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Anophryocephalus inuitorum sp. nov. and *A. arcticensis* sp. nov. (Eucestoda: Tetrabothriidae) in Ringed Seals (*Phoca hispida hispida*) and Harp Seals (*Phoca groenlandica*) from High-Latitude Seas of Eastern Canada and the Arctic Basin

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Abstract: ***Anophryocephalus inuitorum*** sp.nov. and ***A. arcticensis*** sp.nov. are described from ringed seals (*Phoca hispida hispida*) in the eastern Canadian Arctic; the latter species is also reported from harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence. *Anophryocephalus inuitorum* is most similar to *A. skrjabini*, but can be distinguished by fewer testes (14–27) and smaller dimensions of the strobila, neck (3.0–5.9 mm long), and cirrus sac (31–70 μm long), diameter of the genital atrium (44–68 μm), and length of the male canal (23–42 μm long). *Anophryocephalus arcticensis* resembles *A. nunivakensis* in the structure of the scolex, but is readily distinguished by a longer neck (8.9–14.7 mm), an elongate cirrus sac (60–98 × 44–73 μm) with a substantially thicker muscular wall, a more globular vitelline gland, and larger embryophores (29–41 μm long) and oncospheres (24–34 μm long). These are the first species of *Anophryocephalus* to be described from phocines in the eastern Canadian Arctic, and are included in a revised key for the genus.

Résumé : On trouvera ici la description d'***Anophryocephalus inuitorum*** sp.nov. et d'***A. arcticensis*** sp.nov., rencontrés chez des Phoques annelés (*Phoca hispida hispida*) dans l'est de l'Arctique canadien; la seconde espèce a également été trouvée chez des Phoques du Groenland (*Phoca groenlandica*) dans le golfe du Saint-Laurent. *Anophryocephalus inuitorum* s'apparente surtout à *A. skrjabini*, mais s'en distingue par le nombre plus restreint de ses testicules (14–27) et les dimensions plus réduites des composantes de son strobila, cou (3,0–5,9 mm longueur), sac du cirre (31–70 μm), atrium génital (44–68 μm de diamètre), canal mâle (23–42 μm de longueur). *Anophryocephalus articensis* ressemble à *A. nunivakensis* par la structure de son scolex, mais s'en distingue facilement par un cou plus long (8,9–14,7 mm de longueur), par son sac du cirre allongé (60–98 × 44–73 μm) à la paroi musculaire beaucoup plus épaisse, par sa glande vitelline plus globuleuse et par la taille plus importante de ses embryophores (29–41 μm de longueur) et de ses oncosphères (24–34 μm de longueur). Il s'agit là des premières espèces d'*Anophryocephalus* jamais trouvées chez des Phocinae dans l'est de l'Arctique canadien; la clé du genre a été amendée de façon à inclure les nouvelles espèces.
[Traduit par la Rédaction]

Introduction

The genus *Anophryocephalus* Baylis, 1922 currently contains 5 species that are restricted to high latitudes (Subarctic and Arctic) of the northern hemisphere (Hoberg et al. 1991). Among these, 3 species are characteristic of phocids, primarily those of the tribe Phocini and genus *Phoca* (see Wyss 1988), and include *Anophryocephalus anophrys* Baylis, 1922 (Palearctic–Atlantic sector of the Arctic basin), *A. skrjabini* (Krotov and Deliamure, 1955), and *A. nunivakensis* Hoberg, Adams, and Rausch, 1991 (both endemic to the North Pacific basin). Additional species, *A. ochotensis* Deliamure and Krotov, 1955 and *A. eumetopii* Hoberg, Adams and Rausch, 1991, are exclusively parasites of the otariid *Eumetopias jubatus* (Schreber), primarily in the Bering Sea and Sea of Okhotsk (Hoberg and Adams 1992).

Although cestodes of *Phoca* spp. in the North Pacific

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basin have been studied extensively, there has been relatively little information from the insular areas of the Canadian Arctic (reviewed in Adams 1988; Hoberg et al. 1991; Hoberg and Adams 1992). Previous limited collections from the Canadian Arctic had not revealed any information about the cestode fauna of pinnipeds in the region (McLaren 1958; Finley et al. 1983). However, the distribution of hosts and parasites and the postulated history of local isolation of populations of ringed seals (and other *Phoca* species, e.g., *P. largha* (see Shaughnessy and Fay 1977)) in conjunction with phylogenetic and biogeographic analyses suggested that additional species of *Anophryocephalus* might be found among the Phocini in the Arctic Basin or North Pacific (Hoberg and Adams 1992; Hoberg 1992).

During the summers of 1992 and 1993, one of us (L.N.M) initiated the first strictly parasitological surveys in the eastern Canadian Arctic (Measures and Gosselin 1994). Field studies in the region of Hudson Strait resulted in the collection of two undescribed species of *Anophryocephalus* in ringed seals (*Phoca hispida hispida* Schreber). Subsequently, cestodes of one of these species were also found in harp seals (*Phoca groenlandica* Erxleben) on the winter foraging grounds in the St. Lawrence River estuary near Les Escoumins, Quebec. These cestodes, described in the current study, represent the second and third species of *Anophryocephalus* apparently endemic to the Arctic and Subarctic regions of the Atlantic basin (Hoberg 1995).

Materials and methods

Mature and gravid specimens of two undescribed species of *Anophryocephalus* were collected (by L.N.M.) from ringed seals in the area of Hudson Strait, northern Quebec, during the late summer of 1992 and 1993. On 25–28 August 1992, very small cestodes were collected from two young-of-the-year ringed seals (approximately 4–5 months in age, based on the usual pupping time of mid-March to mid-April, according to McLaren (1958), Smith (1973, 1987), and King (1983)), taken by Inuit hunters near Salluit, Quebec. Subsequently, between 4 and 9 September 1993 an additional adult and 14 young-of-the-year ringed seals were collected and necropsied in the region (Sugluk Inlet, Hudson Strait, 62°13′N, 75°39′W; Deception Bay, 62°10′N, 74°42′W). Among 5 of 15 seals (from 19 collected) examined for cestodes in 1993, specimens of a small and a very large species of *Anophryocephalus* were found. In both years, the seals were shot adjacent to the village and dissected several hours after collection. Cestodes were recovered alive and allowed to relax in tap water overnight prior to fixation in buffered 10% formalin and storage in acetic acid – alcohol formalin (AFA). Cestodes were stained in either Schneider's or Semichon's acetic carmine and mounted in Permount or Canada balsam. Descriptions are based on (*i*) 8 complete cestodes with scolices and 2 incomplete strobilae, lacking the holdfast but with unequivocal diagnostic characters for the species (small form), and (*ii*) 3 gravid and 1 early mature specimen along with 2 additional scolices and large fragments of gravid strobila (large form). Specimens were prepared as whole mounts, with regions of mature and gravid strobila (with exact counts of segments) retained for sectioning (5 and 2 specimens, respectively). Thick transverse sections were prepared by hand with a razor blade for examination of the longitudinal musculature and genital atrium. Determination of the ontogeny of the genital system and strobila and maximum dimensions of specific organs (with reference to degree of maturity) was consistent with criteria developed by Hoberg (1987*a*) and Hoberg et al. (1991) (see also Murav'eva and Popov 1976). All measurements are presented as length × width (in micrometres unless specified otherwise). The sample size (n) and the mean ± 1 SD, in parentheses, accompany major mensural and numerical characters.

