

UDC 569.745.3“6235”(261.2)

NEW SPECIES OF *PRAEPUSA* (CARNIVORA, PHOCIDAE, PHOCINAE) FROM THE NETHERLANDS SUPPORTS EAST TO WEST NEOGENE DISPERSAL OF TRUE SEALS

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New Species of *Praepusa* (Carnivora, Phocidae, Phocinae) from the Netherlands Supports East to West Neogene Dispersal of True Seals. Koretsky, I. A., Peters, N., Rahmat, S. — Examination of new fossils (humerus and sacrum) from The Netherlands reveals morphologically-distinctive characters, allowing the description of a new Late Miocene — Early Pliocene representative (*Praepusa boeska* sp.n.) of the subfamily Phocinae. Diagnostic humeral differences in shape of the coronoid (oval in males vs triangular in females) and depth of the olecranon fossae (shallow in males vs deep in females), as well as the presence of a rounded first ventral foramen and thick lateral wall in the male sacrum, reveal the first evidence of sexual dimorphism in the genus *Praepusa*. The newly described species adds information on the distribution of true seals, supporting the westward dispersal of this genus across the Paratethys. Strong endemism from closure of the Paratethys, and climatic, geological and stratigraphic differences indicate that *Praepusa* first inhabited the Eastern Paratethys (Early — Middle Miocene, 16.5–13.6 Ma) before dispersing to the Central (Middle Miocene, 13.6–11.2 Ma) and, later, Western (Late Miocene — Early Pliocene, 11.6–3.6 Ma) Paratethys. The *Pr. boeska* fossils are the youngest to date and have been found the furthest west of any previously described material of this genus. These findings help explain the origin and dispersal among described species of the genus *Praepusa* in comparison with other genera of the subfamily Phocinae.

Key words: seals; Phocinae; Miocene; Pliocene; Paratethys; North Atlantic.

Новый вид *Praepusa* (Carnivora, Phocidae, Phocinae) из Нидерландов, подтверждающий распространение настоящих тюленей в неогене с востока на запад. Корецкая И. А., Петерс Н., Рахмат С. — Исследование новых ископаемых остатков (плечевой кости и крестца) из Нидерландов показывает морфологически отличительные признаки, позволяющие описать нового представителя подсемейства Phocinae (*Praepusa boeska* sp.n.) из позднего миоцена — раннего плиоцена. Диагностические различия в форме клювовидного отростка плечевой кости (овальной у самцов по сравнению с треугольной у самок), глубине ямки локтевого отростка (мелкой у самцов по сравнению с глубокой у самок), а также наличии округлого первого вентрального отверстия и толстой боковой стенки в крестце самцов обнаруживают первые доказательства полового диморфизма у представителей рода *Praepusa*. Описанный вид добавляет информацию о распространении настоящих тюленей, подтверждая расселение этого рода на запад через Паратетис. Высокая степень эндемизма вследствие изоляции Паратетиса и климатические, геологические и стратиграфические отличия указывают, что проникновение *Praepusa* в Восточный Паратетис (ранний — средний миоцен, 16,5–13,6 млн лет назад) произошло до заселения им Центрального (средний миоцен 13,6–11,2 млн лет назад), а позже и Западного Паратетиса (поздний миоцен — начало плиоцена, 11,6–3,6 млн лет назад). Ископаемые остатки *Pr. boeska* являются наиболее ранними из остатков известных на сегодняшний день представителей этого рода и были обнаружены намного западнее ранее описанного палеонтологического материала. Эти находки помогают объяснить происхождение и расселение описанных видов рода *Praepusa* по сравнению с другими родами подсемейства Phocinae.

Ключевые слова: тюлени, Phocinae, миоцен, плиоцен, Паратетис, Северная Атлантика.

