

A new monachine seal
(Monachinae, Phocidae, Mammalia)
from the Miocene of Cerro La Bruja
(Ica department, Peru)

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A new monachine seal (Monachinae, Phocidae, Mammalia) from the Miocene of Cerro La Bruja (Ica department, Peru)

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ABSTRACT

In the present study, we present a new monachine phocid, *Magophoca brevirostris* n. gen., n. sp., the fifth monachine described from the Pisco Formation (Peru). Coming from the Cerro la Bruja level at the locality of the same name, *Magophoca* n. gen. is the geologically oldest known seal from the Neogene of the southeast Pacific, dated at least to the late Tortonian, c. 8.4 Ma. *Magophoca* n. gen. is the second Monachinae (with *Noriphoca gaudini*) found to possess six upper incisors instead of four as in the other members of the sub-family. Further characters, such as the deep fossa for the *m. triceps brachii caput mediale* below the humeral head, on the posterior aspect of the proximal extremity of the diaphysis of the humerus, strongly support close relationships with *Piscophoca* from the latest Miocene and earliest Pliocene of the Pisco Formation at Sud Sacaco (Peru), but more interestingly, with *Frisiphoca aberrata* from the Tortonian of Belgium. In addition, the presence of an entepicondylar foramen is shared between *Frisiphoca* and *Magophoca* n. gen., but rare among other Monachinae, further strengthening the link between both. Although the fossil record of *Frisiphoca aberrata* is too incomplete to draw conclusions, these marked similarities allow us to hypothesize a dispersal link between both regions, across the late Miocene North Atlantic and Central American Seaway. The phylogenetic analysis retrieved *Magophoca* n. gen. as closely related to *Hadrokirus* and *Piscophoca* from younger levels in the Pisco Formation. This phylogenetic analysis also returned *Kawas* from the Miocene of Argentina as a sister genus of *Homiphoca* from the Pliocene of South Africa, thus radically departing from the previous classification of *Kawas* as a phocine seal.

KEY WORDS

Lobodontini,
Monachinae,
Phocidae,
Pisco Formation,
Peru,
Cerro la Bruja,
Tortonian,
new genus,
new species.

RÉSUMÉ

Un nouveau phocidé monachiné (Monachinae, Phocidae, Mammalia) de la Formation Pisco (Pérou, Miocène). Le présent travail étudie un nouveau phocidé monachiné, *Magophoca brevirostris* n. gen., n. sp., qui constitue le cinquième monachiné décrit provenant de la Formation Pisco (Pérou). Provenant du niveau Cerro La Bruja (CLB) de la localité du même nom, *Magophoca* n. gen. est le phocidé le plus ancien connu du Néogène du Pacifique du sud-est, daté au moins du Tortonien supérieur, environ 8,4 Ma. *Magophoca* n. gen. est le second monachiné (avec *Noriphoca gaudini*) connu, possédant six incisives supérieures au lieu de quatre comme chez les autres membres de la sous-famille. D'autres caractères comme une profonde fosse pour le triceps brachii caput mediale sous la tête humérale sur la face postérieure de l'extrémité proximale de la diaphyse de l'humérus plaident en faveur de relations étroites avec *Piscophoca* du Miocène terminal et Pliocène basal de la Formation Pisco à Sud Sacaco (Pérou), mais de façon plus intéressante avec *Frisiphoca aberrata* du Tortonien de Belgique. De plus, la présence d'un foramen entépicondylien est un caractère présent chez *Magophoca* n. gen. et *Frisiphoca* mais rare chez les autres monachinés ce qui renforce les liens entre les deux genres. Bien que le registre fossile de *Frisiphoca aberrata* est trop incomplet pour en tirer des conclusions, ces ressemblances permettent d'émettre l'hypothèse d'un lien migratoire entre les deux genres de l'Atlantique nord vers le Pacifique sud via le bras de mer de l'Amérique centrale au Miocène supérieur. L'analyse phylogénétique révèle un lien de parenté étroit entre *Magophoca* n. gen. d'une part et *Piscophoca* et *Hadrokirus*, d'autre part, des genres provenant de niveaux plus récents de la Formation Pisco. De cette analyse phylogénétique, résulte également que *Kawas*, du Miocène d'Argentine, est un genre frère d'*Homiphoca* du Pliocène d'Afrique du Sud, une interprétation radicalement différente de la classification précédente de *Kawas* parmi les Phocinae.

MOTS CLÉS
Lobodontini,
Monachinae,
Phocidae,
Formation Pisco,
Pérou,
Cerro la Bruja,
Tortonien,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Pinnipeds originated in the eastern North Pacific during the late Oligocene/early Miocene, in the area of today's northern California, Oregon, and Washington (e.g., Deméré *et al.* 2003; Berta *et al.* 2018; and references therein). At the time, the Central American Seaway (CAS) separated North and South America, allowing the ancestors of Phocidae, or earless seals, or the earliest Phocidae to migrate from the Cenozoic North Pacific to the North Atlantic. Indeed, the oldest known confirmed phocid fossils are *Leptophoca* specimens from the early middle Miocene Langhian, and possibly from the late early Miocene Burdigalian from North America and the Netherlands, and the genus *Devinophoca* from the early middle Miocene of the Paratethys in Slovakia (True 1906; Koretsky & Holec 2002; Koretsky *et al.* 2012; Koretsky & Rahmat 2015). Earlier dates, suggested for certain specimens, have been presented, such as a Lutetian (middle Eocene) age for *Praephoca bendullensis* from Germany (Diedrich 2011), a Chattian (late Oligocene) age for *Noriphoca gaudini* from Italy (Dewaele *et al.* 2018a), and also a Chattian age for unnamed specimens from South Carolina (Koretsky & Sanders 2002), but have also shown to be uncertain (Peredo & Uhen 2016; Dewaele *et al.* 2017a). The North Atlantic Ocean is the probable place where phocid seals diversified into the two subfamilies, Monachinae and Phocinae, and thrived during the Miocene (see e.g., Ray 1976; Muizon 1982; Deméré *et al.* 2003; Berta *et al.* 2018, Rule *et al.* 2020a). However, whereas a North Atlantic origin had been suggested for both, recently-discovered fossils from Australasia suggest a Southern Pacific origin and initial dispersal and diversification of (crown) Monachinae (Rule *et al.* 2020b, c, d).

Since the 1980s, four extinct species of monachines have been described from the Neogene of Peru: *Acrophoca longirostris*, *Piscophoca pacifica*, *Hadrokirus martini*, and *Australophoca changorum* (Muizon 1981; Amson & Muizon 2014; Valenzuela-Toro *et al.* 2016), showing that a diverse monachine seal fauna was present in the Neogene eastern South Pacific as well. In light of the dichotomy between the long-presumed North Atlantic origin of monachines (Muizon 1982; Deméré *et al.* 2003; Berta *et al.* 2018) and the recent hypothesis of a South Pacific origin of monachines (Rule *et al.* 2020b), the study of new fossil phocid material from the Neogene of Peru is necessary to bring more clarity. To date, the exact taxonomic and phylogenetic relationships between the fossil phocids from the eastern South Pacific and other fossil seals, as well as the exact timing of the colonization of the eastern South Pacific remain topics of debate. Studies show a close relationship between the Peruvian fossil monachines and the four Antarctic lobodontin monachines (Muizon 1981; Amson & Muizon 2014; Govender 2015), but other studies consider them to be stem monachines (Berta *et al.* 2015; Rule *et al.* 2020b). The former hypothesis suggests that the Neogene Peruvian seals may be ancestral to present-day Antarctic seals of the tribe Lobodontini (e.g., Muizon 1981, 1982; Deméré *et al.* 2003), warranting the importance of understanding their evolutionary history in light of ongoing climate change. In the present study, fossil material of a new genus and species from the Cerro la Bruja locality in the Ica Department of Peru is examined, providing clues to evolutionary and temporal pathways of the Neogene conquest of the Southern Hemisphere by Monachinae.

MATERIAL AND METHODS

PALEONTOLOGICAL AND BIOLOGICAL SAMPLE

The present study focuses on fossil phocid specimens housed at the Muséum national d'Histoire naturelle, Paris, France (MNHN) and referred here to a new taxon. Comparison material includes all extant phocid species with the exception of *Phoca largha* which was not available to us. Nevertheless, its sister taxon *Phoca vitulina* within the same genus is included in the study. Extinct taxa include all published South American phocids taxa, including the monachines *Acrophoca longirostris*, *Hadrokirus martini*, and *Piscophoca pacifica* from Peru, *Australophoca changorum* from Chile and Peru, the monachine *Properitychus argentinus*, and the – allegedly – phocine *Kawas benegasorum* from Argentina. However, the latter, *Australophoca* and *Properitychus* are only highly incompletely known. Other monachine taxa represented by good material include the South African *Homiphoca capensis* and the Mediterranean *Pliophoca etrusca*, and the less complete *Eomonachus belegaerensis* from New Zealand and *Sarcodectes magnus* from the east coast of North America. Other extinct Phocidae are poorly known: they are considered in this study, but their usefulness remains generally limited because of the limited diagnostic value of isolated (long) bones for phocid identification and comparison (Churchill & Uhen 2019).

All taxonomic names (genus and species), cited in the present study, are listed with their taxonomic authorities in Appendix 1. A detailed list of specimens used for comparison is provided in Appendix 2.

ANATOMICAL TERMINOLOGY

To maintain consistency with other recent systematic paleontological descriptions of extinct Monachinae, the osteological nomenclature follows the nomenclature used by Amson & Muizon (2014) for the description of *Hadrokirus martini* and by Berta *et al.* (2015) for the redescription of *Pliophoca etrusca*. When osteological descriptors are needed that have not been used by the aforementioned studies, the nomenclature used draws from Evans & Lahunta (2013), and Dewaele *et al.* (2017a, 2017b; 2018a, 2018b).

PHYLOGENETIC ANALYSIS

The phylogenetic analysis of *Hadrokirus martini* from Amson & Muizon (2014) forms the basis of the phylogenetic analysis in the present study. The data matrix includes 93 characters, which are listed in Appendix 3; all are equal weighted and all but two are unordered (char. 39, 42). Of the 93 phylogenetic characters used, 35 (char. 1–35) are cranial characters, two (char. 36, 37) are mandibular characters, 14 (char. 38–51) are dental, and 42 (char. 52–93) are postcranial.

The phylogenetic analysis includes 24 taxa. These include four outgroups from outside Phocidae. The extinct *Pteronarcotus goedertae* represents non-pinniped pinnipedimorphs. Of the three families of Pinnipedia, Odobenidae, Otariidae, and Phocidae, representatives of Odobenidae and Otariidae have been included as outgroup taxa too. The extant *Odobenus rosmarus* represents Odobenidae. *Arctocephalus pusillus*, and

Otaria byronia represents two extant representatives of Otariidae, respectively. For the Phocidae, 20 taxa are included in the phylogenetic analysis. The subfamily Phocinae is represented by four species, including the extant *Erignathus barbatus*, *Halichoerus grypus*, *Pagophilus groenlandicus*, and *Phoca vitulina*. Monachinae are represented by seven extant species, representing the three commonly accepted monachine tribes: Lobodontini, with *Hydrurga leptonyx*, *Leptonychotes weddellii*, *Lobodon carcinophaga*, and *Ommatophoca rossii*; Miroungini, represented by *Mirounga leonina*; and Monachini, represented by *Monachus monachus* and *Neomonachus schauinslandi*. Nine extinct Monachinae included in the present phylogenetic analysis are *Acrophoca longirostris*, *Eomonachus belegaerensis*, *Hadrokirus martini*, *Homiphoca pacifica*, *Piscophoca pacifica*, *Pliophoca etrusca*, and *Sarcodectes magnus*, as well as the newly described species *Magophoca brevirostris* n. gen., n. sp. from Cerro La Bruja (Peru). In addition, this phylogenetic analysis includes *Kawas benegasorum*. Cozzuol (2001) described this species as the first phocine from the southern hemisphere. This identification has only been tested once, with Rule *et al.* (2020b) retrieving *Kawas* as a stem-phocid. We argue that a reappraisal of the holotype of *Kawas benegasorum* is urgently needed to test the conclusions of Cozzuol (2001) and Rule *et al.* (2020b).

The phylogenetic matrix is built using Mesquite 3.5.1 (Maddison & Maddison 2019) and analyzed using heuristic parsimony searches in PAUP* version 4.0a (build 169) for Macintosh (X86) (Swofford 2002) with a heuristic search option and using the tree-bisection-reconnection algorithm (TBR). A backbone constraint for extant Pinnipedia (plus *Pteronarcotus goedertae*) has been adapted from Rule *et al.* (2020b). Character states are optimized using the accelerated transformation criterion (ACCTRAN). Homoplasy is downweighed through implied weighing using the Goloboff criterion, with the k-value set at three. The stability of the resulting tree(s) is studied using the bootstrap test with a full heuristic search with 10 000 replications with random number seed zero and the best tree being saved for each replication.

SUPPLEMENTARY DATA

A nexus file of the data matrix is available as supplementary data (Appendix 4) at the following address: https://doi.org/10.5852/geodiversitas2024v46a3_s1

Certain phylogenetic characters are mentioned in the section describing *Magophoca brevirostris* n. gen., n. sp. and comparing it with other taxa, below.

INSTITUTIONAL ABBREVIATIONS

NHMUK	Natural History Museum, London, United Kingdom;
CMM	Calvert marine Museum, Solomons, Maryland, United States;
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium;
MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina;
MEF	Museo paleontológico “Edigio Feruglio”, Trelew, Chubut, Argentina;
MER	Museo de Entre Ríos, Paraná, Argentina;
MNHN	Muséum national d'Histoire naturelle, Paris, France;

MSNUP	Museo di Storia naturale, Università di Pisa, Italy;
MUSM	Museo de Historia natural, Universidad Nacional Mayor de San Marcos, Lima, Peru;
SAM	Iziko South African Museum, Cape Town, South Africa;
USNM	United States national Museum of natural History, Washington, D.C., United States.

STRATIGRAPHIC AND GEOGRAPHIC SETTING

The specimens described here have been collected at the locality of Cerro La Bruja (CLB) in the Pisco-Ica sub-basin of the Pisco Formation (Fig. 1). The Cerro la Bruja locality has yielded vertebrate fossil remains representing various marine tetrapod taxa, including the type specimens of the cetaceans *Atocetus iquensis*, *Belonodelphis peruanus*, *Brujadelphis ankylorostris*, and *Brachydelphis mazeasi*, and the penguin *Spheniscus muizoni*. Muizon & DeVries (1985) and Amson & Muizon (2014) mentioned an undescribed monachine phocid seal from CLB, which the present study intends to formally describe.

