

The immature stages of central European species of *Nicrophorus* (Coleoptera, Silphidae)

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Morphology, taxonomy, larval keys

Abstract. All the three larval instars of 5 species of *Nicrophorus* Fabricius are described, illustrated and keyed: *N. vespillo* (L.), *N. vespilloides* Herbst, *N. humator* Ol., *N. investigator* Zett. and *N. fossor* Er. Detailed morphological characterization of all the immature stages at generic level is given.

INTRODUCTION

Burying beetles are well known for their interesting biology, especially for their well-developed parental care of larvae (reviewed in Milne & Milne, 1976; Scott, 1990) or the fighting ability for corpses (Barlett & Ashworth, 1988; Otronen, 1988). Further, data about pheromone emission of males were presented by Mueller & Eggert, 1987. On the other hand, only limited data about the morphology of immature stages are available.

At generic level, larvae of *Nicrophorus* Fabricius were keyed by Hatch (1972a), Byzova (1964) and Klausnitzer & Zerche (1978).

Papers containing isolated descriptions of larvae were reviewed in Pukowski (1934). A short key to the identification of the L₃* of four species (*N. vespilloides*, *N. vespillo*, *N. humator* and *N. investigator*) was given by Henriksen (1922) and adopted by Hatch (1927b). All three larval instars of *N. germanicus* were illustrated by Pukowski (1933). A key of the L₃ of 6 species (*N. vespilloides*, *N. vespillo*, *N. humator*, *N. fossor*, *N. investigator* and *N. germanicus*) was presented by Pukowski (1934). A brief description of the L₃ of *N. humator* was given by Paulian (1941). Photographs of all three larval instars of *N. fossor* were published by Roussel (1964a) and those of *N. vespillo* by Roussel (1964b). Unfortunately, all these descriptions were too brief and don't guarantee correct recognition of the species concerned.

The only recent and relevant paper upon larvae of *Nicrophorus* was that of Anderson (1982). The author presented detailed descriptions and a key to the L₃ of ten North American species (including *N. investigator* and partly *N. vespilloides*). Generic descrip-

* The following abbreviations are used throughout the text: E - egg; L₁, L₂, L₃ - larva of instar I, II, III; L - larva; P - pupa. L₁ and L₂ are collectively designated as "young larvae" L₃ as "mature larvae".

tions based upon L₃ of *Nicrophorus* Fabricius and the related *Ptomascopus* Kraatz were included, as well as a characterization of the L₃ of subfamily Nicrophorinae. Evolutionary relationships of most N. American species were proposed and some characters of evolutionary importance were discussed. A key and brief descriptions of the larvae of N. American *Nicrophorus* can be found in Anderson & Peck (1985), and phylogenetic relationships of Nearctic *Nicrophorus* based also on L₃ morphology were studied by Peck & Anderson (1985).

The aim of this paper is to complete data on immature stages of central European species of *Nicrophorus* (with the exception of *N. germanicus* (L.), *N. sepultor* Charp., *N. vestigator* Herschel and *N. antennatus* Reitt.) and to make an attempt to place these species in existing species groups, based upon the larval morphology.

MATERIAL AND METHODS

All the material used for the description of the immature stages was reared during 1985-1988. Breeding pairs collected in the field were from various localities from Bohemia and more precise data accompanies the descriptions of individual species.

Two methods of rearing were used. During 1985-1987 a modified method, after Špicarová (1969) and Anderson (1982), under natural conditions was employed. With this method, only L₃ and P were obtained. Therefore during 1987-1988, a second method was used: breeding pairs or single females were kept in glass vessels (with diameter about 10-15 cm) on a layer of soil with a piece of fish for nourishment, placed in dark in natural or laboratory conditions. Adults did not bury the carcass and built no crypt. Eggs were then laid in soil and larvae of all instars were taken directly from a shallow depression on the top of the carcass. Pupae were reared from single mature larvae, kept in Petri-dishes with a layer of soil under laboratory conditions.

The material was killed and preserved in Pampel's Fluid, after Švácha & Danilevsky (1987). Some details of the larvae were studied from dissected parts of the head, mounted in Canada balsam on microscope slides. All material examined is deposited in the author's collection.

In the descriptions of larval instars I and II only differences from the third instar are given. Morphological terms follow those of Anderson (1982) and Švácha & Danilevsky (1987).

General morphology of immature stages of the genus *Nicrophorus*

E g g s (Fig. 63) white to yellow, strongly elongated. Chorion without perceptible surface structures under high magnification (about x 10,000).

L a r v a e campodeiform, oval and eruciform, mature larvae dorsoventrally depressed (Fig. 5). Body white to yellow, unsclerotized with the exception of the head; reduced scutal and strongly reduced ventral sclerites; sclerotization in regions surrounding the spiracles, urogomphi and legs; mature larva possesses strongly sclerotized mandibles, sclerotization around their articulation and apical part of labrum.

H e a d (Figs 1, 4, 6-9, 13; Plate I, Figs 3-4)* prognathous, dorsoventrally depressed. Cranium always wider than long, widest behind stemmata. Coronal suture short, straight

* Plates I-II will be found at the end of this issue

(Fig. 4:1). Frontal suture convexly bent in an S-shape (especially in mature larvae). In younger larvae suture virtually continuous or, at most, interrupted in the middle only (Figs 8,9), turned laterally before antenna, in mature larvae anteriorly indistinct (Fig. 6). A fovea is developed laterally of frontal suture, marking the attachment of dorsal tentorial arms (Fig. 4:3).

F r o n s (Fig. 4:4) triangular, sclerotized medially. In mature larvae elevated medioanteriorly and, sometimes in this region, more strongly sclerotized; posteriorly rounded, imperfectly delimited laterally. Posteriorly, equipped with 1 pair, and laterally with 2-3 pairs, of primary setae, anteriorly with another pair of secondary setae and 1 pair of sensillae. Separated from clypeus by epistomal suture laterally only. Protentorial pits lie at medial extremities of both valves of epistomal suture (Fig. 4:10).

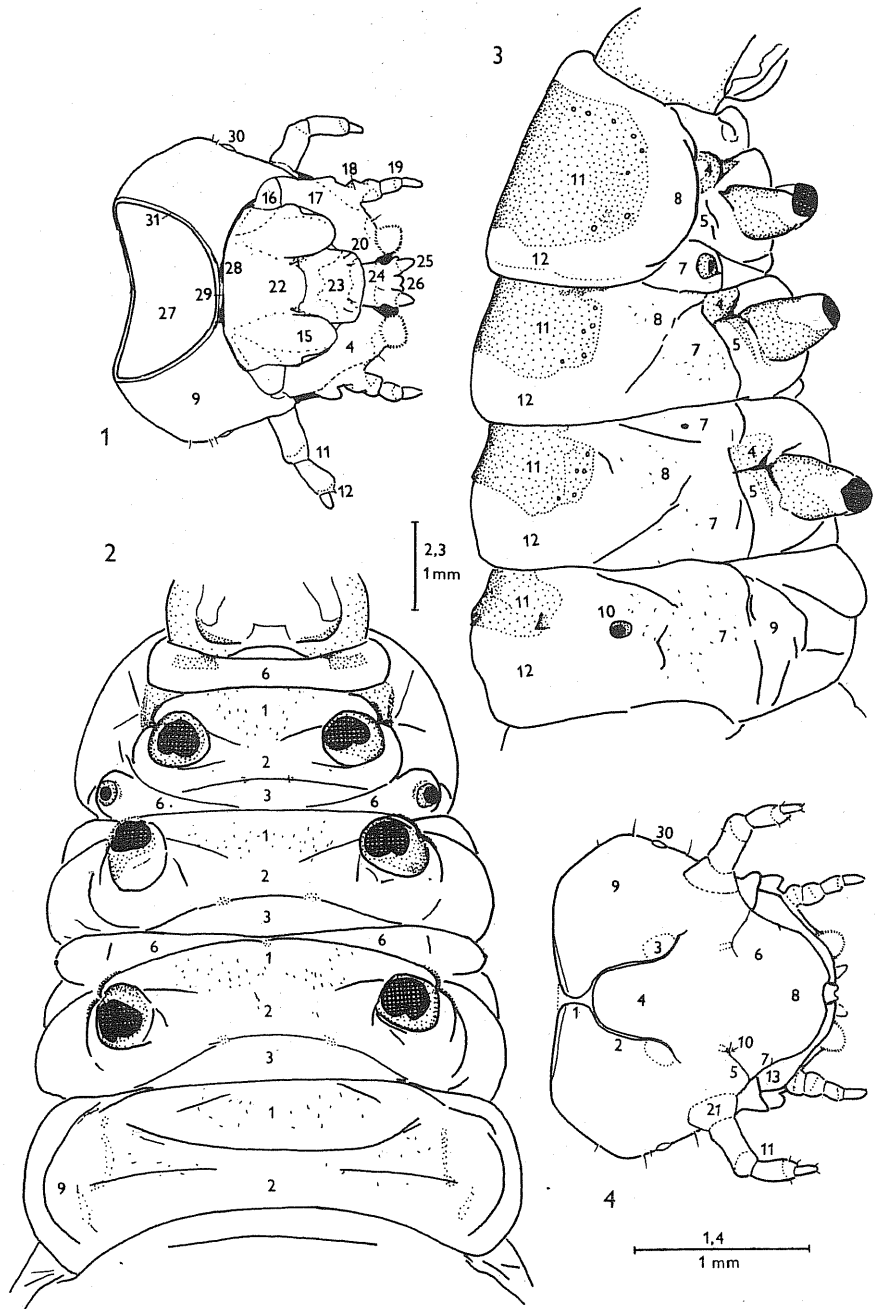
C l y p e u s (Fig. 25) transverse, hexagonal in form, sclerotized as strongly as frons. In mature larvae, the central part has a raised semicircular area, sometimes with a central transverse, darker region whose posterior margin is irregular, medially more or less emarginate and diffuse; laterally this region joined with epistomal suture. Clypeus equipped medially with 2 pairs of primary setae.

L a b r u m pentagonal, separated from clypeus by laterally distinct clypeolabral suture (Fig. 4:7), in younger larvae sclerotized uniformly and as strongly as the clypeus, with two unsclerotized wedge-shaped bands laterobasally (Figs 8,9), in mature larvae unsclerotized laterally and sometimes medially, with slight sclerotization anterolaterally on margin and with very strongly sclerotized trapezoidal area apically (Figs 6, 25). Furnished with 3 pairs of primary setae and 1 pair of sensillae.

