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A new species of *Sarcotaces* (Copepoda: Cyclopoida: Philichthyidae) from *Antimora rostrata* (Actinopterygii: Gadiformes: Moridae)

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Abstract

Parasitic copepods of the genus *Sarcotaces* occur in galls inside the skeletal musculature of fishes. The gall, hosting a highly metamorphosed drop-shaped female contains also a black fluid capable of staining the fish tissues during filleting. Their marine fish hosts are globally distributed and until recently, eight nominal species have been described from fish hosts representing eight fish families. Females are quite similar in their morphology, therefore the males are used for the species determination. The aim of this study was to provide a detailed morphological characterization of the *Sarcotaces* specimens found in muscles of the blue antimora, *Antimora rostrata* (Günther, 1878) originating from deep open waters of the Atlantic. The present paper describes and illustrates *Sarcotaces antimori* **sp. nov.** The new species differs from its congeners in the shape of the cephalothorax, relative proportions and structure of the caudal rami, and in the setal formula of the antennulae of the male.

Keywords

Antimora rostrata, copepod taxonomy, endoparasite, host–parasite relation, mesoparasite

Introduction

Parasitic copepods (Copepoda: Philichthyidae) of the genus *Sarcotaces* Olsson, 1872 are highly metamorphosed and sexually dimorphic organisms infecting marine fishes. They can be found in galls inside the skeletal muscles of fishes. The gall, hosting a highly metamorphosed drop-shaped female is also filled with a black fluid known to stain the fish tissues during filleting. Despite their spectacular appearance they are rather rarely found (Piasecki et al. 2020, 2022).

There are eight nominal species representing the genus *Sarcotaces* namely, *Sarcotaces arcticus* Collett, 1874; *Sarcotaces verrucosus* Olsson, 1872; *Sarcotaces pacificus* Komai, 1924; *Sarcotaces komaii* Shiino, 1953; *Sarcotaces japonicus* Izawa, 1974; *Sarcotaces shiinoi* Izawa, 1974; *Sarcotaces namibiensis* Reimer, 1991; and *Sarcotaces izawai* Piasecki, Barcikowska, Panicz, Eljasik et Kochmański, 2022. There has been no comprehensive revision of this genus and only one species (*S. izawai*) has also been defined genetically (Piasecki et al. 2022).

Materials and methods

The gall hosting both specimens (male and female) was embedded in the flank of a blue antimora, *Antimora rostrata* (Günther, 1878), caught on the RRS *DISCOVERY* cruise D252 (13–30 April 2001), Stn No. 13951#40 (49°49.9′N, 012°10.8′W), at a depth of 1631–1653 m in the Goban Spur, northwest Atlantic. The parasite gall was collected by R.A. Bray.

The male specimen was examined under a compound light microscope Olympus BX50 using a modified "wooden slide" method of Humes and Gooding (1964) and lactic acid as a clearing medium. The male was stained with lignin pink. The drawings were made using a drawing tube (Olympus). The female was observed under a dissecting microscope and photographed.

Morphological terminology follows, Kabata (1979), and Huys and Boxshall (1991). Thoracic and abdominal somites are numbered using Roman numerals and abbreviated th and abd, respectively.

Two separate attempts were made to extract genetic material from the female. Both attempts were unsuccessful. The types were deposited at the Natural History Museum, London, UK.

Results

The gall dissected from the host fish contained a single female and a single male of a sexually dimorphic copepod parasite. No eggs or nauplius stages were found. It was explicitly identified as representing the genus *Sarcotaces* but it did not resemble any of the hitherto known species. We therefore concluded that these specimens represent a species unknown to science. In the present paper, we provide principal data on all nominal species and illustrated descriptions (Table 1). We also compare principal morphological data of all *Sarcotaces* species (Table 2).

Taxonomy

Phylum Arthropoda
Subphylum Crustacea
Subclass Copepoda
Order Cyclopoida Burmeister, 1835
Family Philichthyidae Vogt, 1877
Genus *Sarcotaces* Olsson, 1872

Sarcotaces antimori sp. nov.

https://zoobank.org/1ACD2032-14ED-42C8-AC32-1E111FD318D8
Figs. 1–3

Locality. Goban Spur, northwestern Atlantic (49°49.9′N, 012°10.8′W)

Host fish. blue antimora, *Antimora rostrata* (Günther, 1878)

Infection site. lateral musculature (flank)

Type material. NHMUK 2022.198 holotype (male) and NHMUK 2022.199 allotype (female)

Description of female. Body highly metamorphosed, semi-pyriform/semi-quadrangular with deep transverse furrows marking apparent segmentation, and without visible appendages. Surface of cephalosome and thoracic somites covered by papilliform protrusions. Deep transverse furrows without papilliform protrusions

Table 1. Available (illustrated) descriptions of nominal species of the genus *Sarcotaces*. [Modified from Piasecki et al 2022].

