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Supplementary data and micrographs follow the references.

Diversity of Tetrabothriidae (Eucestoda) among Holarctic Alcidae (Charadriiformes): Resolution of the *Tetrabothrius jagerskioeldi* Cryptic Species Complex—Cestodes of Alcinae—Provides Insights on the Dynamic Nature of Tapeworm and Marine Bird Faunas under the Stockholm Paradigm

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Abstract

We begin resolution of the *Tetrabothrius jagerskioeldi*–species complex with descriptions of *Tetrabothrius alcae* n. sp. based on numerous specimens, primarily in murre (species of *Uria*), from the greater North Pacific basin and *Tetrabothrius sinistralis* n. sp. based on cestodes in guillemots (species of *Cephus*) from the central Bering Sea and West Greenland. These tetrabothriids are characterized, among 44 species of *Tetrabothrius* in avian hosts, by attributes of the scolex, male and female organ systems, structure and dimensions of the vitelline gland, numbers of testes, configuration of the genital atrium, genital papillae and the male and female atrial canals, position of the genital ducts relative to the poral osmoregulatory canals, structure, dimensions and position of the vaginal seminal receptacle, and dimensions of the embryophore and oncosphere, in addition to a broader array of characters. Remarkably, *T. alcae*, *T. sinistralis*, and a cryptic complex had remained unrecognized for the past century, given that these species are unequivocally differentiated by multiple suites of unique structural attributes relative to *T. jagerskioeldi*. Alcids and cestodes of the *T. jagerskioeldi*–complex are restricted to cold marine systems of advection and upwelling along coastal margins adjacent to the continental shelf or are associated with archipelagos (especially the Aleutian Arc), isolated islands and rocky headlands of the Bering Sea, Chukchi Sea, Gulf of Alaska, Sea of Okhotsk, and Sea of Japan. *Tetrabothrius alcae*, *T. jagerskioeldi*, and *T. sinistralis* may occur in sympatry but with minimal overlap in the faunas associated with murre (Alcini) and guillemots (Cepphini). Transmission for cestodes and persistence of this fauna is expected to be associated with pelagic and neritic systems adjacent to colony sites in zones where critical prey species are concentrated or secondarily dispersed downstream by predictable advective and upwelling processes and become available to foraging birds. Faunal assembly represents the outcomes of oscillating climate, shifting ranges (breakdown in isolation, ecological fitting, and exploration modes for cestodes) and the changing interfaces for resource availability maintained by trophic and habitat overlaps. Dynamics at these ecotones constitute the nexus of opportunity and capacity for infection by species of *Tetrabothrius* among avian hosts where capacity appears broad and opportunity is ecologically restricted in space and

time. Life history pathways for cestodes are tied to trophic associations and dynamics at mesoscales across marine domains and provinces. Resilience and connectivity through ecological fitting strongly suggest the influence of multiple trophic pathways for transmission and persistence of this complex fauna through differing assemblages of zooplankters, fishes, and cephalopods depending on locality, oceanographic conditions, and temporal variability. Changing conditions, especially ecological perturbations driven by climate oscillations, directly determine production cycles and distributions of micro- and macro-zooplankton, forage fishes, cephalopods, and trophic structure in high-latitude marine ecosystems. Expanding regimes of accelerating change emphasize the critical importance of field collections, archives, and baselines to assess biological outcomes across temporal and spatial scales. Parasite assemblages reveal macro- to meso-scale connectivity serving as adjuncts and proxies in recognizing and understanding outcomes for episodes of environmental oscillation and directional atmospheric and oceanic warming in marine ecosystems.

Keywords: *Tetrabothrius alcae* n. sp., *Tetrabothrius sinistralis* n. sp., Alcidae, marine diversity, faunal assembly, climate, Stockholm paradigm dynamics

Introduction

Large robust cestodes attributable to species of *Tetrabothrius* Rudolphi, 1819 appear as characteristic parasites among charadriiform seabirds of the family Alcidae across high-latitude seas of the Holarctic (Hoberg and Soudachanh, 2020). A single oceanographically widespread species, *Tetrabothrius jagerskioeldi* Nybelin, 1916, had generally been regarded to have a considerable host range among alcids (e.g., Baer, 1954; Temirova and Skryabin, 1978; Muzzafar and Jones, 2004). In contrast, Hoberg and Soudachanh (2020), in a synthesis of 40 years of geographically extensive field inventories, demonstrated that a species complex, minimally including 3 unrecognized and undescribed taxa, has been hidden within *T. jagerskioeldi* for the past century.

In our evaluations of diversity, specimens of *T. jagerskioeldi*, in addition to the original type series (including *T. intrepidus* Baylis, 1919) from Sweden and the Barents Sea (Nybelin, 1916; Baylis, 1919), were identified primarily among guillemots (Cepphini), species of *Cephus* Pallas [pigeon guillemot, *C. columba* Pallas, 1811; spectacled guillemot, *C. carbo* Pallas, 1811; and black guillemot, *C. grylle* (Linnaeus, 1758); prevalence of 37%, 50%, and 12.5%, respectively] occurring at 6 insular localities spanning the North Pacific basin across the northern Sea of Okhotsk, Bering Sea, and Gulf of Alaska (Hoberg and Soudachanh, 2020). We confirmed the identity of *T. jagerskioeldi* and a patchy distribution for this tetrabothriid among alcid (6 species), larid (glaucous-winged gull, *Larus glaucescens* Naumann, 1840), and phalacrocoracid [pelagic shag, *Urile pelagicus* (Pallas, 1811)] hosts based on these collections and direct comparisons to the type series of Nybelin

(1916). Alcids, other than guillemots, were rarely observed as hosts, and cestodes occurred in single specimens of common murre [*Uria aalge* (Pontoppidan, 1763)], marbled murrelet [*Brachyramphus marmoratus* (Gmelin, 1789)], and rhinoceros auklet [*Cerorhinca monocerata* (Pallas, 1811)]. Specimens of *T. jagerskioeldi* were not collected nor identified in other species of auks (Alcini), puffins (Fratrunculini), auklets (Aethiini), or murrelets (Brachyramphini and Synthliboramphini) from the North Pacific basin (Hoberg and Soudachanh, 2020). Following the original description of *T. jagerskioeldi*, a broad oceanographic range across seas of the Holarctic has been established for this tetrabothriid.

Tetrabothrius jagerskioeldi, consistent with a conventional understanding of marine parasite diversity and the otherwise traditional model for cospeciation (see for discussion Nylin et al., 2018; Brooks et al., 2019), would have been predicted as a common helminth among murre species of *Uria* Brisson, 1760 (e.g., Muzzafar and Jones, 2004). In our ongoing studies, however, authoritative identification of *T. jagerskioeldi* revealed this cestode species in 1 of 276 specimens of common murre (<1%) and none among 150 specimens of thick-billed murre, *U. lomvia* (Linnaeus, 1758), across localities from the greater North Pacific basin (Hoberg and Soudachanh, 2020). Because of the recognition of a putative species complex and a nearly uniform absence of archived specimens on which to establish identity in global museum collections, prior records of *T. jagerskioeldi* in murre species, especially from the Arctic Basin and North Atlantic (e.g., Belopol'skaia, 1952; Threlfall, 1971), and other species of alcids are equivocal and can now rarely be substantiated (Hoberg and Soudachanh 2020).

In our current study, we have updated and revised our records for host and geographic occurrence and preva-

lence for species of the *T. jagerskioeldi*-complex arising from the original inventories between 1950 and 1992 across the North Pacific (Hoberg and Soudachanh, 2020). Data encompassing additional specimens of seabirds collected after 1992 from the Bering Sea and Aleutian Islands are summarized. These latter observations broaden the baseline originally reported by Hoberg and Soudachanh (2020) to include 1,871 seabirds of 34 species across 55 localities, and 1,345 Alcidae of 18 species (Supplementary Data Tables 1–3). Cestodes of the complex are now documented, based on inventory, in 102 of 1,871 seabirds examined (5%) and among 1,345 alcids (8%) of 12 species (Supplementary Data Table 3). An additional occurrence for a previously undescribed *Tetrabothrius* has been linked to specimens originally attributed to *T. jagerskioeldi* collected by J. G. Baer during July 1955 in 1 of 3 black guillemots adjacent to Kangerluk (formerly Diskofjord), West Greenland (ca. 69°29'N, 53°56'W) (Baer, 1956); further, 2 specimens of *C. grylle* examined on 20 August 1955 from Kronprinsens Ejland, Qaasuitsup, West Greenland (ca. 69°01'N, 53°19'W) were not infected. We also note a corrected record for specimens of an unknown species of *Tetrabothrius* in Scripp's murrelets [*Synthliboramphus scrippsi* (Green and Arnold, 1939)] which had been erroneously referred to the complex by Hoberg and Soudachanh (2020) (Supplementary Data Tables 3 and 4).

Overall, 13 of 20 avian species that have been examined among the 24 extant members of the Alcidae [25 species with inclusion of the extinct great auk, *Pinguinus impennis* (Linnaeus, 1758)] across Holarctic seas were identified as hosts for cestodes of the *T. jagerskioeldi*-complex (Hoberg and Soudachanh, 2020). These cestodes, other than *T. jagerskioeldi*, were not observed in avian taxa beyond the Alcidae, including sympatric species of Stercorariidae, Laridae, and Phalacrocoracidae. Species of the complex appear to have limited host ranges among the Alcidae and, further, have not been collected or observed among an assemblage of Procellariiform seabirds in sympatry across the North Pacific Ocean and Bering Sea ecosystem during the boreal summer (E.P. Hoberg, unpublished data).

The general absence of archived specimens in alcids from most localities in the greater North Atlantic basin and from Russian and Japanese localities in the northwestern Pacific currently precludes a synoptic understanding of the broader host and geographic distribution of tetrabothriid cestodes, including those of the *T. jagerskioeldi*-complex (Hoberg and Soudachanh, 2020). Specimens of robust tetrabothriids in murrens appear historically to have been largely misattributed to *T. jagerskioeldi* (see Temirova

and Skrjabin, 1978; Muzzafar and Jones, 2004). Among these, an undescribed species of *Tetrabothrius*, as a component of the *T. jagerskioeldi*-complex, occurred in 53 of 1,345 avian specimens (4%), composing 5 of 18 species of Alcidae examined [predominantly in common murre and thick-billed murre; infrequently in pigeon guillemot, ancient murrelet [*Synthliboramphus antiquus* (Gmelin, 1789)], and parakeet auklet [*Aethia psittacula* (Pallas, 1769)] from 11 of 55 localities across the greater North Pacific basin, representing marine inventory between 1950 and 2002 (Supplementary Data Tables 1–3). A broad oceanographic distribution is documented, encompassing the region from Humboldt Bay, California, in the eastern North Pacific through the Gulf of Alaska, Bering Sea, Chukchi Sea, and Aleutian Islands to the northern Sea of Okhotsk in the west. Cestode specimens necessary to examine potential distributions in the Arctic basin and adjacent North Atlantic are not available.

It is also now evident that multiple species of large *Tetrabothrius*, including *T. jagerskioeldi*, occur in guillemots (Hoberg and Soudachanh, 2020) (Supplementary Data Table 3). Among these, an apparently rare cestode, a second distinct species in the complex, is represented by 3 fully developed specimens collected at single localities from the central Bering Sea (in pigeon guillemot at St. Matthew Island, Alaska; overall, 1 of 1,345 alcids, <1.0%; 1 of 22 *C. columba* but not in *C. carbo* or *C. grylle* from the North Pacific basin) and from West Greenland as noted previously (in black guillemot). The latter specimens held in the Museum d'Histoire Naturelle (MHN), Geneva had originally been identified as *T. jagerskioeldi* by Baer (1956).

In our expanding exploration of diversity, 2 previously unrecognized species of *Tetrabothrius*, primarily among murrens and guillemots (Alcinae), are characterized through comparative morphological approaches; 2 additional undescribed species primarily among the Fraterculinae will be designated in a subsequent study. Specimens or tissues suitable for molecular systematics and integrated analyses are not available. Cestode specimens, respectively, from the MHN and an assemblage of alcid hosts now archived in the Parasitology Division, Museum of Southwestern Biology, University of New Mexico (MSB), contribute to our present observations and descriptions. Taxonomic resolution provides an opportunity to explore the historical, ecological, and biogeographical parameters for assembly of the tetrabothriid fauna among North Pacific seabirds, along with consequences for restructuring of nektonic communities under climate oscillation and anthropogenic warming in high-latitude oceans.

Methods and Materials

Specimens Examined

We update and incorporate new field data (Supplementary Data Tables 2 and 3) from 1992 to 2002 into summaries previously outlined in Hoberg and Soudachanah (2020). Cestode specimens examined in the course of a comprehensive redescription of *T. jagerskioeldi*, as a basis for establishing morphological and taxonomic limits within the species complex, were outlined by Hoberg and Soudachanh (2020). Specimens now designated in the type and voucher series for 2 previously unrecognized species within the complex, described in our current study, are archived in the Parasitology Division, Museum of Southwestern Biology, University of New Mexico, Albuquerque (Supplementary Data Table 4). Primary data for field collections, including host occurrence and georeferenced localities (Supplementary Data Tables 2 and 3), are held in the Arctos data platform (<http://arctos.database.museum>). Host taxonomic nomenclature follows Chesser et al. (2020) for species of Alcidae, Laridae, Stercorariidae, and genera and species of Procellariiformes and Kennedy and Spencer (2014) for Phalacrocoracidae (shags and cormorants).

Cestode specimens from inventory collections of seabirds between 1975 and 2002 were usually fixed in buffered 10% formalin or 70% ethanol; specimens collected by other field biologists prior to 1975 were fixed in 10% formalin. Prior to fixation, cestodes immediately recovered from avian specimens during field collections were allowed to relax for an extended period of time in water at ambient temperature. Cestodes were heat-killed in either H₂O or in fixative. Strobilate specimens were generally prepared as whole mounts stained in Semichon's acetic carmine, destained in 70% ethanol and HCl, dehydrated through a series of ethanol, cleared in terpineol or xylene, and mounted in Permout or Canada balsam. Tegument was stripped from the strobila of some series of specimens at the time of clearing to facilitate examination of internal anatomy in whole mounts. Handcut thick sections were generally prepared from each strobila coincidental with clearing. Transverse sections were prepared in reference to ontogeny of the male and female reproductive systems to view the progressive development of the genital atrium, male and female genital ducts and uterus, and to confirm the position of the genital ducts and transverse uterus relative to the poral osmoregulatory canals. Designation of immature, mature, postmature, pregravid, and gravid proglottids follow definitions proposed in prior taxonomic studies of tetrabothriids (Murav'eva and Popov, 1976; Hoberg, 1987b; Hoberg et al., 1991) and provide the basis for

direct comparisons of genital organ systems at comparable stages of ontogeny (Rawson, 1964). Identifications for this series of specimens were limited to comparative morphological approaches. Molecular phylogenetic analyses were not possible for specimens because of their age and time frames for field collections in the 1950s to 2002, and a long history of storage at ambient temperatures in 10% formalin, varying grades of ethanol, and other reagents.

Results

Expanding Diversity in the *T. jagerskioeldi*-Complex, Cestodes in Murres

A previously unrecognized species of *Tetrabothrius*, a component of the *T. jagerskioeldi*-complex, occurred in 5 species of Alcidae among 18 examined and from 11 of 55 localities across the greater North Pacific basin (encompassing the region from Humboldt Bay, California, in the east through the Bering Sea, Chukchi Sea, and Aleutian Islands to the northern Sea of Okhotsk, Russia, in the west) representing inventory between 1950 and 2002 (Supplementary Data Table 3).

Cestodes we attribute to *Tetrabothrius alcae* n. sp. were found as parasites in 53 hosts among 1,345 (4%) alcids examined. These cestodes were predominantly observed in species of murres and among 49 of 426 of these seabirds, irrespective of age or breeding status (prevalence 11.5%), as summarized in Supplementary Data Table 3. Among common murres, *T. alcae* occurred in 32 of 276 (12%; intensity = 1–19 cestodes per host) across 6 of 17 localities where this avian species was collected. Among thick-billed murres, cestodes were found in 17 of 150 examined (11%; intensity = 1–16) across 7 of 14 sites. *Tetrabothrius alcae* occurred sporadically in other species of alcids. We discovered *T. alcae* in a pigeon guillemot (1 of 22, 4.5%; single gravid specimen at St. Lawrence Island) but not in *C. carbo* (4 examined) or *C. grylle* (8); in ancient murrelets (2 of 51, 4%; with single gravid cestode specimens, respectively, at St. Lawrence Island and from pelagic waters south of the western Aleutian Islands) but not in *S. scrippsi* (4); and in a parakeet auklet (1 of 56, 2%, 3 postlarval specimens from Talan Island). Specimens attributable to *T. alcae* (or *T. jagerskioeldi*) were generally not found among Fraterculinae, including other species of auklets (Aethiini), *Aethia* Merrem, 1788, and *Ptychoramphus* Brandt, 1837, nor among puffins (Fraterculini) of the genera *Cerorhinca* Bonaparte, 1828 and *Fratercula* Brisson, 1760 (Supplementary Data Table 3). Specimens of *T. alcae* were observed in multiple host species in sympatry (but not consistently synchronic) from pelagic waters south of the Aleutian Islands (*U. lomvia*,

S. antiquus), St. Lawrence Island (*U. lomvia*, *C. columba*, *S. antiquus*), St. Matthew Island (*U. aalge*, *U. lomvia*), and Talan Island (*U. aalge*, *U. lomvia*, *A. psittacula*).

Among all species of murre, relative to breeding status and age of hosts, specimens of *T. alcae* were discovered in 24 of 356 breeding adult birds (7%), 13 of 37 nonbreeding subadults (35%), and 12 of 33 chicks at fledging (36%). Among common murre across all localities, *T. alcae* occurred in 11 of 216 breeding adult birds (5%), 10 of 29 subadults (34%), and 11 of 31 chicks at the time of fledging (35%). Among thick-billed murre, cestodes were found in 13 of 140 adults (9%), 3 of 8 subadults (37%), and 1 of 2 fledglings.

Primary materials representing *T. alcae* include specimens in 40 alcid hosts (24 *U. aalge*, 12 *U. lomvia*, 2 *S. antiquus*, and single *C. columba* and *A. psittacula*), with 47 cestodes on 91 slides in the type series on which the description is based (Supplementary Data Table 4); specimens in one ancient murrelet and a parakeet auklet are excluded from the type series and are included as vouchers. Additionally, there are 67 stained and mounted vouchers, primarily postlarval or immature specimens, on 37 slides, identified based on the characteristic configuration and structure of the scolex. Additional unmounted specimens from the type and voucher series are held in vials in 70% or greater ethanol.

Description—*Tetrabothrius alcae* n. sp.

Figures 1–29

General Description: (Based on complete and partial observations and measurements from 47 specimens in the type series.) Large, robust, tetrabothriids; maximum length of strobila 127–210 mm, with 529–700 proglottids in gravid specimens. Segments wider than long throughout strobila; 94–182 long × 1,636–2,457 wide in immature proglottids; 195–455 × 3,003–5,005 in mature; 455–1,105 × 4,355–6,166 in gravid. Length:width ratio 1:9.29–17.98 in immature; 1:9.63–15.68 in mature; 1:4.86–13.43 in gravid. Scolex rectangular, consistently wider than long (n = 40) 190–392 (297) long × 201–422 (359) wide; auricles not prominent. Bothridia suckerlike, deep, well developed, (n = 146) 152–255 (212) long × 103–198 (168) wide, with muscular margins. Apical region hypertrophied, domelike, expanded anterior to auricles. Neck, as measured from base of scolex to first indication of internal segmentation, relatively long, (n = 32) 500–1,550 (843) in length × 274–577 (428) wide, often appearing inflated. Ventral osmoregulatory canals 41–169

in diameter; transverse canal 16–74, often with multiple anastomoses; dorsal canals 17–41 in diameter. Dorsal canal shifted mediad relative to ventral canal. Occasionally 3 dorsal canals present, with one pair situated in poral 1/3 of segment. Anastomoses of osmoregulatory system visible in scolex, extending into neck. Genital pores unilateral, dextral in dorsal orientation of strobila, situated marginally in middle third of proglottid. Male and female genital ducts and extensions of transverse uterus pass ventrally to poral osmoregulatory canals.

Longitudinal Musculature: Musculature prominent in transverse sections of proglottids; inner and outer bundles arranged in single layers. Inner bundles large in diameter; (n = 22) 95–177 (139) in number; (n = 55) 9–72 (35) fibers per bundle. Outer bundles relatively small in diameter; (n = 10) 183–235 (217) in number; (n = 100) 2–15 (7) fibers per bundle. Numbers of muscle bundles maximum in mature proglottids, diminishing in number posteriad in postmature and gravid segments.

Male Genitalia: Genital anlagen visible immediately posterior to neck, protandrous; first testes observed in 130th–160th segment; mature in 250th–300th segment. Testes positioned dorsally in 1–2 layers surrounding and partially overlapping female organs, with gap along anterior margin of vitelline gland and ovary; (n = 130) 52–105 (74) in diameter. Testes (n = 230 segments from 17 strobila) 75–134 (100) in number in immature segments, decreasing posteriad to (n = 110 segments from 10 strobila) 66–111 (87) in number with maturation of male and female organs; overall (n = 340 segments) 66–134 (96). Vas deferens prominent, highly convoluted, distended adjacent to poral osmoregulatory canals. Cirrus sac ovoid, situated in dorsal aspect of genital atrium, (n = 500) 80–137 (107) increasing in diameter posteriad in strobila, attaining maximum dimensions in late maturity; muscular wall thickened, (n = 50) 5–10 (8). Cirrus sac contains extension of convoluted vas deferens and cirrus armed with miniscule but prominent spines. Genital atrium ovoid, highly muscularized (n = 400) 140–304 (218) attaining maximum diameter in late maturity. Male genital canal, as viewed in transverse sections, dorsal, extending through wall of atrium, with slight ventral curve, opening through prominent, weakly bilobed papilla in center of atrial lumen; sphincters not observed. Length of male genital canal increases with age of proglottid and development of genital atrium; (n = 29) 44–68 (55) long in early maturity; (n = 94) 65–94 (77) in late mature to pregravid segments; overall (n = 123) 44–94 (72) in length.

Figures 1–2. *Tetrabothrius alcae* n. sp. **Fig. 1.** Scolex in dorso-ventral view from paratype specimen (2640-3A); note structure of weakly developed, laterally directed auricles near anterior margins of deep, strongly developed, suckerlike bothridia and domelike apical region. **Fig. 2.** Scolex in lateral view from paratype specimen (2640-4A); note disposition of inconspicuous auricles.

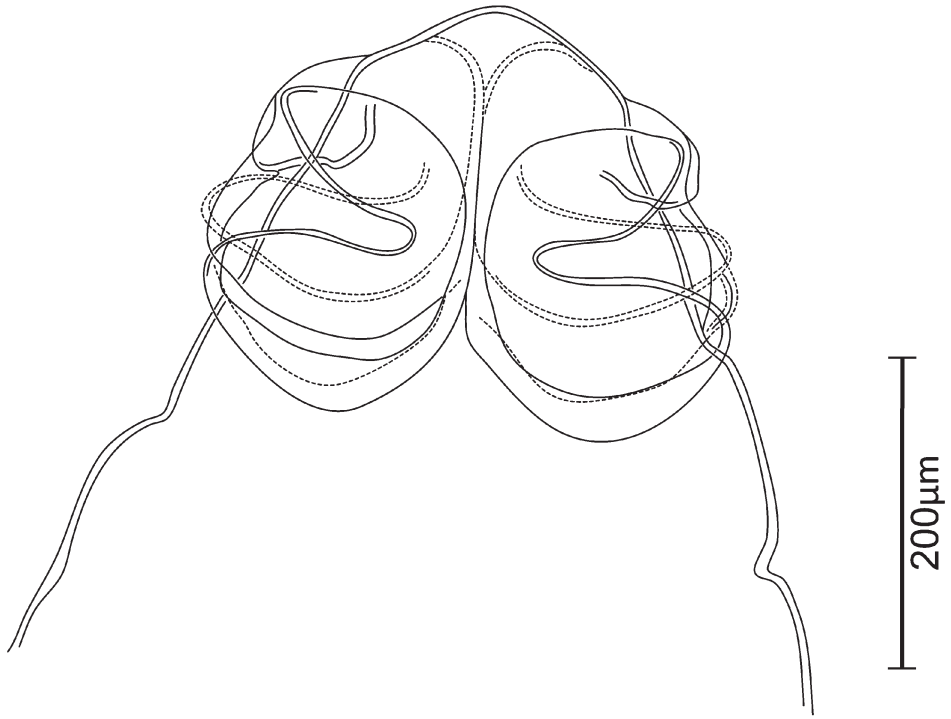
Figures 3–4. *Tetrabothrius alcae* n. sp., showing structure of proglottids and configuration of male and female organ systems. **Fig. 3.** Proglottid in early maturity in dorsal view, whole mount from holotype (2640-1A); note dextral genital pore, ventral genital ducts and nascent uterus, distribution of testes, and elongate vitelline gland on anterior margin of lobate, biwinged ovary. **Fig. 4.** Proglottid in maturity, dorsal view, whole mount from holotype (2640-1A), showing region from near midline to genital pore margin; note ventral position of genital ducts and uterine stem relative to poral osmoregulatory canals, elongate and cylindrical to pyriform vaginal seminal receptacle, voluminous and convoluted vas deferens, and prominent subspherical genital atrium and cirrus sac.

Figures 5–7. *Tetrabothrius alcae* n. sp., showing configuration of the genital atrium and relative positions of the cirrus sac, terminal vagina, and male and female atrial canals. **Fig. 5.** Genital atrium in early maturity, dorsal view, whole mount, from holotype (2640-1A); note position of cirrus sac with convoluted vas deferens and cirrus, ventral vagina, and weakly bilobed genital papilla in dorsal aspect of atrium, and developing uterine stem. **Fig. 6.** Genital atrium in maturity, dorsal view, whole mount, from holotype (2640-1A); note ventral positions of the vagina, vas deferens, and uterine stem relative to poral osmoregulatory canals, structure of bilobed genital papilla, and apertures of the male and female genital canals. **Fig. 7.** Genital atrium in pregravid condition, dorsal view, whole mount, from holotype (2640-1A); note bilobed genital papilla, subspherical cirrus sac, and male canal positioned dorsally to terminal vagina with expansion of atrial seminal receptacle.

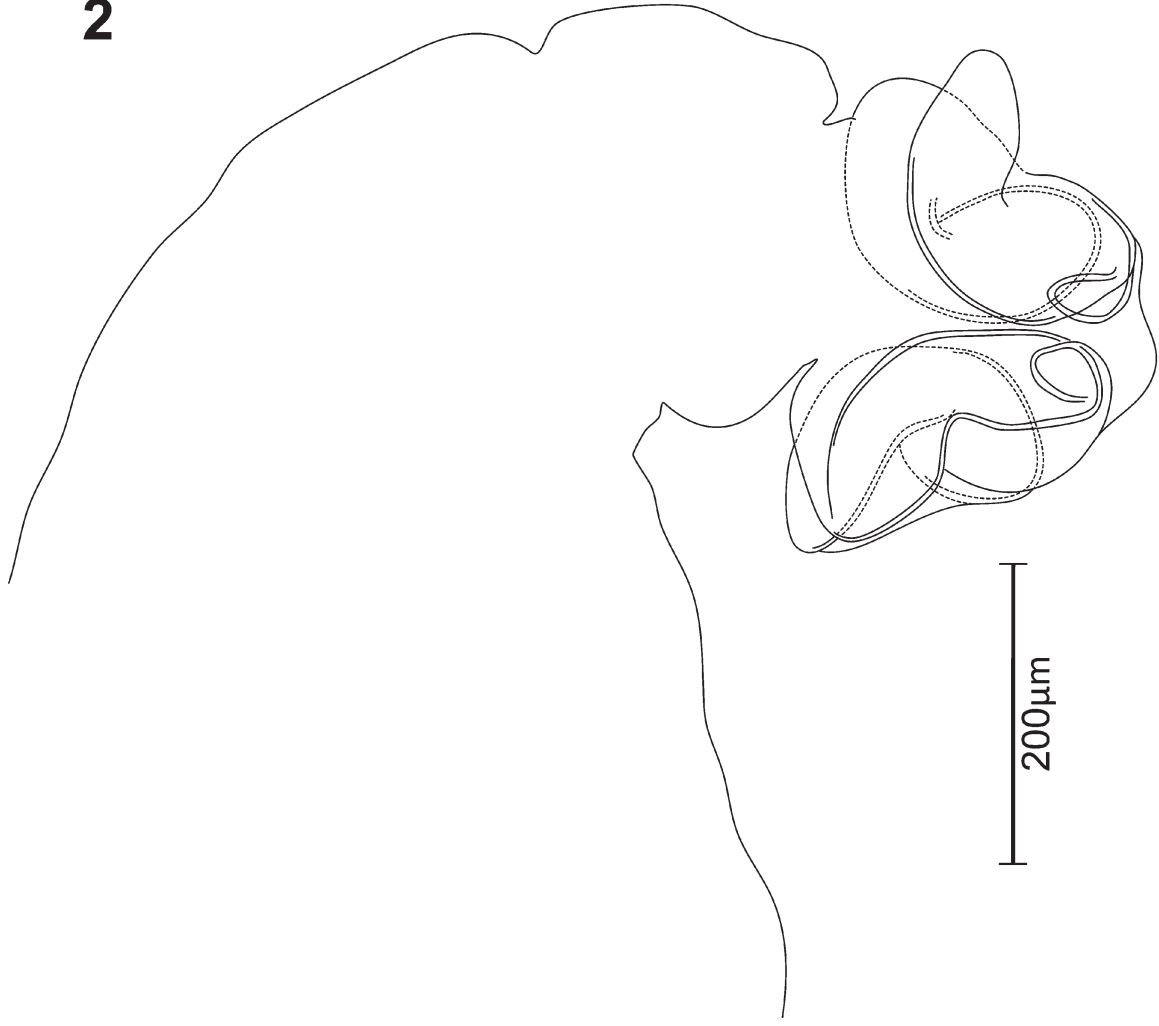
Figures 8–9. *Tetrabothrius alcae* n. sp., showing configuration of the genital atrium and relative positions of the cirrus sac, terminal vagina, and male and female genital atrial canals from hand-cut transverse sections. **Fig. 8.** Genital atrium in early maturity, dorsal to top, from holotype specimen (2640-1B); note relative position of the cirrus sac, weakly curved male atrial canal, terminal vagina and thick-walled female canal, entering muscular atrium at 90° to male system. **Fig. 9.** Genital atrium and poral margin of proglottid in post maturity, dorsal to top, from holotype specimen (2640-1C); note positions and structure of the outer and inner bundles of longitudinal musculature, ventral position of the genital ducts relative to the dorsal and ventral osmoregulatory canals, strongly muscular genital atrium, weakly curved male canal, terminal vagina turning 90° at entry to atrial wall, and expansion of atrial seminal receptacle.

Figures 10–11. *Tetrabothrius alcae* n. sp., showing details of female organ systems and egg. **Fig. 10.** Female genital ducts in early maturity, ventral view from paratype (018-75 A-2), showing the configuration of the vagina, internal seminal receptacle, ovarian duct, common vitelline duct, ascending uterine stem, and transverse uterine stem relative to the ovary and vitelline gland. **Fig. 11.** Egg, showing structure from holotype specimen (2640-1G), with granular capsule, ellipsoidal hyaline embryophore, oncosphere, and oncospherical hooks.

