



A new genus of Herpyllobiidae (Copepoda: Cyclopoida) from a deep-living annelid (Polychaeta: Sigalionidae)

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Abstract A taxonomic study of deep-sea polychaetes collected at a depth of 2,805 m off the northern coast of California revealed a scaleworm of the family Sigalionidae with an attached parasitic copepod. The copepod represents an undescribed genus of the family Herpyllobiidae, comprising mesoparasitic copepods chiefly recorded from polychaetes of the family Polynoidae. *Blakerius* **gen. nov.** diverges from the other herpyllobiid genera by its possession of 1) a chalice-shaped ectosoma with several protuberances along the posterior margin and a long cylindrical shaft with a hyaline coating and integumental sculpturing, a short stalk with a small, anteriorly placed sclerotized ring, 2) a relatively large, discoid-shaped endosoma with digitiform process, and 3) attached male copepodids with 3-segmented antennules, containing limbless sac-like males. The new genus is compared with other herpyllobiids. This discovery increases the number of known herpyllobiid genera to six and is the first record of a herpyllobiid parasitizing a sigalionid polychaete.

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Introduction

Scaleworms are involved in symbiotic relationships with many other organisms, either as parasites or as hosts (Martin & Britayev, 2018; Mikac et al., 2020). Numerous copepod taxa have been recorded symbiotically associated with scaleworms, and these copepods have been studied since the 19th century (Boxshall et al., 2019). Currently, there are over 120 species of more than 20 copepod families that have been recorded as external or internal parasites of polychaete annelids (Boxshall & Halsey, 2004; Conradi et al., 2015; Björnberg & Radashevsky, 2011; Kim et al., 2013; Boxshall et al., 2019). Many of them are recognized as mesoparasites, a mode of life defined by the females having a highly transformed body, part of which is embedded in the host tissue. One of the better-known families of mesoparasitic annelidicolous copepods is the Herpyllobiidae Hansen, 1892, currently containing five valid genera: *Eurysilenium* Sars M., 1870, *Gottoniella* López-González, Bresciani & Conradi, 2006, *Herpyllobius* Steenstrup & Lütken, 1861, *Phallusiella* Leigh-Sharpe, 1926, and *Thylacoides* Gravier, 1912. The latter two genera are poorly known.

The most diverse herpyllobiid genus is *Herpyllobius*, with 21 valid species (Suárez-Morales & Salazar-Vallejo, 2022; 2024; Walter & Boxshall, 2024). Herpyllobiid copepods have been recorded chiefly as parasites of annelid polychaetes of the family Polynoidae Kinberg (Lützen, 1964; López-González

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& Bresciani, 2001; Conradi et al., 2015; Boxshall et al., 2019), but also in Iphionidae Kinberg (Suárez-Morales & Salazar-Vallejo, 2022), and more recently in Flabelligeridae de Saint-Joseph (Suárez-Morales & Salazar-Vallejo, 2024). The only previous record of copepods parasitizing scaleworms of the family Sigalionidae Kinberg is of the cyclopoid *Leaniricola rotundata* M'Intosh, 1885 (M'Intosh, 1885; Huys, 2016), an external parasite exhibiting an oral cone and modified gnathobases to anchor in the host, *Leanira areolata* M'Intosh, integument (Huys, 2016). The type specimen of *L. rotundata* was revisited by Huys (2016), who described the new family Leaniricolidae Huys, 2016. No mesoparasitic copepods have been hitherto reported from sigalionid scaleworms.

The taxonomic study of a scaleworm specimen of the genus *Sthenolepis* Willey, revealed a parasitic copepod attached to the dorsal surface of the host. A closer analysis of the parasite revealed that it represents an undescribed genus of the cyclopoid copepod family Herpyllobiidae. We provide a full description of this copepod and the morphological characters supporting its inclusion among herpyllobiids.

