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ACARINA (ARTHROPODA: ARACHNIDA) ASSOCIATED WITH SELECTED MICHIGAN SILPHIDAE (COLEOPTERA)

By

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ABSTRACT

ACARINA (ARTHROPODA: ARACHNIDA) ASSOCIATED WITH SELECTED MICHIGAN SILPHIDAE (COLEOPTERA)

By

Wayne Alva Yoder

The systematics of the Acarina associated with Michigan *Nicrophorus*, *Silpha*, and *Necrodes* are presented. Beetles were collected from cans baited with carrion of various types.

A total of 11,743 mites were identified from 246 beetles. Eleven species of mites were collected in numbers of forty or more, including four of *Poecilochirus*, three of *Macrocheles*, and four of Anoetidae. Four new species are described: *Poecilochirus longisetosa*, *P. silphaphila*, *Macrocheles breviseta*, and *M. necrophoraphila*.

Each species of mite is discussed in relation to: (1) total numbers collected, (2) range in numbers on each beetle species, (3) percent of beetles infested, (4) average number of mites/beetle from those beetles having mites, and (5) site preferences on beetles.

Wayne Alva Yoder

The biology and phoretic behavior of anoetids and Poecilochirus found on Silphidae are discussed. A life history of Macrocheles necrophoraphila is given, including comments on its biology.

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INTRODUCTION

Mites were first reported on silphid beetles from Europe by Müller (1859). Since that time scattered papers have reported the occurrence of several mite families on carrion beetles, the Silphidae, especially on the genus *Nicrophorus*. Despite these reports, no one has undertaken a systematic study of the mites associated with Silphidae to this time. The first part of this study deals with the systematics of Acarina associated with Silphidae in Michigan. Part II examines the interactions of these mites with silphid beetles, and some aspects of their biology.

PART I

A SYSTEMATIC SURVEY OF THE ACARINA ASSOCIATED WITH MICHIGAN SILPHIDAE

LITERATURE REVIEW

Six genera of mites representing three families have been found commonly associated with Michigan Silphidae. The genus *Poecilochirus* (Parasitidae) was originally described by G. and R. Canestrini (1882) from specimens on a *Carabus*. Since then Vitzthum (1930), Neumann (1943), Holzmann (1969), and Micherdzinski (1969) have published systematic works pertaining to *Poecilochirus*. The keys in Holzmann (1969) and Micherdzinski (1969) include all six valid species of *Poecilochirus* described until this study was initiated.

Macrocheles (Macrochelidae), another genus of mites common on silphids, was described by Latreille (1829), but major systematic studies on the genus did not follow until Berlese (1903, 1910, 1918). However, most of his publications lack illustrations, and are somewhat limited in usefulness. More recent illustrated systematic articles on *Macrocheles* include those of Evans and Browning (1956), Ryke and Meyer (1958), Bregatova and Koroleva (1960), Filipponi and Pegazzano (1962, 1963), Krantz (1962), Evans and Hyatt (1963), and Krantz and

Fillipponi (1964). Keys included in Evans and Browning (1956), Bregetova and Koroleva (1960), and the illustrations in Evans and Hyatt (1963) make these publications most useful in identifying species.

Deutonymphs of the genera Histiostoma, Pelzneria, Spinanoetus, and Anoetus (Family Anoetidae) are frequently found on Michigan Silphidae. The two major systematic treatises dealing with this family are Scheucher (1957) and Hughes and Jackson (1958). Keys in both of these publications are very useful in determining species.

MITE METHODS

In order to determine mites to species, specimens must be specially prepared for microscopic examination with a compound microscope. Beetles for this study were collected in 80 percent ethyl alcohol. Removal of mites from the beetles was also done in 80 percent ethyl alcohol by use of a dissecting microscope at nine and twenty-seven magnifications. For all mites, the beetle host was recorded, along with the site of attachment, date, and locality information. Mites were stored in small vials until prepared further for slides, or treated immediately as indicated in the following paragraphs.

Mesostigmata, including species of *Poecilochirus*, *Macrocheles*, and Uropodidae, were dissected before placing on microslides. Prior to dissection, specimens were placed into a spot plate in a solution of lactophenol made up of lactic acid-50 parts, liquid phenol-25 parts, and water-25 parts. Spot plates were placed in an oven and heated at 44°C from two to twelve hours, until the pleural membranes of the mites were softened sufficiently for dissection.

Dissections were accomplished using either 27 or 54 magnifications of the dissecting microscope. To do this a mite submerged in lactophenol in a spot plate was grasped lightly with a jewelers forceps so that its pleural membrane was facing upward. A minuten needle was then used to pierce the pleural membrane joining the dorsal and ventral shields of the mite. For *Poecilochirus* and Uropodidae this initial piercing of the membrane was done between the dorsal shield and the peritreme, because the peritreme is more closely attached to the ventral half of the mite. For *Macrocheles*, the initial piercing was between the peritreme and a leg attachment, since the peritreme fastens directly to the dorsal shield at its anterior end. After the initial piercing, the grip with the forceps was released, and a second minuten needle was inserted into the opening along with the first needle. By using the two needles in a series of lightly opposing pulls toward opposite ends of the mite, the membrane joining dorsal and ventral shields was slowly cut. Experience proved that cutting the membrane along one side of the mite at a time worked best. After the membrane was cut on both sides, the dorsal and ventral halves of the body separated easily. A bit more care had to be taken in cutting the membrane around the anterior end of the mite above the mouth parts, because the shields in this area were less sclerotized, and easily broken. Also, in Macrocheles the peritremes which attach anteriorly can easily be torn loose from the dorsal shield unless caution is exercised in cutting the membrane.

After the dorsal and ventral halves were separated the internal organs were scraped from each half with needles. Then the halves were transferred to another depression in the spot plate to be rinsed with distilled water. (The "eye" end of a small sewing needle made a useful instrument for such transfers.) Two or three rinses were made to remove lactophenol from the mite, as any remaining lactic acid caused crystals to form when a mite was mounted in Hoyer's solution.

When the rinses were completed the mite halves were transferred to a drop of Hoyer's solution in the center of a 0.8x75x25 mm. microscope slide. At this point the ventral half of the mite was held lightly against the slide with a needle while a second minuten needle was used to push the chelicerae from the body. The needle was inserted into the posterior end of a chelicera, and pushed anteriorly until the chelicera was loosened from the body. Then the mite halves were oriented with the external side upward and a 0 thickness, 12 mm. diameter cover glass applied.

Two labels were applied to all mite slides. The left label bears family and species names, and the right label contains all date, locality, and host information.

After examining a considerable number of *Poecilochirus*, it became possible to identify species without dissection. From this time on, described species, namely *Poecilochirus necrophori* Vitzthum and *P. subterraneus* (Müller), were simply stored in small vials in 80 percent ethyl alcohol with date, locality, and host information rather than mounted on slides.

Although mites of the Anoetidae do not require dissection for determination, they do require special chemical treatment before mounting in Hoyer's solution. Anoetids tend to accumulate a crystalline material in body spaces which makes them opaque and conceals finer cuticular details which must be seen for determination. Two methods of removing crystals were used successfully.

The first involved heating the hypopi in Keifer's clearing agent as suggested by Hughes and Jackson (1958). This treatment required placement of hypopi into the clearing agent in an oven at 44°C over night. Following this they were transferred to a slide into a drop of Hoyer's mountant.

The second method involved heating hypopi in 0.5-1.0 N HCl for one to two hours at 44°C. Following the acid treatment, mites were rinsed once in distilled water and mounted in a drop of Hoyer's solution on a slide. Usually 15-20 anoetid hypopi were put on one slide because they are relatively small and they frequently numbered several hundred at one site of attachment on a beetle. On examination with the compound microscope, it was not unusual to find that more than one species had been placed on the same slide; but because of the small size of the mites, species characteristics could not be seen with a dissecting microscope.

After mounting all species of mites in Hoyer's solution, the slides were allowed to "cure" at room temperature for one to two weeks before placing them in an oven at 44°C to dry for two to three more weeks. When the drying period was complete, slides were removed from the oven, allowed to cool, and the cover glasses ringed with a compound to seal them. Most commonly fingernail polish was used as a ringing compound. Several named brands of ringing compounds were tried but discarded as being unsatisfactory.

Depositions of type specimens are given under each species. The remainder of the slides are either retained by the author for future investigations, or are deposited in the Entomology Museum of Michigan State University.

In the account which follows, the systematics are presented for the mites found on 246 silphid beetles collected in Michigan. Beetles from which each mite species was collected are given along with date and locality data. More detailed information regarding percent of beetles infested, numbers of mites/beetle, and site preferences of mites on beetles are reported in Part II of this thesis. A total of 11,743 mites were taken from the 246 beetles. Individual species examined were as follows: 40 Nicrophorus tomentosus Weber, 17 N. americanus Olivier, 6 N. vespilloides Herbst, 7 N. pustulatus Herschel, 9 N. orbicollis Say, 13 N. marginatus Fabricius; 54 Silpha americana Linnaeus, 53 S. noveboracensis Forster, 16 S. lapponica Herbst, 13 S. inaequalis Fabricius; 18 Necrodes surinamensis Fabricius. Approximately equal numbers of male and female beetles were examined, except in the case of N. vespilloides, where only six males were collected.

ORDER ACARINA

Family Parasitidae

Poecilochirus necrophori Vitzthum

Poecilochirus necrophori Vitzthum, 1930. Zool. Jahrb., Syst. 60: 381.

Gamasoides eurasiaticus Trägardh, 1937. In part (only the Lapplandic deutonymph, not the south Mongolian), Ark. Zool., 29: 1.

nec. *Poecilochirus necrophori* Vitzthum sensu Neumann, 1943 = *P. carabi* Canestr. (after Holzmann, 1969. Acarologie, Folge 13:7).

Poecilochirus necrophori has been rather widely reported from *Nicrophorus* in Europe by the above authors. Additional reports include those of Theodorides (1955) from France, Belozerov (1957) from the U.S.S.R., and Mrciak (1964) from Finland.

P. necrophori collected in Michigan correspond to European descriptions of the species. The total of 448 deutonymphs were distributed on the silphids as follows:

Nicrophorus tomentosus (124), N. marginatus (37), N. americanus (1), N. vespilloides (52), N. pustulatus (168), N. orbicollis (30), Silpha americana (17), S. noveboracensis (18), and Necrodes surinamensis (1).

Beetles bearing P. necrophori were collected in the following counties. N. tomentosus: Eaton, Ingham, Kalamazoo, St. Joseph, Shiawassee (19 June-18 Oct.). N. americanus: Bay (14 Oct.). N. marginatus: Jackson, Kalamazoo (16 June-14 July). N. vespilloides: Ingham, Shiawassee (4 June-4 Oct.). N. pustulatus: Kalamazoo, St. Joseph (31 May-23 Aug.). Silpha americana: Ingham, Kalamazoo, St. Joseph (9 July-9 Sept.). S. noveboracensis: Kalamazoo (28 June-14 July). Necrodes surinamensis: Kalamazoo (9 July).

All P. necrophori collected were found active on the beetles, and frequently were seen leaving and returning to the beetles as described by previous authors.

Poecilochirus subterraneus (J. Müller)

Porrhostaspis subterranea J. Müller, 1859. Jahrb. mahr. schles. Gesellsch. Brunn: 176.

Parasitus subterraneus sensu Oudemans, 1902. Ent. Ber. 1: 238.

Gamasoides subterraneus sensu Berlese, 1903. Redia 1: 258.

<u>Poecilochirus</u> <u>subterraneus</u> Vitzthum, 1930. Zool. Jahrb., Syst. 60: 381.

In addition to reports by the above European authors, <u>P</u>. <u>subterraneus</u> has been reported by Theodorides (1955) from France. In all cases the mites were taken from <u>Nicrophorus</u>. <u>P</u>. <u>subterraneus</u> collected in Michigan from three species of <u>Nicrophorus</u> are in agreement with previously published descriptions. A total of 346 deutonymphs were distributed on silphids as follows: <u>N</u>. <u>pustulatus</u> (183), <u>N</u>. <u>tomentosus</u> (159), <u>N</u>. <u>vespilloides</u> (4).

Beetles bearing <u>P</u>. <u>subterraneus</u> were collected in the following counties. <u>N</u>. <u>pustulatus</u>: Kalamazoo (23-28 June). <u>N</u>. <u>tomentosus</u>: Clinton, Eaton, Kalamazoo, St. Joseph, Shiawassee (19 June-23 Aug.). <u>N</u>. <u>vespilloides</u>: Ingham, Shiawassee (4-7 June).

Most <u>P</u>. <u>subterraneus</u> were found active on beetles. It was not uncommon, however, to find them under the elytra or metathoracic wings of the beetles.

<u>Poecilochirus</u> <u>longisetosa</u> new species

<u>Deutonymph</u> (Figures 1-3): Brownish-amber color. With two closely joined dorsal shields; total length of dorsal shields 0.844-0.974 mm. (average 0.949 mm.); width 0.598-0.775 mm. (average 0.723 mm.) at level of

most posterior marginal setae on podonotal shield; podonotal shield with 20 pairs of setae with relative lengths and distribution as in Figure 1, all 20 pairs commonly pilose to plumose, or with the two smaller anterior marginal pairs sometimes smooth; opisthonotal shield mostly with 13 or 14 pairs of pilose to plumose setae, although one seta frequently is added or subtracted along the right or left margin of the shield by variations in its sclerotization; both dorsal shields finely punctate, and with heavier scale-like to reticulate markings.

Dorsal integument in live specimens commonly extending beyond the opisthonotal shield up to one-third its length; dorsal integument with numerous simple to slightly setose setae.

Sternal shield 0.314-0.360 mm. long (average 0.343 mm.); width 0.184-0.238 mm. (average 0.219 mm.) at level of second set of pores; entire shield lightly punctate, and with heavier network of markings (Figure 2); transverse band most heavily sclerotized part of shield, with anterior marginal continuation of band to setae 1 nearly as heavily sclerotized; with posterior marginal continuation of sclerotization somewhat irregular, but generally lighter than either the anterior continuation or the transverse band, extending beyond sternal setae 4, but not quite to posterior edge of shield. Sternal setae lightly pilose.

Anal shield elliptical to oval, lightly punctate, marked posteriorly with six rows of tooth-like markings; somewhat concentric lines around anal valves; with three simple setae about the length of the anal valves.

Peritrematal shield unattached to other shields, extending anteriorly to between the two small marginal setae of the podonotal shield, and posteriorly to mid-level of coxae III. Presternal shields a somewhat straightened s-shape, their length extending nearly half the width of the sternal shield; tritosternum with length of laciniae nearly equal or up to one-third longer than base; gnathosoma with 14 rows of deutosternal teeth, seven of which may be less well developed.

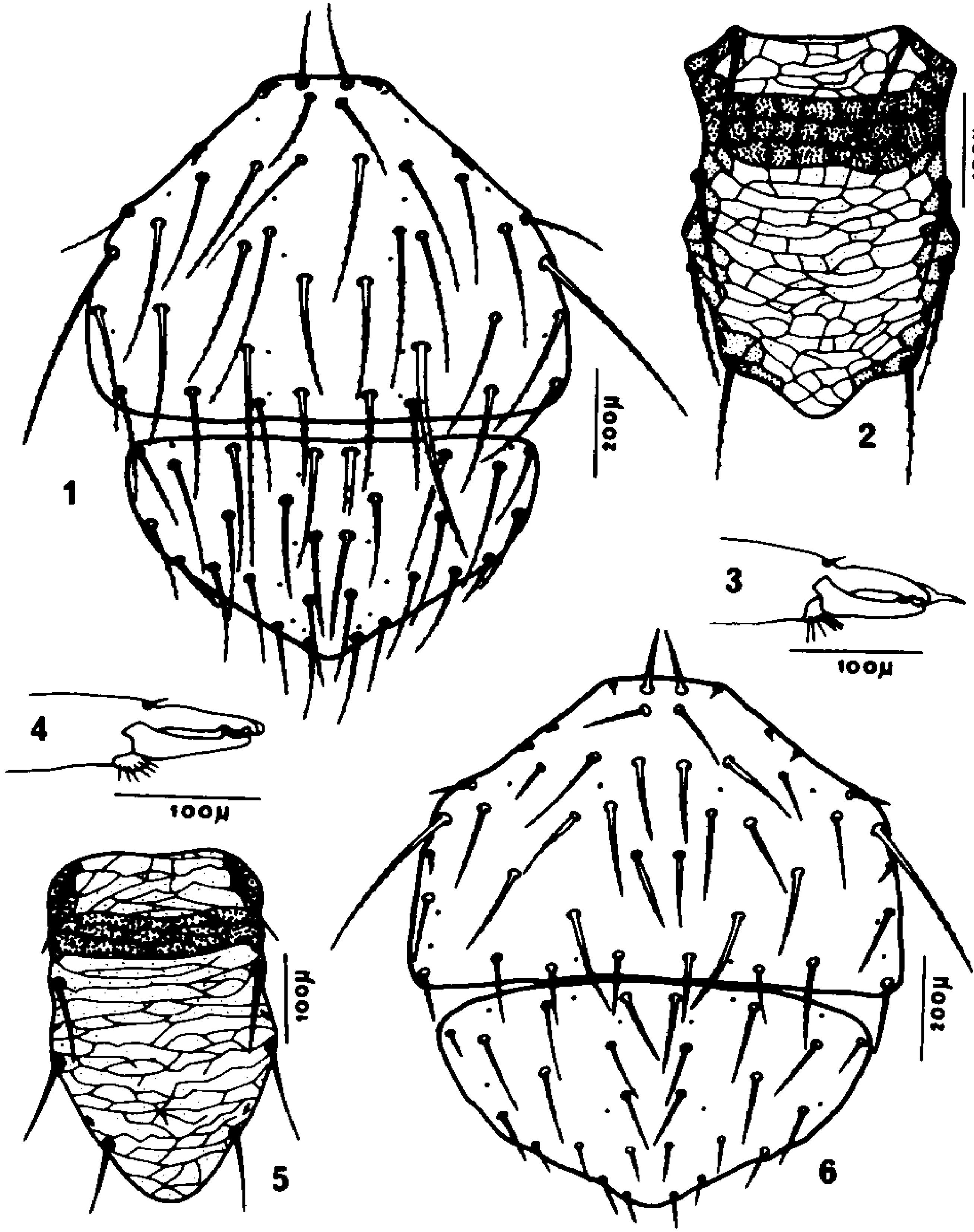
Fixed digit of chelicera with a distal membranous apophysis shaped as in Figure 3; with two well developed teeth ventro-medially and two ventro-laterally; movable digit with one large subterminal tooth; dorsal seta of fixed digit simple.

