. Eggs and pharate pupae, at least in the laboratory, were often killed by molds.

MITE RELATIONSHIPS

The role played by the mites that are usually associated with *N. surinamensis* and other silphids has not been definitely established. *Poecilochirus* sp. (Parasitidae) were commonly found on the sternal regions of adult beetles and, in fewer numbers, on various parts of the body of larvae and pharate pupae; they were rarely seen associated with pupae. Deutonymphs were always seen, except for one instance when a large aggregation of protonymphs was found on a pharate pupa.

It is theorized that the mites are feeding on essentially the same food as the beetles (ectocommensals) and not on the beetles (ectoparasitic). The mites are phoretic commensals acting as scavengers and feeding on the debris and decaying matter that often adheres to carrion beetles. As a result, mites are most frequently found on the adults and larvae which have the greatest amount of decayed material sticking to their bodies. They are encountered less frequently on pharate pupae because active feeding (and accumulation of food material) has ceased.

In one instance in the laboratory, after an adult *N. surinamensis* had discarded the remains of a maggot it had fed upon, a mite quickly approached and began feeding on the remains of the maggot. Feeding continued for about five minutes.

BEHAVIOR

Observations on behavior were conducted in the field and in the laboratory under variable conditions in light, temperature and humidity. Insects have rigidly fixed, species specific behavior

actions, and the results obtained are not meant to establish *THE* behavioral pattern of *N. surinamensis* as it was observed all too frequently that there did not appear to be a definite pattern of sequential and predictable behavioral events as has been recorded for some other beetles. Furthermore, no behavioral comparison with other silphids was attempted.

The results obtained are largely dependent on the health and number of individuals observed and their responses to the observational conditions. The behavior noted is species typical, but more research is needed to define what is species specific.

Based on discrepancies in attraction experiments, Shubeck (1968) suggested it is possible that different populations of Silphidae develop different patterns of behavior; if this is true, it would complicate the results obtained (when only one population was considered) for any one species. This hypothesis is not unreasonable when one considers that a species occupying a large range, as *N. surinamensis*, has to cope with a multiplicity of environmental and climatological differences. Much investigation needs to be yet completed before Shubeck's theory can be effectively evaluated. At this point it is not known how much intra-specific variation exists in behavior.

GROOMING. — Grooming in adult *N. surinamensis* was observed in the laboratory for periods as long as two hours. Whether they groom this extensively at one time at carrion is unknown. Grooming at lights was seen but was never extensive. Cleaning behavior is stereotyped, and definite, though usually fragmentary, patterns of cleaning exist. There is a tendency for cleaning to begin with the protarsi and then proceed caudad to the antennae, meso- and metatarsi, tip of the abdomen and elytra, and the wings.

The protarsi are cleaned by being drawn through the mouthparts which scrape off accumulating debris; they may also be rubbed together. The antennae are groomed after the protarsi but not each time the tarsi are cleaned. Each foreleg grooms the antenna by reaching up, bending it down and scraping it in the process; the antennae may be pulled down several times and for as long as 15 seconds each time. Each antennae is alternately cleaned and, regardless of intermittent grooming, one antenna is

never cleaned twice consecutively. Antennae are never cleaned simultaneously.

The pro- and mesotarsi are rubbed together infrequently as are the meso- and metatarsi. The most common cleaning actions are rubbing together of the metatarsi and brushing the dorsal surface of the tip of the abdomen with the metatarsi. The tip of the abdomen is extended during the latter action, and both tarsi may rub it simultaneously or one at a time. The metatarsi are often brought down over the elytra and move caudad over the tip of the abdomen.

N. surinamensis grooming also includes what might be best termed comfort movements. The beetles extend and arch the abdomen dorsad and then relax; the elytra raise slightly, and the wings are extended posteriorly and refolded. Either of these actions may be performed unaccompanied by the other.

It was noticed in the laboratory that beetles always cleaned their protarsi after contact with maggots, even in mere passing encounters.

