A late surviving ‘southern seal’ from high latitudes of the North Atlantic realm: a late Pliocene monachine seal on the southern margin of the North Sea (#24029)

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A late surviving 'southern seal' from high latitudes of the North Atlantic realm: a late Pliocene monachine seal on the southern margin of the North Sea

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Background: The family of true seals, the Phocidae, is subdivided into two subfamilies: the 'southern seals' or Monachinae, and the 'northern seals' or Phocinae. These common names refer to the subfamilies' current distribution: while the extant Monachinae are largely restricted to the (sub-)antarctic and the eastern Pacific, the fossil record shows that Monachinae were common in the North Atlantic realm during the late Miocene and early Pliocene. Until now, only one late Pliocene record is known from the Mediterranean, *Pliophoca etrusca* from Tuscany, Italy, but none from farther north in the North Atlantic. **Methods:** We present the description of one partial phocid humerus collected in the early 20th century from the Antwerp area (Belgium), with an assessment of its stratigraphic origin using data from the literature. **Results:** The studied humerus was recovered during construction works at the former Lefèvre dock in the Antwerp harbour (currently part of the America dock). Confronting the information associated to the specimen with data from the literature and from local boreholes, the upper Pliocene Lillo Formation is ascertained as the lithological unit from which the specimen originates. Morphologically, among other features the shape of the deltopectoral crest indicates a monachine attribution for this specimen. The development of the deltopectoral crest is closer to the condition in extant Monachinae than in extinct Monachinae. **Discussion:** The presented specimen is definitely a monachine seal and a literature study clearly shows that it came from the upper Pliocene Lillo Formation. This is the first known monachine specimen from the late Pliocene of the North Sea, and more broadly from the northern part of the North Atlantic realm. This humerus differs from the humerus of *Pliophoca etrusca* and suggests a higher diversity of Monachinae in the late Pliocene than previously assumed.

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Abstract

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Keywords: Mammalia, Phocidae, Monachinae, Pliocene, North Atlantic, North Sea

Introduction

True seals (Mammalia, Pinnipedia, Phocidae) are subdivided into two extant subfamilies: Monachinae Gray, 1869 and Phocinae Gray, 1821. Morphologically, both are clearly distinct from each other (e.g., King, 1964; Berta & Wyss, 1994). Additionally, both subfamilies are characterized by different biogeographic ranges for the extant taxa, which are reflected in their common names (King, 1964). Monachinae are sometimes referred to as ‘southern seals’, while Phocinae are usually called ‘northern seals’ (King, 1964). Indeed, the geographic range of Phocinae is restricted to the Arctic and Northern temperate zones, including the Caspian Sea (*Pusa caspica* (Gmelin, 1788)) and Lake Baikal (*Pusa sibirica* (Gmelin, 1788)), while most Monachinae live more southerly (e.g., King, 1964; Jefferson et al., 2008; Perrin et al., 2017). The Lobodontini Gray, 1869 tribe lives in the Antarctic and sub-Antarctic waters. The elephant seals of the genus *Mirounga* Gray, 1827 live in sub-Antarctic waters and along the western shores of South America, but also in the Northeast Pacific, from California to Alaska. The monk seals (genus *Monachus* Fleming, 1822) have a sub-tropical to tropical distribution, restricted to the Mediterranean (*Monachus monachus* Hermann, 1779), the Caribbean Sea (*Monachus tropicalis*

Gray, 1850 recently extinct) and the Hawaiian Islands, in the central Pacific Ocean (*Monachus schauinslandi* Matschie 1905) (e.g., King, 1964; Jefferson et al., 2008; Perrin et al., 2017).

However, the current distribution of extant Monachinae does not reflect the past distribution of Monachinae and Phocinae. Indeed, during the Neogene, multiple monachine taxa lived in the North Atlantic realm, with fossils of *Auroraphoca atlantica* Dewaele, Peredo, Meyvisch & Louwye, in press, *Callophoca obscura* Van Beneden, 1876, and *Virginiaphoca magurai* Dewaele, Peredo, Meyvisch & Louwye, in press, from late Miocene deposits from Belgium and late Miocene and early Pliocene deposits from the east coast of North America (Van Beneden, 1876, 1877; Ray, 1976; Koretsky & Ray, 2008; Dewaele et al., in press). Historically, the youngest published fossil monachine taxon of the Northern Hemisphere is the holotype of *Pliophoca etrusca* Tavani, 1941 from the Piacenzian (late Pliocene) of Tuscany, Italy (Tavani, 1941; Berta et al., 2015).

Materials and Method

Biological sample

This study focuses on specimen IRSNB M2308. In addition, fossil comparison material includes all known late Miocene-early Pliocene Monachinae from the North Atlantic realm: *Auroraphoca atlantica*, *Callophoca obscura*, *Homiphoca* (*capensis*), *Pliophoca etrusca*, and *Virginiaphoca magurai*, as well as other Neogene Monachinae from the Southern Hemisphere: *Acrophoca longirostris* Muizon, 1981, *Australophoca changorum* Valenzuela-Toro, Pyenson, Gutstein & Suárez, 2016, *Piscophoca pacifica* Muizon 1981, and *Properitpychus argentinus* (Ameghino, 1893). Comparisons are based on personal observations (*Ac. longirostris*, *Aur. atlantica*, *C.*

obscura, *Pi. pacifica*, and *V. magurai*) and bibliographic data (*Ac. longirostris*, *Aus. changorum*, *Homiphoca* spp., *Pi. pacifica*, *Pl. etrusca*, and *Pr. argentinus*; Muizon & Hendey, 1980; Muizon, 1981; Muizon & Bond, 1982; Berta et al., 2015; Valenzuela-Toro et al., 2016).

