PREFACE

The first International Symposium on the Biology of the Seal was held at the University of Guelph, Ontario, Canada from 13 to 17 August 1972. The symposium developed from discussions originating in Dublin in 1969 at the meeting of the Marine Mammals Committee of the International Council for the Exploration of the Sea (ICES). The culmination of three years' organization resulted in the first international meeting, and this volume. The president of ICES Professor W. Cieglewicz, offered admirable support as well as honouring the participants by attending the symposium.

The programme committee was composed of experts representing the major international sponsors. W. N. Bonner, Head, Seals Research Division, Institute for Marine Environmental Research (IMER), represented ICES; A. W. Mansfield, Director, Arctic Biological Station, Fisheries Research Board of Canada (FRB) represented the International Commission for Northwest Atlantic Fisheries (ICNAF); and K. S. Norris, Director, Marine Mammal Council Executive Committee, represented the International Biological Program (IBP). The Food and Agriculture Organization of the United Nations (FAO) also offered its support to the programme and ICNAF has contributed to the financing of this volume.

Sponsors of national origin were the Fisheries Research Board of Canada (FRB), the National Research Council of Canada (NRCC), the Canadian National Sportsmen's Show (CNSS), the World Wildlife Fund (Canada) (WWF), and the University of Guelph.

In his preliminary remarks Professor Ronald introduced the representatives of these groups; namely J. R. Weir, Chairman, Fisheries Research Board of Canada; S. Bata, International Director and J. S. McCormack, Director, World Wildlife Fund (Canada); and R. T. D. Birchall, President, Canadian National Sportsmen's Show and a Director of WWF (Canada).

W. C. Winegard, President of the University of Guelph, welcomed participants to the symposium and commented particularly on how pleased he was to welcome representatives from so many countries. Later, at a banquet sponsored by the Department of the Environment, Canada, he offered an invitation to the group to return in 1975 for a Second International Seal Symposium.

Altogether 62 papers were presented. A further 14 papers were read by title and are included either in full or abstract form in this volume. The 139 participants represented 16 countries, permitting scientific interchange of a truly international nature.

In his opening address, V. B. Scheffer suggested that a dream was becoming a reality with a meeting of such a large group of pinniped biologists. This he felt was very relevant at a time when the relationship of marine mammals and man was being closely examined on biological, political and ethical grounds.

The scientific session commenced with a seven paper section on evolution chaired by E. D. Mitchell which showed the origins and subsequent development of this amphibious group of higher vertebrates. Many of the arguments for particular evolutionary trends are speculative in nature and different interpretations can be attached to the same fossil material. Readers of this volume should be aware of such differences when reading the papers in this section. The twelve papers of S. H. Ridgway's section on functional anatomy illustrated the fundamental structure of the seal, as well as its associated control mechanisms. R. J. Schusterman followed this theme by introducing ten papers on behaviour. He established a major focus on social organization and communication and their association with the functional anatomy of the pinnipeds. D. E. Sergeant chaired the population dynamics section of seven papers, covering the modelling of populations and method of analysis of seal populations around the world. In the fifth section, J. R. Geraci, by means of papers and a panel discussion dealt with the care and management of captive pinnipeds. W. N. Bonner coordinated a presentation in the broad area of ecology, and was able to bring together studies on environmental factors and their associated behavioural and genetic control systems. The physiology section was chaired by H. T. Andersen, his introductory remarks forming the initial paper of the section. The other six papers of his section emphasized the underwater responses of seals. The final and general section, chaired by J. E. King, offered a broad coverage of several of the more interesting areas in various disciplines.

A. W. Mansfield acted as rapporteur for the entire programme, and his report stressed the need for continued cooperation by all biologists so that they might understand seals and their importance to environmental studies.

This volume includes with one exception, those pa-
pers either presented, read by title, or abstracted, but
the continuing discussion on the biology of the seals
led to one further paper that is included here. Some
of the discussion was formal and, where recordable, is
included here, but by far the greater part of discussions
was informal and hence must remain as extremely
valuable, but merely mental recollections of the par-
ticipants in the symposium.

The symposium achieved its purpose of bringing
together scientists interested in the Pinnipedia and it
offered leads into the international examination of
marine mammals.

The editors with little apology recognized that they
have not reached a completely uniform format in this
volume since they have allowed use of both English
and metric systems of measurement and both English
and North American word usage for the sake of har-
mony. The main editorial structure has been the con-
sistency of usage throughout a particular paper.

Attempts have also been made to attain a fairly
uniform taxonomy for the species, but where there has
been any doubt caution has not overridden clarity. As
in other mammalian groups, the systematics of the
Pinnipedia are still open to much interpretation. The
references are cited according to an Annotated Biblio-
graphy on the Pinnipedia*. The ‘List of the marine
mammals of the world’ by D. W. Rice and V. B.
Scheffer (U.S. Fish and Wildlife Service, Washing-
ton, 1968) has been used as the standard reference on
nomenclature.

The work of the chairmen of each of the seven sec-
tions of this volume is especially recognized. As well,
the convenor wishes to thank the programme com-
mittee for their ability to support a somewhat unortho-
dox procedural system, and particularly the sponsors
ICES, ICNAF, IBP, CNSS, FRB, NRCC, WWF (Ca-
nada), FAO, and the University of Guelph for their
valuable financial assistance.

The convenor is most grateful to Mr. H. Tambs-
Lyche, General Secretary of ICES, for his advice and
encouragement from the embryonic stages of the sym-
posium to the publication of the proceedings; he also
recognizes the considerable amount of expert help pro-
vided by A. W. Mansfield in co-editing this volume.

Finally, the effort put into both the symposium and
this volume by Mrs. Ginny Bandesen has been beyond
measure, but I hope that she will accept the results of
the symposium recorded here as tangible proof of her
most valuable contribution. To the members of the
Dean of the College of Biological Science’s office, the
university support staff and our host Dr. W. C. Wine-
gard, I express on behalf of the participants and my-
self, our sincerest thanks.