DEFENSE. — Reed (1958) accurately noted that *N. surinamensis* differ from other silphids in being more alert, quicker to hide and more rapidly moving. These traits are the primary protective measures used by the adults to escape danger. When escaping, *N. surinamensis* run away and rarely fly. They are also capable of ejecting from the anus a brown, vile-smelling fluid. Reed reported the beetles able to squirt a distance of ten inches, and observations in this study confirmed that distance. Accuracy is fairly good, at least with objects the size of a hand. If an attempt is made to pick the beetles up from the direction of the head, they arch their abdomens cephalad and still manage to hit their target. After the initial discharge, however, the beetles no longer perform in this manner for several hours because they apparently use all of the fluid in one action. Physical contact with the beetle is not a necessary prelude for discharge as they will squirt at an approaching object.

Thanatosis is generally not a mechanism used by *N. surinamensis* adults for defense; it occurs rarely and then only for a few seconds. Thanatosis can be observed in the larvae to a slightly greater extent but, like the adults, for only a few seconds.

The principal larval defense consists of writhing violently when attacked. It is, at best, tenuous protection. Larvae can also exude from the anus what appears to be the same liquid possessed by the adults; they cannot eject it forcefully, and its defensive value appears dubious.

MATING.—The mating behavior of *N. surinamensis* has evolved to further facilitate fertilization. Consequently the beetles are gregarious at carcasses, very promiscuous and mate repeatedly. Sexual contacts occur at carrion or lights by accidental contact and usually result as a part of the search for food.

There is little sexual dimorphism in *N. surinamensis*, and sexual recognition can probably be accomplished only by direct contact. On several occasions two beetles of the opposite sex were seen to touch maxillary palps, but copulation did not follow. How recognition is effected, short of attempted copulation, is unknown. Similarly, the role of pheromones (if any) and tactile and visual stimuli in aiding recognition are unknown.

Prior to copulation males chase what they may believe are females for short distances. When a female is overtaken, males attempt to mount from the left or right sides or from the posterior. Males grasp the females just behind the base of the first and second pair of femurs while the metatarsi press against the abdominal sternites of the female. Females may resist by attempting to escape or rejecting copulation. Males often fail at insertion and may continue to try or give up. When a female is receptive she extends and raises the genitalia, and the male inserts the aedeagus into the vagina.

Males performed the only display acts observed. These consisted of rubbing palps against the pronotum of the female, genital probing and, more rarely, pulling back on the female's antenna with the mandibles. All of these actions occurred while the male is mounted.

Riding time varies with the disposition of the female; it normally lasts for only a few minutes but can continue for up to ten minutes. Activity during this period ranges from continual walking by the female to immobility interrupted only by genital probing.

Males do not engage in reproductive combat. Possibly because

of the difficulty of sex recognition, brief attempts at homosexual copulation are common; these terminate rapidly when the sex of the partner is discovered.

MOULTING.—When carrion is in active decay, moulting usually takes place adjacent to the carcass or on top of it. In the later stages of decay moulting tends to occur beneath or in the carcass in the caverns and hollow spaces that have formed. These latter areas are preferred for ecdysis and offer shelter to the larvae.

Larvae near the beginning or midway through an instar have a dark and shiny cuticle whereas those preparing to moult possess dull, non-shiny, slightly wrinkled cuticles which are in the process of becoming loosened from the epidermis of the new instar.

Internal stresses eventually cause the old cuticle to split over the dorsal shield of the thorax (Fig. 35). The rupture proceeds caudad, and the new instar withdraws its abdomen, thorax and legs from the exuvium. The head is the last to be freed from the old cuticle. During this time larvae are usually on their backs or sides while the legs are used to push anteriorly against the constraining exuvium. Periodically there are short bursts of activity in which the legs push and the abdomen whips about as the insect attempts to free its head. Duration of the moulting process is from 30 to 45 minutes. Newly emerged larvae are light grayish-brown in color.

After escaping completely from the old cuticle, larvae remain somewhat quiescent for a short time while sclerotization occurs. This normally is completed in two to four hours, and feeding often resumes before hardening is completed.

