

The Fossil Monk Seal *Pontophoca sarmatica* (Alekseev) (Mammalia: Phocidae: Monachinae) from the Miocene of Eastern Europe

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ABSTRACT

We present a phylogenetic analysis of the middle Miocene European seal *Pontophoca sarmatica* (Alekseev) based upon characters of the mandible, humerus (both described herein for the first time), and femur. The diagnoses of the subfamily Monachinae and the genus *Pontophoca* are emended to include the postcranial characters. *Pontophoca*, as revised, is proposed as the sister group of the modern *Monachus* and is included in the monophyletic subfamily Monachinae. We also include in this subfamily two extinct taxa that occur in both the eastern United States and western Europe: *Callophoca* and *Pliophoca*.

Introduction

The purpose of this study is to clarify the taxonomic status of *Pontophoca sarmatica* (Alekseev, 1924) in light of new material found in the last 30 years and of previously undescribed bones in various European collections.

The most numerous fossil remains of true, or earless, seals (Phocidae) in the Old World have been found in the middle Sarmatian–Maeotian, and probably Pontian, deposits of the European part of the former USSR, especially in the northern coastal region of the Black Sea in Ukraine, Moldavia, and Romania. In this study we seek to improve the state of knowledge of Monachinae of the middle Sarmatian and Maeotian, and possibly of the early Sarmatian and Pontian, as well as (within limits) of the subfamily as a whole. We also present a phylogenetic analysis and classification based upon morphological characters of the mandible, humerus, and femur of the Monachinae.

The age of the material of *Pontophoca sarmatica* was con-

sidered to be late Tertiary by Eichwald (1850) and von Nordmann (1858–1860), whereas Andrusov (1893) specified the age more precisely as Upper Miocene (Sarmatian).

Further studies on Sarmatian marine mammals were made early in the last century. Alekseev (1924, 1926) described two new species, *Phoca sarmatica* and *Phoca novorossica*. About the same time, in his study of true seals of the northern littoral region of the Black Sea, Simionescu (1925) also described two other species—*P. maeotica* and *P. pontica*. As can be judged by the illustrations of the femur in his study (pl. 1: fig. 2), Simionescu included in "*P.*" *pontica* the seal described previously by Alekseev (1924) as *P. sarmatica* and noted that these finds date from the Sarmatian period. Following Simionescu (1925), Macarovici and Oescu (1942) and Macarovici (1942) published short reviews of information on fossil seals of the European Sarmatian, which only confused the picture.

Meanwhile, Kretzoi (1941), who tried to classify the Neogene seals of this region, proposed three new genera: *Praepusa*, *Pontophoca*, and *Monachopsis*. The importance of Kretzoi's work is that he attempted for the first time to make comparisons of previously known fossil material. Unfortunately, he did not succeed completely.

King (1956), in her monographic review of monk seals, presented the first description of bones of the postcranial skeleton as well as descriptions and measurements of the skulls and mandibles of modern species of Monachinae. Of special interest in this context is an article by McLaren (1960), who, on the basis of previous publications, revised the two subfamilies of true seals of the northern Black Sea coastal region of the former USSR. King (1964), in the first edition of her monograph on seals of the world, presented her conception of fossil seals of the Miocene of the northern Black Sea coastal region, separating them into four species of *Phoca* and two other species referred to *Monotherium* and *Pontophoca*. Subsequently, King (1983) changed her views on classification of the true seals, but she considered only their classification above the rank of tribe. Grigorescu (1977), in his article on the seals of

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Paratethys, presented a detailed description of postcranial bones from southern Romania. He also discussed the evolution and phylogeny of Sarmatian seals. Miocene seals in the Northern Hemisphere were reviewed by Ray (1977), who also considered routes of penetration of Phocidae into the North Atlantic during the Neogene.

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REPOSITORIES.—The following abbreviations are used for institutions housing specimens used in this study:

IZUAN	Institute of Zoology (named after I.I. Shmalhausen) of the Academy of Sciences of the Ukraine, Kiev
JaU	Department of Geology, University of Jassy, Romania
MZHF	Museum of Zoology, Helsinki, Finland
OGUM	Paleontological Museum (named after I.I. Mechnikov), Odessa State University, Ukraine
PIN	Paleontological Institute of the Academy of Sciences of Russia, Moscow
TGPI	Tiraspol State Pedagogical Institute, Moldavia
UBFG	Faculty of Geography-Geology, University of Bucharest, Romania
USNM	Collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (includes collections of the former United States National Museum)
ZIN	Zoological Institute of the Academy of Sciences of Russia, Saint Petersburg
ZKM	Zaporozhye Museum of Regional Studies, Zaporozhye, Ukraine

MATERIAL AND METHODS

For solving diagnostic problems, we used the methods of Asanin (1936), Chapskii (1952, 1967), and Antoniuk (1970, 1972). Morphometric analysis of skulls and mandibles was based upon the methods of Chapskii (1955, 1974), Semenov (1981), Andreescu and Murariu (1985), and the methods described below. Bones of the postcranial skeleton and skulls of both Miocene and extant Monachinae were measured according to the schemes of Marcoci and Popa (1957), Dornesco and Marcoci (1958), Sergienko (1967), Piérard (1971), Driesch (1976), Muizon (1981), Antoniuk and Koretsky (1984), Koretsky (1987), and Koretsky and Ray (1994). Anatomical terminology follows the *International Anatomical Nomenclature* edited by Michaylov (1980), the *Anatomical Atlas* by Sinelnikov (1963), and Piérard (1971).

The information presented below on geographic location and geologic age of the finds as well as on collectors and institutional repositories is compiled from data published by Kellogg (1922), Pidoplichko (1956), Gromova et al. (1962), Godina (1973), Dubrovo and Kapelist (1979), Korotkevich et al. (1985), and Semenenko (1987) and from our unpublished data.

In this study we use the stratigraphic scheme of eastern Paratethys published by Chepalyga et al. (1985).

This cladistic study is intended to clarify the phylogenetic relationships among modern and fossil species of monachine seals. Six species of Monachinae were analyzed, along with one species of Cystophorinae (*Cystophora cristata*) and one species of Phocinae (*Leptophoca lenis*) as outgroups, using 48 cranial and postcranial morphological characters. Originally, 62 characters were examined, but 14 were eliminated because they could not be examined in the fossil taxa. The 48 informative characters were analyzed with the Hennig86 computer program (Farris, 1988).

Systematic Paleontology

Superfamily PHOCOIDEA Smirnov, 1908

Family PHOCIDAE Gray, 1825

Subfamily MONACHINAE Trouessart, 1897

TYPE GENUS.—*Monachus* Fleming, 1822; present distribution: Mediterranean Basin, Atlantic Ocean (North Africa), Hawaiian Islands, Gulf of Mexico, Caribbean Sea (probably extinct in the last two areas).

DISTRIBUTION.—Middle Miocene to the present; Mediterranean Basin, North Atlantic, North Pacific, Antarctic region.