K. Ronald,
Convenor

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PARALLELISM AND CONVERGENCE IN THE EVOLUTION OF OTARIIDAE AND PHOCIDAE

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INTRODUCTION

In marked contrast to the situation obtaining less than fifteen years ago, there is now a sufficient number of fossil pinnipeds known by formal descriptions or in museum collections and actively being worked on, to allow useful speculation on pinniped evolution. For example, at the time that Downs wrote on *Atopotarus* (1956), the study of fossil pinnipeds was truly at the descriptive level. However, a number of fossils, otariids and some phocids, have been described since then.

It is probably true that the fossil record of otariids is much the more complete at the moment. This is particularly so, not only because a greater number of fossil otariids, including complete skeletons have been collected but because there are more investigators searching in rocks that are likely to contain them. For these reasons, I have taken the approach in this paper of summarizing the evidence for a detailed phylogeny reflecting the evolution of Otariidae. Against this framework I speculate on adaptive trends seen in the evolutionary divergences of Otariidae, and compare them with the trends inferred in the evolution of Phocidae.

I will not pretend in this essay to put together an overview of phocid evolution since this has been done by McLaren in the present volume. However, it should be noted that McLaren’s views are based upon much evidence from living species in the absence of critical and detailed analyses of fossil phocids. A recent paper by Hendey and Repenning (1972) gives data and interpretations regarding one aspect of phocid evolution, but the fossil record of the diverse species presently living in the antarctic region is almost completely unknown.

I have taken the approach in this paper of working on the subfamily level, as I earlier defined these taxa for otariids (1968a) and as McLaren (this volume) discusses the presently recognized two subfamilies of Phocidae. Below I give a brief account of each subfamily covering salient points from recent literature. In the otariids, particularly, I discuss some details of my evaluation of fossil specimens newly described by others in order to make clear my interpretation of some evolutionary relationships. I will use this phylogeny of otariids as a basis for comments on the rather more fragmentary and poorly known phocid record.

I have purposely used technical terminology throughout, particularly at the level of subfamily, genus and species, in order to avoid confusion as to which fossils and taxa, and what interpretation, I am discussing.

OTARIIDAE

I have elsewhere presented evidence for my interpretation of otariid taxonomy and phylogeny (Mitchell 1968a). Much new work is being carried out by Barnes (1970, 1971, 1972, work in progress), Repenning (this volume, work in progress), Clayton Ray (work in progress), Shikama and Hasegawa (work in progress), Mitchell and Tedford (1973), and others. A summary of otariid phylogeny, and an indication of the subfamilies currently recognized (Mitchell 1968a) is presented in Figure 1.

DESMATOPHOCINAE

*Desmatophoca oregonensis* is the name applied to a species of sea lion from early or middle Miocene rocks on the coast of Oregon. It was first described by Condon (1906) and is under study by me (Mitchell 1966a, and in progress). The skull of the holotype specimen has been prepared and an illustration is presented here preliminary to the redescription of the specimen (Fig. 2). The species represents in many ways a generalized otariid pinniped that has retained many features of even more primitive ancestry. For example, the paroccipital and mastoid processes are separate entities, unlike the condition in a contemporary species (Mitchell and Tedford 1973) which represents a new subfamily more closely allied with the
Figure 1. Phylogeny of Otariidae. Interpretation of the interrelationships of species and unnamed taxa based upon evidence cited by Mitchell (1968a) and including a re-evaluation of new fossils described and interpreted by Barnes (1970, 1972) and Mitchell and Tedford (1973).

living sea lions (Otariinae). Thus *D. oregonensis* should be regarded not as the earliest of the ancestral otariids, but rather as a representative of one of at least two separate lines of evolution in the early to middle Miocene.

It would appear that *D. oregonensis* is related to *Allodesmus kernensis* (Kellogg 1922, 1931; Mitchell 1966a; Barnes 1972) with a common ancestor most probably in the late Oligocene or earliest Miocene. It is most probably a relict form, surviving as a primitive and somewhat generalized species.

As I recognize the subfamily Desmatophocinae, it contains only this one genus at the present time, a view that is not accepted by Repenning (this volume). Barnes (1972) and Repenning have interpreted the subfamily Desmatophocinae rather more broadly; Repenning would elevate it to family rank, while Barnes has included within it my (1968a) Alloidesminae and also referred other specimens to it, some of which I would refer to other subfamilies.

The relationships of the Desmatophocinae, as I have defined it (Mitchell 1968a), are relatively clear: on the one hand, there is a close relationship, probably in the nature of direct descent, between Desmatophocinae and Alloidesminae; on the other hand, the true living walruses (Odobeninae) have probably evolved from within, or in parallel with, the Desmatophocinae lineage.

The relationship of Desmatophocinae to Dusignathinae is less straightforward, but Dusignathinae, Alloidesminae and Desmatophocinae are all generally interrelated. Dusignathinae represents a late surviving specialization of the Desmatophocinae. The Desmatophocinae group, then, is related to Odobeninae, Dusi-
Figure 2. Ventral view of holotype of *Desmatophoca oregonensis* (Condon 1906); subfamily Desmatophocinae. Line drawing by Mrs. Betty Osborne, scale is 10 cm in length.

gnathinae, and Allodesminae. The more advanced sea lions (the Imagotarinae and Otariinae) are much more distantly related.

