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Molecular and morphological confirmation of Profilicollis altmani as the cause of acanthocephalan peritonitis in California sea otters (Enhydra lutris nereis)

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ABSTRACT

Acanthocephalan peritonitis (AP; trans-intestinal migration of acanthocephalan parasites into the peritoneal cavity resulting in severe peritonitis), is a common cause of mortality in southern sea otters (*Enhydra lutris nereis*). Although *Profilicollis* spp. acanthocephalans have been implicated in these infections, the species causing AP has been an important unresolved question for decades. We used morphological and molecular techniques to characterize acanthocephalans from the gastrointestinal (GI) tract and peritoneal omentum of eighty necropsied southern sea otters. Only *P. altmani* was found to have perforated through the intestinal wall and migrated into the peritoneal cavity of examined sea otters, resulting in AP. Morphological and molecular criteria confirmed that *Profilicollis kenti* was synonymous with *P. altmani*. A second *Profilicollis* sp., likely *P. botulus*, was present only in the intestinal lumen, did not penetrate through the intestinal wall, and was not associated with AP.

1. Introduction

Southern sea otters are known to harbor two genera of parasites in the phylum Acanthocephala: *Corynosoma* and *Profilicollis*. *Corynosoma enhydri* is found in the intestines of nearly all necropsied non-neonate sea otters; although it can contribute to sublethal morbidity, it is generally not associated with mortality (Mayer et al., 2003; Rausch, 1953; Shanebeck and Lagrue, 2020), as it does not penetrate the intestinal serosa. Sea otters are definitive hosts for *C. enhydri* (Shanebeck and Lagrue, 2020), and the intermediate crustacean host is unknown. Hennessy (1972), Hennessy and Morejohn (1977), and Mayer et al. (2003) reported infection by three species of acanthocephalans in the *Profilicollis* genus based on gross examination of the GI tracts of southern sea otters (Fig. 1.). *Profilicollis* parasites can inhabit the entire length of the GI tract in sea otters from the lower duodenum to the colon and are typically at highest densities in the jejunum (R. Grewelle., personal observation). Sea otters are not the definitive hosts for *Profilicollis* spp., but these parasites can be transmitted to sea otters when they consume Pacific sand crabs (*Emerita analoga)* or spiny mole crabs (*Blepharipoda occidentalis*; Lafferty and Torchin, 1997). Avian taxa, such as larids, anatids, and charadriiformes, are definitive hosts of *Profilicollis* spp. Mortality events linked to high density infections and coelomitis have been observed in terns, gulls, and other bird species, though full migration of the parasite into the body cavity is not observed as it is in southern sea otters (La Sala and Martorelli, 2007; La Sala et al., 2013; Patton et al., 2017). Mammals, such as rats and dogs have been experimentally infected, but are not known to harbor reproductive *Profilicollis* adults (Tantaleán et al., 2002).

Acanthocephalan peritonitis (AP) is considered a cause of death in sea otters when moderate to high numbers of *Profilicollis* spp. acanthocephalans are observed in the peritoneal cavity in conjunction with peritonitis (Miller et al., 2020). In affected animals, death can be due to a robust host foreign body reaction to the parasites, secondary bacterial peritonitis, intestinal mural necrosis with adhesions, and severe emaciation (Mayer et al., 2003; Kreuder et al; Miller et al., 2020). Although a recent longitudinal study identified acanthocephalan peritonitis (AP) as contributing to one-quarter (n = 127/541) of southern sea otter deaths; the highest among infectious diseases affecting this population (Miller et al., 2020), the taxonomy of the parasites causing these peritoneal infections has been unresolved for decades (Hennessy and Morejohn,

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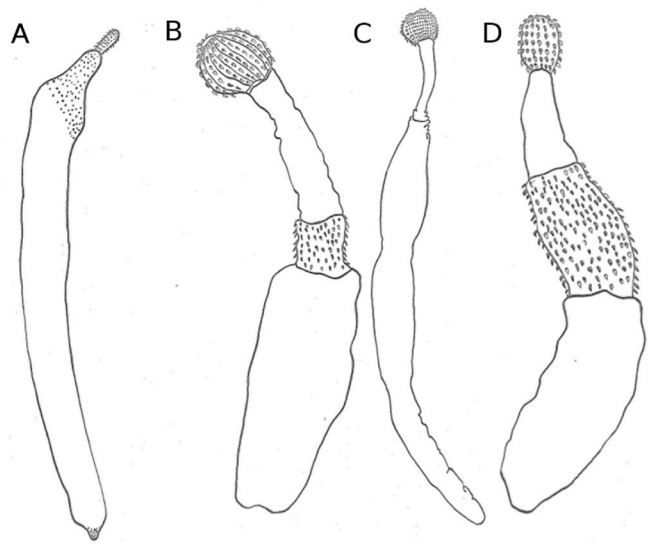

