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Lacunicambarus dalyae: a new species of burrowing crayfish (Decapoda: Cambaridae) from the southeastern United States

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Abstract

The Jewel Mudbug, *Lacunicambarus dalyae* **sp. nov.**, is a large, colorful primary burrowing crayfish found in Alabama, Florida, Georgia, Mississippi and Tennessee. This species is most similar in appearance to the Paintedhand Mudbug, *L. polychromatus*, a species found across the Midwestern United States. The ranges of the two species overlap minimally, and they can be distinguished from each other based on several characters, the most notable of which is the much longer central projection of the gonopod in Form I and II males of *L. dalyae* **sp. nov.** relative to *L. polychromatus*. Like its congeners, *L. dalyae* **sp. nov.** is commonly found in burrows in the banks and floodplains of streams and is resilient to a moderate amount of anthropogenic habitat degradation, being occasionally collected from burrows in roadside ditches and urban lawns.

Key words: *polychromatus*, *diogenes*, paintedhand mudbug, devil crayfish, jewel mudbug, taxonomy, systematics

Introduction

Freshwater crayfishes in general and primary burrowing crayfishes in particular are becoming increasingly imperiled for reasons that include habitat degradation and biological invasions (Lodge *et al.,* 2000; Taylor *et al.,* 2007; Richman *et al.,* 2015). High taxonomic resolution is important in the face of such threats, as a truly widespread species is likely to be buffered against a certain amount of anthropogenic and natural stressors, and therefore requires less immediate conservation attention (IUCN, 2012; Hossain, 2018). Contrarily, if a purportedly widespread species is actually multiple more-narrowly distributed species, more urgent conservation attention may be warranted for each of these species but inadvertently withheld (Crandall *et al.,* 2009; Richman *et al.,* 2015; Bland, 2017). It is therefore critical for taxonomists to differentiate between these two scenarios and describe the diversity that they discover; however, North American primary burrowing crayfish taxonomy has proven difficult to establish because of how challenging these animals are to find and collect relative to their stream-dwelling counterparts (Hobbs, 1989; Jezerinac, 1993). This has led to the formation of numerous species complexes, where similar-looking crayfishes from a large range are regarded as a single species (e.g., Taylor, 2000; Ainscough *et al*., 2013; Thoma *et al*., 2016). Fortunately, a recent surge in research interest in primary burrowing crayfishes along with increases in the sophistication and availability of molecular techniques have paved the way for much needed taxonomic revisions.

The genus *Lacunicambarus* is in the midst of such a revision after more than a century of researchers using the binomial "*Cambarus diogenes*" as a catchall for many large North American burrowing crayfishes that are now recognized as distinct species in their own genus. Until recently, the species that are now in the genus *Lacunicambarus* were ascribed to the *Cambarus* subgenera *Lacunicambarus* (Hobbs, 1969) and *Tubericambarus* (Jezerinac, 1993). Species in these subgenera are morphologically and ecologically similar, but Jezerinac, 1993 split *Tubericambarus* from *Lacunicambarus* based on differing tuberculation patterns on the dorsomesial surface of the palm of the chela. In a pivotal paper investigating the phylogenetics of *Cambarus*, Breinholt *et al*., 2012 raised concerns about the

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monophyly of most of the *Cambarus* subgenera, leading Crandall & De Grave, 2017 to advise against their usage. As part of a systematic revision of what is now recognized as *Lacunicambarus diogenes* (Girard, 1852), Glon *et al.,* 2018 further investigated the subgenera *Lacunicambarus* and *Tubericambarus*, confirming that neither were independently monophyletic but finding that they together formed a clade distinct from *Cambarus*. Glon *et al.*, 2018 elevated *Lacunicambarus* to generic rank to encompass the species from these rejected subgenera. Throughout this work on *Lacunicambarus*, the presence of several potential undescribed species became apparent, generating the current paper.

We first collected *Lacunicambarus dalyae* **sp. nov.**, described herein, in August 2017 while sampling for burrowing crayfishes in the Duck River Basin of Tennessee. Subsequent correspondences with a number of researchers revealed to us that this species had previously been collected and studied but ascribed to either *L. diogenes* or more frequently *L. polychromatus* (Thoma *et al.,* 2005). One exception is Thoma *et al.*, 2005, who made a brief reference to an undescribed species occurring in Alabama, Mississippi and Tennessee that resembles *L. polychromatus* which we believe to be *L. dalyae* **sp. nov**. Upon our first examination of this species, we likewise noted its similarity to *L. polychromatus*. However, our familiarity with *L. polychromatus* from throughout its range in the midwestern United States allowed us to identify several discordant morphological characters (described below), leading us to suspect that the specimens at hand were of a distinct species from *L. polychromatus*. Our subsequent examination of additional specimens as well as our molecular systematic work as part of a broader revision of *Lacunicambarus* has provided additional evidence to corroborate our initial suspicions and expanded the known range of this new species to Alabama, Florida, Georgia, and Mississippi.

Methods

Sampling. We used a combination of freshly collected and museum specimens in our analyses. Between 2017 and 2019, we collected specimens in Tennessee and Alabama from burrows which we pumped by hand or excavated with a gardening pickaxe or shovel. Shortly following capture, we used heat-sterilized forceps to remove gill tissue from each specimen, which we preserved in tubes of 100% ethanol and froze as soon as possible for subsequent molecular analyses. We preserved voucher specimens in jars of 70% ethanol and later deposited them in the Ohio State University Museum of Biological Diversity (OSUMC) Crustacean Collection and the North Carolina Museum of Natural Sciences (NCSM) Non-Molluscan Invertebrate Collection. We also obtained additional specimens and tissue samples from other researchers which helped fill gaps in our own sampling. Lastly, we examined a large number of specimens from the Smithsonian Museum of Natural History's (NMNH) Invertebrate Collection that were discovered while sorting through and identifying lots catalogued as "*Cambarus diogenes*" in Fall 2018.

Note on absence of molecular analyses. We did not run any new molecular analyses for this study, as two previously published molecular phylogenies of *Lacunicambarus* based on three mitochondrial DNA loci (12S, 16S, and COI) recover all specimens of *L. dalyae* **sp. nov.** in a maximally supported clade (see Glon *et al.,* 2018 Figure 1 and Glon *et al.* 2019 Figure 2; in both cases *L. dalyae* **sp. nov.** is the clade labelled "*L.* aff. *polychromatus*" directly above *L. ludovicianus*). An updated *Lacunicambarus* phylogeny with additional *L. dalyae* **sp. nov.** specimens is currently being prepared and will be presented in an upcoming manuscript (MGG, unpublished data).

Morphometric analyses. In order to quantitatively differentiate *L. dalyae* **sp. nov.** from *L. polychromatus*, we measured a standard set of 30 morphological and meristic characters (see e.g., Fetzner & Taylor, 2018 and Loughman & Williams 2018) from specimens of each species using digital calipers and a dissecting microscope (*L. dalyae* **sp. nov**: n = 49, Form I male = 24, Form II male= 10, female = 15; *L. polychromatus*: n = 51, Form I male = 25, Form II male= 10, female = 16). Where appropriate, we standardized continuous measurements to account for size variation amongst our specimens by dividing them by a reference body part such as carapace length or gonopod length (e.g., mesial process length / gonopod length). We then calculated the means and standard deviations of each measurement and used these statistics as well as our direct observations to select measurements that we hypothesized to differ between species (Table 1). We checked for normality of these measurements using Shapiro-Wilk Tests, then accordingly used one-tailed Welch's t-tests or Wilcoxon Rank Sum Tests to test for statistically significant differences between species at an alpha value of 0.05. We conducted all of our analyses in R (R Core Team, 2017).

