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NEOLEBOURIA MULLINEAUXAE N. SP. (TREMATODA: DIGENEA) AND ANOTHER OPECOELID FROM DEEP-SEA HYDROTHERMAL VENT FIELDS OFF CENTRAL AMERICA AND PAPUA NEW GUINEA, WITH SPECIES KEYS AND A COMPARISON TO MESOBATHYLEBOURIA

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KEY WORDS ABSTRACT

28S
East Pacific Rise
Eulepetopsis vitrea
Host records
ITS2
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Morphological variation
Opcoelidae
Phylogeny
Pyrolycus manusanus
Thermarces cerberus
Zoarcidae

Neolebouria mullineauxae n. sp. (Digenea: Opcoelidae), exhibiting remarkable morphological variation (i.e., 2 distinctive morphotypes), is described from the intestine of the zoarcid eelpout or pink vent fish, *Thermarces cerberus*, collected from deep-sea hydrothermal vent fields along the East Pacific Rise (EPR) off the west coast of Central America. It can be distinguished from its congeners by having a unique diagnostic combination of features including a small body and gonads that are smaller relative to body size, a prebifurcal genital pore, a cirrus pouch that extends posteriorly as far as the posterior margin of the ventral sucker while the anterior margin of the latter is either close to or overlaps the intestinal bifurcation, confluent vitelline fields within the posttesticular space, and vitelline follicles and eggs that are not as dense and few to moderate in number, respectively. This report introduces a new family (Zoarcidae) and genus (*Thermarces*) of fish infected by the genus *Neolebouria*, a new host record in that this is the first taxonomic description of a digenetic trematode from *T. cerberus*; a new geographic locality for *Neolebouria* (*sensu stricto*)—the East Pacific Ocean off the coast of Central America—and a life cycle of the new species within the hydrothermal vent biome is postulated, including the sporocyst stage which utilizes the glass limpet, *Eulepetopsis vitrea*, as a first intermediate host. Two immature digeneans (cf. Opcoelidae) are described herein, collected from vent fields off Papua New Guinea, and represent a new host record in that this is the first report of a digenetic trematode from the zoarcid eelpout, *Pyrolycus manusanus*. Based on molecular analysis of the 28S gene, *N. mullineauxae* n. sp. was 99.92% (1,218/1,219 base pairs [bp]) similar to *Neolebouria georgiensis*. It was genetically closer to a previously described vent digenean, *Buticulotrema thermichthysi*, than to *Mesobathylebouria lanceolata*, despite the new species sharing morphological characteristics with the genus *Mesobathylebouria*. The 2 distinctive morphotypes of *N. mullineauxae* n. sp. were genetically identical in the 28S and ITS2 barcoding regions, supporting their identity as a single species. Given the similarity of *N. mullineauxae* n. sp. to members of *Mesobathylebouria* morphologically and ecologically, a thorough comparison of both genera is presented, as well as new keys to species, and a plea offered for a more efficacious diagnostic suite of morphological characters to distinguish both genera.

Since its erection almost 50 yr ago, *Neolebouria* Gibson, 1976 (Opcoelidae Ozaki, 1925) has seen its share of taxonomic confusion, to put it mildly, with wide fluctuations in the number of

species recognized as well as varied distinct combinations of diagnostic morphological features, resulting over time in several ambitious revisions we briefly review here. This genus included as many as 14 species when it was erected by Gibson (1976) for plagioporeine opcoelids that parasitize the gastrointestinal tract of marine teleosts and are similar to *Podocotyle* Dujardin, 1845 in possessing a lobed ovary and to *Plagioporus* Stafford, 1904 in having vitellaria that are confluent dorsally within the forebody. Cribb (2005)

Version of Record, first published online with fixed content and layout, in compliance with ICZN Arts. 8.1.3.2, 8.5, and 21.8.2 as amended, 2012. ZooBank publication registration: [urn:lsid:zoobank.org/pub:C2EAD9F3-7A66-428F-9D39-0B05B7DED794](https://zoobank.org/pub:C2EAD9F3-7A66-428F-9D39-0B05B7DED794).

defined members of *Neolebouria* in part as possessing 2 tandem to oblique testes, a distinct lobed ovary, vitelline follicles that enter the forebody and extend posteriorly beyond the testes to the posterior extremity, an excretory vesicle that extends to the ovary, and members parasitize marine fishes. Bray and Justine (2009) considered the key generic features of *Neolebouria* to be a lobed ovary and vitellarium in the forebody—whether confluent or not—and they recognized as many as 22 species. For a thorough taxonomic review of this genus, the reader is referred to Dronen et al. (2014).

Martin et al. (2018a) originally considered *Neolebouria* to comprise 11 species; however, after examining molecular phylogenetic data (see Faltýnková et al., 2017; Martin et al., 2017), they concluded that this genus must represent at least 2 genera because *Neolebouria georgiensis* Gibson, 1976, the type species, and *Neolebouria lanceolata* (Price, 1934) Reimer, 1987 did not resolve together. Four species were retained in *Neolebouria*: *Neolebouria antarctica* (Szidat and Graefe, 1967) Zdzitowiecki, 1990 (syn. *Crassicutis antarcticus* Szidat and Graefe, 1967) found in an Antarctic dragonfish, *Parachaenichthys charcoti* (Vaillant, 1906) (Bathydraconidae) (Szidat and Graefe, 1967); *N. georgiensis* parasitizing the Antarctic dragonfish, *Parachaenichthys georgianus* (Fischer, 1885) (Bathydraconidae), and the blackfin icefish, *Chaenoccephalus aceratus* (Lönnberg, 1906) (Channichthyidae) (Gibson, 1976); *Neolebouria merretti* Gibson and Bray, 1982 infecting the deep-sea tripod fish, *Bathytrophops sewelli* (Norman, 1939) (Ipnopidae) (Gibson and Bray, 1982); and *Neolebouria terranovaensis* Zdzitowiecki, Pisano and Vacchi, 1993 found in the crocodile icefish, *Chionodraco hamatus* (Lönnberg, 1905) (Channichthyidae), the Mawson's dragonfish, *Cygnodraco mawsoni* Waite, 1916 (Bathydraconidae), the sharp-spined notothenia, *Trematomus pennellii* Regan, 1914 (syn. *Trematomus centronotus* Regan, 1914) (Nototheniidae), and the saddlepack plunderfish, *Pogonophryne scotti* Regan, 1914 (Artedidraconidae) (Zdzitowiecki et al., 1993). These 4 species were noted by Martin et al. (2018a) as large (1,800–4,800 µm long), robust, having thick tegument, gonads that are medial and irregularly lobed, large eggs (>80 µm long) and possessing a cirrus pouch that extends to the level of the posterior margin of the ventral sucker or a little beyond into the hindbody. (Note: *N. antarctica* has a much shorter cirrus pouch). Martin et al. (2018a) also declared and/or recognized 2 species to be *incertae sedis*: *Neolebouria leiognathi* (Wang, Wang and Zhang, 1992) Bray, 2002 described from the deep pugnose ponyfish, *Deveximentum ruconius* (Hamilton, 1822) (syn. *Leiognathus ruconius* [Hamilton, 1822]) (Leiognathidae); and *Neolebouria maorum* (Allison, 1966) Gibson, 1976 parasitizing the mantle cavity as well as the kidney lobes and coelom of the Maori or New Zealand octopus, *Macroctopus maorum* (Hutton, 1880) (syn. *Octopus maorum* Hutton, 1880) (Octopodidae)—a very unique definitive host, indeed (Allison, 1966; Wang et al., 1992). Five of the remaining 6 species of *Neolebouria* were placed by Martin et al. (2018a) into the new genus *Mesobathylebouria* Martin, Huston, Cutmore, and Cribb, 2018 (Opecoelidae). This genus was erected for species of *Neolebouria* that are morphologically similar to *Neolebouria* (*sensu stricto*), parasitize marine fishes from lower epipelagic (100–200 m) to mesopelagic (200–1,000 m) depths (see Marshall, 1979), and do not parasitize notothenioids or other Antarctic and sub-Antarctic fishes. The final species, *Neolebouria pentacerotis* Machida and Araki, 2002, collected from the intestine of the Japanese armorhead, *Pentaceros japonicus* Steindachner, 1883 (Acropomatiformes: Pentacerotidae), from deep

waters off Nago, Okinawa Prefecture, Japan, was moved by Martin et al. (2018a) into *Choerodonicola* Cribb, 2005 (Opecoelidae) as *Choerodonicola pentacerotis* (Machida and Araki, 2002) Martin, Huston, Cutmore and Cribb, 2018.

WoRMS (2025) currently lists 5 species of *Neolebouria*: *N. antarctica*, *N. georgiensis*, *N. leiognathi*, *N. maorum* (not recognizing their status as *incertae sedis*—see Martin et al., 2018a) and *N. merretti*. Although Martin et al. (2018a) recognizes *N. terranovaensis*, WoRMS (2025) supports the conclusion of Faltýnková et al. (2022) that this species is a junior synonym of the type species, *N. georgiensis*.

The purpose of this study was to help clear the “turbid taxonomic waters” of *Neolebouria* as well as add to our knowledge of this marine digenean genus with the description of a new species exhibiting remarkable morphological variation and found to infect the intestine of the zoarcid eelpout or pink vent fish, *Thermarces cerberus* Rosenblatt and Cohen, 1986 (Perciformes: Zoarcidae), collected from deep-sea hydrothermal vent fields along the East Pacific Rise (EPR) off the west coast of Central America. We also describe 2 immature specimens of an opecoelid infecting another zoarcid eelpout, *Pyrolycus manusanus* Machida and Hashimoto, 2002 (Perciformes: Zoarcidae), found within the Manus Basin off the coast of Papua New Guinea. Molecular sequence data from 2 rDNA regions (28S and ITS2) are presented as additional evidence for the new taxon. We introduce a key to the species we recognize within *Neolebouria* as well as to those within *Mesobathylebouria*, a genus that our material is similar to morphologically and ecologically yet different from molecularly. We comment on applicable new host and parasite records, postulate a possible life cycle for the new digenean within the hydrothermal vent biome, and present ecological speculations regarding both genera in the deep-sea environment.

MATERIALS AND METHODS

Eleven individuals of the zoarcid eelpout, *T. cerberus*, were collected by deep-submergence vehicles HOV *Alvin* and ROV *Jason* in December 2019 and in March–April 2021 and examined for parasites (see Dykman et al., 2023a, 2023b). Fish were collected by benthic trap or with a slurp gun from 2,511–2,519-m depth at the hydrothermal vent sites ‘Riftia Mound,’ ‘Tica,’ and ‘Crab Spa’ in the 9°50'N vent field on the EPR, in the Pacific Ocean off Central America. Specimens of *T. cerberus* were immediately either examined for parasites fresh aboard ship or were flash frozen (–80 °C) before being transferred back to the laboratory for necropsy. An additional 5 *T. cerberus* were earlier collected in 1999 and 2001 from 2,491–2,499-m depth at the hydrothermal vent sites ‘Train Station’ and ‘East Wall’ along the northern EPR. Six specimens of another zoarcid eelpout species, *Pyrolycus manusanus*, were obtained in August of 2007 at 1,399-m depth along the ‘South Su’ vent field within the Manus Basin off the coast of Papua New Guinea. These fish were collected using an ROV suction sampler, fixed in formalin, and preserved in 70% ethanol for later study (see Collins et al., 2012; Moravec et al., 2023).

Morphological study

Of a total of 349 digeneans collected, a subset of 110 was selected for morphological study, stained in Semichon's carmine,

destained and neutralized in acid alcohol and sodium bicarbonate solutions, dehydrated in a graded ethanol series, cleared in clove oil, and mounted in Canada balsam. Measurements and drawings were done with the aid of an Olympus CH30 compound microscope (Olympus Corporation, Center Valley, Pennsylvania) using a drawing tube and a Nikon Superhigh-Performance 3 Zoom Coolpix 990 digital camera (Nikon Corporation, Melville, New York) and image software system. Additional measurements and drawings were done with the aid of an Olympus BX53F2 compound microscope equipped with DIC/Nomarski Optics using a drawing tube and an Olympus EP50 digital and image software system. Measurements are in micrometers (μm) with the range followed by the mean in parentheses; the number [n] of measurements is also noted where needed. Two-dimensional measurements are given with the length before the width. Comparative measurements were taken from the original species descriptions or redescrptions unless otherwise stated. Some critical measurements that were not available or obviously in error in the original descriptions were calculated from original illustrations and identified herein; if needed, measurements were compared to museum specimens (see Dronen et al., 2014). Fish classification and authorities follow FishBase (Froese and Pauly, 2024), and digenean authorities follow Cribb (2005). Digenean identification is based on Cribb (2005), Dronen et al. (2014), and Martin et al. (2018a), and ecological terms follow Bush et al. (1997).

Molecular study

A subset of 30 digenean individuals was selected for molecular study. DNA was extracted from ethanol-preserved specimens using the DNeasy Blood and Tissue Kit (QUIAGEN, Beverly, Massachusetts) following the manufacturer's instructions. Polymerase chain reaction (PCR) was carried out in 25- μl volumes containing 12.5 μl GoTaq Master Mix (Promega Corporation, Madison, Wisconsin), 2.5 μl of each primer, 6.5 μl nuclease-free water, and 1 μl of sample. The 28S rDNA region was used to compare the new material to previously described species, and the ITS2 rDNA region was used to demonstrate further that specimens of our new species were conspecific despite high morphological variability. Partial 28S rDNA was amplified with the primers ZX-1 (5'-ACC CGC TGA ATT TAA GCA TAT-3') or LSU5' (5'-TAG GTC GAC CCG CTG AAY TTA AGC A-3') and 1500R (5'-GCT ATC CTG AGG GAA ACT TCG-3') (Tkach et al., 2003; Bray et al., 2009). The following touchdown cycling protocol was used for the 28S reactions: 95 C for 3 min; 14 "touchdown" cycles of 95 C for 30 sec, 65 C to 52 C for 30 sec (dropping 1 C each cycle), and 72 C for 1 min; 20 cycles of 95 C for 30 sec, 52 C for 30 sec, 72 C for 1 min; and a final extension at 72 C for 7 min. Whole ITS2 rDNA was amplified with the primers 3S (5'-GGT ACC GGT GGA TCA CGT GGC TAG TG-3') (Morgan and Blair, 1995) and ITS2.2 (5'-CCT GGT TAG TTT CTT TTC CTC CGC-3') (Cribb et al., 1998). For the ITS2 reactions, the following protocol from Martin et al. (2017) was used: 1 $\times$ (3 min at 95 C, 2 min at 45 C, 90 sec at 72 C), 4 $\times$ (45 sec at 95 C, 45 sec at 50 C, 90 sec at 72 C), 30 $\times$ (20 sec at 95 C, 20 sec at 52 C, 90 sec at 72 C), 1 $\times$ (5 min extension only at 72 C). Successful amplification was confirmed with gel electrophoresis, and PCR product was sent to Sequagen DNA Sequencing (Worcester, Massachusetts) for Sanger sequencing. Consensus sequences were created using Sequencher Ver. 5.4.6 (Gene Codes Corporation,

Ann Arbor, Michigan). Of the 30 individual digeneans selected for molecular study, 17 yielded high-quality sequences that were submitted to GenBank.

Reference sequences were gathered from NCBI, including the closest matches in the NCBI nr/nt database to the new vent specimens and all sequences from previously described vent digeneans (Bray et al., 2014). Sequences were aligned using the software clustalo v1.2.2 (Goujon et al., 2010; Sievers and Higgins, 2021) and manually trimmed to remove all gaps. After alignment and trimming, a 1,061-base pair (bp) segment was used for 28S analysis and a 435-bp segment was used for ITS2 analysis with full coverage. Trees were generated using the software iqtree v2.2.0 (Nguyen et al., 2015). Branch supports were estimated using the ultrafast bootstrap with 1,000 replicates (Hoang et al., 2018) as in Sokolov et al. (2019), and the best-fit model was selected based on the Bayesian information criterion (BIC) using the program ModelFinder v2.2.0 (Kalyaanamoorthy et al., 2017). The best model for the 28S tree was GTR+F+G4 (BIC = 25,752.210). A tree was not generated for the ITS2 sequences because all such sequences from the new species were identical and there is no reference sequence representing the genus.

Although we understand that in situ fixation of digeneans is not ideal (i.e., flash freezing or cold fixation of the host in formalin/ethanol), specimens selected and measured herein were in good condition upon close examination. Furthermore, because of the inherent rarity of this material, we felt the benefits that this study provided to our limited knowledge of helminth communities within the deep sea, in general, and within hydrothermal vents, in particular, justified the completion of this work.

Type and voucher digenean specimens used in this study were deposited in the Harold W. Manter Laboratory of Parasitology (HWM), University of Nebraska–Lincoln, Lincoln, Nebraska; the Parasite Collection, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution (USNM); and the Natural History Collections, Parasitology Section, Corpus Christi Museum of Science and History (CCM), Corpus Christi, Texas.

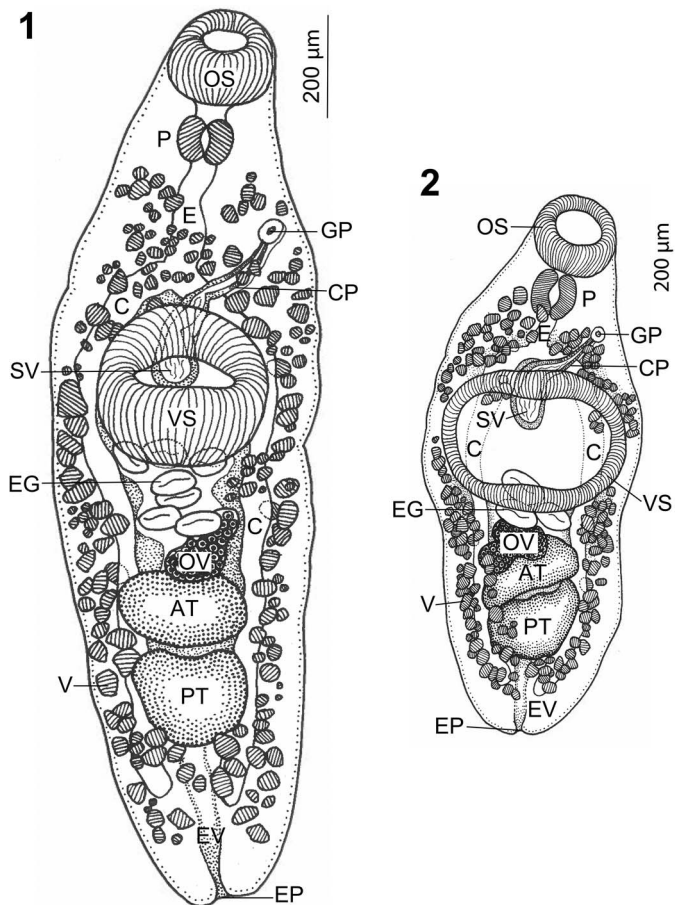
DESCRIPTION

Neolebouria mullineauxae n. sp.

