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Larval morphology of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope (Coleoptera: Silphidae: Nicrophorinae)

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Abstract

Larval morphology of all three instars of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831 (Coleoptera: Silphidae: Nicrophorinae) is described and illustrated, based on reared larvae. The eastern Palaearctic and Oriental *N.* (*N.*) *nepalensis* is similar to the western Palaearctic *N.* (*N.*) *humator* (Gleditsch, 1767) in a number of larval characters. This is congruent with recent classification of the genus *Nicrophorus* Fabricius, 1775 by Sikes, who suggested a close phylogenetic affinity of the *N. nepalensis* species group (with 16 species) with the *N. humator* species group (2 species). The generic description of larvae of *Nicrophorus* Fabricius, 1775 is expanded, based on detailed SEM observation.

Key words: larval morphology, burying beetles, Silphidae, Nicrophorinae, *Nicrophorus nepalensis*, Oriental Region

Introduction

The burying beetles of the genus *Nicrophorus* Fabricius, 1775 (Silphidae: Nicrophorinae) are known for their advanced biparental care of larvae, and burial of small vertebrate carcasses (Scott 1998). Within the genus, two subgenera are recognised: *Necroxenus* Semenov-Tian-Shanskiy, 1933 (containing only two endemic Chinese species) and the nominotypical subgenus (with 66 species, distributed world-wide, but absent from Antarctica, Australia and sub-Saharan Africa) (Sikes *et al.* 2002; Sikes & Venables 2013a, Sikes *et al.* 2016; Sikes & Barclay 2017). The subgenus *Nicrophorus* is divided into 13 informal species groups (Sikes & Venables 2013a). The *N. nepalensis* group with 16 species is the second most species-rich lineage (Sikes *et al.* 2006; Sikes & Venables 2013a). It is distributed from Pakistan and India to the Far East of Russia and Japan, and through Malay Peninsula to Papua New Guinea and the Solomon Islands; most of the species are local montane species (Sikes *et al.* 2006; Sikes & Mousseau 2013; Sikes & Venables 2013b). Within this group, *N.* (*N.*) *nepalensis* Hope, 1831 is the only widely distributed species, known from Pakistan and India to China, Japan (Ryukyu Archipelago), Philippines, Malaysia and Indonesia (Sikes *et al.* 2002; Sikes & Venables 2013b). This species is also known to have a broad ecological niche, being distributed from lowlands to mountain habitats (Hwang & Koh 2013).

Larvae have only been described for a small portion of *Nicrophorus* species, mostly Western Palaearctic and Nearctic (summarized in Anderson 1982; Anderson & Peck 1985; Růžička 1992). Other older, usually quite superficial descriptions are summarized by Růžička (1992). Subsequently, only a few papers providing isolated larval descriptions of additional *Nicrophorus* species have been published (Hayashi 1986; Palestrini *et al.* 1996; Parkhomenko 2000a,b; Nishikawa 2001). Altogether, larval descriptions are currently available for 21 of 68 species of *Nicrophorus* (J. Růžička, unpubl.).

The only paper formally describing a larva of a member of the *N. nepalensis* group was published by Nishikawa (2001), who described a third instar larva of *N.* (*N.*) *maculifrons* Kraatz, 1877 from Japan.

The present paper provides detailed morphological descriptions of all three larval instars of *N.* (*N.*) *nepalensis*, and compares these with related species with known larval morphology, based on the phylogeny reconstructed by Sikes & Venables (2013a). Additionally, the generic description of *Nicrophorus* is supplemented by details observed using SEM.

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Materials and methods

Rearing insects. Adults of *N.* (*N.*) *nepalensis* were collected on May 16, 2011 by P. Šípek and D. Vondráček near Tanah Rata, Cameron Highlands, Malaysia (04°28.01‘75“N 101°22‘37.88“E), at an altitude of 1450 m. They used pitfall traps baited with fish and prawn meat. Eight males and 11 females were collected, transported to the laboratory at Charles University, and reared following the breeding protocol provided by Růžička (1992). Adults were identified using the key of Sikes *et al.* (2006); the identity of larvae obtained by breeding is therefore assured. Voucher specimens of some of the adults and reared larvae are deposited in the collection of Jan Růžička, Prague, Czech Republic. Breeding pairs or single females were kept in plastic containers (30×30 cm) on a 3 cm layer of soil, each provided with one mouse (*Mus musculus* Linnaeus, 1758, app. 25 g). The containers were then placed outdoors and kept in complete darkness. Average day temperature was 18.6 °C; max. 30.5 °C, min. 9.1 °C in June 2011, 17.9 °C; max. 30.9 °C, min. 9.0 °C in July 2011. The breeding boxes were inspected at least once a day.

Optical imaging. The immature specimens were killed in hot water and fixed in Pampel’s fluid (after Švácha & Danilevsky 1987). After one month, material was transferred into 75% ethanol, for permanent deposition. Before documentation, selected specimens were treated with ultrasonic cleaner for a short period of time (up to 1 min.) and gently cleared using a fine brush. Images of habitus were taken with specimens immersed in ethanol using a Canon macro photo lens EF-S 60mm on a Canon 550D body, multiple layers of focus were combined in the Zerene Stacker 1.04 software. Photographs of smaller details of external morphology were taken on temporarily dried specimens under a Keyence VHX-6000 digital microscope with VH-Z20R and VH-ZST lenses. Body length and head width were measured using an ocular micrometre under a dissecting microscope, with relative units converted to mm. Measurements of antennomeres and urogomphal segments were taken using a Keyence VHX-6000 digital microscope and its software. In total, 3 L1, 11 L2 and 28 L3 were measured for body length and cranial width, 3 L1, 9 L2 and 10 L3 for proportion of antennomeres and urogomphi. Morphological terminology follows Lawrence & Ślipiński (2013).

Electron imaging. Fine details of external morphology were examined at the Faculty of Science of Charles University in Prague using a JSM-6380LV (JEOL) scanning electron microscope (SEM) with a high resolution of 10.0 nm (with accelerating voltage 10–15 kW). The methodology follows Novák (2017). Before imaging, the specimens were first dehydrated through a series of increasing alcohol concentrations. The samples were transferred sequentially to 60%, 70%, 80%, 90%, and 95% alcohol for ca. 0.5 h each. Dehydrated samples were then dried using the critical point drying method. Dry samples were subsequently attached to an aluminium disk target and coated with gold in Bal-Tec Sputter Coater SCD 050, to ensure conductivity.

