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RARE LATE MIOCENE SEAL TAXA (CARNIVORA, PHOCIDAE) FROM THE NORTH SEA BASIN

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Rare Late Miocene Seal Taxa (Carnivora, Phocidae) from the North Sea Basin. Koretsky, I., Rahmat, S., Peters, N. — The discovery of new late Miocene fossil true seals from the North Sea Basin in Northern Europe provides important information regarding the radiation of monachines and phocines in the Eastern Atlantic. Examination of the first fossil seal remains from the Gram Formation, western Denmark, allowed redescriptions and emended diagnoses of several taxa. Analysis of diagnostic material recovered from western Denmark and The Netherlands shows the presence of at least three phocid genera and reveals new information on the taxonomic variability of true seals. Due to the close relationships that exist between these phocid faunas, a correlation was demonstrated between different localities of Northern and Western Europe and provides the opportunity to associate localities of the Western and Central Paratethys with the eastern and western shores of the North Atlantic. Morphological analyses of postcranial material identified three new late Miocene species (*Pontophoca jutlandica*, Subfamily Monachinae; *Gryphoca nordica* and *Platyphoca danica*, both Subfamily Phocinae), suggesting that the maximum evolutionary diversity of mid-Tertiary phocids occurred first in the Paratethys and later in the North Atlantic Basins.

Key words: seals, Miocene, Phocidae, Paratethys, Denmark, Belgium, The Netherlands.

Редкие позднемиоценовые таксоны тюленя (Carnivora, Phocidae) из бассейна Северного моря. Корецкая И., Рахмат С., Петерс Н. — Открытие новых позднемиоценовых ископаемых настоящих тюленей в бассейне Северного моря в Северной Европе даёт важные сведения о распространении представителей подсемейств Monachinae и Phocinae в Восточной Атлантике. Исследование первых остатков ископаемых тюленей из грамской свиты в западной Дании позволило переопределить несколько таксонов и уточнить их диагнозы. Анализ диагностического материала из западной Дании и Нидерландов показывает наличие как минимум трёх родов и предоставляет новые данные о таксономической изменчивости настоящих тюленей. Благодаря близким взаимоотношениям этих фаун показана корреляция между различными местонахождениями Северной и Западной Европы, что даёт возможность ассоциировать местонахождения Западного и Центрального Паратетиса с восточными и западными побережьями Северной Атлантики. При помощи морфологического анализа посткраниального материала обнаружены три новых вида из позднего миоцена (*Pontophoca jutlandica*, подсемейство Monachinae; *Gryphoca nordica* и *Platyphoca danica*, оба из подсемейства Phocinae), что указывает на то, что максимальное эволюционное разнообразие средне-третичных тюленей впервые развилось в Паратетисе и лишь позднее — в Северо-Атлантическом бассейне.

Ключевые слова: тюлени, миоцен, Phocidae, Паратетис, Дания, Бельгия, Нидерланды.

Introduction

The Family Phocidae was traditionally divided into three subfamilies: Phocinae, Monachinae and Cystophorinae (Gray, 1844–1875; Trouessart, 1897). Subsequent studies (Grassé, 1955; Scheffer, 1958; King, 1964; Chapskii, 1974) examined the morphology of various seals and supported the existence of three subfamilies. Specifically, the broad-ranging studies of Chapskii (1955, 1961, 1974) described diagnostic cranial characters, notably the number of incisors, that maintain the division of true seals into three subfamilies (Koretsky,

Rahmat, 2013). While many studies have diverged from the three-subfamily scheme (King, 1966; Burns, Fay, 1970; Muizon, 1982; Bininda-Emonds, Russell, 1996; Árnason et al., 2006), some molecular biologists have determined a need for re-evaluating pinniped morphology (Higdon et al., 2007). Due to the controversial taxonomic relationships within Phocidae, this study will continue with the more classical classification of seals in which the Family Phocidae includes carnivorans divided into three extant subfamilies (Phocinae, Monachinae, and Cystophorinae) in addition to the recently-described extinct Subfamily Devinophocinae.

In contrast with numerous Miocene true seals (= Phocidae) found in the Western Paratethys (Koretsky, 2001), occurrences of fossil seals in the northern part of Europe remain scarce. Sparse remnants of extinct seals from the late Miocene of the North Sea Basin were mainly restricted to Belgium and The Netherlands (Schneider, Heissig, 2005; Koretsky, Peters, 2008). However, the phocid fauna from Denmark, Belgium and The Netherlands described herein provides new information on taxonomic variability of true seals, demonstrating a correlation between different localities of Northern and Western Europe and providing the opportunity to associate localities of the Western and Central Paratethys with the eastern shore of the North Atlantic due to the close relationships that exist between these phocid assemblages (Koretsky, Ray, 2008; Koretsky et al., 2012). Similar species are now known from Belgium (Beneden, 1876 a, b; 1877), from The Netherlands (Schneider, Heissig, 2005; Koretsky, Peters, 2008; Koretsky et al., 2012), from France (Ginsburg, Janvier, 1975; 1999), from the Black Sea region (Simionescu, 1925; McLaren, 1960; Grigorescu, 1977; Koretsky, Grigorescu, 2002; Koretsky, Rahmat, 2013), and also from the eastern shore of the United States (Ray, 1976; Koretsky, Barnes, 2008; Koretsky, Ray, 2008). In 2008, Koretsky and Ray revised the systematic position of the Neogene seals from Western Europe by re-examining Van Beneden's (1877) material, housed in the Royal Belgian Institute of Natural Sciences in Brussels. Van Beneden was the first to mention and illustrate the majority of Neogene species from Belgium.