The Pisco Formation was deposited during a series of marine transgressions along the tectonically active west coast of South America. It is famous for its exceptionally well-preserved fossil record of marine tetrapods, including marine birds, cetaceans, pinnipeds and marine sloths (e.g., Bianucci *et al.* 2016a, b, and references therein). The fossils are largely preserved at discrete vertebrate levels, named after different localities: Cerro la Bruja (CLB), El Jahuay (ELJ), Aguada de Lomas (AGL), Montemar (MTM), Sacaco Sud (SAS), and Sacaco (SAO) (e.g., Muizon & DeVries 1985; Brand *et al.* 2011; Ehret *et al.* 2012). The CLB vertebrate level is the third oldest vertebrate level of the Pisco Formation, being younger than the rich vertebrate level at Cerro Colorado and the oldest vertebrate level of the Pisco Formation at Santa Rosa (Muizon & DeVries 1985; Muizon 1988; Brand *et al.* 2011; Ehret *et al.* 2012, Bianucci *et al.* 2016a, Marx *et al.* 2017). A geologic age of 11–13 Ma has been suggested for CLB on the basis of the mollusk and marine mammal fauna (Muizon & DeVries 1985; Muizon 1988). Radiometric dating of a volcanic ash layer approximately 50 m above the CLB vertebrate level yielded an absolute age of 9.2 Ma (Brand *et al.* 2011). This dating concludes to likely middle Miocene Serravallian age (11–13 Ma), but definitely no younger than an early late Miocene Tortonian age (9.2 Ma).

More recent studies by Di Celma *et al.* (2017), have re-evaluated the calibration of the upper Miocene beds of the Pisco Formation in the Ica desert. These authors, based on the occurrence of three widespread erosional surfaces, have subdivided the Pisco Formation in this area into three depositional sequences named, from the oldest to the youngest, P0, P1, and P2. The P2 sequence has been subdivided into 10 units (P2-1 to P2-10) based on 10 distinctive stratigraphic markers. As seen on Fig. 1, the CLB level as defined by Muizon (1988) corresponds to the most basal sediments of the P2-1 (Di Celma *et al.* 2017), which are as old as 8.4 Ma (Bosio *et al.* 2020).

However, the situation is complicated by an apparent mismatch between faunal and radiometric data from the Pisco-Ica and Sacaco sub-Basins. The oldest vertebrate level in the Sacaco sub-Basin is that of El Jahuay (ELJ), the age of which is bracketed between 9.6 and 9 Ma (Muizon & Bellon 1986; Ehret *et al.* 2012; Stanton 2014; Ochoa *et al.* 2022). A basin-wide tuff dated at 9.3 Ma, has been referred to by Ochoa *et al.* (2022) in, both the Ica-Pisco and Sacaco sub-basins and is regarded by these authors as slightly older than the base of the P2. This tuff corresponds to the tuff dated by Muizon & Bellon (1986). Therefore, the age of the ELJ level would be older than that of the CLB level. However, comparison of the vertebrate faunas of these levels indicates a different relative age of the two levels, CLB being older than ELJ. The absence of phocoenids, and the occurrence of kentriodontids at Cerro La Bruja, whereas phocoenids are present and kentriodontids are absent at El Jahuay, favor this interpretation.

Awaiting a revision of the calibration of the Pisco Formation beds in the Sacaco sub-basin, it is expressed here that the fossils of the CLB faunistic level are, at least, 8.4 Ma old and therefore at least, late Tortonian in age. However, we believe that several faunistic data could indicate an older age, such as early Tortonian or late Serravalian.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Clade PINNIPEDIA Illiger, 1811
Family PHOCIDAE Gray, 1821
Subfamily MONACHINAE Gray, 1869
Tribe Lobodontini Gray, 1869

Genus *Magophoca* n. gen.

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TYPE AND ONLY SPECIES INCLUDED. — *Magophoca brevirostris* n. sp.

ETYMOLOGY. — From ancient Greek ‘mágos’ (m.), magician, sorcerer, and ‘phoké’ (f.), seal. The prefix referring to magician, sorcerer, comes from the Cerro la Bruja locality is the type locality for the type (and only) species in this genus, *Magophoca brevirostris* n. gen., n. sp., ‘Bruja’ is the Spanish word for witch, sorceress.

DIAGNOSIS. — As for the type species, *Magophoca brevirostris* n. gen., n. sp.

Magophoca brevirostris n. gen., n. sp.
(Figs 2–45; Tables 1–27; Appendices 1–4)

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HOLOTYPE. — MNHN.FPPI276, partial skeleton of a male. Associated elements include the partial left rostrum, fragmentary horizontal ramus of left mandible, left M1; all cervical vertebrae, including subcomplete atlas, partial axis, and Ce3–7 in various conditions of preservation, four thoracic and three lumbar vertebrae

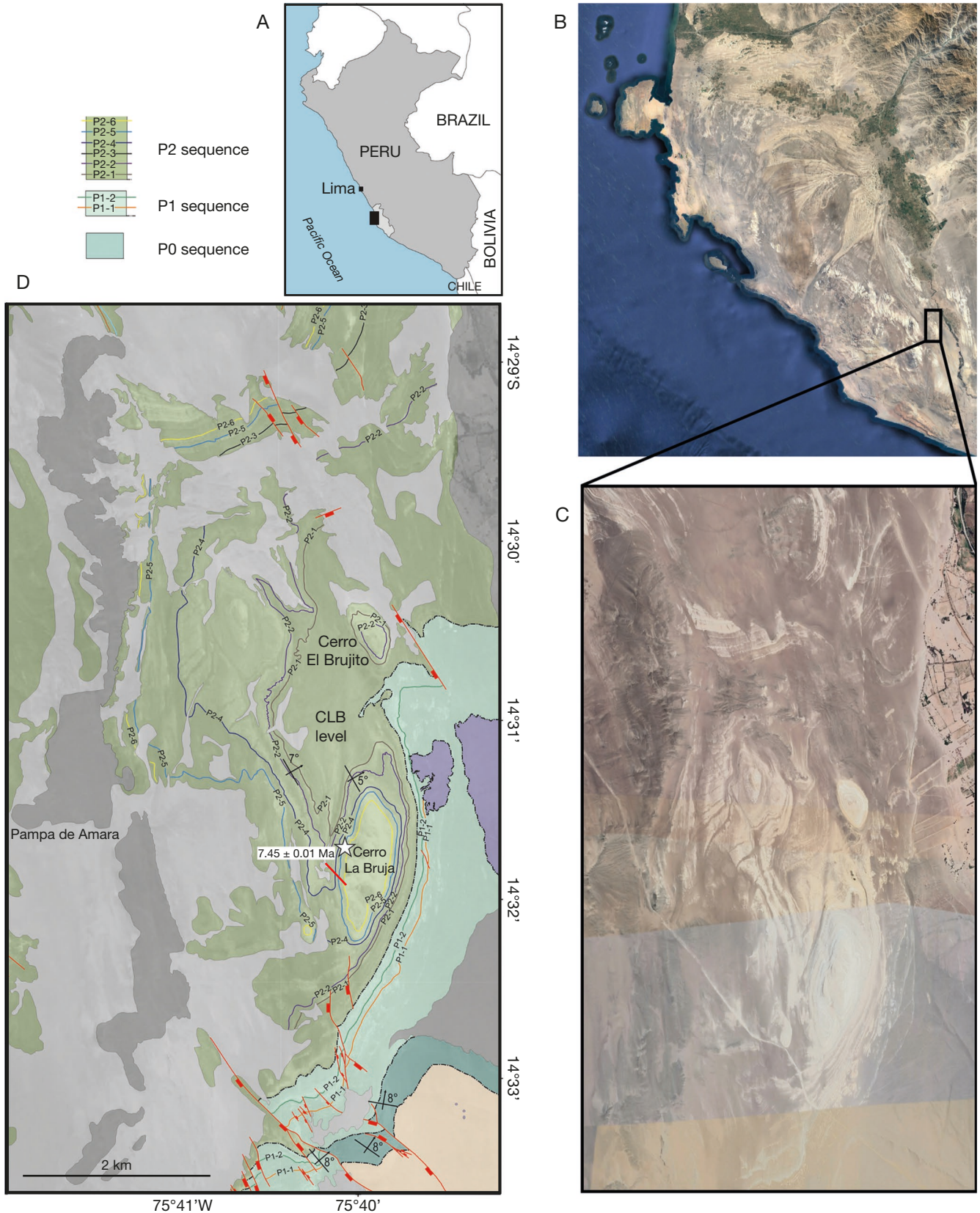


FIG. 1. — Geography and geology of the Cerro La Bruja Locality: **A**, geographic location of the study area of Cerro La Bruja; **B**, **C**, Google Earth photographs of the locality; **D**, geological map indicating the CLB level in the Cerro La Bruja locality, modified from Di Celma *et al.* (2017: appendix 2, fig. 2).

in various conditions of preservation, multiple fragments of ribs, partial sacrum, six (seven?) caudal vertebrae in various conditions of preservation; complete left scapula, articular portion of the right scapula, subcomplete left and right humerus, incomplete left and right radii consisting of separated proximal epiphysis and distal extremity, abraded proximal half of the left ulna, and right ulna without olecranon process; anterior portion of right innominate, severely abraded portion of left innominate, partial baculum, left and right femur and (probably) right patella, (proximally fused) left and right tibia and fibula, subcomplete left and right astragalus, subcomplete left and right calcaneum, subcomplete left cuboid, partial right cuboid, subcomplete left navicular, partial right navicular, partial left and right ectocuneiforms, left Mt I-V, proximal portion of right Mt II, three complete phalanges and fragments pertaining to multiple phalanges

PARATYPES. — MNHN.F.PPI269, subcomplete but slightly crushed cranium including left malleus; complete left and right mandibles dentition consisting of upper left I2, P3, and M1, upper right C, P1-P4, lower left c, p1, p3, p4, m1, and lower right c, p1-p4, m1; cervical vertebrae, including atlas, axis, and Ce3; manubrium; left scapholunar; proximal half of right Mc III and IV.

MNHN.F.PPI277, partial skull consisting of the partial left rostrum and moderately fractured braincase.

DIAGNOSIS. — A comparatively small lobodontin (i.e., Lobodontini), diagnosed by the following unique characters: six upper incisors (also in Phocinae, but four in other Monachinae, except *Noriphoca gaudini*), and the lower and upper branch of the transverse processes of Ce3-7 are clearly separated (also in Phocinae). *Magophoca brevirostris* n. gen., n. sp. is also characterized among Lobodontini by the following unique set of characters: an extended premaxilla-nasal contact (also in *Acrophoca*, *Hadrokirus*, and *Homiphoca*), the alveolar process of the maxilla facing anteroventrally posterior to P1 (also in *Hadrokirus*, *Homiphoca*, *Piscophoca*, and *Ommatophoca*), an insertion area for *m. supraspinatus* on the scapula that is equal to or smaller than the insertion areas for *m. infraspinatus* and *m. teres major* (also in *Hydrurga*), a greater tubercle reaching the level of the humeral head (also in *Homiphoca* and *Piscophoca*), the lack of a bicipital bar on the humerus (also in *Acrophoca*, *Lobodon*, *Ommatophoca*, and *Pliophoca*), a well-developed supinator ridge (also in *Homiphoca*, *Kawas*, *Leptonychotes*, *Lobodon*, and *Piscophoca*), the presence of an entepicondylar foramen (also in *Homiphoca* and *Kawas*, and in *Frisiphoca*, a monachine genus of unknown tribal affinities), a deep groove for the *m. extensor digitorum communis* tendon on the radius (also in *Acrophoca* and *Piscophoca*), an antero-dorsal iliac process located posterodorsal to the anteroventral iliac process (also in *Ommatophoca*), a large and strongly protruding posteroventral iliac process (also in *Kawas*), and a little reduced trochanteric fossa on the femur (also in *Homiphoca*, *Kawas*, *Lobodon*, and *Piscophoca*).

ETYMOLOGY. — The specific name *brevirostris* comes from the Latin adjective 'brevis', short, and noun 'rostrum', snout, thus meaning short snout. The specific name is an anatomically descriptive name, highlighting the comparatively short snout of the species compared to other Monachinae.

TYPE LOCALITY. — All the specimens are from the locality of Cerro La Bruja in the Ica desert, and were discovered at the foot of the hill.

TYPE HORIZON AND AGE. — All the specimens are from the CLB level as defined by Muizon & DeVries (1985). This faunistic level corresponds to the very base (unit P2-1) of the P2 sequence of the Pisco Formation, which is as old as 8.4 Ma (Bosio *et al.* 2020).

OTHER REFERRED SPECIMENS. — MNHN.F.PPI278, a partial rostrum including left C, P1 and P2, and right P1, partial horizontal rami of the left and right mandibles;

MNHN.F.PPI279, subcomplete right humerus, highly incomplete left humerus preserved as separated proximal and distal portions, pathologic distal half of radius, proximal epiphysis of right radius, left Mc I, fragments of indeterminate phalanges, five anterior thoracic vertebrae, several rib fragments, and three sternebrae; MNHN.F.PPI280, partial left radius missing the distal epiphysis, partial right ulna missing the distal portion; MNHN.F.PPI281, isolated subcomplete right femur; MNHN.F.PPI282, partial right hind limb with distal portions of tibia and fibula, astragalus, calcaneum, navicular, incomplete cuboid; MNHN.F.PPI283, distal portion of left humerus; MNHN.F.PPI284, left partial hind limb with strongly weathered femur, proximal portion of tibia, astragalus and calcaneum; MNHN.F.PPI285, proximal half a right ulna; MNHN.F.PPI286, proximal and distal extremities of right tibia; MNHN.F.PPI287, strongly weathered elements of hind limbs including distal extremity of right tibia, right and left partial astragali; right and left almost complete calcanea, right navicular, right incomplete cuboid, right and left ectocuneiforms; proximal extremity of left Mt II and III; complete left Mt IV and V, proximal half of right Mt IV; MNHN.F.PPI288, left innominate strongly weathered medially and missing posterior ends of pubis and ischium; MNHN.F.PPI289, partial right innominate (missing ventral angle of ilium and posterior parts of ischium and pubis) and complete right femur with unfused epiphyses; MNHN.F.PPI290, limb elements of a juvenile individual (all lacking epiphyses): distal part of right scapula, right and left humeri, right radius, right innominate missing posterior parts of pubis and ischium, left tibia; MNHN.F.PPI291, left innominate of juvenile; MNHN.F.PPI292 Proximal half of severely weathered left humerus; MNHN.F.PPI293 complete left astragalus and right astragalus missing talus (same individual); MNHN.F.PPI294, fragmentary skull (including well-preserved left ear region), partial mandible, atlas and centrum of axis; MNHN.F.PPI295, three anterior thoracic vertebrae, some rib fragments, right scapholunar, magnum, trapezium, trapezoid, right McII, IV, and V, left McI, and III, one right proximal phalanx, proximal part of left proximal phalanx, one right (?) middle phalanx, two ungual phalanges missing distal apex; MNHN.F.PPI296, isolated incomplete left femur. MNHN.F.PPI297, right McI missing proximal epiphysis

DESCRIPTION AND COMPARISON

SKULL

General

Our cranial sample of *Magophoca brevirostris* n. gen., n. sp. consists of four specimens, including the holotype (MNHN.F.PPI276), two paratypes (MNHN.F.PPI269, MNHN.F.PPI277), and an anterior portion of a rostrum (MNHN.F.PPI278). The holotype includes a toothless partial left rostrum (maxilla and premaxilla). Paratype MNHN.F.PPI269 is subcomplete (skull and mandibles) but significantly fractured and distorted. Paratype MNHN.F.PPI277 is a left maxilla and associated moderately fractured braincase and basicranium. MNHN.F.PPI269 and MNHN.F.PPI278 are referred to *Magophoca* n. gen., based on the presence of three upper incisors as on the holotype. This is an uncommon feature among Monachinae, which is present only in *Noriphoca gaudini* from the early (?) Miocene of the Abruzzo region (Italy) (Guiscardi 1871; Dewaele *et al.* 2018a). Other fossil and extant Monachinae have two upper incisors (see below). Phocinae also have three upper incisors, but sev-

