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1946 and Checklist of Parasites from *Lycodes*
cortezianus (Perciformes: Zoarcidae)

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REVIEW

***Pseudopecoelus mccauleyi* n. sp. and *Podocotyle* sp. (Digenea: Opecoelidae) from the deep waters off Oregon and British Columbia with an updated key to the species of *Pseudopecoelus* von Wicklen, 1946 and checklist of parasites from *Lycodes cortezianus* (Perciformes: Zoarcidae)**

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Abstract

Pseudopecoelus mccauleyi n. sp. (Opecoelidae: Opecoelinae) is described from the intestine of the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890) (Perciformes: Zoarcidae), collected at 200–800 m depths in the Northeastern Pacific Ocean off Oregon and Vancouver Island, British Columbia. The new species is distinguished by possessing a unique combination of the following diagnostic characters: vitelline fields that extend to the posterior margin of the ventral sucker; a slender, tubular and sinuous seminal vesicle that extends some distance into the hindbody; an unspecialized, protuberant ventral sucker; a genital pore at pharynx level; lobed to deeply multi-lobed testes; a lobed ovary; and an egg size of 68–80 µm × 30–46 µm. A single specimen of *Podocotyle* Dujardin, 1845 (Digenea: Plagioporinae) is also described from the intestine of an individual *Coryphaenoides* sp. (Gadiformes: Macrouridae) collected at 2,800 m depth off Oregon. A listing of parasites from the bigfin eelpout as well as observations of parasite diversity within relevant hosts are offered, new host and locality records are noted, and a brief discussion of *Pseudopecoelus* von Wicklen, 1946 in the deep sea is presented taking note of the low level of host specificity recorded (i.e. spp. of *Pseudopecoelus* are now known to parasitize deep-water fish from at least 20 piscine families). A new dichotomous key to the 39 recognized species of *Pseudopecoelus* is introduced.

Keywords

British Columbia, *Coryphaenoides* sp., Digenea, Key, *Lycodes cortezianus*, Macrouridae, Opecoelidae, Opecoelinae, Oregon, Plagioporinae, *Podocotyle* sp., *Pseudopecoelus mccauleyi* n. sp., Vancouver Island, Zoarcidae

Introduction

Pseudopecoelus von Wicklen, 1946 is a large opecoelid genus within the Opecoelinae Ozaki, 1925 comprised of almost 40 species. Its members possess a combination of unexceptional characters representative of the archetypal opecoeline condition including an unspecialized and sessile, protuberant or pe-

dunculate ventral sucker, blindly-ending caeca, a cirrus pouch that is either small or absent, and a sinistral genital pore located in the forebody (Cribb 2005). *Pseudopecoelus* was erected by von Wicklen (1946) after she undertook a study of the genus *Cymbephallus* Linton, 1934 and concluded the latter genus to be a junior synonym of *Opecoeloides* Odhner, 1928. With the suppression of *Cymbephallus*, she established

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Pseudopecoelus by moving four species of *Cymbephallus* into the new genus: *Pseudopecoelus elongatus* (Yamaguti, 1938) von Wicklen, 1946; *Pseudopecoelus japonicus* (Yamaguti, 1938) von Wicklen, 1946; and *Pseudopecoelus vulgaris* (Manter, 1934) von Wicklen, 1946 as the type species. Von Wicklen (1946) also deduced that *Cymbephallus fimbriatus* Linton, 1934 of Manter, 1934 belonged in *Pseudopecoelus* and proposed *Pseudopecoelus tortugae* von Wicklen, 1946 for this species based on its type locality – off Tortugas, Florida (see Manter 1934). The four species von Wicklen (1946) recognized in *Pseudopecoelus* (formerly in *Cymbephallus*) differed from species of *Opecoeloides* in lacking an accessory sucker immediately posterior to the genital pore, papillae on the ventral sucker, and a uroproct – all features still recognized among species of *Opecoeloides* today (see Cribb 2005) – and the etymology of *Pseudopecoelus* reflected its resemblance to *Opecoelus* Ozaki, 1925 in sharing a protuberant ventral sucker and lacking an accessory sucker but differed in the former possessing blindly-ending caeca (not a common anus) and lacking acetabular papillae.

Within a decade of the erection of *Pseudopecoelus*, the genus had grown to include nine species, and Manter (1954) proposed one of the earliest keys to the species of this genus. Yamaguti (1958, 1971) recognized ten and 21 species, respectively, of *Pseudopecoelus*, while in his study of the digenetic trematodes off Hawaii, Yamaguti (1970) recognized five species of *Pseudopecoelus* from this region. Bray (1987) established six morphological groups (A–F) in his attempt to taxonomically organize *Pseudopecoelus*, which by then had grown to include 28 nominal species. Thirty years have passed since Bray (1987), and two newer keys to the species within *Pseudopecoelus* have been produced. Bray and Justine (2010) devised a visual key to 35 species of *Pseudopecoelus* (see their Fig. 2) using metric data accumulated from 12 criteria (see p. 46–47 of Bray and Justine 2010) presented as histograms (see their Figs 1, 2). Later that same year Madhavi and Lakshmi (2010) produced a more conventional, dichotomous key to the 37 species of *Pseudopecoelus* they recognized. To our knowledge, Madhavi and Lakshmi (2010) represent the latest key devised and new species described, *Pseudopecoelus brayi* Madhavi and Lakshmi, 2010, for this genus. Currently, Gibson (2014b) recognizes 37 species in *Pseudopecoelus*; however, the most recent species described, *P. brayi*, is not included in Gibson (2014b), and we include it herein. Thus, we recognize a total of 38 spp. of *Pseudopecoelus* in this report (Table I).

The purpose of this study was to add to our knowledge of *Pseudopecoelus* with the description of a new species from the intestine of the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890) (Zoarcidae), collected from deep waters off Oregon and British Columbia. We also briefly describe a single individual of an unidentified species of *Podocotyle* Dujardin, 1845 from the intestine of *Coryphaenoides* sp. (Macrouridae) collected off Oregon. We present an updated key to the species of *Pseudopecoelus* and provide a listing of the parasites known from *L. cortezianus* (Table II).

Materials and Methods

An unknown number of bigfin eelpout, *L. cortezianus*, and a single individual of an unidentified grenadier species of *Coryphaenoides* Gunnerus, 1765 (Macrouridae) were collected aboard ship and examined for parasites by the late Dr. James E. McCauley, Dept. of Oceanography, Oregon State Univ., Corvallis, Oregon, USA. Fish were collected by otter trawl from depths of 200–2,800 m within the northeastern Pacific Ocean approximately 40–105 km west of Newport, Lincoln County, Oregon. Specimens of *L. cortezianus* and *Coryphaenoides* sp. were immediately fixed at sea by injecting the body cavity, mouth and anus with AFA or 4% seawater formaldehyde and preserved in 10% neutral seawater-formalin before being transferred back to the laboratory for autopsy (see Eagle and McCauley 1964; McCauley 1964, 1968). Digeneans from these two host species were stained with either Mayer's carmalum or Van Cleave's hematoxylin combination and mounted in Canada balsam (see McCauley and Pequegnat 1968). Eight slides (2 whole mounts + 6 sections) were also examined that had been housed in the British Museum (Natural History) Collection (BMNH/NHMUK) at The Natural History Museum, London, UK. These digeneans were obtained from the intestine of an unknown number of *L. cortezianus* collected off Vancouver Island, British Columbia, Canada (date[s] of collection, depth[s] and geographic coordinates unavailable), apparently stained in Van Cleave's hematoxylin, and donated to the museum by Dr. Hisao P. Arai (Dept. of Biology, Univ. of Calgary, Alberta, Canada) (David I. Gibson and Eileen Harris – pers. comm.). Drawings were done with the aid of an Olympus CH30 compound microscope using a drawing tube and a Nikon Superhigh-Performance 3 Zoom Coolpix 990 digital camera and image software system. Measurements are in micrometres (µm) with the holotype followed by the means and ranges in parentheses; the number [n] of measurements is also noted where needed. Two-dimensional measurements are given with the length before the width. Holotype selection of the new species was based on choosing the single individual that best exhibited the combination of morphological features unique to the new species. Comparative measurements were taken from the original species descriptions or re-descriptions unless otherwise stated. If needed, some critical measurements that were not available or were obviously in error in the original descriptions were calculated from original illustrations and are identified herein. Fish classification and authorities follow FishBase (Froese and Pauly 2017). Digenean identification was based on Cribb (2005) and ecological terms followed Bush *et al.* (1997).

While we understand that *in situ* fixation of digeneans is not ideal, specimens measured herein appeared in good condition upon close examination. Furthermore, we felt that because of the inherent rarity of this material (i.e. from the deep sea) the benefits to our limited knowledge of deep-sea helminth communities afforded by this study justified the completion of this work.

Table I. List of species of *Pseudopecoelus* von Wicklen, 1946 we recognize with hosts, infection sites, localities and references from the type descriptions

Parasite Species	Host species	Infection Site	Locality	Reference
<i>Pseudopecoelus ablennesi</i> Bray, 1987	Flat needlefish, <i>Ablennes hians</i> (Valenciennes, 1846) (Belonidae)	Anterior intestine	Off Durban, South Africa	Bray (1987)
<i>Pseudopecoelus acanthuri</i> Yamaguti, 1970	Convict surgeonfish, <i>Acanthurus triostegus</i> (Linnaeus, 1758) (Acanthuridae)	Gall bladder	Off Hawaii	Yamaguti (1970)
<i>Pseudopecoelus akamachi</i> Machida and Araki, 2002	Deepwater longtail red snapper, <i>Etelis coruscans</i> ¹ Valenciennes, 1862 (Lutjanidae)	Pyloric caeca and upper intestine	Off Koniya, Kagoshiima Prefecture, Japan and Palau, western Caroline Islands	Machida and Araki (2002)
<i>Pseudopecoelus alectis</i> Shen, 1990	African pompano, <i>Alectis ciliaris</i> (Bloch, 1787) (Carangidae)	Stomach	Off Hainan Island, China	Shen (1990)
<i>Pseudopecoelus ariusi</i> Parukhin, 1983	Giant catfish, <i>Netuma thalassina</i> (Rüppell, 1837) (Ariidae)	Intestine and stomach	Off Oman in Arabian Sea	Parukhin (1983)
<i>Pseudopecoelus barkeri</i> Hanson, 1950	Squirrelfish, <i>Holocentrus adscensionis</i> (Osbeck, 1765) (Holocentridae)	GI tract ²	Off Bermuda	Hanson (1950)
<i>Pseudopecoelus bilqeesae</i> Ahmad and Dhar, 1987	Malabar trevally, <i>Carangoides malabaricus</i> (Bloch and Schneider, 1801) (Carangidae)	Anterior small intestine	Off Puri, Odisha (Orissa), India, in Bay of Bengal	Ahmad and Dhar (1987)
<i>Pseudopecoelus brayi</i> Madhavi and Lakshmi, 2010	Shoulderbar soldierfish, <i>Myripristis kuntzei</i> Valenciennes, 1831 (Holocentridae)	Intestine	Off Visakhapatnam, Andhra Pradesh, India, in Bay of Bengal	Madhavi and Lakshmi (2010)
<i>Pseudopecoelus brevivesic- ulatus</i> Hanson, 1955	Honeycomb filefish, <i>Cantherhines pardalis</i> (Rüppell, 1837) Monacanthi- dae [type host]; Black triggerfish, <i>Melichthys niger</i> (Bloch, 1786) (Balistidae)	Intestine	Off Hawaii	Hanson (1955)
<i>Pseudopecoelus dollfusi</i> Ahmad and Dhar, 1987	Largescaled terapon, <i>Terapon theraps</i> Cuvier, 1829 (Terapontidae)	Middle small intestine	Off Puri, Odisha (Orissa), India, in Bay of Bengal	Ahmad and Dhar (1987)
<i>Pseudopecoelus elongatus</i> (Yamaguti, 1938) von Wicklen, 1946	Gnomefish, <i>Scombrops boops</i> (Houttuyn, 1782) (Scombroptidae)	Small intestine	Off Maisaka, Siduoka Prefecture, Japan	Yamaguti (1938)
<i>Pseudopecoelus epinepheli</i> Wang, 1982	Hong Kong grouper, <i>Epinephelus akaara</i> (Temminck and Schlegel, 1842) (Serranidae)	Intestine	Off Fujian Province, China	Wang (1982)
<i>Pseudopecoelus ghanensis</i> Fischthal and Thomas, 1970	Law croaker, <i>Pseudotolithus senegallus</i> (Cuvier, 1830) (Sciaenidae)	Small intestine	Off Tema and Cape Coast, Ghana	Fischthal and Thomas (1970)
<i>Pseudopecoelus gibbonsiae</i> Manter and van Cleave, 1951	Striped kelpfish, <i>Gibbonsia metzi</i> Hubbs, 1927 (Clinidae)	Intestine	Off La Jolla, California	Manter and van Cleave (1951)
<i>Pseudopecoelus gymnothoracis</i> Nahhas and Cable, 1964	Spotted moray, <i>Gymnothorax moringa</i> (Cuvier, 1829) (Muraenidae)	Intestine	Off Curaçao in Caribbean Sea	Nahhas and Cable (1964)
<i>Pseudopecoelus hemilobatus</i> Manter, 1954	Silver dory, <i>Cyttus australis</i> (Richardson, 1843) (Cyttidae)	Intestine	Off Portobello, New Zealand	Manter (1954)
<i>Pseudopecoelus holocentri</i> Nahhas and Cable, 1964	Squirrelfish, <i>Holocentrus adscensionis</i> (Osbeck, 1765) (Holocentridae)	Intestine	Off Curaçao in Caribbean Sea	Nahhas and Cable (1964)

