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Historical biogeography and modes of speciation across high-latitude seas of the Holarctic: concepts for host – parasite coevolution among the Phocini (Phocidae) and Tetrabotheiidae (Eucestoda)

Eric P. Hoberg

Abstract: Species of *Anophryocephalus* are host-specific parasites of pinnipeds in the Holarctic. Phylogenetic analysis of 7 species postulates *A. anophrys* as the basal taxon and *A. inuitorum* as basal to *A. skrjabini*; *A. arcticensis* is basal to *A. nunivakensis* and *A. eumetopii* + *A. ochotensis* (single tree; consistency index = 74.4%; homoplasy slope ratio = 36.45%). Evaluation of host and geographic distributions postulates ringed seals of the Atlantic–Arctic as ancestral hosts, and the Arctic basin as a paraphyletic area with respect to the North Pacific. Cospeciation within this assemblage was dependent on intense isolation of small effective populations of definitive hosts during the late Tertiary and Pleistocene glacial stages. Rapid modes of parasite speciation, compatible with microallopatry and peripheral isolation, appear to have been associated with isolation of pinniped populations in refugial habitats of the Arctic basin and Beringia. The biogeography of host–parasite assemblages among pinnipeds and Alcidae (Charadriiformes) during the Pliocene and Quaternary contrasts in part with the history elucidated for some free-living invertebrate taxa in the Arctic basin.

Résumé : Les *Anophryocephalus* sont des parasites spécifiques à certaines espèces de pinnipèdes dans la région holarctique. L'analyse phylogénétique de sept espèces indique qu'*A. anophrys* est probablement le taxon ancestral et qu'*A. inuitorum* est un taxon ancestral d'*A. skrjabini*; *A. arcticensis* est un taxon ancestral d'*A. nunivakensis* et d'*A. eumetopii* + *A. ochotensis* (arbre unique; indice de compatibilité, CI = 74,4%; coefficient d'homoplasie, HSR = 36,45%). L'étude des hôtes et de leurs répartitions géographiques indique que les Phoques annelés de l'Atlantique–Arctique sont les hôtes ancestraux et que le bassin de l'Arctique constitue probablement la région paraphylétique par rapport au Pacifique Nord. La cospéciation au sein de cette association résulte de l'isolement important de petites populations productives des hôtes terminaux au cours des époques glaciaires de la fin du Tertiaire et du Pleistocène. La spéciation rapide des parasites, phénomène compatible avec les hypothèses de la microallopatrie et de l'isolement périphérique, a probablement résulté de l'isolement de populations de pinnipèdes dans des refuges du bassin de l'Arctique et de la Béringie. La biogéographie des associations hôtes-parasites chez les pinnipèdes et chez les Alcidae (Charadriiformes) au cours du Pliocène et du Quaternaire, contredit partiellement l'histoire évolutive de certains taxons d'invertébrés non parasites qui vivent dans le bassin de l'Arctique.

[Traduit par la Rédaction]

Introduction

The host-distribution and historical biogeography of the tetrabotheiid cestodes of the genus *Anophryocephalus* Baylis, 1922 is consistent with a relatively recent radiation in the Holarctic since the Late Pliocene (Hoberg and Adams 1992). The macroevolutionary history of this assemblage of hosts and parasites has involved extensive colonization and specia-

tion among the Phocini of the North Atlantic, Arctic, and North Pacific basins. Among the 7 species of *Anophryocephalus*, 5 are characteristic of the tribe Phocini and genus *Phoca* (classification according to Wyss 1988) and include *Anophryocephalus anophrys* Baylis, 1922, *A. inuitorum* Hoberg and Measures, 1995, and *A. arcticensis* Hoberg and Measures, 1995 from the Atlantic sector of the Arctic basin, and *A. skrjabini* (Krotov and Deliamure, 1955) and *A. nunivakensis* Hoberg, Adams, and Rausch, 1991, which are endemic to the northern 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; Hoberg and Measures 1995).

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Table 1. Character matrix for species of *Anophryocephalus*.

	Character																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Tetrabothriid out-groups ^a	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
<i>A. anophrys</i>	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. ochotensis</i>	1	0	0	1	1	0	0	1	1	0	1	1	1	1	2	2	2	1	1	1	1	1	0	0	0	1
<i>A. skrjabini</i>	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	1	1	0	0	1	1
<i>A. nunivakensis</i>	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	0	0	1	0	1
<i>A. eumetopii</i>	1	0	1	0	1	0	0	1	1	0	1	1	1	0	2	2	2	1	1	1	1	1	0	0	0	1
<i>A. inuitorum</i>	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0
<i>A. arcticensis</i>	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0	1

NOTE: Characters are consistent with those presented by Hoberg and Adams (1992) unless specified otherwise in the Materials and methods: 1, apical region (development); 2 and 3, opercula associated with bothridia; 4, auricles on bothridia (confluence); 5, parenchymal envelopes associated with bothridia; 6, osmoregulatory canals (ventral transverse); 7, osmoregulatory canals (dorsal); 8, osmoregulatory canals (ventral); 9 and 10, neck (length); 11, genital pore (position); 12, genital pore (structure); 13, cirrus sac (form); 14, cirrus sac (wall); 15, genital atrium (genital papilla); 16, genital atrium (genital papilla); 17, genital atrium (muscular pad); 18, testes (number); 19, testes (position); 20, male canal (direction); 21, vagina (atrial armature); 22, vaginal seminal receptacle; 23, testes (distribution); 24, bothridia (anterior gap); 25, vitelline gland (lobation); 26, genital ducts (position).

^aIncluding *Tetrabothrius* spp., *Chaetophallus* spp., and *Trigonocotyle* spp.

