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A new species of *Leptophoca* (Carnivora, Phocidae, Phocinae) from both sides of the North Atlantic Ocean (Miocene seals of the Netherlands, part I)

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New material of *Leptophoca* from The Netherlands, studied in relation to fossil seals from the east coast of North America, sheds new light on past distribution of true seals in the North Atlantic. Based on recent discoveries and additional information, we try here to widen and deepen understanding of pinniped paleogeography. Among the specimens studied are two size clusters. Even the small series of remains justifies distinguishing two sexes. *Leptophoca amphiatlantica* new species originated on the coast of western Europe (The Netherlands, 15.8 - 16.4 Ma), dispersed across the Atlantic westward, to in the western shore of the North Atlantic, at first in Calvert time (14.2 - 15 Ma) and spread southward in St. Mary's time (8.5 - 10.5 Ma).

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INTRODUCTION

For many years the study of fossil phocids was severely limited by scarcity of specimens from Western Europe. Even when material was collected, very often the precise locality and geological age were unknown, as in the case of France: Lublé (Middle Miocene); Malta: Gozo (Late Miocene); Austria: Heiligenstadt (Middle Miocene); Belgium: Brussels, Antwerp Basin (Late Miocene); Borgerhout, Rumst-reet (Late Miocene), Deurne, Steendorp (?Miocene-Pliocene), Nachtegalen Park (Middle Miocene), vicinity of Antwerp; private collection of Dr. Paul Gigase; Italy: Roccamorice, vicinity of Naples (Late Miocene); and Netherlands: Leiden, Borne, Morselt, Groenlo (Miocene) (Koretsky 2001).

Fortunately, a recent Geological Survey of

the south-eastern part of the Netherlands has resulted in the recovery of new and interesting material of seals. Among the specimens brought recently by one of us (NP) for study to the Smithsonian Institution's National Museum of Natural History was a series of bones representing phocines, monachines, and even cystophorines. All of these are attributable to new species, some even to new genera.

