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THE BIOLOGY AND DISTRIBUTION OF THE
SILPHIDAE AND AGYRTIDAE OF CANADA AND ALASKA
(INSECTA: COLEOPTERA)

by

ROBERT SAMUEL ANDERSON, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

Department of Biology
Carleton University
Ottawa, Ontario.
April 2, 1981

The undersigned recommend to the Faculty
of Graduate Studies acceptance of the thesis
"The biology and distribution of the Silphidae and
Agyrtidae of Canada and Alaska (Insecta: Coleoptera)"
submitted by Robert Samuel Anderson, B.Sc.,
in partial fulfilment of the requirements for
the degree of Master of Science.

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April 27, 1981

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ABSTRACT

Diagnoses, keys, biologies, distributions, geographic variation and synonymy are given for the eight species of Agyrtidae and twenty-five species of Silphidae known to occur in Canada and Alaska. Similar information is presented at the generic, tribal and familial levels, although emphasis in these cases is on the world fauna.

The following synonymies are proposed as new;

Pelatinus Cockerell = Ipelates Reitter; Protonecrodes Portevin = Necrodes Leach; Philas Portevin, Silphosoma Portevin, Chalcossilpha Portevin = Thanatophilus Leach; Blitophaga Reitter = Aclypea Reitter; Isossilpha Portevin = Oiceoptoma Leach; Eusilpha Semenov-Tian-Shanskij, Calossilpha Portevin, Deutossilpha Portevin, Chrysossilpha Portevin, Deuterosilpha Hatch = Necrophila Kirby and Spence; Necrocharis Portevin, Necroxenus Semenov-Tian-Shanskij, Eunecrophorus Semenov-Tian-Shanskij, Necrocleptes Semenov-Tian-Shanskij, Necrophorindus Semenov-Tian-Shanskij, Necrophoriscus Semenov-Tian-Shanskij, Nesonecrophorus Semenov-Tian-Shanskij, Necropter Semenov-Tian-Shanskij, Nesonecropter Semenov-Tian-Shanskij, Stictonecropter Semenov-Tian-Shanskij, Neonicrophorus Hatch = Nicrophorus Fabricius; Necrophorus hecate Bland = Nicrophorus guttula Motschoulsky; Necrophorus ruficornis Motschoulsky = Nicrophorus nigrita Mannerheim. Phylogenetic relationships and possible evolutionary histories are also discussed for most taxa of Silphidae in Canada and Alaska.

Resource partitioning and ecological interactions in the silphid fauna of southern Ontario are examined in detail, using baited pitfall traps placed in four different habitats. Twelve species were found in the course of the study, five in the tribe Silphini and seven in the tribe Nicrophorini, genus Nicrophorus. The roles of different seasonal patterns and habitat specificity in resource partitioning are discussed for all species in both an ecological and evolutionary context. The use of phylogenetic analyses of both ecological and morphological attributes of species in analyzing the origin and evolution of species' assemblages is also discussed.

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Mr. L.E.C. Ling took the Scanning Electron Micrographs.

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INTRODUCTION

Members of the family Silphidae are generally large beetles that are frequently found associated with decaying organic material. They are commonly encountered at dead vertebrate carcasses and hence have become commonly known as carrion beetles. Other common names by which they are known are the sexton beetles and burying beetles. These names are associated with the habits of some members of the family that inter small vertebrate carcasses in the soil.

The family was first recognized by Leach (1815) and included the genera Nicrophorus Fabricius, Silpha Linnaeus, Oiceoptoma Leach, Necrodes Leach and Thanatophilus Leach. Lacordaire (1854) expanded family boundaries to include taxa which are now placed in the Leiodidae and the Clambidae. He also included the first members of the genus Agyrtes Frölich. Horn (1880) maintained this classification but also included members of the genera Necrophilus Latreille, Pelates Horn, Sphaerites Duftschmid, Pteroloma Gyllenhal and Apatetica Westwood in the tribe Silphini. Horn also considered the applicability of the generic concepts of the Europeans, in particular Leach, but declined to use the names, and placed all North American species in the genus Silpha. Subsequent North American workers have maintained this usage of Silpha, but have employed the other names at the subgeneric level (Arnett 1944).

The situation has remained as outlined until recent

revisionary work by Dr. R.B. Madge (unpublished), which has placed the members of the North American fauna in the various genera utilized in Europe. I have followed Dr. Madge's suggested classification, hence all changes and new synonymies should be credited to him.

The same is true for the higher classification. Hatch (1927a) recognizes four tribes in the Silphidae, these being the Lyrosomini, Agyrtini, Silphini and Microphorini. Madge, in his unpublished work, reunites the tribes Lyrosomini and Agyrtini as the Agyrtini, and maintains the recognition of the Microphorini and the Silphini. Here again, I have concurred in part with Madge's work, in recognizing the tribes Silphini and Microphorini.

Likewise, Dr. A.F. Newton, Jr., in an unpublished manuscript has proposed that the Agyrtini should be given familial ranking, and that they are not closely related to the Silphidae, but are closer to the Leiodidae. He has also suggested, following Hatch (1927c), recognition of the Silphidae as a subfamily of the Staphylinidae. I have followed Newton in recognizing the Agyrtidae as a distinct family, but not in recognizing the Silphidae as a subfamily of the Staphylinidae.

The information on the biology of the Agyrtidae is very limited, with most information coming from specimen data and not from detailed studies of life histories.

In contrast to the Agyrtidae, much has been published on the Silphidae, although at present no large work exists which brings together all of this information on a world wide or even regional basis. Consequently ecologists now working with silphids speak of the diffuse and widespread nature of the information. Paleontologists also find it frustrating to be presented with identifiable fossils (see Matthews 1974, 1975, 1977, Coope and Angus 1975, Coope et al 1979, and Miller and Peck 1979) yet can not find information of the present day ecologies and biologies which are essential for their use as paleoclimatic or paleoenvironmental indicators.

It is hoped that this present work will not only bring together our knowledge of silphid and agyrtid biology and ecology, but also add to it. The work should also serve to alleviate errors and inconsistencies in identification by providing a clear, concise treatment of the systematics of the species found in North America, but more particularly of Canada and Alaska.

The paper is divided into two sections. The first brings together information on silphid and agyrtid biology, provides distributions, an up to date treatment of the systematics of the species in Canada and Alaska and some comments on evolutionary history and phylogenetic relationships. The second part concentrates on improving our understanding of the mechanisms of resource partitioning in the silphid fauna of northeastern North America. The

results are discussed in both ecological and evolutionary terms with special consideration being given to the use of phylogenetic data in analyzing the origin of species assemblages or communities and in elucidating evolutionary histories of the constituent taxa.

The information presented should serve the ecologist, systematist, biogeographer and paleontologist alike, not only in providing background information, but also in providing stimulation and encouragement for further research on these beetles.

(5)

PART I:

THE BIOLOGY, DISTRIBUTION AND TAXONOMY
OF THE SILPHIDAE AND AGYRTIDAE OF CANADA
AND ALASKA, WITH COMMENTS ON PHYLOGENETIC
RELATIONSHIPS AND A LIST OF SYNONYMY

MATERIALS AND METHODS

The format for this section is essentially similar to that of the recent Insects and Arachnids of Canada handbook series (eg. Wood et al 1979), with sections on systematics including keys, distribution, biology, geographic variation and phylogenetic affinities, being presented for all species of Silphidae. Similar information is given for the Agyrtidae, but a section on phylogenetic affinities is not included because of the current reclassification of the family that is being carried out by Newton.

A short diagnosis of each taxon is provided which was prepared through personal examination of specimens. These diagnoses should augment the keys, and together they should provide a means of easily and reliably identifying members of the two families found within the range of the study. Diagnoses are given only for those species occurring in Canada and Alaska, but all known species in North America, north of Mexico are included in the keys. Those which do not occur in Canada or Alaska are noted and are not treated further here.

The distribution of each higher taxon is given for the world, while the distribution of each species is given in detail for Canada and Alaska, based on personal examination of specimens, and generally for the United States also based in part on personal examination of specimens. These specimens were acquired on loan from the various institutions and

individuals listed in Appendix I. References to comprehensive systematic papers concerning the world as well as the North American fauna are also given where available. It should however be emphasized, that our understanding of North American silphid taxonomy has changed markedly in many cases, and that only the present keys and those of Peck (in press) and Miller and Peck (1979) incorporate any recent changes.

Information on the biology, ecology and in some cases on the behavior of all taxa is also presented. This information not only includes that which is already present in the literature, but also that which is representative of the author's own results. For the higher taxa, all available information is presented, but not discussed at great length. Only for the Canadian and Alaskan species are detailed data presented and discussed.

In view of the emphasis in current systematics on evolutionary history and phylogeny, it is important that all possible life stages be examined, thereby increasing the number of characters available for analysis. For the above reasons, the present status of the taxonomy of the immature forms of each taxon is also provided.

Another important aid in understanding certain aspects of evolution is a good knowledge of morphological variation within a given species. This information is given for all species, and in some cases possible causative mechanisms and adaptive significance are

presented and discussed in terms of the evolutionary history of the species.

Finally a section is presented wherein inferences are made concerning the possible evolutionary history and phylogenetic relationships of each taxon of silphid.

The author acknowledges the necessity of knowledge of phylogeny in the form of a cladogram preceeding any comments on biogeography or evolutionary history.

Unfortunately, the construction of such a cladogram for all species of silphids is not now possible. Preliminary cladistic analyses however, of the genera of Silphini in North America and of the species of Nicrophorus in North America are presented. These cladistic analyses as well as the basis for their construction are given, and thus represent hypotheses testable by the inclusion of taxa occurring outside North America and by a more extensive knowledge of the taxonomy of the immature stages.

A list of the synonymies for each taxon is also provided, following Hatch (1928) although some new synonymies are proposed. In these lists, the names for the aberrations of species in the genus Nicrophorus proposed by Hatch are not treated. According to Hatch (1940), these names are used in an infrasubspecific manner and thus are excluded from the provisions of the code. Portevin's intended ranking of aberrations is not made clear by him, and since they appear as trinomials they must be considered of subspecific ranking and thus require consideration.

KEY TO FAMILIES

Agyrtids and silphids are members of the superfamily Staphylinoidea, and according to Crowson (1967) can be distinguished from all other Staphylinoidea by the following characters; Small (5-13 mm in length) to large (14-35 mm in length) species with 11 segmented antennae. Fore coxae large, conical and projecting; fore coxal cavities open behind. Hind coxae lacking femoral plates. Abdomen with 3 or more tergites membranous at base.

The two families as treated here, can then be distinguished by the following key:

- 1a Elytra with 9 or 10 striae; covering entire abdomen.....Agyrtidae (Page 10)
- 1b Elytra plain or tricostate, never distinctly striate; truncate, usually exposing at least one abdominal segment and often more.....
.....Silphidae (Page 33)

AGYRTIDAE

DIAGNOSIS: Brownish beetles, 5-13 mm in length. Elytra with 9 or 10 striae; covering entire abdomen. Antennae filiform to gradually clavate.

DISTRIBUTION: . In North America, agyrtids are found primarily in the western coastal areas of Washington, Oregon, California, British Columbia and Alaska, and inland to Alberta, Montana and Idaho. One species is found in the Appalachian states, northward to extreme southern Ontario. Outside of North America, they are found in Mexico, Europe, southeast Asia and New Zealand.

Sixty-three species are known, eleven of which occur in North America, north of Mexico. These eleven species are in six genera.

BIOLOGY: Little is known of the biologies of these beetles. They appear to be scavengers in wet habitats, particularly in wet coastal areas. They are most frequently collected in gravel and moss along the edges of mountain streams and ponds, in deep forest litter and on snowfields, particularly at high elevations. Most species appear to be active during the winter months or during cooler periods.

IMMATURE STAGES: No comprehensive papers on the taxonomy of the immature stages exist, with the very few descriptions that do exist being found in various publications cited elsewhere in the text.

KEY TO THE GENERA OF AGYRTIDAE IN NORTH AMERICA,
NORTH OF MEXICO

- 1a Mandible with 1 or 2 large preapical teeth on inner margin (Figs. 1, 2), 2 or more preapical antennal segments lacking an apical groove (Fig. 8).....5
- 1b Mandible lacking preapical teeth (Figs. 3, 5), 2 or more preapical antennal segments each with an apical groove containing a dense concentration of setae (Fig. 7).....2
- 2a Elytra with 10 striae, last segment of maxillary palpus swollen (Fig. 3), dorsal ridge of elytral epipleuron depressed behind shoulder.....Agyrtes Frölich (Page 15)
- 2b Elytra with 9 striae, last segment of maxillary palpus not swollen, cylindrical (Figs. 4, 5), dorsal ridge of elytral epipleuron evenly rounded.....3
- 3a Body form elongate, pronotum cordiform (Fig. 9), widest in anterior half, not as wide as elytra at baseLyrosoma Mannerheim (Page 13)
- 3b Body form ovoid, pronotum not cordiform, almost as wide as elytra at base, explanate.....4
- 4a Lateral margins of pronotum broadly explanate, (larger beetles), greater than 8 mm long....Necrophilus Latreille
(Page 28)
- 4b Lateral margins of pronotum narrowly explanate, (smaller beetles), 8 mm in length or less.....Ipelates Reitter
(Page 18)

- 5a Pronotum with rounded fovea at middle of base and in posterior corners (Fig. 6), aedeagus with basal piece and parameres.....Pteroloma Gyllenhal (Page 20)
- 5b Pronotum evenly rounded, lacking fovea, aedeagus lacking basal piece and parameres.....Apteroloma Hatch (Page 24)

LYROSOMA MANNERHEIM

Lyrosoma Mannerheim, 1853:174

DIAGNOSIS: Elongate, brownish beetles with clypeus transversely pentagonal in shape, labrum prominent, mandibles lacking preapical teeth. Antennae filiform to very gradually clavate, eyes not prominent. Elytra with 9 striae, pronotum cordiform (Fig. 9), much narrower than elytra at base, not explanate. Hind coxae slightly separated.

DISTRIBUTION: The 8 species in this Holarctic genus were last revised by Hlisnikovsky (1964a). One species occurs in North America.

BIOLOGY: Little has been recorded on the biology of any of the Palearctic species. Lewis (1893) records the habitat of Lyrosoma tripartitum Lewis as under stones on the ocean shore.

IMMATURE STAGES: Larvae and pupae of all species are unknown.

LYROSOMA OPACUM MANNERHEIM

Lyrosoma opacum Mannerheim, 1853:175

DIAGNOSIS: Elongate, brownish beetles, 8-9 mm in length. Antennae long, reaching as far as the anterior $\frac{1}{3}$ of the pronotum; very gradually clavate, segment three about twice as long as segment two. Elytral intervals dull, with prominent isodiametric microsculpture. Apterous.

DISTRIBUTION: Found on the western Aleutian Islands (Fig. 68), this species also extends into coastal and insular areas of Siberia southward to Japan (Hatch 1927a).

BIOLOGY: It has been recorded from rotting kelp and other seaweed on beaches and shore areas which are frequently inundated by high tides (Hatch 1927a, Van Dyke 1921). Kellogg (1914) records it from murre nests and among broken eggs left after the nest has been abandoned. Van Dyke (in Kellogg 1914) believes that the distribution of the beetles on many of the isolated and recently formed islands of the north Pacific area can be explained by the beetles being transported in the plumage of the birds.

It is probably a scavenger in the aforementioned habitats, feeding on decaying organic material. It is primarily active in the summer months.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

AGYRTES FRÖLICH

Agyrtes Frölich, 1799:15; Peck, 1974; Hlisnikovsky, 1964b

Agyrtecanus Reitter, 1901:102

Lendomus Casey, 1924:185

DIAGNOSIS: Elongate, brownish beetles with the clypeus transversely rectangular in shape, labrum not prominent, mandibles lacking preapical teeth (Fig. 3). Last segment of maxillary palpi swollen, oval (Fig. 3). Antennae clavate, eyes not prominent. Elytra with 10 striae; with epipleural ridge depressed behind shoulder. Pronotum slightly wider than long; as wide as elytra at base. Hind coxae slightly separated.

DISTRIBUTION: The seven species in this Holarctic genus were last revised by Hlisnikovsky (1964b). Two species occur in North America (Peck 1974), one of which reaches Canada and Alaska.

BIOLOGY: Little has been recorded on the biology of the Palearctic species. They have been most commonly found under bark, in moss and at rotting mushrooms (Peck 1974). Agyrtes bicolor Laporte has been recorded among the masses of larvae of Bibio marci (Diptera; Bibionidae) which appear on the ground during warm winter days in Europe (Berce and Brisout 1872, Laboulbene 1872).

IMMATURE STAGES: Unknown.

KEY TO THE SPECIES OF AGYRTES IN NORTH
AMERICA, NORTH OF MEXICO

- 1a Antennal club with four segments, posterior angles of
pronotum sharp, elytral epipleuron glabrous.....
.....longulus (LeConte) (Page 17)
- 1b Antennal club with five segments, posterior angles of
pronotum rounded, elytral epipleuron hairy.....
.....similis Fall

AGYRTES LONGULUS (LECONTE)

Necrophilus longulus Leconte, 1859:282; Peck, 1974

Lendomus politus Casey, 1924:185

DIAGNOSIS: Dark brown, elongate beetles, 5-7 mm in length. Antennae short, scarcely reaching the middle of the pronotum; with club of four segments; third antennal segment longer than the second. Elytral intervals shiny with no apparent microsculpture.

DISTRIBUTION: This species is widely distributed in coastal areas from the Alaskan Panhandle southward to British Columbia (Fig. 69) and in the United States to southern California (Fig. 69).

BIOLOGY: This species has been collected on snow, flood debris and from under the bark of living oak, Engelmann spruce and Western larch. It has also been collected in association with Bibio larvae, as previously noted for Agyrtes bicolor. It is presumably associated with forested habitats (Peck 1974) and is most active in the winter months.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

IPELATES REITTER

Ipelates Reitter, 1884:90

Pelatines Cockerell, 1906:240 (for Pelates Horn, 1880:244,
not Fischer, not Cuvier) NEW SYNONYMY

DIAGNOSIS: Oval, brownish beetles with the clypeus transversely pentagonal in shape, labrum not prominent and the mandibles lacking preapical teeth (Fig. 4). Antennae clavate. Elytra with 9 striae, pronotum wider than long; explanate, as wide as elytra at base. Hind coxae contiguous.

The new synonymy is adopted based on studies of Madge (unpublished), who has examined specimens of the genera Ipelates and Pelatines and considers them to be synonymous.

DISTRIBUTION: This genus is Holarctic with nine species currently recognized (Newton pers. comm.). Only one species occurs in North America.

BIOLOGY: Only Lewis (1893) records any biological data for the Palearctic species, when he notes the collection of Ipelates striatipennis Lewis from an old rotten log and from foliage.

IMMATURE STAGES: Unknown.

IPELATES LATUS (MANNERHEIM)Necrophilus latus Mannerheim, 1852:331

DIAGNOSIS: Brownish, oval beetles, 4-6 mm in length. Antennae short, reaching almost to base of pronotum, gradually clavate; segment three only slightly longer than segment two. Elytral intervals shiny, smooth, with no prominent microsculpture.

DISTRIBUTION: Widely distributed in British Columbia and western Alberta, northward to the Alaskan panhandle and the southeastern Northwest Territories (Fig. 70). In the United States it is found from Washington, Oregon and California, inland to Montana and Idaho (Fig. 70).

BIOLOGY: It is apparently a general scavenger in leaf litter. This species is most commonly collected by sifting moist, primarily deciduous, leaf litter at mid elevations inland and in lowland coastal areas.

Tenerals appear to be most common in late July and August, indicative of emergence at these times. In subsequent weeks adults are frequently found associated with mushrooms, often around the bases of lodgepole pine and douglas fir. These mushrooms could be the possible site of oviposition and subsequent larval development, but could also be sites of adult feeding. Adults are also often collected from under the bark of decaying trees and from debris along the edges of streams.

IMMATURE STAGES: Larvae are known, but not described. They are in the collection of Dr. A.F. Newton, Jr.

GEOGRAPHIC VARIATION: None noted.

PTEROLOMA GYLLENHAL

Pteroloma Gyllenhal, 1827:418 ; Hatch, 1928

Adolus Fischer von Waldheim 1828:242

Holocnemis Schilling 1829:93

DIAGNOSIS: Elongate, brownish beetles with the clypeus transversely rectangular; labrum prominent, almost as long as clypeus (Fig. 2); mandibles each with 1 or 2 large preapical teeth on inner edge (Fig. 2). Antennae clavate, preapical segments longer than wide. Elytra with 9 striae; pronotum quadrate, not explanate, not as wide as elytra at base, with rounded fovea at middle of base and in posterior corners (Fig. 6). Aedeagus with basal piece and parameres. Hind coxae contiguous.

DISTRIBUTION: The genus is Holarctic, with ten species currently recognized (Newton pers. comm.). Only one species occurs in North America, north of Mexico.

BIOLOGY: Biological data on the Palearctic species are scattered. Lewis (1893) records the habitat of Pteroloma discicolle Lewis as under small stones on a mountain summit. Holdhaus and Lindroth (1939) present information on the biology of Pteroloma forstroemi Gyllenhal of Europe. They state that the species is found at high altitudes, among damp stones and leaves in the vicinity of ponds. Individuals are active in sunny weather and are inactive during cool or cloudy periods. This is corroborated by Scholtz (1934), who notes that the species is primarily active during bright periods. He found it at rest under moss, rocks and gravel

near the water's edge. Egg carrying females were also found in the moss and it is likely that this is the site of oviposition (see notes under Pteroloma nebrioides). Brundin (1934) also has collected it in shaded, moss covered stream banks.

IMMATURE STAGES: Unknown.

PTEROLOMA NEBRIOIDES BROWN

Pteroloma nebrioides Brown, 1933:213

DIAGNOSIS: Brownish, elongate beetles, 5-7 mm in length. Antennae long, extending to the anterior one third of the elytra; segment three approximately twice as long as segment two. Dorsal surface of head coarsely, sparsely punctate, frons with irregular fovea. Elytra with epipleuron coarsely, irregularly punctate; intervals shiny with no apparent microsculpture..

DISTRIBUTION: This species is found in the southern montane areas of eastern British Columbia and western Alberta (Fig. 71). In the United States it is known only from extreme northwestern Montana.

BIOLOGY: The species occurs in mosses and amongst rocks and gravel along the banks of shaded montane streams of 3-5 metres width, apparently only at elevations between 4000-6000 feet. Although often common amongst the rocks, large series have been collected from mossy banks which are overhanging the water. This may represent an area where food, presumably organic material carried by the stream, is deposited. The insects may therefore be congregating in these areas to feed.

Individuals are active primarily in late spring and early summer. It is at this time that mating and egg-laying take place. The females each appear to lay 2 large eggs (1.5 mm in diameter) in damp moss. The larvae appear to feed as scavengers or predators on other insects in the banks that may have been deposited by stream drift.

Other seasonal or life history data are at present unknown.

IMMATURE STAGES: Larvae are known and in the collection of Dr. A.F. Newton Jr.

GEOGRAPHIC VARIATION: None noted.

APTEROLOMA HATCH

Apteroloma Hatch, 1927c:12

DIAGNOSIS: Elongate, brownish beetles with the clypeus transversely rectangular; labrum prominent, as long as clypeus; mandibles each with one large preapical tooth on inner edge (Fig. 1). Antennae clavate, preapical segments wider than long. Elytra with 9 striae; pronotum quadrate not explanate, of variable width. Aedeagus lacking basal piece and parameres. Hind coxae contiguous.

DISTRIBUTION: The genus is Holarctic, with 22 species currently recognized (Newton pers. comm.). Four of these occur in North America, north of Mexico (Van Dyke 1928).

BIOLOGY: Biological data on the Palearctic and Mexican species are sparse. Jeannel (1935) records Apteroloma sillemi Jeannel on a glacier at 4125 metres elevation. Bolivar y Pieltan and Hendrichs (1972) in describing some new Mexican species, which they initially placed in the genus Pteroloma, record them from under stones and detritus above tree line on the high peaks of the Mexican Plateau. They were especially common along snow runoff streams, alpine lakeshores and in foggy areas.

The distributions of the other species would indicate that they are found in similar montane areas.

IMMATURE STAGES: Unknown.

KEY TO THE SPECIES OF APTEROLOMA IN NORTH
AMERICA, NORTH OF MEXICO

- 1a Elytral epipleuron impunctate.....2
- 1b Elytral epipleuron punctate.....3
- 2a Internal sutural angle of elytron with a distinct
tooth present (Fig. 10); pronotum narrow, base less
than one and one third times the length along the midline
.....caraboides (Fall) (Page 26)
- 2b Internal sutural angle of elytra rounded, lacking tooth
(Fig. 11); pronotum broad, base less than one and one
half times the length along the midline.....tahoecum (Fall)
- 3a Posterior angles of pronotum obtusely angulate.....
.....arizonicum (Van Dyke)
- 3b Posterior angles of pronotum rounded.....
.....tenuicorne (LeConte) (Page 27)

APTEROLOMA CARABOIDES (FALL)

Pteroloma caraboides Fall, 1927:235

DIAGNOSIS: Brownish, elongate beetles, 8-10 mm in length. Antennae long, extending to the anterior one third of the elytra, segment three approximately twice as long as segment two. Pronotum with base less than one and one third times the length along the midline, narrower than elytra at base. Elytral epipleuron impunctate, sutural apices truncate, with sharp tooth on inner margin (Fig. 10), intervals with prominent reticulate microsculpture.

DISTRIBUTION: This species is found in Canada from central to southern British Columbia, west of the main ridge of the Rockies (Fig. 73). In the United States it is found from northern Washington and Idaho, southward to northern California (Fig. 73).

BIOLOGY: It is a rare inhabitant of stream and river banks. Some specimens are occasionally collected amongst drift on beaches and lakeshores. In more southern localities it is locally common on snowfields at higher elevations, both nocturnally and diurnally (Dr. D.H. Kavanaugh, pers. comm.). It is probably a scavenger in the aforementioned areas.

No seasonal or life history data are available, although label data indicate that it is primarily active in summer.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

APTEROLOMA TENUICORNE (LECONTE)

Necrophilus tenuicornis Leconte, 1859b:84

DIAGNOSIS: Brownish, elongate beetles, 5-7 mm in length. Antennae short, extending to base of elytra or only slightly beyond; segment 3 approximately twice the length of segment 2. Pronotum with base approximately one and one half times the length along the midline, as wide as elytra at base. Elytral epipleuron punctate, sutural apices of elytra evenly rounded, intervals glabrous.

DISTRIBUTION: This species is found in Canada from southern British Columbia inland to southern Alberta (Fig. 72). In the United States it is found from Washington and Idaho, southward to California and Colorado (Fig. 72).

BIOLOGY: It is a rare inhabitant of damp or wet habitats, particularly streamsides, lakeshores, beaches and nocturnally at the edges and upon melting snowfields (Hatch 1940, 1957). It has also been collected on fresh snow banks in prairie areas, along the edges of rivers. No seasonal or life history data are available.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: Horn (1880) records some variation in surface lustre and sculpture, and it is probable that he had specimens of Apteroloma caraboides confused with those of A. tenuicorne. I have not noted any geographic variation in Apteroloma tenuicorne.

NECROPHILUS LATREILLE

Necrophilus Latreille, 1829:500 ; Madge, 1980

Necrobius Gistel, 1834:147

DIAGNOSIS: Oval, brownish beetles with the clypeus transversely pentagonal (Fig. 5); labrum prominent; mandibles lacking preapical teeth (Fig. 5). Antennae clavate, preapical two or more segments with an apical groove containing a dense concentration of setae (Fig. 7). Pronotum broadly explanate, about as broad as elytra at base. Hind coxae contiguous.

DISTRIBUTION: The genus is primarily Holarctic, although one species occurs in New Zealand. There are four species in the genus, with two of these occurring in North America.

BIOLOGY: The biology of Necrophilus subterraneus (Dahl) of Europe has been described by Rade (1893). He found the species breeding on dead land snails (Helix sp.) and noted a period of 5 weeks for development from egg to adult. There were two weeks of active larval feeding. Will (1886) also records larvae of this species feeding on well decayed snails. Horion (1949) records the adults from carrion and fungi.

IMMATURE STAGES: The immature stages of the species occurring outside of North America are unknown.

KEY TO THE SPECIES OF NECROPHILUS IN NORTH AMERICA

- la Wingless; elytral striae with deep, distinct punctures;
intervals 2, 4 and 6 convex; sutural angles of elytra
truncate, each with a prominent sharp tooth at the
inner angle.....pettitii Horn (Page 30)
- ✓ lb Winged; elytral striae with shallow, indistinct punctures;
intervals uniformly very slightly convex; sutural angles
of elytra evenly rounded.....hydrophiloides Guérin-Ménéville
(Page 32)

NECROPHILUS PETTITII HORN

Necrophilus pettitii Horn, 1880:243

DIAGNOSIS: Oval, brownish beetles, 9-12 mm in length.

Antennae with segment 8 noticeably wider than segment 7.

Eyes not prominent. Pronotum broadly explanate, with the margins reflexed upwards. Metasternum short, wingless.

Elytra with striae punctures large, deep; intervals 2,4 and 6 convex. Elytral apices truncate, each with a prominent sutural tooth.

DISTRIBUTION: In Canada this species is known only from the type locality in extreme southern Ontario. In the United States it is widespread in the Appalachian states from New York, Michigan and Illinois southward to Alabama, Georgia and northern Florida (Fig. 74).

