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First step towards understanding the specific identity of fish muscle parasites of the genus *Sarcotaces* (Copepoda: Philichthyidae)—New species and first molecular ID in the genus

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ABSTRACT

Parasitic copepods of the genus *Sarcotaces* are remarkable. They occur in galls inside skeletal muscles of fishes and it is virtually impossible to overlook them, especially during fish handling and processing. The galls contain an intensively black ink-like substance that may stain fish tissue during filleting. They have a global distribution and until recently, seven nominal species had been described, each from a host representing a different fish family. Females of valid species are quite similar in their morphology, therefore the males are essential for species determination. Even though such a task may be difficult, because of the existing inadequate descriptions that additionally hinder correct identification. The aim of this study was to provide a detailed morphological and molecular characterization of the *Sarcotaces* specimens found in muscles of the common mora, *Mora moro* (Risso, 1810), most probably originating from southern Australia. The additional aim was to indicate possible mode and strategy of infection for the parasitic copepods of the genus *Sarcotaces*. The present paper not only describes and illustrates *Sarcotaces izawai* sp. nov. but also provides its molecular ID based on the *COI* gene. In addition to traditional light microscopy studies, Scanning Electron Microscopy (SEM) was also used. Males of *Sarcotaces izawai* sp. nov. differ from those of its congeners: in the host fish family, in the relative proportions of the caudal rami, and in the setal formula of the antennulae. For the first time in this genus, we described the maxillulae. We also discussed the possible mode and strategy of infection and redefined mesoparasitism.

1. Introduction

Fish parasites representing the family Philichthyidae are mesoparasites sensu Kabata (1976). Although they are completely (or almost completely) hidden within the host's body, they cannot be considered endoparasites because of their constant contact with the external environment. According to Boxshall and Halsey (2004), philichthyid copepods are classified in nine valid genera: *Colobomatoides* Essafi et Raibaut, 1980; *Colobomatus* Hesse, 1873; *Ichthyotaces* Shiino, 1932; *Lepospilus* Hesse, 1866; *Lernaeascus* Claus, 1886; *Philichthys* Steenstrup, 1862; *Procolobomatus* Castro-Romero, 1994; *Sarcotaces* Olsson, 1872; and *Sphaerifer* Richardi, 1876. Those copepods live either in the subcutaneous spaces associated with the sensory canals/mucous canals of the lateral line (*Colobomatoides*, *Colobomatus*, *Lepospilus*, *Lernaeascus*, *Procolobomatus*, *Sphaerifer*) (Uyeno et al., 2015), inside the cranial bones of actinopterygian fishes (*Philichthys*) (Rolbiecki et al., 2021), or in galls inside fish tissues (*Ichthyotaces*, *Sarcotaces*) (see Shiino, 1932). Copepods of the genus *Sarcotaces* are very spectacular. Their highly-metamorphosed females attain substantial sizes, up to 50 mm or even 90 mm in length (Berland, 1970), and occur in a gall surrounded by a thin-walled envelope, inside skeletal muscles of bony fishes (Actinopterygii: Teleostei). Those galls (sometimes referred to as a cyst) contain black fluid which is likely to stain the fish muscles during the process of filleting. Therefore, German fishermen used to call those muscle

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parasites Tintenbeutel [ink bag] (Amlacher, 1958; Priebe, 1963). A small aperture connects the gall with the external environment. It is essential in releasing the offspring (at the nauplius stage) and also in attracting and receiving the opposite sex. Priebe (1963) illustrated the tip of a female's body protruding through such skin opening. Quite often the gall contains also small-size male(s).

Like many other copepods parasitic on fishes, *Sarcotaces* also show very distinct sexual dimorphism. Females are disproportionally large, in this case, 10–20 times longer than males. The females exhibit obliterated segmentation and extreme reduction of appendages. Males, in turn, are less altered and their appendages, although modified, are well visible.

It is quite easy to identify a *Sarcotaces* because the females are uniform in shape and structure. Males have many characters of potential taxonomic value but like females, they show high phenotypic plasticity in some of their body parts. Until recently, only seven nominal species had been described. Unfortunately, the morphology of the majority of nominal species has been inadequately described and illustrated.

We assumed that *Sarcotaces*, like other highly metamorphosed copepod species including species of the family Philichthyidae, exhibit a narrow host specificity (at the host family level). Therefore, the only way to determine the species identity would be to study its molecular ID, and such data are not available for known species.

We collected *Sarcotaces* specimens of both sexes and their nauplii from fillets of a marine fish. The whole consignment was mislabeled in terms of the host species identity ("*Pseudophycis bachus*", family Moridae) and most probably also the fish origin ("the Falklands"). The hosts were identified genetically as *Mora moro* (Risso, 1810) (GenBank: *Mora moro* voucher Ml_Mm_2; Acc. No. MT318699 and *Mora moro* voucher Ml_Mm_2 Acc. No. MT318700) (Piasecki et al., 2020).

2. Materials and methods

The parasites were recovered from 29 preselected, frozen fish all showing signs of the infection and delivered by the County Veterinary Inspector [Powiatowy Lekarz Weterynarii] of Szczecin, Poland. The fish were decapitated, finless, and gutted (so-called pan-dressed fish) and they were probably frozen and thawed more than three times. All fish delivered showed gross symptoms of a subdermal infection or ugly-looking black-stained areas in their muscles. Some fillets featured only the black-stained voids in the muscles and the parasites were probably lost during the mechanical processing. The *Sarcotaces* galls were dissected and the black fluid surrounding them was strained through a fine gauze to separate putative microscopic-size parasite stages (larvae and adult males). Details of the procedure were described in Piasecki et al. (2020). One of the males was designated as the holotype. The best preserved female, measuring 40 mm in total length was designated as the allotype. The collected specimens were 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 copepods were stained in lignin pink. The drawings were made using a drawing tube (Olympus). Two male specimens were examined in a Scanning Electron Microscope (SEM). They were rinsed in 75% ethanol to remove lactic acid remains and dehydrated through a graded acetone series (30%, 50%, 75%, 90%, and 100%). Final drying was performed using CO_2 critical point dryer Polaron E3000 (Quorum Technologies, Laughton, East Sussex, UK). Dry samples were covered with Au–Pd alloy using thermal evaporator JEOL JEE-4X (JEOL, Tokyo, Japan). Scanning Electron Microscopy (SEM) observations were performed using a field emission microscope Hitachi SU-70 (Hitachi, Naka, Japan) at an accelerating voltage of 1.5 kV.

Morphological terminology follows Delamare Deboutteville (1962), Kabata (1979), and Huys and Boxshall (1991).

2.1. Molecular study

Samples of *Sarcotaces* tissues were collected also for molecular studies. Due to the scarcity of the material DNA isolation was performed based on a single female only. High Pure PCR Template Preparation Kit (Roche, Switzerland) was used for DNA extraction according to the manufacturer's instructions. The quantity and quality of the extract were assessed by spectrophotometric measurements using the NanoDrop 2000 (Thermo Scientific, USA) and electrophoresis in 1.5% agarose gel. The amplification of the selected region was conducted using universal primers LCO1490: 5′-GGTCAACAAATCATAAAGATATTGG-3′ and HCO2198: 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′, targeting *cytochrome oxidase subunit I* (*COI*) (Folmer et al., 1994) under the following conditions: 1 step of 5 min at 94 °C followed by 35 cycles at 94 °C for 30 s, 58 °C for 30 s, 72 °C for 60 s, and a final extension at 72 °C for 7 min. The PCR reaction was conducted on T100™ Thermal Cycler (Bio-Rad, USA) using the GoTaq PCR kit (Promega, USA), including 5 μL of Green GoTaq® Flexi Buffer, 2.5 μL of $MgCl_2$ (25 mM Solution), 0.5 μL of PCR Nucleotide Mix (10 mM), 0.125 μL of GoTaq® DNA Polymerase (5 u/μL), 0.5 μM of each primer and 5 μL of DNA template in the final volume of 25 μL. The results of amplification were assessed by separating the PCR products analyzed on 2% agarose gel and samples were cut from the gel purified with Gel-Out kit (A&A Biotechnology, Poland). Next, PCR products were cloned to DNA plasmid pUC19 (A&A Biotechnology, Poland), plasmids extracted using Plasmid Mini AX kit (A&A Biotechnology, Poland) and stabilized in 10 mM Tris-HCl pH 8.0 buffer. Samples were sent for bidirectional sequencing to Genomed company (Poland). The raw reads were assembled with Geneious 8.0 (Kearse et al., 2012) and compared against the GenBank sequences using BLAST (Altschul et al., 1990).