Institutional Abbreviations

IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **MSNUP**, Museo di Storia naturale, Università di Pisa, Pisa, Italy; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Historical and geological context of humerus IRSNB M2308

Humerus IRSNB M2308 was discovered in 1904 by the private collector Georges Hasse. The collection of the latter entered into the RBINS collection in the 1910s. The data provided by the labels adjoining specimen IRSNB M2308 state only ‘Anvers’ (Antwerp) and ‘bassin-canal’ as the locality of the specimen (Fig. 1). The specimen was originally considered to represent a humerus of *Prophoca* Van Beneden, 1876

Originally, the specimen has been stratigraphically assigned to the ‘Poederlian’ (Poederlien, Fig. 1A). However, the ‘Poederlian’ is currently a disused regional Neogene stage (Laga & Louwye, 2006). Laga & Louwye (2006) argue that the stage has never been defined properly, that different historic authors employed different interpretations of the stage, and that the type locality is unsuitable for a stage type section. The ‘Poederlian’ is named after the Belgian village of Poederlee, roughly 30 kilometers east of Antwerp, and the so-called

'Poederlian' deposits in the Antwerp harbour area were correlated to the deposits at Poederlee by Vincent (1889). Later authors disagreed with Vincent (1889), and considered the 'Poederlian' in the Antwerp harbour area to represent the upper substage of the Scaldisian (Leriche, 1922).

Fortunately, Hasse (1909) described 'Poederlian' walruses from the Antwerp harbour area, providing geographic maps, photographs of stratigraphic sections, and a detailed description of the lithology. Hasse (1909) states that these walrus specimens were discovered during construction works for new docks ('bassin' in French) in 1902-5, alongside other fossil mammal remains including phocid remains (presented as '*Phoca*'). The time interval, location data, and stratigraphic data from Hasse (1909) match perfectly the labels of IRSNB M2308 (Fig. 1), and it can be safely assumed that specimen IRSNB M2308 had been found at the same locality, and in the same levels ('Poederlian'), as the walruses that he described (now attributed to *Ontocetus emmonsi*, see Kohno & Ray, 2008). Hasse (1909) pinpointed the geographic setting to the Lefèvre dock (Bassin Lefèvre). Currently, the Lefèvre dock is merged into the America dock, forming its southeastern portion. Additionally, Hasse (1909) presented malacological data for the Lefèvre dock fossil-bearing level; one of the most common taxa is the gastropod *Fusus contrarius* (Linnaeus, 1771). More recent research renamed the fossil '*F. contrarius*' to *Neptunea angulata* (Wood, 1848) to make the distinction with extant *F. contrarius*. In Neogene deposits of the Antwerp area, *N. angulate* is considered a characteristic taxon for the Oorderen Sands and the overlying Kruisschans Sands members of the Pliocene Lillo Formation (Fig. 2A) (Nyst, 1843; Marquet, 1993, 1997, 1998). The Oorderen Sands Member overlies the Luchtbal Sands Member, the lowest member of the Lillo Formation, conformably. Another mollusc from the locality and level listed by Hasse (1909) is the bivalve *Cardium parkinsoni*, which Tavernier & Heinzelin (1962) restricted to the Kruisschans Sands and Merksem Sands members (Fig. 2A).

Borehole logs (GEO-04/169-BRO-B1 and kb15d28w-B211; Dienst Ondergrond Vlaanderen, www.dov.vlaanderen.be) within close proximity of the locality analysed by Hasse have shown that the lower – upper Pliocene Lillo Formation is underlain by the lower Pliocene Kattendijk Formation in the area. However, the boundary between the Lillo and Kattendijk formations is consistently located at ten meters or more below the core top, while Hasse (1909) clearly stated that the walrus fossils (and associated phocid material) he found came from less than three meters below the top of the section (Fig. 2B). Consequently, all arguments confirm the Lillo Formation as the origin of both the walruses described by Hasse (1909) (for more details see Kohno & Ray, 2008) and the phocid humerus IRSNB M2308.

Dinoflagellate cyst biostratigraphy by De Schepper, Head & Louwye (2009) dated the Oorderen Sands Member no younger than 2.72-2.74 Ma, but not older than the maximum possible age of 3.71 Ma for the Lillo Formation, and the upper boundary of the Kruisschans Sands Member to be no younger than 2.58 Ma. These two members are thus included in an interval ranging from the latest Zanclean (late early Pliocene) to the Piacenzian (late Pliocene). Considering the presence of the Luchtbal Sands Member under the Oorderen Sands, a late Pliocene age is proposed for IRSNB M2308, originating either from the latter member or from the Kruisschans Sands Member.

Systematic paleontology

Pinnipedia Illiger, 1811

Phocidae Gray, 1825

Monachinae Gray, 1869

Indeterminate Monachinae

Referred Specimen—IRSNB M2308, right humerus, Oorderen Sands or Kruisschans Sands members, Lillo Formation, America dock, Antwerp, Belgium.

