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Phylogeny, historical biogeography, and ecology of *Anophryocephalus* spp. (Eucestoda: Tetrabothriidae) among pinnipeds of the Holarctic during the late Tertiary and Pleistocene

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Phylogenetic systematic analyses of *Anophryocephalus* spp. resulted in a single most-parsimonious cladogram (consistency index: 80%). Cladograms for pinniped hosts (phocids and otariids) and *Anophryocephalus* spp. were highly incongruent, corroborating a hypothesis for colonization as a dominant determinant of parasite diversification. *Phoca* (*Pusa*) spp. in the Atlantic basin are postulated as the initial hosts; range expansion for hosts and parasites into the Pacific basin through the Arctic (ca. 3.0–2.5 million years ago) was followed by radiation of *Anophryocephalus* spp. among *Phoca* spp. and subsequent colonization of otariids (*Eumetopias jubatus* as typical hosts; ca. 2.0 million years ago). Host phylogeny and historical biogeography in conjunction with host distributions of these cestodes indicate evolution of *Anophryocephalus* was associated with dispersal and radiation of *Phoca* spp. in the Holarctic during the Late Pliocene and Pleistocene. Isolation in regional refugia and vicariance (during stadials) and subsequent range expansion and sequential colonization (interstadials) are postulated as the primary determinants of host–parasite diversification in the North Pacific during the late Tertiary and Quaternary. Colonization is regarded as a central theme in the development of cestode faunas among marine homeotherms.

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Des analyses systématiques phylogénétiques d'*Anophryocephalus* spp. ont donné lieu à un seul cladogramme très parcimonieux (CI = 80%). Les cladogrammes établis pour les *Anophryocephalus* spp. et les pinnipèdes qui leur servent d'hôtes (phocidés et otariidés) ne montrent aucune congruence, ce qui corrobore l'hypothèse de la colonisation comme principal facteur déterminant de la diversification des parasites. Les diverses espèces de *Phoca* (*Pusa*) dans le bassin atlantique constituent probablement les hôtes d'origine; la dispersion des hôtes et des parasites dans le bassin du Pacifique et dans l'Arctique (ca. 3,0–2,5 millions d'années) a été suivie par la radiation des *Anophryocephalus* spp. chez les espèces de *Phoca* et par la colonisation subséquente des otariidés (*Eumetopias jubatus* comme hôte type; ca. 2,0 millions d'années). La philogénie des hôtes et leur évolution biogéographique, combinées à la répartition des cestodes chez ces hôtes, indiquent que l'évolution d'*Anophryocephalus* est associée à la dispersion et à la radiation des espèces de *Phoca* dans la zone holarctique à la fin du Pliocène et durant le Pléistocène. L'isolement dans des refuges régionaux et la vicariance durant les glaciations, suivis d'une expansion de la répartition et d'une colonisation séquentielle au cours des périodes interglaciaires, constituent probablement les principaux facteurs déterminants de la diversification hôtes-parasites dans le Pacifique Nord à la fin du Tertiaire et durant le Quaternaire. La colonisation est considérée comme la principale voie de développement des faunes de cestodes chez les homéothermes marins.

[Traduit par la rédaction]

Introduction

Phylogenetic systematics (Hennig 1966; Wiley 1981) forms the basis for evaluations of coevolutionary and historical ecological mechanisms associated with the organization and structure of helminthic parasite faunas among vertebrate hosts (see Brooks and McLennan 1991 and references therein). Analyses of such macroevolutionary processes in the development of helminth faunas have centered upon archaic and coevolved systems (e.g., Brooks 1979a; Brooks *et al.* 1981; Brooks and Bandoni 1988; Bandoni and Brooks 1987). In contrast, few parasite assemblages have been studied that are relatively young and structured by colonization or host switching, and in which diversification has been predominately controlled by historical ecological processes (Hoberg 1986, 1987, 1989).

The family Tetrabothriidae Linton, 1891 is a relatively young monophyletic group of cestodes in which host switching has strongly influenced diversification (Hoberg 1987; Galkin 1987). Hypotheses for the evolution of the tetrabothriids, which are widely distributed among seabirds and marine mammals, indicate an origin in marine homeotherms via colonization from elasmobranchs during the Tertiary (Hoberg 1987). The distribution of certain genera of the tetrabothriids has also suggested that host switching was a significant factor in the later radiation of the family among seabirds, cetaceans, and pinnipeds (Baer 1954; Temirova and Skrjabin 1978; Hoberg 1987; Galkin 1987).

Hoberg (1989) completed the first phylogenetic analyses of the tetrabothriids and supported the validity of the genera *Tetra-*

bothrius Rudolphi, 1819; *Chaetophallus* Nybelin, 1916; *Trigonocotyle* Baer, 1932; *Anophryocephalus* Baylis, 1922; *Strobilocephalus* Baer, 1932; and *Priapocephalus* Nybelin, 1922. The last three genera were recognized as an inclusive group designated as the *Anophryocephalus*-clade (Hoberg 1989), in which *Anophryocephalus* was postulated as the sister-group for *Strobilocephalus* + *Priapocephalus*. The history of this group is of particular interest, as members of these genera have host distributions restricted solely to marine mammals (Temirova and Skrjabin 1978 and others).

Hoberg *et al.* (1991) revised the genus *Anophryocephalus*, provided descriptions of two previously unrecognized species, and reviewed host and geographic ranges for these cestodes among pinnipeds. *Anophryocephalus* spp. are host-specific parasites of phocids (*Anophryocephalus anophrys* Baylis, 1922 in *Phoca (Pusa) hispida* Schreber; *Anophryocephalus skrjabini* (Krotov and Deliamure 1955) in *Phoca* spp.; and *Anophryocephalus nunivakensis* Hoberg, Adams, and Rausch, 1991 in *Phoca largha* Pallas) and otariids (*Anophryocephalus ochotensis* Deliamure and Krotov, 1955 and *Anophryocephalus eumetopii* Hoberg, Adams, and Rausch, 1991 in *Eumetopias jubatus* (Schreber)) in subarctic to arctic latitudes of the North Pacific and Atlantic basins. Among the phocids, *Cystophora cristata* (Erxleben), the northwest atlantic subspecies of *Phoca vitulina* Linnaeus, and *Phoca (Pagophilus) groenlandica* Erxleben are recognized as facultative or incidental hosts of *A. anophrys*, whereas among the otariids, *Callorhinus ursinus* (Linnaeus) is considered to represent a facultative host for *A. ochotensis*. Otherwise, species of *Anophryocephalus* have severely limited distributions among pinnipeds and have not been reported among the Odobenidae, other genera and species of the Otariidae, and the majority of the Phocidae (Hoberg *et al.* 1991). Additionally, the genus is restricted to high latitudes of the Holarctic and is not represented in the southern hemisphere (Deliamure 1955; Temirova and Skrjabin 1978; Hoberg *et al.* 1991).

The narrow host and geographic distributions for *Anophryocephalus* spp. are distinctive, and certain observations suggest a historical association for hosts and parasites: (i) congruence of geographic ranges for particular species of hosts and parasites, (ii) highly defined host distributions for *Anophryocephalus* spp. among phocids and otariids, and (iii) the historical biogeography and phylogenetic history of the extant pinnipeds. Considering these factors, it is suggested that these cestodes either represent numerical relicts (*sensu* Brooks and Bandoni 1988) among their pinniped hosts or that the fauna is historically depauperate (see Hoberg 1986). As such, these alternatives represent hypotheses for the diversification of *Anophryocephalus* wherein coevolution versus colonization (with infrequent coevolution) can be postulated as the dominant determinants in controlling the radiation of this host-parasite assemblage.

In the current study, phylogenetic analysis among the five species of *Anophryocephalus* was conducted. Alternative hypotheses for coevolution and colonization were evaluated by a direct comparison of the congruence and consistency of host and parasite phylogenies (see Brooks and McLennan 1991 and references therein). Well-corroborated hypotheses for the historical biogeography and ecology of *Anophryocephalus* among phocids and otariids in the Holarctic during the late Tertiary and Pleistocene are presented. Estimates for the temporal associations of *Anophryocephalus* spp. and the clade (see Hoberg 1986) were developed with respect to host distri-

butions of parasites and the phylogenetic and biogeographic history of the pinnipeds (Repenning *et al.* 1979; DeMuizon 1982; Berta and Deméré 1986; Wyss 1988a; Berta *et al.* 1989; and others). These concepts were also extended to consideration of the broader host associations of the *Anophryocephalus*-clade and the role of colonization in the evolution of helminth faunas among marine homeotherms (see Hoberg 1986, 1987, 1989).

Methods and materials

Phylogenetic systematics or cladistics (Hennig 1966; Wiley 1981) was used to analyze relationships among the five species of *Anophryocephalus*. Parsimony criteria were used to construct phylogenetic hypotheses with the PAUP computer systematics program (version 2.4; Swofford 1985). Analyses were conducted with the ALLTREES option, rooted with a designated ancestor and employed Farris optimization. Host-parasite interactions and historical biogeography were examined by mapping and the development of area cladograms.

Specimens examined

Specimens of all *Anophryocephalus* spp. and representatives of basal tetrabothriid genera were examined. A detailed listing of specimens of *A. anophrys*, *A. skrjabini*, *A. nunivakensis*, *A. ochotensis*, and *A. eumetopii* was presented previously (Hoberg *et al.* 1991). Specimens of *Tetrabothrius* spp. and *Trigonocotyle* spp. included those studied during generic-level analyses of the Tetrabothriidae (Hoberg 1989, 1992). Additional specimens included those of *Chaetophallus umbrella* (Fuhrmann, 1898) from *Diomedea exulans* Linnaeus, provided by the British Museum (Natural History) (BMNH 1975.1.13.125–129), and *Trigonocotyle sextesticulae* Hoberg, 1990 from *Feresa attenuata* Gray (see Hoberg 1990). The structural aspects of all pertinent characters for *Anophryocephalus* spp. and other tetrabothriids were illustrated previously (Hoberg *et al.* 1991; Hoberg 1992).

Character analysis

Homologous characters used in the analysis were derived from direct examination of specimens representing all species of *Anophryocephalus*. Reference to original descriptions (Baylis 1922; Deliamure 1955; Hoberg *et al.* 1991) and redescrptions (Baer 1954; Murav'eva and Popov 1976; Temirova and Skrjabin 1978; Hoberg *et al.* 1991) augmented the analysis. The out-group method (Lundberg 1972; Wiley 1981) was used in polarization of character states. Taxonomic out-groups included tetrabothriids in the genera *Tetrabothrius*, *Chaetophallus*, and *Trigonocotyle*; *Trigonocotyle* spp. were considered the primary out-group based on a well-corroborated hypothesis for a sister-group relationship with the *Anophryocephalus*-clade (Hoberg 1989).

In the analysis all binary and multistate characters were ordered. The polarity of two characters (unique within *Anophryocephalus*), including the condition of the ventral osmoregulatory canals (8) and the structure of the genital atrium (16), was evaluated secondarily with reference to the functional outgroup (*A. anophrys*). Functional coding was based on recognition of the most basal member of the genus in preliminary analyses (Watrous and Wheeler 1981). Additionally, a single character, the structure of the bothridial apertures (2, 3), was split to recognize the potential for independent derivation from the plesiomorphic condition. The 20 homologous characters, including 24 character transformations, are presented below and in a numerical matrix (Table 1). Plesiomorphic states are coded as 0, and apomorphic states as 1 or 2. Values for the consistency index (CI) (Farris 1970) were calculated for individual characters (Table 2) and for overall relationships among the species.