Species	Sex or stage	Locality	Valid name of host fish	Fish family	Order	Reference
S. verrucosus	**F**	**St. Barthelemy, Caribbean**	***Acanthurus* sp.**	**Acanthuridae**	**Perciformes**	**Olsson 1872**
S. verrucosus	F	Martinique, Caribbean	*Halichoeres radiatus* (Linnaeus, 1758)	Labridae	Perciformes	Dollfus 1928
S. verrucosus	F + M + N	San Matías Gulf, Argentina	*Pseudopercis semifasciata* (Cuvier, 1829)	Pinguipedidae	Perciformes	González and Tanzola 2000
S. arcticus	**F** (no fig.)	**Øksfjord, Finmark, Norway**	***Molva dypterygia* (Pennant, 1784)**	**Lotidae**	**Gadiformes**	**Collett 1874**
S. arcticus	F + N	Collett's material	***Molva dypterygia* (Pennant, 1784)**	Lotidae	Gadiformes	Hjort 1895
S. arcticus	M	Aberdeen, Scotland	***Molva dypterygia* (Pennant, 1784)**	Lotidae	Gadiformes	Aitken 1942
S. arcticus	F + M	Norway	***Molva dypterygia* (Pennant, 1784)**	Lotidae	Gadiformes	Moser et al. 1985
S. arcticus	F + M + N	British Columbia	*Sebastes ruberrimus* (Cramer, 1895)	Sebastidae	Scorpaeniformes	Kuitunen-Ekbaum 1949
S. arcticus	F + M + N	Alaska? California?	*Sebastes* spp.	Sebastidae	Scorpaeniformes	Moser et al. 1985
S. arcticus	F + M	British Columbia	*Sebastes* sp.	Sebastidae	Scorpaeniformes	Kabata 1988
S. pacificus	**F + M + N**	**Tanabe Bay, Japan**	***Antennarius striatus* (Shaw, 1794)**	**Antennariidae**	**Lophiiformes**	**Komai 1924**
S. pacificus	F + M	Sagami, Musaki, Saogiro, Japan	***Antennarius* sp.**	Antennariidae	Lophiiformes	Heegaard 1947
S. pacificus	F + M	Shirama, (near type locality)	***Antennarius striatus* (Shaw, 1794)**	Antennariidae	Lophiiformes	Shiino 1953
S. pacificus	N + C	Tanabe Bay, Japan	***Antennarius striatus* (Shaw, 1794)**	Antennariidae	Lophiiformes	Izawa 1973
S. pacificus	F + M	Tanabe Bay, Japan	***Antennarius striatus* (Shaw, 1794)**	Antennariidae	Lophiiformes	Izawa 1974
S. komaii	**F + M**	**Tosa Bay, Japan**	***Scalicus hians* (Gilbert et Cramer, 1897)**	**Peristediidae**	**Perciformes**	**Shiino 1953**
S. komaii	F + M	Shiino's type material	***Scalicus hians* (Gilbert et Cramer, 1897)**	**Peristediidae**	**Perciformes**	Izawa 1974
S. komaii	F	Cuba	*Sparisoma rubripinne* (Valenciennes, 1840)	Scaridae	Perciformes	Ezpeleta Herce 1974
S. komaii	F + M	Pacific coasts of Japan	*Antimora rostrata* (Günther, 1878)	Moridae	Gadiformes	Avdeev and Avdeev 1975
S. japonicus	**F + M + N**	**Tanabe Bay, Japan**	***Gymnothorax kidako* (Temminck et Schlegel, 1846)**	**Muraenidae**	**Anguilliformes**	**Izawa 1974**
S. shiinoi	**F + M**	**Kumano Sea**	***Acromycter nezumi* (Asano, 1958)**	**Congridae**	**Anguilliformes**	**Izawa 1974**
S. namibiensis	**F + M**	**Namibian coast**	***Selachophidium guentheri* Gilchrist, 1903**	**Ophidiidae**	**Ophidiiformes**	**Reimer 1991**
S. izawai	**F + M + N**	**"Falklands"? Australia?**	***Mora moro* (Risso, 1810)**	**Moridae**	**Gadiformes**	**Piasecki et al. 2022**
***S. antimori* sp. nov.**	**F + M**	**Northwestern Atlantic**	***Antimora rostrata* (Günther, 1878)**	**Moridae**	**Gadiformes**	**This study**

Sarcotaces species in bold represent original descriptions. Fish names in bold are records from the type-host species. Fish names in regular font show records form a fish other than their type-host; F = female, M = male, N = nauplius, C = copepodid. Originally Komai (1924) described only a female and a nauplius. However, Shiino (1953) reported that Komai after reexamination of his material also found a male.