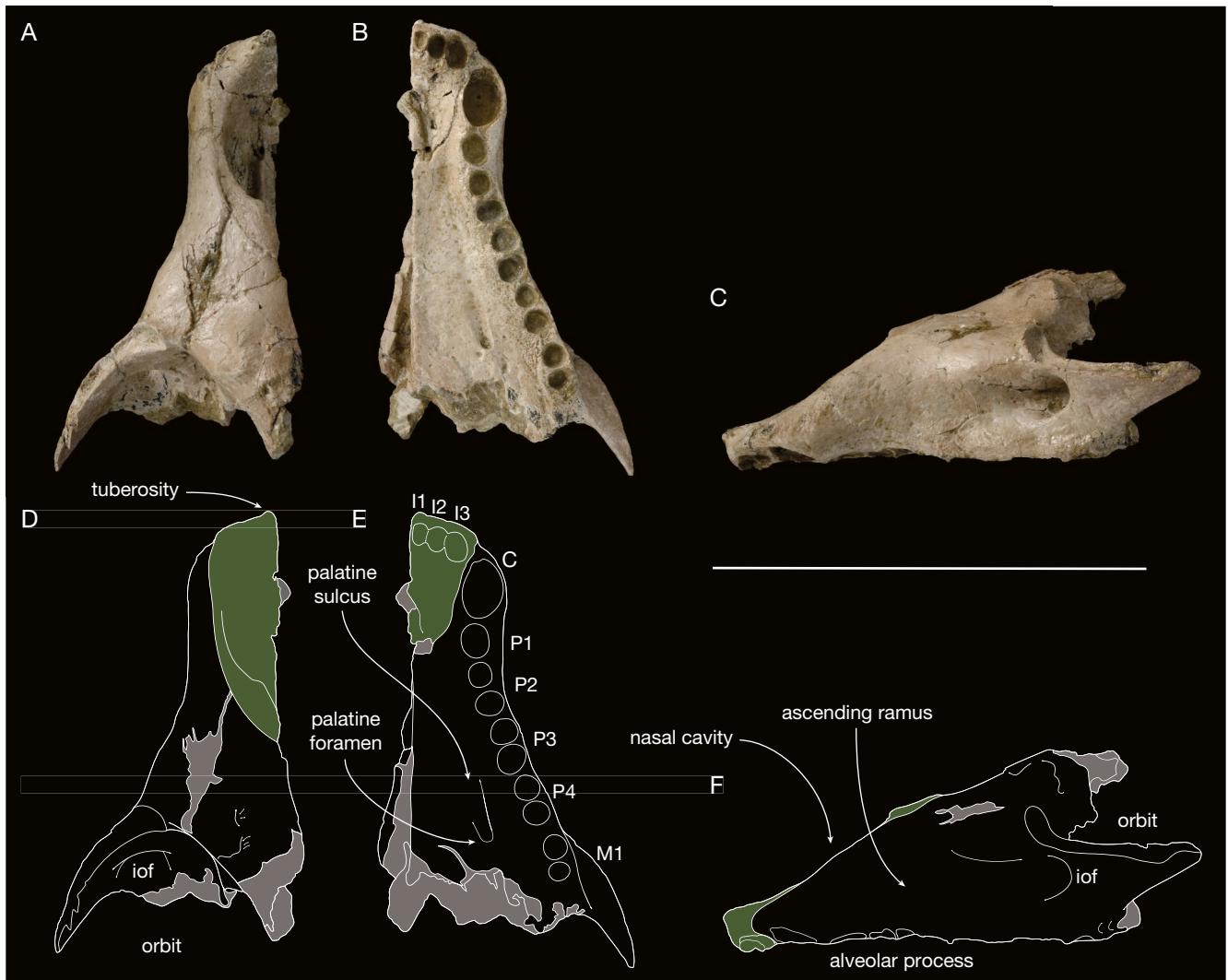


FIG. 2. — Rostrum of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, rostrum in dorsal view; **B**, same rostrum in ventral view; **C**, same rostrum in left lateral view; **D-F**, corresponding labelled line drawings. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxilla in green. Abbreviations of the teeth follow the convention used in the main text. Other abbreviation: **iof**, infraorbital foramen. Scale bar: 10 cm.

eral other features of MNHN.F.PPI276, MNHN.F.PPI269, MNHN.F.PPI277, and MNHN.F.PPI278 also support their identification as monachines (see below). MNHN.F.PPI277 is referred to *Magophoca* n. gen. based on similarities on the basicranium and maxilla (see below).

The dental formula of *Magophoca* n. gen. is $I3/2\ C1/1\ 4/4P\ 1/1M$ (char. 39[0], 42[0], 51[1]).

Most of the specimens lack the incisors. Only left I1 and I3 are present in MNHN.F.PPI278 and left I2 is preserved on MNHN.F.PPI276. None of the lower incisors are known. The dental formula of *Magophoca* n. gen. corresponds to that of the general condition in Phocinae. The general dental formula of Monachinae (other than *Magophoca* n. gen. and *Noriphoca*) is $I2/2\ C1/1\ P4/4\ M1/1$ with two upper incisors instead of three. Exceptions are the extant monachine genus *Mirounga* and the extant phocine species *Cystophora cristata*, which have dental formulas $I2/1\ C1/1\ P4/4\ M1/1$, with two upper and one lower incisor (e.g., King 1966; Berta & Wyss

1994; Bininda-Emonds & Russell 1996). The retention of a third upper incisors in *Magophoca* n. gen. and *Noriphoca* is a plesiomorphy present in all Pinnipedia, except other Monachinae (Berta & Wyss 1994).

CRANIUM (Figs 2-10; Tables 1-3)

General

Within our sample of four specimens of *Magophoca brevirostris* n. gen., n. sp. including cranial remains, MNHN.F.PPI278 is the largest, followed by the holotype. The rostrum of paratype MNHN.F.PPI277 is incompletely preserved, but the size of the braincase and basicranium suggests that the individuals MNHN.F.PPI269 and MNHN.F.PPI277 are of similar size. Ranking the four specimens according to size: MNHN.F.PPI269 (paratype) $\approx$ MNHN.F.PPI277 (paratype) $<$ MNHN.F.PPI276 (holotype) $<$ MNHN.F.PPI278. Because the holotype is a male (since the specimen includes a baculum) we suggest that the large rostrum of MNHN.F.PPI278 is that of a male

TABLE 1. — Comparative measurement (in mm) in the four specimens of *Magophoca brevirostris* n. gen., n. sp. including cranial remains. Abbreviations: **LLTR**, length of the lower cheek tooth row; **LP1-3**, length of upper P1-3 tooth row; **LUTR**, length of upper cheek tooth row; **WAC**, maximum width of the alveolus of upper canine; **WRC**, maximum width of rostrum at the level of the canines; **WUC**, width of upper canine.

Specimen	WRC	WAC	LUTR	LP1-3	LLTR	WUC
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI276; male)	22.5 × 2 = 45,0	9.7	63.5	36.0	60.5	–
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI278; male?)	46.0	10.1		38.0	63.0	8.2
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI277; female?)	–	8.5e	60.2	33.0	–	–
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI269; female?)	21.0 × 2 = 42.0	8.8	60.5	32.3	56.8	7.1

TABLE 2. — Comparative measurements (in mm) of the crania of *Magophoca brevirostris* n. gen., n. sp. in comparison with other Monachinae and selected Phocinae. Abbreviations: **BZW**, bizygomatic width; **BCW**, bicondylar width; **GLFW**, width at level of lateral edges of glenoid fossae; **MPW**, width between mastoid processes; **PLWM1**, palate width at level of posterior root of M1s; **WAC**, maximum width of alveolus of upper canine; **WRPP**, width of rostrum at preorbital processes; **e**, estimate.

Specimen	BZW	MPW	WRPP	PLWM1	BCW	GLFW
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI276; male)	–	–	–	31.9 × 2 = 63.8	–	–
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI278; male?)	–	–	–	–	–	–
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI277; female?)	132e	120.7	–	–	58.3	122.6
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI269; female?)	136	129.5	49e	63e	60.3	130
Other extinct Monachinae						
<i>Acrophoca longirostris</i> (MNHN.F.SAS563)	63 × 2 = 126e	38.75 × 2 = 77.5e	–	41.2	31.5 × 2 = 63e	63 × 2 = 126e
<i>Acrophoca longirostris</i> (MNHN.F.SAS1654)	66 × 2 = 132e	58 × 2 = 116e	57e	–	30.5 × 2 = 61e	60 × 2 = 120e
<i>Hadrokirus martini</i> (MUSM 1662)	140	122	113.6	66.6	47e	129.2
<i>Hadrokirus martini</i> (MUSM 340)	200.5	170.5	–	87.5	71.1	190.6
<i>Homiphoca capensis</i> (SAM-PQ-L30080)	145	128.5	85.3	61	57.5	130.5
<i>Piscophoca pacifica</i> (MNHN.F.SAS564)	152	139e	72.5	69.2	63.8	144.1
Extant Monachini						
<i>Monachus monachus</i> (USNM 219059)	194.8	172.6	71.1	71.4	62.4	183.0
<i>Monachus monachus</i> (MNHN-ZM-AC-A7953)	214	181.5	81	76.5	71.2	191
<i>Neomonachus schauinslandi</i> (USNM 243838; male)	157.4	158.6	47.9	68.2	60.7	152.6
<i>Neomonachus schauinslandi</i> (USNM 243839; female)	155.9	152.3	50.8	71.5	62.0	148.2
<i>Neomonachus tropicalis</i> (USNM 100363; male)	167.0	147.6	46.3	71.4	62.4	157.4
<i>Neomonachus tropicalis</i> (USNM 100371; female)	167.3	147.9	49.4	73.3	65.3	154.7
Extant Lobodontini						
<i>Hydrurga leptonyx</i> (USNM 396931)	219.6	184.1	108.5	95.2	75.8	205.9
<i>Hydrurga leptonyx</i> (USNM 550360; male)	190.0	193.4	98.4	78.7	80.6	193.4
<i>Leptonychotes weddellii</i> (USNM 269526; male)	154.7	174.1	49.1	52.6	75.5	154.2
<i>Leptonychotes weddellii</i> (USNM 269526; female)	165.5	172.1	49.6	57.3	77.6	160.5
<i>Leptonychotes weddellii</i> (USNM 395811)	152.9	170.6	51.7	51.7	74.0	153.4
<i>Lobodon carcinophaga</i> (USNM 550080; female)	131.7	147.8	76.4	61.7	76.3	136.3
<i>Lobodon carcinophaga</i> (USNM 550083; male)	140.0	152.8	80.1	62.7	78.9	138.6
<i>Ommatophoca rossii</i> (USNM 275206; male)	160.3	160.4	75.9	58.6	79.0	150.1
<i>Ommatophoca rossii</i> (US3NM 339989; female)	151.9	157.5	71.3	53.4	77.4	146.1
Extant Phocinae						
<i>Pagophilus groenlandicus</i> (USNM 188790; male)	111.3	111.6	30.0	43.7	58.0	105.4
<i>Pagophilus groenlandicus</i> (USNM 188791; female)	102.8	109.7	27.0	45.0	57.6	101.2
<i>Phoca vitulina concolor</i> (USNM 504298; male)	130.4	125.1	34.3	54.5	56.1	114.0
<i>Phoca vitulina concolor</i> (USNM 593947; female)	126.3	117.5	33.4	49.4	58.6	109.3
<i>Phoca vitulina concolor</i> (USNM 594207; female)	125.8	114.9	27.8	55.2	55.5	106.7

too. Therefore, the two paratypes, which are distinctly smaller than the holotype could be females since sexual dimorphism is widespread among pinnipeds (e.g., Jefferson *et al.* 2008). Quantitative data supporting this hypothesis are provided in Table 1, in which all the measurements of the male and inferred male are greater than those of the inferred females.

Skull dimensions of *Magophoca* n. gen. are smaller than for most other Monachinae (Tables 2; 3). A notable exception is *Australophoca*, which does not have any published skull, but is

the smallest monachine based on postcranial remains. Based on these measurements, it can be argued that *Magophoca* n. gen. was slightly smaller in size than the average extant monachine seal. Using the equations from Churchill *et al.* (2014) to calculate the estimated body size of *Magophoca* n. gen., the estimated body size of specimen MNHN.F.PPI269 is *c.* 223 cm, conforming this statement. Considering that the first equation used total basal skull length and that this could not be measured for any of the preserved skulls, only the second equation, below, has been used.

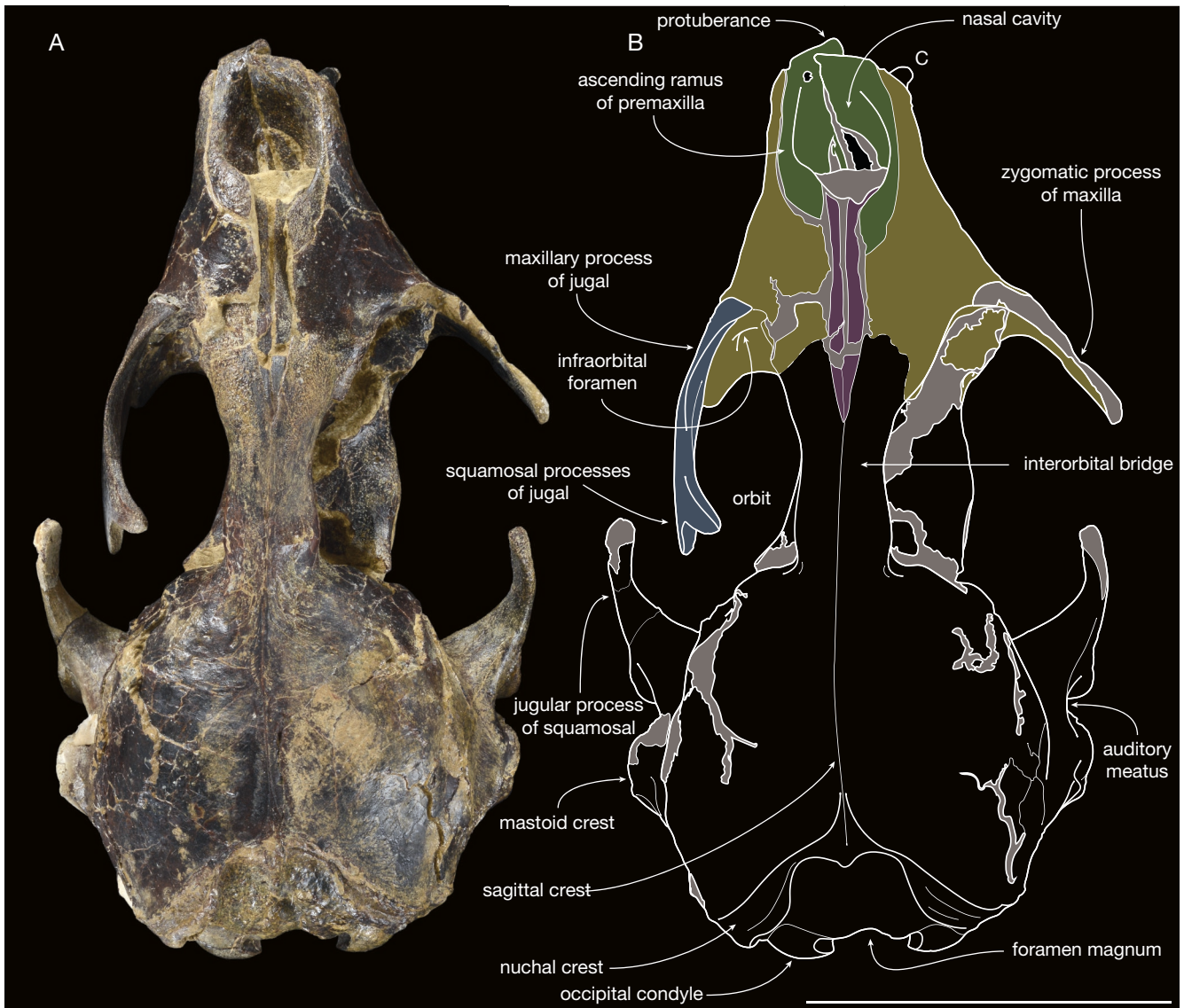


FIG. 3. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, cranium in dorsal view; **B**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, maxillae in yellow, nasals in purple, jugal in blue. Other bones not colored due to the fusion or incomplete preservation of the sutures separating the bones. Dashed lines represent the presumed sutures between the maxillae and frontals. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm.