Materials and methods

During the examination of approximately 60 sigalionid specimens of *Sthenolepis* sp. by one of us (CC-G), it was discovered that one individual had a mesoparasitic copepod attached to the dorsal surface of an anterior body segment. The host specimen was collected from off Northern California, as part of a long-term monitoring survey carried out at the San Francisco Deep-Ocean Dredged Material Disposal Site (SF-DODS). The parasitized specimen was collected with a 0.25-m² box core at 2,805 m and recovered by sieving a sediment subcore. It was sorted under a stereomicroscope, fixed in 10% formalin in the field, and then transferred to 70% ethanol (ETOH) for preservation within 48 h after fixation (Blake et al., 2009).

The copepod was photographed still attached to the dorsum of the host, as well as the anterior region of the scaleworm for illustration and processed for further study. A series of photographs at different planes of focus was taken and then processed as a stack using Helicon-Focus software. Line drawings of the copepod were prepared with the aid of a camera

lucida attached to an Olympus BX51 microscope. Due to the fragility of the body, during the dissection, the endosoma was separated from the ectosoma. However, this was helpful during manipulation while line drawing. The specimen was processed for cold-stage or cryo-SEM technique, involving controlled dehydration series and the quick freezing of the specimen (Wightman, 2022). The specimen was observed at high vacuum in a JEOL-JSM-6010LA scanning electron microscope at ECOSUR-Chetumal.

Once the parasite was separated from the host, the copepod was kept in a separate vial from the scale worm. Host and parasite lots were deposited in the Natural History Museum of Los Angeles County (LACM) section Crustacea and Annelida, respectively.

Results

Class Copepoda Milne-Edwards, 1840

Order Cyclopoida Burmeister, 1834

Family Herpyllobiidae Hansen, 1892

Blakerius gen. nov.

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Differential morphological diagnosis

Adult female with chalice-shaped ectosoma, with prominent paired genital swellings and adjacent lateral protuberances along posterior margin. No vestiges of limbs in adult female. Ectosoma ornamented with scattered wart-like integumental processes and with diagonal lateral grooves. Posterior ectosomal section connecting to long cylindrical shaft anteriorly leading to short, narrow stalk. Integument of shaft ornamented with wrinkles. Stalk leading to small, discoid endosoma with irregular edges. Small sclerotized ring present at the junction with endosoma. Endosoma discoid, with single digitiform expansion. Endosoma larger than posterior part of ectosoma. Egg sacs absent. Late stage male copepodids attached around female genital swellings. Copepodid body comprising anterior ovoid prosome and slender 3-segmented urosome; bearing 3-segmented antennules, 3 pairs of legs plus paired caudal rami. Limbless adult male visible within copepodid exuvium, attached to host by the anterior tip.

Etymology: The name of the new genus is an eponym to honor Dr. James A. Blake, a polychaete specialist, who processed the host specimen and allowed us to examine this material. Gender masculine.

Specimens studied: Adult female holotype (LACM:DISCO:35064-) female, parasitizing *Sthenolepis* sp., off San Francisco, California, U.S.A. (Sta. 27. August 28th, 2016, 37°40.9920'N, 123°32.0044'W, 2,805 m). Specimen incomplete, ectosome missing, lost during SEM processing.

Type species: *Blakerius calyciformis* gen. nov. sp. nov., by original designation.

Type host: *Sthenolepis* sp.

Blakerius calyciformis gen. nov. sp. nov.

(Figs. 1–4)

Diagnosis. — As for monotypic genus.

Description of female holotype. — Ectosoma comprising two sections; posterior chalice-shaped section (length = 0.64 mm, maximum width at posterior margin = 0.4 mm) and elongate (0.67 mm) anterior section with narrow (width = 0.12 mm) cylindrical shaft covered by hyaline cuticle (Fig. 1B, hc in Fig. 2A). Posterior end of chalice-shaped ectosomal section with pair of sclerotized genital swellings, and

