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A REDESCRIPTION OF THE FIRST INSTAR OF *RHANTUS CALIDUS* (FABRICIUS) (COLEOPTERA: DYTISCIDAE) WITH NOTES ON ITS BIOLOGY

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ABSTRACT

First instars of *Rhantus calidus* (Fabricius) representing a Georgia population are described and illustrated. Dimensions are provided along with an analysis of the primary chaetotaxy of legs, head, and last abdominal segment. The presence of first instars at the study site demonstrated that *R. calidus* either requires or is at least tolerant of warmer temperatures for completion of its life cycle. Habitats with temperatures comparable to this site were likely present in a warm Atlantic coastal enclave during the last glacial maximum (LGM), making it probable that the LGM dytiscid fauna of Georgia included *R. calidus*.

Key words: Georgia, *Rhantus*, larva, habitat, distribution.

INTRODUCTION

Although there are 10 North American species of *Rhantus* Dejean (1), *Rhantus calidus* (Fabricius) is the only species reported for Georgia with adult records from Coastal Plain and Piedmont counties (2). *Rhantus calidus* has an extensive distribution through much of South America, into the West Indies, Central America, southern Baja California, parts of southern Mexico, and into the eastern United States where it ranges along the Gulf and Atlantic coastal states into New York. It displays regional differences in adult morphology (3), leading to the inference that *R. calidus* may represent a species complex.

Some general descriptive information is available for the mature larva of *R. calidus* (4, 5) as well as specific information dealing with mandibular geometry (6). An extensive analysis (7) of primary and secondary larval morphology of *Rhantus* with an emphasis on chaetotaxy includes *R. calidus*. However, only a single first instar of *R. calidus* was available for that analysis, and there were some apparent inconsistencies in the application of descriptive information attributed to this first instar in that study. First instar (primary) morphological studies (*e.g.*, 7, 8, 9, 10, 11, 12) have provided important information for the development and testing of systematic hypotheses. Thus, an objective of this study was to provide a description of the external morphology of the first instar of *R. calidus* that is based on a larger sample size than that available to Alarie *et al*. (7), permitting greater insight into variation. An additional objective was to describe elements of the life cycle of this central Georgia population of *R. calidus* and to evaluate its implications for the historical distribution of the species in Georgia.

MATERIALS AND METHODS

Descriptions are of ten first instars of *R. calidus* collected 21 July 2007 in Bibb County, Georgia (N 32° 52.033', W 83° 47.999'). Identification of first instars as *R. calidus* was based on their association with third instars from this habitat that had been cultured into the adult stage.

Observations and measurements were of dismembered specimens preserved in 70 per cent glycerated ethyl alcohol. Head lengths were measured dorsally from the posterior margin of the head capsule to the distal margin of the frontoclypeus, excluding the frontoclypeal sensilla. Head widths were measured dorsally at the widest point of the head. Mandibular lengths were determined by measuring ventrally from the apex to the center of the ball of articulation with gape measured ventrally from the center of the balls of the right and left mandibular articulations (6). Other measurements were taken along the greatest length of each structure. Lengths for legs are sums of the lengths of the individual segments, excluding trochanters and tarsal claws.

Primary sensilla are identified and coded according to systems developed by Nilsson (8) and Alarie (9, 10). Other morphometric terms employed are those of Larson *et al*. (1), Snodgrass (13), and Wolfe and Roughley (14).

Description Of First Instar

Color. Preserved specimens with membranous areas generally translucent, sclerotized areas light yellowish-tan.