Additionally, representatives of one of these species were incidentally recovered from 3 of 56 harp seals collected in the winter of 1991–1992 near Les Escoumins, Quebec, in the St. Lawrence River estuary (48°21′N, 69°24′W) and from a single host at Sept-Îles, Quebec (ca. 50°12′N, 66°23′W), in June 1992. The cestode material was highly fragmented and macerated, having been collected from seals that had been frozen and thawed prior to necropsy. Scolices and mature and gravid strobilae were recovered that appear consistent with the large form of *Anophryocephalus* spp. from ringed seals. Owing to their condition, however, these specimens could not be used in preparing the description.

Representative specimens, including the type series and vouchers from *P. hispida* and vouchers from *P. groenlandica*, have been deposited in the collections of the U.S. National Parasite Collection, U.S. Department of Argiculture, Beltsville, Maryland, U.S.A. (USNPC), the Canadian Museum of Nature, Parasite Collection, Ottawa, Canada (CMNP), and the Maurice Lamontagne Institute, Department of Fisheries and Oceans, Mont Joli, Quebec, Canada (MLI).

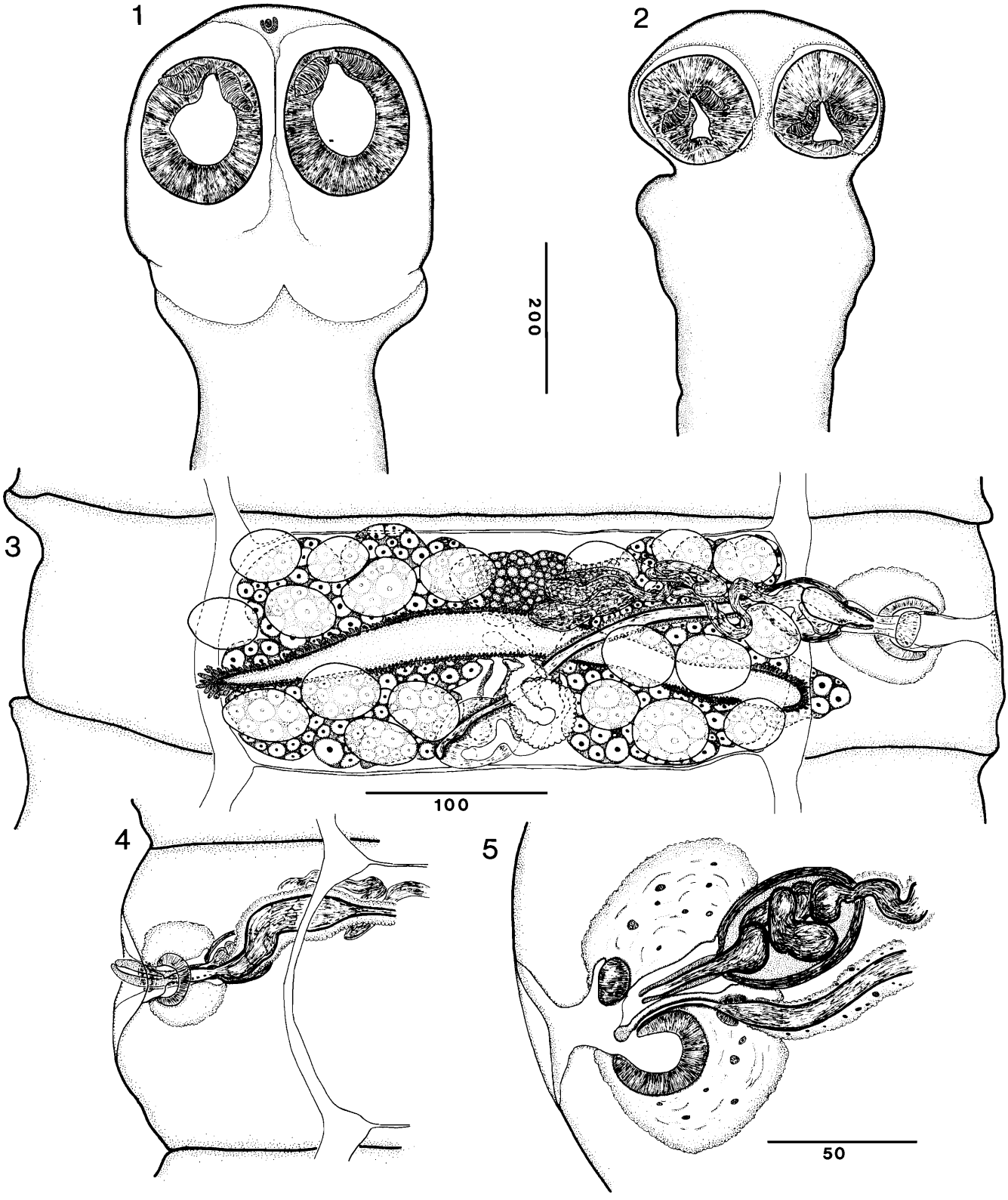
Results

Anophryocephalus inuitorum sp.nov. Figs. 1–5, 12, 13

General description

Small, weakly craspidote cestodes, 59.5–84.1 mm in maximum length, 935 in width, and with 418–533 segments in nearly gravid specimens. Proglottids wider than long in immature and mature strobilae, becoming nearly equal in dimensions when gravid; 100–185 × 380–605 in mature and 185–700 × 480–935 in pregravid to gravid segments. Length:width ratio in mature segments 1:2.49–6.05 and in pregravid to gravid segments 1:1.0–3.74. Scolex round to rectangular, usually wider than long, (n = 7) 195–416 (275 ± 84.42) × 273–468 (353 ± 68.32), with prominent rounded apical region sometimes evident (dependent on degree of contraction); pedicle or former point of attachment of apical sucker visible in one specimen. Suckerlike bothridia lacking opercula or gaps along anterior margin and not situated in parenchymal invaginations; (n = 27) 138–216 (165 ± 24.81) × 99–192 (140 ± 28.92). Paired auricular appendages with independent origins, not confluent, along anterior margins of bothridia; lateral appendages, (n = 5) 65–81 (70 ± 6.19) in length; medial appendages, (n = 4) 62–70 (67.5 ± 4.93). Neck approximately 3.0–5.9 mm in length. Osmoregulatory canals completely developed in neck; maximum diameter of dorsal canals, 3–5, attained in the neck immediately posterior to scolex, becoming atrophied in earliest immature segments and absent posteriad; ventral canals 5–94 in diameter, with maximum observed in pregravid to

