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Burying beetle larvae: Nearctic *Nicrophorus* and Oriental *Ptomascopus morio* (Silphidae)

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ABSTRACT. Third instar larvae are described for the first time for the following species: *Nicrophorus defodiens* Mannerheim, *N.guttula* Motschulsky, *N.hybridus* Hatch and Angell, *N.marginatus* Fabricius, *N.nigrita* Mannerheim, *N.obscurus* Kirby, *N.orbicollis* Say and *N.sayi* Laporte, and are redescribed for *N.investigator* Zetterstedt, *N.tomentosus* Weber and *Ptomascopus morio* Kraatz. Keys are provided to larvae of the subfamilies of Silphidae, genera of Nicrophorinae and the known third instar larvae of Nearctic *Nicrophorus*.

A subfamilial description of the larvae of the Nicrophorinae and a generic description of the larvae of *Nicrophorus* are presented. Evolutionary trends within the larvae of Nicrophorinae and phylogenetic relationships among Nearctic *Nicrophorus* are discussed.

Larvae of *Nicrophorus* are very similar, differing from *Ptomascopus* primarily in the reduced sclerotization and by possession of spines in place of the tergal lobes of the latter. This trend towards reduced sclerotization continues within *Nicrophorus*, with species groups being recognizable on the basis of the form and extent of the ventral abdominal sclerotization, positioning and sclerotization of the labial palpi and the presence or absence of sutures at the bases of the urogomphi.

Introduction

Members of the family Silphidae (*sensu* Newton, unpublished) are large beetles (10–35 mm in length), which are commonly called carrion beetles because of their common occurrence at vertebrate carcasses. There are two subfamilies recognized within the family in this study, the Silphinae, for which larvae of many Nearctic species have been well treated by Dorsey (1940), and the Nicrophorinae. Within the Nicrophorinae, two genera are recognized, the Oriental *Ptomascopus* and the widely distributed *Nicrophorus*.

The life history of *Ptomascopus morio* has only recently become known (Peck, personal communication), while that of *Nicrophorus* should be familiar to most coleopterists. *Nicrophorus* are commonly called burying beetles or sexton beetles because of their habits of interring small vertebrate carcasses. Eggs are then laid in the underground chamber, and the larvae feed upon the decaying flesh of the carcass. They are thought to have the most advanced form of parental care in beetles. More detailed information on the biology of *Nicrophorus* can be found in Pukowski (1933), Balduf (1935), Milne & Milne (1944, 1976), Leech (1934) and Anderson (1981).

As part of studies on the biology, distribution and systematics of North American Silphidae (Anderson, 1981), an examination of the literature revealed a lack of information on the larval stages of most *Nicrophorus*. Within the North American fauna, only the

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larvae of *Nicrophorus tomentosus* Weber (Schaupp, 1881), *N.investigator* Zetterstedt (Pukowski, 1934) and *N.vespilloides* Herbst (Pukowski, 1934) have been described. All three descriptions are insufficient, however, to permit accurate species identification. Also lacking is a complete description of the larvae of the genus *Ptomascopus*, essential for making any comments on evolutionary relationships within *Nicrophorus* using larval characters.

The purpose of this paper is to fill, in part, the gap in our knowledge of nicrophorine larvae by providing descriptions of most Nearctic species of *Nicrophorus* and of *Ptomascopus morio*. On this basis, larvae of the Nicrophorinae and *Nicrophorus* can then be characterized and the evolutionary relationships of most Nearctic species of *Nicrophorus* be inferred.

This study considers larvae of all Nearctic species of *Nicrophorus* with the exception of *N.americanus* Olivier, *N.carolinus* (Linnaeus), *N.mexicanus* Matthews, *N.pustulatus* Herschel and *N.vespilloides* Herbst, although the latter is considered in part.

Materials and Methods

Larvae of five species of *Nicrophorus* were acquired through a generous loan from Dr R. B. Madge, Commonwealth Institute of Entomology, London. Larvae of *N.sayi* were reared and loaned by Dr D. S. Wilson, Michigan State University and Dr A. F. Newton, Jr, Harvard University, while larvae of *N.nigrita* were loaned by Mr S. E. Miller, Harvard University. The larvae of the remaining three species were reared by the author. Rearing was accomplished by placing a dead mouse in a plastic 2 litre ice cream container, filled with approximately 15 cm of moist, sandy soil. A single pair of beetles was then placed in the container and left undisturbed for 2–3 weeks. Subsequent exhumation of the crypt yielded larvae, some of which were preserved for systematic purposes. Others were left to continue development as part of studies on the life history of the group. Larvae of *Ptomascopus morio* were reared by Dr S. B. Peck, Carleton University, during his studies on the life history of that species.

Larvae were killed in boiling water and then preserved in 70–80% alcohol. Larvae were examined in alcohol using a dissecting microscope. Detailed examination of the head and mouthparts of representative specimens of all species was made using a compound microscope at magnifications of up to 400×. For these detailed examinations, the mouthparts were first dissected from the head, and both placed in a hot 10% KOH solution to clear the structures of any musculature. Specimens were then placed in glycerine on cavity slides, covered with a coverslip and examined. All absolute and relative measurements were made using an ocular micrometer.

Structural terms follow those of Dorsey (1940).

Systematics

The higher classification and phylogeny of silphids is at present under investigation by Dr A. F. Newton, Jr. In view of this, a detailed and lengthy discussion of the phylogenetic relationships of the Nicrophorinae will not be attempted. Evolutionary relationships within *Nicrophorus* will be discussed, and this will necessitate reference to character states in larvae of the other genus in the subfamily, *Ptomascopus*.

Larvae of the Silphidae can be distinguished from all other coleopterous larvae by the following combination of characters (Böving & Craighead, 1930; Crowson, 1967; Kasule, 1966): Mandibles lacking a molar part; mala fused to stipes, divided at apex into galeal and lacinial lobes, the galeal lobe bearing a large brush of setae, the lacinial lobe spinose only on the lateral margin; ligula bilobed; bearing well developed, usually articulated, two-segmented urogomphi. All members of the family, so far as is known, undergo three larval instars.

Two subfamilies are recognized, and their larvae can be distinguished by the following key (Böving & Craighead, 1930):

Tergites small, those on the abdomen quadrispinose; ventral surface whitish and soft, lacking large sternites; with a single, unpigmented ocellus on each side of the head . . . . . *Nicrophorinae*

Tergites large, laterally produced with the posterior angles usually acuminate; ventral surface with the sternites large, well developed; with six pigmented ocelli on each side of the head . . . . . *Silphinae*

The taxonomy of Nearctic silphine larvae has been well treated by Dorsey (1940), although not all Nearctic species are included. In this paper, Dorsey considers all of the Nearctic species to be in the genus *Silpha*. Recent studies by Dr R. B. Madge (unpublished) have since placed the Nearctic species in the generic concepts utilized for the Palearctic species. Thus Dorsey's generic description of *Silpha* must be considered applicable at the subfamilial level, and not at the generic level as it was originally intended.