Head (Fig. 1A, C). Length 0.81-0.96 mm ($\bar{x}$= 0.89 ± 0.05 mm); width

0.96-1.02 mm ($\bar{x}$= 1.00 ± 0.02 mm), widest near origins of antennae; gape (6), 0.70-0.81 mm ($\bar{x}$= 0.78 ± 0.04 mm); posteroventral emargination pronounced; frontoclypeus 0.33-0.50 mm, ($\bar{x}$= 0.43 ± 0.05 mm), without microspinulae, egg-bursters present but obscure, nasale not extending beyond apices of adnasaliae (anterolateral lobes), 15-19 spine-like frontoclypeal sensilla (Fig. 1B); coronal suture 0.39-0.50 mm ($\bar{x}$= 0.45 ± 0.03 mm); parietals with numerous scale-like dorsolateral microspinulae, an abbreviated anteroventral ecdysial cleavage line, prominent lateral keel or ridge between occipital suture and stemmatal region; corneal lenses (15), 1-4 elongate and dorsal, lens 5 anteroventral and ovoid, lens 6 (16) ventrolateral and smaller than dorsal lenses (Figs 1A, C). Antenna. Length, excluding palpifer, 0.83-1.04 mm ($\bar{x}$= 1.00 ± 0.04 mm), without microspinulae; antennomere (AN) 1, 0.19-0.22 mm ($\bar{x}$= 0.21 ± 0.01 mm), AN2 0.23-0.28 mm ($\bar{x}$= 0.27 ± 0.02 mm), AN3 0.26-0.30 mm ($\bar{x}$= 0.28 ± 0.01 mm) without protruding accessory appendage (A3′), AN4 0.22-0.26 mm ($\bar{x}$= 0.25 ± 0.01 mm), AN4 significantly ($p < 0.0001$) shorter than AN3.

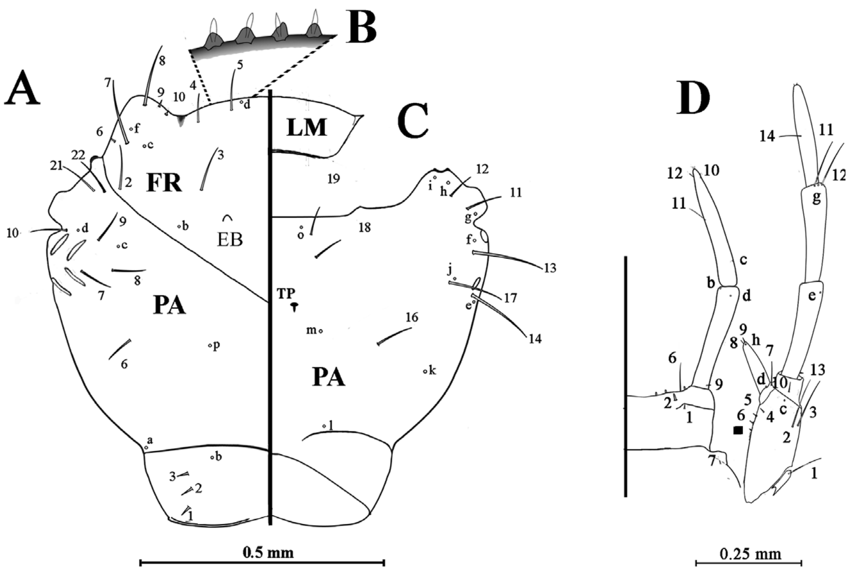

Figure 1. Dorsal (A) and ventral (C) views of cranium, frontoclypeal sensilla (B) and ventral views (D) of the labium and maxilla of *Rhantus calidus*. Numbers and lowercase letters identify respectively ancestral primary spiniform and campaniform (pores) sensilla. Legend: EB, egg bursters; FR, frontoclypeus, LM, labrum; PA, parietal; TP, posterior tentorial pit.

