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A review of the genus *Zonophryxus* Richardson, 1903 (Crustacea: Isopoda: Dajidae) with recognition of *Colypurus agassizi* Richardson, 1905 (Crustacea: Isopoda: Colypuridae) as a synonym of *Zonophryxus similis* Searle, 1914 and the requisite sinking of Colypuridae

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Abstract.—All species in the epicaridean isopod genus *Zonophryxus* Richardson, 1903 are reviewed, and information regarding host choice is summarized. The enigmatic species *Colypurus agassizi* Richardson, 1905 is shown to be synonymous with *Zonophryxus similis* Searle, 1914, and *Colypurus* Richardson, 1905 and Colypuridae Richardson, 1905 are synonymized with *Zonophryxus* and Dajidae, respectively. The correct name for the species is *Zonophryxus agassizi*, new combination. The existence of two distinct male morphotypes in at least some species of *Zonophryxus* is confirmed and discussed. Type and other material of *Zonophryxus retrodens* Richardson, 1903 and *Zonophryxus trilobus* Richardson, 1910 were examined, and these species are discussed and illustrated, including description of morphological structures either erroneously or not previously reported. New material of *Zonophryxus dodecapus* Holthuis, 1949 is reported on, with the discovery that females of the species can have either five or six pairs of pereopods independent of their developmental stage. A new species, *Zonophryxus probisowa*, is described from Peruvian material and named in honor of The Proceedings of the Biological Society of Washington on the occasion of this, its final volume.

Keywords: dajid, deep-water, Epicaridea, isopod, new species, parasite, shrimp hosts

Most isopods belonging to Dajidae G. O. Sars, 1883 (59 species) are ectoparasitic on euphausids, mysids, and shrimp as definitive hosts, although some are known from isopods, anomurans, and brachyurans with a number of species described without known hosts (Boyko et al. 2008 onwards). As with other epicarideans, dajid life cycles also include copepods as intermediate hosts (Coyle & Mueller 1981). Typically, adult females attach to the dorsal carapace (euphausids and shrimp) or within the marsupia (mysids) of hosts; however, in some cases they attach to the eyestalks, antennules or pereopods of definitive hosts (Williams & Boyko 2021). Regardless of position on the hosts, all dajid females pierce the cuticle with styliform mandibles and feed on hemolymph of hosts and some have been shown to reduce reproduction and impact secondary sexual characters (e.g., Field 1969,

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Shields & Gómez-Gutierrez 1996, Nagler et al. 2020).

The genus *Zonophryxus* Richardson, 1903 is currently comprised of six species (Boyko et al. 2008 onwards), most known parasitizing caridean hosts primarily in Pandalidae and rarely in Nematocarcinidae in relatively deep water (210–1401 m) in the Atlantic, Pacific, and Antarctic (Southern) Oceans. The bodies of females are ovate and dorsally swollen, often showing little to no dorsal segmentation, with no visible appendages in dorsal view, and with a row of triangularly-shaped processes along the posterior border of the body, giving the posterior end a "notched" appearance (Kensley 1979). Females of *Zonophryxus* are oriented with their head toward the posterior end of the host and with mouthparts positioned toward the posterior end of the dorsal surface of the host carapace (see Fig. 4), corresponding to the region of the heart of the host into which they insert their mouthparts. They possess five or six pairs of pereopods for attachment to the host cuticle. The first five pairs of pereopods are clustered around the head and used to clutch onto the host carapace with their dactyli, possibly aided by the ventral surface being closely applied to the carapace and acting as a "suction-cup" (Brandt & Janssen 1994, Nagler et al. 2020). When present, the sixth pair of pereopods is positioned at the base of the sixth oostegite; it is not known if these posterior pereopods also aid in attachment.

Males of *Zonophryxus* species are of two types, probably part of a developmental series: one similar to those seen in other dajid genera (e.g., *Holophryxus* Richardson 1905a) and another that is quite different, with larger pereomeres, a head bearing dorsal lobes, and a ventrally displaced pleon with all pleomeres fused into a single segment. The unusual morphology of this second type of male led Richardson (1905b) to remark that the holotype of *Colypurus agassizi* Richardson, 1905 did "not seem to belong to any of the known families of the order," although she did not specify what characters she considered distinctive. Because of the novel morphology of this specimen, Richardson (1905b) used it as the basis for her description of a new species, genus, and family of uncertain relationships with other isopods. Richardson (1905b) did not make note of the sex of the specimen and thought that the specimen was a parasite; this is not strictly correct as only epicaridean females directly parasitize their hosts (i.e., pierce the host and feed on hemolymph).

In the present paper, we show that *Colypurus agassizi* Richardson, 1905 is the male of *Zonophryxus similis* Searle, 1914, and that *Colypurus* Richardson, 1905 and Colypuridae Richardson, 1905 are junior synonyms of *Zonophryxus* and Dajidae, respectively. Additionally, we describe a new species based on a pair of specimens collected in Peruvian waters. We also review all the species in the genus and provide morphological details about species that were incompletely described and/or illustrated in earlier publications. Finally, we discuss the variable number of pereopods found in females, a feature previously considered a species-specific character but shown herein to represent phenotypic plasticity. A key to species is provided based on female characters because mature and immature males are not known for all species.

Materials and Methods

Line drawings were made with a camera lucida drawing tube attached to Olympus compound or dissecting microscopes. Final images were created by tracing a scanned copy of the original sketch with a Wacom tablet or Wacom Cintiq pen display using Adobe Illustrator. In addition to conventional light micrographs, the holotype of *Zonophryxus similis* Searle, 1914 (USNM 46432) was imaged with a Macropod Pro kit (MacroscopicSolutions), and resulting pictures were aligned

and stacked with the focus stacking software Zerene Stacker (10 images from bottom to top of specimen).

Note that when Harriet Richardson married William Searle in 1913, she took his name as Harriet Richardson Searle but published only three papers using the latter name (Damkaer 2000). The 1914 paper in which *Z. similis* was described is often cited as "Richardson 1914," but the header on alternating pages reads "Searle: Isopoda" and so we attribute authorship of the species to Searle, rather than Richardson or Richardson Searle.

Specimens were borrowed from and deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). References are provided for taxonomic authorities of isopod taxa but not for those of decapod hosts. This work is registered in ZooBank with the registration number urn:lsid:zoobank.org:pub:E208CA4D-D822-4B14-828A-73EED7A8FE38.

Systematic Account

Isopoda Latreille, 1817

Epicaridea Latreille, 1825

Cryptoniscoidea Kossmann, 1880

Dajidae G. O. Sars, 1883

Dajidae G. O. Sars, 1883:19.
Colypuridae Richardson, 1905b:105 (n. syn.).

Remarks.—As shown below, the male holotype of *Colypurus agassizi* belongs to the same species as the female holotype of *Zonophryxus similis* Searle, 1914 and, consequently, Colypuridae is a junior synonym of Dajidae.

Zonophryxus Richardson, 1903

Zonophryxus Richardson, 1903
Colypurus Richardson, 1905b:105–106 (n. syn.).

Type species.—*Colypurus agassizi* Richardson, 1905 by monotypy; *Zonophryxus retrodens* Richardson, 1903 by original designation.

Diagnosis.—Female. Body symmetrical, ovate, longer than broad, dorsally convex; body regions indistinct in dorsal view; appendages not visible in dorsal view; head, pereon, and pleon fused. Well-developed anterior margin (frontal lamina) and thin lateral margins on ventral surface. Antennules as recurved flat lobes, posteriorly tapering and surrounding buccal cone. Antennae small, digitiform. Sternal plate distinct. Six pairs of oostegites but sixth pair variously fused to posterior margin of fifth. Adults with five or six pairs of isomorphic pereopods; sixth pair (if present) near posterior margin of body at bases of oostegite 6 pair. Pleon lacking appendages or uropods. Posterior margin of body with row of triangularly-shaped processes (margin appears "notched").

Male body flattened. Head ovate, fused with first segment of pereon. Antennules minute, rounded; antennae elongate, blade-like. Pereon with 6 free segments. Seven pairs of isomorphic pereopods. Pleomeres fused with pleotelson into single ovate pleon, without segmentation or appendages. Type 1 male ("*Zonophryxus*-type") head ovate, sloping from posterior to anterior, more or less smooth. Pereomere 7 smaller than pereomere 2. Pleon extending posteriorly from pereomere 7. Type 2 male ("*Colypurus*-type") head with distinct medial and lateral lobes. Pereomere 7 larger than pereomere 2. Pleon ventrally displaced under pereomere 7.

Remarks.—As shown below, the male holotype of *Colypurus agassizi* belongs to the same species as the female holotype of *Zonophryxus similis* and, consequently, *Colypurus* is a junior synonym of *Zonophryxus*. The only clear synapomorphy for *Zonophryxus* is the presence of the triangularly-shaped processes on the posterior of the body in females; it is possible that the type 2 male morphology, not known to occur in males of other dajid genera, is also a synapomorphy for the genus, but this

male form has not been found in all species to date. However, this is perhaps not surprising as the number of specimens known for any of the species in the genus is small.

