

**A DESCRIPTION OF THE FIRST INSTAR OF *HOPERIUS PLANATUS* FALL, 1927
(COLEOPTERA: DYTISCIDAE: COLYMBETINAE: COLYMBETINI),
WITH PHYLOGENETIC IMPLICATIONS**

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ABSTRACT

The first instar of *Hoperius planatus* Fall, 1927 is described and illustrated for the first time with an emphasis on the chaetotaxy of the head capsule, head appendages, legs, last abdominal segment, and urogomphi. *Hoperius planatus* is characterized by the presence of additional campaniform sensilla (pores) on the frontoclypeus, representing a unique character state within the tribe Colymbetini (Colymbetinae). A phylogenetic analysis based on 42 first-instar characters using the program TNT reinforces the hypothesis of monophyletic origin of the Colymbetini and suggests a placement of *Hoperius* Fall, 1927 as sister to a clade comprised of *Neoscutopterus* J. Balfour-Browne, 1943, *Meladema* Laporte, 1835, and *Bunites* Spangler, 1972. Members of this clade are uniquely characterized within the Colymbetini by the presence of a large number of additional spiniform sensilla on the urogomphus.

Key Words: predaceous diving beetle, *Hoperius*, larvae, morphology, chaetotaxy, mandibular geometry

The North American endemic genus *Hoperius* Fall, 1927 is included in the tribe Colymbetini along with six other genera: *Bunites* Spangler, 1972, *Colymbetes* Clairville, 1806, *Meladema* Laporte, 1835, *Melanodytes* Seidlitz, 1887, *Neoscutopterus* J. Balfour-Browne, 1943, and *Rhantus* Dejean, 1833 (Nilsson 2013). The cosmopolitan *Rhantus* and the Holarctic *Colymbetes* are speciose taxa, containing the majority of the species of Colymbetini. Each of the other four genera contains substantially fewer species and is more localized. *Hoperius* is monotypic, containing only the rare (Spangler 1973) *Hoperius planatus* Fall, 1927, originally identified from material collected in Arkansas within the

interior highlands of the eastern USA (Allen 1990). It has also been collected in Alabama (Folkerts and Donovan 1974), Georgia (Turnbow and Smith 1983), Tennessee (Wolfe, unpublished data), east Texas (Jasper and Vogtsberger 1996), Maryland, South Carolina, and Virginia (Spangler 1973).

Although the inclusion of *Hoperius* within the Colymbetini appears well-supported, its placement within this tribe is uncertain (Alarie and Hughes 2006). Recognition of the potential value of the relative stability of primary larval chaetotaxal systems to systematics (Nilsson 1988) has resulted in a number of informative studies emphasizing or dedicated exclusively to first instar (primary)

morphology of dytiscid larvae (e.g., Alarie 1995, 1998; Michat 2005; Alarie *et al.* 2009). Therefore, the purposes of this study were to: 1) describe the first instar of *H. planatus* with an emphasis on chaetotaxy; 2) incorporate descriptive information into a phylogenetic analysis along with primary characters of representative Colymbetini; and 3) provide comments on elements of its natural history in Georgia.

MATERIAL AND METHODS

Descriptions are of three first instars collected on 16 February 2006 in Baldwin County, GA (N 32°99.151' W 83°07.263'), USA and killed with 95% ethyl alcohol before storage in 70% glycerated ethyl alcohol. First instars were identified by association with third instars collected concurrently from the same habitat and identified as *H. planatus* on the basis of descriptions by Spangler (1973), Alarie and Hughes (2006), and Barman *et al.* (2006). This material is stored in the Georgia College & State University Insect Museum (GCIM).

Specimens were dismembered and mounted on concave slides to minimize distortions. One specimen was cleared in lactic acid and mounted on glass slides with polyvinyl-lacto-glycerol after dissection. Illustrations were prepared using Motic Imaging and Adobe Illustrator 10 and Photoshop CS5 or drawings were made with a camera lucida attached to an Olympus CX31, scanned, and digitally edited.

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 width was measured dorsally at the level of antennal origins, and the occipital foramen width was measured dorsally along its posterior margin. Inter-mandibular distance (\approx gape) was measured ventrally from the center of the ball of the right and left mandibular articulations, and mandibular length approximations were determined by measuring ventrally along line a-b (Fig. 1) from the center of the ball to the mandibular apex (Wall *et al.* 2006). Lengths of the antennae and maxillary and labial palpi were determined by summing the lengths of individual segments. Siphon lengths were estimated by subtracting the ventral lengths from dorsal lengths of the eighth abdominal segment.

Ancestral and additional setal and campaniform (pore-like) sensilla were identified for the cranium, cranial appendages, legs, abdominal segment 8, and urogomphus, using methodologies proposed by Alarie (1995, 1998). Individual ancestral sensilla are coded with two capital letters followed by either a number (setal sensilla) or lower case letter (pores).