LIFE CYCLE

N. surinamensis adults, after locating carrion, feed actively on the dipterous larvae that are present. During the one to seven days the beetles are at the carcass they mate, and the females oviposit the large, cream colored eggs randomly on the soil adjacent to the carcass and one at a time. Protection of the eggs is enhanced as they gradually change to the color of the soil on which they rest. Excavation of the soil for ovipositional purposes was never seen and probably does not occur. In the laboratory

a number of hours elapsed between each oviposition, but, considering the very large number of larvae encountered in field carcasses and the relatively short time the adults are present there, it is probable that oviposition progresses at a much more rapid rate in the field. Oviposition continues for most of the time the female is present at a carcass. Howden (1950) indicated that, in general, there is usually a clear relationship between the size of a female insect and the number of eggs which it can develop. A shortage of food during larval life may decrease fecundity because the size-fecundity relationship probably operates through the size of the foodstore accumulated during development and converted later to egg yolk. Smaller females of *N. surinamensis* were seen to lay slightly smaller eggs, but total number of eggs laid seemed to depend on overall health, longevity and amount of food available.

Because eggs are laid over a span of several days, larvae of different instars are found on the same carcass. Larvae normally hatch from the eggs from two to four days after deposition and immediately seek the shelter of the carcass to begin feeding. Temperature was seen to influence hatching. During one period of prolonged cool, damp, cloudy weather, eggs took six to eight days to hatch. Because of the usually rapid decay cycles in most carcasses, it is conjectured that hatching from the egg occurs faster than has previously been suspected for silphids. If this were not the case, maggots and other carrion insects might consume such a great amount of food as to offer rigorous competition to the lately emerging larvae, and predators would take a considerably larger toll of *N. surinamensis* eggs.

Under favorable conditions first instar larvae (Fig. 15) moult after approximately 24 hours, but under some laboratory conditions (and conceivably some field conditions) larvae did not moult for eight days. First instars are notable in that the lateral flaring of the dorsal plates is not yet developed.

The stadium of the second instar (Fig. 16) usually lasts from one to two days and may extend to 15 days and possibly longer when the food source is poor. Duration of the third instar (Fig. 17) is normally two to three days, but individuals were observed 20 days into this stage without moulting because of unfavorable

conditions. Fourth instar was never attained in these individuals, and death followed. The longest-lived larva in the laboratory, a third instar suffering from arrested development because of an inadequate food source, lived for 30 days.

It was frequently observed in laboratory colonies that when the substrate became wet, as it would after a rain, the appendages and mouthparts of the larvae often became caked with mud which then dried and rendered them incapable of normal movement or feeding. Larval grooming does not appear to be extensive, and, unless these deposits are removed, the larvae may die as some actually did. Others in this condition were removed, washed and returned to their enclosures, and development continued as usual.

The length of the fourth instar (Fig. 18) is more difficult to ascertain as they burrow into the ground prior to pupation and pass through a prepupal or pharate pupal (Hinton, 1946) stage. The fourth instar probably lasts three to five days and, as in all previous stages, may be greatly extended due to adverse circumstances. When ready to pupate the larvae wander away from the carcass to form earthen pupal cells (Fig. 21) in the ground or beneath logs, rocks or debris. Pupae were never found in the soil beneath carrion. Soil density (type) may significantly affect the depth at which the cell is formed or even prevent its formation.

It is believed the cell is formed by the sharp, convulsive thrashing of the abdomen which forms an oval, hollow chamber. The violent movements of the abdomen serve to pack the soil on the walls of the cell to firmness. A secretion of some kind is probably used to cement or reinforce the walls, but no trace of this could be found in any of the cells examined. The size of the chamber is dependent on the size of the larva making it. Typical measurements range between 11 to 18 mm deep and 16 to 21 mm long. Pupal cells in the laboratory were found 5 cm below the surface.

After construction of the pupal cell a period of quiescence follows which lasts from 5 to 8 days or, in some instances, 14 days and possibly longer. During this interval of rest, larvae contract slightly causing the intersegmental membrane to wrinkle; the head gradually becomes turned ventrad. The beetle during this period usually orients itself horizontally on its dorsum or

side and is highly sensitive to sounds or vibrations to which it responds by wriggling the abdomen rapidly. At this juncture the insect is usually termed a prepupa, but the pharate pupa (Fig. 20) of Hinton is preferable (pharate characterizing that phase of an instar which is enclosed within the cuticle of the previous instar). Mortality of pharate pupae in the laboratory was seen to be relatively high, the cause remaining undiscovered.