Approximate lengths of legs (excluding pretarsi) are: I-1.166 mm.; II-0.836 mm.; III-0.936 mm.; IV-1.258 mm.

Diagnosis: The deutonymph of P. longisetosa is easily distinguished from other Poecilochirus deutonymphs by the long dorsal setae, the pattern of the heavier sclerotization of the sternal shield, and the

Figs. 1-3. _Poecilochirus longisetosa_ new species, deutonymph. 1. Dorsal shields. 2. Sternal shield. 3. Chelicera.

Figs. 4-6. _Poecilochirus silphaphila_ new species, deutonymph. 4. Chelicera. 5. Sternal shield. 6. Dorsal shields.


1
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2
100µ
3
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4
100µ
5
100µ
6
200µ

form of the membranous apophysis of the fixed digit of the chelicerae.

Material: Holotype deutonymph with the following data: Kalamazoo Co., Michigan; Kellogg Biol. Sta.; T1S: R9W:S9; W. A. Yoder, coll.; ex. Nicrophorus marginatus male WY346, loose in coll. vial; 3 July 1969. Sixteen paratype deutonymphs from same locality as holotype, also ex. Nicrophorus marginatus, 30 June-14 July 1969. One paratype deutonymph from Ingham Co., Michigan; T4N: R1E:S4; G. Manley, coll.; ex. Nicrophorus vespilloides male WY358; loose in coll. vial; 4 June 1971.

The holotype and paratypes will be deposited in the collection of the U.S. National Museum, Washington, D.C. Paratypes will also be deposited in the following institutions: British Museum (Natural History), London; The Institute of Acarology, Ohio State University, Columbus; Michigan State University, Entomology Museum, East Lansing.

Poecilochirus silphaphila new species

Deutonymph (Figures 4-6): Brownish-amber color. With two closely joined dorsal shields; total length of dorsal shields 0.675-0.874 mm. (average 0.790 mm.); width 0.598-0.752 mm. (average 0.677 mm.) at level of most posterior marginal setae on podonotal shield; podonotal shield with 22 pairs of pilose setae, the three smaller anterior marginal pairs often appearing simple (Figure 6); opisthonotal shield mostly with 13 pairs of simple to pilose setae, although one or two setae are frequently added to the right or left margin of the shield by variations in its extent of sclerotization; setae of both dorsal shields relatively wide at base and tapering uniformly to the tip, or widening to about one-third the distance from the base and then tapering uniformly to the tip; both dorsal shields finely punctate and with heavier scale-like markings in irregular rows.

Dorsal integument of live specimens commonly extending beyond the opisthonotal shield by up to one-fourth its length; dorsal integument with numerous simple, occasionally pilose setae.

Sternal shield 0.261-0.307 mm. long (average 0.285 mm.); width 0.161-0.199 mm. (average 0.179 mm.) at level of second set of pores; entire shield lightly punctate and with heavier network of markings (Figure 5); transverse band of sternum more heavily sclerotized, with its anterior prolongation to sternal setae 1 nearly as heavily sclerotized. Sternal setae acuminate.

Anal shield oval, lightly punctate, marked posteriorly with six rows of tooth-like structures; light, somewhat concentric lines around anal valves; with three setae about one-fourth the length of anal shield.

Peritrematal shields unattached to other shields, extending anteriorly to between the two most anterior small marginal setae and posteriorly to rear edge of coxae III. Presternal shields somewhat straightened s-shape, their length equal to 0.6 the width of sternal shield; tritosternum with length of laciniae nearly equal to base; gnathosoma with 14 rows of deutosternal teeth, six to eight of which may be less well developed.

Fixed digit of chelicera with rather small distal membranous cap as in Figure 4; with ridge-like tooth ventro-medially and ventro-laterally, or ridge sometimes appearing as two somewhat divided teeth; movable digit with a large submedian tooth and two smaller teeth distad to it; dorsal seta of fixed digit simple.

Approximate lengths of legs (excluding pretarsi) are: I-1.005 mm.; II-0.690 mm.; III-0.805 mm.; IV-1.089 mm.

Diagnosis: Deutonymph of P. silphaphila is easily separated from deutonymph of P. necrophori which it most closely resembles and from other Poecilochirus deutonymphs by small distal membranous cap of the chelicera, length and shape of dorsal setae, and sclerotization pattern of sternal shield.

Material: Holotype deutonymph with the following data: Eaton Co., Michigan; Pine Lake, Olivet College Biol. Preserve; T1N:R5W:S31; W. A. Yoder, coll.; ex.

Nicrophorus tomentosus female WY211, loose in coll. vial; 23 Aug. 1970. Fifteen paratype deutonymphs from same locality as holotype, also ex. *Nicrophorus tomentosus*, 23 Aug. 1970. Three paratype deutonymphs from Marquette Co., Michigan; Van Riper State Park near Michigamme; T4N:R30W:S24; D. D. Wilder, coll.; ex. *Nicrophorus vespilloides* male WY316, loose in coll. vial, 25 July 1971. Seven paratype deutonymphs from Mackinac Co., Michigan; Cedarville, T41N:R1E:S6; D. D. Wilder, coll.; ex. *Nicrophorus orbicollis* male WY317, loose in coll. vial, 23 July 1971.

The holotype and paratypes will be deposited in the collection of the U.S. National Museum. Paratypes will also be deposited in the following institutions: British Museum (Natural History), London; The Institute of Acarology, Ohio State University, Columbus; Michigan State University, Entomology Museum, East Lansing.

Family Macrochelidae

Macrocheles dimidiatus Berlese

Macrocheles dimidiatus Berlese, 1918. Redia 13: 115.

Only two speciments of this species were found on Michigan Silphidae, one on *S. americana* from Jackson Co., 31 July 1970, and one on *N. americanus* from Midland

Co. Their occurrence may have been "accidental" as other species of Macrocheles were found in considerably larger numbers. Previous records (Evans and Hyatt, 1963) are mostly from Phaneus.

Macrocheles vespillo Berlese

Macrocheles vespillo Berlese, 1918. Redia 13: 115.

This species was described from mites taken from two species of Nicrophorus from Texas. Krantz (1971) also has specimens from N. marginatus from Iowa. The 111 M. vespillo females collected were distributed on Michigan silphids as follows: N. americanus (97), N. marginatus (13), N. tomentosus (1). Nearly all specimens were attached under the wings of the beetles.

Beetles bearing M. vespillo were collected in the following counties. N. americanus: Kalamazoo (22 June-21 July). N. marginatus: Eaton, Jackson (16 June-24 Aug.). N. tomentosus: Eaton (24 Aug.).

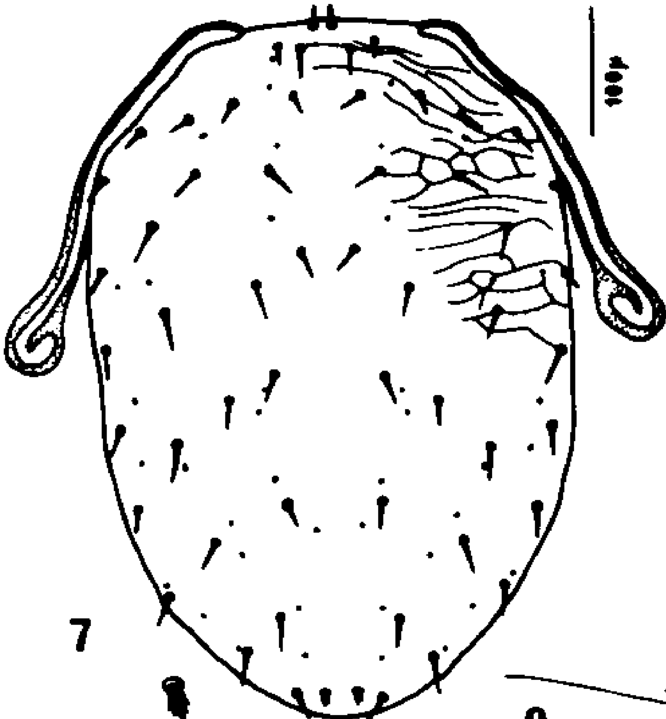
Macrocheles breviseta new species

Female (Figures 7-9): Pale brown. Single dorsal shield 0.468-0.552 mm. long (average 0.509 mm.), width 0.291-0.368 mm. (average 0.323 mm.) at level of setae Mg_2; finely punctate and with heavier punctations and

Figs. 7-9. *Macrocheles breviseta* new species, female. 7. Dorsal shield with enlarged detail of seta D_8. 8. Ventral shields. 9. Chelicera.

Figs. 10-12. *Macrocheles necrophoraphila* new species, female. 10. Dorsal shield with enlarged detail of seta D_8. 11. Ventral shields. 12. Chelicera.

Figs. 13-14. *Macrocheles necrophoraphila* new species, larva. 13. Venter of opisthosoma. 14. Dorsum of opisthosoma.



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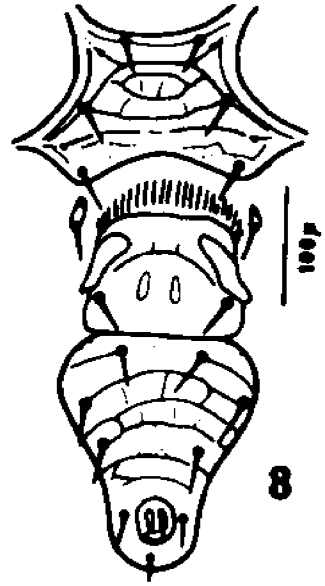

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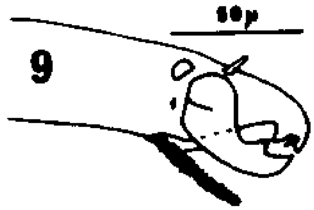

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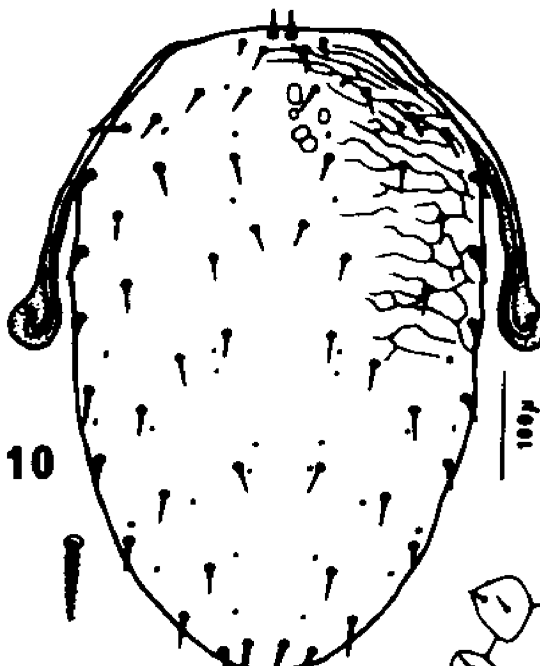

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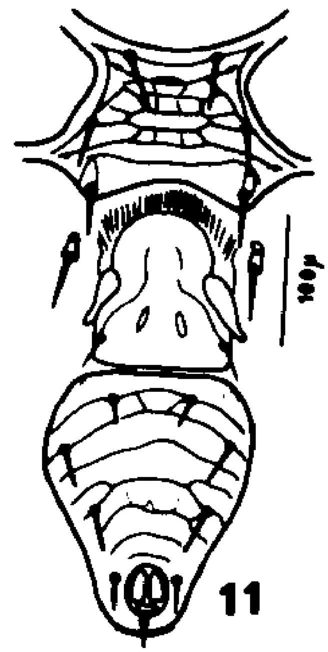

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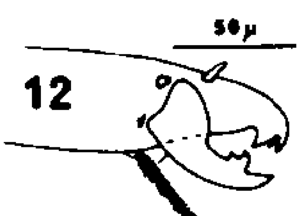

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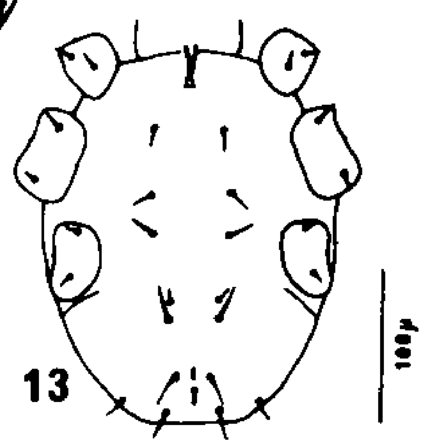

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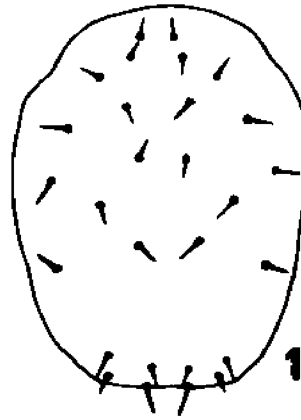

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lines forming reticulate pattern over entire shield; with 28 pairs of setae, all acuminate except D_1 and D_8; D_1 acuminate to somewhat blunted, D_8 shorter and rather palmate; relative lengths and distribution of setae as in Figure 7. Integumental setae acuminate, mostly not as long as dorsal setae. Peritrematal shields fused anteriorly to dorsal shield, extending to anterior edge of shield near setae M_1, and posteriorly to about the middle of coxae IV.

Sternal shield 0.086-0.098 mm. long at midline (average 0.091 mm.); width 0.101-0.114 mm. (average 0.108 mm.) at narrowest point between sternal setae 1 and 2 (Figure 8); sternal setae acuminate; metasternal setae like sternals and inserted on small irregular metasternal shields.

Epigynial shield finely punctate with transverse crescent of markings near the midline (Figure 8); the pair of acuminate epigynial setae somewhat shorter than sternals.

Ventrianal shield ornamented as in Figure 8; 0.144-0.193 mm. long (average 0.177 mm.); width 0.107-0.141 mm. (average 0.128 mm.) at level between ventrianal setae 1 and 2; with nine acuminate setae which are only about 0.67 the length of sternals. Ventral integument with numerous simple setae, most of which are shorter than ventrianals.

Tectum tripartite, with central element divided distally. Gnathosoma with five rows of deutosternal teeth with five to seven teeth per row; two transverse ridges without teeth anterior to the toothed rows.

Movable digit of chelicera with one large submedian tooth and a smaller tooth touching it proximally (Figure 9); fixed digit with one large subterminal tooth and sometimes a small subterminal tooth distad to it; dorsal seta of fixed digit simple.

Approximate lengths of legs (excluding pretarsi) are: I-0.376 mm.; II-0.360 mm.; III-0.330 mm.; IV-0.437 mm.

Males and immatures: Unknown.

Diagnosis: *M. breviseta* appears to represent a new species in the broad concept of the *M. dimidiatus* group. Females can be separated from other *Macrocheles* females by the dorsal chaetotaxy (all setae simple, except D_8 palmate and shorter), and the pattern of sternal and ventrianal ornamentation.

Material: Holotype female with the following data: Eaton Co., Michigan; Pine Lake, Olivet College Biol. Preserve; T1N:R5W:S31; W. A. Yoder, coll.; ex. *Nicrophorus tomentosus* female WY274, loose in coll. vial; 24 Aug. 1970. Sixteen paratype females from same locality as holotype, ex. *Nicrophorus marginatus*, 24 Aug. 1970. Two paratype females from Kalamazoo Co., Michigan; Kellogg

Biol. Sta.; T1S:R9W:S9; W. A. Yoder, coll.; ex. Nicrophorus marginatus, loose in coll. vial; 30 June 1969 and 14 July 1969. Five paratype females from Kalamazoo Co., Michigan; Kellogg Biol. Sta., T1S:R9W:S22; ex. Nicrophorus marginatus female WY35; loose in coll. vial; 9 July 1969.