<i>Pseudopocoelus japonicus</i> (Yamaguti, 1938) von Wicklen, 1946	Pacific jellynose fish, <i>Ateleopus japonicus</i> ¹ Bleeker, 1853 (Ateleopodidae); Sea bass sp., <i>Chelidoperca hirundinacea</i> (Valenciennes, 1831) (Serranidae); Greeneye sp., <i>Chlorophthalmus albatrossis</i> ¹ Jordan and Starks, 1904 (Chlorophthalmidae); Japanese thread-sail fish, <i>Hime japonica</i> (Günther, 1877) (Aulopidae); Snipe eel sp., <i>Nemichthys</i> sp. ¹ (Nemichthyidae); Japanese perchlet, <i>Plectranthias japonicus</i> ¹ (Steindachner, 1883) (Serranidae) [type host]; Silver eye, <i>Polymixia japonica</i> ¹ Günther, 1877 (Polymixiidae); Fivespot flounder, <i>Pseudorhombus pentophthalmus</i> Günther, 1862 (Paralichthyidae); Golden cusk, <i>Siremba imberbis</i> (Temminck and Schlegel, 1846) (Ophidiidae); Blackmouth splitfin, <i>Synagrops japonicus</i> ¹ (Döderlein, 1883) (Acropomatidae); Atlantic horse mackerel, <i>Trachurus trachurus</i> (Linnaeus, 1758) (Carangidae); Mirror dory, <i>Zenopsis nebulosa</i> ¹ (Temminck and Schlegel, 1845) (Zeidae)	Small intestine, stomach and encysted in peribuccal connective tissue	Off Maisaka and Suruga Bay, Shizuoka (= Siduoka) Prefecture, Japan	Yamaguti (1938)
<i>Pseudopocoelus littoralis</i> Caballero and Caballero, 1976	White croaker, <i>Genyonemus lineatus</i> (Ayres, 1855) (Sciaenidae)	Intestine	Off Ocean Park, California	Caballero and Caballero (1976)
<i>Pseudopocoelus manteri</i> Sogandares-Bernal and Hutton, 1959	Silver perch, <i>Bairdiella chrysoura</i> (Lacepède, 1802) (Sciaenidae)	Pyloric caeca	Off Tarpon Key, Boca Ciega Bay, Florida	Sogandares-Bernal and Hutton (1959)
<i>Pseudopocoelus maomao</i> Yamaguti, 1970	Green damselfish, <i>Abudefduf abdominalis</i> (Quoy and Gaimard, 1825) (Pomacentridae)	Intestine	Off Hawaii	Yamaguti (1970)
<i>Pseudopocoelus mccauleyi</i> n. sp.	Bigfin eelpout, <i>Lycodes cortezianus</i> (Gilbert, 1890) (Zoarcidae)	Intestine	Off Oregon and Vancouver Island, British Columbia	Present study
<i>Pseudopocoelus minutus</i> Nahhas and Cable, 1964	Dwarf wrasse, <i>Doratonotus megalepis</i> Günther, 1862 (Labridae)	Intestine	Off Curaçao in Caribbean Sea	Nahhas and Cable (1964)
<i>Pseudopocoelus nossamani</i> Kruse, 1977	Pacific halibut, <i>Hippoglossus stenolepis</i> Schmidt, 1904 (Pleuronectidae)	GI tract ²	Off Amchitka Island, Alaska, in Bering Sea	Kruse (1977)
<i>Pseudopocoelus odeningi</i> Ahmad, 1987	Belanger's croaker, <i>Johnius belangerii</i> (Cuvier, 1830) (Sciaenidae)	Intestine	Off Puri, Odisha (Orissa), India, in Bay of Bengal	Ahmad (1987)
<i>Pseudopocoelus priacanthi</i> (MacCallum, 1921) Manter, 1947	Atlantic bigeye, <i>Priacanthus arenatus</i> Cuvier, 1829 (Priacanthidae)	Intestine	Off Key West, Florida, and New York Aquarium	MacCallum (1921)
<i>Pseudopocoelus pritchardae</i> Gupta and Sayal, 1979	Squirrelfish sp., <i>Holocentrus</i> sp. (Holocentridae)	"Gut"	Off Kavaratti Island, Lakshadweep, India, in Arabian Sea	Gupta and Sayal (1979)
<i>Pseudopocoelus puhipaka</i> Yamaguti, 1970	Yellow-edged moray, <i>Gymnothorax flavimarginatus</i> (Rüppell, 1830) (Muraenidae)	Intestine	Off Hawaii	Yamaguti (1970)
<i>Pseudopocoelus pyriformis</i> Prudhoe and Bray, 1973	Splendid sea perch, <i>Callanthias allporti</i> Günther, 1876 (Callanthiidae)	GI tract ²	Off Maria Island, Tasmania, Australia	Prudhoe and Bray (1973)
<i>Pseudopocoelus scorpaenae</i> (Manter, 1947) Overstreet, 1969	Barbfish, <i>Scorpaena brasiliensis</i> Cuvier, 1829 (Scorpaenidae); Plumed scorpionfish, <i>Scorpaena grandicornis</i> Cuvier, 1829 (Scorpaenidae) [type host]	Intestine	Off Tortugas, Florida	Manter (1947)

<i>Pseudopecoelus sesokoensis</i> Dyer, Williams and Williams, 1988	Trout sweetlips, <i>Plectorhinchus pictus</i> (Tortonese, 1936) (Haemulidae)	Intestine	Off north coast of Sesoko-jima, Motobu-cho, Okinawa, Ryukyu Islands, Japan	Dyer <i>et al.</i> (1988)
<i>Pseudopecoelus sewelli</i> Bray, 1990	Orange roughy, <i>Hoplostethus atlanticus</i> ¹ Collett, 1889 (Trachichthyidae)	Intestine	Off Tasmania, South Australia and Victoria, Australia	Bray (1990b)
<i>Pseudopecoelus sosoae</i> Bray and Justine, 2010	Lanternbelly sp., <i>Neoscombrops pacificus</i> ³ Mochizuki, 1979 (Acropomatidae)	Digestive tract	Off Nouméa, New Caledonia	Bray and Justine (2010)
<i>Pseudopecoelus sphyraenae</i> Yamaguti, 1970	Great barracuda, <i>Sphyraena barracuda</i> (Edwards, 1771) (Sphyraenidae)	Intestine	Off Hawaii	Yamaguti (1970)
<i>Pseudopecoelus stunkardi</i> Ahmad, 1990	False trevally, <i>Lactarius lactarius</i> (Bloch and Schneider, 1801) (Lactariidae)	Posterior part of intestine	Off Panjim, Goa, India	Ahmad (1990)
<i>Pseudopecoelus tortugae</i> von Wicklen, 1946	Hollowsnout grenadier, <i>Coelorinchus caelorhincus</i> ^{1,4} (Risso, 1810) (Macrouridae)	Intestine	Off Tortugas, Florida	Manter (1934)
<i>Pseudopecoelus umbrinae</i> Manter and van Cleave, 1951	Yellowfin drum, <i>Umbrina roncadore</i> Jordan and Gilbert, 1882 (Sciaenidae)	Intestine	Off La Jolla, California	Manter and van Cleave (1951)
<i>Pseudopecoelus vitellozonatus</i> Pritchard, 1966	Bluespine unicornfish, <i>Naso unicornis</i> (Forsskål, 1775) (Acanthuridae) [type host]; Hawaiian squirrelfish, <i>Sargocentron xantherythrum</i> (Jordan and Evermann, 1903) (Holocentridae)	Intestine	Off Oahu Island, Hawaii	Pritchard (1966)
<i>Pseudopecoelus vulgaris</i> (Manter, 1934) von Wicklen, 1946 [type species]	Three-eye flounder, <i>Ancylopsetta dilecta</i> (Goode and Bean, 1883) (Paralichthyidae); Horned searobin, <i>Bellator militaris</i> (Goode and Bean, 1896) (Triglidae); Goby flathead, <i>Bembrops gobioides</i> (Goode, 1880) (Percophidae); Simony's frostfish, <i>Benthodesmus simonyi</i> ¹ (Steindachner, 1891) (Trichiuridae); Bearded brotula, <i>Brotula barbata</i> (Bloch and Schneider, 1801) (Ophidiidae); Blackbelly rosefish, <i>Helicolenus dactylopterus</i> ¹ (Delaroche, 1809) (Sebastidae); Shortbeard codling, <i>Laemonema barbatulum</i> Goode and Bean, 1883 (Moridae); Armored or flathead searobin/ gurnard spp., <i>Peristedion brevirostre</i> ¹ (Günther, 1860), <i>Peristedion imberbe</i> ¹ Poey, 1861, <i>Peristedion miniatum</i> ¹ Goode, 1880 (Peristediidae); Longspine scorpionfish, <i>Pontinus longispinis</i> Goode and Bean, 1896 (Scorpaenidae); Spiny searobin, <i>Prionotus alatus</i> Goode and Bean, 1883 (Triglidae); Shortwing searobin, <i>Prionotus stearnsi</i> Jordan and Swain, 1885 (Triglidae); Sea bass sp., <i>Pronotogrammus</i> sp. (Serranidae); Atlantic thornyhead, <i>Trachyscorpia cristulata cristulata</i> Goode and Bean, 1896 (Sebastidae); Unidentified sp.	Intestine and rarely in stomach	Off Tortugas, Florida	Manter (1934)

¹Froese and Pauly (2017) identify this host species as an inhabitant of deep water.

²Type description of this particular parasite species had no information for this characteristic, so the most likely infection site is given where possible.

³While Bray and Justine (2010) examined a single individual of this host species caught at 200–400 m depth, Froese and Pauly (2017) do not list *N. pacificus* as a deep water species, though they list its depth range as 60–500 m.

⁴Manter (1934, p. 295) noted that either the hollowsnout grenadier, *Coelorinchus caelorhincus* (Risso, 1810) (as *Coelorhynchus carminatus* [Goode, 1880]), or the Western softhead grenadier, *Malacocephalus occidentalis* Goode and Bean, 1885 (as *Chalinura occidentalis* [Goode and Bean, 1885]) (Macrouridae), was the host for the single specimen he possessed of *Pseudopecoelus tortugae* (as *Cymbephallus fimbriatus* Linton, 1934 of Manter, 1934); however, Manter (1947, p. 292, 371) confirmed the host of this individual worm as *C. caelorhincus*.

Table II. Parasites reported from the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890), including infection sites, localities and references

Host / Parasite Species ¹	Infection Site	Locality	Reference
A ² - <i>Echinorhynchus gadi</i> Zoega in Müller, 1776	Intestine	NW Atlantic Ocean along east coast of N. America; Off coast of British Columbia, Canada, in Pacific Ocean	Arai (1967, 1969, 1989 ³); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³); Amin (1998 ³)
C ² - <i>Bothriocephalus scorpii</i> (Müller, 1776) Rudolphi, 1808 (larvae)	Intestine	Off British Columbia, Canada	Arai (1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³)
C - <i>Nybelinia surmenicola</i> Okada in Dollfus, 1929 (larvae)	Intestine	Off British Columbia, Canada	Arai (1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³); Bates (1990 ³)
C - <i>Phyllobothrium</i> sp. (larvae)	Intestine	Burke Channel, coast of British Columbia, Canada	Arai (1967, 1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³)
D ² - <i>Lecithaster gibbosus</i> (Rudolphi, 1802) Lühe, 1901	Intestine; pyloric caeca	Burke Channel, coast of British Columbia, Canada	Arai (1967, 1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³); Gibson (1996 ³)
D - <i>Parahemiurus merus</i> (Linton, 1910) Woolcock, 1935	Intestine; pyloric caeca; stomach	Burke Channel, coast of British Columbia, Canada	Arai (1967, 1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³); Bray (1990a ³); Gibson (1996 ³)
D - <i>Podocotyle</i> sp. (immature)	Intestine	Burke Channel, coast of British Columbia, Canada	Arai (1967, 1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³)
D - <i>Pseudopocoelus mccauleyi</i> n. sp.	Intestine; stomach	NE Pacific Ocean off Newport, Lincoln County, Oregon; Off Vancouver Island, British Columbia, Canada, in Pacific Ocean	Gibson (1996 ³) ⁴ ; Present study; BM(NH) Coll. (Access. # 1987.5.11.1-3) ^{5,6} ; HWML Coll. (Access. # 42794, 42814, 42848-42850, 42853, 42961) ⁵
M ² - Monogenea	Gills	NE Pacific Ocean ⁷	HWML Coll. (Access. # 42845) ⁵
N ² - <i>Capillaria</i> sp.	Stomach	Off British Columbia, Canada	Arai (1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³)
N - <i>Contracaecum</i> sp. (larvae)	Body cavity	Burke Channel, coast of British Columbia, Canada	Arai (1967, 1969); Love and Moser (1976 ³ , 1983 ³); Margolis and Arthur (1979 ³)

¹Following Froese and Pauly (2017), the following host synonymies were also searched: *L. cortezianus*-*Aprodon corteziana* Gilbert, 1890, *Aprodon cortezianus* Gilbert, 1890. For the parasites listed, we attempted to use the most up-to-date taxonomic designation for each species using the World Register of Marine Species (www.marinespecies.org).

²A—Acanthocephala; C—Cestoda; D—Digenea; M—Monogenea; N—Nematoda.

³These references are host-parasite checklists and should not be considered as original records.

⁴Gibson (1996, p. 165), in his key to the species of *Pseudopocoelus* von Wicklen, 1946 from Canadian waters, examined specimens he tentatively identified as *P. japonicus* collected from *Aprodon* (= *Lycodes*) *cortezianus* that were in the BM(NH) and originally collected by Dr. H.P. Arai (see Arai 1967, 1969, 1989); we found these specimens to be *P. mccauleyi* n. sp.