Morphotype A

(Syns. DIGE08, DIGE16, SPOR01 of Dykman, 2023 and Dykman et al., 2023a, 2023b; DIGE08, SPOR01 of Dykman et al., 2025) (Figs. 1, 3–7)

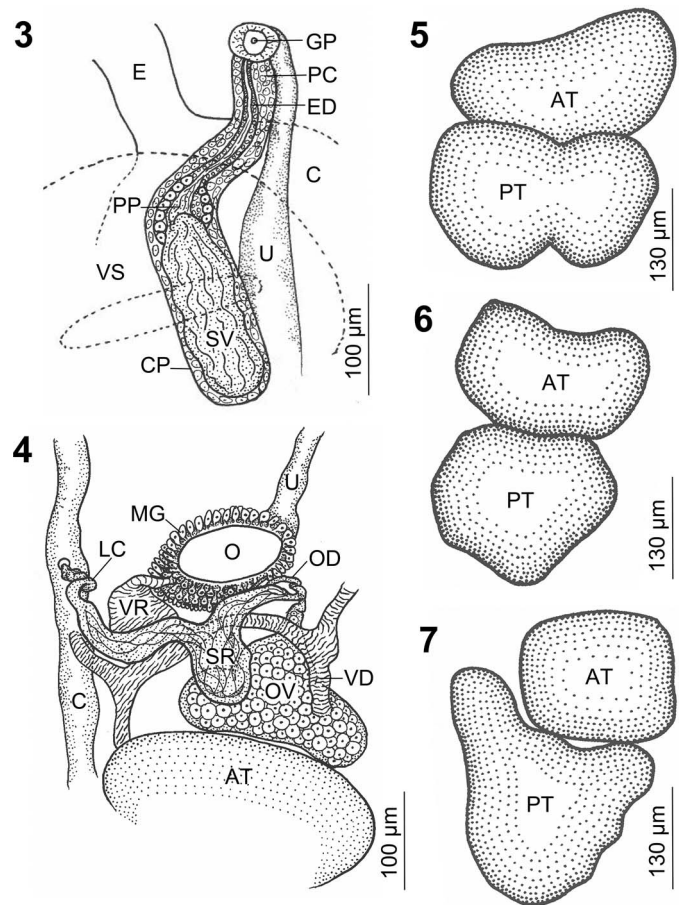
Description: Digenea, Opecoelidae. Measurements based on 32 adult, whole-mounted specimens; see Table I. With the characteristics of the genus. Body elongate-oval; widest at or near junction of anterior and middle one-third of body. Forebody attenuated to rounded extremity; hindbody gradually attenuated to broadly curved almost truncate extremity. Tegument smooth. Preoral lobe absent. Oral sucker moderate in size, globular, oval, circular to subcircular, slightly protuberant; mouth subterminal (54% of specimens measured) or terminal (46%). Ventral sucker moderate in size, median, slightly puckered to protuberant, round to subcircular, with thick conspicuous muscular rim and narrow aperture, larger than oral sucker, in middle third of body. Prepharynx short, at times overlapped by posterior margin of oral sucker.



Figures 1, 2. *Neolebouria mullineauxae* n. sp. Morphotypes A and B (Digenea: Opcoelidae) in *Thermarces cerberus* from the East Pacific Rise. (1) Whole mount of the holotype (Morphotype A); ventral view. (2) Whole mount of paratype (Morphotype B); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SV, seminal vesicle; V, vitellarium; VS, ventral sucker.

Pharynx distinct, moderate in size, muscular, globular, round, oval or dolioform, anterior margin rarely overlapped by posterior margin of oral sucker. Esophagus distinct, wide, thick-walled, straight, sinuous or slightly arcuate. Intestinal bifurcation in posterior forebody, anterior to ventral sucker. Ceca moderately wide, thick-walled, conspicuous, extend posteriorly near lateral margins to terminate blindly in posterior one-fifth of body often near posterior extremity (ceca with expanded dilations at posterior ends [$n = 1$]).

Testes 2, moderate in size, median, tandem (oblique [$n = 8$ specimens]), contiguous or almost so, smooth or indented or lobed, globular, oval to circular (note: testes shape markedly variable: cuboidal [$n = 1$]; dumbbell [$n = 3$]; irregular [$n = 1$]; reniform [$n = 2$]; subtriangular [$n = 2$]; posterior testis with extended anterior lobe of 336 long [$n = 1$]), in posterior one-third of body. Cirrus pouch conspicuous, clavate to sigmoid (retroflexed [$n = 1$]), with dense numbers of prostatic gland cells, extends postero-dextrally along transverse course in forebody to midlevel of ventral sucker (extends almost to level of anterior one-third of ventral sucker [$n = 1$]; extends to posterior margin of ventral sucker [$n = 3$]). Seminal vesicle occupies majority of proximal portion of cirrus



Figures 3–7. *Neolebouria mullineauxae* n. sp. Morphotype A (Digenea: Opcoelidae) in *Thermarces cerberus* from the East Pacific Rise. (3) Male system of paratype; ventral view. (4) Female system of paratype; dorsal view. (5–7) Testes of paratypes showing variation in lobation and orientation to each other; (5) dorsal view; (6, 7) ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; ED, ejaculatory duct; GP, genital pore; LC, Laurer's canal; MG, Mehlis' gland; O, oötype; OD, oviduct; OV, ovary; PC, prostatic cells; PP, pars prostatica; PT, posterior testis; SR, seminal receptacle; SV, seminal vesicle; U, uterus; VD, vitelline duct; VR, vitelline reservoir; VS, ventral sucker.

pouch, saccate in most specimens (reniform [$n = 4$]; elongate-oval [$n = 1$]). Pars prostatica circular to oval, inconspicuous, immediately distal to seminal vesicle, surrounded by prostatic gland cells, filled with bleb-like cells that line wall of interior. Ejaculatory duct distinct, long, narrow, tubular, distal to pars prostatica, wider proximally then narrows towards distal end; unspined cirrus present, occasionally everted. Genital atrium deep, distinct, cylindrical to circular; genital pore submedian, sinistral near midpoint between midline and left margin, anterior to ventral sucker and prebifurcal at level of mid- to lower esophagus (at level of anterior esophagus [$n = 1$]), often puckered above ventral surface of worm.

Ovary median to slightly sinistrally or dextrally submedian, contiguous with or overlaps anterior margin of anterior testis (ovary immediately to right of anterior testis and directly anterior to posterior testis [$n = 2$ specimens with oblique testes]), smooth or indented or 3- to 4-lobed, globular, round to oval to subcircular (note: ovary shape markedly variable: bilobed and heart-shaped [$n = 3$]; campaniform [$n = 2$]; subtriangular [$n = 4$]), in

Table 1. Dimensions of *Neolebouria mullineauxae* n. sp. Morphotypes A and B from the eelpout *Thermarces cerberus** Rosenblatt and Cohen, 1986 (Perciformes: Zoarcidae) collected from hydrothermal vents along the East Pacific Rise (EPR) off Central America either in 2019 and 2021 or in 1999 and 2001.†

Morphotype Year of collection	A 2019/2021	B 2019/2021	A 1999/2001	B 1999/2001
n =	30	13	2	9
Body L	1,000–1,680 (1,368)	704–900 (822) [n = 12]	800–1,400 (1,100)	875–1,575 (1,286)
Body W at pharynx	152–368 (238)	120–320 (202)	248–344 (296)	100–300 (226)
Body W at VS	264–544 (414)	320–400 (352)	336–464 (400)	350–600 (482)
Body W at PT	200–448 (325)	192–320 (259)	232–320 (276)	272–590 (380)
Forebody L	264–480 (390)	200–336 (268) [n = 12]	336–600 (468)	295–470 (405)
Hindbody L	496–944 (712)	280–408 (337)	464–800 (632)	580–1,105 (881)
Oral sucker (OS) L	124–184 (159)	88–152 (122) [n = 12]	184–248 (216)	120–200 (167)
OS W	124–184 (162)	120–168 (140) [n = 12]	160–264 (212)	100–210 (164)
Prepharynx L	16–56 (32) [n = 26]	8–28 (18) [n = 10]	0	0 [n = 8]§
Pharynx L	72–108 (97)	72–124 (87)	112–168 (140)	80–105 (93)
Pharynx W	80–112 (100)	60–84 (71)	88–128 (108)	65–105 (93)
Esophagus L	60–184 (139) [n = 28]	44–92 (67) [n = 9]	60–152 (106)	115–185 (141) [n = 5]
Intestinal bifurcation anterior to VS	12–212 (56) [n = 27]	16–64 (30) [n = 10]	0	0–35 (11) [n = 7]
Postcecal region L	32–168 (90)	47–140 (77) [n = 12]	144–224 (184)	100–235 (149)
VS L	228–400 (316)	200–264 (230)	164–232 (198)	200–375 (317)
VS W	212–380 (305)	248–372 (325)	168–256 (212)	280–460 (371)
AT L	116–220 (159)	64–132 (94)	184–200 (192)	80–175 (120)
AT W	140–304 (197)	84–216 (169)	160–176 (168)	120–275 (220)
PT L	140–264 (184)	92–132 (109)	96–152 (124)	80–190 (125)
PT W	136–316 (207)	100–220 (158)	140–172 (156)	110–295 (203)
PTR L	128–328 (223)	92–188 (126)	52–120 (86)	150–355 (215)
PTR W at midpoint	144–340 (241)	148–232 (186)	164–212 (188)	205–370 (274)
CP L	236–404 (315) [n = 26]	124–260 (181) [n = 11]	316 [n = 1]	212–300 (254) [n = 6]
CP W	50–110 (71) [n = 26]	50–80 (66) [n = 12]	64 (64)	55–100 (75) [n = 6]
Seminal vesicle L	67–188 (136) [n = 25]	50–108 (88)	116 [n = 1]	47–125 (101) [n = 4]
Seminal vesicle W	47–80 (60) [n = 25]	40–75 (52)	60 [n = 1]	37–85 (64) [n = 4]
Pars prostatica L	25–105 (50) [n = 16]	27–48 (34) [n = 3]	84 [n = 1]	25–85 (53) [n = 4]
Pars prostatica W	27–60 (43) [n = 16]	20–30 (25) [n = 3]	24 [n = 1]	22–28 (25) [n = 4]
Ejaculatory duct L	75–188 (134) [n = 22]	55–125 (92) [n = 6]	34 [n = 1]	65–95 (77) [n = 4]
Ejaculatory duct W	7–15 (11) [n = 23]	5–13 (9) [n = 8]	6 [n = 1]	7–30 (16) [n = 4]
GP to lateral margin	20–144 (74) [n = 26]	28–128 (81) [n = 11]	196 [n = 1]	45–110 (79) [n = 6]
GP anterior to VS	28–192 (113)	44–84 (67) [n = 11]	132 [n = 1]	75–135 (114) [n = 6]
GP to anterior extremity	224–380 (313)	176–268 (225) [n = 11]	480 [n = 1]	210–380 (308) [n = 5]
Preovarian region L	608–984 (827)	440–595 (514) [n = 12]	496–880 (688)	510–990 (797)
OV L	64–152 (107)	48–76 (62)	60–96 (78)	50–120 (79)
OV W	56–265 (133)	40–140 (88)	52–60 (56)	80–190 (133)
VS to OV L	60–272 (146)	0–100 (28)	32–48 (40)	25–140 (80)
Seminal receptacle L	60–166 (96) [n = 16]	47–75 (62) [n = 4]	50 [n = 1]	130 [n = 1]
Seminal receptacle W	40–73 (57) [n = 17]	37–53 (44) [n = 4]	44 [n = 1]	55 [n = 1]
Vitelline follicle L	20–92 (54) [n = 149]	24–64 (40) [n = 65]	22–44 (36) [n = 9]	30–80 (42) [n = 44]
Vitelline follicle W	20–76 (40) [n = 149]	12–52 (30) [n = 65]	16–32 (24) [n = 9]	20–60 (35) [n = 44]
Previtelline field L	216–372 (283)	120–252 (206) [n = 12]	196–480 (338)	210–380 (312)
Postvitelline field L	32–136 (68)	32–88 (58)	140–328 (234)	45–115 (86)
Vitelline reservoir L	50–125 (81) [n = 28]	46–96 (68)	52–56 (54)	50–130 (83) [n = 6]
Vitelline reservoir W	35–108 (65) [n = 28]	32–92 (57)	42–48 (45)	48–75 (61) [n = 6]
Uterus L	416–728 (573)	304–388 (353) [n = 12]	408 [n = 1]	360–640 (542) [n = 6]
Uterus W	92–264 (184) [n = 29]	92–204 (149) [n = 12]	176–256 (216)	192–385 (267) [n = 9]
PUR L	400–680 (523)	240–364 (291)	308–504 (406)	280–580 (435)
Egg L	80–104 (93.2) [n = 122]	76–96 (84.8) [n = 33]	66–76 (73.3) [n = 6]	80–95 (90.8) [n = 30]
Egg W	36–52 (43.6) [n = 131]	34–52 (42.9) [n = 39]	40–42 (41.3) [n = 6]	40–57 (49.1) [n = 31]
Excretory vesicle L	400–660 (498) [n = 16]	232–344 (288) [n = 10]	248–420 (334)	280 [n = 1]
Excretory vesicle W	25–68 (45) [n = 23]	27–65 (44) [n = 10]	48–92 (70)	20–100 (52) [n = 52]
Body W at VS %‡	23.0–35.8% (30.2%)	36.4–51.1% (43.3%) [n = 12]	33.1–42.0% (37.6%)	28.9–42.4% (37.6%)
Forebody L %‡	21.9–32.9% (28.6%)	25.0–38.2% (32.6%) [n = 12]	42.0–42.9% (42.4%)	27.7–35.0% (31.6%)
OS L %‡	9.2–13.8% (11.6%)	10.4–18.9% (15.3%) [n = 11]	17.7–23.0% (20.4%)	9.1–16.0% (13.2%)
Pharynx L %‡	4.9–8.4% (7.1%)	8.4–14.1% (10.7%) [n = 12]	12.0–14.0% (13.0%)	6.2–9.1% (7.4%)
OS:pharynx W ratio	1:1.24–1.95 (1:1.62)	1:1.71–2.19 (1:1.95) [n = 12]	1:1.82–2.06 (1:1.94)	1:1.43–2.10 (1:1.77)
Esophagus L %‡	3.8–13.3% (10.1%) [n = 28]	5.6–11.5% (8.3%) [n = 9]	7.5–10.9% (9.2%)	7.3–14.3% (11.0%) [n = 5]
VS L %‡	20.3–26.7% (23.2%)	25.0–31.5% (28.1%) [n = 12]	16.6–20.5% (18.5%)	21.4–25.9% (24.7%)
Sucker W ratio	1:1.40–2.19 (1:1.89)	1:2.07–2.63 (1:2.33) [n = 12]	1:0.97–1.05 (1:1.01)	1:2.00–2.80 (1:2.30)
CP L %‡	15.1–28.6% (23.1%) [n = 26]	15.9–29.8% (22.2%) [n = 11]	22.6% [n = 1]	15.9–24.3% (20.1%) [n = 6]
AT L %‡	7.6–14.9% (11.7%)	8.6–15.9% (11.6%) [n = 12]	14.3–23.0% (18.7%)	6.9–12.1% (9.5%)
PT L %‡	10.0–22.4% (13.5%)	10.2–16.9% (13.5%) [n = 12]	10.9–12.0% (11.4%)	6.9–13.1% (9.7%)

Table I. Continued.

Morphotype	A	B	A	B
Year of collection	2019/2021	2019/2021	1999/2001	1999/2001
Body W at PT %‡	17.2–29.5% (23.6%)	23.6–41.1% (32.1%) [n = 12]	22.9–29.0% (25.9%)	19.3–37.5% (29.4%)
PTR L %‡	10.7–20.9% (16.3%)	12.3–20.9% (15.3%) [n = 12]	6.5–8.6% (7.5%)	10.3–24.5% (16.7%)
OV L %‡	6.0–11.4% (7.8%)	6.2–9.2% (7.7%) [n = 12]	6.9–7.5% (7.2%)	3.8–7.6% (6.2%)
VS to OV L %‡	4.3–17.2% (10.6%)	0.0–11.4% (3.3%) [n = 12]	3.4–4.0% (3.7%)	2.8–9.2% (6.1%)
Previtelline field L %‡	14.7–25.8% (20.9%)	17.1–30.5% (25.0%) [n = 12]	24.5–34.3% (29.4%)	18.4–28.8% (24.4%)
Postvitelline field L %‡	2.7–9.0% (4.9%)	3.6–9.8% (7.0%) [n = 12]	17.5–23.4% (20.5%)	4.4–8.8% (6.7%)
PUR L %‡	32.4–46.0% (38.2%)	29.5–40.4% (35.7%) [n = 12]	36.0–38.5% (37.3%)	29.1–37.2% (33.6%)

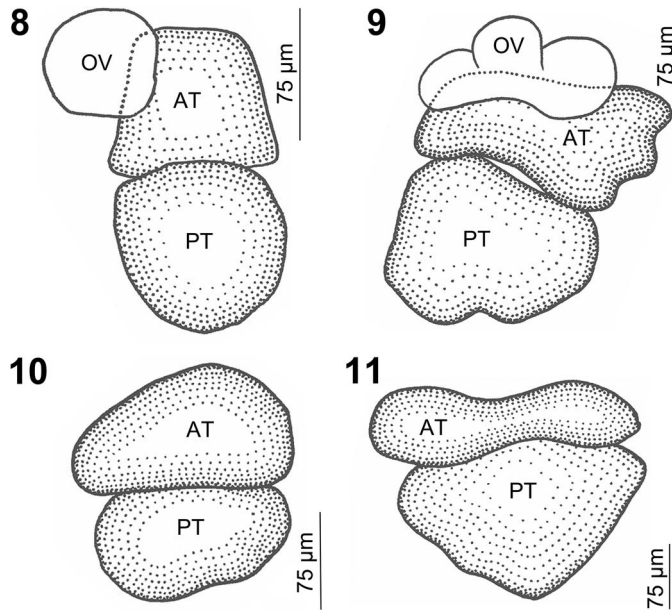
* Based on Froese and Pauly (2024) there are no synonyms for this species.
† Because of differences in fixation used in collection of host specimens in 2019 and 2021 vs. 1999 and 2001 (i.e., fish examined fresh or flash frozen vs. fixed and preserved in formalin and ethanol; see text), measurements and allometries of Morphotypes A and B from both sets of hosts were kept separate for comparative reasons and to document any differences resulting from fixation artifacts. AT, anterior testis; CP, cirrus pouch; GP, genital pore; L, length; OS, oral sucker; OV, ovary; PT, posterior testis; PTR, posttesticular region; PUR, postuterine region; VS, ventral sucker; W, width; ranges followed by means in parentheses where applicable; number [n] of measurements provided if different from total number of worms examined.
‡ Proportion of body length.
§ Prepharynx length in 1 specimen = 15 µm; however, forebody appeared somewhat distended.

middle one-third of body. Seminal receptacle canalicular, large, median, circular, elongate-oval, clavate, teardrop-, or dumbbell-shaped, often overlapped by uterus, confined to area proximate to ovary but can extend posteriorly to dorsally overlap anterior half of anterior testis (seminal receptacle opposite of ovary and distinctly at left side of worm [n = 1]). Laurer's canal present, coiled, proceeds left from seminal receptacle to near median wall of left cecum then runs anterior a short distance to terminate at pore that overlaps left cecum. Mehlis' gland cells conspicuous, either to left of and/or anterior to ovary. Oviduct passes anterior from either middle lobe or right margin of ovary, receives sperm and vitelline ducts, and passes into oötype located immediately anterior to ovary or either directly to left of or antero-dextral to it. Uterus conspicuous, primarily intercecal, median, coiled, extends from level of esophagus to midlevel of ovary, occasionally extends further posterior to midlevel of anterior testis, loops widest in region between ovary and ventral sucker then narrows over left margin of latter as it passes antero-sinistrally. Metraterm runs alongside distal end of cirrus pouch. Vitellarium follicular, extensive, ventral and dorsal to ceca, run along lateral margins, from mid-esophageal level (from level of pharynx [n = 2]) to level of cecal ends or to near posterior extremity, overlaps lateral margins of gonads, uterus, and sometimes ventral sucker; vitelline fields either confluent or not in forebody and can overlap anterior half of ventral sucker, have occasional gaps on 1 or both sides of sucker, are almost confluent in region between ventral sucker and ovary (completely confluent immediately posterior to ventral sucker [n = 1]), and are confluent in posttesticular region except directly over midline in some specimens (follicles extend to testes level but not into posttesticular region [n = 1]); follicles dense, irregular, globular, subcircular to round and small to large (some follicles as large as 120 × 80). Vitelline reservoir distinct, circular, oval to subtriangular (reniform [n = 1]), median to sinistrally submedian, either opposite to or dorsally overlapping ovary and posterior uterus, anterior to or dorsally overlapping anterior margin of anterior testis (overlaps left margin of anterior testis [n = 1]). Paired vitelline ducts proceed medially from lateral vitelline fields to join vitelline reservoir and can overlap ovary and/or anterior margin of anterior testis; transverse vitelline ducts pass from vitelline reservoir laterally to near medial margins of ceca, then bifurcate into vitelline ducts that run anterior and posterior along longitudinal axis of

worm. Eggs large, relatively few to moderate in number, oval, crenulated, operculate, amber, nonfilamented, nonembryonated. Excretory vesicle I-shaped, extends to level of ovary, narrow at posterior end, gradually widens anteriorly to anterior extremity which then balloons in width (cf. cul-de-sac), anterior border of vesicle demarcated by dark-staining cells. Excretory pore terminal.