Locality—Historically 'Anvers (bassin-canal)', but currently reconsidered as the southeastern area of the America dock in the Antwerp Harbour area, north to northwest of the city of Antwerp, Antwerp province, Belgium, following data from Hasse (1909) (see discussion above).

Stratigraphy and Age—Historically 'Poederlien', but currently reconsidered to belong to either the Oorderen Sands or the Kruisschans Sands members of the Lillo Formation, following data from Hasse (1909) and De Schepper, Head & Louwye (2009), between 2.58 Ma and 3.71 Ma (see discussion above). This entails a Piacenzian age (late Pliocene), although a latest Zanclean (latest early Pliocene) age cannot be completely ruled out.

Description and Comparison—Specimen IRSNB M2308 was found isolated, and no other phocid remains are currently known from the late Pliocene Lillo Formation of Antwerp, Belgium. IRSNB M2308 is a partial right humerus, lacking the distal epiphysis. The distal portion of the diaphysis is fractured, with the internal bone structure clearly visible. Consequently, it is clear that the distal part is not missing due to skeletal immaturity and non-fusion of the distal epiphysis.

The preserved portion of humerus IRSNB M2308 is 123.2 mm long, allowing to assume that the length of the complete humerus should have been 140-150 mm, and that the individual must have been comparable in size to the extant Weddell seal *Leptonychotes weddellii* (2.7 – 3.3 m total length; from King, 1964). However, this is still considerably smaller than the humerus of *Callophoca obscura* from the early Pliocene Kattendijk Formation, underlying the Lillo

Formation in the Antwerp harbour area, and the Yorktown Formation in the Lee Creek Mine, Aurora, North Carolina (Fig. 3A-D, versus Fig. 3E). The illustrated humerus of *Callophoca obscura* is approximately 200 mm long (Fig. 4F). The length of humerus IRSNB M2308 is comparable to that of *Homiphoca* spp. and *Pliophoca etrusca* (see Muizon & Hendey, 1980; Berta et al., 2015). The humeral head is prominent and hemispherical in IRSNB M2308, with a clear, sharp distinction between the head and the neck, similar to the extant *Leptonychotes weddellii* (Lesson, 1826), and the extinct *Piscophoca pacifica* and *Pliophoca etrusca*, but slightly better developed than in other Monachinae. Contrastingly, in the contemporaneous *Pliophoca etrusca*, the head strongly overhangs the diaphysis posteriorly, while this is not the case in IRSNB M2308. The humeral head is slightly compressed anteroproximally (height-to-width ratio is 42.1 mm : 44.6 mm; Table 1). The head is directed anteriorly to the same extent as in the extant *Monachus monachus* and *Leptonychotes weddellii*, and the extinct *Acrophoca longirostris* and *Piscophoca pacifica*. The posterodistal margin of the humeral head is sub-triangular in IRSNB M2308. We observed a similar condition in *Monachus monachus*, while it tends to be more smoothly-rounded in Lobodontini.

Both the lesser and the greater tubercle do not reach the level of the humeral head, proximally. These conditions vary between extant and extinct Monachinae (Muizon, 1981; Dewaele et al., in press). Apart from *Monachus monachus*, all extant Monachinae have a lesser tubercle that is well-developed, exceeding the proximal level of the humeral head; while in extinct Monachinae, the lesser tubercle usually does not exceed the proximal level of the humeral head, except in *Callophoca obscura*, *Homiphoca* spp. (Hendey & Repenning, 1972), *Pliophoca etrusca*, *Properiptychus argentinus* and *Virginiaphoca magurai* (Muizon & Hendey, 1980; Muizon, 1981; Muizon & Bond, 1982; Berta et al., 2015; Dewaele et al., in press). The greater tubercle is generally little-developed in extant Monachinae, not exceeding the proximal level of the humeral head (Muizon, 1981). However, in extinct Monachinae, this condition varies, with the greater tubercle exceeding the proximal level of the humeral head in most taxa (*Acrophoca longirostris*, *Auroraphoca atlantica*, *C. obscura*, *Homiphoca* spp. Muizon & Hendey, 1980, and *Piscophoca pacifica*), but not in others (IRSNB M2308, *Pl. etrusca*, and *Pr. argentinus* (Ameghino, 1893)) (Muizon, 1981; Muizon & Bond, 1982; Berta et al., 2015; Dewaele et al., in press). The proximal portion of the deltopectoral crest of IRSNB M2308 is strongly curved medially, yielding a deep and relatively narrow bicipital groove, i.e., that is as deep as it is wide. This condition differs from other Monachinae, having bicipital grooves that are usually wider than deep. This groove is moderately deep in *Hydrurga leptonyx* (Blainville, 1820) and *Leptonychotes weddellii* (see Muizon, 1981). The bicipital groove of IRSNB M2308 is smooth, as in *H. leptonyx*, and *L. weddellii*, while other extant and extinct Monachinae have a transverse bar at the proximal portion of the bicipital groove (see Muizon, 1981; Dewaele et al., in press).