Ecdysis eventually occurs (Fig. 22) disclosing the cream-white pupa. Orientation and pupal movements are the same as those of a pharate pupa. The length of the pupal period varies from 12 to 17 days.

As eclosion approaches the eyes become pigmented first, followed by the gradual darkening of the remainder of the insect, especially the elytra. Convulsive movements of the body and legs cause the pupal cuticle to split. It appears initially over the pronotum and extends longitudinally from this point to the head and caudad. The cuticle is eventually shed from the posterior end of the imago with the assistance of the hind legs. The wings, having been feebly extended in the confining space of the pupal cell, are folded when they have become hardened. Pigmentation is usually completed after 24 hours. At this time, or after another day or two has passed, the imago begins to dig its way out of the cell to begin its adult life.

The length of adult life is variable and can only be approximated, especially since all the factors affecting longevity are not appreciated. In the laboratory adults lived for about three weeks on the average, some not feeding that entire time. Newly emerged imagos frequently died within two to three days after escaping from their chambers; their food requirements at this point may be more demanding than allowed for. The longest-lived adult in the laboratory attained an age of 35 days.

N. surinamensis overwinter as adults beneath stones, boards and any other object that provides sufficient protection. Blatchley (1910) reported imagos hibernating beneath logs close to carrion, but this cannot be possible all the time. The factor(s) responsible for initiating diapause remain unknown.

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REFERENCES CITED

- ARNETT, R. H. 1944. A revision of the nearctic Silphini and Nicrophorini based on female genitalia. *J. New York Ent. Soc.* 52(1):1-25.
- . 1946. Coleoptera notes 1: Silphidae. *Canadian Ent.* 78(7, 8):131-34.
- . 1968. The beetles of the United States (a manual for identification). *American Ent. Inst. Ann Arbor, Mich.* 112 p.
- BALDUF, V. W. 1935. The bionomics of entomophagous Coleoptera. John S. Swift Co., St. Louis. 220 p.
- BELL. 1873. A glimpse of insect life. *Canadian Ent.* 5(5):94-5.
- BLACKWELDER, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, part 1. *Bull. United States Nat. Mus.* 185:1-99.
- BLATCHLEY, W. S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana. *Indiana Dept. Geol. and Nat. Res. Bull.* 1:1-1386.
- BORNEMISSZA, G. F. 1957. An analysis of Arthropod succession in carrion and the effect of its decomposition on the soil fauna. *Australian J. Zool.* 5(1):1-12.