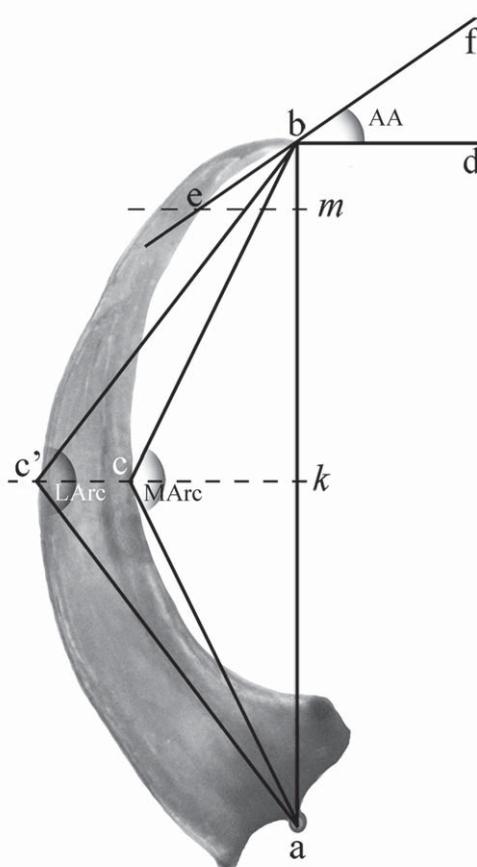


Fig. 1. *Hoperius planatus*, first-instar mandible, ventral view, with methodology for estimating angle of attack (AA) and lateral (LArc) and medial (Marc) arcs.

Letters represent the area or structure of origin, with the following abbreviations used: AN, antenna; AB, abdominal segment; CO, coxa; FE, femur; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietal; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter; UR, urogomphus. Ancestral sensilla were identified by comparison with the chaetotaxal ground-plan of the subfamilies Agabinae and Colymbetinae (Alarie 1995, 1998), with homologies evaluated using the criterion of similarity of position (Wiley 1981). Additional sensilla are enumerated but not coded as above. Sensilla on the cranium, labium, and abdominal segment 8 are reported for each half either to the right or left of the sagittal plane.

Geometric parameters for mandibles were computed from images produced with Motic Images 2000 1.3 for Windows connected to a National DC3-420T digital microscope. All images were standardized to 14-cm lengths. Lateral (LArc) and medial Arcs (Marc) were determined using a simplification (Fig. 1) of techniques proposed by

Feduccia (1993) and Wall *et al.* (2006). Both were determined by establishing a positive 90° line drawn from the midpoint (*k*) of line (a-b) to intersect the medial (c) and lateral (c') boundaries of the mandible. The angles acb and/or ac'b were inserted into the following formulae: $\text{Marc} = 360^\circ - 2(\text{angle acb})$ or $\text{Larc} = 360^\circ - 2(\text{angle ac'b})$. Angle of attack (AA), representing apical curvature, was determined (Fig. 1) by extending a negative 90° line (b-d) from line (a-b) at the apex (b). A positive 90° line was extended from a point (*m*) to intersect with the medial curvature of the mandible at point (e). Point *m* is 1/10 of the length of a-b from the apex. A line from point (e) through point (b) was established with the resulting angle bdf taken as an estimate of the angle of attack.

In evaluating the phylogenetic relationship of *Hoperius* within the Colymbetini, first instars of *H. planatus* and representatives of seven other genera and subgenera were coded for parsimony analysis. Data were scored directly from specimens, except for *Melanodytes pustulatus* (Rossi, 1792) for which data were taken from the literature (De Marzo 1974; Nilsson 1988; Nilsson and Hilsenhoff 1991). Miller (2001) suggested that the subfamily Agabinae, previously considered as a tribe of Colymbetinae, represents a basal lineage with respect to the Colymbetini. Therefore, *Agabus anthracinus* Mannerheim, 1852 was included as the out-group. All characters were treated as unordered and equally weighted, and multistate characters were treated as non-additive. The data matrix was analyzed using the program TNT (Goloboff *et al.* 2008). The small size of the matrix allowed for the implementation of an exact solution algorithm (implicit enumeration). Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated, increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching *et al.* 1998). Jackknife values were calculated with 2000 replicates and *P* (removal probability) = 36.