Overall, the deltopectoral crest of IRSNB M2308 is typically monachine in lateral view, in that the deltopectoral crest curves smoothly into the diaphysis, distally (e.g., King, 1964; Muizon, 1981; Berta & Wyss, 1994) (Fig. 3A-G, versus Fig. 3H). The maximum breadth of the deltopectoral crest is located at approximately 1/3 of the total length of the bone in IRSNB M2308. The shape of this deltopectoral crest in lateral view varies at the genus level among Monachinae. An overall trend appears to be that the anterior projection of this crest is more pronounced in extant and some Pliocene Monachinae compared to other Pliocene and Miocene Monachinae in which this projection is less pronounced and located slightly more distal (see Valenzuela-Toro et al., 2016: fig. 4). Consequently, a better developed deltopectoral crest yields a stronger curvature at the distal tapering of the crest. Indeed, Miocene Monachinae, such as *Acrophoca longirostris*, *Australophoca changorum* Valenzuela-Toro, Pyenson, Gutstein & Suárez, 2015, *Piscophoca pacifica*, and *Properiptychus argentinus* have a deltopectoral crest that does not expand as strongly anteriorly as in extant Monachinae, and the extinct *Callophoca obscura*, and *Homiphoca* spp. (see Berta & Wyss, 1994). An exception is *Pliophoca etrusca*, from the late Pliocene, which does not seem to have a strongly-expanded deltopectoral crest (Fig. 3E). The humerus IRSNM M2308 has a strongly anteriorly-expanded deltopectoral crest, as in most Pliocene and extant Monachinae. However, the distal portion of the deltopectoral crest tapers more gradually to the distal epiphysis than in extant Monachinae (except *Monachus* spp. and *Ommatophoca rossii* Gray, 1844).

In anterior view, the proximal portion of the deltopectoral crest of IRSNB M2308 is weakly bifurcate. Among other Monachinae, this condition varies between a relatively smoothly-curving margin in *Leptonychotes weddellii* and a strongly-pronounced bifurcation in *Ommatophoca rossii*. However, other known extant and extinct Monachinae show intermediate conditions, comparable to the condition in IRSNB M2308.

The deltoid crest on the deltopectoral crest is smooth and elongate, approximately twice as long as it is wide (approximately 6 cm long and 3 cm wide). The proximal and distal edges of this deltoid crest are rounded. This condition varies among Monachinae, but the deltoid crest of IRSNB M2308 appears to resemble that of *Piscophoca pacifica* the best (compare Muizon, 1981). Another characteristic of the deltopectoral crest of IRSNB M2308 is the strong development of a mammillary tubercle proximal on the anteroproximal margin of the deltopectoral crest. This tubercle is strongly turned medially and can be assumed to be the insertion area of the atlantoscapularis muscle (see Howell, 1929; Muizon, 1981). A similar condition has only been observed in *Monachus monachus* and *Ommatophoca rossi*, and it is developed to a lesser extent in *Lobodon carcinophaga* (Gray, 1844).

In posterior view, the diaphysis of IRSNB M2308 is roughly comparable in shape to most other Monachinae, but noticeably transversely more slender than in *Callophoca obscura*. On the posterior surface of the diaphysis, just distal to the humeral head and lesser tubercle, there is a moderately well-developed fossa for the origin of the triceps brachii muscles. Among Monachine, Muizon (1981) only observed a similar condition in *Piscophoca pacifica*. Muizon (1981) also observed this condition in *Monotherium aberratum*, but recent research suggests that *M. aberratum* is not a monachine but a phocine seal (Dewaele et al., in prep.). The distal epiphysis is largely missing. Only the most proximal portion of the supinator crest is preserved, indicating that this crest was poorly developed. This supinator crest is consistently poorly developed among Monachinae (Muizon, 1981; Berta & Wyss, 1994). Only the extinct *Homiphoca* spp. appears to have a moderately well-developed crest, but not to the same extent as in Phocinae (L.D., pers. obs.).