Taxonomic summary

Type host: *Thermarces cerberus* Rosenblatt and Cohen, 1986 (Perciformes: Zoarcidae); zoarcid eelpout or pink vent fish.
Localities/collection dates: Eastern Pacific Ocean off Central America in the 9° 50' N vent field along the East Pacific Rise: 'Train Station' vent site, 9° 49' 38.6" N, 104° 17' 21.1" W, depth = 2,491 m, 1999; 'East Wall' vent site, 9° 50' 31.9" N, 104° 17' 31.2" W, depth = 2,499 m, 2001; 'Tica' vent site, 9° 50' 24.5" N, 104° 17' 30.1" W, depth = 2,519 m, 28 December 2019 [Type locality]; 'Riftia Mound' vent site, 9° 50' 17.4" N, 104° 17' 29.0" W, depth = 2,512 m, 24 December 2019; 'Crab Spa' vent site, 9° 50' 23.7" N, 104° 17' 29.6" W, depth = 2,511 m, 15 April 2021.
Site of infection: Intestine.
First intermediate host: *Eulepetopsis vitrea* McLean, 1990 (Gastropoda: Neolepetopsidae); glass limpet.
Prevalence: 8 of 11 (72.7%) fish in 2019/2021. Data only available for Morph A and B combined = 5 of 5 (100%) fish in 1999/2001.
Intensity: 2–120 worms in fish in 2019/2021. Data only available for Morph A and B combined = 3–7 worms in fish in 1999/2001.
Mean intensity: 26.9 (215 worms within 8 infected fish) in 2019/2021. Data only available for Morph A and B combined = 4.8 (24 worms within 5 infected fish) in 1999/2001.
Relative density/abundance: 19.5 (215 worms within 11 total fish examined) in 2019/2021. Data only available for Morph A and B combined = 4.8 (24 worms within 5 total fish examined) in 1999/2001.
Specimens deposited: Holotype HWML 217927 (1 slide), paratypes HWML 217928 (10 specimens on 10 slides), vouchers HWML 217929 (7 specimens on 7 slides); paratypes USNM 1741983–1741992 and 1742020–1742021 (12 specimens on 12 slides), vouchers USNM 1741993–1741998 and 1742022–1742034 (19 specimens on



Figures 8–11. *Neolebouria mullineauxae* n. sp. Morphotype B (Digenea: Opecoelidae) in *Thermarces cerberus* from the East Pacific Rise. (8, 9) Ovary and testes of paratypes showing variation in lobation and orientation to each other; ventral view. (10, 11) Testes of paratypes showing variation in lobation and orientation to each other; dorsal view. Abbreviations: AT, anterior testis; OV, ovary; PT, posterior testis.

19 slides); paratypes CCM2024.07.01–09 (9 specimens on 9 slides); vouchers CCM2024.07.10–15 (6 specimens on 6 slides).

ZooBank registration: urn:lsid:zoobank.org:act:46DA5334-524F-4B83-9A7F-219D90E03CC3.

Representative DNA sequences: One sequence deposited in GenBank for the 28S region (accession number: PQ454158); 8 sequences deposited in GenBank for the ITS2 region (accession numbers: PQ454176, PQ454177, PQ454178, PQ454179, PQ454180, PQ454181, PQ454182, PQ454190); 2 sequences deposited in GenBank for the 18S region as described in Dykman et al. (2025) (accession numbers: PQ454130, PQ454137).

Etymology: The species is named in honor of Dr. Lauren Mullineaux, Woods Hole Oceanographic Institution (WHOI), for her esteemed career and extensive contributions to deep-sea vent ecology, larval biology, and education.

Morphotype B

(Figs. 2, 8–11)

Description: Digenea, Opecoelidae. Measurements based on 22 adult, whole-mounted specimens; see Table I. With the characteristics of the genus and Morphotype A. Body small, elongate-oval. Oral sucker large. Ventral sucker large, almost as wide or wider than body width, oval to transversely elongate, over twice as large as oral sucker. Prepharynx absent or short. Pharynx large. Esophagus distinct. Intestinal bifurcation in posterior forebody. Ceca terminate blindly in posterior one-fourth of body.

Testes 2, large, wider than long, tandem to slightly oblique, contiguous, indented or slightly lobate, globular, oval to transversely elongate (note: testes shape variable: subrectangular [$n = 1$]; dumbbell [$n = 1$]; subtriangular [$n = 3$]), in posterior one-third of body. Cirrus pouch thick-walled, clavate, wider posteriorly, prostatic

gland cells most dense in proximal portion, reaches to either anterior margin, midlevel or posterior margin of ventral sucker. Seminal vesicle large, saccate, anterior end of seminal vesicle often looped back over posterior end. Pars prostatica thick-walled. Ejaculatory duct distinct; cirrus present. Genital atrium inconspicuous to quite distinct; genital pore submedian, at level of esophagus.

Ovary contiguous with, overlaps anterior margin of, or antero-dextral to anterior testis, smooth to lobate (distinctly 3-lobed [$n = 7$]), oval, globular to irregular, wider than long, in posterior portion of middle one-third of body. Seminal receptacle submedian, posterior to ovary, opposite it, or at midlevel between testes. Laurer's canal present. Mehli's gland cells conspicuous. Oötype antero-sinistral to or overlaps anterior margin of ovary. Uterus extends to level of ovary or anterior margin of anterior testis, loops widest between anterior testis and ventral sucker. Metratrum present. Vitellarium from level of pharynx or midesophagus to level of cecal ends or posterior extremity; vitelline fields confluent in forebody, present at level of ventral sucker or have occasional gaps on 1 or both sides of sucker, confluent in posttesticular region except directly over midline; follicles large with occasional smaller follicles. Vitelline reservoir large, globular, circular or oval, opposite ovary at level of posterior margin of ventral sucker or area from anterior margin of ovary to anterior testis. Eggs mainly in proximal portion of uterus.

Excretory vesicle I-shaped, indistinct, extends to level of ovary, anterior extremity can balloon in width (e.g., 108 wide). Excretory pore terminal, often surrounded by dark-stained cells and at medial point furthest anterior when posterior end invaginated.

Taxonomic summary

Host: *Thermarces cerberus* Rosenblatt and Cohen, 1986 (Perciformes: Zoarcidae); zoarcid eelpout or pink vent fish.

Localities/collection dates: Eastern Pacific Ocean off Central America in the 9°50'N vent field along the East Pacific Rise: 'Train Station' vent site, 9°49'38.6"N, 104°17'21.1"W, depth = 2,491 m, 1999; 'East Wall' vent site, 9°50'31.9"N, 104°17'31.2"W, depth = 2,499 m, 2001; 'Tica' vent site, 9°50'24.5"N, 104°17'30.1"W, depth = 2,519 m, 28 December 2019; 'Crab Spa' vent site, 9°50'23.7"N, 104°17'29.6"W, depth = 2,511 m, 15 April 2021.

Sites of infection: Intestine and stomach.

First intermediate host: *Eulepetopsis vitrea* McLean, 1990 (Gastropoda: Neolepetopsidae); glass limpet.

Prevalence: 2 of 11 (18.2%) fish in 2019/2021.

Intensity: 3–131 worms in fish in 2019/2021.

Mean intensity: 67.0 (134 worms within 2 infected fish) in 2019/2021.

Relative density/abundance: 12.2 (134 worms within 11 total fish examined) in 2019/2021.

Specimens deposited: Paratypes HWML 217930 (5 specimens on 5 slides), vouchers HWML 217931 (8 specimens on 8 slides); paratypes USNM 1741999–1742002 and 1742011–1742019 (13 specimens on 13 slides), vouchers USNM 1742003–1742010 (8 specimens on 8 slides); paratypes CCM2024.07.16–19 (4 specimens on 4 slides); vouchers CCM2024.07.20–27 (8 specimens on 8 slides).

Representative DNA sequences: One sequence deposited in GenBank for the 28S region (accession number: PQ454160); 9 sequences deposited in GenBank for the ITS2 region (accession numbers: PQ454186, PQ454187, PQ454188, PQ454191, PQ454192, PQ454193,

PQ454194, PQ454195, PQ454196); 7 sequences deposited in GenBank for the 18S region as described in Dykman et al. (2025) (accession numbers: PQ454133, PQ454134, PQ454135, PQ454138, PQ454139, PQ454140, PQ454141).

Remarks

The new species belongs within *Neolebouria* based on the following diagnostic combination of features: a well-developed, muscular cirrus pouch with a seminal vesicle that is not bipartite; canalicular seminal receptacle; eggs lacking polar filaments and $>40\text{ }\mu\text{m}$ long; ceca end blindly; ventral sucker round, lacks lamellar lips, neither possesses stalk (i.e., not pedunculate) nor fleshy fold; vitelline fields ventral and dorsal to ceca, extend to near posterior extremity and into forebody; testes 2, tandem or oblique; ovary deeply lobed (can also be smooth or indented); oral sucker not funnel-shaped; excretory vesicle does not enter forebody; submedian genital pore; pretesticular uterus; and *N. mullineauxae* infects a deep water marine teleost (*T. cerberus* [Zoarcidae]) that is not within the Macrouridae (Bonaparte, 1831) (grenadiers or rattails) (Cribb, 2005). In addition, *N. mullineauxae* possesses medial, irregularly lobed gonads, a large egg ($\geq 80\text{ }\mu\text{m}$ long), and a cirrus pouch not extending posterior to the ventral sucker (Martin et al., 2018a).

Although we identified the new species morphologically as belonging to *Neolebouria* (and our molecular data strongly indicated this as well; see the following), we noted several differences relative to the 6 congeners we recognize herein (Martin et al., 2018a; WoRMS, 2025; see Tables I, II). Two of the main features Martin et al. (2018a, p. 19) used to define the 4 species of *Neolebouria* they recognized (*N. antarctica*, *N. georgiensis*, *N. merretti*, and *N. terranovaensis*) included a large (1,800–4,800 μm long) and robust body; a large body size is seen also in *N. leiognathi* (1,920–2,000) and *N. maorum* (3,200–3,700). The body size of *N. mullineauxae* is smaller (800–1,680 μm long) and it has an elongate-oval body. The entire esophagus of *N. georgiensis* and *N. merretti*, along with the anterior region of the ceca in the latter species, is lined with especially dense gland cells, and the seminal vesicle of both species is broad and dilate proximally becoming long, thin, coiled and duct-like before the pars-prostatica and ejaculatory duct. The esophagus lacked gland cells, and the seminal vesicle was saccate in *N. mullineauxae*. Additionally, *N. antarctica* and *N. maorum* have a shorter esophagus, markedly more lobation along the posterior margin of the ovary and testes, and a genital pore at or below the level of the intestinal bifurcation. The ventral sucker size relative to body size is smaller in *N. georgiensis*, *N. leiognathi*, *N. merretti*, and *N. maorum*, the distance between this sucker and the intestinal bifurcation is greater in *N. leiognathi* and *N. maorum*; and the gonads are larger relative to body size in *N. terranovaensis*. All previously recognized species of *Neolebouria* possess denser and more numerous vitelline follicles and eggs as well. The new species parasitizes a member of the Zoarcidae, not known to host *Neolebouria* species, and is unique in that it was found within a host inhabiting hydrothermal vent communities.

The remote location of the host species, *T. cerberus*, for *N. mullineauxae*—the hydrothermal vent environment off the west coast of Central America at very deep depths of 2,491–2,519 m is notable (*T. cerberus* is known down to a depth of 2,630 m). No hosts

for species of *Neolebouria* come from depths this deep nor are known from vent communities, with 1 exception: *N. merretti* infects the deep-sea tripod fish, *Bathytrophops sewelli*, which is known to have a depth range of 2,980–4,200 m; however, this teleost is neither known from vent fields nor the Pacific Ocean (Gibson and Bray, 1982; Froese and Pauly, 2024). We further suspect that *N. mullineauxae* is new because of the lack of gene flow expected with the geographic and vertical isolation of its host, a zoarcid eelpout, within the abyss.

Based on overall morphology and molecular evidence from 2 barcoding regions, we infer that *N. mullineauxae* exists as 2 morphotypes (A and B): morphologically distinguishable (i.e., exhibiting morphological variation) yet molecularly (i.e., genotypically) identical (see Fig. 12). Indeed, the morphological differences between these 2 morphs were so noticeable that, at first, we believed they were 2 separate congeneric species. We recognize that poor fixation of our material may account for at least some of these differences; however, we noted across all specimens examined consistency in these differing morphological features (e.g., large ventral sucker). For in situ fixation to produce such specific and consistent artifacts across our study, while possible, we feel is not likely. A collection of additional, live-fixed specimens in the future would be ideal. We also want to suggest that the *cox1* gene may be of use in further investigation as this gene can better distinguish species than *ITS2* (Bray et al., 2023); however, *cox1* can vary significantly across genera, species, and populations. *ITS2* is sufficient for delineating species in most cases (e.g., Martin et al., 2018b), and in some instances, variation in *cox1* has been interpreted as interspecific variation (Magro et al., 2023). Given the incongruency between morphology and the available genetic sequences, and because we were unable to sequence the *cox1* gene at the time, we elected to describe the morphs as 1 species while keeping our morphological observations, measurements, and comparisons separate for the 2 morphs. This will better facilitate division into 2 species if further molecular data become available (see the following and Table I).

When comparing Morph A and Morph B, the latter possesses a conspicuously larger ventral sucker relative to body size and is itself smaller overall. We also noted differences in body shape (distinctly elongate oval vs. a stout, more compact elongate oval body), testes texture (Morph A observed to possess smooth testes whereas this was not seen in Morph B), and the size and extent of the cirrus pouch between both morphs. We noted differences in lengths of the hindbody, testes, uterus, excretory vesicle, ventral sucker to ovary distance, and the preovarian and postuterine regions between both morphs as well as differences in several allometric measures including body width, pharynx, ventral sucker, and ventral sucker to ovary lengths as a percentage of body length (BL), along with a larger sucker width ratio in Morph B reflecting its much larger ventral sucker (see Figs. 1, 2; Table I). Of the *T. cerberus* examined, just 1 individual had a co-infection of both Morphs A and B. This fish was collected from the type locality, the ‘Tica’ vent site, and the majority of digeneans found in this fish were Morph B.

At the time of writing, nucleotide sequences were available on NCBI GenBank for the species *N. georgiensis* (4 *COI* and 5 28S sequences), *N. maorum* (1 28S sequence), and *Mesobathylebouria lanceolata* (Price, 1934) Martin, Huston, Cutmore and Cribb, 2018 (1 28S sequence [labeled as *Neolebouria lanceolata* in

Table II. Dimensions of the 6* species of *Neolebouria* Gibson, 1976 we recognize prior to this study.†

Parasite	<i>N. antarctica</i> (Szidat and Graefe, 1967, fig. 2)	<i>N. georgiensis</i> (Gibson, 1976, fig. 24)	<i>N. leiognathi</i> (Wang, Wang, and Zhang, 1992, fig. 16)	<i>N. maorum</i> (Allison, 1966, fig. 1)	<i>N. merretti</i> (Gibson and Bray, 1982, fig. 9)	<i>N. terranovaensis</i> (Zdzitowiecki, Pisano & Vacchi, 1993, fig. 1)
Locality	Off South Shetland Islands, Antarctica	Off South Georgia, sub-Antarctic	Off Fujian Province, China	Off Kaikoura, New Zealand	SW of Canary Islands off Africa	Terra Nova Bay, Ross Sea, Antarctica
n =	1	10	?	≤61#	14	39
Body L	2,300 [2,240] {2,160}§	2,500–4,800	1,920–2,000	3,200–3,700	1,800–3,800	1,190–3,600
Body W	1,100 [1,080]	820–1,400	460–512	1,150–1,200	1,100–2,100	610–1,300
Forebody L	{472}	600–980	{621}	926	969	722
Hindbody L	1,818	3,125	1,329	2,274	2,750	3,056
OS L	[280]	170–360	112–176	282	200–340	164–337
OS W	300 [330] {239}	220–310	112–192	300	180–310	207–373
Prepharynx L	0	≤60	{0}	0	20–60	30
Pharynx L	[190]	120–230	80–112	200	120–160	104–198
Pharynx W	[180] {157}	130–180	84–90	100	140–190	93–183
Esophagus L	45	150–470	240–302	60	280–380	90–240
Intestinal bifurcation anterior to VS	45	63	171	342	0–94	28
Postcecal region L	136	531	107	242	438	333
VS L	[440]	330–470	144–208	403	340–530	262–460
VS W	550 [580] {572}	450–680	144–192	470	300–520	303–592
AT L	227	380–650 (both testes)	128–160	302	170–640 (both testes)	140–580
AT W	568	420–820 (both testes)	168–176	242	550–1,120 (both testes)	360–810
PT L	250		112–128	322		180–870
PT W	409		84–112	342		300–770
PTR L	{502}	1,000	{386}	886	781	806
PTR W at midpoint	682	625	386	845	1,563	750
CP L	{440}	844	406–560	342	530–1,000	348–804
CP W	197	188	80	161	180–210	95–244
Seminal vesicle L				181	469	239
Seminal vesicle W				81	250	148
Pars prostatica L					188	125
Pars prostatica W					63	23
Ejaculatory duct L				141	157	91
Ejaculatory duct W				20	16	23
GP to lateral margin	76	94	107	161	156	278
GP anterior to VS	45	281	364	201	281	306
GP to anterior extremity	409	625	279	725	781	500
Preovarian region L	1,205	1,688	1,071	1,650	1,906	1,417
OV L	136	150–300	98–112	181	375	110–300
OV W	523	360–750	112–160	342	563	240–770
VS to OV L	295	500	300	342	406	278
Seminal receptacle L	91		107	101		307
Seminal receptacle W	45		43	40		182
Vitelline follicle L	45–61 (51) [n = 5]†	31–125 (100) [n = 5]	43 (43) [n = 5]	60–101 (68) [n = 5]	31–125 (88) [n = 5]	83–139 (105) [n = 5]
Vitelline follicle W	30–45 (42) [n = 5]	31–93 (63) [n = 5]	21–43 (25) [n = 5]	40–81 (52) [n = 5]	31–94 (63) [n = 5]	56–83 (72) [n = 5]
Previtelline field L	348	719	386	282	688	444
Postvitelline field L	45	125	64	60	469	83
Vitelline reservoir L				121		
Vitelline reservoir W				60		
Uterus L	750	1,188	814	926	1,313	1,056
Uterus W	614	750	214	463	1,094	528

Table II. Continued.

Parasite	<i>N. antarctica</i> (Sádat and Graefe, 1967, fig. 2)	<i>N. georgiensis</i> (Gibson, 1976, fig. 24)	<i>N. leiognathi</i> (Wang, Wang, and Zhang, 1992, fig. 16)	<i>N. maorum</i> (Allison, 1966, fig. 1)	<i>N. merretti</i> (Gibson and Bray, 1982, fig. 9)	<i>N. terranovaensis</i> (Zdzitowiecki, Pisano & Vacchi, 1993, fig. 1)
Locality	Off South Shetland Islands, Antarctica	Off South Georgia, sub-Antarctic	Off Fujian Province, China	Off Kaikoura, New Zealand	SW of Canary Islands off Africa	Terra Nova Bay, Ross Sea, Antarctica
PUR L	1,114	2281	857	1,550	1,656	2,333
Egg L	50–60 [95–99] {82–95}	90–102 (95)	92–98	60	80–92	76–111
Egg W	25–30 [43–53] {38–50}	51–57 (55)	52–54	30	44–56	40–55
Excretory vesicle L			≥386	1,389	1,313	458¶
Excretory vesicle W			43	141	125	69¶
Body W %‡	47.8%	29.2–32.8%	24.0–25.6%	32.4–35.9%	55.3–61.1%	36.1–51.3%
Forebody L %‡	{21.9%}	{20.4–24.0%}	25.0% {32.3%}	33.3% {29.0%}	20.0–30.0%	19.1% {20.0%}
OS L %‡	12.5%	6.8–7.5%	5.8–8.8%	8.8%	8.9–11.1%	9.4–13.8%
Pharynx L %‡	8.5%	4.8%	4.2–5.6%	6.3%	4.2–6.7%	5.5–8.7%
OS:pharynx W ratio	{1:1.52}	{1:1.69–1.72}	{1:1.33–2.13}	1:3.00 {1:1.70–1.80}	{1:1.29–1.63}	{1:2.03–2.26}
Esophagus L %‡	2.0%	6.0–9.8%	12.5–15.1%	1.9%	10.0–15.6%	6.7–7.6%
VS L %‡	19.6%	9.8–13.2%	7.5–10.4%	12.6%	13.9–18.9%	12.8–22.0%
Sucker W ratio	{1:2.40}	{1:2.05–2.19}	1:1.16 {1:1.00–1.29 (1:1.15)}	1:1.57	1:1.67 {1:1.50–2.60}	{1:1.46–1.59}
CPL L %‡	{20.4%}	21.3% {19%}	{21.1–28.0%}	{10.7%}	{26.3–29.4%}	{22.3–29.2%}
AT L %‡	9.9%	13.5–15.2% (both testes)	6.7–8.0%	9.4%	9.4–16.8% (both testes)	11.8–16.1%
PT L %‡	10.9%		5.8–6.4%	10.1%		15.1–24.2%
PTL L %‡	{23.2%}	25.2% {24%}	{20.1%}	{27.7%}	21.0% {20.0%}	21.3% {23.0%}
OV L %‡	5.9%	6.0–6.3%	5.1–5.6%	5.7%	10.1%	8.3–9.2%
VS to OV L %‡	12.8%	12.6%	15.6%	10.7%	10.9%	7.4%
Previtelline field L %‡	15.1%	18.1%	20.0%	8.8%	18.5%	11.8%
Postvitelline field L %‡	2.0%	3.1%	3.3%	1.9%	12.6%	2.2%
PUR L %‡	48.4%	57.5%	44.4%	48.4%	44.5%	61.8%

* Based on Martin et al. (2018a) and WoRMS (2025).

