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# A Description of the Mature Larva of *Neoporus dimidiatus* (Gemminger and Harold, 1868) (Coleoptera: Dytiscidae: Hydroporinae) with Notes on its Natural History

## **Cover Page Footnote**

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**A DESCRIPTION OF THE MATURE LARVA OF *Neoporus dimidiatus* (GEMMINGER AND HAROLD, 1868) (COLEOPTERA: DYTISCIDAE: HYDROPORINAE) WITH NOTES ON ITS NATURAL HISTORY**

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**ABSTRACT**

Mature larvae of *Neoporus* Guignot, 1931 collected from an Oklahoma stock pond and outlet stream were cultured into the adult stage, and identified as *N. solitarius* (Gemminger and Harold, 1868). Chaetotaxy of legs and urogomphi is comparable to that of previously described *Neoporus*, including secondary sensilla on the proximal urogomphal segment. Mandibular geometric parameters were as follows: MMD/ML,  $0.10 \pm 0.02$ ; MBD/ML,  $0.27 \pm 0.03$ ; angle of attack (AA),  $46.6 \pm 1.9^\circ$ ; lateral arc (Larc),  $119.6 \pm 2.9^\circ$ ; medial arc (Marc),  $78.2 \pm 5.2^\circ$ . Respective cranial temporal curvature and orientation were  $73.2 \pm 8.6^\circ$  and  $13.9 \pm 1.3^\circ$ . Significant differences between dorsal and ventral intermandibular distances (DID =  $0.71 \pm 0.04$  mm vs. VID =  $0.49 \pm 0.03$  mm) appear to be major architectural and geometric features facilitating the oblique opening and closure of mandibles during prey capture and feeding.

**Keywords:** Larval morphology, chaetotaxy, cranial architecture, mandibular geometry

**INTRODUCTION**

Hydroporinae Aubé, 1836 with adults ranging in size from 1.0–7.2 mm (Larson et al. 2000) is the largest dytiscid subfamily with about 1500 species and a worldwide distribution (Nilsson and Holmen 1995). Hydroporine larvae are easily recognized because of a prominent anterior extension of the frontoclypeus margin (nasale) that extends well beyond the origins of the antennae and mandibles (Larson et al. 2000). This taxon includes the endemic Nearctic *Neoporus* Guignot, 1931 containing about 40 species with most having ranges that are restricted to the Appalachian region of North America (Wolfe 1984). The distribution of *N. dimidiatus* is exceptional in that its range extends from northern Georgia (Turnbow and Smith 1983) into eastern Canada and westward to Alberta and then south to Oklahoma, Texas, New Mexico, and Arizona (Larson et al. 2000). *Neoporus* with *Heterosternuta* Strand, 1935 form a monophyletic lineage that is supported by a combination of diagnostic characters, including the presence of secondary sensilla on the proximal urogomphal segment and the absence of an apparent homologue of TR<sub>2</sub> on each trochanter (Alarie 1991). Mature larvae of *Neoporus* and *Heterosternuta* also lack thoracic and lateral abdominal spiracles as noted by Barman (1972) and confirmed by Alarie (1991). Third instars of these taxa are

separated by the presence of natatory (swimming) sensilla on tibiae and tarsi of *Neoporus* and their absence on *Heterosternuta* (Alarie 1991).