TABLE 1. Morphological and meristic variables compared between *L. dalyae* **sp. nov.** and *L. polychromatus*, along with means and standard deviations, test statistics of Wilcoxon Rank Sum Test or Welch's t-test, and resulting p-values. Asterisks denote statistically significant difference between species at alpha = 0.05. Abbreviations: CL, carapace length; FI, Form I male; FII, Form II male; L, length; *L.*, *Lacunicambarus*; W, width.

Measurement	*L. dalyae* mean	*L. dalyae* standard deviation	*L. polychromatus* mean	*L. polychromatus* standard deviation	Test statistic	p-value
Subpalmar tubercles	1.220	1.294	0.778	0.765	W = 1148.5	0.03*
Rostrum eye W / CL	0.117	0.008	0.122	0.009	W = 845	< 0.01*
Rostrum L / CL	0.166	0.008	0.174	0.036	W = 933	0.02*
Antennal scale L / W	3.010	0.196	2.812	0.153	W = 1891	< 0.001*
Propodus L / CL	0.788	0.074	0.751	0.090	W = 1135	0.2
Palm W / propodus L	0.457	0.021	0.472	0.028	W = 548	< 0.001*
Annulus ventralis L / W	0.825	0.089	0.833	0.085	$t_{28.591} = -0.23778$	0.59
Gonopod umbo W / L (FI)	0.269	0.014	0.243	0.014	$t_{45.946} = 6.2804$	< 0.001*
Gonopod central projection L / gonopod L (FI)	0.284	0.017	0.231	0.015	$t_{45.18} = 11.832$	< 0.001*
Gonopod mesial process L / gonopod L (FI)	0.298	0.021	0.284	0.018	$t_{45.215} = 3.5686$	< 0.01*
Gonopod central projection L / gonopod mesial process L (FI)	0.955	0.041	0.815	0.041	W = 574	< 0.001*
Gonopod umbo W / L (FII)	0.259	0.018	0.245	0.011	$t_{15.074} = 2.0065$	0.03*
Gonopod central projection L / gonopod L (FII)	0.297	0.020	0.245	0.009	$t_{12.784} = 7.3925$	< 0.001*
Gonopod mesial process L / gonopod L (FII)	0.310	0.014	0.310	0.012	$t_{17.444} = -0.31915$	0.49
Gonopod central projection L / gonopod mesial process L (FII)	0.961	0.081	0.792	0.039	$t_{12.9} = 5.976$	< 0.001*

Results

Morphometric analyses. We tested for differences between *L. dalyae* **sp. nov.** and *L. polychromatus* for 15 measurements based on our examination of specimens and comparisons of means and standard deviations. Of these, 13 were statistically significantly different between species (Table 1). Of these 13 measurements, five are different between species for Form I and II males as well as females. Specifically, the chela of *Lacunicambarus dalyae* **sp. nov.** has a greater number of subpalmar tubercles and a more slender palm than that of *L. polychromatus.* In addition, *L. dalyae* **sp. nov.** has a narrower and shorter rostrum than *L. polychromatus*. Lastly, the antennal scale of *L. dalyae* **sp. nov.** is slightly wider than that of *L. polychromatus*. The remaining characters pertain only to males. Specifically, male *L. dalyae* **sp. nov.** of both Forms have a wider gonopod umbo and a longer central projection that is approximately the same length as the mesial process. In contrast, the central projection of *L. polychromatus* of both Forms is considerably shorter than the mesial process. Lastly, the mesial process of *L. dalyae* **sp. nov.** is significantly longer than that of *L. polychromatus*, but only for Form I males.

Taxonomy

Family Cambaridae Hobbs 1942

Genus *Lacunicambarus* (Hobbs, 1969)

Lacunicambarus dalyae Glon, Williams and Loughman sp. nov (Figures 1–4, 6)

Cambarus (*Tubericambarus*) sp. A—Jezerinac 1993: 535 [in part].
Cambarus sp. A—Taylor & Schuster 2004: 126 [in part].
Cambarus polychromatus—Taylor *et al.* 2007:383 [in part]. Schuster *et al.* 2008:502. Simon 2011:77 [in part]. Smith *et al.* 2011:38. Miller & Stewart 2013:270.
Cambarus (*Tubericambarus*) *polychromatus*—Taylor & Schuster 2007:8. Miller & Stewart 2013:276. Miller *et al.* 2014:15.
Cambarus (*Tubericambarus*) sp. B—Heath *et al.* 2010:150.
Cambarus diogenes—Helms *et al.* 2013:1333 [in part]. Clay *et al.* 2017:1177.
Cambarus (*Lacunicambarus*) *erythrodactylus*—Simon *et al.* 2015:576 [in part]
Lacunicambarus aff. *polychromatus*—Glon *et al.* 2018:604 [in part]. Glon *et al.* 2019:456 [in part].

Diagnosis.—Eyes pigmented, not reduced. Rostrum narrow, moderately deflected, curving downward in lateral view, margins moderately thickened to acumen, lacking marginal spines or tubercles and median carina, shallowly excavated. Acumen distinctly delimited basally by 45° angles. Cephalothorax subcylindrical, laterally compressed, with 1–10 (mean: 6) adpressed tubercles lining posterior margin of cervical groove. Suborbital angle acute. Postorbital ridges developed, ending cephalically in small tubercle. Areola obliterated, constituting in adults 40–45% (mean: 42%) of entire length of cephalothorax. Antennal scale 2.7 to 3.6 (mean: 3.0) times as long as wide, broadest at mid-length, antennal spine strongly developed. Dorsomesial 1/4–1/3 surface of palm of chela studded with distinct to adpressed tubercles, mesial-most row consisting of 6–9 (mean: 8). Opposable margin of dactyl with concavity just proximal to midpoint. Ratio of dactyl length to palm length 1.6–2.0 (mean: 1.8). Dorsomesial longitudinal ridges of dactyl and propodus weakly developed. Dorsolateral impression at base of propodus weak. Ventral surface of chela with 0–7 (mean: 1) subpalmar tubercles. Mesial ramus of uropod with distomesial spine not reaching caudal margin. Gonopods of Form I males contiguous at base, with pronounced umbo near mid-length of caudal surface; terminal elements consisting of 1) long central projection lacking subapical notch, slightly tapered at mid-length, distally rounded, slightly shorter than mesial process, directed caudally at approximately 90°, overreaching margin of umbo by noticeable amount, 2) long mesial process with conical base, tapering slightly near mid-length, tipped with protruding finger, directed caudally at approximately 90° and overreaching margin of umbo by noticeable amount, 3) inconspicuous caudal knob protruding from caudolateral base of central projection. Hook on ischium of third pereiopod only. Female with annulus ventralis subcircular or subquadrangular, slightly wider than long, deeply embedded in sternum, with anterior half mildly pliable and posterior half sclerotized.