BIOLOGY: Little is recorded in the literature on the biology of this species. Reed (1958) records it from Tennessee on dried dog carcasses and notes the slow movement that appears typical of most agyrtids. Blatchley (1910) has recorded it from decaying fungi as has Pettit (1869).

Dr. J.A. Payne (unpublished) records the following detailed biological information. A number of adults in copula were collected from Peromyscus leucopus (deer mouse) feces at Perry, Georgia on December 7, 1969. Adults were offered decaying squirrel meat and mouse feces, but did not feed. Approximately 20 small larvae were noticed on December 14, indicating a maximum of 7 days in the egg stage. These larvae fed primarily on the mouse feces, but also on the squirrel meat.

The first adults emerged on February 1, 1970, indicative of an egg to adult period of about eight weeks. Payne also records the species from various vertebrate carrion in both the dry and decay stages (see Payne 1965 for a description of the various decay stages).

Nearly all records are in the winter months, from November through March.

IMMATURE STAGES: The larvae are known and in the collection of Dr. A.F. Newton, Jr.

GEOGRAPHIC VARIATION: None noted.

NECROPHILUS HYDROPHILOIDES GUÉRIN-MÉNEVILLE

Necrophilus hydrophiloides Guérin-Ménéville, 1835:Pl.17,
Fig. 12

DIAGNOSIS: Oval, brownish beetles, 10-13 mm in length. Antennae with segments 7 and 8 equal in width. Eyes prominent (Fig. 5). Pronotum broadly explanate, evenly convex. Metasternum of normal length; winged. Elytra with stria punctures shallow, indistinct; intervals only slightly convex. Elytral apices evenly rounded.

DISTRIBUTION: This species is found in the coastal areas of Canada and Alaska, from the panhandle and the Queen Charlotte Islands southward to southern British Columbia (Fig. 75). In the United States it is found from Washington and Idaho, southward to southern coastal California (Fig. 75).

BIOLOGY: This species is primarily a scavenger of decaying organic material in wet, coastal forests. It has been caught commonly on carrion, in garbage and in decaying vegetable material. Although no rigorous data exist on seasonality, specimen data indicates that the species is more active in the winter months, from November to May.

IMMATURE STAGES: Larvae are known, but not described. They are in the collection of Dr. A.F. Newton, Jr. The pupal stage has been described by Blaisdell (1901).

GEOGRAPHIC VARIATION: None noted.

SILPHIDAE

DIAGNOSIS: Large beetles, 10-35 mm in length, generally blackish, but often with orange or red color patterns on the elytra. Elytra tricostate, costae sometimes obsolete or lacking. Antennae clavate, some species with a distinct club.

DISTRIBUTION: There are approximately 227 species in this family. Most species are found in north temperate areas, with those that are in the tropics being found predominantly at higher elevations. A few species are found in the south temperate zone or in the lowland tropics. There are 29 species in 7 genera in North America, north of Mexico.

Comprehensive works on the North American species are those of LeConte (1853), Horn (1880), Hatch (1927a), Arnett (1944), Miller and Peck (1979) and Peck (in press). Major publications on the world species are Portevin (1926) and Hatch (1928).

BIOLOGY: The vast majority of the Silphidae are necrophagous. Some genera are snail or caterpillar predators (Dendroxena Motschulsky and some Silpha Linnaeus), while others in the genus Aclypea Reitter are phytophagous. Others are often collected at fungi or decaying vegetable material. All larvae of the necrophagous forms appear to feed exclusively on decaying animal material. The adults of some of the primarily necrophagous species have been shown to feed on both decaying flesh and other insects, especially fly larvae (Balduf 1935, Clark 1895 and Steele 1927).

Studies on a few species have shown that olfaction is of primary importance in food finding (Dethier 1947, Abbott 1927a and b), with the antennae, more precisely the sensilla coelosphaerica of the terminal antennal segments, being the principal structures involved (Boeckh 1962, Ernst 1969, 1972 and Waldow 1973). These sensilla have been found to be receptive to H_2S and some other cyclic compounds (Waldow 1973). The role of wind in the orientation behavior of the beetles to the food source has also been examined (Shubeck 1968, Petruska 1975 and Sanborne 1977).

Some European species have been shown to carry various parasitic nematodes and cestodes, although none of these are known to infect man or domestic animals (Prokopic and Bily 1975). Studies have also been carried out to investigate the possibility that they could carry and possibly even act as disseminators of rabies virus or anthrax bacilli. These studies showed that rabies virus is inactivated in the gut of Nicrophorus (Sidor 1975) and that anthrax bacilli can be disseminated by silphids (Osinskii 1940). They are also important components of ecosystems as they assist in the promotion of nutrient recycling.

IMMATURE STAGES: In general, the state of knowledge of silphid larvae is quite poor, as it is with most beetle families. Large works on silphid larvae are as follows; Paulian (1941) on some European species, Henriksen (1922) on European species, Klausnitzer (1978) with a key to the European genera, Hatch (1927a) on some European species and Kawada et al (1959) on some Japanese species.

PHYLOGENETIC AFFINITIES: The phylogenetic position and relationships of the Silphidae have long been debated. The recent work of Newton (unpublished), as well as that of Hatch (1927c) has shown them to be most closely related to the Staphylinidae. Cladistic analysis has shown that they should be regarded as a subfamily of the Staphylinidae.

KEY TO THE TRIBES OF SILPHIDAE

- 1a Elytra not truncate, stridulatory files absent, epistomal suture absent (Fig. 12), second antennal segment distinctSilphini (Page 37)
- 1b Elytra truncate, exposing 3 or 4 abdominal tergites, stridulatory files present on dorsum of abdominal segment 5 (Fig. 48), epistomal suture present (Fig. 47), second antennal segment small, indistinct.....Nicrophorini (Page 82)

SILPHINI

DIAGNOSIS: Ovoid, generally blackish, dorsoventrally compressed beetles, 12-25 mm long. Epistomal suture absent, gula strongly constricted medially, but sutures distinctly separate. Antennae with segment 2 large; clavate. Pronotum transverse, broadly explanate, almost as wide as elytra at base. Elytra not truncate, although last two or three abdominal tergites are sometimes exposed; usually tricostate, although some or rarely all of the costae may be effaced. Legs elongate, slender, not suited for digging.

DISTRIBUTION: There are approximately 140 species in 12 genera known. Most species are found in north temperate areas, although the genera Ptomaphila Kirby and Spence (in Australia and New Guinea) and Oxelytrum Gistel (in Central and South America) are found in the southern hemisphere. The genus Diamesus Hope is found in New Guinea and Formosa through India, while some species of the genera Silpha and Thanatophilus are found in Africa.

Fourteen species in 6 genera are known from North America, north of Mexico, excluding Oxelytrum discicolle Brulle which was recently recorded from Texas (Davis 1980), and any of those species which may have been man introduced.

BIOLOGY: Unlike the Nicrophorini, the Silphini are not all necrophagous as larvae. The genera Dendroxena and Silpha (in part) are predatory in habit (Heymons et al 1927, 1928, 1932), while the genus Aclypea is phytophagous (Heymons et al

1929, 1930).

Of the two life cycle strategies which have been developed in the Silphidae, that of the Silphini is the less complex.

This basic life cycle can be summarized as follows: Beetles, upon finding a dead animal will mate, with the females subsequently ovipositing in the soil around the carcass. Larvae upon hatching migrate to the carcass and begin to feed. There are three larval instars, with pupation taking place in the soil. Unlike the Nicrophorus, these beetles appear to avoid competition with numerous fly larvae by waiting until the fly larvae have finished feeding. This is accomplished by having the eggs hatch at a time when the fly larvae are migrating to the soil to pupate, approximately 5 days after oviposition by both taxa has occurred. Upon eclosure the silphine larvae feed on the remains of the carcasses (Dorsey 1940, Johnson 1974). The adults during this time may feed on both carrion and fly larvae at the carcass. Silphines are also occasionally found as adults on dung and in garbage.

Phoretic mites are few on the silphines and the complex and tight relationships that seem to exist in Nicrophorus do not appear. This would be expected as the life cycle does not require the presence of the mites, which are hypothesized to kill fly competitors in the food resources of Nicrophorus (Springett 1968).

~~These~~ beetles partition the food resources as do Nicrophorus, however studies on the ecological interactions amongst members of this group are few, with the only

exceptions being the studies of Katakura and Fukuda (1975) on Japanese species and Petruska (1968a) on European species. In North America, only Pirone (1974) and Shubeck (1968, 1969, 1971, 1976) and Shubeck et al (1977) have considered interspecific interactions in any detail. Cole (1942) does present some observations on different seasonal and temporal strategies of resource usage. Detailed studies on this aspect of silphid biology are presented in Part II for the species occurring in eastern North America.

Most species appear to be diurnal, or else active throughout most of the day and night. Exceptions to this are the genera Necrodes and Oxelytrum which are primarily nocturnal.

IMMATURE STAGES: Numerous Palearctic larvae have been described, with the most notable contributions being those mentioned in the discussion under Silphidae. Dorsey (1940) presents keys and descriptions of the North American species.

PHYLOGENETIC AFFINITIES: The synapomorphic character state of the absence of the epistomal suture would appear to be indicative of the monophyly of this tribe. Most other characters appear to be sympleisiomorphic.

Figure 101 shows a proposed phylogeny of the genera of Silphini of North America, with the evidence for constructing the phylogeny as depicted given under each discussion of the phylogenetic relationships of the genera, and also summarized in Figure 103A. Outgroup comparisons of other Silphidae were made through the personal examination of specimens, while comparisons with the Staphylinidae were made using Blackwelder (1936).

KEY TO THE GENERA OF SILPHINI IN NORTH AMERICA,
NORTH OF MEXICO

- 1a Eyes large, propleural lobe very short, rounded (Fig. 37),
pronotum orbicular, widest towards the middle (Fig. 14);
large males with hind femora expanded.....
.....Necrodes Leach (Page 41)
- 1b Eyes small, propleural lobe well developed, pronotum
not orbicular, widest towards the base.....2
- 2a Head with a short row of long, more erect setae behind
the eyes (Fig. 12).....3
- 2b Head lacking the row of setae behind the eyes.....5
- 3a Elytral shoulders toothed (Fig. 42), inner face of the
metafemora lacking carinae; elytra lacking reticulate
sculpturing.....Oiceoptoma Leach (Page 66)
- 3b Elytral shoulders rounded, metafemora with two carinae
on the inner face; elytra with reticulate sculpturing
(Fig. 18).....4
- 4a Pronotum uniformly black, punctures round.....
.....Heterosilpha Portevin (Page 74)
- 4b Pronotal disc black with distinct yellow margins,
punctures "V" shaped.....Necrophila Kirby and Spence
(Page 78)
- 5a Labrum deeply emarginate (Fig. 13), mesocoxae narrowly
separated.....Aclypea Reitter (Page 58)
- 5b Labrum shallowly emarginate, mesocoxae widely separated
.....Thanatophilus Leach (Page 46)

NECRODES LEACH

Necrodes Leach, 1815:88 ; Hatch, 1928

Asbolus Bergroth, 1884:229

Protonecrodes Portevin, 1922:508 NEW SYNONYMY

DIAGNOSIS: Elongate beetles, 12-25 mm in length. Eyes large, labrum moderately emarginate. Pronotum orbicular, widest near the middle; punctate; narrowly explanate (Fig. 14). Elytra tricostate, elongate. Mesocoxae widely separated.

I have examined specimens of both Protonecrodes and Necrodes and feel that the differences used by Portevin (1922, 1926) are not sufficient to warrant separate generic status.

DISTRIBUTION: This genus has 5 species distributed in the Holarctic and Oriental regions. It has also been recorded from the Neotropical region (Hatch 1928, Portevin 1926, Ratcliffe 1972), although this is questionable due to the unavailability or recent or reliable old records. Only one species occurs in North America.

BIOLOGY: The biology of the North American species has been well documented by Ratcliffe (1972), but no information appears to be available on the Palearctic and Oriental species.

IMMATURE STAGES: The larva of the Palearctic Necrodes littoralis (Linnaeus) has been described in detail by Paulian (1941) and that of Necrodes nigricornis Harold by Kawada et al (1959).

PHYLOGENETIC AFFINITIES: This genus has been placed in a separate tribe, the Necrodini (Portevin 1926) along with the genus Diamesus. This tribe is not presently recognized, with both of these genera now considered as in the Silphini, based on a better understanding of the relationships within the family. The sister genus to Necrodes would appear to be Diamesus, based on the synapomorphic character states of large eyes, the short propleural lobe and the swollen metafemora in the males. The relationships between these genera and the genera Ptomaphila and Oxelytrum have not yet been closely examined.

NECRODES SURINAMENSIS (FABRICIUS)

Silpha surinamensis Fabricius, 1775:72 ; Hatch, 1928

Protonecrodes surinamensis ab. bizonatus Portevin 1926:165

DIAGNOSIS: Pronotum black, orbicular. Elytra black with red markings present in apical one quarter, occasionally with red markings along lateral margin near mid-length. Large beetles, 15-25 mm in length.

DISTRIBUTION: Found in southern Canada from Newfoundland and Nova Scotia, westward to British Columbia, although apparently only locally common in the west (Fig. 76). It is very widely distributed in the United States (Fig. 76). It has also been recorded from South America, although these records are doubtful.

BIOLOGY: The biology of this species has been well documented by Ratcliffe (1972) in Nebraska. The adults emerge very early in April, mating and oviposition ensues, with eggs being laid singly in the soil surrounding a carcass. Upon hatching 2-4 days later, the young larvae move to the carcass to feed. The first instar (considered by Ratcliffe as ~~two~~ distinct instars) may last from 3 to 15 days, the second instar from 3 to 20 days and the third from 3 to 5 days, although this could be extended due to periods of adversity. There is a 5-8 day prepupal period, and the pupal period lasts 12-17 days. It is the adult stage which overwinters. It was not ascertained how many generations there were per year, but this may vary with geographic locality. In Canada and the more northerly United States, there is probably only one period of reproductive

activity, such as has been recorded for Necrophila americana.

This species is nocturnal, often being caught commonly at lights. It is found on larger sized carcasses (e.g. dog, bear, moose, deer etc.), which appear to be the sole size used in nature for reproductive purposes. By using the larger carcasses, the problem of food resources as a limiting factor may be reduced or eliminated, and thus may be responsible for its widespread distribution.

Mite relationships, behavior, natural enemies and other aspects of the natural history are discussed by Ratcliffe (1972).

It should be noted here that in all silphids studied, only three larval instars are present. Ratcliffe's study however, indicates the presence of four larval instars. Although I have not reared this species, and cannot give direct evidence to the contrary, a careful examination of Ratcliffe's Table 1 (1972;373) indicates that what he recognizes as the first and second instars are in fact only one instar. It has been well documented, (Mackay 1978 and references) that as insect larvae moult, the head capsule width increases by a factor of approximately 1.4 at each moult. If Ratcliffe's first and second instar measurements are examined, they clearly differ by a factor much less than 1.4. Should these be pooled, the difference factor is very close to 1.4. His other data correlate well with the expected ratio and thus appear to represent distinct instars.

IMMATURE STAGES: The larvae of this species have been described by Wickham (1895), Dorsey (1940) and subsequently by Ratcliffe (1972). Ratcliffe also gives descriptions of

the other immature stages.

GEOGRAPHIC VARIATION: There is a great deal of variation evident in the elytral patterns of the species (Ratcliffe 1972: Fig. 30). In some specimens the elytra is immaculate, while in others two red bands, or lines of spots are present. There has been no attempt at correlating these patterns with geographic locality, although studies on the variation in elytral patterns of Nicrophorus indicate a correlation between wet and cool coastal conditions and reduction in pattern (Anderson, unpublished).

PHYLOGENETIC AFFINITIES: This species is probably closely related to Necrodes littoralis (Linnaeus), with which it has often been confused (Ratcliffe 1972, Arnett 1946).

THANATOPHILUS LEACHThanatophilus Leach, 1815:89 ; Hatch, 1928Pseudopelta Bergroth, 1884:229Philas Portevin, 1903:331 NEW SYNONYMYSilphosoma Portevin, 1903:333 NEW SYNONYMYChalcosilpha Portevin, 1926:31 NEW SYNONYMY

DIAGNOSIS: Obovate beetles, 8-15 mm in length. Head without a short row of long erect hairs behind the eyes. Eyes relatively small, labrum shallowly emarginate. Pronotum pubescent; explanate, but not broadly. Elytra tricostate, with some or occasionally all of the costae effaced. Mesocoxae widely separated. Females generally with sutural apices of the elytra prolonged and rounded, males with apices evenly rounded.

I have examined specimens of these genera, and feel that the characters used by Portevin (1926) are not sufficient to warrant separate generic status.

DISTRIBUTION: This genus has approximately 28 species distributed in the Holarctic, Ethiopian and Oriental regions. Five species occur in North America, north of Mexico, four of which reach into Canada and Alaska.

BIOLOGY: There is no information available on the members of this genus which occur outside of North America.

IMMATURE STAGES: Larvae of the African species T. micans (Fabricius) and the widespread Palearctic T. sinuatus (Fabricius) are described by Paulian (1941), those of T. rugosa (Linnaeus) and T. dispar (Herbst) by Henriksen (1922) and T. auropilosa Portevin by Kawada et al (1959).

The latter three species are not described in great detail.

PHYLOGENETIC AFFINITIES: The lineage composed of Oiceoptoma, Heterosilpha, Necrophila and Aclypea (Fig. 101) is characterized elsewhere (see under Aclypea), and together with Thanatophilus composes a monophyletic lineage. This placement is based on the synapomorphic character state of having the stylus preapical on the coxite in the female genitalia (Figs. 22-26).

KEY TO THE SPECIES OF THANATOPHILUS IN NORTH AMERICA,
NORTH OF MEXICO

- 1a Elytra without costae, apices truncate....truncata (Say)
- 1b Elytra with costae, apices rounded in males, prolonged
in females.....2
- 2a Elytra with tubercles interspersed between the costae
(Fig. 15).....lapponicus (Herbst) (Page 55)
- 2b Elytra lacking tubercles between costae.....3
- 3a Inner two elytral costae effaced near base, pronotum
lacking pubescence, eighth abdominal segment orange..
.....coloradensis (Wickham) (Page 49)
- 3b Inner two elytral costae entire, pronotal pubescence
greyish, eighth abdominal segment black.....4
- 4a Outer elytral costa extending beyond apical callus (Fig. 17),
propleural lobe pointed (Fig. 39).....sagax (Mannerheim)
(Page 53)
- 4b Outer elytral costa terminating at apical callus (Fig. 16),
propleural lobe rounded (Fig. 38).....trituberculatus
(Kirby) (Page 51)

THANATOPHILUS COLORADENSIS (WICKHAM)

Silpha coloradensis Wickham, 1902:180 ; Hatch, 1928

Thanatophilus obalskii Portevin 1920a:507

DIAGNOSIS: Head and pronotum black, lacking pubescence, evenly, densely punctate. Propleural lobe pointed. Sternal pubescence sparse, brown. Elytra black, intervals flat, inner two costae effaced near base. Last abdominal segment orange. Moderately sized, 11-14 mm in length.

DISTRIBUTION: This species has been rarely collected in central Alaska and northern British Columbia (Fig. 77). It is also found in the United States at high elevations above tree line in the states of Colorado, New Mexico, Utah, Montana, and Wyoming (Fig. 77). Matthews (1975, 1979) records fossils of this species from the Yukon Territory and Alaska of age 80,000-39,000 years BP (Matthews pers. comm.).

BIOLOGY: Very little is known of the biology of this species. Peck (pers. comm.) has caught very large series in carrion baited pitfall traps in rocky alpine tundra at elevations of 13,000 feet in the aforementioned states. It is probably dependent on the carcasses of the common burrowing alpine rodents (eg ground squirrels, pikas, marmots etc.) for reproductive purposes. It appears to be adapted to very cold, extreme environmental conditions, as evidenced by its occurrence at the high elevations where even Thanatophilus lapponicus, another cold adapted species does not occur commonly. This may be responsible for the apparent change in relative abundance of these two species during the Pleistocene period as has been noted by Matthews (1975, 1979). It is possible that

these changes in abundance are due to Thanatophilus coloradensis being the dominant species during the colder glacial periods in northern refugia and T. lapponicus being dominant during the milder interglacials (see also discussion under T. lapponicus).

IMMATURE STAGES: Larvae are known, but not described. They are in the author's collection and the collection of Dr. A.F. Newton, Jr.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: This species is most likely closely related to the Tibetan T. robrowskii Jakowlew, with which it shares the apomorphic character state of having the last abdominal segment orange. Although detailed information is not available on the habitat of T. robrowskii, it is most likely a species of high elevation tundra, as is T. coloradensis. Ranges of these species were most likely expanded during the cold periods of the early Pleistocene and late Pliocene, and may have been contiguous, forming one large ancestral population. The subsequent fragmentation of this range due to warming trends may have resulted in divergence in the morphology apparently characterizing the two species.

It should also be noted that it is possible that these two species are conspecific since no detailed examinations of the comparative morphology have yet been carried out.

THANATOPHILUS TRITUBERCULATUS (KIRBY)

Oiceoptoma trituberculatum Kirby, 1837:101

DIAGNOSIS: Head and pronotum black, covered with short grey pubescence. Propleural lobe rounded (Fig. 38). Sternal pubescence brown. Elytra black, intervals flat, outer elytral costa ending at apical callus (Fig. 16). Smaller beetles 8-11 mm in length.

DISTRIBUTION: It is found in central Canada, from southern Saskatchewan, Alberta and Manitoba, north into the Northwest Territories, west to Alaska and east to Ontario (Fig. 78). I have not seen any records from the United States, although Hatch (1957) and Hatch and Rueter (1934) record it from the Pacific Northwest. These records most likely represent T. sagax, a more widely distributed species that is often confused with T. trituberculatus. Hatch (1927b) also records it from Minnesota, and while this may be a valid record of T. trituberculatus, the possibility of it being T. sagax still exists.

Fossils of T. trituberculatus have been recorded from Sibley County, Minnesota (age 13,000 years BP) (Ashworth in litt.) and Ennadai Lake, Keewatin in the Northwest Territories (age 5,500 years BP) (Elias pers. comm.). The record of Ashworth is from a pioneering assemblage that colonized southern Minnesota after the retreat of the Wisconsin ice, (Ashworth in litt.) and indicates that the distribution of the species was displaced to the south during times of ice cover.

BIOLOGY: This species is primarily northern and appears to be cold adapted like T. sagax, although it is not as widely distributed as the latter. It is most often found on carrion and under debris along lakeshores and riversides. Specimen data indicate that it is active from May to August. (see also under discussion of the biology of T. lapponicus)

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: See under Phylogenetic Affinities of Thanatophilus sagax.

THANATOPHILUS SAGAX (MANNERHEIM)

Silpha sagax Mannerheim, 1853:173

DIAGNOSIS: Head and pronotum black, covered with short grey pubescence. Propleural lobe pointed (Fig. 39). Sternal pubescence brown. Elytra black, intervals flat, outer elytral costa extending beyond the apical callus (Fig. 17). Smaller beetles, 10-13 mm in length.

DISTRIBUTION: It is widely distributed in the north, from west Alaska, southward to southern British Columbia and then eastward to eastern Quebec (Fig. 79). In the United States, it is found in the west from Washington south to California (Hatch 1957 as T. trituberculatus); also in the central states from North Dakota southward into Colorado (Fig. 79). Matthews (1968, 1974a) records fossils of this species from interior Alaska of ages 24,400 years BP and 8,000-4,000 years BP.

BIOLOGY: This species is primarily northern and appears to be cold adapted like most other members of the genus in North America. Most specimens have been found under debris or on carrion along the shores of lakes, rivers and alkali sloughs. Specimen data indicate activity from May to September. (See also under discussion of the biology of T. lapponicus)

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted, although some specimens may lack hair on the head or pronotum. This is most likely due to the hair being worn off.

PHYLOGENETIC AFFINITIES: This species is probably most closely related to T. trituberculatus, but this may be due to sympleisiomorphy and is therefore not indicative of monophyly. Many more members of this large genus should be examined before relationships within the genus may be elucidated.

THANATOPHILUS LAPPONICUS (HERBST)

Silpha lapponica Herbst, 1793:209 ; Hatch, 1928

Silpha caudata Say 1823:192

Silpha tuberculata Germar 1824:81

Silpha californica Mannerheim 1843:253

DIAGNOSIS: Head and pronotum black, covered with a dense grey pubescence. Propleural lobe broadly rounded. Sternal pubescence grey, dense. Elytra black, intervals tuberculate (Fig. 15). Smaller beetles, 10-14 mm in length.

DISTRIBUTION: Very widely distributed in Canada and Alaska (Fig. 80). In the United States, it is found primarily in the northern states, but southward in the west to California, New Mexico and Arizona (Fig. 80). The same species is also very widely distributed in the Palearctic.

BIOLOGY: This species is an early spring breeder, with the first adults appearing in late April in Ontario. It is the dominant species of open land habitats throughout its range, particularly in the northern areas where it is often the sole silphid collected.

In Ontario there are two generations per year, in contrast to the other eastern species which all have only one. The first mating and egg-laying occurs from late April to late May, with larvae also present throughout these times. In early June, teneral adults are present in the population and very soon thereafter mating and egg-laying occurs again, continuing throughout late July. Teneral adults continue to be present until early September whereupon numbers begin to decrease rapidly. This would

appear to indicate overwintering in the adult stage.

Females lay approximately 10 eggs each in the soil around a carcass, and larvae upon hatching migrate to the carcass to feed. Based solely on field observations, the egg stage lasts 5-6 days, the first instar about 7 days, the second instar 8-10 days and the third instar 10-12 days. No pupae were observed.

Thanatophilus lapponicus is a cold adapted species, which in the west occurs southward at high elevations into California. In most of its range in northern Canada and Alaska it occurs with T. sagax and T. trituberculatus, two rare species for which there is little ecological or biological information. It also occurs with T. coloradensis in Alaska, but this latter species is extremely rare. This situation appears to have been reversed in the late Pleistocene, with T. coloradensis dominating in the region of interior Alaska (Matthews 1975, 1979) and T. lapponicus being rare or absent. In other areas of the north T. sagax and T. trituberculatus are the only silphid fossils recorded during these late Pleistocene periods (Matthews 1968, 1974a, Ashworth in litt., Elias pers. comm.). The lack of T. lapponicus fossils appears odd in view of its present distribution, habits and abundance and may be a result of the qualitative changes in the tundra ecosystem during Pleistocene times as proposed by Matthews (1974b, 1979). Detailed study of the biology and ecology of T. sagax and T. trituberculatus would certainly contribute to a better understanding of the situation.

In Asia, T. lapponicus has been regarded as being injurious to furs, meats and dried fish (Emetz 1975).

IMMATURE STAGES: Larvae have been described by Dorsey (1940).

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: The species is probably most closely related to T. graniger (Chevrovat), a very similar species found only in the transverse volcanic belt of Mexico. The fact that only T. graniger and T. lapponicus possess distinct tubercles between the elytral costae would appear to be indicative of a sister species relationship. Portevin (1926) states that T. sachalinicus Kieseritzky of Japan also has tubercles, although not distinct. This taxon may be the sister group to T. lapponicus and T. graniger.

ACLYPEA REITTER

Aclypea Reitter, 1884:74

Blitophaga Reitter, 1884:82 NEW SYNONOMY

DIAGNOSIS: Obovate beetles, 10-17 mm in length. Head without a short row of hairs behind the eyes (Fig. 13). Labrum deeply emarginate (Fig. 13). Pronotum uniformly punctate, with occasional glabrous areas; pubescent; explanate, but not broadly. Elytra tricostate, usually pubescent. Mesocoxae narrowly separated. Males with a large recurved metatibial spine.

The differences used by Reitter (1884) to distinguish Aclypea from Blitophaga appear to me to not be sufficient to warrant separate generic status.

DISTRIBUTION: This Holartic genus contains 27 species, two of which occur in North America.

BIOLOGY: Members of this genus are strictly phytophagous, in marked contrast to the necrophagous habits of most of the other Silphidae. They feed primarily on Chenopodiaceae, but are often found on various cultivated plants in both Eurasia and North America. Some species are considered pests of sugar beets, spinach and other crops.

Detailed biological information is available on two of these pest species in Europe (Heymons et al 1928, 1930, Martin 1945), these being Aclypea undata (Muller) and A. opaca (L.). According to Martin, adults of both species overwinter, emerging in the spring when the sugar beets are germinating. Larvae appear about two weeks later and feed externally on the young shoots and leaves. When mature, larvae move into the

soil to pupate. Adults emerge 10-15 days later and will also feed on the plants, but not as extensively as the larvae.

IMMATURE STAGES: Heymons et al (1930) has described the immature stages of Aclypea undata, and has also (1928) described the immature stages of the Holarctic A. opaca. Martin (1945) also describes the immatures of both species.

PHYLOGENETIC AFFINITIES: The exclusively phytophagous habit and the structure of the labrum distinctly separate this genus from all other silphids. Members of the genus Silpha are in part phytophagous and therefore may be closely allied to Aclypea. However, an examination of the female genitalia reveals that in at least some Silpha, the stylus is apical on the coxite, while in Aclypea it is distinctly preapical (Fig. 23). It is therefore likely that the similar feeding habits represent convergence or sympleisiomorphy.