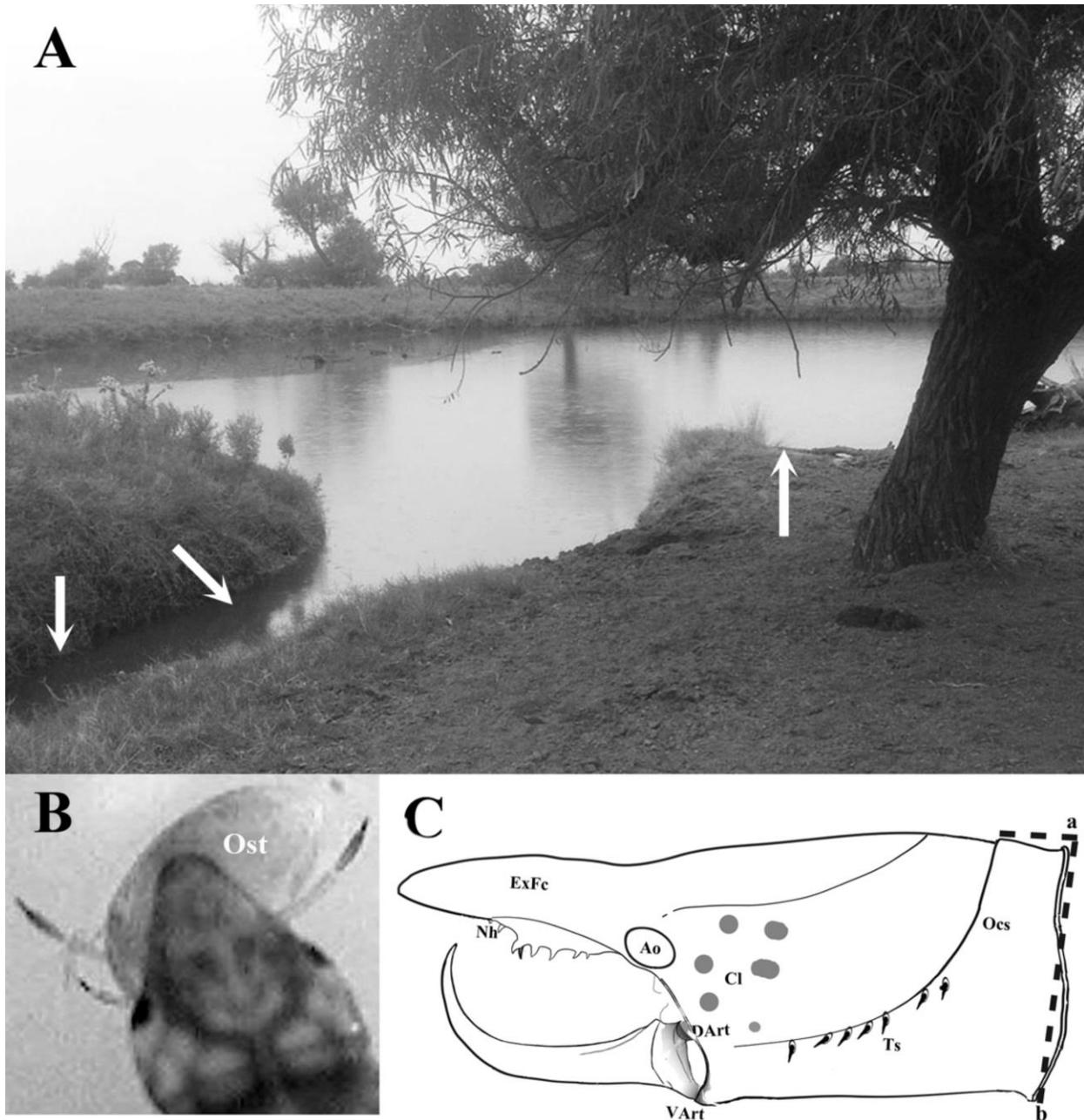
In general *Neoporus* species have been associated with lotic systems although the habitat of the widely distributed and nearly ubiquitous eastern species *N. undulatus* (Say, 1823) has been described as permanent with some restricted water movements. However, statements concerning Nearctic dytiscid reproductive habitat preferences are often based on the occurrence of adults (Larson et al. 2000) in a limited number of habitats. Large numbers of adults, including gravid specimens, present in a system do not necessarily indicate that the system has served or will serve as a preferred or successful reproductive site. Eggs were deposited by *Coptotomus interrogatus* (Fabricius, 1801) collected from a very small system that was dry 14 days after collection (Barman 2004), making completion of larval development unlikely within that system. Adults of *N. undulatus* were numerous in a small permanent upstate New York pond, but larvae were collected only in a nearby temporary habitat and neither adults nor larvae were observed in a lotic habitat that transected the frequently monitored study area (Barman 1996).

Larvae of *N. dimidiatus* were described as *H. solitarius* Sharp, 1882 (Barman 1972), but this description includes errors and lacks the morphological detail required for identification of larval material as well as for comparative and geographical studies. The purpose of this study was, in part, to describe general larval morphology with an emphasis on sensilla of legs and urogomphi of an Oklahoma population of *N. dimidiatus*. Observations on selected aspects of larval cranial architecture and mandibular geometry were included because these data may provide insights into the interaction of mandibles and the extended frontoclypeus in capture and feeding by hydrophiline larvae. Mandibular geometry and cranial architecture may also be indicative of differences in intrasystem larval distributions and behaviors (Barman et al. 2016). Observations on general bionomics of the Oklahoma and New York populations of *N. dimidiatus* also afforded an opportunity of assessing some aspects of geographic variation in reproductive habitats.