⁵Specimens of this parasite species are currently housed in the Natural History Museum Collections (BM[NH]), London, U.K. and in the Harold W. Manter Laboratory of Parasitology (HWML), Univ. of Nebraska-Lincoln, Lincoln, Nebraska, U.S.A (Accession numbers given where available).

⁶These 8 slides (6 of sections) of *P. mccauleyi* n. sp. are the same specimens earlier identified as *P. nossamani* and *P. japonicus* (see Gibson 1996); these were collected from *Aprodon* (= *Lycodes*) *cortezianus* from off British Columbia, Canada, housed in the BM(NH), and donated to the museum by Dr. H.P. Arai (Eileen Harris and Rodney Bray – pers. comm.).

⁷This particular parasite record had no information for this characteristic, so the most likely locality was given.

Digenean specimens used in this study are currently housed in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska-Lincoln, Lincoln, Nebraska, USA (Original HWML Nos. 42774, 42794, 42814, 42848, 42849, 42850, 42853, 42961) and in the BMNH (BMNH 1987.5.11.1–3). Specimens of species of *Pseudopecoelus* and *Podocotyle* also were borrowed and examined from the BMNH, HWML, and the United States National Parasite Collection, Smithsonian National Museum of Natural History (NMNH), Washington, DC, USA (USNM – formerly USNPC). Borrowed materials included: *Podocotyle angulata* Dujardin, 1845 (BMNH 1982.6.8.14–28, 1982.9.28.57–59); *Podocotyle atomon* (Rudolphi, 1802) Odhner, 1905 (BMNH 1976.4.8.186, 1976.11.5.40, 1979.1.12.15, 1983.10.10.60–65, 1989.4.13.47–64; USNM 008220.00, 008222.00, 008224.00, 008227.00, 008228.00, 051794.00; HWML 1047–1049, 37798–37805, 45392); *Podocotyle reflexa* (Creplin, 1825) Odhner, 1905 (BMNH 1932.11.28.24, 1967.6.19.2–3, 1980.6.2.8–9, 1982.6.9.2; USNM 078271.00–078273.00; HWML 37807–37809, 37818–37824); and *Pseudopecoelus nossamani* Kruse, 1977 (USNM 1369684/USNPC 074121).

Results

Class: Trematoda Rudolphi, 1808

Subclass: Digenea Carus, 1863

Order: Plagiorchiida La Rue, 1957

Family: Opecoelidae Ozaki, 1925

Subfamily: Opecoelinae Ozaki, 1925

Genus: *Pseudopecoelus* von Wicklen, 1946

Pseudopecoelus mccauleyi n. sp. (Figs 1–7)

Synonym: *Pseudopecoelus japonicus* of Gibson 1996, p. 165.

Description based on 34 whole-mounted specimens. Measurements and proportions given in Table III. With characteristics of genus. Body elongate to elongate oval, flattened dorsoventrally, widest at junction of first and second 1/4 of body (2 specimens widest at junction of second and third 1/3 of body) and then constricts just posterior to this point to produce an arrow-shaped anterior end in some specimens, sides run parallel for most of length of body then attenuate to rounded anterior and posterior extremities. Forebody about 1/5 length of body. Hindbody with parallel sides, attenuate in posterior 1/4 of body. Tegument aspinose. Pre-oral lobe not observed. Oral sucker subterminal, circular to subspherical to oval, unspecialized (3 individuals with terminal mouth; 1 specimen with triangular-shaped mouth). Ventral sucker large, oval to subspherical to transversely elongate, unspecialized, protuberant (pronounced in lateral view; 2 specimens with protuberant ventral sucker on raised/elevated surface), conspicuous muscular border around perimeter that can appear bloated at times, wider than long and larger than oral sucker,

pre-equatorial at junction of first and second 1/4 to 1/5 of body. Prepharynx absent to very short. Pharynx muscular, oval to dolioform, anterior end occasionally ventrally-overlapped by oral sucker. Oesophagus conspicuous, thick-walled, straight, sometimes with slight curve longitudinally, longer than pharynx. Intestinal bifurcation short distance anterior to ventral sucker in posterior half of forebody (1 specimen with intestinal bifurcation just ventrally overlapped by anterior margin of ventral sucker). Caeca parallel, slightly variable in width, mostly narrow, terminates blindly near posterior extremity in last 1/5 of body.

Testes 2, tandem (1 specimen with slightly diagonal testes), median, lobed to deeply multi-lobed, occasionally indented (2 specimens with smooth and/or oval testes, 1 specimen with triangular-shaped anterior testis and heart-shaped posterior testis; 1 specimen with posterior testis longitudinally elongate, 1 specimen with testes that appear pulled apart/highly distorted – teratological individuals?), not commonly contiguous (5 specimens with contiguous testes), mostly intercaecal, postequatorial and separated from posterior end. Post-testicular region confined to posterior 1/3 to 1/5 of body. Cirrus pouch absent. Seminal vesicle tubular, free in parenchyma, naked (no membranous portion), very long, thin anteriorly and widens further posteriorly to become dilated or swollen posterior to ventral sucker, winds and becomes quite convoluted dorsal to ventral sucker and slightly posterior to it, extends some distance into hindbody. Pars prostatica fairly inconspicuous, short, thin-walled, appears as slight dilation at distal end of seminal vesicle, not much wider than latter, lined with large, bleb-like cells aligned at angle to longitudinal axis of worm; ejaculatory duct thick-walled, short; cirrus present. Genital pore conspicuous, submedian (sinistral), pre-acetabular, pre-bifurcal at level of pharynx (1 specimen at pre-pharynx level), lateral position approaches midline of worm or ventrally overlaps left edge of pharynx or is between pharynx and left margin. Genital atrium distinct, small, round, deep, surrounded by dark-stained cells; atrium wall striated in appearance and in lateral view appears elevated (i.e. "puckered") above ventral surface of worm.

Ovary 3- to 4-lobed (1 specimen with irregular-shaped ovary), median to slightly dextral, anterior to but not contiguous with anterior testis (in 4 specimens anterior testis extends anterior to posterior margin of ovary; 4 specimens with distance ≤ 12 between ovary and anterior testis), mostly intercaecal, testes can either ventrally overlap caeca (11, 19 and 17 specimens, respectively, with ovary, anterior testis and posterior testis that overlap caeca) or extend lateral to caeca (extracaecal) (8, 4 and 8 specimens, respectively, with ovary, anterior testis and posterior testis that extend lateral to caeca), equatorial in middle third of body. Seminal receptacle uterine. Laurer's canal present, extensive, joins oviduct immediately anterior to right lobe of ovary and to side of vitelline reservoir, terminates at dorsal pore midway between left caecum and left margin of worm. Vitelline reservoir sub-triangular, oval to clavate (1 specimen with lemon-shaped reservoir), median to submedian (sinistral), im-

Table III. Dimensions of *Pseudopecoelus mccauleyi* n. sp. from *Lycodes cortezianus* (Gilbert, 1890), *Pseudopecoelus nossamani* Kruse, 1977 from *Hippoglossus stenolepis* Schmidt, 1904 and *Podocotyle* sp. from *Coryphaenoides* sp. from off Oregon, British Columbia and Alaska

Parasite	<i>Pseudopecoelus mccauleyi</i> n. sp. ¹	<i>Pseudopecoelus mccauleyi</i> n. sp. ²	<i>Pseudopecoelus mccauleyi</i> n. sp. ^{1,3}	<i>Pseudopecoelus nossamani</i> Kruse, 1977 ⁴	<i>Podocotyle</i> sp.
n =	31	1	2	1	1
Length	3,280 (3,083, 2,200–4,440)	4,460	5,120 (4,800–5,440)	2,940	2,220
Width at pharynx	336 (262, 208–392)	232	304 (288–320)	184	424
Width at VS ⁵	648 (547, 408–656)	544	772 (768–776)	440	704
Width at PT ⁵	544 (404, 264–568)	272	940 (896–984)	368	888
Forebody L ⁵	580 (618, 440–860)	880	950 (840–1,060)	640	580
Hindbody L	2,300 (2,159, 1,460–3,340)	3,480	3,860 (3,640–4,080)	2,080	1,240
Oral sucker (OS) L	160 (181, 144–224)	208	240 (240)	176	272
OS W ⁵	180 (163, 128–192)	172	216 (208–224)	160	232
Prepharynx L	0 (7, 0–80)	48	0	8	32
Pharynx L	96 (107, 88–136)	108	134 (124–144)	100	240
Pharynx W	108 (103, 72–132)	144	142 (136–148)	108	160
Oesophagus L	248 (255, 128–380) [n = 30]	400	444 (376–512)	208	96
IB ⁵ to anterior end L	532 (540, 424–740) [n = 30]	736	812 (728–896)	432	648
IB L anterior to VS	60 (117, 52–256) [n = 30]	176	160 (128–192)	248	0
VS L	392 (330, 260–392)	344	320 (312–328)	228	392
VS W	432 (374, 296–452)	316	360 (336–384)	284	496
AT ⁵ L	328 (267, 184–340)	248	532 (408–656)	340	100
AT W	272 (249, 152–320)	280	440 (432–448)	204	364
PT L	296 (294, 196–476)	340	576 (512–640)	300	172
PT W	264 (258, 176–312)	240	452 (424–480)	220	364
AT to PT	56 (52, 4–104) [n = 28]	224	0	176	0
Post-testicular region (PTR) L	880 (851, 512–1,240)	1,160	1,640 (1,640)	520	624
PTR W at mid-point	440 (317, 192–440)	240	830 (800–860)	352	728
Seminal vesicle (SV) L	920 (948, 628–1,624) [n = 28]	1,584	1,760 (1,472–2,048)	776 ⁴	156
SV W	20 (38, 16–76)	56	80 (72–88)	52	96
SV L posterior to VS	236 (295, 128–688) [n = 28]	944	892 (616–1,168)	152 ⁴	0
Pars prostatica L	98 (66, 42–98) [n = 29]	–	160 (120–200)	124	–
Pars prostatica W	24 (23, 18–32) [n = 29]	–	48 (40–56)	20	–
Genital pore (GP) to anterior end L	236 (247, 196–324)	320	348 (320–376)	416	464
GP L anterior to VS	380 (396, 256–576)	576	612 (528–696)	232	144
Ovary (OV) L	176 (156, 80–208) [n = 30]	160	220 (192–248)	188	216
OV W	224 (188, 76–244) [n = 30]	100	308 (304–312)	112	312
Pre-OV region L	1,580 (1,484, 1,080–2,120)	2,220	2,310 (2,120–2,500)	1,500	1,100
VS to OV L	640 (577, 312–1,100)	1,220	1,040 (960–1,120)	640	184
OV to AT L	56 (55, 4–128) [n = 29]	176	32 (0–64)	0	0
Vitelline follicle L	55, 46–70 [n = 5] (53, 24–88) [n = 155] ⁶	62 (52–70) [n = 5] ²	75 (56–92) [n = 10] ⁷	66 (56–84) [n = 10] ⁷	68 (48–96) [n = 10] ⁷
Vitelline follicle W	44, 40–50 [n = 5] (41, 18–76) [n = 155] ⁶	46 (42–50) [n = 5] ²	54 (40–68) [n = 10] ⁷	40 (24–56) [n = 10] ⁷	50 (40–64) [n = 10] ⁷

Vitellarium to anterior end L	940 (900, 672–1,168) [n = 30]	980	1,350 (1,300–1,400)	880	672
Vitelline reservoir L	160 (106, 64–160) [n = 29]	80	136 (100–172)	88	–
Vitelline reservoir W	52 (70, 44–104) [n = 29]	72	102 (84–120)	54	–
Uterus L	1,380 (1,246, 880–1,860)	1,860	2,000 (1,820–2,180)	1,100	736
Uterus W at widest point	272 (196, 120–320)	248	448 (416–480)	360	512
Post-uterine region (PUR) L	1,680 (1,593, 1,100–2,340)	2,260	2,800 (2,660–2,940)	1,420	1,040
Egg L	70 (73.3, 68–80) [n = 81]	71.2 (68–74) [n = 5] ²	73.5 (70–80) [n = 12] ⁷	81.2 (78–84) [n = 10] ⁷	69.0 (62–74) [n = 10] ⁷
Egg W	30 (38.0, 30–46) [n = 90]	35.2 (34–36) [n = 5] ²	32.0 (30–36) [n = 12] ⁷	40.8 (38–44) [n = 10] ⁷	35.4 (32–38) [n = 10] ⁷
Post-caecal region L	124 (151, 64–240) [n = 24]	192	372 (328–416)	64	264
Exc. bladder L	1,600 (1,483, 1,040–2,080) [n = 30]	2,120	2,480 [n = 1]	1,320	608
Exc. bladder W	152 (92, 18–176) [n = 30]	80	58 (56–60)	40	92
Body W at VS % ⁸	19.8 (18.0, 13.0–23.3)	12.2	15.1 (14.3–16.0)	15.0	31.7
Body W at PT % ⁸	16.6 (13.3, 8.7–21.5)	6.1	18.5 (16.5–20.5)	12.5	40.0
Forebody L % ⁸	17.7 (20.2, 16.3–25.8)	19.7	18.5 (17.5–19.5)	21.8	26.1
OS:pharynx width ratio	1:1.67 (1:1.59, 1:1.25–1.83)	1:1.19	1:1.52 (1:1.51–1.53)	1:1.48	1:1.45
Oesophagus % ⁸	7.6 (8.2, 4.2–10.8) [n = 30]	9.0	8.6 (7.8–9.4)	7.1	4.3
IB to anterior end L % ⁸	16.2 (17.6, 13.8–21.2) [n = 30]	16.5	15.8 (15.2–16.5)	14.7	29.2
IB L anterior to VS % ⁸	1.8 (3.8, 1.6–8.1) [n = 30]	3.9	3.1 (2.7–3.5)	8.4	0
Sucker-width ratio	1:2.40 (1:2.31, 1:1.71–2.83)	1:1.84	1:1.66 (1:1.62–1.71)	1:1.78	1:2.14
AT to PT % ⁸	1.7 (1.7, 0.2–3.0) [n = 28]	5.0	0	6.0	0
PTR % ⁸	26.8 (27.5, 19.7–34.1)	26.0	32.2 (30.1–34.2)	17.7	28.1
SV L % ⁸	28.0 (30.2, 24.9–41.2) [n = 28]	35.5	34.9 (27.1–42.7)	26.4 ⁴	7.0
Genital pore (GP) to anterior end L % ⁸	7.2 (8.1, 6.8–10.0)	7.2	6.8 (6.7–6.9)	14.2	20.9
GP L anterior to VS % ⁸	11.6 (12.9, 9.6–17.4)	12.9	11.9 (11.0–12.8)	7.9	6.5
Pre-OV region L % ⁸	48.2 (48.3, 43.0–54.6)	49.8	45.1 (44.2–46.0)	51.0	49.6
VS to OV L % ⁸	19.5 (18.5, 12.6–24.8)	27.4	20.3 (20.0–20.6)	21.8	8.3
OV to AT L % ⁸	1.7 (1.7, 0.2–3.9) [n = 29]	3.9	0.7 (0–1.3)	0	0
Vitellarium to anterior end L % ⁸	28.7 (29.7, 25.1–34.9) [n = 30]	22.0	26.4 (25.7–27.1)	29.9	30.3
PUR L % ⁸	51.2 (51.6, 45.4–58.8)	50.7	54.7 (54.0–55.4)	48.3	46.9