Due to the rarity of cranial remains, fossil seals have been classified using mainly postcranial elements, with emphasis on morphological characters of individual dissociated bones (usually the humerus or femur). Finding cranial material of fossil seals is rare due to the fragility of their skull bones, which are seldom preserved. Until now, only 12 fossil seal skulls have ever been described. Thus, postcranial bones, which are relatively abundant and well preserved and show specific ecomorphological characteristics, have commonly been used for taxonomic classification of seals (Muizon, 1981; Koretsky, 2001; Koretsky, Grigorescu, 2002; Koretsky, Ray, 2008; Koretsky, Rahmat, 2013). But in the absence of good cranial material, seals have remained one of the most controversial groups of large mammals to classify.

Where available, the humeri of different fossil seal species have most often been selected as the holotypes due to their relatively character-rich morphology among postcranial elements (e. g., Van Beneden's species). While some of these Belgian phocid specimens are not highly diagnostic due to fragmentation, they compare favorably with taxa known from the Paratethys and the eastern shore of North America. This study is a preliminary assessment of the pinniped fauna of new marine mammal collections from the Gram Formation of Jutland (Denmark), from the Antwerp area (Belgium), and from Mill-Langenboom (The Netherlands). These new and diverse assemblages consist mainly of cetaceans and late Miocene phocid pinnipeds. Although only three genera are discussed here, the actual diversity of fossil seals is much higher (Schneider, Heissig, 2005; Koretsky, Peters, 2008; Diedrich, 2011; Koretsky et al., 2012).

In this study, we describe species of several phocid genera from the late Miocene of Northern Europe, some of them previously studied by Nordmann (1860), Van Beneden (1877), and Alekseev (1924). The examination of new fossil remains from the late Miocene of the Gram Formation, Western Denmark, allowed redescrptions and emended diagnoses of several taxa, based on prior published work on North American and European material of the genera *Platyphoca*, *Gryphoca*, and *Pontophoca* (Koretsky, Grigorescu, 2002; Koretsky, Barnes, 2006; Koretsky, Ray, 2008). This study does not attempt to discuss questions about phylogenetic relationships of the described species and refrains from cladistic analysis at this time, but focuses on solving concrete alpha-systematic problems. Only after this has been done will it be possible to understand what is included under a given specific name and to initiate broader discussions of phylogenetic relationships and higher levels of classification. Details of the infra-familial arrangement of Phocidae can be found in Koretsky and Ray (2008) and in Koretsky and Barnes (2008). Herein, we describe some species from the late Miocene of Northern Europe, compare this material with seals from Western Europe and, if possible, with North American material, and also revise relevant taxa.

Material and methods

The material was collected during several years of excavation in the clay pits of Gram (Denmark) and the sandpit of Mill-Langenboom (The Netherlands) from the 1990s onwards until 2009. Geological and stratigraphic descriptions of the excavation sites in Denmark (Hansen, Hansen, 2003) and The Netherlands (Koretsky et al., 2008) have been previously given. The Danish specimens in this study are housed in the Midtønderjyllands Museum, Gram Slot and in the Geological Museum in Copenhagen, while the Dutch material is in Oertijdmuseum De Groene Poort in Boxtel (The Netherlands). These collections include 32 individual bones representing three new species of the subfamilies Monachinae and Phocinae.

Anatomical nomenclature and updated morphometric analysis of the bones of the postcranial skeleton was carried out using the methods of Aristov and Barushnikov (2001) and Koretsky (1986, 1987, 2001).

The emended diagnosis for *Pontophoca sarmatica* is based on general review of this taxon with additional information from new material from Denmark.

Abbreviations. GM — Geological Museum (Copenhagen, Denmark); MAB — Museum de Groene Poort (Boxtel, The Netherlands); MSM — Midtsønderjyllands Museum (Gram Slot, Gram, Denmark); USNM — National Museum of Natural History (Smithsonian Institution, Washington DC, USA).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Superfamily Phocoidea Smirnov 1908

Family Phocidae Gray, 1825

Subfamily Monachinae Trouessart, 1897

Genus *Pontophoca* Mc Laren, 1960

1860 (atlas 1858) *Phoca* — von Nordmann: 317, 356–357, pl. 23, fig. 3, 7; pl. 24, fig. 1; 1922 *Phoca* — Kellogg: 120 (part); 1924 *Phoca* — Alekseev: 203, fig. 4–7; 1925 *Phoca* — Simionescu: 180, 188, 190–191, fig. 5P; pl. 1, fig. 2; 1941 *Phoca* — Macarovici, Oescu: 351–352, 363–367, 378–379, fig. 7, 8; pl. 2, fig. 13, 19; 1941 *Pontophoca* — Kretzoi: 354, fig. 3.2 (nom. nud.); 1942 *Phoca* — Macarovici: 262–263, 267, pl. 2, fig. 18.1; 1947 *Phoca* — Friant: 12; 1947 *Monachus* — Friant: 6, 16, 47–50, pl. 1, fig. 1a–c; 1956 *Phoca* — Pidoplichko: 142; 1960 *Phoca* — McLaren: 51, 52; *1960 *Pontophoca* — McLaren: 47, 52, fig. 1g, h, I; 1961 *Phoca* — Kirpichnikov: 29, 32, 34, 36; 1964 *Pontophoca* — King: 131; 1965 *Phoca* — Aslanova: 52; 1977 *Phoca* — Grigorescu: 407, 411, 413–418, fig. 5D; 1979 *Phoca* — Dubrovo, Kapelist: 36; 1985 *Phoca* — Trelea, Simionescu: 19; 1992 *Phoca* — Muizon: 35; 2002 *Pontophoca* — Koretsky, Grigorescu: 149–162, fig. 1–3.

Type species: *Phoca sarmatica* Alekseev, 1924 (pl. 1, 1A, 1B). Holotype from Kishinev, Moldova, Eastern Europe (Alekseev, 1924), Middle Miocene, middle Sarmatian.