$$0.37 \times \text{Log width of skull across canines} + \\ 0.80 \times \text{Log width across occipital condyles} + 1.39$$

Rostrum

The rostrum of *Magophoca brevirostris* n. gen., n. sp. is short and stout (Figs 2; 3; 9). In *Magophoca* n. gen., the premaxilla forms the medial wall of the nasal cavity. In the median part of the nasal cavity, the ascending ramus of the premaxilla remains within the nasal cavity and, consequently, only the posterodorsal portion of the ascending ramus of the premaxilla is visible in lateral view (char. 2[1]). In other words, the maxilla-premaxilla suture runs on the dorsal edge of the nasal cavity in its median portion and therefore is not (or barely) visible in lateral view. This corresponds with the general condition in Monachinae and contrasts with the condition

in Phocinae. Among Phocinae, the ascending ramus of the premaxilla is visible in lateral view along the entire length of the nasal cavity and the maxilla-premaxilla suture is observed on the lateral aspect of the wall of the nasal cavity. However, exceptions exist: among the phocines *Histiophoca* and *Pagophilus*, the anteroventral portion of the ascending ramus of the premaxilla remains visible in lateral view, but becomes marginally thin in its median part (Bininda-Emonds & Russell 1996). In addition, in the monachine genus *Mirounga* and the phocine *Cystophora*, only the anterior portion of the premaxilla is visible in lateral view, a condition likely correlated to the cranial adaptations to accommodate a proboscis.

The anterior tips of the premaxillae end in a distinct, anterodorsally protruding tuberosity in *Magophoca* n. gen. The tuberosity is small in MNHN.F.PPI269, but is robust and well

TABLE 3. — Measurements (in mm) of the cranium of *Magophoca brevirostris* n. gen., n. sp. Abbreviations; e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype, left)	MNHN.F.PPI269 (paratype)		MNHN.F.PPI277 (paratype)	
		left	right	left	right
Overall, length	n/a	> 252.3		n/a	
Overall, bizygomatic width	n/a	61.3 × 2 = 122.6e		n/a	
Rostrum, width across canines	22.1 × 2 = 44.2e	20.4 × 2 = 40.8e		n/a	
Rostrum, width across maximum constriction	17.8 × 2 = 35.6e	25.7e		n/a	
Rostrum, width across widest portion	33.0 × 2 = 66.0e	65.6e		n/a	
I1, alveolus length	4.1	5.0	n/a	n/a	n/a
I1, alveolus width	2.7	3.0	n/a	n/a	n/a
I2, alveolus length	5.7	6.1	n/a	n/a	n/a
I2, alveolus width	3.9	3.7	n/a	n/a	n/a
I3, alveolus length	6.6	7.3	n/a	n/a	n/a
I3, alveolus width	5.1	5.8	n/a	n/a	n/a
C, alveolus length	1.7	14.4	14.1	n/a	n/a
C, alveolus width	9.4	8.3	7.8	n/a	n/a
P1, alveolus length	7.7	7.2	7.2	n/a	n/a
P1, alveolus width	6.1	5.9	5.4	n/a	n/a
P2, alveolus length	12.4	11.6	10.6	n/a	n/a
P2, alveolus width	6.7	5.9	5.3	n/a	n/a
P3, alveolus length	12.8	12.4	11.8	11.3	n/a
P3, alveolus width	6.4	5.2	5.1	5.2e	n/a
P4, alveolus length	12.4	11.6	11.1	11.5	n/a
P4, alveolus width	5.9	5.8	5.3	5.2	n/a
M1, alveolus length	10.9	11.4	12.0	11.8	n/a
M1, alveolus width	5.9	5.8	5.7	5.4	n/a
Postcanine toothrow, length	62.4	60.8	61.0	n/a	n/a
Infraorbital foramen, width	9.9	10.6	9.7	8.3	
Premaxilla, length ventral portion at sagittal suture	n/a	30.7		n/a	
Maxilla, length of palatine process at sagittal suture	n/a	42.8		n/a	
Tympanic bulla, width	n/a	42.9	40.5	37.7	37.0
Tympanic bulla, length	n/a	n/a	45.1	42.2	43.4
Tympanic bullae, width between	n/a	35.5		34.4	
Naris, horizontal length	n/a	44.5		n/a	
Interorbital septum, least width	n/a	22.1		20.4	
Glenoid fossae, width	n/a	26.3		25.2	
Glenoid fossae, length	n/a	18.1	18.1	18.1	18.1
Braincase, length	n/a	101.6		97.6	
Braincase, width	n/a	99.7e		105.7e	
Mastoids, width across	n/a	128.1		119.5	
Occipital condyles, width across	n/a	n/a		58.2	
Occipital condyles, height	n/a	n/a		28.7	
Foramen magnum, width	n/a	n/a		n/a	
Foramen magnum, height	n/a	n/a		n/a	

developed in MNHN.P.PPI278, in which it is almost as large as in *Homiphoca* (Fig. 9). Such a tuberosity is strongly reduced or even absent in other Monachinae, with the exception of the extant *Hydrurga*, and the extinct *Acrophoca*, *Hadrokirus*, *Homiphoca*, and *Piscophoca*. In *Homiphoca*, this tuberosity strongly projects anteriorly.

In lateral view, the margin of the nasal cavity of *Magophoca* n. gen. appears rather strongly concave (char. 4[1]). The nasal cavity opens more dorsally than anteriorly (char. 3[1]). This condition corresponds with other Monachinae, with the exception of *Ommatophoca*, which has a rather anteriorly-facing nasal cavity.

The posterodorsal tip of the ascending ramus of the premaxilla broadly contacts the nasal (char. 1[0]). This characteristic is a plesiomorphy shared with Phocinae (except *Cystophora*) and some extinct Monachinae: *Acrophoca*, *Hadrokirus*, *Homiphoca*, and *Sarcodectes*. Among other Monachinae, a reduced contact is observed in *Leptonychotes*, *Piscophoca*, and the tribe Monachini; it is absent in *Hydrurga*, *Lobodon*, and *Ommatophoca*.

The palatal part of the premaxilla is roughly triangular (Figs 2; 5). The incisors are arranged in a weakly-curved arch. The incisive foramen forms a deep groove, entirely located within the premaxillary portion of the palate, and the left and right foramina are separated by a well-developed septum. Except for the extinct *Eomonachus*, *Hadrokirus*, *Piscophoca*, and *Sarcodectes* and the extant *Hydrurga*, and *Ommatophoca*, these incisive foramina are shallow or even vestigial in other Monachinae.

The nasals are elongate, forming a long and narrow V-shaped wedge terminating roughly mid-way between the level of the anterior margin of the orbit and the posterodorsal process of the jugal, well posterior to the level of the anterior margin of the orbito-temporal fossa, ventrally (char. 5[1], 6[1]), (Fig. 3). Among other Phocidae, the distal termination is generally sharply V-shaped too, except for *Neomonachus schauinslandi* and the extant phocine *Erignathus* (see, Bininda-Emonds & Russell 1996). In the latter two, the nasals form a V-shaped wedge between the frontals, but the distal termination is blunter, more rounded.

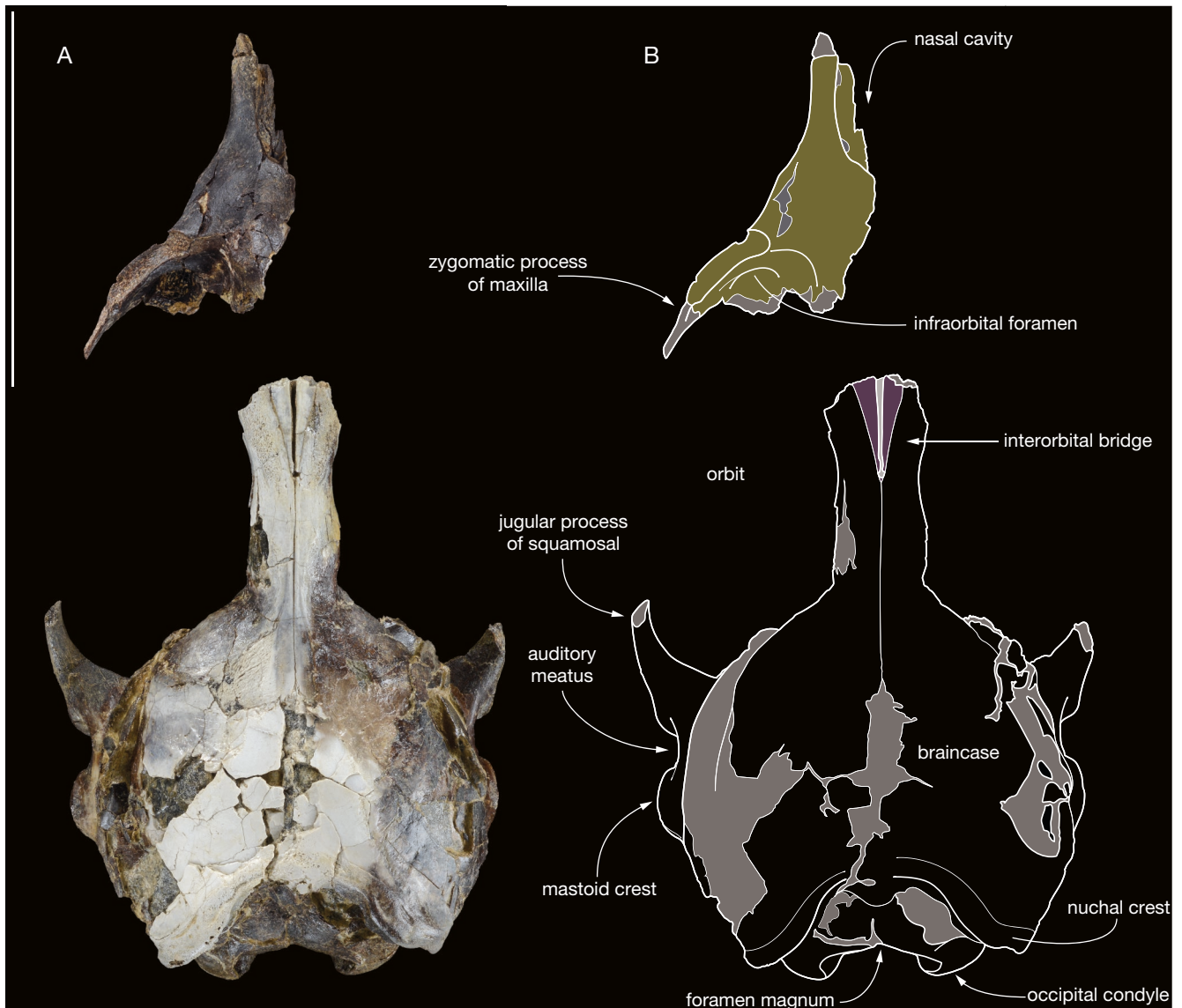


FIG. 4. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI277): **A**, cranium in dorsal view; **B**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Maxilla in yellow, nasals in purple. Other bones not colored due to the fusion or incomplete preservation of the sutures separating the bones. Scale bar: 10 cm.

The extension of the posterior termination of the nasals varies among Monachinae. This character appears to vary considerably, intraspecifically, but generally the posterior end of the nasals reaches or is posterior to the level of the anterior margin of the orbito-temporal fossa ventrally in many monachines. It extends well posterior to this edge in *Acrophoca* and *Ommatophoca*. It does not extend posterior (or barely) to the level of the anterior margin of the orbito-temporal fossa ventrally in *Hadrokirus*, *Homiphoca*, *Mirounga*, Monachini, and *Sarcodectes*.

Although the rostrum is broken at key areas, it appears that the maxilla-nasal contact is slightly longer than the nasal-frontal contact. The anterior margin of the nasal over the naris is distinctly V-shaped with the lateral branch of the V longer than the medial one; therefore, the anterior margin of the combined nasals is clearly W-shaped.

The palatal processes of the maxillae of the paratype MNHN.F.PPI269 have been displaced during fossilization and the bones of the rostrum are not in anatomical disposition (Fig. 5). However, the palatal process of the maxilla is straight, and we hypothesize that the alveolar process (i.e., maxillary toothrow) was facing slightly anteroventrally (char. 18[1]). This condition is also observed in the extinct Monachinae *Hadrokirus*, *Homiphoca*, and *Piscophoca*, and the extant *Ommatophoca*, in which the palate and the maxillary toothrow are strongly upturned anteroventrally (Muizon & Hendey 1980; Muizon 1981; Amson & Muizon 2014; Govender 2015). In most other extant Monachinae the alveolar process of the maxilla faces roughly ventrally.

