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**MORPHOLOGY AND SYSTEMATICS OF MIOCENE PHOCINAE
(MAMMALIA: CARNIVORA) FROM PARATETHYS
AND THE NORTH ATLANTIC REGION**

BUDAPEST, 2001

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Abstract

This manuscript provides a systematic revision of North Atlantic and Paratethyan Phocinae (true seals; Mammalia; Carnivora), based on associations of isolated skeletal elements, which are hypothesized by analogy with ecomorphs of Recent seals. In fossil and Recent phocines, five main ecomorphotypes of mandibular, humeral, and femoral structure can be distinguished, and they are defined and considered in detail herein.

Historically, the genus *Phoca* has included both large seals with a monachine type of organization of the postcranial elements and small seals of a phocine type. In this study special attention is drawn to the possibility of using differences in morphology of the postcranial skeleton for the purpose of generic, and to a lesser degree, of specific diagnosis of Phocinae.

This analysis provides a foundation for revision of the group, and clarification of the systematic characteristics of its members. Based on this revision, I have reclassified certain species. In addition, I describe fossil materials from the southern European region of the former USSR, Eastern and Western Europe, and the eastern part of North America. New material allows revision of generic diagnoses, permitting a partial revision of the subfamily Phocinae, and proposes a method for description and morphometric treatment of this group. This corresponds to methods used in analyses both of Recent representatives of this subfamily and, with some modifications, of fossil material. Some problems of classification and phylogenetic relationships of the phocids are considered also.

Introduction

In modern paleozoology a transition is occurring from studies of faunas to the investigation of separate groups of animals. Studies of separate groups allow the solution of many biological problems, and lead as a rule to important and useful stratigraphic and paleogeographic conclusions. However, the small number of specimens available for some groups frequently precludes a satisfactory conclusion. It follows that there is an obvious need for study of larger numbers of these representatives of Neogene faunas.

Many marine and continental Neogene deposits have not been well studied. Particularly insufficient are studies of Neogene marine deposits of the Ukraine, especially studies of their stratigraphic correlation with Neogene continental deposits of adjacent and distant regions.

This study concentrates upon Miocene (from 23.8 to 5.3 million years ago) marine deposits, which are the ones most extensively represented in southwestern Ukraine. The thick marine layers exposed in this region are as a rule not very rich in fossil animal remains other than molluscs, but some areas are well characterized geologically. In similar-aged continental deposits of the Ukraine, some large Miocene hipparion faunas have been found. This suggested the southwestern Ukraine as an especially interesting location for paleozoological investigation.

One of the least investigated and most complicated groups of large Miocene mammals is the subfamily Phocinae (Order Carnivora, Family Phocidae = true seals). This situation may be explained partly by the great rarity and the usually unsatisfactory preservation of postcranial and especially cranial remains of these animals as compared even with terrestrial carnivores. At present, Miocene true seals are of interest for the solution of some theoretical problems of biology — of general problems of evolutionary theory, of phylogenetic relationships among pinnipeds (BERTA 1991; BERTA and WYSS 1990, 1994), and of the history of global faunal development. Studies of taxonomy, morphology, and phylogeny of Phocinae may be useful in biogeography (HENDEY 1972; GRIGORESCU 1977; RAY 1977a; REPENNING, RAY and GRIGORESCU 1979; MUIZON 1982) and in correlation of European and North American Neogene deposits.

The geographic ranges of some modern pinniped species are very large and often extend through several zoogeographical regions. Fossil species likewise are widespread, and of particular zoogeographic interest are the true seals (Phocinae), whose fossils are very numerous in Miocene coastal-marine faunas of the northern Black Sea littoral region. In the former Soviet Union, remains of these animals have been found at localities in the Transcaucasus and in Kazakhstan, but the most numerous finds are in the Middle Sarmatian (13.6–10.0 m.y. ago) to Maeotian (9.88–7.6 m.y. ago), and probably Pontian (7.5–5.5 m.y. ago), deposits of the European part of the former USSR and especially in the northern littoral region of the Black Sea in the Ukraine and in Moldavia. In Western and Central Europe, remains of fossil seals are regularly found in France, The Netherlands, Belgium, Austria, Hungary, Romania, Czech Republic, and Slovakia. Isolated finds are known from Turkey and Italy (TAVANI 1942) (Fig. 1). Fossil phocines are also known in the United States; the oldest is *Leptophoca lenis* TRUE 1906, from the Middle Miocene of Maryland and Virginia.

Pinnipeds in general are widely distributed, their remains are relatively numerous, and they have been investigated for a long time. However, up to the present, many important problems of phocine phylogeny, ecology, morphology, and distribution have not solved. Moreover, in studies of pinnipeds, difficulties arise from the absence of generally accepted procedures for description and identification of their remains. As a result, data in various publications cannot be compared because of the complicated nomenclature and absence of useful diagnoses.

The available specimens, for the most part dissociated and fragmentary, include representation of essentially every element of the skeleton. I have concentrated here on humeri, femora, mandibles, teeth, and cranial bones, including the temporal bone with the auditory region, because of their taxonomic usefulness. I have given lesser attention to the innominate, radius, tibia and fibula, and still less to other elements due the lack of association. An overview of the entire

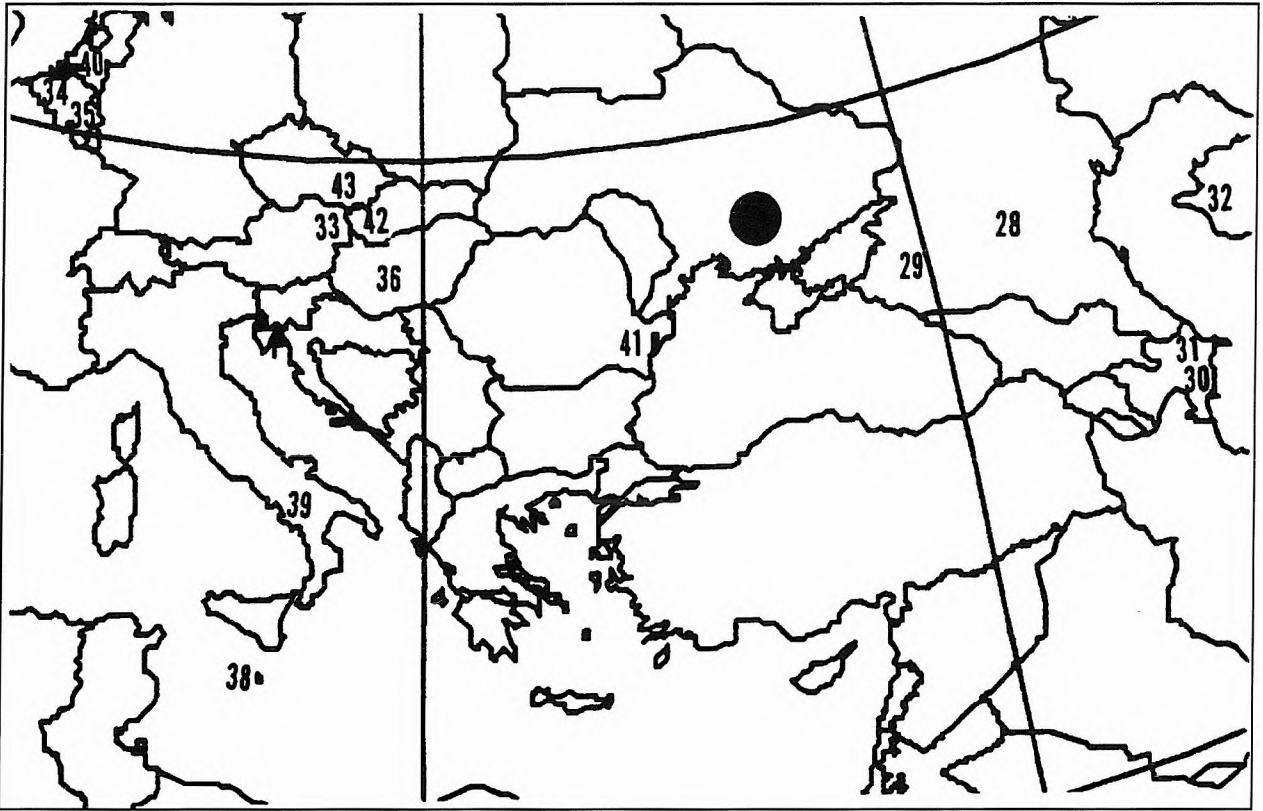


Figure 1. Main localities of Miocene Phocinae of Paratethys

28 — Stavropol; 29 — Tsymlyansk; 30 — Eldar; 31 — Perekishkul; 32 — Mangyshlak Peninsula; 33 — Heiligenstadt; 34 — Brussels; 35 — Borgerhout; 36 — Črd; 37 — Lublé; 38 — Malta; 39 — Roccamorice; 40 — Leiden; 41 — Dobrogea; 42 — Holič; 43 — Neusdorf; Northern Black Sea region indicated by black circle

collection shows that many parts of the skeleton are diagnostic at least to the subfamilial level, but much more work (in progress) is required to determine their reliability and the taxonomic level of their utility.

Determination of the overall phylogeny of the pinnipeds is necessary to build a common system of classification for the Recent and fossil seals. However, classification of modern true seals is based exclusively on skull morphology, and the mandible and bones of the postcranial skeleton have not been adequately described. Therefore, it has been practically impossible to compare descriptions of fossil and Recent Phocinae. As a result, in most monographic reviews and catalogs, either fossil or modern taxa are excluded (OGNEV 1935; HEPTNER et al. 1976; GROMOV and BARANOVA 1981; PAVLINOV and ROSSOLIMO 1987; RIDGWAY and HARRISON 1981; WOZENCRAFT 1989).

Contemporary literature contains many specific and generic names, which cannot be used because they are composite taxa (VAN BENEDEN's taxa), or because a particular work provides no more than a basic description (ALEKSEEV 1924a, b; KRETZOI 1941; THENIUS, 1958). What is needed is to determine the range of specific, sexual, age, and individual variability, and then proceed with a cladistic analysis of the Recent and fossil pinnipeds. The current cladistic literature addresses only Recent taxa (WYSS 1988a; PERRY et al. 1995; BININDA-EMONDS and RUSSELL 1996). This leads to no definitive result, with every year seemingly producing new phylogenetic (cladistic) schemes.

In my opinion, the foregoing considerations demonstrate the timeliness of the present study. My purpose here is to improve the state of knowledge of true seals of the Middle Sarmatian – Maeotic, and partly of the Early Sarmatian and Pontian, of the Northern Hemisphere, emphasizing the eastern part of the USA, Europe, and especially the northern Black Sea littoral region of the Ukraine, as well as (within limits) to increase knowledge of the group as a whole. I have analyzed the taxonomic characters that have been used for classification of the Phocinae, and have established that the genus *Phoca*, as applied to extinct seals, is a composite taxon that includes representatives of three subfamilies, Phocinae, Monachinae, and Cystophorinae, whose only common characteristic is a generally similar structure of the postcranial skeleton.

A working hypothesis basic to this study is that there exist among Recent phocines several distinct skeletal morphotypes, which are also distinct ecologically; and that these and similar morphotypes can also be identified among fossil phocines (see Chapter 4). These hypothesized morphotypes form a critical part of the basis for my associating of isolated bones into separate species. Obviously there is also a strong implication here that the fossil species were ecological-

ly similar to their recent counterparts displaying the same morphotypes. However, this ecological equivalence cannot be considered demonstrable given our present limited understanding of phocine functional anatomy, and must instead await future studies, especially of living seals, in order for my working hypothesis to be properly tested. Such tests of this hypothesis are beyond the scope of the present work, which is not conceptually based on the (presumably) ecological explanation of the empirically — observed morphotypes, but only on the “correlations of parts” which these represent.

Results of this analysis have allowed the establishment of a foundation for revision of the group, and clarification of the systematic characteristics of its members. Moreover, these results have provided the basis for revision of the generic and species diagnoses of true seals and suggested a procedure for the study of their cranial and postcranial remains. Based on this revision, I have reclassified certain species. In addition, I describe fossil materials from the southern European region of the former USSR, Eastern and Western Europe, and the eastern part of North America. Some problems of classification and phylogenetic relationships of the phocids are considered also. The methods developed in my studies for description and morphometric treatment can be applied equally well to modern and fossil representatives of the subfamily Phocinae.

This study was begun in the I. I. Shmalhausen Institute of Zoology of the Academy of Sciences of the Ukraine, Kiev. The materials were collected during many years of excavations carried out by expeditions of the Department of Vertebrate Paleozoology and of the Paleontological Museum of that institute, in which I participated from 1977 to 1988.

Chapter 1
History of investigation and the present state of systematics
of fossil representatives of the subfamily Phocinae

Despite more than 100 years of investigations of fossil true seals, paleontological understanding of this group of marine mammals has not improved significantly. Many investigators have presented only descriptive information and have not paid due attention to problems of systematics, phylogeny, and elaboration of procedures for diagnosing taxa. These particular publications often have poor definitions and lack useful description. Often, determination of remains is erroneous and serves only to further complicate the nomenclature and classification of subfamilies of true seals, and makes it impossible to compare data from the literature. New discoveries of limited material too often have led to erection of new species or, rarely, genera that have proven spurious.

The unsatisfactory state of phocid systematics is also the result of the following. For a long time, classification of fossil Phocinae was based on the morphology of the postcranial skeleton. This situation is explained partly by the better preservation of humeri and femora compared with skull bones, and their correspondingly greater availability for study. Many investigators have not paid due attention to skull morphology in their description of new fossil taxa. On the other hand, classification of modern true seals is based exclusively on skull morphology. As a rule, the mandible and bones of the postcranial skeleton are not adequately described for modern taxa. For these reasons, comparing the classifications of Neogene and Recent phocids has been practically impossible. As a result, in most monographic reviews and catalogs, either fossil or modern taxa are excluded (OGNEV 1935; HEPTNER et al. 1976; GROMOV and BARANOVA 1981; RIDGWAY and HARRISON 1981; PAVLINOV and ROSSOLIMO 1987; WOZENCRAFT 1989).

A detailed description of the history of investigation and of problems of systematics of true seals is presented by investigators such as McLAREN (1960), KIRPICHNIKOV (1953, 1961, 1964), CHAPSKII (1952, 1955a, b, 1961, 1967, 1970, 1971, 1974), GRIGORESCU (1977), RAY (1976, 1977a, b), ANTONIUK and KORETSKY (1984), KORETSKY (1986, 1987a, b, 1988) and KORETSKY and RAY (1994).

TROUESSART (1897, 1904, 1905) proposed a clear system of classification of the carnivoran suborder Pinnipedia, and in particular the Phocidae. In his classification [TROUESSART (1898–1904)], the Monachinae included the antarctic phocids, *Lobodon* GRAY, 1844; *Ommatophoca* GRAY, 1844; *Hydrurga* GISTEL, 1848; and *Leptonychotes* GILL, 1872. However, in the classification of SIMPSON (1945), the antarctic phocids were separated, for example *Lobodon* and the other genera mentioned above were included in a subfamily Lobodontinae.

Except for the introduction of the subfamily Lobodontinae the classification system proposed by SIMPSON (1945) is essentially only a simplified and not always validated variant of the older system of TROUESSART, and does not completely satisfy modern requirements.

Regrettably, up to the present there has been no clear concept of the subfamilial structure of the true seals and this remains a controversial problem. For example, one group of investigators perceives phocids as comprising only one subfamily, Phocinae (WYSS 1988a; MCKENNA and BELL 1997), while others separate them into two (Phocinae and Cystophorinae, see KING 1983, 1989; BURNS and FAY 1970; MUIZON 1982a; WYSS 1988a, 1994; PERRY et al. 1995; BININDA-EMONDS and RUSSELL 1996), three (OGNEV 1935; GRASSÉ 1955; SCHEFFER 1958; KING 1964; CHAPSKII 1974; PAVLINOV and ROSSOLIMO 1987; KORETSKY and HOLEC, in press), or even four subfamilies: Phocinae, Lobodontinae, Monachinae, and Cystophorinae (e.g., ALLEN 1880; SIMPSON 1945:122–123). Finally, some researchers (SOKOLOV 1979; WOZENCRAFT 1989) do not separate true seals into subfamilies at all.

Classification of the family Phocidae (true seals) into genera is based on morphological differences in the cranium, mandible, and postcranial bones. Based on the assumption of similarity in the postcranial skeletons, many paleontologists historically have referred diverse remains of extinct Phocidae to the single genus *Phoca* (BLAINVILLE 1842; EICHWALD 1850; NORDMANN 1858; GERVAIS 1859; BRÜHL 1860; PETERS 1867; TOULA 1897; TRUE 1906; ALEKSEEV

1924a, b). As a result, this genus has become a “wastebasket” taxon that includes Neogene and Recent representatives of both Monachinae and Phocinae.

For example, from Miocene-Pliocene deposits of the northern littoral of the Black Sea, remains of at least five species of seals have been referred by some authors to the genus *Phoca*. In my opinion this is evidence of insufficient investigation of the group.

It should be noted that SIMPSON (1945) listed some ten genera of Miocene-Pliocene seals in Western Europe, belonging to three subfamilies: *Monachinae*, *Phocinae*, *Cystophorinae*. Therefore it may be supposed that Miocene seals from the northern Black Sea littoral deposits are also not a taxonomically united group (McKENNA and BELL 1997). This was the opinion of KRETZOI (1941), who proposed three new genera: *Praepusa*, *Monachopsis* and *Pontophoca* for the Miocene seals of this region. The remarkable merit of KRETZOI is that he attempted for the first time to unite the two foregoing approaches and to construct a common classification of modern and fossil seals. Unfortunately the state of knowledge at the time precluded complete success.

Since KRETZOI's work, the taxonomy of the Phocidae has undergone considerable change. CHAPSKII (1955a, 1961, 1967, 1971, 1974, 1975) provided a comprehensive analysis of phocine suprageneric systematics. He presented a clear description of diagnostic cranial traits separating true seals into tribes and subtribes, including Phocini, Monachini and Lobodontini. CHAPSKII (1974) proved untenable the hypothesis of KING (1966), according to which the genus *Cystophora* should be transferred from Cystophorinae into Phocinae, and he also disputed KING's placement of the genus *Mirounga* in the subfamily Monachinae (which perhaps is correct). Evidence of the correctness of CHAPSKII's concept was the conclusion of ROBINETTE and STAINS (1970) in their comparative study of the calcaneum of seals. These authors emphasized that separating *Cystophora* and *Mirounga* taxonomically (at the subfamilial level) is inadmissible. Later, their point of view was supported by ANBINDER (1980:76): “Modern analytical methods of chromosome investigations actually do not permit the separation of genera *Cystophora* and *Mirounga*, and this contrasts with the concept of their separate taxonomic status and of inclusion of *Cystophora* in Phocinae”. Apparently MUIZON (1982a, b) was unaware of CHAPSKII's work, and without reservation he accepted the systematics of KING. Thus he returned to the concept of a separate subfamily Cystophorinae. In my view, the problem of the status of the subfamily Cystophorinae is not yet resolved.

In this study, I accept a more traditional classification (SIMPSON 1945; SCHEFFER 1958; CHAPSKII 1955, 1974; KING 1964; HEPTNER et al. 1976), in which the family Phocidae is divided into three subfamilies: Phocinae, Monachinae and Cystophorinae.

In recent years the situation has improved. Of special interest in this context is an article by McLAREN (1960). Based on previous publications, he revised two subfamilies of true seals of the northern Black Sea littoral of the former USSR. KING (1956), in her monographic review of monk seals, for the first time presented a description of bones of the postcranial skeleton as well as descriptions and measurements of the skulls and mandibles of modern species. KING (1964), in the first edition of her monograph on seals of the world, presented her concept of fossil seals of the Miocene of the northern Black Sea littoral, separating them into four species of *Phoca* and two other species referred to *Monotherium* and *Pontophoca*, respectively. Also discussed was the species *Praepusa pannonica* KRETZOI, which KING included in the same modern genus *Phoca* along with *Pusa*. Later she (KING 1983) changed her views on classification of the true seals, but considered only their classification above the rank of tribe.

The European founder of research on extinct true sea was the French paleontologist DE BLAINVILLE. In 1840, he described under the name *Phoca viennensis antiqua* a fossil seal from “perite layers” (Lower or Middle Sarmatian) of the Vienna Basin. As osteological material accumulated, many paleontologists studied the Miocene pinnipeds. Among them were PETERS (1855, 1867), BRÜHL (1860), TOULA (1897) and THENIUS (1950, 1979, 1992). Unfortunately their works were based largely on the same postcranial remains, and with each examination a new species name was created.

Phoca pontica EICHWALD (1850) from Ukraine has had an obscure history and has been mentioned by many researchers. GRIGORESCU (1976:411, 412) suggested that this species had been confused with *Phoca sarmatica*. McLAREN (1960) first transferred this species to the genus *Monachopsis*, and later I (KORETSKY 1987a; 1988) described additional material, and produced an emended diagnosis of *Monachopsis pontica*.

In order to clarify the systematic position of the Neogene seals from Western Europe, DR. CLAYTON E. RAY and I were obligated to revise VAN BENEDEN's material (KORETSKY and RAY, in press).

Of all studies of this group, the most extensive was that of VAN BENEDEN (1876a, b, 1877), which was accompanied by excellent illustrations. Although this study is of purely regional character (Antwerp Basin), the author, on the basis of poor osteological material, identified six new genera in the subfamily Phocinae (*Phocanella*, *Prophoca*, *Platyphoca*, *Gryphoca*, *Mesotaria*, *Callophoca*) from the Late Pliocene (see KORETSKY and RAY, in press), and two genera in the subfamily Monachinae (*Monotherium*, *Paleophoca*) from the Late Miocene.

During the more than one hundred years since the publication of VAN BENEDEN's monograph (1877), his taxa for the most part have not been critically restudied. Generally speaking, the names have merely been carried forward in com-

pendia of a reference character, such as those of TROUESSART (1897, 1904, 1905), DOLLO (1909), KELLOGG (1922), SIMPSON (1945), KING (1964), SAVAGE and RUSSELL (1983), MUIZON (1992) and MCKENNA and BELL (1997).

Obviously related to *Phoca vitulinoides* is "*Phoca*" *vindobonensis* (TOULA 1897) from the Middle Miocene of the Vienna Basin. Its generic affinities were questioned by HENDEY and REPENNING (1972:95), GRIGORESCU (1977a:407) and by RAY (1977a:395). In this study I transfer "*Phoca*" *vindobonensis* to the genus *Praepusa* KRETZOI, 1941.

Further studies on Sarmatian marine mammals were made at the beginning of this century. One of the oldest known fossil phocines is *Leptophoca lenis* TRUE, 1906, from the Calvert Formation (Middle Miocene) in Maryland and Virginia. It was described on the basis of a single humerus, and the last primary research on it was more than 20 years ago (RAY 1976). The latter paper discussed questions of nomenclature and taxonomic history and described some scanty skeletal remains. Additional material has now been collected.

The Smithsonian Institution's Department of Paleobiology has gradually accumulated a large collection of well-preserved fossils that are very important to research on this poorly known species, and on its affinities with other seals of North America and Europe. The collection includes the first nearly complete skulls and skeletons of *Leptophoca lenis*; such complete specimens are extremely rare in the fossil record of seals (BARNES, DOMNING and RAY 1985). The importance of this species lies in the fact that it is the oldest phocid represented by essentially complete skeletons. Although not necessarily the most primitive phocid (it is already identifiably phocine), *L. lenis* provides the best insight into the character states of early phocids.

The North American *L. lenis* specimens are also close to if not conspecific with fossil seals from Western Europe (BRÜHL 1860; TOULA 1897) and Russia (ANTONIUK and KORETSKY 1984), all of which I have previously examined. For example, the species that was originally referred to *Prophoca proxima* VAN BENEDEN (1871a, 1873, 1876b), from Middle Miocene deposits in Belgium, was considered by RAY (1976:Table 1) to be close to *Leptophoca*. VAN BENEDEN (1876b) had noted the very primitive nature of this species. The North American skeletons are therefore additionally important for establishing faunal connections between eastern North America, Europe, and the Eastern Paratethys, and possibly for intercontinental biostratigraphic correlations.

The most complete and reliable review of Miocene and Pliocene pinnipeds of the world was published by KELLOGG (1922). In this study all information on then-known fossil representatives of the order is collected. This study remains valuable even today.

ALEKSEEV (1924a, b; 1926) described for the first time the rostral part of the skull of small seals found near KISHINEV (Moldavia). These were included in the same species "*Phoca*" *pontica* (KORETSKY 1987a, b), although ALEKSEEV also described two new species, "*Phoca*" *sarmatica* (MCLAREN 1960; KORETSKY and RAY 1994) and "*Phoca*" *novorossica* (ALEKSEEV 1924b, 1926).

Pontophoca sarmatica (ALEKSEEV 1924b) was originally named by ALEKSEEV as *Phoca sarmatica* from Middle Miocene (Middle Sarmatian) deposits of Ukraine. SIMIONESCU (1925), and later MACAROVICI and OESCU (1942), incorrectly identified a femur of *Pontophoca sarmatica* as *Phoca pontica*. Later MCLAREN (1960) transferred these species into the genus *Pontophoca*, described by KRETZOI (1941). KORETSKY and GRIGORESCU (in press) revised the previous diagnosis of *Pontophoca sarmatica*, illustrated additional material from Eastern Europe (including a humerus and mandible), and confirmed that this species belongs to the Monachinae.

In his study of true seals of the northern Black Sea littoral, SIMIONESCU (1925), on the basis of fragments of the postcranial skeleton, described a new species, "*Phoca*" *bessarabica*, from the vicinity of Kishinev (Moldavia and Romania).

He also described additional material, which he referred to *Ph. maeotica* and *Ph. pontica*. As may be judged by the illustrations of the femur in his study (SIMIONESCU 1925, table 1; figure 2), SIMIONESCU included in the latter species, "*Ph.*" *pontica*, the seal described previously by ALEKSEEV as *Ph. sarmatica*, and he noted that these finds are of the Sarmatian period. Later, MACAROVICI and OESCU (1942) and MACAROVICI (1942) published short reviews of fossil seals of the European Sarmatian, which only confused the picture.

When KRETZOI (1941) revised the fossil seals of the Sarmatian he proposed two new genera (*Praepusa* and *Monachopsis*) of fossil phocids from Central Paratethys. Moreover, KRETZOI described, based on a single mandible, a new species, *Praepusa pannonica*, from the Lower-Middle Sarmatian of the Érd near Budapest, Hungary. GRIGORESCU (1977:407) questioned the validity of this species, citing the lack of material, but HENDEY and REPENNING (1972:95) reported that it has a primitive dentition. Later, I (KORETSKY 1987b) reviewed this taxon with referred additional material to the species and provided a description and diagnosis.

After the middle of 1920, investigations on true seals of the former USSR ceased until 1950's, although collections enlarged considerably. This cessation of study resulted from invalid systematics based on obsolete data of the last century, which did not correspond to the material accumulated. In this period fossil seals were mentioned only in publications of a reference character, such as those of PIDOPLICHKO (1938a, b, 1953, 1954, 1956), BOGACHEV (1927a, b), KIRPICHNIKOV (1953, 1961, 1964), AKHUNDOV (1962), ASLANOVA (1965, 1966) and BRUZGIN (1966). Only rarely were problems discussed such as the reworking of bones of seals from the Middle Sarmatian deposits into the Kimmerian lay-



Figure 2. Locaties of Miocene Phocinae from the Northern Black Sea region

1 — Nnilozubovo; 2 — Grigoryevka; 3 — Gritsev; 4 — Homutovo; 5 — Kamenka-Dneprovskia; 6 — Kerch Peninsula; 7 — Kirovo; 8 — Kulikovka; 9 — Mount Mitridat; 10 — Nikolaev; 11 — Novoalexandrovka; 12 — Novovorontsovka; 13 — Sevastopol; 14 — Suchaya Kalina; 15 — Tarchankut; 16 — Tyaginka; 17 — Vasilyevka; 18 — Velikaya Lepeticha; 19 — Maryupol (Zhdanov); 20 — Zheltokamenka; 21 — Zolotaya Balka; 22 — Gidigich; 23 — Kalfa; 24 — Kayiry; 25 — Kishinev; 26 — Kuchiyery; 27 — Tiraspol

ers of the Kerch Peninsula. The discovery on this peninsula of bones of the small seal "*Ph.* *pontica*" in a piece of "strong and solid white limestone together with remains of marine Sarmatian fauna (*Maetra* cf. *caspicus* EICHW.)" confirmed proposals by ANDRUSOV (1893, 1929) and KARLOV (1952) about redeposition of these and similar bones of Late Miocene vertebrates with subsequent secondary burial in iron ore. BRUZGIN (1966) mentioned finding fossil seals on the Kerch Peninsula, and said that bones were redeposited (as judged by their abraded condition) in the Kimmerian layer. These conclusions accord with the my discovery of non-abraded bones of fossil seals in Sarmatian and Maeotic deposits at the village of Gornostaevka, and the Kerch deposits of iron ore at Lake Tobechnik (Crimea, Ukraine).

GRIGORESCU (1977), in his article on Paratethyan seals, presented a detailed description of bones of the postcranial skeleton and of the temporal part of the skull of "*Phoca pontica*" from South Romania. Moreover, he described sexual dimorphism in the femora of two species, "*Phoca*" *pontica* and *Monotherium maeotica*. He also discussed problems of evolution and phylogeny of Sarmatian seals. RAY (1977a) studied these problems in regard to the Northern Hemisphere. He and other authors also considered routes of penetration of Phocidae into the Northern Atlantic during the Neogene (BERG 1910, 1928, 1934, 1940; CHAPSKII 1955b, 1970, 1974; BURNS and FAY 1970; BARNES 1970; REPENNING, RAY and GRIGORESCU 1979; MUIZON 1982; FLYNN 1988; BERTA and WYSS 1994; WYSS 1994; BININDA-EMONDS and RUSSELL 1996).

Praepusa tarchankutica KORETSKY, 1984, from the Middle Miocene (Crimea, Ukraine), was interpreted as a phocine.

Another seal, *Cryptophoca maeotica* (NORDMANN, 1860) KORETSKY et RAY, 1994, from the Paratethyan region, has been called *Phoca maeotica* or *Monotherium maeoticum* by different authors. HENDEY (1972:100) considered it to be closely related to *Monachus monachus*, but RAY (1977a:398–399) considered it to be an aberrant phocine.

The paleontological institutions and private collections of the former USSR and Europe contain many remains of true seals. In particular, many fossils are reported from the northern Black Sea littoral (Figs. 1 and 2). These finds have made it possible to clear up some of the foregoing problems of the systematics of the true seals and to propose a new system of classification for this group.

In this study I describe the Miocene species from the east coast of the USA and from Europe; discuss some questions about their taxonomic level; perform a cladistic analysis; and try to solve certain concrete systematic problems. The question of the phylogenetic relationships within the family Phocidae is a very broad and fundamental one that must be studied separately.

The importance of this study lies in the light it sheds on: (a) the morphology of the oldest known phocines; (b) the taxonomic status of numerous taxa of phocine seals; (c) biogeographic aspects of seal evolution in the North Atlantic region; and (d) cladistic relations within the subfamily Phocinae. Comprehensive analysis of this phylogenetically and geographically natural unit (subfamily Phocinae) is now possible for the first time.

Chapter 2
Material and methods

1. List of osteological and paleontological collections and abbreviations used

- AGMI = Azerbaijan State Medical Institute, Baku, Azerbaijan.
 CMM = Calvert Marine Museum, Solomons, Marylans, USA.
 GIKMM = State Museum of History and Regional Studies of Moldavia, Kishinev.
 HGI = Geological and Paleontological Department of Hungarian Geological Institute, Budapest, Hungary.
 HMZ = Museum of Zoology, Paleontological Department, Helsinki, Finland.
 IPUW = Institut für Paläontologie, University of Vienna, Austria.
 IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
 IZGK = Laboratory of Paleozoology, Institute of Zoology and Genofonda of the Academy of Sciences of Kazakhstan, Almaty.
 IZPhM = Institute of Zoology and Physiology of the Academy of Sciences of Moldavia, Kishinev.
 IZUAN = I. I. Shmalhausen Institute of Zoology of the Academy of Sciences of Ukraine, Kiev.
 JaU = Department of Geology, Paleontological Museum of University of Iași, Romania.
 MGRI = Moscow Geological-Prospecting Institute, Pavlov Museum.
 MKM = Maryupol (=Zhdanov) Museum of Regional Studies, Ukraine.
 MPGI = Paleontological Museum of the Mining Institute, Saint-Petersburg, Russia.
 MNHN = Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.
 NMNH = Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands.
 NHMW = Naturhistorisches Museum, Vienna, Austria.
 OGUM = I. I. Mechnikov Paleontological Museum, State University of Odessa, Ukraine.
 PIN = Paleontological Institute of the Academy of Sciences of Russia, Moscow.
 SKM = Stavropol Museum of Regional Studies, Russia.
 SMNH = Slovak Museum of Natural History, Bratislava, Slovakia.
 TGPI = Tiraspol State Pedagogical Institute, Moldavia.
 UBFG = Faculty of Geology and Geography, University of Bucharest, Romania.
 USNM = National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA.
 ZIN = Zoological Institute of Academy of Sciences of Russia, Saint Petersburg.
 ZKM = Zaporozhe Museum of Regional Studies, Ukraine.

2. Localities of Miocene Phocinae in Eurasia

This study is based primarily on the collections of fossil remains of true seals and also on comparative materials of Recent pinnipeds, kept in the Department of Paleozoology of Vertebrates and the Paleontological Museum of the IZUAN and the Departments of Vertebrate Zoology and Paleobiology of the USNM. Collection of materials was carried out by expeditions of the Department of Paleozoology of the IZUAN from 1937 onward. I took an active part in these expeditions from 1975 to 1987. Paleontological and osteological collections of ZIN, PIN, ZKM, OGUM, MPGI, TGPI and other museums and private collections were also used. Casts of type specimens were studied from the collections of the NHMW, IRSNB, IZPhM, SMNH and UBFG. Ten fossil skulls and 16 mandibles in various degrees of preservation were studied. Some 467 postcranial bones were investigated, as well as a small number of other isolated bones of the postcranial skeleton. These remains originated from 32 localities in the European part of the former USSR and from 24 local-

12. Novovorontsovka*, Cherson Region, Novovorontsovsky district; Sarmatian; collections of Alekseev 1924. Present locations unknown [OGUM?].
13. Sevastopol*, Crimea Region; Sarmatian; collections of PRENDEL 1874; MGRI.
14. Suchaya Kalina, Dnepropetrovsk Region, Sinelnikovo district; Middle Sarmatian; collection of 1950; IZUAN.
15. Tarchankut, Crimea Region, Chernomorsk district, Tarhankut Peninsula, 7 kilometers south-east of village of Olenevka; Middle Sarmatian; collections of Antoniuk 1975–1986, of Koretsky 1983–1986; ZIN, IZUAN.
16. Tyaginka, Cherson Region, Berislav district, village of Tyaginka; Late Sarmatian; ZIN, OGUM.
17. Vasilyevka, Zaporozhy Region, Vasilievky district, bank of Kachovka Reservoir, Mount Lysaya, village of Vasilyevka; Middle Sarmatian; collection of 1963; ZKM.
18. Velikaya Lepeticha*, Cherson Region, Velikolepetichsky district, town of Velikaya Lepeticha; Middle Sarmatian; collection of MOLIIVKO 1949; IZUAN.
19. Maryupol* (Zhdanov), Donetsk Region, quarry on the bank of Kalchik River near Maryupol; Sarmatian; collections of Pidoplichko 1931–1934; MKM.
20. Zheltokamenka, Dnepropetrovsk region, Apostolovo district, Zheltokamenka village on Zheltenkaya River, limestone quarry 8-10 meters deep; Middle Sarmatian; collections of Pidoplichko 1938, 1940, 1953–1954; ZIN, IZUAN.
21. Zolotaya Balka, Cherson region, Novovorontsovo district, village of Zolotaya Balka, quarry north of village, upper layer; Middle Sarmatian; collection of Bezuglov 1952; IZUAN.

Moldavia

22. Gidigich*, Strashensky district, Gidigich, 10 kilometers north of Kishinev; Middle Sarmatian; TGPI, OGUM, GIKMM, ZIN.
23. Kalfa*, Novoanensky district, exposed layers in valley of Byk River, north-west of village of Kalfa; Middle Sarmatian; collection of A. Lungu 1960–1975; TGPI.
24. Kayiry*, Gornostayev region, Kayiry village; Middle Sarmatian. Present locations unknown.
25. Kishinev, limestone quarries in the Visternicheny (Golbochika) and Petrikany reef region, vicinity of Kishinev; Middle Sarmatian; collections of von Nordmann 1853, of Sintsov and Alekseev 1924; OGUM, ZIN, TGPI, PIN, JaU, IZUAN.
26. Kuchiyery, Dubossary Region, valley of Dnestr River, village of Kuchiyery; Middle Sarmatian; GIKMM.
27. Tiraspol, vicinity of Tiraspol, Kolkotov gully; Late Sarmatian; collection of Alekseev 1915; OGUM.

Russia

28. Stavropol*; Middle Sarmatian; precise locality unknown. OGUM?, SKM?.
29. Tsymlyansk, on Don River, bank of Kachovka Reservoir (Krachmal gully); Middle Sarmatian; OGUM.

Transcaucasian region

30. Eldar*, Azerbaijan, flood-plains of Pori River; Late Sarmatian; collections of Burchak-Abramovich and Gadjiev 1937, 1951; AGMI.
31. Perekishkul*, Azerbaijan, Apsheron Peninsula, left bank of Sumgait River; Late Sarmatian; collection of Aslanova 1963; AGMI.

Kazakhstan

32. Mangyshlak Peninsula, Karagie Basin, 36 km east of Fort Shevchenko, near Ude; Sarmatian of Eastern Paratethys; collection of IZGK.

Austria

33. Heiligenstadt; Middle Miocene (Sarmatian); collection of Thenius 1950; IPUW, NHMW.

Belgium

34. Brussels, Antwerp Basin; Late Miocene; IRSNB.
35. Borgerhout, Rumst-reet (Late Miocene), Deurne, Steendorp (?Miocene–Pliocene), Nachtehalen Park (Middle Miocene), vicinity of Antwerp; private collection of Dr. Paul Gigasse, Antwerp.

Hungary

36. Érd, vicinity of Budapest, Érd region, limestones 6 meters deep; Middle Miocene (Middle Sarmatian = Astaracian); collection of F. Bitter; HGI, present location unknown.

France

37. Lublé; Middle Miocene (Middle Sarmatian = Astaracian); MNHN.

Malta

38. Gozo; Late Miocene; British Museum of Natural History, London; precise locality unknown*.

Italy

39. Roccamorice*, vicinity of Naples; Late Miocene; precise location unknown.

Netherlands

40. Leiden, Borne, Morselt, Groenlo; Miocene; precise locality unknown*.

Romania

41. Dobrogea: villages of Adamclici, Andacata, Cavarna, Ciobănița, Credința, South Dobrogea, Constanța and Varna regions; Sarmatian (Bessarabian stage of Eastern Paratethys); collections of Grigorescu, Dode, Chiriac, Simionescu; UBFG.

Slovakia

42. Holíč, southern Moravia, on Morava River, not far from Breslaw (Czech Republic) and border between Czech and Slovak Republics; Late Miocene; NHMW.

43. Neussdorf-Sandberg Austria, vicinity of Vienna (now vicinity of Bratislava, Slovakia, village of Devínska Nova Vés); early Middle Miocene (Vienna basin) (Badenian); collection of NHMW.

USA

44. Maryland, Calvert County, Lower-Middle Miocene (Calvert Formation); Virginia, Westmoreland County, (Calvert Formation); collection of USNM.

3. Methods of investigation

The major aim of this study is to build a common system of classification for Recent and fossil seals. Recent Phocidae taxonomy has until now been based on skull morphology alone, while fossil seal taxonomy has been based on dissociated parts of postcranial skeletons, or in rare cases on mandibles.

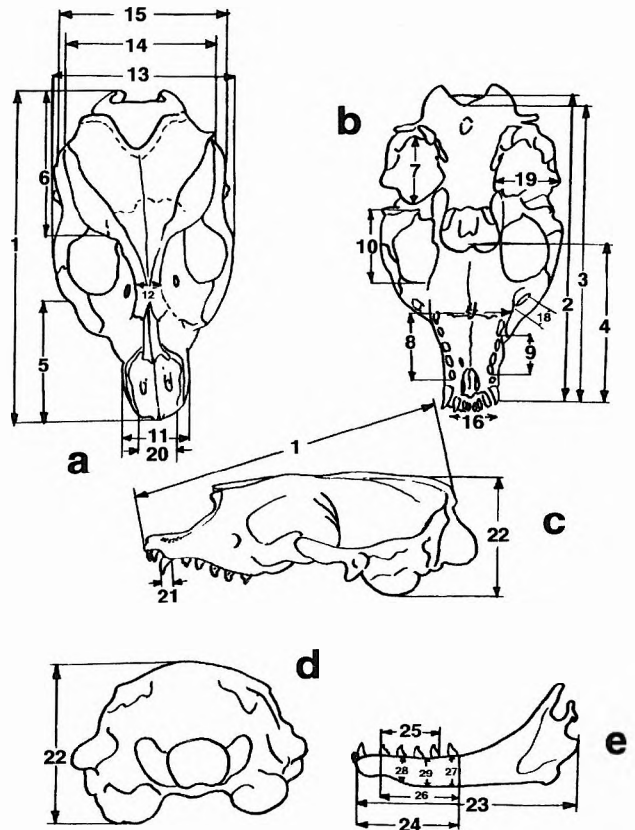
First, it is necessary to eliminate (based in part on comparisons with Recent species) the possibility that the present nomenclature includes misdetermined fossil taxa, which in reality simply represent either sexual or ontogenetic variability.

Second, it is necessary to determine, which types of humerus, femur and mandible belong together. This is done by direct association wherever possible, but also by analogy with Recent material. The modern seals form natural morphological units recognizable from associated bones of the postcranial skeleton and mandible; and each morphotype has a specific ecological niche. (This hypothesis is formally proposed and defended in Chapter 4 below). The working assumption that fossil seals had similar natural morphological units makes it possible to associate the many dissociated humeri, femora, and mandibles, according to the classic principle of “correlation of parts”. (However, the question of the extent to which the fossil taxa were ecologically similar to their Recent morphological analogues is beyond the scope of this taxonomic revision.)

The most novel feature of this study is this application of conclusions derived from “gamma systematics” (i.e., hypotheses about the ecomorphology of Recent seals) in solving problems of the “alpha systematics” (species definition) of fossil members of the same group.

Figure 3. Schema of the measurements of the skull and mandible of true seals

a, b, c, d = skull, e = mandible. 1 — total length; 2 — condylobasal length; 3 — basic length; 4 — length of palatal process; 5 — length of rostral part, measured from antero-upper corner of orbit; 6 — length of braincase, measured from posterior corner of orbit; 7 — width of tympanic bulla; 8 — length of toothrow, P1 - M1; 9 — length of toothrow, P2 - P4; 10 — length of orbit; 11 — width of rostrum across canines; 12 — maximal infraorbital width; 13 — zygomatic width; 14 — width of braincase; 15 — mastoid width; 16 — width of palatine process between P1s; 17 — maximum width of palatine process; 18 — maximum diameter of infraorbital foramen; 19 — width of tympanic bulla; 20 — width of rostrum; 21 — diameter of alveolus of upper canines; 22 — height in region of tympanic bulla; 23 — total length of mandible; 24 — length of toothrow i1 - m1; 25 — length of toothrow p1 - p4; 26 — length of toothrow p1 - m1; 27 — depth under m1; 28 — depth under p1; 29 — depth between p3 - p4



Third, these morphological units can then be labeled, i.e., I can make a nomenclatural revision of previously described species, associate known parts of a skeleton, redescribe them, and produce modern diagnoses.

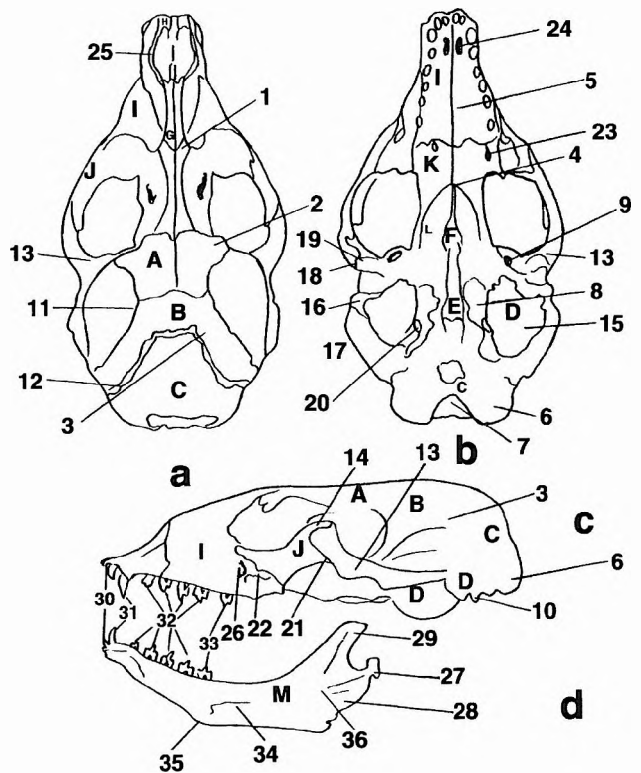
Fourth, cladistic analysis of these redefined species can then be used to group the fossil and modern phocines into genera and tribes.

After this it will be possible to produce a new, modern system of classification including both Recent and fossil phocines. It will also be possible to discuss ecomorphs among both fossil and Recent species, and to interpret convergences and community structure.

For solving diagnostic problems, the methods of ASTANIN (1936), HEPTNER (1947), CHAPSKII (1952; 1967) and ANTONIUK (1970; 1972) were used. Morphometric analysis of skulls and mandibles (Fig. 3) was carried out using the methods of CHAPSKII (1955a; 1974), KOSYGIN and POTELOV (1971), VON DEN DRIESCH (1976), SEMENOV (1981), ANDREESCU and MURARIU (1985), TRELEA and SIMIONESCU (1985), and the method described below (Fig. 4). The determination of sexual dimorphism among fossil humeri and femora was made using the collection of IZUAN, which included 48 bones of females and 25 bones of males from the type locality

Figure 4. Schema of the arrangement of the bones of the skull and mandible of true seals

a, b, c = skull; d = mandible. Skull: A = frontal; B = parietal; C = occipital; D = temporal; E = basisphenoid; F = presphenoid; G = nasal; H = incisivum; I = maxilla; J = zygoma; K = palatal; L = pterygoid; M = mandible. 1 — nasal process of frontal bone; 2 — postorbital process of frontal bone; 3 — temporal fossa; 4 — medial palatal process; 5 — palatal process of maxilla; 6 — occipital condyle; 7 — foramen magnum; 8 — jugular foramen; 9 — oval foramen; 10 — jugular process; 11 — temporal line; 12 — occipital crest; 13 — zygomatic process of temporal bone; 14 — frontal process of zygoma; 15 — bullae; 16 — external acoustic meatus; 17 — mastoid process; 18 — postglenoid process; 19 — glenoid fossa; 20 — carotid canal; 21 — temporal process of zygoma; 22 — zygomatic process of maxilla; 23 — greater palatal canal; 24 — incisor foramen; 25 — nasal process of intermaxilla; 26 — infraorbital foramen; 27 — condyloid process; 28 — angular process; 29 — coronoid process; 30 — incisors; 31 — canines; 32 — praemolars; 33 — molars; 34 — body of mandible; 35 — mental tuberosity



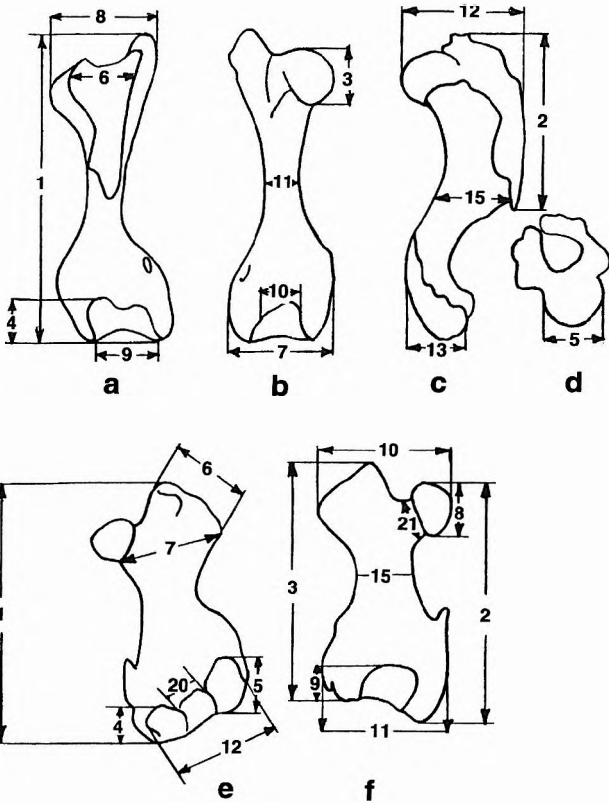


Figure 5. Nomenclature of the humerus (a-d) and femur (e-f) of true seals

a-d: 1 — deltoid crest; 2 — lateral condyle; 3 — medial condyle; 4 — head of humerus; 5 — ridge of trochlea; 6 — trochlea; 7 — greater tubercle; 8 — olecranon fossa; 9 — intertubercular groove; 10 — neck; 11 — anconeal crest; 12 — entepicondylar foramen. e-f: 13 — head of femur; 14 — neck; 15 — greater trochanter; 16 — intertrochanteric line; 17 — lateral epicondyle; 18 — medial epicondyle; 19 — lateral condyle; 20 — medial condyle; 21 — intercondyloid fossa; 22 — patellar surface

the schemes of LYON (1937), CHAPSKII (1955a, b; 1974), SERGIENKO (1967), BURNS and FAY (1970), PIÉRARD (1971), VON DEN DRIESCH (1976), MUIZON (1981a), ANTONIUK and KORETSKY (1984), TRELEA and SIMIONESCU (1985), VAN BREE and ERDBRINK (1987), KORETSKY (1986; 1987a; 1988) and KORETSKY and RAY (1994) (Fig. 6).

Statistical treatment of the results was carried out on a "Electronica B3-21" microcomputer using the programs by FRANCEVICH (1979) and the method of LAKIN (1973), and on a Casio FX-82L microcomputer.

Osteological terminology is presented according to the International Anatomical Nomenclature edited by MICHAYLOV (1980) and the Nomina Anatomica Veterinaria (1988), Piérard (1971), and the Illustrated Veterinary Anatomical Nomenclature (ed. SCHALLER 1992), except that I anglicize all Latin terminology.

For the cladistic analysis I used Hennig86, version 1.5 (FARRIS 1988), installed in the laboratory of Dr. D. DOMNING at Howard University. The analysis incorporated all available osteological and dental characters (62 unweighted characters of the skull, mandible, dentition, and limb bones), and include representatives of all adequately known species of living and fossil Phocinae (9 fossil taxa and 11 Recent taxa).

of the species *Monachopsis pontica* (Kerch Peninsula), and also the UBF, IPUW, and USNM collections. Comparative material used included modern representatives of the genera *Phoca* and *Pusa*: 31 femora and 23 humeri of males, 19 femora and 20 humeri of females. These bones belong to osteologically and sexually mature animals; these materials are kept in the collections of ZIN, PIN, IZUAN, and USNM. I chose representatives of the genera *Phoca* and *Pusa* because these were the most accessible for investigation.

Morphometric analysis of the postcranial skeletons of both Miocene and Recent Phocinae (Fig. 5) was carried out by measurement of a series of these remains according to

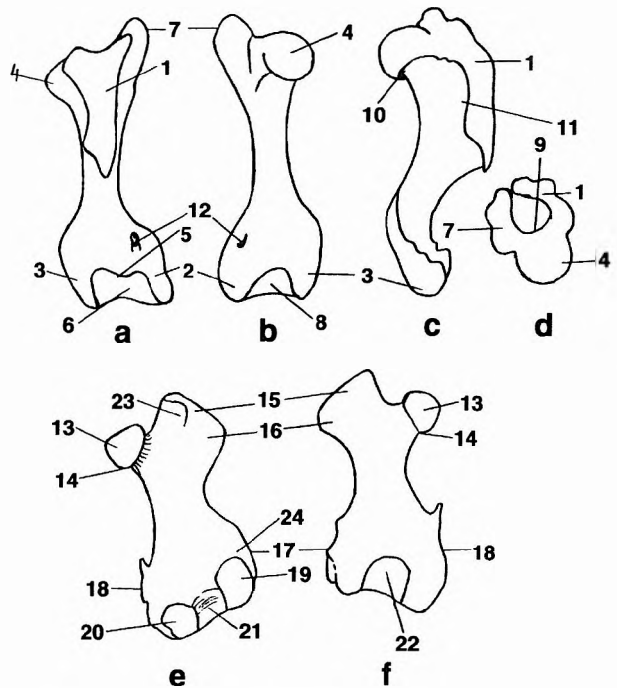


Figure 6. Scheme of measurements of humerus (a-d) and femur (e-f) of true seals

a-d: 1 — total length; 2 — length of deltoid crest; 3 — height of head; 4 — height of trochlea; 5 — width of head; 6 — width of deltoid crest; 7 — width of distal epiphysis; 8 — width of proximal epiphysis; 9 — width of trochlea distally; 10 — width of trochlea, anterior view; 11 — transverse width of diaphysis; 12 — thickness of proximal epiphysis; 13 — thickness of medial condyle; 14 — thickness of lateral condyle; 15 — diameter of diaphysis with deltoid crest. e-f: 1 — total length; 2 — medial length; 3 — lateral length; 4 — length of medial condyle; 5 — length of lateral condyle; 6 — length of greater trochanter; 7 — intertrochanter length; 8 — height of head; 9 — height of patellar surface; 10 — width of proximal epiphysis; 11 — width of distal epiphysis; 12 — width of condyles; 13 — width of trochanter; 14 — width of head; 15 — width of diaphysis; 16 — thickness of diaphysis, anteroposterior view; 17 — thickness of medial condyle; 18 — thickness of lateral condyle; 19 — thickness of proximal epiphysis; 20 — distance between condyles; 21 — diameter of neck

Chapter 3

Some special features of phocine morphology

As noted previously, morphology of the postcranial skeleton is of major importance for the classification of seals. However, it should be analyzed only together with the mandible and, if possible, the skull. It is especially important in studies on phylogenetically closely-related groups of pinnipeds, which, on every taxonomic level, demonstrate parallelism in features associated with the functional activities of mastication and locomotion (MITCHELL 1975). Taking for example the genera *Phoca* and *Pusa*, it is difficult to separate these genera without using combined data of morphology of the skull, the mandible and the postcranial skeleton (CHAPSKII 1955a, 1971; YABLOKOV and SERGEANT 1963; KHUZIN 1967; ANTONIUK 1972, 1979). Investigations of modern true seals have shown that the locomotor system is not always useful for generic diagnosis (HOWELL 1928, 1930; GADJIEV 1957; BURNS and FAY 1970; TARASOFF 1972; CHAPSKII 1975; ENGLISH 1975; HOWARD 1975). However, in many publications on extinct true seals, no information is given on the structure of the skull and mandible, or only scanty data are presented with some occasional measurements (EICHWALD 1850; VAN BENEDEN 1859, 1871a, b, 1876a, b, 1877; KRETZOI 1941; MACAROVICI 1942; MACAROVICI and OESCU 1942; FRIANT 1944, 1947; KIRPICHNIKOV 1964). Moreover, many species of seals were described based on fragments of the postcranial skeleton that often cannot be classified even to genus (GERVAIS 1848–1852; VAN BENEDEN 1877; ALEKSEEV 1926; FRIANT 1944, 1947). Sometimes when humeri and femora were studied, no taxonomic importance was attached to these bones. Generally accepted measurements of humeri and femora, as well as consistent terminology for their description, were lacking. In this situation comparing the data of various authors is impossible. This has hampered to a considerable extent the study of phocids, at all levels.

Studies of the morphological classification of true seals by various specialists (TROUSSERT, 1904, 1905; SIMPSON, 1945; SCHEFFER, 1958), extending over many decades, culminated in the publications of CHAPSKII (1952-1975). In these studies a system of classification of pinnipeds was formulated, based on the above foundations and reinforced by diagnoses of higher taxa (from family to genus). This system still remains valid almost without change. The work of CHAPSKII (1955a, 1971, 1974), which summarized and systematized the previous studies of seal systematics, had an immense impact on the formation of modern ideas on systematics of true seals and of principles of their classification. Indeed, subsequent studies in this area were continuations of CHAPSKII's investigations (GADJIEV 1957, 1982; KHUZIN 1967; SERGIENKO 1967; BURNS and FAY 1970; KING 1983; ANDREESCU and MURARIU 1985; ANTONIUK 1986; PAVLINOV and ROSSOLIMO 1987; WOZENCRAFT 1989; KORETSKY 1986, 1987a, b; KORETSKY and RAY 1994; KORETSKY and GRIGORESCU [in press], KORETSKY and HOLEC [in press], KORETSKY and RAY [in press]).

These and other, more modern studies provide the basis for my analysis of characters of the skull, mandible and postcranial skeleton for classification of the subfamily Phocinae. Important differences were thereby identified among the fossil genera *Monachopsis*, *Praepusa*, *Monotherium*, *Pontophoca*, *Cryptophoca*, *Leptophoca*, *Prophoca*, and other phocines from the studied region. This has allowed revision of the generic and specific diagnoses, permitted a partial revision of the subfamily Phocinae, and has established the worth of previously used and new characters. The same method has been used in my studies both of Recent representatives of this subfamily and, with some modifications, of fossil material. The main results of this analysis are presented below, as well as an analysis of the structure of the extremities of some species that are of special interest for classification of true seals.

Structure of the skull, of the mandible, of humeri and femora as well as schemes of their measurements are presented in Figures 3–6.

In the classification of the subfamily Phocinae, great importance is usually accorded to skull morphology, to the number of whiskers, to characteristics and coloration of the pelage, and to the form and dimensions of the claws. It is obvious that many of these characters may at best be used only for classification of modern seals. In the analysis of palaeontological material it is hardly possible to use even such features as the number of sacral vertebrae, the number of incisors or the form of the tympanic bulla (for its extremely rare preservation).

Thus, of major importance in the classification of fossil Phocinae are: form of rostral part of skull, of tympanic bulla and of palatal process of maxilla; size ratios among alveoli P4 - M1 and p4 - m1; form and position of the chin prominence; form and dimensions of head of humerus and dimensions of deltoid crest; distance between humeral epicondyles; shape and dimensions of greater trochanter and head of femur (CHAPSKII 1955a; GRIGORESCU 1977; ANTONIUK and KORETSKY 1984).

Incomplete preservation restricts significantly the diagnostic value of the characters mentioned. However, some features of the postcranial skeleton in some cases allow diagnoses of fossil taxa. For example, among phocines, in *Monachopsis* the limb bones are very short, in *Praepusa* they are small and elongated, in *Cryptophoca* they are large and broad; whereas in the monachine *Pontophoca* they are almost "round" distally (see Chapter 5). That these features are found in different combinations in the genera mentioned above is evidence of the fact that both large seals with a monachine type of postcranial skeletal structure and small seals of a phocine type have until now been referred to the genus *Phoca* (EICHWALD 1850; SIMIONESCU 1925; MACAROVICI and OESCU 1942; FRIANT 1947; KING 1964; SAVAGE and RUSSELL 1983).

Characters of the skull of Phocidae were analyzed in detail by OGNEV (1935), DORNESCO and MARCOCI (1958), KONDAKOV (1960), KHUZIN (1967), SHUSTOV and YABLOKOV (1967), BURNS and FAY (1970), MITCHELL and TEDFORD (1973), CHAPSKII (1974), KING (1983), KORETSKY (1988), KORETSKY and HOLEC (in press), who took into account age and sexual differences.