Figs. 1–5. *Anophryocephalus inuitorum* sp.nov. (drawn from the holotype unless specified otherwise; all scale bars are in micrometres; the scale is the same in Figs. 3 and 4). Fig. 1. Scolex, completely developed in a pregravid specimen, showing typical form when relaxed (paratype); note the relatively large fleshy auricular appendages that are not confluent across the anterior margin of the bothridia and remnants of the apical pedicle or point attachment of apical sucker in the plerocercoid. Fig. 2. Scolex, showing the form in a contracted specimen; note the flaps, formed by contraction of the basal region of the scolex, extending across the posterior margins of the bothridia. Fig. 3. Proglottis in a late stage of maturity, dorsal view. Fig. 4. Margin of mature proglottis, showing the genital atrium, cirrus sac, and vagina in ventral view; note the position and structure of vaginal sphincters and vaginal seminal receptacle (ovary, testes, and transverse uterine stem are not depicted). Fig. 5. Genital atrium in transverse section, viewed from anterior (paratype).



gravid segments; ventral transverse canals minuscule, 1–5 in diameter. Genital ducts pass dorsal to the ventral osmoregulatory canal. Genital pores weakly suckerlike, unilateral, marginal on the right side, ventrolateral, in the middle to anterior 1/3 of segment.

Longitudinal musculature

Musculature prominent; inner bundles arranged in single layer; outer in 1 or 2 layers. Inner bundles large, 33–48 in number and with 6–23 fibers per bundle. Outer bundles small, often single fibers, 89–111 in number and with 1–7 fibers per bundle.

Male genitalia

Genital Anlagen visible in earliest proglottids; testes discernible in 20–30th segment; genital pore patent and maturity attained by 130–170th segment. Testes (n = 114 segments in 7 strobila) 14–27 (19 ± 2.8) in number; (n = 160) 29–60 (42 ± 7.09) in greater diameter; situated dorsally in a single layer (rarely 2 layers), completely overlapping ovary and female organs in poral and antiporal regions of proglottis. Vas deferens highly convoluted situated dorsal to poral testes, extending to the median line, in anterior part of segment. Cirrus sac elongate, consistently longer than wide in all stages of development (may be distorted to near ovoid by expansion of uterus in gravid proglottids), maximum dimensions attained in postmaturity, (n = 350) 31–70 (49 ± 7.16) × 23–52 (36 ± 5.87); generally slightly overlapping poral ventral osmoregulatory canal. Cirrus sac with muscular wall, 8 in maximum thickness, containing vas deferens and muscular cirrus. Genital atrium ovoid, weakly muscular, (n = 158) 44–68 (57 ± 5.14) in diameter as determined in whole mounts, maximum dimensions attained in postmature segments. Cirrus sac situated in mediodorsal wall of genital atrium; cirrus extends into atrial lumen through dorsal, straight to slightly curved, laterally directed male canal; (n = 97) 23–42 (32 ± 4.54) in length, attaining maximum in postmaturity. Length of cirrus sac : length of male canal 1:0.47–0.82; diameter of genital atrium : length of male canal 1:0.52–0.62. Prominent, solid muscular pad located dorsal to aperture of male canal.

Female genitalia

Ovary multilobate, with 2 prominent wings, evident by 60th segment; developed by 150th segment; 198–390 in length when mature and filling entire segment, extending ventrally beyond ventral osmoregulatory canals in late maturity. Vitelline gland generally globular, transversely elongate, (n = 156) 57–135 (92 ± 15.68) × 29–68 (47 ± 9.73), located anteroventral to ovary on midline. Single broad vitelline duct extends posteriad ventral to ovary. Mehlis' gland located either poral or antiporal to the midline, posterior and dorsal to the ovarian isthmus; (n = 92) 29–57 (41 ± 5.88) in diameter. Inner seminal receptacle ellipsoidal, situated ventral to Mehlis' gland near the median line; (n = 106) 31–68 (49 ± 7.88) in diameter. Vagina extends porad from the inner seminal receptacle, passing dorsally to transverse stem of uterus; covered by a thick cellular epithelium. Vaginal seminal receptacle present as dilatated region where vagina crosses poral osmoregulatory canal. Atrial region of vagina aspinose, extending through genital atrium ventral to cirrus sac; sphincters near vaginal aperture well developed. Vaginal aperture with weak papilliform structure, opening immediately ventral to male canal and dorsal to prominent muscular chamber that is confluent with the ventral wall of genital atrium; inside diameter of chamber as determined in entire specimens, (n = 172) 16–36 (26 ± 5.18); maximum attained in late mature segments, variable in dimensions in gravid proglottids; diameter of genital atrium : diameter of muscular chamber 1:0.36–0.53. Ascending uterine stem extends dorsally from Mehlis' gland to join transverse tubular uterus visible in 100th segment; Anlagen of uterine pore evident in immature segments. Transverse uterus extends ventral to testes and vagina but dorsal to ovary; irregular sacculate structure evident in 220–370th segment. Preformed uterine pore intermittently patent by 278–448th segment but before gravid state is attained. Pregravid to gravid uterus extends dorsally beyond ventral osmoregulatory canals.

Eggs

Membranous uterine capsules, (n = 25) 65–83 (76 ± 5.84) in diameter; containing embryophore, (n = 25) 36–46 (40 ± 2.40) × 24–37 (29 ± 3.63) and oncosphere, (n = 50) 26–34 (30 ± 2.30) × 18–31 (23 ± 2.21). Oncospheral hooks of dissimilar lengths; medial hooks, (n = 50) 15–18 (16 ± 0.99) long and lateral hooks, (n = 60) 16–19 (18 ± 1.0).

HOST: Type host *Phoca hispida hispida* Schreber; in 1992 collected from 2 young-of-the-year seals (4 young of the year and 1 adult examined); in 1993 collected from among 5 of 15 seals infected with *Anophryocephalus* spp.; prevalence undetermined, as individual host records were not maintained.