Stratigraphical range. Aside from the type locality the genus is also known from the late Miocene (early-middle Tortonian, 8.0–11.5 ma) of Denmark, northern Europe.

Included species. Until now, only the type species was included in this genus. Here, we introduce a second species, *Pontophoca jutlandica* Koretsky et al., sp. n.

Referred material. Mandible, scapula, tibiae and fibulae, femora, humeri, innominates (Koretsky, Grigorescu, 2002).

Emended diagnosis. Lower premolars p1 and p2 double-rooted, placed parallel to tooth row axis; protoconid on p2 triangular; diastemata present; metaconid and basal cingulum weakly developed. Deltoid crest of humerus terminates in middle of diaphysis, its proximal part averted in dorsal direction; distal epiphysis considerably inflated compared to proximal epiphysis; lesser tubercle located higher than proximal end of deltoid crest and head; index of head's height (ratio of head width/head height) near 100%; supracondylar crest strongly developed. Height of femoral greater trochanter slightly exceeds that of head; its distal end narrower than its proximal end; head very small compared with the otherwise massive bone and seated on narrow neck; minimal width of diaphysis located in proximal part of bone between neck and distal part of greater trochanter; distal end of femur 1.4–1.5 times broader than proximal end; condyles widely separated; maximal distance between epicondyles about or more than 70% of bone's length.

Pontophoca jutlandica Koretsky, Rahmat et Peters, **sp. n.** (pl. 1, 2A, 2B; table 1)

Holotype. Incomplete right femur MSM 1788, Midtsønderjyllands Museum, Gram Slot, Denmark.

Type locality. Gram, Jutland, Denmark, claypit of Gram Teglværk (55.29°17' N, 9.05°2' E); Gram Formation, late Miocene (early-middle Tortonian, 8.0–11.5 ma).

Etymology. After Jutland, the English name for *Jylland* (Danish: noun, neuter), Latinized to *jutlandica* (adj.) = from Jutland, the type area of the new species.

Diagnosis. Femoral trochanteric fossa deep (in contrast to *P. sarmatica*), reaching half of greater trochanter's thickness; maximal distance across epicondyles 71.0 % of absolute length; condyles very different in size; plantar fossa very distinctive and deep, outlined by thin lateral border of lateral epicondyle.

Discussion. A monachine of small size, similar to *P. sarmatica* (Koretsky, Grigorescu, 2002). Differences from *P. sarmatica* (pl. 1, 1A, 1B): The distal end of the greater trochanter

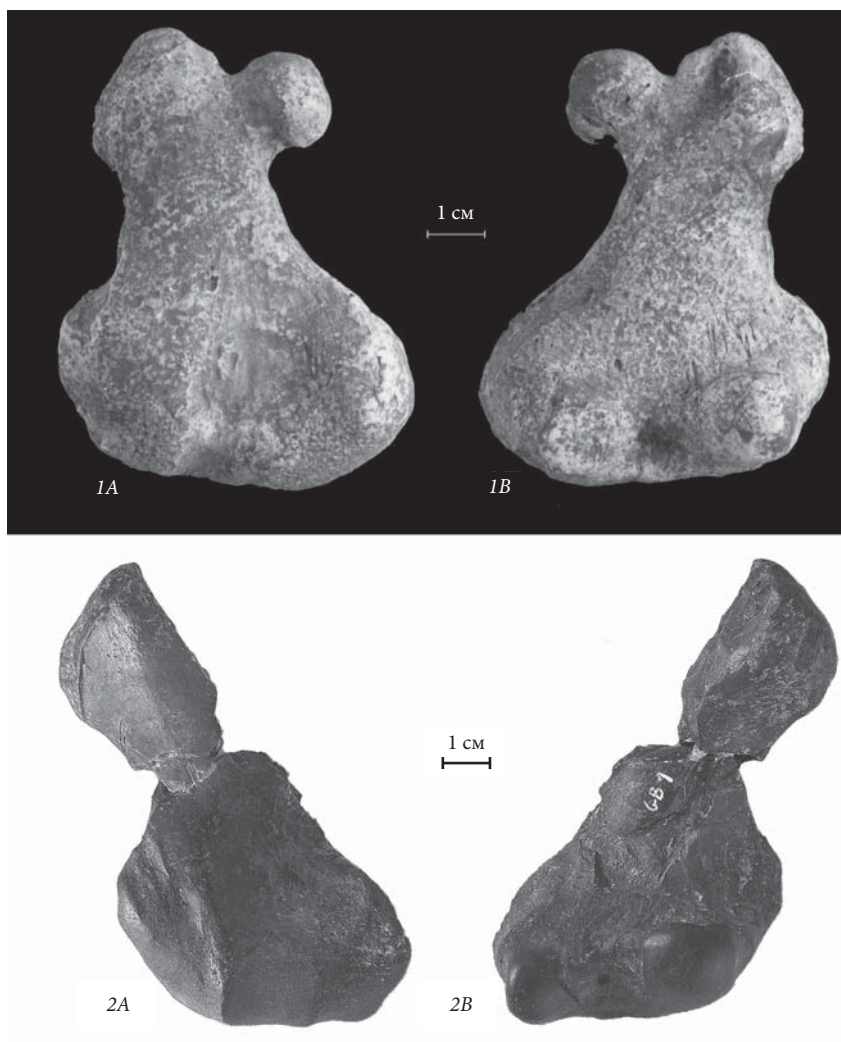


Plate 1.

Fig. 1. *Pontophoca sarmatica*, right femur; Kishinev, Moldavia (Middle Miocene, middle Sarmatian); after Koretsky, Grigorescu (2002: fig. 3); USNM 214980: 1A — cranial; 1B — caudal view.