Mouthparts. Mandible, length 0.49-0.66 mm ($\bar{x}$= 0.56 ± 0.04 mm) about 2.5 times width, pronounced lateral and medial arcs and acute angle of attack (6); mandibular channel present, medial edge with minute teeth and a small tuft of hair-like spinulae. Maxilla (Fig. 1D). Cardo reduced; stipes prominent; galea finger-like and elongate, approximately half the length of palpomere (MP) 1; palpus length, excluding palpifer, 0.63-0.68 mm ($\bar{x}$= 0.67 ± 0.02 mm), MP1 0.20-0.26 mm ($\bar{x}$= 0.23 ± 0.02 mm), MP2 0.18-0.22 mm ($\bar{x}$= 0.21 ± 0.01 mm), MP3 0.19-0.25 mm ($\bar{x}$= 0.23 ± 0.02 mm). Labium (Fig. 1D). Prementum short, approximately twice as wide as long, ventrodistal margin between palpi straight to moderately concave, palpus 0.45-0.59 mm ($\bar{x}$= 0.53 ± 0.05 mm), palpomere (LP)1 0.20-0.28 mm ($\bar{x}$= 0.24 ± 0.03 mm), LP2 0.25-0.32 mm ($\bar{x}$= 0.29 ± 0.02 mm; n = 9).

Thorax. Protergum widest near mid-length, meso- and metaterga widest posteriorly; protergum longer and wider than meso- and metaterga, meso- and metaterga sub-equal in length; protergum with posterotransverse carina weakly developed medially, meso- and metaterga with anterotransverse and poorly developed posterotransverse carinae; terga spinulate, protergum with numerous small hair-like interior and marginal sensilla; meso- and metatertga with small hair-like sensilla on postero-lateral margins; spiracular openings absent. Legs (Figs. 2A, B). Respective lengths of pro-, meso-, and metalegs, 1.64-2.02 mm ($\bar{x}$= 1.81 ± 0.14 mm), 1.79-2.17 mm ($\bar{x}$= 1.98 ± 0.13 mm), 1.81-2.54 mm ($\bar{x}$= 2.13 ± 0.19 mm); natatory sensilla absent; ventral spinulae well-developed on protibia and protarsus, present but less well developed on remaining legs; small spinulae on surface of all segments, more numerous on protarsus; coxa robust and elongate, coxal sutures present; trochanter divided into two regions; tarsal claws sub-equal in length, anterior claw slightly longer than posterior, each with ventroproximal spinulae.

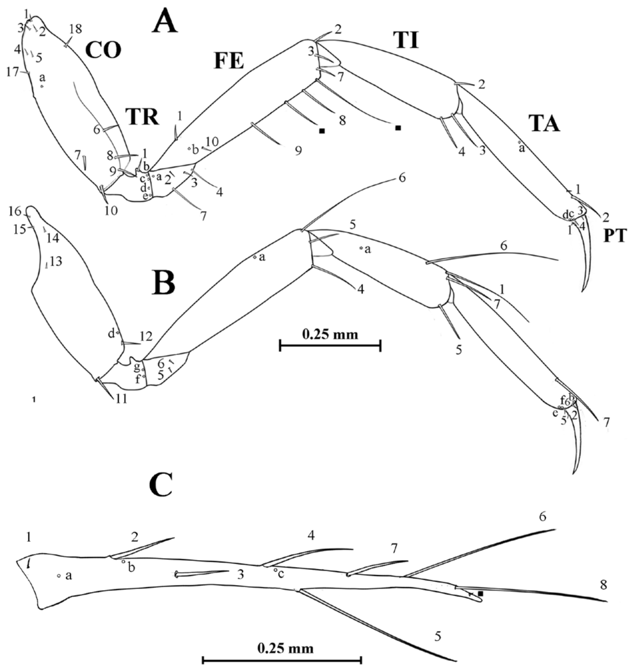

Figure 2. Anterior (A) and posterior (B) views of a metathoracic leg and a dorsal (C) view of the uroghompus of *Rhantus calidus*. Numbers and lowercase letters identify respectively ancestral primary spiniform and campaniform (pores) sensilla with ■ indicating additional primary sensilla. Legend: CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter.