¹All measurements are in micrometres (µm); where holotype is included, the means and ranges are in parentheses, otherwise, the range is in parentheses; the number [n] of measurements is noted if different from the total number of worms examined [n = 31 or 2].

²This particular specimen was quite large and appeared stretched / distorted; resultantly, we elected to keep it separate from the other paratypes. Means and ranges of vitelline follicles and eggs [n = 5] are given with the latter measurements in parentheses.

³These 2 individuals of the new species were housed at the BMNH (BMNH 1987.5.11.1–3) and previously identified as *P. nossamani* (Rodney Bray and Eileen Harris – pers. comm.) and *P. japonicus* (Gibson 1996) – see text. This lot of specimens also included 6 slides of sectioned material.

⁴This individual is the holotype of *P. nossamani* (USNM 1369684 / USNPC 074121). The uterus / opaque eggs occluded most of the seminal vesicle posterior to the ventral sucker in this specimen, so the length(s) provided are for what we could observe (i.e. not total length).

⁵AT, anterior testis; IB, intestinal bifurcation; L, length; PT, posterior testis; VS, ventral sucker; W, width.

⁶Means and ranges of vitelline follicles are given both for the holotype [n = 5] and in parentheses for the paratype specimens [n = 155].

⁷Means and ranges of vitelline follicles and eggs [n = 10 or 12] are given with the latter measurements in parentheses.

⁸Proportion of body length.

mediately preovarian or dorsally overlaps ovary. Longitudinal vitelline ducts run parallel with and alongside medial margins of caeca; lateral ducts proceed from vitelline reservoir at level of anterior margin of ovary, loop anteriorly, then pass posteriorly to bifurcate at level of anterior lobe(s) of anterior testis; main vitelline duct proceeds anteriorly from anterior margin of vitelline reservoir toward Mehlis' gland/oötype complex. Oviduct convoluted, located dextral and anterior to vitelline reservoir, passes anteriorly from anteromedial lobe of ovary, takes an anterodextral course, occasionally loops, then turns sharply left to enter Mehlis' gland/oötype complex after it first receives Laurer's canal followed by main vitelline duct. Mehlis' gland cells conspicuous, dense, located immediately anterior to ovary and vitelline reservoir, occasionally ventrally overlaps anterior margin of latter, bulk of cells at times just right or left of midline; oötype large, median, anterior to and/or dorsally overlapped by vitelline reservoir. Uterus intercaecal, winds with relatively narrow loops, restricted to area between ovary and genital pore; proximal portion of uterus filled with sperm and originates from sinistral to posterosinistral region of Mehlis' gland/oötype complex; distal portion runs parallel with, dorsal to, and to left of distal portion of seminal vesicle and pars prostatica to enter genital atrium after male and female ducts join in common, thick-walled duct (observable in lateral view). Metraterm inconspicuous except in lateral view, thick-walled with thickest walls at distal end near entrance to genital atrium, 140–162 (151) [$n = 2$] $\times$ 6 (6) [$n = 2$]. Vitelline follicles oval to circular to irregular, mostly large, a few follicles per individual can be quite large, moderate in density, circumcaecal, restricted to hindbody, extends from posterior extremity (or just short of it) anteriorly up to level of posterior margin of ventral sucker (1 specimen with right band of follicles short of ventral sucker by 160 [3.6% of body length]; 2 specimens with left band of follicles short of ventral sucker by 90 and 136 [3.2% and 2.5% of body length]; 2 specimens with both bands of follicles short of ventral sucker by 56 and 100 [1.5% and 2.1% of body length]; 2 specimens with either right or left band of follicles that extend to mid-level of ventral sucker; 2 specimens with both bands of follicles that extend to mid-level of ventral sucker), encroach over lateral margins of gonads, run in longitudinal bands along sides of worm and interrupted lateral to gonads (17 specimens with vitelline gap on one side of ovary; 11 specimens with gaps on both sides of ovary; 11 specimens with gap on one side of anterior testis; 7 specimens with gaps on both sides of anterior testis; 10 specimens with gap on one side of posterior testis; 16 specimens with gaps on both sides of posterior testis) and pre-ovarian space, not laterally confluent in pre-ovarian region (1 specimen with confluent follicles just posterior to ventral sucker), in space between ovary and anterior testis, and in inter-testicular region (4 specimens with confluent follicles in this region), confluent in post-testicular region. Eggs oval, majority collapsed and/or crenulated in distal uterus while bloated in proximal uterus, moderate in size and number, operculate, amber, non-filamented, non-embryonated, small nib on one pole.

Excretory bladder tubular, extends to ovary, narrow posteriorly and gradually widens anteriorly, dorsally overlaps testes (2 specimens with vesicle that passes to left side of testes); excretory pore subterminal, dorsal, surrounded by dark-stained cells.

Taxonomic summary

Type-host: *Lycodes cortezianus* (Gilbert, 1890); Perciformes: Zoarcidae; bigfin eelpout.

Type-locality: Northeastern Pacific Ocean, approx. 40 km (25 miles) west of Newport, Oregon, USA, 44°37'N, 124°34' W (approx.); depth = 200 m; dates of collection = 27 April 1963, 19 February 1964.

Other locality: Northeastern Pacific Ocean, approx. 63 km (39 miles) west of Newport, Oregon, USA, 44°37'N, 124°46' W (approx.); depth = 800 m; dates of collection = 14 February 1964, 19 February 1964. Northeastern Pacific Ocean, off Vancouver Island, British Columbia, Canada – geographic coordinates, depth(s) and date(s) of collection not available.

Site of infection: Intestine.

Deposited specimens: Holotype HWML 103034 (1 slide); paratypes HWML 42961, 103035–103038 (31 specimens on 30 slides); paratypes BMNH 1987.5.11.1–3 (2 whole specimens on 2 slides, 6 slides of sectioned material); vouchers HWML 42814, 42848–42850, 42853, 103033 (95 specimens on 88 slides).

Etymology: The species designation is named in honor of the late Dr. James E. McCauley, Department of Oceanography, Oregon State University, who collected this material, deposited it the HWML, and made significant contributions in the field of deep-sea parasitology.

Differential Diagnosis

Based on the complete absence of both a cirrus pouch and a canalicular seminal receptacle (*Pseudopecoelus mccauleyi* n. sp. possesses a uterine seminal receptacle), the new species is assigned to the Opecoelinae within the Opecoelidae (Cribb 2005). It keys out to the genus *Pseudopecoelus* based on its possession of the following diagnostic combination of characters: blindly-ending caeca; no "accessory sucker" closely posterior to the genital pore; a pars prostatica that is not especially large; a submedian genital pore; tandem testes; no cirrus pouch or membranous sac enclosing a seminal vesicle; a ventral sucker without prominent anterior and posterior lobes; and no deep cleft at the excretory pore (Cribb 2005).

Specimens of *P. mccauleyi* n. sp. described herein were obtained from the bigfin eelpout, *L. cortezianus*, found in two locations roughly 575 km apart – off Newport, Oregon, and off Vancouver Island, British Columbia. While we determined digeneans from both localities to be conspecific, we did note a few minor differences between both "sets" of specimens. The two individuals of *P. mccauleyi* n. sp. from off Vancouver Island (BMNH 1987.5.11.1–3) were larger in overall size

Figs 1–3. *Pseudopecoelus mccauleyi* n. sp. from the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890) (Perciformes: Zoarcidae). **1** – Whole view of holotype, ventral view (proximal, bulbous end of seminal vesicle is dorsal to uterus, but drawn ventral for viewing). **2** – Composite drawing of terminal genitalia, lateral view. **3** – Proximal female genital complex, ventral view (ovary is most ventral feature in this figure, but it and caeca are drawn dorsal to all features for ease of viewing; Laurer's canal is dorsal to the vitelline reservoir, but the former is drawn ventral for viewing). Abbreviations: At, anterior testis; C, caecum; Cgd, common genital duct; E, egg; Eb, excretory bladder; Ed, ejaculatory duct; Ep, excretory pore; Gp, genital pore; Lc, Laurer's canal; M, metraterm; Mg, Mehlis' gland; O, ovary; Oes, oesophagus; Os, oral sucker; Ot, oötype; Ov, oviduct; P, pharynx; Pp, pars prostatica; Pt, posterior testis; Sv, seminal vesicle; U, uterus; Utr, uterine seminal receptacle; V, vitelline follicles; Vr, vitelline reservoir; Vs, ventral sucker. Scale bars = 655 µm, 70 µm, 185 µm

(4,800–5,440 vs 2,200–4,440) and in the size of several morphological features measured (see Table III); however, the general appearance of these features was the same and egg sizes overlapped (70–80 × 30–36 vs 68–80 × 30–46). We also noted that all allometric measurements and ratios overlapped between specimens from both locations (see Table III) with the exception of the sucker width ratio, which was slightly smaller in the two individuals from off Canada (1:1.62–1.71 vs 1:1.71–2.83). Most obvious to us in the Canadian material was the more pronounced "arrow-shaped" anterior end (caused by a lateral constriction in the anterior hindbody), a protuberant ventral sucker located on the slightly raised/elevated ventral surface of the worms, and the conspicuous, multi-lobed appearance of the testes; we feel the multi-lobed nature of the testes contributed to their overlap with each other and with the ovary (i.e. contiguous testes and the anterior testis longitudinally overlaps the ovary). The differences just discussed between the two specimens of *P. mccauleyi* n. sp. found off British Columbia and the remaining 127 conspecific specimens found off Oregon we believe to be a result of age – the Canadian worms are likely older and larger individuals, reflecting developmental and maturational changes in this species.

We were unable to identify our material using the latest key to the species of *Pseudopicoelus* by Madhavi and Lakshmi (2010). *Pseudopicoelus mccauleyi* n. sp. possesses vitelline follicles that do not extend anterior to the ventral sucker (follicles extend as far as the posterior margin of the ventral sucker), a long, slender body (neither fusiform nor wide), no papillae on the lips of the ventral sucker, lobed testes, and vitelline follicles that are interrupted opposite the gonads. With these features, the new species is closest to *Pseudopicoelus nossamani*, described from the Pacific halibut, *Hippoglossus stenolepis* Schmidt, 1904 (Pleuronectidae), from the Bering Sea (Kruse 1977; see also Blaylock *et al.* 1998), and to *Pseudopicoelus holocentri* Nahhas and Cable, 1964, described from the squirrelfish, *Holocentrus adscensionis* (Osbeck, 1765) (Holocentridae), from off Curaçao in the Caribbean Sea (Nahhas and Cable 1964) (see our Table I, couplet #31 in key of Madhavi and Lakshmi 2010). While the new species has a sucker ratio that overlaps that of *P. nossamani* and *P. holocentri* (1:1.62–2.83 vs 1:1.72 and 1:2.00–2.15), the egg size of *P. mccauleyi* n. sp. falls between both species (68–80 × 30–46 vs 80–84 × 44 and 52–54 × 27–30). The genital pore of *P. nossamani* was described by Kruse (1977, Fig. 3) as "slightly to left of cecal bifurcation" (= bifurcal) (see Bray 1990b, p. 200; Gibson 1996, p. 165 where the bifurcal location of the genital pore in the type material of *P. nossamani* was confirmed, and this feature was used, in part, to distinguish *Pseudopicoelus sewelli* Bray, 1990 from this species), and its testes appear smooth to slightly indented (see Fig. 3 of Kruse 1977). We examined the holotype of *P. nossamani* (USNM 1369684/USNPC 074121; see Table III) and can confirm that both the genital pore is bifurcal and the testes are smooth to slightly indented (i.e. neither located at