## MATERIAL AND METHODS

Larval descriptions are based on mature larvae collected 30-31 December 1971 from beneath ice on a stock pond and from a lotic exit tributary of this pond (Figure 1A) on 25-26 December 1995 located on the Wayne Harrel farm, Elgin, Comanche County, Oklahoma, USA. Natural history observations are based on these populations and larvae collected 6 August 1969 and 25 July 1970 from Onondaga Creek 1.6 km west of Cardiff, Onondaga County, New York, USA. Larvae of both populations were identified as *N. dimidiatus* after adult eclosion. Vouchers are deposited in the Georgia College & State University Insect Museum (GCIM).

Descriptions were of 10 (unless noted otherwise) Oklahoma specimens and three damaged New York larvae preserved in 70% glycerated ethyl alcohol. Heads and legs were disarticulated and examined with a WILD M5A dissecting microscope equipped with a micrometer eyepiece or a Meiji (MI2000) microscope with an external micrometer. To minimize distortions, all material was examined on concave slides.



**Figure 1.** A. Oklahoma larval habitat(s) for *Neoporus dimidiatus*. Collection locales are indicated by arrows. B. Dorsal view (Barman et al. 2007) of the cranium of a mature hydroporine larva feeding on an ostracod (Ost). C. Lateral view of the cranium of *Neoporus dimidiatus*. Abbreviations include the following: Ao, antennal origin; Cl, corneal lenses; DArt, dorsal mandibular articulation; ExFc, extended frontoclypeus; Nh, notch; Ocs, occipital suture; Ts, temporal spines (the only sensilla shown); VArt, ventral mandibular articulation. Line **ab** drawn along the lateral-posterior margin of the occipital region is used to estimate cranial orientation.

Parameters measured included the following:

Head length (HL): measured dorsally from the posterior margin along the coronal suture to the anterior margin of the frontoclypeus.

Head width (HW): measured dorsally at the widest point of the head.

Mandibular length (ML): measured ventrally along a straight line from the apex to the center of the ventral ball of articulation (Wall et al. 2006).

Intermandibular distance (ID): measured ventrally (VID) and dorsally (DID) from the center point of articulation of one mandible to the same point of the other mandible (Wall et al. 2006; Mathias et al. 2016).

Midmandibular depth (MMD), mandibular basal depth (MBD), angle of attack (>(AA), and lateral (Larc) and medial arcs (Marc): estimated from enlarged images of ventral views of disarticulated mandibles (Mathias et al. 2016).

Temporal curvatures (TC): estimated (Barman et al. 2013) from enlarged dorsal cranial images and using the following formula:  $TC = 360^\circ - 2(\text{angle } \mathbf{acb})$  for computation of TC for both temporal regions of each larva. The TC for each larva is then presented as an average of these two computations.

Cranial orientation (CO): calculated from enlarged lateral images using a base line drawn along the lateral-posterior margin with its length (line **ab**; Figure 1C) determined by the maximum lateral depth of the occipital region. A second line was extended at  $90^\circ$  from the midpoint of line **ab** to terminate beyond the cranial anterior margin at point. An angle representing the ventral (or dorsal) departure of the center of the ball component of the dorsal articulation of the right or left mandible was taken as an estimation of CO (Mathias et al. 2016) with angles above the  $90^\circ$  line designated as negative (-) and those below as positive (+).

Chaetotaxy: Sensilla of legs and urogomphi are identified and enumerated by region or area of origin, using a version of systems (Wolfe and Roughley 1985; Nilsson 1988; Alarie et al. 1990; Alarie 1991) that rely on commonly used anatomical terms to designate individual sensilla or groups of sensilla. Sensilla of legs (Figures 2A, B) are described according to their origin within four general areas: anterior dorsal (AD) and ventral (AV) and posterior dorsal (PD) and ventral (PV) on each coxa (CO), femur (FE), tibia (TI), and tarsus (TA). The sensilla present on mature larvae include apparent homologues of ancestral (primary) sensilla that were present on first instars. Some primary sensilla are tentatively identified with appropriate Arabic numerals (Alarie 1991; Nilsson 1988; Alarie et al. 1990) and used to determine boundaries (dashed lines, Figures 2A, B) between dorsal and ventral regions of each leg segment. Because of their small size and apparent persistence on specimens, homologues of ancestral CO<sub>1-5</sub>, 13-17 and TA<sub>3-6</sub> are also shown with Arabic numerals (Figures 2A, B) but excluded from tabulations.