**ALLODESMINAE**

*Allodesmus kernensis* (Kellogg 1922) is a large otariid known by many hundreds of bones, including a complete skeleton from middle Miocene rocks in south central California and elsewhere (Fig. 3). Mitchell (1966a) described a new species, *A. kelloggi*, based on a complete skeleton from the Sharktooth Hill bone bed in the Round Mountain silt, south central California (Figs 3–6). The characters used to separate this species from *A. kernensis* (Kellogg 1922, 1931), were based mainly on spacing of dental alveoli and proportions of the lower jaw. Barnes (1970, 1972) has re-evaluated the status of this species on the basis of much additional material, and has demonstrated that the specimen on which *A. kelloggi* is based is an extreme individual in the morphological spectrum of the species while the holotype of *A. kernensis* represents the other extreme. Specimens which Barnes documented from the same set of rocks show that the diastema between postcanine four and five, characteristic of *A. kelloggi* may instead occur between other cheek teeth, that the cheek teeth can be variably spaced and more than one diastema can be found on a side, that the number of teeth in the lower jaw is also variable and may range from six postcanine teeth to four postcanine teeth in specimens broadly referable to *A. kernensis*, and that there is likewise extreme variation in the placement of the two incisors of the lower jaw.

It is apparent that other features of the *A. kelloggi* holotype are a reflection of age and sex differences; for example, the relative deepness of the jaw and the sloping nature of the symphysis as well as the angle that the canine makes with the horizontal ramus are likely all related to the age changes within one sex and possibly to sex differences within the species (Barnes, 1972). A collection of the remains of approximately 25 dentary bones showing a wide range of variation are now available from this one deposit and will allow a complete re-evaluation of all these taxonomic characters.

The new specimen that Barnes (1972) referred to *A. kernensis*, appears to be a larger individual than the holotype of *A. kelloggi*, but it also appears to be a relatively younger individual in terms of absolute chronological age. The skull is much longer (as Barnes reconstructed it in the snout region), and there are other differences: for example, in the angle the glenoid process makes with the axis of the skull, and in the relative width across the mastoid processes. The two individuals are decidedly different osteologically, but can be referred to the same species.

*Allodesmus kernensis* probably represents a highly specialized species that was undergoing rapid change or unusual variability at the time of deposition of the Sharktooth Hill bone bed. It can be considered very advanced on the basis of its elongated and highly arched palate, its relatively large cheek teeth spread out over a very long cheektooth row, the beginnings of loss of the fifth and sixth postcanine teeth, and the
enlarged upper and lower canines. For example, features in the orbital region such as the patent interorbital foramen or optic foramen are found only in modern Otariinae and in *Allodesmus kernensis* (specimen UCMP 81708, Barnes 1972). On the other hand, *A. kernensis* shows a number of generalized or primitive features, particularly in the basicranium, that are characteristic of the Desmatophocinae at the time it gave rise to Alldesminae. Such characters as the distinct mastoid process remaining separate from the paroccipital process, the flattened and relatively uninflated auditory bullae (Fig. 6), the long interorbital region with a nearly complete lack of supraorbital processes, and features of the middle ear (especially the shape of the promontorium) are all indicative of the desmatophocine ancestry of the species.

*Allodesmus kernensis* shows a number of specializations that may be related to its feeding habits. For example, a deepened, mortised junction of the zygomatic process of the squamosal with the bifurcate posterior end of the jugal bone (Figs 4 and 5) is probably related to some changes in masseter and other muscle arrangements. The lengthy jaw, the straight tooth row, the enlarged rostral platform, the highly arched palate, and the cheek teeth of large diameter, all indicate a feeding mechanism quite different from that presumably found in the ancestors of the lineage, the Desmatophocinae.

Barnes (1972) has described another species of otariid from these same rocks, which he terms "Desmatophocine species C." This is a portion of a mandible, mainly the symphyseal region and anterior half of the horizontal ramus with teeth broken out, from the Sharktooth Hill bone bed, specimen UCMP 86136. Barnes refers this mandible to a species different from *Allodesmus* or "Desmatophocinae" (in his 1972 terminology) near *Alldesmus packardi* (Barnes 1972). This seems reasonable in view of characters such as the increased or enhanced curvature of the horizontal ramus, relative to the plane of the surfaces posterolaterally. The canine tooth, at the level of the bottom of the incisor alveolus, is nearly solid, but shows a small hole which would open out into the expanded funnel-shaped pulp cavity below. The canine tooth is, at that level, bilobed or dumbbell shaped, a character slightly different from most specimens of *A. kernensis* in collections that I have examined.

Barnes (1972) has described yet another mandible from these collections, indicating that other species may be represented in the Sharktooth Hill bone bed fauna. This mandible he terms "Desmatophocine species B", a specimen in the Department of Geology of Bakersfield College, No. F-1310. Barnes states that the fossil is presumably from the Round Mountain silt, and characterizes this mandible as being different from that of *A. kernensis* in having only five postcanine teeth (not six as commonly found in *Allodesmus kernensis*), a relatively massive horizontal ramus particularly at the anterior end, and, most importantly, an extremely rugose symphyseal region and a dorsoanteriortly blunt chin region. The incisor count and the size and shape of the canine is otherwise similar to that of *A. kernensis*.

Barnes compares this specimen with *Prorosmarus alleni* (Berry and Gregory 1906) and *A. kernensis* and concludes that it is intermediate between these
two species. It is difficult to reconcile this view, since the \textit{P. alleni} jaw is much more massive with a horizontal mandibular ramus that is curved transversely, and has round rather than ovate cheekteeth that are not as deeply rooted as the cheekteeth in the "species B" jaw. \textit{Prorosmarus alleni} also has a vertical canine positioned far out anteriorly on the symphysis, unlike "species B", which has a deeply rooted, large canine, running down in the mandible within the symphyseal region. In "species B" there are many foramina in the jaw associated with the mental foramen, unlike the single large and few very minor foramina in the \textit{P. alleni} jaw. The main similarity between \textit{P. alleni} and "species B" is in the symphysis which is extremely rugose, presumably for more rigid attachment of the two dentary bones. This feature may be related to the relatively large size of the teeth in both species, indicating a functional similarity not necessarily of phyletic importance.