EMENDED DIAGNOSIS.—Large seals with eight incisors (I=2/2). Mastoid with wide convexity; convexity not strongly laterally protruding and not turned abruptly downward behind mastoid process (King, 1966). Maxilla anterior to orbits slightly concave. Anterior palatal foramen tending to disappear, according to Chapskii (1974). Mandibular chin prominence present; posterior symphysis border reaching at least to middle of alveolus for p3. Middle of internal crest of humeral trochlea raised arch-like over coronoid fossa; width of distal epiphysis exceeding width of proximal epiphysis by one-fifth to one-sixth. Width of distal femoral epiphysis greater than that of proximal epiphysis by one-quarter to one-fifth; minimum width of femoral shaft more than two-thirds of the proximal epiphysis width; intertrochanteric crest weakly developed.

INCLUDED TRIBES.—Monachini Scheffer, 1958; Lobodontini Scheffer, 1958.

COMPARISONS.—The interorbital width at the frontal bones in Monachinae is wider than in Phocinae, although not as wide as in Cystophorinae. The anterior part of the frontal has a fossa that is directed medially. On the midline at the fronto-nasal suture is the origin of the very low sagittal crest, which is completely absent in the other two subfamilies. In contrast to the

condition in Cystophorinae, the part of the maxilla located between the nares and orbits is wide. Just as in Phocinae, an interval is present between the external auditory meatus and the postglenoid process. The jugal bone, as in Cystophorinae, has an antero-orbital process. The bolster-like convexity of the mastoid is strongly compressed and is directed laterally. The anterior palatal foramina tend to disappear.

The symphyseal part of the mandible is very strongly developed; it is straight and its posterior edge is considerably displaced posteriorly relative to its position in the other subfamilies.

The middle of the crest of the humeral trochlea, unlike that in Phocinae, is arch-like in shape and raised over the coronal foramen.

Both distal condyles of the femur are of equal dimensions, unlike those in Phocinae. The difference in width of the distal and proximal epiphyses is significant.

DISCUSSION.—Up to the present there has been no clear conception of the relationships within this subfamily. Previously, in accordance with the classification of Trouessart (1897), the subfamily Monachinae contained the genera *Lobodon* Gray, 1844; *Ommatophoca* Gray, 1844; *Hydrurga* Gistel, 1848; and *Leptonychotes* Gill, 1872. Simpson (1945), however, placed *Lobodon* and the other three genera mentioned above in the subfamily Lobodontinae. Placement of these four genera is still a controversial problem. One group of investigators has assigned them to a single subfamily (Ognev, 1935; Grassé, 1955; King, 1964, 1983; Tedford, 1977; Muizon, 1982), whereas others (Wyss, 1988; Muizon, 1992) have separated them into two subfamilies. Finally, some investigators (Sokolov, 1979; Pavlinov and Rossolimo, 1987; Wozencraft, 1989) have chosen not to separate true seals (Phocidae) into subfamilies at all.

Chapskii (1955, 1961, 1971, 1974) presented a comprehensive series of analyses of the suprageneric systematics of pinnipeds. Analyzing the crania, he clearly described diagnostic characters that separate true seals into three subfamilies: Phocinae, Monachinae, and Cystophorinae, which he in turn divided into tribes and subtribes. This is also true for the tribes Monachini and Lobodontini. Chapskii's (1974) detailed analysis proved King's (1966) hypothesis to be untenable; however, King (1983) persisted in her hypothesis that the genus *Cystophora* should be transferred from the subfamily Cystophorinae into the subfamily Phocinae, and that the genus *Mirounga* should be moved into the subfamily Monachinae. It may be assumed that Muizon (1982) was unaware of the study by Chapskii (1974) because he accepted the systematics of King (1964, 1966) without any reservations, and thus he returned to the concept of subdivision of the subfamily Cystophorinae.

Chapskii's concept is supported by the conclusion of Robinette and Stains (1970) in their comparative study of the pinniped calcaneus. These authors emphasized that it is inadmissible to separate the hooded seal and the elephant seal taxonomically. This point of view was supported by Anbinder (1980:76) who noted that "modern analytical methods of chro-

mosome 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." In our view, the problem of the status of the Cystophorinae is solved, and we support Chapskii's point of view that the subfamily Cystophorinae is valid.

Tribe MONACHINI Scheffer, 1958

TYPE GENUS.—*Monachus* Fleming, 1822; present distribution: Mediterranean Basin, southern North Atlantic, North Pacific.

DISTRIBUTION.—Middle Miocene to the present; Europe, southern North Atlantic, North Pacific.

DIAGNOSIS.—Maxillary process of jugal bone clearly outlined. Lower edge (masseteric margin) of jugal bone arched upward, elevated to greatest degree in middle part of bone. Antero-upper process of jugal bone reaching level of infraorbital foramen, terminating almost over inferior edge of infraorbital foramen. Lower edge of orbit at same level as infraorbital foramen.

Nasal bones not united with each other; frontal contact of nasals not longer than maxillary contact. Turbinals (fontanelles) in presphenoid region huge and round (see Chapskii, 1971:311).

INCLUDED GENERA.—*Monachus* Fleming, 1822; *Monatherium* Van Beneden, 1877; *Callophoca* Van Beneden, 1877; *Pliophoca* Tavani, 1941; *Pontophoca* Kretzoi, 1941.

COMPARISONS.—Representatives of the Monachini are distinguished from the Lobodontini by (1) an arch-like bending of the jugal bone, (2) the position of the infraorbital foramen on a level with the greatest deflection of the upper border of the jugal bone, and (3) separate nasal bones.

DISCUSSION.—Several other genera were earlier included in the Monachinae, but now these assignments are considered uncertain or even wrong. We review the status of some of them below; *Mesotaria* Van Beneden (1877) and *Pristiphoca* Gervais and Serres (1847) will be discussed in detail by Koretsky and Ray (in prep.).

Although the author of "*Miophoca*" *vetusta* (Zapfe, 1937), as well as Simpson (1945), Thenius (1950, 1952), King (1964), and Holec et al. (1987), assigned this western European genus to the subfamily Monachinae and dated it to the middle Miocene, other investigators (Kirpichnikov, 1961; Ray, 1977; Muizon, 1982; Savage and Russell, 1983) did not mention this genus at all in their reviews of Tertiary seals of Europe. Thenius (1950, 1952) assigned this species to *Pristiphoca*, and Holec et al. (1987) supported the opinion of Thenius with new cranial remains from Devinská Nová, Slovakia. The uncertainty of the taxonomic position is because of the incompletely known morphology of "*Miophoca*," which also precludes a detailed comparison between "*Miophoca*" and *Pontophoca*. It should be pointed out, however, that in accord with the opinion of Zapfe (1937), the very distinctive, characteristic morphotype

of the mandible shows that representatives of the genus "*Miophoca*" are undoubtedly ancestral to *Cystophora*. The problem of whether "*Miophoca*" belongs in the subfamily Monachinae still remains open, however.

Genus *Monachus* Fleming, 1822

EMENDED DIAGNOSIS.—Condylbasal length of skull not exceeding 200 mm. Facial part of skull markedly lower than occipital part, and with large infraorbital processes. P1 single rooted. Diastemata between teeth absent. Basal cingulum well developed. Main cusp on all cheek teeth sharp-triangular in form. Supplementary cusps weakly developed. Carotid canal displaced almost to bottom of triangular tympanic bulla. Bony blade of external auditory meatus relatively weakly developed. Foramen ovale more or less covered by hamular process of sphenoid bone. Transverse measurement of glenoid fossa of mandible equal to or slightly exceeding longitudinal dimension of tympanic bulla. Jugular process not conjoined with mastoid process, and with a convexity on anterolateral part.