Introduction

This study is the third in a series of publications under one general title: “Miocene Seals of The Netherlands”. The first paper, “A new species of *Leptophoca* (Carnivora, Phocidae, Phocinae) from both sides of the North Atlantic Region” (Koretsky et al., 2012), detailed the geology of the south-eastern part of the province

of Noord-Brabant in The Netherlands. The second publication, “A new genus *Batavipusa* (Carnivora, Phocidae, Phocinae) from the eastern shore of the North Atlantic Ocean” (Koretsky, Peters, 2008) described a new genus named *Batavipusa* and explained the history of the genus *Phocanella* (Van Beneden, 1877).

Among Neogene seals, phocine fossil remains from the Middle, and especially from the Late, Miocene deposits of the Western Paratethys are relatively numerous, particularly in Belgium (Van Beneden, 1876, 1877; Koretsky, Ray, 2008), the Vienna Basin (Blainville, 1842), France (Friant, 1942, 1947; Ginsburg, Janvier, 1975, 1999), and now in The Netherlands (Schneider, Heissig, 2005; Koretsky, Peters, 2008; Koretsky et al., 2012). Despite the wide distribution of seals of the subfamily Phocinae, the abundance of recovered fossil remains, and numerous previous studies, many important aspects of morphology, phylogeny and systematics of the subfamily remain obscure. This ambiguity holds true for the genus *Praepusa* described by Kretzoi in 1941. After that first description, another species (*Pr. tarchankutica* Antoniuk et Koretsky, 1984) was reported, leading to the first diagnosis for the genus *Praepusa* that compared it with remaining genera of the subfamily Phocinae. Consequent studies by Koretsky (2001, 2003) revised material that historically was assigned to this taxon, described several additional species, and generated a diagnosis and re-description of the partial fossil skeleton, changing the knowledge of geographical distribution and geological implications of *Praepusa*.

Recently, a small collection of fossils from the Western Paratethys has been accumulated, including postcranial bones referable to this genus. The new material enabled a more precise and detailed diagnosis, the redescription of some fossil material, and defined the distribution of the genus *Praepusa*. Thus, different species from Kazakhstan, the Vienna Basin, Hungary, and The Netherlands have been reassigned to the genus *Praepusa* (Koretsky, 2001, 2003). This approach increases the degree of nomenclature stability in Phocinae rather than erecting a new genus from material that is similar in morphology and originated from relatively comparable geological deposits. In this study, we describe a previously unknown Late Miocene — Early Pliocene representative of the subfamily Phocinae from Holland and Belgium, and discuss its relationship with other phocids. We provide the first description of sexual dimorphism within *Praepusa* and its biogeographical implications, including the likely dispersal pattern of this genus across the Paratethys from east to west.

In 1975, the curator of the Natural History Museum in Leiden, D. A. Hooijer, described a small partial seal sacrum that was dug up by a shell dredging ship from the Westerschelde. There appeared to be a striking resemblance between this bone and the sacrum of *Phocanella minor*, a small seal found in the sediments of Antwerpen, Belgium that was described by Van Beneden (1877; plate 14, fig. 18 and 19). More than 35 years later, the present curator of the Naturalis Biodiversity Centre (Dr. John de Vos) recently showed us another sacrum that did not originate from the Westerschelde. This sacrum is more complete and better preserved than the two pieces that were found earlier. The sacrum was uncovered in 1980 during the construction of a sewage purifying plant in Boeichout, located in the south-east region of Antwerpen, Belgium, from Oorderen sands, Lillo formation, now called Zanclean-Piacenzian (Pliocene). This specimen was donated to the Naturalis Biodiversity Centre in Leiden. To clarify phylogenetic relationships within *Praepusa*, there needs to be a re-examination of fossils previously attributed to this genus and their comparison with new *Praepusa* fossils found in recent years (Antwerpen, Mill-Langenboom).

According to the stratigraphy of the Mill-Langenboom locality as described by Wijnker et al. (2008), we can determine that the remains of fossil true seals from the “de Kuilen” sandpit (fig. 1) have an age that ranges from Late Miocene to Early Pliocene, (between about 11.5–3.5 Ma). The ex-situ finds originated from early-middle Tortonian sediments to early Piacenzian.