The "Desmatophocinae species B" jaw affords bet-
ter comparison with *Dusignathus santacruzensis*. In this species the mandible is very deep and laterally thin, and the postcanine teeth are extremely large in diameter. Significantly, they are ovate and deeply rooted as in "species B". The symphysis is long and sloping as in the Allodesminae, but it is relatively rugose as far as preserved. The postcanines are reduced to five in number as in *D. santacruzensis*. "Species B" resembles *A. kernensis* in the diastema between postcanines four and five, a feature commonly found in many of the *Allodesmus* jaws from the Sharktooth Hill bone bed.

The above comparisons suggest that "Desmatophocinae Species B" has converged upon or evolved in parallel with *D. santacruzensis* from as yet undetermined Allodesminae or possibly Desmatophocinae stock.

Barnes (1972) has nicely compared the mandible of "Desmatophocinae species B" with the morphological sequence proposed between *Allodesmus* and *Dusignathus* (Mitchell 1966a). He appears to agree that the comparisons are interesting but not especially significant in terms of actual phylogeny. His discussion emphasizes the fact that there has apparently been a series of adaptive radiations at different organizational grades and at different times in the evolution of the Otariidae, and that within the Desmatophocinae and the Allodesminae there have been successive bursts of adaptive radiation which are as yet very poorly known.

The Allodesminae species group, comprised of *Allodesmus packardi* Barnes (1972), *A. kernensis* (= *A. kelloggi*), *A. (Atopotarus) courseni*, and "Desmatophocinae species B" Barnes (1972) represents an adaptive radiation in the early and middle Miocene which evidently persisted late into the Miocene. Although the group itself appears to be cohesive the relationship of the Allodesminae to *Desmatophoca oregonensis*, and the recognition of the separate subfamilies (Allodesminae and Desmatophocinae) are subject to further discussion and possibly revision. Mitchell (1968a) recognized the
two subfamilies and pointed out that the Allodesminae species group probably represented a specialization of the generalized situation in *D. oregonensis*.

**DUSIGNATHINAE**

*Dusignathus santacruzensis* was first called a sea lion by Kellogg, the original describer (1927). The only known specimen is the holotype, and I would now refer to this species the bones previously referred to by Mitchell (1962) as “Odobenid, new genus and species” (Mitchell, manuscript in preparation). My interpretation of the holotype, in which I have prepared the middle ear region (Fig. 7), is that it represents either a lineage descended from the desmatophocines in parallel with the Odobeninae, or a very early offshoot from the common Odobeninae stock which then paralleled them. It may be regarded as walrus-like, but adapted to a different mode of feeding. The emphasis was on large cheekteeth, suited not for crushing but for grasping, which were arranged in line in a deep-bodied jaw with a very large lower canine. Both the upper and lower canines were large and caniniform. This is in marked contrast to the true walruses (Odobeninae), in which the upper canine becomes greatly enlarged into a tusk, while the lower canine becomes peg-like and is functionally incorporated into a row of crushing teeth. Thus the differences are related to particular modes of feeding.

One indication of the affinities of this species depends on the interpretation of Barnes’ (1972) “Desmatophocinae species B” within the *Allodesmus* species group. In that specimen there is a parallel in the development of the large postcanine teeth, splayed out from the center of the ramus both anteriorly and posteriorly, and a long sloping symphysis with a deep, thin horizontal ramus and anteriorly directed canine. It is possible that “Desmatophocinae species B” is a species representing an adaptive trend parallel to *D. santacruzensis* on the subfamily level, or the similarities may imply a closer genetic relationship. The chronology of occurrence is right for an ancestor-descendent relationship since “Desmatophocinae species B” is middle Miocene in age (presumably from the Sharktooth Hill bone bed, although this assumption is not proven by Barnes 1972), and *D. santacruzensis* is from late Miocene or early Pliocene rocks in the west central part of California. However, morphological features preclude this relationship. The “Desmatophocinae species B” specimen (Barnes 1972, UCMP 93049) probably represents parallelism or convergence with the morphological situation in the lower jaw of *D. santacruzensis*, in which large cheekteeth have been evolved and closely appressed in the tooth row of the horizontal ramus. It cannot be considered to be directly ancestral to *D. santacruzensis* because of the completely different shape of the mandibular symphysis, which in *Dusignathus* is subquadrate with the widest area ventral-most (near genial tuberosity) and which in “species B” is just the opposite, subquadrate with the widest area dorsanteriorly in the jaw. In this feature it is reminiscent of more advanced species in the Imagotariinae and Otariinae.

Thus otariids with large, non-crushing cheekteeth evolved many times in the Miocene. *Dusignathus santacruzensis* represents one such lineage, the exact relationships of which remain unknown.

Figure 8 represents a reconstruction of the skull of *D. santacruzensis*, made by placing plaster casts of the various skull fragments described by Kellogg (1927) within a clay model and drawing the entire outline by means of an optical pantograph. The drawing shows what I think an intact skull would look like viewed orthographically; hence the jaw outline does not accord exactly with the view given by Kellogg. Most pieces were interrelated by articulations except for the fragment of the lambdoid crest, the critical placement of which is open to conjecture.

Considering the overall skull morphology, an alternative interpretation of the habitus of *D. santacruzensis* is that, instead of being a close analogue of the walrus, it was a “killer sea lion” that may have preyed upon other pinnipeds. This speculation is based upon the fact that it has a very strong set of jaws with deep

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**Figure 7. Ventral view of the squamosal bone and ear region of *Dusignathus santacruzensis*, a Pliocene otariid from the vicinity of Santa Cruz, west central California. Line drawing by Mrs. Betty Osborne, scale is 1 cm in length.**
rami, large upper and lower canines and deep-rooted cheekteeth that are round in cross-section; both upper and lower cheekteeth have long or high crowns, though it is not known whether accessory cusps were present or not. The dentition appears to be adapted for grasping and tearing, suggesting the possibility that the species performed a role in the adaptive spectrum of pinnipeds analogous to the killer whale within the Delphinidae.