LOCALITY: Type locality Sugluk Inlet, Hudson Strait, near Salluit, northern Quebec, Canada (62°13′N, 75°39′W).

HABITAT: Small intestine.

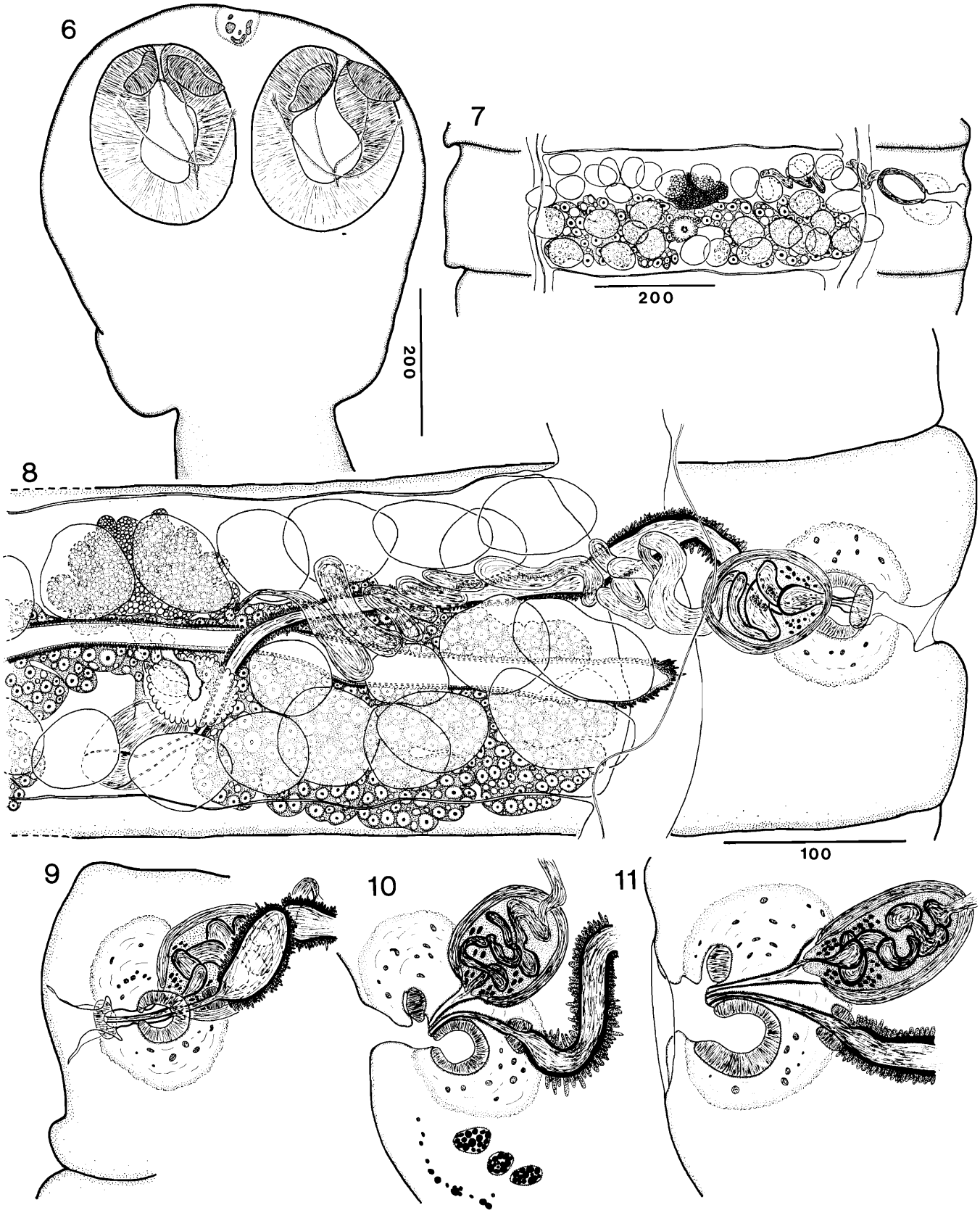
SPECIMENS: From type host and locality, collected by L.N. Measures, 25 August 1992: holotype CMNP No. 1993-0031; Paratypes CMNP Nos. 1993-0032-0034 and 0035-0037 (2 specimens; 3 slides each); USNPC Nos. 82826, 82827, 82828 (3 specimens with 3, 3, and 4 slides each) and a paratype and voucher in the collection of MLI. Additional vouchers include 4 specimens from among 5 of 15 ringed seals collected during 4–9 September 1993 (not used in the description): USNPC Nos. 83740, 83741, 83742, 83743.

ETYMOLOGY: The specific name *inuitorum* (latinization of the noun "Inuit," to form the genitive plural; translated as "the people") refers to the Inuit of Arctic Canada and acknowledges their contributions to zoological research in the North.

Comments

Specimens of *Anophryocephalus inuitorum* sp.nov. may be differentiated from those of *A. nunivakensis*, *A. eumetopii*, and *A. ochotensis* by the absence of parenchymal invaginations associated with the bothridia, the presence of an elongate cirrus sac, a straight rather than ventrally decurved male canal and atrial region of the vagina, substantially fewer testes, and specific combinations of other characters. It may be distinguished from *A. anophrys* primarily by the absence of bothridial opercula, the structure of the genital atrium (solid versus bipartite muscular pad; relatively long male canal; presence of atrial vaginal sphincters), and distribution of the testes and ovary.

Figs. 6–11. *Anophryocephalus arcticensis* sp.nov. (drawn from the holotype; all scale bars are in micrometres; the scale is the same in Figs. 8–11). Fig. 6. Scolex, showing muscular bothridia with opercula and contained within parenchymal invaginations; also note vestiges of the apical pedicle. Fig. 7. Mature proglottis in dorsal view, showing the overall distribution of the testes and the position of the ovary. Fig. 8. Mature proglottis in dorsal view, showing detail of male and female systems in the poral half of the segment.



Note the minuscule dorsal osmoregulatory canal and position of the genital ducts. Fig. 9. Genital atrium in ventral view; note the dilatation of the proximal vagina, vaginal sphincter, and muscular chamber. Fig. 10. Genital atrium, viewed from the anterior, showing the structure and disposition of the male canal, ventral chamber, and vaginal sphincter in a mature proglottis. Fig. 11. Genital atrium, viewed from the anterior, showing the structure in a pregravid proglottis.

Table 1. Comparison of specimens of *Anophryocephalus inuitorum* sp.nov. from Quebec and *A. skrjabini* from the Alaskan Arctic and eastern Bering Sea.