Deltoid crest of humerus short, not reaching middle of the shaft, and distended in proximal quarter; lesser tubercle oval shaped, with height exceeding height of head; head flattened proximodistally; ratio of width to height of head greater than 0.90; intertubercular sulcus narrow and deep; epicondyles strongly developed; distal epiphysis wider than the proximal epiphysis; coronoid fossa shallow.

Greater trochanter of femur slightly higher than femur head and square in form; slightly distended in proximal part; trochanteric fossa shallow, rounded, and ending in anterior one-third of trochanter. Minimal width of shaft in middle of femur. Distal condyles similar in size and placed widely apart; maximal distance across epicondyles 0.61 times length of femur; intercondylar area flat; distal end of femur wider than proximal end by ~115%.

DISCUSSION.—This is the first time that characters of the humerus and femur have been included in the diagnosis of *Monachus*, except for the short general description by King (1956: 239, 241). Because the material of the other fossil taxa needed for analysis is totally lacking or is fragmentary, we cannot make a more detailed comparison with genera in the tribe Monachini. For example, there is no information on skull fragments, mandibles, or femora of the genus *Monatherium*, and the fossils assigned to *Paleophoca* represent a cetacean (Koretsky and Ray, in prep.).

Genus *Pontophoca* Kretzoi, 1941

TYPE SPECIES.—*Phoca sarmatica* Alekseev, 1924; middle Sarmatian of Kishinev.

DISTRIBUTION.—Middle Miocene of eastern Europe.

EMENDED DIAGNOSIS.—p3 and p4 double rooted, placed parallel to the tooth-row axis. Protoconid on p4 triangular. Di-

astemata present. Metaconid and basal cingulum weakly developed.

Deltoid crest of humerus terminating lower than middle of shaft; proximal part of crest recurved posterodorsally; distal end of bone considerably wider than proximal end; lesser tubercle located higher than proximal end of deltoid crest and head; ratio of width to height of head about 1.00; supracondylar crest strongly developed.

Greater trochanter of femur slightly higher than head and very oblique; distal end of greater trochanter narrower than proximal end. Distal end of femur broader than proximal end by 111%–114%; trochanteric fossa shallow and elongated along femur axis; head of femur very small relative to massive bone and seated on narrow neck; minimal width of shaft located in proximal part of femur between head and distal part of greater trochanter; distal condyles widely separated; maximal distance across epicondyles ~70% of femur length.

INCLUDED SPECIES.—In the middle Sarmatian of the northern Black Sea littoral region, only one monachine species (the type species) is recorded—"*Phoca*" *sarmatica* from Moldavia and possibly from the middle part of the Don River (Alekseev, 1924).

COMPARISONS.—Among the modern and fossil representatives of the subfamily Monachinae, the extinct genus *Pontophoca* can be compared only with *Monachus*, *Pliophoca*, *Callophoca*, and partly with *Monatherium*. It differs from all of these taxa as follows: (1) The teeth are oriented parallel to the axis of tooth row, with diastemata between the teeth; cheek teeth have one anterior and one posterior accessory cusp (except in *M. monachus*); basal cingulum is weakly developed (except in *Monachus*). (2) The deltoid crest of the humerus is shorter (except in *Monachus*); the distal part of the deltoid crest is narrow, and the proximal part is averted posterodorsally; the development of a coronoid fossa and intertubercular sulcus is rudimentary (except in *Callophoca* and *Monatherium*); the lesser tubercle is elongated; the head is more spherical; the development of the medial supracondyles is relatively stronger. (3) The medial border of the femoral body is distended; the supracondyles are of different heights and are thickened at the points of attachment of both heads of the gastrocnemius muscle; the lateral supracondyle, however, is thickened only at the point of attachment of *m. extensor digitorum longus*.

Apart from these characters, this genus differs from *Monatherium* as follows: the width of the distal end of the humerus is greater than that of the proximal end; the lesser tubercle extends above the head and above the proximal part of the deltoid crest; and development of the lateral epicondyloid crest is considerably stronger.

It differs from *Pliophoca* as follows: The body of the mandible is higher. The lesser tubercle extends above the head of the humerus; the radial sulcus is absent; the deltoid crest is widest in its proximal part. The trochanteric fossa of the femur is shallow and wide; the least width of the shaft is in the proximal part of the bone; and the condyles are widely spaced and flat.

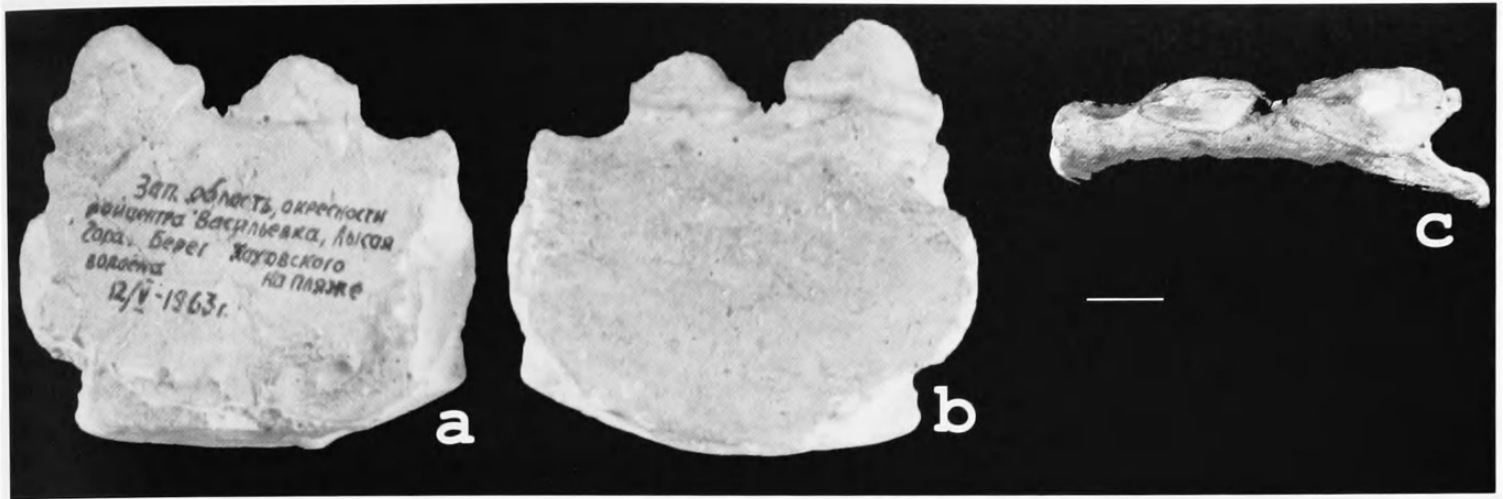


FIGURE 1.—Mandible of *Pontophoca sarmatica*. Cast of fragment of R. mandible, collection of ZKM, unnumbered (with p3, p4) from village of Vasilyevka, Zaporozhye Region, bank of Kachovka Reservoir (Mount Lysaya), Ukraine. In labial (a), lingual (b), and occlusal (c) aspects. (Scale bar=1 cm.)