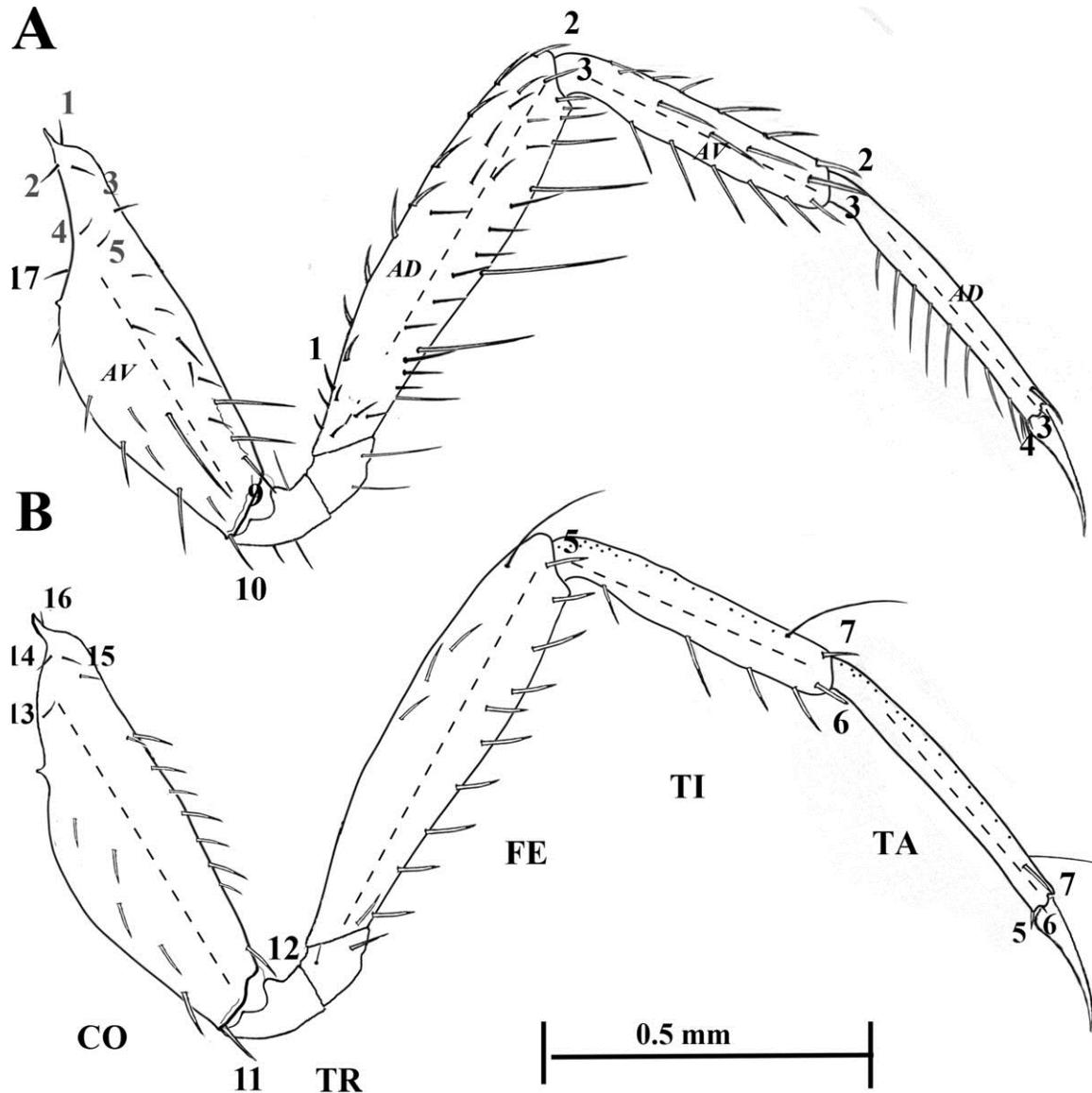
Data analysis was with GraphPad InStat, version 3.10 for Windows; GraphPad Software, San Diego, California, USA.

### **LARVAL DESCRIPTION** (Tables I, II, III; Figures. 1B, C, 2A, B)

**Body.** Widest at or the near base of first abdominal segment, length (alcohol preserved specimens) about 6 mm excluding urogomphi; sclerotized areas yellowish-brown with irregular areas on head, body, and cerci darker brown.

