A NEW SPECIES OF NEOALBIONELLA (COPEPODA: SIPHONOSTOMATOIDEA: LERNAEOPODIDAE) FROM SKIN OF THE GULPER SHARK, CENTROPHORUS GRANULOSUS (SQUALIFORMES: CENTROPHORIDAE) IN THE NORTHERN GULF OF MEXICO

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KEY WORDS
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New Species
Siphonostomatoida

ABSTRACT
Using light and scanning electron microscopy of male and female copepods, we herein describe a new species of Neoalbionella Özdiœmen, 2008 (Copepoda: Lernaeopodidae), Neoalbionella benzipirata n. sp., infecting the skin of the gulper shark, Centrophorus granulosus (Bloch and Schneider, 1801), in the northern Gulf of Mexico. Females of the new species were assigned to Neoalbionella by having 3 setae on the maxillule lateral palp (vs. 2 setae in Lernaeopoda Nordmann, 1832) and a single accessory denticle on the maxilliped subchela claw (vs. ≥2 denticles in Lernaeopoda). Females of the new species resemble those of Neoalbionella longicaudata (Hansen, 1923) Özdiœmen, 2008 but can be differentiated from them and those of all congeners by having a unique configuration of 16 dorsocephalic sensilla; an antennule terminal segment having 6 apical setae comprising tubercles 1 and 3, digitiform seta 4, 2 subequal setae of complex 5, and flagelliform seta 6; an antenna exopod with a thickened dorsal ridge, smooth (convex) outer surface with 2 short papillae, and rugose (concave) inner surface plus a terminal endopodal segment having a large dorsal hook, medial spine, bifid distal tubercle, and spinulose ventral process; a mandible having the formula P1, S1, P1, S1, P1, S1, B5; and a single pair of anterolateral spines on the mouth cone labium. Males attached to the posteroventral surface of the females’ genital trunk were assigned to Neoalbionella by having tapered (not inflated) caudal rami directed posteroventrally. They were differentiated from previously reported congenere males by having an antennule with the same number and configuration of apical setae as the female; an antenna with a spatulate exopod having minute spinules along its apex plus a terminal endopodal segment with components the same as the female; a mandible with formula P2, S1, P1, S1, B5; a labium with 1 pair of anterolateral spines like the female; and a conspicuous mediative process with bifid tip. Detail of the dorsocephalic shield (in females) and mouth cone labium (in both sexes) previously had not been used to diagnose Neoalbionella spp. We also dissected voucher specimens of “Neoalbionella longicaudata” (collected from gulper sharks in the western Pacific Ocean off Japan by Shiino in 1956), which we morphologically diagnosed as an innominate species, Neoalbionella sp. This is the first report of a species of Neoalbionella from the Gulf of Mexico and the second species of Neoalbionella reported from C. granulosus, a deepwater shark seldom encountered and surveyed for parasitology.

Neoalbionella Özdiœmen, 2008 comprises 7 nominal (Benz, 1991b; Hogans and Marques, 1994) and 3 innominate (Shiino, 1956; Rodríguez et al., 2010; Bakopoulos et al., 2018; present study) species that collectively infect skin and gill of squaliform and carcharhiniform sharks of 5 families, 6 genera, and 10 species (Table I). Nominal species of Neoalbionella reportedly exhibit high host specificity: 5 infect a single host species and 2 infect several. Of those, Neoalbionella longicaudata (Hansen, 1923) Özdiœmen, 2008 is reported from 2 species of Centrophorus Müller and Henle, 1837 (Table I), which inhabit insular slopes and outer continental shelves at depths of up to 2,350 m but also as shallow as 50 m in the...
Table I. Summary of hosts, males, sites of infection, and locality records for species of *Neoalbionella* Öz dikmen, 2008 (ordered alphabetically).

<table>
<thead>
<tr>
<th>Species*</th>
<th>Host family</th>
<th>Type host</th>
<th>Other hosts</th>
<th>Male described</th>
<th>Site of infection</th>
<th>Type locality†</th>
<th>Other localities</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Neoalbionella benzipirata</em> n. sp.</td>
<td>Centrophoridae</td>
<td><em>Centrophorus granulosus</em> (Bloch &amp; Schneider, 1801)</td>
<td>—‡</td>
<td>Yes</td>
<td>Bases of fins; body surface</td>
<td>Off Florida shelf, NEG</td>
<td>Mississippi Canyon, NGM</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Neoalbionella centroscyllii</em> (Hansen, 1923)</td>
<td>Etmopteridae</td>
<td><em>Centroscyllium fabricii</em> (Reinhardt, 1825)</td>
<td>C. fabricii</td>
<td>Yes</td>
<td>Near cloaca; bases of fins</td>
<td>Davis Straight, off Newfoundland, NWA</td>
<td>—</td>
<td>Hansen, 1923; Kabata, 1964; Rubec and Hogans, 1988</td>
</tr>
<tr>
<td><em>Neoalbionella etmopteri</em> (Yamaguti, 1939)</td>
<td>Etmopteridae</td>
<td><em>Etmopterus lucifer</em> Jordan &amp; Snyder, 1902</td>
<td>Etmopterus sp.</td>
<td>Yes</td>
<td>Gill; dorsal body surface</td>
<td>Off Japan, NPO</td>
<td>Off South Africa, SEA</td>
<td>Yamaguti, 1939; Shiino, 1956; Benz, 1991a Rubec and Hogans, 1988</td>
</tr>
<tr>
<td><em>Neoalbionella fabricii</em> (Rubec and Hogans, 1988)</td>
<td>Etmopteridae</td>
<td><em>C. fabricii</em></td>
<td>—</td>
<td>Yes</td>
<td>Gill</td>
<td>Gulf of St. Lawrence, off Newfoundland, NWA</td>
<td>—</td>
<td>Rubec and Hogans, 1988</td>
</tr>
<tr>
<td><em>Neoalbionella globosa</em> (Leigh-Sharpe, 1918)</td>
<td>Scyliorhinidae</td>
<td><em>Scyliorhinus canicula</em> (Linnaeus, 1758)</td>
<td>—</td>
<td>Yes</td>
<td>Nasal fossae; near spiracle</td>
<td>Off Plymouth, United Kingdom, NEA</td>
<td>—</td>
<td>Leigh-Sharpe, 1918; Kabata, 1979</td>
</tr>
<tr>
<td><em>Neoalbionella longicaudata</em> (Hansen, 1923)</td>
<td>Centrophoridae</td>
<td><em>Centrophorus squamosus</em> (Bornattere, 1788)</td>
<td><em>C. granulosus</em></td>
<td>Yes</td>
<td>Fins; body surface</td>
<td>Off Iceland, NAO</td>
<td>Off Spain, NEA</td>
<td>Hansen, 1923; Fernández-Ovies, 1992 Shiino, 1956; Benz, 1991b</td>
</tr>
<tr>
<td><em>Neoalbionella oviformis</em> (Shiino, 1956)</td>
<td>Squalidae</td>
<td><em>Squalus mitsukurii</em> Jordan &amp; Snyder, 1903</td>
<td>—</td>
<td>No</td>
<td>Body surface</td>
<td>Off Japan, NPO</td>
<td>—</td>
<td>Shiino, 1956; present study</td>
</tr>
<tr>
<td><em>Neoalbionella sp.</em></td>
<td>Centrophoridae</td>
<td><em>C. granulosus</em></td>
<td>Centrophorus atromarginatus Garman, 1913</td>
<td>Yes</td>
<td>Body surface</td>
<td>Off Japan, WPO</td>
<td>—</td>
<td>Shiino, 1956; present study</td>
</tr>
<tr>
<td><em>Neoalbionella sp.</em></td>
<td>Etmopteridae</td>
<td><em>Etmopterus granulosus</em> (Günther, 1880)</td>
<td>—</td>
<td>No</td>
<td>Dorsal fin</td>
<td>Off Juan Fernández Archipelago, Chile, SPO</td>
<td>—</td>
<td>Rodríguez et al., 2010</td>
</tr>
<tr>
<td><em>Neoalbionella sp.</em></td>
<td>Scyliorhinidae</td>
<td><em>S. canicula</em></td>
<td>—</td>
<td>No</td>
<td>Peri-genital area; Pterygiopodia</td>
<td>Off Lesvos Island, NAS</td>
<td>—</td>
<td>Bakopoulos et al., 2018</td>
</tr>
</tbody>
</table>