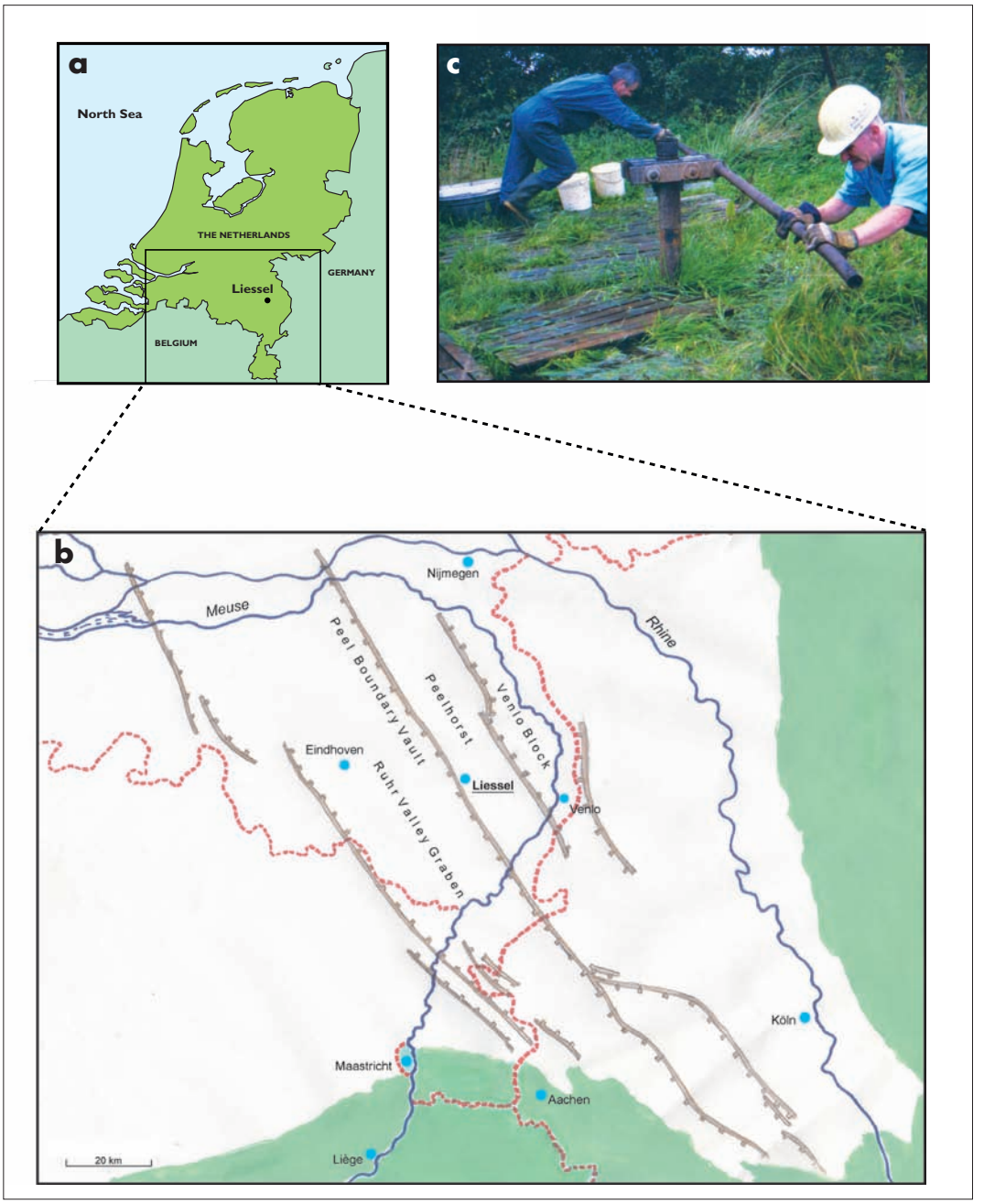

Figure 1 The Netherlands (**a**), showing the location of Liessel in the eastern North Brabant region (**b**). Coring was done manually (**c**).

The present study is part of a proposed series of papers under one general title 'Miocene seals of The Netherlands'. Based on recent discoveries and additional information, we try here to widen and deepen understanding of pinniped paleogeography. This new material from the eastern shore of the North Atlantic, studied in relation to fossil seals from the western shore, sheds new light on the distribution of the true seals in the North Atlantic (Ray 1976, 1977; Repenning *et al.* 1979; Ärnason 2006; Koretsky & Barnes 2006). Their dispersal in the North Atlantic was a matter of expanding ranges through population increase under favorable conditions to occupy all suitable and accessible habitat. Many of these Miocene and Pliocene phocines were distributed more or less continuously around the northern perimeter of the North Atlantic, with considerable and easy gene flow through the whole range.

The Smithsonian Institution houses a huge collection of Pliocene seals (from the Lee Creek Mine, North Carolina) which shows the connection between the old and new worlds (Koretsky & Ray 2008). Today, we have in our possession new material from the late Oligocene and early Miocene, which supports the idea of one common origin of the true seals in the North Atlantic region (Koretsky 2001; Koretsky & Sanders 2002).

Moreover, after more than a century since the description of *Leptophoca lenis* TRUE, 1906, during which almost nothing has been added in print to knowledge of this seal, abundant material has accumulated, primary in the NMNH and CMM, representing almost every part of the skeleton, in some instances from partial, associated skeletons, which include humeri and femora (Koretsky 2001). This knowledge laid the foundation for describing another kind of femur as a new species. This abundant material has been published in small part (Ray 1976; Barnes *et al.* 1985; Koretsky 2001, 2006; Koretsky & Peters 2008) and is under continuing study. Meanwhile, it has become clear that more than one taxon is present in the Calvert Formation (Gottfried *et al.* 1994). The purpose of the present communication is to place a part of that information on record in connection with a first report on relevant material from The Netherlands.

ABBREVIATIONS

Specimens from the following institutions have been examined for this review:
CMM - Calvert Marine Museum, Solomons, MD, USA; MAB - Museum de Groene Poort (formerly Museum Ammonietenhoeve), Boxtel, The Netherlands; RMNH - National Centre for Biodiversity Naturalis, Leiden, The Netherlands; NMNH (USNM) - National Museum of Natural History (formerly the United States National Museum), Smithsonian Institution, Washington, D.C., USA.

In reference to bones, distance, and absolute age: L - left, R - right; mm - millimeters; m - meters; Ma - mega-annum (million years), both as age of the fossils and as age of the rocks.