3. Results

Only nine fish specimens out of 29, preselected by the County Veterinary Inspector, hosted in their muscles characteristic parasitic galls. Only a single gall per fish was observed in the muscles of the posterior part of the body of those nine hosts. Other "carcasses" showed black-stained voids where the parasites were removed by automated processing of the fish (Fig. 1A). Some voids were double suggesting infection by two parasite females. The parasite galls were pyriform (drop-shaped) containing a tightly-fitting single female (Fig. 1B and C). The limited space between the gall wall and the parasite was filled with a distinctly black ink-like fluid. The fluid, after straining through a fine gauze revealed, eggs, newly hatched nauplius stages, and cylindrical males (Fig. 1D) of very small size. The long axes of the galls/females were oriented at an acute angle to the fish skin, pointing backward. Each gall was linked to a minute opening in the fish skin, penetrating through a hole in a scale. All galls were situated in the posterior part of the host, in the presumed lateral line area.

We collected a total of nine females of which four were extensively damaged or distorted. One of the largest females was best preserved. A total of 20 males were collected. Two of them were found in a female, measuring 40 mm in total length (designated as the allotype), and as many as 18 in other female not measured because of extensive damage (Piasecki et al., 2020).

3.1. Taxonomy

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

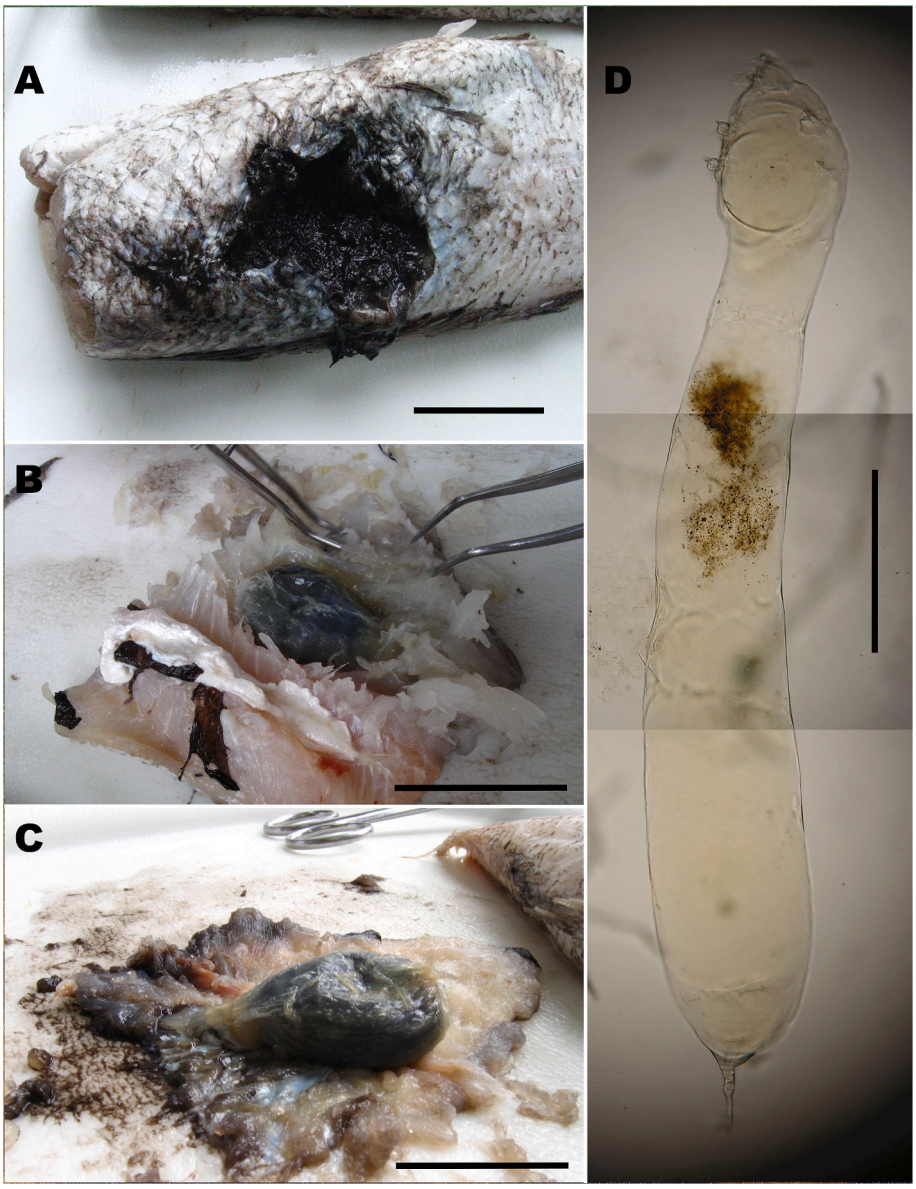

Fig. 1. Photographs documenting copepod (*Sarcotaces izawai* sp. nov.) infection of fish (*Mora moro*); (**A**) Parasite-induced black-stained void in the body of host fish, (**B**) parasite gall in the muscles of host fish, (**C**) The same with myomeres removed, (**D**) Composite microphotograph of the male parasite, lateral view. Scale bars: A–C = 30 mm, D = 0.5 mm. Photos A–C: by Karolina Półtorak.

3.2. Locality

"The Falklands" (Most probably southern Australia; see Discussion).

3.3. Host fish

Mora moro (Risso, 1810) (GenBank: *Mora moro* voucher Ml_Mm_2; Acc. No. MT318699 and *Mora moro* voucher Ml_Mm_2 Acc. No. MT318700) (Piasecki et al., 2020).

3.4. Infection site

Posterolateral skeletal muscles.

3.5. Type material

The types, have been deposited in the Crustacea Collection of the Museum für Naturkunde, Berlin, Germany. The type material included holotype male (ZMB 34609), allotype female (ZMB 34610), and paratypes (ZMB 34611) (4 complete male specimens, 2 complete female specimens, 2 male specimens studied using SEM, and 2 partly dissected males).

3.6. ZooBank registration

http://zoobank.org/3ACAAAB2-E0CD-4B54-A3B4-D2AFB8357B63.

3.7. Species COI barcode

Analysis of the raw reads allowed to obtain a 658 bp sequence of *COI*, which was deposited in GenBank under accession number OM681152.

3.8. Description of female

Body elongate, pyriform (drop shaped) with anterior part gently rounded, posterior part distinctly tapering into pointed process