RESULTS

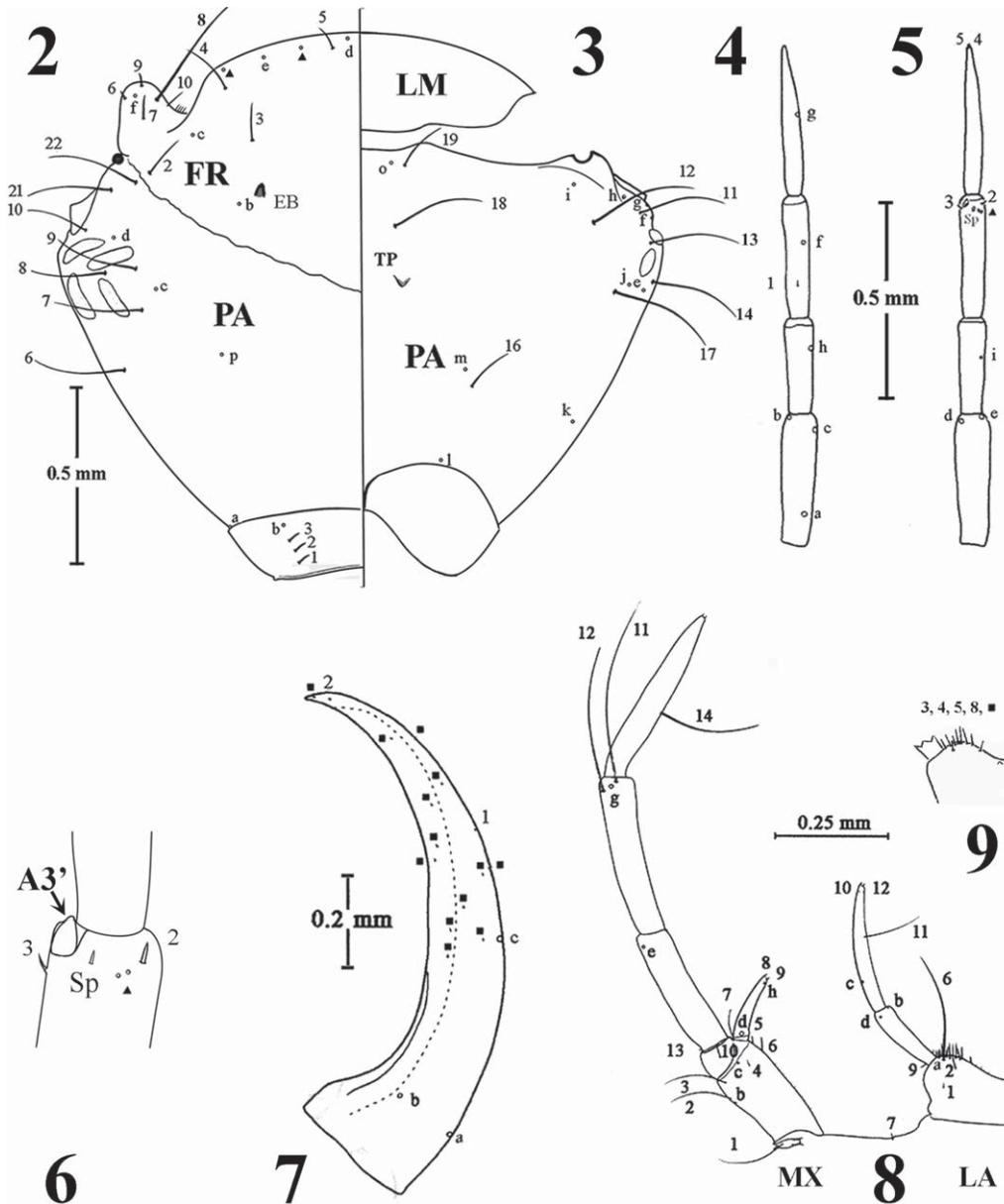
Hoperius planatus Fall, 1927

first instar
(Figs. 1–15)

Diagnosis. The first instar of *H. planatus* can be distinguished from those of other Colymbetini by its restricted geographic distribution and the following combination of characters: cranial dorsoventral silhouette approximating that of an irregular convex hexagon; limited lateral expansion of temporal regions (Figs. 2, 3); frontoclypeus with

FRe present, anterior margin with additional pores (Fig. 2), and 48–50 spatulate sensilla; mandible with additional minute setae (Fig. 7); stipes relatively narrow, subcylindrical (Fig. 8); anterior margin of prementum deeply emarginated with 4–5 additional setae (Figs. 8, 9); labial palpomere 2 with two minute additional dorsoapical setae; femur with elongate and hair-like FE5 and FE6, additional dorsal, anterodorsal, and posteroventral setae; tibia with elongate and hair-like TI6 and TI7; tibia and tarsus with anteroventral, and posteroventral additional setae (Figs. 10, 11); abdominal segment 8 with additional dorsal pores (Fig. 13) and 1–2 additional ventral setae (Fig. 14); urogomphus with additional setae and pores (Fig. 15).

