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SPECIFIC ANTIQUITY OF THE SUCKING LICE AND EVOLUTION OF OTARIID SEALS[1]

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INTRODUCTION

In the Symposium on the Biology of the Seal a significant correlation was recognized among the conclusions of the three papers which we presented. These papers discussed evolution of the otariid seals based upon the fossil record (Repenning, 1975), an interpretation of possible phylogenetic sequence of the otariids based upon the bacula of the living forms (Morejohn, 1975), and the ecology and morphological adaption of the sucking lice on the northern fur seal (Kim, 1975). In the last paper those lice endemic to the living genera of otariid seals were listed, and their host specificity was discussed. The conclusions of the three papers were mutually corroborative, and provided further evidence for evolution of otariid seals. At the same time the known chronology of the fossil record of otariid seals provides rather compelling suggestion of the antiquity of the louse-seal association.

Here, the conclusions of the three papers are collaborated and synthesized to document this greater understanding of the evolution of the otariid seals and of their sucking-louse fauna. The significance of the host specificity and diversity of the sucking lice (Echinophthiriidae, Anoplura) on the Pinnipedia is emphasized.

THE FOSSIL RECORD

The phylogenetic history of the otariid seals is better documented by the fossil record, than it is for many other mammalian groups. This does not result from a great abundance of fossil material but rather from the conservative nature of the evolutionary diversifications of these marine carnivores. Thus a relatively few fossils reveal the phylogenetic history.

In this discussion we are concerned only with the last 5 or 6 million years of otariid evolution. Records now available suggest that the sea lions (Subfamily Otariinae) evolved from the more primitive fur seals (Subfamily Arctocephalinae) possibly as long ago as 3 million years. This suggestion is based on an arbitrary definition of the fur seals and the earliest records of living taxa of sea lions.

The more primitive otariids, whose history dates back at least 12 and possibly 15 million years, are all small forms in comparison with living sea lions. They have skeletal limb proportions more comparable to living fur seals, and they have double-routed cheek teeth. These conditions lead to the assumption that they are best considered primitive fur seals rather than sea lions. In addition, the fur seals are presumed to be the more primitive otariids because abundant underfur obviously has insulating advantages in water only to moderate depths where hydrostatic pressure would not greatly compress the air it traps. Thus, thick underfur is found in many shallow-water mammals, in the Rodentia as well as in the Carnivora. Among marine mammals, that feed in deep-water under great hydrostatic pressure, the value of underfur is lost because of the compression of the trapped air, and conservation of body heat must depend on relatively imcompressible subcutaneous adipose tissue. A thick envelope of subcutaneous fat covers the body of all living marine mammals except *Enhydra* which feeds only in shallow water.

Although most living otariids have at least some single-rooted cheek teeth, the tendency toward single (or fused) roots is much stronger in living sea lions than in living fur seals. The earliest otariid fossils with single-rooted cheek teeth are between 3 and 4 million years old, based upon the approximate correlation with zebrine horses found elsewhere in the same stratigraphic unit (Burleson, 1948; Allison *in* Leffler, 1964). Fossil otariids with all cheek teeth bearing two roots are known in deposits 4 to 5 million years old based upon associated pliohippine horses (L. G. Barnes, personal communication). Remains of living genera of sea lions are known in the North Pacific Basin in deposits possibly 2 million years old. It is thus presumed that the sea lions may have diverged from the ancestral fur seals about 3 million years ago.

The earliest records of living genera of sea lions in the Southern Hemisphere are less than one million years old. However, because they are generically distinct from the sea lions of the Northern Hemisphere and because living genera are known to have lived between 1 and 2 million years ago to the north, it is presumed that the sea lions dispersed to the Southern Hemisphere perhaps 2 million years ago and there evolved into the living taxa.

In addition, the three southern sea lion genera, *Phocarctos*, *Neophoca* and *Otaria*, harbor the same sucking louse, *Antarctophthirus microchir* (Troussart and Neumann), as do the two northern genera, *Eumetopias* and *Zalophus*. This fact requires the interpretation that the southern sea lions did not evolve separately from some fur seal in the Southern Hemisphere, rather a common origin of all sea lion genera is indicated, presumably in the North Pacific Basin.

THE BACULUM

The present fossil record helps little in learning the events involved in the development of the two living genera of fur seals, *Arctocephalus* and *Callorhinus*. Some aspects of fossil fur seals 7 to 9 million years old suggest relationship to *Callorhinus* and others to *Arctocephalus;* there are no known fossils which are clearly ancestral to only one of the living genera. However, consideration of the bacula of living otariids and of one fossil otariid, provides some evidence of probable evolutionary patterns.