Holotypic male, Form I (Catalogue # OSUMC 10855; Figures 1, 2A–D, G–I, K, 6; Table 2).—Cephalothorax bullet-shaped in dorsal view (Figure 2G), width 93% of depth. Abdomen narrower than cephalothorax (19.1 and 22.5 mm, respectively; Figure 1); maximum width of cephalothorax less than depth at caudodorsal margin of cervical groove (22.5 and 24.3 mm, respectively). Areola obliterated; length 42% of total length of cephalothorax (Figure 2G). Rostrum moderately deflected and curved downwards in lateral view, margins slightly thickened; acumen distinctly delimited basally by 45° angles, anterior tip upturned, not reaching ultimate podomere of antennular peduncle; dorsal surface of rostrum shallowly concave with minute punctations forming single row along margins. Subrostral ridge moderate, evident in lateral aspect along entire length of rostrum. Postorbital ridges developed, grooved dorsolaterally, ending cephalically in small tubercle. Suborbital angle acute; branchiostegal spine absent (Figure 2A). Posterior margin of cervical groove lined by collar of 9 adpressed tubercles. Branchiostegal region granulate. Anteroventral branchiostegal region with 14 small tubercles. Hepatic region with scattered granules and tubercles. Remainder of cephalothorax with slight punctations dorsally and laterally. Abdomen longer than cephalothorax (52.4 and 50.5 mm, respectively), 2.7 times as long as wide; pleura short, rounded caudoventrally or ventrally. Cephalic section of telson with 2 spines in caudolateral corners, mesial spine slightly moveable. Proximal segment of lateral ramus of uropod with border of 17 spines on distal margin, second-most lateral spine distinctly longer than others; mesial ramus of uropod with prominent median rib ending distally as strong distomesial spine not reaching margin of ramus, laterodistal spine of ramus strong.

FIGURE 1. Dorsal view of Form I holotypic male of *Lacunicambarus dalyae* **sp. nov.** (OSUMC 10855).

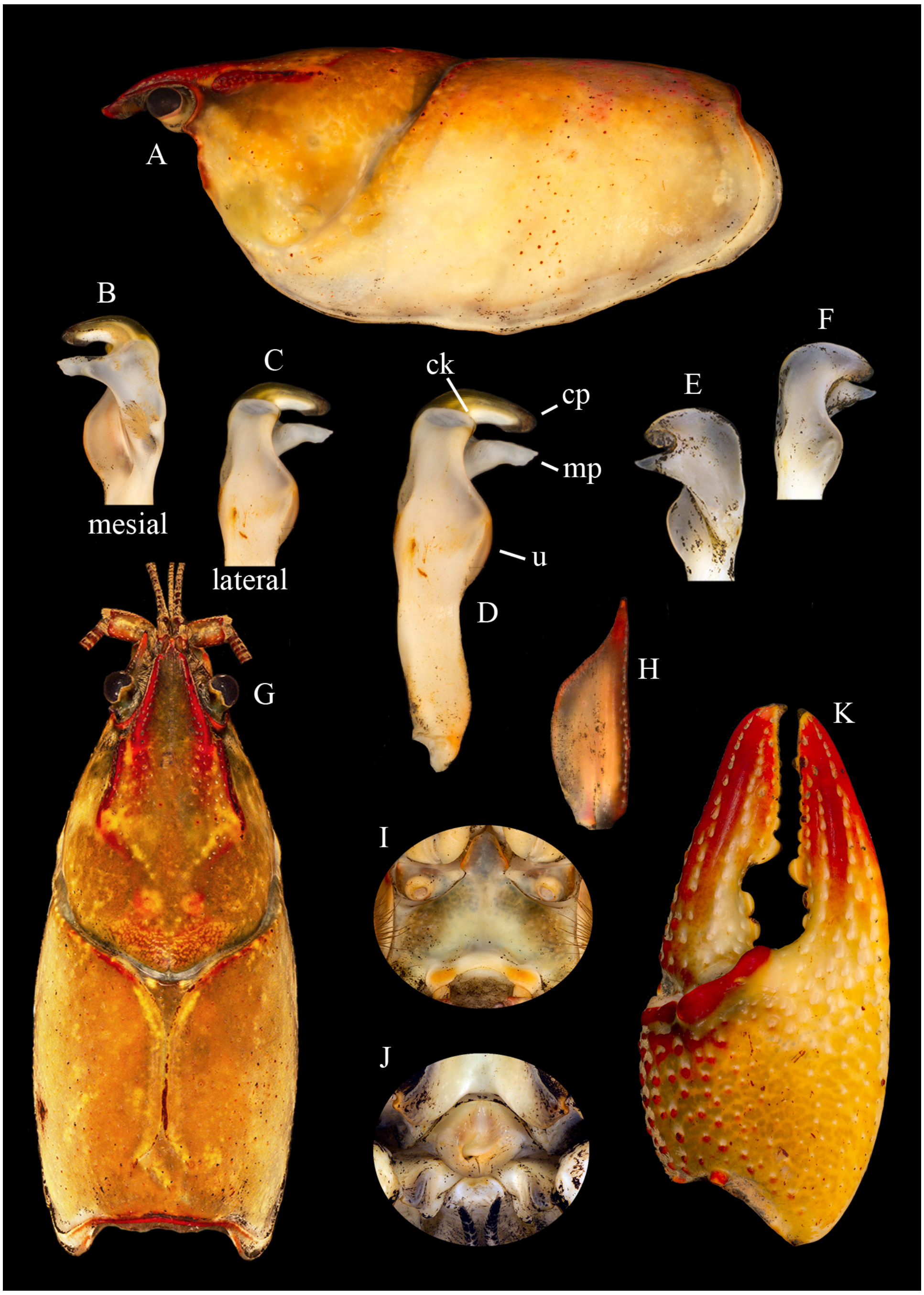

FIGURE 2. *Lacunicambarus dalyae* **sp. nov**. (A) Lateral cephalothorax; (B) mesial and (C–D) lateral Form I gonopod; (E) mesial and (F) lateral Form II gonopod; (G) dorsal cephalothorax; (H) antennal scale; (I) epistome; (J) annulus ventralis; (K) dorsal right chela. A–D, G–I, and K from holotype (OSUMC 10855); E–F from morphotype (OSUMC 10856); J from allotype (OSUMC 10857). Abbreviations: ck, caudal knob; cp, central projection; mp, mesial process; u, umbo.

Cephalomesial lobe of epistome (Figure 2I) bell-shaped with uniform raised margins, ventral surface shallowly concave; main body of epistome with shallow fovea; epistomal zygoma arched. Ventral surface of antennular peduncle's proximal podomere with small spine at mid-length. Antennal peduncle without spines. Antennal scale 3.0 times as long as wide (Figure 2H), broadest near mid-length, lateral margin straight from basal area to broadest distal point, ending in strongly developed antennal spine reaching past proximal margin of ultimate podomore of antennal peduncle. Ventral surface of entire third maxilliped densely studded with long, flexible setae; distolateral angle not acute.

Length of right chela (Figure 2K) 89% of cephalothorax length; chela width 46% of chela length; palm length 33% of chela length; dactyl length 1.9 times palm length. Dorsomesial 1/3 surface of palm of chela studded with distinct to adpressed tubercles, most strongly developed mesially, mesial-most row consisting of 7; proximal dorsolateral half smooth, distolateral area punctate, punctations deep, large in vicinity of dorsolateral base of propodus; lateral margin of propodus not costate; ventromesial surface of palm with small punctations, 2 bulbous tubercles on articular rim opposite base of dactyl, lateral-most spiniform; 1 subpalmar tubercle. Both fingers of chela with weakly developed dorsomedian longitudinal ridges. Opposable margin of propodus with row of 9 tubercles, decreasing in size from base except for 3rd from base which is greatly enlarged over adjacent tubercles, ultimate tubercle with corneous tip, larger than penultimate tubercle, positioned ventrally relative to adjacent tubercles; single row of minute denticles extending distally from fifth tubercle. Opposable margin of dactyl with row of 12 tubercles decreasing in size from base except for 3rd from base which is greatly enlarged over adjacent tubercles; conspicuous gap between 2nd and 3rd tubercles; single row of minute denticles extends distally from 7th tubercle; mesial surface of dactyl studded with 15 tubercles proximally, not forming distinct rows, giving way to punctations distally. Dorsolateral impression at base of propodus weak.