The holotype and paratypes will be deposited in the collection of the U.S. National Museum, Washington, D.C. Paratypes will also be deposited in the following institutions: British Museum (Natural History), London; The Institute of Acarology, Ohio State University, Columbus; Oregon State University, Corvallis; Michigan State University, Entomology Museum, East Lansing.

Macrocheles necrophoraphila new species

Egg: Ovoid, translucent white, longest dimension 0.221-0.255 mm.

Larva (Figures 13-14): White, weakly sclerotized, lacking discernable shields. Idiosoma 0.255-0.298 mm. long (average 0.272 mm.), width 0.190-0.230 mm. (average 0.212 mm.) at level of legs II. Dorsum bearing 14 pairs of simple setae (Figure 14) and two pairs of additional setae inserted ventrally.

Venter (Figure 13) bearing three pairs of sternal setae, and two pairs of opisthogastric setae, of which posterior pair are much longer than anterior pair. Anus represented by slit; paranal setae nearly twice as long as postanal seta; anal shield indicated by very light line on several specimens. Tritoseternum with base about equal in length to laciniae. Gnathosoma and chelicerae somewhat less sclerotized than legs.

Legs, especially II and III are short and stumpy; approximate lengths of legs (excluding pretarsi) are: I-0.233 mm.; II-0.212 mm.; III-0.196 mm.

Protonymph (Figures 19-20): White, somewhat more heavily sclerotized than larva. Dorsum covered by two shields; podonotal shield 0.421-0.476 mm. long (average 0.452 mm.), 0.383-0.506 mm. wide (average 0.447 mm.) at level between two most posterior marginal setae; podonotal shield bears 11 pairs of setae all of which may be acuminate or with several pairs spinose as in Figure 20. Opisthonotal shield 0.176-0.222 mm. long (average 0.202 mm.), 0.245-0.322 mm. wide (average 0.284 mm.) at anterior end; bears six pairs of setae, all but most medial of which are plumose as in Figure 20; posterior edge of shield more heavily sclerotized in a crescent shape.

Sternal shield very weakly sclerotized, gradually widening to insertions of sternal setae 2 (Figure 19), bearing three pairs of simple setae. Anal shield somewhat more sclerotized than sternal shield, with three simple setae. Ventral integument surrounding anal shield with five pairs of simple setae.

Gnathosoma with five rows of weakly developed deutosternal teeth. Approximate lengths of legs (excluding pretarsi) are: I-0.255 mm.; II-0.218 mm.; III-0.200 mm.; IV-0.261 mm.

Deutonymph (Figures 21-22): White, all shields more sclerotized than protonymph, but considerably less than female or male. Dorsum covered by single shield, with wide incisions at margin indicating podonotal and opisthonotal areas (Figure 22); 0.353-0.407 mm. long (average 0.372 mm.); 0.169-0.230 mm. wide (average 0.207 mm.) at level of setae Mg_2 (chaetotaxy follows Evans and Browning, 1956); dorsal shield bears 18 pairs of podonotal setae, 10 pairs of opisthonotal setae, same complement found in adult males and females; all dorsal setae except D_8 acuminate, with D_8 shorter and plumose, approaching shape of those in adults.

Sternal shield (Figure 21) 0.160-0.187 mm. long (average 0.176 mm.), 0.080-0.092 mm. wide (average 0.086 mm.) between sternal setae 2 and 3; with four pairs of acuminate setae.

Anal shield irregularly rounded, with three acuminate setae. Ventral integument with 11 pairs of acuminate setae distributed as in Figure 21.

Approximate lengths of legs (excluding pretarsi) are: I-0.345 mm.; II-0.276 mm.; III-0.238 mm.; IV-0.345 mm.

<u>Female</u> (Figures 10-12): Pale brown. Dorsal shield 0.506-0.567 mm. long (average 0.538 mm.) and 0.291-0.345 mm. wide (average 0.320 mm.) at level of setae Mg_2; with fine punctations and moderately heavy reticulate pattern over entire shield (Figure 10). Bearing 28 pairs of setae of which 26 are acuminate; setae D_1 acuminate to slightly blunted; D_8 pilose to plumose; distribution and relative lengths of dorsal setae as in Figure 10. Integumental setae acuminate and of same length as dorsal setae. Peritrematal shields fused anteriorly to dorsal shield, extending anteriorly to between setae M_1 and M_2, and posteriorly to between coxae III and IV.

Sternal shield (Figure 11) 0.083-0.095 mm. long (average 0.089 mm.) at midline and 0.098-0.120 mm. wide (average 0.109 mm.) at narrowest point between sternal setae 1 and 2; fine punctations over entire surface, ornamented by fine lines and moderately large punctures as in Figure 11; more heavily sclerotized around coxae II. Sternal setae acuminate; metasternal setae like sternals, inserted on small irregular metasternal shields.

Epigynial shield finely punctate, with fine markings as in Figure 11, epigynial setae smooth, slightly shorter than sternals.

Ventrianal shield 0.172-0.206 mm. long (average 0.189 mm.), and 0.129-0.153 mm. wide (average 0.140 mm.)

at level of second pair of setae; ornamented by light lines as in Figure 11; with nine smooth setae which may be only 0.75 as long as sternal setae. Ventral integumental setae simple, somewhat shorter than any of those on the ventral shields.

Tectum tripartite, with central element distally divided. Gnathosoma bears five rows of deutosternal teeth, in front of which are two transverse ridges without teeth.

Movable digit of chelicera bearing one large subterminal tooth and smaller tooth proximally to it (Figure 12); fixed digit with one large subterminal tooth and smaller one distad to it; internal cheliceral brush extending about 0.75 the length of movable digit; dorsal seta of fixed digit simple.

Approximate lengths of legs (excluding pretarsi) are: I-0.391 mm.; II-0.360 mm.; III-0.337 mm.; IV-0.460 mm.

Male (Figures 15-18): Pale brown. Dorsal shield 0.414-0.491 mm. long (average 0.455 mm.) and 0.245-0.330 mm. wide (average 0.281 mm.) at level of setae Mg_2; finely punctate and ornamented as in Figure 16; bearing 28 pairs of setae, most of which are acuminate; setae D_1, D_8, L_1, Mg_1, and Mg_{10} rather plumose, Mg_8 and Mg_9 simple to plumose; distribution and relative setal lengths as in Figure 16. Peritrematal shields joined anteriorly to dorsal shield.

Figs. 15-18. *Macrocheles necrophoraphila* new species, male. 15. Ventral shield. 16. Dorsal shield. 17. Leg II (excluding pretarsus). 18. Chelicera.

Figs. 19-20. *Macrocheles necrophoraphila* new species, protonymph. 19. Venter of opisthosoma. 20. Dorsum of opisthosoma.

Figs. 21-22. *Macrocheles necrophoraphila* new species, deutonymph. 21. Venter of opisthosoma. 22. Dorsum of opisthosoma.

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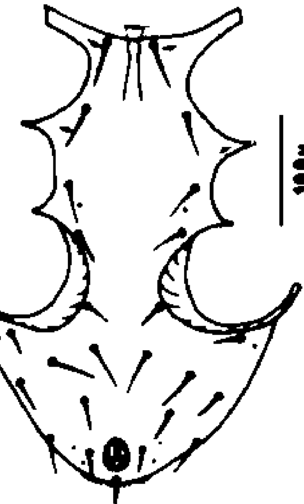

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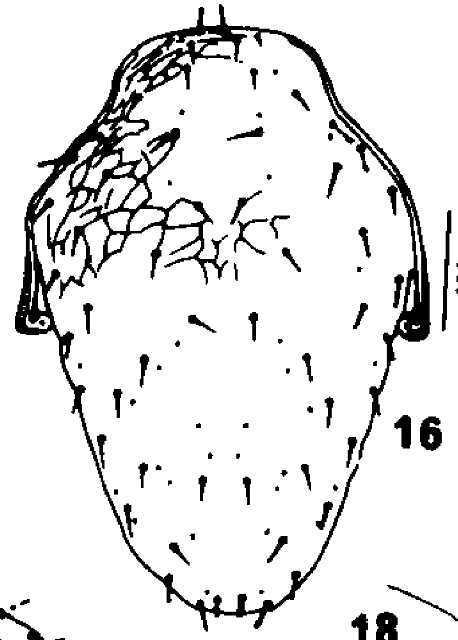

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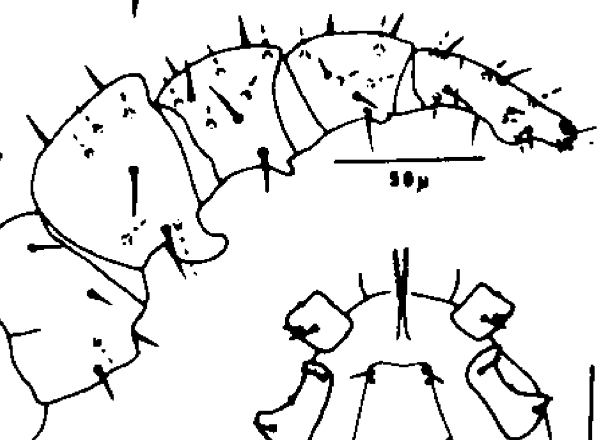

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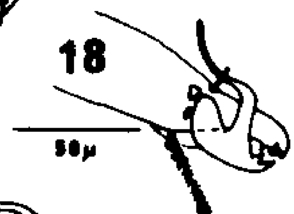

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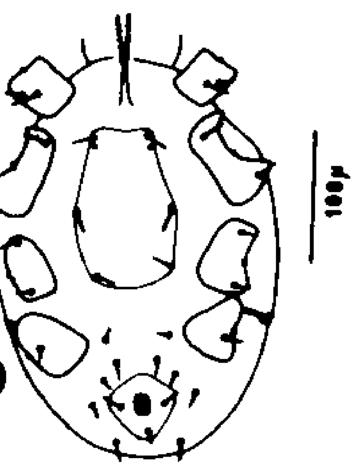

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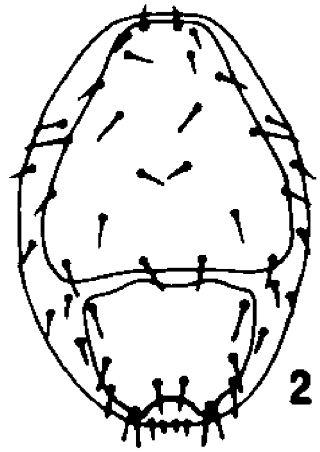

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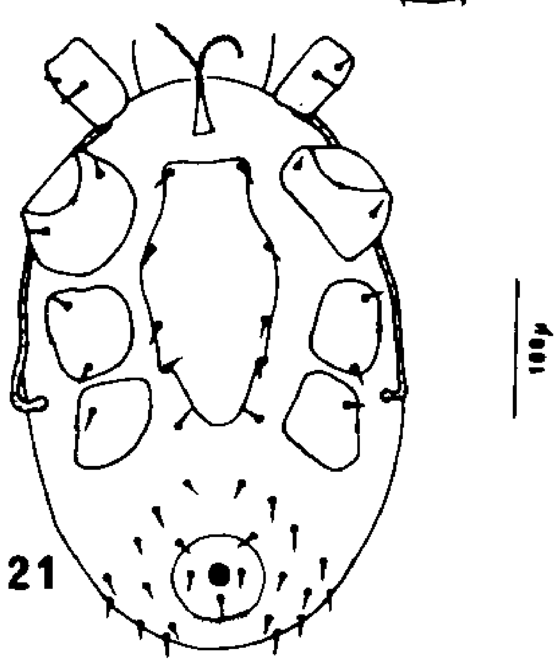

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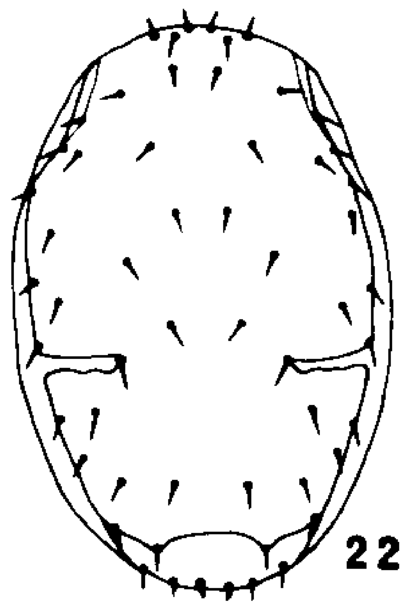

Venter (Figure 15) fused as one solid shield; length 0.330-0.391 mm. (average 0.352 mm.), width at level of sternal setae 3 equals 0.253-0.314 mm. (average 0.285 mm.); with 25 acuminate setae of approximately equal length and similar to female; shield lightly ornamented at anterior end and around anal area. Male genital opening boardered anteriorly by a sclerotic crescent.

Deutosternal teeth and tectum as in female. Movable digit of chelicera bears curved spermatophoral process whose length exceeds digit (Figure 18) and a well developed tooth distad to process; fixed digit with one well developed tooth and two less well developed teeth distad to it; dorsal seta of fixed digit slightly bifurcated; cheliceral brush extending slightly beyond base of spermatophoral process.

Approximate lengths of legs (excluding pretarsi) are: I-0.391 mm.; II-0.322 mm.; III-0.291 mm.; IV-0.391 mm. Leg II bears spur-like process on posterior surface of the femur and small spur on genu and tibia (Figure 17); leg IV also bears spur on posterior aspect of femur.

Diagnosis: *M. necrophoraphila* appears to represent a new species in the *M. subbadius* group, and is close to *M. merdarius*. Females can be separated from other *Macrocheles* females by dorsal chaetotaxy (all setae simple, except D_8 pilose), and pattern of sternal and ventrianal ornamentation.

Material: Holotype female with the following data: Eaton Co., Michigan; Pine Lake, Olivet College Biol. Preserve; T1N:R5W:S31; W. A. Yoder, coll.; ex. Nicrophorus orbicollis female WY215, on pleural membrane I-II; 23 Aug. 1970. Allotype male reared in laboratory from female collected in Ingham Co., Michigan; Michigan State University, Toumey Woodlot; T4N:R1W:S30; W. A. Yoder, coll.; ex. Nicrophorus orbicollis male WY313; 31 May 1971. Paratypes include ten females, eleven males, eight larvae, 18 protonymphs, 16 deutonymphs. Three paratype females with same information as holotype. Three paratype females from Kalamazoo Co., Michigan; W. K. Kellogg Biol. Sta.; T1S:R9W:S22; ex. Nicrophorus orbicollis male WY352, on terga III-5; 23 Aug. 1969. All remaining paratype females, males, larvae, protonymphs, and deutonymphs reared in laboratory from same original female as allotype male.

The holotype, allotype, and paratypes of all instars will be deposited in the collection of the U.S. National Museum. Paratypes of all instars will also be deposited in the following institutions: British Museum (Natural History), London; The Institute of Acarology, Ohio State University, Columbus; Oregon State University, Corvallis; Michigan State University, Entomology Museum, East Lansing.

Family Anoetidae

Woodring and Moser (1970) discussed the validity of the generic names *Anoetus* and *Histiostoma*. I have chosen to follow Scheucher (1957) in separating *Histiostoma* from *Anoetus* on the basis of the suckers (or discs) on coxal plates I and III of *Histiostoma* hypopi where *Anoetus* hypopi bear setae or setal sockets in place of discs.

Histiostoma cyrtandrae (Vitzthum)

Anoetus cyrtandrae Vitzthum, 1931. Arch. Hydrol. 2: 59.

Histiostoma cyrtandrae Hughes & Jackson, 1958. Va. Jour. Sci. 9: 59.

Hypopi collected from coxal cavities of single *N. pustulatus* (Eaton Co., 24 Aug.) and *N. orbicollis* (Kalamazoo Co., 23 Aug.) compare well with specimens of Hughes' collection except for a slight difference in the shape of the tarsal seta ta 16 (Heinemann, 1972).

Pelzneria crenulata (Oudemans)

Anoetus crenulatus Oudemans, 1909. Ent. Ber. 3: 23.

Histiostoma crenlatus Buitendijk, 1945. Zool. Meded. XXIV: 281.

Pelzneria crenulata Scheucher, 1957. Beitrage zur Systematik und Ökologie mitteleuropäischer Acarina: 347.

Scheucher (1957) established the genus *Pelzneria* to include those hypopi in which the anterior edge of the notogaster is crenulate, which separates them from the undifferentiated notogaster as found in *Histiostoma*. Both species which she placed in the genus were collected from *Nicrophorus* in Europe.

The 6511 *P. crenulata* hypopi collected made it the most frequently occurring mite on Michigan Silphidae. They were distributed on the beetles as follows: *N. tomentosus* (3411), *N. americanus* (967), *N. pustulatus* (782), *N. marginatus* (449), *N. vespilloides* (79), *N. orbicollis* (10), *S. noveboracensis* (574), *S. inaequalis* (190), *S. americana* (30), *S. lapponica* (6), *Necrodes surinamensis* (21). *P. crenulata* were regularly attached to the underside of the elytra, to the terga, and in coxal cavities.