Host and geographic ranges for parasites

The geographic and host ranges for species of *Anophryocephalus* were determined from museum records (U.S. National Museum and British Museum (Natural History)), published and unpublished records for collections from pinnipeds in the North Pacific basin by

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
Tetrabothriid outgroups*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. anophrys</i> Baylis, 1922	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	1
<i>A. ochotensis</i> Deliamure and Krotov, 1955	1	0	0	1	1	0	0	1	0	1	1	1	0	2	2	2	0	1	1	0
<i>A. skrjabini</i> (Krotov and Deliamure, 1955)	0	0	0	1	1	0	0	0	2	1	0	0	0	1	0	1	1	0	0	0
<i>A. nunivakensis</i> Hoberg, Adams, and Rausch, 1991	0	0	1	0	1	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1
<i>A. eumetopii</i> Hoberg, Adams, and Rausch, 1991	1	0	1	0	1	0	0	1	0	1	1	1	1	2	2	2	1	1	1	0

*Including *Tetrabothrius* spp., *Chaetophallus* spp., and *Trigonocotyle* spp.TABLE 2. Consistency indices for individual characters used in the analysis of *Anophryocephalus* spp.

Character No.	Character	Consistency index
1	Apical region (development)	1.0
2	Bothridial opercula	1.0
3	Bothridial opercula	0.50
4	Auricles (confluence)	0.50
5	Parenchymal envelope	1.0
6	Ventral transverse canals	1.0
7	Dorsal canals	1.0
8	Ventral canals	1.0
9	Neck (length)	0.667
10	Genital pore (position)	1.0
11	Genital pore (structure)	1.0
12	Cirrus sac (form)	1.0
13	Cirrus sac (wall)	0.50
14	Genital atrium (papilla)	1.0
15	Genital atrium (papilla)	1.0
16	Genital atrium (muscular pad)	1.0
17	Testes (number)	0.50
18	Testes (position)	1.0
19	Male canal	1.0
20	Vagina (armature)	0.50

F. H. Fay and L. M. Shults, and the literature (see Hoberg *et al.* 1991). Additionally, three new geographic records for *A. nunivakensis* are reported and the following specimens deposited as vouchers in the helminthological collections of the U.S. National Museum (USNM), U.S. Department of Agriculture, Beltsville, Maryland: (1) USNM 81904 from a male *Phoca largha*, collected 24 April 1976 in the Bering Sea (ca. 56°02.2'N, 162°57.4'W) by F. H. Fay (FHF 42037); (2) USNM 81905 from a male *P. largha*, collected 28 May 1978 in the Bering Sea (ca. 63°25.8'N, 173°05.6'W) by F. H. Fay (FHF 42453); and (3) USNM 81906 from a female *P. largha*, collected on 7 June 1978 in the Bering Sea (ca. 64°20.9'N, 167°07.9'W) by F. H. Fay (FHF 42483).

Host-parasite evolution and historical biogeography

Interpretations of host evolution and historical biogeography were derived from the literature. Host-group cladograms, which formed the basis for determination of congruence of host and parasite phylogenies, were modified from studies of the pinnipeds by Wyss (1987, 1988a, 1989), Berta *et al.* (1989), and DeMuizon (1982). Analyses of the historical biogeography of the Phocidae by Davies (1958), Repenning *et al.* (1979), Ray (1976), and DeMuizon (1982) were considered in developing hypotheses for the associations of *Anophryocephalus* spp. among the pinnipeds. The estimated temporal duration of assemblages or time of divergence of host and parasite groups is indicated in millions of years ago.

Results

Character analysis

1. Apical region (development). 0 = minimal; 1 = hypertrophied.

2, 3. Operculum (presence and structure of aperture). States of this character were split into separate transformation series to account for postulated independent derivation from the plesiomorphic condition. A tegumental operculum is absent in *Tetrabothrius*, *Chaetophallus*, and *Trigonocotyle*. Among *Anophryocephalus* spp., opercula are absent in *A. ochotensis* (0, 0) and *A. skrjabini* (0, 0), but present in *A. anophrys* (1, 0), *A. nunivakensis* (0, 1), and *A. eumetopii* (0, 1). Character 2: 0 = absent; 1 = present, with a longitudinal slit-like aperture not extending beyond the muscular margin of the bothridium. Character 3: 0 = absent; 1 = present, with a longitudinal or diagonal aperture that opens to the anterior.

4. Auricles (anterior confluence). 0 = auricular appendages with independent origins; 1 = lateral and medial auricles confluent along anterior margin of bothridium.

5. Parenchymal envelope on posterior aspect of bothridium. 0 = bothridia not contained in envelope; 1 = bothridia contained in envelope.

6. Osmoregulatory canals (ventral transverse). 0 = minute transverse canal present; 1 = transverse canal absent.

7. Osmoregulatory canals (dorsal). 0 = atrophied dorsal canal present; 1 = absent.

8. Osmoregulatory canals (ventral). Coded with reference to the functional out-group, *A. anophrys*: 0 = hypertrophied; 1 = not hypertrophied.

9. Neck (length). 0 = short (near 2 mm); 1 = of medium length (5–10 mm); 2 = exceptionally long (>16 mm). Among basal tetrabothriids the neck is typically very short (<1.0 mm), whereas a long neck (≥2.0 mm) is a characteristic of *Anophryocephalus* (Hoberg 1989). However, within the genus the length of the neck varies considerably from relatively short to unusually long.

10. Genital pore (position). 0 = lateral; 1 = ventrolateral.

11. Genital pore (structure). 0 = weakly developed; 1 = developed as an extrusible suckerlike organ.

12. Cirrus sac (form). 0 = elongate to pyriform; 1 = ovoid.

13. Cirrus sac (wall). 0 = thick, heavily muscularized; 1 = thin, weakly muscular.

14. Genital atrium (genital papilla). 0 = papilla absent; 1 = rudimentary development; 2 = strongly developed.

15. Genital atrium (genital papilla). 0 = papilla absent or not directed ventrally; 1 = papilla directed weakly ventrad; 2 = papilla strongly decurved ventrally.

16. Genital atrium (muscular pad). Coded with reference to

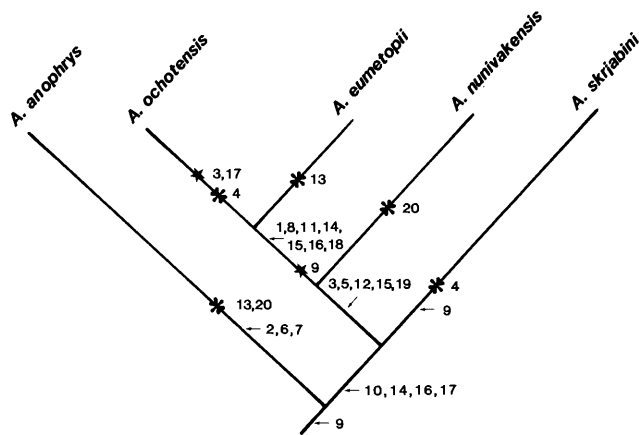


FIG. 1. Cladogram depicting the postulated relationships among *Anophryocephalus* species. Apomorphic characters have been mapped onto the tree and are designated by arrows. Apparent homoplasy in specific characters is indicated by an asterisk (parallel development) or a star (reversals). The hypothesis has a consistency index of 80%, with a minimum of 24 steps and 30 postulated changes required to define the topology of the tree.

the functional out-group, *A. anophrys*: 0 = bifurcate and prominent; 1 = ellipsoidal, massive; 2 = ellipsoidal, minuscule.

17. Testes (number). 0 = 20–30; 1 = >34.

18. Testes (position). 0 = surround the ovary; 1 = completely overlap female organs.

19. Male canal (direction). 0 = straight; 1 = ventrally decurved.

20. Vagina (atrial armature). 0 = atrial region spinose; 1 = atrial region aspinose.

Phylogeny of *Anophryocephalus* species

Monophyly for the genus was previously established by synapomorphies for structural characters of the scolex (paired auricular appendages), atrophy of the dorsal osmoregulatory canals, and basic configuration of the genital atrium (Hoberg 1989). These attributes represented constant characters within the study group and as such were excluded from the analysis.

A single cladogram resulted from the analysis and was supported by 20 homologous attributes and 24 character transformations (Fig. 1). This phylogenetic hypothesis was well corroborated with a CI of 80% (24 steps minimum; 30 changes postulated). Consistency values for individual characters are summarized in Table 2. Homoplasy was evident in six characters with three postulated reversals (3: structure of the operculum; 9: length of neck; 17: number of testes) and three cases of parallel development (4: confluence of auricles; 13: wall of cirrus sac; 20: vaginal armature).

Anophryocephalus anophrys is postulated to have had a common ancestor with the remaining *Anophryocephalus* species. *Anophryocephalus skrabini* is recognized as the sister-species for a more inclusive group including *A. nunivakensis*, *A. eumetopii*, and *A. ochotensis*. The internal branches and nodes of this cladogram are strongly supported; homoplasy is typically associated with terminal branches and character distributions defining individual species (Fig. 1).

Discussion

Anophryocephalus has been recognized as a monophyletic taxon within the Tetrabothriidae (Hoberg 1989). Evaluation of generic- and species-level relationships has a bearing on

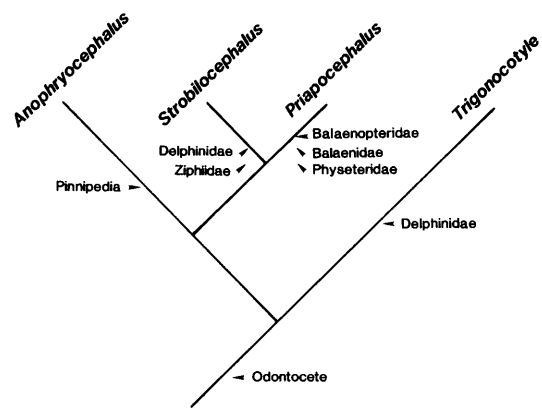


FIG. 2. Cladogram showing relationships of the *Anophryocephalus*-clade (modified from Hoberg 1989). Association of hosts and parasites is indicated by the distribution of host taxa that have been mapped onto the cladogram. Relationships depicted are compatible with a hypothesis for colonization of the pinnipeds by a tetrabothriid of odontocetes.

understanding the evolution of the family and the temporal and historical aspects of the development of host–parasite associations among tetrabothriids and avian and mammalian hosts in marine communities. These points are expanded in a discussion of the origins of the Tetrabothriidae, the *Anophryocephalus*-clade (see Hoberg 1989), and a comparison of the phylogenetic relationships of *Anophryocephalus* species and their pinniped hosts. It is only through detailed comparisons of host–parasite phylogenies that hypotheses for historical biogeography and historical ecology can be assessed with respect to the evolution of complex symbiotic assemblages (Brooks 1979b, 1981, 1985, 1988, 1990; Brooks and McLennan 1991; Hoberg 1986). Additionally, historical biogeography of the host group in conjunction with phylogenetic hypotheses for hosts and parasites provides the context for elucidating the temporal duration of an assemblage (Hoberg 1986; Brooks and Bandoni 1988).

Origin of Tetrabothriidae and generic diversification

The origin of the tetrabothriids is postulated to be associated with colonization of marine homeotherms (seabirds or marine mammals) by a derived tetrabothriid ancestor occurring among elasmobranchs (Hoberg 1987; Galkin 1987). Diversification of the family during the Tertiary resulted in six genera among marine birds (*Tetrabothrius*, *Chaetophallus*), cetaceans (*Tetrabothrius*, *Trigonocotyle*, *Strobilocephalus*, and *Priapocephalus*), and pinnipeds (*Anophryocephalus*). Relationships indicated by cladistic analysis at the generic level supported recognition of *Tetrabothrius* spp. as the most basal tetrabothriids but do not currently provide compelling evidence for elucidating the basal host–parasite associations for the family (Hoberg 1989).

Baer (1932) previously outlined hypotheses for the affinities of *Mesocestoides* Vaillant, 1863 and *Anophryocephalus*, with the latter representing a basal taxon within the tetrabothriids. Thus, it was postulated that marine mammals were the primary hosts for tetrabothriids, that there was a coevolutionary association among cestodes of terrestrial carnivores and those characteristic of pinnipeds, and that continued diversification involved colonization and radiation among avian hosts (Baer 1932).