E p i p h a r y n x (Fig. 26), with the exception of the medial part, covered by dense microtrichia oriented posteriorly and medially. Anterior part emarginate, at its lateral angles with 1 pair of conical primary setae. Anteriorly, in first porous area, there are 4 pairs of larger sensillae and 1-2 pairs of smaller ones (Fig. 28), posteriorly of these are one pair of second porous areas, each with a triad of sensillae (Fig. 27) and a transverse and irregular row of variable number of sensillae (quinqueporous area sensu Anderson, 1982). Most posteriorly is a pair of porous areas, each with 5 sensillae (Fig. 29), and an asymmetrically localized pair of small conical primary setae. Anterolaterally the epipharyngeal margin has 1-2 pairs of main conical setae.

E p i c r a n i u m strongly developed, forming the widest part of the head. Laterally extended, with a single stemma located anteriorly, before the widest part (Fig. 1:30); directly behind the dorsal mandibular articulation in mature larvae a sharp protuberance is sometimes found, environs of articulation strongly sclerotized. The anterior margin of epicranium (between mandibular articulations) strengthened, in middle projecting into a slender sclerotized apodeme, below its origin branches off a short sclerotized posteriorly directed ledge. Epicranium ventrally from this line with massive protuberance. Epicranium dorsally furnished with 3 pairs, posteriorly with another 3 pairs, of primary setae. Stemma surrounded posteriorly with 5-6 primary setae.

T e n t o r i u m with large, strongly sclerotized V-shaped protentorial arms, which



Figs 1-4: 1 - *Nicrophorus vespilloides*, L3, head, ventral view, schematized; 2 - *N. humator*, L3, thorax and abdominal segment I, ventral view; 3 - *N. humator*, L3, ditto, lateral view; 4 - *N. vespilloides*, L3, head, dorsal view, schematized.

are oval in cross-section, extended in sagittal plane. Dorsal tentorial arms, branching off in two thirds of protentorial arms, are thin and weakly sclerotized. Ventrally tentorium broadens into corpotentorium, the posterior tentorial arms short but bulky. Metatentorial bridge laterally formed by two diverging apodemes, connected posteriorly by a very thin, dorsally elevated arch.

Antennae short and minute, three-segmented (Figs 10-12). Segments cylindrical, with sclerotized rings. Segment I with 4 sensillae, segment II with one sensilla basally and 3 setae subapically. Apically with 3 sensillae (Plate II, Fig. 4): the first one large, conspicuous, conic, and situated apically; the remaining two are small, one visible at high magnifications only (about x 500). Segment III of antenna located asymmetrically, subapically furnished with a group of 5 setae, apically with another group of setae: 2 short and one filamentous, elongate. Antenna inserted on side of head, with connecting membrane wide, slightly conically elongated.

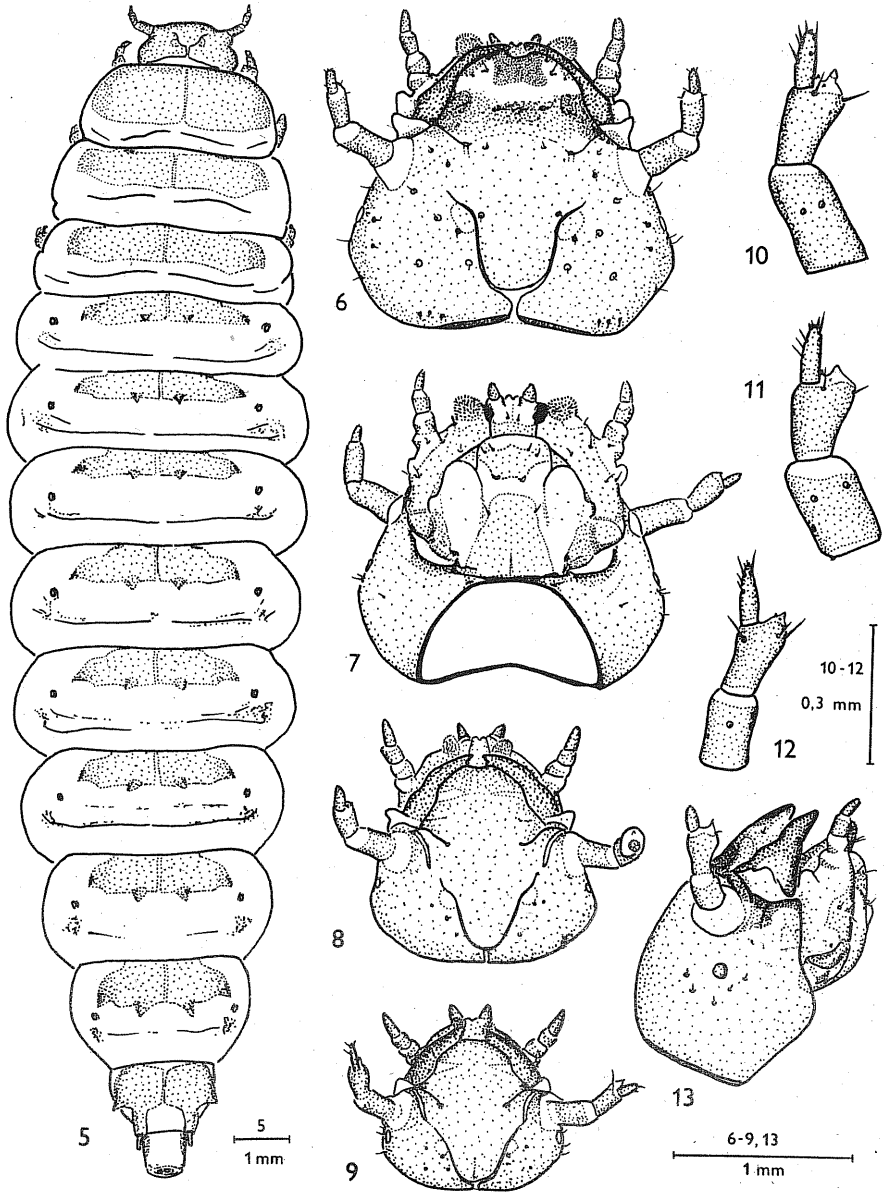
Mandible (Figs 64-66) strongly sclerotized. Dorsal and ventral articulations respectively sited laterally and on anterolateral projection of epicranium. Epicranium curved laterally, but base of mandible straight, connected with epicranium by a triangular membrane. Mandible at base triangular in cross-section, medially projecting into the head by a strongly sclerotized apodeme for attachment of a mandibular adductor. Mandible almost triangular from dorsal view in younger larvae (Figs 65,66), in mature larvae the mandible is elongate, with apex broadened (Fig. 64). The apex with several variably developed teeth (Figs 67-69). Basal part of mandible without mola, dorsolaterally with one robust primary seta, more apically with two small primary setae, at inner basal region one sensilla.

Labiomaxillary complex composed of maxillae and labium, fused at base and strongly elevated ventrally (Fig. 13; Plate II, Fig. 1). Between maxilla and labium there is a distinct, wide and unsclerotized connecting lobe (Fig. 1:15; Plate I, Fig. 4), anterior part broadened and bearing a longitudinal ridge; at base fused with submentum and anteriorly extending to half the length of the mentum.

Maxillae relatively strongly sclerotized. Cardo triangular in ventral view, with one primary seta posteriorly. Posteroventral region of cardo sclerotized and posteriorly projected into an arc. Stipes robust, elongate and strongly sclerotized ventrally, with 5 pairs of primary setae (Figs 14, 19). Palpiger in the form of a conical process attached laterally on maxilla, separated by wide unsclerotized line. Palpiger sclerotized posteriorly and dorsally in narrow strip only. Maxillary palpi three-segmented, segments I and II cylindrical, segment III conic. All segments annular and sclerotized, but segment I sometimes unsclerotized ventrally. On the last segment there is a close-fitting digitiform

1,4: 1 - coronal suture, 2 - frontal suture, 3 - fovea, 4 - frontale, 5 - epistomal suture, 6 - clypeus, 7 - clypeolabral suture, 8 - labrum, 9 - epicranium, 10 - protentorial pit, 11 - antenna, 12 - conical sensilla, 13 - mandible, 14 - maxilla, 15 - connecting lobe, 16 - cardo, 17 - stipes, 18 - palpiger, 19 - maxillary palpus, 20 - mala, 21 - connecting membrane of antenna, 22 - submentum, 23 - mentum, 24 - praementum, 25 - labial palpus, 26 - ligula, 27 - foramen occipitale, 28 - metatentorial pit, 29 - gula, 30 - stemma, 31 - postoccipt.

2,3: 1 - basisternum, 2 - sternellum, 3 - spinasternum, 4 - episternum, 5 - epimeron, 6 - praesternum, 7 - epipleurum, 8 - alar lobe, 9 - pleural lobe, 10 - spiracular area, 11 - scutal sclerite, 12 - scutellum.



Figs 5-13: *Nicrophorus vespilloides*. 5 - mature larva, dorsal view, schematized; 6 - L3, head, dorsal view; 7 - L3, head, ventral view; 8 - L2, head, dorsal view; 9 - L1, head, dorsal view; 10 - L3, right antenna, lateral view; 11 - L2, ditto; 12 - L1, ditto; 13 - L3, head, lateral view.

sensilla laterally, apically group of about 12 sensillae.

M a l a preapically broadened, only apically divided into free lacinia and galea, ventrally sclerotized, with longitudinal groove (Plate II, Fig. 2). Medial sclerotization lacking on dorsal side (Fig. 15).

L a c i n i a dorsally with strongly sclerotized basal edge, laterally with process projected as a narrow, oval, variably pronounced protuberance, which has 2-3 teeth at its apex. Apex of lacinia with 3-5 strong teeth, dorsal and median margins of protuberance densely covered with microtrichia, dorsobasally with a second, small conical process.

G a l e a wide, ventroapically with oval, transverse area of dense setae (Plate II, Fig. 1), more extensive ventrally than dorsally. Posterior area separated by unsclerotized, and wide wedge-shaped line. Galea with strongly sclerotized process dorsobasally.