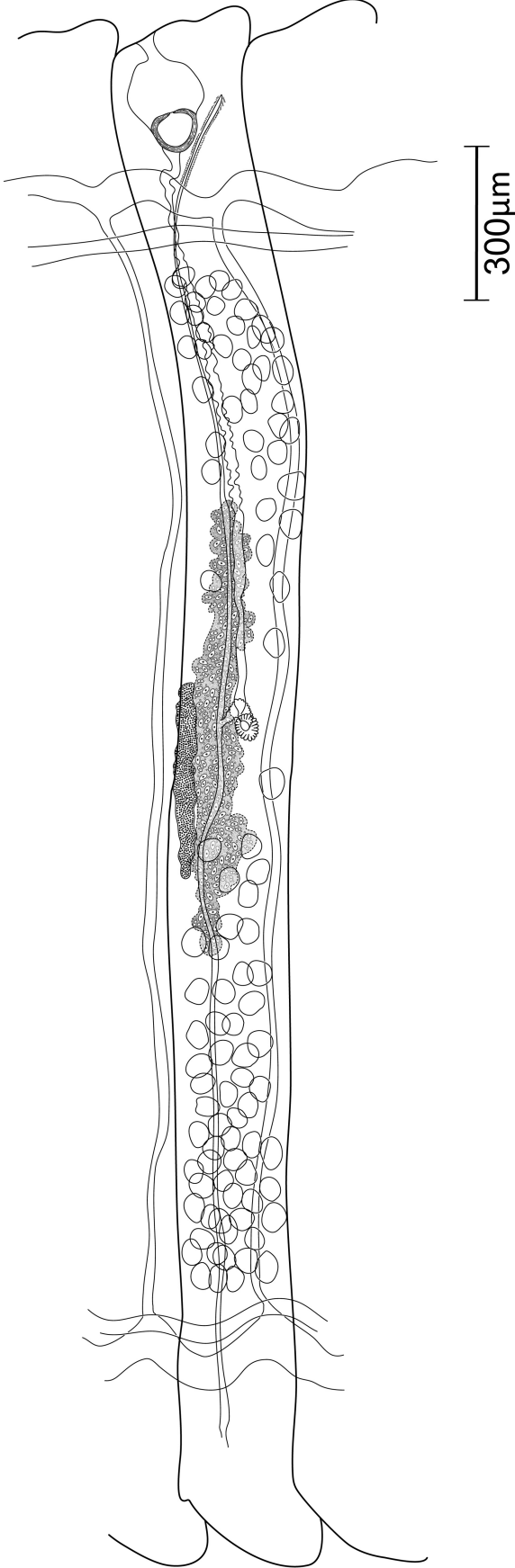
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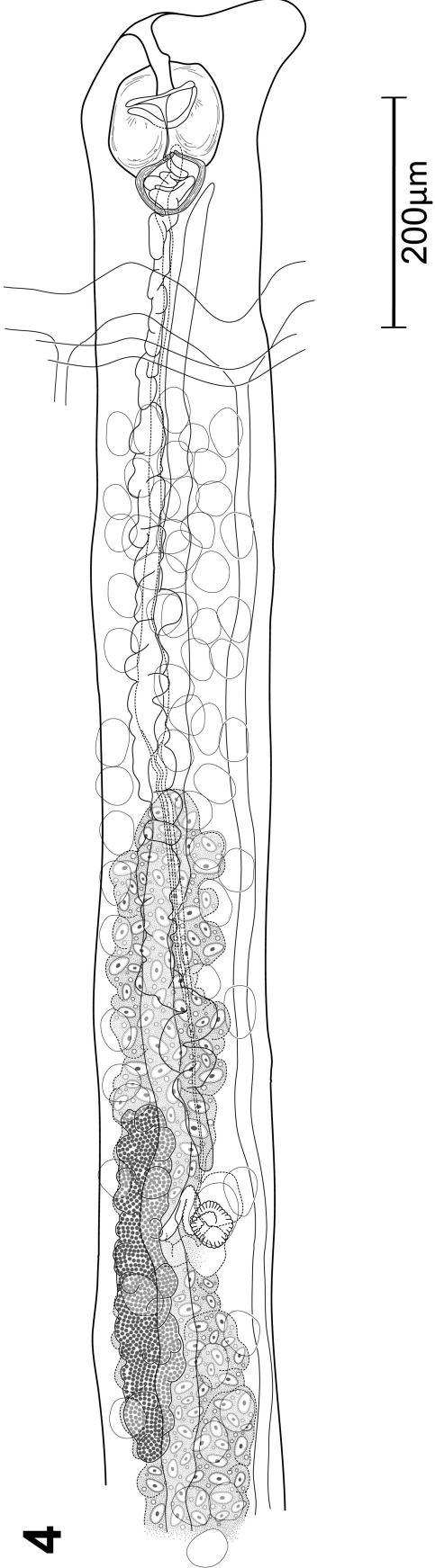
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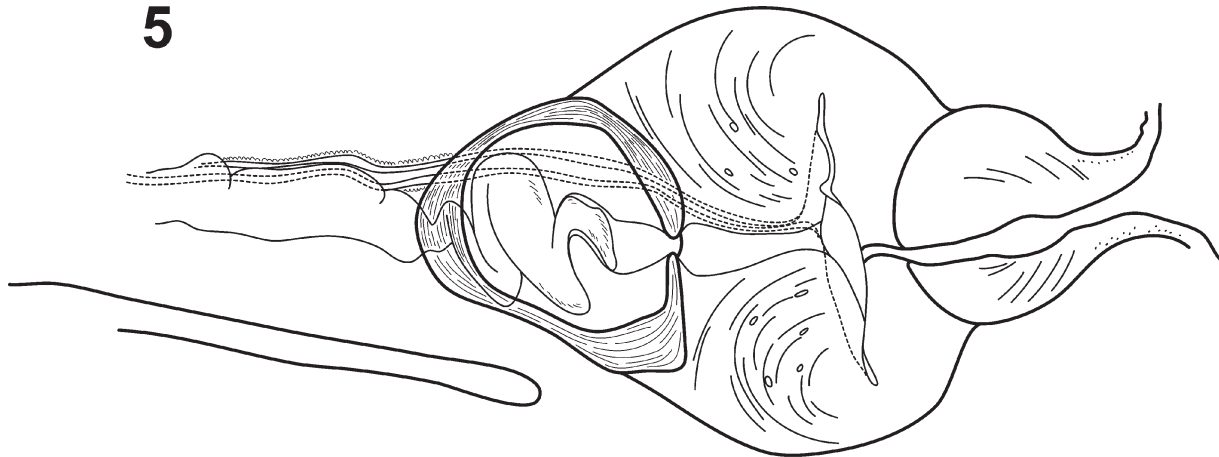
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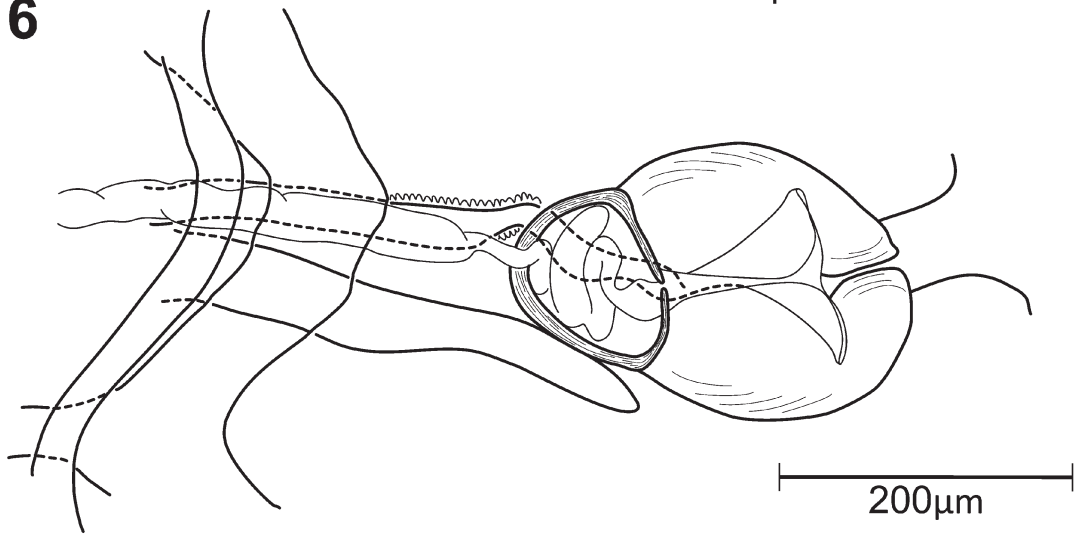


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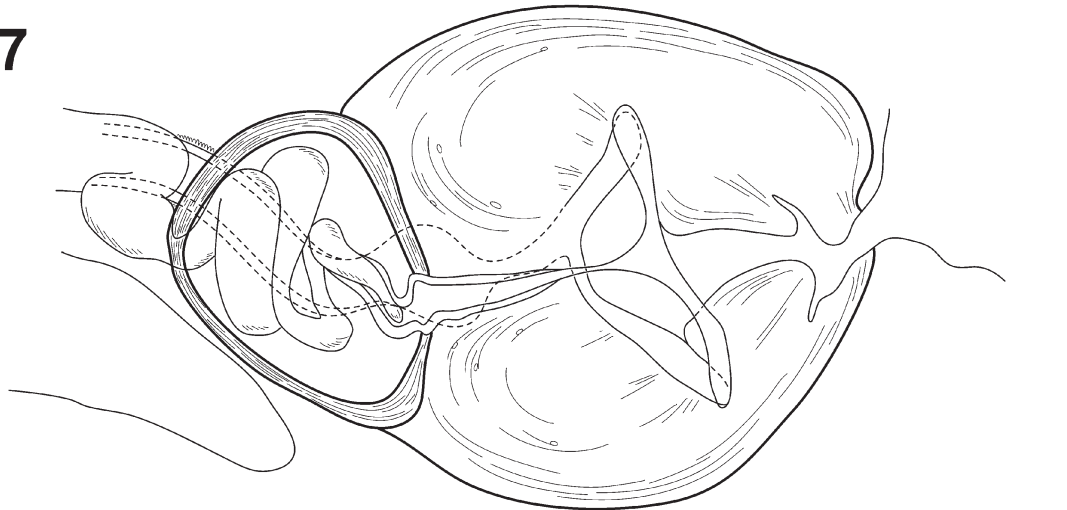
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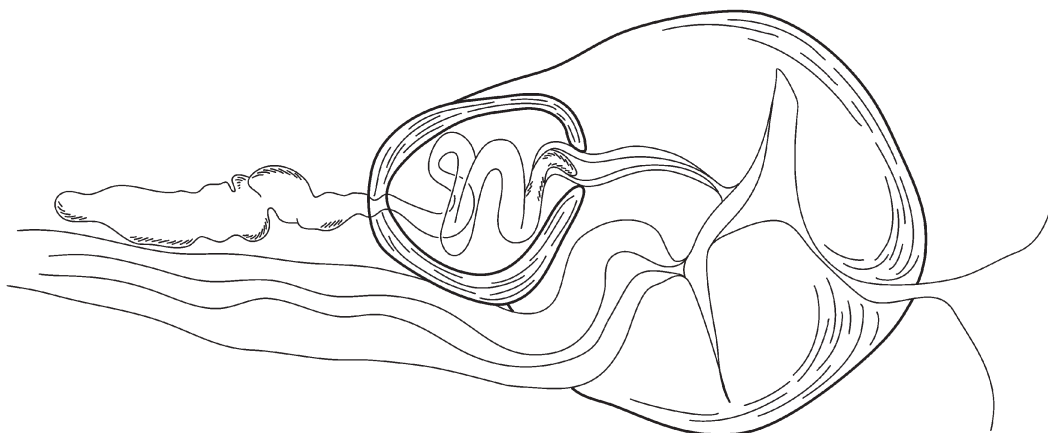
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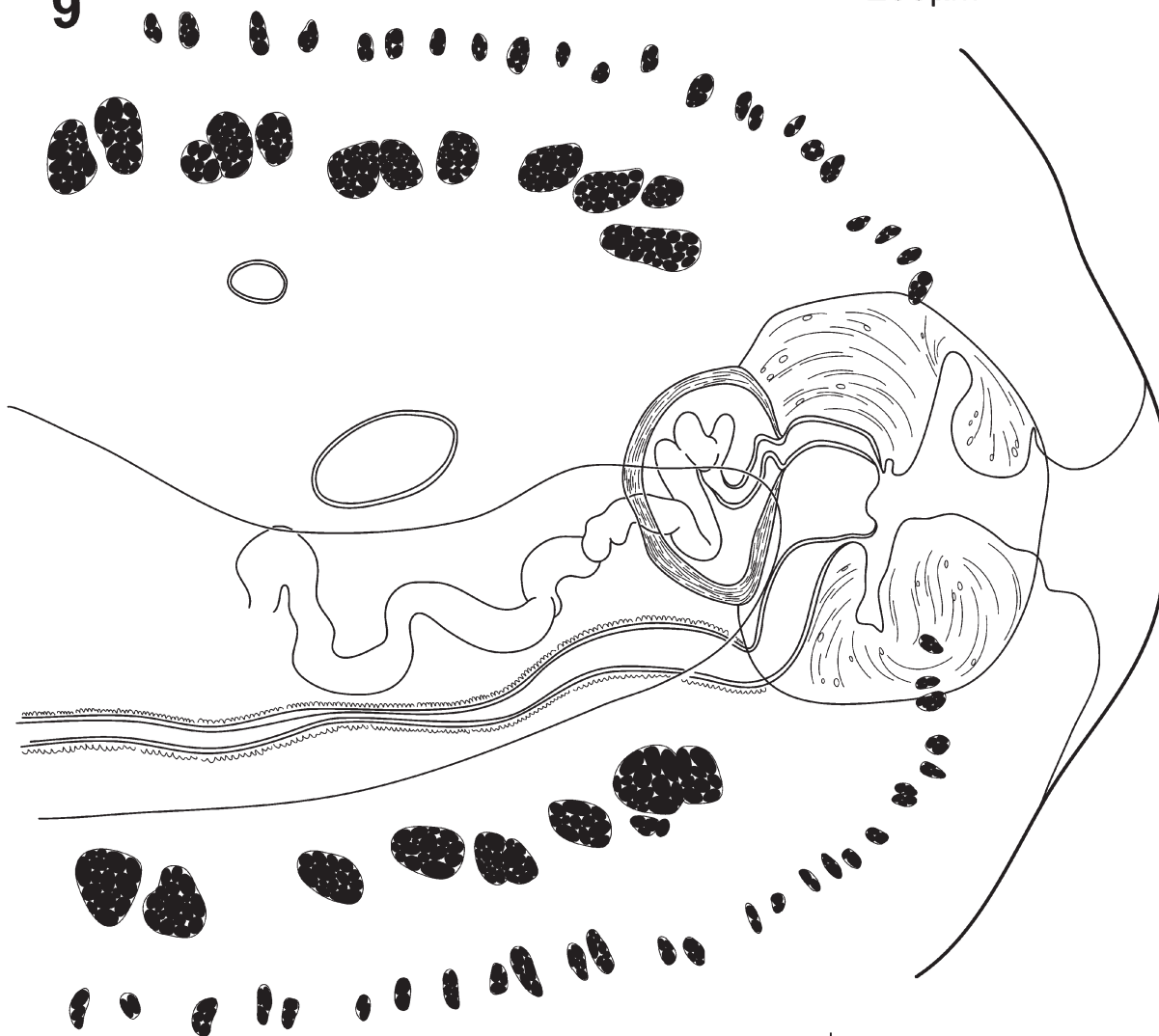
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8



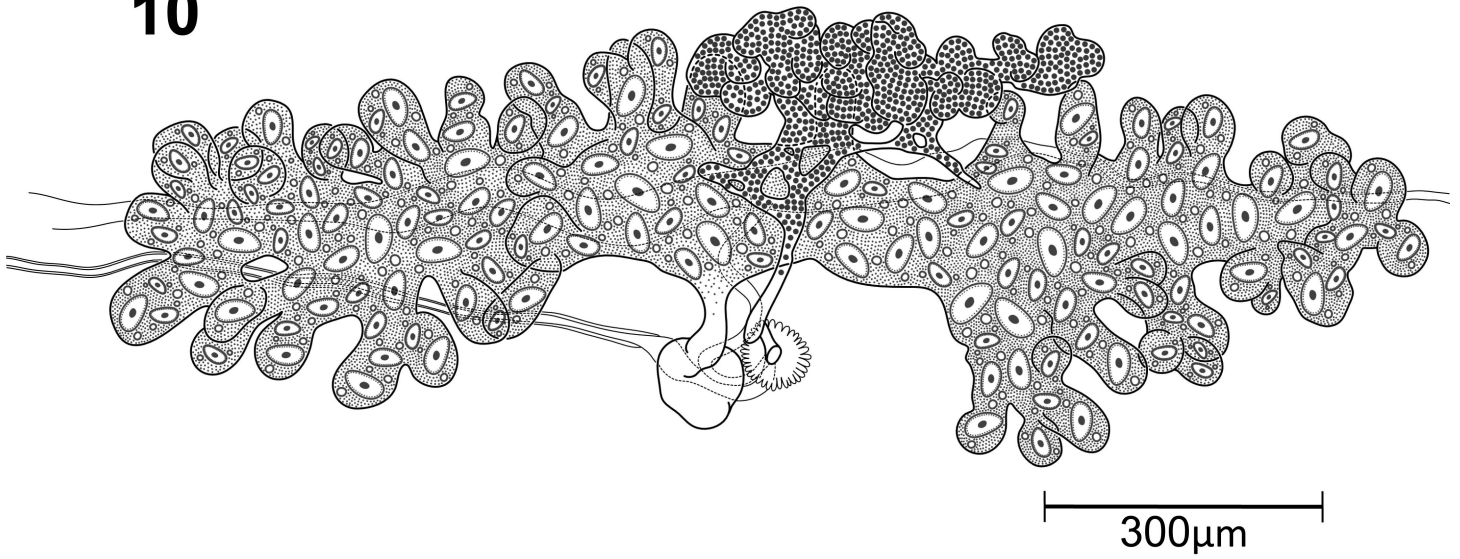
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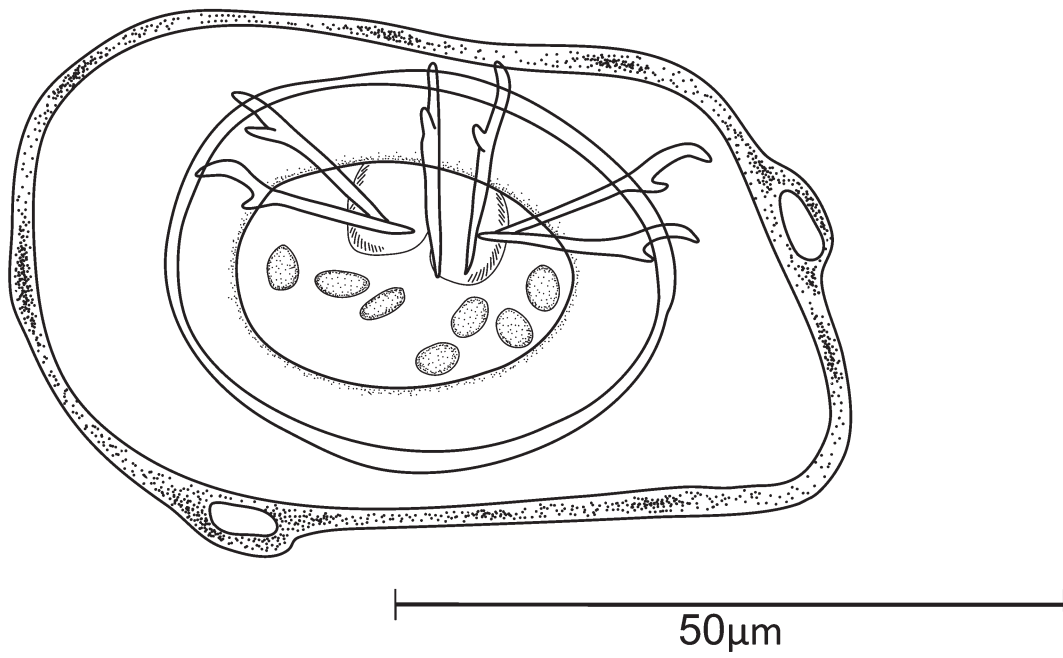


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10



11



Figures 12–15. *Tetrabothrius alcae* n. sp., showing structure of scolex and bothridia from micrographs of whole-mounted strobilate, gravid specimens (scale bars in micrometers). **Fig. 12.** Scolex and elongate neck region in paratype specimen (2640-3A), dorso-ventral view. **Fig. 13.** Scolex detail showing strongly developed suckerlike bothridia and reduced auricles; note the prominent domelike apical region. **Fig. 14.** Scolex and elongate neck region in paratype specimen (018-75-A), showing lateral view of suckerlike bothridia. **Fig. 15.** Scolex showing muscular structure of bothridia in lateral view.

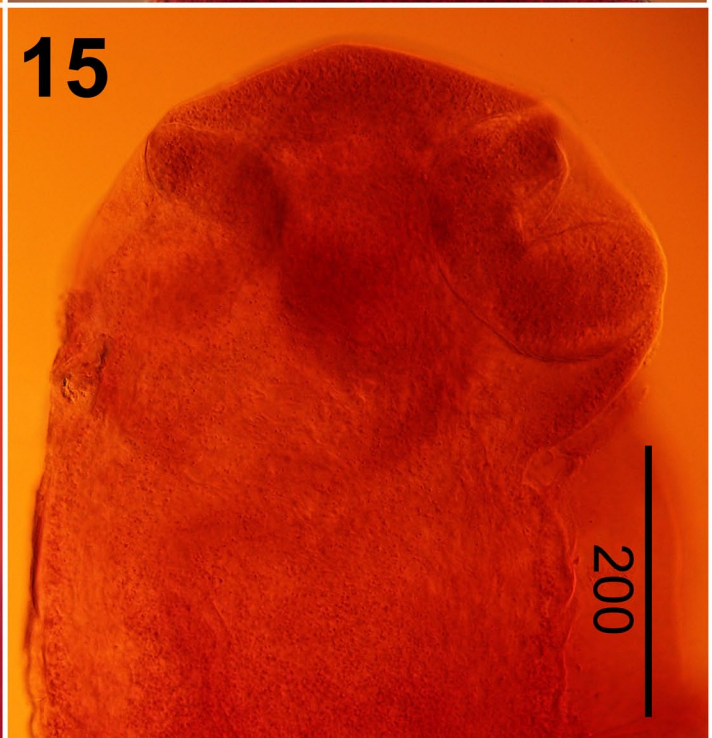
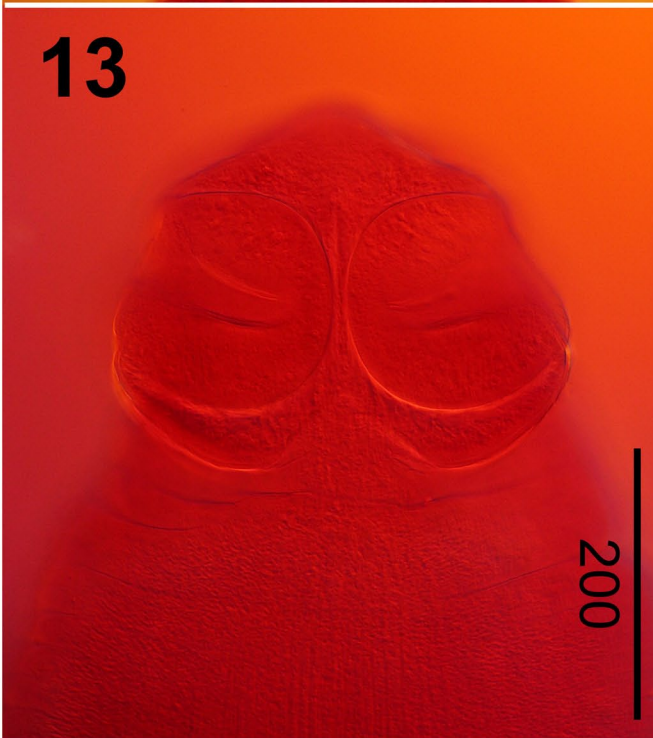
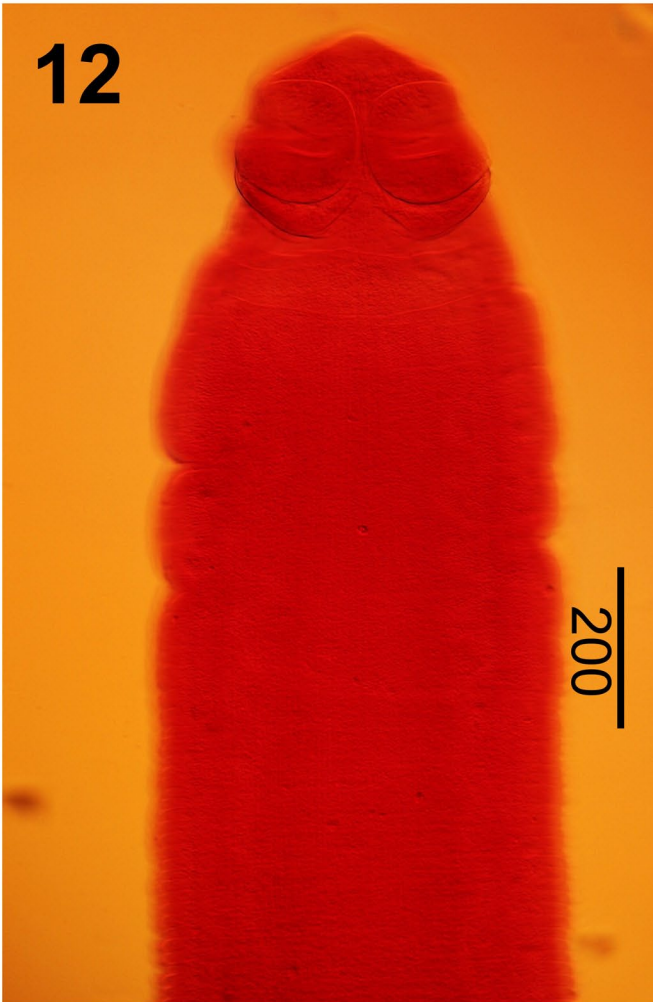
Figures 16–18. *Tetrabothrius alcae* n. sp., showing structure of proglottids at progressive stages of ontogeny and positions of male and female organ systems from micrographs of whole-mounted specimens (scale bars in micrometers). **Fig. 16.** Proglottids in early maturity (holotype, 2640-1A), dorsal view, showing dextral position of genital pore, disposition of testes surrounding female system with gap in distribution along anterior margin of dendritic ovary and follicular vitelline gland. **Fig. 17.** Proglottids in maturity (paratype 018-75-A), ventral view, showing bilobed dendritic ovary and follicular anteroventral vitelline gland. **Fig. 18.** Proglottids in maturity (holotype, 2640-1A), dorsal view (poral aspect of segments from midline to marginal genital pore), showing position of testes, genital ducts relative to poral osmoregulatory canals, initial development of transverse uterine stem, and prominent dextral genital pore.

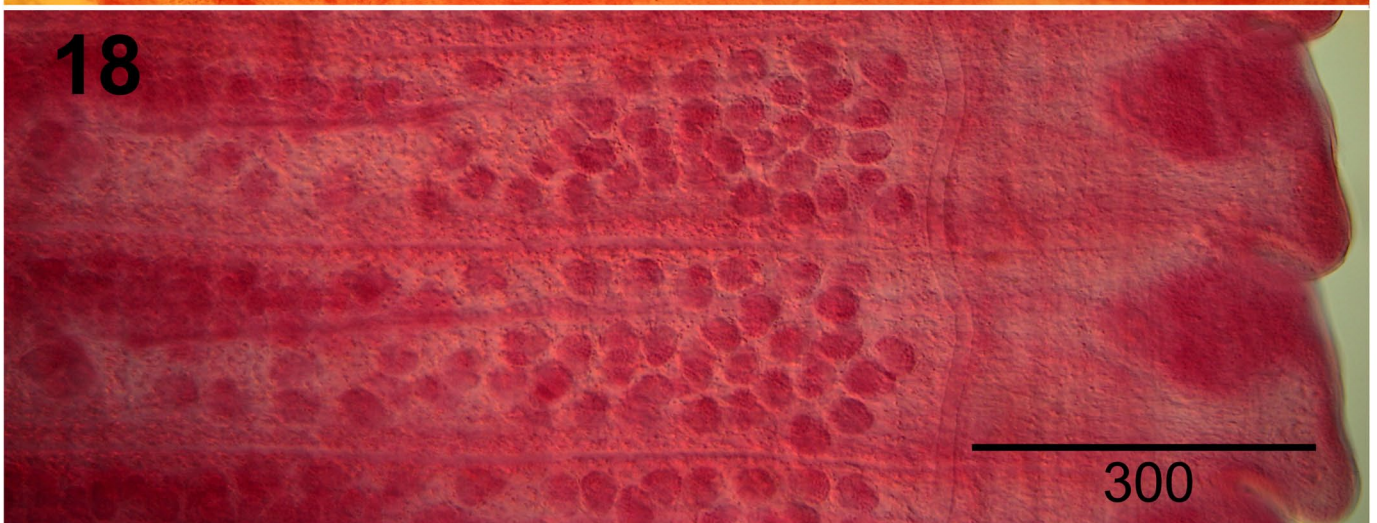
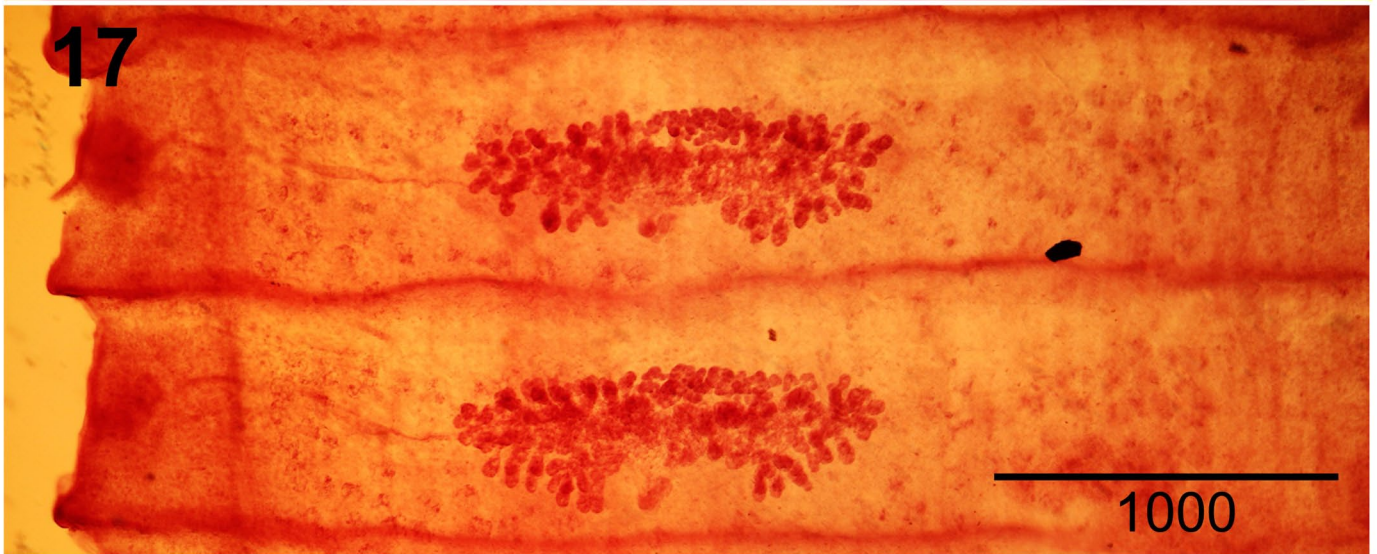
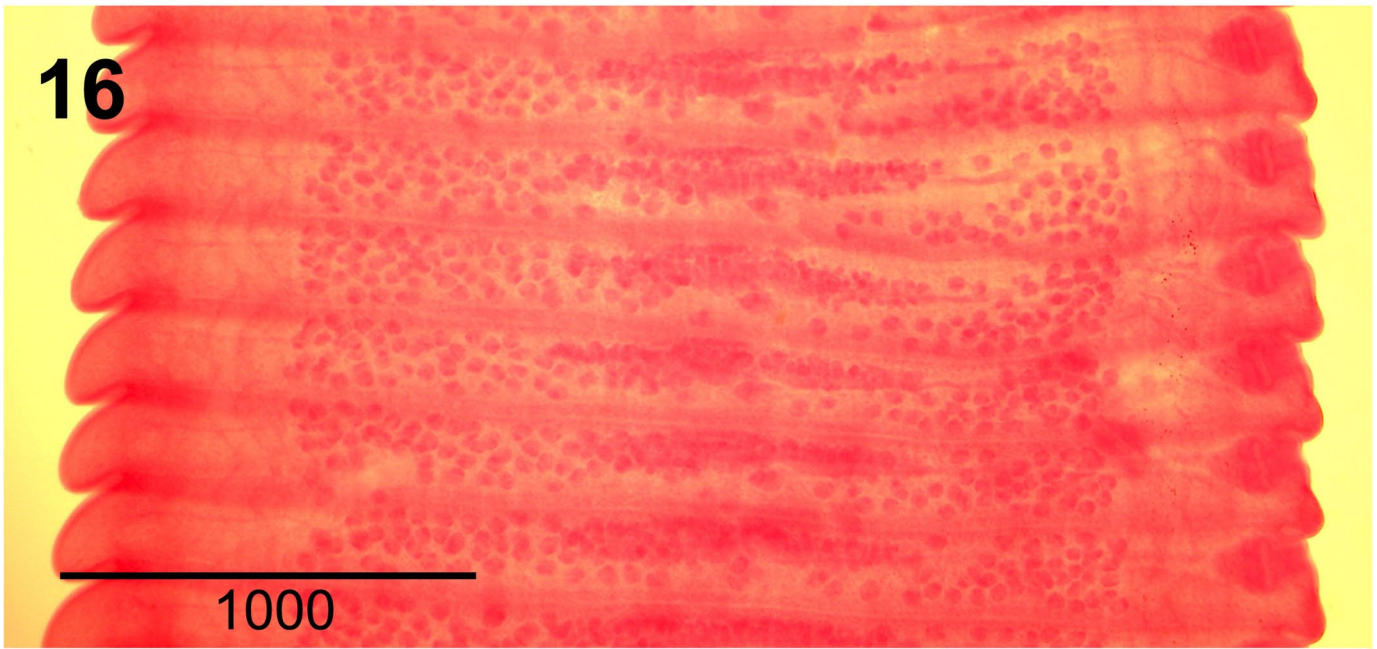
Figures 19–21. *Tetrabothrius alcae* n. sp., showing structure of female organ systems in ventral view from micrographs of a whole-mounted specimen (scale bars in micrometers). **Fig. 19.** Structure of strongly dendritic and bilobed ovary (ov); highly elongate, follicular vitelline gland (vt); and granular uterine stem (ut) (paratype 018-75-A) in early maturity. **Fig. 20.** Ovary (ov), anteroventral vitelline gland (vt), and position of Mehlis' gland (me) (paratype 018-75-A) in maturity. **Fig. 21.** Genital duct systems and transverse uterine stem (paratype 018-75-A) in region between poral wing of ovary (ov) and genital pore; note highly convoluted male vas deferens (vd), narrow vagina and expanding, elongate to pyriform vaginal seminal receptacle (vsr); and transverse uterine stem (ut) passing ventral to the poral osmoregulatory canals (osm) in maturity.

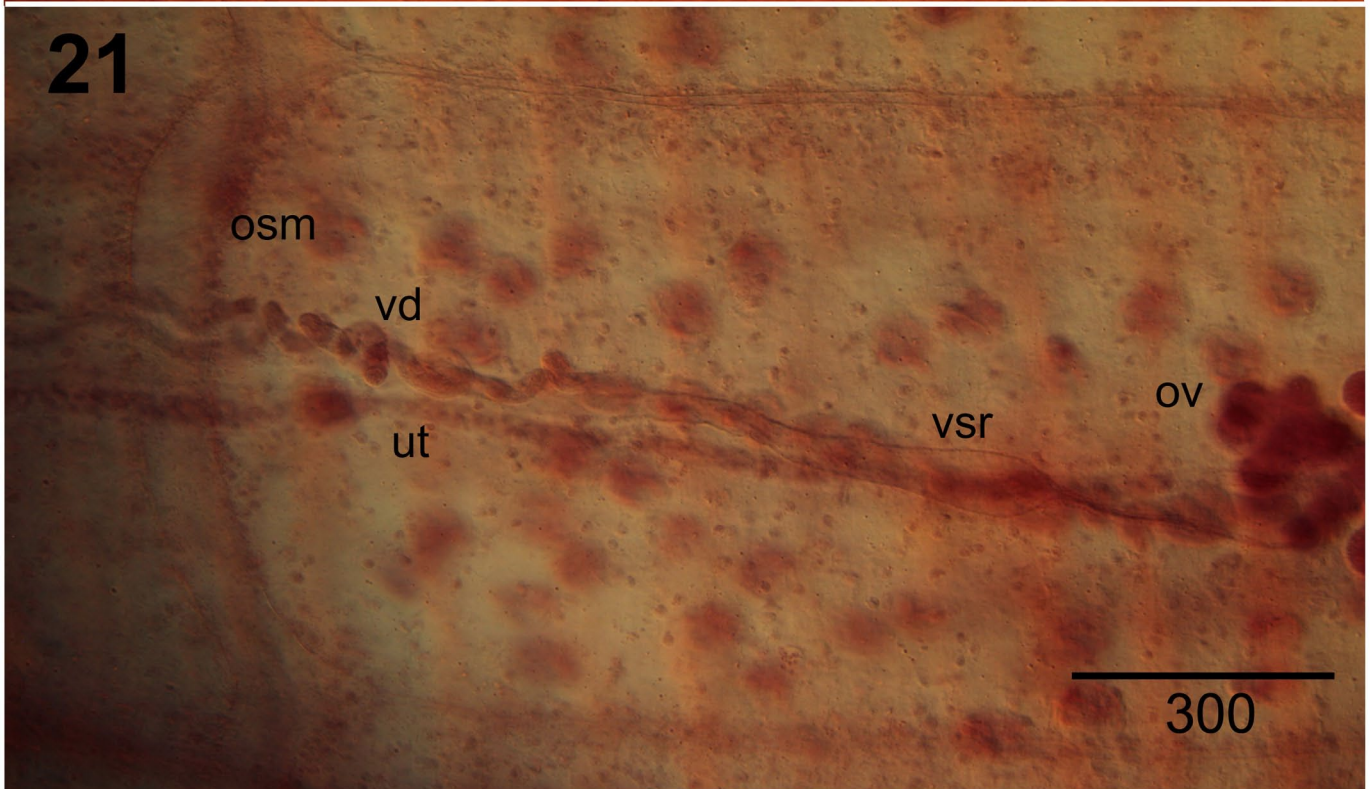
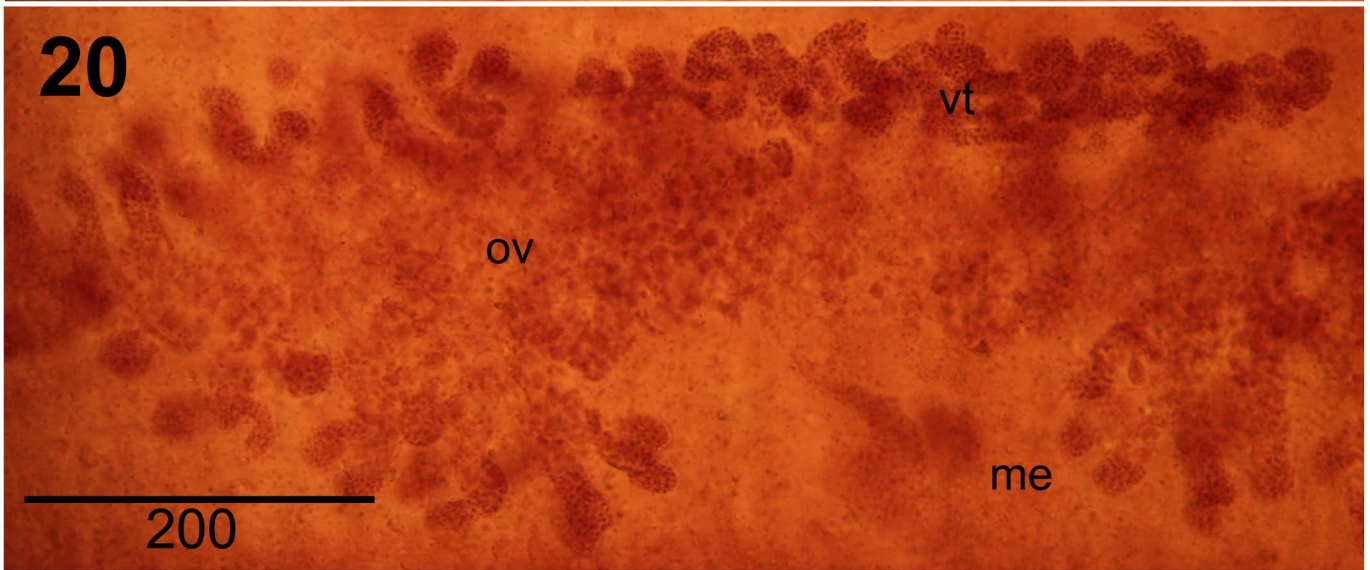
Figures 22–23. *Tetrabothrius alcae* n. sp., showing structure of genital atrium, cirrus sac, male atrial canal, and vagina from micrographs of a whole-mount specimen and hand-cut transverse sections in postmature to pregravid development (scale bars in micrometers). **Fig. 22.** Genital pore and atrium in dorsal view from whole mount (holotype 2640-1A), showing marginal position of the genital pore (ge); genital atrium (ga) with bilobed papilla; and prominent, strongly muscularized cirrus sac (cs). **Fig. 23.** Genital atrium in transverse section (holotype 2640-1C), viewed from posterior (dorsal to top), showing structure of cirrus sac (cs), genital atrium (ga), genital papillae, weakly curved male genital canal and position of atrial seminal receptacle (asr), and 90° turn in vagina adjacent to the cirrus sac. Apertures of the male and ventrally disposed female canal open centrally and near the base of the genital papillae. The uterus (ut), vas deferens (vd), and vagina (va) pass ventrally to the dorsal (dosm) and ventral (vosm) osmoregulatory canals. Note the position, dimensions, and distribution of the inner (im) and outer (om) bundles of longitudinal musculature.