Final images from both optical and electron imaging were processed using CorelPHOTO-PAINT 2018; plates were arranged in CorelDRAW 2018. Graphs were compiled using R ver. 3.5.1.

Abbreviations. Larval instars are briefly marked as L1, L2 and L3 through the text. AI to AIII is used for antennomere I to III, UI and UII is used for urogomphal segment I and II.

Results

Larval morphology of *Nicrophorus* Fabricius, 1775

Anderson (1982) and Růžička (1992) provide generic descriptions of larvae of *Nicrophorus*, based on Nearctic and western-Palaearctic species. Here, we provide some additional details, based on thorough observation under SEM. **Head** prognathous, with short epicranial stem and bent frontal arms (Fig. 7D), medial endocarina extends beyond epicranial stem (Fig. 7D). Clypeus transverse, hexagonal in shape (Fig. 6A, cl). Labrum trapezoidal, with emarginate anterior part (Fig. 6A). Antenna three-segmented, antennomere II subapically with two setae and two sensory structures—one pointed sensorium and a large, peg-like sensilla (Fig. 7F). Maxillolabial complex strongly extended ventrally (Fig. 7E). Maxilla with stipes basally with prominent, sharp lateral lobe (Fig. 6F). Maxillary palpus three-segmented, with a short basal palpifer; palpomere III with basal close-fitting digitiform sensilla laterally (Fig. 6D), apex with a transverse field of ca. 12 sensillae (Figs. 6B, D). Apex of galea densely setose (Fig. 6F). Labial palpi two-segmented, palpomere II apically again with transverse field of ca. 12 sensillae (Fig. 7G).

Thorax. Pronotum irregularly folded (Fig. 7A), anterior part of prothorax with transversely folded membrane (Figs. 7A, B). Metasternum with a large spiraculum, surrounded by a heavily sclerotized ring, bearing a single seta; atrium of spiracle padded with multi-branched filtration hairs (Figs. 8C, D). Leg on prothorax short, with a high number of mostly ventrally oriented setae (Fig. 6C, 7C). Pretarsus short, sickle-shaped, with longitudinal microsculpture (Fig. 6E).

Abdomen. Tergum with large scutal sclerite, posteriorly with two pairs of dorsal and lateral lobes (Fig. 8A). Segment IX with only lateral pair of small spines and dorsal two-segmented urogomphi (Fig. 8B). Basal segment of urogomphi usually only partly separated from scutal sclerite of segment IX, urogomphal suture incomplete in the middle (Fig. 8B).

Biology and larval description of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831

(Figs 1–9)

Reproduction and development. Eight breeding pairs were raised along with 3 single females kept in separate boxes. One breeding pair and the 3 single females were unsuccessful in reproduction and died without producing any offspring. During the initial phase, the adults did not bury the carcass nor build a crypt. During the first 17 days (May 25–June 11, 2011) breeding was unsuccessful, and the mouse carcasses had to be replaced with fresh ones. After 4 days (on June 16, 2011), several eggs were observed in the containers. Observations were made in the joint broods for each breeding pair; estimates of the larval instar durations are thus only approximate. After another 4 days (on June 20, 2011), L1 larvae (3 specimens) emerged, and the same day L2 larvae (12 spec.) appeared, thus the length of development between L1 and L2 is only a few hours. L3 larvae (32 spec.) were observed after an additional 6–10 days (first on June 26, 2011). After another 11 days, the larvae burrowed into the soil and transformed into immobile prepupae followed by pupation (21 spec.). Adults (2 spec.) emerged from another colony 20 days after pupation (on June 27, 2011). Thus, the complete development time from egg to teneral adult takes about 41 days.

Morphometry. Total body length increases isometrically in larvae of *N.* (*N.*) *nepalensis*, but the values overlap widely between instars (Fig. 9A). The same isometric trend is observed in the width of the head capsule, which can be used for reliable instar identification, with no overlaps between instars (Fig. 9B). Proportions of appendages are negatively correlated with size: the ratio of antennomere III to antennomere I can be also used for instar identification, with no overlap between instars (Fig. 9C); a similar trend is visible in the ratio of segment II to segment I of the urogomphi, but with wide overlaps, specifically between L1 and L2 (Fig. 9D).

Morphology. L3 (Figs. 3A–C): Body length 14.0–26.0 mm. Head: cranial width 1.8–2.0 mm. Epipharynx with 1 or 2 lateral peg setae. Antennomere I 2.11–2.24 times as long as antennomere III. Mandible apically with 6 teeth. Maxilla: palpifer sclerotized only laterally (Fig. 4A), palpomere I sclerotized ventrally (Fig. 4A), palpomere II only slightly longer than palpomere I (Fig. 4A). Labium: Width of labium 0.34 mm, prementum with ventral part unsclerotized, narrow sclerotization present only laterally (Fig. 4A). Distance between bases of labial palpi approximately equal to width of basal labial palpomere (Fig. 4A), which is only narrowly sclerotized at base in ventral view (Figs. 4A, B). Ligula simple, without small lateral lobes (Figs. 4A, 7G).

Thorax (Figs. 3A–C): meso- and metanotum only weakly notched postero-laterally (Fig. 3A,B).

Abdomen (Figs. 3A–C): lateral and mid-dorsal spines (lobes) of tergites equal in length (Fig. 5B). Ventral part only weakly sclerotized, sclerites on segments II–VIII strongly reduced in ventral view (Fig. 3C, 5D). Urogomphus with articulation suture (urogomphal suture) only lacking in the middle (Figs. 5E, 8B). Basal segment of urogomphus 1.88–2.00 times as long as distal one (Fig. 5E). Ventrite IX completely sclerotized, only weakly emarginate at lateral margins; weakly notched medio-basally (Figs. 3C, 5C), with only one pair of setae centrally (Fig. 5C). Segment X with completely sclerotized ventral part at base as well as apically, without separately sclerotized Y-shaped area (Figs. 3B,C, 5A).

L2 (Figs. 2A–C): Body length 6.90–15.40 mm. Head: cranial width 1.2–1.3 mm. Antennomere I 1.76–1.89 times as long as antennomere III. Maxilla: palpomere II only slightly longer than palpomere I (Fig. 4C). Labium: Distance between bases of labial palpi less than a half of width of basal labial palpomere (Fig. 4C).

Thorax (Figs. 2A–C): meso- and metanotum not notched postero-laterally (Figs. 2A,B).