FIGURE 3. Dorsal view of female specimen of *Lacunicambarus dalyae* **sp. nov.** from Humphreys County, Tennessee demonstrating color variation present in the species.

Cheliped carpus with distinct dorsal furrow; dorsomesial surface with 5 scattered tubercles; dorsolateral surface punctate; mesial surface with 5 scattered tubercles plus 1 large procurved spine near distal margin; ventral surface with spine on distal articular rim. Merus with 2 pre-marginal spines dorsally, ventrolateral margin with row of 3 spines, ventromesial margin with row of 11 spines, increasing in size from base. Basioischial segment of first pereiopod with 3 small tubercles on ventral margin. Ischium of 3rd pereiopod with simple hook extending proximally to basioischial margin, not opposed by tubercles on basis. Coxa of 4th pereiopod with setiferous, caudomesial boss, ventral surface calcified; coxa of 5th pereiopod lacking boss, ventral surface membranous.

Gonopods contiguous at base, reaching past caudomesial boss of 4th pereiopod; terminal elements as described in diagnosis (Figure 2B–D).

Dextral gonopod and antennal scale separated from specimen and placed in vials inside specimen jar. One gill has been extracted from sinistral gill chamber of specimen, preserved in 100% ethanol and frozen at OSUMC for future DNA extractions (MGG 668).

FIGURE 4. Dorsal view of Form II male specimen of *Lacunicambarus dalyae* **sp. nov.** from Humphreys County, Tennessee demonstrating color variation present in the species.

TABLE 2. Measurements (mm) of holotype, morphotype, and allotype of *Lacunicambarus dalyae* **sp. nov.** (OSUMC 10855–10857).

Character	Holotype	Morphotype	Allotype
Carapace:			
Depth	24.3	22.9	21.7
Width	22.5	22.6	20.2
Length	50.5	47.4	45.6
Areola:			
Length	21.2	20.2	19.5
Rostrum:			
Width at eyes	5.7	5.4	5.5
Length	8.2	7.6	7.6
Postorbital ridge:			
Width	9.4	9.1	8.5
Chela (right):			
Length of propodus	45.1	39.0	32.7
Length of palm	15.0	13.1	10.9
Width of palm	20.9	18.0	15.5
Length of dactyl	28.3	23.4	21.2
Abdomen:			
Length	52.4	48.3	49.0
Width	19.1	18.4	18.1
Gonopod:			
Length	12.0	11.8	NA
Width at umbo	3.2	3.0	NA
Annulus ventralis:			
Length	NA	NA	3.3
Width	NA	NA	4.1
Antennal scale:			
Length	7.3	6.4	6.7
Width	2.4	2.4	2.3

Allotypic female (Catalogue # OSUMC 10857; Figure 2J; Table 2).—The allotypic female differs from the holotype as follows: Areola length 43% of total length of cephalothorax. Anterior tip of rostrum acumen overreaching proximal margin of ultimate podomere of antennular peduncle. Posterior margin of cervical groove lined by collar of 6 adpressed tubercles. Anteroventral branchiostegal region with 11 small tubercles. Proximal segment of lateral ramus of uropod with border of 16 spines on distal margin. Antennal scale 2.9 times as long as wide. Length of right chela 72% cephalothorax length; chela width 48% of length; dactyl length 1.4 times palm length. Mesial-most row of tubercles on dorsomesial surface of palm of chela consisting of 8 tubercles, chela with 2 subpalmar tubercles. Opposable margin of dactyl with row of 15 tubercles, decreasing in size from the 5th tubercle; no conspicuous gap between tubercles of proximal half. Mesial surface of dactyl studded with 17 tubercles, decreasing in size distally. Dorsomesial surface of cheliped carpus with 7 scattered tubercles; mesial surface with 5 spiniform tubercles plus 1 large procurved spine near distal margin. Merus with 5 pre-marginal spines dorsally, 2 of which are considerably larger than others; ventrolateral margin with row of 4 spines.

Annulus ventralis (Figure 2J) as in diagnosis; 1.3 times wider than long, with bifurcated leathery ridge mesially located in anterior half; tongue extending from sclerotized lingual (sinistral) wall into fossa of sclerotized supralingual (dextral) wall; supralingual wall more swollen caudomesially than lingual wall, both walls curved on outer margin. Posterior margin of annulus ventralis reaching anterior margin of oblong, approximately symmetrical postannular sclerite, lacking setae. First pleopods overreaching distal edge of annulus ventralis when abdomen flexed.

Morphotypic male, Form II (Catalogue # OSUMC 10856; Figure 2E–F; Table 2).—The morphotypic Form II male differs from the holotype as follows: cephalothorax width 99% of depth; areola length 43% of total length of cephalothorax. Anterior tip of rostrum acumen overreaching proximal margin of ultimate podomere of antennular peduncle. Posterior margin of cervical groove lined by collar of 6 adpressed tubercles. Anteroventral branchiostegal region with 8 small tubercles. Abdomen 2.6 times as long as wide. Proximal segment of lateral ramus of uropod with border of 15 spines on distal margin. Antennal scale 2.6 times as long as wide; lateral margin slightly concave. Length of right chela 80% of cephalothorax length; palm length 34% of chela length; dactyl length 1.8 times palm length. Opposable margin of propodus with row of 8 tubercles. Opposable margin of dactyl with row of 9 tubercles. Mesial surface of dactyl studded with 14 tubercles. Dorsomesial surface of cheliped carpus with 7 scattered tubercles; mesial surface with 4 scattered tubercles plus 1 large procurved spine near distal margin. Merus ventrolateral margin with row of 2 spines, ventromesial margin with row of 10 spines.

Form II gonopod central projection non-corneous, rounded, slightly shorter than mesial process, overreaching margin of umbo (Figure 2E–F). Mesial process conical at base, tapering to a thin tip, overreaching margin of umbo. Caudal knob not visible. Dextral gonopod separated from specimen, placed in glass vial inside specimen jar. Sinistral chela regenerated, extreme tip of dactyl of dextral chela damaged.

Coloration and color pattern. Like many cambarid crayfishes, *L. dalyae* **sp. nov.** exhibits a notable ontogenetic shift in its coloration and color pattern (MGG, personal observation).

Large adult specimens resemble the holotype and exhibit the most striking coloration found in this species (Figure 1). The background coloration of the cephalothorax and chela of these large specimens is predominantly golden. The dorsal surface of the cephalothorax is darker than the lateral surfaces, which are subtly mottled. The legs of large adults are a light amber or cream color. The background coloration of the abdomen is typically darker than the cephalothorax, ranging from ocher to bronze. The background color of the crayfish is complemented by polychromatic highlights throughout the body. The dorsal surface of the carpus and merus are highlighted in shades of turquoise and emerald. The surfaces of the telson and rami of clean (i.e., recently molted) specimens are blue with white speckles. Much of the crayfish is highlighted in a ruby red color, including the tips of the chela, the tubercles and spines of the chela, merus and carpus, and the margins of the antennal scales, rostrum, postorbital ridge, pereiopods 2–5, abdomen, telson and uropods. The dorsal side of the cephalothorax and abdomen is adorned by a single longitudinal gladiate stripe that is typically yellow. Lastly, the dorsal side of the cephalon is adorned by a diamond-shaped pattern formed anteriorly by the ruby red highlights of the rostral margins and postorbital ridge and posteriorly by two ruby red to orange diagonal lines running from the distal ends of the postorbital ridge to a convergence point just anterior to the cervical groove.