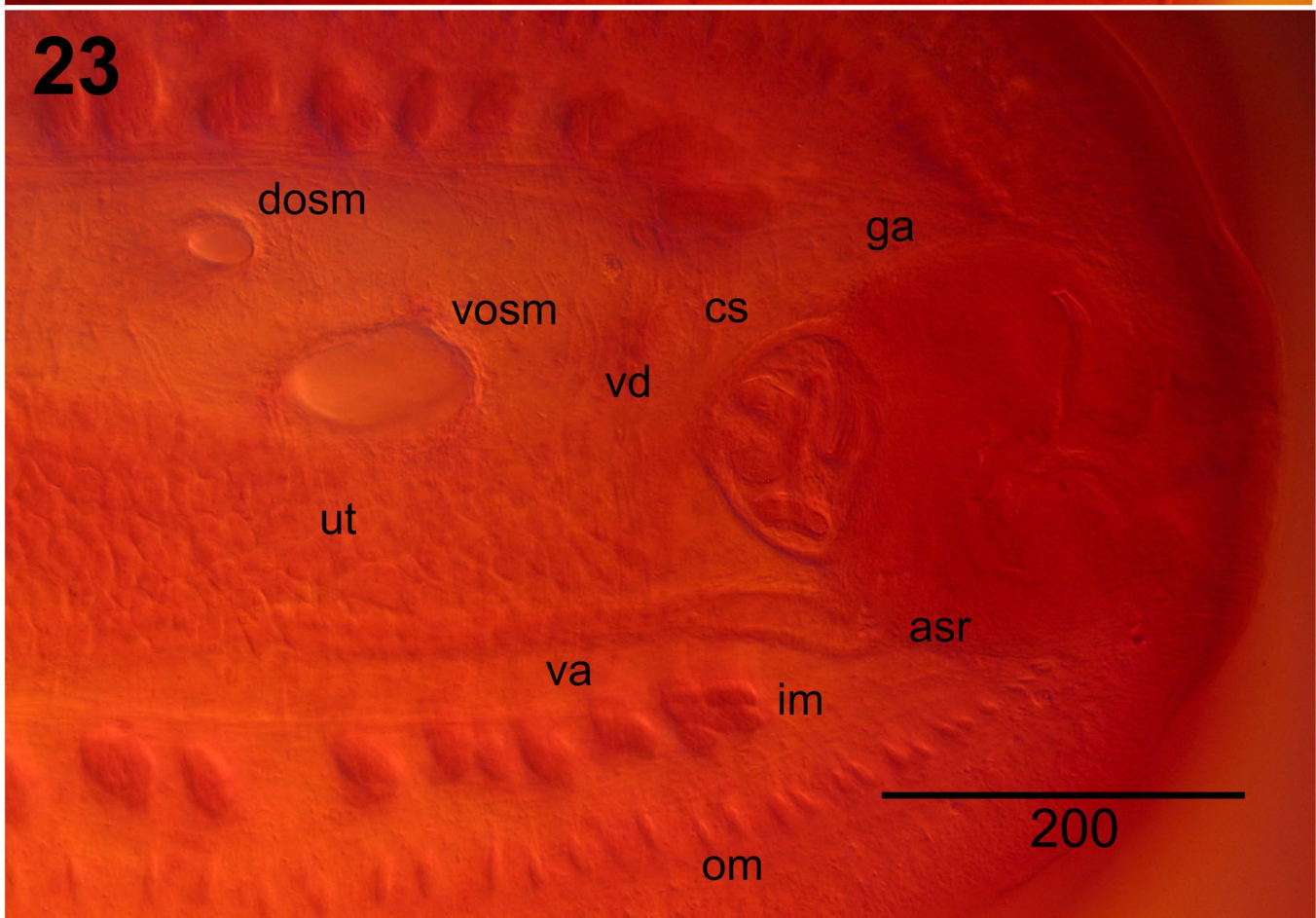
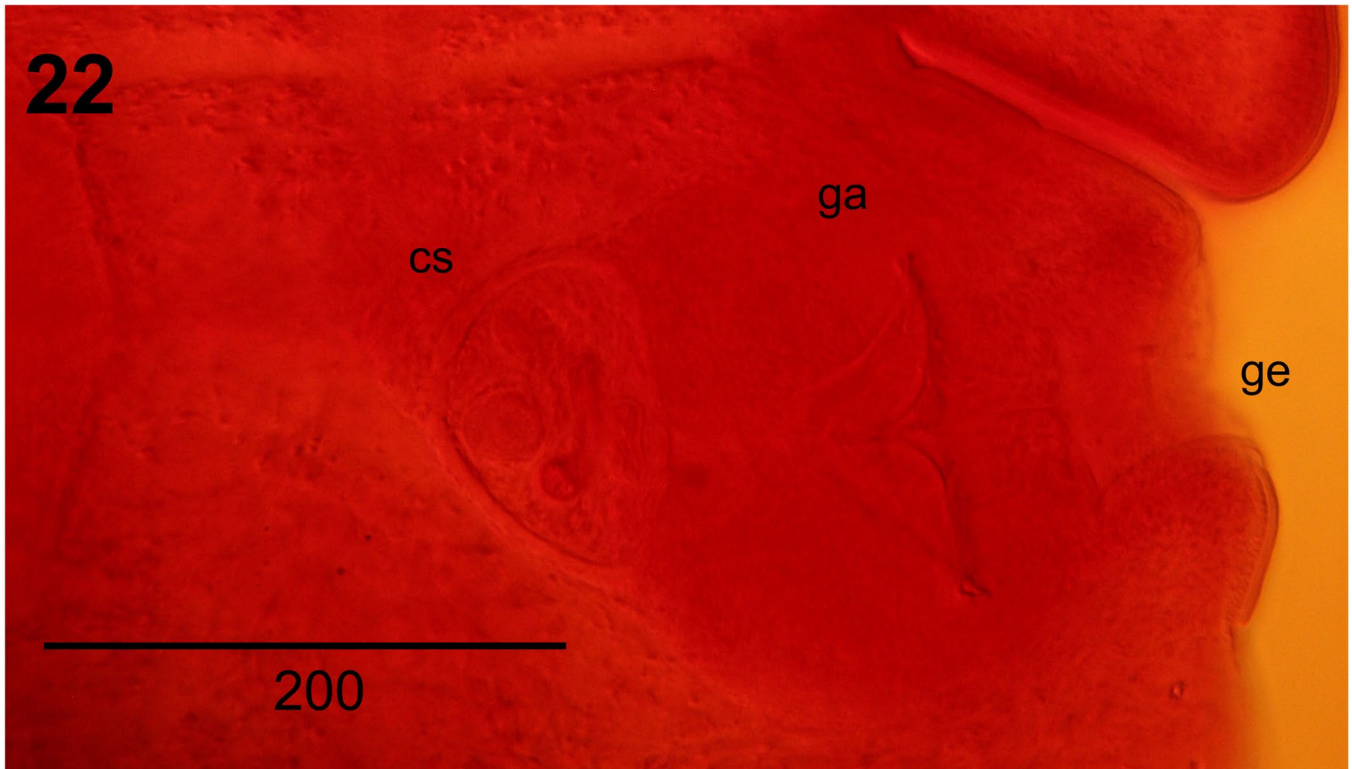
Figures 24–25. *Tetrabothrius alcae* n. sp., showing structure of genital atrium, cirrus sac, vagina, and genital ducts in transverse hand-cut sections, viewed from anterior, from micrographs of the holotype specimen (dorsal to top; scale bars in micrometers). **Fig. 24.** Genital atrium (holotype 2640-1C), showing relative positions of genital ducts, expanding uterus ventral to the osmoregulatory canals. Vagina, with thick wall and expanded atrial seminal receptacle (asr) enters genital atrium in 90° turn; female canal opens ventral, not strongly adjacent, to orifice of male canal. Cirrus sac on lateral border of genital atrium with slightly curved male canal opening between weakly bilobed papilla in center of atrium. **Fig. 25.** Genital atrium (holotype 2640-1C), showing relationships of cirrus sac (cs) (containing highly convoluted vas deferens and retracted cirrus), genital atrium (ga) with male and female genital canals (arrows), genital papillae (gp), and atrial vagina.

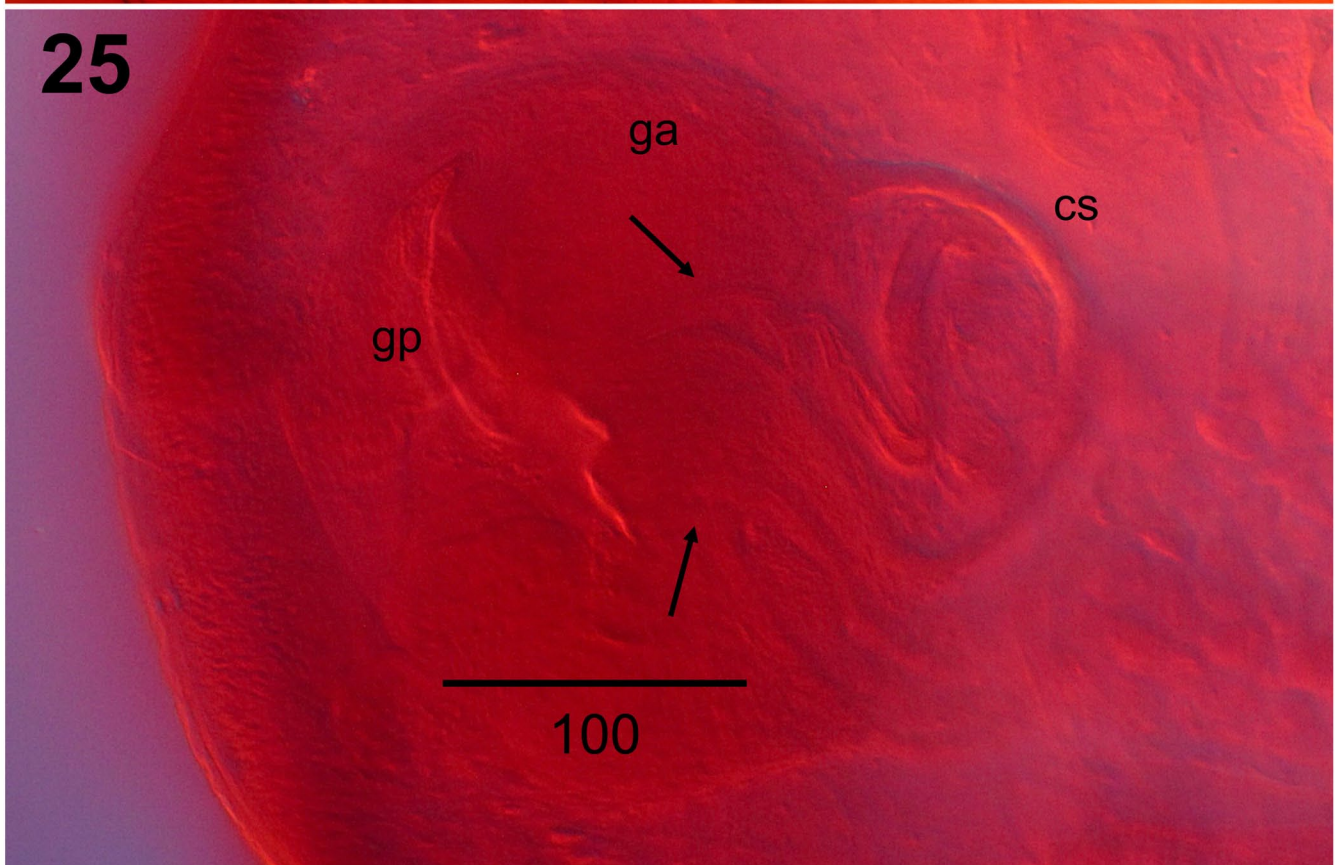
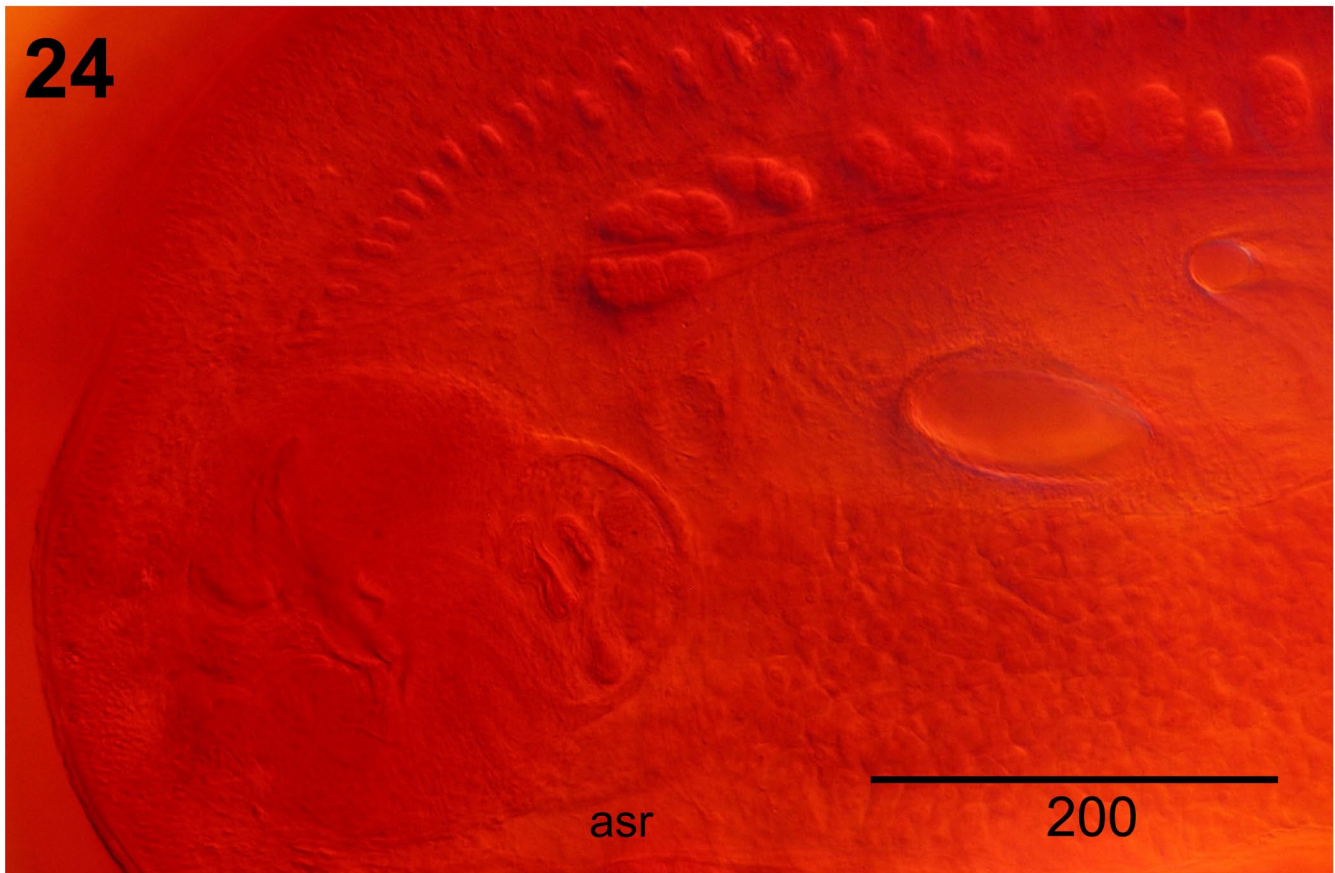
Figures 26–29. *Tetrabothrius alcae* n. sp., showing structure of gravid uterus from micrographs of whole-mounted specimens (scale bars in micrometers). **Fig. 26.** Uterus (paratype 2640-3C), dorsal view, showing strongly lobate, saccular structure (ut) during late development, extending beyond poral osmoregulatory canals to level of cirrus sac, genital pore (ge). **Fig. 27.** Gravid uterus (paratype 2640-3C), dorsal view (scale as in Fig. 26), showing completely developed, broad sacculate structure, at stage with fully developed oncospheres, extending to margins of proglottid. **Fig. 28.** Gravid uterus (paratype 2640-3G), dorsal view, showing position passing ventrally to poral osmoregulatory canals (arrows denote ventral osmoregulatory canal). **Fig. 29.** Uterine pore (paratype 2640-3C), dorsal view, showing developing dehiscence (arrows) on the midline near anterior margin of successive gravid proglottids.

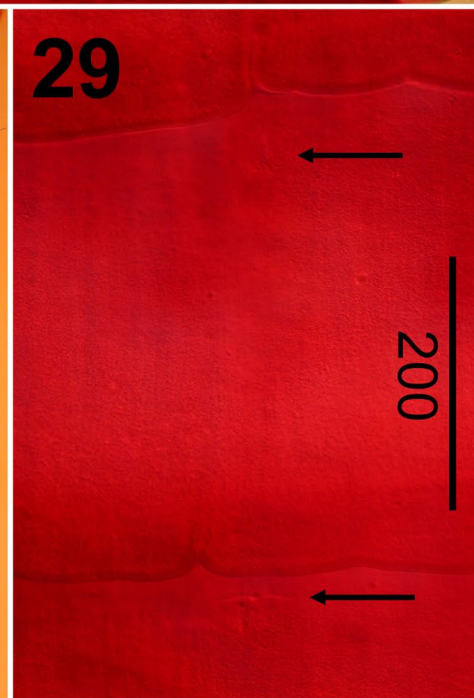
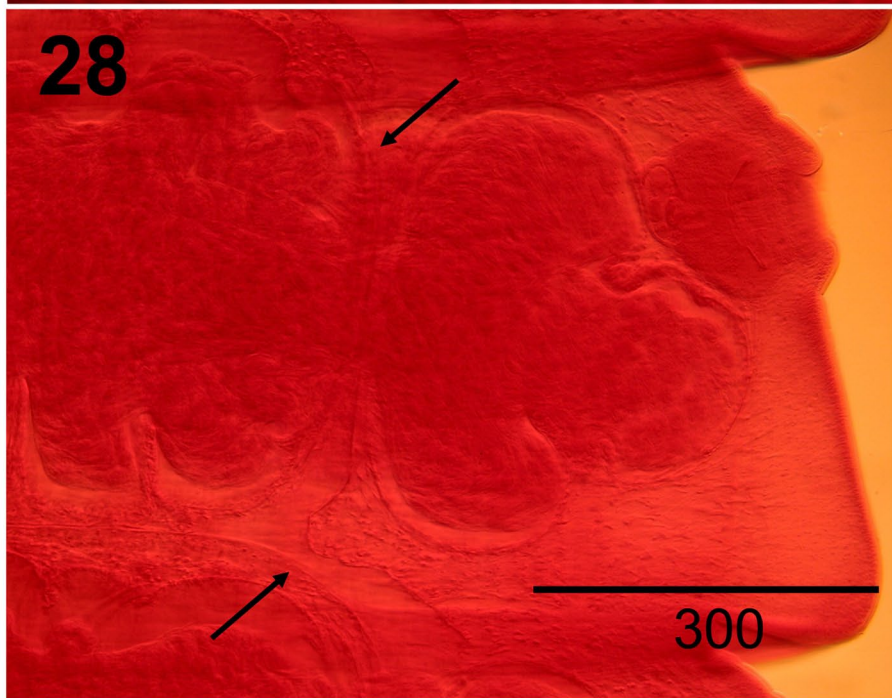
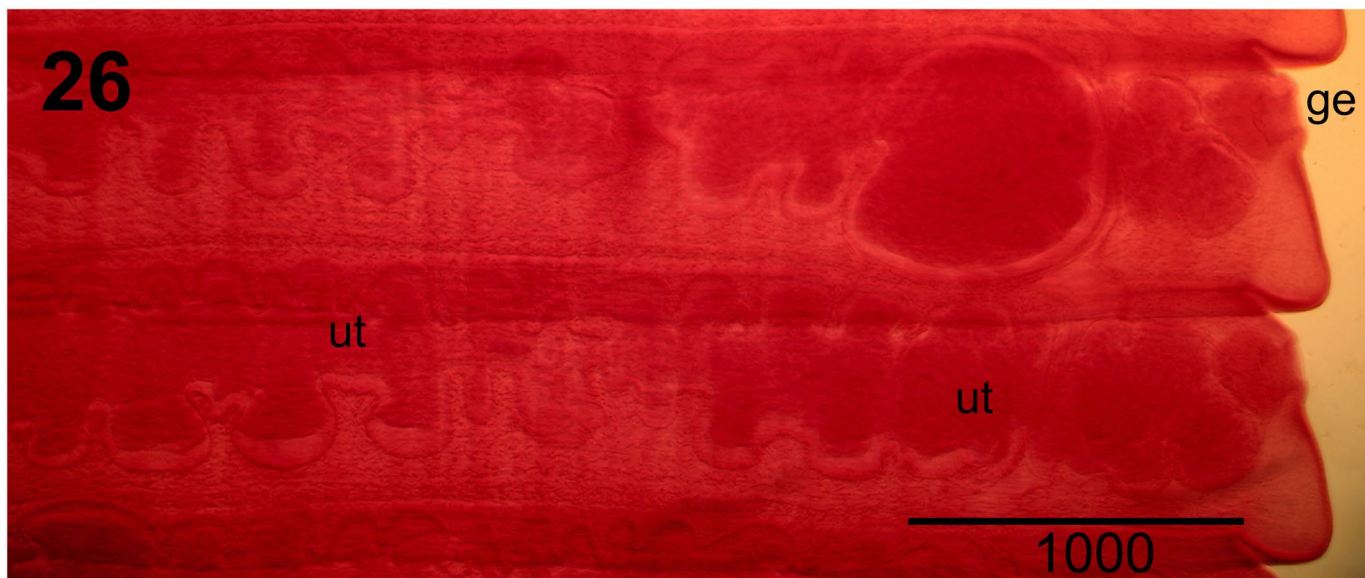












Female Genitalia: Ovary dendritic, multilobate, with 2 prominent wings, initially visible in 150th–170th segment; fully developed in 280th–330th segment; (n = 150) 892–1820 (1,396) in width from early to late maturity; situated in anterior 2/3 of segment with center of female organs (ovary and Mehlis gland) shifted slightly porad of midline; not extending to osmoregulatory canals. Vitelline gland extremely elongate, narrow, (n = 300) 301–1,018 (556) wide × 52–156 (104) long; situated anteroventral to ovary, shifted under antiporal wing of ovary, with center of organ near midline; follicular structure with multiple reticulate, anastomosing ducts fusing to form broad common vitelline duct passing ventral to ovary. Common vitelline duct extends posteriad becoming confluent with common vaginal and ovarian duct to ventrally enter prominent Mehlis' gland, (n = 105) 52–94 (75) in diameter; nascent ascending, convoluted, uterine stem extends dorsally from Mehlis' gland. Proximal vagina terminates with expansion as thin-walled, ellipsoidal inner seminal receptacle receiving broad ovarian duct slightly dorso-lateral to Mehlis' gland. Vagina extends porad from internal seminal receptacle as thin tube dorsal to ovary, ventral to testes. Vaginal seminal receptacle develops as a voluminous, elongate, cylindrical to weakly pyriform, saccular dilatation of vagina with thin, membranous wall, extending from near level of poral wing of ovary (occasionally attains ovarian wing in pregravid), tapering porad, confluent with terminal vagina beyond level of osmoregulatory canals; maximum diameter and length (n = 40) 36–110 (77) × 520–1,350 (869) (in 4 strobila) attained in mature to pregravid segments; sphincter demarking antiporal end. Distal vagina with thickened muscular wall, often expanded as atrial seminal receptacle, enters genital atrium in sinuous curve, ascending and at about 90° ventral to cirrus sac. Female genital canal parallel to male duct, opening ventrally near base of weakly bilobed papilla; orifice ventral to aperture of male canal, not immediately adjacent; atrial vagina spinose. Ascending uterus extends anteriorly from dorsal aspect of Mehlis' gland; transverse tubular uterine stem initially visible coinciding with ovarian development, dorsal to ovary, ventral to testes. Mature uterus, a broad, lobate, sacculate structure lined with cellular epithelium, situated dorsally in proglottid, extending ventrally beyond osmoregulatory canals, attaining margins of segment; gravid by 520th to 640th segment. Uterine pore median, initially visible dorsally as a miniscule dehiscence near anterior margin of proglottid on midline; patent in pregravid strobila; segments anapolytic. Mature eggs contained within irregular capsule with granular membrane. Hyaline embryophore elliptical (n = 50) 36–56 (44) wide × 25–46 long (34) con-

tains oncosphere (n = 100) 28–45 (36) wide × 21–34 (26) long. Embryonic hooks (n = 50) 17–20 (18) for medial pairs, (n = 50) 20–21 (20) for lateral groups.

Taxonomic Summary

Hosts: Type host—Common murre, *Uria aalge* (Pontopidan, 1763). Other known hosts—Thick-billed murre, *Uria lomvia* (Linnaeus, 1758); ancient murrelet, *Synthliboramphus antiquus* (Gmelin, 1789); pigeon guillemot, *Cephus columba* Pallas, 1811; and parakeet auklet *Aethia psittacula* (Pallas, 1769).

Localities: Type locality—Talan Island, northern Sea of Okhotsk, Russia, ca. 59°19'N, 149°06'E, in type host on 25 July 1988. Other known localities—St. Lawrence Island, Alaska (Savoonga and Gambell); Cape Thompson, eastern Chukchi Sea, Alaska; Cape Lisburne, eastern Chukchi Sea, Alaska; St. Matthew Island, Bering Sea, Alaska; Buldir Island, western Aleutian Islands, Alaska; Pelagic waters south and adjacent to western Aleutian Islands; Kodiak Island (Chiniak Bay), Gulf of Alaska, Alaska; Ugaiushak Island, Gulf of Alaska, Alaska; Humboldt Bay, eastern North Pacific, California; Pelagic waters over Grays Marine Canyon, eastern North Pacific, Washington (Supplementary Data Tables 2–4).

Specimens: Holotype—in type host (subadult male), from type locality collected by E. P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, and S. Bondarenko (field number 2640-1-A through 2640-1-G, single specimen on 7 slides including scolex, strobila, and hand-cut thick sections); identification by EPH. Museum of Southwestern Biology, Collection Catalogue No. MSB PARA-29629. Specific MSB PARA Collection data for paratype series and vouchers with georeferenced localities (linked to original field designations), hosts, dates, numbers of specimens (and slides), field collectors, and identifiers are summarized in Supplementary Data Table 4 and online in the Arctos database platform.

Zoobank Name Registration for *Tetrabothrius alcae*:

LSID urn:lsid:zoobank.org:pub:
35C7B2E7-DE5B-4E06-8640-29B948DBE4AF

Symbiotype: Host specimens or tissues not retained and archived.

Etymology: *Tetrabothrius alcae* is derived from *álka*, denoting colonial diving birds in the Icelandic dialect obtained from Old Norse; northern hemisphere seabirds are now referred to the family Alcidae.

Table 1. Morphological Data, Hosts, and Geographic Localities for Differentiation of *Tetrabothrius jagerskioeldi* Nybelin, 1916, *T. alcae* n. sp., and *T. sinistralis* n. sp. among Alciidae

| Character | <i>Tetrabothrius jagerskioeldi</i> ^{1,2} | <i>Tetrabothrius jagerskioeldi</i> ³ | <i>Tetrabothrius alcae</i> n. sp. ⁴ | <i>Tetrabothrius sinistralis</i> n. sp. ⁵ |
|---|--|---|--|--|
| Host(s) Species | <i>Cepphus grylle</i> (type host) | <i>Brachyramphus marmoratus</i> , <i>Cepphus grylle</i> , <i>Cepphus carbo</i> , <i>Cepphus columba</i> , <i>Cerorhinca monocerata</i> , <i>Uria aalge</i> | <i>Uria aalge</i> (type host), <i>Uria lomvia</i> , <i>Cepphus columba</i> , <i>Synthliboramphus antiquus</i> , <i>Aethia psittacula</i> | <i>Cepphus columba</i> (type host), <i>Cepphus grylle</i> |
| Geographic Locality | Kristineberg, Sweden (type); Väderöarna, Sweden (*) | North Pacific Basin; Gulf of Alaska; Bering Sea; Aleutian Islands; Sea of Okhotsk | Talan Island, Sea of Okhotsk (type); Cape Thompson, Eastern Chukchi Sea; Cape Lisburne, Eastern Chukchi Sea; St. Lawrence Island, Bering Sea; St. Matthew Island, Bering Sea; Buldir Island, Aleutian Islands; Western Aleutian Islands, Pelagic Zone; Kodiak Island, Gulf of Alaska; Ugaiushak Island, Gulf of Alaska; Humboldt Bay, Eastern North Pacific Ocean; Grays Marine Canyon, Pelagic Zone, Eastern North Pacific Ocean | St. Matthew Island, Bering Sea (type); Kangerluk (Diskofjord), West Greenland |
| Strobila (L × W, maximum) | 90 mm × 4 mm | 85–203 mm × 3.9 mm | 127–210 mm × 4.35–6.16 mm | 111–180 mm × 3.5–4.47 mm |
| Muscle bundles, outer (#) | 202–221 (*) | 185–237 (204) | 183–235 (217) | 213–238 (226) |
| Fibers/bundle, outer (#) | 3–12 (*) | 3–11 (7) | 2–15 (7) | 1–5 (3) |
| Muscle bundles, inner (#) | 118–125 (*) | 99–146 (114) | 95–177 (139) | 111–119 (115) |
| Fibers/bundle, inner (#) | 5–53 (*) | 6–37 (19) | 9–72 (35) | 5–20 (11) |
| Scolex (L) | 510 (original); 325 (*) | 350–580 (489) | 190–392 (297) | 355–420 (388) |
| Scolex (W) | 560 (original); 430 (*) | 490–700 (580) | 201–422 (359) | 376–490 (421) |
| Bothridia (L) | 285–300 (*) | 240–500 (406) | 152–255 (212) | 240–340 (298) |
| Bothridia (W) | 195–215 (*) | 235–370 (277) | 103–198 (168) | 209–240 (225) |
| Neck (L) | short (*) | short | 500–1,550 (843) | 200–480 |
| Genital pore (position) | Dextral in dorsal view (*) | Dextral in dorsal view | Dextral in dorsal view | Sinistral in dorsal view |
| Genital ducts (relation to osmoregulatory canals) | Between (*) | Between | Ventral to poral osmoregulatory canals | Between |
| Cirrus pouch (diameter) | 100–111 (original); 70–114 (*) (mature to gravid) | 65–110 (88) (mature); 75–130 (94) (pregravid); 78–152 (107) (gravid) | 80–137 (107), increasing in diameter through ontogeny, maximum in late mature | 71–120 (92), increasing in diameter through ontogeny, maximum in pregravid to gravid |
| Genital atrium (diameter) | 117–169 (*) (mature to gravid) | 125–190 (154) (mature); 112–230 (169) (pregravid); 142–205 (176) (gravid) | 140–304 (218), maximum diameter in late mature to pregravid | 138–230 (178), increasing in diameter through ontogeny, maximum in pregravid to gravid |

Table 1. (continued)

| Character | <i>Tetrabothrius jagerskioeldi</i> ^{1,2} | <i>Tetrabothrius jagerskioeldi</i> ³ | <i>Tetrabothrius alcae</i> n. sp. ⁴ | <i>Tetrabothrius sinistralis</i> n. sp. ⁵ |
|---|---|--|---|---|
| Structure male papilla | Triangular (*) | Triangular | Weakly bilobed (dorso-ventral view) | Weakly bilobed (dorso-ventral view) |
| Genital ducts (position in genital atrium) | Male, female canals straight; opening center of papilla (male); female at base, ventral (*) | Male, female canals straight; opening center of papilla (male); female at base, ventral | Male—weakly curved, opening through weakly bilobed papilla; female—sinuous curve, passing through atrial wall at 90° ventral to cirrus sac, opening ventral to male canal | Male—strongly decurved opening near ventral apex of prominent, bulbous, weakly bilobed papilla; female—passing through atrial wall in 90° curve parallel to male canal in genital atrium, opening ventral to papilla/aperture of male canal |
| Male canal (L) | 39–57 (*) (mature); 44–49 (*) (gravid) | 41–50 (45) (mature); 37–62 (47) (late mature to pregravid) | 44–68 (55) (early maturity); 65–94 (77) (late mature to pregravid); 44–94 (72) (all stages of ontogeny) | 70–100 (91), maximum in late mature; 75–88 (81), decreasing in pregravid to gravid |
| Testes (#) | 58–62 (original); 46–58 (*) | 40–70 (54) | 75–134 (100) (immature); 66–111 (87) (late mature) | 47–70 (58) (immature to early mature) |
| Center female organs | Midline | Midline | Shifted porad of midline | Midline |
| Ovary (W) | 410–600 (mature) (*) | 420–980 (694) (maximum, mature to pregravid) | 892–1,820 (1,396) (maximum, early mature to late mature) | 559–1,310 (915) (maximum, mature to late mature) |
| Vitelline gland (W × L) | 101–192 × 44–120 (*) (mature) | 120–400 (204) × 48–170 (107) (mature to pregravid) | 301–1,018 (556) × 52–156 (104) (mature to pregravid) | 157–460 (268) × 50–177 (102) (mature to pregravid) |
| Vitelline gland (structure) | Compact, globular (*) | Compact, globular | Follicular, highly elongate | Compact to weakly follicular |
| Vitelline duct | Single (*) | Single | Multiple, reticulate | Single |
| Vaginal seminal (L × W) receptacle | Spindle-shaped; level of osmoregulatory canals (*) | 100–170 (132) length in mature; spindle-shaped, short; with thickened epithelium; crossing between osmoregulatory canals | 520–1,350 (869) × 36–110 (77) in mature to pregravid; cylindrical to weakly pyriform, highly elongate, thin-walled; tapering porad, crossing poral osmoregulatory canals | 78–470 (305) × 40–90 (64); spindle-shaped, elongate, thin-walled; attaining, seldom crossing poral osmoregulatory canals |
| Uterus position (relative to osmoregulatory canals) | Between (*) | Between | Ventral to poral and antiporal osmoregulatory canals | Ventral to poral and antiporal osmoregulatory canals |
| Embryophore (L × W) | Not observed | 28–35 (30) × 34–43 (39) | 25–46 (34) × 36–56 (44) | 37.5–45 (40) × 50–57.5 (52) |
| Oncosphere (L × W) | Not observed | 20–26 (23) × 28–39 (32) | 21–34 (26) × 28–45 (36) | 27.5–35 (30.5) × 35–45 (39) |

Notes:

¹Nybelin (1916) from original description; asterisk (*) indicates new observations from type and voucher specimens summarized by Hoberg and Soudachanh (2020); throughout the table, all measurements are reported in micrometers unless specified otherwise, with the range followed by the mean in parentheses when available.