Discussion

The shape of the deltopectoral crest in the humerus IRSNB M2308 allows to identify the specimen as a monachine seal: it is rounded in lateral view and gradually tapers to the distal epiphysis. However, it is radically different from the other Pliocene monachines from the North Atlantic and Mediterranean, *Auroraphoca atlantica*, *Callophoca obscura*, *Homiphoca* spp., and *Pliophoca etrusca*: the maximum breadth of the deltopectoral crest is located relatively proximally. *A atlantica*, from the early Pliocene Yorktown Formation at Lee Creek Mine, Aurora, North Carolina, differs strongly from IRSNB M2308 in the particular shape of the deltopectoral crest, extending much more distal, and the strong development of the lesser tubercle. The early Pliocene *C. obscura*, representing the stratigraphically second youngest monachine from the Antwerp area, next to IRSNB M2308, is noticeably larger and has a more robust humeral diaphysis, and *Homiphoca* spp. has a less pronounced deltopectoral crest. Representing the only contemporaneous monachine taxon to IRSNB M2308 from the Northern Hemisphere, *P. etrusca* differs notably in having a humeral head that strongly overlaps the diaphysis posteriorly, as well as a less developed deltopectoral crest. Consequently, humerus IRSNB M2308 most likely represents a new monachine species, the first known ‘southern seal’ from the late Pliocene (or latest early Pliocene) of the North Sea (3.71 to 2.58 Ma), and thus the latest occurrence of Monachinae from higher latitudes of the North Atlantic (Fig. 4). Although humeri have historically often been used as type specimens of phocids (e.g., Koretsky, 2001; Koretsky and Ray, 2008), we are reluctant to diagnose a new taxon, despite the presence of multiple characteristics that distinguishes IRSNB M2308 from other monachine humeri. A proper diagnosis awaits more complete skeletal remains to be discovered. In the North Atlantic realm, monachine seals went extinct before the Pleistocene, with the exception of the extant *Monachus monachus* in the Mediterranean Sea and along the western shore of North Africa (Deméré, Berta & Adams, 2003), and today the higher latitudes of the North Atlantic Ocean are exclusively occupied by phocine seals (e.g., King, 1964). Although the exact triggers of the extinction of Monachinae in higher northern latitudes are unknown, it can be assumed that Pliocene North Atlantic lineages of Monachinae could not adapt to decreasing seawater temperatures related to the global, Pliocene to Pleistocene decline in temperatures (see Zachos, Dickens & Zeebe, 2008). Similarly, late Pliocene – Pleistocene climatic changes impacting the distribution and diversity of other groups of marine mammals, both regionally and globally, have been accounted for in the literature (Boessenecker, 2013; Churchill, Kohno & Clementz, 2014; Poust & Boessenecker, 2017; Slater, Goldbogen & Pyenson, 2017; Tsai et al., 2017), including the pinniped faunal turnover in the southeastern Pacific (Valenzuela-Toro et al., 2013). Different hypotheses regarding the causes of diversity changes across the Plio-Pleistocene boundary have been invoked. Deméré, Berta & Adams (2003) argued that North Atlantic lineages of Pliocene Monachinae did not evolve the pagophilic evolution observed in phocines and lobodontins in response to Pleistocene glacioeustatic events. In the context of that hypothesis, ongoing climatic change will most likely profoundly affect the survival and distribution of North Atlantic and Arctic phocids; relying on ice for pupping and nursing, pagophilic species are greatly threatened, whereas more temperate species may potentially broaden their range in higher latitudes (e.g., Johnston et al., 2012; Stenson & Hammill, 2014). Although a study of the paleobiogeographic evolution of Monachinae in response to climatic change is beyond the scope of this paper, Churchill, Kohno & Clementz (2014) showed that global temperature changes during the late Neogene and Quaternary were important drivers for changes in otariid biogeography. For cetaceans Marx & Uhen (2010) and Bisconti (2003) argued the presence of a link between higher primary productivity during the Pliocene than during the Quaternary, and reduced interspecific competition pressure. Consequently, more ecological niches were available during the Pliocene than thereafter. This reasoning may or may not be extrapolated to the evolution of Monachinae from the North Atlantic.

Conclusions

Specimen IRSNB M2308 was discovered by Georges Hasse during construction works at the Lefèvre dock in Antwerp, Belgium, in the early 1900s. A reassessment of the geographic and stratigraphic settings and the local molluscan assemblage indicates that specimen IRSNB M2308 originates from the upper Pliocene Lillo Formation. This is the first late Pliocene phocid described from the higher latitutes of the North Atlantic realm (north to the Mediterranean). The shape of the deltopectoral crest allows an attribution of the monachine subfamily, and the overall morphology indicates that the specimen does not represent either previously described early Pliocene monachines from the North Atlantic (*Auroraphoca atlantica*, *Callophoca obscura*, or *Homiphoca* spp.) or contemporaneous *Pliophoca etrusca* from the late Pliocene of the Mediterranean. This further increases the diversity of Monachinae during the Pliocene (and more specifically the late Pliocene), prior to the final extinction of the clade in higher latitudes of the North Atlantic.

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FIGURE 1. Labels found associated to the humerus IRSNB M2308, Monachinae indet. **A**, original label, stating Antwerp ('Anvers') as the origin of the specimen and 1904 as the year of discovery. A provisional, unpublished and unsupported identification returned *Prophoca* Van Beneden, 1876; **B**, more recent label, stating the more precise locality as one of the docks in the Antwerp harbour area ('bassin-canal').

FIGURE 2. Pliocene stratigraphy of the Antwerp harbour region. **A**, stratigraphic column showing the succession of the different members of the uppermost lower and upper Pliocene Lillo Formation in the Antwerp harbour area. **B**, simplified lithology of the section from Lefèvre Dock where Hasse (1909) discovered specimen IRSNB M2308. Litholog drawn after descriptions by Hasse (1909).

FIGURE 3. Humerus IRSNB M2308 and comparison material. **A-D**, right humerus IRSNB M2308, Monachinae indet. (Antwerp, Belgium; late Pliocene), in **A**, medial view; **B**, anterior view; **C**, lateral view; **D**, posterior view. **E**, left humerus of *Pliophoca etrusca* (MSNUP I-13993, holotype) (Casa Nuova, Tuscany, Italy; Piacenzian) in medial view; **F**, left humerus of *Callophoca obscura* (USNM 186944) (Aurora, North Carolina, U.S.A.; Zanclean) in medial

view; **G**, schematic drawing of left humerus of the extant monachine *Monachus monachus*; **H**, schematic drawing of left humerus of the extant phocine *Phoca vitulina*. Scale bar equals 5 cm.

FIGURE 4. Geographic distribution of late Miocene to recent Monachinae in the North Atlantic realm (including Mediterranean Sea). Localities of fossil Monachinae are indicated by a black dot. *Auroraphoca atlantica* and *Callophoca obscura* are known from the late Miocene and early Pliocene of Antwerp, Belgium (*C. obscura*), and the early Pliocene of Lee Creek Mine, North Carolina, USA (*A. atlantica* and *C. obscura*) (Koretsky & Ray, 2008; Dewaele et al., in press); specimen IRSNB M2308, Monachinae indet., from the late Pliocene of Antwerp, Belgium (this study); *Pliophoca etrusca* from the late Pliocene of Tuscany, Italy (Berta et al., 2015). Geographic ranges of the extant *Monachus monachus* and the recently extinct *Monachus tropicalis* are indicated in dark gray, following data presented by Jefferson, Webber & Pitman (2008) for *M. monachus* and Timm, Salazar & Peterson (1997) for *M. tropicalis*.