Richardson (1903) incorrectly interpreted the sixth oostegites of the female as a pair of pleopods; examination of specimens bearing six pairs of pereopods clearly shows that these are oostegites. She also identified the row of triangularly-shaped processes at the posterior end of the body as "coalesced abdominal segments" but they represent the remnants of only the lateral margins of the pleon (see Kensley 1979: Fig. 2).

Prior to the present study, no females of any species of *Zonophryxus* have been reported as ovigerous. We are not aware of any other documented cases of dajids with two morphological types of males such as the presumed immature type 1 males and mature type 2 males found in species of *Zonophryxus*. Developmental studies are needed to determine whether molt(s) are involved and verify the sexual immaturity/maturity of the morphotypes. We know of one species that possesses two male morphotypes in Bopyridae (see *Parathelges aniculi* (Whitelegge, 1897) in Williams & Boyko 2016), but this may represent a case of cryptic species rather than development.

Zonophryxus agassizi (Richardson, 1905), new combination
Figs. 1, 2

Colypurus agassizi Richardson, 1905b:106, Figs. 1, 2 (06°36′N, 81°44′W, off Mariato Point, south of Coiba Island, Panama (Pacific).—Searle, 1914:370–371 (description after Richardson 1905b).—Nierstrasz & Brender à Brandis, 1923:112 (list).—Brusca, 1987:273 (mention).—Markham, 2020:150 (list).

Zonophryxus similis Searle, 1914:369–370, Fig. 16 (06°36′N, 81°44′W, off Mariato Point, south of Coiba Island, Panama (Pacific).—Holthuis, 1949:212 (mention).—Danforth, 1970c:31 (mention), 52 (list), 155 (key), Fig. 44f, g (after Searle, 1914).—Lopretto, 1983:96 (key).—Brandt & Janssen, 1994:343, 350 (mention).—Shimomura et al., 2010:9, 10 (list).—Markham, 2020:151 (list).—Nagler et al., 2020:342 (list).

Zonophryxus similes [*sic*] Raupach & Thatje, 2006:439 (mention).

Material examined.—Mature holotype male (5.0 mm TL) of *Colypurus agassizi*, "Albatross" Sta. 4621, 06°36′N, 81°44′W, off Mariato Point, south of Coiba Island, south coast of Panama (Pacific), 581 fms (=1063 m), 21 Oct 1904 (USNM 46433). Mature holotype female (17.4 mm TL) of *Zonophryxus similis*, "Albatross" Sta. 4621, 06°36′N, 81°44′W, off Mariato Point, south of Coiba Island, Panama (Pacific), 581 fms (=1063 m), 21 Oct 1904 (USNM 46432).

Type locality.—06°36′N, 81°44′W, off Mariato Point, south of Coiba Island, Panama (Pacific).

Range.—Known only from the type locality.

Depth.—1063 m.

Size.—Female 17.4 mm TL; male 5.0 mm TL.

Host.—Unknown (no shrimp species from "Albatross" Station 4621 in the USNM online catalog).

Redescription.—Female body ovate, head, pereon, and pleon fused, widest in middle, dorsally convex (Fig. 1A, B); small notches visible on lateral margins indicating some pereon segments; eleven closely approximated triangularly shaped processes on posterior margin of body short, not visible in dorsal view (Fig. 1A, F). Ventral side of body concave, with five pairs of isomorphic pereopods closely approximated from head to midpoint of body (Fig. 1A, D, E). Antennules as recurved flat lobes, posteriorly tapering and surrounding buccal cone (Fig. 1A, C). Antennae

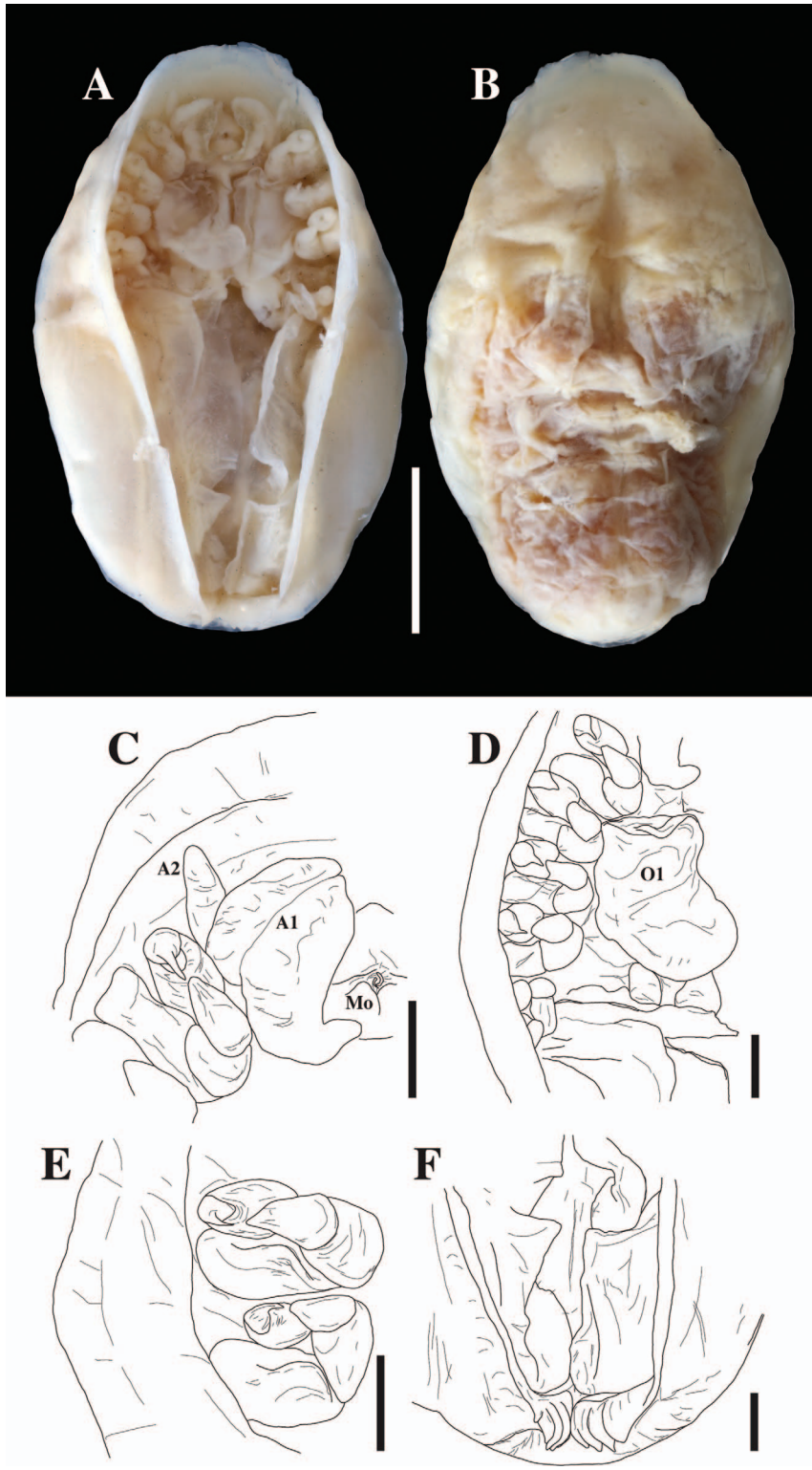

Fig. 1. *Zonophryxus similis* Searle, 1914 (= *Zonophryxus agassizi* (Richardson, 1905) holotype female (A–F) (USNM 46432). A, ventral view. B, dorsal view. C, mouthparts (Mo), antennule (A1), antenna (A2), and pereopod 1, right side. D, oostegite 1 (O1) and pereopods 1–5, right side. E, pereopods 4 and 5, right side. F, posterior end, ventral view, showing oostegite 6 and triangularly-shaped processes on posterior margin. Scale bars: A, B = 5 mm; C–F = 1 mm.