²Data reported in the literature for *T. jagerskioeldi* by Baer (1954), Temirova and Skrijabin (1978), and Ryzhikov et al. (1985) and for the synonym *T. intrepidus* Baylis, 1919 were discussed in detail by Hoberg and Soudachanh (2020) and are not repeated in the current study.

³North Pacific, specimens of *T. jagerskioeldi* in Alciidae hosts. Confirmed based on direct comparisons to type specimens, reported and summarized by Hoberg and Soudachanh (2020). Morphological and meristic data for specimens in Laridae and Phalacrocoracidae are not outlined here but are reported in Hoberg and Soudachanh (2020).

⁴Original comparative data for *Tetrabothrius alcae* n. sp.

⁵Original comparative data for *Tetrabothrius sinistralis* n. sp.

Remarks and Diagnosis

Among the 50 currently known nominal species in the genus (42 among avian hosts; 8 among mammalian hosts), specimens of *Tetrabothrius alcae* n. sp. are morphologically most similar to those of *T. jagerskioeldi* (see Mariaux et al., 2017; Hoberg and Soudachanh, 2020). Both species are characterized by a robust and large strobila and otherwise share considerable superficial similarity. A suite of structural and mensural characters allows unequivocal differentiation of these cestodes in the species-complex historically represented by *T. jagerskioeldi*. Specimens of *T. alcae* are distinguished from those of *T. jagerskioeldi* by attributes of the scolex; male and female organ systems; structure and dimensions of the vitelline gland; numbers of testes; configuration of the genital atrium; genital papillae and the male and female atrial canals; position of the genital ducts relative to the poral osmoregulatory canals; structure, dimensions, and position of the vaginal seminal receptacle; and dimensions of the embryophore and oncosphere, in addition to a broader array of characters. Some suites of characters—such as the structure and position of the vaginal seminal receptacle, relative positions of the poral osmoregulatory canals, and position of the female organs relative to the midline and structure of the vitelline gland—are applied for the first time in differentiation among species of *Tetrabothrius* (Table 1, Figs. 1–29; for *T. jagerskioeldi*, Supplementary Data File 5, Figs. 1–15) (Hoberg and Soudachanh, 2020).

The substantially smaller scolex of *T. alcae* possesses strongly developed, suckerlike bothridia with reduced auricles and a domelike, hypertrophied apical zone (Figs. 1–4; Figs. 12–15). In *T. jagerskioeldi* the scolex has typically broad, concave bothridia with strongly muscularized and prominent auricular appendages. The elongate and inflated neck region further contrasts with *T. jagerskioeldi*. Anastomoses of the osmoregulatory canals, observed in the scolex and neck region of *T. alcae*, are absent in *T. jagerskioeldi*. In *T. alcae* the dorsal osmoregulatory canals (poral) are shifted mediad relative to the ventral canals; in *T. jagerskioeldi* the poral canals are positioned equidistant from the proglottid margin.

Genital systems and organs are distinct in *T. alcae*. The genital ducts and uterine stem (and mature sacculate uterus) are consistently ventral to the osmoregulatory canals at all stages of development (Fig. 9; Figs. 23 and 25); in *T. jagerskioeldi* the ducts and uterus pass between the poral canals. The position of the center of the female organs (defined by the position of the Mehlis' gland, isthmus connecting the wings of the bilobed ovary, and vitelline gland) is shifted porad of the midline; in *T. jagerskioeldi* these systems reside on the midline of the

proglottid. In *T. alcae* the developing and mature ovary is strongly dendritic, and the vitelline gland is highly elongate and follicular, with a reticulate anastomosing duct structure that coalesces into a single descending duct (Figs. 3–4, 10, 19–20); the mature ovary is multilobate, not dendritic, and a compact globular structure of the vitelline gland, whereas a single duct is typical in *T. jagerskioeldi*. In *T. alcae* the vaginal seminal receptacle (vsr) is highly elongate, expanded, cylindrical to pyriform, and sacculate with a thin wall, lacking epithelium, that extends from near the poral wing of the ovary to beyond the poral osmoregulatory canals (Figs. 3–4, 21); in *T. jagerskioeldi* the vsr is a spindle-shaped expansion, with a well-developed epithelium, that crosses between the dorsal and ventral osmoregulatory canals. In *T. alcae* the atrial seminal receptacle (a defined expansion contained in the wall of the genital atrium) is well developed; it is weakly developed in *T. jagerskioeldi*. In *T. alcae* the sinuous ascending vagina enters the genital atrium at 90° to the cirrus sac and male atrial genital canal (Figs. 8–9, 23–25). In *T. jagerskioeldi* the terminal vagina is relatively straight entering the wall of the genital atrium, with the female genital canal becoming slightly curved in parallel to the cirrus sac and male canal. In gravid specimens, fully developed embryophores, oncospheres, and embryonic hooks are larger in *T. alcae* relative to those in *T. jagerskioeldi*.

Specimens of *T. alcae* have a substantially greater number of testes than *T. jagerskioeldi*. In *T. alcae* the numbers of testes are >75, maximum = 134, mean determined in immature proglottids = 100; overall from immature to pre-gravid proglottids = 96. In specimens of *T. jagerskioeldi* among alcid, larid, and phalacrocoracid hosts, the range for numbers of testes was demonstrated as 40–73 (only exceptionally exceeding 60 in number) with a mean \pm 55 (Hoberg and Soudachanh, 2020). Testes surround the female organs laterally and to the posterior in *T. alcae*, with a gap in distribution directly anterior to the vitelline gland and ovary; distribution anterior to the female organs is without a gap in *T. jagerskioeldi*.

In *T. alcae* the male and female atrial genital canals are weakly curved ventrally (as observed in transverse sections), opening through a dorsally oriented, bilobed genital papilla; apertures of genital ducts are not in close proximity (Figs. 8–9, 23–25). Lateral muscular processes, directed ventrally bordering the genital papilla are absent; a single prominent, triangular genital papilla is absent. In *T. jagerskioeldi* the male and female genital canals are relatively straight, opening ventrally below the apex of a prominent triangular genital papilla; male and female canal apertures are adjacent. Lateral muscular processes are prominent (in transverse section, appearing as a dorsal bar in dorso-

ventral view), extending ventrally and bordering the anterior edge of the genital papilla. The male atrial canal is substantially greater in length at all stages of ontogeny in specimens of *T. alcae*.

Among the series of specimens of *T. alcae* examined during our current study, we noted no variation in the ventral position of the genital ducts, transverse uterine stem, and fully developed gravid uterus. The typical position, among nearly all species of *Tetrabothrius* in avian hosts in which these characters have been documented is between the canals, as has been observed consistently in specimens of *T. jagerskioeldi* (e.g., Hoberg and Soudachanh, 2020) and in nearly all nominal species in the genus (Baer, 1954; Temirova and Skrjabin, 1978). A ventral position for the genital ducts relative to the osmoregulatory canals is rare among the 6 genera and 71 species of tetrabothriids, with inclusion of *T. alcae* (Mariaux et al., 2017). A ventral position for the ducts is apparent among species of *Priapocephalus* Nybelin, 1922, large cestodes of baleen whales (Hoberg, 1994). Among the 51 recognized nominal species of *Tetrabothrius* (8 among cetaceans, 43 among avian hosts with inclusion of *T. alcae*), a ventral position has been described in *T. eudyptidis* (Lönnerberg, 1896) among sphenisciform birds and in *T. arsenyevi* Deliamure, 1955; *T. egregius* Skrjabin and Murav'eva, 1971; *T. ruudi* Nybelin, 1928; and *T. schaeferi* Markowski, 1955 among baleen whales. These 4 latter species, among a larger assemblage of cestodes in avian and cetacean hosts, have been provisionally referred to the subgenus *Oriana* Leiper and Atkinson, 1914 (see Mariaux et al., 2017). The placement of the genital ducts relative to the dorsal and ventral osmoregulatory canals thus appears to be a stable character contributing to species-level identity among tetrabothriids.

Expanding Diversity in the *T. jagerskioeldi*-Complex, Cestodes in Guillemots

Primary materials representing *T. sinistralis* n. sp. include specimens in 2 alcid hosts (single specimen in *C. columba* from the central Bering Sea and 2 specimens in *C. grylle* from West Greenland), with 3 cestodes on 6 slides in the type series on which the description is based (Supplementary Data Table 4); additional vouchers are not currently recognized. In the North Pacific basin, this species was found only in a pigeon guillemot (1 of 22, 4.5%). Specimens attributable to *T. sinistralis* were not recognized among additional species of *Cephus*, other alcids, nor a broader assemblage of marine birds, occurring in 1 of 1,345

alcid specimens examined (<1.0%) from 1 of 55 localities (Supplementary Data Tables 2 and 3).

Description—*Tetrabothrius sinistralis* n. sp.

Figures 30–49

General Description: Large, robust, tetrabothriids; maximum length of strobila 111–180 mm, maximum width of 4,475 attained in pregravid segments; with (n = 2) 377–544 proglottids in gravid specimens. Segments wider than long throughout strobila; 150–234 long × 811–1,750 wide in immature proglottids; 275–520 × 1,261–4,100 in mature (including early to postmature); 585–1,450 × 3,500–4,425 in gravid. Length:width ratio 1:3.88–9.0 in immature; 1:4.04–10.8 in mature; 1:2.41–6.9 in pregravid to gravid. Scolex rectangular, wider than long (n = 3) 355–420 (388) long × 376–490 (421) wide; auricles not prominent. Bothridia well developed, (n = 8) 240–340 (298) long × 209–240 (225) wide, flattened to concave with muscular margins; square across anterior margins of prominent auricles and bothridia. Apical region hypertrophied, domelike, expanded anterior to auricles. Neck, as measured from base of scolex to first indication of internal segmentation, short, 200–480 long × 365–450 wide. Ventral osmoregulatory canals 25–183 in diameter, width increasing posteriad in strobila; transverse canal 10–15, seldom with multiple anastomoses; dorsal canals 10–28 in diameter with limited variation throughout strobila. Dorsal canal overlies ventral canal. Genital pores unilateral, sinistral in dorsal orientation of strobila, marginal, situated in middle third of proglottid. Male and female genital ducts passing between poral osmoregulatory canals; transverse uterine stem and gravid uterus passing ventral to poral and antiporal osmoregulatory canals.

Longitudinal Musculature: Musculature prominent in transverse sections of proglottids; inner and outer bundles arranged in single layers. Inner bundles large in diameter; (n = 4) 111–119 (115) in number; (n = 15) 5–20 (11) fibers per bundle. Outer bundles relatively small in diameter; (n = 4) 213–238 (226) in number; (n = 15) 1–5 (3) fibers per bundle. Numbers of muscle bundles maximum in mature proglottids, diminishing in number posteriad in postmature and gravid segments.

Male Genitalia: Genital anlagen visible immediately posterior to neck, protandrous; first testes observed in 110th–120th segment; male fully mature in 210th–250th segment. Testes positioned dorsally in 1–2 layers surrounding and partially overlapping female organs laterally and along

posterior margin of ovary, gap in distribution of testes along anterior margin of ovary and vitelline gland; (n = 90) 63–105 (80) in diameter. Testes (n = 45 segments from 3 strobila) 47–70 (58) in number counted in immature to early mature segments. Vas deferens prominent, highly convoluted, distended adjacent to poral osmoregulatory canals. Cirrus sac ovoid, situated in dorsal aspect of genital atrium, (n = 125) 71–120 (92) in diameter overall across all stages of ontogeny, increasing in dimensions posteriad with progressive development, attaining maximum dimensions in late maturity. Cirrus sac diameter in maturity (n = 86) 71–120 (88); in pregravid (n = 29) 79–120 (100); in gravid (n = 10) 90–110 (101). Muscular wall of cirrus sac thickened, (n = 55) 7.5–18 (12). Cirrus sac contains extension of convoluted vas deferens and cirrus armed with miniscule but prominent spines. Genital atrium ovoid, highly muscularized (n = 145) 138–230 (178) in diameter overall across all stages of ontogeny, attaining maximum diameter in pregravid to gravid. Genital atrium diameter in maturity (n = 105) 138–200 (168); in pregravid (n = 30) 171–230 (201); in gravid (n = 10) 200–220 (205). Male genital canal, dorsal, extending through wall of atrium, strongly decurved ventrally to open subventrally near apex of prominent, bulbous, bilobed papilla in center of atrial lumen; sphincters not observed. Length of male genital canal increases with age of proglottid and development of genital atrium, attaining maximum in late maturity; (n = 9) 70–100 (91); length in pregravid to gravid segments (n = 9) 75–88 (81).

Female Genitalia: Ovary multilobate, with 2 prominent wings, ovarian development and transverse uterine stem visible in 145th–160th segment; ovary fully developed in 275th–320th segment; (n = 60) 559–1,310 (915) in maximum width increasing in dimensions from mature to pregravid proglottids; situated in anterior 2/3 of segment with center of female organs on midline; not extending to osmoregulatory canals. Vitelline gland compact to weakly follicular, relatively narrow, 50–177 (102) long (n = 115) × 157–460 (268) wide, increasing in dimensions from mature to pregravid proglottids; situated anteroventral to ovary, with center of organ on midline; with single broad common vitelline duct passing ventral to ovary. Common vitelline duct extends posteriad becoming confluent with common vaginal and ovarian duct to ventrally enter prominent Mehlis' gland, (n = 35) 39–75 (57) in diameter; nascent ascending, convoluted, uterine stem extends dorsally from Mehlis' gland. Proximal vagina terminates with expansion as thin-walled, ellipsoidal inner seminal receptacle, (n = 15) 55–71 (81) in diameter in mature to late mature proglottids, receiving broad ovarian duct slightly dorso-lateral to Mehlis' gland. Vagina extends porad from internal seminal receptacle as thin tube dorsal to

ovary, ventral to testes. Vaginal seminal receptacle (vsr) present as highly elongate, spindle-shaped expansion of vagina with thin, membranous wall, lacking prominent epithelium when fully developed; originating and extending mediad from near level of poral osmoregulatory canals, attaining but seldom crossing poral canals in late mature to pregravid condition, not attaining poral wing of ovary; tubular vagina with initial expansion of vaginal seminal receptacle near 275th segment; maximum diameter of vsr (n = 45) 40–90 (64) wide × 78–470 long (305); increasing in dimensions from mature to pregravid proglottids, rapidly diminishes in diameter from pregravid to gravid segments. Distal vagina with thickened muscular wall, enters genital atrium in sinus curve about 90°, ascending ventral to cirrus sac. Female genital canal parallel to male duct, opening ventrally near base of bulbous bilobed papilla; orifice ventral to aperture of male canal, not immediately adjacent; expanded distally as well-developed atrial seminal receptacle; atrial vagina spinose. Ascending uterus extends anteriad from dorsal aspect of Mehlis' gland; transverse tubular uterine stem initially visible dorsal to ovary and ventral to testes coinciding with ovarian development. Initial tubular expansion in about 295th segment (in cestode specimen with 544 proglottids); first egg about 320th; lobate expansion of uterus about 390th. Nascent dorsal uterine pore visible about 410th segment, initially situated as ovoid protruding bulge and lengthwise dehiscence along midline near anterior margin of proglottid. Fully developed uterus, a broad sacculate structure lined with cellular epithelium, situated dorsally in proglottid, extending ventrally beyond osmoregulatory canals; gravid by 500th segment. Uterine pore median, dorsal, ovoid aperture (n = 5) 190–370 (236) in diameter when fully patent in gravid strobila; segments anapolytic; eggs released near 510th segment to termination of strobila leaving lobate sac largely devoid of eggs. Mature eggs contained within ovoid to irregular capsule with thickened granular membrane. Hyaline embryophore elliptical, (n = 30) 50–57.5 (52) wide × 37.5–45 (40) long, contains oncosphere (n = 30) 35–45 (39) wide × 27.5–35 (30.5) long. Embryonic hooks (n = 50) 16.5–22.5 (19) in length for medial pairs, (n = 50) 17.5–24 (22) for lateral groups.

Taxonomic Summary

Hosts: Type host—Pigeon guillemot, *Cephus columba* Pallas, 1811. Other known host(s)—black guillemot, *Cephus grylle* (Linnaeus, 1758).

Localities: Type locality—St. Matthew Island, Central Bering Sea, Alaska, ca. 60°20'N, 171°00'W on 27 July 1982. Other known localities—Adjacent to Kangerluk (formerly, Diskofjord), West Greenland, ca. 69°29'N, 53°56'W, on 27 July 1955.

Figures 30–32. *Tetrabothrius sinistralis* n. sp. scolex and mature proglottid. **Fig. 30.** Scolex, dorsoventral view, in holotype specimen (1301) in *Cepphus columba*. **Fig. 31.** Scolex, dorsoventral view in paratype (108-60) in *C. grylle*; note expanded apical region and vestigial apical organ. **Fig. 32.** Proglottid in ventral view in mature region of strobila from paratype. Note sinistral position of genital pore and terminal genitalia (when in dorsal orientation), position of uterine stem ventral to osmoregulatory canals, and genital ducts passing between osmoregulatory canals.

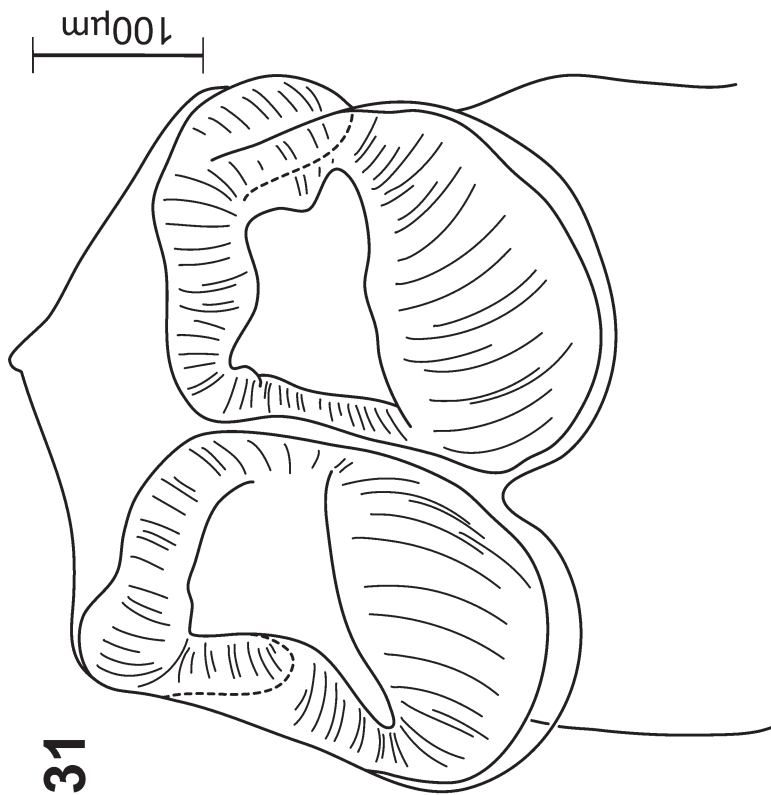
Figures 33–36. *Tetrabothrius sinistralis* n. sp. genital atrium in whole mount and in transverse section and the fully developed egg with oncosphere. **Fig. 33.** Genital atrium, ventral view in whole mount in late maturity from paratype in *Cepphus grylle* (108-60). **Fig. 34.** Genital atrium, ventral view in whole mount in pregravid condition (108-60). **Fig. 35.** Genital atrium in transverse section in late maturity from holotype in *C. columba* (1301). Note relative positions of the male and female genital ducts; strongly decurved male canal opening subventrally on weakly bilobed papilla. **Fig. 36.** Egg.

Figures 37–40. *Tetrabothrius sinistralis* n. sp., showing scolex and attributes of the genital atrium (scale bars in micrometers). **Fig. 37.** Scolex in dorsoventral view from whole-mounted specimen (holotype 1301-1A), showing bothridia and prominent muscularized auricles. **Fig. 38.** Proglottid margin in lateral view, transverse section from posterior, dorsal to top (holotype 1301-1B), showing sinistral genital pore (ge) and genital atrium (ga), with position of vas deferens (vd), vagina (va), and expanding uterus (ut) relative to dorsal (dosm) and ventral (vosm) osmoregulatory canals in late maturity. Cirrus sac (cs) on lateral border of genital atrium (ga), with strongly decurved male atrial canal (arrow) opens on subventral apex of prominent genital papilla (gp); aperture of female canal and vagina is adjacent and ventral. **Fig. 39.** Proglottid margin from transverse section, from posterior (holotype 1301-1D) in pregravid stage, showing sinistral genital pore, terminal genitalia, and position of sacculate, expanding uterus relative to osmoregulatory canals. **Fig. 40.** Proglottid margin from transverse section (holotype 1301-1D) in gravid stage, showing genital atrium (ga), terminal genitalia, and position of sacculate uterus (ut) ventral to osmoregulatory canals (osm).

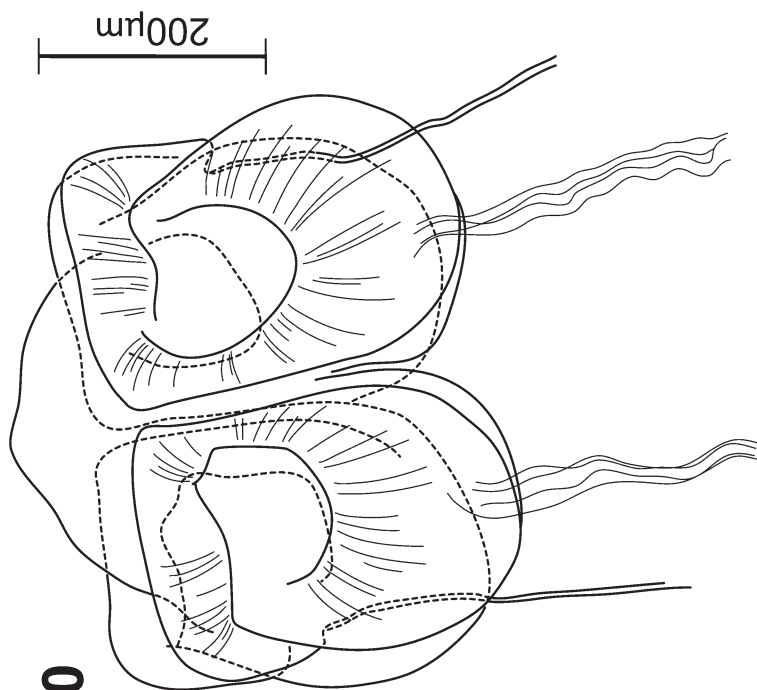
Figures 41–43. *Tetrabothrius sinistralis* n. sp., showing proglottids at successive stages of ontogeny and positions of male and female systems, from a whole-mounted specimen in dorsal orientation (scale bars in micrometers). **Fig. 41.** Proglottids in immature strobila (holotype 1301-1A) showing distribution of testes with gap along anterior margins of vitelline gland and ovary. **Fig. 42.** Proglottids in early maturity (holotype 1301-1A) showing structure of ovary and vitelline gland. **Fig. 43.** Proglottids in maturity (holotype 1301-1B) showing region from near midline to marginal, sinistral genital pore (ge), including genital atrium (ga), cirrus sac (cs), transverse uterine stem (ut), and margin of ovary (ov).

Figures 44–45. *Tetrabothrius sinistralis* n. sp., showing male and female ducts in dorsal view with detail of cirrus pouch, genital atrium, and vaginal seminal receptacle (scale bars in micrometers). **Fig. 44.** Cirrus sac (cs), genital atrium (ga), and genital pore (ge) in dextral-lateral aspect of pregravid proglottid showing relative position of osmoregulatory canals (osm) and vaginal seminal receptacle (vsr) (holotype 1301-1A). **Fig. 45.** Expanded vaginal seminal receptacle attaining and extending between poral osmoregulatory canals in pregravid condition of segments, also showing ventral position of the uterus (ut) (holotype 1301-1A).

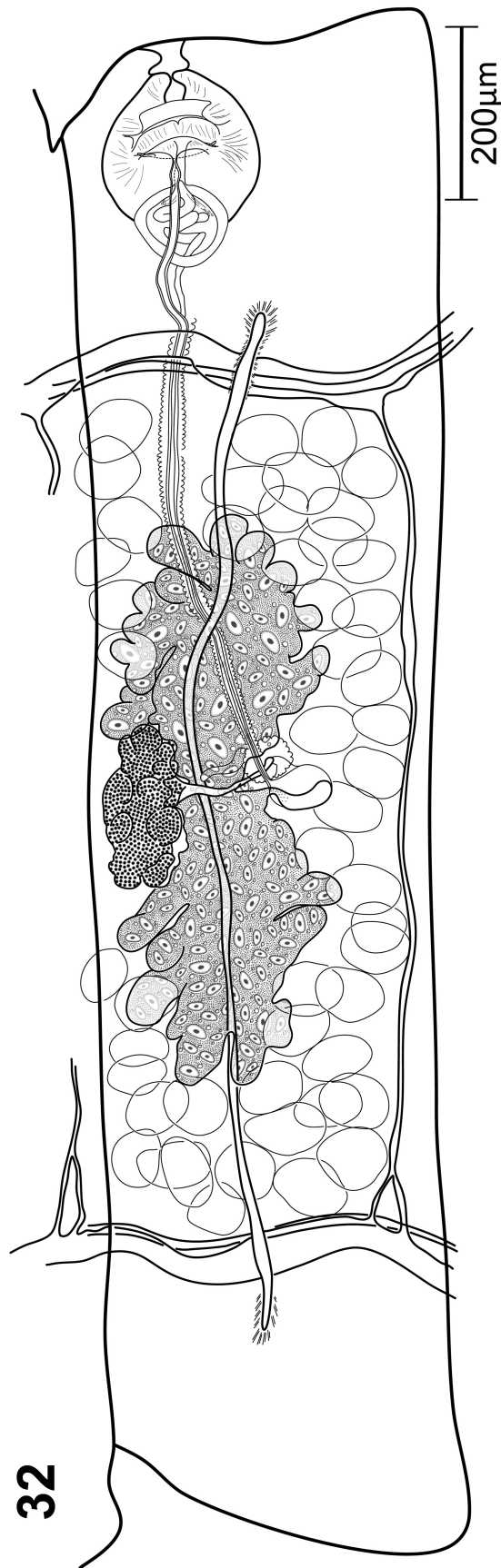
Figures 46–49. *Tetrabothrius sinistralis* n. sp., showing gravid proglottids from whole-mounted specimen in dorsal orientation (holotype 1301-1E) (scale bars in micrometers). **Fig. 46.** Gravid proglottids showing lobate saccular uterus, at stage with fully developed oncospheres, extending beyond osmoregulatory canals. **Fig. 47.** Uterine pore at stage of full patency (arrows), showing structure on midline near anterior margins of successive gravid proglottids. **Fig. 48.** Oncospheres contained within capsules and embryophores in passage through patent uterine pore. **Fig. 49.** Embryophores containing fully developed oncospheres showing medial and lateral hooks.



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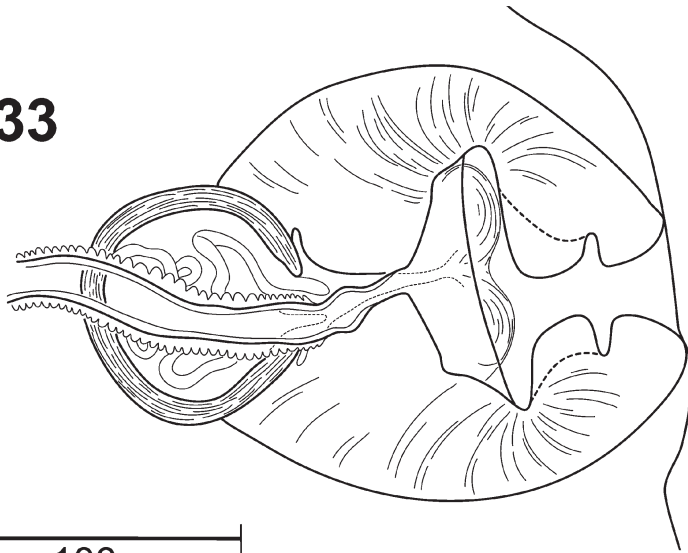


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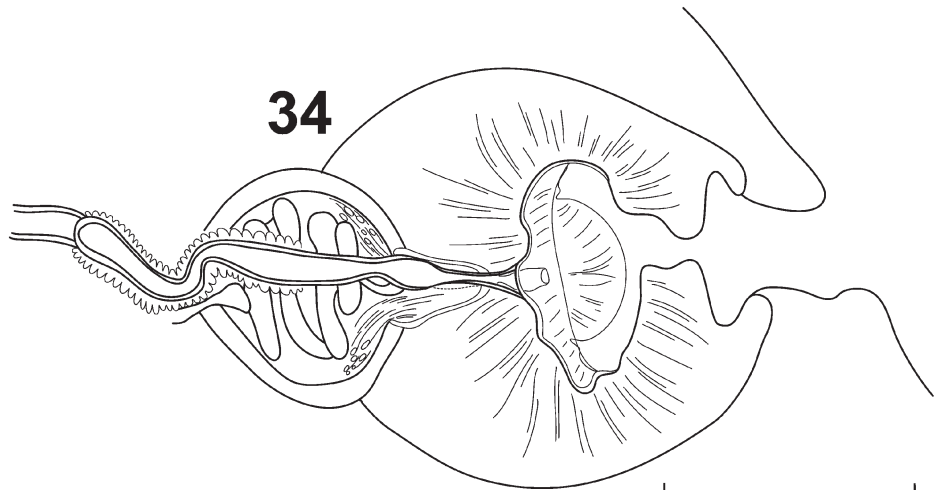
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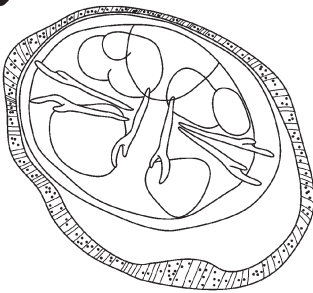
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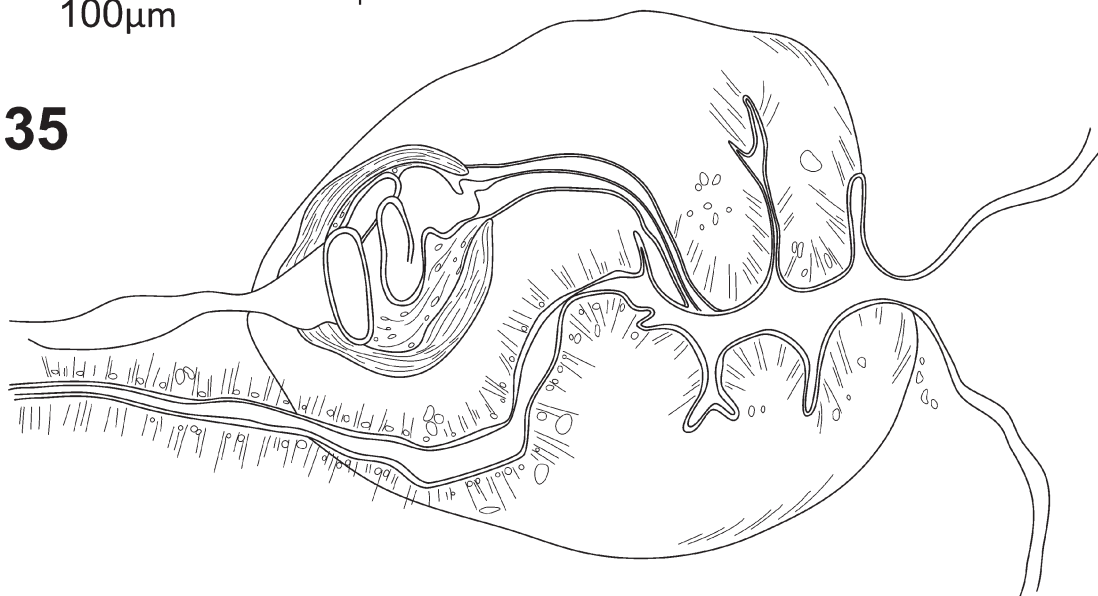
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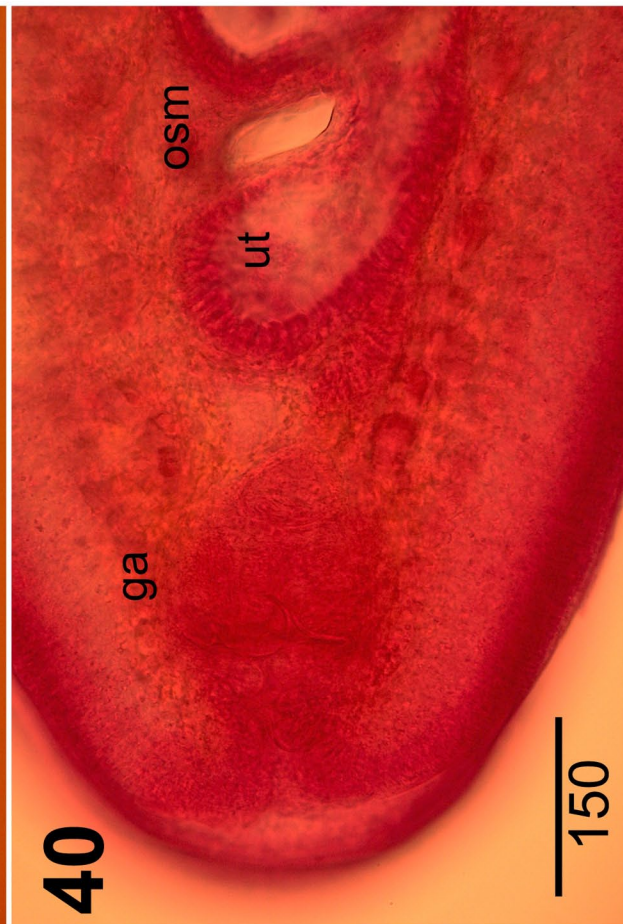
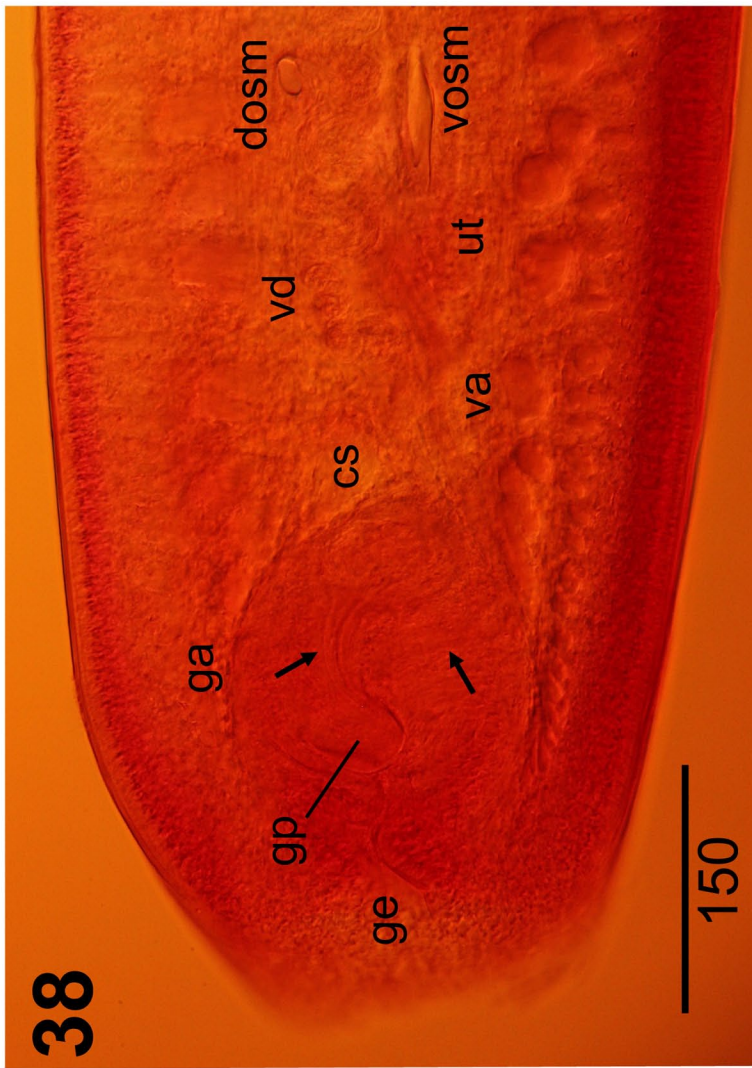
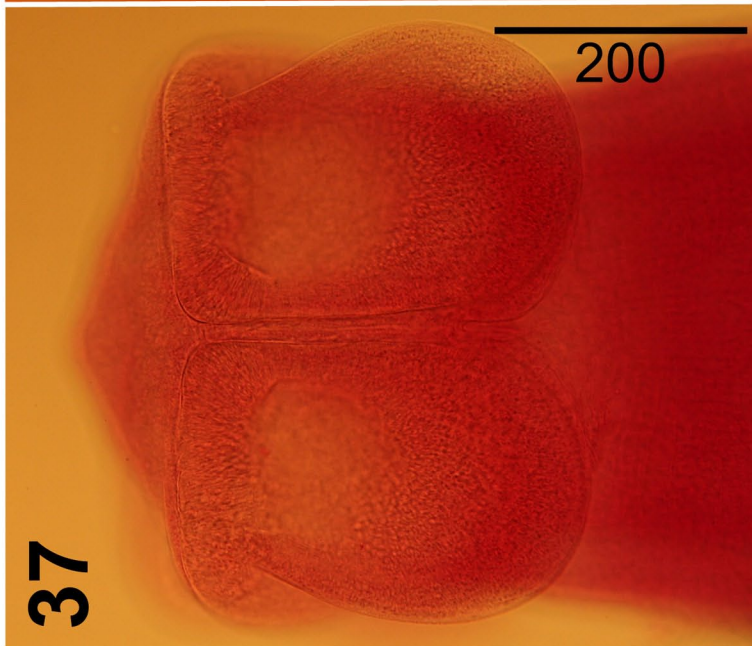