	A. skrjabini[a]	*A. inuitorum*
Strobila (length)	576 mm	59.5–84.1 mm
Scolex (width)	372–515	273–468
Bothridia		
Length	214–260 (235)	138–216 (165)
Width	170–238 (201)	99–192 (140)
Neck (length)	16–28 mm	3.0–5.9 mm
Testes (number)	24–41 (32)	14–27 (19)
Cirrus sac (length)	68–106 (88)	31–70 (49)
Genital atrium (diam.)	68–135 (95)	44–68 (57)
Genital ducts[b]	Between	Dorsal
Male canal (length)	28–52 (40)	23–42 (32)
Cirrus sac : male canal[c]	0.28–0.56	0.47–0.82
Atrium : male canal[d]	0.33–0.53	0.52–0.62
Ovary (position)[e]	Posterior 2/3	Fills segment
Chamber (diam.)[f]	20–29 (25)	16–36 (26)
Atrium : chamber[g]	0.21–0.29	0.36–0.53
Oncosphere		
Length	17–27 (22)	26–34 (30)
Width	10–15 (13)	18–31 (23)
Oncospheral hooks, medial (length)	11–13 (12)	15–18 (16)

NOTE: Numbers in parentheses are means.

[a]Data include corrected values for data originally presented in Table 2 of Hoberg et al. (1991) for specimens from Alaska.

[b]Position with respect to the osmoregulatory canals.

[c]Ratio of cirrus sac length to male canal length; indicative that the male canal is relatively longer in *A. inuitorum*.

[d]Ratio of genital atrium diameter to male canal length; indicative that the male canal is relatively longer in *A. inuitorum*.

[e]Position in the segment with respect to the anterior and posterior margins of the proglottis.

[f]Diameter of ventral muscular chamber determined in whole mounted specimens.

[g]Ratio of diameter of genital atrium to inside diameter of ventral chamber; indicative that the ventral chamber is relatively larger in *A. inuitorum*.

Specimens of *A. inuitorum* resemble those of *A. skrjabini*, based on similarities of the scolex in these species. Although the scolex is round to rectangular, with prominent muscular bothridia lacking opercula or parenchymal invaginations, the large and fleshy auricular appendages characteristic of *A. inuitorum* are not confluent in the anterior. Discounting the overall similarity of the holdfast in these species, *A. inuitorum* is readily distinguished by smaller dimensions of the neck, strobila, and most organs of the genital system (Table 1). The dorsal osmoregulatory system becomes atrophied earlier in *A. inuitorum* than in *A. skrjabini*, where it continues to be present in mature proglottids, and the genital ducts pass between the dorsal and ventral canals. In the male system, there are fewer testes (distributed in a single layer rather than in 2–3 layers) and the dimensions of the cirrus sac, diameter of the genital atrium, and length of the male canal are smaller than in *A. skrjabini*, but the relative length of the male canal is greater (determined from ratios of the cirrus sac to the male canal and the genital atrium to the male canal). The attributes of the female system also differ substantially in *A. inuitorum*, where the proportion of the mature proglottis filled by the ovary is greater, a vaginal sphincter is present, the atrial vagina is aspinose and there are larger embryophores, oncospheres, and oncospheral hooks than in *A. skrjabini*. Additionally, although the dimensions of the ventral chamber overlap substantially, the ratio of the diameter of the genital atrium to the ventral chamber indicates that this structure is relatively larger in *A. inuitorum*.