Abbreviations: NL — The Netherlands; MAB — Museum de Groene Poort; RGM — Nationaal Natuurhistorisch Museum.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Superfamily Phocoidea Gray, 1821

Family Phocidae Gray, 1821

Subfamily Phocinae Gray, 1821

Genus *Praepusa* Kretzoi, 1941

Phoca Blainville, 1840 : 41–42, pl.10, fig. 1; Brühl, 1860 : 1–16, fig. 2; Peters, 1867 : 110–111; Toula, 1897 : 55–70, pl. 2, fig. 9–11; Trouessart, 1897 : 385, 1904 : 286; Kellogg, 1922 : 119–120; Alekseev, 1924 : 32; Bogachev, 1927 : 141–143, 145; Kretzoi, 1941 : 350–356, fig. 1; Friant, 1947 : 7, 12, 16, 45, 47, table 2, fig. 1a–c; King, 1964 : 131; Thenius, 1969 : 319; McLaren, 1960 : 51–52, 56, 58; Hendey, Repenning, 1972 : 85; Ray, 1977 : 395, 398; Grigorescu, 1977 : 407, 412, 417; Nicolas, 1978 : 456; Muizon, 1982:190, 205.

“*Phoca*” — McLaren, 1975 : 44; Mitchell, 1975:23.

Praepusa Kretzoi, 1941 : 351–356, fig. 1; McLaren, 1960 : 55–56, 59; Thenius, 1969 : 404; Grigorescu, 1977: 407, 412, 417; Antoniuk, Koretsky, 1984 : 27–29, fig. 1–3; Koretsky, 1987 b : 3–6, fig.1; 2001 : 46–55, fig. 18–30; 2003 : 63–70, fig. 1–4; Koretsky, Ray, 1994 : 20; McKenna, Bell, 1997 : 257.

Leptophoca? — Ray, 1977 : 395, 398; Savage, Russell, 1983 : 292; Muizon, 1992 : 35.

Type species. *Praepusa pannonica* Kretzoi, 1941:351–356, fig. 1.

Included species. *Praepusa pannonica* Kretzoi, 1941, from the early-middle Sarmatian (Middle Miocene) of Hungary and from the middle Sarmatian of Moldova; *Praepusa vindobonensis* Toulou, 1897 from the early Sarmatian of Austria (Nussdorf) and from the middle Sarmatian of the Ukraine and Moldova; *Pr. magyaricus* Koretsky, 2003, Sarmatian age of the Vienna Basin. *Praepusa boeska* sp.n., from the Late Miocene — Late Pliocene (Tortonian–Piacenzian Stages, 11.5–3.5 Ma) sandpit de Kuilen, Mill-Langenboom, Noord-Brabant, S. E. Netherlands; and Pliocene and Miocene? of the Antwerp Basin, Belgium.

Emended and expanded diagnosis. Cranial diagnosis the same as for *Praepusa vindobonensis*; mandibular diagnosis the same as for *Pr. pannonica*.

Deltoid crest of humerus has shape of sharp blade; lesser tubercle elongated along axis of bone; head width to height ratio greater than 0.964; lateral epicondyle reaches distal part of deltoid crest.

Greater trochanter of femur considerably higher than head; its proximal and distal parts approximately of equal width; trochanteric fossa wide and medially open, but deep; head slightly deflected distally and seated on narrow, long neck; minimal width of diaphysis in middle part of bone; maximal intercondylar distance 12.0–15.8 % of femoral length.

Sacrum consists of three fused short vertebrae with smaller alae, and narrower bases than in *Phocanella*; cranial articular processes (*processus articularis cranialis*) shorter, flattened with square bases; foramina smaller, wider and shorter, base not round, but rectangular shape; lateral sacral crests oblong in shape, more elongated and reaching above second dorsal foraminae, in contrast to *Phocanella pumilla* where crests reach only lower (distal) part of foramina.