It differs from *Callophoca* in the following characteristics: the greater trochanter of the femur extends higher above the head, and the condyles are flat.

DISCUSSION.—Like most taxa erected by Kretzoi, the genus *Pontophoca* was not diagnosed satisfactorily. For this reason, until recently this genus was recognized by only a few specialists, such as McLaren (1960) and Kirpichnikov (1961). Representatives of this genus were usually assigned either to *Phoca* or to *Monachus*. Some species included in these genera undoubtedly belong to *Pontophoca*.

Von Nordmann (1858) was the first investigator who analyzed the bones of the extremities of *Pontophoca sarmatica*, but he described them under the name *Phoca maeotica*, together with the remainder of his material. Alekseev (1924) separated these specimens from the Nordmann collection, supplemented them with material kept at Odessa University (Ukraine), and described them as *Phoca sarmatica*. Some authors (Grigorescu, 1977; Trelea and Simionescu, 1985; Muizon, 1992) still use the name *Phoca* when referring to them. We view this assignment as incorrect, because the femur and humerus differ so distinctly from those of *Phoca* that the possibility of confusion is practically excluded. The importance of Grigorescu's (1977) work is that he recognized characters diagnostic of the Monachinae in bones of *Pontophoca sarmatica*. In his opinion, the strong development of the gastrocnemius muscle and the location of its attachment stimulated considerable expansion of the distal part of the femur. Our material confirms this, but all femora that we studied also have a very well developed plantar fossa, the place for attachment of the plantaris muscle, so we can add that not only the gastrocnemius muscle but also the plantaris contributed to expansion of the distal part of the femur.

To remove some doubts on the correctness of the assignment of *Pontophoca* to the subfamily Monachinae, we compared its femora with those of young individuals of *Monachus mona-*

chus. These femora are very similar to those of *Pontophoca sarmatica* in the form of the bone, the obliqueness of the greater trochanter, the narrow neck, and the relatively small head. For these reasons we consider the assignment of "*Phoca*" *sarmatica* to the Monachinae to be well founded.

In the "Comparisons" section above we drew attention to the common structural features of the mandibles in *P. sarmatica*, *M. monachus*, *M. tropicalis*, and *M. schauinslandi*. These common features are evidence of the common origin of these four species (Repenning and Ray, 1977) and also suggest that *Pontophoca* might be ancestral to the genus *Monachus*. The cladistic analysis below confirms this (Figure 5).

Pontophoca sarmatica (Alekseev, 1924) McLaren, 1960

FIGURES 1–4; TABLES 1–3

- Phoca maeotica* Nordmann, 1860:356–357, pl. 23: figs. 3, 7; pl. 24: fig. 1.
Phoca maeotica [sic].—Nordmann, 1860:317.
Phoca pontica.—Kellogg, 1922:120 [in part].—Simionescu, 1925:180, 188, 190–191, fig. 5P; pl. 1: fig. 2.—Macarovici and Oescu, 1942:351–352, 363–367, 378–379, figs. 7, 8; pl. 2: figs. 18, 19.—Macarovici, 1942:262–263.—McLaren, 1960:51.
Phoca sarmatica.—Alekseev, 1924:203, figs. 4–7.—Friant, 1947:12.—Pidoplichko, 1956:142.—McLaren, 1960:57.—Kirpichnikov, 1961:29, 32, 34, 36.—Aslanova, 1965:52.—Grigorescu, 1977:407–411, 413–418, fig. 5D.—Dubrovo and Kapelist, 1979:36.—Trelea and Simionescu, 1985:19.—Muizon, 1992:35.
Phoca pontica var. *sarmatica*.—Macarovici, 1942:263, 267, pl. 2: fig. 18.1.
Pontophoca simionescui.—Kretzoi, 1941:354, fig. 3.2.
Monachus [sic].—Friant, 1947:6, 16, 47–50, pl. 1: fig. 1a–c.
Pontophoca sarmatica.—McLaren, 1960:47, 52, 57, fig. 1g,h,i.—King, 1964:131.

HOLOTYPE.—Femur described and illustrated by Alekseev (1924:202, fig. 6). *Phoca sarmatica* (McLaren, 1960:57); collection of OGUM, Moldavia, middle Sarmatian.

DISTRIBUTION.—Middle Sarmatian of northern Black Sea coastal region (southern Ukraine and possibly Russia).

TABLE 1.—Measurements (mm) of mandible and lower dentition of *Pontophoca sarmatica*, collection of ZKM, unnumbered, incomplete right ramus with p3 and p4.

Character	Measurement
p3 length	14.0
p4 length	20.0
Ramus depth under p4	36.5
p3 height	8.7
p4 height	15.0
p3 width	7.0
p4 width	10.0
Diastema length between p3 and p4	4.5

REFERRED MATERIAL.—Kishinev: PIN 1713/10, R. humerus and L. femur from one individual; PIN 1713/23, femur from another individual; OGUM 23, two humeri, eight femora (R. and L.); OGUM 53–57, one scapula, two fused tibiae and fibulae, five isolated tibiae, three isolated fibulae, and two pelvic bones (this material was described by Alekseev (1926)); ZIN 4, one femur, collection of von Nordmann; ZIN 8, one femur, collection of von Nordmann; UBFG 259, L. and R. femora, collection of Simionescu; USNM 214980, cast of R. femur (original UBFG 259, collection of Simionescu); JaU MS20L, femur, collection of Simionescu (this material was described and illustrated as *Phoca pontica* by Macarovici and Oescu (1942: 351–352, 363–367, 378–379, figs. 7, 8, pl. 2: figs. 18, 19);

TABLE 2.—Measurements (in mm) of humeri of *Pontophoca sarmatica*.

Character	n	x	Range
Total length	7	111.1	100.5–120.0
Length of deltoid crest	7	67.0	64.0–73.0
Height of head	5	25.8	25.5–28.0
Height of trochlea	5	20.1	19.5–23.0
Width of head	5	25.1	23.0–27.5
Width of deltoid crest	5	30.8	27.0–33.0
Width of proximal epiphysis	7	33.3	28.0–38.0
Width of distal epiphysis	7	36.1	30.1–47.0
Width of trochlea distally	5	20.1	20.0–24.0
Width of trochlea, anteriorly	5	17.0	16.5–18.0
Transverse width of diaphysis	8	16.9	15.3–19.1
Thickness of proximal epiphysis	7	38.7	37.3–43.0
Thickness of medial condyle	7	18.1	15.0–22.0
Thickness of lateral condyle	5	18.2	16.5–22.0
Diameter of diaphysis with deltoid crest	8	35.2	31.0–45.0

MZHF 1811, R. humerus, illustrated by von Nordmann (1858, pl. 23: fig. 3) and described by him (1860:317, 356–357) as *Phoca maeotica*; UBFG unnumbered, two L. and one R. femora; UBFG 249, L. humerus; MZHF unnumbered, five R. femora, collection of von Nordmann.

Vicinity of Tiraspol, Moldavia: OGUM 6, 23–25, six humeri (two of which are unnumbered).

Stanitsa Tsymlyansk on the Don River: OGUM 9, humerus.