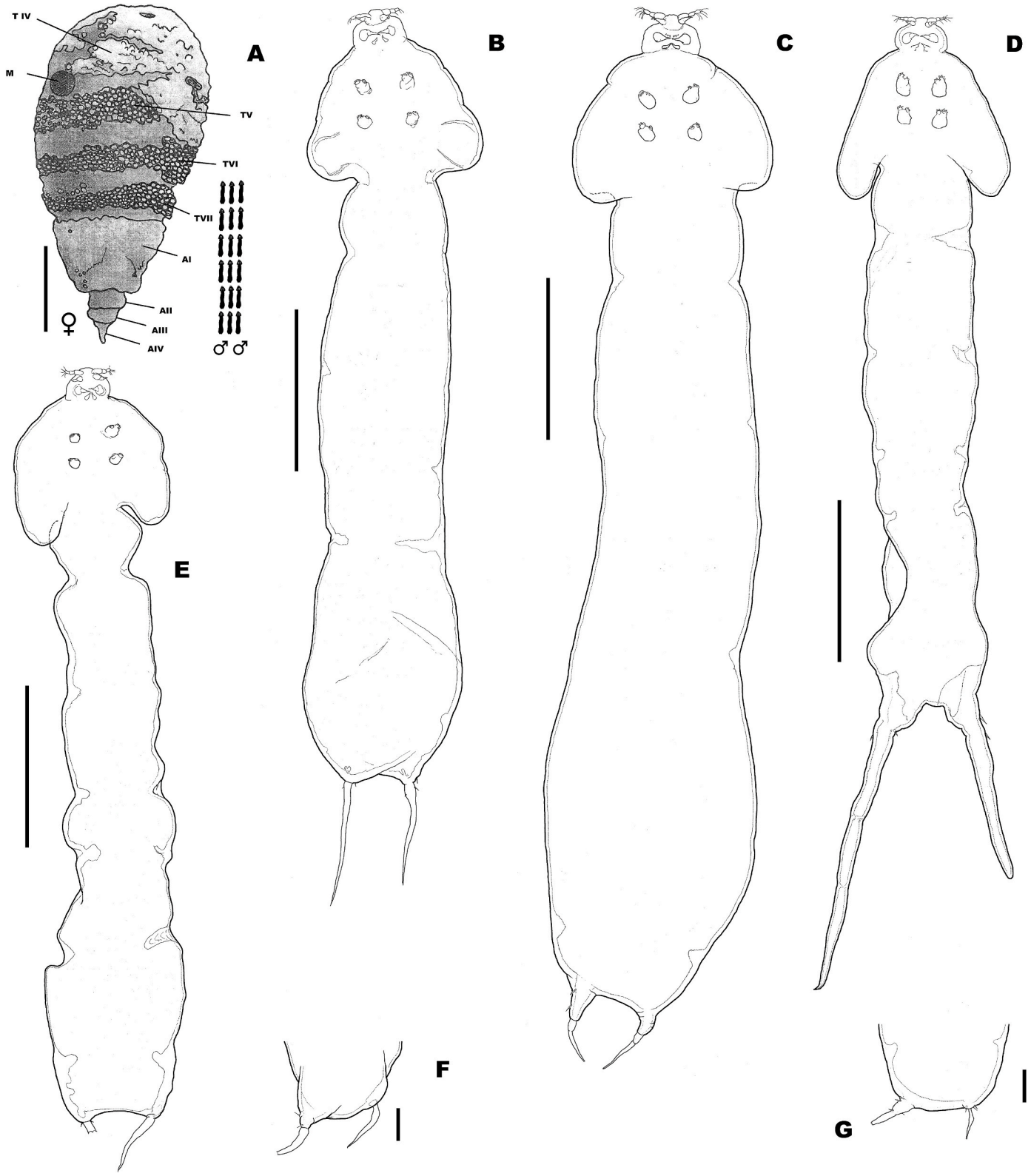

Fig. 2. Line drawings of *Sarcotaces izawai* sp. nov.; (**A**) Female (allotype), habitus, semi-ventral view; small black silhouettes on the right represent the males at the same scale (the highest number found in a single gall), (**B**) Male (holotype), habitus, ventral, (**C, D, E**) Other males, habitus, ventral, (**F, G**) Caudal rami of other male specimens; Abbreviations: M = mouth area, TIV–TVII = thoracic somites, AI–AIV = abdominal somites; Scale bars: A = 10 mm, B–E = 0.5 mm, F–G = 0.1 mm.

(Fig. 2A). Total length (n = 5) reaching 25–48 mm (35.8 ± 8.1 mm); total width 10–19 mm (15.6 ± 3.0 mm) (mean ± standard deviation). Body highly metamorphosed, with obliterated segmentation and appendages, in some places covered with lobate, indistinctly bifurcated protrusions. Presumed borders between somites marked by areas without protrusions. Protrusions well developed in anterior part, reduced in abdominal part. Dorsal "segmentation" not consistently matching ventral one. Mouth area positioned ventrally on cephalosome. Presumed somites th II—th III poorly distinguishable and displaced in front of mouth area. Somites th IV, th V, th VI, and th VII relatively short, of similar length, located posterior to mouth opening and covered with papillary protrusions. Abdominal somites lacking papillary protrusions. First abdominal somite (abd I) very long, resembling truncated cone of height similar to diameter. Abrupt setoff between abd I and abd II; abd III very small, and abd IV very small in form of terminal sharp spike. Appendages not visible.

3.9. Description of male

Males (Figs. 1D, 2B–G, 3, 4, 5) distinctly smaller than females, differing substantially in their structure. Body very strongly elongate, subcylindrical, unsegmented, with smooth surface. Cephalothoracic appendages well developed and consisting of antennulae, antennae, mandibles, maxillulae, maxillae, and 2 pairs of legs. Total length of males (n = 11), excluding caudal rami, reaching 2.15–3.52 mm (2.56 ± 0.38 mm), total width 0.36–0.60 mm (0.47 ± 0.083 mm). Caudal rami 0.039–0.9 mm (0.41 ± 0.197 mm) (mean ± standard deviation), constituting 9.41% of body length. Distinct asymmetry visible in 8 out of 11 specimens (Figs. 2B, C, D, F, G, 3B, C, E, 5). In one case setation on one side absent completely (Fig. 3E). Only in three cases caudal rami symmetrical (Figs. 2E and 3A, D). Anterior part of body (head) small and semicircular, with dorsal shield with sensory setules (Figs. 4A and C) with four pairs of appendages (Fig. 2B–E, 4B). Rest of cephalothorax semi-triangular/oval, abruptly widening in dorsal view, having two prominent posterolateral lobes, and bearing two pairs of simplified legs (Fig. 2B–E). Legless trunk cylindrical, distinctly narrower than preceding somites; gradually widening posteriorly, in ventral view and gently narrowing towards posterior end. Internally, traces of segmentation visible, marked by areas with thicker cuticle. Thickest cuticle in posterior part, especially in specimen with largest caudal rami (Fig. 2E). Holotype depicted in Fig. 2B. Caudal rami extremely variable in shape, size, and armament (Fig. 2B–G, 3A–E, 5E), usually consisting of apparently bipartite semi-conical process ("seta") (Fig. 5F) armed at base with 2–4 setules. Antennule (Figs. 3F and 4D, E) four segmented. First segment longest with four robust short setae ventrally; second segment slightly longer than wide with single seta posteriorly, short seta and two longer setae ventrally; third segment almost twice as long as wide with one short and one long seta anteriorly; fourth segment short with six long and one short setae terminally. Antenna (Figs. 3G and 4F) uniramous, comprising protopodal part (coxa and basis) and 3-segmented endopod. Endopod with two large claws bearing indistinct process at bases. Protopodal basis with single robust, short, round-tip seta and several tiny sharp denticles ventrally (Fig. 4E and F). Mandible (Figs. 3H and 5A, B) large, uniramous, subchelate, indistinctly two-segmented. Protopodal part robust, wide at base; second segment smaller, slightly elongate and armed with powerful claw. Supramandibular ridges (SMR) having few denticles located anterior to both mandibles at close proximity. SMRs separated medially be tight gap. Maxillulae (Fig. 5A and B)