four rounded lateral protuberances, three on one side, one on other (lp in Figs. 2A, 3A); posterior margin 3 times wider than anterior connection to elongate anterior section; medial lateral margin with deep diagonal groove (lg in Fig. 4A). Ectosoma integument smooth except for scattered wart-like processes (Fig. 4A). Paired genital swellings sclerotized, moderately prominent (gsw in Figs. 2A, 3A). Genital swellings lacking egg sacs. Intergenital surface weakly concave (Fig. 3A). Anterior shaft with integumental sculpturing, tapering into short neck; anterior end of shaft tapering towards junction with endosoma (ip in Fig. 2B) and with small, sclerotized ring (sr in Figs. 2A, 4B, D). Endosoma discoid, 0.95 mm in maximum width, with regular rounded edges except for single digitiform process (dp in Fig. 2B), endosoma originating from underside of ectosoma close to mid-body (Fig. 2B).

Holotype female with three dwarf males copepod individuals attached close to genital swellings (M1–3 in Fig. 3B). Males of slightly different body lengths (0.10–0.12 mm) and seemingly distinct developmental stages; males' body globose, composed by wide, oviform cephalothorax and poorly defined

Fig. 1 Digital photographs of *Blakerius calyciformis* gen. nov. sp. nov. infecting *Sthenolepis* sp. from off California. A. complete body of the host, dorsal view with attached *B. calyciformis*. B. habitus of *B. calyciformis* showing hyaline membrane (hc). C. anterior dorsal view of *Sthenolepis* sp.

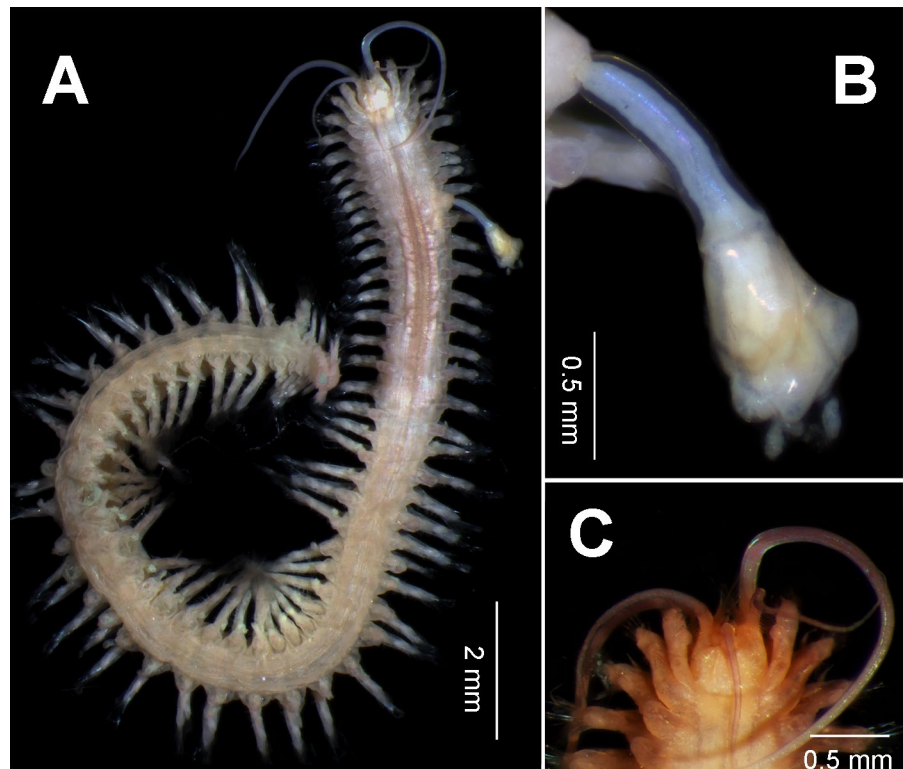
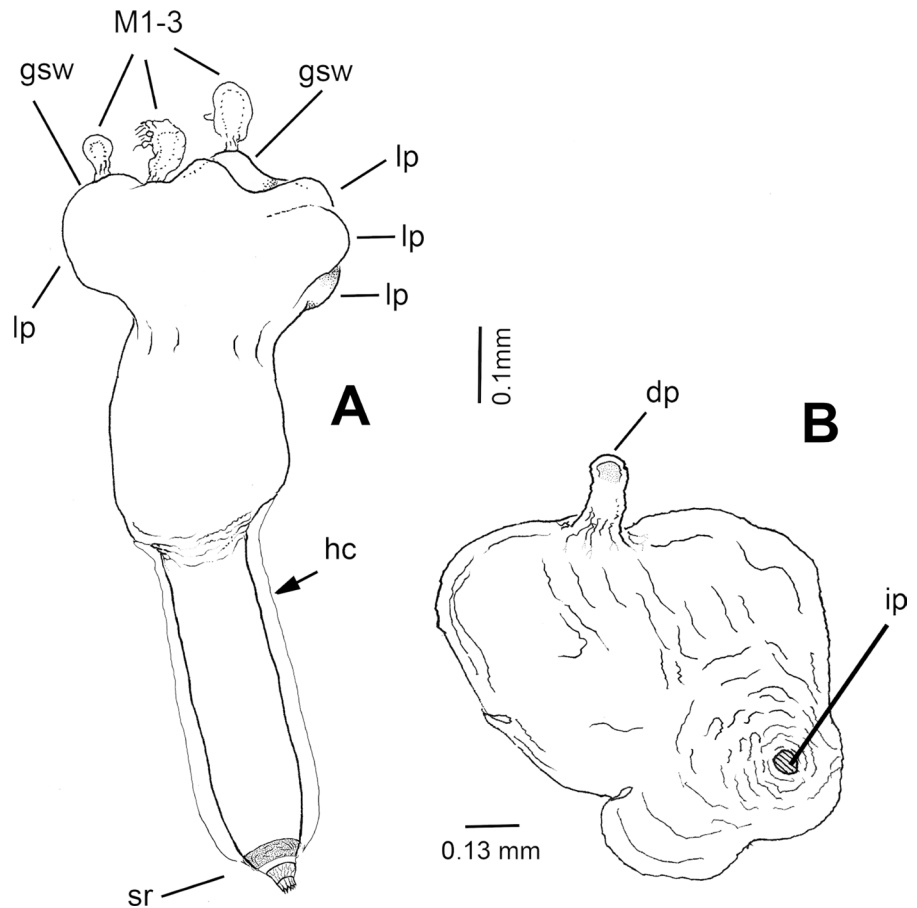