Aclypea appears to form a monophyletic group with the genera Oiceoptoma, Heterosilpha and Necrophila, based on the synapomorphic character state of having the second abdominal sternite in the larvae complete (Fig. 32). This is in contrast to the case in the genera Thanatophilus, Necrodes, Oxelytrum and Ptomaphila, where the sternite is broken into three separate sclerites (Fig. 31).

All published descriptions of larval Aclypea cited here, note the presence of two segmented urogomphi. Personal examination of North American Aclypea larvae reveals this to be incorrect. There is actually only one segment, a character state found only in one other silphid genus, whose larvae I have examined, this being Heterosilpha. This does not appear to be indicative of common ancestry, but more likely represents convergence.

KEY TO THE SPECIES OF ACLYPEA IN NORTH AMERICA

- 1a Elytra with punctures shallow, but distinct, the distance between punctures never being less than the width of the punctures (Fig. 20); isodiametric microsculpture of pronotum and elytra prominent, genitalia usually lightly sclerotized.....
.....opaca (Linnaeus) (Page 61)
- 1b Elytra with punctures deep, the distance between punctures often less than the width of the punctures; punctures often confluent, especially near the base (Fig.19); isodiametric microsculpture not prominent, genitalia heavily sclerotized.....bituberosa (LeConte) (Page 63)

ACLYPEA OPACA (LINNAEUS)

Silpha opaca Linnaeus, 1758:361 ; Hatch, 1928

Silpha hirta Schaeffer 1769:pl.93 Fig.6

Silpha tomentosa Villers 1789:89

Silpha villosa Naezen 1792:168

Blitophaga opaca var. binotata Portevin 1926:59

Blitophaga opaca var. samnitica Fiori 1898:161

DIAGNOSIS: Color blackish to brown, occasionally clothed with yellow hairs dorsally. Pronotum with the anterior margin usually narrow, lateral margins not distinctly raised; with occasional impunctate areas being present behind the eyes. Elytra with punctures shallow, the distance between them never less than their width (Fig. 20). Microsculpture of pronotum and elytra prominent. Genitalia in both sexes lightly sclerotized. Small beetles, 12-15 mm in length.

DISTRIBUTION: This species is known in North America from very few specimens in Alaska and the Northwest Territories (Fig. 81). It has been recorded from various localities in the United States (Horn 1880, Hatch 1927a) but these all appear to be misidentifications of Aclypea bituberosa. The species also occurs throughout the northern areas of the Palearctic region.

BIOLOGY: Like other Aclypea, it is phytophagous on Chenopodiaceae. It has long been recorded as a pest of sugar beets in Europe (Martin 1945). It is a cold adapted species and appears to be active very early in the season.

The biology has been well documented by Heymons et al (1928)

and Martin (1945) in Europe. Even though detailed studies have not yet been carried out on the North American population, there would seem to be no reason to expect differences.

IMMATURE STAGES: The immature stages have been described by Heymons et al (1928) and Martin (1945), however see also the notes under phylogenetic affinities of Aclypea.

GEOGRAPHIC VARIATION: Many specimens possess varying patterns of impunctate spots on the pronotum, although a correlation with geographic distribution has not yet been attempted.

PHYLOGENETIC AFFINITIES: It appears to be very closely related and possibly even conspecific with Aclypea bituberosa with which it is commonly confused. See also the notes under phylogenetic affinities and geographic variation of Aclypea bituberosa.

ACLYPEA BITUBEROSA (LECONTE)

Silpha bituberosa Leconte, 1859c:6

DIAGNOSIS: Color blackish to brown, occasionally clothed with yellow hairs dorsally. Pronotum with anterior margin thick, lateral margins distinctly elevated; with occasional impunctate areas but never with any behind the eyes. Elytra with punctures deep, often confluent, especially towards the base (Fig. 19). Microsculpture of pronotum and elytra not prominent. Genitalia in both sexes heavily sclerotized. Moderately sized beetles, 14-17 mm in length.

DISTRIBUTION: In Canada, this species is found throughout the provinces of Alberta, Saskatchewan and Manitoba, extending northward into southern Northwest Territories. It is also found at high elevations and in the interior valleys of British Columbia (Fig. 82). In the United States it occurs throughout most of the northern midwest into the western coastal states (Fig. 82).

BIOLOGY: The biology of this species has been well documented by Cooley (1917). It is phytophagous, feeding on Chenopodium, Monolepis and other native Chenopodiaceae, as well as Solanum (Solanaceae) (Hatch 1957, Cooley 1917). It has also been recorded from beet fields and spinach and is considered a serious pest of these crops in some areas.

Adults emerge very early in the spring, and lay eggs in the soil, which hatch about 5 days later. Larvae feed on the leaves and shoots of the young plants during the day, returning to the soil to hide during the night. The first

instar lasts about 5 days, the second also 5 days and the third about 15 days. Pupation takes place in the soil and adults emerge about three weeks later. These new adults feed, but do not lay eggs, returning to the soil to overwinter.

Most specimens are recorded from prairie areas, but some have been caught at high elevations, particularly in the coastal states. This tendency to move up to higher elevations is probably due to the cold adapted habits as evidenced by the early season activity, which may be necessitated by the feeding habits of the larvae on young, tender shoots of the food plants which would be available only at this time of the year.

IMMATURE STAGES: The immature stages have been described by Cooley (1917).

GEOGRAPHIC VARIATION: Based on examination of very few specimens, beetles from the higher elevations are smaller and have a much less convex elytra than those from lowland areas. In these forms, the genitalia tend to be heavily sclerotized as they are in all A. bituberosa, however the punctures of the elytra tend to become smaller and shallower, thus approaching the state in A. opaca. The punctures at the base of the elytra remain large and deep, yet are rarely confluent.

These patterns of variation can apparently be correlated with a change to alpine habitats and may have an ecophenotypic or ecogenotypic basis. The possibility of a continuous morphocline existing between the northern A. opaca and the southern A. bituberosa through these alpine populations cannot be excluded, although collection data at present

indicates the existence of a narrow zone where neither species occurs. Proof for the existence of such a cline may be indicative of conspecificity, as this is the only character state I have found that reliably distinguishes the two species.

PHYLOGENETIC AFFINITIES: The sister species to A. bituberosa would appear to be A. opaca. The slight divergence in morphology has probably taken place as a result of displacement of populations into more southerly localities during the Pleistocene glacial stadia. The Holarctic A. opaca probably persisted in Beringean refugia during these times having arrived at a previous time when the Beringean land bridge was exposed. The lack of northern specimens of A. bituberosa indicates that it probably did not survive glaciation in the northern refugia, but only in areas south of the ice sheet.

The two species appear to be presently narrowly allopatric, based on distributional data presented within (Figs. 81,82). This may represent an artifact of inadequate collecting in these areas.

OICEOPTOMA LEACHOiceoptoma Leach, 1815:89 ; Hatch, 1928Oeceoptoma Agassiz, 1847:256Isosilpha Portevin, 1920b:396 NEW SYNONYMY

DIAGNOSIS: Obovate beetles, 12-15 mm in length. Head with a short row of long erect hairs behind the eyes. Labrum moderately emarginate. Pronotum uniformly punctate, pubescent; explanate, but not broadly. Elytra tricostate, shoulders toothed (Fig. 42). Mesocoxae widely separated. Females with sutural apices of elytra prolonged to a sharp point, males with apices broadly rounded.

I feel that the characters used by Portevin (1926) to distinguish Isosilpha and Oiceoptoma are artificial and not sufficient to warrant separate generic status. The shared apomorphic character state of toothed elytral shoulders appears to indicate that they should be regarded as congeneric.

DISTRIBUTION: Nine species are known in this Holarctic and Oriental genus, three of which occur in North America. Two species occur in Canada.

BIOLOGY: The only Palearctic species for which biological information is available is O. thoracica (Linnaeus) (Heymons et al 1931).

IMMATURE STAGES: Larvae of O. thoracica have been described by Heymons et al (1931) and those of O. nigropunctata Lewis by Kawada et al (1959).

PHYLOGENETIC AFFINITIES: The synapomorphic character state of the presence of a row of hairs behind the eyes indicates a monophyletic relationship between this genus,

Heterosilpha and Necrophila. Adults of the species Necrophila americana and Oiceoptoma noveboracense exhibit similar behavior during periods of mating and reproduction. This behavior appears to be unique in the Silphidae and may occur only in this monophyletic group. The genus Heterosilpha, sister to Necrophila, would therefore be expected to exhibit this same type of behavior. This was not noted by Brewer and Bacon (1975), yet this does not mean that it does not occur.

KEY TO THE SPECIES OF OICEOPTOMA IN NORTH AMERICA

- 1a Pronotal disc black, with distinct orange red margin...
boveboracense (Forster) (Page 71)
- 1b Pronotal disc uniformly black.....2
- 2a Elytra epipleuron wide in posterior one half, the upper
 oblique portion being twice the width of the lower
 vertical portion (Fig. 40).....inaequale (Fabricius)
 (Page 69)
- 2b Elytral epipleuron narrow, the upper oblique portion
 approximately equal in width to the lower vertical
 portion throughout its length (Fig. 41); elytral intervals
 occasionally with transverse rugose sculpturing.....
rugulosum Portevin

OICEOPTOMA INAEQUALE (FABRICIUS)

Silpha inaequalis Fabricius, 1781:87

DIAGNOSIS: Pronotum with disc black, covered with very fine black pubescence. Elytra black, epipleuron narrow. Moderately sized, 13-15 mm in length.

DISTRIBUTION: In Canada, the species occurs in extreme southern Ontario and Quebec (Fig. 83). It is also widely distributed in the eastern United States (Fig. 83).

BIOLOGY: This species is a spring breeder, emerging very early in the season. The first adults appear from late April to early May in Ontario and New Jersey (Shubeck 1976). In more southern localities emergence occurs earlier, with adults appearing in early to mid February in Tennessee (Reed 1958) and in Maryland (Howden 1950). It is rare or absent in most northern localities and occurs commonly with O. noveboracense throughout most of the central part of its range.

There appears to be one generation per year (Reed 1958, Howden 1950), with egg laying occurring during May in the north and during February and March in the south. The subsequent peaks of adult emergence are in June through early July in the north, and are presumably earlier in the southern areas. Overwintering is accomplished in the adult stage.

Data are not available on the details of the life history, but the observations by Cole (1942) indicate an egg stage duration of 7 days and a larval stage duration of about 20 days. This data combined with the seasonal data of Shubeck (1976) would indicate a pupal period of 2 to 3 weeks.

It is almost entirely restricted to deciduous forest habitats, although it is occasionally found in open areas (Cole 1942). Cole also gives observations on seasonal activity. These indicate that O. inaequale is active on carcasses before both O. noveboracense and Necrophila americana in areas where all three may occur together. The different times of the bulk of the reproductive activity and the habitat preferences, should minimize interactions between N. americana and O. inaequale, whose ranges are broadly sympatric. Allopatry appears to be the predominant factor in minimizing interactions between O. inaequale and O. noveboracense.

Shubeck (1971) indicates that it is primarily diurnal.

IMMATURE STAGES: Larvae have been described by Dorsey (1940).

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: This species and O. rugulosum of the southern gulf coastal plains, from Florida and Georgia, west to Texas, appear to be sister species. The close relationship may be attributed to a recent divergence through isolation of a population in insular Florida, possibly during the Pleistocene period, as has been outlined for other taxa by Hubbell (1961).

OICEOPTOMA NOVEBORACENSE (FORSTER)

Silpha noveboracensis Forster, 1771:17 ; Hatch, 1928

Silpha marginalis Fabricius 1776:215

Oiceoptoma marginata Kirby 1837:100

DIAGNOSIS: Pronotum with disc black, margins orange red. Elytra brownish to black. Moderately sized, 13-15 mm in length.

DISTRIBUTION: In Canada the species occurs very commonly in the southern areas, from Manitoba eastward to the coast (Fig. 84). It also occurs westward to Alberta, but only rarely. It is also widespread in the northeastern United States (Fig. 84).

BIOLOGY: This species is a spring breeder, with the first adults appearing very early in the year. In Ontario, New York (Pirone 1974) and New Jersey (Shubeck 1976) they appear in mid April. In more southerly areas emergence occurs earlier, with the adults appearing in late February in Tennessee (Reed 1958) and early March in Maryland (Howden 1950).

In the more northerly localities it is the dominant early season species in forested habitats where O. inaequale is rare or absent (Pirone 1974). Throughout central parts of the range it occurs with O. inaequale, but the latter precedes O. noveboracense in emergence by a few days (Cole 1942). In southern areas O. noveboracense is absent and O. inaequale is the dominant spring breeder, while in extreme southern areas, O. rugulosum appears to be the sole species present.

There is one generation per year with mating and egg laying occurring from mid April to late May. Females each lay 8-10 eggs in the soil around the carcass. These eggs hatch in 5-6 days and the newly emerged larvae crawl to the carcass to feed. Based on both laboratory and field observations, the first instar lasts approximately 4-5 days, the second 7-8 days and the third 10 days, whereupon the larvae dig into the soil to pupate. No pupae were observed, although seasonal data indicates a generation period of 6-8 weeks (as in Pirone 1974), thereby indicating approximately 2-3 weeks for pupal development.

The second peak of activity occurs throughout most of the month of July, and is composed of many teneral and no egg carrying females. This indicates lack of a second larval brood and subsequent overwintering as adults.

The species, although commonly found in all habitats sampled, appears to show a preference for forested areas instead of open habitats. This factor minimizes its interaction with Thanatophilus lapponicus and Necrophila americana.

It has been recorded as being primarily diurnal (Shubeck 1971).

In the early spring, prior to and during the mating season, adults of this species are very commonly seen paired, with the males mounted on top of the females. This position is apparently maintained by both members for sustained lengths of time, although copulation is not actively occurring. A closer examination reveals that the male has firmly grasped

one of the antennae of the female in its mandibles. This position is maintained until copulation occurs. At this time the male lets go of the antenna of the female and moves backward on the female's elytra. He uses his antennae to drum or stroke the pronotum of the female while probing and eventually inserting the aedeagus. Once copulation has terminated, the male returns to his original position on the female, and once again grasps one of her antennae in his mandibles. This pattern of behavior continues until the female lays eggs. When eggs and larvae are present few pairs are seen in this position. It appears that this behavior, which terminates at oviposition is a method by which the male insures his reproductive investment (see Alcock 1979).

This behavior also occurs in the species Necrophila americana.

IMMATURE STAGES: Larvae have been described by Dorsey (1940).

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: I have only seen one species from the Palearctic and thus cannot offer any comments on the placement of O. noveboracense.

HETEROSILPHA PORTEVIN

Heterosilpha Portevin, 1926:83

DIAGNOSIS: Obovate beetles, 14-18 mm in length. Head with a short row of long erect hairs behind the eyes. Labrum moderately emarginate. Pronotum uniformly densely punctate; strongly margined laterally; lacking pubescence. Elytra with reticulate sculpturing (Fig. 18). Inner face of metafemora with two carinae.

DISTRIBUTION: This genus has only two species, both of which occur in North America. Matthews (1977) records a fossil of Miocene age of Heterosilpha from Meighen Island in the Canadian arctic. Close examination of this fossil reveals that it is not conspecific with either of the extant species. The punctures on the pronota of the extant species are finely punctate, whereas the fossil specimen has large, confluent punctures. Undoubtedly the genus was more widely distributed in the past, when conditions in the far north may have been more suited to insect life.

BIOLOGY: No information is available on the Californian species H. aenescens (Casey), although its habits are probably similar to those of H. ramosa (Say).

IMMATURE STAGES: The immature stages of H. aenescens are not known.

PHYLOGENETIC AFFINITIES: This genus is closely related to Necrophila and Oiceoptoma, as discussed under the phylogenetic affinities of Necrophila.

KEY TO THE SPECIES OF HETEROSILPHA IN NORTH AMERICA

- la Males with pro- and mesotarsal segments one through four broadly expanded, females with elytra drawn out at apex; male genitalia thick and broad, parameres with apices thick and curved down; elytra without metallic shininess.....*...ramosa (Say); (Page 76)
- lb Males With pro- and mesotarsal segments not expanded; male genitalia thin and slender, parameres with apices more narrow and straight; elytra often with metallic shininess.....aenescens (Casey)

HETEROSILPHA RAMOSA (SAY)

Silpha ramosa Say, 1823:193 ; Hatch, 1928

Silpha cervaria Mannerheim 1843:252

DIAGNOSIS: Pronotum black, finely densely punctate. Elytra black, not metallic. Males with pro and mesotarsal segments one to four laterally expanded. Female with elytral apices drawn out. Moderately sized beetles, 14-18 mm in length.

DISTRIBUTION: In Canada, it is found from extreme north western Ontario and Manitoba, westward to coastal British Columbia (Fig. 85). It is also widely distributed in the western United States (Fig. 85).

BIOLOGY: The biology of H. ramosa in Colorado has been worked out by Brewer and Bacon (1975). Their study shows that the species overwinters as adults, with the first individuals becoming active in mid-April of the following year. Mating takes place and eggs are laid in the soil around the carcass. There are two generations per year with the second peak of activity in late July and August. The egg to adult period takes about 30 days; the egg stage lasting 5 days, the first instar 4-5 days, the second instar 5-6 days, the third instar 8-10 days and the pupal stage 8-9 days. Observations are also given on mating behavior and feeding habits.

Other studies on the biology of this species include Gissler (1880) and Goe (1919), who erroneously calls it O. inaequale. Linsley (1942) records H. ramosa as feeding on dead grasshoppers in California, but it is possible that these

observations refer to H. aenescens (Miller and Peck 1979).

Heterosilpha ramosa appears to be most common in the aspen groves that are characteristic of prairie-forest interfaces.

IMMATURE STAGES: The larva was initially described by Gissler (1880) and subsequently by Dorsey (1940). Brewer and Bacon (1975) also present notes on the morphology of the immature stages.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: Heterosilpha ramosa is very closely related to H. aenescens, the only other species in the genus. The very similar morphology may be indicative of a recent divergence.

Fossils of H. ramosa of age 30,000 years BP have been found in California (Miller and Peck 1979).

NECROPHILA KIRBY AND SPENCE

Necrophila Kirby and Spence, 1828:509 ; Madge, 1980

Necrobora Hope, 1840:151

Necrotropha Gistel, 1848:121

Eusilpha Semenov-Tian-Shanskij, 1891:229 NEW SYNONYMY

Calosilpha Portevin, 1920b:396 NEW SYNONYMY

Deutosilpha Portevin, 1920b:396 NEW SYNONYMY

Chrysosilpha Portevin, 1921:538 NEW SYNONYMY

Deuterosilpha Hatch, 1928:112 NEW SYNONYMY

DIAGNOSIS: Oval beetles, 15-20 mm in length. Head with a short row of long, erect hairs behind the eyes (Fig. 127), with a large, distinct fovea on frons, midway between the eyes. Labrum moderately emarginate. Pronotum punctate, more densely so laterally; lacking pubescence; strongly margined laterally, widely explanate. Inner face of metafemora with two carinae. Elytral sculpture variable.

I have examined a small number of specimens from the genera Eusilpha, Calosilpha, Deutosilpha and Chrysosilpha and feel that the characters used by Portevin (1926) to differentiate the genera are not sufficient to warrant generic status. The name Deuterosilpha Hatch is a misspelling of Deutosilpha Portevin.

DISTRIBUTION: There are approximately 20 species in this genus which is found in both the Holarctic and Oriental regions. Only one species is found in North America.

BIOLOGY: Nothing has been recorded on the biology of any of the Palearctic or Oriental species.

IMMATURE STAGES: The larva of N. brunneicollis Kraatz has been described by Kawada et al (1959).

PHYLOGENETIC AFFINITIES: The genus is most closely related to Oiceoptoma and Heterosilpha, based on the synapomorphic character state in the adults of possessing a row of long, erect hairs behind the eyes (Fig. 12). The genera Necrophila and Heterosilpha appear to be sister taxa based on the synapomorphic character states of possessing two carinae on the inner face of the metafemora in the adults and having the sensory apparatus on the second antennal segment in the larvae composed of one or more plates (Fig. 33).

NECROPHILA AMERICANA (LINNAEUS)

Silpha americana Linnaeus, 1758:360 ; Hatch, 1928

Scarabaeus peltata Catesby 1771:Pl. 10, Fig. 7

Oiceoptoma terminata Kirby 1837:103

Oiceoptoma affine Kirby 1837:103

Oiceoptoma canadensis Kirby 1837:104

DIAGNOSIS: Pronotum with margins yellow, disc black, punctures "V" shaped. Elytra black, with reticulate sculpturing. Females with elytral apices prolonged. Large beetles, 15-20 mm in length.

DISTRIBUTION: It is found in Canada from Nova Scotia westward to central Manitoba (Fig. 86). It is also widely distributed in the eastern United States (Fig. 86).

BIOLOGY: This species is a late spring and early summer breeder, with the first adults appearing in mid to late May in Ontario, New York (Pirone 1974) and New Jersey (Shubeck 1976). In more southern areas emergence occurs in late March (Reed 1958).

The period of reproduction is from late May through mid July, with the bulk of larval emergence from late May to mid June. The eggs are laid in the soil around the carcass and the larvae upon hatching crawl to the carcass to feed. There is only one generation per year, with an egg to adult duration of approximately 10-12 weeks. It appears to exhibit continuous activity throughout the summer, with no pronounced peaks of adult activity being evident. Teneral, which are present from mid July to early September are indicative of adult

emergence at these times and subsequent overwintering as adults. This pattern conforms in general to those found by Pirone (1974) and Shubeck (1976) for this species.

It is primarily found in mesic, open habitats, but is also often common in forested areas (Shubeck 1969, Pirone 1974, Walker 1957). Its occurrence in open areas would serve to minimize interactions with O. noveboracense and O. inaequale, while its preference for warmer and wetter areas would minimize interactions with T. lapponicus. It is also of importance when considering coexistence, that the reproductive period of this species does not overlap with any of the other eastern silphines for which information is available.

It has been recorded as primarily diurnal (Shubeck 1971).

The mating and pre-mating behavior is similar to that noted for O. noveboracense.

IMMATURE STAGES: Larvae have been described by Dorsey (1940).

GEOGRAPHIC VARIATION: Specimens from southern localities tend to be much wider and more oval than those from the north. The apices of the elytra, which are tipped with yellow in the northern areas, are uniformly black in these southern populations. Variations in the size and shape of the black pronotal spot have also been recorded (Hatch 1927a).

PHYLOGENETIC AFFINITIES: This species appears to be highly autapomorphic and thus difficult to place in view of the fact I have seen only a few of the other species in the genus.

2

A

NICROPHORINI

DIAGNOSIS: Elongate beetles, 12-35 mm in length. Epistomal suture present (Fig. 47), gular sutures fused for at least the first one half of their length. Antennae with second segment small, indistinct. Pronotum cordate, orbicular or transverse, not explanate, not as wide as elytra at base. Elytra truncate, exposing three or four abdominal tergites; lacking costae. Abdomen with a pair of stridulatory files on the mid-dorsum of segment five (Fig. 48). Legs short, stout, suited for digging.

DISTRIBUTION: There are approximately 87 species in two genera in this tribe which is distributed nearly worldwide, except in Australia or sub-Saharan Africa. Only one of these two genera occurs in North America.

BIOLOGY: Of the two genera in this tribe, only Nicrophorus has had its ecology, biology, development etc. reasonably well documented. The natural history of the other genus, Ptomascopus Kraatz of Japan and China, was unknown until only recently, when Peck (in prep.) made detailed observations on the life history and general biology of Ptomascopus morio Kraatz. Unlike Nicrophorus, there is no burial of carrion, no parental care or even extended larval-adult association and no localized feeding of larvae. Eggs are laid in the soil and the larvae feed externally on the carcass.

IMMATURE STAGES: Larvae have been described for very few members of this tribe, with most descriptions restricted to the genus Nicrophorus. The larvae of Ptomascopus morio are

also described (Kawada et al 1959), but not in great detail.

PHYLOGENETIC AFFINITIES: This tribe can be characterized as a monophyletic group by the reduced sclerotization and form of the larvae, the reduction in the number of ocelli in the larvae, the presence of stridulatory files on abdominal segment 5, the presence of the clypeal membrane and the small second antennal segment in the adults.

NICROPHORUS FABRICIUS

Nicrophorus Fabricius, 1775:71 ; Hatch, 1928; Madge, 1980

Necrophorus Thunberg, 1789:7

Necrophagus Leach, 1815:88

Cyrtoscelis Hope, 1840:149

Acanthopsilus Portevin, 1914:223

Necrocharis Portevin, 1923:141 NEW SYNONYMY

Necroxenus Semenov-Tian-Shanskij, 1926:46 NEW SYNONYMY

Eunecrophorus Semenov-Tian-Shanskij, 1933:152 NEW SYNONYMY

Necrocleptes Semenov-Tian-Shanskij, 1933:153 NEW SYNONYMY

Necrophorindus Semenov-Tian-Shanskij, 1933:153 NEW SYNONYMY

Necrophoriscus Semenov-Tian-Shanskij, 1933:152 NEW SYNONYMY

Nesonecrophorus Semenov-Tian-Shanskij, 1933:153 NEW SYNONYMY

Necropter Semenov-Tian-Shanskij, 1933:154 NEW SYNONYMY

Nesonecropter Semenov-Tian-Shanskij, 1933:154 NEW SYNONYMY

Stictonecropter Semenov-Tian-Shanskij, 1933:154 NEW SYNONYMY

Neonicrophorus Hatch, 1946:99 NEW SYNONYMY

DIAGNOSIS: Elongate beetles, 12-25 mm in length, with orange markings on the elytra. Antennae with a distinct four segmented club. Stridulatory files well developed, extending the entire length of abdominal segment five.

The names proposed by Semenov-Tian-Shanskij, Portevin and Hatch, appear not to represent natural groupings within Nicrophorus, and hence are synonymized with the latter.

DISTRIBUTION: There are about 85 species in this genus, distributed worldwide, except Australia and sub-Saharan Africa. Fifteen species occur in North America, north of Mexico, fourteen of which occur in Canada and Alaska.

BIOLOGY: Of the life cycle strategies that have been developed in the Silphidae, that of Nicrophorus is the more complex pattern. This basic life cycle, first elucidated by Pukowski (1933), can be summarized as follows. It should be noted that her work was carried out on six European species, and that only recently have the biologies of some North American species been verified in detail (Wilson, pers. comm.).

Beetles, upon finding a dead animal will crawl over and under the carcass, activities which have been interpreted as assessing the suitability of the carcass for burial. The carcass, if suitable, will be buried where it lies, or may be moved to a place where the substrate will permit burial. The methods by which the beetles move carcasses have been documented by Milne and Milne (1976). Burial is accomplished by the beetles burrowing into the soil under the carcass, pushing the soil out the other side as they emerge from the substrate. This behavior is continued until the carcass sinks into the cavity, or is pulled in by the beetles from below. Subsequent movements by the beetles around the carcass after it has been buried result in a crypt-like chamber, with the carcass lying in the center.

Usually only a pair of beetles is associated with a carcass, however more than one pair or even more than one species may be present. Should there be more than a single pair present, fighting ensues with only one pair remaining to use the resource for reproductive purposes. This fighting usually takes place after the food source is buried. The victorious pair will then prepare the carcass by moulding it into a sphere and stripping

it of any fur which may be present. The female then excavates a passage leading off in a lateral direction from the crypt, where she will eventually lay up to 20 eggs in the walls of the passage. After oviposition the male always leaves the crypt. However, if the female is removed, the male will remain with the brood (D.S. Wilson pers. comm.). I feel that this behavior, which parallels the riding behavior of males on females in some Silphini, is a means by which the male insures his reproductive investment.

When the larvae hatch, they migrate to the food source, whereupon the female will chew a hole in the exterior surface of the carrion ball, thereby exposing the inner contents. The larvae then crawl into this hole, but do not yet feed on the contents. At this time the female beetle will crawl to the side of the ball and regurgitate a liquid which is imbibed by the larvae through the contact of mouthparts. This continues for about 5 or 6 hours, at which time the larvae begin to feed on their own. Reciprocal feeding also takes place after the first and second moults, but does not appear obligatory, since the larvae will mature normally should both adults be removed.

There are three larval instars, the first lasting about 12 hours, the second about 24 hours, and the third from 5 to 15 days depending on the species and conditions. Upon completing larval development, the larvae crawl into the surrounding soil to pupate, a stage which lasts from 13 to 15 days. It is at this time that the female leaves the crypt.

D.S. Wilson (pers. comm.) has also made some interesting

observations on the life cycle of some of the North American species. He notes that during the moulding of the carcass into a ball, phoretic nematodes are transferred from the beetle to the ball. These nematodes rapidly proliferate and spread over the entire surface, and may act as antifungal or antimicrobial agents. In such a manner they may be acting to decrease the rate of decomposition as has been noted by Leech (1934). They may also act, through the secretion of toxins, to render the exterior of the ball unsuitable for consumption and thus protect the food from other competitors.

Phoretic mites are also invariably present on the beetles and may act in a similar symbiotic manner by feeding on fly eggs that may be in the surrounding soil or on the carcass (Springett 1968). This relationship is at present under intensive investigation by Wilson, who is attempting to formulate a model of coevolution of the beetles and their phoretic associates.