L a b i u m with well defined submentum, mentum and praementum. Submentum (Fig. 1:22) at base trapezoidally sclerotized, distally with one pair of primary setae. Mentum (Fig. 1:23) transversely weakly sclerotized, basally with 2 pairs of primary setae, dorsally with small and central hypopharyngeal sclerome, connected 2 sclerotized lines on each side with base of dorsal mandibular articulation and laterally with epicranium. Dorsal side apically densely covered with microtrichia.

P r a e m e n t u m transverse, sclerotized laterally, sometimes partially also ventrally. Dorsobasally with strongly sclerotized, curved transverse line. Labial palpi two-segmented. Segment I cylindrical, either with a more or less wide sclerotized zone at base or sclerotized laterally only. Segment II conic, sclerotized, apically with crescentic area of about 12 miniature sensillae. Ligula narrow or very wide, depending upon species, divided by a vestigial medial line, sclerotized laterally, with only a few dispersed sensillae apically.

T h o r a x (Figs 2,3; Plate I, Figs 1,2) cylindrical, flattened dorsoventrally. Pro-, meso- and metathorax of similar construction so they are described together with the main differences noted.

Each **n o t u m** divided into anterior scutal sclerite (fused praescutum and scutum, Fig. 3:11) and posterior unsclerotized scutellum (Fig. 3:12). Sclerite strongly sclerotized, medially interrupted by unsclerotized line. Marginal regions, in particular, with a number of small primary setae. Sclerite irregularly folded (Plate I, Fig. 1), attachments of muscles visible as paler or darker spots. In mature larvae the sclerite is reduced. Proscutal sclerite most developed (Figs 43, 48, 53), not reduced, those of meso- and metascutum similar, but shorter and sometimes notched on both sides posteriorly (Figs 44, 49, 54). Posterior margin of scutum straight, scutal sclerite not projected in lobes and/or spines.

Notum adjacent to unsclerotized lateral **a l a r l o b e** (Fig. 3:8), largest and rounded on prothorax, on meso- and metathorax shorter and wedge-shaped, dividing epipleurum (Fig. 3:7) into anterior and posterior parts. On mesothorax anterior epipleurum bears an annular spiracle whereas on metathorax only a laterally sited vestigial spiracle is perceptible as small sclerotized area.

Pleuron consists anteriorly of sclerotized episternum (Fig. 3:4), posteriorly of epimeron (Fig. 3:5). Proepimeron unsclerotized, meso- and metepimeron with triangular sclerotized area, tapered posteriorly. Pleural suture strongly sclerotized.

Thoracic segment (Fig. 2) divided ventrally by transsternal suture into anterior basisternum and posterior sternellum and spinasternum. Sometimes, in mature larvae, particularly in the prothorax, a postcoxal region is delineated by a transverse line. On each segment is an anterior and distinct praesternum. On prothorax this is transverse, wide and laterally with a sclerotized area. On meso- and metathorax this is particularly developed laterally and appears to be interrupted medially.

Each thoracic sternum posteriorly with well developed transverse spinasternum. Before spinasternum lie two paired and one medial unpaired impressions, these are probably remnants of a reduced thoracic endoskeleton. Basisternum and alar lobe covered by small setae.

Legs (Figs 40-42) relatively short, heavily sclerotized, with the exception of a medial unsclerotized region with a high number of small setae. Coxa large and conical, trochanter short and triangular. Femur cylindrical, elongate and with longer setae ventrally. Tibiotarsus always shorter and narrower than femur, in apical part with a higher number of sensillae and longer setae. Praetarsus slender, shorter than tibiotarsus, basal part wider with 2 short setae ventrally, apical part slender, bearing a bent claw (Plate II, Fig. 3).

Abdomen ten-segmented, segments I-VI short, cylindrical, dorsoventrally flattened. Segments VII and VIII gradually longer and narrower, IX considerably modified, X converted into an anal tube.

Notum divided dorsally by a transverse suture into anterior scutal sclerite (the fused praescutum and scutum, Fig. 3:11) and posterior short unsclerotized scutellum (Fig. 3:12). Scutal sclerite almost as long as that of metathorax, but distinctly narrower (Fig. 5), medially with paler lengthwise line. In younger larvae sclerite extends to half the length of the notum and in mature larvae, to the first third only. Posterior margin extended to form one pair each of lateral and dorsal lobes or spines. Dorsal pair of spines always longer than lateral and the ratio of their lengths differs for each segment (Figs 45, 46; 50, 51; 55, 56). Spines short on first abdominal segments, more or less elongate caudally in some species. In younger larvae, spines longer than those of mature larvae. Particularly in mature larvae considerable traumatical variability occurs; thus, spines are not used in larval taxonomy. Sclerite on posterior margin between lateral and dorsal spine with a large seta. Spine with numerous setae, the largest one situated apically.

Laterally the segments have a separated **spiracular area** (Fig. 3:10). Spiracle on segments I-VIII, annular, sclerotized, smaller than on mesothorax.

Epipleurum (Fig. 3:7) extended laterally to form a distinct lobe (called an epipleural lobe), apically with 1-2 setae. In younger larvae of a few species (e.g. *N. vespilloides*, *N. fossor*) with small sclerite but in mature instars it is always unsclerotized.

Ventrolaterally there is a **pleural lobe** (Figs 2:9, 3:9) with one large seta and

a number of small setae apically, in younger larvae of most species (with exception of *N. vespillo*) the lobe is with an oval, lengthwise extended sclerite.

S t e r n u m divided by transsternal suture into anterior basisternum (Fig. 2:1) and posterior sternellum (Fig. 2:2). In mature larvae a coxal lobe separated by a more or less distinct suture. Sternum laterally defined by heavy, lengthwise indentations (the attachments of abdominal muscles). On lateral region of segment I only, the basisternum possesses an anterior vestigial line. Sternum medially with small, reduced, rhomboid sclerite, lacking on segment I. Sclerite size constant in all instars, but relatively strongly reduced in mature larvae due to growth of segment width. In L₁ on its posterior margin, and in L₂ and L₃, in a transverse row, are 3 pairs of longer setae. Sternum with many microscopic setae on surface. Sclerite sometimes divided into a number of small sclerotized areas.

S e g m e n t I X smaller than preceding ones. Dorsally with transverse sclerite, on posterior margin with lateral pair of spines and two-segmented urogomphi (Figs 47, 52, 57). First segment robust, longer than the second. Base of segment I separated from sclerite by suture, sometimes incomplete in the middle of the urogomphus width or wholly lacking. Urogomphus with higher number of setae, one long located apically. Sternum of segment IX fused ventrally with pleural lobe, bearing one big sclerite (Figs 35-39), with 5 pairs of setae posteriorly, higher number of setae marginally, and a group or a pair of setae centrally. Sclerite sometimes reduced laterally, in the most advanced case fragmented (Fig. 36).

S e g m e n t X reduced to a cylindrical anal tube. Unsclerotized dorsally, sclerotized laterally and in part ventrally. Venter at base sclerotized, sometimes apically with triangular or Y-shaped sclerotized area (Figs 30, 31, 34), in advanced cases wholly unsclerotized ventrally (Fig. 33). Furnished with a high number of sometimes asymmetrically located setae. Anus margined by three retractable papillae (two laterodorsally and one ventrally), covered densely by microtrichia.

P u p a e (Figs 58-60): the type of pupa exarata libera, white to yellow. Strongly sclerotized (and thus brown in colour) in older pupae are eyes, mandibles, apical part of clypeus, mouthparts, mesonotum, claws, spines on tibiae and long spines on pronotum and abdomen; the latter spines very strongly sclerotized in distal half. Just before eclosion the second pair of wings become grey. Pupa flattened dorsoventrally, habitus like that of adult beetle. Pronotum bent forward, head with mouthparts directed to the venter of body.

H e a d laterally above the eyes with 3 pairs of long spines. Eye laterally with sigmoid distinctive line. Maxillary and labial palpi with indicated segmentation. Antennae pressed to the head, dorsally pointed, with indicated segmentation. Antennal club sited under the extended margin of pronotum.

S h a p e o f p r o n o t u m like that of adult. Anteriorly with 3-4 pairs of short spines, anterolaterally with 1 small pair of spines, marginally with 3 pairs of robust spines, posterior margin with 2-3 pairs of spines.

Mesonotum large, triangular, metanotum extended posteriorly into a sharp projection, laterally with semicircular line. Wings pressed to the body. The first pair abbreviated, with indication of longitudinal striae. Legs free, tibia with spines apically, tarsi segmented and directed posteriorly.

A b d o m e n strongly flattened dorsoventrally, only segments I-IV with spiracles which are located laterodorsally. Segment I narrow. Segments I-VIII dorsally with a pair of small spines, segments II-VII with a second pair of robust spines laterally. Segment VIII convex dorsally, without spines. Segments IX and X modified. Segment IX extended into a pair of conical lobes laterally, each with large, posteriorly oriented apical spine. Rudiments of male or female genitalia visible ventrally (Figs 61, 62).

Differential diagnosis of particular instars

L1: Body length 4.5-9.6 mm, cranial width 0.85-1.10 mm. Clypeal width at base 0.55-0.65 mm, labrum uniformly sclerotized. Antennal segment I 0.90-1.50 times as long as segment III. Pronotal width 1.10-1.40 mm. Basal segment of urogomphus 1.00-1.80 times as long as distal one. With the exception of *N. vespillo*, abdominal segments I-VIII on pleural lobe with oval sclerite.

L2: Body length 7.9-15.5 mm, cranial width 1.20-1.65 mm. Clypeal width at base 0.65-0.90 mm, labrum uniformly sclerotized. Antennal segment I 1.15-2.00 times longer than segment III. Pronotal width 1.65-2.50 mm. Basal segment of urogomphus 1.45-2.30 times longer than distal. Abdominal segments I-VIII on pleural lobe with (*N. fossor*, *N. investigator*) or without (other species examined) oval sclerite.

L3: Body length 16.1-32.6 mm, cranial width 1.60-2.40 mm. Clypeal width at base 1.00-1.30 mm, labrum apically with main sclerotized area, wide unsclerotized zone laterally. Antennal segment I 1.60-3.35 times longer the segment III. Pronotal width 2.75-4.60 mm. Basal segment of urogomphus 1.80-3.30 times longer than distal. Abdominal segments I-VIII on pleural lobe always without sclerotization.