the level of the pharynx [= pre-bifurcal] nor with lobed to deeply multi-lobed testes as in *P. mccauleyi* n. sp.). In addition, the holotype of *P. nossamani* differs from the new species in having the intestinal bifurcation located midway between the suckers instead of in the posterior half of the forebody a short distance from the ventral sucker, an ovary that is contiguous with the anterior testis, a longer and more prominent, thick-walled pars prostatica that along with the distal portion of the seminal vesicle is surrounded by conspicuous and large prostatic gland cells, vitelline follicles that are variable in their anterior extent (i.e. right band of follicles extend to mid-level of ventral sucker; left band of follicles 112 µm [3.8% of body length] short of sucker), are not interrupted lateral to the ovary (they are interrupted lateral to the testes – see Kruse 1977) and that are confluent in the pre-ovarian space, and the holotype specimen has a terminal vs dorsally subterminal excretory pore. It is important to note that some of our measurements, proportions and/or ranges for the sizes of several features in the holotype of *P. nossamani* (see Table III) differed from those given for the same features in the type description by Kruse (1977) (e.g. we measured the oral sucker length to be 176 and observed a terminal mouth, but in Kruse 1977 it is 140–160 long and described as subterminal; we measured the pharynx width to be 108, but it is described having a width of 76–96; post-testicular region length 520 vs 375–510; egg width 38–44 vs 44; forebody length 1/5 [21.8%] vs 1/4 of body length). Kruse (1977) described the seminal receptacle as lacking but a uterine seminal receptacle is present, and sadly, almost every egg in the holotype appeared opaque/black causing the occlusion of some features (e.g. the proximal portion of the seminal vesicle). We did see a couple of transparent, amber-colored eggs in the very proximal end of the uterus near the ovary; however, all of these were severely contracted/collapsed. Along with having a smaller egg than the new species, *P. holocentri* was described by Nahhas and Cable (1964) as having a "slightly irregular" ovary (i.e. not lobed), a terminal excretory pore and it was found parasitizing the squirrelfish, *H. adscensionis* – a species that usually inhabits depths of only 8–30 m (Froese and Pauly 2017) – from the Caribbean Sea off Venezuela (Curaçao). *Pseudopicoelus mccauleyi* n. sp. possesses a 3–4 lobed ovary, an excretory pore that is distinctly, dorsally subterminal and it was found infecting the bigfin eelpout, *L. cortezianus* (Zoarcidae), from much deeper waters (200 and 800 m, respectively) within the Northeast Pacific Ocean off Oregon and British Columbia.

There has been only one report in the literature of a species of *Pseudopicoelus* from *Lycodes cortezianus* – this being Gibson (1996, p. 165) where he examined specimens of *Pseudopicoelus* collected from the intestine of this fish found off Vancouver Island, British Columbia (see Table II) and that were donated by Dr. Hisao P. Arai (Dept. of Biology, Univ. of Calgary, Alberta, Canada) to the BMNH (see Arai 1967, 1969, 1989). Gibson confirmed (pers. comm.) to one of us (CKB) that the specimens he had tentatively identified as *P. japonicus* in that report are the specimens housed in the BMNH

Figs 4–6. *Pseudopecoelus mccauleyi* n. sp. from the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890) (Perciformes: Zoarcidae). **4** – Whole view of older adult specimen from off British Columbia, Canada, ventral view. **5** – Longitudinally-distorted testes in teratological specimen, ventral view. **6** – Midbody of specimen illustrating bifurcation and course of longitudinal vitelline ducts along median margins of caeca, ventral view. Abbreviations: At, anterior testis; C, caecum; Eb, excretory bladder; Ep, excretory pore; Gp, genital pore; Lvd, longitudinal vitelline duct; O, ovary; Oes, oesophagus; Os, oral sucker; P, pharynx; Pp, pars prostatica; Pt, posterior testis; U, uterus; V, vitelline follicles; Vr, vitelline reservoir; Vs, ventral sucker. Scale bars = 890 μ m, 425 μ m, 515 μ m

under accession # BMNH 1987.5.11.1–3; it is these specimens that we have identified herein, in part, as the new species (see Taxonomic summary above). It is important to also note that these same individuals were taxonomically identified by Dr. Arai and catalogued for a time at the BMNH as *P. nossamani* (Rodney Bray and Eileen Harris – pers. comm.). As far as we are aware, *P. mccauleyi* n. sp. is the only species of *Pseudopecoelus* known from the bigfin eelpout, *L. cortezianus* (Table II).

There are three species of *Pseudopecoelus* originally described from areas proximate to Oregon and British Columbia in the Northeast Pacific Ocean: *Pseudopecoelus gibbonsiae* Manter and van Cleave, 1951; *Pseudopecoelus littoralis* Caballero and Caballero, 1976; and *Pseudopecoelus umbrinae* Manter and van Cleave, 1951 – all from off the coast of California (Table I). *Pseudopecoelus gibbonsiae* parasitizes the intestine of the striped kelpfish, *Gibbonsia metzi* Hubbs, 1927 (Clinidae), off La Jolla, California (Manter and van Cleave 1951). It differs from *P. mccauleyi* n. sp. in having vitelline follicles that extend to a point midway between the pharynx and ventral sucker and that are not interrupted lateral to the gonads, lacking a metraterm, a larger egg length (90–92 vs 68–80), a globular and smooth ovary that is contiguous with the anterior testis instead of a lobed ovary that is not contiguous with the anterior testis, testes that are smooth, subspherical and contiguous instead of lobed to deeply multi-lobed testes that are not contiguous, a larger pharynx in relation to overall body size (see Fig. 6 of Manter and van Cleave 1951), a smaller oral sucker:pharynx width ratio (1:1.0 vs 1:1.3–1.8), and a larger forebody ("about one-third body length" vs 16.3%–25.8% of body length). *Pseudopecoelus littoralis* was described from the intestine of the white croaker, *Genyonemus lineatus* (Ayres, 1855) (Sciaenidae), from off Ocean Park, California (Caballero and Caballero 1976). This species differs from *P. mccauleyi* n. sp. in the following characteristics: a smaller overall body size (1,069–1,231 vs 2,200–5,440) and size of internal features (e.g. oral and ventral suckers, pharynx, oesophagus, testes, etc.); a "cuadrangular-shaped" (cuboidal or square-shaped) oral sucker; a larger forebody (36.4%–39.5% vs 16.3%–25.8% of body length); oblique testes that are "trapezoidal" (couplet #13a in key of Madhavi and Lakshmi 2010 describes testes as "triangular"); an ovary that is lateral and to the right of the anterior testis and not completely anterior to it (see Fig. 2 of Caballero and Caballero 1976); a uterus that extends further posterior overlapping the anterior halves of the anterior testis and ovary instead of being completely pre-ovarian and pre-testicular; and the vitelline follicles extend anterior to the ventral sucker to the level of the intestinal bifurcation and are not interrupted lateral to the gonads. *Pseudopecoelus umbrinae* was found by Manter and van Cleave (1951) in the intestine of the yellowfin drum, *Umbri- rina roncadore* Jordan and Gilbert, 1882 (Sciaenidae), from off La Jolla, California. It differs from the new species in having a more oval vs elongate to elongate oval shape resulting in a shorter (1,037–2,420 vs 2,200–5,440) body, testes that are di-

agonal (though they can be tandem), contiguous, smooth or slightly irregular in outline, a seminal vesicle that does not extend posterior to the ventral sucker vs one that extends some distance posterior to it into the hindbody, an ovary that is "partly to the right and partly anterior to anterior testis" appearing lateral and to the right of the anterior testis (not fully pre-testicular) in Fig. 8 of Manter and van Cleave (1951), a uterus "beginning to left of ovary, mostly preovarian" and not entirely pre-ovarian, neither seminal receptacle nor metraterm present (though most likely a uterine seminal receptacle), and the vitelline follicles extend anterior to the ventral sucker to the level of the posterior oesophagus and are not interrupted lateral to the gonads.

Pseudopecoelus mccauleyi n. sp. was found in deeper water (200 and 800 m, respectively); there are six species of *Pseudopecoelus* that also were originally or subsequently reported from deep-water fish, yet none are known from *L. cortezianus* (Table I, also see Froese and Pauly 2017). *Pseudopecoelus akamachi* Machida and Araki, 2002 was reported from the pyloric caeca and upper intestine of the deep-water longtail red snapper, *Etelis coruscans* Valenciennes, 1862 (Lutjanidae), from off Koniya, Kagoshima Prefecture, Japan and from off Palau, western Caroline Islands, Micronesia (Machida and Araki 2002). This species differs from *P. mccauleyi* n. sp. in several features: a larger overall body size (7,700 × 1,530 [holotype] and 770–1,130 wide [paratypes] vs 2,200–5,440 × 208–984) and size of most internal features (e.g. suckers, pharynx, etc.); an intestinal bifurcation located either much nearer the oral than ventral sucker (holotype) or midway between the suckers (paratypes) vs located only a short distance anterior to the ventral sucker in the posterior half of the forebody; a smaller sucker width ratio (1:1.1–1.3 vs 1:1.6–2.8); a longer forebody (29%–36% of body length [paratypes] vs 16%–26%; note: holotype of *P. akamachi* with forebody = 23% of body length); ovoid and smooth vs lobed to deeply multi-lobed testes (see Fig. 5 of Machida and Araki 2002); a larger post-testicular region (PTR) (40% of body length [holotype] vs 20%–34%; note: paratypes of *P. akamachi* with PTR = 22%–31% of body length); a two partitioned seminal vesicle (= bipartite), the anterior (portion) saccular and the posterior (portion) tubular; a pre-pharyngeal genital pore that is at the level of the posterosinistral edge of the oral sucker (holotype) vs at the level of the pharynx (note: paratypes of *P. akamachi* have a genital pore sinistral to the pharynx – see Fig. 6 of Machida and Araki 2002); an ovoid, smooth ovary that is contiguous with the anterior testis vs a 3- to 4-lobed ovary that is not contiguous with the anterior testis; vitelline follicles that are not interrupted lateral to the gonads; a shorter egg (53–58 [holotype] and 48–55 [paratypes] long vs 68–80 long); and a terminal vs subterminal and dorsal excretory pore. *Pseudopecoelus japonicus* was originally described by Yamaguti (1938) as *Cymbephallus japonicus* Yamaguti, 1938 from the small intestine, stomach and peribuccal connective tissue (i.e. a single "fully gravid worm in doubled-up position" was found inside a "subglobular cyst") of 12 piscine

Figs 7–8. *Pseudopecoelus mccauleyi* n. sp. from the bigfin eelpout, *Lycodes cortezianus* (Gilbert, 1890) (Perciformes: Zoarcidae) and *Podocotyle* sp. from *Coryphaenoides* sp. (Gadiformes: Macrouridae). **7** – Larger, extended specimen of *P. mccauleyi* n. sp. illustrating protuberant ventral sucker, long and convoluted seminal vesicle dorsal and posterior to ventral sucker, and bloated eggs in proximal uterus, lateral view (posterior uterine loops not drawn for ease of viewing of seminal vesicle). **8** – Whole view of *Podocotyle* sp., ventral view. Abbreviations: At, anterior testis; C, caecum; Cp, cirrus pouch; E, egg; Eb, excretory bladder; Ep, excretory pore; Gp, genital pore; M, metraterm; O, ovary; Oes, oesophagus; Os, oral sucker; P, pharynx; Pp, pars prostatica; Pr, prepharynx; Pt, posterior testis; Sv, seminal vesicle; U, uterus; V, vitelline follicles; Vr, vitelline reservoir; Vs, ventral sucker. Scale bars = 490 μ m, 435 μ m

host species, seven of which inhabit deeper waters, from off Maisaka and Suruga Bay, Shizuoka (= Siduoka) Prefecture, Japan (see Table I). Subsequently, *P. japonicus* has been reported from 11 fish species, 8 of which are inhabitants of the deep sea, collected off Portobello, New Zealand, Mozambique, Africa, Suruga Bay (off the Pacific coast of Japan) and the South Atlantic (Manter 1954; Parukhin 1976a, 1976b, 1978; Reimer 1987; Machida and Kamegai 1997). This species differs from *P. mccauleyi* n. sp. in having vitelline follicles that extend to the level of the anterior margin of the ventral sucker and that are not interrupted lateral to the gonads, a small cirrus pouch (= "muscular sheath") enclosing the pars prostatica and a short cirrus, an excretory bladder that is sigmoid in combination with oblique testes that are irregularly indented (1 of 34 [2.9%] specimens of *P. mccauleyi* n. sp. have slightly diagonal testes but remainder [97.1%] have distinctly tandem testes, while 2 of 34 [5.9%] specimens of the new species possess an excretory bladder that passes to the left side of the testes and is not sigmoid/winding between them; the testes of *P. mccauleyi* n. sp. are lobed to deeply multi-lobed), and *P. japonicus* has a smaller sucker width ratio (1:1.4–1.5 vs 1:1.6–2.8) (see Fig. 28 of Yamaguti 1938). *Pseudopecoelus sewelli* is known from the intestine of the orange roughy, *Hoplostethus atlanticus* Collett, 1889 (Trachichthyidae), from off Tasmania and Victoria, Australia, as well as from the digestive tract of the lanternbelly *Neoscombrops pacificus* Mochizuki, 1979 (Acropomatidae) from off Nouméa, New Caledonia (Bray 1990b; Bray and Justine 2010). This species can grow to a maximum size somewhat larger than that of *P. mccauleyi* n. sp. (8,820 × 1,140 vs 5,440 × 984) and some of its internal features (e.g. testes, ovary) have a larger maximum size than the new species, it has a shorter forebody (15% vs 16–26% of body length), a ventral sucker that is on a distinct peduncle (see Fig. 1 of Bray 1990b and couplet #4a in key of Madhavi and Lakshmi 2010), a terminal excretory pore that is surrounded by a sphincter (described as ventrally subterminal by Bray and Justine 2010), its egg can be up to 93 × 60 in size, and the vitelline follicles can extend to between the level of the mid-oesophagus (anterior to the ventral sucker) and the anterior hindbody. *Pseudopecoelus sosoae* Bray and Justine, 2010 also parasitizes the digestive tract of *N. pacificus* from the deep waters off Nouméa, New Caledonia (Bray and Justine 2010). Froese and Pauly (2017) do not recognize *N. pacificus* as a deep water species (its depth range is listed as 60–500 m), but Bray and Justine (2010) examined a single individual of this host species from a depth of 200–400 m (the same individual fish parasitized by *P. sewelli* mentioned earlier); therefore, we have elected to include *P. sosoae* in our comparative analyses here. *Pseudopecoelus sosoae* differs from *P. mccauleyi* n. sp. in having a longer body overall (4,307–5,878 vs 2,200–5,440), a shorter forebody (13%–14% vs 16%–26% of body length), an intestinal bifurcation that is dorsal to the anterior part of the ventral sucker vs completely pre-acetabular, smooth and oval testes, a seminal vesicle that extends only a slight distance posterior to the ventral sucker (see couplet #20a