Fig. 2 Morphology of *Blakerius calyciformis* **gen. nov. sp. nov.**, holotype female from off California. A. adult female ectosoma showing genital swellings (gsw), lateral protuberances (lp), hyaline cuticle (hc), sclerotized ring (sr) and attached males M1-3. B. endosoma with digitiform process (dp) and insertion point (ip)



segmentation, all of them attached to female by the anterior end. First male (M1) with 3-segmented antennules at attachment point, antennule with 3 apical elements, followed posteriorly by biramous swimming leg 1 with unarmed protopod and with one ramus armed with single seta and the other with two; leg 1 followed posteriorly by 2-segmented, uniramous leg 2 carrying 2 distal setae. The most posterior appendage of this male individual being a 3-segmented urosome carrying rounded caudal rami armed with 4 distal setae (Fig. 3C). Second male (M2) lacking antennules; remnants of three pairs of swimming legs present posteriorly; legs 1 and 2 broken off, with distal segments missing; putative leg 3 1-segmented, armed with two short apical setae; posterior end of M2 with median structure, possible remnants of urosome. Male M3 represents an incomplete exuvium retaining first swimming leg only, as in M1 (Fig. 3B). Limbless ovoid adult male visible through exuvium of last copepodid specimens M1 and M2.

Remarks

The new genus is proposed as a member of the family Herpyllobiidae because it possesses the following characters distinctive of the family (Lützen, 1964; Boxshall & Halsey, 2004; Boxshall et al., 2019): body lacking any external trace of segmentation, ectosoma bilaterally symmetrical, spherical, ovoid or heart-shaped, limbless; posterior end with paired sclerotized genital swellings; intergenital area flat or moderately protuberant; stalk arising from the midline of the underside; at the point it pierces the host skin, it exhibits a holdfast with serrated edges; the shape and size of the endosoma is highly variable, usually branched or with lobes. Males attached to female ectosoma.