- BRIMLEY, C. S. 1938. The insects of North Carolina. North Carolina Dept. Agr., Raleigh. 560 p.
- BRITTON, W. E. 1920. Check-list of the insects of Connecticut. State Geol. and Nat. Hist. Surv. Bull. 31:1-397.
- CARR, F. S. 1920. An annotated list of the Coleoptera of northern Alberta. Alberta Nat. Hist. Soc. 8 p.
- CHAGNON, G. 1917. A preliminary list of the insects of the province of Quebec (part 3). Suppl. to Rep. Quebec Soc. Prot. Plants, p. 160-277.
- CHAMPLAIN, A. B. 1909. Coleoptera collecting by gas-light. Ent. News 20(4):179-181.
- CLARK, C. U. 1895. On the food habits of certain dung and carrion beetles. J. New York Ent. Soc. 3(2):3-61.
- DAVIS, W. T. 1915. *Silpha surinamensis* and *Creophilus villosus* as pre-daceous insects. J. New York Ent. Soc. 23(2):150-1.
- DILLON, E. S. AND L. S. DILLON. 1961. A manual of common beetles of eastern North America. Row, Peterson and Co., Evanston. 884 p.
- DORSEY, C. K. 1940. A comparative study of the larvae of six species of *Silpha* (Silphidae). Ann. Ent. Soc. America 33(1):120-139.
- DURY, C. 1902. A revised list of the Coleoptera observed near Cincinnati, Ohio, with notes on localities, bibliographical references and description of six new species. J. Cincinnati Soc. Nat. Hist. 20(3): 107-196.
- FABRICIUS, J. C. 1775. Systema entomologiae. Lipsiae. 832 p.
- FATTIG, P. W. 1936. The Coleoptera or beetles of Georgia, II. Ent. News 47(1):15-20.
- FICHTER, G. S. 1948. The bionomics of *Creophilus maxillosus* (L.). Unpubl. Thesis, North Carolina State Coll. 53 p.
- FORBES, T. M. 1922. The wing-venation of the Coleoptera. Ann. Ent. Soc. America. 15(4):328-352.
- FULLER, M. E. 1934. The insect inhabitants of carrion: a study in animal ecology. Bull. Australian Council Sci. and Ind. Res. 82:1-62.
- HATCH, M. H. 1927. Studies on the Silphini. J. New York Ent. Soc. 35(4):331-371.
- . 1928. Coleopterorum Catalogus, pars 95, Silphidae II. p. 63-244.
- . 1933. Records of Coleoptera from Montana. Canadian Ent. 65(1):5-15.
- . 1957. The beetles of the Pacific Northwest, part II. Univ. Washington Press, Seattle. 384 p.
- HINTON, H. E. 1946. Concealed phases in the metamorphosis of insects. Nature 157(3991):552-3.
- HOWDEN, A. T. 1950. The succession of beetles on carrion. Unpubl. Thesis, North Carolina State Coll. 83 p.
- JAQUES, H. E. 1951. How to know the beetles. W. C. Brown and Co., Dubuque. 372 p.

- KIRBY, W. 1837. Fauna Boreali-Americana: Insecta IV. Canadian Ent. 3(7):134-137.
- KNUDSEN, J. W. 1959. *Necrodes surinamensis* (Silphidae) in western Washington. Coleop. Bull. 13:110.
- LEACH, W. E. 1815. The Zoological miscellany; being descriptions of new, or interesting animals, vol. 2. London. 154 pp.
- LENG, C. W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York. 470 p.
- MALKIN, B. 1953. Western records of *Silpha surinamensis*. Coleop. Bull. 7(6):50-1.
- MESERVE, F. G. 1936. The Silphidae of Nebraska. Ent. News 47(5): 132-4.
- PAYNE, J. A. 1965. A summer carrion study of the baby pig *Sus scrofa* L. Ecology 46(5):592-602.
- PORTEVIN, G. 1922. Note sur quelques silphides des collections du museum. Bull. Mus. Nat. Hist. Natur. 28(7):505-8.
- . 1926. Les grandes necrophages du globe. Encycl. Ent. VI. 270 p.
- RAUTERBERG, F. 1885. Coleoptera of Wisconsin. Proc. Nat. Hist. Soc. Wisconsin (December, 1885). p. 48-62.
- REED, H. B., JR. 1958. A study of dog carcass communities in Tennessee, with special reference to the insects. American Midl. Nat. 59(1): 213-245.
- SHUBECK, P. P. 1968. Orientation of carrion beetles to carrion: random or non-random. J. New York Ent. Soc. 76(4):253-265.
- STAIG, R. A. 1931. The Fabrician types of insects in the Hunterian collection at Glasgow University. Coleoptera, part I. Cambridge Univ. Press, London. 110 p.
- STEELE, F. S. 1927. Notes on the feeding habits of carrion beetles. J. New York Ent. Soc. 35(1):77-81.
- WALKER, T. J. 1957. Ecological studies of the Arthropods associated with certain decaying materials in four habitats. Ecology 38(2): 262-276.
- WICKHAM, H. F. 1895a. On the larvae of *Hydrocharis obtusatus* and *Silpha surinamensis*. Ent. News 6(5):168-171.
- . 1895b. A list of Coleoptera from the southern shore of Lake Superior with remarks on geographical distribution. Proc. Davenport Acad. Nat. Sci. 6:125-169.
- WIGGLESWORTH, V. B. 1950. The principles of insect physiology, 4th ed. Methuen and Co., London. 544 p.