† AT, anterior testis; CP, cirrus pouch; GP, genital pore; L, length; OS, oral sucker; OV, ovary; PT, posterior testis; PTR, posttesticular region; PUR, postuterine region; VS, ventral sucker; W, width; ranges followed by mean in parentheses where applicable; number [n] of measurements provided if different from total number of worms examined. Additional morphological and allometric measurements for species of *Neolebouria* included within this table obtained from Dronen et al. (2014) and Jaiswal et al. (2014) and are indicated by {} as well as from figures from original descriptions.

‡ Proportion of body length.

§ Additional measurements and observations of *Neolebouria antarctica* obtained from Zdzitowiecki (1990, fig. 1a) indicated by [] and from reevaluation of holotype specimen by Dronen et al. (2014) indicated by {}.|| Wang et al. (1992) did not provide for *N. leiognathi* the number of specimens examined.# Allison (1966) stated that the examination of the definitive host, the Maori octopus, *Macroctopus (=Octopus) maorum* (Hutton, 1880), produced 3 trematode specimens from material previously obtained by P. Johns as well as 52 and 6 additional specimens, respectively, from *M. maorum* found off Kaikoura, New Zealand; however, the exact number of specimens measured in the description was not provided.

¶ Measured from Zdzitowiecki et al. (1993; fig. 1d); while immature, this was the only specimen with excretory bladder illustrated.

GenBank]). We focused on the 28S rDNA region for comparison between species because 28S sequences were available for all *Neolebouria* and *Mesobathylebouria* species represented in GenBank, in addition to other closely related opecoelids. We compared the ITS2 barcoding region for *N. mullineauxae* Morphs A and B because this region provides higher resolution at the species level (Nolan and Cribb, 2005). For the 28S barcoding region (Fig. 12), *N. mullineauxae* Morphs A and B were genetically identical (100% similarity, 1,236/1,236 bp) and were 99.92% (1,218/1,219 bp) similar to *N. georgiensis*. *Neolebouria mullineauxae* also grouped closely with *Podocotyle atomon* (Rudolphi, 1802) Odhner, 1905 (97.69% similarity, 1,185/1,213 bp) as well as with *Buticulotrema thermichthysi* Bray, Waeschenbach, Dyal, Littlewood and Morand, 2014 (96.73% similarity, 1,182/1,222 bp), which was described in a different hydrothermal vent fish, the livebearing brotula *Thermichthys hollisi* (Cohen, Rosenblatt and Moser, 1990) (Ophidiiformes: Bythitidae). In contrast, *N. mullineauxae* was genetically distant (92.33% similarity, 1,131/1,225 bp) from *M. lanceolata*, the only available sequence for this genus. The sequence for *N. maorum* was not long enough to include in the phylogenetic tree but the overlapping region shared 86.42% (471/545 bp) similarity with *N. mullineauxae*. All ITS2 sequences from *N. mullineauxae* Morphs A and B were genetically identical (100% similarity, 435/435 bp), further supporting their status as a single species.

There are a handful of parasite reports from *T. cerberus*. De Buron et al. (2000) reported the acanthocephalan *Hypoechinorhynchus thermaceri* de Buron, 1988 from the intestine of *T. cerberus* collected on the EPR 13°N. One of us (L.N.D.) has also reported parasites from this host (Dykman, 2023; Dykman et al., 2023a, 2023b, 2025) including 2 new nematode species, *Ascarophis justinei* Moravec, Dykman and Davis, 2023 and *Ascarophis globuligera* Moravec, Dykman and Davis, 2023. To our knowledge, the present report is the first description of a digenetic trematode species from *T. cerberus*.

With the description herein of a seventh species of *Neolebouria*, we now present a key to the species we recognize within this genus.

Key to species of *Neolebouria* (based on Dronen et al., 2014)

- 1a. Genital pore prebifurcal 2
- 1b. Genital pore bifurcal or postbifurcal 5
- 2a. Cirrus pouch extends posteriorly as far as the posterior margin of ventral sucker 3
- 2b. Cirrus pouch extends beyond posterior margin of ventral sucker
..... *Neolebouria georgiensis* Gibson, 1976 (type species of genus) (Fig. 13; egg size: 90–102 × 51–57)
- 3a. Vitelline fields confluent in posttesticular space; anterior margin of ventral sucker either close to or overlapping intestinal bifurcation 4
- 3b. Vitelline fields not confluent in posttesticular space; ventral sucker some distance posterior to intestinal bifurcation
..... *Neolebouria leiognathi* (Wang, Wang and Zhang, 1992) Bray, 2002* (syn. *Plagioporus leiognathi* Wang, Wang and Zhang, 1992) (Fig. 14; egg size: 92–98 × 52–54)
- 4a. Body relatively large (1,190–3,600); gonads larger in relation to body size; vitelline follicles dense and

- eggs numerous
..... *Neolebouria terranovaensis* Zdzitowiecki, Pisano and Vacchi, 1993† (Fig. 15; egg size: 76–111 × 40–55)
- 4b. Body relatively small (704–1,680); gonads smaller relative to body size; vitelline follicles not as dense and eggs few to moderate in number
..... *Neolebouria mullineauxae* (Figs. 1–11; egg size: 76–104 × 34–52)
- 5a. Genital pore at, or near, to the level of intestinal bifurcation 6
- 5b. Genital pore clearly postbifurcal
..... *Neolebouria maorum* (Allison, 1966) Gibson, 1976 *(syns. *Plagioporus maorum* Allison, 1966; *Plagioporus* (*Plagioporus*) *maorum* Allison, 1966) (Fig. 16; egg size: 60 × 30)
- 6a. Cirrus pouch terminates anterior to midlevel of ventral sucker
..... *Neolebouria antarctica* (Szidat and Graefe, 1967) Zdzitowiecki, 1990 (syns. *Crassicutis antarcticus* Szidat and Graefe, 1967; *Plagioporus lobatus georgianus* Gaevskaja and Kovaljova, 1976) (Fig. 17; egg size: 50–60 × 25–30)‡
- 6b. Cirrus pouch terminates at the level of posterior margin of ventral sucker or slightly more posterior
..... *Neolebouria merretti* Gibson and Bray, 1982 (Fig. 18; egg size: 80–92 × 44–56)

* This species was recognized as *incertae sedis* by Martin et al. (2018a), but is fully recognized by WoRMS (2025).

† Martin et al. (2018a) recognized *N. terranovaensis*; however, WoRMS (2025) supports Faltýnková et al. (2022) that this species is a junior synonym of *N. georgiensis*.

‡ Zdzitowiecki (1990, fig. 1a) redescribed *N. antarctica* noting a larger egg size (95–99 × 43–53) and commented that the cirrus pouch did not end anterior to the ventral sucker (as illustrated by Szidat and Graefe, 1967, fig. 2), but it runs posteriorly, dorsal to the ventral sucker.

We also describe 2 immature specimens of an opecoelid from another zoarcid eelpout, *Pyrolycus manusanus*, found along the South Su vent field within the Manus Basin off the coast of Papua New Guinea.

Opecoelidae sp.

(Figs. 19–20)

Description: Digenea, Opecoelidae. Measurements based on 2 immature, whole-mounted specimens, 1 specimen slightly rolled, second specimen with slight tear of syncytium posteriorly; see Table III. With the characteristics of family. Body small, stout, elongate-oval, with parallel margins in middle one-third of body. Forebody and hindbody attenuated to rounded extremity; 1 individual constricted about one-fourth body length from anterior extremity and with more truncate posterior extremity. Tegument smooth. Preoral lobe absent. Oral sucker large, sub-spherical, protuberant; mouth subterminal. Ventral sucker distinct, moderate in size, median (rolled to left in 1 specimen), sub-spherical with prominent muscular perimeter, slightly smaller than oral sucker, in middle third of body. Prepharynx absent. Pharynx large, muscular, oval to dolioform, overlapped by posterior margin of oral sucker. Esophagus distinct, thick-walled, short, straight,

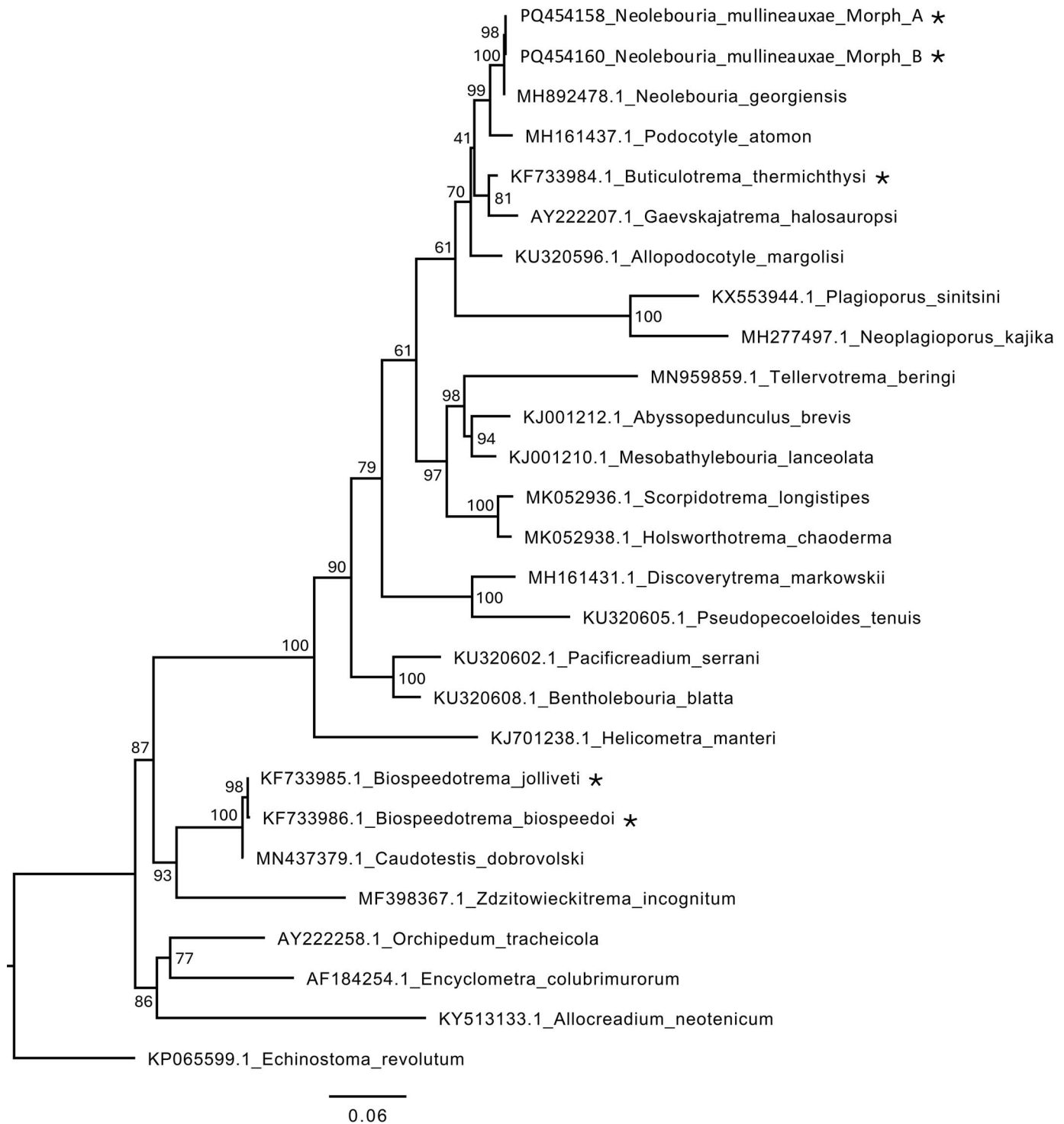
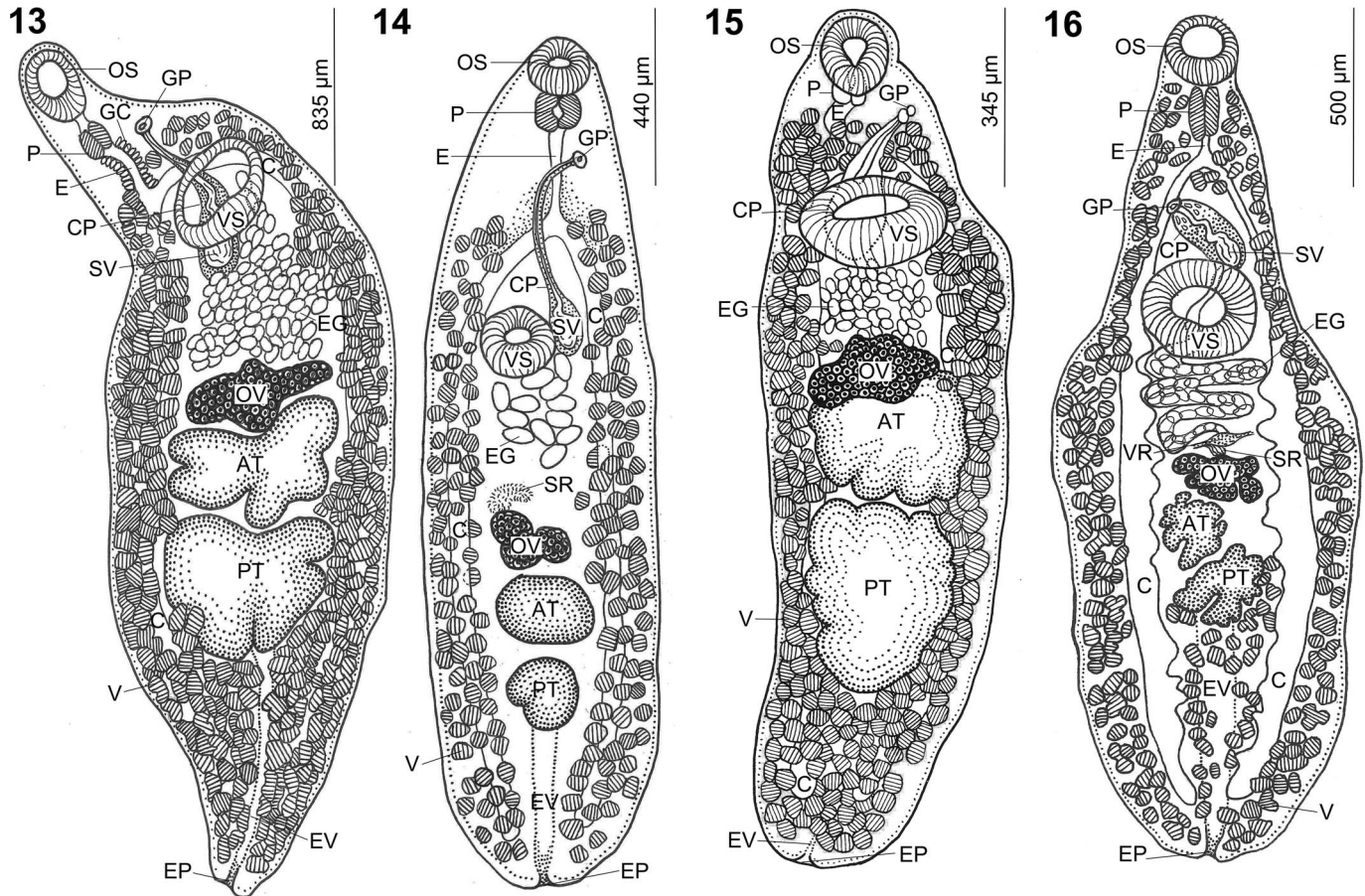


Figure 12. Phylogenetic tree resulting from maximum-likelihood analysis of the partial 28S rDNA alignment. This analysis places the new species in context with sequences from genera *Neolebouria* and *Mesobathylebouria*, other known vent digenean species (*), and other closely related marine digeneans, with *Echinostoma revolutum* (Fröhlich, 1802) Looss, 1899 as an outgroup. Support values generated with 1,000 bootstraps are shown at the tree branches. The scale bar indicates the expected number of substitutions per site. GenBank accession numbers are shown before the species names.

wide. Intestinal bifurcation in posterior forebody, just anterior to ventral sucker (overlapped by ventral sucker in rolled specimen). Gland cells distinct, lateral to pharynx and esophagus. Ceca wide, conspicuous, extend posteriorly to terminate blindly in or near

posterior one-fourth of body, 1 specimen with dilated ceca at posterior ends.

Testes 2, symmetrical, median (slightly dextrally submedian in rolled specimen), longer than wide, contiguous, smooth, globular



Figures 13, 14. *Neolebouria georgiensis* Gibson, 1976 and *Neolebouria leiognathi* (Wang, Wang and Zhang, 1992) Bray, 2002 (Digenea: Opecoelidae). (13) Whole specimen of *N. georgiensis* based on fig. 24 of Gibson (1976); ventral view. (14) Whole specimen of *N. leiognathi* based on fig. 16 of Wang et al. (1992); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GC, gland cells; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SR, seminal receptacle; SV, seminal vesicle; V, vitellarium; VS, ventral sucker.

Figures 15, 16. *Neolebouria terranovaensis* Zdzitowiecki, Pisano and Vacchi, 1993 and *Neolebouria maorum* (Allison, 1966) Gibson, 1976 (Digenea: Opecoelidae). (15) Whole specimen of *N. terranovaensis* based on fig. 1b of Zdzitowiecki et al. (1993); ventral view. (16) Whole specimen of *N. maorum* based on fig. 1 of Allison (1966); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SR, seminal receptacle; SV, seminal vesicle; V, vitellarium; VR, vitelline reservoir; VS, ventral sucker.

to oval, at or near level of cecal ends in posterior one-third of body. Cirrus pouch and its contents not observed. Genital atrium and genital pore not observed.

Ovary median, immediately postacetabular and separated from testes, smooth, oval to elongate oval (i.e., longitudinally stretched in 1 specimen), dark stained, in middle one-third of body. Proximal female system not observed. Uterus median, extends anterior from level of ovary to pass dorsal to ventral sucker. Vitellarium and vitelline reservoir not observed. Rudimentary transverse vitelline duct observed in 1 specimen near level of ovary. Eggs absent.

Excretory vesicle I-shaped, extends to or near level of ventral sucker. Excretory pore subterminal, dorsal, surrounded by dark-stained cells.

Taxonomic summary

Host: *Pyrolycus manusanus* Machida and Hashimoto, 2002 (Perciformes: Zoarcidae); zoarcid eelpout.

Locality/collection date: Western Pacific Ocean off the coast of Papua New Guinea in the 'South Su' vent field within the Manus Basin, 3°48'39.6"S, 152°6'14.4"E, depth = 1,399 m, 4 August 2007.

Site of infection: Intestine.

Prevalence: 2 of 6 (33.3%) fish.

Intensity: 1 worm in each infected fish.

Mean intensity: 1.0 (2 worms within 2 infected fish).