The coloration and color pattern of young adult specimens differs slightly from adults (Figures 3, 4). Firstly, these specimens exhibit more pronounced mottling on their cephalothoraxes and abdomens. In addition, the background coloration of these younger specimens is less vibrant, ranging from burnt orange to olive. These specimens have more conspicuous turquoise and emerald highlights on their merus, carpus and chela than large adults. Lastly, the diamond-shaped pattern on the cephalon is sometimes less clearly delineated in these specimens, but it is typically still present.

Juvenile specimens are the darkest and most mottled specimens of the species. The background color of their entire body including the chela ranges from bronze to brown. They have conspicuous mottling on the lateral surfaces of the abdomen and cephalothorax which is of a muted goldenrod color. These specimens still bear characteristic markings of the species, including the dorsal longitudinal gladiate stripe, which is also a goldenrod color, and the diamond-shaped pattern on the cephalon. Lastly, these specimens have similar, albeit more muted, ruby red highlights on the margins of somites throughout the body.

Size. The largest *L. dalyae* **sp. nov.** that we have examined is a Form I male from Prentiss County, Mississippi that measures 53.4 mm carapace length (CL). The average ± standard deviation size of specimens that we examined was 43.0 ± 5.2 mm CL for Form I males, 38.4 ± 4.5 mm CL for Form II males, and 42.4 ± 3.5 mm CL for Females. The smallest Form I male that we examined measured 33.9 mm CL; however, Miller *et al.* (2014) recorded collecting a Form I male specimen measuring 27.4 mm CL.

Variation. There is a moderate amount of morphological variation across the range of *L. dalyae* **sp. nov**. We have examined specimens from Tennessee with lanceolate rostrums lacking clearly delimited acumens and others with rostral margins that remain thickened and entire to the tip of the acumen. One specimen from Pike County, Alabama has distinctly concave rostral margins. Some specimens from across the range have a very slight depression at the tip of the central projection that one might label as a subapical notch, but we hesitate to do so as this feature is considerably more subtle than the deep and conspicuous subapical notch found in some other members of the genus (see key below). We have also seen variation across the species' range in the distal end of the mesial process, which is occasionally tipped with one or more minute, finger-like tubercles, sometimes oriented laterally creating a fork. In some specimens, the lateral-most of the 2 bulbous tubercles on the articular rim opposite the ventral base of the dactyl is topped with a sharp spine oriented distally. One specimen from Lee County, Georgia exhibited an impressive and highly unusual 23 subpalmar tubercles, and a specimen from Walton County, Florida bore uncharacteristically long and thin chelae that did not appear to have been regenerated. Lastly, two specimens from Davidson County, Tennessee have remarkably thin antennal scales.

As mentioned above, much of the color variation found in *L. dalyae* **sp. nov.** is ontogenetic in nature; however, there appears to be a fair amount of color variation across this species' range. Particularly noteworthy are specimens from Alabama whose background colors are bright green or orange, rather than the usual gold (Guenter A. Schuster, personal communication). Despite this color variation, these specimens were still recognizable by their longitudinal gladiate stripe and diamond-shaped pattern on the cephalon, suggesting that the color pattern of this species is more characteristic than the color itself.

Disposition of Types. The holotype, morphotype and allotype are deposited in the OSUMC (OSUMC 10855–10857). Paratypes are deposited in the NCSM (NCSM 90130–90132).

Type locality. We collected the holotype and allotype from the banks of Big Richland Creek, a tributary of the Tennessee River in Humphreys County, Tennessee (36.1576° N, 87.8203° W). Most of the burrows at this site were within 1 meter of the stream channel and relatively shallow. These burrows were surrounded by dense ground vegetation and occasional young trees. The soil at this site was primarily clay mixed with a small amount of sand and pebbles.

We collected the morphotype and paratypes from burrows in and above the floodplain of Hurricane Creek, a tributary to the Duck River in Humphreys County, Tennessee (35.9823° N, 87.8148° W). The burrows that we excavated at this site were up to 10 m away from the stream channel and surrounded by ground vegetation (including a large amount of poison ivy) and mature trees. The terrain beyond the floodplain of Hurricane Creek at this site is steeply sloped causing some burrow entrances to be over 2 m above the water table and therefore particularly difficult to collect crayfishes from. The soil at this site was mostly clay loam with some sand.

Range. This species is widely distributed across the southeastern United States, having so far been found in Alabama, Florida, Georgia, Mississippi and Tennessee (Figure 5). The western limit of its range appears to be the Mississippi River, as we are not yet aware of any records of *L. dalyae* **sp. nov.** from Louisiana, Arkansas or Missouri. The eastern limit of this species' range is less clearly defined; we have numerous samples of this species from the Florida panhandle and the Upper Coastal Plain in Georgia, but further sampling will be required to more thoroughly determine its range in these states. Similarly, the northern extent of the species' range is unclear. It is found in West and Middle Tennessee, but we have not yet located it in East Tennessee or Kentucky. Kentucky is inhabited by a number of other *Lacunicambarus* species, including the closely-related *L. polychromatus*, so it is possible that competitive exclusion has prevented *L. dalyae* **sp. nov.** from expanding its range into this State. Similarly, East Tennessee is occupied by *L.* aff. *thomai* (Jezerinac, 1993) and *L. acanthura* (Hobbs, 1981), and this region is also characterized by an increase in topographic relief and associated change in hydrology, to which *L. dalyae* **sp. nov.** may not be adapted. Overall, this species' range does not correspond cleanly with any major drainage basin or ecoregion, but most of its range is within the confines of the South-Atlantic Gulf River Basin and the Southeastern Plains and Interior Plateau regions of the Southeastern USA Plains (sensu Wiken *et al.,* 2011).

Specimens examined. We examined a total of 175 specimens from 31 counties in five States. See Table 3 for information on these specimens.

Conservation status. *Lacunicambarus dalyae* **sp. nov.** is widely distributed throughout the southeastern United States and common in appropriate habitat. It appears to persist amidst a moderate amount of anthropogenic habitat degradation, as evidenced by specimens collected from burrows in roadside ditches and urban lawns. We suggest that it be considered Currently Stable following the American Fisheries Society's Endangered Species Crayfish Subcommittee criteria (Taylor *et al.,* 2007) and of Least Concern following the IUCN criteria (IUCN, 2012), but also recommend that potential threats to this species, including from pet trade collectors, be preemptively examined.

TABLE 3. Data (sorted by State and County) on examined specimens of *Lacunicambarus dalyae* **sp. nov.** including field/catalogue number, State and County of collection, GPS coordinates in decimal degrees, collection date, number of specimens of each sex and Form, whether sample included gravid females, and other crayfish species found at collection site. Asterisks denote type locality. Please note that some museum specimens were not associated with GPS coordinates so we estimated them based on provided locality information. Abbreviations: aff., affinis; AJ, Alan Jeon; AL, Alabama; AUM, Auburn University Museum of Natural History; *C.*, *Cambarus*; DF, Daniel Folds; FL, Florida; GA, Georgia; *L.*, *Lacunicambarus*; MGG, Mael Gianni Glon; MS, Mississippi; OSUMC; Ohio State University Museum of Biological Diversity Crustacean Collection; PM, Paul Moler; TN, Tennessee; USNM, Smithsonian National Museum of Natural History.