Diversification of this parasite assemblage appears to have been strongly influenced by a history of restricted breeding populations of phocine seals in the Holarctic (Hoberg 1992). Since the Late Pliocene, radiation of these tetrabothriids has been associated only with pinnipeds from high-latitude seas of the Holarctic (Hoberg and Adams 1992). Among recognized hosts of *Anophryocephalus*, ringed seals (*Phoca (Pusa) hispida* Schreber) were apparently one of few species of marine mammals to remain in the Arctic basin during glacial maxima (Davies 1958). Putative sub-specific differentiation of ringed seals, particularly around the margins of the Arctic basin but also in the Bering Sea and Sea of Okhotsk, is indicative of historical isolation of numerous populations since the Pliocene (Anderson 1942; Davies 1958; Ray 1976; King 1983). Contemporary isolation of local populations has been further reinforced by the largely sedentary habits of these seals (McLaren 1958; Finley et al. 1983).

Isolation of populations of definitive hosts is a putative driving mechanism for allopatric speciation of parasites, a hypothesis examined in detail in the current study. In this respect, *A. anophrys* is associated with *Phoca hispida hispida* (and several incidental phocid hosts) in the Palearctic–Atlantic sector of the Arctic, whereas *A. skrjabini* is found in *P. h. krascheninnikovi* Naumov and Smirnov (Bering Strait region) and *P. h. ochotensis* Pallas (Sea of Okhotsk) from the North Pacific in addition to *P. largha* Pallas, *P. fasciata* Zimmerman, and *Phoca vitulina richardsi* (Gray). The distribution of hosts and parasites and the postulated history of local isolation of populations of ringed seals suggested that additional species of *Anophryocephalus* might be found among the Phocini in the Holarctic (Hoberg and Adams 1992). This was confirmed with the discovery of *A. inuitorum* and *A. arcticensis* in *P. h. hispida* and *P. groenlandica* Erxleben in the Nearctic–Atlantic sector of the Arctic (Hoberg and Measures 1995).

In the current study, I present a revised phylogenetic analysis of the genus *Anophryocephalus*, including the recently discovered species from the eastern Canadian Arctic (Hoberg

and Measures 1995). The results of this analysis promote a more refined hypothesis to be developed for host–parasite coevolution and historical biogeography of *Anophryocephalus* among the Phocini and constitute an extension of concepts presented by Hoberg and Adams (1992). Additionally, the distributional history postulated for this parasite–host assemblage is compared with that which has been elucidated for free-living marine taxa in benthic and pelagic environments of the Holarctic (North Pacific, Arctic Basin, North Atlantic) by Briggs (1970), Marinovich et al. (1990), and Dunton (1992) in an attempt to identify replicated historical patterns in the region.

Materials and methods

Phylogenetic analysis (Hennig 1966; Wiley 1981) of 5 nominal species of *Anophryocephalus* (*A. anophrys*, *A. skrjabini*, *A. nunivakensis*, *A. ochotensis*, and *A. eumetopii*) was previously conducted by Hoberg and Adams (1992). In the current study, a revised analysis of 7 taxa is presented and includes *A. inuitorum* and *A. arcticensis*. Twenty-six morphological characters, representing 29 states (0 = plesiomorphic; 1 or 2 = apomorphic), were included in the analysis and are consistent with those used by Hoberg and Adams (1992) unless specified otherwise (Table 1). The current study also entailed reexamination of all species of *Anophryocephalus* (see Hoberg et al. 1991) as a basis for comparison. Out-groups included basal genera of the Tetrabothriidae, *Tetrabothrius* Rudolphi, 1819, *Chaetophallus* Nybelin, 1916, and *Trigonocotyle* Baer, 1932, as indicated by previous phylogenetic analysis (Hoberg 1989). More precise definitions or coding were developed for 6 characters, and 5 new characters (22–26) are included in the analysis (Table 1). The potential influence of these changes in character coding is considered.

Characters were analyzed with PAUP 2.4.1 (Swofford 1985) using the ALLTREES option and rooted with ANCESTOR (tetrabothriid out-groups) and employed FARRIS optimization; multistate transformation series were ordered. Associated measures of homoplasy were calculated for the complete

analysis and included the consistency index (CI) (Kluge and Farris 1969; Farris 1970), the homoplasy slope ratio (HSR) (Meier et al. 1991), the mean random CI (CI_{random}), and adjusted CI ($CI_{\text{adjusted}} = CI_{\text{actual}} - CI_{\text{random}}$) (Klassen et al. 1991). The HSR (defined by Meier et al. (1991) as “the average level of homoplasy that would be displayed in a series of analyses based on random data sets of the same size”) and CI_{random} (defined by Klassen et al. (1991) as “the minimum value real data sets should exceed to be considered to contain phylogenetic information”) constitute indicators of the degree to which a phylogenetic hypothesis departs from random.

Results

Character argumentation

In the phylogenetic analysis of *Anophryocephalus* presented herein, refined or more precise definitions were developed for 6 characters originally evaluated by Hoberg and Adams (1992); other characters are consistent with the previous study. Additionally, 5 new characters, not previously recognized or considered (22–26), are analyzed. These attributes are presented below and in a numerical matrix along with abbreviated definitions (Table 1).

Character 7. Osmoregulatory canals (dorsal). 0 = atrophied dorsal canal present and discernible in mature segments; 1 = atrophied dorsal canal present in neck, absent posteriad. No changes in coding resulted, but this definition more strictly specifies the relationship for the development of the dorsal osmoregulatory canals.

Characters 9 and 10. Neck (length). Originally coded as a single multistate character with respect to the taxonomic out-groups, this attribute is now coded with reference to the functional out-group, *A. anophrys*. Additionally, this attribute was split into separate transformation series to allow postulated independent derivation of short (≤ 3.0 mm: 1,0) and long necks (≥ 10.0 mm: 0,1) with reference to the plesiomorphic condition of medium length (≈ 7.0 mm; 0,0). Character 9. 0 = medium or long; 1 = short. Character 10. 0 = medium or short; 1 = long.

Character 14. Cirrus sac (wall). 0 = thick, heavily muscularized; 1 = relatively thin, weakly muscularized. This character was incorrectly coded in the original analysis, as determined by examination of specimens during the current study (new coding is presented for all in-group taxa).

Character 18. Testes (number). 0 = mean number < 25 ; 1 = mean number > 30 . A more accurate definition of this character was based on a comparison of the mean number of testes (new coding was required only for *A. ochotensis* = 1).

