



The deep-sea fish digenean genus *Tellervotrema* Gibson & Bray, 1982 (Opecoelidae: Plagioporinae): Re-evaluation of the type species, *T. armstrongi* Gibson & Bray, 1982 and *T. beringi* (Mamaev, 1965)

CHARLES K. BLEND¹, NORMAN O. DRONEN², SCOTT L. GARDNER³,
GABOR R. RACZ³ & HOWARD W. ARMSTRONG²

¹58 Rock Creek Dr., Corpus Christi, Texas 78412-4214, U.S.A. E-mail: ilovethesea@att.net

²Laboratory of Parasitology, Department of Wildlife and Fisheries Sciences, College of Agriculture and Life Sciences, Texas A&M University, 2258 TAMU, College Station, Texas 77843-2258, U.S.A. E-mail: n-dronen@tamu.edu

³Harold W. Manter Laboratory of Parasitology, W 529 Nebraska Hall, University of Nebraska-Lincoln, Lincoln, Nebraska 68588-0514, U.S.A. E-mail: slg@unl.edu, grac2@unl.edu

Abstract

Tellervotrema Gibson & Bray, 1982 (Digenea: Opecoelidae) was erected for *Podocotyle*-like species that possess a symmetrical pair of isolated groups of vitelline follicles in the posterior forebody, lack them dorsal to the caeca and parasitize archybenthal macrourid fishes. *Tellervotrema armstrongi* Gibson & Bray, 1982 is redescribed from the type host, the common Atlantic grenadier, *Nezumia aequalis* (Günther), *N. cyrano* Marshall & Iwamoto, and from an unidentified macrourid collected from the northern Gulf of Mexico. *Tellervotrema beringi* (Mamaev, 1965) is redescribed from the giant grenadier, *Albatrossia pectoralis* (Gilbert), and *Coryphaenoides* sp. obtained from off Oregon. The following six features are suggested to distinguish *T. armstrongi* and *T. beringi*: egg size; position of the genital pore; posterior extent of the cirrus-sac relative to the ventral sucker; testes volume relative to hindbody size; anterior extent of the paired vitelline groups in the forebody; and geographic locality. The generic diagnosis of *Tellervotrema* is amended to include circumcaecal vitelline follicles, and the presence of the vitelline gap itself was found to be a more consistent diagnostic generic character than the location of the resulting pair of distinct, isolated groups of vitelline follicles created by the gap. A neotype and paraneotypes are designated for *T. beringi*. The following new host and locality records are established: first original report of *T. armstrongi* from *N. cyrano*; first report of a member of *Tellervotrema* from the giant grenadier, *A. pectoralis*; and the waters off Oregon are a new locality record for *Tellervotrema*, a genus in the North Pacific Ocean known only from the Bering Sea and off Japan. A comprehensive listing of all parasites previously reported from the four macrourid species examined herein is given and intermediate hosts are postulated through which species of *Tellervotrema* may complete their life cycles in the deep.

Key words: *Albatrossia pectoralis*, *Coryphaenoides* sp., deep sea, Digenea, Gulf of Mexico, Macrouridae, *Nezumia aequalis*, *Nezumia cyrano*, Opecoelidae, Oregon, Plagioporinae, redescription, *Tellervotrema armstrongi*, *Tellervotrema beringi*

Introduction

Gibson & Bray (1982) erected the trematode genus *Tellervotrema* Gibson & Bray, 1982 for *Podocotyle*-like species that possess a symmetrical pair of isolated groups of vitelline follicles in the posterior forebody, lack them dorsal to the caeca and parasitize archybenthal macrourid fishes (also known as grenadiers or rattails). The type species, *Tellervotrema armstrongi* Gibson & Bray, 1982 was described from the intestine of the common Atlantic grenadier, *Nezumia aequalis* (Günther), collected from 820–1,000 m depth off the west coast of Scotland (Gibson & Bray 1982). These authors also noted what appeared to be *T. armstrongi*, described earlier as “*Plagioporus* sp. n. #1” by Armstrong (1974, p. 82–86), obtained from the intestine of *N. aequalis* and an unidentified macrourid collected from 548–732 m depth from the northeastern Gulf of Mexico. Gibson & Bray (1982) further speculated that “*Plagioporus* sp. n. #2”, also described by Armstrong (1974, p. 86–89) and acquired from the intestine of a single

N. aequalis collected from 713 m depth from the northeastern Gulf of Mexico, may have been a smaller and/or contracted form of *T. armstrongi*. In recognition that this digenean species was first described and illustrated by Armstrong (1974) in his unpublished doctoral dissertation, Gibson & Bray (1982) erected *T. armstrongi* as a patronym for Dr. Howard W. Armstrong. Blend (1996, p. 141–145) later reported *T. armstrongi* from the intestine and pyloric caecum of *N. aequalis* and *Nezumia cyrano* Marshall & Iwamoto obtained from depths of 473–1,170 m in the northcentral to northeastern Gulf of Mexico. Recently, Bray & Kuchta (2006) reported this digenean from *N. aequalis* collected at 1,000–1,050 m depth off the Outer Hebrides, Scotland.

Tellervotrema beringi (Mamaev, 1965) was established by Gibson & Bray (1982) as the second species within this genus. *Tellervotrema beringi*, originally described by Mamaev (1965) as *Plagioporus beringi* Mamaev, 1965 was collected from the stomach of seven specimens of an unidentified macrourid of the genus *Coryphaenoides* Gunnerus obtained from 30 miles west of the Pribilof Islands, Alaska, and near Cape Navarin, Russia, in the Bering Sea at 150–500 m depth. Additional reports are few and include a listing of *P. beringi* by Yamaguti (1971, p. 183), and a report of either species of *Tellervotrema* within four, non-original checklists focusing on the helminth parasites of fishes from the deep sea (Bray 1995; Klimpel *et al.* 2001, 2009) and from the Gulf of Mexico (Overstreet *et al.* 2009, p. 459).

Tellervotrema katadara (Kuramochi, 2001) was first described as *Plagioporus katadara* Kuramochi, 2001 from the intestine of the bathygadine macrourid *Gadomus colletti* Jordan & Gilbert from 500–600 m depth in Tosa Bay, Japan (Kuramochi 2001). Kuramochi (2009) later transferred *P. katadara* to *Tellervotrema* based on observation of eight gravid specimens of the parasite collected from the intestine of the longfin grenadier, *Coryphaenoides longifilis* Günther, found at 1,196 m depth off the Pacific coast of northern Honshu, Japan. Recently, Kuramochi (2011) suppressed *T. katadara* as a junior synonym of *T. beringi* based on work with ten additional parasite specimens he found in the pyloric caecum of the short-tailed grenadier, *Nezumia proxima* (Smith & Radcliffe), obtained from off Jōgashima Island, Japan. We contacted Dr. Toshiaki Kuramochi, who graciously sent us his specimens of *T. beringi* (= *T. katadara*) from Japan, and the taxonomic status of this material will be investigated in a subsequent report. Besides *T. armstrongi* and *T. beringi*, there are no other nominal species within *Tellervotrema*.

The purpose of this study was to add to our knowledge of *Tellervotrema* and re-evaluate the diagnostic combination of characteristics that distinguish this genus through the examination and redescription of unpublished specimens of *T. armstrongi* and *T. beringi*. In addition, this paper documents new and original host and locality records for this parasite genus and provides a comprehensive listing of all parasites reported from the three nominal macrourid species examined in this study (Table 1).

TABLE 1. Parasites reported from the macrourids *Albatrossia pectoralis* (Gilbert, 1892), *Coryphaenoides* sp., *Nezumia aequalis* (Günther, 1878), and *Nezumia cyrano* Marshall & Iwamoto, 1973.

Host / Parasite Species	Infection Site	Locality	Reference(s)
<i>Albatrossia pectoralis</i> (Gilbert, 1892)			
¹ CO – <i>Brachiella annulata</i> Markevich, 1940	Mouth	Off California coast	Noble 1973
CO – <i>Brachiella</i> (= <i>Neo-brachiella nitida</i>) (Wilson, 1915)	Mouth	N. Pacific	Wilson 1915, 1935; Yamaguti 1963b ² ; Love & Moser 1976 ² , 1983 ²
¹ D – <i>Brachyphallus crenatus</i> (Rudolphi, 1802)	Stomach	Coast of Japan off eastern Hokkaido	Machida & Araki 1994
D – <i>Derogenes macrostoma</i> Yamaguti, 1938	Stomach	Northern Honshu, Japan	Kuramochi 2009
D – <i>Dinosoma lophiomi</i> Toman, 1973	Stomach	Northern Honshu, Japan	Kuramochi 2009
D – <i>Dinosoma manteri</i> Yamaguti, 1938	Stomach	Northern Honshu, Japan	Kuramochi 2009

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
D – <i>Dinosoma oregonensis</i> McCauley & Pequegnat, 1968	Stomach	Coast of Oregon	McCauley & Pequegnat 1968; Yamaguti 1971 ² ; Love & Moser 1976 ² , 1983 ² ; Bray 1995 ² ; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; HWML Coll. (Access. #42544, 42546); USNPC Coll. (Access. #71290) ³
D – <i>Dinosoma pectoralis</i> McCauley & Pequegnat, 1968	Stomach	Coast of Oregon	McCauley & Pequegnat 1968; Yamaguti 1971 ² ; Love & Moser 1976 ² , 1983 ² ; Bray 1995 ² ; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; HWML Coll. (Access. #42529, 42531–42534); USNPC Coll. (Access. #71291)
D – <i>Gonocerca crassa</i> Man- ter, 1934	Stomach	Northern Honshu, Japan	Kuramochi 2009
D – <i>Gonocerca oregonensis</i> McCauley, Pequegnat & Brownell, 1970	Stomach	Coast of Oregon	McCauley <i>et al.</i> 1970; Yamaguti 1971 ² ; Love & Moser 1976 ² , 1983 ² ; Bray 1995 ² ; Blend 1996 ² ; HWML Coll. (Access. #42538)
D – <i>Gonocerca oshoro</i> Shi- mazu, 1970	Ovary	Gulf of Alaska, Emperor Range, Pacific Ocean	Shimazu 1970; Love & Moser 1976 ² , 1983 ² ; Moles 1982 ² ; Korotaeva 1985, 1990; Kurochkin 1985; Bray 1995 ² ; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²
D – <i>Lepidapedon coelo- rhynchi</i> Yamaguti, 1938	Intestine	Northern Honshu, Japan	Kuramochi 2009
D – <i>Lepidapedon elongatum</i> (Lebour, 1908)	Intestine, pyloric caecum	Coast of Japan off east- ern Hokkaido	Machida & Araki 1994
D – Lepocreadiidae sp. (= <i>Tellervotrema beringi</i> (Mamaev, 1965))	Intestine	NE Pacific Ocean	Present study; HWML Coll. (Access. #42665)
D – <i>Pseudoplagioporus</i> sp.	Intestine	Northern Honshu, Japan	Kuramochi 2009
D – <i>Tellervotrema beringi</i> (Mamaev, 1965)	Intestine	Coast of Oregon	Present study
D – Digenean Genus <i>incertae sedis</i> or undetermined	GI tract ⁴ ; stom- ach	Off California coast, northern Pacific Ocean	Noble 1973; Bray 1995 ² ; Blend 1996 ² ; HWML Coll. (Access. #42957)
¹ M – <i>Cyclocotyloides pinguis</i> (Linton, 1940)	Mouth, gills	Coast of Oregon; off Agattu Island in Aleutian chain, NW Pacific Ocean	Linton 1940; Price 1943; Yamaguti 1963a ² ; McCauley & Smoker 1969; Noble 1973; Love & Moser 1976 ² , 1983 ² ; Mamaev & Avdeev 1981; Moles 1982 ² ; Blend 1996 ² ; Kritsky & Klimpel 2007 ⁵ ; HWML Coll. (Access. #23526, 42645); USNPC Coll. (Access. #08157, 08158, 70427)
¹ MY – <i>Auerbachia pulchra</i> Lom, Noble & Laird, 1975	Gall bladder	Off northern California	Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977d
MY – <i>Auerbachia</i> sp.	Gall bladder	Off central California	Noble 1973; Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Klimpel <i>et al.</i> 2009 ²
MY – <i>Bipteria minima</i> Kova- leva, Zubchenko & Krasin, 1983	Urinary bladder	Okhotsk Sea	Kovaleva <i>et al.</i> 1983
MY – <i>Ceratomyxa rara</i> Kovaleva, Gaevskaya & Kra- sin, 1986	Gall bladder	Near the Kuril Isles, northern Pacific Ocean	Kovaleva <i>et al.</i> 1986; Klimpel <i>et al.</i> 2001 ² , 2009 ²

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
MY – <i>Davisia aurita</i> Koval-eva, Gaevskaya & Krasin, 1986	Urinary bladder	Okhotsk Sea	Kovaleva <i>et al.</i> 1986; Klimpel <i>et al.</i> 2001 ² , 2009 ²
MY – <i>Davisia coryphanoidea</i> Yoshino & Noble, 1973	Kidney tubules, urinary bladder	Off coast of northern California & Washington	Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977d; Klimpel <i>et al.</i> 2009 ²
MY – <i>Davisia pectoralis</i> (Moser & Noble, 1975)	Kidney tubules, urinary bladder	Off northern California	Moser & Noble 1975, 1977d; Love & Moser 1976 ² , 1983 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²
MY – <i>Leptotheca armatura</i> Yoshino & Moser, 1974	Gall bladder, kidney tubules, urinary bladder	Off central and northern California & Washington	Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1976; Klimpel <i>et al.</i> 2009 ²
MY – <i>Leptotheca informis</i> Auerbach, 1910	Gall bladder	Off central and northern California & Washington	Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1976; Klimpel <i>et al.</i> 2009 ²
MY – <i>Leptotheca</i> sp.	Gall bladder	Off California coast	Noble 1973
MY – <i>Myxoproteus californicus</i> Yoshino & Noble, 1973	Kidney tubules, urinary bladder	Off northern California & Washington	Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977c; Klimpel <i>et al.</i> 2009 ²
MY – <i>Sinuolinea magna</i> Yoshino & Noble, 1973	Urinary bladder	Off northern California	Yoshino & Moser 1974; Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977a; Klimpel <i>et al.</i> 2009 ²
MY – <i>Sinuolinea triangulata</i> Schulmar, 1966	Kidney	Off northern California	Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977a
MY – <i>Zschokkella meglitschi</i> Moser & Noble, 1977	Urinary bladder	Off central California	Love & Moser 1976 ² , 1983 ² ; Moser & Noble 1977b
¹ N – <i>Anisakis</i> sp. larvae	Mesenteries, peritoneum, viscera ⁴	Off California coast	Noble 1973; Blend 1996 ²
N – <i>Capillaria</i> sp.	Stomach	Off California coast	Noble 1973; Blend 1996 ²
N – <i>Neoscaraphis insulana</i> (Solov'eva, 1991)	Stomach	Near northern Kuril Islands, Sea of Okhotsk, NW Pacific Ocean	Solov'eva 1991; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²
N – Nematoda <i>Coryphaenoides</i> sp.	Stomach	NE Pacific Ocean	HWML Coll. (Access. #42586, 42870)
¹ A – <i>Corynosoma reductum</i> (Linstow, 1905)	Intestine	Bering Sea	Mamaev 1965; Blend 1996 ²
A – <i>Echinorhynchus gadi</i> Zoega in Müller, 1776	Intestine	Bering Sea	Mamaev 1965; Blend 1996 ²
¹ C – Abothriinae gen. sp.	Intestine	Bering Sea	Mamaev 1965; Blend 1996 ²
C – <i>Grillotia erinacea</i> Beneden, 1858	Body cavity, stomach wall	Bering Sea	Mamaev 1965; Blend 1996 ²
C – <i>Nybelinia surmenicola</i> Okada, 1929 larva	Body cavity, stomach wall, intestine	Bering Sea	Mamaev 1965; Blend 1996 ²
C – <i>Phyllobothrium</i> sp. larvae	Intestine	Bering Sea	Mamaev 1965; Blend 1996 ²
C – <i>Scolex pleuronectis</i> (Müller, 1788)	Intestine, gall bladder	Bering Sea	Mamaev 1965; Blend 1996 ²