**Cranium** (Figures 1B, C). Pear-shaped in dorsal view, frontoclypeus extended well beyond the origins of the mandibles to form a prominent projection (nasale),

temporal curvature (TC)  $65.0\text{--}86.0^\circ$  ( $73.2 \pm 8.6^\circ$ ); cranial orientation  $12.0\text{--}15.5^\circ$  ( $13.9 \pm 1.3^\circ$ ); the mean DID was  $0.71 \pm 0.04$  mm and the mean VID was  $0.49 \pm 0.03$  mm (Table II); occipital suture prominent, extending anteriorly along lateral surfaces, no constriction between the occipital suture and the cranial posterior margin; extended frontoclypeus with prominent lateral notches, anterior to serrated marginal area; venter extensively sclerotized, labrum not evident; stemmatal area with six corneal lenses arranged laterally in an oval; gular sutures obscure; posterior tentorial pits visible



**Figure 2.** Metathoracic leg of *Neoporus dimidiatus*; anterior (A) and posterior (B) views with sensilla tentatively identified as homologues of ancestral sensilla indicated with Arabic numerals. Abbreviations include the following: anterior dorsal, AD; anterior ventral, AV; coxa, CO; femur, FE; trochanter, TR; tibia, TI; and tarsus, TA. Origins of natatory sensilla are shown as dots on posterior views of the tibia and tarsus.

ventrally; prominent sensilla include *lamellae chypeales* on frontoclypeal anteroventral margin; seven to 10 temporal spines parallel to occipital sutures; antenna with accessory sensorial appendage present on 3<sup>rd</sup> segment.

**Mouth parts** (Tables I, II). Mandible, slender, falcate, with two prominent lateral sensilla, no medial teeth, MMD/ML = 0.07–0.12 ( $0.10 \pm 0.02$ ); MBD/ML = 0.23–0.29 ( $0.27 \pm 0.03$ ); directed dorsomedially (Figure 1C) to cross beneath anterior margin of frontoclypeus; angle of attack (AA), 43.5–48.5° ( $46.6 \pm 1.9^\circ$ ); lateral arc (Larc), 117.0–124.0° ( $119.6 \pm 2.9^\circ$ ); medial arc (Marc), 72.0–85.0° ( $78.2 \pm 5.2^\circ$ ) (Table II); maxilla with obscure cardo bearing one prominent sensillum; stipes short, fingerlike, ventrolateral surface with two prominent sensilla, medial surface without sensilla; galea absent, maxillary palps, 1<sup>st</sup> with basal spinule and distal pore, 2<sup>nd</sup> with two prominent sensilla, 3<sup>rd</sup> with one prominent sensillum; labium, prementum small, trapezoidal, narrowest posteriorly, lateral margins distant from medial margins of maxillary stipes, three prominent distolateral hair-like sensilla near origin of each labial palp, two small basal spines, lateral spinules present; postlabium relatively short, broad based, separated from maxillary bases by two low but prominent protuberances, one small sensillum between each protuberance and stipes.

**Thorax.** Pronotum about one and a half times longer than either meso- or metanota, widest posteriorly, pronotal venter membranous, with long hair-like sensilla on the margins anteriorly, laterally, and posteriorly, irregularly distributed interior sensilla; meso- and metanota about equal in length, hair-like sensilla within interior and forming fringe on the lateral and posterior margins. Spiracles absent on thorax. Legs (Tables I, III; Figures IIA, B) with coxal sutures obscure; ventral spinules (combs) present on protarsi and protibiae, vestigial distally on meso- and metatarsi and tibiae; trochanter, 1TR (proximal region) with 2-3 sensilla, 2TR (distal region) with four sensilla, apparent homologues of TR<sub>2</sub> and TR<sub>3</sub> absent. Apparent homologues of CO<sub>1-3,4,5,13-17</sub> and TA<sub>3-6</sub> consistently present. Number and distribution of prominent spiniform sensilla on pro- and metalegs as in Table III; sensillar distributions on metathoracic (Figures 2A, B) and mesothoracic legs are similar, only more numerous on former; complex sensilla, bearing unicellular processes present, more numerous ventrally and distally on femoral and tibial segments; posterior tarsal claws shorter than anterior claws.

**Abdomen.** Segments 1-5 with heavily sclerotized and distinct dorsal plates, membranous laterally and ventrally, 6 heavily sclerotized dorsally and laterally, segments 7 and 8 completely sclerotized; sensilla numerous on all segments with shorter sensilla dominant ventrally; spiracular openings absent on 1-7; segment 8 dorsal length 0.38-0.52 mm ( $\bar{x} = 0.46 \text{ mm} \pm 0.05$ , n = 7); siphon well-defined with broad base, length 0.08-0.14 mm ( $\bar{x} = 0.11 \pm 0.02 \text{ mm}$ ). Urogomphus, two segmented; proximal segment, 1.34-1.59 mm ( $\bar{x} = 1.44 \pm 0.08 \text{ mm}$ , n = 7) with numerous primary (ancestral) and secondary sensilla similar to that shown for *N. undulatus* (Alarie 1991); segment 2, length 0.90-1.04 mm ( $\bar{x} = 0.95 \pm 0.05 \text{ mm}$ , n = 6), with a hair-like sensillum arising distally.