In this section my major purpose is to provide metric and morphological comparisons of the separate bones of the skeleton. The present state of systematics of fossil true seals, however, allows the analysis of only the most frequently occurring elements.

1. Some morphological characters

Cranial region

Main proportions of skull. The relation between lengths of facial and cranial regions of the skull, and at the same time, the degree of shortening of the facial (= rostral) part of the skull to the level of the posterior alveolus of P1 can be used for diagnosis, although this feature is individually and ontogenetically variable.

Form of rostral region and of maxillary bones of the skull. In combination with width of the skull above the canines and with the width of the palate at P1, the form of the profile of the preorbital part of the maxilla, as in terrestrial carnivores, characterizes the strength of the masticatory apparatus (in Phocinae the maxillae are convex and bulging).

Differences in length and in shape of the jugular and postglenoid processes.

Relative dimensions of orbit. Ratio of orbit diameter and width of the rostral part of the skull above the canines is comparatively insensitive to the quality of skull preservation. The large orbital diameter in representatives of some genera of true seals suggests that these predators lived under conditions of reduced illumination, i.e., that they dove deeply.

Form and diameter of external acoustic meatus.

Form of tympanic bulla. Character of swelling of the tympanic bullae, their length and the distance between them.

Relative width of the palatine bone. The most convenient index is the ratio of the length of tooth row P1 - P4 to the width of the palatine. The degree of lateral extension of the palatine bone and the form of its swelling are useful characters.

Depth of retropalatal notch. Location of the retropalatal notch and the shape of the anterior border of the notch in Phocinae show considerable ontogenetic, individual and species variability and have no taxonomic importance.

Structure of the body of the mandible. In phocids, five types of structure of the body of the mandible may be distinguished; they will be presented in more detail in Chapter 4. They differ in degree of concavity of the body of the mandible and of intensity of the chin prominence (= mental tubercle), in the shape and development of the symphyseal part of the mandible (Fig. 22), and in the shape and dimensions of the alveoli and the diastemata between them. Another very important character is the ratio between diameters of alveoli of p4 and m1. All special features mentioned above are adequately represented by the index of the form of the body of the mandible (the ratio of the height of mandible between p3 and p4 to the height under p2).

Location and relative dimensions of teeth. The absolute dimensions of the teeth, just as those of the skull, of the mandible and of the extremities, can be used for diagnosis. In all representatives of the Phocinae the external (lateral) incisors are enlarged to various degrees. However, location and relative dimensions of the other incisors may also be useful characters.

The reduction of basal cingula (= collars) on cheek teeth and, in rare cases, on incisors is one of the characters indicating specialization of predators to feeding on meat (as in terrestrial carnivorans). In fossil Phocinae, basal cingula are better developed than in extant forms. Since objective evaluation of the feature is difficult, this character is almost impossible to use.

Other taxonomic characters are relative dimensions of the diastemata between all teeth and, in particular, the diastemata P3 - P4, p3 - p4, P4 - M1, p4 - m1 and the length of row P1 - M1, p1 - m1. The number of additional cusps and roots on premolars and the ratio of the alveoli P4/M1 and p4/m1 can be used for diagnosis.

Postcranial Skeleton

Use of postcranial characters seems logical, since classification of fossil seals was originally based on morphology of femora and more rarely of humeri. Moreover, these limb bones show considerable sexual and age variability. However, as a rule, in their descriptions of new taxa specialists have not paid much attention to these characters. In seals, four main ecomorphotypes (or ecophenotypes; see SCHOCH 1986:87) of structure of humeri and femora can be distinguished, and they will be considered in detail below.

Structure of humerus. Ratio of the anteroposterior width of the middle part of the trochlear crest to the depth of the coronoid fossa is a useful character.

Taxa of Phocinae may be distinguished by the following: ratio of the heights of the lesser tubercle and the head; the height of the head relative to the proximal part of the deltoid crest; degree and direction of compression of the head; form and length of the deltoid crest relative to absolute length of bone; degree of development of intertubercular groove and of lateral epicondylid crest.

The depth of the coronoid fossa, although there is sexual variability, may be a useful character, as well as the relative dimensions of the capitulum and trochlea of the humerus (Figs. 5–6).

Structure of femur. Ratios of the dimensions of lateral and medial condyles and of distal and proximal epiphyses are useful for diagnosis. The most pronounced and convenient characters are the shape and degree of development of the greater trochanter; the depth and location of the trochanteric fossa; the relative thickness of the neck; and the distance between epicondyles. Relative dimensions of the head and dorsoventral thickness of condyles can also be used (Figs. 5–6).

2. Ontogenetic changes

As was already mentioned, many characters are related significantly to the age of the individuals studied. Considerable attention to problems of age and sexual variability of cranial characters was paid by OGNEV (1935), ASTANIN (1936), HEPTNER (1947), and CHAPSKII (1952). ASTANIN investigated ontogenetic changes in the postcranial skeleton also. My materials confirmed fully the conclusions of these investigators, with insignificant additions. In the present study all analyzed individuals are separated into two age groups, in accordance with the degree of fusion of epiphyses of limb bones and relative sizes of proximal and distal epiphyses, as well as with specific features of skull development:

— “young” individuals – epiphyses of bones are not fused, and difference between distal and proximal epiphyses is not very pronounced;

— “adult” – epiphyses are fused and the distal end of the bone is distended considerably as compared with the proximal end.

In “young” individuals the tympanic bullae are swollen, and the rostral part of the skull is relatively short as compared with those of older animals (Fig. 7).

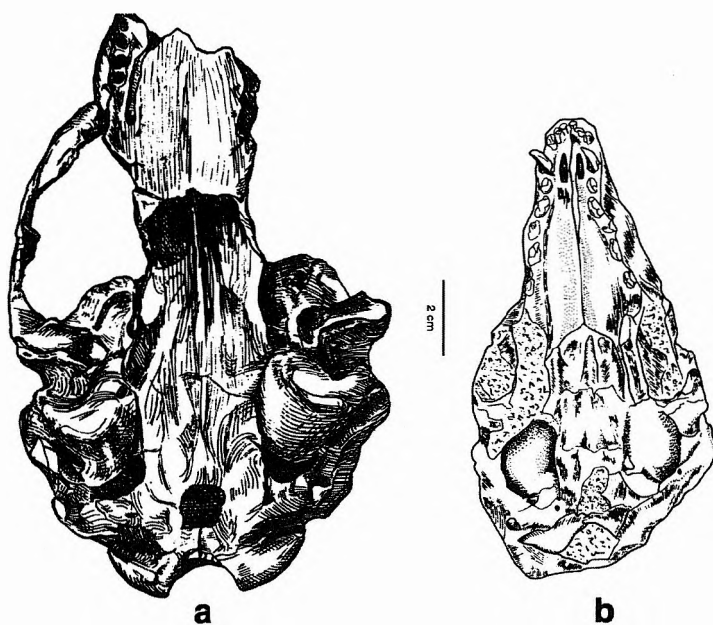


Figure 7. Ontogenetic variation. Skulls of *Praepusa vindobonensis* in occlusal view

a = Adult, IZUAN 64-469, from Tarchankut Peninsula, Crimea, Ukraine. b = Juvenile, IZUAN 64-468, from the same locality. This was illustrated by ANTONIUK and KORETSKY as *Praepusa tarchankutica* (1984, figs. 1–2)

A further characteristic of young individuals is the arrangement of incisors in the form of a half-circle, located at the alveolar margin of the maxilla (Fig. 7, b); in adult animals this is changed generally into a straight row with a bony prominence in front of the incisors. Length of skull increases as a result of growth of its rostral part, and this significantly influences ratios of the length of facial and cerebral parts of the skull in young and adult individuals (Fig. 7). In accordance with the development of the facial part of the skull and with strengthening of musculature in the course of aging, relative increases in zygomatic (= jugal) width occur, as well as increases in width of the rostrum at the level of the upper canines, in width of the palate at P1, in greatest width of the palatine bone, and in many other measurements. Growth of the mandible also occurs in an irregular manner, in particular the depth of the masseteric fossa. The irregular growth of the skull causes a significant increase in dimensions of the ascending ramus of the mandible: the length of the condylar process and the height of the coronoid process. Considerable increase in the length of the tooth row (i1 - m1) occurs, the height and thickness of the body of the mandible under m1 increase, and maximal height of the body of the mandible and the diastema between c and p1 also increase. The length of row p1 - p4 increases insignificantly. The index of the form of the mandibular body (ratio of height between p3 and p4 to height under p2) also changes. However, dimensions of the alveoli of teeth in young and old individuals remain essentially constant.

In bones of the extremities the following ontogenetic changes occur: the lesser tubercle of the humerus is extended along the bone axis, the intertubercular groove and the coronoid fossa assume a more compressed form, and the deltoid crest increases in size. The patellar surface of the femur becomes lower and wider.

Consequently these ontogenetic variations of the skull and of the postcranial skeleton lower considerably the diagnostic value of remains of younger animals. All these ontogenetic changes are very similar to those in terrestrial Carnivora.

Studying these age groups in Recent seals allowed me to confirm the ontogenetic variation in the modern skulls and to note ontogenetic variations in the mandibles and in some parts of the postcranial skeleton. I assume in this study that the same ontogenetic changes occur in the fossil taxa, which are closely related to the modern ones.

These findings allow the conclusion that in true seals and in the majority of terrestrial carnivores, identical ontogenetic transformations of the masticatory system occur - increase of zygomatic width of the skull and of the width of the bony palate. At the same time a reduction of the relative height of the facial part of the skull occurs, as well as increases in the length of the tooth row and of the height and thickness of the mandibular body. The adaptation of true seals for swimming results in greater compactness (shape and flattening) and in widening of the femora during growth. All of this variability makes difficult the redetermination and redescription of materials presented in some publications (ALEKSEEV 1924a, b; SIMIONESCU 1925; KRETZOI 1941; FRIANT 1944, 1947; KIRPICHNIKOV 1964).

3. Sexual dimorphism

In past investigations of true seals, sexual dimorphism was analyzed only among the Recent Phocinae, based mainly on cranial material (CHAPSKII 1952, 1967; KHUZIN 1967). More recently, GADJIEV (1982) has analyzed sexual variability of the sacral bones of the Caspian seal, and VAN BREE and ERDBRINK (1987) briefly described this in a postcranial skeleton of the harbour and grey seals. In fossil Phocinae, only I have studied sexual dimorphism, an understanding of which is necessary to construct a correct classification (KORETSKY 1987a).

Fossil remains of pinnipeds usually consist of isolated limb bones, mainly the humerus and femur. In my study of a series of these bones attributed to *Monachopsis pontica* (KORETSKY 1987a), the following sexual differences were identified (many of the same differences can be observed in modern representatives of the genera *Phoca* and *Pusa*).

Humerus (Figs. 8-9, Table 2). The absolute length of the bone in males of all genera studied is greater than in females, and the head is larger and more spherical, while in females it is com-

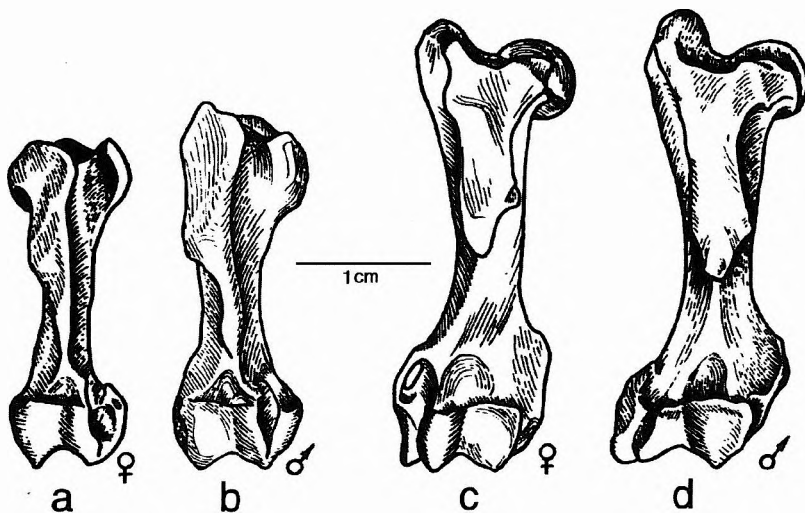


Figure 8. Sexual dimorphism. Humeri, cranial aspect
Monachopsis: a = female, b = male. Pusa: c = female, d = male

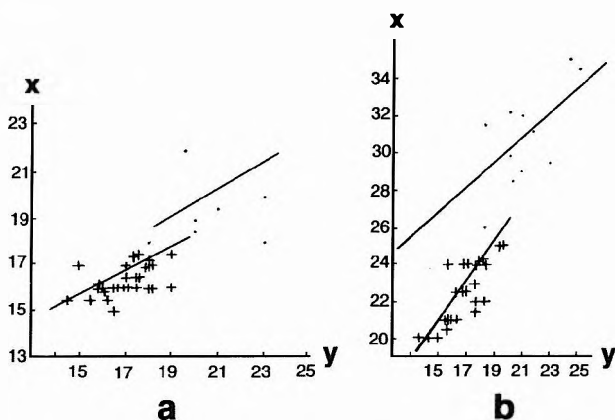


Figure 9. The ratio between the height of the head of the humerus (X) and the width of the head of the humerus (Y)

a = *Monachopsis*, b = *Pusa*, + = females, • = males

pressed in a dorsoventral direction (Table 6). The ratio of the greatest width of the head to the greatest width of the proximal epiphysis in male *M. pontica* is 0.76; in females it is 0.66. The deltoid crest in male *M. pontica* is a little longer than in females. In modern species of *Phoca* and *Pusa*, no sexual differences in structure of the distal part of the deltoid crest were noted.

The fossa located mediiodistal to the head seen in caudal aspect (between the lesser tubercle and the head) is deeper in males. The enormous head of the triceps muscle arises from this fossa on the medial side of the neck of the humerus, and it inserts onto the dorsal part of the olecranon of the ulna (HOWELL 1930; ENGLISH 1975). The action of the triceps medialis muscle is to extend the elbow joint (MILLER 1964).

The heads of the humeri of male *M. pontica* (Table 2) are bent caudally to a lesser degree than bones of females (Figs. 8–9); this is probably also a sexual difference. However, in modern seals this difference is not pronounced.

In females, although the dimensions of the deltoid crest are smaller, the deltoid tuberosity is more developed. Laterodistally from the head of the humerus, behind the deltoid tuberosity, the fossa for the origin of the brachialis muscle is located (HOWELL 1930; PIÉRARD 1971; TARASOFF 1972; ENGLISH 1975; HOWARD 1975). This muscle, judging from the depth of the fossa, is more highly developed in males. In fossils this character is much less pronounced, evidently as a result of wear of the available material. In females the medial epicondyle is compressed in its peripheral (= lateral) part and is not bent in a caudal olecranon of the ulna (HOWELL 1930; ENGLISH 1975). The direction; at the same time, the lateral epicondyle is shorter and narrower than in males. However, the presence or absence of an entepicondylar foramen is an individual variation.

The shape of the coronoid fossa in representatives of *Phoca* and *Pusa* does not depend on sex. Its depth is somewhat greater in females. In *M. pontica*, however, the form of this fossa differs in males and females: in the former it is of sharp triangular form; in the latter it is of rounded-triangular or semi-rounded form (Figs. 8–9).

Femur (Figs. 10–12, Tables 3, 7). The absolute length of this bone in males of modern and fossil genera is greater than in females. However, in females the antero-posterior diameter of the diaphysis is greater than in males (Table 3). In contrast, GRIGORESCU (1977) presumed that the diaphyses of the females of *Monachopsis pontica* and *Cryptophoca maeotica* were more compressed than in males. However, my materials indicate that it is the males who have the more compressed diaphyses (Figs. 11–12, Table 7). Sexual dimorphism in the structure of the diaphysis is associated with various degrees of development of the vastus intermedius and medialis muscles in cranial aspect (see PIÉRARD 1971:73), and of the adductor cranialis muscle (= adductor anticus in HOWELL 1930) in caudal aspect. The action of the vastus intermedius and

Table 2

Means ($\bar{X} \pm SE$) and range for measurements (mm) of number in sample (n) of humeri of *Phoca* and *Monachopsis*

Characters	Phoca				Monachopsis				
	Males		Females		Males		Females		
	n	$\bar{X} \pm SE$	Range	n	$\bar{X} \pm SE$	Range	n	$\bar{X} \pm SE$	
Height of head/Width of head	21	105.9±3.2	87.5–127.5	13	91.5±1.8	80.6–102.1	6	91.0±2.5	80.4–97.7
Width of head/Thickness of proximal epiphysis	21	101.6±1.1	94.0–111.1	13	101.5±1.4	92.3–107.7	7	65.8±1.9	57.1–72.9
Length of deltoid crest/Absolute length	21	54.5±0.5	49.3–57.1	13	59.1±0.6	49.0–55.6	1	–	72.7
Height of trochlea/Width of trochlea, frontal view	19	104.8±3.0	81.1–125.0	13	110.0±2.3	100.0–128.0	2	–	94.4; 105.6
							19	88.3±1.8	77.8–100.0

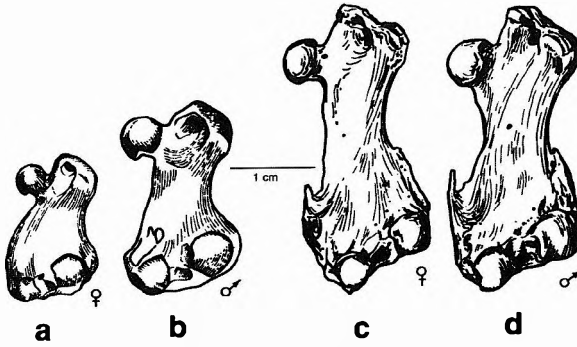


Figure 10. Sexual dimorphism. Femora, caudal aspect
 Monachopsis: a = female, b = male. Pusa: c = female, d = male

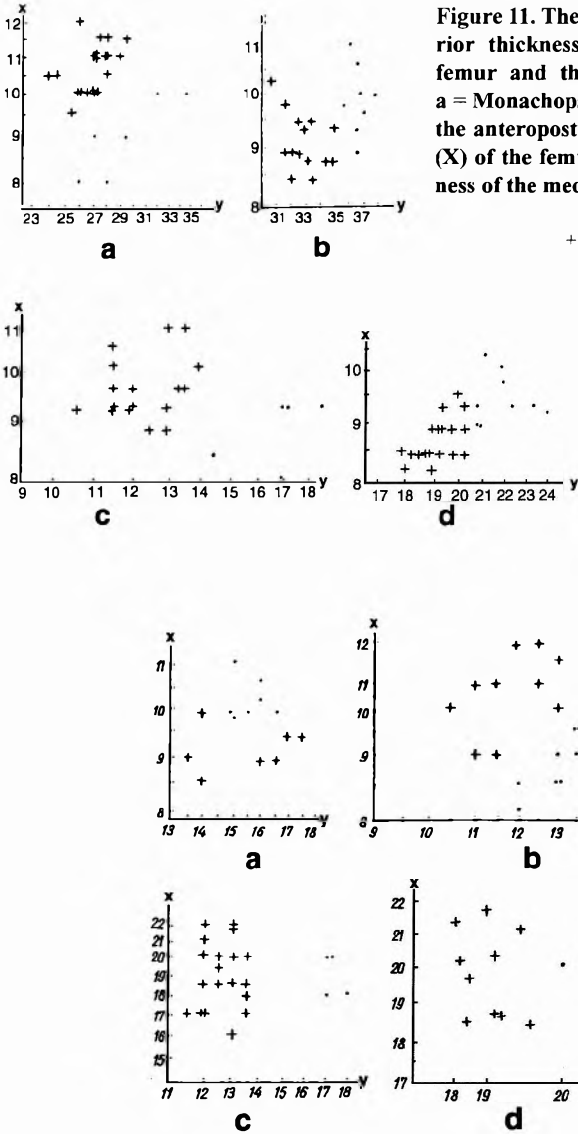


Figure 11. The ratio between the anteroposterior thickness (X) of the diaphysis of the femur and the width of the condyles (Y), a = Monachopsis, b = Pusa. The ratio between the anteroposterior thickness of the diaphysis (X) of the femur to the anteroposterior thickness of the medial condyle (Y), c = Monachopsis, d = Pusa

+ = females, • = males

Figure 12. The ratio between the anteroposterior thickness of the diaphysis (X) of the femur and the height of the head (Y), a = Monachopsis, b = Pusa. The ratio between the width of the diaphysis (X) of the femur and the anteroposterior thickness of the medial condyle (Y), c = Monachopsis, d = Pusa

+ = females, • = males

Table 3

Means ($\bar{X} \pm SE$) and range for measurements (mm) of number in sample (n) of femora of Pusa and Monachopsis

Characters	Pusa				Monachopsis					
	Males		Females		Males		Females			
	n	Range	$\bar{X} \pm SE$	n	Range	$\bar{X} \pm SE$	n	Range		
Anteroposterior thickness of intercondylois depression/Length of lateral condyle	21	68.3–75.7	71.3±1.2	15	65.8–81.3	57.0±2.0	26	50.0–66.7	56.6±1.4	41.9–69.2
Height of articular area of patella surface/Width of distal epiphysis	25	38.5–46.9	40.7±0.8	13	37.0–45.9	42.8±1.2	28	38.1–47.4	40.5±0.5	33.3–47.3
Diameter of neck/Absolute length	25	14.0–18.3	15.6±0.3	15	13.5–17.3	18.0±0.8	9	15.0–19.1	18.0±0.4	15.7–19.5
Width of greater trochanter/Length of greater trochanter	28	51.0–60.0	58.0±1.0	15	54.0–65.2	66.0±1.1	16	58.5–73.7	—	64.7; 75.0
Width of head/Height of head	27	87.5–109.7	99.0±0.8	15	93.8–103.4	98.8±0.7	14	96.2–104.2	—	100.0; 114.3

medialis muscles is to extend the knee via the patella and its patellar tendon. Insertion of these muscles is on the proximal half of the patella. The action of the adductor cranialis muscle (part of the quadriceps muscle of the thigh) is to adduct the femur. This muscle arises from the external surface of the ischium and pubis, and inserts by a tendon onto the posteromedial (caudal) aspect of the femur (HOWARD 1975).

In both Recent and fossil seals, the neck of the femur is shorter and wider in males. The neck forms nearly a right angle with the long axis of the femur in females, but in males the angle is greater than 90 degrees. Males have more compressed diaphyses and the head of the bone is larger, while in females the reverse is true (Figs. 10–12). The average widths of the diaphyses in both sexes are nearly equal, while the distal epiphysis is more developed in males (Figs. 10–12, Tables 2–3). The ratio of the transverse (= dorsoventral) diameter of the proximal epiphysis to the greatest width of the distal epiphysis in females of *M. pontica* ($n = 10$) is 0.89 (0.83–0.97); in males ($n = 5$) it is 1.09 (1.03–1.13).

The greater trochanter is wider and longer in males than in females, except for *Pusa caspica* in which the trochanter's width is the same in both sexes and the measurements of its length are overlapping (Table 3). A similar pattern is observed in *M. pontica*, but the range of overlap in Recent species is somewhat smaller. The distal part of the greater trochanter in females terminates more sharply or acutely (is V-shaped), while in males it is frequently rounded, almost oval.

The gluteus medius and gluteus minimus muscles, insert onto the cranial side of the greater trochanter while the piriformis muscle is attached to the caudal side; all of these are significantly more developed in males (HOWELL 1930; PIÉRARD 1971; HOWARD 1975). Consequently, the trochanter is stronger in males. The action of the gluteal muscles is to abduct, extend, and internally rotate the femur. The action of the piriformis muscle is not just to abduct, but also to extend and laterally rotate the femur. All these muscles originate from the wing of the ilium (HOWARD 1975).

HOWELL (1928, 1930), PIÉRARD (1971), and HOWARD (1975) described the trochanteric fossa as a place of attachment of the obturator internus and externus muscles, which share a common tendon of insertion with the two gemelli muscles, the superior and inferior. The gemelli and obturator externus muscles arise from the lateral border of the obturator foramen and its membrane. The two gemelli join with the obturator internus muscle to form a common tendon for insertion. PIÉRARD (1971) however, concluded that the origin of the tendon of the obturator internus muscle is a shallow groove on the middle third of the pubic border. The action of the obturator externus muscle is to rotate the femur laterally. The actions of the gemelli and obturator internus muscles are to abduct and also rotate the femur externally (PIÉRARD 1971; KORETSKY and SANDERS, in press). In females, compared with males, the obturator externus and gemelli muscles are more developed, and as a result the trochanteric fossa is deeper and more closed.

In females of *Phoca* and *Pusa*, the plantar fossa above the lateral condyle is wider and deeper and is bordered by a very thin edge of bone. This is especially well defined in young and subadult individuals. The plantar fossa itself is the place of origin of the plantaris and lateral head of the gastrocnemius muscles. Contraction of the gastrocnemius muscle causes strong plantar flexion of the foot. The action of the plantaris muscle is to plantarflex the foot and also to flex the digits through the flexor digitorum brevis complex (HOWARD 1975). In males this plantar fossa is weakly outlined and is not bounded on the medial side. However, this sexual differences is not observed in *M. pontica*. All differences mentioned above apply also to fossil bones, although they are not clearly defined in worn specimens (Figs. 9, 11–12).

The diameter of the patellar surface (measured in the long axis) is greater in the males, except in *P. caspica*, where the ranges of diameters in the two sexes overlap. The condyles are also relatively larger in the males.

In general, variations of femur and humerus in the Miocene genus *Monachopsis* coincide with those in modern *Phoca* and *Pusa*.

For determination of sex on humerus and femur, the following characters can be used:

Humerus — overall size; length of deltoid crest and width of its middle part; depth and shape of the coronoid fossa, depth of the fossa located caudal to the medial side of the neck of the humerus, distal to the lesser tubercle.

Femur — overall size; anteroposterior width, or dorsoventral thickness of diaphysis; length and thickness of neck; length and width of greater trochanter; anteroposterior diameter of distal epiphysis.

The most reliable characters for sex determination are: depth of the fossa for the triceps medialis muscle on the humerus and degree of compression of the femoral shaft.

The features noted here are characteristic for adult animals. In young and subadult individuals they are not nearly as pronounced. Despite this, the established differences and variations are fairly (sufficiently) constant, and allow researchers to separate elements of the extremities according to sex.

Chapter 4

Ecomorphotype hypothesis based on predominant types of mandible, humerus, and femur among fossil and recent species of seals

Each Recent species of phocine seal has a specific ecological niche reflected in bones of the postcranial skeleton and mandible. As the most common dissociated elements of fossil phocines are the mandible, humerus and femur, the modern phocines were separated into morphoecological units on the characteristics of these elements. Since remains of fossil seals fall into analogous morphologic groups (which may or may not have been ecologically identical to their Recent analogues), they may be particularly compared with similar groups of modern true seals.

The working hypothesis that fossil phocine seals had natural morphological units similar to those of the Recent species provide a rationale for associating the many dissociated fossil elements. These remains of fossil seals fall into morphologic groups comparable to those among extant phocine seals.

The most important characters on which this classification into ecomorphotypes is based are the following:

— Mandibles: Form of the symphyseal region; location of the chin prominence and the degree of its development; degree of compression and height of the body; presence or absence of diastemata and dimensions of teeth.

— Humeri: Ratios of heights of the head and the lesser tubercle; shape of the lesser tubercle; degree of compression of the intertubercular groove; location of maximal width of the deltoid crest.

— Femora: Ratios of heights of the head and greater trochanter; shape of the greater trochanter; location of the intertrochanteric crest; and overall shape of the bone.

To the first morphological group (Fig. 13) I assign the modern species *Erignathus barbatus*, and conditions of this type are observed in the mandibles of *Praepusa pannonica* from the Middle Sarmatian (Middle Miocene) of Moldavia (Kishinev) (Table 1). The following conditions of the mandible are characteristic for this morphological type: symphyseal part acute; chin prominence pronounced, and bent in a labial direction. The latter prominence extends from the alveolus of p2 to back of the alveolus of p4; maximal height of body of mandible situated between alveoli of p3 and p4 or at anterior end of alveolus p4; alveoli of teeth shallow; diastemata absent or insignificant; p1 with one root.

In humeri: lesser tubercle is enlarged and equal in height to the head or insignificantly higher than the head; intertubercular groove partially shallow; maximal enlargement of deltoid crest is in its middle part.

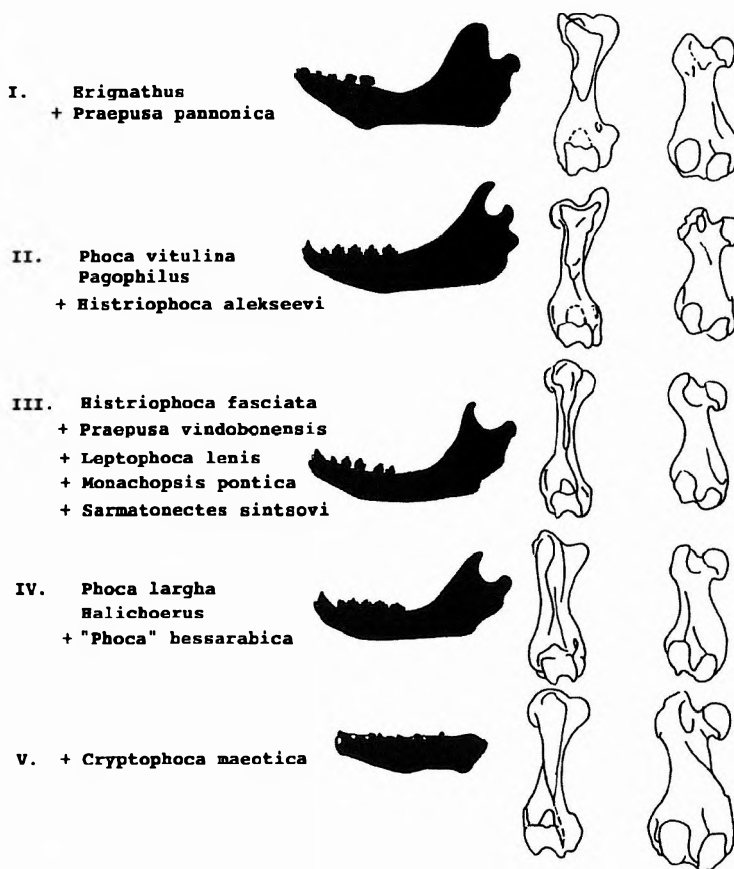


Figure 13. Predominant morphological types of bones of Recent and fossil seals

In femora: greater trochanter strong, slightly higher than the head, and enlarged in its proximal part; intertrochanteric crest well developed and lower than the head.

Ecological characters of the modern members of this group: predominantly bottom feeding on crustaceans (40%), mollusks (12%), and worms (23%) in waters approximately 60 meters deep, but may dive to 100 meters (HEPTNER et al. 1976; RIDGWAY and HARRISON 1981; RIEDMAN 1990).

The second morphological group (Fig. 13) is represented by a series of modern species, including *Pusa* ssp., *Phoca vitulina*, and *Pagophilus groenlandica*. Mandible of this type are observed in the extinct species *Histriophoca alekseevi* from the Middle Sarmatian of Moldavia (Kishinev).

Characteristics of this morphological group are:

In mandible: symphyseal part acute. Chin prominence not pronounced, and bent labially; it is located at a level between anterior alveolus p4 and posterior alveolus m1. Maximal height of body of mandible is in the middle or below the anterior portion of alveolus m1. Alveoli of teeth shallow with small or absent diastemata; p1 may have two united roots.

In humerus: lesser tubercle very much higher than the head, and extended along the bone's axis; intertubercular groove broad and shallow; maximal width of deltoid crest is in its proximal part.

In femur: height of greater trochanter exceeds considerably that of head; its proximal part is broader than the distal part. Trochanteric crest weakly developed; it has the form of a fold, and ends on the same level as the head.

Ecological characters of the Recent members of this group: Representatives of *Pusa* and *Phoca* are mostly piscivorous and to a lesser degree feed on crustaceans (BIGG 1981; RONALD and HEALEY 1981; RIEDMAN 1990). They prey on animals living in dense masses and in upper layers of the water, although they may dive to nearly 90 meters (HEPTNER et al. 1976). In one species of the modern genus *Pagophilus* the feeding habits vary by season. In summer they feed on zooplankton, in autumn and in winter on fish. They can dive to depths of 150-200 meters (HEPTNER et al. 1976; BIGG 1981; RONALD and HEALEY 1981; RIEDMAN 1990).

To the third morphological group (Fig. 13) belongs the modern species *Histriophoca fasciata*: this also seems to have been true for representatives of the extinct taxa *Leptophoca*, *Sarmatonectes*, *Praepusa vindobonensis* and *Monachopsis*. This group differs little in structure from the previous one, though it has the following distinctive characteristics in the mandible: symphyseal part acute and weakly pronounced; chin prominence weakly outlined and not bent labially, and located beneath posterior alveoli p2 and p4; maximal height of body of mandible located below the p3 and p4; alveoli of teeth shallow, without diastemata, sometimes with united roots.

In humerus: lesser tubercle slightly higher than the head, and extended along the bone's axis; intertubercular groove not pronounced but instead narrowed; maximal width of the deltoid crest is in its middle part or more rarely in its proximal part.

In femur: greater trochanter slightly higher than the head; its proximal part is beveled; intertrochanteric crest shortened, and lowered on the bony diaphysis a little below trochanteric fossa.

Ecological characters: representatives of the modern genus *Histriophoca* feed near and on the bottom on invertebrates (crabs, shrimp, mollusks, amphipods) and to a lesser extent on fish. The depth in their habitats reaches 50–100 meters and more (HEPTNER et al. 1976; RIDGWAY and HARRISON 1981; RIEDMAN 1990).

To the fourth morphological group (Fig. 13) are assigned the modern species *Phoca largha* and *Halichoerus grypus*. Similar morphology are observed in mandibles from the Middle Sarmatian of Moldavia and in the limb bones of the extinct species "*Phoca?*" *bessarabica* from the Middle Sarmatian (Middle Miocene) of Moldavia (Kishinev) (Table 1). The bones of of this group have highly distinctive form: the limb bones are short and wide, having a bulbous appearance, while the mandibles are nearly "round" in cross section.

Characters of mandible: symphyseal part bluntly rounded: chin prominence absent or weakly outlined; maximal height of body of mandible usually under p4; alveoli of teeth rounded, large, with equal diastemata between them; p1 single- or double-rooted, p2 single-rooted, m1 single- or double-rooted; m2 may also be single-rooted.

In humerus: lesser tubercle considerably higher than the head and of rounded form; intertubercular groove small, not deep; maximal width of deltoid crest not pronounced along its entire length (i.e., deltoid crest of approximately uniform width along its length).

In femur: greater trochanter much higher than the head and with widened proximal part; intertrochanteric crest reaches the head and is oriented transverse to the bone's axis.

Ecological characters of modern members of this group include feeding mostly on large pelagic fishes (75–82%), crustaceans (11–13%), and to a lesser degree on mollusks (7–12%). They feed in shallow and in deep waters, and dive to 150-300 meters (HEPTNER et al. 1976; BIGG 1981; RIEDMAN 1990).

A fifth morphological group (Fig. 13), not known among extant seals, is represented by the fossil species *Cryptophoca maeotica* from the Middle Sarmatian of the northern Black Sea region (Moldavia, Ukraine), and by a series of mandibles from the Middle Sarmatian of Moldavia (Kishinev) (Table 1).

Since are no Recent species with this skeletal morphotype, I characterize this group here, as follows:

Mandible: Symphyseal part straight, considerably thickened; chin prominence weak, without a labial bend, located below the interval from anterior alveolus of p3 to posterior alveolus of p4; maximal height of mandible located below alveoli p3 - p4; alveoli small with large diastemata; p1 single-rooted, with small alveolus.

Humerus: Lesser tubercle oval and equal in size to head or insignificantly higher than it; intertubercular groove not pronounced; maximal width of deltoid crest in proximal part.

Femur: Greater trochanter much higher than head, and nearly rectangular in cross-section; intertrochanteric crest below trochanteric fossa and located on middle axis of bone.

Available material shows that, in the size and character of mandible and limb bones, the genus *Cryptophoca* has some similarity with *Pagophilus*, but not enough to put them together in one group.

Prophoca proxima from the Middle Miocene (Anversian) of Belgium possesses similar osteological characteristics of the extremities. For this reason it may also be assigned to this morphological group.

There is information on the form and structure of the teeth of *Cryptophoca*. Consequently, it is difficult to postulated ecological characteristics of this group. It can only be assumed that these animals were fast-moving.

My findings suggest that these morphotypes include both Recent and fossil phocines. The proposed association of fossil seal bones in these groups, based on the classic comparative-anatomical principle of "correlation of parts", helps to determine the correct assignment of limb bones and mandibles to individual taxa. Previous classification of fossil true seals was based on disassociated bones, such as humerus and femur, and in rare cases, on the mandible, whereas the classification of modern seals is based on skull morphology and soft anatomy. The recognition of morphotypes among Recent phocines allows the association of the limb bones with each other and with mandibles in fossil material. Only after this association is made it possible to delimit species and start resolving the problems of nomenclature. Although the resulting taxonomic associations of fossil seal bones are hypothetical, they help in defining individual taxa, and in making referrals of isolated elements, which would otherwise, in many cases, have no objective basis. Thus, I propose that recognition of morphotypes not only provides a foundation for future paleoecological reconstructions, but also allows (in the present work) an indirect solution to the otherwise intractable problems of alpha systematics and classification of fossil Phocinae.

However, it must be stressed that at the present time there is not an adequate basis for interpreting ecological traits from the morphological characters of these morphotypic categories; the studies of functional anatomy necessary to link morphology with ecology have simply not been done. Therefore, in the remainder of this work, these categories are referred to simply as "morphotypes". The fact that ecological differences are observed among the Recent exemplars of these morphotypes is suggestive of possible ecological resemblances with the fossil forms; but it would be premature to uncritically apply the ecological traits listed above directly to the fossil taxa assigned to the same morphotypes. That potential application remains to be worked out in detail in future studies.

Ecomorphotypes are not so readily recognizable in the other subfamilies, Monachinae and Cystophorinae. They show a mixture of the characters described above, and do not fit any of these groups. I hypothesize that this is due to a lack of sympatric competition among the members of these subfamilies, whereas some species of phocines are geographically sympatric and are specialized to exploit different food resources based primarily on water depth.

The biomechanical and ecological significance of the traits defining each group remain to be elucidated by future research, which will thereby provide tests of this set of hypotheses. Direct tests of my hypothesized taxonomic associations of bones will, of course, come when associated skeleton are discovered. Such association are already verified by a recently found associated parts in *Leptophoca lenis* now in the collection of the NMNH.

List of fossil taxa, which I used ecomorphotype hypothesis to define

Monachopsis pontica

Praepusa pannonica

Praepusa vindobonensis

Cryptophoca maeotica

Sarmatonectes sintsovi

Leptophoca lenis

Chapter 5 Systematics

This chapter is devoted to systematic relationships in the subfamily Phocinae. Only a comparatively small subset of this taxon is considered.

Until recently, no definite criteria for classification of this subfamily into tribes, genera or even species had been proposed. For example, the species *Pusa sibirica*, which was always assigned to the genus *Phoca*, according to morphologic characteristics of the mandible, teeth and postcranial skeleton, is in fact distinct from the genus *Phoca*. The question still remains open of classification of representatives of "*Monotherium*" *maeutica*. Do they belong to Phocinae or to Monachinae? Many other classification problems need clarification. The considerable importance of the postcranial skeleton for classification of fossil pinnipeds is beyond doubt. However, it cannot be analyzed without taking into account the morphology of the skull and the mandible. Such an approach is especially necessary and timely now that the systematics of the fossil forms has been well grounded on extensive factual material. This allows one to make comparisons with the systematics of Recent groups. On the basis of such a systematic revision, some phylogenetic conclusions can be drawn (see Chapter 8).

Four subfamilies of phocids are recognized here: Devinophocinae KORETSKY et HOLEC (in press); Phocinae GRAY, 1821; Monachinae GRAY, 1869; Cystophorinae GRAY, 1866.

Comparison of families of true seals with eared seals and with walruses is beyond the scope of this investigation. Moreover, the materials that I am analyzing do not allow full comparison of these taxa. Those features of the skull, mandible and postcranial skeleton that formed the basis of classification of the Phocidae into ten-incisor, eight-incisor and six-incisor seals (HEPTNER et al. 1976) were established on modern representatives of the subfamilies and consequently may not always be useful for diagnosis of extinct species. This is due mainly to the existence in the fossil record of intermediate forms, but even some modern species cannot be assigned to subfamilies on diagnostic criteria such as those given above for the Phocinae.

Some investigators (SIMPSON 1945; GRASSÉ 1955) differentiate in the subfamily Monachinae another subfamily — Lobodontinae. I use the generally accepted system, in which separation into subfamilies is based on number of incisors and on similar morphology of the skull (TROUESSART 1905; SCHEFFER 1958; ANDERSON and JONES 1967; CHAPSKII 1974; MUIZON 1982). Determination of the taxonomic boundaries of the subfamilies Devinophocinae, Phocinae, Monachinae and Cystophorinae is beyond the scope of this investigation.

ORDER CARNIVORA BOWDICH, 1821 SUPERFAMILY PHOCOIDEA SMIRNOV, 1908 FAMILY PHOCIDAE GRAY, 1825

Type genus: *Phoca* LINNAEUS, 1758; Early Pliocene to Recent of Eurasia, North Pacific and North Atlantic.

Included genera: Apart from the type genus *Phoca* L. 1758, the subfamily includes: *Pusa* SCOPOLI, 1777; *Histiophoca* GILL, 1873; *Pagophilus* GRAY, 1844; *Halichoerus* NILSSON, 1820; *Erignathus* GILL, 1866; *Platyphoca* VAN BENEDEN, 1877; *Phocanella* VAN BENEDEN, 1877; *Cryptophoca* KORETSKY and RAY, 1994; *Praepusa* KRETZOI, 1941; *Monachopsis* KRETZOI, 1941; *Prophoca* VAN BENEDEN, 1877; *Leptophoca* TRUE, 1906.

Emended diagnosis: "Pinnipeds" of small and medium size (1.0–2.5 meters) to large size (6.5 meters). Tympanic bulla relatively large, with well-developed bony auditory canal. Mastoid process relatively small, not united with paroccipital process and not directed downward. Nasal bones end posteriorly in one common, wedge-like termination, protruding between anterior parts of frontal bones. Zygomatic bones without a pronounced anterior-interior process.

Most cheek teeth in maxilla and mandible have two roots and divided crown. Tooth formula I3-2/2-1, C1/1, P4/4, M1/1-2, according to HEPTNER (1976).

Proximal part of deltoid crest (greater tubercle of the humerus) relatively weakly developed, lesser tubercle pronounced.

Lesser trochanter of femur absent or weakly developed.

Distribution: Late-Early Miocene to Recent of Europe, Asia and America (North Atlantic, North Pacific, and Arctic Ocean); Late Pliocene to Recent of Africa; Recent, waters of Antarctic.

Subfamily Phocinae GRAY, 1821

Type genus: *Phoca* LINNAEUS, 1758; Late-Early Miocene to Recent, Pacific (Asia, America) and North Atlantic (America, Europe).

Diagnosis: Seals of small and medium size. Ten incisors (I3/2). Mastoid very pronounced, narrow, cylindrical. Its width is not greater than half the length of the tympanic bulla and it is, as a rule, bulla directed sharply downward behind the mastoid process. Maxilla immediately swollen in front of orbit; its lateral contour is convex. Anterior palatal foramen well-developed, with a more or less pronounced groove-like shape, according to CHAPSKII (1974).

Chin prominence usually present (except in *Halichoerus*); symphyseal part of mandible reaches anterior or posterior alveolus p2.

Middle part of crest of humeral trochlea located on a level with the coronal fossa, and concave.

Medial and lateral condyles of femur of different dimensions; distal and proximal epiphyses of nearly the same width; intertrochanteric crest usually absent or very weakly developed.

Content of subfamily: The subfamily includes the tribes and subtribes: tribe Phocini CHAPSKII, 1955, which has been divided into the subtribes: Phocina and Histriophocina; tribe Erignathini CHAPSKII, 1955.

Comparison: The body size of ten-incisored seals is much smaller than that of representatives of the other two living subfamilies. However, some genera (*Erignathus*, *Halichoerus*) are near to Monachinae and Cystophorinae in dimensions of the skull, of the mandible and of the postcranial skeleton. A characteristic of Phocinae is narrowing of the space between the orbits. Some increase of this space is characteristic of *Erignathus* and *Halichoerus*. The anterior orbital processes are weakly outlined. The part of the skull in front of the orbits is convex and wide, in contrast to Cystophorinae; the auditory canal and the retroglenoid process are widely separated. Auditory bullae are triangular, and relatively less swollen. In all Phocinae there is a bolsterlike convexity of the posterior mastoid, and the mastoid process is bent downwards; palatal fossa is well developed. The principal characters by which Phocinae differ from other taxa of the Phocidae are differences in number of incisors (10, 8 and 6 in the Phocinae, Monachinae, and Cystophorinae, respectively).

The differences in structure of the mandible, humerus and femur are not numerous and not very pronounced. The principal taxonomic characters are expressed in the diagnosis of the subfamily.

Discussion: Many of the characteristics presented are described in detail by CHAPSKII (1955, 1967, 1975). It is impossible to determine the state of many of these characters on most fossil materials in view of their fragmentary nature. It is also difficult to determine these character states and to make appropriate taxonomic determinations on the basis of most published descriptions and illustrations.

Distribution: Late-Early Miocene – Recent, in Eurasia and North America (North Pacific, North Atlantic).

Genus *Phoca* LINNAEUS, 1758

Phoca: LINNAEUS, 1758:37.; PALLAS, 1811:113.; SCHEFFER, 1958:8.
Pusa: SCOPOLI, 1777:490.; TROUSSERT, 1904:288.

Type species: *Phoca vitulina* LINNAEUS, 1758; Recent; amphiboreal, in temperate and subarctic latitudes of North Atlantic and Pacific Oceans.

Included species: According to CHAPSKII (1967, on skull morphology), ROBINETTE and STAINS (1970, on calcanea), PERRY et al. (1995, on mitochondrial DNA sequences), BININDA-EMONDS and RUSSELL (1996, on phylogenetic analysis), two species are recognized: *Phoca vitulina* L., 1758 (Recent, Atlantic waters of Europe, Canada, USA, and Greenland and American Pacific coast) and *Phoca largha* PALLAS, 1811 (Recent, eastern part of Sea of Japan, Okhotsk Sea, Bering Sea, and areas of the Chukchi Sea).

Emended diagnosis: Condylbasal length of adult skull exceeds 200 mm. Interorbital width twice the diameter of infraorbital foramen. Longitudinal diameter of alveolus of maxillary canine 1.5–2.0 times more than maximal width of

infraorbital foramen. Total width of nasal bones (at level of frontal-maxillary suture) not less than 20.0% of total length of skull. Length of tympanic bulla less than distance between them. Foramen ovale not covered by tympanic bulla. Teeth with 3–4 cusps, these additional cusps weakly developed.

Symphyseal part of mandible blunt and rounded; alveolar part massive and swollen. Chin prominence weakly pronounced, extending from anterior alveolus p3 to posterior alveolus p4. Tooth alveoli rounded, with equal diastemata between them.

Deltoid crest of humerus longer than half-length of bone, its maximal width located at proximal end. Lesser tubercle considerably higher than head and proximal part of deltoid crest. Index of head's height (ratio of the head's width to its height) = 0.83. Lateral supracondylar crest strongly developed, reaching level of distal end of deltoid crest.

Greater trochanter of femur considerably higher than head, its proximal end slightly wider than distal. Trochanteric fossa open medially, not deep. Head of femur not bent in distal direction, and attached to short, wide neck. Maximal distance between epicondyles 50.0–54.0% of the bone's length.

Comparison: In characters of the mandible and postcranial skeleton, *Phoca* differs from other genera of true seals as follows: shortened vomer (except *Pusa*, *Halichoerus*, *Erignathus*, *Monachopsis*); blunt and rounded form of symphyseal part of the mandible (except *Halichoerus* and *Praepusa*); massive and swollen body of the mandible (except *Halichoerus*). Shortened deltoid crest of humerus (except *Pusa* and *Erignathus*); absence of dorsal eversion of deltoid crest of the humerus (except *Pusa*, *Praepusa*, *Erignathus*) and enlargement of its proximal end (except *Praepusa*, *Halichoerus*, *Cryptophoca*, *Monachopsis*); lesser tubercle extended along the length of the bone, its height greatly exceeding the head (except *Pusa*, *Histiophoca*, *Pagophilus*); absence of a well-developed intertrochanteric crest of the humerus (except *Pusa* and *Halichoerus*); relatively narrow humeral neck (except *Pusa*, *Pagophilus*, *Praepusa*, *Monachopsis*). *Phoca* differs from most genera (except *Halichoerus*, *Erignathus* and all fossil genera) in the shape of the humeral head (dorsoventrally compressed). Apart from the foregoing characters, this genus differs:

From *Pusa* by: prolonged condylobasal length of skull and larger size of the bones of the postcranial skeleton; broadened interorbital area; considerably larger diameter of alveolus of maxillary canine as compared with maximal width of infraorbital foramen; greater width of nasal bones on the level of the frontal-maxillary suture; relatively smaller distance between tympanic bullae. Longer deltoid crest of the humerus; larger lateral supracondylar crest. Shallow trochanteric fossa of the femur; relatively bigger femoral head; and relatively greater intertrochanteric width.

From *Halichoerus* by: considerably smaller size; shortened and not raised facial part of the skull; narrowed interorbital area; enlarged infraorbital foramen, dorsally visible; double-rooted teeth; absence of significant diastema between P4 and M1; different shape of the tympanic bulla. Sharp symphyseal part of the mandible; compacted body of the mandible with presence of weakly developed chin prominence. Narrower deltoid crest of the humerus; shallow spiral and wider intertubercular grooves. Shallow trochanteric fossa of the femur, reaching the middle of the trochanter; and different shape of the trochanter.

From *Erignathus* by: transversely compressed alveoli of the upper incisors; absence of S-formed curvature of the line of the alveoli of upper teeth; markedly narrower interorbital space; smaller oval fossa (which is located in suture between the squamosal and basisphenoid bones); presence of a prominent inframeatal lip forming the ventral margin of the external auditory meatus; infraorbital fossa compressed dorsoventrally, its width being less than the longitudinal diameter of the upper canine; absence of pronounced chin prominence; swelling of alveolar border. Presence of the intertubercular groove of the humerus. Narrower proximal epiphysis of the femur; rounded femoral head; and relatively smaller femoral condyles.

From *Pagophilus* by: presence of a deep angular incision on the posterior border of the palatine; the length of the crowns of maxillary premolars exceeding their width. More anterior location of chin prominence of the mandible. Relatively wider distal end of the greater trochanter of the femur; shallow trochanteric fossa, reaching the middle of the greater trochanter; smaller intercondylar distance; and narrower distal epiphysis.

From *Histiophoca* by: larger size; prolonged facial part of the skull; presence of a deep angular incision on posterior border of the palatine; unequal ratio of the width of the infraorbital foramen and the longitudinal diameter of the alveolus of the maxillary canine; foramen ovale not covered by tympanic bulla; presence of additional cusps on the posterior cheek-teeth. Reduced distance between condyloid and coronoid processes of the mandible; less pronounced chin prominence. Relatively smaller medial supracondylar crest of the humerus. Medially open trochanteric fossa of the femur; relatively larger condyles, with wider intercondylar width; and different shape of the femur.

From *Monachopsis* by: considerably larger size; lesser swelling of the palatal process of the maxilla; absence of diastemata between the teeth. Relatively larger medial supracondylar crest of the humerus. Proximal extension of the trochanter of the femur; femoral head not bent distally; relatively wider femoral neck; absence of plantar fossa; and lesser width of diaphysis located at the middle of the bone.

From *Praepusa* by: considerably larger size; absence of a well-developed jugular process; presence of connecting the mastoid and zygomatic processes of the squamosal. Swollen alveolar part of the mandible; p1 and m1 with mul-

tiple cusps; equal size of alveoli p4/P4 and m1/M1. Presence of intertubercular groove of the humerus. Distended proximal end of the femoral trochanter; short femoral neck; and relatively thin femoral supracondylar crest.

From *Cryptophoca* by: greater height of the body of the mandible under p2; double-rooted p1; equal size of alveoli p4 and m1. Presence of intertubercular groove of the humerus; better developed medial supracondylar crest of the humerus. Relatively larger greater trochanter of the femur; larger femoral condyles and intercondylar width; and different shape of the femur.

Distribution: Recent, in the arctic and subarctic Atlantic and northern and northeastern parts of the Pacific.

Genus *Histriophoca* GILL, 1873

Phoca: ZIMMERMAN, 1783:277.; RIDGWAY and HARRISON, 1981:89–109.

Histriophoca: GILL, 1873:178–179.; SCHEFFER, 1958:102.; CHAPSKII, 1955a:170., 190.; 1961:142.; 1974:150.; KING, 1964:3–4., 64–66.; BININDA-EMONDS and RUSSELL, 1996:8., 12., 74–75., 172–173.

Phoca (*Histriophoca*): HEPTNER et al., 1976:328–340.; PAVLINOV and ROSSOLIMO, 1987:82.

Type species: *Histriophoca fasciata* (ZIMMERMANN, 1783); Recent, Kuril Islands (North Pacific).

Included species: *Phoca fasciata* ZIMMERMANN, 1783; Recent, Kuril Islands. *Histriophoca alekseevi* KORETSKY, sp. nov., Middle Sarmatian of Moldavia.

Emended diagnosis: Condylbasal length of adult skull 190.7–191.7 mm. Vomer does not reach posterior border of palate. Length of nasal opening $\frac{1}{3}$ less than width of palatal bone. Intermaxillaries considerably shortened. Length of facial part of skull $\frac{1}{2}$ of length of cerebral part. Longitudinal diameter of alveolus of maxillary canine less than maximal width of infraorbital foramen. Symphyseal part of mandible oblique; chin prominence present, very weak; body of mandible compressed, not high. Femur and humerus are known only in *Histriophoca fasciata*.

Deltoid crest shorter than half length of humerus and expanded in the middle. Lesser tubercle slightly higher than head; ratio of the head to its height 0.86–0.94. Supracondylar crest weakly developed.

Greater trochanter of femur slightly higher than head. Proximal part of greater trochanter wider than distal part. Trochanteric fossa elongated along bone's axis and reaches middle of greater trochanter. Intercondylar width 13.0–14.5% of bone's length.

Comparison: *Histriophoca* differs from all other known seals in the following features: shortened facial part of the skull and premaxillae; shape and size of the swelling of the palatal process of the maxilla; almost equal diameters of the infraorbital foramen and of alveolus of the maxillary canine (except genus *Pusa*). Thinness of the alveolar border of the mandible; oblique symphyseal part of the mandible. Considerably smaller body size (except in comparison with *Phoca*, *Pusa*, *Monachopsis*, and *Praepusa*). Lower placement of the lesser tubercle of the humerus relative to the head (except *Pusa*, *Erignathus*, *Halichoerus*, and *Sarmatonectes*); more compressed humeral head (except *Pusa*, *Erignathus*, and *Cryptophoca*); relatively shortened deltoid crest (except *Pusa*, *Erignathus*, and *Pagophilus*), absence of expansion on its proximal border (except *Pagophilus*, *Monachopsis*, *Praepusa*), and eversion of the crest in the sagittal plane. Small, narrowly seated condyles of the femur; relatively shortened and thick femoral neck (except *Monachopsis*, *Halichoerus*, *Phoca*, and *Sarmatonectes*). Moreover, this genus differs as follows:

From *Phoca* by: smaller ratio between the separation of the auditory bullae and their length. Compacted body of the mandible; shorter condyloid process of the mandible. Medially covered femoral trochanteric fossa.

From *Pusa* by: the width of the orbit greatly exceeding the width of palatine; considerably more developed jugular processes. More anterior location of chin prominence of the mandible; lesser depth of the masseteric fossa; greater length and width of the condyloid process. Swollen medial epicondyles of the humerus; absence of spiral groove on the humerus. Larger swelling of the intertrochanteric crest and wide femoral epicondyles; relatively larger femoral head.

From *Erignathus* by: compacted alveoli of upper incisors; absence of S-formed curvature of the line of upper premolars, with buccal side of the alveolar border not forming a sharp ridge. Weakly pronounced chin prominence of the mandible, not bent labially; shortened symphyseal part; lower height of the mandibular ramus. Less compressed head of the humerus; weaker development of the lateral condyle. Trochanteric fossa covered from medial side; oblique proximal border of greater trochanter; weaker development of femoral intertrochanteric crest; more concave medial border of the femur.

From *Halichoerus* by: relatively lower height of the facial part of the skull; visibility of infraorbital foramen in dorsal view; double-rooted teeth (except p1, P1); compact mandible with chin prominence; straight toothrow; length of tooth crown exceeding its height. Wide and flat intertubercular groove of the humerus; weaker distension of supracondylar crest. Stronger development of femoral intertrochanteric crest; small trochanteric fossa, reaching the middle of the trochanter; relatively weak development of trochanter; shorter and thicker epicondyles; strongly concave medial border of the femur.

From *Pagophilus* by: shortened vomer not reaching the posterior border of the palatine; length of tooth crown exceeding its height; weaker development of jugular processes; absence of additional cusps on teeth. Lesser height and thickness of the mandible. Narrower distal epiphysis of the humerus. Displacement of the trochanteric fossa towards the distal border of the femur; narrower and longer intertrochanteric crest.

From *Monachopsis* by: considerably greater size; double-rooted p4, P4 and m1, M1; flatter palatal process of the maxilla. Higher location of the head relative to the lesser tubercle of the humerus. Expanded proximal part of greater trochanter of the femur; elongation of trochanteric fossa along the bone's axis; different shape of the femur (Figure 10); relatively smaller intercondylar width.

From *Praepusa* by: considerably greater size; less development of the jugular processes, which are adjacent to mastoids; more inflated auditory bullae; double-rooted m1/M1 and single-cusped teeth; presence of crests connecting the zygomatic processes of the squamosal and the mastoids; straight tooth row. Wider distal epiphysis of the humerus. Expanded proximal part of femoral trochanter; concave medial border of femur.

From *Cryptophoca* by: relatively shorter tooth row. Expanded proximal part of femoral greater trochanter; location of smallest width of diaphysis in the middle of the femur.

Distribution: Miocene–Recent in North Pacific, northern Black Sea littoral (Moldavia).

Histriophoca alekseevi KORETSKY, new sp.

Figure 14; Tables 4–5

Phoca pontica: ALEKSEEV, 1924a:26–33., figs. 1–3 (not *Phoca pontica* EICHWALD, 1850.); MCLAREN, 1960:47–65., fig. 3a.; KIRPICHNIKOV, 1961:25–40.

Holotype: Facial part of the skull; ALEKSEEV, 1924a:26–33, fig. 1, 2. *Phoca pontica*; IZUAN, collection 40–121.; Kishinev, Middle Sarmatian.

Etymology: “alekseevi”, in honor of Dr. A. K. ALEKSEEV for his contribution to the study of this material.

Referred material: Vicinity of city of Kishinev (Moldavia); Sarmatian limestone, collection of OGUM: incomplete body of mandible with p4 and m1 evidently from the same individual as the holotype, found in the same location (ALEKSEEV, 1924a) (Fig. 14).

Diagnosis: Alveoli of second and third upper incisors of equal length; alveolus of first incisor is half as wide as and shorter than either external alveolus; distance from posterior palatal fossa to lateral notch of palatine is 3mm; palatal process of maxilla swollen; diastemata between all teeth large and similar in size; length of alveolus M1/m1 larger than that of P4/p4; shallow chin prominence of mandible located under m1.