Abdomen (Figs. 2A–C): sclerites on segments II–VIII fully reduced (Fig. 2C). Basal segment of urogomphus 1.26–1.40 times as long as distal one.

L1 (Figs. 1A–C): Body length 5.60–9.80 mm. Head: cranial width 0.9 mm. Antennomere I 1.38–1.56 times as long as antennomere III. Maxilla: palpomere II distinctly longer than palpomere I (Fig. 4D). Labium: Distance between bases of labial palpi only one third of width of basal labial palpomere (Fig. 4D).

Thorax (Figs. 1A–C): meso- and metanotum not notched postero-laterally (Figs. 2A,B).

Abdomen (Figs. 1A–C): sclerites on segments II–VIII fully reduced (Fig. 1C). Basal segment of urogomphus 1.24–1.28 times as long as distal one.

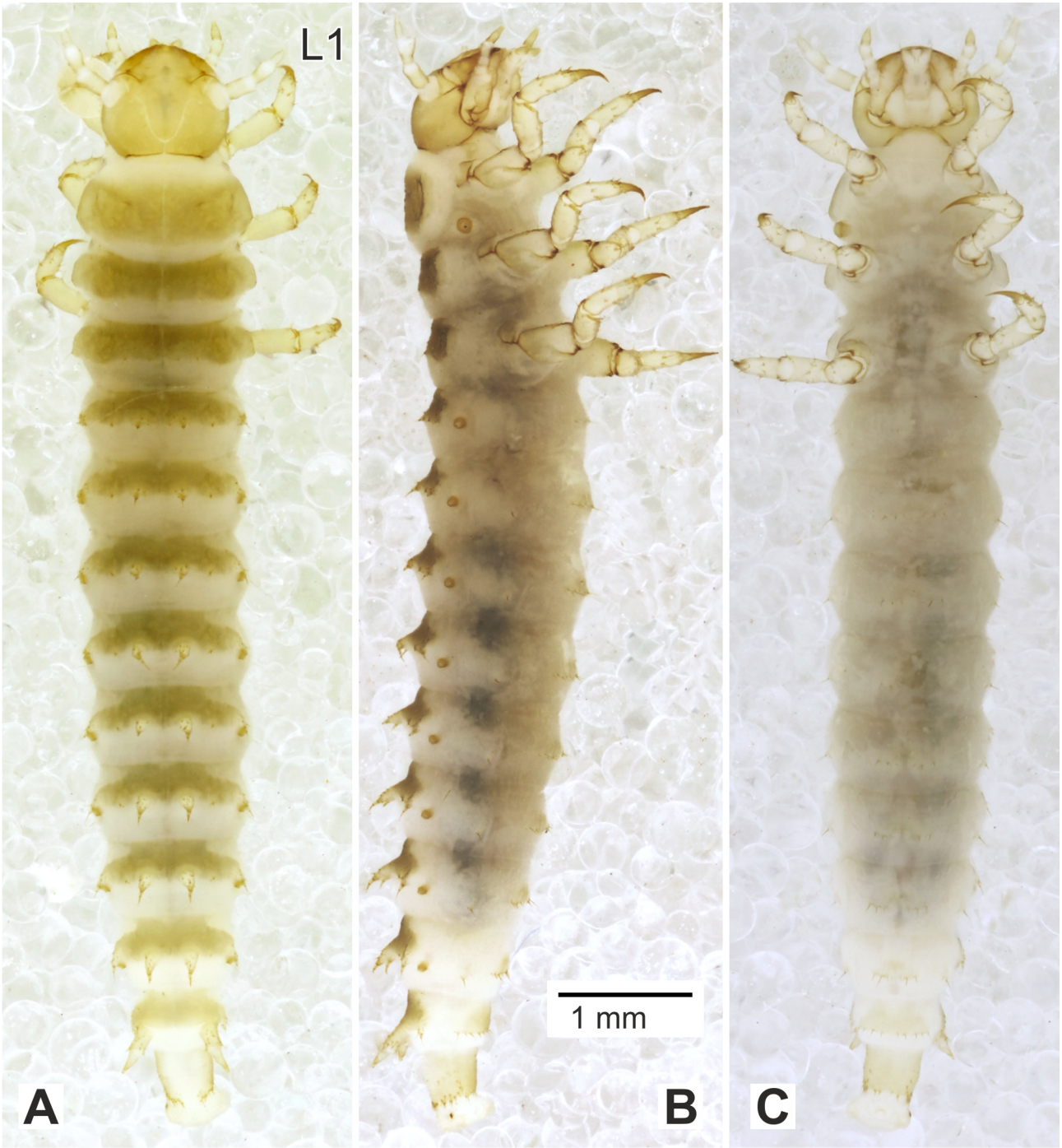

FIGURE 1. A–C. Habitus of the first instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—dorsal view, B—lateral view, C—ventral view.

