Article

ZOOTAXA

Redescription of *Deltamysis holmquistae* Bowman & Orsi, 1992 (Crustacea: Mysida: Mysidae), a mysid species new to the Atlantic Ocean with observations on the taxonomic status of *Kochimysis* Panampunnayil & Biju, 2007

MATTHEW J. SCRIPTER[1], W. WAYNE PRICE[2] & RICHARD W. HEARD[3]

[1]*Ecological Associates, Inc., Jensen Beach, Florida 34958, USA. matts@ecological-associates.com*
[2]*Department of Biology, University of Tampa, Tampa, Florida 33606, USA. wprice@ut.edu*
[3]*Department of Coastal Sciences, University of Southern Mississippi, Ocean Springs, Mississippi 39566, USA.*
richard.heard@usm.edu

Abstract:

The first occurrences of the estuarine mysid *Deltamysis holmquistae* Bowman & Orsi from the Atlantic Ocean are documented from sites on the eastern Florida and northwest Gulf of Mexico (Texas) coasts of North America. Based on examination of type material and specimens from Florida and Texas, considerable morphological variability and additional characters were observed necessitating a rediagnosis of the monotypic genus *Deltamysis* and a redescription of *D. holmquistae*. As a result of these new taxonomic criteria, the Indian Ocean species, *Kochimysis pillaii* Panampunnayil & Biju, described from southwest coastal India, is subsumed as a junior synonym of *D. holmquistae*. The current distribution of this apparently invasive species is probably due to maritime commerce. The geographical location of the endemic or source populations of *D. holmquistae* remains undetermined; however, its co-occurrence in California with three introduced Asian mysids suggests a northern Indian Ocean or northwest Pacific origin.

Key words: Taxonomy, Invasive Species, India, California, Texas, Florida

Introduction

The Atlantic coast of the U.S. has a long history of biological invasions due to the early arrival of European transatlantic ships (Fofonoff *et al*. 2009; Ruiz *et al*. 2011; Ojaveer *et al*. 2018). Subtropical Florida contains more introduced plants and animals than any other region in the continental US (Ewel 1986). While invasive charismatic megafauna may garner the most attention, small cryptic organisms are potentially the most invasive since they are transported via mundane commercial routes and escape notice until becoming established (Carlton 1996).

This article documents the first occurrence in the Atlantic Ocean of the invasive mysid species *Deltamysis holmquistae* Bowman & Orsi, 1992, specifically from the coastal waters of the southeastern Atlantic and Gulf coasts of the United States. This article also reviews the taxonomic standing of *Kochimysis pillaii* Panampunnayil & Biju, 2007—a brackish species described from India. The morphologically variable *D. holmquistae* is redescribed from paratypes and newly collected specimens from Florida and Texas.

Historical Review

Deltamysis holmquistae was originally described from the Sacramento–San Joaquin Delta in California by Bowman & Orsi (1992). In their original description, Bowman & Orsi (1992) concluded that *D. holmquistae* might be a cryptic native or an exotic invader (i.e., cryptogenic), but provided little evidence to support either conclusion.

A similar genus and species, *K. pillaii*, was described and reported from brackish water habitats in the state of Kerala on the southwest coast of India (Panampunnayil & Biju 2007; Biju & Panampunnayil 2010; Manojkumar & Pavithran 2016). Panampunnayil & Biju (2007) mentioned the similarity of the genus *Kochimysis* to *Deltamysis*, but they did not consider the two taxa to be congeneric.

Little published biological or ecological information is available for the monotypic genera *Deltamysis* and *Kochimysis*. Although continuous zooplankton sampling was conducted in the Sacramento–San Joaquin estuary from 1968–1987, the first recorded capture of *D. holmquistae* was not until 1977 (Bowman & Orsi 1992). It was collected every year after that (through 1987), but always in low numbers (1 to 39/year). The limited information on its ecology is confined to the original publication by Bowman & Orsi (1992) and Mecum (2006). The former authors reported the occurrence of this species in a salinity range of 0 to 18.7 ‰, but indicated that most of the specimens collected occurred in 1.1–2.2 ‰. Mecum (2006) found *D. holmquistae* in salinities of 0–6 PSU and, although rare, most abundant in December and January in the upper San Francisco Estuary. The Indian populations of *K. pillaii* occurred in low abundances (0.3 individuals/ m³) in zooplankton tows in a tropical estuary (Kochi backwater) in which temperatures and salinities ranged from 25.0–32.5 °C and 0–32.5 PSU, respectively (Panampunnayil & Biju 2007; Biju & Panampunnayil 2010). The species was also found in the stomachs of the greater lizardfish, *Saurida tumbil* Bloch captured north of Kochi (Manojkumar & Pavithran 2016).

Methods

Two separate collection methods, using either plankton nets or Ponar benthic grabs, were employed in the capture of specimens of *D. holmquistae* from the Florida and Texas study sites (Figure 1). Sampling was funded by private industry as part of required regulatory compliance reporting, and confidentiality constraints preclude reporting precise sampling coordinates at the four sites where *D. holmquistae* occurred.

Fort Lauderdale & Port St. John, Florida, and Freeport, Texas: Collections were made using proprietary plankton collection equipment designed to comply with Environmental Protection Agency (EPA) Clean Water Act (CWA) Section 316(b) (US EPA 1977) rules. The collection system for these three sites used a size-selective intake pipe in front of a water withdrawal structure to pull water from mid-depths, record precise water volumes using an in-line flowmeter, and filter water using a standard 3:1 length-to-diameter 505 μm mesh plankton net suspended in a 1514-liter (400-gallon) buffer chamber. A 13 hp 4" Honda trash pump (Model #3994–96) pulled water through the sampling apparatus with minimal damage to zooplankton and ichthyoplankton. A Hach Quanta water quality meter was used to measure specific conductance (mS/cm), temperature (°C), salinity (PSU), pH, and dissolved oxygen (mg/L) during sampling from the buffer chamber. When sampling was complete, the filtered organisms were washed into the cod end of the net and preserved in a 10% buffered formalin solution. The collections at each tidal event filtered ~50 m³ of water, with a target filtered volume of 100 m³ for the combined day or night samples. **Fort Lauderdale, FL:** Every two weeks, sampling occurred from 11 November 2015 through 6 November 2017, for a total of 52 sampling events and 104 collections. Samples taken at high and low tides were combined into diurnal or nocturnal composite samples to accommodate tidal variability in species number and diversity. **Port St. John, FL:** Every two weeks, sampling occurred from 14 June 2017 through 18 June 2018, for a total of 26 sampling events and 52 collections incorporating high and low tides for day and night collections. **Freeport, TX:** Sampling occurred twice monthly in September 2016, May through September 2017, and June through August 2018. Monthly collections occurred from October 2016 through April 2017, August 2017, and October 2017 through May 2018. In all, 33 sampling events took place and 66 collections containing a high and low tide sample from either day or night were analyzed.

Jacksonville, Florida: Collections made as part of this ecological assessment followed Florida Department of Environmental Protection (FDEP) Standard Operating Procedures (SOP) FS7450 for benthic macroinvertebrate sampling (FDEP, 2017). Three replicates were taken using a 225 cm² Petite Ponar grab. Sediments were passed through a 0.5950 mm sieve (U.S. Standard No. 30) to remove fine particles and retained organisms were preserved in a 10% buffered formalin solution. A Hach Quanta water quality meter was used to measure specific conductance (milli-Siemens per centimeter [mS/cm]), temperature (°C), salinity (PSU), pH (units), and dissolved oxygen (milligrams per liter [mg/L]) during the quarterly benthic sampling events. Benthic sampling was conducted quarterly from 10 July 2014 through 14 July 2016, for 8 sampling events and 144 individual collections.