Description: Judging from the rostral part of the skull (Fig. 14, Table 4) and the mandible, this species is close in size to the modern *Histriophoca fasciata*. The right maxilla is broken away. The dental formula is the same as in other phocines. On the dorsal side of the premaxilla are located two well-developed little spurs, which are elongated antero-laterally. Dorsally the premaxilla forms a broad, flat platform, whose maximal width over the canines is 25 mm. The nasal aperture is round. The preorbital parts of the maxilla, between the nasal aperture and the orbits, are long and convex, the same shape as in the other Phocinae. The premaxillae bordering the nasal aperture ascend vertically toward the nasal bones. The ascending part of the nasal process of the premaxillae end at the level of the anterior edge of the alveolus of P1.

The palatal process of the maxilla is slightly swollen. The shallow palatal groove is pronounced along its total length and connects the anterior and

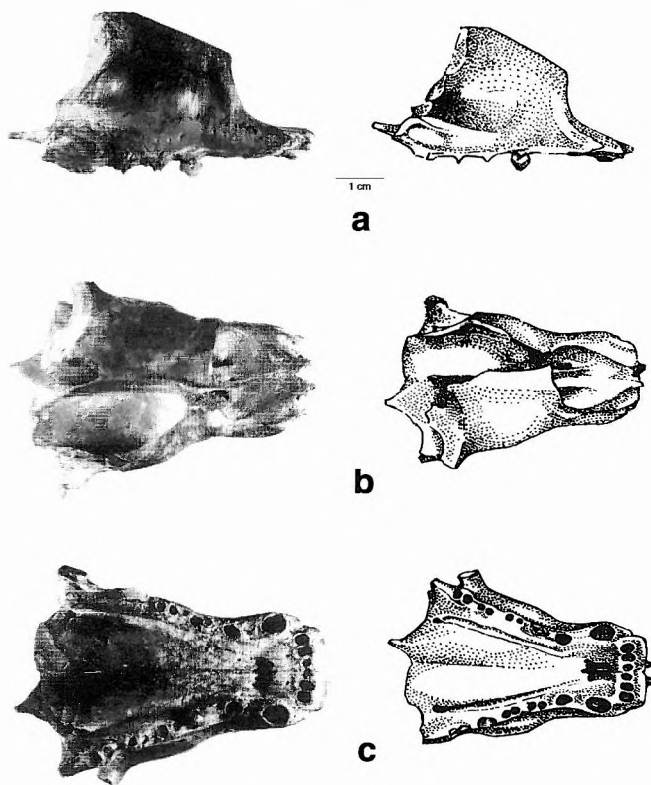


Figure 14. *Histriophoca alekseevi*, new species, rostral part of skull, holotype #IZUAN 40-121

a = skull and its drawing in lateral view, b = skull and its drawing in occlusal view, c = skull and its drawing in dorsal view

Cranial measurements (in mm) in the skulls

Characters	<i>Devinophoca claytoni</i>	<i>Histriophoca</i>		<i>Praepusa vindobonensis</i>		<i>Leptophoca lenis</i>
		<i>fasciata</i>	<i>alekseevi</i>	juv.	ad.	
1. Total length	119.9	184.0–185.0	–	116.0	–	220.0
2. Condylobasal length	119.3	183.0–184.0	–	127.0	–	208.0
3. Length of processus palatinus	71.0	51.0–69.0	55.5	65.0	–	83.0
4. Length of rostral part, measured from antero-upper corner of orbit	49.0	66.0	52.0	47.0	–	63.7; 69.0
5. Length of braincase, measured from anterior corner of orbit	93.5	139.5	–	83.0	110.0	84.0
6. Length of bulla tympanica	38.5	41.5	–	23.0	28.0	29.0; 35.0
7. Length of tooth-row, P1 to M1	49.0 (L), 53.2 (R)	40.0; 40.0	35.0	34.0	–	60.0
8. Length of tooth-row, P2 to P4	32.5 (L), 34.5 (R)	23.0	20.5	20.5	–	38.0; 40.0
9. Maximum diameter of infraorbital foramen	7.5 (L), 11.2 (R)	–	–	–	–	11.0; 9.0
10. Length of temporal fossa	61.5	65.5	–	38.5	49.0	63.6; 68.0
11. Width of rostrum across canines	40.0	27.0; 27.0	24.5	19.5	–	33.0–36.0; 47.0
12. Maximal infraorbital width	25.5	–	–	–	–	16.0–22.0
13. Minimal infraorbital width	14.0	17.0	–	5.5	6.5	12.7; 15.0
14. Width of skull across of processus zygomaticum of squamosal	124.0	–	–	66.0	–	112.0; 116.0
15. Width of braincase	88.0	95.0	–	65.0	77.0	85.0; 114.0
16. Mastoid width	113.0	123.0	–	68.5	87.0	92.0; 140.0
17. Width of processus palatinus between P1s	10.5	20.0	13.5	9.0	–	15.5–19.0; 24.0
18. Maximum width of processus palatinus	55.5	53.0	44.0	35.0	29.5	45.3–50.5
19. Maximum anteroposterior width of foramen infraorbitale	9.0 (L), 10.0 (R)	10.0	10.0	7.0	8.0	9.0; 7.0
20. Width of bulla tympanica	49.3	37.5	–	22.5	27.0	28.3–35.0
21. Width of rostrum	37.0	27.5	18.0	15.0	–	25.0–30.0; 40.0
22. Height of skull in region of bulla tympanica	80.0	80.0	–	52.0	58.0	69.0; 71.0
23. Distance from center of stylomastoid foramen to center of postglenoid foramen	15.1	–	–	14.5	13.0	19.5–20.0
Ratios of measurements						
meas. 14 / meas. 1	103.4	–	–	51.6	–	51.1; 52.7
meas. 4 / meas. 5	52.4	47.3	–	56.6	–	75.8; 82.1
meas. 18 / meas. 9	160.9	230.4	214.6	170.7	–	126.3

posterior palatal foramina. The anterior palatal foramen forms a narrow groove-like tube which continues toward the incisors. The posterior palatal foramen is located 3mm from the lateral notch of the palatal bone.

The zygomatic process of the maxilla arises from the side of the skull between P4 and M1.

Maximum diameter of the infraorbital foramen is larger than the diameter of the alveolus of the maxillary canine.

The alveoli of the upper incisors are markedly compressed mediolaterally. I1 in its length and width is little more than half the size of I2 and I3; the latter differ insignificantly from each other and only by their width. The alveolar row is straight.

P1 is single-rooted in contrast to the remaining cheek teeth. The toothrow is straight. The diastema between canine and P1 is larger than between the remaining teeth. The alveolar length of P4 is 70% of the length of alveolus M1. The teeth are well worn, with one main cusp, the lingual basal cingulum is well-developed.

Judging from its size and pattern of tooth wear, the mandible (ALEKSEEV 1924a:30., fig. 3, table 5) belongs to the same individual as the skull. The body of the mandible on the labial side is thickened along its middle part; on the lingual side it is flat. The teeth are aligned parallel to the axis of the toothrow.

Both p4 and m1 have one main cusp; the protoconid on p4 is triangular. The shallow chin prominence is located under m1. The length of p4 alveolus is 70.0% of the length of m1 alveolus. The retromolar space is shortened.

Comparison: The species described here differs from the type species of *Histriophoca fasciata* by equal lengths of the second and third alveoli of upper incisors; by arrangement of upper incisors in a straight line; by equal diastemata between all cheek teeth; by shorter distance from the posterior palatal foramen to lateral notch of the palatal bone; by a different ratio of lengths of alveoli m1/M1 and p4/P4; by a shorter rostrum; by smaller size of the nasal aperture; by more posterior location of the chin prominence of the mandible.

Discussion: These fragments of maxilla and mandible were described by ALEKSEEV (1924a), who presented a detailed description and measurements. Unfortunately, however, ALEKSEEV, on the basis of EICHWALD's (1850) study, supplemented the cranial part of the skull of "*Phoca pontica*" illustrated in EICHWALD's atlas with the facial part of this small seal that was in his possession. ALEKSEEV considered this material referable to the species described by EICHWALD. Subsequent investigators did not examine these specimens, and they continued to assign them to the foregoing species (MCLAREN 1960; KIRPICHNIKOV 1961). During comparison of these materials with skulls and mandibles of representatives of both Recent and fossil genera, I concluded that the mandible (of which I regrettably possess only measurements and pictures) practically does not differ from the mandible of *Pagophilus groenlandica*.

The facial part of the skull of *Histriophoca alekseevi* has many morphological characters in common with *H. fasciata* — the shortened facial part, the vertical outline of the nasal aperture (in lateral view), the similar shape of swelling of the palatal process of the maxilla, the nearly equal size of the alveolus of the maxillary canine and the diameter of the infraorbital foramen. I think these characters are sufficient for assigning the remains to the genus *Histriophoca*.

CHAPSKII (1955a) pointed out the following categories of intergeneric craniological differences between Greenland and Ribbon seals: 1. Structure of teeth. 2. Shapes of the auditory bulla. 3. Structure of the mandible. 4. Characters of the rostral part of the skull. Based on these features, *Histriophoca alekseevi* occupies an intermediate position between two closely related taxa, *Pagophilus groenlandica* and *Histriophoca fasciata*. Considering the fact that both these genera are contained in the subtribe Histriophocina, the new species likewise belongs in this taxonomic group. The single intergeneric difference observable in the fragmentary material is a dimension of the vomer, which may reach (in *Pagophilus*) or not reach (in *Histriophoca fasciata* and in *H. alekseevi*) the posterior border of the palatine.

As to the postcranial skeleton, at present I can only provisionally assign to *H. alekseevi* some isolated bones of extremities from the collections of PIN and IZUAN. By analogy with ecomorphological types of the mandible and teeth, and in view of their similarity to the same bones in the genera *Phoca*, *Pusa*, and *Pagophilus* (see Chapter 4), I can hypothesize which postcranial features should be diagnostic of *Histriophoca alekseevi*:

Humerus: the lesser tubercle is elongated along the bone's axis; it is located above a round head; the intertubercular groove is wide and flattened; the deltoid crest is distended either in its middle part or on its distal border.

Femur: the trochanter is triangular; its height slightly exceeds that of the head; an intertrochanteric crest is displaced toward the trochanter's distal border.

Analysis of additional, more nearly complete material would show with greater certainty whether this Miocene seal is ancestral to the Greenland and/or Ribbon seals. At this time it can only be pointed out that, according to their morphology, the cranial remains from Kishinev do not belong to the modern species *H. fasciata*. Consequently, proposing a new taxon of species rank is necessary — *Histriophoca alekseevi*.

Geological age and distribution: Middle Sarmatian of northern Black Sea littoral (Moldavia).

Genus *Monachopsis* KRETZOI, 1941

Phoca: EICHWALD, 1850:210–218, pl. 13, figs. 17, 26.; ALEKSEEV, 1924b:201, 205; 1926:140.; MCLAREN, 1960:50–56, fig. 1A.; KING, 1964:131.; GRIGORESCU (in part), 1977:407–409, 411–414, 416, 417, fig. 5A.; MUIZON, 1982a:188, 190; 1992:35, 36.; SAVAGE and RUSSELL, 1983:293.

Monachopsis: KRETZOI, 1941:353, fig. 3.; MCLAREN, 1960:57, 58.; KORETSKY, 1987; 1988.

Type species: *Phoca pontica* EICHWALD, 1850:211. Ukraine, Crimea, Kerch Peninsula, Kerch, Mount Mitridat; the eastern end of the Kerch peninsula, top layer of molasse formation.

Included species: The genus is monotypic. In the Late Miocene (Sarmatian) of the Ukraine, Romania, and Turkey, only the type species "*Phoca*" *pontica* is recorded.

Emended diagnosis: Phocinae of very small size; P4-M1 single-rooted; diastemata between teeth absent; palatal process of maxilla highly swollen; infraorbital foramen visible in dorsal view.

Lesser tubercle of humerus located on same level as proximal part of deltoid crest, higher than head. Ratio of head's width to its height near 103%. Deltoid crest strongly developed, reaches coronoid fossa; epicondyloid crest weakly developed.

Greater trochanter of femur slightly higher than head, its proximal part narrower than distal; trochanteric fossa shallow, located transversely relative to bone's axis; head strongly bent distally; neck short; minimal width of diaphysis shifted proximally; greatest breadth across condyles 49.9–58.9% of bone length.

Comparison: This genus differs from other known phocines by: smaller size, single-rooted and single-cusped P1 (except *Phoca*, *Halichoerus*, *Histriophoca*, and *Cryptophoca*), single-rooted P4 and M1, absence of diastemata between maxillary cheek teeth, arrangement of cheek teeth in a straight line, relatively shorter length of tooth-row, greater swelling of palatal process of maxilla, and shape of the palatal process (except *Erignathus*, *Halichoerus*, *Pagophilus*,

and *Cryptophoca*). By compression of the head of the humerus in a parasagittal plane (except *Praepusa* and *Sarmatonectes*); ratio between the height of the head and its width; ratios of heights of lesser tubercle, of deltoid crest and of the head (except *Histriophoca* and *Praepusa*); deltoid crest everted dorsally (except *Praepusa*) and reaching the coronoid fossa. By ratio of heights of the greater trochanter and the head of femur; proximal part of the greater trochanter narrower than the distal part, the minimum width of the diaphysis being shifted proximally, and ratio of distance between condyles and bone's length. In addition, this genus differs distinctly from other genera as follows:

From *Pusa* by: location and height of lesser tubercle of humerus; weak development of epicondylar crest. By shallow trochanteric fossa, located along the greater trochanter of femur; thicker and shorter neck; and smaller dimensions of femoral condyles.

From *Phoca* by: weak development of the supracondylar crest of humerus. By the femoral head being strongly bent in a distal direction and seated on a short neck; and the presence of a supracondylar (= plantar) fossa.

From *Erignathus* by: not sharply turned downward alveolar process of the maxilla. By presence of the intertubercular groove of the humerus; maximal width of deltoid crest located in its proximal part. And by the relative distance between condyles of femur.

From *Halichoerus* by: location of the infraorbital foramen. By the presence of a wide and flat intertubercular groove of the humerus; weak development of the lateral epicondylar crest. By small condyles and weakly developed lateral epicondyle of femur.

From *Pagophilus* by: distention of proximal part of the deltoid crest of humerus. By smaller femoral condyles with narrow intercondylar width.

From *Histriophoca* by: the absence of double-rooted M1.

From *Praepusa* by: lesser tubercle of humerus located slightly higher than the head; shorter length of deltoid crest. By femoral head strongly bent in a distal direction, and fixed on a short neck; and a different shape of the femur (Figure 10).

From *Cryptophoca* by: elongated deltoid crest of humerus; compressed head of this bone; narrow medial epicondylar crest. By narrowed proximal part of femur; shallow trochanteric fossa; relatively wider neck and proximal epiphysis; and greater intercondylar width.

Distribution: Late Miocene – ?Early Pliocene (?Middle Sarmatian – Maeotian) of eastern Europe, Ukraine, Romania, and Turkey.

Monachopsis pontica (EICHWALD, 1850)

Figures 15–17; Tables 2–4a, 6, 7

Phoca pontica: EICHWALD, 1850:210–218, pl. 13, figs. 17, 26.; ALEKSEEV, 1924b:201, 205; 1926:140.; McLAREN, 1960:50–56, fig. 1A.; KING, 1964:131.; GRIGORESCU (in part), 1977:407–409, 411–414, 416, 417, fig. 5A.; MUIZON, 1982a:188, 190; 1992:35, 36.; SAVAGE and RUSSELL, 1983:293.

Monachopsis pontica: KRETZOL, 1941:353, fig. 3.; McLAREN, 1960:57, 58.; KORETSKY, 1987, 1988.

Neotype: Left humerus: EICHWALD, 1850:214, Plate 13, fig. 17; collection of MPGI 17–113; ?Late Sarmatian, Kerch Peninsula, Ukraine.

Referred material: Collection of IZUAN, Ukraine, Crimea, Kerch Peninsula; collection 64–516: maxilla with P1, littoral of Lake Uzunlar (?Late Sarmatian).

Collection 64, iron-ore mine of Kamysh-Burun district, quarry “E”: humeri, male: ##71, 100, 102–105, 130, 245, 248, 310.

Humeri, female: ##73, 101, 108–122, 125–6, 129, 131, 133–4, 320, 464–7; from the region of Novyi Karantin: ##123, 127, 135, 247; from Lake Uzunlar: #170; from Lake Tobechnik: ##174, 249; from village Ossoviny: #309; from village Kyz-Aul: ##317, 319.

Femora, male, iron-ore mine of Kamysh-Burun district, quarry “E”: ##7, 8, 18, 19, 21, 56, 65–68, 305, 314, 324, 358, 401–406, 409–411, 413–416, 470, and from village Ossoviny #308.

Femora, female, iron-ore mine of Kamysh-Burun district, quarry “E”: ##1–5, 14, 22, 28, 42–44, 69, 119, 145, 166, 168, 350–353, 400, 407–8, 412, 424, 433–450; from Lake Uzunlar: ##46, 169; from village Ossoviny: #307; from village Kyz-Aul: #315.

Collection of PIN: humerus 565–3 and four femora 299–42, 299–66, 299–69, one femur without number, from Peninsula Hronya (Kerch Peninsula, Crimea, Ukraine).

Collection of UFG: two humeri from village Giobanita: ##9, 242, and one from village Credința: #148; eight femora from Dobrogea (Romania): ##4, 11(243), 12, 44, 157(10), 158(9), 255.

Diagnosis: As for the genus.

Table 5a

Means (\bar{X}) and range for measurements (mm) of number in sample (n) of the mandibles

Characters	<i>Cryptophoca maeotica</i>		<i>Leptophoca lenis</i>		
	Range	n	\bar{X}	Range	
				n	\bar{X}
Total length	—	3	134.0	130.0–138.9	
Length of toothrow i1–m1	—	4	60.2	56.0–63.5	
Length of toothrow p1–p4	35.5–40.0	9	38.2	33.0–43.5	
Length of toothrow p1–m1	7.0	9	50.0	47.0–51.0	
Depth under m1	20.5–26.0	9	19.6	18.0–21.5	
Depth under p2	18.0–19.0	9	18.2	16.5–19.0	
Depth behind m1	18.5–18.5	8	18.0	17.4–19.5	
Depth between p3–p4	20.0–24.0	9	17.8	16.5–18.3	
Thickness of mandible under m1	9.0–11.0	11	7.4	7.0–8.5	
Diastema between p4–m1	6.5–9.0	9	2.4	1.5–5.0	
Diastema between p1–p2	—	9	2.2	1.1–3.5	
Diastema between p1–c	—	7	2	1.5–2.5	

Table 5b

Means (\bar{X}) and range for measurements (mm) of number in sample (n) of the lower dentition

Characters		<i>Cryptophoca maeotica</i>			<i>Leptophoca lenis</i>		
		n	\bar{X}	Range	n	\bar{X}	Range
i1	length	—	—	—	3	4.2	3.4–5.0
	width	—	—	—	3	2.6	2.3–3.0
i2	length	—	—	—	3	3.5	3.0–3.8
	width	—	—	—	3	3.0	2.5–3.5
c	length	2	—	7.0; 7.0	7	8.6	7.8–10.0
	width	2	6.5	6.0; 7.0	8	6.5	5.8–8.0
p1	length	1	—	5.5	9	6.5	6.0–7.0
	width	1	—	4.5	9	5	4.8–5.5
p2	length	4	8.4	8.0–9.0	10	9.8	9.0–11.0
	width	4	3.4	3.0–4.0	10	5.0	4.5–5.5
p3	length	3	8.5	8.0–9.0	11	9.8	9.0–11.0
	width	3	3.0	3.0	11	5.0	4.5–5.5
p4	length	4	8.5	8.0–9.0	11	9.9	9.0–11.0
	width	2	—	3.0; 3.0	12	5.0	4.0–5.0
m1	length	2	6.5	6.0; 7.0	12	10.0	9.0–11.5
	width	2	—	3.0	13	4.7	4.0–5.6

Humerus (Fig. 16, Table 6). The lesser tubercle is higher than the head, on the same level as the proximal part of the deltoid crest. It is elongated along the bone's axis and is slightly bent backwards and laterally. Its proximal border is directed toward that of the deltoid crest, reminiscent of the humerus of *Pusa caspica*. The head is compressed in a dorsoventral direction and in males the head is considerably larger. The ratio of the head's width to its height is approximately 1.03. The intertubercular groove is wide and flat. The deltoid crest is strongly developed, and its distal part reaches the coronoid fossa; in males it is considerably larger. The maximum distension of the deltoid crest is in its proximal part. The deltoid tuberosity is located along the middle of the diaphysis. The lateral epicondyle is very narrow; it is elongated along the bone's axis and is higher than the distal part of the deltoid crest. The medial epicondyle is short and flattened. The presence of an entepicondylar foramen is an individually variable feature, and not a specific character, as EICHWALD assumed.

Femur (Fig. 17, Table 7). The femur of *M. pontica* is similar in size to that of the Baikal seal, modern *Pusa sibirica*. The greater trochanter extends proximally higher than the femoral head. In males this difference reaches $M = 5.45$ mm, $n = 10$; in females there is no such difference, with $M = 1.5$ mm, $n = 20$. The proximal part is narrower than the

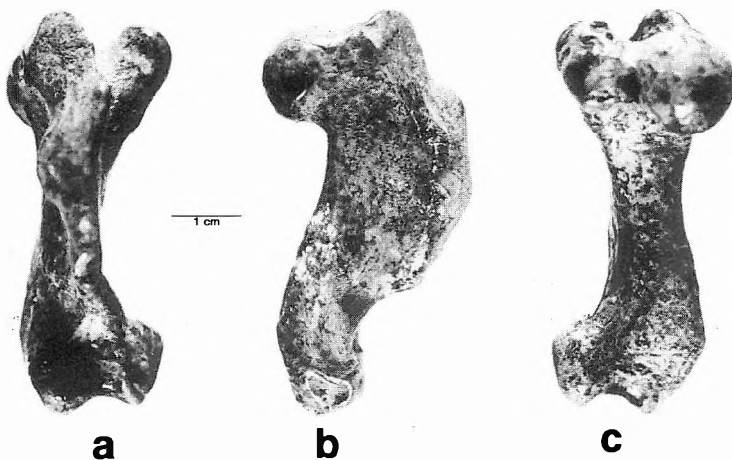


Figure 16. *Monachopsis pontica*, humerus, # IZUAN 64-309

a = in cranial; b = in lateral; c = in caudal aspects

distal part. The strong "swelling" of the greater trochanter (KRETZOI 1941) is observed only in bones of males; in females the greater trochanter is more skewed (Figs. 17, b–e). The trochanteric fossa is shallow and wide open, actually reaching the distal 1/3 of the greater trochanter. The intertrochanteric crest is not expanded. The trochanteric proximal part is wide and elongated. The femoral head in females is considerably smaller than in males. It is strongly bent in a distal direction, and seated on a narrow, short neck. The supracondylar fossa is located above the medial condyle. The dimensions of this fossa vary from a barely noticeable depression to a large fossa. Maximal intercondyloid width is 47.9–58.9% of the bone's length. The smallest width of the diaphysis is shifted distally.

Table 4a

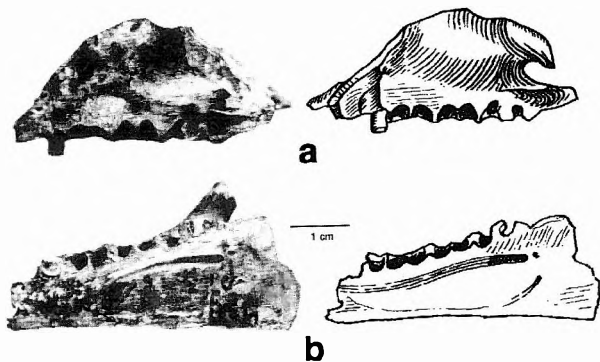


Figure 15. *Monachopsis pontica*, photographs and drawing of fragment of skull, #IZUAN 64-516

a = lateral view; b = occlusal view

Description: The rostral fragment of the skull (Fig. 15, Table 4a) belongs to a very small seal. In the exemplar available for study, the crown of P1 is worn straight across. The palatal sutures are obliterated, consequently this fragment of the skull belongs to an adult individual. P1, P4 and M1 are single-rooted, in contrast to the remaining teeth. The tooth-row forms a straight line, and is considerably shortened. Diastemata are practically absent: between the alveoli of P4 and M1 the distance is about 2 mm, between other alveoli the distance is even shorter. The body of the maxilla from the posterior edge of the alveolus of P2 to the posterior border of the alveolus of M1 is strongly swollen. The palatal (= sagittal) groove is well defined along its total length, and reaches the anterior palatal foramen. The distance from the posterior palatal foramen to the lateral notch of the palatal bone is about 2/3 of the distance from the same notch of the palatal bone to the junction of intermaxillary and transverse sutures (Figure 15, Table 4a).

Cranial measurements (mm) in the skulls of *Monachopsis pontica*

Length of tooth-row, P1 to M1		29.0
Width of processus palatinus between P1s		17.0
Length of processus palatinus between M1s		30.0
Maximum anteroposterior width of infraorbital foramen		7.9
Maximum width of processus palatinus		38.0
Distance from oposterior palatine foramen to the lateral notch of the maxilla		9.4
P1 alveolus	length	4.0
	width	5.0
P2 crown	length	8.5
	width	5.0
P3 crown	length	8.0
	width	4.0
P4 crown	length	4.0
	width	4.0
M1 crown	length	3.0
	width	3.0

Table 5

Means (\bar{X}) and range for measurements (mm) of number in sample (n) of the mandibles and lower dentition

Characters	<i>Histriophoca</i>		<i>Praepusa</i>					
	<i>fasciata</i>	<i>alekseevi</i>	<i>pannonica</i>			<i>vindobonensis</i>		
	Range	Range	n	\bar{X}	Range	juv.	ad.	
Total length	105.0; 105.9	—	—	—	—	79.0	—	
Length of toothrow i1–m1	47.5; 47.5	—	2	—	35.5; 48.0	40.0	—	
Length of toothrow p1–p4	28.0; 29.0	—	1	—	28.0	15.0	—	
Length of toothrow p1–m1	37.0; 38.0	—	2	—	31.5; 38.0	34.0	—	
Depth under m1	16.0; 16.5	16.0	3	13.7	10.0–16.0	10.5	12.0	
Depth under p2	12.0; 13.0	—	2	—	9.0; 11.5	10.5	—	
Depth behind m1	16.0; 16.0	14.0	4	13.0	9.0–15.0	9.5	10.5	
Depth between p3–p4	16.0; 16.5	13.3	4	14.6	11.0–16.0	12.0	12.0	
Thickness of mandible under m1	4.5; 4.5	6.2	3	5.7	4.5–6.5	4.5	4.0	
Diastema between p4–m1	1.0; 2.0	2.1	4	2.9	2.0–3.5	2.0	2.5	
Diastema between p1–p2	—	—	—	—	—	—	—	
Diastema between p1–c	—	—	—	—	—	—	—	
p3	length	—	—	—	8.0	7.0	—	
	width	4.0; 4.5	—	—	—	3.5	—	
p4	length	7.5; 8.0	5.6	4	8.6	7.0–10.0	6.0	7.0
	width	—	—	—	—	—	—	
m1	length	7.0; 8.0	6.5	4	7.4	7.0–8.0	5.5	6.0
	width	3.0; 3.0	—	—	—	2.7	3.0	—

Means (\bar{X}) and range for measurements (mm) of number in sample (n) of humeri of *Monachopsis pontica*

Characters	Males			Females		
	n	\bar{X}	Range	n	\bar{X}	Range
Absolute length	1	0	80.5	13	66.3	60.0–71.5
Length of deltoid crest	1	0	58.5	21	46.7	44.5–58.0
Height of head	8	19.8	18.0–23.0	31	17.4	15.5–19.0
Height of trochlea	3	16.2	15.5–17.0	19	13.2	10.5–16.0
Width of head	9	20.8	18.0–23.0	32	17.0	15.0–19.0
Width of deltoid crest	6	21.6	18.0–24.0	21	16.3	14.0–19.0
Width of distal epiphysis	3	27.7	27.0–28.0	19	23.8	21.0–26.5
Width of proximal epiphysis	7	31.4	28.5–35.0	24	22.5	20.0–26.0
Width of trochlea distally	2	0	12.5; 13.0	17	12.8	10.5–14.0
Width of trochlea, frontal view	3	18.3	17.5–19.0	17	16.1	13.0–19.0
Transverse width of diaphysis	4	13.6	13.0–15.0	27	11.5	8.5–14.5
Thickness of proximal epiphysis	4	35.4	34.5–36.5	22	27.0	24.0–29.5
Thickness of medial condyle	2	0	15.0; 16.0	18	12.8	10.5–14.0
Thickness of lateral condyle	3	13.5	12.0–14.5	19	12.0	10.0–14.0
Diameter of diaphysis with deltoid crest	8	26.5	25.0–28.5	24	23.2	21.0–26.0

Sexual dimorphism in bones of the extremities is described in detail in Chapter 3.3 (Tables 2–3).

Discussion: In the 150 years that have passed since the description of *M. pontica* (EICHWALD 1850), only three reports have been published containing information on cranial remains of this species, which were found in various locations. ALEKSEEV (1924a) was the first author who attempted to associate the rostral part of the skull of a Middle Sarmatian seal from Kishinev with an illustration of the cerebral part of the cranium of "*Ph.*" *pontica*, presented by EICHWALD in his first description. Unfortunately, this comparative analysis was unsuccessful, as the species overall was incompletely characterized and the description of the cranium was imprecise. Based on comparison with the example from the Kerch Peninsula, I note that the seal from the Middle Sarmatian of Kishinev differs considerably from all other known members of the subfamily Phocinae, including the genus *Monachopsis* from the Crimean Peninsula. In this chapter I redescribe the rostral part of the skull that was previously published by ALEKSEEV (1924a), and I assign it to a new species, *Histriophoca alekseevi*.

Table 6a

Means ($\bar{X} \pm SE$) and range for measurements (mm) of number in sample (n) of humeri

Characters	<i>Cryptophoca maeotica</i>			<i>Praepusa vindobonensis</i>		
	n	$\bar{X} \pm SE$	Range	n	$\bar{X} \pm SE$	Range
Absolute length	5	107.1 \pm 1.5	99.0–123.5	19	86.3 \pm 1.55	75.0–101.0
Length of deltoid crest	5	75.9 \pm 0.7	73.0– 80.4	19	57.0 \pm 0.16	52.0– 73.0
Height of head	4	25.1 \pm 0.2	24.0– 28.0	29	17.0 \pm 0.60	15.0– 24.0
Height of trochlea	4	20.1 \pm 0.7	19.0– 21.5	27	13.9 \pm 0.41	10.5– 16.0
Width of head	4	25.0 \pm 0.9	23.0– 28.0	30	18.4 \pm 0.40	17.0– 22.5
Width of deltoid crest	4	28.6 \pm 0.2	28.0– 30.0	22	18.6 \pm 0.52	18.0– 23.5
Width of distal epiphysis	5	37.0 \pm 1.8	30.0– 45.0	30	27.6 \pm 0.50	26.5– 31.1
Width of proximal epiphysis	7	34.2 \pm 2.0	29.0– 38.5	34	25.6 \pm 0.61	21.0– 30.0
Width of trochlea distally	4	19.1 \pm 0.6	18.0– 20.0	28	15.7 \pm 0.35	14.5– 18.0
Width of trochlea, frontal view	4	23.1 \pm 0.8	22.0– 25.0	34	13.1 \pm 0.18	11.0– 14.5
Transverse width of diaphysis	5	14.5 \pm 0.9	12.0– 17.0	19	10.6 \pm 0.42	10.0– 13.5
Thickness of proximal epiphysis	7	40.5 \pm 0.4	33.8– 46.0	29	29.0 \pm 0.76	23.0– 34.0
Thickness of medial condyle	4	19.6 \pm 0.6	18.5– 20.5	27	14.0 \pm 0.31	12.0– 15.0
Thickness of lateral condyle	4	17.4 \pm 0.4	16.4– 8.5	27	15.2 \pm 0.43	13.0– 18.0
Diameter of diaphysis with deltoid crest	6	33.5 \pm 1.6	29.0– 38.0	8	24.2 \pm 1.60	18.0– 28.5

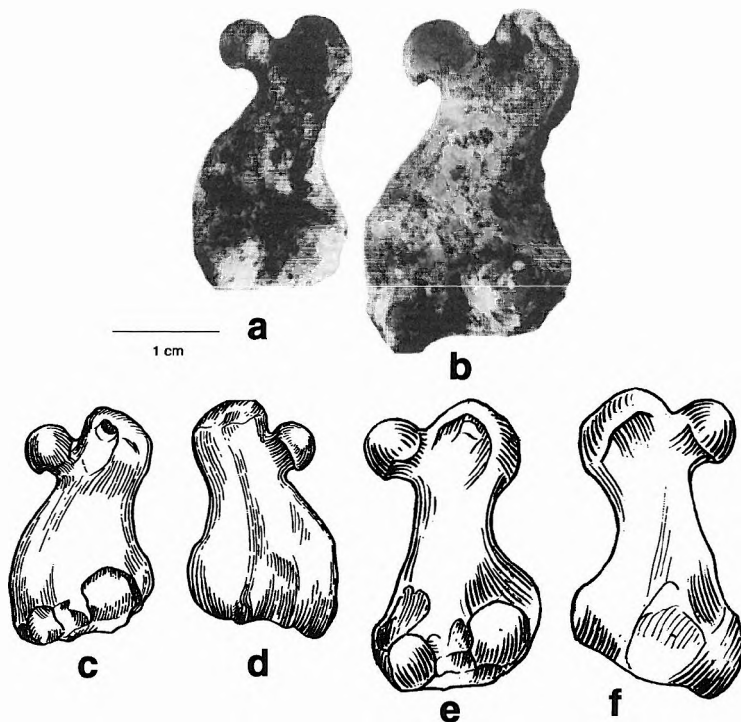


Figure 17. *Monachopsis pontica*, femur

a = female, #PIN 299-69 in caudal aspect, b = male, #PIN 299-65 in caudal aspect, c = drawing of femur, female, # IZUAN 64-445, in caudal, and d = in cranial aspects; e = drawing of femur, male, # IZUAN 64-314, in caudal, and f = in cranial aspects

SIMIONESCU (1925) described bones of the extremities of *Ph. pontica* found in Sarmatian limestone near Kishinev. However, as may be judged by his illustration of the femur (figure 5; plate 1, figure 2, this author erroneously assigned to this species the seal previously described by ALEKSEEV (1924b) as *Ph. sarmatica*, and this introduced additional complications into this species concept. I have presented above a detailed analysis of confusion in the literature associated with this species, and I will not dwell on all citations of this species in the literature.

KRETZOI (1941) proposed the new genus *Monachopsis* with "*Phoca*" *pontica* as its type species. However, like most taxa described by this investigator, this genus was not recognized by other specialists, since a lectotype was not described, a diagnosis was not given, and no osteological comparison was made. Of all morphological features, only two were mentioned: the strong development of the humeral deltoid crest and considerable "protrusion" of the femoral greater trochanter. It should be pointed out, however, that of this genus proposed by KRETZOI was validated by subsequent discoveries.

Consequently, MCLAREN (1960), in his revision of the Paratethyan seals, convincingly-

Table 7

Means (\bar{X}) and range for measurements (mm) of number in sample (n) of femora of *Monachopsis pontica*

	Characters Males			Females		
	n	\bar{X}	Range	n	\bar{X}	Range
Absolute length	5	68.3	65.0-70.0	20	58.5	51.0-65.0
Medial length	3	65.5	63.0-67.5	11	55.0	49.0-59.5
Lateral length	10	60.6	55.0-67.0	20	54.8	49.0-60.5
Length of medial condyle	12	11.7	10.5-13.5	26	10.1	9.5-11.0
Length of greater trochanter	18	19.8	18.0-21.0	31	18.0	16.0-19.5
Intertrochanter length	15	24.3	21.0-27.0	23	21.1	17.0-25.0
Height of head	14	13.3	11.0-15.5	17	11.5	10.0-13.0
Height of articular area of patella surface	10	14.8	12.0-13.0	32	12.8	11.0-15.0
Width of proximal epiphysis	14	32.8	29.5-36.0	12	28.7	25.0-32.5
Width of distal epiphysis	15	34	30.0-38.0	34	31.5	27.0-35.0
Width of condyles	13	29.5	25.0-34.5	29	26.4	23.0-29.0
Width of greater trochanter	22	13.2	11.5-15.0	34	12.6	10.5-14.0
Width of head	15	13.2	12.0-15.0	17	11.5	10.0-13.0
Width of diaphysis	19	18.1	17.0-20.0	35	18.8	16.0-22.0
Anteroposterior thickness of diaphysis	21	9.7	8.0-11.5	30	10.6	9.5-12.0
Thickness of medial condyle	8	16.6	13.5-19.0	26	12.5	11.0-14.0
Thickness of lateral condyle	15	18.9	17.0-20.5	32	16.4	14.5-18.0
Distance between condyles	14	8.3	7.0-10.0	30	8.1	6.5-10.0
Diameter of neck	17	11.5	9.0-13.0	18	10.8	9.0-12.5

Means ($X \pm SE$) and range for measurements (mm) of number in sample (n) of femora

Measurements	<i>Cryptophoca maeotica</i>			<i>Praepusa vindobonensis</i>		
	n	$X \pm SE$	Range	n	$X \pm SE$	Range
Absolute length	23	106.0 \pm 2.4	93.0–138.0	22	72.8 \pm 1.9	63.0–82.5
Medial length	13	96.0 \pm 3.2	87.0–110.4	15	69.2 \pm 2.1	66.5–80.0
Lateral length	12	92.9 \pm 2.8	82.0–110.4	20	67.3 \pm 2.1	62.5–80.0
Length of medial condyle	19	18.8 \pm 0.4	17.0– 21.0	23	12.9 \pm 0.4	11.0–14.5
Length of lateral condyle	22	22.4 \pm 0.5	18.0– 26.5	28	14.7 \pm 0.5	13.0–16.0
Length of greater trochanter	23	26.9 \pm 0.8	25.0– 33.5	29	20.3 \pm 0.8	18.0–22.5
Intertrochanter length	9	31.2 \pm 1.2	24.0– 34.5	32	26.7 \pm 0.7	24.5–30.5
Height of head	17	20.0 \pm 0.5	18.0– 23.0	25	13.3 \pm 0.4	11.5–14.5
Height of articular area of patella surface	17	22.5 \pm 0.7	18.5– 25.0	25	15.2 \pm 0.6	12.0–17.0
Width of proximal epiphysis	23	51.8 \pm 1.2	44.3– 64.2	29	36.5 \pm 0.7	32.0–38.0
Width of distal epiphysis	25	53.4 \pm 0.6	47.0– 62.3	30	37.5 \pm 0.9	30.0–39.0
Width of condyles	23	42.3 \pm 0.7	38.0– 49.0	27	31.0 \pm 0.7	27.0–32.5
Width of greater trochanter	24	18.7 \pm 0.4	16.0– 22.0	32	13.6 \pm 0.4	11.0–14.0
Width of head	22	21.7 \pm 0.5	18.5– 25.0	28	14.6 \pm 0.4	13.0–15.5
Width of diaphysis	30	27.6 \pm 0.4	23.0– 33.0	34	18.4 \pm 0.4	16.0–20.0
Anteroposterior thickness of diaphysis	12	12.4 \pm 0.6	12.0– 17.0	31	10.4 \pm 0.3	7.5–11.0
Thickness of medial condyle	12	23.7 \pm 0.7	21.0– 27.5	21	18.7 \pm 0.6	15.0–19.0
Thickness of lateral condyle	15	26.1 \pm 0.7	23.5– 29.0	28	20.4 \pm 0.5	18.5–21.5
Distance between condyles	18	11.1 \pm 1.3	8.0– 12.0	28	11.6 \pm 0.3	9.0–12.5
Diameter of neck	22	16.2 \pm 0.4	14.0– 19.5	28	11.0 \pm 0.4	9.0–13.0

ly established a lectotype on the basis of the picture of the cranium in EICHWALD's publication (1850, pl. 13, fig. 1), and used the generic name given by KRETZOI. Unfortunately, this skull fragment was destroyed during the Second World War. At that time EICHWALD's collection was kept in the Geological Museum of the Mining Institute (St. Petersburg, Russia). When I found this material, only the left humerus remained. Consequently, I choose it as a neotype on the following basis: it was part of the Eichwald collection on which the nominal taxon was originally based, and hence a paratype; it was from the type locality; and it was described and illustrated by EICHWALD.

KIRPICHNIKOV (1964) made a comparison of a composite skeleton and skull of "*Ph.*" *pontica* from the Kerch Peninsula (collection of PIN) with *Ph. caspica*. Regrettably, this author presented neither illustrations nor bone measurements, nor references to the collection numbers. For these reasons, it is impossible to find and to revise the materials described by KIRPICHNIKOV; his data may be considered as unreliable.

Later, GRIGORESCU (1977) described a series of teeth, temporal bones, a fragment of palatal arch, and part of a postcranial skeleton of "*Ph.*" *pontica* from the Middle Sarmatian deposit in Romania (Bessarabian Formation of Eastern Paratethys). In all features this seal differs considerably from *M. pontica* from the type locality. Specifically, it has double-rooted P1 - M1, large size of alveoli, another type and size of the swelling of the palatal process of the maxilla, and a much shorter distance from the posterior palatal foramen to the lateral notch of the palatal bone (2.5–2.7 mm). The particulars of the morphology, as well as the more ancient age of the Romanian find, allow the conclusion that the materials published by GRIGORESCU do not belong to *M. pontica*.

I acknowledge uncertainty in the assignment of the foregoing rostral fragment from the Crimea (IZUAN 64-516) to *M. pontica*. However, at present it is necessary to define precisely the morphological characters of this species and its taxonomic status. For these reasons the assignment to this taxon of the material found geographically and stratigraphically close to the type locality is in my opinion much more justified than identification of materials from other regions of the Black Sea littoral with *M. pontica*. This approach is justified by the presence at Lake Uzunlar of a large number of bones of extremities that do not differ morphologically from the type materials of EICHWALD.

Geological age and distribution: Late Miocene (Sarmatian–Maeotian) of eastern Europe. ?Late Sarmatian of Ukraine, Kerch Peninsula; Romania (South Dobrogea); Turkey.

Table 7b

Genus *Praepusa* KRETZOI, 1941Means (\bar{X}) and range for measurements (mm) of number in sample (n) of femora

Measurements	<i>Sarmatonectes sintsovi</i>	<i>Leptophoca lenis</i>		
	Range	n	\bar{X}	Range
Absolute length	89.5; 94.5	2	—	119.0; 120.0
Medial length	88.0	2	—	109.0; 112.0
Lateral length	80.0; 87.5	6	104.8	101.5–112.0
Length of medial condyle	16.0; 16.5	2	—	21.5; 22.0
Length of lateral condyle	19.0; 19.0	5	22.9	21.0–24.5
Length of greater trochanter	26.0; 26.0	4	33.3	28.5–37.0
Intertrochanter length	32.0; 36.0	8	44.0	42.0–48.0
Height of head	16.0	2	—	23.5; 254.5
Height of articular area of patella surface	18.0; 19.0	6	23.8	23.5–24.0
Width of proximal epiphysis	43.0	8	53.9	51.0–59.0
Width of distal epiphysis	47.5; 48.0	4	55.3	54.0–62.0
Width of condyles	40.0; 43.0	3	50.7	45.0–54.5
Width of greater trochanter	15.0; 17.0	7	18.8	16.5–22.5
Width of head	17.0	7	20.5	18.0–23.5
Width of diaphysis	21.0; 22.5	9	28.1	26.0–35.0
Anteroposterior thickness of diaphysis	13.0; 13.0	9	15.2	14.0–17.0
Thickness of medial condyle	20.5; 21.0	3	27.3	27.0–27.5
Thickness of lateral condyle	23.5; 25.5	8	28.3	27.0–31.5
Distance between condyles	11.0; 13.5	8	14.3	13.0–17.5
Diameter of neck	12.5	9	16.2	14.5–18.0

of equal width; trochanteric fossa wide and medially open, but deep; head slightly deflected distally and seated on narrow, long neck; minimal width of diaphysis in middle part of bone; maximal intercondylar distance 12.0–15.8% of bone's length.

Comparison: In their cranial dimensions the representatives of this genus are near to those of Recent *Pusa*. The genus differs from other known phocines by: lesser height of the mandible under p2 (except *Erignathus*, *Histriophoca*); more anterior location of the chin prominence (except *Erignathus*, *Histriophoca*, *Halichoerus*); three-cusped p2/P2 and p4/P4 (except *Pusa* and *Phoca*); the alveolar length of m1 smaller than that of p4 (except *Erignathus*, *Pagophilus*, *Halichoerus*). In humeral morphology they differ from all known phocines by: their long deltoid crest which smoothly descends to the condyles; relatively narrow intertubercular groove; the head which is compressed mediolaterally; and location of the lesser tubercle at the same level as the head (except *Erignathus*, *Pagophilus*, *Histriophoca*, *Cryptophoca*). Morphology of the femur differs by: the nearly equal widths of proximal and distal parts of the greater trochanter (except *Sarmatonectes*), and a thin and long neck (except *Pagophilus*). Apart from this, the genus differs:

From *Pusa* by: single-cusped p1/P1 and m1/M1; relatively lesser width of the occipital bone; greater length of the extero-posterior wall of the tympanic bulla; an oval-shaped opening of the external auditory canal; location of the oval

Phoca: BLAINVILLE, 1842:41–42, pl.10, fig. 1.; BRÜHL, 1860:1–16, fig. 2.; PETERS, 1867:110–111.; TOULA, 1897:55–71, pl. 2, figs. 9–11.; TROUËSSART, 1897: 385; 1904:286.; KELLOGG, 1922:119–120.; ALEKSEEV, 1924a:32.; BOGACHEV, 1927:141–143, 145.; KRETZOI, 1941:350–356, fig. 1.; FRIANT, 1947:7, 12, 16, 45, 47, tabl. 2, figs. 1a–c.; KING, 1964:131.; THENIUS, 1969:319.; McLAREN, 1960:51–52, 56, 58.; HENDEY and REPENNING, 1972:85.; Ray, 1977:395, 398.; GRIGORESCU, 1977:407, 412, 417.; NICOLAS, 1978:456.; MUIZON, 1982a:190, 205.

"*Phoca*": McLAREN, 1975:44.; MITCHELL, 1975:23.

Praepusa: KRETZOI, 1941:351–356, fig. 1.; McLAREN, 1960:55–56, 59.; THENIUS, 1969:404.; GRIGORESCU, 1977:407, 412, 417.; ANTONIUK and KORETSKY, 1984:27–29, figs. 1–3.; KORETSKY, 1987b:3–6, fig. 1.; KORETSKY and RAY, 1994:20.; MCKENNA and BELL, 1997:257.

Leptophoca?: RAY, 1977:395, 398.; SAVAGE and RUSSELL, 1983:292.; MUIZON, 1992:35.

Type species: *Praepusa pannonica* KRETZOI, 1941:351–356, fig. 1; Early–Middle Sarmatian of Hungary.

Included species: *Praepusa pannonica* KRETZOI, 1941, from the Early–Middle Sarmatian of Hungary and from the Middle Sarmatian of Moldavia; *Praepusa vindobonensis* TOULA, 1898, from the Early Sarmatian of Austria (Nussdorf) and from the Middle Sarmatian of the Ukraine and Moldavia.

Emended diagnosis: Diagnosis of skull the same as for *Praepusa vindobonensis*; diagnosis of mandible the same as for *Praepusa pannonica*. Femur and humerus known only for *P. vindobonensis*.

Deltoid crest of humerus has shape of sharp blade, which smoothly descends to condyles; maximal distention of deltoid crest in its proximal end; lesser tubercle elongated along axis of the bone, and located at same level as head; ratio of head's width to its height, 0.964; lateral epicondyle reaches distal part of deltoid crest.

Greater trochanter of femur considerably higher than head; its proximal and distal parts approximately

fossa at the same level as the anterior end of the tympanic bulla. By the absence of spiral groove of the humerus. By relatively larger condylar width of the femur; and strong swelling of its intertrochanteric crest.

From *Phoca* by: smaller size; single-cusped p1/P1 and m1/M1. By considerable thickening of epicondyles of the femur; and stronger swelling of its intertrochanteric crest.

From *Erignathus* by: lowered facial part of the skull; absence on the posterior border of the palatine bone of a tongue-shaped prominence; a thicker ventral lip of the opening of the exterior auditory canal; relatively lesser thickness of the mandible; a bluntly rounded symphyseal part; a weakly pronounced chin prominence and by elongated retromolar space; single-cusped p1. By location of maximal width of deltoid crest of the humerus in its proximal part, and lateral location of this crest. By a larger greater trochanter relative to the femoral head; and the femur's relatively larger intercondylar width.

From *Halichoerus* by: lowered and shortened facial part of the skull; greater compactness of the mandible; presence of a chin prominence; very small teeth seated along the axis of the mandible; double-rooted p2 and p3; elongated retromolar space. By relatively greater intercondylar width of the femur; and thinned femoral epicondyles.

From *Pagophilus* by: lower and shortened facial part of the skull; greater compactness of the mandible; a bluntly rounded symphyseal part. By location of maximal width of deltoid crest of the humerus in its proximal part, and lateral location of this crest; deeper and wider trochanteric fossa of the femur; relatively lesser swelling of intertrochanteric crest and width of its condyles.

From *Histriophoca* by: closely spaced cheek-teeth; parallel location of long axes of the tympanic bullae and their triangular shape. By the absence of distention of the middle part of the deltoid crest of the humerus and presence of its lateral eversion. By thinness of femoral epicondyles; and a trochanteric fossa of the femur which opens medially.

From *Monachopsis* by: absence of swelling of the palatal process of the maxilla; double-rooted p4/P4 and m1/M1; the presence of diastemata between premolars and molars. By narrower deltoid crest of the humerus. By greater height of the greater trochanter relative to the head of the femur; position of the smallest diameter of the diaphysis in the middle of the femur; and relatively smaller intercondylar width.

From *Cryptophoca* by: considerably smaller size; premolars in a skewed position relative to the axis of the tooth row; the bluntly-rounded shape of the symphyseal part of the mandible. By the oval shape of the lesser tubercle of the humerus. By the wide and deep trochanteric fossa of the femur; and smallest width of femoral diaphysis displaced towards proximal epiphysis.

Discussion: Despite the wide distribution of Phocinae, abundant remains, and prolonged studies, many important aspects of morphology, phylogeny and systematics of the subfamily remain confused. These remarks may be fully applied also to the genus *Praepusa*, described by KRETZOI (1941).

KRETZOI described the holotype *Praepusa pannonica*, and presented a schematic illustration of the mandible and some of its measurements. He considered this information sufficient for establishing a new taxon of generic rank. Also, for the first time, and on the basis of fragmentary fossil materials, KRETZOI attempted to combine cranial morphology with the morphology of the mandible and the bones of extremities of modern and extinct seals.

In the description of the species *Praepusa tarchankutica*, ANTONIUK and KORETSKY (1984) diagnosed the genus *Praepusa* and compared it with remaining genera of the subfamily Phocinae. However, in more recent years a large collection from the northern Black Sea region has accumulated, including some bones referable to this genus. This allows presentation of a much more precise and detailed diagnosis, redescription of the material, and delineation of the distribution of this taxon.

Geological age and distribution: Early-Middle Sarmatian of the southern part of Eastern and Central Europe.

Praepusa pannonica KRETZOI, 1941

Figure 18; Table 5

Praepusa pannonica: KRETZOI, 1941: 350–356, figs. 1–2.; THENIUS, 1969: 404.; McLAREN, 1960:55–56.; GRIGORESCU, 1976:407.; KORETSKY, 1987b: 3–6, fig.1.

Phoca pannonica: KING, 1964:131.

Holotype: Mandible with m1 and alveoli i2 - p4; collection of HGS, #Aw n1; illustrated and described by KRETZOI (1941:351, fig. 1) as *Praepusa pannonica*.

Type locality: Early-Middle Sarmatian of Hungary (region of Érd near Budapest).

Originally referred material: Proximal end of tibia and fibula; collection of HGI; illustrated and described by KRETZOI (1941:353, fig. 2.1) as *Praepusa pannonica*.

Newly referred material: Kishinev (Moldavia): collection of TGPI; incomplete left ramus of the mandible without teeth, without number (Fig. 18, a–b); collection of PIN — incomplete right ramus of the mandible, without teeth, without number.

Emended diagnosis: Chin prominence located between p3 and p4, directed lingually. Length of alveolus p4 exceeds the length of alveolus m1. Diastema between p3 and p4 shorter than between p4 and m1.

Description: Small seal, in size near to the modern genus *Pusa*. The body of the mandible (Fig. 18; Table 5) is low and thin, symphyseal part bluntly rounded; the chin prominence is well-marked, located between p3 and p4, and directed lingually. The mandible under p3 is slightly concave. The ramus of the mandible is not preserved. Cheek teeth (Table 5) are located along the axis of the mandible with short diastemata, except between p4 and m1, where the length of diastema reaches 3.5 mm. The p1 is single-rooted; all remaining teeth are double-rooted. The alveolus of p4 is larger than the alveolus of m1.

Measurements of the tibia and fibula, which KRETZOI considered as a paratype: width of proximal epiphysis = 35mm; width of distal epiphysis = 17 mm.

Comparison: The type species differs from *Praepusa vindobonensis* by larger size of the mandible under p2 and larger tooth alveoli, by higher chin prominence and by longer row of p1 - m1. Although some measurements such as mandibular height behind m1, length of row i1 - m1 and some others are overlapping, even such a small collection of bony remains allows the conclusion that these species are distinct.

Discussion: The lack of additional materials and incomplete description of the type species raise some doubts about the assignment of remains from Moldavia to *P. pannonica* (Fig. 18, a-b). Actually, according to published information, the Moldavian finds could not be diagnosed more precisely than Phocini. However, on the basis of remains preserved and on illustrations published by KRETZOI, the height and form of the mandible, sizes of tooth alveoli and lengths of diastemata between them, as well as location of the chin prominence, allow, with a great degree of probability, assignment of this seal to *P. pannonica* (Fig. 18, c-d). In my opinion, this approach is more justified than establishment of a new taxon.

Geological age and distribution: Early-Middle Sarmatian of Hungary (region of Érd near Budapest); Middle Sarmatian of Moldavia (limestone quarry in the vicinity of Kishinev).

Praepusa vindobonensis (TOULA, 1897), new combination

Figures 19-31; Tables 4-5, 6a-7a, 8-12

Phoca viennensis antiqua: BLAINVILLE, 1842:42-51, pl. 10.; KELLOGG, 1922:119.; KRETZOI, 1941:350, 353.

Phoca holitschensis: BRÜHL, 1860:1-16, fig. 2.; TROUESSART, 904:286; 1897:385.; KELLOGG, 1922:119.; KRETZOI, 1941:350, 352,353.

Phoca halithensis (sic; lapsus): ALEKSEEV, 1924a:32.

Phoca holitchensis (sic; lapsus): KING, 1964:131.

Phoca pontica: PETERS, 1867:110-111.

Phoca vindobonensis: TOULA, 1897:55-66, pls. 1-3.; TROUESSART, 1904: 286.; KELLOGG, 1922:119.; ALEKSEEV, 1924a:32.; BOGACHEV, 1927:141-143.; KRETZOI, 1941:352.; FRIANT, 1947:10, 12, pl. 2, figs. 1a-c.; TOTH, 1948:183-194.; MCLAREN, 1960:51-52, 58.; KING, 1964:131.; THENIUS, 1969: 319.;— HENDEY and REPENNING, 1972:85.; RAY, 1976:19.; GRIGORESCU, 1977:412, 417.; NICOLAS, 1978:456.

Leptophoca? vindobonensis: RAY, 1977:395, 398.; SAVAGE and RUSSELL, 1983:292-293.; MUIZON, 1992:36.

"*Phoca*" *vindobonensis*: KRETZOI, 1941:353.; HENDEY and REPENNING, 1972:85.; MCLAREN, 1975:44.; MITCHELL, 1975:23.; MUIZON, 1982a:190, 205.

Phoca (Phoca) vindobonensis (sic; lapsus): FRIANT, 1947:7.

Phoca (Phoca) holitchensis: FRIANT, 1947:7.

Praepusa tarchankutica: ANTONIUK and KORETSKY, 1984:27-31, figs. 1-3.

Lectotype: Femur; collection of NHMW; illustrated and described by TOULA (1897: 47-71, pl. 2, fig. 2) as *Phoca vindobonensis*.

Type locality: Neussdorf (Vienna) Austria, Early Sarmatian of Vienna Basin.

Referred material:

Ukraine, Tarchankut: IZUAN, collection #64 — two skulls, adult and juvenile, two mandibles (juv.) without ascending rami, scapulae, two humeri, two radii; material partly described by ANTONIUK and KORETSKY (1984); collection of ZIN — three humeri, incomplete mandible, two ulnae (#31873 and without number), fragment of humerus without number.

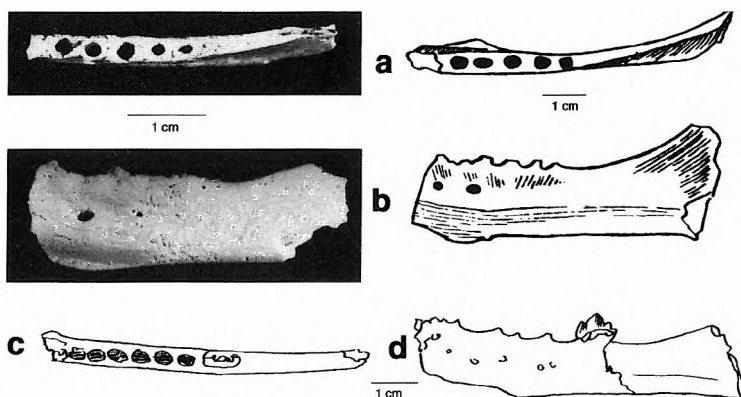


Figure 18. *Praepusa pannonica*, incomplete mandible from Moldavia, without number

a = in occlusal and b = in labial views; fragment of mandible, illustrated by Kretzoi (1941:351, fig. 1 = from Hungary; c = in occlusal and d = in labial views

Kerch Peninsula (Kamysh-Burun region, Lake Tobechik): IZUAN collection #64 — six femora and three humeri.

Village of Gritzev: IZUAN collection #64 — two femora.

Village of Kirovo, Odessa region: IZUAN collection #64 — two humeri.

Village of Suchaya Kalina: IZUAN collection #64 — humerus. IZUAN collection #2223 — humerus. Exact locality unknown for this specimen.

Moldavia: City of Kishinev, IZUAN collection #64 — humerus; ZIN — femur #1, material described by NORDMANN (1858).

Kazakhstan, Mangyshlak Peninsula: IZGK, collection of Laboratory of Paleozoology, humeri ##104, 105, 107, 544 and 545 [last two humeri from the same individual as L. and R. radii (##546-547),

L. and R. ulnae (##548-549), L. and R. femora (##542-543), L. and R. tibiae and fibulae (##551-552) and phalanges], ##553-557, 10 fragments without numbers, one humerus without number (from the same individual as innominate).

5 fragments of scapulae without numbers, one fragment without number (from the same individual as humerus and innominate).

Ulnae ##3344-86, 3347-86, and 2 fragments without numbers.

Innominate ##102, 2890 and 6 fragments without numbers, one fragment without number (from the same individual as humerus and scapula).

Femora ##19, 20, 50, 54, 64, 106, 218, 282, 560, 563, 565 and 17 fragments without numbers.

Tibiae and fibulae ##190, 202, 206, 566, 567, 568, 810 and 13 fragments without numbers.

Austria, Nussdorf, NHMW: casts of two femora: ##A 3966, A 3967; humeri R. and L. #243(1957); two humeri, R. and L. from one individual: ##1890/XXI, 1859/XXVII.