Figure 1

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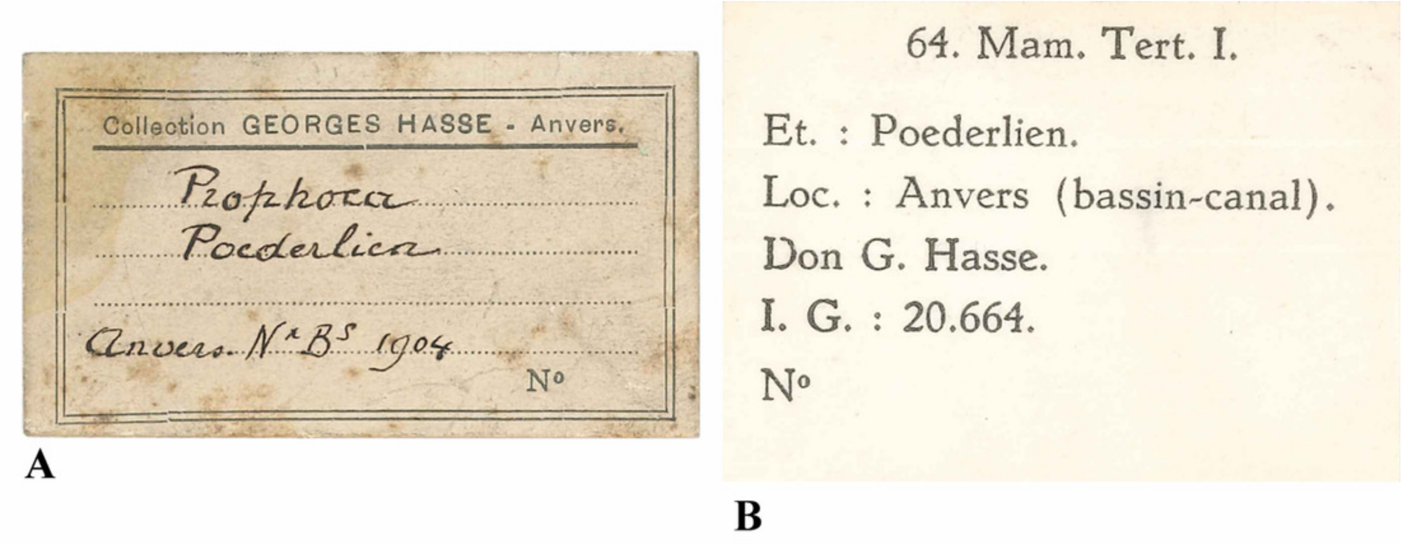


Collection GEORGES HASSE - Anvers.

Prophoca

Poederlien

Anvers N^x B^s 1904

N°

64. Mam. Tert. I.

Et. : Poederlien.

Loc. : Anvers (bassin-canal).

Don G. Hasse.

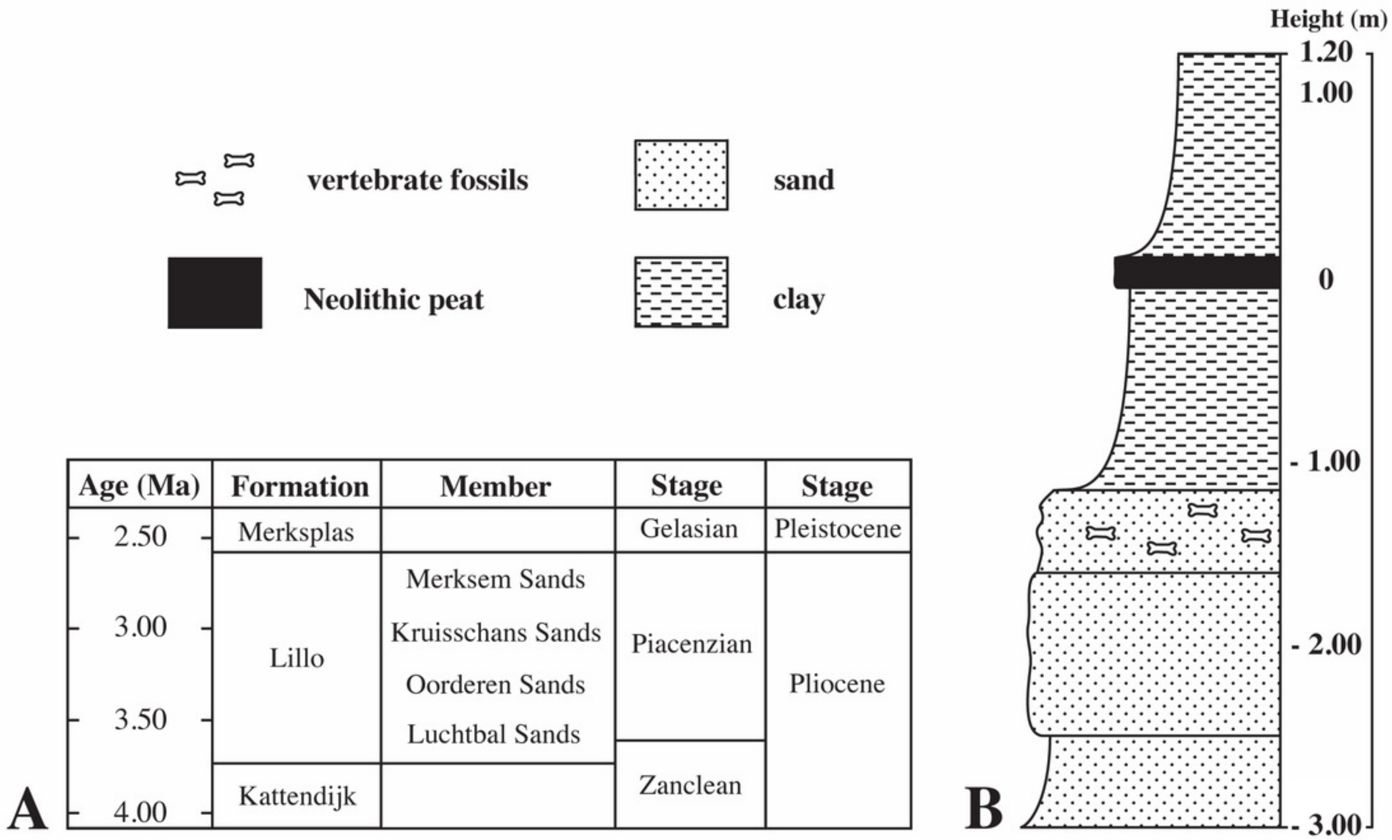
I. G. : 20.664.