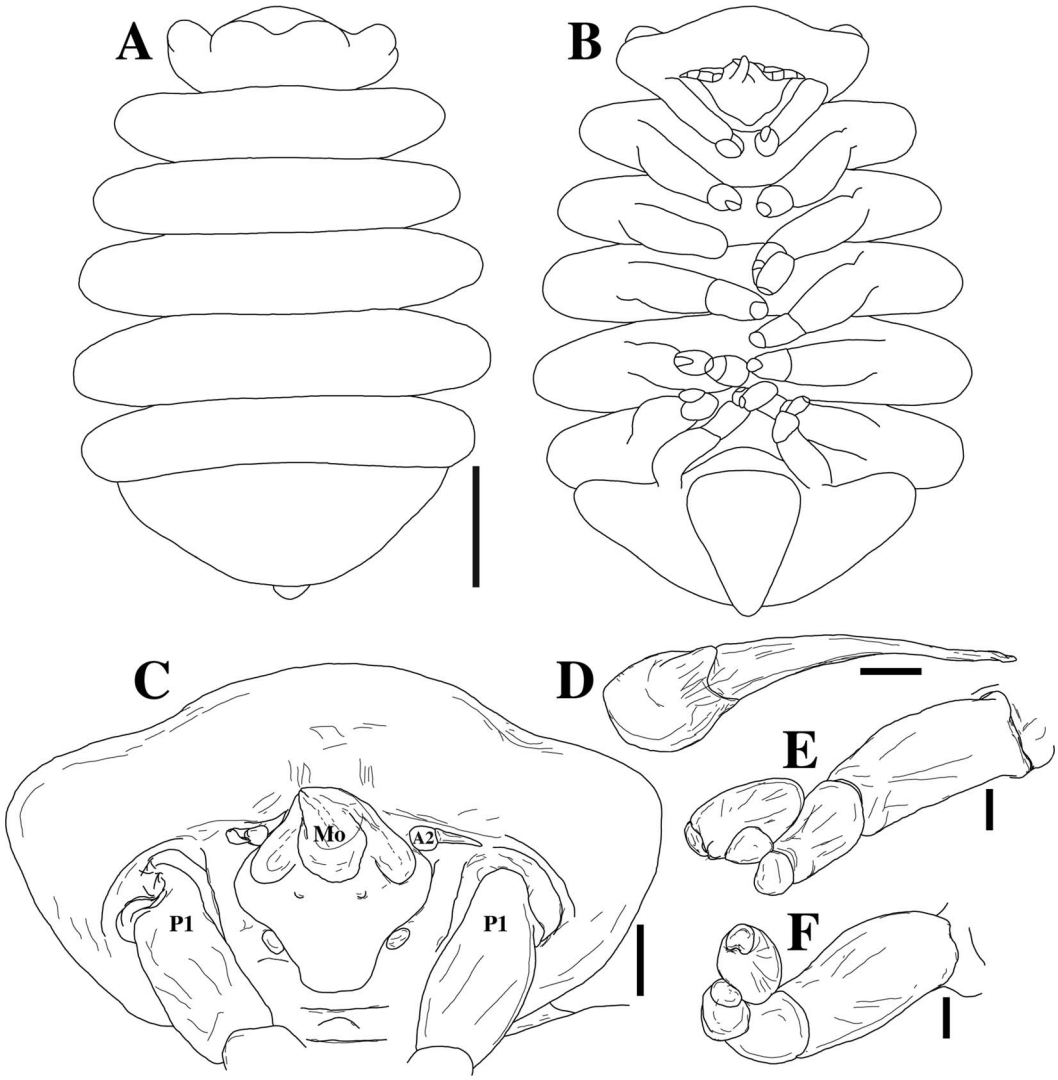

Fig. 2. *Colypurus agassizi* Richardson, 1905 (= *Zonophryxus agassizi* (Richardson, 1905)), holotype type 2 male (A–F) (USNM 46433). A, dorsal view. B, ventral view. C, mouthparts (Mo), antenna (A2, labeled only on left side), and basis of pereopod 1 (P1). D, antennae, left side. E, pereopod 1, right side (rotated). F, pereopod 7, left side. A, B redrawn from Richardson (1905b). Scale bars: A, B = 1 mm; C = 200 μm; D = 50 μm; E, F = 100 μm.

small, digitiform, situated behind and extending anterolaterally from antennules (Fig. 1C). Maxilliped not dissected out. Sternal plate distinct below oral cone, triangular in shape at anterior end and continuing as ridge between oostegites (Fig. 1A). Oostegite 1 large with subquadrate anterior lobe and rounded posterior lobe (Fig. 1D); oostegite 5 large, subquadrate, basally fused to small, subquadrate oostegite 6 (Fig. 1A, F), both with some minute setae on margins.

Type 2 male dorsoventrally flattened (Fig. 2A, B). Head with lateral rounded extensions, narrower than pereomere 1, dorsal surface with two large lobes (Fig. 2A). Antennule a small indistinct lobe bearing few setae, merged with frontal

margin (not visible in figures). Antennae of two segments, tapering blade-like distal segment more than four times as long as rounded basal segment (Fig. 2C, D). First pereomere fused with head, followed by six free pereomeres, slightly wider posteriorly; all pereomeres laterally directed (Fig. 2A). Seven isomorphic pereopods present (Fig. 2B, E, F). Pleomeres fused with pleotelson, forming single ovate, elongate pleon (Fig. 2A, B). Pleon ventrally displaced, affixed near anteroventral margin of pereomere 7 and extending posteriorly, slightly visible in dorsal view, lacking pleopods or uropods (Fig. 2A, B).

Remarks.—The male holotype of *C. agassizi* is a type 2 male and is very similar to one of the male morphotypes found in *Z. quinquedens* (see Lopretto 1983, Brandt & Janssen 1994) and, as such, is easily recognizable as a male belonging to *Zonophryxus*; *Colypurus* and *Zonophryxus* are therefore synonymous. The male of *C. agassizi* was likely paired with the female holotype of *Z. similis* in life; this is inferred based on the fact that they were collected from the same station on the same day. Given the rarity of *Zonophryxus* species in samples, the likelihood of a second species in the genus occurring in the same sample is small, and we consider the two species synonymous as well. Although *Colypurus* is a junior synonym of *Zonophryxus*, the specific name *C. agassizi* is the senior synonym of *Z. similis* and so the correct name for the species is *Zonophryxus agassizi*.

Richardson (1905b) stated that the holotype of *C. agassizi* was in the Museum of Comparative Zoölogy (Harvard University), but for reasons unknown, it was deposited in the USNM; Searle (1914) cited the catalog of the specimen as USNM 46433. Intriguingly, the USNM catalog numbers of the two holotypes are sequential, despite their being described nine years apart. Was this merely a coincidence or did Searle (née Richardson) recognize the relationship between the two specimens but never publish on it?

Searle (1914) stated of the female of *Z. similis* that "the antennae are widely separated and seem to be composed of three articles. The antennulae are concealed by the maxillipeds." It appears that Searle (1914) interpreted the antenna and antennule as one structure, hence the supposed three segments. The antennule is not obscured by the maxilliped in any species of *Zonophryxus*. Only the type 2 male is known from this species.

Zonophryxus retrodens Richardson, 1903
Fig. 3A–L

Zonophryxus retrodens Richardson, 1903:52, Figs. 4, 5 (Oahu, Hawaii), 1904:678, 679, Figs 32, 33 (after Richardson, 1903), 1910:41 (mention).—Koehler, 1911:18, 21, 22, 33 (mention).—Searle, 1914:370 (mention).—Holthuis, 1949:212 (mention).—Danforth, 1970a:27 (mention), 1970b:462 (mention), 1970c:31, 32, 52 (mention), 128 (description after Richardson, 1903), 155 (key), Fig. 44C–E (figures after Richardson, 1903), 1976:79 (mention).—Brandt & Janssen, 1994:350 (mention).—Moore, 2004:82 (list).—McLaughlin et al., 2005:189 (list).—Raupach & Thatje, 2006:439 (mention).—Shimomura et al., 2010:9–17, Figs. 1–7 (32°09.015′N, 129°30.259′E–32°09.034′N, 129°31.725′E, 499–496 m, ex *Plesionika semilaevis* Spence Bate, 1888).—Shimomura, 2017:110 (mention).—Markham, 2020:151 (list).

Material examined.—Mature syntype female (12.4 mm TL), mature syntype male (3.4 mm TL), "Albatross" Sta. 3815, south coast, southeast of Diamond Head, Oahu Island, Hawaii, 228–312 fms (=417–571 m), 28 Mar 1902 (USNM 28970).

Type locality.—Off Oahu Island, Hawaii, 417–571 m.

Range.—Hawaii and Japan.