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
C – Cestoda	Intestine	NE Pacific Ocean	HWML Coll. (Access. #42573, 42575)
CO – <i>Clavella adunca</i> (Ström, 1762)	Gills	Coast of Chile, Pacific Ocean	Castro-Romero 1994; Klimpel <i>et al.</i> 2001 ² , 2009 ²
CO – <i>Luetkenia astrodermi</i> Claus, 1864	Surface of fish	Messina, Italy	Claus 1864; Yamaguti 1963b ²
D – Allocreadiidae sp.	Stomach	NE Pacific Ocean	HWML Coll. (Access. #42644)
D – <i>Derogenes varicus</i> (Müller, 1784)	Stomach	Bering Sea	Mamaev 1965; Bray 1995 ² ; Blend 1996 ²
D – <i>Dinosoma oregonensis</i> McCauley & Pequegnat, 1968	Stomach	NE Pacific Ocean	HWML Coll. (Access. #42548)
D – <i>Dinosoma pectoralis</i> McCauley & Pequegnat, 1968	Stomach	NE Pacific Ocean	HWML Coll. (Access. #42530)
D – <i>Dinosoma tortum</i> Yamaguti, 1938	Stomach	Bering Sea	Mamaev 1965; Bray 1995 ² ; Blend 1996 ²
D – <i>Gonocerca oregonensis</i> McCauley, Pequegnat & Brownell, 1970	Stomach	NE Pacific Ocean	HWML Coll. (Access. #42539, 42540, 42542)
D – <i>Lepidapedon abyssensis</i> (McCauley, 1968) ⁶	Intestine	Pacific Ocean, 65 miles west of Newport, Oregon	McCauley 1964, 1968; Yamaguti 1971 ² ; Love & Moser 1976 ² , 1983 ² ; Bray 1995 ² ; Blend 1996 ² ; USNPC Coll. (Access. #60182)
D – <i>Lepidapedon desotoensis</i> Blend, Dronen & Armstrong, 2000	Intestine, pyloric caecum	NE Gulf of Mexico	Armstrong 1974; Bray 1995 ² ; Bray & Gibson 1995; Blend 1996 ² ; Blend <i>et al.</i> 2000; Klimpel <i>et al.</i> 2009 ² ; Overstreet <i>et al.</i> 2009 ²
D – <i>Lepidapedon filiformis</i> McCauley, 1968	Intestine	NE Pacific Ocean	HWML Coll. (Access. #42675)
D – <i>Lepidapedon gadi</i> Yamaguti, 1934	Intestine	Bering Sea	Mamaev 1965; Bray 1995 ² ; Blend 1996 ²
D – <i>Lepidapedon luteum</i> Yamaguti, 1938	Intestine	Maisaka, Japan; NE Pacific Ocean	Yamaguti 1938, 1958 ² , 1971 ² ; Bray 1995 ² ; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; HWML Coll. (Access. #42618–42620, 42622, 42629, 42632, 42633, 42636, 42637, 42642, 42679, 42681, 42692, 42693, 42732, 42733, 42745, 42749)
D – <i>Lepidapedon oregonensis</i> McCauley, 1968	Intestine	NE Pacific Ocean	HWML Coll. (Access. #42695–42698, 42702–42704, 42706, 42707, 42711, 42715, 42717, 42721, 42755, 42762)
D – <i>Lepidapedon yaquina</i> McCauley, 1968	Intestine	NE Pacific Ocean	HWML Coll. (Access. #42728)
D – <i>Lepidapedon</i> sp. (= <i>Tellervotrema beringi</i> (Mamaev, 1965) for HWML Access. #42743)	Intestine, stomach	NE Pacific Ocean	Present study; HWML Coll. (Access. #42735, 42736, 42741–42744, 42746, 42748, 42751, 42752, 42754)
D – <i>Paraccacladium</i> sp.	Rectum ⁴	NE Atlantic Ocean	Gibson 1977; Blend 1996 ²
D – <i>Tellervotrema beringi</i> (Mamaev, 1965)	Intestine, stomach	Bering Sea; coast of Oregon	Mamaev 1965; Yamaguti 1971 ² ; Gibson & Bray 1982; Bray 1995 ² ; Blend 1996 ² ; Present study
D – <i>Tubulovesicula lindbergi</i> (Layman, 1930)	Stomach	Bering Sea	Mamaev 1965; Bray 1995 ² ; Blend 1996 ²

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
D – Digenea (= <i>Tellervotrema beringi</i> (Mamaev, 1965) for HWML Access. #42855)	Intestine, stomach	NE Pacific Ocean	Present study; HWML Coll. (Access. #42772, 42774, 42775, 42855, 42959, 42960)
M – <i>Cyclocotyloides pinguis</i> (Linton, 1940)	Buccal cavity; gills	Bering Sea, USSR; Gulf of California, Mexico, NW slope of Guaymas Basin; NE Pacific Ocean	Mamaev & Lyadov 1975; Payne 1987; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Kritsky & Klimpel 2007 ⁵ ; HWML Coll. (Access. #23525, 23528, 23531–23534, 42646, 42654, 48332)
M – <i>Diclidophoropsis tissieri</i> Gallien, 1937	Gills	Bering Sea	Mamaev 1965; Blend 1996 ²
M – <i>Macruricotyle clavipes</i> Mamaev & Lyadov, 1975	Gills	Antarctic waters; Indian Ocean	Mamaev & Lyadov 1975; Mamaev & Avdeev 1984; Klimpel <i>et al.</i> 2001 ² , 2009 ²
MY – <i>Myxidium coryphaenoidium</i> Noble, 1966	Gall bladder	Off coast of Mexico, Pacific Ocean	Noble 1966; Klimpel <i>et al.</i> 2001 ² , 2009 ²
MY – <i>Myxidium</i> spp.	Gall bladder ⁴	Coast of California, Mexico & Central America, Pacific Ocean	Noble & Collard 1970; Klimpel <i>et al.</i> 2001 ² , 2009 ²
N – <i>Anisakis</i> sp. larvae	Body cavity, wall of internal organs	Bering Sea; off Japan	Yamaguti 1941; Mamaev 1965; Blend 1996 ²
N – <i>Contracaecum aduncum</i> Rudolphi, 1802 larvae	GI tract, mesenteries ⁴	Bering Sea	Mamaev 1965; Blend 1996 ²
N – Nematoda	Intestine, stomach	NE Pacific Ocean	HWML Coll. (Access. #42579, 42581, 42585, 42592, 42597, 42603)
<i>Nezumia aequalis</i> (Günther, 1878)			
C – <i>Nybelinia</i> sp pleurocercoid, forms I & II ⁷	Mesenteries, peritoneum of stomach & intestine, stomach wall	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – <i>Nybelinia</i> sp. pleurocercoid, form III	Free in body cavity, mesenteries, peritoneum of stomach & body cavity	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – Pleurocercoid, form I (<i>incertae sedis</i>)	Body cavity, mesenteries, peritoneum of stomach & intestine	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – Pleurocercoid, form II (<i>incertae sedis</i>)	Mesenteries, stomach wall	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – Pleurocercus, form II	Mesenteries	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – <i>Scolex pleuronectis</i> (Müller, 1788), form I	Intestine, pyloric caeca, rectum	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ² ; Jensen 2009 ²
C – Cestoda larvae	Stomach	Rockall Trough off west coast of British Isles	Mauchline & Gordon 1984; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
D – <i>Buticulotrema stenauchenus</i> Blend, Dronen & McEachran, 1993	Intestine, pyloric caeca	NE Gulf of Mexico	Blend <i>et al.</i> 1993; Bray 1995 ² ; Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ² ; USNPC Coll. (Access. #82540)
D – <i>Dissosaccus laevis</i> (Linton, 1898)	Stomach	NE Gulf of Mexico	Armstrong 1974; Bray 1995 ² ; Blend 1996 ²
D – Genus novum B, sp. n. (Opecoelidae)	Intestine	NE Gulf of Mexico	Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ²
D – <i>Glomicirrus macrouri</i> (Gaevskaya, 1975)	Intestine, stomach	Caribbean Sea off Panama; Northcentral to NE Gulf of Mexico; West coast of British Isles off Tory Island, NW Ireland	Armstrong 1974; Gibson & Bray 1986; Bray 1995 ² ; Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ² ; BMNH Coll. (Access. #1983.12.13.9) ³
D – <i>Glomicirrus</i> sp.	Stomach	Off Ireland, NE Atlantic Ocean	BMNH Coll. (Access. #1992.10.8.22)
D – <i>Gonocerca minuta</i> Campbell & Munroe, 1977	Stomach	Rosemary Bank, Tory Island, NE Atlantic Ocean	BMNH Coll. (Access. #1990.6.28.32–33 & 43)
D – <i>Gonocerca phycidis</i> Manter, 1925	Branchial chamber, intestine, stomach	Caribbean Sea off Honduras & Panama; NE Gulf of Mexico	Armstrong 1974; Bray 1995 ² ; Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ²
D – <i>Lepidapedon nezumiatis</i> Blend, Dronen & Armstrong, 2000	Intestine	NE Gulf of Mexico	Armstrong 1974; Bray 1995 ² ; Bray & Gibson 1995; Blend 1996 ² ; Blend <i>et al.</i> 2000; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ²
D – <i>Podocotyle (Neopodocotyle)</i> sp. n.	Intestine	NE Gulf of Mexico	Armstrong 1974; Bray 1995 ² ; Blend 1996 ²
D – <i>Tellervotrema armstrongi</i> Gibson & Bray, 1982	Intestine, pyloric caeca	Northcentral to NE Gulf of Mexico; off west coast of Scotland/Outer Hebrides and Ireland, NE Atlantic Ocean	Armstrong 1974; Gibson & Bray 1982; Bray 1995 ² ; Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Bray & Kuchta 2006; Overstreet <i>et al.</i> 2009 ² ; Present study; BMNH Coll. (Access. #1981.12.4.12–27, 1992.10.8.16–18); USNPC Coll. (Access. #97378)
¹ I – <i>Syscenus infelix</i> Harger, 1881	Dorsal midline, immediately behind first dorsal fin	NW Atlantic Ocean	Ross <i>et al.</i> 2001
M – <i>Macrouridophora nezumiae</i> (Munroe, Campbell & Zwerner, 1981)	Gills	NE & NW Atlantic Ocean	Rubec & Dronen 1994; Blend 1996 ²
M – <i>Polycliphora nezumiae</i> Lambert & Euzet, 1980	Gills	Off coast of Senegal; NE Atlantic Ocean	Lambert & Euzet 1980; Vassiliades 1985; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²
M – <i>Syncoelicotyloides macruri</i> Mamaev & Brashovyan, 1989	Gills	Walvis Ridge, SE Atlantic Ocean	Mamaev & Brashovyan 1989 ⁸
MY – <i>Myxobolus mexicanus</i> Yoshino & Noble, 1973	Kidney	Gulf of Mexico	Moser & Noble 1977a
N – <i>Anisakis</i> type larva, form I	Mesenteries, peritoneum of stomach & intestine, stomach wall	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²

continued next page

TABLE 1. (continued)

Host / Parasite Species	Infection Site	Locality	Reference(s)
N – <i>Anisakis</i> type larva, form II	Mesenteries	NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Ascarophis</i> sp. n. #1	Intestine, pyloric caeca, stomach	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Contracaecum</i> type larva, form I	Mesenteries	NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Contracaecum</i> type larva, form II	Peritoneum of stomach, intestine, pyloric caeca & in mesenteries	Caribbean Sea off Panama; NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Contracaecum</i> type larva, form III	Mesenteries	NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Contracaecum</i> type larva, form IV	Mesenteries	NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – <i>Johnstonmawsonia</i> sp. n. #2	Gall bladder, pyloric caeca	NE Gulf of Mexico	Armstrong 1974; Blend 1996 ²
N – Nematoda	Stomach	Rockall Trough off west coast of British Isles	Mauchline & Gordon 1984; Blend 1996 ² ; Klimpel <i>et al.</i> 2001 ² , 2009 ²
<i>Nezumia cyrano</i> Marshall & Iwamoto, 1973			
D – <i>Dissosaccus laevis</i> (Linton, 1898)	Stomach	Gulf of Mexico	Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ²
D – <i>Lepidapedon nezumiatis</i> Blend, Dronen & Armstrong, 2000	Intestine	NE Gulf of Mexico	Blend 1996; Blend <i>et al.</i> 2000; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ² ; HWML Coll. (Access. #39933); USNPC Coll. (Access. #88280)
D – <i>Tellervotrema armstrongi</i> Gibson & Bray, 1982	Intestine, pyloric caeca	Northcentral to NE Gulf of Mexico	Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ² ; Overstreet <i>et al.</i> 2009 ² ; Present study
D – Unidentified Trematode C	Body cavity, liver	Northcentral to NE Gulf of Mexico	Blend 1996; Klimpel <i>et al.</i> 2001 ² , 2009 ²
MY – <i>Sphaeromyxa intermedia</i> Moser & Noble, 1977	Gall bladder	Caribbean Sea	Moser & Noble 1977a

¹A—Acanthocephala; C—Cestoda; CO—Copepoda; D—Digenea; I—Isopoda; M—Monogenea; MY—Myxosporida; N—Nematoda.

²These references are host-parasite checklists and should not be considered as original records. See Appendix 1 of Blend (1996, p. 202–303).

³Specimens of this parasite species collected from this host species are currently housed in the Natural History Museum (BMNH) Collections, London, U.K.; Harold W. Manter Laboratory of Parasitology (HWML), Univ. of Nebraska-Lincoln, Lincoln, Nebraska, U.S.A.; United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A. (Accession numbers given where available).

⁴Record(s) for this particular parasite species had no information for this characteristic, so the most likely infection site is given where possible.

⁵See Materials & Methods of Kritsky & Klimpel (2007).

⁶*Lepidapedon luteum* var. *abyssensis* var. nov. McCauley, 1964 & *Lepidapedon luteum abyssensis* McCauley, 1968 are considered junior synonyms of this species (see Yamaguti [1971, p. 159]).

⁷Armstrong (1974, p. 179–180) listed both forms together as it was a “mixed infection.”

⁸While the host species reported is *Macrurus holotrachys* (non Günther, 1878) (= *N. aequalis*), Rubec *et al.* (1995, p. 959), stated that the host is most likely the ridge scaled rattail, *Macrurus carinatus* (Günther, 1878). According to Cohen *et al.* (1990), *M. holotrachys* is strictly known from the Patagonian slope in the southwestern Atlantic and is frequently confused with *M. carinatus*, a closely related species widely distributed in the southern Atlantic.

Material and methods

Eighty-eight specimens of the common Atlantic grenadier, *Nezumia aequalis*, and 14 specimens of *Nezumia cyrano* were examined for parasites. Parasites from both species of *Nezumia* Jordan described herein were collected aboard ship or procured from fishes housed in the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University, College Station, Texas, USA. Specimens of *N. aequalis* relevant to this study were obtained and examined by one of us (HWA) from the upper slope of the northeastern Gulf of Mexico off Florida and Alabama in the DeSoto Canyon area. Specimens of *N. aequalis* collected from off Florida by the National Marine Fisheries Service (NMFS), Pascagoula, Mississippi, USA and GI tracts of *N. aequalis* along with a single unidentified macrourid obtained from off Florida by Dr. Thomas Bright (retired), Department of Oceanography, Texas A&M University, were given to and examined by HWA. Additional *N. aequalis* specimens were obtained by HWA from the northeastern Gulf of Mexico and housed in the TCWC until examined by two of us (CKB & NOD). Specimens of *N. cyrano* relevant to this study were from the LGL Collection (LGL) housed at the TCWC and obtained from off Florida and Louisiana. An unknown number of the giant grenadier, *Albatrossia pectoralis* (Gilbert), and two individuals of an unidentified macrourid species of *Coryphaenoides* were collected aboard ship and examined for parasites by Dr. James E. McCauley (deceased), Department of Oceanography, Oregon State University, Corvallis, Oregon, USA. Three sets of specimens of *Tellervotrema* from these two hosts are currently housed in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska-Lincoln, Lincoln, Nebraska, USA (HWML 42665, 42743, 42855). These digeneans were collected from three locations within the northeastern Pacific Ocean: 80.5 km west of Waldport, Oregon; 104.6 km west of Newport, Oregon; and 136.8 km west of Newport, Oregon. All fish were collected by otter trawl. Specimens of *N. aequalis* and *N. cyrano* collected by HWA were examined for parasites onboard ship, either with live specimens being removed from the GI tract and heat-fixed under slight coverslip pressure in hot AFA and preserved in 70% ethanol, or freshly-caught fish were injected at the mouth, anus and body cavity with AFA to live fix endohelminths, preserved in 10% formalin onboard ship, and transported back to the university where fish were transferred to and stored in 70% ethanol prior to dissection. Entire specimens and GI tracts of *N. aequalis* and an unidentified macrourid obtained from NMFS and Dr. Bright as well as individuals of *N. cyrano* from LGL were presumably cold-fixed in 10% formalin and preserved in either 70% ethanol or formalin. Digenea from *Nezumia* spp. were stained in Semichon's carmine or alum cochineal, sometimes counterstained in fast green and mounted in Kleermount or Permount. Specimens of *A. pectoralis* 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 & McCauley 1964; McCauley 1964, 1968). Digeneans from these two macrourid host species were stained with either Mayer's carmalum or Van Cleave's hematoxylin combination and mounted in Canada balsam (see McCauley & Pequegnat 1968). Drawings were made with the aid of a drawing tube and photographs were taken with a Nikon Superhigh-Performance 3× Zoom Coolpix 990 digital camera. Measurements are in micrometers (µm) with the range followed by the mean in parentheses; the number [n] of measurements is also noted. Measurements from conspecific specimens fixed *in situ* were used only if they generally did not appear to be significantly different from measurements of those individuals heat-fixed live. The identification of the fish for this study was based on Cohen *et al.* (1990), and the fish classification and authorities follow FishBase (Froese & Pauly 2012). The identification of the digeneans was based on Gibson & Bray (1982) and Cribb (2005), and ecological terms follow Bush *et al.* (1997).