Character 19. Testes (position). 0 = surround ovary; 1 = completely overlap female organs. This character was incorrectly coded for *A. skrjabini* in the original analysis, as it was subsequently determined that the testes completely overlap rather than surround the female organs (new coding for *A. skrjabini* = 1).

Character 21. Vagina (atrial armature). 0 = atrial region of vagina aspinose; 1 = atrial region of vagina spinose. This attribute was originally coded with reference to the taxonomic out-group. However, the presence of vaginal armature is variable among other genera and species of tetrabothriids,

consequently more precise coding in the analysis of *Anophryocephalus* spp. could be determined with reference to the functional out-group, *A. anophrys* (new coding for all in-group taxa).

Character 22. Vaginal seminal receptacle. 0 = present and well developed as a dilatation in the atrial region of the vagina; 1 = reduced or absent.

Character 23. Testes (distribution). 0 = multiple layers of testes, usually 2 or 3; 1 = single layer of testes.

Character 24. Bothridia (anterior gap). 0 = bothridia lacking prominent gap along anterior margin; 1 = bothridia with prominent gap.

Character 25. Vitelline gland (lobation). 0 = highly lobed; 1 = margins of gland smooth.

Character 26. Genital ducts (position). This character is coded with reference to the functional out-group, *A. anophrys*. 0 = genital ducts entirely dorsal to osmoregulatory system (owing to complete atrophy of dorsal system); 1 = genital ducts between dorsal and ventral canals in mature segments.

Phylogenetic analysis

Monophyly for the genus *Anophryocephalus* continues to be supported with the inclusion of *A. inuitorum* and *A. arcticensis* and is based on synapomorphies for the structure of the bothridia, osmoregulatory canals, and genital atrium which were excluded from the analysis (Hoberg and Adams 1992; Hoberg 1992). A single cladogram (Fig. 1) was produced from the analysis of 26 transformation series representing 29 character states (see Hoberg and Adams 1992). The current hypothesis was well supported with a CI of 74.4% (29 steps minimum; 39 steps postulated), HSR of 36.45% (see Meier et al. 1991), CI_{random} of 47.72%, and CI_{adjusted} of 26.68% (see Klassen et al. 1991). The CI, excluding autapomorphies (characters 2, 6, 23, and 25), is 71.4%. Homoplasy was evident in 10 characters. There were 6 postulated reversals: character 3, structure of opercula; character 7, dorsal osmoregulatory canals; character 10, neck length; character 14, wall of cirrus sac; character 19, position of testes; and character 24, bothridia with anterior gap; there were 4 postulated parallelisms: character 4, confluence of auricles; character 8, ventral osmoregulatory canals; character 21, vaginal spination; and character 22, vaginal seminal receptacle.

Anophryocephalus anophrys is postulated as the basal member of the clade, and *A. inuitorum* is basal to *A. skrjabini* + *A. arcticensis* + *A. nunivakensis* + *A. ochotensis* and *A. eumetopii* (Fig. 1). The overall topology of the tree is consistent with the original analysis of *Anophryocephalus* spp. by Hoberg and Adams (1992).

Recoding of the 6 characters as defined and justified above did not result in an overall increase in the CI with respect to the original analysis of 5 taxa (80%) (Hoberg and Adams 1992). Considering the consistency of individual characters, there was no change in characters 14 and 21 (CI = 0.50; homoplasy postulated to be reversal and reversal or parallelism, respectively). There was a reduction in consistency of characters 7 and 19 (CI = 0.50; homoplasy postulated to be reversal or parallelism and reversal, respectively) and an increase only in character 18 (CI = 1.0).

Fig. 1. Cladogram showing the relationships postulated for *Anophryocephalus* spp. Characters have been mapped onto the tree and are indicated as follows: apomorphic characters are designated by arrows, with multistate transformation being indicated by ' and "; homoplasy is designated as either reversal (star) or parallelism (asterisk). The hypothesis has CI = 74.4%, HSR = 36.45%, $CI_{\text{random}} = 47.72\%$, and $CI_{\text{adjusted}} = 26.68\%$. AANO, *A. anophrys*; AINU, *A. inuitorum*; ASKR, *A. skrjabini*; AARC, *A. arcticensis*; ANUN, *A. nunivakensis*; AEUM, *A. eumetopii*; AOCH, *A. ochotensis*.

Character 9, split into independent transformation series (characters 9 and 10) resulted in no net increase in the CI. Thus, the overall CI was not artificially inflated nor the topology of the tree altered by these changes in character state polarity.

Discussion

Allopatric speciation of pinnipeds, seabirds, and helminth parasites in the Holarctic was driven by isolation in response to habitat disruption during cyclical glacial stages through the late Tertiary and Pleistocene (Hoberg 1986, 1992). In this regime, colonization of *Phoca* sp. in the Atlantic sector of the Arctic basin in the Late Pliocene, and subsequent speciation of *Anophryocephalus* coincided with range expansion and radiation of phocines in the North Pacific during the Quaternary (Hoberg and Adams 1992; Hoberg 1992).

The historical biogeography of this host-parasite assemblage is intricate. Radiation of the 5 species of *Anophryocephalus* among phocines has had both a coevolutionary and a historical ecological component (Hoberg and Adams 1992; Hoberg 1992). With recognition of *P. hispida*, *P. fasciata*, *P. groenlandica*, *P. largha*, and *Phoca vitulina richardsi* as hosts, it is apparent that during the summer season all except *P. vitulina* forage in pelagic environments and commonly exploit zooplankton (Davies 1958; King 1983). The host specificity of parasites and foraging behavior of some phocines have constituted limitations on the potential for host switching and broad radiation of *Anophryocephalus* among Holarctic pinnipeds (Hoberg and Adams 1992).

A minimum of three species of *Anophryocephalus* are postulated to have coevolved with *Phoca hispida* (Fig. 2). The diversification of basal species of *Anophryocephalus* was associated with isolation of populations of ringed seals in the Atlantic sector of the Arctic basin (*A. anophrys*,

A. inuitorum) and North Pacific (*A. skrjabini*). Subsequent range expansion from the Bering Sea into the Arctic basin and vicariance accounting for the distribution of *A. arcticensis* coincided with movements of either *P. hispida* or the putative common ancestor of *P. fasciata* and *P. groenlandica* (as discussed in detail below). Diversification of the three species of cestodes endemic to the Arctic occurred in the absence of concomitant host speciation, but was dependent on the existence of refugial habitats.