Table 2. Principal morphological data of nominal species of the genus *Sarcotaces*.

Species	FEMALE	MALE							Reference
	Length [mm]	Comments	Body length [mm] (mean)	Caudal ramus length [mm] (mean)	Total length [mm] (mean)	Caudal ramus percentage of total length/body length (mean values) [%]	Antennule	Caudal ramus	
S. verrucosus	15.0	—	—	—	—	—	—	—	Olsson 1872
S. arcticus	39.15	—	—	—	—	—	—	—	Collett 1874
	10.0–90.0	—	—	—	—	—	—	—	Berland 1970
	—	Triangular cephalothorax; posterior somite abruptly narrowing	<3.0	**<1.1**	**<4.1**	**26.6/36.7**	Inadequate description	Single seta, variable in size	Aitken 1942
	—	Triangular (?) cephalothorax	—	—	—	—	3, 2, ?, ?	—	Moser et al. 1985
S. arcticus	5.0–70.0	Host: *Sebastes ruberrimus*; illustrated male with double caudal setae is 3.19/5.07 mm long	1.0–1.28	**?**	**?**	**?**	0, 1, 1, 1, 4	Very high variability (including double setae and no seta et all)	Kuitunen-Ekbaum_1949
S. pacificus	5.0–15.0	—	—	—	—	—	—	—	Komai 1924
	10.0–15.0	Semi-trapezoid cephalothorax; posterior somite abruptly narrowing	**0.94**	**0.35**	**1.29**	**27.1/37.2**	Inadequate description	Strong, 2-segmented seta +2 setules	Heegaard 1947
	1.9–13.0	Semi-triangular/oval cephalothorax; posterior somite abruptly narrowing	1.0–1.4 (1.25) **1.0–1.24 (1.14)**	**0.47–0.55 (0.52)**	**1.53–1.79 (1.67)**	**31.1/45.6**	3, 3, 3, 7	Strong, 2-segmented seta +3 setules; High variability	Izawa 1974
S. komaii	<12.3	Semi-triangular cephalothorax; posterior somite abruptly narrowing	>2.0?	—	—	**41.1/69.8**	Inadequate description	Thin, vermicular	Shiino 1953
	9.5–25.0	Semi-triangular/oval cephalothorax; posterior somite abruptly narrowing	1.3–2.0 (1.62) **1.29–1.98 (1.29)**	**0.94–1.52 (1.16)**	**2.23–2.81 (2.45)**	**54.9/89.9**	4, 4, 3, 9	High variability	Izawa 1974 based on Shiino's type material
S. japonicus	9.0–22.0 (14.7)	Pyriform cephalothorax; posterior somite abruptly narrowing	1.0–1.1 **1.04–1.22 (1.12)**	**0.73–0.79 (0.77)**	**1.82–2.01 (1.88)**	**42.8/68.8**	4, 4, 0, 10	Strong, 2-segmented seta +4 setules	Izawa 1974
S. shiinoi	8.6–21.1	Semi-triangular cephalothorax	1.5–1.8 (1.65) **1.22–1.47 (1.35)**	**0.76–1.05 (0.91)**	**1.98–2.52 (2.25)**	**40.4/67.4**	1, 2, 4, 6	Strong, 2-segmented seta +3 setules	Izawa 1974
S. namibiensis	20.0–32.0	Semi-triangular cephalothorax; posterior somite abruptly narrowing	1.8 **1.74**	**1.04**	**2.78**	**37.4/58.4**	Inadequate description	2-segmented seta	Reimer 1991
S. izawai	25.0–48.0 (35.8)	Semi-triangular/oval cephalothorax; posterior somite not narrowing	2.15–3.52 (2.56)	0.04–0.9 (0.41)	(2.97)	13.8/16.0	4, 4, 2, 7	High variability	Piasecki et al. 2022
S. antimori sp. nov.	15.1	Semi-triangular cephalothorax with very distinct lateral indentations possibly marking traces of thoracic segmentation; posterior somite not narrowing	2.07	0.83	2.90	28.6/40.1	0, 1, 2, 6	Strong seta with small setule	This study