N°

Figure 2

Pliocene stratigraphy of the Antwerp harbour region.

A, stratigraphic column showing the succession of the different members of the uppermost lower and upper Pliocene Lillo Formation in the Antwerp harbour area. The Kattendijk and Merksplas formations are not divided into members. **B**, simplified lithology of the section from Lefèvre Dock where Hasse (1909) discovered specimen IRSNB M2308. Litholog drawn after descriptions by Hasse (1909).



Age (Ma)	Formation	Member	Stage	Stage
2.50	Merksplas		Gelasian	Pleistocene
	Lillo	Merksem Sands	Piacenzian	Pliocene
3.00		Kruisschans Sands		
		Oorderen Sands		
3.50		Luchtbal Sands		
4.00	Kattendijk		Zanclean	

Figure 3

Humerus IRSNB M2308 and comparison material.

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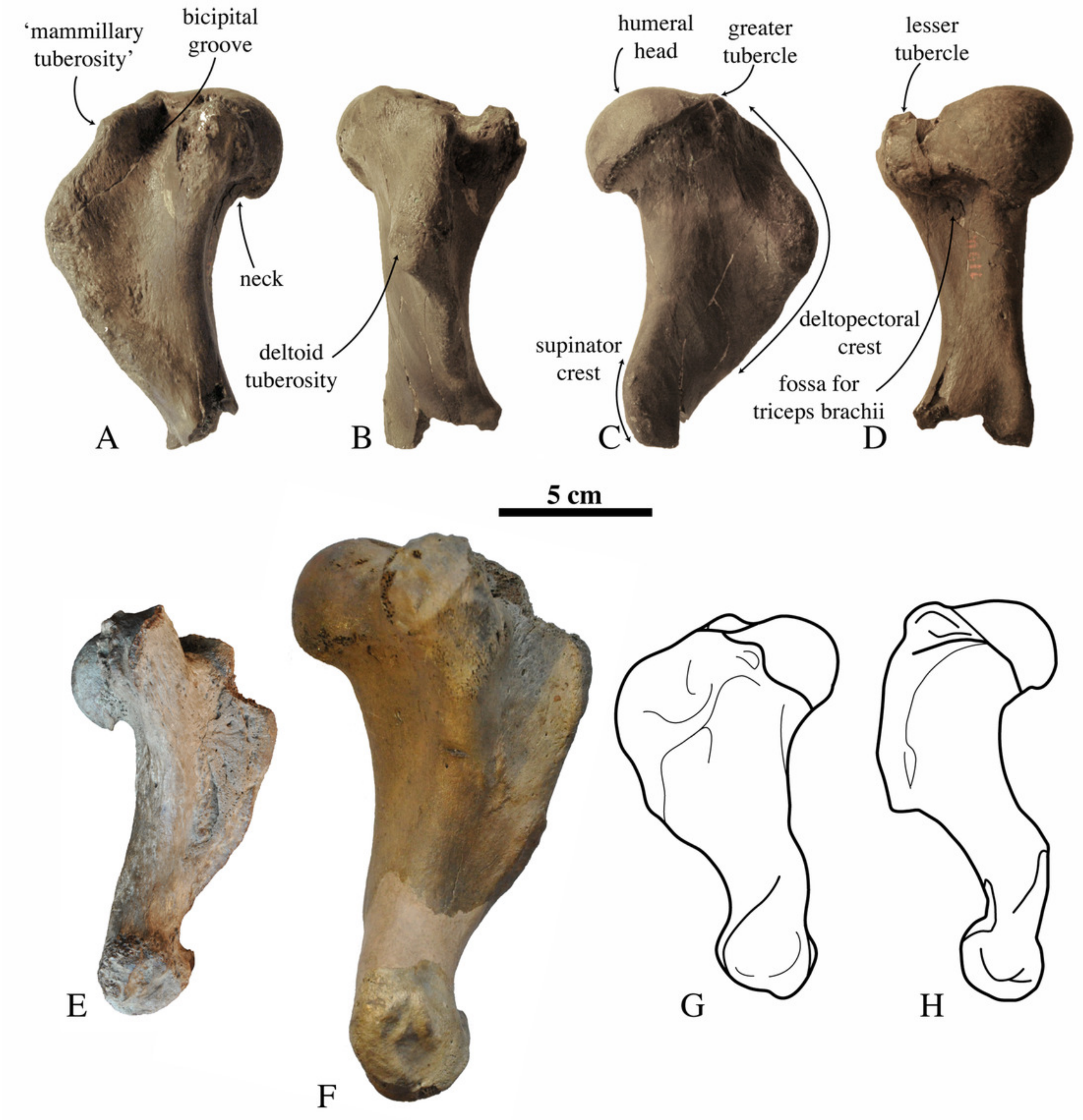
'mammillary tuberosity'
bicipital groove
neck
deltoid tuberosity
humeral head
greater tubercle
supinator crest
deltopectoral crest
lesser tubercle
fossa for triceps brachii
A
B
C
D
5 cm
E
F
G
H