Abdomen. Segments 1 to 7 strongly sclerotized dorsally with antero- and posterotransverse carinae, membranous laterally, and ventrally, and bearing long, widely dispersed hair-like sensilla, primarily along tergal margins; segment 7, 0.21-0.37 mm ($\bar{x}$= 0.30 ± 0.05 mm); segment 8 (LAS) completely sclerotized, anterotransverse carina present but poorly developed, dorsal length 0.68-0.92 mm ($\bar{x}$= 0.85 ± 0.07 mm) with well developed siphon, length 0.16-0.26 mm ($\bar{x}$= 0.21 ± 0.03 mm); sclerotized areas of all segments with microspinulae. Urogomphus (Fig. 2C). One-segmented, spinulate, length 0.68-0.85 mm ($\bar{x}$= 0.75 ± 0.06 mm).

Chaetotaxy. All coded primary sensilla (Figs. 1 and 2) as described by Alarie *et al*. (7) for *R. calidus*, urogomphal primary sensilla exhibiting subtle individual variation; pro-, meso-, metafemur respectively with 1-2, 2-3, and 1-2 additional anteroventral spine-like sensilla, additional sensillum with origin between FE_7 and FE_8, present on all legs of all specimens, spine-like on proleg and elongate and hair-like on the meso- and metalegs of all but one specimen.

Bionomics

Although no adults were collected, larvae of *R. calidus* were numerous in this central Georgia man-made eutrophic ephemeral habitat that was described briefly by Jackson *et al*. (17). Clays are suspended in the water column, resulting in the water having a reddish-brown color. Larvae of *Laccophilus fasciatus* Aubé were abundant during late spring and early summer with larvae of *Coptotomus* sp. indet. and *Acilius* sp. indet. present sporadically during the same period. First instars of *R. calidus* were present between 31 June and 21 July 2007 when central lower Piedmont average air temperatures for June and July were respectively 26 and 27°C (18). Mature larvae of *R. calidus* and *Hydaticus bimarginatus* (Say) were collected concurrently in the habitat with the latter present from early July until mid-September (17).

DISCUSSION

Heavily sclerotized areas of all first instars collected from the Georgia habitat were light yellowish-tan, providing an obvious contrast with the glossy black sclerotized areas of the Cuban larva studied by Alarie *et al*. (7). Zimmerman and Smith (3) indicated that *R. calidus* displays regional differences in adult morphology, and color and color patterns may be important in *Rhantus* adult systematics (1). However, the value of larval color as an analytical character or as an indicator of geographic variation may be limited. Wesenburg-Lund (19) observed that larvae of some dytiscid species were black when collected from boggy, tree shaded pools but others of the same species were less intensely pigmented when taken from ditches draining clay soils. Barman (20) also reported differences in the intensity of larval pigmentation of larvae of the same species collected from different habitats as well as different areas of the same relatively small habitat.

The morphology of the crania and mouthparts of the Georgia specimens appear to correspond in general with that of the Cuban specimen. However, there were some inconsistencies in the application of descriptive information attributed to the first instar of *R. calidus* (7) that may cause confusion. Although the frontoclypeus was described (7, page 27) and illustrated (7, Fig. 40) in that study as extending anteriorly only to or slightly below the level of the apices of the adnasaliae, this character was coded in the phylogenetic analysis (Tables 2 and 3, character 05) as extending beyond the adnasaliae. In addition, the number of lamellae clypeales for the Cuban larva was given as 16 (7, page 27), within the range of 15-19 reported herein, and as 15-35 (7, page 11) for first instars of *Rhantus* examined therein. However, couplet 5 of the Alarie key has *R. calidus* with less than 14 lamellae clypeales. Additional ventroapical pores on antennomere 3 were not observed on the Georgia specimens and were reported as absent on the Cuban larva (7, page 27), but this character is coded (7, Tables 2 and 3, character 12) as present. The anterodorsal primary sensilla of the prementum are minute on Georgia larvae and were described as minute within the description of the first instar

(7, page 27) but coded (7, Table 2 and 3, character 28) as elongate for the phylogenetic analysis.