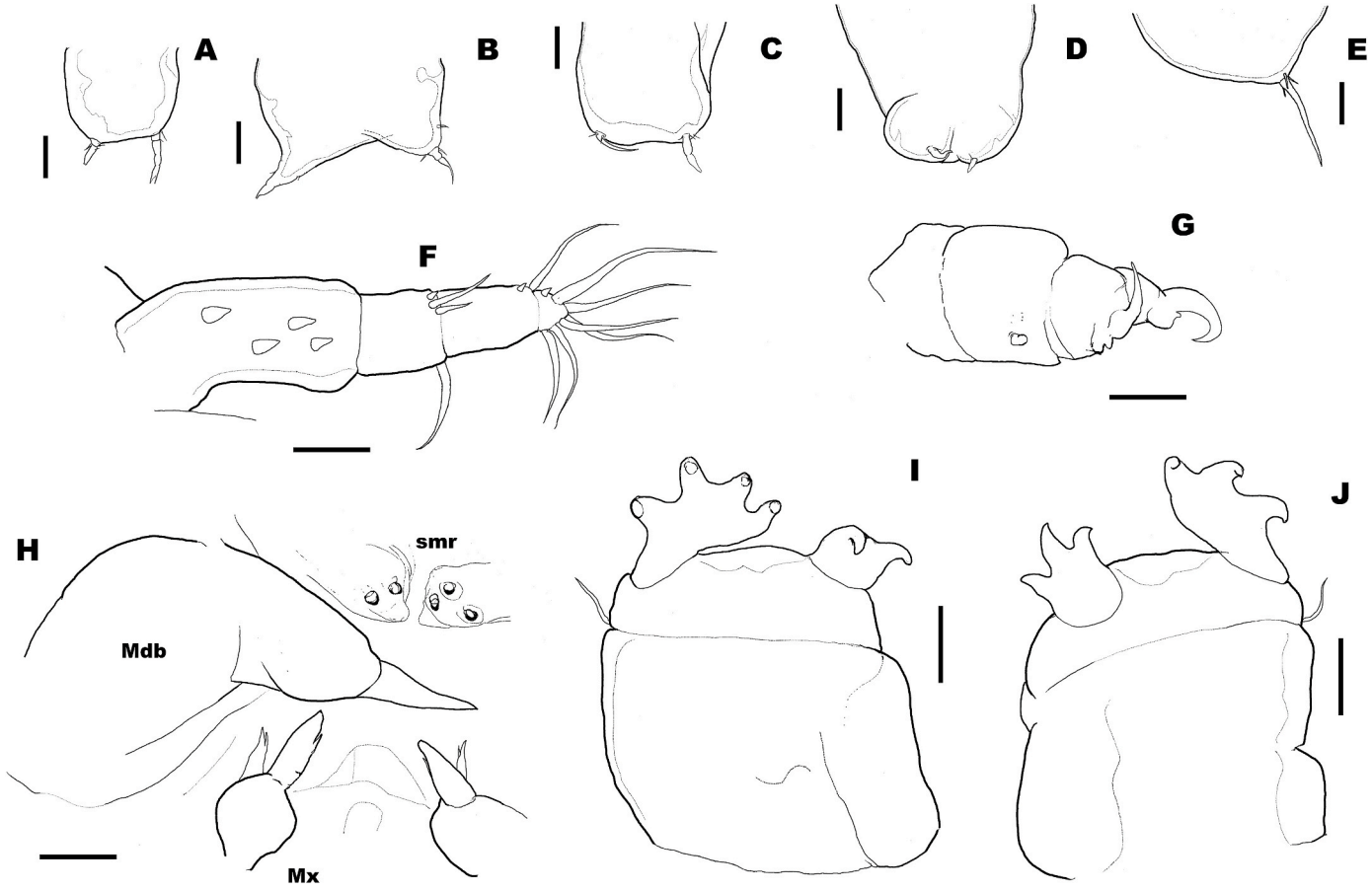

Fig. 3. Line drawings of *Sarcotaces izawai* sp. nov.; male; (**A–E**) Caudal rami of other male specimens, ventral; (**F**) Antennule, ventral; (**G**) Antenna, ventral; (**H**) Mandible (Mdb), and maxillae (Mx), ventral; above—protuberances of supramandibular ridge; left mandible omitted), (**I**) First leg (right side), ventral, (**J**) Second leg (left side), ventral; Scale bars: A–E = 0.1 mm, F–J = 0.01 mm.

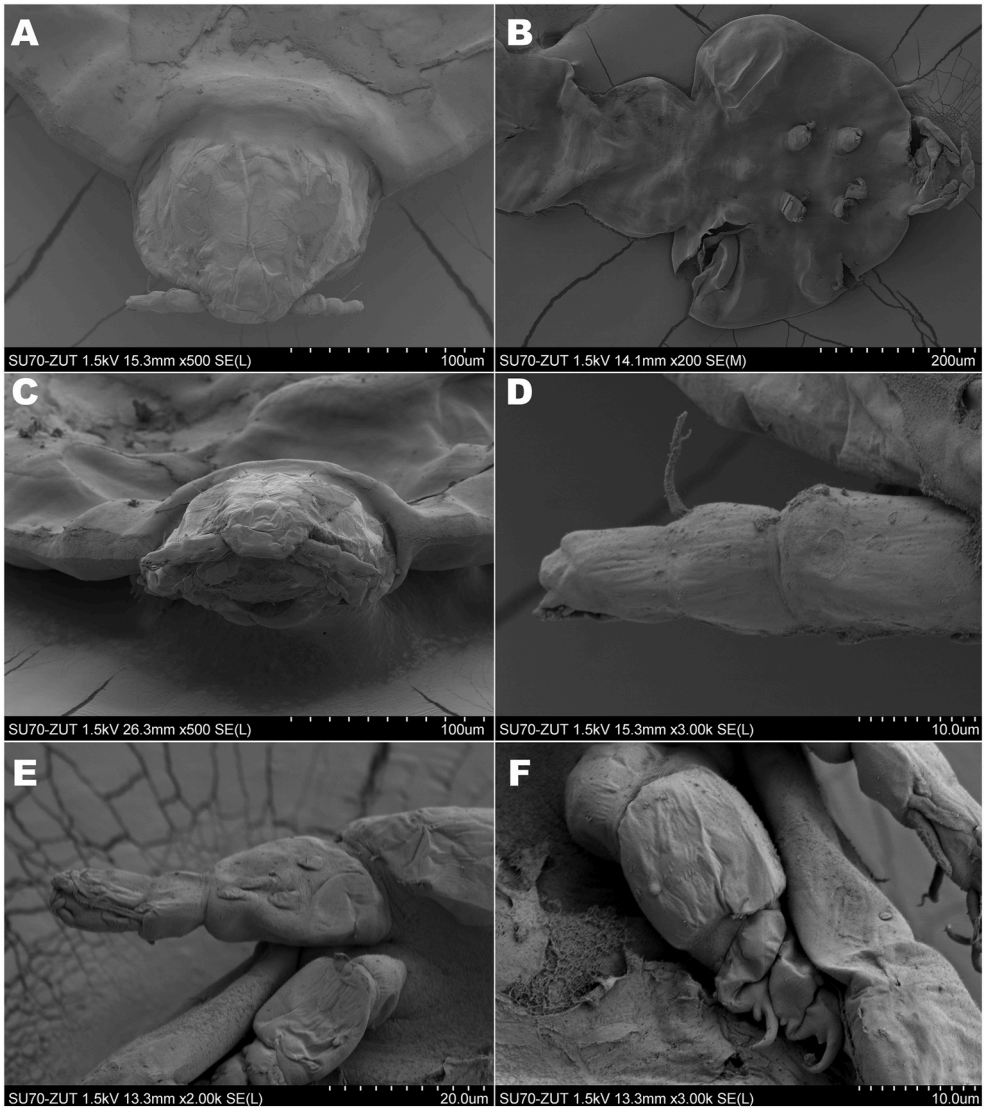

Fig. 4. SEM micrographs of *Sarcotaces izawai* sp. nov.; male; (**A**) Cephalon, dorsal, (**B**) Cephalothorax, ventral, (**C**) Cephalon, anterior view, (**D**) Antennule, dorsal, (**E**) Antennule, ventral, (**F**) Antenna, ventral.

reduced, minute, bilobed, partly obscured by mandibular claw. Maxillae (Figs. 3H and 5C) small, uniramous, with oval base surmounted with two blade-like terminal segments; posterior larger, conical with 4–5 denticles; anterior slim with bifid tip. First leg (Fig. 3I) biramous with semi-quadrangular two-segmented protopodal part (coxa and basis). Exopod one segmented armed with four stout claws (Fig. 5D) and single seta at basis laterally; endopod one segmented with two stout claws. Second leg (Fig. 3J) similar to first leg. Exopod with three stout claws (with single seta at basis laterally); endopod with three stout claws.

3.10. Etymology

The specific name *izawai* is intended to honor Dr Kunihiko Izawa for his contribution to copepodology and to the knowledge of the genus *Sarcotaces* in particular.

4. Discussion

There are seven nominal species belonging to the genus *Sarcotaces*: *S. arcticus* Collett (1874); *S. verrucosus* Olsson (1872); *S. pacificus* Komai (1924); *S. komaii* Shiino (1953); *S. japonicus* Izawa (1974); *S. shiinoi* Izawa (1974); and *S. namibiensis* Reimer (1991).