Laboratory methods: Body lengths (L) of *D. holmquistae* were measured from the anterodorsal margin of the carapace to the posterior margin of the telson, excluding setae. Males were considered adults upon confirmation of developed penes and the setiferous male lobe. Females were considered adults if they had developed oöstegites. All illustrations are from Northwest Atlantic material. Most of the specimens examined in the study are being main-

tained in the collections of Ecological Associates, Inc. and some representative specimens are deposited in the Gulf Coast Research Laboratory (GCRL 6602).
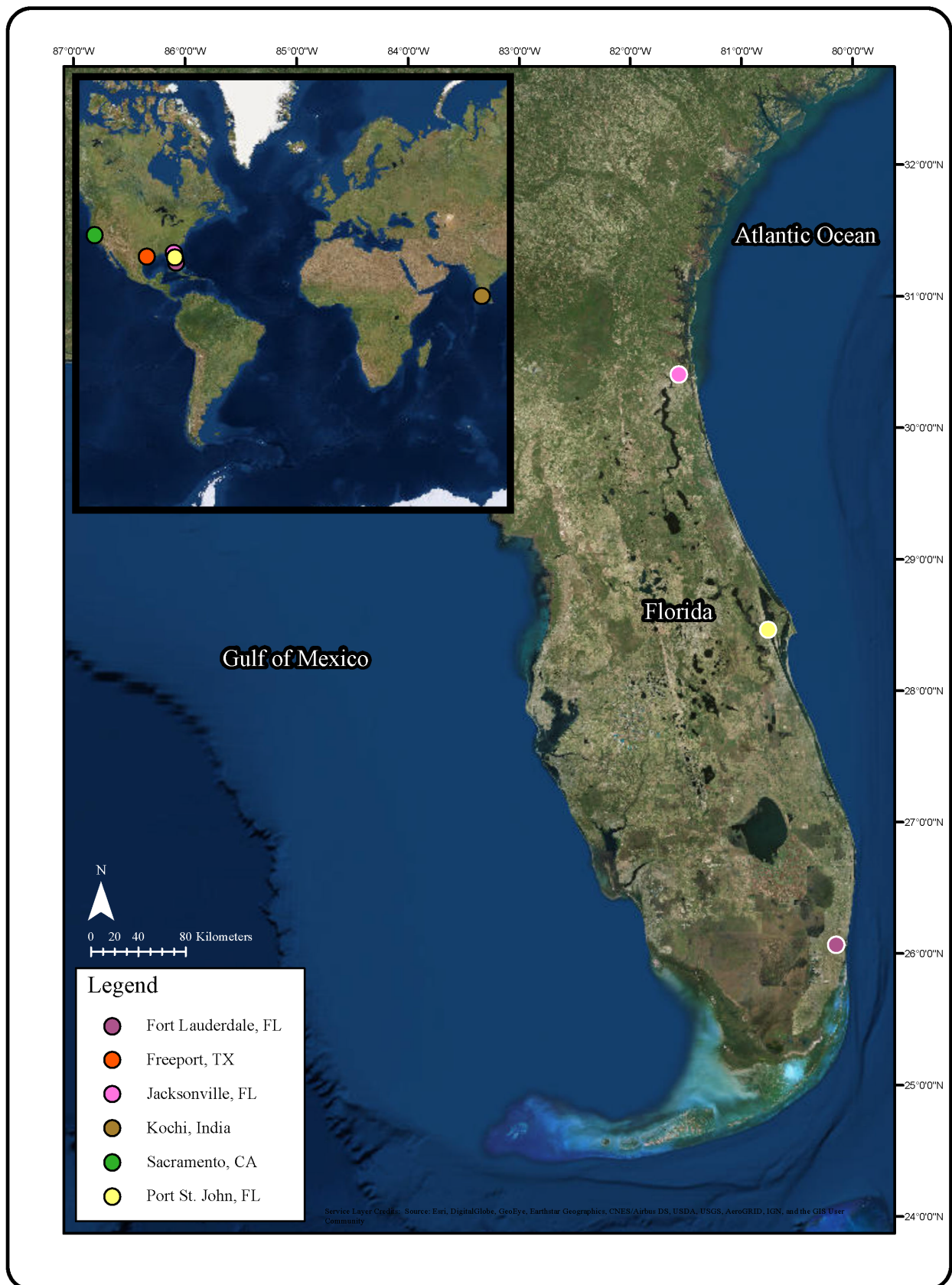

FIGURE 1. Capture locations for *Deltamysis holmquistae* with an emphasis on Florida sites.

Descriptions and locations of collection sites

Florida. Fort Lauderdale: Sampling occurred in the brackish-to-fresh Dania Cut-Off (C–10) Canal just east of its intersection with the South Fork New River Canal terminus. The Dania Cut-Off Canal enters the Intracoastal Waterway at the south end of Port Everglades. **Port St. John:** Sampling took place in a canal on the western shoreline of the Indian River 7 km north of the Barge Canal. The Port Canaveral locks open into the Banana River lagoon, and due west the Barge Canal connects the Banana River with the northern Indian River. **Jacksonville:** Sampling occurred at five stations along the St. Johns River north of Blount Island and another in San Carlos Creek. With the exception of the latter station, all sample stations were located on the narrow mud shelf alongside the main deep-water shipping channel. **Texas. Freeport:** Sampling occurred adjacent to the mainland opposite Brazos Harbor Inlet. The inlet and harbor area are a deep-water port for large shipping vessels with direct access to the open waters of the Gulf of Mexico.

Results

Taxonomy and Systematics

Order Mysida Boas, 1883

Family Mysidae Haworth, 1825

Subfamily Heteromysinae Norman, 1892

Tribe Mysidetini Holt & Tattersall, 1906

Genus *Deltamysis* Bowman & Orsi, 1992

Synonym: *Kochimysis* Panampunnayil & Biju, 2007

Emended diagnosis (Based on adult *D. holmquistae* paratypes and western Atlantic material): Carapace with anterior margin produced into a short, rounded rostrum. Male antennular peduncle, article 3 with reduced, rounded, sometimes indistinct, setiferous lobe. Antennal scale with transverse suture, separating short distal article. Thoracic endopod 2 with carpus and propodus simple in female; with papillations on lateral margins in male. Thoracic endopod 3 not stouter than other thoracic endopods. Thoracic endopods 3 and 4 with carpopropodus divided into 3 subarticles. Thoracic endopods 5–8 with carpopropodus divided into 4 subarticles. Pleopods rudimentary in both sexes. Uropodal endopod without spiniform setae along medial margin in region of statocyst. Penis of moderate size, extending forward to bases of thoracopods 4–5. Telson entire, lateral margins armed along posterior 0.25–0.37 length with 6–9 spiniform setae per margin (including apical setae); apex with 2 pairs of spiniform setae, inner pair 0.25–0.50 times as long as outer pair.

    Remarks: We compared our morphological observations on the paratypes of *D. holmquistae* from northeastern Pacific (California) and northwest Atlantic specimens (Florida and Texas) examined during the present study with the specific description of *K. pillaii* from the northern Indian Ocean. There was a significant degree of intraspecific morphological variation observed within the type series of *D. holmquistae*, as well as, in specimens from the northwest Atlantic (see Table 1). These observations demonstrated a high degree of overlap for the characters used in the generic and specific designations for *K. pillaii* and these findings strongly indicate that the two taxa represent a single variable and geographically dispersed species (see Discussion). Based on these comparisons and the morphological similarities, we herein formally subsume the monotypic genus *Kochimysis* Panampunnayil & Biju, 2007, as a junior subjective synonym of *Deltamysis* Bowman & Orsi, 1992.

Deltamysis holmquistae **Bowman & Orsi, 1992**
(Figs. 2, 3, 4, & 5)

Synonymy: *Deltamysis holmquistae* Bowman & Orsi, 1992: 734, figs. 2–4.—Cohen & Carlton 1995: 81.—Modlin & Orsi 1997: 439.—Bollens *et al*. 2002: 91, (Table 2).—Price 2004: 68.—Dean *et al*. 2005: 5, (Table 1).—Petryashev 2005: 14, (Table 1).—Mecum 2006: 1, pl. 2.—Modlin 2007: 492 (key), fig. 221C.—Panampunnayil & Biju 2007: 1962.—Carlton 2009: 35 (table 2.4C).—Ruiz *et al*. 2011:231, (Appendix 1). Winder & Jassby 2011: 684, (table 3).—Brown *et al*. 2016: 11 (Table 2).—Hiebert & Rasmusson 2016a: 541.—Hiebert & Rasmusson 2016b: 548.—Price 2016: 706 (key), pls.16.191.02E, 16.191.03J.—Mees & Meland 2012 (in list).
Deltamysis **sp. A.** [? *holmquistae*] Ranasinghe *et al*. 2005: 681 (tables 1, 4).
Kochimysis pillaii Panampunnayil & Biju, 2007: 1957, figs. 2–5.—Biju & Panampunnayil 2010: 50, table 1.—Manojkumar & Pavithran 2016: 42.—Mees & Meland 2012 (in list).