Key to species for larval instar I

- 1 (2) Segment II of maxillary palpus distinctly longer than segment I (as on Fig. 18). Tenth abdominal segment with venter sclerotized only in apical region, unsclerotized at base. Ninth sternite fragmented.....*N. vespilo*.
- 2 (1) Segment II of maxillary palpus only slightly longer than segment I (Fig. 17). Tenth abdominal segment with venter sclerotized at least at base. Ninth sternite entire.
- 3 (4) Basal segment of both labial and maxillary palpus (not palpiger !) unsclerotized ventrally (Fig. 17). Meso- and metanotum distinctly notched laterally in posterior regions.....*N. vespilloides*.
- 4 (3) Basal segment of both labial and maxillary palpus with venter sclerotized, at least at base. Meso- and metanotum laterally straight in posterior region or only shallowly emarginate.
- 5 (6) Praementum with venter unsclerotized, distance between bases of labial palpi slightly shorter than width of basal segment of labial palpi. Urogomphus with suture at base complete.....*N. humator*.
- 6 (5) Praementum with venter sclerotized at base, distance between bases of labial palpi 1.3-1.5 times wider than width of basal segment of labial palpi. Urogomphus with suture at base complete or incomplete in middle.
- 7 (8) Pleural lobe of abdominal segments I-VIII with large, oval sclerite, epipleural lobe without sclerite.....*N. investigator*.

- 8 (7) Pleural lobe of abdominal segments I-VIII with oval sclerite, epipleural lobe with minute sclerite.....
 *N. fossor*

Key to species for larval instars II and III

- 1 (2) Segment II of maxillary palpus distinctly longer than segment I (Fig. 18). Tenth abdominal sement unsclerotized ventrally (Fig. 33), ninth sternite fragmented (Fig. 36)*N. vespillo*
 2 (1) Segment II of maxillary palpus only slightly longer than segment I (Figs 14, 16, 19). Tenth adominal segment with venter sclerotized at least at base (Figs 30-32, 34), ninth sternite entire (Figs 35, 37-39).
 3 (4) Basal segment of both labial and maxillary palpus (not palpiger !) unsclerotized ventrally (Figs 14,16, 22, 23). Urogomphus lacking basal suture (Figs 47, 52).....*N. vespilloides*
 4 (3) Basal segment of both labial and maxillary palpus with venter sclerotized at least at base (Figs 18-21). Urogomphus with suture at base complete or lacking in middle only.
 5 (6) Praementum with venter unsclerotized, distance between bases of labial palpi approximately equal to width of basal segment of labial palpi (Fig. 20). Tenth abdominal segment with venter sclerotized at base only, apically unsclerotized (Fig. 32)*N. humator*
 6 (5) Praementum with venter widely sclerotized at base, sometimes with unsclerotized line medially. Distance between bases of labial palpi at least twice the width of basal segment of labial palpus (Fig. 21). Tenth abdominal segment with venter sclerotized apically, too (Figs 30, 31).
 7 (10) Labrum uniformly sclerotized. Pleural lobe of abdominal segments I-VIII with oval sclerite. Tenth abdominal segment with triangular sclerite ventroapically.
 8 (9) Epipleural lobe of abdominal segments I-VIII without sclerite*N. investigator*, L₂
 9 (8) Epipleural lobe of abdominal segments I-VIII with minute sclerite..... *N. fossor*, L₂
 10 (7) Labrum sclerotized more heavily apically than laterally. Pleural lobe of abdominal segments I-VIII without sclerite. Tenth abdominal segment with Y-shaped sometimes fragmented d sclerite ventroapically.
 11 (12) Praementum sclerotized without interruption ventrally (Fig. 21). Urogomphus with complete suture at base. Ninth sternite with 3-4 pairs of setae centrally (Fig. 37). Tenth abdominal segment with venter widely sclerotized at base, Y-shaped area always fused with basal sclerotization anteriorly (Fig. 30).....
*N. investigator*, L₃
 12 (11) Praementum with venter with unsclerotized line medially. Urogomphus with suture at base incomplete in middle. Ninth sternite with only 1 pair of setae centrally (Fig. 39). Tenth abdominal segment with venter sclerotized narrowly at base, Y-shaped area sometimes fragmented and never fused with basal sclerotization (Fig. 31)*N. fossor*, L₃

Survey of species

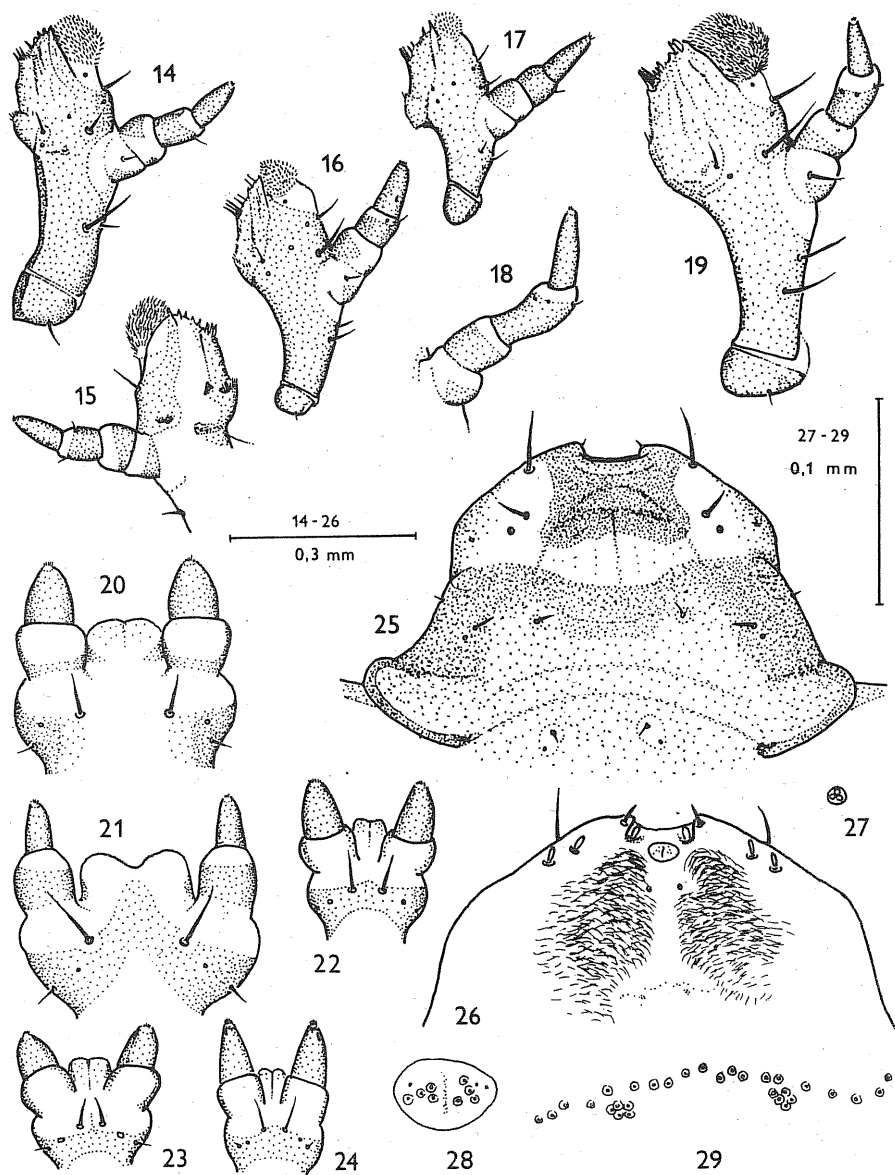
Nicrophorus vespillo (Linné, 1758)

(L₃ - Figs 18, 26-29, 33, 36)

Description:

L₃: Body length 19.8-25.4 mm. Length of head 1.35-1.90 mm, cranial width 1.70-2.20 mm (average in 10 specimens 1.90 mm). Width of clypeus 1.00-1.25 mm. Epipharynx marginally with 2 pairs of setae (Fig. 26). Segment I of antenna 1.65-2.65 times longer than segment III. Basal segment of maxillary palpus sclerotized ventrally, segment II distinctly longer than segment I (Fig. 18). Width of labium 0.40-0.50 mm, praementum unsclerotized only medioventrally, distance between bases of labial palpi approximately twice width of basal segment of labial palpus which is sclerotized ventrally.

Pronotal width 3.10-4.10 mm. Nota laterally not notched in posterior part. Width of notum of abdominal segment IV 2.00-2.75 mm. Abdomen only slightly sclerotized



Figs 14-29: 14 - *Nicrophorus vespilloides*, L3, left maxilla, ventral view; 15 - *N. vespilloides*, L3, left maxilla, dorsal view; 16 - *N. vespilloides*, L2, left maxilla, ventral view; 17 - *N. vespilloides*, L1, ditto; 18 - *N. vespillo*, L3, left maxillar palpus, ventral view; 19 - *N. fossor*, L3, left maxilla, ventral view; 20-24 - labium, ventral view: 20 - *N. humator*, L3; 21 - *N. investigator*, L3; 22 - *N. vespilloides*, L2; 23 - *N. vespilloides*, L3; 24 - *N. vespilloides*, L1; 25 - *N. vespilloides*, L3, clypeus and labrum, dorsal view; 26 - *N. vespillo*, L3, epipharynx, ventral view; 27 - *N. vespillo*, L3, second porous area, detail; 28 - *N. vespillo*, L3, first porous area, detail; 29 - *N. vespillo*, L3, quinque-porous area, detail.

ventrally, sclerites more reduced than in other species. Urogomphus with suture at base incomplete in middle, basal segment 1.85-2.65 times longer than distal. Ninth sternite fragmented (Fig. 36), with higher number of setae centrally. Tenth abdominal segment with venter quite unsclerotized (Fig. 33).

L₂: Body length 7.90-11.45 mm. Length of head 1.10-1.25 mm, cranial width 1.35-1.45 mm (average in 5 specimens 1.42 mm). Width of clypeus 0.80-0.85 mm. Segment I of antenna 1.45-2.00 times longer than segment III. Width of labium 0.30-0.35 mm.

Pronotal width 1.65-1.90 mm. Width of notum of abdominal segment IV 1.45-1.50 mm. Basal segment of urogomphus 1.45-1.65 times longer than distal.

L₁: Body length 6.20-7.75 mm. Length of head 0.75-0.80 mm, cranial width 0.85-0.90 mm (average in 5 specimens 0.88 mm). Width of clypeus 0.55 mm. Segment I of antenna 1.00-1.50 times as long as segment III. Width of labium 0.20 mm.