in key of Madhavi and Lakshmi 2010), a genital pore at the level of the anterior oesophagus, a sub-oval and entire ovary that is contiguous with the anterior testis (ovary can be slightly separated from anterior testis), much larger eggs (104–153 × 43–86 vs 68–80 × 30–46), an excretory pore that is ventrally vs dorsally subterminal, and the vitelline follicles do not extend to the ventral sucker (post-acetabular) vs extending to the level of the posterior margin of the sucker (note: the type description of *P. sosoae* does not state if the vitelline follicles of this species are interrupted lateral to the gonads – we expect if gaps were present consistently, they would be mentioned; however, in Fig. 3 of Bray and Justine 2010, there does appear to be a single gap in the follicles anterosinistral to the ovary, immediately dextral to the anterior portion of the anterior testis, and directly sinistral to the left margin of the posterior testis). *Pseudopecoelus tortugae* (= *Cymbephallus fimbriatus* Linton, 1934 of Manter, 1934) was found in the intestine of the hollowsnout grenadier, *Coelorhynchus caelorhynchus* (Risso, 1810) (= *Coelorhynchus carminatus* [Goode, 1880]) (Macrouridae), from a depth of 366 m off Tortugas, Florida (Manter 1934, 1947, see Table I). This species differs from *P. mccauleyi* n. sp. in the following combination of features originally described: a terminal vs subterminal oral sucker (note: the oral sucker of *P. tortugae* illustrated in Fig. 48 of Manter 1934 appears subterminal); a ventral sucker encircled by a fold of the body wall (see Fig. 48); an oesophagus that is about the same length as the pharynx or a little longer vs an oesophagus length (128–512) that is conspicuously greater than that of the pharynx (88–144); a genital pore located at the mid-oesophagus level; testes that are only slightly indented and not lobed to deeply multi-lobed; a smooth and globular ovary; vitelline follicles that are not interrupted lateral to the gonads and do not reach the ventral sucker; and *P. tortugae* has a shorter egg (57–66 vs 68–80). We note that the sucker width ratio for *P. tortugae* was 1:1.62 (calculated from oral and ventral sucker widths of 156 and 252 given in the type description); couplet #36b in the key of Madhavi and Lakshmi (2010) gives the sucker width ratio of this species as 1:1.26–1.94. *Pseudopecoelus vulgaris*, the type species of the genus, was described from the intestine and stomach of 16 piscine species, five of which are endemic to the deep sea, from depths of 91–578 m (16 spp.)/183–576 m (5 deep-sea spp.) off Tortugas, Florida (Manter 1934; Froese and Pauly 2017; see Table I). Subsequently, this digenean has been discovered in two additional deep-sea fish species found off the Straits of Florida and in Tosa Bay, Japan (Overstreet and Martin 1974; Kuramochi 2001). *Pseudopecoelus mccauleyi* n. sp. differs from *P. vulgaris* in that gravid individuals of the latter species can be as short as 1,300 vs 2,200, its body is "usually indented opposite [the] testis" and possesses "folds, especially in the form of a lip-like anterior fold, developed in connection with [the] ventral sucker" (see Figs 42, 44, 45 of Manter 1934), its testes are very close together, practically contiguous (Figs 42, 43, 45), its egg is much larger (90–127 × 50–76), and while the vitelline follicles are "sometimes slightly

interrupted opposite [the] testes", there is neither mention in the description of *P. vulgaris* nor evidence in Figs 42–45 that there are gaps in the follicles lateral to the ovary and pre-ovarian space as is in *P. mccauleyi* n. sp.

Pseudopocoelus mccauleyi n. sp. exhibits a fair amount of intraspecific variability. We suspect (and expect) the presence of teratological individuals among our almost 130 specimens of the new species examined, and as is true for soft-bodied animals, the possibility of contraction as a contributing factor cannot be ruled out; however, the frequency, extent and variety of features we observed to exhibit plasticity in *P. mccauleyi* n. sp. was quite pronounced. Phenotypic plasticity has been observed in other species of *Pseudopocoelus*. Bray (1990b) documented considerable variation in *P. sewelli* in the anterior extent of the vitelline follicles, the presence and/or number of gaps in the vitelline follicles lateral to the gonads, sucker ratio and in egg size. In *P. mccauleyi* n. sp., intraspecific variability was noted in the position (subterminal or terminal) of the oral sucker, the location of the intestinal bifurcation relative to the ventral sucker, the position (tandem or diagonal, contiguous or not), texture (lobation) and shape of the testes, the site (level of pharynx or pre-pharynx) of the genital pore, the shape (lobed or irregular) and location (pre-testicular) of the ovary and its position along with the testes relative to the caeca (intercaecal, overlapping caeca or extracaecal), the shape of the vitelline reservoir, the anterior course of the excretory bladder (passing either directly dorsal to or to left of testes), and it is similar to *P. sewelli* in the variability observed in the anterior extent of the vitelline follicles relative to the ventral sucker, the number of gaps (one or both sides) in vitelline follicles lateral to the gonads, and whether the follicles were confluent or not in the pre-ovarian and inter-testicular regions.

Subfamily: Plagioporinae Manter, 1947

Genus: *Podocotyle* Dujardin, 1845

***Podocotyle* sp.** (Fig. 8)

Description based on 1 slightly contracted specimen with small tear on left margin at level of ventral sucker. Measurements and proportions given in Table III. With characteristics of genus. Body elongate, oval to almost clavate, flattened dorsoventrally, widest in region around junction of middle and posterior 1/3 body; anterior end attenuated to tightly curved extremity; posterior end less attenuated with broader, rounded extremity. Forebody short, attenuate, about 1/4 body length. Hindbody wide, gradually narrows in posterior 1/3 of body. Tegument smooth. Pre-oral lobe absent. Oral sucker subterminal, longitudinally extended to almost pyriform, unspecialized. Ventral sucker conspicuous, muscular, transversely oval, unspecialized, wider than long and about 1.5× longer and 2× wider than oral sucker, at junction near first and second 1/3 of body; ventral surface of worm elevated immediately anterior to ventral sucker that makes sucker appear slightly raised. Prepharynx short. Pharynx large, muscular, oval; pharyngeal

gland cells around anterior half of pharynx. Oesophagus short, thick-walled, straight, overlapped by ventral sucker and ventrally-elevated region of worm anterior to sucker. Intestinal bifurcation overlapped by anterior 1/2 of ventral sucker. Caeca wide, slightly arcuate, lined with dense numbers of cells that give fibrous appearance to inner walls, terminates blindly near posterior extremity.

Testes 2, median, tandem, smooth to slightly indented, irregular and transversely elongate, contiguous, intercaecal, post-equatorial, at junction of middle and posterior 1/3 of body; anterior testis appears longitudinally compressed; posterior testis longer than anterior testis. Post-testicular region large, wider than long, confined to posterior 1/3 of body. Cirrus pouch distinct, thin-walled, clavate and slightly curved towards midline posteriorly, 352 long × 120 wide; posterior extent of cirrus pouch extends to mid-level of ventral sucker. Seminal vesicle internal, bi-partite; proximal portion large, wide, saccate; distal portion tubular, runs anteriorly from proximal portion and curves. Pars prostatica located in mid-region of cirrus pouch; ejaculatory duct long and wide; cirrus located in anterior portion of cirrus pouch. Prostatic gland cells numerous and distributed throughout cirrus pouch. Genital pore submedian (sinistral), pre-acetabular, at mid-pharynx level and about midway between midline and left margin of worm. Genital atrium distinct, round.

Ovary 3-lobed (lobes not pronounced), median, equatorial, post-acetabular, contiguous to and immediately anterior to anterior testis, intercaecal but left edge of ovary and anterior testis ventrally overlap medial wall of left caecum. Seminal receptacle canalicular, large, voluminous, round (appears to resemble a pomegranate), directly dorsal to ovary, median to just dextral to midline, 112 long × 140 wide. From seminal receptacle, relatively short terminal portion of Laurer's canal proceeds anteriorly, turns slightly to right, loops dorsally over anterior margin of ovary, and joins oviduct; majority of Laurer's canal proceeds anterosinistrally from seminal receptacle in a very long, convoluted and tortuous path that loops dorsally over anterior margin of ovary before it proceeds over left side of uterus to terminate at dorsal pore located longitudinally at a position slightly anterior to midpoint between ventral sucker and ovary and sinistral to medial margin of left caecum by 32 long. Vitelline reservoir median, elongate, dorsally overlaps center of ovary and ventrally overlaps seminal receptacle; vitelline ducts converge directly dorsal to lateral margins of ovary (on both sides) and run longitudinally along lateral margins of caeca. Oviduct arises anteriorly from ovary, receives both Laurer's canal and main vitelline duct, then enters oötype which is itself directly anterior to and overlaps anterior margin of ovary; Mehlis' gland cells inconspicuous. Uterus large, pre-ovarian, intercaecal (a few loops of uterus extracaecal near level of posterior margin of ventral sucker, but this is due to small tear and resultant stretching on left margin of worm there); wide loops proceed anteriorly from level of anterior margin of ovary and ventrally overlap both caeca but do not extend lateral to them, loops then narrow and pass

dorsally over ventral sucker, take a distinct anterosinistral course at level of intestinal bifurcation, and pass ventrally over left margin of cirrus pouch before distal portion enters genital atrium. Metraterm not observed. Vitelline follicles large, dense, elongate and/or irregular, circumcaecal with majority of follicles ventral and lesser number dorsal to caeca, extend longitudinally in 2 uninterrupted lateral bands from posterior extremity anteriorly up to mid-level of ventral sucker, encroach over lateral margins of gonads and into inter-testicular space, not confluent in pre-ovarian region, in space between ovary and anterior testis and in inter-testicular region, confluent in post-testicular region. Eggs collapsed and/or crenulated, operculate, amber, non-embryonated, non-filamented, numerous and densely packed in uterus.

Excretory bladder tubular, extends to mid-level of posterior testis. Excretory pore subterminal, dorsal.

Taxonomic summary

Host: *Coryphaenoides* sp.; Gadiformes: Macrouridae.

Locality: Northeastern Pacific Ocean, approx. 105 km (65 miles) west of Newport, Oregon, USA, 44°37'N, 125°12' W (approx.); depth = 2,800 m; date of collection = 20 February 1964.

Site of infection: Intestine.

Deposited specimen: HWML 42774.

Differential Diagnosis

Based on its possession of a canalicular seminal receptacle and a well-developed cirrus pouch enclosing an internal seminal vesicle, this individual is assigned to the Plagioporidae within the Opecoelidae (Cribb 2005). We have placed this specimen in the genus *Podocotyle* based on its possession of the following diagnostic combination of morphological characters: an egg lacking a unipolar filament and having a length > 40–50 µm; blindly-ending ceca; a round to transversely oval, non-pedunculate and unspecialized ventral sucker; vitelline follicles that are restricted to the hindbody (they extend to the mid-level of the ventral sucker), post-testicular and extend to the posterior end of the body; two tandem testes; an oral sucker that is not funnel-shaped; an excretory bladder that is neither diverticulate nor enters the forebody; a clearly submedian genital pore; a pre-testicular uterus; and an ovary that is deeply lobed (Cribb 2005).

It is impossible to observe any intra-specific variation with only a single specimen and we cannot rule out the possibility of an accidental infection in this case, so any detailed comparative analyses of this specimen with accepted species of *Podocotyle* would be of limited value. This specimen is also slightly damaged (it is somewhat contracted and there is a small tear on the left margin at the level of the ventral sucker – see Fig. 8). Resultantly, we have elected to designate this digenean from *Coryphaenoides* sp. simply as *Podocotyle* sp. The taxonomic status of *Podocotyle* has been reviewed re-

cently by Blend and Dronen (2015), and Blend *et al.* (2016) described *Podocotyle nimoyi* Blend, Dronen and Armstrong, 2016. Currently Gibson (2014a) recognizes 27 species in *Podocotyle*, and we concur with his assessment (see also Table I of Blend and Dronen 2015).

Future parasitological studies of species of *Coryphaenoides* from the deeper waters off Oregon are recommended in hopes of obtaining additional specimens of this species of *Podocotyle* so that any intraspecific variability can be observed, a complete species identification can be obtained and/or a new species documented – potentially, the sixth species of *Podocotyle* known from the deep sea.