GEOLOGY

Between 1997 and 2001, a manual coring was carried out in the vicinity of the sandpit of the 'Hoogdonk' brickyard in Liessel (Noord-Brabant) in the Netherlands (Fig. 1). The aim of the coring project was to get a better insight into the local stratigraphy of the Peelhorst area. Although during previous years lots of fossils were dredged from the sandpit, the precise stratigraphic origin of these remained uncertain; partly of course because fossils were mixed up in the dredging process (none of them was found *in situ*), partly because the geological setting can differ locally from what is known for the region as a whole. Going down to a depth of almost 45 meters, the coring yielded not only lithological information, but also numerous macro- and micro-fossils of plants (e.g. seeds, pollen) and animals (e.g. bones, teeth, shells) (Peters *et al.* 2004; Peters 2009).

The lithological data combined with the floral and animal remains show that the local stratigraphy of the Peelhorst is more or less

as was expected in advance. Late Pliocene deposits were found under the Pleistocene (Beegden) Meuse-sediment (0-8 m). These Pliocene deposits (8-12.5 m) showed a terrestrial facies.

Older marine layers were found below the Late Pliocene deposits. On the basis of the calcareous shells of mollusks and foraminifera (Peters *et al.* 2004; Peters 2009) these layers are of Late Miocene age in the deepest part of the section (43-45 m). Deposits between 12.5 and 43 meters also have a Late Miocene age, because at 32 meters a massive concentration of *Pyrgo simplex*, a foraminifer of supposedly Tortonian age, was found. Moreover, dinoflagellates that were studied recently in sand samples from the 12.5 - 43 m traject all showed Late Miocene characteristics (Munsterman 2007).

In general, one of the two formations that were deposited during Miocene and Pliocene time in The Netherlands (Fig. 1) is the Breda Formation. This Formation consists mainly of glauconitic sands (as in the Hoogdonk sandpit) that were deposited in shallow seas or coastal regions (Wijnker *et al.* 2008). A zonation of the Breda Formation, based on dinoflagellate cyst distribution was carried out by Munsterman & Brinkhuis (2004). Our study indicated that the age of the partial femur MAB 2129 is about 15.8-16.4 Ma. But previous study indicated that the age of the majority of the marine fossils that were found in the Liessel sandpit is from 7 - 11 Ma. Because most of them were not found in situ this particular femur has probably been redeposited from older sediments, which in fact happens quite often. So, this uncertainty of precise geological age must be kept in mind.

PALEOENVIRONMENTS OF CALVERT CLIFFS

A few bones that belong to a new species of *Leptophoca* are known from the eastern shore of USA, found in the Calvert Formation of Maryland (the western shore of the North Atlantic). The paleoenvironmental condition in Calvert time (between 18 and 11 Ma) suggests a warm-temperature terrestrial flora with some subtropical elements (Gottfried *et*