Discussion. Extensive investigations of seal fossils from several Middle — Late Miocene deposits of Western Europe allow a more accurate diagnosis of the genus *Prae-*



Fig. 1. Sandpit de Kuilen, location of Mill-Langenboom, in the eastern Noord-Brabant, The Netherlands (Late Miocene).

Рис. 1. Песчаный подводный карьер «Де-Кейлен», муниципалитет Милл-Лангенбом, провинция Северный Брабант, Голландия (поздний миоцен).

pusa due to similar humeral characters in: 1) *Praepusa vindobonensis* Toulou, 1897: from Austria, Kazakhstan, Ukraine, and Moldova (Middle Miocene); 2) *Pr. pannonica* Kretzoi, 1941: from the early-middle Sarmatian (Middle Miocene) of Hungary and Moldova; and 3) *Pr. magyaricus* Koretsky, 2003: from the Middle Miocene of the Vienna Basin.

Geological age and distribution. Middle Miocene of the southern part of Eastern and Central Europe; Late Miocene to Late Pliocene (Tortonian–Piacenzian Stages, 11.5–3.5 Ma) of the Eastern shore of the North Atlantic, The Netherlands and Belgium.

***Praepusa boeska* Koretsky, Peters et Rahmat, sp.n.** (fig. 2–3; tables 1–2)

Holotype. Right humerus MAB 4686 (♀), collection of the Museum de Groene Poort, Boxtel (NL), found in Antwerp harbour (Belgium), not in-situ. Miocene? The Antwerp Basin, Belgium.

Paratype. Sacrum RGM 629552, collection of the Naturalis Biodiversity Center in Leiden (NL). Miocene — Pliocene, The Antwerp Basin, Belgium.

Etymology. *boeska*, in reference to its finder Mr. K. A. Boes, The Netherlands (= Holland).

Type Locality. The Antwerp Basin, Belgium.

Referred material. In addition to the type material, the following specimens were found in The Netherlands: Humeri MAB 4687, distal half of left humerus, ♂; MAB 4688, distal half of left humerus, ♂; MAB 4689, distal half of left humerus, cast, ♂; MAB 4690, dis-



Fig. 2. Humeri of *Praepusa boeska* sp. n., MAB 4686 holotype, right humerus, female, Miocene ? the Antwerp Basin, Belgium; A — cranial view; B — lateral view; C — medial view; and MAB 4687, left humerus, male, Late Miocene — Early Pliocene (Tortonian–Piacenzian Stages, 11.5–3.5 Ma), sandpit de Kuilen (municipality of Mill-Langenboom), Noord-Brabant, S. E. Netherlands; D — cranial view; E — lateral view; F — caudal view.

Рис. 2. Плечевые *Praepusa boeska* sp. n., голотип, MAB 4648, правая плечевая кость, самка, миоцен ?, Антверпен бассейн, Бельгия: А — вид спереди; В — вид с латеральной стороны; С — вид с медиальной стороны; и MAB 4687, левая плечевая кость, самец, поздний миоцен — ранний плиоцен (тортоний-пьяцензиан, 11,5–3,5 млн лет назад), песчаный подводный карьер «Де-Кёйлен» (муниципалитет Милл-Лангенбом), провинция Северный Брабант, юго-восточная Голландия; D — вид спереди; E — вид с латеральной стороны; F — вид сзади.

Table 1. Measurements of humeri of *Praepusa boeska*, mmТаблица 1. Измерения плечевых костей *Praepusa boeska*, мм

Characters	Male	Female	n	Mean	Range
Absolute length		81.1	1		81.1
Length of deltoid crest		50.4	1		50.4
Height of head		18.6	1		18.6
Height of trochlea	14.7	13.2	5	14.1	13.0–17.3
Width of head		19.4	1		19.4
Width of deltoid crest		13.5	1		13.5
Width of distal epiphysis	30.5	21.2	5	27.1	21.2–32.7
Width of proximal epiphysis		23.5	1		23.5
Width of trochlea distally	16.9	18.2	5	16.9	14.6–18.7
Width of trochlea, anterior view	20.5	16.7	5	19.0	15.7–22.2
Transverse width of diaphysis	14.6	11.3	5	12.7	10.9–17.6
Thickness of proximal epiphysis		22.9	1		22.9
Thickness of medial condyle	16.2	16.9	5	16.5	14.4–19.0
Thickness of lateral condyle	15.3	13.9	5	14.8	12.7–16.1
Diameter of diaphysis with deltoid crest		21.1	1		21.1

