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FIRST RECORD OF FOSSIL CYSTOPHORINAE (CARNIVORA, PHOCIDAE): MIDDLE MIOCENE SEALS FROM THE NORTHERN PARATETHYS

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Abstract. Despite a long history of phocid studies, no fossil members of the Subfamily Cystophorinae have ever been described. New fossil material from the Middle Sarmatian (11.2-12.3 Ma) in the Paratethyan Basin of Ukraine allows emended diagnoses and redescriptions to help clarify phylogenetic relationships within the Family Phocidae. After cladistic and morphological analyses of the material, a new genus (*Pachyphoca*) was erected, with two new species of extinct fossil true seals (*Pachyphoca ukrainica* and *Pachyphoca chapskii*), belonging to the Subfamily Cystophorinae. This new material shows exceptional pachyosteosclerotic bones, which is uncommon for the family as a whole. The new Miocene genus shares numerous characters with several Recent species of *Cystophora* and *Mirounga*, providing the first opportunity to study sexual dimorphism of limb bones and mandibles in the Subfamily Cystophorinae. Sexual dimorphism in postcranial bones and mandibles in living members of Cystophorinae is more obvious than in other representatives of true seals. Examination of anatomical traits demonstrated that both new species are more primitive and better adapted for terrestrial locomotion than any living representatives of Cystophorinae. The smaller *Pachyphoca ukrainica* is more adapted to terrestrial locomotion than its larger relative, *P. chapskii*. Phylogenetic analysis suggests that seals with 10 incisors (Phocinae) are more primitive than those with 8 (Monachinae), and that Monachinae are more primitive than seals with 6 incisors (Cystophorinae). These findings indicate that the Subfamily Cystophorinae includes not only elephant and hooded seals, but also the two new Middle Sarmatian pachyosteosclerotic seals.

Riassunto. Nonostante la lunga storia dello studio dei focidi, non era mai stato descritto un membro della Sottofamiglia Cystophorinae. Nuovo materiale fossile dal Sarmatiano Medio (11.2-12.3 Ma) del Bacino della Paratetide dell'Ucraina permette ora di emendare diagnosi e descrizioni in modo da aiutare a chiarire i rapporti filogenetici all'interno della famiglia Phocidae. In seguito all'analisi morfologica e cladistica del materiale è stato istituito un nuovo genere (*Pachyphoca*), con due nuove specie di foche in senso stretto estinte (*Pachyphoca ukrainica* e *Pachyphoca chapskii*), appartenenti alla Sottofamiglia Cystophorinae. Questo nuovo materiale mostra ossa pachiosteosclerotiche eccezionali, inusuali per l'intera famiglia. Il nuovo genere del Miocene condivide numerosi caratteri con diverse specie Recenti di *Cystophora* e *Mirounga,* ed offre la prima opportunità di studiare il dimorfismo sessuale delle ossa degli arti e delle mandibole nella Sottofamiglia Cystophorinae. Il dimorfismo sessuale nelle ossa postcraniali e nelle mandibole è maggiormente evidente nei membri attuali di Cystophorinae rispetto agli altri rappresentanti delle foche in senso stretto. L'analisi dei tratti anatomici ha dimostrato che entrambe le nuove specie sono più primitive e meglio adattate per la locomozione terrestre di qualsiasi altro rappresentante vivente di Cystophorinae. *Pachyphoca ukrainica*, più piccola, è meglio adattata alla locomozione terrestre rispetto alla specie più grande *P. chapskii*. L'analisi filogenetica suggerisce che le foche con 10 incisivi (Phocinae) sono più primitive di quelle con 8 (Monachinae), e che i Monachinae sono più primitivi delle foche con 6 incisivi (Cystophorinae). Questi ritrovamenti indicano che la Sottofamiglia Cystophorinae include non solo elefanti marini e foche dal cappuccio, ma anche le due nuove foche pachiosteosclerotiche del Sarmatiano Medio.

Introduction

The study of fossil seals of the northern Black Sea region (Fig. 1A) began in the mid 19th century with work by Eichwald (1850, 1853) and Nordmann (1860), and was continued by Andrusov (1893), Alekseev (1924), Simionescu (1925), Macarovici and Oescu (1941), McLaren (1960), Kirpichnikov (1961), Koretsky (2001), and Koretsky and Grigorescu (2002). A diverse mix of true seals (Phocidae) has been reported in these studies, but no members of the Otariidae.

Despite the abundance and broad distribution of Phocidae, many problems persist in interpreting the systematics of this group, with the taxonomic history of *Cystophora* being especially confusing (Koretsky & Holec 2002). Gray (1866) and Trouessart (1897) divided Phocidae into three subfamilies: Phocinae, Monachinae

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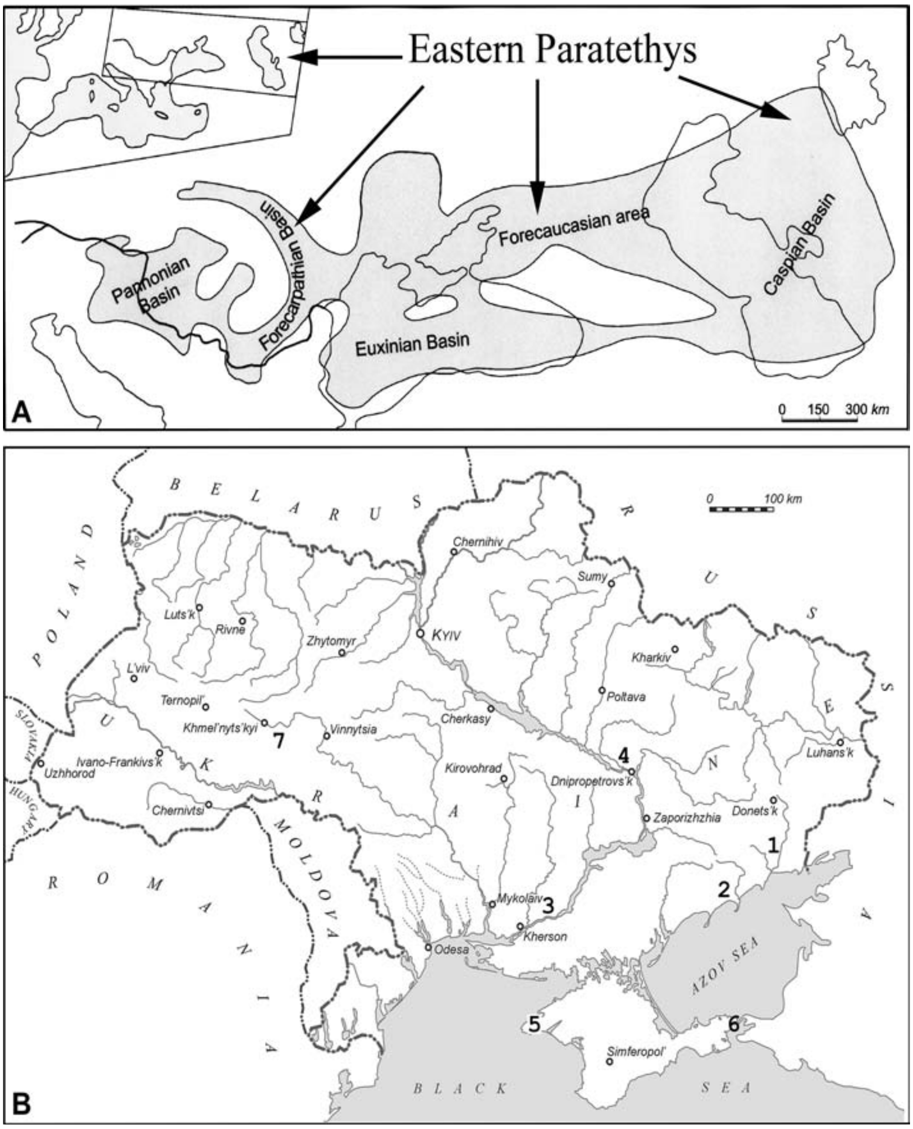


Fig. 1 - A) Paleogeographic sketch-map of the Eastern Paratethys for the duration of the Sarmatian Sea (12.3 – 9.36 Ma) with reduced salinity and strong endemism (map modified after Ivanov et al., 2007). B) Generalized geographical map of Ukraine showing the principal fossil localities of the genus *Pachyphoca* from Middle Miocene (Sarmatian) of Ukraine mentioned in the text:
1) Khomutovo Village (47°16'11.4"N 38°09'36.1"E).
2) Gnylozubovo (47°06'56.3"N 37°31'65.8"E).
3) Zolotaya Balka (47°22'46.9" N 33°58'23.5"E.).
4) Zheltokamenka (47°41'34.2"N 33°50'06.8"E).
5) Tarchankut (45°20'46.9"N 32°29'23.5"E).
6) Uzunlar (45°15'80.1"N 36°22'27.0"E).
7) Gritsev (49°58'05.2"N 27°10'03"E).

and Cystophorinae. While there has never been universal acceptance of this classification, it was followed by many subsequent workers including Ognev (1935), Grassé (1955), Scheffer (1958), King (1964) and Chapskii (1974). Characters supporting the existence of three subfamilies mainly derive from analyses of cranial, dental and pelage morphology. In particular, a comprehensive analysis of suprageneric systematics is found in the studies of Chapskii (1955, 1961, 1971, 1974). He described diagnostic cranial characters (number of incisors, shape of maxilla, form of anterior palatal foramina, and some others) supporting the separation of true seals into three subfamilies, which he in turn divided into tribes and sub-tribes.

Therefore, seals with six incisors belong to the Subfamily Cystophorinae (Gill 1866), comprising the genera *Cystophora* Nilsson, 1820 (hooded seal) and *Mirounga* Gray, 1827 (elephant seal or sea elephant). This classification is based on several synapomorphies between *Cystophora* and *Mirounga*: 1) reduction of the incisors to 2/1; 2) possession of an inflatable nasal sac; 3) non-differentiated shape (homodonty) of the postcanine teeth; 4) shape and direction of mastoid process; and 5) shape of the maxilla. Allen (1880), followed by Simpson (1945), created an additional subfamily, Lobodontinae, for southern seals that Chapskii and previous workers regarded as a tribe within Monachinae.

Major divergences from the three-subfamily scheme began with the work of King (1966) and Burns and Fay (1970). Chapskii (1974) also proved that King's (1966) hypothesis of reassigning the genus *Cystophora* from the Subfamily Cystophorinae into the Subfamily Phocinae and the genus *Mirounga* into the Subfamily Monachinae is untenable. Muizon (1982) accepted the systematics of King, and returned to dismissing the Subfamily Cystophorinae as a whole. The correctness of Chapskii's concept was corroborated by Robinette and Stains (1970) and Polly (2008) in their comparative studies of the pinniped calcaneus, emphasizing that it is inadmissible to taxonomically separate the hooded seal and the sea elephant. Later, this point of view was also supported by Anbinder (1980:76): "... 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". However, recent molecular and karyological studies do not support this point of view and place *Cystophora* into the Subfamily Phocinae and *Mirounga* into the Subfamily Monachinae as separate clades (Bininda-Emonds & Russell 1996; Ärnasson et al. 2006; Fulton & Strobeck 2010). Even molecular biologists conclude the need for a re-evaluation of pinniped taxonomy (Higdon et. al. 2007). Our morphological data indicates that the new fossil seals from the Middle Miocene (*Pachyphoca*) have a combination of cystophorine and miroungini characters, re-opening the discussion once again about the subfamilial relationships of seals.

King (1964), Burns and Fay (1970), Carr and Perry (1994), and later Ärnason et al. (2006) assigned *Cystophora* to the Tribe Cystophorini, while McKenna and Bell (1997) included *Cystophora* in the Tribe Phocini. Even today, the exact taxonomic relationships of seals within Phocidae are still controversial (Wyss 1994; Koretsky & Grigorescu 2002; Koretsky & Holec 2002). Various scientists either separate phocids into: only one subfamily, Phocinae (Wyss 1988; McKenna & Bell 1997); two subfamilies, Phocinae and Monachinae (Burns & Fay 1970; Muizon 1982, 1992; King 1983, 1989; Wyss 1994; Perry et al. 1995; Bininda-Emonds & Russell 1996; Berta & Sumich 1999); or do not separate true seals into subfamilies at all (Sokolov 1979; Wozencraft 1989). Therefore, this study will continue to follow the "classical" classification of Scheffer and Chapskii by placing *Cystophora* into the Subfamily Cystophorinae – the six-incisor seals.

Because of the paucity of cranial remains, the study of fossil seals has been based mainly on the use of postcranial characters, specifically the morphology of individual dissociated bones (mainly the femur or humerus). Interpretation of postcranial elements is aided by analysis of specific ecological niches that are reflected in bones of the postcranial skeleton and mandible of Recent seals (Koretsky 2001). This has allowed separation of modern phocines into morphological groups based on characters from the most common dissociated elements (more than 1000 bones, mainly mandible, humerus, and femur). In addition, other publications show associated parts of seal skeletons (Muizon 1981; Koretsky 2001; Cozzoul 2001; Koretsky & Grigorescu 2002; Koretsky & Ray 2008) that also can be used as a foundation of alpha classification. This information was the basis to associate individual bones from the Middle Sarmatian of Ukraine into two taxonomical units. Another hurdle for finding cranial fossil seal material (as for today, only 10 known fossil seal skulls have ever been found and described) is that the survival rate of fossil seal skulls is extremely low due to the paper-thin thickness of skull bones. A similar condition appears in otaridae, but fossil otaridae skull bones are much denser and have a higher survival rate.

Due to the great rarity and usually unsatisfactory preservation of postcranial, and especially cranial, fossil remains of seals, compared to terrestrial carnivores, this remains one of the least investigated and most complicated groups of large mammals. This study focused on describing previously unknown extinct representatives of Cystophorinae and clarifying their relationships with other seals of the Family Phocidae and its four subfamilies (Phocinae, Monachinae, Cystophorinae, and Devinophocinae).