Fig. 2. *Pontophoca jutlandica* sp. n., holotype, incomplete right femur; Gram, Jutland, Denmark. Clay pit of Gram Teglværk, Gram Formation (late Miocene, early-middle Tortonian, 8.0–11.5 ma); MSM 1788: 2A — cranial; 2B — caudal view.

Рис. 1. *Pontophoca sarmatica*, правая бедренная кость; Кишинев, Молдова (средний миоцен, средний сармат); по: Koretsky, Grigorescu (2002: рис. 3); USNM 214980: 1A — вид спереди; 1B — вид сзади.

Рис. 2. *Pontophoca jutlandica* sp. n., голотип, неполная правая бедренная кость; Грам, Ютландия, Дания. Карьер Грамского кирпичного завода, грамская свита (поздний миоцен, верхний-средний тортон, 8,0–11,5 млн лет назад); MSM 1788: 1A — вид спереди; 1B — вид сзади.

Table 1. Measurements of femora

Таблица 1. Измерения бедренных костей

Characters, mm	Pontophoca	
	sarmatica	jutlandica
Absolute length	76.5–96.0	
Medial length	74.0–88.0	
Lateral length	71.5–80.5	84.7
Length of medial condyle	15.0–21.0	15.4
Length of lateral condyle	16.0–22.0	21.0
Length of greater trochanter	25.0–30.0	31.8
Intertrochanteric length	28.5–38.0	
Height of head	17.2–23.0	
Height of articular area of patellar surface	15.9–22.0	19.0
Width of proximal epiphysis	36.0–44.0	
Width of distal epiphysis	54.5–66.0	54.5
Width of condyles	42.6–50.5	43.1
Width of greater trochanter	14.5–18.0	16.5
Width of head	17.5–20.7	
Width of diaphysis	24.5–29.5	
Thickness of diaphysis, anteroposterior	11.0–12.5	13.0
Thickness of medial condyle	16.0–20.0	16.6
Thickness of lateral condyle	24.0–27.0	25.2
Distance between condyles	12.0–15.5	16.7
Diameter of neck	14.0–17.5	

is narrower and has a V-shaped termination. The trochanteric fossa is deep, elongated along the femoral axis, wide, and reaches the middle of the greater trochanter's length. This fossa is open on the proximal side of the greater trochanter. The condyles are very widely spaced (maximal distance across them is 71.1 % of the bone's length). In contrast to *P. sarmatica*, the condyles are very different in size. The plantar fossa is located medial to the lateral epicondyle, making the outside border of the lateral epicondyle very thin.

The anatomical features and size of this femur are compatible with the similar bone of the type species of *Pontophoca* (table 1). We assign the femur to a new species, as it comes from the same geological time as the confidently referred material of *Pontophoca sarmatica*. The comparison with material of *P. sarmatica* is limited since the femur of *P. jutlandica* lacks the medial part of the bone. However, the preserved section of the femur bears enough distinct characters to distinguish it as a new species of *Pontophoca*. For detailed study and descriptions of humerus, femur, and other postcranial elements of *Pontophoca sarmatica* see Koretsky and Grigorescu (2002).

Family Phocidae Gray, 1825

Subfamily Phocinae Gill, 1866

Genus *Gryphoca* Van Beneden, 1877

1876 a *Gryphoca* — Van Beneden: 798 (nom. nud.); *1877 *Gryphoca* Van Beneden: 69, atlas pl. 13; 1897 *Gryphoca* — Toula: 52, 55; 1897 *Halichoerus (Gryphoca)*: Trouessart, p. 382; 1909 *Gryphoca* — Dollo: 118; 1922 *Gryphoca* — Kellogg: 115; 1945 *Gryphoca* — Simpson: 122; 1947 *Halichoerus (Gryphoca)*: Friant, p. 6; 1958 *Gryphoca* — Misonne: 22; 1964 *Gryphoca* — King: 131; 1977 *Gryphoca* — Ray: 394; 1983 *Gryphoca* — Savage, Russell: 294; 1992 *Gryphoca* — Muizon: 36; 1997 *Gryphoca* — McKenna, Bell: 258; 2008 *Gryphoca* — Koretsky, Ray: 89–90.

Type species and locality: *Gryphoca similis* Van Beneden, 1877, holotype from the 3rd section of Borgerhout, Antwerp area, Belgium.

Stratigraphical range. Apart from the type locality of *Gryphoca similis*, the genus *Gryphoca* is known from the Pliocene (Scaldisian) of the Antwerp area, Belgium, from the late

Miocene (early-middle Tortonian, 8.0–11.5 ma) Gram Formation of Gram, Jutland, western Denmark, from the late Miocene or early Pliocene of Mill-Langenboom, The Netherlands, and from the Pliocene (5.0–5.8 ma) Yorktown Formation, eastern United States.

Referred material. Humeri, scapula, innominate, femora, tibia and fibula from the Antwerp area, Belgium, from western Denmark, from Mill-Langenboom, The Netherlands, and from the eastern United States (Koretsky, Ray, 2008).

Emended diagnosis. Phocine of medium size similar to modern *Halichoerus grypus*. Deltoid crest of humerus short, narrow, and thin, terminating about 1/2 length of bone; its distal end gently broadening and somewhat overhanging the bone; lesser tubercle located slightly above head and proximal part of deltoid crest; intertubercular groove narrow and deep; medial epicondyle reaches distal end of deltoid crest; entepicondylar foramen present. Femoral greater trochanter higher than head; minimal width of shaft located in middle part of femur; epicondyles very thin

Discussion. The rare taxon *Gryphoca similis* is represented in Van Beneden's collection only by a few fragmentary bones: humeri and femora, scapula, innominate, tibia and fibula. All bones show very distinctive morphological features and the same applies to the material from the eastern United States (Koretsky, Ray, 2008). Although the morphologies of the fossils from Western Denmark and The Netherlands described in this paper are very similar, the bones also differ in several aspects. Nonetheless, we are sure about the assignment of these new fossils to a new species of the genus *Gryphoca*.