Emended diagnosis: This seal is smaller than the type species, with condylobasal length of cranium near 127 mm; upper incisors form u-shaped arcade; preorbital part of maxilla with very short, pronounced convexity; frontal contact of nasal bones much shorter than maxillary contact; interorbital space narrowing between anterior parts of orbits and broader more posteriorly; interorbital width less than 10% of mastoid width; diameter of infraorbital foramen greater than diameter of alveolus of upper canine; vomer overlaps preclinoid process; anterior palatal foramina oval-shaped and shallow; palatal groove shallow but well defined; anteroposterior length of tympanic bulla lesser than distance between bullae; jugular process well developed; width of mastoid process less than half length of tympanic bulla; mastoid convexity does not turn down behind mastoid process; connection between zygomatic process of squamosal and mastoid process absent. Dimensions of p4, P4 exceed those of m1, M1; cusp of p1 reaches 2/3 of canine's height; cheek teeth with three cusps, except p1 - m1 and P1 - M1. Symphyseal part of mandible bluntly rounded; chin prominence located between p3 and p4.

Diagnostic features of humerus and femur as for the genus.

Description: This species is smaller in body size than modern *Pusa sibirica*. Its dental formula is the same as in other

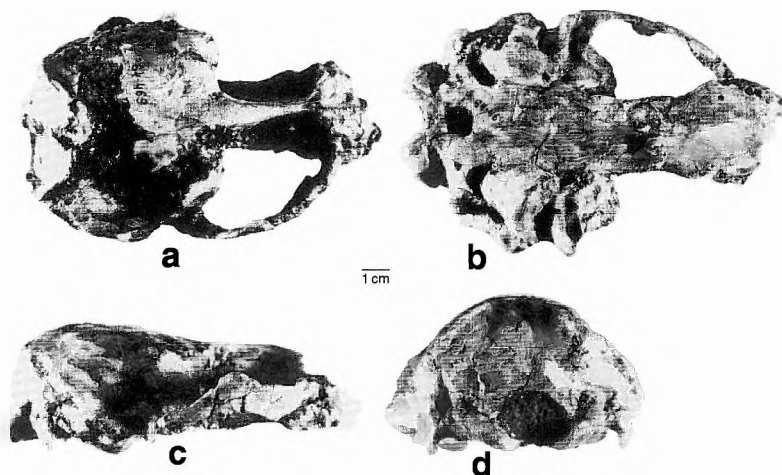


Figure 19. *Praepusa vindobonensis* new comb., skull, #IZUAN N64-469, adult individual

a = in dorsal; b = ventral; c = lateral; and d = caudal views

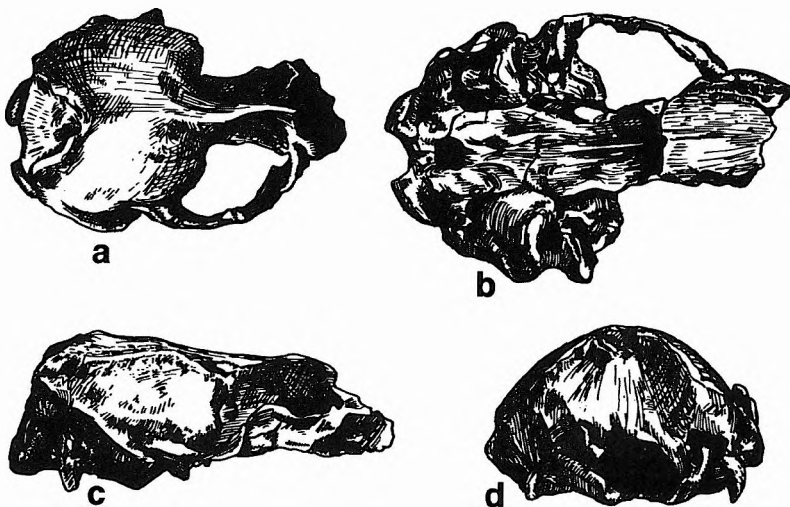


Figure 20. *Praepusa vindobonensis* new comb., skull, #IZUAN N64-469, adult individual; drawing of the photograph

a = in dorsal; b = ventral; c = lateral; and d = caudal views

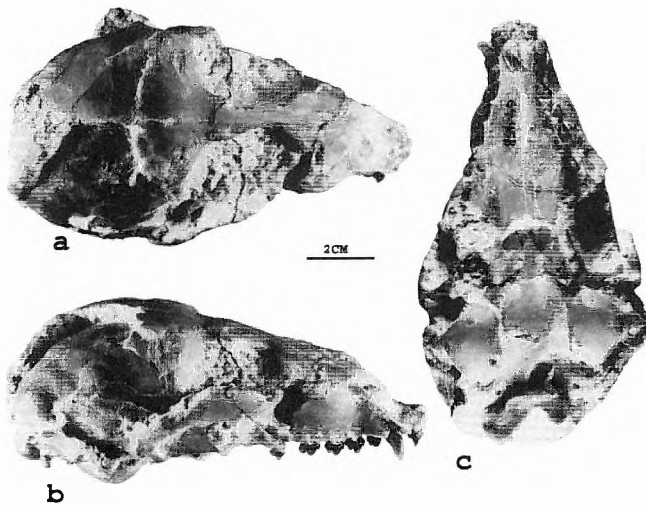


Figure 21. *Praepusa vindobonensis* new comb., skull, #IZUAN N64-468, juvenile
a = in dorsal; b = lateral; and c = ventral views

between the frontal bones. The width of the nasal bones is much less than their whole length.

The infraorbital foramen lies above M1. The diameter of the alveolus of the maxillary canine is less than 1/4 of the diameter of the infraorbital foramen.

The palatal process of the maxilla is a flat plate. The anterior palatal foramen is oval and shallow as for other phocids (WOZENCRAFT 1989). The posterior palatal foramen is caudal to M1. The anterior and posterior palatal foramina are connected by a shallow anteroposteriorly-aligned groove.

Laterally, the bulla (Figs. 20, 22) is extended as a short tube, with a prominent ventral lip forming the ventral margin of the external auditory meatus. This opening is oval and protrudes obliquely in an anterior direction. The rim of the external auditory meatus is in contact with the mastoid process.

The postglenoid process lies 9mm from the ventral lip of the external auditory meatus. The postglenoid process and mastoid are combined and form a pronounced prominence extending laterally from the tympanic bulla. The postglenoid foramen is well developed.

In *Praepusa vindobonensis*, a shallow and short groove extends anterolaterally from the stylomastoid foramen between the meatal tube of the bulla and the mastoid process (as in all phocids).

In ventral view, the tympanic bulla (Figs. 19, b – 20, b; 21, c; 22, b) is oval-triangular in outline, and has a smoothly convex ventral surface. It is slightly inflated in its anterolateral parts (in the adult) and slopes uniformly toward the external auditory meatus. The antero-posterior length of the tympanic bulla is less than the distance between the bullae; this ratio is similar to that of the genus *Phoca*. The length of the tympanic bulla (34mm) is 4.2 times the anteroposterior width of the glenoid fossa (8mm), whereas in other phocines it is 2.5–3.0 times greater than the width.

As in *Devinophoca*, the inflated anterior portion of the bulla (presumably the ectotympanic) is separated from the more flattened posterior portion (presumably entotympanic) by a distinct ridge instead of a sulcus.

The carotid foramen is visible in ventral view as in *Devinophoca*, in contrast to other phocines (BERTA and WYSS 1994). The posterior carotid foramen does not

phocines. The vomer overlaps the preclinoid process (Figs. 19–22, Table 4). In the adult it reaches the middle part of the tympanic bulla; in juveniles it reaches the oval foramen, which is formed by the temporal bone. The rostral part of the adult skull is unknown. In the young individual the width of the rostral part of the skull is 3.5 times smaller than the mastoid width. The skull is lower in its facial than in its occipital part. The preorbital part of the maxilla is short and convex, and the same shape as in the other Phocinae (CHAPSKII 1974).

The anterior edge of the orbit lies behind M1 (Fig. 19). In young individuals, the supraorbital process of the frontal and the anteroposterior process on the anterior margin of the maxilla are represented by small tubercles.

The frontal contact of the nasal bone is much shorter than the maxillary contact, as in other Phocinae (CHAPSKII 1974). Posteriorly, the nasal bones together form a V-shaped projection, inserted

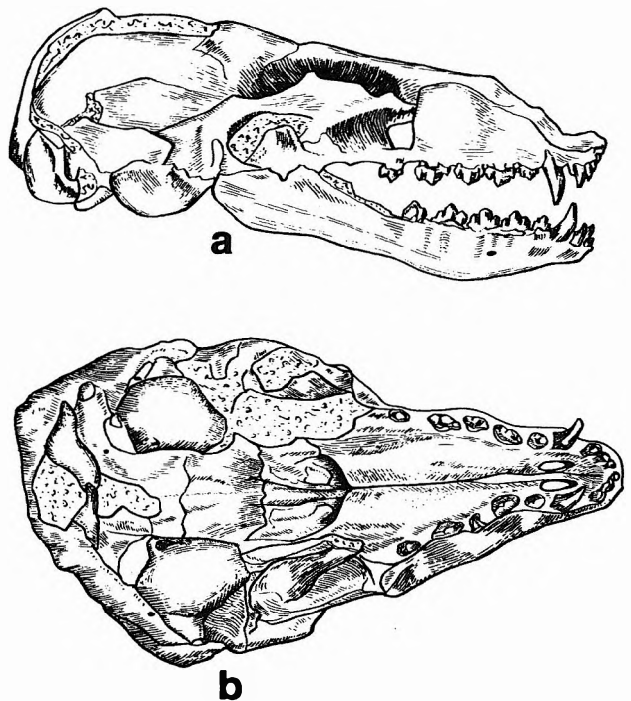


Figure 22. *Praepusa vindobonensis* new comb., skull, #IZUAN N64-468, juvenile; drawing of the photograph
a = in lateral and b = ventral views

open into a common fossa with the posterior lacerate foramen (as in *Devinophoca*).

The posterior lacerate foramen, as in *Devinophoca*, does not reach the base of the paroccipital process as in other phocids (MITCHELL and TEDFORD 1973). The posterior lacerate foramen surrounds the posteromedial portion of the bulla.

The mastoid process does not extend far laterally, nor does it obscure the bulla in lateral view. The inflation of the lateral side of the squamosal, between the paroccipital and mastoid process, is present in *Pr. vindobonensis* also. The small crest connecting the paroccipital process and mastoid is present. The connection between the zygomatic process of the squamosal and mastoid is absent, in contrast to other Recent species of phocines.

The paroccipital process (Fig. 20, c–d) is large (its height is 9 mm; this is nearly equal to the height of the tympanic bulla), and does not border upon the mastoid process. In its anterior part it is convex. In the juvenile individual the height of the paroccipital process is 6mm.

Maxillary canine is insignificantly smaller than mandibular ones; their shape is identical to the shape of the canine in *Pusa*. P1 is single-rooted, without basal cingula (its metacone is barely outlined). The P2 - P4 are double-rooted teeth with broad basal cingula. Their paracones are considerably smaller than the metacones. M1 is a double-rooted tooth with a single cusp; its crown is triangular in lateral view, without basal cingula. Its length is 74% of the length of P4 (Table 4).

Mandible (Fig. 23, Table 5). Incisors correspond in shape and size to those of representatives of the Tribe Phocini. The canines are small, and the main cusp of p1 barely reaches two-thirds of the canine's height. Premolars are seated obliquely relative to the axis of the tooth row, with the posterior part of the tooth displaced labially. On cheek teeth (except m1), additional cusps reach two-thirds of the main cusp's height; p2 - p4 are double-rooted, and the main cusp is rounded-triangular; m1 is single-cusped with the main cusp of triangular shape. The chin prominence is located between p3 and p4. The length of alveolus m1 is shorter than that of p4; the retromolar space is elongated.

Humerus (Figs. 24, 28; Table 6a). The lesser tubercle is slightly elongated along the bone's axis and is barely at the same level as the head, but lower than the greater tubercle. The intertubercular groove is very narrow and deep. The head is compressed mediolaterally. The ratio of the head's width to its height is 103%. The deltoid crest has the form of a sharp band smoothly descending to the condyles, where it ends at the coronoid fossa. The maximal width of the deltoid crest is in its proximal part, at the level of the lesser tubercle. The entepicondylar foramen is small, with a wide bridge over it. The coronoid fossa is shallow, and lies at the same level as the lateral epicondyle.

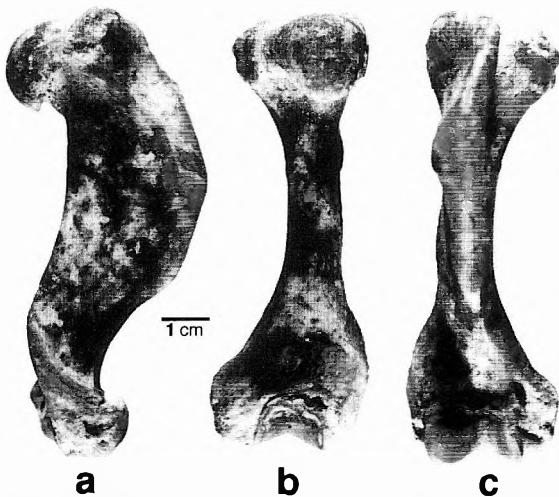


Figure 24. *Praeypusa vindobonensis* new comb., humerus, #IZUAN N64-2, adult

a = in lateral; b = caudal; and c = in cranial views

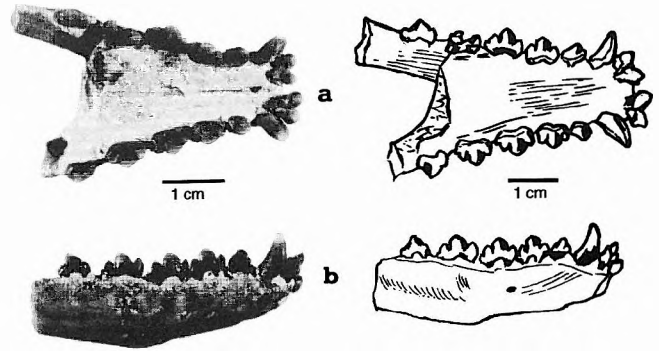


Figure 23. *Praeypusa vindobonensis* new comb., mandible, #IZUAN N64-468, juvenile

a = in occlusal view and its drawing; b = in lateral view and its drawing

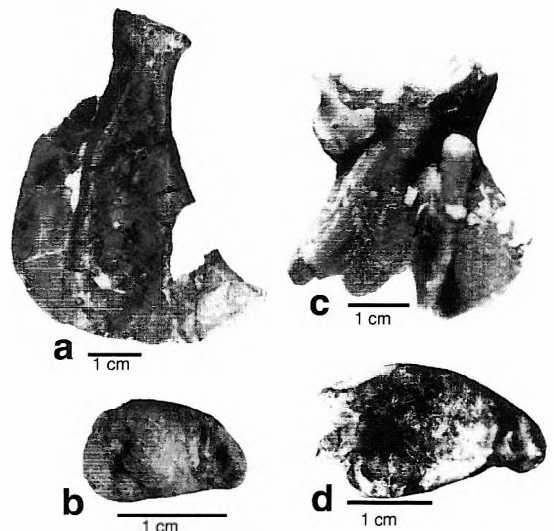


Figure 25. *Praeypusa vindobonensis* new comb., scapulae, #IZUAN N64-468, juvenile

a = in lateral and b = in glenoidal views; Fragment of scapula from Tarchankut, adult; c = in lateral and d = in glenoidal views

Table 8

Means ($X \pm SE$) and range for measurements (mm) of number in samples (n) of scapulae

Measurements	<i>Praepusa vindobonensis</i>				<i>Leptophoca lenis</i>
	juv.	ad.			
		n	$X \pm SE$	Range	
Absolute length	62.0	0	—	—	138.0
Width of collum	12.0	5	18.4	16.5–22.0	33.0
Anteroposterior diameter of cavitas glenoidale	8.0	5	14.2	13.5–15.0	33.0
Transverse diameter of cavitas glenoidale	9.5	5	21.5	19.0–28.5	22.0
Anteroposterior diameter of vertebral border	15.0	0	—	—	155.0
Distance from the base to vertebral end of spine	6.5	0	—	—	16.0
Maximal thickness of scapula in its spine	6.5	1	0	22.0	34.0

Scapula (Figs. 25, 28; Table 8). The scapular spine ends smoothly, and does not reach the cranial angle. The acromion is well developed, and does not reach the ventral angle. In the cervical region, the infra-articular tuberosity (in the juvenile individual) is not pronounced, in contrast to the adult. The infraspinous fossa is wider and deeper than the supraspinous. The vertebral border of the scapula is strictly perpendicular to the scapular spine. The maximal width of the scapula is 77.4% of its total length (in juvenile).

Ulna (Fig. 26, Table 9). The caudal border of the bone is sharpened and acute. The cranial surface is rounded and somewhat concave. The anterior end of the olecranon is not preserved. The olecranon is short and abruptly passes onto the diaphysis of the bone. On the medial surface, the proximal tuberosity has only one barely visible prominence. On its lateral surface, the fossa for attachment of the abductor pollicis longus muscle (PIÉRARD 1971) is absent. The coronoid process protrudes slightly forward over the radial notch (GROMOVA 1950:159). The radial notch is not pronounced. On the medial surface of the diaphysis is located a 150mm long groove along the lower border of the coronoid process. This groove is surrounded by sharp crests. The interosseous crest is swollen to form a prominence which markedly protrudes externally. The styloid process posteriorly is slightly turned toward the lateral surface.



Figure 26. *Praepusa vindobonensis* new comb., ulna, #IZUAN N64-468, juvenile

a = in lateral and b = in cranial views

Table 9
Means (X) and range for measurements (mm) of numbers in sample (n) of ulna of *Praepusa vindobonensis*

Measurements	juv.	ad.		
		n	X	Range
Absolute length	106.5	1	0	99.0
Width of incisura trochlearis in upper part	8.5	7	10.1	9.0–11.0
Width of incisura trochlearis in lower part	7.5	6	8.2	7.5–11.0
Maximal width of middle part of diaphysis	10.5	3	11.0	10.0–12.5
Maximal width of distal epiphysis	12.6	2	13.0	12.0–14.0
Width of bone at the level of lower part of incisura trochlearis	17.0	4	15.5	15.5–17.5
Width of olecranon	7.0	2	36.5	35.0–38.0
Transverse diameter of proximal epiphysis at the level of processus anconeus	25.0	2	21.0	19.0–23.0

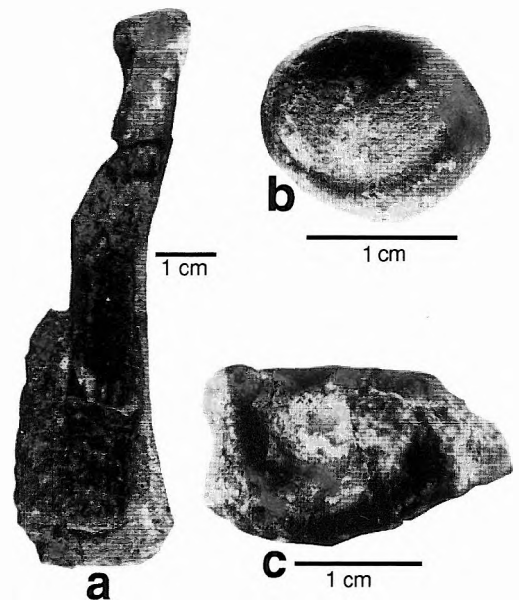


Figure 27. *Praepusa vindobonensis* new comb., radius, IZUAN, without number, adult

a = in medial; b = in proximal; and c = in distal views

Radius (Figs. 27–28; Table 10). The radial tuberosity is not pronounced, but has a narrow spine-like ridge. It is elongated along the axis of the bone. In other respects, the bone does not differ from those of Recent phocines.

Innominate (Fig. 29; Table 11). The ilium is thin, and the iliac crest is only slightly everted and excavated on its exterior surface.

The iliac tuberosity and caudal dorsal iliac spine are very well developed for the size of the bone. The iliopectineal eminence is well

expressed, and situated lower than the proximal border of the acetabular fossa. The greater ischiatic notch is very short and concave. At the level of the caudal dorsal iliac spine on the body of the ilium is located a shallow fossa. However, the degree of development of this fossa varies individually. The edges of the acetabular fossa rise above the surface of the body. The acetabulum is deep and circular, with a well-marked cotyloid notch. The eminence for the musculus gluteus medius is poorly developed and terminates on the same level with the iliac tuberosity.

The ischium and pubis are not preserved.

Femur (Fig. 30; Table 7a). In their size, femora of *P. vindobonensis* are similar to those of the modern *Pusa sibirica*. The greater trochanter extends proximally much higher than the head ($M = 4.3$ mm, $n = 7$); its proximal and distal parts are

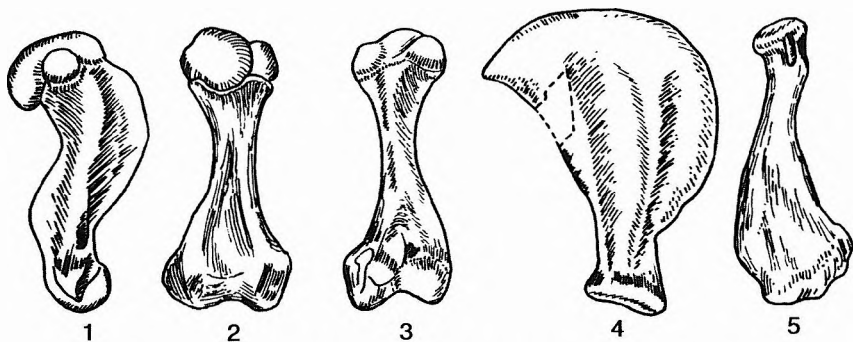


Figure 28. *Praepusa vindobonensis* new comb., #IZUAN N64-468, juvenile
1 — humerus in medial, 2 — caudal, and 3 — in cranial views, 4 — scapula from the same individual in lateral view, 5 — radius from the same individual in medial view

Table 10

Means (\bar{X}) and range for measurements (mm) of numbers in sample (n) of radius of *Praepusa vindobonensis*

Measurements	juv.			ad.		
	n	\bar{X}	Range	n	\bar{X}	Range
Absolute length	3	76.2	56.0–79.0	2	0	91.5; 88.5
Width of diaphysis	3	13.8	10.0–16.0	5	13.3	11.0–16.5
Width of distal epiphysis	3	22.8	20.5–25.5	7	24.5	22.0–27.0
Width of articulation surface of distal epiphysis	2	10.8	9.5; 12.0	7	12.2	11.5–13.0
Width of articulation surface, disposition of medial from articulation cavity	2	8.3	8.0–8.5	7	7.9	6.5–10.5
Lesser diameter of caput	3	9.8	8.0–11.0	3	13.2	12.5–14.0
Least width of proximal epiphysis	3	8.3	7.0–9.0	3	9.3	9.0–9.5
Greater diameter of caput	3	12.5	11.0–13.5	3	15.5	14.0–17.0
Anteroposterior diameter of distal epiphysis	3	13.0	12.5–13.5	9	12.4	11.0–15.0

Table 10a

Means (\bar{X}) and range for measurements (mm) of number in samples (n) of radii

Measurements	<i>Prophoca proxima</i>	<i>Leptophoca lenis</i>		
	Range	n	\bar{X}	Range
Absolute length	0	1	—	114.0
Width of diaphysis	19.3	6	15.4	15.0–16.0
Width of distal epiphysis	39.3	4	34.3	30.0–42.0
Width of articulation surface of distal epiphysis	0	—	—	—
Width of articulation surface, disposition of medial from articulation cavity	0	—	—	—
Lesser diameter of caput	19.3	4	16.8	15.5–18.0
Least width of proximal epiphysis	16.9	6	14.1	12.0–15.5
Greater diameter of caput	21.0	4	19.0	18.0–20.0
Anteroposterior diameter of distal epiphysis	21.1	3	17.4	12.0–19.0



Figure 29. *Praepusa vindobonensis* new comb., innominate, #IZUAN N64-468, juvenile; in lateral view

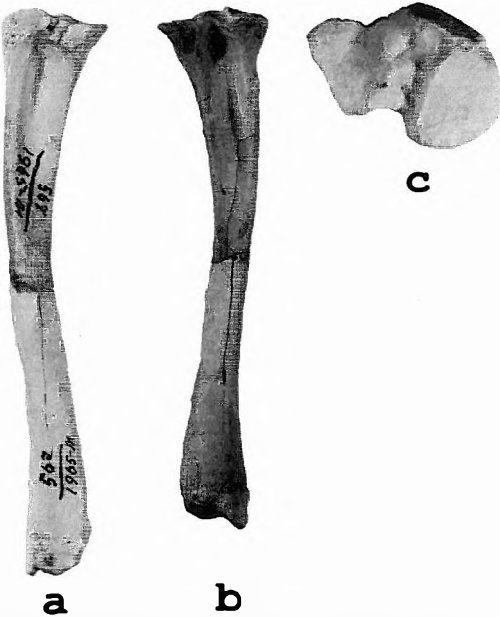


Figure 31. *Praepusa vindobonensis* new comb., tibia and fibula, adult, from Kazakhstan, #IZGK 567/1965-M

a = caudal, b = cranial, and c = sagittal views

Table 11

Means (X) and range (OR) for measurements (mm) of number in samples (n) of innominates

Species	From center of acetabulum to iliac crest = A	Width of level of iliac crest = O	Percentage O/A × 100
<i>Praepusa vindobonensis</i>	$n = 1$ $X = 41.0$	$n = 3$ $X = 37.5$ $OR = 35.5-39.0$	91.5
<i>Leptophoca lenis</i>	$n = 6$ $X = 73.8$ $OR = 66.0-83.0$	$n = 5$ $X = 59.4$ $OR = 52.0-76.0$	80.5

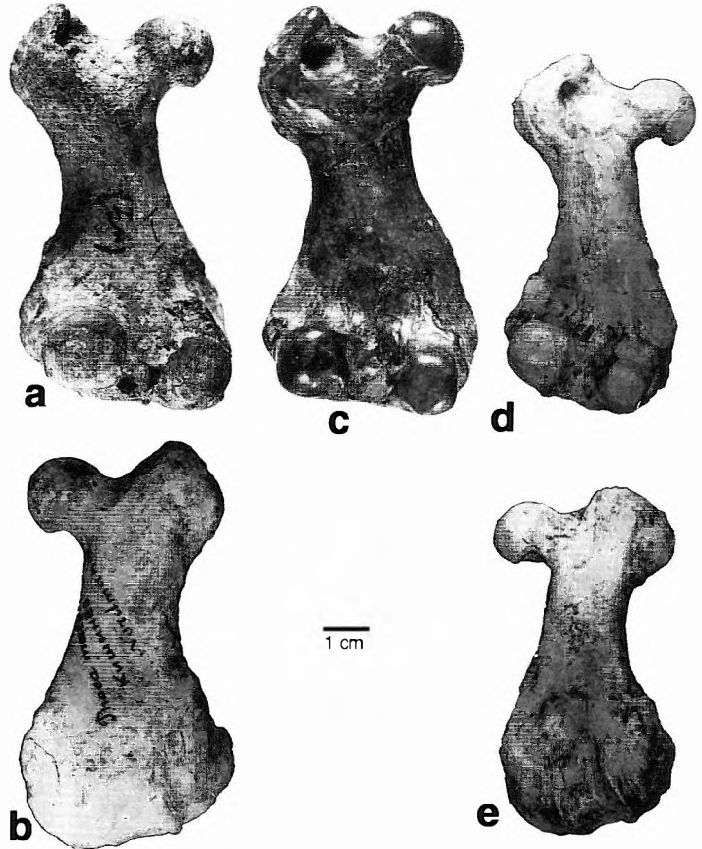


Figure 30. *Praepusa vindobonensis* new comb., femora, adult, collection of Nordmann, ZIN #1, from Moldavia

a = in caudal and b = in cranial views. Femur from Ukraine, #IZUAN 64-455, c = in caudal view. Cast of femur from Austria, #A 3967 by (illustrated Toulou, 1898, pl. 2, fig. 2), d = in caudal and e = cranial views

Table 12

Means (X) and range for measurements (mm) of number in samples (n) of tibia

Measurements	<i>Praepusa vindobonensis</i>			<i>Leptophoca lenis</i>		
	n	X	Range	n	X	Range
Width of proximal epiphysis	8	30.4	28.0-34.5	16	46.3	44.0-58.0
Width of distal epiphysis	10	18.1	17.0-21.0	7	28.3	25.0-33.0

of the same width. The trochanteric fossa is deep and widely open, reaching the middle of the greater trochanter. The intertrochanteric crest is relatively strongly developed and extends to the middle of the bone, much lower than the distal part of the neck. The head in females is considerably smaller than in males, and is seated on a long narrow neck. The condyles are relatively small, and are widely separated. Above the medial condyle, the plantar fossa is weakly pronounced. Both epicondyles are considerably thinned. The minimal width of the diaphysis is in the middle of the bone.

Tibia and fibula (Fig. 31; Table 12). The two condyles are weakly concave in their centers, and ellipsoidal in shape.

The intercondyloid eminence is weak and low, with borders only slightly raised above the two lateral perimeters of the condyles.

The popliteal notch is shallow and quite narrow, but well marked. The tibial crest is enlarged. On the cranial aspect of the tibia, the tibial tuberosity is flattened, extended transverse to the axis of the bone, and almost square in shape. The muscular groove is flattened and broad. The distal articular surface is ellipsoidal and deep. Posteriorly, proximal to the medial malleolus, is a shallow, wide groove for the tendon of *m. flexor digitorum longus*.

Comparison: The small series of remains that I analyzed allow the conclusion that *Praepusa vindobonensis* differs from the type species by its smaller size; by the lack of substantial difference between diastemata of p3 - p4 and p4 - m1; and by higher index of the form of the mandibular body (the ratio between the height of the mandibular body between p3 - p4 and the height under p2) — respectively, 122.3% and in *P. pannonica* — 114.3%.

Discussion: In publications of GERVAIS (1852; 1853), VAN BENEDEN (1877), ALEKSEEV (1924a), ZAPFE (1937), KRETZOI (1941), MUIZON and HENDEY (1980), and MUIZON (1981a), only eight fragments of mandibles are described of fossil representatives of the family Phocidae. They are assigned to the genera *Phoca*, *Pristiphoca*, *Miophoca*, *Praepusa*, *Callophoca*, *Piscophoca*, *Homiphoca* and *Acrophoca*. However, the great similarity between the mandible of the Tarchankut seal and those of the genus *Praepusa*, described by KRETZOI from the Middle Sarmatian of Hungary, allows me to assign the Crimean finds to this genus.

Despite the wide distribution of *P. vindobonensis*, this species was represented only by bones of the extremities from the Vienna Basin, described under the name "*Phoca*" *viennensis antiqua* by BLAINVILLE (1842). It should be noted that BLAINVILLE did not present measurements or morphological characters of the new species. Following this, BRÜHL (1860), confusing the left and right sides of the animal's body based on material of BLAINVILLE, described the new species *Phoca holitschensis*. TOULA (1897) drew attention to this error, coined the new name *vindobonensis* (which he apparently considered a justified emendation of *viennensis*), and proposed to consider *holitschensis* as a synonym of *vindobonensis*. TOULA presented a detailed description and measurements of bones of the girdles with extremities, most vertebrae, sternum, and some ribs. Evidently for these reasons, many authors (see synonymies) referred to the seal of the Vienna Basin as *Ph. vindobonensis*. I consider this name quite justified, as did KRETZOI (1941). Since it has been used by all recent authors in preference to *viennensis*, despite the priority principle (see International Code of Zoological Nomenclature, 1985, Articles 23b, 79c, and 80), I maintain the existing usage of the species name, *Ph. vindobonensis* for this animal.

The extensive investigations of fossil remains of seals from the Middle Sarmatian deposits of the Southern European part of the former Soviet Union allow, on one hand, a more accurate diagnosis of the genus *Praepusa*, since morphologic characters of the mandibles from this region actually do not differ from those of the mandible of the type species from Hungary described by KRETZOI. And, on the other hand, they allow comparison between this taxon and other genera of the subfamily Phocinae.

From analysis of the casts of Vienna Basin humeri and femora from the NHMW, I came to the conclusion that these remains are in no way different from those of the seal from the Crimea. Since we (ANTONIUK and KORETSKY 1984) previously assigned the Tarchankut seal to the genus *Praepusa*, species *tarchankutica*, this species name, as a junior synonym, is no longer valid. Clearly, the reassignment of the species "*Phoca*" *vindobonensis* to another genus (*Praepusa*) is also justifiable and well founded. This approach seems more reasonable than recognizing two or more species originating from deposits close in age and similar in morphology, and allows some degree of stabilization of the nomenclature of the subfamily.

Geological age and distribution: Early Sarmatian of Vienna Basin (Vienna, Nussdorf); Middle Sarmatian of Ukraine (Kerch Peninsula: Kamysh-Burun, Lake Tobechik; Tarchankut Peninsula); village of Gritzev; Middle Sarmatian of Moldavia (vicinity of Kishinev).

The identification of remains from the Vienna Basin, Moldavia and Ukraine as conspecific allow confirms of the statements of ANDRUSOV (1929) and BRUZGIN (1966) regarding the redeposition of seal bones in several localities of the Kerch Peninsula from Middle Sarmatian into Kimmerian horizons.

Genus *Cryptophoca* KORETSKY and RAY, 1994

Phoca: EICHWALD, 1850 (in part):210–218, 1853 (in part):391–400.; NORDMANN, 1858: pl. 23, figs. 1, 2, 8–10; 1860 (in part):320–321, 356–357.; VAN BENEDEEN, 1877:26.; TOULA, 1898:50.; ALEKSEEV, 1924b:202; 1926: 138–143.; SAVAGE and RUSSELL, 1983:292–294.
Monotherium: TROUESSART, 1897:380; 1904:283.; FRIANT, 1947:50 (non pl. 1, figs. 2a–c).; KING, 1964:131; 1983:132.
Monotherium: KELLOGG, 1922:114.; KRETZOL, 1941:353.; MCLAREN, 1960:50–52, 56–57, fig. 1e.; GRIGORESCU, 1977:407. 413–415, 417, fig. 5b.; MUIZON, 1982:202–205.; GRIGORESCU, 1977:407.
 “*Monotherium*”: MUIZON, 1992:37.
Cryptophoca: KORETSKY and RAY, 1994:17–26.

Type species: *Phoca maeotica* NORDMANN, 1860:321, pl. 23, figs. 8, 9; Kishinev, Middle Sarmatian of Moldavia.

Included species: Only the type species.

Diagnosis: Lower canine and p1 very large (Tables 5a, b), p1 single-rooted; symphysis straight, its inner part enlarged from anterior alveolus p2 to canine; mental protuberance located between p3 and p4. Deltoid crest up to 1/4 of humeral length, not reaching coronoid fossa; proximal border of deltoid crest is its widest part; lesser tubercle of humerus located on same level as proximal border of deltoid crest; head round. Femur with almost rectangular greater trochanter; trochanteric fossa deep and open; head of femur large (Table 7a), situated on relatively narrow, short neck; minimal width of diaphysis shifted toward proximal epiphysis; greatest breadth across condyles 20–21% of bone length; proximal epiphysis narrower than the distal by 2–8%.

Comparison: The materials in my possession at present allow only the conclusion that, as judged by dimensions and characters of the mandible and bones of the extremities, representatives of this genus are closely related to the modern species of the genus *Pagophilus*. *Cryptophoca* differs from other known true seals by: straight shape of symphyseal part of mandible (except for *Pagophilus*), smaller height of body of mandible under p2 (except for *Phoca*, *Halichoerus*, and *Pagophilus*); lower position of lesser tubercle of humerus relative to head and its location on same level with proximal border of deltoid crest (except for *Erignathus*, *Pagophilus*, and *Monachopsis*); large rectangular greater trochanter (except for *Erignathus*, *Praepusa*, and *Sarmatonectes*); peculiar shape of both humerus and femur (Table 6a–7a).

In addition this genus differs distinctly from other genera as follows:

From *Pusa* by: larger dimensions; greater depth of body of mandible under p2; forward-shifted mental protuberance. Absence of intertubercular groove of humerus; large head of humerus; greater length of deltoid crest. Large swelling of intertrochanteric crest; deeper and wider trochanteric fossa; relatively larger head of femur (Fig. 9).

From *Phoca* by: flattened body of mandible; mental protuberance not labially bent; greater length of p4 alveolus relative to m1 alveolus; larger diastemata between teeth; single-rooted p1. Relatively greater length of deltoid crest of humerus. Larger size of intertrochanteric crest; relatively smaller condyles of femur.

From *Erignathus* by: smaller dimensions; mental protuberance of mandible slightly pronounced, shifted forward and not labially bent. Relatively greater length of deltoid crest of humerus and widening of latter's proximal border; round shape of head of humerus. Greater height of greater trochanter relative to femoral head; smaller size of neck; relatively narrower proximal epiphysis.

From *Halichoerus* by: greater mandibular flattening; pronounced mental protuberance; double-rooted p2-m1. Lateral position of deltoid crest of humerus; absence of intertubercular groove; round head of humerus. Presence of intertrochanteric crest of femur.

From *Pagophilus* by: forward-shifted mental protuberance. Lateral position of deltoid crest of humerus and widening of its proximal border. Deeper and wider trochanteric fossa of femur.

From *Histiophoca* by: far greater dimensions; longer tooth row. Lengthened deltoid crest of humerus with widening of its proximal border. Minimal width of femoral diaphysis shifted towards proximal epiphysis; more widely placed condyles.

From *Praepusa* by: far greater dimensions; greater height of body of mandible under p2; widening of tooth row from posterior alveolus p3 to canine. Alignment of lesser tubercle of humerus with proximal border of deltoid crest; slightly greater index of humeral head width. Least width of femoral diaphysis shifted toward proximal epiphysis; relatively smaller width of proximal epiphysis; large but relatively more closely placed condyles.

From *Monachopsis* by: far greater dimensions; double-rooted p2-m1 with large diastemata. Round head of humerus; short deltoid crest; higher and wider medial epicondyle. Deeper and more elongated trochanteric fossa of femur; relatively more narrow proximal epiphysis.

Discussion: NORDMANN (1860:313–326) described the species *Phoca maeotica* on the basis of dissociated postcranial bones extracted from material originally assigned by EICHWALD (1850) to his *Phoca pontica*. NORDMANN suggested a close affinity of this large seal with the monk seal. Later, TROUESSART (1898–1899, 1904), never questioning this relationship, transferred the species to the genus *Monotherium*, belonging to the subfamily Monachinae. However, the taxonomic position of this species has since been questioned. For instance, some systematists (KELLOGG 1922; MCLAREN 1960; GRIGORESCU

1976; MUIZON 1992), on the basis of the size of the distal epiphysis of the femur, classified *Phoca maeotica* with the monachine seals, whereas others (ALEKSEEV 1924a, b, 1926; BOGACHEV 1927; KIRPICHNIKOV 1961; RAY 1977; SAVAGE and RUSSELL 1983) considered it to be a phocine seal, or did not mention the placement of this species (MUIZON 1982).

In recent years, discoveries of cranial and postcranial remains of *Phoca maeotica* in the northern Black Sea region have greatly augmented the classic collection of von Nordmann. Although several taxa of phocids occur in the same deposits with the nominal species *Phoca maeotica*, I feel confident in my assignment here of the mandible and humeri on the basis of similarity in size and morphology and analogy with modern phocids. Making use of all available material, I conclude that the Kishinev seal belongs to the Subfamily Phocinae on the basis of: extension

of the symphyseal part of the mandible to the anterior border of the alveolus of p2; presence of the mental protuberance; trochlear crest of the humerus not separated from the coronoid fossa by a distinct lip; different size of the femoral condyles; small difference in the width of proximal and distal epiphyses; and absence or poor development of an intertrochanteric crest.

Furthermore, my study of *Phoca maeotica* not only corroborates its specific distinctness, but also requires distinguishing it as a new genus as described by KORETSKY and RAY (1994).

Distribution: Middle Sarmatian of the northern Black Sea littoral of the Ukraine, Moldavia, and Romania.

Cryptophoca maeotica (NORDMANN, 1860) KORETSKY and RAY, 1994

Figures 32–35; Tables 5a, b; 6a–7a

Phoca pontica: EICHWALD, 1850 (in part):210–218; 1853 (in part):391–400.

Phoca maeotica: NORDMANN, 1860 (in part):320–321, 356–357.; VAN BENEDEN, 1877:26.; TOULA, 1898:50.; ALEKSEEV, 1924b:202; 1926:138–143.; SAVAGE and RUSSELL, 1983:292–294.

Monotherium maeoticum: TROUSSART, 1897:380; 1904:283.; FRIANT, 1947:50 (non pl. 1, figs. 2a–c); KING, 1964:131; 1983:132.

Monotherium maeoticum: KELLOGG, 1922:114.; KRETZOI, 1941:353.; MCLAREN, 1960:50–52, 56–57, fig. 1e.; GRIGORESCU, 1977:407, 413–415, 417, fig. 5b.; MUIZON, 1982:202–205.

Monotherium maeotica: GRIGORESCU, 1977:407.

"*Monotherium*" *maesticum* (sic): MUIZON, 1992:37.

Cryptophoca maeotica: KORETSKY and RAY, 1994:17–26.

Lectotype: Left femur #1815, HMZ; illustrated by NORDMANN (1858: pl. 23, figs. 8, 9) as *Phoca* and described and named as *Phoca maeotica* in 1860. (Fig. 32)

Type locality: Middle Sarmatian of northern Black Sea littoral (Moldavia, Kishinev).

Referred material: Moldavia (Kishinev): ZIN, (collection of von Nordmann) eight femora, a part of the material described by von NORDMANN (1860), three humeri, without numbers; PIN, collection #1713 — nine femora, 1713/1329 and 1713/1330 — two incomplete

mandibular rami; OGUM — five femora, the materials described by ALEKSEEV (1926); IZUAN, collection #64 — one humerus; TGPI — ramus of the left mandible, without numbers (collections of A. N. Lungu); HMZ, (collection of von Nordmann) right humerus #1812

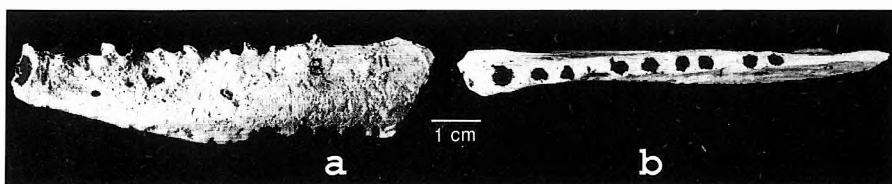


Figure 33. *Cryptophoca maeotica*, cast of the left mandibular ramus, without number, TGPI, Moldavia

a = labial and b = occlusal views

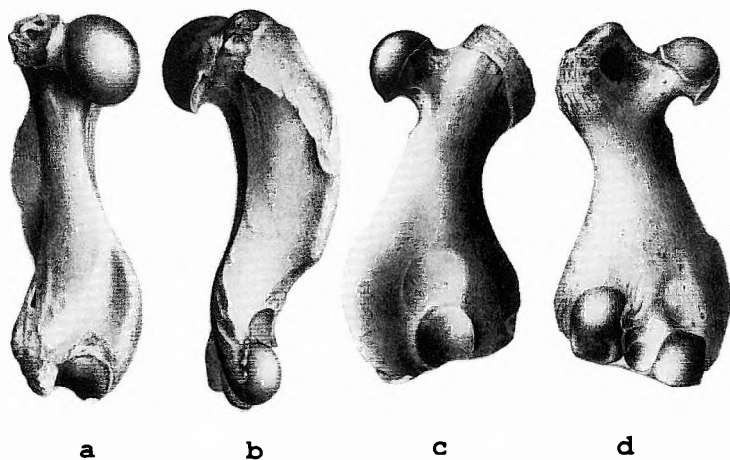


Figure 32. *Cryptophoca maeotica*. Right humerus from Kishinev (Moldavia), from NORDMANN (1858: pl. 23, figs. 1, 2), #HMZ 1812

a = caudal, b = lateral views. *Cryptophoca maeotica*. Lectotype, left femur from KISHINEV (Moldavia), from NORDMANN (1858: pl. 23, figs. 8,9), #HMZ 1812: c = cranial, d = caudal views

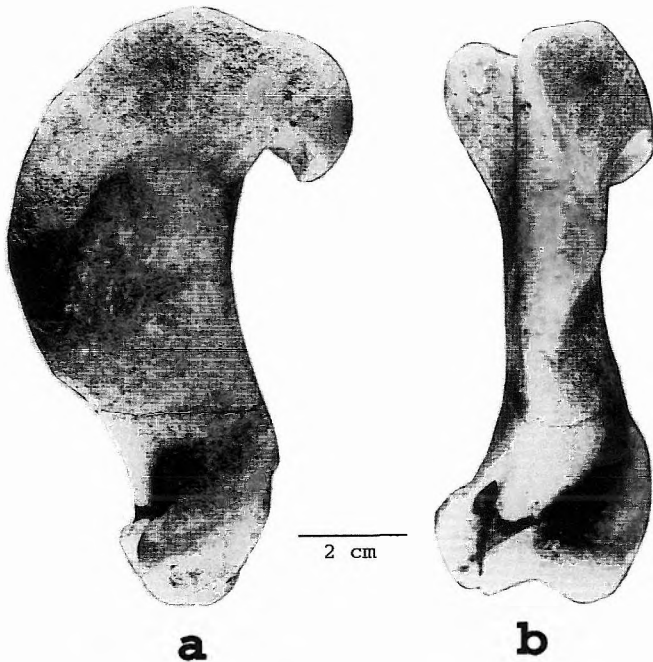


Figure 34. *Cryptophoca maeotica*. Left humerus from Kishinev (Moldavia), #IZUAN 64-530
a = lateral and b = cranial views

Humerus (Fig. 34; Table 6a). Lesser tubercle of humerus is slightly elongated and deviates only slightly from bone's axis. Intertubercular groove only slightly discernible. Deltoid crest widest proximally. Deltoid tuberosity located along middle of diaphysis. Coronoid fossa narrow and shallow. Lateral epicondyle reaches distal part of deltoid crest; medial epicondyle spreads from lower part of entepicondyle and ends below lateral epicondyle. Spiral groove not pronounced.

Femur (Fig. 35; Table 7a). Greater trochanter much higher than head, approaching a rectangular shape. Trochanteric fossa wide, deep, and open. Intertrochanteric crest located along middle part of femur, below trochanteric fossa. Smallest width of diaphysis is shifted to proximal part of femur.

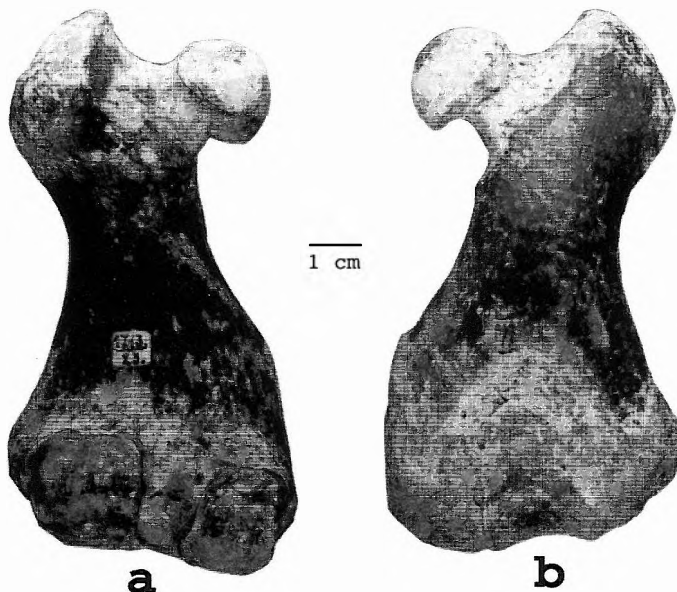


Figure 35. *Cryptophoca maeotica*. Left femur from Kishinev (Moldavia), #PIN 1713/23, Kishinev
a = caudal and b = cranial views

(illustrated by von NORDMANN 1858: pl. 23, fig. 10), left femur #1815 (illustrated by von NORDMANN 1858: pl. 23, figs. 8, 9), six femora without numbers (not illustrated); USNM (collection of Simionescu) — cast of left femur (original in UBFG #259/II, 5c).

Ukraine, Crimea, Kerch Peninsula (Kamysh-Burun): IZUAN, collection 64 — three femora.

Diagnosis: As for the genus.

Description: True seal, close in body size to modern genus *Pagophilus*.

Mandible (Fig. 33; Tables 5a, b). Not high, flat on lingual side. On labial side, body of mandible thickened in the middle from level of anterior alveolus of p2 to beginning of ascending ramus. All teeth arranged in alignment with the tooth row axis. Alveolar length of m1 smaller than that of p4; retro-molar space shortened. Mental protuberance located between anterior alveolus of p3 and anterior alveolus of p4. Maximal height of mandible between alveoli of p2 and p4. Symphyseal part straight and thick, i.e., the lower border of the mandible is not elevated with respect to alveolus of canine. Alveolus of p1 similar to canine alveolus, is very large. Evidently for this reason the mandible in its symphyseal part is considerably thickened.

Geological age and distribution: Upper Miocene, Middle Sarmatian (Bessarabian Formation) of the northern Black Sea littoral of the Ukraine, Moldavia, and Romania.

Sarmatonectes, new genus

Type species: *Sarmatonectes sintsovi* new species.

Included species: The genus is monotypic.

Etymology: Sarmato, in reference to the Sarmatian stage-age; and nectes, from Greek "nektes", swimmer.

Diagnosis: Deltoid crest extends more than 2/3 of humeral length; maximal width of deltoid crest located in its proximal portion; lesser tubercle of humerus located distal to proximal border of deltoid crest; head compressed craniocaudally; lateral epicondyle reaches middle of diaphysis. Proximal and distal parts of greater trochanter of femur approximately of equal width; trochanteric fossa shallow and opened medioproximally; lesser trochanter

small, located at same level as distal border of greater trochanter; head small, situated on relatively wide, short neck; minimum width of diaphysis located in middle part of bone; maximum intercondylar distance 12.3–14.3% of bone's length.

Comparison: The genus *Sarmatonectes* differs from other known seals by: distal location of the lesser tubercle of the humerus relative to the proximal border of the deltoid crest and to the head (except for *Leptophoca*); extension of the lateral epicondyle to the middle of the diaphysis; slight craniocaudal compression of the humeral head (except for *Halichoerus*, *Pusa*, *Monachopsis*, *Prophoca*, *Leptophoca*); relatively narrow and deep intertubercular groove of the humerus (except for *Phoca*, *Pusa*, *Pagophilus*, *Histriophoca*). By approximately equal width of proximal and distal parts of the greater trochanter of the femur (except for *Praepusa*, *Cryptophoca*); location of the insignificant lesser trochanter at the same level as the distal border of the greater trochanter (except for *Leptophoca*); smaller head relative to the bone's mass (except for *Phoca*, *Histriophoca*, *Praepusa*, *Monachopsis*); and smaller intercondylar distance compared to the bone's length (except for *Histriophoca*, *Halichoerus*, *Cryptophoca*).

In addition, this genus differs distinctly from other genera as follows:

From *Pusa* by: proximally wider deltoid crest of the humerus; longer, not dorsally averted deltoid crest relative to the absolute length of the bone.

From *Erignathus* by: smaller size; proximally wider deltoid crest of the humerus; longer, not dorsally averted deltoid crest relative to the absolute length of the bone; lateral epicondyle twice the length of the medial condyle; relatively higher and deeper coronoid fossa. By absence of the fovea capitis of the femur.

From *Halichoerus* by: smaller size; longer, not dorsally averted deltoid crest of the humerus relative to the absolute length of the bone. By shallow trochanteric fossa of the femur; presence of the intertrochanteric crest.

From *Pagophilus* by: smaller size; not dorsally averted deltoid crest; proximally wider deltoid crest. By shallow, but wide trochanteric fossa of the femur, which opens medially; relatively wide, short femoral neck.

From *Histriophoca* by: the deltoid crest extending more than 2/3 of humeral length.

From *Praepusa* by: greater size; location of the lesser tubercle of the humerus only slightly distal to the head; higher coronoid fossa. By shallow trochanteric fossa of the femur; wide and short neck.

From *Monachopsis* by greater size. By presence of intertrochanteric crest of the femur; least width of diaphysis being located in the middle of the femur.

From *Cryptophoca* by: smaller size; deeper and higher coronoid fossa of the humerus, reaching the middle of the lateral condyle. By shallow trochanteric fossa of the femur; least width of diaphysis being located in the middle of the femur.

From *Prophoca* by: smaller size; longer deltoid crest relative to the absolute length of the humerus; deeper and higher coronoid fossa, reaching the middle of the lateral condyle, ending proximally to medial epicondyle.

From *Leptophoca* by: smaller size; absence of a musculospiral groove on the humerus; deeper and higher coronoid fossa; deeper olecranon fossa. By shallow trochanteric fossa of the femur; more distally located lesser trochanter; least width of diaphysis being located in the middle of the femur.

Discussion: Some doubts might be raised about the wisdom of basing a new taxon, *S. sintsovi*, on such limited material as two femora and a humerus. However, according to my ecomorphotype hypothesis these bones belong to the same group. Thus, I can assign them to ecomorphotype III on the basis of characters such as: lesser tubercle slightly higher than the head of the humerus, and extended along the bone's axis; intertubercular groove not pronounced but instead compressed; maximum width of the deltoid crest is in its proximal part; greater trochanter slightly higher than the head of the femur; intertrochanteric crest shortened, and lowered on the diaphysis a little below the trochanteric fossa. Ecomorphological analysis is here applied on the level of alpha systematics, and I believe this approach justifies establishing a new taxon.

Distribution: Middle Miocene (Sarmatian) of the Eastern Paratethys.

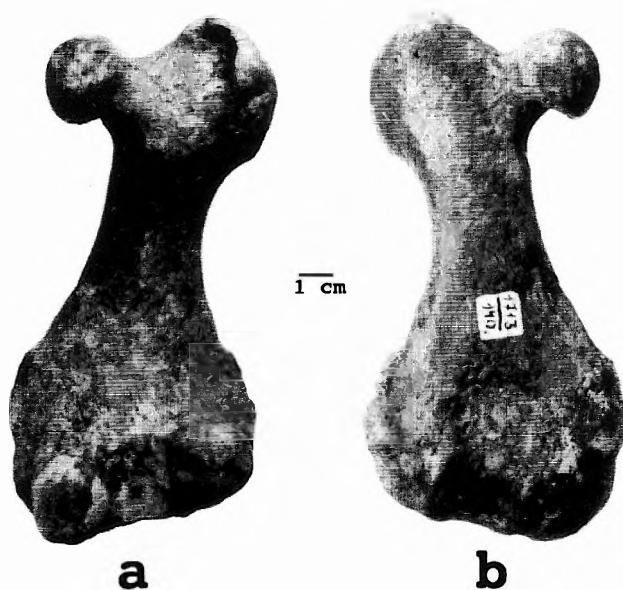


Figure 36. *Sarmatonectes sintsovi*. Right femur from Kishinev (Moldavia), #PIN 1713/140
a = caudal and b = cranial views

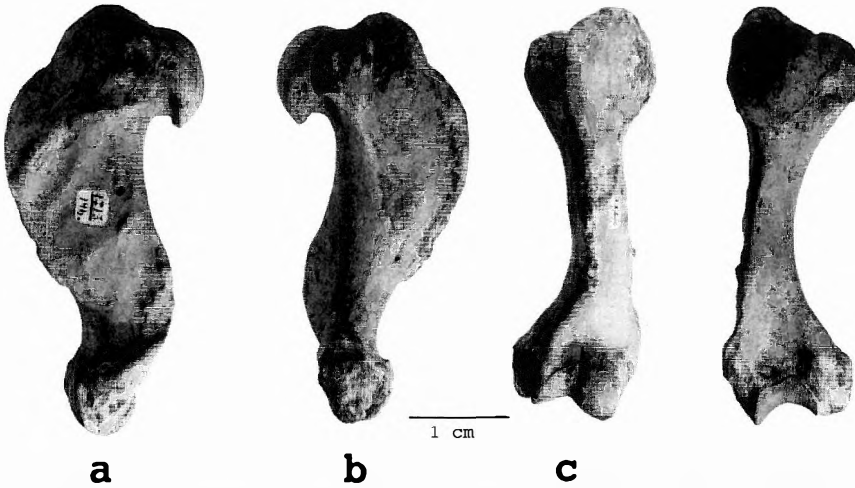


Figure 37. *Sarmatonectes sintsovi*. Left humerus from Kishinev (Moldavia), #PIN 1713/146

a = lateral; b = medial; c = cranial; and d = caudal views

Diagnosis: As for the genus.

Description:

Humerus (Fig. 37; Table 6b). The intertubercular groove is narrow and deep. The deltoid crest is widest proximally, and extends more than 2/3 of the length of the bone. The deltoid tuberosity is located proximal to the middle of the diaphysis. The lesser tubercle is slightly elongated along the bone's axis, well developed and located scarcely distal to the head of the humerus, and considerably below the greater tubercle. The head is slightly compressed craniocaudally. The musculospiral groove is not expressed. The lateral epicondyle is well developed, reaching beyond the distal part of the deltoid crest to the middle of the diaphysis, and extends 2" times farther proximally than the medial. The medial epicondyle is flattened, spreading from the lower part of the entepicondylar foramen and ending below the middle of the coronoid fossa. The coronoid fossa is deep, and forms a triangular depression extending proximal to the medial epicondyle, reaching the middle of the lateral epicondyle. The entepicondylar foramen is small and oval, with a very narrow bridge over it. The olecranon fossa is very deep.

Femur (Fig. 36; Table 7b). The femur of *Sarmatonectes sintsovi* is similar in size to those of the modern ringed seal, *Pusa hispida*. The greater trochanter extends proximally higher than the femoral head; its proximal and distal parts are equal in width. The trochanteric fossa is shallow and open (not covered laterally by the trochanter), reaching the distal 2/3 of the greater trochanter. The insubstantial intertrochanteric crest is located along the lateral side of the femur, below the trochanteric fossa, and does not reach the lesser trochanter. The lesser trochanter is very small and is located on the posterior side of the bone, at the same level as the distal border of the greater trochanter. The femoral head is small relative to the bone's mass, and seated on a wide, short neck. The least width of the diaphysis is located in the middle of the femur. The supracondylar fossa located above the lateral condyle is shallow but wide; the supracondylar fossa located above the medial condyle is deeper, but its radius is very small. The maximal intercondyloid width is 0.15 of the bone's length.

Geological age and distribution:

Middle Miocene (Middle Sarmatian) of the northern Black Sea littoral (Moldavia).

Sarmatonectes sintsovi, new species

Figures 36–37; Tables 6b–7b

Holotype: Right femur #1713/140, PIN, collection of Sintsov, Kishinev (Moldavia), Middle Sarmatian (Fig. 36).

Etymology: Named in honor of Dr. I. F. SINTSOV, collector of these and other materials of fossil seals.

Type locality: Middle Sarmatian of the northern Black Sea littoral, limestone quarries in the vicinity of Kishinev (Moldavia).

Referred material: Collection of PIN, Kishinev (Moldavia); left humerus #1713/146, femur #1713/1352.

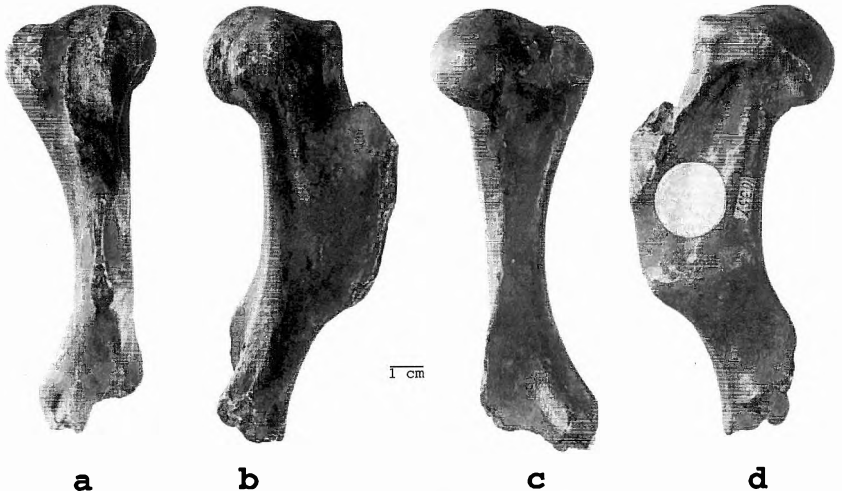


Figure 38. *Prophoca proxima*. Right humerus from Borderhout (Belgium), #IRSN 1146, Ct. M. 279, cast USNM 10357

a = cranial, b = medial, c = caudal, and d = lateral views

Genus *Prophoca* VAN BENEDEN, 1877

Prophoca: VAN BENEDEN, 1876a:802; 1876b:205 (nomen nudum).