Among Neogene marine mammals, the remains of phocine seals (in comparison with monachines and cystophorines) are relatively numerous in the Middle Sarmatian-Maeotian deposits of the Central and Eastern Paratethys (Fig. 1). Such remains are found in the Ukraine, Moldavia, Romania, Kazakhstan, Slovakia, Austria, Hungary, and even in Turkey (Eichwald 1850; Nordmann 1860; Alekseev 1924; Simionescu 1925; McLaren 1960; Grigorescu 1977; Grigorescu et al. 1986; Koretsky 1986, 1987a, b, 2001; Koretsky & Grigorescu 2002). In spite of the abundance and broad distribution of true seals, many problems persist in interpreting the systematics of these animals (Koretsky 1987a). Among the three "traditional" subfamilies of Phocidae (Phocinae, Monachinae, Cystophorinae) and the more recently described subfamily Devinophocinae (Koretsky & Holec 2002), fossil remains of Cystophorinae have never been found, illustrated or described. The extensive investigations of fossil seals from the Middle Miocene deposits of Ukraine now allow a more accurate diagnosis of the Subfamily Cystophorinae, and comparisons between this taxon and other genera of the Family Phocidae can help determine the phylogenetic relations among the subfamilies.

This study will improve the classification and knowledge of the general morphology of true seals, with special emphasis on previously unknown fossil representatives of the Subfamily Cystophorinae from the Middle Sarmatian (12.3-11.2 Ma) of the Eastern Paratethys, notably in the northern Black Sea littoral region of the Ukraine. Taxonomic characters used for the classification of Phocidae (Koretsky 2001; Koretsky & Grigorescu 2002; Koretsky & Ray 2008) will be analyzed in order to determine which subfamily our two new species belong in and the relationships they have with other true seals. Thus, the new fossil evidence presented in this study also can be used to determine the relationships within the Subfamily Cystophorinae, and provides a unique opportunity to study sexual dimorphism of the limb bones and mandibles in living members of this subfamily.

Abbreviations

Specimens from the following institutions and departments have been examined for this manuscript:

AMNH, American Museum of Natural History, New York, USA.

NMNHU-P, National Museum of Natural History at the National Academy of Science of Ukraine, Kiev, Ukraine.

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

ZIN, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

In reference to bones:

L. – left; **R.** - right, **m.** – muscle.

Northern Black Sea marine mammal localities

The Mediterranean, Black, Caspian and Aral Seas are remnants of the ancient Tethys seaway which, during much of Miocene time (23 to 5.2 Ma), extended continuously from Western Europe into Central Asia (Fig. 1A). The northern shore of this seaway extended across the area that is now southern Ukraine. Sediments deposited in, and on the shores of, this ancient seaway are rich in the remains of fossil mammals. Near the present northern shore of the Black Sea are thick sections of predominantly marine strata, with several localities (Tarchankut, Kerch, Odessa) having an abundance of fossil marine mammal remains, including pinnipeds (seals) and cetaceans (whales, porpoises), as well as some continental deposits with land mammal remains (Pidoplichko 1956; Dubrovo & Kapelist 1979; Koretsky 1986, 1987).

Farther to the north, deposits are predominantly continental with remains of land mammals preserved at many localities (Sevastopol, Velikomichailovka, Berislav, Grebeniki, Augustovka, Cubanka). The several localities (Gricev, Zolotaya Balka, Zheltokamenka, Tyaginka; Fig. 1B) where land mammals and marine mammals are associated (Koretsky 2001) are especially important.

At certain intervals during the Neogene, the fossil record shows that the land mammalian fauna of the northern continents was quite cosmopolitan, indicating periods when it was possible for land mammals to disperse freely between Europe and Asia as well as to North America via Beringia (Bernor et. al. 1990). Naturally, the dispersal pattern for marine mammals is very different, as fossil seals and whales of the Tethys could range across the North Atlantic to eastern North American coastal waters (Koretsky & Barnes 2006; Koretsky & Ray 2008; Koretsky et al. 2012). Fossil seal taxa found in Paratethyan localities across Europe also have been discovered in deposits along the eastern seaboard of North America, with terrestrial mammalian association at some localities. These associations give the potential for two cross-checking systems (one through land records via Asia, and the other through marine records via the North Atlantic) of biochronological correlation between Eurasia and North America (Koretsky et al. 2012).

The geographic ranges of some modern pinniped species are very large and often extend through several zoogeographical regions. Likewise, fossil species are widespread. True seals (Phocidae) are of particular zoogeographic interest as their 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 in the Transcaucasus and Kazakhstan, with the most numerous finds from the northern littoral region of the Black Sea in the Ukraine and Moldavia from the Middle Sarmatian (12.3 – 11.2 Ma). In Western and Central Europe, remains of fossil seals are regularly found in France (Friant 1942, 1947; Ginsburg & Janvier 1975, 1999), The Netherlands (Springhorn 1978; Koretsky & Peters 2008; Koretsky et al. 2012), Belgium (Koretsky & Ray 2008), Denmark (Koretsky, in press), Austria (Zapfe 1937), Hungary (Koretsky 2003), Romania (Grigorescu 1977; Koretsky & Grigorescu 2002), Czech Republic (Holec et al. 1987; Holec & Sabol 1996; Holec et al. 1997), and Slovakia (Koretsky & Holec 2002). Isolated finds are known from Turkey (Koretsky, unpublished data), Italy (Tavani 1942) and Malta (Bianucci et. al. 2011). Fossil Miocene seals are also known in the eastern United States (Koretsky and Ray, 2008), with the most primitive being *Leptophoca lenis* True, 1906, from the Middle Miocene of Maryland and Virginia (Ray 1976; Koretsky 2001; Koretsky et al. 2012) and recently discovered in North Africa in Libya (Koretsky and Domning, in press).

Many marine and continental Neogene deposits have not been thoroughly studied. Particularly insufficient are studies of Neogene marine deposits of the Ukraine, especially their stratigraphic correlation with continental deposits of adjacent and distant regions. This study will concentrate upon Miocene (23.8 – 5.2 Ma) marine deposits in southwestern Ukraine, which are the most extensively represented, but least characterized geologically. The thick marine layers exposed in this region are, almost as a rule, not very rich in fossil animal remains other than mollusks. In similar-aged continental deposits of the Ukraine, some large Miocene hipparion faunas have been found, suggesting that southwestern Ukraine is an important location for paleozoological investigations.

Since Alekseev (1924), a significant fossil seal collection from Eastern Paratethys has accumulated in Kiev's National Museum of Natural History at the National Academy of Science. These fossils have been referred to as *Phoca* sp. (Pidoplichko 1956; Dubrovo & Kapelist 1979). However, this collection of very pachyosteosclerotic postcranial elements must be revised and "redescribed" in order to broaden general knowledge and understand the specific distribution of cystophorines and their relationship with other subfamilies. This revision will yield a much more precise and detailed diagnosis of the material and delineate the distribution of this taxon. The information presented below on geographical locations, their geological age, collec-

Characters	*Pachyphoca*	
	ukrainica	*chapskii*
Maximal length	118.5	121.0
Anteroposterior diameter of cavitas glenoidalis	17.5; 18.0	19.0
Transverse diameter of cavitas glenoidalis	21.0; 21.0	30.0
Maximal thickness of sapula in its spine	21.0; 19.0	24.5
Width of cervix	21.5; 24.0	26.5
Transverse width of body	60.0	75.5

Tab. 1 - Measurements (mm) of scapulae.

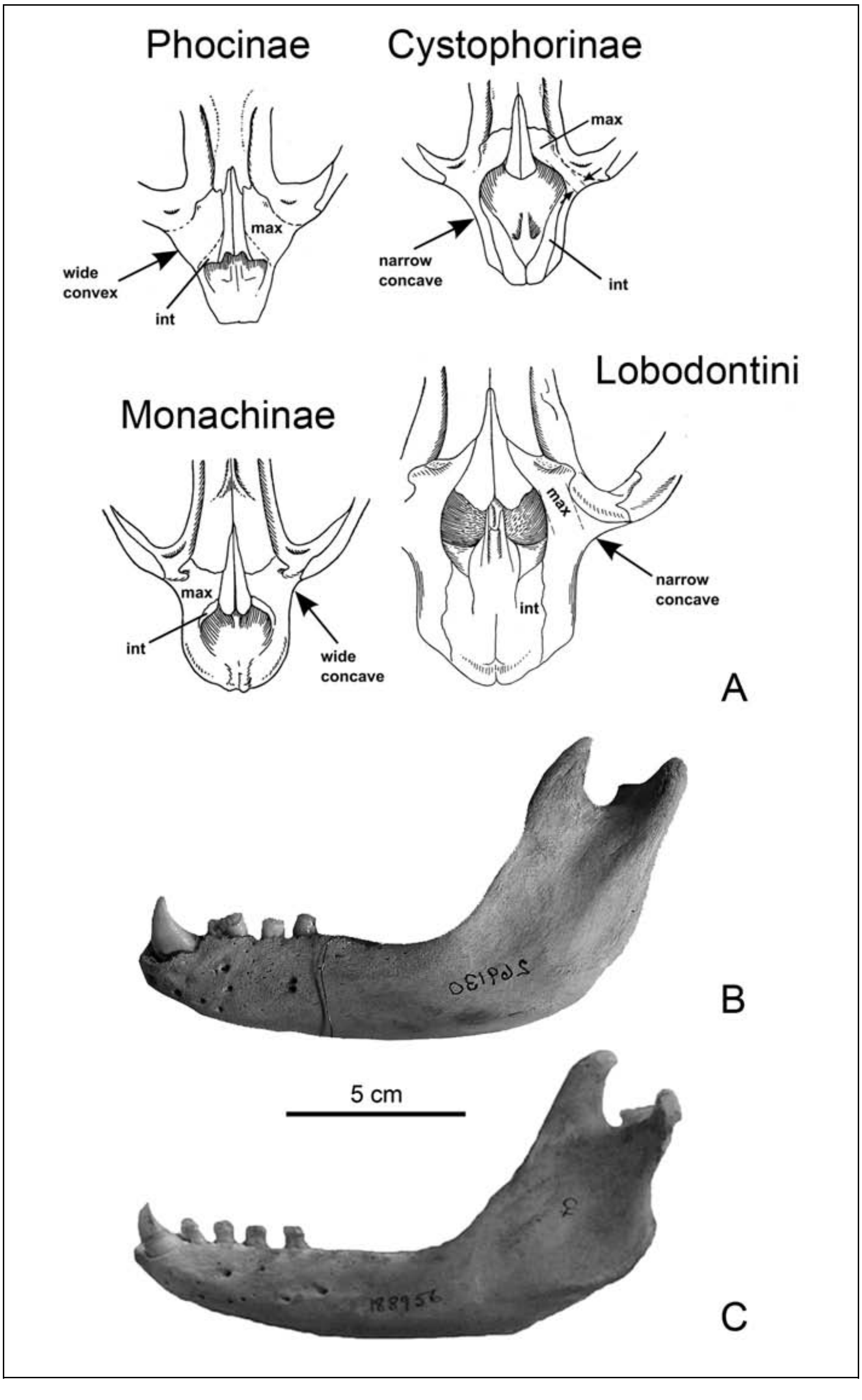


Fig. 2 - Rostral part of Recent seal maxillae in A) Dorsal views (modified after Chapskii, 1974). Labial views of *Cystophora cristata* mandibles: B) male (USNM 269130; reversed) and C) female (USNM 188956). Abbreviations: int, nasal process of intermaxilla; max, maxilla.

tors, and institutions where material is stored was compiled using published data (Pidoplichko 1956; Dubrovo & Kapelist 1979).

Earlier, Koretsky (2001) showed that there are several localities (Gricev, Chomutovo, Zolotaya Balka, Zheltokamenka, and Tyaginka) in Ukraine where seal bones with pronounced pachyosteosclerosis are especially noteworthy (Fig. 1B). These and others are as follows:

Zheltokamenka: Dnepropetrovsk region, Apostolovo district, Zheltokamenka village on Zeltenkaya River, limestone quarry 8-10 m deep; Middle Sarmatian (Bessarabian; 12.3 – 11.2 Ma); expeditions of Pidoplichko 1938, 1940; Bezuglui 1953-54; and Semenov 2001; collection of NMNHU-P. Other mammalian remains, besides pinnipeds, such as *Machairodus*, *Mastodon*, *Achtiaria* and *Cetotheium* were found in this quarry in the 1940s. Some bones of the marine mammals (seals and whales) are very much rolled and abraded, which means that they were deposited in shallow water near the shore (shelf zone).

Khomutovo Village: Donetsk region, Novoazov district; limestone quarry 6-7 m deep; Upper Miocene (Pontian); collection of 1959; NMNHU-P.

Tarchankut: Crimea region, Chernomorsk district, Tarchankut Peninsula, 7 km south-east of village of Olenevka; Middle Sarmatian; collections of Antoniuk 1975-1986; and Koretsky 1983-1986; ZIN, NMNHU-P.

Uzunlar: Crimea, Kerch Peninsula; Middle Sarmatian; collection 1952; NMNHU-P.

Zolotaya Balka: Cherson region, Novovorontsovo district, right bank of the Dnieper River, south of city of Nikopol; limestone quarry north of village, upper layer, 7 m deep, Middle Sarmatian; collection of Bezuglui 1952; NMNHU-P.

Gnylozubov: Donetsk region, Mariupol district, left bank of Kalmius River; village of Bobrinets; limestone quarry, Middle Sarmatian; collection of 1936; NMNHU-P.

Gritsev: Chmelnitsky region, Shepetovka district, 3 km west of village of Gritsev; karst deposits in limestone quarry on right bank of Chomora River; Middle Sarmatian; collection of Semenov 1983-1985; NMNHU-P.

Novovorontsovo: Cherson region, Novovorontsovsky district; clay; Middle Miocene; collection of Bezuglui 1952; NMNHU-P.

Nikolaev: Nikolaev region, vicinity of city of Nikolaev; Early Sarmatian; collection of 1935; NMNHU-P.

The material was collected and gradually accumulated during many years (1932 – 2003) of excavations carried out by expeditions of the Department of Paleontology of the NMNHU-P. The collection includes 58 individual postcranial bones representing the new genus and two new species of the Subfamily Cystophorinae, all housed in the Department of Paleontology of the NMNHU-P.

Systematic Paleontology

Superfamily Phocoidea Smirnov, 1908
Family Phocidae Gray, 1825
Subfamily Cystophorinae Gray, 1866

Type Genus: *Cystophora* Nilsson, 1820; present distribution: Arctic and subarctic North Atlantic oceans; circumpolar in subantarctic region.

Distribution: Middle Miocene (Sarmatian) in Eastern Paratethys; Recent in Arctic and Antarctic Oceans.