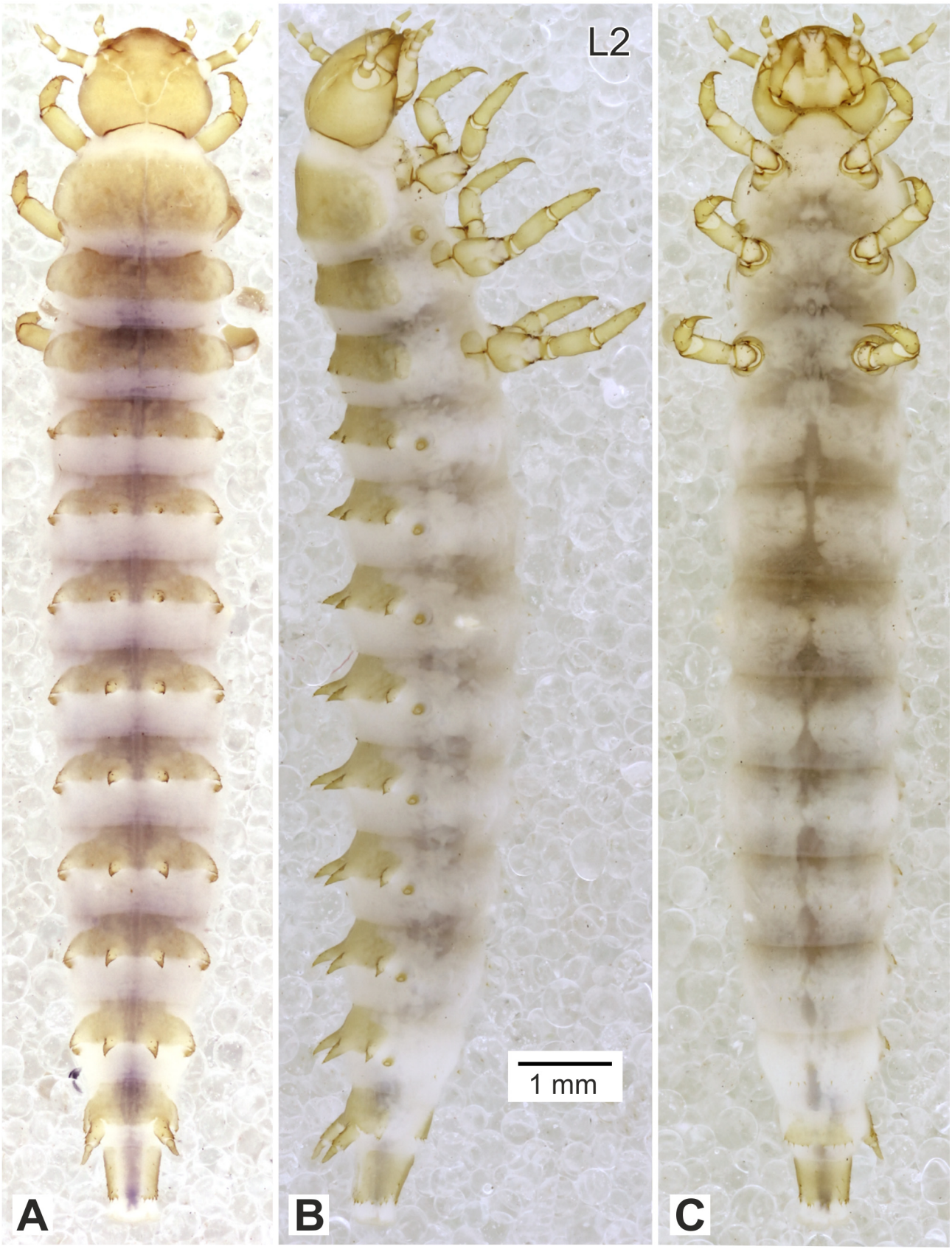

FIGURE 2. A–C. Habitus of the second instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—dorsal view, B—lateral view, C—ventral view.

FIGURE 3. A–C. Habitus of the third instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—dorsal view, B—lateral view, C—ventral view.

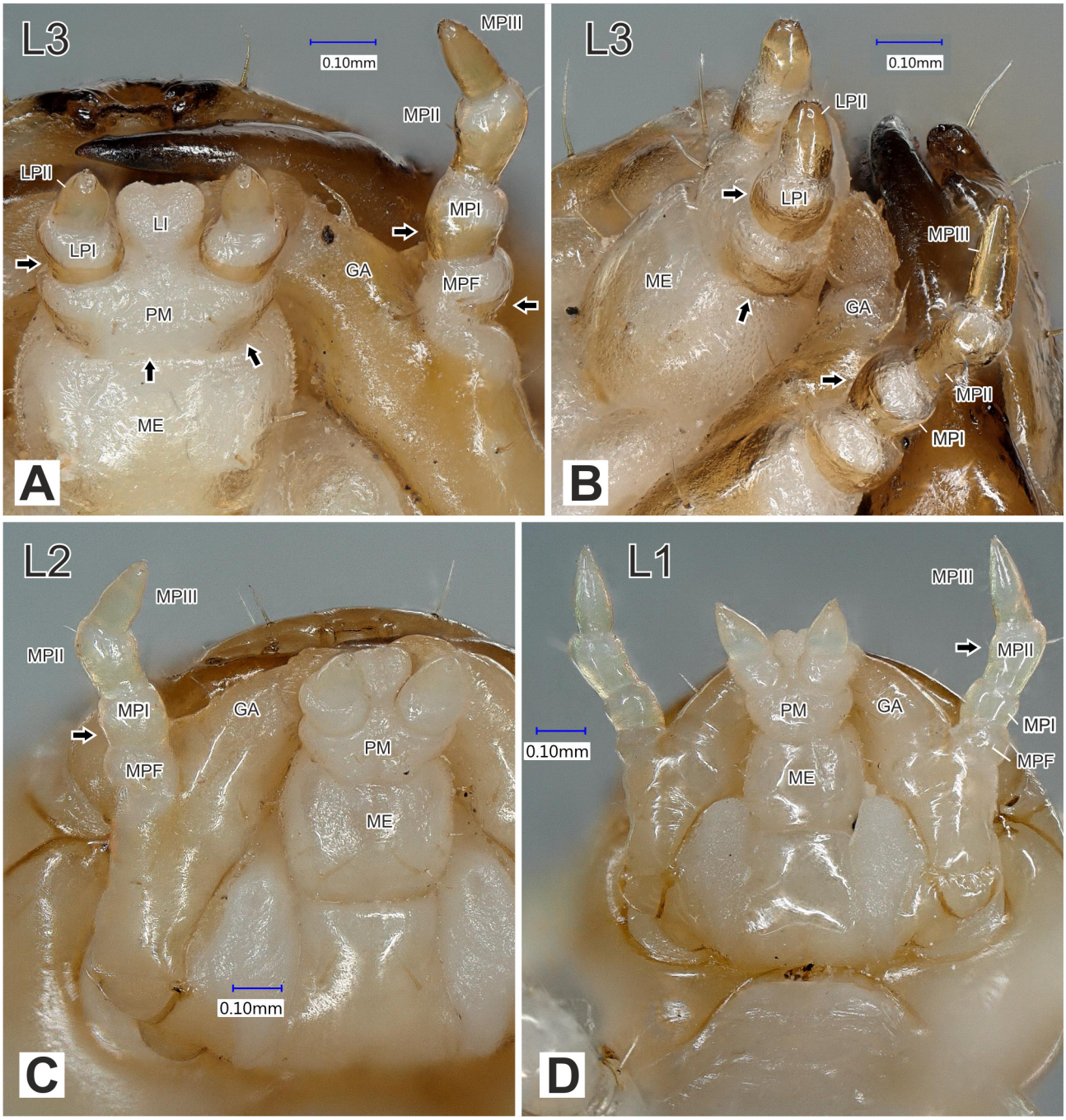

FIGURE 4. A–D. Maxillo-labial complex of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A, B—third instar, ventral and lateral view, C—second instar, ventral view, D—first instar, ventral view. Abbreviations: GA—galea, LI—ligula, LPI, LPII—labial palpomere I and II, ME—mentum, MPF—palpifer of maxilla, MPI to MPIII—maxillary palpomere I to III, PM—prementum.