Pronotal width 1.10-1.20 mm. Width of notum of abdominal segment IV 1.00-1.10 mm. Urogomphus with suture at base either complete or incomplete in middle. Basal segment 1.20-1.50 times longer than distal. Venter of tenth abdominal segment occasionally with sclerotized area apically, mostly fragmented.

Material examined: 5 E, 24 L₁, 9 L₂, 75 L₃, 2 P, obtained from breeding pairs found in Bohemia centr., Vlašim env., Nové Mlýny, 9.v.1986, 1 ♂, 1 ♀; the same locality, 24.vii.1987, 1 ♂, 1 ♀; Bohemia c., Zbraslav, 18.v.1986, 1 ♂, 1 ♀; Bohemia c., Cerhovice, 1.v.1988, 3 ♂, 3 ♀; the same locality, 29.v.1988, 1 ♂, 1 ♀.

Nicrophorus vespilloides Herbst, 1784

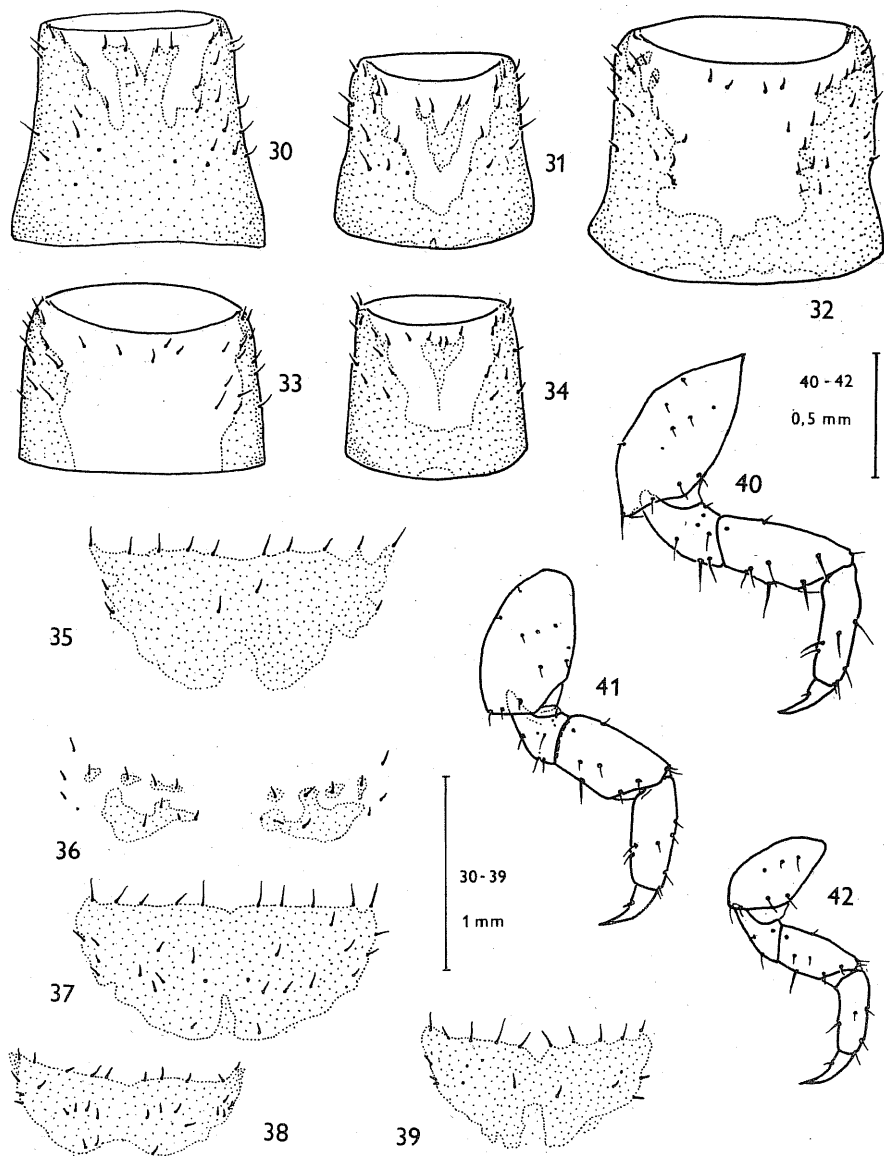
(L₁ - Figs 9,12,17,24,42,53-57,66,67; L₂ - Figs 8,11,16,22,41,48-52,65,68; L₃ - Figs 1,4-7,10,13-15, 23,25,34,40,43-47,64,69, Plate II, Figs 1,2,4; P - Figs 58-62)

Description:

L₃: Body length 17.4-21.9 mm. Length of head 1.30-1.60 mm, cranial width 1.60-2.05 mm (average in 10 specimens 1.87 mm). Width of clypeus 1.00-1.20 mm. Epipharynx marginally with 1 pair of setae. Segment I of antenna 1.60-2.50 times longer than segment III. Basal segment of maxillary palpus unsclerotized ventrally, segment II not distinctly longer than segment I (Fig. 14). Width of labium 0.25-0.30 mm. Praementum sclerotized ventrobasally, sclerotization projecting medioanteriorly. Distance between bases of labial palpi narrower than width of basal segment of labial palpus which is unsclerotized ventrally (Fig. 23).

Pronotal width 2.75-3.55 mm. Nota laterally not notched posteriorly (Figs 43,44). Width of notum of abdominal segment IV 2.40-3.50 mm. Urogomphus with suture at base lacking, basal segment 2.25-3.30 times longer than distal. Ninth sternite entire, slightly emarginate mediobasally, with 2-5 pairs of setae centrally (Fig. 38). Tenth segment with venter sclerotized at base as well as apically, bearing a Y-shaped area (Fig. 34), sometimes fused with basal sclerotization anteriorly.

L₂: Body length 8.05-11.15 mm. Length of head 1.00-1.15 mm, cranial width 1.20-1.40 mm (average in 5 specimens 1.28 mm). Width of clypeus 0.65-0.70 mm. Segment I of



Figs 30-42: 30-34 - L3, abdominal segment X, ventral view: 30 - *Nicrophorus investigator*; 31 - *N. fossor*; 32 - *N. humator*; 33 - *N. vespillo*; 34 - *N. vespilloides*; 35-39 - L3, sclerite of abdominal segment IX, ventral view: 35 - *N. humator*; 36 - *N. vespillo*; 37 - *N. investigator*; 38 - *N. vespilloides*; 39 - *N. fossor*; 40-42 - *N. vespilloides*; right leg of metathorax, posterior view: 40 - L3; 41 - L2; 42 - L1.

antenna 1.50-1.75 times longer than segment III. Width of labium 0.20-0.25 mm. Distance between bases of labial palpi approximately half width of basal segment of labial palpus (Fig. 22).

Pronotal width 1.75-2.10 mm. Meso- and metanotum notched laterally in posterior parts (Fig. 49). Width of notum of abdominal segment IV 1.70-2.00 mm. Basal segment of urogomphus 1.45-1.75 times longer than distal.

L₁: Body length 4.50-7.45 mm. Length of head 0.70-0.80 mm, cranial width 0.95-1.00 mm (average in 5 specimens 0.98 mm). Width of clypeus 0.55-0.60 mm. Segment I of antenna 1.00-1.35 times as long as segment III. Width of labium 0.15-0.20 mm, distance between bases of labial palpi narrower than half width of basal segment of labial palpus (Fig. 24).

Pronotal width 1.20-1.35 mm. Meso- and metanotum emarginate laterally posteriorly (Fig. 54). Width of notum of abdominal segment IV 1.10-1.45 mm. Pleural lobe of abdominal segments I-VIII with relatively large, oval sclerite, and epipleural lobe with minute sclerite. Urogomphus with suture at base either complete or incomplete in middle (Fig. 57). Basal segment 1.35-1.80 times longer than distal. Tenth abdominal segment sclerotized ventrally.

Material examined: 15 L₁, 31 L₂, 142 L₃, 17 P, obtained from breeding pairs found in Bohemia centr., Vlašim env., Nové Mlýny, 17.v.1986, 1 ♂, 1 ♀; the same locality, 20-25.vii.1987, 2 ♂, 2 ♀; Bohemia c., Praha - Háje, 4-9.v.1986, 1 ♀; Bohemia c., Cerhovice, 1.v.1988, 6 ♂, 6 ♀.

Nicrophorus humator Olivier, 1790

(E - Fig. 63; L₃ - Figs 20,32,35; Plate I, Figs 1-4; Plate II, Fig. 3)

Description:

L₃: Body length 21.7-32.6 mm. Length of head 1.75-2.15 mm, cranial width 2.05-2.35 mm (average in 10 specimens 2.15 mm). Width of clypeus 1.10-1.30 mm. Epipharynx marginally with 1 pair of setae. Segment I of antenna 1.85-2.75 times longer than segment III. Basal segment of maxillary palpus sclerotized ventrally, segment II not distinctly longer than segment I. Width of labium 0.40-0.50 mm, praementum with venter unsclerotized (Fig. 20). Distance between bases of labial palpi only slightly longer than width of basal segment of labial palpi which is sclerotized only narrowly at base ventrally (Fig. 20).

Pronotal width 3.70-4.60 mm. Notum laterally not truncate posteriorly. Width of notum of abdominal segment IV 3.15-3.85 mm. Urogomphus with suture at base complete, basal segment 2.10-3.15 times longer than distal. Ninth sternite entire, sometimes only slightly emarginate at lateral margins, notched mediobasally, with 1 pair of setae centrally (Fig. 35). Tenth segment with venter sclerotized only narrowly and irregularly at base (Fig. 32), sclerotization sometimes interrupted medially.

L₂: Body length 8.70-15.50 mm. Length of head 1.35-1.45 mm, cranial width 1.45-1.60 mm (average in 5 specimens 1.53 mm). Width of clypeus 0.80-0.90 mm. Segment I of

antenna 1.50-1.80 times longer than segment III. Width of labium 0.30-0.35 mm. Distance between bases of labial palpi slightly shorter than width of basal segment of labial palpus.

Pronotal width 2.05-2.35 mm. Width of notum of abdominal segment IV 2.00-2.40 mm. Basal segment of urogomphus 1.50-1.90 times longer than distal. Tenth abdominal segment with venter sometimes in apical half with sclerotized area.