Emended Diagnosis: Large seals (length up to 5 m) with six incisors (I=2/1; in contrast to Monachinae with 8 incisors and Phocinae with 10 incisors); paroccipital process of skull poorly developed (in contrast to Devinophocinae); anteroposterior length of auditory bulla less than distance between bullae (in contrast to Phocinae and Devinophocinae); infraorbital process present; interorbital space wide; interorbital width less than 30%, but equal to or greater than 25% of mastoid width (as in Devinophocinae); anterior palatal foramina oval (as in Devinophocinae) and shallow; preorbital part of maxilla with narrow concavity (similar to Lobodontini; in contrast to Monachinae, Phocinae, and Devinophocinae). Upper second incisors tend to enlarge rather than first incisors.

Mandibular chin prominence absent; alveoli of p4 bigger than alveoli of m1; coronoid process very narrow and turned caudally, especially in male; condyloid process not well marked; symphysis reaches posterior alveolus of p1; mandibular notch very narrow; retromandibular space elongated (~3.5 cm in females and ~ 3 cm in males).

Middle of internal crest of humeral trochlea rises wave-like over coronoid fossa; widths of distal and proximal epiphyses almost equal.

Medial and lateral femoral condyles almost equal in size; lesser trochanter present in males; minimum width of femoral shaft 1.4-1.9 times width of proximal epiphysis.

Included Genera: *Cystophora* Nilsson, 1820; *Mirounga* Gray, 1827.

Comparisons. The interorbital portion of the frontal bone in Cystophorinae (as in Devinophocinae), but in contrast to Phocinae, is widened (apomorphic or derived condition), even to a greater degree than in Monachinae. On the anterior part of the frontal bone, the origin of the temporal crest is present, in contrast to the other three subfamilies. The part of the maxilla (Fig. 2A) situated between the nasal meatus and orbits has a narrow concavity, as in Devinophocinae, and contrasts with Phocinae (with a short convexity) and Monachinae (with a long concavity). In contrast to the other three subfamilies, an interval is absent between the external auditory meatus and the anterior crest of the mandibular fossa. The lacrimal bone has an antero-orbital process strongly protruding to a greater degree than in Monachinae. The convexity of the mastoid is not robustly expressed and is directed cranio-caudally. The foramen ovale is ventrally covered by the presphenoid bone, and laterally by the postglenoid process. The

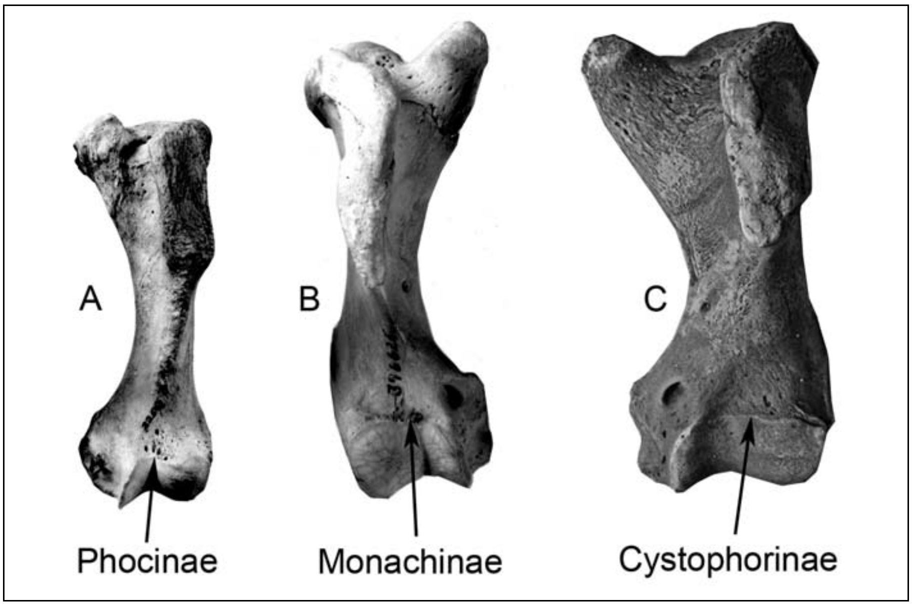


Fig. 3 - Tip of the arrow points to the middle of the humeral trochlear crest; A) in Phocinae, at the level of the coronoid fossa; B) in Monachinae, arch-like elevated over the coronoid fossa; C) in Cystophorinae, wave-like raised over the coronoid fossa.

antero-inferior process of the jugal bone is located almost at the level of the middle of the orbit, in contrast to the other subfamilies. The anterior palatal foramina are oval as in Devinophocinae and tend to disappear as in Monachinae.

The upper second incisors, in contrast to the other subfamilies, are much bigger than the first ones, and almost reach the size of the canines. The teeth are very small in comparison to the size of the mandible, p4 is bigger than m1, but the largest tooth is p3; P2, p2 are single-rooted; p2 – m1 have fused roots, and the alveoli are shallow.

In Cystophorinae, the body of the mandible, and especially the ramus, are very unique, compared to the other subfamilies. The mandibular body is very thick, but not high. The ramus of the mandible is also very thick, wide, and high in contrast to the other subfamilies, as is the absence of the mandibular chin prominence. The condyloid process is especially short, narrow, and not pronounced. Although we believe that Cystophorinae and Mirounga belong to the same taxon, some ecomorphological characteristics do differ, such as the Cystophorine coronoid process of the mandible being very sleek and turned caudally, the presence of a very narrow mandibular notch, and an elongated retromandibular space, compared to those found in *Mirounga*.

The middle of the humeral crest of the trochlea (Fig. 3) in Cystophorinae is wave-like and elevated over the coronoid fossa, in contrast to that in Phocinae, which is at the level of the coronoid fossa, or in Monachinae, where it is arch-like and concavely raised over the coronoid fossa.

The femoral condyles are almost equal in size (but less so than in Monachinae), in contrast to Phocinae. The minimum width of the diaphysis is almost twice as great as the width of the proximal epiphysis.

Discussion. Other taxa have been suggested to be closely related to members of Cystophorinae. Zapfe (1937) proposed that the representatives of the genus *Miophoca* are undoubtedly ancestral to Cystophorinae. While Simpson (1945), Thenius (1950, 1952), King (1964), and McKenna and Bell (1997) assigned *Miophoca vetusta* to the Subfamily Monachinae, other investigators (Ray 1977; Muizon 1982; Savage & Russell 1983) did not mention this taxon at all in their reviews of the Tertiary seals of Europe. Thenius (1950, 1952), without any explanation, transferred *Miophoca vetusta* to another genus, *Pristiphoca*. Later, Holec et al. (1987, 1996) supported this opinion with a proposal to reassign genus *Miophoca* to the Tribe Cystophorini. However, the distinctive morphological mandibular characters (Koretsky et al. in press), especially the similar degree of the condyloid angle (12°-15°), shows that *Miophoca vetusta* clearly belongs to the Subfamily Monachinae.

Sexual Dimorphism in *Cystophora cristata*

In prior studies of true seals, sexual dimorphism was only examined on cranial material of Recent Phocinae (Ognev 1935; Chapskii 1952, 1967; Khuzin 1967). However, fossil remains of seals usually consist of isolated limb bones, mainly the femur and humerus. The lack of fossil cranial material makes the use of postcranial elements even more important in the proper classification of specimens and in examining the sexual variability (dimorphism) of various bones. Studies determining ontogenetic and sexual variation based on postcranial elements of modern and fossil seals were done by Gadjiev 1982, Koretsky 1987a, Van Bree and Erdbrink 1987 and Koretsky 2001.

Characters	*Pachyphoca*				*Cystophora cristata*					
	ukrainica			*chapskii*	female			male		
	n	M	OR		n	M	OR	n	M	OR
Absolute length	2		85.0; 89.0	-	4	148.2	143.0-153.3	3	153.1	152.0-154.0
Length of deltoid crest	2		55.0; 56.0	-	4	81.0	78.0-83.9	3	83.3	82.6-83.4
Height of head	4	20.8	19.5-23.0	-	4	30.4	28.9-31.5	3	30.7	28.7-34.5
Height of trochlea	3	15.0	14.0-16.0	21.0	4	29.5	28.0-31.0	3	27.8	27.7-28.0
Width of head	4	23.3	22.0-25.0	-	4	34.5	34.0-35.1	3	35.9	34.6-38.0
Width of deltoid crest	2		19.5; 20.0	-	4	36.8	31.0-41.5	3	45.5	44.1-50.0
Width of distal epiphysis	2		33.0; 34.5	-	4	57.3	55.0-60.0	3	57.2	56.7-63.0
Width of proximal epiphysis	2		29.0; 32.0	-	4	53.8	49.5-58.0	3	56.0	53.5-60.0
Width of trochlea below	3	18.0	17.0-19.0	-	4	31.3	30.6-32.0	3	33.1	30.6-38.0
Width of trochlea, frontal view	3	21.3	20.0-23.0	49.5	4	31.7	28.0-34.0	3	35.9	35.0-37.7
Transverse width of diaphysis	4	18.3	16.5-21.5	27.0	4	23.6	23.2-24.0	3	23.9	22.2-27.0
Thickness of proximal epiphysis	2		29.0; 35.0	-	4	49.1	44.7-53.5	3	53.9	53.7-68.0
Thickness of medial condyle	3	16.3	15.5-17.0	23.0	4	25.0	24.0-26.1	3	25.7	24.1-27.0
Thickness of lateral condyle	3	15.2	15.0-5.5	20.0	4	28.2	26.4-30.0	3	27.8	27.0-31.0
Diameter of diaphysis with deltoid crest	2		31.5; 33.0	-	4	53.8	53.0-55.0	3	58.4	53.2-66.0

Tab. 2 - Measurements (mm) of humeri.

Sexual dimorphism in the postcranial bones and mandibles of the Subfamily Cystophorinae (Fig. 4; Tabs 2, 6), especially in *Mirounga*, is more obvious than in other true seals. Prior to this study, there have never been any fossil remains found and described within Cystophorinae. The new fossil postcranial bones (58 individual bones) examined in this study show obvious dimensional and morphological diversity and fell into two size classes that do not fit previously described patterns of individual, ontogenetic, or sexual variations. Previously, Koretsky (1987a, 2001) studied sexual dimorphism in the skull, mandible, humerus, and femur of Recent Phocinae and compared them to fossil material. The finds of fossil Cystophorinae provided a unique opportunity to study the sexual dimorphism in the limb bones and mandibles in extinct, as well as living, members of the Subfamily. The following sexual differences were identified (similar differences can be observed in modern and fossil Phocinae).

Mandible (Figs 2B, C). The sexual dimorphism in *Cystophora cristata* is discernible not just in size but in the different proportions of the ramus and the body of the mandible. In addition, the male retromandibular space is even more elongated than in females, as well as in both sexes in other representatives of Phocidae, with the coronoid crest less inclined. The coronoid process in males is much lower, is turned caudally, and ends at almost the same level as the condyloid process (in contrast to other subfamilies). The angular process is more developed in females than in males; in contrast, the mandibular notch in males is wider than in females. The masseteric fossa in females is also deeper and better outlined than in males. The condyloid angle (the position of the condyloid process in relation to the axis of the alveolar row) of 25 specimens were examined, with the average measurements being 53° in females and 40° in males (see detailed explanation in Koretsky et al. in press).

Humerus (Figs 4A, B; Tab. 2). This bone in males of *Cystophora* is absolutely longer and more robust than in females, and the head is compressed in a dorso-ventral direction, while in females it is larger and more spherical (contrary to Phocinae; Tab. 2). The ratio of the greatest width of the head to the height in the male of *Cystophora cristata* is 0.85; in the females it is 0.80. Despite the taller bone in a male, the length of the deltoid crest is equal to that in females, but the distal part of the deltoid crest in a female ends as a narrow V, while in a male it is wider, U-like (Fig. 3A). The head of the humerus of the male *C. cristata* (Tab. 2) is bent caudally to a greater degree than that of females, indicating probable sexual dimorphism also. However, in the humerus of modern Phocinae this difference is not pronounced.

The fossa located medio-distal to the head seen in caudal aspect (between the lesser tubercle and the head) is deeper in males (as in Phocinae). The enormous medial head of the *triceps* muscle arises from this fossa on the medial side of the neck of the humerus, and inserts onto the dorsal part of the olecranon of the ulna (Howell 1930; English 1977). The action of the *triceps medialis* muscle is to extend the elbow joint (Miller et al. 1964).

In females, although the deltoid crest is bigger in comparison to the rest of the bone (contrary to Phocinae), the deltoid tuberosity, which is part of the deltoid crest, is more developed (similar to Phocinae). The musculospiral groove, where the *brachialis* muscle originates (Howell 1930; Piérard 1971; Tarasoff 1972; Howard 1975; English 1977), is deeper in males. In fossils, this character is much less pronounced, evidently as a result of wear on the available material.

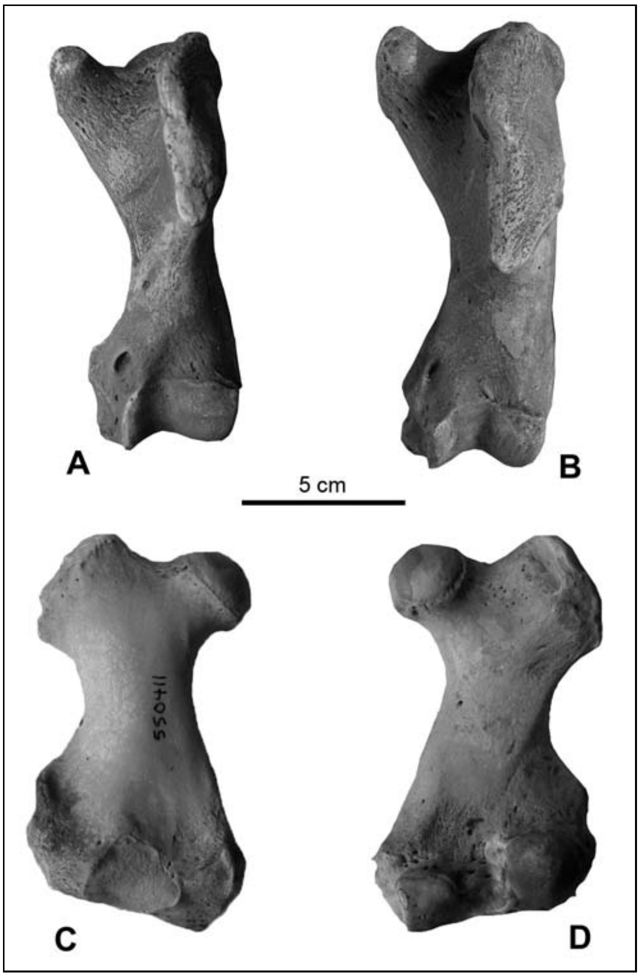


Fig. 4 - Sexual dimorphism of Recent *Cystophora cristata*. Humerus, cranial view of A) female (AMNH 184660, L.) and B) male (AMNH 184659, L.). Male femur (USNM 550411, R.) in C) cranial and D) caudal views.