Anophryocephalus arcticensis sp.nov. Figs. 6–11, 14, 15

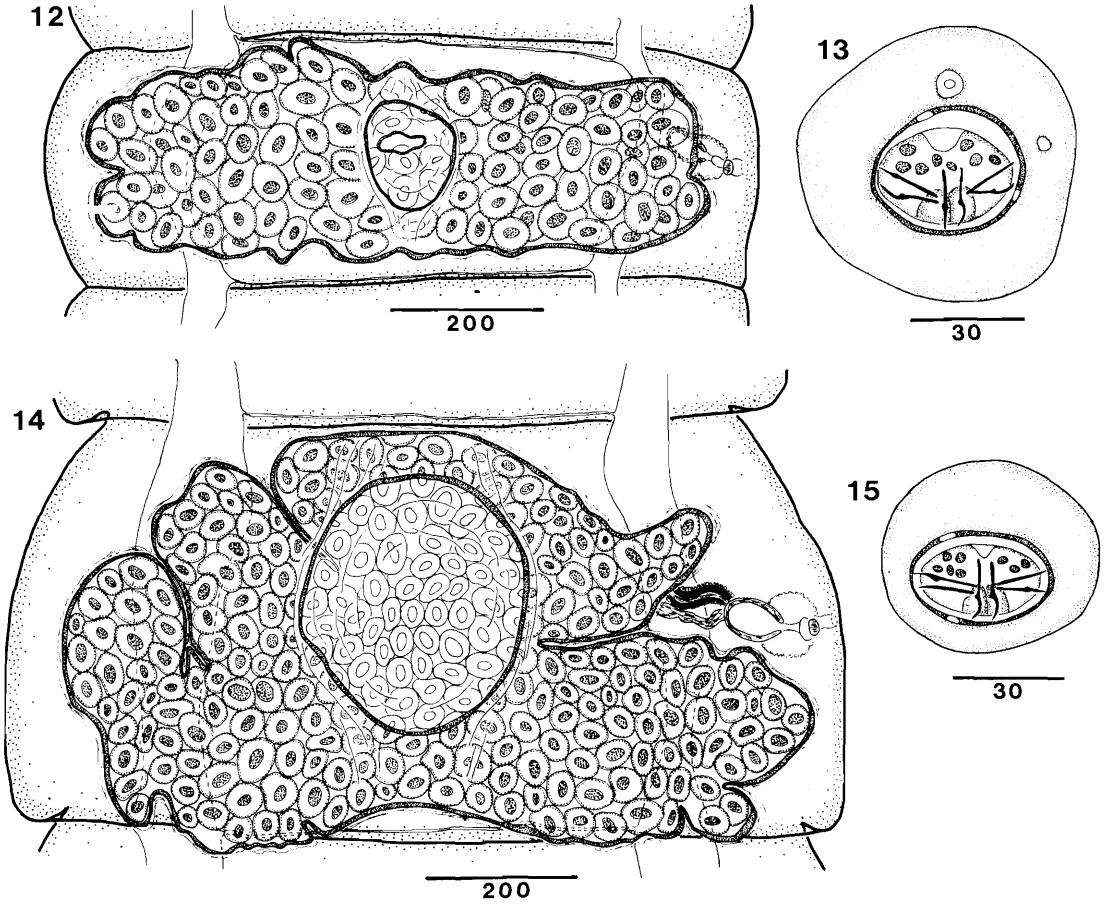
General description

Large, weakly craspidote cestodes, 246.9–319.5 mm in maximum length, 1420 in width, and with up to 1847 segments in gravid specimens. Proglottids wider than long in immature and mature strobila, increasing in length when gravid; 200–280 × 850–1110 in mature and 550–700 × 1125–1420 in pregravid to gravid segments. Length:width ratio 1:3.09–5.55 in mature segments, 1:1.88–2.58 in pregravid to gravid segments. Scolex round to rectangular, slightly wider than long, (n = 6) 450–535 (505 ± 31.30) × 490–560 (524 ± 29.87), with prominent rounded apical region; pedicle or former point of attachment of apical sucker visible in 4 specimens. Suckerlike bothridia with opercula; with prominent gaps along anterior margin; situated in shallow parenchymal invaginations; (n = 24) 182–263 (236 ± 23.74) × 172–224 (195 ± 11.76). Paired auricular appendages with independent origins, not confluent, along anterior margins of bothridia; lateral and medial appendages nearly equal in length; (n = 23) 62–86 (78 ± 6.64). Neck approximately 8.85–14.70 mm in length. Osmoregulatory canals completely developed in neck; maximum diameter of dorsal canals, 2–5, attained in the neck immediately posterior to scolex, becoming atrophied in mature segments and absent posteriad; ventral canals 8–156 in diameter, with maximum observed in pregravid to gravid segments; ventral transverse canals minuscule, 1–3 in diameter. Genital ducts pass between osmoregulatory canals in mature segments. Genital pores weakly suckerlike, unilateral, marginal on the right side, ventrolateral, in middle 1/3 of segment.

Longitudinal musculature

Musculature prominent; inner bundles arranged in single layer; outer in 1 or 2 layers. Inner bundles large, 49–58 in number and with 6–25 fibers per bundle. Outer bundles small, often single fibers, 114–142 in number and with 1–5 fibers per bundle.

Figs. 12–15. Gravid proglottids and eggs of *Anophryocephalus inuitorum* sp.nov. and *A. arcticensis* sp.nov. (all scale bars are in micrometres). Fig. 12. Gravid segment of *A. inuitorum* in dorsal view, showing median uterine pore and extent of gravid uterus. Fig. 13. Oncosphere, embryophore, and capsule typical of *A. inuitorum*. Fig. 14. Gravid segment of *A. arcticensis* in dorsal view, showing the median expansion of the uterus through the uterine pore, and the extent of the gravid uterus. Fig. 15. Oncosphere, embryophore, and capsule typical of *A. arcticensis*.



Male genitalia

Genital Anlagen visible in earliest proglottids; testes discernible in 150–200th segment; genital pore patent and maturity attained by 1100th segment. Testes (n = 100 segments in 4 strobila) 24–44 (32 ± 3.64) in number; (n = 150) 36–70 (53 ± 8.68) in greater diameter; situated dorsally in 2–3 layers, completely overlapping ovary and female organs. Vas deferens highly convoluted, situated dorsal to poral testes, extending to the median line, in anterior part of segment. Cirrus sac elongate, consistently longer than wide in all stages of development, maximum dimensions attained in postmaturity, (n = 269) 60–98 (76 ± 6.48) × 44–73 (57 ± 4.55); generally not attaining poral ventral osmoregulatory canal. Cirrus sac with muscular wall, 10–16 in maximum thickness, containing vas deferens and muscular, aspinose cirrus. Genital atrium ovoid, weakly muscular, (n = 175) 65–104 (81 ± 8.17) in diameter as determined in whole mounts, maximum dimensions attained in postmature segments. Cirrus sac situated in mediodorsal wall of genital atrium; cirrus extends into atrial lumen through dorsal, straight to slightly curved, laterally directed male canal; (n = 88) 33–57 (44 ± 5.30) in length, attaining maximum in postmaturity. Aperture of male canal opening on weakly developed papilla. Length of cirrus sac : length of male canal 1:0.42–0.71; diameter of genital atrium : length of male canal 1:0.40–0.75. Prominent, solid muscular pad located dorsal to aperture of male canal.

Female genitalia

Ovary multilobate, with 2 prominent wings, evident by 400th segment; developed by 900–1000th segment; 382–750 in length when mature and filling posterior 2/3 of segment, extending laterally to ventral osmoregulatory canals in late maturity. Vitelline gland globular to transversely elongate, with lobation, (n = 150) 68–150 (113 ± 14.15) × 47–91 (65 ± 10.39), located anteroventral to ovary on midline. Single broad vitelline duct extends posteriad ventral to ovary. Mehlis' gland located either poral or antiporal to the midline, posterior and dorsal to ovarian isthmus; (n = 140) 39–70 (53 ± 6.51) in diameter. Inner seminal receptacle ellipsoidal, situated ventral to Mehlis' gland near median line; (n = 30) 44–78 (65 ± 6.99) in greater diameter. Vagina extends porad from the inner seminal receptacle, passing dorsally to transverse stem of uterus; covered by a thick cellular epithelium. Vaginal seminal receptacle present as dilatated region where vagina crosses poral osmoregulatory canal. Atrial region of vagina aspinose, extending through genital atrium ventral to cirrus sac; sphincters near vaginal

aperture well developed. Vaginal aperture with weak papilliform structure, opening immediately ventral to male canal and dorsal to prominent muscular chamber that is confluent with ventral wall of genital atrium; inside diameter of chamber as determined in entire specimens, (n = 180) 10–29 (19 ± 3.63); maximum attained in late mature segments, variable in dimensions in gravid proglottids; diameter of genital atrium : diameter of muscular chamber 1:0.13–0.36. Ascending uterine stem extends dorsally from Mehlis' gland to join transverse tubular uterus visible in about 900th segment; Anlagen of uterine pore evident in immature segments. Transverse uterus extends ventral to testes and vagina but dorsal to ovary; irregular sacculate structure evident in 1200–1250th segment. Preformed uterine pore intermittently patent by 1250th segment but before gravid state is attained. Pregravid to gravid uterus, a lobate sac, extending dorsally beyond ventral osmoregulatory canals.

Eggs

Membranous uterine capsules not determined; containing embryophore, (n = 50) 29–41 (36 ± 3.08) × 20–29 (25 ± 2.87) and oncosphere, (n = 50) 24–34 (30 ± 2.96) × 14–21 (19 ± 1.63). Oncospheral hooks of dissimilar lengths; medial hooks, (n = 40) 13–16 (15 ± 0.66) long and lateral hooks, (n = 50) 15–18 (16 ± 0.84).