Prophoca: VAN BENEDEN, 1877:78 (part), 80–81.; MOURLON 1877:609.; TOULA, 1898:53.; DOLLO, 1909:114.; KELLOGG, 1922:116.; SIMPSON, 1945:122.; FRIANT, 1946:7, 13.; MISONNE, 1958:15 (part).; KING, 1964:132.; RAY, 1976:394–395.; MUIZON, 1980: 124.; MCKENNA and BELL, 1998:257.

Leptophoca: RAY, 1976:394–395.; SAVAGE and RUSSELL, 1983:292.

Type species: *Prophoca proxima* VAN BENEDEN, 1877:80–81. Atlas pl. 18, figs. 12–16.

Included species: The type species only.

Diagnosis: Deltoid crest extends distally more than $\frac{2}{3}$ of humeral length, not reaching coronoid fossa; lesser tubercle of humerus located distally to the head but on same level as proximal border of deltoid crest; head compressed mediolaterally; lateral epicondyle reaches distal end of deltoid crest (Fig. 38).

Comparison: The genus *Prophoca* differs from other known seals by: distal location of the lesser tubercle of the humerus relative to the head (except for *Leptophoca*); location of the proximal borders of the lesser tubercle and deltoid crest at the same level (except for *Leptophoca* and *Cryptophoca*); extension of the deltoid crest distally more than $\frac{2}{3}$ of humeral length (except for *Praeypusa* and *Sarmatonectes*); mediolateral compression of the humeral head (except for *Phoca*, *Monachopsis*, and *Leptophoca*).

In addition, this genus differs distinctly from other genera as follows:

From *Pusa* by: greater size; longer deltoid crest; extension of the lateral epicondyle to the distal end of the deltoid crest.

From *Phoca* by: greater size; longer deltoid crest; termination of the medial epicondyle distal to the coronoid fossa.

From *Erignathus* by: smaller size; extension of the lateral epicondyle to the distal end of the deltoid crest.

From *Pagophilus* by: longer deltoid crest; termination of the medial epicondyle distal to the coronoid fossa.

From *Praeypusa* by: shorter and abruptly ended deltoid crest.

From *Monachopsis* by: the deltoid crest not reaching the coronoid fossa; larger and better-developed epicondyles.

From *Sarmatonectes* by: shorter lateral epicondyle.

From *Leptophoca* by: longer deltoid crest; termination of the medial epicondyle distal to the coronoid fossa.

Discussion: Besides the type species, VAN BENEDEN (1876a:802) assigned to the genus *Prophoca* a larger species, *P. rousseaui* (1876a:801). Unfortunately, at that time he gave no description, measurements, collection numbers or even illustrations. One year later, VAN BENEDEN (1877:78) described these two species as primitive phocines and illustrated the material in his Atlas (1877: pl. 18). Therefore, VAN BENEDEN'S (1876a) name were *nomina nuda* until his 1877 publication.

This rare taxon (*P. proxima*) from Van Beneden's collection is represented only by a few fragmentary and rolled bones, but has very distinctive morphological features. Unfortunately, the humeral distal epiphysis was missing, resulting in the absence of important diagnostic characters. Although this genus is known to researchers by name, no one except RAY (1976) seems to have reexamined the original material critically. When RAY visited the Institut Royal des Sciences Naturelles de Belgique in Brussels, Belgium in 1972 he noted that material described by VAN BENEDEN as *Prophoca* belongs to two different subfamilies. RAY (1976) later suggested that VAN BENEDEN'S two species were related to primitive phocines, although he now agrees with me (oral communication) in assigning the smaller seal (*Prophoca proxima*) to the Phocinae, but placing the larger seal ("*P. rousseaui*") in the Monachinae. This large monachine, "*P. rousseaui*", from the Miocene of Western Europe, will ultimately require a new generic name.

Although none of the specimens in VAN BENEDEN'S original collection is truly satisfactory, I choose the humerus as the best available lectotype. I believe, however, that this name *P. proxima* represents an identifiable species and genus, as shown above and attributed to VAN BENEDEN.

Distribution: Middle Miocene (Anversian) of Western Europe (Belgium).

Prophoca proxima VAN BENEDEN, 1877

Figures 38–39; Tables 6b; 10a

Prophoca proxima: VAN BENEDEN, 1876a:802; 1876b:205 (nomen nudum).

Prophoca proxima: VAN BENEDEN, 1877:80–81.; MOURLON 1877:609.; TOULA, 1898:53.; DOLLO, 1909:114.; FRIANT, 1946:7, 13.; MISONNE, 1958:15.; KING, 1964:132.; RAY, 1976:394–395.

Leptophoca proxima: RAY, 1976:394–395.; SAVAGE and RUSSELL, 1983:292.

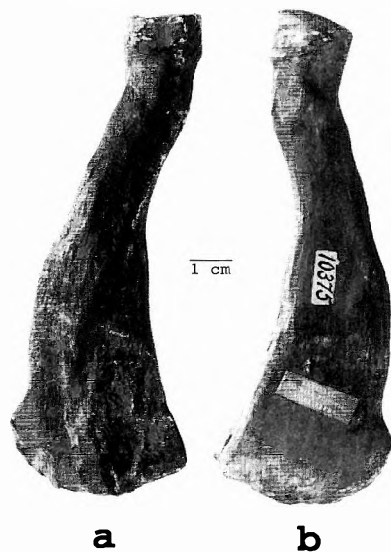


Figure 39. *Prophoca proxima*. Radius from Borderhout (Belgium), #IRSN 10375, Ct. M. 280A, cast USNM 10375
a = lateral and b = medial

Lectotype: R. humerus, IRSN 1146, Ct. M. 279, cast #10357, collection of USNM (illustrated by VAN BENEDEEN, 1877, pl. 18, figs. 12–14).

Type locality: Borderhout, Belgium (black sands in third section); Middle Miocene (Anversian).

Original material: In addition to lectotype:

Radius: IRSN 10375, Ct. M. 280A, cast #10375, collection of USNM (illustrated by VAN BENEDEEN, 1877, pl. 18, fig. 15) (Fig. 39).

Innominate: IRSN 10356, Ct. M. 280B, cast #10356, collection of USNM (illustrated by VAN BENEDEEN, 1877, pl. 18, fig. 16).

Diagnosis: As for the genus.

Description: The humerus of *Prophoca proxima* is similar in size to those of the modern grey seal, *Halichoerus grypus*. Humerus (Fig. 38; Table 6b). The intertubercular groove is wide and shallow. The deltoid crest is not preserved proximally, but extends more than half the length of the bone. The deltoid tuberosity is located in the proximal half of the bone. The lesser tubercle is well developed, oval, and located distal to the head, and at the same level as the greater tubercle. The head is compressed mediolaterally. The musculospiral groove is very deep. The lateral epicondyle is well developed, reaching the distal part of the deltoid crest, and extends twice as far distally as the medial. The medial epicondyle spreads over the entepicondylar foramen but ends distal to the coronoid fossa. The entepicondylar foramen is large and oval, with a wide bridge over it. The olecranon fossa is not preserved.

Radius (Fig. 39, Table 10a). The radial tuberosity is relatively large and circular, but flattened. The articular circumference is higher on its medial than on its lateral aspect. The bone belongs to a subadult animal (the distal epiphysis is not fused with the shaft of the bone), although the grooves for all the tendons are very deep. The insertion of the m. pronator teres is weak, and mostly absent.

Geological age and distribution: Middle Miocene (Anversian) of the Antwerp Basin, Belgium.

Genus *Leptophoca* TRUE, 1906

Leptophoca: TRUE, 1906:836, pl. 75, figs. 1–4.; KELLOGG, 1922:123.; SIMPSON, 1945:122.; SCHEFFER, 1958:34.; KING, 1964:132; 1983:133.; HENDEY and REPENNING, 1972:94.; MITCHELL, 1975:22, 23.; McLAREN, 1975:44.; RAY, 1976:20–22, pls. 8–11, fig. 4; 1977:395, 397–398.; HEPTNER et al., 1976:19,118.; REPENNING and RAY, 1977: 679–680.; REPENNING, RAY and GRIGORESCU, 1979:361–363.; MUZION, 1982a:186, 205; 1992:35.; SAVAGE and RUSSELL, 1983:272.; BARNES, DOMNING, and RAY, 1985:41.; MCKENNA and BELL, 1997:257.

Type species: *Leptophoca lenis* TRUE, 1906.

Included species: only the type species.

Emended diagnosis: Phocine of medium size, with total skull length near 235 mm; upper incisors form u-shaped arcade; P2-M1 double-rooted with posterior alveoli larger than anterior; p4, P4 larger than m1, M1; cheek teeth except p1, P1 with three and more cusps; diastemata present between teeth; preorbital part of maxilla with long, pronounced convexity; small antorbital process present on anterior margin of orbit; frontal contact of nasal bones twice as long as maxillary contact; interorbital space narrowing between anterior part of orbits and much narrowed in most posterior part of interorbital area; interorbital width 11.4% of width of skull at mastoid processes; sagittal crest begins at posterior end of orbit and becomes deeper at middle of braincase; infraorbital foramen not visible in dorsal view; diameter of infraorbital foramen equal to diameter of alveolus of upper canine; palatal process of maxilla flat; anterior palatal foramina oval and deep; palatal groove shallow but well defined; anteroposterior length of tympanic bulla lesser than smallest distance between bullae; jugular process well developed; width of mastoid process less than half length of tympanic bulla; mastoid convexity not turned down behind mastoid process; connection present between zygomatic process of squamosal and mastoid process.

Body of mandible swollen and thick, symphyseal part not pronounced; chin prominence absent; ramus of mandible thin and low; cheek teeth aligned parallel to axis of mandible with equal diastemata; alveoli of p4 equal in size to alveoli of m1.

Lesser tubercle of humerus located distal to proximal part of deltoid crest and head; head compressed craniocaudally; deltoid crest extends less than 2/3 of humeral length; maximum width of deltoid crest located in its proximal end; lateral epicondyle reaches distal part of deltoid crest.

Greater trochanter of femur higher than head, its proximal part wider than its distal; distinct lesser trochanter located far below distal border of greater trochanter; trochanteric fossa deep, wide, and covered medioproximally; head large, seated on narrow, short neck; minimum width of diaphysis shifted proximally; greatest breadth across condyles 65.0–66.0% of bone's length.

Comparison: *Leptophoca* differs from all other known seals by: frontal contact of nasal bones twice as long as maxillary; posterior part of interorbital area narrowed; sagittal crest present (except *Praepusa*); long, pronounced convexity

on preorbital part of maxilla (except *Halichoerus*, *Histriophoca*, and *Erignathus*); antorbital process present (except *Pusa*, *Halichoerus*, *Erignathus* and *Pagophilus*); interorbital area narrow (less than 25% of width at mastoid processes) (except *Pagophilus*); infraorbital foramen invisible in dorsal view (except *Praepusa*); diameters of infraorbital foramen and alveolus of upper canine equal (except *Pagophilus*); anterior palatal foramina deep (except *Phoca*, *Halichoerus*, and *Erignathus*); palatal groove shallow but well defined (except *Histriophoca* and *Praepusa*); anteroposterior length of tympanic bulla less than distance between bullae (except *Phoca*, *Halichoerus*, *Pagophilus*, and *Praepusa*); jugular process well developed (except *Erignathus*, *Pagophilus*, and *Praepusa*); symphyseal part of mandible not pronounced (except *Pusa*); chin prominence absent (except *Halichoerus*); alveoli of p4 and m1 equal in length (except *Phoca*); lesser tubercle of the humerus placed lower relative to the head and proximal part of deltoid crest (except *Sarmatonectes*); head compressed mediolaterally (except *Histriophoca*, *Praepusa*, and *Prophoca*); deltoid crest relatively longer (except *Halichoerus*, *Monachopsis*, *Praepusa*, *Cryptophoca*, and *Prophoca*); lateral epicondyle better developed (except *Halichoerus*, *Pagophilus*, *Praepusa*, and *Prophoca*); lesser trochanter of femur distinct; trochanteric fossa wide and covered medioproximally (except *Pagophilus*); femoral head seated on narrow neck (except *Halichoerus*, *Pagophilus*, and *Cryptophoca*); minimum width of diaphysis shifted proximally (except *Phoca*, *Monachopsis*, and *Cryptophoca*).

In addition, *Leptophoca* differs distinctly from other genera as follows:

From *Pusa* by: larger size; U-shape of upper incisor arcade; by swollen and thick body of mandible; cheek teeth located along axis of mandible. By larger femoral head with a short neck.

From *Phoca* by: larger size; U-shaped of upper incisor arcade. By deep trochanteric fossa of femur; greater breadth across femoral condyles.

From *Erignathus* by: p4, P4 larger than m1, M1; cheek teeth multicusped (except p1, P1); width of mastoid process less than half length of tympanic bulla. By thin and low ramus of mandible. By wider proximal end of deltoid crest of humerus. By proximal part of greater trochanter of femur wider than distal; deep trochanteric fossa.

From *Halichoerus* by: double-rooted, multicusped cheek teeth (except p1, P1); p4, P4 larger than m1, M1; presence of diastemata between teeth; width of mastoid process less than half length of tympanic bulla. By equal diastemata between the cheek teeth, which are located along axis of mandible. By shorter deltoid crest of humerus.

From *Pagophilus* by: larger posterior than anterior alveoli of postcanine teeth; single-cusped p1, P1. By thin and low ramus of mandible; equal diastemata between the cheek teeth.

From *Histriophoca* by: larger size; multicusped cheek teeth (except p1, P1); p4, P4 larger than m1, M1; flattened palatal process of maxilla; oval-shaped anterior palatal foramina. By swollen and thick body of mandible. By wider proximal end of deltoid crest of humerus. By deep trochanteric fossa of femur; greater breadth across femoral condyles.

From *Praepusa* by: larger size; deep anterior palatal foramina; presence of a connection between zygomatic process of squamosal and mastoid process. By swollen and thick body of mandible; equal diastemata between the cheek teeth. By shorter deltoid crest of humerus. By proximal part of greater trochanter of femur wider than distal; deep trochanteric fossa; larger femoral head with a short neck.

From *Monachopsis* by: larger size; double-rooted postcanine teeth with posterior alveoli larger than anterior; presence of diastemata between teeth; flattened palatal process of maxilla. By relatively shorter deltoid crest of humerus. By proximal part of greater trochanter of femur wider than distal; deep trochanteric fossa; larger head; breadth across femoral condyles.

From *Cryptophoca* by: absence of mental protuberance of mandible. By proximal part of greater trochanter of femur wider than distal; greater breadth across femoral condyles.

From *Sarmatonectes* by: shorter deltoid crest of humerus. By the greater trochanter of femur higher than head, and its proximal part wider than its distal; deep trochanteric fossa; larger femoral head.

From *Prophoca* by: shorter deltoid crest of humerus.

Discussion: The name *Leptophoca* is widely known to researchers, but material of this genus has heretofore never been described, except for the humerus, radius, and a fragment of the innominate. Dr. Clayton RAY has assembled additional material collected over the last 30 years. As a result, the USNM collection now includes an almost complete associated skeleton of this genus, which is very rare for any fossil seal taxon.

However, as can be seen from the "Comparison" made here, it is hard to compare some taxa, especially when only a fragment of skull is available (as in the case of *Monachopsis*), or no cranial material at all (as in the case of *Cryptophoca* and *Prophoca*).

Geological age and distribution: Lower and lower-Middle Miocene (Calvert Formation) of the eastern shore of the United States.

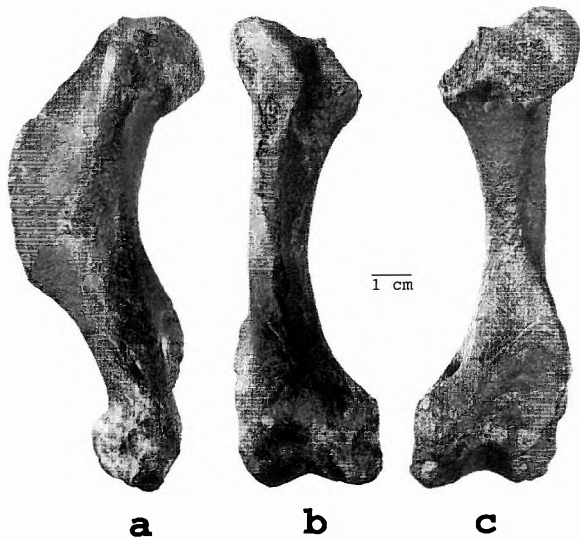


Figure 40. *Leptophoca lenis*. Right humerus from Maryland, USA, USNM 5359 (illustrated by True, 1906: pls. 75, figs. 2-4)

a = medial; b = cranial; and d = caudal views

Vertebra: fifth lumbar, Chesapeake Beach, USNM 5363 (illustrated by TRUE, 1906, pl. 76, fig. 3).

Newly referred material: USA, Early Miocene, Calvert Formation, collection of USNM:

Skeletons: #263648 (skull, scapula, radius, innominate, femur, tibia and fibula, ribs (8), vertebrae (29), baculum (1), phalanges (7), metatarsal and metacarpal bones (8), tarsal and carpal bones (5)); #375737 (skull and large part of skeleton).

Skulls: Maryland, Calvert County, Randle Cliff, rostral part, #460122; Scientists' Cliffs, fragment of R. maxilla with alveoli P1-P2, #25921; Scientists' Cliffs, Port Republic, skull with 8 teeth and with mandibles and 7 vertebrae, # CMM-V-2021.

Upper dentitions: Maryland, Calvert County, between Brownie's Beach and Randle Cliff, #454906; Chesapeake Beach, Brownie's Beach, M1 ##412122, 412123; Randle Cliff, upper canine #299725, Kaufman Camp, I3 #375710. Virginia, Stratford Harbor, #498750; Mill Pond, Gravitts Mill, I2 #413905.

Mandibles: Maryland, Calvert County, Plum Point, L. mandible with c and p3, #498752; Governor's Run, fragment of L. mandible with alveolus of m1, #187238; Camp Roosevelt, L. mandible with c, p3, m1, #498751; Scientists' Cliffs, fragment of L. mandible with c and alveoli p1-m1, #412116; Scientists' Cliffs, Port Republic, R. and L. mandibles with c, p2-m1 (skull and 7 vertebrae), # CMM-V-2021. Randle Cliff, R. mandible with c, p3, and alveoli of p1, p2, and m1, #482299. Virginia, Stratford Hall, R. mandible with alveoli p1-m1, #244117; Stratford Harbor, R. mandible with p2, m1, and alveoli p3-p4, #498749.

Lower dentition: Maryland, Calvert County, Plum Point beach, p3 or p4 ##437640; Governor's Run, #321937; Flag Ponds State Park, p4 #454908, m1 #405591.

Humeri: Maryland, Calvert County, Chesapeake Beach, ##23232, 23450, 306522, 412115; Parker's Creek, Port Republic, ##23241, 23242, 49875. Virginia, Westmoreland County, Pope's Creek in Stratford Bluffs, ##23061, 284721; Richmond, Ballard Street, #187409.

Radii: Maryland, Calvert County, Chesapeake Beach, north of Scientists' Cliffs, #23238, without number (proximal epiphysis), #306523; Parker's Creek, #329114; St. Leonard, #412119; Prince Georges County, Tinker Creek, #421761.

Innominate: Maryland, Calvert County, Governor's Run, #360419; Scientists' Cliffs, ##306527, 482298; Parker Creek, ##23224, 23225, 25825 (cervical vertebra with the same number); Plum Point, #214896; Calvert Beach, #360397. Virginia, Stratford, ##215206; 321934; Hanover County, south bank of Pamunkey River, 305247, 307602.

Femora: Maryland, Calvert County, Chesapeake Beach, Parker Creek, #23228; Governor's Run, ##321936, 329112 (distal epiphysis), 392055 (immature); Plum Point, ##23236, 205499; north of Scientists' Cliffs, ##23223. Virginia, Westmoreland County, Westmoreland State Park, Stratford Hall, ##454770, 321934 (distal epiphysis; from the same individual — proximal epiphysis of tibia and caudal vertebra); Homini Cliffs, #170882 (distal end).

Tibiae and fibulae: Maryland, Calvert County, Chesapeake Beach, north of Scientists' Cliffs, #263648; Governor's Run, ##175578, 23226, 23239, 457374; Parker's Creek, ##23243, 187238 (from the same individual — mandible), 263650, 360420, 372545; Willow Beach Colony, #306524, 306525; Chesapeake Ranch Club, #372547; Matoaka Cottages (500 yd. N. of Kings Creek), #374263; Flag Pond, #454524. Virginia, Westmoreland County,

Leptophoca lenis TRUE, 1906

Figures 40–50; Tables 4, 5a, b–7a, 8, 10a, 11–12

Leptophoca lenis: TRUE, 1906:836, pl. 75, figs. 1–4.; KELLOGG, 1922:123.; SCHEFFER, 1958:34.; KING, 1964:132; 1983:133.; HENDEY and REPENNING, 1972:94.; MITCHELL, 1975:22, 23.; RAY, 1976:20–22, pls. 8–11, figs.4; 1977: 395, 397–398.; REPENNING and RAY, 1977: 679–680.; REPENNING, RAY and GRIGORESCU, 1979:361–363.; MUIZON, 1982a:186, 205.; SAVAGE and RUSSELL, 1983:272.; BARNES, DOMNING, and RAY, 1985:41.

Holotype: R. humerus; USNM 5359; illustrated and described by TRUE (1906:835–840, pls. 75, figs. 2–4) as *Leptophoca lenis* (Fig. 40).

Type locality: Between Chesapeake Beach (Bed 5) and Plum Point (Bed 10), Calvert Formation, Late-Early Miocene (~18 Ma), Calvert County, Maryland (USA).

Original material: In addition to the holotype, the following specimens were part of the original hypodigm:

Radius: Chesapeake Beach, north of Scientists' Cliffs, USNM 5362 (immature; illustrated by TRUE, 1906, pl. 76, fig. 1).

Tibia and fibula: north of Scientists' Cliffs, USNM 5361 (proximal half; illustrated by TRUE, 1906, pl. 76, fig. 2).

Westmoreland State Park, Stratford Hall, #321934 (proximal epiphysis; from the same individual — distal epiphysis of femur and caudal vertebra), and one bone without number; beach near Mill Wheel, #452646.

Atlas: Maryland, Calvert County, Chesapeake Beach, north of Parker's Creek, #305246; Governor's Run, #411889.

Axis: Maryland, Calvert County, Chesapeake Beach, south of Parker's Creek, #250303 (from the same individual — third cervical vertebra).

Cervical vertebra: Maryland, Calvert County Parker's Creek, #25825 (innominate with the same number); Scientists' Cliffs, Port Republic, 7 vertebrae (from the same individual as a skull and mandibles), # CMM-V-2021.

Sacrum: Maryland, Calvert County, Chesapeake Beach, ##23231, 23234.

Caudal vertebra: Virginia, Stratford, #321934 (innominate with the same number).

Emended diagnosis: As for the genus until other species are described.

Description: The bones of *Leptophoca lenis* are similar in size to those of the modern harp seal, *Pagophilus groenlandica*.

The available relatively complete skull (Fig. 41, Table 4) of *Leptophoca lenis* (USNM 263648) represents a young adult individual based on its incompletely obliterated sutures; fragments from another skull (USNM 375737) belong to an individual of about the same age. The teeth of USNM 263648 have fallen out; on the left side of the skull the maxilla (present partly in Fig. 41) and the jugal bones are missing, while on the right side the parietal and part of the occipital bones are partly broken away.

The postorbital (77.0 mm) part of the cranium is longer than the preorbital (68.5 mm) part. The lateral outline of the braincase is rounded. In lateral profile, the top of the braincase is slightly concave. The left half of the braincase above the external auditory meatus is 68.5 mm wide. The preorbital parts of the maxilla (Fig. 41, c–e), between the nasal aperture and the orbits, are long and convex, the same shape as in the other Phocinae (CHAPSKII 1974). The palatal parts of the premaxillo-maxillary sutures are fused, but still clearly visible. The ascending process of the premaxilla is deformed.

On the right maxilla at the anterior margin of the orbit is a small but distinct antorbital process. The fronto-maxillary suture is far forward of the anterior rim of the orbit. The supraorbital process of the frontal bone is represented only by a small ridge.

The nasal bones (Fig. 41, a) are very short, and not fused to each other along the midline; their maxillary contact is about as long as the frontal contact (15:28). The posterior limit of the nasal bones is far behind the frontal-maxillary contact. The maxillary part of the nasal bone is wider than the frontal part. Posteriorly, the nasal bones together form a short W-shaped projection inserted between the frontal bones. This shape is more similar to that of the Phocinae (especially *Histiophoca fasciata*), but the ratio between the frontal and maxillary parts (28:15) of the nasal bones is the same as in Monachinae (primitive character state).

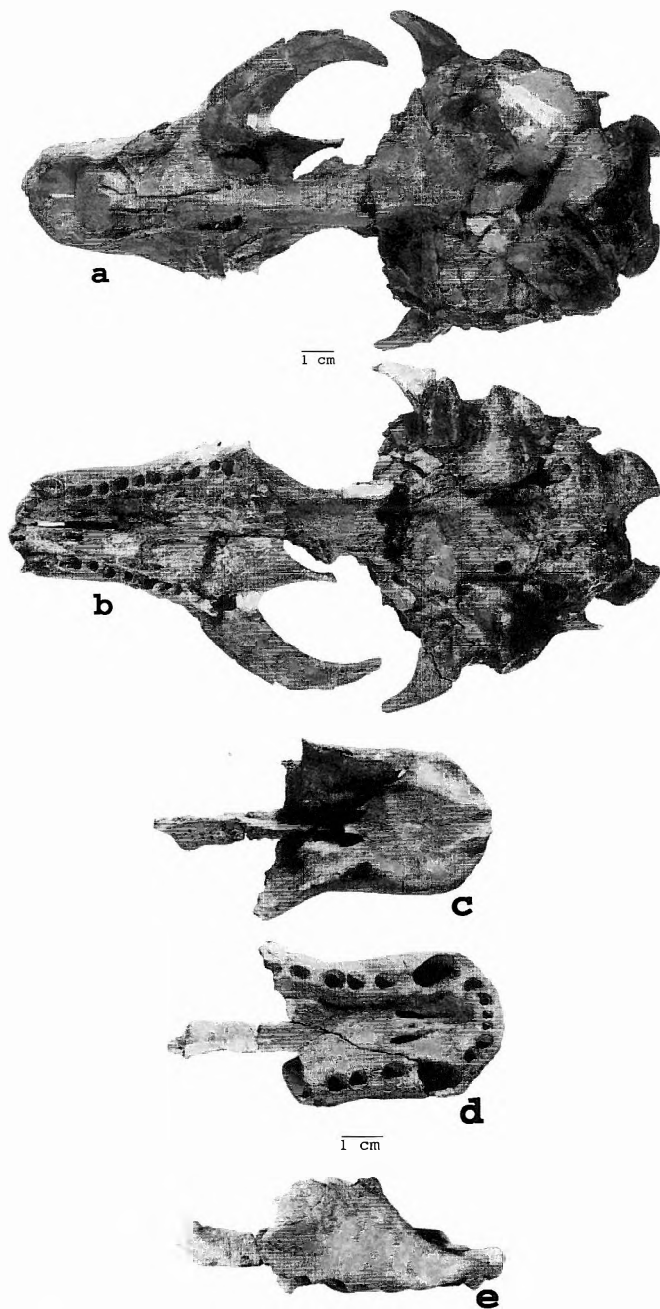


Figure 41. *Leptophoca lenis*. Skull from Maryland, USA, CMM-V-2021

a = in dorsal; and b = ventral views. Rostral part of maxilla from Maryland, USA, USNM 460122, c = dorsal; d = ventral; and e = lateral views

The interorbital region is slightly narrowed in its most anterior portion; the least interorbital width occurs in the most posterior portion of the interorbital area (where the braincase begins). The widest part of the interorbital area (16 mm) is located in the middle of the orbits. This primitive feature is typical for terrestrial carnivorans (BERTA and WYSS 1994). The least width of the interorbital area is about 11.4% of the mastoid width (140 mm [70×2]), very similar to the ratio in *Phoca vitulina*.

The sagittal crest (Fig. 41, a) begins anteriorly at the narrowest part of the interorbital area (at the posterior end of the orbits), and continues to the lambdoidal crest. The depression on either side of the sagittal crest becomes deeper at the middle of the braincase. The maximum height of the sagittal crest is about 2.5 mm.

The infraorbital foramen is located above the alveolus of M1; it is oval and relatively large (anteroposterior width 6.5 mm, mediolateral width 12 mm). The diameter of the alveolus of the upper canine (12 mm) is equal to the anteroposterior width of the infraorbital foramen, as in other Phocinae. When the skull is viewed dorsally, the posterior opening of the infraorbital canal in the orbit cannot be seen. The ventral floor of the infraorbital foramen is deformed.

The palatal process of the maxilla is a flat plate (Fig. 41, b, d). The anterior palatal foramina (= fissurae palatinae) are located between the P1 and are oval and deep, in contrast to other phocids (WOZENCRAFT 1989). Between the canines the palate is narrower and more concave (17.7 mm wide and 7 mm high), and descends smoothly to the posterior margin of the incisor arcade. The lingual alveolar margins of the canine and the posterior incisors are on the same level as those of the cheek teeth. The palatal bone and posterior palatine foramen are deformed. At the anterior palatine foramen begins a shallow, straight groove (= sulcus palatinus). The intermaxillary suture (36.5 mm) is shorter than the midline length of the palatine bone (67.5 mm), including the pterygoid process. The posterior border of the horizontal plate of the maxilla is long, turning ventrally about 10 mm behind M1.

The anterior edge of the orbit is above the middle of M1. The zygomatic process of the squamosal ascends anteriorly, and is not tapered anteriorly as in *Devinophoca*; the length of this process in front of the glenoid fossa is 33 mm.

The glenoid fossa measures 11 mm anteroposteriorly and 20 mm transversely. Its posterior border forms a very shallow, hardly visible postglenoid groove in the tympanic bone. A postglenoid foramen is located 2 mm from the postglenoid process in this groove, and is not floored by the tympanic as in *Devinophoca*. The postglenoid process itself is unusually short (17.7 mm) and is located 9 mm forward of the meatal tube. As I noted elsewhere (KORETSKY and HOLEC, in press) I consider the presence of a postglenoid foramen as a primitive condition in Phocinae, in contrast to the opinion of WYSS and FLYNN (1993).

Laterally (Fig. 41, b), the bulla is extended as a long tube (7.3 mm), with a prominent ventral lip forming the ventral margin of the external auditory meatus; this opening is slightly oval. The rim of the external auditory meatus is separated by a deep but short notch from the mastoid process (as in other carnivores). As in other phocids (MITCHELL and TEDFORD 1973), this notch continues as a well-defined groove extending anterolaterally from the stylomastoid foramen along the side of the external auditory meatus. This groove is a synapomorphy of phocids (KORETSKY and HOLEC, in press). The pit for the tympanohyal ligament is separated from the stylomastoid foramen (a primitive character state) and is anterolateral to the latter (as in *Lutra*: see MUIZON 1982).

In ventral view (Fig. 41, b), the tympanic bulla is roughly triangular in outline, has a smoothly convex ventral surface, is slightly inflated in its anterior (= ectotympanic) parts, and slopes uniformly to the posterolateral parts. The length of the auditory bulla (33.5 mm) is, as in other phocines, 2.7 times the anteroposterior width of the glenoid fossa (12.5 mm), in contrast to *Devinophoca* (3.4 times). The long axis of the bulla is slightly oblique to the midline of the skull. The median lacerate foramen and musculotubular canal with petrotympanic fissure (groove) are separated by a thick septum (5.0 mm) above the anteromedial corner of the bulla. The inflated ectotympanic part is much smaller than the entotympanic. Caudally, the entotympanic is more flattened than the ectotympanic along the anteroposterior axis, and is separated from the ectotympanic part of the bulla by a distinct ridge instead of a sulcus. This flatter entotympanic is in contrast to the more inflated entotympanic of Mustelinae and other Phocidae, as noted by WOZENCRAFT (1989).

The medial portion of the entotympanic close to the petrosal forms a deep, long fissure around the medial side of the bulla, and the carotid foramen is separated from the posterior lacerate foramen by a thick wall. The carotid canal is partially concealed in the posteromedial wall of the bulla, considerably anterior to the posterior lacerate foramen (the primitive conditions, see TEDFORD 1977), almost reaching the level of the stylomastoid foramen. In contrast to other phocines (BERTA and WYSS 1994), but similar to *Devinophoca claytoni* (KORETSKY and HOLEC, in press), the posterior opening and the posteromedial process of the carotid canal are visible in ventral view (RAY 1976). In *Leptophoca lenis*, similar to *D. claytoni* the carotid canal is parallel to the surface of the basioccipital, but in contrast to *D. claytoni* its posterior aperture opens in a ventral direction (derived condition, as in other phocines), and has a fully formed margin at its medial side (this is the primitive condition).

The posterior lacerate foramen is impossible to describe because the basioccipital bone is partially broken away. However, the septum between the carotid canal and the posterior lacerate foramen is present (in contrast to ursids, otariids, and also primitive musteloids; see MITCHELL and TEDFORD 1973; TEDFORD 1977; WOLSAN 1993).

The mastoid process is narrow, and does not extend far laterally as it does in *Monachinae*, but it does form a pronounced prominence anterolateral to the auditory bulla. The mastoid is not so inflated that it obscures the bulla in lateral view; this is the condition described for phocines by CHAPSKII (1974), RAY (1976), and KING (1983). There is a complete fusion of the posterolateral portion of the meatal lip to the mastoid process as in other carnivores, but the shallow sulcus between these two parts is present.

The continuous crest extending from the mastoid process over the external auditory meatus to the postglenoid process is very well developed (Fig. 41, b). From the base of the jugular (= paroccipital) process arise two separate ridges that merge at the tip of the process; these two ridges form a depression between them. The width of the jugular process at the base is 9.5 mm, the medial height is 12.5 mm, and the process itself is not curved. A uniquely phocid feature (MITCHELL and TEDFORD 1973), is that the inflation of the lateral side of the squamosal between the paroccipital and mastoid processes, is absent in the skull of *Leptophoca lenis*. On the contrary, a deep depression is present at this site. The thin and low lambdoidal crest is continued as a weak supramastoid crest.

The occipital bone (Fig. 41, b) is mostly broken away. The occipital condyles are 38 mm apart in the upper part of the foramen magnum and are approximately 29 mm apart below the foramen. The dorsal border of the foramen magnum is rounded, and the intercondylar notch is thick dorsally (4.8 mm). The large condyloid foramen (5 mm × 4.5 mm) is located at the base of the condyle.

The upper dental formula is I3, C1, P4, M1 (Fig. 41, b, d). The incisor alveoli form a wide U-shaped arcade. Based on size of alveoli, I3 is much larger than I2, which in turn is larger than I1. The upper canines were relatively large and projected more anteriorly than ventrally, judging from the curvature of the anterior surface of their alveoli.

P1 has a single root, circular in cross section. The posterior alveoli of the postcanines are slightly larger than the anterior.

The crown of P4 is triangular in occlusal view, and the buccal side is convex. A cingulum is located on the lingual side. The main cusp is turned caudally. Two small cusps, which are located on either side of the major cusp, are worn out with age. The two roots of the tooth are short and very inflated, and round (bulbous) in cross-section.

The double-rooted M1 is much smaller than P4. It has two alveoli, but the posterior alveolus is bilobed, indicating that the posterior root is made up of two fused roots.

Mandible (Fig. 42, Tables 5a, b). The body of the mandible is swollen, thick, but not high; the retromolar space is shortened. The ramus of the mandible is very thin and low (63 mm high); the condyloid process is especially short and narrow (22.6 × 8.2). The mandibular notch is indistinct.

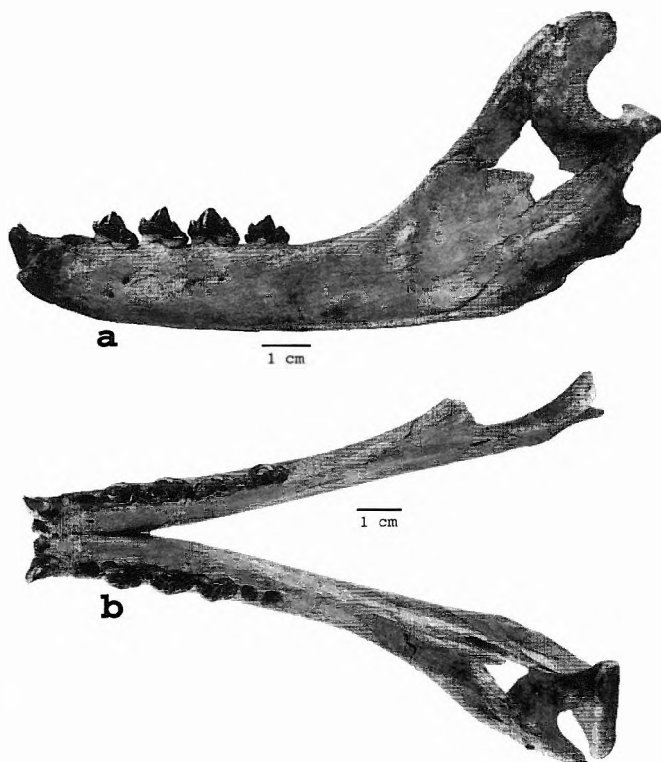


Figure 42. *Leptophoca lenis*. Mandible from Maryland, USA, CMM-V-2021

a = medial; and b = occlusal views

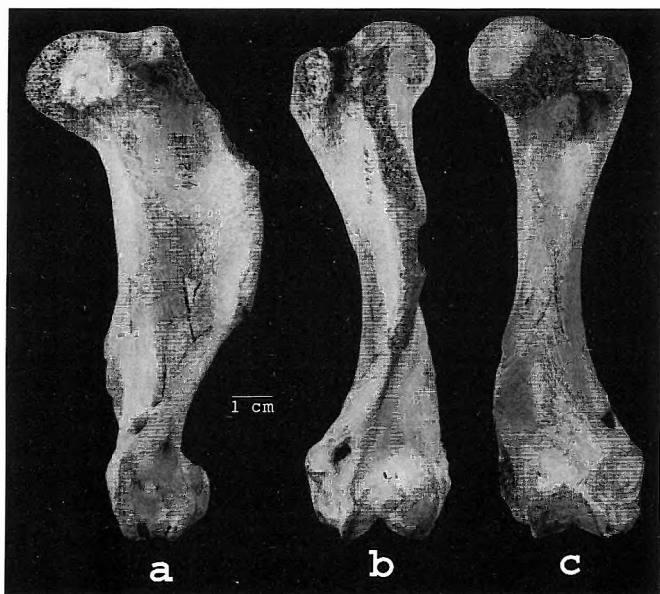


Figure 43. *Leptophoca lenis*. Humerus from Maryland, USA, USNM 412115

a = medial; b = cranial; and d = caudal views

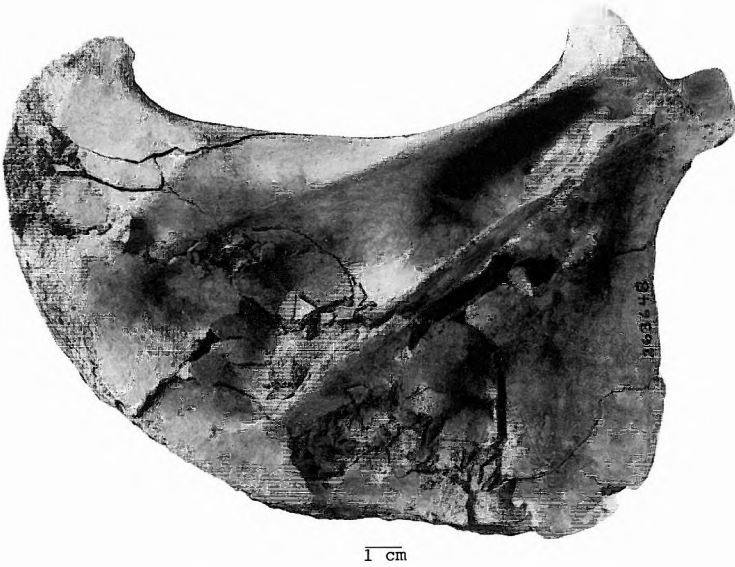


Figure 44. *Leptophoca lenis*. Scapula from Maryland, USA, USNM 263648; in lateral view

scapula is convex and not perpendicular to the scapular spine. The acromion is not high, but does reach the ventral angle. In the cervical region of the bone, the infra-articular tuberosity is pronounced as a long ridge, which connects with the very sharp muscular line on the infraspinous fossa. The coracoid process is much shorter medially than the caudal end of the glenoid cavity; the scapular tuberosity is very large, square, and very wide. The infraspinous fossa is narrow, but deeper than the supraspinous. The caudal angle forms a wide, open hook.

Humerus (Fig. 43, Table 6b). The intertubercular groove is narrow and shallow. The deltoid crest is widest proximally, extends less than $2/3$ of the length of the bone, and smoothly descends to the condyles as a sharp blade. The deltoid tuberosity is located proximal to the middle of the diaphysis. The lesser tubercle is well developed, round, and located considerably distal to the head of the humerus and greater tubercle. The head is compressed craniocaudally. The musculospiral groove is well expressed. The lateral epicondyle is well developed, reaching the distal part of the deltoid crest, and extends more than twice as far proximally as the medial. The medial epicondyle is flattened, spreading from lower part of the entepicondylar foramen, and ending at the level of the middle of the coronoid fossa. The coronoid fossa is deep, and forms a rounded triangular depression extending farther proximally than the medial epicondyle. The entepicondylar foramen is large and oval, with a wide bridge over it. The olecranon fossa is very flat, wide, and not well developed.

Radius (Fig. 45, Table 10a). The radial tuberosity is very large, prominent, and round; the neck is relatively wide. The grooves for all tendons are shallow, but the insertion of *m. pronator teres* is very well developed. The groove for the tendon of *m. abductor pollicis longus* is wide and shallow, whereas ridge the *extensor digitorum communis* is protruding.

Innominate (Fig. 46, Table 11). The ilium is thin, and the iliac crest is only slightly averted and excavated on its exterior surface. The iliac tuberosity and caudal dorsal iliac spine are very well developed compared to the size of the bone. The iliopectineal eminence is well expressed, and situated higher than the proximal border of the acetabular fossa. The greater ischiatic notch is concave, with a well-developed caudal dorsal ischial spine. On the lateral aspect of the wing of the ilium is located a deep and wide fossa for *m. gluteus medius*. However, the degree of development

The symphyseal part of the mandible is very small, and reaches the anterior alveoli of p2; the chin prominence is absent. The diastemata between teeth are equal in length.

The lower canines are very small, smaller than the upper canines, and oval in cross section. The cheek tooth row is oriented parallel to the axis of the symphyseal part of the mandible. The alveoli are round and equal in dimensions.

On the mandible, i1 and i2 are equal in size; i2 lies behind i1, and both adjoin the canine. The crowns of the cheek teeth are very narrow; p2, p4, and m1 are three-cusped and double-rooted; p3 has one or two additional cusps on a basal cingulum. The basal cingula are very well developed, especially on the lingual side. The lengths of alveoli of m1 and p4 are equal.

Scapula (Fig. 44, Table 8). The scapular spine ends smoothly, and does not reach the vertebral border. The vertebral border of the



Figure 45. *Leptophoca lenis*. Radius from Maryland, USA, USNM 329114

a = in medial and b = lateral views

of this fossa varies individually. On the medial aspect, at the level of the caudal dorsal iliac spine on the body of the ilium, is located a deep, wide fossa (facies auricularis) for insertion of the mm. psoas minor and (cranial to this) psoas major, and for m. quadratus lumborum. The edges of the acetabular fossa are raised slightly above the plane surface of the bone. The acetabulum is deep and circular, with a well-marked cotyloid notch. The obturator foramen is long and narrow, and its greatest width corresponds with that of other phocines. The pubic edge of the obturator foramen is much thicker and more rounded than the ischial edge. The pubic symphysis is very long and its limits are well defined.

Sexual dimorphism is strongly pronounced in development of the body of the ilium and in size of the acetabular fossa.

Femur (Fig. 47, Table 7b). The greater trochanter extends proximally higher than the femoral head; its proximal part is wider than the distal part. The trochanteric fossa is deep, wide, and covered proximally by the trochanter, reaching the distal half of the greater trochanter. The insubstantial intertrochanteric crest is located along the middle part of the femur, below the trochanteric fossa, and does not reach the lesser trochanter. The lesser trochanter is very well developed and is located on the posteromedial side of the bone, far below the distal border of the greater trochanter. The femoral head is large relative to the bone's mass, and seated on a narrow, short neck. The smallest width of the diaphysis is slightly shifted toward the proximal half of the femur. The supracondylar fossa located above the lateral condyle is barely noticeable. The maximum intercondyloid width is 0.65–0.66 of the bone's length.

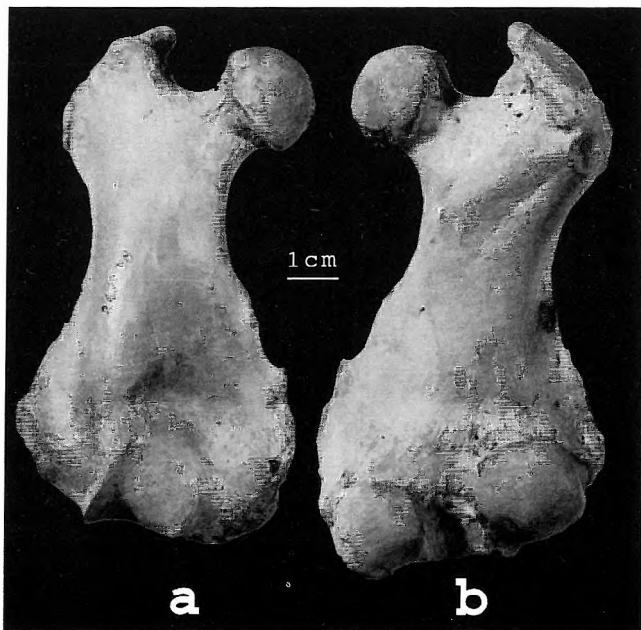


Figure 47. *Leptophoca lenis*. Femur from Maryland, USA, USNM 263648

a = cranial; and b = caudal views

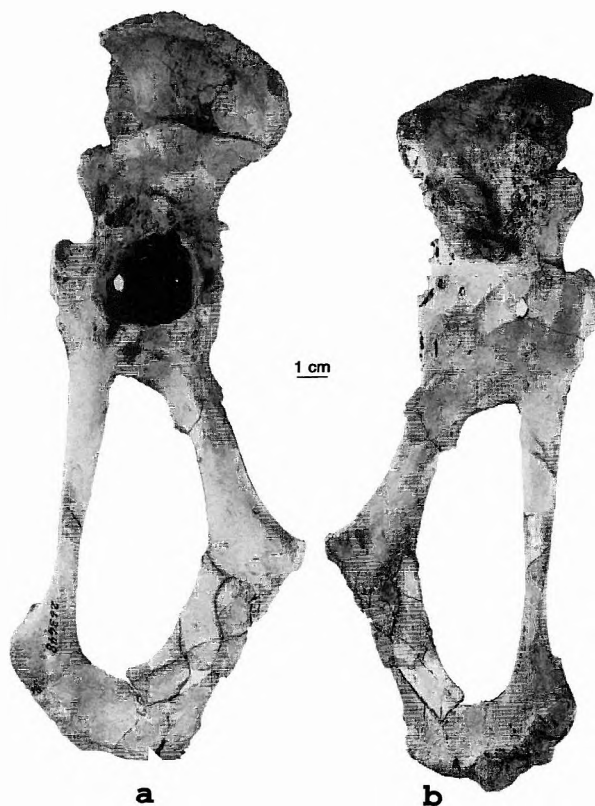


Figure 46. *Leptophoca lenis*. Innominate from Maryland, USA, USNM 263648

a = in medial and b = lateral views

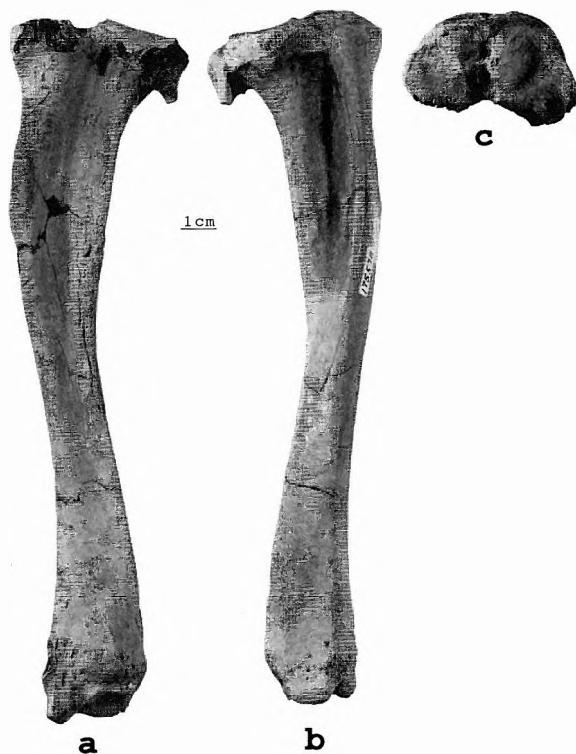


Figure 48. *Leptophoca lenis*. Tibia and fibula from Maryland, USA, USNM 175578

a = caudal; b = cranial; and c = sagittal views

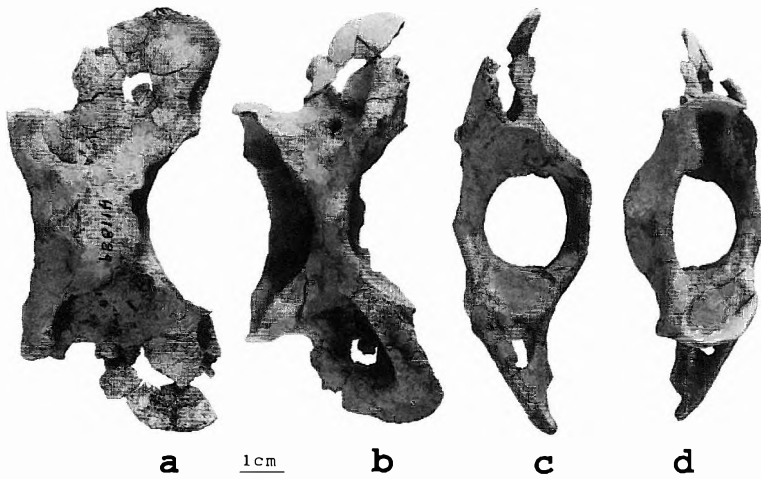


Figure 49. *Leptophoca lenis*. Atlas (C1) from Maryland, USA, USNM 411889
a = in dorsal; b = ventral; c = caudal; and d = cranial views

articular surface is round, and not deep. Caudal to the medial malleolus is a deep, wide groove for the tendon of *m. flexor digitorum longus*, with elevated medial and lateral borders forming distinct crests.

Vertebrae: The vertebral column in Phocinae has the formula C7, T15, L5, S4, Ca8-15. The bodies (centra) are oval in cross section, not circular as in Monachinae (KING 1956); the ventral surfaces have a flat ventral tubercle on all vertebrae (in contrast to Monachinae where this tubercle does not exist on the atlas). Compared with the sea lions (HOWELL 1930), the cervical transverse processes of the seals are narrower, reflecting lesser complexity of the *m. longus colli*. The spinous processes are also less developed.

Sexual dimorphism in bones of the extremities is described in detail in the Chapter 3.3, KORETSKY (1987), and VAN BREE and ERDBRINK (1987).

Tibia and fibula (Fig. 48, Table 12). The two condyles are weakly concave in their centers, shortened, and round.

The intercondyloid eminence is weak and only slightly raised above the two lateral, well-developed borders of the condyles. The popliteal notch is deep, wide, and well marked. The tibial crest is very sharp, but slightly flattened in the dorsomedial direction. On the ventral side of the tibia, the tibial tuberosity is well marked and round. The muscular groove is deep and narrow. The distal

Table 13

Morphological features in axial skeleton of some representatives of Phocidae

Some segments of axial skeleton	Phocinae	Monachinae	Cystophorinae
Atlas (C1):			
Position of lateral border of the transverse process	craniolateral	caudolateral	<i>Cystophora</i> – craniocaudal <i>Mirounga</i> – caudolateral
Axis (C2):			
Angle of spinous process dorsally	more than 10 degrees	less than 10 degrees	<i>Cystophora</i> – more than 10 degrees <i>Mirounga</i> – less than 10 degrees
Sacrum:	fused from 4 vertebrae	fused from 2–3 vertebrae	<i>Cystophora</i> – fused from 4 vertebrae <i>Mirounga</i> – fused from 3 vertebrae
Promotorium	lower than wings	higher than wings	<i>Cystophora</i> – lower than wings <i>Mirounga</i> – higher than wings
Greater width with wings	less than 4 times absolute length	more than 4 times absolute length	<i>Cystophora</i> – less than 0.4 absolute length <i>Mirounga</i> – more than 0.4 absolute length
Ribs:			
Articular surface of the head	equal or slightly greater than articular surface of tubercle	much greater than articular of tubercle	<i>Cystophora</i> – equal with tubercle <i>Mirounga</i> – much greater than articular surface of tubercle
Sternum:			
Shape of the segments	almost square-shaped, height equal or greater than width	dorsoventrally flattened height is 1/3 less than width	<i>Cystophora</i> – almost square-shaped, height greater than width <i>Mirounga</i> – flattened dorsoventrally, height is 1/3 less than width

Atlas (Fig. 49; Table 13). The atlas (C1) is heavy, measuring 99 mm in width and 37.5 mm in dorsoventral height. Its dorsal and ventral tubercles are well marked. The vertebral arch is round, with the same radius anteriorly and posteriorly. The transverse process is massive; cranially the costal element is expanded and directed vertically (as noted by ANTONIUK 1971; 1972; 1979, Table 13 in this text), while caudally it is inclined, as in monachines (KING 1956). The intervertebral foramen is large, measuring 11.3 mm in diameter caudally, while cranially it forms an enormous depression (19.6 mm wide and 1.5 mm high). The alar notch is not present, in contrast to land carnivores.

Axis (Table 13): Measures 73 mm in absolute craniocaudal length, 70.5 mm in length of spinous process, 36.6 mm in length of the body, 67 mm in maximum dorsoventral height, and 45 mm in width; its dens (17.5 mm) accounts for less than 1/3 of the absolute length (in contrast to Monachinae, PIÉRARD 1971). No accessory process (anapophysis) can be seen; this is in contrast to the condition described in *Phoca* (HOWELL 1929, PIÉRARD 1971). The vertebral arch is narrow, oval, and with almost the same width anteriorly and posteriorly.

The thin spinous process of the axis is elongated craniocaudally (backwards), and is relatively high dorsoventrally if compared with land carnivores; its dorsal edge is separated from the caudal articular process by a narrow (in contrast to Monachinae) notch. The spinous process of the axis is expanded caudally and forms an angle of more than 15° to the base (dorsal crura of the lamina, as in monachines; see ANTONIUK 1979; Table 13 in this text).

The transverse process of the axis is thick and rounded (not thin and pointed as in monachines; KING 1956).

Sacrum (Fig. 50; Table 13): Consists of 4 fused vertebrae, with 164 mm absolute length, and 112.7 mm width. The maximum width of the wings is more than 40% of the length of the sacrum, which according to ANTONIUK (1979) is a monachine character. However, the promontory is lower than the wings of the sacrum, similar to other Phocinae (see ANTONIUK 1979; Table 13 in this text). On S2, a well-defined mammillo-articular process (intermediate sacral crest) is present, and a long spinous process extends caudally. S3 shows a short spinous process and a less developed mammillo-articular process, while on S4 the mammillo-articular process is larger than those on S2, and the spinous process is very weak.

Ribs: The articular surface of the head is much larger than that of the tubercle, as in Monachinae (see ANTONIUK 1979; Table 13 in this text).

Discussion: The well-preserved skull and the skeleton of *Leptophoca lenis* (USNM ##460122, 263648, 375737), together with assorted bones from different individuals, show a mix of derived and primitive characters. The primitive features are: (skull) a well-developed sagittal crest, an antorbital process, a pit for the tympanohyal ligament separated from the stylomastoid foramen, and the position of the stylomastoid foramen (MUIZON 1982, WOLSAN 1993); (humerus) a large entepicondylar foramen; (femur) well-developed lesser trochanter, deep intertrochanteric fossa. The derived features are: (skull) a posterior aperture of the carotid canal opening ventrally (BERTA and WYSS 1994), with fully formed margins at its medial side (RAY 1976).

Moreover, this species has a few mixed subfamilial characters. For instance, the features it shares with Phocinae are: a weakly pronounced mastoid process, the shape of the preorbital part of the skull, a narrowed interorbital part, short naso-frontal contact, and an inflated ectotympanic (CHAPSKII 1974; TEDFORD 1977; WOZENCRAFT 1989). The characters similar to Cystophorinae are: the oval and deep anterior palatine foramina, and the presence of the antorbital process

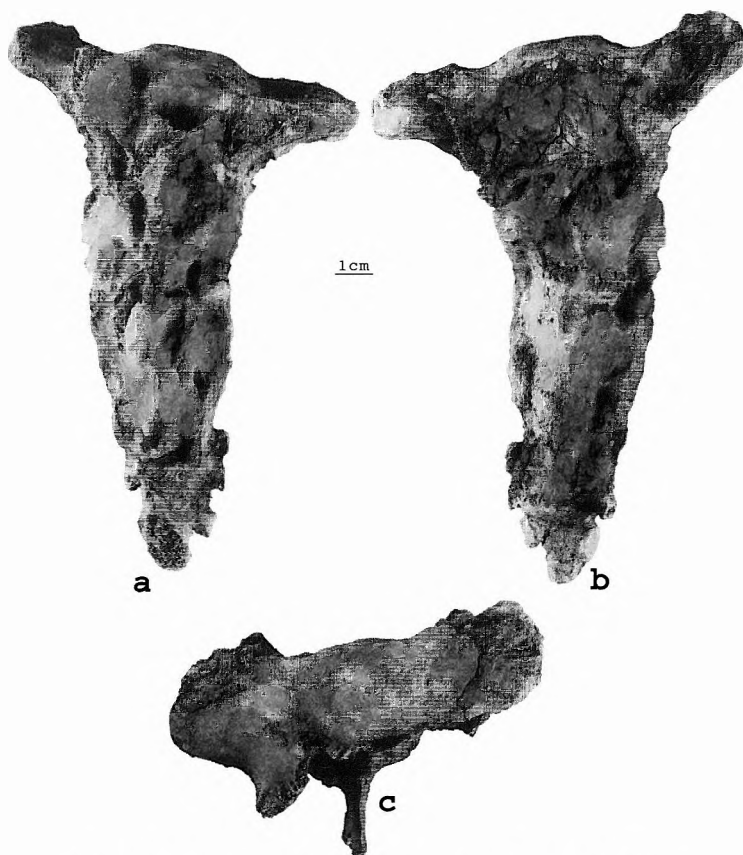


Figure 50. *Leptophoca lenis*. Sacrum from Maryland, USA

a = in dorsal; b = ventral; c = lateral; and d = caudal views

(similar to Monachinae also). Features shared with Monachinae are: the ratio between the maximum width of the wings and the total length of the sacrum; thin and pointed transverse process of the axis (KING 1956; ANTONIUK 1979; see Table 13 in this manuscript). This is not so surprising because *L. lenis* is one of the oldest known representatives of the Phocinae.