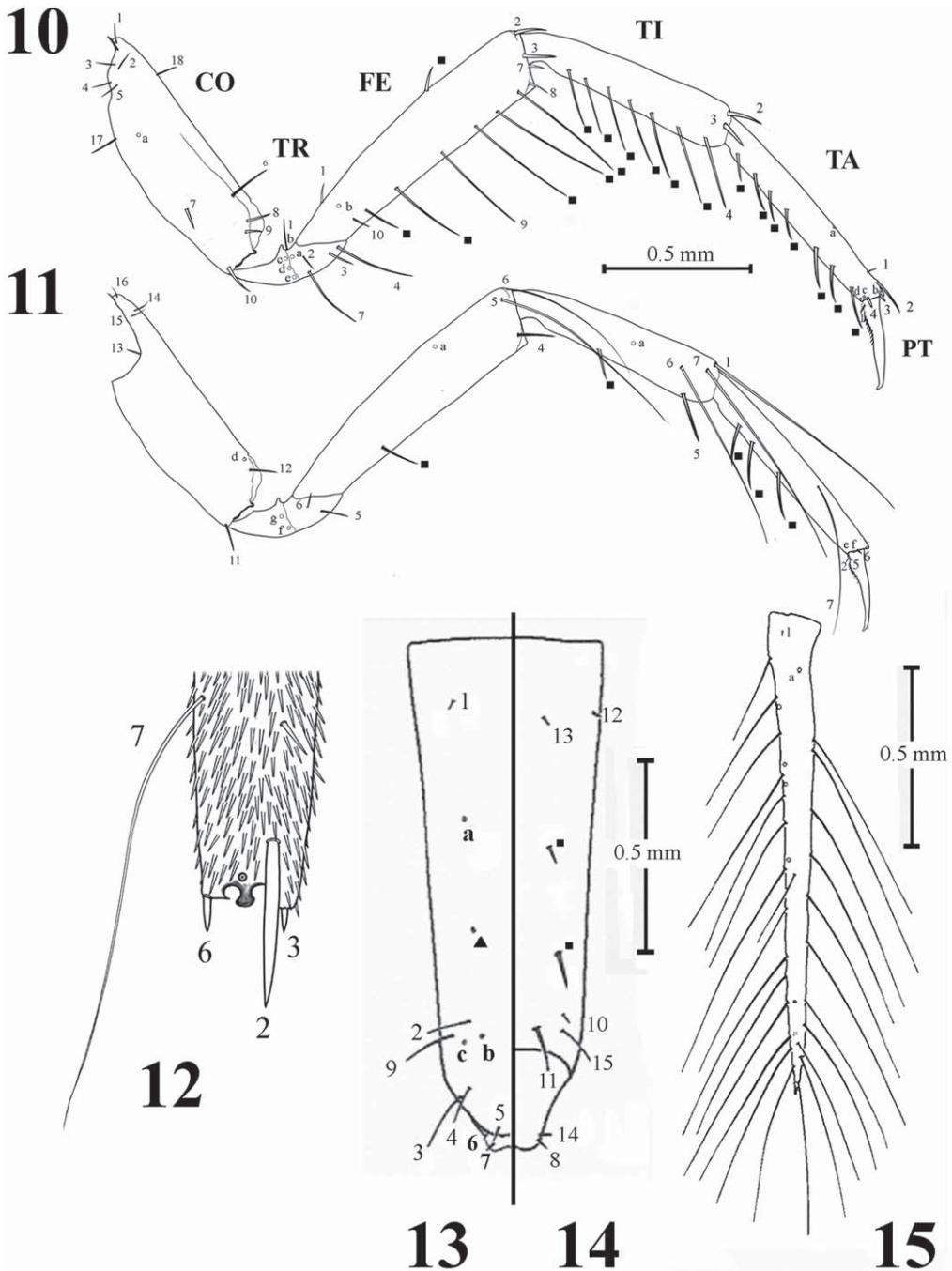
Description. Body: Subcylindrical, narrowing toward abdominal apex, length (near end of first stadium and excluding urogomphi) about 10 mm. **Color:** Sclerotized areas uniformly testaceous to light brown, without color pattern, membranous areas pale yellow. **Cranium** (Figs. 2, 3): Dorsoventral silhouette approximating that of an irregular convex hexagon, length 1.54–1.58 mm, maximum width 1.58–1.63 mm, occipital foramen width 0.52–0.61 mm; limited lateral expansion of temporal regions; intermandibular distance 1.30–1.37 mm; labrum prominent, directed posteroventrally; occipital suture confluent ventrally with a pronounced posteroventral indentation of the occipital foramen; frontoclypeal length 0.72–0.77 mm, broadly triangular in dorsal view, extending beyond well-developed rounded anterolateral lobes, with 48–50 anterior lamellate sensilla, egg bursters, and numerous spinulae; coronal suture length 0.79–0.82 mm, dividing spinulate parietals; temporal spines absent; corneal lenses in two convex columns of three each, ventrolateral lenses smaller and less elongate than dorsolateral lenses; posterior tentorial pits visible ventrally. **Antenna** (Figs. 4–6): Length, excluding palpifer, 1.23–1.31 mm; antennomere (A) 1 0.33–0.35 mm, A2 0.24–0.27 mm, A3 0.31–0.32 mm, accessory appendage (A3') small and scale-like (Fig. 6), A4 0.35–0.37 mm. **Mandible** (Figs. 1, 7): Falciform, length 1.04–1.15 mm, lateral arc $150\text{--}154^\circ$, medial arc $100\text{--}103^\circ$, angle of attack $34\text{--}40^\circ$, channel present, spinulate distally and medially. **Maxilla** (Fig. 8): Cardo reduced; stipes prominent, subcylindrical with length exceeding width, lateral and medial margins somewhat parallel, medial surface spinulate; lacinia absent; galea prominent, subconical, curved inward, length slightly over half that of palpomere (MP) 1, palpus length, excluding prominent palpifer, 1.06–1.14 mm, MP1 0.30–0.35 mm, MP2 0.35–0.36 mm, MP3 0.41–0.43 mm. **Labium** (Figs. 8, 9): Prementum approximately twice as wide as long, strongly emarginated medially, small relative to maxilla