ODOBENINAE

The living walrus *Odobenus rosmarus* represents a phyletic lineage of walruses in which there has been an emphasis on development of the upper tusks and reduction in size of the lower canines. The north Atlantic genera of walruses, *Alachtherium* and *Trichecodon*, are closely related to the living walrus and without doubt represent the same phyletic lineage. This is only one part of odobenid diversity, however. Another lineage was termed a separate subfamily, the Dusignathinae (Mitchell 1968a). Aberrant walruses are also known (Mitchell 1961, and in preparation) but their cranial structure and exact affinities are unknown (cf. Fig. 1, *Valenictus imperialensis*).

*Prorosmarus alleni* (Berry and Gregory 1906) appears to fall naturally within Odobeninae representing a good morphological stage and probably a phyletic stage in the evolution of this group from somewhere within the Desmatophocinae or Allodesminae. Mitchell (1966a) studied the jaw of *Prorosmarus alleni* and stressed its similarities to the jaws of both *D. santacruzensis* and *A. kernensis (= A. kelloggi)*. Earlier, Mitchell (1962) described some walrus bones termed “Odobenid, new genus and species” from Pliocene rocks in the vicinity of Santa Cruz, California. In view of the diversity of generalized otariid pinnipeds recognized and newly reinterpreted since the time of that writing, these bones are now attributed to the subfamily Dusignathinae, possibly representing *D. santacruzensis* known from the same rock unit (Mitchell, in preparation).

The relationship of Odobeninae to Dusignathinae is close, but the two taxa were considered as separate (Mitchell 1968a) in order to emphasize the parallelism in their evolution, especially the enhancement or suppression of the lower canines. Both taxa are related broadly to the Desmatophocinae and the Imagotariinae.

ENALIARCTINAE

At present, the new subfamily Enaliarctinae (Mitchell and Tedford 1973) is based on only one species, an otter-like sea bear which was restored by Mitchell (1966b). New material, currently being prepared by C. Ray and L. Barnes will probably help to confirm that this new subfamily is a cohesive and tightly interrelated group.

Mitchell and Tedford compared the new taxon especially with the Arctocephalini, emphasizing the many similarities to such fur seals as *Arctocephalus* sp. and *Callorhinus ursinus*. They also suggested that
Figure 9. Basicranium of holotype of *Pontolis magnus* True. Line drawing by Mrs. Betty Osborne, scale is 10 cm in length.

*Neotherium mirum* might be related more to the new subfamily than to the Otariini.

*Neotherium mirum* has remained a problematical species since Kellogg first described it in 1931. Downs (1956) even doubted that it was a valid genus, but Mitchell (1961) illustrated a humerus possibly referable to this species.

A tooth illustrated by Kellogg (1922) and referred to *Alodesmus kernensis* presumably as part of the hypodigm, is more probably referable to the species *Neotherium mirum* or some related species (Mitchell 1966a).

It appears that a number of possibilities are open at the present time regarding the structure and relationships of *Neotherium mirum*. The species may be related to the terminal adaptive radiation of a lineage represented by Enaliarctinae. It may be related to the origin and early diversification of the Otariinae, and specifically to the origin of the Otariini. It may in fact be related to both of these lineages and possibly could form the intermediate or connecting taxon through which the new subfamily can be linked with the origin of the Otariini.

Thus the relationships of the Enaliarctinae lie on the one hand with the Otariinae, the lineage leading to living fur seals and sea lions and on the other hand with the bear-dogs, specifically *Cephalogale*. There appears to be little room in this lineage, from fissiped to otariid pinniped, for the origin of Phocidae; hence it comprises indirect evidence for the polyphyletic origin of pinnipeds.

It is not certain whether *Neotherium mirum* should be intercalated somewhere in this lineage or whether it is representative of a split from the Enaliarctinae on the lineage that evolved into Imagotariinae, as recognized by Mitchell (1968a). More fossils, particularly bones referable to the skull of *Neotherium mirum*, are needed before any judgment can be made.

**IMAGOTARIINAE**

The Imagotariinae is a subfamily probably derived from ancestry in the Desmatophocinae. They were
large animals which converged to a high degree upon the living sea lions (subfamily Otariinae). Mitchell (1968a) restricted the use of this subfamily to the holotype species Imagotaria downsi and speculated that Pontolis magnus (True 1909) might prove, on preparation and restudy, to be allied with Imagotaria downsi.

Pontolis magnus is a large sea lion, described first by True as an early otariine. Further study of this specimen, following preparation of the basicranium (Fig. 9) confirms the general relationship of P. magnus to I. downsi and the Imagotariinae (Mitchell, in preparation). The species most likely represents continuation or slight divergence in the adaptive trend found in the Imagotariinae, which leads through Imagotaria downsi to large pinnipeds paralleling Otariini and evolving many cingular and accessory cusps in front of and behind the main tooth cusp (Mitchell 1968a, and see Barnes 1971).

Barnes (1972) has described the anterior portion of the dentary bone of a taxon he terms “Desmatophocinae species A” (1972, specimen UCMP 85197). This jaw has a flange on the anterointernal edge of the symphysis, and a canine with a carina on the posterior edge of the crown and an external, lateral sulcus along the canine root. The postcanine teeth were partially or completely double-rooted. The specimen is from the Santa Margarita Formation.

Barnes considers that it represents a species evolved from Desmatophocinae related more to D. oregonensis than to A. kernensis. This interpretation is based on the long, sloping and narrow symphysis, and the relatively thin and deep-bodied horizontal ramus. These features may be highly adaptive, and therefore related to type of teeth and general feeding mechanisms.