**Table I.** Dimensions ( $n = 10$ , unless noted otherwise) of crania and cranial and thoracic appendages of Oklahoma third instars of *Neoporus dimidiatus*

	<u>Range (mm)</u>	<u>Mean <math>\pm</math> SD</u>
Head Length (HL)	1.12–1.20	1.15 $\pm$ 0.02
Maximum Head Width (HW)	0.84–0.99	0.93 $\pm$ 0.04
Maximum Head Depth (HD); $n = 5$	0.41–0.53	0.50 $\pm$ 0.05
Frons Length (FL)	0.84–0.98	0.88 $\pm$ 0.04
Coronal Suture Length (CS)	0.18–0.32	0.26 $\pm$ 0.04
Mandibular Length (ML)	0.54–0.62	0.59 $\pm$ 0.03
Mandibular Mid-depth (MMD); $n = 8$	0.04–0.07	0.06 $\pm$ 0.01
Mandibular Basal Depth (MBD); $n = 8$	0.14–0.17	0.16 $\pm$ 0.01
Antennal Length (AL)	0.58–0.64	0.62 $\pm$ 0.02
Antennal Segment 1	0.09–0.14	0.11 $\pm$ 0.02
Antennal Segment 2	0.20–0.23	0.22 $\pm$ 0.01
Antennal Segment 3	0.20–0.22	0.21 $\pm$ 0.01
Antennal Segment 4	0.06–0.08	0.07 $\pm$ 0.01
Maxillary Palp Length	0.48–0.57	0.53 $\pm$ 0.03
Maxillary Palp Segment 1	0.24–0.29	0.26 $\pm$ 0.02
Maxillary Palp Segment 2	0.15–0.21	0.19 $\pm$ 0.02
Maxillary Palp Segment 3	0.05–0.09	0.07 $\pm$ 0.01
Labial Palp Length	0.38–0.49	0.44 $\pm$ 0.03
Labial Palp Segment 1	0.21–0.28	0.25 $\pm$ 0.02
Labial Palp Segment 2	0.17–0.21	0.19 $\pm$ 0.02
Procoxa	0.60–0.66	0.64 $\pm$ 0.02
Mesocoxa; $n = 8$	0.63–0.74	0.69 $\pm$ 0.04
Metacoxa; $n = 9$	0.65–0.77	0.72 $\pm$ 0.04
Protrochanter; $n = 9$ )	0.20–0.26	0.23 $\pm$ 0.02
Mesotrochanter	0.22–0.28	0.24 $\pm$ 0.02
Metatrochanter	0.24–0.31	0.26 $\pm$ 0.02
Profemur	0.53–0.62	0.57 $\pm$ 0.03
Mesofemur	0.63–0.71	0.68 $\pm$ 0.03
Metafemur	0.72–0.80	0.76 $\pm$ 0.02
Protibia	0.26–0.32	0.28 $\pm$ 0.02
Mesotibia	0.36–0.43	0.40 $\pm$ 0.02
Metatibia	0.47–0.56	0.52 $\pm$ 0.03
Protarsus	0.24–0.32	0.28 $\pm$ 0.03
Mesotarsus	0.35–0.41	0.38 $\pm$ 0.01
Metatarsus	0.47–0.54	0.52 $\pm$ 0.03
Proleg, total length; $n = 9$	1.68–1.89	1.80 $\pm$ 0.07
Mesoleg, total length; $n = 8$	2.01–2.23	2.14 $\pm$ 0.07
Metaleg, total length; $n = 9$	2.36–2.66	2.53 $\pm$ 0.08

**Table II.** Selected cranial and mandibular geometric and proportional dimensions for Oklahoma third instars of *Neoporus dimidiatus*

	<u>Range</u>	<u>Mean ± SD</u>
Cranial Orientation (CO); <i>n</i> = 5	12.0–15.5°	13.9 ± 1.3°
Cranial Temporal Curvature (TC); <i>n</i> = 5	65.0–86.0°	73.2 ± 8.6°
Dorsal Intermandibular Distance (DID); <i>n</i> = 5	0.65–0.76 mm	0.71 ± 0.04 mm
Ventral Intermandibular Distance (VID); <i>n</i> = 5	0.44–0.55 mm	0.49 ± 0.03 mm
MMD/ML; <i>n</i> = 8	0.07–0.12	0.10 ± 0.02
MBD/ML; <i>n</i> = 8	0.23–0.29	0.27 ± 0.03
Mandibular angle of Attack (AA); <i>n</i> = 5	43.5–48.5°	46.6 ± 1.9°
Mandibular Lateral Arc (Larc); <i>n</i> = 5	117.0–124.0°	119.6 ± 2.9°
Mandibular Medial Arc (Marc); <i>n</i> = 5	72.0–85.0°	78.2 ± 5.2°