Fig. 1. Four acanthocephalan morphotypes and their prior identities observed in necropsied sea otters. (A) *Corynosoma enhydri* adult, (B) *Profilicollis altmani*, (C) *Profilicollis kenti*, (D) *Profilicollis major*. Modified from Hennessy (1972).

1977; Mayer et al., 2003; Kreuder et al; Miller et al., 2020). The gross and microscopic characteristics of this condition, and demographical, temporal, and geographical risk factors for sea otter infection have been described in detail in other studies (Mayer et al., 2003; Kreuder et al; Miller et al., 2020), and were not the focus of the current study.

Conservation policy and ecological and epidemiological research would greatly benefit from clarification of the acanthocephalan species associated with AP in sea otters. In addition, due to taxonomic uncertainty in the phylum Acanthocephala and the genus *Profilicollis* implicated in AP (Amin, 2013), concurrent assessment of morphological and molecular characteristics of acanthocephalans infecting the gastrointestinal (GI) tract and peritoneal omentum of sea otters would be very beneficial (García-Varela et al., 2013).

In a prior study (Mayer et al., 2003) two species, *P. altmani* and *P. kenti*, were historically implicated in sea otter AP cases because both were found to be perforating the intestinal wall or were present within the omentum or peritoneal cavity at necropsy. However, intraspecific morphological variation not previously noted – because the type-species of these two parasites were identified in different host taxa (Perry, 1942; Van Cleave, 1947) – may have resulted in erroneous classification of morphotypes as separate species. Recent morphological evidence suggests synonymizing *P. altmani* and *P. kenti* (Amin, 2013; Amin et al., 2022). *Profilicollis major* was also identified in necropsied southern sea otters, but this presumed species was never implicated in AP cases (Hennessy, 1972; Mayer et al., 2003). Several recent studies have clarified the relationships among *Profilicollis* species, though the taxonomic relationships between *P. major* and *P. kenti* remained unresolved (Rodríguez and D'Elía, 2017, Rodríguez et al., 2017a; Rodríguez et al., 2017b; Lorenti et al., 2018). The core objective of the current study was to use combined morphological and molecular characterization methods to identify the acanthocephalan species that have perforated through the intestinal wall and were present in the peritoneal cavity of southern sea otters, as well as acanthocephalan species that were present in the intestinal tract but did not perforate through the intestinal wall. Phylogenetic analysis was necessary to resolve species identification among *Profilicollis* morphotypes infecting southern sea otters and to distinguish the species responsible for intestinal perforations leading to AP.

2. Materials and methods

Stranded southern sea otters in California have been examined and systematically documented since 1968, with most animals receiving at least a cursory necropsy (protocol replicated from Pattison et al., 1997). Causes of death are assessed for full necropsies via pathological and histological examination of major organs, including the GI tract (see Miller et al., 2020). Intestinal perforations due to *Profilicollis* spp. acanthocephalan infection are linked mainly to severe peritoneal foreign body reactions, secondary bacterial infection, and emaciation, leading to sea otter death (Mayer et al., 2003; Kreuder et al; Miller et al., 2020).