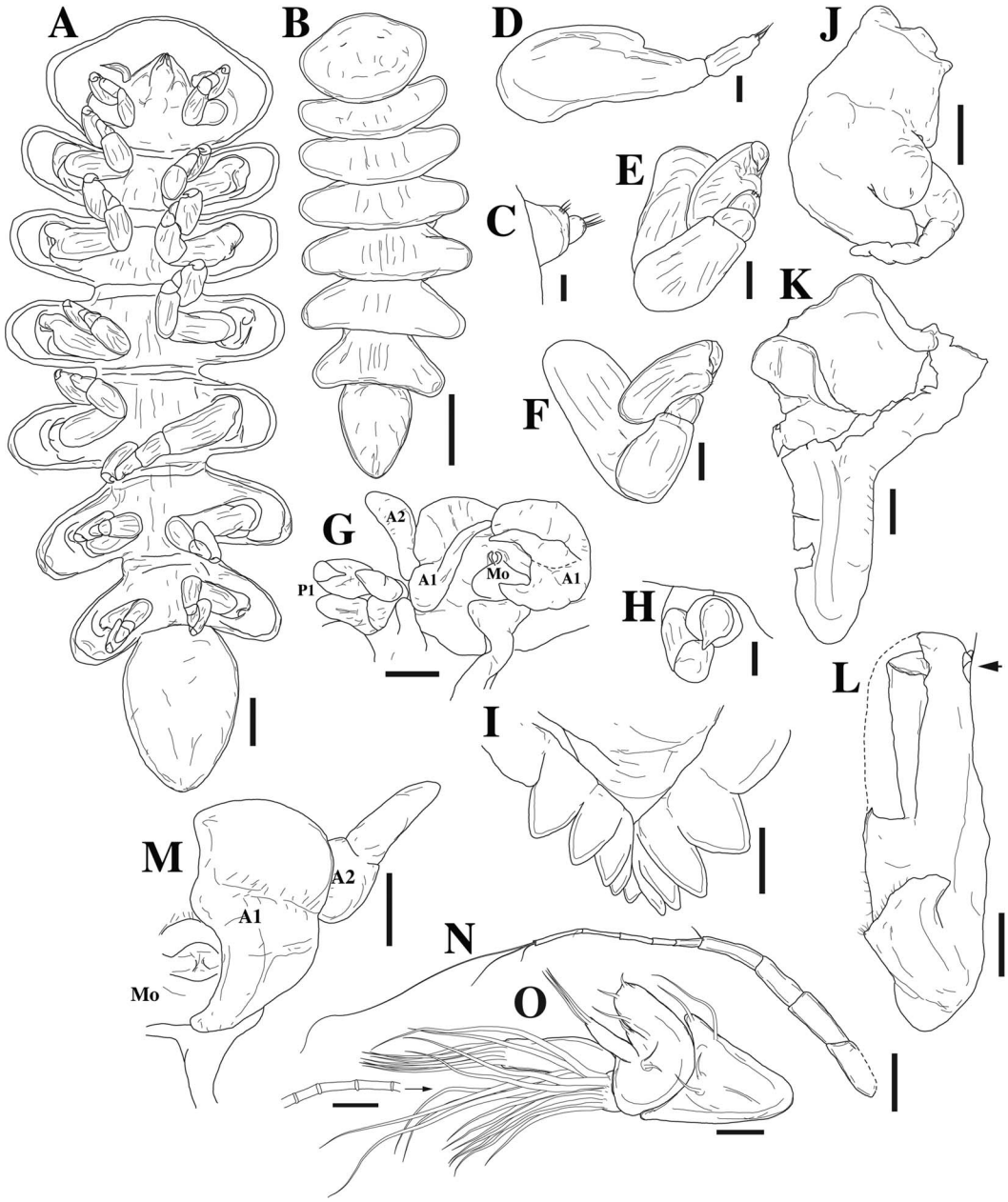

Fig. 3. *Zonophryxus retrodens* Richardson, 1903, male (A–F) and female (G–L) (USNM 28970) and *Zonophryxus trilobus* Richardson, 1910, female holotype (M) and cryptoniscus larva (N, O) (USNM 189065). A, ventral view. B, dorsal view. C, antennule, left side. D, antenna, left side. E, pereopod 1, right side. F, pereopod 7, left side. G, mouthparts (Mo), antennule (A1), antenna (A2, shown only on right side), and pereopod 1 (P1). H, pereopod 5, right side. I, posterior end, ventral view, showing terminal teeth. J, left maxilliped and appendix (sensu Rustad 1935). K, left oostegite 1. L, oostegites 5 and 6, arrow shows pereopod 5. M, mouthparts (Mo), antennule (A1), antenna (A2, shown only on left side). N, right antenna, dashed line shows portion of basal segment obscured by antennule. O, right antennule; inset shows ridges along brush setae. Scale bars: A = 200 μm; B, G, I, K–M = 500 μm; C = 10 μm; D, H, O = 20 μm (O inset = 10 μm); E, F, N = 50 μm; J = 1 mm.

Depth range.—417–571 m.

Size range.—Female to 12.4 mm TL; male to 3.4 mm TL.

Hosts.—Type host unknown (but see Remarks); also found on *Plesionika semilaevis* Spence Bate, 1888.

Redescription.—Female body ovate, head, pereon and pleon fused, widest in middle, dorsally convex; small notches visible on lateral margins indicating some pereon segments; nine triangularly-shaped processes on posterior margin of body short, scarcely visible in dorsal view, broadly separated laterally (Fig. 3I); small notches visible on lateral margins indicating some pereonal segments. Ventral side of body concave with five pairs of isomorphic pereopods closely approximated from head to midpoint of body (Fig. 3G, H). Antennules as recurved flat lobes, posteriorly tapering and surrounding buccal cone (Fig. 3G). Antennae small, digitiform, situated behind and extending anterolaterally from antennules (Fig. 3G). Maxilliped of two ovate lobes, anterior margin irregular, posterior margin rounded; appendix digitiform, slightly curved, attached to side of posterior lobe (Fig. 3J), hooked around oostegite 1 when in situ. Sternal plate distinct below oral cone, triangular in shape at anterior end and continuing as ridge between oostegites (Fig. 3G). Oostegite 1 large with subquadrate anterior lobe and recurved, tapering posterior lobe (Fig. 3K), internal ridge smooth; oostegite 5 large, subquadrate, basally fused to small, ovate oostegite 6 (Fig. 5L), both with setose margins.

Type 1 male dorsoventrally flattened (Fig. 3A, B). Head ovate, fused with pereomere 1. Antennule small, rounded, bearing few terminal setae, superficially appearing to be composed of two articles (Fig. 6C; see Remarks); antennae with two articles, large basal article with anterior notch and small digitiform terminal article with setae (Fig. 3D). Pereomeres 2–6 free, maximal width at pereomere 4; pereomeres 2 and 3 anterolaterally curved, 4 and 5 laterally directed, 6 and 7 posterolaterally directed (Fig. 3A, B). Seven isomorphic pereopods present (Fig. 3E, F). Pleomeres fused with pleotelson, forming single ovate, elongate pleon, lacking pleopods or uropods (Fig. 3A, B).

Remarks.—The type host is unknown, but two potential species, cataloged in the USNM with the same collection and station data as the syntypes, are *Heterocarpus ensifer* A. Milne-Edwards, 1881 and *Aristeus semidentatus* Spence Bate, 1881.

Only the type 1 male is known from this species. The largest female reported by Shimomura et al. (2010) was the same size as the female syntype and the types match in most respects the redescription by these authors, although there is a large geographical distance separating the two collection localities. Shimomura et al. (2010) also used SEM to examine fine morphological details, including setules on the antennae and other structures of females, observed herein for this species and the others studied (as well as for *Z. quinquedens* by Brandt & Janssen 1994). Shimomura et al. (2010: Fig. 2C) incorrectly drew the antennule and antenna of the female, showing the anterior portion of the antennule as contiguous with the antenna rather than the posterior portion of the antennule (see Fig. 3G herein); however, their description and SEM image of these structures were accurate. The antennules are similar to those in species of the genus *Holophryxus*, and Rustad (1935) suggested they "probably serve as stuffing during sucking, thus increasing the sucktive power" while feeding on host hemolymph. This conclusion has recently been supported by Nagler et al. (2020) who also suggested that additional mouthparts function in sealing the wound to enhance sucking during feeding. In addition, the maxilliped and appendix are similar between species of *Zonophryxus* and those of other dajid genera; the appendix hooks around oostegite 1 and the presumed function is to regulate water flow and

prevent the escape of ova and larvae (Rustad 1935, Williams & Boyko 2021).

The antennules of the male (Fig. 3C) each appear to have two segments, but this may represent a crease in the cuticle; both specimens examined by Shimomura et al. (2010; Fig. 7B, C) have a single rounded lobe, as does the male of the new species of *Zonophryxus* (Fig. 6D) described herein.

Zonophryxus trilobus Richardson, 1910
Fig. 3M–O

Zonophryxus trilobus Richardson, 1910:41, Fig. 39 (off Caluya Island, Philippines, 571 m).—Searle, 1914:370 (mention).—Holthuis, 1949:212 (mention).—Danforth, 1976:79 (mention).—Kensley, 1979:665–670, Figs. 1–3 (Makyan Islands, Indonesia, 503 m, ex *Heterocarpus gibbosus* Spence Bate, 1888).—Lopretto, 1983:96 (key).—Brusca & Wilson, 1991:160 (mention).—Brandt & Janssen, 1994:350 (mention).—Trilles, 1999:284, 298, Figs. 8.4C, 8.18 (figured after Kensley 1979).—Raupach & Thatje, 2006:439 (mention).—Shimomura et al., 2010:9, 10, 17 (mention).—Sidabalok, 2013:61 (list).—Suharsono, 2014:156 (list).