Beetles bearing *P. crenulata* were collected in the following counties. *N. tomentosus*: Clinton, Eaton, Ingham, Kalamazoo, St. Joseph, Shiawassee (19 June-8 Oct.). *N. americanus*: Kalamazoo, Midland (22 June-21 July). *N. pustulatus*: Eaton, Kalamazoo, Macomb (22 June-24 Aug.). *N. marginatus*: Eaton, Jackson, Kalamazoo (16 June-24 Aug.). *N. vespilloides*: Ingham, Marquette (4 June-4 Oct.). *N. orbicollis*: Eaton, Kalamazoo, Macomb, St. Joseph (31 July-25 Aug.). S. noveboracensis: Kalamazoo, Shiawassee, Van Buren (9 April-3 July). S. lapponica: Kalamazoo (9-14 July).

Spinanoetus pelznerae Scheucher

Spinanoetus pelznerae Scheucher, 1957. Beitrage zur Systematik und Ökologie mitteleuropäischer Acarina: 358.

Michigan hypopi agree well with Scheucher (1957), the only previous report. She collected the species from Nicrophorus, Thanatophilus, and Geotrupes from Europe.

The 2679 S. pelznerae hypopi collected made it the second most common mite on Michigan silphids. They were distributed on the beetles as follows: S. noveboracensis (2149), S. inaequalis (79), S. americana (14), S. lapponica (1), Necrodes surinamensis (422), Nicrophorus marginatus (9), N. tomentosus (4), N. americanus (1). Its most common attachment sites were the abdominal terga and the underside of the elytra.

Beetles bearing S. pelznerae were collected in the following counties. S. noveboracensis: Clinton, Ingham, Kalamazoo, Shiawassee, Van Buren (9 April-22 July). S. inaequalis: Kalamazoo, Van Buren (9 April-5 July). S. americana: Kalamazoo, St. Joseph (28 June-31 July). S. lapponica: Kalamazoo (3 July). Necrodes surinamensis: Benzie, Kalamazoo (28 June-24 July). N. marginatus:

Eaton, Jackson, Kalamazoo (16 June-24 Aug.). _N_. _tomentosus_: Kalamazoo, Shiawassee (19 June-30 July). _N_. _americanus_: Midland (8 July).

Anoetus _turcastanae_ Oudemans

Anoetus _turcastanae_ Oudemans, 1917. Ent. Ber. 4: 391.

Hypopi from five species of _Nicrophorus_, _S_. _americana_, and _Necrodes_ _surinamensis_ from Michigan agree with Oudemans (1917) figures, except the Michigan specimens do not have the sterna st3 and st4 fused as they are in his drawings. The majority of individuals of this species were attached to the abdominal sterna and terga, undersides of the elytra, or coxal cavities.

The total 604 _A_. _turcastanae_ were distributed on silphids as follows: _N_. _marginatus_ (593), _N_. _americanus_ (4), _N_. _vespilloides_ (1), _N_. _orbicollis_ (1), _N_. _tomentosus_ (2), _S_. _americana_ (2), _Necrodes_ _surinamensis_ (1).

Beetles bearing _A_. _trucastanae_ were collected in the following counties. _N_. _marginatus_: Eaton, Jackson, Kalamazoo (16 June-24 Aug.). _N_. _americanus_: Kalamazoo, Midland (22 June-8 July). _N_. _vespilloides_: Ingham (4 Oct.). _N_. _orbicollis_: Kalamazoo (23 Aug.). _N_. _tomentosus_: Kalamazoo (30 June-14 July). _S_. _americana_: St. Joseph (31 July). _Necrodes_ _surinamensis_: Kalamazoo (14 July).

ACARINA OCCURRING INFREQUENTLY ON MICHIGAN SILPHIDAE

Mites collected infrequently from Silphidae during this study are listed in Table 1. As most were taken only occasionally, they were considered to be "accidental" and not regularly associated with the beetles. Their identifications and names follow Krantz (1970). The following brief comments concerning their biology are offered only as possible explanations for the collection of each group on the beetles.

TABLE 1. Acarina occurring infrequently on Michigan Silphidae.

	Number of specimens
Suborder Mesostigmata	
Rhodacaridae	3
Ascaidae	1
Uropodidae	31
Suborder Prostigmata	
Pyemotidae	2
Hydrachnidae	1
Suborder Astigmata	
Acaridae	7
Saproglyphidae	4
Labidophoridae	1
Analgidae	1
Unidentifiable	2
Suborder Cryptostigmata	2

Rhodacaridae and Ascaidae are frequently collected from leaf litter. It is not unusual that several individuals were found active on the dorsum of silphids. The Uropodidae are generally thought to be fungivores as adults, and deutonymphs often attach to the cuticle of insects by an anal pedicel (Krantz, 1970). The phoresy by deutonymphs of this group on Silphidae may merit further examination, as seen by the 31 sessile specimens collected. The systematics of the group are a problem at this time, however, and could not be included in the scope of this study.

Representatives of the Pyemotidae, Acaridae, and Saproglyphidae are all commonly found in decaying materials, and many are fungivorous. It is not surprising that they might be found in habitats common to Silphidae.

The single labidophorid found was taken from a <u>Silpha noveboracensis</u> collected on a dead muskrat. Labidophorid hypopi have been reported from muskrats (Krantz, 1970), and perhaps this specimen crawled from the muskrat to the beetle.

One hydrachnid was taken from a <u>Nicrophorus orbicollis</u> collected at an ultraviolet light trap. It probably came to the light on an aquatic insect, and there found its way onto the silphid. The two Cryptostigmata taken from beetles were probably normal soil inhabitants of an area where collections were made from ground level baited cans.

PART II

THE BIOLOGY OF ACARINA ASSOCIATED WITH MICHIGAN SILPHIDAE

INTRODUCTION

The decomposition of dead animals is a natural process involving a succession of organisms. Under given conditions a dead body will be reduced quickly from a fresh state to dry remains of skin, cartilage, hair, and bones. But any major disturbance of the natural order could have serious consequences upon this succession. Since carrion is a breeding site for many insect vectors of disease (Faust, *et al.*, 1962; and Symes, *et al.*, 1962), a potentially serious public health hazard could result if carrion degradation did not occur quickly. For example, Stonier (1964) reported outbreaks of enormous populations of flies following the atomic bombings of Hiroshima and Nagasaki. United States diseases bred or carried by animals on carrion include dysenteries, scrub typhus, and plague, among others (Symes, *et al.*, 1962).

Carrion beetles, the Silphidae, by their eating of carrion and fly larvae living in carrion, chewing of tissues, and intermixing of decay bacteria, play an important role in the decomposition of dead animals. However, the common association of mites with silphids has remained largely unstudied, and their possible importance in animal degradation has been, therefore, unknown. For this reason, I undertook a study to examine the acarine fauna found on Michigan silphid species of the genera Silpha, Necrodes, and Nicrophorus, and the types of associations between mites and these beetles.

LITERATURE PERTAINING TO SILPHIDAE AND CARRION DECOMPOSITION

Numerous studies have reported the insects found on carrion, including studies which have considered the succession of insects over time. Jaques (1915) examined the fish-feeding Coleoptera from the beaches of Cedar Point, Ohio. Six species of silphids contributed to the rapid reduction of fish to bones and scales. He found that fish removed from the beach to shady places under trees attracted Coleoptera in much larger numbers, representing more species. Fuller (1934) discussed the insect inhabitants of carrion in Australia and their succession during different seasons. She was particularly interested in calliphorid flies and their possible biological control.

Howden (1950), following beetle succession on carrion, found 98 species from 14 families. She stated that at least half of these were primarily predacious on dipterous larvae and puparia; the other half were necrophagous or of dubious food habits. The moisture condition, size, and shape of carcasses were important in determining what beetles were found on them. Scaly, cornified or unclothed skins inhibited insect succession, while tender skin or skin with hair or feathers facilitated it. Also the larger the natural and artificial openings into the carcass, the more rapid was the succession.

Bornemissza (1957) wrote concerning succession of carrion frequenting organisms on guinea pigs in Australia, and examined the influence of carrion on the typical soil fauna of a woodland. Decomposition of carrion had a maried effect on the normal soil fauna to a depth of 14 cm., causing many normal soil arthropods to leave the carrion area. Reinvasion of the carrion zone by soil arthropods remained incomplete one year after original carrion placement.

Walker (1957) investigated arthropods attracted to unbaited cans, and those baited with cornmeal, cantaloupe, and fish in four different habitat areas. Four species of Silphidae were attracted only to the fish, and no silphid species was attracted to fish in an abandoned field with little cover.

Reed (1958) studied dog carcass communities in Tennessee. Adults of six silphid species were found on carcasses in the earlier, moist stages of decay. Few adults were found on carcasses in a dry stage, but larvae were found only on carcasses in drier stages. He observed, as Walker, that insect populations in general were smaller at carcasses in non-wooded areas than in wooded. Ordinarily succession proceeded more rapidly in pastures than in wooded areas.

Payne (1965) compared decomposition of baby pig carcasses decaying with a normal succession of arthropods to decomposition when arthropods were excluded from the carrion by screen. Carrion screened from insects decomposed and dried very slowly, taking on a mummified appearance which it retained as long as two months. While 90 percent of the carrion open to insects was removed in six days, 20 percent of mummified carcasses unexposed to insects remained after 100 days. Maggots of the Sarcophagidae, Calliphoridae, and Muscidae were the primary insects responsible for removal of carrion. Silphidae fed on the maggots as well as the carrion.

Payne and Crossley (1966) gave a list of the animal species found in Payne's 1965 study. A total of 522 animal species were listed, including six species of Nicrophorus, three of Silpha, and Necrodes surinamensis. Their relative abundance was indicated for the five stages of carrion decay. They summarized the role and habits of the major groups found on carrion, and divided them into five groups on the basis of feeding and habits. Mites were treated only casually in this study, with five genera having been collected. Payne, et al. (1968) examined arthropod succession and decomposition of pigs buried at 50-100 cm. in clay soil of a forest. No

Silphidae were collected under these conditions. Twenty-six of the 48 arthropod species collected were found only on buried pigs and not on dead pigs above the ground surface. Buried carcasses were reduced to 20 percent of their original weight in six to eight weeks.

Shubeck (1969) baited for silphids with chicken legs. He found no apparent succession of Silphidae during the time required for total decomposition of the meat, because the amounts were small. He did note a seasonal pattern, however, with Silpha novebaracensis being the species dominant in numbers during early summer, but virtually disappearing by mid-summer. Nicrophorus orbicollis and N. tomentosus on the other hand increased steadily and became dominant in numbers by middle summer.

The biology of the Silphidae has been studied in some detail. According to Pukowski (1933), Gleditsch (1752) was first to report of the striking behavior of Nicrophorus to bury small dead animals. Pukowski (1933) has written the most extensive article about the genus, reporting on six German species of Nicrophoorus. This rather extensive article discusses the attraction of Nicrophorus to carrion, their mating, burial and preparation of carrion for oviposition, development of immatures including brood care by the parents, and the biology of Nicrophorus in general.

Balduf (1935) gives an English summary of Pukowski's work on Nicrophorus. In addition he summarizes information about American species of Nicrophorus and Silpha. His work along with that of Leech (1934) and Milne and Milne (1944) present the most extensive publications concerning the biology of American silphids. Leech (1934) studied the life history of Nicrophorus conversator in British Columbia, describing burying behavior, development of immatures, and feeding. Milne and Milne (1944) concentrated primarily on burying behavior of six species of Nicrophorus in Ontario.

The feeding habits of Nicrophorus, Silpha, and Necrodes have been observed by numerous authors, and can be classified into three main categories: (1) those feeding on carrion, (2) those feeding on fly larvae living on carrion, (3) those feeding on both carrion and maggots. It is quite possible that many species should be placed into the third category, as few authors have experimented to see whether the beetles actually show a preference for either carrion or maggots, or will feed only on one. Authors who have reported silphids feeding on carrion only include Leech (1934), Dorsey (1940), and Cole (1942). Species in these studies included Silpha americana, S. inaequalis, S. noveboracensis, Nicrophorus orbicollis, N. tomentosus, and N. conversator. Larvae of S. americana and S. inaequalis were noted as feeding on drier carrion than adults.

More authors have observed Silphidae feeding on fly larvae than on carrion. Among these are Bell (1873), Selous (1911), Jaques (1915), Goe (1919), Illingworth (1926), and Steele (1927). Species noted feeding on maggots were Silpha americana, S. rugosa, S. sinuata, S. inaequalis, S. noveboracensis, Necrodes littoralis, Nicrophorus orbicollis, N. tomentosus, N. vespillo, and N. humator. Clark (1895) stated that Nicrophorus marginatus and Silpha lapponica fed almost exclusively on larvae. Illingworth also noted that Silpha and Nicrophorus larvae ate some sarcophagid pupae, and Steele observed that Nicrophorus orbicollis ate the smaller N. tomentosus when they were put together in the same container.

Five species are common to the separate groupings above and therefore, can probably be said to feed regularly on both carrion and fly maggots. In addition to these five, Reed (1958) lists Necrodes surinamensis as feeding on both. But Clark (1895) and Davis (1915) state that this species indicates a definite preference for fly larvae.

Several investigators have examined the orientation of Silphidae to carrion. Selous (1911) noticed that most of the beetles attracted to carrion came in the direction opposite from which the wind was blowing, suggesting that they sensed an odor carried by the wind. Abbott (1927, 1927a) studied the role of the antennae and palpi of *Nicrophorus* for detection of carrion in cages. His studies were not controlled as well as Dethier's (1947), however, who concluded that the antennae bear the olfactory receptors for long-range perception, and the palpi bear receptors suited to perception within thirty inches. Dethier (1947) also demonstrated by mark, release, and recapture methods that the three apical segments of the antennae possess the receptors for long range olfactory perception. Ernst (1969) has studied the fine structure of the olfactory hairs (sensilla basiconica) located on these three club segments.

Shubeck (1968) used a mark, release, and recapture method to study whether orientation of *S. noveboracensis*, *N. orbicollis*, and *N. tomentosus* to carrion was random or non-random. He concluded that rate of return of *S. noveboracensis* from 5 to 75 meters was apparently due to random wandering and not related to orientation to odors. There was a significant increase in ability to return to carrion below two meters. *S. noveboracensis* was fourteen times more apt in returning to carrion from five meters than *N. orbicollis* and *N. tomentosus* combined, whereas in Dethier (1947) about equal returns were noted. Dethier also obtained a greater overall return to silphids to carrion, which Shubeck suggested was due to Dethier's suspension of carrion five feet above ground. Odors from the carrion were thus more easily carried by wind currents attracting silphids.

Shubeck (1970) studied attraction of silphids to carrion baited cans on the ground versus cans suspended 1.5 meters in the air. He found that N. tomentosus was attracted primarily to cans in the air, while N. orbicollis, S. americana, and S. noveboracensis were attracted primarily to ground cans.

Ratcliffe and Luedtke (1969) compared the attractiveness to Silphidae of carrion covered with tree bark versus uncovered. Three species were more attracted to covered carrion and four species were more attracted to uncovered carrion. Shubeck (1971) found certain species were more frequently trapped nocturnally than diurnally, and stated that covered carrion of Ratcliffe and Luedtke (1969) could be analogous to nocturnal activity, and uncovered carrion analogous to diurnal activity since they offered similar light conditions.

Authors who have contributed descriptive work on either adult or larval American Silphidae include Schaupp (1881, 1882), Wickham (1895), Blackburn (1936), and Dorsey (1940). Sharp and Muir (1912), Arnett (1944), and Bliss (1949) have done studies pertaining especially to sexual characteristics of Silphidae. R. Heymons and V. H. Lengerken published numerous descriptive and life history studies on European silphids in the 1920's and 1930's.

DISTRIBUTION OF MICHIGAN SILPHIDAE

The range of Michigan's 11 species of carrion beetles extends in all directions beyond the borders of the state. For this reason, no attempt was made in this study to systematically collect silphids throughout the state. Agassiz (1850) included the Coleoptera in his study of the Lake Superior area. Hubbard and Schwarz (1878) reported on Michigan Coleoptera. Major works which have given the distribution of Silphidae throughout the United States include Le Conte (1853), Horn (1880), Leng (1920), and Hatch (1927a).

COLLECTION PROCEDURES FOR BEETLES

The collection of silphid beetles and their mite associates is made relatively easy, although a bit unpleasant, due to their attraction to carrion odors. Primary collection sites for this study in Michigan from 1969-71 included: W. K. Kellogg Gull Lake Biological Station, Kalamazoo County; Rose Lake Wildlife Research Area, Clinton County and Shiawassee County; Olivet College Biological Preserve at Pine Lake, Eaton County; and Michigan State University, Toumey Woodlot, Ingham County. Occasional collections were made throughout various parts of Michigan by the author and others. Collections at the primary sites were usually made between 9 A.M. and noon or early afternoon.