Gryphoca nordica Koretsky, Rahmat et Peters, **sp. n.** (pl. 2, 2A–2D, 3A–3D; table 2)

Holotype. Incomplete right humerus MAB 4602 (pl. 2, 2A–2D), Oertijdmuseum de Groene Poort, Boxtel, The Netherlands.

Paratypes. From the type locality: *R. humerus* (distal half) MAB 4604; *L. humerus* (distal half) MAB 4700; *L. humerus* (proximal half) MAB 460. All in Oertijdmuseum de Groene Poort, Boxtel (51.61°36' N, 5.32°19' E).

From Gram, claypit of Gram Teglværk, Jutland, Denmark, marine Gram Formation: *R. humerus* MSM 1404x1 (pl. 2, 3A–3D); *L. femur* (distal part) MSM 1004x1; both in Midtønderjyllands Museum, Gram Slot, Denmark.

Type locality. Underwater sandpit “de Kuilen”, Mill-Langenboom, province of Noord Brabant, The Netherlands, late Miocene — early Pliocene.

Stratigraphical range. Late Miocene — early Pliocene of Mill-Langenboom, The Netherlands (Wijnker et al., 2008) and late Miocene (early–middle Tortonian, 8.0–11.5 ma) of Gram, Jutland, Denmark (Hansen, Hansen, 2003).

Etymology. After *nord* (Danish: noun, neuter) = the North, Latinized to *nordica* (adj.) = from the North, referring to the northern part of Europe.

Diagnosis. Deltoid crest of humerus with ventral border very sharp and sculptured, overhanging deep spiral groove; lesser tubercle flattened, rectangular, deviates almost 45° from bone's axis; head compressed in cranio-caudal direction; ratio of head width / head height — 97 %.

Description and comparison. Postcranial elements of *Gryphoca nordica* belong to a medium-sized representative of Phocinae, equivalent in size to Recent *Histiophoca fasciata*. Morphological characters similar to *Gryphoca similis* (pl. 2, 2A–2D) are: the deltoid crest is strongly developed, with its maximum width in its proximal part at the level of the lesser tubercle. The deltoid tuberosity is weakly developed, but clearly seen on the proximal part of the deltoid crest. The intertubercular groove is narrow and deep. The ventral border of the deltoid crest is very sharp and sculptured, overhanging as an anconeal crest (ac, pl. 2, 1D). The radial groove (= musculospiral groove) is strongly developed (sg, pl. 2, 1D).

The new species *G. nordica* differs from *Gryphoca similis* by its smaller size. In addition, the head of the humerus is compressed in the cranio-caudal direction, not round in shape.

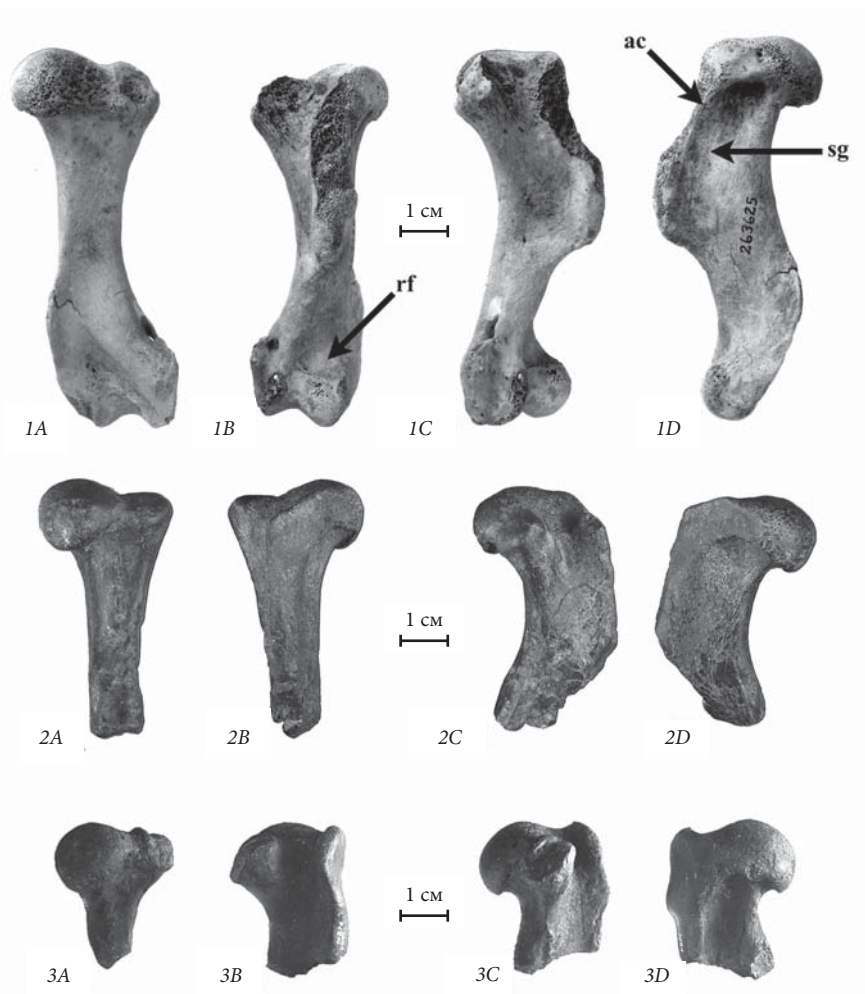


Plate 2.

Fig. 1. *Gryphoca similis*, left humerus. Lee Creek Mine Yorktown Formation (Pliocene, 5.0–5.8 ma); after Koretsky, Ray (2008: fig. 16–18); USNM 263625: 1A — caudal; 1B — cranial; 1C — medial; 1D — lateral view.