Material examined.—Mature holotype female (13 mm TL), "Albatross" Sta. 5259, off Caluya Island, Philippines, 11°57′30″N, 121°42′15″E, 312 fms (=571 m), 3 June 1908 (USNM 40927).—3 immature females (3.0–5.0 mm TL), 2 mature males (1.4 mm TL each), 1 cryptoniscus larva (1.0 mm TL), "Albatross" Sta. 5622, west of Halmahera, Makyan Islands, Indonesia, 0°19′20″N, 127°28′30″E, 503 m, 29 Nov 1909 (USNM 189065).

Type locality.—Off Caluya Island, Philippines, 11°57′30″N, 121°42′15″E, 571 m.

Range.—Philippines and Indonesia; possibly from Western Samoa (see Remarks).

Depth range.—503–571 m.

Hosts.—Type host unknown; *Heterocarpus gibbosus* Spence Bate, 1888.

Size range.—Females to 13 mm TL; males to 1.4 mm TL.

Redescription.—See Kensley (1979).

Remarks.—The host of the holotype is unknown; however, Chace (1985) identified the potential hosts from Sta. 5259, the station at which the holotype was collected, as *Plesionika bifurca* Alcock & Anderson, 1894, *Plesionika semilaevis* Spence Bate, 1888, and *Plesionika spinidorsalis* (Rathbun, 1906).

No specimens of *Heterocarpus gibbosus* Spence Bate, 1888, the host of Kensley's (1979) specimens, were cited from this station. The hosts for Kensley's (1979) non-type specimens are not in the vial with the parasites, but two of three of the immature females were said to each be attached to a *H. gibbosus* (Kensley 1979; size and sex of host unknown). Chace (1985) cited nine male (13.1–33 mm CL) and 12 female (27.2–32.2 mm CL) *H. gibbosus* from the same station as the parasites from this station of which at least two probably the same host specimens cited by Kensley (1979).

A few details of the description by Kensley (1979) require clarification. He noted that the female holotype had an antenna with "a simple digitiform process attached to outer region of antennular lamella." However, the antenna is not fused (unless very basally, see Fig. 3M), it is clearly separated from the antennule (unlike in his Fig. 3A which shows the antennules and antennae as one large plate). Kensley (1979) drew the antennule of the cryptoniscus larva accurately (compare his Fig. 1A with Fig. 3O herein); however, he described the second segment of the antennule as "tripartite" (cited by Brusca & Wilson (1991) as a "trilobed second article") but which is not of three parts as this segment bears a small, slender articulated ramus on the distomedial margin that is not, strictly speaking, part of the segment. Additionally, Kensley (1979) drew the antenna of the cryptoniscus larva with four basal and two flagellar

segments and described them as "of 4 relatively elongate proximal segments, and few distal articles (some possibly missing)," but the right antenna (Fig. 3N) shows the characteristic 4+5 basal and flagellar segment count of dajids (Boyko & Williams 2015). Only the type 1 male is known from this species.

There is a female specimen, probably of this species, in the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie; RMNH.CRUS.I.6430; not examined) with an erroneous spelling of the species name as "tribbus" on the label; it was collected from Western Samoa ex *Heterocarpus sibogae* de Man, 1917. Given that Kensley's (1979) specimens were obtained from *H. gibbosus*, the occurrence of the species on *H. sibogae* is not surprising. The specimen should be examined, but we were unable to borrow it during the COVID 19 pandemic (Pennisi 2020).

Brandt & Janssen (1994) stated that "*Zonophryxus dodecapus* and *Z. trilobus* are characterized by six pereopods" but as far as is known only the immature females of *Z. trilobus* have six pairs of pereopods whereas the mature females have five pairs; this is in contrast to the mature females of *Z. dodecapus* which can have five or six pairs when mature (see Remarks under that species below).

Zonophryxus grimaldii Koehler, 1911

Zonophryxus grimaldii Koehler, 1911:16–22, 31, Figs. 13, 14 (36°14′N, 08°06′W, 1401 m).—Searle, 1914:370 (mention).—Holthuis, 1949:212, 213 (mention).—Danforth, 1976:78, 79 (mention).—Brandt & Janssen, 1994:350 (mention).—Junoy & Castillo, 2003:304 (list).—Raupach & Thatje, 2006:439 (mention).—Shimomura et al., 2010:9, 10 (mention).—Diego, 2012:133 (mention).—Nagler et al., 2020:342 (mention).

Type material.—Mature holotype female (16 mm TL) (most likely deposited in the Oceanographic Museum of Monaco but this has not been verified).

Type locality.—36°14′N, 08°06′W, 1401 m.

Range.—Known only from the type locality.

Depth range.—1401 m.

Size.—Female, 16 mm TL.

Host.—*Heterocarpus grimaldii* A. Milne-Edwards & Bouvier, 1900 (probable; see Remarks).

Description.—See Koehler (1911).

Remarks.—This species is only known from the female holotype, and this is the only species in the genus to have been described from, and remain known only from, a single specimen. Koehler (1911) provided a lengthy description of the female but only provided ventral and lateral whole body illustrations. The type host was not known for certain by Koehler (1911), but he thought *H. grimaldii* was likely, based on the number of specimens of that species collected with the holotype of *Z. grimaldii*.

Zonophryxus quinquedens Barnard, 1914

Zonophryxus quinquedens Barnard, 1914:228–230, pl. 22 (Cape Point, South Africa, 470–700 fms (=860–1280 m), ex *Nematocarcinus* sp. (see Remarks).—Stebbing, 1914:48 (mention).—Barnard, 1940:495 (list).—Holthuis, 1949:210, 212 (mention).—Barnard, 1950:674 (mention).—Taberly, 1954:9, 10 (mention).—Danforth, 1976:79 (mention).—Lopretto, 1983:87–97, Figs. 1–45 (off South Orkney Island, 62°48′W).—Brandt & Janssen, 1994:343–350, Figs. 1–5 (Weddell Sea, 69°58.9′S, 05°08.5′E, 665 m).—Raupach & Thatje, 2006:439–442, Fig. 1 (Weddell Sea, 71°18′S, 13°56′W–71°18′S, 13°58′W, 900–1040 m, ex *Nematocarcinus lanceopes* Spence Bate, 1888).—Wilson, 2009:179–183, 186–189, 191 (phylogenetic placement).—Shimomura et al., 2010:9, 10 (mention).—Boyko et al.,

2013:499, Figs. 1, 2 (placement in phylogenetic tree).—Vogt, 2016:1409, Fig. 7B (mention, figure reproduced from Raupach & Thatje 2006).—Gómez-Gutierrez et al., 2017:164 (mention).—Zhang et al., 2019:1806 (phylogenetic placement).—Nagler et al., 2020:340, 342, 348.

Type material.—4 mature females, 1 juvenile female, 1 male, 3 cryptoniscus larvae (all syntypes) (SAM A270-1, A2276 fide Barnard, 1914; now SAM 16641, 16782, 17101 *fide* Brandt & Janssen 1994).

Type locality.—"Cape Point NE. by E. distant 36 miles, 650–700 fathoms"/"Cape Point ENE., distant 36 miles, 66 fathoms"/"Cape Point NE. ¾ E., distant 29 miles, 470 fathoms."

Range.—South Africa, Weddell Sea.

Depth range.—860–1280 m.

Host.—Type host probably *Nematocarcinus longirostris* Spence Bate, 1888 (see Remarks); *Nematocarcinus lanceopes* Spence Bate, 1888.

Size range.—Females to 27 mm, males to 7 mm (fide Lopretto, 1983).

Redescription.—See Lopretto (1983) and Brandt & Janssen (1994).

Remarks.—The identity of the type host is not known, but Barnard (1914) stated that several potential host species were in the same bottles as the syntypes but that one bottle with a single female *Z. quinquedens* contained only an unidentified species of *Nematocarcinus* A. Milne-Edwards, 1881 (later identified as *N. longirostris* Spence Bate, 1888; see Barnard 1950); this led Barnard (1914) to conclude that *N. longirostris* was the likely host. The finding of *Z. quinquedens* on a specimen of *N. longirostris* by Brandt & Janssen (1994) supports Barnard's (1914) conclusion; however, Brandt & Janssen (1994) apparently were unaware of Barnard's (1950) paper in which he identified his earlier (1914) record of *Nematocarcinus* sp. as *N. longirostris*. This species is the only one in the genus known to parasitize hosts outside of Pandalidae.

Lopretto (1983) provided a thorough redescription of the species but did not state at what depth or from what hosts his specimens were collected. Both the type 1 and type 2 males are known from this species (Lopretto 1983).

Raupach & Thatje (2006) reported their specimens from *Nematocarcinus lanceopes*, a host they stated was previously known for *Z. quinquedens* from Brandt & Janssen's (1994) paper, but the species cited as host in the latter paper was actually *N. longirostris*. The notation in Boyko et al. (2013) that the 18s rDNA sequence for this species was novel was incorrect as it originated from the data of Raupach & Thatje (2006).