Additional abbreviations used are: BM(NH), The British Museum (Natural History) Collection at The Natural History Museum, London, UK; USNPC, The United States National Parasite Collection, Beltsville, Maryland, USA; HWA, Dr. Howard W. Armstrong; JEM, Dr. James E. McCauley.

Results

Family Opecoelidae Ozaki, 1925

Subfamily Plagioporinae Manter, 1947

Genus *Tellervotrema* Gibson & Bray, 1982***Tellervotrema armstrongi* Gibson & Bray, 1982**

(Figs. 1–3)

Synonyms: *Plagioporus* sp. n. #1 & #2 of Armstrong (1974).**Type-host:** *Nezumia aequalis* (Günther); Gadiformes: Macrouridae: Macrourinae; common Atlantic grenadier.**Other hosts:** *Nezumia cyrano* Marshall & Iwamoto; Gadiformes: Macrouridae: Macrourinae. Unidentified macrourid; Gadiformes: Macrouridae.**Localities:** *N. aequalis*: Northeastern Gulf of Mexico, 28°02'N, 85°37'W, depth = 585 m, 24/June/1971; 28°15'N, 86°06'W, depth = 589 m, 26/June/1971; 28°22'N, 86°31'W, depth = 713 m, 26/June/1971; 28°31'N, 86°33'W, depth = 534, 27/June/1971; 28°36'N, 86°36'W, depth = 473 m, 27/June/1971; 28°36'N, 86°55'W, depth = 695 m, 28/June/1971; 28°42'N, 86°46'W, depth = 548 m, 28/June/1971; 28°53'N, 86°57'W, depth = 655 m, 29/June/1971; 28°54'N, 86°55'W, depth = 640 m, 12/February/1970; 28°59'N, 86°49'W, depth = 519 m, 29/June/1971; 29°27'N, 86°57.1'W, depth = 585–732 m, 19/July/1967. *N. cyrano*: Northcentral and northeastern Gulf of Mexico, 27°31.1'N, 89°48.9'W, depth = 1,064 m, 15/November/1984; 28°06'N, 86°35.3'W, depth = 1,170 m, 18/April/1984. Unidentified macrourid: Northeastern Gulf of Mexico, 29°27'N, 86°57.1'W, depth = 637 m, 19/July/1967.**Site:** Intestine; pyloric caecum.**Deposited Specimens:** Collector HWA, NMFS & Dr. Thomas Bright, BM(NH) vouchers NHMUK 2012.3.7.1–19 (21 adult & 6 immature), USNPC vouchers 105330.00–105335.00 (8 adult & 6 immature), HWML vouchers 49746 & 49747 (7 adult & 5 immature); Collector LGL, BM(NH) vouchers NHMUK 2012.3.7.20–30 (11 adult); Collector Dr. Thomas Bright, BM(NH) voucher NHMUK 2012.3.7.31 (1 adult).**Prevalence:** *N. aequalis*: 19 of 88 host specimens (21.6% infected); *N. cyrano*: 9 of 14 host specimens (64.3%) infected; unidentified macrourid: 1 of 1 host specimen (100% infected).**Intensity:** *N. aequalis*: 1–11 worms/specimen; *N. cyrano*: 1–2 worms/specimen; unidentified macrourid: only 1 specimen found.**Mean intensity:** *N. aequalis*: 54 worms in 19 specimens or 2.8 worms/infected fish; *N. cyrano*: 11 worms in 9 specimens or 1.2 worms/inf. fish; unidentified macrourid: 1 worm in 1 specimen or 1 worm/inf. fish.**Relative density/abundance:** *N. aequalis*: 54 worms in 88 specimens or 0.6 worms/total fish examined; *N. cyrano*: 11 worms in 14 specimens or 0.8 worms/t.f.ex.; unidentified macrourid: 1 worm in 1 specimen or 1.0 worm/t.f.ex.**Records:** 1. Armstrong (1974); 2. Gibson & Bray (1982); 3. Bray (1995); 4. Blend (1996); 5. Klimpel *et al.* (2001); 6. Bray & Kuchta (2006); 7. Klimpel *et al.* (2009); 8. Overstreet *et al.* (2009); 9. Present study.**Descriptions:** 1, 2, 4, 9.**Redescription.** [Based on 48 specimens. Measurements and proportions are given in Table 2.] Body elongate-oval, widest postequatorially; lateral margins occasionally foliate or crinkled, especially in posterior region. Forebody tapered anteriorly. Hindbody either slightly truncate or plump and rounded posteriorly. Tegument smooth. Pre-oral lobe absent. Oral sucker spherical to subspherical, subterminal. Ventral sucker sessile, transversely elongate or oval, wider than long, larger than oral sucker, preequatorial. Prepharynx quite short. Pharynx muscular, oval, longer than wide. Oesophagus distinct, with tegumental lining, straight in most individuals (92%), slightly convoluted rarely in others (8%). Intestinal bifurcation located 3/4 to 4/5 distance between anterior extremity and ventral sucker. Caeca narrow, unbranched, with thickened walls, ending blindly near posterior extremity.

Testes 2, lobed or irregularly indented or smooth, subspherical to transversely elongate or oval, tandem, median, intercaecal, postequatorial in posterior third of body, contiguous in most individuals (58%) but can be separated by short distance (42%). Post-testicular region fairly sizeable, occupying posterior third of body. Cirrus-sac thin-walled, clavate, straight, entirely preacetabular (can extend to midacetabular level in contracted specimens), extending posterodextrally from point midway between left lateral body edge and midline to terminate at or just posterior to level of intestinal bifurcation near midline. Seminal vesicle bipartite; posterior portion saccular and occupying most of cirrus-sac; anterior portion tubular, looping over posterior portion before extending anteriorly in to narrow, distal portion of cirrus-sac to terminate in small genital atrium. Prostate gland-cells well developed,

TABLE 2. Dimensions of *Tellervotrema armstrongi* Gibson & Bray, 1982 from *Nezumia aequalis*, *N. cyrano* and an unidentified macrourid from the northern Gulf of Mexico.

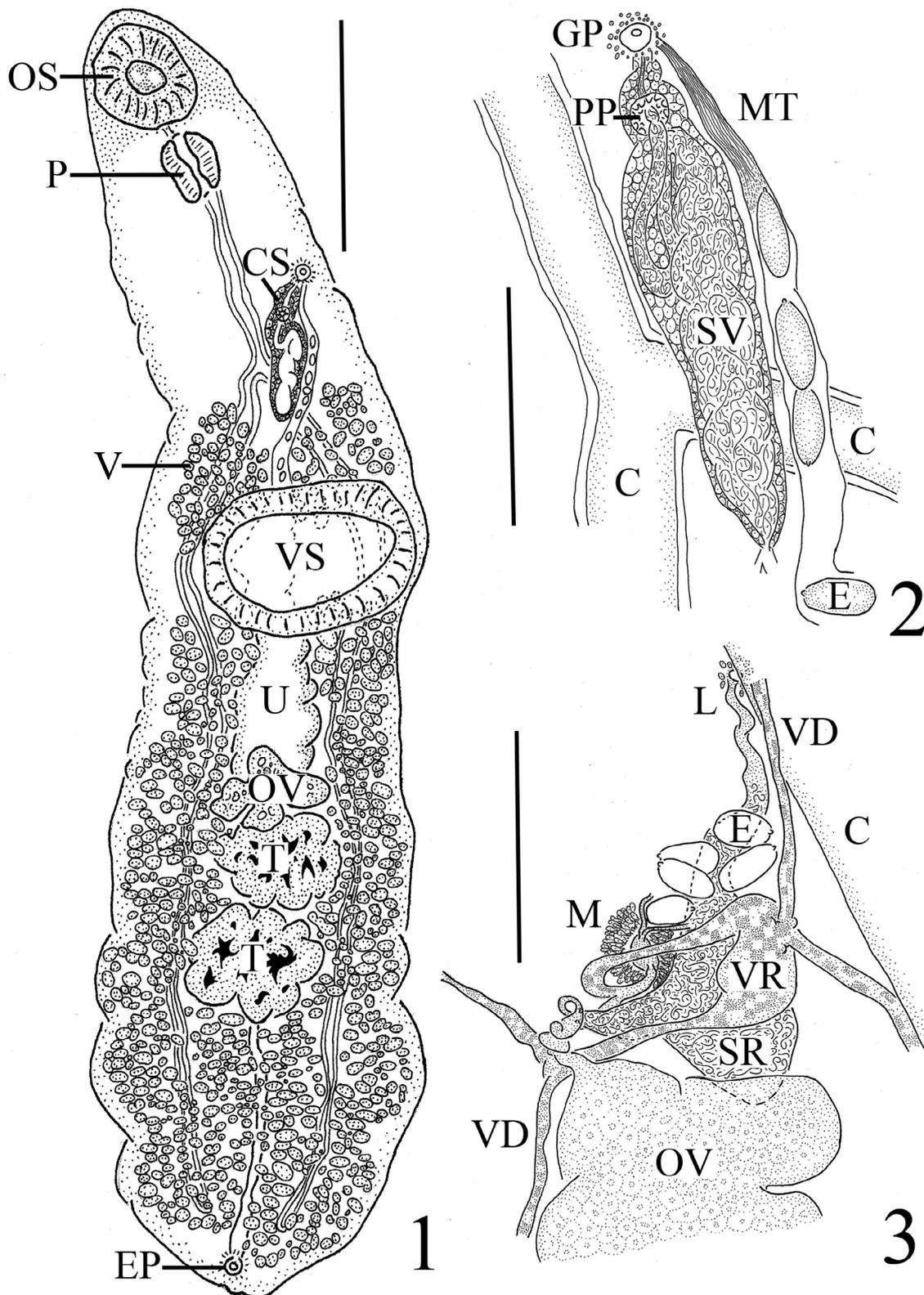
Parasite	<i>T. armstrongi</i> ¹		<i>T. armstrongi</i> ²		<i>T. armstrongi</i>	
	n	18	1	3	15	11
Host		<i>Nezumia aequalis</i>	Unidentified macrourid	<i>Nezumia aequalis</i>	<i>Nezumia aequalis</i>	<i>Nezumia cyrano</i>
Source of data		Armstrong (1974)	Armstrong (1974)	Armstrong (1974)	Blend (1996)	Blend (1996)
Collector & fixation		HWA, heat & host AFA injection; Bright, formalin	Bright, formalin	HWA, heat & host AFA injection	HWA, heat & host AFA injection	LGL, formalin
Length		2,168–3,700 (2,813) [n = 10] ³	1,840	1,000–1,232 (1,099)	1,862–3,112 (2,533)	1,678–4,116 (2,710) [n = 10]
Width at pharynx		240–656 (382) [n = 17]	296	160–208 (189)	160–450 (324) [n = 14]	220–772 (494)
at VS		520–880 (732) [n = 11]	592	352–408 (376)	380–790 (567)	430–1,152 (810) [n = 10]
at PT		504–1,032 (806) [n = 11]	632	360–424 (395)	430–956 (716) [n = 13]	540–1,510 (990) [n = 10]
Forebody	l ³	800–1,320 (1,069) [n = 11]	760	272–376 (323)	680–1,180 (997) [n = 13]	600–1,650 (1,042)
Hindbody	l	584–2,300 (1,374) [n = 16]	784	520–592 (549)	960–1,680 (1,308) [n = 12]	680–2,200 (1,248) [n = 9]
Oral sucker (OS)	l	208–376 (260)	160	94–136 (111)	220–310 (264) [n = 12]	150–370 (268)
	w ³	176–304 (256)	176	100–130 (117)	180–300 (241) [n = 12]	180–380 (286)
Prepharynx	l	0–84 (24) [n = 15]	40	12–40 (27)	52–88 (67) [n = 8]	0–56 (9)
Pharynx	l	116–200 (150) [n = 17]	100	50–70 (61)	100–160 (134)	110–280 (189) [n = 10]
	w	102–164 (133) [n = 17]	110	52–68 (61)	60–150 (121)	90–200 (140) [n = 10]
Oesophagus	l	320–520 (435) [n = 11]	280	112–120 (116) [n = 2]	110–620 (429) [n = 14]	190–680 (427)
Ventral Sucker	l	288–488 (374)	260	160–264 (227)	220–405 (330)	220–490 (362)
(VS)	w	360–656 (502)	384	328–392 (349)	290–580 (437)	260–600 (420)
Cirrus-sac (CS)	l	174–456 (309) [n = 15]	226	152–244 (198) [n = 2]	110–405 (251) [n = 13]	125–400 (258) [n = 7]
	w	60–120 (91) [n = 16]	70	34–50 (42) [n = 2]	50–125 (81) [n = 14]	37–113 (66) [n = 7]
CS anterior to VS		22–280 (133) [n = 16]	108	not observed	60–200 (118) [n = 12]	16–224 (98) [n = 6]
Ejaculatory duct	w	6–16 (12) [n = 12]	10	6–12 (9) [n = 2]	8–22 (17) [n = 12]	12–16 (14) [n = 2]
in distal CS						
Genital pore to lateral margin		40–244 (112) [n = 14]	80	24–56 (40) [n = 2]	66–158 (120) [n = 11]	106–224 (147) [n = 5]
Pre-ovarian region	l	1,448–2,140 (1,744) [n = 11]	1,300	568–760 (637)	1,400–1,980 (1,675) [n = 12]	1,080–2,520 (1,653) [n = 10]
Ovary (OV)	l	46–240 (155)	68	84–136 (117)	87–203 (149) [n = 13]	50–285 (134)
	w	62–376 (240)	214	132–188 (155)	120–313 (223) [n = 13]	110–320 (204)
VS to OV		160–560 (297) [n = 12]	272	56–120 (88)	160–432 (263) [n = 13]	104–560 (237) [n = 10]
Vitelline follicles	l	40–80 (55) [n = 75]	36–44 (40) [n = 5]	40–62 (52) [n = 13]	26–96 (52) [n = 75]	22–88 (53) [n = 51]
	w	16–48 (30) [n = 82]	24–34 (29) [n = 5]	20–36 (27) [n = 12]	16–40 (27) [n = 75]	14–56 (30) [n = 51]

continued next page

TABLE 2. (continued)