In contrast, Baer (1954), Delamure (1955), and Rees

TABLE 3. Host distribution and geographic range for *Anophryocephalus* spp. among the pinnipeds

Host	Parasite	Range ^a
Otariidae ^b		
<i>Eumetopias jubatus</i>	<i>Anophryocephalus ochotensis</i>	P
	<i>Anophryocephalus eumetopii</i>	P
<i>Callorhinus ursinus</i> ^c	<i>Anophryocephalus ochotensis</i>	P
Odobenidae	Absent	—
Phocidae		
Monachinae ^d	Absent	—
Phocinae ^e		
<i>Erignathus barbatus</i>	Absent	—
<i>Cystophora cristata</i> ^f	<i>Anophryocephalus anophrys</i>	At
<i>Halichoerus grypus</i>	Absent	—
<i>Phoca (Pusa) hispida</i>	<i>Anophryocephalus anophrys</i>	At
	<i>Anophryocephalus skrjabini</i>	P, Ar
<i>Phoca (Pusa) sibirica</i>	Absent	—
<i>Phoca (Pusa) caspica</i>	Absent	—
<i>Phoca (Histriophoca) fasciata</i>	<i>Anophryocephalus skrjabini</i>	P
<i>Phoca (Pagophilus) groenlandica</i> ^g	<i>Anophryocephalus anophrys</i>	At
<i>Phoca largha</i>	<i>Anophryocephalus skrjabini</i>	P
	<i>Anophryocephalus nunivakensis</i>	P
<i>Phoca vitulina</i> ^h	<i>Anophryocephalus skrjabini</i>	P

NOTE: Distribution reviewed in Hoberg *et al.* (1991) and references cited therein, including corrections to some previous reports in the North Pacific. Hosts listed in Margolis and Arai (1989) are considered incidental.

^aP, Pacific basin endemic (high boreal to arctic); At, subarctic to arctic of the Atlantic basin; Ar, western (Alaskan) Arctic.

^bNot reported from other Otariidae including *Arctocephalus* spp., *Zalophus californianus* (Lesson), *Otaria byronia* (Blainville), *Neophoca cinerea* (Péron), and *Phocarcus hookeri* (Gray).

^cRecord by Iurakhno (1987), only from the Komandorskii Islands and not from the Pribilof and Kurile islands (also see Deliamure 1955; Neiland 1961; Keyes 1965), is consistent with the northern fur seal being regarded as a facultative host for *Anophryocephalus ochotensis*.

^dAccording to Wyss (1988a), including *Monachus* spp., *Mirounga* spp., *Hydrurga leptonyx* (Blainville), *Lobodon carcinophaga* (Hombron and Jacquinot), *Ommatophoca rossi* Gray, and *Leptonychotes weddelli* (Lesson).

^eAccording to Burns and Fay (1970) and Wyss (1988a), including the genera *Erignathus*, *Cystophora*, and the tribe Phocini with the genera *Halichoerus*, and *Phoca* (including the subgenera *Histriophoca*, *Pagophilus*, and *Pusa*).

^fConsidered a facultative host (see Deliamure and Treshchev 1966).

^gSingle host record (Smith and Threlfall 1973), indicating harp seals may be regarded as facultative hosts for *A. anophrys*.

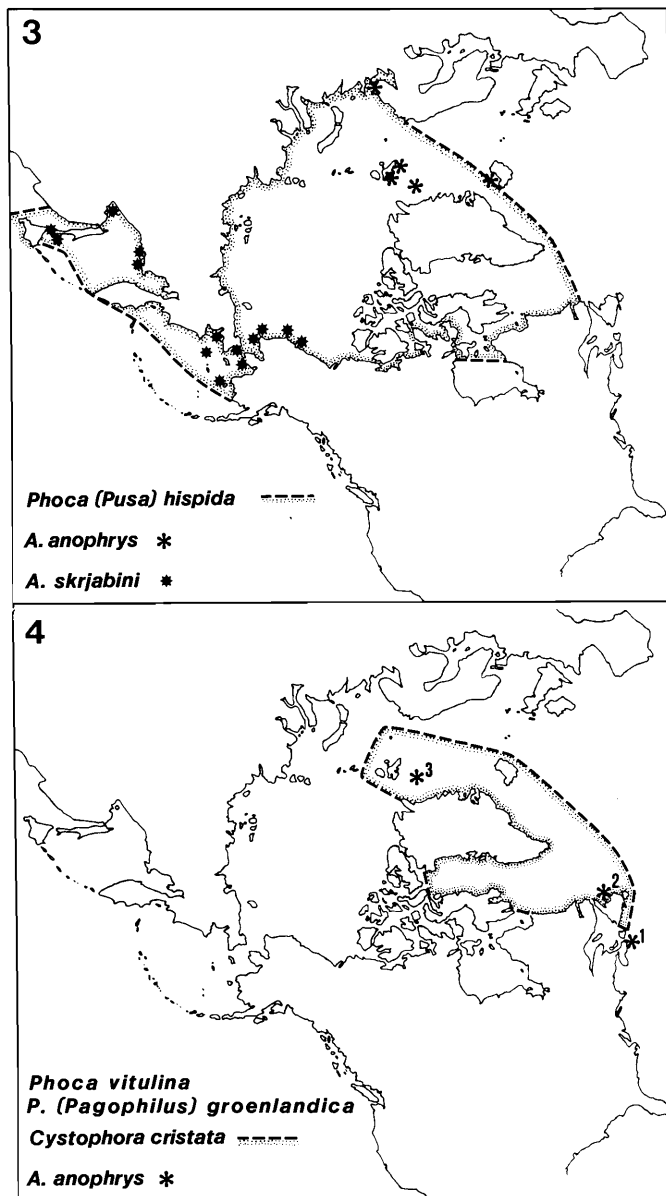
^hOnly in *Phoca vitulina richardsi* in the North Pacific (see Margolis 1956; Dailey and Fallace 1989). McClelland (1980) reported an *Anophryocephala* sp. (= *Anophryocephalus* sp.) from a captive harbor seal in Nova Scotia. This record is equivocal because of the inadequate history for the host (e.g., length of time in captivity and diet), and an incomplete identification of the cestode. *Phoca vitulina* subspecies in the North Atlantic are regarded as facultative hosts, as this represents the sole record from harbor seals in this region.

(1956) considered seabirds to be ancestral hosts for *Tetrabothrius*, with subsequent colonization and diversification resulting in the origin of genera typical of mammalian hosts. These authorities suggested that the genera characteristic of marine mammals (*Trigonocotyle*, *Anophryocephalus*, *Strobilocephalus*, and probably *Priapocephalus*) were evolutionarily derived with respect to *Tetrabothrius*. Temirova and Skrjabin (1978) accepted *Tetrabothrius* as relatively ancestral but stated that a reliable decision was not yet possible in reference to the sequence of colonization among avian or mammalian hosts.

Galkin (1987) argued for recognition of odontocete cetaceans as the original host group and suggested that seabirds and pinnipeds were independently colonized. This contention was based upon the morphological attributes of some *Tetrabothrius* spp. among cetaceans (massive scolex, vitelline gland tending to be follicular), the occurrence of larval phyllobothriids as tissue parasites in some cetaceans (Skrjabin 1972; also see Skrjabin and Iurakhno 1987), and a high degree of generic-level diversification of cestodes among marine mammals (and concurrent minimal generic radiation among avian hosts). Additionally, Galkin (1987) suggested it was improbable that colonization had occurred from avian to mammalian hosts due

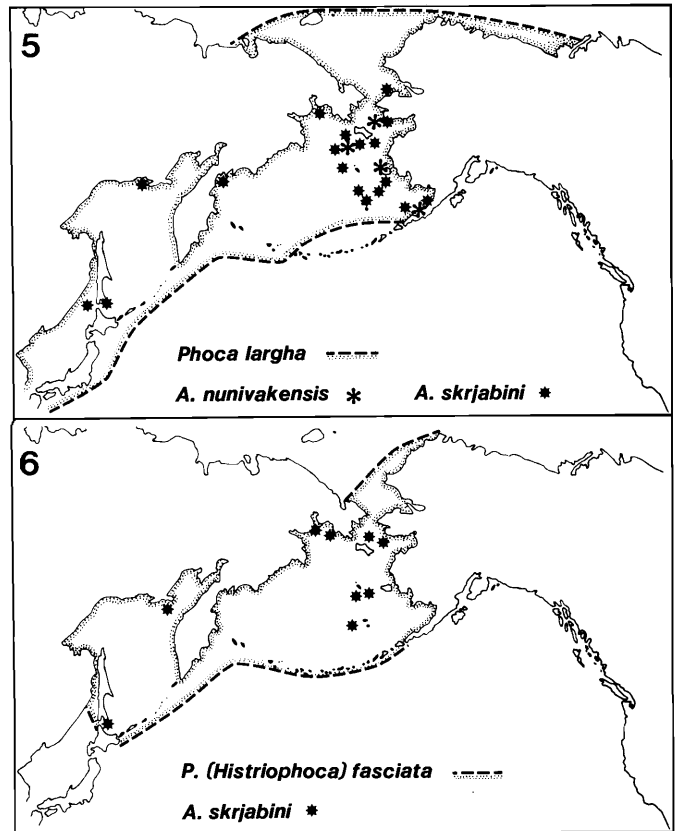
to minimal overlap in trophic associations (see Hoberg 1987 for alternative opinion). Galkin (1987) also maintained the *Anophryocephalus* was "relatively primitive" with respect to the structure of the scolex, but "intermediate" in the degree of complexity of the genital atrium. These morphological attributes were considered to have remained constant following the early isolation of the genus among pinnipeds.

Cladistic analyses of the *Tetrabothriidae* have supported the basal status of *Tetrabothrius* (Hoberg 1989), but it is apparent that a combination of colonization (with subsequent speciation) and coevolution and later diversification of the group would have been dictated by the time frames of initial host switching of, and cladogenesis among, avian and mammalian hosts and respective groups of cestodes. Initial hosts for the *tetrabothriids* remain enigmatic because members of the basal genus *Tetrabothrius* occur in avian and mammalian hosts (species are highly segregated). These caveats aside, the limited distribution of *Tetrabothrius* spp. among marine mammals (8 species, versus 42 species among avian hosts) and the occurrence of evolutionarily derived genera among cetaceans (*Trigonocotyle*, *Strobilocephalus*, and *Priapocephalus*) and pinnipeds (*Anophryocephalus*) may provide support for recog-



FIGS. 3 and 4. Geographic distributions of *Anophryocephalus* spp. and pinniped hosts. Fig. 3. Geographic distribution of *Phoca (Pusa) hispida* (from King 1983) and minimum ranges of *A. anophrys* (asterisks) and *A. skrjabini* (stars) as determined by localities of collection (from Temirova and Skrjabin 1978; Adams 1988; Hoberg *et al.* 1991). Localities indicated on the range map may include multiple host records. Fig. 4. Approximate overlapping geographic distributions for *Phoca vitulina*, *Phoca (Pagophilus) groenlandica*, and *Cystophora cristata* (from King 1983) and single localities of collection for *A. anophrys* (asterisks) in *P. vitulina* (1), *P. groenlandica* (2), and *C. cristata* (3) (see Deliamure and Treshchev 1966; Smith and Threlfall 1973; McClelland 1980).

nition of seabirds as initial hosts for ancestral tetrabothriids (Hoberg 1987, 1989). Subsequent associations among marine mammals would have developed via host switching, thus the origin of the *Anophryocephalus*-clade is of particular interest. With the recognition of the *Anophryocephalus*-clade (*Anophryocephalus*, *Strobilocephalus*, and *Priapocephalus*), it becomes possible to delineate maximum limits on the length of temporal associations among hosts and parasites when aspects of the phylogeny and biogeography of the pinnipeds are evaluated. Additionally, some broad aspects of the rela-