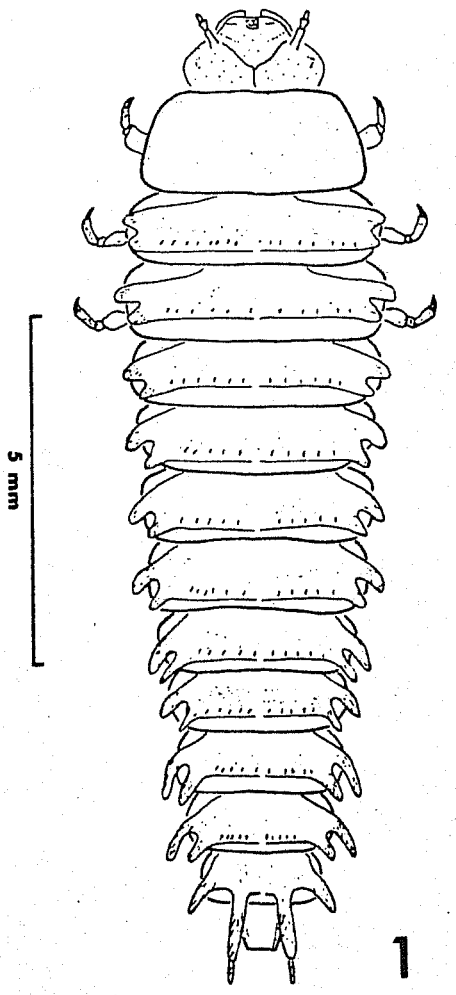
However, a subfamilial description is lacking for the Nicrophorinae and would appear appropriate in view of the diverse amount of material that has become available during this study.

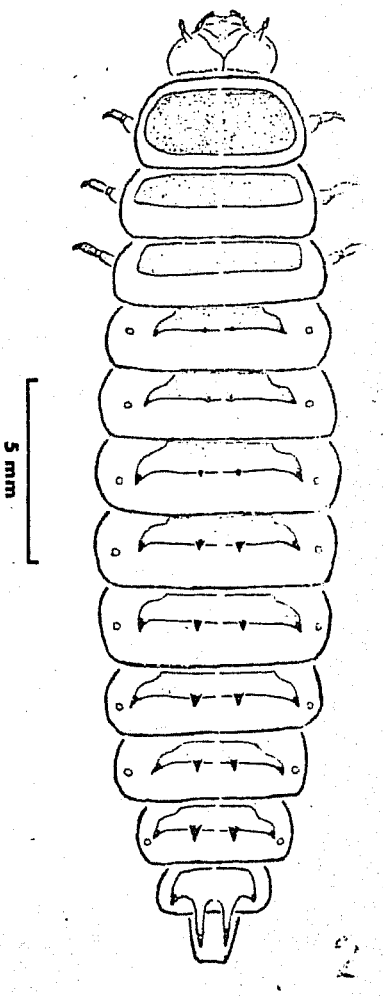
NICROPHORINAE

Description of third instar larva (Figs. 1 and 2).

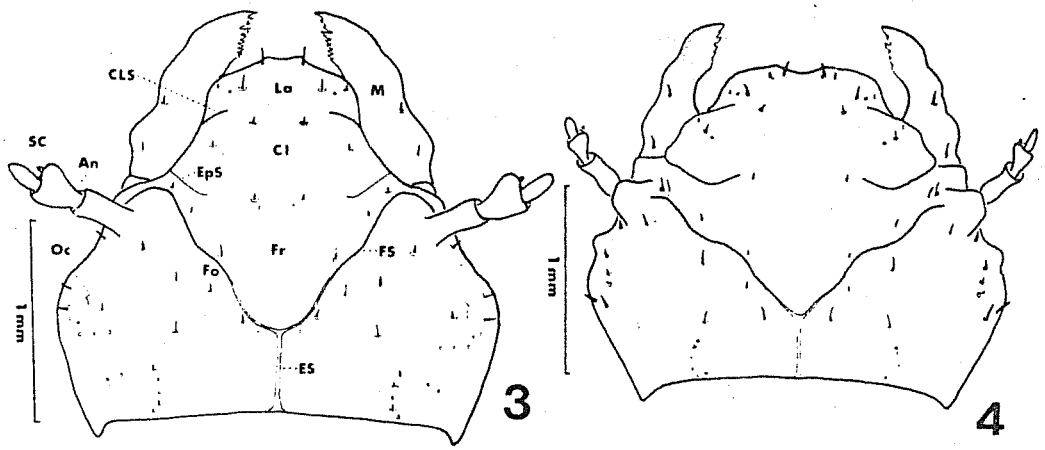
Body eruciform, tapering posteriorly; all thoracic and abdominal segments generally cylindrical in cross-section.

Head (Figs. 3 and 4) with setation sparse, short; with broad fovea (Fo; a shallow pit) lateral to mid-point of each frontal suture (FS); yellow-brown in colour; with a single unpigmented ocellus (Oc) on each side, located posterior to base of antenna (An). Frontal and epicranial sutures distinct, deeply impressed; frontal sutures converging medially, forming 'V' shaped posterior angle on frons; epicranial suture (ES) short, approximately one third





FIGS. 1–2. Dorsal habitus of third instar larvae: 1, *Ptomascopus morio*; 2, *Nicrophorus investigator*.

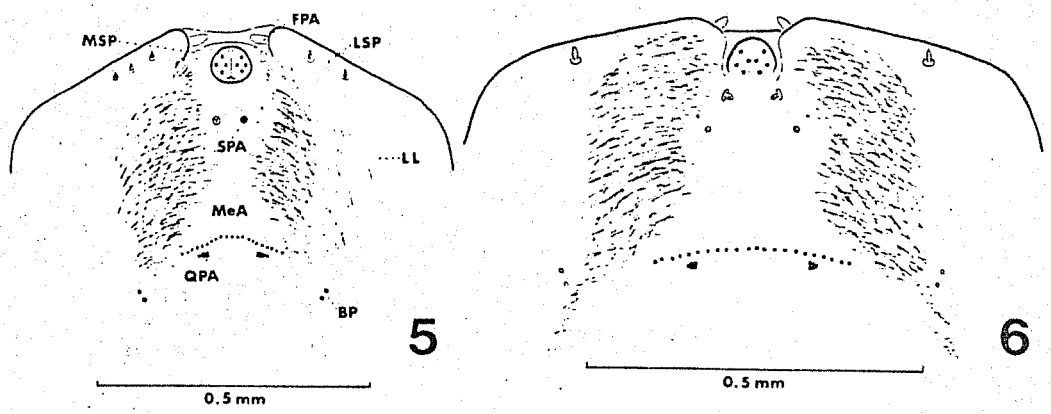


FIGS. 3–4. Dorsal view of head of third instar larvae: 3, *Nicrophorus marginatus*, An, antenna; Cl, clypeus; CLS, clypeo-labral suture; EpS, epistomal suture; ES, epicranial suture; Fo, fovea; Fr, frons; FS, frontal suture; La, labrum; M, mandible; Oc, ocellus; SC, sensory cone. 4, *Ptomascopus morio*.

length of frontal suture. Frons (Fr) slightly elevated anteriorly at middle; medially produced anteriorly; setation sparse, short; colour darker. Epistomal suture (EpS) absent medially, represented laterally by an internal ridge extending from anterior tentorial attachment to dorsal mandibular articulation. Clypeal area (Cl) transversely hexagonal in shape, colour dark. Clypeo-labral suture (CLS) indistinct medially, deeply impressed laterally. Labrum (La) quadrate, broader than long, moderately medially prolonged; broadly emarginate at middle; median area dark in colour, occasionally feebly concave longitudinally. Genae with basal areas inwardly prolonged, not meeting; separated by wide, short, broadly rounded gula; light brown in colour.