The maxilla strongly narrows anteriorly, at the level of the P1 (char. 19[1]). Therefore, the maxillary toothrow strongly diverge from the sagittal plane posteriorly; the palate is the narrowest

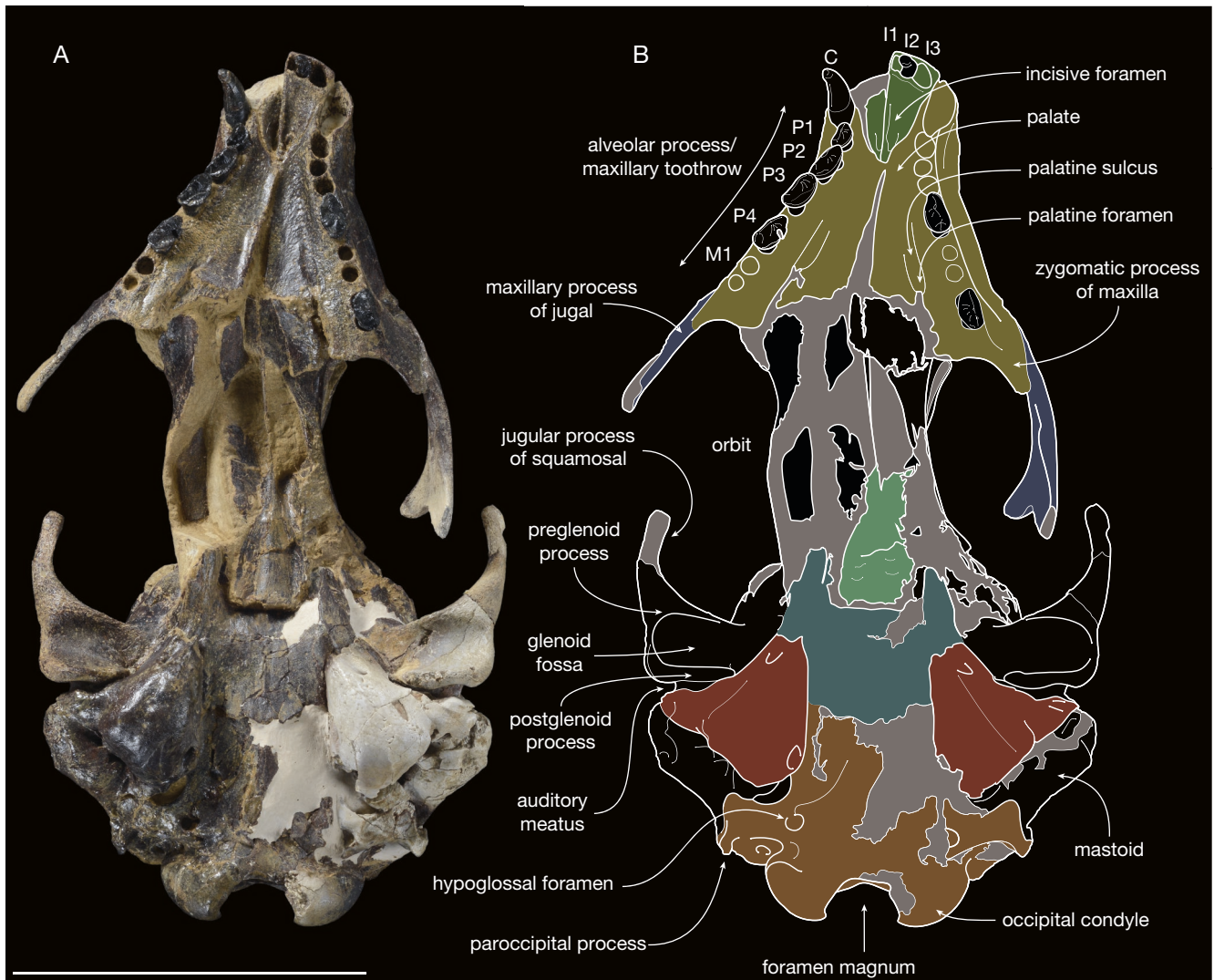


FIG. 5. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, cranium in ventral view; **B**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, maxillae in yellow, jugals in blue, presphenoid in milky green, basisphenoid in teal, tympanic bullae in red, basioccipital in brown. Other bones not colored due to the fusion or incomplete preservation of the sutures; but the glenoid area and mastoid, together with the tympanic bulla, comprises the temporal. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm.

at the level of P1 and at least twice as wide at the level of M1, where it is the widest (Table 3). Among other Monachinae, maxillary toothrows are generally strongly divergent, and do not depart much from the condition in *Magophoca* n. gen. (char. 38[2]). The degree to which the maxillary toothrow diverges in monachines largely correlates to the elongation of the toothrow. For instance, the maxillary toothrow is twice as wide at the widest point than it is at the narrowest point in *Acrophoca*, just as in *Magophoca* n. gen., but the difference between both lies in the extreme elongation of the maxillary toothrow in the former. *Hydrurga*, *Mirounga*, and to a lesser extent *Lobodon*, form exceptions with virtually straight and only slightly diverging maxillary toothrows.

The palate is almost entirely flat, arching only a little. The palatine sulcus is shallow and weakly outlined, terminating posteriorly in a small, rounded palatine foramen at the level of the diastema between P4 and M1. The palatine

foramen is located anterior to the palatamaxillary suture (MNHN.F.PPI276; Fig. 2B, E) or on the palatamaxillary suture (MNHN.F.PPI269; Fig. 5). The position of this palatine foramen differs strongly within Phocidae. In Phocinae, it terminates well posterior to the level M1 and is located on the palatine bone or at the suture between the maxilla and the palatine. The exception is the genus *Phoca*, in which it terminates at the level between P4 and M1 and anterior to the palatamaxillary suture. The condition in *Magophoca* n. gen. differs little from that in the other Monachinae, but, in the latter, the position of the palatine foramen varies from the level between P3 and P4 in *Hydrurga* to a level medial or posterior to M1 in *Homiphoca* and *Mirounga*. Also, among other Monachinae, this foramen is located in the maxillary, with the exception of *Piscophoca*, where it is located at the palatamaxillary suture, and *Homiphoca*, where it is located posterior to the palatamaxillary suture, therefore in the palatine.

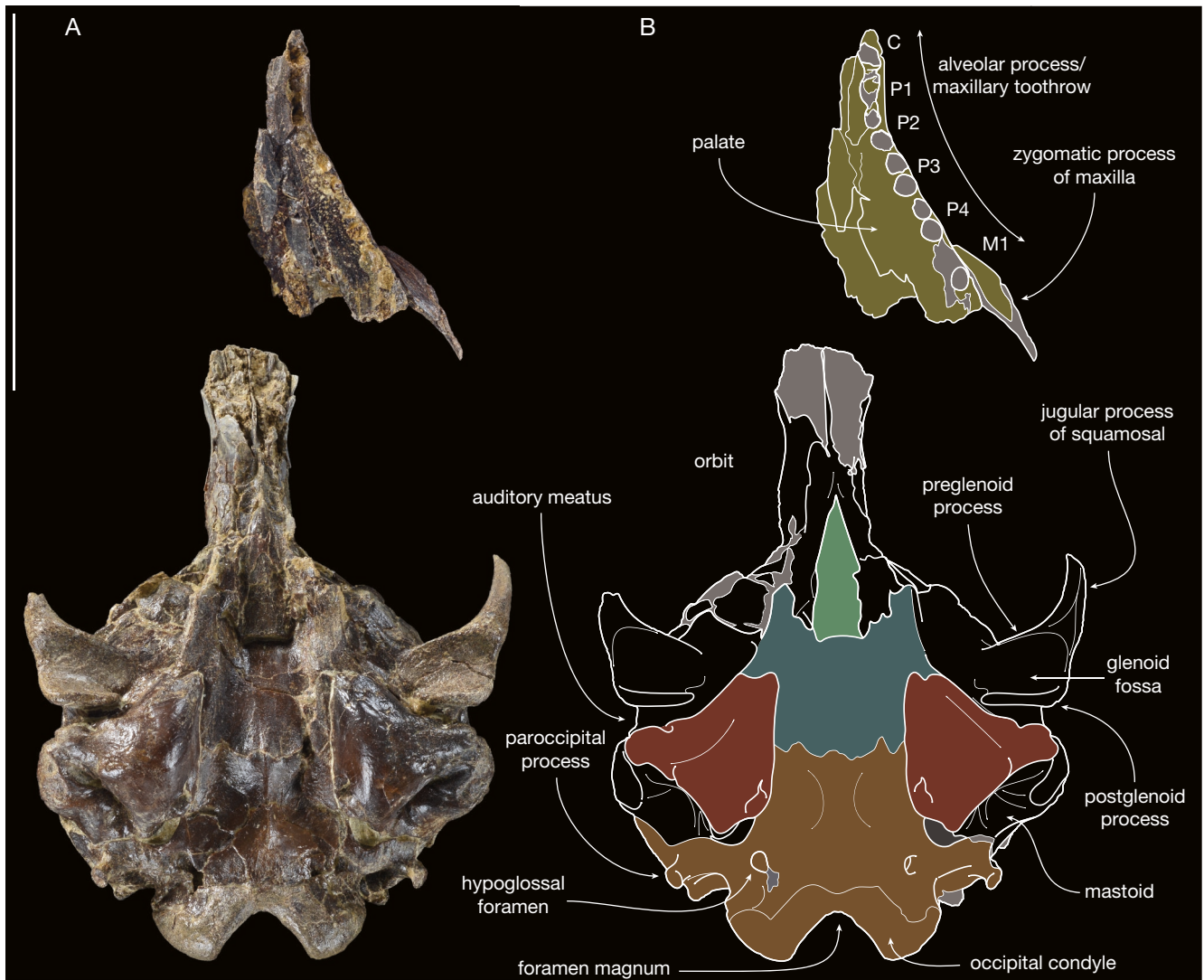


FIG. 6. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PP1277): **A**, cranium in ventral view; **B**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Maxillae in yellow, presphenoid in milky green, basisphenoid in teal, tympanic bullae in red, basioccipital in brown. Other bones not colored due to the fusion or incomplete preservation of the sutures; but the glenoid area and mastoid, together with the tympanic bulla, comprises the temporal. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm.

Orbits. The anterior opening of the infraorbital foramen on the lateral margin of the maxilla, at the base of the zygomatic process is subcircular and large in *Magophoca brevirostris* n. gen., n. sp. (Figs 2; 7; 8). Among Monachinae, the characteristic of a subcircular infraorbital foramen is shared with *Acrophoca*, *Hadrokirus*, *Leptonychotes*, and Monachini; but it has an oval outline in other Monachinae.

In *Magophoca* n. gen., the infraorbital foramen is located just dorsal to M1, following the condition in other Phocidae, except for the extant Lobodontini, in which this foramen is located slightly anterodorsal to M1, and *Mirounga* and *Sarcodectes* in which it is located posterodorsal to M1 (char. 11[1]).

The area between the zygomatic process of the maxilla just ventral to the infraorbital foramen and the alveolar process of the maxilla is flat to slightly convex in *Magophoca brevirostris*

n. gen., n. sp., as in other Monachinae. It is generally strongly concave in Phocinae.

Overall, the zygomatic process of the maxilla is gracile and forms a relatively thin dorsolateral edge of the infraorbital foramen. This process extends and tapers posteriorly. It has a long and almost straight horizontal contact with the medial edge of the maxillary process of the jugal. The jugo-maxillary suture is markedly oblique as in most monachines, and differing from the condition in phocines in which it is only slightly oblique or subvertical (char. 12[0]). Noteworthy exceptions among Monachinae are *Hadrokirus* and *Mirounga*, which have a subvertical jugo-maxillary suture.

The zygomatic process of the maxilla of *Magophoca* n. gen. projects horizontally to slightly dorsally and the zygomatic arch is at a level above the alveolar plane, in lateral view (char. 14[0]). This corresponds with the condition in other Phocidae,

except for *Acrophoca*, *Homiphoca*, extant Lobodontini (except *Hydrurga*), and *N. schauinslandi*, in which the ventral edge of the zygomatic arch is at the same level of, or is ventral to, the maxillary tooth row. In *Hydrurga*, the zygomatic process of the maxilla curves ventrally, but does not reach the level of the alveolar plane of the maxilla. Consequently, the jugo-maxillary suture is visible in lateral view along the entire length of the contact.

The lateral expansion of the orbits in *Magophoca brevirostris* n. gen., n. sp. does not differ from the average monachine. Exceptional monachines are *Acrophoca* and *Hydrurga*, having elongated skulls with comparatively narrow orbits, and *Monachus monachus* and *Ommatophoca rossii* having skulls with comparatively wide and large orbits.

The preorbital process is small and low, but easily identifiable at the anteromedial side of the orbit. Among other Phocidae, the preorbital process is generally also, either small and reduced to a small ridge or roughening of the maxilla, or absent altogether, as observed in *Neomonachus*. Exceptions are *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Hydrurga*, and *Piscophoca*, in which this process is comparatively prominent and well developed.

The maxillary process of the jugal is smoothly tapering anteriorly, and the anterior limit of the process extends above the dorsomedial edge of the infraorbital foramen (char. 13[1]). This condition is shared with Monachini and other extinct Monachinae, except *Homiphoca* and *Piscophoca*; but differs starkly from other Phocidae, in which the apex process is lateral to the infraorbital foramen or, at the most, dorsal to its lateral edge.

The jugal is transversely slender and distally splitting in a superior and inferior squamosal process, forming a mortized jugulosquamosal contact (char. 12[0], char. 15[1]). The latter is incomplete on the only preserved specimen (MNHN.F.PPI269) and lacks its apex (Fig. 7). The superior squamosal process is more slender than the inferior one, as usual in phocids. The zygomatic process of the squamosal is too abraded in the different specimens to make inferences about the jugo-squamosal contact in MNHN.F.PPI269, and by extension, in *Magophoca* n. gen.

The zygomatic process of the squamosal projects anterodorsally (Fig. 7). Its dorsal component is moderate as in *Acrophoca* and *Homiphoca*. It is intermediate between the condition in other Monachinae, which have, either a rather anteriorly-projecting zygomatic process (*Hydrurga*, *Leptonychotes*, *Lobodon*, *Neomonachus schauinslandi*, and *Sarcodectes*) or a more strongly dorsally-projecting zygomatic process (*Eomonachus*, *Hadrokirus*, *Mirounga*, *Monachus*, *Neomonachus tropicalis*, *Ommatophoca*, and *Piscophoca*).

The glenoid fossa of *Magophoca* n. gen. is shallow and very open, with a weakly developed preglenoid process. This condition is comparable to that in other Monachinae, except for *Hadrokirus*, *Hydrurga*, *Piscophoca*, and *Sarcodectes*, which have a more semi-cylindrical glenoid fossa with a better developed preglenoid process. The postglenoid process in *Magophoca* n. gen. is moderately thick, as in other Monachinae, except for extant Lobodontini, in which it is comparatively much

thicker. Interestingly, the postglenoid process in paratype MNHN.F.PPI269 appears to have a slightly concave posterior side, corresponding with the anteriorly projected lateral extremity of the ectotympanic. This condition is not observed in paratype MNHN.F.PPI277.

The long axes of the glenoid fossae for articulation with the mandibles are parallel to each other in *Magophoca* n. gen., a characteristic shared with other Monachinae, but contrasting to Phocinae, in which the long axes of the glenoid fossae converge posteriorly (char. 20[0]).

The frontals are incompletely preserved in both paratypes, MNHN.F.PPI269 and MNHN.F.PPI277 (Figs 3; 4). The supraorbital process is almost indiscernible, reduced to a small tuberosity on the interorbital bridge, just anterior to the level of the distal tip of the nasals between the frontals (char. 9[1]). This condition varies among other Monachinae, in which the supraorbital process is either absent or vestigial. The interorbital bridge is long and narrow, and the narrowest portion is in the central part of the bridge (char. 16[0], char. 17[1]). At the extreme posterior end of the interorbital bridge, the posteriorly-widening bar is abruptly constricted. Among other Phocidae, the transverse width of the interorbital bridge varies, but it is generally as narrow or slightly less narrow than in *Magophoca* n. gen. Exceptions are the phocine tribe Histriophocini and genus *Pusa*, having a remarkably thin interorbital bridge; and, *Cystophora*, *Erignathus*, *Homiphoca*, *Lobodon*, and *Ommatophoca*, having a notably broad interorbital bar. In addition, the shape of the interorbital bridge largely varies between Monachinae and Phocinae. In Monachinae, except for *Ommatophoca*, the central and posterior portions of the interorbital bridge are generally the narrowest and the bar roughly retains its width throughout, before expanding into the braincase. In Phocinae and *Ommatophoca*, the central or anterior portion of the interorbital bridge is narrowest and the bar gradually widens posteriorly, progressing into the braincase. *Magophoca* n. gen. follows the condition observed in Monachinae.