Parasite	<i>T. armstrongi</i> ¹	<i>T. armstrongi</i> ²	<i>T. armstrongi</i> ²	<i>T. armstrongi</i>	<i>T. armstrongi</i>
Vitelline reservoir	l 66–172 (106) [n = 15]	110	70–108 (88)	58–140 (89) [n = 9]	34–192 (93) [n = 3]
	w 24–84 (53) [n = 15]	44	26–40 (35)	24–48 (36) [n = 9]	34–56 (45) [n = 3]
Uterus	l 776–1,440 (1,055) [n = 11]	824	384–504 (444) [n = 2]	656–1,300 (1,019) [n = 11]	616–1,480 (990) [n = 8]
	w 240–400 (303) [n = 12]	384	180–272 (212)	152–280 (230) [n = 14]	180–480 (289) [n = 6]
Post-uterine region (PUR)	l 488–1,960 (1,052) [n = 17]	480	352–376 (365)	688–1,248 (999) [n = 13]	560–1,600 (1,012) [n = 9]
Anterior testis (AT)	l 76–496 (204)	112	94–120 (105)	100–238 (162) [n = 14]	72–263 (156)
	w 232–400 (311) [n = 12]	256	190–212 (203)	147–368 (255) [n = 14]	122–380 (264) [n = 10]
Posterior testis (PT)	l 136–336 (223) [n = 12]	150	116–130 (123) [n = 2]	125–273 (195) [n = 12]	70–240 (155)
	w 240–400 (329) [n = 12]	352	168–208 (188) [n = 2]	162–363 (286) [n = 12]	130–380 (273)
AT to PT	0–96 (13) [n = 17]	30	0	8–58 (22) [n = 8]	18–96 (54) [n = 9]
Post-testicular region (PTR)	l 272–840 (493) [n = 17]	160	128–216 (181)	330–640 (514) [n = 13]	300–1,130 (653) [n = 10]
	w 248–840 (559) [n = 17]	560	224–280 (261)	367–780 (640) [n = 13]	470–1,300 (870) [n = 10]
Post-caecal region	l 100–368 (178) [n = 16]	128	not observed	104–226 (168) [n = 12]	120–608 (249) [n = 10]
	w 48–66 (57.7) [n = 81]	52–62 (56.8) [n = 10]	48–54 (51.8) [n = 11]	47.5–60 (54.7) [n = 49]	50–62.5 (56.9) [n = 31]
Egg	l 26–38 (31.1) [n = 80]	32–42 (38.0) [n = 10]	24–28 (26.1) [n = 14]	25–30 (27.7) [n = 48]	25–32.5 (27.9) [n = 31]
	w 528–1,680 (1,035) [n = 3]	not observed	not observed	704–1,032 (872) [n = 3]	632–768 (700) [n = 2]
Excretory vesicle	l 22–88 (46) [n = 12]	not observed	20 [n = 1]	16–52 (32) [n = 13]	18–52 (39) [n = 8]
	w 31.0–44.9 (38.4) [n = 10]	41.3	25.6–32.0 (29.4)	30.7–47.1 (38.7) [n = 13]	36.8–44.6 (41.4) [n = 9]
Forebody % ⁴	l 1.6–2.5 (2.0)	2.2	2.5–3.3 (3.0)	1.6–2.1 (2.0) [n = 12]	1.1–1.9 (1.5)
Sucker width ratio	l 1.6–2.5 (2.0) [n = 12]	1.6	1.8–2.0 (1.9)	1.5–2.1 (1.8) [n = 11]	1.4–2.6 (2.1) [n = 10]
OS:pharynx width ratio	l 12.4–18.5 (15.7) [n = 10]	15.2	10.5–12.0 (11.3) [n = 2]	11.4–23.9 (16.9) [n = 12]	11.3–18.1 (15.3) [n = 10]
Oesophagus % ⁴	l 8.3–15.1 (11.1) [n = 10]	14.8	5.3–9.7 (7.9)	6.2–13.9 (10.1) [n = 12]	6.1–13.6 (8.2) [n = 9]
VS to OV % ⁴	l 28.1–52.4 (37.8) [n = 16]	26.1	29.9–35.3 (33.5)	33.7–43.3 (38.6) [n = 12]	33.4–44.4 (38.4) [n = 9]
PUR % ⁴	l 16.9–41.6 (29.0) [n = 10]	34.4	33.8–40.0 (36.1)	23.3–35.5 (29.6) [n = 11]	28.2–45.6 (37.3) [n = 9]
Width at PT % ⁴	l 13.9–26.4 (17.7) [n = 16]	8.7	12.8–18.8 (16.4)	17.1–23.8 (20.0) [n = 12]	17.6–31.4 (23.4) [n = 10]
	w				

¹ Identified as *Plagioporus* sp. n. #1 by Armstrong (1974, p. 82–86).² Identified as *Plagioporus* sp. n. #2 by Armstrong (1974, p. 86–89). These specimens exhibited evidence of contraction (see text).³ l, length; w, width; mean (parentheses); number [n] of measurements indicated where different from [n] in column heading.⁴ Proportion of body length.



FIGURES 1–3. *Tellervotrema armstrongi* Gibson & Bray, 1982 from the common Atlantic grenadier, *Nezumia aequalis*. **1.** Whole specimen, ventral view. **2.** Composite drawing of male terminal genitalia, ventral view. **3.** Composite drawing of oötype region, ventral view. Abbreviations: C, cecum; CS, cirrus-sac; E, egg; EP, excretory pore; GP, genital pore; L, Laurer's canal; M, Mehlis' gland; MT, metraterm; OS, oral sucker; OV, ovary; P, pharynx; PP, pars prostatica; SR, seminal receptacle; SV, seminal vesicle; T, testes; U, uterus; V, vitelline follicles; VD, vitelline duct; VR, vitelline reservoir; VS, ventral sucker. Scale-bars: 1, 600 μ m; 2, 155 μ m; 3, 180 μ m.

numerous in cirrus-sac. Pars prostatica, narrow ejaculatory duct, and cirrus present. Genital pore submedian, sinistral, midway between body margin and midline but can be nearer to lateral margin in some individuals, prebifurcal in region between mid-oesophagus and intestinal bifurcation, preacetabular and midway between oral and ventral suckers; dark-stained cells surrounding pore.

Ovary deeply 3- to 4-lobed and clover-leaf-shaped, median, intercaecal, immediately pretesticular, contiguous with anterior testis, postequatorial and located near junction of middle and posterior thirds of body. Oviduct arises anteriorly from anterodextral lobe of ovary. Oötype located on median line or immediately anterosinistral and dorsal to ovary. Seminal receptacle canalicular, ovoid to teardrop-shaped, dorsosinistral and either completely anterior to or overlapping anterior margin of ovary. Laurer's canal wide and winding, passing anteriorly from seminal receptacle to overlap posterosinistral loops of uterus, terminating directly dorsal to or just medial of left cecum on dorsal surface; dark-stained cells around canal opening. Vitellaria follicular, circumcaecal, extending posterolaterally from level at or just posterior to intestinal bifurcation to posterior extremity; vitelline field interrupted around level of ventral sucker producing two paired, non-confluent, isolated patches of vitelline follicles extending from bifurcal level to anterior margin of ventral sucker (paired anterior vitelline patches can be confluent and extend 3/4 distance over ventral sucker in contracted specimens); remainder of vitelline follicles commencing at level of posterior margin of ventral sucker, running posterolaterally to testes and ovary, not confluent in immediate preovarian space, between ovary and anterior testis or in intertesticular area, confluent in posttesticular region. Vitelline reservoir medial to sinistral, dorsally overlapping anterior margin of ovary or immediately preovarian, often ventrally overlapping seminal receptacle. Uterus tightly coiled, winding, intercaecal, wide loops running anteriorly from ovary up through middle of ventral sucker where loops narrow; distal loop turning anterosinistrally to run up along left side of cirrus-sac before terminating at genital pore. Metraterm straight, thin-walled, weakly developed, narrower than remainder of uterus, 1/5 to 1/3 length of cirrus-sac and running anterior along left side of it. Eggs smooth, oval, partially to severely collapsed in many specimens, yellow, non-filamented, operculate, with conspicuous knob or boss on one pole.

Excretory vesicle tubular, I-shaped, terminating at ovary or in region between ovary and anterior testis. Excretory pore dorsal, subterminal, opening via a small sphincter; elongated, dark-stained cells surrounding pore.

Remarks: With the presence of a well-developed cirrus-sac enclosing a seminal vesicle and a canalicular seminal receptacle, our specimens belong within the opecoelid subfamily Plagioporinae. Based on the key by Cribb (2005), these same specimens can be identified as belonging to the genus *Tellervotrema*, distinguished from other plagioporines by the presence of the following combination of diagnostic characteristics: non-filamented eggs that are > 40 µm long (ours ranged from 47.5–66 µm long); blind caeca; an elliptical, non-pedunculate ventral sucker that lacks lamellar lips, “fleshy folds” or an accessory attachment organ; vitelline follicles that extend to the posterior end of the body, well into the forebody, and are distinctly interrupted at the level of the ventral sucker; tandem and paired testes; an oral sucker that is not funnel-shaped; an excretory vesicle that is not diverticulate and does not extend to the pharynx but terminates inside the hindbody at about the level of the ovary; a clearly submedian genital pore; a pre-testicular uterus; and our specimens were found in macrourid hosts.

Our specimens compare favourably to *T. armstrongi* as described by Gibson & Bray (1982) in almost every aspect including overall appearance, the presence of a symmetrical pair of isolated groups of follicles in the posterior forebody proximate to the ventral sucker, a sinistral genital pore, a conspicuous trilobed ovary (4-lobes also observed, see Figs. 18–19), tandem and paired testes that may be contiguous or separated by a short gap, a unique dorsally subterminal excretory pore opening via a sphincter surrounded by gland cells, and our specimens were obtained from the intestine of two nominal species of macrourid hosts (the type host species, *N. aequalis*, and *N. cyrano*) as well as from an unidentified macrourid species. We noted a few differences between the description of the type specimens of *T. armstrongi* and our specimens. *Tellervotrema armstrongi* was described as possessing in part the following characteristics: a distinct prepharynx which could reach up to half the length of the pharynx; irregularly lobed testes; and vitelline follicles that do not occur dorsally to the caeca (Gibson & Bray 1982). Observations of our specimens revealed more variability in the first two characteristics mentioned immediately above—while some individuals possessed a distinct, short prepharynx (Fig. 1), we were not able to observe this feature in others (0–88 µm long), and we noticed a breadth of testes textures, ranging from smooth to irregularly indented to lobed (see Figs. 20 & 21). Most significant was the presence of circumcaecal vitelline follicles in our material. While there is a tendency for the more posterior vitelline follicles to be restricted to only the ventral side of the caeca, we noticed at times circumcaecal vitelline follicles in this location. More numerous were the circumcaecal

follicles making up the two isolated anterior vitelline groups (see Figs. 8–10). Gibson & Bray (1982) noted that species of this genus have vitelline follicles that do not occur dorsally to the caeca and they illustrated this in Figure 12 B–C. However, these transverse sections were taken from the levels of the anterior testis and the middle of the post-testicular region, respectively—levels posterior to the two anterior isolated vitelline groups characteristic of *Tellervotrema*. Had sectioned material been illustrated in this anterior region of the worm, the circumcaecal nature of the vitelline follicles might have been more evident.

This report includes the original specimens described and illustrated as “*Plagioporus* sp. n. #1 & #2” by one of us (HWA) (see Armstrong 1974, p. 82–89). We have confirmed the speculation noted earlier by Gibson & Bray (1982, p. 551) that these two species of *Plagioporus* are indeed conspecific and represent *T. armstrongi*. “*Plagioporus* sp. n. #2” is a contracted form of “*Plagioporus* sp. n. #1” (= *T. armstrongi*). This is evident in Table 2 by the smaller size ranges of several features for these three specimens of *T. armstrongi*. The host species and geographic locality for “*Plagioporus* sp. n. #1 & #2” were the same—the type host, *N. aequalis*, and the northeastern Gulf of Mexico. Finally, the three specimens of “*Plagioporus* sp. n. #2” were found in co-infection with one specimen of “*Plagioporus* sp. n. #1” (Armstrong 1974, p. 89).

This account represents a new host record in that this is the first original report of *T. armstrongi* from the macrourid *N. cyrano*. This digenean species has already been documented in the northeastern Gulf of Mexico (Gibson & Bray 1982).

***Tellervotrema beringi* (Mamaev, 1965)**

(Figs. 4–7)

Synonyms: *Plagioporus beringi* Mamaev, 1965.

Hosts: *Albatrossia pectoralis* (Gilbert); Gadiformes: Macrouridae: Macrourinae; giant grenadier. *Coryphaenoides* sp.; Gadiformes: Macrouridae: Macrourinae.

Localities: *A. pectoralis*: Northeastern Pacific Ocean, 44°25'N, 125°07'W, depth = 1,530 m, 14/August/1964. *Coryphaenoides* sp.: Northeastern Pacific Ocean, 44°38'N, 125°25'W, depth = 2,800 m, 20/February/1964; 44°38'N, 125°50'W, depth = 2,800 m, 30/December/1963.

Site: Intestine.

Deposited Specimens: Collector JEM, HWML neotype 49709 (1 adult [McCauley ID # OTB-42-F-1-11]), HWML paraneotypes 42665 (19 adult), HWML vouchers 42665 (2 adult & 6 immature); Collector JEM, HWML paraneotypes 42743, 42855 (2 adult).

Prevalence: *Coryphaenoides* sp.: 2 of 2 host specimens (100% infected).

Intensity: *Coryphaenoides* sp.: only 1 specimen found in each fish.

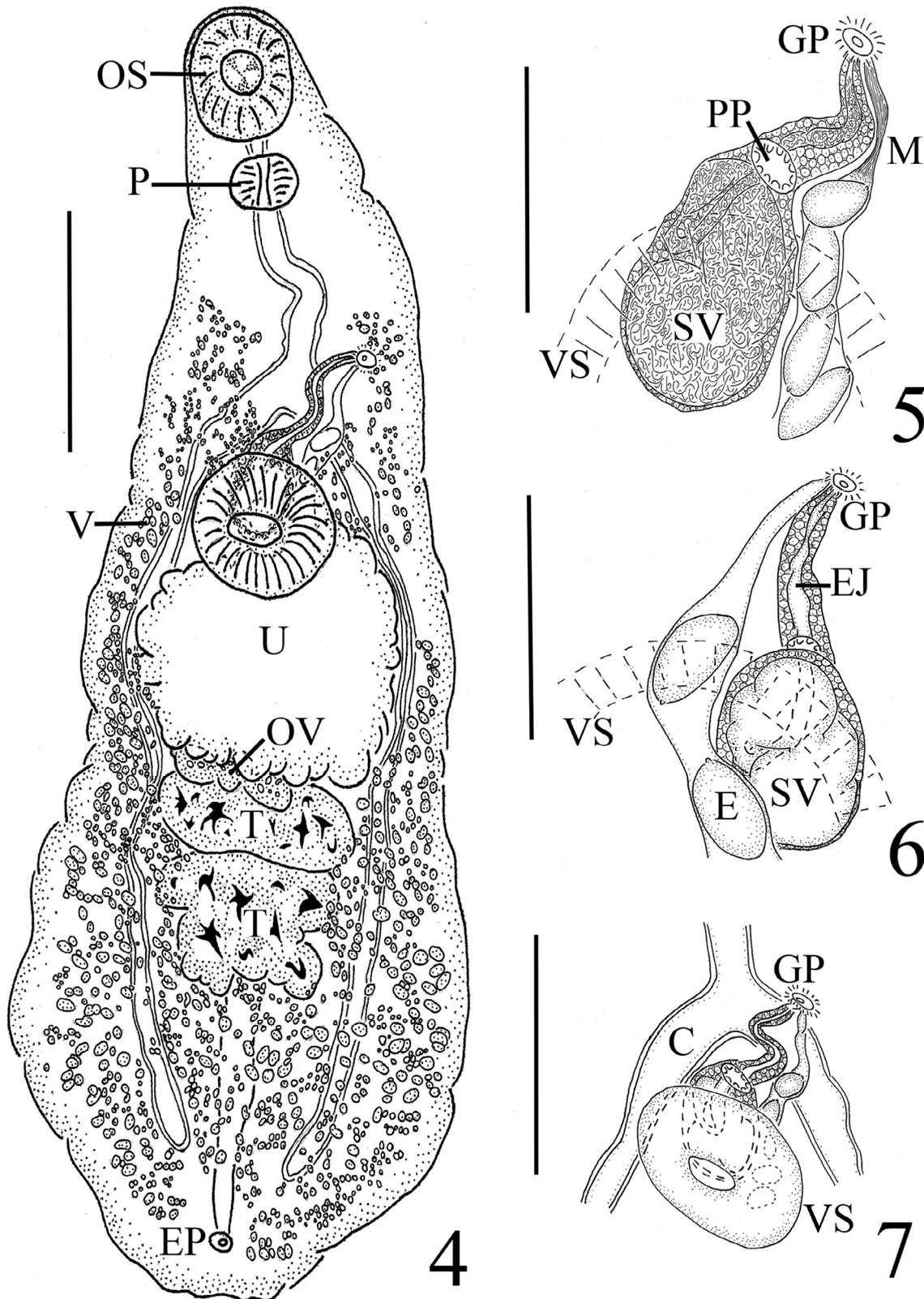
Mean intensity: *Coryphaenoides* sp.: 2 worms in 2 specimens or 1 worm/infected fish.