Antennae (An) three-segmented, short; segment 1 cylindrical, as long as segments 2 and 3 combined; segment 2 triangular, with single large apical sensory cone (SC) on inner lobe, also with 2 or 3 minute sensory structures in a close group, approximately 1½ times length of segment 3; segment 3 cylindrical, broadly rounded at apex.

Mandibles (M) with broad, subtriangular base; elongate, tapering to incisor lobe which possesses 6–10 teeth. First (apical) and third (occasionally fourth) teeth equal in length, 1½ times length of others. Molar areas lacking,



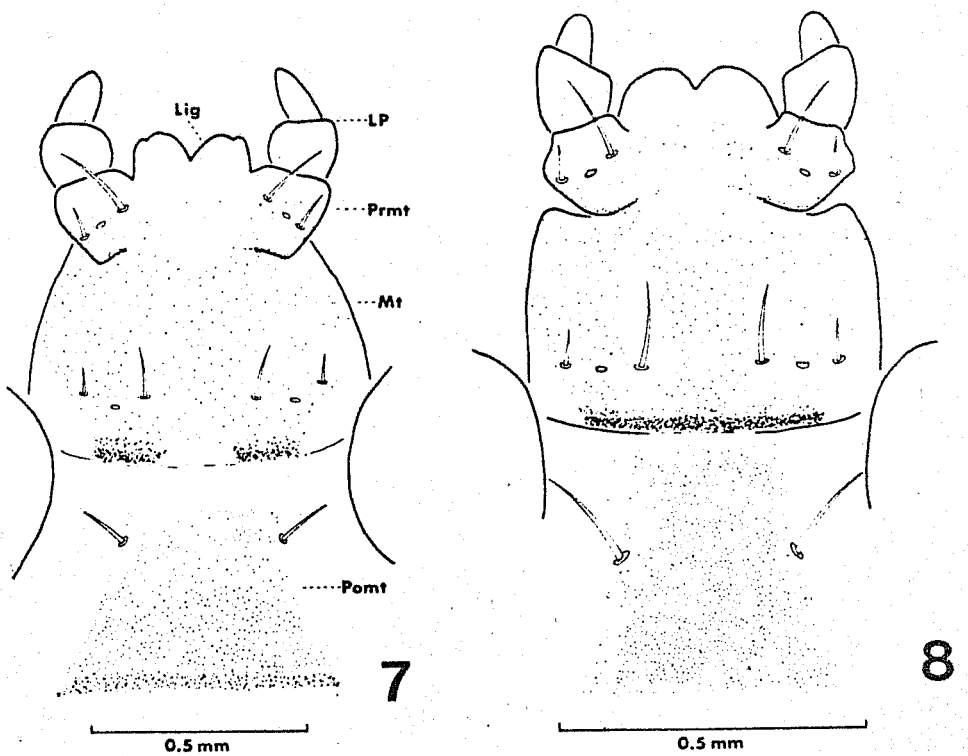
FIGS. 5–6. Ventral view of epipharynx of third instar larvae: 5, *Nicrophorus marginatus*, BP, bilobate pegs; FPA, first porous area; LL, lateral lobe; LSP, lateral sensory pegs; MeA, median area; MSP, median sensory peg; QPA, quinque porous area; SPA, second porous area. 6, *Ptomascopus morio*.

inner margin evenly rounded to base; outer margin sinuate, with two prominent setae on dorsal surface, one situated near base, other at first sinuation.

Maxillae (Figs. 9–11) with cardo, stripes, mala (fused galea and lacinia) and maxillary palpi. Cardo trapezoidal, longer than wide, furnished apically with one seta. Stipes (St) elongate, slightly expanded preapically; ventral setation as in Fig. 11. Mala (Ma) with lacinia and galea fused throughout much of their length, free at apex. Lacinial lobe ventrally medially prolonged to prominent point, slightly longer than wide; inner margin near base with numerous spiculi or elongate setae which extend on to dorsal surface; with two or three elongate teeth at inner apex (IAL); outer oblique portion of apex (OAL) with four stout, short teeth. Galeal lobe with apex broadly rounded, densely setose (GaB); with prominent lateral projection (LaP) on outer margin and shorter, dorsally directed projection (DP) near inner margin, both projections near base; with single seta at mid-length on outer margin. Maxillary palpi (MP) four-segmented; segments 3 and 4 approximately equal in length, each slightly longer than segments 1 or 2. Segments 1–3 cylindrical, expanded very slightly towards their apices; apices obliquely truncate. Segment 4 conical. Segment 1 furnished with single ventral seta.

Labium (Figs. 7 and 8) with well-defined postmentum, mentum and prementum. Venter with large trapezoidal postmentum (Pomt), possessing single seta on outer margin in apical half; base 1½–2 times as wide as apex. Mentum (Mt) short, quadrate to subquadrate, possessing two setae and one sensory pore on each side at mid-length. Prementum (Prmt) with posterolateral angles bearing two setae and one sensory pore; bearing a pair of two-segmented palpi which extend slightly beyond apex of ligula. Segment 1 of palpi broad, almost spherical; segment 2 conical. Ligula (Lig) medially cleft; dorsolaterally with dense hairs, sparsely setose medially. Hypopharyngeal scleromes absent, hypopharyngeal rod and bracon strongly defined. Hypopharynx densely setose laterally and apically.

Epipharynx (Figs. 5 and 6) with lateral



FIGS. 7–8. Ventral view of labium of third instar larvae: 7, *Nicrophorus marginatus*, Lig, ligula; LP, labial palp; Mt, mentum; Pomt, postmentum; Prmt, prementum. 8, *Ptomascopus morio*.

lobes (LL) densely setose, except near base, where there is a triangular, bald area possessing two bilobate pegs (BP) at inner angle; broadly rounded apically, diverging and becoming narrower near base. Medial area (MeA) with setation sparse, near base with broadly parabolic row of 16–22 pores, bounded posteriorly on each side by a group of 5 pores (QPA, quinque porous area of Dorsey, 1940); with prominent sensory papilla (FPA, first porous area of Dorsey, 1940) at apex, divided longitudinally, each half possessing 3 or 4 pores; with 1 median sensory peg (MSP) on each side of the papilla; also with two preapical sensory pores (SPA, second porous area of Dorsey, 1940), each located posterolaterally of sensory papilla and bounded anterolaterally by smaller pore which is often concealed among setae of lateral lobe. Anterolateral margin of epipharynx with 1–3 lateral sensory pegs (LSP) per side.

Thorax three-segmented, each segment bearing one pair of legs. Legs five-segmented, with coxa, trochanter, femora, tibia and tarsungulus. Coxa large, projecting, subquadrate; with scattered setae; inner margin about two-thirds length of femora. Femora trapezoidal, with scattered setae; approximately equal to length of tibia and tarsungulus combined. Tibia cylindrical, with scattered setae. Thorax with sclerotization greatly reduced. Ventrally, with pro-, meso- and metasternum possessing scattered setae between bases of legs. Prosternum anterolaterally with single, small sclerite, bordered laterally by a pair of setae. Other thoracic sterna lacking sclerites. Laterally, all segments bearing small, subquadrate episternum above bases of coxae; meso- and metepimera present or absent; proepimeron lacking. Mesothorax bearing single pair of functional spiracles located posterolaterally to prothoracic legs; spiracular opening annular, with an inwardly directed lobe, bearing a single seta. Mesothorax posterolaterally with spiracular remnant. Dorsally all segments bearing single, large, transversely rectangular tergite; with prominent mid-dorsal suture; broadly rounded laterally. Prothorax with tergite 3 times as wide as long; meso- and metathoracic tergites 5 times as wide as long; all with scattered setae around margins.