FIGURE 2.—Humerus of *Pontophoca sarmatica*. Cast of R. humerus, collection of MZHF 1811, from Kishinev, Moldavia. This was illustrated by von Nordmann (1858, pl. 23: fig. 3) and described by him (1860:317, 356–357) as *Phoca maeotica*. In cranial (a), caudal (b), medial (c), and lateral (d) aspects. (Scale bar=1 cm.)

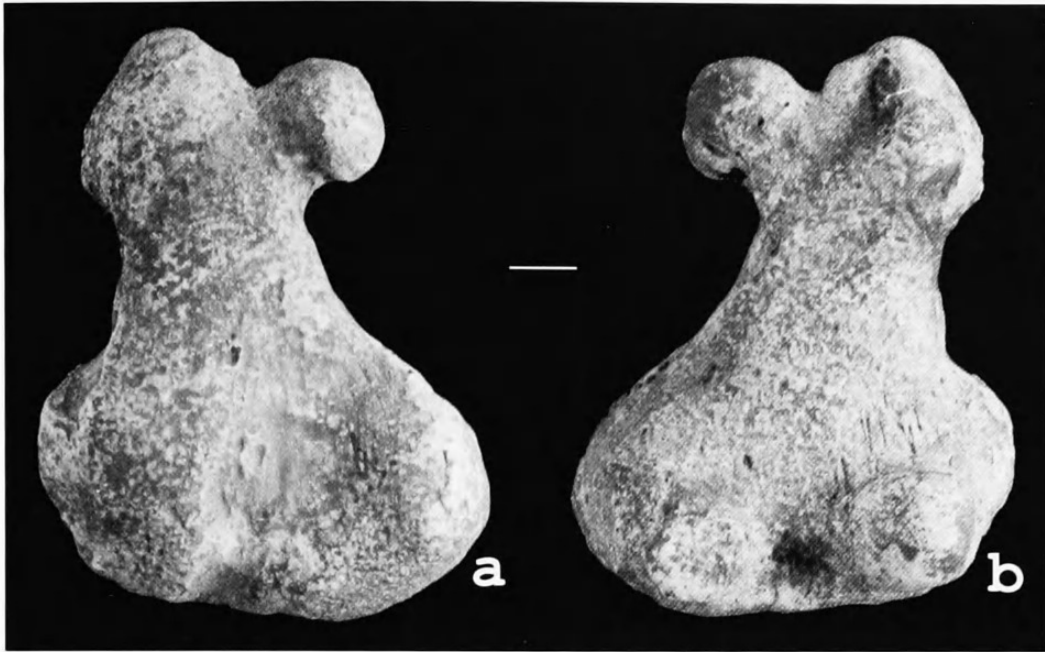


FIGURE 3.—Femur of *Pontophoca sarmatica*. Cast of R. femur, USNM 214980 (original UFG 259, collection of Simionescu), from Kishinev, Moldavia. In cranial (a) and caudal (b) aspects. (Scale bar=1 cm.)

Like the material from the foregoing localities, this material was described by Alekseev (1924).

Kerch Peninsula (Kamysh-Burun): IZUAN 64-357, 64-361, 64-362, three femora.

Village of Vasilyevka, Zaporozhye region; bank of Kachovka Reservoir (Mount Lysaya): ZKM unnumbered, incomplete R. ramus of mandible with p3 and p4.

DIAGNOSIS.—Same as for the genus.

DESCRIPTION.—*Mandible* (Figure 1, Table 1): The long axes of the teeth are parallel to the tooth-row axis. The distema between p3 and the alveolus of p2 is longer than the distema between p3 and p4. Lower p4 is considerably larger than p3. The height of p3 exceeds by only 3.0 mm the paracoid on p4. The basal cingulum and metaconid are weakly developed on both teeth.

Scapula: “Its distinctive features are the strong development of the muscular spine, thickened summit and thick, massive acromion. The articular surface is very narrow; the tuberculum supraglenoidale and cervix scapulae are very weakly pronounced” (Alekseev, 1924:202).

Humerus (Figures 2, 4, Table 2): The lesser tubercle is large, elongate parallel to the bone’s axis, and proximally higher than the head, practically on the same level as the proximal border of the deltoid crest. The intertubercular sulcus is absent. The head is spherical. In well-preserved specimens, the ratio between the length and the width of the head is almost 1.00. The deltoid crista ends in the distal one-third of the bone. This crest is markedly convex, and the deltoid tuberosity is strongly swollen. The coronoid fossa is barely outlined in smaller (i.e., juvenile) bones; in larger individuals it is absent. The radial sulcus is absent. In well-preserved bones, significant

distention of the two epicondyles is clearly seen. The lateral epicondyle is wide; in height it practically reaches the distal part of the deltoid crest. The medial epicondyle in a large individual (evidently an adult) barely reaches the height of the lateral supracondyle. The entepicondylar fossa is seen on all specimens, but in sexually mature individuals this fossa is covered on its medial side by a thicker and wider wall.

Pelvis: The ilia are considerably thickened and distended. “The acetabulum is very deep. Its diameter is rather small, less than in “*Phoca*” *maeotica* and with very pronounced borders” (Alekseev, 1924:202; 1926:138–143).

Femur (Figures 3, 4, Table 3): The femora are closely similar in size to those of the living seal of the genus *Histriophoca*. The greater trochanter is higher than the head, very obliquely oriented, and elongated along the bone’s long axis. In smaller individuals from the Kerch Peninsula (these individuals probably were younger; see Astanin, 1936; Heptner, 1947), it is less oblique and, consequently, more protruding. In its distal part the greater trochanter has a V-shaped end. The length of the greater trochanter varies considerably (from 19.5 mm to 52.0 mm), depending upon the individual’s age. The trochanteric fossa is shallow and wide and reaches the middle of the greater trochanter’s length. This fossa is open on the proximal side of the greater trochanter. Relative to the bone’s mass, the femoral head is very small and is placed on a narrow, long neck. The least width of the shaft is located in the proximal part of the bone. The distal condyles are flat and very widely spaced. The maximum distance between them (10.0–15.5 mm) is 60%–80% of the bone’s length. In young individuals a plantar fossa is present on top of the lateral epicondyle. In adult individuals a considerable swelling of the bone is seen at this loca-