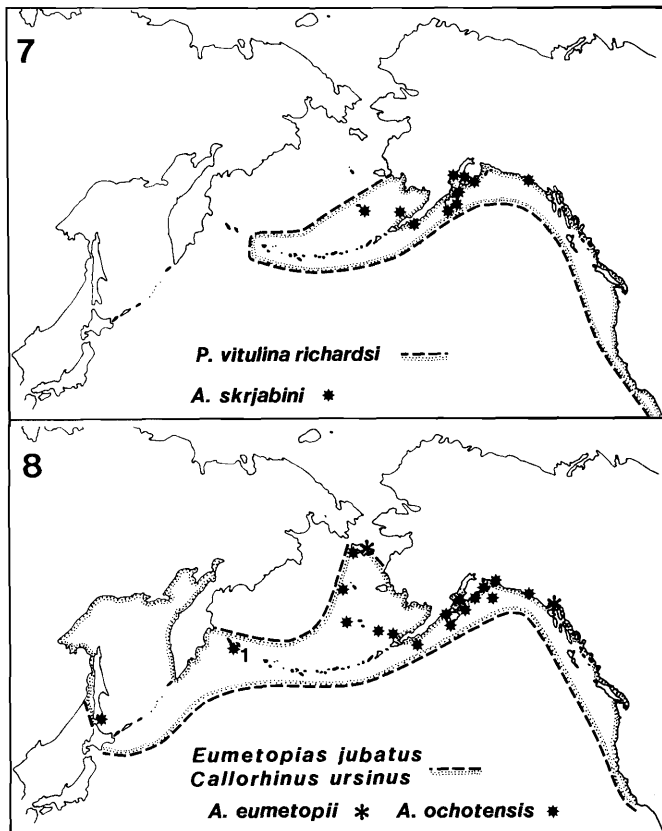
FIGS. 5 and 6. Geographic distributions of *Anophryocephalus* spp. and pinniped hosts in the North Pacific. Fig. 5. Geographic distribution for *Phoca largha* (from King 1983) and minimum ranges of *A. skrjabini* (stars) and *A. nunivakensis* (asterisks) as determined by localities of collection (see Shults 1982; Deliamure *et al.* 1984; Hoberg *et al.* 1991). Localities for *A. skrjabini* may include multiple host records. The type locality for *A. nunivakensis* was at Nunivak Island in the eastern Bering Sea (Hoberg *et al.* 1991). Previously unpublished records presented here (northern Bering Sea and Bristol Bay) were derived from specimens and locality data recently deposited at the U.S. National Museum by F. H. Fay and L. M. Shults. Fig. 6. Geographic distribution for *Phoca (Histriophoca) fasciata* (from King 1983) and minimum range for *A. skrjabini* (stars) as indicated by localities of collection (see Shults and Frost 1988; Hoberg *et al.* 1991); this represents multiple host records at each locality and includes data deposited at the USNM by L. M. Shults.

tionships of cestodes among cetaceans and pinnipeds may be considered.

The *Anophryocephalus*-clade

The *Anophryocephalus*-clade represents an inclusive group of tetrabothriids with apparently restricted distributions among pinnipeds and cetaceans (Fig. 2). The putative sister-group for the clade is the genus *Trigonocotyle*, which contains species that are exclusively parasites of the Delphinidae (Hoberg 1989, 1990). Such a relationship is consistent with the hypothesis that *Anophryocephalus* (the basal member of the clade) had a common ancestor with cestodes of odontocetes. Following colonization, diversification of *Anophryocephalus* spp. was limited to pinnipeds, whereas cetaceans became characteristic hosts for *Strobilocephalus* (Delphinidae, Ziphiidae) and *Priapocephalus* (Physeteridae, Eschrichtiidae, Balaeonidae, Balaenopteridae) (Fig. 2) (Hoberg 1989; Temirova and Skrjabin 1978).

Considering the genus *Anophryocephalus*, a degree of spe-



FIGS. 7 and 8. Geographic distributions of *Anophryocephalus* spp. among pinnipeds in the North Pacific. Fig. 7. Geographic distribution of *Phoca vitulina richardsi* (from King 1983) and minimum range for *A. skrjabini* (stars). This figure was based solely upon previously unpublished records from harbor seals, deposited in the USNM by L. M. Shults. Identity of the cestodes was based on the examination of voucher specimens (see Hoberg *et al.* 1991). Fig. 8. Approximate overlapping geographic ranges for *Eumetopias jubatus* and *Callorhinus ursinus* (from King 1983) and minimum range for *A. eumetopii* (asterisks) and *A. ochotensis* (stars). Records from *E. jubatus* are according to Shults (1986) and Hoberg *et al.* (1991) and include additional details of host occurrence from data deposited by L. M. Shults in the USNM. The single report of *A. ochotensis* from *C. ursinus* (1) in the Komandorskii Islands is attributable to Iurakhno (1987).

cificity is apparent in the host distributions of the five species. Hoberg *et al.* (1991) reviewed host and geographic ranges for species among phocids (*A. anophrys*, *A. nunivakensis*, *A. skrjabini*) and otariids (*A. eumetopii*, *A. ochotensis*) in the Holarctic Region (Table 3, Figs. 3–8). Species of this genus are absent from boreal latitudes of the Atlantic and Pacific and appear to be restricted to the subarctic and arctic. Among the Phocidae, *Anophryocephalus* is limited to the subfamily Phocinae, specifically *Cystophora cristata* + *Phoca* spp. of the tribe Phocini (classification is consistent with Wyss 1988a), whereas among the Otariidae only *E. jubatus* (subfamily Otariinae) has been recognized as a typical host. Based on single host records of *A. anophrys* in *C. cristata*, *P. (Pagophilus) groenlandica* and *P. vitulina* (from the Northwest Atlantic) and a recent report of *A. ochotensis* in *C. ursinus* (subfamily Arctocephalinae) (Komandorskii Islands, western Bering Sea), these pinnipeds are recognized as facultative, ecological hosts (Deliamure and Treschev 1966; Smith and Threlfall 1973; McClelland 1980; Iurakhno 1987) (Table 3, Figs. 4 and 8). Notably, *Anophryocephalus* spp. are absent

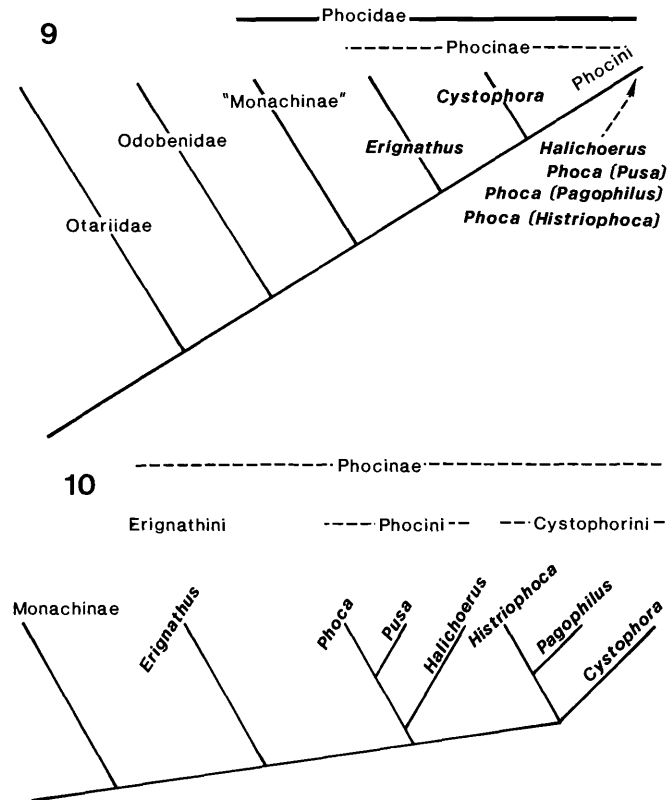


FIG. 9. Cladogram depicting the phylogenetic hypothesis for relationships among the Pinnipedia (modified from Wyss 1987, 1988a, 1989; Berta *et al.* 1989). "Monachinae" are not considered to be monophyletic; *Cystophora* is recognized as the sister-group for the monophyletic tribe Phocini that includes *Halichoerus* and subgenera of *Phoca*. FIG. 10. Cladogram depicting an alternative phylogenetic hypothesis for the Phocinae (modified from DeMuizon 1982). It differs from postulated relationships shown in Fig. 9 in recognizing monophyly for the Monachinae as the sister-group of the Phocinae. The concept of the Phocini and Cystophorini presented in this figure differs from most current classifications. With respect to this hypothesis, the traditional Phocini would be polyphyletic; additionally, *Cystophora* is considered to be highly derived.

among the Odobenidae, all other Otariidae (only 2 of 14, or 14% of otariids are known hosts, with 1 being facultative), and the majority of the Phocidae (only 6 of 19, or 32% of phocids are known hosts, with 3 being facultative), including the Monachinae and a substantial number of genera, species, and subspecies referred to the Phocinae (Table 3).

Additionally, there are no records of this group of cestodes from the southern hemisphere (Deliamure 1955; Markowski 1952a, 1952b, 1971; Temirova and Skrjabin 1978; and others). In contrast, some other platyhelminths, including the pseudophyllidean *Diphyllbothrium* Cobbold, 1858 and the campulid digenean *Orthosplanchnus* Odhner, 1905, have broad host and geographic distributions among pinnipeds in the northern and southern hemispheres (Deliamure 1955; Markowski 1952a, 1952b; Adams and Rausch 1989; Schmidt 1986).

The absence of species of *Anophryocephalus* from the southern hemisphere and other regions where collections of phocids and otariids have been extensive supports the contention that colonization occurred subsequent to the divergence of the Otariidae (including the Otariinae and Arctocephalinae), the Odobenidae, and the Phocidae (see Wyss 1987), and to the

establishment of the seals, sea lions, and fur seals in the Southern Ocean, thus following hemispherical segregation and isolation of pinniped populations about 3–5 million years ago (see Repenning *et al.* 1979). Consequently a basis is provided for establishing a maximum age for the origin of the *Anophryocephalus*-clade. Radiation of *Anophryocephalus* spp., *Strobilocephalus*, and *Priapocephalus* would necessarily have been limited to the Late Pliocene – Pleistocene, with all groups having origins substantially more recent than had been previously considered (Baer 1954; Temirova and Skrjabin 1978; Galkin 1987). This also indicates an older association of diphyllobothriids and campulids among pinnipeds.

Further implications of the evolution of *Strobilocephalus* and *Priapocephalus*, along with other platyhelminths mentioned above, will not be considered here. However, it is possible to examine in detail the evolution and historical biogeography of *Anophryocephalus* among the pinnipeds and in doing so to define more restrictive limits on the temporal duration of this assemblage. A requisite component of the analysis is consideration of the phylogeny and biogeography of the pinnipeds to provide a context for interpreting the distributional and evolutionary history of *Anophryocephalus* spp. (see Hoberg 1986; Brooks 1985).

Pinniped phylogeny and biogeography

Salient conclusions of recent phylogenetic studies of the pinnipeds are summarized below (Figs. 9 and 10). These provide a foundation for an assessment of host–parasite evolution and historical biogeography of *Anophryocephalus* spp. among the otariids and phocids (particularly the Phocinae).

