A new species of parasitic copepod (Siphonostomatoida: Lernaeopodidae: Neoalbionella Özdikmen, 2008) infecting the skin of a gulper shark, Centrophorus sp. (Squaliformes: Centrophoridae), in the Gulf of Mexico, with a key to species of Neoalbionella

Carlos F. Ruiz and Stephen A. Bullard
Aquatic Parasitology Laboratory, School of Fisheries, Aquaculture, and Aquatic Sciences, College of Agriculture, Auburn University, 203 Swingle Hall, Auburn, Alabama 36849
Correspondence: S.A. Bullard; e-mail: ash.bullard@auburn.edu
(Received 26 February 2019; accepted 23 May 2019)

ABSTRACT

We describe male and female specimens of a species of Neoalbionella Özdikmen, 2008 (Siphonostomatoida, Lernaeopodidae), Neoalbionella dannytangi sp. nov., infecting the skin of a gulper shark Centrophorus sp. (Centrophoridae) in the northern Gulf of Mexico. Females of the new species most closely resemble those of Neoalbionella globosa (Leigh-Sharp, 1918) but are unique among congeners by having the combination of 1) terminal endopodal segment of antenna with a reduced distal tubercle having a minute protuberance, 2) maxillule with a spinulose lateral palp and praecoxal endite, 3) maxilla with a swollen tip nearly parallel with the distal surface of the bulla, and 4) maxilliped with a sub-circular spinulose pad along the proximal myxal margin of the corpus maxillipedis. The male copepod was attached to the tip of a female’s posterior process and was assigned to Neoalbionella by having a cephalosome nearly equal in length to the trunk and tapered caudal rami directed posteroventrally (swollen and directed anterodorsally in males of Lernaeopoda von Nordmann, 1832). It was distinct from those of all other congeners by having 1) an antenna terminal endopodal segment and maxillule similar to that of the female, 2) a maxilla syncoxa with an anteromedial process having seven large, conical denticles, 3) a bifid mediative process approximately as wide as the length of the shortest lobe, and 5) a caudal ramus with a unique configuration and number of setae. This is the second report of a species of Neoalbionella from the Gulf of Mexico and the third nominal species of Neoalbionella reported from gulper sharks (Centrophorus spp.). We also provide keys to females and males of Neoalbionella.

Key Words: deep water, dichotomy, ectoparasites, elasmobranchs, morphology, taxonomy

INTRODUCTION

The Lernaeopodidae H. Milne-Edwards, 1840 (Copepoda, Siphonostomatoida) comprises 48 genera (41 marine; seven freshwater) of ectoparasitic copepods, 20 of which infect epidermal sites of elasmobranch, holocephalan, and teleost hosts in North America (Wilson, 1915; Kabata & Bowman, 1961; Hoffman, 1999; Boxshall & Halsey, 2004). Species of Acespadia Leigh-Sharp, 1933 (monotypic), Briandella Wilson, 1915 (monotypic; Dippenaar et al., 2004), Charopinus Krøyer, 1864 (three species; Kabata, 1979), Dentritapta Kabata, 1964 (two subspecies; Dippenaar et al., 2004), Lernaeopoda de Blainville, 1822 (ca. eight species; this genus requires revision and at least two species require redescriptions; Kabata, 1979), Lernaeopodina Wilson, 1915 (four species; Kabata, 2004), Neoalbionella Özdikmen, 2008 (eight species; Ruiz et al., 2019), Omnatoxoa Leigh-Sharp, 1926 (monotypic), and Pseudocharopinus Kabata, 1964 (11 species; Dippenaar, 2012) infect elasmobranchs only (Boxshall & Halsey, 2004). Members of Schistobrachia Kabata, 1964 (six species Dippenaar et al., 2004; Dippenaar, 2016) infect both elasmobranchs and holocephalans; species of Vanbenedenia Malm, 1860 (four species (Wilson, 1915;
Ruiz and dissected while submersed in lactic acid (Benz acid. Specimens were stained with a pinch of lignin pink for 4 h and lactic acid, with lactic acid added periodically to replenish
Wild M5A stereo-dissecting microscope (Wild Heerbrugg, Gais, and preserved in 95% ethanol (EtOH). The habitus of the holo-
were removed from the dorsal fin of an infected gulper shark
species.

ruiz et al. (2019) summarized host and locality records for each of the eight nominal species of Neoolithonella and described a new species, N. benzipirata ruiz et al. (2019) (on skin of gulper shark, Centrophorus granulosus (Bloch & Schneider, 1801) (Centrophoridae). The report of ruiz et al. (2019) gave the first account of a speci-
ies of Neoolithonella from the Gulf of Mexico. They also reported morphological features that differentiated the female and male of N. benzipirata from morphologically similar congeners in the Atlantic and Pacific oceans, described features seldom used to dif-
ferentiate species, and discussed characters shared between con-
specific females and males of Neoolithonella. We herein describe the ninth species of Neoolithonella, this one infecting a species of
Centrophorus Müller & Heule, 1837 (Neoselachii, Squaliformes, Centrotdoridae).