These mites are representative of four families, the Parasitidae, the Anoetidae, the Uropodidae and the Macrochelidae (Roeder 1972). The Poecilochirus mites of the family Parasitidae are the largest and the most active mites on the beetles, and the group that are implicated by Springett (1968) as being involved in a symbiotic relationship with the beetles. The relationships and the possible roles of the other mites have not yet been examined.

It therefore appears that the Nicrophorus avoid competition with the flies and other scavengers by burying the food sources and by having an assemblage of associates which render the

resource unsuitable for consumption by competitors. This is in marked contrast to the strategy that is employed by the Silphini to alleviate competition.

For reasons of size limitations, only small carcasses can be used for reproductive purposes, and thus these beetles are not competing with the Silphini for food. Occasionally Nicrophorus are found on larger carcasses where they are either eating the carrion or are eating the fly larvae which are invariably present. For similar reasons, adult Nicrophorus may also be found in dung or fungi.

They appear to divide up the available resources through differential habitat utilization and by having different seasonal patterns of development. Studies on this aspect of the ecology of the North American species are few, however the second part of this paper presents a detailed analysis of resource partitioning in eastern North American Nicrophorus and Silphini. The Europeans have studied the ecology of Nicrophorus in much greater detail. Of particular note are the studies of Pukowski (1933), Cantonnet and Lecordair (1947), Mroczkowski (1949), Theodorides and Van Heerdt (1950), Petruska (1968b), Novak (1965a, b), Paulian (1946) and Katakura and Fukuda (1975), all of which deal with various aspects of the ecological interactions among species.

Detailed studies on the biology of Palearctic species have been carried out by Pukowski (1933), Sidor (1966) and Benick (1912). Other studies on various aspects of larval development are Roussel (1964a, b) and Spicarova (1971, 1973).

Spicarova (1972, 1974) in Europe and Katakura and Fukuda (1975) in Japan, have looked at the role of light in controlling daily activity patterns.

All Nicrophorus possess a pair of stridulatory files on the fifth abdominal tergite, the morphology of which is characteristic of the species (Schumacher 1973). These files when rubbed on the apex of the elytra produce a scraping sound which can be used for defense as well as playing a possible communicatory role (Schumacher 1973, Niemitz 1972). When disturbed, the beetles will not only stridulate, thereby sounding like a bee, but will also go into a state of thanatosis, lying still with all legs rigidly extended. On occasion they will also move the apical segments of the abdomen in much the same way that a bee does when evertng a stinger (Lane and Rothschild 1965). When in a state of thanatosis they will also emit a foul smelling fluid from the anus, which presumably is foul tasting or possibly even toxic to any organisms which may ingest it. The contrasting red and black color pattern may also play a defensive role, apparently being aposematic and thus warning of the foul taste and deterring predation by birds as has been noted by Jones (1932). Diffraction gratings, producing an irridescant color pattern may also deter or confuse predators Hinton (1969).

IMMATURE STAGES: Larvae of some Palearctic species have been described, the most notable contribution being that of Pukowski (1934). In this paper, the larvae of N. germanicus (Linnaeus), N. fossor Erichson, N. investigator Zetterstedt,

N. vespilloides Herbst, N. vespillo (Linnaeus) and N. humator Olivier are keyed, with the last four species being described, although poorly. Hatch (1927a) also presents keys to the same four species that Pukowski describes. Larvae of N. humator have subsequently been described in detail by Paulian (1941) and those of N. vestigator Herschel by Benick (1912).

The larvae of the North American species have not yet been described in detail.

PHYLOGENETIC AFFINITIES: The sister genus to Nicrophorus, and only other genus in the tribe, is Ptomascopus, with two species distributed in the Oriental region. It was more widely distributed in the past as evidenced by Oligocene fossils of the genus from France (Hatch 1927a). Of the two genera, Nicrophorus appears to be the more autapomorphic taxon, being characterized not only by the more complex life history, but by such apomorphic character states as the four segmented antennal club in the adults and the reduced sclerotization in the larvae which lacks the lateral flanges of the tergites of other Silphidae.

Hypothesized relationships among the North American species of Nicrophorus are depicted in Figure 102, along with the evidence on which the placement is based (Fig. 103B). Three lineages appear to be present, the investigator, orbicollis and marginatus lineages, within which various groups can be delimited. Further discussion is presented under the Phylogenetic Affinities section for all species.

KEY TO THE SPECIES OF NICROPHORUS IN NORTH AMERICA,
NORTH OF MEXICO

- 1a Pronotum without an anterior transverse impression; with
extremely narrow lateral margins (Fig. 49); elytral
epipleuron very narrow (Fig. 61).....
.....carolinus (Linnaeus) (Page 95)
- 1b Pronotum with an anterior transverse impression, lateral
margins not narrow (Figs. 51-53); elytral epipleuron
wide.....2
- 2a Frons and pronotal disc red; tarsal empodium quadrisetose
(Fig. 45).....americanus Olivier (Page 97)
- 2b Frons and pronotal disc black; tarsal empodium bisetose
(Fig. 46).....3
- 3a Pronotum covered with dense yellow pubescence, except
occasionally for two small areas on disc.....
.....tomentosus Weber (Page 99)
- 3b Pronotum glabrous, or with only sparse hair on anterior
or lateral margins.....4
- 4a Posterior lobe of metepimeron with dense yellow pubescence
(Fig. 50); pronotum cordate (Fig. 52).....5
- 4b Posterior lobe of metepimeron glabrous, or with dark hairs
or only a few yellow hairs, pronotum variable.....7
- 5a Anterior face of procoxae with short hairs on basal
half.....marginatus Fabricius (Page 101)
- 5b Anterior face of procoxae with long hairs on basal half
.....6

- 6a Penultimate antennal segment with outer edge deeply emarginate (Fig. 35); basal segment of antennal club black; anterior black band of elytra reaching epipleural ridge, but not crossing onto epipleuron (Fig. 64)....
.....obscurus Kirby (Page 105)
- 6b Penultimate antennal segment with outer edge shallowly emarginate (Fig. 36); basal segment of the antennal club black or red; if red, then the anterior black elytral band crosses over the epipleural ridge into the epipleuron (Fig. 62), if black then the elytral maculations are reduced or absent, except for reddish marking on the elytral shoulder (Fig. 62E).....guttula Motschulsky
(Page 103)
- 7a Metatibia distinctly curved; anterior black band not reaching the epipleuron (Fig. 57).....sayi Laporte
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- 7b Metatibia straight; the anterior black band of elytra usually reaching the epipleuron.....8
- 8a Elytral epipleuron unicolored, either entirely black or orange.....9
- 8b Elytral epipleuron distinctly bicolored, partly black and partly orange.....13
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- 10a Elytra with long hairs over the dorsal surface; epipleural ridge short, reaching only to the level of the tip of the scutellum (Fig. 55).....orbicollis Say (Page 108)

- 10b Elytra lacking long hairs over most of dorsal surface;
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- 11a Elytra immaculate; metasternal pubescence long, dense,
brown.....nigrita Mannerheim (Page 111)
- 11b Elytra maculate, with small lateral anterior spots and two
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metasternal pubescence sparse, yellow-brown.....
.....pustulatus Herschel (Page 113)
- 12a Metasternum with elongate, bald patch just behind the
mesocoxae (Fig. 54); with continuous multiple and irregular
rows of short, stout, erect hairs running around elytral
shoulder to base of epipleural ridge (Fig. 43).....
.....hybridus Hatch and Angell (Page 115)
- 12b Metasternum without an elongate bald patch; with
continuous multiple irregular rows of hairs around elytral
shoulder, but ending well before the base of the
epipleural ridge (Fig. 44); elytral maculations often
reduced (Figs. 65C-F).....investigator Zetterstedt
(Page 117)
- 13a Metasternal pubescence brown; apical three segments of the
antennal club red.....mexicanus Matthews
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antennal club black.....14
- 14a Base of elytral epipleuron orange, with a prebasal black
spot (Fig. 59A,B); upper and lower faces of antennal
segments nine and ten with a patch of dense white hairs

arranged in a figure eight pattern.....

.....vespilloides Herbst (Page 121)

14b Base of elytral epipleuron entirely black* (Fig, 60);
upper and lower faces of antennal segments nine and ten

• without dense white hairs, although the figure eight
pattern may be present as a vestige.....

.....defodiens Mannerheim (Page 125)

NICROPHORUS CAROLINUS. (LINNAEUS)Silpha carolina Linnaeus, 1771:530 ; Hatch, 1928Necrophorus mediatus Fabricius, 1801:334Necrophorus mysticallis Angell, 1912:307Necrophorus carolinus ab. scapulatus Portevin, 1923:142Necrophorus carolinus var. dolosus Portevin, 1923:142

DIAGNOSIS: Pronotum cordate, lateral margins extremely narrow except at base, basal margins moderately wide; anterior transverse impression lacking (Fig. 49). Antennal club with all four segments orange. Metasternal pubescence yellow, metepimeron glabrous. Hind tibiae very slightly curved. Elytral epipleuron very narrow (Fig. 61). Moderately sized, 15-20 mm in length.

DISTRIBUTION: In Canada, it is known from a single specimen from southeast Alberta. It is widely distributed in the central states, southward to Texas, then eastward along the Gulf Coastal Plains, then northward along the Atlantic Coastal Plains to Virginia (Fig. 87). It has also been collected at Tuba City, Arizona.

BIOLOGY: Arnett (1946) recorded observations of this species burying a dead snake. It appears restricted to sandy soil in open or sparsely forested areas, although this requires verification. No data are available on seasonal patterns.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: The typical elytral color pattern (Fig. 61A) is the commonest throughout its range in the southeastern states. In areas of the north central states, the

maculations are broken and reduced (Fig. 61B), while populations in the vicinity of Tuba City, Arizona are entirely black.

This is one species of Nicrophorus that exhibits melanism in an inland locality. The other cases appear to be correlated with coastal areas and their associated climatic patterns. The case of N. carolinus may be the result of a pattern which evolved in a coastal area, but has since undergone a shift in range.

PHYLOGENETIC AFFINITIES: This species has formerly been regarded as belonging to a distinct genus, Necrocharis Portevin. Recently, Madge (1958) has suggested placement near Nicrophorus marginatus based on pronotal shape, curved hind legs and the shortened length of the elytra. The lack of yellow hairs on the metepimeron would not support inclusion in the marginatus group, and the characters mentioned by Madge are either pleisiomorphic (cordate pronotum, shortened elytra) or are weak and subject to convergence.

I tentatively place it at the base of the marginatus lineage (Fig. 102) and anticipate that the species will possess the larval characters defining that group.

NICROPHORUS AMERICANUS OLIVIER

Nicrophorus americanus Olivier, 1790:6 ; Hatch, 1928

Necrophorus grandis Fabricius 1801:247

Nicrophorus virginicus Frölich 1792:123

DIAGNOSIS: Pronotum orbicular, lateral and basal margins broad, with an anterior transverse impression. Pronotal disc and frons red. Antennal club with all four segments orange. Metasternal pubescence yellow-brown; metepimeron with pubescence sparse, brown. Hind tibia slightly curved. Elytral pattern as in Fig. 58. Large beetles 25-35 mm in length.

DISTRIBUTION: In Canada this species is known from a few localities in extreme southern Ontario and Quebec (Fig. 88). In the United States, it was once widely distributed in the eastern states (Fig. 88), but now appears restricted to isolated localities (Anderson in press; Davis 1980).

BIOLOGY: Although N. americanus is one of the most distinctive and commonly recognized members of our fauna, virtually nothing has been recorded on its biology. It has been recorded at carrion in Tennessee (Walker 1957) and Ohio (Jaques 1915). It was also the subject of some crude experiments on the olfactory senses of carrion beetles (Abbott 1927a). I have made in another publication (Anderson 1982) some inferences on its biology based on its large size and what is known of the habits of other large Nicrophorus. Its decline over the last 50 years can be attributed to this large size and appears to be due to the deforestation of eastern North America which has removed

mature climax forests from all but a few isolated localities.

It is nocturnal, with most specimens having been collected in light traps and not at carrion.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: It appears to be most closely related to the European species N. germanicus, however this relationship needs to be more closely investigated. At present only the large size and the orbicular pronotum are evidence of affinity.

In North America, the relationships among the three species with orbicular pronota is unclear (Fig. 102). Perhaps an attempt at construction of a cladogram of the world species of Nicrophorus would solve these problems.

NICROPHORUS TOMENTOSUS WEBERNecrophorus tomentosus Weber, 1801:47 ; Hatch, 1928Necrophorus velutinus Fabricius 1801:334Necrophorus velutinus ab. angustefasciatus Portevin 1925:170Necrophorus velutinus ab. aurigaster Portevin 1925:170

DIAGNOSIS: Pronotum sub-quadrate, not strongly cordate, with wide lateral and basal margins; covered with dense yellow pubescence except occasionally for two spots in the center of the disc. Antennal club with all four segments black. Metasternal pubescence yellow, with bald spots behind mesocoxae; metepimeron with only a few yellow hairs. Hind tibiae straight. Elytral pattern as in Fig. 67. A small species, 12-18 mm in length.

DISTRIBUTION: In Canada, it is common from Nova Scotia and New Brunswick, westward to southern Saskatchewan (Fig. 89). It is widely distributed in the eastern United States (Fig. 89).

BIOLOGY: This species is summer active, first appearing in late June and early July in Ontario, New Jersey (Shubeck 1976) and New York (Pirone 1974). This is a pattern unlike those of the other eastern North American Nicrophorus, for which life history data are available. The presence of teneral during this period of emergence is indicative of overwintering in a stage other than the adult.

Upon emerging, the adults pass through the typical life cycle of the genus, but they do not bury the carcass. Rather, they make a shallow pit into which the carcass sinks, but is not covered with soil. Instead the pit is often covered with leaf litter and other debris. After migrating into the

surrounding soil, the mature larvae do not pupate, but remain quiescent in the third instar (as prepupae), later turning a dark yellow color. The winter is passed in this form, with pupation occurring in the spring, later followed by the adult emergence. What the environmental cues are that initiate and terminate diapause have not yet been determined.

The species is very common in all habitats sampled, a fact probably due to the emergence at a time when no other eastern Nicrophorus are known to be reproductively active.

It is diurnal (Shubeck 1971) and has been recorded as a mimic of Bombus (Hymenoptera: Apidae) (Milne and Milne 1944), which it greatly resembles when in flight. This diurnal flight behavior may also be an important component of resource partitioning.

IMMATURE STAGES: The larva has been described by Schaup (1881), but very superficially.

GEOGRAPHIC VARIATION: There are occasionally sporadic variations in the extent of the elytral maculations.

PHYLOGENETIC AFFINITIES: The characteristics of the life cycle would appear to place the species in the investigator group (Fig. 102). It lacks the quadrate pronotum found in N. investigator, N. mexicanus and N. nigrita, and is therefore not a member of that monophyletic group. It appears to be most closely related to N. hybridus, with which it shares the apomorphic character state of the possession of a bald spot behind the mesocoxae (Fig. 54).

NICROPHORUS MARGINATUS FABRICIUS

Necrophorus marginatus Fabricius, 1801:334 ; Hatch, 1928 ;

Miller and Peck, 1979.

Necrophorus requiescator Gistel, 1848:190

Necrophorus montezumae Matthews, 1888:92

Necrophorus marginatus ab. cordiger Portevin, 1924:84

Necrophorus guttula labreae Pierce, 1949:63

Necrophorus mckittricki Pierce, 1949:66

Necrophorus obtusiscutellum Pierce, 1949:67

Necrophorus investigator latifrons Pierce, 1949:67

DIAGNOSIS: Pronotum strongly cordate, with narrow lateral margins and wide basal margin (Fig. 52). Antennal club with all four segments orange. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence (Fig. 50). Hind tibiae slightly curved. Elytral pattern as in Fig. 63. Moderately sized, 15-22 mm in length.

DISTRIBUTION: In Canada this species is found in extreme southern Ontario and Quebec, as well as Manitoba, Saskatchewan, Alberta and British Columbia (Fig. 90). It is very widely distributed in the United States, ranging southward into northern Mexico (Fig. 90).

BIOLOGY: This species is initially active in mid to late spring in Ontario, with the first individuals appearing in early May. Reproduction occurs from late May through June, with teners appearing in July and August. The individuals from this second period of activity subsequently overwinter.

In eastern Canada, it is the only species that is found commonly in open habitats, especially the meadows. The

only other species which occurs frequently in these habitats is N. tomentosus, which is found more commonly in the other habitats. This is also at a time when N. marginatus has completed reproductive activity, so competition for food resources would appear not to occur.

In the western provinces, N. marginatus is an inhabitant of prairie areas, along with N. guttula, N. obscurus, N. hybridus and N. investigator. The ecological relationships among these five species need to be examined in more detail in order to detect if there are any mechanisms of resource partitioning.

It has not been determined if the species is nocturnal or diurnal.

IMMATURE STAGES: Larvae are known, but not described. They are in the author's collection.

GEOGRAPHIC VARIATION: There is slight variation in the typical pattern of the elytral maculations, with the anterior and the posterior bands occasionally being fused.

PHYLOGENETIC AFFINITIES: This species is very closely related to N. guttula and N. obscurus (Fig. 102). This group can be characterized as monophyletic by the possession of the synapomorphic character states of dense yellow hair on the metepimeron (Fig. 50) and incomplete ventral sclerotization on the last segment in the larvae (Fig. 30).

Nicrophorus marginatus may have been limited to the western prairies until man provided cleared habitats in the eastern United States and Canada, whereupon it has spread eastward. This same pattern has been documented for Carabidae by Lindroth (1971).

NICROPHORUS GUTTULA MOTSCHOUJSKY

Necrophorus guttula Motschoulsky, 1845:53 ; Miller and Peck,
1979

Necrophorus hecate Bland, 1865:382 , NEW SYNONYMY

Nicrophorus guttula punctostriatus Pierce, 1949:66

Nicrophorus hecate immaculosus Hatch, 1957:15 NEW SYNONYMY

DIAGNOSIS: Pronotum strongly cordate, with narrow lateral and wide basal margins. Antennal club with either all segments black, or with the basal segment black and the apical three segments orange. Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibiae straight. Elytral pattern within Canada usually as in Fig. 62B. Moderately sized, 14-20 mm in length.

Nicrophorus hecate and N. guttula have long been considered separate species based on the different color patterns of the elytra. Recent evidence (Anderson, unpublished) demonstrates that this variation is clinal and that intermediates exist. In view of these facts, the two forms should be considered conspecific.

DISTRIBUTION: In Canada, the species is found in the southern areas of British Columbia, Alberta and Saskatchewan (Fig. 92). It is widely distributed in the western states, particularly in the south (Fig. 92).

BIOLOGY: This species is apparently an inhabitant of dry forest and prairies, especially where soils are sandy. It is diurnal and has been caught at human and coyote dung as well as carrion. Specimen data indicate activity in the summer months of May through September, and thus probable

overwintering in the adult stage.

IMMATURE STAGES: Larvae are known, but not described.

They are in the collection of Dr. R.B. Madge, British Museum.

GEOGRAPHIC VARIATION: This species exhibits extreme variation in elytral color pattern and in the color of the antennal club (Figs. 62A-E, Hatch 1957). The forms in Canada are mostly of the maculated pattern (Fig. 62B), but in the southwestern coastal areas of the United States melanic forms occur (Figs. 62C-E). These melanic forms can be contrasted with increasingly maculated forms in inland desert areas (Fig. 62A), with an apparent correlation between the climate and the color pattern being evident (Anderson, unpublished).

PHYLOGENETIC AFFINITIES: This species is a member of the marginatus group (Fig. 102). It appears to be most closely related to N. obscurus due to the synapomorphic character state in the adults of possession of long hairs on the anterior face of the procoxae. Both species also possess dense punctures on the pronotum.

Nicrophorus vespillo, N. interruptus Stephens and N. vestigator, all of the Palearctic region also possess the dense yellow hairs on the metepimeron in the adults that are characteristic of this group. The larvae are described only for N. vespillo (Pukowski 1934), and from this description it is evident that this species possesses the reduced ventral sclerotization of the last abdominal segment in the larva (Fig. 30) that is also characteristic of this lineage. This concordance between the two character states serves to support the monophyly of the marginatus lineage.

NICROPHORUS OBSCURUS KIRBY

Necrophorus obscurus Kirby, 1837:97

DIAGNOSIS: Pronotum strongly cordate, with narrow lateral margins and wide basal margin. Antennal club with the apical three segments orange; basal segment black; with the penultimate segment with the outer edge deeply emarginate (Fig. 35). Metasternal pubescence dense, yellow; metepimeron with dense yellow pubescence. Hind tibiae very slightly curved. Moderately sized, 15-25 mm in length.

DISTRIBUTION: In Canada it is found in the southern areas of Alberta, Saskatchewan and Manitoba (Fig. 91). It is also widely distributed in the north central states (Fig. 91).

BIOLOGY: An inhabitant of prairie areas, it appears to be active early in the year, from May to June. It is diurnal and has been collected at both carrion and human dung. Further biological or ecological information is lacking.

IMMATURE STAGES: Larvae are known, but not described. They are in the collection of Dr. R.B. Madge, British Museum.

GEOGRAPHIC VARIATION: Most specimens have the typical pattern of Fig. 64A, however some have the maculations reduced (Fig. 64B).

PHYLOGENETIC AFFINITIES: This species is most closely related to N. guttula.

NICROPHORUS SAYI LAPORTE

Necrophorus sayi Laporte, 1840:2 ; Hatch, 1928

Necrophorus lunulatus Gistel 1848:189

Necrophorus lunatus LeConte 1853:277

Necrophorus luniger Harold 1868:104

DIAGNOSIS: Pronotum orbicular, with wide lateral and basal margins. Antennal club with the apical three segments orange; basal segment black. Metasternal pubescence sparse, yellow-brown; metepimeron with a few short black hairs. Hind tibiae strongly curved. Elytral pattern as in Fig. 57. Moderately sized, 15-23 mm in length.

DISTRIBUTION: In Canada it is found from Newfoundland and Nova Scotia westward to central Alberta (Fig. 93). It is also widely distributed in the northeastern United States (Fig. 93).

BIOLOGY: This species is active in very early spring, being the first Nicrophorus to appear. I have caught specimens while there was still snow on the ground.

In southern Ontario, the first individuals appear in mid April. These individuals are reproductively active, since the next peak of adult activity, which occurs in late July through early September, is characterized by a high number of teneralis. These will then overwinter in the adult stage.

It is found in the open and forested areas, but exhibits a strong preference for the latter. It appears to minimize interactions with the other species of eastern Nicrophorus, especially N. orbicollis, by emerging 2-3 weeks earlier in the season. By emerging early, it may be specializing on

the carcasses of animals that have died due to the extreme conditions imposed by winter. Its southern limit of distribution may be influenced by this factor, since the strategy would not be of much use in areas where winter conditions are not extreme, and animal deaths over the winter may be less frequent. This may explain the primarily northern distribution and the absence of the species from the studies of Shubeck (1976, 1977), Pirone (1974), Howden (1950) and Walker (1957), carried out in southern areas.

It is nocturnal, often being attracted to lights.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: The presence of an orbicular pronotum would appear to indicate inclusion in the orbicollis lineage (Fig. 102). The relationships between N. orbicollis, N. americanus and N. sayi are at present unclear.

NICROPHORUS ORBICOLLIS SAY

Necrophorus orbicollis Say, 1825:177 ; Hatch, 1928

Necrophorus hallii Kirby 1837:98

Necrophorus quadrisignatus Laporte 1840:1

DIAGNOSIS: Pronotum orbicular, with wide lateral and basal margins (Fig. 51). Antennal club with the apical three segments orange; basal segment black. Metasternal pubescence dense, brown; metepimeron with sparse brown hairs. Hind-tibiae straight. Dorsal surface of elytra with long hairs over the entire surface. Elytral pattern as in Fig. 55. Moderately sized, 15-22 mm in length.

DISTRIBUTION: In Canada it is common from Nova Scotia and New Brunswick, westward to south eastern Saskatchewan (Fig. 94). It is also widely distributed in the eastern United States, westward to Texas, Oklahoma and Nebraska (Fig. 94).

BIOLOGY: This species is active early in the season, with the first adults appearing in mid to late May in Ontario, New York (Pirone 1974) and New Jersey (1976). They are reproductively active at this time, with the teneral adults appearing in late July and early August until September. It is the adult stage that overwinters.

It is found in both open and forested habitats, although exhibiting a preference for the latter, a factor which minimizes interaction with the species of marsh or meadow. The different patterns of seasonal development serve to reduce interactions with N. sayi and N. tomentosus, the species with which it is most often encountered.

It has been reared using mice placed in a small plastic

container filled with about 8 cm of sandy soil. A pair of beetles can usually bury the mouse within 3 or 4 hours. Eggs are then laid, the exact position of which has not yet been determined. These hatch in about 5 days, with the first instar larvae moving to the food to feed. The first instar is of short duration, apparently lasting on the order of 1 day. The second and third instars are longer, and while exact determinations of their duration have not been made, appear to be about 3-5 days each. Upon completing larval development, or when the food supply is exhausted, they migrate into the soil to pupate. No adults were reared therefore it was not possible to ascertain the duration of the pupal stage. The average brood contains 12-16 larvae, of which a smaller number usually survive. This is apparently related to the size of the resource and competition between the larvae for food. Spicarova (1971, 1973) has also shown that the size of the resource will determine how many eggs, or in some cases how many clutches of eggs are laid in the European species N. vespillo. This was not examined in N. orbicollis.

It is nocturnal (Shubeck 1971), often being caught in light traps.

IMMATURE STAGES: Larvae are known, but not described. They are in the author's collection.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: The presence of elytral pubescence and the short epipleural ridge of the elytra, both apomorphic character states, are evidence of relationships with the Neotropical species N. didymus Brulle, N. scrutator Blanchard,

N. olidus Matthews and N. quadrimaculatus Matthews.

Members of this monophyletic group also possess an orbicular pronotum. The relationships amongst the species in this group have not been closely examined, but it appears that N. orbicollis is most closely related to N. didymus due to the shared possession of the apparently apomorphic character state of having the outer apex of the hind tibiae prolonged and tipped with 5 or 6 short, stout spines.

Within North America, three species possess an orbicular pronotum (Fig. 102). The relationships amongst these species are at present unclear.

NICROPHORUS NIGRITA MANNERHEIM

Necrophorus nigrita Mannerheim, 1843:251 ; Hatch, 1928 ;

Miller and Peck, 1979

Necrophorus ruficornis Motschoulsky, 1869:352 NEW SYNONOMY

Nicrophorus investigator alpha Pierce, 1949:67.

DIAGNOSIS: Pronotum quadrate, with wide lateral and basal margins. Antennal club with the apical three segments orange, the basal segment black. Metasternal pubescence dense, brown; metepimeron glabrous. Hind tibiae straight. Elytra entirely black. Smaller species, 13-18 mm in length.

Nicrophorus ruficornis, which was synonymized by Hatch (1928) under Nicrophorus guttula, is in fact a synonym of N. nigrita as is quite clear from the original description.

DISTRIBUTION: In Canada, this species is found rarely in southwestern British Columbia and Vancouver Island (Fig. 95). It is widely distributed in the coastal areas of Oregon, Washington and California (Fig. 95).

BIOLOGY: This species appears to be found in the dryer coastal forests, although there are no strong data to support this statement. Specimen data from southern localities indicate that it is primarily active in the winter months of September through May. This may explain why it is rare in northern localities.

IMMATURE STAGES: Larvae are known, but not described. They are in the collection of Scott Miller, Santa Barbara Museum of Natural History.

GEOGRAPHIC VARIATION: None noted.

PHYLOGENETIC AFFINITIES: This species appears closely related to N. mexicanus and N. investigator based on the synapomorphic character state of the quadrate pronotum in the adults. They are very similar and have even been treated as subspecies (Madge 1958).

The species N. nigrita and N. mexicanus can be recognized as sister species due to the synapomorphic character state (relative to other Nicrophorus) of brown metasternal pubescence in the adults. These two species differ only in the color of the elytra, but as no intermediates have yet been recorded, their status as distinct species should be maintained.

The two forms appear to be the result of fragmentation of a larger ancestral population, into a desert element and a western coastal element. This pattern of distribution conforms well with the distribution that would be expected from the theoretical models of allopatric or parapatric speciation of Bush (1975).

NICROPHORUS PUSTULATUS HERSCHEL

Necrophorus pustulatus Herschel, 1807:271 ; Hatch, 1928

Necrophorus bicolon Newman, 1838:385

Necrophorus tardus Mannerheim, 1853:170

Necrophorus marginatus ab. fasciatus Portevin, 1924:86

Necrophorus marginatus ab. unicolor Portevin, 1924:86

DIAGNOSIS: Pronotum transverse, subquadrate; with basal and lateral margins wide. Antennal club with the apical segments orange, the basal segment black. Metasternal pubescence sparse, yellow-brown; metepimeron glabrous. Hind tibiae straight. Elytral pattern usually as in Fig. 56. Moderately sized, 15-20 mm in length.

DISTRIBUTION: In Canada this species is found in southern areas, from Nova Scotia and New Brunswick, westward to Alberta (Fig. 96). It is also widely distributed in the eastern United States (Fig. 96).

BIOLOGY: This is generally considered to be one of the rarer species of Nicrophorus. It appears to emerge early in the season, with the first adults appearing in late April and early May in Ontario. It is reproductively active at this time, with the first adults of the new brood appearing as tenerals in late July and early August. These then overwinter in the adult stage. Although both Shubeck (1977) and Pirone (1974) record the presence of this species, their first records of it are in July. It thus appears that they missed the spring period of activity and only recorded the later peak of activity as the new adults emerged.