* The identity of 3 innominate species of *Neoalbionella* infecting squaliform sharks (see Remarks; Shiino, 1956; Rodríguez et al., 2010; Bakopoulos et al., 2018) will be treated elsewhere.
† Abbreviations: NAS (Northeastern Aegean Sea); NAO (North Atlantic Ocean); NEA (Northeast Atlantic Ocean); NEG (Northeastern Gulf of Mexico); NGM (Northern Gulf of Mexico); NPO (Northwest Pacific Ocean); NWA (Northwest Atlantic Ocean); SEA (Southeast Atlantic Ocean); SPO (Southeastern Pacific Ocean); WPO (West Pacific Ocean).
‡ (—) indicates No data.
Atlantic and Pacific oceans (Verissimo et al., 2014). Because these copepods infect “deepwater” sharks that are seldom captured (Castro, 2011), relatively few anatomical studies of Neoalbionella spp. have been published. Moreover, because of the rarity of obtaining infected sharks and the low infection intensity typically reported in deepwater fishes (Klimpel et al., 2001), some species accounts within Neoalbionella are based on only 1 or 2 specimens (Benz and Izawa, 1990; Hogans and Marques, 1994).

We herein propose a new species of Neoalbionella from the skin of Centrophorus granulosus (Bloch and Schneider, 1801) (Squaliformes: Centrophoridae) in the Gulf of Mexico (the second congener infecting C. granulosus). We also compare the new species to vouchers of “N. longicaudata” Shiino (1956) collected from gulper sharks in the Pacific Ocean off Japan, discuss morphological characters seldom or arbitrarily described for congeners, and highlight non-sexually dimorphic features.

MATERIALS AND METHODS

During March and April 2015, National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service personnel deployed experimental bottom-longline gear from the NOAA Research Vessel Oregon II on the continental shelf off Florida and Alabama, Gulf of Mexico, at depths of 19–857 m (609 ± 318 m). A total of 11 gulper sharks were captured (1,091–1,585 mm [1,309.6 ± 154.1 mm] stretch total length (TL); all females (at least 1 female may have been reproductively mature based on maximum size estimates provided by White et al., 2013) from 5 localities (28°11′56.40″N, 86°9′4.20″W; 28°12′10.80″N, 86°28′30.60″W; 28°20′53.40″N, 86°42′17.40″W; 28°31′27.60″N, 86°52′40.80″W; 28°54′38.40″N, 88°26′10.20″W). Although 10 infected gulper sharks were sampled during 2 mo in 2015, we considered that year as a single collection event because those fisheries data are logged as a distinct survey (spanning 3 wk) with a unique cruise code; therefore, we calculated prevalence and mean intensity without separating hosts by month of capture in 2015. In March 2017, 3 additional gulper sharks (all infected) (1,040–1,206 mm [1,135.7 ± 85.9 mm] TL; all mature males based on clasper length and manual protraction of claspers) were captured from the Mississippi Canyon off Louisiana (28°22′58.80″N, 89°34′7.32″W) at a depth of 780 m. Sharks were field-identified based on the following combination of characters: first dorsal fin high and angular, with origin over pectoral fin inner margin; second dorsal fin spine slightly longer than first; pectoral fin free, rear tip elongated; without ventral inter pelvic-caudal keel; free posterior tips of pectoral fins elongated and extending beyond first dorsal fin spine; space between insertion of second dorsal fin and caudal peduncle approximately 7% of TL (Carpenter, 2002). The body surface of all sharks was examined and sampled for ectoparasites before each shark was fin-clipped, tagged, and released alive.

Copepods were collected using fine forceps, taking special care to remove each copepod specimen intact (including the bulla), and fixed directly in 10% neutral buffered formalin or preserved in 95% ethanol (EtOH). Copepods intended for morphology were cleaned of host tissue using horsehair brushes and repeated rinsing with 70% EtOH and stored in vials of 70% EtOH plus 1% glycerin. Specimens were cleared by initially immersing them in an open container with equal parts 95% EtOH and lactic acid, with lactic acid added periodically to replace evaporated EtOH until resulting solution was 100% lactic acid. After clearing for 8–12 hr in lactic acid, specimens were stained by dissolving a pinch of lignin pink into the lactic acid (Benz et al., 2000). With the aid of a stereo-dissecting microscope and minuten (insect) pins mounted on wooden dowels, each copepod appendage was excised from the stained copepod submerged in lactic acid. Each appendage was then mounted in a drop of lactic acid using the hanging drop wooden slide method of Humes and Gooding (1964) and illustrated with the aid of Leica DM-2500 and Leica DMR compound microscopes (Leica Microsystems Inc., Buffalo Grove, Illinois), each equipped with differential interference contrast (DIC) optical components and a drawing tube. The habits of intact copepods was illustrated with the aid of a Wild M5A stereodissecting microscope (Wild Heerbrugg, Gais, Switzerland) with a drawing tube. The holotype and allotype were neither cleared in lactic acid nor stained with lignin pink. Formalin-fixed copepods for scanning electron microscopy (SEM) were washed in deionized water, dissected or left intact, dehydrated through a graded series of ethanol, dried using a Tousimis SAMDR1® PVT-3D Critical Point Dryer (Tousimis, Rockville, Maryland), mounted on aluminum SEM stubs with double-sided carbon tape, sputter-coated with gold palladium (19.32 g/cm3; 25 mA), and examined with a Zeiss EVO 50VP SEM (Zeiss USA, Thornwood, New York). Measurements are reported in micrometers (µm) unless otherwise noted and reported as a range followed in parentheses by the mean, standard deviation, and number of specimens measured. Measurements reported to the tenth of a millimeter were obtained with the aid of a stereo-dissecting microscope and digital caliper. Copepod total length was calculated by summing the length of the cephalosome with that of the trunk, inclusive of the female posterior processes (“rami” sensu Benz and Izawa, 1990; Hogans and Marques, 1994) or male caudal rami.