Discussion

Table II offers a comprehensive listing of all parasites that we found in the literature reported from the bigfin eelpout, *L. cortezianus*; to our knowledge, this is the first compilation of parasites from this fish. We refer the reader to Table I of Blend *et al.* (2012) for a comprehensive listing of all parasites reported from *Coryphaenoides* sp. (note: an additional report of myxosporidan trophic stages was reported from the eastern Pacific Ocean by Noble and Collard 1970). From this, we can draw several conclusions about parasite diversity in both hosts relevant to this study. There are a total of 38 known parasite species documented from, as of yet, unidentified species of *Coryphaenoides* (Table I of Blend *et al.* 2012). Specifically, digeneans appear the most diverse with 19 species documented, followed by cestodes (6 spp.), monogeneans, myxosporidians and nematodes (3 spp. each), and acanthocephalans and copepods (2 spp. each). We are aware of at least 11 parasite species from *L. cortezianus*: digeneans (4 spp.), cestodes (3 spp.), nematodes (2 spp.) and acanthocephalans and monogeneans (1 sp. each) – see Table II. This study focused on digeneans, and this group of parasites is fairly diverse in both hosts. In particular, digeneans from the following seven families (with number of species in each) are known to parasitize the hosts relevant to this study: Accacoeliidae Odhner, 1911 (1 sp.); Alloeacardiidae Looss, 1902 (1 sp. – this report is dubious as alloeacardiids have freshwater life histories); Derogenidae Nicoll, 1910 (2 spp.); Hemiuridae Looss, 1899 (5 spp.); Lecithasteridae Odhner, 1905 (1 sp.); Lepidapedidae Yamaguti, 1958 (8 spp.); Opecoelidae Ozaki, 1925 (4 spp.); and an unidentified Digenea Carus, 1863 (1 sp.). Members of the Lepidapedidae, and exclusively species within the genus *Lepidapedon* Stafford, 1904, have been most commonly reported, followed by the Hemiuridae and the Opecoelidae – the digenean family relevant to this study; the remaining four digenean families are represented by only one or two species each.

This report documents new host and locality records. Our study represents the second documentation of a species of *Pseudopecoelus* from *L. cortezianus*. As stated earlier, Gibson (1996, p. 165, Fig. 74) provided a somewhat tentative listing of *P. japonicus* from *L. cortezianus* in a key to the two

species of *Pseudopecoelus* he recognized in Canadian waters; the specimens he examined are those included in this study (BMNH 1987.5.11.1-3) and determined to be the new species. Thus, *P. mccauleyi* n. sp. is the only species of *Pseudopecoelus* known from the bigfin eelpout, *L. cortezi*anus (Table II). Our study also reports the second known opcoelid from this fish (Table II). As far as we are aware, the unidentified individual of *Podocotyle* described herein is the first report of a member of a species of *Podocotyle* parasitizing a species of *Coryphaenoides* from off Oregon (we note that the type host for *Podocotyle harrisae* Bray and Campbell, 1996 was *Coryphaenoides carapinus* Goode and Bean, 1883, but this host was captured from the New York/New Jersey Bight in the NW Atlantic Ocean – see Bray and Campbell 1996).

Pseudopecoelus mccauleyi n. sp. is the 39th species in *Pseudopecoelus*. As discussed earlier, we now recognize seven (18%) species of *Pseudopecoelus* from deeper waters: *P. akamachi*, *P. japonicus*, *P. mccauleyi* n. sp., *P. sewelli*, *P. sosoae*, *P. tortugae* and *P. vulgaris*. Bray and Justine (2010) provided an interesting discussion of *Pseudopecoelus* in the deep sea, and while noting that members of this genus can occur down to depths approaching 700 m (see Overstreet and Martin 1974), they speculated that *Pseudopecoelus hemilobatus* Manter, 1954 and *P. nossamani* also may occur in the deep sea. *Pseudopecoelus hemilobatus* was originally described from the intestine of the silver dory, *Cyttus australis* (Richardson, 1843) (Cyttidae), from off Portobello, New Zealand (Manter 1954). Froese and Pauly (2017), while not listing this fish as a deep-sea species, give a depth range of 10–350 m for *C. australis*. In addition, *P. nossamani*, detailed earlier, is known from the Pacific halibut, *H. stenolepis*, from off Alaska in the Bering Sea (Kruse 1977). Froese and Pauly (2017) do not list *H. stenolepis* as from the deep sea either, but a depth range of 0–1,200 m is given for this species. Thus, while not exclusive inhabitants of the deep sea (≥ 200 m depth – see Bray 2004), it is likely that *C. australis* and *H. stenolepis* while foraging acquire at least some of their parasites from deeper waters, among which may include the two species of *Pseudopecoelus* relevant here. Given this, there may be currently as many as nine (23%) species of *Pseudopecoelus* inhabiting the deep sea. Bray and Justine (2010) also concluded that "there is little indication of a host-preference as species [of *Pseudopecoelus*] are reported from 17 fish orders." Our research of this opcoelid genus within the deep sea also concluded little host specificity as we have documented herein (see Table I and text) that members of *Pseudopecoelus* parasitize deepwater fish belonging to at least 20 families.

With the low level of host specificity among deepwater species of *Pseudopecoelus* and the remarkable number of host families utilized by members of this genus as a whole (Table I), it is understandable that one may question the true validity of this genus. Cribb (2005) postulated that it seems likely that a large number of *Pseudopecoelus* species may not be each other's nearest neighbor, and we agree with his prediction that this genus will eventually be divided up. Given the large num-

ber of fish hosts, their broad phylogenetic diversity, and the varied diets of the fish reported, we believe it is unlikely that members of a single genus could evolve such a wide array of life histories (i.e. utilize dissimilar intermediate hosts). For example, *Pseudopecoelus ablennesi* Bray, 1987 parasitizes the flat needlefish, *Ablennes hians* (Valenciennes, 1846) (Belontiidae), that feeds on small fishes; *Pseudopecoelus acanthuri* Yamaguti, 1970 parasitizes the convict surgeonfish, *Acanthurus triostegus* (Linnaeus, 1758) (Acanthuridae), a fish that feeds on filamentous algae growing on rocks; while *Pseudopecoelus barkeri* Hanson, 1950 parasitizes the squirrelfish, *H. adscensionis*, that preys upon crabs and other small crustaceans (Froese and Pauly 2017). If we narrow the focus to deep-sea species of *Pseudopecoelus* and ask if they might form a clade distinct from those species infecting shallow-water fishes, the picture remains murky. Concerning the diets of the many families of deepwater fishes known to harbor *Pseudopecoelus*, both benthic and pelagic items are represented and they vary widely, including, in part, fish, squid, crustaceans, euphasiids, echinoderms, mysids, amphipods, polychaetes and gastropods. Many of these deepwater fish have unknown diets (see Froese and Pauly 2017), while the extensive variety of hosts, and resultantly their diets, documented for *P. japonicus* and *P. vulgaris* include representatives from both deep and shallow waters (Table I). Another striking fact is the difference in host diversity among species of *Pseudopecoelus*; some species infect many fish (12–15 spp.) while others have much narrower (1 sp.) ranges (Table I). Whether this is either an artifact of sampling or might reflect unrecognized taxonomic distinctions within *Pseudopecoelus* is hard to confirm at this point; this genus has been studied only morphometrically. GenBank contains no DNA sequence information for any species of *Pseudopecoelus*. Therefore, in order to ascertain the true validity of *Pseudopecoelus*, we feel that this genus would be an ideal candidate for future studies combining molecular, morphological and life history data.

Given the fact that *Pseudopecoelus* is quite speciose (39 recognized species), we propose here a new key to the species of *Pseudopecoelus*. Our key is based, in part, on the key by Madhavi and Lakshmi (2010) as well as on a taxonomically informative set of simple characters we chose to use in a repetitive nested fashion throughout the key (see Dronen and Blend 2015 where relatively simple characters were used in a repetitive nested fashion in the keys to the Cyclocoelidae Stossich, 1902).

Key to species of *Pseudopecoelus* based in part on Madhavi and Lakshmi (2010)¹

- 1a. Vitelline fields extend anterior to ventral sucker (into forebody) 2
- 1b. Vitelline fields extend to level of ventral sucker or further posterior (in hindbody) 18
- 2a. Posterior extent of seminal vesicle to level of ventral sucker 3

- 2b. Posterior extent of seminal vesicle into hindbody . . . 11
- 3a. Seminal vesicle long, slender, tubular and/or sinuous (unipartite) 4
- 3b. Seminal vesicle distinctly saccular or claviform (unipartite) 7
- 4a. Genital pore position at pharynx level or further anterior (oral sucker, etc.) 5
- 4b. Genital pore position further posterior at oesophageal level; egg 52–56 × 28–30; sucker width ratio 1:1.2–1.5 *P. brayi*² Madhavi and Lakshmi, 2010 (Figs 1,2)
- 5a. Testes lobed (deep or irregularly) 6
- 5b. Testes smooth or indented; egg 61–71 (rarely to 80) × 27–49 (collapsed eggs 61–68 × 27–32; uncollapsed eggs near ovary probably more nearly representing the size of living eggs, 68–71 × 42–49); sucker width ratio 1:1.65–2.00 *P. umbrinae*² Manter and van Cleave, 1951 (Figs 8,9 of Plate 12)
- 6a. Testes oblique, trapezoidal, with slightly lobed edges; oral sucker quadrangular; uterus overlaps anterior half of anterior testis and ovary; egg 66 × 41–48; sucker width ratio: 1:2.09–2.37 *P. littoralis* Caballero and Caballero 1976 (Fig. 2)
- 6b. Testes tandem, deeply and many lobed; oral sucker round; uterus entirely pre-ovarian and pre-testicular; somewhat collapsed eggs, 58–77 × 32–48 (more rounded and colorless eggs near ovary, 56–74 × 42–64); sucker width ratio: 1:1.00–1.25 *P. vitellozonatus* Pritchard, 1966 (Figs 11,12a–c)
- 7a. Genital pore position at pharynx level; egg 46–50 × 23–25; sucker width ratio 1:1.00–1.09 *P. dollfusi* Ahmad and Dhar, 1987 (Figs 5A–D)
- 7b. Genital pore position further posterior (oesophagus, intestinal bifurcation, etc.) 8
- 8a. Cirrus sac present 9
- 8b. Cirrus sac absent; egg 67–70 × 33–40; sucker width ratio 1:2.69 *P. ariusi* Parukhin, 1983 (Fig. A)
- 9a. Oral sucker subterminal; vitelline follicles not interrupted lateral to gonads 10
- 9b. Oral sucker terminal; vitelline follicles may be interrupted; egg 54–68 × 26–37 (usually 58–61 × 28–34); sucker width ratio: 1:1.22–1.57 (1:1.37–1.39 based on sucker widths in description) .. *P. brevivesiculatus*^{2,3} Hanson 1955 (Figs 4,5)
- 10a. Seminal vesicle relatively small in relation to body size; forebody 29% and post-testicular region 26% of body length; egg 53–59 × 30–33; sucker width ratio: 1:1.25–2.30 (1:1.50–1.67 based on sucker widths in description) *P. acanthuri*^{2,3} Yamaguti 1970 (Fig. 113)
- 10b. Seminal vesicle massive/wide in proximal portion in relation to body size; forebody 34% and post-testicular region 17% of body length; egg 56–59 × 32–35; sucker width ratio: 1:1.42 *P. puhipaka*^{2,3} Yamaguti 1970 (Fig. 114)
- 11a. Seminal vesicle unipartite (long, slender, tubular and/or sinuous) 12
- 11b. Seminal vesicle bipartite (tubular and saccular portions); egg 48–60 × 28–36 (collapsed); sucker width ratio 1:0.9–1.1 (1:1.60–1.83 based on sucker widths in description) *P. manteri*² Sogandares-Bernal and Hutton, 1959 (Fig. 9)
- (Note: The bipartite or unipartite nature of the seminal vesicle of *P. manteri* was not described; however, this feature appears bipartite in Fig. 9 where it possesses a saccular proximal portion and a narrow, tubular distal portion)
- 12a. Genital pore position at pharynx level or further anterior (oral sucker, etc.) 13
- 12b. Genital pore position further posterior (oesophagus, intestinal bifurcation, etc.) 16
- 13a. Testes lobed (deeply or irregularly) 14
- 13b. Testes smooth or indented 15
- 14a. Ovary lobed; egg 66–93 × 29–60; sucker width ratio 1:1.76–2.69 *P. sewelli*^{3,4} Bray, 1990 (Figs 1, 2)
- 14b. Ovary not lobed; egg 56–62 × 32–38; sucker width ratio 1:1.7–2.2 . . . *P. pyriformis*⁵ Prudhoe and Bray, 1973 (Fig. 10)
- 15a. Ovary lobed; egg 44–53 × 23–29; sucker width ratio 1:1.50–1.53 *P. bilgeesae* Ahmad and Dhar, 1987 (Figs 6A–D)
- 15b. Ovary not lobed; egg 90–92 × 36–47 (uncollapsed 90–92 × 43–47); sucker depth ratio 1:2.04–2.20 (based on depth/thickness of suckers as holotype illustration in lateral view) *P. gibbonsiae* Manter and van Cleave, 1951 (Figs 6,7 of Plate 12)
- 16a. Testes lobed (deeply or irregularly) 17
- 16b. Testes smooth; egg 45–54 × 22–30; sucker width ratio 1:1.7–2.0 *P. minutus*³ Nahhas and Cable, 1964 (Fig. 29)
- 17a. Cirrus sac present; egg 34–60 × 25–46; sucker width ratio 1:1.35–1.50 (1:1.16–1.27 based on sucker widths in description) *P. pritchardae*² Gupta and Sayal, 1979 (Figs 5, 6)
- 17b. Cirrus sac absent; egg 54–69 × 30–45 (usually 63–67 × 37–42); sucker width ratio 1:1.7–2.1 *P. gymnothoracis* Nahhas and Cable, 1964 (Fig. 28)
- 18a. Posterior extent of seminal vesicle to level of ventral sucker 19
- 18b. Posterior extent of seminal vesicle into hindbody . . . 20
- 19a. Seminal vesicle tubular, convoluted; egg 46–56 × 28–40; sucker width ratio 1:1.68–2.06 *P. sphyraenae*^{2,6} Yamaguti, 1970 (Figs 116A–C)
- 19b. Seminal vesicle saccular; egg 38–50 × 22–25; sucker width ratio 1:1.72–1.80 (1:1.66–1.73 based on sucker widths in description) *P. odeningi* Ahmad, 1987 (Fig. 2)
- 20a. Seminal vesicle bipartite (tubular and saccular portions) .. 21
- 20b. Seminal vesicle unipartite (either tubular/sinuous or saccular/clavate) 23
- 21a. Testes smooth or indented 22
- 21b. Testes lobed; egg 50–59 × 33–38; sucker width ratio 1:1.92–1.93 *P. ghanensis* Fischthal and Thomas, 1970 (Figs 3,4)