For this study most of the beetles were collected by placing various dead vertebrates into one gallon metal cans such as are readily available from cafeteria kitchens. The different kinds of carrion included dead fish, mice, birds, snakes, and frogs. After preliminary studies dead fish was most commonly used as bait, because it was readily available and was found to produce the strongest odor detectable by the author in a short time. Other types of carrion were used as available.

After placing the carrion into a gallon can, a wire screen with one-inch mesh was fastened over the opening to prevent vertebrate scavengers from removing the bait. In cases where small animal bodies such as mice were used for bait, a wire mesh smaller than one inch was needed to prevent Nicrophorus from removing the bodies from the cans for burial.

Occasionally silphids were also collected at lights and by examining road kills and vertebrates found dead of natural causes. Dead animals lying at road sides seldom had silphids on them, however.

For all beetles collected the following information was recorded: species and sex, date and site of collection, general habitat type, and kind of carrion from which collected. In addition, all beetles collected from a single dead body were kept together until examined for mites. In this way comparisons could be made to see if beetles collected at one site carried the same or different mites as there is a possibility for exchange of mites between beetles at a common carrion site. The general habitat type was recorded for all beetle collection sites, in order to examine possible beetle preferences.

Beetles were identified using keys from Horn (1880), Hatch (1927, 1927a), and Arnett (1944). Hatch (1927a) includes keys to aberrations of species (variations in color pattern) which were not used in this study, because it was not thought that sub-specific identification would add significantly to the information obtained.

Beetles were collected from the baited cans by grasping one of their hind legs with a forceps. The complement of mites found on each beetle was disturbed very little in this way. Unless a beetle or mites on it were to be retained for rearing, each beetle was placed into a vial of 80 percent ethyl alcohol. Separate vials were used for each beetle to retain specific host data. Upon placement into alcohol, <u>Poecilochirus</u> and <u>Macrocheles</u> mites frequently fell from the beetle into the alcohol. This was due to the fact that they were not holding onto the beetle with their chelicerae, but simply holding to the dorsum of the beetle with their legs. Mites found on the beetle at sites other than the dorsum usually remained in place.

Beetles and mites which were to be retained for rearing were collected into dry baby food jars. Care had to be taken to prevent the mites from becoming fastened to the bottom of the jar in the liquid excretions which silphids frequently give off when confined in a small container. A small piece of paper toweling in the bottom of the jar usually solved this problem.

When it was desirable to remove live mites from beetles, carbon dioxide gas was used to anesthetize both the mites and silphids. In this way the beetles would lie still while they were being examined under the wings, in coxal cavities, etc. for mites. Also the mites could be easily picked up with a moist camel hair brush and transferred to a culture dish.

PROCEDURE FOR EXAMINATION OF BEETLES FOR MITES

Removal of both live and dead mites from silphids was accomplished by use of a dissecting microscope at 9 and 27 magifications. Each beetle examined for mites was given a number for future reference starting with WY1, WY2, WY3. . . . For those beetles collected in alcohol, removal of mites was also done in 80 percent alcohol. Several sizes of pipettes were used to suck up the mites as they were gently prodded to loosen them from a beetle. The site of mite attachment to the beetle was recorded for all mites in order to examine their preferences. Terminology used in describing the silphid anatomy follows Blackburn (1936).

The same sequence was followed in probing the parts of each beetle to insure a thorough examination. In order to hold a beetle under alcohol during examination, one of the hind legs was grasped with a forceps, leaving one hand free to probe the parts of the beetle and suck up the mites. First the beetle was laid on its back and the legs, coxal cavities, and membranous areas between thoracic sternal sclerites, pleural sclerites, and cervical areas were examined. Next the abdominal sternites were examined, particularly the intersegmental membranes. Then the area between the hind coxae and abdomen was pressed apart to determine if mites were attached there. Following examination of the ventral side, the silphid was turned over for examination of the dorsum. The elytra were lifted, one at a time, and one side of the dorsum was examined before lifting the second elytron and repeating the examination on the second half. First the under-side of the elytron was examined. Very commonly large numbers of anoetids were attached there. Then the wing bases, scutellar area and thoracic terga were probed, followed by examination of the abdominal terga. Frequently anoetid mites were attached to these terga, especially at the intersegmental membranes. Finally, the terminal segments of the abdomen bearing the genitalia were examined. Mites and nematodes were often concealed on those segments until the segments were drawn out a bit with forceps, as the segments were withdrawn within one another.

Following removal of the mites from the beetles, they were treated for microscopic examination as described under the preceding section on "Mite Methods."

Beetles from which mites were removed are either deposited in the Michigan State University Entomology Museum or are retained by the author for future study.

RESULTS AND DISCUSSION

During this study the acarine fauna found on 246 silphid beetles representing eleven species collected in Michigan was examined. A total of 11,743 mites were taken from these beetles. Individual beetle species examined were as follows: 40 *Nicrophorus tomentosus* Weber, 17 *N. americanus* Olivier, 6 *N. vespilloides* Herbst, 7 *N. pustulatus* Herschel, 9 *N. orbicollis* Say, 13 *N. marginatus* Fabricius; 54 *Silpha americana* Linnaeus, 53 *S. noveboracensis* Forster, 16 *S. lapponica* Herbst, 13 *S. inaequalis* Fabricius; 18 *Necrodes surinamensis* Fabricius. Approximately equal numbers of male and female beetles were examined, except in the case of *Nicrophorus vespilloides*, where only six males were collected.

Larger numbers of *N. tomentosus*, *S. americana*, and *S. noveboracensis* were examined since these species were more frequently collected. Preliminary studies also showed that of the commonly collected silphids *N. tomentosus* and *S. noveboracensis* had a greater frequency of infestation by mite species and individuals. *Nicrophorus americanus* was never collected by the author during this study, and all data for this species are from museum specimens. Although museum records show it has occurred in the past in the same areas collected in this study, no live specimens were seen during the time of this investigation.

The various types of carrion attracting each silphid species in this study are shown in Figure 23. Dead fish and mice were the only two baits used regularly, as they were readily available and attracted all species. Based on field observations alone, dead fish, which gave off the strongest odor detectable by the author, seemed to attract the most beetles. However, no quantitative data were recorded. Dead *Peromyscus* sp. also served quite well as bait when six to ten adults were placed into one can. Birds, snakes, frogs, and turtles were used as bait when available, but this was too infrequent to predict whether or not all species would be attracted to them. On one occasion, a partially disinterred horse was found with several *Necrodes surinamensis* on it. Other large mammals which at times were found inhabited by silphids included deer, opposum, dog, and muskrat. When the large variety of dead animals used in this study and others reported in previous literature are considered, it becomes apparent that most groups of dead vertebrates attract Silphidae.

BEETLE SPECIES	Fish	Mice	Birds	Large Mammals	Snakes	Frogs	Light
Silpha americana	X	X	X	Deer			
S. nove-boracensis	X	X	X	Deer, Dog Opossum Muskrat			
S. inaequalis	X	X	X	Deer Muskrat		X	
S. lapponica	X	X	X			X	
Necrodes surinamensis	X	X		Horse	X		X
Nicrophorus tomentosus	X	X			X	X	
N. orbicollis	X	X					X
N. pustulatus	X	X					X
N. vespil-loides	X	X	X				X
N. marginatus	X	X					

Figure 23. Attractants of Silphidae in Michigan.

As many as four silphid species, often representing two or three genera, were attracted to a single baited can during this study. How many of these species would have remained to reproduce was never determined. But Pukowski (1933) reported that normally only one *Nicrophorus* female or a breeding pair would remain on dead moles to reproduce, all others being driven off before the burial of the mole was completed and eggs were laid. His experiments were confined to cages, and perhaps more work should be done in a natural setting to determine whether his observations apply to a natural situation.

The percent of each species of beetle infested by mites is given in Figure 24. This graph also shows the average number of mite species found on each beetle. All species of *Nicrophorus* showed a high infestation of mites, with 89 percent infestation of *N. orbicollis* the lowest. Three species showed 100 percent infestation. The average number of mite species on different species of *Nicrophorus* having mites ranged from 2.4 to 3.8. This is in contrast to *Silpha* which ranged from 1.0 to 1.9 mite species/beetle species for infested beetles. The percent infestation of all species of Silpha was also less than any *Nicrophorus*. *Silpha noveboraensis* had the highest infestation with 85 percent while *S. americana* had the lowest infestation of all silphids collected with only 44 percent having mites.

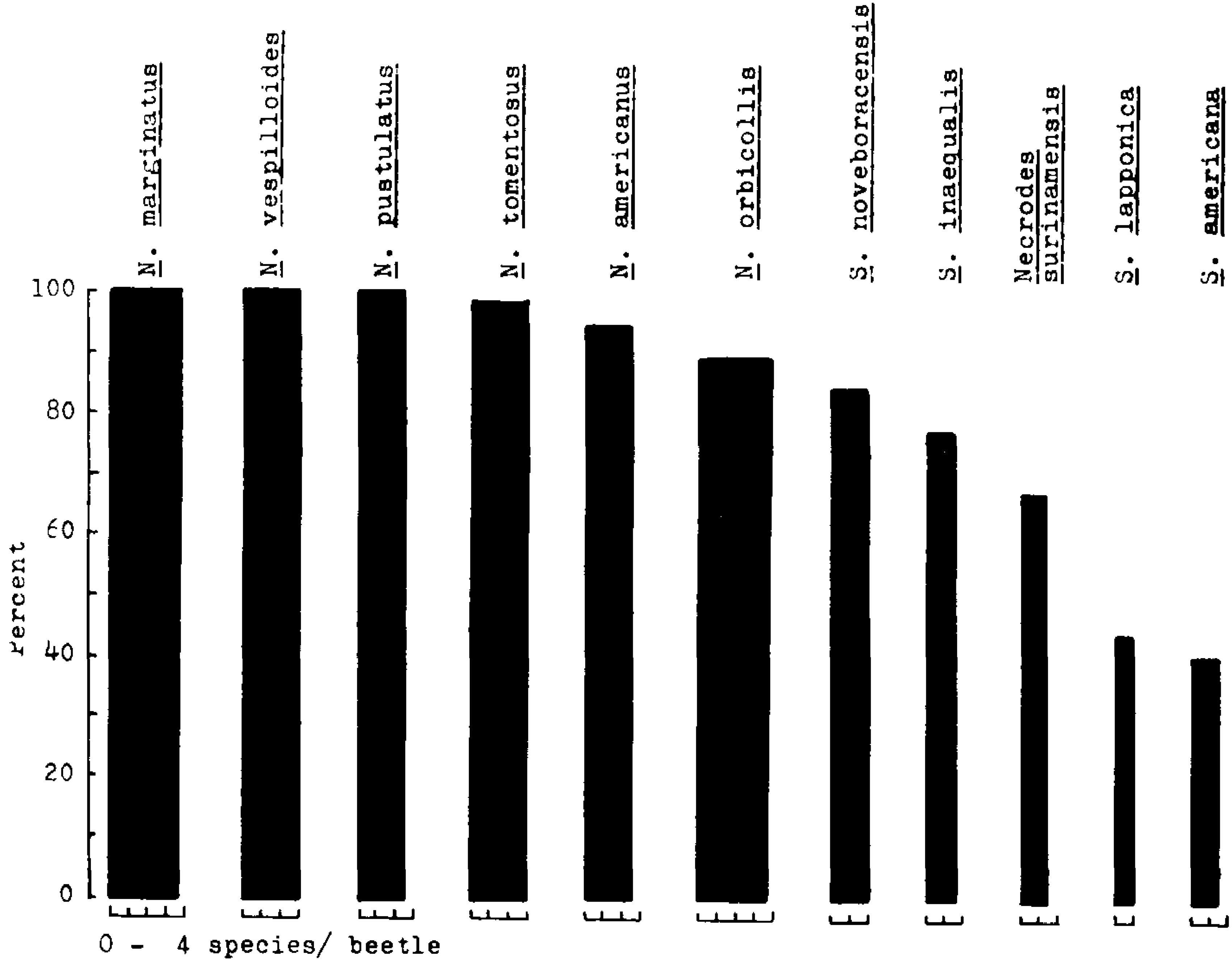

Figure 24. Percent of Silphidae infested by mites, and mean number of mite species per beetle for beetles having mites.

While factors affecting the preferential attraction of mites to the eleven different silphid species were beyond the scope of this study, several possibilities are suggested. Differences in beetle size or structure may make one beetle species more attractive than another. For example, the indentation in the elytra of *Necrodes surinamensis* provided an attachment site for 15 percent of all the *Spinanoetus pelznerae* collected. Habits of the different beetle species may make one more attractive than another. Food regurgitations of *Nicrophorus* could serve as a stimulus to bring mites to them which would not be drawn to *Silpha*. Likewise, the burying behavior of *Nicrophorus* could keep them in an environment more suitable for mite associations than *Silpha* and *Necrodes* which spend most of their time near the surface of the ground. The question of why one beetle species is more attractive to mites than another is part of a more basic question of why are mites attracted to beetles at all, which will be discussed later.

MITE ASSOCIATIONS WITH SILPHIDAE

Eleven mite species were found on Michigan Silphidae in numbers of 40 or more. The number of beetle species hosting each mite species is presented in Figure 25. Their distribution follows a normal pattern with *Pelzneria crenulata* being found on all eleven silphid species, while *Macrocheles breviseta* and *Poecilochirus longisetosa* were found on only two beetle species. The remaining seven species were distributed on intermediate numbers of beetles.

In the following discussion, each of these mite species will be discussed in relation to: (1) its total number collected, (2) range in numbers on beetle species, (3) percent of beetles infested, (4) average number of mites/beetle from those beetles having mites, (5) site preferences on beetles. For each mite being considered, the reader is referred to Table 2 for the percent of each beetle infested by given species of mites, and to Table 3 for the mean number of mites/beetle. Locations of mites on beetles are given in Table 4.

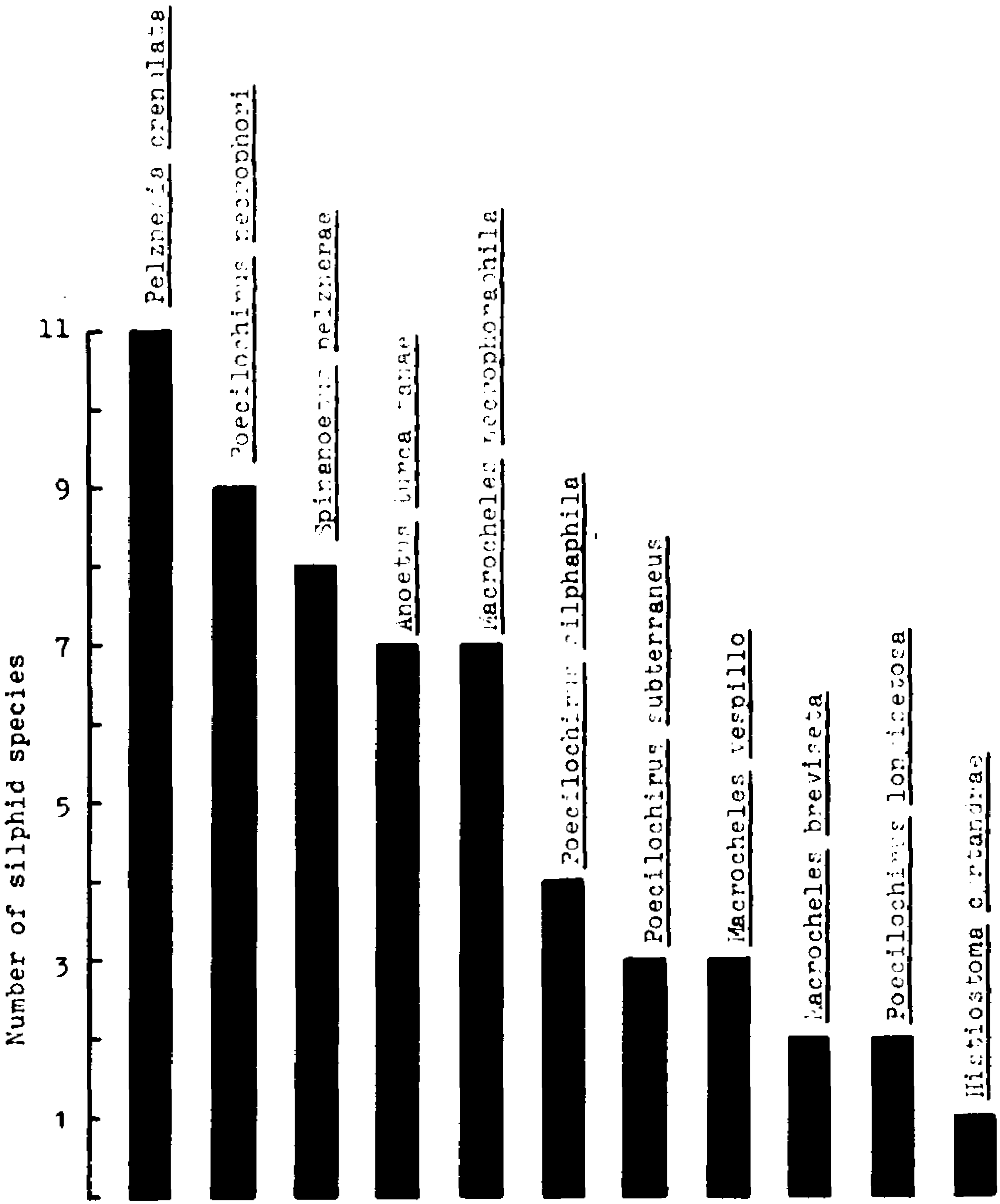

Figure 25. Number of silphid species on which given mite species were found.