Voucher specimens were deposited in the National Museum of Natural History’s Invertebrate Zoology Collection (USNM, Smithsonian Institution, Washington, D.C.). USNM collection nos. 1501697-1501711.

Because original type materials of N. longicaudata are no longer extant (D. Eibye-Jacobsen, Zoological Museum, Natural History Museum, Copenhagen, Denmark, pers. comm.), we compared our specimens of the new species with the original descriptions of N. longicaudata provided by Hansen (1923). Further, we borrowed and were given permission to dissect 1 female and 1 male voucher specimen identified as Neoalbionella (Lernaeopoda) longicaudata by Shiino (1956) accessioned at the National Museum of Nature and Science (NMST), Division of Marine Invertebrates, Tsukuba, Japan.

Scientific names for fishes are derived from Fricke et al. (2018) and morphological terminology of copepod appendages follow Kabata (1979), Piasecki (1989), Benz and Izawa (1990), and Huys and Boxshall (1991).

DESCRIPTION

Neoalbionella benzzipirata n. sp. Ruiz and Bullard
(Figs. 1–62)

Description of ovigerous adult female specimens (based on 16 total individuals; 11 plus 5 specimens studied with light and SEM, respectively [USNM 1501697-1501703, 1501709-1501711]) (Figs. 1–33): Body having lernaeopodid habitus, with cephalosome (bearing antennules, antennae, buccal apparatus, maxillules,
Figures 1, 2. Adult female of Neoalbionella benzipirata n. sp. (Copepoda: Lernaeopodidae) from skin of gulper shark, Centrophorus granulosus, in the northern Gulf of Mexico. (1) Habitus showing attached male and position of pediger 1 (diagonal arrowhead) and pediger 2 (horizontal arrowhead). Paratype female and paratype male USNM 1501709. Lateral view. (2) Habitus (allotype removed) showing level of tubercle (cf. opening of maxillary gland) (arrowhead). Holotype USNM 1051697. Dorsal view.
maxillae, and maxillipeds) plus trunk (including neck-like region [herein termed “neck” throughout description] and genital trunk) and short abdomen (=anal somite) bearing posterior processes, 16.2–20.6 mm (18.9 ± 1.5 mm; 8) in total length (Figs. 1, 2).

Cephalosome declining ventrally approximately 30–45 degrees relative to trunk axis, much shorter than trunk, longer than broad, 2.3–3.0 mm (2.6 ± 0.3 mm; 8) long, 1.4–1.9 mm (1.7 ± 0.2 mm; 8) in maximum width, broadly rounded posteriorly, dorsoventrally-flattened (Figs. 1, 3, 4), demarcated from trunk by neck (Figs. 1, 2), with slight outline of dorsal cephalic shield in dorsal and lateral views (Figs. 1, 2, 4–6); dorsocephalic shield having dorsocephalic sensilla (sensu Piasecki, 1989); sensilla minute, approximately 10 μm long (Fig. 7), 8 in number per side of dorsocephalic shield (16 total sensillae), having bilaterally symmetrical distribution (Figs. 2, 4–6), each centering on crater-like depression; depression comprising translucent cuticle sealing a channel; channel visible with dissecting microscope in non-cleaned specimens (Figs. 4, 5), best viewed with DIC in cleared and stained specimens.

Antennule having 4 segments, anteroventral to antenna (Fig. 4), typically extending anteriad beyond anterodorsal margin of cephalosome (Figs. 5, 6, 8); basal (first) segment swollen near junction with antepenultimate (second) segment; antepenultimate segment with whip near junction with penultimate (third) segment; whip 50–68 μm (60 ± 9 μm; 3) long; penultimate segment with short solus on inner lateral margin near junction with terminal segment; solus 16–23 μm (18 ± 4 μm; 3) long or 24–46% whip length; terminal segment with apical setae; apical setae 6 in number, comprising tubercles 1 and 3, digitiform seta 4, complex setae 5 (having 2 subequal setae originating from common base), and flagelliform seta 6 (Figs. 10, 11); tubercle 1 typically shorter than tubercle 3, adjacent to base of digitiform seta 4, 10–16 μm (13 ± 3 μm; 3) long; tubercle 2 absent; tubercle 3 adjacent to base of flagelliform seta 6 or flanking short seta of complex 5, 12–23 μm (18 ± 6 μm; 3) long; digitiform seta 4 widest at base relative to all other apical setae (Figs. 10, 11), 32–40 μm (37 ± 5 μm; 3) long; complex setae 5 (5.1, 5.2) originating from common base, with seta 5.1 longer (37–40 μm [38 ± 2 μm; 3]) than seta 5.2 (15–25 μm [22 ± 6 μm; 3]); flagelliform seta 6 approximately as long as digitiform seta 4 and seta 5.1, 32–43 μm (38 ± 6 μm; 3) long.

Antenna comprised of sympod, exopod, and endopod (Fig. 12), originating posteroadial to antennule (Fig. 4), capable of extending anteriad beyond anterodorsal margin of dorsocephalic shield (Figs. 4, 5); sympod naked (without spinulose pad); exopod spatulate, extending beyond distal margin of endopod, consisting of 1 segment, with thickened dorsal ridge (Figs. 12, 13, 22, 23), having a smooth outer (lateral) surface and rugose inner (medial) surface, lacking distinct lobes and minute spinules, with 2 abbreviated papillae of approximately equal length and shape (Figs. 12, 13); exopod papillae 10–15 μm (13 ± 3 μm; 6) long, conical; endopod having distinct basal and terminal segments (Fig. 12); basal endopodal segment naked; terminal endopodal segment having an elongate ventral process, spinulose ventral process, distal tubercular process, medial spine, and dorsal hook (Figs. 14, 24); elongate ventral process 17–18 μm (18 ± 1 μm; 3) long; distal tubercular process squat, bifid; medial spine ≥ elongate ventral process length, 15–20 μm (17 ± 3 μm; 3) long; dorsal hook longer than medial spine and elongate ventral process, 30–45 μm (39 ± 8 μm; 3) long.