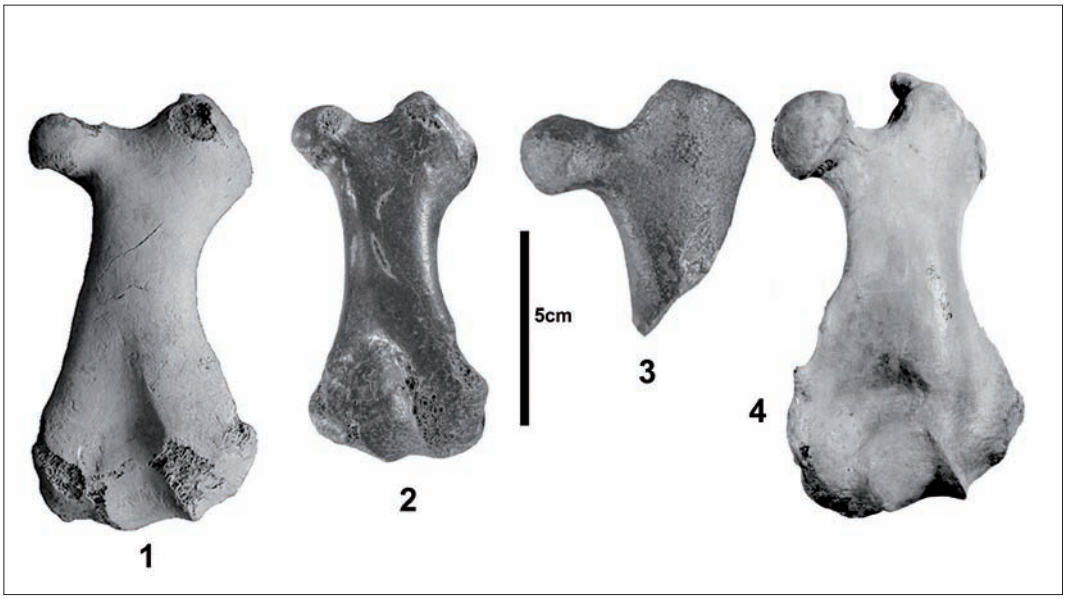

Figure 2 **1-3**: Femora of *Leptophoca amphiatlantica* n.sp., in ventral aspect; **1** holotype, right femur, male, USNM 23227 from Maryland, USA (reversed); **2** left femur, female, USNM 321926, from Maryland USA; **3** paratype, left distal half of femur, male, MAB 2129 from Liessel, S.E. Netherlands; **4** right femur of *L. lenis*, USNM 263648 from Maryland, USA (reversed).

al. 1994), with open marine, gently sloping seafloor of about 150 m water depth. Zone 12 (some of our material originates from this zone) reflects the deepest water and includes marine mammals, fish, reptiles, abundant mollusks, and diverse micro-plankton (Kidwell 2006). The Calvert record indicates many repeated regression-transgression cycles, each having a maximum water depth that is shallower than that of previous cycle.

Other material described here comes from the St. Mary's Formation (Zone 23-22) of the Calvert Cliffs, deposited between 11 and 8.5 Ma Sediments of the St. Mary's Formation are medium to coarse sands and pebble beds, with abundant wood and other plant debris and small shells, that represent mixed marine and freshwater conditions in a tide-influenced coastal environment (Kidwell 2006).

Marginal marine environments are less diverse, and include species that are typical of low-salinity estuaries (Barnes *et al.* 2006; Ward 2006). A sharp temperature decrease in the Late Miocene is indicated by a shift to a cooler-water fish fauna during St. Mary's time (Gottfried *et al.* 1994).

SYSTEMATIC PALEONTOLOGY

Order Carnivora BOWDICH, 1821
Superfamily Phocoidea SMIRNOV, 1908
Family Phocidae GRAY, 1825
Subfamily Phocinae GRAY, 1821
Genus *Leptophoca* TRUE, 1906

Leptophoca: True 1906, p. 836, pl. 75, figs. 1-4; Kellogg 1922, p.123; Simpson 1945, p.122; Scheffer 1958, p. 34; King 1964, p.132; King 1983, p.133; Hendey & Repenning 1972, p. 94; Mitchell 1975, p. 22, 23; McLaren 1975, p. 44; Ray 1976, p. 20-22, pls. 8-11, fig.4; Ray 1977, p. 395, 397-398; Heptner *et al.* 1976, p. 9,118; Repenning & Ray 1977, p. 679-680; Repenning *et al.* 1979, p. 361-363; De Muizon 1982, p. 186, 205; De Muizon 1992, p. 35; Savage & Russell 1983, p. 272; Barnes *et al.* 1985, p. 41; McKenna & Bell 1997, p. 257; Koretsky 2001, p. 62-72; Koretsky 2006, p. 22; Ärnason *et al.* 2006, p. 351.

Type species *Leptophoca lenis* TRUE, 1906

Included species *Leptophoca lenis* TRUE, 1906, from the Lower-Middle Miocene (Calvert Formation; c. 11-18 Ma) of the