Field/catalogue #	State	County	Latitude	Longitude	Collection date	Form I males	Form II males	Females	Gravid?	Juveniles	Other species
USNM 130777	AL	Chambers	32.7734	-85.2261	14/04/1970		1				
Zac-181023-03	AL	Clarke	31.7447	-88.0224	23/10/2018			1			
USNM 146495	AL	Conecuh	31.4248	-87.0655	11/04/1975			1	yes		
USNM 209053	AL	Conecuh	31.3731	-87.0266	27/07/1967			1		2	
USNM 209315	AL	Conecuh	31.4145	-87.2180	26/07/1967	1				1	
USNM 145302	AL	Conecuh	31.4271	-86.8364	6/04/1974	1				8	
USNM 209047	AL	Conecuh	31.3085	-86.7279	12/05/1968		1			2	*L.* aff. *diogenes*
USNM 147256	AL	Elmore	32.5610	-86.2085	12/08/1976	1				4	
MGG-170830-01	AL	Lee	32.5010	-85.4361	21/04/2017		2			2	
AJ-4	AL	Lee	32.5929	-85.4956	17/10/2018	1					
USNM 144745	AL	Lee	32.6011	-85.4877	12/05/1972	1	2	5		7	
USNM 144752	AL	Lee	32.6954	-85.4903	8/03/1973	3					
USNM 145290	AL	Lee	32.6674	-85.4893	31/03/1973	2	4	5		4	
USNM 145198	AL	Lee	32.6082	-85.4810	9/06/1973	2		1			
USNM 145291	AL	Lee	32.5587	-85.5273	12/03/1973	1	1				*L.* aff. *diogenes*
AUM 22881	AL	Macon	32.4681	-85.6719	26/03/2009	1					
AUM 22903	AL	Macon	32.4681	-85.6719	30/03/2011			1			
AUM 23041	AL	Macon	32.4681	-85.6719	25/08/2011		1				
DF-3	AL	Perry	32.4959	-87.3758	21/07/2018					1	
USNM 130812	AL	Pike	31.8088	-85.9724	16/04/1970			1			
AJ-3	AL	Russell	32.2899	-85.4154	10/10/2018		1				
USNM 130789	AL	Russell	32.4478	-85.2376	15/04/1970		1	1		1	
PM-8	FL	Holmes	30.9681	-85.6079	18/03/2019			2	yes		*C. striatus*

...*Continued next page*

TABLE 3. (*Continued*)

Field/catalogue #	State	County	Latitude	Longitude	Collection date	Form I males	Form II males	Females	Gravid?	Juveniles	Other species
PM-11	FL	Jackson	30.9468	-85.2600	18/03/2019	1					*C. striatus, L.* aff. *diogenes*
PM-2	FL	Jackson	30.7925	-85.2219	20/09/2018					2	
USNM 1462936	FL	Liberty	30.5697	-84.9480	1/12/1939	1					
PM-12	FL	Walton	30.9691	-86.3205	13/03/2019	1		1	yes		
AJ-2	GA	Bibb	32.8094	-83.7587	21/10/2018					2	
USNM 146970	GA	Early	31.0899	-84.9831	25/06/1975		1				
USNM 146975	GA	Early	31.1834	-85.0379	25/06/1975		1			2	
USNM 132616	GA	Lee	31.7322	-84.1247	26/10/1981	1	1			4	
USNM 129671	GA	Lee	31.9070	-84.2449	14/04/1968		1				
USNM 129688	GA	Miller	31.1701	-84.7107	16/04/1968		1	1		1	
USNM 129681	GA	Schley	32.2095	-84.3159	15/04/1968			3		1	
USNM 260496	MS	Alcorn	34.9603	-88.4805	27/08/1936			2	yes		
USNM 208820	MS	Bolivar	33.7395	-90.9821	28/06/1967			1		7	
USNM 178478	MS	Lauderdale	32.4024	-88.5578	5/06/1982	1				5	
OSUMC 6210	MS	Prentiss	34.5594	-88.4419	24/03/1985	1		1			
OSUMC 6753	TN	Davidson	36.1713	-86.7308	5/06/2007		3	3			
OSUMC 2486	TN	Gibson	36.0751	-88.7452	22/03/1987		1				
OSUMC 6980	TN	Hardeman	35.1561	-88.8819	4/05/2008	1					
USNM 130153	TN	Hardin	35.2445	-88.1228	21/04/1969	1	1	1		1	
USNM 176980	TN	Hardin	35.0409	-88.2911	9/05/1976			1			
OSUMC 7083	TN	Henry	36.4425	-87.5772	21/04/2009	1		1			
MGG-170807-052	TN	Humphreys	35.9317	-87.7475	7/08/2017		1				
MGG-170807-054	TN	Humphreys	35.9823	-87.8148	7/08/2017	1	3	2			
MGG-190521-03	TN	Humphreys	36.1576	-87.8203	21/05/2019	5		2			*C. striatus*
OSUMC 7077	TN	Madison	35.5042	-88.6923	23/04/2009	3		1			

....*Continued next page*

ABLE 3. (*Continued*)

Field/catalogue #	State	County	Latitude	Longitude	Collection date	Form I males	Form II males	Females	Gravid?	Juveniles	Other species
OSUMC 7094	TN	Madison	35.5063	-88.6763	23/04/2009		1	1			
OSUMC 6756	TN	McNairy	35.0662	-88.6557	6/06/2007			1			
OSUMC 6759	TN	McNairy	35.1553	-88.5808	6/06/2007	1					
OSUMC 6961	TN	McNairy	35.0668	-88.6569	4/05/2008	1	2				
OSUMC 6758	TN	Mcnairy	35.1554	-88.5808	6/06/2007	1	1	3		1	
OSUMC 6761	TN	McNairy	35.0748	-88.5621	6/06/2007		1	3			
USNM 130585	TN	McNairy	35.1588	-88.5799	20/04/1969			1			
OSUMC 7041	TN	McNairy	35.0752	-88.5625	4/05/2008			1			

Life history notes. A detailed life history of *L. dalyae* **sp. nov.** in Alabama has previously been published (Miller *et al.,* 2014). Amongst their findings, Miller *et al.*, 2014 reported that mating of *L. dalyae* **sp. nov.** occurs in burrows during autumn or winter, with females extruding up to 171 eggs at the end of that same winter. Our examination of specimens largely corroborates this timing except for a single gravid female from Alcorn County, Mississippi that was collected on August 27th, 1936. Overall, this phenology is similar to what has been documented for other *Lacunicambarus* species (e.g., Fitzpatrick, 1978; Thoma *et al.,* 2005; Glon *et al.,* 2019). In addition, Miller *et al.*, 2014 found that juvenile *L. dalyae* **sp. nov.** are released and spend a period time in open water habitats before emerging to dig their first burrows in the banks or floodplain, which is a dispersal strategy that may contribute to the wide range of *L. dalyae* **sp. nov.** and other *Lacunicambarus* species (Helms *et al.,* 2013; Clay *et al.,* 2017; Glon *et al.,* 2018). Based on their length-frequency histograms, Miller *et al.*, 2014 suggested that the minimum lifespan of this species is 4 years. We do not have a reliable way of aging our specimens, but we expect that the maximum lifespan of this species could be as much as twice this minimum lifespan estimate based on our observations of other *Lacunicambarus* species (e.g., Glon *et al.,* 2019).