Zonophryxus dodecapus Holthuis, 1949
Fig. 4

Zonophryxus dodecapus Holthuis, 1949:3–8, Figs. 1, 2, pl. 1 (Los Cristianos, Tenerife, Canary Islands, 210 m, ex *Parapandalus narval* (J. C. Fabricius, 1787) (= *Plesionika narval* (J. C. Fabricius, 1787)).—Danforth, 1970c:33 (mention).—Kensley, 1979:670 (mention).—Lopretto, 1983:93, 95, 96, 97 (mention).—Brandt & Janssen, 1994:343, 347 (mention).—González Pérez, 1995:100 (mention), Fig. 52 (color photograph in situ on *Plesionika narval* (J. C. Fabricius, 1787).—González & Santana, 1996:179 (record from off La Gomera, Canary Islands, ex *P. narval*).—Trilles, 1999:287, 299, 300, Figs. 8.5B, C, 8.19A, B, 8.21C (figured after Holthuis 1949).—Raupach & Thatje, 2006:439 (mention).—Castello & Junoy, 2007:26 (list).—Shimomura et al., 2010:9, 10, 17 (mention).—Boyko & Williams, 2012:401 (mention).—Diego, 2012:132, 133, Fig. 1 (Cantabrian Sea, ex *Plesionika heterocarpus* (A. Costa, 1871)).—Boyko et al., 2013:499, Figs. 1, 2 (placement in

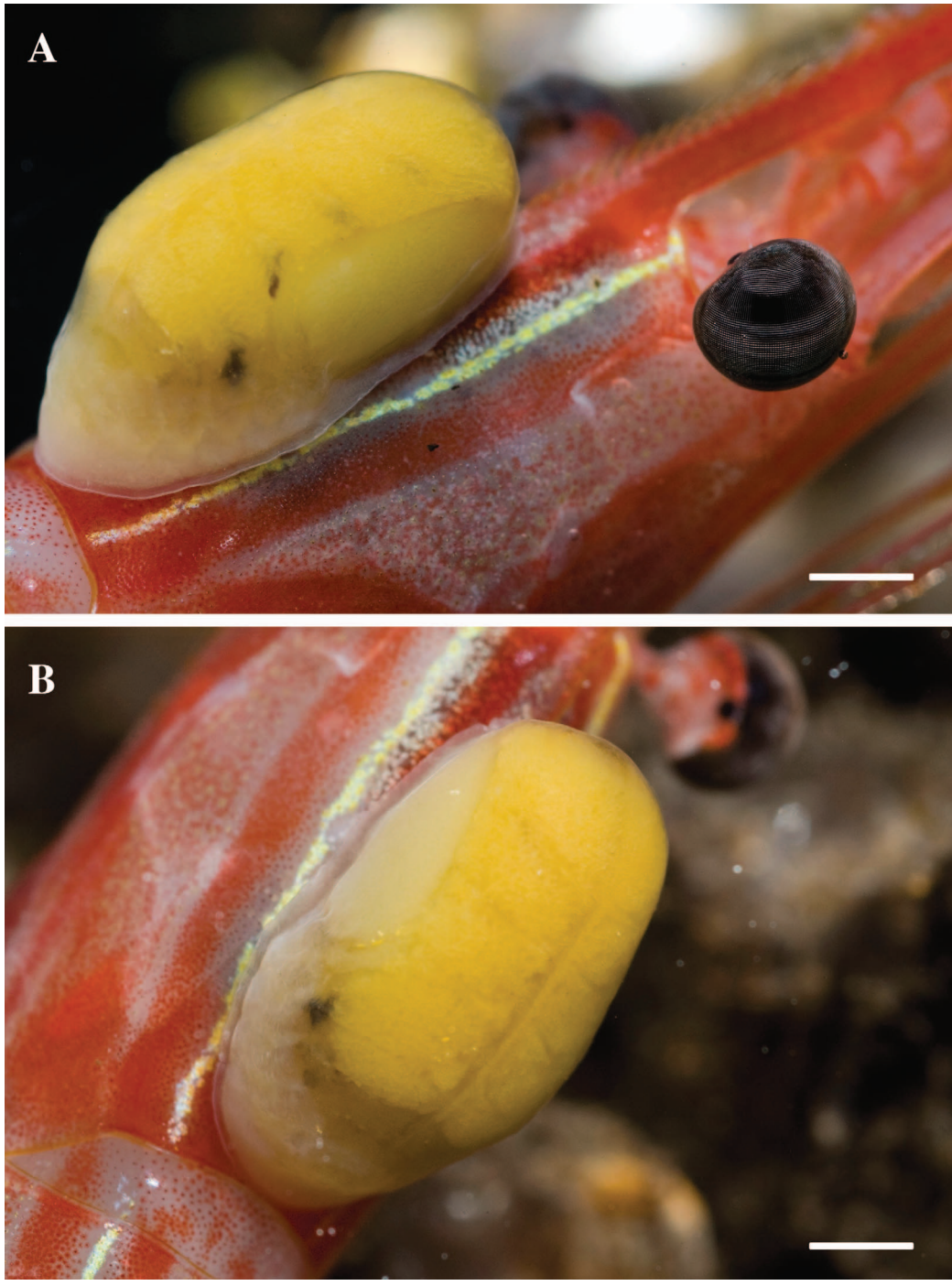

Fig. 4. *Zonophryxus dodecapus* Holthuis, 1949 (USNM 1659607—5-legged specimen), photographs taken while alive in situ on dorsal carapace of host *Plesionika narval* (J. C. Fabricius, 1787). A, lateral view, right side. B, oblique view, left side. Scale bars = 2 mm. Photographs by L. Moro Abad.

phylogenetic tree).—González, 2015:6 (mention).—Zhang et al., 2019:1806, Fig. 5 (placement in phylogenetic tree).

Zonophryxus dodecarpus [sic] Brandt & Janssen, 1994:350 (mention).

Not *Zonophryxus dodecapus*: Danforth, 1976:78, 79 (Guam, 274 m, ex *Heterocarpus ensifer* A. Milne-Edwards, 1881).—Ross, 1983:167 (list) (? = *Zonophryxus retrodens* Richardson, 1903).

Material examined.—1 ovigerous female with 6 pairs of pereopods (12.0 mm TL), 1 mature male (2.8 mm TL), ex *Plesionika narval* (J. C. Fabricius, 1787), 12.0 mm CL (excluding rostrum; head only, cannot sex), Candelaria, Tenerife, Canary Islands, ca. 150 m depth, coll. L. M. Abad, 10 Jan 2010 (USNM 1659606). 1 ovigerous female with 5 pairs of pereopods (11.0 mm TL), 1 mature male (2.7 mm TL), ex *P. narval*, 13.5 mm CL (excluding rostrum; head only, cannot sex), Candelaria, Tenerife, Canary Islands, ca. 150 m depth, coll. L. Moro Abad, 10 Jan 2010 (USNM 1659607).

Type material.—5 females and 2 males (1 syntype is RMNH.CRUS.I.1712; see Remarks) (not examined).

Type locality.—Los Cristianos, Tenerife, Canary Islands, 210 m depth.

Range.—Canary Islands and Cantabrian Sea.

Depth range.—150–210 m.

Hosts.—*Plesionika narval* (J. C. Fabricius, 1787) (type host); *Plesionika heterocarpus* (A. Costa, 1871).

Size range.—Females to 12 mm TL; males to 3 mm.

Description.—See Holthuis (1949).

Remarks.—Examination of the two pairs of specimens cited above shows that characters of both the males and females are in agreement with the description of the species by Holthuis (1949) with the notable exception that one female has only five pairs of pereopods, not the six pairs that are the basis of the species name. This variability in pereopod number is similar to that seen in females of species in the genus *Holophryxus*, although in that case, the sixth pereopods are said to be lost during development (Rustad 1935, Butler 1964, Coyle & Mueller 1981, Wasmer 1988). In *Z. dodecapus*, the presence/absence of the sixth pereopods may represent phenotypic plasticity, not a developmental loss, as both females examined here were ovigerous. Identification of specimens of *Zonophryxus* should therefore not rely on presence of six pairs of pereopods as a species-level character. The specimen with five pairs of pereopods (Fig. 4) was preserved in 100% ethanol and was the source of the 18s rDNA molecular data (GenBank number KF765768) for the species given in Boyko et al. (2013); the specimen with six pairs of pleopods was formalin-fixed. Only the type 1 male is known from this species.