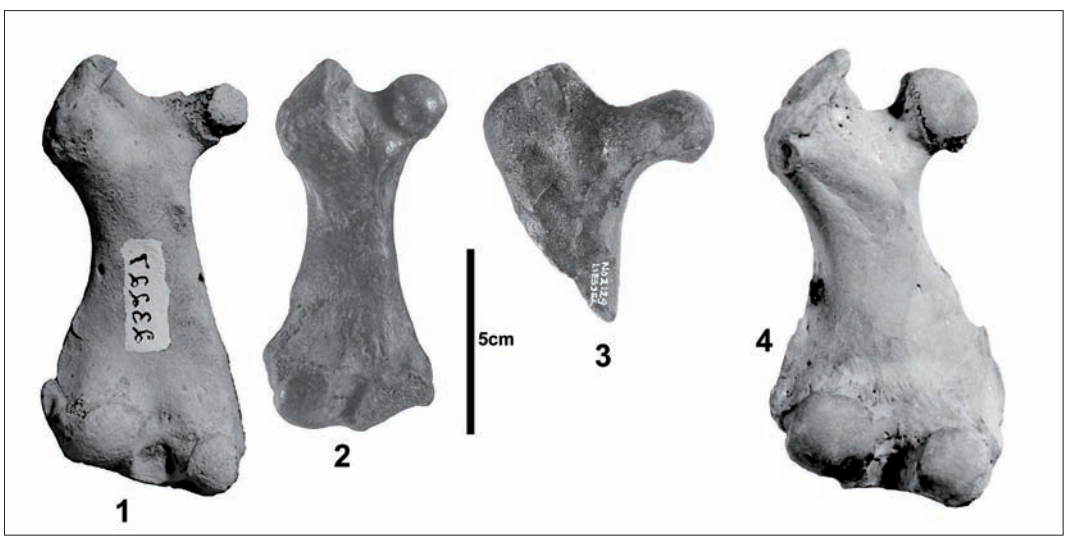

Figure 3 **1-3**: Femora of *Leptophoca amphiatlantica* n.sp., in dorsal aspect; **1** holotype, right femur, male, USNM 23227 from Maryland, USA (reversed); **2** left femur, female, USNM 321926, from Maryland USA; **3** paratype, left distal half of femur, male, MAB 2129 from Liessel, South East Netherlands; **4** Right femur of *L. lenis*, USNM 263648 from Maryland, USA (reversed).

east coast of the United States of the North Atlantic (Virginia and Maryland). *Leptophoca amphiatlantica* n.sp., from the Lower-Middle Miocene (St. Mary's and Calvert Formation; c. 8.5-18 Ma) of east coast of the United States, Virginia and Maryland, and from the Middle Miocene (Breda Formation, Zones 5-10; c. 15.8-16.4 Ma) of The Netherlands.

Expanded and emended diagnosis Phocine of medium size. Greater trochanter of femur higher than head, its proximal part wider than its distal; distinct lesser trochanter located far below distal border of greater trochanter; trochanteric fossa deep, wide, and overhanging medioproximally; head large in relation to size of femur; minimum width of diaphysis situated proximally.

Comparison of femora *Leptophoca* differs distinctly from other representatives of subfamily Phocinae by the following characters: deep tro-