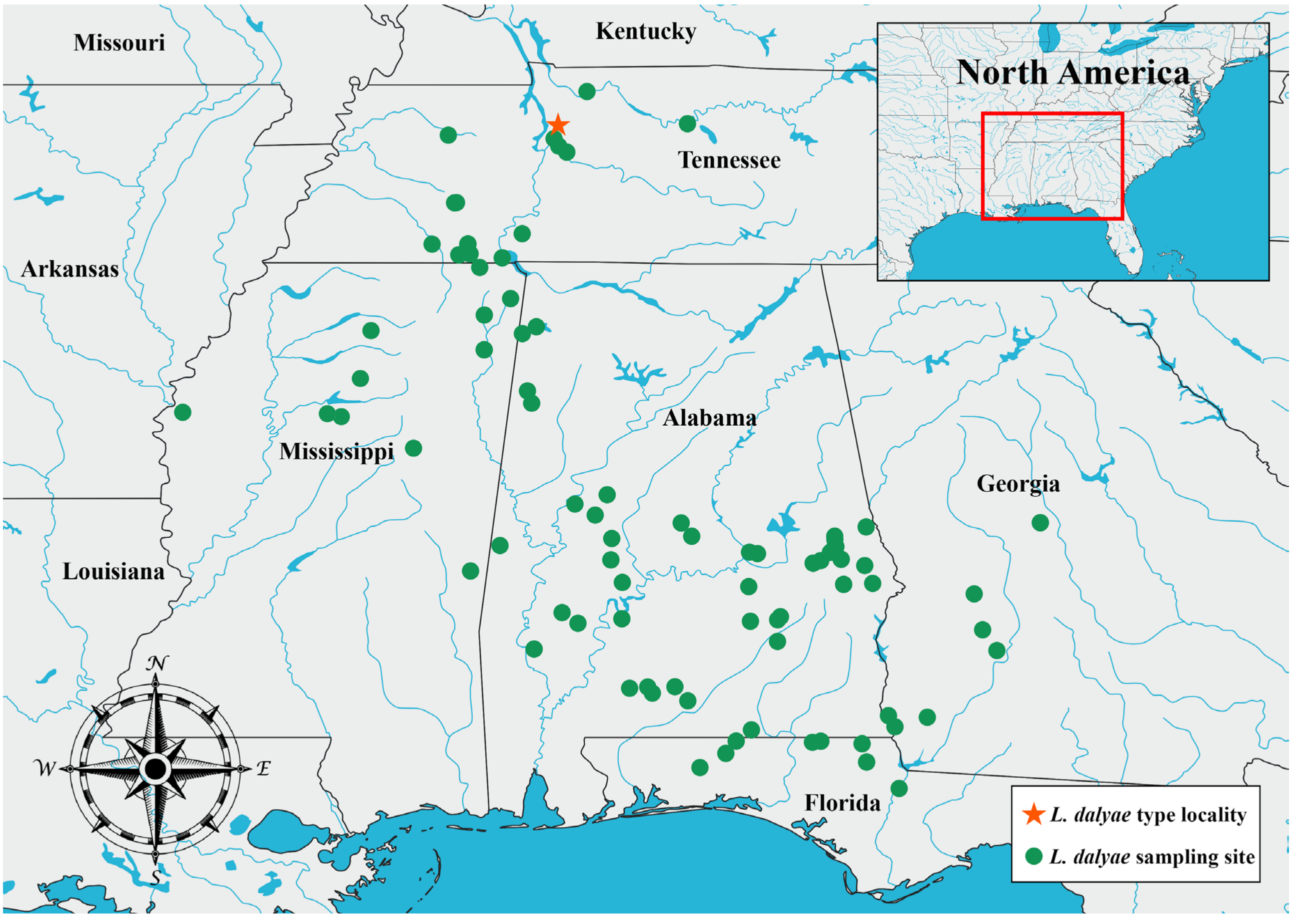

FIGURE 5. Range map of *Lacunicambarus dalyae* **sp. nov.** based on examined specimens. Localities for historical museum specimens lacking GPS coordinates estimated given available information. Green dots indicate sampling site and the orange star denotes the type locality of the species.

Ecological notes. *Lacunicambarus dalyae* **sp. nov.** is a primary burrowing crayfish typically found burrowing in alluvial soils of stream floodplains. Populations of this species are also frequently found burrowing in anthropogenically altered habitats like roadside ditches, the banks of ponds, and urban lawns. Like most of its congeners, this species excavates moderately complex burrows that consist of one or more surface openings (Miller *et al.,* 2014 found a range of 1–5 with a mean of 2.1) leading to tunnels that converge into a central tunnel approximately 30-50 cm below the surface. The depth attained by the central tunnel is largely dependent on the depth of the water table and substrate but can be greater than 2 m for adults. Depending on the time of year and weather conditions, burrow openings may be open or plugged, and one or more of these openings may be topped by a conspicuous chimney made of mud pellets excavated from the burrow.

Like its congeners and most other cambarid crayfishes, *L. dalyae* **sp. nov.** appears to be an opportunistic omnivore (Reynolds *et al*., 2013). We have not collected dietary data for this species *in situ* but individuals that we have kept in captivity have thrived when fed a diet consisting of a mixture of foods including leaf detritus, live invertebrates, and shrimp- and spirulina-based commercial fish foods.