tal end of right humerus, ♀; MAB 4691, distal end of left humerus, cast, ♀. All referred material comes from the S. E. Netherlands, Noord-Brabant, Late Miocene — Late Pliocene (Tortonian–Piacenzian Stages, 11.5–3.5 Ma), sandpit de Kuilen, village of Mill-Langenboom.

Diagnosis. Deltoid crest sharp-bladed and extends to 2/3 of humeral length, not reaching coronoid fossa; maximal width of deltoid crest located in its middle portion; lesser tubercle of humerus located slightly above proximal border of deltoid crest, round in shape and not deviated from humeral axis; head compressed medio-laterally; ratio of head width to its height 0.98; lateral epicondyle does not reach middle of diaphysis, but reaches distal part of deltoid crest.

Sacrum-based diagnosis is same as for the genus *Praepusa* described above.

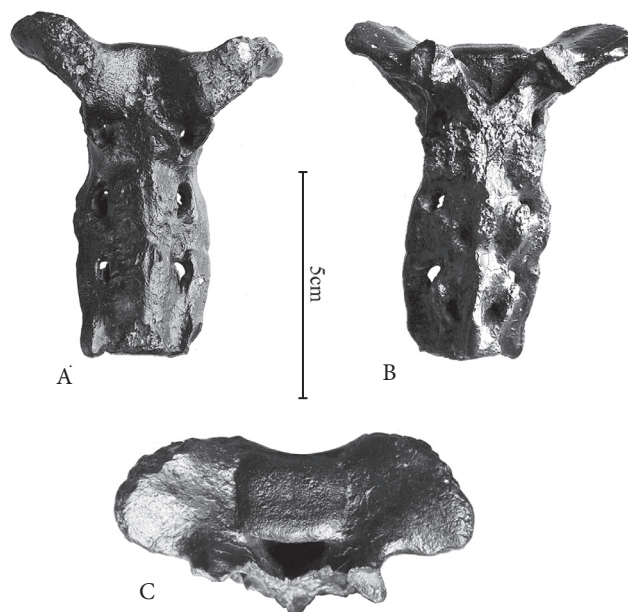


Fig. 3. Sacrum of *Praepusa boeska* sp. n., RGM 629552, collection of the Naturalis Biodiversity Center in Leiden (NL). Zancian–Piacenzian (Pliocene), Antwerp Basin, Belgium: A — ventral view; B — dorsal view; C — cranial view.

Рис. 3. Крестец *Praepusa boeska* sp. n., RGM 629552, коллекция Национального центра биологического разнообразия в Лейдене (NL), занклиан–пьяцензиан (плиоцен), Антверпенский бассейн, Бельгия: А — вид снизу; В — вид сверху; С — вид спереди.

Table 2. Measurements of sacrum of *Praepusa boeska*, mmТаблица 2. Измерения крестцовых костей *Praepusa boeska*, мм

Characters	n	Mean	Range
Total length (measured over the axis)	1		63.0
Combined Length of S1 + S2	3	33.0	29.0–39.0
Width over the wings of S1	3	48.2	47.0–57.6
Width over sacral foramina S1	3	26.7	24.3–30.0
Width over sacral foramina S2	1		27.4
Width over sacral foramina S3	1		27.5
Height of centrum S2	3	15.7	15.0–17.0
Height of wings S1	3	25.0	23.2–28.0

Description. Small seal that has dimensions close to Recent *Pusa*.

