SPECIFIC ANTIQUITY OF THE SUCKING LICE AND EVOLUTION OF OTARIID SEALS

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INTRODUCTION

In the Symposium on the Biology of the Seal a signifi-
cant correlation was recognized among the conclu-
sions of the three papers which we presented. These
discussions focused on the evolution of the otarid se-
als based upon the fossil record (Repenning, 1955), an
interpretation of possible phylogenetic sequence of the
otarids based upon the bacula of the living forms
(Morejohn, 1975), and the ecology and morphological
adaptation of the sucking lice on the northern fur seal
(Kim, 1975). In the last paper those lice endemic to the
living genera of otarid seals were discussed and their
host specificity was discussed. The conclusions of the
three papers were mutually corroborative, and pro-
vided further evidence for evolution of otarid seals.

At the same time the known chronology of the fossil
record of otarid seals provides rather compelling sug-
gestion of the antiquity of the host-lice association.

Here, the conclusions of the three papers are colla-
borated and synthesized to document this greater un-
derstanding of the evolution of the otarid seals and of
their sucking-louse fauna. The significance of the host
specificity and diversity of the sucking lice (Hippoboscidae,
Anoplura) on the Primates is emphasized.

THE FOSSIL RECORD

The phylogenetic history of the otarid seals is bet-
ter 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 diversification
of these marine carnivores. Thus a relatively few fos-
sils reveal the phylogenetic history.

In this discussion we are concerned only with the
first 3 or 6 million years of otarid 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
to 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-rotated cheek teeth.

These characteristics suggest that these animals were
considered more primitive than sea lions.

In addition, the fur seals are presumed to be the
more primitive otariids because abundant underfossil
material has insinuated advantages in water only to moder-
ate depths where hydrostatic pressure would not greatly
compress the air it traps. Thus, thick underfossil 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 pres-
sure, the value of underfossil is lost because of the com-
pression of the trapped air, and conservation of body
heat must depend on relatively incompressible sub-
cutaneous adipose tissue. A thick envelope of subcu-
taneous fat covers the body of all living marine mam-
mals except Eusphyra which feeds only in shallow
water.

Although most living otariids have at least some
single-rooted cheek teeth, the tendency toward single
(rooted) roots is much stronger in living sea lions
than in living fur seals. The earliest otarid fossils with
single-rooted cheek teeth are between 3 and 4 million
years old, based upon the approximate correlation with
zebra horses found elsewhere in the same stratigraphic
unit (Burton, 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
phalangipine horses (L. G. Bornes, personal commu-
nication).

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 have dispersed 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 geographically dis-

tinct 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 then
evolved into the living taxa.

In addition, the three southern sea lion genera, Phoca-
retes, Neophoca and Otaria, harbor the same sucking
louse, Antarctophilus micros (Tromsøe and Neum-
mann). As do the two northern genera, Eumetopias
and Zalophus. This fact implies the interpretation
that the southern sea lions did not evolve separately
from the sea lions of the Northern Hemisphere, rather
a common origin of all sea lion genera is indicated,
preumably in the North Pacific Basin.

THE BACULUM

The present fossil record helps little in learning the
evolutionary position 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
considered ancestral to only one of the living genera.

However, it is clear from the bacula of living otariids
and of one fossil otarid, 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 tri-
angular 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 Phocaenets and Eumetopias. The sea
lions, Zalophus, and the fur seal, Arctocephalus, have
bacula essentially identical in apex morphology, al-
thought that of Zalophus is usually smaller and broad-
er. Both dorsal and ventral knobs are of approximate
ly equal width and, when viewed anteriorly, the
baculae are parallel-sided in most individuals.

However, a growth series of Eumetopias bacula shows
that it develops first from an Arctocephalus or Zal-
ophus-like condition, and then continues to grow
through a transversely broadened condition like that
of the bacula of Otaria and Neophoca, and later
as a subadult, though the adult condition of
Phocaenets. Finally, with full matuinity, Eumetopias
develops an essentially circular outline when viewed
in anterior aspect.