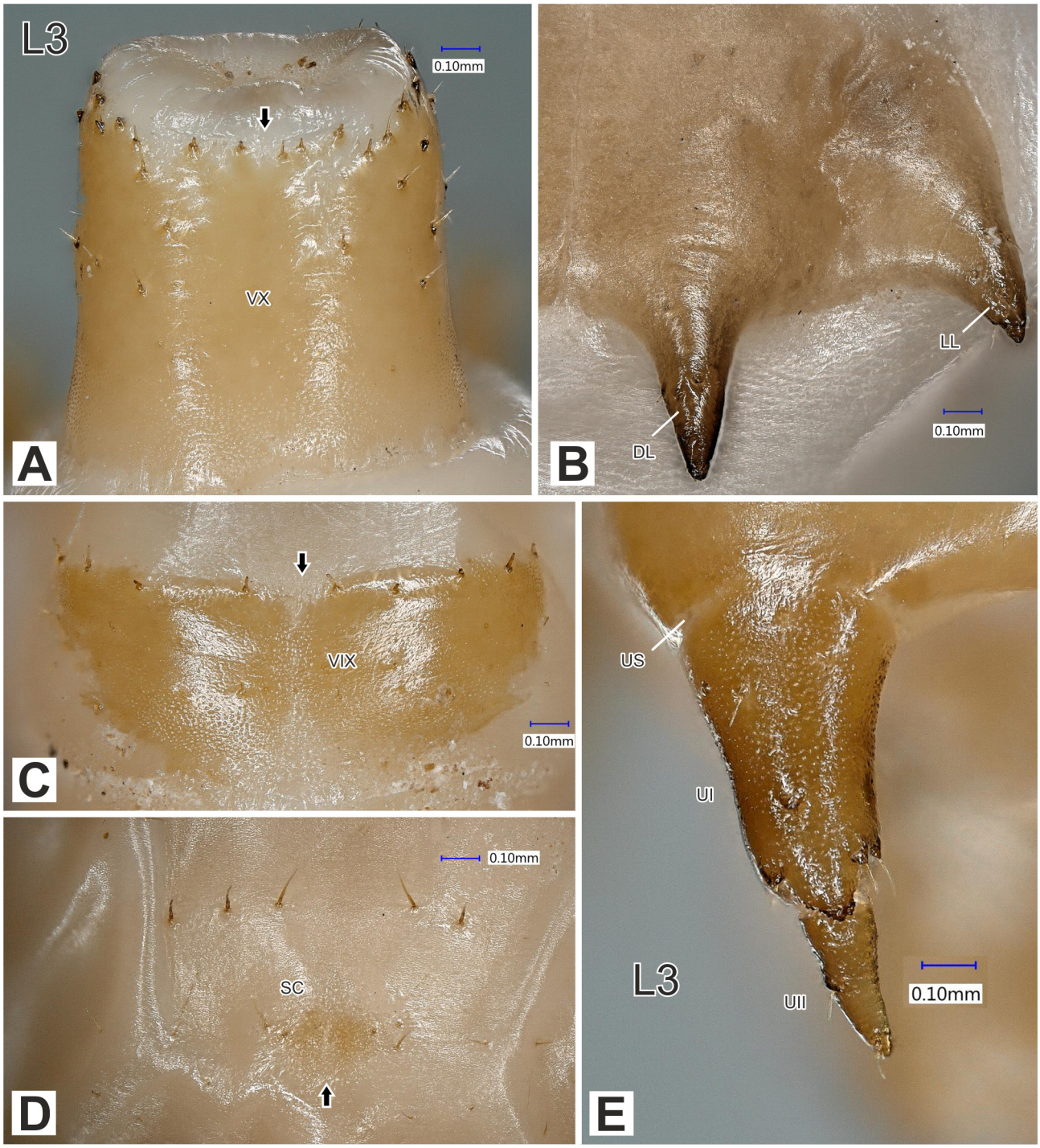

FIGURE 5. A–E. Details of third instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—segment X, ventral view, B—lateral portion of abdominal segment IV, dorsal view, C—ventrite IX, ventral view, D—ventrite IV, ventral view, E—urogomphus, dorsal view. Abbreviations: DL—dorsal lobe, LL—lateral lobe, SC—ventral sclerite, UI and UII—urogomphal segment I and II, US—urogomphal suture, VIX—ventrite IX, VX—ventrite X.