Concepts for the origins and relationships of the extant higher taxa among the Pinnipedia (Otariidae, Odobenidae, and Phocidae) recognize terrestrial arctoid carnivorans (e.g., ursids and mustelids, among others) as the ancestors of these marine mammals (Tedford 1976; Berta *et al.* 1989; and others). Hypotheses for diphyletic derivation of the Otariidae and Odobenidae (from ursids) and the Phocidae (from mustelids) have been presented (Tedford 1976; Repenning *et al.* 1979; Barnes *et al.* 1985; Repenning 1990; and others). In contrast, a considerable body of molecular and morphological data provides strong support for recognition of the pinnipeds as a monophyletic group derived from a common arctoid ancestor (Arnason and Widegren 1986; Wyss 1988b, 1989; Berta *et al.* 1989; Berta and Wyss 1990; and others). Within the context of a monophyletic Pinnipedia, the otariids are considered a basal group with respect to the odobenids and phocids (Wyss 1987, 1988a, 1989; Berta *et al.* 1989) (Fig. 9). Although debate continues over the relationships of the sea lions, fur seals, and walruses (Repenning 1976; Berta and Deméré 1986; Wyss 1987), monophyly of the Phocidae has been widely accepted (Wyss 1988a, DeMuizon 1982).

The phocids are typically divided into the subfamilies Phocinae (“northern” phocids) and Monachinae (“southern” phocids) (King 1983; DeMuizon 1982; Wyss 1988a). Monophyly of the subfamilies was supported by analyses by DeMuizon (1982), who considered them to be sister-groups (Fig. 10). However, Wyss (1988a) concluded that the “monachines” were paraphyletic, while recognizing monophyly for the phocines (Fig. 9).

Although the monophyly of the Phocinae is undisputed, there is considerable disagreement over the relationships of the tribes and genera referred to the subfamily. Three tribes (Erignathini, Cystophorini, and Phocini) have been estab-

lished (King 1983). In the traditional classification, the Erignathini (with *Erignathus barbatus* (Erxleben), the bearded seal) and Cystophorini (with *C. cristata*, the hooded seal) are monotypic, whereas the Phocini typically includes species of *Phoca* Linnaeus (harbor seals), *Pusa* Scopoli, *Halichoerus grypus* Fabricius (gray seal), *Pagophilus groenlandica* (Erxleben) (harp seal), and *Histiophoca fasciata* Zimmermann (ribbon seal). Burns and Fay (1970) have reduced all of the Phocini (except *Halichoerus*) to subgenera of *Phoca*, although this opinion is not universally accepted (see DeMuizon 1982).

In a cladistic analysis of the phocids, DeMuizon (1982) postulated that *Erignathus* was the basal member of the Phocinae. The Phocini (*Halichoerus*, *Pusa*, and *Phoca*) shared a sister-group association with the Cystophorini (*Cystophora*, *Pagophilus*, and *Histiophoca*) (Fig. 10). Thus, acceptance of the traditional concept of the Phocini resulted in the tribe being polyphyletic (DeMuizon 1982). In contrast, Wyss (1988a) concluded from phylogenetic analyses that *Erignathus* and *Cystophora* were basal taxa, with the latter being the sister-group for a monophyletic Phocini (Fig. 9).

Although there continues to be a dispute over some aspects of pinniped phylogeny, the biogeographic history of the otariids and phocids (as principal hosts of *Anophryocephalus* spp.) has been elucidated to a considerable degree (Davies 1958; McClaren 1960, 1966; Ray 1976; Repenning *et al.* 1979; DeMuizon 1982; and others). The evolutionary history of these families is apparently one of long-term isolation in early centers of diversification in the North Pacific (otariids) and North Atlantic (phocids) with minimal interchange through the late Tertiary (Repenning *et al.* 1979).

The earliest recognized otariids are Mid-Miocene in age (~11–12 million years ago) from the North Pacific basin (Repenning 1976; Barnes *et al.* 1985; Berta and Deméré 1986). According to Repenning (1976) these early taxa are considered directly ancestral to the fur seals (*Arctocephalus* Geoffroy and Cuvier), and by 6 million years ago, diversification leading to the Alaskan fur seal (*Callorhinus* Gray) is recognized (Repenning *et al.* 1979). The sea lions diverged as a distinct lineage by about 3 million years ago (or perhaps >5 million years ago as implied by Berta and Deméré 1986) and represent the most recently derived of the otariids. Although fur seals had dispersed to the southern hemisphere by about 5 million years ago, the sea lions crossed the equator within the past 3 million years. Diversification of the sea lions proceeded subsequent to isolation of populations in the northern and southern hemispheres (Pacific basin), leading to the radiation of *Zalophus* Gill and *Eumetopias* Gill in the north and *Neophoca* Gray, *Otaria* Person, and *Phocarcos* Peters in the south (Kim *et al.* 1975; Repenning *et al.* 1979).

Berta and Deméré (1986) presented a somewhat different view of otariid relationships, postulating a sister-group association for the Arctocephalinae and Otariinae. The Otariinae contained five traditional genera, with *Zalophus* considered to be the basal genus and with *Eumetopias*, *Neophoca*, *Phocarcos*, and *Otaria* diverging later. The results of this analysis might imply a somewhat earlier origin for *Eumetopias* than had been previously suggested (also see Repenning 1976) but do not appear to significantly alter the current understanding of late-otariid biogeography.

The phocids appear to have an evolutionary history equal in duration to that of the otariids (DeMuizon 1982; Barnes *et al.* 1985) and have seemingly been confined to the North Atlantic

during much of their diversification (Ray 1976; Repenning *et al.* 1979; DeMuizon 1982). However, the putative sister-group of the phocids (Odobenidae) originated in the Pacific, and the earliest branch of the phocid cladogram is also a Pacific endemic (see Wyss 1987, 1988a), potentially implying the importance of this region (or the Tethys Sea?) in the initial diversification of the group. Phocines and monachines are recognized in the earliest fossil record of phocids from the Atlantic (Ray 1976; Repenning *et al.* 1979; DeMuizon 1982). The phylogenetic and biogeographic histories of the two subfamilies of phocids are complex, but it is clear that the lineages have been independent and distinct since the Mid-Miocene (Ray 1976).

Monachines had origins in the North Atlantic; however, their greatest diversification occurred in the middle latitudes of the northern tropics (tribe Monachini), along the coast of the western neotropics (tribe Miroungini), and in the Southern Ocean (tribe Lobodontini) (DeMuizon 1982). Ancestors of these latter groups dispersed into the southern hemisphere about 5 million years ago and entered the South Atlantic to establish a circumantarctic distribution by 4.5 million years ago. The Monachini became distributed through the middle latitudes of the Pacific and Caribbean starting 15 million years ago (Ray 1976; Repenning *et al.* 1979; DeMuizon 1982). Consequently the monachines have been phylogenetically distinct and geographically isolated from the northern phocines for 5–10 million years.

Although the phocines were contemporaneous with the monachines for much of their late Tertiary history in the North Atlantic, they did not disperse to the south but diversified in the boreal to subarctic (Ray 1976). Members of extant genera, now restricted to high latitudes of the northern hemisphere (DeMuizon 1982; King 1983), did not disperse to the Pacific basin through the Central American Seaway (open until 3 million years ago) but entered the North Pacific through the Arctic basin following the first opening of Bering Strait, which occurred about 3.0–3.5 million years ago (Barnes and Mitchell 1975; Ray 1976; Repenning *et al.* 1979; Herman and Hopkins 1980; Matthews 1981). Radiation of modern phocines (particularly *Phoca* spp.) occurred during the latest Pliocene and Pleistocene (Burns and Fay 1970; Ray 1976; King 1983; and others) coincidental with the inception of the major cycles of glaciation in the northern hemisphere (Herman and Hopkins 1980).

Extant species of the Phocinae that are the hosts of *Anophryocephalus* are referred either to the Phocini + *Cystophora* (Wyss 1988a; Fig. 9) or to the Cystophorini and Phocini (DeMuizon 1982; Fig. 10). The history and evolution of *C. cristata*, and *Phoca* spp. in the Holarctic are particularly intricate and have yet to be fully elucidated (Davies 1958; McLaren 1966; Grigorescu 1976; Ray 1976; King 1983; and others).

Hooded seals are considered to be the sister-group of *Phoca* (*Histiophoca*) + *Phoca* (*Pagophilus*) (DeMuizon 1982) (Fig. 10) or basal phocines as the sister-group for the Phocini (Wyss 1988a; Fig. 9). A single species of *Cystophora*, lacking geographic differentiation, occurs at high latitudes of the Atlantic basin, and apparently never successfully dispersed to the Pacific basin (Davies 1958; Ray 1976). In contrast, species of the genus *Phoca* became widely distributed in the Holarctic Region.

Phocines, represented by *Phoca* (*Pusa*), entered the Bering Sea from the Arctic basin about 2.5–3.0 million years ago

(Ray 1976; Repenning *et al.* 1979). Radiation of phocines in the Bering Sea, Okhotsk Sea, and the subarctic and boreal Pacific resulted in the differentiation of *P. (Pusa) hispida* ssp., *P. largha*, *P. (Histiophoca) fasciata*, and *P. vitulina* ssp. (King 1983). Biogeographic studies by Davies (1958), McLaren (1960, 1966), and Ray (1976), in conjunction with cladistic analyses by DeMuizon (1982), indicate that evolution of this assemblage was dependent on sequential episodes of dispersal (from the Atlantic via the Arctic) and subsequent vicariance. Cyclic fluctuations in glacial maxima (with concomitant eustatic variation in sea level) through the Pleistocene mediated range expansions and contractions for *Phoca* spp., the latter ultimately leading to isolation in refugial centers (Arctic, Okhotsk, Aleutian, etc.) and divergence of populations. The dispersal and speciation process would also have been influenced by variation in sea surface temperatures and changes in the distribution of key prey organisms (Davies 1958).

Phoca (Pusa) hispida appears closely allied with the Baikal and Caspian seals (*Phoca (Pusa) sibirica* Gmelin and *Phoca (Pusa) caspica* Gmelin), but its relationship with other *Phoca* species is not clear (Davies 1958; McLaren 1966; Repenning *et al.* 1979). A potential for derivation from the Paratethyan seals has been suggested (Grigorescu 1976; Repenning *et al.* 1979), as has a later relationship with *P. largha* (McLaren 1966). DeMuizon (1982) considered *Phoca* and *Pusa* as sister-groups but did not discuss the biogeographic implications. A high degree of differentiation of local populations suggested to Davies (1958) that *P. hispida* was among the earliest to enter the Pacific basin (see Repenning *et al.* 1979).

Phoca (Histiophoca) fasciata in the Pacific and *P. (Pagophilus) groenlandica* in the Atlantic may represent a vicariant species pair (Davis 1958; DeMuizon 1982). This association, along with a putative relationship of *Halichoerus* and *Phoca* + *Pusa* (DeMuizon 1982) and the potential that *Phoca vitulina richardsi* (Gray) + *Phoca vitulina stejnegeri* Allen (in the Pacific) have closer affinities with North Atlantic populations of *P. vitulina* than with *P. largha* (Shaughnessy and Fay 1977), suggests the importance of multiple events of dispersal (from the Atlantic) and vicariance during the Mid to Late Pleistocene. Additionally, the *P. vitulina*-group is considered to represent an actively radiating species swarm (Ray 1976). Thus, it is apparent that the history of *Phoca* in the North Pacific basin is relatively recent, extending only over the past 2.5–3.0 million years.

Host–parasite associations

The historical or ecological foundation for the host and geographical ranges of *Anophryocephalus* spp. may be viewed within the context of alternative hypotheses (not mutually exclusive) for coevolution or colonization. A coevolutionary relationship would be supported by a high degree of consistency and congruence in the phylogenies of *Anophryocephalus* spp. and their pinniped hosts (Brooks 1979b, 1981, 1988; Brooks and McLennan 1991). Additionally, an early association of *Anophryocephalus* among the otariids with subsequent cospeciation and coadaptation among the phocids would be expected. Absence of these cestodes among most otariids (only 2 species, or 14%, are hosts, including 1 facultative), odobenids, monachine phocids, and many phocines (only 6 species, or 32%, are hosts, including 3 facultative) would be attributable to a considerable level of secondary loss. Extant *Anophryocephalus* spp. would thus represent coevolved

numerical relicts as determined by host-trophic ecology (see Brooks and Bandoni 1988). Alternatively, corroboration of a hypothesis for host switching as a dominant influence on host-parasite evolution would be indicated by a low degree of consistency and congruence in the respective phylogenies (Brooks and McLennan 1991). Evolutionary associations attributable to colonization would account for geographically delimited faunas occurring among ecologically similar hosts. Varying degrees of coevolution may be postulated as a function of the timing of initial colonization of the host group.