HOST: Type host *Phoca hispida hispida* Schreber; collected from among 5 of 15 seals; prevalence and intensity not determined, as individual host records were not maintained. Also reported from harp seals, *Phoca groenlandica* Erxleben; collected from 4 of 57 seals in the St. Lawrence River estuary, Canada.

LOCALITY: Type locality Hudson Strait, near Salluit, northern Quebec, Canada (62°13′N, 75°39′W), including Sugluk Inlet (62°13′N, 75°39′W) and Deception Bay (62°10′N, 74°42′W). Also reported from the St. Lawrence River estuary near Les Escoumins, Quebec (48°21′N, 69°24′W), and Sept-Îsles, Quebec (ca. 50°12′N, 66°23′W).

HABITAT: Small intestine.

SPECIMENS: From type host and locality, collected by L.N. Measures on 4–9 September 1993: holotype, CMNP No. 1994-0028 (8 slides); paratypes, CMNP Nos. 1994-0029, 1994-0030 (single slides), 1994-0031 (2 slides); USNPC Nos. 83744 (8 slides), 83745 (9 slides), 83737, 83738 (single slides), 83739 (2 slides); and vouchers, CMNP Nos. 1994-0032, 1994-0033 (single slides). Additional vouchers from harp seals (not used in the description): CMNP Nos. 1994-0035-0039, 1994-0044-0053, 1994-0040-0043, 1994-0034. Unmounted fragments of strobila from *P. hispida* and *P. groenlandica* were deposited at MLI.

ETYMOLOGY: The specific name *arcticensis* refers to the high boreal to Arctic latitudes of eastern Canada where this cestode is known to occur.

Comments

Specimens of *Anophryocephalus arcticensis* sp.nov. may be differentiated from those of *A. anophrys*, *A. skrjabini*, and *A. inuitorum* by the presence of parenchymal invaginations associated with the bothridia. The species is further distinguished from *A. anophrys* on the basis of the structure of the bothridial opercula, genital atrium (presence of a solid muscular pad, longer male canal), greater numbers of testes, an atrial vaginal sphincter, and longer neck. Additional attributes that separate *A. arcticensis* and *A. inuitorum* include the presence of bothridial opercula, substantially larger dimensions of the strobila, neck, and most organs, greater numbers of testes, testes distributed in 2 or 3 layers, genital ducts that pass between the osmoregulatory canals, and an ovary that does not fill the entire proglottis when mature. Although the morphology of the reproductive organs and genital atrium is relatively similar in *A. arcticensis* and *A. skrjabini*, the former species is identified by the presence of bothridial opercula, a shorter neck region, the presence of a vaginal sphincter, and substantially larger embryophores and oncospheres.

Anophryocephalus arcticensis is distinguished from both *A. eumetopii* and *A. ochotensis* by the structure of the scolex, a longer neck, the presence of an elongate cirrus sac, a straight rather than ventrally decurved male canal and atrial region of the vagina, the presence of a vaginal sphincter, and an aspinose vagina. In contrast to *A. arcticensis*, bothridial opercula characteristic of *A. eumetopii* are of a different structure, and they are absent in *A. ochotensis*.

Table 2. Comparison of specimens of *Anophryocephalus arcticensis* sp.nov. from Quebec and *A. nunivakensis* from the eastern Bering Sea.

	A. nunivakensis[a]	*A. arcticensis*
Strobila (length)	532 mm	246.9–319.5 mm
Scolex (width)	333–606	490–560
Bothridia		
Length	174–243 (212)	182–263 (236)
Width	136–223 (171)	177–224 (195)
Neck (length)	4.6–9.9 mm	8.85–14.7 mm
Testes (number)	26–56 (36)	24–44 (32)
Cirrus sac (length)[b]	57–95 (78)	60–98 (76)
Genital atrium (diam.)	68–109 (86)	65–104 (81)
Genital ducts[c]	Between	Between
Male canal (length)	26–60 (42)	33–57 (44)
Cirrus sac : male canal[d]	0.40–0.63	0.42–0.71
Atrium : male canal[e]	0.38–0.55	0.40–0.75
Ovary (position)[f]	Posterior 2/3	Posterior 2/3
Chamber (diam.)[g]	14–36 (26)	10–29 (19)
Atrium:chamber[h]	0.20–0.33	0.13–0.36
Oncosphere		
Length	18–24 (22)	24–34 (30)
Width	12–16 (13)	14–21 (19)
Oncospheral hooks, medial (length)	11–12 (11.5)	13–16 (15)

NOTE: Numbers in parentheses are means.

[a]Data are from Hoberg et al. (1991).

[b]The cirrus sac is spheroidal rather than elongate in *A. nunivakensis*; this measurement is given as the diameter.

[c]Position with respect to the osmoregulatory canals.

[d]Ratio of cirrus sac length to male canal length.

[e]Ratio of genital atrium diameter to male canal length.

[f]Position in segment with respect to the anterior and posterior margins of the proglottis.

[g]Diameter of ventral muscular chamber determined in whole mounted specimens.

[h]Ratio of diameter of genital atrium to inside diameter of ventral chamber.

Specimens of *A. arcticensis* most closely resemble those of *A. nunivakensis*, based on similarities of the scolex in these species. The scolex is round to rectangular, the prominent muscular bothridia have opercula open to the anterior and are contained in shallow parenchymal invaginations, and the large and fleshy auricular appendages are not confluent in the anterior. Discounting the overall similarity of the holdfast and attributes of the reproductive organs in these species, *A. arcticensis* is readily distinguished by the greater dimensions of the neck, an elongate cirrus sac with a substantially thicker muscular wall, a more globular vitelline gland, and larger embryophores and oncospheres (Table 2).