In females, the medial epicondyle is more compressed and narrow in its lateral part (Howell 1930; English 1977). At the same time, the lateral epicondyle is shorter and narrower than in males, as in Phocinae. The entepicondylar foramen is always present in both sexes.

The shape of the humeral coronoid fossa of *Cystophora* depends on sex, with males having a sharp triangular form and females having a rounded-triangular or semi-rounded form (Fig. 4A); its depth is somewhat greater in females.

Femur (Figs 4C, D; Tab. 6). The absolute length of this bone in males of *C. cristata* is less than in females (in contrast to Phocinae); however, the male femur is more robust and wider. Moreover, in females of *C. cristata* the anteroposterior diameter of the diaphysis is greater than in males, but the least width of the diaphysis in females is located in the middle of the shaft, while in males it is shifted to the proximal portion of the shaft.

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 *m. adductor cranialis* (= *adductor anticus* in Howell 1930) in caudal aspect. A detailed description of the actions of these muscles can be found in Koretsky (2001).

In males, the head of the femur is larger and the diaphysis is less compressed, while in females it is the reverse. The average width of the diaphysis is smaller in females, while the distal epiphysis is more developed in males. One unique and very primitive character of *C. cristata* is that the lesser trochanter in males is well developed, while in females it is not.

In contrast to Phocinae, the neck of the femur of *C. cristata* is shorter and wider in females. Therefore (as in Phocinae), the neck forms nearly a right angle with the long axis of the bone in females, but in males the angle is greater than 90°.

The greater trochanter is wider and longer in males than in females. The distal part of the greater trochanter in females terminates more sharply or acutely (being V-shaped), while in males it is frequently rounded (U-shaped).

The *gluteus medius* and *gluteus minimus* muscles insert onto the cranial side of the greater trochanter, while the *m. piriformis* is attached to the caudal side. The attachment sites of these muscles are significantly more developed in males (Howell 1930; Piérard 1971; Howard 1975; Koretsky 2002), and consequently, the trochanter also is more developed in males.

Howell (1928, 1930), Piérard (1971), and Howard (1975) described the trochanteric fossa as a place of attachment for the *obturator internus* and *externus* muscles, which share a common tendon of insertion with the superior and inferior *gemelli* muscles (Koretsky & Sanders 2002). The *obturator externus* and *gemelli* muscles are more developed in females than in males, resulting in a deeper and more closed trochanteric fossa (as in Phocinae).

In females of *C. cristata*, the plantar fossa above the lateral condyle is wider and deeper and is bordered by a very thin edge of bone. The plantar fossa itself is the place of origin of the *plantaris* and lateral head of the *gastrocnemius* muscles. Although the patellar surface is larger in males, the sizes of the condyles are almost equal in both sexes. For detailed functional analysis of these muscles see Howard (1975) and Koretsky (2001).

For determining the sex using the humerus and femur in the Subfamily Cystophorinae, the following characters can be used: 1) 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 (similar to Phocinae) and 2)

Femur – overall size; anteroposterior width (=dorsoventral thickness) of diaphysis; length and thickness of neck; length and width of greater trochanter; anteroposterior diameter of distal epiphysis; presence of lesser trochanter.

The most reliable characters for sex determination in Cystophorinae are: in males, the absence of the mental tubercle; the height of the first incisor almost equaling the dimensions of the canine; width of the distal epiphysis on the humerus; and presence of the lesser trochanter of the femur.

While the features noted above are characteristic for adult animals, they are not nearly as pronounced in young and subadult individuals. Overall, the established differences and variations of characteristics are fairly constant, allowing researchers to separate individual elements of the extremities according to sex.

Pachyphoca gen. n.

Type species: *Pachyphoca ukrainica*; Middle Sarmatian of Ukraine

Etymology: *Pachys*, Greek, thick (referring to bone hypertrophy); *phoca*, Latin, from the Greek *phoke*, seal (f.).

Diagnosis: Lesser tubercle of humerus small, round, and located distal to head and greater tubercle; head compressed craniocaudally; intertubercular groove wide and shallow; medial epicondyle flattened, spreading from lower part of entepicondylar foramen; olecranon fossa deep and narrow.

Greater trochanter of femur slightly higher than head; trochanteric fossa deep; intertrochanteric crest flat, wide, and thick, reaching lesser trochanter; head large, seated on distinct lip (shaped like mushroom) and wide neck; minimum width of diaphysis shifted proximally; body of femur swollen, thick, husky, heavy, and pachyosteosclerotic; condyles almost equal in size.

Scapular spine ends smoothly; infraspinous fossa deeper and wider than supraspinous.

Medial surface of ulna flattened, not concave; olecranon short and thick; radial notch deep and long.

Ilium thick; iliac crest not averted, and excavated on its ventral surface as in other Monachinae and Cystophorinae; iliopectineal eminence flattened; fossa for *m. gluteus medius* shallow; auricular fossa deep; alar spine robust; iliac tuberosity and caudal dorsal iliac spine not very well developed; caudal dorsal ischial spine rounded and wide, not protruding; alar spine robust; acetabulum shallow.

Popliteal notch of tibia shallow and wide; tibial crest rounded in dorsomedial direction; tibial tuberosity flattened; muscular groove wide; grooves on distal end shallow and flattened.

All bones are thick, husky, and pachyosteosclerotic.

Included species: In the Middle Sarmatian (12.3-11.2 Ma) of the Northern Black Sea littoral region, southern Ukraine, two new cystophorine species are recorded: *Pachyphoca ukrainica* and *P. chapskii*.

Range: Middle Miocene, Middle Sarmatian (Bessarabian Stage; 11.2-12.3 Ma), the Northern Black Sea region, Ukraine, Eastern Paratethys.

Comparisons. *Pachyphoca* has characters similar to other representatives of the Subfamily Cystophorinae such as: absence of the musculospiral groove of the humerus; the protruding femoral intertrochanteric crest extending more proximal than the head; the presence of the lesser trochanter; almost equal-sized condyles. Other specific similarities to *Cystophora* include: cranio-caudal depression of the humeral head; short deltoid crest; enlargement of the deltoid crest in the middle; and presence of the entepicondylar foramen.

Similarities to *Mirounga* are: shallow and wide intertubercular groove of humerus; shallow, oval coronoid fossa extending to the same level as medial epicondyle; noticeable femoral intertrochanteric line; very deep intercondylar groove.

In addition, *Pachyphoca* differs from these two genera of the Subfamily Cystophorinae by: much smaller size; position and shape of the lesser tubercle of the humerus; presence of a distinct lip between the femoral head and the neck; and deeper trochanteric fossa. Specifically, *Pachyphoca* differs from *Cystophora* by the reverse relationship between lateral and medial epicondyles and from *Mirounga* by: the presence of the entepicondylar foramen of the humerus; shorter deltoid crest; protruding lesser trochanter of the femur; higher position of the greater trochanter; shorter femoral neck and larger head compared to the size of the bone.

Pachyphoca ukrainica gen. n sp. n.

Figs 5-10, Tabs 1-8

Etymology: *ukrainica*, from Latinized form of Ukraine.

Holotype: Right humerus, NMNHU-P 64-701, Middle Sarmatian.

Type Locality: Khomutovo Village, Donetsk region, Novoazov district, Ukraine.

Range: Middle Sarmatian (Bessarabian Stage, 11.2-12.3 Ma) deposits of the Northern Black Sea Region, Ukraine.

Diagnosis: Maximal enlargement of humeral deltoid crest located in middle; deltoid crest shorter than ½ of bone length; lateral epicondyle shorter and lower than medial (in contrast to *P. chapskii*), does not reach proximal part of medial epicondyle; medial epicondyle extending more proximal than coronoid fossa; entepicondylar foramen located above coronoid fossa; coronoid fossa oval.

Proximal part of femoral greater trochanter wider than distal; trochanteric fossa narrow; lesser trochanter well developed; head massive, seated on distinct lip on wide neck; supracondylar fossa deep, wide, rectangular.

Referred Specimens: In addition to the holotype, the following specimens were found in Ukraine: **humeri**: NMNHU-P 64-246 (L.), Uzunlar; 64-703 (L.), 64-713 (L.), Zolotaya Balka; **scapulae**: NMNHU-P, 64-477 (L.), 64-702 (R.), Zolotaya Balka; **radii**: NMNHU-P 64-481 (L., immature), 64-482 (L., immature), Zolotaya Balka; **ulnae**: NMNHU-P 64-705 (L.), Zolotaya Balka; 64-383 (R.), 64-710 (R., possibly from the same individual as holotype), Khomutovo; 64-711, (R., from the same individual as rib 64-711, not described), 64-712 (R.), Zheltokamenka; **innominata**: NMNHU-P 64-479 (L.), 64-348 (L.), Zolotaya Balka; **femora**: NMNHU-P 64-354(R.), Zolotaya Balka; NMNHU-P 64-166 (R.), Gnylozubov; 64-471 (L.), Zolotaya Balka; **tibiae and fibulae**: NMNHU-P 64-472 (R., proximal fragment), 64-473 (L.), 64-478 (L., proximal fragment), Zolotaya Balka; **vertebra**: NMNHU-P 64-704 (thoracic), Zolotaya Balka.

Description. Scapula (Figs 5A-C; Tab. 1): The scapular spine ends smoothly and does not reach the

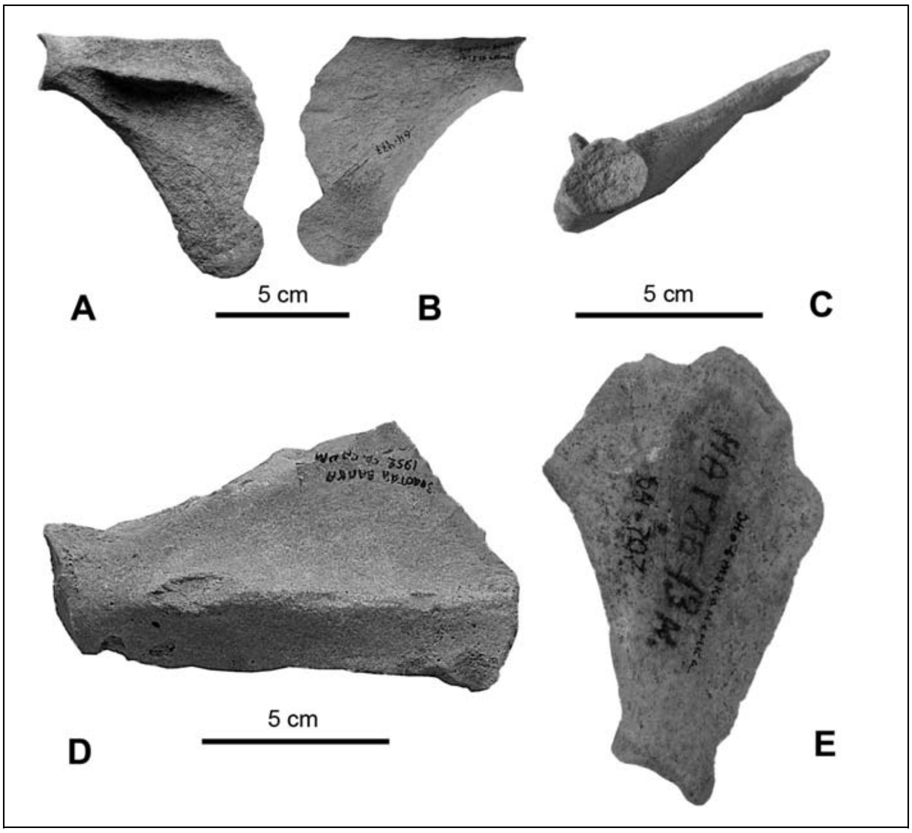


Fig. 5 - Scapula of *Pachyphoca ukrainica* (NMNHU-P, 64-477, L.) in A, dorsal B) ventral and C, glenoid views. Scapula of *P. chapskii* (NMNHU-P 64-707) in D) dorsal and E) ventral views.

vertebral border, which is partially broken in available specimens. The acromion is not developed and does not reach the ventral angle. In the cervical region, the infraarticular tuberosity shows as a long ridge connected with a thick and distinct muscular line on the infraspinous fossa. The coracoid process and scapular tuberosity are not developed either. The infraspinous fossa is deeper and wider than the supraspinous. The distal border of the supraspinous fossa ends as a straight line. In the infraspinous fossa the caudal angle forms a thin, round edge at the vertebral border. The glenoid fossa is deep with a thin mushroom-like lip. The complete bone is very thick at the lateral border and becomes much thinner at the vertebral border.

Humerus (Figs 6A, B; Tab. 2): The intertubercular groove is shallow and wide. The widest portion of the deltoid crest is located in the middle; the crest extends about half the length of the bone, and smoothly descends to the condyles as a flat, almost invisible ridge. The deltoid tuberosity is small and located at the middle of the deltoid crest proximal to the middle of the diaphysis. The lesser tubercle is weakly developed, round, and located considerably inferior to the greater tubercle, just distal to the head, which is compressed craniocaudally. The musculospiral groove is absent. The lateral epicondyle is shorter and lower than the medial, and does not reach the distal part of the deltoid crest. The medial epicondyle is flattened, spreading from the lower part of the entepicondylar foramen, extending higher than the coronoid fossa. The entepicondylar foramen is located above the coronoid fossa, with a laterally-located wide wall. The coronoid fossa is shallow, oval, extends further proximally than the lateral epicondyle, and ends at the same level as the medial epicondyle. The olecranon fossa is deep and narrow. The complete bone is extremely husky with a very pachyosclerotic condition.

Radius (Figs 7A, B; Tab. 3): The radial tuberosity is very large, wide, flat, and does not protrude laterally. The groove for all tendons including the tendon of the *m. abductor pollicis longus* is wide and shallow, whereas the ridge for the *m. extensor digitorum communis* is only shallow. Both available bones belong to subadult animals.