Relative density/abundance: *Coryphaenoides* sp.: 2 worms in 2 specimens or 1.0 worm/total fish examined.

Records: 1. Mamaev (1965); 2. Yamaguti (1971); 3. Gibson & Bray (1982); 4. Bray (1995); 5. Blend (1996); 6. Present study.

Descriptions: 1, 6.

Redescription. [Based on 22 specimens. Measurements and proportions are given in Table 3.] Body elongate-oval, clavate or lanceolate, widest postequatorially; some individuals slightly hour-glass-shaped with narrowing of body around equatorial level. Forebody attenuated anteriorly, narrowing at bifurcal level. Hindbody rounded posteriorly and wider than forebody. Tegument smooth. Pre-oral lobe absent. Oral sucker subspherical, subterminal (terminal in a few specimens). Ventral sucker sessile, spherical to subspherical, wider than long in most specimens, larger than oral sucker, postbifurcal, preequatorial and located near junction of anterior and middle thirds of body. Prepharynx quite short. Pharynx muscular, elongate oval, majority wider than long. Oesophagus with tegumental lining, straight in most specimens (67%) while sinuous in others (33%). Intestinal bifurcation short distance anterior to ventral sucker. Caeca narrow yet distal ends can be inflated, unbranched, with thickened walls, running posteriorly along lateral sides of worm to end blindly near posterior extremity; ends of caeca arcuate in some individuals.



FIGURES 4–7. *Tellervotrema beringi* (Mamaev, 1965) from the giant grenadier, *Albatrossia pectoralis*. **4.** Whole specimen, ventral view. **5.** Composite drawing of male terminal genitalia, ventral view. **6.** Cirrus-sac showing straight distal portion running anterior to ventral sucker, dorsal view. **7.** Cirrus-sac showing markedly curved distal portion running anterior to ventral sucker, ventral view. Abbreviations: C, cecum; E, egg; EJ, ejaculatory duct; EP, excretory pore; GP, genital pore; M, metraterm; OS, oral sucker; OV, ovary; P, pharynx; PP, pars prostatica; SV, seminal vesicle; T, testes; U, uterus; V, vitelline follicles; VS, ventral sucker. Scale-bars: 4, 550 μm ; 5, 230 μm ; 6, 200 μm ; 7, 460 μm .

Testes 2, tandem, irregularly indented to deeply lobed, transversely elongate, median, intercaecal, postequatatorial, contiguous (91%), rarely separated (9%). Post-testicular region fairly sizeable, occupying posterior third of body. Cirrus-sac thin-walled, distinctly elongate in anterior portion, clavate to pyriform in shape, extending from point midway between left lateral body edge and midline in a long and either nearly straight or markedly curved posterodextral line beyond anterior margin of ventral sucker to overlap 1/5 to 3/4 length of ventral sucker, terminating well posterior to level of intestinal bifurcation near midline. Seminal vesicle bipartite; posterior portion saccular; anterior portion tubular, narrow, looping back and ventrally overlapping posterior portion before passing anterosinistrally in long straight line from near midline of worm to enter distal portion of cirrus-sac, which itself either continues anterosinistrally or turns sharply anteriorly over left cecum at level of intestinal bifurcation to proceed anteriorly to terminate in small, subcircular genital atrium. Prostate gland-cells well developed, numerous in cirrus-sac. Pars prostatica conspicuous and just anterior to or dorsally overlapping anterior margin of ventral sucker; narrow ejaculatory duct and cirrus present. Genital pore submedian, sinistral, midway between body margin and midline but can be either nearer to lateral margin or nearer to midline in some individuals, at level of intestinal bifurcation but can reach level of posterior oesophagus, preacetabular and closer to ventral sucker than oral sucker.

TABLE 3. Dimensions of *Tellervotrema beringi* (Mamaev, 1965) from *Coryphaenoides* sp. and from *Albatrossia pectoralis* collected off the coast of Oregon.

Parasite	<i>T. beringi</i>	<i>T. beringi</i>
n	2	20
Host	<i>Coryphaenoides</i> sp.	<i>Albatrossia pectoralis</i>
Source of data	HWML 42743 & 42855 ¹	HWML 49709 & 42665 ¹
Collector & fixation	McCauley, host AFA injection	McCauley, host AFA injection
Length	2,540–2,960 (2,750)	1,680–3,440 (2,524) [n = 18] ²
Width at pharynx	356–405 (381)	316–599 (476) [n = 19]
at VS	567–802 (685)	591–1,004 (751)
at PT	543–786 (665)	664–1,269 (931) [n = 19]
Forebody	l ² 851–891 (871)	608–1,288 (862) [n = 19]
Hindbody	l 1,689–2,069 (1,879)	1,072–2,369 (1,637) [n = 19]
Oral sucker (OS)	l 216–272 (244)	148–308 (246) [n = 19]
	w ² 244–260 (252)	164–332 (247) [n = 19]
Prepharynx	l 16–36 (26)	0–80 (27) [n = 19]
Pharynx	l 124–148 (136)	76–168 (117) [n = 19]
	w 96–108 (102)	124–192 (153) [n = 19]
Oesophagus	l 220–316 (268)	162–592 (328) [n = 17]
Ventral Sucker (VS)	l 276–332 (304)	260–462 (350) [n = 19]
	w 276–389 (333)	284–567 (375) [n = 19]
Cirrus-sac (CS)	l 336–412 (374)	264–632 (443) [n = 19]
	w 136 (136)	100–256 (161) [n = 19]
CS overlap VS	52–122 (87)	112–360 (211) [n = 17]
Ejaculatory ductw in distal CS	26 [n = 1]	6–24 (14) [n = 17]
Genital pore to lateral margin	124–184 (154)	68–288 (175) [n = 17]
Pre-ovarian region	l 1,360–1,460 (1,410)	1,045–2,000 (1,478) [n = 19]
Ovary (OV)	l 180–192 (186)	60–204 (124)
	w 232–332 (282)	164–344 (256)

continued next page

TABLE 3. (continued)

Parasite		<i>T. beringi</i>	<i>T. beringi</i>
VS to OV		236–243 (240)	128–559 (297) [n = 19]
Vitelline follicles	l	56–100 (70) [n = 10]	42–98 (66) [n = 92]
	w	28–50 (39) [n = 10]	16–56 (31) [n = 97]
Vitelline reservoir	l	94–128 (111)	60–136 (86) [n = 18]
	w	58–100 (79)	80–180 (119) [n = 18]
Uterus	l	745–778 (762)	575–1,134 (853)
	w	316–454 (385)	365–745 (567)
Post-uterine region (PUR)	l	1,158–1,540 (1,349)	551–1,420 (980) [n = 19]
Anterior testis (AT)	l	132–244 (188)	120–320 (203)
	w	180–332 (256)	296–548 (420)
Posterior testis (PT)	l	156–340 (248)	160–340 (246)
	w	256–336 (296)	280–524 (425)
AT to PT		44–92 (68)	0
Post-testicular region (PTR)	l	689–800 (745)	211–810 (522) [n = 19]
	w	437–720 (579)	583–1,037 (766) [n = 19]
Post-caecal region	l	146–340 (243)	89–405 (241) [n = 17]
Egg	l	88–96 (92) [n = 10]	80–102 (93) [n = 90]
	w	52–60 (55) [n = 10]	40–56 (48) [n = 84]
Excretory vesicle	l	1,458 [n = 1]	851–1,240 (1,024) [n = 3]
	w	36–56 (46)	10–52 (24) [n = 5]
Forebody % ³		30.1–33.5 (31.8)	27.3–38.8 (34.3) [n = 18]
Sucker width ratio		1.1–1.5 (1.3)	1.2–2.0 (1.5) [n = 18]
OS:pharynx width ratio		2.4–2.5 (2.5)	1.2–2.0 (1.6) [n = 19]
Oesophagus % ³		8.7–10.7 (9.7)	8.3–17.8 (12.9) [n = 17]
VS to OV % ³		8.2–9.3 (8.8)	7.1–20.0 (11.7) [n = 17]
PUR % ³		45.6–52.0 (48.8)	32.8–49.6 (39.3) [n = 18]
Width at PT % ³		21.4–26.6 (24.0)	25.9–51.3 (38.5) [n = 17]
PTR % ³		27.0 (27.0)	12.5–38.5 (21.6) [n = 18]

¹These specimens were collected by Dr. James M. McCauley (deceased), Oregon State University, and housed at the Harold W. Manter Laboratory (HWML) under these accession numbers.

²l, length; w, width; mean (parentheses); number [n] of measurements indicated where different from [n] in column heading.

³ Proportion of body length.

Ovary deeply 3- to 4-lobed and clover-leaf-shaped, flattened longitudinally in several individuals, median to submedian, intercaecal, immediately pretesticular, contiguous with anterior testis, postequatorial in posterior portion of middle third of body. Oötype located anterodorsal to ovary. Seminal receptacle canalicular, anterosinistral and dorsal to ovary. Laurer's canal opening proximate to left cecum. Vitellaria follicular, circumcaecal, circular or elongate oval or globular in shape, extending posterolaterally from level anterior to intestinal bifurcation to posterior extremity; interruption in vitelline field approximate to ventral sucker variable in number (0, 1 or 2 gaps), symmetry (gaps directly opposite ventral sucker, oblique to ventral sucker, or displaced longitudinally to near level of gonads) and location (near body margin or displaced medially to near midline of worm), producing two paired, non-confluent, isolated patches of vitelline follicles extending from prebifurcal level to region spanning distance between ovary and posterior margin of ventral sucker; remainder of vitelline follicles running posterolateral to

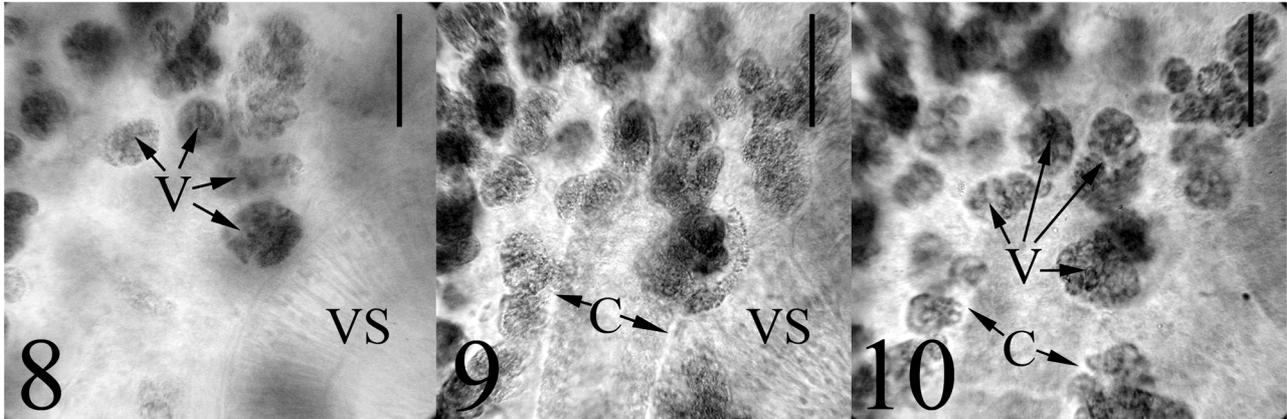
ovary and testes, not confluent but encroaching somewhat in to immediate preovarian region, space between ovary and anterior testis and in to intertesticular area, completely confluent in posttesticular region. Vitelline reservoir elongate oval to subtriangular, median to submedian, dorsally overlapping anterior margin of ovary or immediately anterosinistral to it. Vitelline ducts overlap lateral margins of uterus, ovary and anterior testis. Uterus winding, intercaecal and filling up almost entire space between ovary and ventral sucker, proximal loops running anteriorly from ovary and narrowing over ventral sucker, distal loop turning anterosinistral to terminate at genital pore. Metraterm straight, distal end noticeably curved toward genital pore in a few individuals, thin-walled, weakly developed, longitudinal fibers evident along wall. Eggs smooth, oval, slightly collapsed or crenulated in some specimens, yellow, non-filamented, operculate, with conspicuous knob or boss on one pole.

Excretory vesicle tubular, I-shaped, thin in width, reaching to ovary along midline of worm. Excretory pore dorsal, subterminal, opening via a small sphincter; dark-stained cells surrounding pore.

Remarks: Based on the same combination of diagnostic characteristics given above, these specimens key out to the genus *Tellervotrema* within Plagioporinae (Gibson & Bray 1982; Cribb 2005). We also have identified those individuals of *Tellervotrema* collected from *A. pectoralis* and *Coryphaenoides* sp. as *T. beringi*. As far as we are aware, there exists only one published description of *T. beringi* - the brief type description, given in Russian and originally named *Plagioporus beringi* by Mamaev (1965), who found intensities of 2–34 of these worms parasitizing seven individuals of *Coryphaenoides* sp. from the Bering Sea. Gibson & Bray (1982, p. 550–551) gave a brief list and table of features used to distinguish *T. armstrongi* from *T. beringi*, including in the latter species a larger egg size (100–110 × 50–60 µm vs 50.6–64 × 24–35 µm), a smaller sucker width ratio (1:1.4 vs 1:1.6–2.1), a more posteriorly situated genital pore (opening at the level of intestinal bifurcation vs opening at the level of about 30% of the distance between the intestinal bifurcation and the pharynx), a more posteriorly-extended cirrus-sac and lateral gaps in the vitelline fields (cirrus sac reaches the rear edge of the ventral sucker and the vitelline gap is near this same level vs a cirrus-sac that is entirely anterior to or only reaches to the middle of the ventral sucker and the vitelline gap is at midacetabular level) and *T. beringi* possesses entire (smooth) rather than irregularly lobed testes. In almost all of these features as well as in overall appearance, our specimens described herein more closely match *T. beringi* than *T. armstrongi*. Also, the type host (*Coryphaenoides* sp.) and locality (Bering Sea) for *T. beringi* is more similar to the hosts (*Coryphaenoides* sp. and *A. pectoralis*) and locality (Pacific Ocean off Oregon) of our specimens; *T. armstrongi* is known primarily from macrourids of the genus *Nezumia* from the North Atlantic Ocean. Finally, these particular specimens possess a conspicuous knob or boss on one pole of the egg (Fig. 17), described by Mamaev (1965) as a “носик” or “little nose, spout or bill” (Shporkin pers. comm.). This feature is also apparent on the eggs of our specimens of *T. armstrongi* and was noted by Armstrong (1974) on the egg of “*Plagioporus* sp. n. #1”; however, this knob or boss was not mentioned in Gibson & Bray (1982), probably because their material contained collapsed or severely distorted eggs.