TABLE 2. Percent of beetles infested with given mite species. (Numbers in parentheses following species names indicate number of specimens.)

Beetle species \ Mite species	Poecilochirus necrophori (446)	Poecilochirus subterraneus (346)	Poecilochirus longisetosa ([illegible])	Poecilochirus silphaphila ([illegible])	Macrocheles necropophila ([illegible]62)	Macrocheles breviseta (6[illegible])	Macrocheles vespillo (111)	Pelzneria crenulata (5519)	Spinanoetus pelznerae (2579)	Anoetus tirgastanae (604)
Nicrophorus tomentosus (40)	70	68	13	28	5	3	3	83	10	5
Nicrophorus americanus (17)	6	0	0	12	77	0	24	59	6	12
Nicrophorus vespilloides (6)	50	33	0	17	83	0	0	67	0	17
Nicrophorus pustulatus (7)	29	57	0	0	14	0	0	86	0	0
Nicrophorus orbicollis (9)	45	0	0	22	67	0	0	44	0	11
Nicrophorus marginatus (13)	31	0	62	0	0	63	23	69	39	69
Silpha americana (54)	11	0	0	0	2	0	0	11	9	4
Silpha noveboracensis (53)	17	0	0	0	2	0	0	57	76	0
Silpha lapponica (16)	0	0	0	0	0	0	0	25	6	0
Silpha inaequalis (13)	0	0	0	0	0	0	0	77	38	0
Necrodes surinamensis (18)	6	0	0	0	0	0	0	11	67	6

TABLE 3. Mean number of mites/beetle from those beetles having mites. (Numbers in parentheses following species names indicates number of specimens.)

Beetle species \ Mite species	Poecilochirus necrophori (448)	Poecilochirus subterraneus (346)	Poecilochirus longisetosa (56)	Poecilochirus silphaphila (52)	Macrocheles necrophoraphila (762)	Macrocheles breviseta (65)	Macrocheles vespillo (111)	Pelzneria crenulata (6519)	Spinanoetus pelznerae (2679)	Anoetus turcastanae (604)
Nicrophorus tomentosus (40)	4.4	5.7	2.6	3.5	3.5	2.0	1.0	103.4	1.0	1.0
N. americanus (17)	1.0	0	0	1.0	45.4	0	24.3	96.7	1.0	2.0
N. vespilloides (6)	17.3	2.0	0	3.0	4.2	0	0	19.8	0	1.0
N. pustulatus (7)	84.0	45.8	0	0	25.0	0	0	130.3	0	0
N. orbicollis (9)	7.5	0	0	4.5	19.3	0	0	2.5	0	1.0
N. marginatus (13)	9.3	0	5.4	0	0	7.9	4.3	49.1	1.8	65.9
Silpha americana (54)	2.9	0	0	0	1.0	0	0	5.0	2.8	1.0
S. noveboracensis (53)	2.0	0	0	0	1.0	0	0	19.1	53.8	0
S. lapponica (16)	0	0	0	0	0	0	0	1.5	1.0	0
S. inaequalis (13)	0	0	0	0	0	0	0	19.0	15.8	0
Necrodes surinamensis (18)	1.0	0	0	0	0	0	0	10.5	35.2	1.0

TABLE 4. Locations of mite species on beetles by percent. (Numbers in parentheses following species names indicate number of specimens.)

Location \ Mite species	*Poecilochirus necrophori* (448)	*Poecilochirus subterraneus* (346)	*Poecilochirus longisetosa* (56)	*Poecilochirus silphaphila* (52)	*Macrocheles necrophoraphila* (762)	*Macrocheles breviseta* (65)	*Macrocheles vespillo* (111)	*Pelzneria crenulata* (6519)	*Spinanoetus pelznerae* (2679)	*Anoetus furcastanae* (604)
Loose	100	62.9	98.2	92.3	8.8	29.2	1.8	18.9	7.1	13.8
Abdominal terga	0	6.1	0	5.8	8.0	0	2.7	15.5	67.1	6.1
Thoracic terga	0	12.2	0	0	9.5	0	0	0	0	0.2
Abdominal sterna	0	0	1.8	0	3.8	0	8.2	1.6	0.2	46.3
Thoracic sterna	0	0	0	0	0	0	0	0.5	0	0.2
Coxal cavities	0	0	0	0	0	0	0	32.9	0.2	6.8
Underside of elytra	0	18.8	0	0	1.7	0	0	25.1	25.4	26.6
Spiracles	0	0	0	1.9	67.2	0	80.9	0	0	0
Genitalia	0	0	0	0	0	0	0	3.4	0	0.2
Posterior edge of pleuron I	0	0	0	0	0	70.8	6.4	0	0	0
Other	0	0	0	0	1.0	0	0	2.0	0	0.4

FAMILY ANOETIDAE

Members of the Anoetidae were found on silphids in greater numbers than any of the other families. They were found only in the deutonymph or hypopus instar, attached by their suckers to various parts of the beetles.

Pelzneria crenulata (Oudemans)

Anoetus crenulatus Oudemans, 1909: 23.

Histiostoma crenulatus Buitendijk, 1945: 281.

Pelzneria crenulata Scheucher, 1957: 347.

The 6519 *P. crenulata* specimens were the largest number of any mite species collected. It was found on all eleven silphid species ranging in numbers from 1 to 574 individuals/beetle. Infestation ranged between 86 percent of *Nicrophorus pustulatus* and 11 percent of *Silpha americana* and *Necrodes surinamenis*. The highest average number of *P. crenulata*/beetle species was found on *N. pustulatus*, with 130.3/beetle, and the lowest average was 1.5/beetle on *Silpha lapponica*. High average numbers per beetle were also recorded for *N. tomentosus* (103.4), *N. americanus* (96.7), and *N. marginatus* (49.1).

Lower averages were recorded for N. vespilloides (19.8), S. noveboracensis (19.1), S. inaequalis (19.0), and Necrodes surinamensis (10.5). Overall, much higher average numbers of P. crenulata were found on Nicrophorus than on Silpha or Necrodes.

Of all the P. crenulata collected, 32.9 percent were found in coxal cavities I and II of the beetles. They were usually attached to the medial and posterior surfaces of the coxal cavities, although when in larger numbers they would cover the entire surfaces of the cavities. Twenty-five percent of the P. crenulata were found attached to the underside of silphid elytra. Most often they were clustered toward the proximal end of the elytra, but extended two-thirds of the way toward the distal end when in larger numbers, coating the entire surface of the elytra to that boundary. The abdominal terga were the attachment site for 15.5 percent of the P. crenulata collected. Only the terga covered by the elytra when at rest were occupied by mites in most cases. They would cluster toward the intersegmental membranes unless larger numbers were present, and forced onto the more sclerotized surfaces of the terga. The genital sclerites were the sites of attachment for 3.4 percent of this species. It was the only species which was found there with any frequency. It is interesting to speculate as to whether they reached the genitalia by crawling there after they were on some other part of the beetle, or if their original site of entrance onto the beetle may have been the genitalia. All but one of 221 *P. crenulata* taken from the genitalia were on female beetles, so the possibility exists that these mites could have crawled onto the ovipositors of females as they were depositing eggs at a carrion site. When beetles were placed into collecting vials containing alcohol, 18.9 percent of the *P. crenulata* became dislodged from their attachment site. Such mites were all combined into a category called "loose" in Table 4, for this and following species.

Spinanoetus pelznerae Scheucher

Spinanoetus pelznerae Scheucher, 1957: 358.

The total of 2679 *S. pelznerae* collected made it the second most commonly collected mite species. It was found on eight of the eleven silphid species. Numbers found on a single beetle ranged from 1 to 281, the highest number being found on *S. noveboracensis*. Seventy-six percent infestation of *S. noveboracensis* was also the highest infestation by this mite on any species of beetle, and only 6 percent of *N. americanus* and *S. lapponica* carried this species. Only three species of beetles had a high average number of this mite/beetle:

S. noveboracensis, 53.8; Necrodes surinamensis, 35.2; and S. inaequalis, 15.8. It is interesting to note that this was the only mite species which infested Silpha and Necrodes in greater numbers than Nicrophorus for reasons unknown.

S. pelznerae was found primarily in two locations on silphids. The abdominal terga were the attachment sites of 67.1 percent of the species, and 25.4 percent were found on the underside of the elytra. Fifteen percent of the specimens were attached to the elytra of Necrodes surinamensis, even though only 16 percent of the total were found on this beetle. The elytra of N. surinamensis bear an indentation, lacking in other silphids, which perhaps makes them a more attractive or suitable attachment site for hypopi. For some reason, S. pelznerae was the only anoetid mite which was not frequently found in the coxal cavities, and which showed only two clear site preferences on the beetles.

Anoetus turcastanae Oudemans

Anoetus turcastanae Oudemans, 1917: 391.

Only 604 A. turcastanae were collected in contrast to much larger numbers of the preceding anoetid mites. It was found on seven silphid species. Nicrophorus marginatus was the only beetle which had more than three of this mite on it, one specimen having 387 individuals. *N. marginatus* had 69 percent infestation, with the other species having only 4 to 12 percent infestation. *N. marginatus* having *A. turcastanae* averaged 65.9 mites/beetle, but no other beetle averaged greater than two/beetle.

This species was generally distributed over the beetles with the abdominal sterna bearing 46.3 percent, the underside of the elytra 26.6 percent, coxal cavities 6.8 percent, and the abdominal terga 6.1 percent.

Histiostoma cyrtandrae (Vitzthum)

Anoetus cyrtandrae Vitzthum, 1931: 59.

Histiostoma cyrtandrae Hughes & Jackson, 1958: 59.

Forty specimens of *H. cyrtandrae* were collected from a single *Nicrophorus pustulatus*. Twenty of these were found in coxal cavities I and II, and twenty were detached from the beetle in the collecting fluid. It is unusual that such a large number of a species should be collected from only one beetle during the entire study. No explanation can be given for it at this time. Many other beetles were collected from the same area during a period of one week.

FAMILY PARASITIDAE

Representatives of this family were found on silphids only as deutonymphs. Most frequently the mites would be running about freely on the dorsum of beetles when collected, although they were also commonly clinging to the undersides.

Poecilochirus necrophori Vitzthum

Poecilochirus necrophori Vitzthum, 1930: 381.

Poecilochirus necrophori was the largest mite species collected from Silphidae. A total of 448 specimens were collected from nine siliphid species, making it the second most commonly collected mesostigmatic species. It was never collected from *Silpha inaequalis* or *S. lapponica*, but was found on all other Michigan silphids. Infestations ranged from one mite/beetle to a high of 146 mites/beetle on a *Nicrophorus pustulatus*. Excluding that one individual, the highest infestation was 32 mites/ beetle. Seventy percent of *Nicrophorus tomentosus* carried this species, but only 6 percent of *Necrodes surinamensis* had it. Only 6 percent of *Nicrophorus americanus* carried it as well, but all *N. americanus* were museum specimens, and probably were placed in cyanide killing jars rather than in vials of alcohol, as were the rest of the beetles in this study. If so, it is quite likely that a number of P. necrophori would have been lost in collection. All Nicrophorus except N. americanus had at least 29 percent infestation of P. necrophori, and the collection method could account for its being much lower. The only two Silpha carrying P. necrophori, S. americana and S. noveboracensis, had only 11 percent and 17 percent infestation respectively.

For those beetles bearing P. necrophori, the average number/beetle for Nicrophorus ranged from 1.0 on N. americanus to 84.0 on N. pustulatus. Again, however, a more reliable estimate of the average number would probably exclude the museum specimens of N. americanus. Then N. tomentosus would have the lowest average number/beetle with 4.4. This is still considerably higher than the 2.9 and 2.0 mites/beetle found on Silpha americana and S. noveboracensis. Both average numbers of P. necrophori/beetle and percent infestation suggest that this mite species has a definite preference for Nicrophorus over Silpha or Necrodes. In addition, this was the only one of four species of Poecilochirus found on Silpha and Necrodes at all. Possible reasons for this preferential attraction will be discussed later.

All P. necrophori were in a "loose" association with silphids, running on the beetles, or off the beetles onto carrion, feeding, and returning to the beetles. They seldom remained stationary on a beetle, and were seldom seen holding onto a beetle while a beetle was on the ground. For this reason, the mites fell off when the beetles were placed into vials of alcohol. Occasionally a mite was seen with a beetle seta in its chelicerae, indicating that perhaps this was their method of holding to a beetle during its flight. But there were no indications of site preferences on the beetles.

Poecilochirus subterraneus (Müller)

Porrhostaspis subterranea Müller, 1859: 176.

Parasitus subterraneus Oudemans, 1902: 238.

Gamasoides subterraneus Berlese, 1903: 258.

Poecilochirus subterraneus Vitzthum, 1930: 381.

Three hundred forty-six P. subterraneus were collected from only three species of Nicrophorus. Their numbers ranged from one mite/beetle, to 132 mites/beetle on one N. pustulatus. N. tomentosus had the highest percent infestation with 27 percent while N. pustulatus and N. vespilloides had only 4 percent and 2 percent infestation each. Of the beetles bearing P. subterraneus, N. pustulatus had the highest average number with 45.8/ beetle, while N. tomentosus had 5.7/beetle and N. vespilloides 2.0/beetle.

P. subterraneus was distinct from the other three Poecilochirus in its site preferences on the beetles. Only 62.9 percent of P. subterraneus were in "loose" association with the beetles and fell off when placed in alcohol, compared to 92-100 percent of the other three species. The remaining 37.1 percent not "loose" were found on thoracic or abdominal terga under the elytra, or between the elytra and membranous wings. The fact that *P*. *subterraneus* is only about half the size of other *Poecilochirus* probably allows it to crawl under the elytra onto the terga where the others cannot easily go. When on several occasions it was noted that there were also nematodes under the wings, the question was raised of whether the mites were simply under the wings seeking attachment sites for phoresy, or whether they might be seeking nematodes as a food source. Until now nothing has been published concerning food habits of *P*. *subterraneus*, including this study. But this would probably be a profitable area for investigation.

Poecilochirus longisetosa new species

Nicrophorus marginatus and *N*. *tomentosus* carried a total of 56 *P*. *longisetosa*. It ranged in number from one mite/beetle to 32/beetle on one *N*. *marginatus*. Thirteen percent of *N*. *tomentosus* and 62 percent of *N*. *marginatus* carried it. The average number per beetle for those having this species was 2.6 for *N*. *tomentosus* and 5.4 for *N*. *marginatus*.

A single specimen of *P. longisetosa* was found holding to an abdominal sternite. All others fell off the beetles when collected into alcohol, as was typical for most individuals of the genus.

Poecilochirus silphaphila new species

A total of 52 *P. silphaphila* were collected from four species of *Nicrophorus*. It ranged in number from one to eight mites/beetle. Percent infestation by species was less than for any other *Poecilochirus*, with 28 percent infestation of *N. tomentosus* being the highest. *N. americanus* carried the lowest average number of mites/ beetle with 1.0, while *N. orbicollis* averaged 4.5 mites/ beetle for specimens with it.

This species showed little site preference on beetles as 92.3 percent were loose after collection into alcohol. One specimen was found holding to the edge of a thoracic spiracle and 5.8 percent were found on abdominal terga under the elytra.

FAMILY MACROCHELIDAE

This family was represented on Michigan Silphidae by five species of *Macrocheles*. They were found on the beetles only as adult females.

Macrocheles vespillo Berlese

Macrocheles vespillo Berlese, 1918: 115.

One hundred eleven specimens of this species were taken from three species of *Nicrophorus*. Their numbers per beetle ranged from one to a high of 47 on one specimen of *N. americanus*. Twenty-four percent of *N. americanus* and 23 percent of *N. marginatus* examined carried *M. vespillo*, while only a single *N. tomentosus* had one specimen on it. The average number per beetle was 4.3 on *N. marginatus* and 24.3 on *N. americanus*. The spiracles of *N. americanus* were the attachment site of 80.9 percent of this species. This was a much higher percentage than was found on any other sites on all beetles, with only 8.2 percent being found on the abdominal sterna, 6.4 percent under the posterior edge of pleuron I, 2.7 percent on the abdominal terga, and 1.8 percent loose in the collection vials. The high percentage found clustered around the spiracles would suggest that perhaps a certain gas or humidity concentration found there was more suitable for *M. vespillo*. A high percentage of *M. necrophoraphila*, which follows in this discussion, was also found in greatest numbers at the spiracular openings. The same stimulus might have attracted both species of *Macrocheles* to the spiracles.