Material examined

Type material. Paratypes: All samples from Sacramento–San Joaquin Estuary, collected between Brown's Island and Jersey Island; bottom to surface tows using a 505 μm plankton net; USNM 251609, 1 adult male (Length [L] 4.5 mm), 4 non-ovigerous females (L 3.6, 3.8, 4.2 mm, 1 damaged), exact location and date unknown, J. J. Orsi coll.; USNM 251618, 2 adult males (L 3.8 mm, 1 damaged), 2 ovigerous females (damaged), 5 non-ovigerous females (L 3.5, 3.7 mm, 3 damaged), Sta. 56, north of Brown's Island, date unknown, J. J. Orsi coll.; USNM 251619, 1 adult male (L 3.2 mm), 1 ovigerous female (damaged), 2 non-ovigerous females (L 3.2, 1 damaged), 1 female (head only), exact location unknown, 29 May 1990, J. J. Orsi coll.

Northwest Atlantic material. Jacksonville, Florida: 11 males (L 2.6–2.9 mm), 14 ovigerous females (L 2.8–3.2 mm), 15 non-ovigerous females (L 1.9–2.9 mm), 7 juveniles (L 1.4–2.0 mm), 14–15 Oct 2014, temperature 26.6–26.9 °C, salinity 7.1–11.0 PSU, dissolved oxygen 6.0–6.7 mg/L; 2 ovigerous females (L 2.9, 3.0 mm), 1 non-ovigerous female (L 2.3 mm), 2 damaged, 14–16 Jan 2015, temperature 13.7–14.5 °C, salinity 20.9–22.2 PSU, dissolved oxygen 7.8–8.0 mg/L; 3 males (L 2.1–2.7 mm), 15 July 2015, temperature 29.1 °C, salinity 29.7 PSU, dissolved oxygen 5.4 mg/L; 1 male (L 2.6 mm), 1 non-ovigerous female (L 2.3 mm), 15 Oct 2015, temperature 25.8 °C, salinity 5.6 PSU, dissolved oxygen 6.2 mg/L; 2 males (L 2.2 mm, 1 damaged), 2 ovigerous females (L 3.5 mm, 1 damaged), 1 non-ovigerous female (L 2.1), 12 July 2016, temperature 32.3 °C, salinity 24.3 PSU, dissolved oxygen 5.5 mg/L. **Port St. John, Florida:** 1 non-ovigerous female (L 3.2 mm), 21 Mar 2018, temperature 21.4 °C, salinity 26.2 PSU, dissolved oxygen 7.8 mg/L; 1 male (L 2.2 mm), 1 ovigerous female (L 2.8 mm), 1 non-ovigerous female (L 2.5 mm), 4 Apr 2018, temperature 25.7 °C, salinity 26.4 PSU, dissolved oxygen 6.4 mg/L; 1 male (L 1.9 mm), 4 June 2018, temperature 29.6 °C, salinity 23.2 PSU, dissolved oxygen 5.1 mg/L. **Fort Lauderdale, Florida:** 1 non-ovigerous female (L 2.6 mm), 23 Nov. 2015, temperature 26.5 °C, salinity 2.8 PSU, dissolved oxygen 5.3 mg/L; 1 ovigerous female (L 3.4 mm), 2 non-ovigerous females (L 2.1, 2.6 mm), 29 Mar 2016, temperature 26.9 °C, salinity 1.0 PSU, dissolved oxygen 4.9 mg/L; 2 males (L 2.5, 2.6 mm), 2 non-ovigerous females (L 2.5, 3.3 mm), 7 Apr 2017, temperature 31.2 °C, salinity 0.5 PSU, dissolved oxygen 4.5 mg/L. **Freeport, Texas:** Water quality data not available, 2 males (L 2.1mm, 1 damaged), 21 Oct 2016; 1 non-ovigerous female (L 3.0 mm), 13 July 2017; 1 non-ovigerous female (L 3.2 mm), 20 Nov 2017.

Redescription: General body form: (Fig. 2A) moderately slender; length of adult males 2.6–4.5 mm; adult females 2.8–3.8 mm. Note: In the redescription and associated comments, the citations for Bowman & Orsi (1992) and Panampunnayil & Biju (2007) are abbreviated as B & O and P & B, respectively.

Carapace: Anterior margin produced into a short, rounded rostrum; posterodorsal margin emarginated, exposing thoracic somite 8, and at times 7 (Fig. 2A) (see B & O, Figs. 2A, B; P & B, Figs. 2A, B).

Comment: P & B described the posterodorsal margin of the carapace as "leaving last three thoracic somites dorsally exposed." Somite 6 was never exposed in the material that we examined. Based on the authors' experience and personal observations, this difference may have been due to the process of preservation, osmotic postmortem swelling, or some other artifact in the process of specimen collection.

Antennular peduncle: Generally as described and illustrated by B & O (Fig. 2D, E) and P & B (Figs. 2A–E).

Comment: There was, however, a difference in the interpretation by B & O of the presence of a "male lobe." They described article 3 of the male as having a tuft of setae on the distoventral surface, but lacking a lobe. The material that we examined, including the paratypes of *D. holmquistae*, agreed with that of P & B (Fig. 2C, D) in having a reduced, rounded, sometimes indistinct, setiferous lobe on the ventral surface.

Antenna: Both sexes with scale having length 2.5–3.6 times greatest width, apex with transverse suture (faint at times) separating short distal article, 0.10–0.14 times scale length; antennal peduncle subequal to slightly longer than scale, article 2 0.75–1.20 times length of article 3.
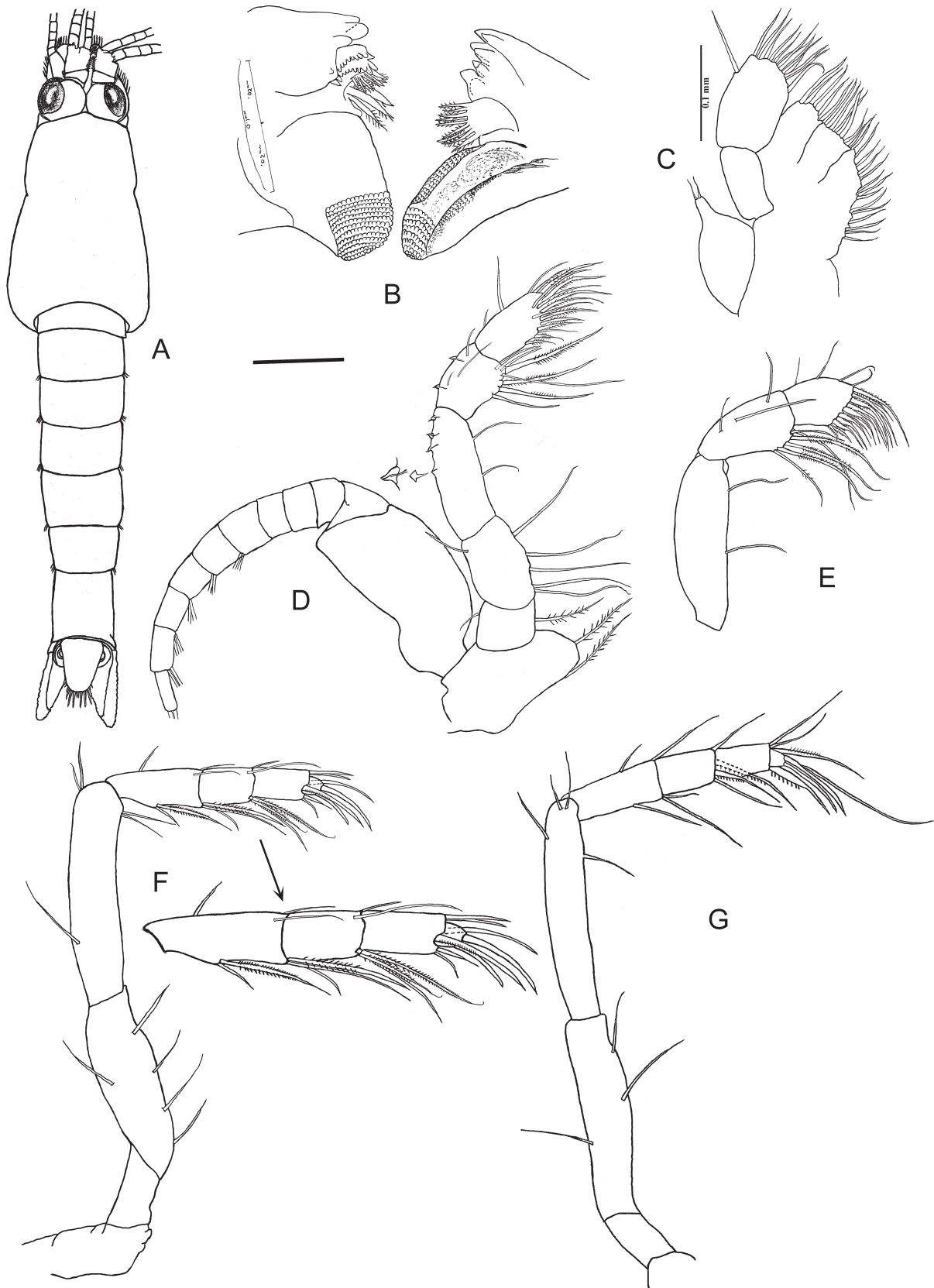
FIGURE 2. *Deltamysis holmquistae* female, 3.5 mm (A, E, G); female, damaged (B & C), male, 2.9mm (D, F); Jacksonville, Florida. A. Dorsal view. B. Mandibles, gnathobasic processes, posterior (caudal) view. C. Maxilla, coxal endite omitted. D. Thoracopod 2, male with enlargement of papillation. E. Thoracic endopod 2, distal end, female. F. Thoracic endopod 3 with enlargement of distal end. G. Thoracic endopod 4. Scale: A, 0.5 mm; B, 0.15; C-G, 0.1.