MATERIALS AND METHODS

Gulper sharks (N = 40; ≤ ca. 143 cm total length) were captured using a bottom-longline off Fort Morgan, Alabama, USA, northern Gulf of Mexico (30°00′3.24″N, 87°58′48.60″W) (depth ca. 400–600 m) in August 2016. Sharks were measured, photographed, and opportunistically examined for external parasites before being tagged and released alive. The live sharks were field-
identified as Centrophorus sp. by having 1) a spiralike directly post-
to the eye, 2) five gill slits anterior to the pectoral fin, 3) two dor-
sal fins each with a grooved spine along the anterior margin (dorsal fin spines approximately equal in length), 4) origin of first dor-
sal fin far anterior to that of the pelvic fin and over the free rear tip of the pectoral fin, and 5) distinctly heterocercal caudal fin with a subterminal notch on its upper lobe as well as by the absence of an anal fin, precaudal pit, and caudal keel (Carpenter, 2002). The lack of taxonomic resolution among gulper sharks (bañón et al., 2008; moura et al., 2008, 2015; white et al., 2013; vérissimo et al., 2014; wienerroither et al., 2015; lieff et al., 2017) and the fact that the sharks did not fit the diagnosis of any named gulper shark prevented a definitive identification. It also is also possible that these gulper sharks comprised a hitherto unnamed species.

Two ovigerous female and one male lernaeopodid copepods were removed from the dorsal fin of an infected gulper shark and preserved in 95% ethanol (EtOH). The habitus of the holotype and that of the allotype was illustrated with the aid of a Wild M5A stereo-dissecting microscope (Wild Heerbrugg, Gais, Switzerland) equipped with a drawing tube. Specimens were cleared by immersing them in a glass dish with 50:50 95% EtOH and lactic acid, with lactic acid added periodically to replenish evaporated EtOH until the resulting solution was 80–100% lactic acid. Specimens were stained with a pinch of lignin pink for 4 h and dissected while submerged in lactic acid (benz et al., 2000; ruiz et al., 2019). Illustrations of appendages were made using the hanging-drop method (humes & gooding, 1964) and with the aid of Leica DM-2500 and Leica DMR compound light micro-
scopes (Leica, Wetzlar, Germany), each with differential interfer-
cence contrast (DIC) optical components and a drawing tube. Measurements are reported in micrometers (μm) unless otherwise noted as a range followed in parentheses by the mean, standard deviation, and number of subjects measured. Single measure-
ment values are of illustrated appendages corresponding to the holotype or allotype. Copepod total length was calculated by adding cephalosome, trunk, and abdomen lengths inclusive of the female’s posterior processes or of the male’s caudal rami (benz & izawa, 1990; hogans & marques, 1994; ruiz et al., 2019).

Specimens of the new species were stored in 70% EtOH and ultimately deposited in the Invertebrate Zoology Collection, National Museum of Natural History’s Smithsonian Institution, USNM 1550564-1550566. CFR processed and approved the manuscript that was revised by the editor-in-chief, and SAB handled the copy-edited manuscript, specimen deposition, and page proofs.


SYSTEMATICS

Order Siphonostomatoida Thorell, 1859
Family Lernaeopodidae Milne Edwards, 1840
Neoolithonella Özdikmen, 2008

Neoolithonella dannytangi sp. nov. (Figs. 1–5)

Type material: Holotype (10.3 mm), USNM 1550564 (partly dis-
sected); sinistral maxilliped, dextral antenna, and dextral maxillule left on cephalosome); paratype female (11.4 mm), USNM 1550565 (dissected); allotype (2.9 mm), USNM 1550566 (dissected).

Type and only known locality: Northern Gulf of Mexico, 25 km south of Fort Morgan, AL, USA (30°00′3.24″N, 87°58′48.60″W), 2 August 2016.

Type host: Centrophorus sp. (Squaliformes, Centrophoridae).