It seems likely, therefore, that the baculum of
Arctocephalus is a fur seal and the baculum of Zal-
ophus 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 strik-
ingly similar to Zalophus (Repenning, Peterson, and
Hubbs, 1971). In addition, Zalophus Californicus and
Arctocephalus pacificus have been 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 pacificus is more like
a sea lion than a fur seal, despite the presence of
underfur.

The developmental stages of the bacalce apex of Callorhinus are similar to those of Arctocephalus and Zal-
ophus as subadults and adults. However, the adult
baculum of Callorhinus, resembles a "figure eight" in terminal view. The ventral knob is consider-
ably expanded laterally and the dorsal knob less so.
A marked waist between dorsal and ventral knobs is
obvious. Thus, Callorhinus has a baculum form un-
commonly exhibited by other otarid genera. The growth series and appears to represent a specialized
offshoot of the Arctocephalus stem. Other taxa
shared by the other otarid also suggest this: 1) milk
teeth begin to be shed while still in utero (Schel-
fer, and Kraus, 1961); 2) lactation time is shortened
to about 5 months (Peterson, 1968); 3) cartilaginous
tubeworms 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 nude to female
size disparity of 4.5 to 1 (Schelle, 1958), probably
greater than in any other otarid.

One fossil baculum is known from an otarid of
roughly 8 million years ago, and it 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 otarid evolution proceeded from the
Arctocephalus condition to further modification of the
bacalce apex.
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 remained constant in *Arctocephalus* since this divergence of the sea lions from the stem lineage of the otarids occurred.

**The Sucking Lice**

The sucking lice of the family Echinophthiridae 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 echinophthirids depends solely upon the survival of the host animal and upon the microenvironment that host provides.

The pinniped-infecting 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 echinophthirids must have evolved with the pinnipeds since the ancestral scales ventured into marine life. Unquestionably, this specialization that obsoles taxonomic relationships is the result of adaptation to the marine environment by the Echinophthiridae, as the sucking lice in general are essentially terrestrial ectoparasites. However, fish-eating carnivores are usually infected with biting lice (Mallophaga) but not with sucking lice. The single exception is in the Canidae, on which two species of Echinophthiridae 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 Echinophthiridae 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 setae 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 tibias, and the abdomen is completely membranous.

The Echinophthiridae includes four distinct genera at present (Table 131). *Arctocephalus* is the most diverse taxon and includes six known species from a wide range of hosts: Otariidae, Odobenidae, and the Monachinae. *Prochrocephalus* is found exclusively on the Arctocephalinae and includes two known species, *P. fusca* (Ferris) on Callorhinus ursinus and *P. zumpti* (Wernec) on Arctocephalus pusillus. *Echinophthirus* is monotypic and exclusively parasitic upon the Phocidae; *E. horridus* (von Oerst) is known from Cystophora cristata, Erignathus barbatus, Halichoerus grypus, Pagophilus groenlandicus, Phoca vitulina, P. hispida, and Pusa sibirica. The fourth genus, *Lepidophthirus*, is comprised of two species: *L. microhiri* Enderlein inhabits only on Mirounga leonina and *L. piniformis* Blagoveschensky on Monachus monachus.

Unlike other pinnipeds, the northern fur seal, *Callorhinus ursinus*, hosts two species of sucking lice: *Arctocephalus californicus* (Okada) inhabiting the naked skin and *Prochrocephalus flatus* (Ferris) in the fur or underfur habitat (Kim, 1971; 1972). The second species of *Prochrocephalus*, *P. zumpti* Wernec, is found on *Arctocephalus pusillus* and presumed to inhabit the underfur, but no species of *Echinophthirus* is yet known from the southern fur seal.

*Arctocephalus microchir* (Trouessart and Néumann) is the sole species known from the living sea lions, including all genera of both northern and southern hemisphere: *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.