The new genus *Blakerius* **gen. nov.** diverges from the other valid herpyllobiid genera (viz., *Herpyllobius*, *Eurysilenium*, *Phallusiella*, *Thylacoides* and *Gottoniella*) in several characters, including: the

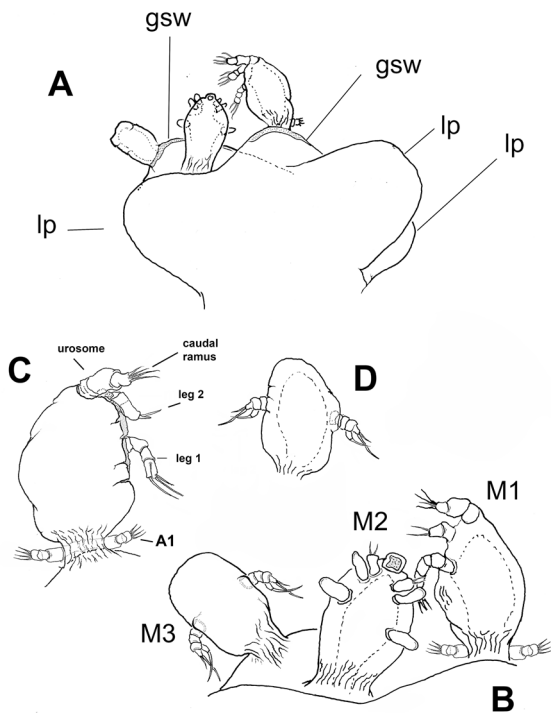


Fig. 3 Morphology of *Blakerius calyciformis* gen. nov. sp. nov., holotype female from off California and details of the attached male copepodids. A. posterior part of female ectosoma with lateral protuberances (lp), genital swellings (gsw), and male copepodids. B. detail of male copepodids M1-3. C. male M1 showing antennules (A1), swimming legs (sl), urosome (ur), and caudal rami (cr). D. male M2 showing single swimming leg (sl)

shape of the ectosoma and endosoma of the female, and in details of the males. Its female ectosoma differs from that of the poorly known *Phalusiella*, which is distinctively bilobed or branched (Leigh-Sharpe, 1926; Boxshall & Halsey, 2004). In *Gottoniella* the ectosoma is laterally expanded and the endosoma is bifurcate and tubular (López-González et al., 2006) and in *Eurysilenium* the endosoma tapers towards its tip, both differing from the pattern found in the new genus *Blakerius* gen. nov. The males of *Gottoniella* have a distinct metasome and retain robust 3-segmented maxillipeds (López-González et al., 2006) while the males of *Eurysilenium* carry modified caudal rami at the posterior end of a distinct, 4- to 5-segmented post-cephalic trunk.

Thylacoides was found on a syllid host, and it is so poorly known that the type species, *T. sarsi* Gravier, 1912, was considered to be a species inquirendum