Relative density/abundance: 0.3 (2 worms within 6 total fish examined).

Specimens deposited: Vouchers HWML 217932 (2 specimens on 2 slides).

Remarks

Identification of these 2 immature specimens from the intestine of *P. manusanus* could be made only to the family Opecoelidae, and they are quite similar to each other in overall morphology (see Figs. 19, 20; Table III). Both specimens possessed a relatively large pharynx and suckers, distinct gland cells lateral to the

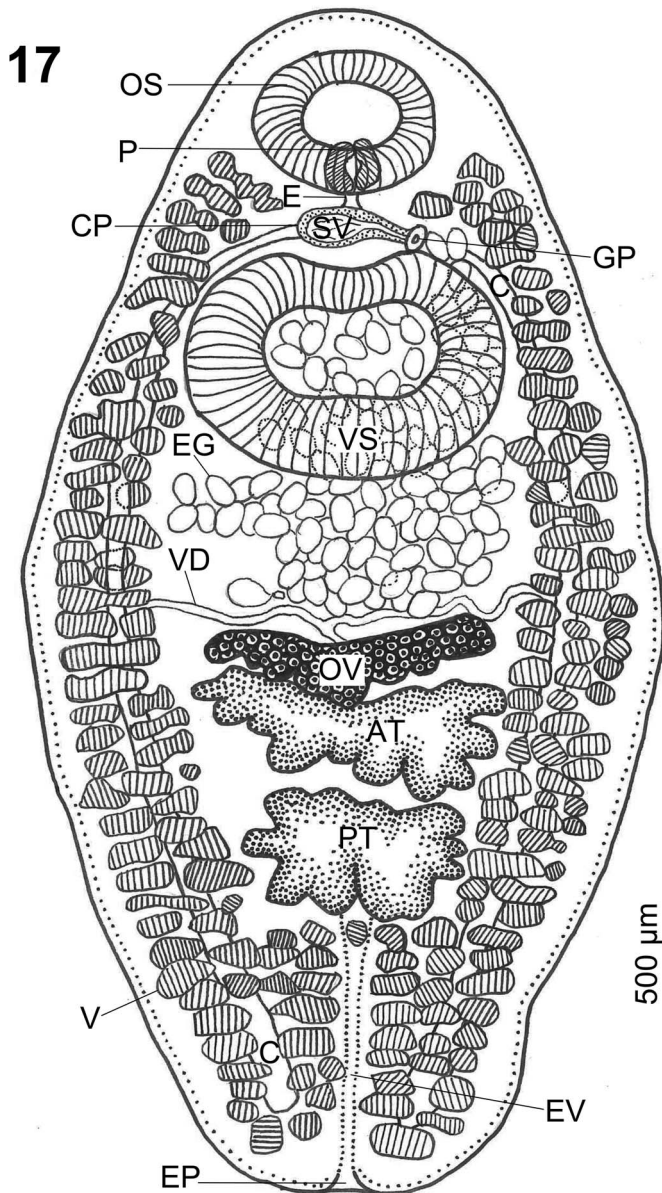


Figure 17. *Neolebouria antarctica* (Szidat and Graefe, 1967) Zdzitowiecki, 1990 (Digenea: Opcoelidae). Whole specimen based on fig. 2 of Szidat and Graefe (1967); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SV, seminal vesicle; V, vitellarium; VD, vitelline duct; VS, ventral sucker.

pharynx and esophagus, symmetrical and globular to oval testes, an I-shaped excretory vesicle, and an elongate-oval body.

We are aware of 1 previous report of a parasite from *P. manusanus* and that study was recently published from material related to this study. Moravec et al. (2023) described the nematode, *Ascarophis monofilamentosa* Moravec, Dykman, and Davis, 2023, from the large intestine of *P. manusanus* found at 1,399 m depth in the Manus Basin near Papua New Guinea. We believe the 2 immature digeneans of the present study to be the first report of a digenetic trematode from *P. manusanus*.

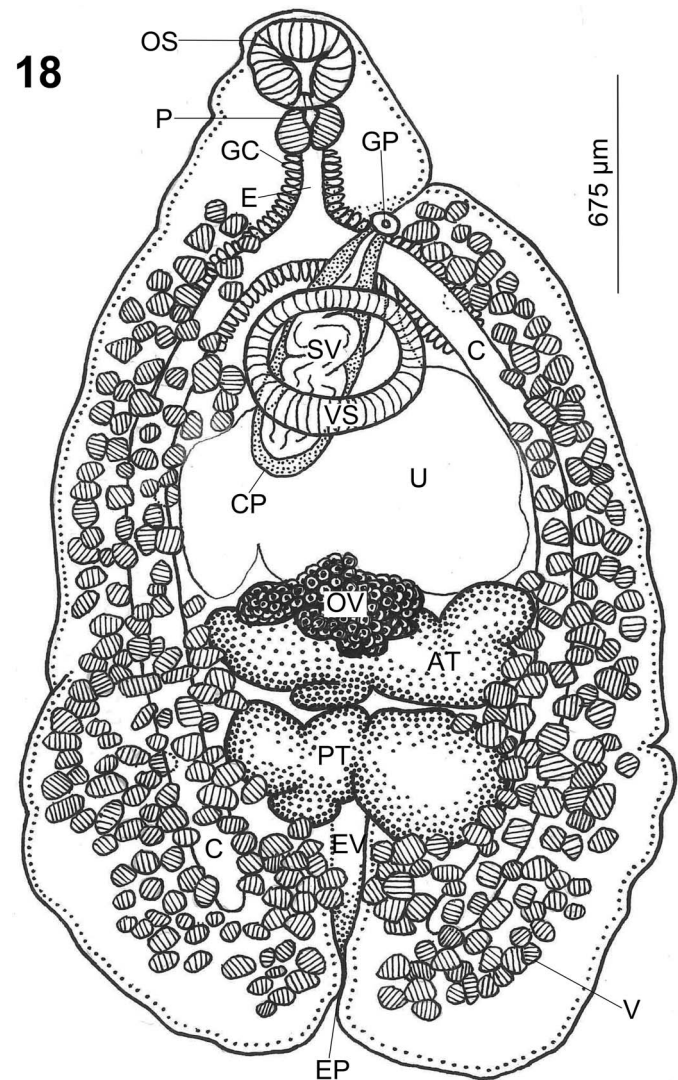
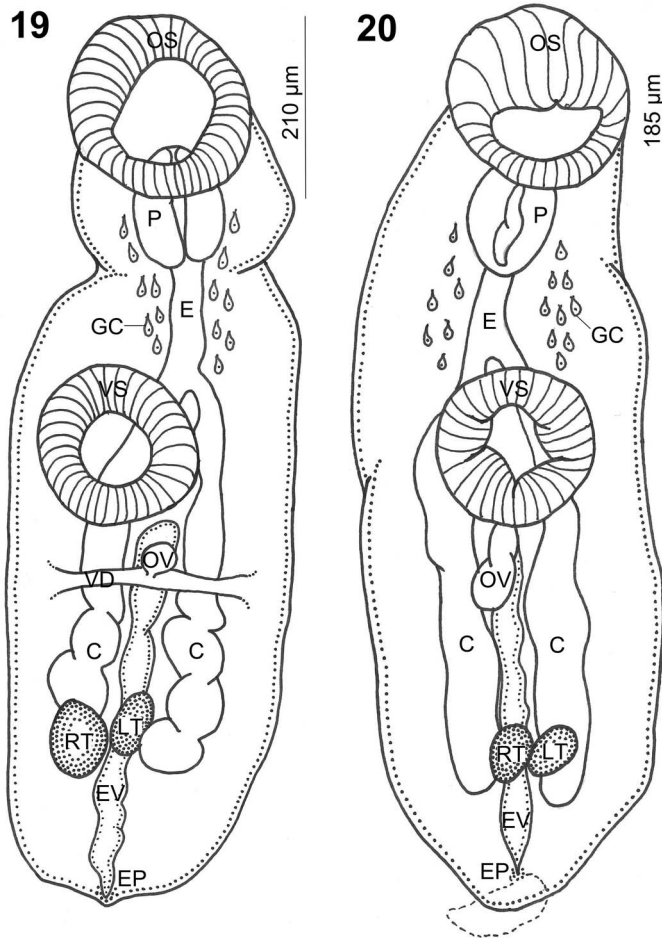


Figure 18. *Neolebouria merretti* Gibson and Bray, 1982 (Digenea: Opcoelidae). Whole specimen is based on fig. 9A of Gibson and Bray (1982); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EP, excretory pore; EV, excretory vesicle; GC, gland cells; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SV, seminal vesicle; U, uterus; V, vitellarium; VS, ventral sucker.

DISCUSSION

This report introduces a new host family (Zoarcidae Swainson, 1839) and genus (*Thermarces* Rosenblatt and Cohen, 1986) of fish infected by this digenean group. The new species described herein, *N. mullineauxae*, represents the first taxonomic description of a new digenean species infecting the zoarcid, *T. cerberus*, and the finding of an opcoelid from the zoarcid, *P. manusanus*, represents a new host record (note: 2 species of *Ascarophis* van Beneden, 1871 [Nematoda: Cystidicolidae] were recently described from *T. cerberus* and 1 from *P. manusanus* by Moravec et al., 2023 as part of this same project). This report also introduces a new geographic locality for *Neolebouria* (*sensu stricto*), the East Pacific Ocean off the coast of Central America.



Figures 19, 20. Opecoelidae sp. in *Pyroliscus manusanus* from off Papua New Guinea. (19) Whole mount of first of 2 immature specimens collected; ventral view. (20) Whole mount of the second of 2 immature specimens collected with a slight tear in syncytium at the posterior extremity; ventral view. Abbreviations: C, cecum; E, esophagus; EP, excretory pore; EV, excretory vesicle; GC, gland cells; LT, left testis; OS, oral sucker; OV, ovary; P, pharynx; RT, right testis; VD, vitelline duct; VS, ventral sucker.

The presence of *Neolebouria* in deep water

Neolebouria is well represented in the deep sea (see Table IV; Froese and Pauly, 2024; Palomares and Pauly, 2024). The 7 species of this genus have radiated into at least 4 orders of fishes and 1 order of cephalopods with the majority parasitizing perciforms (Table IV). This also includes at least 10 families, 26 genera, and 37 species of fishes and cephalopods known to inhabit the deep sea that harbor members of this digenean genus. *Neolebouria antarctica* has been reported from the greatest number of hosts, and we noted that different species of *Neolebouria* infect the same host species in the deep sea. Host specificity in the deep sea is relatively high with 22 of the 37 (60%) known host species harboring 1 species only of *Neolebouria*. It is interesting to note that Wang et al. (1992) described *N. leiognathi* from the deep pugnose ponyfish, *Deveximentum ruconius* (Hamilton, 1822) (syn. *Leiognathus ruconius* [Hamilton, 1822]) (Acanthuriformes: Leiognathidae), off Fujian Province, China; a piscine species not known from deep waters (maximum depth of 60 m, respectively). Two other hosts,

Table III. Dimensions of 2 immature individuals of a species of Opecoelidae Ozaki, 1925 from the eelpout, *Pyroliscus manusanus** Machida and Hashimoto, 2002 (Perciformes: Zoarcidae), collected from hydrothermal vents within the Manus Basin off the coast of Papua, New Guinea in 2007.†

Parasite	Specimen 1	Specimen 2
Body L	944	912
Body W at pharynx	224	224
Body W at VS	296	296
Body W at testes	288	280
Forebody L	368	352
Hindbody L	576	560
OS L	180	188
OS W	184	180
Prepharynx L	0	0
Pharynx L	132	116
Pharynx W	104	84
Esophagus L	96	72
Intestinal bifurcation anterior to VS	0	10
Postcecal region L	152	152
VS L	180	160
VS W	176	164
RT L	76	62
RT W	64	46
LT L	72	50
LT W	44	48
Intertesticular region	0	2
PTR L	160	190
PTR W at midpoint	222	156
Preovarian region L	544	504
OV L	44	82
OV W	28	28
VS to OV L	24	0
OV to testes	132	124
PUR L	400	344
Excretory vesicle L	440	448
Excretory vesicle W	56	32
Body W at VS %‡	31.4%	32.5%
Forebody L %‡	39.0%	38.6%
OS L %‡	19.1%	20.6%
Pharynx L %‡	14.0%	12.7%
OS:pharynx W ratio	1:1.77	1:2.14
Esophagus L %‡	10.2%	7.9%
VS L %‡	19.1%	17.5%
Sucker W ratio	1:0.96	1:0.91
RT L %‡	8.1%	6.8%
LT L %‡	7.6%	5.5%
Body W at testes %‡	30.5%	30.7%
PTR L %‡	17.0%	20.8%
OV L %‡	4.7%	9.0%
VS to OV L %‡	2.5%	0.0%
PUR L %‡	42.4%	37.7%

* Based on Froese and Pauly (2024), there are no synonyms for this species.

† L, length; LT, left testis; OS, oral sucker; OV, ovary; PTR, posttesticular region; PUR, postuterine region; RT, right testis; VS, ventral sucker; W, width.

‡ Proportion of body length.

the yellowbelly rockcod, *Notothenia neglecta* Nybelin, 1951 (Perciformes: Nototheniidae), proximate to Antarctica and parasitized by *N. antarctica*, and the hammer octopus, *Octopus australis* Hoyle, 1885 (syn. *Robsonella australis* [Hoyle, 1885]) (Octopoda: Octopodidae), from off Portobello, New Zealand and parasitized by *N. maorum*, are not known from the deep sea either.

Life history of *N. mullineauxae* within hydrothermal vents

The zoarcid eelpout or pink vent fish, *T. cerberus*, is a bathydemersal species found at depths down to 2,630 m in the East

Table IV. Hosts of species of *Neolebouria* Gibson, 1976 known to inhabit the deep sea.*

Parasite species	Host order†	Host family†	Host species†	Known depth range (m)†
<i>Neolebouria antarctica</i> (Sizdat and Graefe, 1967) Zdzitowiecki, 1990	Perciformes Bleeker, 1863	Bathydraconidae Regan, 1913 [Antarctic dragonfishes]	<i>Gerlachea australis</i> Dollo, 1900 [Antarctic dragonfish]	200–670
			<i>Gymnodraco acuticeps</i> Boulenger, 1902 [ploughfish]	0–550
			<i>Parachaenichthys charcoti</i> (Vaillant, 1906) [Antarctic dragonfish]	5–400
			<i>Parachaenichthys georgianus</i> (Fischer, 1885) [Antarctic dragonfish]	5–270
			<i>Psilodraco breviceps</i> Norman, 1937 [Antarctic dragonfish]	60–345
			<i>Chaenocephalus aceratus</i> (Lönnberg, 1906) [blackfin icefish]	5–770
		Channichthyidae Gill, 1861 [crocodile icefishes]	<i>Chaenodraco wilsoni</i> Regan, 1914 [spiny icefish]	200–800
			<i>Champsoscephalus gunnari</i> Lönnberg, 1905 [mackerel icefish]	0–700
			<i>Chionodraco rastrispinosus</i> DeWitt and Hureau, 1979 [ocel-lated icefish]	0–1,000
			<i>Neopagetopsis tonah</i> Nybelin, 1947 [Jonah's icefish]	20–900
			<i>Pagetodes antarcticus</i> (Dollo, 1900) [long-fingered icefish]	90–600
			<i>Pseudochaenichthys georgianus</i> Norman, 1937 [South Georgia icefish]	0–475
			<i>Paraliparis meganchus</i> Andriashev, 1982 [slit branchial paraliparis]	220–1,145
		Nototheniidae Günther, 1861 [cod icefishes]	<i>Dissostichus eleginoides</i> Smitt, 1898 [Patagonian toothfish]	0–2,144
			<i>Dissostichus mawsoni</i> Norman, 1937 [Antarctic toothfish]	0–2,200
			<i>Gobionotothen gibberifrons</i> (Lönnberg, 1905) [humped rockcod]	6–429
			<i>Lepidonotothen squamifrons</i> (Günther, 1880) [grey rockcod]	10–900
			<i>Notothenia coriiceps</i> Richardson, 1844 [black rockcod]	0–550
			<i>Notothenia neglecta</i> Nybelin, 1951 [yellowbelly rockcod]	1–95‡
			<i>Notothenia rossii</i> Richardson, 1944 [marbled rockcod]	5–350
			<i>Nototheniops larseni</i> (Lönnberg, 1905) [painted notie]	30–750
			<i>Nototheniops nudifrons</i> (Lönnberg, 1905) [yellowfin notie]	3–400
			<i>Trematomus bernacchii</i> Boulenger, 1902 [emerald rockcod]	0–700
<i>Neolebouria georgiensis</i> Gibson, 1976§	Perciformes Bleeker, 1863	Bathydraconidae Regan, 1913 [Antarctic dragonfishes]	<i>Trematomus eulpidotus</i> Regan, 1914 [blunt scalyhead]	70–650
			<i>Trematomus hansonii</i> Boulenger, 1902 [striped rockcod]	6–549
			<i>Trematomus newnesi</i> Boulenger, 1902 [dusky rockcod]	0–400
			<i>Parachaenichthys charcoti</i> (Vaillant, 1906) [Antarctic dragonfish]	5–400
			<i>Parachaenichthys georgianus</i> (Fischer, 1885) [Antarctic dragonfish]	5–270

Table IV. Continued.

Parasite species	Host order†	Host family†	Host species†	Known depth range (m)†
		Channichthyidae Gill, 1861 [crocodile icefishes]		
			<i>Chionocephalus aceratus</i> (Lönnberg, 1906) [blackfin icefish]	5–770
			<i>Champsoscephalus gunnari</i> Lönnberg, 1905 [mackerel icefish]	0–700
			<i>Chionodracon hamatus</i> (Lönnberg, 1905) [crocodile icefish]	4–600
			<i>Chionodracon rastrispinosus</i> DeWitt and Hureau, 1979 [ocel- lated icefish]	0–1,000
			<i>Pagetodus antarcticus</i> (Dollo, 1900) [long-fingered icefish]	90–600
			<i>Pseudochannichthys georgianus</i> Norman, 1937 [South Georgia icefish]	0–475
		Nototheniidae Günther, 1861 [cod icefishes]		
			<i>Dissostichus eleginoides</i> Smitt, 1898 [Patagonian toothfish]	0–2,144
			<i>Notothenia coriiceps</i> Richardson, 1844 [black rockcod]	0–550
			<i>Notothenia rossii</i> Richardson, 1844 [marbled rockcod]	5–350
			<i>Trematomus hansonii</i> Boulenger, 1902 [striped rockcod]	6–549
			<i>Trematomus newnesi</i> Boulenger, 1902 [dusky rockcod]	0–400
<i>Neolebouria leiognathi</i> (Wang, Wang and Zhang, 1992) Bray, 2002	Acanthuriformes Jordan, 1923	Leiognathidae Gill, 1893 [slimys, slipmouths, ponyfishes]	<i>Deveximentum ruconius</i> (Hamilton, 1822) [deep pugnose ponyfish]	3–60‡
<i>Neolebouria maorum</i> (Allison, 1966) Gibson, 1976	Octopoda Leach, 1818	Octopodidae Orbigny, 1839 [octopuses]	<i>Macroctopus maorum</i> (Hutton, 1880) [Maori octopus] <i>Octopus australis</i> Hoyle, 1885 [hammer octopus]	0–549 3–140‡
<i>Neolebouria merretti</i> Gibson and Bray, 1982	Aulopiformes Rosen, 1973	Ipnopidae Gill, 1884 [deep-sea tripod fishes]	<i>Bathytrophops sewelli</i> (Norman, 1939) [deep-sea tripod fish]	2,980–4,200
<i>Neolebouria mullineuxae</i> n. sp.	Perciformes Bleeker, 1863	Zoaridae Swainson, 1839 [eelpouts]	<i>Thermarces cerberus</i> Rosenblatt and Cohen, 1986 [eelpout]	2,300–2,630
<i>Neolebouria terranovaensis</i> Zdzitowiecki, Pisano and Vacchi, 1993§	Gadiformes Goodrich, 1909	Muraenolepididae Regan, 1903 [eel cods]	<i>Muraenolepis marmorata</i> Günther, 1880 [marbled moray cod]	30–1,600
	Perciformes Bleeker, 1863	Artedidraconidae Eakin, 1988 [barbled plunderfishes]	<i>Pogonophryne scotti</i> Regan, 1914 [saddleback plunderfish]	100–1,180
		Bathydraconidae Regan, 1913 [Antarctic dragonfishes]		

Table IV. Continued.