L₁: Body length 7.45-9.60 mm. Length of head 0.80-0.95 mm, cranial width 0.95-1.10 mm (average in 5 specimens 1.01 mm). Width of clypeus 0.55-0.60 mm. Segment I of antenna 1.00-1.20 times as long as segment III. Width of labium 0.20-0.25 mm, distance between bases of labial palpi slightly shorter than width of basal segment of labial palpi.

Pronotal width 1.30-1.40 mm. Width of notum of abdominal segment IV 1.30-1.40 mm. Pleural lobe of abdominal segments I-VIII with oval sclerite. Basal segment of urogomphus 1.00-1.30 times as long as distal. Tenth abdominal segment sclerotized ventrally.

Material examined: 11 E, 15 L₁, 8 L₂, 23 L₃, 2 P, obtained from breeding pairs found in Bohemia centr., Vlašim env., Nové Mlýny, 25.iv.1986, 3 ♂, 3 ♀; the same locality, 4.v.1986, 1 ♂, 1 ♀; the same locality, 24.iv.1988, 2 ♀; Bohemia c., Praha - Háje, 4.v.1986, 1 ♂, 1 ♀.

Nicrophorus investigator Zetterstedt, 1824

(L₃ - Figs 21,30,37)

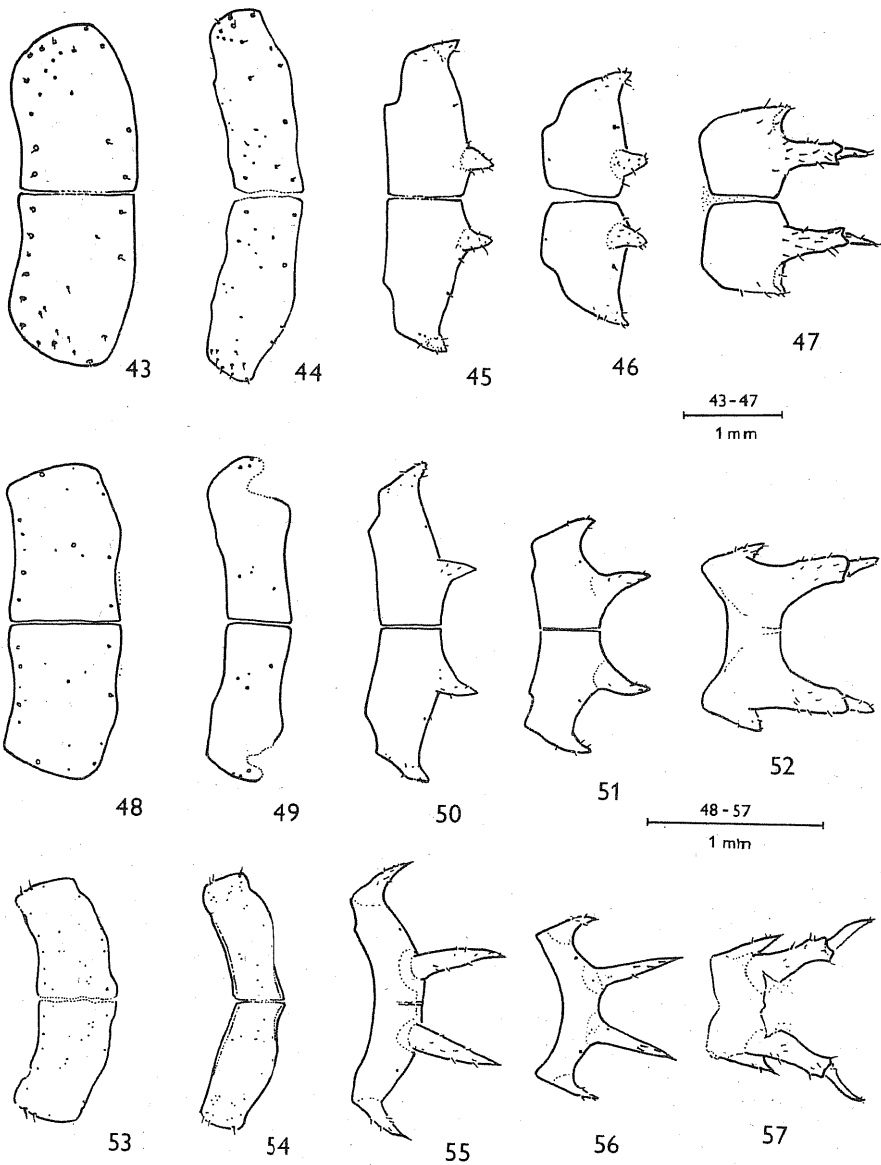
Description:

L₃: Body length 16.1-28.7 mm. Length of head 1.75-2.05 mm, cranial width 2.15-2.40 mm (average in 10 specimens 2.25 mm). Width of clypeus 1.20-1.30 mm. Epipharynx marginally with 1 pair of setae. Segment I of antenna 1.60-2.20 times longer than segment III. Basal segment of maxillary palpus only narrowly sclerotized ventrally, segment II not distinctly longer than segment I. Width of labium 0.50-0.55 mm. Praementum widely sclerotized ventrally, sclerotization extended apically onto the base of ligula (Fig. 21). Distance between bases of labial palpi more than twice as long as the width of basal segment of labial palpus which is widely sclerotized basoventrally.

Pronotal width 3.70-4.30 mm. Nota laterally not emarginate in posterior part. Width of notum of abdominal segment IV 3.55-4.15 mm. Urogomphus with suture at base complete, basal segment 2.00-2.60 times longer than distal. Ninth sternite entire, deeply but narrowly notched at base, sometimes with lighter line medially, with 3-4 pairs of setae centrally (Fig. 37). Tenth segment with venter sclerotized widely at base as well as apically, bearing a Y-shaped area, always fused with basal sclerotization anteriorly (Fig. 30).

L₂: Body length 11.45-13.35 mm. Length of head 1.25-1.35 mm, cranial width 1.50-1.65 mm (average in 5 specimens 1.57 mm). Width of clypeus 0.85-0.90 mm. Segment I of antenna 1.15-1.50 times longer than segment III. Width of labium 0.37 mm.

Pronotal width 2.20-2.50 mm. Width of notum of abdominal segment IV 2.25-2.40 mm. Pleural lobe of abdominal segments I-VIII with minute oval sclerite. Venter of each segment with small sclerotized area centrally (as in other species) and with higher



Figs 43-57: *Nicrophorus vespilloides*: 43-47 - L3; 48-52 - L2; 53-57 - L1; 43,48,53 - scutal sclerite of pronotum, dorsal view; 44,49,54 - scutal sclerite of mesonotum, dorsal view; 45,50,55 - scutal sclerite of abdominal segment IV, dorsal view; 46,51,56 - scutal sclerite of abdominal segment VIII, dorsal view; 47,52,57 - scutal sclerite of abdominal segment IX and urogomphi, dorsal view.

number of small areas at posterior row of setae. Urogomphus with suture at base incomplete in middle, basal segment 1.60-1.80 times longer than distal. Ninth sternite only very slightly emarginate medially at base, with 1 pair of longer setae centrally, other setae very short, rather indistinct. Tenth segment with venter widely sclerotized, apically with short, triangular area.

L₁: Body length 6.20-6.80 mm. Length of head 0.80-0.85 mm, cranial width 1.00-1.10 mm (average in 5 specimens 1.06 mm). Width of clypeus 0.60-0.65 mm. Segment I of antenna 0.90-1.20 times longer than segment III. Width of labium 0.20-0.25 mm, distance between bases of labial palpi 1.3 times longer than width of basal segment of labial palpus.

Pronotal width 1.25-1.35 mm. Width of notum of abdominal segment IV 1.35-1.60 mm. Pleural lobe of abdominal segments I-VIII with large, oval sclerite, epipleural lobe without sclerite. Urogomphus with suture at base either complete or incomplete in middle. Basal segment 1.25-1.50 times longer than distal. Ninth sternite straight at base, with 1 pair of longer setae centrally, remaining setae short and rather indistinct. Tenth segment with venter sclerotized, lateroapically only slightly emarginate.

Material examined: 1 E, 7 L₁, 7 L₂, 38 L₃, 8 P, obtained from females found in Bohemia centr., Louňovice p. Blaníkem env., Býkovicce, 25.vii.1987, 1 ♀; the same locality, 9.viii.1987, 2 ♀.

Nicrophorus fossor Erichson, 1837

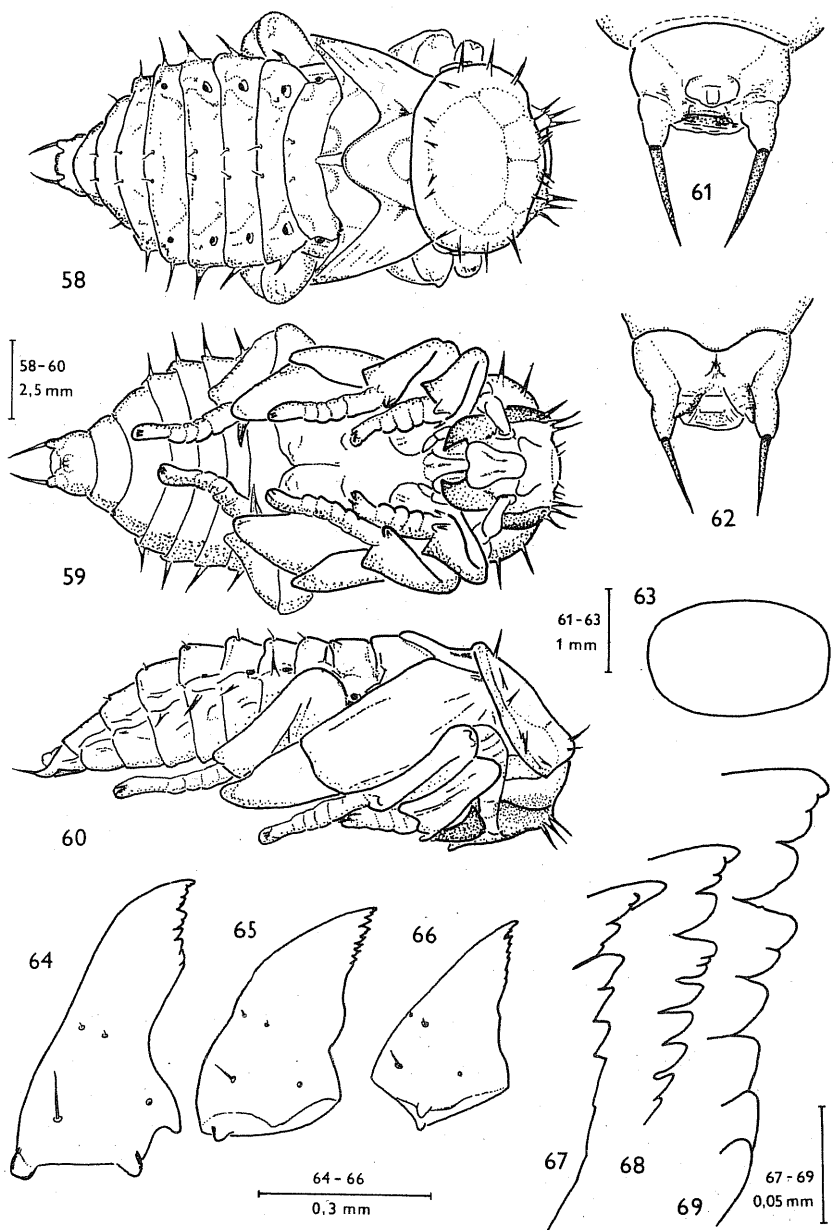
(L₃ - Figs 19,31,39)