Macrocheles necrophoraphila new species

The 762 specimens of *M. necrophoraphila* collected made it the most common *Macrocheles* on silphids. It was taken from seven species of beetles in numbers ranging from 1 to a high of 282 on a single *N. americanus*. Percent infestation ranged from 2 percent on *S. americana* and *S. noveboracensis* to 83 percent on *N. vespilloides*. *N. americanus* had 77 percent infestation and *N. orbicollis* 67 percent, while *N. pustulatus* and *N. tomentosus* had only 14 percent and 5 percent respectively. For those beetles bearing mites, the average number per beetle ranged from 1.0/beetle for *S. americana* and *S. noveboracensis* to 45.4 mites/beetle for *N. americanus*. This was the only species of *Macrocheles* for which any specimens were found on *Silpha*. *N. pustulatus* and *N. orbicollis* had high infestations with 25.0 and 19.3 *M. necrophoraphila*/beetle respectively. *N. vespilloides* carried only 4.2/beetle, and *N. tomentosus* 3.5/beetle.

The spiracles of *Nicrophorus* were the attachment site of 67.2 percent of this species collected. The spiracles of *N. americanus* alone accounted for 66.7 percent of the specimens. As mentioned in the discussion of *M. vespillo*, a common stimulus may have attracted these two mite species in large numbers to the spiracles of *N. americanus*. Since *N. americanus* beetles were all museum specimens, it is quite possible that they were killed with cyanide gas, and perhaps the mites were attracted to the beetles spiracles as their oxygen supply was diminished. However, this would not explain the greatest percentage of both species being attracted to N. americanus initially. Ideas concerning the initial attraction of mites to beetles will be discussed later. In addition to the M. necrophoraphila found attracted to the spiracles, 19.2 percent of this species were found either on the thoracic or abdominal terga or under the elytra, away from the spiracles. Combined with those specimens found at the spiracles, 86.4 percent of this species were found under the wings of silphids. Most of the remainder had fallen off the beetles into the alcohol when collected.

Macrocheles breviseta new species

Sixty-three M. breviseta were found on N. marginatus and two on N. tomentosus. The highest number on any beetle was 21. M. breviseta infested 62 percent of N. marginatus, and only a single specimen of N. tomentosus. The average number of mites on N. marginatus was 7.9. The inside of the posterior edge of pleuron I was the attachment site for 70.8 percent of this species, all on N. marginatus. This sclerite, connected by a membrane to the rest of the body wall, provided enough room for at least 21 mites to crawl snuggly under it, almost concealing them completely from observation from the outside. Beetles were taken on four different dates and from two counties with this species under the edge of the pleuron. The 29.2 percent not found under the pleuron had fallen from the beetles into the collecting fluid.

THE BIOLOGY AND PHORETIC BEHAVIOR OF ANOETID MITES ON SILPHIDAE

Although the biology of Anoetidae found on silphids was not examined in detail, knowledge of other anoetids allows reasonable assumptions regarding the role of silphids in the biology of anoetids found on them. It is well known that hypopi do not possess functional mouth parts and, therefore, the anoetids which were collected from silphids in this study could not be feeding on the beetles or other materials found on them. Hughes and Jackson (1958) state in regard to the other instars of the family that for nearly all species encountered so far "they appear to thrive best when fermentation of organic matter is evident. They are surface feeders, and most seem to prefer a thin film of fluid in which to wade while feeding. It is presumed that they engulf yeasts, and other microorganisms." In most cases, carrion becomes quite moist during the early stages of decay, and probably forms a suitable habitat for anoetid reproduction. Woodring (1963) reported that when the anoetid food medium dries, hypopi form in ever increasing numbers. And when fresh medium is again made available, most hypopi molt to tritonymph. So it is quite possible that hypopi carried by silphids could leave the beetles when they reach a new, moist carrion site, complete their life cycle, and reproduce new young. The new young upon reaching the hypopal stage could attach to silphids, and emigrate to new carrion sites as the old carrion dried, and the adult beetles left it. Factors controlling the formation of hypopi in the life cycles of anoetids are not well understood (Woodring, 1963), but the formation of hypopi probably has adaptive benefit for anoetids in getting them to new wetter habitats as their old habitat dries. A great deal of work remains to be done in order to understand the problems of anoetid nutrition and hypopal formation and termination, and to correlate this with their phoresy on silphids.

THE BIOLOGY AND PHORETIC BEHAVIOR OF *POECILOCHIRUS*

A study was undertaken from 13 August to 6 September 1971, in Michigan State University's Toumey Woodlot to determine whether *Poecilochirus* would be found on carrion which had not been visited by beetles. Limited observations by Springett (1968) indicated that *P. necrophori* was not found on dead terns on the Farne Islands until *Nicrophorus* had visited the dead birds.

For this study two six-foot square screen cages were erected in the woodlot several hundred feet apart. The screen, a mesh 20 lines per inch, excluded beetles but not mites. A gallon can baited with dead mice was placed inside each cage. Outside each cage, thirty feet from them, a similarly baited control can was placed. Cans were collected one or two days after freshly killed mice were placed into them, and the mites recorded from caged cans and uncaged controls.

Results and Discussion

Nicrophorus were found in all control cans, or there was definite evidence that they had visited the cans and left. In several of the control cans no Nicrophorus were collected, but the mice were chewed in a way that had previously been observed as characteristic for Nicrophorus.

Comparison of the total mites collected in caged versus uncaged cans shows that 0 Poecilochirus were collected in nine caged cans where Nicrophorus were excluded, whereas 113 Poecilochirus were collected in the uncaged cans. This indicates, as was suggested by Springett (1968), that Poecilochirus are carried to carrion initially by silphids, and are not simply a normal part of the soil fauna. They are dependent on beetles for their transport and dispersal from one carrion site to another.

A total of five mites other than Poecilochirus were collected from the total 18 cans. These mites were all members of groups that would normally be expected in soil or leaf litter, and therefore, probably could be considered accidental visitors of the carrion. They did not require silphids to carry them to the carrion site.

Only two investigators have studied the feeding habits of Poecilochirus in any detail, and their results are opposed. Neumann (1943) reported that P. necrophori (reported by Holzmann (1969) to have been P. carabi) could be reared to adults very easily on crushed fly maggots in the absence of silphids. Springett (1968) concluded that P. necrophori are apparently unable to produce young in the absence of Nicrophorus, although he stated that his observations were preliminary. He noted that on one occasion _P. necrophori_ protonymphs were observed feeding on the brown fluid regurgitated by _Nicrophorus_, and implied that this fluid or other beetle excretions may be very important to the mites. Their diet of fly eggs and small larvae in the absence of beetles apparently did not supply all requirements for reproduction.

In some preliminary experiments during this study, 14 _P. necrophori_ deutonymphs were maintained in the laboratory apart from beetles in order to compare results with those of Springett (1968). They were kept on a moist plaster of Paris-charcoal substrate at 21-27°C, and offered a diet of crushed _Tenebrio molitor_ larvae, nematodes, and eggs and larvae of _Calliphora_ sp. Although all mentioned food items were accepted to at least some degree and all mites fed regularly on one or more of the items, none ever molted and reached the adult instar before its death. The number of days from placement in culture to death ranged from 27-92 days. This would have been adequate time for their molt and reproduction if conditions were proper, as Neumann (1943) reported a generation time of only 8-9 days for _P. carabi_. While these results are preliminary at best, they suggest that _P. necrophori_ may not be capable of reproduction in the absence of _Nicrophorus_. Adults and immatures probably feed on nematodes and fly larvae on the carrion, and deutonymphs are transported from one carrion site to another. At the new carrion site apparently some still unknown interaction between the silphids and deutonymphs of *P. necrophori* is necessary before they will molt to adulthood and reproduce. Such possible interactions should be investigated further.

A LIFE HISTORY STUDY OF *MACROCHELES* *NECROPHORAPHILA* NEW SPECIES

Two female *Macrocheles necrophoraphila* new species were taken from a male *Nicrophorus orbicollis* collected in Michigan State University's Toumey Woodlot, East Lansing, Michigan on 31 May 1971. These females were collected live and transferred to culture cells to obtain specimens of their immature instars and to study the life history of their offspring.

Methods and Materials

Culture cells were made by cutting the bottom off one-inch diameter plastic vials and setting them into a plaster of Paris-charcoal mixture. This mixture was made up of nine parts plaster of Paris: one part fine bone charcoal. Water was added to make it a soupy consistency into which the vials were set. As the plaster set, the vials became firmly anchored. The plaster and vials can be set in different sized containers, depending on how many vials are desired in one unit. For this study, plastic containers 8 cm. high, 10 cm. diameter were found to be a convenient size for holding four vials as a unit.

Holes were cut into the lid of the containers so that the four vials could protrude above it, and the lid could prevent rapid evaporation of water from the plaster. In order to maintain a high relative humidity in the vials, distilled water was added to the plaster every one to four days, keeping it nearly saturated. A one-fourth-inch diameter hole was drilled into the lid of each vial to allow ventilation, and covered with a nylon mesh 400 lines/inch to prevent escape of mites.

Culture cells were kept at constant temperatures of 10, 15, 21, and 27°C (all ± 1°C) to determine the effect of different temperatures on development rates of the *Macrocheles*. Growth chambers Model R30BI from Sherer-Gillett Company, Marshall, Michigan, were used. The growth chambers had no artificial light in them, so mites were in constant darkness except when being examined under the microscope. *Macrocheles* lack eye spots, so it was thought the constant darkness might not affect them appreciably. However, possible effects of light on *Macrocheles* could be a subject for future study, especially since it is known to affect the silphid beetles on which these mites are found.

The *M. necrophoraphila* were fed a diet of nematodes, *Rhabditella* sp., which they were regularly observed ingesting. The *Rhabditella* in turn were reared within each vial on torn mealworms, *Tenebrio molitor*.

Rhabditella were originally extracted from rotting fruits lying on soil. Stock cultures of *Rhabditella* were maintained in jars of oatmeal on a wet sand substrate, modifying a method used by Singh and Rodriguez (1966). After an initial culture of nematodes was transferred to torn mealworms, they reproduced, and no addition of nematodes was necessary to maintain an adequate supply of worms for growth and reproduction of *M. necrophoraphila*. Weekly, one-half of a late instar *Tenebrio* was added to each culture vial to insure a suitable reproductive medium for the *Rhabditella*, and consequently, an adequate *Rhabditella* supply for the *M. necrophoraphila*.

There was some problem with mold development in these cultures. Each time vials were checked for development of mites, mold was wiped out with a small wad of paper toweling held in a forceps. This was done under a dissecting microscope to insure that no mites or eggs were crushed. It was noted during the latter parts of the study that if large numbers of *M. necrophoraphila* were kept in one vial, there was seldom any problem with development of mold. The reasons for this are unknown at this time, and should be investigated to see if related to the mites' diet.

All culture vials were checked daily for production of eggs by females, and to determine the length of the mite stadia. Eggs and individuals whose life histories were to be observed were isolated from parent females to new cells. Transfers were most easily accomplished by using a camel hair brush cut to three to five bristles. Eggs were frequently deposited in small holes of the plaster of Paris, and small bits of plaster often had to be chipped away from the egg with a fine needle before it could be picked up on a brush. Many times the eggs were nearly as large as the hole or even larger, leading one to believe that they must expand a bit after deposit by the female.

Individual mites which had reached maturity were checked every two to four days thereafter to determine the length of their life span, and the number of offspring produced by a single female.

Descriptions of the adult and immature *M. necrophoraphila* obtained from these cultures are given in the systematic portion of this thesis.

Results and Discussion

The fact that *M. necrophoraphila* reproduces successfully on a nematode diet in the laboratory is probably related to its natural diet in a carrion habitat. While their feeding in a natural setting cannot be easily observed, it is quite easy to observe masses of nematodes on decaying carrion, and it is likely that they form a large part of the mites' diet there as well. Singh and Rodriguez (1966) reported three other species of *Macrocheles* which they successfully reared on nematodes. One of these was *M. muscaedomesticae* whose biology Axtell (1969) has studied rather extensively as a possible biological control for synanthropic flies. Although the adults of this species preferred house fly eggs over namatodes, its protonymphs and deutonymphs under the same conditions preferred nematodes (Rodriguez, *et al.*, 1962). While *M. necrophoraphila* can be successfully reared on nematodes, additional studies need to be done to determine more precisely its food preferences in a carrion habitat.

M. necrophoraphila reproduces both bisexually and parthenogenetically. In this study unfertilized females produced only males, and females which were apparently fertilized produced females, as is normal for most species of *Macrocheles* (Oliver, 1971).

Mean development times from egg to the various instars of *M. necrophoraphila* are shown in Figure 26. Development times for immature instars were considerably longer at 15 than at 21 or 27°C. Time for larvae to hatch from eggs was 1.5 days at 15° compared to 0.7 days at 21° and 27°. Times from egg to protonymph were 2.8 days at 15°, 1.2 days at 21° and 27°. Females required 4.3 days to reach the deutonymph at 15°, 2.1 days at 21°, and 2.4 days at 27°, whereas males required 4.2 days at 15°, 2.2 days at 21°, and 1.9 days at 27°. For both males and females development was also considerably faster at 21°

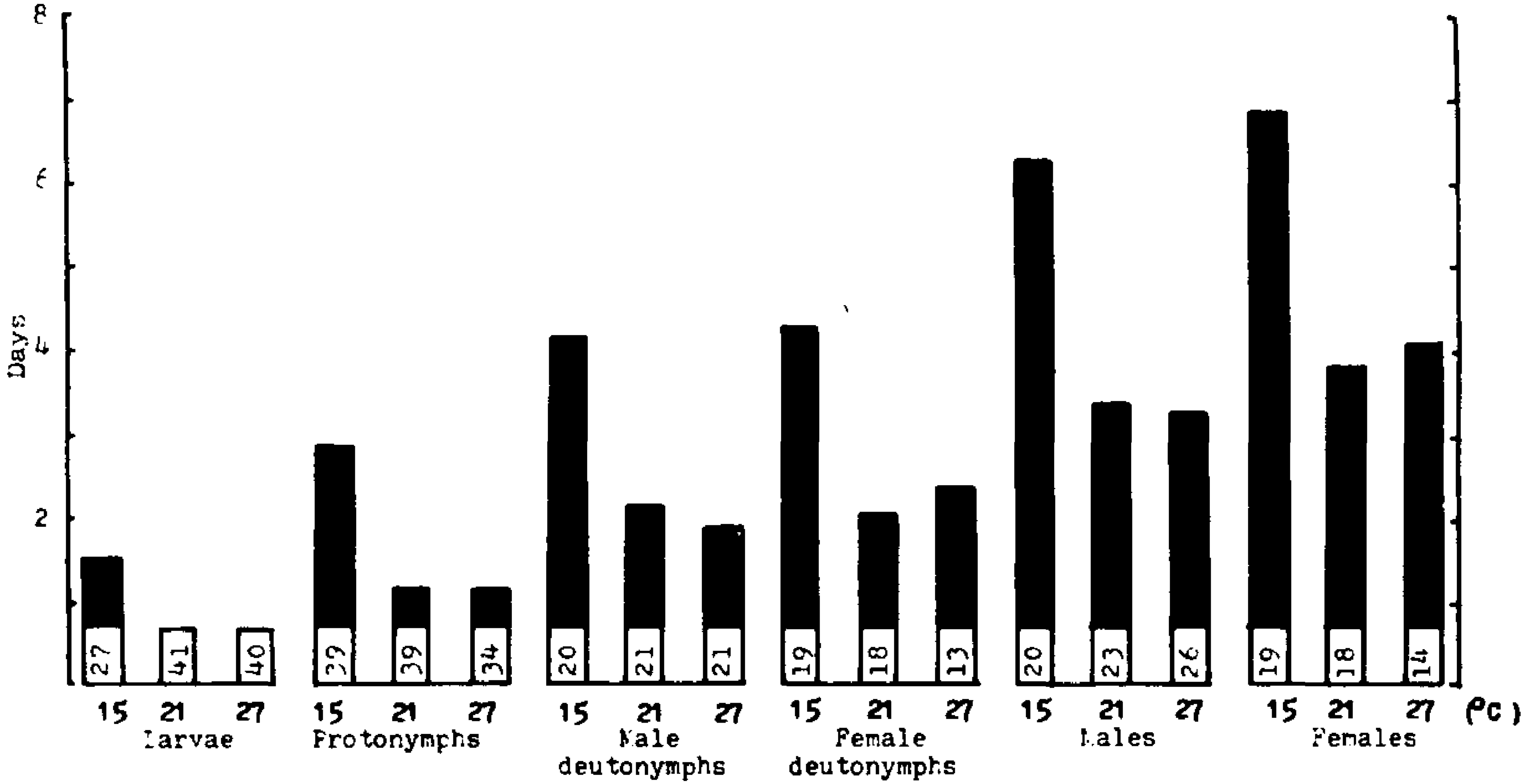

Figure 26. Mean development time for Macrocheles necrophoraphila from egg to each instar at three different temperatures. (Numbers within bars indicate number of specimens).

and 27°C than it was at 15°. Females reached adulthood slightly faster at 21° (3.8 days) than at 27° (4.2 days). In contrast, they required 6.8 days to develop at 15°C.

Males reached adulthood sooner at 27° (3.3 days) than at 21° (3.4 days). As with females, males had considerably shorter development time at 21° and 27°C than at 15° (6.3 days).