Site of infection: Dorsal fin.

Intensity of infection: 2 females, 1 male (male attached to posterior process of holotype female) specimens of the new species infected a single gulper shark.

Etymology: The specific epithet honors Dr. Danny Tang (Orange County Sanitation District, Fountain Valley, California) for his contributions to our knowledge of parasitic as well as free-living copepods.

Diagnosis: Female body having lernaeopodid habitus, with cephalosome (inclusive of antennules, antennae, buccal apparatus, maxillules, maxillae, maxillipeds) plus trunk (neck, genital trunk), short abdomen (anal somite issuing posterior processes); maxillule having lateral palp with 3 apical setae; maxilliped with subchela claw having accessory denticle.

Male with cephalosome bearing appendages as in female, with distinct trunk plus genital area plus abdomen issuing caudal rami; maxillule having lateral palp with 3 apical setae; caudal rami tapered, not inflated, directed posterocentrally.

Description of adult female: Body 10.3–11.4 mm (10.8 ± 0.7 mm; N = 2) long (Figs. 1A–31).

Cephalosome declining ventrally approximately 90−135° (paratype, holotype, respectively) relative to trunk axis, shorter than trunk, slightly longer than broad, 2.6–2.8 mm (2.7 ± 0.2 mm, N = 2) long, 2.2−2.4 mm (2.3 ± 0.2 mm; N = 2) in maximum width, broadly rounded posteriorly, dorsoventrally flattened (Figs. 1A; 2A; 3A), demarcated from trunk by short neck (Figs. 2A, 3A), having en-face groove accommodating retracted antennules, antennae, with outline of dorsal cephalic shield in dorsal, lateral views (Fig. 2A, B); dorsocephalic shield having pores (presence of sensilla; see ruiz et al., 2019) could not be confirmed without SEM); dorsocephalic pores minute, not observable without
A bar. Paratype female USNM 1550565. Ventral view of habitus (Fig. 1). Lernaeopodidae) from the skin of Centrophorus sp. (Squaliformes, Centrophoridae) in the northern Gulf of Mexico. Scale values aside each bar. Paratype female USNM 1550565. Ventral view of habitus (A).

Antennule anteromedial to antenna, 4-segmented (Fig. 3B); basal segment slightly swollen distally; second segment with whip (47 μm long) distomedially; third segment with solus (4 μm long, approximately 8.5% whip length) distomedially; terminal segment with 6 setae including tubercle 1 (8–10 μm (9.0 ± 1.4 μm; N = 2) long), tubercle 3 (15–15 μm (14.0 ± 1.4 μm; N = 2) long), digitiform seta 4 (35–39 μm (37.0 ± 2.8 μm; N = 2) long), complex 5 with 2 subequal setae (24–25 μm (24.5 ± 0.7 μm; N = 2) and 22–27 μm (16.5 ± 0.7 μm; N = 2) long), and flagelliform seta 6 (35–38 μm (39.0 ± 1.4 μm; N = 2) long) (Fig. 3C, D).

Antenna posterolateral to antennule, comprised of sympod, exopod, endopod (Fig. 3E); sympod naked; exopod somewhat spatulate, 1-segmented, extending beyond terminal segment of endopod, without thickened or rugose dorsal ridge, having smooth lateral, medial surfaces, lacking distinct lobes, with minute spinules along apex plus 2 lateral setae (“papillae” sensu Kabata, 1979) of approximately equal length (30–35 μm (32.5 ± 3.5 μm; N = 2)); endopod 2-segmented; basal endopodal segment with spinulose pad (conspicuous in paratype female; most spinules were missing in holotype); terminal endopodal segment having dorsal hook 1 (51–52 μm (51.5 ± 0.7 μm; N = 2) long), spiniform medial seta 2 (29–35 μm (24.0 ± 1.4 μm; N = 2) long), reduced distal tubercle 3 with minute protuberance, elongated ventral process 4 (25–26 μm (25.5 ± 0.7 μm; N = 2) long), inflated spinulose ventral process 5 (Fig. 3F).

Buccal apparatus subterminal on cephalosome, comprised of fused labrum, labium plus paired mandibles; labrum with rounded anterior margin, having dense set of setules partially concealing triangular rostriform process (Fig. 3G); mandible having dental formula P1, S1, P1, S1, P1, S1, B4 (holotype) or B5 (paratype), 363 long (Fig. 3H), with field of minute rice-shaped denticles posterior to basal teeth; labium with setules fringing anterior margin, having field of minute spines dorsally (4 total) directly posterior to origin of fringing setules; inner (medial) spine shorter, thinner than truncated outer spine (Fig. 3I).