The Atlantic basin and Arctic fauna

During Pleistocene glacial maxima, the extent of Laurentide ice over the eastern Canadian Islands eliminated these areas as potential marine refugia (CLIMAP Project Members 1976; Stravers et al. 1992; Peltier 1994). Full glaciation of the Hudson Strait area resulted in an easterly shift and restriction in the range of ringed seals to Baffin Bay and Davis Strait (Dorf 1959; Dillon 1956; Cronin et al. 1981). Subsequent range expansion associated with postglacial dispersal into Hudson Strait may have enhanced or maintained isolation of an *Anophryocephalus* sp. with a local population of *P. hispida*. Thus, isolation and vicariance of an ancestral *Anophryocephalus* species in ringed seals (leading to the divergence of *A. anophrys* and *A. inuitorum*) coincided with populations of *P. hispida* in (i) refugia in Davis Strait along unglaciated habitats of Baffin Island (Matthews 1979; Pielou 1991) and (ii) east of Greenland into the Barents Sea. Speciation resulted from vicariance, microallopatry, or peripheral isolation in refugial environments (see below). The degree to which polynias were involved in maintaining or promoting isolation of the assemblage is not known.

Refugia also existed to the south along the coasts of the Gaspé Peninsula, Newfoundland, and glacial Sable Island, including isolated ice-free islands and peninsulas (Matthews 1979; Pielou 1991; Peltier 1994). Small ephemeral coastal

Fig. 2. Cladogram for *Anophryocephalus* spp., showing host and geographic distributions mapped onto the parasite tree (for an explanation of abbreviations of parasite names see Fig. 1). These relationships are compatible with *Anophryocephalus* spp. initially colonizing *Phoca hispida* in the Atlantic sector of the Arctic Basin. Range expansion of *Anophryocephalus* spp. with *P. hispida* into the North Pacific Basin, followed by vicariance, resulted in the development of ASKR. The relationships of AARC provide the only evidence of secondary range expansion from the Pacific to the Arctic–Atlantic. ANUN represents a peripheral isolate in *P. largha* from the eastern Bering Sea. Colonization of the Otariidae and speciation of AEUM and AOCK in *Eumetopias jubatus* were outlined previously (Hoberg and Adams 1992). Facultative hosts for *Anophryocephalus* spp. are not presented on the cladogram, as they have not been implicated in the history of host–parasite diversification (see Hoberg and Adams 1992; Hoberg 1992).

refugia existed at sea level along the narrow exposed continental shelf. The highly isolated Goldthwait Sea (existing from 20 to 18 ka) and the Champlain Sea (from 10 to 12 ka) (extensions of the Gulf of St. Lawrence) provided habitats for a high latitude marine mammal assemblage (Matthews 1979; Pielou 1991; Whitmore 1994). The occurrence of ringed seals, harp seals, other pinnipeds, and cetaceans including narwhals (*Monodon monocerus* Linnaeus), beluga (*Delphinapterus leucas* (Pallas)), and bowhead whales (*Balaena mysticetus* Linnaeus) indicates the high productivity of macrozooplankton such as euphausiids in these ice-floe environments. It can be assumed that similar marine refugia were intermittently present, coinciding with glacial maxima through the Pleistocene. The recognized potential for speciation in marginal, ephemeral refugia (e.g., the Goldthwait Sea and southern Davis Strait) and postglacial expansion into currently occupied habitats reinforces the hypothesis of vicariance across the North Atlantic basin, leading to the development of *A. anophrys* and *A. inuitorum* in association with ringed seals.

Considering the coevolution of ringed seals and cestodes, Anderson (1942) and Davies (1958) recognized 4 discrete but poorly differentiated marine subspecies of *P. hispida* in the Arctic basin, 2 populations in the Canadian and Alaskan Arctic and 2 in the Russian and Siberian Arctic. However, currently only the nominal subspecies, *P. h. hispida*, is considered to reside across this region. *Anophryocephalus anophrys* has only been found thus far in the zone extending from Iceland and eastern Greenland to the White Sea (Hoberg et al. 1991; Hoberg and Adams 1992; Hoberg and Measures 1995). If through continued collections, *A. inuitorum* and *A. arcticensis* are found to have relatively limited

distributions in *P. hispida* in the eastern Canadian Arctic this would suggest relative isolation of populations of ringed seals in the Arctic (Russian/European versus eastern Canadian). Recognition of poorly differentiated but isolated populations of *P. hispida* in the Arctic basin and of the localized and sedentary habits of ringed seals is compatible with microallopatry being important in diversification of this cestode fauna (McLaren 1958; Davies 1958; Finley et al. 1983). Consequently, the possibility that additional, currently unrecognized species of *Anophryocephalus* may be distributed in this region should also be considered.

Phoca hispida hispida is recognized as the principal host for *A. inuitorum* and *A. anophrys*. Such a distribution constitutes a form of cospeciation (see Brooks and McLennan 1991) when host populations are isolated to the extent that sufficient time allows divergence of parasites but not of hosts. These events apparently predate the Pleistocene as a sequence of Late Pliocene glacials (at 3.4 and 2.5 Ma; Herman and Hopkins 1980) could have promoted vicariance and isolation of seal populations. The putative history of this assemblage in the Arctic basin is further compatible with either (i) a secondary loss of *Anophryocephalus* spp. in lacustrine subspecies of *P. hispida* (e.g., *P. h. ladogensis* Nordquist; *P. h. saimensis* Nordquist) and species of *Phoca* (*Pusa*) (e.g., *P. sibirica* Gmelin in Lake Baikal; *P. caspica* Gmelin in the Caspian Sea) or (ii) initial colonization of marine ringed seals following divergence of the *Phoca* (*Pusa*) complex (see Repenning et al. 1979; Deliamure et al. 1982; Kurochkin 1975). More refined knowledge of the phylogeny and temporal setting for speciation in the host group in the Arctic is required in order to evaluate this hypothesis.