Humerus (fig. 2; table 1). The deltoid crest is long and slender, extending for about 2/3 of the length of the bone; the lesser tubercle is visible and is located distal to the head of the humerus, barely above the greater tubercle; it does not deviate from the humeral axis, is round in shape and well developed; the musculospiral groove is not expressed; the lesser tubercle is below the level of the head, but the intertubercular groove is very narrow and deep; the head is slightly compressed medio-laterally; the ratio of the head width to its height is 102 %; the deltoid crest has the form of a sharp blade and does not reach the condyles; the maximal width of the deltoid crest is in its middle part; the lateral epicondyle is well developed, reaches the distal part of the deltoid crest just below the middle of the diaphysis and extends twice as far proximally as the medial epicondyle; the medial epicondyle is flattened, spreading from the lower part of the entepicondylar foramen and ending at the middle of the coronoid fossa; the coronoid fossa is shallow and forms an oval in ♂ or triangular in ♀ depression extending proximally to the medial epicondyle, ending below the lateral epicondyle; the entepicondylar foramen is present, large and oval, open, but the narrow bridge over it is broken away; the olecranon fossa is very shallow in ♂ and deep in ♀. Detailed description of sexual dimorphism in the mandible and postcranial elements for the subfamily Phocinae (Koretsky, 1987 a, 2001) and subfamily Monachinae (Koretsky, Ray, 2008) has previously been published.

Sacrum (fig. 3; table 2). Consists of three fused vertebrae, with an absolute length of 63.0 mm and width of 57.6 mm. The maximum width of the wings is 86.2 % of the length of the sacrum, which according to Antoniuk (1979) is a diagnostic character of Phocidae. The sacral promontory is concave and not pronounced. The proximal surface of the first centrum is lower than the wings of the sacrum, a configuration that is similar to other Phocinae, including *Leptophoca* (Antoniuk, 1979, table 2; Koretsky, 2001, table 13). The ala (= wing) is thin and higher than the proximal surface of the first centrum like in phocines, but in contrast to monachines where the ala is lower than the centrum (Antoniuk, 1979). On S1–S3, a well-defined mammillo-articular process (= intermediate sacral crest) is present; S3 has a less developed mammillo-articular process. The median sacral crest, which is formed by several un-fused spinous processes, is very short and extends caudally. Dorsal and ventral sacral foraminae are equal in size.

According to sexual dimorphism in sacral bones described by Gadjiev (1982), RGM 629552 belongs to an adult male because its first ventral foramen is rounded and the lateral wall is very thick. The body of the sacrum is slender and narrow.

Comparison. The bones of the postcranial skeleton of *Praepusa boeska* are smaller than those of *Pr. vindobonensis* and *Pr. magyricus* and are similar to those of Recent *Pusa*. In humeral morphology, the new species differs from *Pr. vindobonensis* and *Pr. magyricus* in its lesser tubercle being positioned lower than the head, and slightly above the greater tubercle; deltoid crest being shorter, not reaching the condyles, and widest in its middle part; larger entepicondylar foramen; and coronoid fossa being shorter and terminating lower than the lateral epicondyle. In contrast to *Pr. magyricus*, the humerus of *Pr. boeska* has a head that is medio-laterally compressed.

Discussion. Antoniuk and Koretsky (1984) previously assigned the seal from Tarchankut Peninsula (Ukraine) to the genus *Praepusa*, species *tarchankutica*. They described an almost complete skeleton, mandible, and skull belonging to a subadult individual in comparison with another skull belonging to an adult individual. The mandible is very similar to *Praepusa vindobonensis* Toulou 1897, and for this reason the name *tarchankutica*, as a junior synonym, is no longer valid (Koretsky, 2001).

Only few fossil sacral bones of the subfamily Phocinae have been described or illustrated previously. These include: *Pusa caspica* (Gadjiev, 1982), *Phocanella*, “*Phoca*” and *Prophoca* (Van-Beneden, 1877; Atlas pl.14; 15; 18), and *Leptophoca* (Koretsky, 2001; 2006). Several sacral bones have been described from the subfamily Monachinae: *Callophoca* (Koretsky, Ray, 2008), *Monaterium* (Van-Beneden, 1877; Atlas pl.16), *Acrophoca* (de Muizon, 1981) and several sacral bones are known from the Subfamily cystophorinae (Koretsky, Rahmat, 2013). However, the rather well-preserved condition of the found *Praepusa* sacrum from the Western Paratethys, and its morphologically distinguishing characteristics make it possible to separate this bone from other phocine species from the other areas of the Paratethys.