Maxillule bilobate, with lateral palp plus inner (medial) praecoxal endite; lateral palp tipped with 5 apical setae, having minute spinules; praecoxal endite with 3 terminal papillae each with elongated apical seta, having field of minute spinules dorsally (Fig. 3J); sinistral praecoxal endite of holotype was damaged.

Maxilla connecting to base of cephalosome at trunk junction, not fused, 4.3–5.3 mm (4.7 ± 0.7 mm; N = 2) in total length including bulla, 0.9–1.2 mm (0.9 ± 0.1 mm; N = 2) wide, having proximal tubercle (opening of maxillary gland) (Fig. 2A, B), with inflated distal tips at connection with bulla, having short manubrium; bulla sub-circular, not stellate, margins smooth (Fig. 2B), without posterior indentation, distal surface smooth, flat (bulla damaged in paratype female).

Maxilliped comprised of corpus maxillipedis plus subchela (Fig. 3K), positioned anteriad between insertions of maxillae (Figs. 2A; 3A); corpus maxillipedis having swollen base at connection with cephalosome, with proximal, distal spinulose pads separated by seta with swollen base along myxal (medial) margin; proximal spinulose pad sub-circular; distal spinulose pad wishbone-shaped; subchela 377 μm long (exclusive of claw), having proximal ventral process, with sinuous row of fine serrations immediately posterior to base of barb (“distomedial seta” sensu Ruiz et al. (2019)) (Fig. 3K, L); barb extending anteriad beyond tip of accessory denticle of claw (146 μm long; approximately 38.7% length of subchela).

Trunk comprising wide neck bearing vestigial leg 1 plus large genital trunk bearing vestigial leg 2, 7.7–8.6 mm (8.1 ± 0.6 mm; N = 2) long, 3.7–4.3 mm (4.0 ± 0.5 mm; 2) wide, 2.5 μm deep (Fig. 3A), approximately 2.5–3.0 times longer than cephalosome,
broadening posteriorly, having broadly rounded posterolateral margins (Fig. 2A), with slight mid-dorsal longitudinal raised welt lateral inflations (Figs. 2A, 3A); neck 0.9–1.3 mm (1.1 ± 0.3 mm; N = 2) long, 1.4–1.8 mm (1.6 ± 0.3 mm; N = 2) wide; vestigial leg 1 positioned anteriorly on ventrolateral margin of neck (Fig. 3A), with cylindrical base, with seta; vestigial leg 2 posterior to neck on ventrolateral margin of genital trunk (Fig. 3A), having cylindrical base, with 2 setae (one seta shorter (30 μm; N = 1) than the other (59 μm; N = 1)).

Abdomen extending posteriad relative to oviduct orifices (dorsal aspect), paired copulatory pores (ventral aspect), terminating as pair of semispherical protuberances each issuing posterior process; posterior process ventral to egg sacs, extending posteroventrally from lateral margins of abdomen (Figs. 1A, 2A, 3A); 1.7–2.2 mm (1.9 ± 0.4 mm; N = 2) long, 0.8–0.9 mm (0.8 ± 0.1 mm; N = 2) wide; sausage-shaped, without apical seta; egg sac issuing from dorsolateral oviduct orifice positioned anterior to origin of posterior process, 10–13 mm (11.5 ± 2.1 mm; N = 2) long, 1.7–1.8 mm (1.8 ± 0.1 mm; N = 2) wide, multiseriate.

Description of adult male:

Body 2.9 mm long (Figs. 2A, B, 4A−5P). Cephalosome declining ventrally at approximately 90° relative to trunk axis, approximately equal to length of trunk, longer than broad, 1.4 mm long, 0.8 mm maximum width, broadly rounded posteriorly, dorsally flattened (Fig. 4A), demarcated from trunk by slight constriction, with outline of dorsocephalic shield in dorsal, lateral views (Fig. 4A, B); dorsal cephalic shield without pores, with oxbow-like cuticular folds along posterior margin (Fig. 4B).