The North Pacific and Beringian fauna

In the northern North Pacific, subspecific differentiation of *P. hispida* occurred subsequent to speciation of *A. anophrys* and *A. inuitorum* in the Arctic basin, suggesting that vicariance of a widespread population of *P. hispida* occurred in the High Arctic before ringed seals entered the North Pacific. In this situation isolation was insufficient for host speciation.

In contrast, the broad geographic range of *A. skrjabini* in *P. h. krascheninnikovi* (Bering Strait region) and *P. h. ochotensis* (Okhotsk Sea) indicates coadaptation (Brooks and McLennan 1991) at the level of host subspecies following entry to the North Pacific <2.5 Ma (Hoberg 1992) (Fig. 2). Coadaptation also explains the occurrence of *A. skrjabini* in largha seals in the Sea of Okhotsk and Bering Sea, if *P. hispida* and *P. largha* had a common ancestor (see McLaren 1966; Hoberg and Adams 1992). The basal coevolutionary relationship of *A. skrjabini* and the subspecies of *P. hispida* in the North Pacific basin provides additional support for host association by colonization for this species in *P. v. richardsi* (northern Gulf of Alaska and southeastern Bering Sea) and *P. fasciata* (Bering Sea and Sea of Okhotsk) (Hoberg and Adams 1992; Hoberg 1992) (Fig. 2). Although *P. v. richardsi* exhibits some degree of regional variation (a complex of many apparently sedentary local breeding populations) indicative of potential for local or clinal differentiation (Shaughnessy and Fay 1977), speciation of *Anophryocephalus* has apparently not occurred in this subspecies.

The distribution of *A. arcticensis* provides the only evidence for secondary movement of *Anophryocephalus* spp. with *Phoca* spp. from the North Pacific to the North Atlantic sector of the Arctic during a Pleistocene interglacial stage (Fig. 2). The occurrence of this species in both *P. h. hispida* in the Hudson Strait area and *P. groenlandica* in the Gulf of St. Lawrence suggests a complex history. This may be related to a coevolutionary association with *P. hispida* and subsequent colonization of harp seals. A putative coevolutionary association with *P. hispida* is suggested by the distribution of *A. skrjabini* in this phocine along the Alaskan–Arctic coast (Hoberg and Adams 1992). The distribution of the latter species of *Anophryocephalus* indicates the potential that existed for range expansion of hosts and parasites from west to east across the Canadian Arctic during an earlier interglacial. Thus, the contemporary range of *A. arcticensis* may have resulted from such an event, with vicariance and isolation in the eastern Canadian Arctic coinciding with the development of glacial conditions and the emergence of Beringia.

In this case, *P. groenlandica* could represent a facultative host for this cestode, but current evidence does not support this conclusion. Although relatively few seals in the St. Lawrence River estuary were found to be infected, substantial infections were evident, involving fully developed mature and gravid specimens (Hoberg and Measures 1995). Harp seals, in addition to ringed seals, may be typical hosts for *A. arcticensis*. A relatively low prevalence of infection on the wintering grounds would be compatible with harp seals acquiring cestodes during the summer when their distribution extends to High Arctic latitudes (Ronald and Dougan 1982), overlapping that of *P. hispida*. However, the potential that the cycle of *A. arcticensis* may be completed across the winter range of the western herd of harp seals, from New-

foundland into the Gulf of St. Lawrence, should not be discounted.

An alternative explanation for the occurrence of *A. arcticensis* follows from the putative sister-species association of *P. groenlandica* and *P. fasciata* (Davies 1958; DeMuizon 1982). The common ancestor of these phocines could have been infected with a species of *Anophryocephalus* in the North Pacific, with subsequent range expansion through the Arctic basin and vicariance leading to the origin of *A. arcticensis*.

Anophryocephalus nunivakensis is the only other species known from phocines in the North Pacific and its distribution appears to be limited to largha seals in the Bering Sea (Hoberg et al. 1991; Hoberg and Adams 1992) (Fig. 2). Shaughnessy and Fay (1977) recognized 8 disjunct geographic breeding populations of *P. largha* extending from the Sea of Japan through the Bering Sea. The distribution of *A. nunivakensis* corresponds roughly to the range of *P. largha* associated with the pack ice of the southeastern Bering Sea (Shaughnessy and Fay 1977; King 1983). Speciation of *A. nunivakensis* may have occurred in this region (see Hoberg and Adams 1992). However, isolation of populations of phocine hosts was insufficient to promote speciation. Post-glacial expansion had to have occurred even for such putative peripheral isolates as *A. nunivakensis*, which now occupies an area in the eastern Bering Sea that was a constituent of an emergent Beringia during eustatic reductions in sea level.

During glacial maxima the Beringian region was characterized by extremely low sea surface temperatures (Baldauf 1982). The southern coast of Beringia apparently had an Arctic climate, with ice existing for extended periods through the year. Such conditions are considered inhospitable to marine mammals that pup on land or ice floes. As a consequence the importance of the Aleutian Islands, Sea of Okhotsk, coastal Alaska, and British Columbia as refugial areas is reinforced. Many ephemeral shoreline refugia existed along the North Pacific coast and included the Queen Charlotte Islands and West Vancouver Island.

In the North Pacific, isolation of hosts and parasites occurred in these ephemeral and marginal habitats south of Beringia. The primary mode of speciation resulted from intense isolation of ancestral populations of phocine hosts and parasites in a stadial refugium. Extinction rates and speciation rates would have been concomitantly high (Vrba and Gould 1986; Warheit and Lindberg 1988; Warheit 1992). Speciation in a refugium accounts for the origin of a now widespread species. Contemporary distributions of host–parasite assemblages were subsequently determined by post-glacial range expansion from refugial centers into newly available habitat coinciding with rising sea levels since 14 ka (Hopkins 1971, 1982).