Geological age and distribution. Eastern shore of the Atlantic Ocean (Western Europe); Late Miocene (early-middle Tortonian Stage) — Pliocene (Zanclean–Piacenzian Stages) sandpit “de Kuilen”, Mill-Langenboom, 11.5–3.5 Ma, Noord-Brabant, S. E. Netherlands. Late Pliocene (Scaldisian), Anvers 3rd Section, Antwerp Basin, Belgium.

Discussion and conclusions

The Paratethyan seaway extended from western Kazakhstan across north-western Europe to the western shore of the Atlantic Ocean from the Early to Late Miocene (23.0 to 9.3 Ma), allowing marine mammals to travel and inhabit different niches (Rögl, Steininger, 1984; Koretsky, 2001). Rapid changes of marine connections during the Badenian (Koretsky, Holec, 2002) and Sarmatian (Koretsky, Grigorescu, 2002) resulted in varying marine and terrestrial biotas, as evidenced by the fossil record (Koretsky, 2001; Koretsky, Rahmat, 2013). During the Sarmatian, strong endemism with reduced salinity is evident in fossil material as the Paratethys divided into isolated basins containing endemic faunas. Sediments deposited in, and on the shores of, this ancient seaway are rich in the remains of fossil seals.

Modern pinnipeds have large geographic ranges that regularly extend through several zoogeographical regions. Likewise, fossil species are widespread. Fossil true seals (Phocidae) are very numerous in Miocene coastal-marine faunas in localities that used to lie on the path of the Paratethys. In the Late Miocene — Early Pliocene including the Messinian (7.2–5.6 Ma) salinity crisis (Rögl, Steininger, 1984; Koretsky, 2001), the seaway became closed and basins were separated by land masses, forcing marine mammals to be confined to the habitat they were living in at that time. This explains the discovery of the following *Praepusa* fossils from different isolated localities across Europe and Asia (fig. 4):

Praepusa vindobonensis: Western Kazakhstan and Austria; Middle Miocene, early Sarmatian (16.5–11.2 Ma; Toulou 1897; 1 in fig. 4); Ukraine and Moldova; Middle Miocene, middle Sarmatian (13.6–12.3 Ma; Antoniuk, Koretsky, 1984; 2 in fig. 4).

Pr. pannonica: Moldova and Hungary; Middle Miocene, early-middle Sarmatian (12.3–11.2 Ma; Kretzoi, 1941; 3 in fig. 4).

Pr. magyaricus: Vienna Basin; Sarmatian, Middle Miocene (13.6–12.3 Ma; Koretsky, 2003; 4 in fig. 4).

Pr. boeska: The Netherlands and Belgium; Late Miocene — Late Pliocene (11.6–3.2 Ma), described in the current paper (5 in fig. 4).

The endemism due to closure of the Paratethyan seaway, and climatic, geological and stratigraphic differences of localities support our hypothesis that the genus *Praepusa* first inhabited the Eastern Paratethys (Early — Middle Miocene, 16.5–13.6 Ma) before dispersing to the Central (Middle Miocene, 13.6–11.2 Ma) and, later, Western (Late Miocene — Early Pliocene, 11.6–3.6 Ma) Paratethys. The newly described *Pr. boeska* is the youngest species