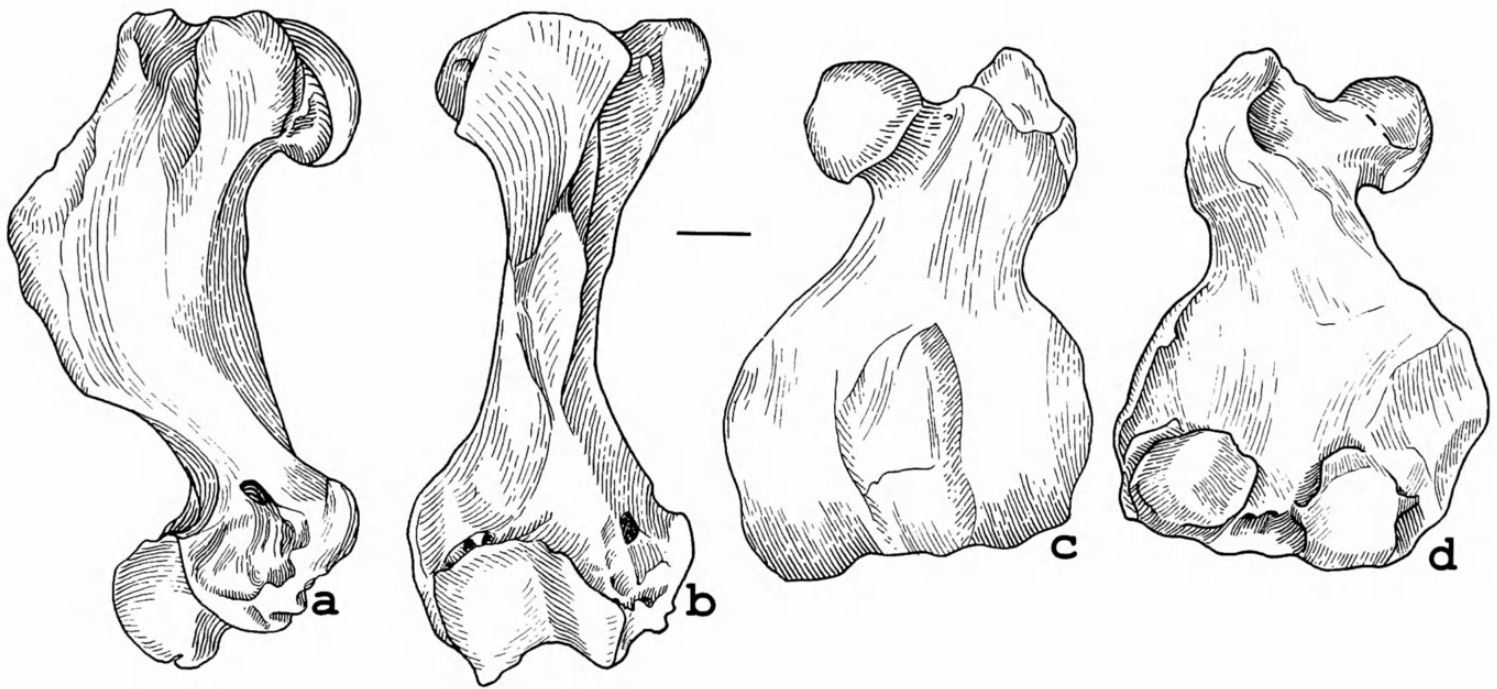


FIGURE 4.—Humerus and femur of *Pontophoca sarmatica* from one individual, originals, collection of PIN 1713/10, from Kishinev, Moldavia. Illustrations of R. humerus in medial (a) and cranial (b) aspects; L. femur in cranial (c) and caudal (d) aspects. (Scale bar=1 cm.)

tion. The characteristic, distinctive feature of this species is significant distention (expansion) of the distal part of the bone, which in adult individuals is 1.4–1.5 times wider than the proximal part (in juveniles 1.2 times).

Tibia and Fibula: Distinctive features are a narrower diaphysis and markedly thickened epiphysis; “the distal condyles of the femur are, consequently, widely placed; the articular surface bordering this distal end of the femur is significantly distended” (Alekseev, 1924:202).

DISCUSSION.—According to published data, this type species is a widely known representative of the Monachinae. It has not, however, been adequately described. In particular, the limits of its dimensions are unknown, as are most of the bones of its skeleton. McLaren (1960) thus stated that it is of smaller dimensions than *Cryptophoca maeotica* (formerly *Phoca maeotica*), which was revised by Koretsky and Ray (1994); but Alekseev (1924) stated that some bones (pelvis) are of equal dimensions with those of the latter species. Kretzoi (1941) illustrated the femur of *Pontophoca sarmatica* as being smaller than that of “*Phoca*” *pontica*. According to our information, however, *P. sarmatica* is considerably larger than *C. maeotica*, and even more so than *Phoca pontica*. Although detailed studies were made of femora of *P. sarmatica*, no one except Alekseev has studied other skeletal parts. We have described herein for the first time a humerus and femur belonging to one individual (PIN 1713/10 from Kishinev). The fact that these bones have the same pathology (not described) and were found not far from each other in one bed supports our opinion that they belong to the same individual. The skeletal parts (the scapula, pelvis, tibia, and fibula) described and illustrated by Alekseev

(1924, 1926) were not cited as associated and were never studied by other authors (e.g., Kretzoi, 1941; Friant, 1947; McLaren, 1960); therefore, at present we cannot supplement their descriptions by our materials or confirm their species assignment. To describe this species more completely, we used the description of Alekseev for these missing skeletal parts of *Pontophoca sarmatica*. Future analysis of supplementary materials may show this hypodigm to be a composite, particularly in view of the considerable intraspecific variability of the humerus and femur, and of the rather narrow geographic distribution (eastern Europe) of this seal as herein recognized. Also, there are no reliable records from the banks of the Don River, although Alekseev reported finding this species in the Lower Don. In addition, more than one large seal is known from the Sarmatian deposits. Alekseev’s scapula, pelvis, tibia, and fibula can be questionably assigned to the same species.

Cladistic Analysis

CHARACTERS USED FOR SUBFAMILY MONACHINAE

The data matrix for the 48 included characters is shown in Table 4. Characters and character states for Monachinae are listed below; 0 designates the most primitive state among the taxa studied; 1 and 2 are derived states; – indicates unknown or missing data.

Skull

1. Mastoid process: (0) not strongly pronounced; (1) pronounced.

TABLE 3.—Measurements (in mm) of femora of *Pontophoca sarmatica*.

Measurement	Adult			Juvenile		
	<i>n</i>	<i>x</i>	Range	<i>n</i>	<i>x</i>	Range
Total length	16	82.5	76.5–96.0	2	–	68.0; 68.5
Medial length	8	78.3	74.0–88.0	2	–	64.5; 68.0
Lateral length	9	75.3	71.5–80.5	3	60.7	58.0–62.5
Length of medial condyle	13	16.6	15.0–21.0	2	–	12.0; 12.0
Length of lateral condyle	17	18.0	16.0–22.0	3	16.8	16.0–18.0
Length of greater trochanter	15	28.0	25.0–30.0	3	21.3	20.5–22.0
Height of head	6	18.5	17.2–23.0	2	–	15.0; 15.5
Height of articular area of patella surface	6	17.2	15.9–22.0	2	–	16.5; 20.0
Intertrochanteric width	9	29.0	28.5–38.0	3	25.5	25.0–26.0
Width of proximal epiphysis	13	40.8	36.0–44.0	2	–	34.0; 35.0
Width of distal epiphysis	19	59.2	54.5–66.0	2	–	39.0; 39.5
Width of condyles	13	46.8	42.6–50.5	2	–	33.0; 35.0
Width of greater trochanter	16	16.1	14.5–18.0	3	13.7	13.0–14.0
Width of head	11	18.9	17.5–20.7	2	–	15.0; 15.5
Width of shaft	15	26.0	24.5–29.5	3	18.7	18.0–19.0
Anteroposterior thickness of shaft	12	11.7	11.0–12.5	3	11.2	10.5–12.0
Thickness of medial condyle	8	17.5	16.0–20.0	2	–	15.0; 15.5
Thickness of lateral condyle	13	25.3	24.0–27.0	2	–	17.0; 23.0
Distance between condyles	16	12.7	12.0–15.5	2	–	11.0; 11.0
Diameter of head	13	15.9	14.0–17.5	2	–	12.5; 14.0

2. Mastoid process: (0) narrow; (1) wide (Chapskii, 1974:301; polarity opposite to Berta and Wyss, 1994:48).

3. Maxilla: (0) convexity anterior to the orbits; (1) short concavity; (2) long concavity (polarity opposite that of Berta and Wyss, 1994:46).