Comment: P & B reported the antennal scale with no distal suture, the antennal peduncle much longer than the antennal scale, and articles 2 and 3 of the peduncle as being subequal (P & B, Figs. 2F, G). In contrast, we, as well as, B & O (Fig. 2G), found distal sutures on all specimens examined, and noted greater variation in the latter two characteristics than reported by P & B (see Table 1).

Eye: (Fig. 2A) as described and illustrated by B & O (Fig. 2A) and P &B (Figs. 2A, B).

Comment: We found little variation in the corneal eyestalk width to eyestalk width ratio (0.70–0.96), which is only a marginally wider range than values reported previously.

Mandible: Left mandible (Fig. 2B, Fig. 5B, D, & F): incisor and lacinia mobilis with 3–4 teeth; spine row with 8–9 serrated spines; well-developed molar process. Right mandible (Fig. 2B, Fig. 5A, C, & E): incisor with 4 teeth; lacinia mobilis somewhat rectangular with a series of 7–8 tubercles on the long sides and a pair of acute teeth at either end; spine row with 3 large and 8–9 smaller, more slender serrated spines; well-developed molar process. Mandibular palp (Fig. 4F & G): 3-articulated; article 1 small, article 2 expanded medially, length 2.1–2.9 times greatest width, about twice as long as article 3, with 3 simple setae on medial margin, 1 short proximolateral simple seta and 1 long simple seta on distolateral margin, 3 setae on distal margin; article 3 with 1 long, strong pennate seta at apex and a series of shorter pennate setae along distomedial margin.
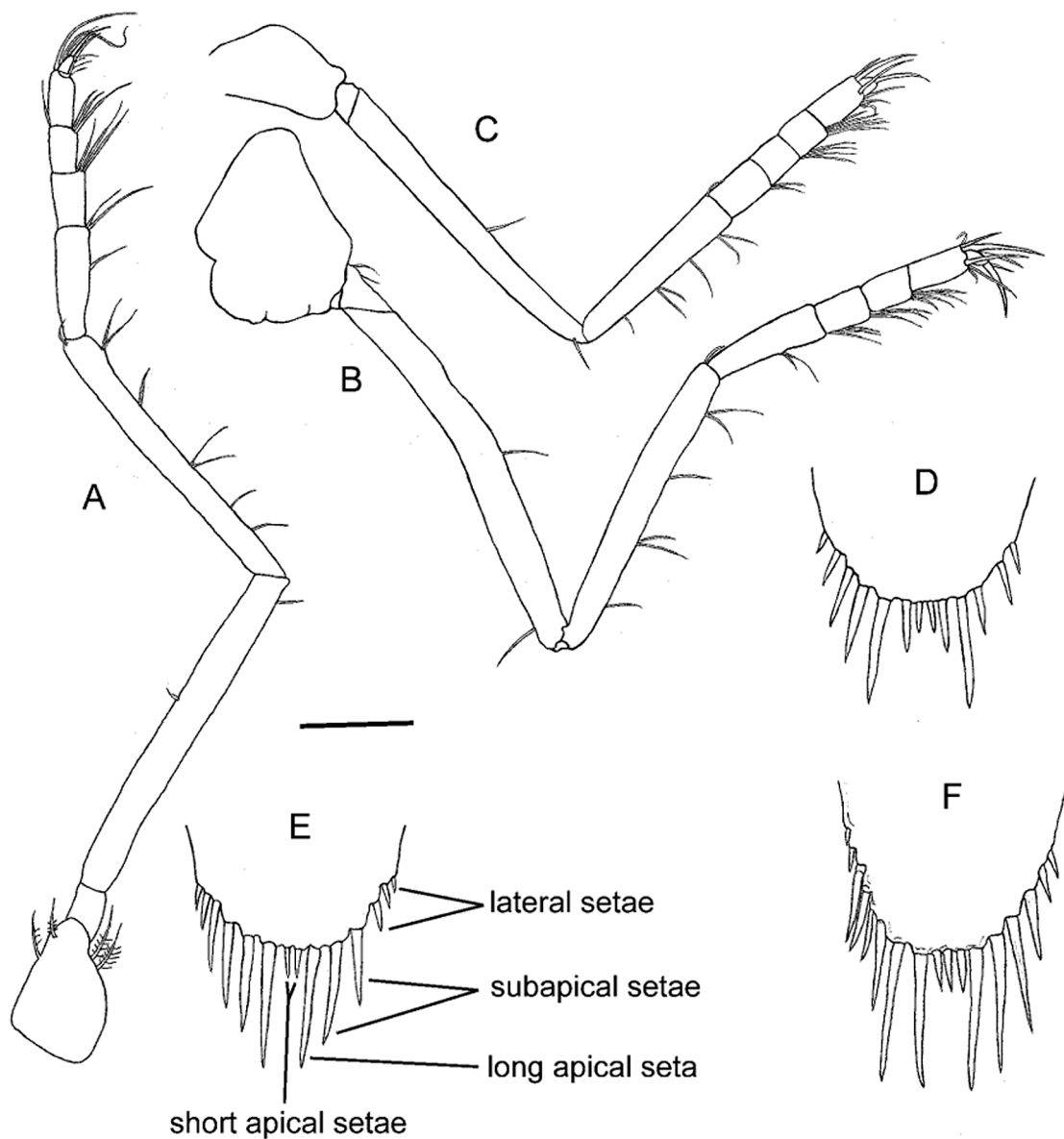