Abdomen ten-segmented, segments 1–8 decreasing slightly in width and length posteriorly; segments 9 and 10 strongly decreasing in width and length. Ventrally, segments 2–8 with small, median sclerite, bounded posteriorly by row of 6 setae. Segment 9 with transversely rectangular midventral sclerite; larger than those of segments 2–8; usually bearing setae. Segment 10 cylindrical, sclerotized laterally, variable ventrally; with numerous short setae throughout sclerotized areas. Segments 1–8 each with a pair of annular spiracles located laterally at mid-length of each segment. Dorsally, segments 1–8 each bearing transversely rectangular tergite; with prominent mid-dorsal suture; truncate laterally; each tergite bearing four lobes or spines. Tergite of segment 9 with lobe or spine in each posterolateral corner and two-segmented articulated urogomphus on each side of mid-dorsal suture on hind margin. Segment 10 with dorsum unsclerotized.

Remarks

Larvae of the subfamily Nicrophorinae can easily be distinguished by their greatly reduced sclerotization, especially ventrally, and the quadrispinose abdominal tergites. The lacinial lobe, which possesses 6–10 stout teeth in the Silphinae, is divided into inner and outer areas, each area bearing its own complement of teeth. There is also a reduction in the number of ocelli from 6 pigmented ocelli per side of the head in Silphinae, to a single unpigmented ocellus per side of the head in the Nicrophorinae. Larvae of the Nicrophorinae are generally less mobile, and are more cylindrical in form than the Silphinae, characteristics that can be associated with the unusual life history of most members of the group.

Key to genera of larvae of Nicrophorinae

1 Abdominal, meso- and metathoracic tergites with lateral margins prolonged into two rounded lobes (Fig. 1); tergites large, almost as wide as the abdominal segment and covering the anterior three-quarters of each segment . . . *Promascopus*

– Abdominal tergites (never the thoracic tergites) with a small spine in each posterolateral corner, also with a single spine located on each side of the mid-dorsal suture (Fig. 2); tergites smaller, only slightly greater than half as wide as the abdominal segment, only covering the anterior half to third of the segment . . . . . *Nicrophorus*

In order that the polarity of character states within the larvae of *Nicrophorus* can be recognized, it is necessary to know what the character state is in the sister taxon. In the case of *Nicrophorus*, this taxon is *Ptomascopus* and it is therefore necessary to redescribe (previously described in Kawada *et al.*, 1959) the third instar larva of a species representative of this genus, *Ptomascopus morio* Kraatz.

Ptomascopus morio Kraatz

Length of larva 14–16 mm; width of head capsule 1.85–1.90 mm.

Head (Fig. 4) with setal pattern as in Fig. 4. Anterior margin of clypeus unsclerotized at sides; medially with transversely subtriangular sclerite. Labrum unsclerotized in basal two-thirds on either side of midline, otherwise heavily sclerotized. Mandibles with 6 teeth, first and third equal in length; first and second, and fifth and sixth broadly joined at bases.

Maxillae (Fig. 9) with lacinial lobe with inner margin at base with elongate setae; galeal lobe with setose area prolonged basally on the dorsum at middle.

Labium (Fig. 8) with postmentum bearing pair of setae located only slightly anterior of mid-length; width of base 1½ times width of apex. Mentum quadrate, with almost entire basal margin heavily sclerotized. Membranous areas located laterally of mentum and postmentum sclerotized at middle, slightly convex. Labial palpi with segment 1 distinctly longer than segment 2.

Epipharynx (Fig. 6) with single median sensory peg on each side, located posterolaterally of sensory papilla; sensory papilla with margin incomplete posteriorly; anterolateral pores of second porous area distinct, not situated among setae of lateral lobes; with two prominent, inwardly directed spines at sides of apical emargination.

Thorax with episterna very lightly sclerotized; mes- and metepimera indistinct, apparently lacking. Ventrally and laterally with numerous setae. Metathorax with spiracular remnant present as small, rounded, sclerotized cone. Dorsally, with tergites large, covering anterior three-quarters on meso- and metathorax and almost entire dorsal surface on prothorax. Lateral margins of meso- and metathoracic tergites each bearing a pair of rounded, setose lobes (as found on abdominal tergites 1–8), those on metathorax slightly larger than those on mesothorax.

Abdomen with ninth sternite with 10 setae along posterior margin, and with scattered setae throughout (Fig. 16). Tenth segment (Fig. 12) sclerotized ventrally at base. Dorsally with tergites large, almost as wide as abdominal segment, covering apical three-quarters of each segment. Each tergite with two lateral lobes per side; lobes covered with scattered, appressed, posteriorly directed setae; with similar setae along posterior margin of each tergite. Segments 1–6 with length of anterior lobe approximately equal to length of posterior lobe; segments 7 and 8 with anterior lobe very slightly longer than posterior lobe. All lobes with broad suture at base. Tergite of segment 9 approximately twice as wide as long, bearing pair of long, two-segmented urogomphi which extend slightly beyond the apex of segment 10. Urogomphi approximately twice as long as lateral lobes. Segment 1 of urogomphi 4 times length of segment 2. Laterally all segments bearing numerous small setae.

Material examined. Thirty-five larvae reared from adults collected by Dr S. B. Peck in Japan during the late summer of 1980. Specimens are in the author's collection and that of SBP.

Remarks. Larvae of *Ptomascopus morio* can easily be distinguished from *Nicrophorus* larvae by the characters mentioned in the key. They also differ from *Nicrophorus* in certain aspects of the setation of the head, the absence of a complete margin around the sensory papilla (first porous area) of the epipharynx, the position of the median sensory pegs of the epipharynx, the form of the setae on the basal angles of the inner margin of the lacinial lobe of the maxilla and in the form of the apical setose area of the galeal lobe of the maxilla.

Larvae of *P.morio* are generally smaller, are not as cylindrical and are more sclerotized than *Nicrophorus* larvae and appear to possess a life cycle probably representative of that which preceded the complex life cycle of *Nicrophorus* (Peck, personal communication). This life cycle of *P.morio* necessitates

more mobility than that of *Nicrophorus*, hence the less cylindrical form, and more exposure to the air (since the larval food is not completely buried), hence the greater degree of sclerotization.

Larvae of *Ptomascopus plagiatus* Ménétriés, also from the Oriental region, are undescribed.

Nicrophorus Fabricius

Description of third instar larva

Head (Fig. 3) with setal pattern as in Fig. 3. Anterior margin of clypeus unsclerotized at sides; medially, sclerotization confluent with that of labrum. Labrum unsclerotized or very lightly sclerotized laterally, heavily so medially.

Maxillae (Figs. 10 and 11) with lacinial lobe with inner margin with numerous small spiculi throughout length, as well as at base; galeal lobe lacking dorsal prolongation of apical setose area.

Labium (Fig. 7) with postmentum bearing pair of setae located at anterior third. Mentum subquadrate, basal margin with heavily sclerotized areas confined to outer angles. Labial palpi with segments 1 and 2 equal in length.

Epipharynx (Fig. 5) with median sensory pegs (MSP) located anterolaterally of sensory papilla (FPA); sensory papilla with margin complete; anterolateral pore of second porous area small, indistinct, located among setae of lateral lobe; with two inwardly directed setae at sides of apical emargination.