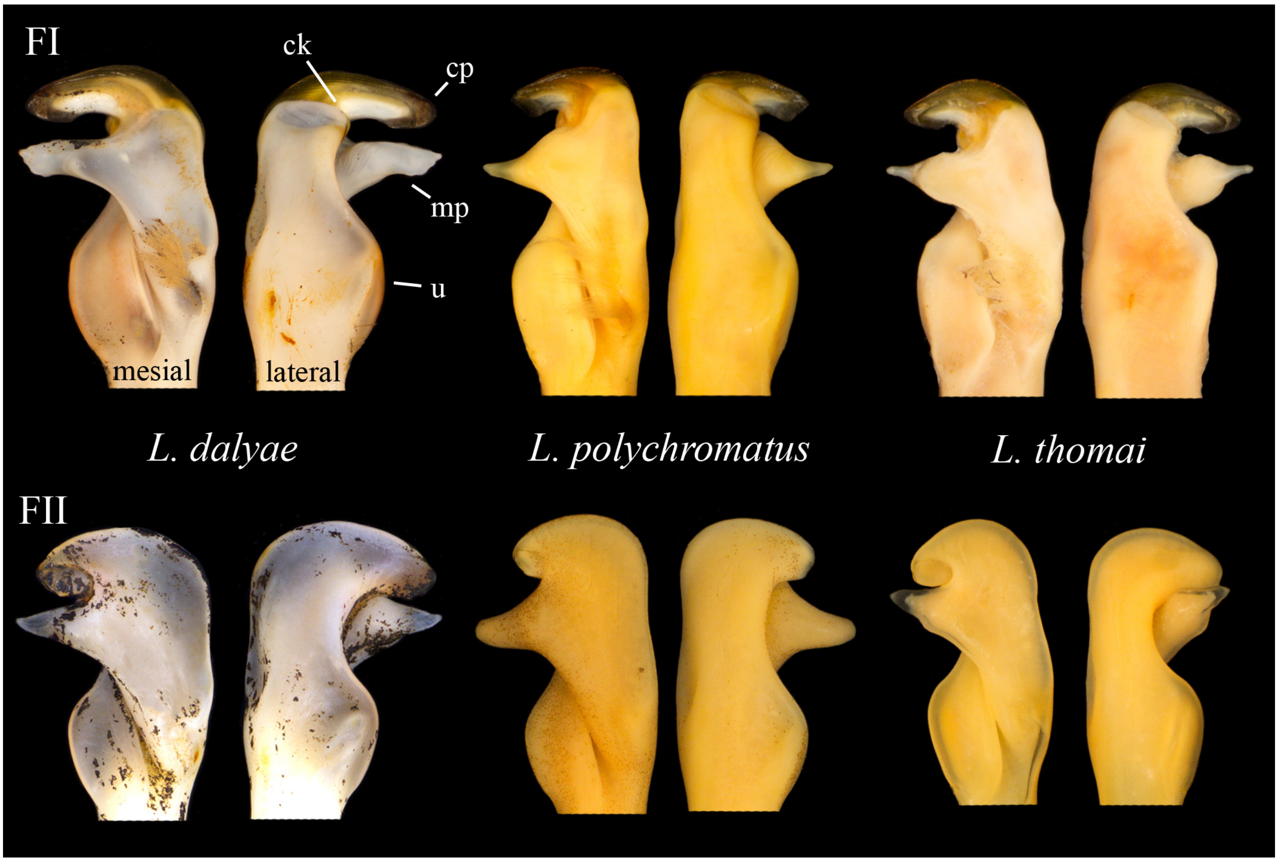

FIGURE 6. Mesial and lateral views of Form I (top row) and Form II (bottom row) gonopods of *L. dalyae* **sp. nov.**, *L. polychromatus*, and *L. thomai*. Abbreviations: ck, caudal knob; cp, central projection; FI, Form I; FII, Form II, mp, mesial process; u, umbo.

Updated key to *Lacunicambarus*

The following key is modified from Glon *et al*., 2019 and is based on Form I male specimens with at least one original chela.

1. Median spine on mesial ramus of uropod overreaching caudal margin of ramus . . . . *Lacunicambarus acanthura*

\- Median spine on mesial ramus of uropod not overreaching caudal margin of ramus 2

2(1). Dorsomesial margin of palm of chela with two parallel rows of well-developed tubercles, usually numbering 6–8 each, plus a third row running diagonally from mesial base of palm to lateral dactyl articulation, additional scattered tubercles usually present between second and third rows 3

\- Dorsomesial margin of palm of chela with dorsomesial 1/4–1/3 studded with tubercles not forming distinct rows 6

3(2). Form I male gonopod with pronounced subapical notch on central projection; rostrum narrow with sides strongly concave, forming hourglass shape; abdomen reduced in width 4

\- Form I male gonopod lacking or with very weak subapical notch on central projection; rostrum broad with sides straight or weakly concave; abdomen not reduced in width 5

4(3). Cephalic lobe of epistome apically truncate; life colors include single longitudinal gladiate stripe on dorsum of abdomen . . . . *Lacunicambarus miltus* (Fitzpatrick, 1978)

\- Cephalic lobe of epistome rounded or subtriangular; life colors include three brightly-colored longitudinal stripes on dorsum of abdomen, mesial of which is gladiate. . . . . *Lacunicambarus ludovicianus* (Faxon, 1884)

5(3). Spines on ventrolateral row of merus ranging from 0–4 (mean: 2); gonopod terminal elements moderately long (central projection / gonopod length mean ± standard deviation: 0.29 ± 0.00; mesial process / gonopod length mean ± standard deviation: 0.31 ± 0.00); longitudinal gladiate stripe never present on dorsum of abdomen . . . . *Lacunicambarus diogenes* (Girard, 1852)

- Spines on ventrolateral row of merus ranging from 2–9 (mean: 5); gonopod terminal elements short (central projection / gonopod length mean ± standard deviation: 0.22 ± 0.00; mesial process / gonopod length mean ± standard deviation: 0.26 ± 0.00); longitudinal gladiate stripe usually present on dorsum of abdomen . . *Lacunicambarus chimera* Glon & Thoma *in* Glon *et al.*, 2019

6(2). Rostrum straight in lateral view. Life colors olive to brown, occasionally with red or orange highlights on rostral margins and tips of chela, but body typically monochromatic and almost never adorned with longitudinal gladiate stripe on dorsum of abdomen . . . . *Lacunicambarus thomai* (Jezerinac, 1993)

- Rostrum moderately to strongly deflected in lateral view (e.g., Figure 2A). Life colors vary but body typically polychromatic and adorned with longitudinal gladiate stripe on dorsum of abdomen 7

7(6). Central projection and mesial process of Form I male gonopod long, both distinctly overreaching umbo; central projection approximately equal in length to mesial process (mean ± standard deviation central projection / mesial process: 0.96 ± 0.04; Figure 6) . . . . *Lacunicambarus dalyae* **sp. nov.**

- Mesial process of Form I male gonopod overreaching umbo, but central projection not overreaching umbo; central projection conspicuously shorter than mesial process (mean ± standard deviation central projection / mesial process: 0.82 ± 0.04; Figure 6). . . . . *Lacunicambarus polychromatus* (Thoma *et al.,* 2005)

Crayfish associates. Given that *L. dalyae* **sp. nov.** is broadly distributed across the most crayfish species-rich region of the world, an exhaustive list of crayfish associates would be intractable. Adults of burrowing crayfish species like *L. dalyae* **sp. nov.** often live in clustered colonies (Clay *et al.,* 2017), but multiple burrowing crayfish species may also live in close proximity to one another in partially or completely overlapping colonies. For instance, we have collected *C. gentryi* Hobbs, 1970 and *C. striatus* Hay, 1902 from burrows directly adjacent to those of *L. dalyae* **sp. nov.** in Tennessee. Colleagues of ours have collected *L. dalyae* **sp. nov.** and its congener *L.* aff. *diogenes* from numerous sites in Mississippi and Florida (Susie Adams & Paul Moler, personal communication). Similarly, Miller *et al.*, 2014 reported collecting *Creaserinus fodiens* (Cottle, 1863), *C. striatus*, *C. latimanus* (Le Conte, 1856), and *Procambarus acutissimus* (Girard, 1852) from burrows in the vicinity of *L. dalyae* **sp. nov.** burrows in Alabama. In short, a large number of southeastern primary or secondary burrowing crayfishes could be found occurring in sympatry with *L. dalyae* **sp. nov.** so long as the habitat is suitable.

Etymology. It is with great pleasure that we name this crayfish after Dr. Marymegan Daly, a Professor in the Department of Evolution, Ecology, and Organismal Biology and Director of the Museum of Biological Diversity at The Ohio State University. It is thanks to the opportunity presented by Dr. Daly to the lead author to join her lab, as well as her continued guidance and instruction on topics such as zoological nomenclature and systematics, that the recent revisionary work on *Lacunicambarus* was ever undertaken. Dr. Daly is an accomplished invertebrate zoologist and systematist who has greatly advanced her field during her ongoing career and is also a thoughtful and caring person who strives for equality and justice in this turbulent world. The crayfish described herein does not possess nematocysts, but we trust that Dr. Daly will be captivated by it all the same!

We suggest the common name “Jewel Mudbug” for this species as a testament to its magnificent color pattern. This crayfish’s golden background color and polychromatic highlights gives the impression that it has been cast in gold and adorned with precious stones. We refer to this crayfish as a mudbug to denote that it is a primary burrowing crayfish.

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