The species is nocturnal, commonly being caught at lights.

This common occurrence at lights, yet its apparent rareness in pitfall trapping may be indicative of it possessing a different biology than the other Nicrophorus. It is also often found at large carcasses and occasionally in pitfall traps where Necrodes surinamensis (also rare in pitfalls) has been caught. This may be indicative of these two species possessing similar foraging habits and of the use of large carcasses by N. pustulatus for reproductive purposes. How this could be accomplished, or even if it occurs, has not yet been examined.

It appears to be found in most habitats, but this is based on the collection of few specimens.

IMMATURE STAGES: Unknown.

GEOGRAPHIC VARIATION: Slight variations are present in the typical elytral pattern (Fig. 56). The anterior spot can be of varying sizes, although never very large. The posterior spots, which are usually separate are occasionally fused to form one larger spot.

PHYLOGENETIC AFFINITIES: This species is very difficult to place in the North American fauna, and probably has all of its close relatives in the Old World. Its placement is therefore best left as questionable (Fig. 102).

NICROPHORUS HYBRIDUS HATCH AND ANGELL

Nicrophorus hybridus Hatch and Angell, 1925:216

DIAGNOSIS: Pronotum sub-quadrate, not strongly cordate, with wide lateral and basal margins. Antennal club with apical segments orange, the basal segment black. Metasternal pubescence yellow, with bald spots behind the mesocoxae (Fig. 54); metepimeron glabrous. Hind tibiae straight. Elytral pattern usually as in Fig. 66. Moderately sized, 15-20 mm in length.

DISTRIBUTION: In Canada, it occurs in the southern areas of the prairie provinces, westward into western British Columbia (Fig. 97). In the United States it is widely distributed in the north central states (Fig. 97).

BIOLOGY: This species is an inhabitant of prairie areas and is reproductively active later in the season, when most other prairie Nicrophorus have completed reproduction. This late season activity is probably due to overwintering in the prepupal stage, as has been noted for N. tomentosus and N. investigator.

It appears to be primarily, if not exclusively diurnal.

IMMATURE STAGES: Larvae are known, but not described. They are in the collection of Dr. R.B. Madge, British Museum.

GEOGRAPHIC VARIATION: Most individuals have the elytral pattern as in Fig. 66, however some have the anterior and posterior maculations fused.

PHYLOGENETIC AFFINITIES: The yellow metasternal pubescence and the reduced, but not incomplete ventral sclerotization on the last abdominal segment in the larva place this species in

the investigator lineage. Within this lineage, the apomorphic character state of prepupal overwintering places it in the investigator group (Fig. 102). It is most closely related to N. tomentosus due to the synapomorphic character state of the possession of a bald spot behind the mesocoxae.

NICROPHORUS INVESTIGATOR ZETTERSTEDT

Necrophorus investigator Zetterstedt, 1824:154 ; Hatch, 1928

Necrophorus maritimus Guérin-Méneville, 1835:Pl.17, Fig. 12

Necrophorus melsheimeri Kirby, 1837:97

Necrophorus ruspator Erichson, 1837:225

Necrophorus aleuticus Gistel, 1848:190

Necrophorus pollinator Mannerheim, 1853:169

Necrophorus infodiens Mannerheim, 1853:170

Necrophorus confossor LeConte, 1854:20

Necrophorus sibiricus Motschoulsky, 1860:126

Necrophorus labiatus Motschoulsky, 1860:126

Necrophorus microcephalus Thomson, 1862:9

Necrophorus particeps Fischer von Waldheim, 1884:139

Necrophorus investigator var. funeror Reitter, 1884:87

Necrophorus functor Fauvel, 1890:348

Necrophorus investigator var. intermedius Reitter, 1895:327

Necrophorus investigator var. variolosus Portevin, 1924:149

Necrophorus investigator var. lutescens Portevin, 1924:150

DIAGNOSIS: Pronotum quadrate, with wide lateral and basal margins (Fig. 53). Antennal club with the apical three segments orange, the basal segment black. Metasternal pubescence yellow; metepimeron glabrous. Hind tibiae straight. Elytral pattern variable. Moderately sized, 13-18 mm in length.

DISTRIBUTION: This species is widely distributed throughout Canada and Alaska, although in eastern Canada it is found primarily in the northern areas (Fig. 98). It is also

widely distributed in the western United States (Fig. 98) and throughout most of the Palearctic region.

BIOLOGY: Virtually nothing has been published on the biology of the species in North America, however work has been done on the biology in Europe (Pukowski 1933, Mrockowski 1949) and Japan (Katakura and Fukuda 1975). These studies showed that the adults first appear in mid-June and early July. They are reproductively active at this time, with the subsequent brood overwintering in the prepupal stage.

This pattern of activity also occurs in North American populations and may allow it to occupy most areas where either N. tomentosus or N. hybridus are absent. An examination of the distributions of these species indicates that N. tomentosus and N. investigator are at most only narrowly sympatric. It thus appears that competitive exclusion is operating to inhibit coexistence of these two species. Nicrophorus investigator and N. hybridus occur sympatrically throughout much of the range of the latter and thus some mechanism of resource partitioning must be operating. This could be explained by N. investigator being primarily a forest species (which in the prairies may only occur in gallery forests) as the bulk of its distribution and collecting data appear to indicate, and by N. hybridus being a prairie species as has been noted. This however, requires more detailed study in the areas where both occur.

It appears to be primarily diurnal in North America, although this may vary due to local conditions as noted by

Katakura and Fukuda (1975).

IMMATURE STAGES: The larvae have been described by Pukowski (1934), although poorly.

GEOGRAPHIC VARIATION: Variation in the elytral pattern is extensive, with darker forms (Figs. 65C-F) occurring on the north west coast of North America. This melanism appears to be correlated with the cooler and wetter conditions typical of these coastal areas. Dark patterns are especially common and pronounced in the northern areas of the Queen Charlotte Islands, coastal and insular Alaska and the Aleutian Islands. In the southern areas of the coast, only the normally maculated forms (Fig. 65A,B) are found. This appears to be due to the diurnal flight habits of this species, which in these areas will be active at a time when the temperatures are near their highest values and humidity and percentage cloud cover are near their lowest values. This is in contrast to the case in the northern areas, where temperatures are consistently colder, humidities and percentage cloud cover are higher throughout the entire day (Dominion Bureau of Statistics 1962). This high humidity and percentage cloud cover will serve to radically reduce solar radiation and thus more melanistic forms (Fig. 65C-F) should be selected for in these areas, since this will increase the ability of the individual to acquire and retain the internal heat levels that are necessary to permit flight.

In the inland localities of British Columbia, and throughout the rest of the range, the normally maculated form is the only form present. In some desert areas of the southern United

States the maculations tend to fuse to form a pattern like that discussed previously for other species.

A more detailed study of the distribution and cause of melanism in North American Nicrophorus is in preparation (Anderson in prep.).

PHYLOGENETIC AFFINITIES: The tendency towards a quadrate pronotum and the reduced, but not incomplete ventral sclerotization of the last abdominal segment in the larvae (Fig. 29) characterize the lineage to which this species belongs (Fig. 102). Within the lineage, the investigator group can be characterized by the presence of a prepupal overwintering stage, or in the case of southern species, activity primarily throughout the winter months.

It is closely related to N. mexicanus and N. nigrita due to the shared possession of a quadrate pronotum. Closer relatives to N. investigator are very likely present in the Palearctic region, although this has not been examined closely.

NICROPHORUS VESPILLOIDES HERBST

- Nicrophorus vespilloides Herbst, 1783:32 ; Hatch, 1928
- Nicrophorus mortuorum Fabricius, 1792:248
- Nicrophorus aurora Motschoulsky, 1860:126 .
- Nicrophorus vespilloides ab. altumi Westhoff, 1881:108
- Nicrophorus vespilloides var. sylvaticus Reitter, 1895:328
- Nicrophorus vespilloides var. silvivagus Reitter, 1897:48
- Nicrophorus vespilloides ab. steinfeldi Smirnov, 1908:42
- Nicrophorus vespilloides var. fractus Portevin, 1914:195
- Nicrophorus vespilloides var. borealis Portevin, 1914:195
- Nicrophorus vespilloides var. subfaciatus Portevin, 1914:195
- Nicrophorus subinterruptus Pic, 1917:21
- Nicrophorus vespilloides var. tristis Portevin, 1924:375
- Nicrophorus vespilloides var. andrewesi Portevin, 1926:235
- Nicrophorus mortuorum ab. maculatus Willoughby-Ellis, 1926:3
- Nicrophorus mortuorum ab. disjunctus Willoughby-Ellis, 1926:3

DIAGNOSIS: Pronotum subquadrate, with wide lateral and basal margins. Antennal club with all four segments black; upper and lower surfaces of antennal segments 9 and 10 with a dense patch of white hairs arranged in a figure eight pattern. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibiae straight. Elytral pattern variable. Smaller sized beetles, 12-16 mm in length.

DISTRIBUTION: In Canada and Alaska, this species is widely distributed (Fig. 99), but has only been recorded from a few localities in the northeastern United States (Fig. 99).

It is also common throughout the Palearctic region.

BIOLOGY: This species is initially active early in May and appears to reproduce at this time. The subsequent generation of adults emerges in August and September and then overwinters in this stage. This pattern conforms well with that documented by Christie (1980) for the same species in England.

It is a species of varying habitat preferences. In North America it is found only in swampy or boggy areas throughout the boreal forest region, while in Europe it is found exclusively in dry coniferous forests (Pukowski 1933). In Japan it appears to be found in all habitats that were sampled (Katakura and Fukuda 1975). This variability is most likely due to the ecological requirements and habitat preferences of the species with which it coexists.

It does not appear to bury carcasses, but instead digs a shallow pit and covers the food resources with leaf litter or other debris. It is both diurnal and nocturnal, depending on the time of year at which it is active (Katakura and Fukuda 1975).

IMMATURE STAGES: Larvae have been described by Pukowski (1934) although poorly.

GEOGRAPHIC VARIATION: In some coastal areas in north western Alaska and in insular Alaska, including the Aleutian Islands, there is a reduction of maculations in the typical pattern (Figs. 57A,B). The reduction also results in disjunction of the humeral orange spot and the rest of the orange pattern of the elytral epipleuron. This is most likely due to the colder

and wetter conditions in these areas as discussed for N. investigator.

PHYLOGENETIC AFFINITIES: The yellow metasternal pubescence and subquadrate pronotum in the adult, and the reduced ventral sclerotization in the larva place this species in the investigator lineage. Nicrophorus vespilloides can be distinguished from the members of the investigator group by lacking the prepupal overwintering stage. It is very closely related to N. defodiens as evidenced by the synapomorphic character state of having the base of the urogomphi, in the larvae, lacking a suture where they join the ninth tergite. These two species have long been regarded as conspecific, and only recently have they been distinguished as distinct species.

The good knowledge of distributions, habitat preferences and phylogenetic relationships of these two species presents a situation which is conducive to biogeographic analysis. Nicrophorus vespilloides is Holarctic in its distribution. It is however, found in marshes in North America, but in dry forests in the Palearctic. Nicrophorus defodiens is only found in North America, primarily in the dry coniferous forest region. A close examination of the morphology reveals that N. defodiens is the more primitive of the two species. Thus N. vespilloides cannot be the ancestor, and only N. defodiens, or a form unlike either could be. It is then logical to assume that the forest inhabiting strategy is plesiomorphic. From this information, the following hypothesis of evolutionary history can then be presented.

The initial ancestor was widely spread in northern North America. During Miocene or Pliocene times Asia and North America were united through Beringia, and this permitted dispersal of the ancestor into the Old World. Subsequent divergence in morphology occurred while the two forms were separated. The reunion of Asia and North America during the Pleistocene would have resulted in the introduction of the Palearctic form into North America. Once in North America it would find the ancestral habitat occupied and would therefore be required to shift to a new habitat, this being the marshes and bogs. It has then dispersed widely throughout the boreal forest area where boggy areas are common.

If alternative evolutionary histories are reconstructed, they are less parsimonious, requiring more dispersals or more habitat changes.

NICROPHORUS DEFODIENS MANNERHEIM

Necrophorus defodiens, Mannerheim, 1846:513 ; Hatch, 1928

Necrophorus hebes Kirby, 1837:96

Necrophorus pigmaeus Kirby, 1837:98

Necrophorus pollinator LeConte, 1854:19

Necrophorus plagiatus Motschoulsky, 1869:352

Necrophorus conversator Walker, 1866:320

Necrophorus defodiens ab. binotatus Portevin, 1926:236

Necrophorus defodiens ab. kadjakensis Portevin, 1926:236

Necrophorus defodiens ab. mannerheimi Portevin, 1926:236

DIAGNOSIS: Pronotum subquadrate, with wide lateral and basal margins. Antennal club with all four segments black. Metasternal pubescence dense, yellow; metepimeron glabrous. Hind tibiae straight. Elytral pattern variable. Smaller sized beetles, 12-18 mm in length.

DISTRIBUTION: This species is very widely distributed in Canada and Alaska (Fig. 100). It is also found in the western coastal and Rocky Mountain states, and in the north central and eastern states southward along the Appalachian Mountains to Tennessee and North Carolina (Fig. 100).

BIOLOGY: The pattern of seasonal development is very like N. vespilloides, with the first adults appearing in mid May. These individuals will mate and reproduce, with the offspring from this brood appearing as adults in August.

The species is found primarily in the dry, boreal forest throughout its range, but also occurs in the montane and coastal forests of British Columbia and the western states. Habitat specificity serves to reduce interaction with N. vespilloides

in the north and with any of the eastern deciduous forest species in the eastern states, most of which are reproductively active in the spring. Interactions with the widespread N. investigator and N. tomentosus are minimized due to the different patterns of seasonal development.

The species does not bury carcasses, but like N. vespilloides, conceals them under leaf litter or debris. Details of the life history are presented by Leech (1934).

It is active at dusk throughout most of its range.

IMMATURE STAGES: Larvae are known, but not described.

They are in the collection of Dr. R.B. Madge.

GEOGRAPHIC VARIATION: Variations in the elytral patterns of this species are very extensive (Figs. 60-A-D), and many forms can be represented in a single brood (Leech 1934). The normally maculated form (Fig. 60A), which characterizes inland and eastern coastal areas, grades into the melanistic forms in the western coastal areas. Elytral maculations in these western coastal areas vary from slight reduction (Fig. 60B) to great reduction in size and fragmentation (Figs. 60C-D). Some individuals in western areas may be entirely black.

This melanism in coastal areas has been well documented for Lepidoptera by Hovanitz (1941), the correlation appearing to be one of colder, wetter, humid and cloudy conditions with increasing melanism. This appears to be the case with N. defodiens. It is crepuscular, being active in the evenings, prior to and just after dusk. During the day, the land will be heated by the sun, the hot air will rise, and an on-shore breeze will be generated. Temperatures will decrease as the

humidity and cloud cover increases, and thus there will be a selective advantage to being darker in these areas (see discussion of geographic variation of N. investigator).

Although N. defodiens and N. investigator occur together in many areas along the west coast, the former will be melanistic in areas where the latter is not. This is due to the different flight periods of the two species.

PHYLOGENETIC AFFINITIES: See discussion of the phylogenetic affinities of N. vespilloides.

PART II:

HABITAT PREFERENCES, SEASONALITY AND RESOURCE
PARTITIONING IN THE CARRION BEETLE FAUNA OF
SOUTHERN ONTARIO (COLEOPTERA: SILPHIDAE):
ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

INTRODUCTION

Most past studies of carrion community ecology have been concerned with such questions as faunal succession (Johnson 1974, Bornemissza 1957, Payne 1965, Howden 1950), general ecological interactions amongst all taxa (Pirone 1974, Cornaby 1974, Putman 1978, McKinnerney 1979) and faunal surveys (Payne and King 1969, Payne and King 1970, Payne and Mason 1971, Payne et al 1968). Others, (Walker 1957) have looked at how certain environmental conditions affect the distribution of carrion feeding arthropods in different habitats. Few works have been concerned with the ecological interactions among closely related taxa, or members of a specific taxon. Exceptions to this are the studies by Denno and Cothran (1975, 1976) on the necrophagous flies of the families Calliphoridae and Sarcophagidae, by Young (1978) on the neotropical necrophagous beetles of the family Scarabaeidae and by Shubeck (1968, 1969, 1971, 1976) on some of the Nearctic Silphidae.

The ecological interactions among European Silphidae, especially Nicrophorus, have been examined by Pukowski (1933), Mroczkowski (1949), Theodorides and Van Heerdt (1950), Paulian (1946) and Cantonnet and Lecordair (1947). Katakura and Fukuda (1975) have done the same for the Japanese Silphidae.

None of these studies addresses the specific question of resource partitioning, even though the data are in many cases indicative of such a principle in operation, structuring the

assemblage or guild such that ecological interactions among closely related, coexisting taxa are minimized.

Recently, Schoener (1974) has reviewed the literature on resource partitioning in both vertebrates and invertebrates, noting the significant niche dimensions along which coexisting taxa usually space themselves, so that competition is reduced.

These important niche dimensions include body size of the organism, available habitat types, available food types and sizes, and possible patterns of seasonal and temporal activity. Most of these studies cited by Schoener concern vertebrates and can be extremely complex. Furthermore, the taxa included in the study are often not closely related, let alone monophyletic, a fact that will be stressed later.

The following study was then undertaken to ascertain how the species of Silphidae in the eastern North American carrion community are acting to minimize interactions amongst themselves, such that all can coexist, and how these interactions may have affected the evolution of the various elements of the assemblage

Special consideration is given to the following, the first four as outlined by Schoener;

- 1) Is it actually competition that is resulting in the observed patterns of differential niche utilization, and not effects of predation or pressures towards reproductive isolation?
- 2) What is the availability of the different values along the various niche dimensions, and how are

PART II:

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these filled by the organisms present?

- 3) Along which niche dimensions does variation occur and what are the relative importances of the various niche dimensions in permitting coexistence?
- 4) Are there any limitations in the availability of certain niche dimensions or values of a niche dimension due to the morphology or physiology of the organism?
- 5) What, if any, are the evolutionary implications of resource partitioning and can a knowledge of present ecological relationships contribute to an understanding of the evolutionary history of a group of closely related species, or possibly even community?

AREA OF STUDY

The area chosen for study was to the northeast of Metropolitan Toronto, in the vicinity of the town of Markham. Four sites were selected on the basis of habitat differences and two baited pitfall traps were installed at each locality. The four sites chosen can be described as follows.

SITE #1: DECIDUOUS FOREST

This area was a lowland forest with rich, moist soil that was high in humus content, due to the abundance of leaf litter. The dominant tree species was Acer saccharum. Ferns were abundant in the early part of the season and the herb species had a continuous moderate cover. There was a patchy distribution in the shrub layer, with most being Cornus or Acer saplings. The forest was situated in a valley, with slopes having some Tsuga canadensis (hemlock) and less of a herb cover. On the slopes, the soil was better drained and ferns were absent.

SITE #2: OLD FIELD/MEADOW

This area was an old field and a grassy meadow that were separated by a hedgerow. The hedgerow was approximately 12 feet wide and extended the length of the field. The field was typical of a successional assemblage invading a cultivated lot that had been left unused for 4 or 5 years. There was a continuous herb cover which averaged about 1 metre in height.

Solidago spp. was common as were Asclepias syriaca, Verbascum thapsis, Daucus carota and Linaria vulgaris. Various grasses were present in the field and were the dominant, if not the sole plants present in the meadow. Identification of these grasses was not attempted.

SITE #3: MARSH

This area was a typical Typha marsh, which undergoes a seasonal inundation, with water accumulating in the spring after the snow had melted or after heavy rainfall. The cover was nearly 100% Typha spp. with scattered individuals of other herbs being present. Salix sp. and Populus tremuloides were present further back into the marsh, as was Sambucus canadensis.

SITE #4: CONIFEROUS FOREST

This area was a red pine (Pinus resinosa) plantation with an extremely dry litter layer covering a very sandy soil. The understory was open and included scattered Acer saccharum and Fraxinus americanus seedlings. Herb cover was low and confined to the open canopy areas, which were initially unplanted or were areas where trees had fallen.

MATERIAL AND METHODS

Beetles were collected in baited pitfall traps of size 14 cm diameter and 17 cm depth with a solution of 50:50 glycol:water mixture in the bottom into which the insects would fall (Newton and Peck 1975, Southwood 1978). These were baited with approximately 200 gms of white sucker, and serviced at weekly intervals, with the old bait removed and placed in a container for subsequent disposal far from the trapping site. The insects in the solution of glycol were sieved through a tea strainer and placed in FAA solution (Norris and Upton 1974:11) to preserve the internal reproductive systems. The glycol was then poured back into the trap, and the trap reset. The same solution of glycol was used until it became noticeably diluted, whereupon it was replaced.

Silphids were sorted and removed from the trap residues and placed in a fresh solution of FAA. The residues were discarded.

Sampling was begun on May 7, 1979 and terminated November 3, 1979. In 1980, the sampling was started earlier, since the traps of May 7 were already capturing silphids. This began on April 12, and continued until May 24, thus providing the early season data which were lacking ~~and~~ enough of an overlap between the yearly sampling periods to permit year to year comparisons.

After 7 days in the FAA solution, the beetles were

transferred to an 80% ethanol solution, where they were maintained until examined. Examination, following the methods of Barlow (1970, 1973), consisted of identification and enumeration of the adults and larvae of each species found in each trap, sexing of the adult individuals, enumeration of teneral individuals, and dissection of the females in order to ascertain their reproductive state.

These data were recorded on tables (see Appendix II) for each of the 12 species collected during the study and subsequently were presented as graphs (Figs. 104-120). The data used in the construction of these graphs represents the pooled samples (2) from each site for each weekly period.

RESULTS

Over the course of the study, 9549 specimens, representing 12 species of Silphidae were collected. Of these 12 species, 5 were members of the tribe Silphini and 7 members of the tribe Nicrophorini, genus Nicrophorus.

In the Silphini, the most numerous species was Oiceoptoma noveboracense, followed by Necrophila americana and Thanatophilus lapponicus. The two other species, Oiceoptoma inaequale and Necrodes surinamensis were collected in small numbers.

Of the Nicrophorus, the most commonly collected species was N. tomentosus, followed by N. orbicollis and then N. sayi. Nicrophorus marginatus was also quite numerous, while N. pustulatus, N. defodiens and N. vespilloides were rarely captured.

The relative abundance of all Silphidae collected is summarized on Table 1.

SEASONAL DEVELOPMENT AND PHENOLOGY

The most numerous silphine, Oiceoptoma noveboracense, was found to be active very early in the season, with the first adults appearing in early to mid-April (Fig. 104). Many of these females were carrying eggs, indicative of reproductive activity. This was further evidenced by the presence of larvae in the traps in early May (Fig. 116). The numbers of adults declined in June, with a subsequent

peak of adult activity occurring throughout July. Many of these were teneral and thus probably the progeny of the early season generation. Activity declined into September and since no eggs were laid or larvae were noted, overwintering must occur in the adult stage.

The next most abundant silphine, Necrophila americana, was found to possess a similar life cycle to O. noveboracense, although in this case emergence of the overwintering adults began in mid-May, 2-3 weeks after the emergence of the latter (Fig. 105). Egg carrying females were numerous at this time and were present until early July. Throughout this same time larvae were numerous, but their initial emergence occurred noticeably later than in any other species (Fig. 116). In late July through August, tenerals were present, indicative of emergence of the first brood of larvae. No eggs or larvae were noted at this time, with the overwintering taking place in the adult stage.

The other common silphine, Thanatophilus lapponicus, does not show a pattern similar to those already discussed. This species emerges early in the season, with the first adults appearing in mid-late April (Fig. 106). The larvae are found in early May, appearing to be the earliest silphine larvae to appear (Fig. 116). Egg carrying females are also present at this time and continue to be present into early June. Tenerals first appear in mid-June and are present throughout the duration of adult activity, which lasts until mid-September. The appearance of more egg carrying females

in late June and early July, along with the increased presence of larvae is indicative of a second period of reproductive activity. The continued presence of teneral, as well as the occasional late season activity is indicative of overwintering in the adult stage.

The remaining two species of silphine were rarely collected, and thus the patterns of development are difficult to clearly document. It appears that O. inaequale follows a pattern very similar to that of O. noveboracense (Fig. 107), with emergence of overwintering adults early in the season.

Reproductive activity takes place at this time as evidenced by the presence of egg carrying females, and the subsequent presence of teneral individuals in July and August.

Necrodes surinamensis was very rarely collected and little can be elucidated except that it is a summer active species (Fig 108). The presence of teneral among the first individuals recorded may be indicative of overwintering in a stage other than the adult.

In the Nicrophorus burying beetles, the most numerous species, N. tomentosus, is a late season emerger, with the first adults appearing in mid-late June (Fig. 109). Teneral were present at this time and continue through July and into August. Peak numbers of adults appear in mid-late August, with activity continuing into September, but stopping by early October. This pattern is indicative of overwintering in a stage other than the adult.

Nicrophorus orbicollis, the next most abundant species,

emerges early in the season, with the first adults appearing in mid-late May (Fig. 110). Peak numbers occur in early June through July. In late July and August, activity begins to decline and teneral appear. Like most other silphids, this pattern is indicative of overwintering in the adult stage.

The other common species, N. sayi, appears very early in the season, with the first adults appearing in mid April (Fig. 111). Peak numbers occur soon after, followed by a decline in activity into June. Tenerals appear in July, and activity increases, continuing into October and November. The adult stage would again appear to be the stage that overwinters.

Nicrophorus marginatus is also an early emerger, with the first adults appearing in mid-late May (Fig 112). Activity declines throughout June, but increases in July through August and into September. Teneral are present in mid July and in late August, and overwintering would appear to be in the adult stage.

Of the rarer species, N. pustulatus first appears in early May (Fig. 113). Activity is initially sporadic, but increases from mid July through mid September. Teneral are present from mid August through early September. Both N. defodiens and N. vespilloides appear to have similar patterns of activity. They are both active early in the season, however N. defodiens (Fig. 114) appears later than N. vespilloides (Fig. 115). The former first appears in

late May, while the latter first appears in early May. They are both active throughout the summer, although apparently sporadically. In N. defodiens, activity ceases in early September, while in N. vespilloides it continues into early October.

In all of the Nicrophorus caught and examined, no females were found to possess eggs.

HABITAT PREFERENCES

In the Silphini, O. noveboracense was found in all habitats sampled (Fig. 117), although was more common in the coniferous forest area. It was found uncommonly in the marsh, and was slightly more common in the deciduous forest than in the meadow. Necrophila americana is also found in all habitats sampled (Fig. 118), although in this case is much more common in the marsh. It is also rare in the meadow, and is about equally abundant in the two forest areas.

Thanatophilus lapponicus is found only in the open habitats (Fig. 117). It is more common in the meadow than in the marsh. Oiceoptoma inaequale is found in the deciduous forest and the marsh, however very rarely in the latter habitat (Fig. 117). The one remaining silphine, Necrodes surinamensis, is found in both the coniferous forest and the meadow (Fig. 118).

In the Nicrophorus, N. tomentosus is found commonly in all habitats (Fig. 118), being more common in the coniferous forest and the meadow. In contrast to this is the pattern shown by N. orbicollis (Fig. 120). This species, although found in all habitats is more common in the two forested areas.

It is also quite common in the open habitats, where it is slightly more common in the marsh. Nicrophorus sayi, like N. orbicollis, is more common in the forested areas (Fig. 120), although much more so in the coniferous forest. It is much less common in the open habitats than N. orbicollis. Nicrophorus marginatus is very habitat specific (Fig. 119). It is found only in the open habitats and is much more common in the meadow. Only a few individuals are found in the marsh, and this is late in the season as this habitat dries up. Both N. defodiens and N. vespilloides are highly habitat specific. The former is found exclusively in the coniferous forest (Fig. 119) and the latter only in the marsh (Fig. 120). The last species, N. pustulatus, is found in approximately equal abundance in the two forested areas (Fig. 119). It is also present in the meadow, although it is not common.

DISCUSSIONS

METHODOLOGY

The initial intent of this study was to follow the methods of Barlow (1970, 1973) and Vlijm and van Dijk (1967) in studies on phenology in Carabidae, and use these methods to interpret the various ecological interactions, or lack thereof among the coexisting species of Silphidae. In the course of the study however, problems were encountered which limited the applicability of these methodologies to the present study.

Carabids, the subjects of the previous studies, possess polytrophic ovarioles which lend themselves well to the determination and recognition of female reproductive states. In the Silphidae, the ovarioles are telotrophic (Suzzoni 1979) and thus a distinct corpus luteum is not present as a yellow band at the base of the ovarioles after eggs have been laid.

In the Silphini this problem did not affect the total number of states of the female system that could be recognized, although it did result in a lowered confidence in recognizing non-teneral females as spent or pre-reproductive. The three recognizable states used in this study were; teneral, non-teneral lacking eggs and non-teneral possessing eggs.