Thorax with episterna heavily sclerotized, mes- and metepimera distinct, elongate, triangular, separated from episterna by deep, heavily sclerotized sulcus; laterally asetose; ventrally with but few scattered setae. Metathorax with spiracular remnant present as small, open, sclerotized ring. Dorsally with tergites moderately large, those on meso- and metathorax covering only anterior half of segment, those on prothorax covering almost entire dorsal surface; all three tergites equal in width, rounded laterally and lacking spines or lobes.

Abdomen with ninth sternite variable. Tenth segment sclerotized or unsclerotized ventrally at base. Dorsally with tergites small, never as wide as abdominal segment, covering anterior third to half of each segment. Each tergite with 4 spines; one in each posterolateral corner and one on either side of mid-dorsal suture; spines of variable sizes, lacking sutures at bases. Tergite of segment 9 bearing small spine in each posterolateral corner and larger two-segmented urogomphus on each side of mid-dorsal suture. Urogomphus never extending beyond apex of segment 10; segment 1 approximately 3 times length of segment 2. Laterally all segments appearing asetose.

Remarks. Larvae of *Nicrophorus* can be distinguished by their greatly reduced sclerotization and the quadrispinose abdominal tergites. Within the genus, this trend towards reduced sclerotization continues, with certain species groups being characterized by the form of the ventral abdominal sclerotization. Another character, which appears to be of use in separating species, but not for determining phylogenetic relationships, is the relative position and size of the spines on abdominal segments 1–9.

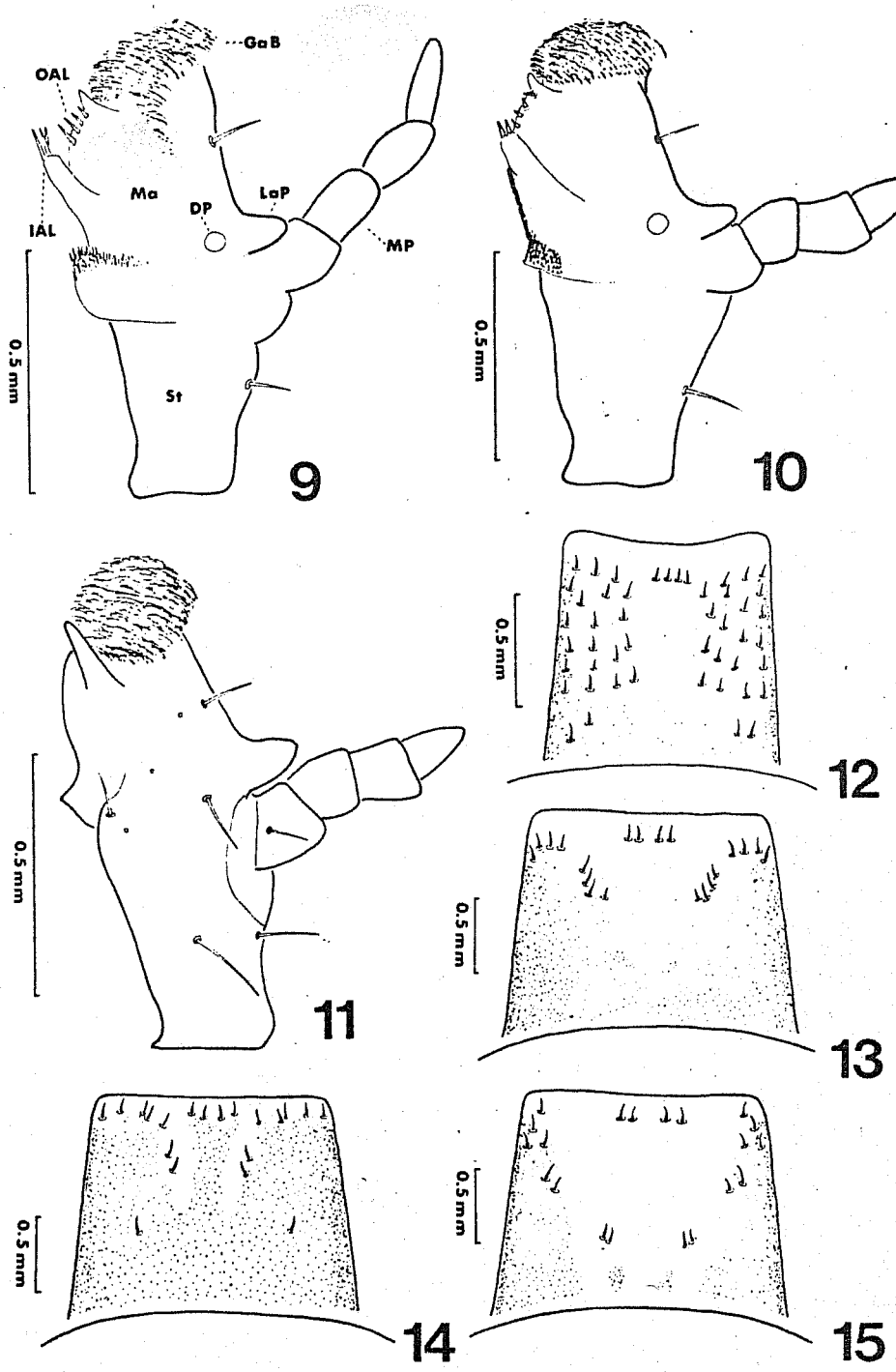
The form of the life cycle in *Nicrophorus* would appear responsible for the reduced sclerotization and mobility. These losses are common in many endoparasitic or endophytic insect larvae and are apparently the result of the relaxation of selection pressures responsible for their maintenance in other insect larvae. Endoparasitic or endophytic larvae also often develop posteriorly directed spines which aid in movement in the food source. Similar structures have been developed in *Nicrophorus*, these being the tergal spines, apparently derived from and therefore homologous with the lateral tergal lobes of *Ptomascopus*.

Based upon descriptions of third instar larvae presented later, the following key to the known larvae of Nearctic *Nicrophorus* is presented.

Key to third instar larvae of Nearctic *Nicrophorus*

1 Venter of abdominal segment 10 unsclerotized at base (Fig. 15); sternite of abdominal segment 9 truncate at the lateral margins (Figs. 18 and 19), or else fragmented (Fig. 20) 2

– Venter of abdominal segment 10 sclerotized at base (Fig. 13); sternite of abdominal segment 9



FIGS. 9–11. Maxillae of third instar larvae: 9, Dorsal view, *Ptomascopus morio*, DP, dorsal projection; GaB, galeal brush; IAL, inner apex of lacinial lobe; LP, lateral projection; Ma, mala; MP, maxillary palp; OAL, outer apex of lacinial lobe; St, stipes. 10, Dorsal view, *Nicrophorus marginatus*. 11, Ventral view, *Nicrophorus marginatus*.