We examined a subset of sea otters (n = 80) during gross necropsy between 2018 and 2020 to assess acanthocephalan prevalence, intensity, and morphology, replicating procedures outlined in Hennessy and Morejohn (1977) and Mayer et al. (2003) but with higher precision, and incorporating molecular methods for parasite characterization. Gastrointestinal (GI) tracts (duodenum to rectum) were removed, segmented, cut longitudinally, and rinsed with tap water. Following gross necropsy where the entire peritoneal cavity was examined for parasites, and the omentum was removed for detailed examination because it rapidly accumulates peritoneal acanthocephalan parasites that have migrated through the intestinal wall and progressively metabolizes the parasites through pyogranulomatous inflammation; thus it is the most reliable peritoneal tissue for diagnosing AP (M Miller, Pers. commun.). Omenta were removed, laid out, and examined for attached acanthocephalans and omental hyperemia, thickening, and discoloration indicative of host inflammatory response to the parasites and associated bacteria. All acanthocephalans were counted and, when available, ten or more Profilicollis spp. specimens were collected at random across the length of each GI tract with forceps, washed with tap water, and stored in 95% ethanol-filled screw cap collection tubes for later morphological and/or molecular identification. Intact specimens found attached to the omentum were collected separately and preserved in the same manner. Based on the results of prior studies (Mayer et al., 2003; Kreuder et al; Miller et al., 2020), all acanthocephalans present in the omentum at necropsy were considered indicative of GI perforation and AP. In total, 215 of the 1136 Profilicollis spp. specimens with intact proboscises collected were examined under a compound light microscope to count the longitudinal rows of hooks and hooks per row on each proboscis. For each specimen the body shape, trunk spines, and length were also noted.

We designed five sets of primers, four targeting rRNA loci and one targeting cytochrome C oxidase I (COI), using *P. altmani* GenBank accession ID KF835281.1 (Goulding and Sarah Cohen, 2014). Forward and reverse primer descriptions are available in Supplementary Table S1. We extracted genomic DNA by emulsifying individual parasites in an Eppendorf tube using a sterile pestle. Each sample was digested overnight with proteinase K at 50 °C. Phenol-chloroform extraction was facilitated by use of sterilized vacuum grease for phase separation. After ethanol precipitation, DNA pellets were suspended in 10 mM Tris-HCl (pH 8.5) and stored at −20 °C. The DNA concentration was measured using a NanoDrop spectrophotometer. Five separate PCR reactions were performed for each individual parasite; one for each locus. The volume for all reactions was 50 μL: 5 μL Taq buffer, 1 μL dNTP, 1 μL template DNA at 10 ng/μL, 0.25 μL Taq polymerase, 40.75 μL RNase free water, 1 μL forward primer at 50 pM, and 1 μL reverse primer at 50 pM. Thirty PCR cycles at 56 °C annealing temperature were performed for each reaction mixture. Five microliters of each sample were run on EtBr agarose gel (1%) and PCR reactions were repeated until either a distinct band was visible within the gel, or no band was visualized after three sequential PCR runs.

We performed Sanger sequencing (GeneWiz) on all amplified loci for 23 *P. altmani*, 6 *P. botulus/P. major*, and 3 *C. enhydri* samples. Indigo (Gear Genomics, supported by EMBL) was used to call alleles in single nucleotide variant (SNV) discovery compared to the *P. altmani* GenBank accession ID KF835281.1 reference sequence for each locus. Fifty nucleotides were trimmed on forward and reverse ends, and chromatograms were visually inspected during allele calling. We constructed an unrooted phylogeny with the PhyML maximum likelihood algorithm

(Guindon and Gascuel, 2003; Anisimova and Gascuel, 2006; Dereeper et al., 2008) (HKY85 substitution model), concatenating the recovered alleles for loci B,C, and D and comparing to concatenated representative GenBank sequences for *P. altmani* and *P. botulus*, all other available members of the *Profilicollis* and *Polymorphus* genera, and *C.enhydri*, with the rotifer *Adineta vaga* as an outgroup (Fig. 2). Concatenated sequences were aligned using MUSCLE (Edgar, 2004). A GenBank reference sequence for locus C was unavailable for *P. botulus*, so an unrooted phylogeny was also generated by concatenating loci B and D, including a *P. botulus* reference (Fig. 3). Gene trees were constructed using all available sequences (Supplementary Figs. S1–S5) to examine gene tree discordance, and the position of *P. altmani* within its clade was verified using all five loci (Supplementary Fig. S6). Phylogenies were visualized using FigTree v1.4.4.

3. Results and discussion

Thirty-five of 80 southern sea otters examined had *Profilicollis* parasites present in the GI tract and/or omentum. Smaller and less mature *Profilicollis* sp. acanthocephalans were often found in the upper part of the jejunum when the infection intensity was high. Of the eighty sea otters included, forty-four were female and thirty-six were male (Table 1). Sampling across age classes was spread evenly between immature and adult age classes, with fewer pups and aged adults sampled. This distribution reflects broad-scale characteristics of the living sea otter population and risk of overall mortality between age classes (Young and Harris, 2021), and major trends were comparable to results from prior mortality surveys (Kreuder et al; Miller et al., 2020). However, due to the nature of carcass recovery, opportunistically and usually from sandy beaches this is not a random sample of the southern sea otter population. Infection prevalence was highest in males and younger age classes, and the highest intensity infections were observed in immature otters.