In the Nicrophorus, a further problem was encountered. No females of any species of Nicrophorus collected were found to possess eggs. This can be attributed to the different life cycle and reproductive strategy that these beetles employ

(Pukowski 1933, Milne and Milne 1944, 1976). Unlike the Silphini, which lay their eggs in the soil around a food source that is exposed on the soil surface and utilized by many individuals, Nicrophorus bury the food source, prepare the food for consumption by a single brood of larvae and lay eggs in a specially constructed underground tunnel. After a carcass is buried, there appears to be a period of inactivity that precedes egg laying. During this period, the eggs are probably matured and mating takes place. Since only a single pair of beetles will utilize a carcass, should more than a single pair be present, fighting will take place to determine who will get possession of the resource. The delayed maturation of eggs may therefore be a physiological characteristic that ensures that eggs are not prematurely developed and carried by a female who has not yet secured a suitable food source. It would also ensure that a female, should she have to fight for possession of a carcass or forage extensively, would not have valuable energy stored in the eggs. Thus in Nicrophorus, only two reproductive states can be detected in the females, these being teneral and non-tenerals.

Recently, (Christie 1980) in a study of the phenology of N. vespilloides in England, succeeded in recognizing four different classes of the reproductive states of the females. She did not however, give the criterion used to recognize the states, nor does she discuss the trapping method used to acquire the specimens.

Another problem which occurred infrequently was the removal of bait or the disturbance of the trap. This occurred in only two cases, trap 3B, May 7-14, 1979 and trap 4B, September 15-22, 1979. The problem induced is one of how to treat the data collected in traps 3A and 4A during these time periods. Since the traps were set only 100 meters apart, and silphids have been shown to be receptive to odors from large distances (Petruska 1975), there is obviously a relationship between the numbers present in each of the traps. The removal of one of the traps would surely increase the numbers that would be collected in the other trap. Thus the only alternative is to assign a value of one half of that caught in the active trap to the lost trap. This will not be entirely accurate, due to the 100 meter distance between traps, which will result in a slight difference in the areas from which each trap is drawing the insects, yet it is the only available solution. These altered figures give a much better fit to the seasonal patterns based on the rest of the data.

Close examination of the data sheets (Appendix II) reveals that the replicability between the two samples in any given habitat is often low. This may be due to differential attractiveness of the traps, which may have arisen because the bait in one trap is more decayed and thus releasing more odors than the other. This situation could have resulted, should fly larvae have succeeded in entering and feeding on the bait, thus enhancing decomposition. These traps would then have possessed a large number of fly

larvae and could be easily noticed. In this study no such cases were recorded.

It is more likely that wind direction is playing a role in determining which trap a beetle will first encounter. When foraging, silphids tend to fly low over the substrate in an upwind direction until they detect odors to which they can then orient. This type of foraging strategy is typical for many insects, most notably dung beetles (Fincher 1972), and blood feeding insects such as mosquitoes (Gillet 1971). If the wind is blowing parallel to the direction along which the traps are oriented, one trap will be encountered first and will therefore have a larger catch. If the wind is blowing at an angle to the direction of orientation of the traps, they will be encountered equally and will possess a similar catch. Winds may also affect the size of the area sampled with a strong wind attracting beetles from a greater distance.

It is also difficult to ascertain whether a Nicrophorus individual is attracted to a carcass to feed or to use the carcass for reproductive purposes. Since only one pair of any one species will use the food source, it is also difficult to know which species would have succeeded in securing the carcass.

In order to overcome these problems, D.S. Wilson (pers. comm.) places dead mice in the field which are tied by a long string of dental floss to a small stake. In this manner the species of beetle that secures the carcass can be actually

determined, and not inferred as it is in the present study, based on relative abundance data. It is also possible to determine if any food resources end up colonized by flies, other silphines or vertebrate scavengers.

In future studies, the use of both pitfall traps and staked mice should be attempted. It would also be informative to stage competitive experiments between species of Nicrophorus artificially in the laboratory.

These constituted the main problems associated with the use of pitfall traps in the present study. However, further problems inherent in the usage of pitfall traps are discussed in Southwood (1978:247-249), although many are invalidated by the use of baited traps and single year studies.

NICHE DIMENSIONS OF THE COMMUNITY: ECOLOGICAL CONSIDERATIONS

Schoener (1974) has outlined the various niche dimensions along which variation usually exists so that coexistence can occur between closely related species. Although the present study has only examined in detail the roles of seasonal patterns and habitat preferences, discussions based on the literature and the author's own observations concerning the other niche dimensions are also included.

Food Type and Size

All members of this family collected during the study are primarily necrophagous as larvae. The one possible exception is Nicrophorus pustulatus, for which little information is

available on trophic habits. A radical divergence from the usual life history of the genus would be highly unlikely.

In the case of carrion feeding insects, the availability of and competition for food would appear to be the most important factor responsible for the generation of ecological character displacement. Although no rigorous data are available to demonstrate the lack of this food item in nature, all evidence, albeit circumstantial, certainly indicates that it is rare. Furthermore, it would be randomly distributed in space and time and not a predictable resource. An exception to this may be in the spring, when large numbers of carcasses would be expected to be available due to the increased mortality in the vertebrates over the winter season.

In the Silphidae, two patterns of resource utilization, pertaining directly to the use of food for reproductive purposes have been developed. Both are concerned primarily with minimizing interactions between the flies and the beetles, and not as might be expected, in minimizing interactions between the different groups of beetles.

Individuals of the tribe Silphini, appear to arrive at a carcass during the early to middle stages of decay (Payne 1965, Johnson 1974). Eggs are then laid in the soil around the carcass, which hatch in 4-5 days. It is during this time that the flies are also arriving and ovipositing on the carcass. Fly eggs hatch almost immediately (Denno and Cothran 1975, 1976) and the larvae begin to feed, often being present in great numbers. These larvae digest their

food externally, liquifying the decaying material with a digestive enzyme which is released through the mouthparts. This fluid is subsequently reingested by the larvae. They complete development rapidly, migrating from the carcass to pupate in 3-5 days, depending on the species and the temperature (Denno and Cothran 1976), the time at which the silphid larvae are hatching. These newly emerged larvae then feed only on that part of the resource not eaten by the fly larvae, this being small pieces of flesh left on the bones and on the moist, inside face of the skin (Dorsey 1940, Johnson 1974). The egg laying habits of the silphines are also related to this strategy, with oviposition occurring in the soil and not directly on the carcass, where they would probably be destroyed by the fly larvae.

Silphines appear most commonly at large carcasses, especially the species Nicrodes surinamensis. This is undoubtedly due to the availability of food, with the smaller carcasses tending to have little utilizable material left after the flies have finished feeding. Larger carcasses can provide sufficient food resources for the larger number of beetles that are usually present.

In contrast to the Silphini, the Nicrophorus avoid direct competition with the flies by getting to the food source before or concurrently with the flies. They will then bury the carcass in the soil or under leaf litter, and at the same time kill and eat any fly larvae that may be present (Steele 1927, Clark 1895). They also carry a load of phoretic mites which have been shown to feed on and destroy

any fly eggs and thus aid the beetles in providing a competition free environment in which to rear their larvae (Springett 1968). Once the carcass is buried, eggs are laid, and the larvae, when they hatch, feed on the carrion. Smaller carcasses are thus the only food resources capable of being used by the beetles since larger sizes would be impossible for the beetles to bury.

Within these higher taxa, there appears to be no resource partitioning with regard to food type, size or stage of decay. Shubeck (1976) has examined the possible existence of selection for poikilothermic carrion or homeothermic carrion in the Silphidae. He found that there was little evidence to suggest that any selection was taking place, and that the beetles were probably utilizing what was available. Similarly, work on succession of beetles on carrion (Johnson 1974, Payne 1965, Howden 1950) shows no differences between the stage of decay at which specific species of Silphidae occur.

Body Size of the Organism

The use of differing body sizes as a mechanism of resource partitioning has been examined extensively in numerous studies (see Schoener 1974 for a review). The great majority of these studies are concerned with the coexistence of predators, who are selecting different sized prey items, due either to their own morphological limitations or the availability of the prey. This is reflected in a recent paper by Wilson (1975), examining the role of body size as a mechanism of resource

partitioning, where all examples are drawn from predator-prey studies.

In the case of the Silphidae, it is difficult to see how differing body sizes could result in the usage of different food resources, since the food is not available as discrete, individual units such as prey items or seeds. Only in the genus Nicrophorus could body size play a possible role, where the larger species would be able to bury larger carcasses. The variation in size is often great within a species (Spicarova 1971) and thus would appear not to play a significant role in minimizing ecological interactions.

Patterns of Seasonal and Temporal Activity

Most temperate insect species reproduce seasonally, with peak periods of adult activity occurring only at certain times of the year. The spacing of these periods along a seasonal niche dimension should serve to reduce direct competition and permit coexistence of closely related taxa, if the finding of food for reproductive purposes is required. The results from the present study indicate that this is the case with the Silphidae, with variation in the periods of activity being evident among the members of both tribes.

In the Silphini, Necrophila americana, Oiceoptoma noveboracense and Thanatophilus lapponicus are all reproductively active at different times of the year (Figs. 104-106). This is especially evident when the periods of larval activity are examined (Fig. 116). Thanatophilus lapponicus also possesses

a second period of reproductive activity later in the year, a characteristic exhibited by no other Silphidae in this assemblage. This strategy may be the result of the unpredictable and highly limited resource characteristics of the northern environments where it is most often found. Insects which survive there must be opportunistic and adapted for rapid reproduction whenever possible. The other Silphidae, most of which possess distributions primarily centered in southern areas, have only one generation per year.

The other two species, Oiceoptoma inaequale and Necrodes surinamensis, which were rarely collected, also appear to be early season breeders. However, with all time periods already occupied by one of the aforementioned common species, it is probable that their periods of reproductive activity will overlap. This may be reflected in the apparent rarity of these species. Necrodes surinamensis possesses food habits, which have already been discussed that appear to be the primary means through which resource partitioning is achieved. The distribution of O. inaequale and its absence from the studies of Pirone (1974) would appear to indicate that the study was carried out near the northern limit of its range. In southern areas, where it is more common, it emerges earlier in the year than any of the other species with which it coexists (Reed 1958, Howden 1950). It is possible that the environmental conditions associated with increasing latitude place restrictions on its strategy of resource utilization, thus forcing it to occur at the same time as O. noveboracense, by which it may be eventually competitively excluded in the

northern areas.

The ecological attributes of all Silphini collected are summarized in Table 2.

Past studies (Shubeck 1969, 1976, Pirone 1974) have noted patterns in the seasonal development of O. noveboracense and N. americana to be similar to those recorded here. Only Pirone briefly considers the role of such patterns in resource partitioning.

In the Nicrophorus, similar patterns occur, with certain species being reproductively active at different times of the year. Shubeck and Pirone have both noted the different activity periods of N. tomentosus and N. orbicollis. Nicrophorus tomentosus is reproductively active later in the year, when no other Nicrophorus in this assemblage are. These studies also noted the presence of N. pustulatus, but as in this study, it was rarely collected. This certainly poses a problem in attempting to analyse the ecological interactions among the species. It appears to be a spring breeder and hence would overlap with the periods of reproductive activity of the other species. The fact that it is rarely caught in pitfall traps, yet is apparently common in the area, as evidenced by light collecting, would be indicative of it possessing unusual biological characteristics. Presumably, these are sufficient to minimize interactions with the other species in the assemblage.

The other Nicrophorus are all reproductively active in the spring, with N. sayi being the earliest to emerge. The other four species, N. marginatus, N. defodiens, N. vespilloides

and N. orbicollis all emerge at similar times and would appear to overlap in their periods of reproductive activity.

Table 3 summarizes the ecological attributes of the 7 species of Nicrophorus collected.

Another factor which should be mentioned is temporal activity. In the Silphini, this will not be important since the length of larval life will cover many days and thus would permit occurrence of various species on a single resource. In Nicrophorus, this may be important since these beetles can bury the food overnight. The only species in this assemblage which is diurnal is N. tomentosus (Shubeck 1971) and since it occurs at a time when no other species are reproducing it is unlikely that this is an important component of resource partitioning.

Habitat Preferences

The availability of distinct habitats within an area offers another mechanism by which species can partition resources and therefore coexist. By concentrating reproductive activity in a single habitat, a species can minimize interactions with other species should they be selecting a different habitat. Even if they are not, the concentration of reproductive efforts in a single habitat will place selection pressures on other species to become habitat specific themselves (Crowell and Pimm 1976).

In this study, many species were found to possess distinct habitat preferences, which when considered in

conjunction with the seasonal patterns eliminated ecological interactions by defining unique, non-overlapping niches.

In the Silphini, only N. americana and O. noveboracense occurred in all habitats, although N. americana was more common in the marsh and O. noveboracense in the forests. The fact that both occur commonly in the same areas (Pirone 1974, Shubeck 1969, 1976) may be accounted for by the seasonal differences. Oiceoptoma inaequale was found in the forests and appears to be rare in areas where O. noveboracense is common. Thanatophilus lapponicus is a species of open habitats. This specificity combined with the seasonal pattern place this species in a non-interactive position.

The habitat preferences of Necrodes surinamensis are unclear, but for reasons pertaining to food habits it would not appear to be in direct competition with any of the other species.

In the Nicrophorus, there is also a high degree of habitat specificity with N. marginatus, N. vespilloides and N. defodiens being found only in the meadow, marsh and coniferous forest respectively. Nicrophorus marginatus is probably a prairie species that has spread eastward, while N. vespilloides and N. defodiens are primarily northern species. They appear to coexist throughout their range by utilizing different habitats.

The other four species are primarily southern in their distributions and are found in most habitats. In the case of N. tomentosus, habitat preference is not a concern, since it has no competitors that are active at the same time. It should be expected to be eurytopic and is. Nicrophorus sayi and N. orbicollis are both primarily found in forested areas

although they do occur in other habitats. This would appear to minimize competition with the other early season species that are habitat specific. The circumstances surrounding N. pustulatus have already been discussed.

AVAILABILITY OF SPECIFIC VALUES OF NICHE DIMENSIONS

Having already outlined the ways in which the Silphidae are spaced along some niche dimensions, attention should now be devoted to ensuring that this spacing is the result of selection of particular niche dimension values, and not the required usage of that value based on limited availability regardless of the presence of competitors.

In the assemblage of species being considered here, the role of food as a limiting resource has already been stressed. Although no data are available on the seasonal distribution, abundance etc. of carcasses in nature, it seems reasonable to assume that the largest numbers of carcasses will be available in the spring. It may be for this reason, that most species of Silphidae overwinter as adults. It is also possible that during periods of reproductive activity, vertebrate mortality increase due to increased physiological and energetic strains on the organism. This will lead to seasonality in the availability of type and possibly size of food resource, and will depend on local climatic conditions and the faunal structure of the local vertebrate community.

In the area of study, the winter period lasts from late November to early April, and will limit the activity of the

Silphidae to the remaining months. Within this season, there would appear to be little reason to expect that activity should not be continuous. Physiological limitations to development however, may reduce the number of available strategies. This may be evidenced by the occurrence of only two modes of overwintering in the assemblage being studied; the adult and the prepupal stage. The possibility for passage of the winter season in another life history stage appears remote for other reasons as well. In Nicrophorus, the apparent necessity or at least advantage of adult-larval interaction would inhibit the overwintering of the eggs or immature larvae, which would subsequently have to feed, unless of course adults were present. This would lead to a complex life history structure, which would be highly risky since food would have to be acquired in the fall, and maintained over the winter.

In the Silphini, the similar unpredictable nature of the food source would confer a high risk factor on this type of strategy. Competition with flies would also be a problem, since the strategy that the Silphini have adopted to reduce interaction with the former would now be lost.

The availability of different habitats is quite extensive since the study was carried out in an area where the deciduous forest grades into the boreal and where cleared lands abound. The high diversity of habitats in the area certainly contributes to the co-occurrence of species which would otherwise not naturally coexist. This is evidenced by the distributions of N. vespilloides and N. defodiens

which are primarily boreal and N. marginatus which is a western prairie species. Thanatophilus lapponicus is also boreal, while the other species are all found primarily in the southeastern United States. The assemblage of species in this study can then best be characterized not as a closely integrated, co-evolved community, but as a mixture of species from different communities which have retained their original habitat preferences, yet are permitted to coexist due to the transitional nature of the area. This case would therefore indicate the necessity of ensuring consistency of the assemblage over a larger geographic area. Elements of the present assemblage, when grouped by habitat do appear to be discreet assemblages which have persisted for long time periods and may represent coevolved communities.

EVOLUTIONARY CONSIDERATIONS

Theoretical studies of community origin and evolution have stressed the importance of allopatric speciation contributing to, and in turn being controlled by the species diversity within a community (Rosenzweig 1975). Also regulating diversity and speciation rates may be the ecological attributes of organisms (Eldredge 1979). Stenotopes tend to be more diverse, with their rigid ecological requirements usually permitting coexistence. Eurytopes, on the other hand, are ecological generalists and usually exclude each other in competitive situations.

Other studies (Cody 1974, 1975, Diamond 1975, MacArthur and Wilson 1967) have concentrated on the importance of immigration and extinction rates, both as random and as regulated by the existence of already resident competitors.

These views tend to represent both ends of a continuum along which many of the different concepts of a community fit. One end will be recognized as an extremely closely associated complex of species, while the other will be recognized as a random assemblage, where few interactions are or have taken place. Clearly a dogmatic approach is illogical, with most "real" communities falling somewhere in between.

In past studies these assemblages have been delimited taxonomically, geographically, ecologically and by various combinations of these characters. This in turn may be reflected in the position that the assemblage will take along the continuum.

The present assemblage as a whole can be seen to encompass different habitats, which exist together simply due to the transitional nature of the area. Misinterpretation of the origin of the assemblage is therefore very easy to make should the assemblage not be recognized as an artifact of the random association of habitats and their constituent species. Subsequent attempts to analyse the role of niche relationships in structuring the assemblage would lead to incorrect results, should this distributional data be lacking. It is quite clear that the division of the area into

the individual habitats and their constituent species assemblages which demonstrate geographical consistency, which are then analyzed, would be much more informative. If this is done with the present assemblage some interesting patterns become apparent.

Phylogenetic analysis of the evolutionary relationships (Hennig 1966, Eldredge and Cracraft 1980) among the species collected indicates that the affinities lie in many different areas (see Part I). The lack of sister species relationships (with the exception of N. defodiens and N. vespilloides) would certainly argue against the in situ model of community evolution, or the entry of species which may have diverged in allopatry or parapatry back into the assemblage, provided that the extant species were those that were present when the assemblage was first put together.

If the individual elements, according to habitat, of the assemblage are considered, possible patterns of their origin and assembly can be understood, but only in the light of data on the phylogenetic relationships and ecological attributes of the species under consideration.

When considering the eastern deciduous forest element (see distributions presented in Part I), the members N. sayi, N. pustulatus, Necrodes surinamensis, Oiceoptoma noveboracense and Necrophila americana would all appear to have their closest relatives in southeast Asia or Europe, the ecological attributes of which are unknown. This pattern of relationship has been noted for numerous other taxa as well (Thorne 1972, Darlington 1957), although at a higher taxonomic level in many

cases. The most commonly accepted explanation of this pattern is the recognition of the presence of an ancestral assemblage of taxa or a community which was formerly widely distributed. Fragmentation of the habitat resulted in divergence in the constituent taxa, or more simply speciation. The fact that the Silphidae show these close relationships in more than a few species is supportive of such a hypothesis. It is very unlikely that most species in the assemblage would all possess close relatives in the other if the distribution patterns were due to dispersal alone. It therefore seems probable that the eastern deciduous forest assemblage has been derived as the result of a vicariant event (sensu Nelson and Platnick 1980), which has fragmented the ancestral assemblage. This resulted in the formation of homologous, but not analogous assemblages (as in Pianka 1975).

The species that exist in the assemblage today are therefore not those that were initially present and interacting when the assemblage originated. This will then make analysis of the original assembly, based on present ecological attributes of extant species invalid, unless evidence can be presented showing that the ancestral species possessed similar ecological traits. Knowledge of the ecological attributes of the sister species to those in the assemblage may provide this information.

If both species had the same niche in the homologous assemblages, there would be little reason to suspect that the ancestor would have had a different niche. Outgroup

comparison and the knowledge of the ecological attributes of the outgroup, should these again be similar, would tend to more strongly support the hypothesis. Should differences in the ecological attributes of the sister species be present, the outgroup comparison is essential in order to indicate which species has changed, and thus the probable niche occupied by the ancestor. Similar analysis of all species pairs in an assemblage would lead to recognition of any changes which may have occurred in the ecological relationships among the extant constituent taxa. Continuing this pattern of analysis for all members in a monophyletic lineage should provide a scenario of the changes in the ecological relationships that have occurred throughout the evolutionary history of the group. If this is done for all taxa in a community, the origin of that community can then, and only then be clearly documented.

For obvious reasons this type of analysis would only be possible should many conditions be ideally met. The present state of knowledge in the Silphidae does not allow such an analysis but does represent a possible case for future study. The only other work which I am aware of that incorporates phylogenetics in a study of evolution of ecological attributes are those of Andersen (1979) and Andersen and Polhemus (1980), but these are at the family level and are not of use in interpreting community assembly.

There are exceptions however, amongst the species in the present study of the eastern deciduous element that do not conform to the vicariant model. One of these is N. tomentosus

which at present appears to be most closely related to N. hybridus of western North American prairies. It is at present not possible to say whether N. tomentosus has entered the assemblage after its original assembly, or whether N. hybridus has diverged from an ancestor in the assemblage that is now present as N. tomentosus. The use of the aforementioned outgroup analysis should solve this problem.

Another type of case exists with regard to Oiceoptoma inaequale. The apparent sister taxon is O. rugulosum of the southeastern United States. At a higher level, the sister taxon would appear to occur in the Old World. Thus the ancestor was probably within the assemblage at the time of vicariance, with the divergence of the two species O. inaequale and O. rugulosum taking place after such an event had occurred.

The final member of the assemblage collected is N. orbicollis, which has its affinities in South and Central America. At present ecological data on the related species is nil, and thus further analysis is impossible.

Of the remaining species found in the area, N. marginatus has already been sufficiently discussed, but it is interesting to note that the closest relatives of this species are sympatric with it in western North America, and this may be an example of in situ evolution of community structure.

Thanatophilus lapponicus, N. defodiens and N. vespilloides are all northern boreal, or tundra species. The relationships of T. lapponicus are at high elevations in Mexico and in the northern areas of the Old World. Again, ecological data are

lacking on the sister groups, as well as other tundra Silphini. The work of Matthews (1974b) on the evolution of the tundra ecosystem may make this the topic of a potentially very informative study, since data would be available on the historical distribution of the habitat and the absolute age of the assemblage.

Nicrophorus defodiens and N. vespilloides are the only sister species pair found in the study. In this case the outgroups are at present unrecognizable, yet it is still possible to detect the possible ancestor. This is done through an examination of comparative morphology (Eldredge and Cracraft 1980:137-146). Their evolutionary history, which demonstrates quite clearly the use of a form of the methodology is presented elsewhere in the paper (Phylogenetic Affinities of N. vespilloides in Part I).

In other studies, Bush (1975) has shown the uses of knowledge of ecology in aiding in the elucidation of possible modes of speciation. Species that morphologically diverge during allopatry tend to possess similar ecological attributes, while those that diverge during sympatry or parapatry will differ in their ecological attributes. Of course, it would be impossible to distinguish the latter from those cases where subsequent invasion has occurred after allopatric speciation. In the Silphidae, the probability of sympatric speciation is low, since there would appear to be no mechanism of insuring homogametic mating. Only by way of an allochronic mode could sympatric speciation occur. The

lack of sister species relationships in the assemblage being studied differing in seasonal patterns of development indicate that this has not occurred.

In the present study it would therefore appear that competition between the ancestors of the extant species in the assemblage may have been the dominant force resulting in the observed patterns of variation along a specific niche dimension and subsequent coexistence. Predation pressures, which would operate to promote variation by selectively removing individuals of one species at a particular time or in a particular habitat do not appear to be strong. The limited data on Nicrophorus indicates that they are unpalatable and are avoided by birds in laboratory studies (Jones 1932) and may represent a Mullerian type color pattern. Similar diel patterns and the similar food habits would also appear to expose all species equally to predation, and thus preclude a predator from becoming species specific.

Similarly, the role of pressures in maintaining reproductive isolation does not appear to play a large role in the present assemblage, since few species are very closely related. It may however, have been important in the formation of the assemblage, if all the members were from a monophyletic group and if speciation was via a non-vicariant event.

CONCLUSIONS

Eastern Canadian Silphidae partition resources primarily along three niche dimensions. At a high taxonomic level, food type and size is important, while at the specific level, variation occurs in seasonality and habitat preferences. Habitat variations are due to the transitional nature of the area where the study was carried out, while seasonal variations are probably the result of competition, or selection for reproductive isolation among the ancestors of the extant species that were present when the assemblage originally evolved.

Component species of the separate habitats, especially the eastern deciduous forest assemblage, demonstrate similar patterns of biogeographic affinity, indicative of homologous assemblages, and taxonomic consistency of these assemblages over long term evolutionary time. In order to achieve an understanding of the ecological interactions present throughout the evolutionary history of the component species; the ecological attributes of these species and their close relatives must be known. The ecological attributes of the ancestors can then be elucidated through phylogenetic analysis of these characteristics, and any changes which may have occurred be recognized. This will then contribute to our knowledge of the evolution of these species, and eventually, if all taxa are considered, to our knowledge of the origin and evolution of the assemblage or even the entire community.

REFERENCES

- Abbott, C.E. 1927a Experimental data on the olfactory sense of Coleoptera, with special reference to the Necrophorini. Ann. Ent. Soc. Amer. 20:207-216.
- _____ 1927b Further observations on the olfactory powers of the Necrophorini. Ann. Ent. Soc. Amer. 20:550-553.
- Agassiz, L. 1847 Nomenclatoris Zoologici Index Universalis. Soloduri. viii+393 pp.
- Alcock, J. 1979 Multiple mating in Calopteryx maculata (Odonata:Calopterygidae), and the advantage of non-contact guarding by males. J. Nat. Hist. 13:439-446.
- Andersen, N.M. 1979 Phylogenetic inference as applied to the study of evolutionary diversification of semi-aquatic bugs (Hemiptera:Gerromorpha). Syst. Zool. 28:554-578.
- Andersen, N.M. and J.T. Polhemus 1980 Four new genera of Mesoveliidae (Hemiptera:Gerromorpha) and the phylogeny and classification of the family. Ent. Scand. 11:369-392.
- Anderson, R.S. in press On the decreasing abundance of Nicrophorus americanus Olivier in eastern North America. Coleop. Bull. (in press).
- Angell, J.W. 1912 Two new North American Nicrophorus. Ent. News 23:307.
- Arnett, R.H. 1944 A revision of the Nearctic Silphini and Nicrophorini based upon the female genitalia. J. N.Y. Ent. Soc. 52(1):1-25.
- _____ 1946 Coleoptera notes I: Silphidae. Can. Ent. 78:131-134.
- Balduf, W.V. 1935 The bionomics of Entomophagous Coleoptera. J. B. Swift Pub. Co., St. Louis. 220 pp.
- Barlow, C.A. 1970 Phenology and distribution of some Pterostichus of eastern Canada. J. N.Y. Ent. Soc. 78(4):215-236.
- _____ 1973 Phenology and distribution of Carabus nemoralis in eastern Canada. Nat. Can. 100:361-369.

- Benick, L. 1912 Zur biologie des Necrophorus vestigator Herschel nebst Beschreibung der Larve und Nympe.
Ent. Blatter 8/9:197-203.
- Berce, J.E. and C. Brisout de Barneville 1872 Des conditions dans lesquelles on recontre l'Agyrtes bicolor. Ann. Ent. Soc. France (5)2:v-vi.
- Bergroth, E. 1884 Bemerkungen zur dritten Auflage des Catalogus Coleopterorum Europae auctoribus L. v. Heyden, E. Reitter et J. Weise. Berliner Ent. Zeit. 28:225-230.
- Blackwelder, R.E. 1936 Morphology of the Coleopterous family Staphylinidae. Smith: Misc. Coll. 94(12):1-102.
- Blaisdell, F.E. 1901 Pupa of Necrophilus hydrophiloides. Ent. News 12:263-264 + 1 pl.
- Bland, J.H.B. 1865 Descriptions of several new species of North American Coleoptera. Proc. Ent. Soc. Phila. 4:381-384.
- Blatchely, W.S. 1910 An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana. Nature Publishing Co., Indianapolis, Indiana. 1386 pp.
- Boeckh, J. 1962 Elektrophysiologische Untersuchungen an einzelnen Geruchsrezeptoren auf den Antennen des Totengräber (Nicrophorus: Coleoptera). Z. Vergl. Physiol. 46:212-248.
- Bolivar y Pieltan, C. and J. Hendrichs 1972 Distribución en Norteamérica del género holártico Pteroloma y estudio de tres nuevas formas mexicanas. Ciencia Mex. 27(6): 207-216.
- Bornemissza, G.F. 1957 An analysis of Arthropod succession in carrion and the effect of its decomposition on the soil fauna. Aust. J. Zool. 5:1-12.
- Brewer, J.W. and T.R. Bacon 1975 Biology of the carrion beetle, Silpha ramosa. Ann. Ent. Soc. Amer. 68(5): 786-790.
- Brown, W.J. 1933 Two undescribed species of the old family Silphidae with notes on some characters that have been used to divide the group. Can. Ent. 65:213-215.
- Brundin, L. 1934 Die Coleopteren der Tornetraskgebietes. PhD Thesis, Lund. 436 pp.
- Bush, G.L. 1975 Modes of animal speciation. Ann. Rev. Ecol. Syst. 6:339-364.