- 22a. Forebody 23% and post-testicular region 40% of body length; egg 53–58 × 33–36 (egg in young adult 48–55 × 33–36); sucker width ratio 1:1.2 *P. akamachi* Machida and Araki, 2002 (Figs 5–7)
- 22b. Forebody 20%–25% and post-testicular region 20%–25% of body length; egg 44–51 × 31–34; sucker width ratio 1:2.24–2.44 *P. barkeri* Hanson, 1950 (Fig. 8)
- 23a. Seminal vesicle long, slender, tubular and/or sinuous . . . 24
- 23b. Seminal vesicle distinctly saccular or claviform 37
- 24a. Ventral sucker possesses a posterior lip with one pair of short muscular papillae and a single, median, bilobed, non-muscular papilla; egg 68–71 × 39–44; sucker width ratio 1:2.0–2.2 *P. hemilobatus*^{2,7} Manter, 1954 (Figs 30,31)
- 24b. Ventral sucker not as above 25
- 25a. Genital pore position at pharynx level or further anterior (oral sucker, etc.) 26
- 25b. Genital pore position further posterior (oesophagus, intestinal bifurcation, etc.) 33
- 26a. Testes lobed (deeply or irregularly) 27
- 26b. Testes smooth or indented 30
- 27a. Ovary lobed 28
- 27b. Ovary not lobed; egg 52–54 × 27–30; sucker width ratio 1:2.00–2.15 *P. holocentri* Nahhas and Cable, 1964 (Fig. 27)
- 28a. Ventral sucker either non-pedunculate (sessile) or protuberant 29
- 28b. Ventral sucker markedly pedunculate; egg 45–50 × 22–28; sucker width ratio 1:1.00–1.08 *P. stunkardi* Ahmad, 1990 (Figs 14–18)
- 29a. Body folds, especially in the form of a lip-like anterior fold, developed in connection with ventral sucker; forebody 16%–25% and post-testicular region almost always longer than forebody; egg large, 90–127 × 50–76 (in very young individuals eggs may be as small as 78 × 40 but whenever eggs of 78–80 in length occur, the specimen can be recognized as young); sucker width ratio 1:2.0–3.0 *P. vulgaris* (Manter, 1934) von Wicklen, 1946 [type species] (Figs 42–47 of Manter 1934)
- 29b. No body folds in the form of a lip-like fold anterior to or in connection with ventral sucker (not to be confused with the slightly raised/elevated ventral surface producing protuberant ventral sucker); forebody 16%–26% and post-testicular region 20%–34% of body length; egg small, 68–80 × 30–46; sucker width ratio 1:1.62–2.83 *P. mccauleyi* n. sp. (Figs 1–7)
- 30a. Ovary not lobed 31
- 30b. Ovary lobed; egg 63–84 × 36–54; sucker width ratio 1:1.41–1.46 *P. japonicus*² (Yamaguti, 1938) von Wicklen, 1946 (Fig. 28 of Yamaguti 1938)
- 31a. Ventral sucker markedly pedunculate 32
- 31b. Ventral sucker non-pedunculate or protuberant; egg 50–53 × 30–32; sucker width ratio 1:2.1–3.0 *P. scorpaenae*^{2,8} (Manter, 1947) Overstreet, 1969 (Figs 41,42 of Manter 1947)
- 32a. Vitelline follicles noticeably interrupted lateral to gonads; post-testicular region 12% of body length; egg 48–51 × 24–33; sucker width ratio 1:1.03 (1:1.27 based on sucker widths in description) . . . *P. alectis* Shen, 1990 (Fig. 73)
- 32b. Vitelline follicles not interrupted lateral to gonads; post-testicular region 33% of body length; egg 50 × 30; sucker width ratio 1:2.3–2.7 *P. priacanthi*⁹ (MacCallum, 1921) Manter, 1947 (Fig. 73 of MacCallum 1921)
- 33a. Testes smooth or indented 34
- 33b. Testes lobed; egg 64–72 × 35–45; sucker width ratio 1:1.6 *P. epinepheli*¹⁰ Wang, 1982 (Fig. 13)
- 34a. Ovary not lobed 35
- 34b. Ovary lobed; egg 80–84 × 44; sucker width ratio 1:1.72 (1:1.73–2.65 based on sucker widths in description) *P. nossamani*² Kruse, 1977 (Figs 3,4)
- 35a. Vitelline follicles not interrupted lateral to gonads . . . 36
- 35b. Vitelline follicles noticeably interrupted lateral to gonads; egg 54–60 × 33–36; sucker width ratio 1:1.43–1.67 . . . *P. elongatus*² (Yamaguti, 1938) von Wicklen, 1946 (Fig. 30 of Yamaguti 1938)
- 36a. Ventral sucker encircled by a fold of the body wall; forebody 18% and post-testicular region 35% of body length; egg small, 57–66 × 39–44; sucker width ratio 1:1.62 *P. tortugae* von Wicklen, 1946 (see Manter 1934, Fig. 48)
- 36b. Ventral sucker not encircled by a fold of the body wall; forebody 13%–14% and post-testicular region 22%–29% of body length; egg large, 104–153 × 43–86; sucker width ratio 1:1.7–2.0 *P. sosoae* Bray and Justine, 2010 (Figs 3,4)
- 37a. Genital pore position at pharynx level or further anterior (oral sucker, etc.) 38
- 37b. Genital pore position further posterior; egg 82–86 long (collapsed in worms with ovary) and 64–66 × 30–38 (worms with no discernable ovary); sucker width ratio 1:1.06 *P. ablenesi*² Bray, 1987 (Figs 1A,B)
- 38a. Vitelline follicles noticeably interrupted lateral to gonads; egg 44–56 × 28–35; sucker width ratio 1:0.81–0.92 *P. maomao*^{2,3,11} Yamaguti, 1970 (Figs 115A,B)
- 38b. Vitelline follicles not interrupted lateral to gonads; egg 53–62 × 37–40; sucker width ratio 1:1.65–1.79 *P. sesokoensis*^{2,3} Dyer, Williams and Williams, 1988 (Fig. 1)

¹Figure(s) listed in parentheses at the end of each couplet refer to those included in the type description as indicated by the authority for each species. Where more than one authority is given or another reference is used, the source of the figure(s) is also indicated. *Pseudopecoelus scomberi* (Hafeezullah, 1971) Madhavi, 1975 is considered by Gibson (2014b) to belong in the genus *Pseudopecoeloides* Yamaguti, 1940; however, Madhavi and Lakshmi (2010), after re-examining material of this species available to them, did not observe a uroproct and concluded it belongs in *Pseudopecoelus*. Clearly, the status of this species needs to be clarified. In addition, Gib-

son (2014b) lists *Pseudopecoelus xishaensis* Gu and Shen, 1983 as a member of *Pseudopecoelina* Yamaguti, 1942.

²The following species were described with a cirrus pouch and/or no seminal receptacle: *P. ablennesi*, *P. acanthuri*, *P. brayi*, *P. brevivesiculatus*, *P. elongatus* ("feebly muscular sheath"), *P. hemilobatus*, *P. japonicus* ("muscular sheath"), *P. manteri*, *P. maomao*, *P. nossamani*, *P. pritchardae*, *P. puhipaka*, *P. scorpaenae*, *P. sesokoensis*, *P. sphyraenae*, and *P. umbrinae* (Yamaguti 1938; Manter 1947, 1954; Manter and van Cleave 1951; Hanson 1955; Sogandares-Bernal and Hut-ton 1959; Yamaguti 1970; Kruse 1977; Gupta and Sayal 1979; Bray 1987; Dyer *et al.* 1988; Madhavi and Lakshmi 2010). Cribb (2005) describes members of *Pseudopecoelus* as either possessing a small cirrus pouch or lacking one entirely. The seminal receptacle in these species is uterine and not canalic-ular, which might have led these authors to believe that the particular species they described lacked this feature. We agree with Gibson (2014b) and recognize herein these species in *Pseudopecoelus*.

³The pars prostatica was neither differentiated nor evident in *P. acanthuri*, *P. minutus*, *P. puhipaka*, *P. maomao*, *P. sesokoensis* and in *P. sewelli* (Nahhas and Cable 1964; Yamaguti 1970; Dyer *et al.* 1988; Bray 1990b). This feature in *P. brevivesiculatus* was neither described nor illustrated in Figs 4, 5 of Hanson (1955).

⁴Bray (1990b) noted that the anterior extent of the vitelline follicles in *P. sewelli* is quite variable – ranging from the mid-oesophagus (pre-acetabular) to the anterior hindbody. Among his type material, 13 worms had vitelline follicles that extended into the forebody, while 17 worms had vitelline folli-cles that either reached the level of the ventral sucker or were confined to the hindbody. He also stated that the position of the ventral sucker peduncle could have caused, in part, this vari-ation. Based on the holotype illustration of this species (see his Fig. 1A), we have elected in our key to include *P. sewelli* as possessing vitelline follicles extending anterior to the ven-tral sucker (see Couplet 1a); however, the reader should be aware that this particular character is quite variable in this species.

⁵*P. pyriformis* was described by Prudhoe and Bray (1973) with a body shape that varies from roughly triangular to broadly pyriform; however, the authors also commented that the seven specimens they measured were "in a contracted con-dition", and this is apparent in Fig. 10. This contraction prob-ably affected the appearance of certain features such as the testes, which were described as "transversely elongate – no doubt due to the contraction of the body", ovary, "transverse striations" in the hindbody, the presence of which "is probably due to contraction of the body", etc. Prudhoe and Bray (1973) also described that "anteriorly to the ventral sucker [in *P. pyri-formis*] there is a second transverse slit-like depression on the surface of the body" (see their Fig. 10). As with *P. hemiloba-tus*, this "transverse slit-like depression" is reminiscent of a similar feature in *Podocotyle bathyhelminthos* Blend and Dron-en, 2015 which possesses a "small transverse ridge" on the

ventral surface immediately anterior to the ventral sucker (Blend and Dronen 2015).

⁶*P. sphyraenae* was described by Yamaguti (1970) as pos-sessing a genital pore "ventral to pharynx or anterior part of esophagus". As the holotype of this species is illustrated (Fig 116A) with the genital pore at the level of the posterior phar-ynx, we have considered this species in our key to have a gen-ital pore at the pharynx level instead of further posterior.

⁷The genital pore position relative to the pharynx for *P. hemilobatus* was found to be a weak character as this feature was described by Manter (1954) as "opposite posterior half of pharynx or a little posterior to pharynx"; thus, the genital pore is neither exclusively at the pharynx level nor further posterior. Fig. 30 of Manter (1954) shows the genital pore posterior to the pharynx. In addition, *P. hemilobatus* was described as pos-sessing "a transverse groove in the ventral surface just anterior to the acetabulum [that] might be more than a fold but its aper-ture does not have a definite boundary nor musculature" (see Fig. 30 of Manter 1954). This groove is very reminiscent of what was noted by two of us (CKB, NOD) in *Podocotyle ba-thyhelminthos* Blend and Dronen, 2015; we described in this species a "small transverse ridge" on the ventral surface im-mediately anterior to the ventral sucker that made the sucker slightly elevated (Blend and Dronen 2015).

⁸*P. scorpaenae* was originally described by Manter (1947) as *Neopecoelus scorpaenae* Manter, 1947 and it possesses "narrow ceca [that] open through two ani which lie dorsally near [the] posterior end...these ani are inconspicuous in pre-served specimens but were clearly observed in living speci-mens." Overstreet (1969) produced serial sagittal sections of a specimen of this species he collected and did not observe ani; therefore, he moved this species into *Pseudopecoelus* and declared *Neopecoelus* a junior synonym of *Pseudopecoelus*.

⁹*P. priacanthi* was originally described by MacCallum (1921) as *Allocreadium priacanthi* MacCallum, 1921 and it possessed a "fairly large cirrus sac"; however, Manter (1947) moved this species to *Pseudopecoelus* stating that "it cannot belong in the genus *Allocreadium* because of its lack of a cir-rus sac."

¹⁰*P. epinepheli* was described and illustrated (Fig. 13) by Wang (1982) as possessing a "slightly pointed anterior end and truncate posterior end"; however, we cannot rule out the possi-bility here that this might be an artifact of contraction/fixation.

¹¹*P. maomao* was described by Yamaguti (1970) having a sucker width ratio of 1:1.1–1.5. This cannot be correct given the widths provided for both suckers (oral sucker width 120–160, ventral sucker width 110–130) and the type description that stated "acetabulum smaller than oral sucker".

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