FIGURE 3. *Deltamysis holmquistae* male, B & D (2.9 mm); Jacksonville, Florida, females, A & E (3.0 mm), C (2.3 mm); Jacksonville, Florida; F (3.2 mm); Port St. John, Florida. A. Thoracic endopod 5. B. Thoracic endopod 6. C. Thoracic endopod 7. Telsons, posterior ends D–F. Scale: A–F, 0.1 mm.
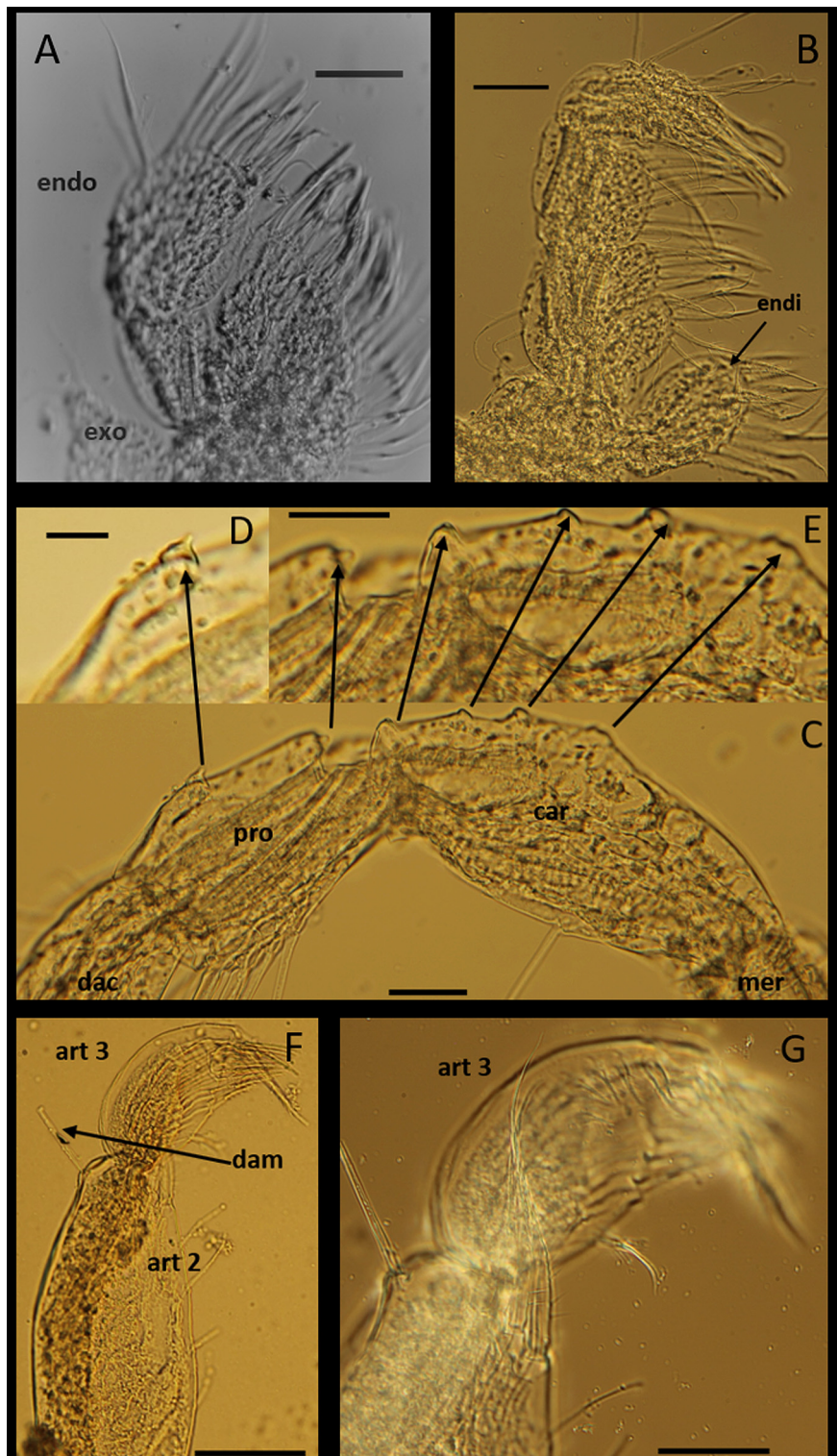
FIGURE 4. Photomicrographs of *Deltamysis holmquistae* appendages. Length of scale bar is given in parentheses for each photo. A) Maxilla (0.05 mm); B) thoracic endopod 1 (0.05); C, D, & E) male thoracic endopod 2 (0.05, 0.01, & 0.02); F & G) mandibular palps (0.05 & 0.03). Abbreviations: car, carpus; dac, dactylus; endi, endite; endo, endopod; exo, exopod; mer, merus; pro, propodus; dam, damaged seta; art, article.

Comment: B & O reported the absence of a lacinia mobilis on the right mandible. For the paratype and northwest Atlantic material, we found this structure on both mandibles as did P & B (Fig. 3B). More variation was recorded in the spination of the spine row of our material (right, 11–12 spines: left, 8–9 spines) as compared to either B & O (8, 8) or P & B (3, 4). The length: width ratio of article 2 of the mandibular palp of our material showed more

variation than the single illustration of P & B (2.1–2.9 vs. 2.4, Fig. 3A); however, these ratios were much less than the ratio (3.4) illustrated by B & O (Fig. 2 H) that depicted a rather narrow article 2. In addition, the setal (or setation) variation of article 2 of our material was greater than that found in either original description.

Labrum: As described and illustrated by P & B (Fig. 3C); middle half of bilobed posterior margin with cluster of short fine setae on one side of emargination and short coarse setae on the other.

Maxillule: Outer lobe apex with 9–10 stout spiniform setae and three subterminal simple (smooth) setae; inner lobe with 3 long plumose setae and 7–9 simple setae (B & O, Fig. 2J; P & B, Fig. 3D).

Maxilla **(Fig. 2C, 4A):** Sympod and sympodal endites as described and illustrated by B & O (Fig. 3A) and P & B (Fig. 3E); endopod 2-articulated, proximal article 0.44–0.75 times as long as oval distal article; exopod with 2–5 setae on apex and outer margin, extending beyond proximal margin of article 1 of endopod (P & B, Fig. 3E).

Comments: The endopod and exopod of the paratype and western Atlantic material exhibited more variation than the descriptions and illustrations of P & B or B & O, but more closely resembled the former. The ratio of endopod lengths of article 1: article 2 was 0.44–0.75 for all material except for those of B & O (<0.25). B & O also reported the exopod not reaching the proximal margin of article 1 of the endopod, whereas it exceeded the margin for all other material. The authors may have misinterpreted the placement of the proximal margin of article 1, thus accounting for these differences.

Thoracic endopods: Endopods generally increasing in length posteriorly, with 6th the longest.

Thoracic endopod 1 (Fig. 4B): As described and illustrated by B & O (Fig. 3B) and P & B (Fig. 3F).

Thoracic endopod 2 (Figs. 2D, E, 4C, D, & E): Ischium 0.5–0.6 times length of merus, medial margin with 1 plumose seta; merus 0.7–0.8 times length of carpus, median margin with 3–6 simple or sparsely plumose setae. Carpus subequal in length to combined lengths of propodus and dactylus, medial margin with 2 simple setae; male having 4 papillations along lateral margin; female lacking papillations on lateral margin. Propodus with 4–7 simple setae and serrate setae furnished with bilateral series of spine-like setules along distomedial margin; females with 3 simple setae and no papillations on lateral margin; males with 3 simple seta and 2 papillations along lateral margin; dactylus with 13–16 bilaterally serrate and simple setae on distal and distomedial margin, claw absent.

Comments: The paratypes of *D. holmquistae* and the western Atlantic material examined most closely resembled the Indian material (Figs. 3G, H). Males in all three collections have papillations ("notches" of P & B) on the carpus and propodus; all females examined lack these papillate structures. B & O did not describe or illustrate thoracic endopod 2 of males. Either they did not examine the second thoracic endopods of the males in detail or failed to note the exclusive occurrence of these structures in only males.

Thoracic endopod 3 (Fig. 2F): ischium about 2 times length of preischium, medial margin with 4–6 simple setae, lateral margin with 1 simple seta; merus slightly longer than ischium and subequal to 3-articulated carpopropodus, distomedial margin with 2 simple setae, lateral margin with 1 simple seta on proximal half and two simple setae near distolateral margin; carpopropodus proximal article 1.4–1.5 times length of articles 2 and 3, respectively, medial margin with one bilaterally serrate seta and one simple setae at midpoint and another bilaterally serrate seta and two simple setae on distomedial corner, three simple setae on lateral margin; distomedial margin of article 2 with two bilaterally serrate setae and two simple setae (one not shown on Fig. 2F), distolateral margin with one short and one long simple seta; distal margin of article 3 surrounded by simple setae and one spiniform seta with a unilateral row of thin setules proximally; dactylus with 2 simple setae on apex.