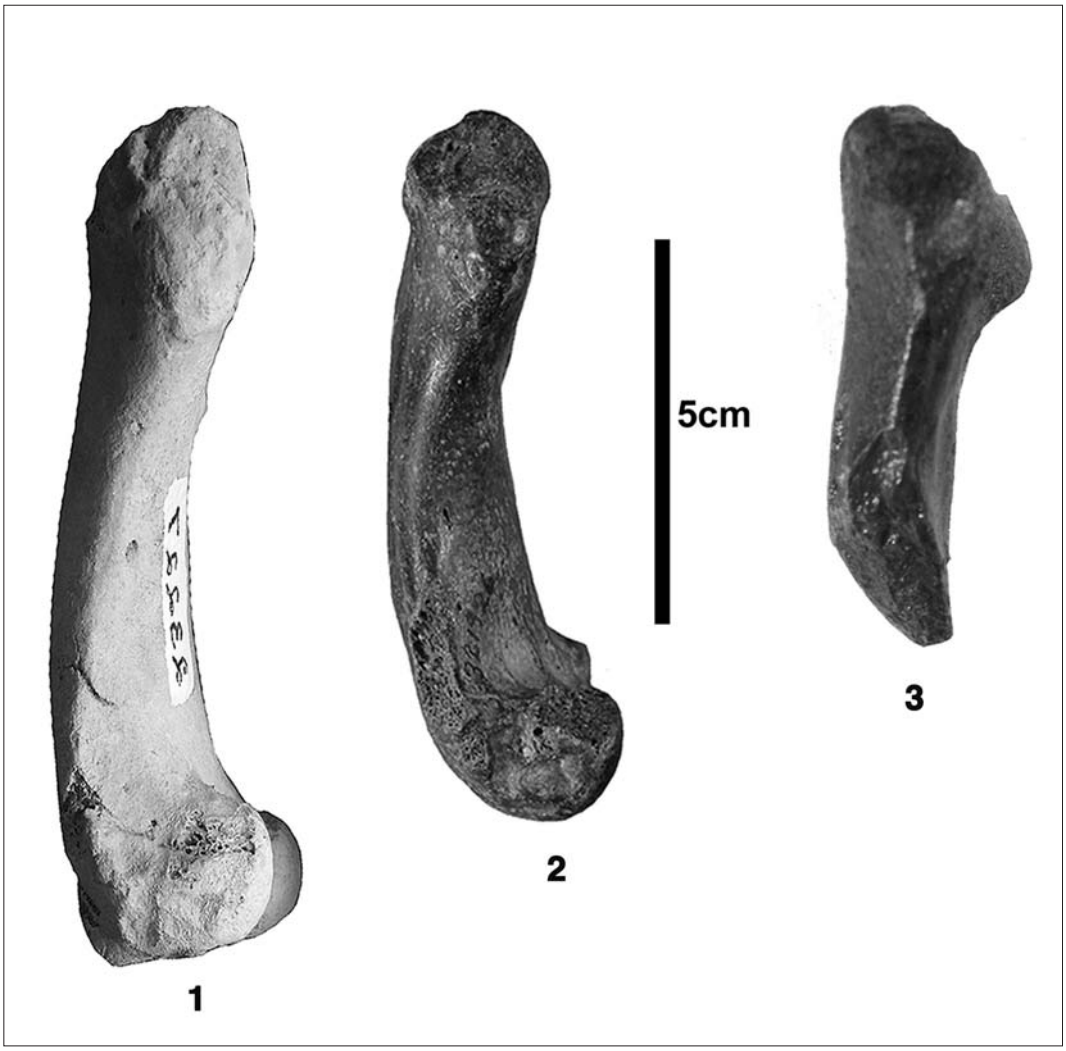

Figure 4 Femora of *Leptophoca amphiatlantica* n.sp., in lateral aspect; **1** holotype, right femur, male, USNM 23227 from Maryland, USA (reversed); **2** left femur, female, USNM 321926, from Maryland, USA; **3** paratype, left distal half of femur, male, MAB 2129 from Liessel, South East Netherlands.

chanteric fossa (except *Pusa*, *Cryptophoca*), proximal part of greater trochanter of femur wider than distal (except *Histriophoca*); femoral head larger, compared to overall size of bone (except *Phoca*, *Erignathus*, *Histriopohoca*, *Monachopsis*, *Cryptophoca*); lesser trochanter of femur very distinct; trochanteric fossa wide and overhanging medioproximally (except *Pagophilus*); minimum width of diaphysis shifted proximally (except *Phoca*, *Monachopsis*, and *Cryptophoca*). Moreover, this genus differs from *Halichoerus* by the shorter greater trochanter, and from *Sarmatonectes* by the greater trochanter of femur, which higher than the head.

Discussion Among the large collection of *Leptophoca*, mostly referable to *L. lenis*, stored in the USNM, we found several bones, also from Calvert Cliffs, which are morphologically very similar, but which do not belong to the same species.

Detailed comparison of the genus *Leptophoca* with known representatives of the subfamily Phocinae was made by Koretsky (2001: 62-72). However, as can be seen from the 'Comparison' above, it is hard to compare some taxa, especially when holotypes are not homologous elements, when only partial skeletons are available (as in the case of *Monachopsis*), or when some parts of the skeleton are unknown (as in the case of *Prophoca*).

Geological age and distribution Miocene (Calvert and St. Mary's Formations) of the western shore of the North Atlantic, United States, and from the Eastern shore of the North Atlantic, The Netherlands (Breda Formation).

Leptophoca amphiatlantica, new species

Figures 2-4; Table 1

Holotype USNM 23227, right femur, USA, middle Miocene, Maryland, Calvert County, Calvert Formation, Parker's Creek (Bed 12).

Paratype MAB 2129, distal half of left femur, The Netherlands, Upper North Sea Group, Noord-Brabant, Breda Formation, Zone 5-10 (c. 15.8 - 16.4 Ma), Village of Liessel, Hoogdonk sandpit (gravel, greensand).

Etymology *amphiatlantica*, from Greek *amphi* (= on both sides), in reference to its occurrence on both sides of the Atlantic Ocean.

Type Locality Parker's Creek (Bed 12, c. 15 Ma), Calvert Cliffs, middle Miocene, Calvert County, Maryland (USA).

Referred material In addition to the type material, the following specimens found in the USA: USNM 214897, left femur, early Miocene, Virginia, Westmoreland County, Stratford Harbor Beach, Chesapeake Group, Calvert Formation; USNM 321926, left femur, early Miocene, Maryland, Saint Mary's County, Calvert Cliffs near Lighthouse, Chesapeake Group, St Mary's Formation (Zones 23-22, c. 8.5 - 11.0 Ma).