Despite almost 70 published records of *Sarcotaces* (see Piasecki et al., 2020) only some papers contain morphological descriptions and illustrations. Not all of the latter papers, however, can be used for taxonomic purposes for different reasons. The major reason is the host-specificity. Many copepods parasitic on fishes show a narrow host specificity, for example, species of the family Lernaeopodidae (see Piasecki et al., 2010). Such phenomenon has also been reported for the family Philichthyidae (see Delamare Deboutteville, 1962; Grabda and Linkowski, 1978; West, 1992). The narrow host-specificity of *Sarcotaces* seems to be indirectly confirmed also by its relative "rarity". The number of known records is relatively low (Piasecki et al., 2020), considering how spectacular and readily visible those infections are. Until a further evidence is provided we assume that also *Sarcotaces* species are host specific (at the host family level). In view of the above, all *Sarcotaces* cases reported, re-described, and illustrated from fishes different than the type species (or a type-species family) seem to be unreliable. This concerns: Dollfus (1928, 1929), Causey (1955), and González and Tanzola (2000) [for "*S. verucosus*"]; Kuitunen-Ekbaum (1949), Sekerak (1970), Avdeev and Avdeev (1975), Sekerak and Arai (1977), Moser et al. (1985; records from Sebastidae), Kazačenko (1986), and Stanley and Kronlund (2005) [for "*S. arcticus*"]; Ezpeleta Herce (1974), Avdeev and Avdeev (1975), and Kazačenko (2015) [for "*S. komaii*"]. Also, the majority of other

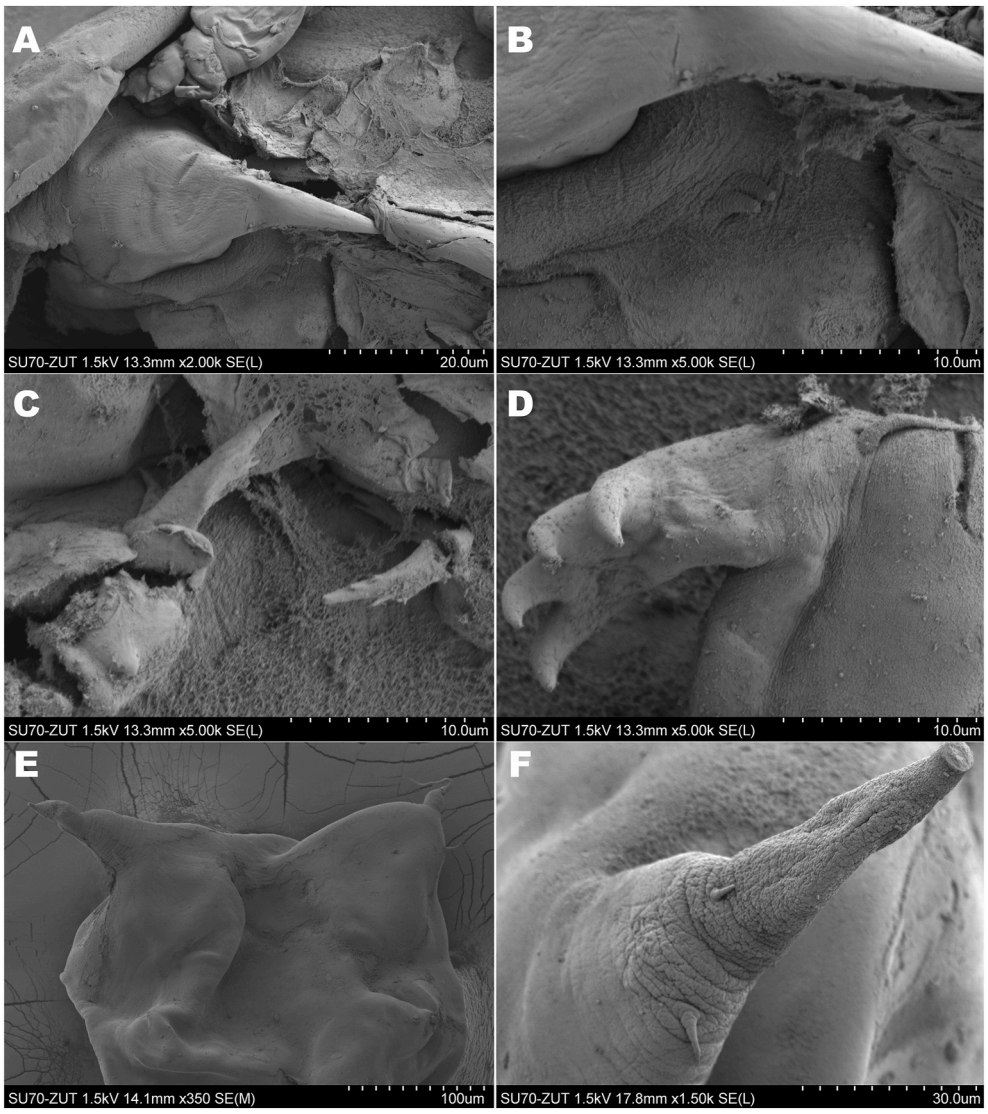

Fig. 5. SEM micrographs of *Sarcotaces izawai* sp. nov.; male; (**A**) Antenna, mandible and maxillule, ventral, (**B**) Mandibular claw and maxillule, ventral, (**C**) Maxillae, ventral, (**D**) Exopod of first thoracopod (left side), (**E**) Caudal rami of other male specimens, ventral, (**F**) Caudal ramus of another male specimens, ventral.

non-descriptive, mostly faunistic records from non-type host fishes is doubtful (for the list see Piasecki et al., 2020). The females of *Sarcotaces* are large and spectacular while the males are inconspicuous, often absent, or overlooked because of their microscopic size. The "old" descriptions were based on females only, until Heegaard (1947) announced that he described and illustrated the first-ever male of *Sarcotaces* (*S. pacificus*). In fact, the first male description in the genus was by Aitken (1942) for *S. arcticus*. Consequently, all subsequent descriptors included also the male. Because females of all species are very similar and show extensive phenotypic variability in terms of their size, we now understand that species differentiation must be based on the male morphology. Also, for the holotypes males rather than females should be selected (e.g., Uyeno et al., 2015).

Sarcotaces verucosus was originally described from *Acanthurus* sp. (Perciformes: Acanthuridae) captured off St. Barthelemy, Caribbean (Olsson, 1872). Unfortunately, the original description included only the female and there have been no subsequent descriptions based on the acanthurid fishes that would cover also the male. One of the best-illustrated descriptions of a *Sarcotaces* species is that of "*S. verucosus*" published by González and Tanzola (2000). Unfortunately, the above-mentioned paper was based on copepods collected from Argentine sandperch, *Pseudopercis semifasciata* (Cuvier, 1829) (Perciformes: Pinguipedidae), and not on the host type species of *S. verucosus*. While discussing this copepod specificity, González and Tanzola (2000) stated that "*S. verucosus*" does not infect other fishes in the area and is therefore specific to the sandperch but they forgot, however, that the original *S. verucosus* was collected not from the sandperch but from a fish representing another family coming from a quite distant locality. Unfortunately, those authors did not explain why do they think that their copepods represent *S. verucosus*. After rejecting the descriptions from non-type hosts (Dollfus, 1928; González and Tanzola, 2000) we suggest that the identity of *S. verucosus* cannot be confirmed at present.

Sarcotaces arcticus was described from *Molva dypterygia* (Pennant, 1784) (Gadiformes: Lotidae) collected at Øksfjord, Finmark, Norway by Collett (1874). The original description covered only the female and unfortunately, the author failed to illustrate the new species. Collet's material, however, was used subsequently in Hjort (1895) where the female and a nauplius were described and illustrated. The male was described much later (Aitken 1942) also from the same fish species landed in Aberdeen, Scotland. Unfortunately, the description and the drawings were inadequate in terms of the standards of modern copepod taxonomy. Selected parts of the male morphology of *S. arcticus* were nicely SEM illustrated by Moser et al. (1985) based on the material from

the host type species from Norway. A complete description of *S. arcticus*, unfortunately is not available. According to Berland (1970), the prevalence of *S. arcticus* in Norway was quite low, reaching 9% for smaller fish and only 3.4% for the larger ones. He examined several thousand fish and about two thousand parasite galls.