Comments: The illustration of P & B (Fig. 4A) differs from the paratype and western Atlantic material in the arrangement of the serrated setae on articles 1 and 2 of the carpopropodus, the lack of a serrated seta on article 3, and the setation (plumose vs. simple) of the medial margin of the ischium.

Thoracic endopod 4 (Fig. 2G): Ischium about 3 times length of preischium, medial margin with 2–5 simple setae, lateral margin with 1 simple seta; merus 0.9–1.2 times as long as ischium and subequal to 3-articulated carpopropodus, distomedial and distolateral margins with 1 simple seta each, distal margin with 2 simple setae; carpopropodus proximal article 1.8–2.2 times length of articles 2 and 3, respectively, medial and lateral margins with simple setae only; distomedial margin of article 2 with two bilaterally serrate setae and 1–2 simple setae, distolateral margin with one simple seta; distal margin of article 3 surrounded by simple setae and two spiniform setae with unilateral rows of setules proximally; dactylus with 2 simple setae on apex.

Comment: The serrate setae on the carpopropodus occurred on all material that we examined, but were not described or illustrated by B & O or P & B.
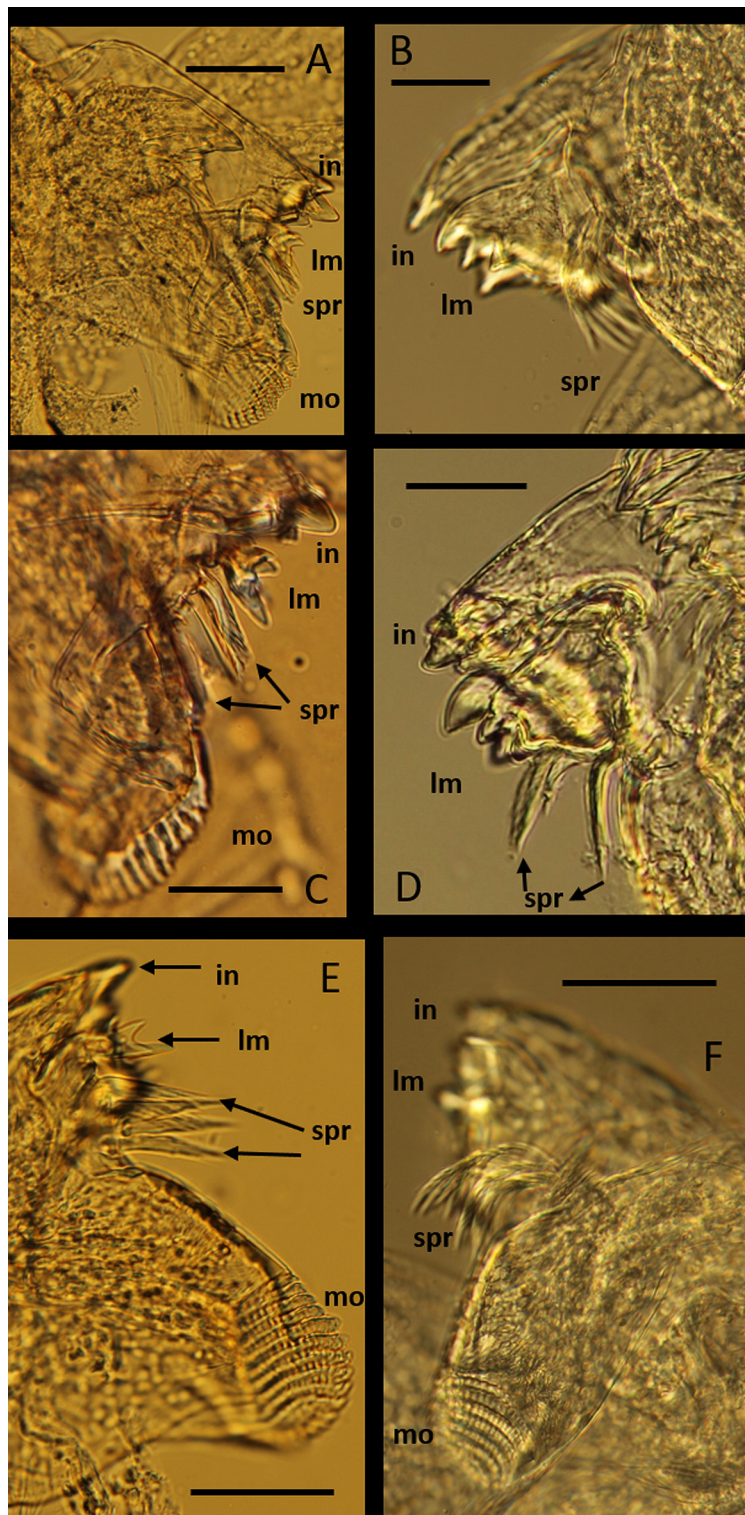
FIGURE 5. Photomicrographs of *Deltamysis holmquistae* appendages. Length of scale bar is given in parentheses for each photo. A) right mandible (0.07 mm); B) left mandible (0.05); C) right mandible (0.05); D) left mandible (0.04); E) right mandible (0.05); and F) left mandible (0.05). Abbreviations: in, incisor; lm, lacinia mobilis; mo, molar; spr, spine row.

Thoracic endopods 5–6 (Figs. 3A, B)**:** Ischium 1.0–1.3 times length of merus, distomedial margin with 1 simple seta, lateral margin with 1 simple seta on distal half; merus 1.1–1.3 times length of carpopropodus, medial margin with 6–8 simple setae along border, distolateral margin with 1 simple seta; carpopropodus 4-articulated, articles 2–4 subequal, each 0.4–0.6 times as long as proximal article, distomedial margin of each article with 2–5 simple setae; dactylus surrounded by simple setae, armed with moderately robust claw (see P & B, Fig. 4C).

TABLE 1. Comparison of diagnostic morphological characters of mature *Deltamysis holmquistae*.

Characters	*D. holmquistae* Bowman & Orsi, 1992	*K. pillaii* Panampunnayil & Biju, 2007	*D. holmquistae* paratypes; present study	*D. holmquistae*, NW Atlantic; present study
Anterior margin of carapace	Short, rounded	Broadly triangular	Short, rounded	Short, rounded
Cornea W/eyestalk W**	0.9*; Fig. 2 A	0.75–0.88*; Fig. 2 A, B	0.84–0.96	0.7–0.9
A 1 setiferous male lobe	Lobe not developed	Small setose lobe developed	Most males with small setose lobe developed	Most males with small setose lobe developed
A 2 scale distal suture	Suture present	Suture absent	Suture present	Suture present
A 2 scale: L***/W	~3.0	3.2*–3.5; Fig. 2 F, G	2.5–3.6	2.5–3.6
A 2 peduncle L: A 2 scale L	~ 1.10* Fig. 2 G	1.18–1.24 Figs.2 F, G	1.10–1.25	1.17–1.44
A 2 peduncle: article 2 L/article 3 L	~0.75–0.78*; Fig. 2 G	0.96–1.02; Figs, 2 F, G	0.80–1.01	0.8–1.2
Mandibular palp, article 2: L/W	3.4*; Fig. 2 H	2.4*; Fig. 3A	2.10–2.75	2.1–2.9
Lacinia mobilis	Right: absent Left: present	Right: present Left: present	Right: present Left: present	Right: present Left: present
Mandible spine row: no. spines	Right: 8 spines Left: 8 spines	Right: 3 spines Left: 4 spines	Right: 11–12 spines Left: 8–9 spines	Right: 11–12 spines Left: 8–9 spines
Mx 2 endopod: article 1 L/ article 2 L	<0.25	0.9*; Fig. 3E	0.44–0.75	0.5–0.7
Male thoracic endopod 2 with papillations	No mention of papillations	Papillations on carpus and propodus	Papillations on carpus and propodus	Papillations on carpus and propodus
Thoracic endopod 3 serrated setation	No mention of setation on carpopropodus	Carpopropodus with 4 serrated setae on articles 1 and 2; Fig. 4 A*	Carpopropodus with 5 serrated setae on articles 1–3	Carpopropodus with 5 serrated setae on articles 1–3
Thoracic endopod 4 serrated setation	No mention of setation	No mention of setation	Carpopropodus with 4 serrated setae on articles 2 and 3	Carpopropodus with 4 serrated setae on articles 2 and 3
Carapace: postero-dorsal margin	Thoracic somite 8 exposed	Thoracic somites 6–8 exposed	Thoracic somite 8 exposed; somite 7 may be partially exposed	Thoracic somite 8 exposed; somite 7 may be partially exposed
Penis L/W	~5.0	~4.4*; Fig.4D	5.5–7.0	5.8–6.5
Anterior reach of penis	"Slightly beyond basis of pereopod 7" (thoracopod 8); Fig. 3 F	No mention	To base of thoracic leg 5	To base of thoracic legs 4–5
Telson:				
Abdominal somite 6 L/telson L	No mention	Telson "longer than last abdominal segment"	0.95–1.10	1.0–1.2
L/W	1.2	~1.1*; Fig. 5 H	1.1–.3	1.1–1.3