**Table III.** Number and distribution of spine-like sensilla on pro- and metalegs of mature larvae of Oklahoma *Neoporus dimidiatus*, excluding apparent homologues of CO<sub>1-5, 13-17</sub> and TA<sub>3-6</sub>. Abbreviations employed include the following: AD, anterodorsal; AV, anteroventral; AT, total number of sensilla on the anterior face; hrl, hair-like; PD, posterodorsal; PV, posteroventral; PT, total number of sensilla on the anterior face, excluding NS, natatory sensilla

<u>Appendage</u>	<u>Location</u>	<u>Coxa</u>	<u>Femur</u>	<u>Tibia</u>	<u>Tarsus</u>
Proleg	AD	7–8	7–8	1	1
	AV	6–8	14–17	2	0–1
	AT	13–16	21–25	3	1–2
	PD	6–8	2–4 + 1 hrl + 1	2–3 + 1 hrl + 1	2–3 + 1 hrl + 1
	PV	5–6	6–10	4–5	4–5
	PT	11–14	10–16	8–9	8–10
	NS	0	0	5–7	2–3
Metaleg	AD	7–11	15–21	7–10	1
	AV	6–10	17–23	7–9	7–9
	AT	13–21	32–44	14–19	8–10
	PD	6–9	3–5 + 1 hrl	1 hrl + 1	1 hrl + 1
	PV	6–10	8–11	4–6	0–1
	PT <sup>1</sup>	12–19	12–17	6–8	2–3
	NS	0	0	17–23	15–24

### BIONOMICS

Mature larvae and adults of *N. dimidiatus* were concurrent in small pools and backwater areas of Onondaga Creek (central New York) in July (1970) and August (1969). Collection site substrates were characterized by gravel and rubble and supported neither macrophytes nor noticeable growths of filamentous algae. In the laboratory, with the exception of activity during limited feeding, larvae were quiescent, remaining near small stones in the rearing containers. Although ostracods and other planktonic organisms were provided, larvae were observed feeding only on small chironomid

larvae. Mature larvae were collected from beneath relatively ephemeral ice ( $\approx 2.5$  cm) on the Oklahoma stock pond in December 1971. In December 1995 the pond was not frozen over. Neither larvae nor adults were present in the pond although mature larvae (but not adults) were common in and amongst dense growths of filamentous algae along the length of a lotic out-flow ditch leading from this pond (Figure 1A). A few teneral adults were present but only in nearby stock ponds.

## DISCUSSION

Larval cranial lengths and widths of the Oklahoma larvae are marginally greater than those of larvae collected in New York. Western adults of *N. dimidiatus* are also larger than and “look different” from those representing eastern populations, but no adult character discontinuities have been observed that support a change in species status or recognition of subspecies (Larson et al. 2000). There were no discernible differences in the general appearance of the chaetotaxy of legs and urogomphi between the western and eastern populations although the small number ( $n = 3$ ) of and the poor condition of the New York larvae made the comparison tentative. In general, the urogomphal and leg chaetotaxy of representatives of both populations are similar to that provided for previously described *Neoporus* (Alarie 1991; Scott et al. 2004). There was, however, some interspecific variation on meso- and metatarsal chaetotaxy that may assist in identification of mature larvae, at least from local or regional populations. The metatarsus of *N. undulatus* has well-developed AV and PV sensillar series while *N. dimidiatus*, *N. carolinus* (Fall, 1917) (Alarie 1991), and *N. clypealis* (Sharp, 1882) (Scott et al. 2004) have only the AV series.

The Oklahoma and New York populations, however, did exhibit notable differences as to when and where larvae were present. The total developmental period for a central New York population of *N. undulatus* was 30–44 days (Barman 1996), suggesting that oviposition for the New York *N. dimidiatus* population may have been underway as early as the first few days of June. Oviposition for the Oklahoma third instars collected would have occurred in late November or early December if *N. dimidiatus* and *N. undulatus* have similar lifecycles. The ice covered pond and algal “choked” lotic habitats from which the western specimens were collected are strikingly different from those in New York that were characterized by gravel and rubble and supported neither macrophytes nor noticeable growths of filamentous algae. However, because of general inattention to the reproductive behavior of Nearctic dytiscids, this may represent only “expected” variation in life-history responses to very different climates and landscapes. In addition, the presence of larvae should be considered a successful reproductive effort only if development continues so as to produce viable adults capable of parenting the next generation. The presence of mature larvae of *N. dimidiatus* under ice in Oklahoma in midwinter may represent a futile reproductive effort near the margin of the extensive range of this species.