Key to the species of *Anophryocephalus* Baylis, 1922

1 (8) Scolex with bothridial opercula

2 (3) Opercula with narrow, slitlike longitudinal apertures not extending beyond margins of bothridia; cirrus sac elongate; genital papilla absent; muscular pad of atrium bifurcate; parasites of *Phoca hispida* and *Cystophora cristata*, Palearctic sector of the North Atlantic and Arctic basin ..... *Anophryocephalus anophrys*

3 (2) Opercula with apertures extending beyond muscular margins of bothridia; bothridia contained in invaginations of parenchyma; muscular pad solid; genital papilla present

4 (5) Apertures of opercula diagonal; genital papilla prominent; male canal strongly decurved ventrally; atrial vagina spinose, lacking sphincter; cestodes of *Eumetopias jubatus*, Bering Sea and northern North Pacific basin ..... *Anophryocephalus eumetopii*

5 (4) Apertures of opercula longitudinal, opening broadly to anterior; bothridia with marginal gap anteriorly; genital papilla weakly developed; vagina aspinose, with sphincter

6 (7) Cirrus sac ovoid; neck relatively short (<10 mm); oncospheres 18–24 μm long; cestodes of *Phoca largha*, Bering Sea ..... *Anophryocephalus nunivakensis*

7 (6) Cirrus sac elongate; neck long (9–15 mm); oncospheres 24–34 μm long; cestodes of *Phoca hispida* and *Phoca groenlandica*, Nearctic sector of the North Atlantic and Arctic basin ..... *Anophryocephalus arcticensis* sp.nov.

8 (1) Scolex lacking bothridial opercula

9 (10) Scolex rounded; bothridia contained within parenchymal invaginations; neck short (≈2 mm); cirrus sac ovoid; genital papilla prominent; muscular pad minuscule; male canal strongly decurved ventrally; cestodes of *Eumetopias jubatus*, Bering Sea and northern North Pacific basin ..... *Anophryocephalus ochotensis*

10 (9) Scolex rectangular, bothridia lacking parenchymal invaginations; cirrus sac elongate; genital papilla weakly developed

11 (12) Neck exceptionally long (>16 mm); auricular appendages confluent in anterior; testes 26–56 in number; ovary occupies posterior region of proglottis; cestodes of *Phoca* spp., Bering Sea and northern North Pacific basin ..... *Anophryocephalus skrjabini*

12 (11) Neck relatively short (<6 mm); auricular appendages not confluent; testes 14–27 in number; ovary filling entire proglottis; cestodes of *Phoca hispida*, eastern Canada, Nearctic sector of Arctic basin ..... *Anophryocephalus inuitorum* sp.nov.

Discussion

Anophryocephalus inuitorum sp.nov. and *Anophryocephalus arcticensis* sp.nov. are the first species of this genus to be described from ringed seals in the Arctic basin of eastern Canada. Although both species were collected during the 1993 field season at Salluit, Quebec, it cannot be determined from collection records whether they occurred in mixed infections in individual ringed seals. In the North Pacific, where 4 species of *Anophryocephalus* are sympatric, infections involving multiple species in a phocid or otariid host have not been recorded (Hoberg et al. 1991).

Previously, only *A. anophrys* had been recognized from phocines at high latitudes in the Atlantic basin (Baylis 1922; Temirova and Skrjabin 1978). However, this species appears to be primarily a parasite of *P. hispida* in the eastern Atlantic sector of the Arctic (Hoberg and Adams 1992). With the discovery of *A. inuitorum* and *A. arcticensis* in phocines of the Canadian Arctic and Subarctic, previous reports of *A. anophrys* from this region are equivocal. Specifically, the single report of *A. anophrys* in *P. groenlandica* from coastal Newfoundland was not accompanied by voucher material (Smith and Threlfall 1973) and may be referrable to *A. arcticensis*, based on the results of the current study and the occurrence of the latter species in harp seals from the Gulf of St. Lawrence.

Specimens from the current collection allow further consideration of hypotheses concerning the ontogeny of tetrabothriid cestodes (Hoberg 1987*b*; Hoberg et al. 1991). The presence of a residual pedicle or other vestiges of an apical sucker at the apex of the scolex in 5 specimens of *A. inuitorum* (Fig. 1) and 4 specimens of *A. arcticensis* (Fig. 6) provides further indication of the uniformity in postlarval development of the adult holdfast in species of *Anophryocephalus* and *Tetrabothrius* (Hoberg 1987*b*). Rapid development of strobilate specimens of *A. inuitorum* and *A. arcticensis* is also indicated by the young age of some definitive hosts in the current study. This appears consistent with the recognition of an apical sucker (or its vestiges) among specimens of *A. skrjabini* and *A. nunivakensis* (Hoberg et al. 1991). The contention that infective metacestodes (plerocercoids) in the intermediate or paratenic host

should possess an apical sucker, with development of bothridia occurring subsequent to ingestion by the pinniped definitive host, is not refuted (Hoberg 1987*b*). Consequently, the pattern of heterochronic development in the holdfast of tetrabothriids is not consistent with the identification of "*Anophryocephalus*" plerocercoids with fully formed adult scolices (lacking an apical sucker) in piscine paratenic hosts as reported by Avdeeva (1989) (see also Hoberg and Adams 1992).

A life cycle involving 2 or 3 hosts has previously been postulated for *Anophryocephalus*, with macrozooplankton such as euphausiids as first intermediate hosts (Murav'eva and Popov 1976; Hoberg 1987*b*; Hoberg and Adams 1992). In this regard, Dunbar (1949) and McLaren (1958) reported a wide variety of pelagic crustaceans and fishes as food items for *P. hispida*, but the predominant prey were amphipods (*Parathemisto libellula* (Lichtenstein)), mysids (*Mysis oculata* (Fabricius)), and polar cod (*Boreogadus saida* (Lepechin)); the 5 ringed seals examined in 1992 had full stomachs containing *M. oculata*. Prey selection by ringed seals and other ice-dwelling phocines such as *P. largha* may vary locally and seasonally (Lowry and Frost 1981; Frost and Lowry 1984) and can depend on whether populations are associated with pack or fast ice. Such variation in foraging and food habits has a direct influence on the focal nature of helminth faunas in seals (Finley et al. 1983; Deliamure et al. 1984; Hoberg 1992). Although prey selection appears opportunistic (Davies 1958; King 1983), the dynamics of food webs in ice-edge communities of the high Arctic suggest that polar cod could function as important paratenic hosts for *Anophryocephalus* spp. in these environments (Bradstreet 1982; Bradstreet and Cross 1982).

A more diverse prey base is exploited by harp seals of the western Atlantic, and food habits change with age and annual seasonal distribution. Fishes and pelagic crustaceans are the predominant prey, with *Mallotus villosus* (Müller) and euphausiids being taken on the wintering grounds from Newfoundland into the Gulf of St. Lawrence. In the Subarctic and Arctic, *Boreogadus saida*, amphipods, and mysids constitute the primary prey during the summer (Sergeant 1991; Murie and Lavigne 1991). Foraging occurs primarily in pelagic environments, although adult seals may feed on some demersal fishes and crustaceans (Sergeant 1991). As with ringed seals, such food habits are compatible with pelagic crustaceans serving as intermediate hosts and fishes as paratenic hosts for *Anophryocephalus* spp.

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