....Continued next page

TABLE 1 (Continued)

Characters	*D. holmquistae* Bowman & Orsi, 1992	*K. pillaii* Panampunnayil & Biju, 2007	*D. holmquistae* paratypes; present study	*D. holmquistae*, NW Atlantic; present study
Lateral telson setae (apical setae included)	posterior 0.3*; Fig.2 C; 14–16	posterior 0.25-0.33; Fig.5H; 16	posterior 0.25–0.37; 14–16	posterior 0.25–0.32; 12–17
No. of posterior setae- short apical: long apical: subapical: lateral setae	2:2:4:6–8	2:2:4:8	2:2:4:6–8	2-3:2:4:4–8
Short apical setal L: long apical setal L	0.3–0.4; Fig. 2C	0.36–0.38; Fig. 5 H, I	0.25–0.40	0.25–0.38
Long apical setal L: telson L	0.2*; Fig. 2 C	0.35–0.40*; Fig. 5 F, H	0.2–0.3	0.3–0.4
Long apical setal L: more posterior subapical setal L	1.10–1.15*; Fig. Fig 2C	1.25–1.40*; Fig. 5 H, I	0.90–1.25	1.0–1.2
Long apical setal L: more anterior subapical setal L	1.4–1.6*; Fig. 2C	1.4–1.7*; Fig. 5 H, I	1.20–1.55	1.2–1.4

* Information from illustrations only; W** width; L*** length

Thoracic endopods 7–8 (Fig. 3C)**:** Ischium 1.4–1.6 times length of merus, distomedial margin with 1 simple seta, lateral margin with 1 simple seta on distal half; merus 1.1–1.2 times length of carpopropodus, medial margin with 6–8 simple setae along border, distolateral margin with 1 simple seta; carpopropodus 4-articulated, endopod 7, articles 2 and 3 subequal, articles 1 and 4 subequal, 2 and 3 each 0.6–0.7 times as long as 1 or 4; endopod 8, articles 2–4 subequal, each 0.5–0.7 times as long as proximal article; dactylus surrounded by simple setae, armed with moderately robust claw (see B & O, Fig.3E; P & B, Fig. 4D).

Thoracic exopods (Fig. 2D)**:** Flagella of exopod 1 with 8 articles, flagella of exopods 2–8 with 9 articles.

Marsupium: Females with pairs of fully developed oöstegites on bases of the medial margins of thoracopods 7 and 8, respectively, pair of small, linguiform oöstegites on thoracopod 6; all oöstegites with sparse plumose setae on ventral and anterior borders.

Penes: Cylindrical, moderate size, stiff with smooth cuticle; 4.4–7.0 times longer than greatest width; extending forward to bases of thoracopods 4–5.

Comment: The length: width ratio of the penis for our material was greater and more variable (5.5–7.0) than reported by B & O (~5.0; Fig. 3F) or illustrated by P & B (4.4; Fig. 4D). In addition, the penes extended anteriorly to thoracopod 4–5 for our specimens, but only slightly anterior to thoracopod 8 for B & O's material.

Pleopods: As described and illustrated by B & O (Fig. 4) and P & B (Fig. 5A–E).

Uropods: As described and illustrated by B & O (Fig. 2C) and P & B (Fig. 5F, G).

Telson (Fig. 3D–F)**:** Entire; length 0.95–1.20 times length of abdominal somite 6; 1.0–1.3 times as long as maximum (basal) width; lateral and apical margins armed along posterior 0.25–0.37 length with 12–17 spiniform setae; posterior end truncate or broadly rounded with two pairs of apical setae, inner short setae (2, rarely 3) 0.25–0.40 length of adjacent longer setae, which are 0.2–0.4 times telson length; longer apical setae 0.9–1.7 times lengths of adjacent two pairs of subapical setae which are usually followed by 3–4 pairs of lateral setae that decrease in length anteriorly (see B & O, Fig. 2C; P & B, Fig. 5 F, H, I).

Comment: P & B state that differences exist between *D. holmquistae* and *K. pillaii* in reference to the ratios of short and long apical setal lengths of the telson. An examination of the two original descriptions (text and illustrations), *D. holmquistae* paratypes, and northwest Atlantic material shows greater variation of this character than reported previously and considerable overlap among the four sources (Table 1).

Concluding Remarks:

To briefly reiterate, Panampunnayil & Biju (2007) state that although *Kochimysis* and *Deltamysis* are closely related, the former genus could be distinguished from the latter by a number of characters involving the morphology of the eyes, antennule, antenna, mandibles, maxilla, thoracic endopod 2, and telson. Our research of the paratypes of *Deltamysis*, northwest Atlantic material, and the two original descriptions revealed that many of these "differences" were due to errors or omissions made in the original descriptions. An examination of other characters (e.g., eyes, antenna, telson, etc.) showed greater variation than previously reported and overlap among the specimen sources (see Redescription and Table 2). The result of the taxonomic data presented above, lead us to emending the diagnosis of *Deltamysis*, the redescription of *D. holmquistae*, and to the conclusion that it is a senior synonym of *Kochimysis pillai*.

Discussion

Forty-one years have elapsed since *D. holmquistae* was first collected in the eastern Pacific coastal waters of California in 1977 (Bowman & Orsi 1992). At present, records for this euryhaline species are confined to the Northern Hemisphere regions of the eastern Pacific, Indian (as *Kochimysis pillaii*), and northwest Atlantic Oceans as reported herein.

Based on our comparisons of type and collected specimens, we consider the monotypic genera *Deltamysis* and *Kochimysis,* and their nominal species as synonyms that represent a single, variable species. Notwithstanding, there remains a possibility that *D. holmquistae sensu lato* could represent two or more very similar cryptic species. DNA analyses of specimens from various disjunct Pacific and Atlantic locations, and especially those from a currently-unknown, endemic parent population, are necessary to determine definitively whether *D. holmquistae* as defined herein represents a single species. Genetic work may also shed light on whether Atlantic populations originate from the California population or a presumed endemic parent population.

The geographical origin of *D. holmquistae* remains uncertain. The new records for *D. holmquistae* from the Florida and Texas coastal waters represent the third occurrence of an invasive mysid species in eastern North America. The first, *Praunus flexuosus* (Müller, 1776), is endemic to European waters (see Wigley 1963; Ruiz *et al*. 2011), and now is present along the Northeast US coast. The second, *Hemimysis anomala* Sars, 1907*,* from the Ponto–Caspian Region, has invaded the Great Lakes–St. Lawrence ecosystem and surrounding inland lakes (Sinclair *et al*. 2016). But the original discovery location of *D. holmquistae* suggests its native range is likely Asia as hinted by Bowman & Orsi (1992). Three other confirmed exotic marine mysids found in the brackish Sacramento–San Joaquin Estuary or San Francisco Bay downstream hailed from Asia. *Hyperacanthomysis longirostris* (Ii, 1936) and *Orientomysis aspera* (Ii, 1964), both discovered in the Sacramento–San Joaquin Estuary in 1997, are endemic to the coasts of Japan, China, and Korea (Modlin & Orsi 1997). *Orientomysis hwanhaiensis* (Ii, 1964), which was reported from the San Francisco Estuary, originates from Chinese and Korean waters (see Modlin & Orsi 2000). A fourth Asian mysid, *Neomysis japonica* Nakazawa, 1910, also may be present in the San Francisco Estuary, but its identity has yet to be confirmed (Mecum 2006; Modlin 2007; Price 2016). The co-occurrence of *D. holmquistae* with Asian mysids in California in 1977 (Bowman & Orsi 1992) and its discovery only as early as 2014 in the well-studied northwest Atlantic (see Material Examined) is evidence that this species is not endemic to North America.