Alternatively, if speciation of cestodes occurred in post-glacial or interstadial environments, this would be a consequence of hosts having highly sedentary and localized populations (e.g., both *Phoca largha* in the North Pacific and *P. hispida* across the circumpolar region). Under a regime of secondary isolation, divergence and speciation of cestodes is dependent on the length of the interstade and the degree of gene flow. We would predict numerous poorly differentiated species of cestodes associated with discrete host populations.

Differentiation of some local cestode populations may not

be definable morphologically. For instance, consider the sibling species complexes of *Pseudoterranova decipiens* (Krabbe, 1878) and *Contracaecum osculatum* (Rudolphi, 1802) in North Atlantic phocids (Nascetti et al. 1993, Paggi et al. 1991). Whether this obtains with *Anophryocephalus* spp. would have to be determined via biochemical or molecular level analyses (Baverstock et al. 1985). Biochemically distinct populations of cestodes coinciding with definable host populations provide evidence for postglacial divergence driven by host isolation following the Pleistocene.

These patterns are distinguishable with reference to the topology of a cladogram. Poorly differentiated, polychotomous species swarms are compatible with multiple species originating from a widespread common ancestor via speciation of peripheral isolates (Wiley 1981; Brooks and McLennan 1991; Frey 1993). Such patterns are also compatible with secondary divergence (postglacial) of a population that became widespread and later underwent local isolation. Conversely, a hierarchical and dichotomous arrangement, such as that found in the present study, is compatible with a restricted origin in an isolated refugium with secondary postglacial expansion and host switching during interstadials.

A role for intermediate hosts?

Hypotheses of allopatric speciation of *Anophryocephalus* have considered isolation of populations or species of phocine definitive hosts to be a determining factor in parasite diversification. These hypotheses followed from empirical evidence derived from the phylogenies of parasites and hosts, patterns of host and parasite association, and historical biogeography of phocines (Hoberg 1986; Hoberg and Adams 1992). However, a putative role for intermediate and paratenic hosts in influencing parasite speciation must be evaluated (Hoberg 1992). To achieve this, the taxa involved, their vagility, historical biogeography, and the associated implications for isolation or range expansion and gene flow must be considered. Cospeciation analysis, however, would not predict constant rates of speciation among an assemblage of disparate taxa, involved in the maintenance of a host–parasite assemblage, following the origin of a specific life cycle association.

Among species of *Anophryocephalus* in the Sea of Okhotsk, the Subarctic, and Transition zones of the North Pacific, euphausiids, principally species of *Thysanoessa* Brandt and *Euphausia pacifica* Hansen, have been implicated as intermediate hosts (Murav'eva and Popov 1986) and fishes as paratenic hosts (Hoberg 1987; Hoberg and Adams 1992). The distributional patterns exhibited by some macrozooplankton and pelagic and semidemersal fishes are indicative of historically continuous populations connecting the Atlantic and Pacific through the Arctic basin, and ranges for many taxa, including calanoid copepods, some species of *Thysanoessa*, and subspecies of herring (*Clupea harengus* Linnaeus), were determined during the Quaternary (Ekman 1953; Ponomareva 1963; Frost 1974; Reid et al. 1978; Outer Continental Shelf Environmental Assessment Program (OCSEAP) 1986). However, the Holarctic distributions of euphausiids (e.g., *T. inermis* (Kröyer) and *T. raschii* (Sars)) (Ponomareva 1963) and the exceptionally broad ranges exhibited by a wide array of zooplankton species (Reid et al. 1978) suggest that climatic fluctuations over the past 3 Ma

generally resulted in minimal diversification. This contrasts with evidence for intense isolation and vicariance of seabird (Hoberg 1986, 1992; Siegel-Causey 1991; Warheit 1992) and pinniped populations (Shaughnessey and Fay 1977) during the late Tertiary and Pleistocene.

Pelagic macrozooplankters, including euphausiids, have severely limited abilities for rapid dispersal (Brinton 1976). Changing foraging habits, associated with development, and across a dispersal trajectory also markedly determine their potential as intermediate hosts. The longevity of individuals, up to 2 years for some species, promotes relatively slow but substantial long-distance transport via advection (e.g., an estimated 200 days' transit time for *E. pacifica* from the Subarctic Gyre to coastal Baja California) (Brinton 1976; McGowan 1977). However, this may not necessarily increase the potential for transmission of cestodes, owing to the vast pelagic populations of these crustaceans (see Cielecka et al. 1992). Zooplankters also have patchy distributions confined to relatively large, oceanic circulation systems (McGowan 1974, 1977; Reid et al. 1978). Consequently, relatively homogeneous populations of zooplanktonic Crustacea will be of limited importance in dispersal or in the maintenance of cohesion within specific parasite populations through gene flow.

In contrast, some putative piscine hosts for *Anophryocephalus* spp., including herring, walleye pollock (*Theragra chalcogramma* (Pallas)), ocean perch (*Sebastes alutus* (Gilbert)), and other pelagic and semidemersal fishes have predictable patterns of migration and regionally defined populations in the North Pacific (Smith 1981; OCSEAP 1986). Although there is potential for rapid dispersal, differentiation of stocks is attributed to barriers and the isolating effects of geographical distance. Consequently, the localized distributions of some key prey species of phocids (Lowry and Frost 1981) could enhance the regional isolation of parasites. However, completion and continuity of the life cycle is dependent on the coincidental occurrence of the entire host–parasite assemblage.

Sympatry for such marine parasite assemblages is reinforced through focal feeding by pinnipeds and seabirds. Foraging zones are often correlated with predictable regions of frontal circulation, upwelling, and tidal eddy systems near islands utilized as colony and haul-out sites (Calkins 1986; Hunt and Schneider 1987; Hunt et al. 1988). Thus, insular marine systems and adjacent pelagic waters represent foci for parasite transmission and are areas where predictable assemblages of parasites and intermediate and definitive hosts are concentrated. In these environments, isolation and speciation of *Anophryocephalus* and pinniped hosts could have proceeded independently of that of more broadly distributed populations of intermediate and paratenic hosts. Parasite populations appear to be strongly influenced by the distributions of relatively vagile definitive hosts that disseminate infective stages for the intermediate host (Hoberg 1986; Hoberg and Adams 1992). Consequently, cohesion within broadly distributed species of macrozooplankton or pelagic fishes is a process that must be decoupled from gene flow within parasite populations.