Ulna (Figs 7C-E; Tab. 4): The medial surface of the bone is flattened and not concave; the olecranon is short and thick, gradually connecting to the proximal half of the bone. On the lateral surface, there is barely any visible prominence of the rugosity for brachialis muscle insertion. Rather than a fossa for origin of the *m. abductor pollicis longus*, a protuberance is present. Caudal to the articular surface is another deep, wide, and short groove; this groove is surrounded by a circular (sharp) crest. On the bone's radial aspect, the coronoid process only slightly protrudes forward over the radial notch; the radial notch is deep and long. The interosseous crest is swollen, forming a prominence that protrudes only slightly. The head is not preserved.

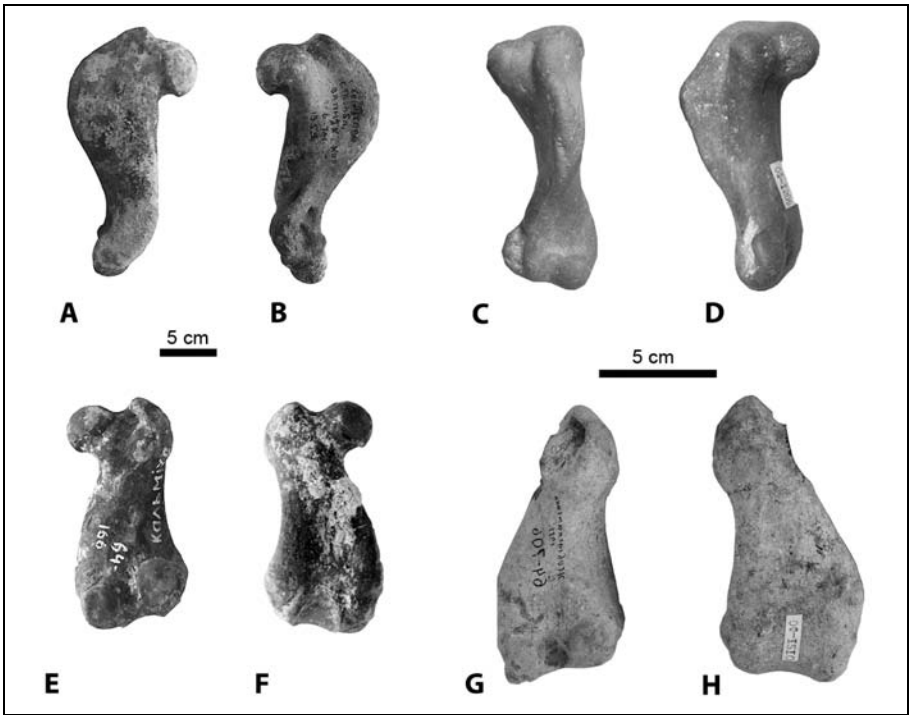


Fig. 6 - *Pachyphoca ukrainica* humerus (NMNHU-P 64-246, L.) in A) lateral and B) medial views. *P. ukrainica* femur (NMNHU-P 64-166, R.) in E) caudal and F) cranial views. *P. chapskii* humerus (NMNHU-P 64-523, L.) in C) lateral and D) medial views. *P. chapskii* femur (NMNHU-P 64-706, L., reversed) in G) caudal and H) cranial views.

Characters	OR
Absolute length	80.0; 85.0
Width of diaphysis	12.5; 14.0
Width of distal epiphysis	23.0; 24.0
Width of articulation surface of distal epiphysis	16.0; 16.0
Width of articulation surface, disposition of medial from articulation cavity	9.0; 12.0
Lesser diameter of caput	13.0; 13.5
Least width of proximal epiphysis	10.5; 11.0
Greater diameter of caput	16.0; 16.5
Anteroposterior diameter of distal epiphysis	16.0; 16.0

Tab. 3 - Measurements (mm) of radii of *Pachyphoca ukraina*.

Characters	*Pachyphoca*			
	ukrainica			*chapskii*
	n	M	OR	
Absolute length	2		113.0; 120.0	170.0; 155.0
Width of incisura trochlearis in upper part	4	12.3	10.0 - 13.5	14.0; 16.5
Width of incisura trochlearis in lower part	4	9.0	6.0 - 11.0	11.5; 12.0
Maximal width of middle part of diaphysis	4	14.7	13.0 - 18.5	18.5; 19.0
Width of bone at the level of incisura trochlearis	4	23.0	12.0 - 31.5	34.0; 35.0
Width of olecranon	4	35.3	30.5 - 40.0	45.5; 46.5
Transverse width of olecranon	4	13.3	12.0 - 14.0	16.5; 19.0
Maximal width of distal epiphysis	2		15.0; 17.5	19.5; 21.0

Tab. 4 - Measurements (mm) of ulnae.

Innominate (Figs 8C, D; Tab. 5): As in other Monachinae and Cystophorinae, the ilium is thick and the iliac crest is not averted and not excavated on its ventral surface. The iliopectineal eminence is small, situated higher than the proximal border of the acetabular fossa. The greater ischial notch is slightly concave, almost straight. A shallow depression (fossa) for the *m. gluteus medius* is located on the medial aspect of the ilial wing; on its lateral aspect is a deep and narrow auricular fossa for origin of the *m. psoas major*. The alar spine does not protrude very far. The iliopectineal eminence is absent, as is the pectineal tubercle. The edges of the acetabular fossa are not raised above the plane surface of the bone; the acetabulum is circular with a slightly marked cotyloid notch. The ischium is thick, wide and robust; the ischial spine is large, rounded and well developed for attachment of the *m. biceps femoris*. The pubis is not preserved.

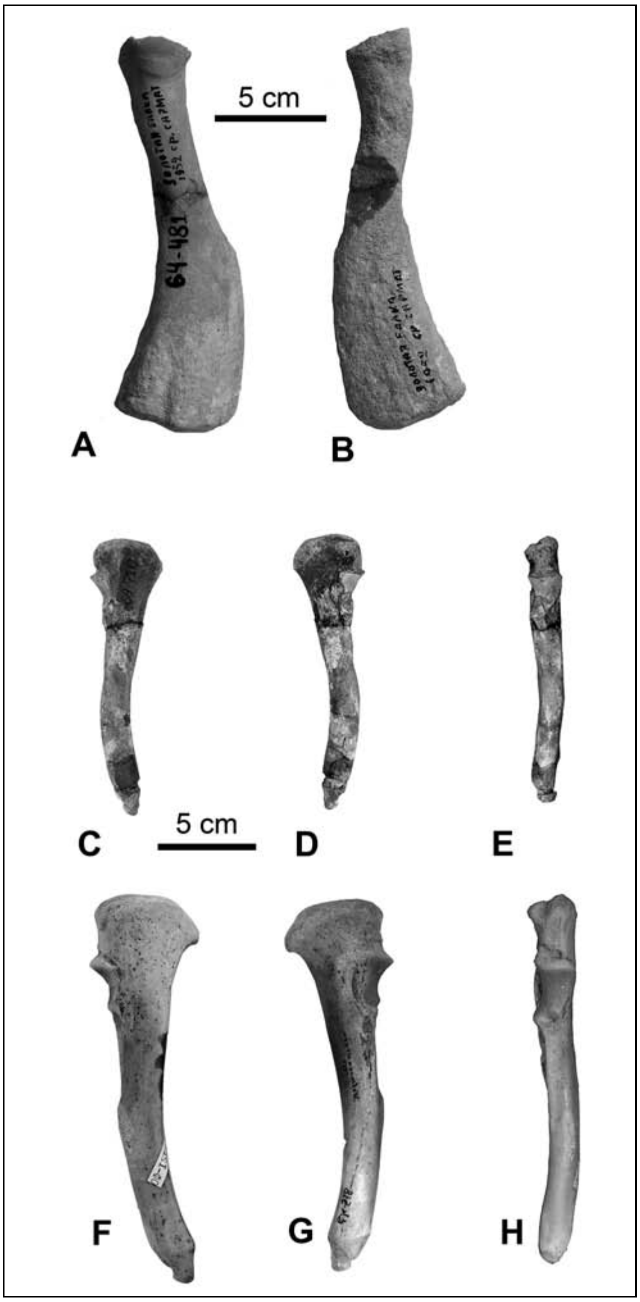


Fig. 7 - *Pachyphoca ukrainica* radius (NMNHU-P 64-481, L.) in A) dorsal and B) ventral views. *P. ukrainica* ulna (NMNHU-P 64-710, R.) in C) medial; D) lateral; and E) cranial views. *P. chapskii* ulna (NMNHU-P 64-518, R.) in F) medial; G) lateral; and H) cranial views.

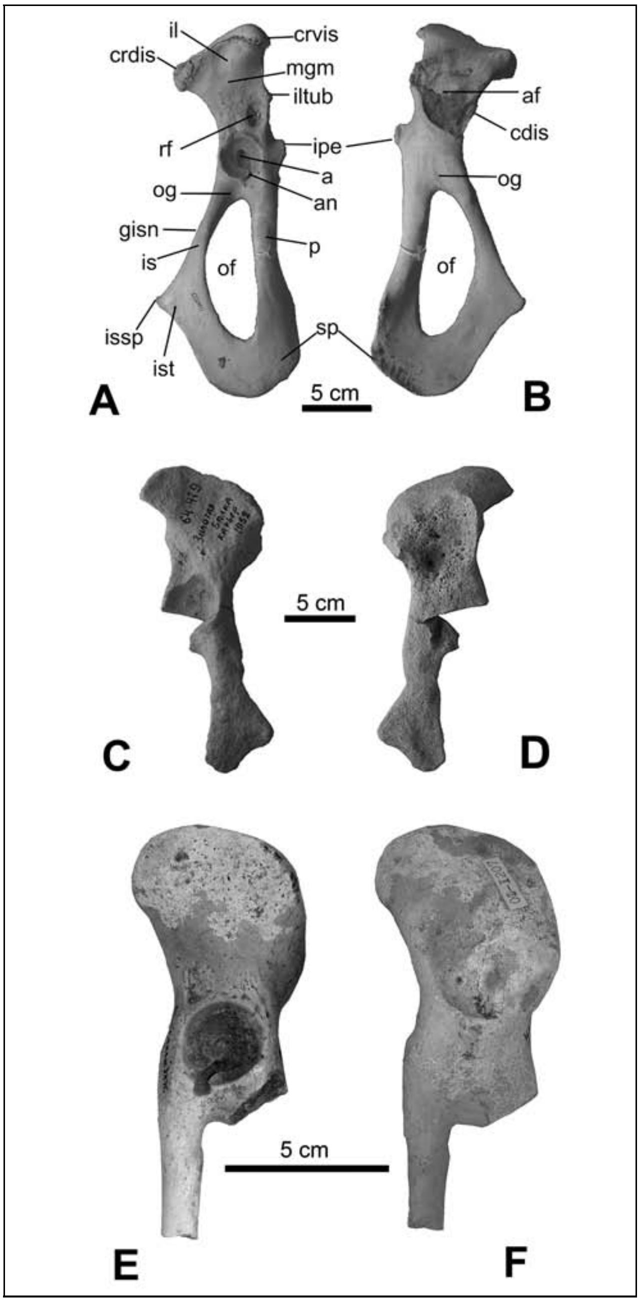


Fig. 8 - Innominate bone in A) lateral (=ventral) and B) medial (=dorsal) views of Recent *Cystophora cristata* (USNM 550411, ♂, R.). Innominate bone of Middle Miocene *Pachyphoca ukrainica* (NMNHU-P 64-479, L.) in C) lateral and D) medial views. Innominate bone of *P. chapskii* (NMNHU-P 64-525, R.) in E) lateral and F) medial views. Abbreviations: a, acetabulum; af, auricular fossa; an, acetabular notch; cdis, caudal dorsal iliac spine; crdis, cranial dorsal iliac spine; crvis, cranial ventral iliac spine; gisn, greater ischial sciatic notch; il, ilium; iltub, iliac tuberosity; ipe, iliopectineal eminence; is, ischium; issp, ischial spine; ist, ischial tuberosity; mgm, m. gluteus medius; of, obturator foramen; og, obturator groove; p, pubis; rf, m. rectus femoris attachment; sp, symphysis pubis.

Femur (Fig. 6E, F; Tab. 6): The greater trochanter extends proximally slightly higher than the head; its proximal part is somewhat wider than the distal. The trochanteric fossa is deep, narrow and open proximally, reaching the distal half of the greater trochanter. The flat, wide and thick intertrochanteric crest reaches the lesser trochanter, which serves for insertion of the *m. iliopsoas*. The lesser trochanter is very visible, thick, and not separated from the crest; the lesser trochanter reaches below the distal border of the greater trochanter and ends at the same level as the distal border of the head (or slightly higher than the head). The femoral head is large, relative to the bone's mass, and seated on a very short, thick, and wide neck; between the head and neck is a distinct lip. The smallest width of the

Characters	*P. ukrainica*	*P. chapskii*
	OR	
Length from center of acetabulum to iliac crest	52.5	70.5
Length of pubic from center of acetabulum	61.0	-
Width of level of iliac crest	45.0	53.0
Width of pubic	60.0; 67.0	44.0
Thickness of pubic	11.0; 13.5	14.0
Ratio		
1 : 3	117.6	133.0

Tab. 5 - Measurements (mm) of innominate of *Pachyphoca*.

diaphysis is shifted toward the proximal end of the bone. The supracondylar fossa is located above the medial condyle and is deep, wide, and rectangular; the condyles are almost equal in size**.**

Tibia (Figs. 9A-C; Tab. 7): The two condyles are weakly concave in their centers, shortened and oval. The intercondyloid eminences are weak and only slightly raised above the two lateral, well-developed borders of the condyles. The popliteal notch is shallow and wide, but well marked. The tibial crest is rounded in a dorsomedial direction. On the ventral side of the tibia, the tibial tuberosity is flattened and not well marked. The muscular groove is flat and wide; the grooves on the distal end are shallow and flattened.

Discussion. The innominate bone of *Pachyphoca ukrainica* has several very primitive characteristics, such as:

- The femoral lesser trochanter is present, for insertion of the *m. iliopsoas* (which flexes and laterally rotates the femur, tilts the pelvis forward, flexes the thigh upon the pelvis, and adducts the femur; Koretsky & Sanders 2002).
- The greater ischial notch of the *os coxa* is almost straight.
- A deep and narrow auricular fossa is present for insertion of the *m. psoas major* (a flexor of the hip joint).
- The ischial spine is large, rounded, and well developed for attachment of the *m. biceps femoris* (an extensor of the hip joint).