My own interpretation of “Desmatophocinae species A” is that it may be less closely related to Allodesminae (in my terminology), and is more likely a derivative of Desmatophocinae very close to, or possibly included within, the Imagotariinae.

The Imagotariinae are allied with the Desmatophocinae, Allodesminae and Dusignathinae, and most closely to the Odobeninae. On the other hand they resemble the Otariinae in many more ways than can be explained by simple convergence. Their ancestry within the Enaliarctinae (Mitchell and Tedford 1973) is probably the best interpretation, with their resemblances to Desmatophocinae and the other subfamilies resulting from heritage features in common between the Enaliarctinae and the Desmatophocinae.

Relationships of the Imagotariinae lie on the one hand with the Desmatophocinae, probably their ancestral group, and on the other hand as a parallel offshoot of the Desmatophocinae, with the living walruses and extinct “pseudo-walruses”, Odobeninae and Dusignathinae. The Imagotariinae are convergent upon the living Otariinae.

OTARIINAE

This subfamily includes living sea lions (Otariini) and living fur seals (Arctocephalini), and is equivalent to Repenning’s Otariidae (this volume). There are few Tertiary fossils relevant to a discussion of the origin and evolution of the subfamily. Japanese finds were reviewed by Mitchell (1968a).

The Otariini are represented by a diversity of living species, the interrelationships of which have only recently been re-examined in some detail (Mitchell 1968a, Morejohn, this volume). There are few described fossils from the North Pacific basin that bear on the Pleistocene or late Pliocene history of this group. This paucity of described fossils is more a reflection of
lack of interest and effort on the part of investigators than on the scarcity of fossils in the geological column. The relationships between Arctocephalini and Otariini, the time of their divergence, the general evolutionary trends within each lineage and their direct ancestry are all points that can be resolved only after many additional fossils have been described and interpreted.

In a study of a new subfamily, the Enaliarctinae (Mitchell and Tedford 1973) much emphasis was placed on comparisons of the type species with the Arctocephalini. The new subfamily can be taken as broadly ancestral to the Otariinae. In the absence of other evidence, it is reasonable to assume that the fur seal lineage (Arctocephalini) is directly descended from the type species of the Enaliarctinae.

A major portion of the record of the Otariinae is in the Pleistocene, and in the recent flowering of living species. One significant fossil that bears upon phyletic trends within the group is the holotype and hypodigm of Pitbantarary starr, described by Kellogg (1925; and see Fig. 10). Kellogg correctly emphasized the relationships of this species to the Arctocephalini by comparing it with a young fur seal skeleton. The fossils are from late Miocene or early Pliocene rocks in the region of Santa Barbara, California, from the same deposits that yielded the holotype of Imagonia downsii. The skull of Pitbantarary resembles that of living fur seals. Thus in the late Miocene or early Pliocene there was a species evolved that may not have been directly ancestral to living species, but which was certainly on the mainline of Arctocephalini evolution. This would imply that a mix of species were evolved at this time, broadly ancestral to Arctocephalini. By implication, the Otariini may have become differentiated by this time also.

Repenning (this volume) has pointed out that the Otariini may have evolved very much more recently from the grade of organization now recognized as Arctocephalini. He places this divergence of Otariini and Arctocephalini in the Plio-Pleistocene, and states that it involves little more than the loss of double roots in some or all postcanine teeth, particularly, in PC2-PC4. This hypothesis would help explain the apparent lack of fossils referable to Otariini (sensu stricto, Mitchell 1968a) in the late Miocene and Pliocene of the northeastern North Pacific.

An alternative hypothesis is that the Otariini evolved in an area other than the northeastern north Pacific and used the eastern Pacific corridor to invade the North Pacific in the Plio-Pleistocene. This hypothesis is confirmed in part by findings (Mitchell 1968a) that some of the sea lions in the southern hemisphere particularly Phocarctos, are more generalized, and possibly represent a group nearer the original stock of Otariini. The present lack of fossils indicates that caution should be used in interpreting the history of the Otariinae. Present morphological diversity of the Otariini indicates a longer evolutionary history than the early Pleistocene. Dependence on single characters related to feeding mechanisms, such as development of single roots in cheekteeth, is not reliable considering the trend from double to single roots in Desmatophocinae to Alloodesminae, Odobeninae and Dysgnathinae, and within the Imagotarianinae and its ancestry. Otariini may have had a long and diverse history, dating from within the Pliocene or earlier.

**PHOCIDAE**

Little can be said of the evolution of the Phocidae until there has been a critical re-evaluation of the fossil species of seals from late Tertiary rocks in Belgium (Van Beneden 1877). Clayton Ray has undertaken this study and, pending publication of his results, detailed discussion of the relatively incomplete phocid fossil record would be inconclusive.

As Hendey and Repenning (1972) point out, there are few fossil phocids for which the skulls are even partially known. These include Pliophoca etrusca Taverni (1942; skull), Phoca pontica Eichwald (1853, cranium), Phoca pontica Alekseev (1924; rostrum), and Prionodelphis capensis Hendey and Repenning (1972).

The earliest phocids recorded are known from the region of the northern Atlantic Ocean. This is in keeping with theories calling for their origin and early deployment in the Atlantic and Tethyan region (McLaren 1960a). There are many such fossils from late Miocene and early Pliocene rocks in this region (reviewed by McLaren 1960b). The earliest recorded phocid may be Leptophoca lenis from Miocene rocks of the eastern United States (True 1906), the holotype of which is a humerus. The specimen appears to represent a fully adapted marine phocid, indicating that an important middle or early Miocene flowering of Phocidae remains to be elucidated in this region.

All previous records of fossils from California attributed to Phocidae are incorrectly identified, and the only late Cenozoic species of Phocinae from the northeastern Pacific region, represented by a number of fossils, is Phoca vitulina (Barnes and Mitchell, this volume).