Some data are estimated from the illustrations (**bold** type); the antenna was inadequately described for the majority of species, the mandible (subchelate claw) is uniform in all species; maxillules were only reported for *S. izawai*; the maxillae structure has not been adequately determined in any species; the structure of legs 1 and leg 2 is similar in five species (*S. pacificus*, *S. japonicus*, *S. shiinoi*, *S. izawai*, and *S. antimori* sp. nov.) and in *S. komaii* (where a seta at the base of the exopod of both legs was not reported) and *S. antimori* sp. nov. (where a seta at the base of the exopod of the first leg was not observed).

(Fig. 1A, 1B). Abdominal somites without papilliform protrusions covering surface. Total length reaching 15.1 mm; total width 8.1 mm (Table 2). Body consisting of two parts equal in length. Anterior part semi-cylindrical, blunt, with frontal margin constituting straight line perpendicular to body axis; posterior part slightly wider, semi-conical (tapering posteriorly). Anterior part divided into 5 tightly packed (short) divisions covered with papilliform protrusions and separated by surface furrows. Apparent "segmentation" on dorsal surface not consistently matching furrows on ventral surface. Posterior part of body with two prominent, well-defined somites, diminishing in diameter, and conical abdominal part comprising three somites (abd II–abd IV) tapering stepwise towards conical tip. Surface of posterior part with few papilliform protrusions on dorsal side (Figs. 1B, 2A). Oral lobe located anteriorly on ventral surface, doughnut-shaped, densely covered with papillae around perimeter. Two larger processes present on body surface immediately posterior to oral lobe (Figs. 1A, 2B).

Description of male. Body (Fig. 3A) markedly smaller than that of female, and substantially different in structure; strongly elongate, subcylindrical, unsegmented, with smooth surface. Body consisting of two