Buccal apparatus subterminal on cephalosome, comprising paired mandibles and mouth cone derived from fused labrum and labium; labrum with rounded anterior margin, having dense set of bristle-like setules partially covering rostriform process along anterior margin (Figs. 15, 17) (caution: the rostriform process is fragile, and if its tip is broken the dense setules would mask its presence; observed in 4 of 11 specimens with light microscopy), with blunt tips of buccal styles visible through cuticle in cleared and stained specimens (Fig. 15); mandible 373–400 μm (388 ± 11 μm; 4) long, having dental formula P1, S1, P1, S1, P1, S1, B5; with basal teeth decreasing in length posteriorly (Fig. 16), with field of rice-shaped spinules posterior to basal teeth; labium with thin and finely-striated setules fringing margin, bearing 2 anterolateral spines posterior to origin of fringing setules (Fig. 17).

Maxillule bilobate, with small lateral palpal (exopod sensu Kabata, 1969) and large inner praeocular endite (endopod sensu Kabata, 1964); palp tipped with 3 apical setae; praeocular endite with 3 terminal papillae (i.e., dorsal, medial, ventral) each with an elongate apical seta (Fig. 17), with field of minute spinules on dorsal margin spanning from base of dorsal papilla to level of palp (not figured herein).

Maxilla connecting to base of cephalosome at trunk junction, 23.5–43.4 mm (33.3 ± 7.3 mm; 6) in total length including fused and non-fused sections, 0.8–1.1 mm (0.9 ± 0.1 mm; 6) wide, fused for most of length (83–87%), approximately cylindrical through-out fused section; proximal non-fused section comprising 8–13% of total length of maxillae, having tubercle (perhaps homologous to opening of maxillary gland sensu Huys and Boxshall [1991]) along ventrolateral margin slightly distal to connection with cephalosome (Figs. 2, 25); distal non-fused section proximal to connection with manubrium of bulla, comprising 3–5% of total length of maxillae (Figs. 18, 26), without inflated tips at proximal connection, having an abbreviated (vs. elongate) manubrium; bulla sub-circular, with irregular and slightly thickened margins (Fig. 18) and smooth and flat distal surface.

Maxilliped comprising corpus maxillipeds and subchela (Figs. 19, 27), pair located on ventral surface of cephalosome between insertions of maxillae (Figs. 4, 8); corpus maxillipeds having swollen base at connection with cephalosome (Fig. 8), with 2 medial spinulose pads nearly equal in length in lateral profile; each spinulose pad with serrated perimeter distinct from ventrally-directed spinules loosely distributed across surface area of pads in no discernible pattern (Fig. 28); seta positioned between spinulose pads along medial margin of maxilliped (Figs. 19, 27), longer than wide, sub-triangular in lateral profile, lacking distal outgrowths; subchela 432–436 μm (434 ± 3 μm; 3) long (exclusive of claw), with proximal ventral seta and distomedial...
seta posterior to base of claw, with 2 sinuous rows of fine serrations proximal to base of distal seta (Fig. 20); distal seta slender and elongate, extending anteriad beyond origin of accessory denticle of claw; claw comprising approximately 40% of length of remainder of subchela, 180–182 μm (181 ± 1 μm; 3) long, with single, robust, accessory denticle (Fig. 20) (note that the accessory denticle is fragile and may appear missing or broken [Fig. 19; observed in 3 of 11 specimens using light microscopy]).

Trunk comprising narrow neck bearing pediger 1 and large genital trunk bearing pediger 2, 6.6–10.0 mm (8.2 ± 1.2 mm; 8) long, 2.7–4.1 mm (3.4 ± 0.6 mm; 7) wide, 1.6–3.4 mm (2.6 ± 0.8 mm; 4) deep (Figs. 1, 2), 3.1–3.3x longer than cephalosome, posterolateral margins rounded, having cylindrical (Fig. 1) to orbicular profile in lateral view, without mid-dorsal longitudinal raised welts, lacking ventrolateral inflations; neck 1.1–3.0 mm (1.8 ± 0.8 mm; 5) long (Figs. 1–3), 1.7–1.9 mm (1.8 ± 0.1 mm; 5) wide; pediger 1 positioned anteriorly on ventrolateral margin of neck, with cylindrical base having elongate seta (longer than cylindrical base) (Fig. 29); pediger 2 positioned immediately posterior to neck on ventrolateral margin where genital trunk begins to widen (Fig. 1), tipped with 1 elongate seta, cylindrical, slightly more robust than pediger 1.

Abdomen appearing as pair of posteriorly-round protuberances, bearing paired elongate posterior processes, extending posteriad relative to oviduct orifices (dorsal aspect) and copulatory pores (ventral aspect); posterior processes ventral to egg sacs, extending posteroventrally from lateral margins of abdomen (Figs. 30–32), 7.2–8.7 mm (8.2 ± 0.5 mm; 7) long, 0.7–1.2 mm (0.9 ± 0.1 mm; 7) wide, sausage-shaped (Figs. 1, 2), each tipped with 1 seta (Fig. 33); egg sacs 7.7–21.9 mm (15.5 ± 7.2; 3) long, 1.2–1.6 mm (1.4 ± 0.2; 3) wide, multiseriate, issuing from oviduct
orifices positioned anterior to origin of posterior processes (Figs. 1, 30).

Description of adult male specimens (based on 16 total individuals; 12 plus 4 specimens studied with light and scanning electron microscopy, respectively [USNM 150704-1501711]) (Figs. 34–62): Body having cephalosome bearing appendages as in female, with distinct trunk terminating in genital area and abdomen (anal somite issuing caudal rami), 2.9–3.2 mm (3.0 \( \pm \) 0.1 mm; 4) in total length (Figs. 34–36), attached to ventral surface of female genital trunk (at level of paired copulatory pores) between origins of posterior processes (Figs. 1, 49, 50).

Cephalosome declining ventrally at approximately 40–60° relative to trunk axis, approximately equal to length of trunk, longer than broad, 1.3–1.4 mm (1.4 \( \pm \) 0.1 mm; 4) long, 0.7–0.8 mm (0.8 \( \pm \) 0.1 mm; 4) in maximum width, broadly rounded posteriorly, dorsoventrally-flattened (Figs. 34, 49, 50), demarcated from trunk by slight constriction, with conspicuous outline of dorocephalic shield in dorsal and lateral views (Figs. 34, 35, 49, 50); dorsal cephalic shield without dorocephalic sensilla.