Of the *Profilicollis* spp. specimens examined, there were two distinct morphotypes: *P. altmani/P. kenti* and *P. major/P. botulus*. The *P. altmani/P. kenti* morphotype constituted nearly 90% (n = 190/215) of specimens and was characterized by a slender, elongated neck and spherical proboscis possessing 23–30 distinguishable longitudinal rows of hooks and 12 or more hooks per row. For the *P. altmani/P. kenti* morphotype, we also noted clear morphological transitions as the parasites matured from cystacanths to mature adults and took on characteristics originally prescribed to *P. kenti* (Karl, 1967). This includes a more spherical proboscis, parasite lengthening and clearer body segmentation, and an increased number and greater variability of the numbers of rows of hooks. There was otherwise no clear morphological distinction between these parasites; rather the *P. kenti* phenotype was associated with parasite maturity, as confirmed by visible gonads. Of the forty-four intact specimens found in the omentum, all forty-four exhibited the *P. altmani/P. kenti* morphotype.

The *P. Major/P. botulus* morphotype (n = 25/215) was only found within the GI tract and characterized by a shorter neck and ovate proboscis possessing 16 longitudinal rows and 7–9 hooks per row. Variation in body length was observed for the *P. major/P. botulus* morphotype, but no clear association was found between body length and the number of hooks or rows of hooks on the proboscis. This morphotype was also indistinguishable from prior descriptions of *P. botulus* in avian hosts.

PCR primers successfully amplified all five loci for *P. altmani/P. kenti* specimens, loci B-D for *P. major/P. botulus* specimens, and locus D for *C. enhydri* specimens. Phylogenetic results using loci B-D revealed definitive separation of *P. altmani/P. kenti* and *P. major/P. botulus* haplotypes (Fig. 2). This result was further supported with an expanded phylogeny including other reference congeners using loci B and D (Fig. 3). Both sampled *P. major/P. botulus* haplotypes and the *P. botulus* reference haplotype were monophyletic. *Profilicollis bullocki* was the closest relative to *P. altmani*, a relationship generally supported by each gene tree with discordance at locus D alone (Supplementary Fig. S4). Minor allelic variation was observed for *P. altmani/P. kenti* at locus A, and major allelic variation was observed for *P. major/P.botulus* at locus B. This major variation resulted in paraphyletic assortment of the two alleles (Supplementary Fig. S2), which was a property not conserved as additional loci were concatenated. With five concatenated loci, clades separated as anticipated by taxonomic assignment (Supplementary Fig. S6). Morphological variation in the proboscis of *P. altmani/P. kenti* was consistent with maturation rather than speciation, confirmed by 100% molecular identity across morphological variants.