In contrast, Orecchia et al. (1994) postulated a role for intermediate and paratenic hosts and complex life cycles in enhancing gene flow and range expansion for anisakine

nematodes in pinnipeds of the Arctic and Antarctic (Paggi et al. 1991; Nascetti et al. 1993). However, the potential for successful gene flow is variable and dependent on (i) vagility of intermediate and paratenic hosts (via horizontal transport or advection); (ii) longevity (survivorship) in the water column or water mass; (iii) foraging behavior, and age-specific food habits of macrozooplankton and fishes, which may determine levels of infection; (iv) population size of crustacean and piscine hosts; (v) migratory patterns of hosts; and (vi) focality of foraging by definitive hosts, the influence of a dilution effect in marine systems, and isolation due to distance.

Under these criteria the importance of intermediate hosts and their movements in maintaining gene flow is minimal during both interstadial and stadial conditions (in contrast to Orrechia et al. 1994). This obtains because of the postulated high level of focality for transmission associated with localized colonies and oceanic dilution between colony sites, which would directly influence the availability of infected prey. As a consequence, in pelagic marine systems of the Subarctic the putative role of intermediate hosts is neutral with respect to gene flow or isolation of parasite populations. In contrast, paratenic hosts may act as mediators of the opportunity for successful transmission and, as such, constitute "moderators" of gene flow, potentially enhancing regional isolation. Thus, speciation of cestodes appears to be driven by the *limiting factor* of the ranges occupied by pinniped definitive hosts.

Additionally, parasite speciation is not directly determined by host speciation (either definitive or intermediate hosts), i.e., there is no general expectation of reciprocal cospeciation. Under the assumptions of an allopatric model, divergence and speciation among parasites are functions of the isolation of populations of the definitive host. Parasites can speciate independently of the host if sufficient breakdown of cohesion occurs across the range of the ancestral parasite species.

Modes of speciation

The driving mechanism of host-parasite diversification in the Holarctic and specifically in the North Pacific/Beringian region during the Late Pliocene and through the Quaternary is viewed as extremes in climate leading to environmental perturbations and eustatic fluctuation in sea level with concomitant habitat disruption and discontinuity. The intricate history of eustatic variation in sea level, associated with glacial maxima and interglacial stages over the last 3 Ma (Matthews 1979; Herman and Hopkins 1980; Marincovich et al. 1990; Pielou 1991), resulted in the development of refugia for hosts and parasites in the Arctic Basin and the North Pacific (Hoberg 1992).

Under the extremes of cyclical stadia and interstadia, two modes of speciation are postulated. A rapid, or "major," mode occurring during stadia is associated with harsh environments, habitat instability, and fragmentation. Numerous refugia and ephemeral habitats are produced, where small effective populations are highly segregated and gene flow is minimal. Fragmentation of populations would result from vicariance or range retraction. In such a setting the potential for local extinction or speciation would have been great, and directly influenced by the stability, geographic extent and temporal duration of refugia. In contrast, a slow, or

"minor," mode of speciation would be expected during interstadia, associated with larger effective populations occupying more extensive geographic ranges across relatively stable habitats (following postglacial expansion), with greater levels of gene flow and a lower expectation of local extinction or speciation. Fragmentation of populations would be minimal and largely driven or maintained by local isolation of host populations via sedentary habits or philopatry. Speciation may eventually occur under such circumstances, given sufficient time or duration of the interstadium. Secondary refugial effects may be pronounced, where expansion from historical refugial centers has been minimal, thus promoting continued isolation.

Current models of rapid speciation describe the observed distributions of *Anophryocephalus* spp. in phocines (also *A. eumetopii* and *A. ochotensis* in the otariid *E. jubatus*) (see Wiley 1981; Brooks and McLennan 1991; Hoberg and Adams 1992; Frey 1993). In these instances, local and regional isolation of populations of hosts during stadia appears to have been instrumental in promoting rapid speciation of associated parasites. Rapid diversification is described by the Type II allopatric (peripheral isolates) and Type III allopatric speciation models of Wiley (1981). The latter model is one of microallopatry and may explain the initial development of *A. anophrys* + *A. inuitorum*, and *A. skrjabini* + *A. arcticensis*, in semi-isolated or isolated populations of ringed seals. Type II, peripheral-isolates speciation, is compatible with the distribution of *A. nunivakensis* in largha seals in the eastern Bering Sea (Hoberg and Adams 1992; Hoberg 1992). In each situation in the genus *Anophryocephalus*, microallopatry of hosts has led to parasite speciation occurring independently of the host group, often resulting in multiple species of cestodes in single host species across a broad geographic range.

Frey (1993) further outlined predictions from phylogenetic analysis that were necessary to recognize or postulate speciation by peripheral isolation. Relationships for *Anophryocephalus* spp. correspond to a peripheral isolates model involving sequential dispersal or limited range retraction. The phylogeny is dichotomous, reflecting the sequence of speciation, and the central population is relatively plesiomorphic with respect to the relatively apomorphic peripheral population (Fig. 2) (Wiley 1981; Brooks and McLennan 1991; Frey 1993). Speciation in the peripheral populations is considered to be rapid.

The model of rapid diversification of species of *Anophryocephalus* is additionally supported by parasite and host biology. Speciation of cestodes may have been promoted by short generation times and high population turnover compared with those of phocine hosts. The patchy distribution of intermediate hosts (macrozooplankton and fishes) would also have constituted a restriction of gene flow in cestode populations that would be dependent on localized and sedentary seals for dispersal (Hoberg 1992). Geographic differences in prey selection and limited vagility of zooplanktonic intermediate hosts and seals would drive the development of regional parasite faunas. The latter conclusion is supported by parasitological differences observed between populations of seals inhabiting fast ice versus pack ice in both the Arctic (*P. hispida*; Finley et al. 1983) and Bering Sea (*P. largha*; Deliamure et al. 1984).