FIGS. 12–15. Ventral view of tenth abdominal segment of third instar larvae: 12, *Ptomascopus morio*; 13, *Nicrophorus defodiens*; 14, *Nicrophorus investigator*; 15, *Nicrophorus marginatus*.

entire, with the posterior margin straight, the anterior margin broadly arcuate, emarginate at middle (Fig. 17) 4

2 Sternite of abdominal segment 9 entire, with the lateral margins truncated (Figs. 18 and 19) . . 3

– Sternite of abdominal segment 9 fragmented (Fig. 20) . . . . . *marginatus*

3 Lateral and mid-dorsal spines on abdominal segment 3 equal in length; ligula lacking lateral lobes . . . . . *obscurus*

– Mid-dorsal spines of abdominal segment 3 approximately 3 times length of lateral spines; ligula with very small lateral lobes . . . . *guttula*

4 Segment 1 of labial palpus unsclerotized ventrally; distance between bases of labial palpi approximately half width of segment 1 of palpus . . . 5

– Segment 1 of labial palpus sclerotized ventrally; distance between bases of labial palpi twice width of segment 1 of palpus 6

5 Bases of urogomphi lacking sutures where they join the tergite; mid-dorsal spines of abdominal segments 2–8 at least twice as long as lateral spines . . . . . *defodiens**

– Bases of urogomphi with sutures where they join the tergite, however often incomplete at middle; mid-dorsal spines of abdominal segments 4–8 at least twice as long as lateral spines . . *sayi*

6 Abdominal segment 10 mid-ventrally sclerotized in apical half, the sclerite 'Y' shaped, extending to bases of innermost pair of apical setae (Fig. 14) 7

– Abdominal segment 10 unsclerotized mid-ventrally in apical half (Fig. 13) 8

7 Lateral spines of abdominal segments 3–8 approximately half length of mid-dorsal spines; lateral spines of segment 9 large, distance to base of urogomphus from base of lateral spine equal to length of lateral spine . . . . . *investigator*

– Lateral spines of abdominal segments 7 and 8 approximately half length of mid-dorsal spines; lateral spines of segment 9 shorter, distance to base of urogomphus from base of lateral spine equal to twice length of lateral spine . . . *nigrita*

8 Lateral and mid-dorsal spines of abdominal segment 1 equal in size; mid-dorsal spines of segments 2–8 at least twice as long as lateral spines; lateral spines of segments 1–8 small, not exceeding diameter of spiracle . . . *tomentosus*

– Lateral spines of abdominal segments 1–3 very slightly longer of equal to length of mid-dorsal spines: mid-dorsal spines of segments 4–8 at least twice as long as lateral spines; lateral spines of segments 1–8 larger, approximately twice diameter of spiracle on segments 6–8 9

9 Lateral spines of abdominal segment 9 large, distance to base of urogomphus from base of lateral spine approximately equal to length of lateral spine . . . . . *hybridus*

– Lateral spines of abdominal segment 9 minute, appearing only as small cones, distance to base of urogomphus from base of lateral spine 4 times or more length of lateral spine . . . . . *orbicollis*

*Characters of *N. vespilloides* discussed by Pukowski (1934) and Hatch (1927) indicate that this species will key out to *defodiens* in the above key. Unfortunately I have not seen larvae of *vespilloides* and therefore cannot distinguish between it and *defodiens*.

Nicrophorus marginatus Fabricius

Length of larva 22 mm; width of head capsule 2.3 mm.

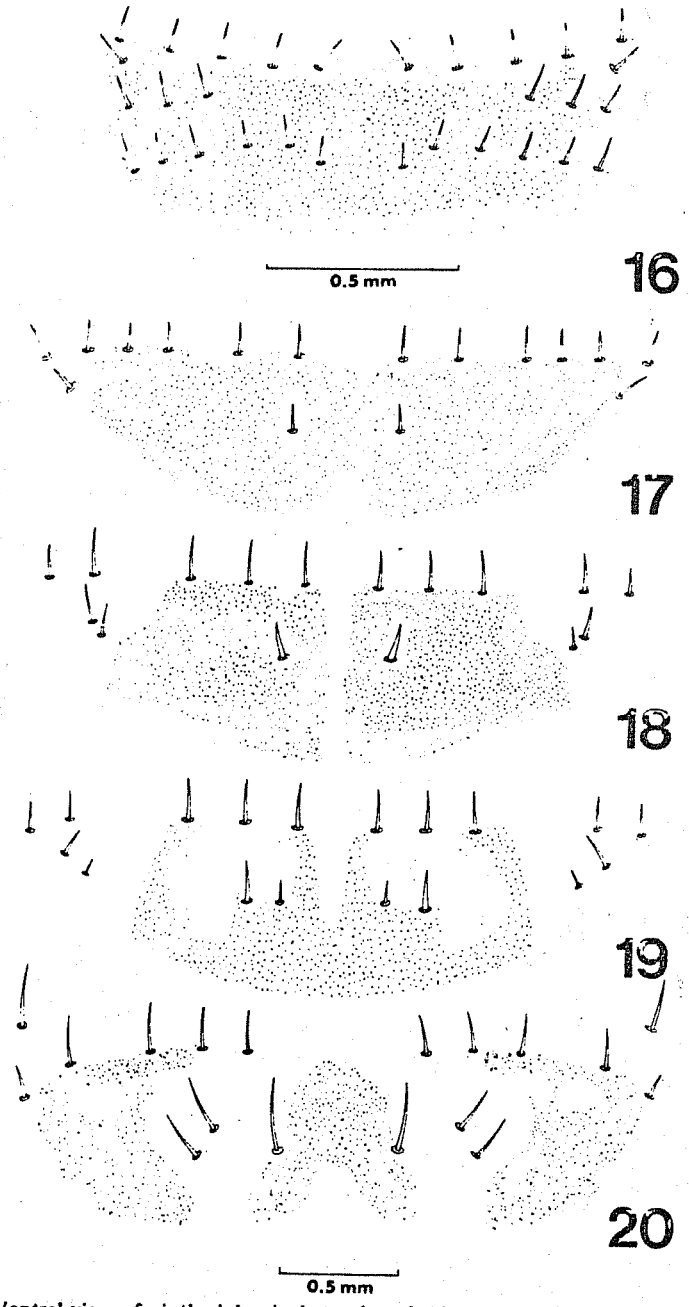
Mandibles with 10 teeth, first and fourth equal in length; fourth recurved anteriorly, broadly joined at base to fifth. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula with small lateral lobes. Epipharynx with anterolateral margins each bearing 3 lateral sensory pegs; apical emargination moderately deep, with pair of prominent, inwardly directed stout setae.

Abdomen with lateral and mid-dorsal spines of segment 1 equal in size, approximately half diameter of spiracle in length; lateral and mid-dorsal spines of segment 2 equal in size, very slightly larger than those on segment 1; lateral and mid-dorsal spines of segment 3 equal in size, approximately equal in length to diameter of spiracle; lateral spines of segments 4–8 approximately third length of mid-dorsal spines, equal in length to diameter of spiracle on segment 4, slightly greater than diameter of spiracle on segment 5, and 1½ times diameter of spiracle on segments 6–8. Ninth tergite with lateral spines moderate in size, distance to base of urogomphus approximately twice length of lateral spine. Urogomphus with suture at base incomplete at middle; segment 1 about twice as long as segment 2. Ninth sternite fragmented (Fig. 20). Segment 10 with venter unsclerotized at base (Fig. 15).

Material examined. One larva, reared by the author from adults collected at Markham, Ontario, Canada, 1.vi.1979. Specimen in author's collection.

Nicrophorus obscurus Kirby

Length of larva 23–34 mm; width of head capsule 2.1–2.4 mm.



FIGS. 16–20. Ventral view of ninth abdominal sternite of third instar larvae: 16, *Promascopus morio*; 17, *Nicrophorus defodiens*; 18, *Nicrophorus obscurus*; 19, *Nicrophorus guttula*; 20, *Nicrophorus marginatus*.

Mandibles with eight teeth, first and fourth equal in length; fourth very slightly recurved anteriorly, broadly joined at base to fifth. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula lacking lateral lobes. Epipharynx with anterolateral margins

each bearing 2 or 3 lateral sensory pegs; apical emargination moderately shallow, with pair of indistinct, inwardly directed setae.