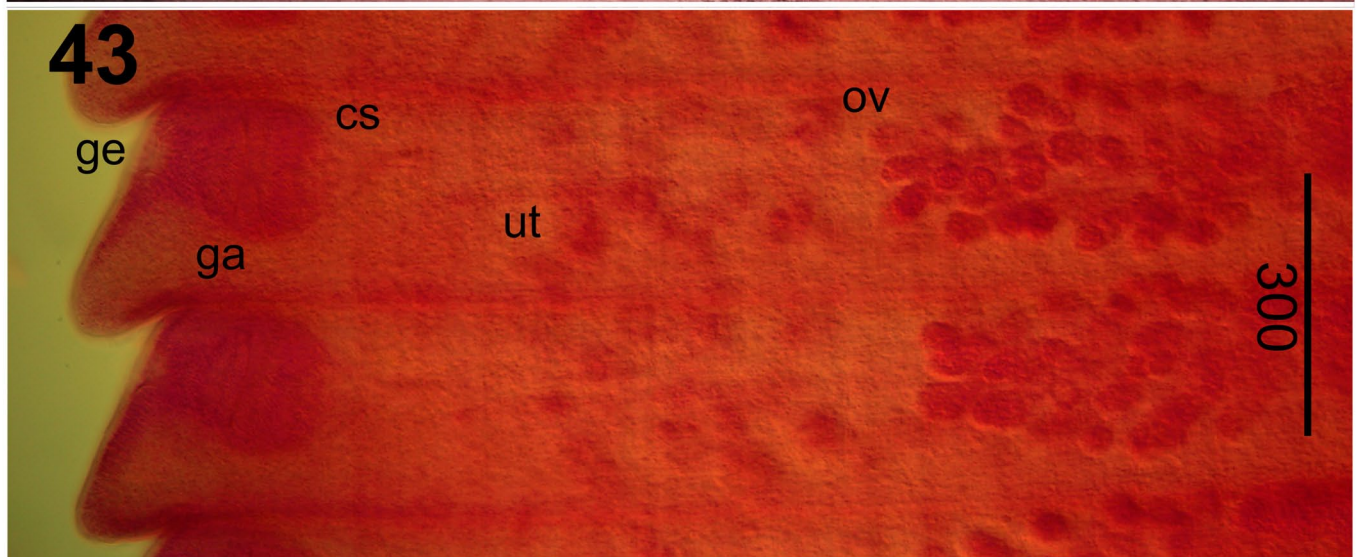
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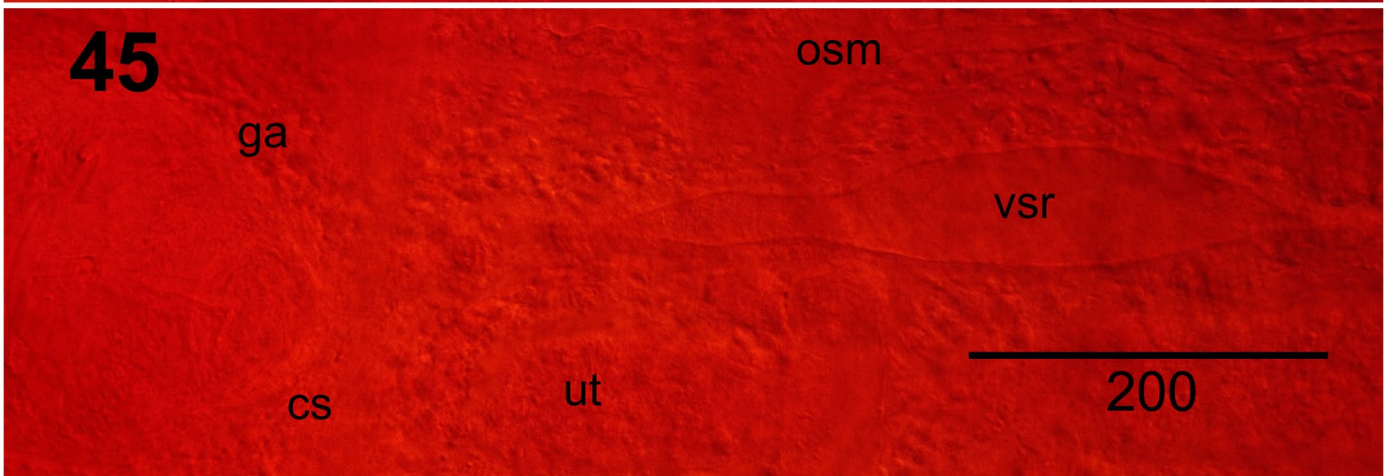
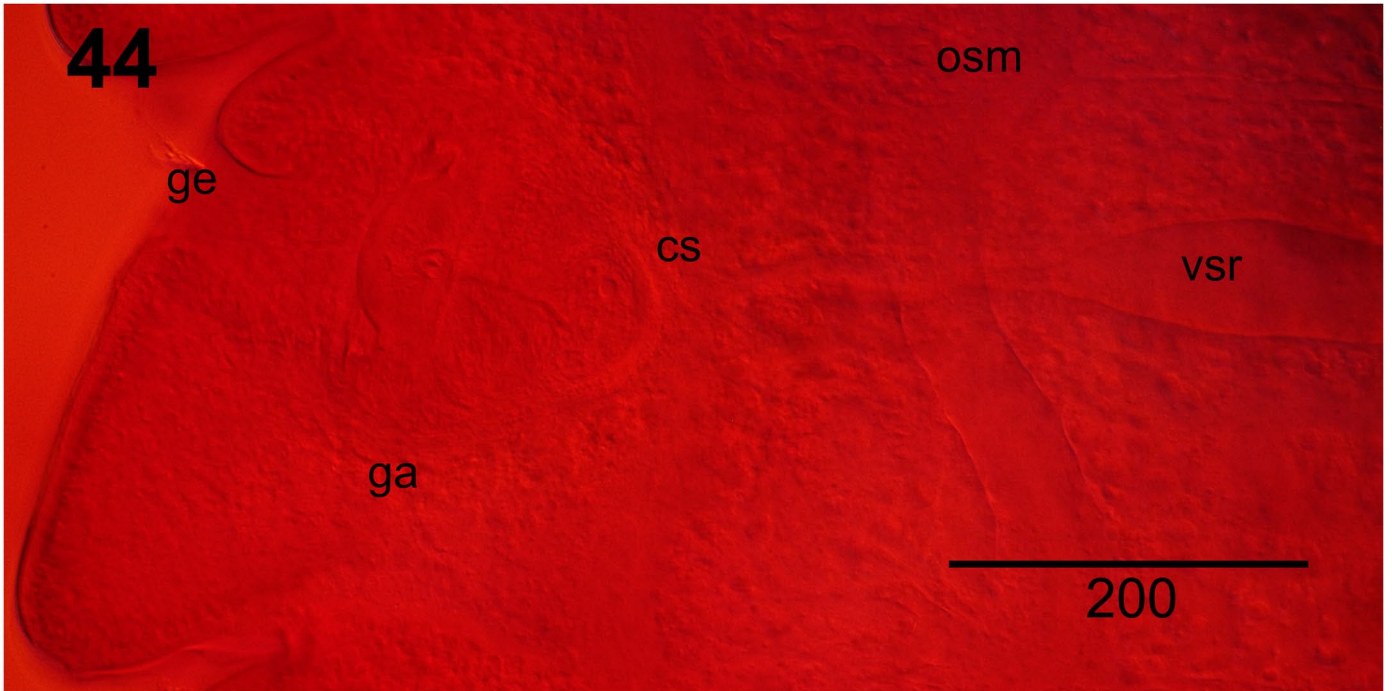
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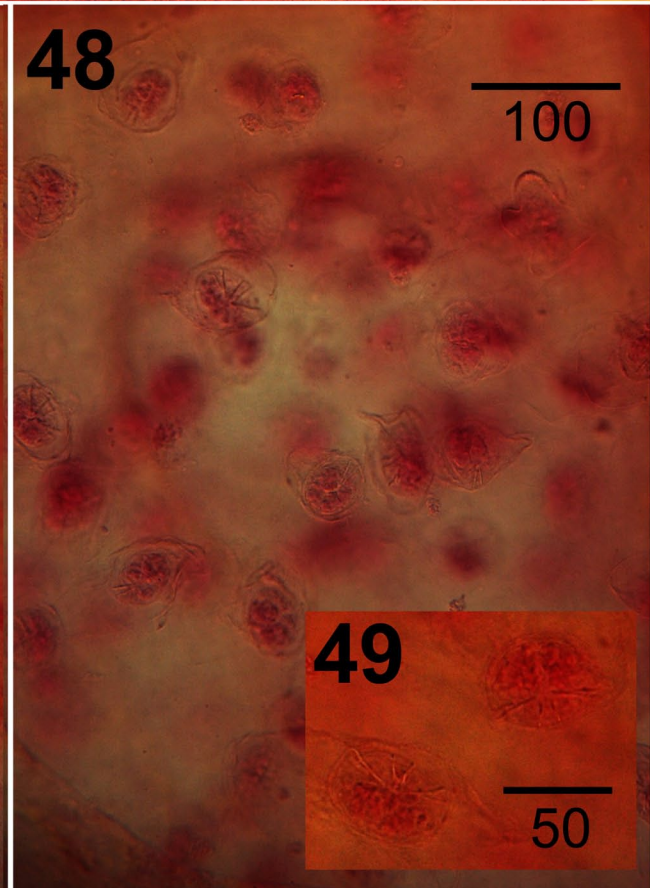
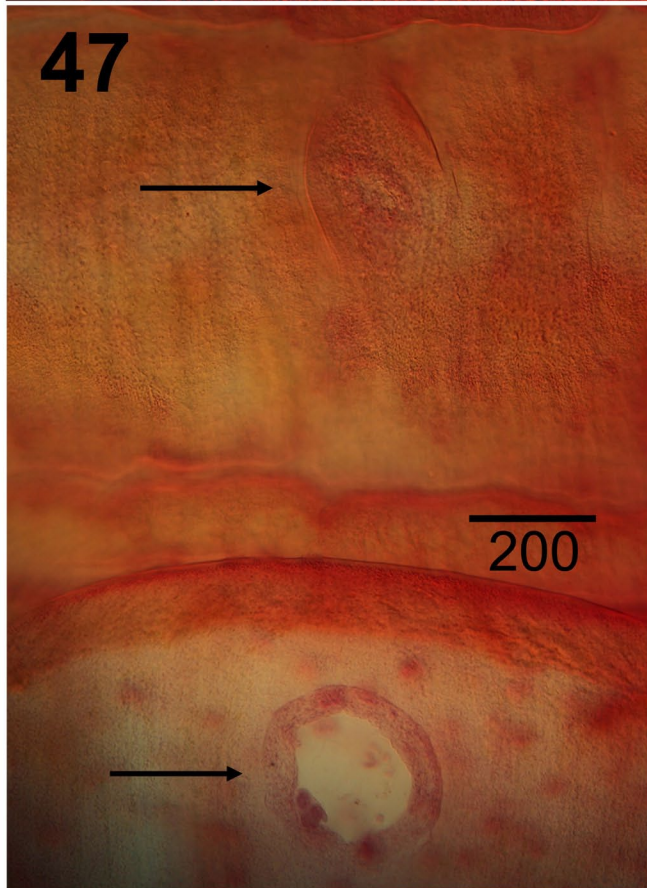
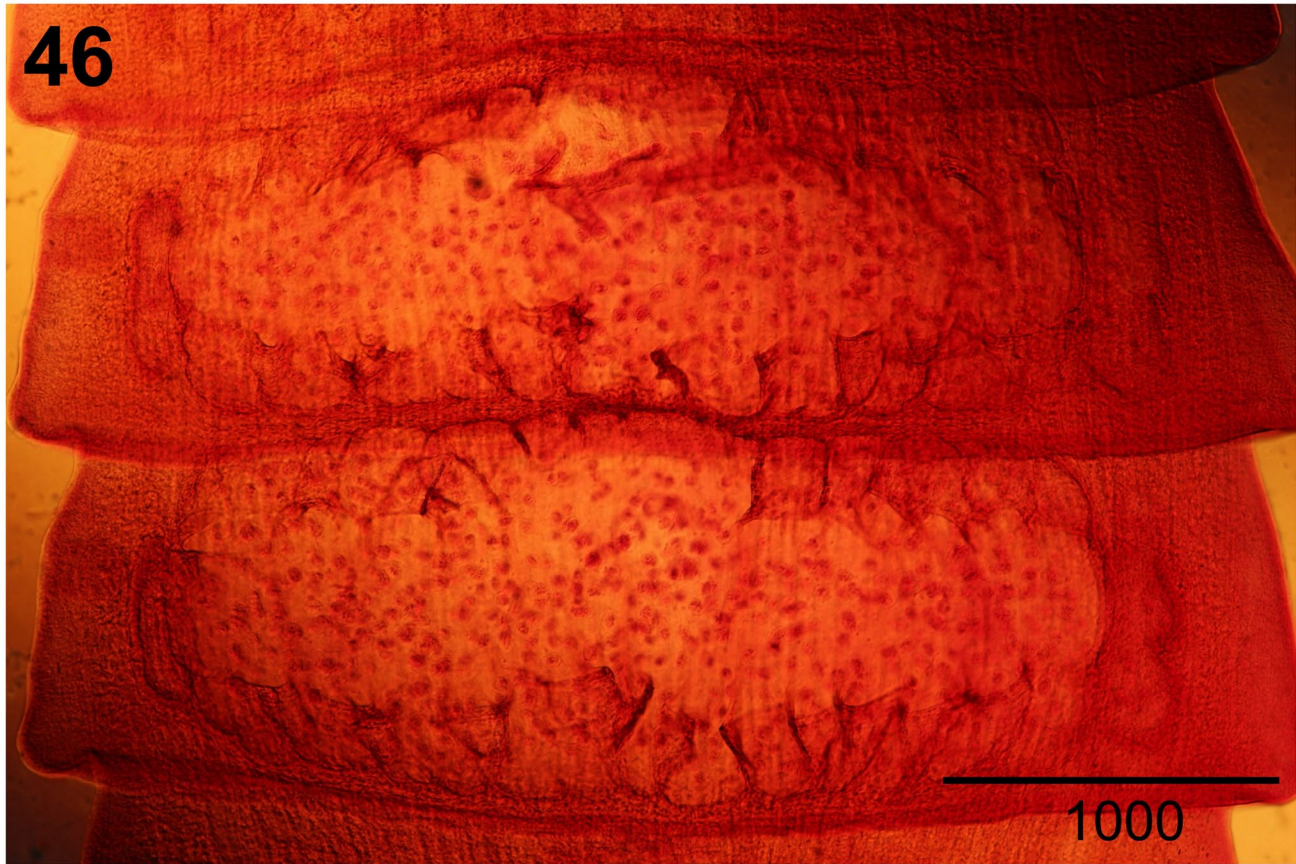


200µm









Specimens: Holotype—in type host (adult male), from type locality collected by E. P. Hoberg, (field number 1301-1-A through 1301-1-D; single gravid specimen on 5 slides including scolex, strobila, and hand-cut thick sections); identification by EPH. Museum of Southwestern Biology, MSB Collection Catalogue No. 29677. Paratype specimens—Paratype 1 and Paratype 2, including 2 complete specimens on 1 slide, formerly attributed to *Tetrabothrius jagerskioeldi* Nybelin, 1916, Museum d'Histoire Naturelle, Geneva (No. 108/60), from West Greenland collected by J. G. Baer on 27 July 1955; identification by EPH.

Zoobank Name Registration for *Tetrabothrius*

***sinistralis*:** [LSID urn:lsid:zoobank.](https://zoobank.org/LSID:urn:lsid:zoobank.org:act:23C47EF6-C595-4BB6-96AE-46C3ECB92AF2)

[org:act:23C47EF6-C595-4BB6-96AE-46C3ECB92AF2](https://zoobank.org/act:23C47EF6-C595-4BB6-96AE-46C3ECB92AF2)

Symbiotype: Host specimens or tissues not retained and archived.

Etymology: *Tetrabothrius sinistralis* n. sp. is derived from *sinistra* in Latin and Medieval Latin, denoting the unique position of the genital pore “on the left side” of each proglottid in dorsal view.

Remarks and Diagnosis

Specimens of *Tetrabothrius sinistralis* n. sp. are immediately distinguished from all species of *Tetrabothrius*, including 43 (with inclusion of *T. alcae*) and 8 congeners recognized respectively in avian and mammalian hosts. The sinistral-marginal position of the genital pore, in dorsal orientation of the strobila, contrasts with a dextro-marginal orientation which is observed among all nominal species. We note that Yamaguti (1935) reported irregular alternation in the position of the genital pore in some specimens of *T. lari* Yamaguti, 1935 (junior synonym of *T. erostris* Lönnerberg, 1896). In those specimens, reversal of an otherwise dextral position occurred rarely in single segments or in short series of contiguous segments but did not consistently involve orientation in the entire strobila.

Among the current 44 nominal species in avian hosts, cestodes representing *T. sinistralis* are most similar to specimens of *T. jagerskioeldi* and *T. alcae* in overall dimensions of the strobila and scolex, with the latter being consistently wider than long. The numbers of testes are similar in *T. sinistralis* and *T. jagerskioeldi*, and the dorsal and ventral osmoregulatory canals (poral) are positioned with near equidistance from the proglottid margin. Relative to *T. jagerskioeldi*, specimens of *T. sinistralis* are distinguished by smaller dimensions of the scolex (490–700 µm in width among specimens of *T. jagerskioeldi* from the North Pacific), attributes of the genital atrium, genital papilla and

ducts, position of the uterus, structure of the vitelline gland, and dimensions of the embryophore and oncosphere (Table 1; Hoberg and Soudachanh, 2020; for *T. jagerskioeldi*, Supplementary Data File 5, Figs. 1–15). Although the male and female genital ducts are positioned between the poral osmoregulatory canals in *T. sinistralis* and *T. jagerskioeldi*, the transverse uterine stem, and uterus at all stages of development in the former species, pass ventral to the canals (Figs. 32, 38–40, 45). In *T. sinistralis* the elongate, spindle-shaped, thin-walled, vaginal seminal receptacle attains but seldom crosses the poral osmoregulatory canals (considerably smaller, thick-walled, and positioned between the canals in *T. jagerskioeldi*) and does not attain the ovarian wing (Figs. 44–45). The vitelline gland is weakly follicular and relatively elongate in *T. sinistralis*, contrasting with the compact and globular condition in *T. jagerskioeldi* (Figs. 41–42). The testes surround the female organs in *T. sinistralis* and *T. jagerskioeldi*, although there is a gap in continuous distribution along the anterior margin of the vitelline gland and ovary in the former species. The genital atrium in *T. sinistralis* is characterized by a bulbous, weakly bilobed, but prominent genital papilla and a ventrally directed, strongly decurved, male canal with a subventral aperture near the apex between the lobes (Figs. 35, 38–39); the aperture of the female genital canal is ventral to and adjacent to that of the male canal. The vagina enters the genital atrium in a 90° curve in *T. sinistralis*; in *T. jagerskioeldi* the vagina attains a slight curve. In *T. jagerskioeldi* the male and female genital canals are relatively straight and parallel, opening ventrally below the apex of a single, prominent triangular genital papilla. The length of the male canal is substantially greater in *T. sinistralis* relative to *T. jagerskioeldi*. The embryophore and oncosphere are substantially larger in *T. sinistralis*.

Specimens of *T. sinistralis* and *T. alcae* are distinguished by dimensions and structure of the scolex and neck region; numbers of testes; position of the genital ducts; structure of the genital atrium, genital papilla, ducts, and distal vagina; and in the form and length of the vaginal seminal receptacle (Table 1). In *T. sinistralis* the scolex is flattened dorso-ventrally and possesses slightly concave bothridia with strongly developed auricles (Figs. 30–31, 37); the neck region is short. In contrast, *T. alcae* has powerfully muscular suckerlike bothridia with reduced auricles; the neck region is elongate and inflated. The dimensions of the scolex in *T. sinistralis* are notably larger. The position of the dorsal and ventral osmoregulatory canals is equidistant from the poral margin of the proglottid in *T. sinistralis*; the dorsal canal is shifted mediad in *T. alcae* (Figs. 35, 38). The male (vas deferens) and female (vagina) ducts pass between the poral osmoregulatory canals in *T. sinistralis*, and only the uterus is ventral in position. Alternatively, in *T. alcae* the

genital ducts and the uterus are entirely ventral to the canals. The female organ systems are centered on the midline in *T. sinistralis*, whereas the center of the ovary and Mehlis' gland is shifted porad and the center of the vitelline gland is shifted to the antiporal ovarian wing in *T. alcae*. In *T. sinistralis* the ovary is lobate but not dendritic, and the vitelline gland is weakly follicular; in *T. alcae* the ovary is strongly dendritic, and the vitelline gland is highly elongate and follicular. The vaginal seminal receptacle is spindle-shaped and elongate in *T. sinistralis*, differing from the voluminous pyriform to cylindrical condition in *T. alcae* (Figs. 44–45). The numbers of testes are considerably fewer in specimens of *T. sinistralis*. Dimensions of the cirrus sac and muscular genital atrium overlap, although these organs tend to be smaller in specimens of *T. sinistralis* at comparable stages of development. The length of the male atrial canal overlaps between the species; however, the structure differs considerably. In *T. sinistralis* the male genital canal is strongly decurved ventrally, opening subventrally near the apex of a bulbous, weakly bilobed papilla (Figs. 35, 38–39). In *T. alcae* the male canal is weakly curved, opening near the base of a dorsally disposed bilobed genital papilla in the center of the atrium. In *T. sinistralis* and *T. alcae* the vagina passes through the wall of the genital atrium in a 90° curve ventral to the cirrus sac.

Tetrabothrius sinistralis can also be distinguished from 4 additional species of *Tetrabothrius* that may circulate among larids and other seabirds, including some cestodes that have been sporadically reported among alcid hosts from the North Pacific basin and Holarctic seas (Linton, 1927; Belopol'skaia, 1952; Baer, 1954; Temirova and Skrjabin, 1978; see Hoberg and Soudachanh, 2020). Specimens of species discussed in this and the following paragraphs (and *T. jagerskioeldi*) all have well-developed scolexes that are consistently wider than long and with typical flattened to concave bothridia and prominent auricular appendages. Among these, specimens of *T. sinistralis* differ from *T. cylindraceus* Rudolphi, 1819 based on dimensions and structure of the strobila (highly serrate, ± 50 mm long for gravid specimens of *T. cylindraceus*) and scolex (about 250 μm wide), the numbers of testes (about 20), smaller dimensions of most organ systems, and the structure of the genital atrium (male and female genital canals are parallel and ventrally curved throughout the length and open on a prominent strongly decurved genital papilla) (Linton, 1927; Baer, 1954; Temirova and Skrjabin, 1978).

Specimens of *T. sinistralis* differ from those of *T. erostris* based on generally smaller dimensions in the latter for the scolex (280 μm in width in *T. erostris*), genital atrium (140 μm greater diameter), cirrus sac (mean diameter = 80 μm), ovary (480 μm , maximum width), and vitelline gland

(125–175 μm , maximum width, compact and globular) and in having fewer testes (37–40, maximum = 50). The spindle-shaped vaginal seminal receptacle is positioned between the poral osmoregulatory canals in *T. erostris*. The genital atrium is similar in these species, with the male canal being ventrally decurved and opening near the apex of a genital papilla (Baer, 1954; Temirova and Skrjabin, 1978).

Specimens of *T. sinistralis* differ from those of *T. macrocephalus* Rudolphi, 1819 based on a series of characters in the latter species including substantially longer strobila (maximum 300 mm in *T. macrocephalus*), larger scolex (1,020–1,420 μm in width), relatively smaller genital atrium (140–210 μm , in greater diameter) and cirrus sac (range 57–75 μm , 86 μm maximum, greater diameter), fewer testes (35–40 in number), short male atrial canal (64 μm in length), and a strongly compact vitelline gland. The muscular genital atrium lacks a prominent papilla, and the male (dorsal) and female (ventral) canals are parallel, straight, and open centrally in the atrium (Linton, 1927; Baer, 1954; Temirova and Skrjabin, 1978).

Specimens of *T. sinistralis* differ from those of *T. morschtini* Murav'eva, 1968 in reference to a series of characters in the latter, including a smaller strobila, a substantially larger scolex (mean = 580 μm , maximum 840 μm in width in *T. morschtini*), smaller genital atrium (98–138 μm) and cirrus sac (75–90 μm), a strongly compact vitelline gland, and substantially fewer testes (32–34 in number). The vaginal seminal receptacle in *T. morschtini* is spindle-shaped and elongate, and does not attain the poral osmoregulatory canals. The structure of the genital atrium is also similar to *T. sinistralis* where the male canal is decurved ventrally, opening near the apex of a bulbous genital papilla, with the aperture of the vagina ventral and adjacent (Murav'eva, 1968).

Metacestodes and Scolex Ontogeny among Species of *Tetrabothrius*

Among specimens of *T. alcae*, postlarval cestodes, ranging from a few primary immature proglottids to initial appearance of genital anlagen and protandrous development of the testes, were identified based on structural characteristics of the scolex and powerful suckerlike bothridia. Among specimens of *T. sinistralis*, structural characters associated with developing metacestodes in the definitive host were not recognized. Attributes of metacestode or postlarval scolexes in *T. alcae* were defined by an expanded apical region, vestigial pedicle, apical pore, and padlike to ovoid apical organ (Figs. 50–57); a terminal apical sucker was not

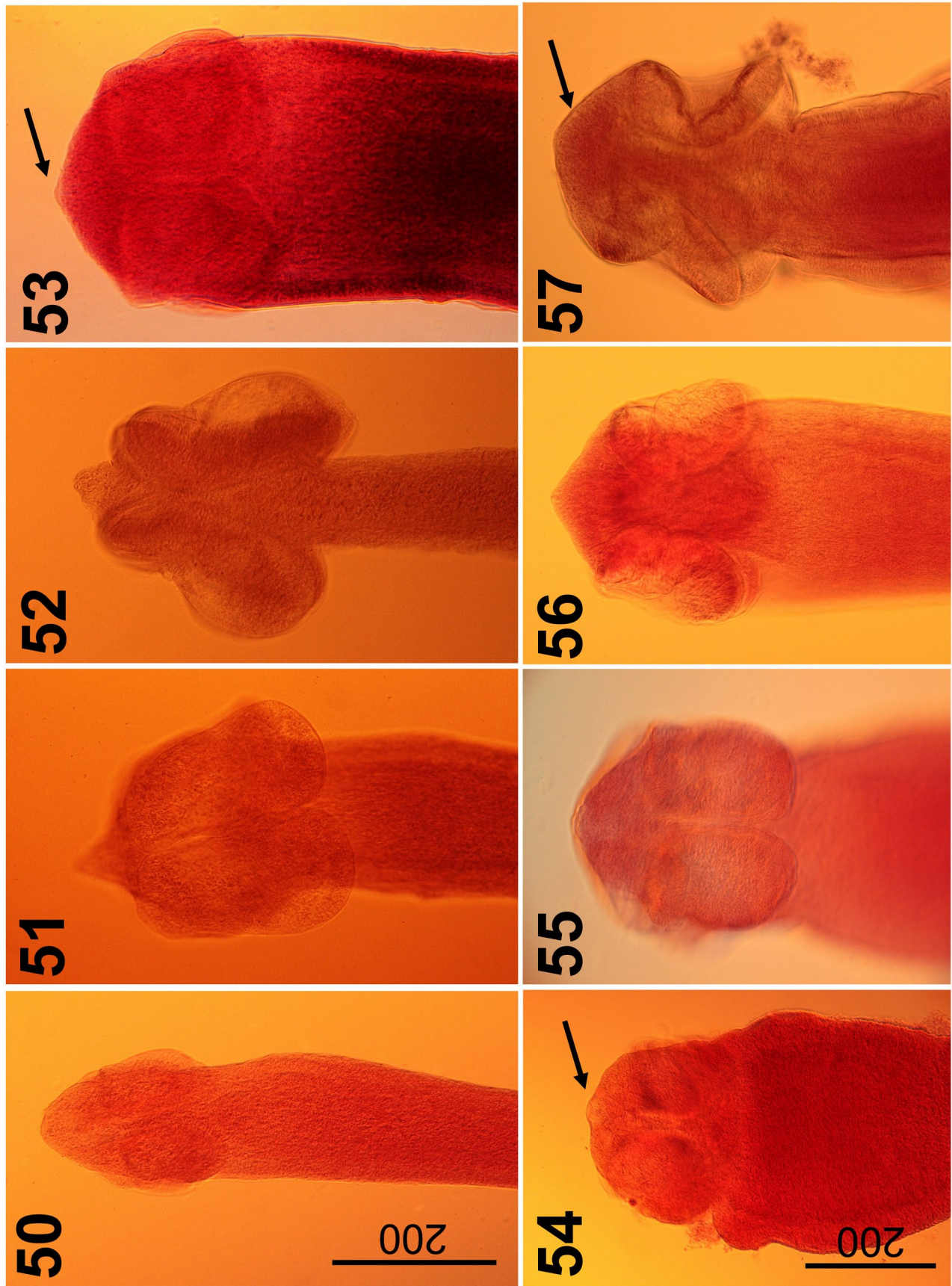
observed in any specimens. Postlarval specimens, with minimal development, were collected from 16 adult hosts (8 *U. aalge*, 6 *U. lomvia*, 1 *A. psittacula*, and 1 *S. antiquus*) at sites spanning the North Pacific and Bering Sea (Sea of Okhotsk, Aleutian Islands, central and Northern Bering Sea, Gulf of Alaska, and eastern Pacific from Grays Marine Canyon to Humboldt Bay) (Figs. 50–57) (Supplementary Data Table 4). Additionally, cestode specimens with larval attributes and strobilization with minimal development of early mature proglottids were observed predominantly among chicks of common (8) and thick-billed murres (1) near the time of fledging prior to dispersal from nesting cliffs adjacent to marine habitats on Talan Island; and in an adult ancient murrelet in the pelagic zone south of the Aleutian Islands (Figs. 58–61). A pigeon guillemot chick at St. Lawrence Island was infected by a fully developed cestode. Adult strobilate and gravid cestodes in which the scolex retained larval attributes (including the holotype) were observed in 4 subadult or adult murres (*U. aalge* and *U. lomvia*) at Talan Island and in pelagic waters south of the Aleutian Islands. The occurrence of postlarval specimens and strobilate cestodes with larval characters encompasses an extensive spatial distribution and among 5 species of alcids, indicating that the life cycle is broadly completed within the North Pacific ecosystem.

An ontogenetic progression associated with cestodes recently acquired in the definitive host accounts for the degree of development of the inflated apical zone, apical organ, and vestigial apical pedicle and dimensions of individual scolexes (e.g., Hoberg, 1987a; Galkin, 1987). Generally, these developing scolexes were consistently wider than long ($n = 23$; 170–370 μm [mean = 293] in length, 165–400 [297] in width) and in the most developed specimens approached dimensions observed in large strobilate and adult cestodes (e.g., Figs 1–2; Figs. 12–15). Bothridia were strongly muscularized and suckerlike with relatively inconspicuous auricular appendages, ($n = 52$) 125–280 (205) in length and 75–190 (138) in width. An elongate, inflated neck region was typical, and varying degrees of primary strobilization were evident (Figs. 50–57; Figs. 58–61). Apical expansion or hypertrophy indicative of recent infection and accelerated development and strobilization were also observed in strobilate adult and gravid specimens of cestodes in the type and voucher series. (e.g., the holotype and associated paratypes from Talan Island).

An intact apical sucker was not observed among fully developed (strobilate) or immature specimens of *T. alcae*. A rudimentary pedicle and vestiges of this organ following loss of the apical sucker in the definitive host were observed in some specimens consistent with scolex ontogeny among other Tetrabothriidae (e.g., Galkin, 1987; Hoberg, 1987a, 1989; Hoberg and Ryan, 1989; Hoberg et al., 1991; Hoberg and Measures, 1995). A single apical sucker, and vestiges of the apical organ system, have been described in immature and fully developed strobilate cestodes among multiple genera and species of *Tetrabothrius* and *Anophryocephalus* Baylis, 1922 in avian and pinniped hosts. The occurrence of a fully developed apical sucker, or hypertrophied apical region with a pedicle, serves to further confirm the uniformity of an accelerated ontogenetic pathway within the Tetrabothriidae (Hoberg, 1994). The scolex of the metacestode in the intermediate host is undifferentiated, with a prominent muscular apical sucker at the apex of an unsegmented body of the plerocercoid (Hoberg, 1987a; Galkin, 1987). Structural characters of the bothridia are attained through rapid development of the adult scolex, coinciding with or following initial strobilization, secondary to establishment in the avian or mammalian definitive host. Among specimens of *T. alcae*, patterns of accelerated differentiation for the scolex and strobila are further indicated by already strobilate specimens of tapeworms occurring in young common and thick-billed murres at the time of fledging (near 15–18 days of age, 8 birds; about 20 days, 2 birds) as evident at Talan Island. The typical fledging time for murres is about 20–22 days (range in reported duration prior to departure, 16–30 days), with young birds leaving the cliff-face ledges prior to attaining capacity for flight (Harris et al., 1997; Harris and Birkhead, 1985; Boekelheide et al., 1990). Thus, acquisition of parasites occurs before young birds have departed colony sites and become established in marine environments, being dependent on prey (usually piscine; e.g., Boekelheide et al., 1990; Piatt et al., 2020), which serve as intermediate or possibly paratenic hosts, provided directly by adult birds (e.g., Hoberg, 1992a, 1996). Prey species diversity varies regionally; for example, in the Farallon Gulf system off California, juvenile rockfish (species of *Sebastes* Cuvier, 1829) are a dominant resource for developing chicks, whereas in the Bering Sea sandlance (species of *Ammodytes* Linnaeus, 1758) are essential (Ainley and Sanger, 1979; Ainley, 1990; Piatt et al., 2020).