It is interesting to note that males reached the adult instar from 0.4-0.9 day sooner than females. Costa (1966) noted that in _Macrocheles robustulus_, males matured nearly one day earlier than females, and also mounted deutonymphs as if preparing for copulation. _M. necrophoraphila_ displayed the same mounting behavior. Costa observed that insemination of females took place after their final molt, and that females could not be inseminated very long after the molt if their exoskeleton had time to harden. Therefore, mature males would have to be waiting to copulate with females soon after their final molt if they were to be inseminated. Faster male development time would make the chances for this greater.

The effect of temperature on development is more marked in the time which females require to produce eggs than in development of the mites themselves. Egg to egg generation time (for 16 females) at 15° averaged 18.4 days, whereas it averaged only 7.3 days (for 18 females) at 21° and 8.3 days (for 15 females) at 27°C.

TABLE 5. Survival time of *M. necrophoraphila* at 10°C. (Time is number of days after placement into 10° cells from 21° cells)

Instar	No. Mites	Average Survival (Days)	Range in Survival (Days)
Larva	3	3.3	2-4
Protonymphs	5	8.0	2-12
Deutonymphs	8	23.0	9-66
Males	4	30.5	9-69
Females	5	91.4	51-170

M. necrophoraphila did not reproduce, nor did immatures molt at 10°. The survival time of the various instars at 10° is given in Table 5.

From these data it can be seen that the older the instar, the better it was able to survive at this colder temperature. Females survived three times longer than males, but even though their average survival time after placement into 10° was 91.4 days, not a single female produced eggs. At 15° the average female produced its first egg 11.6 days after reaching adulthood, at 21° in 3.5 days, and in 4.1 days at 27°. These numbers indicated that apparently something in the egg development processes of the females stops at a temperature between 10 and 15°. A number of implications for the life cycle of the mite follow from this fact.

The silphid species found in Michigan have a wide geographic range, both farther north and south. It would be interesting to see how much farther north than Michigan _M. necrophoraphila_ is found on these beetles since its reproduction ceases between 10 and 15°C. Perhaps in colder, more northern areas _M. necrophoraphila_ is replaced on silphids by other mites which can reproduce at colder temperatures. Also certain silphid species such as _S. noveboracensis_ are more predominantly spring species, while several species of _Nicrophorus_ are more common during summer months. Further studies are needed to determine whether a possible seasonal occurrence of mite species is related to seasonal frequency of the beetles.

Survival by adult and nymphal instars of _M. necrophoraphila_ for over a week at 10°C could certainly help to adapt this mite to survive temperature fluctuations that are likely to occur during its active period, especially in spring and autumn. Its influence in a carrion habitat must be related to the numbers of individuals present, which in turn are related to factors regulating its reproduction.

CONCLUDING COMMENTS

Although the factors which initially attract mites to Silphidae and cause them to attach to the beetles were beyond the scope of this study, the discussion would be incomplete without mentioning that these factors provide very basic areas for research. Farish and Axtell (1971) reviewed previous investigations of phoretic behavior in mites, and noted that additional studies were justified. Their study and that of Rapp (1959) are the most extensive and both deal with phoresy of mites on insects from manure.

It should be noted that a phoretic mite receives competitive stimuli. These stimuli attract it to attach to an insect; or they oppose the insect attraction, causing the mite to leave an insect or to remain on a substrate off the insect. Farish and Axtell (1971) theorize that a mite becomes a phoretic when its substrate's attractiveness becomes less than that of its potential insect transport. Possible factors mentioned which stimulate attachment were air currents caused by insect wing movement, emission of carbon dioxide by an insect, and undetermined chemical attractions from an insect. All of these are possibilities in the case of mites on silphid beetles. The excretions of silphid beetles could well be investigated as an attractant.

Possible detachment factors given by Farish and Axtell (1971) which could cause mites to leave insects included hunger of the mite, chemical attractants and/or moisture in the substrate inhabited by the transporting insect. These are other possible stimuli for mites on Silphidae which remain for future investigation.

SUMMARY

The mite fauna found on 246 Michigan silphid beetles represented by six species of *Nicrophorus*, four species of *Silpha*, and *Necrodes surinamensis* was examined. Beetles were collected from cans baited with carrion of various types.

A total of 11,743 mites were identified from these beetles. Eleven mite species were found in numbers of forty or more. These included four species of *Poecilochirus*, three species of *Macrocheles*, *Histiostoma cyrtandrae*, *Pelzneria crenulata*, *Spinanoetus pelznerae*, and *Anoetus turcastanae*. Four new species are described: *Poecilochirus longisetosa*, *P. silphaphila*, *Macrocheles breviseta*, and *M. necrophoraphila*.

Each mite species is discussed in relation to: (1) total numbers collected, (2) variation in numbers on each beetle species, (3) percent of beetles infested, (4) average number of mites/beetle, (5) locational preferences on beetles.

All species of *Nicrophorus* showed at least 89 percent infestation by mites. Three species were 100

percent infested. The average number of mite species on the various species of *Nicrophorus* ranged from 2.4-3.8 species/beetle. Infestation of *Silpha* ranged from 44-85 percent of the specimens. The various species of *Silpha* averaged 1.0-1.9 mite species/beetle.

The biology and phoretic behavior of anoetids and *Poecilochirus* found on Silphidae are discussed. A life history study of *Macrocheles necrophoraphila* new species is given, including comments on its biology. Egg to egg generation time averaged 7.3 days at 21°C and 18.4 days at 15°C. It failed to reproduce, and immatures did not molt at 10°C.

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APPENDICES

APPENDIX 1. Mite species found on each beetle species.

Mite species	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
	Found on 40 *Microphorus tomentosus*.					
Poecilochirus necrophori	28	70	124	1-19	4.4	3.1
P. subterraneus	27	68	159	1-28	5.7	3.9
P. longisetosa	5	13	13	1-6	2.6	0.3
P. silphaphila	11	28	38	1-8	3.5	1.0
Pelzneria crenulata	33	83	3411	1-574	103.4	85.3
Spinanoetus pelznerae	4	10	6	1	1.5	0.2
Anoetus turcastanae	2	5	2	1	1.0	0.1
Macrocheles necrophoraphila	2	5	7	1-6	3.5	0.2
M. breviseta	1	3	2	2	2.0	0.1
M. vespillo	1	3	1	1	1.0	0.0
Acaridae	3	8	3	1	1.0	0.1
Oribatei	1	3	1	1	1.0	0.0
Analgidae	1	3	1	1	1.0	0.0

APPENDIX 1. cont'd.

Mite species	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
	Found on 17 *Nicrophorus americanus*.					
Poecilochirus necrophori	1	6	1	1	1.0	0.1
P. silphaphila	2	12	2	1	1.0	0.1
Macrocheles dimidiatus	1	6	1	1	1.0	0.1
M. necrophoraphila	13	77	591	1-282	45.4	34.8
M. vespillo	4	24	97	1-47	24.3	5.7
Pelzneria crenulata	10	59	967	2-206	96.7	56.8
Uropodidae	2	12	6	1-5	3.0	0.4
Spinanoetus pelznerae	1	6	1	1	1.0	0.1
Anoetus turcastanae	2	12	4	1-3	2.0	0.2
Acaridae	1	6	2	2	2.0	0.1
	Found on 6 *Nicrophorus vespilloides*.					
Poecilochirus necrophori	3	50	52	4-26	17.3	8.3
P. subterraneus	2	33	4	1-3	2.0	0.7
P. silphaphila	1	17	3	3	3.0	0.5
Macrocheles necrophoraphila	5	83	21	1-9	4.2	3.5
Pelzneria crenulata	4	67	79	3-34	19.8	13.1
Anoetus turcastanae	1	17	1	1	1.0	0.2
Uropodidae	1	17	1	1	1.0	0.2
Rhodacaridae	1	17	2	2	2.0	0.2

APPENDIX 1. cont'd.

Mite species	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
	Found on 7 *Nicrophorus pustulatus*.					
Poecilochirus necrophori	2	29	168	22-146	84.0	24.0
P. subterraneus	4	57	183	1-132	45.8	26.2
Pelzneria crinulata	6	86	782	9-460	130.3	111.7
Histiostoma cyrtandrae	1	14	40	40	40.0	5.7
Macrocheles nicrophoraphila	1	14	25	25	25.0	3.6
Uropodidae	1	14	6	6	6.0	0.9
Acaridae	2	29	2	1	1.0	0.3
	Found on 9 *Nicrophorus orbicollis*.					
Poecilochirus necrophori	4	45	30	1-17	7.5	3.3
P. silphaphila	2	22	9	2-7	4.5	1.0
Macrocheles necrophoraphila	6	67	116	1-101	19.3	12.9
Pelzneria crenulata	4	44	10	1-4	2.5	1.1
Anoetus turcastanae	1	11	1	1	1.0	0.1
Uropodidae	3	33	16	1-5	5.3	1.8
Hydrachnidae	1	11	1	1	1.0	0.1
Oribatei	1	11	1	1	1.0	0.1
Astigmata	1	11	1	1	1.0	0.1

APPENDIX 1. cont'd.

Mite species	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
	Found on 13 *Nicrophorus marginatus*.					
Poecilochirus necrophori	4	31	37	1-32	9.3	2.8
P. longisetosa	8	62	43	1-8	5.4	3.3
Macrocheles breviseta	8	62	63	1-21	7.9	4.8
M. vespillo	3	23	13	2-6	4.3	1.0
Pelzneria crenulata	9	69	442	1-224	49.1	34.0
Spinanoetus pelznerae	5	39	9	1-4	1.8	0.7
Anoetus turcastanae	9	69	593	1-387	65.9	45.6
Uropodidae	1	8	1	1	1.0	0.1
	Found on 18 *Necrodes surinamensis*.					
Poecilochirus necrophori	1	6	1	1	1.0	0.1
Pelzneria crenulata	2	11	21	1-19	10.5	1.2
Spinanoetus pelznerae	12	67	422	5-108	35.2	23.4
Anoetus turcastanae	1	6	1	1	1.0	0.1
Saproglyphidae	1	6	4	4	4.0	0.2
	Found on 13 *Silpha inaequalis*.					
Pelzneria crenulata	10	77	190	1-81	19.0	14.6
Spinanoetus pelznerae	5	38	79	4-29	15.8	6.1

APPENDIX 1. cont'd.

Mite species	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
	Found on 54 *Silpha americana*.					
Poecilochirus necrophori	6	11	17	1-10	2.9	0.3
Macrocheles dimidiatus	1	2	1	1	1.0	0.0
M. necrocheles	1	2	1	1	1.0	0.0
Pelzneria crenulata	6	11	30	1-20	5.0	0.6
Spinanoetus pelznerae	5	9	14	1-8	2.8	0.3
Anoetus turcastanae	2	4	2	1	1.0	0.0
Uropodidae	1	2	1	1	1.0	0.0
Acaridae	2	4	2	1	1.0	0.0
Pyemotidae	2	4	2	1	1.0	0.0
Ascaidae	1	2	1	1	1.0	0.0
	Found on 53 *Silpha noveboracensis*.					
Poecilochirus necrophori	9	17	18	1-3	2.0	0.3
Macrocheles necrophoraphila	1	2	1	1	1.0	0.0
Pelzneria crenulata	30	57	573	1-39	19.1	10.8
Spinanoetus pelznerae	40	76	2149	1-281	53.8	40.6
Acaridae	1	2	1	1	1.0	0.0
Labidophoridae	1	2	1	1	1.0	0.0
	Found on 16 *Silpha lapponica*.					
Poecilochirus silphaphila	1	6	1	1	1.0	0.1
Pelzneria crenulata	4	25	6	1-2	1.5	0.4
Spinanoetus pelznerae	1	6	1	1	1.0	0.1
Rhodacaridae	1	6	1	1	1.0	0.1

APPENDIX 2. Beetle species bearing each mite species. (Numbers in parentheses following beetle species indicate number of specimens.)

	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
***Poecilochirus necrophori* on:**						
Nicrophorus tomentosus (40)	28	70	124	1-19	4.4	3.1
N. marginatus (13)	4	31	37	1-32	9.3	2.8
N. americanus (17)	1	6	1	1	1.0	0.1
N. vespilloides (6)	3	50	52	4-26	17.3	8.3
N. pustulatus (7)	2	29	168	22-146	84.0	24.0
N. orbicollis (9)	4	45	30	1-17	7.5	3.3
Silpha americana (54)	6	11	17	1-10	2.9	0.3
S. noveboracensis (53)	9	17	18	1-3	2.0	0.3
Necrodes surinamensis (18)	1	6	1	1	1.0	0.1
***Poecilochirus subterraneus* on:**						
Nicrophorus pustulatus (7)	4	57	183	1-132	45.8	26.2
N. tomentosus (40)	27	68	159	1-28	5.7	3.9
N. vespilloides (6)	2	33	4	1-3	2.0	0.7
***Poecilochirus longisetosa* on:**						
Nicrophorus marginatus (13)	4	31	43	1-32	9.3	2.8
N. tomentosus (40)	5	13	13	1-6	2.6	0.3

APPENDIX 2. cont'd.

	No. beetles with mite species	% of beetles with mite	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
Poecilochirus silphaphila on:						
Nicrophorus tomentosus (40)	11	28	38	1-8	3.5	1.0
N. orbicollis (9)	2	22	9	2-7	4.5	1.0
N. vespilloides (6)	1	17	3	3	3.0	0.5
N. americanus (17)	2	12	2	1	1.0	0.1
Macrocheles necrophoraphila on:						
Nicrophorus americanus (17)	13	77	591	1-282	45.4	34.8
N. orbicollis (9)	6	67	116	1-101	19.3	12.9
N. pustulatus (7)	1	14	25	25	25.0	3.6
N. vespilloides (6)	5	83	21	1-9	4.2	3.3
N. tomentosus (40)	2	5	7	1-6	3.5	0.2
Silpha americana (54)	1	2	1	1	1.0	0.0
S. noveboracensis (53)	1	2	1	1	1.0	0.0
Macrocheles breviseta on:						
Nicrophorus marginatus (13)	8	62	63	1-21	7.9	4.8
N. tomentosus (40)	1	3	2	2	2.0	0.1
Macrocheles vespillo on:						
Nicrophorus americanus (17)	4	24	97	1-47	24.3	5.7
N. marginatus (13)	3	23	13	2-6	4.3	1.0
N. tomentosus (40)	1	3	1	1	1.0	0.0

APPENDIX 2. cont'd.

	No. beetles with mite species	% of beetles with mite	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
***Pelzneria crenulata* on:**						
Nicrophorus pustulatus (7)	6	86	782	9-460	130.3	111.7
N. tomentosus (40)	33	83	3411	1-574	103.4	85.3
N. americanus (17)	10	59	967	2-206	96.7	56.8
N. marginatus (13)	9	69	449	1-224	49.1	34.0
N. vespilloides (6)	4	67	79	3-34	19.8	13.1
N. orbicollis (9)	4	44	10	1-4	2.5	1.1
Silpha inaequalis (13)	10	77	190	1-81	19.0	14.6
S. noveboracensis (53)	30	57	574	1-99	19.1	10.8
S. americana (54)	6	11	30	1-20	5.0	0.6
S. lapponica (16)	4	25	6	1-2	1.5	0.4
Necrodes surinamensis (18)	2	11	21	1-19	10.5	1.2
***Anoetus turcastanae* on:**						
Nicrophorus marginatus (13)	9	69	593	1-387	65.9	45.6
N. americanus (17)	2	12	4	1-3	2.0	0.2
N. vespilloides (6)	1	17	1	1	1.0	0.2
N. orbicollis (9)	1	11	1	1	1.0	0.1
N. tomentosus (40)	2	5	2	1	1.0	0.1
Silpha americana (54)	2	4	2	1	1.0	0.0
Necrodes surinamensis (18)	1	6	1	1	1.0	0.1

APPENDIX 2. cont'd.

	No. beetles with mite species	% beetles with mites	Total no. mites	Range mites/ beetle	Mean no. mites for beetles with mites	Mean no. mites for all beetles
<u>Spinanoetus</u> <u>pelznerae</u> on:						
<u>Silpha</u> <u>nove-boracensis</u> (53)	40	76	2149	1-281	53.8	40.6
<u>S.</u> <u>inaequalis</u> (13)	5	38	79	4-59	15.8	6.1
<u>S.</u> <u>americana</u> (54)	5	9	14	1-8	2.8	0.3
<u>S.</u> <u>lapponica</u> (16)	1	6	1	1	1.0	0.1
<u>Necrodes</u> <u>surinamensis</u> (18)	12	67	422	5-108	35.2	23.4
<u>Nicrophorus</u> <u>marginatus</u> (13)	5	39	9	1-4	1.8	0.7
<u>N.</u> <u>tomentosus</u> (40)	4	10	4	1	1.0	0.2
<u>N.</u> <u>americanus</u> (17)	1	6	1	1	1.0	0.1
<u>Histiostoma</u> <u>cyrtandrae</u> on:						
<u>Nicrophorus</u> <u>pustulatus</u> (7)	1	14	40	40	40.0	5.7