The bacula of living otariids possess, at maturity, both dorsal and ventral knobs on the apex and have a shaft that varies from round, through oval, to triangular in cross section. The apex is transversely broader in most of the living sea lions than in the fur seals, and this condition is most accentuated in the sea lion genera *Phocarctos* and *Eumetopias*. The sea lion, *Zalophus*, and the fur seal, *Arctocephalus*, have bacula essentially identical in apex morphology, although that of *Zalophus* is usually stouter and broader. Both dorsal and ventral knobs are of approximately equal width and, when viewed anteriorly, the bacular apices are parallel-sided in most individuals. However, a growth series of *Eumetopias* bacula shows that it develops first from an *Arctocephalus* or *Zalophus*-like condition, and with continued lateral swelling, passes through a transversely broadened condition like that of the bacula of *Otaria* and *Neophoca*, and later as a subadult, through the adult condition of *Phocarctos*. Finally, with full maturity, *Eumetopias* develops an essentially circular outline when viewed in anterior aspect.

It seems possible, therefore, that the baculum of *Arctocephalus* as a fur seal and the baculum of *Zalophus* as a sea lion are the most primitive of those found in the living otariids. In fact, the cheek teeth and skulls of some species of *Arctocephalus* are strikingly similar to *Zalophus* (Repenning, Peterson, and Hubbs, 1971). In addition, *Zalophus californianus* and *Arctocephalus pusillus* have bred in captivity and produced several intergeneric offspring (Mohr, 1952). *Zalophus*, in several respects, could be considered a fur seal without fur and may be of the living genera, the form closest to the archetypal sea lion. Stirling and Warneke (1971) cite a number of lines of evidence which suggest that *Arctocephalus pusillus* is more like a sea lion than a fur seal, despite the presence of underfur.

The developmental stages of the bacular apex of *Callorhinus* are similar to *Arctocephalus* and *Zalophus* as subadults and adults. However, the adult bacular apex of *Callorhinus*, resembles a "figure eight" in terminal view. The ventral knob is considerably expanded laterally and the dorsal knob less so. A marked waist between dorsal and ventral knobs is obvious. Thus, *Callorhinus* has a bacular form unknown in other otariids either as adults or in their growth series and appears to represent a specialized offshoot of the Arctocephaline stem. Other traits not shared by the other otariids also suggest this: 1) milk teeth begin to be shed while still *in utero* (Scheffer and Kraus, 1964); 2) lactation time is shortened to about 4 months (Peterson, 1968); 3) cartilaginous and skin extensions of flippers are markedly greater than in all other otariids; 4) the species undergoes the most extensive annual pelagic migrations (Kenyon and Wilkie, 1953); and 5) the species has a male to female size disparity of 4·5 to 1 (Scheffer, 1958), probably greater than in any other otariid.

One fossil baculum is known from an otariid of roughly 8 million years ago, and this most resembles that of *Callorhinus*. The suggestion is, therefore, that the lineage leading to *Callorhinus* diverged from the stem lineage earlier than did the sea lion, while the main branch of otariid evolution proceeded from the *Arctocephalus* condition to further modification of the bacular apex.

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With the later divergence from this lineage, broadening of the apex developed in the sea lions and has progressed to the most advanced condition seen in *Phocarctos* and *Eumetopias*. The primitive pattern of the bacular apex, the retention of underfur and of primitive limb proportions, and the reduced rate of development of single-rooted cheek teeth apparently has remained constant in *Arctocephalus* since this divergence of the sea lions from the stem lineage of the otariids occurred.

THE SUCKING LICE

The sucking lice of the family Echinophthiriidae are obligate, permanent ectoparasites exclusively on the aquatic carnivora mainly Pinnipedia. They are fierce blood suckers, and their entire life cycle is completed on the host. The lice are host-specific, and inhabit the skin and the pelage of pinnipeds. Thus, survival of the echinophthiriids depends solely upon the survival of the host animal and upon the microenvironment their host provides.

The pinniped-infesting sucking lice are so highly specialized that their affinity is quite obscure. The fact that they have unique morphological traits and host specificity to the pinnipeds suggests that the echinophthiriids must have evolved with the pinnipeds since the ancestral seals ventured into marine life. Unquestionably, this specialization that obscures taxonomic relationships is the result of adaption to the marine environment by the Echinophthiriidae, as the sucking lice in general are essentially terrestrial ectoparasites. However, fissiped carnivores are usually infested with biting lice (Mallophaga) but not with sucking lice. The single exception is in the Canidae, on which two species of sucking lice are known. These belong to the genus *Linognathus*, which is specific to the Bovidae and the Cervidae (Artiodactyla), and the acquisition of *Linognathus* by canids is therefore recent.

The echinophthiriid lice are unique in that the body is more or less thickly beset with various setae, some of which are modified as scales; the thoracic and abdominal spiracles are of distinctive type with a long, more or less membranous atrium and a highly specialized closing apparatus; the fore legs are usually small and slender, with an acuminate claw; the middle and hind legs have very stout tibiotarsi, and the abdomen is completely membranous.