Figs. 2–9. *Hoperius planatus*, first instar. **2)** Cranium, dorsal view; **3)** Cranium, ventral view; **4)** Right antenna, dorsum; **5)** Left antenna, venter; **6)** Antennomere 3, distal aspect; **7)** Right mandible, dorsum; **8)** Maxilla and labium, venter; **9)** Prementum, dorsal view. Abbreviations: A3' = ventrolateral apical process of antennomere 3; EB = egg burster; FR = frontoclypeus; LA = labium; LM = labrum; MX = maxilla; PA = parietal; Sp = spinula; TP = posterior tentorial pit. Solid squares refer to additional setae; solid triangles refer to additional pores.

and mandible, lateral margin distant from medial margin of stipes; surface with densely distributed microspinulae; postmentum, short with an expansive base; palpus 0.43–0.48 mm, palpomere (LP) 1 0.17–0.19 mm, LP2 0.26–0.29 mm. **Thorax:** Ecdysial suture present, protergal length subequal

to the combined length of meso- and metaterga, meso- and metaterga subequal in length; protergum with posterior transverse carina, continuous laterally; meso- and metaterga with anterior and posterior carinae, posterior carinae continuous laterally; protergum with hair-like marginal and interior setae,



Figs. 10–15. *Hoperius planatus*, first instar. **10)** Metathoracic leg, anterior view; **11)** Metathoracic leg, posterior view; **12)** Metathoracic tarsus, dorsodistal aspect; **13)** Abdominal segment 8, dorsal view; **14)** Abdominal segment 8, ventral view; **15)** Urogomphus, dorsal aspect. Abbreviations: CO = coxa; FE = femur; PT = pretarsus; TA = tarsus; TI = tibia; TR = trochanter. Solid squares refer to additional setae; solid triangles refer to additional pores. URb, URc, and additional sensilla on the urogomphus are not labeled.

sparse hair-like setae on posterior and lateral margins of meso- and metaterga; minute densely distributed mirospinulae on terga; spiracles absent. **Legs** (Figs. 10–12): Natatory sensilla absent; series of ventral spinulae well-developed on pro-tibia and tarsus only; numerous small spinulae on surface of all leg segments (Fig. 12), numbers increasing ventrally on distal segments; abbreviated coxal sutures present; trochanter divided into 2 regions ($_1$ Tr; $_2$ Tr); respective lengths of individual seg-

ments of pro-, meso-, and metathoracic legs: coxae 0.81–0.86, 0.84–0.89, 0.85–0.90 mm; trochanters 0.35–0.36, 0.36–0.42, 0.38–0.42 mm; femora 0.88–0.93, 0.96–1.02, 1.04–1.08 mm; tibiae 0.50–0.56, 0.62–0.70, 0.78–0.86 mm; tarsi 0.52–0.55, 0.64–0.67, 0.78–0.84 mm; anterior/posterior tarsal claws on pro- (0.52–0.53/0.64–0.68 mm), meso- (0.67–0.69/0.59–0.63 mm), and metathoracic legs (0.74–0.77/0.74–0.78 mm); each claw with ventroproximal spinulae. **Abdomen:**

Table 1. Characters and states used for phylogenetic analysis of 11 terminal taxa of first instars of Colymbetini. Abbreviations: A = antennomere; AD = anterodorsal; Adi = anterodistal; AV = anteroventral; D = dorsal; PV = posteroventral; V = ventral.