The importance of coevolution and (or) colonization as determinants of structure and organization within this parasite-host assemblage may be determined by the degree of congruence in the phylogenies of *Anophryocephalus* spp. and the pinnipeds. Ancillary evidence for assessing the temporal duration of the assemblage may be gained through a consideration of the host and geographic ranges of *Anophryocephalus* spp.

The phylogenetic histories of *Anophryocephalus* species and their pinniped hosts are inconsistent and incongruent, thus strongly corroborating a hypothesis for the dominance of colonization in the evolution of this assemblage (Figs. 11, 12, 13). The origin and later diversification of *Anophryocephalus* spp. among pinnipeds was a function of colonization, sequential host switching, and subsequent coevolution (including cospeciation and coadaptation) (see Brooks 1979b; Brooks and McLennan 1991). The broader relationships of the *Anophryocephalus*-clade (as previously outlined) suggest that the genus *Anophryocephalus* was derived from the tetrabotheiids of odontocete cetaceans via colonization of pinnipeds. The initial hosts of *Anophryocephalus* were phocines, specifically species of *Phoca*, in the Atlantic basin, whereas diversification followed host switching (and coevolution) among *Phoca* spp. and colonization of otariids (*E. jubatus*) in the North Pacific basin (Figs. 11, 12, 13).

Colonization of pinnipeds and the diversification of *Anophryocephalus* were dependent upon guild associations (see Hoberg 1986, 1987), initially between odontocetes and pinnipeds and later among phocines and otariids. The sister-group for the *Anophryocephalus*-clade is considered to be *Trigonocotyle*, a group of cestodes among the Delphinidae. Although initial radiation of the odontocetes and pinnipeds occurred in the late Oligocene (Barnes *et al.* 1985), available evidence suggests that tetrabotheiids may not have been associated with the former host group during that period. Host switching from odontocetes to pinnipeds occurred relatively late in the evolutionary history of the latter group.

Consequently, the distribution of *Anophryocephalus* among phocids and otariids has no bearing on corroboration of the hypothesis for pinniped monophyly. Additionally, evidence is lacking that could elucidate a possible sister-group relationship for the Odobenidae and Phocidae (see Wyss 1987). Although a definable cestode fauna exists in pinnipeds, it is marine rather than terrestrial in origin (see Hoberg 1987). The depauperate contemporary cestode fauna of the Phocinae (see Wyss 1988a) and otariids was acquired following invasion of marine communities by terrestrial arctoid ancestors of the pinnipeds. It is likely that most components of the helminth fauna typical of terrestrial carnivorans were lost prior to the broad diversification of the pinnipeds. Thus, there are no known cestodes that provide a definable link between terrestrial and marine carnivorans, although some nematodes may have been retained following an invasion of marine habitats (see Deliamure 1955).

Otariids and phocids appear to have been isolated in highly segregated allopatric centers of diversification in the Pacific and Atlantic, respectively (Repenning *et al.* 1979; King 1983; Wyss 1989), through much of the late Tertiary. The degree of isolation is tenuously supported by a relatively poor fossil record, although the barriers to dispersal, particularly through the Central American Seaway, are not completely understood (Wyss 1989). However, it is of interest that the latter region also appears to have been a significant obstruction to the dispersal of early members of the Alcidae and their parasites, which were restricted to the North Atlantic and North Pacific for much of their early evolutionary history (see Hoberg 1984, 1986).

The broader context of the parasitological record may provide some concept for linkage of these pinniped faunas, as genera and species of ectoparasitic echinophthiriid lice are specific to sea lions, walruses, and seals, and perhaps indicative of a long coevolutionary association with their hosts (Kim *et al.* 1975). In contrast, the helminth fauna of phocids, otariids, and odobenids appears to be largely structured by ecological interactions of the hosts (Deliamure 1955).

Although the bipolar distributions of acanthocephalans (particularly *Corynosoma* spp.), anisakines, diphyllbothriids, and campulids suggest a protracted history with pinnipeds (see Markowski 1952a, 1952b; Deliamure 1955; Zdzitowiecki 1986; Adams and Rausch 1989), there do not appear to be phylogenetic associations with hosts that would unequivocally link these early centers of diversification. In this regard, Fagerholm and Gibson (1987) suggested that the distribution of *Contracaecum ogmorhini* Johnston and Mawson, 1941 supported the hypothesis of diphyletic origins of the phocids and otariids. This anisakid is a parasite of otariids and has morphological similarities with species of *Contracaecum* from avian hosts, suggesting that it is not closely related to *C. osculatum* Rudolphi, 1802 from odobenids and phocids. This led Fagerholm and Gibson (1987) to propose independent origins for *Contracaecum* spp. in otariids and phocids. Phylogenetic hypotheses have not been developed for *Contracaecum* spp. and related anisakids; thus, the postulated relationship (and morphological similarities) for *C. ogmorhini* and species from avian hosts could be based on plesiomorphic characters. However, the contention that *C. ogmorhini* represents a colonizer acquired from seabirds appears supportable (see Fagerholm and Gibson 1987).

Consequently, with respect to the considerable corroboration for pinniped monophyly, the lack of a close phylogenetic association for *C. osculatum* and *C. ogmorhini* implies that the host switch (from marine birds) to basal otariids occurred following divergence from other pinnipeds but prior to cladogenesis of the Arctocephalinae and Otariinae (see Berta and Deméré 1986). However, the relationship and origin of *C. osculatum* among odobenids and phocids remain obscure, and to complicate the situation, Berland (1963) advocated referral of this species to *Phocascaris* Host, 1932. It is possible that the distribution of *C. osculatum* among phocids and odobenids (Deliamure 1955; and others) could be indicative of a sister-group relationship for these families as postulated by Wyss (1987, 1988a). Phylogenetic analysis of *Contracaecum* spp. and related anisakids would be essential to resolve this issue. Additionally, detailed studies of other helminth taxa in pinnipeds are still required. In the case of *Anophryocephalus*, radiation of phocids and otariids had been extensive prior to the origin of the host-parasite assemblage.

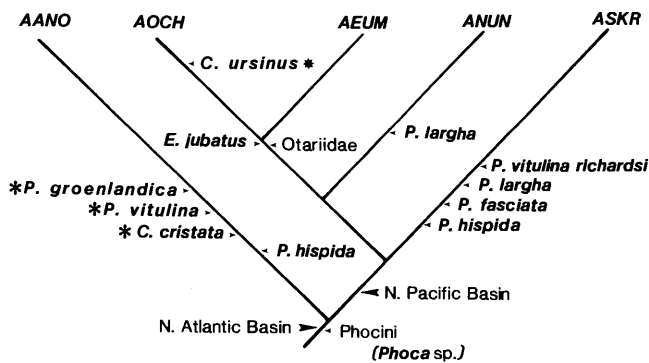


FIG. 11. Cladogram of *Anophryocephalus* spp., showing host and geographic relationships mapped onto the parasite tree. Relationships shown here are compatible with *Anophryocephalus* initially colonizing the Phocini (*Phoca*) in the North Atlantic. *Anophryocephalus anophrys* (AANO) developed in *Phoca* (*Pusa*), and the occurrence of *Cystophora cristata*, *Phoca vitulina*, and *Phoca* (*Phagophilus*) *groenlandica* represents contemporary shifts to facultative ecological hosts in the western Atlantic. *Anophryocephalus* entered the North Pacific via the Arctic basin with *Phoca* (*Pusa*) and later radiated among *Phoca* spp., resulting in the diversification of *A. skrjabini* (ASKR) and *A. nunivakensis* (ANUN). Most recently the otariids (specifically *Eumetopias jubatus*) were colonized by the common ancestor of *A. ochotensis* (AOCH) and *A. eumetopii* (AEUM), and the occurrence of the former species in *Callorhinus ursinus* (star) in the Komandorskii Islands is consistent with a contemporary distribution in a facultative host.

Species-level relationships

The host and geographic distributions of *Anophryocephalus* spp. were largely determined by climatic fluctuations and cyclic variation in the sea level that characterized the Late Pliocene and Pleistocene (Hopkins 1967, 1971; Matthews 1981). Patterns of vicariance, range expansion and isolation in regional refugia, and sequential colonization (specifically in the Pacific basin) dominated the evolution and host-associations of *Anophryocephalus* spp. among the phocids and otariids (Figs. 11–14). With respect to the alternative hypotheses for the relationships among the Phocinae (Figs. 9, 10), colonization is a dominant factor in determining the structure of host associations for *Anophryocephalus* spp. However, in the phylogenetic hypothesis developed by DeMeuzon (1982), a minimum of one additional colonization event is required to explain the distribution of *Anophryocephalus* spp. among the Phocinae (Figs. 12, 13).

The most basal species of *Anophryocephalus*, *A. anophrys* is endemic to the subarctic of the Atlantic basin and the eastern Arctic basin (Figs. 3, 4, 14). It has a narrow host range in ringed seals, with the hooded, harp, and harbor seals being considered facultative ecological hosts, due to the paucity of records (Delamure and Treschev 1966; Smith and Threlfall 1973; McClelland 1980). In this respect, *A. anophrys* is considered a host-specific parasite of *P. (Pusa) hispida*, as it has not been reported from any of the other Phocinae in the Atlantic basin (Hoberg *et al.* 1991). These relationships indicate that a maximum temporal limit can be defined for the association of *Anophryocephalus* and the Phocinae.

The initial appearance of *Phoca* (*Pusa*) in the Arctic basin was approximately 3.0 million years ago (Repenning *et al.* 1979; Ray 1976). Consequently, the absence of *Anophryocephalus* from other phocines of the Atlantic is compatible with colonization of *Phoca* (*Pusa*) in the Arctic basin no