Kuitunen-Ekbaum (1949) was the first researcher to describe "*S. arcticus*" from *Sebastes ruberrimus* (Cramer, 1895) (Scorpaeniformes: Sebastidae) from the Pacific (British Columbia). The assumption that the *Sarcotaces* specimens from the Pacific sebastids are indeed *S. arcticus*, persisted for decades and it was reflected in the re-descriptions by Moser et al. (1985) and Kabata (1988) and also in numerous parasitological surveys (for the complete list see Piasecki et al., 2020). Moser et al. (1985) studied *Sarcotaces* morphology using SEM and they compared the specimens from Pacific sebastids with those from the type species (*M. dypterygia*). Unfortunately, their SEM micrographs were not backed up by a description and/or morphological discussion. Virtually without explanation, they synonymized *S. arcticus*, *S. verrucosus*, and *S. komaii* without even examining the two latter species. While analyzing SEM micrographs published by Moser et al. (1985) we noticed that the described "*S. arcticus*" from sebastid fishes has semi-triangular/oval cephalothorax in contrast to the triangular one depicted by Aitken (1942) for the real *S. arcticus*. Therefore *Sarcotaces* specimens collected from Pacific sebastids probably represent another, hitherto undescribed species.

Chronologically, the third known species was *S. pacificus*, described (as a female and nauplius) from *Antennarius striatus* (Shaw, 1794) (Lophiiformes: Antennariidae) captured in Tanabe Bay, Japan (Komai, 1924). More than two decades later Heegaard (1947) came up with a redescription of the male. The host fish was *Antennarius* sp. from Japan. Unfortunately, the morphological details described and illustrated were inadequate for the needs of modern taxonomy and for the differentiation of the species. Fortunately, subsequent studies of Izawa (1974) on the specimens collected from the type host species and from the type locality added a lot to our knowledge on females and males of *S. pacificus*. The same author described and illustrated also developmental stages (nauplius, copepodid) of this parasite (Izawa 1973).

The fourth species of its genus was *S. komaii*, recovered from *Scalicus hians* (Gilbert et Cramer, 1897) (Scorpaeniformes: Platycephaloidei), captured in Tosa Bay, Japan, and described by Shiino (1953). This description included both sexes of this copepod. The second reliable description of *S. komaii*, from the same host and locality, was by Izawa (1974). The other two records of "*S. komaii*" were by Ezpeleta Herce (1974) and Avdeev and Avdeev (1975). The former described "*S. komaii*" from *Sparisoma rubripinne* (Valenciennes, 1840) (Perciformes: Scaridae) from Cuba, while the latter—from *Antimora rostrata* (Günther, 1878) (Gadiformes: Moridae) from the Pacific coasts of Japan. For the reasons mentioned earlier, descriptions by Ezpeleta Herce (1974) and Avdeev and Avdeev (1975) cannot be considered.

Three, most recently added, species of *Sarcotaces* were reported only by their original descriptors. *Sarcotaces japonicus* found in *Gymnothorax kidako* (Temminck et Schlegel, 1846) (Anguilliformes: Muraenidae), captured in Tanabe Bay, Japan, was described by Izawa (1974). *Sarcotaces shiinoi* was also described by Izawa (1974) from *Acromycter nezumi* (Asano, 1958) (Anguilliformes: Congridae) caught at the Kumano Sea, Japan. *Sarcotaces namibiensis* was found by Reimer (1991) in *Selachophidium guentheri* Gilchrist, 1903 (Ophidiiformes: Ophidiidae) from the costs of Namibia. Unfortunately, the quality of the description of *S. namibiensis* is substandard, so it is not suitable for species differentiation and requires a redescription.

Each nominal species was described from a fish representing a different family. Each of those families belongs to a different order, except for *S. japonicus* and *S. shiinoi* which both originate from fishes of the order Anguilliformes (Muraenidae and Congridae, respectively) and *S. arcticus* and *S. izawai* sp. nov., which hosts represent the order Gadiformes and families Lotidae and Moridae, respectively.

Despite the chronological progress in the quality of the available descriptions of species of genus *Sarcotaces* the vast majority of them seem to be inadequate to determine the intraspecific morphological differences. Definitely, the best ones are those provided by Izawa (1974) for *S. pacificus*, *S. komaii*, *S. japonicus*, and *S. shiinoi*. They were all based solely on light microscopy. For the remaining species (*S. verucosus*, *S. arcticus*, *S. namibiensis*) descriptions/illustrations of comparable quality are not available. SEM illustrations of selected body parts of the male of *S. arcticus* were provided by Moser et al. (1985). Those authors also illustrated "*S. arcticus*" from Pacific sebastid fishes but those illustrations cannot be used for discussing the valid species of *Sarcotaces*. Description and SEM data of "*S. verucosus*" from a sandperch by González and Tanzola (2000) cannot be used either (see Table 1).

The size of females differs among the species and it is highly variable (Table 2). The variability was higher in cases where more specimens were collected. Moreover, their body length values tend to overlap among the nominal species. Even though, females of five species (*S. verucosus*, *S. pacificus*, *S. komaii*, *S. japonicus*, *S. shiinoi*) are smaller (25 mm or less) while three others (*S. arcticus*, *S. namibiensis*, and *S. izawai* sp. nov.) are larger, exceed the length of 30 mm. Also, the details of female morphology, in our opinion, are not suitable for species differentiation. Because of the bad quality and the scarcity of the presently reported material we were not able to study the females in more detail.

The shape, size, and morphological details of the male seem to be more helpful. The total length (excluding caudal rami) of S. *pacificus*, *S. komaii*, *S. japonicus*, *S. shiinoi*, *S. namibiensis* does not exceed 2 mm (Table 2). Only *S. arcticus* reported by Aitken (1942) was longer (<3 mm). The body length of the presently described *S. izawai* sp. nov. was 2.15–3.52 mm. Another important feature is the shape of the cephalothorax. It is almost triangular in *S. arcticus* and semi-trapezoid in *S. japonicus*, while in all other species it is semi-triangular/oval.

Sarcotaces izawai sp. nov. male distinctly differs from males all other valid species by the relative length of caudal rami (with setae). The length of caudal rami approximates 70% in *S. komaii*, *S. japonicus*, and *S. namibiensis*, 60% in *S. shiinoi*, and 50% in *S. pacificus*. According to Aitken (1942) the caudal rami constituted 37% of the body length of *S. arcticus*. No reliable data are available for *S. verucosus*. In *S. izawai* sp. nov. the caudal rami are the smallest and represent 9.41% of the body length and this mean value includes an abnormal specimen with excessively long caudal setae, depicted in Fig. 2D. Without this specimen, it would be much lower. Many authors mentioned or simply illustrated some variability in caudal rami but nobody has indicated comparably extensive structural variability as we did in *S. izawai* sp. nov. We also noticed that there is usually a single big caudal seta with a variable number of setules, originating on the proximal portion of this seta (setules on the seta) (Figs. 2D, F, G, 3B, 5E, F). The ancestral number of setae is 6. They usually differ in length, but they always originate from a 'common base'. This is not the case in *S. izawai* sp. nov. where probably the 'common base' was incorporated into the main seta, as its proximal "segment". This fact may be confirmed in Fig. 2D where some "segmentation" or pseudo articulation of the main seta can be visible. Therefore, it is suggested that the first "segment" is in fact an elongated "common base". We observed an extreme asymmetry visible in 8 out of 11 specimens (Figs. 2B, C, D, F, G, 3B, C, E). In one case, the setation on one side was absent (Fig. 3E).

The most uniform male appendages are the mandibles. Their shape reported from all known species is virtually the same. Also, the legs have probably the same structure in all nominal species. This was confirmed for the males of three species (*S. pacificus*, *S. japonicus*, *S. shiinoi*) by Izawa (1974) and for *S. izawai* sp. nov. (present paper). The same leg structures were also observed by Shiino (1953) for the male of *S. komaii* without, however, reporting the small setule at the base of the exopod.