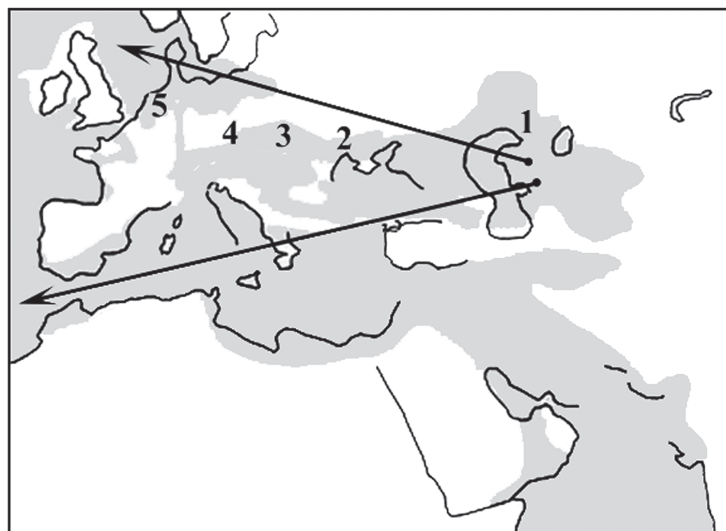


Fig. 4. Geographical and palaeogeographical locations of the studied area with arrows indicating dispersals of different species of the genus *Praepusa* from the Eastern Paratethys westward: 1 — *Praepusa vindobonensis*: Western Kazakhstan and Austria, Middle Miocene, early Sarmatian (16.5–11.2 Ma); 2 — *Pr. vindobonensis* (= *tarchankutica*): Ukraine and Moldova, Middle Miocene, middle Sarmatian (13.6–12.3 Ma); 3 — *Pr. pannonica*: Moldova and Hungary, Middle Miocene, early-middle Sarmatian (12.3–11.2 Ma); 4 — *Pr. magyarus*: Vienna Basin, middle Sarmatian, Middle Miocene (13.6–12.3 Ma); 5 — *Pr. boeska*: The Netherlands and Belgium, Late Miocene — Early Pliocene (11.6–3.2 Ma).

Рис. 4. Географические и палеогеографические местонахождения в изучаемом регионе, стрелкой указано направление распространения различных видов рода *Praepusa* из Восточного Паратетиса на запад: 1 — *Praepusa vindobonensis*: Западный Казахстан и Австрия, средний миоцен, нижний сармат (16,5–11,2 млн лет назад); 2 — *Pr. vindobonensis* (= *tarchankutica*): Украина и Молдова, средний миоцен, средний сармат (13,6–12,3 млн лет назад); 3 — *Pr. pannonica*: Молдова и Венгрия, средний миоцен, нижний–средний сармат (12,3–11,2 млн лет назад); 4 — *Pr. magyarus*: Венский бассейн, средний миоцен, средний сармат (13,6–12,3 млн лет назад); 5 — *Pr. boeska*: Голландия и Бельгия, поздний миоцен — ранний плиоцен (11,6–3,2 млн лет назад).

of *Praepusa* to date and is dispersed the furthest west of any previously described members of this genus. These findings help explain the origin, dispersal, and phylogenetic relations among described species of the genus *Praepusa*.

Pr. boeska is smaller than any other described member of the genus *Praepusa*. Although the material is insufficient for assessing the variability of this specific taxon, the size and morphology of the postcranial bones from the Tortonian–Piacenzian Stages from The Netherlands permits, with a great degree of confidence, the assignment of this true seal to the genus *Praepusa*. Future investigations of fossil seals from the Middle Miocene deposits of Western Europe can expand the diagnosis of the genus *Praepusa* and enable more detailed comparison of this taxon with other genera of the subfamily Phocinae to better clarify their phylogenetic relationships.

First we wish to thank all donors, collectors, and organizations as follows: Jan Boes, Frank van Esch, Harold van der Steen, Dick Hofman, Hans Wijnstekers, Wim van de Broek, and the Naturalis Biodiversity Center in Leiden, The Netherlands. We thank Dave Bohaska for critical help with specimens in the National Museum of Natural History, USA. Some financial support for this project was provided by The Netherlands Organization for Scientific Research.

We thank the senior editor and all reviewers for suggestions which significantly improved the manuscript.

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Received 12 May 2014

Accepted 26 November 2014