Diagnosis New species of *Leptophoca* of smaller body size than *L. lenis*. The femur is having a short intertrochanteric crest which does not reach lesser trochanter; the head is small and seated on a narrow, long neck; the smallest width of the diaphysis is shifted toward the proximal half of the femur; maximum intercondyloid width is 14-15% of the bone's length.

Description The femora of *Leptophoca amphiatlantica* are similar is size to those of the modern ribbon seal, *Histriophoca fasciata*. The greater trochanter of the femur (Figs. 2-4, Table 1) extends proximally higher than the femoral head; its proximal part is wider than the distal part. The trochanteric fossa is deep, wide, and overhung proximally by the greater trochanter; it does not reach the distal half of the greater trochanter. The insubstantial, short intertrochanteric crest is located along the middle part of the femur, below the trochanteric fossa, and does not reach the lesser

trochanter. The lesser trochanter is very well developed and is located on the posteromedial side of the bone, not far below the distal border of the greater trochanter. The femoral head is small relative to the bone's mass, and seated on a narrow, long neck. The smallest width of the diaphysis is slightly shifted toward the proximal half of the femur. The supracondylar fossa, located above the lateral condyle, is weakly developed. The maximum intercondyloid width is 14-15% of the bone's length.

Comparison *Leptophoca amphiatlantica* differs from *L. lenis* as follows: the overall smaller size (Table 1); the trochanteric fossa is shifted medially on the trochanter, and it is shorter than half of the greater trochanter; the intertrochanteric crest is shorter than in *L. lenis*, located below the trochanteric fossa, and does not reach the lesser trochanter and middle part of the femur; the well developed lesser trochanter is located not far below the distal border of the greater trochanter, much higher than in *L. lenis*; the femoral head is smaller and seated on a narrow, longer neck; the smallest width of the diaphysis is shifted more toward the proximal half of the femur; the supracondylar fossa, located above the lateral condyle, is deeper; the maximum intercondylar width, is smaller, as are the condyles.

Discussion Unfortunately, humeri of *Leptophoca* representing a species distinct from *L. lenis* have not yet been found in Maryland or The Netherlands. Fortunately, femora confidently referred to *L. lenis* are available for comparison with those here described as a new species.

The well-preserved femora of *Leptophoca amphiatlantica* from the USA (USNM 23227, 321926, 214897), and from the Netherlands (MAB 2129) show several primitive features, including their well-developed lesser trochanter and deep intertrochanteric fossa. This is not surprising because *Leptophoca* is one of the oldest known and most primitive representatives of the Phocinae.

Among the material studied are two size clusters, one belonging to smaller, and one to larger individuals. Even the small series of remains justifies distinguishing two sexes. The distinctions in size and morphology (see Table 1) are here interpreted as a sexual dimorphism. These distinctions include: overall size difference in dorsoventral thickness of the diaphysis, length and thickness of the neck, and length and thickness of the greater trochanter. In addition, the trochanter is stronger in specimens regarded as males (Figs. 2-3). The distal part of the greater trochanter in putative females terminates acutely (V–shaped), whereas in males it is more rounded (Figure 4). In females, the supracondylar fossa above the lateral condyle is wider, and deeper (Figs. 3.1, 3.2). The diameter of the patellar surface is greater in supposed males (Figs. 2.1, 2.2).

Thus, we conclude, that femora USNM 321926 and 32129 belong to females, and USNM 23227 and 214897 to males. Femur MAB 2129 from the Netherlands also is regarded as belonging to a male. Sexual dimorphism in bones of phocines of the extremities is described in detail by Koretsky (1987, 2001: 26-29).

Geological age and distribution Eastern shore of the Atlantic Ocean, province of North-Brabant, The Netherlands, in the Upper North Sea Group, Breda Formation, Zone 5-10 (c. 15.8 - 16.4 Ma). Western shore of the Atlantic Ocean, USA, Early-Middle Miocene, Calvert Formation, Zone 14 corresponding to Langhian Stage (c. 14.2 Ma). Late Miocene St. Mary's Formation, Zone 23-22 corresponding to Tortonian Stage (8.5 - 10.5 Ma) (Barnes *et al.* 2006; Kidwell 2006; Ward 2006).

CONCLUSION

There are two distinctive kind of seals known in the Calvert and St. Mary's Formations (Ray 1976), indicating a well-marked divergence between phocines and monachines by that time (c. 18 Ma). The monachine seal *Monotherium? wymani* from the St. Mary's

Table 1 Measurements (mm) of femora of *Leptophoca amphiatlantica*.