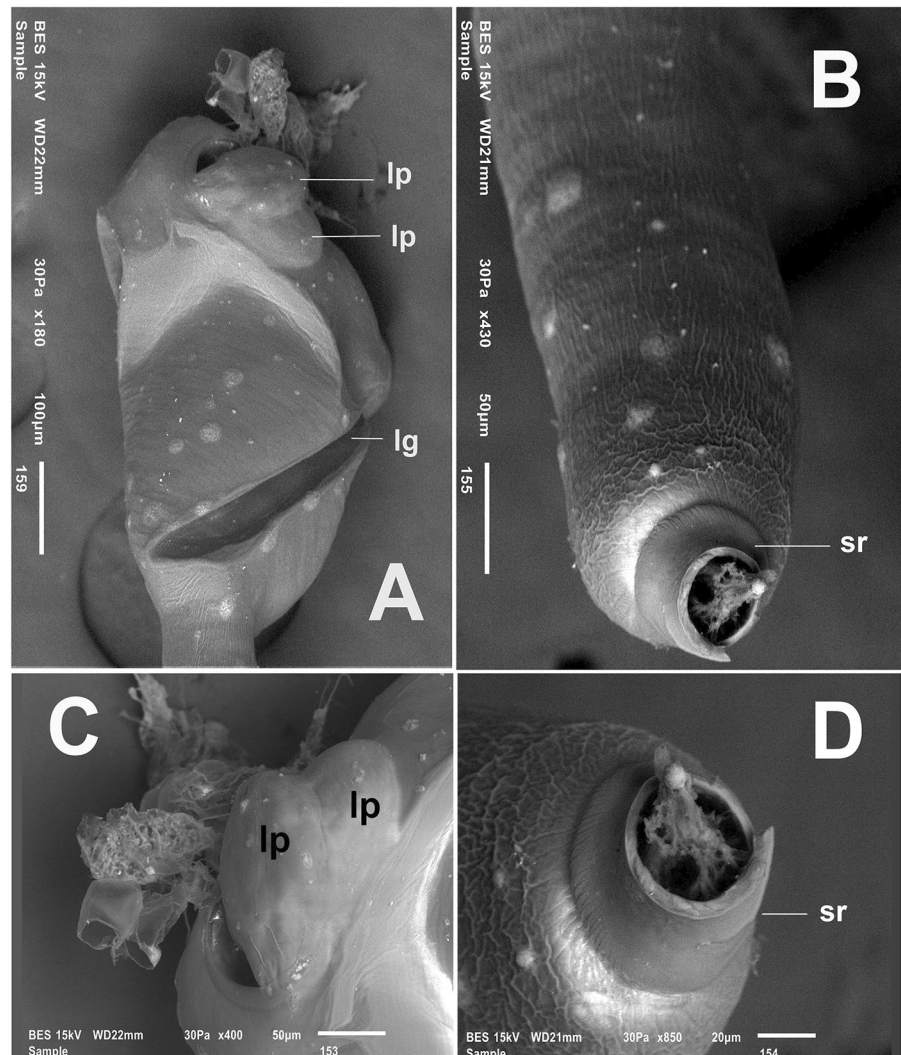
by Boxshall et al. (2019). There are no conspicuous similarities between the females of the new genus and *Thylacoides*. The males of *Thylacoides* have a clear body segmentation and bear two pairs of tubercles plus two curved hooks on the final body segment (Gravier, 1912), whereas the male of the new genus is limbless.

The new genus differs from *Herpyllobius* in the form of the female ectosoma. The division of the ectosoma in *Blakerius* gen. nov. into broad posterior section bearing the genital swellings and a slender anterior shaft is a unique attribute serving to distinguish between the genera. The males of *Herpyllobius* are typically limbless, represented by bottle-shaped individuals anteriorly attached to the female genital area (López-González & Bresciani, 2001). We consider that the adult males of *Blakerius* gen. nov. are similar, even though in our material the adult is still enclosed within the exuvium of the preceding last male copepodid stage.

Detailed comparisons are problematic because of the incomplete state of the exuvia of the three late male copepodids attached to the female of *Blakerius* gen. nov. However, the presence of 3-segmented antennules is shared with *Herpyllobius* males but the only other paired limbs present in copepodids of the new genus are two pairs of legs positioned posteriorly on the prosome. The most anterior pair has a well-defined 2-segmented protopod while the posterior-most pair is lobate and armed 2 apical setae. The absence of antennae and/or maxillipeds may be due to the state of the exuvium-based material. Late copepodids of *Herpyllobius* typically have 3 pairs of biramous legs, as in *H. arcticus* Steenstrup & Lütken, 1861 (see Boxshall et al., 2019) whereas the third leg pair in *Blakerius* gen. nov. comprises a single segment bearing 2 apical setae. We consider these differences in both sexes to be sufficient to distinguish the new genus from *Herpyllobius*.