Parasite species	Host order†	Host family‡	Host species†	Known depth range (m)†
		Channichthyidae Gill, 1861 [crocodile icefishes]	<i>Cynodraco mawsoni</i> Waite, 1916 [Mawson's dragonfish] <i>Gymnodraco acuticeps</i> Boulenger, 1902 [ploughfish]	110–300 0–550
		Liparidae Gill, 1861 [snailfishes]	<i>Chionodraco hamatus</i> (Lönnberg, 1905) [crocodile icefish] <i>Pagetodes antarcticus</i> (Dollo, 1900) [long-fingered icefish]	4–600 90–600
		Nototheniidae Günther, 1861 [cod icefishes]	<i>Paraliparis antarcticus</i> Regan, 1914 [snailfish]	300–782
			<i>Notothenia coriiceps</i> Richardson, 1844 [black rockcod] <i>Trematomus bernacchii</i> Boulenger, 1902 [emerald rockcod] <i>Trematomus hansonii</i> Boulenger, 1902 [striped rockcod] <i>Trematomus newnesi</i> Boulenger, 1902 [dusky rockcod] <i>Trematomus pennellii</i> Regan, 1914 [sharp-spined notothenia]	0–550 0–700 6–549 0–400 0–732

* The deep sea is defined as ocean waters that are ≥ 200 m in depth (Marshall, 1979).
† Based on Froese and Pauly (2024) and Palomares and Pauly (2024).
‡ Not a deep-water species.
§ While Martin et al. (2018a) recognized *N. terranovaensis*, WoRMS (2025) lists this species as a junior synonym of *N. georgiensis*.
|| For this study, *N. mullineauxae* n. sp. was found in *T. cerberus* at 2,491–2,519-m depth.

Pacific Ocean along the East Pacific Rise and Galápagos Rift (Froese and Pauly, 2024). We documented a variety of prey items from *T. cerberus* examined including identified gastropods (*Cyathernia* Warén and Bouchet, 1989 [cf. *Cyathernia naticoides* Warén and Bouchet, 1989]; *Lepetodrilus* McLean, 1988 [cf. *L. elevatus* McLean, 1988]) and crustaceans (*Dahlella* Hessler, 1984; *Ventiella sulfuris* Barnard and Ingram, 1990) as well as unidentified pieces of amphipods, copepods, other crustaceans (shrimp carapace and megalope larvae), polychaetes and partially degraded chaetae (chitinous bristles of an annelid worm). Bray (2020) and Bray et al. (1999) noted that opecoelid digeneans utilize gastropods as the first intermediate host, and amphipods, decapods, mysids, and fish are second or subsequent intermediate hosts. Indeed, Zdzitowiecki (1997) reported *N. antarctica* from the mysid, *Antarctomysis maxima* (Holt and Tattersall, 1906) (Malacostraca: Mysidae). Furthermore, Dykman et al. (2025), as part of an ongoing study of parasites utilizing heteroxenous life cycles along the EPR, provided molecular evidence to demonstrate that the sporocyst stage (SPOR01) of *N. mullineauxae* (DIGE08) utilizes the glass limpet, *Eulepetopsis vitrea* McLean, 1990 (Gastropoda: Neolepetopsidae), as a first intermediate host. As the diet of *T. cerberus* overlaps some of these groups of organisms that can serve as second or subsequent intermediate hosts (e.g., amphipod [*Ventiella*] and decapod [shrimp and megalope (crab)] crustacean species), *N. mullineauxae* may utilize some or all of these hosts along with *E. vitrea* and *T. cerberus* to complete its life cycle among the hydrothermal vents of the East Pacific Rise (see also Dykman et al., 2023a, 2023b; Moravec et al., 2023).

Molecular phylogeny of *Neolebouria*

Although molecular data from the genus *Neolebouria* are sparse, we can conclude that *N. mullineauxae* is very closely related to *N. georgiensis*, which has been recorded in the Antarctic dragonfish and blackfin icefish off South Georgia in the sub-Antarctic. The geographic and ecological distance of the host species is remarkable for such closely related parasite species. Deep-sea vents are extremely isolated systems with endemic fauna that have adapted to specialize in the harsh thermal and chemical environment, so it is unlikely there is much interaction or exchange between these species in the present era; however, they presumably shared a recent ancestor. The lack of sequences from other *Neolebouria* species unfortunately limits the conclusions we might draw about the origins of diversity within *Neolebouria*. The only other *Neolebouria* sequence available was for *N. maorum*, which was quite short and could not be placed in full phylogenetic context, but the overlapping genetic area did not match closely to the other *Neolebouria* species, indicating the genus may still be polyphyletic. *Mesobathylebouria lanceolata*, which has previously been classified as *Neolebouria*, does not cluster with the 2 *Neolebouria* specimens for which we have high-quality sequences. The high morphological similarity yet genetic distance between these 2 genera suggests that genetic evidence will be critical to include in future species descriptions within either genus to prevent further taxonomic confusion. Genetic evidence proved important for our study in several ways, not only because Morphotypes A and B would have been classified as separate species morphologically (i.e., ventral sucker size) yet were genetically identical, but also because, initially, our material appeared to group morphologically with *Mesobathylebouria*.

Examination of *Mesobathylebouria*

Morphological and ecological comparison: It is important to mention that, based on morphological features, we had previously identified the new species described herein as a member of *Mesobathylebouria* (Opecoelidae), a genus established by Martin et al. (2018a) for species of *Neolebouria* that are morphologically similar to *Neolebouria* (*sensu stricto*) and found in marine fishes from the lower epipelagic (100–200 m) to the mesopelagic zone (200–1,000 m) (see Marshall, 1979). Furthermore, *Mesobathylebouria* spp. are not known to parasitize notothenioids or other Antarctic and sub-Antarctic fishes (i.e., species of *Neolebouria* [*sensu stricto*]), yet our molecular evidence was quite conclusive that the new taxon belonged within *Neolebouria*. We feel that given this perceived incongruency between morphological and molecular observations as related to *N. mullineauxae*, a thorough examination herein of *Mesobathylebouria* is warranted.

There are 5 species recognized within this genus: *Mesobathylebouria acanthogobii* (Yamaguti, 1951) Martin, Huston, Cutmore and Cribb, 2018 (syns. *Neolebouria acanthogobii* (Yamaguti, 1951) Gibson, 1976; *Plagioporus acanthogobii* Yamaguti, 1951); *Mesobathylebouria lanceolata* (type species) (syns. *Neolebouria lanceolata*; *Podocotyle lanceolata* Price, 1934); *Mesobathylebouria lobata* (Yamaguti, 1934) Martin, Huston, Cutmore and Cribb, 2018 (syns. *Lebouria lobata* Yamaguti, 1934; *Neolebouria lobata* [Yamaguti, 1934] Gibson, 1976; *Plagioporus lobata* [Yamaguti, 1934] Manter, 1947; *Plagioporus lobatus* [Yamaguti, 1934] Manter, 1947); *Mesobathylebouria tinkerbella* (Thompson and Margolis, 1987) Martin, Huston, Cutmore and Cribb, 2018 (syn. *Neolebouria tinkerbella* Thompson and Margolis, 1987); and *Mesobathylebouria tohei* (Yamaguti, 1970) Martin, Huston, Cutmore and Cribb, 2018 (syns. *Neolebouria tohei* [Yamaguti, 1970] Gibson, 1976; *Plagioporus tohei* Yamaguti, 1970; *Plagioporus* (*Plagioporus*) *tohei* Yamaguti, 1970; *Podocotyle tohei* [Yamaguti, 1970] Bartoli, Bray and Gibson, 2003) (see Price, 1934; Yamaguti, 1934, 1951, 1970; Thompson and Margolis, 1987; Martin et al., 2018a; WoRMS, 2025).

Species of *Mesobathylebouria* infect a diverse taxonomic array of definitive hosts, many of which are known from the deep sea (see Table V; Froese and Pauly, 2024; Palomares and Pauly, 2024). The 5 species of this genus have radiated into at least 12 orders of fish (Table V). This includes at least 17 families, 19 genera, and 22 species of fishes; 14 of which are known from the deep sea. *Mesobathylebouria lobata* has been reported from the greatest number of hosts, and unlike *Neolebouria*, there is no overlap in host species infected with ≥ 2 species of *Mesobathylebouria* (i.e., do not parasitize conspecific hosts); thus, we noted marked host specificity across species of this genus. At least 4 host species harboring *Mesobathylebouria* species are restricted to shallow waters (Froese and Pauly, 2024). The Azurio tuskfish, *Choerodon azurio* (Jordan and Snyder, 1901) (Eupercaria: Labridae), known to a depth of 50 m, was reported by Wang et al. (1992) to harbor *M. lanceolata* from Fujian Province, China. *Mesobathylebouria lobata* was found to parasitize the pyloric ceca and small intestine of the bluefin gurnard, *Chelidonichthys kumu* (Cuvier, 1829) (Perciformes: Triglidae) (depth range to 200 m), in Toyama Bay, Japan (Yamaguti, 1934). *Mesobathylebouria tinkerbella* was discovered in the intestine of 3 experimentally infected fish, 2 of which are restricted to depths of 200 m or less: the 3-spined stickleback, *Gasterosteus aculeatus*

Linnaeus, 1758 (Perciformes: Gasterosteidae) (depth range to 100 m); and the Pacific staghorn sculpin, *Leptocottus armatus* Girard, 1854 (Perciformes: Cottidae) (depth range to 156 m). These 3 hosts had been fed metacercariae found infecting the heart and somatic musculature of the cold-water prawn, ocean, or smooth pink shrimp, *Pandalus jordani* Rathbun, 1902 (Decapoda: Pandalidae), collected in the Barkley Sound off Vancouver Island, British Columbia, Canada (Thompson and Margolis, 1987).

Neolebouria mullineauxae shares striking ecological and morphological similarities to species of *Mesobathylebouria*. As noted earlier, members of *Mesobathylebouria* occur in a broad range of non-notothenioid fishes in deeper waters outside of Antarctic and sub-Antarctic waters; *N. mullineauxae* was found in a species of zoarcid eelpout from along the EPR at 2,491–2,519 m depth off the Pacific coast of Central America. Species of *Mesobathylebouria* generally differ morphologically from those of *Neolebouria* (*sensu stricto*), yet are similar to *N. mullineauxae* in having a less robust body, a dextro-submedian ovary and smooth testes in some species, and a cirrus pouch that does not extend posterior to the ventral sucker (Martin et al., 2017, 2018a).

However, *N. mullineauxae* can be distinguished from *Mesobathylebouria* spp. by a variety of morphological and allometric characters (see Tables I and VI), including body length, the sizes of particular features (e.g., testes, preovarian region, uterus, excretory vesicle, postcecal and posttesticular region [PTR] lengths, ventral sucker [Morphotype B], forebody, genital pore to anterior extremity and previtelline field lengths), the position of the intestinal bifurcation within the forebody, testes texture (i.e., smooth, indented, lobed), ovary lobation (i.e., smooth, indented, 3- to 4-lobed), and vitelline follicle distribution. The cirrus pouch relative to the ventral sucker extends primarily to the midlevel of the ventral sucker in *N. mullineauxae*, but in *M. acanthogobii*, *M. lobata*, and *M. tohei* the cirrus pouch is entirely preacetabular; whereas in *M. lanceolata* it extends to or slightly posterior to the posterior margin of the ventral sucker, and *M. tinkerbella* possesses a cirrus pouch of variable length, extending from the anterior margin of the ventral sucker to two-thirds the length of it. A saccate seminal vesicle was observed in *N. mullineauxae*, but this feature in *M. acanthogobii* is tubular and looped (cf. *M. lobata* [syns. *Plagioporus lobatus* (Yamaguti, 1934) Manter, 1947; *Neolebouria lobata* (Yamaguti, 1934) Gibson, 1976]), convoluted in *M. lobata* (described by Yamaguti, 1951, p. 249 as ‘looped’ and cf. *M. acanthogobii*), *M. tinkerbella* has a bipartite seminal vesicle consisting of an ovoid proximal portion and a longer, tubular, distal portion that is recurved at the junction with the proximal portion to form a loop on the right side of the latter (Thompson and Margolis, 1987, fig. 2), and this feature in *M. tohei* is fusiform to elliptical or sigmoid. A pars prostatica is absent in *M. acanthogobii* and *M. lobata*. Eggs are few to moderate in number and $76\text{--}104 \times 34\text{--}52$ in size in *N. mullineauxae*; however, in *M. acanthogobii*, *M. lanceolata*, *M. lobata*, and *M. tohei* the eggs are numerous and $63\text{--}78$ long, 56×30 , 63 and $46\text{--}63$ long, respectively; *M. tinkerbella* has an egg with a small, rounded knob at the anopercular pole measuring $5\text{ }\mu\text{m}$ wide. Well-developed cervical glands with ducts containing fine secretory particles and a distinctly muscular esophagus are seen in *M. tohei* (see Yamaguti, 1970, fig. 72A)—neither are in the new species. Unique in *M. tinkerbella* is the “possible existence of muscular attachments between [the] posterior end of [the] ceca and excretory vesicle, but no

Table V. Hosts of species of *Mesobathylebouria* Martin, Huston, Cutmore and Cribb, 2018 known to inhabit the deep sea*.

Parasite species	Host order†	Host family†	Host species†	Known depth range (m)†
<i>Mesobathylebouria acanthogobii</i> (Yamaguti, 1951) Martin, Huston, Cutmore and Cribb, 2018	Cypriniformes Bleeker, 1859	Xenocypridae Günther, 1868 [East Asian minnows]	<i>Xenocypris macrolepis</i> Bleeker, 1871 [yellowfin]	—‡
	Gobiiformes Günther, 1880	Gobiidae Cuvier, 11816 [gobies]	<i>Acanthogobius hasta</i> (Temminck and Schlegel, 1845 [goby]) <i>Amblychaeturichthys hexanema</i> (Bleeker, 1853) [goby]	—‡
	Lophiiformes Garman, 1899	Chaunacidae Gill, 1863 [sea toads, coffinfishes]	<i>Chaunax pictus</i> Lowe, 1846 [pink frogmouth]	200–1,000
	Tetraodontiformes Berg, 1940	Ostraciidae Rafinesque, 1810 [boxfishes]	<i>Ostracion cubicum</i> Linnaeus, 1758 [yellow boxfish]	1–280
	Eupercaria incertae sedis	Labridae Cuvier, 1816 [wrasses]	<i>Choerodon azurio</i> (Jordan and Snyder, 1901) [Azurio tuskfish]	8–50§
<i>Mesobathylebouria lanceolata</i> (Price, 1934) Martin, Huston, Cutmore and Cribb, 2018§	Polymixiiformes Rosen and Patterson, 1969	Polymixiidae Bleeker, 1859 [beardfishes]	<i>Polymixia lowei</i> Günther, 1859 [beardfish] <i>Polymixia nobilis</i> Lowe, 1836 [stout beardfish] <i>Polymixia</i> sp. [beardfish]	50–600 100–770 —
	Anguilliformes Berg, 1943	Congridae Kaup, 1856 [conger and garden eels]	<i>Gnathophtis nystromi</i> (Jordan and Snyder, 1901) [conger eel]	250–355
		Nettastomatidae Kaup, 1859 [duckbill eels]	<i>Venefica proboscidea</i> (Vallant, 1888) [whipsnout sorcerer]	385–2,200
		Ipnopidae Gill, 1884 [deep-sea tripod fishes]	<i>Bathypterois phenax</i> Parr, 1928 [blackfin spiderfish]	800–2,657
		Ophidiidae Rafinesque, 1810 [cusk-eels]	<i>Selachophidium guentheri</i> Gilchrist, 1903 [barbed brotula]	200–980
<i>Mesobathylebouria lobata</i> (Yamaguti, 1934) Martin, Huston, Cutmore and Cribb, 2018		Hoplichthyidae Kaup, 1873 [ghost flatheads]		

Table V. Continued.

Parasite species	Host order†	Host family†	Host species‡	Known depth range (m)†
<i>Mesobathylebouria tinkerbellae</i> (Thompson and Margolis, 1987) Martin, Huston, Cutmore and Cribb, 2018	Stomiiformes Regan, 1909	Triglidae Rafinesque, 1815 [searobins]	<i>Hoplichthys acanthopleurus</i> Regan, 1908 [ghost flathead]	120–457
			<i>Chelidonichthys kumu</i> (Cuvier, 1829) [bluefin gurnard]	1–200§
			<i>Chelidonichthys spinosus</i> (McClelland, 1844) [spiny red gurnard]	25–615
	Zeiformes Regan, 1909	Phosichthyidae Weitzman, 1974 [lightfishes]	<i>Polymetme corythaeola</i> (Alcock, 1898) [rendezvous fish]	165–800
			<i>Zeus faber</i> Linnaeus, 1758 [John dory]	5–400
	Perciformes Bleeker, 1863	Cottidae Bonaparte, 1831 [sculpins]	<i>Leptocottus armatus</i> Girard, 1854 [Pacific staghorn sculpin]	0–156§ #
			Gasterosteidae Bonaparte, 1831 [sticklebacks and tubenouts]	0–100§ #
		Pleuronectiformes Refinesque, 1815	Pleuronectidae Cuvier, 1816 [righteye flounders]	<i>Gasterosteus aculeatus</i> Linnaeus, 1758 [three-spined stickleback]
	<i>Platichthys stellatus</i> (Pallas, 1787) [starry flounder]			0–375#
	<i>Mesobathylebouria tohei</i> (Yamaguti, 1970) Martin, Huston, Cutmore and Cribb, 2018	Anguilliformes Berg, 1943	Congridae Kaup, 1856 [conger and garden eels]	<i>Conger</i> sp. [conger eel]

* The deep sea is defined as ocean waters that are ≥ 200 m in depth (Marshall, 1979).

† Based on Froese and Pauly (2024) and Palomares and Pauly (2024).

‡ Depth information not provided in Froese and Pauly (2024).

§ Not a deep-water species.

|| Price (1934) described *M. lanceolata* (syn. *Podocotyle lanceolata* Price, 1934) from the intestine of an unidentified species of *Polymixia* Lowe, 1836 (Polymixiiformes: Polymixiidae) found off Puerto Rico. He did not provide any depth information for this host, but we infer that the fish was caught in deeper waters as this parasite was collected on the Johnson-Smithsonian Deep-Sea Expedition to the Puerto Rican Deep.# Thompson and Margolis (1987) experimentally infected this fish species with *M. tinkerbellae* having fed it metacercariae found parasitizing the heart and somatic musculature of the cold-water prawn, ocean, or smooth pink shrimp, *Pandalus jordani* Rathbun, 1902 (Decapoda: Pandalidae), from Barkley Sound off Vancouver Island, British Columbia, Canada.¶ Yamaguti (1970) described *M. tohei* (syn. *Plagioporus [Plagioporus] tohei* Yamaguti, 1970) from the intestine of an unidentified conger eel species of *Conger* Bosc, 1817 (Anguilliformes: Congridae) found off Hawaii, and he mentioned that the local name for this fish was “tohei.” Using this common name, Froese and Pauly (2024) identify this fish as the Hawaiian mustache conger, *Conger marginatus* Valenciennes, 1850 (Anguilliformes: Congridae); however, no depth information was provided for this species.