The taxonomy of the *Profilicollis* genus has changed dramatically

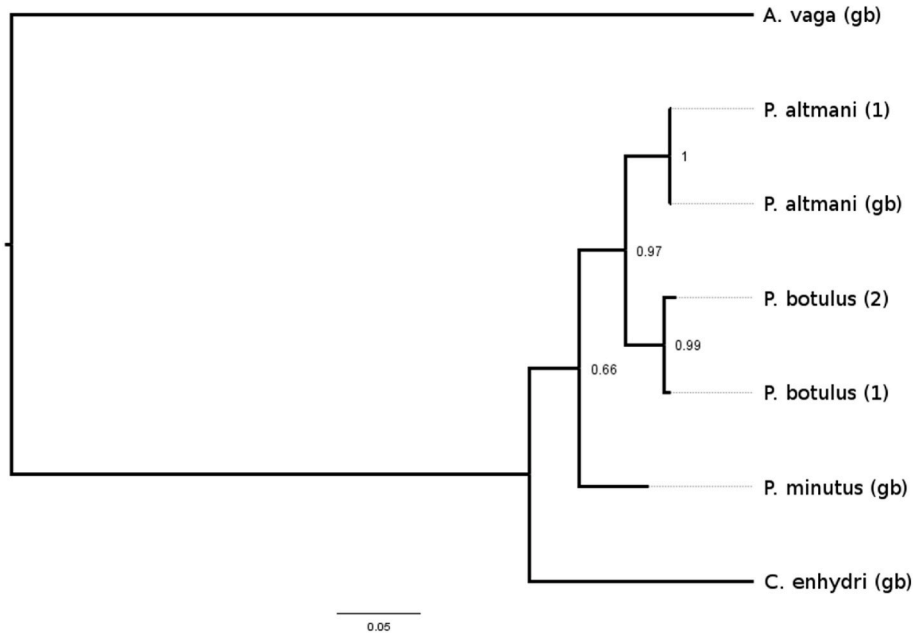

Fig. 2. Maximum likelihood phylogeny generated from the concatenation of sequences of loci B, C, D. Species analyzed include: *Adineta vaga*, *Profilicollis altmani* (sample haplotype 1 and GenBank (gb)), *Profilicollis botulus/Profilicollis major* (sample haplotypes 1 and 2), *Polymorphus minutus*, and *Corynosoma enhydri*. Branch lengths are scaled to phylogenetic distance and nodes are labeled with bootstrap support values (n = 100 replicates).

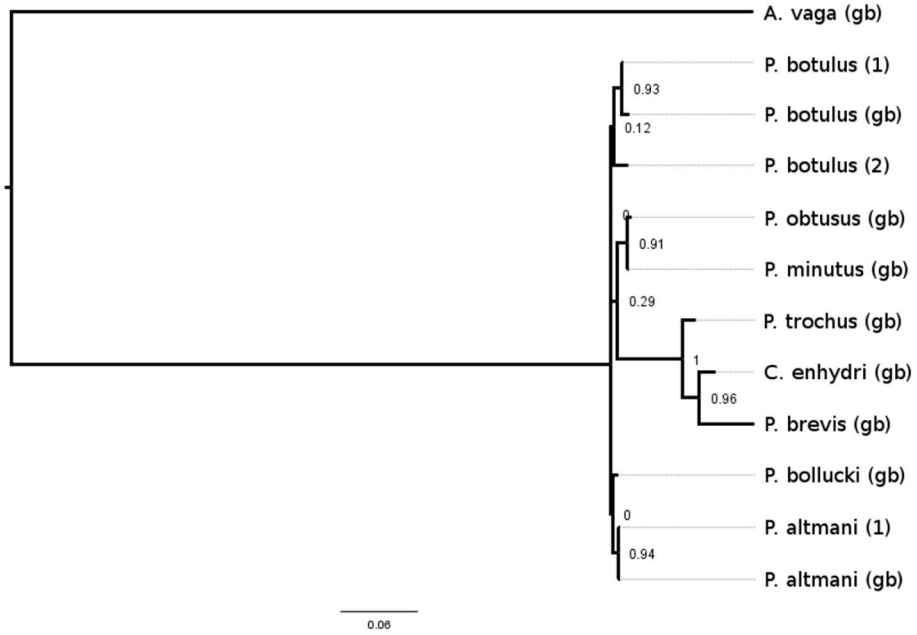

Fig. 3. Maximum likelihood phylogeny generated from the concatenation of sequences of loci B and D. Species analyzed include: *Adineta vaga*, *Profilicollis botulus/Profilicollis major* (sample haplotypes 1 and 2 and GenBank (gb)), *Polymorphus obtusus*, *Polymorphus minutus*, *Polymorphus trochus*, *Corynosoma enhydri, Polymorphus brevis, Profilicollis bullocki, and Profilicollis altmani* (sample haplotype 1 and GenBank). Branch lengths are scaled to phylogenetic distance and nodes are labeled with bootstrap support values (n = 100 replicates).

Table 1
Profilicollis spp. infections and peritonitis by demographic group. The presence/absence of acanthocephalan peritonitis as a cause of death was assessed for each case prior to gastrointestinal tract dissection and Profilicollis spp. counts for each sea otter.