Character	States
00 Occipital suture	0 = Absent; 1 = Present
01 FRe	0 = Present; 1 = Absent
02 Additional setae on FR	0 = Absent; 1 = Present on anterior margin; 2 = Present on lateromedial portion
03 Additional pores on FR	0 = Absent; 1 = Present
04 Additional D setae on PA	0 = Absent; 1 = Present
05 Additional V setae on PA	0 = Absent; 1 = Present
06 Ventroapical spinula on A3	0 = Present; 1 = Absent
07 Additional ventroapical pores on A3	0 = Absent; 1 = Present
08 Apical lateroventral process (A3') of A3	0 = Protuding; 1 = Not protruding
09 ANg	0 = Located basally; 1 = Located medially
10 Additional small setae on mandible	0 = Absent; 1 = Present
11 MXa	0 = Present; 1 = Absent
12 Additional setae on stipes	0 = Absent; 1 = Present
13 Anterior margin of prementum	0 = Straight to shallowly emarginate; 1 = Deeply emarginate
14 Additional setae on ADi margin of prementum	0 = Up to three on each side; 1 = Four or more on each side
15 Insertion of CO7 on proleg	0 = Proximal; 1 = Distal
16 Additional seta near CO10	0 = Absent; 1 = Present
17 Additional setae on TR	0 = Absent; 1 = Present
18 Insertion of FE1	0 = Proximal; 1 = Distal
19 Additional D setae on FE	0 = Absent; 1 = Present
20 Additional PV setae on FE	0 = Absent; 1 = One; 2 = Two or more
21 Mesofemoral FE5	0 = Short, spiniform; 1 = Elongate, setiform
22 Metafemoral FE5	0 = Short, spiniform; 1 = Elongate, setiform
23 Metafemoral FE6	0 = Short, spiniform; 1 = Elongate, setiform
24 Additional AD setae on tibia	0 = Absent; 1 = Present
25 Additional AV setae on tibia	0 = Absent; 1 = Present
26 Additional PV setae on tibia	0 = Absent; 1 = Present
27 TI4	0 = More proximal on foreleg; 1 = Not more proximal on foreleg
28 TI6	0 = Short, spiniform; 1 = Elongate, setiform
29 TI7	0 = Short, spiniform; 1 = Elongate, setiform
30 Additional AV setae on tarsus	0 = Absent; 1 = Present
31 Additional PV setae on tarsus	0 = Absent; 1 = Present
32 Series of V spinulae on meso- and metatibiae	0 = Well developed; 1 = Absent or reduced
33 Basoventral spinulae on claws	0 = Absent; 1 = Present
34 AB7	0 = Incompletely sclerotized; 1 = Completely sclerotized
35 Additional setae on AB8	0 = Absent; 1 = Short, spiniform; 2 = Elongate, setiform
36 Additional D pores on AB8	0 = Absent; 1 = Present
37 Urogomphus	0 = Two-segmented; 1 = One-segmented
38 Additional setae on urogomphus	0 = Absent; 1 = One (minute, subapical); 2 = Numerous prominent setae
39 URb	0 = Proximal to sensillum UR2; 1 = Distal to sensillum UR2
40 URc	0 = Proximal to sensillum UR4; 1 = Distal to sensillum UR4
41 Additional pores on urogomphus	0 = Absent; 1 = Present

Terga with densely distributed microspinulae, segments 1–7 lacking spiracles; segments 1–6 strongly sclerotized dorsally with anterior and posterior carinae, posterior carinae continuous laterally; membranous laterally and ventrally, terga with setae of variable lengths, primarily along posterior carinae, segments 4–6 with prominent ventral setae; segments 7–8 completely sclerotized, segment 7 with prominent posterior dorsal and ventral setae; dorsal length of segment 8 (Figs. 13, 14) 1.28–1.37 mm, with siphon length 0.30–0.32 mm. **Urogomphus** (Fig. 15): One-segmented, length 1.32–1.42 mm, densely covered with microspinulae. **Chaetotaxy** (Figs. 2–15; Tables 1, 2): Notable similarities with and variation from the chaetotaxy of *A. anthracinus* (Alarie 1995, 1998) and representatives of Colymbetini (Table 2) include: Frontoclypeus with FRe present, 2 additional submarginal pores (Fig. 2); antennomere A3 with an additional ventroapical spinula and 2 ventroapical pores (Fig. 6); mandible with about 10 additional minute setae (Fig. 7); maxilla with MXa absent; labium with prementum with 8–9 relatively elongate spine-like anterodorsal setae (LA3, LA4, LA5, LA8 + 4–5 additional setae) (Fig. 9), LP2 with 2 additional minute, dorsoapical setae near LA10 and LA12; femora with FE5 and FE6 elongate and hair-like, additional setae of 1 dorsal, 1 posteroventral, 3–5 anteroventrals; tibiae with TI6 and TI7 elongate and hair-like, additional setae of 6–7 anteroventrals and 2–3 posteroventrals; tarsi with TA1 small with subapical anterodorsal origin, TA2 anterodorsal distal and spiniform, TA7 elongate hair-like with proximal posterodorsal origin (Figs. 10–12), additional setae of 6–8 anteroventrals and 3 posteroventrals. Abdominal segment 8 with 1–2 asymmetrically distributed additional setae (Fig. 14); urogomphus with UR1 and URa present, identification of URb and URc prevented by 4–6 additional pores, one minute subapical seta

and 18–19 additional lateral, medial, and dorsal spine-like and/or hair-like setae.

Character Analysis. Forty-two first-instar characters were included in the phylogenetic analysis, with 38 coded as binary and four as multistate (Table 1). The analysis of the data matrix (Table 2) using TNT resulted in four most parsimonious trees of 67 steps (CI = 0.69; RI = 0.70). These equally parsimonious trees differed in the relative positions of *Colymbetes*, *Melanodytes*, and some *Rhantus* species. For this reason, the strict consensus was calculated, in which the genus *Hoperius* was recovered as sister to a clade formed by the genera *Neoscutopterus*, *Meladema*, and *Bunites* (Fig. 16). Characters were mapped in one of the most parsimonious cladograms (Fig. 17).