Description:

L₃: Body length 16.8-26.8 mm. Length of head 1.65-1.85 mm, cranial width 2.10-2.30 mm (average in 10 specimens 2.25 mm). Width of clypeus 1.05-1.25 mm. Epipharynx marginally with 1-2 pairs of setae. Segment I of antenna 2.45-3.35 times longer than segment III. Basal segment of maxillary palpus only narrowly sclerotized ventrally, segment II not distinctly longer than segment I (Fig. 19). Width of labium 0.40-0.50 mm. Praementum widely sclerotized ventrally (as in *N. investigator*) but with unsclerotized line medially. Distance between bases of labial palpi more than twice width of basal segment of labial palpus which is widely sclerotized ventrally.

Pronotal width 3.30-4.00 mm. Nota laterally not emarginate posteriorly. Width of notum of abdominal segment IV 2.90-3.55 mm. Urogomphus with suture at base incomplete in middle, basal segment 1.80-2.50 times longer than distal. Ninth sternite entire, strongly notched basomedially, with 1 pair of setae centrally (Fig. 39). Tenth segment with venter sclerotized narrowly at base as well as apically, bearing a Y-shaped area (Fig. 31), often asymmetrically reduced to a number of small areas, never fused with basal sclerotization anteriorly.

L₂: Body length 10.55-12.70 mm. Length of head 1.10-1.30 mm, cranial width 1.40-1.50 mm (average in 5 specimens 1.48 mm). Width of clypeus 0.80-0.90 mm. Segment I of antenna 1.40-1.55 times longer than segment III. Width of labium 0.30-0.35 mm. Distance between bases of labial palpi nearly twice longer than width of basal segment of labial palpi.



Figs 58-69: 58-60 - *Nicrophorus vespilloides*, pupa: 58 - dorsal view; 59 - ventral view; 60 - lateral view; 61 - *N. vespilloides*, pupa, abdominal segments IX and X, ventral view, male; 62 - ditto, female; 63 - *N. humator*, egg, lateral view; 64-66 - *N. vespilloides*, left mandible, dorsal view: 64 - L3; 65 - L2; 66 - L1; 67-69 - *N. vespilloides*, detail of apical part of left mandible, dorsal view: 67 - L1; 68 - L2; 69 - L3.

Pronotal width 2.10-2.20 mm. Meso- and metanotum only very slightly emarginate posterolaterally. Width of notum of abdominal segment IV 2.00-2.15 mm. Pleural lobe of each abdominal segment I-VIII with oval sclerite, epipleural lobe of segments II-V with minute sclerite. Abdominal segments ventrally sclerotized as in *N. investigator*. Urogomphus with suture at base either widely incomplete in middle or absent. Basal segment 2.00-2.30 times longer than distal. Ninth sternite only slightly emarginate basomedially. Tenth segment ventroapically with triangular area more or less fused with basal sclerotization anteriorly.

L₁: Body length 5.25-7.75 mm. Length of head 0.70-0.80 mm, cranial width 0.90-0.95 mm (average in 5 specimens 0.92 mm). Width of clypeus 0.55-0.60 mm. Segment I of antenna 1.00-1.20 times as long as segment III. Width of labium 0.20 mm, distance between bases of labial palpi about 1.5 times longer than width of basal segment of labial palpus.

Pronotal width 1.15-1.20 mm. Meso- and metanotum only very slightly emarginate posterolaterally. Width of notum of abdominal segment I-VIII 1.30-1.35 mm. Pleural lobe of segments I-VIII with oval sclerite, epipleural lobe with minute sclerite. Urogomphus at base with suture either complete or incomplete in middle. Basal segment 1.15-1.35 times longer than distal. Ninth sternite straight basomedially. Tenth segment with venter sclerotized, lateroapically notched.

Material examined: 9 L₁, 9 L₂, 17 L₃, obtained from breeding pairs found in Bohemia centr., Vlašim env., Nové Mlýny, 24.vii.1987, 1 ♀; Bohemia centr., Louňovice p. Blaníkem, env., Býkovice, 9.viii.1987, 1 ♂, 1 ♀; Bohemia c., Praha - Hrnčíře, 20.viii.1987, 1 ♂, 1 ♀.

Notes on taxonomy

Morphological characters of evolutionary importance and polarity of their states are summarized in Table 1. The distribution of polarity of characters of the species studied is given in Table 2. Characters 1-7 are taken after Anderson, 1982, the polarity of states of characters 1 and 3-7 after the same paper.

Characters are considered to be in plesiomorphic state in L₃ of *Ptomascopus morio*, the species of the more primitive sister genus of *Nicrophorus* (after Anderson, 1982) with one exception: the author does not agree with Anderson (l.c., p. 263) in the evaluation of the polarity of the state in character 2 (the sclerotization of apical part of venter of segment X). The venter is unsclerotized in L₃ of *Ptomascopus morio* but sclerotized in all L₁ of species studied of *Nicrophorus* and in different states in L₂ and L₃ (see Table 2). So it appears to be more probable that the venter apically is sclerotized plesiomorphically and unsclerotized apomorphically.

According to results taken from Table 2, the European species investigated here are placed into the existing species groups (sensu Anderson, 1982; Peck & Anderson, 1985) as follows:

N. vespillo on the basis of the synapomorphy of characters 1 and 7 (base of venter of

TABLE 1. Morphological characters of larvae of *Nicrophorus*.

Character	State	
	plesiomorphic	apomorphic
1 base of venter of segment X	sclerotized	unsclerotized
2 apical part of venter of segment X	sclerotized	unsclerotized
3 suture at base of urogomphus	complete	incomplete medially or absent
4 suture at base or urogomphus	complete or incomplete medially	absent
5 bases of labial palpi	widely separated	narrowly separated
6 ventral surface of basal segment of labial palpus	sclerotized	unsclerotized
7 sternite of segment IX	entire	laterally notched or fragmented
8 ventral surface of base of praementum	sclerotized	unsclerotized
9 ventral surface of basal segment of maxillary palpus	sclerotized	unsclerotized

TABLE 2. Character states of particular instars and species of larvae of *Nicrophorus*.

Instar	Species	Character								
		1	2	3	4	5	6	7	8	9
L1	<i>N. vespilloides</i>	-	-	-+	-	+	+	-	-	+
	<i>N. vespillo</i>	+	-	-+	-	-	-	+	+	-
	<i>N. humator</i>	-	-	-	-	+	-	-	+	-
	<i>N. investigator</i>	-	-	-+	-	-	-	-	-	-
	<i>N. fossor</i>	-	-	-+	-	-	-	-	-	-
L2	<i>N. vespilloides</i>	-	-	+	+	+	+	-	-	+
	<i>N. vespillo</i>	+	+	+	-	-	-	+	+	-
	<i>N. humator</i>	-	+	-	-	+	-	-	+	-
	<i>N. investigator</i>	-	-	+	-	-	-	-	-	-
	<i>N. fossor</i>	-	-	+	-	-	-	-	-	-
L3	<i>N. vespilloides</i>	-	-	+	+	+	+	-	-	+
	<i>N. vespillo</i>	+	+	+	-	-	-	+	+	-
	<i>N. humator</i>	-	+	-	-	+	-	-	+	-
	<i>N. investigator</i>	-	-	-	-	-	-	-	-	-
	<i>N. fossor</i>	-	-	+	-	-	-	-	-	-

- plesiomorphic; + apomorphic; -+ in material of L1 present both in plesiomorphic and apomorphic states (individual variability).

segment X unsclerotized, sternite of segment IX fragmented) is placed in the *marginatus* group.

It is possible to verify the placement of *N. vespilloides* in the *defodiens* group (Peck & Anderson, 1985) based on the synapomorphy of character 6 (ventral surface of basal segment of labial palpus unsclerotized). However, the apomorphic state of character 5 (bases of labial palpi narrowly separated) is exhibited in *N. humator* also and, therefore, cannot be used for the characterization of the *defodiens* group (i.e., p. 274).

The other two species, *N. investigator* and *N. fossor* can be placed in the *investigator* group. Members of this group can be defined by overwintering as praepupa only (vide l.c., p. 275), but no morphological characters exist for characterization of this group - character 2 (base of segment X sclerotized) is shared with *N. vespilloides* and is plesiomorphic.

No apomorphic larval characters can be found to place *N. humator* to any species group.

A c k n o w l e d g m e n t s . I would like to thank Prof Karel Hůrka for his valuable advice and support in my work and to Dr Petr Švácha and Ing Milan Tůma for comments and for their help with the SEM photographs.