4. Anterior palatine foramina: (0) faintly marked; (1) oval and shallow (Burns and Fay, 1970:372).

5. Interorbital width: (0) less than 25.0% width of skull across mastoids; (1) less than 30.0%, but equal to or greater than 25.0% of mastoid width; (2) equal to or greater than 30.0% of mastoid width (Burns and Fay, 1970:370; Chapskii, 1974:299).

6. Jugular process: (0) poorly developed; (1) well developed.

7. Rostrum: (0) elongate; (1) short, compared with cranium (Chapskii, 1974:300).

8. Diameter of infraorbital foramen: (0) less than diameter of alveolus of maxillary canine; (1) approximately equal to diameter of alveolus of maxillary canine; (2) greater than diameter of alveolus of maxillary canine (polarity opposite that of Berta and Wyss, 1994:47).

9. Anteroposterior length of auditory bullae: (0) greater than distance between them; (1) less than distance between them; (2) about equal to distance between them (Burns and Fay, 1970:382; Chapskii, 1974:300) (unordered character).

Mandible

10. Symphyseal part: (0) continues at least to the middle of the alveolus of p3; (1) reaches only to the alveolus of p2; (2) reaches only to the alveolus of p1.

11. Lateral outline of symphyseal region: (0) square, symphysis thin; (1) rounded, symphysis thick; (2) straight, symphysis thick.

12. Chin prominence: (0) pronounced; (1) absent or weakly outlined.

13. Chin prominence: (0) extends from the anterior or posterior alveolus of p2 to the posterior or anterior alveolus of p4; (1) extends from the anterior alveolus of p2 to anterior alveolus of p3.

14. Maximum height of body of mandible: (0) between p2 and p3; (1) in the middle or at the posterior portion of p2 (Korotky and Ray, 1994:21); (2) situated between alveoli of p4-m1.

15. Diastemata and tooth alveoli: (0) alveoli small, with equal diastemata; (1) alveoli round and large, with equal diastemata between them; (2) alveoli shallow, and diastemata unequal.

16. 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).

17. Retromandibular space: (0) long; (1) short.

Teeth

18. Number of incisors: (0) 3/2; (1) 2/2; (2) 2/1 (Chapskii, 1974:289; polarity opposite that of Burns and Fay, 1970:380).

19. Roots of postcanine teeth (P,p 2–P,p 4): (0) one root, divided partially at the base; (1) two (polarity opposite that of Berta and Wyss, 1994:51).

20. Crowns of postcanine teeth: (0) single cusped; (1) multicusped (polarity opposite that of Berta and Wyss, 1994:51) (reversal to primitive condition, unordered character).

21. Relative dimensions of postcanine teeth: (0) large; (1) small.

22. Relative dimensions of canine: (0) large; (1) small.

23. Basal cingulum of postcanine teeth: (0) well developed; (1) not developed.

TABLE 4.—Matrix of character-state data for monachine taxa and outgroups analyzed. (*=outgroup.)

Species	Character																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Leptophoca lenis</i> *	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	1		
<i>Cystophora cristata</i> *	1	1	1	0	1	0	0	0	0	0	1	1	0	2	1	1	0	2	0	0	1	0	0	2	
<i>Pontophoca sarmatica</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1			—	—	1	0	0	—	0	0	
<i>Monachus monachus</i>	1	1	2	0	0	1	1	0	2	1	2	1	1	2	2	2	1	1	1	1	1	0	0	0	
<i>Monachus schauinslandi</i>	1	1	2	0	0	0	1	1	1	2	1	1	1	1	2	2	1	1	1	1	1	1	0	1	
<i>Monachus tropicalis</i>	1	0	2	1	0	1	1	2	2	2	1	0	1	1	0	2	1	1	1	1	1	0	0	1	
<i>Pliophoca etrusca</i>	0	0	2	0	2	0	0	1	0	1	2	0	0	0	1	0	0	1	1	1	1	0	1	0	1
<i>Callophoca obscura</i>	0	0	2	0	1	0	0	0	0	1	0	1	1	0	2	0	0	1	0	1	0	0	0	1	

Species	Character																							
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
<i>Leptophoca lenis</i> *	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0
<i>Cystophora cristata</i> *	0	1	1	1	1	1	2	1	1	0	0	1	0	0	2	1	0	1	2	0	0	1	1	1
<i>Pontophoca sarmatica</i>	0	—	—	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
<i>Monachus monachus</i>	1	0	1	1	0	1	0	0	2	1	1	2	1	1	0	0	1	1	0	1	1	0	0	1
<i>Monachus schauinslandi</i>	1	0	1	1	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1
<i>Monachus tropicalis</i>	0	0	1	1	0	1	0	0	1	1	1	2	1	1	0	0	1	1	0	1	1	1	1	1
<i>Pliophoca etrusca</i>	1	0	1	1	0	0	1	2	2	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1
<i>Callophoca obscura</i>	1	0	2	1	0	0	1	1	1	2	0	1	0	0	0	0	1	0	1	1	1	0	0	1

24. Number of additional cusps of premolars: (0) two; (1) more than two; (2) no additional cusps (unordered character).

25. Premolars: (0) seated parallel to axis of tooth row; (1) seated obliquely.

26. Upper incisors: (0) form a curved line; (1) form a straight line.

27. Second and third (or first) upper incisors: (0) third larger than second; (1) second larger than third (or first); (2) incisors equal in size (unordered character).

Humerus

28. Lesser tubercle: (0) pronounced; (0) not pronounced (polarity opposite that of Berta and Wyss, 1994:52).

29. Trochlear crest: (0) raised arch-like over coronoid fossa; (1) not separated from coronoid fossa by a distinct lip.

30. Lesser tubercle and head: (0) equal in height or tubercle insignificantly higher than head; (1) tubercle very much higher than head.

31. Lesser tubercle: (0) rounded; (1) extended along the bone's axis; (2) oval.

32. Head: (0) mediolaterally compressed; (1) rounded; (2) flattened proximodistally.

33. Deltoid crest: (0) maximal enlargement is in its proximal part; (1) neither part noticeably enlarged; (2) maximal enlargement is in its middle part.

34. Deltoid crest: (0) shorter than one-half length of the bone, confined to the proximal half of the bone; (1) longer than one-half length of the bone but not reaching coronoid fossa; (2) reaches coronoid fossa (in contrast to that of Berta and Wyss, 1994:52).

35. Coronoid fossa: (0) deep; (1) shallow.

36. Head and trochlea: (0) head wider than trochlea; (1) head almost equal in width to trochlea; (2) trochlea wider than head (polarity opposite that of Berta and Wyss, 1994:53).