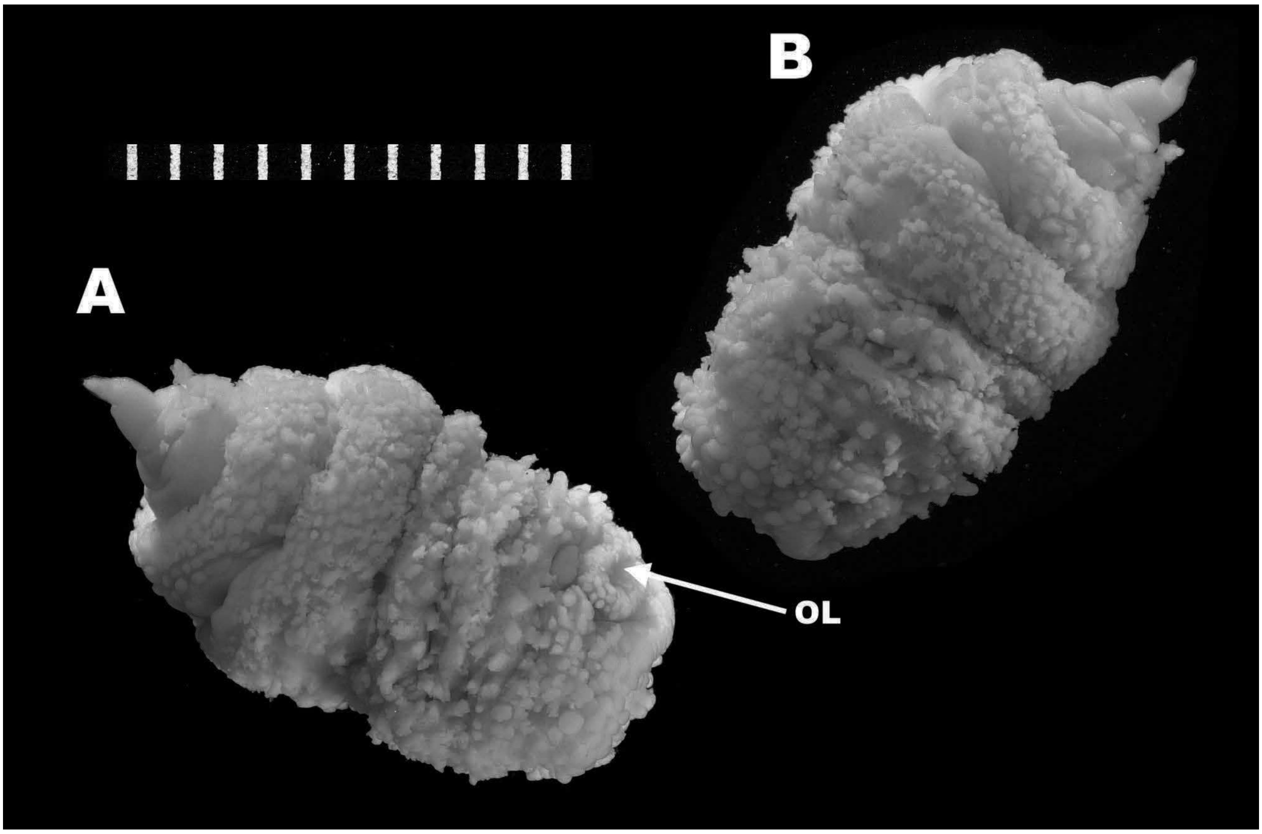

Figure 1. Female of *Sarcotaces antimori* sp. nov. (allotype) from blue antimora, *Antimora rostrata*. (**A**) ventrolateral view; (**B**) dorsolateral view. OL = oral lobe. Scale: 10 mm. Photo: Harry Taylor (NHM Photo Studio, London, UK).

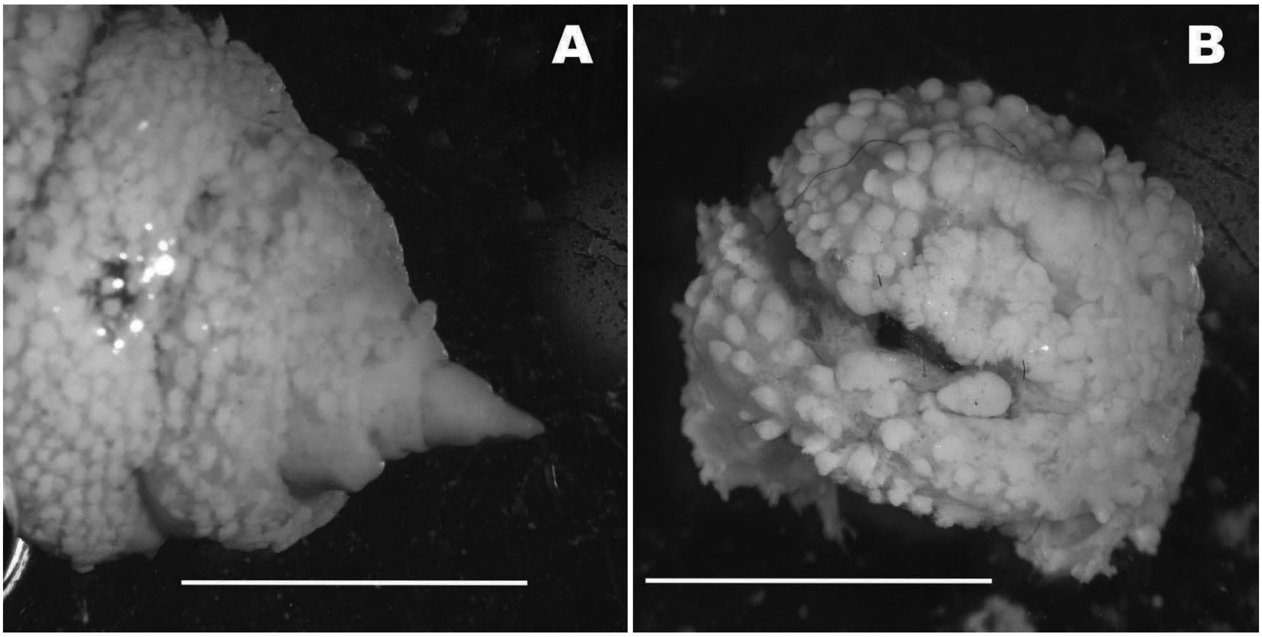

Figure 2. Female of *Sarcotaces antimori* sp. nov. (allotype) from blue antimora, *Antimora rostrata*. (**A**) posterior part; dorsal view; (**B**) Anterior part; vental view. Scale bars: 5 mm. Photo: Dr Brygida Wawrzyniak-Wydrowska (University of Szczecin, Poland).