Abdomen with lateral and mid-dorsal spines of segment 1 equal in length, approximately half diameter of spiracle in length; lateral spines of segment 2 very slightly greater in length than mid-dorsal spines, half diameter of spiracle in length; lateral and mid-dorsal spines of segment 3 equal in length, approximately three-quarters diameter of spiracle in length; lateral spines of segments 4–8 approximately third length of mid-dorsal spines, approximately three-quarters diameter of spiracle in length. Ninth tergite with lateral spines small, distance to base of urogomphus 3 times length of lateral spine. Urogomphus with suture at base incomplete at middle; segment 1 approximately 2½ times length of segment 2. Ninth sternite entire, truncate at lateral margins; divided medially in posterior half (Fig. 18). Segment 10 as in *N.marginatus*.

Material examined. Nineteen larvae reared from adults collected by Dr R. B. Madge at Calgary, Alberta, Canada, 8.vi.1964. Specimens are in the collection of RBM.

Nicrophorus guttula Motschulsky

Length of larva 20–23 mm; width of head capsule 1.9–2.0 mm.

Mandibles as in *N.obscurus*. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula with small lateral lobes. Epipharynx with anterolateral margins each bearing 2 or 3 lateral sensory pegs; apical emargination moderately shallow, with pair of indistinct, inwardly directed short setae.

Abdomen with lateral and mid-dorsal spines of segment 1 equal in length, approximately third diameter of spiracle in length; lateral spines of segment 2 very slightly shorter than mid-dorsal spines, approximately half diameter of spiracle in length; lateral spines of segment 3 approximately third as long as mid-dorsal spines, approximately half diameter of spiracle in length; lateral spines of segments 4–8 approximately quarter as long as mid-dorsal spines, approximately equal to diameter of spiracle in length. Ninth tergite with lateral spines moderate in size, distance to base of urogomphus about twice length of lateral spine. Urogomphus with suture at base incomplete at middle; segment 1 twice length of segment 2. Ninth sternite entire, truncate at lateral margins; divided medially in posterior half (Fig. 19). Segment 10 as in *N.marginatus*.

Material examined. Twenty-four larvae reared from adults collected by Dr R. B. Madge at Oliver, British Columbia, Canada, 4.vi.1959. Specimens are in the collection of RBM.

Nicrophorus defodiens Mannerheim

Length of larva 17–19 mm; width of head capsule 1.6–1.8 mm.

Mandibles as in *Ptomascopus morio*. Basal segment of labial palpus unsclerotized ventrally; distance between bases of labial palpi approximately half width of basal segment of labial palpus. Ligula not distinctly cleft, sclerotized laterally, lacking lateral lobes. Epipharynx with anterolateral margins each bearing 1 lateral sensory peg; apical emargination deep, apparently lacking inwardly directed setae.

Abdomen with lateral spines of segment 1 slightly shorter than mid-dorsal spines, approximately equal to diameter of spiracle in length; lateral spines of segments 2–5 approximately half length of mid-dorsal spines, approximately 1⅓ times diameter of spiracle in length; lateral spines of segments 6–8 approximately third length of mid-dorsal spines, 1½ times diameter of spiracle in length. Ninth tergite with lateral spines moderately large, distance to base of urogomphus approximately equal to length of lateral spine. Urogomphus with suture at base lacking; segment 1 approximately twice length of segment 2. Ninth sternite entire; with posterior margin straight, anterior margin broadly arcuate, emarginate medially (Fig. 17). Segment 10 with venter unsclerotized at base (Fig. 13).

Material examined. Five larvae reared by Dr R. B. Madge from adults collected at Edmonton, Alberta, Canada, 14.vii.1960. Specimens are in the collection of RBM.

Nicrophorus sayi Laporte

Length of larva 18–32 mm; widith of head capsule 1.7–2.1 mm.

Mandibles lacking teeth (probably worn). Basal segment of labial palpus unsclerotized ventrally; distance between bases of labial palpi approximately half width of basal segment of labial palpus. Ligula lacking lateral lobes. Epipharynx with anterolateral margins each bearing 1 lateral sensory peg; apical emargination shallow, apparently lacking inwardly directed setae.

Abdomen with lateral spines of segment 1 very slightly longer than mid-dorsal spines, approximately half diameter of spiracle in length; lateral and mid-dorsal spines of segments 2 and 3 equal in length, approximately equal to diameter of spiracle in length; lateral spines of segment 4 approximately half length of mid-dorsal spines, approximately equal to diameter of spiracle in length; lateral spines of segments 5–8 approximately third length of mid-dorsal spines, very slightly greater than diameter of spiracle in length. Ninth tergite with lateral spine moderate in size, distance to base of urogomphus approximately equal to length of lateral spine. Urogomphus with suture at base either complete or incomplete at middle; segment 1 about twice length of segment 2. Ninth sternite entire (as in Fig. 17), although sometimes with reduced sclerotization in anterolateral angles. Segment 10 with venter unsclerotized at base.

Material examined. Fifty-one larvae reared from adults collected by Dr D. S. Wilson at Hickory Corners, Michigan, United States, v.1981 and one larva reared from adults collected by Dr A. F. Newton, Jr, at Carroll Co., New Hampshire, United States, 15.vi. 1981. Specimens are in the author's collection.

Nicrophorus investigator Zetterstedt

Length of larva 26–29 mm; width of head capsule 2.1–2.2 mm.

Mandibles as in *N.obscurus*. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula with small lateral lobes. Epipharynx with anterolateral margins bearing 1 lateral sensory peg; apical emargination shallow, apparently lacking inwardly directed setae.

Abdomen with lateral and mid-dorsal spines of segment 1 equal in length, approximately equal to diameter of spiracle in length; lateral spines of segment 2 approximately half length of mid-dorsal spines, very slightly larger than diameter of spiracle in length; lateral spines of segments 3–8 approximately half length of mid-dorsal spines, increasing from 1⅓ to 1½ times diameter of spiracle in length on posterior segments. Ninth tergite with lateral spines moderately large, distance to base of urogomphus approximately equal to length of lateral spine. Urogomphus with suture at base complete; segment 1 about twice as long as segment 2. Ninth sternite as in *N.defodiens*. Tenth segment with venter sclerotized in apical half as well as at base (Fig. 14).

Material examined. Eleven larvae reared from adults collected by Dr R. B. Madge at Edmonton, Alberta, Canada, 9–16.viii.1964. Specimens are in the collection of RBM.

Nicrophorus nigrita Mannerheim

Length of larva 28 mm; width of head capsule 2.0 mm.

Mandibles as in *N.sayi* (probably worn). Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Epipharynx with anterolateral margins each bearing 1 or 2 lateral sensory pegs (single available specimen has 1 peg on right margin and 2 pegs on left margin); apical emargination shallow, apparently lacking inwardly directed setae.

Abdomen with lateral and mid-dorsal spines of segments 1–4 equal in length, very slightly shorter than the diameter of spiracle in length lateral spines of segments 5 and 6 very slightly shorter than mid-dorsal spines, approximately equal to diameter of spiracle in length; lateral spines of segments 7 and 8 approximately half length of mid-dorsal spines, approximately equal to diameter of spiracle in length. Ninth tergite with lateral spines small, distance to base of urogomphus twice length of lateral spine. Urogomphus with suture at base complete; segment 1 approximately twice length

of segment 2. Ninth sternite as in *N.defodiens*. Tenth segment with ventral sclerotization as in *N.investigator*.