Antennule similar to female, having 4 segments, originating anterodorsal to origin of antenna (Figs. 34–36), extending anteriad beyond anterodorsal margin of cephalosome, capable of extending to, and making contact with, surface of female trunk when in copula (Fig. 51); basal segment not swollen near junction with antepenultimate segment; antepenultimate segment with whip on medial margin near junction with penultimate segment; whip 38–41 \( \mu \)m (38 \( \pm \) 3 \( \mu \)m; 3) long; penultimate segment with solus on medial margin near junction with terminal segment; solus 27–30 \( \mu \)m (28 \( \pm \) 2 \( \mu \)m; 3) long or approximately 66–79% whip length; terminal segment with apical setae; apical setae 6 in number, comprising tubercles 1 and 3, digitiform seta 4, complex setae 5 (having 2 subequal setae originating from common base), and flagelliform seta 6 (Fig. 38); tubercle 1 adjacent to base of digitiform seta 4, 19–22 \( \mu \)m (21 \( \pm \) 2 \( \mu \)m; 3) long; tubercle 2 absent; tubercle 3 adjacent to base of flagelliform seta 6 or flanking short seta of complex 5, 16–22 \( \mu \)m (19 \( \pm \) 3 \( \mu \)m; 3) long; digitiform seta 4 widest at base relative to all other apical setae, 38–46 \( \mu \)m (42 \( \pm \) 4 \( \mu \)m; 3) long; complex setae 5 (5.1, 5.2) originating from common base, with seta 5.1 longer (30–35 \( \mu \)m [32 \( \pm \) 3 \( \mu \)m; 3]) than seta 5.2 (19–24 \( \mu \)m [22 \( \pm \) 3 \( \mu \)m; 3]); flagelliform seta 6 approximately as long as digitiform seta 4, 38–51 \( \mu \)m (46 \( \pm \) 7 \( \mu \)m; 3) long.

Antenna comprised of sympod, exopod, and endopod (Fig. 39), originating posteroverentral to antennule (Figs. 34–36, 50), capable of reaching surface of female trunk when in copula (Fig. 51); sympod with spinulose pad (Figs. 39, 52); exopod spatulate, not extending beyond reach of endopod, consisting of 1 segment, without thickened dorsal ridge, lacking distinct lobes, with minute spines along dorsal and apical margins, with 2 elongate papillae of approximately equal length and shape (Figs. 40, 53); exopod papillae 17–25 \( \mu \)m (21 \( \pm \) 4 \( \mu \)m; 3) long, flagelliform; endopod having distinct basal and terminal segments (Figs. 39, 51, 52); basal endopodal segment with pad bearing minute spines; spinulose pad more elevated relative to that of the sympod; terminal endopodal segment having an elongate ventral

process, spinulose ventral process, tubercular process, medial spine, and dorsal hook (Fig. 41); elongate ventral process 13–15 μm (14 ± 1 μm; 3 long; spinulose ventral process separate from elongate process (we note that spinules of process are fragile and may be missing, and could be artifact of specimen processing; observed in 2 of 12 and 1 of 4 specimens processed for light microscopy and SEM, respectively [Fig. 55]); tubercular process bifid (we observed that tubercular process tips are fragile and subject to artifact and may appear blunted; observed in 5 of 12 specimens processed for light microscopy and 1 of 4 specimens processed for SEM, respectively); medial spine > length of elongate ventral process, 24–28 μm (26 ± 2 μm; 3 long; dorsal hook longer than medial spine and elongate ventral process, 67–77 μm (72 ± 5 μm; 3 long).

Buccal apparatus subterminal on cephalosome comprising paired mandibles and mouth cone derived from labrum and labium; labrum with rounded anterior margin, having dense field of bristles partially covering elongate rostriform process along anterior margin (Figs. 42, 57), with blunt tips of buccal stylettes visible through cuticle in cleared and stained specimens; mandible 238–249 μm (244 ± 6 μm; 3 long, having dental formula P2, S1, P1, S1, B5 (number of basal teeth matches the female) (Fig. 43); labium with thin setules fringing margin, with 2 anterolateral spines posterior to origin of fringing setules as in female (Figs. 56, 57).

Maxillule comprising lateral palp and praeacodal endite (Fig. 44); palp tipped with 3 apical setae; praeacodal endite bearing 3 terminal papillae (dorsal, medial, ventral), each with an elongate apical seta, with prominent patch of spinules immediately posterior to base of dorsal papilla.

Maxilla comprised of syncoxa (proximal segment) and basis, positioned directly anterior to mediate process on ventral surface of cephalosome (Fig. 45); syncoxa broad and robust relative to surface area of maxilliped in ventral view, with 2 rugose proterubrances accommodating tip of claw (Fig. 45), having small ventral tubercle (cf. maxillary gland opening) posterior to rugose proterubrances; basis forming claw, with thickened cuticular membrane near articulation with syncoxa; tip of claw inserted anterior to level of copulatory pores of female when in copula (Fig. 32).

Mediate process (sensu Kabata, 1979) positioned between maxillae and maxillipeds on cephalosome, 150–159 μm (155 ± 5 μm; 3 long, 80–84 μm (82 ± 2 μm; 3 wide at base (lateral), bifid (Fig. 46), with 1 lobe typically more bulbous than the other.

Maxilliped comprised of corpus maxillipedis and subchela (Figs. 47, 48), positioned posterior to mediate process; corpus maxillipedis with mid-medial denticle and apical process (Figs. 47, 48); apical projection triangular, with medial indentation accommodating tip of claw of subchela; medial indentation with rice-shaped denticulations (Figs. 47, 48, 58) and 1 spine-like proterubrence positioned on mid-lateral margin of indentation; subchela with 1 lateral seta and 1 medial seta proximal to base of claw (Fig. 47, 48).

Trunk bearing pedigers 1 and 2 and terminating in genital area, 1.1–1.3 mm (1.2 ± 0.1 mm; 4) long, 0.5–0.6 mm (0.6 ± 0.1 mm; 4) wide, approximately equal to length of cephalosome, having irregular margins, indistinctly segmented, with thin translucent cuticle (Figs. 34–36); pedigers 1 and 2 each bearing a single seta (Figs. 59, 60); genital area comprising paired genital processes and paired genital plates; genital process juxtaposed to lateral margin of genital plate, boot-shaped (Fig. 61); genital plate with indistinct margin partially concealed by genital process and translucent cuticle of trunk.

Abdomen appearing as pair of posteriorly-rounded protuberances issuing paired caudal rami, extending posteriorly relative to genital processes; caudal ramus directed posteriorly, 0.4–0.5 mm (0.5 ± 0.1 mm; 4) long, not inflated, setiform (Fig. 62), with denticulations on distal half, bearing 3 elongate dorsal setae plus 2 abbreviated lateral setae and 2 abbreviated ventral setae.

**Taxonomic Summary**

*Type host:* Gulper shark, *Centrophorus granulosus* (Bloch and Schneider, 1801) (Squaliformes: Centrophoridae).

*Type locality:* 28°20’53.40″N, 86°42’17.40″W; Florida shelf, northeastern Gulf of Mexico (GOM), 220 km southwest of Panama City, Florida.