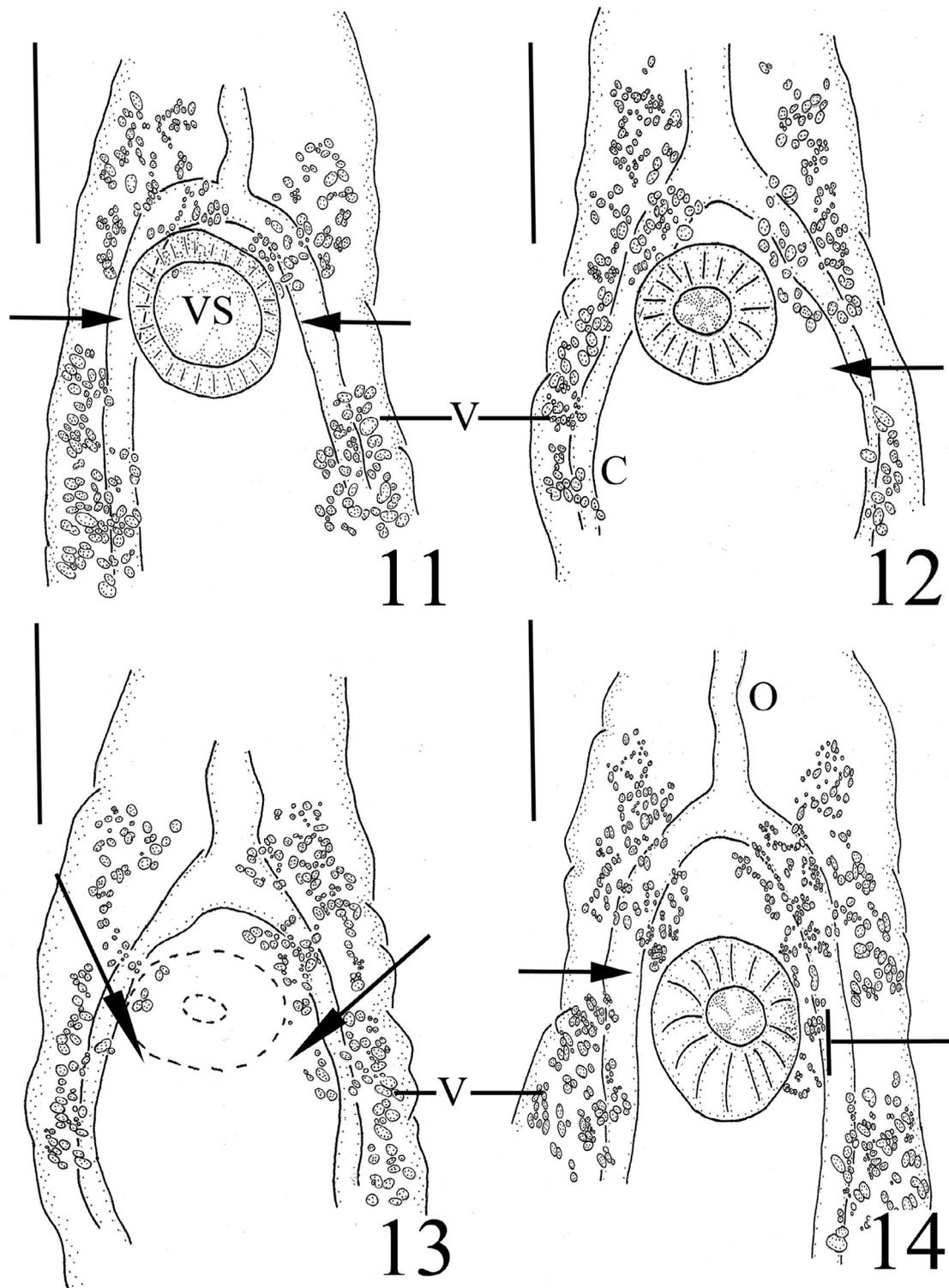
There are a few minor differences between the type description of *T. beringi* and our specimens (see Table 3). *Tellervotrema beringi* was described and illustrated by Mamaev (1965, Fig. 1) as possessing in-part the following characteristics: a short prepharynx; large and smooth testes; a vitelline gap at the level of the posterior margin of the ventral sucker; and a large egg (100–110 × 50–60 µm). Observations of our specimens of *T. beringi* revealed more variability in these features. Some individuals possessed a distinct, short prepharynx (Fig. 4), yet we were not able to observe this feature in others (0–80 µm long). While the absence of a prepharynx may be the result of contraction, we were unable to locate this feature in several specimens of *T. beringi* that showed no sign of contraction and the apparent lack of a prepharynx was noticeable in 1/3 of the measured specimens parasitising *A. pectoralis*. The testes in our specimens were somewhat smaller (120–340 × 180–548 µm vs 360–380 × 750–780 µm) and irregularly indented to deeply lobed; we did not observe any that were smooth. This might reflect the plasticity of this character in this genus as testes texture varied in *T. armstrongi* from smooth to irregularly indented to lobed. Combining our observations with Mamaev (1965), the testes texture of *T. beringi* varied from smooth to irregularly indented to deeply lobed (see Figs. 22–23). A third difference was the highly variable location of the vitelline gap which produced contrasting appearances in the *Tellervotrema*-like, paired, isolated, anterior vitelline groups. While we observed the presence of a vitelline gap at about the level of the posterior margin of the ventral sucker, the gap itself was quite variable in number (0, 1 or 2 gaps), symmetry (gaps directly opposite ventral sucker, oblique to ventral sucker, or displaced longitudinally to near level of gonads) and location (near body margin or displaced medially to near midline of worm) (see Figs. 11–16). Mamaev (1965) noted that almost all the trematodes of *T. beringi* that he found had the same gap within the vitelline field at the level of the ventral sucker, as seen in the “type

form” (holotype), yet in several “copies” (paratypes or other specimens), he also noted that [they] did not have [this same pattern of vitelline follicles], indicative of the variability in the position of the vitelline gap. Finally, while the egg size of our specimens was smaller in length and barely overlapped that of the type measurement (80–102 μm vs 100–110 μm), the width of the egg was the same as in *T. beringi* (40–60 μm vs 50–60 μm) and the egg of our specimens of *T. beringi* was larger than that of *T. armstrongi* (50.6–64 \times 24–35 μm [Gibson & Bray 1982—Table 1] and 47.5–66 \times 25–42 μm in specimens described herein).

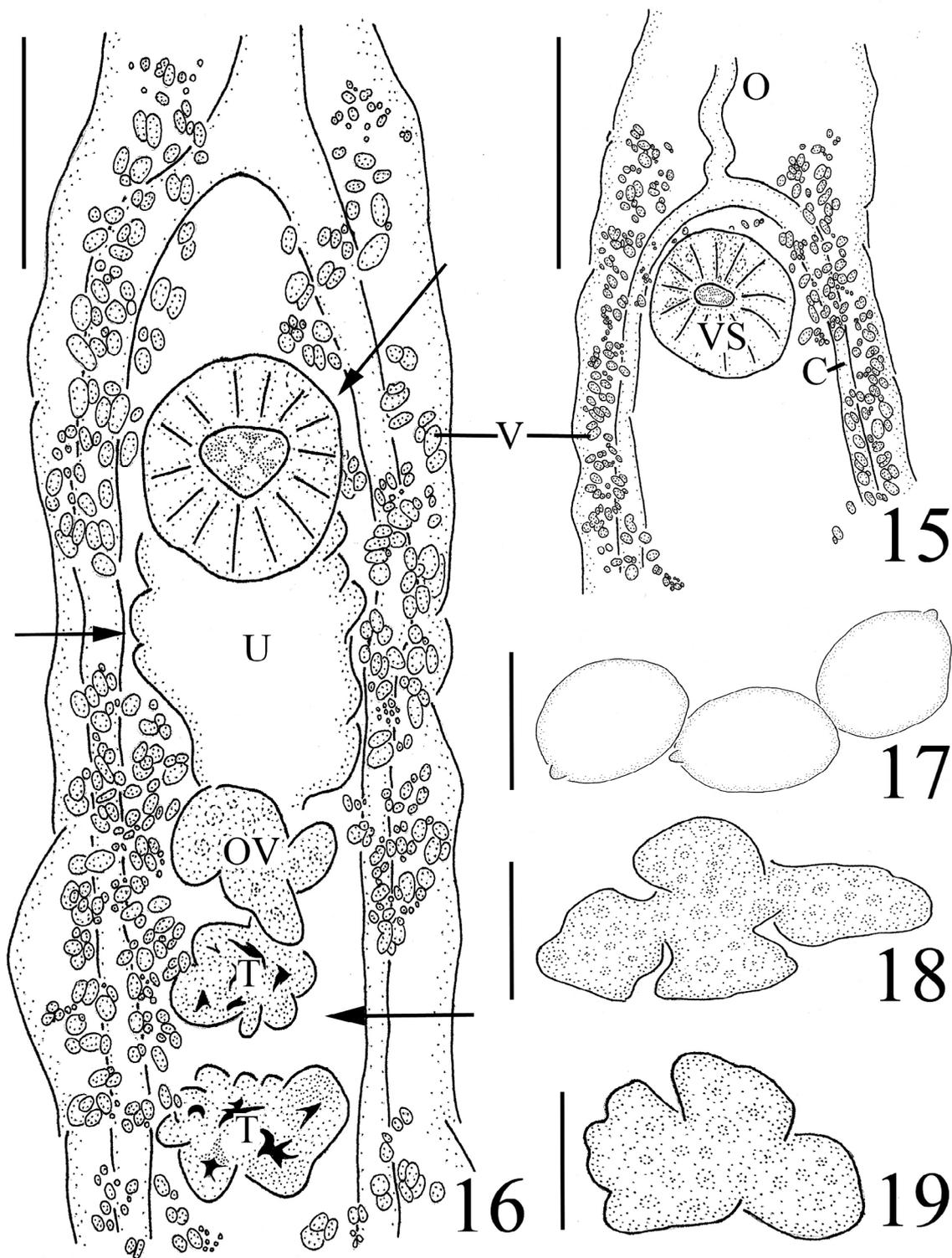


FIGURES 8–10. Circumcaecal vitelline follicles in a single specimen of *Tellervotrema beringi* (Mamaev, 1965) from the giant grenadier, *Albatrossia pectoralis*. **8.** Photograph of vitelline follicles located ventral to cecum. **9.** Photograph of cecum located directly dorsal to vitelline follicles in Fig. 8. **10.** Photograph of vitelline follicles located dorsal to vitelline follicles and cecum in Figs. 8 & 9. Abbreviations: C, cecum; V, vitelline follicles; VS, ventral sucker. Scale-bars: 8–10, 110 μm .

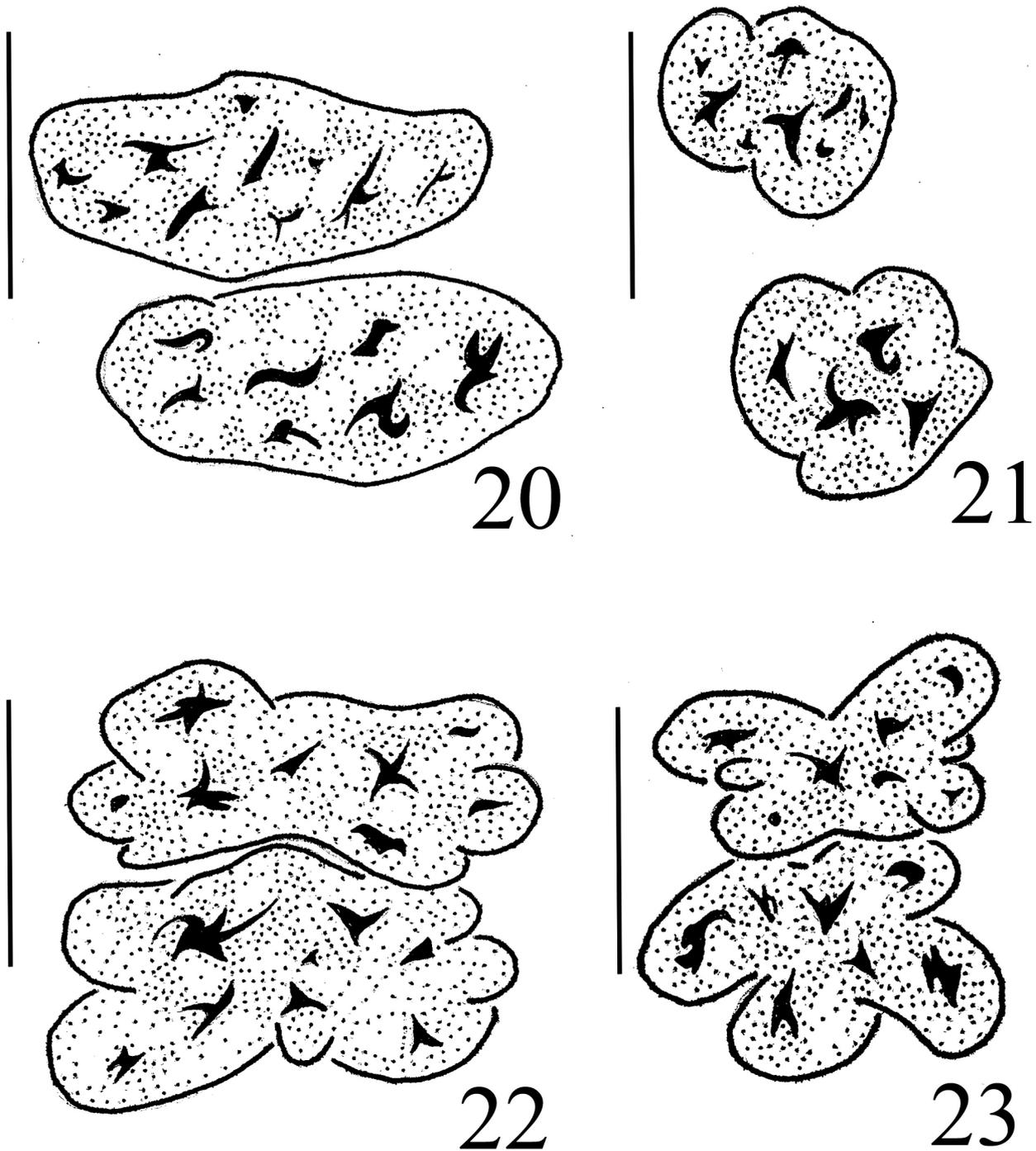
We noted some variability between our specimens of *T. beringi* from *A. pectoralis* and from *Coryphaenoides* sp. Most conspicuous are those characteristics in which there is little or no overlap in measurements or proportions between both sets of *T. beringi* specimens (see Table 3); however, we believe these differences to be attributable to intraspecific variability and minimized in importance when compared to the inherent intraspecific variability already noted by previous authors for *T. armstrongi* (Gibson & Bray 1982). For example, there was an apparent difference in inter-testicular distance (AT to PT) between those specimens of *T. beringi* from *Coryphaenoides* sp. (44–92 μm) and from *A. pectoralis* (testes are contiguous). However, this species and *T. armstrongi* are known to have testes that can be either contiguous or that can be separated by a short distance. The distance that the cirrus-sac extended beyond the anterior margin of the ventral sucker in *T. beringi* also varied: 52–122 μm (1/5 to 1/3 ventral sucker length) in worms from *Coryphaenoides* sp. vs 112–360 μm (1/3 to 3/4 ventral sucker length) in worms from *A. pectoralis*. While variable ($\Delta = 55\%$ of ventral sucker length), both sets of specimens are comparable to the variability in this same feature described by Gibson & Bray (1982) for *T. armstrongi* (cirrus-sac entirely anterior to (0%) or extending to 50% of ventral sucker length beyond anterior margin of ventral sucker). We discerned a difference in the length of the excretory vesicle between both sets of specimens of *T. beringi* (1,458 μm vs 851–1,240 μm). This can be attributed in-part to a very low number of observed measurements for this feature ($n = 1$ & $n = 3$, respectively) due to the gonads and, at times, the uterus occluding the view of the anterior extent of the excretory vesicle. Had more measurements been able to be obtained, this difference might have been nullified. The critical taxonomic importance of this feature in distinguishing *Tellervotrema* from other genera, the excretory vesicle extends to the level of the ovary (Gibson & Bray 1982; Cribb 2005), was confirmed for both sets of specimens of *T. beringi*. Perhaps the least explainable difference in Table 3 was the oral sucker (OS) to pharynx width ratio (2.4–2.5 vs 1.2–2.0). While there is overlap in the width of the oral sucker (244–260 vs 164–332), there is a difference in the width of the pharynx (96–108 μm vs 124–192 μm) between both sets of specimens. There is also a dissimilarity in the relationship of pharynx length to width between *T. beringi* from each host: 124–148 \times 96–108 μm (length > width) vs 76–168 \times 124–192 μm (width > length). The variability in these measurements may in-part explain the difference in OS:pharynx width ratio, but we remain uncertain as to the cause of this difference. We stress that the majority of all other dimensions measured, including egg size (see Table 3), between both sets of specimens of *T. beringi* overlapped in size and / or were practically identical to each other. Lastly, while one set of *T. beringi* had a low number of specimens ($n = 2$), these same specimens were collected from the type host genus (*Coryphaenoides*) and locality (North Pacific Ocean) as originally reported by Mamaev (1965). To further support our analysis, more congeneric parasite material is needed from species of *Coryphaenoides* inhabiting the deep waters off Oregon and elsewhere in the North Pacific Ocean (i.e. Kuramochi 2001, 2009, 2011).



FIGURES 11–14. Variability in number, symmetry and location of vitelline gap(s) in *Tellervotrema beringi* (Mamaev, 1965) from the giant grenadier, *Albatrossia pectoralis*. **11.** Ventral view of horizontally symmetrical gaps (2; gaps indicated by arrows) at about level of posterior margin of ventral sucker producing *Tellervotrema*-like, paired, isolated, anterior vitelline groups. **12.** Ventral view of 1 gap, located on left side at level of posterior margin of ventral sucker; no gap on right side. **13.** Dorsal view of diagonally symmetrical gaps (2) at level of ventral sucker. **14.** Ventral view of asymmetrical gaps (2) located oblique to ventral sucker; complete horizontal gap on right side (arrow) and incomplete gap on left side with medially-displaced vitelline follicles (bar). Abbreviations: C, cecum; O, oesophagus; V, vitelline follicles; VS, ventral sucker. Scale-bars: 11, 490 μm ; 12, 575 μm ; 13, 640 μm ; 14, 500 μm .