Material examined. One larva (in poor condition) reared from adults collected by S. E. Miller on Santa Barbara Island, California, United States, 5–9.iii.1979. Specimen is in the collection of SEM.

Nicrophorus tomentosus Weber

Length of larva 23–25 mm; width of head capsule 1.8–1.9 mm.

Mandibles as in *N.obscurus*. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula with small lateral lobes. Epipharynx with anterolateral margins each bearing 1 lateral sensory peg; apical emargination shallow, apparently lacking inwardly directed setae.

Abdomen with lateral and mid-dorsal spines of segment 1 equal in length, approximately half diameter of spiracle in length; lateral spines of segment 2 approximately half length of mid-dorsal spines, approximately half diameter of spiracle in length; lateral spines of segment 3 approximately third length of mid-dorsal spines, approximately half diameter of spiracle in length; lateral spines of segments 4–8 approximately third length of mid-dorsal spines, approximately three-quarters diameter of spiracle in length. Ninth tergite with lateral spines small, distance to base of urogomphus approximately 3 times length of lateral spine. Urogomphus with suture at base complete; segment 1 approximately 2½ times length of segment 2. Ninth and tenth sternites as in *N.defodiens*.

Material examined. Two larvae reared by the author from adults collected at Chaffey's Locks, Ontario, Canada, 8.ix.1980. Specimens are in the author's collection.

Nicrophorus hybridus Hatch and Angell

Length of larva 23–27 mm; width of head capsule 2.0–2.3 mm.

Mandibles as in *N.obscurus*. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula lacking lateral lobes. Epipharynx with anterolateral margins each bearing 1 or 2 lateral sensory pegs; apical emargination shallow, with pair of indistinct, inwardly directed, very short setae.

Abdomen with lateral spines of segments 1 and 2 slightly greater in length than mid-dorsal spines, approximately equal to diameter of spiracle in length; lateral and mid-dorsal spines of segment 3 equal in length, approximately 1⅓ times diameter of spiracle in length; lateral spines of segment 4 approximately half length of mid-dorsal spines, approximately 1⅓ times diameter of spiracle in length; lateral spines of segments 5–8 slightly less than half length of mid-dorsal spines, approximately 1½ times diameter of spiracle in length. Ninth tergite with lateral spines moderately large, distance to base of urogomphus equal to length of lateral spine. Urogomphus with suture at base complete; segment 1 twice length of segment 2. Ninth and tenth sternites as in *N.defodiens*.

Material examined. Five larvae reared from adults collected by Dr R. B. Madge at Brandon, Manitoba, Canada, 19.viii.1958. Specimens are in the collection of RBM.

Nicrophorus orbicollis Say

Length of larva 19–23 mm; width of head capsule 1.9–2.2 mm.

Mandibles as in *N.obscurus*. Basal segment of labial palpus sclerotized ventrally; distance between bases of labial palpi approximately twice width of basal segment of labial palpus. Ligula lacking lateral lobes. Epipharynx with anterolateral margins each bearing 2 or 3 lateral sensory pegs; apical emargination moderately deep, with pair of indistinct, inwardly directed setae.

Abdomen with lateral spines of segment 1 slightly longer than mid-dorsal spines, approximately equal to diameter of spiracle in length; lateral and mid-dorsal spines of segments 2 and 3 equal in length, approximately 1⅓ times diameter of spiracle in length; lateral spines of segments 4–8 approximately half length of mid-dorsal spines, approximately 1½ times diameter of spiracle in length. Ninth tergite

TABLE 1. Characters of larvae of *Nicrophorus*.

		Plesiomorphic state	Apomorphic state
1	Base of venter of segment 10	Sclerotized (Figs. 12 and 13)	Unsclerotized (Fig. 15)
2	Apex of venter of segment 10	Unsclerotized (Figs. 12 and 13)	Sclerotized (Fig. 14)
3	Suture at base of urogomphus	Complete	Incomplete at middle or lacking
4	Suture at base of urogomphus	Complete or incomplete at middle	Lacking
5	Bases of labial palpi	Widely separated	Narrowly separated
6	Ventral surface of basal segment of labial palpi	Sclerotized	Unsclerotized
7	Sternite of segment 9	Entire, outer angles acute (Figs. 16 and 17)	Laterally truncate or fragmented (Figs. 18–20)

with lateral spines minute, distance to base of urogomphus 4 times length of lateral spine. Urogomphus with suture at base complete; segment 1 twice length of segment 2. Ninth and tenth sternites as in *N. defodiens*.

Material examined. Three larvae reared from adults collected by the author at Markham, Ontario, Canada, 12.vi.1979. Specimens are in the author's collection.

Phylogeny

From this study, it is now quite apparent that there are few differences between the larvae of species of *Nicrophorus*, and that many of these differences are unimportant in recognizing phylogenetic affinity. An example of this type of character is the relative lengths of the abdominal spines. There are, however, some trends in various characters within the genus that do appear to be phylogenetically important.

In the present study, the sister genus to *Nicrophorus*, and therefore the most suitable out-group for the determination of character state polarity within *Nicrophorus*, is the genus *Ptomascopus*.

A summary of the phylogenetically important characters of *Nicrophorus* and the polarity of their states is presented in Table 1. An examination of the distribution of the apomorphic and plesiomorphic states of these characters (Table 2) reveals strong affinities between certain species.

Nicrophorus marginatus, *guttula* and *obscurus* possess the synapomorphic character state of reduced sclerotization on the venter of segments 9 and 10, indicative of a close relationship. The truncate form of the ninth sternite on *guttula* and *obscurus* may also be indicative of these two species being more closely related to each other, than either is to *marginatus*.

Among the other species, *defodiens* and *vespilloides* appear to be very closely related, since they share the apomorphic character state of the lack of a suture at the base of the urogomphus. These two species also lack ventral sclerotization on the basal segment of the labial palpus and have the palpi situated very close together. These apomorphic character states are also found in *sayi*, indicating that this latter species is also closely related to *defodiens* and *vespilloides*. Some larvae of *sayi* also have the suture at the base of the urogomphus incomplete at the middle and thus are approaching the state where the suture is completely absent. Members of the *marginatus* group (previously delimited) also

TABLE 2. Character states among larvae of nearctic *Nicrophorus* (+, apomorphic; –, plesiomorphic).

	1	2	3	4	5	6	7
marginatus	+	–	+	–	–	–	+
obscurus	+	–	+	–	–	–	+
guttula	+	–	+	–	–	–	+
defodiens	–	–	+	+	+	+	–
*vespilloides**	–	–	+	+	+	+	–
sayi	–	–	+	–	+	+	–
investigator	–	+	–	–	–	–	–
nigrita	–	+	–	–	–	–	–
tomentosus	–	–	–	–	–	–	–
hybridus	–	–	–	–	–	–	–
orbicollis	–	–	–	–	–	–	–

*I have not seen larvae of *N. vespilloides* but indications as to the state of these characters are found in Pukowski (1934) and Hatch (1927).

have the suture incomplete at the middle and may prove to be sister to the *sayi, defodiens* and *vespilloides* group.

Nicrophorus investigator and *nigrita* are another pair of species which appear to be closely related since they possess the synapomorphic character state of possession of apical sclerotization on the middle of the venter of segment 10.

Unfortunately characters were not found which would allow the placement of the remaining species or which would allow for the recognition of affinities between the above groups.

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