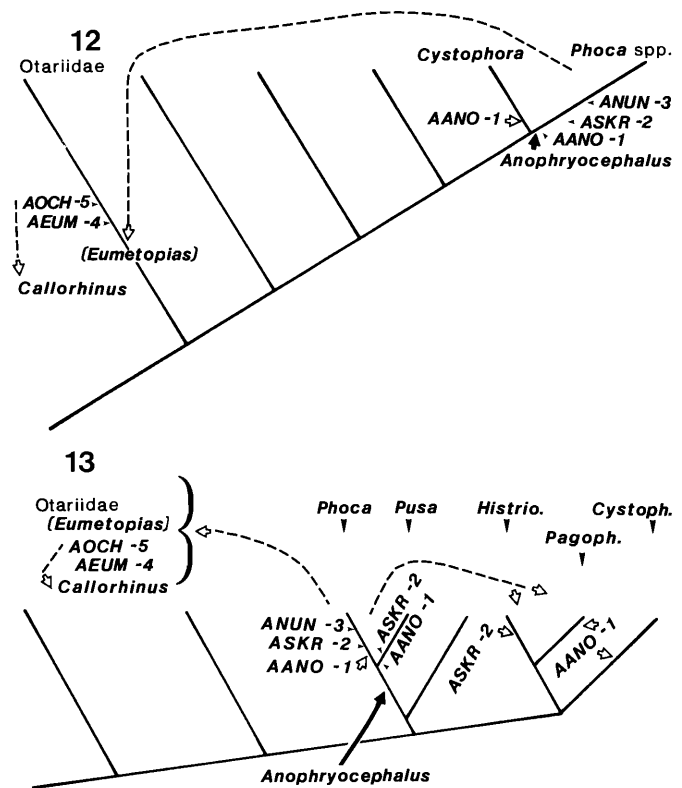


FIG. 12. Host cladogram (consult Fig. 9), with sequential associations of *Anophryocephalus* spp. indicated among the Phocinae and Otariidae. Numbers indicate the sequence of speciation among *Anophryocephalus* spp. The solid arrow indicates the original colonization of *Phoca*. *Anophryocephalus anophrys* (AANO-1), *A. skrjabini* (ASKR-2), and *A. nunivakensis* (ANUN-3) are restricted to the Phocini; *Cystophora* was subsequently colonized by AANO (open arrow) (other contemporary facultative hosts for AANO in the North Atlantic, including *Phoca vitulina* and *Phoca* (*Pagophilus*) *groenlandica* are not shown). Otariids (only *Eumetopias*) were colonized by *Anophryocephalus* from phocines (broken line, open arrow); subsequent specific differentiation resulted in the development of *A. eumetopii* (AEUM-4) and *A. ochotensis* (AOCH-5); distribution of the latter species in *Callorhinus* is postulated to be a contemporary host shift (broken line, open arrow). These relationships require a minimum of four events of colonization among the Phocini + *Cystophora* (including three contemporary host shifts involving AANO in *Cystophora*, *P. vitulina*, and *P. groenlandica*) and a more recent independent colonization of the otariids (*Eumetopias*) and later host shift of AOCH to *Callorhinus*. FIG. 13. Host cladogram (consult Fig. 10) with sequential associations of *Anophryocephalus* spp. among the Phocini, Cystophorini, and Otariidae (sea lions and fur seals are not included on the cladogram). The solid arrow indicates the initial colonization by *Anophryocephalus* in the common ancestor for *Phoca* + *Pusa*. Later differentiation resulted in the development of *A. anophrys* (AANO-1), *A. skrjabini* (ASKR-2), and *A. nunivakensis* (ANUN-3). These host relationships require independent colonization of *Histiophoca* (by ASKR) in the Pacific and later contemporary host shifts by AANO to *Cystophora*, *Phoca*, and *Pagophilus* in the Atlantic (broken lines, open arrows). Later *Eumetopias* would have been colonized from *Phoca*, thus accounting for the distribution of *A. eumetopii* (AEUM-4) and *A. ochotensis* (AOCH-5), and a contemporary host shift to *Callorhinus* is consistent with the occurrence of the latter species in fur seals (broken lines, open arrows). These relationships require a minimum of five events of colonization among the Phocini + Cystophorini (with three contemporary host shifts of AANO to *Cystophora*, *Phoca*, and *Pagophilus*) and a more recent independent colonization of the otariids (with a secondary shift to *Callorhinus*).

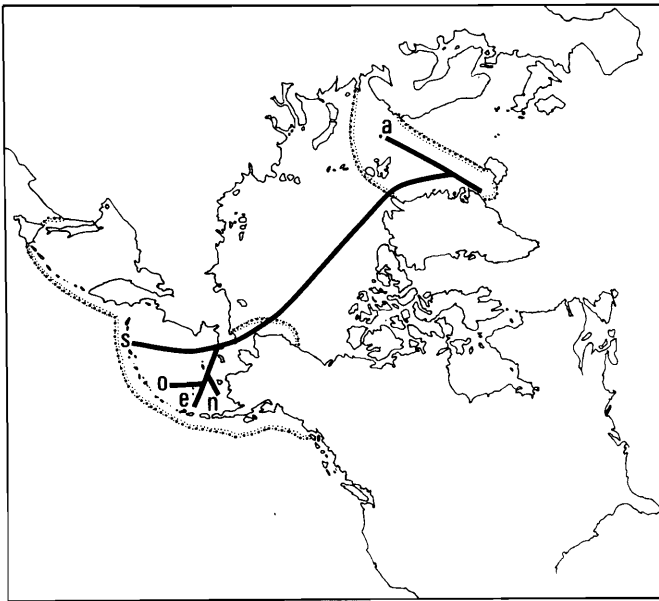


FIG. 14. Area cladogram for *Anophryocephalus* species in the Holarctic Region. The area of endemism for *A. anophrys* (a) is in the arctic sector of the North Atlantic basin. Overall relationships shown in the figure suggest the importance of vicariance in the diversification of *Anophryocephalus*. *Anophryocephalus* sp. would have been broadly distributed in the Arctic basin prior to entry into the Pacific. Vicariance of this population is postulated to have resulted in the differentiation of *A. anophrys* and later radiation of species in the arctic and subarctic of the Pacific basin, including *A. skrjabini* (s), *A. nunivakensis* (n), *A. ochotensis* (o), and *A. eumetopii* (e). Apparent restriction of *A. nunivakensis* to the eastern Bering Sea could indicate that the origin of this species is attributable to peripheral isolation; other Pacific endemics appear to be broadly distributed in the Bering Sea, Gulf of Alaska, and Sea of Okhotsk.

earlier than 3.0 million years ago. Following the initial event of host switching in the arctic sector of the North Atlantic, *Anophryocephalus* attained a broad geographic range with *P. (Pusa) hispida* in the Arctic basin. The high arctic was clear of perennial sea ice until 700 000 years ago (Worseley and Herman 1970; Herman and Hopkins 1980), and even after deterioration of conditions during the Late Pleistocene this region apparently remained suitable for ringed seals, the only phocines adapted to high arctic conditions (Davies 1958; King 1983). With the initial opening of Bering Strait in the Late Pliocene (3.0–3.5 million years ago; Matthews 1981), it became possible for phocines (and *Anophryocephalus*) to enter the North Pacific basin for the first time, although this may not have occurred until 2.5 million years ago (Ray 1976; Repenning 1979; DeMuizon 1982; and others). The subsequent history of this assemblage was determined by radiation of *Phoca* spp. and *Anophryocephalus* spp. during the Late Pliocene and Pleistocene in the North Pacific basin.

The initial pattern evident in the evolution of *Anophryocephalus* spp. is vicariance. Separation and isolation of an early Holarctic population of *Anophryocephalus* in the Arctic basin and North Pacific accounts for the development of *A. anophrys* and *A. skrjabini* (Figs. 11–14). This vicariance event would have been associated with an Early Pleistocene closure of Bering Strait mediated by eustatic changes in sea level. Although periodic emergence of Beringia occurred through the Pleistocene (Hopkins 1967, 1971; Matthews

1981), later disruptions to marine dispersal apparently did not influence the overall distribution of *Anophryocephalus* in the Holarctic. However, the subsequent partitioning of the Bering Sea and Sea of Okhotsk and North Pacific into regional refugial zones (Udvardy 1963; Davies 1958; Warner *et al.* 1982) during glacial maxima directly influenced isolation and speciation of this parasite–host assemblage.

The initial divergence of *A. anophrys* and *A. skrjabini* was associated with separation of a population of an early *Phoca* (*Pusa*) sp.; however, the broad host and geographic distribution of the latter species of cestode in the North Pacific could be explained by coevolution or colonization. The range of *A. skrjabini* is amphipacific (Figs. 3, 5, 6, 7, 14) and coincides with the distributions of *P. (Pusa) hispida*, *P. largha*, *P. (Histriophoca) fasciata* and *P. vitulina richardsi* (for the latter, only in the Gulf of Alaska and Bering Sea). If the contention of DeMuizon (1982) is correct and “*Phoca*” is polyphyletic then the host distribution is a consequence of ecological factors (host food habits) and colonization (Figs. 10, 13). However, if *Phoca* is monophyletic (the Phocini) (Wyss 1988a), then the assemblage may have developed at least in part through coadaptation (Figs. 9, 12).

Considering the detailed outline for phocid evolution presented earlier, coadaptation explains the occurrence of *A. skrjabini* in *P. hispida* and *P. largha* if, as McLaren (1966) contended, the spotted or largha seal is closely related to the former species (divergence 2–3 million years ago). Host switching among *Phoca* spp. provides a more parsimonious explanation for the occurrence of *A. skrjabini* in *P. vitulina richardsi* and *P. (Histriophoca) fasciata*. Harbor seals appear most closely related to the North Atlantic subspecies of *P. vitulina* (Shaugnessey and Fay 1977) and may be part of a still actively speciating swarm (Ray 1976). Thus, a relatively late association of *A. skrjabini* and *P. vitulina richardsi* appears supported by available data. Additionally, the putative relationship for *P. (Histriophoca) fasciata* and *P. (Pagophilus) groenlandica* (Davies 1958; DeMuizon 1982) suggests that these represent a vicariant species pair in which colonization by *A. skrjabini* and a contemporary host shift by *A. anophrys* occurred, following cladogenesis of the common ancestor of ribbon and harp seals, respectively (Figs. 10, 13).

The host and geographic distribution of *A. nunivakensis* is compatible with parasite speciation without concomitant host speciation (Figs. 5, 11–14). The primary hosts are spotted or largha seals. *Anophryocephalus nunivakensis* could represent a peripheral isolate (with respect to the broadly distributed *A. skrjabini*) that speciated in a refugial situation (see Wiley 1981), coinciding with isolation of a host population (possibly corresponding with a range contraction of *P. largha*) during an Early Pleistocene glacial stage. Support for this hypothesis will require clarification of records for *A. nunivakensis* and *A. skrjabini* in *Phoca* spp. from other areas of the North Pacific basin.

Radiation of *Anophryocephalus* spp. among phocines resulted in the evolution of three species, whereas two additional species were derived from a relatively recent colonization of otariids (specifically *E. jubatus*) (Figs. 11–14). The single report from *C. ursinus* in the Komandorskii Islands (Iurakhno 1987) and a paucity of records from other localities (see Stiles and Hassal 1899; Deliamure 1955; Neiland 1961; Keyes 1965; Iurakhno 1987) are compatible with recognizing northern fur seals as facultative ecological hosts for *A. ochotensis*. Thus, the absence of *Anophryocephalus* from all other

otariids (including sea lions and fur seals of the northern and southern hemispheres) implies that Steller's sea lions became hosts for these cestodes following the divergence of the Otariinae from the Arctocephalinae and *Eumetopias* from other otariines in the Pleistocene (≈ 2.0 million years ago) (Kim *et al.* 1975; Barnes *et al.* 1985; Berta and Deméré 1986).

The genus *Eumetopias* has a temporal range extending to 2.0 million years ago, based on deposits in Japan (Repenning 1976; Kim *et al.* 1975; Barnes *et al.* 1985). Sea lions referable to *E. jubatus* diverged somewhat later, providing a maximum age of the association with *Anophryocephalus* at not more than 2.0 million years ago. The geographic range of *E. jubatus* is amphi-Pacific, extending from subarctic to boreal latitudes, and local populations are not recognized (Davies 1958). Cestodes in Steller's sea lions, *A. eumetopii* and *A. ochotensis*, are considered to be host specific and appear to have broad ranges coinciding with that of their pinniped host only in the subarctic (Figs. 8, 11–14). These sister-species may have originated from vicariance of a widespread *Anophryocephalus* sp. in *Eumetopias*. Alternatively, isolation and divergence of populations in refugial settings in the Okhotsk, Aleutian arc, or Gulf of Alaska, followed by postglacial expansion of ranges of hosts and parasites, could also explain the distribution. Evolution of *Anophryocephalus* in sea lions represents another instance of parasite speciation without concomitant host speciation. The apparent limited occurrence of *A. ochotensis* in *Callorhinus* (Iurakhno 1987) is postulated to have resulted from a recent, contemporary host shift.