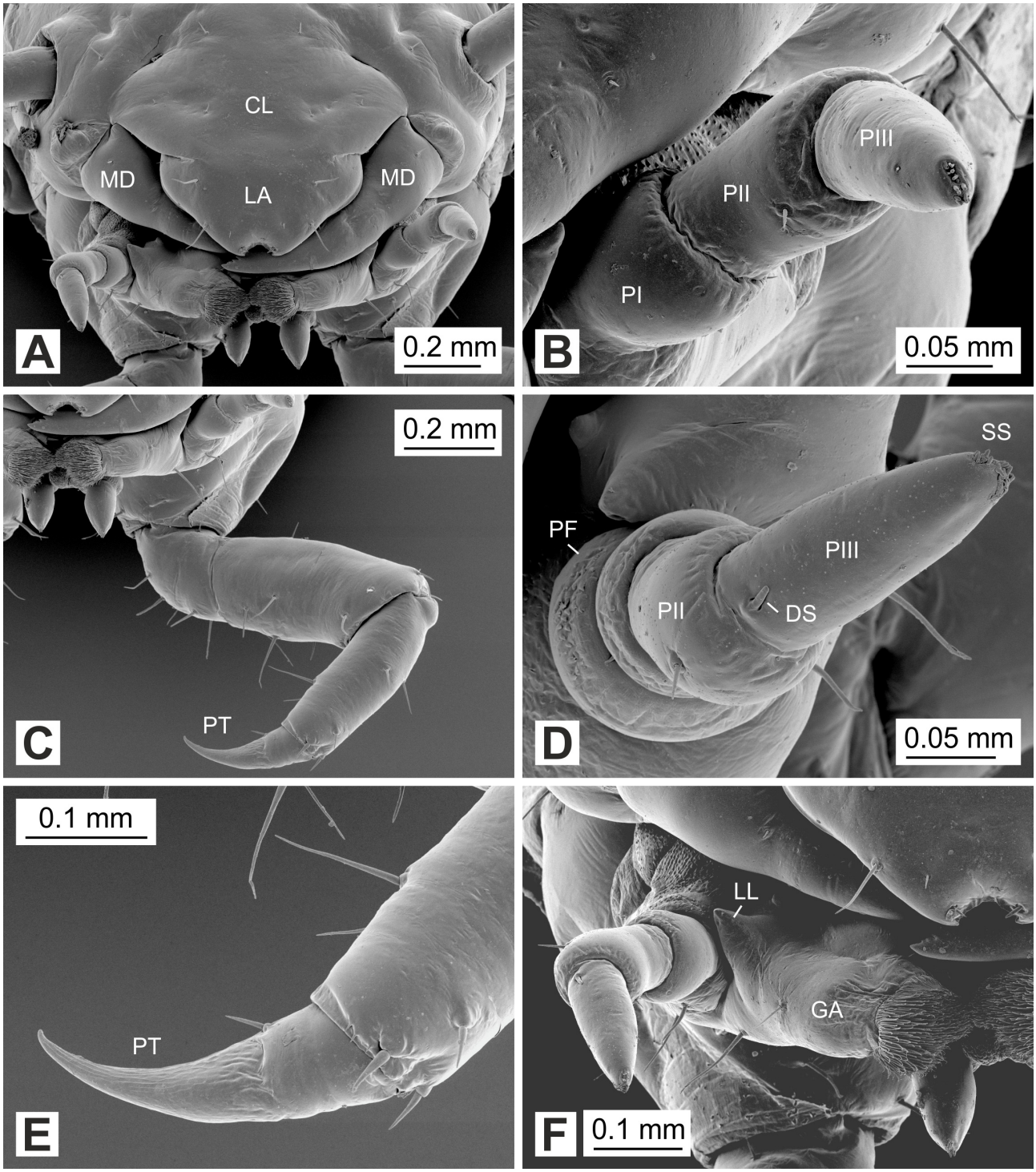

FIGURE 6. SEM of second instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—head antero-dorsally, B—maxillary palpus, lateral view of palpomeres I and II, C—leg on prothorax, lateral view, D—maxillary palpus, lateral view of palpomere III, E—leg on prothorax, tarsal claw, lateral view, F—maxilla, antero-dorsal view. Abbreviations: CL—clypeus, DS—digitiform seta, GA—galea, LA—labrum, LL—lateral lobe of maxilla, MD—mandible, PF—palpifer, PI to PIII—maxillary palpomere I to III, PT—pretarsus, SS—sensillae.

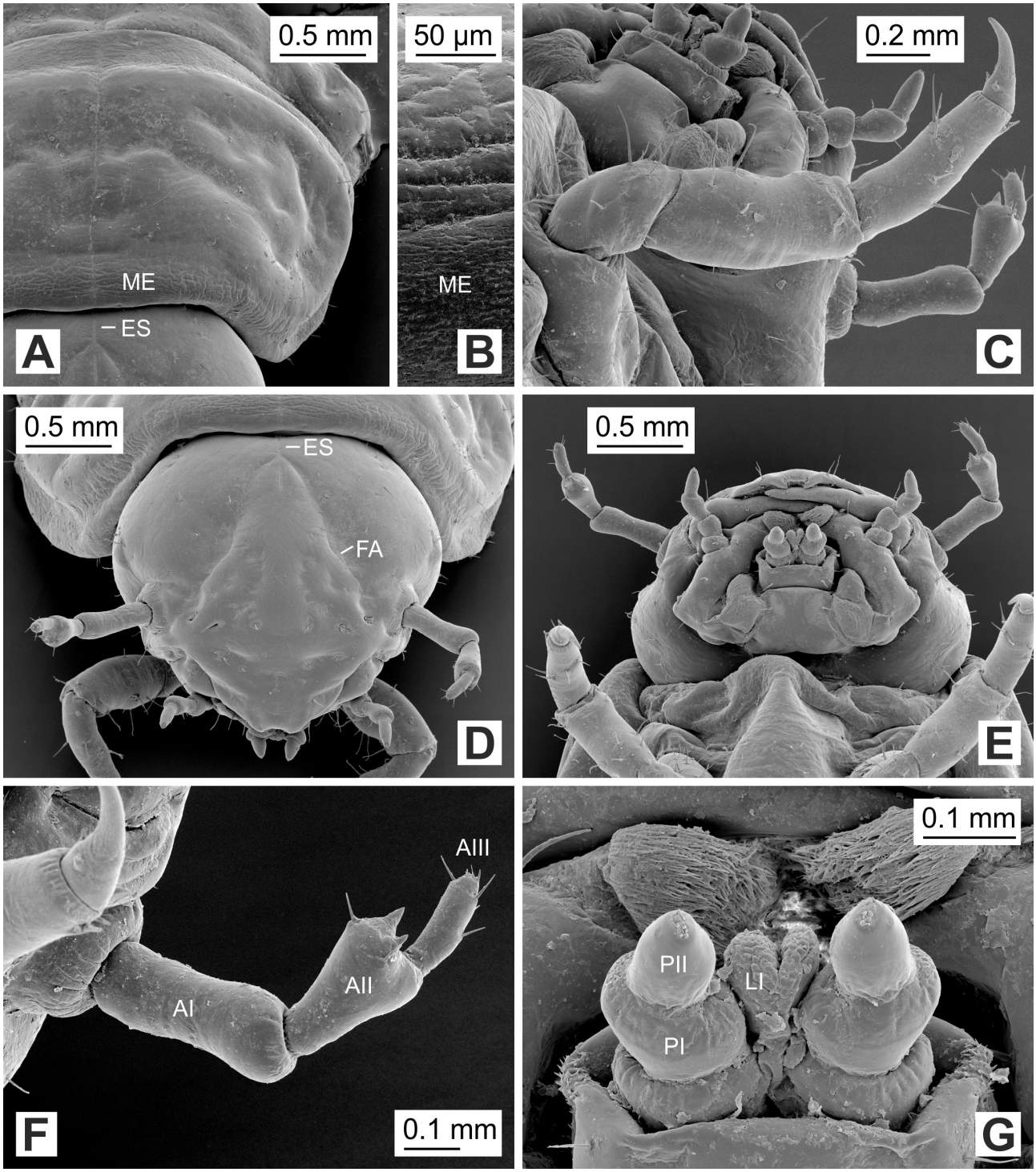

FIGURE 7. SEM of third instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—pronotum in dorsal view, B—detail of anterior part of pronotum in dorsal view, C—leg on prothorax in lateral view, D—head in dorsal view, E—head in ventral view, F—antenna in lateral view, G—apex of labium in antero-ventral view. Abbreviations: AI to AIII—antennomere I to III, ES—epicranial stem, FA—frontal arms, LI—ligula, ME—membrane on prothorax, PI and PII—labial palpomere I and II.