Estuarine species with disjunct populations suddenly appearing near ports suggests that a species spreads due to maritime commerce (Seebens *et al*. 2013). There is a remote possibility that a benthic mysid such as *D. holmquistae* could have gone undetected due to sampling bias; however, both regions of the US West and East Coasts where this species has been collected have been subject to earlier studies on mysids (Stuck *et al*. 1979a, b; Price 1982; Bowman & Orsi 1992; Heard *et al*. 2006; Price & Heard 2009; M. Scripter, W. Price & R. Heard, per. observ. since 1975). Further, the possibility of it being introduced into Indian waters in the state of Kerala is supported by its absence in several earlier surveys and publications on the mysids from this coastal region prior to the 2007 report of Panampunnayil & Biju (see Pillai 1965; 1973). The sudden appearance of *D. holmquistae* in California, India, Florida, and Texas coastal waters is almost certainly due to a hypothesized maritime commerce-driven range extension from ports where *D. holmquistae* occurs and its subsequent colonization of new ports via ballast water discharge (Seebens *et al*. 2013). Freeport is an industrial port in the Northwest Gulf of Mexico and Jacksonville is a major port in North-

east Florida. In southeast Florida, the Fort Lauderdale sampling site is part of the canal system feeding into Port Everglades, a major shipping port, and the Port St. John collection site in the Indian River Lagoon is just northwest of Port Canaveral. Presumably, the Panama Canal would serve as either a transmission route or nearest brackish-water source population for *D. holmquistae* discovered in the northwest Atlantic, if the direct parent population of the Atlantic *D. holmquistae* populations are from the eastern Pacific.

The known range of *D. holmquistae* along the northwest Atlantic coast is currently restricted to the four sites reported herein. Between 2014 and 2018, however, one of us (MJS) was responsible for the taxonomic work from similar plankton and benthic surveys conducted at 12 additional sites along the Gulf of Mexico and Atlantic coasts of North America. Comparable plankton sampling occurred in Corpus Christi Bay (2016–2018), the lower Missis-sippi River (2 sites, 2016–2018), the Caloosahatchee River estuary on the west coast of Florida (2017–2018), Port Everglades (2017–2018), the Port of West Palm Beach (2016–2017), the nearshore ocean waters near Stuart, FL (2017–2018), and the James River estuary in Virginia (2017–2018). Comparable benthic Ponar grab sampling took place at the Indian River Lagoon at Vero Beach, Florida (2016), 2 rivers draining into the Mobile Bay, Alabama estuary (2017), and a harbor in Milford, Connecticut (2017). To date, however, *D. holmquistae* has only been rec-ognized from the four sites reported herein.

A total of 79 specimens of *D. holmquistae* occurred at four sites—Jacksonville, Ft. Lauderdale, and Port St. John, FL, and Freeport, TX. Most (62) were incidental captures at Jacksonville during a benthic macroinvertebrate sampling program. *Deltamysis holmquistae* was collected in 17 of 144 Ponar grab samples taken there and repre-sented the only mysid species captured during the study. Other mysid species common in the Jacksonville region of the St. Johns River estuary are *Neomysis americana* (Smith, 1873) *Americamysis bahia* (Molenock, 1969), and *A. almyra* (Bowman, 1964). At Freeport, TX, only 4 *D. holmquistae* were collected from 66 plankton collections that captured 7760 other mysids. The Freeport native mysid community was comprised of *Metamysidopsis swifti* Băcescu, 1969, *Americamysis alleni* Price, Heard & Stuck, 1994, *Brasilomysis castroi* Băcescu, 1968, and *Promysis atlantica* Tattersall, 1923. At Fort Lauderdale, FL, 8 *D. holmquistae* were captured by an even larger sampling ef-fort over 2 years in a study in which 5458 mysids were collected representing four native species: *Mysidopsis furca* Bowman (1957), *A. bahia*, *A. almyra*, and *Chlamydopleon dissimile* (Coifmann, 1937). Five *D. holmquistae*, out of 1936 other mysids, were captured in 52 plankton samples in the Port St. John study that yielded only one other my-sid species, *Coifmanniella mexicana* (Tattersall, 1951). In all sampling regimes except Jacksonville, *D. holmquistae* was an extremely rare component of the pelagic mysid assemblage which suggests a habitat preference is driving the observed distribution and abundance patterns.

Deltamysis holmquistae from the Florida sites were collected within the following salinity, temperature, and dissolved oxygen ranges: 0.5–29.7 PSU, 13.7–32.3 °C, and 4.5–8.0 mg/L. Prior to this study, there were few eco-logical field observations of abiotic factors in relation to this species. No information exists concerning dissolved oxygen and there is only one record with respect to temperature. Indian specimens of *D. holmquistae* (= *K. pillaii*) were collected in temperatures ranging from 25.0–32.5 °C in the Kochi backwater along the southwest coast of In-dia (Panampunnayil & Biju 2007; Biju & Panampunnayil 2010). However, the present and previous studies indicate that *D. holmquistae* is a euryhaline species capable of living in a wide range of salinities varying from freshwater to 32.5 PSU (Bowman & Orsi 1992; Mecum 2006; Panampunnayil & Biju 2007; Biju & Panampunnayil 2010). Environmental tolerance and a tendency to occupy niches unoccupied by native mysids may contribute to the docu-mented invasiveness of *D. holmquistae*.

Based on *D. holmquistae* abundance in the Port of Jacksonville collections, the lower St. Johns River and sur-rounding St. Johns estuarine system appears to support a viable, established population of this estuarine invader. Capturing these mysids in a benthic Ponar grab is evidence for an epibenthic habitat preference, which concurs with the habitat preference posited by Bowman & Orsi (1992). Epibenthic mysids are potentially potent transfer agents of benthic nutrients to mobile predators (Jumars, 2007; Rodríguez-Graña *et al.* 2008), and their abundance at the Jacksonville collection stations in the St. Johns River may indicate a positive or even substantial contribution to energy flow in the estuary. Further studies in the lower St. Johns River estuary, including diurnal surface and bottom plankton collections, are needed to estimate the relative abundance and population size of *D. holmquistae* and its co-occurrence with local mysid species. Mysids are important prey for fish (Darnell 1958, Sheridan1979; Holstens & Mees 1999; Waggy *et al.* 2007; Castro *et al.* 2013), and a follow-up ecological impact study in fish species with benthic feeding habits is ongoing in two of the collection regions by the primary author.

Ecological Consequences: The successful colonization by *D. holmquistae* may come at the expense of indige-

nous mysid species. There may be negative competitive interactions if this introduced population of *D. holmquistae* becomes well-established and has an overlapping niche with one or more of the common native epibenthic mysid species, *Americamysis almyra*, *A. bahia*, and *Neomysis americana* (see Heard *et al*. 2006). Feeding selectivity studies and other ecological observations are needed to determine if *D. holmquistae* occupies a similar or different ecological niche (feeding, spatial, temporal) as compared to these co-occurring endemic mysid species. Unfortunately, mysid studies *in situ* are difficult due to collection and observation problems (Mayor *et al*. 2017).

When prevention fails, early detection of invasive species is critical if an attempt to eradicate or prevent the further spread of invasive species is the goal (Ojaveer *et al*. 2018). Routine biological monitoring at ports may be a necessary biosecurity precaution in addition to ballast water control regulations (Wooldridge *et al*. 1999; Lehtiniemi *et al*. 2015). Transparency or a reporting requirement of biological assessment reports performed for regulatory compliance (e.g., at power plants, prior to dredging for port maintenance or expansion, etc.) would speed the recognition of new invasive species. Biological invaders are potentially devastating to local ecosystems and often carry a hefty price tag for control. Global climate change may indeed result in the range expansion of species, but such changes are glacial in comparison to the swift spread of invasive species via anthropogenic travel and shipping.

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