As one of the most primitive representatives of the true seals, *L. lenis* shares some characters with other genera of Phocinae, such as: the shape of the posterior portion of the nasal bones — with *Histriophoca*; the width of the interorbital region compared to the width at the mastoid processes — with *Phoca*; the diameter of the infraorbital foramen equal to the diameter of the alveolus of the upper canine — with *Pagophilus*; the location of the lesser tubercle of the humerus — with *Sarmatonectes*; and other features (see “Comparison”).

The presence of a sagittal crest and strong lambdoid crest, the simplicity of the teeth, and a long rostrum all indicate that the feeding mechanism of *Leptophoca lenis* was adapted for rapid jaw closure (for fish-eating), with possibly more powerful closing of the jaws.

Geological age and distribution: Late-Early – Early-Middle Miocene (Calvert Formation):

Maryland (USA), Calvert County: Plum Point (Bed 10), Parker Creek (Bed 12), Scientist’s Cliffs (Bed 13), Port Republic, Camp Roosevelt, Kaufman Camp, Brownie’s Beach, Randle Cliffs, Flag Ponds, 0.5 mi. N. of Governor’s Run (Bed 14), Governor’s Run (Bed 15), St. Leonard, Willow Beach Colony, Chesapeake Ranch Club, Prince Georges County: Tinker Creek, Matoaka Cottages (N. Of Kings Creek) (Bed 17).

Virginia (USA), Westmoreland County: Westmoreland State Park, Stratford Hall Plantation, Homini Cliffs, Stratford Harbor, Pope’s Creek in Stratford Beuffs, Mill Pond, Gravitts Mill (Bed 12 or 14), beach near Mill Wheel; Hanover County: south bank of Pamunkey River; Richmond, Ballard Street (RAY 1984; GOTTFRIED et al. 1994).

“Manatus maeoticus” EICHWALD, 1850

“Manatus”: EICHWALD, 1840:35, pl. 2, figs. 3–6.; BLAINVILLE, 1844:118, pl. 10g.

“Manatus maeoticus”: EICHWALD, 1850:174–175, pl. 23, fig. 38 (nomen dubium).; NORDMANN, 1860:328–333, pl. 25, figs. 1–7; 1861:581–582, pl. 11, figs 2–3.; SINZOV, 1900.; SIMIONESCU, 1931: 146, 154–155, 157.; MACAROVICI and OESCU, 1942:351, 353, 376–379, 382, pl. 7, figs. 6–12.; REINHART, 1976:281–282.; DOMNING, 1996:103, 247, 393, 527.

Type locality: Late? Sarmatian of Ukraine, Kerch Peninsula.

Other localities: Sarmatian of Kishinev, Moldavia; Middle Miocene of Balcic, Romania (now Balchik, Bulgaria).

Discussion: The type specimens of *“Manatus maeoticus”* EICHWALD, 1850 consisted of two rib fragments found in Kerch. Because they resembled the pachyosteosclerotic ribs of sirenians, EICHWALD used for them the generic name *Manatus*, a genus of Sirenia, and coined a new specific name. Later writers referred ribs, vertebrae, scapulae, and ster-na to this nominal species. In particular, NORDMANN (1860:330–333) described and referred to *“M. maeoticus”* ribs, two scapulae, and 26 vertebrae from the stone quarries of Kishinev (Moldavia). From the shape of the ribs it seems more likely that they belong to a phocine rather than to a sirenian, in contrast to the opinion of REINHART (1976). Unfortunately, identifying the ribs to genus and species is impossible without other associated material.

Later, several authors mentioned this specific name only in reference to EICHWALD’s material. However, DOMNING (1996), in agreement with BLAINVILLE (1844) and EICHWALD (1850), concluded that the specimens possibly belong to phocids. I regard the specimens as phocine but indeterminate and therefore conclude that the name *“Manatus maeoticus”* EICHWALD, 1850 is a nomen dubium. In my opinion, there is no basis for placing such material in any particular known phocine species.

Chapter 6

Cladistic analysis

Within the past 30 years there has been an increase of interest in pinniped phylogenetic relationships (MITCHELL 1966; 1968, 1975; SARICH 1969a, b; REPENNING 1975, 1976, 1990; REPENNING and TEDFORD 1977; BARNES 1972, 1979, 1987, 1988, 1989, 1990; BARNES and MITCHELL 1975; WYSS 1987, 1988b; FLYNN et al. 1988, WOZENCRAFT 1989; BERTA et al., 1989; BERTA and WYSS 1990; BININDA-EMONDS and RUSSELL 1996), and this has been largely the result of an impressive expansion in the numbers of fossil pinniped specimens available in museum collections (see BARNES et al. 1985).

Some investigators have postulated a non-carnivoran origin for pinnipeds; for example, WORTMAN (1894; 1906) proposed that they evolved from oxyaenid creodonts. Most researchers, however, have concluded that pinnipeds evolved from arctoid fissiped carnivorans (MATTHEW 1909 [dental and osteological characters]; WEBER 1904 [soft anatomical features]; FISH 1903 [brains]; ARNASON 1977 [karyotypes]; TEDFORD 1976 [dentitions, cranial anatomy]; HUNT and BARNES 1984 [basicranial circulation]).

However, there has been continuing controversy (KELLOGG 1922; HOWELL 1930; MITCHELL 1967) over whether pinnipeds evolved from a single aquatic ancestor (monophyletic origin) or had two independent origins (diphyletic origin). The theory of the diphyletic origin of pinnipeds proposes that true seals (Phocidae) had a North Atlantic origin and are most closely related to mustelids, whereas sea lions and walruses (Otariidae and Odobenidae) had a North Pacific origin and are related to ursids (MIVART 1885; McLAREN 1960b; MITCHELL 1967; TEDFORD 1976; MUIZON 1982b; WOLZAN 1993). The monophyletic viewpoint contends that all pinnipeds shared a single common aquatic ancestry (SIMPSON 1945; DAVIES 1958; SCHEFFER 1958; ARNASON 1977; KING 1983) and were derived from terrestrial arctoids, usually with ursids being the most likely sister group (WYSS 1987; FLYNN et al. 1989; BERTA et al. 1989).

WYSS (1987) reviewed osteological evidence for walrus relationships, and concluded that pinnipeds are monophyletic. He proposed that phocids had their closest relationships with the most derived of the animals that have traditionally been classified as Otarioidea, the allodesmines and the walruses.

This is diametrically the opposite of even the traditional monophyletic proposals that the shared common ancestry of Phocidae and Otariidae was very ancient and involved very primitive carnivorans (e.g., DAVIES 1958; SCHEFFER 1958; KING 1964, 1983), rather than otarioids that are usually considered relatively highly derived.

In support of pinniped monophyly WYSS (1988a; 1994), BERTA et al. (1989), and WYSS and FLYNN (1993) interpreted skeletal features of various fossil and living pinnipeds and proposed the taxon Pinnipedimorpha, to contain the fossil Enaliarctos and all other pinnipeds, including phocids, otariids and odobenids. This classification is not supported by karyotypic data (ANBINDER 1980), nor by a recently published cladistic analysis of the phocids' phylogenetic relationships based on skeletal morphology (BININDA-EMONDS and RUSSELL 1996). For example, according to the karyosystematic analysis of ANBINDER (1980:108) all pinnipeds are monophyletic; however, even his own data (1980:109, fig. 32) do not seem to support this conclusion. As stated by ANBINDER, all pinnipeds differ from each other in having very specific karyotypes, just as in other carnivores such as Canoidea and Feloidea. At some level, of course, all carnivorans are monophyletic, because at some early geological age they would appear to have been derived from a primitive form of Fissipedia.

However, MITCHELL (1967), McLAREN (1960b), TEDFORD (1976), BARNES (1987b), and WOZENCRAFT (1989) have come to a different conclusion. They argued that the Pinnipedia, whether a suborder or an order, is an artificial taxon. WOZENCRAFT (1989), in a phylogenetic analysis of Recent Carnivora, followed TEDFORD (1976) and MUIZON (1982) in supporting a close relationship between mustelids and phocids, although he differed from these authors in details of the interrelationships of these groups. In addition, WOZENCRAFT (1989) followed the traditional practice of uniting ursids and otarioids as a monophyletic group.

Matrix of character-state data for

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1 <i>Allodesmus kelloggi</i>	0	1	0	1	0	0	1	1	1	1	0	2	2	1	0	1	0	0	1	0	0	0	0
2 <i>Enaliarctos emlongi</i>	0	1	1	1	0	0	1	1	2	0	1	0	2	0	0	1	1	0	0	0	0	1	1
3 <i>Lutra canadensis</i>	0	1	0	1	0	0	1	1	1	1	0	2	2	1	0	1	0	0	1	0	0	0	0
4 <i>Desmatophoca oregonensis</i>	0	1	1	0	1	0	1	1	2	1	0	2	2	0	0	1	1	0	1	0	1	2	1
5 <i>Devinophoca claytoni</i>	0	0	1	0	0	0	0	0	0	0	1	2	1	0	0	?	1	1	0	0	0	0	1
6 <i>Monachus schauinslandi</i>	0	0	1	0	1	1	0	1	0	1	1	2	2	0	1	0	0	0	0	1	1	1	1
7 <i>Callophoca obscura</i>	1	1	1	0	0	0	1	1	1	0	1	2	2	1	0	0	0	1	0	1	0	0	1
8 <i>Cystophora cristata</i>	1	0	1	1	1	1	1	1	2	0	0	1	1	1	0	0	1	1	0	0	0	2	0
9 <i>Pagophilus groenlandica</i>	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	2	0	1	1
10 <i>Histiophoca fasciata</i>	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	2	0	0	0
11 <i>Histiophoca alekseevi</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	?	?	?	1	2	?	0	2
12 <i>Pusa caspica</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0
13 <i>Pusa sibirica</i>	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0
14 <i>Pusa hispida</i>	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	0
15 <i>Phoca largha</i>	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1	0
16 <i>Phoca vitulina</i>	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	2	1	0	1
17 <i>Halichoerus crypus</i>	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0	0	1
18 <i>Erignathus barbatus</i>	1	1	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	0	2	1	0	1
19 <i>Leptophoca lenis</i>	0	0	?	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	0	1
20 <i>Praepusa vindobonensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	2	1	0	1
21 <i>Praepusa pannonica</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
22 <i>Cryptophoca maeotica</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2
23 <i>Monachopsis pontica</i>	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	?	?	?	0	?	?	?	?
24 <i>Prophoca proxima</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
25 <i>Sarmatonectes simtsovi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Phylogenetically, the phocids are very close to the Carnivora from whose more primitive members they undoubtedly evolved in the Late Oligocene or earlier. Moreover, a phocid has been discovered recently in Late Oligocene deposits of South Carolina (KORETSKY and SANDERS, in press). This creature stands very close to the land or semiaquatic carnivores that could serve as the ancestral form for the evolution of Phocidae.

Here, I interpret the pinnipeds to be diphyletic, at least as far back in time as when the arctoid ancestors of each group first invaded the aquatic environment, and therefore treat the family Otariidae as strictly monophyletic. This group includes the subfamilies Enaliarctinae, Desmatophocinae, and Allodesminae, which I include in this cladistic analysis as outgroups. The differences between the proposed hypotheses for pinniped relationships reflect differences in the interpretations of the polarity of characters, their level of analysis, and the extent to which convergence affects the assessment of relationships (HOWELL 1930; BARNES 1972, 1989; MITCHELL 1975; BERTA et al. 1989; REPENNING 1990; BERTA and WYSS 1990).

Taxa and characters used in cladistic analysis of subfamily Phocinae

The matrix of character-state data for twenty-one species of fossil and modern phocids is given in Table 14; in addition, four outgroup taxa used. These outgroup taxa are the fossil otarioids *Allodesmus kelloggi*, *Enaliarctos emlongi*, and *Desmatophoca oregonensis*, and the Recent mustelid *Lutra canadensis*, reflecting the competing hypotheses of pinniped relationships: monophyly (WYSS and FLYNN 1993; BERTA and WYSS 1994) or diphyletic (MCLAREN 1960; MITCHELL 1966; TEDFORD 1977). Allodesmines are highly evolved otariids, widely evolutionary diversified in the Middle Miocene, and possess many derived marine carnivore features (BARNES and HIROTA 1995).

Points where the nodes of the present tree correspond to traditionally recognized phocid taxa are indicated. Only a few new names are introduced here: inclusion of *Devinophoca* within the Phocidae requires recognition of the new sub-

Table 14

Phociane taxa and outgroups analyzed

24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	
2	1	0	0	1	1	0	0	0	2	0	0	0	1	0	1	1	0	0	0	1	2	0	1	1	1	0	1	2	1	0	1	0	1	0	0	0	1	
1	1	1	0	2	1	2	0	1	0	1	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	0	1	2	0	1	1	0	0	?	0	1	1	
2	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	1	2	0	0	0	0	1	1	0	1	1	
0	1	1	0	2	?	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	2	2	2	1	2	?	?	?	?	?	?	?	?	?	?	?	?	
0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	0	1	0	0	0	2	1	0	1	0	0	0	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	
1	1	0	1	1	0	2	0	0	1	0	1	0	0	1	0	2	1	0	0	1	1	1	2	0	1	0	0	0	0	1	0	1	1	1	0	0	1	
1	1	0	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	0	2	1	1	0	0	1	0	0	1	1	1	1	2	0	0	1	1	1	
0	1	1	1	2	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	1	1	2	0	1	1	1	0	0	0	1	1	1	1	1	2	1	0	0
1	0	0	2	0	0	0	1	1	1	1	0	1	1	0	0	0	0	1	0	1	2	2	0	1	2	1	0	1	0	0	1	2	0	1	0	1	1	
1	0	0	2	1	1	0	0	1	1	1	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
1	0	2	0	2	1	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	1	1	0	1	0	1	1	2	1	1	1	0	1	
0	0	2	0	2	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	2	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1
0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	2	0	1	1	0	0	0	0	0	2	1	0	1	0	1	1	0	1	1	1	0	1	1
1	0	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0	1	1	2	1	1	0	0	0	
1	0	1	1	2	0	0	1	1	2	0	1	1	1	1	0	2	0	1	1	2	2	0	0	1	1	1	0	1	0	1	1	2	0	2	0	1	1	
1	1	1	1	1	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	2	2	2	0	1	1	1	0	1	0	1	1	2	1	1	1	1	1	
1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0	
0	0	0	2	2	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	1	0	1	0	1	
0	0	0	2	2	?	?	0	0	1	?	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
0	0	0	0	2	?	?	0	?	1	1	1	?	?	0	?	?	0	1	0	1	1	0	1	1	2	0	0	1	0	1	1	0	0	0	0	1	1	
?	?	?	2	2	?	0	0	1	2	1	0	?	1	0	?	?	0	1	1	1	0	0	2	1	1	1	0	0	0	1	1	0	0	0	1	1	0	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	1	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0	1	

family Devinoxocinae; a new taxon of Phocinae (*Sarmatonectes sintsovi*) is described; and new fossil species of *Histiophoca* (*H. alekseevi*) described.

This analysis of these taxa used 61 unordered and unweighted cranial, dental and postcranial skeletal characters as shown in Table 14.

Characters and character-states for Phocinae are listed below. "0" designates the most primitive state among the taxa studied; "1" and "2" are alternate derived states; "?" indicates unknown or missing data.

Skull

1. Tympanic bulla: (0) small; (1) large.
2. External auditory meatus: (0) inframeatal lip well developed; (1) poorly developed.
3. Mastoid process: (0) not united with paroccipital process; (1) united with paroccipital process.
4. Mastoid process: (0) axis of mastoid convexity not directed ventrally; (1) directed ventrally.
5. Mastoid process: (0) prominence lateral to auditory bulla not strongly pronounced; (1) pronounced.
6. Mastoid process: (0) narrow (width of the process less than length of process itself); (1) wide (CHAPSKII 1974 :301; in contrast to BERTA and WYSS 1994:48).
7. Mastoid process: (0) round in cross-section; (1) cylindrical.
8. Mastoid process: (0) width less than or equal to half of length of tympanic bulla; (1) width greater than half of length of tympanic bulla.
9. Mastoid convexity: (0) not turned down, obscuring tympanic; . moderately turned down behind mastoid process; (2) directed sharply downward behind mastoid process.
10. Nasal bones: (0) anterior ends form one common termination; (1) anterior ends separated.

11. Nasal bone: (0) maxillary contact longer than frontal contact; (1) frontal and maxillary contacts almost equal in length.
12. Maxilla: (0) has very pronounced convexity anterior to orbits; (1) has short concavity; (2) has long concavity (CHAPSKII 1974; in contrast to BERTA and WYSS 1994:46).
13. Anterior palatine foramen: (0) round and deep; (1) oval and shallow; (2) indistinctly marked (BURNS and FAY 1970:72).
14. Palatal groove: (0) present; (1) absent.
15. Palatal process of maxilla: (0) flattened; (1) convex.
16. Oval foramen: (0) hidden under hamular process of pterygoid bone; (1) exposed, not hidden.
17. Interorbital area: (0) width less than 25.0% of mastoid width of skull; (1) width less than 30.0% but equal to or greater than 25.0% of mastoid width; (2) width equal to or greater than 30.0% of mastoid width (BURNS and FAY 1970:370; CHAPSKII 1974:299).
18. Paroccipital process: (0) well developed; (1) poorly developed or absent.
19. Rostrum: (0) short, relative to cranium; (1) elongated (CHAPSKII 1974).
20. Diameter of infraorbital foramen: (0) less than diameter of upper canine alveolus; (1) equal to diameter of upper canine alveolus; (2) greater than diameter of upper canine alveolus.
21. Length of auditory bulla: (0) equal to or greater than distance between bullae; (1) less than distance between them (BURNS and FAY 1970:382; CHAPSKII 1974:300).

Mandible

22. Symphyseal part: (0) continues at least to middle of alveolus of p3; (1) reaches only to alveolus of p2; (2) reaches only to alveolus of p1.
23. Lateral outline of symphyseal region: (0) square, symphysis thin; (1) rounded, symphysis thick; (2) straight, symphysis thick.
24. Chin prominence: (0) pronounced; (1) absent or weakly outlined.
25. Chin prominence: (0) extends from anterior or posterior alveolus of p2 to anterior or posterior alveolus of p4; (1) extends from anterior alveolus of p2 to anterior alveolus of p3.
26. Maximum height of body of mandible: (0) situated between alveoli p2-p3; (1) situated in middle or at posterior portion of alveolus p2; (2) situated between alveoli p4-m1 (KORETSKY and RAY 1994).
27. Diastemata and tooth alveoli: (0) alveoli are small with equal diastemata; (1) alveoli are round and large, with equal diastemata between them; (2) alveoli are shallow, diastemata are unequal.
28. Alveoli of p4 and m1: (0) alveoli similar in size; (1) alveoli of p4 smaller than alveoli of m1; (2) alveoli of p4 larger than alveoli of m1 (unordered character).
29. Retromandibular space: (0) elongated; (1) short.

Teeth

30. Number of incisors: (0) 3/2; (1) 2/2; (2) 3-2/1 (Chapskii 1974:289; in contrast to Burns and Fay 1970:380) (unordered character).
31. Roots of postcanine teeth (P, p2 – P, p3): (0) two; (1) one (fused) (in contrast to BERTA and WYSS 1994:51).
32. Crowns of postcanine teeth: (0) multicuspidate; (1) single-cusped (in contrast to BERTA and WYSS 1994:51).
33. Roots of P 4: (0) three; (1) two; (2) one.
34. Relative dimensions of postcanine teeth as compared to size and massivity of skull: (0) large; (1) small.
35. Size of canine diameter relative to skull: (0) small; (1) large.
36. Basal cingulum of postcanine teeth: (0) well developed; (1) weakly developed or absent.
37. Number of additional cusps of premolars: (0) more than two; (1) no additional cusps.
38. Premolars: (0) aligned parallel to axis of tooth-row; (1) seated obliquely.
39. Upper incisors: (0) arranged in curved arcade; (1) arrange in straight line.
40. Second and third upper incisors: (0) third larger than second; (1) second larger than third, (2) all upper incisors equal in size.

Humerus

41. Lesser tubercle: (0) pronounced; (1) not pronounced (in contrast to BERTA and WYSS 1994:52).
42. Trochlear crest: (0) raised arch-like over coronoid fossa; (1) not separated from coronoid fossa by a distinct lip.

43. Lesser tubercle and head: (0) equal in height or tubercle insignificantly higher than head; (1) tubercle very much higher than head.
44. Lesser tubercle: (0) rounded; (1) extended along bone's axis; (2) oval (unordered character).
45. Head: (0) mediolaterally compressed; (1) round; (2) flattened proximo-distally.
46. Deltoid crest: (0) maximal enlargement in proximal part; (1) neither part noticeably enlarged; (2) maximal enlargement in middle part.
47. Deltoid crest: (0) shorter than " length of bone, confined to proximal half of bone; (1) equal to or longer than " length of bone, but not reaching coronoid fossa; (2) reaches coronoid fossa (in contrast to BERTA and WYSS 1994:52).
48. Coronoid fossa: (0) deep; (1) shallow.
49. Head and trochlea: (0) head is wider than trochlea; (1) head almost equal in width to trochlea; (2) trochlea is wider (in contrast to BERTA and WYSS 1994:53).

Femur

50. Lesser trochanter: (0) present; (1) absent (BERTA and WYSS 1994:54).
51. Condyles: (0) different in size; (1) similar in size.
52. Epiphyses: (0) distal epiphysis wider than proximal by $L^{-1/5}$; (1) widths of proximal and distal epiphyses about equal; (2) proximal epiphysis wider than distal.
53. Diaphysis: (0) minimum width less than or about equal to $2/3$ width of proximal epiphysis; (1) minimum width more than $2/3$ width of proximal epiphysis.
54. Intertrochanteric crest: (0) well developed; (1) absent or poorly developed.
55. Intertrochanteric crest: (0) reaches lower than head; (1) short, ends on same level as distal edge of head or fovea capitis.
56. Head: (0) round; (1) flattened in dorsoventral direction; (2) compressed mediolaterally (unordered).
57. Intercondylar area: (0) narrow, deep; (1) wide, shallow.
58. Greater trochanter: (0) maximum width in middle part; (1) maximum width in proximal part; (2) enlarged, triangular (KORETSKY 1987).
59. Head and greater trochanter: (0) both reach same level; (1) greater trochanter higher than head.
60. Neck: (0) long, slender; (1) short, wide.
61. Diaphysis: (0) minimum width in proximal part; (1) minimum width in middle part.

Results of cladistic analysis

The mh*; routine in Hennig86 (FARRIS 1988) produced two maximally parsimonious trees, each 295 steps long with a consistency index of 0.55 and a retention index of 0.48.

Use of Hennig86's successive-weighting option reduced the number of trees from two to one, leaving a portion of the tree much better resolved (Fig. 51).

The nodes of the cladogram shown in Fig. 51 are supported by the following character transformations:

Node 1 (family Phocidae): 34(1) small relative dimensions of postcanine teeth as compared to size and massivity of skull; 50(1) absence of lesser trochanter of femur; 52(0 or 1) width of proximal and distal epiphyses about equal, or distal is wider than proximal by $1/4-1/5$.

Node 2 (family Otariidae; one branch forms the possibly paraphyletic subfamilies): 12(2), 16(1), 22(1.2), 52(2).

Node 3 (paraphyletic subfamily Devinophocinae): 12(2) maxilla has a long concavity anterior to orbit (shared with Monachinae); 17(1) width of interorbital area equal or greater than 25% of mastoid width (shared with Cystophorinae); 36(1) absence of basal cingulum on postcanine teeth (shared with Cystophorinae and Phocinae).

Node 4 (paraphyletic subfamily Cystophorinae): 22(2) symphyseal part of the mandible reaches only to the alveolus of p1 (autapomorphy); 44(2) lesser tubercle of humerus oval (shared with Halichoerus and Erignathus).

Node 5 (paraphyletic subfamily Monachinae): 12(2) maxilla has a long concavity (shared with Devinophocinae); 13(2) anterior palatine foramina indistinctly marked; 42(0) middle of internal crest of the humeral trochlea raised arch-like over coronoid fossa; 54(1) intertrochanteric crest of femur absent.

Node 6 (subfamily Phocinae and tribe Phocini): 20(1 or 2) diameter of the infraorbital foramen equal to or greater than diameter of upper canine alveolus; 41(0) lesser tubercle of humerus pronounced; 48(1) coronoid fossa shallow; 58(2) greater trochanter of femur enlarged and triangular.

Node 7 (genus Histriophoca): 27(2) alveoli shallow, diastemata unequal (shared with Praepusa and Monachopsis).

Node 8 (tribe Erignathini): 44(2) lesser tubercle of humerus oval (shared with Halichoerus and Cystophora).

Node 9 (paraphyletic subtribe Phocini, in part): 13(1) anterior palatal foramina round and deep; 28(2) alveoli of p4 larger than alveoli of m1; 39(1) upper incisors arranged in a straight line (shared with Cystophora).

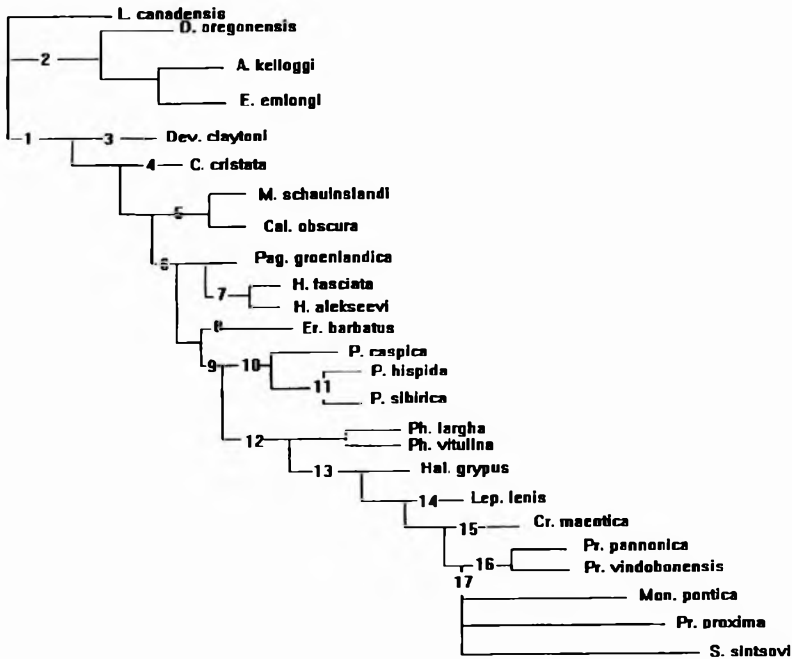


Figure 51. Nelson consensus tree of two trees of the hypothesized phylogenetic relationships among taxa of Phocidae and four outgroups, generated by Hennig86 using 61 characters and the successive weighting option

Tree length, 295 steps; consistency index, 0.55; retention index, 0.48. Character states are given in Table 14

Node 15 (genus *Cryptophoca*): 23(2) lateral outline of symphyseal region straight, symphysis thick (shared with *Histriophoca*); 49(2) trochlea of humerus wider than head (shared with *Phoca*, *Pusa* and *Histriophoca*).

Node 16 (genus *Praepusa*): 27(2) alveoli shallow, diastemata unequal.

Node 17: 33(2) postcanine teeth single-rooted (shared with *Halichoerus*).

Node 10: (genus *Pusa*): 26(2) maximum height of body of mandible situated between alveoli p4-m1; 38(1) premaxillars seated obliquely (shared with *Halichoerus*, *Praepusa* and *Erignathus*).

Node 11: 45(2) head of humerus flattened proximo-distally (shared with *Halichoerus*, *Erignathus*, and *Histriophoca*).

Node 12 (paraphyletic genus *Phoca*): 44(0) lesser tubercle of humerus rounded; 48(0) coronoid fossa deep.

Node 13 (genus *Halichoerus*): 33(2) P4 single-rooted (shared with *Monachopsis*; 40(2) all upper incisors equal in size (shared with *Phoca* and *Callophoca*); 44(2) lesser tubercle of humerus oval (shared with *Erignathus* and *Cystophora*); 58(2) greater trochanter of femur enlarged and triangular (shared with *Pagophilus*).

Node 14 (genus *Leptophoca*): 9(1) mastoid convexity moderately turned down behind mastoid process (shared with *Phoca* and *Callophoca*); 19(1) rostrum elongated (shared with *Halichoerus* and *Histriophoca*).

Chapter 7

Remarks on phocid classification

As mentioned in Chapter 2.2, the major aim of this study is to construct a common system of classification for Recent and fossil seals. By eliminating (based on morphology, ontogeny, and sexual dimorphism) wrongly determined fossil taxa, and by associating many isolated postcranial and cranial bones (according to ecomorphotypes), it has been possible to produce a new, contemporary system of classification that includes both Recent and fossil phocids (Table 15).

The Recent Phocinae are predominantly small, northern, near-shore or lake-dwelling animals that are usually considered to be relatively generalized (but see WYSS 1994 for a contradictory opinion that phocines have undergone retrogressive evolution). In contrast to the Phocinae, the Monachinae have distribution that is predominantly in the lower latitude of the Northern Hemisphere and high latitude of the Southern Hemisphere (*Monachus* ssp., *Mirounga angustirostris*). Some species are more pelagic, and the group includes some of the most highly derived of the phocids, such as the crabeater seal, *Lobodon carcinophagus*, and the elephant seals, *Mirounga* ssp. The Monachinae also include the monk seals, *Monachus* ssp., which have been regarded both as relatively primitive and as derived (WYSS 1988a; BERTA and WYSS 1994). In fact, *Monachus* appears to be a generalized monachine with some unique apomorphies (KORETSKY and GRIGORESCU, in press).

Primitive fossil Phocinae

The later Miocene species "*Phoca*" *bessarabica* SIMIONESCU, 1925, from Romania, is a very unusual seal; it was originally described from an isolated humerus. This species is not well known to most authors, but additional material has now been collected, showing that this species has more cystophorine or monachine than phocine features.

"*Phoca novorossica*" ALEKSEEV, 1924, from the Middle/Late Miocene (Sarmatian) of Ukraine, is poorly described and illustrated. However, the original material, plus additional referred material presently unpublished, suggest a close relationship to Cystophorinae.

Tribe Phocini

The species in the Tribe Phocini are small or middle-sized Northern Hemisphere seals related to *Phoca*. The Recent seals included in this tribe have been placed in three separate genera, *Pagophilus*, *Histriophoca*, and *Pusa*, as well as all classified in one genus, *Phoca* (DOUTT 1942; SIMPSON 1945; SCHEFFER 1958; CHAPSKII 1960, 1974; KING 1964, 1983; ANTONIUK 1979; RIDGWAY and HARRISON, ed. 1981). For example, in her 1964 book, KING recognized *Phoca*, *Pusa*, *Pagophilus*, and *Histriophoca* as separate genera, but later (1983) she used only the genus *Phoca*.

Based on comparative morphology, and because similar morphologic diversity is accorded generic rank within the Otariidae, I recognize *Phoca*, *Pusa*, *Pagophilus*, and *Histriophoca* as separate genera. They have cranial differences of a magnitude similar to those that are considered generic differences in the Otariinae, and they appear to have had separate evolutionary histories for a significant chronologic interval. Recognition of these separate genera also allows the grouping of the closely related *Phoca vitulina* and *P. largha* in one genus, and *Pusa hispida*, *Pusa sibirica*, and *Pusa caspica* in another genus.

BARNES and MITCHELL (1975) reported various isolated latest Pliocene and Pleistocene phocid bones from the west coast of North America that closely resemble those of harbour seals, and identified them as *Phoca*, cf. *P. vitulina*. These bones are rare and, if correctly identified, constitute the only phocine fossils from the eastern North Pacific. The only fossil Phocidae from the western North Pacific are identified as *Phoca* and were found in Late Pleistocene cave deposits near the northern tip of Honshu, Japan (HASEGAWA et al. 1988). Such records indicate that harbor seals entered the North

Phocid classification

Muizon, 1982			Present study		
Subfamily	Tribe	Genera et species	Tribe	Genera et species	Subfamily
Phocinae	Erignathini	<i>Erignathus</i>	Erignathini	<i>Erignathus</i> † <i>Platyphoca vulgaris</i>	Phocinae
	Phocini	<i>Phoca</i> <i>Pusa</i> <i>Halichoerus</i>	Phocini	<i>Phoca</i> <i>Pusa</i> <i>Halichoerus</i> <i>Histriophoca fasciata</i> † <i>H. alekseevi</i> † <i>Monachopsis pontica</i> † <i>Praepusa pannonica</i> † <i>Pr. Vindobonensis</i> † <i>Cryptophoca maeotica</i> † <i>Gryphoca similis</i> † <i>Phocanella pumila</i> † <i>Leptophoca lenis</i> † <i>Prophoca proxima</i> † <i>Sarmatonectes sintsovi</i>	
	Cystophorini	<i>Pagophoca</i> <i>Cystophora</i> <i>Histriophoca</i>			
	Undetermined tribe	† „ <i>Phoca</i> ” <i>pontica</i> † <i>Phocanella</i> † „ <i>Ph.</i> ” <i>vindobonensis</i> † <i>Leptophoca</i> † <i>Platyphoca</i> † <i>Gryphoca</i>			
Incertae sedis		† „ <i>Ph.</i> ” <i>bessarabica</i> † „ <i>Mon.</i> ” <i>meoticum</i> † „ <i>Mon.</i> ” <i>gaudini</i> † <i>Prophoca rosseaui</i>	Incertae sedis	† „ <i>Ph.</i> ” <i>bessarabica</i> † „ <i>Ph.</i> ” <i>novorossica</i> † „ <i>Monotherium</i> <i>gaudini</i>	
Monachinae	Monachini	† <i>Pliophoca</i> † <i>Pristiphoca</i> <i>Monachus</i>	Monachini	† <i>Pliophoca etrusca</i> † <i>Pristiphoca nom. dubius</i> <i>Monachus</i> † <i>Pontophoca sarmatica</i> † <i>Messiphoca mauretanic</i> † <i>Properiphthychus argentinus</i> † <i>Callophoca obscura</i>	Monachinae
			Undetermined tribe	† <i>Monotherum affine</i> † <i>Monotherum delognii</i> † <i>Monotherum wymani</i> † <i>Monotherum abberatum</i> † <i>Piscophoca</i> † „ <i>Prophoca</i> ” <i>rosseaui</i>	
	Lobodontini	† <i>Monotherium</i> † <i>Homiphoca</i> † <i>Acrophoca</i> † <i>Piscophoca</i> <i>Lobodon</i> <i>Hydryga</i> <i>Leptonychotes</i> <i>Ommatophoca</i>	Lobodontini	† <i>Homiphoca</i> † <i>Acrophoca</i> <i>Lobodon</i> <i>Hydryga</i> <i>Leptonychotes</i> <i>Ommatophoca</i>	
	Miroungini	† <i>Callophoca</i> <i>Mirounga</i>		† <i>Miophoca vetusta</i> <i>Cystophora</i> <i>Mirounga</i>	Cystophorinae
				† <i>Devinophoca claytoni</i>	Devinophocinae

Pacific in latest Pliocene time and probably not before. The phocid record is much older in the Atlantic, and is consistent with theories that this is the area of origin and primary evolution of the group.

The living species of *Phoca* include only *P. vitulina* and *P. largha*, and these are very generalized morphologically, even when compared to *Pusa* and *Histriophoca*. Many fossil species that were initially classified as species of *Phoca* have been subsequently transferred to other genera; in fact, some are monachines (KORETSKY 1986). *Phoca insularis* was described by BELKIN (1964) as a Recent species from the Far East of Russia (Ochotsk Sea). This species has not been recognized by most authors (PAVLINOV and ROSSOLIMO 1987; WOZENCRAFT 1989; WILSON and REEDER 1993), with whom I agree; there is not enough evidence to warrant a separate species. Thus this taxon is regarded here as a variant of *Phoca largha*.

An uncritical look at the published fossils attributed to the genus *Phoca* would lead to an incorrect impression of the fossil history of the genus. *Phoca vitulinoides* VAN BENEDEN, 1871, originally based on Middle Pliocene fossils from the Antwerp Basin, is a medium-sized phocine apparently related to Recent *Phoca vitulina* (see KORETSKY and RAY, in press). Earlier, RAY (1976:Table 1) had incorrectly indicated that it might be the same species as *Phocanella minor* VAN BENEDEN, 1877.

Pusa was used as a genus by SCHEFFER (1958) and KING (1964), as a subgenus of *Phoca* by CHAPSKII (1955) and McLAREN (1960:48), and was omitted by KING (1983). The predominantly marine ringed seal, *Pusa hispida*, has two subspecies: *P. h. saimensis* in Lake Saimaa (Finland), and *P. h. ladogensis* (incorrectly spelled lagodensis in FROST and LOWRY 1981) in Lake Ladoga (Russia). The Lake Baikal seal, *Pusa sibirica*, and the Caspian seal, *Pusa caspica*, are isolated populations in landlocked water bodies; NORDQUIST (1899) concluded that the two are more closely related to each other than either is to *P. hispida*. CHAPSKII (1955), ANTONIUK (1974), and KORETSKY (unpublished data) disagree, concluding that *P. sibirica* is closer to *P. hispida* than either is to *P. caspica* (Fig. 51). TIMOSHENKO (1975:164) determined otherwise, that *P. caspica* and *P. hispida* are the two most closely related species, so this question is still open for discussion (see also Chapter 9 below).

The grey seal, *Halichoerus grypus*, has been placed in the Phocini by CHAPSKII (1955), but it has aberrant cranial morphology (the skull is robust and osteosclerotic). Its cheek teeth are large, single-cusped, and have a single root composed of two fused roots (KING 1964: fig. 15a), quite different from those of "typical phocines" like *Phoca* and *Pusa*. Young and neonatal specimens, however, have small cusps anterior and posterior to the main cusp of the deciduous cheek teeth (RAY et al. 1968:pl. 1), and this indicate the basic phocine cusp pattern. RAY et al. (1964) reported the species, associated with walrus, in a Late Pleistocene deposit in coastal Virginia, which they suggested represented a cooler glacial interval.

Gryphoca similis VAN BENEDEN, 1877, is a Late Pliocene phocine from Europe (Scaldisian, first found near Antwerp, Belgium) and the eastern coast of North America. VAN BENEDEN (1877) allied it with *Halichoerus*, SIMPSON (1945:122) classified it in the Phocinae, but RAY (1976:table 1) regarded it as close to *Phocanella pumila* VAN BENEDEN, 1877. Subsequently RAY and KORETSKY (in press) have classified it as a phocine, closely related to *Halichoerus grypus*.

Phocanella originally included two named species, *P. pumila* VAN BENEDEN, 1877, and *P. minor* VAN BENEDEN, 1877, from Middle (?) Pliocene deposits of Belgium. RAY (1976:table 1) reported *P. pumila* from the earliest Pliocene Yorktown Formation on the east coast of North America. VAN BENEDEN (1877) had allied both species with *Pusa hispida*. SIMPSON (1945) placed them in the Phocinae, and RAY (1976:table 1) considered them to be generalized phocines near *Phoca*. RAY and KORETSKY (in press) concluded that *Phocanella minor* is a synonym of *Phocanella pumila*, and that the species is closely related to *Phoca largha*. In the same paper another species, *Phocanella couffoni* FRIANT, 1947, is interpreted as a nomen nudum. It had been named based on a very poorly preserved femur from France.

The Late Miocene seal from the city of Kerch, Crimea (Ukraine) called *Phoca pontica* by EICHWALD (1850:210) has had a confusing history and has been mentioned by many authors. EICHWALD (1850, 1853) also studied isolated bones of the extremities and skull fragments of the true seals found in "... upper layer of molasse formation, ... in sediments of Mount Mithridate and in limestone layers of Cape Akbourun". Following this investigation, von NORDMANN (1860) was the first to note the presence of the genus *Phoca* (species *Ph. maeotica*) in "molasses limestone" on the northern coast of Kerch Strait (Cape Kamysh-Bourun, Crimea, Ukraine). In this so-called "molasses formation" EICHWALD and von NORDMANN recognized deposits of the Tertiary period; its upper layer corresponds to deposits of the Upper Miocene and Pliocene. The studies of ANDRUSOV (1888, 1893, 1929) were very important for the accurate determination of the stratigraphic location of seal remains of the Kerch Peninsula, and showed that these finds belong to the Sarmatian.

GRIGORESCU (1977:411, 412) pointed out that *Phoca pontica* had been confused with *Phoca sarmatica*. McLAREN (1960) first transferred this species to the genus *Monachopsis*, and later KORETSKY (1987a; 1988) described additional cranial and postcranial material, and produced a diagnosis of *Monachopsis pontica*.

Praepusa pannonica KRETZOI, 1941, is an Early-Middle Sarmatian phocine that was described on the basis of a single mandible from near Budapest, Hungary. GRIGORESCU (1976:407) questioned the validity of this species, citing the paucity of material, but HENDEY and REPENNING (1972:95) stated that it has a primitive dentition with cheek teeth hav-

ing a single cusp on both the anterior and posterior sides of the central main cusp. This species has been reviewed by KORETSKY (1987b), who referred additional material to the species and provided a description and diagnosis.

An apparently related species is *Praepusa vindobonensis* (TOULA 1898) from the Vienna Basin (KORETSKY, unpublished data). This Middle Miocene (Early Sarmatian) species was originally called *Phoca vindobonensis* by TOULA (1898), but its generic affinities were questioned by HENDEY and REPENNING (1972:95), who interpreted the humerus as having both monachine and phocine characters; by GRIGORESCU (1976:407), who considered it to be closely related to *Monachopsis pontica* (previously *Phoca pontica*); and by RAY (1976:395), who said that it was “possibly referable to *Leptophoca*”. Both RAY (1976:400) and GRIGORESCU (1976: fig. 8) mistakenly concluded that *Praepusa* (“*Phoca*”) *vindobonensis* (TOULA 1898) was the ancestor of the phocine radiation in the Paratethyan realm, and therefore would be the ancestor of *Monachopsis pontica* and *Pontophoca sarmatica*. Here I conclude that *Phoca vindobonensis* belongs to the genus *Praepusa* KRETZOI, 1941.

A Middle Miocene (Sarmatian) seal from Tarchankut, Crimea, Ukraine, *Praepusa tarchankutica* KORETSKY, 1984, was described on the basis of two skulls with associated postcranial remains. This material represents both adult and juvenile individuals, and is interpreted as a phocine. Here I synonymize this species with *Pr. vindobonensis*.

Cryptophoca maeotica (NORDMANN, 1860) (KORETSKY and RAY, 1994), from the Middle/Late Miocene (Middle Sarmatian) of the Paratethyan region, has been called *Phoca maeotica* or *Monotherium maeoticum* by different authors. HENDEY (1972:100) considered it to be closely related to *Monachus monachus*. RAY (1976: 398–399) considered it to be an aberrant phocine, stating that there is no reason to call it *Monotherium*. GRIGORESCU (1976: 407, 413) reported that it is the most abundant phocid in deposits in Romania, comprising up to 70% of the phocids in collections from there. The genus *Cryptophoca* was named in 1994 by KORETSKY and RAY, and it is classified below as a primitive species of Phocinae.

One of the well known fossil phocines is *Leptophoca lenis* TRUE, 1906, from the Calvert Formation (Middle Miocene) in Maryland and Virginia. The holotype is an isolated humerus, but additional material has now been collected (RAY 1976; see Chapters 1 and 5). The species that was originally called *Prophoca proxima* VAN BENEDEN 1876, from Middle Miocene deposits in Belgium, was wrongly considered by RAY (1976:table 1) to be close to *Leptophoca*. VAN BENEDEN (1876) had recognized the very primitive nature of *Prophoca proxima* when he named it (see phylogenetic tree in Fig. 51).

Sarmatonectes sintsovi, new species (see Chapter 5), from the Middle Miocene (Sarmatian) of Moldavia, is a middle-sized seal and shares certain similarities in morphology of the extremities with extinct *Prophoca* and Recent *Phoca* (Fig. 51).

Subtribe Histriophocini

Histriophoca fasciata has been placed by CHAPSKII (1955) in the subtribe Histriophocini, which included two genera: *Pagophilus* and *Histriophoca*. According to my cladogram (Fig. 51), subdivision of the tribe Phocini is confirmed and *Histriophoca fasciata*, as well as another Middle Sarmatian species, *Histriophoca alekseevi*, and *Pagophilus* form a clade that can be recognized as a subtribe.

The harp seal, *Pagophilus groenlandica*, is justifiably placed in a genus separate from *Phoca*, because it has different cranial proportions, widely separated parasagittal crests rather than a single median crest, larger orbits, narrower interorbital region, smaller and narrower rostrum, and cheek teeth that are more derived compared to species of *Phoca* (compare figures in CHAPSKII 1955, and RONALD and HEALEY 1981, with BIGGS 1981). There is no fossil record of the species, but it is morphologically more derived than *Phoca* ssp. and would be expected to have had a lengthy separate evolutionary history.

Tribe Erignathini

MCLAREN (1960a:47) considered the bearded seal, *Erignathus barbatus* (ERXLEBEN 1777), to represent a highly specialized phocine lineage that had become separated very early in its evolutionary history from the other Phocinae. KING (1966) concluded that *Erignathus* occupies a primitive position among the Phocinae, and shares certain similarities with the Monachinae, especially with *Monachus*. REPENNING (1972) reported a few bones of this genus from Pleistocene deposits in Alaska. It is unique among the Phocinae in not having the anterior end of the ilium bent laterally (a derived character of all other Phocinae; KING 1966; HENDEY and REPENNING 1972:94). CHAPSKII (1955) and later KING (1964) recognized the unique nature of *Erignathus* by classifying it in its own Tribe Erignathini, and so do I.

Despite recognition of two subspecies, the Atlantic (*Erignathus barbatus barbatus*) and the Pacific (*E. b. nauticus*), quite long ago (OGNEV 1935; SMIRNOV 1935; SCHEFFER 1958; CHAPSKII 1963), not many authors cited the morphological features that characterize them, except RAY (1981) and RAY et al. (1982).

Platyphoca vulgaris VAN BENEDEN, 1877, originally named on the basis of Middle (?) Pliocene fossils from Belgium, was classified by SIMPSON (1945) in the Phocinae. RAY (1976:table 1) considered it to be a large, aberrant phocine, and agreed with VAN BENEDEN's (1877) conclusion that it is related to *Erignathus*. It has also been reported from Early Pliocene deposits on the east coast of North America (RAY 1976:table 1), and is redescribed and illustrated by KORETSKY and RAY (in press).

SUBFAMILY MONACHINAE

KING (1956) emphasized the generally primitive structure of the genus *Monachus* relative to the Phocinae. *Monotherium* (?) *wymani* (LEIDY 1853) from the Lower/Middle Miocene of Virginia, is the most primitive monachine. The species may belong in a different genus and its occurrence suggests that the subfamily originated in the Northern Hemisphere from Phocinae.

Tribe undetermined

Monotherium delognii, *Monotherium affine*, and *Monotherium aberratum* are large, medium, and small-sized primitive monachines, respectively, that were described by VAN BENEDEN (1876) from the Late Miocene (Diestian, Borgerhout) of Belgium, but their specific status remains uncertain for today genus requires revision. According to RAY (1976), additional material of *Monotherium* has been collected from the Calvert Formation and questioned St. Mary's Formation (RAY 1976) and Gay Head Greensand in eastern North America. LYELL (1877) reported supposed bones of this genus from Tertiary strata of Martha's Vineyard, Massachusetts.

"*Prophoca*" *rousseaui* VAN BENEDEN, 1876 (and see VAN BENEDEN 1877:78) is a primitive monachine from Belgium (SIMPSON 1945:122; RAY 1976:table 1). Some authors incorrectly cite its age as Late Miocene, but it is from a deposit that is correlative with the Middle Miocene. RAY (1976:table 1) indicated that the species is probably also represented by specimens from the Calvert Formation of Maryland and Virginia.

Piscophoca pacifica MUIZON, 1981, from the Early Pliocene of Peru, is close to *Monotherium aberratum* and related to the Lobodontini by apomorphies of the auditory region.

Tribe Monachini

The tribe Monachini has been recognized by several authors, and seems to be a natural grouping among the Monachinae. HENDEY and REPENNING (1972:95) concluded that *Monachus* has a primitive ear structure compared with that of other phocids. The genus *Monachus* has three species. KING (1956) concluded that *Monachus tropicalis* and *Monachus schauinslandi* are more closely related to each other than either is to *Monachus monachus*. REPENNING and RAY (1977) concluded that *M. schauinslandi* is the most primitive species of *Monachus*.

Two well-known species from the Early Pliocene of Belgium, *Callophoca obscura* and *Mesotaria ambigua*, were described and illustrated by VAN BENEDEN in 1877. RAY (1976) recognized these species as being synonyms, differentiated only by sexual dimorphism. Additional material, recently collected from Lee Creek, North Carolina, supports RAY's idea. About 60% of the phocid material from this locality belongs to *Callophoca obscura* (KORETSKY and RAY, in press).

An Early Pliocene seal first described from Italy by TAVANI (1941) and additional material from the eastern coast of North America was called *Pliophoca etrusca*. Abundant material referred to this species from the Yorktown Formation in North Carolina includes cranial and postcranial bones described by KORETSKY and RAY (in press).

A seemingly related species is *Messiphoca mauretania* MUIZON, 1981, from the Late Miocene of Algeria. According to its author, this species is close to the origin of *Pliophoca* and *Monachus*.

Properiptychus argentinus (AMEGHINO 1893), from the Middle Miocene of Argentina, was classified by MUIZON (1982) as close to *Pristiphoca*, but this latter genus is not valid.

Pontophoca sarmatica (ALEKSEEV 1924) was originally named by ALEKSEEV as *Phoca sarmatica* from Middle Miocene (Middle Sarmatian) deposits of Ukraine. This species is easily recognized because the distal end of the femur is wider than the proximal one, the femoral head is relatively small, and the distal condyles are flat and widely spaced. The humerus has a long, well developed deltoid crest that reaches the coronoid fossa. SIMIONESCU (1926), and later MACAROVICI and OESCU (1941), incorrectly identified a femur of *Pontophoca sarmatica* as *Phoca pontica*. Later McLAREN (1960) transferred these species into the genus *Pontophoca*, named by KRETZOI (1941). KORETSKY and GRIGORESCU (in press) revised the previous diagnosis of *Pontophoca sarmatica* and illustrated additional material from Eastern Europe, including a humerus and mandible.

According to KORETSKY and RAY (in press), the name *Pristiphoca occitana* (GERVAIS and SERRES, 1847) GERVAIS, 1848–1852 is a nomen dubium, because it was based on an isolated canine tooth of an indeterminate carnivore, not to be found at present.

Tribe Lobodontini

This tribe has been used by authors to unite the Antarctic monachine seals (*Lobodon*, *Hydrurga*, *Ommatophoca*, and *Leptonychotes*). The maxillary process is not distinct from the body of the zygomatic bone. The lower border of the zygomatic bone is straight, or with a slight arch only in its posterior part. The antero-dorsal end (= lacrimal process) of the zygomatic bone does not reach the infraorbital foramen; it terminates behind and at the same level as the foramen. The greatest downward flexure of the upper edge (= masseteric margin) of the zygomatic bone is lower than the infraorbital foramen. The nasal bones are usually fused; their frontal part is longer than the maxillary part. The double fontanelle in the presphenoid region narrows in its anterior and posterior parts, and is slitlike (cf. CHAPSKII 1971:315). These animals lack an entepicondylar foramen on the humerus; this is a derived character of the group. While the presence or absence of the entepicondylar foramen has been used for phocid systematics, this requires some qualification. The foramen is always absent in Monachinae, always present in Cystophorinae, and mostly present but variable (and in some individuals, even present on one side and absent on the other) in Phocinae. I consider the phocine and cystophorine conditions as being primitive and the monachine condition (absence of the foramen) to be derived. This is in opposition to the conclusion of WYSS (1994) and results in the opposite polarity of the character.

Homiphoca capensis (HENDEY and REPENNING 1972) from the Pliocene of South Africa was first described as *Prionodelphis capensis*. The age of this species is uncertain. For example, according to RAY (1976:400) this species is Middle Pliocene in age, but HENDEY (1976, 1978) concluded that the specimens are Late Pliocene. MUIZON (1981) simply stated that this deposit is Pliocene, although earlier (1980) he had stated that it is Late Miocene/Early Pliocene. The latter opinion was also expressed by BERTA and WYSS (1994). According to MUIZON and HENDEY (1982), *Homiphoca capensis* is morphologically intermediate between the extant Monachini and Lobodontini, but more closely related to *Lobodon* than to any other living seal. The Monachinae appear to have a range from Middle Miocene to Recent, and RAY (1976:400) reported bones resembling those of *Homiphoca capensis* from the latest Miocene or Early Pliocene Yorktown Formation in Virginia (KORETSKY and RAY, in press).

Acrophoca longirostris MUIZON, 1981, from the Early Pliocene of Peru, also belongs in the Lobodontini. It possesses a skull with a very long rostrum, while morphology of the postcranial skeleton indicates a lesser adaptation to swimming than that of the living Lobodontini.

Prionodelphis rovereti FRENGUELLI, 1922, from the Miocene/Early Pliocene of Argentina, is a nomen dubium, because, according to MUIZON and HENDEY (1980), this name was based on two isolated teeth, one of which (the lectotype of the species) belongs to a delphinoid cetacean, while the other is a monachine seal tooth with low diagnostic value (KORETSKY and RAY, in press).

SUBFAMILY CYSTOPHORINAE

The classification of the subfamily Cystophorinae, in its traditionally accepted form, and as adopted here, is simple. It consists of two genera, *Cystophora* and *Mirounga*, the latter with two species, *M. leonina* and *M. angustirostris*. Some recommended fundamental changes in the structure of the family, concerning also the Subfamily Cystophorinae (KING 1966), as mentioned above, cannot yet be accepted (HEPTNER et al. 1976). In my classification, the Cystophorinae includes the living *Cystophora cristata*, and *Mirounga* ssp., and the fossil *Miophoca vetusta*.

Cystophora is a highly evolved phocid with an interesting combination of characters. It has a palate like that of *Pagophilus*, and single-rooted cheek teeth like those of *Mirounga*. Its basicranium is of the phocine type. It has often been placed in the separate Subfamily Cystophorinae with *Mirounga* (e.g., SIMPSON 1945:123; SCHEFFER 1958; KING 1964; CHAPSKII 1974; KORETSKY and GRIGORESCU, in press); I prefer this arrangement to placing it in the Tribe Cystophorini as was proposed by BURNS and FAY (1970).

The elephant seals, *Mirounga* ssp., are the most highly evolved phocids in their behavior, feeding habits, and morphology. They have been included in their own subfamily or, alternatively, in the Monachinae, sometimes in a tribe Miroungini. No matter how they are classified, they are definitely the epitome of monachine (and of phocid) evolution. They are highly pelagic, specialized to feed at great depths on squid, and are morphologically very modified from the ancestral phocid anatomy. The northern and southern species exhibit classic antitropical distribution. The only reported

fossil Monachinae in the North Pacific are isolated bones of *Mirounga*, known from shallow-water, near-shore deposits of latest Pliocene and Pleistocene age in the coastal region of California (MILLER 1969).

Miophoca vetusta ZAPFE, 1937 (= *Pristiphoca vetusta* (THENIUS 1950)), from the early Middle Miocene (Badenian) of Slovakia, was described as closely related to *Pristiphoca*. Later THENIUS (1950), with no stated reason, transferred this species to the genus *Pristiphoca*. As previously discussed, I cannot accept this transfer, because the genus *Pristiphoca* is a nomen nudum.

SUBFAMILY DEVINOPHOCINAE

A well-preserved skull of *Devinophoca claytoni* (KORETSKY and HOLEC, in press) from the early Middle Miocene at Devinska Nova Vés (formerly Neudorf an der March), Slovakia, shows a mixture of subfamilial characters. Features shared with Phocinae are: number of incisors, and lack of a strongly pronounced mastoid process. Characters similar to Monachinae are: shape of maxillae, ratio between frontal and maxillary contacts of nasal bones. Characters shared with Cystophorinae are: ratio between interorbital width and mastoid width, and (also shared with Phocinae) ratio between length of auditory bullae and distance between them. Moreover, this skull has primitive features that are not known in any of the other three subfamilies: M1 is triangular, with three cusps and three roots; in P2-P4 the larger posterior roots are clearly made up of two fused roots, and the posterior alveoli are larger than the anterior; the incisors form a curved line; the anterior palatal foramina are deep and oval; and the sagittal crest is very well developed.

Thus, the plesiomorphic *D. claytoni* is considered a sister taxon to the three extant subfamilies of Phocidae, and referred to a new subfamily, Devinophocinae (KORETSKY and HOLEC, in press). Because of its young age, *D. claytoni* cannot be ancestral to the more advanced phocids. However, its primitive characters, in combination with the characters it shares with the other subfamilies, suggest that it might approximate the common ancestral morphotype.

Although the earliest known pinnipeds along the Atlantic coast of North America are Late Oligocene to Early Miocene in age, no phocine remains from this early time have yet been recognized in the North Pacific.