FIGURES 15–19. **15.** Ventral view showing 0 vitelline gaps in specimen of *Tellervotrema beringi* (Mamaev, 1965) from the giant grenadier, *Albatrossia pectoralis*. **16.** Ventral view of vitelline gaps (3) distributed randomly (diagonal gap running anterosinistral to ventral sucker; horizontal gap on right side just posterior to ventral sucker; horizontal gap on left side displaced longitudinally to level of testes) in specimen of *T. beringi* from *Coryphaenoides* sp. **17.** Ventral view of eggs showing conspicuous knob or boss on one pole of each from specimen of *T. beringi* from *A. pectoralis*. **18–19.** Ventral views of 4- and 3-lobed ovary from *T. armstrongi* Gibson & Bray, 1982 from the common Atlantic grenadier, *Nezumia aequalis*. Abbreviations: C, cecum; O, oesophagus; OV, ovary; T, testes; U, uterus; V, vitelline follicles; VS, ventral sucker. Scale-bars: 15, 600 μ m; 16, 280 μ m; 17, 80 μ m; 18, 150 μ m; 19, 100 μ m.



FIGURES 20–23. Variability in testes texture and position in species of *Tellervotrema*. **20.** Smooth and barely separated testes in *T. armstrongi* from the common Atlantic grenadier, *Nezumia aequalis*, ventral view. **21.** Slightly indented and separated testes in *T. armstrongi* from *N. aequalis*, ventral view. **22.** Lobed and contiguous testes in *T. beringi* from the giant grenadier, *Albatrossia pectoralis*, ventral view. **23.** Deeply lobed and contiguous testes in *T. beringi* from *A. pectoralis*, ventral view. Scale-bars: 20, 105 μm ; 21, 400 μm ; 22, 315 μm ; 23, 280 μm .

We were unable to provide ecological data (prevalence, intensity, mean intensity and relative density/abundance) for *T. beringi* in *A. pectoralis*. After investigating records at the HWML for Collection # 42665, we were unable to obtain data on the total number of specimens of *A. pectoralis* collected by JEM, the number of *A. pectoralis* infected with *T. beringi*, or the intensity of infection. As a result, we were unable to calculate mean intensity and relative density/abundance for this host species. We were unable to find in Mamaev (1965) any indication of

what type specimens were deposited for *T. beringi* (as *Plagioporus beringi*). Two of us (CKB & NOD) obtained a published list (Mamaev 1975) of specimens housed at the Laboratory of General Helminthology (now the Laboratory of Parasitology) in Vladivostok, Russia, but *T. beringi* (listed as *Plagioporus beringi*, see p. 229 of Mamaev 1975), the type host, *Coryphaenoides* sp. and locality (Bering Sea), were all that was listed with no accession numbers. We then attempted to obtain type material by contacting the Laboratory of Parasitology in Vladivostok, Russia, where helminths of fish from the Bering Sea are housed and where Dr. Yu. L. Mamaev was curator. We were informed that the type specimens of *P. beringi* are believed to be lost (Ermolenko pers. comm.). Thus, we were neither capable of obtaining specimens for comparative examination nor able to acquire accession numbers for the type specimens of *T. beringi*. Because we are unaware of a holotype or other type materials for *T. beringi*, we have designated a neotype (HWML 49709 [McCauley ID # OTB-42-F-1-11]) to serve as the single, name-bearing type specimen for this species and assigned 21 additional adult specimens as paraneotypes (HWML 42665, 42743, 42855). This represents the first report of a species of *Tellervotrema* from the giant grenadier, *A. pectoralis*; the only species in the macrourid genus *Albatrossia* Jordan & Evermann. This study also represents a new locality record (off Oregon) for *Tellervotrema*, a parasite genus that until now only has been documented in the Bering Sea (Mamaev 1965) and off Japan (Kuramochi 2001, 2009, 2011).

Discussion

This re-evaluation of *Tellervotrema* adds to our knowledge of this rarely-encountered genus and the validity of the diagnostic combination of characteristics currently used to distinguish this genus from other plagioporines. As first proposed by Gibson & Bray (1982, p. 551), our results indicated that egg size, a more posteriorly situated genital pore and the posterior extent of the cirrus-sac remained good characters to distinguish both species. Indeed, the difference in the posterior extent of the cirrus-sac between both species is quite striking due to the long and either straight or markedly posterodextrally curved anterior portion of the cirrus-sac in *T. beringi* (Figs. 5–7) resulting in the cirrus-sac continuing much further posterior than in *T. armstrongi*. There were features suggested by Gibson & Bray (1982) to distinguish both species that were not supported in our study. We found there to be overlap in the sucker width ratio between both species (1:1.1–2.5 vs 1:1.1–2.0). Table 1 of Gibson & Bray (1982) showed non-overlapping sucker width ratios for *T. armstrongi* (1:1.6–2.1) and *T. beringi* (1:1.4), yet both values fall within the range of the sucker width ratio for our specimens. Another feature was testes texture; *T. armstrongi* possessed irregularly lobed testes (Gibson & Bray 1982) while *T. beringi* had entire (smooth) testes (Mamaev 1965, Fig. 1). As noted above, testes texture varied in our specimens of *T. armstrongi* from smooth to irregularly indented to lobed, and when combined with the observations of Mamaev (1965), the testes texture of *T. beringi* varied from smooth to irregularly indented to deeply lobed (Figs. 20–23). The position of the lateral gaps in the vitelline fields which produces the characteristic *Tellervotrema*-like, paired, isolated anterior vitelline groups, also showed overlap. The vitelline gap in our specimens of *T. armstrongi* was consistently located around the level of the ventral sucker, but appeared more variable in location in *T. beringi*. We observed the vitelline gap in many of our specimens of *T. beringi* to be at about the level of the posterior margin of the ventral sucker, the same as noted by Mamaev (1965) and Gibson & Bray (1982). However, the gap in other specimens of *T. beringi* varied in number (0, 1 or 2 gaps), symmetry (gaps directly opposite ventral sucker [= *T. armstrongi*], oblique to ventral sucker, or displaced longitudinally to near level of gonads) and location (near body margin or displaced medially to near midline of worm) (Figs 11–16). While not a distinguishing feature between both species, we noted that *T. armstrongi* and *T. beringi* were originally described as possessing a “distinct” and “short” prepharynx, respectively (Mamaev 1965; Gibson & Bray 1982). Although many of our specimens of both species did possess a distinct, short prepharynx (up to 88 µm in length), this feature may be difficult to see in some individuals.

Besides egg size, genital pore location and posterior extent of the cirrus-sac, we found additional features which we feel can be used to differentiate both species. The testes appear to take up a much larger volume of the hindbody in *T. beringi*. This is evident when comparing Figs. 1 & 4 in our material and even more so in comparing Fig. 12A of Gibson & Bray (1982) and Figure 1 of Mamaev (1965). Another peculiarity was the anterior extent of the distinctive, paired, isolated vitelline groups in the forebody. These begin in *T. armstrongi* at or just posterior to the level of the intestinal bifurcation (Fig. 1); whereas, in *T. beringi*, they begin noticeably anterior to this (Figs. 4, 11–16). Finally, both species occupy a different geographic locality—*T. armstrongi* inhabits the North Atlantic

Ocean (off Scotland and in the Gulf of Mexico) while *T. beringi* resides in the North Pacific Ocean (Bering Sea, Japan and off Oregon). In summary, we suggest the following six features to distinguish *T. armstrongi* and *T. beringi*: (1) egg size; (2) position of the genital pore; (3) posterior extent of the cirrus-sac relative to the ventral sucker; (4) testes volume relative to hindbody size; (5) anterior extent of the paired vitelline patches in the forebody; and (6) geographic locality.

Our observations allowed us to comment on the generic diagnostic combination of characteristics used to erect and distinguish *Tellervotrema*. *Tellervotrema* was “erected for *Podocotyle*-like species which occur in archybenthal fishes (macrourids) and possess no vitelline follicles dorsal to the gut-caeca, but do have a symmetrical pair of isolated groups of follicles in the posterior forebody” (Gibson & Bray 1982). We found the species of this genus remain restricted to macrourids, yet the vitelline follicles are not limited to the dorsal side of the caeca but are circumcaecal throughout. While there is a tendency for the vitelline follicles to be primarily ventral to the caeca more posteriorly, the paired, anterior vitelline groups are noticeably circumcaecal (Figs. 8–10). We already noted that in *T. beringi* the vitelline groups in the posterior forebody can vary in number, symmetry and location to the extent that they can reach in to the hindbody (as defined by Manter [1970]). As a result, we feel that the diagnosis of *Tellervotrema* given by Gibson & Bray (1982) and Cribb (2005) should be amended to include circumcaecal vitelline follicles, especially within the isolated vitelline groups anteriorly, and the presence of a vitelline gap. This latter amendment stresses what we feel is the more important diagnostic generic feature - the *presence* of a gap in the lateral vitelline fields - rather than the *location* of the resultant groups of follicles created by the gap, which can be quite variable. Couplet 50a of Cribb (2005, p. 525), the “key” distinguishing couplet for *Tellervotrema*, states: “Vitelline follicles entirely ventral to caeca, enter forebody but are distinctly interrupted at level of ventral sucker; in macrourids.” We propose a slight alteration in this couplet to read “Vitelline follicles circumcaecal, enter forebody but are distinctly interrupted; in macrourids.” We also amend the generic diagnosis of Gibson & Bray (1982, p. 547) to include entire to deeply lobed testes.

Table 1 lists parasites reported from the three nominal macrourid species relevant to this study (*Albatrossia pectoralis*, *Nezumia aequalis*, *Nezumia cyrano*) including a listing of parasites from “*Coryphaenoides* sp.” While it is certain that “*Coryphaenoides* sp.” refers to several or perhaps many species of macrourids, we feel that including this information is relevant to this study because an unidentified species of *Coryphaenoides* was the type host for *T. beringi*, we found *T. beringi* in *Coryphaenoides* sp. collected by JEM (see Table 3), and from this information we can draw conclusions on parasite diversity (see below). All but *N. cyrano* exhibit a diverse parasite fauna with at least 36, 32 and 36 different parasite species reported from *A. pectoralis*, *N. aequalis* and “*Coryphaenoides* sp.”, respectively. Digeneans appear to dominate the parasite fauna reported from these two nominal host species (15 and 10 spp., respectively) and from unidentified species of *Coryphaenoides* (18 spp.). There are 14 myxosporidan species known from *A. pectoralis* followed by 4 nematodes, 2 copepods and 1 monogenean. Helminths appear to dominate the parasite fauna of *N. aequalis* with 9 nematodes, 8 cestodes, 3 monogeneans and a single species each of a myxosporidan and an isopod reported. Opecoelids are common in *N. aequalis* and include *Buticulotrema stenauchenus* Blend, Dronen & McEachran, 1993, “Genus novum B, sp. n.” (Opecoelidae), “*Podocotyle* (*Neopodocotyle*) sp. n.” and *Tellervotrema armstrongi*. Digenean species diversity is distantly followed in “*Coryphaenoides* sp.” by 6 cestodes, 3 monogeneans, 3 nematodes, 2 myxosporidians, 2 copepods, and the only 2 acanthocephalans known from the hosts in this study (see Table 1). There has been 1 opecoelid previously reported from “*Coryphaenoides* sp.”, and it is *Tellervotrema beringi*. There are 4 digeneans, including *T. armstrongi*, and a myxosporidan known to infect *N. cyrano*. Clearly, *N. cyrano* did not exhibit the parasite species diversity that was observed in the other macrourids examined. We attribute this as an artifact due to the small sample size (n = 14 fish) for this host species used in previous parasite studies, the majority of which have been carried out by CKB (Blend 1996; Blend *et al.* 2000; Present study). The sole myxosporidan, *Sphaeromyxa intermediata* Moser & Noble, 1977, was collected from a single specimen of *N. cyrano* (Moser & Noble 1977a, Table 1).

Cohen *et al.* (1990) and Froese & Pauly (2012) listed dietary items reported from *A. pectoralis*, *N. aequalis* and the Pacific grenadier, *Coryphaenoides acrolepis* (Bean); neither reference documented food items for *N. cyrano*. *Coryphaenoides acrolepis* is a likely candidate for the species of *Coryphaenoides* collected by JEM herein as it is a large fish species, one of the most common grenadier in the North Pacific Ocean, and it forms a small local fishery off northern California (Cohen *et al.* 1990). *Albatrossia pectoralis* and *N. aequalis* are known to ingest echinoderms, crabs and polychaetes, while both fish species and *C. acrolepis* typically ingest shrimp and amphipods. Opecoelids are known to utilize either a crustacean or a fish as a second intermediate host (Bray *et al.* 1999). It is

likely that species of *Tellervotrema* utilize one or more of these marine crustaceans (crabs, shrimp, amphipods) as intermediate hosts in their life cycles. Macrourids, serving as definitive hosts, become infected by preying upon one or more of these crustacean species.

Acknowledgments

The authors wish to thank Drs. Kathryn Vaughan, Dept. of Biology, and John D. McEachran (Prof. Emeritis), Dept. of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas, for assistance in identifying host fish and providing access to fish in the TCWC. We are grateful to Dr. Mark Pokras and Robert Ertsgard, Cummings School of Veterinary Medicine, and the Tisch Library, Tufts University, Medford, Massachusetts, for access to and use of their on-line literature databases. Dr. Rodney Bray & Mrs. Eileen Harris, BM(NH), kindly passed along accession numbers as well as taxonomic and locality information for several of the parasites included in Table 1. We also thank Mrs. Harris and Mrs. Patricia Pilitt, USNPC, for help in depositing specimens and appreciate the help offered us by Dr. Toshiaki Kuramochi, Dept. of Zoology, National Museum of Nature and Science, Tokyo, Japan. We are especially grateful to Dr. Alexey V. Ermolenko, Laboratory of Parasitology, Institute of Biology & Soil Science, Far East Branch, Russian Academy of Sciences, Vladivostok, Russia for attempting to locate type specimens of *P. beringi* and inquiring with Dr. Yu. L. Mamaev as to their whereabouts. Belated thanks to Dr. Thomas Bright (retired), Dept. of Oceanography, Texas A&M University; the personnel of NMFS, Pascagoula, Mississippi; and the crew of the *R/V Alaminos* & *R/V Oregon II* for their assistance in collection of fish and donation of macrourid GI tracts. Mr. Boris Shporkin, Ahavat Shalom, Corpus Christi, Texas provided translation of the Russian term for the knob or boss on the egg. Final thanks are given to the three reviewers who provided helpful comments to improve the manuscript and to Gordon College, Wenham, Massachusetts, for the loan of microscopes and other equipment to CKB. This study was completed as part of a sabbatical approved by the Faculty Development Committee and funded in-part by Gordon College.