Femur

37. Lesser trochanter: (0) present; (1) absent (Berta and Wyss, 1994:54).

38. Condyles: (0) different in size; (1) similar in size.

39. Epiphyses: (0) distal epiphysis wider than proximal by one-fourth to one-fifth; (1) widths of proximal and distal epiphyses about equal; (2) proximal epiphysis wider than distal one.

40. Shaft: (0) minimum width less than or about equal to two-thirds width of proximal epiphysis; (1) minimum width more than two-thirds width of proximal epiphysis.

41. Intertrochanteric crest: (0) well developed; (1) absent or poorly developed.

42. Intertrochanteric crest: (0) reaches lower than head; (1) short, ends on same level as distal edge of head or fovea capitis.

43. Head: (0) rounded; (1) flattened in proximodistal direction; (2) compressed in mediolateral direction.

44. Intercondylar area: (0) narrow, deep; (1) wide, flattened.

45. Greater trochanter: (0) maximum width in its middle part; (1) maximum width in its proximal part (Koretsky, 1987:75).

46. Head and greater trochanter: (0) same height; (1) greater trochanter higher than head.

47. Neck: (0) long, slender; (1) short, wide.

48. Shaft: (0) minimum width in its proximal part; (1) minimum width in its middle part.

RESULTS

The analysis of these taxa using Hennig86 and the 48 unweighted characters shown above produced a single tree, 45 steps long, with consistency index of 0.84 and retention index

of 0.83 (Figure 5). The matrix of character-state data for six species of fossil and living monachine seals is given in Table 4, together with data on two outgroup taxa. *Leptophoca lenis* is representative of the oldest known Phocinae (Repenning and Ray, 1977), and *Cystophora cristata* represents the Cystophorinae (as mentioned above).

The nodes of the tree corresponding to taxa recognized by us are indicated; only one new name, *Pontophoca sarmatica*, has been added to those previously recognized: inclusion of *Pontophoca sarmatica* within the Monachinae supports the recognition of the monotypic genus *Pontophoca*. The nodes of the cladogram shown in Figure 5 are supported by the following character transformations:

Node 1. (Subfamily Monachinae) one branch forms the possibly paraphyletic subfamily: 3(2); 18(1); 32(1.2).

Node 2. 41(1) (intertrochanteric crest of the femur poorly developed).

Node 3. 43(1) (head of the femur flattened in dorsoventral direction).

Node 4. (Genus *Monachus*): 7(1); 16(2); 17(1); 37(1); 38(1). Also, character 10(2) is homoplasious in *M. tropicalis* and *M. schauinslandi*; character 35(1) shares the homoplasy of *L. lenis*.

Node 5. 6(1); 9(2); 36(2). Also, character 45(1) shares the homoplasy of *Callophoca obscura* and *Leptophoca lenis*.

As can be seen from the tree (Figure 5), the assignment of *Pontophoca* to the Monachinae is confirmed. Thus, the characters and their polarities that we used on every level of taxonomy are working. Moreover, *Pontophoca sarmatica* (consisting of a new description of the mandible and humerus) is a closely related sister group to *Monachus* and other Monachinae.

In contrast to Berta and Wyss (1994:43), we treated *Monachus schauinslandi* as a not-so-close sister taxon (Flynn, 1988). At the same time, we agree with their conclusion that the subfamily Monachinae is monophyletic (tribe Lobodontini not considered). In this subfamily we include just the three Holocene species of *Monachus*, as well as two Pliocene fossil genera (*Callophoca* and *Pliophoca*) and one middle Miocene genus (*Pontophoca*).

Conclusions

The family Phocidae separated from Carnivora, probably in the early Oligocene (Davies, 1958), became widely distributed during the middle and (especially) late Miocene, and practically ceased to exist in the European part of the former USSR (Black Sea region) in the early Pliocene (Chapskii, 1955, 1970, 1971, 1975; Repenning et al., 1979). Shared derived features of the morphology of the skull, and the relatively early geological age of these Miocene seals, allow the conclusion that these animals are broadly ancestral forms of presently living true seals. A direct relationship between known Miocene seals and modern genera is very uncertain, however. Probably, together with other Phocidae, monachine seals are descendants of some Oligocene or even Eocene semiaquatic mustelid. It should be

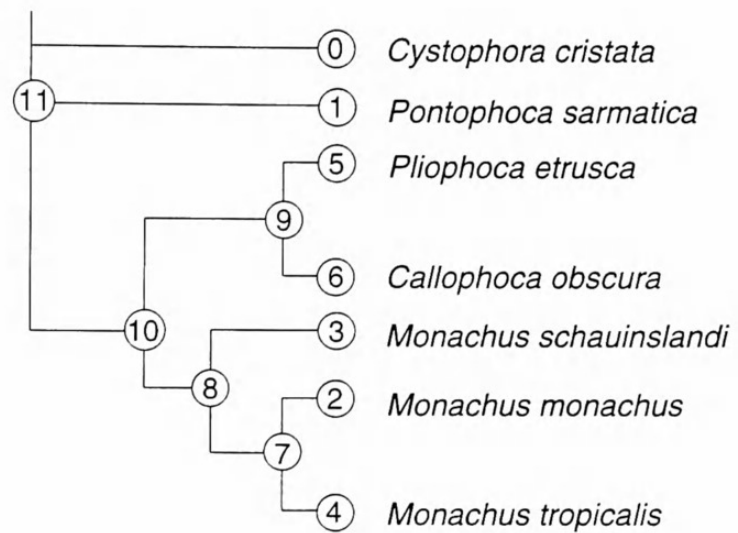


FIGURE 5.—Single most-parsimonious tree of monachine taxa and two outgroups, generated by Hennig86 using 48 unweighted characters. Tree length, 45 steps; consistency index, 0.84; retention index, 0.83.

pointed out, however, that the only Oligocene representatives of this family yet found are two fragments of femora from the late Oligocene of South Carolina (see Koretsky and Sanders, 2002). The most ancient fossil phocids known from good, informative material are from the early middle Miocene (Holec et al., 1987; Koretsky and Holec, 2002). By that time these animals were fully recognizable members of subfamilies to which modern pinnipeds belong.

Middle Miocene seals did not differ very much from modern species, and in most morphological characteristics they are not especially similar to any of the terrestrial or semiaquatic carnivorans that might have been the ancestors of phocids. The analysis of the dentition allows us to conclude that monachines have long been separated from the common stem of pinnipeds and formed a separate phylogenetic branch that has existed until now.

Clearly, the geographical and geological distributions of taxa are of considerable interest for biostratigraphy and for correlations of middle Miocene to early Pliocene marine deposits of Eurasia. At present, however, in view of insufficient investigation of Western European and Asiatic materials, these findings may be used mainly for more precise control of the geological age of the true seals in the European part of the former USSR, and of the stratigraphic distribution of Monachinae in the middle Sarmatian to Pontian of this region.

Moreover, the majority of problems of systematics and morphology of Monachinae are not solved completely (Barnes et al., 1985). In this respect the present study is of a preliminary character that opens up new perspectives in investigations of the groups of predators analyzed. We hope that the results presented herein will draw the specialist's attention and will allow the investigation, from new and different viewpoints, of many problems of classification of both ancient and modern representatives of the subfamily Monachinae.

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