CLASSIFICATION OF PHOCIDAE

Order Carnivora BOWDICH, 1821

Suborder Caniformia KRETZOI, 1943

Infraorder Arctoidea FLOWER, 1869

Superfamily Phocoidea SMIRNOV, 1908

Family Phocidae (BROOKES, 1828) GRAY, 1825

Subfamily Phocinae GILL, 1866

Tribe and Genus undetermined

†*Phoca* "bessarabica" SIMIONESCU, 1925

†*Phoca novorossica*" ALEKSEEV, 1924

Tribe Phocini CHAPSKII, 1955

Subtribe Phocini CHAPSKII, 1955

Phoca LINNAEUS, 1758

Phoca vitulina LINNAEUS, 1758

Phoca largha PALLAS, 1811 (including *Phoca insularis* BELKIN, 1964)

†*Phoca?*" *vitulinoides* VAN BENEDEN, 1871

Pusa SCOPOLI, 1777

Pusa hispida (SCHREBER, 1775)

Pusa sibirica (GMELIN, 1788)

Pusa caspica (GMELIN, 1788)

Halichoerus NILSSON, 1820

Halichoerus grypus (FABRICIUS, 1791)

†*Gryphoca* VAN BENEDEN, 1877

†*Gryphoca similis* VAN BENEDEN, 1877

†*Phocanella* VAN BENEDEN, 1877

†*Phocanella pumila* VAN BENEDEN, 1877 (including †*Phocanella minor* VAN BENEDEN, 1877)

†*Monachopsis* KRETZOI, 1941

- †*Monachopsis pontica* (EICHWALD, 1850)
- †*Praepusa* KRETZOI, 1941
 - †*Praepusa pannonica* KRETZOI, 1941
 - †*Praepusa vindobonensis* (TOULA, 1898) 1941 (including †*Praepusa tarchankutica* KORETSKY, 1984)
- †*Cryptophoca* KORETSKY and RAY, 1994
 - †*Cryptophoca maeotica* (NORDMANN, 1858)
- †*Prophoca* VAN BENEDEN, 1877
 - †*Prophoca proxima* VAN BENEDEN, 1876
- †*Leptophoca* TRUE, 1906
 - †*Leptophoca lenis* TRUE, 1906
- †*Sarmatonectes*, new genus
 - †*Sarmatonectes sintsovi*, new species
- Subtribe *Histriophocini* CHAPSKII, 1955
 - Histriophoca* GILL, 1873
 - Histriophoca fasciata* (ZIMMERMANN, 1783)
 - †*Histriophoca alekseevi* new species
 - Pagophilus* GRAY, 1844
 - Pagophilus groenlandica* (ERXLEBEN, 1777)
- Tribe *Erignathini* CHAPSKII, 1955
 - Erignathus* GILL, 1866
 - Erignathus barbatus* (ERXLEBEN, 1777)
 - Erignathus barbatus barbatus* ERXLEBEN, 1777 (including *Erignathus barbatus nauticus* PALLAS, 1811)
 - †*Platyphoca* VAN BENEDEN, 1877
 - †*Platyphoca vulgaris* VAN BENEDEN, 1877
- Subfamily *Monachinae* GRAY, 1869
 - Tribe undetermined
 - †*Monotherium* VAN BENEDEN, 1877
 - †*Monotherium?* *wymani* (LEIDY, 1853)
 - †*Monotherium delognii* VAN BENEDEN, 1876
 - †*Monotherium aberratum* VAN BENEDEN, 1876
 - †*Monotherium affine* VAN BENEDEN, 1876
 - †“*Prophoca*” *rousseaui* VAN BENEDEN, 1876
 - †*Piscophoca* MUIZON, 1981
 - †*Piscophoca pacifica* MUIZON, 1981
 - Tribe *Monachini* (GRAY, 1869) SCHEFFER, 1958
 - Monachus* FLEMING, 1822
 - Monachus monachus* (HERMANN, 1779)
 - Monachus tropicalis* (GRAY, 1850)
 - Monachus schauinslandi* (MATSCHIE, 1905)
 - †*Callophoca* VAN BENEDEN, 1877
 - †*Callophoca obscura* VAN BENEDEN, 1877 (including *Mesotaria ambigua* VAN BENEDEN, 1877)
 - †*Pliophoca* TAVANI, 1941
 - †*Pliophoca etrusca* TAVANI, 1941
 - †*Messiphoca* MUIZON, 1981
 - †*Messiphoca mauretanic* (MUIZON, 1981)
 - †*Properiptychus* AMEGHINO, 1897
 - †*Properiptychus argentinus* (AMEGHINO, 1893)
 - †*Pontophoca* KRETZOI, 1941
 - †*Pontophoca sarmatica* (ALEKSEEV, 1924) McLAREN, 1960
 - Tribe *Lobodontini* (GRAY, 1869) SCHEFFER, 1958
 - Lobodon* GRAY, 1844
 - Lobodon carcinophagus* (HOMBRON and JACQUINOT, 1842)
 - Hydrurga* GISTEL, 1848
 - Hydrurga leptonyx* (BLAINVILLE, 1820)
 - Ommatophoca* GRAY, 1844
 - Ommatophoca rossi* GRAY, 1844

Leptonychotes GILL, 1872

Leptonychotes weddelli (LESSON, 1826)

†Homiphoca MUIZON and HENDEY, 1980

†*Homiphoca capensis* (HENDEY and REPENNING, 1972)

†Acrophoca MUIZON, 1981

†*Acrophoca longirostris* MUIZON, 1981

Subfamily Cystophorinae GRAY, 1866

Cystophora NILSSON, 1820

Cystophora cristata (ERXLEBEN, 1777)

Mirounga GRAY, 1827

Mirounga leonina LINNAEUS, 1758

Mirounga angustirostris GILL, 1866

†Miophoca ZAPFE, 1937 (= *Pristiphoca* sensu THENIUS, 1950)

†*Miophoca vetusta* ZAPFE, 1937

Subfamily †Devinophocinae (KORETSKY and HOLEC, in press)

†Devinophoca (KORETSKY and HOLEC, in press)

†*Devinophoca claytoni* (KORETSKY and HOLEC, in press)

Chapter 8
Paratethyan geology and biogeography

The Paratethys seaway (a remnant of the Mesozoic Tethys Sea) extended from western Switzerland eastward to the Aral Sea in Asia (Kazakhstan, Uzbekistan). Marine and terrestrial biotas of the Paratethys were strongly influenced by rapid facies changes. These are directly correlated to changing seaways and the distribution of water masses. These constant changes, resulting in the development of differing ecosystems, account for the major subdivisions: Western Paratethys (from the Rhone Valley to Bavaria); Central Paratethys (Alpine–Carpathian region and intramontane basins from Austria to the Ukraine and Moldavia); Eastern Paratethys (Ponto–Caspian or Euxinian region, the area of the Black Sea and the Caspian Sea to the Aral Sea) (Fig. 50) (RÖGL and STEININGER 1984; RÖGL 1998).

From the Oligocene to the Early Miocene, Paratethyan marine sedimentation was characterized by connections to open seas and oceans (Figs. 52, 53). The Late Oligocene – Early Miocene marine cycle exhibited elongated basins with a west–east orientation and connected with the Mediterranean and Indo-Pacific (RÖGL 1998). At this time the

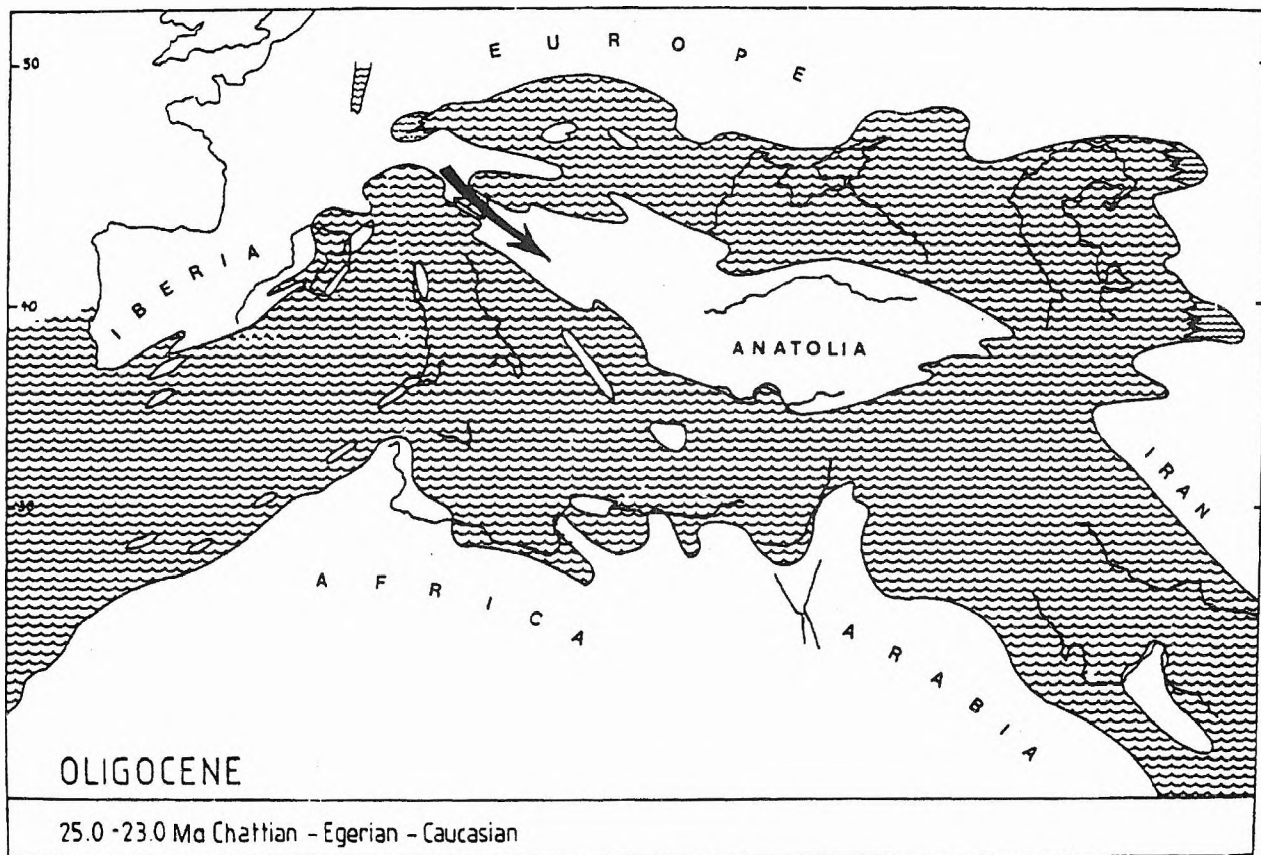


Figure 52. Palaeogeographic reconstruction of the circum-Mediterranean region in the Late Oligocene. Eurasia and Africa have been separated by an open marine realm between the Atlantic and Indo-Pacific Oceans (from RÖGL and STEININGER 1984)

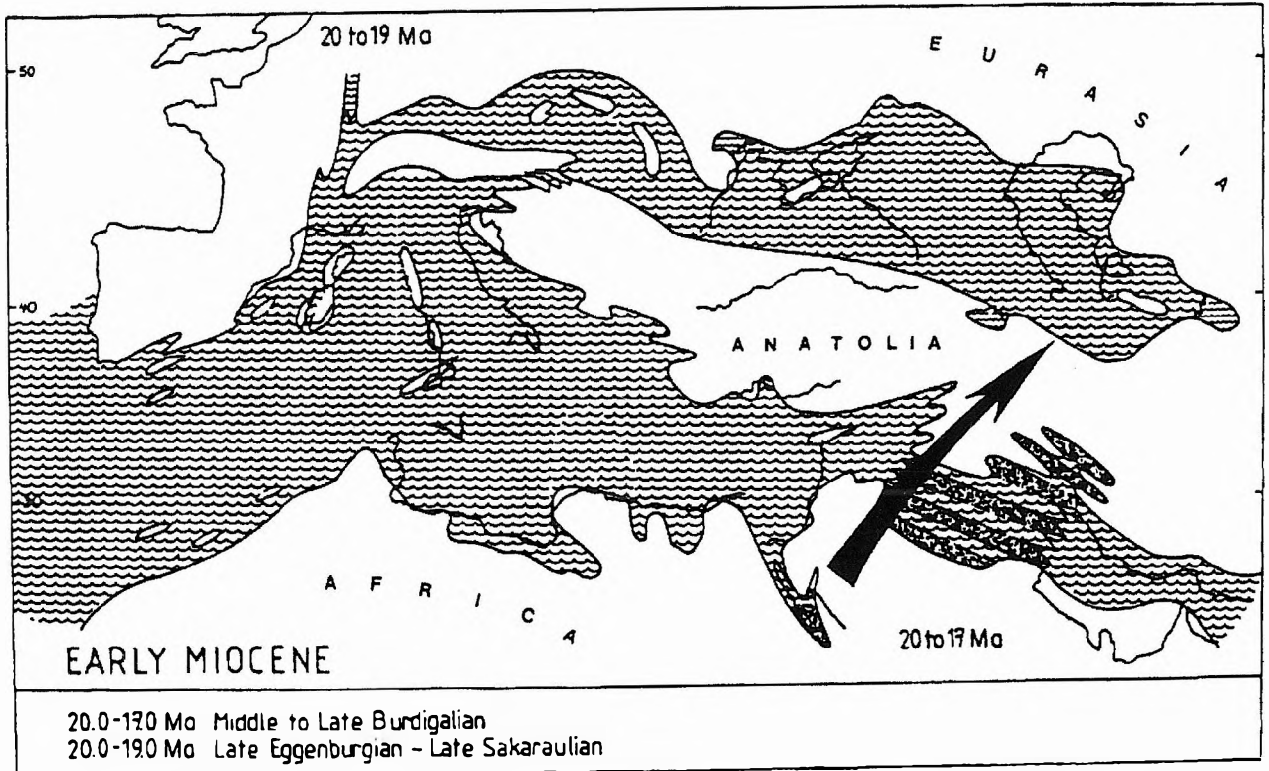


Figure 53. The closure of the seaway to the Indo-Pacific in the Early Miocene (from RÖGL and STEININGER 1984)

Mediterranean/Tethys seaway was still open to the Indian Ocean in the east. A worldwide cooling phase had ended (BERNOR et al. 1996), and in the circum-Mediterranean region tropical to subtropical climates were restored.

Western Paratethys

At the end of the first Miocene cycle (23.8–16.49 Ma), the Indo-Pacific gateway to the Eastern Paratethys closed, and with it the Mediterranean connection along the northern Alpine region. The only remaining marine connection to the Mediterranean passed through northern Yugoslavia.

At the end of the Early Miocene (= Ottnangian, 17 Ma to 19 Ma) the Western Paratethys came under the influence of continental conditions. Only the most central part of the Pannonian Basin remained a marine area, connected with the Mediterranean Basin through northern Yugoslavia (STEININGER et al. 1996).

The collapse of the circum-equatorial circulation systems of the world oceans as a result of the closing of the Eastern Mediterranean also strongly influenced marine biotas and climate around the new basins. While the Paratethys remained open, a new short-lived seaway developed along the western Alpine area to the Rhone Valley and connecting the Antwerp Basin to the Mediterranean (SINITSYN 1965) (Fig.53).

Central Paratethys

The Central Paratethys had rapidly changing marine connections throughout the Early and Middle Miocene. In the Early Miocene (Karpatian transgression, 16.4–17.0 Ma) the reorganization of the Central Paratethys began with the formation of intramontane basins (STEININGER and PAPP 1979). The east–west orientation of the Oligocene–Miocene marine basins disappeared.

The interruption of marine connections in the Ponto-Caspian region resulted in a second period of reduced salinity with endemic mollusc faunas in the Middle Badenian stage (14.5–15.0 Ma). At the same time the marine connections to the Mediterranean along the northern Yugoslavian corridor were retained.

The first geological record of a seal from the Paratethys (Devinska Nova Vés sandhill, Slovakia) is dated to 14.8 Ma (Badenian; lower Zone MN 6 = Langian regression). This was more than one million years earlier than the isolation of

the Paratethys from the eastern Tethys, which occurred at the boundary between Badenian and Sarmatian at 13.6 Ma. At this time extensive biogeographic interchanges took place between Eurasia and Africa (RÖGL and STEININGER 1984).

Changes in marine conditions influenced terrestrial biotas as well. In Central Europe a vegetation dominated by small-leaved forms indicates dry conditions in mammal zone MN 6/7 (Fig. 54). The salinity crises continued only a few hundred thousand years. In the Late Badenian the entire Paratethys was again flooded (GRIGORESCU et al. 1986).

In the Early Miocene, the Central Paratethys Eggenburgian Sea formed an "aquatic bridge" connecting the Mediterranean with the basin of today's Black and Caspian Seas (= the Euxinian Basin). This large seaway was interrupted during Early Miocene times by regional tectonics associated with the Alpine orogeny, changing the distribution of water masses.

The marine conditions in the Pannonian Basin continued until the Late Badenian (circa 13.6 Ma), when the marine reflooding ended. A last opening of the Indo-Pacific connections resulted in a continuous marine environment through the Eastern and Central Paratethys. The gateway to the Mediterranean at the northern Yugoslavian corridor was closed.

By the Middle Miocene, entirely different sedimentation developed in the Euxinian Basin. At this time (Early Badenian stage; Fig. 55) the marine restoration started to occur. The reopening of the seaway to the Indo-Pacific also flooded the entire Central Paratethys, and the Vienna, Pannonian and Transylvanian Basins began to form.

There has been considerable uncertainty surrounding the age of latest Miocene sediments in this region. Currently, it is believed that the Central Paratethys Pannonian/Pontian boundary lies somewhere between 8 and 7 Ma (BERNOR et al. 1996). In the Eastern Paratethys this boundary has been radioisotopically placed at around 7.1 Ma. The top of the Pontian in Azerbaijan has been dated (BERNOR et al. 1996) and is younger (5.4 Ma) than that in the Black Sea region; in the Central Paratethys it is estimated to be ca. 5.6 Ma. The progressive development of land areas in Pontian time reduced the aquatic biotas of the Paratethys, with only the Ponto-Caspian region remaining under marine influence. Around 5.6 Ma the Mediterranean Sea underwent its final Miocene regression, becoming a deep desiccated basin. Concurrent with this terminal Messinian event, Paratethys began to break up in Pontian time into isolated basins with very low salinity (as indicated by freshwater gastropods). At the end of the Messinian crisis, brackish-water sediments were widely distributed in the Mediterranean basin.

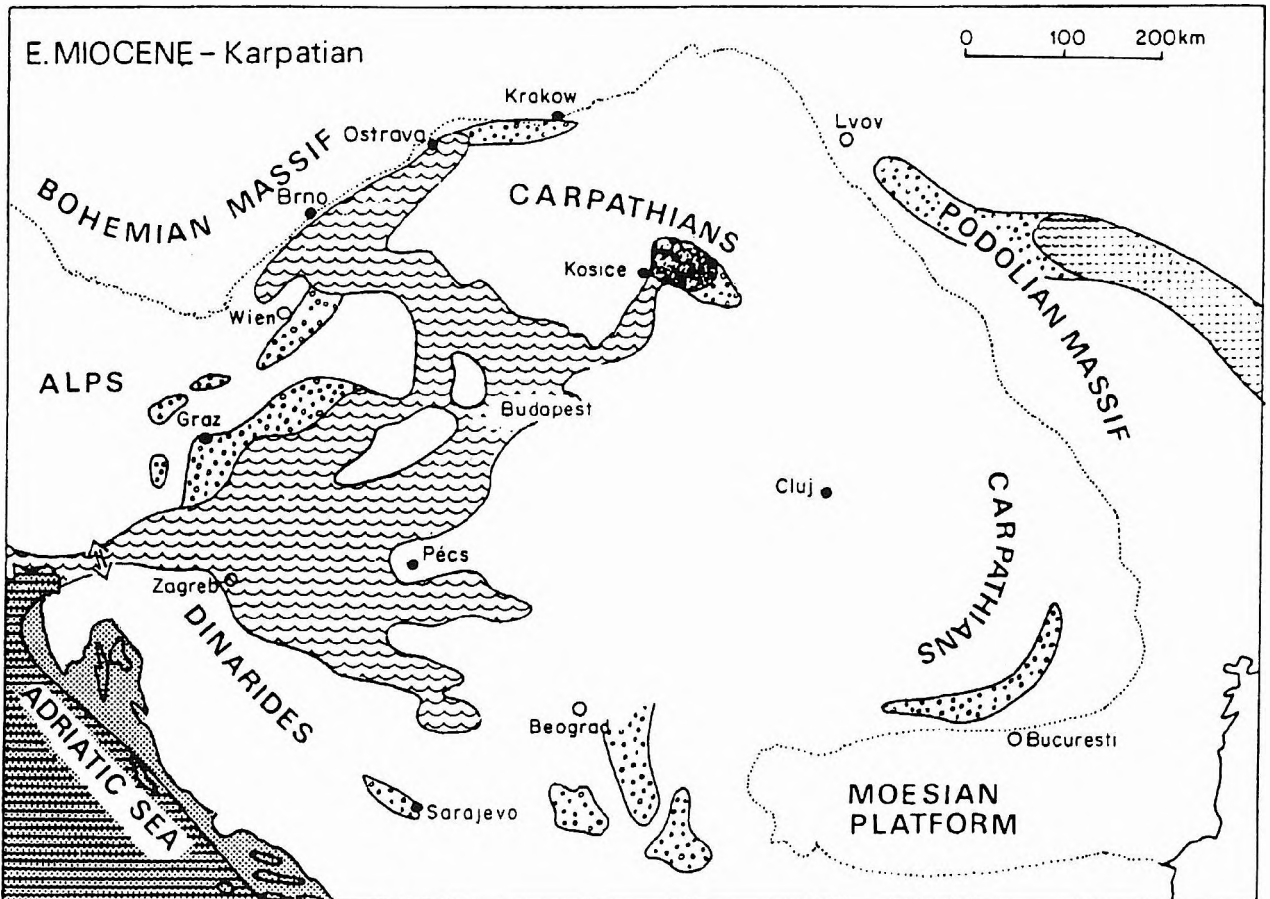


Figure 54. The Karpatian transgression in the Early Miocene. The reorganization of the Central Paratethys began with the formation of intramontane basins (from RÖGL and STEININGER 1984)

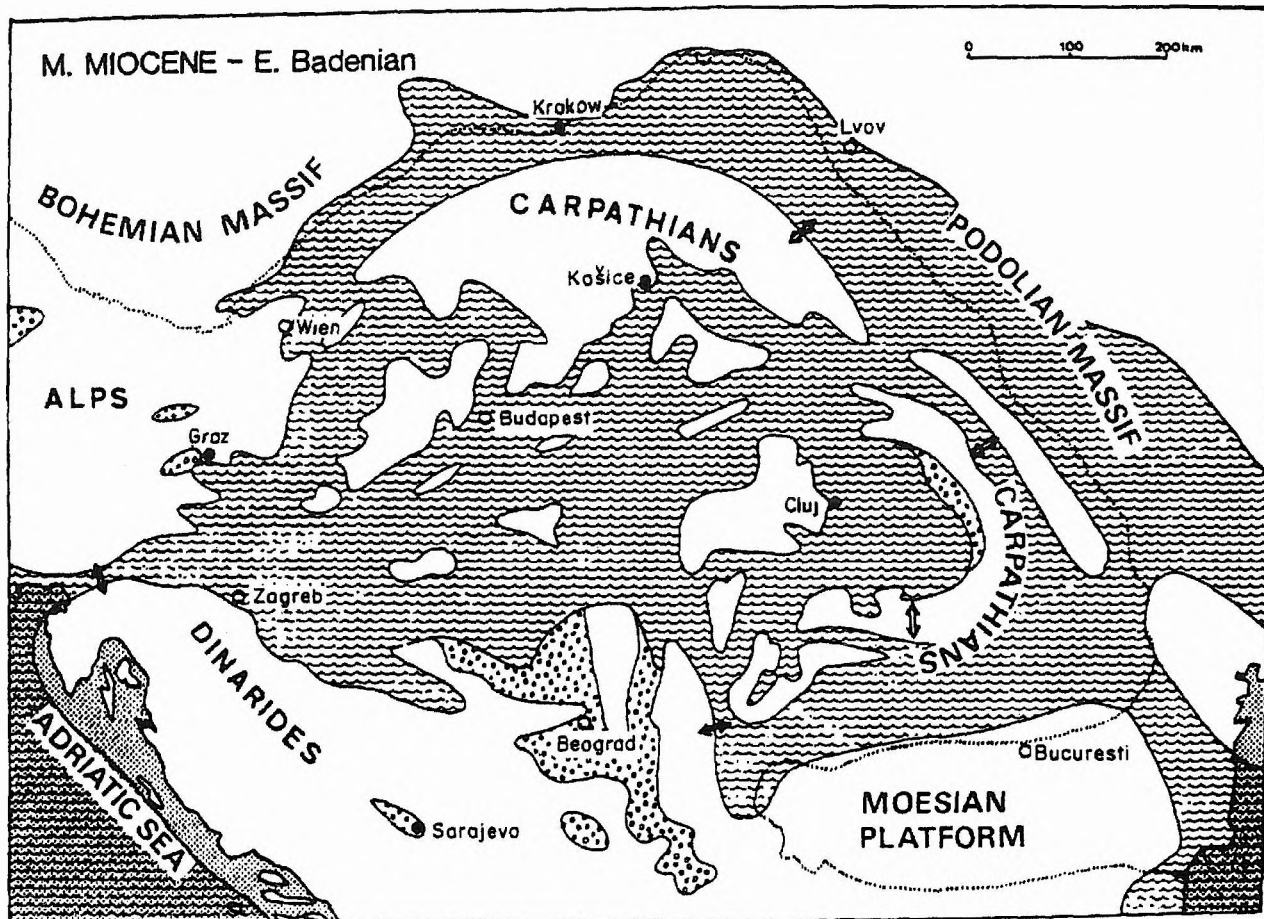


Figure 55. The Middle Miocene marine restoration. The reopening of the seaways to the Indo-Pacific also flooded the entire Central Paratethys, Vienna, Pannonian, and Transylvanian basins (from RÖGL and STEININGER 1984)

With the development of Paratethys endemic faunas, some regional correlations become possible (Fig. 56), while similar stages developed in both the Central and the Eastern Paratethys, despite asynchronous chronology of their development. The Pannonian Basin (Hungary) and its surroundings became the limited Central Paratethys, the freshwater Pannonian lake, in the Late Miocene. Also in the Sarmatian stage, to the east of the Carpathian Mountains a sea with reduced salinity stretched as far as the Caspian Basin.

Eastern Paratethys

In the Eastern Paratethys, a facies showing reduced salinity began to develop in the late Early Miocene (in the period from 16.4 to 19.0 Ma), and the Eastern Paratethys finally degenerated into a low-salinity facies by Middle Burdigalian time (circa 19 Ma). In this stage a brief interruption of the Indo-Pacific connection with the Eastern Paratethys resulted in evaporite formation (= Paratethys salinity crisis) in the Carpathian region and in the neighboring basins of eastern Slovakia and Transylvania (Fig. 57).

The Early/Middle Miocene boundary corresponds to the base of the Badenian and is estimated to be about 16.4 Ma. The Badenian/Sarmatian boundary is dated at 13.6 Ma, and the Sarmatian s.s./Pannonian boundary is estimated to be 11.5 Ma (RÖGL and DAXNER-HÖCK 1996; STEININGER et al. 1996). The Austrian Middle Miocene (Badenian–Sarmatian) includes several localities with age-characteristic species-diverse large mammal faunas.

Around 14 Ma the marine phase of the Paratethys ended and a system of independent basins developed. The Sarmatian salinity reductions led to loss of some marine groups. Endemics began to spread, starting from the Vienna and Pannonian Basins and developing different assemblages in each basin (Fig. 58).

Throughout the Early and Middle Miocene, a sporadic land corridor between Arabia and Asia Minor allowed a series of migration waves of the terrestrial biota between the adjoining continents (Fig. 53).

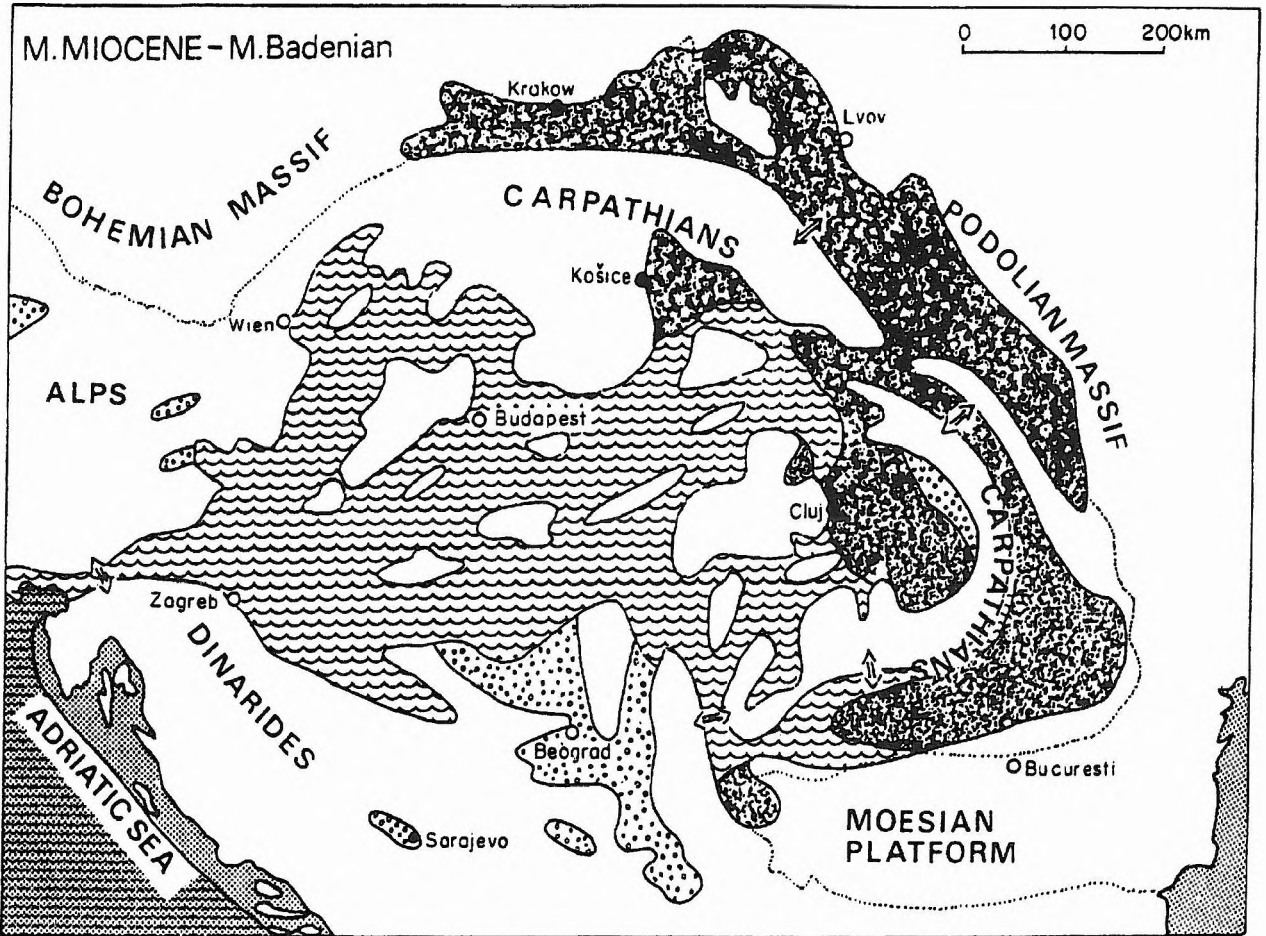


Figure 56. The Middle Miocene Paratethys salinity crisis. A brief interruption of the Indo-Pacific seaway and the connection to the Eastern Paratethys resulted in vast areas of evaporite formation in the basins of eastern Slovakia and Transylvania (from RÖGL and STEININGER 1984)

The second major marine cycle began in the Middle Miocene. Marine conditions were found throughout the Central and Eastern Paratethys. This condition persisted for only a short interval and was followed by another Paratethys salinity crisis. During the Middle Miocene (i.e., at the end of the Badenian stage, 13.6 Ma), biogeographic connection of the Central Paratethys to marine areas stopped, and widely distributed endemic aquatic faunas developed. Low-salinity facies also arose again in the Late Badenian of the Eastern Paratethys (STEININGER et al. 1996).

At the boundary between Badenian and Sarmatian (*sensu strictu*) stages (13.6 Ma), fully marine conditions in the Paratethys ended; this was not accompanied by a major change in the paleogeographical situation (Fig. 59). Only the seaway from the Eastern Paratethys to the Indo-Pacific became narrower. The Paratethys still existed in Sarmatian time, although its salinity was reduced from 30 per mille to 16 per mille at the end of this time (POR 1989).

The marine biotas changed in the Paratethys due to a further reduction of marine connections. The Carpathian area was uplifted. In the Pannonian Basin and adjoining basins the endemic brackish-water facies of the Pannonian stage developed. In the Dacian Basin and in the Eastern Paratethys the “Sarmatian” (more fully marine) facies are continued.

In the Eastern Paratethys the reduction in salinity led to the Sarmatian endemic stage (Fig. 59), from which most of the fossil material discussed here was derived. During the early portion of this stage, the Volhynian substage (from 13.6 to 12.2 Ma), the same conditions prevailed from the Caspian Sea region to the Vienna Basin. The Sarmatian stage continued further on in the more elongated Eastern Paratethys, from the Carpathian Mountains to the Caspian Basin.

Because the Sarmatian stage conditions continued longer in the east, the term “Sarmatian *sensu lato*” was established. This term has also been constantly used for time equivalents of the Pannonian stage of the Vienna and Pannonian Basins. The “Sarmatian s.l.” has been subdivided in the Eastern Paratethys to include the Volhynian, Bessarabian and Khersonian substages. These substages are correlated with the Late Serravallian – Early Tortonian stages of the Mediterranean time-scale (Fig. 56).

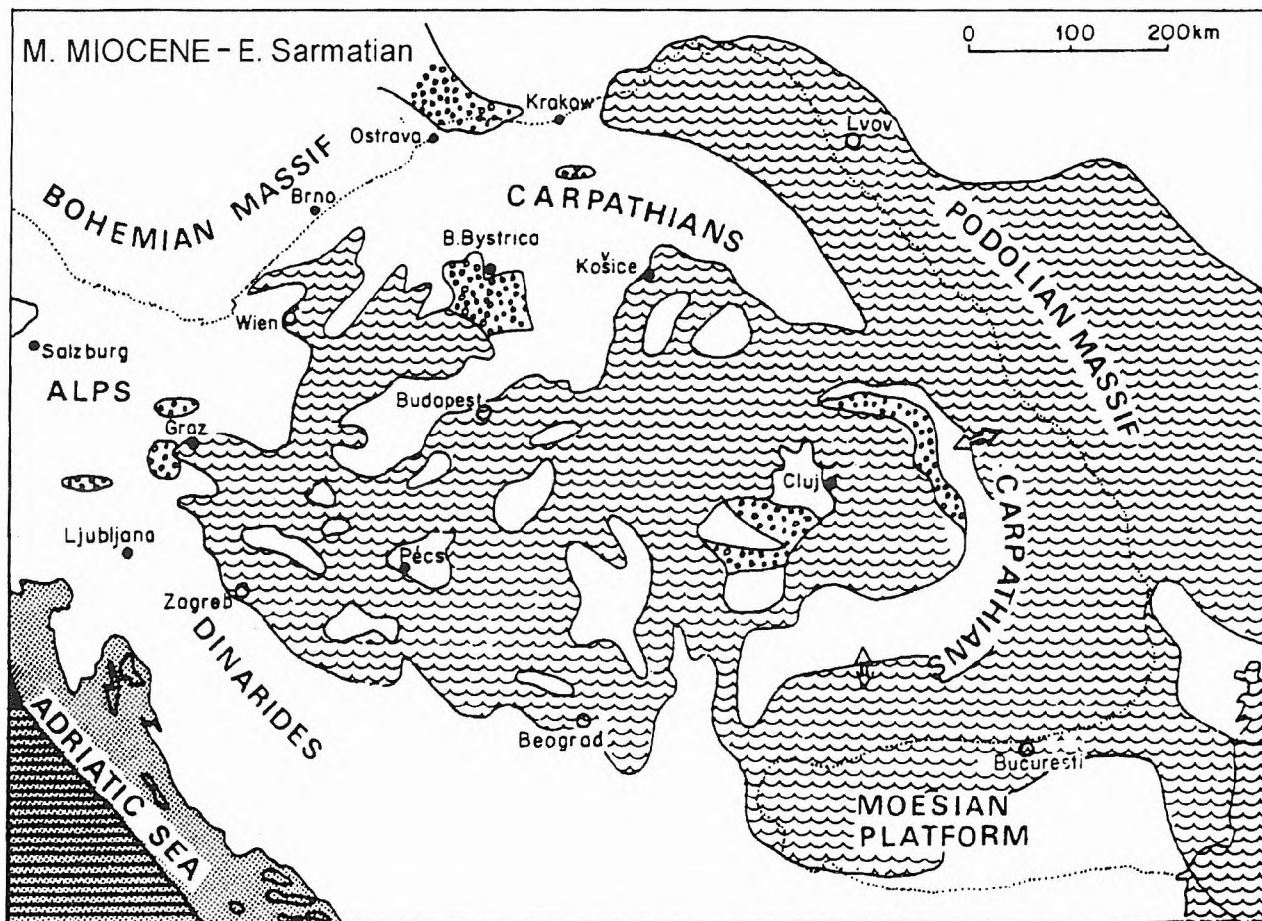


Figure 57. The Early Sarmatian marine region with reduced salinity (from RÖGL and STEININGER 1984)

The subdivision of the Sarmatian s.l. substages in the Eastern Paratethys is important for correlation with equivalent-aged strata in the Vienna Basin: the Volhynian/Bessarabian boundary is ca. 12.2 Ma; the Bessarabian/Khersonian boundary is ca. 10.2 Ma; the Khersonian/Maeotian boundary is 9.88 Ma.

The confusion in correlation of the Middle to Late Miocene between the Central and Eastern Paratethys arises due to improper use of the Sarmatian stage in the Eastern Paratethys. Its stratotypic characterization is actually in the Central Paratethys. The Sarmatian stage s.l. in the Eastern Paratethys is dated from 13.6 Ma to 9.8 Ma.

The Late–Early to Early–Middle Miocene global warming permits fine-scaled biostratigraphic subdivision.

The Middle Miocene (16.49–11.2 Ma) transgression extended all over the Mediterranean and Paratethys, reopening the seaway to the Indo-Pacific. Circum-equatorial water circulation was reestablished. Open seaways continued by way of Eastern Paratethys to the Indo-Pacific, while those to the Mediterranean remained open too. All marine organisms became extinct in the Pannonian Basin and Eastern Paratethys by Khersonian time due to the reduction in salinity (to 0.03–0.04 per mille) (Fig. 58). This environmental shift was followed by a new marine cycle in the Maeotian (from 9.88 to 7.1 Ma). Again, strong endemism resulted, but by the end of the Maeotian the large Eastern Paratethys Sea was reduced to a series of smaller isolated basins. A nearly freshwater stage followed, with significantly similar faunal assemblages in the Pannonian Basin and eastern, Euxinian area. Recognition of this faunal similarity in Central and Eastern Paratethys led to identification of the Pontian stage (from 7.1. to 5.4 Ma)

The Late Miocene of subtropical and transitional regions can help to provide regional correlation between these two regions at the Miocene/Pliocene boundary (5.3 Ma).

Finally, the sea withdrew from the Alpine–Carpathian basin and only the most central part in Hungary remained marine. A marine period, with a continuation into the Austrian–Bohemian channel, was formed in the Pannonian Basin (SEMENENKO 1987; 1993).

The closure of the Atlantic–Western Mediterranean gateway (6.0–5.5 Ma = Messinian – Late Pontian crisis) started the Mediterranean desiccation and well-known salt formation in all deep basins (Fig. 60). The Paratethys split into isolated basins with endemic faunas in Late Pontian time.

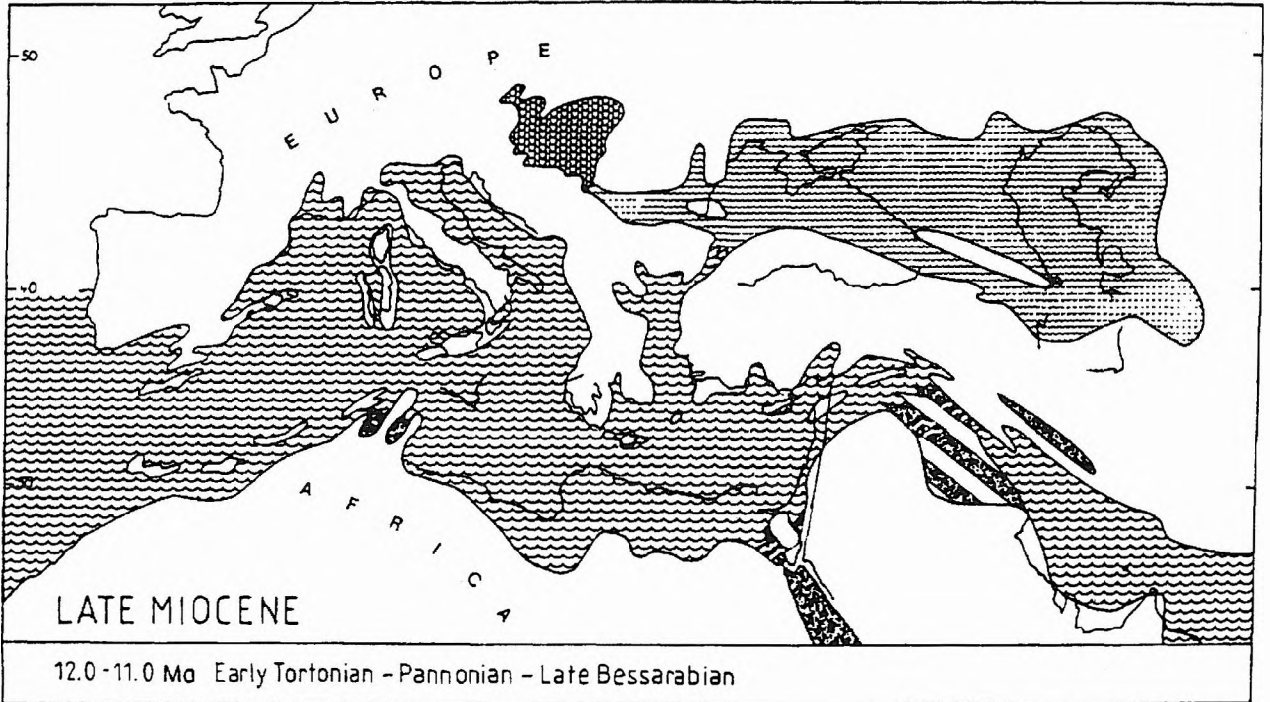


Figure 58. The final closure of the Indo-Pacific seaways in the Late Miocene permitted migrations of terrestrial mammals (arrow) (from RÖGL and STEININGER 1984)

Thus, the Paratethyan species of seals were adapted to flowing, highly oxygenated water, of shallow littoral areas, and underwent endemic speciation near the river basins. They were ecologically well adapted to temperate close to river systems and to basically stable environments, with the possibility of up- or downstream retreat.

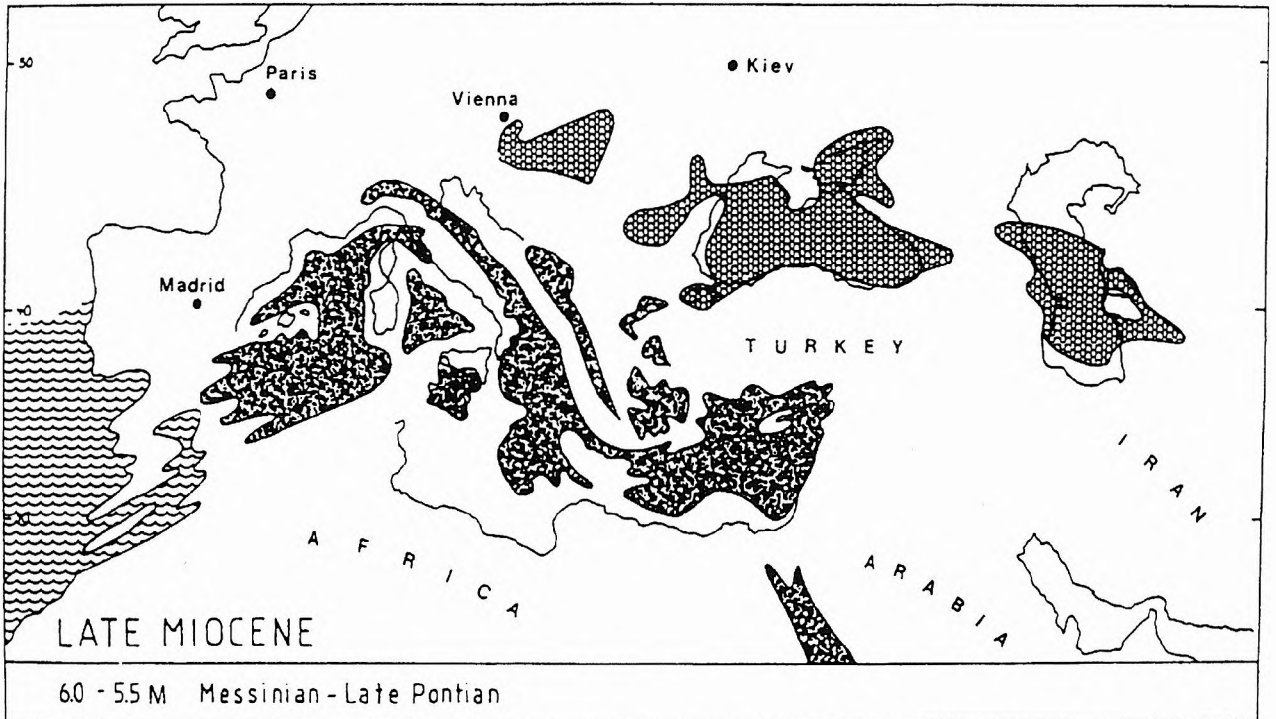
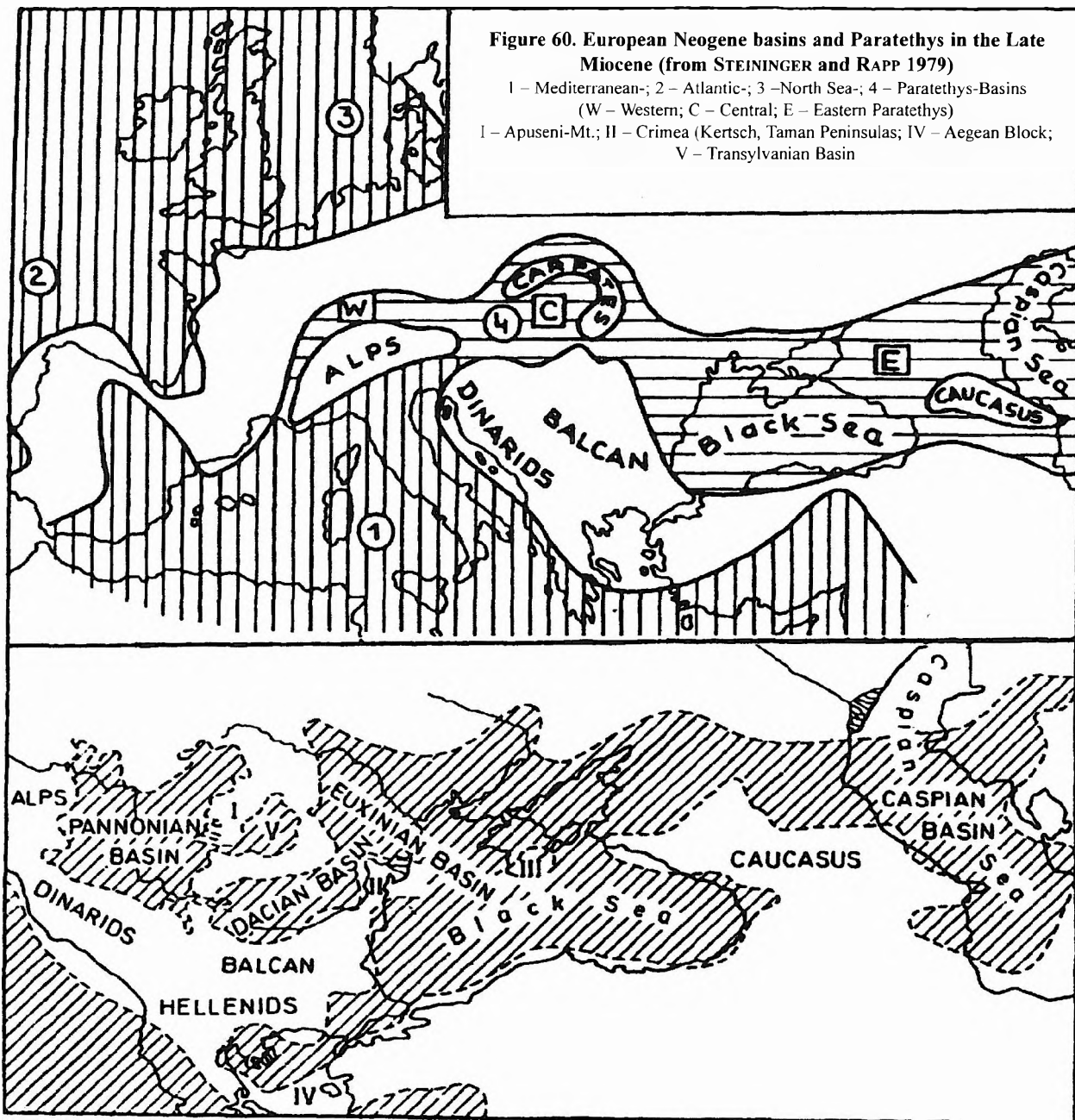


Figure 59. The Messinian salinity crisis. The closure of the Atlantic-Western Mediterranean gateway initiated the Mediterranean desiccation and salt formation in all deep basins. The Paratethys split into isolated basins with endemic faunas in Late Pontian time (from RÖGL and STEININGER 1984)



Biogeography of some Paratethyan seals

One long-debated evolutionary aspect of the Paratethyan seals is connected with the temperature of the water during the Sarmatian. The extensive development of reefs and the rich fossiliferous limestone formed by the calcified shells of mollusks through the entire Paratethys during Sarmatian time is clear evidence for warm, subtropical waters. The earliest Paratethyan seals were thermophilic, and this is reflected in their ecomorphology. The pagophilic forms emerged following adaptation to post-Miocene climatic changes (as exemplified in the Antwerp Basin). The associated invertebrate fossils show that the known fossil pinnipeds lived in warmer waters than do most of their modern analogues. The degree of cold-water preference showed by most modern pinnipeds has apparently increased as the Neogene though Pleistocene cooling trend has progressed.

The Paratethys was characterized by flora and fauna of subtropical aspect. Some authors have assumed that the seals somehow originated in tropical Tethys. On the other hand, others suggested that part of the Paratethys was arctic because of the cold-water adaptations of living forms. Associated invertebrate fossils, particularly in South Dobrogea (Romania),

Kishinev (Moldavia), and Tarchankut (Ukraine), indicate that the Sarmatian Paratethyan seals lived in warm water, and thus the cold-water adaptation of modern seals derived from these must have resulted from global cooling.

It is reasonable to assume that as a result of the change of salinity of waters, a sharp reduction occurred in the number of pinniped lineages.

About 17 Ma one primitive Paratethyan Phocoid moved from this area into the North Sea. It there evolved into a number of endemic forms, most of which have become extinct, but some of which evolved into the genus *Pusa*, still living as a relict in the Caspian Sea (a remnant of Paratethys) (Fig. 61). From the North Sea it dispersed to the North Atlantic and North Pacific by way of the Arctic Ocean about 3 Ma (GRIGORESCU 1977; RAY 1977a; REPENNING et al. 1979).

From 16.5 to at least 8 Ma, phocine seals evolved in isolation in Paratethys, which had at most only restricted and very temporary connections with Tethys. The Paratethys was formed by several basins, at times partially separated by

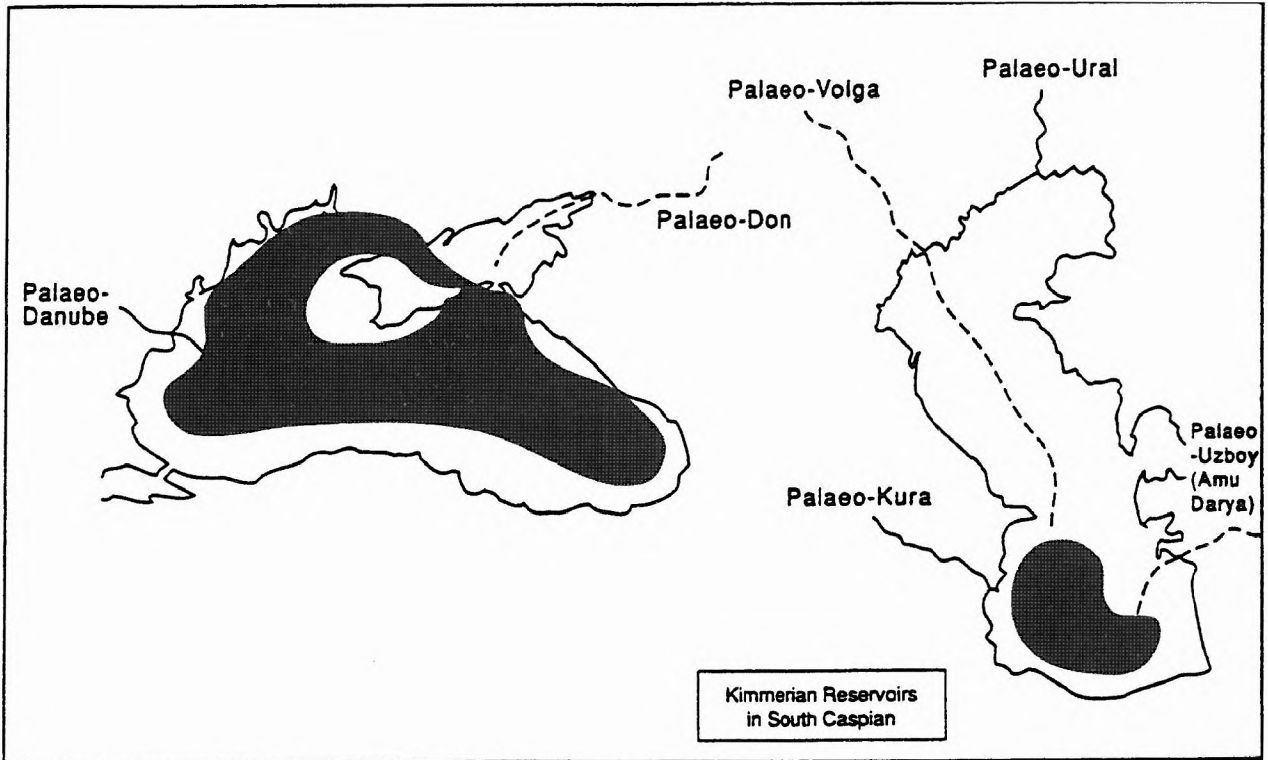


Figure 61. Paleogeographic reconstruction of Eastern Paratethys in latest Miocene-Pliocene (from RÖGL and STEININGER, 1984)

larger and smaller islands (some formed by bryozoan reefs). Possibly as a result of this discontinuity of basins and isolation from Tethys, several Paratethyan seals developed interesting specializations. Some members of *Praepusa*, which are closely related to modern *Pusa*, entered the Paratethys from the Danube Delta and Vienna Basin (from 12.2 to 13.6 Ma).

BERG (1910; 1928; 1940) and McLAREN (1960a) also discussed the biogeography of several species of *Pusa*, and considered two possible mechanisms for their dispersal:

1. via watercourses established during the Pleistocene, and
2. as relicts of more southerly Late Miocene populations that had occupied the Paratethyan Seaway. McLAREN favored the former, as do I (but only partially), because if *P. caspica* and *P. sibirica* had originated or separated from *Pusa hispida* as early as 10 million years ago, I would expect them to be more morphologically diverse. But, according to morphology and phylogenetic analyses (see Chapter 4 and BININDA-EMONDS and RUSSELL (1996:171, fig. 25e), *P. sibirica* is morphologically more similar to *P. hispida*. This observation partially supports McLAREN's theory of dispersal. Also, there is no record of the genus *Pusa* having existed as Early as Late Miocene time. The oldest supposed record (Late Pliocene) of the genus *Pusa* is a single radius (REPENNING and TEDFORD 1977); some specimens have also been reported from Pleistocene deposits on Alaska's North Slope (REPENNING 1983).

Remarks on biogeography of *Pusa*

The modern species of the genus *Pusa* are *P. hispida* (Arctic Ocean), *P. caspica* (Caspian Sea; this water-body is a remnant of the ancient Paratethys), and *P. sibirica* (Lake Baikal). It is most reasonable that *P. sibirica* (which is closely related to Arctic *P. hispida*) gained access to the freshwater Lake Baikal from the more brackish water-body (Caspian

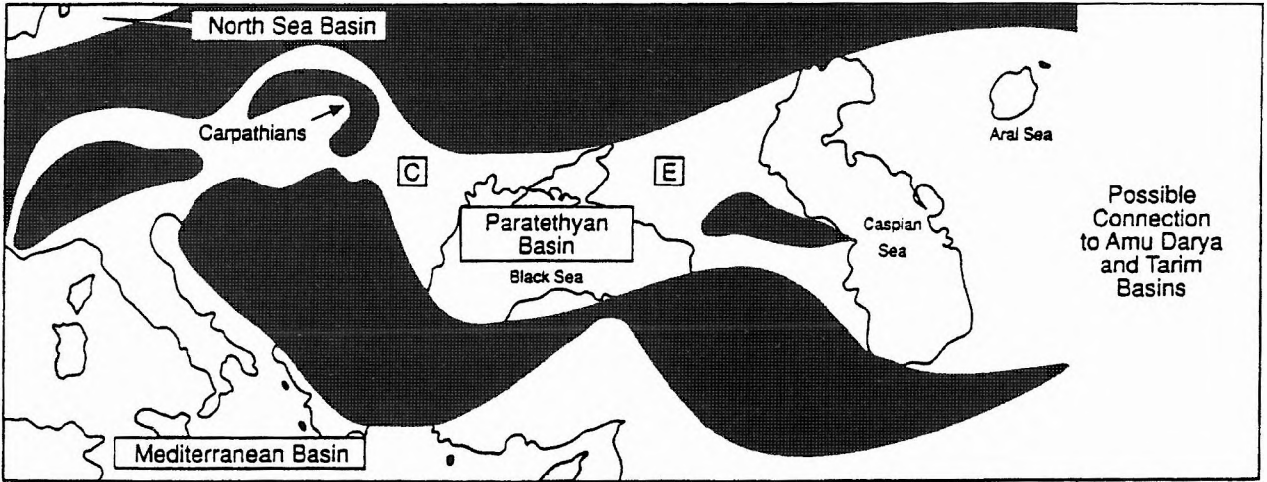


Figure 62. Geological reconstruction of the Paratethyan basin in the Oligocene

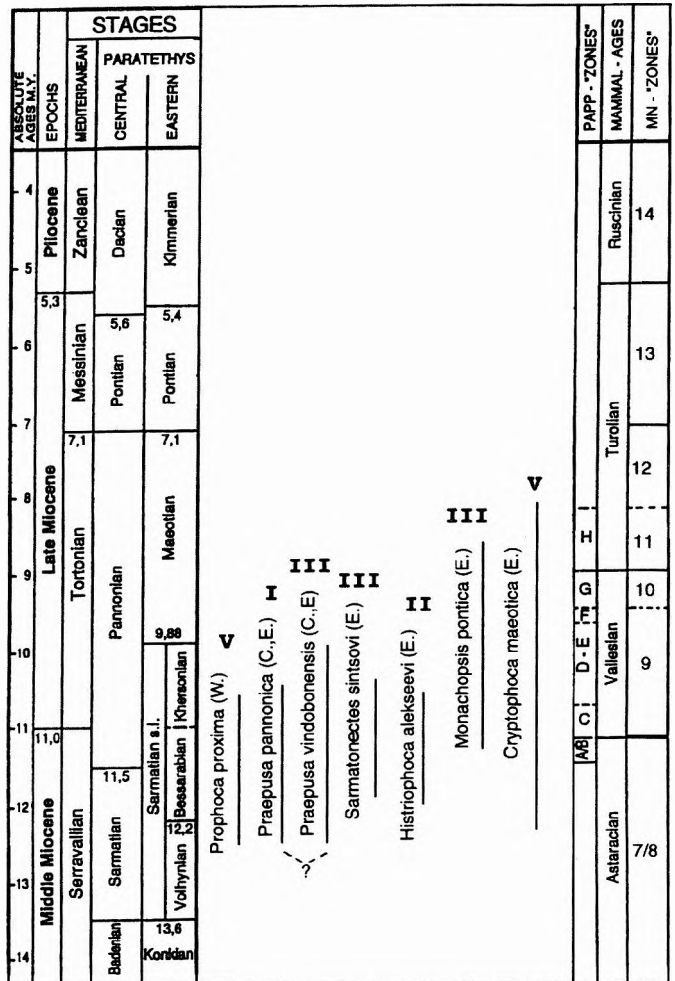
C = Central Paratethys; E = Eastern Paratethys, including the Pontian (Black Sea) Basin and the Caspian Basin (from RÖGL and STEININGER 1984)

Sea) through the remnants of the ancient Paratethys waterway (REPENNING et al. 1979). Throughout most of the Miocene, the eastern limit of the Paratethyan Basin was presumably the Caspian Basin (JONES and SIMMONS 1996), but in the Late Pliocene at least it was probably farther east, with possible connections to the Amu Darya and Tarim basins (Fig. 62). Paleogeographically, at about 3 Ma the present Caspian Sea was greatly enlarged, extending along the western border of the Ural Mountains northward to approximately 55° N latitude. At this time the Arctic Ocean had transgressed southward across northern Russia well below the Arctic Circle to about 61° N latitude (REPENNING et al. 1979). These two aquatic extensions were within 300 miles of each other at the western base of the Urals, and were separated by the lowlands along the present course of the Kama River.