Fig. 2. *Gryphoca nordica* sp. n., holotype, incomplete right humerus (reversed); underwater sandpit 'de Kuilen', Mill-Langenboom, province of Noord Brabant, The Netherlands (late Miocene); Oertijdmuseum de Groene Poort, Boxtel; MAB 4602: 2A — caudal; 2B — cranial; 2C — medial; 2D: lateral view.

Fig. 3. *Gryphoca nordica* sp. n., paratype, proximal part of right humerus (reversed); Gram, Jutland, Denmark. Clay pit of Gram Teglvaerk, Gram Formation (late Miocene, early-middle Tortonian, 8.0–11.5 ma); MSM 1404x1 (cast in Geological Museum, Copenhagen, Denmark): 3A — caudal; 3B — cranial; 3C — medial; 3D — lateral view. Abbreviations: ac — anconeal crest; rf — radial fossa; sg — spiral groove.

Рис. 1. *Gryphoca similis*, левая плечевая кость из Ли-Крик, формация Йорктаун (плиоцен, 5.0–5.8 млн лет назад); по: Koretsky, Ray (2008: рис. 16–18); USNM 263625: 1A — вид спереди; 1B — вид сзади; 1C — вид с медиальной стороны; 1D — вид с латеральной стороны.

Рис. 2. *Gryphoca nordica* sp. n., голотип, неполная правая бедренная кость (перевернута); песчаный подводный карьер «Де-Кейлен», Милл-Лангенбом, провинция Северный Брабант, Голландия (поздний миоцен); Доисторический музей Груне-Порт, Бокстел; МАВ 4602: 2A — вид сзади; 2B — вид спереди; 2C — вид с медиальной стороны; 2D — вид с латеральной стороны.

Рис. 3. *Gryphoca nordica* sp. n., паратип, проксимальная часть правой плечевой кости (перевернута); Грам, Ютландия, Дания; карьер Грамского кирпичного завода, грамская свита (поздний миоцен, верхний-средний тортон, 8.0–11.5 млн лет назад); MSM 1404x1 (копия из Геологического музея, Копенгаген, Дания): 3A — вид сзади; 3B — вид спереди; 3C — вид с медиальной стороны; 3D — вид с латеральной стороны. Сокращения: ac — локтевой гребень; rf — лучевая ямка; sg — спиральная борозда.

The proximal part of the deltoid crest is located at the same level as the lesser tubercle and slightly above the head. The lesser tubercle resembles a flattened rectangle, deviates almost 45° from the bone's axis, and is situated slightly above the head, but higher than the greater tubercle.

The supracondylar fossa of the femur, located above the lateral condyle, is easily visible. The patellar surface is very pronounced, sharp and has a prominent outlinesculptural compared to the bone's overall surface.

Discussion. The rare genus *Gryphoca* was introduced by Van Beneden (1877) based on material from the Antwerp area, Belgium. Although the genus is known to researchers by name, it appears that no one except Ray (1976) has re-examined the original material critically. Koretsky and Ray (2008) re-evaluated, described and compared West European and North American material, and proposed a diagnosis for the genus *Gryphoca*. In this study, we assign a new, smaller species, *G. nordica*, to the genus *Gryphoca* on the basis of only a few fragmentary and rolled bones (but with very distinctive morphological features) from the late Miocene of Northern and Western Europe.

Because none of the specimens in the Denmark collection is complete, we choose the humerus from The Netherlands (with the same geological age, better preservation, and apparently the same morphology; see pl. 2, 2A–2D, and table 2) as the best available holotype.

The fragmentary remains, as well as the lack of further postcranial elements, may raise some doubts about their assignment to the genus *Gryphoca*. However, the preserved material (four humeri and a femur) and previous publications based on the Western European and eastern United States material (Beneden, 1877; Koretsky, Ray, 2008), allow, with a high degree of probability, assignment of this seal to the genus *Gryphoca* and the introduction of a new taxon of specific rank. We think this approach is more justified than establishment of a new taxon of generic rank.

Furthermore, according to the ecomorphotype hypothesis of Koretsky (2001), these bones belong to the same group (ecomorphotype V) on the basis of characters such as: lesser tubercle slightly higher than or at same level as the head of the humerus, and deviates from the bone's axis; intertubercular groove narrow; maximum width of the deltoid crest located in its proximal part. Ecomorphological analysis is here applied on the level of alpha systematics.

Subfamily Phocinae Gill, 1866

Genus *Platyphoca* Van Beneden, 1877

1876 a *Platyphoca* Van Beneden: 798 (nom. nud.); *1877 *Platyphoca* Van Beneden: 67–68; 1904 *Phoca* (*Platyphoca*) Trouessart: 285; 1909 *Platyphoca* Dollo: 118; 1922 *Platyphoca* Kellogg: 117; 1945 *Platyphoca* Simpson: 122; 1947 *Phoca* (*Platyphoca*) Friant: 7, 10, 14; 1958 *Platyphoca* Misonne: 22; 1964 *Platyphoca* King: 131; 1977 *Platyphoca* Ray: 94; 1983 *Platyphoca* Savage, Russell: 294; 1992 *Platyphoca* Muizon: 36; 1997 *Platyphoca* McKenna, Bell: 258; 2008 *Platyphoca* Koretsky, Ray: 84–85, 103–105.

Type species: *Platyphoca vulgaris* Van Beneden, 1877, by original monotypy. Holotype from middle (?) Pliocene (Scaldisian) deposits in the Antwerp area, Belgium.

Stratigraphical range. The type species is also known from the Pliocene (5.0–5.8 ma) Yorktown Formation of the eastern United States. Herein, we introduce a new species from the late Miocene (early-middle Tortonian, 8.0–11.5 ma) Gram Formation of Gram and Skærum Mølle, Jutland, western Denmark.