The proximity of the prementum to each maxilla on *N. dimidiatus* is similar to that shown for *N. clypealis* (Figure 3A in Scott et al. 2004) and observed on *N. undulatus*. The stipes and prementum of *Hydroporus signatus* (Mannerheim, 1853) are much closer together (Figure 3A in Scott et al. 2004) than on these three *Neoporus* species. This suggests that the relative positions of the prementum and maxillae may provide a diagnostic character for separation of *Hydroporus* and *Neoporus* larvae, at least within Georgia. Evaluations of mandibular geometry and cranial architecture (e.g.,

Wall et al. 2006; Brannen et al. 2012; Barman et al. 2016) have indicated that cranial architecture and mandibular geometry are responsive to the morphology and behavior of prey characteristic of preferred reproductive habitats. Since labia have a role in larval feeding, it seems probable that the morphology of labia will also be responsive to differences in prey morphology and behavior characteristic of preferred reproductive habitats. Thus, differences in labial morphology may have some diagnostic value as well as serving as indicators of ecological interactions.

The dicondylic mandibles interact with the frontoclypeus (nasale) to form a characteristic capture and feeding system employed by most dytiscid larvae. On some nonhydroporine species (e.g., Agabinae, Colymbetinae, and some Dytiscinae) the frontoclypeus is broadly rounded and its leading edge usually extends only slightly beyond the mandibular origins. Those mandibles open and close in a horizontal plane during capture and feeding (De Marzo and Nilsson 1986). However, the horizontal abduction and adduction of the mandibles will not suffice for *N. dimidiatus* larvae, and probably those of most other Hydroporinae, because of the notably extended frontoclypeus and its importance in predation. After impalement, hydroporine prey are held between the mandibular apices and the undersurface of the frontoclypeus near its distal margin. In order to maintain the essential proximity of mandibles and anterior nasale on *N. dimidiatus*, abduction and adduction mandibles of *N. dimidiatus* must be oblique rather than horizontal. There should be differences in either geometry of the mandibular shaft and/or cranial architecture between those larvae that open and close mandibles horizontally and those that move mandibles obliquely.

The morphology of the shaft and base of mandibles of *N. dimidiatus* appears comparable to that shown for *Hydroporus limbatus* Aubé, 1838 (De Marzo 1978), displaying the same linearity and the same general locations for mandibular articulation sites. The general appearance of mandibles of *Hydroporus limbatus* Aubé, 1838 (De Marzo 1978) and *N. dimidiatus* is similar. Although mandibles of *D. carolinus* Aubé, 1838 are about 5x the length (Mathias et al. 2016) of those of *N. dimidiatus* and *H. limbatus*, mandibles of these species are comparable in general appearance. *Neoporus dimidiatus* and *D. carolinus* also display similar MBD/ML and MMD/ML ratios (Table II) (Mathias et al. 2016). There are, however, major differences between larvae of *N. dimidiatus* and those of some nonhydroporine species with regard to cranial articulation locations.

Mandibular articulation sites of *D. carolinus* (Mathias et al. 2016) and larvae of some other medium and large dytiscids define nearly vertical parallelogram spaces with dorsal and ventral bases that are more or less equal in width. This arrangement permits the horizontal abduction and adduction of the mandibles. For *N. dimidiatus* strict horizontal movements of the mandibles would not permit of the proximity of mandibular apices and the anterior frontoclypeal margin that appears to be essential for hydroporine predation. However, the mandibular articulation sites of mature larvae of *N. dimidiatus* define trapezoidal spaces because ventral bases ( $VID = 0.49 \pm 0.03$  mm) are much shorter than dorsal bases ( $DID = 0.71 \pm 0.04$  mm) (Table II). Thus, the legs of the trapezoidal space are directed medially so that the mandibles of *N. dimidiatus* are moved obliquely rather than horizontally. Consequently, after adduction mandibular apices are just below and posterior to the frontoclypeal margin (Figure 1C). The notable differences between the dorsal and ventral intermandibular distances then are largely responsible for the oblique movements of the mandibles of *N. dimidiatus*.

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