- Cantonnet, F. and C. Lecordair 1947 Note biologique sur les Necrophorus en foret d'Ardaine (Orne). L'Entomologiste 3:134-136.
- Casey, T.L. 1886 Descriptive notices of North American Coleoptera. Bull. California Acad. Sci. 2(6):157-264.
- 1924 Memoirs on the Coleoptera. XI. Lancaster Press Inc., Lancaster, Pa. 364 pp.
- Catesby, M. 1771 The natural history of Carolina, Florida, and the Bahama Islands. Vol. II (1743), 100 pp. and appendix (1748), 20 pp. Author, London. Edition III, Geo. Edwards editor, London.
- Christie, J. 1980 Mites associated with British Nicrophorus Fabricius, 1775 beetles (Coleoptera: Silphidae): An interim report. Manuscript.
- Clark, C.U. 1895 On the food habits of certain dung and carrion beetles. J. N.Y. Ent. Soc. 3:61.
- Cockerell, T.D.A. 1906 Preoccupied generic names of Coleoptera. Ent. News 17:240-244.
- Cody, M.L. 1974 Competition and the structure of bird communities. Monog. Pop. Biol. 7, Princeton University Press, Princeton, N.J. 318 pp.
- 1975 Towards a theory of continental species diversity. In: Eds. M.L. Cody and J.M. Diamond. Ecology and evolution of communities. pp. 214-257. Belknap Press, Harvard University, Cambridge, Mass.
- Cole, A.C. 1942 Observations of three species of Silpha. Amer. Mid. Nat. 28:161-163.
- Cooley, R.A. 1917 The spinach carrion beetle: Silpha bituberosa. J. Econ. Ent. 10:94-102.
- Coope, G.R. and R.B. Angus 1975 An ecological study of a temperate interlude in the middle of the last glaciation, based on fossil Coleoptera from Isleworth, Middlesex. J. Anim. Ecol. 44:365-391.
- Coope, G.R., J.H. Dickson, J.A. McCutcheon and G.F. Mitchell 1979 The lateglacial and early postglacial deposit at Drumurcher, Co. Monaghan. Proc. Irish Acad. Sci. 79B:63-85.
- Cornaby, B.W. 1974 Carrion reduction by animals in contrasting tropical habitats. Biotropica 6(1):51-63.
- Crowell, R.L. and S.L. Pimm 1976 Competition and niche shifts of mice introduced onto small islands. Oikos 27(2):251-258
- Crowson, R.A. 1967 The natural classification of the families of Coleoptera. E.W. Classey Ltd, Middlesex, 214 pp.

- Darlington, P.J. 1957 Zoogeography; The geographical distribution of animals. 675 pp. J. Wiley Pub. Co. N.Y.
- Davis, L.R. Jr. 1980 Notes on beetle distributions, with a discussion of Nicrophorus americanus Olivier and its abundance in collections (Coleoptera: Scarabaeidae, Lampyridae and Silphidae). Coleop. Bull 34:245-249.
- Denno, R.F. and W.R. Cothran 1975 Niche relationships of a guild of necrophagous flies. Ann. Ent. Soc. Amer. 68(4):741-754.
- 1976 Competitive interactions and ecological strategies of sarcophagid and calliphorid flies inhabiting rabbit carrion. Ann. Ent. Soc. Amer. 69(1):109-113.
- Dethier, V.G. 1947 The role of the antennae in the orientation of carrion beetles to odors. J. N.Y. Ent. Soc. 55:285-293.
- Diamond, J.M. 1975 Assembly of species communities. In: Eds. M.L. Cody and J.M. Diamond. Ecology and Evolution of Communities. pp. 342-444. Belknap Press, Harvard University, Cambridge, Mass.
- Dominion Bureau of Statistics 1962 The climate of Canada. Meteorological Branch, Air Services Department of Transport, Toronto, Canada pp. 1-74.
- Dorsey, C.K. 1940 A comparative study of the larvae of six species of Silpha. Ann. Ent. Soc. Amer. 33:120-139.
- Eldredge, N. 1979 Alternative approaches to evolutionary theory. In: Eds. J.H. Schwartz and H.B. Rollins. Models and methodologies in evolutionary theory. pp. 7-19. Bull. Carnegie Museum of Nat. Hist. #13.
- Eldredge, N. and J. Cracraft 1980 Phylogenetic patterns and the evolutionary process. Columbia University Press, N.Y. 349 pp.
- Emetz, V. 1975 Ergebnisse der zoologischen Forschungen van Dr. Z. Kaszab in der Mongolei Nr. 358: Silphidae and Lioididae. Folia Ent. Hungarica 28(1):57-71
- Ernst, K.D. 1969 Die Feinstruktur von Riechensensillen auf der Antenne des Aaskäfers Nicrophorus. Z. Zellforsch 94:72-102.
- 1972 Sensillum coelasphaericum, die Feinstruktur eines neuen olfaktorischen Sensillentyps. Z. Zellforsch 132:95:106.

- Erichson, W.F. 1837 Die Käfer der Mark Brandenburg.
Vol. 1, Pt. 1, pp. 1-384. F.H. Morin, Berlin.
- Fabricius, J.C. 1775 Systema Entomologiae. Flensburgii
et Lipsiae, Korte, (28), 1-832 pp.
- _____ 1776 Genera Insectorum. Chilonii,
Bartsch. xiv + 1-310 pp.
- _____ 1781 Species Insectorum. Hamburgii
and Kilonii, Bohn. Tomus 1, viii + 1-552 pp.
- _____ 1792 Entomologia Systematica. Tomus 1,
pars 1, Hafniae, Prost., xx + 1-330 pp.
- _____ 1801 Systema Eleutheratorum secundum
ordines, genera, species. Tomus 1. Bibliopolii
Academici Novi, Kiliae. 506 pp.
- Fall, H.C. 1907 New Coleoptera from the southwest, III.
Can. Ent. 34:235-243.
- _____ 1927 New Coleoptera, XII. Can. Ent. 59:
136-141.
- _____ 1937 Miscellaneous notes and descriptions
(Coleoptera). Can. Ent. 69:29-32.
- Fauvel, A. 1890 Tableaux analytiques des Coleoptères
d'Europe, Necrophages. Revue d'Entomol. 9:345-348.
- Fincher, G.T. 1972 Notes on the biology of Phaneus
vindex (Coleoptera:Scarabaeidae). J. Georgia Ent. Soc.
7(2):128-133.
- Fiori, A. 1898 Fauna Entomologica Italiana Coleotteri
nuovi o poco conosciuti. Atti. Soc. Nat. Modena 16:
153-164.
- Fischer von Waldheim, G. 1828 Entomographica Imperii
Rossici. A. Semen, Moscow 3: viii + 3-314, pl. 1-14.
- _____ 1844 Spicilegium Entomographiae
Rossicae. Bull. Soc. Nat. Hist. Moscow 17:3-144.
- Forster, J.R. 1771 Novae species Insectorum. Canturia I.
Davies and White, London. viii + 100 pp.
- Frölich, J.A. 1799 Einige neue attungen und Arten von
Käfern. Der Naturforscher 28:1-65.
- Germar, E.F. 1824 Insectorum Species. Hendelii, Halae.
xxiv + 1-624 pp.

- Gillet, J.D. 1971 Mosquitoes. Weidenfeld and Nicolson, London, England. 274 pp.
- Gissler, C.F. 1880 Biological studies on Silpha ramosa. Amer. Ent. 3:265-267.
- Gistel, J. 1834 Entomologische Notizen. Faunus 1:128-151.
- _____ 1848 Naturgeschichte des Thierreichs für höhere Schulen. Stuttgart. xvi + 1-216 +(4) pp., pl. 1-32.
- Goe, M.T. 1919 Life history and habits of Silpha inaequalis. Ent. News 30(9):253-255.
- Guérin-Méneville, M.F.E. 1835 Iconographie du Règne Animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables, et souvent non encore figures, de chaque genre d'animaux. Insects. Vol. 7. Bailliere, Paris. 576 pp. 104 pl. (Title page date 1829-1838).
- Gyllenhal, L. 1827 Insecta Suecica. Classis I. Coleoptera sive Eleuterata. Tomus 1, pars IV. Eleischer, Lipsiae, viii + 1-761 pp.
- Harold, E.V. 1868 Abänderungen vergebener Namen. Coleoptersche Heft, 4:104.
- Hatch, M.H. 1927a Studies on the Silphinae. J. N.Y. Ent. Soc. 35:331-371.
- _____ 1927b Studies on the carrion beetles of Minnesota, including new species. Univ. Minn. Agric. Exp. Stn. Bull. 48:3-7.
- _____ 1927c Studies on the carrion beetles of Minnesota. II. An inquiry into the position of the Silphinae in the Staphylinoid series. Univ. Minn. Agric. Exp. Stn. Bull. 48:8-12.
- _____ 1928 Coleopterorum Catalogus. Fam. Silphidae II. 95:1-244.
- _____ 1940 Observations on Silphinae with a note on intraspecific variations and their designation. J. N.Y. Ent. Soc. 48:233-244.
- _____ 1946 Mr. Ross H. Arnett's "Revision of the Nearctic Silphini and Necrophorini" J. N.Y. Ent. Soc. 56:99-103.
- _____ 1957 The beetles of the Pacific Northwest. Part II: Staphyliniformia. University of Washington Publications in Biology, Vol. 16. University of Washington Press, Seattle, Wash. 386 pp.

- Hatch, M.H. and J.W. Angell 1925 A new North American Nicrophorus. J. N.Y. Ent. Soc. 23:216.
- Hatch, M.H. and W. Reuter 1934 Coleoptera of Washington: Silphidae. University of Washington Publications in Biology, Vol. 1:151-161.
- Hennig, W. 1966 Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois. 263 pp.
- Henriksen, K. 1922 Larver. Danmarks Fauna 26:249-273.
- Herbst, J.F. 1783 Kritisches Verzeichniss meiner Insectensammlung. pp. 1-151. Archiv. der Insectengeschichte II, Heft 4.
- _____ 1793 Natursystem aller bekannten in-und ausländischen Insecten als eine Fortsetzung der von Buffonschen Naturgeschichte. Der Käfer. Volume 5. Pauli-Berlin. xvi + 1-392 pp.
- Herschel, K. 1807 Der Europäischen arten von Nicrophorus mid unterscheidung einer neuen Art: Nicrophorus vestigator. Magazin für Insektenkunde 6:268-276.
- Heymons, R., H. von Lengerken and M. Bayer 1927 Studien über die Lebenserscheinungen der Silphini. II. Phosphuga atrata L. Zeits. Morphol. Okol. Tiere 9:271-312.
- _____ 1928 Studien über die Lebenserscheinungen der Silphini. III. Xylodrepa quadripunctata L. Zeits. Morphol. Okol. Tiere 10:330-352.
- _____ 1929 Studien über die Lebenserscheinungen der Silphini. IV. Blitophaga opaca L. Zeits. Morphol. Okol. Tiere 14:234-260.
- _____ 1930 Studien über die Lebenserscheinungen der Silphini. VI. Blitophaga undata Mull. Zeits. Morphol. Okol. Tiere 18:170-188.
- _____ 1931 Studien über die Lebenserscheinungen der Silphini. VII. Oeceoptoma thoracica L. Zeits. Morphol. Okol. Tiere 20:691-706.
- _____ 1932 Studien über die Lebenserscheinungen der Silphini. VIII. Ablattaria laevigata F. Zeits. Morphol. Okol. Tiere. 24:259-287.
- Hinton, H.E. 1969 Diffraction gratings in burying beetles (Nicrophorus). The Entomol. 102:185-189.

- Hlisnikovsky, J. 1964a Die Gattung Lyrosoma Mann.
der Tribus Pterolomini (Coleoptera:Silphidae).
Acta. Soc. Ent. Czech. 61(1):39-42.
- _____ 1964b Zur Kenntnis der gattung
Agyrtes Lap. Reichenbachia 2(62):275-278.
- Holdhaus, K. and C. Lindroth 1939 Die Europäischer
Coleopteren mit Boreoalpiner Verbreitung. Ann. Nat.
Mus. Wien 50 Bd., 5:123-293
- Hope, F.W. 1840 The Coleopterist's manual, part the
third, containing various families, genera and species
of beetles recorded by Linnaeus and Fabricius.
Bridgewater, London. pp. 1-191 + pl. 3.
- Horion, A. 1949 Faunistik der Mitteleuropäichen,
Käfer 2:86-90.
- Horn, G.H. 1880 Synopsis of the Silphidae of the
United States with reference to the genera of other
countries. Trans. Amer. Ent. Soc. 8:219-322.
- Hovanitz, W. 1941 Parallel ecogenotypical color variation
in butterflies. Ecology 22(3):259-284.
- Howden, A.T. 1950 The succession of beetles on carrion.
MSc Thesis, University of North Carolina. 83 pp.
- Hubbell, T.H. 1961 Endemism and speciation in relation
to Pleistocene changes in Florida and the Southeastern
Coastal Plain. pp. 466-469 In: XI Internationaler
Kongress für Entomologie, Wien 1960. Sonderdruck
aus den Verhandlungen, Bd. 1.
- Jaques, H.E. 1915 The fish feeding Coleoptera of
Cedar Point. Ohio Nat. 15:525-528.
- Jeanel, R. 1935 Apteroloma. In: Eds. P.C. Visser and
J. Visser-Hooft. Wissenschaftliche Ergebnisse der
Niederländischen Expedition in der Karakorum I:283-287.
- Johnson, M.D. 1974 Seasonal and microseral variations
in the insect populations on carrion. Amer. Mid. Nat.
93(1):79-90.
- Jones, F.M. 1932 Insect coloration and the relative
acceptability of insects to birds. Trans. Ent. Soc.
London 80(II):345-386.
- Katakura, H. and H. Fukuda 1975 Faunal makeup of ground
and carrion beetles in Komiotoinneppu, Hokkaido University
Nakagawa Experimental Forest, northern Japan, with some
notes on related problems. Hokkaido University, Research
Bull. of the College Expt. Forests. 32(1):75-92.

- Kawada, A., et al 1959 Illustrated Insect larvae of Japan. Hokuryukan Co. Ltd. Tokyo. 712 pp. + indexes.
- Kellogg, V. 1914 Beetles becoming parasites. Science 34(1001):360-361.
- Kirby, W. 1837 Northern Zoology, Part 4: The Insects. xxxix + 1-325 pp. + 8 pl. Fletcher, Norwich. In: J. Richardson. Fauna Boreali-Americana; or the Zoology of the northern parts of British America.
- Kirby, W. and W. Spence 1828 An Introduction to Entomology, 5th. Edn. Longmass, Rees, Orme Brown and Green, London. 4:iv + 1-683 pp.
- Klausnitzer, B. et al 1978 Family Silphidae In: Ordnung Coleoptera (Larven). Dr. W. Junk Pub. The Hague, Netherlands.
- Laboulbene, A. 1872 Note sur l'apparition d'une tres grande quantite de Dipteres noirs. Ann. Ent. Soc. Fr. 12:209-211.
- Lacordaire, J.T. 1854 Histoire Naturelle des Insectes, Genera des Coleopteres, Pars 1: Adephaga-Palpicornia
- Lane, C. and M. Rothschild 1965 A case of Mullerian mimicry of sound. Proc. R. Ent. Soc. London (A) 40 (10-12):156-158, 4 pl.
- Laporte, F.L. de comte de Castelnau 1840 Histoire naturelle des Insectes, Coleopteres. Tome 2. 563 pp. Dumenil, Paris.
- Latreille, P.A. 1829 Les Crustaces, les Arachnides et les Insectes, distribues en Familles Naturelles, ouvrage formant les tomes 4 et 5 de celui de M. Le Baron Cuvier sur Le Regne Animal (deuxieme edition). Tome I. xxvii + 1-584 pp. Deterville, Paris.
- Leach, W.E. 1815 Article Entomology. In: Brewster, The Edinburgh Encyclopedia. Edinburgh 9:57-172.
- LeConte, J.L. 1853 Synopsis of the Silphales of America, north of Mexico. Proc. Acad. Nat. Sci. Phila. 6:274-287.
- 1854 Descriptions of some new Coleoptera from Oregon, collected by Dr. J.G. Cooper of the North Pacific R.R. expedition, under Governor J.J. Stevens, Proc. Acad. Nat. Sci. Phila. 7:16-20.

- 1859a Additions to the Coleopterous fauna of Northern California and Oregon. Proc. Acad. Nat. Sci. Phila. 1859:281-292.
- 1859b Catalogue of the Coleoptera of Ft. Tejon, California. Proc. Acad. Nat. Sci. Phila. 1859:69-90
- 1859c The Coleoptera of Kansas and Eastern New Mexico. Smith. Contrib. Know. 11(6):1-66 + 3 Pl.
- Leech, H.B. 1934 The family history of Nicrophorus conversator Walker. Proc. Ent. Soc. B.C. 31:36-40.
- Lewis, G. 1893 On some new Japanese Coleoptera. Ann. Mag. Nat. Hist. 6(11):354-357.
- Lindroth, C. 1971 On the occurrence of a continental element in the ground beetle fauna of Eastern Ontario (Coleoptera:Carabidae). Can. Ent. 103:1455-1462.
- Linnaeus, C. 1758 Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10, Vol. 1. Holmiae. 823 pp.
- 1771 Mantissa plantarum altera generum editionis VI et specierum editionis II. Laurentii Salvii, Holmiae. vii + 144-582 pp.
- Linsley, E.G. 1942 Notes on the habits of some beetles from the vicinity of Yosemite National Park. Bull. S. Cal. Acad. Sci. 42(3):164-166.
- MacArthur, R.H. and E.O. Wilson 1967 The theory of island biogeography. Monog. Pop. Biol. 1. Princeton University Press, Princeton, N.J. 203 pp.
- Mackay, R.J. 1978 Larval identification and instar association in some species of Hydropsyche and Cheumatopsyche. Ann. Ent. Soc. Amer. 71(4):499-509.
- Madge, R.B. 1958 A taxonomic study of the genus Nicrophorus in America, north of Mexico. MSc thesis, University of Illinois, Urbana. 77 pp. + 7 Pl.
- 1980 A catalogue of the type-species in the family Silphidae (Coleoptera). Ent. Scand. 11:353-362.
- Mannerheim, C.G. 1843 Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sitkha und New-Californiens. Bull. Soc. Imp. Nat. Moscow 16(2):175-314.
- 1846 Nachtrag zur Kaefer-Fauna der Aleutischen Inseln und der Insel Sitkha. Bull. Soc. Imp. Nat. Moscow 19:501-516.

- 1852 Zweiter Nachtrag zur Kaefer-Fauna
der Nord-Amerikanischer Laender des Russischen Reiches.
Bull. Soc. Imp. Nat. Moscow 25:283-387.
- 1853 Dritter Nachtrag zur Kaefer-Fauna
der Nord-Amerikanischer Laender des Russischen Reiches.
Bull. Soc. Imp. Nat. Moscow 26:95-273.
- Martin, H. 1945 Contribution a l'etude des Silphes
de la betterave en Suisse. Landwirtschaftliches Jahrbach
der Schweiz 59:757-819.
- Matthews, A. 1888 Family Silphidae. Biologia Centrali-
Americana. Coleoptera. Vol. 1 Pt. 2, pp. 72-101. 3 pl.
- Matthews, J.V. Jr. 1968 A paleoenvironmental analysis
of three late Pleistocene Coleopterous assemblages from
Fairbanks, Alaska. Quaest. Ent. 4:202-224.
- 1974a Wisconsinan environment of
interior Alaska: Pollen and macrofossil analysis of a
27 meter core from the Isabella Basin (Fairbanks, Alaska).
Can. J. Earth Sci. 11(6):828-841.
- 1974b Quaternary environments at
Cape Deceit (Seward Peninsula, Alaska): Evolution
of a Tundra ecosystem. Bull. Geol. Soc. Amer. 85:
1353-1384.
- 1975 Insects and plant macrofossils
from two Quaternary exposures in the Old Crow-Porcupine
region, Y.T., Canada. Arc. and Alp. Res. 7(3):249-259
- 1977 Tertiary Coleoptera fossils
from the North American Arctic. Coleop. Bull. 31(4):
297-308.
- 1979 Paleoeecology of the Arctic Steppe
Mammoth biome: Beringea during the late Pleistocene;
Arctic steppe, or discontinuous herb tundra? A review
of the Paleontological evidence. Preprint-Geological
Survey of Canada #649.
- McKinnerney, M. 1978 Carrion communities in the
northern Chihuahan Desert. Southwestern Nat. 23(4):
563-576.
- Miller, S.E. and S.B. Peck 1979 Fossil carrion beetles
of Pleistocene California asphalt deposits, with a
synopsis of recent California Silphidae. Trans. San
Diego Soc. Nat. Hist. 19(8):85-106.
- Milne, L.J. and M.J. Milne 1944 Notes on the behavior
of burying beetles (Nicrophorus spp.). J. N.Y. Ent.
Soc. 52:311-327.

- _____ 1976 The social behavior
of burying beetles. Sci. Amer. 235(2):84-89.
- Motschoulsky, V. 1845 Die Coleopterologischen
Verhaeltnisse und die Kaefer Russlands. Bull. Soc.
Imp. Nat. Moscow 18:1-127.
- _____ 1860 Coleopteres de la Siberie
orientale et en particulier des rives de l'Amour.
Schrenck, Reissen u. Forschungenim Amurlande St.
Petersburg 2:77-257.
- _____ 1869 Enumeration des nouvelles especes
de Coleopterés rapportes de ses voyages. VIII.
Bull. Soc. Imp. Nat. Moscow 42:348-410.
- Mroczkowski, M. 1949 Notes on the successive appearance
of some species of the genera Nicrophorus and Neonicrophorus.
Polskie Pismo Ent. 19:196-199.
- Naezen D.E. 1792 Beskrifning pa nagra, vid umeå funde,
okande arter bland. Skalbaggarne Vetensk. Acad. nya
Handl. 13:167-174.
- Nelson, G.H. and N.I. Platnick 1980 A vicariance
approach to historical biogeography. Bioscience 30(5):
339-343.
- Newton, A.F. and S.B. Peck 1975 Baited pitfall traps
for beetles. Coleop. Bull. 29(1):45-46.
- Newman, E. 1838 Entomological Notes. The Entomol.
Mag. 5:372-402.
- Niemitz, C. 1972 Bioacoustical, behavioral and
morphological studies on Necrophorus vespillo.
Forma et Functio 5(3):209-230.
- Norris, K.R. and M.S. Upton 1974 The collection and
preservation of insects. Aust. Ent. Soc. Misc. Pub.
#3:1-33.
- Novak, B. 1965a Abundanzänderungen unserer
Feldbewohnenden Totengräber als Folge der Dezimierung
durch den Fallenfang (Coleoptera:Silphidae), Zmęny hustoty
nasich polnich hroborku jako nasledek decimace zemnimi
pastmi (Coleoptera:Silphidae). Acta Univer. Palack.
Oloum. Fac. Rer. Nat. 19:99-119.
- _____ 1965b Faunistik-ekologicka studie o
hrobarkich z polnich biotopu hane (Coleoptera:Silphidae).
Acta. Univer. Palack. Oloum. Fac. Rer. Nat. 19:121-152.

3

A

- Olivier, M. 1790 Entomologie, ou histoire naturelle des Insectes. Vol. 2. Coleoptera No. 10. 8 pp., Baudouin, Paris.
- Osinskii, S.O. 1940 The roles of insects that attack carcasses in the preservation and spread of the bacilli of Anthrax in nature. Rev. Appl. Ent. B. 28:256 (Abstract).
- Paulian, R. 1941 Les premieres etats des Staphylinoidea. VII. Famille Silphidae. Memoirs Mus. Nat. Hist. Natur. Paris 15:109-121.
- _____ 1946 Essai de bionomie quantitative sur les Necrophores. Rev. Fran. Ent. 13(3):93-98.
- Payne, J.A. 1965 A summer carrion study of the baby pig, Sus scrofa. Ecology 46(5):592-602.
- Payne, J.A. and E.W. King 1969 Lepidoptera associated with pig carrion. J. Lep. Soc. 23:191-195.
- _____ 1970 Coleoptera associated with pig carrion. Ent. Mon. Mag. 105:224-232.
- Payne, J.A. and W.R.M. Mason 1971 Hymenoptera associated with pig carrion. Proc. Ent. Soc. Wash. 73:132-141.
- Payne, J.A., F.W. Mead and E.W. King 1968 Hemiptera associated with pig carrion. Ann. Ent. Soc. Amer. 61:565-567.
- Peck, S.B. 1974 A review of the Agyrtes of North America. Psyche 81(3):501-506.
- _____ in press Silphidae and the associated families Agyrtidae and Leiodidae. In: Soil Biology Guide. Ed. D. Dindal. J. Wiley and Sons. (in press).
- _____ in prep. The life history of Ptomascopus morio and the origins of parental care in Nicrophorus (Coleoptera: Silphidae). (in preparation).
- Petruska, F. 1968a Prislusnici skupiny Silphini jako soucast entomofauny repnych poli unicovske rovny (Coleoptera: Silphidae). Acta Univer. Palack. Oloum. Fac. Rer. Nat. 28:189-200.
- _____ 1968b Hrobarici jako soucast entomofauny poli unicovske rovny (Coleoptera: Silphidae). Acta. Univer. Palack. Oloum. Fac. Rer. Nat. 28:159-187.

- 1975 Vliv prevládajících smeru vetru
na nalet některých druhů brouků z čeledi Silphidae do
zemních pastí. Acta. Univer. Palack. Oloum. Fac. Rer.
Nat. 51:155-176.
- Pettit, J. 1869 Notes on a few beetles. Can. Ent. 2:20
- Pianka, E.R. 1975 Niche relations of desert lizards.
In: Eds. M.L. Cody and J.M. Diamond. Ecology and evolution
of communities. pp.292-314. Belknap Press, Harvard University,
Cambridge, Mass.
- Pic, M. 1917 Notes diverses, descriptions et diagnoses.
Echange Moulins 33:21.
- Pierce, W.D. 1949 Fossil Arthropods of California.
17. The silphid burying beetles in the asphalt
deposits. Bull. S. Cal. Acad. Sci. 48(2):55-70.
- Pirone, D.J. 1974 Ecology of necrophilus and carpophilus
Coleoptera in a southern New York woodland (Phenology,
Aspection, Trophic and Habitat preferences) PhD thesis,
Fordham University, 769 pp.
- Portevin, M.G. 1903 Remarques sur les Necrophages du
Museum et description d'espèces nouvelles. Bull. Mus.
Nat. Hist. Paris. 9:329-336.
- 1914 Silphides et Lioides nouveaux.
Ann. Ent. Soc. Belg. 58:190-198.
- 1920a Silphides nouveaux de la collection
du museum. Bull. Mus. Nat. Hist. Paris. 26:505-508.
- 1920b Revision des Silphini et Necrophorini
de la région Indo-Malaise. Bull. Mus. Nat. Hist. Paris.
26:395-401.
- 1921 Note sur quelques Silphides et
Lioides de la collection Grouvelle. Bull. Mus. Nat.
Hist. Paris. 27:535-538.
- 1922 Note sur quelques Silphides des
collection du museum. Bull. Mus. Nat. Hist. Paris.
28:506-508.
- 1923 Revision des Necrophorini du Globe.
Bull. Mus. Nat. Hist. Paris. 29:64-71, 141-146, 226-233,
303-309.
- 1924 Revision des Necrophorini du Globe.
Bull. Mus. Nat. Hist. Paris. 30:83-87, 374-377.
- 1925 Revision des Necrophorini du Globe.
Bull. Mus. Nat. Hist. Paris. 31:165-170.

- 1926 Les grandes Necrophages du Globe.
 Encyc. Ent. 6:1-270. Lechevalier, Paris.
- Prokopic, J. and S. Bily 1975 Beetles as new intermediate
 hosts of helminths. Vestn. Cesk. Spol. Zool. 39(3):
 224-230.
- Pukowski, E. 1933 Oekologische Untersuchungen an
Necrophorus F. Zeits. Morphol. Okol. Tiere 27:518-586.
- 1934 Zur Systematik der Necrophorus
 Larven. Stettiner Ent. Zeitung 95:53-60.
- Putman, R.J. 1978 The role of carrion frequenting
 arthropods in the decay process. Ecol. Ent. 3:133-139.
- Rade, A. 1893 Necrophilus subterraneus Dej. und
 Andre Käfer des Göttinger Gebietes. Ent. Nachr. 19(23):
 357-363.
- Ratcliffe, B.C. 1972 The natural history of Necrodes
surinamensis. Trans. Amer. Ent. Soc. 98:359-410.
- Reed, H.B. 1958 A study of dog carcass communities in
 Tennessee; with special reference to the insects.
 Amer. Mid. Nat. 59:213-245.
- Reitter, E. 1884 Bestimmungs-Tabellen der Europäischen
 Coleopteren 12: Necrophaga. (Platypsyllidae, Leptinidae,
 Silphidae, Anisotomidae und Clambidae). Verh. Natur.
 Ver. Brunn. 23:3-122.
- 1895 Uebersicht der Arten der Coleopteren-
 gattung Necrophorus Fabr. aus der Palaeartischen Fauna.
 Ent. Nachr. 21(21):323-330.
- 1897 Coleopterologische Notizen. Wiener
 Entomol. Zeit. 16:48-49.
- 1901 Uebersicht der bekannten Agyrtes-Arten.
 Wien. Entomol. Zeit. 20:102.
- Roeder, W.A. 1972 Acarina associated with selected
 Michigan Silphidae. PhD Thesis, Michigan State University.
 120 pp.
- Rosenzweig, M.L. 1975 On continental steady states of
 species diversity. In: Eds. M.L. Cody and J.M. Diamond.
 Ecology and evolution of communities. pp. 121-140
 Belknap Press, Harvard University, Cambridge,
 Mass.