The Echinophthiriidae includes four distinct genera at present (Table 131). *Antarctophthirus* is the most diverse taxon and includes six known species from a wide range of hosts; Otariidae, Odobenidae, and the Monachinae. *Proechinophthirus* is found exclusively on the Arctocephalinae and includes two known species, *P. fluctus* (Ferris) on *Callorhinus ursinus* and *P. zumpti* (Werneck) on *Arctocephalus pusillus*. *Echinophthirius* is monotypic and exclusively parasitic upon the Phocidae; *E. horridus* (von Olfers) is known from *Cystophora cristata, Erignathus barbatus, Halichoerus grypus, Pagophilus groenlandicus, Phoca vitulina, Pusa hispida,* and *Pusa sibirica*. The fourth genus, *Lepidophthirus,* is comprised of two species: *L. macrorhini* Enderlein is found only on *Mirounga leonina* and *L. piriformis* Blagoveschensky on *Monachus manachus*.

Unlike other pinnipeds, the northern fur seal, *Callorhinus ursinus,* hosts two species of sucking lice; *Antarctophthirus callorhini* (Osborn) inhabiting the naked skin and *Proechinophthirus fluctus* (Ferris) in the fur or underfur habitat (Kim, 1971; 1972). The second species of *Proechinophthirus, P. zumpti* Werneck, is found on *Arctocephalus pusillus* and presumed to inhabit the underfur, but no species of *Antarctophthirus* is yet known from the southern fur seal.

Antarctophthirus microchir (Troussart and Neumann) is the sole species known from the living sea lions, including all genera of both northern and southern hemispheres; *Eumetopias, Zalophus, Otaria,* and *Phocarctos* (Ferris, 1951) as well as *Neophoca* (B. J. Marlow, personal communication). *A. microchir* inhabits the naked parts of the skin, namely flippers, of these living sea lions. This species is not found on other pinniped hosts.

Proechinophthirus is closely related to *Echinophthirius* in several morphological traits: 1) no abdominal scales: 2) antenae four-segmented; 3) pseudopenis of the male round without distinct apical process; and 4) abdomen elongated; however, *Proechinophthirus* differs from *Echinophthirius* in morphological details of the fore legs and chaetotaxy. All legs of *Echinophthirius* are similar in shape and size and their claws are blunt, and the setae on the body and head are short. *Lepidophthirus* is a highly specialized taxon among the known echinophthiriids, and differs from others in having a short abdomen with a dense cover of scales, a pseudopenis that is disconnected at the apex, and claws of the middle and hind legs that are pointed. *Antarctophthirus,* on the other hand, shares some morphological similarities to *Proechinophthirus* and somewhat to *Lepidophthirus*; it has an elongate abdomen which is, in contrast to *Proechinophthirus,* covered with scales and has different setae, the pseudopenis is complete but has a short apical process, the antennae are four-segmented in nymphs but are five-segmented in the adult, and claws of the middle and hind legs are blunt.

EVOLUTION OF OTARIID SEALS AND THEIR LICE

The fossil records suggest that the sea lions dispersed to the southern hemisphere perhaps 2 million years ago, and there evolved into the three southern genera of living sea lions, while the two northern sea lion genera evolved in the northern hemisphere. Both northern and southern sea lions harbor a single polytypic species of louse, *Antarctophthirus microchir.* This fact suggests that *A. microchir* has existed on the sea lion for more than 2 million years, since the time when this mammal became a distinct evolutionary lineage and prior to dispersal of this lineage to the southern hemisphere between 1 and 2 million years ago. The evolution of this lineage of the sucking lice was exceedingly slow relative to that of the sea lions.

The presence of *Proechinophthirus* as a unique parasite on both *Callorhinus ursinus* of the northern hemisphere and on *Arctocephalus pusillus* of the southern hemisphere suggests that this lineage is of as great an antiquity as is the fur seal lineage. *Proechinophthirus* is definitely the most generalized taxon showing many primitive morphological traits, and may be considered to be closer to the ancestral echinophthiriid, a condition quite comparable to that already indicated for their host, the fur seals. If the rate of evolution of *Proechinophthirus* has been comparable to that of *Antarctophthirus,* the fact that two species have evolved, *P. fluctus* endemic on *Callorhinus* and *P. zumpti* on *Arctocephalus pusillus,* would certainly suggest that the two fur seals have evolved along separate lineages much more ancient than the sea lion lineage; a suggestion already indicated by the study of their bacula.