Antennule anterodorsal to origin of antenna (Fig. 4A, 5A); basal segment not swollen distally; second segment with whip (65 μm long; longer than that of holotype); third segment with solus (12 μm long or approximately 18.5% whip length; longer than in holotype); terminal segment with 6 apical setae: tubercle 1 (11–13 μm (12 ± 1.4 μm; N = 2) long), tubercle 2 (14–16 μm (15 ± 1.4 μm; N = 2) long), digitiform seta 3 (38–40 μm (39 ± 1.4 μm; N = 2) long), complex 5 with 2 subequal setae (32–35 μm (33.5 ± 2.1 μm; N = 2) and 22–27 μm (24.5 ± 3.5 μm; N = 2) long), flagelliform seta 6 (35–38 μm (36.5 ± 2.1 μm; N = 2) long) (Fig. 5B, C).

Antenna posteroventral to antennule (Fig. 4A); sympod with spinulose pad (Fig. 5D); exopod slightly spatulate, 1-segmented, not extending beyond reach of endopod, lacking distinct lobes, with minute spinules along anterodorsal margin, with 2 subequal setae (11–27 μm (18 ± 8.2 μm; N = 3) long) (Fig. 5D); endopod 2-segmented; basal endopodal segment with spinulose pad; terminal endopodal segment having dorsal hook 1 (46–49 μm (47.5 ± 2.1 μm; N = 2) long), spiniform medial seta 2 (approximately 14 μm long, tip broken on sinistral endopod; Fig. 5E); reduced distal tubercle 3 with minute protuberance, elongate ventral process 4 (sinistral process approximately 25 μm long, tip of ventral process is broken on dextral endopod), inflated spinulose ventral process 5 (most spinules blunt or missing in allotype; Fig. 5E).

Buccal apparatus subterminal on cephalosome; labrum similar to that of the female (not figured); mandible 237 long, having dental formula P2, S1, P1, S1, B4 (number of basal teeth matches the holotype) (Fig. 5F); labium similar to that of the female, inner spine longer, thinner than truncated outer spine (not figured).

Maxillule similar to that of the female (Fig. 5G).

Maxilla comprised of syncoxa plus basis, positioned on midventral surface of cephalosome, anterior to mediative process (Fig. 4A, C); syncoxa robust relative to size of maxilliped,
having pronounced, bifid ventral tubercle (opening of maxillary gland), with anteromedial process having 7 conical denticles bordering medial indentation accommodating tip of basis claw (Fig. 5H–J); basis without proximal thickened cuticle, tapering to form curved claw.

Mediative process bifid, with lobe long, narrow relative to the other, 224 μm long, 157 μm wide at base (lateral view), width nearly equal to length of shorter lobe (Fig. 5K).

Maxilliped with corpus maxillipedis without mid-medial denticle, with raised myxal area accommodating tip of subchela claw (Fig. 5L); tip of dextral claw damaged in allotype; myxal area with medial indentation having minute denticles plus spine-like protuberance; subchela with proximal seta plus distal seta (Fig. 5L, M).

Trunk with vestigial legs 1, 2 terminating in genital area, 1.1 mm long (excluding caudal ramus length), 0.7 mm wide, approximately equal to length of cephalosome, having irregular margins, with indistinct segmentation, having translucent cuticle (Fig. 4D–F); vestigial legs similar to those of female (Fig. 5N, O); genital area with paired genital processes, paired genital plates. Abdomen extending posterior relative to genital area, terminating as pair of semi-spherical protuberances each issuing caudal ramus; caudal ramus 0.4 mm long, 0.07 mm wide (Fig. 5P), with 4 setae (1 anterodorsal, 1 mid-lateral, 1 posterolateral, 1 posteromedial) plus minute denticles posteriorly.

Nomenclatural statement: A life science identifier number (LSID) was obtained for the new species: urn:lsid:zoobank.org:pub:B902C8AC-F73E-4F9A-AC56-6185990C23F3.

**DISCUSSION**

This is the third species of *Neoalbionella* described from a gulper shark and the second of *Neoalbionella* from the Gulf of Mexico (Ruiz et al., 2019).

The female and male of the new species most closely resemble those of *Neoalbionella globosa* (Leigh-Sharpe, 1918) (from lesser spotted dogfish, *Scyliorhinus canicula* (Linnaeus, 1758) (Carcharhiniformes, Scyliorhinidae) by having 1) cephalosome approximately 1/3 trunk length in females including posterior processes (approximately equal in males), 2) antennule with four segments (both sexes), 3) maxilla with swollen distal tips (“collars” sensu Kabata, 1986), and 4) posteromedian process 1/4–1/3 trunk length in females (caudal ramus <1/2 trunk length in males).
Figure 4. Adult male of Neoalbionella dannytangii sp. nov. (Copepoda: Lernaeopodidae) from the skin of Centroscyllium fabricii (Squaliformes, Centrophoridae) in the northern Gulf of Mexico. Allotype USNM 1550566. Scale values aside each bar. Lateral view of habitus showing level of vestigial leg 1 (horizontal arrowhead) and vestigial leg 2 (vertical arrowhead) (A). Dorsal view of habitus (B). Ventral view of habitus showing mediative process with tethered spermatophore (s) (C).