Phylogenetic hypotheses for helminth parasites are also

Fig. 3. Area cladogram showing biogeographic relationships for *Anophryocephalus* spp. (for an explanation of abbreviations see Fig. 1). Depicted is the cladogram of the genus *Anophryocephalus* mapped onto the Holarctic region, with the extent of emergent continental shelf (stippled region) at glacial maxima (from Wise and Schopf 1981); the dotted line represents the Arctic Circle and hatching indicates overall known distribution of species of *Anophryocephalus* in the Arctic–Atlantic and North Pacific basins. Relationships are consistent with vicariance or microallopatry of an ancestral parasite population in *P. hispida* in the Arctic Basin (resulting in *A. anophrys* and *A. inuitorum*). Dispersal with *P. hispida* to the North Pacific was followed by vicariance and isolation in refugia, resulting in *A. skrjabini*, *A. nunivakensis*, *A. ochotensis*, and *A. eumetopii*. The distribution of *A. arcticensis* represents a secondary range expansion from the North Pacific to the Arctic with phocine hosts. The apparently limited distribution of *A. nunivakensis* in the eastern Bering Sea may be compatible with peripheral-isolates speciation. Historical biogeographic patterns support recognition of a paraphyletic area relationship for the Arctic Basin (with respect to the North Pacific) and the Atlantic sector of the Arctic as the putative ancestral area for the genus *Anophryocephalus*.

useful in elucidating historical biogeography of host groups (Brooks and McLennan 1991; Hoberg 1995) and as indicators of incipient speciation and speciation of host groups. Congeneric species of parasites may be employed in identification of “cryptic” isolation events (and potential ancestral

areas of diversification) that are not evident in an examination of contemporary host populations. Examples from helminths of marine mammals and seabirds include those for *Anophryocephalus* spp. (also *A. eumetopii* and *A. ochotensis* in *E. jubatus*; see Hoberg and Adams 1992; Hoberg 1992)

and species of *Alcataenia* Spasskaya, 1971 among murre (*Uria aalge* (Pontoppidan) and *Uria lomvia* (Linnaeus)) (Hoberg 1986). Parapatric distributions of parasites appear indicative of a widespread host population that has undergone vicariance without speciation and may not yet have recovered from the isolation event. In contrast, sympatric species of parasites in a contiguous host population are indicative of historical isolation of some segment of that population through either microallopatry or vicariance. Other distributions of congeneric parasites that are not closely related in a single host species may be attributable to colonization (Brooks and McLennan 1991).

Recognition of a cryptic history for populations of a particular host species as indicated by the phylogeny and distribution of specific parasites is also a function of taxonomic scale (Klassen 1992). Specifically, relative taxonomic rank of hosts or parasites may directly influence interpretations of parasite distribution and speciation (Klassen 1992). In the case outlined above, analysis at the level of host subspecies does not allow for maximum resolution of the historical interactions of species of *Anophryocephalus* in ringed seals. In this situation it is the insufficient knowledge of the history of the host group (and limited morphological differentiation) that is masked by the present taxonomy of the genus *Phoca* (e.g., recognition of a single subspecies, *P. h. hispida*, inhabiting the Arctic basin). The phylogeny and putative history of species of *Anophryocephalus* provide the context in which to interpret host biogeography and isolation of populations.

The present analysis leads to a refined hypothesis for the historical biogeography of *Anophryocephalus* spp. among the tribe Phocini (Figs. 2 and 3). The contention that the Atlantic sector of the Arctic was the ancestral area for the genus and that ringed seals were the initial hosts is not refuted (Hoberg and Adams 1992; Hoberg 1992). This is particularly evident if the Arctic basin is recognized as a paraphyletic area (with the basal endemic species *A. anophrys* and *A. inuitorum*) with respect to the North Pacific basin (with *A. skrjabini* and *A. nunivakensis* in phocines and *A. ochotensis* and *A. eumetopii* in Steller sea lions). This is also consistent with host–parasite relationships and models of speciation outlined above. This complex history indicates the potential for discovery of additional species of *Anophryocephalus* among phocines of the Arctic basin.

Arctic basin biogeography

Considering the Arctic marine fauna from a broader perspective, the Pliocene and Pleistocene history of the region was strongly dominated by cyclic glaciation and extreme environmental disruption (Hopkins 1971; Herman and Hopkins 1980; Marinovich et al. 1990; Hoberg 1992; Dunton 1992). Although geographically congruent with host–parasite assemblages that have been studied in the region (Hoberg 1986, 1992), benthic marine faunas of the Arctic basin appear to be strikingly of North Pacific affinities (Dunton 1992), and are considerably younger and poorly established (Dayton et al. 1994). This is in contrast to the apparent paraphyletic area relationships that may be recognized for cestode faunas of pinnipeds (Fig. 3) and alcids (Hoberg 1986, 1992; Hoberg and Adams 1992).

Hosts and parasites had Atlantic–Arctic origins, whereas

the major constituents of the nearshore benthic marine fauna and pelagic fauna are of Pacific origin (Briggs 1970; Marinovich et al. 1990; Vermeij 1991). Additionally, this free-living fauna (and flora) appears to have been largely eradicated from the Arctic basin during successive glacial stages through the Pleistocene. Diversification of this fauna was limited during the Pleistocene and contemporary taxa are considered to represent survivors (of refugia in the Beaufort and eastern Siberian Seas) or to have reinvaded the region following glacial maxima in the Holocene (Dunton 1992). This may parallel the depauperate molluscan assemblage of the western North Atlantic, where successive waves of extinction and adaptation structured the community (Stanley and Campbell 1981; Stanley 1985).

Radiation of hosts and parasites in Subarctic to Arctic refugia during the Quaternary contrasts with the history of the free-living marine fauna. Diversification of these host–parasite assemblages during the Pliocene and Quaternary is reinforced by patterns of speciation postulated for *Contracaecum osculatum* and *Pseudoterranova decipiens* of the Subarctic and Arctic – North Atlantic over the last 3 Ma (Paggi et al. 1991; Nascetti et al. 1993; Orecchia et al. 1994). The history of pinnipeds, alcids, and their respective parasite faunas provides a counterpoint to that of free-living marine taxa across Holarctic seas.

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