A sharp constriction of the interorbital bridge at its posterior end, as in *Magophoca brevirostris* n. gen., n. sp. has also been observed in *Neomonachus* and *Piscophoca*, albeit to a lesser extent.

Basicranium and braincase

The tympanic bulla of *Magophoca brevirostris* n. gen., n. sp. is isosceles triangular in outline in ventral view, but with a pronounced anteriorly turned lateral lip of the ectotympanic covering the auditory meatus and extending further laterally than mid-width of the glenoid fossa (char. 22[1]). This gives the anterolateral margin of the tympanic bulla, the anterior margin of the ectotympanic, a slightly concave appearance in ventral view (Figs 5; 6; 10).

A markedly triangular tympanic bulla is a shared feature with other Monachinae, but differs from Phocinae, in which the strong inflation of the tympanic bulla yields a rounder, “inflated” outline in ventral view, holding the middle between a triangular and a circular shape. On the other side of the spectrum, the inflation of the tympanic bulla in *Acrophoca* is less than in other Monachinae.

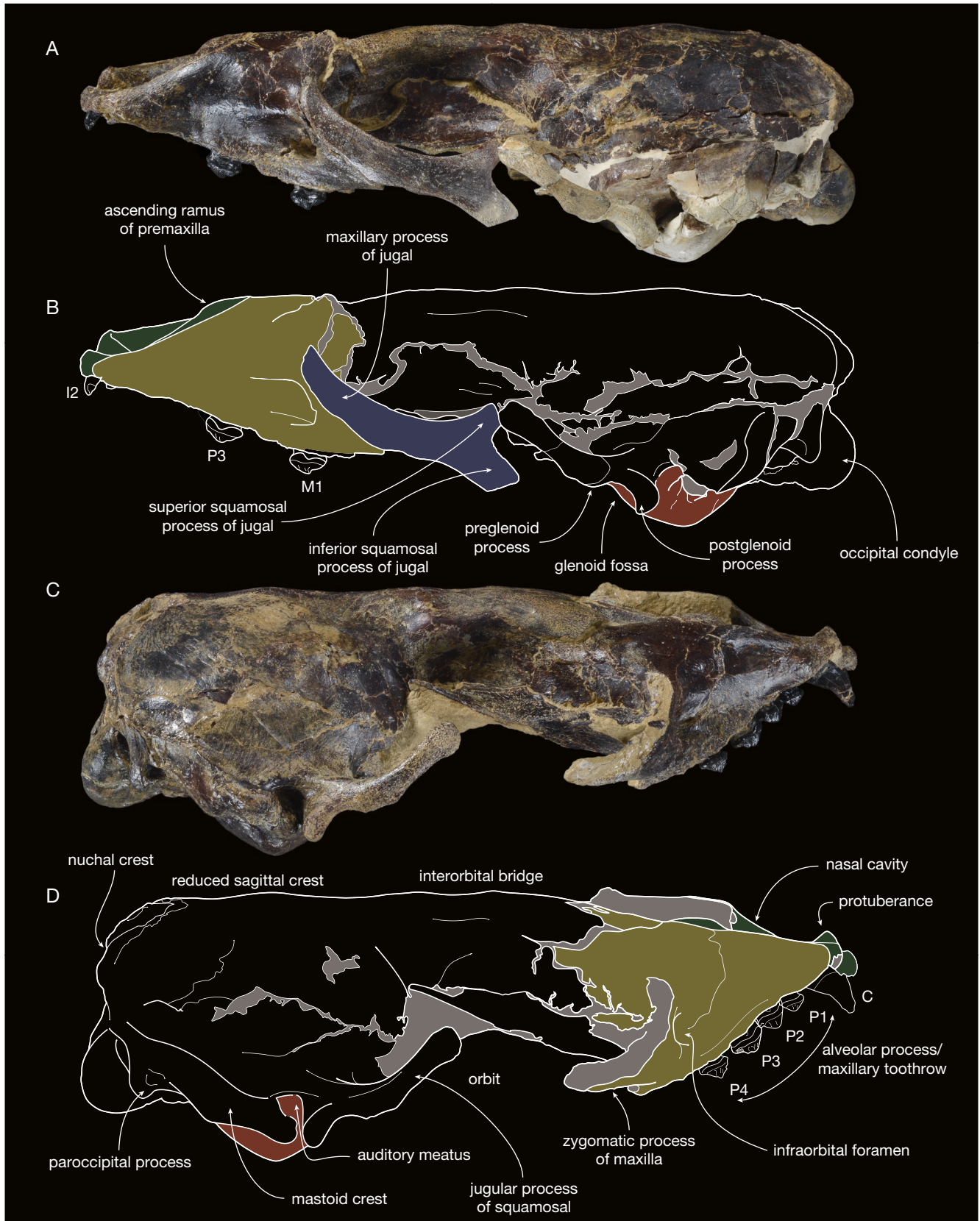


FIG. 7. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, cranium in left lateral view; **B**, corresponding labelled line drawing; **C**, same cranium in right lateral view; **D**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, maxillae in yellow, jugal in blue, tympanic bullae in red. Other bones not colored due to the fusion or incomplete preservation of the sutures; but the glenoid area and mastoid, together with the tympanic bulla, comprises the temporal. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm.

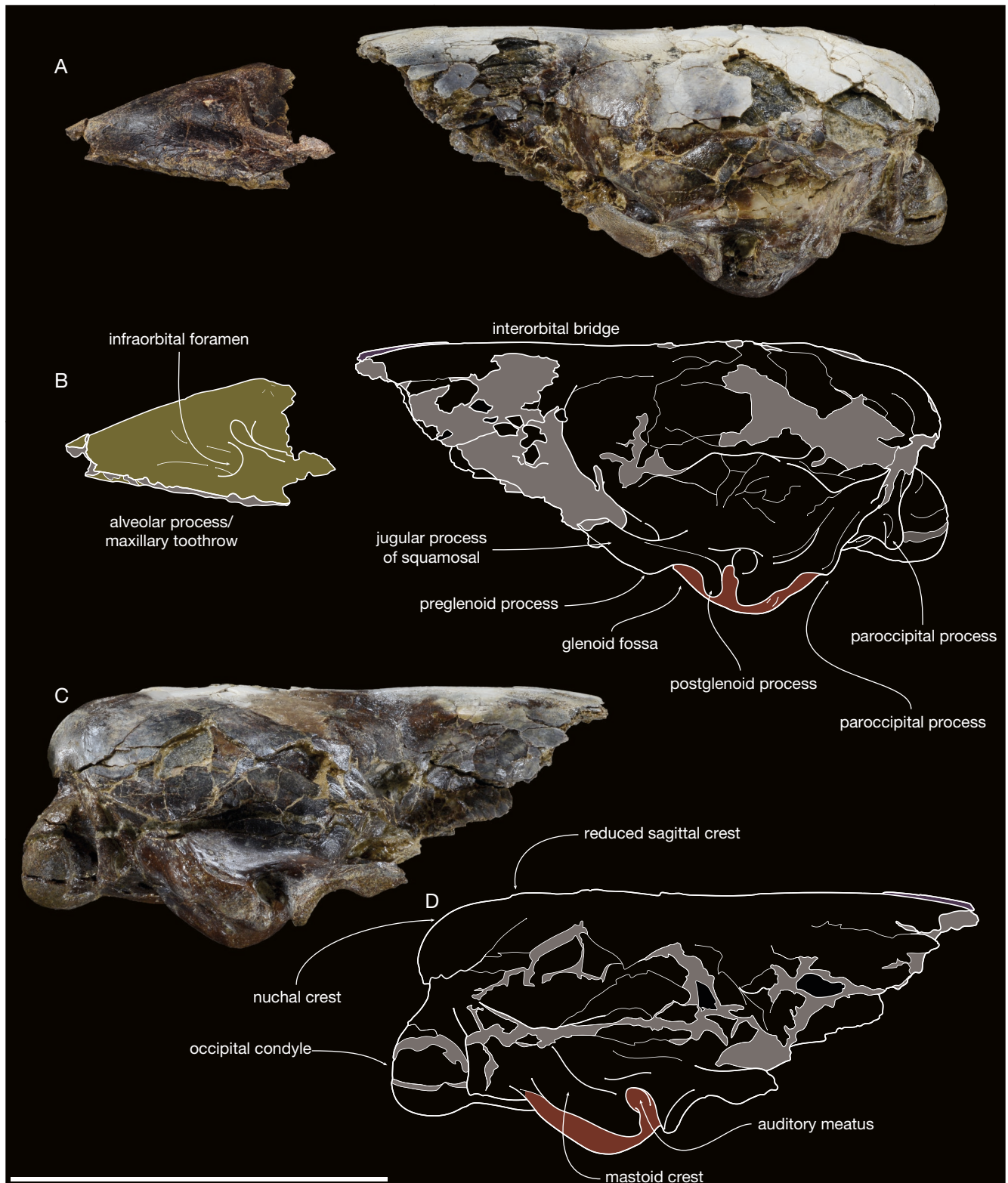


FIG. 8. — Cranium of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI277): **A**, cranium in left lateral view; **B**, corresponding labelled line drawing; **C**, same cranium in right lateral view; **D**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Maxilla in yellow, nasals in purple, tympanic bullae in red. Other bones not colored due to the fusion or incomplete preservation of the sutures; but the glenoid area and mastoid, together with the tympanic bulla, comprises the temporal. Scale bar: 10 cm.

The medial margins of the tympanic bullae are parasagittal and parallel (char. 21[1]). This is a characteristic shared with extant and extinct Lobodontini. Amson & Muizon (2014)

listed this character as one of the diagnostic characters of this tribe. In other Phocidae, the medial margins of the tympanic bullae diverge posteriorly.

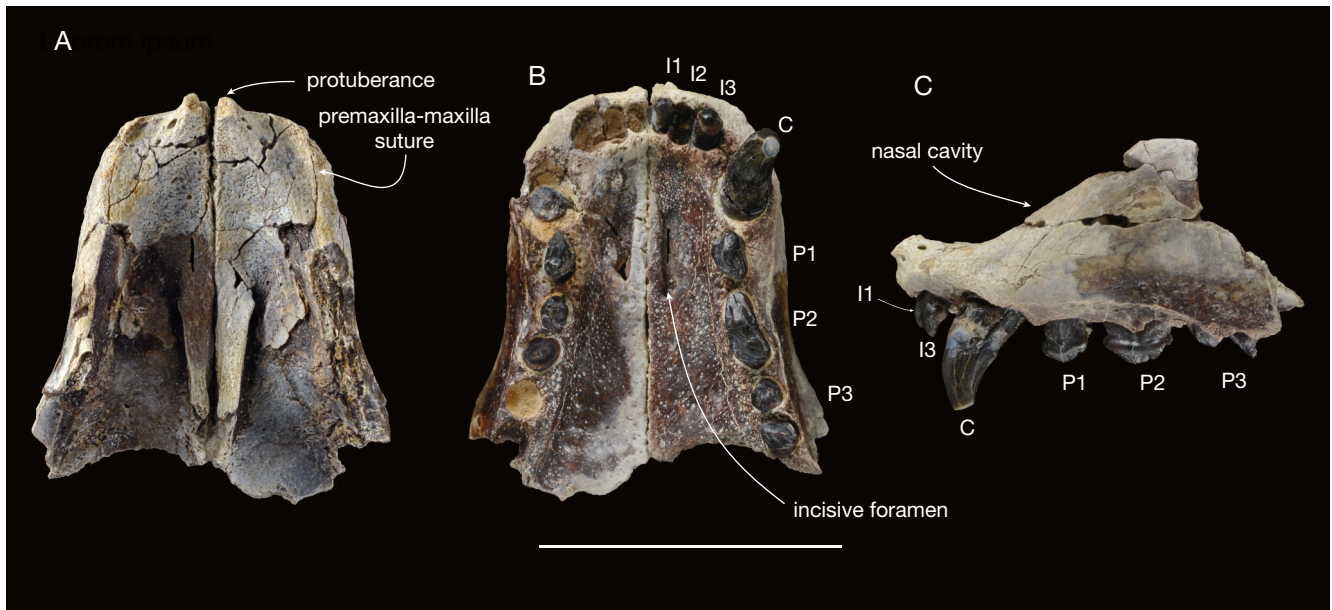


FIG. 9. — Rostrum of *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI278): **A**, rostrum in dorsal view; **B**, same rostrum in ventral view; **C**, same rostrum in left lateral view. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 5 cm.

The entotympanic of *Magophoca* n. gen. is moderately inflated (char. 23[1]). A pitted faint groove is observed along the anterior half of the tympanic bulla and corresponds to the fused suture of the ecto- and ento-tympanic. Posteriorly the suture is totally obliterated.

The ectotympanic is strongly convex medial to the tympanohyal groove forming a hump which is roughly at the same elevation as the entotympanic medially. This inflation of the tympanic bulla is not much different from that in other Monachinae (char. 23[1]), with the notable exception of *Acrophoca*, which has a much less inflated tympanic bulla. This condition differs from that in Phocinae in which the entotympanic is usually much more strongly inflated. As noted above, the ectotympanic lip extends laterally, prominently. However, it is gracile and maintains a fair distance from the postglenoid process. A repercussion of this, is that the lateral lip of the ectotympanic only covers the posteroventral portion of the auditory meatus, leaving the anteroventral portion open.

The carotid canal is located on the posteromedial region of the entotympanic, visible in ventral view, and opening posteromedially (char. 29[0]). The carotid canal does not contribute to the basioccipital or posterior lacerate foramen and is separated from it by a thin lamina of the tympanic bulla (char. 30[0]). These two characters unite *Magophoca* n. gen. with other Monachinae (the latter with Phocidae as a whole). In Phocinae, the carotid canal is not visible in ventral view. In MNHN.F.PPI277, the anterior margin of the carotid canal is invaginated, forming an acute angle. This condition is absent in the paratype MNHN.F.PPI269 and in MNHN.F.PPI294 but is observed on the holotype of *Piscophoca*. The posterior margin of the carotid canal is robust, extending into a wall abutting the anterior margin of the posterior lacerate foramen.

The posterior lacerate foramen is strongly reniform, concave anterolaterally, and located at the posteromedial tip of the tympanic bulla. The posterior lacerate foramen of *Magophoca brevirostris* n. gen., n. sp. does not extend medial to the tympanic bulla, as in other Monachinae (char. 31[0]).