Therefore, it can be concluded that this animal was well adapted for terrestrial locomotion due to the presence of these muscular attachments.

Pachyphoca chapskii gen. n. sp. n.

Figs 5-10, Tabs 1, 2, 4-9

Etymology: Named in honor of the late K. K. Chapskii (of the Zoological Institute, St. Petersburg, Russia) in recognition of his numerous contributions to the study of fossil and modern true seals.

Holotype: Left femur, NMNHU-P 64-706, Middle Sarmatian.

Type Locality: Zheltokamenka, village on Zheltenkaya River, Dnepropetrovsk region, Apostolovo district, Ukraine.

Range: Middle Sarmatian (Bessarabian Stage, 11.2-12.3 Ma) deposit of the Northern Black Sea Region, Ukraine.

Diagnosis: Medial epicondyle does not reach coronoid fossa (in contrast to *P. ukrainica*); coronoid fossa wide, not well outlined, does not reach proximal end of lateral epicondyle.

Greater trochanter of femur is oblique; its distal part is wider than the proximal; trochanteric fossa is wide and reaches middle of greater trochanter; lesser trochanter is wide, not separated from intertrochanteric crest; condyles flat, small, widely spaced; instead of plantar fossa, plantar eminence present; supracondylar fossa has thick protuberance.

Characters	*Pachyphoca*				*Cystophora cristata*					
	ukrainica			*chapskii*	female			male		
	n	M	OR		n	M	OR	n	M	OR
Absolute length	3	80.3	78.0 - 82.5	120	6	131.0	130.0-132.0	3	132.4	131.0-133.5
Medial length	2		74.5; 78.0	-	6	119.5	119.0-120.0	3	121.2	119.0-122.6
Lateral length	3	75.3	72.5; 78.0	11	6	115.7	115.0-116.0	3	117.6	115.0-120.0
Length of medial condyle	3	15.3	14.0 - 18.0	22.5	6	22.2	22.0-26.0	3	24.3	22.1- 28.0
Length of lateral condyle	3	16.0	15.0 - 17.0	24	6	28.4	27.6-29.0	3	28.9	27.5- 30.0
Length of greater trochanter	2		22.0; 26.0	37	6	39.3	39.0-40.0	3	42.0	41.0- 43.5
Intertrochanter length	3	33.5	33.0 - 34.0	39	6	54.8	54.0-55.0	3	55.8	54.5- 58.0
Height of head	2		16.6; 16.5	-	6	25.7	25.0-26.5	3	27.2	26.1- 28.0
Height of articular area of patella surface	3	16.0	14.5 - 18.0	20.5	6	31.2	30.0-32.0	3	31.2	30.0- 33.0
Width of proximal epiphysis	2		36.5; 39.0	-	6	35.8	65.0-66.0	3	67.8	65.8- 69.0
Width of distal epiphysis	3	38.5	36.5 - 41.0	56	6	74.5	73.5-75.0	3	72.5	69.6- 75.0
Width of condyles	3	33.9	33.0 - 37.0	58	6	60.9	57.0-63.0	3	57.9	56.1- 61.0
Width of greater trochanter	2		15.5; 17.0	24	6	25.0	23.0-27.0	3	26.0	23.6- 30.0
Width of head	2		16.5; 16.5	-	6	26.2	24.0-30.5	3	28.4	25.5- 34.2
Width of diaphysis	3	24.3	22.0 - 26.0	33.5	6	33.1	32.0-34.0	3	34.4	33.5- 35.0
Anteroposterior thickness of diaphysis	3	14.3	12.0 - 17.0	21.5	6	25.0	20.5-27.0	3	24.6	19.6- 29.2
Thickness of medial condyle	3	17.5	17.0 - 18.0	27	6	26.6	24.0-27.5	3	30.9	25.0- 36.0
Thickness of lateral condyle	2		20.0; 22.5	30	6	37.0	35.0-39.0	3	37.8	35.8- 40.0
Distance between condyles	3	9.5	8.5 - 11.0	15.5	6	18.2	17.0-20.0	3	17.5	16.0- 19.0
Diameter of neck	2		16.0; 17.0	-	6	20.8	15.0-23.0	3	27.0	26.4- 28.0
Sex ratio										
09:11	3	41.6	37.8 - 47.4	36.7	6	41.9	39.8-43.2	3	43.0	41.0- 44.0
20:01	2		20.0; 20.6	-	6	15.9	14.2-17.3	3	20.5	19.8- 21.4
13:06	2	77.3		65.9	6	63.6	56.8-67.7	3	62.0	57.1- 69.7

Tab. 6 - Measurements (mm) of femura.

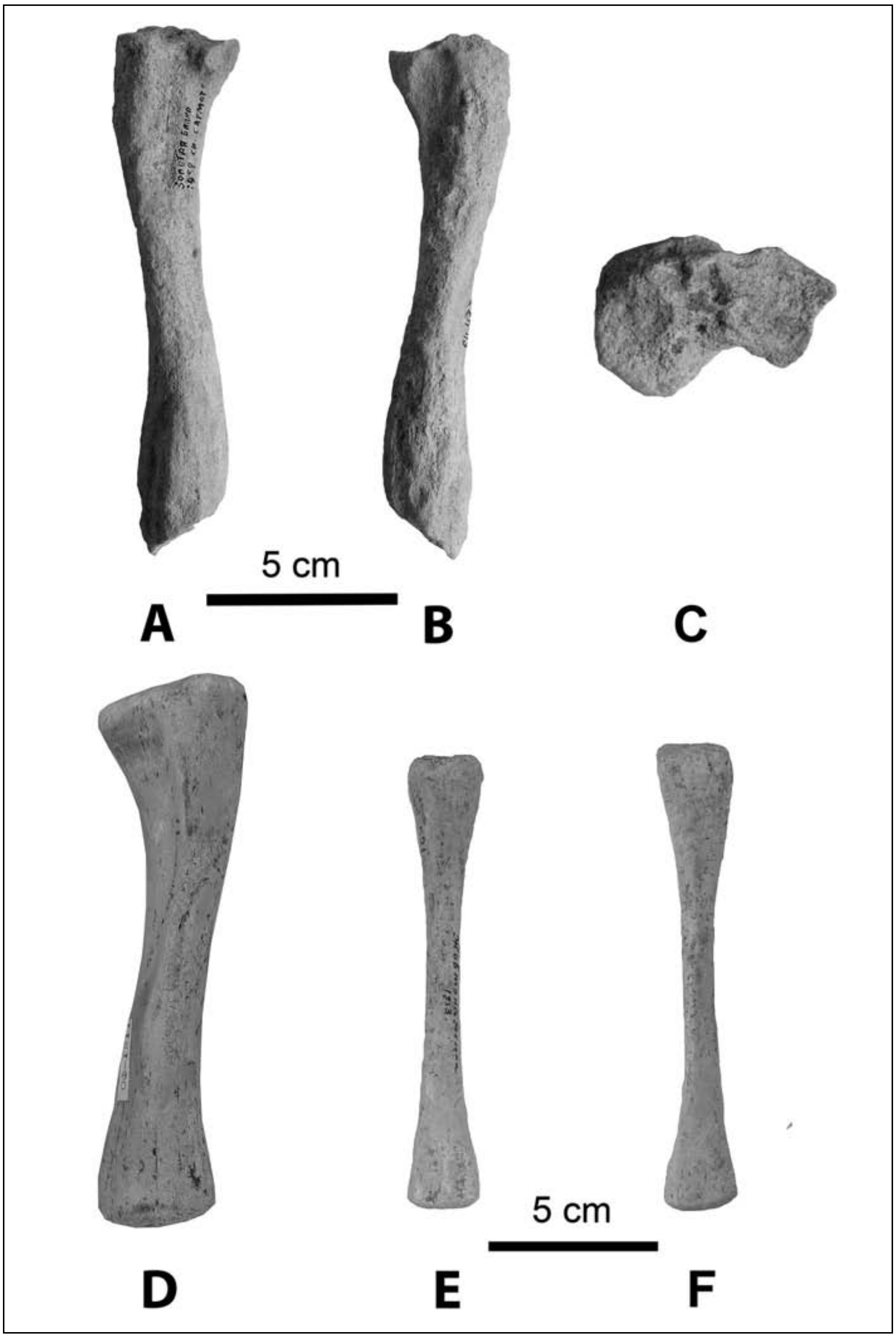


Fig. 9 - *Pachyphoca ukrainica* (NMNHU-P 64-473, L.) tibia in A) caudal; B) cranial and C) proximal views. D) *P. chapskii* tibia (NMNH-P 64-520, L., immature) in caudal view. *P. chapskii* fibula (NMNHU-P 64-521, L., immature, from the same individual as 64-520) in E) caudal and F) cranial views.

Characters	*Pachyphoca*			
	ukrainica			*chapskii*
	n	M	OR	
Width of proximal epiphysis	3	33.2	32.0 - 35.0	40.0
Height of proximal epiphysis	3	20.0	18.0 - 22.0	27.0
Width of distal epiphysis	2		20.5; 21.5	31.5

Tab. 7 - Measurements (mm) of tibiae.

Referred Specimens: In addition to the holotype, the following specimens were found in Ukraine: **humeri**: NMNHU-P 64-708 (R., distal end), 64-523 (L.), Zheltokamenka; **scapula**: NMNHU-P, 64-707 (L.), Zheltokamenka; **ulnae**: NMNHU-P 64-518 (R.), 64-519 (R.), Zheltokamenka; **innominate**: NMNHU-P 64-525 (R.), Zheltokamenka; **tibia**: NMNH-P 64-520 (L., immature), Zheltokamenka; **fibula**: NMNHU-P 64-521 (L., immature, from the same individual as 64-520), Zheltokamenka.; **vertebra**: NMNHU-P 64-528 (lumbar), Zheltokamenka; **sacrum**: NMNHU-P 64-527, Zheltokamenka; **IMtc 2nd phalange**: NMNHU-P 64-517, Zheltokamenka.

Description. Scapula (Figs 5D, E; Tab. 1): The scapular spine ends smoothly, reaching the vertebral border as a small, almost flat ridge; the vertebral border is broken on the available specimen. The acromion is present as a small hook, ending at the same level and height as the scapular spine.

In the cervical region, the infra-articular tuberosity is present as a thick, wide protuberance. The muscular line on the infraspinous fossa is pronounced as a long, very well developed ridge (bigger and stronger than in *P. ukrainica*). The infraspinous fossa is deep and wider than the supraspinous fossa. In contrast to *P. ukrainica*, the coracoid process is thick, short, and wide.

The distal border of the supraspinous fossa ends as a straight line (as in *P. ukrainica*); the caudal angle is not preserved. The glenoid fossa is shallow (deep in *P. ukrainica*), without a pronounced lip, and without a border (in contrast to *P. ukrainica*).

The complete bone is very thick, heavy, and much bigger and thicker than in *P. ukrainica*.

Humerus (Figs 6C, D; Tab. 2): The lateral epicondyle is much higher and wider than the medial. The middle part of the trochlea is raised wave-like over the coronoid fossa. The small, oval entepicondylar foramen has a very wide bridge over the medial epicondyle, and extends lower than both the coronoid fossa and the lateral epicondyle.

The medial epicondyle is flattened, spreading from the lower part of the entepicondylar foramen, and it does not reach the coronoid fossa. The medial epicondyle is lower than the coronoid fossa; the coronoid fossa is shallow, wide and not well defined (=outlined); it extends far proximally, but it does not reach the proximal end of the lateral epicondyle.

The olecranon fossa is deep, long, and narrow, seated transversely to the bone axis. Situated on the anterior-medial side of the humerus is a thick protrusion, located medial to the trochlea and adjacent to the olecranon fossa. The bone is big, strong, and heavy like a stone.

Ulna (Figs 7F-H; Tab. 4): The medial surface is flattened and not concave (as in *P. ukrainica*). The olecranon is short, thick, and forms a hook at the caudal end. The rugosity for the brachialis muscle insertion has a very well developed prominence. On the lateral surface, the fossa for the *m. abductor pollicis longus* is present. Another narrow and long groove is located caudal to the articular surface; this groove is not surrounded by a sharp crest, but very smoothly transitions into the diaphysis, reaching the ulnar protuberance (in contrast to the ulna of *P. ukrainica*). The trochlear notch is flattened and not visible on the radial aspect of the bone. The coronoid process greatly protrudes forward, at almost 90°, over the radial notch; the radial notch is deep and long. The anconeal process is very large, wide, and protruding. The ulnar tuberosity, situated on the middle of the diaphysis, reaches the rugosity for the tendon. The big, long, and wide interosseous crest is located on the middle of the diaphysis. The head and styloid process are preserved.