The most promising structure, in terms of its suitability for species verification, is the antennule. It is evident (Table 2) that the number of setae is different in individual species at least in the best-studied ones (*S. pacificus*, *S. komaii*, *S. japonicus*, *S. shiinoi*, and *S. izawai* sp. nov.).

Table 1
Available (illustrated) descriptions of nominal species of the genus *Sarcotaces*.

Species	Sex or stage	Locality	Valid name of host fish	Fish family	Order	Reference
S. verucosus	**F**	**St. Barthelemy, Caribbean**	***Acanthurus* sp.**	**Acanthuridae**	**Perciformes**	**Olsson (1872)**
	F	Martinique, Caribbean	*Halichoeres radiatus* (Linnaeus, 1758)	Labridae	Perciformes	Dollfus (1928)**
	F+M+N	San Matías Gulf, Argentina	*Pseudopercis semifasciata* (Cuvier, 1829)	Pinguipedidae	Perciformes	González and Tanzola (2000)**
S. arcticus	**F**	**Øksfjord, Finmark, Norway**	***Molva dypterygia* (Pennant, 1784)**	**Lotidae**	**Gadiformes**	**Collett (1874)**
	F	Collett's material only female	*Molva dypterygia* (Pennant, 1784)	Lotidae	Gadiformes	Hjort (1895)*
	M	Aberdeen, Scotland	*Molva dypterygia* (Pennant, 1784)	Lotidae	Gadiformes	Aitken (1942)*
	F+M	British Columbia	*Sebastes ruberrimus* (Cramer, 1895)	Sebastidae	Scorpaeniformes	Kuitunen-Ekbaum (1949)**
	F+M+N	Alaska? California?	*Sebastes* spp.	Sebastidae	Scorpaeniformes	Moser et al. (1985)**
	F+M	Norway	*Molva dypterygia* (Pennant, 1784)	Lotidae	Gadiformes	Moser et al. (1985)*
	F+M	British Columbia	*Sebastes* sp.	Sebastidae	Scorpaeniformes	Kabata (1988)**
S. pacificus	**F+N**	**Tanabe Bay, Japan**	***Antennarius striatus* (Shaw, 1794)**	**Antennariidae**	**Lophiiformes**	**Komai (1923)**
	F+M	Sagami, Musaki, Saogiro, Japan	*Antennarius* sp.	Antennariidae	Lophiiformes	Heegaard (1947)*
	N+C	Tanabe Bay, Japan	*Antennarius striatus* (Shaw, 1794)	Antennariidae	Lophiiformes	Izawa (1973)*
	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)**	**Platycephaloidei**	**Scorpaeniformes**	**Shiino (1953)**
	F	Cuba	*Sparisoma rubripinne* (Valenciennes, 1840)	Scaridae	Perciformes	Ezpeleta Herce (1974)**
	F+M	Kumano Sea	*Scalicus hians* (Gilbert et Cramer, 1897)	Platycephaloidei	Scorpaeniformes	Izawa (1974)*
	F+M	Pacific coasts of Japan	*Antimora rostrata* (Günther, 1878)	Moridae	Gadiformes	Avdeev and Avdeev (1975)**
S. japonicus	**F+M**	**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* sp. nov.**	**F+M**	**"Falklands"?**	***Mora moro* (Risso, 1810)**	**Moridae**	**Gadiformes**	**Present paper**

Bold font denotes original descriptions.
* = description form the type-host fish.
** = description form a fish other than type-host; F = female, M = male, N = nauplius.

Future researchers should also focus on the distribution pattern of the stout and short setae of the first segment of the antenna. In the antenna, the variability of the fine denticles on the protopodal basis may also be helpful.

We described for the first time the paired, sparsely denticulated structure that we named the supramandibular ridge (SMR). A similar structure is visible on a SEM micrograph in Moser et al. (1985) for "*S. arcticus*" from *Sebastes* spp. and in González and Tanzola (2000) for "*S. verucosus*". The authors of those two publications apparently failed to notice the above-mentioned structure. The SMR may also have potential value in identifying species.

We also described for the first time (in the genus) the maxillulae, which is a minute appendage usually obscured by a large mandibular claw. Again, it may be noticed on an SEM micrograph published in Moser et al. (1985) for "*S. arcticus*" from *Sebastes* spp. who did not refer to it in the text.

The structure of the maxillae has not been adequately determined in any valid species. On an SEM micrograph, however, published in Moser et al. (1985) for "*S. arcticus*" from *Sebastes* spp. and in González and Tanzola (2000) for "*S. verucosus*" the maxillae are well illustrated. In both papers the denticulation of the posterior part of the maxilla is visible and also the anterior bifid part can be observed (labeled as seta). In the presently reported *S. izawai* sp. nov. we had only two male specimens at our disposal (for SEM studies). In one specimen only we were able to see the maxillae, but they were partly damaged (Fig. 5C). Its structure is similar to the maxillae depicted in Moser et al. (1985) and González and Tanzola (2000). It is, however, unlikely that this appendage can be used in the future for species differentiation.

Copepods of the genus *Sarcotaces* are quite enigmatic and very little is known about their biology. The early developmental stages of *S. pacificus* were described by Izawa (1973), who isolated eggs from a female gall and incubated them in filtered seawater. The eggs soon hatched and within 45 h 5 consecutive nauplius stages were observed. After that, the nauplii molted into copepodids. On the yolk reserves, they survived at least 9 days. After that time a small host fish was exposed to some 100 copepodids. After 20 min the majority of copepodids vanished from the experimental bowl. The author (Izawa, 1973), without any direct observation, concluded that the larvae infected the fish. We presume that at least some (if not all) copepodids might have been eaten by the fish.

Finding the host seems to be a crucial part of the life cycle of copepod parasites of fishes. The majority of them, in the course of evolution, became specific to their host fishes. Therefore they have a limited number of the target fish and the chances diminish with time and with the dispersal of the infective stages in the water. Therefore the time between the hatching (or releasing the infective larvae) and infection must be limited. Parasitic copepods tend to limit the number of naupliar stages, because they are less effective in finding the host than copepodids (Piasecki, 1989). It is therefore very likely that in *Sarcotaces*, the molting of all nauplius stages and the appearance of the copepodid takes place inside the female gall. The next question is how the infection stages are released into the water? The gall has a connection to the external environment through a small aperture in the scale. Priebe (1963) observed that this aperture is plugged by the small conical end of the female body. Potentially, the aperture can be blocked this way most of the time, and this "plug" may be retracted for an important reason, such as the release of the infective stages (copepodids) when they are ready. Premature opening of the aperture would cause the release of

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

Species	FEMALE	MALE							Reference
	Length [mm]	Comments	Body length [mm]	Antennule	Antenna	Leg 1	Leg 2	Caudal ramus	
S. verucosus	15.0	–	–	–	–	–	–	–	Olsson (1872)
S. arcticus	39.15	–	–	–	–	–	–	–	Collett (1874)
	10.0–90.0	–	–	–	–	–	–	–	Berland (1970)
	–	Triangular cephalothorax; posterior somite abruptly narrowing	<3.0	Inadequate description	Inadequate description	–	–	Single seta, variable in size; 37% of body length	Aitken (1942)
	–	Triangular (?) cephalothorax	–	3, 2, ?, ?	3 protopodal processes, 2 endpodal claws	–	–	–	Moser et al. (1985)
S. pacificus	5.0–15.0	–	–	–	–	–	–	–	Komai 1924
	10.0–15.0	Semi-trapezoid cephalothorax; posterior somite abruptly narrow	<1.0	Inadequate description	Inadequate illustration	Reduced, biramous	Reduced, biramous	Strong, 2-segmented seta +2 setules; 37% of body length	Heegaard (1947)
	1.9–13.0	Semi-triangular/oval cephalothorax; posterior somite abruptly narrowing	1.0–1.4	3, 3, 3, 7	1 protopodal process, 2 endpodal claws	B1, Ex**4**, En**2**	B1, Ex**3**, En**3**	Strong, 2-segmented seta +3 setules; 41%–51% (46%) of body length	Izawa (1974)
S. komaii	12.3	Semi-triangular cephalothorax; posterior somite abruptly narrow	1.0	Inadequate description	Inadequate description	Ex**4**, En**2**	Ex**3**, En**3**		Shiino (1953)
	9.5–25.0	Semi-triangular/oval cephalothorax; posterior somite abruptly narrowing	1.3–2.0	4, 4, 3, 9	1 protopodal process, 2 endpodal claws	–	–	62%–84% (71%) of body length	Izawa (1974)
S. japonicus	9.0–22.0	Semi-trapezoid cephalothorax; posterior somite abruptly narrowing	1.0–1.1	4, 4, 0, 10	2 protopodal processes, 2 endpodal claws	B1, Ex**4**, En**2**	B1, Ex**3**, En**3**	Strong, 2-segmented seta +4 setules; 53%–82% (72%) of body length	Izawa (1974)
S. shiinoi	8.6–21.1	Semi-triangular cephalothorax	1.5–1.8	1, 2, 4, 6	1 protopodal process, 2 endpodal claws	B1, Ex**4**, En**2**	B1, Ex**3**, En**3**	Strong, 2-segmented seta +3 setules; 58%–66% of body length	Izawa (1974)
S. namibiensis	20.0–32.0	Semi-triangular cephalothorax	1.8	Inadequate description	Inadequate description	Inadequate description	Inadequate description	70% of body length	Reimer (1991)
S. izawai sp. nov.	25.0–48.0	Semi-triangular/oval cephalothorax; posterior somite not narrowing	2.15–3.52	4, 4, 2, 7	1 protopodal process, 2 endpodal claws	B1, Ex**4**, En**2**	B1, Ex**3**, En**3**	9.41% of body length	Present paper