Table VI. Dimensions of the 5* species of *Mesobathylebouria* Martin, Huston, Cutmore and Cribb, 2018 recognized prior to this study.†

Parasite	<i>M. acanthogobii</i> (Yamaguti, 1951, fig. 2)	<i>M. lanceolata</i> (Price, 1934, fig. 5)	<i>M. lobata</i> (Yamaguti, 1934, fig. 16)	<i>M. tinkerbella</i> (Thompson and Margolis, 1987, figs. 1–3)	<i>M. tohei</i> (Yamaguti, 1970, fig. 72)
n =	‡§	3+§	3§	17	25
Body L	1,500–3,400†	1,950–2,000	1,140 {1,400 and 1,470}#	1,440–2,680 (2,010)	1,400–1,900
Body W	650–1,000	645–850	600	370–550 (450)	600–700
Forebody L	780	508	316	566	584
Hindbody L	1,350	1,314	611	1,183	754
OS L	160–225	195	110 {130}#	122–181 (153)	180–220
OS W	170–250	100–189	150 {170}#	126–185 (147)	180–240
Prepharynx L	10	0		16–39 (25)	21
Pharynx L	84–110	88–100	63 {74–84}#	81–118 (99)	100–160
Pharynx W	75–120	88	74 {80–95}#	70–104 (85)	90–140
Esophagus L	50–80	160–200	53 {74–120}#	120–238 (170)	110–260
Intestinal bifurcation anterior to VS	320	42	57	100	106
Postcecal region L	100	212	155	59–148 (105)	117
VS L	250–330	220–240	210 {230–240}#	215–307 (244)	298
VS W	270–380	240–280	270 {290–320}#	233–315 (261)	310–370
AT L	150–310 (both testes)	160	150	141–226 (184)	140–320 (both testes)
AT W	370–580 (both testes)	260–280	330	159–252 (207)	130–260 (both testes)
PT L		160–180	140	144–255 (201)	
PT W		260–320	249	170–255 (216)	
PTR L	60–400	576	181	367	149
PTR W at midpoint	540	373	389	258	319
CP L	330–600	400	180	211–344 (286)	200–450
CP W	70–95	100–120	53	59–93 (73)	60–100
Seminal vesicle L				51–137 (94) (proximal portion)	
Seminal vesicle W	50–80			36–78 (54) (proximal portion)	55–90
Pars prostatica L				112	
Pars prostatica W				15	
Ejaculatory duct L				38	
Ejaculatory duct W				6	
GP to lateral margin	100	59	88	50	64
GP anterior to VS	430	153	145	217	213
GP to anterior extremity	390	364	192	367	468
Preovarian region L	1,380	966	653	1,050	1,031
OV L	210–350	140	130	89–211 (144)	60–150
OV W	100–240	240–320	170	141–266 (199)	120–200
VS to OV L	320	254	119	258	159
Seminal receptacle L				132	
Seminal receptacle W	84			46–75 (58)	42
Vitelline follicle L	20–80 (46) [n = 5]†	34–59 (47) [n = 5]	21–47 (33) [n = 5]	25–50 (42) [n = 5]	32–64 (45) [n = 5]
Vitelline follicle W	20–50 (34) [n = 5]	25–34 (29) [n = 5]	16–31 (23) [n = 5]	17–50 (33) [n = 5]	11–43 (30) [n = 5]
Previtelline field L	350	492	140	400	510
Postvitelline field L	30	127	16	42	21
Vitelline reservoir L	120			55–127 (84)	
Vitelline reservoir W	100			29–68 (47)	
Uterus L	1,290	703	518	692	669
Uterus W	730	220	202	183	308
PUR L	860	924	451	917	574
Egg L	63–78	56	63	85–111 (98)	46–63
Egg W	39–45	30	39	33–48 (43)	35–42
Excretory vesicle L	950		451	900	563
Excretory vesicle W	100		67	50	74
Body W %‡	29.4–43.3%	33.1–42.5%	52.6%	20.5–25.7%	36.8–42.9%
Forebody L %‡	31.8%	~25.2%	27.7%	28.8%	35.7%
OS L %‡	6.6–10.7%	9.7%	9.6%	6.8–8.5%	11.6–12.9%
Pharynx L %‡	3.2–5.6%	4.5–5.0%	5.5%	4.4–5.6%	7.1–8.4%
OS:pharynx W ratio	1:2.08–2.27	1:1.64	1:2.03	1:1.78–1.80	1:1.71–2.00
Esophagus L %‡	2.4–3.3%	8.2–10.0%	4.6%	8.3–8.9%	7.9–13.7%
VS L %‡	9.7–16.7%	11.3–12.0%	18.4%	11.5–14.9%	18.2%
Sucker W ratio	1:1.40–1.60	1:1.48–2.40	1:1.80	1:1.50–2.12 (1:1.78)	1:1.40–2.40
CP L %‡	17.6–22.0%	20.3%	15.8%	12.8–14.7%	14.3–23.7%
AT L %‡	9.1–10.0% (both testes)	8.1%	13.2%	8.4–9.8%	10.0–16.8% (both testes)
PT L %‡		8.2–9.0%	12.3%	9.5–10.0%	
PTR L %‡	4.0–11.8%	28.6%	15.9%	18.7%	9.1%

Table VI. Continued.

Parasite	<i>M. acanthogobii</i> (Yamaguti, 1951, fig. 2)	<i>M. lanceolata</i> (Price, 1934, fig. 5)	<i>M. lobata</i> (Yamaguti, 1934, fig. 16)	<i>M. tinkerbellae</i> (Thompson and Margolis, 1987, figs. 1–3)	<i>M. tohei</i> (Yamaguti, 1970, fig. 72)
OV L %‡	10.3–14.0%	7.1%	11.4%	6.2–7.9%	4.3–7.9%
VS to OV L %‡	13.1%	12.6%	10.4%	13.1%	9.7%
Previtelline field L %‡	14.3%	24.4%	12.3%	20.3%	31.2%
Postvitelline field L %‡	1.2%	6.3%	1.4%	2.1%	1.3%
PUR L %‡	35.1%	45.8%	39.6%	46.6%	35.1%

* Based on WoRMS (2025).

† AT, anterior testis; CP, cirrus pouch; GP, genital pore; L, length; OS, oral sucker; OV, ovary; PT, posterior testis; PTR, posttesticular region; PUR, postuterine region; VS, ventral sucker; W, width; ranges followed by mean in parentheses where applicable; number [n] of measurements provided if different from total number of worms examined.

‡ Proportion of body length.

§ Yamaguti (1951, p. 249) did not give number of specimens examined; only “[n]umerous gravid specimens fixed in acetic sublimate . . .”. Price (1934) listed accession numbers for a holotype and paratypes but did not provide a specific number of specimens examined. Yamaguti (1934) gave dimensions for 1 holotype and 2 paratypes; values given in table are from holotype specimen unless otherwise indicated (see below).

|| Due to suspected error(s) in the published scale bar values and/or because this information was not provided in the description, we calculated these measurements and allometries from Yamaguti (1934, fig. 16; 1951, Plate 1, fig. 2; 1970, figs. 72A,B), Price (1934, Plate 1, fig. 5), or Thompson and Margolis (1987, figs. 1–3).

Measurements in {} are from 2 paratypes of *M. lobata* described by Yamaguti (1934).

actual connection [is] present between ceca and excretory vesicle” (see Thomas and Margolis, 1987, p. 190), and although *N. mulleuxae* possesses an intercecal uterus, *M. acanthogobii* has uterine loops that are extracecal ventrally and separated from the body margin by a narrow band of vitelline follicles (see Yamaguti, 1951, fig. 2). Finally, the new species has a terminal excretory pore, but this feature is dorsoterminal in *M. acanthogobii* and *M. tohei* [note: excretory pore of *M. tohei* is terminal in Yamaguti, 1970, fig. 72A].

Molecular comparison: We recognized only 1 gene sequence on GenBank for this genus; a partial sequence of the 28S rDNA gene from *M. lanceolata* (syn. *Neolebouria lanceolata* Price, 1934) submitted by Andres et al. (2014). When Martin et al. (2018a, fig. 1) established *Mesobathylebouria*, they used this gene sequence with many others to generate a phylogram that showed *M. lanceolata* to couple with another deep-sea opecoelid trematode, *Abyssopedunculus brevis* (Andres and Overstreet, 2013) Martin, Huston, Cutmore and Cribb, 2018 (syn. *Podocotyloides brevis* Andres and Overstreet, 2013), which was collected from the intestine of the grey conger, *Conger esculentus* Poey, 1861 (Anguilliformes: Congridae), found at 200-m depth in the Caribbean Sea off Mayagüez, Puerto Rico (Andres and Overstreet, 2013). Martin et al. (2018a) conceded that both species remained inadequately accommodated, and although both taxa are sister to the Stenakrinae Yamaguti, 1970, they may require a new subfamily; however, it was unclear which morphological and/or ecological characters would distinguish this latter group. Sokolov et al. (2020, fig. 2) partially sequenced the 28S rDNA gene from the deep-water digenean, *Tellervotrema beringi* (Mamaev, 1965) Gibson and Bray, 1982 (Opecoelidae: Podocotylineae), found in the intestine of the finescale mora, *Antimora microlepis* Bean, 1890 (Gadiformes: Moridae), collected off the Kuril Islands in the Northwest Pacific Ocean. They found *T. beringi* to cluster with *M. lanceolata* and *A. brevis* (i.e., “Clade D”), still sister to the Stenakrinae, and probably represented a separate subfamily as postulated by Martin et al. (2018a). However, morphological synapomorphies of “Clade D” remained elusive, and Sokolov

et al. (2020) noted that members of this group parasitize fishes from a wide range of depths from sublittoral and reef associated to bathydemersal and bathypelagic hosts, making ecological characterization very ambiguous. More recently, Sokolov et al. (2022) reassessed the status of the Stenakrinae using, in part, specimens identified as belonging to the type species, *Stenakron vetustum* Stafford, 1904 and found it to be distinct from the Stenakrinae *sensu* Martin et al. (2018a). They raised the subfamily to family rank, Stenakridae Yamaguti, 1970, erected the Zdzitowieckitrematidae Sokolov, Shchenkov, Frolov and Gordeev, 2022, and renamed the Stenakrinae *sensu* Martin et al. (2018a), the Scorpidotrematidae Sokolov, Shchenkov, Frolov and Gordeev, 2022 within the Opecoelidae.

In light of the molecular evidence just presented demonstrating a close phylogenetic relationship between *Tellervotrema* Gibson and Bray, 1982 and *Mesobathylebouria* (members of “Clade D”), we noted in the new species of *Neolebouria* described herein as well as in recognized species of *Mesobathylebouria* either a complete (*M. acanthogobii*, *M. lobata*, *M. tinkerbellae*) or partial (*M. tohei*) interruption or gap in the distribution of vitelline follicles at the level of the ventral sucker reminiscent of species of *Tellervotrema* (see Gibson and Bray, 1982; Cribb, 2005). Indeed, 1 of us (C.K.B.) has worked with *Tellervotrema* and found the interruption in the distribution of vitelline follicles at the level of the ventral sucker to be a consistent character across the 3 species currently recognized in this genus: *Tellervotrema armstrongi* Gibson and Bray, 1982; *T. beringi*; and *Tellervotrema katadara* (Kuramochi, 2001) Kuramochi, 2009 (see Blend et al., 2012, 2015; WoRMS, 2025). *Abyssopedunculus brevis*, the type and only species of *Abyssopedunculus* Martin, Huston, Cutmore, and Cribb, 2018, does not exhibit this gap in the vitelline follicles lateral to the ventral sucker; follicles extend anteriorly to a level about midway between the ventral sucker and the ovary and run to the posterior end of the body (Andres and Overstreet, 2013, fig. 1). Ironically, the 1 species in *Mesobathylebouria* that does not exhibit this feature is the type species, *M. lanceolata* (see Price, 1934, fig. 5)—the 1 species for which molecular sequence

data are available. Molecular analyses of more genes and species from all 4 genera, *Abyssopendunculus*, *Mesobathylebouria*, *Neolebouria*, and *Tellervotrema*, are strongly encouraged to elucidate their phylogenetic relationships (i.e., is a new subfamily needed). We also support further studies focusing on the ecology and fine morphological details (e.g., contents of cirrus pouch and ovarian complex of *A. brevis* and *M. lanceolata*—see Sokolov et al., 2020) of relevant taxa needed for the pursuit of these questions.

Future work

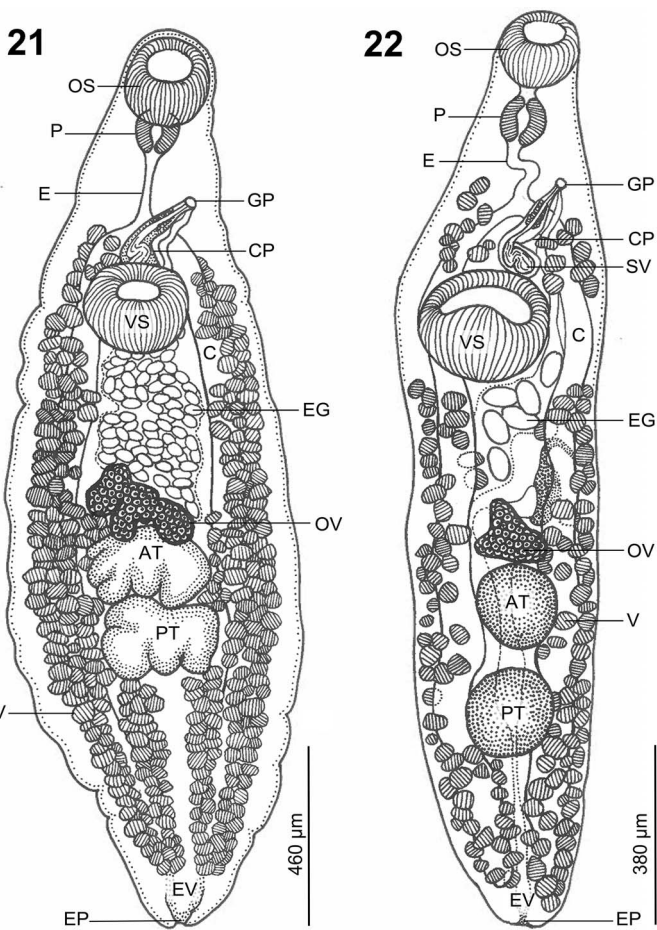
By adding more “sediment” to already “turbid waters,” we feel our overall findings herein— both molecular and morphological— may have further contributed to the “poor taxonomic and phylogenetic visibility” within this group of opecoelids. At present, there is a lack of a definitive diagnostic combination of morphological characters to distinguish species of *Neolebouria* from *Mesobathylebouria*. Our molecular observations found *N. mullineauxae* belongs within *Neolebouria*. However, *N. mullineauxae* possesses a combination of morphological features (see the foregoing) that are more in line with *Mesobathylebouria*. Ecologically, *N. mullineauxae* is more similar to *Mesobathylebouria* in that it does not parasitize notothenioids or other Antarctic and sub-Antarctic fishes; however, the new species is found from depths significantly greater than species of *Mesobathylebouria* (2,491–2,519 m vs. 100–1,000 m) and from a unique habitat (hydrothermal vents). As concluded by Martin et al. (2018a) and Sokolov et al. (2020) in their comparison of *M. lanceolata*, *A. brevis*, and *T. beringi* (i.e., “Clade D”; see the foregoing), we, too, concede that it is unclear which morphological, and to a slightly lesser extent, ecological characters distinguish species of *Neolebouria* from *Mesobathylebouria*. More studies, especially inclusive of a wider range of morphological observations from recognized species of both genera, are needed to help illuminate morphological synapomorphies and, resultantly, contribute to “clearing the waters.”

At present, there is some, albeit weak, genetic evidence to suggest that *Neolebouria* may still be polyphyletic, as the short available sequence for *N. maorum* is genetically distant from the other two sequenced *Neolebouria* species. Unfortunately, there were not enough sequences available for *Mesobathylebouria* to determine whether it was monophyletic. Future collections of specimens in these 2 genera should contribute both morphological and genetic data, particularly in the 28S and ITS2 rDNA genetic regions, which are already represented in open databases. Finally, further genetic inquiry, such as the *cox1* gene, should be completed to explore the morphological separation of the 2 morphotypes of *N. mullineauxae* described in this study, as they may eventually be recognized as 2 species.

Given the close morphological similarities we observed between species of *Neolebouria* and *Mesobathylebouria* as well as the fact that we are not aware of any key to species within the latter genus, we present 1 here for the 5 species we recognize in *Mesobathylebouria* in hopes of helping future researchers.

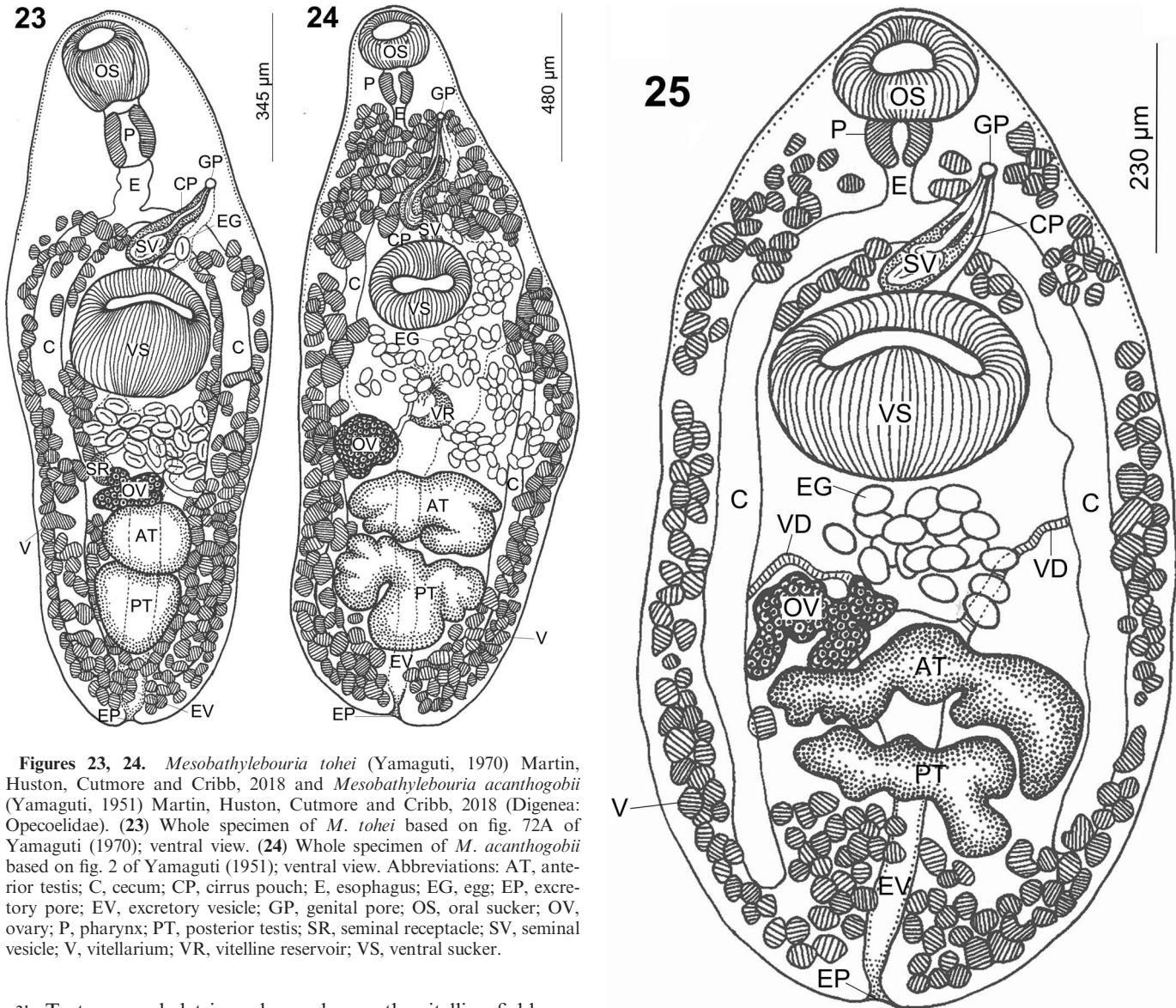
Key to Species of *Mesobathylebouria*

- 1a. Cirrus pouch either entirely anterior to ventral sucker or extends posteriorly as far as 2/3 of the length of sucker 2



Figures 21, 22. *Mesobathylebouria lanceolata* (Price, 1934) Martin, Huston, Cutmore and Cribb, 2018 and *Mesobathylebouria tinkerbellae* (Thompson and Margolis, 1987) Martin, Huston, Cutmore and Cribb, 2018 (Digenea: Opecoelidae). (21) Whole specimen of *M. lanceolata* based on fig. 5 of Price (1934); ventral view. (22) Whole specimen of *M. tinkerbellae* based on fig. 1 of Thompson and Margolis (1987); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SV, seminal vesicle; V, vitelline; VS, ventral sucker.