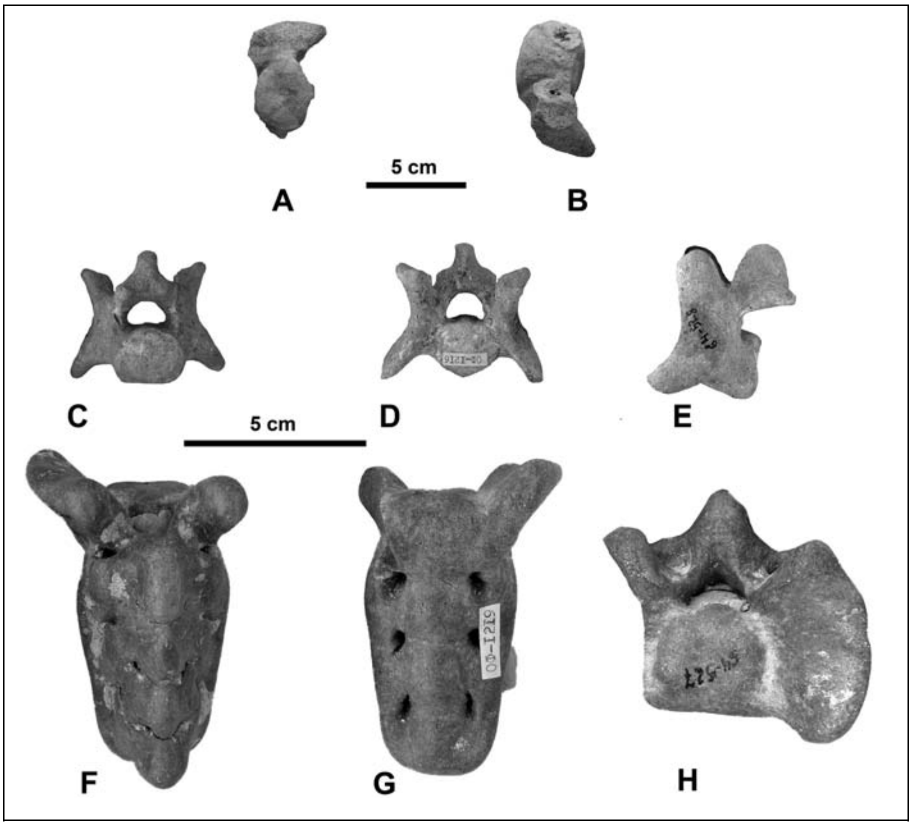
Innominate (Figs 8E, F; Tab. 5): The ilium is thick and flattened, with the iliac crest slightly averted and not excavated on its ventral surface as in other Monachinae and Cystophorinae (similar to *P. ukrainica*). The iliopectineal eminence is wide and not pronounced; the pectineal line is hardly visible. On the medial aspect of the ilium is a shallow depression (compared to size of the bone) for the insertion of the *m. gluteus medius* (this is much smaller and shallower than the same fossa of *P. ukrainica*). On the lateral aspect of the ilial wing is located a deep and wide fossa for insertion of the *m. psoas major.* The alar spine is rounded, robust, and turned posteriorly. The edges of the acetabulum are raised high above the plane surface of the bone (in contrast to *P. ukrainica*); the acetabulum is conical (a primitive character), with a deep and well-marked cotyloid notch. Above the acetabulum, there is a deep and narrow depression for the insertion of the *m. rectus femoris* (in contrast to *P. ukrainica*, where there is a big, flat, and wide depression). The pubis is rounded.

Femur (Figs 6G, H; Tab. 6): The greater trochanter is very obliquely oriented along the bone's axis; its distal part is wider than the proximal and ends in a narrow V-shape. The trochanteric fossa is deep and wide, reaches the middle of the greater trochanter's length, and has a shallow proximal border. The flat, wide, and thick intertrochanteric crest reaches the weakly developed lesser trochanter, which is wide and not separated from the intertrochanteric crest. The condyles are flat and small, compared to the size of the bone, and very widely spaced. Considerable swelling of the bone is seen at the location of the plantar fossa. The supracondylar fossa is not pronounced, but does have a thick protuberance. The smallest width of the diaphysis is shifted toward the proximal end of the bone. The condyles are almost equal in size.

Tibia and fibula (Figs 9D-F; Tab. 7): The two tibial condyles are shortened and oval; the tibial crest is well marked and developed. The intercondyloid eminence is not developed, only slightly raised above the two lateral condyles, with hardly noticeable borders. The popliteal notch is shallow and wide, but not well marked. The tibial crest is well pronounced and rounded in the dorsomedial direction. On the ventral side of the tibia, the tibial tuberosity is flattened, wide, triangular, and extends along the axis of the bone. The muscular groove is deep and wide; grooves on the distal end are shallow and flattened. The fibula is without condyles, but has a well-developed interosseous crest. Both bones probably belong to the same individual animal.

Vertebra (Figs 10D-F; Tab. 8): The body of the lumbar vertebra is flattened in the dorso-ventral direction and heart-shaped; the vertebral foramen is oval in shape. The spinous process is very short and wide, while the transverse processes are directed cranio-ventrally. The caudal articular process is very short and rounded; the mammillary process is thick, wide, and short. The

Fig. 10 - Thoracic vertebra of *Pachyphoca ukrainica* (NMNHU-P 64-704) in A) lateral and B) dorsal views. Lumbar vertebra of *P. chapskii* (NMNHU-P 64-528) caudal; and E) lateral views. Sacrum of *P. chapskii* (NMNHU-P 64-527) in F) dorsal; G) ventral; and H) cranial views.



cranial articular surface is rounded, like a short protuberance.

Sacrum (Figs 10G-I; Tab. 9): The sacrum consists of 4 fused vertebrae as in other cystophorines (with 125 mm absolute length and 72 mm wide). The sacral promontory is almost flat and not pronounced. However, the ala is thick and the anterior surface of the first centrum is lower than the wings of the sacrum (as in miroungini and monachines, but in contrast to cystophorines and phocines, where the ala is on the same level as the centrum; Antoniuk 1979). The maximum width across the wings is 57.6 % of the length of the sacrum, which according to Antoniuk (1979) is a miroungine character, as the percentage in cystophorines should be less than 40%. On S2 are located thick, wide, and well-defined transverse processes. The median sacral crest, which is formed by the spinous processes, is fused between S1 and S2. All spinous processes become progressively smaller from S1 to S4, with immense, thick bases. Dorsal sacral foramina are smaller than ventral.

According to the sexually dimorphic characters of sacral bones described by Gadjiev (1982), this particular bone should belong to an adult male because its first ventral foramen is rounded and the lateral wall is very thick. The bone is partially rolled, but it is very distinctive and unusual. The body of the sacrum is short, wide, and very pachyosteosclerotic.

Cladistic Analysis

The data matrix for the 48 included characters of Phocidae is shown in Tab. 10. In this matrix, 0 designates the most primitive state among the taxa studied; 1-2, derived states; ?, unknown or missing data. Some characters have the opposite polarity to that of Berta and Wyss (1994) and Burns and Fay (1970), while some characters have the same polarity as that of Chapskii (1974). For a detailed discussion of polarities of the characters, see Koretsky and Grigorescu (2002).

Skull

1. Mastoid process: (0) prominence lateral to auditory bulla not strongly pronounced; (1) pronounced.
2. Mastoid process: (1) narrow (width of the process less than length of process itself); (0) wide (Chapskii 1974:301; in contrast to Berta and Wyss 1994:48).
3. Maxilla: (0) has very pronounced convexity anterior to the orbits; (1) short concavity; (2) long concavity (Chapskii 1974; in contrast to Berta and Wyss 1994:46).
4. Anterior palatal foramina: (0) faintly marked (Burns and Fay 1970:72); (1) oval and shallow; (2) round and deep.
5. Interorbital space: (0) less than 25.0% of width of skull across mastoids; (1) less than 30.0%, but equal to or greater than 25.0% of width of skull across mastoids; (2) equal to or greater than 30.0% of width of skull across mastoids (Burns and Fay 1970:370; Chapskii 1974:299).
6. Jugular process: (0) well developed; (1) poorly developed.
7. Rostrum: (0) elongate; (1) short, compared with skull.
8. Diameter of infraorbital foramen: (0) less than diameter of alveolus of maxillary canine; (1) approximately equal to diameter of

Characters	*Pachyphoca*	
	ukrainica	*chapskii*
Height of centrum	21.0	27.5
Width of centrum	20.0	29.0
Thickness of centrum	17.0	33.0

Tab. 8 - Measurements (mm) of lumbar vertebrae.

Characters	*Pachyphoca chapskii*
Absolute length	125.0
Hight of centrum	25.0
Width of centrum	25.0
Thickness of centrum	25.0
Thickness of 4-th vertebra	19.0
Length of ala	46.0
Width of ala	23.5

Tab. 9 - Measurements (mm) of sacrum.

alveolus of maxillary canine; (2) greater than diameter of alveolus of maxillary canine.

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 (unordered character) (Burns and Fay 1970:382; Cahpskii 1974:300).

Mandible

10. Symphyseal part: (0) continues at least to the middle of the alveolus of p3; (1) reaches only the alveolus of p2; (2) reaches only 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; (2) extends from the anterior alveolus of p2 to posterior alveolus of m1 (unordered character).

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

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 (unordered character).

16. Alveoli of p4 and m1: (0) alveoli similar in size; (1) alveolus of p4 smaller than alveoli of m1; (2) alveolus of p4 larger than the alveolus of m1 (unordered character).

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

Teeth

18. Number of incisors: (0) 3/2; (1) 2/2; (2) 2/1 (Chapskii 1974: 289; in contrast to 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 (Berta and Wyss 1994: 51).

20. Crowns of postcanine teeth: (0) single-cusped; (1) multi-cusped (reversal to primitive condition) (Berta and Wyss 1994: 51).

21. Relative dimensions of postcanine teeth to the size and massivity of the skull: (0) large; (1) small.

22. Relative dimensions of canine to the size of the skull: (0) large; (1) small.

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

24. Number of additional cusps of premolars: (0) two; (2) more than two.

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

26. Upper incisors: (0) arranged in curved line; (1) arranged in straight line.

27. Upper incisors: (0) third larger than second (Phocinae); (1) second larger than first (Monachinae); (2) incisors equal in size to canine (Cystophorinae) (unordered character). *Phocinae have 10 incisors (3 upper); Monachinae have 8 incisors (2 upper); and Cystophorinae have 6 incisors (1 upper).

Humerus

28. Lesser tubercle: (0) pronounced; (1) not pronounced (in contrast to Berta and Wyss 1994: 52).

29. Trochlear crest: (0) raised in a wave-like shape over coronoid fossa; (1) raised arch-like over coronoid fossa; (2) 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; (2) tubercle lower than head (unordered character).

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

32. Head: (0) medio-laterally compressed; (1) round; (2) flattened proximo-distally.

33. Deltoid crest: (0) maximum 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 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 (in contrast to 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) round; (1) flattened in proximo-distal direction; (2) compressed in medio-lateral direction.

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

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

46. Head and greater trochanter: (0) both reach same level; (1) greater trochanter higher than head; (2) head higher than greater trochanter.

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

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

The analysis of the phocid taxa used 48 unweighted characters and the Bootstrap analysis. Fig. 11 shows the resulting single most

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Lutra canadensis	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	1
Devinophoca claytoni	0	0	2	1	1	1	1	0	0	?	?	?	?	?	?	?	?	0	0	1	1	1	0	1
Cystophora cristata	1	1	1	0	1	1	0	0	0	0	1	1	0	2	1	2	0	2	0	0	1	0	0	0
Pachyphoca ukrainica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pachyphoca chapskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mirounga angustrirostis	1	1	2	0	0	1	0	0	0	0	1	1	2	2	2	2	0	2	0	0	1	0	1	0
Monachus schauinslandi	1	1	2	0	0	1	1	1	1	2	1	1	1	1	2	2	1	1	1	1	1	1	0	1
Callophoca obscura	0	0	2	0	1	1	0	0	0	1	0	1	1	0	2	0	0	1	0	1	0	0	0	1
Pliophoca etrusca	0	0	2	0	2	1	0	1	0	1	2	0	0	0	1	0	0	1	1	1	0	1	0	1
Pontophoca sarmatica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	0	0	?	0	0
Phoca vitulina	0	0	0	1	0	1	1	2	1	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1
Leptophoca lenis	0	0	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	0	1
Erignathus barbatus	0	1	0	1	0	1	1	2	1	0	1	1	1	1	1	2	0	0	0	1	1	1	1	1

	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Lutra canadensis	0	0	1	0	1	0	1	0	0	1	0	1	0	1	2	0	0	0	0	1	1	0	1	1
Devinophoca claytoni	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cystophora cristata	0	0	1	1	0	1	2	1	1	0	0	1	0	0	2	1	0	1	2	0	0	1	1	1
Pachyphoca ukrainica	?	?	?	1	0	2	0	2	2	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0
Pachyphoca chapskii	?	?	?	?	0	?	?	?	?	?	1	?	1	0	0	0	0	1	?	0	1	?	?	0
Mirounga angustrirostis	0	0	1	0	0	1	2	2	2	1	1	0	1	1	2	1	1	0	2	0	1	2	1	1
Monachus schauinslandi	1	0	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1
Callophoca obscura	1	0	2	1	1	0	1	1	1	2	0	1	0	0	0	0	1	0	1	1	1	0	0	1
Pliophoca etrusca	1	0	1	1	1	0	1	0	2	1	0	0	0	0	0	0	1	1	1	0	0	0	0	1
Pontophoca sarmatica	0	?	?	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0
Phoca vitulina	0	1	2	0	2	1	0	0	0	0	0	2	1	0	1	0	1	1	0	1	1	1	0	1
Leptophoca lenis	0	0	0	0	2	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0
Erignathus barbatus	1	0	0	0	2	1	2	2	2	0	1	1	1	0	1	0	1	1	2	1	1	1	1	1

Tab. 10a, b - Matrix for character-state data for Phocidae taxa and outgroup analyzed.

parsimonious Wagner tree generated by Winclada with length of 157 steps, Consistency Index of 0.43, and Retention Index of 0.46.

The nodes of the cladogram shown in Fig. 11 are supported by the following character transformations:

Node 1 (Family Phocidae): 6(1). This synapomorphic group with an ancestral or primitive character (well developed jugular process) is treated as plesiomorphic for the Family Phocidae. Also, character 33(1,2) is homoplasious in *Pachyphoca ukrainica* (which belongs to the Subfamily Cystophorinae), *Pliophoca etrusca* (which belongs to the Subfamily Monachinae), and *Erignathus barbatus* (which belongs to the Subfamily Phocinae).

Node 2 (Subfamily Devinophocinae): 4(1). The anterior palatal foramina are faintly marked.

Node 3 (Subfamily Phocinae): 29(2). Humeral trochlear crest is not separated from coronoid fossa by a distinct lip.

Node 4 (Subfamily Monachinae): 3(2); 18(1); 31(1). Maxilla forms a long concavity; number of incisors reduced; humeral lesser tubercle extends along the bone's axis.

Node 5 (Subfamily Cystophorinae): 3(1); 18(2). Maxilla forms a short concavity; number of incisors further reduced; humeral trochlear crest raised wave-like over coronoid fossa. Also, character 32(2) is similar in *Mirounga angustirostris* and *Pachyphoca ukrainica*.

Discussion and Conclusions

The new genus with two new species (*Pachyphoca ukrainica* and *P. chapskii*) of extinct fossil true seals belongs to the Family Phocidae and the Subfamily Cystophorinae. These species are known only from the Middle Miocene, Middle Sarmatian (12.3 – 11.2 Ma) deposits of southern Ukraine. The new Miocene genus *Pachyphoca* shares numerous characters with species of *Cystophora* and *Mirounga*, such as: the middle of the humeral trochlear internal crest rising wave-like over the coronoid fossa, and the distal and proximal epiphyses of the humerus almost equal in width.