Some data are determined/approximated from the illustrations; data for male mandible (subchelar claw) are uniform for seven species (*S. arcticus*, *S. pacificus*, *S. komaii*, *S. japonicus*, *S. shiinoi*, *S. namibiensis*, *S. izawai* sp. nov.); maxillules were only reported for *S. izawai* sp. nov.; maxillae structure not adequately determined in any species; abbreviations: B1 = 1 seta at exopod base, Ex4 = 4 claws on exopod, En2 = 2 claws on endpod; "protopodal process" is a short and stout seta.

nauplii which might negatively impact the infection success. The ink-like substance surrounding the female is pitch black. This is additional evidence that the aperture is closed most of the time. Otherwise, the "ink" would be diluted by the entering seawater.

Larvae of parasitic copepods cannot feed and they rely on the yolk reserves (Izawa, 1973; Piasecki, 1989). Therefore their lifespan before the infection is limited. Also, the naupliar stages have no morphological adaptations for efficient swimming and they have no adaptations for the attachment to the host. The copepodid is a good swimmer, but that of *Sarcotaces* has limited adaptations for attachment to the host possessing claws only on its antennae. Izawa (1973) did not report any other chelate or subchelate appendages which would aid the attachment like the appendages of copepodids of Lernaeopodidae (see Piasecki, 1989; Piasecki and Kuźmińska, 2007) or Caligidae (see Piasecki, 1996). The *Sarcotaces* copepodid not having a frontal filament, occurring in most siphonostomatoids (Piasecki and Kuźmińska, 2007), seem to be "handicapped". How to link then such an "inefficient" infective stage with the apparent success of the species evidenced by large females embedded deep in the fish muscles? A possible answer is following the evolutionary achievements of their ancestral philichthyids and exploring, as the "port of entry", the openings of the lateral line canals of fishes. Subcutaneous spaces associated with the sensory canals/mucous canals of the lateral line are utilized by other genera of the family, namely *Colobomatoides*, *Colobomatus*, *Leposphilus*, *Lernaeascus*, *Procolobomatus*, *Sphaerifer* (see Uyeno et al., 2015). Perhaps the same infection strategy is being pursued also by the representatives of *Ichthyotaces* and *Sarcotaces* both known to dwell in the galls inside the fish body. The lateral-line canals have little pores connecting them with the external environment. The diameters of those pores may be suitable for entry of *Sarcotaces* copepodids. It is possible, however, that the pores in juvenile fish may be too small for copepodid' entry. Such infection strategy, however, cannot be easily associated with *Philichthys xiphiae* Steenstrup, 1862 living inside the cranial bones of actinopterygian fishes (Rolbiecki et al., 2021).

Why are the prevalence values relatively low? This could be the function of the limited number of copepodids, limited time of their activity, and the dispersal of the host fish. This may also answer the question of why only one or rarely two or three galls can be found in a single fish. Another answer is that the multiple parasites are more likely to kill (eliminate) the infected fish. Berland (1970), studying *S. arcticus* observed the prevalence of 9% in smaller fish and only 3.4% for the larger ones. This may suggest that many of the infected small fish were eliminated by the parasite.

Some females are found with multiple males inside their gall. González and Tanzola (2000) found the maximum number of 26 males associated with one female. We found as many as 18. On the other hand, many females do not have their males. There are two possible explanations for such a phenomenon. The first reason is simply the random distribution of the infective larvae. The other explanation is sex determination. In at least some parasitic copepods the sex determination is non-genetic (Ginsburger-Vogel and Charniaux-Cotton, 1982; Alexander et al., 2015). It is probably aided by pheromones or other chemosignals (Ginsburger-Vogel and Charniaux-Cotton, 1982). The first infective larva/larvae attaching to the host fish becomes a female(s), while all subsequent ones become males (Ginsburger-Vogel and Charniaux-Cotton, 1982). If we have a fish infected with a single female and a random distribution of subsequent infection brings multiple copepodids they attach to the fish and through the aperture enter the gall and become males. The males seem to be associated with females for the rest of their lives because they do not have any other option.

As indicated earlier (and in Piasecki et al., 2020) the presently reported copepods were recovered a fish consignment with mislabeled from content. Piasecki et al. (2020) proved that the original fish species declaration was false (and the correct one was *Mora moro*) and the reported locality "the Falklands" was probably also a false piece of information. According to Piasecki et al. (2020), no landings of this species have been recorded on the Falklands. In Europe, *Mora moro* is "taken as bycatch in mixed-species demersal trawl fisheries in Subareas 6, 7, and 12 and to a lesser extent, 2, 4, and 5". Small bycatch amounts are reported from New Zealand. The only reliable clue for the locality of *S. izawai* sp. nov. might be Australia. West (1992) describing 11 new *Colobomatus* species of the family Philichthyidae stated that "Some members of the family have gained notoriety by becoming commercially important, for example, members of the genus *Sarcotaces* Olsson, 1872, are the "iodine worms" of the Barrier Reef serranids and southern Australian ribaldo *Mora moro* Risso."

The concept of mesoparasitism was introduced by Kabata (1976) and it has been used predominantly in relation to copepods representing the siphonostome families Pennellidae and Sphyriidae. Quite often the usage of the term mesoparasitism creates confusion and we would like to take this opportunity to explain it in detail. Mesoparasites are partly embedded in the host tissues (with the predominant number of somites inside the host's body). *Sarcotaces* females well fit this definition. They are "partly embedded" and almost all their somites (except for the posterior tip) are inside the host's body. Some ectoparasites, such as monogeneans, dwell also within the host's body but in this case, they occur in a natural cavity (gill chamber). Pennellids, sphyriids, and *Sarcotaces*, on the contrary, are embedded in spaces eroded in the host tissue because of parasitism. Cyclopoid copepods of the genus *Lernaea*, however, despite their apparent similarity to pennellids are not mesoparasites because their pedigers are located outside the host body (Zbigniew Kabata, personal communication to WP, 1987). Copepods of the genus *Sarcotaces* cannot be considered endoparasites, because the latter do not maintain contact with the external environment.

The genus *Sarcotaces* requires a complex revision based not only on traditional methods of copepod taxonomy but also including molecular tools and electron microscopy studies. Our work provides the first clue to truly characterize the genus and should be considered as a guideline for future work with *Sarcotaces* species, which should focus also on genome assembly to understand the biology of this unique parasite. Here we provide a molecular *COI* barcode for the single female specimen of the new species named *Sarcotaces izawai* sp. nov. This is the first sequence available in the GenBank (Acc. no. OM681152) both for the genus of *Sarcotaces* and family Philichthyidae. Further studies should include additional specimens to shed more light on species and interspecies genetic diversity as well as to address key questions in ecology and evolution.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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