parts: anterior cephalothorax (20% of body length) and posterior "trunk" (80%). Semi-triangular cephalothorax with three very pronounced lateral indentations marking traces of body segmentation and defining cephalosome from first and second pedigerous somites, the latter bearing prominent posterolateral lobes. Cephalosome with rounded frontal margin produced anteromedially, lateral margins slightly convex; bearing four pairs of appendages. Post-cephalothoracic "trunk" cylindrical and legless, elongate with discrete traces of segmentation; becoming distinctly wider posteriorly and with prominent caudal rami on posterolateral corners. Total body length

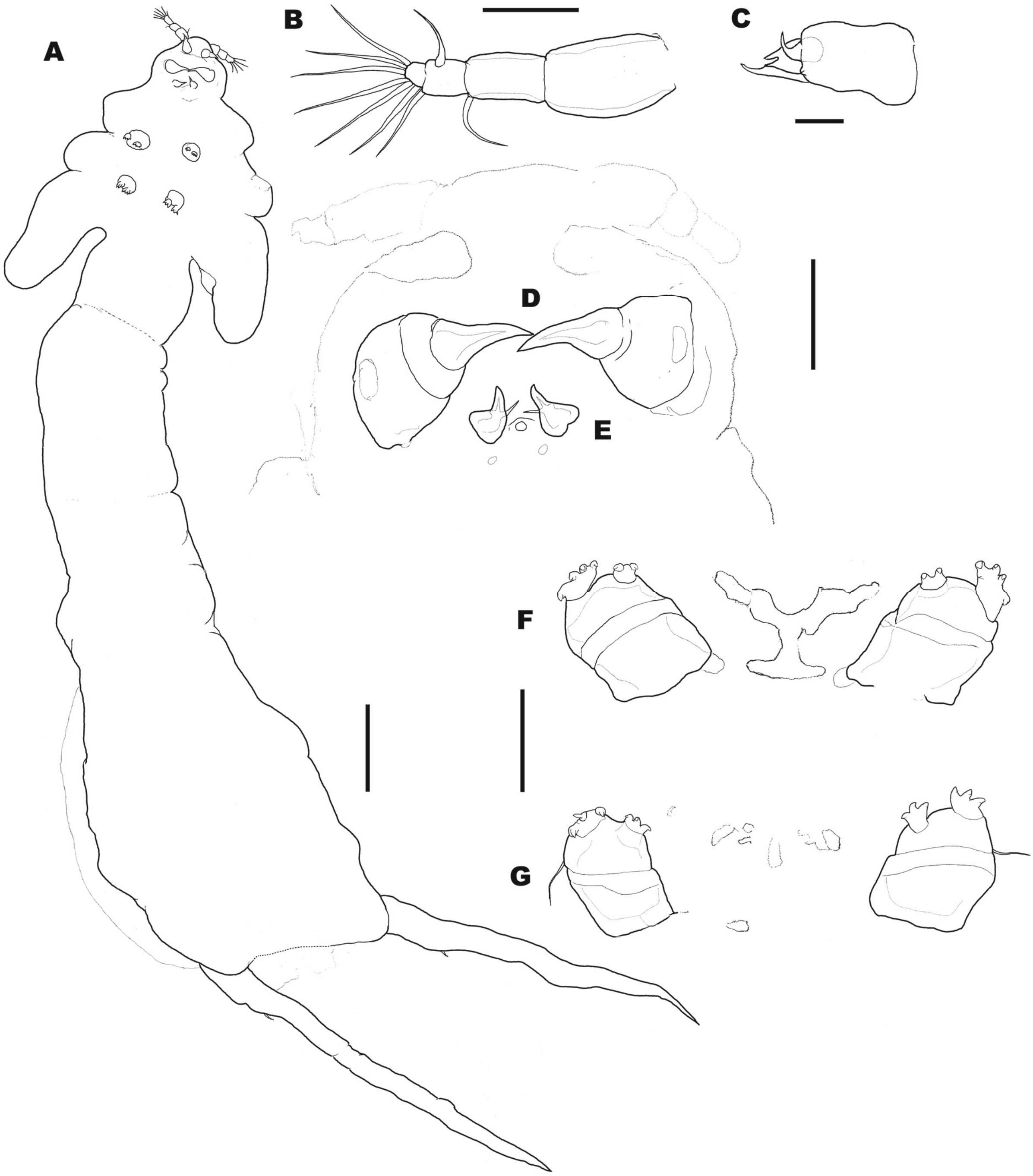

Figure 3. Male of *Sarcotaces antimori* sp. nov. (holotype) from blue antimora, *Antimora rostrata*. Habitus (**A**); antennule (**B**); antenna (**C**); mandibles (**D**); maxillae (**E**); first legs (**F**); second legs (**G**). All images in ventral view. Scale bars: 0.2 mm (A), 0.05 mm (D, E, F, G), 0.02 mm (B), 0.01 mm (C).