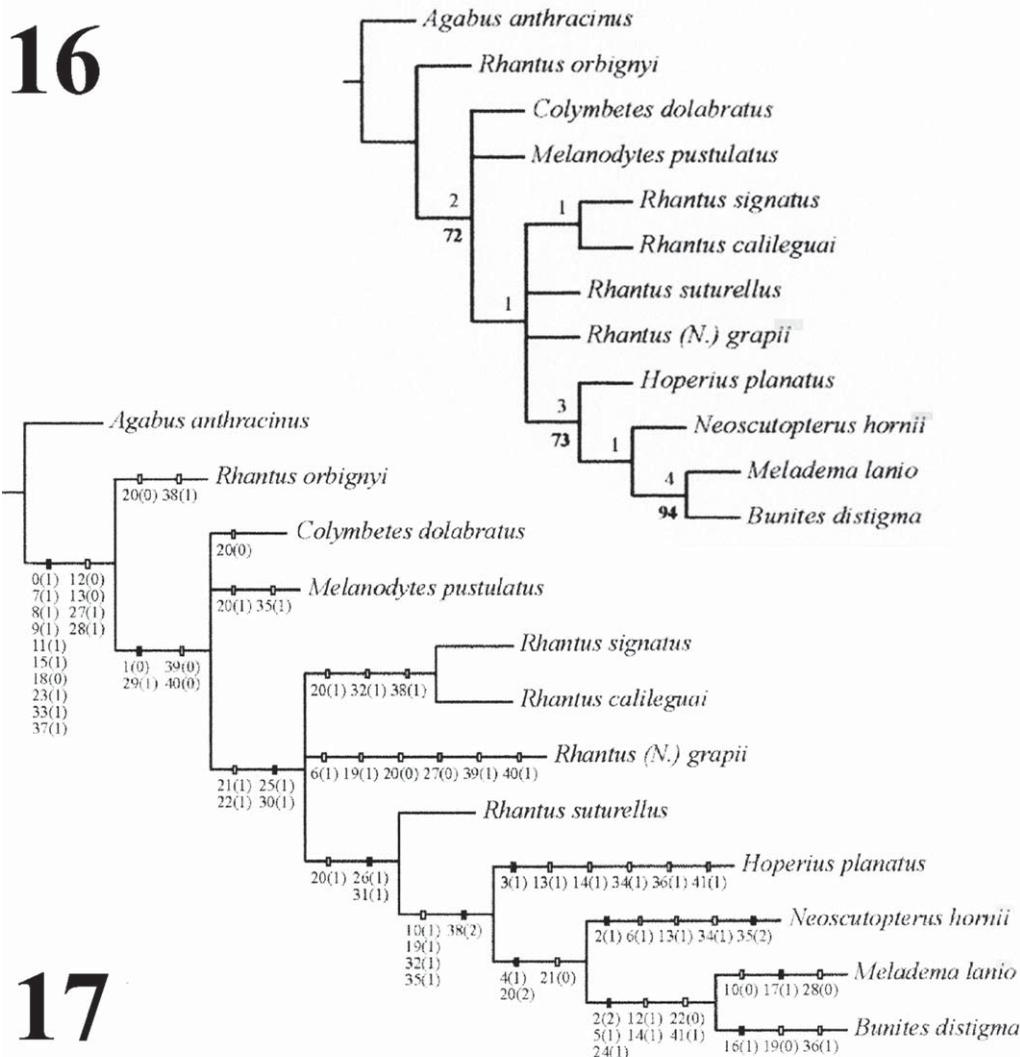
Bionomics. First instars and concurrent second and third instars of *H. planatus* were from a lower Piedmont ephemeral back-pool habitat formed in the channel of Town Creek in Baldwin Co., Georgia. These larvae were the only dytiscids collected. Back-pool habitats are typically flooded only during periods of heavier precipitation in the drainage basin of the creek and are intermittently dry, or nearly so, on one or more occasions annually. Production in these types of systems is typically supported by allochthonous detrital material.

DISCUSSION

The presence of third instars, as well as a third instar collected from a lower Piedmont marsh (Barman *et al.* 1996), indicates that oviposition by *H. planatus* in this area would have begun at least in January, assuming a Type I life cycle (Nilsson 1986) with developmental rates commensurate with other medium-sized dytiscids (Barman 1996). Precipitation rates in the area increase from December through March (Plummer 1983), restoring and/or producing and maintaining numerous

Table 2. Data matrix of 42 first-instar characters for 11 terminal taxa of Colymbetini. Missing data coded with ?.