The pars petrosa of the petrosal is visible in the posterior lacerate foramen, but it is not inflated (char. 33[0]). Amson & Muizon (2014), Berta *et al.* (2015), and Rule *et al.* (2020b) regard an inflated pars petrosa of the petrosal as a characteristic uniting *Eomonachus* from Australasia and *Monachus* and *Pliophoca* from the Mediterranean realm, a feature that is absent in other Monachinae.

The posterolateral margin of the tympanic bulla contacts the mastoid (pars mastoidea of the petrosal), but is separated from it by a deep invagination. This invagination bears multiple grooves, pits and foramina.

The pit for the tympanohyal, in the anterolateral half of this invagination, is located on the ectotympanic and descends into the tympanomastoid contact. The shape of the pit for the tympanohyal on the posterior margin of the ectotympanic varies: it is a wide-open groove in both bullae of MNHN.F.PPI277, but the only completely preserved bulla of MNHN.F.PPI269 (the right one) has a pit for the tympanohyal that is covered by a thin lamina. Among other Monachinae, the pit for the tympanohyal is also (partially) covered by a bony lip in *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Leptonychotes*, *Lobodon*, and *Monachus*.

The stylomastoid foramen is located at the contact between the ectotympanic and the mastoid. From the foramen a deep groove extends anterolaterally at approximately 45° to the sagittal plane. The morphology of this groove varies between MNHN.F.PPI269 and MNHN.F.PPI277. It forms a cylindrical, lateroventrally open gutter in both, open ventrally in

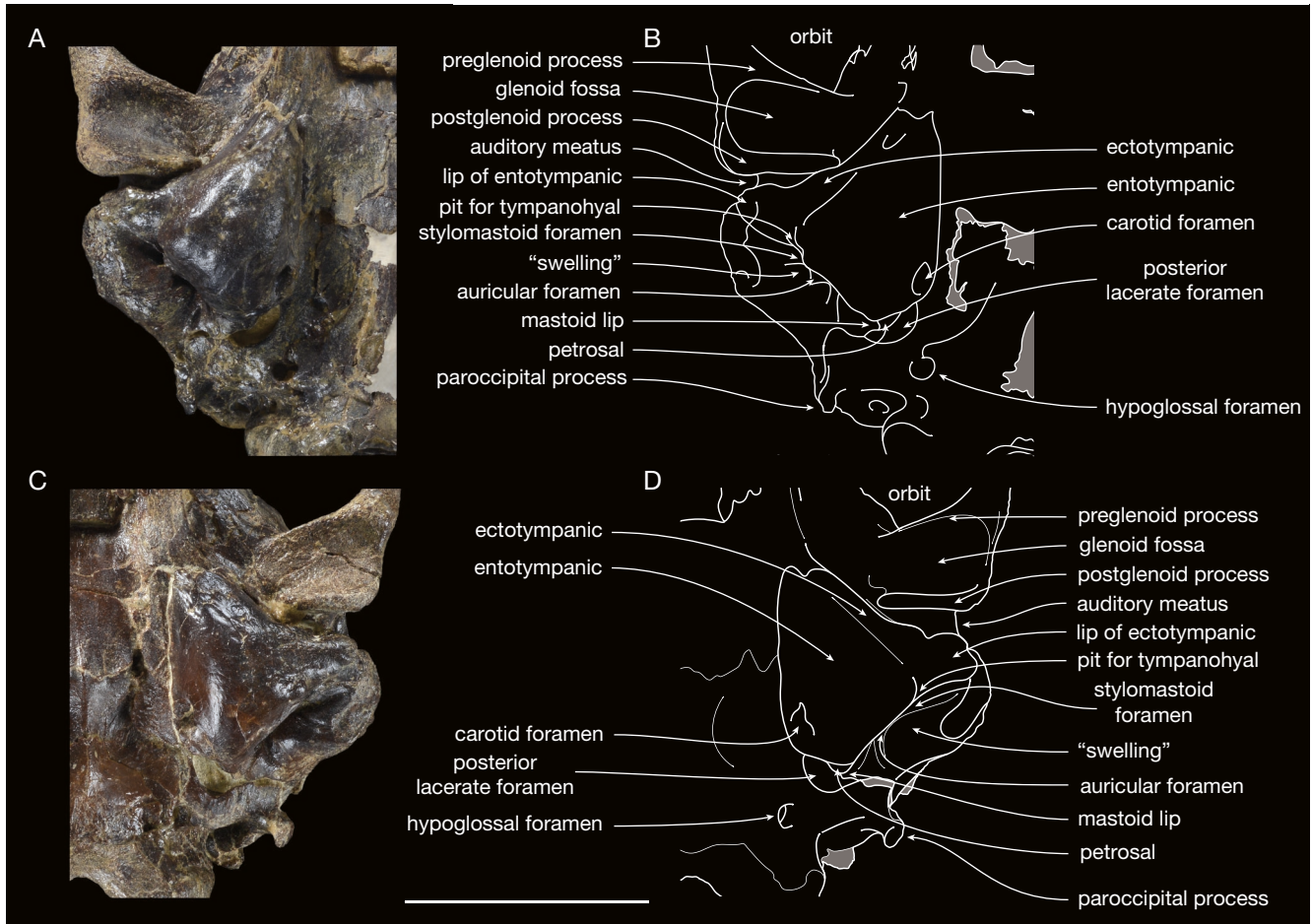


FIG. 10. — Auditory region of *Magophoca brevirostris* n. gen., n. sp.: **A**, right auditory region of paratype MNHN.F.PPI269 in ventral view; **B**, corresponding line drawing; **C**, left auditory region of paratype MNHN.F.PPI277 in ventral view; **D**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix; unless cavities and foramina filled with sediment. Scale bar: 5 cm.

MNHN.F.PPI277, but covered posteriorly by a thin lamina of the mastoid in MNHN.F.PPI269. The facial nerve (CN VII) exits the skull through the stylomastoid foramen and extends on the lateral and dorsal aspect of the skull to innervate the anterior region of the head. A central swelling of the mastoid separates the stylomastoid foramen from the auricular foramen in all Phocidae (Deméré *et al.* 2003), including *Magophoca* n. gen. This lamina in MNHN.F.PPI269 aids in the separation of the stylomastoid foramen from the auricular foramen in the specimen. The auricular foramen conveys the auricular branch of the vagus nerve (CN X), which runs in a groove along posterior angle of the entotympanic, from the posterior lacerate foramen (where the vagus nerve exits) to the facial nerve laterally.

The pars mastoidea of the petrosal is external to the tympanic cavity as in all phocids. It is a robust and contacts the tympanic bulla posterolaterally. The mastoid of *Magophoca* n. gen. exhibits a partial mastoid lip on its medial tip, appressed against the lateral surface of the posterior tip of the tympanic bulla, covering the pars petrosa of the petrosal and the lateral margin of the posterior lacerate foramen (as well as an external cochlear foramen, or a round window, as in other extant and extinct Lobodontini (char. 27[1]), (Fig. 10). However, Rule *et al.* (2021)

drew a distinction between partial mastoid lips and fully sealed mastoid lips. Among extant and extinct Lobodontini, the full mastoid dominates, with only *Hadrokirus*, *Magophoca* n. gen., and *Ommatophoca* having a partial mastoid lip. Considering that the latter condition is shared with certain Monachinae not included in the Lobodontini, such as *Monotherium? wymani*, and *Sarcodectes magnus*, following Rule *et al.* (2021), it can be argued that this characteristic is a plesiomorphy among Monachinae.

The mastoid is not visible in dorsal view of the skull since it is obscured from it by a wide mastoid crest (char. 25[0]). This is a characteristic shared with all other Monachinae, except *Ommatophoca*. In *Ommatophoca* and Phocinae, the mastoid is visible in dorsal view, as a consequence of the medial inflexion of the mastoid crest.

The basioccipital is roughly rectangular between the tympanic bullae, a result from the parasagittal orientation of the medial margins of the tympanic bullae (see above). In the preserved specimens, a serrated suture in the middle between the tympanic bullae separates the basioccipital from the basisphenoid anterior to it. The basioccipital bears a distinct sagittal elevation that is roughly hourglass-shaped, flaring out anteriorly and posteriorly.

On the exoccipital, the paroccipital process forms a moderately well-developed stubby hook-like process. This hook is moderately well-developed, only having a ventral and posterior prominence of a few millimeters (char. 32[1]). Among Monachinae, the development of this process is comparable in most extant and extinct Lobodontini, but better developed in *Hydrurga*, and Monachini. The anterior portion of the process bears a small but well-developed fossa for the muscle attachment. Literature on the myology of Phocidae is scarce, but following Piérard (1971), Bryden (1971), Evans & Lahunta (2013), and Kienle *et al.* (2022) for the musculature of *Leptonychotes weddellii*, *Mirounga leonina* and the domesticated dog, respectively, it can be assumed that *m. digastricus* has its origin on this area. Dorsally, this paroccipital process extends dorsally, transitioning into the nuchal crest. In *Magophoca* n. gen., the hypoglossal foramen is located distal and slightly medial to the posterior lacerate foramen. This condition varies among Monachinae. The hypoglossal foramen is always located posterior to the posterior lacerate foramen: posterior or only slightly posteromedial in *Acrophoca*, extant Lobodontini, and *Piscophoca*; and strongly posteromedial other Monachinae.

The occipital condyles are slender and strongly convex. Lateroventral to the occipital condyle, a distinctly concave ventral condyloid fossa separates the condyle from the paroccipital process. Dorsally, the occipital condyles are strongly diverging (char. 35[1]). The occipital condyles are ventrally fused, and the ventral margin of the foramen magnum is semi-circular. Among other Monachinae, the occipital condyles are also ventrally fused in *Hadrokirus*, *Homiphoca*, *Hydrurga*, Monachini, and *Piscophoca*. In lateral view, the occipital condyles strongly protrude distally in *Magophoca* n. gen. This is due to the combined distal protrusion of the condyles, as well as the rather weak development of the nuchal crests. The nuchal crest does not, or barely, protrude distally past the paroccipital process. The nuchal crest is roughly parabolic in dorsal view, with a rounded flaring progressively more laterally, posteriorly. The angle between both sides is approximately 90°. The crest is lowly-raised, yet robust and rugose. The parabolic nuchal crest of *Magophoca* n. gen. strongly resembles that of *Eomonachus*, *Hadrokirus*, and *Piscophoca*, but differs from the V-shaped nuchal crest of *Acrophoca* (unpublished specimens from MNHN and MUSM). The condition in *Homiphoca* is intermediate between the two morphologies. Among extant monachines a parabolic nuchal crest is present in *Hydrurga*, *Neomonachus schauinslandi*, and *Ommatophoca*, whereas a V-shaped crest is observed in *Leptonychotes*, *Lobodon*, *Monachus*, and *Neomonachus tropicalis*, *Lobodon*, and *Leptonychotes*. The degree of development of the nuchal crest is similar to that in *Acrophoca*, *Homiphoca*, and *Piscophoca*, but less developed than in *Hadrokirus* and *Monachus*. In Phocinae, the nuchal crests are generally much less developed than in Monachinae (except in *Cystophora* and *Halichoerus*).

The sagittal crest is preserved as a low crest at the transition of the interorbital bridge into the braincase, but does not extend onto the braincase to contact the nuchal crest. This does not differ from the general condition among Phocidae.

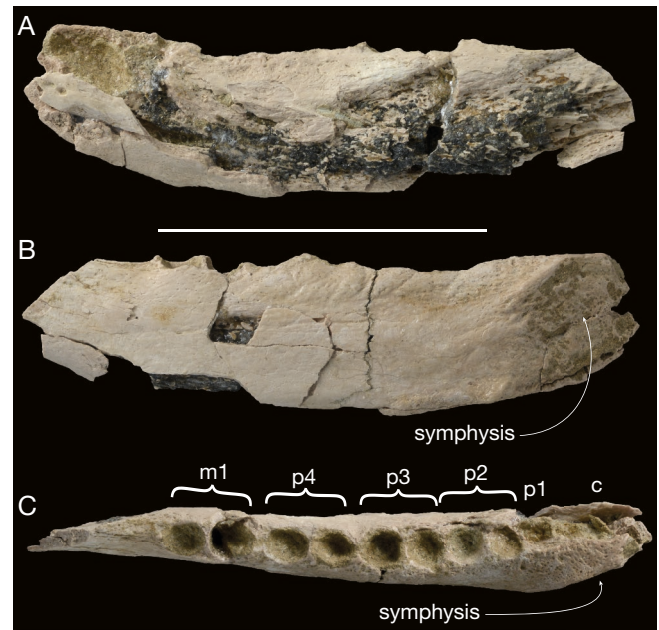


FIG. 11. — Left mandible of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, mandible in lateral view, **B**, same mandible in medial view; **C**, same mandible in occlusal view. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 5 cm.

MANDIBLE (Figs 11-13; Table 4)

The mandible of the paratype, MNHN.F.PPI269, is virtually completely preserved, except for the incisors and left p2 (Fig. 12). The mandible is gracile and mediolaterally thin. The mandibular tooth row extends across the anterior 40-45% of the mandible. Among other Monachinae, the mandibular toothrow is also shorter than half of the total length of the mandible in most extant and other extinct Monachinae. Notable exceptions are *Hydrurga* and *Lobodon*: the mandibles of *Hydrurga* available during in this study show that the mandibular toothrow in this species is approximately half the length of the mandible, and the mandibular toothrow in *Lobodon* is much larger than half the total length of the mandible.