Figures 50–57. *Tetrabothrius alcae* n. sp. postlarval scolexes showing relative progression in development of the adult holdfast (scale bars in micrometers). **Fig. 50.** Scolex, dorsoventral view, during initial development in postlarval cestode in *Uria aalge* (299-A), Chiniak Bay, Kodiak Island. Note extensive inflated apical region and apical organ, suckerlike bothridia in development with rudimentary auricular appendages and inflated neck. **Fig. 51.** Scolex, dorsoventral view, showing retention of apical pedicle and developing bothridia in *U. aalge* (362-78b) at Chiniak Bay, Kodiak Island. **Fig. 52.** Scolex, lateral view, showing development of suckerlike bothridia and retention of apical pedicle in *U. aalge* (362-78a) at Chiniak Bay, Kodiak Island. **Fig. 53.** Scolex, dorsoventral view, showing domed apical region with apical organ and pore (arrow) in *Uria lomvia* (103AB) at Ugaiushak Island, Gulf of Alaska. **Fig. 54.** Scolex, dorsoventral view, showing apical organ and pore (arrow) in *U. lomvia* (1389), St. Matthew Island, Bering Sea. **Fig. 55.** Scolex, dorsoventral view, showing enlarged apical region and apical organ and muscular, suckerlike bothridia in *Aethia psittacula* (2723-2) at Talan Island. **Fig. 56.** Scolex, lateral view, showing domed apical region of holdfast and muscularized suckerlike bothridia in *U. aalge* (2440-2) from Grays Marine Canyon, eastern North Pacific. **Fig. 57.** Scolex, lateral view, with domelike apical region, padlike apical organ with pore (arrow), and strongly muscularized bothridia with rudimentary auricles in *A. psittacula* (2723-3) at Talan Island.

Figures 58–61. *Tetrabothrius alcae* n. sp. early strobilate cestodes (development to early maturity, with primary terminal proglottid) in dorsoventral view. Scolexes retain characteristics of postlarval specimens. **Fig. 58.** Scolex in early mature strobilate cestode retaining a primary proglottid in *U. aalge*, a chick near fledging (2660) at Talan Island. Note ovoid apical organ with padlike structure and apical pore (arrow) with muscular suckerlike bothridia. **Fig. 59.** Scolex in early mature, strobilate cestode. Note inflated neck region lacking segmentation and deep, muscular bothridia with poorly developed auricles, in *U. aalge* (2658-2), a chick near fledging at Talan Island. **Fig. 60.** Scolex in early mature, strobilate cestode, in *U. aalge* (2659-3), a chick near fledging at Talan Island. Note broad, dome-shaped apical region and retention of padlike apical organ and pore. **Fig. 61.** Scolex in lateral view, early mature, strobilate cestode, in *U. aalge* (2657-3) at Talan Island.



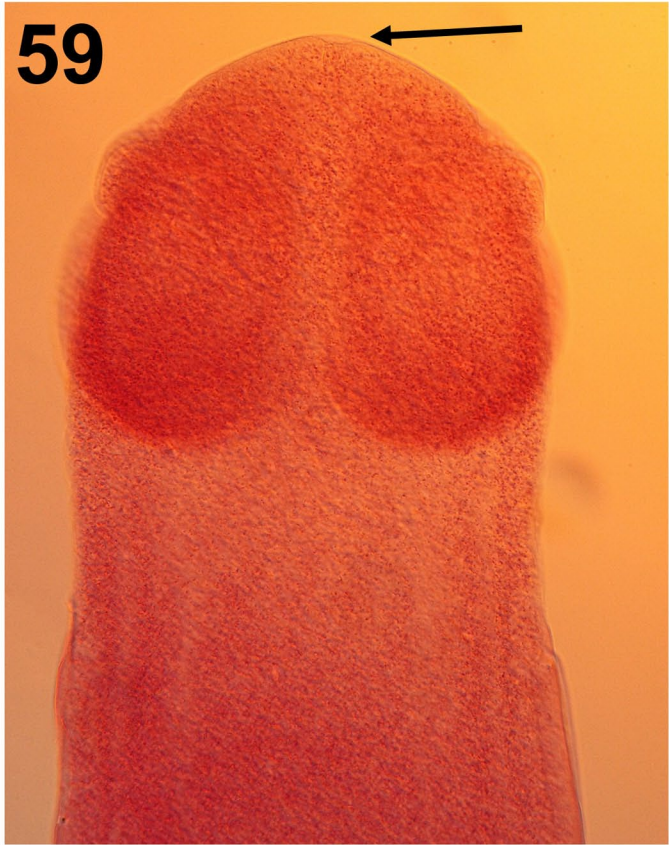


Table 2. Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916, *T. alcae* n. sp., and *T. sinistralis* n. sp. among Alcidae Seabirds

| Avian species | <i>Tetrabothrius jagerskioeldi</i> | <i>Tetrabothrius alcae</i> n. sp. | <i>Tetrabothrius sinistralis</i> n. sp. |
|--|--|--|--|
| Tribe Alcini | | | |
| <i>Alca torda</i> Linnaeus, 1758 | Seven Islands Reserve, Barents Sea (Belopolskaia, 1952) ▲ | Cannot be determined: no specimens are available | Cannot be determined: no specimens are available |
| <i>Alle alle</i> (Linnaeus, 1758) | Northwestern North Atlantic (Threlfall, 1971) ?▲ | Cannot be determined: no specimens are available | Cannot be determined: no specimens are available |
| <i>Uria aalge</i> (Pontoppidan, 1763) | Seven Islands Reserve, Barents Sea (Belopolskaia, 1952) ▲ Northwestern Atlantic (Threlfall, 1971) ▲ Big Bay, Shuyak Island, Gulf of Alaska *★ | Chiniak Bay, Kodiak Island, Gulf of Alaska * St. Matthew Island, Bering Sea * Cape Lisburne, Chukchi Sea * Talan Island, Sea of Okhotsk * Grays Marine Canyon, Eastern North Pacific * Humboldt Bay, Eastern North Pacific * | No current specimens nor records |
| <i>Uria lomvia</i> (Linnaeus, 1758) | Northwestern Atlantic (Threlfall, 1971) ▲ Peter the Great Bay, Russian Far East (Semtanina, 1979, 1981) ▲ | Ugaiushak Island, Gulf of Alaska * Buldir Island, Western Aleutian Islands * Western Aleutian Islands (pelagic) * St. Lawrence Island, Bering Sea * St. Matthew Island, Bering Sea * Cape Thompson, Chukchi Sea * Talan Island, Sea of Okhotsk * | No current specimens nor records |
| † <i>Pinguinus impennis</i> (Linnaeus, 1758) | Host specimen(s) examined: <i>T. jagerskioeldi</i> not discovered | Host specimen(s) examined, <i>T. jagerskioeldi</i> complex not discovered | Host specimen(s) examined, <i>T. jagerskioeldi</i> complex not discovered |
| Tribe Cepphini | | | |
| <i>Cepphus carbo</i> Pallas, 1811 | Sudzukinsky Reserve, Russian Far East (Belopolskaia, 1963a, 1963b) ▲ Peter the Great Bay, Russian Far East (Smetanina, 1979, 1981) ▲ Northern Sea of Okhotsk *★ | No current specimens nor records | No current specimens nor records |
| <i>Cepphus columba</i> Pallas, 1811 | St. Lawrence Island, Bering Sea *⊙★ Uganik Bay, Kodiak Island, Gulf of Alaska *⊙★ Uyak Bay, Kodiak Island, Gulf of Alaska *⊙★ St. Matthew Island, Bering Sea *⊙★ Sledge Island, Bering Sea *⊙★ Ugaiushak Island, Gulf of Alaska *⊙★ | St. Lawrence Island, Bering Sea * | St. Matthew Island, Bering Sea * |
| <i>Cepphus grylle</i> (Linnaeus, 1758) | Kristineberg, Sweden (Nybelin, 1916) * Väderöarna, Sweden * Barents Sea (Baylis, 1918) * Seven Islands Reserve, Barents Sea (Belopolskaia, 1952) ▲ Seven Islands Reserve, Barents Sea (Kuklin and Kuklina, 2005) ▲ Reykjavik, Iceland *★ Boxer Bay, St. Lawrence Island, Bering Sea *★ | No current specimens nor records | Kangerluk, West Greenland (Baer, 1956) * |

† Species of Alcidae lacking parasitological data and which apparently have not been examined for parasites.

▲ Historical record not supported by archival specimens.

* Record substantiated by permanent archived specimens held in an international museum collection; specimens examined during the current study.

⊙ New host record.

★ New geographic record.

Table 2. Cont. Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916, *T. alcae* n. sp., and *T. sinistralis* n. sp. among Alcidae Seabirds

| Avian species | <i>Tetrabothrius jagerskioeldi</i> | <i>Tetrabothrius alcae</i> n. sp. | <i>Tetrabothrius sinistralis</i> n. sp. |
|--|---|---|---|
| Tribe Brachyramphini | | | |
| <i>Brachyramphus marmoratus</i> (Gmelin, 1789) | Chiniak Bay, Kodiak Island, Gulf of Alaska *⊙★ | no current specimens nor records | no current specimens nor records |
| <i>Brachyramphus brevirostris</i> (Vigors, 1829) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens nor records |
| <i>Brachyramphus perditx</i> ⊙ (Pallas, 1811) | | | |
| Tribe Synthliboramphini | | | |
| <i>Synthliboramphus antiquus</i> (Gmelin, 1789) | Sudzukhinsky Reserve, Russian Far East (Belopol'skaia, 1963a, 1963b)▲ Peter the Great Bay, Russian Far East (Smetanina, 1979, 1981)▲ | Western Aleutian Islands (pelagic) * St. Lawrence Island, Bering Sea * | no current specimens nor records |
| <i>Synthliboramphus craveri</i> ⊙ (Salvadori, 1865) | | | |
| <i>Synthliboramphus hypoleucus</i> ⊙ (Xantus de Vesev, 1860) | | | |
| <i>Synthliboramphus scrippsii</i> (Green and Arnold, 1939) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens nor records |
| <i>Synthliboramphus wumizuzume</i> ⊙ Temminck, 1836 | | | |
| Tribe Aethiini | | | |
| <i>Ptychoramphus aleuticus</i> (Pallas, 1811) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens nor records |
| <i>Aethia psittacula</i> (Pallas, 1769) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens nor records |
| <i>Aethia cristatella</i> (Pallas, 1769) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | Talan Island, Sea of Okhotsk * | no current specimens nor records |
| <i>Aethia pygmaea</i> (Gmelin, 1789) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens or records |
| <i>Aethia pusilla</i> (Pallas, 1811) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> Not Discovered | no current specimens nor records | no current specimens nor records |

⊙ Species of Alcidae lacking parasitological data and which apparently have not been examined for parasites.

▲ Historical record not supported by archival specimens.

* Record substantiated by permanent archived specimens held in an international museum collection; specimens examined during the current study.

⊙ New host record.

★ New geographic record.

Table 2. Cont. Records of Host and Geographic Occurrence for *Tetrabothrius jagerskioeldi* Nybelin, 1916, *T. alcae* n. sp., and *T. sinistralis* n. sp. among Alcidae Seabirds

| Avian species | <i>Tetrabothrius jagerskioeldi</i> | <i>Tetrabothrius alcae</i> n. sp. | <i>Tetrabothrius sinistralis</i> n. sp. |
|--|---|---|---|
| Tribe Fraterculini | | | |
| <i>Fratercula arctica</i> (Linnaeus, 1758) | Seven Islands Reserve, Barents Sea (Belopolskaia, 1952)▲ Northwestern Atlantic (Threlfall, 1971)▲ | cannot be determined: no specimens are available | cannot be determined: no specimens are available |
| <i>Fratercula cirrhata</i> (Pallas, 1769) | Russian Far East or Kurile Islands (?) (Temirova and Skryabin, 1978)▲ | no current specimens nor records | no current specimens nor records |
| <i>Fratercula corniculata</i> (Naumann, 1821) | Host Specimen(s) Examined: <i>T. jagerskioeldi</i> : Not Discovered | no current specimens nor records | no current specimens nor records |
| <i>Cerorhinca monocerata</i> (Pallas, 1811) | Shikotan Island, Kurile Islands (Smetanina and Leonov, 1984)▲ Western Aleutian Islands (pelagic) *★ | no current specimens nor records | no current specimens nor records |

◎ Species of Alcidae lacking parasitological data and which apparently have not been examined for parasites.

▲ Historical record not supported by archival specimens.

* Record substantiated by permanent archived specimens held in an international museum collection; specimens examined during the current study.

◎ New host record.

★ New geographic record.

Discussion

We begin the resolution of the *T. jagerskioeldi*-species complex with descriptions of *Tetrabothrius alcae* n. sp. based on numerous specimens from the greater North Pacific basin and *Tetrabothrius sinistralis* n. sp. based on cestodes from the central Bering Sea and West Greenland. These species of *Tetrabothrius* are the first to be described in avian hosts since the late 1980s, indicating the degree to which attention to these dominant marine cestodes has languished. It remains apparent that extensive revision of this group is required, including redescription and validation of the now 52 nominal species in avian and mammalian hosts (e.g., Hoberg, 1987b, 1994, 1996; Mariaux et al., 2017). A principal tenet continues for complete descriptions and redescrptions that adopt a standardized basis for morphological and mensural comparisons reflecting progressive modification of the genital organs during ontogeny (e.g., Rawson, 1964; Murav'eva and Popov, 1976; Hoberg, 1987b; Hoberg et al., 1991). When possible, integrated approaches that embody molecular and genomics data with comparative morphology should be expected, although such will not be a generality in assessing diversity assembled through centuries of collections and with the relatively minimal numbers of specimens now held in museum repositories globally. New and continuing field collections with accumulation of archived specimens, biodiversity information, and robust phylogenetic assessments will be central to resolution of diversity and history for tetrabothriids, species of *Tetrabothrius*, and related genera among the more than 326 species of seabirds (excluding Anseriformes), 91 Cetartiodactyla (suborders Odontoceti and Mysticeti), and 36 Pinnipedia (e.g., Hoberg 1996; Hoberg et al., 2013; Dunnum et al., 2017; Mariaux et al., 2017). Following descriptions of *Tetrabothrius alcae* and *Tetrabothrius sinistralis*, the genus *Tetrabothrius* contains 44 species that are parasites in marine avian hosts with 3 nominal cestode taxa among Alcidae.

Fallacy of Expected Identification

The history of this apparent complex has been confused. Historically, identifications of *T. jagerskioeldi* were based on host association (host identity = parasite identity) directly linked to expectations emerging from cospeciation and assumed specificity (e.g., Nylin et al., 2018; Brooks et al., 2019). Knowledge or assumptions about diversity were derived from a host-centric view and host taxonomy rather than from parasite morphology, genetic data, and phylogeny, a generality which has been apparent across diverse assemblages of hosts and parasites. Parasite taxonomy as a reflection or extension of host range has historically been

a core assumption of parasite biodiversity knowledge. A context linking cospeciation, host specificity, species limits, and taxonomy has been effectively refuted with the advent of phylogenetic/comparative methods (e.g., Hoberg and Brooks, 2008 and references therein; Agosta et al., 2010; Brooks et al., 2019). A context for seabird parasite diversity, and especially published records among the Alcidae, has been strongly influenced by these assumptions over the past century following the description of *T. jagerskioeldi* by Nybelin (Nybelin, 1916).

Superficial resemblance of large tetrabothriid cestodes has been problematic. Thus, any large tetrabothriid in an alcid host would by default be identified as *T. jagerskioeldi*. As we noted, the understanding of the distribution of parasite diversity among alcids and other seabirds has been confounded by the nearly universal absence of a large series of archival vouchers in museum collections (Hoberg and Soudachanh, 2020). Although we refer to this broadening assemblage recognized as a species-complex, that idea currently rests on overall morphological similarity in the absence of a phylogenetic foundation. It will remain to be revealed the degree to which these species of large *Tetrabothrius* among the Alcidae are related as a series of sister species representing a clade within a broader phylogenetic framework that comprises cestodes among the Aequornithae (core water birds—Gaviiformes, Procellariiformes + Sphenisciformes, Suliformes [Phalacrocoracidae, Sulidae, Fregatidae, Anhingidae] + Pelecaniformes [Pelecanidae and others]), Phaethontiformes, Podicipediformes, and other Charadriiformes, in addition to cetaceans and pinnipeds (e.g., Hoberg, 1996; see Jarvis et al. [2014] for entry to current higher avian phylogeny and taxonomy).

A Complex of *Tetrabothrius* Species among Alcidae

Specimens of *T. alcae* were discovered predominantly in common and thick-billed murrelets across a broad distribution encompassing 11 localities from the greater northern North Pacific, Bering Sea, Chukchi Sea, and northern Sea of Okhotsk (Table 2; Supplementary Data Table 3; Supplementary Data Table 4). Cestodes attributed to this species were rarely observed in other species of alcids and included specimens archived from 2 ancient murrelets, a pigeon guillemot, and a parakeet auklet (Supplementary Data Table 3, Supplementary Data Table 4). *Tetrabothrius alcae* is currently unrecognized in the Arctic basin and North Atlantic, although it is likely to have been confused with *T. jagerskioeldi* in prior inventories (e.g., Hoberg and Soudachanh, 2020).

A direct consequence of misidentification is revealed in errors that have emerged in redescrptions and the perpetuation of those conclusions in the literature that influence assumptions about host range (e.g., Baer, 1954;

Temirova and Skrjabin, 1978; Ryzhikov et al., 1985; Muzzafar and Jones, 2004). Specifically, specimen(s) in *Stercorarius parasiticus* (Linnaeus, 1758) from Chukotka, *Cephus carbo* from the Russian Far East, and *Fratercula arctica* (Linnaeus, 1758) from the Barents Sea appear to have contributed to a composite redescription of *T. jagerskioeldi* that likely includes the former taxon, *T. alcae* and another currently undescribed species (see Temirova and Skrjabin, 1978; Hoberg and Soudachanh, 2020). Our contention that the redescription of Temirova and Skrjabin (1978) represents a species chimaera is based on morphological incompatibility (as depicted in the figures from Temirova and Skrjabin) relative to the original type series of *T. jagerskioeldi* and other validated specimens from the North Pacific (discussed in Hoberg and Soudachanh, 2020). Resolving sources for these specimens is also complicated. Specimens in parasitic jaeger appear to be from Chukotka (village of Enurmino, Chukotka Autonomous Okrug, Russia, ca. 66°56'44.80"N, 171°49'29.99"W, based on Temirova and Skrjabin, 1978) rather than Seven Islands, East Murman (as suggested in Hoberg and Soudachanh, 2020), and the original collector is undetermined. Cestodes in *C. carbo*, presumably from the Okhotsk or adjacent seas, are likely attributable to Belopol'skaia (1963a, 1963b), whereas those in Atlantic puffin from the Barents Sea were from earlier collections (Belopol'skaia, 1952).

Absence of archival vouchers, misattribution, and inattentive identification with subsequent uncritical duplication of published records serve to confound our perspective for host and geographic range (e.g., Muzzafar and Jones, 2004). Prior collections attributed to *T. jagerskioeldi* in *Cephus grylle*, *Alca torda*, *Uria aalge*; *Fratercula arctica*; and *Stercorarius parasiticus* from the Seven Islands, Gosudarstvennogo Zapovednik in the Barents Sea, were unaccompanied by morphological descriptions, and any vouchers were later destroyed accidentally (Belopol'skaia, 1952).

Reports of *T. jagerskioeldi* in species of murre (*U. aalge* and *U. lomvia*) appear likely to represent *T. alcae* (e.g., Threlfall, 1971; Belopol'skaia, 1952). Substantiated records of *T. jagerskioeldi* indicate a Holarctic oceanic distribution principally among 3 species of *Cephus* guillemots across a minimum of 15 insular localities based on recognized specimens (Nybelin, 1916; Baylis, 1919; Hoberg and Soudachanh, 2020). Archival specimens, aside from those among the *Cephini* are limited to a single cestode in *U. aalge* at Shuyak Island (Gulf of Alaska), 9 cestodes in *B. marmoratus* at Kodiak Island (Gulf of Alaska), and one in *C. monocerata* from pelagic waters south of the western Aleutian Islands (Table 2; Supplementary Data Table 3). Beyond the Alcidae, in the North Pacific basin *T. jagerskioeldi* is known from a single specimen in *Urile*

pelagicus (Pallas, 1811) (at Buldir Island) and from multiple specimens in *Larus glaucescens* Naumann, 1840 (at Puffin Island and Central Island in the Gulf of Alaska) (Hoberg and Soudachanh, 2020).

A paucity of archived voucher specimens from prior field collections that reported *T. jagerskioeldi* among murre, guillemots, other alcids, and marine charadriiforms from the North Pacific, Arctic, and North Atlantic hinders direct attribution of species identity within the complex (e.g., Belopol'skaia, 1952, 1963a, 1963b; Baer, 1956; Threlfall, 1971; Smetanina, 1979, 1981; Temirova and Skrjabin, 1978; Kuklin and Kuklina, 2005). It seems remarkable that *T. alcae*, *T. sinistralis*, and a cryptic complex had remained unrecognized for the past century, given that these species are unequivocally differentiated by multiple suites of unique structural attributes relative to *T. jagerskioeldi* (Table 1) (Hoberg and Soudachanh, 2020). It is apparent that *T. alcae*, *T. jagerskioeldi*, and *T. sinistralis* may occur in sympatry but with minimal overlap in the faunas associated with murre (Alcini) and guillemots (*Cephini*) (Table 2; Supplementary Data Table 3). Current records for *T. sinistralis* are insufficient to document the actual limits for host and geographic distribution, although this species minimally occurs across the Holarctic with specimens in *C. grylle* from Greenland and *C. columba* from the Bering Sea (Table 2).

Defining Diversity among Tetrabothriids

Complex historical, biological, and physical oceanographic drivers provide explanations of diversity and faunal assembly in tetrabothriid faunas (Hoberg, 1995; Hoberg and Adams, 2000; Hoberg and Brooks, 2008). Deep phylogenetic inference within the Eucestoda, relative to the Cyclophylloidea, indicates considerable age, duration, persistence, and extensive diversification for this fauna among marine birds attributable to episodes of host colonization (Hoberg et al., 1997; Hoberg, Gardner, et al., 1999; Hoberg, Jones, et al., 1999; Hoberg et al., 2001; Caira et al., 2014). Further, episodes of colonization in conjunction with cophylogenetic processes (where cophylogeny is not a synonym for cospeciation—see Brooks et al., 2019), may also determine the foundations of faunal structure for species of *Tetrabothrius* among orders, families, and subfamilies of core water birds (Hoberg, 1989, 1996). The extent and chronology of switching events within cophylogenetic histories of association among genera and species occurring in seabirds, pinnipeds, and cetaceans have yet to be completely elucidated, although colonization appears to be a major component of diversification (Hoberg, 1995; Hoberg, Gardner, et al., 1999; Hoberg and Brooks, 2008; Araujo et al., 2015; Brooks et al., 2019).

Circulation of species of *Tetrabothrius* among alcids (and a larger assemblage of parasites and marine homeotherms) depends on capacity for infection by cestodes and host foraging behaviors and conditions influenced by foodwebs and prey availability that determine opportunity spatially and temporally. Ecological partitions emerging in fitness space can influence host range and are evident across spatial and temporal scales. Ecological interactions directly and indirectly influence connectivity within foodwebs and are seen in (1) aspects of foraging behavior and capacity (distance, depth, time); (2) taxonomic prey spectrum (e.g., adult and larval fishes, macro- and micro-zooplankton, cephalopods, and other invertebrates); (3) prey selection, size, and availability (diel and vertical spatial patterns); and (4) physical oceanographic conditions (water mass structure, zonation, temperature, nearshore and offshore upwelling, advection and current regimes, frontal zones and eddies in relation to islands, and marine stratification and sea ice, especially in the Sea of Okhotsk and Bering Sea) (e.g., Ainley, Strong, et al., 1990; Springer et al., 1999; Piatt and Springer, 2003; Sydeman et al., 2017; Hunt et al., 2018; Piatt et al., 2018, 2020). Regional and seasonal dynamics are at play with shifts by foraging seabirds among and between diverse prey resources over space and time (Ainley, Strong, et al., 1990; Hunt et al., 2018; Kitasky and Hunt, 2018). Ocean-atmosphere interactions, including the shifting thermal regimes of the El Niño Southern Oscillation and the Pacific Decadal Oscillation, further influence marine productivity, temporal and spatial restructuring of foodwebs, and the potential for continuity in life history and life cycles for assemblages of marine parasites (e.g., Chavez et al., 2003; Anderson and Piatt, 1999; Hoberg, 1996, 2005; Mouritsen and Poulin, 2002; Sydeman et al., 2012, 2015; Hoberg et al., 2017). Persistent high-temperature anomalies, or marine heat waves, emerging from global warming are shifting the overall structure and phenology of foodwebs (Schultz et al., 2009; Piatt et al., 2020; Suryan et al., 2021). Changing trajectories, which are now being recognized across the greater North Pacific ecosystem under climate forcing, may constitute physical and biological tipping points (e.g., Lenton et al., 2008, 2019; Brovkin et al., 2021) and are resulting in large-scale mortality events for seabirds and marine mammals (e.g., Jones et al., 2018, 2019; Piatt et al., 2020). These factors of marine biological structure, diversity, and conditions within foodwebs are predicted to either facilitate or dampen transmission dynamics and occurrence of marine parasites, driving previously unrecognized associations and distributions among invertebrate, piscine, and avian hosts (e.g., Hoberg, 1996, 2005; Hoberg et al., 2017; Hoberg and Soudachanh, 2020).

The dynamics of prey resources exploited by seabirds vary biogeographically (Piatt et al., 2018). Availability and prey selection by diverse assemblages of resident breeding and migratory seabirds will be strongly influenced by marine province or domain. Seabirds rely on a broad assemblage of potential prey species but generally exploit a narrow array of piscine and invertebrate species spatially and oceanographically and relative to the breeding cycle (e.g., Ainley and Sanger, 1979). Seasonally the greater North Pacific is not homogeneous; consequently, conditions in the subarctic pelagic domain will be different relative to the Sea of Okhotsk, the Aleutian Arc, islands of the Bering Sea and Chukchi Sea, Gulf of Alaska, and province of the California Current (e.g., Ainley and Sanger, 1979; Hunt, Burgeson, et al., 1981; Hunt et al., 2018; Ogi, 1982; Springer et al., 1999; Piatt and Springer, 2003; Paredes et al., 2012; Piatt et al., 2018). For example, in the upwelling system of the Farallones (California Current), breeding alcids and migrating sooty shearwaters are dependent on what has been termed the “juvenile rockfish economy,” which can drive extensive overlaps in foraging and diets (Ainley, Strong, et al., 1990). In contrast, in systems strongly influenced by advection in the Bering Sea, Aleutian Islands, and northern Gulf of Alaska, distinctly different assemblages of pelagic fishes, zooplankton, and cephalopods are critical resources (e.g., Ainley and Sanger, 1979; Hunt, Burgeson, et al., 1981; Schneider and Hunt, 1982; Springer et al., 1999; Piatt and Springer, 2003; Sydeman et al., 2017).

Diverse potential prey resources across space and time lead us to ask about the common elements of these systems that may contribute to continuity of life cycles for a multispecies complex of *Tetrabothrius* tapeworms on broad oceanographic scales. How do these relationships change across oceanographic provinces and in a regime of warming and extreme events (e.g., Hunt et al., 2018; Sydeman et al., 2017; Kitaysky and Hunt, 2018; Piatt et al., 2020)? This is the interface, viewed through a Darwinian lens, for the nature of the organism and the nature of the conditions that interact in processes of faunal assembly over time (e.g., Brooks et al., 2019; Agosta and Brooks, 2020). Fundamental fitness space—the potential for these cestodes to utilize resources across diverse marine avian species—appears broad, whereas realized fitness space and the actual array of host species that are accessed may be restricted or facilitated at any point in time. These complex relationships in sloppy fitness space that link parasites, invertebrate and piscine intermediate (and paratenic) hosts, and seabirds are reflected through realized host range, an outcome of ecological fitting and oscillation in any particular slice of ecological time (e.g., Agosta et al., 2010; Hoberg et al., 2017; Brooks et al., 2019).

Alcid Tetrabothrius Are Rare

Alcids and cestodes of the *T. jagerskioeldi*-complex are restricted to cold marine systems of advection and upwelling along coastal margins adjacent to the continental shelf or are associated with archipelagos (especially the Aleutians), isolated islands, and rocky headlands of the Bering Sea, Chukchi Sea, Gulf of Alaska, Sea of Okhotsk, and Sea of Japan. Especially important is the eastern boundary current (with an upstream connection to the cold Kurishio Current and the West Wind Drift south of the Aleutians) that extends along the narrow continental shelf on the western coast of North America (Ainley, 1990). As a zone of spectacular marine productivity, these marine provinces support great diversity and populations of breeding alcids, larids, phalacrocoracids, and some procellariids and hydrobatids, while serving as seasonal migration corridors for procellariiforms and other seabirds (Hunt, Burgeson, et al., 1981; Hunt, Eppley, et al., 1981; Hunt, Gould, et al., 1981; Ainley, 1990; Piatt and Springer, 2003). Amphi-Pacific distributions among Alcidae, bounded by cold water systems from the Sea of Japan to the southern reaches of the northeastern Pacific along the California Current (and the seas of the Arctic basin into the North Atlantic), constitute the smallest (most restricted) oceanic range of any seabird group. Transmission for cestodes and persistence of this fauna is expected to be associated with pelagic and neritic systems adjacent to colony sites in zones where critical prey species are concentrated or secondarily dispersed downstream by predictable advective processes and become available to foraging birds (e.g., Hoberg, 1995, 1996, 2005). Life cycles are completed across the extent of the oceanographic distribution for Alcidae and this assemblage of *Tetrabothrius*. Focal zones or metaphorical islands of transmission (concentrating prey, infected intermediate hosts, and seabirds) are indicated by recency of infections and cestodes with scolexes and strobila in early stages of ontogeny collected from multiple hosts, host species, and age classes associated with colony sites spanning the greater North Pacific basin, Bering Sea, and Chukchi Sea (Figs. 50–61; Supplementary Data Table 3; Supplementary Data Table 4). Focality in transmission is consistent with birds returning to predictable regions where foraging has been successful on varying temporal/spatial scales in the context of frontal zones, upwelling, ice edges, and prey aggregations, such as spawning shoals of fishes, zooplankton, or cephalopods (Woo et al., 2008; Elliot et al., 2009; Paredes et al., 2012; Harding et al., 2013; Hunt et al., 2018).

Our inventory indicates that these cestodes occur infrequently when assessed across all species of alcids examined; for *T. alcae* (53 of 1,345 alcids, 4%), *T. sinistralis* (1

of 1,345, <1.0%), and *T. jagerskioeldi* (14 of 1,345, ~1.0%). This obscures the occurrence (and greater prevalence) of respective cestode species within a limited spectrum of hosts, or within particular age classes of a host species (e.g., murre and *T. alcae*; guillemots and *T. jagerskioeldi*) as outlined previously. Among these species of the complex, only *T. jagerskioeldi* has been shown unequivocally (based on validated specimens) to infect avian hosts in other families, including a larid and a phalacrocoracid (Hoberg and Soudachanh, 2020). Absolute (or realized) host range (here the number of species infected) is similar for *T. alcae* (5 species of alcids; most prevalent among 2 species of *Uria*, overall, 11.5%) and *T. jagerskioeldi* (6 alcids; most prevalent among 3 species of *Cephus*, overall, 32%; also in single species of *Urile* Bonaparte, 1855 (see also *Phalacrocorax* Brisson, 1760 and *Sticticarbo* Bonaparte, 1856) and *Larus* Linnaeus, 1758, although the spectrum of host diversity differs (Table 2). These patterns of occurrence parallel the distribution of large *Tetrabothrius* spp. (reported as *T. jagerskioeldi*) among adults of other alcid host species and across oceanographically widespread localities spanning Holarctic seas, where prevalence rarely exceeds 10% and infections are of low intensity (only exceptionally >1–2 cestodes in individual hosts) (e.g., Belopol'skaia, 1952; Threlfall, 1971; Smetanina, 1979, 1981).

Recognition of a cryptic complex emphasizes the rarity of broad host range for any species in this assemblage. Cestode species appear limited to particular subfamilies and tribes within the Alcidae in an arena defined by the dimensions of opportunity (e.g., Alcinae—including Alcini [*T. alcae*] and Cepphini [*T. jagerskioeldi* and *T. sinistralis* (?)]) or Fraterculinae—including Fraterculini and Aethiini [*Tetrabothrius* n. sp., undescribed]). These patterns are also consistent with the distribution and occurrence for species of *Alcataenia* Spasskaia, 1971 (distantly related cyclophylloidean tapeworms in alcids and larids) among murre and a broader assemblage of sympatric alcids in the Holarctic (e.g., Hoberg, 1984, 1992b). For example, as we have noted, *T. jagerskioeldi* occurs primarily among 3 species of guillemots while having a capacity to infect other alcids and nearshore or shelf-edge seabirds minimally, including marble murrelets, rhinoceros auklets, common murre, a larid, and a phalacrocoracid. Likewise, *T. alcae* occurs primarily among 2 species of murre with a capacity to infect a broader assemblage of alcids (e.g., parakeet auklets, ancient murrelets, and pigeon guillemots) based on opportunity.

These patterns demonstrate that host range and transmission among these cestodes is defined by opportunity. Differences in prevalence for *T. alcae* between common and thick-billed murre were not apparent, suggesting ecologically equivalent (but not identical) sources and pathways

for transmission over wide expanses of the North Pacific basin. Variation in exploitation of piscine versus benthic invertebrates as prey does not appear to influence prevalence (see Swartz, 1967; Piatt and Springer, 2003). Essentially, these observations may serve to eliminate amphipods or euphausiids from consideration as intermediate hosts for *T. alcae*. Euphausiids, and particularly species of *Thysanoessa* Brandt, 1851 are recognized intermediate hosts for other cestodes among alcids (species of *Alcataenia*), suggesting these pelagic crustaceans may not be involved in life cycles and transmission among species of *Tetrabothrius* (e.g., Hoberg, 1984, 1996). Differences in prevalence for *Alcataenia* tapeworms in murrelets were attributed to prey selection and greater importance of euphausiids in diets of thick-billed murrelets in contrast to common murrelets from the central Bering Sea.

Murrelets are the dominant avian marine piscivores of the North Pacific, foraging near the continental margins across oceanic (pelagic) environments and over the continental shelf adjacent to colony sites (e.g., Piatt and Springer, 2003; Iverson et al., 2007; Piatt et al., 2018; Piatt et al., 2020). Thick-billed murrelets exploit pelagic fishes over shelf habitats and a wide diversity of oceanic prey, including euphausiids, amphipods, and squid (Ainley and Sanger, 1979). Common murrelets forage almost exclusively on pelagic schooling fish during the summer. Murrelets explore and exploit a greater range of habitats over wider areas and distances compared to guillemots, emphasizing a dependence on mid-depth fishes and midwater schooling prey (e.g., Ainley, Strong, et al., 1990; Boekelheide et al., 1990; Elliot et al., 2009; Piatt and Springer, 2003; Piatt et al., 2020).

Where data are available—for example, for *T. alcae* and murrelets—young birds (near the time of fledging) and subadults (~35% prevalence) are consistently infected with greater frequency than adult breeding birds (7%) (Supplementary Data Table 3). Differences in prevalence between adult birds and young prior to fledging may be expected as a generality (although data are elusive) and are consistent with field observations, indicating selective presentation of energetically valuable piscine prey to developing chicks by breeding birds (e.g., Tuck and Squires, 1955; Spring, 1968). In the high Arctic, adult thick-billed murrelets may forage on amphipods during incubation and then shift to high-energy fishes during chick rearing (Woo et al., 2008; Elliott et al., 2009). Similar disparities in prevalence between fledgling birds and adults for other species of *Tetrabothrius* among larid hosts [*Rissa tridactyla* (Linnaeus), *Larus schistisagus* Stejneger] have also been documented and are considered indicators of differential prey selection (or presentation) of fishes or zooplankton relative to host age (Hoberg, 1992a, 1996).

Guillemots demonstrate less variable foraging ranges in contrast to murrelets. Benthic-littoral fishes and shoals or aggregations of pelagic fishes are exploited through foraging in shallow nearshore and intertidal environments (e.g., Ainley and Sanger, 1979; Ainley, Boekelheide, et al., 1990; Litzow et al., 2004). Considerable selectivity may result in a narrow prey base at some sites and over periods of time (Ainley, Boekelheide, et al., 1990). Although data are minimal, such selectivity appears to extend across the chick-rearing period, and infections recognized for *T. jagerskioeldi* may be more prevalent in young birds versus breeding adults (see Belopol'skaia [1952] for large *Tetrabothrius* in black guillemots). Further, outcomes of prey selection may be compounded by dissimilarities in zooplankton exploited by pelagic and or demersal forage fishes, and variation in these trophic links, relative to avian hosts, could influence potential transmission pathways for cestodes and other parasites. Relative ecological isolation among murrelets, guillemots, and their respective prey assemblages, or factors that determine opportunity through foodwebs and spatial distribution, may have explanatory power for understanding the host ranges for *T. alcae* and *T. jagerskioeldi*, with parasites secondarily revealing insights about the structure of the North Pacific marine ecosystem.