Figure 4

Geographic distribution of late Miocene to recent Monachinae in the North Atlantic realm (including Mediterranean Sea).

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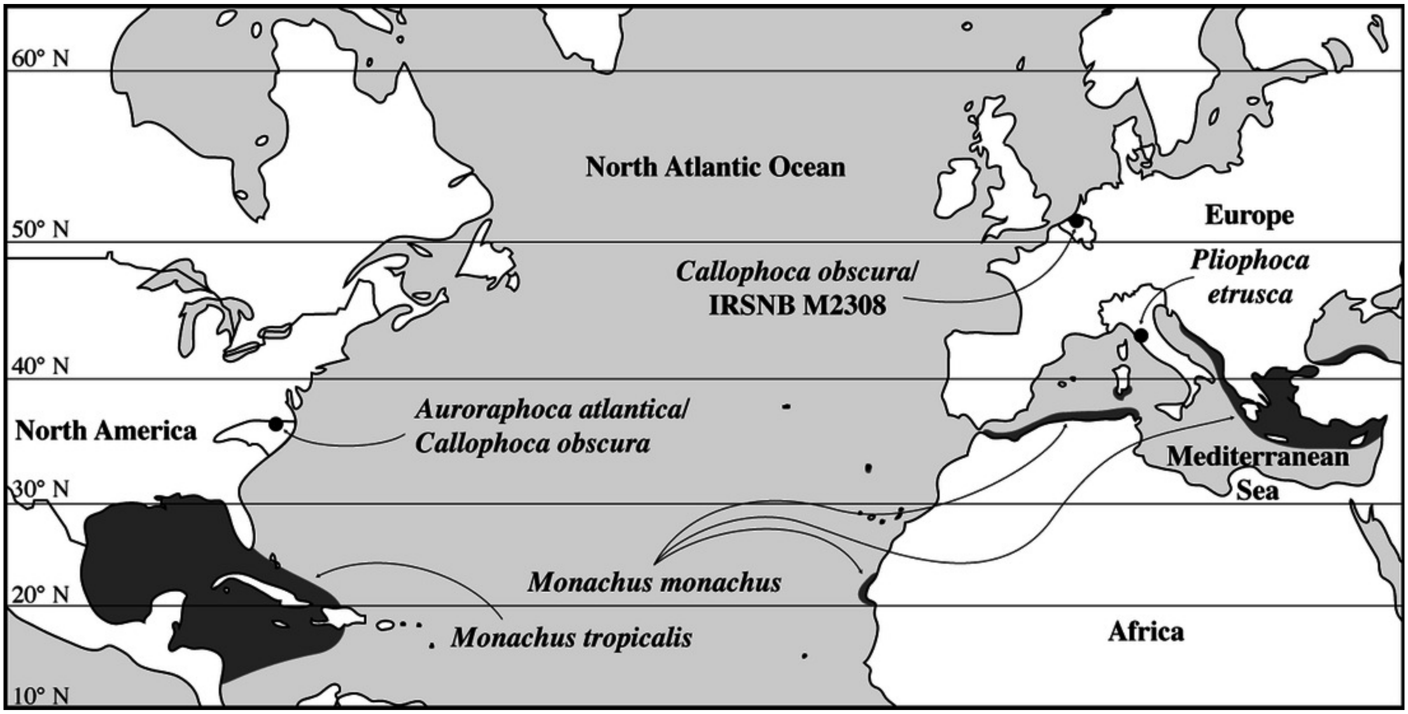

Table 1(on next page)

Measurements of humerus IRSNB M2308.

Measurements taken to the nearest 0.1 mm with an analogous caliper. Taking measurements follows the approach outlined by Koretsky (2001).

Table 1. Measurements of humerus IRSNB M2308. Measurements taken to the nearest 0.1 mm with an analogous caliper. Taking measurements follows the approach outlined by Koretsky (2001).

Character	Length (mm)
Height humeral head	42.1
Width humeral head	44.6
Transverse width proximal epiphysis	63.0
Anteroposterior width	79.9
Proximodistal length deltopectoral crest	92.2
Transverse width diaphysis	27.4