In life, mature female specimens of *Z. dodecapus* exhibit a bright yellow coloration corresponding to the eggs and ovary in the main portion of the body (Fig. 4), with the anterior end and periphery a pale white/translucent coloration; this is similar to the freshly caught but probably not live individual of *Z. dodecapus* photographed by González Pérez (1995: Fig. 52). There are also four dark brown/black spots deeply embedded in the body and obscured by eggs in the posterior region of the photographed specimen; these spots are reminiscent of those described by Field (1969) for the dajid *Notophryxus lateralis* G. O. Sars, 1885. These spots are still visible in the preserved photographed specimen, but no such spots can be seen in the other preserved specimen. Live coloration of females has been described in a few related dajid species, including *Z. retrodens* that exhibits a pale yellow central region (likely corresponding to the developing eggs) and with marginal region of translucent white (Shimomura et al. 2010, Fig. 1). Rustad (1935) and Greve & Johannsessen (1981) reported that females

of *Holophryxus richardi* Koehler, 1911 varied in color with specimens having light yellow, orange, or red coloration, possibly corresponding with maturation; Rustad (1935) indicated that the red coloration matched that of the liver of the host. Huang et al. (2018: Fig. 5A, B) found females of *Holophryxus fusiformis* Shiino, 1937 varied in color with the pereon being white, pale yellow, beige, or orange, whereas the pleon ranged from white to pale green. In fact, they reported that fishermen collecting host shrimp from Taiwan "call these objects 'corn kernels' because of the similarities in color and size" (Huang et al. 2018). Similarly, Butler (1964) described the color of *Holophryxus alaskensis* Richardson, 1905a as "maize."

Danforth (1976) reported on six females and two males from *Heterocarpus ensifer*, collected from 900 ft (=274 m) depth off Guam; he did not figure the specimens but did indicate that the females had six pairs of pereopods and used this as the defining character to place an identification on his specimens. Given that it is unlikely that *Z. dodecapus* occurs in both the Canary Islands and Guam, it is more likely that Danforth (1976) actually had another species. It is possible that the Guam specimens were *Z. retrodens*, although each female had six pairs of pereopods instead of the five found on the holotype and the Japanese specimens of Shimomura et al. (2010) (such plasticity is now documented in females of the genus). This conclusion is supported by the fact that *H. ensifer* was one of the shrimps collected from the same station as the holotype of Z. *retrodens*. Unfortunately, the Guam specimens appear to be lost (Don Cadien, pers. comm.) and recollection is required. The listing of *Z. dodecapus* in Ross (1983) was based only on Danforth's (1976) Guam record.

There is one female in RMNH labeled "paratype," but as Holthuis (1949) did not designate a holotype, it is a syntype; the repository of the other syntypes is not known.

Zonophryxus cf. *dodecapus* Holthuis, 1949

Zonophryxus dodecapus Holthuis, 1949.—Thoma & Heard, n.d.:3, 5 (list).

Material examined.—1 mature female (14.9 mm TL), host unknown, "Pelican" Sta P-11, off Cape Canaveral, FL, 27°54′N, 79°45′W, 235 fms (430 m), 11 Mar 1956 (USNM 99555).

Remarks.—According to the specimen label, this female was found "loose in jar" containing *Hymenopenaeus robustus* Smith, 1885 (= *Pleoticus robustus* (Smith, 1885)), *Plesionika acanthonotus* (Smith, 1902), *Plesionika ensis* (A. Milne-Edwards, 1881), and *Glyphocrangon longleyi* Schmitt, 1931. Based on the host choices of other species of *Zonophryxus*, the most likely host was one of the species of *Plesionika*. Thoma & Heard (n.d.) listed *Z. dodecapus* among the fauna of the South Atlantic Bight but did not cite the source of their record and only reproduced the drawings of Holthuis (1949). The female examined has six pairs of pereopods, as also found in the syntype females of *Z. dodecapus* as well as one of the two females examined during the present study. We are unable to find any obvious morphological differences between the Florida female and those from the Canary Islands; however, due to there being only a single Floridian female lacking a male, as well as the uncertainty of the host, we are noncommittal about the identity of this species at the present time.

Zonophryxus sp.

Zonophryxus [sp. or spp.] Montagne & Cadien, 2001:203, 205 (Southern California Bight, ex *Pantomus affinis* Chace, 1937 and *Plesionika trispinus* Squires & Barragan, 1976).

Remarks.—Both hosts cited above occurred at multiple stations, but the precise localities of those found with parasites was not given by Montagne & Cadien (2001).

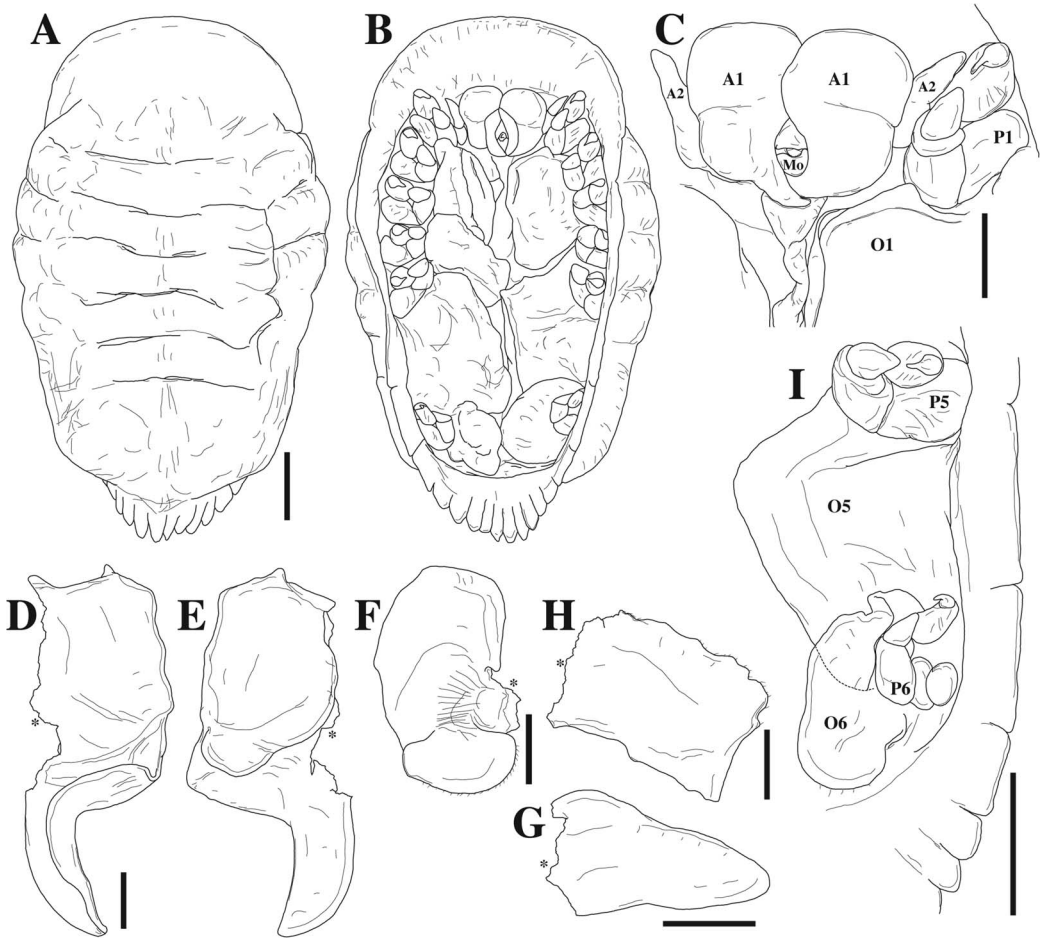

Fig. 5. *Zonophryxus probisowa* n. sp. Holotype female (USNM 235230). A, dorsal view. B, ventral view. C, mouthparts (Mo), antennules (A1), antennae (A2), pereopod 1 (P1), and oostegite 1 (O1). D, oostegite 1, inner view, left side. E, oostegite 1, outer view, left side. F, left maxilliped, outer view (appendix not drawn). G, oostegite 3, left side. H, oostegite 4, left side. I, fifth and sixth oostegites (O5, O6) and pereopods (P5, P6), left side; dashed line shows posterior end of oostegite 5. Asterisk in D–G shows side of attachment where dissected from body. Scale bars: A, B, I = 1 mm; C = 250 μm; D–H = 500 μm.

The identity of these purported specimens of a *Zonophryxus* species, and whether more than one species is present, awaits examination of material from the Southern California Bight.

Zonophryxus probisowa, new species
Figs. 5, 6

ZooBank LSID.—urn:lsid:zoobank.org:pub:E208CA4D-D822-4B14-828A-73EED7A8FE38.

Material examined.—Mature female holotype (8.0 mm TL), mature male allotype (2.5 mm TL), Peru, 03°48′S, 81°22′W, 615 m depth, coll. E. del Solar, 15 Mar 1971, ex *Heterocarpus hostilis* Faxon, 1893, female, 14.3 mm CL (excluding rostrum) (USNM 235230).

Type locality.—Peru, 03°48′S, 81°22′W, 615 m depth.

Range.—Known only from the type locality.

Depth.—615 m.