REFERENCES

- ANDERSON R.S. 1982: Burying beetle larvae: Nearctic *Nicrophorus* and Oriental *Ptomascopus morio* (Silphidae). *Syst. Entomol.*, 7: 249-264.
- ANDERSON R.S. & PECK S.B. 1985: The carrion beetles of Canada and Alaska. Coleoptera: Silphidae and Agrytidae. The Insects and Arachnids of Canada, Part 13. 121 pp., Agriculture Canada, Ottawa.
- BARTLETT J. & ASHWORTH C.M. 1988: Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behav. Ecol. Sociobiol.*, 22: 429-434.
- BYZOVA J. 1964: Silphidae. In Gilyarov M.S. (ed.): *Opredelitel Obitayushchikh v Pochve Lichinok Nasekomykh* (A Key to Insect Larvae Living in Soil). Pp. 212-224, Izd. Nauka, Moskva (in Russian).
- HATCH H. 1927a: Studies of the carrion beetles of Minnesota, including new species. *Univ. Minn. Agric. Exp. Stn. Bull.*, 48: sep. 1-19.
- HATCH H. 1927b: Studies on the Silphidae. *J.N.Y. Entomol. Soc.*, 35: 331-371.
- HENRIKSEN K. 1922: Larver. In Hansen V.: *Biller V. Aadselbiller, Stumpbiller m. m. Danmarks Fauna*. Pp. 249-273, G.E.C. Gaets Forlag, København.
- KLAUSNITZER B. & ZERCHEL. 1978: Silphidae. In Klausnitzer B. (ed.): *Ordnung Coleoptera (Larven)*. Pp. 87-90, Akademie-Verlag, Berlin.
- MILNE L.J. & MILNE M.J. 1976: The social behaviour of burying beetles. *Sci. Amer.* 235: 84-90.
- MUELLER J.K. & Eggert A.K. 1987: Effects of carrion-independent pheromone emission by male burying beetles (Silphidae: *Nicrophorus*). *Ethology*, 76: 297-304.
- OTRONEN M. 1988: The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Ann. Zool. Fennici*, 25: 191-201.
- PAULIAN R. 1941: Les premiers états des Staphylinoidea. *Mém. Mus. Natl. Hist. Nat. (nouv. sér.)*, 15: 1 - 361.
- PECK S.B. & ANDERSON R.S. 1985: Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaest. Entomol.*, 21: 247-317.
- PUKOWSKI E. 1933: Ökologische Untersuchungen an *Nicrophorus* F. *Z. Morphol. Ökol. Tiere (= Z. Wiss. Zool., A)*, 27: 518-586.
- PUKOWSKI E. 1934: Zur Systematik der *Nicrophorus*-Larven. *Stettin. Entomol. Ztg.*, 95: 53-60.
- ROUSSEL J.P. 1964a: Le développement larvaire de *Nicrophorus vespillo* L. *Bull. Soc. Zool. Fr.*, 89: 102-110.

- ROUSSEL J.P. 1964b: Le développement larvaire de *Necrophorus fossor* Er. *Ibid.*, **89**: 111-117.
- SCOTT M.P. 1990: Brood guarding and the evolution of male parental care in burying beetles. *Behav. Ecol. Sociobiol.*, **26**: 31-39.
- ŠPICAROVÁ N. 1969: Chovy hrobaříků za venkovních a laboratorních podmínek (Col. Silphidae) (Zuchten der Necrophoren unter Freiland- und Laborbedingungen). *Acta Univ. Palack. Olomuc. (Fac. Rer. Nat.)*, **31**: 125-130 (in Czech; German abstr.).
- ŠVÁCHA P. & DANILEVSKY M.L. 1987: Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part 1. *Acta Univ. Carol. - Biol.*, **30** (1986): 1-176.

Received May 27; accepted November 28, 1991

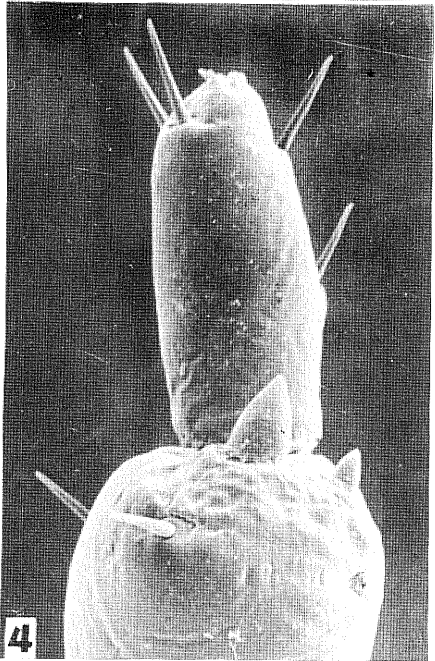
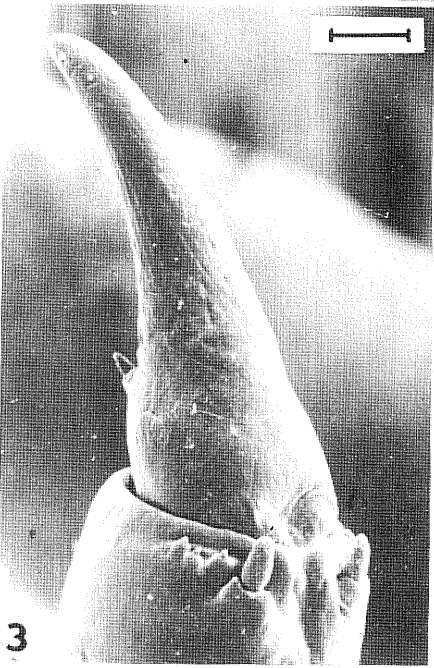
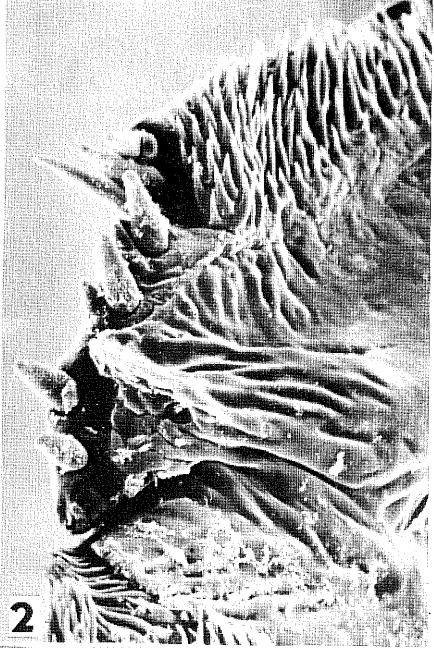


PLATE I, Figs 1-4: *Nicrophorus humator*, L3: 1 - head and thorax, lateral view; 2 - ditto, ventral view; 3 - head, lateral view; 4 - ditto, ventroapical view. Scale: 0.63 mm for Figs 1,2; 0.23 mm for Fig. 3; 0.21 mm for Fig. 4.

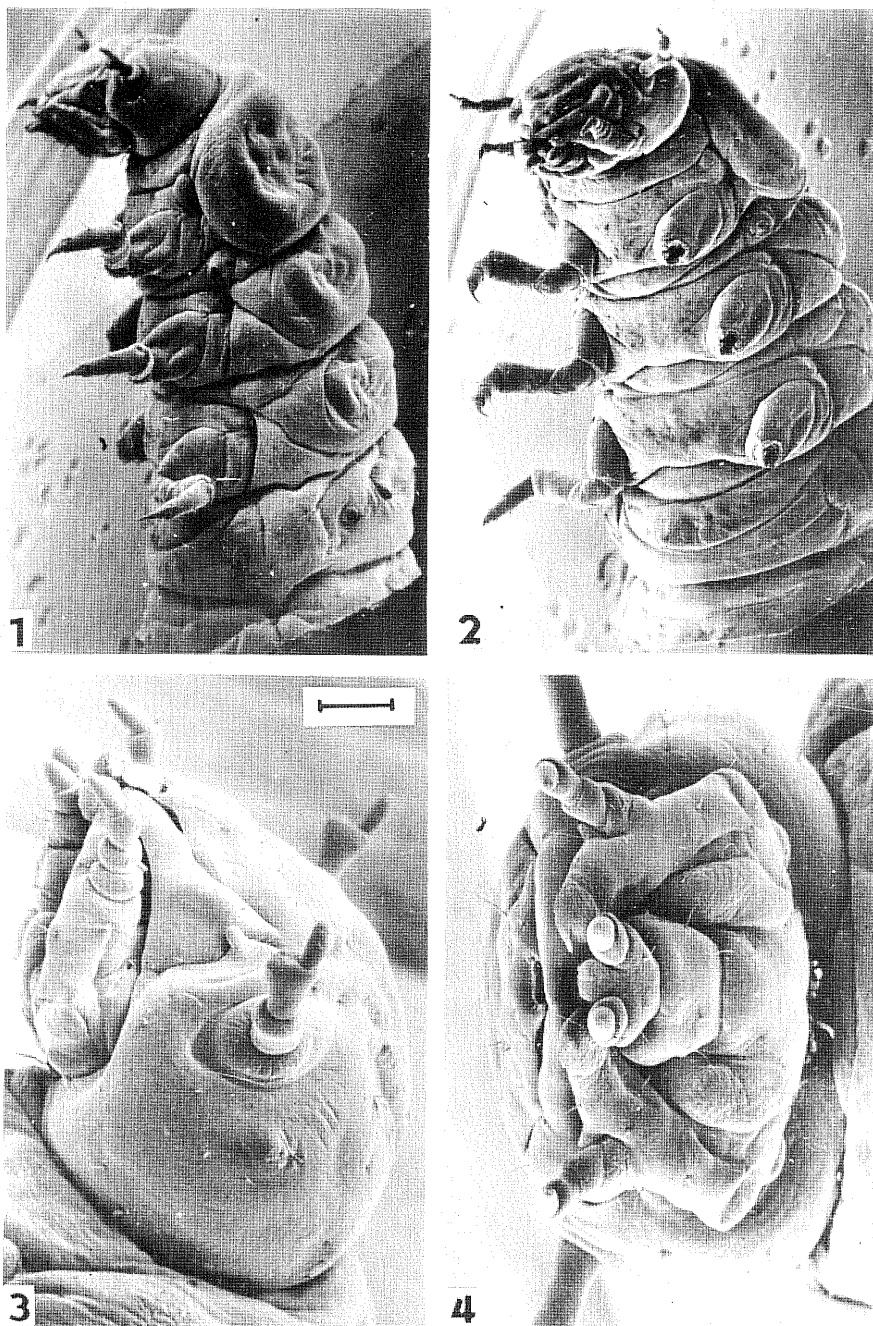


PLATE II, Figs 1-4: 1,2,4 - *Nicrophorus vespilloides*, L3; 3 - *N. humator*, L3: 1 - labiomaxillary complex, dorsal view; 2 - apical part of lacinia, ventral view; 3 - pratarsus, lateral view; 4 - apical part of antenna, ventral view. Scale: 78 μm for Fig. 1; 22 μm for Figs. 2; 36 μm for Fig. 3; 28 μm for Fig. 4.