References

- Armstrong, H.W. (1974) *A study of the helminth parasites of the family Macrouridae from the Gulf of Mexico and Caribbean Sea: their systematics, ecology and zoogeographical implications*, Texas A&M University, College Station, Texas, PhD dissertation, 329 pp.
- Blend, C.K. (1996) *The digenetic trematodes parasitizing macrourid fishes from the Gulf of Mexico and Caribbean Sea: an examination of their systematics, zoogeography and host-parasite ecology*, Texas A&M University, College Station, Texas, M.S. thesis, 305 pp.
- Blend, C.K. Dronen, N.O. & Armstrong, H.W. (2000) Six new species of *Lepidapedon* Stafford, 1904 (Digenea: Lepocreadiidae) from deep-sea macrourid fishes from the Gulf of Mexico and Caribbean Sea, with revised keys to the species of the genus. *Systematic Parasitology*, 45, 29–51.
- Blend, C.K., Dronen, N.O. & McEachran, J.D. (1993) *Buticulotrema stenauchenus* n. gen., n. sp. (Digenea: Opecoelidae) from *Malacocephalus occidentalis* and *Nezumia aequalis* (Macrouridae) from the Gulf of Mexico. *Journal of Parasitology*, 79, 674–676.
- Bray, R.A. (1995) Annotated checklist of digenean parasites of Macrouridae (Teleostei, Gadiformes). *Acta Parasitologica*, 40, 168–192.
- Bray, R.A. & Gibson, D.I. (1995) The Lepocreadiidae (Digenea) of fishes from the north-east Atlantic: a review of the genus *Lepidapedon* Stafford, 1904. *Systematic Parasitology*, 31, 81–132.
- Bray, R.A. & Kuchta, R. (2006) Digeneans from deep-sea marine teleosts off the Outer Hebrides, Scotland, including the description of *Brachyenteron helicoleni* sp. nov. (Zoogonidae). *Acta Parasitologica*, 51, 169–175.
- Bray, R.A., Littlewood, D.T.J., Herniou, E.A., Williams, B. & Henderson, R.E. (1999) Digenean parasites of deep-sea teleosts: A review and case studies of intrageneric phylogenies. *Parasitology*, 119, S125–144.
- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, 83, 575–583.
- Castro-Romero, R. (1994) Two new species and a new record of *Clavella* Oken, 1815 (Copepoda, Lernaeopodidae) parasitic on fishes from the Chilean coast. *Estudios Oceanologicos*, 13, 23–33.
- Claus, C. (1864) Beiträge zur Kenntnis der Schmarotzerkrebse. *Zeitschrift für Wissenschaftliche Zoologie*, 14, 365–382.
- Cohen, D.M., Inada, T., Iwamoto, T. & Scialabba, N. (1990) *Gadiform Fishes of the World (Order Gadiformes). An Annotated and Illustrated Catalogue of Cods, Hakes, Grenadiers and Other Gadiform Fishes Known to Date*. FAO Fisheries Synop-

- sis. FAO, Rome, No. 125, vol 10, 442 pp.
- Cribb, T.H. (2005) Family Opecoelidae Ozaki, 1925. In: Jones, A., Bray, R.A. & Gibson, D.I. (Eds.), *Keys to the Trematoda. Volume 2*. CABI Publishing and the Natural History Museum, Wallingford, pp. 443–531.
- Eagle, R.J. & McCauley, J.E. (1964) Collection of helminths from marine abyssal fishes. *Journal of Parasitology*, 50 (Suppl.), 37. (Abstract).
- Froese, R. & Pauly, D. (editors) (2012) FishBase. World Wide Web electronic publication. Available from <http://www.fishbase.org> (last access Sept 2011).
- Gibson, D.I. (1977) Comments on *Distoma gigas* Nardo and other rare digeneans from oceanic fishes of the Atlantic. *Parasitology*, 75, xxv. (Abstract).
- Gibson, D.I. & Bray, R.A. (1982) A study and reorganization of *Plagioporus* Stafford, 1904 (Digenea: Opecoelidae) and related genera, with special reference to forms from European Atlantic waters. *Journal of Natural History*, 16, 529–559.
- Gibson, D.I. & Bray, R.A. (1986) The Hemiuridae (Digenea) of fishes from the north-east Atlantic. *Bulletin of the British Museum of Natural History (Zoology)*, 51, 1–125.
- Jensen, K. (2009) Cestoda (Platyhelminthes) of the Gulf of Mexico. In: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico origin, waters and biota. Volume 1. Biodiversity*. Texas A&M University Press, College Station, pp. 487–522.
- Klimpel, S., Busch, M.W., Kellermanns, E., Kleinertz, S. & Palm, H.-W. (2009) *Metazoan deep-sea fish parasites*. Verlag Natur & Wissenschaft, Solingen, 384 pp.
- Klimpel, S., Seehagen, A., Palm, H.-W. & Rosenthal, H. (2001) *Deepwater metazoan fish parasites of the world*. Logos Verlag, Berlin, 315 pp.
- Korotaeva, V.D. (1985) Trematodes of commercial fish of the Pacific of practical importance. In: Hargis, W.J., Jr. (Ed.), *Parasitology and pathology of marine organisms of the world ocean*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Springfield, pp. 63–64.
- Korotaeva, V.D. (1990) Fauna of deep-water fish trematodes of the Pacific Ocean. In: Dody, J.M. (Ed.), *Bulletin de la Société Française de Parasitologie. 8. Abstracts of the 7th International Congress of Parasitology*. Société Française de Parasitologie, Paris, p. 273. (Supplement)
- Kovaleva, A.A. Gaevskaia, A.V. & Krasin, V.K. (1986) New species of myxosporidians (Protozoa, Myxosporidia) from macrourids in the northern Pacific Ocean. *Zoologicheskii Zhurnal*, 65, 1571–1573. (In Russian)
- Kovaleva, A.A., Zubchenko, A.V. & Krasin, V.K. (1983) Erection of a new family of myxosporidians (Protozoa, Myxosporidia) and description of two new genera. *Parazitologiya*, 17, 195–202. (In Russian)
- Kritsky, D.C. & Klimpel, S. (2007) *Cyclocotyloides bergstadi* n. sp. (Monogenea: Dicliphoridae: Dicliphoropsinae) from the gills of grenadier, *Coryphænaenoides brevibarbis* (Teleostei: Macrouridae), in the northeast Atlantic Ocean. *Comparative Parasitology*, 74, 23–30.
- Kuramochi, T. (2001) Digenean trematodes of anguilliform and gadiform fishes from deep-sea areas of Tosa Bay, Japan. In: Fujita, T., Saito, H. & Takeda, M. (Eds.), *Deep-sea fauna and pollutants in Tosa Bay*. National Science Museum Monographs, No. 20, Tokyo, pp. 19–30.
- Kuramochi, T. (2009) Digenean trematodes of fishes from deep-sea areas off the Pacific coast of northern Honshu, Japan. In: Fujita, T. (Ed.), *Deep-sea fauna and pollutants off Pacific coast of northern Japan*. National Museum of Nature and Science Monographs, No. 39, Tokyo, pp. 25–37.
- Kuramochi, T. (2011) Digenean trematodes of fishes caught in Sagami Bay, off Izu Islands and off Ogasawara Islands. *Memoirs of the National Science Museum, Tokyo*, 47, 51–63.
- Kurochkin, Yu.V. (1985) Applied and scientific aspects of marine parasitology. In: Hargis, W.J., Jr. (Ed.), *Parasitology and pathology of marine organisms of the world ocean*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Springfield, pp. 15–18.
- Lambert, M. & Euzet, L. (1980) *Polycliphora nezumiae* gen. et sp. nov. (Monogenea: Dicliphoridae) a gill parasite of *Nezumia aequalis* (Macouridae) from Senegal. *Parasitology*, 80, 413–417.
- Linton, E. (1940) Trematodes of fishes mainly from the Woods Hole region, Massachusetts. *Proceedings of the U.S. National Museum*, 88, 1–172.
- Love, M.S. & Moser, M. (1976) *Parasites of California Marine and Estuarine Fish*, University of California, Santa Barbara, 517 pp.
- Love, M.S. & Moser, M. (1983) *A Checklist of Parasites of California, Oregon, and Washington Marine and Estuarine Fishes*, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Seattle, 576 pp.
- Machida, M. & Araki, J. (1994) Some trematodes and cestodes in fishes from off eastern Hokkaido, northern Japan. *Memoirs of the National Science Museum, Tokyo*, 27, 87–92.
- Mamaev, Yu.L. (1965) Helminths of fish from the Bering Sea. In: Leonov, V.A., Mamaev, Yu.L. & Oshmarin, P.G. (Eds.), [Papers presented to Professor A. A. Sobolev on the 40th anniversary of his scientific and teaching ability]. Akademiya Nauk, SSSR, Vladivostok, pp. 168–188. (In Russian)
- Mamaev, Yu.L. (1975) New taxa of helminths described and substantiated by researchers of the Laboratory of General Helminthology, Vladivostok. *Trudy Biologo Pochvennogo Instituta*, 26, 217–238.
- Mamaev, Yu.L. & Avdeev, G.V. (1981) Monogeneans from some bathyal fishes from the northwestern parts of the Pacific Ocean. In: Mamaev, Yu.L. & Demshin, N.I. (Eds.), [Biology and systematics of animal helminths from the Far East]. Akademiya Nauk, SSSR, Vladivostok, pp. 54–70. (In Russian)

- Mamaev, Yu.L. & Avdeev, G.V. (1984) Peculiar attachment of the monogenean *Macruricotyle clavipes* Mamaev et Lyadov, 1975, to the gills of its host. *Materialy nauchnoi konferentsii Vsesoiuznogo obshchestva gel'mintologov [Proceedings of the scientific conferences of the All-Union Society of Helminthologists]*, 34, 35–40. (In Russian)
- Mamaev, Yu.L. & Brashovyan, P.P. (1989) *Syncoelicotyloides macruri* gen. nov., sp. nov., a first representative of the subfamily Syncoelicotylinae from macrurid fish. *Parazitologiya*, 23, 532–536. (In Russian)
- Mamaev, Yu.L. & Lyadov, V.N. (1975) Monogeneans of the subfamily Diclidophoropsinae (Monogenea, Diclidophoridae). In: Lebedev, B.I. (Ed.), [*Helminthological studies of animals and plants*]. Trudy Biologo-Pochvennogo Instituta, No. 26, Vladivostok, pp. 115–125. (In Russian)
- Manter, H.W. (1970) The terminology and occurrence of certain structures of digenetic trematodes, with special reference to the Hemiuroidea. In: Singh, K.S., Tandan, B.K. & Srivastava, H.D. (Eds.), *H. D. Srivastava commemoration volume*. Indian Veterinary Research Institute, Izatnagar, pp. 27–33.
- Mauchline, J. & Gordon, J.D.M. (1984) Incidence of parasitic worms in stomachs of pelagic and demersal fish of the Rockall Trough, northeastern Atlantic Ocean. *Journal of Fish Biology*, 24, 281–285.
- McCauley, J.E. (1964) A deep-sea digenetic trematode. *Journal of Parasitology*, 50, 112–114.
- McCauley, J.E. (1968) Six species of *Lepidapedon* Stafford, 1904 (Trematoda: Lepocreadiidae) from deep-sea fishes. *Journal of Parasitology*, 54, 496–505.
- McCauley, J.E. & Pequegnat, J.E. (1968) Two new species of *Dinosoma* Manter, 1934 (Trematoda: Hemiuridae) from deep-water macrurid fishes off the coast of Oregon. *Journal of Parasitology*, 54, 931–934.
- McCauley, J.E., Pequegnat, J.E. & Brownell, C.L. (1970) A new species of *Gonocerca* Manter, 1925 (Trematoda: Hemiuridae) from the Eastern Pacific. *Proceedings of the Helminthological Society of Washington*, 37, 169–171.
- McCauley, J.E. & Smoker, W.W. (1969) Two diclidophoran trematodes (Monogenea) from deep-sea fishes. *Journal of Parasitology*, 55, 742–746.
- Moles, A. (1982) *Parasite-Host Records of Alaskan Fishes*, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Seattle, 41 pp.
- Moser, M. & Noble, E.R. (1975) The myxosporidan genus *Davisia* in two deep-sea fishes. *Journal of Parasitology*, 61, 691–694.
- Moser, M. & Noble, E.R. (1976) The genus *Leptothecha* (Protozoa: Myxosporida) in macrurid fishes and sablefish, *Anoplopoma fimbria*. *Journal of Protozoology*, 23, 490–492.
- Moser, M. & Noble, E.R. (1977a) Three genera of Myxosporida (Protozoa) in macrurid fishes. *International Journal for Parasitology*, 7, 93–96.
- Moser, M. & Noble, E.R. (1977b) *Zschokkella* (Protozoa: Myxosporida) in macrurid fishes. *International Journal for Parasitology*, 7, 97–100.
- Moser, M. & Noble, E.R. (1977c) The genus *Myxoproteus* (Protozoa: Myxosporida) in macrurid fishes. *International Journal for Parasitology*, 7, 253–255.
- Moser, M. & Noble, E.R. (1977d) Myxosporidan genera *Auerbachia*, *Sphaerospora*, *Davisia* and *Chloromyxum* in macrurid fishes and the sable fish, *Anoplopoma fimbria*. *Zeitschrift für Parasitenkunde*, 51, 159–163.
- Noble, E.R. (1966) Myxosporida in deepwater fishes. *Journal of Parasitology*, 52, 685–690.
- Noble, E.R. (1973) Parasites and fishes in a deep-sea environment. *Advances in Marine Biology*, 11, 121–195.
- Noble, E.R. & Collard, S.B. (1970) The parasites of midwater fishes. In: Snieszko, S.F. (Ed.), *A symposium on diseases of fish and shellfish*. Special Publications of the American Fisheries Society, Washington D.C., pp. 57–68.
- Overstreet, R.M., Cook, J.O. & Heard, R.W. (2009) Trematoda (Platyhelminthes) of the Gulf of Mexico. In: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico origin, waters and biota. Volume 1. Biodiversity*. Texas A&M University Press, College Station, pp. 487–522.
- Payne, R.R. (1987) Some diclidophorid Monogenea (Trematoda), including two new species, from marine fishes of the eastern Pacific Ocean off California, U.S.A. and Baja California, Mexico. *Transactions of the American Microscopical Society*, 106, 256–264.
- Price, E.W. (1943) North American monogenetic trematodes: VI. The family Diclidophoridae (Diclidophoroidea). *Journal of the Washington Academy of Sciences*, 33, 44–54.
- Ross, S.W., Sulak, K.J. & Munroe, T.A. (2001) Association of *Syscenus infelix* (Crustacea: Isopoda: Aegidae) with benthopelagic rattail fishes, *Nezumia* spp. (Macrouridae), along the western North Atlantic continental slope. *Marine Biology (Berlin)*, 138, 595–601.
- Rubec, L.A., Blend, C.K. & Dronen, N.O. (1995) *Syncoelicotyloides zaniophori* n. sp. (Monogenea: Microcotylidae) from the gills of *Coryphaenoides zaniophorus* (Macrouridae) from the Gulf of Mexico. *Journal of Parasitology*, 81, 957–960.
- Rubec, L.A. & Dronen, N.O. (1994) Revision of the genus *Diclidophora* Kroyer, 1838 (Monogenea: Diclidophoridae), with the proposal of *Macrouridophora*. *Systematic Parasitology*, 28, 159–185.
- Shimazu, T. (1970) *Gonocerca oshoro* sp. n. (Trematoda: Hemiuridae) from the ovary of the rattail, *Nematonurus pectoralis* from the Gulf of Alaska. *Japanese Journal of Parasitology*, 19, 278–281.
- Solov'eva, G.F. (1991) *Metabronema insulanum* sp. nov. (Nematoda; Spirurina), a parasite of deep water fish in the Pacific Ocean. *Parazitologiya*, 25, 556–558. (In Russian)
- Vassiliades, G. (1985) Helminthes parasites des poissons de mer des cotes du Senegal. *Bulletin de l'Institute Fondamental d'Afrique Noire*, 44, 78–99. (In French)

TERMS OF USE

This pdf is provided by Magnolia Press for private/research use.
Commercial sale or deposition in a public library or website is prohibited.

- Wilson, C.B. (1915) North American parasitic copepods belonging to the family Lernaepodidae, with a revision of the entire family. *Proceedings of the United States National Museum*, 47, 565–729.
- Wilson, C.B. (1935) Parasitic copepods from the Pacific coast. *American Midland Naturalist*, 16, 776–797.
- Yamaguti, S. (1938) *Studies on the Helminth Fauna of Japan. Part 21. Trematodes of Fishes. IV*, S. Yamaguti, Kyôto, 139 pp.
- Yamaguti, S. (1941) Studies on the helminth fauna of Japan. Part 33. Nematodes of fishes, II. *Japanese Journal of Zoology*, 9, 343–396.
- Yamaguti, S. (1958) *Systema Helminthum. Vol. 1. The digenetic trematodes of vertebrates. Part 1*, Interscience Publishers, New York, 979 pp.
- Yamaguti, S. (1963a) *Systema Helminthum. Vol. 4. Monogenea and Aspidocotylea*, Interscience Publishers, New York, 699 pp.
- Yamaguti, S. (1963b) *Parasitic Copepoda and Branchiura of fishes*, Interscience Publishers, New York, 1,104 p.
- Yamaguti, S. (1971) *Synopsis of digenetic trematodes of vertebrates. Vol. 1*, Keigaku Publishing Company, Tokyo, 1,074 pp.
- Yoshino, T. P., & Moser, M. (1974) Myxosporida (Protozoa) in macrourid fishes (*Coryphaenoides* spp.) of the northeastern Pacific. *Journal of Parasitology*, 60, 655–659.