It is possible to recognize four phases in the evolution of *Anophryocephalus* and the development of this assemblage among pinnipeds (Fig. 14). The initial phase was associated with colonization of *Phoca* (*Pusa*) in the Atlantic sector of the Arctic basin (~ 3.0 million years ago). A later association with *Phoca* (*Pusa*) provides a phylogenetic basis for the absence of *Anophryocephalus* in *Erignathus*, *Halichoerus*, *Cystophora* (the latter considered to be facultative, due to limited records of immature cestodes only; Deliamure and Treshchev 1966), and *Phoca* (*Pagophilus*) and the North Atlantic subspecies of *Phoca vitulina* (both considered facultative due to the paucity of records). The second phase involved range expansion of *Phoca* (*Pusa*) and *Anophryocephalus* into the North Pacific (3.0–2.5 million years ago) and vicariance of host and parasite populations leading to speciation of *A. anophrys* and *A. skrjabini*. Following entry to the Pacific basin, the third phase continued with speciation of *A. nuni-vakensis* (in *P. largha*) and colonization of *Eumetopias* (< 2.0 million years ago) leading to the origin of *A. ochotensis* and *A. eumetopii*. Thus, the evolutionary history of *Anophryocephalus* was largely restricted to the North Pacific basin during the Quaternary. Lack of more extensive differentiation of *Anophryocephalus* in the North Atlantic could be a function of a lower degree of fragmentation in coastal habitats (and formation of refugia) than that documented in the North Pacific basin through the Pleistocene. Broad contemporary geographic ranges for some species of hosts and parasites represent postglacial expansion since the Pleistocene, and variation in seasonal patterns of dispersal for some pinnipeds. The incidental occurrence of *A. anophrys* in hooded, harp, and harbor seals and the limited distribution of *A. ochotensis* in northern fur seals is compatible with contemporary ecologically based host switching.

Historical–ecological components strongly define the structure of this depauperate assemblage; however, additional fac-

tors, including host specificity of parasites and contemporary host ecology, may constitute constraints to broader diversification within this system. The restricted geographic distributions of *Anophryocephalus* in the subarctic and arctic are also considered to be a function of these dual components.

Food habits and feeding patterns among pinnipeds could have limited the initial potential for colonization and the eventual pattern of diversification for *Anophryocephalus* spp. Among the phocines, the primary hosts for *Anophryocephalus* are, to a large extent, zooplanktivores that are pelagic foragers (Davies 1958; King 1983). This suggests that benthic feeders that exploit a wide range of invertebrates, such as *Erignathus* and *Odobenus* Brisson (Lowry *et al.* 1980; Fay 1982), are unlikely to be hosts for *Anophryocephalus*. Although *Anophryocephalus* is considered to have colonized phocines after the divergence of the odobenids and *Erignathus*, food habits provide an ecological constraint on later host switching among *Phoca* spp. and these other pinnipeds.

Euphausiids may constitute primary intermediate hosts for *Anophryocephalus* spp. (Murav'eva and Popov 1976), although pelagic fishes and cephalopods could function as second intermediate or paratenic hosts (see Hoberg 1987; Avdeev and Avdeeva 1986; Skrjabin 1972). Euphausiids and other crustaceans (often pelagic amphipods) are seasonally important prey for *P. hispida*, *P. largha*, and *P. fasciata* (Lowry and Frost 1981; Frost and Lowry 1984), but all are known to exploit a wider base of prey including demersal and pelagic fishes. Murav'eva and Popov (1976) presented evidence that euphausiids were the primary intermediate hosts for *A. skrjabini* among *P. hispida*, *P. largha*, and *P. fasciata* in the Bering Sea and Sea of Okhotsk, although metacestodes resembling undifferentiated tetrabothriids (see Hoberg 1987) have not yet been demonstrated from these pelagic crustaceans (Komaki 1970; Shimazu 1975a, 1975b).

In this regard, reports of plerocercoids referred to *Anophryocephalus* spp. from several species of marine fishes by Avdeeva (1989) require confirmation and are likely to be incorrect. Identification was established solely upon insubstantial similarities in the structure of the scolex and bothridia in these larvae (previously regarded as *Scolex* spp., an otherwise morphologically homogeneous group of tetraphyllidean metacestodes) and adults of *Anophryocephalus* spp., based on a superficial comparison with figures of *A. skrjabini* from Temirova and Skrjabin (1978) (see Avdeeva 1989). Aside from the tenuous nature of the morphological comparison (based on incomplete figures of *Anophryocephalus*; see Hoberg *et al.* 1991), the geographic distributions of the piscine hosts are largely subtropical (southern hemisphere) and thus incompatible with the ranges of known pinniped hosts for *Anophryocephalus* spp. Consequently, a 2- or 3-host cycle, although likely for *Anophryocephalus* spp. (see Hoberg 1987), remains to be confirmed.

Euphausiid intermediates and piscine paratenic hosts would explain the occurrence of *A. skrjabini* in *P. vitulina richardsi*, which is primarily piscivorous (King 1983; Lowry and Frost 1981). Additionally, this would account for the initial colonization of *Eumetopias*, which forages in pelagic habitats on fishes, cephalopods, and large crustaceans (Schusterman 1981; King 1983). The uncommon occurrence of *Anophryocephalus* in northern fur seals may be determined in part by highly pelagic foraging habits and a piscine diet. Further, the absence of *Anophryocephalus* in *Halichoerus* and the infrequency of infections in *Phoca vitulina* ssp. appear to have an

ecological basis, as these seals are primary piscivores (King 1983) with geographic ranges not substantially overlapping those of Arctic–Atlantic phocines. Factors that limit the geographic distribution of *Anophryocephalus* to high latitudes of the North Pacific and Atlantic basins, although likely to have an ecological basis controlled by the distribution of pinnipeds and their prey species, have yet to be elucidated (see Dailey and Fallace 1989).

Although specimens of *P. vitulina richardsi* and *E. jubatus* have been examined in the southern extent of their ranges in the eastern Pacific, the presence of *Anophryocephalus* spp. has never been demonstrated (Dailey and Hill 1970; Margolis 1956; Stroud and Dailey 1978; Dailey and Fallace 1989). Strong limitations exist in the latitudinal distribution of *A. skrjabini* in *P. vitulina richardsi*, and *A. ochotensis* and *A. eumetopii* in *E. jubatus*. The southern periphery of the ranges of these cestodes appears limited to the subarctic of the North Pacific (north of the Subarctic Current and Alaskan Stream, see Dodimead *et al.* 1963), but they occur in host species that have extensive geographic ranges continuing into the southern boreal regions of the eastern Pacific basin (Figs. 7, 8). Similar restrictions in geographic distribution have been noted for other helminths of harbor seals and Steller's sea lions, including *Corynosoma strumosum* (Rudolphi, 1802) and *Diphyllbothrium alasense* (Cobbold, 1858). Such limitations may reflect (i) dietary differences among northern and southern populations of seals and sea lions and (ii) the potential that centers of abundance for key intermediate hosts (specifically pelagic macrozooplankton such as some euphausiids) are limited to the cooler waters and relatively closed biotic system of the Alaskan Domain (see Dodimead *et al.* 1963; McGowan 1974; Cooney 1986; Reed and Schumacher 1986).

In the Atlantic basin the narrow host and latitudinal range of *A. anophrys* may be attributable to host specificity in *P. hispida* and geographically based differences in prey selection among *C. cristata* and *Phoca* spp. The recognition of hooded seals as a facultative ecological host for *A. anophrys* (Deliamure and Treschev 1966) is potentially explained by specificity in ringed seals. Additionally, although harp seals are primary zooplanktivores (euphausiids and amphipods) and their range coincides with that of *P. hispida* in the Atlantic sector of the Arctic, these phocines are not phylogenetically close (King 1983; DeMuizon 1982). Thus, host specificity of *Anophryocephalus* in *P. hispida* may have also constituted a constraint to successful colonization in *P. groenlandica* (see Hoberg 1986). Although *A. skrjabini* occurs in the putative sister species of *P. groenlandica* (*P. fasciata*), colonization in the Pacific basin occurred following divergence of the harp and ribbon seals.

Host specificity among *Anophryocephalus* spp. appears most pronounced in *A. anophrys* (in *P. hispida*), and *A. ochotensis* and *A. eumetopii* (in *E. jubatus*), whereas *A. skrjabini* and *A. nunivakensis* exhibit specificity among *Phoca* sp. (Table 3). Development of strict specificity, particularly with species in Steller's sea lions, appears to have been a rapid phenomenon. In contrast, the concept of specificity has typically been linked to coevolved, often archaic, assemblages of long temporal duration (Mayr 1957; Price 1980; and others). Similar to the distribution of *Alcataenia* among the Alcidae (Hoberg 1986), the *Anophryocephalus*-assemblage is relatively young and has not been substantially influenced by coevolutionary (cospeciation) processes. Brooks (1979b, 1985, 1988) suggested that host specificity may not directly reflect the duration of historical associations between groups

of hosts and parasites. The observation of pronounced specificity in two recently evolved assemblages among phylogenetically disparate host and parasite taxa (Alcidae and dilepidid cestodes; pinnipeds and tetrabothriid cestodes) provides empirical support for this contention.

Colonization represents a unifying theme in the development of parasite faunas among marine homeotherms or contemporary marine taxa with terrestrial origins (Hoberg 1987, 1986). Host switching and subsequent speciation are postulated as the principal mechanisms in the origin and diversification of *Anophryocephalus* spp. among pinnipeds and *Alcataenia* spp. among alcids. Although colonization appears stochastic, the potential for successful transfer to a new host is dependent on predictable trophic associations (trophic guilds and evolutionary time) (Hoberg 1987; Brooks 1988; Brooks and Bandoni 1988).

The results of colonization include diversification (cospeciation, or speciation without concomitant host speciation), coadaptation, and, if unsuccessful, extinction (Brooks 1979b, 1985; Brooks and McLennan 1991). Additionally, distributions of parasites within a host clade may appear relictual but lack a strong historical coevolutionary component (Brooks and Bandoni 1988). Broad diversification of a parasite group via colonization historically reflects a substantial ecological similarity among definitive hosts of the assemblage (Brooks 1985; Brooks and Bandoni 1988). Within the context of colonizing faunas among marine homeotherms, they have been found to be depauperate and geographically delimited as a function of parasite specificity and host ecology (Hoberg 1986, 1987). Among cestodes of alcids and pinnipeds, morphological evolution of parasites may be associated with host switching but it is not a general-level phenomenon (see Brooks *et al.* 1985; Brooks and McLennan 1991). It is also apparent that host specificity may act as a constraint to sequential colonization and radiation of parasites (Hoberg 1986). Thus, in both these colonizing faunas, rapid adaptive radiation has not been associated with the exploitation of a new host group (see Hoberg 1986).

A common history has determined the contemporary biogeography of cestode faunas and the parasite–host assemblages associated with pinnipeds and seabirds of the family Alcidae (Hoberg 1986). The Pleistocene was a dynamic period of climatic fluctuations that strongly influenced paleogeography in coastal habitats (Davies 1958; Hopkins 1971; and others). The effects of climatic change in marine environments was summarized previously with respect to cestodes and marine birds in the Holarctic Region (Hoberg 1986). Udvardy (1963) commented on the similarity in geographic distributions among phocids, otariids, and alcids in the North Pacific basin and suggested that common causal mechanisms determined the ranges for seabirds and marine mammals.

Vrba (1985) postulated a link between maximum climatic variation, environmental disruption (vicariance), and speciation during the late Tertiary. However, it was considered that polar regions would be centers of extinction rather than diversification. Isolation of populations due to eustatic changes in sea level and confinement to refugial centers during the Pleistocene in the North Pacific (and in the Arctic basin) is postulated as a primary determinant of speciation among pinnipeds and some seabirds (Davies 1958; Repenning *et al.* 1979; Hoberg 1986). Additionally, sequential range contraction and expansion coinciding with a cyclic pattern of stadials and interstadials is postulated as the driving mechanism for diversification of marine parasite–host assemblages in the

Holarctic Region (Hoberg 1986). In contrast to the contention by Vrba (1985), climatic fluctuation at high latitudes appears to have directly influenced concurrent radiation of marine homeotherms and their cestode parasites in subpolar and polar regions of the northern hemisphere during the Late Pliocene and Pleistocene. This hypothesis will be expanded and tested in future studies of these assemblages and other components of the marine fauna in the North Pacific and Arctic basin.

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