- 1b. Cirrus pouch extends to posterior margin of ventral sucker or slightly posterior to it
..... *Mesobathylebouria lanceolata* (Price, 1934) Martin, Huston, Cutmore and Cribb, 2018 [type species of genus] (syns. *Neolebouria lanceolata* (Price, 1934) Reimer, 1987; *Podocotyle lanceolata* Price, 1934) (Fig. 21; egg size: 56 × 30)
- 2a. Pars prostatica indistinct, not well differentiated, though prostatic cells present 3
- 2b. Pars prostatica distinct, well-differentiated
..... *Mesobathylebouria tinkerbellae* (Thompson and Margolis, 1987) Martin, Huston, Cutmore and Cribb, 2018 (syn. *Neolebouria tinkerbellae* Thompson and Margolis, 1987) (Fig. 22; egg size, 85–111 × 33–48)
- 3a. Testes transversely elongate and conspicuously lobed; vitelline fields extend anterior to level of pharynx 4



Figures 23, 24. *Mesobathylebouria tohei* (Yamaguti, 1970) Martin, Huston, Cutmore and Cribb, 2018 and *Mesobathylebouria acanthogobii* (Yamaguti, 1951) Martin, Huston, Cutmore and Cribb, 2018 (Digenea: Opecoelidae). (23) Whole specimen of *M. tohei* based on fig. 72A of Yamaguti (1970); ventral view. (24) Whole specimen of *M. acanthogobii* based on fig. 2 of Yamaguti (1951); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SR, seminal receptacle; SV, seminal vesicle; V, vitellarium; VR, vitelline reservoir; VS, ventral sucker.

Figure 25. *Mesobathylebouria lobata* (Yamaguti, 1934) Martin, Huston, Cutmore and Cribb, 2018 (Digenea: Opecoelidae). Whole specimen based on fig. 16 of Yamaguti (1934); ventral view. Abbreviations: AT, anterior testis; C, cecum; CP, cirrus pouch; E, esophagus; EG, egg; EP, excretory pore; EV, excretory vesicle; GP, genital pore; OS, oral sucker; OV, ovary; P, pharynx; PT, posterior testis; SV, seminal vesicle; V, vitellarium; VD, vitelline duct; VS, ventral sucker.

- 3b. Testes rounded triangular and smooth; vitelline fields extend anterior to level of intestinal bifurcation
Mesobathylebouria tohei (Yamaguti, 1970) Martin, Huston, Cutmore and Cribb, 2018 (syns. *Neolebouria tohei* (Yamaguti, 1970) Gibson, 1976; *Plagioporus tohei* Yamaguti, 1970; *Plagioporus* (*Plagioporus*) *tohei* Yamaguti, 1970; *Podocotyle tohei* (Yamaguti, 1970) Bartoli, Bray and Gibson, 2003) (Fig. 23; egg size: 46–63 × 35–42).
- 4a. Body relatively larger, 1,500–3,400 × 650–1,000; uterus overreaching ceca laterally, approaching body wall; sucker width ratio 1:1.4–1.6
Mesobathylebouria acanthogobii (Yamaguti, 1951) Martin, Huston, Cutmore and Cribb, 2018 (syns. *Neolebouria acanthogobii* (Yamaguti, 1951) Gibson, 1976; *Plagioporus acanthogobii* Yamaguti, 1951) (Fig. 24; egg size: 63–78 × 39–45).
- 4b. Body relatively smaller, 1,140 × 600; uterus intercecal; sucker width ratio 1:1.8
Meosbathylebouria lobata (Yamaguti, 1934) Martin,

Huston, Cutmore and Cribb, 2018 (syns. *Lebouria lobata* Yamaguti, 1934; *Neolebouria lobata* (Yamaguti, 1934) Gibson, 1976; *Plagioporus lobata* (Yamaguti, 1934) Manter, 1947 [*lapsus*]; *Plagioporus lobatus* (Yamaguti, 1934) Manter, 1947) (Fig. 25; egg size: 63 × 39).

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LITERATURE CITED

- ALLISON, F. R. 1966. A new species of adult Allocreadiidae (Trematoda) from *Octopus maorum* Hutton. Records of the Canterbury Museum 8: 81–85. doi:10.5555/19670801931.
- ANDRES, M. J., AND R. M. OVERSTREET. 2013. A new species of *Podocotyloides* (Digenea: Opcoelidae) from the grey conger eel, *Conger esculentus*, in the Caribbean Sea. Journal of Parasitology 99: 619–623. doi:10.1645/12-155.1.
- ANDRES, M. J., E. E. PULIS, AND R. M. OVERSTREET. 2014. New genus of opcoelid trematode from *Pristipomoides aquilonaris* (Perciformes: Lutjanidae) and its phylogenetic affinity within the family Opcoelidae. Folia Parasitologica 61: 223–230. doi:10.14411/fp.2014.033.
- BLEND, C. K., N. O. DRONEN, S. L. GARDNER, G. R. RACZ, AND H. W. ARMSTRONG. 2012. The deep-sea fish digenean genus *Tellervotrema* Gibson & Bray, 1982 (Opcoelidae: Plagioporinae): Re-evaluation of the type species, *T. armstrongi* Gibson & Bray, 1982 and *T. beringi* (Mamaev, 1965). Zootaxa 3295: 1–29. doi:10.11646/zootaxa.3295.1.1.
- BLEND, C. K., T. KURAMACHI, AND N. O. DRONEN. 2015. Re-evaluation of *Tellervotrema katadara* (Kuramochi, 2001) Kuramochi, 2009 (Opcoelidae: Plagioporinae) and supplementary morphological data for *T. beringi* (Mamaev, 1965) Gibson & Bray, 1982 with new host and locality. Zootaxa 3986: 435–451. doi:10.11646/zootaxa.3986.4.3.
- BRAY, R. A. 2020. Digenean parasites of deep-sea teleosts: A progress report. International Journal for Parasitology: Parasites and Wildlife 12: 251–264. doi:10.1016/j.ijppaw.2020.01.007.
- BRAY, R. A., S. C. CUTMORE, AND T. H. CRIBB. 2023. Proposal of a new genus, *Doorochen* (Digenea: Lepocreadioidea), for reef-inhabiting members of the genus *Postlepidapedon* Zdzitowiecki, 1993. Parasitology International 93: 102710. doi:10.1016/j.parint.2022.102710.
- BRAY, R. A., AND J.-L. JUSTINE. 2009. Opcoelids (Platyhelminthes, Digenea) from the fork-tailed threadfin bream *Nemipterus furcosus* (Valenciennes, 1830) (Perciformes, Nemipteridae), with preliminary keys to the problematic genera *Macvicaria* Gibson et Bray, 1982 and *Neolebouria* Gibson, 1976. Acta Parasitologica 54: 218–229. doi:10.2478/s11686-009-0041-3.
- BRAY, R. A., D. T. J. LITTLEWOOD, E. A. HERNIOU, B. WILLIAMS, AND R. E. HENDERSON. 1999. Digenean parasites of deep-sea teleosts: A review and case studies of intrageneric phylogenies. Parasitology 119(Suppl.): S125–S144. doi:10.1017/S0031182000084687.
- BRAY, R., A. WAESCHENBACH, T. CRIBB, G. WEEDALL, P. DYAL, AND D. LITTLEWOOD. 2009. The phylogeny of the Lepocreadioidea (Platyhelminthes, Digenea) inferred from nuclear and mitochondrial genes: Implications for their systematics and evolution. Acta Parasitologica 54: 310–329. doi:10.2478/s11686-009-0045-z.
- BRAY, R. A., A. WAESCHENBACH, P. DYAL, D. T. J. LITTLEWOOD, AND S. MORAND. 2014. New digeneans (Opcoelidae) from hydrothermal vent fishes in the south eastern Pacific Ocean, including one new genus and five new species. Zootaxa 3768: 73–87. doi:10.11646/zootaxa.3768.1.5.
- BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83: 575–583. doi:10.2307/3284227.
- COLLINS, P. C., R. KENNEDY, AND C. L. VAN DOVER. 2012. A biological survey method applied to seafloor massive sulphides (SMS) with contagiously distributed hydrothermal-vent fauna. Marine Ecology Progress Series 452: 89–107. doi:10.3354/meps09646.
- CRIBB, T. H. 2005. Family Opcoelidae Ozaki, 1925. In Keys to the Trematoda, Volume 2, A. Jones, R. A. Bray, and D. I. Gibson (eds.). CAB International and Natural History Museum, London, U.K., p. 443–531. doi:10.1079/9780851995878.0443.
- CRIBB, T. H., G. R. ANDERSON, R. D. ADLARD, AND R. A. BRAY. 1998. A DNA-based demonstration of a three-host lifecycle for the Bivesiculidae (Platyhelminthes: Digenea). International Journal for Parasitology 28: 1791–1795. doi:10.1016/S0020-7519(98)00127-1.
- DE BURON, I., J. L. HUNDLEY, AND M. SEGONZAC. 2000. Report of gravid female acanthocephalans in zoarcid fish from EPR 13°N and of a potential amphipod intermediate host for this parasitic worm. International Ridge-Crest Research, Biological Studies 9: 14–15.
- DRONEN, N. O., C. K. BLEND, M. C. OSTROWSKI DE NÚÑEZ, S. K. MALHOTRA, AND N. JAISWAL. 2014. Keys to the species of *Neolebouria* Gibson, 1976 (Digenea: Opcoelidae: Plagioporinae), with a redescription of *Neolebouria truncata* (Linton, 1940). Systematic Parasitology 88: 213–225. doi:10.1007/s11230-014-9498-z.
- DYKMAN, L. N. 2023. Marine parasites in island-like disturbed habitats. Ph.D. Dissertation. Massachusetts Institute of Technology, Woods Hole, Massachusetts, 204 p.
- DYKMAN, L. N., L. S. MULLINEAUX, C. K. TEPOLT, AND A. M. KURIS. 2023a. Dissection data for metazoan parasites and other symbionts from vent-endemic host species collected from the 9°50'N deep-sea hydrothermal vent field. In Biological and Chemical Oceanography Data Management Office (BCO-DMO). (Version 2) Version Date 2023-05-11. K.

- Soenen and A. D. York (data mgrs.). Accessed 19 August 2024. doi:10.26008/1912/bco-dmo.879118.2.
- DYKMAN, L. N., C. K. TEPOLT, C. K. BLEND, AND L. S. MULLINEAUX. 2025. The discovery of indirect parasite life cycles at deep-sea hydrothermal vents. *Marine Ecology Progress Series* 755: 1–14. doi:10.3354/meps14789.
- DYKMAN, L. N., C. K. TEPOLT, A. M. KURIS, A. R. SOLOW, AND L. S. MULLINEAUX. 2023b. Parasite diversity at isolated, disturbed hydrothermal vents. *Proceedings of the Royal Society B* 290: 20230877. doi:10.1098/rspb.2023.0877.
- FALTÝNKOVÁ, A., S. GEORGIEVA, A. KOSTADINOVA, AND R. A. BRAY. 2017. Biodiversity and evolution of digeneans of fishes in the Southern Ocean. In *Biodiversity and Evolution of Parasitic Life in the Southern Ocean* (Parasitology Research Monographs, vol. 9), S. Klimpel, T. Kuhn, and H. Mehlhorn (eds.). Springer, Cham, Switzerland, p. 49–74. doi:10.1007/978-3-319-46343-8_5.
- FALTÝNKOVÁ, A., O. KUDLAI, O. O. SALGANSKIY, E. M. KOROL, AND T. A. KUZMINA. 2022. Trematodes from Antarctic teleost fishes off Argentine Islands, West Antarctica: Molecular and morphological data. *Systematic Parasitology* 99: 491–523. doi:10.1007/s11230-022-10041-9.
- FROESE, R., AND D. PAULY (eds.). 2024. FishBase (version 10/2024). Available at: www.fishbase.org. Accessed 20 January 2025.
- GIBSON, D. I. 1976. Monogenea and Digenea from fishes. *Discovery Reports* 36: 179–266.
- GIBSON, D. I., AND R. A. BRAY. 1982. A study and reorganization of *Plagioporus* Stafford, 1904 (Digenea: Opecoelidae) and related genera, with special reference to forms from European Atlantic waters. *Journal of Natural History* 16: 529–559. doi:10.1080/00222938200770431.
- GOUJON, M., H. MCWILLIAM, W. LI, F. VALENTIN, S. SQUIZZATO, J. PAERN, AND R. LOPEZ. 2010. A new bioinformatics analysis tools framework at EMBL–EBI. *Nucleic Acids Research* 38(Suppl. 2): W695–W699. doi:10.1093/nar/gkq313.
- HOANG, D. T., O. CHERNOMOR, A. VON HAESELER, B. Q. MINH, AND L. S. VINH. 2018. Ufboot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35: 518–522. doi:10.1093/molbev/msx281.
- JAISSAL, N., S. K. UPADHYAY, A. MALHOTRA, C. K. BLEND, N. O. DRONEN, AND S. K. MALHOTRA. 2014. A new species of *Neolebouria* Gibson, 1976 (Opecoelidae: Plagioporinae) from the whitecheek monocle bream, *Scolopsis vosmeri* (Perciformes: Nemipteridae), from the Panjim coast at Goa, with a checklist of parasites previously reported from this fish. *Zootaxa* 3802: 98–108. doi:10.11646/zootaxa.3802.1.8.
- KALYAANAMOORTHY, S., B. Q. MINH, T. K. WONG, A. VON HAESELER, AND L. S. JERMIIN. 2017. Modelfinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. doi:10.1038/nmeth.4285.
- MACHIDA, M., AND J. ARAKI. 2002. Three new species of digenean trematodes found in deep-sea fishes of Japan and adjacent waters. *Bulletin of the National Science Museum, Series A (Zoology)* 28: 195–200.
- MAGRO, L., S. C. CUTMORE, M. CARRASSON, AND T. H. CRIBB. 2023. Integrated characterisation of nine species of the Schistorchiniinae (Trematoda: Apocreadiidae) from Indo-Pacific fishes: Two new species, a new genus, and a resurrected but ‘cryptic’ genus. *Systematic Parasitology* 100: 381–413. doi:10.1007/s11230-023-10093-5.
- MARSHALL, N. B. 1979. *Developments in Deep-Sea Biology*. Blandford Press Limited, Poole, U.K., 566 p.
- MARTIN, S. B., S. C. CUTMORE, AND T. H. CRIBB. 2017. Revision of *Neolebouria* Gibson, 1976 (Digenea: Opecoelidae), with *Trilobovarium* n. g., for species infecting tropical and subtropical shallow-water fishes. *Systematic Parasitology* 94: 307–338. doi:10.1007/s11230-017-9707-7.
- MARTIN, S. B., D. C. HUSTON, S. C. CUTMORE, AND T. H. CRIBB. 2018a. A new classification for deep-sea opecoelid trematodes based on the phylogenetic position of some unusual taxa from shallow-water, herbivorous fishes off south-west Australia. *Zoological Journal of the Linnean Society* 20: 1–29. doi:10.1093/zoolinnean/zly081.
- MARTIN, S. B., D. RIBU, S. C. CUTMORE, AND T. H. CRIBB. 2018b. Opistholobetines (Digenea: Opecoelidae) in Australian tetraodontiform fishes. *Systematic Parasitology* 95: 743–781. doi:10.1007/s11230-018-9826-9.
- MORAVEC, F., L. N. DYKMAN, AND D. B. DAVIS. 2023. Three new species of *Ascarophis* van Beneden, 1871 (Nematoda: Cystidicolidae) from deep-sea hydrothermal vent fishes of the Pacific Ocean. *Systematic Parasitology* 101: 2. doi:10.1007/s11230-023-10130-3.
- MORGAN, J. A. T., AND D. BLAIR. 1995. Nuclear rDNA ITS sequence variation in the trematode genus *Echinostoma*: An aid to establishing relationships within the 37-collar-spine group. *Parasitology* 111: 609–615. doi:10.1017/S003118200007709X.
- NGUYEN, L.-T., H. A. SCHMIDT, A. VON HAESELER, AND B. Q. MINH. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274. doi:10.1093/molbev/msu300.
- NOLAN, M. J., AND T. H. CRIBB. 2005. The use and implications of ribosomal DNA sequencing for the discrimination of digenean species. *Advances in Parasitology* 60: 101–163. doi:10.1016/S0065-308X(05)60002-4.
- PALOMARES, M. L. D., AND D. PAULY (eds.). 2024. SeaLifeBase (version 03/2024). Available at: www.sealifebase.org. Accessed 21 November 2024.
- PRICE, E. W. 1934. New digenetic trematodes from marine fishes. *Smithsonian Miscellaneous Collections* 91: 1–8.
- SIEVERS, F., AND D. G. HIGGINS. 2021. The clustal omega multiple alignment package. *Methods in Molecular Biology* 2231: 3–16. doi:10.1007/978-1-0716-1036-7_1.
- SOKOLOV, S., D. I. LEBEDEVA, I. I. GORDEEV, AND F. KHASANOV. 2019. *Zdzitowieckitrema incognitum* gen. et sp. nov. (Trematoda, Xiphidiata) from the Antarctic fish *Muraenolepis marmorata* Günther, 1880 (Gadiformes: Muraenolepidae): Ordinary morphology but unclear family affiliation. *Marine Biodiversity* 49: 451–462. doi:10.1007/s12526-017-0830-0.
- SOKOLOV, S. G., S. V. SHCHENKOV, E. V. FROLOV, AND I. I. GORDEEV. 2022. A phylogenetic re-evaluation of the stenakrine opecoelids (Trematoda, Digenea: Opecoeloidea) with some taxonomic novelties. *Diversity* 14: 949. doi:10.3390/d14110949.
- SOKOLOV, S. G., S. V. SHCHENKOV, AND I. I. GORDEEV. 2020. Phylogenetic position of deep-sea opecoelid digenean *Tellervotrema beringi* (Mamaev, 1965) (Trematoda: Opecoelidae) based on novel genetic data. *Systematic Parasitology* 97: 379–387. doi:10.1007/s11230-020-09918-4.

- SZIDAT, L., AND G. GRAEFE. 1967. Estudios sobre la fauna de parásitos de peces Antárticos. II. Los parásitos de *Parachaenichthys charcoti*. Servicio de Hidrografía Naval de la Secretaría de la Rep. Argentina, Publico H 911: 4–27.
- THOMPSON, A. B., AND L. MARGOLIS. 1987. Descriptions of *Neolebouria tinkerbella* n. sp. (Trematoda: Digenea: Opcoelidae) from experimental fish hosts, and of metacercariae of *N. tinkerbella* and an unidentified digenean from *Pandalus jordani* (Decapoda: Penaeidae) from the Pacific coast of Canada. Canadian Journal of Zoology 65: 188–193. doi:10.1139/z87-027.
- TKACH, V. V., D. T. J. LITTLEWOOD, P. D. OLSON, J. M. KINSELLA, AND Z. SWIDERSKI. 2003. Molecular phylogenetic analysis of the Microphalloidea Ward, 1901 (Trematoda: Digenea). Systematic Parasitology 56: 1–15. doi:10.1023/A:1025546001611.
- WANG, Y.-Y., P.-Q. WANG, AND W.-H. ZHANG. 1992. Opcoelid trematodes of marine fishes from Fujian Province. Wuyi Science Journal 9: 67–89.
- WoRMS. 2025. World Register of Marine Species. Available at: www.marinespecies.org. Accessed 20 January 2025.
- YAMAGUTI, S. 1934. Studies on the helminth fauna of Japan. Part 2. Trematodes of fishes, I. Japanese Journal of Zoology 5: 249–541.
- YAMAGUTI, S. 1951. Studies on the helminth fauna of Japan. Part 44. Trematodes of fishes, IX. Acta Medica Okayama 7: 247–282. doi:10.18926/amo/31778.
- YAMAGUTI, S. 1970. Digenetic Trematodes of Hawaiian Fishes. Keigaku Publishing Company, Tokyo, Japan, 436 p.
- ZDZITOWIECKI, K. 1990. Reexamination of five Antarctic and subantarctic digenean and acanthocephalan species from Professor Szidat's collection. Acta Parasitologica Polonica 35: 31–36.
- ZDZITOWIECKI, K. 1997. Antarctic Digenea Parasites of Fishes. Synopses of the Antarctic Benthos. Vol. 8. Koeltz Scientific Books, Koenigstein, Germany, 156 pp.
- ZDZITOWIECKI, K., E. PISANO, AND M. VACCHI. 1993. Antarctic representatives of the genus *Neolebouria* Gibson, 1976 (Digenea, Opcoelidae), with description of one new species. Acta Parasitologica 38: 11–14.