King (1966) exhaustively examined osteological similarities and differences between the representatives of the putative subfamily Cystophorinae, and concluded that Cystophora cristata and the two living species of Mirounga were unrelated. Most workers have followed King in abandoning the phocid subfamily Cystophorinae, and regarding Cystophora as a phocine and Mirounga as a monachine.
In the absence of a good fossil record, much of the discussion relating to phocid evolution is based on neontological characters. An overview of some of this evidence is given by McLaren (this volume).

MONACHINAE

Hendey and Repenning (1972) state that "recognition of any tribal subdivision of the Monachinae now seems pointless." They recognize a subfamily Monachinae as was used by King (1966). A comprehensive review of extinct and living Monachinae is badly needed.

Species of the phocid Prionodelphis are known from Pliocene rocks in South America (Frenquelli 1922, 1926) and in South Africa (Hendey and Repenning 1972). The latter authors have compared a new species of this genus with most living species of phocids, and conclude that it is a monachine showing many phocine characters. The age of this find is late Pliocene, perhaps four to five million years old. Prionodelphis rovereti is known from Pliocene rocks in Argentina by only a small number of specimens (Frenquelli 1922, 1926).

In describing their new species, Hendey and Repenning (1972) compared monachine and phocine seals, and concluded that the "ancestral protophocid" from which these two surviving subfamilies evolved, displayed the following diagnostic characters: "dentition with primary cusp flanked by one accessory cusp anteriorly and one posteriorly, much the same as seen in Praepusa pannonica Kretzoi (1941: Fig. 1), ear region much as in living Monachus, and postcranial skeleton unspecialized as in 'Phoca' vindobonensis Toula (1897)." Hendey and Repenning (1972) regard the humerus of Leptophoca lenis and 'Phoca' vindobonensis as representing a primitive pattern from which both monachine and phocine humeri can be derived. Monachine osteological structure, particularly details of the ilium, and the skull, are regarded as more primitive than in the phocines.

The ancestry of the Monachinae is unknown. Hendey and Repenning state that the new species they describe is not clearly ancestral to any of theantarctic monachines. They point out that the great reduction in the last upper postcanine tooth of the new species precludes it from being ancestral to Hydrurga leptonyx or Lobodon carcinophagus. Also the great simplification in the teeth of Leptonychotes weddelli and Ommatophoca rossi "leave(s) little basis for interpretation." This does not necessarily mean that some aspects of the tooth structure of these species might not represent their generalized nature. Hendey and Repenning's statement perhaps assumes too much regarding trends in dentinal evolution. Nevertheless, they conclude that some or all of the antarctic species probably evolved from a related but unknown form.

Hendey (1972) has been more specific, and would derive Lobodon and Hydrurga from the monachine stock before the grade of evolution represented by Prionodelphis was attained. Then Ommatophoca and Leptonychotes were evolved from the monachine stock at a later and more advanced organizational grade.

McLaren (this volume) has given a short summary of the adaptive radiation of the Monachinae, quoting these recent papers by Hendey (1972) and Hendey and Repenning (1972). Hendey's zoogeographic scheme calls for a Mediterranean origin and late Miocene spread of the Monachinae across the south Atlantic from West Africa to South America and through the Central American seaway. A southward spread of monachine stock gave rise to the Antarctic monachines. McLaren concludes that Hendey's arguments are simplistic, and do not take into account the possibility of multiple invasions of the southern hemisphere from a broader Tertiary monachine radiation in the north Atlantic.

A reinterpretation of existing fossils, and discovery and description of new fossils, are needed before significant progress can be made in interpreting the evolution of the Monachinae.

PHOCINAE

The Phocinae have been discussed in great detail most recently by McLaren (this volume). McLaren has summarized the interrelationships of taxa in the tribe Phocini and believes that this is a good natural unit, typified by the occurrence of 32 chromosomes (Arnason 1972) and the presence of a woolly white lanugo. Burns and Fay (1970) have revised the Phocinae, recognizing three tribes: Erignathiini, Cystophorini, and Phocini. As with the Monachinae, however, there is still continuing discussion regarding subfamilial classification of some living species. King (1966) has pointed out that Erignathus barbatus is more similar to Monachus than previously thought and Burns and Fay (1970) have found similarities in some details of the skull.

McLaren points out that E. barbatus has 34 chromosomes (Fay et al. 1967) and, had it been found in temperate waters, would have been classed as Monachinae with some phocine traits. He considers the primitive complement of 34 chromosomes in Cystophora (Arnason 1972) an important point in relation to the possession of the white lanugo by this species. He concludes that no existing genus will suffice as a good morphotype for the derivation of the Phocini, and suggests that Cystophora is a relict of a much older northern seal stock.
McLaren has argued that the origin of the tribe Phocini might be close to the modern *Pusa* (McLaren 1960b, 1966) and that, in spite of contrary evidence from cranial morphology (Burns and Fay 1970), *Pusa* can still be regarded as a good possible ancestor of the grey seal *Halichoerus grypus*.

The occurrence of *Phoca pontica* (Chapskii 1955; McLaren, this volume) has been taken as evidence that seals related to *Pusa hispida* were evolved by the late Miocene, and played a part in the pre-Pleistocene origin of the Caspian seal and the ringed seal. Burns and Fay (1970) have placed *Pagophilus* in a generally central and possibly ancestral position among the smaller Phocini, although McLaren (this volume) takes issue with their interpretation by arguing that conservative basicranial skull features and a banded pelage indicate a closer relationship of *Pagophilus* with *Histriophoca* than with the small Phocini.

As with Monachinae, there is need to carry out a concentrated search for remains of Phocinae. Only with a morphologically-graded series of fossils, from known sequences of rocks in the various amphitheaters of seal origin and diversification, will there be evidence to conclusively argue phocine intrarelationships.