of male 2.07 mm, excluding caudal rami, and 2.90 mm with symmetrical caudal rami; caudal ramus length 0.83 mm (Table 2). Maximum cephalothorax width 0.61 mm. Trunk width ranging from 0.21 to 0.54 mm. Caudal rami constituting 28.6% of total length and 40.1% of body length. Cephalothoracic appendages well developed and consisting of antennulae, antennae, mandibles, maxillae, and 2 pairs of legs. Antennule (Fig. 3B) four-segmented with segments diminishing in length and diameter towards tip: first segment longest lacking setation; second segment slightly shorter with single seta posteriorly; third segment slightly longer than wide with one seta anteriorly and one long seta posteriorly; fourth segment short with three long setae posteriorly and three long setae terminally. Antenna (Fig. 3C) indistinctly three-segmented comprising coxobasis plus two-segmented endopod; endopodal segments each bearing single large terminal claw. Mandible (Fig. 3D) large, subchelate, wide at base; tapering towards powerful distal claw. Maxillulae not observed. Maxillae (Fig. 3E) small, uniramous, with triangular base bearing conical terminal segment armed with small seta at base. Maxillipeds absent. First legs

(Fig. 3F) biramous with semi-quadrangular two-segmented protopod: exopod one-segmented and armed with four stout claws; endopod one-segmented with two stout claws. Elaborate, Y-shaped interpodal sclerite present on ventral body surface between first thoracopods. Second legs (Fig. 3G) similar to first: exopod with three stout claws (with single seta at base laterally); endopod with three stout claws. Interpodal sclerite almost completely reduced. Caudal rami very long, thick powerful gently tapering towards distal tip (Fig. 3A), armed with single minute setule near base.

Remarks. The female of *Sarcotaces antimori* sp. nov. differs from that of all known species by possessing very dense coverage over the surface of the cephalosome and thoracic somites with relatively large papilliform protrusions. Another distinct feature of this species is that the surface of the oral lobe is regularly and densely covered with large papilliform protrusions, similar to those covering the rest of the body. This feature distinguishes *Sarcotaces antimori* sp. nov. from its congeners

The male of *Sarcotaces antimori* sp. nov. differs from that of all known species by the deep indentations in the lateral margins of the cephalothorax. Another distinct character is the shape of the trunk which widens substantially posteriorly. In addition, the antennule has a unique setal formula (0, 1, 2, 6) and the first legs lack the outer protopodal seta at the base of the exopod (Table 2).

Etymology. The specific name *antimori* is an adjective derived from the name of the host genus.

Discussion

While comparing the morphological differences between known species of the genus *Sarcotaces* we need to remember about the importance of the host specificity. According to Piasecki et al. (2022), individual *Sarcotaces* species can only infect a specific host fish or closely related species. Those authors broadly discussed the issue of the host specificity in relation to *Sarcotaces*. One of the new arguments supporting the hypothesis of very narrow host specificity are the results of Osman et. al (2014). He studied fishes representing 18 species from the Persian Gulf and *Sarcotaces* was found only in *Epinephelus chlorostigma* (Valenciennes, 1828). McMillan (unpublished*) after examining some 284 specimens of six species of the genus *Coelorinchus* (Gadiformes) caught off New Zealand found *Sarcotaces* only in *Coelorinchus aspercephalus* Waite, 1911. There are no other records of this parasitic copepod in any of the 149 valid species (Fricke et al. 2024) of the genus *Coelorinchus*. In European waters, *Sarcotaces arcticus* can only be found in *Molva dypterygia* (Pennant, 1784).