	Number of Otters	Prevalence of Infection	Incidence of AP	Mean Intensity of Infection (± standard error)
Female	44	34%	20%	110 ± 50
Male	36	56%	22%	123 ± 73
Pup (0–3 mo)	8	0%	0%	0
Immature (3 mo – 1 yr)	25	68%	28%	240 ± 116
Subadult (1–3 yrs)	20	45%	20%	105 ± 73
Adult (4–9 yrs)	24	17%	21%	46 ± 29
Aged Adult (10+ yrs.)	3	33%	33%	14 ± 14

over decades of investigation due to discoveries of presumed different acanthocephalan species in a variety of avian hosts across a broad geographical area (Karl, 1967; Amin, 2013; Amin et al., 2022). Recent research has helped clarify the taxonomy of many species in the *Profilicollis* genus with molecular identification (Rodríguez et al., 2017a; Rodríguez et al., 2017b; Lorenti et al., 2018). Disparate classification between observers plagued the taxonomy, with *P. altmani* now proposed synonymous with *P. kenti* and *P. texensis* (Amin, 2013; Amin et al., 2022). *Profilicollis bullocki* has also been identified as a synonym (Rodríguez and D'Elía, 2017; Rodríguez et al., 2017a), and genetic evidence from our work shows *P. bullocki* as monophyletic to *P. altmani* haplotypes. *Profilicollis altmani* and *P. kenti* were considered divergent due to differences in body size and shape, and variation in hook counts on the proboscis. However, our observations noted clear morphological transitions as the parasites matured from cystacanths to adults with visible gonads and secondary sexual characteristics (e.g. copulatory bursa) and took on characteristics originally prescribed to *P. kenti*. Our phylogenetic evidence identified no genetic variation between the twenty-three *P. altmani/P. kenti* specimens, despite variation in hook number, row number, and body size that once differentiated *P. altmani* from *P. kenti*. We conclude *P. altmani* and *P. kenti* are synonymous. Similarly, *P. texensis* was identified in a sanderling along the United States Gulf coast (Webster, 1948); although its geographic separation led to distinct categorization, later genetic characterization confirmed the cosmopolitan nature of *P. altmani* infection of *E. analoga* throughout this crustacean's geographic range (Goulding and Sarah Cohen, 2014; Rodríguez and D'Elía, 2017; Rodríguez et al., 2017b), and the *Profilicollis* specimen from the sanderling GI tract was most likely also *P. altmani*.

Previous work identified up to four acanthocephalan species infecting sea otters (*C. enhydri*, *P. altmani*, *P. kenti*, and *P. major*). Mayer et al. (2003) previously implicated *P. altmani* and *P. kenti* in cases of acanthocephalan-induced peritonitis based on detection of morphologically compatible parasites in the omentum or fully penetrating the intestinal wall. In contrast, we found *P. altmani* to be the sole contributor to acanthocephalan peritonitis in sea otters. In agreement with Mayer et al. (2003), we found another *Profilicollis* species inhabiting the GI lumen, but it was not observed to be transmigrating through the intestinal wall and was never detected in the peritoneum or omentum of sea otters. This species was originally identified as *P. major* (Hennessy, 1972). Although morphologically similar to *P. botulus* (Amin et al., 2022), records of *P. major* are from the Atlantic Ocean, while *P. botulus* has been identified on the west coast of North America (Ching, 1989). Together with our molecular evidence, it is likely that this species found in sea otters is either *P. botulus* or a close relative. It is possible that this species does not cause peritonitis because its short neck and relatively wide body prohibit penetration through the intestinal wall. In contrast with *P. altmani, P. botulus* is not known to produce coelomitis in its avian definitive hosts (Ching, 1989). The absence of archival genetic data for *P. major* prohibits further clarification of this relationship.

Resolving the species responsible for causing acanthocephalan peritonitis in southern sea otters is a crucial first step toward clarifying the epidemiology of this fatal disease. Ongoing efforts to restore southern sea otter populations to their historic range will benefit from

detailed examination of sea otter mortality risks, which can now be informed by studying the transmission patterns of *P. altmani,* and the population dynamics of its hosts. Further work on the systematics of the *Profilicollis* and *Polymorphus* genera and the acanthocephalan phylum is needed. Combining morphological and molecular approaches can help resolve additional discrepancies highlighted in this study.

GenBank accession nos

OR345610-OR345613, OR345738-OR345739, OR345861-OR345863, OR346011, OR352164-OR352165.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Richard Grewelle reports financial support was provided by Stanford University. Richard Grewelle reports financial support was provided by Achievement Rewards for College Scientists Foundation Inc. Richard Grewelle reports financial support was provided by Sea Otter Foundation Trust. Richard Grewelle reports financial support was provided by Earl H and Ethel M Myers Oceanographic and Marine Biology Trust. Katherine Greenwald reports financial support was provided by California Sea Otter Voluntary Tax Contribution Fund.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2023.08.003.

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