The host scaleworm individual was almost complete and in good condition: however, most of the scales were missing (Fig. 1A). This is likely unrelated to the infestation, as most of the specimens examined from the same site lack scales. The specimen has 60 segments and measures 18 mm long, and 1.2 mm wide. The parasite was attached dorsally to the 10th right parapodium, a segment that naturally lacks scale; however, when scales are present in segments 9th and 11th and these can

Fig. 4 Photographs with SEM cryo-technique of *Blakerius calyciformis* gen. nov. sp. nov., holotype female. A. ectosoma showing lateral groove (lg) and lateral protuberances (lp). B. distal end of ectosoma shaft showing integumental sculpturing and sclerotized ring (sr). C. detail of posterior end of ectosoma showing lateral protuberances and two attached male copepodids. D. detail of sclerotized ring (sr)



cover these segments. Only a few herpyllobiids, like *H. vanhoeffeni* López-González & Bresciani, 2001 and *H. hartmanae* Lützen & Jones, 1976 have been known to attach to the ventral surface of their hosts (Lützen & Jones, 1976; López-González & Bresciani, 2001). The new copepod *B. calyciformis* gen. nov. sp. nov., likely caused a swelling in the dorsal surface of the parapodium, doubling its regular size; and causing an apparent reduction of the branchia. It should be noted that *Sthenolepis* sp. was frequently recorded on the site between 2002 and 2017 (Blake et al., 2009; Cruz-Gómez & Blake unpublished data), and from approximately 60 specimens examined only one parasitized specimen was found, therefore infestation by *B. calyciformis*

gen. nov. sp. nov., is uncommon. This is the second record of a copepod parasitizing a sigalionid scaleworm, and the first on the genus *Sthenolepis*. *Sthenolepis* can be recognized by having lateral auricles in the median antenna, inner tentacular lobes on the first segment, and three neuropodial lobes in middle and posterior segments (Willey 1905; Pettibone 1970; Aungtonya 2002). In the Eastern Pacific, only two *Sthenolepis* species have been recorded, *S. fimbriarum* (Hartman) and *S. spargens* Fauchald. The morphology of the host differs from the known *Sthenolepis* species by possessing long palps, short tentacular cirri and neurochaetae with long canaliculated blades, and inferior non-canaliculated blades (Fig. 1C). *Sthenolepis* sp. is likely to be a new

species from deep water off Northern California and deserves to be described.

Huys (2016) stated that the copepod *L. rotundata* was found on *Sthenolepis areolata*, but this nomenclatural combination is not valid. Whilst Moore (1910: 391) proposed to move *Leanira areolata* to *Sthenolepis*, Pettibone (1970) erected the name *Neoleanira* Pettibone to include sigalionids with a long dorsal cirrus in segment three, a feature found in M'Intosh's species but lacking in *Sthenolepis*. Huys likely followed the combination available then on the WoRMS site, where there were two combinations for the same species, one for *Sthenolepis* and another for *Neoleanira*. Recently, this error was amended, and the current valid combination of this scaleworm is in *Neoleanira* (Read & Fauchald, 2024; Read Pers. Comm.). Therefore, previous to this study, *Neoleanira* was the only sigalionid genus with a documented record of a parasitic copepod.

Habitat

The host was found in fine sediments, mainly domain by silt and clay at 2.3–7 cm dredged material depth (Blake et al. 2009; Cruz-Gómez & Blake unpublished data).

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Author Contributions Study design: Eduardo Suárez-Morales and Christopher Cruz-Gómez. Analyzed data: Eduardo Suárez-Morales, Christopher Cruz-Gómez and Geoffrey A. Boxshall. Writing, first draft: Eduardo Suárez-Morales and Christopher Cruz-Gómez. Writing, reviewing, and editing: Eduardo Suárez-Morales, Christopher Cruz-Gómez and Geoffrey A. Boxshall. Image editing: Eduardo Suárez-Morales and Christopher Cruz-Gómez.

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Data availability Type material is deposited in the Natural History Museum of Los Angeles County section Crustacea.

Declarations

Competing Interests Authors state no conflict of interest.

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