Three of the nine valid species of *Sarcotaces* (*S. arcticus*, *S. izawai*, and *S. antimori* sp. nov.) have been found in fishes representing the order Gadiformes; two (*S. verrucosus* and *S. komaii*) have been reported from fishes representing Perciformes; and another two (*S. japonicus* and *S. shiinoi*) were collected from Anguilliformes fishes. The remaining parasites were recovered from Lophiiformes (*S. pacificus*) and Ophidiiformes (*S. namibiensis*). Despite sharing the same host-fish order, the majority of *Sarcotaces* species have utilized fishes representing different families. There is only one exception: both *S. izawai* and *S. antimori* sp. nov. share the same host-fish family Moridae but they utilize different species and different genera (Table 1). Taking into account the earlier mentioned hypothesis of the narrow host specificity of *Sarcotaces*, we believe that *Sarcotaces* records representing host fishes of higher taxa different from those of the type species should be treated with caution and verified where possible (e.g., Dollfus 1928; Kuitunen-Ekbaum 1949; Ezpeleta Herce 1974; Avdeev and Avdeev 1975; Moser et al. 1985; Kabata 1988; González and Tanzola 2000). Future descriptions of *Sarcotaces* should also be supported by genetic studies. Unfortunately, the only such study has been Piasecki et al (2022). In the presently reported study, however, despite the efforts of two separate teams, we were not able to extract the genetic material.

Despite sharing the same host species (*Antimora rostrata*), *S. komaii* sensu Avdeev and Avdeev (1975) differs from *S. antimori* sp. nov. In the former species, the female is 4.02 cm long, is regularly drop-shaped, body segmentation is regular, the widest somite is just posterior to the oral lobe, and the oral lobe is characteristic, with four peripheral elements, differing in size and armament. The cephalothorax of the male is semi-triangular with distinctly rounded lateral margins lacking indentations that might correspond to inter-segmental boundaries. The trunk is regularly cylindrical and of uniform diameter. In *S. antimori* sp. nov. the female is 15.1 mm long, less drop-shaped and more semi-quadrangular, body segmentation is irregular, the widest somite is located posteriorly, and the oral lobe is doughnut shaped and densely covered by papilliform protrusions. In the male, the cephalothorax has deep lateral indentations separating the cephalosome from the first pedigerous somite and separating the first and second pedigerous somites, the trunk distinctly increases in diameter posteriorly. *Sarcotaces komaii* sensu Avdeev and Avdeev (1975) has been inadequately described and illustrated but its oral lobe is very similar to that of the nominal species (despite the different host fish).

Only a few nominal species have been originally collected in higher numbers. Among them were *Sarcotaces arcticus* with females 10.0–90.0 mm long (Berland 1970) or *S. izawai* representing lengths of 25.0–48.0 mm. Unfortunately, no author has focused their attention on the size of those females at maturity. Consequently, female size does not seem to be a decisive morphological

* McMillan PJ (1980) New Zealand macrourids of the genus *Coelorinchus* (Pisces: Gadiformes) with detailed descriptions of six common species and notes on aspects of their biology. MSc Thesis; Victoria University of Wellington, New Zealand.

factor. Similarly, we do not know if the size of the protrusions covering the body surface increases with age or not.

In the presently reported study, no nauplius stages were found. Such stages are usually detected when the black fluid surrounding the female in the gall is strained through a fine mesh. Through this procedure also males are detected. The male was found, so it is unlikely that nauplii were overlooked. Nauplius stages are known for *S. arcticus* (see Hjort 1895; Kuitunen-Ekbaum 1949; Moser et al. 1985), *S. pacificus* (see Komai 1924; Izawa 1973), *S. japonicus* (see Izawa 1974), *S. izawai* (see Piasecki et al. 2022), and *S. verrucosus* (see González and Tanzola 2000). The only comprehensive life cycle study was conducted on *S. pacificus* by Izawa (1973) who counted up to 1000 eggs in a gall and reared five nauplius stages followed by a copepodid. The copepodid contains energy reserves in the form of yolk granules, so it is likely that the copepodid represents the infective stage. Nobody has reported egg sacs or their traces. Nauplii were always found freely floating in the black fluid surrounding the female. The hypothetical existence of egg sacs under the particular "safe" conditions of gall seems to be redundant.

Copepods of the genus *Sarcotaces* are mesoparasites sensu Kabata (1976). Even though they are completely hidden inside the host musculature they cannot be referred to as endoparasites because of they maintain constant contact with the external environment via a terminal pore in wall of the gall. The concept of mesoparasitism was widely discussed by Piasecki et al. (2022).

Why do the authors describing *Sarcotaces* females have problems in describing cephalic appendages? We found a possible explanation while watching a video by Jonathan Martin (2009) posted on Flickr. This is the only available footage showing live and moving *Sarcotaces* sp. female. It is evident the oral lobe is hinged anteriorly and can close and open at an angle of 45 degrees. When the lobe is closed, which happens usually in dead females, the cephalic appendages are most likely hidden below it.

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