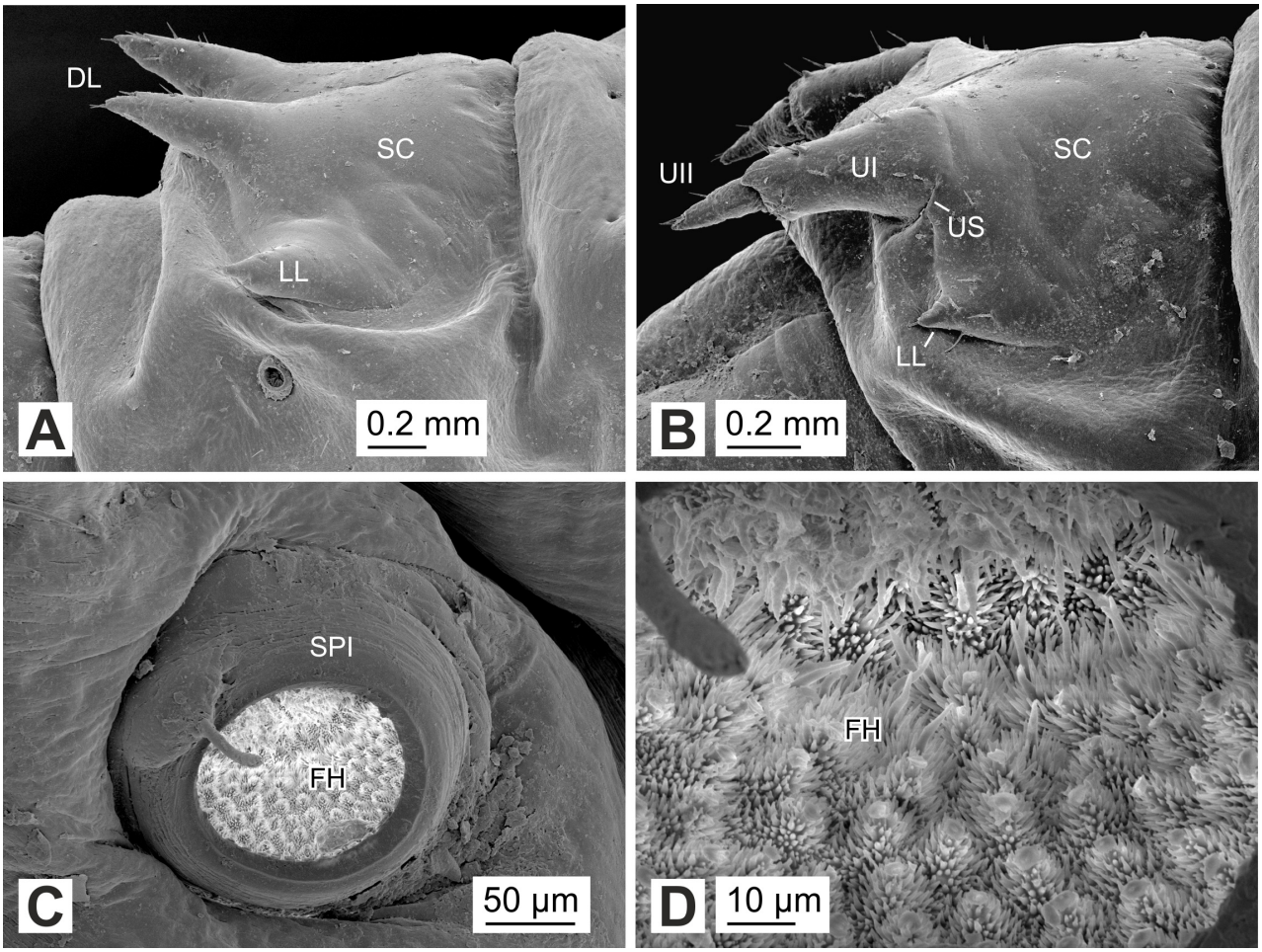

FIGURE 8. SEM of third instar of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—abdominal segment IV in lateral view, B—abdominal segment IX and urogomphi in lateral view, C—metasternal spiraculum in lateral view, D—detail of metasternal spiraculum in lateral view. Abbreviations: DL—dorsal lobe, FH—multi-branched filtration hairs, LL—lateral lobe, SC—scutal sclerite, SPI—spiraculum, UI and UII—urogomphal segment I and II, US—urogomphal suture.

Discussion

A molecular phylogeny of the genus *Nicrophorus* was recently published by Sikes & Venables (2013a). The *Nicrophorus nepalensis* species group was recovered as a monophyletic clade, sister to the European *N*. (*N*.) *humator* (Gleditsch, 1767) (forming *N. humator* species group together with the Nearctic *N*. (*N*.) *sayi* Laporte, 1840) (Sikes & Venables 2013a).

The morphology of the third-instar larva of *N*. (*N*.) *nepalensis* supports this phylogenetic pattern, showing high similarity with *N*. (*N*.) *humator*. Both species share the following character states of larval morphology (comparison based on data in Růžička 1992): (1) maxillary palpomere I sclerotized ventrally; (2) maxillary palpomere II only slightly longer than palpomere I; (3) prementum ventrally unsclerotized; (4) distance between bases of labial palpi approximately equal to width of basal labial palpomere; (5) basal labial palpomere sclerotized only narrowly at base in ventral view; (6) ligula without small lateral lobes; (7) sclerites on segments II–VIII extremely reduced in ventral view; (8) ventrite IX completely sclerotized, only weakly emarginate at lateral margins. Based on Anderson (1982), only one of these character states (for character no. 4) is an apomorphy within *Nicrophorus* sensu stricto. Unfortunately, several other characters were not scored for Nearctic species by Anderson (1982) or Anderson & Peck (1985), although later found to be phylogenetically informative for European species by Růžička (1992).

Larvae of the two species differ in the sclerotization of abdominal segment X in ventral view: in *N*. (*N*.) *humator,* only narrow, irregular sclerotization is present at the base, leaving the apical part unsclerotized (as described by Růžička 1992), but complete sclerotization (base as well as apical part) is developed in *N*. (*N*.) *nepalensis*.