Taxa	Characters									
	00–04	05–09	10–14	15–19	20–24	25–29	30–34	35–39	40–41	
<i>Agabus anthracinus</i>	01000	00000	00110	00010	?0000	00000	00000	00001	10	
<i>Bunites distigma</i>	10201	10111	11101	11000	20011	11111	11110	1112?	?1	
<i>Colymbetes dolabratus</i>	10000	00111	01000	10000	00010	00111	00010	00100	00	
<i>Hoperius planatus</i>	10010	00111	11011	10001	11110	11111	11111	1112?	?1	
<i>Meladema lanio</i>	10201	10111	01101	10101	20011	11?01	11110	1012?	?1	
<i>Melanodytes pustulatus</i>	10000	0??1?	??000	10000	10010	00111	00010	1010?	??	
<i>Neoscutopterus hornii</i>	10101	01111	11010	10001	20110	11111	11111	2012?	?0	
<i>Rhantus calileguai</i>	10000	00111	01000	10000	11110	10111	10110	00110	00	
<i>Rhantus (Nartus) grapii</i>	10000	01111	01000	10001	01110	10011	1?010	00101	10	
<i>Rhantus orbigny</i>	11000	00111	01000	10000	00010	00110	00010	00111	10	
<i>Rhantus signatus</i>	10000	00111	01000	10000	11110	10111	10110	00110	00	
<i>Rhantus suturellus</i>	10000	00111	01000	10000	11110	11111	11010	00100	00	



Figs. 16–17. **16)** Strict consensus cladogram with Bremer support values indicated above branches and jackknife values above 50 indicated below branches; **17)** One of four most parsimonious cladograms with character changes mapped for each clade. Solid rectangles indicate unique character state transformations; open rectangles indicate homoplastic character state transformations.

highly productive temporary pools. Since average January air temperature for the central lower Piedmont is about 7 °C (Anonymous 2013), there is neither substantive nor persistent ice-cover to deter exploitation of these systems by dytiscids and dytiscid prey species. The limited cold tolerance indicated for *H. planatus* that permits oviposition and larval development during central Georgia’s relatively mild winters has also been observed (Barman *et al.* 1996) for other dytiscids (*e.g.*, *Hydroporus signatus* Mannerheim, 1853, *Neoporius undulatus* (Say, 1823), *Platambus stagninus* (Say,

1832), *Agabus disintegratus* (Crotch, 1873) and *Agabus punctatus* Melsheimer, 1844.

The first instar of *H. planatus* is characterized by the presence of additional pores on the frontoclypeus (character 3, Fig. 2), representing a unique character state within the Colymbetini. Reduction in the overall size of the prementum (most evident in the reduced length of the palpi as compared to that of the maxillary palpus) and in the length (height) of the postmentum (Fig. 8) is also important. These traits along with the presence in later instars of a shorter antennomere 2 and of a variable

number of secondary setae on antennomeres 1 and 2 and maxillary palpomere 1 (Alarie and Hughes 2006) make this species very distinctive within this tribe.

Inclusion of the first-instar character states of *H. planatus* into data matrices used in larval studies of phylogenetic relationships of the Colymbetini (Michat 2005; Alarie and Hughes 2006) reinforces the hypothesis of a monophyletic origin for members of this tribe. Larvae of the Colymbetini share a total of 10 non-ambiguous character states with regard to the chosen out-group. These are: (i) presence of an occipital suture (character 00, Fig. 2); (ii) presence of additional ventroapical pores on antennomere 3 (character 07, Fig. 6); (iii) a non-protruding lateroventral process (A3') on antennomere 3 (character 08, Fig. 6); (iv) medial position of ANg (character 09, Fig. 4); (v) absence of MXa (character 11; Fig. 8); (vi) distal articulation of the procoxal CO7 (character 15); (vii) proximal origin of FE1 (character 18, Fig. 10); (viii) elongate and setiform aspect of the metafemoral FE6 (character 23; Fig. 11); (ix) presence of basoventral spinulae on trasal claws (character 33, Figs 10–11); and (x) one-segmented urogomphi (character 37, Fig. 15).

The phylogenetic relationship of *Hoperius* to other Colymbetini genera was deemed equivocal by Alarie and Hughes (2006); however, its position as a sister taxon to a clade comprised of *Neoscutopterus*, *Meladema*, and *Bunites* appears well supported, based on this analysis. Indeed, both Jackknife (73) and Bremer (3) values indicate strong support for the monophyletic origin of these four genera (Fig. 16). First instars of this clade have a large number of additional primary setae on the urogomphus (character 38, Fig. 15), a unique character state within the Colymbetini. It is also noteworthy that first instars of *Hoperius* share with those of *Neoscutopterus*, *Meladema*, and *Bunites* four homoplastic character states: (i) presence of additional setae on the mandible (character 10, Fig. 7); (ii) presence of additional dorsal femoral setae (character 19, Fig. 10); (iii) presence of short, spiniform additional setae on the abdominal segment 8 (character 35, Fig. 14); and (iv) absence of ventral rows of spinulae on the meso- and metatibia (character 32, Figs. 10, 11).

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