The male of the new species differs from that of N. globosa by having 1) an antennule terminal segment with 6 apical setae (versus seven), 2) an antenna terminal endopodal segment having a reduced distal tubercle 3 plus a spinulose ventral process 5 (versus pronounced distal tubercle and without spinulose ventral process), 3) a maxilla shorter than the combined length of the trunk and abdomen including posterior processes (versus maxilla length greater than trunk plus abdomen length), and 4) a maxilliped having a corpus with a sub-circular, proximal spinulose pad (versus elongate spinulose pad). Additional morphological features included herein were not reported in descriptions of N. globosa (see Leigh-Sharpe (1918) and Kabata, (1979)). Neither Leigh-Sharpe (1918) nor Kabata (1979) provided detail of the labium regarding the presence of anterolateral spines; however, the female of the new species clearly has two sets of spines (four total) posterior to the margin of fringing setules.

The single male specimen of the new species was attached to the holotype near the tip of the dextral posterior process and resembled the male of N. globosa in gross morphology. The male of the new species differs from that of N. globosa and those of all congener based on a combination of characters associated with the antennule, antenna, mandible, labium, maxillule, maxilla, mediative process, and caudal ramus. We consider the examined male and female pair to be conspecific because details of five of those features are shared between sexes 1) an antennule terminal segment having six apical setae with similar arrangement, 2) an antenna terminal endopodal segment having a reduced distal tubercle 3 with a minute protruberance, 3) a labium with four anterolateral spines, 4) a mandible with four basal teeth, and 5) a maxillule lateral palp and precoxal endite with spinulation. The male of the new species differs from that of N. globosa by having 1) an antennule with 7 apical setae (versus seven), 2) an antenna terminal endopodal segment with armature similar to that of the female, 3) a mandible with four basal teeth (versus six), 4) a maxilla syncoxa with a pronounced and bifid ventral tubercle (not bifid and reduced) plus an anteromedial process with seven large conical denticles bordering a medial indentation (versus 11 teeth and without a medial indentation), 5) a mediative process that is relatively large, > 200 μm long, and bifid (versus approximately 30 μm long and bifid), and 6) a caudal ramus having four setae (versus three) (see Kabata (1979) for anatomical details of N. globosa).

Females of N. benziplirata are easily distinguished from those of the new species, which is characterized by 1) an antenna exopod without a thickened dorsal ridge and without setules (versus with dorsal ridge and without spinules) plus an endopod with a reduced, non-bifid distal tubercle 3 (versus pronounced and bifid) and 2) a maxilla not fused with the other member and shorter than the trunk length (versus fused with other member and longer than trunk) (see Ruiz et al. (2019) for anatomical details of N. benziplirata). The male of N. benziplirata is very similar to that of the new species regarding morphology of the habitus but differs by having 1) an antenna terminal endopodal segment as in the female, 2) a mandible with four basal teeth (versus five), and 3) a maxilla syncoxa having a pronounced and bifid ventral tubercle (versus reduced and not bifid) plus an anteromedial process having seven large denticles bordering a medial indentation (versus two processes each with a field of denticles) (Ruiz et al., 2019).

Female specimens of the new species differ from those described by Kabata (1964) for female Neoalbionella centroscyllii (Hansen, 1923) (from the black dogfish, Centroscyllium fabricii (Reinhardt, 1825) (Etmopteridae)) by having 1) an antenna exopod setae without tubercular bases (versus with tubercular bases), 2) a maxilla with a swollen tip nearly parallel with the distal surface of the bulla (versus not swollen nor parallel with bulla), and 3) a maxilliped subchela with a barb (versus two) (see Kabata (1964) for details of N. centroscyllii). The male of the new species differs from that of N. centroscyllii (from Kabata, 1964) by having 1) an antennule with six (versus seven) apical setae, 2) a mandible with four (versus five) basal teeth, 3) a maxilla syncoxa having a pronounced and bifid ventral tubercle (versus bifid tubercle absent but ovoid structure present), and 4) two vestigial legs (versus one).