Referred material. Humeri, 2nd phalanx, innominata, metatarsal IV, tibia, and humeri from the Antwerp area, Belgium, from western Denmark, and from the eastern United States (see Koretsky, Ray, 2008).

Emended diagnosis. Deltoid crest of humerus very short and terminating at less than 1/2 of length of bone; from base of lesser tubercle, along medial surface of bone, passes a crest that is only slightly shorter than deltoid crest; maximal enlargement of deltoid

Table 2. Measurements (mm) of humeri

Таблица 2. Измерения (мм) плечевых костей

Characters, mm	Gryphoca		Platyphoca	
	similis	nordicum	vulgaris	danica
Absolute length	125.0			
Length of deltoid crest	68.5–79.0			
Height of head	23.5–26.5	21.2–26.7		
Height of trochlea	20.0–23.0	17.8–20.0	22.0–25.0	24.3
Width of head	21.5–28.5	25.2–28.7		
Width of deltoid crest	20.0	24.9–29.0		
Width of distal epiphysis	35.0–42.0	35.5–41.5	64.5–65.5	52.8
Width of proximal epiphysis	36.0–43.5	38.4–46.2		
Width of trochlea distally	21.5–25.5	18.0–22.4	28.0–29.5	21.5
Width of trochlea, frontal view	24.5–30.0	20.0–28.2	26.0–30.0	20.3
Transverse width of diaphysis	12.0–20.0	15.3–22.6	18.0–26.0	
Thickness of proximal epiphysis	39.0–48.0	41.2		
Thickness of medial condyle	21.5–22.5	17.5–19.0	27.0–28.0	22.6
Thickness of lateral condyle	19.5–23.0	20.1–25.6	26.0–28.0	24.0
Diameter of diaphysis with deltoid crest	30.0–40.0	29.0–31.0	42.0–44.5	

crest in its proximal part; intertubercular groove very shallow and not well defined; both epicondyles well developed and very wide; distal part of each epicondyle flat.

Discussion. *Platyphoca vulgaris* (pl. 3, 1A–1B) was originally mentioned by Van Beneden (1876 a), who considered it to be very close to the Recent *Erignathus barbatus*. The size of the humerus approaches that of *Erignathus* more closely than any other phocid. This poorly known, obscure, but distinctive species was described on the basis of only a few bones of the postcranial skeleton. *P. vulgaris* was a very large animal, perhaps similar in size to the modern species *Cystophora cristata*. This intriguing species has been virtually ignored in the literature except for a few comprehensive works, where *Platyphoca vulgaris* is listed among species from the Pliocene of Europe (e. g. Trouessart, 1904; Kellogg, 1922; Simpson, 1945; King, 1964; Muizon, 1992).

Platyphoca danica Koretsky, Rahmat et Peters, **sp. n.** (pl. 3, 2A–2B; table 2)

Holotype. Distal part of the left humerus (pl. 3, 2A–2B), GM1, Geological Museum, Copenhagen, Denmark. Cast in Museum Midtsønderjyllands Museum, Gram Slot; number refers to collection number of original in Copenhagen.

Type locality. Skærum Mølle, Jutland, Denmark (56.33°20' N, 8.35°21' E).

Stratigraphical range. Gram Formation, late Miocene (early-middle Tortonian, 8.0–11.5 ma).

Etymology. After *Dania* (Latinized, noun, feminine) — Denmark; *danica* (Latinized, adj.) — from Denmark.

Diagnosis. Coronoid and olecranon fossae of humerus wide and shallow; extended more proximally than medial epicondyle, almost reaching distal part of deltoid crest; entepicondylar foramen large, with wide bridge over it; thin lateral epicondyle very elongated, but does not reach distal part of deltoid crest; medial epicondyle wide and flattened, its lateral border forming an oval that is oriented 45° to the bone's axis.

Description and comparison. The humeral trochlea is very pronounced, especially the capitulum. The groove between the trochlea and capitulum (the middle of the internal crest of the humeral trochlear) is flattened near the floor of the coronoid fossa, unlike that in Monachinae (= arch-like) or Cystophorinae (= appearing wave-like over the coronoid fossa) (Koretsky, Rahmat, 2013; fig. 3). The trochlea is higher and more prominent than in *P. vulgaris* (pl. 3, 1A–1B). The coronoid and olecranon fossae are so shallow (in contrast to *P. vulgaris*) that they are barely outlined. They extend more proximal than the