It is presumed, but not yet established, that other species of *Arctocephalus* harbor *Proechinophthirus.* Occasional contact is known between most species, the most remote possibility being that of *Arctocephalus townsendi,* from Mexican and southern California waters, having contact with other species south of the Equator. *Callorhinus* currently breeds on San Miguel Island, California, and *A. townsendi* now visits the island as a wanderer. Remains of both genera are abundant in Indian garbage dumps on the island and, to judge by the number of young individuals, it seems possible that both fur seal genera bred there. *A. townsendi,* therefore, may well have a *Callorhinus*-like louse fauna rather than one typical of other species of the genus.

Antarctophthirus is a typical echinophthiriid and adapted to the microhabitat (naked skin) which is directly influenced by the thermoregulatory activities of the host and by numerous factors of the marine environment. From morphological and ecological evidence it may be concluded that *Antarctophthirus,* prosessing a broad genetic adaptability, established itself on all pinnipeds not host to *Echinophthirius* and

Table 131. List of known species of Anoplura from Pinnipedia

The Sucking Lice (Family Echinophthiriidae)				Host (Order Pinnipedia)
Antarctophthirus	*Proechinophthirus*	*Echinophthirius*	*Lepidophthirus*	Family Otariidae
				Subfamily Arctocephalinae
A. callorhini	*P. fluctus*	–	–	*Callorhinus ursinus*
???	*P. zumpti*	–	–	*Arctocephalus pusillus*
A. microchir				Subfamily Otariinae
»	–	–	–	*Eumetopias jubata*
»	–	–	–	*Phocarctos hookeri*
»	–	–	–	*Otaria bryonia*
»	–	–	–	*Zalophus californianus*
»	–	–	–	*Neophoca cinerea*
				Family Odobenidae
A. trichechi	–	–	–	*Odobenus rosmarus*
				Family Phocidae
				Subfamily Monachinae
–	–	–	*L. piriformis*	*Monachus monachus*
–	–	–	*L. macrorhini*	*Mirounga leonina*
A. ogmorhini	–	–	–	*Hydrurga leptonyx*
»	–	–	–	*Leptonychotes weddelli*
A. lobodontis	–	–	–	*Lobodon carcinophagus*
A. mawsoni	–	–	–	*Ommatophoca rossi*
				Subfamily Phocinae
–	–	*E. horridus*	–	*Cystophora cristata*
–	–	»	–	*Erignathus barbatus*
–	–	»	–	*Halichoerus grypus*
–	–	»	–	*Pagophilus groenlandicus*
–	–	»	–	*Phoca vitulina*
–	–	»	–	*Pusa hispida*
–	–	»	–	*Pusa sibirica*

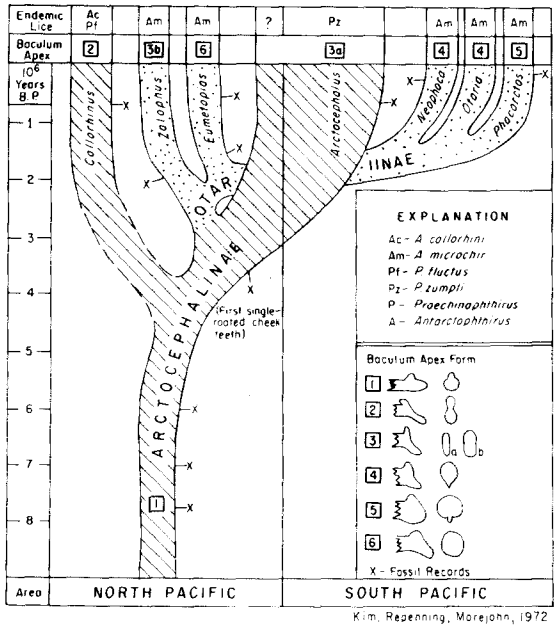

Figure 385. Phylogeny of the Otariidae inferred from the fossil record, form of the baculum, and endemic sucking lice.

Lepidophthirus with the single exception of *Arctocephalus pusillus*. However, it is suspected that *Antarctophthirus* will eventually be found on the southern fur seal (Table 131). Of six known species, *A. callorhini* is the most generalized species of *Antarctophthirus*. The lack of scales on the thoracic sternum in *A. callorhini* is definitely an indication of primitiveness. This fact seems to support the conclusions derived from the fossil record and the bacular anatomy that the ancestral otariids were fur seal-like animals. This should be further substantiated by studying the louse fauna of *Arctocephalus*.

The possible origin of *A. callorhini* on *Callorhinus* is not clearly answerable at this time. This may be a relic from the louse fauna inhabiting the ancestral otariids, now extinct, which still retains some primitive morphological traits, as does its host.

Most significantly, the presence of *A. microchir* as an inhabitant of both the northern and southern taxa of sea lions (Otariinae) suggests that a monospecific lineage of the sucking lice has existed for at least 2 million years, and strongly suggests a monophyletic origin of the sea lions out of an ancestral fur seal. The most probable evolutionary history, in the opinion of the authors, is shown as a phylogenetic diagram in Figure 385.

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