Tetrabothrius in the North Pacific System

Abundance for species of *Tetrabothrius* among alcid hosts is low, prevalence is limited, and cestodes were not demonstrated at all oceanic or geographic sites where intensive sampling was conducted (Supplementary Data Table 2; Supplementary Data Table 3). Sampling error and uneven collections across localities could influence these observations. It is apparent, however, that annual to decadal variation may occur in the diversity and distribution of large *Tetrabothrius* tapeworms among alcids across and within oceanographic provinces (e.g., Hoberg et al., 2013; compare Threlfall [1971] and Muzzafar [2009] for marine systems from the eastern Canadian Arctic to west Greenland; see Belopol'skaia [1952], Galaktionov [1995], and Kuklin and Kuklina [2005] for Barents Sea and East Murman). Fundamentally, this reflects temporal disparities in physical and biological oceanographic determinants for marine productivity, prey spectrum, and availability on regional, provincial, and local scales over time (e.g., Ainley, 1990; Ainley, Strong, et al., 1990; Anderson and Piatt, 1999; Sydeman et al., 2017; Piatt et al., 2018; Hunt et al., 2018). Consequently, the diets of seabirds (at least during breeding cycles) depend on the oceanographic location of a colony site in a physically and biologically heterogeneous ocean (Schneider and Hunt, 1982) which secondarily defines a window of time in which parasite transmission is occurring (e.g., Hoberg, 1996, 2005).

Table 3. Specimens and Localities for Procellariiformes Infected with Species of *Tetrabothrius* from the Greater North Pacific during the Boreal Summer

| Species/Localities ^{1,2} | Number of Hosts ³ |
|--|------------------------------|
| <i>Ardenna creatopus</i> (Coues, 1864) / Pink-footed Shearwater | |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 8 September 1982 | 8 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 31 August 1985 | 20 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 21 August 1987 | 5 |
| <i>Ardenna bulleri</i> (Salvin, 1888) / Buller's Shearwater | |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 31 August 1985 | 1 |
| <i>Ardenna tenuirostris</i> (Temminck, 1836) / Short-tailed Shearwater | |
| Central Bering Sea and Bristol Bay, Bering Sea, Alaska (56°37'N, 170°26'W to 56°55'N, 159°49'W) / August–September 1976 | 4 |
| Kodiak Island region, Gulf of Alaska / June–September 1977 | 23 |
| Western Aleutians, Pelagic / 1981 | 3 |
| Sarichev Island, Shishmaref, Alaska, Chukchi Sea (ca. 69°13'59"N, 166°07'28"W) / August 2019 | 7 |
| <i>Ardenna grisea</i> (Gmelin, 1789) / Sooty Shearwater | |
| Kodiak Island region, Gulf of Alaska / June–September 1977 | 3 |
| Western Aleutians, Pelagic / 1981 | 1 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 31 August 1985 | 1 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 21 August 1987 | 2 |
| <i>Fulmarus glacialis</i> (Linnaeus, 1761) / Northern Fulmar | |
| Bristol Bay, Alaska, Bering Sea / May 1970 | 1 |
| Nunivak Island, Alaska, Bering Sea / 30 August 1949 | 1 |
| Central Bering Sea and Bristol Bay, Bering Sea, Alaska (56°37'N, 170°26'W to 56°55'N, 159°49'W) / August–September 1976 | 1 |
| Western Aleutians, Pelagic / 1981 | 4 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 31 August 1985 | 1 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 21 August 1987 | 6 |
| <i>Oceanodroma furcata</i> (Gmelin, 1789) / Fork-tailed Storm Petrel | |
| Western Aleutians, Pelagic / 1981 | 3 |
| Western Aleutians, Pelagic, south of Tanaga and Adak Island / 1982 | 3 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 8 September 1982 | 2 |
| <i>Phoebastria nigripes</i> (Audubon, 1839) / Black-footed Albatross | |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 8 September 1982 | 1 |
| Grays Marine Canyon, Washington State, Eastern North Pacific / 21 August 1987 | 2 |

Specimens Examined = 103

Species Examined = 7

Notes:

¹Localities correspond to those outlined in Supplementary Data Tables 2 and 3, except Sarichev Island, Shishmaref, Alaska, in 2019, which is noted in the current table.

²Host voucher specimens from Grays Marine Canyon are held in the Burke Memorial Washington State Museum.

³Prevalence for species of *Tetrabothrius* cannot be accurately determined for all host species and localities based on these collections. Prevalence approached 100% in most species and localities, and specimen numbers above reflect all procellariiforms in which *Tetrabothrius* was found or collected.

We can provisionally begin to explore the limits on host and spatial range with explanations about rarity, low abundance, and insular occurrence within an otherwise extensive and simultaneously patchy oceanographic distribution for these species of *Tetrabothrius* among Alcidae. How do rare species of parasites become oceanographically widespread, as is apparent for the *T. jagerskioeldi*-complex in an open system defined by degrees of dilution? Resolving these contrasting observations is at the interface for physical and biological processes: (1) Are there ecologically equivalent but taxonomically diverse zooplankton, cephalopod, and piscine taxa with capacities to serve as appropriate hosts (compatibility across a host assemblage) in varying oceanographic provinces in the context of ecological fitting? In this sense, capacity is equated with compatibility under the perspective of all species (intermediate and definitive) involved in an association. (2) Are there widespread but rare prey species that consistently serve as an assemblage of intermediate host(s) across oceanographic domains? (3) Does rarity reflect dilution by distance from an island focus (colony site) and as an outcome of dispersed but central-place foraging in neritic and pelagic waters (Hoberg, 1996; Elliott et al., 2009; Harding et al., 2013)? and/or (4) Are infections influenced through dilution by advection downstream that may determine the distribution of infective stages in the water column and infected intermediate hosts at increasing distances from islands and foraging zones (Hoberg, 1995)? (5) What are the parameters of passive advection and dispersal for parasites (e.g., Piatt and Springer, 2003) in contrast to connectivity mediated by highly vagile seabirds (see parallels to species of *Anophryocephalus* Baylis, 1922 cestodes in northern pinnipeds; Hoberg, 1995). In this context, when do intermediate and potential paratenic hosts become infected and when are these competent in transmission pathways? Completion of these marine life cycles may be influenced by the limits on foraging behavior, feeding capacity (e.g., physical limitations on particle size or prey dimensions for foraging), and food selection by zooplankters, larval and adult fishes, and cephalopods of different age and size classes and life history patterns at the interface with seabird hosts (e.g., Hoberg, 1996). These are the dimensions in sloppy fitness space for developing metacestodes and opportunity that circumscribes the potential for infections in avian hosts and which defines realized host range within the broader extent of fundamental fitness space (Brooks et al., 2019). Multiple transmission pathways, through ecological fitting, may characterize particular oceanic provinces related to distinct assemblages of invertebrate, piscine, and avian diversity (e.g., Springer et al., 1996; Piatt et al., 2018).

Complexity and Considerations within a Larger Fauna

Prevalence revealed among species of the *T. jagerskioeldi*-complex in alcids is considerably lower than that seen for an assemblage of *Tetrabothrius* among resident species of Laridae and resident and migratory species of Procellariiformes, which may occur in sympatry (e.g., Hoberg, 1992a, 1996; Hoberg and Soudachanh, 2020; Supplementary Data Table 3; Table 3). No matter the species reported—for example, most published inventory records reported as *T. jagerskioeldi* are expected to be largely incorrect—prevalence of large *Tetrabothrius* is largely consistent with a picture of infrequent occurrence in Holarctic alcids. Currently, species typical of a *Tetrabothrius* fauna among Holarctic Laridae (e.g., *T. erostris* and *T. cylindraceus*) are rarely observed among alcids (Hoberg and Soudachanh, 2020); other high-latitude species such as *T. morschtini* have not been recognized in alcids (Murav'eva, 1968; Temirova and Skrjabin, 1978; Galkin, 1994; Hoberg and Soudachanh, 2020). Additionally, species reported in the literature in alcid hosts, including *T. macrocephalus*, have not been directly confirmed based on archived specimens.

Faunas are ecologically segregated and appear spatially structured between nearshore and pelagic environments; substantial differences in diversity, abundance, and prevalence of infection are apparent. For example, large larid gulls (species of *Larus*), with eclectic foraging in neritic and littoral waters and relative proximity to intertidal systems, generally support assemblages of high prevalence (often near 100%) and intensity of infection for multiple species of *Tetrabothrius*, in addition to helminth faunas of great diversity (e.g., Belogurov, 1966; Belogurov et al., 1968; Hoberg, 1992a, 1996, 2005). A departure from this spatial/ecological relationship for helminth diversity in larids is demonstrated among kittiwakes, *Rissa tridactyla*, which forage in pelagic environments and support considerably lower species diversity and prevalence of infection for helminths (summarized in part by Hoberg, 1992a, 2005; Hoberg and Soudachanh, 2020; Supplementary Data Table 3). Patterns of pelagic foraging among these disparate groups of seabirds may explain diversity, relative to nearshore environments, although prevalence and abundance of cestodes among procellariiform hosts appears to be an exception.

Cestodes of the *T. jagerskioeldi*-complex, based on current collections, are absent among resident and transient procellariiform seabirds in the North Pacific basin during the boreal summer (Supplementary Data Table 3). Species of shearwaters including sooty [*Ardenna grisea* (Gmelin, 1789)], short-tailed [*A. tenuirostris* (Temminck, 1836)], and pink-footed [*A. creatopus* (Coues, 1864)] are oceanographically wide-ranging seabirds that breed deep in the southern hemisphere during the austral summer. Subsequently,

following dispersal from colony sites and northward (transequatorial) migration from the southern oceans, shearwaters become a dominant component of the avifauna on neritic and pelagic waters of the subarctic North Pacific and Bering Sea during the boreal summer (Hunt, Gould, et al., 1981; Ogi, 1982). Distributions for a larger assemblage of resident procellariiforms—for example, northern fulmars [*Fulmarus glacialis* (Linnaeus, 1761)], fork-tailed [*Oceanodroma furcata* (Gmelin, 1789)] and Leach's [*O. leucorhoa* Vieillot, 1818] storm petrels, black-footed [*Phoebastria nigripes* (Audubon, 1939)] and Laysan [*P. immutabilis* (Rothschild, 1893)] albatrosses—alcids, larids, and stercorariids, are regionally to locally abundant, becoming sympatric with these species of *Ardenna* seasonally and during migration (e.g., Hunt, Gould, et al., 1981; Chu, 1982; Ogi, 1982).

In the North Pacific and Bering Sea, high prevalence, approaching 100%, with intensity of infection often exceeding 100–200 cestodes in individual hosts, characterized multiple species of *Tetrabothrius* in a diverse assemblage, but relatively limited sample, of pelagic foraging shearwaters and other procellariiforms (Table 3; E.P. Hoberg, unpublished data). These distributions are in contrast to the rarity of cestodes attributed to the *T. jagerskioldi*-complex in alcids (Supplementary Data Table 3); respective cestode faunas remain strongly segregated. Although requiring complete evaluation, species in this tetrabothriid fauna among shearwaters appear distinct from those circulating respectively among alcids and larids and other seabirds that occur in sympatry during the boreal spring, summer, and autumn (E.P. Hoberg, unpublished data).

Faunas explored in great shearwaters [*A. gravis* (O'Reilly, 1818)] from the Atlantic basin serve to emphasize the minimal overlap in cestode species that circulate in the northern and southern hemispheres among migratory and resident procellariiforms (Hoberg and Ryan, 1989). Cestode diversity is represented by different species assemblages in the southern and northern hemispheres with transmission circumscribed by breeding cycles associated with isolated colony sites. Among great shearwaters, the major component of cestode diversity was derived from the South Atlantic Ocean adjacent to breeding grounds (on Gough Island) during the austral spring and summer: 100% prevalence with maximum intensity of infection exceeding 4,000 cestodes in individual hosts. Transequatorial migration from the south brings different assemblages into sympatry, although contact among avian hosts in common foraging zones does not apparently result in colonization by parasites; for example, no species or other elements of these faunas are shared among procellariiforms, larids, and alcids. Inventory data suggested a sequential loss of some elements of this fauna in shearwaters, without replace-

ment, during northward migration and during a period of residency in the North Atlantic (Hoberg and Ryan, 1989; Hoberg, 1996). Despite common trophic resources seasonally exploited by shearwaters, alcids, and larids across the greater North Pacific, these cestode faunas may circulate through ecologically segregated pathways with minimal exchange (Ainley and Sanger, 1979; Ogi, 1982; Chu et al., 1982). Collectively, these observations are consistent with the considerable abundance of tetrabothriid cestodes in pelagic foraging procellariiform seabirds. Concurrently, strong ecological and historical segregation among major groups of marine birds may limit or facilitate opportunity that partitions parasite diversity on regional or provincial scales (see also Hoberg, 1995; Hoberg and Adams, 2000).

Narrow host range with minimal overlap for elements of this fauna are consistent with outcomes of episodes of oceanographic expansion (exploration and host colonization) alternating with bouts of isolation in refugial zones (exploitation and coadaptation) through the late Tertiary period (e.g., Hoberg, 1992b; Hoberg et al., 2012, 2017). Faunal dynamics can be explained within the context of the Stockholm paradigm (e.g., Hoberg and Brooks, 2008; Araujo et al., 2015; Brooks et al., 2019; Agosta and Brooks, 2020). Faunal assembly represents the outcomes of oscillating climate, shifting ranges (breakdown in isolation, ecological fitting, and exploration modes for cestodes), and the changing interfaces for resource availability maintained by trophic and habitat overlaps. Dynamics of these ecotones constitute the nexus of opportunity and capacity for infection among avian hosts in which capacity appears broad and opportunity is ecologically restricted in space and time. Multiple life history pathways are tied to trophic associations and dynamics at mesoscales across marine domains and provinces (consider Gulf of Alaska, Bering and Chukchi Sea, high-latitude gyre systems) (Springer et al., 1996, 1999; Piatt et al., 2018). Resilience and connectivity through ecological fitting strongly suggest the influence of multiple trophic pathways for transmission and persistence (including a history of diversification) of this complex fauna (differing assemblages of zooplankton, fishes, and cephalopods depending on locality, oceanographic conditions, and temporal variability) (e.g., Sydeman et al., 2017; Piatt et al., 2018, 2020).

Returning to the *T. jagerskioldi*-complex, transmission occurs across the extent of the greater Pacific basin (Sea of Okhotsk, Bering Sea, Chukchi Sea, Aleutian Arc, Gulf of Alaska, and California Current systems). These are oceanographically definable domains or provinces (characterized by water mass, advection, and upwelling) with distinct but ecologically equivalent assemblages of zooplankton, cephalopods, and fishes. Provincial-level foodwebs are the foundations for prey selection and resource use by particular

seabirds (e.g., Ainley and Sanger, 1979; Piatt and Springer, 2003; Sydeman et al., 2017; Piatt et al., 2018). Relatively few prey elements are in common or occur consistently across all marine domains. There is broad capacity, however, for completion of life cycles for cestodes across all domains, with transmission circumscribed by breeding cycles and oceanographic location of colonies. These observations are compatible with transmission being limited by opportunity, in the context of partitions in the distribution of tapeworms among particular marine birds (e.g., murre and guillemots), which are to a degree ecologically segregated. Persistence for species of *Tetrabothrius* is driven by a particular host genus, with broad fundamental fitness space (capacity) indicated by sporadic infection in other alcids in sympatry. These interactions describe the relationship of fundamental fitness space (and potential host range), realized fitness space and outcomes for ecological fitting in sloppy fitness space in faunal assembly, and diversification over time as predicted under the Stockholm paradigm (Agosta et al., 2010; Brooks et al., 2019; Agosta and Brooks, 2020).

Alcid tapeworms circulate under the dynamics of capacity (potential observed for broad multispecies host assemblages) with limits imposed by ecological opportunity. Changing conditions, especially ecological perturbations driven by climate oscillations, directly determine production cycles and distributions of micro- and macro-zooplankton, forage fishes, cephalopods, and trophic structure in high-latitude marine ecosystems. Ocean-atmosphere oscillations—or regime shifts from cold to warm cycles, such as the El Niño Southern Oscillation, Pacific Decadal Oscillation, and the North Atlantic Oscillation—drive one scale of episodic ecological reorganization that will influence foodwebs and the potential for persistence and transmission of marine parasites (e.g., Piatt et al., 1998; Anderson and Piatt, 1999; Hurrell et al., 2003; Chavez et al., 2003; Sydeman et al., 2012; Hoberg et al., 2017; Hoberg and Soudachanh, 2020). Climate and ocean warming can drive the potential for local to regional shifts in the host and geographic distribution of this parasite fauna (e.g., Hoberg and Soudachanh, 2020).

Environmental perturbation is a driver of faunal change, in part reflected in persistence through origins of new host and geographic associations, or under catastrophic disruption a context for extirpations and extinctions (Hoberg and Brooks, 2008; Stigall et al., 2017; Brooks et al., 2019; Agosta and Brooks, 2020). Changing conditions that alter opportunity space may lead to broadening of host range, such that when the original host(s) become extinct, the parasite(s) will survive, a principal demonstrated across evolutionary and ecological time in persistence of complex parasite-host assemblages through ecological fitting and colonization

(e.g., Hoberg and Brooks, 2008; Brooks et al., 2019). As a generality, species that persist through major episodes of environmental disruption are those that can leave their original habitats and survive elsewhere based on conserved capacities under a regime of new opportunity (Stigall, 2010, 2012; Stigall et al., 2017; Agosta and Brooks, 2020). In the context of perturbations in the North Pacific ecosystem, such alterations that result in a significant loss of avian species diversity, coincident with a broader reorganization of ecological structure, could produce a small number of surviving avian hosts that support a diverse assemblage of parasites that were not each other's closest relatives, although they might be "related." Under cophylogenetic assumptions, these findings would be consistently misinterpreted as "cophylogeny = cryptic cospeciation" and therefore massive coextinction (Brooks et al., 2019). Consequently, temporal and spatial faunal baselines explored in a backdrop derived from phylogeny can reveal trajectories and new patterns of faunal assembly over time and provide direct insights about systems under dynamic change (e.g., Brooks et al., 2014).

During the past two to three decades, anthropogenic forcing and extensive climate-driven shifts in ecosystem structure have emerged across the greater North Pacific and the provinces of the California Current, Aleutian Arc, Gulf of Alaska, and Bering Sea. Widespread failures of forage fish and high-energy zooplankton, with direct consequences for persistence and reproductive success for marine birds, have been a general outcome for restructuring of nektonic communities (e.g., Schultz et al., 2009; Piatt et al., 2020; Suryan et al., 2021). Persistent high-temperature anomalies, as exemplified by the extreme marine heatwave that unfolded over the years 2014–16, are transforming the entire structure of high-latitude foodwebs, leading to shifts in latitudinal composition and abundance of zooplankton, fishes, and cephalopods, which may reflect cascading physical and biological tipping points (e.g., Jones et al., 2019; Piatt et al., 2020; Suryan et al., 2021; Brovkin et al., 2021). Cascades unfolding from an acceleration in climate forcing and oscillation in marine habitats, with shifting thermal balances and resulting environmental sloshing, are analogous to processes observed in terrestrial systems (Kafle et al., 2020). These expanding regimes of accelerating change emphasize the critical importance of field collections, archives, and baselines to assess biological outcomes across temporal and spatial scales (e.g., Hoberg et al., 2013; Brooks et al., 2014; Dunnum et al., 2017; Cook et al., 2017). Parasite assemblages reveal macro- to meso-scale connectivity serving as adjuncts and proxies in recognizing and understanding outcomes for episodes of environmental oscillation and directional atmospheric and oceanic warming

in marine ecosystems (e.g., Hoberg, 1996; Springer et al., 1996, 2007; Hoberg et al., 2013; Hoberg et al., 2017; Piatt et al., 2018; Hoberg and Soudachanh, 2020).

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Supplementary Data follows.

Supplementary Data Table 1. Avian Specimens (Alcidae, Laridae, Stercorariidae, and Phalacrocoracidae) from the Greater North Pacific Basin Examined for Helminth Parasites (1949–2002)

| Species | Number |
|--|--------|
| Charadriiformes—Alcidae: | |
| (Subfamily Alcinae) | |
| Tribe Alcini | |
| <i>Alle alle</i> (Linnaeus) (dovekie) | 1 |
| <i>Uria aalge</i> (Pontoppidan) (common murre) | 276 |
| <i>Uria lomvia</i> (Linnaeus) (thick-billed murre) | 150 |
| Tribe Cepphini | |
| <i>Cepphus carbo</i> Pallas (spectacled guillemot) | 4 |
| <i>Cepphus columba</i> Pallas (pigeon guillemot) | 22 |
| <i>Cepphus grylle</i> (Linnaeus) (black guillemot) | 8 |
| Tribe Brachyramphini | |
| <i>Brachyramphus marmoratus</i> (Gmelin) (marbled murrelet) | 7 |
| <i>Brachyramphus brevirostris</i> (Vigors) (Kittlitz's murrelet) | 5 |
| Tribe Synthliboramphini | |
| <i>Synthliboramphus antiquus</i> (Gmelin) (ancient murrelet) | 51 |
| <i>Synthliboramphus scrippsi</i> (Green and Arnold) (Scripp's murrelet) | 4 |
| (Subfamily Fraterculinae) | |
| Tribe Aethiini | |
| <i>Ptychoramphus aleuticus</i> Brandt (Cassin's auklet) | 16 |
| <i>Aethia psittacula</i> (Pallas) (parakeet auklet) | 56 |
| <i>Aethia cristatella</i> (Pallas) (crested auklet) | 190 |
| <i>Aethia pygmaea</i> (Gmelin) (whiskered auklet) | 18 |
| <i>Aethia pusilla</i> (Pallas) (least auklet) | 63 |
| Tribe Fraterculini | |
| <i>Cerorhinca monocerata</i> (Pallas) (rhinoceros auklet) | 39 |
| <i>Fratercula cirrhata</i> (Pallas) (tufted puffin) | 286 |
| <i>Fratercula corniculata</i> (Naumann) (horned puffin) | 149 |
| Charadriiformes—Laridae: | |
| <i>Rissa tridactyla</i> (Linnaeus) (black-legged kittiwake) | 211 |
| <i>Rissa brevirostris</i> (Bruch) (red-legged kittiwake) | 2 |
| <i>Larus hyperboreus</i> Gunnerus (glaucous gull) | 13 |
| <i>Larus glaucescens</i> (Naumann) (glaucous-winged gull) | 67 |
| <i>Larus schistisagus</i> Stejneger (slaty-backed gull) | 27 |
| <i>Larus argentatus</i> (Pontoppidan) (herring gull) | 12 |
| <i>Larus heermani</i> Cassin (Heerman's gull) | 6 |
| <i>Sterna paradisaea</i> Pontoppidan (Arctic tern) | 39 |
| <i>Onychoprion aleutica</i> (Baird) (Aleutian tern) | 6 |
| <i>Xema sabini</i> (Sabine) (Sabine's gull) | 34 |
| Charadriiformes—Stercorariidae: | |
| <i>Stercorarius pomarinus</i> Temminck (pomarine jaeger) | 14 |
| <i>Stercorarius parasiticus</i> (Linnaeus) (parasitic jaeger) | 4 |
| <i>Stercorarius longicaudus</i> Vieillot (long-tailed jaeger) | 19 |
| Suliformes—Phalacrocoracidae: | |
| <i>Urile pelagicus</i> (Pallas) (pelagic shag) | 36 |
| <i>Urile "kenyoni"</i> (Siegel-Causey) (Kenyon's shag) = <i>U. pelagicus</i> | 2 |
| <i>Urile urile</i> (Gmelin) (red-faced shag) | 34 |
| Specimens examined = 1,871 | |
| Species examined = 34 | |

Supplementary Data Table 2. Field Data with Georeferences, Dates, and Collectors for Specimens of Alcidae, Some Laridae, and Other Seabirds Examined for Helminth Parasites from the Greater North Pacific Basin (1949–2002)**Aleutian Islands, Alaska**

- Adak Island, Andreanof Islands, Bering Sea (ca. 51°53'N, 176°38'E)
May 1997 / D. Causey
- Amchitka Island, Constantine Harbor, Rat Islands, Bering Sea (ca. 59°30'N, 179°00'E)
12 March 1952 / R.L. Rausch (locality reported by RLR as Kurilof Harbor)
May 1976 / E.P. Hoberg
- Amukta Island, Traders Cove, Islands of the Four Mountains, Bering Sea (ca. 52°29'19"N, 171°15'30"W)
1 September 2002 / D. Causey
- Alaid Island, Semichi Islands, Bering Sea (52°45'46"N, 173°53'53"E)
August 1992 / D. Siegel-Causey
- Attu Island (Holtz Bay), Near Islands, Bering Sea (52°56'50"N, 173°11'31"E)
July 1991, August 1992 / D. Siegel-Causey
- Attu Island (Etienne Bay), Near Islands, Bering Sea (52°53'53"N, 172°34'56"E)
August 1992 / D. Siegel-Causey
- Gibson Islands, adjacent to Attu Island, Near Islands, Bering Sea (52°56'45"N, 173°16'15"E)
6 September 2002 / D. Causey
- Buldir Island, Bering Sea (ca. 52°21'N, 175°56'E)
July 1974 / C.P. Dau, G.V. Byrd, M.H. Dick
August 1975 / E.P. Hoberg
July 1982 / D. Forsell
August 1987 / D. Nysewander
August 1991 / D. Siegel-Causey
- Kiska Island, Kiska Harbor, Bering Sea (51°58'01"N, 177°33'50"E)
August 1992 / D. Siegel-Causey
- Nizki Island (Bozo Cove), Semichi Islands (52°44'28"N, 173°59'08"E)
August 1991 / D. Siegel-Causey
- Seguam Island, Andreanof Islands, Bering Sea (ca. 52° 19' 24" N., 172° 27' 58" W.)
31 August, 2002/ D. Causey
- Tanaga Island, Andreanof Islands, Bering Sea (ca. 51°47'34"N, 177°55'43"W)
3–4 September 1997 / D. Causey
- South of Western Aleutian Islands, Pelagic Habitat, North Pacific (ca. 50–51°N, 172–174°E)
June–July 1981 / P.J. Gearin
28 June 1981 / P.J. Gearin (50°52'4"N, 173°52'1"E)
14 July 1981 / P.J. Gearin (50°03'N, 173°08.6'E)
June 1982 / P.J. Gearin
16, 20 July 1982 / P.J. Gearin
- South of Tanaga Island and Adak Island, Pelagic Habitat, North Pacific
8 July 1982 / P.J. Gearin
- Ulak Island, Andreanof Islands, Bering Sea (ca. 51°21'54"N, 178°56'50"W)
3 September 2002 / D. Causey

(Continued)

Supplementary Data Table 2. (continued)

Arctic Basin and Chukchi Sea

- Little Diomede Island, Bering Strait (65°45'42"N, 168°57'06"W)
15 August 1984 / L. Lowry
- Utqiagvik Alaska (originally as Point Barrow), Chukchi Sea (71°16'N, 156°50'N)
May 1958 / R.L. Rausch
August 1979 / J. Homan
- Cape Thompson, Alaska, Chukchi Sea (ca. 68°06'N, 165°46'W)
June 1959 / L.G. Swartz
June 1960 / L.G. Swartz
July 1976 / D.G. Roseneau, A.M. Springer
July 1977 / D.G. Roseneau, A.M. Springer
- Cape Lisburne, Alaska, Chukchi Sea (ca. 68°52'N, 166°12'W)
July 1977 / D.G. Roseneau, A.M. Springer
- Chaun Bay (Chaun Biological Station), East Siberian Sea, Russia (ca. 68°44'N, 170°36'E)
July–August 1981 / V. Kontrimavichus, S. Bondarenko, A. Ia. Kondratiev, L. Kondratieva, G. Atrashkevich, E.P. Hoberg

Bering Sea

- St. Paul Island (Pribilof Islands), Bering Sea (57°10'N, 170°20'W)
July 1979 / J. Homan
June 1987 / G.V. Byrd
- St. George Island (Pribilof Islands), Bering Sea (56°36'00"N, 169°32'00"W)
June 1987 / G.V. Byrd
- Pribilof Islands, Pelagic (no specific geo coordinates)
August 1974 / US Fish and Wildlife Service
- Nunivak Island, Nash Harbor, Bering Sea (66°00'N, 166°00'W)
August 1949 / P.J. Brandly
- St. Matthew Island, Bering Sea (ca. 60°20'N, 171°00'W)
July–August 1982 / E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseneau
July 1983 / A.M. Springer
July 1997 / D. Causey
- St. Matthew Island (Hall Island), Bering Sea (ca. 60°39'50"N, 173°05'46"W)
July 1997 / D. Causey
- St. Lawrence Island, Bering Sea (ca. 63°45'N, 171°40'W)
May 1950 / E.L. Schiller
18 August 1950 / E.L. Schiller / (63°40'04"N, 170°34'08"W)
22 August 1950 / E.L. Schiller / (Gambell) (63°46'48"N, 171°44'25"W)
5 August 1956 / F.H. Fay / Boxer Bay (63°20'21"N, 171°34'25"W)
July 1959 / R.L. Rausch
August 1964 / J. Bedard / (Gambell) (63°46'48"N, 171°44'25"W)
10 and 27 July 1966 / J. Bédard / (Gambell) (63°46'48"N, 171°44'25"W)
August 1966 / J. Bédard / (Gambell) (63°46'48"N, 171°44'25"W)
August 1968 / J. Bédard / (Gambell) (63°46'48"N, 171°44'25"W)
30–31 May, June 1981 / R. Wilson / (Savoonga) (63°41'48"N, 170°27'39"W)
19 July 1981 / D.G. Roseneau, A. Springer / (Savoonga) (63°41'48"N, 170°27'39"W)
June 1982 / R.L. Rausch / (Savoonga) (63°41'48"N, 170°27'39"W)
June 1983 / R.L. Rausch
18 July 1987 / J. Piatt / ca. (63°47'N, 171°44'W)
- Sledge Island, Bering Sea (64°29'45"N, 166°12'08"W)
July 1969 / R.L. Rausch
- Wales, Alaska, Bering Sea (65°36'N, 168°05'W)
22 March 1966 / R.L. Rausch
- Bering Sea, North Central (no specific coordinates)
1976, 1977 / US Fish and Wildlife Service

(Continued)

Supplementary Data Table 2. (continued)**Gulf of Alaska**

- Ugaiushak Island, Gulf of Alaska (56°47'N, 156°41'W)
May–July 1976 / E.P. Hoberg, D.H.S. Wehle
- Central Island, Gulf of Alaska (56°51'N, 156°53'W)
June 1976 / E.P. Hoberg, D.H.S. Wehle
- Chowiet Island, Semidi Islands, Gulf of Alaska (ca. 56°02'N, 156°45'W)
June 1976 / G.C. Burrell
- Kodiak Island, Uganik Bay, Gulf of Alaska (57°47'21"N, 153°31'47"W)
June 1953 / R.L. Rausch
- Kodiak Island, Uyak Bay, Browns Lagoon, Gulf of Alaska (57°42'52"N, 153°56'51"W)
June 1953 / R.L. Rausch
- Kodiak Island, Chiniak Bay, Gulf of Alaska (57°49'N, 152°30'W)
June–July, 1977 / E.P. Hoberg, D. Nysewander
- Big Koniuji Island, Shumagin Islands, Gulf of Alaska (ca. 55°03'N, 159°35'W)
July 1976 / US Fish and Wildlife Service
- Puffin Island, Kodiak Island, Chiniak Bay, Gulf of Alaska (57°46'N, 152°26'W)
10 July 1977 / E.P. Hoberg
24 July 1977 / E.P. Hoberg
- Sitkalidak Island, Kodiak Island region, Gulf of Alaska (57°07'N, 153°10'W)
8 July 1977 / P. Baird, A. Moe
- Middleton Island, Gulf of Alaska (59°29'N, 146°28'W)
June 1956 / R.L. Rausch
November 1956 / R.L. Rausch
- Shuyak Island, Big Bay, Gulf of Alaska (58°33'23"N, 152°36'14"W)
November 1954 / R.L. Rausch
- Forrester Island, Gulf of Alaska (54°50'N, 133°35'W)
July 1976 / A. DeGange
- Gulf of Alaska, North Central (no specific geo coordinates)
1969, 1970, 1971 / US Fish and Wildlife Service

Eastern North Pacific / Washington State to California**Washington State, USA**

- Grays Marine Canyon (Washington pelagic zone) (46°55'N, 124°46'W)
8 September 1982 / E.P. Hoberg, D.R. Paulson, K.B. Aubry
31 August 1985 / E.P. Hoberg, S. Rohwer, K.B. Aubry, C. Spaa
21 September 1985 / E.P. Hoberg, G. Eddy, S. Rohwer
21 August 1987 / E.P. Hoberg, S. Rohwer, K.B. Aubry
- Protection Island, Washington, Strait of Juan de Fuca (48°08'N, 122°55'W)
July 1981 / R. Fitzner
- Destruction Island, Washington, Eastern North Pacific (47°41'N, 122°55'W)
July 1981 / R. Fitzner
- San Juan Island, Friday Harbor, Washington (48°32'7" N, 123°1'52" W)
January 1981 / E.P. Hoberg
- San Juan Island, Wescott Bay, Washington (ca. 48°30'N, 123°05'W)
February 1982 / W.G. English
- Pt. Roberts (Southern Strait of Georgia [49°00'N, 123°05'W])
January 1964 / R.A. Ryder
- Sequim Bay, Olympic Peninsula, Washington, Strait of Juan de Fuca (ca. 48°05'N, 123°00' W)
November 1981 / E.P. Hoberg, R. Fitzner

(Continued)

Supplementary Data Table 2. (continued)

California, USA

- Humboldt Bay, California, Eastern North Pacific (ca. 40°49'N, 124°10'W)
June 1977 and 1979 / M. Phillips
- Santa Barbara Island (Channel Islands), California, Eastern North Pacific (ca. 33°28'30"N, 119°02'13"W)
10 June 1987 / C. Drost
12 May 1988 / C. Drost

Sea of Okhotsk, Russia

- Magadan, coastal zone (ca. 59°35'N, 150°45'E)
August 1981 / A. Ia. Kondratiev
 - Khmotiyevskogo Peninsula (near Talan Island), northern Sea of Okhotsk (ca. 59°18'N, 148°56'E)
30 July 1988 / L. Kondratieva
 - Talan Island, northern Sea of Okhotsk (ca. 59°19'N, 149°06'E)
July–September 1988 / E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko, A. Kitaysky
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Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | | | |
|---------------------------|-----------------|-----------------------------------|-------------------------------|---------------------------------|-----------------|-------------------------------|-----|------------------------------------|----------------------------|----------------------|-----------------|----------------------------|-----|-----------------|----------------------------|-----|--|
| | | | | Tetrahobothrius fagerskroeldi | | Tetrahobothrius alicae n. sp. | | Tetrahobothrius sinistralis n. sp. | | Tetrahobothrius spp. | | | | | | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | | |
| ALEUTIAN ISLANDS | Amchitka Island | <i>Brachyramphus marmoratus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Aethia cristatella</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | Amchitka Island | <i>Larus glaucescens</i> | 13 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 4 | 1-2 | | | |
| | | <i>Brachyramphus brevirostris</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | Amukta Island | <i>Fratercula corniculata</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Rissa tridactyla</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1+ | | | |
| | Buldir Island | July 1974 | <i>Cephus columba</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | | <i>Aethia pusillata</i> | 5 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | | <i>Aethia cristatella</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | | <i>Aethia pygmaea</i> | 3 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | | <i>Fratercula cirrhata</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | | <i>Fratercula corniculata</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 2 | 1-8 | | |
| | | | <i>Rissa brevirostris</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 6 | | |
| <i>Uria lomvia</i> | | | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| Buldir Island | | | August 1975 | <i>Uria lomvia</i> | 11 | 0 | 0-0 | | 1 | 1 | MSB PARA 29664 | 0 | 0-0 | | 0 | 0-0 | |
| | | | | <i>Fratercula cirrhata</i> | 26 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Buldir Island | August 1987 | <i>Fratercula corniculata</i> | 13 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | | | |
| | | <i>Rissa tridactyla</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 9 | 1-14 | | | |
| | | <i>Rissa brevirostris</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria pelagicus</i> | 4 | 1 | 1 | MSB PARA 27910 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria urile</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Aethia pygmaea</i> | 5 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Aethia pygmaea</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Aethia cristatella</i> | 8 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria pelagicus</i> | 3 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria urile</i> | 4 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| Nizki Island (Bozo Cove) | August 1991 | <i>Uria pelagicus</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria "henyoni"</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| Attu Island (Holtz Bay) | August 1992 | <i>Uria urile</i> | 9 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria urile?</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| Attu Island (Etienne Bay) | September 2002 | <i>Uria pelagicus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Uria pelagicus</i> | 4 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| Seguam Island | August 2002 | <i>Uria urile</i> | 6 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | | <i>Fratercula corniculata</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |

Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | |
|-----------------------------|------------------------------|--|-------------|------------------------------------|-----------------|----------------------------|------------------------------------|-----------------|---|---|-----------------|----------------------------|---------------------------|-----------------|----------------------------|
| | | | | <i>Tetrabothrius fagerskroeldi</i> | | | <i>Tetrabothrius alicae</i> n. sp. | | | <i>Tetrabothrius sinistralis</i> n. sp. | | | <i>Tetrabothrius</i> spp. | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) |
| Tanaga Island | September 1997 | <i>Uria pelagicus</i> | 5 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Ulak Island | September 2002 | <i>Fratercula corniculata</i> <i>Fratercula cirrhata</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Alaid Island | August 1992 | <i>Uria urile</i> <i>Uria pelagicus</i> | 5 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Kiska Island (Kiska Harbor) | August 1992 | <i>Uria pelagicus</i> | 4 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Adak Island | May 1997 | <i>Synthliboramphus antiquus</i> <i>Larus glaucescens</i> <i>Onychoprion aieulica</i> <i>Sterna paradisaea</i> <i>Uria pelagicus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Western Aleutian (Pelagic) | June-July 1981, June 1982 | <i>Uria lomvia</i> (subadult) | 4 | 0 | 0-0 | | 2 | 2-16 | MSB PARA 27219, 29687, 29688, 29689, 29670, 29671 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Synthliboramphus antiquus</i> | 1 | 0 | 0-0 | | 1 | 1 | MSB PARA 29684 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia cristatella</i> <i>Cerorhinca monocerata</i> | 16 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratercula cirrhata</i> (adult) | 30 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratercula cirrhata</i> (subadult) | 23 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratercula corniculata</i> (adult) | 12 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratercula corniculata</i> (subadult) | 7 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | |

Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | |
|--------------------------------------|-----------------|----------------------------------|-------------|---------------------------------|-----------------|----------------------------|------------------------------|-----------------|----------------------------|------------------------------------|-----------------|----------------------------|----------------------|-----------------|----------------------------|
| | | | | Tetrahobothrius jagerskioeldi | | | Tetrahobothrius alcae n. sp. | | | Tetrahobothrius sinistralis n. sp. | | | Tetrahobothrius spp. | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) |
| BERING SEA Wales, Alaska | March 1966 | <i>Uria lomvia</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | July 1969 | <i>Cepphus columba</i> | 1 | 1 | 1 | MSB PARA 27879 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| Nunivak Island (Nash Harbor) | August 1949 | <i>Fratrercula cirrhata</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | August 1974 | <i>Uria lomvia</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Paul Island (Pribilof Islands) | July 1979 | <i>Uria lomvia</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratrercula cirrhata</i> | 7 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratrercula comiculata</i> | 7 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Rissa tridactyla</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Paul Island (Pribilof Islands) | June 1987 | <i>Uria lomvia</i> | 3 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia cristatella</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 4 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 5 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia cristatella</i> | 8 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. George Island (Pribilof Islands) | June 1987 | <i>Aethia cristatella</i> | 8 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 8 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island | May 1960 | <i>Uria lomvia</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Larus hyperboreus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island (Gambell) | August 1960 | <i>Cepphus columba</i> | 4 | 2 | 1 | MSB PARA 27880, 28951 | 1 | 1 | MSB PARA 28647 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Uria lomvia</i> | 1 | 0 | 0-0 | | 1 | 1 | MSB PARA 19115 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Fratrercula cirrhata</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Rissa tridactyla</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | |
| St. Lawrence Island | August 1956 | <i>Cepphus grylle</i> | 1 | 1 | 1 | MSB PARA 1738 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | July 1959 | <i>Uria pelagicus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island | August 1964 | <i>Aethia cristatella</i> | 12 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia pusilla</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island | | <i>Fratrercula cirrhata</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Syrnitroamphipus arcticus</i> | 1 | 0 | 0-0 | | 1 | 1 | MSB PARA 28645 | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island (Gambell) | August 1966 | <i>Fratrercula comiculata</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Uria aalge</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Aethia cristatella</i> | 2 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |

Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | |
|----------------------------------|--------------------|---|----------------------------|---------------------------------|--|----------------------------|---|--|-------------------------------------|---|--|---------------------------------|----------------------------|--|---------------------------------|
| | | | | Tetrabothrius fagerskoei | | | Tetrabothrius alicae n. sp. | | | Tetrabothrius sinistralis n. sp. | | | Tetrabothrius spp. | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) |
| St. Lawrence Island | June 1968 | <i>Alie alle</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island (Savoonga) | May-June-July 1981 | <i>Aethia cristatella</i> <i>Aethia pusilla</i> <i>Aethia psittacula</i> <i>Uria lomvia</i> | 6 4 2 2 | 0 0 0 0 | 0-0 0-0 0-0 0-0 | | 0 0 0 1 | 0-0 0-0 0-0 5 | | 0 0 0 MSB PARA 29646 | 0 0 0 0 | 0-0 0-0 0-0 0-0 | | 0 0 0 0 | 0-0 0-0 0-0 0-0 |
| St. Lawrence Island (Savoonga) | June 1982 | <i>Aethia pusilla</i> | 12 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island | June 1983 | <i>Aethia psittacula</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Lawrence Island | July 1987 | <i>Aethia cristatella</i> | 10 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Matthew Island | July 1982 | <i>Aethia cristatella</i> <i>Aethia pusilla</i> <i>Aethia psittacula</i> <i>Fratercula corniculata</i> <i>Cephus columba</i> | 11 24 6 5 11 | 0 0 0 0 2 | 0-0 0-0 0-0 0-0 1-2 | | 0 0 0 0 MSB PARA 27927, 27919 | 0 0 0 0 0-0 | | 0 0 0 0 MSB PARA 29655, 27252 | 0 0 0 0 1 | 0-0 0-0 0-0 0-0 0-0 | | 0 0 0 0 0 | 0-0 0-0 0-0 0-0 0-0 |
| | | <i>Uria aalge</i> (adult) | 38 | 0 | 0-0 | | 3 | 1 | MSB PARA 29655, 27252 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Uria aalge</i> (subadult) | 4 | 0 | 0-0 | | 1 | 1 | MSB PARA 29685 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Uria lomvia</i> (adult) | 34 | 0 | 0-0 | | 4 | 1-2 | MSB PARA 27004, 29682, 26987, 26996 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Uria lomvia</i> (subadult) | 3 | 0 | 0-0 | | 1 | 1 | MSB PARA 27227 | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Larus hyperboreus</i> | 1 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | <i>Rissa tridactyla</i> | 14 | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| St. Matthew Island | July 1983 | <i>Uria aalge</i> <i>Uria lomvia</i> | 2 1 | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | |
| St. Matthew Island (Hall Island) | July 1997 | <i>Uria aalge</i> <i>Rissa tridactyla</i> | 1 1 | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | | 0 0 | 0-0 0-0 | |
| St. Matthew Island | July 1997 | <i>Fratercula corniculata</i> <i>Aethia pusilla</i> <i>Rissa tridactyla</i> <i>Larus glaucescens</i> <i>Stercorarius longicaudus</i> <i>Uria pelagicus</i> | 1 1 3 1 1 3 | 0 0 0 0 0 0 | 0-0 0-0 0-0 0-0 0-0 0-0 | | 0 0 0 0 0 0 | 0-0 0-0 0-0 0-0 0-0 0-0 | | 0 0 0 0 0 0 | 0-0 0-0 0-0 0-0 0-0 0-0 | | 0 0 0 0 0 0 | 0-0 0-0 0-0 0-0 0-0 0-0 | |
| Bering Sea- North Central | 1976-1977 | <i>Uria aalge</i> <i>Uria lomvia</i> <i>Fratercula cirinata</i> <i>Chrotophaga alutica</i> | 3 5 5 1 | 0 0 0 0 | 0-0 0-0 0-0 0-0 | | 0 0 0 0 | 0-0 0-0 0-0 0-0 | | 0 0 0 0 | 0-0 0-0 0-0 0-0 | | 0 0 0 0 | 0-0 0-0 0-0 0-0 | |

Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | |
|---------------------------------------|----------------------|---|---------------------------------------|---------------------------------|-----------------------|----------------------------|-----------------------------|--|----------------------------|----------------------------------|-----------------|----------------------------|--------------------|-----------------|----------------------------|
| | | | | Tetrabothrius fagerskroeldi | | | Tetrabothrius alicae n. sp. | | | Tetrabothrius sinistralis n. sp. | | | Tetrabothrius spp. | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) |
| SEA OF OKHOTSK Magadan, Russia | August 1981 | <i>Uria aalge</i> | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula cirrhata</i> | 5 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula corniculata</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Rissa tridactyla</i> | 10 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 8 | 1-9 | | |
| | | <i>Larus schistisagus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | | |
| | Talan Island, Russia | July-August 1988 | <i>Aethia cristatella</i> (adult) | 80 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | | <i>Aethia cristatella</i> (fledgling) | 33 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | | <i>Aethia psittacula</i> (adult) | 27 | 0-0 | | 1 | 3 | MSB PARA 29230 | 0 | 0-0 | | 0 | 0-0 | |
| | | | <i>Aethia psittacula</i> (fledgling) | 4 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | | <i>Synthliboramphus ancticus</i> | 46 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| SEA OF OKHOTSK Magadan, Russia | August 1981 | <i>Fratercula cirrhata</i> (adult) | 30 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula cirrhata</i> (fledgling) | 33 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula corniculata</i> (adult) | 30 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula corniculata</i> (fledgling) | 28 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Uria aalge</i> (adult) | 28 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Uria aalge</i> (subadult) | 1 | 0-0 | | 0 | 0-0 | MSB PARA 29629, 29630, 29631, 29632 | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Uria aalge</i> (chicks at fledgling) | 12 | 0-0 | | 8 | 1-4 | MSB PARA 29633, 29634, 29635, 29636, 29637, 29638, 29640, 29641, 29642, 29643, 29644, 29648, 29649, 29650, 29651, 29652, 29653 | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Uria lomvia</i> (adult) | 6 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Uria lomvia</i> (chicks at fledgling) | 2 | 0-0 | | 1 | 1 | MSB PARA 29659 | 0 | 0-0 | | 0 | 0-0 | | |
| | | SEA OF OKHOTSK Magadan, Russia | August 1981 | <i>Rissa tridactyla</i> (adult) | 30 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 |
| <i>Rissa tridactyla</i> (fledgling) | 26 | | | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 5 | 1-8 | | |
| <i>Larus schistisagus</i> (adult) | 21 | | | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 25 | 1-31 | | |
| <i>Larus schistisagus</i> (fledgling) | 5 | | | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 14 | 1-34 | | |
| <i>Uria pelagicus</i> | 3 | | | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 4 | 1-19 | | |
| <i>Cephus carbo</i> | 4 | | | 1-3 | MSB PARA 27912, 29234 | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| <i>Cephus carbo</i> | 4 | | | 1-3 | MSB PARA 27912, 29234 | 2 | 0-0 | | 0 | 0-0 | | 1 | 3 | | |
| <i>Cephus carbo</i> | 4 | | | 1-3 | MSB PARA 27912, 29234 | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| <i>Cephus carbo</i> | 4 | | | 1-3 | MSB PARA 27912, 29234 | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| <i>Cephus carbo</i> | 4 | | | 1-3 | MSB PARA 27912, 29234 | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |

Supplementary Data Table 3. (continued)

| GEOGRAPHIC LOCATION | COLLECTION DATE | AVIAN SPECIES | N= EXAMINED | TETRABOTHRIUS SPECIES INFECTION | | | | | | | | | | | |
|--|--|---------------------------------|-----------------------------------|---------------------------------|-----------------|----------------------------|-----------------------------|-----------------|---|----------------------------------|-----------------|----------------------------|--------------------|-----------------|----------------------------|
| | | | | Tetrabothrius fagerskjoeldi | | | Tetrabothrius alicae n. sp. | | | Tetrabothrius sinistralis n. sp. | | | Tetrabothrius spp. | | |
| | | | | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) | N= | Intensity Range | Museum Catalogue Number(s) |
| EASTERN PACIFIC Grays Marine Canyon, Washington State, Pelagic Zone | September 1982 | <i>Ptychoramphus aleuticus</i> | 4 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | | |
| | | <i>Cerorhinca monocerata</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Fratercula cirrhata</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | August 1985 | <i>Xema sabini</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Stercorarius pomarinus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Brachyramphus marmoratus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | Grays Marine Canyon | <i>Cerorhinca monocerata</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Larus heermanni</i> | 6 | 0-0 | | 0 | 0-0 | | 2 | 1 | | 0 | 0-0 | | |
| | | <i>Stercorarius pomarinus</i> | 6 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Stercorarius longicaudus</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Ptychoramphus aleuticus</i> | 10 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Cerorhinca monocerata</i> | 3 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Stercorarius parasiticus</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Stercorarius pomarinus</i> | 6 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | | |
| | | <i>Xema sabini</i> | 11 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 6 | 2-43 | | |
| <i>Larus argentatus</i> | | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 5 | | | |
| Grays Marine Canyon | August 1987 | <i>Ptychoramphus aleuticus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Cerorhinca monocerata</i> | 9 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 3 | | |
| | | <i>Fratercula cirrhata</i> | 11 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | <i>Uria aalge</i> (adult) | 4 | 0-0 | | 2 | 2-17 | MSB PARA 29680, 29683 | 0 | 0-0 | | 1 | 1 | | | |
| | <i>Uria aalge</i> (subadult) | 4 | 0-0 | | 3 | 1-19 | MSB PARA 29678, 29679 | 0 | 0-0 | | 1 | 5 | | | |
| | <i>Stercorarius pomarinus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | <i>Stercorarius longicaudus</i> | 14 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 1 | | | |
| | <i>Stercorarius parasiticus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | <i>Sterna paradisaea</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | | |
| | <i>Xema sabini</i> | 8 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 5 | 1+ | | | |
| Pt. Roberts, Washington | January 1964 | <i>Brachyramphus marmoratus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 3 | | |
| | | <i>Cerorhinca monocerata</i> | 10 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | July 1981 | <i>Cerorhinca monocerata</i> | 10 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | | <i>Cerorhinca monocerata</i> | 10 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | November 1981 | <i>Uria aalge</i> | 20 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | |
| | San Juan Island, Friday Harbor, Washington | January 1981 | <i>Brachyramphus marmoratus</i> | 1 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | | February 1982 | <i>Cephus columba</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | |
| | Humboldt Bay, California | June 1977 and June 1979 | <i>Uria aalge</i> (adult) | 47 | 0-0 | | 4 | 1-8 | MSB PARA 2724, 29633, 29657, 29658, 29659, 29680, 29681, 29686, 29676 | 0 | 0-0 | | 0 | 0-0 | |
| | | | <i>Uria aalge</i> (fledgling) | 18 | 0-0 | | 3 | 2-14 | MSB PARA 29672, 29673, 29674, 29675, 29681 | 0 | 0-0 | | 0 | 0-0 | |
| | | June 1987 | <i>Synthliboramphus scrippsii</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 20 | MSB PARA 32002 |
| May 1988 | <i>Synthliboramphus scrippsii</i> | 2 | 0-0 | | 0 | 0-0 | | 0 | 0-0 | | 1 | 0-0 | | | |
| TOTAL | | | 1871 | 29 | 53 | 1 | 222 | | | | | | | | |

Supplementary Data Table 4. *Tetrabothrius alcae* n. sp. and *Tetrabothrius sinistralis* n. sp. Type Series and Voucher Specimens Catalogued in the Museum of Southwestern Biology

| MSB PARA # | SCIENTIFIC NAME | IDENTIFIER | COLLECTOR | FIELD CATALOG # | SPECIFIC LOCALITY | Latitude-Longitude | COLLECTION DATE | HOST SPECIES | SPECIMEN TYPE | SLIDE SPECIMEN #s | NUMBER OF SLIDES | COMMENTS |
|----------------|----------------------------|----------------|---|------------------|---|---------------------------------|-------------------------|-----------------------------------|---------------|--|------------------|---|
| MSB-Para-29629 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2640-1 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 July 1988 | <i>Uta aage</i> | HOLOTYPE | 2640-1A to 2640-1G | 7 | subadult female host; 4 TOTAL specimens in 2640. |
| MSB-Para-29630 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2640-2 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 July 1988 | <i>Uta aage</i> | PARATYPE | 2640-2A to 2640-2E | 5 | |
| MSB-Para-29631 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2640-3 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 July 1988 | <i>Uta aage</i> | PARATYPE | 2640-3-A, 2640-3-B, 2640-3-C, 2640-3-C1, 2640-3-D | 5 | |
| MSB-Para-29632 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2640-4 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 July 1988 | <i>Uta aage</i> | PARATYPE | 2640-4-A, 2640-4-B | 2 | |
| MSB-Para-29633 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2672 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 5 September 1988 | <i>Uta lomax</i> | PARATYPE | 2672 | 1 | chick, ca. 20 day host; 1 TOTAL specimen in 2672. |
| MSB-Para-29634 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2655 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 16 August 1988 | <i>Uta aage</i> | PARATYPE | 2655 | 1 | chick, female, ca. 20 day host; 3 TOTAL specimens in 2655. |
| MSB-Para-29635 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2656-1 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2656-1 | 1 | chick, female, ca. 15-18 day host; 3 TOTAL specimens in 2656. |
| MSB-Para-29636 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2656-2 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2656-2 | 1 | |
| MSB-Para-29637 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2656-3 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2656-3 | 1 | |
| MSB-Para-29638 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2657-1 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2657-1 | 1 | chick, female, ca. 15-18 day host; 3 TOTAL specimens in 2657. |
| MSB-Para-29639 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2657-2 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2657-2 | 1 | |
| MSB-Para-29640 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2657-3 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2657-3 | 1 | |
| MSB-Para-29641 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2658-1 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2658-1 | 1 | chick, female, ca. 15-18 day host; 4 TOTAL specimens in 2658. |
| MSB-Para-29642 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2658-2 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2658-2 | 1 | |
| MSB-Para-29643 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2658-3 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2658-3 | 1 | |
| MSB-Para-29644 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2658-4 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2658-4 | 1 | |
| MSB-Para-29645 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 754, 250-B-64 | Saint Lawrence Island, Gambel, Bering Sea | 83° 46' 48" N., 171° 44' 25" W. | 29 July 1984 | <i>Synbranchomphalus antiquus</i> | PARATYPE | 754 | 3 | adult host; 1 TOTAL specimen in 754. |
| MSB-Para-29646 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 847, 5L-2, 81 | Saint Lawrence Island, Savoonga, Bering Sea | 83° 41' 48" N., 170° 27' 39" W. | 19 July 1981 | <i>Uta lomax</i> | PARATYPE | 847 | 3 | adult host; 3 TOTAL specimens in 847; single specimen mounted, 4 in 70% ethanol |
| MSB-Para-29647 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 507, RL-1, 8-221 | Saint Lawrence Island, Gambel, Bering Sea | 83° 46' 48" N., 171° 44' 25" W. | 20 August 1950 | <i>Capillaria colubina</i> | PARATYPE | 507-A, 507-B | 2 | chick host; 1 TOTAL specimen in 507. |
| MSB-Para-29648 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2659-1 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2659-1 | 1 | chick, female, ca. 15-18 day host; 3 TOTAL specimens in 2659. |
| MSB-Para-29649 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2659-2 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2659-2 | 1 | |
| MSB-Para-29650 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2659-3 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2659-3 | 1 | |
| MSB-Para-29651 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2660 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 25 August 1988 | <i>Uta aage</i> | PARATYPE | 2660 | 1 | chick, female, ca. 15-18 day host; 1 TOTAL specimen in 2660. |
| MSB-Para-29652 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2662 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 27 August 1988 | <i>Uta aage</i> | PARATYPE | 2662 | 1 | chick, male, ca. 15 day host; 1 TOTAL specimen in 2662. |
| MSB-Para-29653 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 2663 | Talen Island, Northern Sea of Okhotsk | ca. 59° 19' N., 149° 06' E. | 27 August 1988 | <i>Uta aage</i> | PARATYPE | 2663 | 1 | chick, male, ca. 15 day host; 1 TOTAL specimen in 2663. |
| MSB-Para-29654 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia. Kondratiev, L. Kondratieva, S. Bondarenko | 018-75, JLL-112 | Buler Island, Bering Sea | ca. 52° 21' N., 175° 56' E. | 14 August 1975 | <i>Uta lomax</i> | PARATYPE | 018-75-A, 018-75-A1, 018-75-A2, 018-75-B, 018-75-C | 5 | adult, female host; 1 TOTAL specimen in 018-75. |
| MSB-Para-29655 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1314 | Saint Matthew Island, Bering Sea | ca. 60° 20' N., 171° 00' W. | 27 July 1982 | <i>Uta aage</i> | PARATYPE | 1314 | 1 | adult, male host; 1 TOTAL specimen in 1314. |
| MSB-Para-29656 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1311 | Saint Matthew Island, Bering Sea | ca. 60° 20' N., 171° 00' W. | 27 July 1982 | <i>Uta lomax</i> | PARATYPE | 1311 | 1 | adult, female host; 1 TOTAL specimen in 1311. |
| MSB-Para-29657 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1373 | Saint Matthew Island, Bering Sea | ca. 60° 20' N., 171° 00' W. | 3 August 1982 | <i>Uta aage</i> | PARATYPE | 1373 | 1 | adult, male host; 1 TOTAL specimen in 1373. |
| MSB-Para-29658 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 544, DGR-16977 | Capet Sabine, Alaska, Chukchi Sea | ca. 65° 52' N., 169° 12' W. | July 1977 | <i>Uta aage</i> | PARATYPE | 544-A1 to 544-44 | 4 | adult host; 1 TOTAL specimen in 544. |
| MSB-Para-29659 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083-2 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083-2-A to 1083-2-G | 7 | adult, male host; 8 TOTAL specimens in 1083 plus 3 TOTAL specimens in vial 70% ethanol. |
| MSB-Para-29660 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083-4 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083-3-A, 1083-3-B | 2 | |
| MSB-Para-29661 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083-5 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083-4 | 1 | |
| MSB-Para-29662 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083-6 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083-5 | 1 | |
| MSB-Para-29663 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083-7 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083-6 | 1 | |
| MSB-Para-29664 | <i>Tetrabothrius alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dyes-Hoberg, M.K. Hoberg, D.G. Roseman | 1083 | Humboldt Bay, Eastern North Pacific | ca. 40° 49' N., 124° 10' W. | ca. June 1977-June 1979 | <i>Uta aage</i> | PARATYPE | 1083 | 2 | fragments |

Supplementary Data Table 4. (continued)

Supplementary Data Table 4. *Tetraobolus alcae* n. sp. and *Tetraobolus sinistralis* n. sp. Type Series and Voucher Specimens Catalogued in the Museum of Southwestern Bio

| MSB PARA # | SCIENTIFIC NAME | IDENTIFIER | COLLECTOR | FIELD CATALOG # | SPECIFIC LOCALITY | Latitude-Longitude | COLLECTION DATE | HOST SPECIES | SPECIMEN TYPE | SLIDE SPECIMEN #s | NUMBER OF SLIDES | COMMENTS |
|----------------|--------------------------------|----------------|---|--------------------|--|---------------------------------|---------------------------|------------------------------|---------------|-----------------------|------------------|---|
| MSB Para 28602 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, D. Nysewander | 362-76 | Kodiak Island, Chitnaik Bay, Gulf of Alaska | 57°49' N., 152°30' W. | 20 June 1977 | <i>Uta alage</i> | VOUCHER | 362-76 | 1 | adult, male host; 4 TOTAL specimens in 362. Post-larval |
| MSB Para 28604 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, D. Nysewander | 362-89 | Kodiak Island, Chitnaik Bay, Gulf of Alaska | 57°49' N., 152°30' W. | 20 June 1977 | <i>Uta alage</i> | VOUCHER | 362-89 | 1 | post-larval ectoparasite |
| MSB Para 28605 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, D. Nysewander | 362-1 | Kodiak Island, Chitnaik Bay, Gulf of Alaska | 57°49' N., 152°30' W. | 20 June 1977 | <i>Uta alage</i> | PARATYPE | 362-1 | 1 | post-larval ectoparasite |
| MSB Para 28606 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1088-1 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | PARATYPE | 1088-1A, 1088-1-B | 2 | adult, male host; 1 TOTAL specimen in 1088. |
| MSB Para 28607 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1083-1, P.JG-072 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | 14 July 1981 | <i>Uta lomiva</i> | PARATYPE | 1083-1A, 1083-1-B | 2 | Subadult, male host; 16 TOTAL specimens in 1083. 5 on slides, 11 in vial 70% ethanol. |
| MSB Para 28608 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1083-2, P.JG-072 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | 14 July 1981 | <i>Uta lomiva</i> | PARATYPE | 1083-2A to 1083-2-D | 4 | |
| MSB Para 28609 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1083-3, P.JG-072 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | 14 July 1981 | <i>Uta lomiva</i> | PARATYPE | 1083-3A to 1083-3-C | 3 | |
| MSB Para 28610 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1083-4, P.JG-072 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | 14 July 1981 | <i>Uta lomiva</i> | PARATYPE | 1083-4A to 1083-4-C | 3 | |
| MSB Para 28611 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1083-4A1, P.JG-072 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | 14 July 1981 | <i>Uta lomiva</i> | PARATYPE | 1083-4A | 1 | |
| MSB Para 28612 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1084-1 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | PARATYPE | 1084-1 | 1 | young of the year, female host; 5 TOTAL specimens, 1 in 70% ethanol. |
| MSB Para 28613 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1084-2 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | VOUCHER | 1084-2 | 1 | |
| MSB Para 28614 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1084-3 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | VOUCHER | 1084-3 | 1 | |
| MSB Para 28615 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1084-4 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | VOUCHER | 1084-4 | 1 | |
| MSB Para 28616 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1087 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | 1979 | <i>Uta alage</i> | PARATYPE | 1087 | 2 | Subadult, male host; 3 TOTAL specimens; Fragments in 70% ethanol. |
| MSB Para 28617 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, S. Rowser, K.B. Aubry | 2440 | Greys Marine Canyon, Eastern Pacific | ca. 48°55' N., 124°46' W. | 21 August 1987 | <i>Uta alage</i> | VOUCHER | 2440-1, 2, 3, 4, 6, 7 | 6 | subadult host; 19 TOTAL specimens, post-larval |
| MSB Para 28618 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, S. Rowser, K.B. Aubry | 2442 | Greys Marine Canyon, Eastern Pacific | ca. 48°55' N., 124°46' W. | 21 August 1987 | <i>Uta alage</i> | VOUCHER | 2442 | 1 | young of the year host; 1 specimen, post-larval |
| MSB Para 28619 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, S. Rowser, K.B. Aubry | 2445 | Greys Marine Canyon, Eastern Pacific | ca. 48°55' N., 124°46' W. | 21 August 1987 | <i>Uta alage</i> | VOUCHER | 2445-1, 2 | 2 | adult host; 2 TOTAL specimens, early mature, strobable |
| MSB Para 28620 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, S. Rowser, K.B. Aubry | 2447 | Greys Marine Canyon, Eastern Pacific | ca. 48°55' N., 124°46' W. | 21 August 1987 | <i>Uta alage</i> | VOUCHER | 2447-2, 5, 6, 7 | 4 | Subadult host; 17 TOTAL specimens, post-larval, to early mature |
| MSB Para 28621 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1055 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | ca. June - July 1981 | <i>Symbiolomphus arripus</i> | VOUCHER | 1055 | 1 | adult host; 1 specimen, mature, strobable |
| MSB Para 28622 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, A. Ia, Kondratiev, L. Kondratieva, S. Bondarenko | 2723 | Taim Island, Northern Sea of Okhotsk | ca. 59°19' N., 149°06' E. | 8 June 1988 | <i>Aging pastuscula</i> | VOUCHER | 2723-1, 2, 3 | 3 | adult host; 3 specimens, early mature and post-larval |
| MSB Para 28623 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1383 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 3 August 1982 | <i>Uta alage</i> | VOUCHER | 1383 | 1 | subadult host; 1 specimen, post-larval |
| MSB Para 28624 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1330 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 29 July 1982 | <i>Uta lomiva</i> | VOUCHER | 1330 | 1 | subadult female host; 1 specimen, post-larval |
| MSB Para 28625 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1305 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 27 July 1982 | <i>Uta lomiva</i> | VOUCHER | 1305 | 1 | adult male host; 1 specimen, post-larval |
| MSB Para 28626 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1389 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 3 August 1982 | <i>Uta lomiva</i> | VOUCHER | 1389 | 1 | adult female host; 1 specimen, post-larval |
| MSB Para 28627 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | M. Phillips | 1100 | Humboldt Bay, Eastern North Pacific | ca. 40°49' N., 124°10' W. | ca. June 1977 - June 1979 | <i>Uta alage</i> | VOUCHER | 1100 | 1 | young of the year host; 2 specimens, post-larval |
| MSB Para 28628 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg | 289 | Kodiak Island, Chitnaik Bay, Gulf of Alaska | 57°49' N., 152°30' W. | 22 June 1977 | <i>Uta alage</i> | VOUCHER | 289 | 1 | subadult female host; 2 specimens, post-larval |
| MSB Para 28629 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | P.J. Geasin | 1064 | South of Western Aleutian Islands, Pelagic Zone, North Pacific | 50°03' N., 173°08.6' E. | ca. June - July 1981 | <i>Uta lomiva</i> | VOUCHER | 1064 | 2 | subadult host; 2 specimens, post-larval |
| MSB Para 28630 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.L. Schiller | 513 | Saint Lawrence Island, Gambel, Bering Sea | 63°46'48" N., 177°44'25" W. | August 1950 | <i>Uta lomiva</i> | VOUCHER | 513A | 1 | adult host; 1 specimen, immature |
| MSB Para 28631 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | Eric P. Hoberg, D.H.S. White | 103 | Ugashik Island, Gulf of Alaska | 56°47' N., 156°41' W. | 30 June 1976 | <i>Uta lomiva</i> | VOUCHER | 103-A, B, C, AB, E | 5 | adult host; 5 specimens, post-larval |
| MSB Para 28632 | <i>Tetraobolus alcae</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1390 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 3 August 1982 | <i>Uta lomiva</i> | VOUCHER | 1390 | 1 | adult host; 2 specimens, post-larval |
| MSB Para 28633 | <i>Tetraobolus sinistralis</i> | Eric P. Hoberg | E.P. Hoberg, M. Dykes-Hoberg, M.K. Hoberg, D.G. Roseman | 1301 | Saint Matthew Island, Bering Sea | ca. 60°20' N., 177°00' W. | 27 July 1982 | <i>Cephus columba</i> | HOLOTYPE | 1301-1A to 1301-1D | 5 | adult male host |
| MSB Para 28634 | <i>Tetraobolus sp.</i> | Eric P. Hoberg | Charles Dorst | 2438 | Santa Barbara Island, Channel Islands, CA | ca. 33°28'30" N., 119°02'13" W. | 10 June 1987 | <i>Symbiolomphus arripus</i> | VOUCHER | 2438 | 4 | adult female host; 16 immature post-larval specimens in 2438. 1 specimen, not associated with <i>T. jagarskolei</i> complex |

***Tetrabothrius jagerskioeldi* Nybelin, 1916: Images for Comparative Diagnostics and Identification of Adult Strobilate Tapeworms**

Primary data for hosts, localities of collection, and methods of preparation are summarized in Hoberg and Soudachanh (2020). Scale bars in micrometers.

Figures 1–4. Scolex. **Fig. 1.** Adult scolex in *Uria aalge* (Pontoppidan, 1763) (MSB 5732). Dorso-ventral view, showing flattened bothridia and prominent auricular appendages (Figs. 1–3 same scale). **Fig. 2.** Adult scolex in *Cepphus columba* Pallas, 1811 (MSB 27927). Lateral view; note prominent, muscular auricle. **Fig. 3.** Adult scolex in *C. columba* (MSB 27880). Dorso-ventral view; note inflated apical region, indicative of recent infection and development of the scolex. **Fig. 4.** Scolex in postlarval specimen with early strobilization, attaining immature development in *Cepphus carbo* Pallas, 1811 (MSB 29234). Lateral view of scolex, showing pedicle structure following loss of apical sucker and development of bothridia and auricles.

Figures 5–7. Genital atrium and cirrus sac in development. **Fig. 5.** Proglottids in ventral view showing mature development of cirrus sac (cs), genital atrium (ga), dorsal bar (db), and position of the ventral osmoregulatory canal (vosm) in *Cepphus columba* (MSB 27880). **Fig. 6.** Proglottids in ventral view in mature specimen showing genital pore (ge), cirrus sac (cs), genital atrium (ga), vas deferens (vd), and uterine stem (ut) in *Cerorhinca monocerata* (Pallas, 1811) (MSB 26828). **Fig. 7.** Proglottids in dorsal view in pregravid strobila showing structure of the genital atrium, dorsal bar (db), cirrus sac (cs), and transverse uterus under expansion (ut) in *C. columba* (MSB 27927).

Figures 8–10. Genital atrium in transverse sections (hand-cut). **Fig. 8.** Genital atrium in late maturity, from posterior, dorsal to top, in *Brachyramphus marmoratus* (Gmelin, 1789) (MSB 27916). Shown are relative positions of the cirrus sac (cs), transverse uterine stem (ut) extending between the dorsal (dosm) and ventral (vosm) osmoregulatory canals, vagina (va), muscular genital atrium (ga), genital pore (ge), and inner (im) and outer (om) longitudinal muscle bundles. **Fig. 9.** Genital atrium in late maturity (MSB 27916), showing details of the terminal male and female genital ducts (arrows), position and structure of the muscular dorsal bar (db), cirrus sac (cs), and vagina (va). **Fig. 10.** Genital atrium in pregravid proglottid, from anterior, dorsal to top, in *Uria aalge* (MSB 5732), showing genital ducts, dorsal bar (db), genital pore (ge), cirrus sac (cs), vagina (va), and the inner (im) and outer (om) muscle bundles.

Figures 11–12. Genital organ complex in male and female, from whole mounts. **Fig. 11.** Proglottid in maturity to late maturity showing dorsal view with distribution and structure of organ systems. Note the lobate, biwinged ovary (ov), compact vitelline gland (vt), spindle-shaped vaginal seminal receptacle (vsr with arrow), cirrus sac (cs), and genital atrium (ga), in *Cepphus columba* (27879). **Fig. 12.** Proglottid in maturity to late maturity in dorsal view. Note ovarian wing (ov), vaginal seminal receptacle crossing osmoregulatory canals (between) (osm), in *C. columba* (27879).

Figures 13–15. Gravid proglottids and uterus. **Fig. 13.** Developing lobate uterus, in *Cepphus columba* (MSB 27927), ventral view. Transverse uterus (ut) extends toward poral margin; note relationship to cirrus sac (cs) and genital pore (ge). **Fig. 14.** Patent uterine pores, mid-dorsal near anterior margin, in successive gravid segments near termination of strobila, dorsal view (arrows), in *C. columba* (MSB 27880). **Fig. 15.** Gravid uterus in successive proglottids near termination of strobila, dorsal view, in *C. columba* (MSB 27879-A4). Note uterus extends beyond osmoregulatory systems to fill proglottid; note position of genital pore (ge). Some segments are devoid of eggs, which have been released through the dorsal uterine pores.