*Prochrocephalus* is closely related to *Echinophthirus* in several morphological characters: 1) these lice have three different types of scales; 2) antennae four-segmented; 3) pseudopods of the male round without distinct apical process; and 4) abdomen elongated; however, *Prochrocephalus* differs from *Echinophthirus* in morphological details of the fore legs and chaetotaxy. All legs of *Echinophthirus* are similar in shape and size and their claws are blunt. The head of the *Prochrocephalus* is shorter. *Lepidophthirus* is a highly specialized taxon among the known echinophthirids, and differs from others in having a short abdomen with a dense cover of scales, a pseudopod that is disconnected at the apex, and claws of the middle and hind legs that are pointed. *Arctocephalus*, on the other hand, shares some morphological similarities to *Prochrocephalus* and somewhat to *Lepidophthirus*; it has an elongate abdomen which is, in contrast to *Prochrocephalus*, covered with scales and has different setae, the pseudo-pod 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, *Arctocephalus 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 *Prochrocephalus* 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. *Prochrocephalus* is definitely the most generalized taxon showing many primitive morphological traits, and may be considered to be closer to the ancestral echinophthirid, a condition quite comparable to that already indicated for their host, the fur seals. If the rate of evolution of *Prochrocephalus* has been comparable to that of *Arctocephalus*, the fact that two species have evolved, *P. flatus* 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 these basal clades.

It is presumed, but not yet confirmed, that other species of *Arctocephalus* harbor *Prochrocephalus*. Occasional contact is known among 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 seals bred there. *A. townsendi*, therefore, may well have a Callorhinus-like louse fauna rather than one typical of other species of the genus.

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

### Table 131. List of known species of Anoplura from Pinnipedia

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<thead>
<tr>
<th>Anoplura Species</th>
<th>Prochrocephalus Species</th>
<th>Echinophthirus Species</th>
<th>Lepidophthirus Species</th>
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<tr>
<td><em>A. callorhinii</em></td>
<td><em>P. flatus</em></td>
<td><em>E. microhiri</em></td>
<td><em>L. piniformis</em></td>
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<td><em>A. microhiri</em></td>
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<td><em>L. microhiri</em></td>
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<td><em>A. tridiscis</em></td>
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<td><em>A. squamosus</em></td>
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<td><em>A. ibadnati</em></td>
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<tr>
<td><em>A. masaricus</em></td>
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*Host (Order Pinnipedia)*

- Family Otariidae
- Subfamily Arctocephalinae
- Callorhinus ursinus
- Echinophthirus pusillus
- Subfamily Otariinae
- Eumetopias jubatus
- Phoca vitulina
- *Lepidophthirus*
- *Lepidophthirus* horridus
- Otaria flavescens
- Pagophilus grinnelii
- Phoca vitulina
- *Lepidophthirus californicus*
- *Echinophthirus* microhiri
- Neophoca cinerea
- *Lepidophthirus* horridus
- *Lepidophthirus* neumanni
- *Lepidophthirus* townsendi
- Family Otodontidae
- *Echinophthirus* townsendi
- *Lepidophthirus* horridus
- *Lepidophthirus* neglectus
- Pagophilus groenlandicus
- Phoca hispida
- *Lepidophthirus* piniformis
- *Echinophthirus* horridus
- Echinophthirus pusillus
- *Lepidophthirus* horridus
- *Lepidophthirus* neglectus
- *Echinophthirus* horridus
- *Lepidophthirus* neglectus
- Phoca hispida
- *Lepidophthirus* horridus
- *Lepidophthirus* neglectus
- *Echinophthirus* horridus
- *Lepidophthirus* neglectus
- Phoca hispida
- *Lepidophthirus* horridus
- *Lepidophthirus* neglectus
- *Echinophthirus* horridus
- *Lepidophthirus* neglectus
- Phoca hispida
- *Lepidophthirus* horridus
- *Lepidophthirus* neglectus
- *Echinophthirus* horridus
- *Lepidophthirus* neglectus
- Phoca hispida
Lepidophtherinus with the single exception of Arctocephalus pusillus. However, it is suspected that Antarcotelus will eventually be found on the southern fur seal (Table 131). Of six known species, A. callithrhini is the most generalized species of Antarcotelus. The lack of scales on the thoracic sternum in A. callithrhini 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 otaries were fur seal-like animals. This should be further substantiated by studying the loose fauna of Arctocephalus.

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

Most significantly, the presence of A. microchis as an inhabitant of both the northern and southern taxa of sea lions (Otarinae) suggests that a monospecific lineage of the suckling 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.

REFERENCES