*Other localities:* Haphazardly selected sites (28°11’56.40″N, 86°9’4.20″W; 28°12’10.80″N, 86°28’30.60″W; 28°31’27.60″N, 86°52’40.80″W) on Florida shelf, northeastern GOM; 28°54’38.40″N, 88°26’10.20″W, south of Mississippi-Alabama border, northern GOM. 28°22’58.80″N, 89°34’7.32″W, Mississippi Canyon, approximately 100 km southeast of Grand Isle, Louisiana, northern GOM.

*Sites of infection:* Skin at base of fins and general body surface.

*Prevalence and intensity:* March/April 2015, north/northeastern GOM off Florida and Mississippi–Alabama border, 40 female and 14 male lernaeopodids infected 10 of 11 gulper sharks (91% prevalence; 5.4 mean intensity); March 2017, northern GOM off Mississippi–Alabama border, 4 female and 3 male lernaeopodids infected 3 of 3 gulper sharks (100%; 2.3).

*Specimens deposited:* Holotype (USNM 1501697), allotype (USNM 1501704), 6 paratype females (USNM 1501698-1501703), 4 paratype males (USNM 1501705-1501708), and 3 paratypes of males attached to females (USNM 1501709-1501711).

*Specimens examined:* One female and 1 male voucher of Neoalbionella sp. (NSMT Cr-20469; *Lernaeopoda longicaudata*; lot comprised of 11 females and 1 male specimen).


*Etymology:* The specific epithet honors George W. Benz (1954–2015) (benz)- for his contributions to our knowledge of *Neoalbionella* spp. and his swashbuckling (-pirata) for discovery (Bullard, 2016, 2017).

**Remarks**

This is the second report of an ectoparasite from *C. granulosus* (Dippennaar, 2004; Pollerspöck and Straube, 2012), the second species of *Neoalbionella* Ozdikmen, 2008 from *C. granulosus*, and the first report of a species of *Neoalbionella* from the Gulf of Mexico.

We attempted to verify our generic diagnosis by referring to the key to genera of Lernaeopodidae in Boxshall and Halsey (2004; p. 777–779) but encountered an error that incorrectly lead to *Brianella* Wilson, 1915, *Charopinus Kröyer, 1863,* and *Pseudocharopinus* Kabata, 1964; all of which have posterior processes located dorsal (vs. ventral) to the oviduct openings in the female. If corrected, the second choice in couplet 14 should go to couplet 21 (“branched processes absent”), then 22 (“abdominal region not
distinct” [less than one-quarter length of trunk and shorter than cephalosome]), 23 (“posterior processes present” [inflated or sausage-shaped, elongated, or reduced and ramus-like]), 26 (“cephalothorax [cephalosome] short, dorsoventrally-flattened”), and 27 (“male cephalothorax [cephalosome] without dorsal swelling; caudal rami not inflated or reflexed”) to reach Neoalbionella (“Albionella”).

We think that “cephalosome” rather than “cephalothorax” should be used in future keys and descriptions of lernaeopodid genera and species. The dorsal cephalic shield of a true cephalothorax covers the anterior 7 or more somites of the habitus (5 cephalic somites plus the first thoracic somite bearing the maxillipled and second thoracic somite with first legs [pediger 1]; the dorsal cephalic shield of a true cephalosome incorporates the anterior 6 somites of the habitus (5 cephalic somites plus the first thoracic somite bearing the maxillipled, excluding pediger 1) (Huys and Boxshall, 1991). The cephalosome condition in adult lernaenopodids is interesting because the infective copepodid stage for some species (Achtheres von Nordmann, 1832; Sabincolina Wilson, 1915; Parabrachiella Wilson, 1915; Tracheliastes von Nordmann, 1832) has a cephalothorax incorporating pediger 1 that eventually separates from the cephalic region of the habitus and subsequently transitions into the cephalosome state in progressive developmental stages (Kabata and Cousens, 1973; Piaseeki, 1989; Ho et al., 2007; Piaseeki and Kuźnińska, 2007). Noteworthy is that no infective copepodid stage has yet been discovered for any species of Neoalbionella.

Kabata (1979) established Albionella to accommodate Lernaeopoda centroscyllii Hansen, 1923, Lernaeopoda etmopteri Yamaguhti, 1939, L. longicaudata Hansen, 1923, and Lernaeopoda globosa Leigh-Sharpe, 1918. He differentiated Albionella from Lernaeopoda Blainville, 1822 by the morphology of their males, namely the males of Albionella, which lack a posterodorsal swelling on the cephalosome and have non-inflated, posteriorly-directed caudal rami. Rubec and Hogans (1988) proposed morphological characters that differentiated females of species of these genera (claw of maxilliped with >1 accessory denticle for Lernaeopoda vs. 1 for Albionella; 2 setae on the maxillule palp for Lernaeopoda vs. 3 setae for Albionella). Özüdemir (2008) later recognized that Albionella was a junior homonym of a genus of jumping spider and, as such, established Neoalbionella to accommodate the 7 species of Albionella.

The new species most closely resembles N. longicaudata by having (1) a cephalosome approximately one-third trunk length in females (approximately equal in males), (2) elongate posterior processes that are > one-half length of trunk in females, (3) 4-segmented antennules in both sexes, and (4) extremely elongate maxillae in females (1.2–2.5× > total body length; variability here depends on the extent of relaxation during fixation or preservation of specimens). Females of N. longicaudata and the new species both have maxillae that are fused for most of their length whereas Neoalbionella globosa (Leigh-Sharpe, 1918) Özüdemir, 2008, Neoalbionella centroscyllii (Hansen, 1923) Özüdemir, 2008, Neoalbionella etmopteri (Yamaguhti, 1939) Özüdemir, 2008, Neoalbionella oviformis (Shiino, 1956) Özüdemir, 2008, Neoalbionella fabricii (Rubec and Hogans, 1988) Özüdemir, 2008, and Neoalbionella kabatai (Benz and Izawa, 1990) Özüdemir, 2008 have maxillae that are fused near the buill only (Kabata 1964, 1979; Rubec and Hogans, 1988; Benz and Izawa, 1990; Benz, 1991a, 1991b).