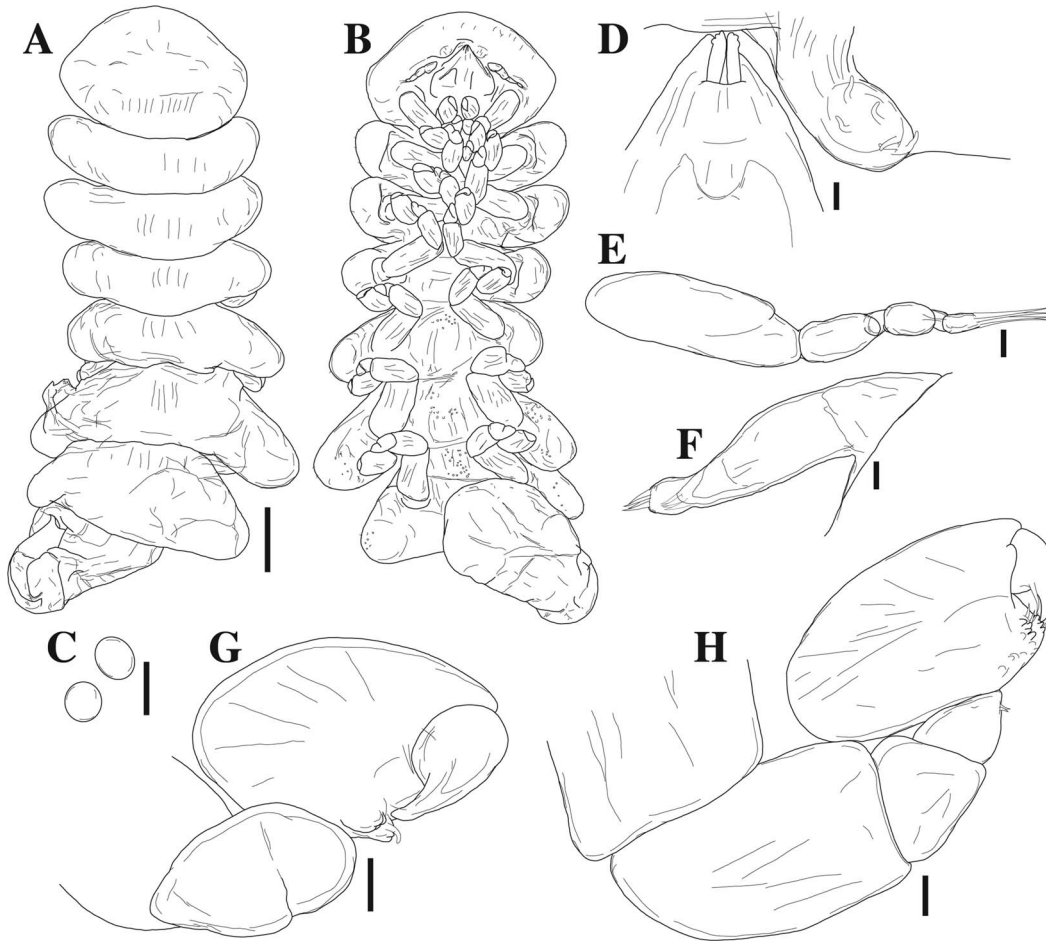

Fig. 6. *Zonophryxus probisowa* n. sp. Allotype male (USNM 235230). A, dorsal view. B, ventral view. C, spherical cells within body. D, mouthparts and antennule, left side. E, antenna, left side. F, antenna, right side. G, pereopod 1, right side. H, pereopod 6, right side. Scale bars: A, B = 250 μm; C–F = 10 μm; G, H = 20 μm.

Host.—*Heterocarpus hostilis* Faxon, 1893.

Size.—Female 8.0 mm TL; male 2.5 mm TL.

Etymology.—The species name is an arbitrary combination of letters used as a word, formed as an acronym of the journal name, Proceedings of the Biological Society of Washington (1880–2021); it is indeclinable.

Description.—Female body ovate (Fig. 5A, B), head, pereon, and pleon fused, widest in middle, dorsally convex with faint traces of segmentation; ventral body surrounded by marginal extension, broad anteriorly and posteriorly, thin laterally; small notches visible on lateral margins indicating some pereonal segments; posterior margin with closely approximated row of nine large triangularly-shaped processes (Fig. 5A, B). Ventral side of body concave with six pairs of isomorphic pereopods, five pairs closely approximated from head to midpoint of body, sixth pair near posterior margin of body at the base of sixth oostegites (Fig 5B). Antennules as recurved flat lobes, posteriorly tapering and surrounding buccal cone (Fig. 5C).

Antennae small, digitiform, situated behind and extending anterolaterally from antennules (Fig. 5C). Maxilliped of two ovate lobes (Fig. 5F), with digitiform, slightly curved appendix (not shown in figure, compare to Fig. 3J). Sternal plate distinct below oral cone, triangular in shape at anterior end and continuing as ridge between oostegites. Oostegite 1 large with subquadrate anterior lobe and recurved, tapering posterior lobe (Fig. 5D, E), internal ridge smooth; oostegites 2 and 3 small, distally tapering (Fig. 5G); oostegite 4 small, subquadrate (Fig. 5H); oostegite 5 large, subquadrate, basally fused to small, ovate oostegite 6 (Fig. 5I).

Type 1 male dorsoventrally flattened (Fig. 6A, B). Head ovate, fused with pereomere 1, dorsal surface slightly concave medially and upturned at distal margin (Fig. 6A). Antennule as small indistinct lobe bearing few setae, merged with frontal margin (Fig. 6D). Antennae non-symmetrical: left antenna of six(?) segments, basal segment as large as others combined; right antenna of two(?) segments, blade-like distal segment more than two times as long as basal triangular segment (Fig. 6F). Pereomeres 2–6 free, gradually increasing in width posteriorly; pereomeres 2 and 3 anterolaterally curved, 4 and 5 laterally directed, 6 and 7 posterolaterally directed (Fig. 6A). Seven isomorphic pereopods present (Fig. 6B, G, H). Spherical cells of indeterminant identity dispersed within pereomeres and pleomeres; 82 $\pm$ 9 μm ($n = 8$) in maximal diameter. Pleomeres fused with pleotelson, forming single ovate, elongate pleon (Fig. 6A, B). Pleon affixed near ventrodistal margin of pereomere 7 and extending posteriorly, lacking pleopods or uropods (Fig. 6A, B).

Remarks.—Although the male is somewhat similar in morphology to that of *Z. retrodens*, the strongly developed, closely approximated, posterior triangularly-shaped processes on the pleon of the female indicates that the two species are distinct, as those processes are short and more widely separated in *Z. retrodens*. The allotype male of *Z. probisowa* n. sp. appears to be going through a molt, as evidenced by the asymmetrical nature of the antennae, the cuticle lifting off posteriorly from pereomere 6, and the "shrunken" appearance of the posterior pereomeres and pleon (Fig. 6A, B). Only the type 1 male is known from this species.

The morphology of the posterior margin of the pleon of the female is unique in the genus and separates *Zonophryxus probisowa* n. sp. from all others previously described. Although the holotype of *Z. probisowa* n. sp. bears six pairs of pereopods, a character state previously reported only in *Z. dodecapus*, the variability in pereopod number in that species reported on herein indicates that this character should not be used to distinguish species.

Key to species of *Zonophryxus* Richardson, 1903 based on females

The only other key to species was given by Lopretto (1983), but most characters in that key, such as antennal segment count and number of pereopods, were either incorrectly interpreted or are variable within at least some species.

1a. Ventrolateral lobes of mature female converging posteriorly, forming v-shape 2

1b. Ventrolateral lobes of mature female not tapering..... 3

2a. Oostegite 6 of mature female separated from oostegite 5 along most of lateral margin .... *Z. grimaldii* Koehler, 1911

2b. Oostegite 6 of mature female fused with oostegite 5 along most of lateral margin .... *Z. trilobus* Richardson, 1910

3a. Oostegite 6 of mature female separated from oostegite 5 along most of lateral margin 4

3b. Oostegite 6 of mature female fused with oostegite 5 along most of lateral margin 6

4a. Triangularly-shaped processes on posterior margin of pleon tightly bunched together, overlapping ... . *Z. agassizi* (Richardson, 1905)

4b. Triangularly-shaped processes on posterior margin of pleon not bunched together, not overlapping 5

5a. Triangularly-shaped processes on posterior margin of pleon short, scarcely visible in dorsal view .... *Z. retrodens* Richardson, 1903

5b. Triangularly-shaped processes on posterior margin of pleon long, distinctly visible in dorsal view.... ..... *Z. probisowa* n. sp.

6a. Sternal plate with posterior knob (see Lopretto, 1983: fig. 23) .... *Z. quinquedens* Barnard, 1914

6b. Sternal plate without posterior knob (see Holthuis, 1949: Fig. 1i)..... ..... *Z. dodecapus* Holthuis, 1949

Acknowledgments

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