Females of Neoalbionella etmopteri (Yamaguti, 1939) following characters given by Benz (1991a) (from the blackbelly lanternshark Etmopterus lucifer Jordan & Snyder, 1902 (Etmopteridae)) are easily differentiated from those of the new species, which have 1) an antennule terminal segment with six (versus nine) apical setae, 2) an antenna exopod with sparse apical spinulation (versus lobate, densely spinulated and unconfined to apex), 3) a vestigial leg 1 with one seta (versus two), and 4) a posterior process that is elongated and sausage-shaped (versus short and tapered) (Yamaguti, 1939). The male of the new species differs from that of N. etmopteri by having 1) an antennule terminal segment with 6 (versus 7) apical setae, 2) an antenna exopod that is bifid (versus 4 basal teeth), and 5) a maxilliped with the corpus without bifid tubercle (versus with bifid tubercle) plus an anterolateral process having a pronounced and bifid ventral tubercle (versus reduced and not bifid) plus an anteromedial process having seven large denticles bordering a medial indentation (versus two processes each with a field of denticles) (Yamaguchi, 2019).

Females of the new species differ from those of Neoalbionella fabricii (Rubec & Hodgans, 1988) (from C. fabricii) by having 1) an antennule with 4 segments (versus 3), 2) an antenna sympod that is naked (versus with spinulose pad) plus a terminal endopodal segment with a reduced distal tubercle 3 (versus pronounced distal tubercle), 3) a mandibular formula P1, S1, P1, S1, P1, S1, B4 or B5 (versus P2, S1, P1, S1, B5), and 4) a maxilliped having a sub-circular proximal spinulose pad (versus elongated and narrow). The male of the new species differs from that of N. fabricii by having 1) an antennule with 4 segments (versus 3), 2) an antenna terminal endopodal segment with a reduced...
NEW LERNAEOPODID COPEPOD WITH KEY TO NEOALBIONELLA SPP

Female specimens of the new species differ from those described by Benz & Izawa (1990) for *Neoalbionella kabatai* (Benz & Izawa, 1990) (from type host, the spatulasnout catshark *Apristurus platyrhynchus* (Tanaka, 1909) (Pentanchidae) and the deepwater catshark *Apristurus profundorum* (Goode & Bean, 1896)) by having 1) an antennule terminal segment with 6 (versus 7) apical setae, 2) a mouth cone labrum with a rostriform process (versus absent), 3) a maxilla that is shorter than the trunk length including posterior processes (versus longer than trunk including posterior processes) plus a bulla with sub-circular anchor (versus ovate), and 4) an elongate posterior process that is sausage-shaped (versus short, tapered, and with ventral spines).

The female of the new species differs from that of *Neoalbionella longicaudata* (Hansen, 1923) (from type host, leafscale gulper shark, *Centrophorus squamosus* (Bonnaterre, 1788) (Centrophoridae); *C. granulosus*) by having 1) a maxilla that is shorter than the trunk length and not fused with the other member (versus fused with other member and longer than trunk length) and 2) a posterior process that is relatively short and without an apical seta (versus long and tipped with apical seta) (Hansen, 1923). The male of the new species differs from that of *N. longicaudata* by having 1) a maxilla syncoxa with an anteromedial process bearing 7 large conical teeth (versus 2 rugose protuberances) and 2) a maxilliped with the corpus maxillipedis lacking a mid-medial denticle (versus present).

Females of the new species differ from those of *Neoalbionella oviformis* (Shiino, 1956) (from the shortspine spurdog *Squalus mitsukurii* Jordan & Snyder, 1903 (Squalidae)) by having 1) an antennule terminal segment with 6 (versus 5) apical setae, 2) a mouth cone labrum with a rostriform process (versus without), 3) a

---

**Figure 5.** Adult male of *Neoalbionella dannytangi* sp. nov. (Copepoda: Lernaeopodidae) from skin of *Centrophorus* sp. (Squaliformes, Centrophoridae) in the northern Gulf of Mexico. Allotype USNM 1550566. Scale values aside each bar. Lateral view of antennule (A). Dorsomedial view of antennule terminal segment (B). Ventral view of antennule terminal segment (C). Lateral view of antenna (dextral) (D). Lateral view of antenna terminal endopodal segment (sinistral) (E). Lateral view of mandible (F). Dorsolateral view of maxillule (G). Ventral view of maxilla showing bifid ventrual tubercle (diagonal arrowhead within boxed area) of maxilla syncoxa (H). Ventral view of boxed area (H) showing 7 conical denticles and bifid ventral tubercle of maxilla syncoxa (I). Lateral view of bifid ventral tubercle of maxilla syncoxa (J). Ventrolateral view of mediative process (K). Ventral view of maxilliped (L). Medial view of maxilliped subchela claw (tip damaged) apposed with raised myxal area of corpus maxillipedis (M). En face view of vestigial leg 1 (N). Lateral view of vestigial leg 2 (O). Dorsolateral view of genital area and abdomen with caudal rami (P).
mandible with 4 or 5 basal teeth (*versus* 6), and 4) vestigial leg 1 with 1 seta (*versus* 2) (Benz, 1991b).