- Roussel, J.P. 1964a Le développement larvaire de
Nicrophorus vespillo L. Bull. Soc. Zool. Fr. 89(2-3):
102-110.
- 1964b Le développement larvaire de
Nicrophorus fossor Er. Bull. Soc. Zool. Fr. 89(2-3):
111-117.
- Sanborne, P.M. 1977 Ecology and behavior of some large
carrion beetles occurring near Ottawa, Ontario (Coleoptera:
Silphidae). BSc Hons. Thesis, Carleton University,
Ottawa. 119 pp.
- Say, T. 1823 Descriptions of Coleopterous insects
collected in the late expedition to the Rocky Mountains,
performed by order of Mr. Calhoun, Secretary of War, under
the command of Mjr. Long. J. Acad. Nat. Sci. Phila.
3:139-216.
- 1825 Descriptions of new Coleopterous insects
inhabiting the United States. J. Acad. Nat. Sci. Phila.
5:160-202.
- Schaeffer, J.C. 1769 Icones Insectorum circa Ratisbonam
indigenorum coloribus naturam referentibus expressae.
Bde. 1, Teil 2. 4y, 50 p.u. 12 p. Taf. 51-100.
- Schaupp, F.G. 1881 Description of the larva of
Nicrophorus tomentosus. Bull. Brook. Ent. Soc. 4:37-38.
- Schilling, P.S. 1829 Holocnemis Carabicornum genus novum.
Beitr. Ent. Schles. Fauna I pp. 93-94.
- Schoener, T.W. 1974 Resource partitioning in ecological
communities. Science 185:27-37.
- Scholtz, R. 1934 Kleine Coleopterologische Mitteilungen.
Ent. Blätter 30(5):190-191.
- Schumacher, R. 1973 Beitrag zur Kenntnis der
Stridulationsapparate einheimischer Nicrophorus-Arten.
Zeits. Morphol. Tiere 75:65-75.
- Semenov-Tian-Shanskij, A. 1891 Diagnosis Coleopterorum
novorum ex Asia centrali et orientali. Honae Societatis
Entomologicae Rossicae 25:262-382.
- 1926 Analecta Coleopterologica
XIX. Entomologiceskoe Obozrenie 20:33-55.
- 1933 De tribu Necrophorini
(Coleoptera; Silphidae), classificanda et de ejua
distributione geographica. Trav. Instit. Zool. Acad.
Sci. URSS 1:149-160.

- Shubeck, P.P. 1968 Orientation of carrion beetles to carrion: Random or non-random? J. N.Y. Ent. Soc. 76(4):253-265.
- _____. 1969 Ecological studies on carrion beetles in Hutcheson Memorial Forest. J. N.Y. Ent. Soc. 77(3): 138-151.
- _____. 1971 Diel periodicities of certain Carrion beetles. Coleop. Bull. 25(2):41-46.
- _____. 1976 Carrion beetle responses to poikilothermic and homiothermic carrion. Ent. News 89:265-269.
- Shubeck, P.P., N.M. Downie, R.L. Wenzel, and S.B. Peck 1977 Species composition of carrion beetles in a mixed-oak forest. William L. Hutcheson Mem. Forest. Bull. 4(1): 12-17.
- Sidor, C. 1966 Prilog proučavanju biologije Necrophorus vespillo u Vojvodini. Zbornik Matice Srpske za Prirodne Nauke 31:62-71.
- _____. 1970 The results of investigations on the role of burying beetles (Necrophorus vespillo) in rabies transmission. Mikrobiologija 7(2):131-138.
- Smirnov, D.A. 1908 Review of the species variability of Necrophorus vespilloides Herbst. Rev. Russe Ent. 8(1):42-43.
- Southwood, T.R.E. 1978 Ecological methods, with particular reference to the study of insect populations. Chapman and Hall, London. 524 pp.
- Spicarova, N. 1971 Dwarf forms of burying beetles and cause of their development. Acta. Univer. Palack. Oloum. Fac. Rer. Nat. 34:193-197.
- _____. 1972 The emergence of burying beetles from the soil after their metamorphosis and its dependence on daylight. Acta. Univer. Palack. Oloum. Fac. Rer. Nat. 39:141-155.
- _____. 1973 Morfoplasticke pusebeni potravniho faktoru na potomstvonekolika druhu rodu Necrophorus F. Acta. Univer. Palack. Oloum. Fac. Rer. Nat. 43:297-335.
- _____. 1974 Diurnal activity of young individuals of Necrophorus germanicus. Acta. Univ. Palack. Oloum. Fac. Rer. Nat. 47:179-187.

- Springett, B.P. 1968 Aspects of the relationship between burying beetles, Necrophorus spp. and the mite Poecilochirus necrophori. J. Anim. Ecol. 37:417-424.
- Steele, B.F. 1927 Notes on the feeding habits of carrion beetles. J. N.Y. Ent. Soc. 35:77-81.
- Suzzoni, J. 1973 Histological study and function of the female reproductive system in Phosphuga atrata. Ann. Sci. Nat. Zool. Biol. Anim. 15(3):271-292.
- Théodoridès, J. and P.F. Van Heerdt 1950 Nouvelles recherches écologiques sur les Nécrophores: Comparaison des résultats du terrain avec du laboratoire (thermopreferendum et hygropreferendum). Physiol. Comp. Oecologia 2(4):297-309.
- Thomson, C.G. 1862 Skandinaviens Insectes. Lund. 392 pp.
- Thorne, R.F. 1972 Major disjunctions in the geographical ranges of seed plants. Quart. Rev. Biol. 47(4):365-411.
- Thunberg, C.P. 1789 Periculum entomologicum, quo characteres generum Insectorum proponit. Dissert. Resp. Tornes 10 Juni 1789, Upsaliae, Edman. pp. 1-16.
- Van Dyke, E.C. 1921 Coleoptera from the Pribilof Islands, Alaska. Proc. Cal. Acad. Sci. 11:156-166.
- 1928 The American species of Pteroloma (Coleoptera:Silphidae) and a new Japanese species. Bull. Brook. Ent. Soc. 23:19-26.
- Villers, C.J. 1789 Caroli Linnaei Entomologia. Lugduni, Piestre et Delamolliere. Bde 1:24u 765 pp. 3 Taf.
- Vlijm, L. and T.S. van Dijk 1967 Ecological studies on carabid beetles II. General patterns of population structure in Calathus melanocephalus (L.) at Schiermonnikoog. Z. Morphol. Okol. Tiere. 58:396-404.
- Waldow, U. 1973 The electrophysiology of a new carrion smell receptor and its role in the behavior of Necrophorus. J. Comp. Physiol. 83(4):415-424.
- Walker, F. 1886 Descriptions of Coleoptera. Lord's Naturalist in Vancouver Island II:309-321.
- Walker, T.J. 1957 Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecology 38(2):262-276.

- Weber, F. 1801 Observations entomologicae, continens
novarum quae condidit generum characteres et nuper
detectarum specierum descriptiones. Bibliopolii
Academici Novi. Kiliae. xii + 116 pp.
- Westhoff, F. 1881 Die Käfer Westfalens. Verh. Naturhist.
Ver. Preuss. Rheinl. 38 ((4.F.)8), Suppl. i-xxviii + 1-140.
- Wickham, H.F. 1895 On the larvae of Hydrocharis
obtusatus and Silpha surinamensis. Ent. News 6(5):
168-171.
- _____ 1902 Two new Silphidae from Colorado.
Can Ent. 34:180-181.
- Will, F. 1886 Zur Entwicklung des Necrophilus
subterraneus. Ent. Nachr. 12:14.
- Willoughby-Ellis, H. 1926 Forms of Necrophorus
mortuorum F. Ent. Rec. 38:3 pl. vi.
- Wilson, D.S. 1975 The adequacy of body size as a niche
difference. Amer. Nat. 109:769-784.
- Wood, D.M., P.T. Dang, and R.A. Ellis 1979 The
Mosquitoes of Canada (Diptera:Culicidae). Part 6.
The Insects and Arachnids of Canada. Agriculture
Canada Research Publication 1686. 390 pp.
- Young, O.P. 1978 Resource partitioning in a Neotropical
necrophagous scarab guild. PhD Thesis, University of
Maryland. 228 pp.
- Zetterstedt, J.W. 1824 Nya Svenska Insect-Arten.
Kungliga Svenska Vetenskaps Akademiens Handlingar.
1824:149-159.

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FIGURE 101: Proposed phylogeny of the genera of Silphini in North America, north of Mexico. Numbers refer to characters in Fig. 103. Black dots represent apomorphic character states.

FIGURE 102: Proposed phylogeny of Nicrophorus species in North America, north of Mexico. Numbers refer to characters in Fig. 103. Black dots represent apomorphic character states.

FIGURE 103A : RELATIVE PLEISIOMORPHY AND
APOMORPHY OF THE CHARACTERS OF THE NORTH
AMERICAN GENERA OF SILPHINI.

CHARACTER	PLEISIOMORPHIC STATE	APOMORPHIC STATE	EVIDENCE
1	presence of epistomal suture (Fig. 47)	absence of epistomal suture (Fig. 12)	outgroup comparison with Microphorini and Staphylinidae
2	apical position of stylus on coxite in female genitalia (Figs. 21,27)	preapical position of stylus (Figs. 22-26)	outgroup comparison with Microphorini and Staphylinidae
3	second abdominal sternite in larvae divided into 3 separate sclerites (Fig. 31)	second abdominal sternite entire (Fig. 32)	outgroup comparison with Staphylinidae, also highly concordant with other characters
4	lack of row of hairs behind the eyes (Fig.13)	presence of a row of hairs (Fig. 12)	outgroup comparison with Microphorini and Staphylinidae
5	absence of carina on inner face of metafemora	two carinae present	outgroup comparison, with Microphorini
6	sensory apparatus on second antennal segment in larvae with 1 cone or peg-like structure (Fig. 34)	sensory apparatus with 1 large or up to 10 small plates (Fig. 33)	outgroup comparison with Microphorini

FIGURE 103B : RELATIVE PLEISIOMORPHY
AND APOMORPHY OF THE CHARACTERS OF THE
NORTH AMERICAN SPECIES OF NICROPHORUS.

CHARACTER	PLEISIOMORPHIC STATE	APOMORPHIC STATE	EVIDENCE
1	absence of clypeal membrane (Fig. 12)	presence of clypeal membrane (Fig. 47)	outgroup comparison with Staphylinidae, Silphini
2	clavate antennae	antennae with four segmented club	outgroup comparison with Staphylinidae, Silphini and <u>Ptomascopus</u>
3	larvae with high degree of sclerotization	larvae with reduced sclerotization	outgroup comparison with Staphylinidae and Silphini
4	larvae with 6 ocelli per side of head	larvae with 1 ocellus per side of head	outgroup comparison with Silphini
5	cordate pronotum (Fig. 52)	orbicular pronotum (Fig. 51)	outgroup comparison with <u>Ptomascopus</u>
6	sternal pubescence brown	sternal pubescence yellow	outgroup comparison with Silphini and <u>Ptomascopus</u>
7	sclerotization of venter of last abdominal segment in the larvae complete (Fig. 28)	sclerotization reduced (Fig. 29)	outgroup comparison with Silphini and <u>Ptomascopus</u>
8	cordate pronotum (Fig. 52)	sub-quadrate pronotum	outgroup comparison with <u>Ptomascopus</u>

9	sclerotization of venter of last abdominal segment in the larvae reduced (Fig. 29)	sclerotization incomplete (Fig. 30)	outgroup comparison with Silphini and <u>Ptomascopus</u> , completion of transformation series
10	metepimeron glabrous or with sparse pubescence	metepimeron with dense yellow pubescence (Fig. 50)	outgroup comparison with Silphini and <u>Ptomascopus</u>
11	anterior face of procoxae with short hairs	anterior face of procoxae with long hairs	outgroup comparison with Silphini and <u>Ptomascopus</u>
12	base of urogomphi in the larvae with suture where it joins the tergite	suture lacking	outgroup comparison with Silphini and <u>Ptomascopus</u>
13	overwinter as an adult	overwinter as a prepupa	outgroup comparison with Silphini
14	lacking a bald spot behind the mesocoxae	bald spot present behind mesocoxae	outgroup comparison with <u>Ptomascopus</u>
15	subquadrate pronotum	quadrate pronotum (Fig. 53)	outgroup comparison with <u>Ptomascopus</u> , completion of transformation series
16	yellow metasternal pubescence	brown metasternal pubescence	highly concordant with other characters

FIGURE 104: THE NUMBER OF ADULT OICEIPTOMA NOVEBORACENSE TRAPPED DURING 1979 AND EARLY 1980

FIGURE 105 : THE NUMBER OF ADULT NECROPHILA AMERICANA TRAPPED DURING 1979 AND EARLY 1980

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FIGURE 116: THE NUMBER OF LARVAL SILPHIDAE TRAPPED DURING 1979 AND EARLY 1980

FIGURE 117: HABITAT ABUNDANCES

FIGURE 118: HABITAT ABUNDANCES

- 1 DECIDUOUS FOREST
- 2 FIELD/MEADOW
- 3 MARSH
- 4 CONIFEROUS FOREST

FIGURE 119: HABITAT ABUNDANCES

FIGURE 120: HABITAT ABUNDANCES

TABLE 1 : RELATIVE ABUNDANCE OF THE
SPECIES OF SILPHIDAE TRAPPED DURING
1979 AND EARLY 1980.

SILPHINI

<i>Oiceoptoma noveboracense</i>	1908
<i>Necrophila americana</i>	1477
<i>Thanatophilus lapponicus</i>	616
<i>Oiceoptoma inaequale</i>	51
<i>Necrodes surinamensis</i>	11

NICROPHORINI

<i>Nicrophorus tomentosus</i>	2306
<i>Nicrophorus orbicollis</i>	1849
<i>Nicrophorus sayi</i>	1123
<i>Nicrophorus marginatus</i>	125
<i>Nicrophorus vespilloides</i>	32
<i>Nicrophorus defodiens</i>	27
<i>Nicrophorus pustulatus</i>	26

TABLE 2: ECOLOGICAL CHARACTERISTICS
OF EASTERN CANADIAN SILPHINI.

SPECIES	CARCASS SIZE	REPRODUCTIVE PERIOD	HABITAT
<i>Oiceoptoma noveboracense</i>	medium- large	early spring	primarily forests
<i>Necrophila americana</i>	medium- large	late spring- early summer	primarily marsh
<i>Thanatophilus lapponicus</i>	medium- large	early spring & late summer	primarily meadow/field
<i>Oiceoptoma inaequale</i>	medium- large	early spring	primarily decid. forest
<i>Necrodes surinamensis</i>	large	early spring ?	??

TABLE 3: ECOLOGICAL CHARACTERISTICS
OF EASTERN CANADIAN Nicrophorus.

SPECIES	CARCASS SIZE	REPRODUCTIVE PERIOD	HABITAT
Nicrophorus tomentosus	small	mid-late summer	all
Nicrophorus orbicollis	small	late spring- early summer	primarily forests
Nicrophorus sayi	small	early spring	primarily conif. forests
Nicrophorus marginatus	small	early-late spring	meadow/field & marsh
Nicrophorus vespilloides	small	early-late spring	marsh
Nicrophorus defodiens	small	early-late spring	coniferous forest
Nicrophorus pustulatus	??	early-late spring ??	all ??

APPENDIX I :

Collections and curators from which
Canadian Silphidae were received and
examined during the present study.

COLLECTION	CURATOR
Agriculture Canada Research Station, Fredericton, N.B.	Dr. L.P. Magasi
Agriculture Canada Research Station, Harrow, Ont.	Dr. W.H. Foott
Agriculture Canada Research Station, Lethbridge, Alta.	Dr. K.W. Richards
Agriculture Canada Research Station, Saskatoon, Sask.	Dr. M.E. Taylor
Agriculture Canada Research Station, Winnipeg, Man.	Dr. G.L. Ayre
British Columbia Provincial Museum, Victoria, B.C.	Mr. R.A. Cannings
California Academy of Sciences, San Francisco, Calif.	Dr. D.H. Kavanaugh
Canadian National Collection, Ottawa, Ont.	Dr. J.M. Campbell
Cornell University, Ithaca, N.Y.	Dr. L.L. Pechuman
Field Museum of Natural History, Chicago, Ill.	Dr. E.H. Smith
Lakehead University, Thunder Bay, Ont.	Dr. R. Freitag

Lyman Entomological Museum, Ste. Anne de Bellevue, Que.	Mr. N. Duffy
Museum of Comparative Zoology, Cambridge, Mass.	Dr. A.F. Newton, Jr.
Nova Scotia Museum, Halifax, N.S.	Dr. B. Wright
Oregon State University, Corvallis, Ore.	Dr. M.D. Schwartz
Royal Ontario Museum, Toronto, Ont.	Dr. G.B. Wiggins
Saskatchewan Provincial Museum, Regina, Sask.	Mr. R.R. Hooper
United States National Museum, Washington D.C.	Dr. T.J. Spilman
University of Alberta, Edmonton, Alta.	Dr. G.E. Ball
University of British Columbia, Vancouver, B.C.	Mr. S.G. Cannings
University of Guelph, Guelph, Ont.	Mr. S.A. Marshall
University of Manitoba, Winnipeg. Man.	Dr. T.D. Galloway

University of Montreal,
Montreal, Que.

Dr. P.P. Harper

University of Saskatchewan,
Saskatoon, Sask.

Dr. D.M. Lehmkuhl

University of Western Ontario,
London, Ont.

Dr. W.W. Judd

PRIVATE COLLECTIONS

Robert S. Anderson, Ottawa, Ont.

John L. Carr, Calgary, Alta.

Stewart B. Peck, Ottawa, Ont.

Henry F. Howden, Ottawa, Ont.

APPENDIX II :

The number of adult male (M),
female (F), teneral males and females (T),
gravid females (G), and larval (L)
Silphidae trapped during 1979 and early 1980.
The number in brackets indicates the total
of adults of that species collected.

ОЦЕОТОМА НОВЕБОРАЦЕНСЕ (1908)

DATE	1A		1B		2A		2B		3A		3B		4A		4B	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
April	12-19	80														
	19-26	80														
	26-3	80														
May	3-10	80	13	9	31	31	20	35	6	7	4	1	3			
	10-17	80	1	2	1				3	2						
	17-24	80	5	2	13	15			6	15	2	5		1	2	
May	7-14	79	9	13	9	19	17	20	2	3	18	32	-	35	52	15
	14-21	79			1			1	1	1	2	3		10	20	1
	21-28	79									1					
June	28-4	79			4	5	7	10	4	11	9	10	3	2	13	19
	4-11	79	2					1				3	1	1	2	1
	11-18	79	2									1	1			
July	18-25	79														
	25-2	79														
	2-9	79	2	2	6	4	1		1			1		1	1	1
August	9-16	79	11	19	9	12			10	8	1	1	2	5	3	3
	16-23	79	16	17	15	14	2	4	4	5	7	2	2	10	5	4
	23-30	79	18	20	20	29		2	12	22	5	3	3	1	10	17
September	30-6	79	18	31	18	20	7	5	20	15	11	7	5	11	19	33
	6-13	79	7	6	2	5	1	2	2	4	2	1	2	3	7	18
	13-20	79	3	1	2	2			4	4	1		1	3	4	1
October	20-27	79	4	5	2	2			4	1	1		1	5	1	4
	27-3	79	1	1	2	1			2		2		1	2	3	1
	3-8	79	1	2	1				1			1		1	1	3
November	8-15	79														
	15-22	79														
	22-29	79														
December	29-6	79														
	6-13	79														
	13-20	79														
January	20-27	79														
	27-3	79														

44

OF / DE

DATE	1A L T G	1B L T G	2A L T G	2B L T G	3A L T G	3B L T G	4A L T G	4B L T G
April								
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19-26 80								
26-3 80								
May								
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17-24 80								
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28-4 79								
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11-18 79								
18-25 79								
25-2 79								
July								
2-9 79								
9-16 79								
16-23 79								
23-30 79								
30-6 79								
August								
6-13 79								
13-20 79								
20-27 79								
27-3 79								
September								
3-8 79								
8-15 79								
15-22 79								
22-29 79								
29-6 79								
October								
6-13 79								
13-20 79								
20-27 79								
27-3 79								

THANATOPHILUS LAPPONICUS (616)

DATE	1A	1B	2A	2B	3A	3B	4A	4B
	M	F	M	F	M	F	M	F
April								
12-19 80								
19-26 80								
26-3 80			6 2	2	1			
May								
3-10 80			11 13	3 2	1			
10-17 80				1	2			
17-24 80			1 1	1	2			
May								
7-14 79			3 10		6 5			
14-21 79			1					
21-28 79				1 1				
28-4 79			5 6	24 16	11 8	1 1		
June				2 2		5 1		
4-11 79								
11-18 79			1 2	1				
18-25 79				1 2	2 4	5 2		
25-2 79								
July								
2-9 79				1 1	2 2	4 4		
9-16 79			7 4	10 19	11 9	6 6		
16-23 79			4 1	18 35	6 12	4 5		
23-30 79			3 2	20 17	4 6	1 1		
August								
30-6 79			1 1	1 4	8 5	2 1		
6-13 79			4 3	23 16	10 5	4 5		
13-20 79			2	7 4	7 1	2 1		
20-27 79				1 2	4 2	2 2		
27-3 79				2 6	3 1	2 2		
September								
3-8 79			1 2	4 2	11 11	7 5		
8-15 79			1		1			
15-22 79								
22-29 79								
29-6 79								
October								
6-13 79								
13-20 79								
20-27 79								
27-3 79								

	1A	1B	2A	2B	3A	3B	4A	4B
	L T G	L T G	L T G	L T G	L T G	L T G	L T G	L T G
April								
12-19 80								
19-26 80								
26-3 80				1				
3-10 80			7	2				
10-17 80								
17-24 80								
May								
7-14 79			19	5	2			
14-21 79			1					
21-28 79								
28-4 79			5	11	1	6	1	
4-11 79				1			1	
11-18 79			2					
18-25 79				3	2	6		
25-2 79					1	2		
2-9 79			1	7	2	1	2	3
9-16 79			14	6	2	2		
16-23 79			3	5	5	1	2	
23-30 79				2	4	2		
30-6 79				1	2	1	2	4
6-13 79			2	1	3	4	1	
13-20 79				3				
20-27 79								
27-3 79			2	2	1			
September								
3-8 79			1	2	4	3		
8-15 79						1		
15-22 79								
22-29 79								
29-6 79								
October								
6-13 79								
13-20 79								
20-27 79								
27-3 79								

DATE	1A	1B	2A	2B	3A	3B	4A	4B
April								
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	L
	L	T	G	L	T	G	L	T
	T	G	L	T	G	L	T	G
	G	L	T	G	L	T	G	

NECRODES SURINAMENSIS (11)

DATE	1A	1B	2A	2B	3A	3B	4A	4B
April	M	F	M	F	M	F	M	F
12-19 80								
19-26 80								
26-3 80								
May								
3-10 80								
10-17 80								
17-24 80								
May								
7-14 79								
14-21 79								
21-28 79								
28-4 79								
June								
4-11 79								
11-18 79								
18-25 79								
25-2 79								
July								
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September								
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29-6 79								
October								
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20-27 79								
27-3 79								

1A 1B 2A 2B 3A 3B 4A 4B
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DATE
April 12-19 80
19-26 80
26-3 80
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10-17 80
17-24 80
May 7-14 79
14-21 79
21-28 79
28-4 79
June 4-11 79
11-18 79
18-25 79
25-2 79
July 2-9 79
9-16 79
16-23 79
23-30 79
30-6 79
August 6-13 79
13-20 79
20-27 79
27-3 79
September 3-8 79
8-15 79
15-22 79
22-29 79
29-6 79
October 6-13 79
13-20 79
20-27 79
27-3 79

MICROPHORUS TOMENTOSUS (2306)

DATE	1A	1B	2A	2B	3A	3B	4A	4B
	M	F	M	F	M	F	M	F
April								
12-19 80								
19-26 80								
26-3 80								
May								
3-10 80								
10-17 80								
17-24 80								
May								
7-14 79								
14-21 79								
21-28 79								
28-4 79								
June								
4-11 79								
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18-25 79								
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August								
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September								
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15-22 79								
22-29 79								
29-6 79								
October								
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20-27 79								
27-3 79								

DATE	1A	1B	2A	2B	3A	3B	4A	4B
April								
	12-19 80							
	19-26 80							
	26-3 80							
May								
	3-10 80							
	10-17 80							
	17-24 80							
May								
	7-14 79							
	14-21 79							
	21-28 79							
	28-4 79							
June								
	4-11 79							
	11-18 79							
	18-25 79							
	25-2 79							
July								
	2-9 79	1	3	1	1	2	2	1
	9-16 79	3		3		1		2
	16-23 79			3		3		
	23-30 79	2	2	3	2	2		
	30-6 79	3						
August								
	6-13 79	2			1	1	1	5
	13-20 79						7	4
	20-27 79				3		4	6
	27-3 79					1	5	
September								
	3-8 79							
	8-15 79							
	15-22 79							
	22-29 79							
	29-6 79							
October								
	6-13 79							
	13-20 79							
	20-27 79							
	27-3 79							

MICROPHORUS SAYI (1123)

DATE	1A		1B		2A		2B		3A		3B		4A		4B	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
April																
12-19 80																
19-26 80																
26-3 80	2	3	1	1	4	1			1				9	10	28	29
3-10 80	3	1	1	1	3					1			1	10	6	7
10-17 80	6	2	6	2			1	1					2	3	12	10
17-24 80	3	1	4	5			1		2	1			10	14	10	18
May																
7-14 79	7	7	20	11	7	5	8	4	2				22	29	22	26
14-21 79	6	4	5	4									11	15	23	30
21-28 79	6	1	3	1					2				7	3	3	7
28-4 79			6	10			2	1		1			19	23	5	12
4-11 79	5	10	1	1					1		2		27	24	5	13
11-18 79	3			2									11	8	1	6
18-25 79	1	1											2	2	3	2
25-2 79	1												5	3	3	6
July													3	4	2	2
2-9 79	1												1	1	3	3
9-16 79			1		1								2			1
16-23 79	2	2	2			1							1	2	1	
23-30 79	14	10	9	8	1								2	9	9	9
30-6 79	23	17	8	14	1	1							4	3	2	1
August																
6-13 79	1	1	1	4					2				1	2	2	3
13-20 79	2	3		2									8	11	13	11
20-27 79	2	1	2		1								6	4	4	2
27-3 79	1	3									1		3	2	5	5
September																
3-8 79	1	2	1	1					2		1		1	1	1	5
8-15 79	1												5	7	-	-
15-22 79	1	1	1	3									2	1	1	2
22-29 79	1			2			1						1	1	1	1
29-6 79	2			1							1		1	1	1	1
October																
6-13 79																
13-20 79	2	1	1	1									2	1	1	1
20-27 79																
27-3 79	1	1		2									1	1	1	1

DATE	1A	1B	2A	2B	3A	3B	4A	4B
April	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G	L T G L T G L T G L T G L T G L T G
12-19 80								
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September								
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20-27 79								
27-3 79								
October								
6-13 79								
13-20 79								
20-27 79								
27-3 79								

MICROPHORUS MARGINATUS (125)

DATE	1A	1B	2A	2B	3A	3B	4A	4B
	M	F	M	F	M	F	M	F
April								
12-19 80								
19-26 80								
26-3 80								
May								
3-10 80								
10-17 80								
17-24 80								
May								
7-14 79			2	1				
14-21 79								
21-28 79								
28-4 79			3	1	2	2		
June								
4-11 79			1					
11-18 79			1	1	2	1		
18-25 79			1					
25-2 79								
July								
2-9 79								1
9-16 79			1	1	3			
16-23 79			3	2	4	7		
23-30 79			2			4		
30-6 79				2	1			
August								
6-13 79			2	2	2			
13-20 79			1					
20-27 79			1	3	5	11	2	1
27-3 79								2
September								
3-8 79			3		3	2	1	
8-15 79					1	2	4	4
15-22 79								6
22-29 79								
29-6 79								1
October								
6-13 79								
13-20 79								
20-27 79								
27-3 79								1

LA 1A 1B 2A 2B 3A 3B 4A 4B
L T G L T G L T G L T G L T G L T G L T G L T G

DATE	LA	1A	1B	2A	2B	3A	3B	4A	4B
April 12-19 80									
19-26 80									
26-3 80									
May 3-10 80									
10-17 80									
17-24 80									
May 7-14 79									
14-21 79									
21-28 79									
28-4 79									
June 4-11 79									
11-18 79									
18-25 79									
25-2 79									
July 2-9 79									
9-16 79									
16-23 79									
23-30 79									
30-6 79									
August 6-13 79									
13-20 79									
20-27 79									
27-3 79									
September 3-8 79									
8-15 79									
15-22 79									
22-29 79									
29-6 79									
October 6-13 79									
13-20 79									
20-27 79									
27-3 79									

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