**CONVERGENT AND PARALLEL EVOLUTION**

It should be emphasized that in discussing pinniped phylogeny and the interpretation of primitive or generalized characters, it is important to remember that there are grades of organization in the basicranial and postcrania area of the skeleton. One such grade, which did not change rapidly after it was first evolved and stabilized and which persisted until perhaps the early Pliocene is shown in the “archaic group” of sea lions represented by the Desmatophocinae and the Allo­desminae. Elsewhere it has been suggested (Mitchell 1968b, 1966b) that the Allo­desminae and other archaic sea lions actually migrated equatorwards at the time of their disappearance from rocks in California, but actual times of their biological extinction have yet to be determined.

The Imagotariinae (Mitchell 1968a), represent an advanced grade of anatomical structure or adaptation which has paralleled trends in the living Otariinae. If Imagotariinae evolved from Desmatophocinae *sensu stricto* (Mitchell 1968a), the similarities could be due to convergence.

The Enaliarctinae (Mitchell and Tedford 1973) represent an apparent discontinuity since their grade of organization includes the presence of species in early Miocene rocks with a mastoid-paroccipital process that is continuous or even fused and directed ventrolaterally from the skull. These animals are found in the same rocks as the Desmatophocinae and Allo­desminae which have separate paroccipital and mastoid processes, connected by a thin or weak ridge but not fused, and directed externally, laterally and perhaps slightly posteriorly from the skull.

These features are very useful in assessing the relationships of the species and indicating their grade of organization. The fusion of the paroccipital-mastoid process and its downward deflection has progressed in the lineage leading on to the Odobeninae, the Otariini, and the Arctocephalini, as well as the Imagotariinae and the Dusignathinae. It is possible that either this grade of organization of the mastoid-paroccipital area was attained independently by all these lineages after the Desmatophocinae and Allo­desminae were evolved, or that the Allo­desminae and Desmatophocinae evolved separately from the other otariid subfamilies.

If the latter occurred then the Enaliarctinae forms a useful ancestral group for the evolution of the Ota­rini, the Imagotariinae and the Odobeninae, whereas the Desmatophocinae forms a useful grade of organization or a phyletic group adequate for the ancestry of Allo­desminae and Dusignathinae. The apparent dichotomy in the evolution of these two putative groups of otariids breaks down when the Dusignathinae are compared with the Odobeninae and Imagotariinae, or when the Desmatophocinae are compared with the Odobeninae and the Enaliarctinae. The simplest conclusion at this time appears to be, that various characters such as crushing teeth and tusks, the shape and confluence of the mastoid and paroccipital processes and the form of structures in the middle ear have all evolved independently of various phyletic lines, and that resemblances are an expression of parallel evolution and perhaps ultimately even convergence.

*Allo­desmus packardi* (Barnes 1972) is also similar in skull morphology to some of the antarctic monachines. The skull grossly resembles *Phoca* and *Monachus* in having a short, wide palate, a short rostrum, a broad cranial area and a similar jugal-squamosal relationship, among many other similar features. The best comparison of *A. packardi* is with *Leptonychotes weddellii* and *Monachus* spp. At first glance the skull is so similar to these modern phocids that it is surprising to realize that it is an otariid. Such adaptive convergence is shown in the great similarity between *A. kermensis* and *Hydrurga leptonyx* but the basicranial features of both species of *Allo­desmus* clearly show that they are otariids.

Burns and Fay (1970) have recognized the new tribe Cystophorini within the Phocinae to receive the hooded seal which was demonstrated by King (1966) to have belonged to an untenable subfamily, the Cysto­phorinae. Resemblances between *Cystophora cristata*
and *M. leonina* and *M. angustirostris*, interpreted now to be Monachinae, can be ascribed to convergent evolution. The shortening of the skull and development of a proboscis are features that have resulted from feeding specializations and sexual selection (McLaren this volume).

The otariid *Allodesmus* also shows convergence on this pattern as a result of feeding specializations and sexual selection (Mitchell 1966a).

*Allodesmus kernensis* (including *A. kelloggi*) evolved a rostral platform which presumably had upon it a proboscis (Mitchell 1966a). In addition, this species exhibits a long, low narrow skull with rather widely splayed zygomatic arches and a peculiar mortised joint between the squamosal and jugal bones. This joint was interpreted by Downs (1956) as a possible abnormality in *Allodesmus* (*Atopotarus* *courseni*). However, Mitchell (1966a) has indicated that the rather deep jugal process of the squamosal is similar to that in *Mirounga* and other monachines. These similarities probably related to a peculiar or at least a specialized feeding mechanism. The comparison between the skull of *A. kernensis* and that of *H. leptonyx* is the closest in this regard, and a detailed study of the functional similarities in this convergent situation is in progress (Mitchell, in preparation).

It is clear that *A. kernensis* and the phocid *Hydrurga leptonyx* are closely convergent. This leads to the interesting speculation that one species might have replaced the other in competition, but this is not borne out by present knowledge of their geographical and chronological distribution.

CONCLUSION

Otariid diversification resulted in a flowering of taxa in the Miocene. The Allodesminae and the Desmatophocinae are closely related, with early Desmatophocinae giving rise to Allodesminae. Similarities can be partly ascribed to parallel evolution. The Otariinae and the Imagotariinae also display either parallel or convergent evolution. The Odobeninae and the Dusignathinae represent parallelism, having had a common ancestry in the Miocene. The adaptive flowering of Allodesminae in the early and middle Miocene resulted in species convergent on monachines such as *Hydrurga*, *Leptonychotes*, and *Mirounga*. By implication, this flowering resulted from niche diversification in waters of great productivity as in the living Monachines. However, times of flowering may have been different, since the evolutionary history of Antarctic Monachines is unknown. Species of Monachines, Phocinae and Allodesminae converged in evolution of a hood or proboscis. Phocid-like "experiments" of Otariidae are now extinct, possibly as a result of competition resulting from phocid invasion of the North Pacific.

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