Three innominate species of *Neoalbionella* reportedly infect squaliform sharks, one of which was treated by Ruiz et al. (2019), who identified one female and one male as *Neoalbionella* sp. (from *C. granulosus*; Pacific Ocean off Japan (Shiino, 1956)). The female of the new species differs from that of Shiino (1956) by having 1) a trunk having having broadly rounded posterolateral margins (rather than being cyndrical or orbicul ar as in other *Neoalbionella* spp.), 2) an antenna terminal endopodal segment with a reduced distal tubercle (3 *versus* distal tubecle pronounced and with conical tip), 3) a mouth cone labium with 2 pairs of anterolateral spines (outer spines are truncated *versus* conical), 4) short and non-fused maxillae, and 5) shorter posterior processes. The male of the new species differs from that of Shiino (1956) by having the same features as those listed for the female. The female of the new species is different from the innominate female of Rodriguez et al. (2010) by having 1) an antennal exopod that is not lobate and with sparse apical spinulation (*versus* lobate and with dense spinulation) and 2) a posterior process that is swollen and elongated (*versus* not swollen, short, and tapered). We did not compare the female of the new species to the female of *Neoalbionella* sp. reported by Bakopoulos et al. (2018) (nor was it included in the dichotomous key provided herein) because their diagnosis only highlighted generic features and provided no detail of any appendage.

Other than intraspecific phenotypic plasticity in the mandibular formula (the holotype of the new species has 5 basal teeth, whereas, the paratype has 4), all other features matched the holotype and paratype female specimens. Females of *N. kabatai* apparently may also have similar plasticity in the mandibular formula. Benz & Izawa (1990) reported 3 basal teeth in the holotype female of *N. kabatai* in the northwest Pacific Ocean, whereas Hogans & Marques (1994) reported four from the female collected in the North Atlantic Ocean. Noteworthy is that these differences are reported from lernaeopodids collected from two species of *Apiratus* Garman, 1913 (Carcharhiniformes, Pentanchidae) from two different ocean basins.

### KEY TO FEMALES OF SPECIES OF *NEOALBIONELLA*

| 1a. Maxillae fused for most of length | 2 |
| 1b. Maxillae not fused for most of length | 3 |
| 2a. Mouth cone labium with 2 anterolateral spines |  |
| - Mandibular formula P1, S1, P1, S1, P1, S1, B5... *N. bennicpata* | |
| 2b. Labium with 4 anterolateral spines (large spines of equal size and shape) | |
| - Mandibular formula P1, S1, P1, S1, P1, S1, B4... *N. longicauda* | |
| 2c. Labium with 4 anterolateral spines (one large spine abutted by small, medial spine) | |
| - Mandibular formula P1, S1, P1, S1, P1, S1, B4 or B5sp. | |
| 3a. Posterior process elongate and sausage-shaped | 4 |
| 3b. Posterior process short and tapered | 5 |
| 4a. Antennule with 5 apical setae | |
| - Mandibular formula P2, S1, P1, S1, B6... *N. weifensis* | |
| 4b. Antennule with 6 or 7 apical setae | 6 |
| 5a. Antenna exopod with lobate, spinulose apex | |
| - Antennule terminal segment with 9 setae | |
| - Mandibular formula P1, S1, P1, S1, P1, S1, B4 | |
| - Vestigial leg 1 with a minute seta | *N. etmopteri* | |
| 5b. Antenna exopod with bluntly rounded-spinulose apex | |
| - Antennule terminal segment with 7 setae | |
| - Mandibular formula P1, S1, P1, S1, P1, S1, B3 (NW Pacific O.) or B4 (North Atlantic O.); | |
| - Vestigial leg 1 with 2 minute setae | *N. kabatai* | |
| 5c. Antenna exopod with lobate, spinulose apex | |
NEW LERNAEOPODID COPEPOD WITH KEY TO NEOALBIONELLA SPP