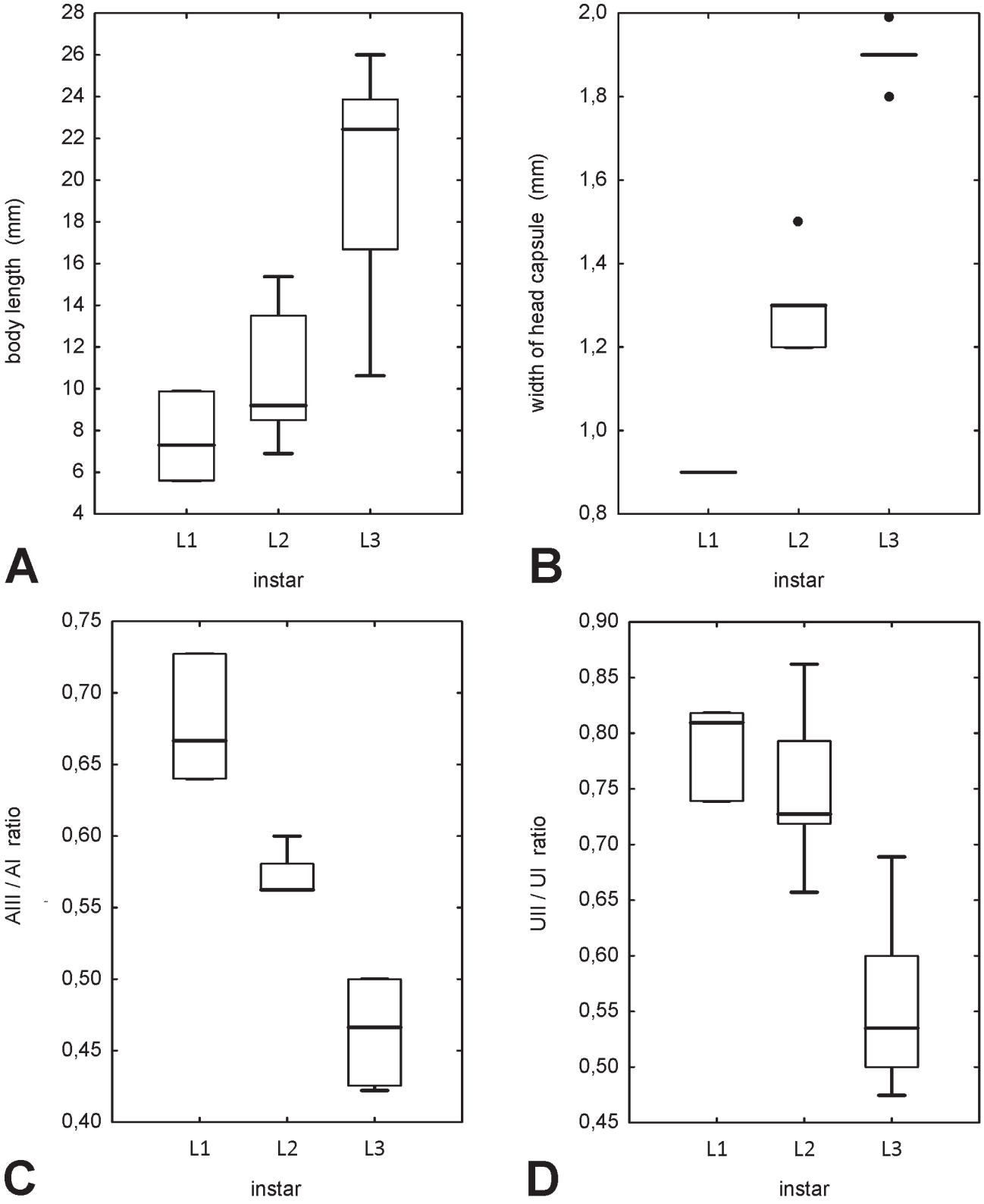

FIGURE 9. Boxplots of measurements of in all three larval instars of *Nicrophorus* (*Nicrophorus*) *nepalensis* Hope, 1831. A—total body length; B—width of head capsule; C—length ratio between antennomeres (AIII / AII); D—length ratio between segments of urogomphi (UII / UI). Horizontal lines within the boxes indicate median values, upper and lower boxes indicate the 75th and 25th percentiles, respectively; whiskers indicate the values with the 1.5 interquartile ranges; black dots are outliers.

Presently, it is difficult to compare the larva of *N.* (*N.*) *nepalensis* with that of *N.* (*N.*) *maculifrons*, the only other species of *N. nepalensis* species group with formally described larvae. Nishikawa (2001) had access to only a single L3 larva. His description and illustrations mentioned the following shared character states for both species: (1) maxillary palpomere II only slightly longer than palpomere I; (2) distance between bases of labial palpi approximately equal to width of basal labial palpomere; (3) ligula without small lateral lobes; (4) ventrite IX completely sclerotized, only weakly emarginate at lateral margins.

Both species show the following differences: (1) basal labial palpomere unsclerotized ventrally in *N.* (*N.*) *maculifrons* (sclerotized in *N.* (*N.*) *nepalensis*); (2) abdominal segment X in ventral view sclerotized at base, apically with Y-shaped sclerotization and deep lateral desclerotized emarginations in *N.* (*N.*) *maculifrons* (complete sclerotization at base as well as in apical part in *N.* (*N.*) *nepalensis*). Morphology of additional species of this species group is needed to fully understand the distribution and polarization of character states within this large lineage.

Nicrophorus is a popular group for study of different evolutionary aspects of biparental care (e.g., Pukowski 1933, Scott 1998, Benowitz & Moore 2016, Pilakouta *et al.* 2018). However, larval morphology is known for less than a third of the species (21 of 68 species; J. Růžička, unpublished). For some burying beetle species with formally described larvae, several characters are not properly scored (Anderson 1982; Hayashi 1986; Palestrini *et al.* 1996; Parkhomenko 2000a,b; Nishikawa 2001). Presently, we know too little about larval morphology of burying beetles to combine it efficiently with molecular data. However, some character states in *N.* (*N.*) *nepalensis* (e.g., complete sclerotization of ventral side of abdominal segment X) are unique within known larvae of *Nicrophorus*, and broaden the known spectrum of variation within the genus. Further studies of carrion beetle larval morphology are thus required.

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