The female of the new species differs from that of N. longicaudata (see Hansen [1923]) off Iceland by having (1) dorsocephalic sensilla (absent in all congeners), (2) an antennule with 6 apical setae (not detailed for N. longicaudata), (3) an antenna with an exopod having a smooth lateral surface and rugose medial surface plus a thickened dorsal ridge (N. longicaudata with exopod having “at least 1 minute spine... end broadly rounded” in Hansen [1923; p. 55]), (4) an antenna with a terminal segment of the endopod having 3 dorsal and 2 ventral elements (N. longicaudata with endopod having “at least 2 spines on the end, one of them somewhat large and curved” in Hansen [1923; p. 55]), (5) a mandible with 5 basal teeth (not reported in Hansen [1923]), and (6) a labium with 2 anterolateral spines posterior to the distal margin of the fringing setules (4 anterolateral spines in N. longicaudata as per Hansen [1923]). Additional female morphological features included herein were omitted from or generalized in descriptions of N. longicaudata (see Hansen [1923]). These differences are not obvious but we do not regard all of them as cryptic, i.e., Hansen (1923) would have seen them if present because he illustrated features of comparable size in males and females. In specific, Hansen (1923) did not detail the labrum regarding the presence or shape of the rostriform process; however, the new species definitively has a narrow rostriform process that extends beyond the margin of the fringing setules. The illustration of the labrum by Hansen (1923) suggests that the rostriform process is absent in N. longicaudata.

The male of the new species differs from that of N. longicaudata by having (1) an antennule with 6 apical setae on the terminal segment (Hansen [1923] did not determine the number of setae and only described the antennule as slender and 4-jointed), (2) an antenna with a terminal segment of the endopod bearing a bifid distal tubercle (not reported for N. longicaudata), (3) the mandibular formula P2, S1, P1, S1, B5 (not reported in Hansen [1923]), (4) a mediative process (apparently absent in N. longicaudata), and (5) a caudal ramus with a denticulated surface (illustrated as smooth and lacking a denticulated surface by Hansen [1923]; although this feature may have been stylized). Noteworthy is that each male of N. benzipirata was attached to a female by the ventral surface of the genital trunk (at the level of the paired copulatory pores) and between the ventral origins of the posterior processes.

The female of the new species differs from that of N. centroscyllii by having (1) 6 (vs. 7) apical setae on the terminal segment of the antennule, (2) a spatulate and naked exopod of the antenna (vs. bulbous and with “fine spinulation”), (3) a bulla with a prominent sub-circular anchor and thin mandibulum (vs. small anchor with thick mandibulum), and (4) a subchela of the maxillipled with 1 (vs. 2) setae (Kabata, 1964).

The male of the new species differs from that of N. centroscyllii by having (1) 6 (vs. 7) apical setae on the terminal segment of the antennule and (2) lacking an “ovoid” structure on the syncoxa of the maxilla (Kabata, 1964). Noteworthy is that the male and female of N. centroscyllii apparently have 2 (vs. 3) apical setae on the maxillule palp (Kabata, 1964). If one accepts the generic characters for females sensu Rubec and Hogans (1988), then Kabata’s (1964) specimens represent a species of Lernaeopoda or a new genus.

The female of the new species differs from that of N. etmopteri by having (1) 6 (vs. 9) setae on the terminal segment of the antennule, (2) a spatulate and naked (vs. lobate and spinulose)
exopod of the antenna, (3) the mandibular formula P1, S1, P1, S1, P1, S1, B5 (vs. P1, S1, P1, S1, P1, S1, B4), iv) a bulla with a sub-circular anchor and a manubrium (vs. broadly circular and without a manubrium), and (4) elongate posterior processes, each armed with 1 apical seta (vs. vestigial, ramus-like, and armed with 3 ventral spines plus 1 apical seta) (Benz, 1991a).

The male of the new species differs from that of *N. etmosteri* by having (1) 6 (vs. 7) apical setae on the terminal segment of the antennule, (2) a spinulose (vs. naked) exopod of the antenna, (3) a syncoxa of the maxilla with 2 rugose protuberances (vs. 1 rugose and 1 smooth protuberance along distomedial margin), (4) a bifid mediative process without bilobed tips (vs. bilobed tips present), (5) a corpus maxillipeds with an anteriorly-directed denticle along medial margin (vs. without denticle), (6) 1 (vs. 2) seta on pedigers 1 and 2, and (7) 7 (vs. 3) total setae on the caudal ramus (Benz, 1991a).

The female of the new species differs from that of *N. globosa* by having (1) 6 (vs. 7) apical setae on the terminal segment of the antennule, (2) a terminal endopodal segment of the antenna bearing a ventral spinulose process (vs. without ventral spinulose process), (3) the mandibular formula P1, S1, P1, S1, P1, S1, B5 (vs. P1, S1, P1, S1, P1, S1, B4), and (4) a prominent bulla with a sub-circular anchor and a manubrium not obscured by tips of the maxillae (vs. expanded into flat, semicircular pads and manubrium obscured by swollen tips) (Kabata, 1979).

The male of the new species differs from that of *N. globosa* by having (1) 6 (vs. 7) apical setae on the terminal segment of the antennule, (2) a spinulose exopod of the antenna (vs. naked), and (3) the mandibular formula P2, S1, P1, S1, B5 (vs. P2, S1, P1, S1, B6) (Kabata, 1979).

The female of the new species differs from that of *N. kabatai* by having (1) a long trunk not widening posteriorly (vs. short trunk slightly longer than the cephalosome that widens posteriorly), (2) 6 (vs. 7) setae on the terminal segment of the antennule, (3) a spatulate and naked (vs. rounded and denticulated) exopod of the antenna, (4) a labrum with rostriform process (vs. labrum without rostriform process), (5) the mandibular formula of P1, S1, P1, S1, P1, S1, B5 (vs. P1, S1, P1, S1, P1, S1, B4), and (6) a bulla with a sub-circular anchor (vs. ovate), (7) 1 (vs. 2) seta on pediger 1, and (8) elongated and inflated posterior processes (vs. short, vestigial, ramus-like) (Benz and Izawa, 1990).

The female of the new species differs from that of *N. oviformis* by having (1) a cylindrical (vs. ovoid) genital trunk in dorsal view, (2) 6 (vs. 5) setae on the terminal segment of the antennule, (3) a spatulate and naked (vs. bulbous and denticulated at apex) exopod of the antenna, (4) a bulla with a sub-circular anchor and a manubrium (vs. broadly circular, without manubrium), (5) the mandibular formula P1, S1, P1, S1, P1, S1, B5 (vs. P2, S1, P1, S1, B6), and (5) 1 (vs. 2) setae on pedigers 1 and 2 (Benz, 1991b).