Discussion of sexual dimorphism in Recent Phocidae has been based mainly on cranial material, with very little attention to postcranial elements. In contrast, the fossil remains of true seals usually consist of isolated limb bones, mainly the humerus and femur. Detailed studies of sexual dimorphism covering both cranial and postcranial elements in both fossil and Recent species have only been performed on members of the Subfamily Phocinae (Koretsky 1987a, 2001). Therefore, this new fossil material provided a unique opportunity to study the sexual dimorphism of limb bones and mandibles of the Subfamily Cystophorinae.

Sexual dimorphism in postcranial bones and mandibles in living members of the Subfamily Cystophorinae is more obvious than in other true seals. The quantity (58 individual bones of the postcranial skeleton) and variety of the new fossil postcranial bones revealed two size classes of specimens that did not fit known patterns of ontogenetic or sexual variation. In addition, most elements of the postcranial skeleton for both new species reveal several very primitive characters, such as: presence of femoral lesser trochanter and visible intertrochanteric line; a deep, long fossa for origin of the *gluteus medius* muscle on the wing of the ilium; well-developed pectineal tuberosity; and a large, deep acetabulum.

Both new species show a mosaic of these primitive characters. For example, the smaller species *(Pachyphoca ukrainica*) has a better-developed lesser trochanter of the femur than the larger species (*P. chapskii*), while the larger has a thicker and bigger intertrochanteric crest. The larger (*P. chapskii*) has innominate bones with a deep, conical acetabulum, and the margins of the acetabular fossa are raised high above the plane surface of the bone. In contrast, the smaller species has a pubis with a big, well-developed ridge for attachment of the *obturator* muscles (which cause outward rotation of the hip joint), a thick, wide and robust ischial spine for attachment of the *biceps femoris* muscle (an extensor of the hip joint), and a deep fossa on the medial aspect of the ilium for attachment of the *gluteus medius* muscle (also an extensor of the hip joint).

The presence of these anatomical traits, and specifically the well-developed lesser trochanter of the femur, implies that the smaller *Pachyphoca ukrainica* was more adapted to terrestrial locomotion (more primitive) than its larger relative. In addition, both new species are more primitive and better adapted for terrestrial locomotion than any living representatives of the Subfamily Cystophorinae. Notably, the sexual dimorphism supposed in the two new species of *Pachyphoca* is more obvious than the similar characters in modern Cystophorinae (see Tabs 2, 6).

This new material of fossil seals from the Middle Miocene (Sarmatian) deposits of the Ukraine allows emended diagnoses, redescriptions, and assessment of geographic distributions to help clarify phylogenetic relationships within the Subfamily Cystophorinae (especially comparisons with the controversial genus *Mirounga*). The fossil record of Cystophorinae from the Northern Black Sea region (Paratethyan Basin) is in agreement with the earlier hypothesis that the origin of Phocidae was in the Atlantic Ocean including Tethys (Koretsky & Barnes 2006). Despite the incomplete fossil evidence for ancient dispersal patterns, our hypothesis, based on this new material, indicates that Cystophorinae originated in the Paratethyan Basin, probably migrated westward about 11.2 million years ago, and subsequently divided into the two modern genera (*Cystophora* and *Mirounga*). Further, *Mirounga* itself divided into the northern and southern elephant seals. Northern elephant seals (*Mirounga angustirostris*) spread through the North Atlantic Ocean with *Cystophora cristata* into the Arctic region. Southern elephant seals (*Mirounga leonina*) dispersed into the Antarctic region via the South Atlantic Ocean. *M. angustirostris* migrated through the Bering Sea and later on became the North Pacific elephant seal, while *C. cristata* became the hooded seals of the Arctic Circle and Northern Pacific. These new findings help explain the origin, dispersal, and phylogenetic relations among the several subfamilies of the Family Phocidae.

Our phylogenetic analysis, based on cranial and postcranial characters of fossil and Recent seals, supports a monophyletic Family Phocidae that includes the subfamilies Devinophocinae, Phocinae, Monachi-

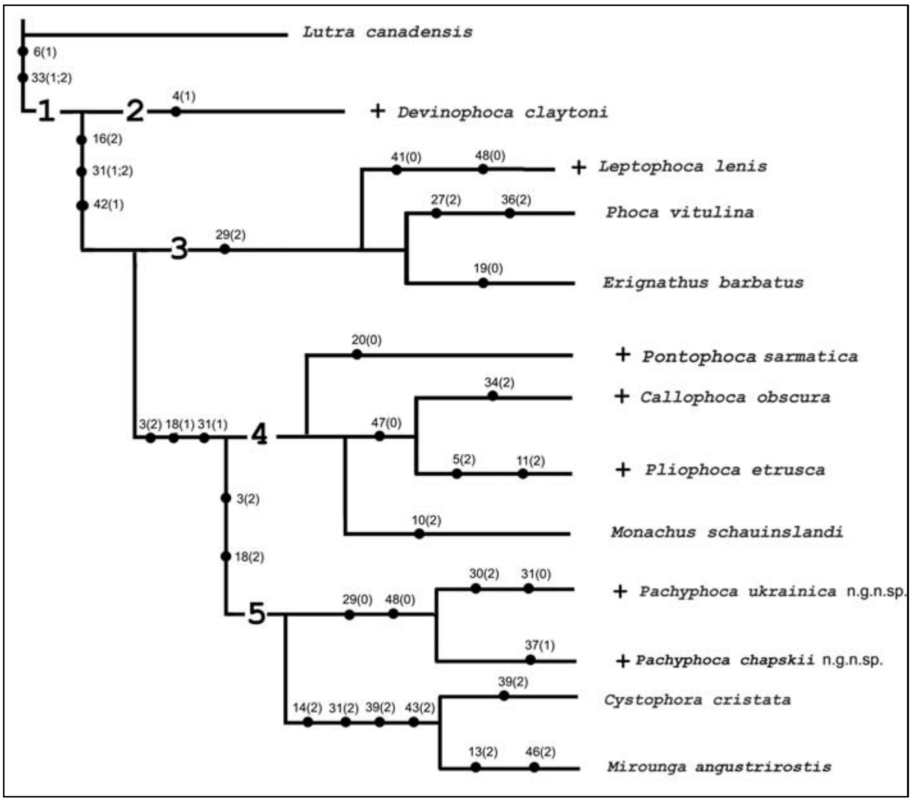


Fig. 11 - Postulated phylogenetic relationships among selected Recent and fossil taxa of the Family Phocidae, including *Pachyphoca ukrainica* and *P. chapskii*, new genera and new species, based on 48 characters explained in the text. This is the resulting single most parsimonious tree with 157 steps, Consistency Index 0.43, Retention Index 0.46, obtained using the Wincla-da option of Hennig86.

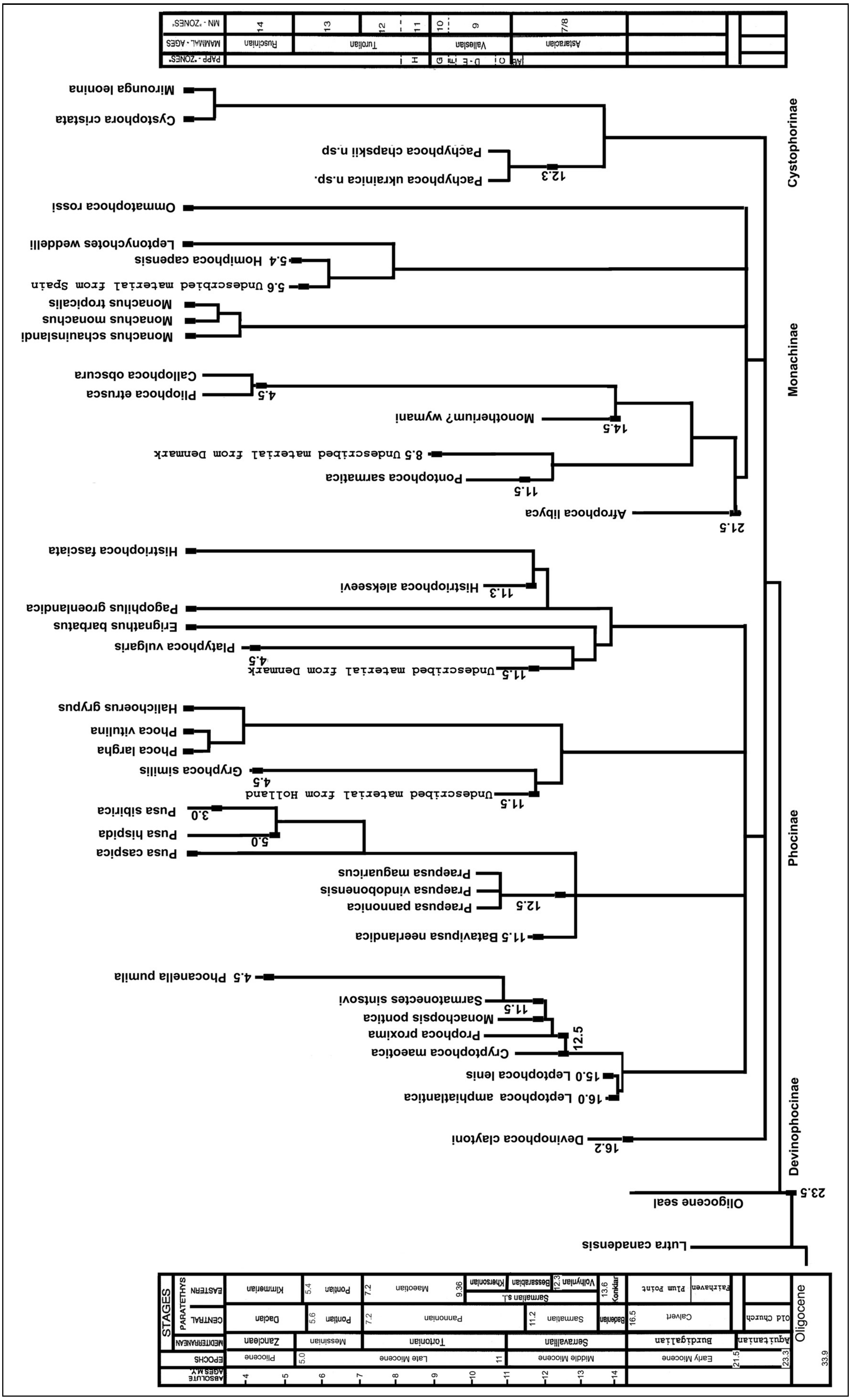


Fig. 12 - Chronologic and stratigraphic correlation chart of extinct and living Phocidae. Branching points are not necessarily correlated with the time scale.

nae, and Cystophorinae. If phocids are indeed monophyletic, there cannot be dual origins and dispersals between Monachinae (North Atlantic coastline of North America) and Phocinae (Paratethys) as suggested by Deméré et. al. (2003). Additionally, these new findings appear to contradict the hypothesis of Ärnason et. al. (2006), where all seals originated on the North Atlantic coast of North America. Numerous fossil seal remains (and their geological ages) in the Paratethyan/Mediterranean regions, collected over the last three decades, do not support either hypothesis mentioned above.

Moreover, the phylogenetic analysis suggests that seals with 10 incisors (Phocinae) are more primitive than those with 8 (Monachinae), which are more primitive than those with 6 (Cystophorinae). Also, it further suggests that the Subfamily Cystophorinae includes hooded (*Cystophora*) and elephant (*Mirounga*) seals, as well as the two new species of the Middle Sarmatian "pachyosteosclerotic" seals (*Pachyphoca*) (Fig. 11).

Some Miocene seal postcranial elements, including ribs, exhibit thick and swollen (pachyosteosclerotic) bones that can be mistaken for those of sirenians such as *Manatus maeoticus* (Koretsky 2001). Paleoecologically, it is possible that hypersaline closed basins developed as the Central and Eastern Paratethys Sea gradually dried, allowing pachyosteosclerotic seals and sirenians to evolve independently in the same time periods. Functionally, the increased skeletal mass would be a likely adaptation for reducing buoyancy and to remain submerged more easily by having high bone density (correlating to feeding habits). It may be reasoned that several species evolved pachyosteosclerotic bones for shallow diving and slow swimming speeds. Pachyosteosclerosis among fossil seals is a relatively new discovery and is hardly remarked at all in literature. The detailed study of pachyosteosclerotic bones of fossil and Recent seals is a planned future project.

It is possible that a few pachyosteosclerotic bones described by Simionescu (1925) as *Phoca bessarabica* from the Early-Middle Sarmatian of Bessarabia (modern Ukraine-Moldavia border) also belong to the Subfamily Cystophorinae. However, the lack of additional materials and incomplete description of the type species raise some questions about the assignment of other seal material from the Paratethys to *Phoca bessarabica*. Since Simionescu (1925), additional collections from the Central and Eastern Paratethys have been accumulated in the NMNHU-P, Kiev, Ukraine, that likely pertains to this species. This added material has never been described or illustrated, with no one even visiting the localities or researching their stratigraphy.

Results of extensive investigations on these fossil remains provide a foundation for revision of the group, and clarification of the systematics of its members. Moreover, these results have provided the basis for revision of the generic and specific diagnoses of true seals and suggest a framework for the unified study of cranial and postcranial elements, including the full range of ontogenetic and sexual morphological variations. The methods developed in these studies can be applied equally well to modern and fossil representatives of the Subfamily Cystophorinae for description and morphometric treatment.

During our review of seals overall, one tree was erected describing the relationships of all currently known extinct and living species, as well as the two species described in this paper (*Pachyphoca ukrainica* and *P. chapskii*). This tree was combined with a chart of stratigraphic and chronologic correlations (Fig. 12) that also includes multiple species that are not discussed in this paper and several undescribed new finds that will be published soon.

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Appendix

A study of 68 individual specimens using the osteological collections of the NMNH, AMNH, and ZIN of Recent (10) and fossil (58) seal bones was performed. All bones examined were from adult animals with fused epiphyses. The catalogue numbers of the Recent seals (*Cystophora cristata*) examined are as follow:

Female: 188956 (USNM); 550317 (USNM); 188959 (USNM); 35052 (AMNH); 30632 (ZIN); 29671 (ZIN).

Males: 188938 (USNM); 269130 (USNM); 504411 (USNM); 27545 (ZIN).