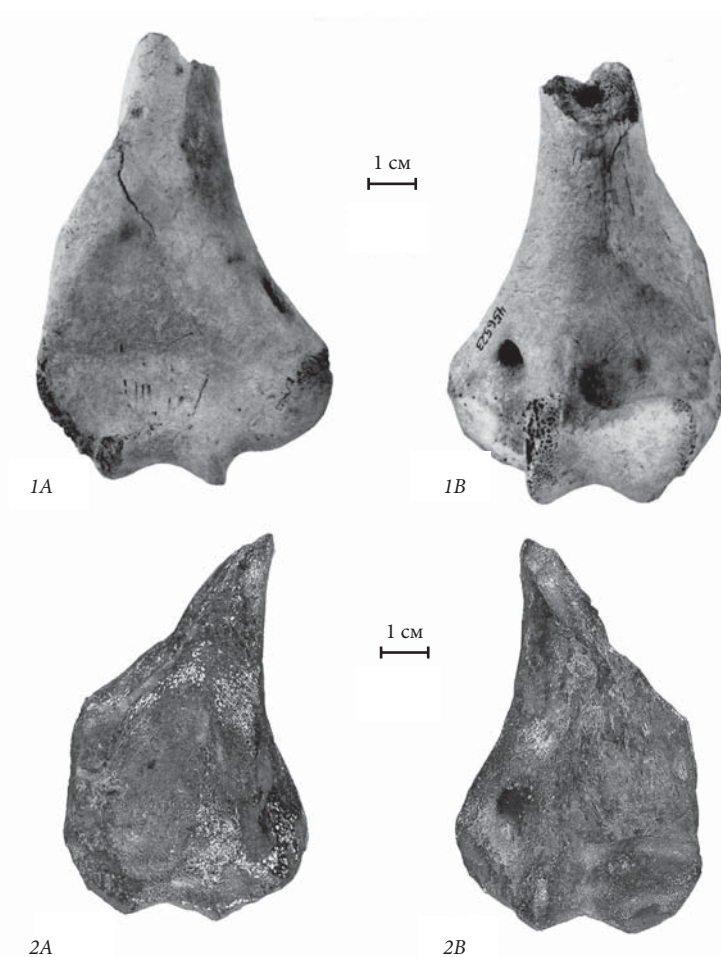


Plate 3.

Fig. 1. *Platyphoca vulgaris*, distal part of left humerus. Lee Creek Mine, Yorktown Formation (Pliocene, 5.0–5.8 ma); after Koretsky, Ray (2008: fig. 2 E–F); USNM 456523: 1A — caudal; 1B — cranial view.

Fig. 2. *Platyphoca danica* sp. n., holotype, distal part of left humerus. Skærum Mølle, Jutland, Denmark, Gram Formation (late Miocene, early-middle Tortonian, 8.0–11.5 ma); GM1: 2A — caudal; 2B — cranial view.

Рис. 1. *Platyphoca vulgaris*, дистальная часть левой плечевой кости; из Ли-Крик, формация Йорктаун (плиоцен, 5,0–5,8 млн лет назад); по: Koretsky, Ray (2008: рис. 2 E–F); USNM 456523: 1A — вид сзади; 1B — вид спереди.

Рис. 2. *Gryphoca danica* sp. n., голотип, дистальная часть левой плечевой кости; Скерум-Мёлле, Ютландия, Дания; грамская свита (поздний миоцен, верхний-средний торгон, 8,0–11,5 млн лет назад); GM1: 2A — вид сзади; 2B — вид спереди.

medial epicondyle and do not reach the distal part of the deltoid crest. The entepicondylar foramen is large, oval (in contrast to *P. vulgaris*), with a broad and flat bridge over it. The lateral epicondyle is narrow, very elongated, and does not reach the distal part of the deltoid crest, but extends farther proximally than the medial epicondyle (as in *P. vulgaris*). The medial epicondyle is oval (in contrast to *P. vulgaris*) and forms a 45° angle with the bone's axis. The distal epiphysis is narrower and thinner than in *P. vulgaris*. The entire bone is unusually flat, and slender. Collectively, these features lend a spatula-like appearance of the distal end of the humerus. The general appearance of the bone suggests that it belongs to the genus *Platyphoca*, as indicated above.

Discussion. Although a comparison with the humerus of *P. vulgaris* is limited due to the absence of the proximal part of the bone as well as by its origin from a different geological age, this Danish humerus is compatible with humeri of *Platyphoca vulgaris* in several anatomical characters and its size. At the same time, the preserved part of the humerus appears to bear enough distinctive characters to describe a new taxon.

Similar to *Gryphoca*, the unusual and rare taxon *Platyphoca* is known to researchers by name and was critically re-examined by Ray (1976) and Koretsky and Ray (2008). Despite the fragmentary representation of this species in Van Beneden's original collection, the examination of additional fossil material from the Lee Creek Mine (USA) shows the same very distinctive morphological features (such as spatula-like distal end of the humerus). The high affinity of this newly described humerus from Denmark with *Platyphoca* and the amount of similar fossil material from other parts of the world indicate that *Platyphoca danica* represents an identifiable species.

Conclusion

Not surprisingly, the majority of phocid material recovered from the late Miocene Gram Formation of Western Denmark is referable to the Subfamily Phocinae. However, the occurrence of the genus *Pontophoca* in the same deposits demonstrates the presence of the Subfamily Monachinae further north along the Atlantic coast of Northern Europe than previously known. While the fragmentary nature of many of the postcranial bones used to classify new seal species can be questioned, specific morphologically-defining features present on these bones (described above) make it possible to clearly differentiate seal taxa. The difficulty in finding well-preserved cranial and sometimes postcranial material has been a persistent problem throughout the study of phocids. Thus, it is unavoidable and commonplace to classify seals based on distinctive characteristics of a few isolated bones (usually the humerus or femur). Obviously, as new material (both cranial and postcranial) becomes available, these results will be revised, as has been the case since the earliest days in this field when whole phylogenies were based on isolated teeth.

Moreover, all the phocid material from Jutland, Denmark, was recovered from late Miocene (early-middle Tortonian) sediments. Therefore, its age is intermediate between the much older seals from the Eastern Paratethys, such as *Pontophoca sarmatica* (middle Sarmatian of the northern Black Sea littoral) and the much younger phocids, such as *Gryphoca similis* and *Platyphoca vulgaris*, from the Pliocene (Scaldisian) of Belgium and the Pliocene (Yorktown Formation) of the eastern United States. These results support the previous suggestion (Koretsky, Barnes, 2006) that the earliest known occurrence and maximum evolutionary diversity of mid-Tertiary phocids occurred first in the Paratethys and later in the North Atlantic Basin.

Therefore, this fossil pinniped material from the North Sea Basin provides important additional information regarding the radiation of monachines and phocines in the Eastern Atlantic. Analysis of the diagnostic material recovered from western Denmark and The Netherlands shows the presence of at least three phocid species belonging to three distinct genera, with the possibility that more species may be represented in yet undescribed material. Until articulated or better-associated fossil material is recovered, the possibility that even more than three species may be represented remains open.

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