Both the male and female of *N. fabricii* have an antennule and mandibular formula unlike that of most members of *Neoalbionella*. Kabata (1979) diagnosed females of *Neoalbionella* (Albionella) and *Lernaeapoda* as having a 4-segmented antennule. Because both sexes of *N. fabricii* have a 3-segmented antennule, the genus may require revision to include a 3 or 4-segmented antennule. Kabata (1979) did not include mandibular dentition in the generic diagnosis of males of *Neoalbionella*. Moreover, Rubec and Hogans (1988) also did not include mandibular dentition as a generic feature for female congeners. The female of *N. fabricii* has a mandibular formula beginning with 2 primary teeth (also in the female of *N. oviformis*; Benz, 1991b) rather than a single primary tooth (as in most *Neoalbionella* spp.) (Rodríguez et al., 2010). The male of *N. fabricii* has 9 primary teeth and lacks secondary and basal teeth (Rubec and Hogans, 1988) whereas all other congeners have 3 primary teeth, 2–3 secondary teeth, and 3–6 basal teeth (Rodríguez et al., 2010).
Shiino [1956] material) or new material collected to verify those features and those associated with the genital area and caudal ramus of the male. The terminal segment of the female antennule had 5 setae and its antenna had an exopod with a granulose surface (“granulose at apex” of Shiino [1956; p. 272]), which is lacking in *N. benzipirata*. We also observed 6 apical setae in the male specimen, as illustrated by Shiino (1956; fig. 3D, p. 274), who described it as, “terminal joint [segment] tipped with few [sic] spines,” (p. 272); which, interestingly, does not match the female. Characterization of the male caudal ramus will require study of more specimens due to putative artifact (broken or lost setae). Given the subtlety of differences between specimens of *N. benzipirata* and *Neoalbionella* sp. (see Shiino, 1956), genetic sequence data could help test the taxonomic usefulness of these morphological features.

We tried to locate Fernández-Ovies’ (1992) voucher specimens of “*N. longicaudata*” that were sent to Roger Cressey (Smithsonian Institution, Department of Invertebrate Zoology). However, those specimens evidently were not accessioned at the museum (C. Walter, USNM, pers. comm.). This record is curious regarding the antennule and maxillule, which are identical between those female and male specimens. Specifically, the antennule terminal segment was illustrated as having 5 apical setae (Fernández-Ovies [1992]; fig. 3, p. 98), and the maxillule lateral exopod is illustrated as having 2 (vs. 3) setae. If details of the antennule are correct, then this species is distinct from *N. benzipirata*. Further, if those details of the maxillule lateral palp are accurate, those specimens may not belong to *Neoalbionella*. We emphasize, however, that the maxillule lateral palp setae are fragile and may be easily missed or damaged. This is likely, given that Fernández-Ovies (1992) illustrated glycerin-mounted appendages of a single male and female pair (out of 13 male–female pairs). Moreover, Fernández-Ovies (1992) did not describe spinulation on the dorsal margin of the praecoxal endite, which is further evidence against conspecificity with the new species in the Gulf of Mexico.

**DISCUSSION**

We herein detail features in the new species that have seldom or previously not been used to compare *Neoalbionella* spp., i.e., details associated with the female’s dorsocephalic shield, the mouth cone labium of both sexes, and the male’s mediative process. The number, shape, size, and distribution of dorsocephalic sensilla, which could be neotenic (present in copepodids and adults), could be an important taxonomic feature for lernaeopodids, but they are seldom described and perhaps commonly missed or overlooked. Piasecki (1989; see figs. 8, 9, p. 192 therein) detailed sensilla on the cephalosome of the copepodid of *Trachelastes maculatus* Kollar, 1835. Dippenaar and Jordaan (2008) reported a series (n = 6) of spherical hyaline papillae symmetrically arranged along the anterior margin of the cephalosome of *Naobranchia kabatana* Dippenaar and Jordaan, 2008. The presence/absence, shape, number, and arrangement of spines on the outer surface of the labium could differentiate *Neoalbionella* spp. and may be informative in diagnosing other genera. Although similar structures associated with the labium are reported from members of other siphonostomatoid families, these features are difficult to see. The labium of *Lernanthropus gisleri* van Beneden, 1852 (*Lernanthropidae*) has 2 sharply-pointed spines (Kabata, 1979; fig. 1061); that of *Endacytina acuta* van
Beneden, 1853 (Eudactylinidae) has 16 thin, elongate “setae” (Kabata, 1979; fig. 1185); and Lernaeocera branchialis (Linnaeus, 1767) (Pennellidae) has a “labium with short distal barb” (Kabata, 1979; fig. 1355). The shape of the mediative process, which is positioned immediately posterior to the bases of maxillae in males, differentiates Neoalbionella spp. The new species has a bifid mediative process. The males of only 5 species of Neoalbionella have been described (Table I): Hansen (1923) and Shiino (1956) did not describe the mediative process in the males of N. longicaudata; Kabata (1964; p. 686) described it as, “a small tubercle known as the mediative process” for N. centrosycyllii; Kabata (1979; p. 381) described it as “process bifid, its branches short, inflated and bulbous” in N. globosa; Rubec and Hogans (1988) did not describe it telegraphically but illustrated the mediative process as a long, thin, and posteriorly-directed structure in N. fabricii; and Benz (1991a; p. 667) characterized it as “process bifid, both tips bilobed, tips of lobes blunt” for N. etmopteri.

We herein documented that the fine details of 4 appendages are similar, if not identical, between sexes of the new species; i.e., details of the setae on the terminal segment of the antennule, armature of the terminal endopodal segment of the antenna, basal tooth number of the mandible, and mouth cone labium. At least 2 other species of Neoalbionella also share similarities with those appendages between sexes. Specifically, the number and configuration of antennule apical setae and the morphology of the terminal endopodal terminal segment are similar for males and females of N. globosa (Kabata, 1979); the number of mandibular basal teeth (n = 5) in males and females of N. centrosycyllii are also identical (Kabata, 1964). Morphology of the labium, however, has not been matched between males and females of any other species of Neoalbionella besides that of the new species.

No worker has compared the number of collected males and their attachment sites on females among Neoalbionella spp. A total of 17 of 44 female specimens (39%) of the new species had males attached and none exhibited signs of decay, indicating that they were alive. All 14 males were attached to the ventral surface of a female at the level of the paired copulatory pores. Nearly all species of Neoalbionella have males that attach in this way; only that of N. fabricii was observed on the tip of the posterior process of a female (Rubec and Hogans, 1988). The original description of the type species, N. globosa, included 3 females, 2 of which had males attached (67%); the males were not treated with the original description of females but Kabata [1979] thoroughly described those museum-deposited male type specimens. Hansen (1923) described a single ovigerous female of N. centrosycyllii whereas Kabata (1964) provided the first account of the male found attached to 1 of 3 ovigerous female specimens (33%). The original description of N. longicaudata (Hansen, 1923) comprised 2 ovigerous females and 1 male (50%; the attachment site of the male was not reported therein). The report provided by Shiino (1956) included 11 females and 1 attached male specimen (9%) of N. longicaudata (Shiino [1956]; fig. 1A). Yamaguti (1939) originally described a single specimen of an adult-ovigerous female (no male was found) of N. etmopteri. Shiino (1956) provided the first description of a single male of N. etmopteri attached to 1 of 3 females (33%). Further, Benz (1991a) reported 11 of 18 females of N. etmopteri with attached males (61%).

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**LITERATURE CITED**