According to some authors (GROSSHEIM and KHSIN 1967), at this time the high mountains separating the Caspian and Black Seas were glaciated. It seems that *Pusa* could have emigrated from the

Figure 63. Stratigraphic correlation chart of the Late Miocene with the Central and Eastern Paratethys regional stage systems (from RÖGL and DAXNER-HÖCK, 1996), suggested phylogeny and distribution of early phocines showing possible relationships to derived taxa. Dashed lines depict inferred but uncertain relationships not yet documented by the known fossil record

W = species distributed in the Western Paratethys; C = species distributed in the Central Paratethys; E = species distributed in the Eastern Paratethys



Caspian Sea to the Arctic Ocean most easily at this time and could also have become adapted to the cold climate before doing so (Fig. 63). Some information indicates that very large lakes existed along 55° N latitude in the region of the Yenisey River. Presumably *Pusa* could have migrated north from Lake Baikal via the Yenisey River to the Arctic Ocean (the coast of which lay as far as south as 61° N; (REPENNING et al. 1979), rather than in the opposite direction, as previously suggested by BERG (1934) and REPENNING et al. (1979).

Chapter 9 Conclusion

This revision of the fossil record of the Phocinae is based in part on material from the Middle Miocene (Sarmatian) of Eastern and Central Europe (ALEKSEEV 1924; McLAREN 1960; GRIGORESCU 1977; KORETSKY 1986, 1987a, b, 1988), one species from the Middle Miocene (Anversian) of western Europe (VAN BENEDEN 1877), and a single taxon from the Late–Early or Early–Middle Miocene (Calvert Formation) of the United States (RAY 1976, 1977a, 1984). Most of this material is not generally known and has not previously been published. It supports a North Atlantic – Paratethyan origin of the Phocidae (REPENNING and TEDFORD 1977; REPENNING et al. 1979; GRIGORESCU 1977; RAY 1977a) and indicates that phocids were primitively of small body size. This observation is contrary to the opinion of WYSS (1994).

Miocene seals were not very similar morphologically to any terrestrial or semiaquatic carnivorans that could have been the original ancestors of phocids. They also did not differ very much from modern species; and structure of the dentition and cranium, as well as the relatively early geological age of these seals, allow the conclusion that these Miocene taxa include the ancestors of some presently living Phocinae.

In regard to Western Paratethys, five species of fossil seals have been identified in the Middle Miocene of Belgium (Antwerp Basin, Western Paratethys): “*Prophoca rousseaui*, *Prophoca proxima*, *Monotherium aberratum*, *M. gaudini* and *M. delognii*”. VAN BENEDEN (1877) described five Pliocene species from Belgium (Antwerp Basin): *Gryphoca similis*, *Callophoca obscura* (= *Mesotaria ambigua*), *Phocanella pumila* (= *Ph. minor*), *Platyphoca vulgaris* and “*Phoca vitulinoides*”, and there is one Pliocene species from Italy (*Pliophoca etrusca* TAVANI, 1941). Their date corresponds to the basal Pliocene (circa 5.3 m. y. ago), and reflects a global cooling event (Messinian crisis).

In the Central Paratethys the first recorded phocid is *Devinophoca claytoni* from Slovakia. Another seal, *Miophoca vetusta*, is from the so-called “Tortonian” age of the Vienna Basin. They both pertain to the Badenian stage (circa 14.8 Ma, MN Zone 6; STEININGER and NEVESSKAYA 1975). *Praepusa pannonica* from Hungary and *Pr. vindobonensis* from the Vienna Basin occur in beds equivalent to the Lower Sarmatian (middle–upper part of the Volhynian substage, 13.6 Ma). The history of Central Paratethyan seals certainly began earlier (maybe in the Early Miocene, or even in the Late Oligocene), but the fossil record is very poor in this area. Distribution of the genus *Praepusa* in the Middle Miocene throughout the Central and Eastern Paratethys confirms the theory of RÖGL and STEININGER (1984) about connection between these two basins.

The rapidly declining salinity during the Sarmatian stage was responsible for the relatively rapid loss of many Miocene marine taxa.

Among the 13 species of seals discovered in the Miocene deposits of Paratethys, seven taxa are described from the Eastern Paratethys in the territory of the Ukraine and Moldavia. They belong to at least five genera of the subfamily Phocinae: *Monachopsis pontica*, *Cryptophoca maeotica*, *Histriophoca alekseevi*, *Praepusa vindobonensis*, *Sarmatonectes sintsovi* n. sp.; “*Phoca novorossica*” and “*Phoca*” *bessarabica*. Although the stratigraphic positions of these fossils were not very carefully recorded, they all correspond to the Sarmatian stage (= between circa 13.6 and 10.0 Ma). The somewhat lesser diversity of fossil seals seen in the Transcaucasus and the Stavropol region is associated with less intense paleontological investigations of these regions.

Together with other true seals, the Phocinae are no doubt descendants of some Oligocene pinnipeds. Indeed, specimens referred to the Phocidae have already been found in the Late Oligocene of South Carolina, USA (KORETSKY and SANDERS, in press).

The subfamilies Phocinae, Monachinae, and Cystophorinae should be considered as separate phylogenetic branches of ancient Phocidae, which separated from ancient Carnivora probably in the Early (?) Oligocene, then became widely distributed in the Late Miocene, and practically ceased to exist in the European part of the former USSR in the Early Pliocene. These fossil animals were completely developed members of the subfamilies to which modern phocids belong.

Clearly, the geographical and geological distributions of individual taxa are of considerable interest for biostratigraphy and for correlations of marine deposits of Late Miocene – Early Pliocene age in Eurasia. However, at present, in view of insufficient investigation of Western European and of Asiatic materials, these findings may be useful mainly for more precise determination of the geological age of some finds in the European part of the former USSR, and of the stratigraphic distribution of Middle Sarmatian–Pontian phocines of this region. This study is mainly a regional review devoted to a relatively small group of Neogene carnivorans. Admittedly, in this study only some of the problems of classification of this subfamily are researched. Moreover, some of the problems of systematics and morphology of true seals are not completely resolved.

In this respect the present study is of an incomplete character, but which opens up new perspectives in investigations of the groups of carnivorans analyzed. I hope that the results presented here will draw the attention of specialists and will allow the investigation, from new and different viewpoints, of many problems of classification of both ancient and modern representatives of the Family Phocidae.

References

- AKHUNDOV, F. M. 1962: Sketch of the history of study fossil seals on the territory of the Soviet Union. — *Uchonie zapisky Azerbaizhanskogo University. Seria biologicheskikh nauk*, 4:51–58. [In Russian.]
- ALEKSEEV, A. K. 1924a: Seals in the Sarmatian deposits of southern Russia. — *Journal Nauchno-Issledovatel'skikh kafedr v Odessa*, 1(5):26–34. [In Russian.]
- 1924b: Seals in the Sarmatian deposits of the southern U.S.S.R. — *Journal Nauchno-Issledovatel'skikh kafedr v Odessa*, 1(10–11):201–205. [In Russian.]
- 1926: Seals of the Sarmatian deposits of the southern U.S.S.R. — *Journal Nauchno-Issledovatel'skikh kafedr v Odessa*, 11(4):138–143. [In Russian.]
- ALLEN, J. A. 1880: History of North American pinnipeds. A monograph of walruses, sea lions, sea bears and seals of North America. — U.S. Geological and Geographical Survey of the Territories. Miscellaneous Publication, 12:1–785, 60 figures. New York; Arno Press 1974.
- ANBINDER, E. M. 1980: Karyology and evolution of the pinnipeds. — 452 pages. Moscow: Nauka. [In Russian.]
- ANDERSON, S. and J. K. JONES JR. eds. 1967: Recent mammals of the world. A synopsis of families. — 453 pages. New York: The Ronald Press Company.
- ANDREESCU, I. and D. MURARIU 1985: Contribution à l'étude du crâne de quelques représentants des familles Otariidae et Phocidae (Mammalia: Pinnipedia). — *Travaux du Muséum d'histoire Naturelle "Grigore Antipa"*. Bucuresti, 27:317–324.
- ANDRUSOV, N. I. 1888: Outline of the evolutionary history of the Caspian Sea and its inhabitants. — *Izvestia Russkogo geographicheskogo obzhestva*, 2:91–113. [In Russian.]
- 1893: Geotectonics of the Kerch Peninsula. — *Material on the Geology of Russia*, 16. [In Russian.]
- 1929: Upper Pliocene of the Black Sea Basin. — *Geology of the USSR*, 3, 4(2), part 2. [In Russian.]
- ANTONIUK, A. A. 1970: Comparative anatomic study of some spinal columns of Pinnipedia. — *Trudy Tichookeanskogo Institute Rybnogo Khoziaistva (TINRO)*, 17:87–95. Vladivostok. [In Russian.]
- 1971: Quantitative changes of vertebrae in the vertebral column of Pinnipeds. — *Trudy Atlantic Nauchno-Issledovatel'skogo Institute Rybnogo Khoziaistva e Okeanography (ATLANTNIRO)*, 39:317–322. Kaliningrad. [In Russian.]
- 1972: Comparative morphology of the axial skeleton of seals of the genus Pusa. — *Tezisy doklady V All-Union Conference on marine mammals. Machatchkala*, 2:24–26. [In Russian.]
- 1975: On the adaptive evolution of pinnipeds. — Abstract of VI All-Union Conference on marine mammals. Kiev, 1:21–22. [In Russian.]
- 1979: Comparative morphology research of the skeleton of pinnipeds. — *Avtoreferat dissertation kandidat biologicheskikh nauk. Moscow*:1–24. [In Russian.]
- 1986: Fossil seals and accompanying faunas from the Sarmatian deposits of the Western Crimea. — *Voprosu Palaeologii*, 9:124–129. Leningrad. [In Russian.]
- ANTONIUK, A. A., and V. M. CHRABRY. 1975: About a new find of seals in the Miocene. — Abstracts of VI All-Union Conference on marine mammals. Kiev, 1:21–22. [In Russian.]
- ANTONIUK, A. A., and I. A. KORETSKAYA (KORETSKY) 1984: A new seal from the Middle Sarmatian deposits of the Crimean district of Ukraine. — *Vestnik Zoologii*, 4:26–31. [In Russian.]
- ARNASON, U. 1977: The relationship between the four principal pinniped karyotypes. — *Hereditas*, 87:227–242.
- ASLANOVA, S. M. 1965: Seal in the Lower Miocene deposits in Azerbaizhan. — *Doklady Akademii Nauk of Azerbaizhanskoy SSR*, 21(6):46–48. [In Russian.]
- 1966: Marine mammals in Lower Miocene deposits in Azerbaizhan. — Abstracts of All-Union Conference on paleontology of mammals. Tbilisi:46–47. [In Russian.]
- ASTANIN, L. P. 1936: Ontogenetic changes of the skeleton of mammals in connection with the question of age determination. — *Izvestia Nauk. Institute*, 19(2):203–231. [In Russian.]
- BARNES, L. G. 1972: Miocene Desmatophocinae (Mammalia: Carnivora) from California. — *University of California Publications in Geological Sciences*, 89:1–68.

- 1979: Fossil enaliarctine pinnipeds (Mammalia: Otariidae) from Pyramid Hill, Kern County, California. — *Contributions in Science, Natural History Museum of Los Angeles County*, 318:1–41.
- 1987: An Early Miocene pinniped of the genus *Desmatophoca* (Mammalia: Otariidae) from Washington. — *Contributions in Science, Natural History Museum of Los Angeles County*, 382:1–20.
- 1988: A new fossil pinniped (Mammalia: Otariidae) from the Middle Miocene Sharktooth Hill Bonebed, California. — *Contributions in Science, Natural History Museum of Los Angeles County*, 396:1–11.
- 1989: A new enaliarctine pinniped from the Astoria Formation Oregon, and classification of the Otariidae (Mammalia: Carnivora). — *Contributions in Science, Natural History Museum of Los Angeles County*, 403:1–26.
- 1990: A new Miocene enaliarctine pinniped of the genus *Pteronarctos* (Mammalia: Otariidae) from the Astoria Formation, Oregon. — *Contributions in Science, Natural History Museum of Los Angeles County*, 422:1–20.
- 1992: A new genus and species of Middle Miocene enaliarctine pinniped (Mammalia, Carnivora, Otariidae) from the Astoria Formation in coastal Oregon. — *Contribution in Science, Natural History Museum of Los Angeles County*, 431:1–27.
- BARNES, L. G., D. P. DOMNING, and C. E. RAY. 1985: Status of studies on fossil marine mammals. — *Marine Mammals Science*, 1(1):15–53.
- BARNES, L. G. and K. HIROTA 1995: Miocene pinnipeds of the otariid subfamily Allodesminae in the North Pacific Ocean: systematics and relationships. — *In* North Pacific. L. G. BARNES, N. INUZUKA, and Y. HASEGAWA (eds.) *The Island Arc, In Evolution and Biogeography of fossil marine vertebrates*, 3(4):329–360.
- BARNES, L. G., and E. D. MITCHELL 1975: Late Cenozoic northeast Pacific Phocidae. — *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, 169:34–42.
- BERG, L. S. 1910: The fauna of Lake Baikal and its origin. — *Biologicheskii Zhurnal*, 1(1):10–45. [In Russian.]
- 1928: On the origin of the northern elements in the fauna of the Caspian sea. — *Doklady Akademii Nauk SSSR*, 7:107–112.
- 1934: About the amphiboreal (intermittent) distribution of the marine fauna in the Northern Hemisphere. — *News of the State Geographic Society*, 66(1):69–78.
- 1940: The origin of the Baikal fauna. — *Priroda*, 4:47–53. [In Russian.]
- BERNOR, R. L., V. FAHLBUSCH, H.-W. MITTMANN, and S. REITSCHEL.
- 1996: The Evolution of Western Eurasian Neogene Mammal Faunas. — The 1992 Schloss Reisenburg Workshop Concept, pages 1–7. *In* BERNOR, R.L., V. FAHLBUSCH, H.-W. Mittmann, ed., *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York.
- BERTA, A. 1987: New Enaliarctos (Pinnipedimorpha) from the Oligocene and Miocene of Oregon and the role of “Enaliarctidae” in pinniped phylogeny. — *Smithsonian Contributions to Paleobiology*, 69:1–33.
- BERTA, A., C. E. RAY, and A. R. WYSS 1989: Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. — *Science*, 244:60–62.
- BERTA, A., and A. R. WYSS 1990: Oldest pinniped. — *Science*, 248(4954):499–500.
- 1994: Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. — *Proceedings of the San Diego Society of Natural History*, 29:33–56.
- BIGG, M. A. 1981: Harbour seal — *Phoca vitulina* and *P. largha*. — *In* Ridgway S. H. and Harrison R. J., eds., *Handbook of marine mammals. Seals*, 2:1–27. Academic Press, Inc., London.
- BININDA-EMONDS, O.R.P., and A.P. RUSSELL 1994: A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). — *Bonner Zoologische nographien*, 41:256 pages.
- BLAINVILLE, H. M. D. de. 1839–1864: Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récent et fossiles pour servir de base à la zoologie et à la géologie. Atlas; Tome deuxième. — Paris, J. B. Baillière et fils—Libraires de l'Académie Impériale de Médecine, 19 (part 7. *Phoca* [= Pinnipeds] published 1840).
- BOGACHOV, V. V. 1927a: The seals in the Miocene of the Caspian Basin. — *Izvestia Azerbaizhan Gosudarstvennogo University. Otdelenie estestvoznaniya e medicine*. Baku, 6:135–148. [In Russian.]
- 1927b: Miocene seals of the Caspian Basin. — *Azerbaizhan oil Economy*. 1. [In Russian.]
- BRÜHL, K. B. 1860: *Phoca holitschensis*, der fossile Phocafuss des Pester Universitäts-Museums, ein Unicum. — *Mittheilungen aus dem K.K. Zoologischen Institut der Universität Pest*. Wien, 2:1–16.
- BRUZGIN, V. V. 1966: On study of the fossil cetaceans and seals of the Kerch Peninsula. — Abstracts of III Science Conference on study of the Kerchensky and other iron-stone sediments of Ukrainian S.S.R.: 87–88. [In Russian.]
- BURNS, J. J., and F. H. FAY 1970: Comparative morphology of the skull of the Ribbon seal, *Histiophoca fasciata*, with remarks on systematics of Phocidae. — *Journal of Zoology* (London), 161(3):363–394.
- CHAPSKII, K. K. 1952: The age and sexual changes in the craniological features and their influence upon the diagnosis of some pinnipeds. — *Izvestia Institute estestvenich Nauk*. Moscow, 25: 78–96. [In Russian.]
- 1955a: An attempt at revision of the systematics and diagnosis of seals of the subfamily Phocinae. — *Trudy Zoologicheskogo Instituta Akademii Nauk S.S.S.R.*, 17:160–199. Leningrad. (English translation by JELETZKY, T. F., Fisheries Research Board of Canada, Translation Series, 114, 57 pages, 1957). [In Russian.]
- 1955b: Contribution to the problem of the history of development of the Caspian and Baikal seals. — *Trudy Zoologicheskogo Instituta Akademii Nauk S.S.S.R.*, 17:200–216. (English translation by Fisheries Research Board of Canada, Translation Series, 174, 26 pages, 1958). [In Russian.]
- 1961: Current status and problems in the systematics of pinnipeds. — *Trudy soveshchaniya ikhtiologicheskoy komissii. Akademya Nauk S.S.S.R.*, 12:138–149. Moscow. English translation by Sayer, U.S. Fish and Wildlife Service, Seattle, Washington). [In Russian.]
- 1967: Morphological-taxonomical nature of the pagetod form of the Bering Sea *largha* seal. — *In*, *Research on marine mammals. Trudy Poliarnogo Nauchno-Issledovatel'skogo Instituta Rybnogo Khoziaistva e Okeanography (PINRO)*, Murmansk, 21:147–177. [In Russian.]

- 1970: The concept of the Arctic origin of pinnipeds and another solution to this problem. — Hydrometeorological Publishers. Leningrad:166–173. [In Russian.]
- 1971: Systematic rank and subgeneric differentiation of seals (of the subfamily Monachinae). — *Trudy Atlanticheskogo Nauchno-Issledovatel'skogo Instituta Rybnogo Khoziaistva e Okeanografiya (ATLANTNIRO)*, 39:305–316. Kaliningrad. English translation, Fisheries Research Board of Canada, Translation Series, 3185, 1974. [In Russian.]
- 1974: Theoretical questions of the systematics and phylogeny of animals. — Leningrad, Nauka: 282–334. [In Russian.]
- 1975: Taxonomy of the seals of genus *Phoca* sensu stricto. In, *Marine mammals*. — Materials VI All-Union Conference. Naukova Dumka. Kiev, 2:159–162. [In Russian.]
- CHEPALYGA, A. L., E. L. KOROTKEVICH, et. al. 1985: Paratethys regional stages and hipparion faunas according to paleomagnetic data. — Abstracts VII Congress of the Regional Committee on Mediterranean Neogene Stratigraphy. Budapest:137–139.
- CHIRIAC, M., and D. GRIGORESCU 1975: Asupra fosilor Bessarabiene din Dobrogea de Sud. — *Studii și Cercetări geologie, geofizica, geographie. Seria geologie*, 20(1):89–110.
- DAVIES, J. L. 1958a: Pleistocene geography and the distribution of northern pinnipeds. — *Ecology*, 39(1):97–113.
- 1958b: The Pinnipedia: an essay in zoogeography. *Geographical Review*, 48(4):474–493.
- DOMNING, D. P. 1996: Bibliography and Index of the Sirenia and Desmostylia. — *Smithsonian Contributions to Paleobiology*, 80:611 pages.
- DOLLO, L. 1909: The fossil vertebrates of Belgium. — *Annals of the New York Academy of Sciences*, 19(4), part 1:99–119.
- DORNESCO, G.-T., and G.-V. MARCOCI. 1958: Étude comparative du crâne des pinnipèdes. — *Annales des Sciences Naturelles. Zoologie*, 11 xx + :158–182.
- DOUTT, J. K. 1942: A review of the genus *Phoca*. — *Annals of the Carnegie Museum*, 29:61–125.
- DRIESCH, A. VON DEN 1975: A guide to the measurement of animal bones from archeological sites. — *Bulletin of the Peabody Museum*, 1:1–137.
- DUBROVO, I. A., and K. V. KAPELIST 1979: Catalogue of the locations of the Tertiary vertebrates of Ukrainian SSR. — 159 pages. Moscow. Nauka. [In Russian.]
- EICHWALD, E. 1850: *Lethaea Rossica*. Saint-Petersburg. — 520 pages. Atlas, 13 pls. [In Russian.]
- 1853: *Lethaea Rossica on Paleontologie de la Russie*. — 3:520 pages. Atlas, 13 pls. Stuttgart, Schweizerbart.
- ENGLISH, A. W. 1975: Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). — *Journal of Zoology*, London, 178:341–364.
- FARRIS, J. S. 1988: Hennig86, version 1.5. — Available from Diana Lipscomb, department of Biology, George Washington University, Washington, DC, 20560.
- FISH, P. A. 1903: The cerebral fissures of the Atlantic walrus. — *Proceedings of the United States National Museum*, 26:675–688.
- FLEMING, J. 1822: Philosophy of zoology, or a general view of the structure function and classification of animals. — Edinburgh, 2:1–187.
- FLYNN, J. J. 1988: Ancestry of sea mammals. — *Nature*, 334:383–384.
- FLYNN, J. J., N. A. NEFF, and R. H. TEDFORD. 1988: Phylogeny of the Carnivora, pp. 73–116. — In, ed. M. J. BENTON. *The Phylogenetic Classification of the Tetrapods. Volume 2 (Mammalia)*, Clarendon Press, Oxford.
- FANCEVICH, L. I. 1975: Processing of the result of the biological experiments on the micro-EVM “Electronica B3-21”. 91 pages. — Kiev: Naukova Dumka. [In Russian.]
- FRIANT, M. 1942: Le fémur des phocidés scaldiens; son interprétation morphologique. — *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 20(12):1–4.
- 1947: Recherches sur le fémur des Phocidae. — *Bulletin du Musée royal d'Histoire naturelle de Belgique*, 23(2):1–51.
- GADJIEV, D. V. 1957: Morphological features in structure of nasal bones in *Phoca caspica* and their taxonomic significance. — *Doklady Akademii Nauk Azerbaizhanskoy S.S.R.*, 13(4):431–435. [In Russian.]
- 1958: New materials from the Eldarskaya fauna. — *Izvestia Akademii Nauk Azerbaizhanskoy S.S.R. Seria geology-geography*, 4:55–65. [In Russian.]
- 1981: Sexual dimorphism in structure of sacral bones in Caspian seals. — *Fauna e Ecologia nazemnych e vodnych zivotnykh Kura-Araxinskoy nizmenosti e Malogo Kavkasa*. Baku:90–95. [In Russian.]
- GERVAIS, P. 1848–1952: *Zoologie et paléontologie françaises (Animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*, 1 (text):18–141; 3 (illustrations).
- 1853: Description de quelques ossements de phoques et de cétacés. — *Mémoires de l'Académie des Sciences de Montpellier*. Paris, 2 (2):307–314.
- 1859: Nouvelles Recherches sur les animaux vertébrés. — *Zoologie et paléontologie françaises*. Paris, Arthus Bertrand, 2nd édition, 2:1–544.
- 1872: *Journal de Zoologie*. — Comprenant les différentes branches de cette science. Tome Premier:64–67.
- GERVAIS, P., and M. de SERRES.
- 1847a: Sur les mammifères fossiles des sables marins tertiaires de Montpellier. — *Comptes Rendus des Séances de l'Académie des Sciences*, Paris, 24(18):799–801 (text identical to 1847b).
- 1847b: Nouvelles observations sur les mammifères dont on trouve les restes fossiles dans les sables marins de Montpellier (2). — *Annales des Sciences Naturelles*, Paris:224–226.
- GILL, T. N. 1866: Prodrôme of a monograph of the pinnipeds. — *Proceedings Essex Institute, Salem, Communications*, 5:3–13.
- 1872: Arrangement of the families of mammals, with analytical tables. — *Smithsonian Miscellaneous Collections*, 11(1):vi+98 pages. (Publication no. 230 of the Smithsonian Institution.)
- GINSBURG, L., and P. JANVIER. 1975: Les mammifères marins des faunes de la Touraine et de l'Anjou: faune, sisemas, et paléobiologie. — *Bulletin de la Société d'Etudes Scientifiques de l'Anjou*. n.s. 9:73–96.

- GODINA, A. Y., and A. I. DAVID. 1970: Localities of Neogene vertebrates in the territory of Moldova. — Kishinau: 107 pages. [In Russian.]
- GOTTFRIED, M. D, D. J. BOHASKA, and F.C. WHITMORE, JR. 1994: Miocene Cetaceans of the Chesapeake Group. In, A. BERTA and T. A. DEMÉRÉ (eds.), Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. — *Proceedings of the San Diego Society of Natural History*, 29.Grassé, Pierre-P. (ed.)
- 1955: Traité de zoologie. Anatomie, systématique, biologique. — Paris, 27:568–668.
- GRAY, J. E. 1825: An outline of an attempt at the disposition of Mammalia into tribes and families, with list of the genera apparently appertaining to each tribe. — *Annals of Philosophy*, N.S., 10 (vol. 26 of the whole series):337–344. London.
- 1844–1875: The zoology of the voyage of H.M.S. Erebus & Terror, under the command of Captain Sir James Clark Ross, N.N., F.R.S., during the years 1839 to 1843. Part I. Mammalia. Longman, Brown, Green, and Longmans, London. 12 pages, 17 plates (:1–8, plates 1–10, 14–17, published 1844, and :9–12, 1875, according to Scheffer, V.B., 1958, Seals, Sea Lions, and Walruses. — Stanford University Press, Stanford.179 pages).
- GRIGORESCU, D. 1977: Paratethyan seals. — *Systematic Zoology*, 25(4) for December, 1976:407–419.
- GRIGORESCU, D., V. CONSTANTINESCU, and L. DRAGOMIRESCU 1985: A Paleoecologic Analysis of the Bessarabian (Middle Sarmatian) Vertebrate Association from Credița and Ciobănița (Southern Dobrogea) Based on the Taphonomic characters processed Through Methods of Numerical Taxonomy. — *Travaux du Muséum d'Histoire naturelle Grigore Antipa*, Bucarest, 28:275–283.
- GROMOV, I. M., and G. I. BARANOVA. 1981: Catalogue of Mammals of the USSR. — Pliocene–Recent. Leningrad, Nauka: 455 pages. [In Russian.]
- GROMOVA, V. I. 1950: Works of the Committee for Studying the Quaternary Period. — Moscow–Leningrad. 9: 239 pages. [In Russian.]
- GROMOVA, V. I., I. A. DUBROVO, and N.M. JANOWSKAYA 1961: Order Pinnipedia: Seals. — *Fundamentals of paleontology. Mammalia*. Moscow, 13: 234–235. [In Russian.]
- GROSSHEIM, V. A., and V. E. KHAIN 1967: Paleogene, Neogene, and Quaternary. — In VINOGRADOV, A. P. ed., Atlas of lithological-paleogeographical maps of the USSR (4): Moscow, Ministry of Geology of the USSR and Academy of Sciences of the USSR. [In Russian.]
- HASEGAWA, Y., Y. TOMIDA, N. KOHNO, K. ONO, H. NOKARIYA, and T. UYENO 1985: Quaternary vertebrates from Shiriya area, Shimokita Peninsula, northeastern Japan. — *Memoirs of the National Science Museum*, 21:17–36.
- HENDEY, Q. B. 1970: The evolution and dispersal of the Monachinae (Mammalia: Pinnipedia). — *Annals of the South African Museum*, 59(5):99–113.
- HENDEY, Q. B., and C. A. REPENNING. 1972: A Pliocene phocid from South Africa. — *Annals of the South African Museum*, 59(4):71–98.
- HEPTNER, V. G. 1947: On the methods of studying age and sexual dimorphism of the mammals. — *Nauchno-metodicheskie zapisky*, 9:151–155. [In Russian.]
- HEPTNER, V. G. K. K. CHAPSKII, and B. A. ARSENIYEV 1976: Mammalia of the Soviet Union. Pinnipeds and Cetacea, 2(3): 717 pages. — Moscow:High School. [In Russian.]
- HOLEC, P., J. KLEMBARA, and S. MESZÁRO 1985: Discovery of new fauna of marine and terrestrial vertebrates in Devínska Nová Ves. — *Geologický Zborník. Geologica Carpathica*, 38(3):349–356. Bratislava.
- HOWELL, A. B. 1928: Contribution to the Comparative Anatomy of the Eared and Earless Seals (Genera *Zalophus* and *Phoca*). — *Proceedings of the United States National Museum*, 73(15):1–42.
- 1930: Aquatic Mammals. Their Adaptations to Life in the Water. — vii+338 pages, 54 figs. Charles C. Thomas, Springfield, IL., and Baltimore, MD. Dover Publications, Inc. New York, 1970.
- HOWARD, L. D. 1975: Muscular Anatomy of the Hind Limb of the Sea Otter (*Enhydra lutris*). — *Proceedings of the California Academy of Sciences*, 40(12):335–416.
- HUNT, R. M., Jr., and BARNES, L. G. 1994: Basicranial evidence for ursid affinity of the oldest pinnipeds. — Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. A. BERTA and T. A. DEMÉRÉ editors, *Proceedings of the San Diego Society of Natural History* 29, 57–67.
- International Commission on Zoological Nomenclature (ICZN)
- 1985: International Code of Zoological Nomenclature. Edition 3. Adopted by the 20th General Assembly of the International Union of Biological Sciences. — 338 pages. Berkeley: University of California Press.
- JONES, R. W., and SIMMONS, M. D. 1996: A review of the stratigraphy of Eastern Paratethys (Oligocene–Holocene). — *Bulletin of Geology, British Museum (Natural History)*, London, 52(1):25–49.
- KARLOV, N. N. 1952: The remains of seals in an iron-mine. — *Priroda*, 41(6):115. [In Russian.]
- KELLOGG, R. 1922: Pinnipeds from Miocene and Pleistocene deposits of California. — *University of California Publications. Bulletin of the Department of Geological Sciences*, 13(4):23–132.
- KHUZIN, P. S. 1967: The variability of craniological characters of the Harp seal. — *Trudy Poliarnogo Nauchno-Issledovatel'skogo Instituta Morskogo Rybnogo Khoziaistva e Okeanography (PINIRO)*, Murmansk, 21:27–50. [In Russian.]
- KING, J. 1956: The monk seals (genus *Monachus*). — *Bulletin of Zoology, British Museum (Natural History)*, London, 3(5):201–256.
- 1964: *Seals of the World*. — 154 pages. London, British Museum (Natural History).
- 1966: Relationships of the hooded and elephant seals (genera *Cystophora* and *Mirounga*). — London: British Museum (Natural History), 148(4):385–398.
- 1983: *Seals of the world*. — Second edition, 240 pages. Ithaca, New York: Cornell University Press.
- 1989: Otariidae and Phocidae. — In WALTON, D.W. and RICHARDSON, B.J. (eds.) *Fauna of Australia*, Mammalia, Canberra 1B:1012–1029.

- KIRPICHNIKOV, A. A. 1953: Caspian seal in the lower Quaternary deposits of the coast of the Azov Sea. — *Doklady Akademii Nauk Ukrainsskoy SSR*, 90(5):883–886. [In Russian].
- 1961: Essay on the history of study of marine mammals of Sarmatian deposit and adjoining countries. — *Trudy ichtiologicheskoy komissii Akademii Nauk SSSR*, 12:25–39. Leningrad. [In Russian].
- 1964: On the origin of the Caspian seal. — *Bulletin Moskovskogo Obzhestva Ispytateley Prurody (MOIP)*, 65(5):136–139. [In Russian].
- KONDAKOV, N. N. 1960: On the problem of the systematic status of the Baikal seal. — *Bulletin Moskovskogo Obzhestva Ispytateley Prurody (MOIP)*, otdelenie biologii, 65(4):120–121. [In Russian].
- KORETSKY (KORETSKAYA), I. A. 1986: Modern status of systematics of Miocene seals of the Family Phocinae of the Northern Black Sea Province. — Abstracts of IX All-Union Conference on marine mammals. Archangelsk:206–207. [In Russian].
- 1987a: Sexual dimorphism in the structure of the humerus and femur of *Monachopsis pontica* (Pinnipedia: Phocinae). — *Vestnik Zoologii*, 4:77–82. [In Russian].
- 1987b: The position of the genus *Præpusa* in the Phocinae system. — Reprint/Akademii Nauk Ukrainian SSR. Institute of Zoology, 87.12:3–7. [In Russian].
- 1988: New record of *Monachopsis pontica* (Pinnipedia: Phocidae) from Neogene deposits of Kerch Peninsula. — *Vestnik Zoologii*, 6:74–76. [In Russian].
- KORETSKY, I. A., and C. E. RAY 1994: *Cryptophoca*, new genus for *Phoca maeotica* (Mammalia: Pinnipedia: Phocinae) from Upper Miocene deposits in the Northern Black Sea region. — *Proceeding of the Biological Society of Washington*, 107(1):17–26.
- KORETSKY, I. A., and A. E. SANDERS (in press): Pinniped bones from the Late Oligocene of South Carolina: the oldest known seal (Carnivora: Phocidae). — *Smithsonian Contributions to Paleobiology*.
- KORETSKY, I. A., and D. GRIGORESCU (in press): The monk seal *Pontophoca sarmatica* (Mammalia: Phocidae: Monachinae) from the Miocene of Eastern Europe. — *Smithsonian Contributions to Paleobiology*.
- KORETSKY, I. A., and P. HOLEC (in press): A primitive seal (Mammalia: Phocidae) from the Badenian Stage (early Middle Miocene) of the Central Paratethys. — *Smithsonian Contributions to Paleobiology*.
- KORETSKY, I. A. and RAY, C. E. (in press): Phocidae of the Pliocene of Eastern North America. — *Smithsonian Contributions to Paleobiology*.
- KOROTKEVICH E. L., V. N. KUSHNIRUK, Y.A. SEMENOV, and A.P. CHEPALYGA 1985: New locality of Middle Sarmatian vertebrates in the Ukraine. — *Vestnik Zoologii*, 3: 81–82. [In Russian].
- KOSYGIN, G. M., and V. A. POTELOV. 1971: Age, sex, and population variability of the craniological characters in Bearded seals. — *Trudy Vsesouznogo Nauchno-Issledovatel'skogo Instituta (VNII) Morskogo Rybnogo Khoziaistva e Okeanography*, 82:266–288. [In Russian].
- KRETZOI, M. 1941: Seehund-Reste aus dem Sarmat von Érd bei Budapest. — *Földtani Közlöny*, 71:350–356.
- LAKIN, G. F. 1973: *Biometria*. — 2nd edition. 343 pages. Moscow, High School. [In Russian].
- LEIDY, J. 1853a. The ancient fauna of Nebraska. — *Smithsonian Contributions to Knowledge*, 6(7): 126 pages.
- 1853b: [Description of *Stenorhynchus vetus*.] — *Academy of Natural Sciences of Philadelphia Proceedings*, 6 (10):377.
- 1857: Notice of remains of two species of seals. — *Academy of Natural Sciences of Philadelphia Proceedings*, 8(6):265.
- 1869: The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. — *Academy of Natural Sciences of Philadelphia Journal*, second series, 7:i–vii + 8–472.
- LUNGU, A. N., and V. A. TARABUKIN. 1966: New facts about Neogene vertebrate faunas of Moldavia. — *Guarding of Nature*, 4:159–160. [In Russian].
- LYON, G. M. 1937: Pinnipeds and a sea otter from the Point Mugu Shell Mound of California. — *University of California Press*, Berkeley, California, 1(8):133–168.
- MACAROVICI, N. 1942: Sur les phoques fossiles du Sarmatien de l'Europe. — *Annales Scientifiques de l'Université de Jassy*. Section 2, 28(10):260–268.
- MACAROVICI, N., and C. V. OESCU. 1942: Quelques vertébrés fossiles trouvés dans les calcaires récifales de Chişinau (Bessarabia). — *Analele Academiei Române*. Memoriile Secţiunii Ştiinţifice. Seria 3, 17(6):351–382.
- MATTHEW, W. D. 1909: The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. — *Memoirs of the American Museum of Natural History*, 9(6):291–567.
- MCKENNA, M. C., and S. K. BELL 1997: Classification of mammals above the species level. — Columbia University Press, New York: 631 pages.
- MCLAREN, I. A. 1960a: On the origin of the Caspian and Baikal seals and the paleoclimatological implication. — *American Journal of Sciences*, 258:47–65.
- 1960b: Are the Pinnipedia biphyletic? — *Systematic Zoology*, 9:18–28.
- 1975: A speculative overview of phocid evolution. — *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, 169:43–48.
- MICHAYLOV, S. S. 1980: International anatomical nomenclature. — Moscow: Medical, 4th edition: 239 pages. [In Russian].
- MILLER, W. E. 1967: Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). — *Bulletin of the Los Angeles County Museum of Natural History, Science*, 10:1–124.
- MITCHELL, E. D. 1966: The Miocene pinniped *Allodesmus*. — *University of California Publications in Geological Sciences*, 61:1–46.
- 1967: Controversy over diphyly in pinnipeds. — *Systematic Zoology*, 16(4):350–351.
- 1975: Parallelism and convergence in the evolution of Otariidae and Phocidae. — *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer*, 169:12–26.

- 1978: Origins of eastern north Pacific sea mammal fauna. In HALEY, D. (ed.) *Marine Mammals of Eastern North Pacific and Arctic Waters*. — Seattle: Pacific Press: 13–20.
- MITCHELL, E. and R. H. TEDFORD 1973: The Enaliarctinae, a new group of extinct aquatic Carnivora and consideration of the origin of the Otariidae. — *Bulletin of the American Museum of Natural History*, 151(3):203–284.
- MIVART, S. G. 1885: Notes on the Pinnipedia. — *Proceedings of the Zoological Society*, London, 1885:484–500.
- MUIZON, C. de 1981a: Les vertébrés fossiles de la formation Pisco (Perou). Première partie: Deux nouveaux Monachinae (Phocidae: Mammalia) du Pliocène de Sud Sacaco. — *Travaux de l'Institut français d'Etudes Andines*, 22: 161 pages.
- 1981b: Premier signales de Monachinae (Phocidae:Mammalia) dans le Sahélien (Miocene Supérieur) d'Oran (Algerie). — *Palaeovertebrata*, 11:181–194.
- 1982a: Phocid phylogeny and dispersal. — *Annals of the South African Museum*. Cape Town, 89, part 2:175–213.
- 1982b: Les relations phylogénétique des Lutrinae (Mustelidae, Mammalia). — *Geobios, Mémoire spécial*, 6:259–277.
- 1987: Paléontologie. — In R. DUGUY and D. ROBINEAU, editors. Band 6: Meeressäuger. Teil II: Robben-Pinnipedia. In, J. NIETHAMMER and F. KRAPP, (eds.) *Handbuch der Säugetiere Europas*, pages 34–41. AULA-Verlag Wiesbaden.
- MUIZON, C. de, and M. BOND. 1982b: Le Phocidae (Mammalia) miocene de la formation Parana (Entre Rios, Argentina). — 4 (3–4):165–207.
- MUIZON, C. de, and Q. B. HENDEY 1980: Late Tertiary seals of the South Atlantic Ocean. — *Annals of the South African Museum*. 82:91–128.
- NICOLAS, J. P. 1978: Un nouveau gisement de vertébrés dans le Chersonien: Kutchuk-Tchekmedje Ouest (Trace turque). — *Comptes Rendus des Séances de l'Académie des Sciences*. Paris, tom 287, Série D (5):455–458.
- NORDMANN, A. D. von. 1860 [1858]: Palaeontologie Südrusslands. — H.C. FRIIC, Helsingfors: 360 pages. Atlas of 24 pls.
- OGNEV, S. I. 1935: Mammals of the USSR and adjacent countries. Carnivora. — (in Russian, English translations by BIRRON, A. & COLES, Z. S. for Israel Program for Scientific translations, 1962). Glavpushnina, Moscow–Leningrad, 3: 752 pages.
- PAVLINOV, I. J., and O. L. ROSSOLIMO. 1987: Systematics of Mammalia of the Soviet Union. — 282 pages. Moscow University. [In Russian.].
- PERRY, E. A., S. M. CARR, S. E. BARLETT, and W. S. DAVIDSON 1995: A phylogenetic perspective on the evolution of reproductive behavior in pagophilic seals of the Northwest Atlantic as indicated by mitochondrial DNA sequences. — *Journal of Mammalogy*, 76(1):22–31.
- PETERS, K. F. 1855: Schildkrötenreste aus der Österreichischen Tertiär-Ablagerungen. — K. Akademie der Wissenschaften, Vienna. Mathematisch-naturwissenschaftlichen Klasse, Denkschriften, 9(2):1–22.
- 1867: *Phoca pontica* Eichw. bei Wien. — Sitzungsberichte Naturwissenschaftlichen-mathematisch Klasse 1, h.k. Akademie Wissenschaften zu Wien. 55(2): 110–112.
- PIDOPLYCHKO, I. G. 1938a: Materials for studying the former faunas of the Ukraine. — *Akademia Nauk*, Kiev, 1: 233 pages. [in Ukrainian].
- 1938b: Eldarskaya paleontological expedition of the Museum of Georgia and Akademii Nauk. — *Izvestia Akademii Nauk Ukrainian SSR*, 1:44–48. [in Ukrainian].
- 1953: About vertebrate fauna from Sarmatian deposits in the area of Kachovskoe water-bodies. — In, X-Scientific section. Kiev: State University. [in Ukrainian].
- 1954: New data about development of the Neogene vertebrates faunas of the southern Ukrainian SSR. — In, XI-Scientific section. Kiev: State University. [in Ukrainian].
- 1956: *Materials for studying of the former faunas of the Ukrainian SSR*. 225 pages, 2nd edition. Naukova Dumka, Kiev.
- PIÉARD, J. 1971: Osteology and myology of the weddell seal *Leptophoca weddelli* (Lesson, 1826), pages 53–108, 59 figs. — In W.H. BURT, ed. *Antarctic Pinnipedia*. Antarctic Research Series. National Academy of Sciences-National Research Center, 18:1–226.
- POR, F. D. 1989: The Legacy of Tethys, An Aquatic Biogeography of the Levant. — In DUMONT, H.J., and M.J.A. WERGER, eds., *Monographie Biologicae*, Kluwer Academic Publishers, The Netherlands, (63):vii + 15.
- RAY, C. E. 1976: *Phoca wymani* and other Tertiary seals (Mammalia: Phocidae) described from the eastern seaboard of North America. — *Smithsonian Contributions to Paleobiology*, 28:1–36.
- 1977a: Geography of phocid evolution. — *Systematic Zoology*, 25(4)(for December 1976):391–406.
- 1977b: Fossil marine mammals of Oregon. — *Systematic Zoology*, 25(4)(for December 1976):420–436.
- 1984: Fossil seals from the Calvert Formation of the Pamunkey River, Hanover County, Virginia. — In, *Stratigraphy and Paleontology of the Outcropping Tertiary Beds in the Pamunkey River region, Central Virginia Coastal Plan*. — :232–235.
- RAY, C. E., and A. E. SPIESS 1981: The Bearded Seal, *Erignathus barbatus*, in the Pleistocene of Maine. — *Journal of Mammalogy*, 62(2):423–427, 2 figures.
- RAY, C. E., F. REINER, D. E. SERGEANT, and C. N. QUESADA 1982: Notes on past and present distribution of the Bearded Seal, *Erignathus barbatus*, around the North Atlantic ocean. — *Série Zoológica*, 2(23):1–32.
- RAY, C. E., A. WETMORE, D. H. DUNKLE, and P. DREZ 1968: Fossil vertebrates from the marine Pleistocene of southeastern Virginia. — *Smithsonian Miscellaneous Collections*, 153(3):1–25.
- REINHART, R. H. 1976: Fossil sirenians and desmostylids from Florida and elsewhere. — *Bulletin Florida State Museum, Biological Sciences*, 20(4):187–300.
- REPENNING, C. A. 1972: Pleistocene deposits in Alaska. Alaskan North Slope. — *Quaternary Research*, 19:356–372.
- 1975: Otarioid evolution. — *Rapports et Procès-verbaux des Reunions, Conseil International pour l'Exploration de la Mer*, 169:27–33.
- 1977: Adaptive evolution of sea lions and walruses. — *Systematic Zoology*, 25(4):375–390.
- 1983: New evidence for the age of the Gubik Formation, Alaskan North Slope. — *Quaternary Research*, 19:356–372.

- 1990: Technical comments. Oldest pinniped. — *Science*, 248(4954):499.
- REPENNING, C. A., C. E. RAY, and D. GRIGORESCU. 1979: Pinniped biogeography. — In, J. GRAY and A. J. BOUCOT, eds. *Historical Biogeography, Plate Tectonics and the Changing Environment*. :359–369. Corvallis: Oregon State University Press.
- REPENNING, C. A., and R. H. TEDFORD 1977: Otariid seals of the Neogene. — U.S. *Geological Survey Professional Paper*, 992:1–93.
- RIEDMAN, M. 1990: The Pinnipeds: Seals, Sea Lions, and Walruses, pages ix + 439. — University of California Press, Berkeley, Los Angeles, Oxford.
- RIDGWAY, S. H., and R. I. HARRISON 1981: *Handbook of Marine Mammals*. — Volume 2: The Seals, pages xv + 359. Academic Press Inc., London.
- ROBINETTE, H., and H. J. STAINS 1970: Comparative study of the calcanea of the Pinnipedia. — *Journal of Mammalogy*, 51(3): 527 pages.
- RÖGL, F. 1998: Paleogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). — *Annalen des Naturhistorisches Museum in Wien* (99A):279–310.
- RÖGL, F., and F. F. STEININGER 1981: Neogene Paratethys, Mediterranean and Indo-Pacific Seaways. — Implications for the Paleobiogeography of Marine and Terrestrial Biotas. In BRENCHELY, P., ed.: *Fossils and Climate*, John Wiley & Sons Ltd., 10:171–200.
- RONALD, K., and J. L. HEALEY 1981: Harp seal — *Phoca groenlandica*. — In RIDGWAY S.H. and HARRISON R.J., eds., *Handbook of marine mammals. Seals*, 2:55–87. Academic Press Inc., London.
- SAVAGE, D. E., and D. E. RUSSELL 1983: *Mammalian Paleofaunas of the World*. — London, Amsterdam, Don Mills, Sydney, Tokyo: Addison-Wesley Publishing Co., Inc. Sarich, V.M.:432 pages.
- 1969a: Pinniped phylogeny. — *Systematic Zoology*, 18:416–422.
- 1969b: Pinniped origins and the rate of evolution of carnivore albumins. — *Systematic Zoology*, 18:286–295. SCHALLER, O. (ed.).
- 1992: *Illustrated Veterinary Anatomical Nomenclature*. — Ferdinand Enke Verlag, Stuttgart, :617 pages.
- SCHAEFFER, V. B. 1958: *Seals, sea lions and walruses: A review of the Pinnipedia*. — Stanford, California: Stanford, University Press, :179 pages.
- SCHOCH, R. M. 1986: *Phylogeny reconstruction in paleontology*. — Boston University, Van Nostrand Reinhold Co., New York: 363 pages.
- SEMENENKO, V. N. 1987: *Stratigraphical correlation of the Upper Miocene and Pliocene of the Eastern Paratethys and Tethys*. 230 pages. — Kiev, Naukova Dumka. [In Russian.]
- 1993: Geological events of the late Miocene of the Eastern Paratethys and Tethys. — *Paleontologia i Evolució*, 26–27:291–292.
- SEMENOV, Y. A. 1981: On the question of the systematic position of the genus *Palhyaena* GERVAIS, 1859 (Carnivora: Hyaenidae). — In, Ecological-morphological specialization of animals and environment of their habitation. *Sbornik nauchnych trudov*. Kiev, Naukova Dumka, :58–61. [In Russian.]
- SERGIENKO, N. I. 1967: On the taxonomic significance of some parts of the postcranial skeleton of the seals of the genus *Pusa*. — *Trudy Poliarnogo Nauchno-Issledovatel'skogo Institute Morskogo Rybnogo Khoziaistva e Okeanography (PINRO)*, Murmansk, 21:185–193. [In Russian.]
- SHUSTOV, A. P., and A. V. YABLOKOV 1967: Comparative-morphological characteristics of the harp and ribbon seals. — *Trudy Poliarnogo Nauchno-Issledovatel'skogo Institute Morskogo Rybnogo Khoziaistva e Okeanography (PINRO)*, Murmansk, 21:51–60. [In Russian.]
- SIMIONESCU, I. 1925: Foci fosile din Sarmatecul de la Chişinau. *Academia Română. Memoriile Secţiunii Ştiinţifice*, 3,3(4):179–191.
- 1931: Mamifere marine din sarmaticul de la Balcic. *Academia Română. Memoriile Secţiunii Ştiinţifice*, 3,8(2):145–154.
- SIMPSON, G. G. 1945: The principles of classification and a classification of mammals. — *Bulletin of the American Museum of Natural History*, 85:350 pages. New York.
- SINELNIKOV, R. D. 1963: *Atlas of the anatomy of man*. — 2nd edition. Moscow, Medical literature, 1:477 pages. [In Russian.]
- SINITSYN, W. M. 1965: *Ancient climates of Europe and Asia. Paleogene and Neogene*. — Leningrad University Press, 1: 165 pages. [In Russian.]
- SMIRNOV, N. A. 1935: Marine Animals of the Arctic Sea. — In *Zveri Arctiki, Glavsevmorpyti*, Leningrad. :455–570. [In Russian.]
- SOKOLOV, W. E. 1975: *Systematics of Mammals: Cetacea, Pinnipedia, Carnivora, Tubulidentata, Tylopoda, Perissodactyla*. 528 pages. — Moscow, High School. [In Russian.]
- 1985: *Dictionary of animal names in five languages. French, Latin, Russian, English, Germany*. Moscow, Russian Language. — 2nd edition: 352 pages.
- STEININGER, F. F., and L.A. NEVESSKAYA 1975: *Stratotypes of Mediterranean Neogene stages*. — Vol. 2. Committee on Mediterranean Neogene Stratigraphy. Bratislava, 364 pages.
- STEININGER, F. F., and A. PAPP 1979: Current Biostratigraphic and Radiometric Correlations of Late Miocene Central Paratethys Stages (Sarmatian s.str., Pannonian s.str., and Pontian) and Mediterranean stages (Tortonian and Messinian) and the Messinian Event in the Paratethys. — *Newsletters on Stratigraphy*. Berlin, Stuttgart, 8(2):100–110.
- STEININGER, F. F., R. L. BERNOR, and V. FAHLBUSCH 1994: European Neogene marine/continental chronologic correlation: 15–46. In: LINDSAY, E. H., V. FAHLBUSCH, and P. MEIN (eds.), *European Neogene Mammal Chronology*. — Plenum Press, New York, 658 pages.
- SZTANÓ, O. 1995: Paleogeographic significance of tidal deposits: an example from an Early Miocene Paratethys embayment, north-east Hungary. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 113:173–187.
- TARASOFF, F. J. 1972: Comparative Aspects of the Hind Limbs of the River Otter, Sea Otter and Seals. — In, R.J. HARRISON (ed.), *Functional Anatomy of Marine Mammals*, Academic Press: London and New York, 1:333–359.
- TAVANI, G. 1941: Revisione dei resti del Pinnipede conservato nel Museo di Geologia di Pisa. — *Palaeontographica Italica, Memorie di Paleontologia*, 40:97–113 (whole volume 40 dated 1942).

- 1942. Revisione dei resti di Pinnipedi conservati nel Museo geo-paleontologica di Firenze. — *Atti della Società Toscana di Scienze Naturali*, 5:3–11. Pisa (whole volume dated 1943).
- TEDFORD, R. H. 1977: Relationships of pinnipeds to the other carnivores (Mammalia). — *Systematic Zoology*, 25(4):363–374.
- THENIUS, E. 1943: Ergebnisse der Neuuntersuchung von *Miophoca vetusta* ZAPFE (Phocidae, Mammalia) aus dem Torton des Wiener Beckens. — *Österreichische Akademie der Wissenschaften, Denkschriften mathematisch-naturwissenschaftlichen Klasse vom 9. März* 1950(5):99–107.
- 1979: *Die Evolution der Säugetiere. Eine Übersicht über Ergebnisse und Probleme*. — Gustav Fischer Verlag, Stuttgart, New York, 270 pages.
- 1992: Neue Befunde und Erkenntnisse zur Verbreitungsgeschichte der Robben (Mammalia: Carnivora: Pinnipedia). — *Anzeiger der Österreichischen Akademie der Wissenschaften, Sitzungsberichte der mathematisch-naturwissenschaftlichen Klasse*, 129:67–73.
- TOTH, G. 1948: Weitere Reste von *Miophoca vetusta* ZAPFE aus dem Torton des Wiener Beckens. — *Paleobiologica*, Wien, 8(3):173–194.
- TOULA, F. 1897: *Phoca vindobonensis* n. sp. von Nussdorf in Wien. — *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients, Mittheilungen des Paläontologischen Instituts der Universität Wien*, 11(2):47–70.
- TRELEA, N. and T. SIMIONESCU 1981: Au sujet de quelques formes de vertébrés des formations sarmatiennes de Șchelia du département de Jassy. — *Analele Științifice ale Universității Iași. Geologie-Geografic*, 31(2):18–20.
- TROUËSSART, E.-L. 1897: Carnivora, Pinnipedia, Rodentia I. — Fascicle II (pages 219–452). In *Catalogus mammalium tam viventium quam fossilium*. Nova editio. Berlin: R. Friedländer & Sohn.
- 1898: Sirenia, Cetacea, Edentata, Marsupialia, Allotheria, Monotremata. — Fascicle V (pages 999–1264). In *Catalogus Mammalium tam viventium quam fossilium*. Nova editio. Berlin: R. Friedländer & Sohn.
- 1904: Primates, Prosimiae, Chiroptera, Insectivora, Carnivora, Pinnipedia. — Fascicle I (iv + 288 pages) In *Catalogus mammalium tam viventium quam fossilium*. Quinquennale supplementum, anno 1904. Berlin: R. Friedländer & Sohn.
- 1905: Cetacea, Edentata, Marsupialia, Allotheria, Monotremata. — Fascicle IV (pages vii + 753–929) In *Catalogus mammalium tam viventium quam fossilium*. Quinquennale supplementum (1899–1904). Index alphabeticus. — Berlin: R. Friedländer & Sohn.
- TRUE, F. W. 1906: Description of a new genus and species of fossil seal from the Miocene of Maryland. — *Proceedings of the United States National Museum*, 30(1475):835–840.
- UGOLINI, R.
- 1900: Di uno scheletro fossile di Foca trovato ad Orciano. — *Atti della Società Toscana di Scienze Naturali*, Pisa, 12:146–148.
- 1902: Il *Monachus albiventer* Bodd. del Pliocene di Orciano. — *Paleontographica Italica. Memorie de Paleontologia*, Pisa, 8:1–21.
- 1903: Resti di foche fossili italiane. — *Atti della Società Toscana di Scienze Naturali. Pisa. Memorie*, 19:80–89.
- VAN BENEDEEN, P.-J. 1853: Note sur dent de phoque fossile du crag d'Anvers. — *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*. 2nd serie, 6(20):255–258.
- 1859: Ossements fossiles découverts a Saint-Nicolas, en *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*. — 2nd serie, 8(11):123–146.
- 1871a: Les phoques de la mer Scaldisienne. — *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*. 2nd serie, 32(7):5–19.
- 1871b: Un sirénien nouveau du terrain rupélien. — *Bulletins de l'Académie Royale des Sciences, des lettres et des Beaux-Arts de Belgique*: 164–178.
- 1872: Paléontologie des Vertébrés. — *Patria Belgica, Encyclopédie Nationale ou Exposé Méthodique de toutes les Connaissances, première partie*, 10:353–388.
- 1876a: Les Phoques Fossiles du bassin d'Anvers. — *Bulletin de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*. 45^{ia} anne, 2ⁿ serie, 41(4):783–802. Brussels.
- 1876b: Les Phoques Fossiles du Bassin D'Anvers. — *Journal de Zoologie Comprenant les différentes Branches de Arte et Science*:188–205. Paris.
- 1877: Description des ossements fossiles des environs d'Anvers, première partie. — *Pinnipèdes ou Amphithériens. Musée Royal d'Histoire Naturelle de Belgique, Annales*, 1:88 pages.
- VAN BREE, P. J. H., and D. P. B. ERDBRINK 1987: Fossil Phocidae in some Dutch collections (Mammalia, Carnivora). — *Beaufortia. Institute of Taxonomic Zoology (Zoological Museum). University of Amsterdam*, 37(3):43–66.
- VOGT, P. R. and R. ESHELMAN 1987: Maryland's Cliffs of Calvert: A Fossiliferous Record of Mid-Miocene Inner Shelf and Coastal Environments. — *Geological Society of America Centennial Field Guide – Northeastern Section*, 3:9–14.
- WEBER, M. 1904: *Die Säugetiere. Einführung in die Anatomie und Systematik der receten und fossilen Mammalia*. — Jena, G. Zischer, xii + 866.
- 1927: *Die Säugetiere. Einführung in die Anatomie und Systematik der receten und fossilen Mammalia*. — Berlin: G. Fischer, 1:4468 pages.
- WIG, R. 1981: On the relationship of pinnipeds to other carnivores. — *Zoologica Scripta*, 12:225–227.
- 1981. Sexual shape dimorphism in the skull of the hooded seal *Cystophora cristata*. — *Zoological Journal of the Linnean Society*, 88:339–347.
- WILSON, D. E., and D. M. REEDER (eds.) 1993: *Mammal species of the world: a taxonomic and geographic reference*. — Second ed. Smithsonian Institution Press, Washington, D.C., 1: 206 pages.
- WOLSAN, M. 1993: Phylogeny and classification of early European Mustelidae (Mammalia: Carnivora). — *Acta Theriologica* 38(4):345–384.

- WORTMAN, J. L. 1894: Osteology of *Patriofelis*. — *Bulletin of the American Museum of Natural History*, 6(5):129–164.
- 1906. A new fossil seal from the marine Miocene of the Oregon coast. — *Science, new series*, 24, 89–92.
- WOZENCRAFT, W. C. 1987: The Phylogeny of the Recent Carnivora. — In, J. L. GITTLEMAN (ed.). *Carnivore Behavior, Ecology, and Evolution*.
- 1988: Cornell University Press, Ithaca, New York. pages 495–593. Wyman, J.
- 1850a: [Some fossil bones of seals.] — *Boston Society of Natural History Proceedings*, 3:241–242.
- 1850b: [other fossil remains of seals.] — *Boston Society of Natural History Proceedings*, 3:323.
- 1850c: Notice of remains of vertebrated animals found at Richmond, Virginia. — *American Journal of Sciences and Arts*, second series, 10(29):228–235.
- WYSS, A. R. 1987: The walrus auditory region and monophyly of pinnipeds. — *American Museum Novitates* 2871:1–31.
- 1988a: On “Retgression” in the Evolution of the Phocinae and Phylogenetic affinities of the Monk Seals. — *American Museum Novitates*, 2924:1–38.
- 1988b: Evidence from flipper structure for a single origin of pinnipeds. — *Nature*, 334:427–428.
- 1989: Flippers and pinniped phylogeny: has the problem of convergence been overrated? — *Marine Mammal Science*, 5:343–375.
- 1987: The Evolution of Body size in Phocids: Some Ontogenetic and Phylogenetic Observations; pp. 69–75. — In, A. BERTA and T.A. DEMÉRÉ (eds.), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* — *Proceedings of the San Diego Society of Natural History*, 29.
- WYSS, A. R., and J. J. 1988: A phylogenetic analysis and definition of the Carnivora; pp. 32–52. — In, F. S. SZALAY, M. J. NOVACEK, and M.C. MCKENNA (eds.), *Mammal phylogeny: Placentals*. — Springer-Verlag, New York.
- YABLOKOV, A. V., and D. E. SERGEANT 1961: Cranial variation in the Harp Seal (*Pagophilus groenlandicus* Erxleben, 1777). — *Zoological Journal*, 42(12):23–132.
- ZAPFE, H. 1937: Ein bemerkenswerter Phocidenfund aus dem Torton des Wiener-Beckens. — *Verhandlungen der K.K. Zoologisch-botanischen Gesellschaft*. Vienna. 86/87:271–276.