Descriptive studies of dytiscid first instars are often by necessity based on few specimens because the larvae are difficult to collect and/or culture. As a result the extent of individual variation is often not apparent, and this may cause some problems when results of these analyses are used to develop or test systematic hypotheses. The larger, but still small, sample available for this analysis made possible the observation of subtle variations in the origin and morphology of urogomphal sensilla. UR_2 was described (7) as "about" the same length as that of UR_3; however, on some Georgia specimens examined UR_2 was longer that UR_3. UR_b is shown on the Cuban larva with its origin distal to UR_2 and about midway between that sensillum and UR_3 (7, Fig. 44). Although the position of UR_b was distal to UR_2 on all specimens examined, its origin varied along the shaft from near the origin of UR_2 (Fig. 2C) to near that of UR_3. UR_5 had a more proximal origin (Fig. 2C) relative to the origin of UR_7 than that attributed to the Cuban larva with variation in the relative origins of UR_5 and UR_7 resulting in asymmetrical urogomphi on one specimen examined.

First instars of *R. calidus* have relatively few additional primary sensilla that are restricted to femoral anteroventral surfaces and the apex of each urogomphus. Alarie *et al.* (7) reported 1 anteroventral additional sensillum on the proleg and 2 anteroventral additional sensilla on each meso- and metaleg of *R. calidus* (Table 4). However, only one additional sensillum is shown for the metaleg (Figure 41) and couplet 5 of the key to first and third instars of *Rhantus* indicates that the Cuban larva had less than 2 AV additional sensilla on the metaleg. The numbers of anteroventral sensilla on the Georgia material ranged from 1-2 on the pro- and metalegs and from 1-3 on the mesoleg, with one specimen having 2 additional sensilla on one mesoleg and 3 on the other. An additional sensillum was present between FE_7 and FE_8 on the Cuban larva and on all legs of all specimens examined in this analysis. However, although this sensillum was consistently spine-like on the proleg, it was elongate and hair-like on the meso- and meta legs of all but one Georgia specimen. With the exception of this hair-like sensillum, the additional primary chaetotaxy of this and previously described material is comparable and consistent with expected individual variation.

The presence of primary spiniform frontoclypeal sensilla provides an overt character that increases the probability of identifying first instars *R. calidus* within the context of the Georgia fauna. *Matus bicarinatus* (Say) and *M. ovatus* Leech also have frontoclypeal sensilla similar to those of *R. calidus* (10, 11, 21) and both are present in Georgia (2). Thus, larvae collected within the state that lack temporal spines and spiracles but have egg-bursters and spiniform sensilla on a broadly rounded frontoclypeus (Figs. 1A, B) are likely to be first instars of *M. ovatus, M. bicarinatus* or *R. calidus*. However, first instars of *M. ovatus* (21) and *M. bicarinatus* (9, 11) have pseudo-chelate proand mesotibial modifications, whereas all tibiae of *R. calidus* are unmodified (as in Figs. 2A, B).

It is likely that *R. calidus* has been a component of the Georgia coastal dytiscid fauna from at least the last glacial maximum (LGM) to the present although no records of the LGM fauna are available. In central Georgia, *R. calidus* appears to be employing a univoltine Type I breeding strategy (22) with incubation and larval development completed in a matter of weeks. Average monthly air temperatures for this reproductive habitat were about 26°C (18), indicating that *R. calidus* may require or is at least tolerant of relatively warm temperatures for initiation and completion of its life cycle. During the LGM, the composition of the Georgia coastal amphibian and reptilian faunas make it obvious that this area was part of a warm thermal enclave (23). The presence of these lower vertebrates, including *Alligator mississippiensis* (Daudin), in that region also indicates that the expanded LGM Georgia coast would have had aquatic systems with temperatures comparable to those of the reproductive habitat used by this extant population of *R. calidus*. Given the enhanced dispersal abilities evidenced by its extensive interglacial distribution (3), the exploitation of these relatively warm LGM coastal habitats by *R. calidus* seems probable.

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