Characters	Europe	USA			USA		
	2129♂	23227♂	321926♀	214897♂	n	mean	range
1. Absolute length	-	118,3	96,0	-	2	107,1	96.0-118.3
2. Medial length	-	109,5	-	-	1	109,5	
3. Lateral length	-	109,4	94,5	-	2	102,0	94.5-109.4
4. Length of medial condyle	-	19,7	-	-	1	19,7	
5. Length of lateral condyle	-	19,8	19,4	-	2	19,6	19.4-19.8
6. Length of greater trochanter	30,5	30,1	27,1	29,2	3	28,8	27.1-30.5
7. Intertrochanteric length	43,2	44,4	38,0	48,8	3	43,8	38.0-48.8
8. Height of caput	19,0	-	18,3	19,0	2	18,7	18.3-19.0
9. Height of articular area of patellar surface	-	23,0	20,0	-	2	21,5	20.0-23.0
10. Width of proximal epiphysis	60,9	58,0	47,1	59,2	3	54,8	47.1-59.2
11. Width of distal epiphysis	-	58,8	46,0	-	2	52,4	46.0-58.8
12. Width of condyles	-	51,0	43,0	-	2	47,0	43.0-51.0
13. Width of greater trochanter	16,3	20,5	18,3	19,0	3	19,7	18.3-20.5
14. Width of caput	23,3	23,0	18,0	-	2	20,5	18.0-23.0
15. Width of diaphysis	27,1	30,9	23,7	-	2	27,3	23.7-30.9
16. Thickness of diaphysis, anteroposterior	15,3	16,5	15,9	15,5	3	16,0	15.5-16.5
17. Thickness of medial condyle	-	30,0	-	-	1	30,0	
18. Thickness of lateral condyle	-	31,0	26,4	-	2	28,7	26.4-31.0
19. Distance between condyles	-	15,8	14,3	-	2	15,1	14.3-15.8
20. Diameter of cervix	17,3	17,8	16,3	18,9	3	17,7	16.3-18.9
Indices:							
11 : 1	-	49,7	47,9	-	2	48,8	47.9-49.7
5 : 4	-	100,5	-	-	1	100,5	
8 : 1	-	-	19,0	-	1	19,0	
15 : 11	-	52,3	51,5	-	2	52,0	51.5-52.0

Formation, Richmond, Virginia, USA, and also the phocine seal Leptophoca (from the same formation) certainly have diverged from a common ancestor before that time, when they settled in the western shore of the Atlantic. This hypothesis is supported by the current molecular data that estimates the time of separation between Monachinae and Phocinae at ≈22 Ma (Ärnason *et al.*, 2006), considerably older than to ≈15-17 Ma as suggested by Fyler *et al.* (2005).

Meanwhile, morphological analysis of these taxa supports the hypothesis that some representatives of the genus *Leptophoca* can be found on both sides of the Atlantic Ocean, in this case in The Netherlands and in Maryland and Virginia (USA).

At the same time, controversial theories of the origin of phocid seals remain a very popular topic of discussion. According to the one hypothesis, supported by Koretsky & Barnes (2006) and Koretsky & Ray (2008), the early phase of phocid evolution took place in the Paratethyan region. But, Ärnason *et al.* (2006) suggested that the Atlantic coast of North America rather than that of Western

Europe or the Paratethys is the place of origin of phocid seals. Moreover, Fyler *et al.* (2005) suggested that basal phocid seals could have made the transition from the North Pacific to the North Atlantic following one of two possible routes: southward through the Central American Seaway or through the Arctic. At the same time and according to their hypothesis, *Monachus* (Monachinae) originated in the Tethys Sea, and dispersed from east to west, first to the Caribbean and then to the Pacific.

If the Phocinae and Monachinae belong to one monophyletic group (De Muizon 1982; McKenna & Bell 1997; Koretsky & Holec 2002; Koretsky & Grigorescu 2002; Ärnason *et al.* 2006), then they must have originated in one place.

Thus, *Leptophoca amphiatlantica* originated in the coastal shore of western Europe (the Netherlands, 15.8 - 16.4 Ma), crossed the Atlantic westward, settled on the western shore of the North Atlantic, first in Calvert time (14.2 - 15 Ma) and spread southward in St. Mary's time (8.5 - 10.5 Ma).

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APPENDIX

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