The horizontal ramus of the mandible of *Magophoca brevirostris* n. gen., n. sp. is dorsoventrally highest and transversely widest at the level of the symphysis. Transversely, the mandible becomes gradually more slender, posteriorly. Dorsoventrally, the mandible is almost equally high along the entire length of the horizontal ramus, only slightly shorter just posterior to m1. The external aspect of the symphysis, i.e., the chin, is smoothly and gently convex. The symphysis is round to teardrop-shaped, terminating at the level of the anterior alveolus of p2. In most other Monachinae, the symphysis terminates at the level of p2 (or just posterior to it) except in *Lobodon*, *Mirounga*, and *Ommatophoca*. In most other Monachinae, the horizontal ramus of the mandible is equally high throughout, except for *Hydrurga* in which the horizontal ramus of the mandible is proportionally significantly higher anteriorly. In *Magophoca brevirostris* n. gen., n. sp., three mental foramina line up horizontally on the labial side of the mandible, ventral to the incisors and canine; two are located

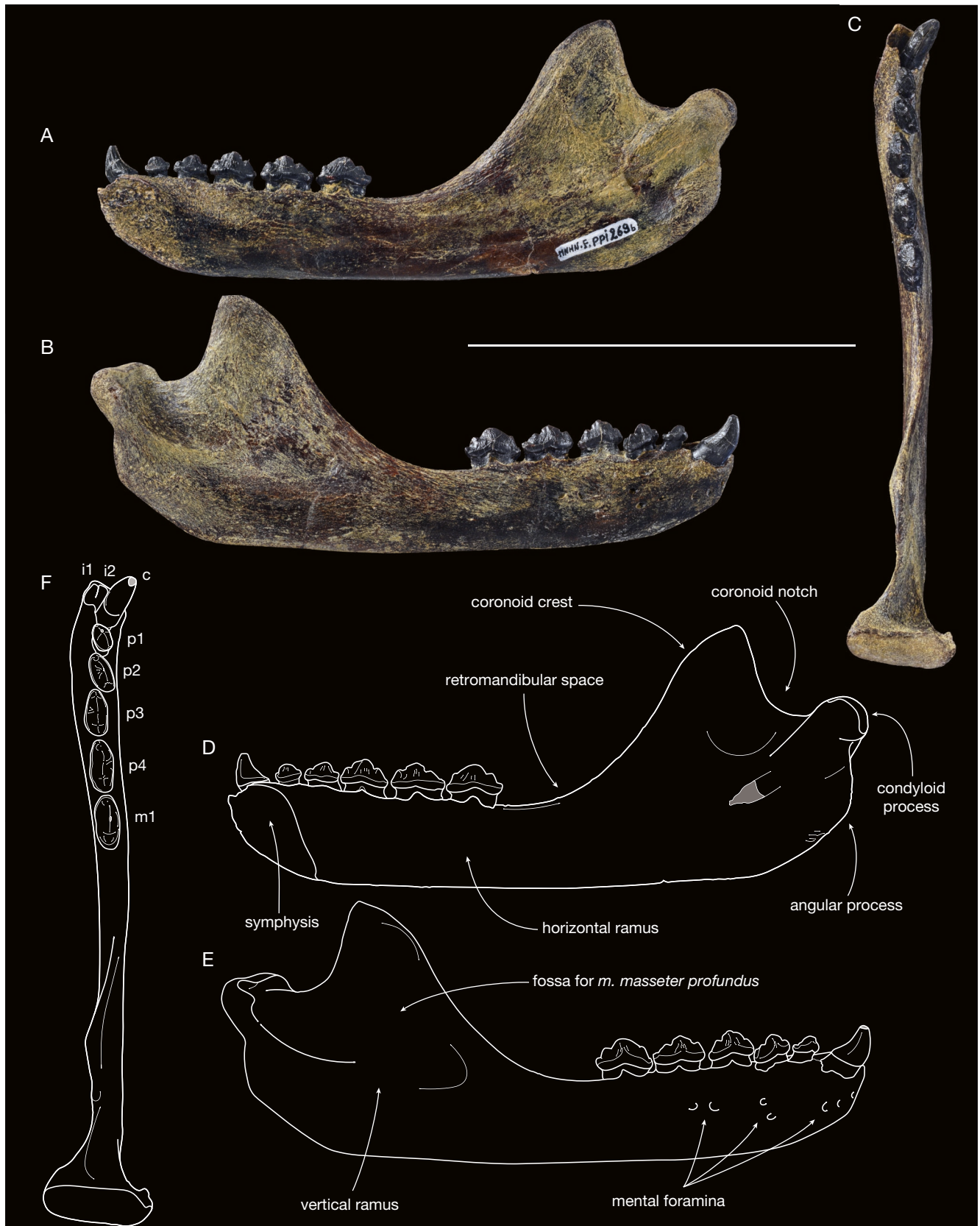


FIG. 12. — Right mandible of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, mandible in lingual view; **B**, the same mandible in labial view; **C**, the same mandible in occlusal view, **D-F**, corresponding labelled line drawings. Areas in gray are abraded or obscured from view by sediment matrix. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm.

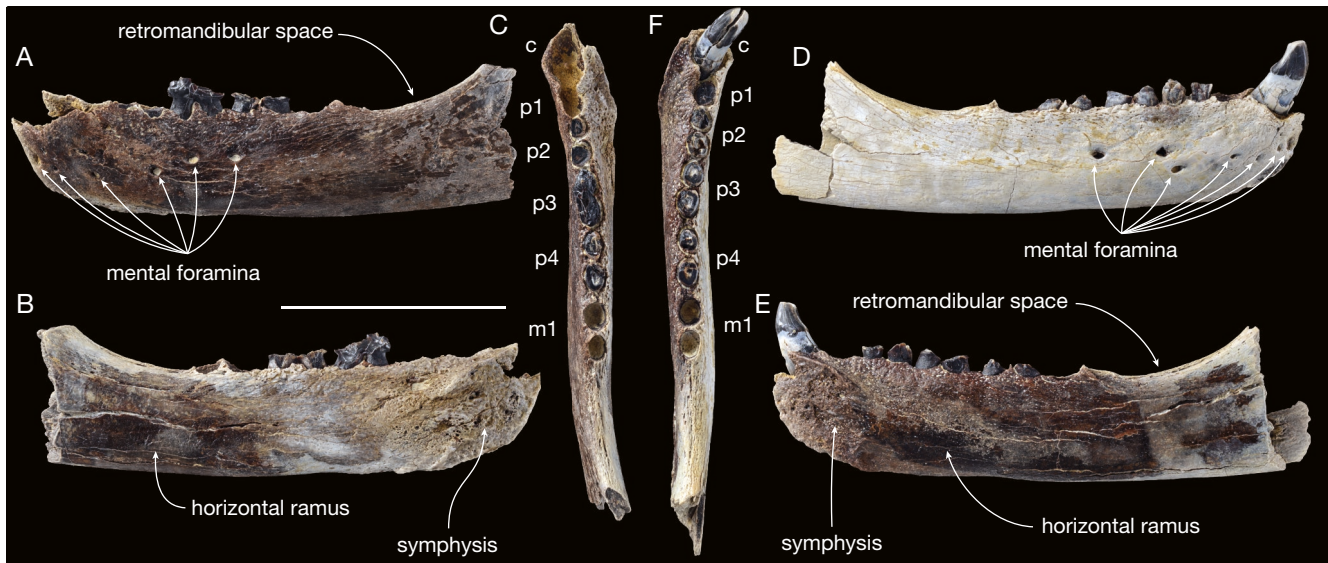


FIG. 13. — Mandibles of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI277): **A**, left horizontal ramus horizontal in lateral view; **B**, the same mandible in medial view; **C**, the same mandible in occlusal view; **D**, right horizontal ramus horizontal in lateral view; **E**, the same mandible in medial view; **F**, the same mandible in occlusal view. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 5 cm.

on a vertical line, ventral to the posterior alveolus of p2; and two line up horizontally at the level of the posterior alveolus of p3 and the anterior alveolus of p4. The retromandibular space is short, with the coronoid crest of the mandible beginning to rise less than one tooth length posterior to the m1. Among other Monachinae, the retromandibular space is also short in *Hadrokirus*, *Hydrurga*, and tribe Monachini. The retromandibular space is moderately long in *Homiphoca*, *Piscophoca*, and *Pliophoca*, and long in all other Monachinae: *Acrophoca*, *Leptonychotes*, *Mirounga*, and *Ommatophoca*. The curvature of the coronoid crest is sigmoidal in *Magophoca brevirostris* n. gen., n. sp. The ventral margin of the mandible is overall straight, only curving dorsally, at the angle of the mandible, posterior to the level of the coronoid process. This largely corresponds with other Monachinae, with the exception of *Homiphoca*, *Leptonychotes*, *Lobodon*, *Mirounga*, and *Ommatophoca*. In *Homiphoca* and *Mirounga*, the angle of the mandible reaches ventral to the ventral margin of the horizontal ramus before curving dorsally. In *Leptonychotes*, the mandible starts to curve dorsally just posterior to the tooththrow, and in *Lobodon* and *Ommatophoca*, the elongated symphysis makes the ventral margin of the mandible curve. The vertical ramus (*ramus mandibularis*) is approximately three times as high as the horizontal ramus (*corpus mandibularis*). Among other Monachinae, such a proportionally high vertical ramus is also present in some extinct Monachinae (e.g., *Hadrokirus*, *Homiphoca*, and *Piscophoca*) and Monachini. In other Monachinae, such as some Lobodontini (e.g., *Hydrurga* and *Lobodon*) and *Mirounga*, the vertical ramus is proportionally not as high since these taxa have a very robust and high horizontal ramus. The coronoid process is transversely thin, and the posterior margin of the process is roughly straight and vertical. The latter contrasts with other extinct Monachinae,

TABLE 4. — Measurements (in mm) of the mandible of *Magophoca brevirostris* n. gen., n. sp. Abbreviations: e, estimate for a character due to minor damage; n/a, a character could not be measured.

Character	MNHN.F. PPI.276 (holotype)	MNHN.F.PPI.269 (paratype)	
	left	left	right
Overall, total length	n/a	168.9	168.8
Overall, length from anterior tip to angular process	n/a	162.7	161.4
Overall, total height	n/a	65.3	65.7
Symphysis, length	n/a	27.5	27.1
Symphysis, height mandible at the distal tip of the symphysis	22.2	25.1	24.3
i1, alveolus length	n/a	n/a	n/a
i1, alveolus width	n/a	n/a	n/a
i2, alveolus length	n/a	n/a	n/a
i2, alveolus width	n/a	n/a	n/a
c, alveolus length	n/a	11.2	11.6
c, alveolus width	n/a	7.3	8.0
p1, alveolus length	n/a	6.6	6.5
p1, alveolus width	n/a	4.5	4.2
p2, alveolus length	10.5e	10.0	10.2
p2, alveolus width	5.4e	4.0	4.3
p3, alveolus length	11.7	10.1	10.5
p3, alveolus width	5.4	4.1	4.3
p4, alveolus length	12.6	11.5	11.5
p4, alveolus width	5.2	4.1	4.2
m1, alveolus length	12.6	11.6	11.5
m1, alveolus width	6.0	4.5	4.5
Horizontal ramus, height at level just posterior to m1	n/a	22.5	22.6
Horizontal ramus, width at level just posterior to m1	n/a	7.3	7.3
Postcanine tooththrow, length	n/a	56.3	55.4
Coronoid, vertical height from the lowest point of the coronoid notch to the apex of the coronoid process	n/a	24.5	24.7
Condylar process, width	n/a	26.7	27.2

TABLE 5. — Measurements (in mm) of the upper dentition of the *Magophoca brevirostris* n. gen., n. sp. paratype (MNHN.F.PPI269). “n/a” signifies that a character could not be measured.

Character	MNHN.F.PPI269 (paratype)	
	left	right
I2, crown height	3.6	n/a
I2, crown length	3.6	n/a
I2, crown width	3.6	n/a
C, crown height	n/a	13.6
C, crown length	n/a	9.7
C, crown width	n/a	6.9
P1, crown height	n/a	4.7
P1, crown length	n/a	8.2
P1, crown width	n/a	5.3
P2, crown height	n/a	5.8
P2, crown length	n/a	11.6
P2, crown width	n/a	6.0
P3, crown height	6.0	6.2
P3, crown length	12.4	12.4
P3, crown width	6.9	7.0
P4, crown height	n/a	6.1
P4, crown length	n/a	12.0
P4, crown width	n/a	6.9
M1, crown height	5.8	n/a
M1, crown length	11.8	n/a
M1, crown width	6.6	n/a

in which the coronoid process forms a ‘hook’, either thin, or thick. This condition varies among extant Monachinae, ranging from a concave ‘hook’ in *Hydrurga*, *Leptonychotes*, and *Neomonachus*; a straight posterior margin in *Lobodon*, *Mirounga*, and *Monachus*, to an anterodorsal-posteroventrally inclined ridge in *Ommatophoca*. Consequently, the coronoid notch of the mandible of *Magophoca brevirostris* n. gen., n. sp. is not as strongly concave as it is in many other Monachinae. The fossa for *m. masseter superficialis* on the lateral surface of the mandible is weakly outlined. In contrast, on the medial surface, the subcircular fossa for *m. temporalis* is deep and well-outlined. Also, on the medial surface, the mandibular foramen is located slightly posteroventral to the level of the apex of the coronoid process. The condyloid process, or condyle, is lateroventrally tilted, as in *Hadrokirus*. It has a slender cylindrical shape and reaches slightly dorsal to the ventral extremity of the coronoid notch and reaches well above the horizontal level of the tooth row. The angular process is strongly reduced, forming a weakly-outlined rugosity and thickening which forms no notable protuberance that can be distinguished from the existing curvature of the posteroventral margin of the mandible in lateral view (char. 36[1]). There is no discernible angular process in *Hydrurga* or *Leptonychotes*. The process is large and strongly protruding posteriorly in *Homiphoca*. The angular process is small in most other Monachinae.

DENTITION

Upper teeth and alveoli (Figs 5-9; 14; Tables 3; 5; 6).

The shapes of the alveoli of the three upper incisors suggest a gradual increase in size from I1 to I3 in *Magophoca brevirostris* n. gen., n. sp. Yet, I3 is still incisiform and not caniniform (char. 40[0]). In addition, whereas the shape of the alveolus of I1 and I2 indicates a transversely flattened root, the shape

TABLE 6. — Measurements (in mm) of the isolated (upper) tooth of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276).

Character	MNHN.F.PPI276 (holotype)
Crown height	7.7
Crown length	14.3
Crown width	6.8
Root height	10.1
Root length	11.9

of the alveolus of I3 suggests an oval to circular root in cross-section (char. 41[1]). This agrees with other Monachinae, in which the roots of the upper incisors are moderately compressed transversely as compared to Phocinae, in which these roots are strongly compressed. On MNHN.F.PPI278, I3 and I1 are preserved. I1 is peg-like (maximum width 3.3 mm; maximum high, as preserved, 4.6 mm) and bears a large wear facet posteroventrally oriented and, which almost reaches the base of the crown distolingually. On the mesiolingual base of the crown part of a lingual cingulum is preserved. In labial view, the distal side of the crown, present a small vertical depression, which reveals that a hint of a distal cuspule was probably present. The I3 has a circular root. The crown has a triangular asymmetrical shape, its mesial edge being more ventral than the distal edge. The lingual side of the tooth bears a pronounced cingulum, with a small median cuspule. Both mesial and distal edges of the crown form a relatively sharp crest and the distal crest is slightly cusped at its base. The I3 is 6.2 mm high and its maximum width is 4.6 mm. The I2 is preserved on MNHN.F.PPI269. It has a transversely compressed root. Its crown is more peg-like and less asymmetrical than that of I3. Except for a small facet at apex, it is unworn. Consequently, a distinct cingulum can be observed on its lingual side, with a median cuspule. The cingulum extends on the mesiolabial and distolabial angles of the crown but does not run along all the labial side of the tooth. Its crown is 4.7 mm high and 3.6 mm wide as preserved.

It is noteworthy that the fact that the I1 of MNHN.F.PPI278 is approximately of the same size as the I2 of MNHN.F.PPI269 and is likely related to sexual dimorphism, the former being a probable male and the latter a probable female (see, Table 1).

Two upper canines are known in situ, the right one in MNHN.F.PPI269 and the left one in MNHN.F.PPI278. Both upper canines are slightly compressed transversely and posteriorly recurved. They bear weak, yet noticeably lingual and distal carinae. Both canines have a small horizontal wear facet at the apex.

The upper postcanine teeth are little adapted to specialized aquatic feeding techniques (see Hocking *et al.* 2017) and not fully homodont. This contrast with most extant Monachinae, except for the tribe Monachini. Among other extinct Monachinae, the postcanine teeth are homodont and specialized in some taxa, i.e., *Acrophoca*, and *Hadrokirus*, but less so in others, i.e., *Homiphoca*, *Piscophoca*, and *Pliophoca*.

In *Magophoca* n. gen., the first premolar, P1, is single-rooted, and all other postcanine teeth are double-rooted (char. 47[1], 50[0]). A single-rooted P1 is common among other Phoci-

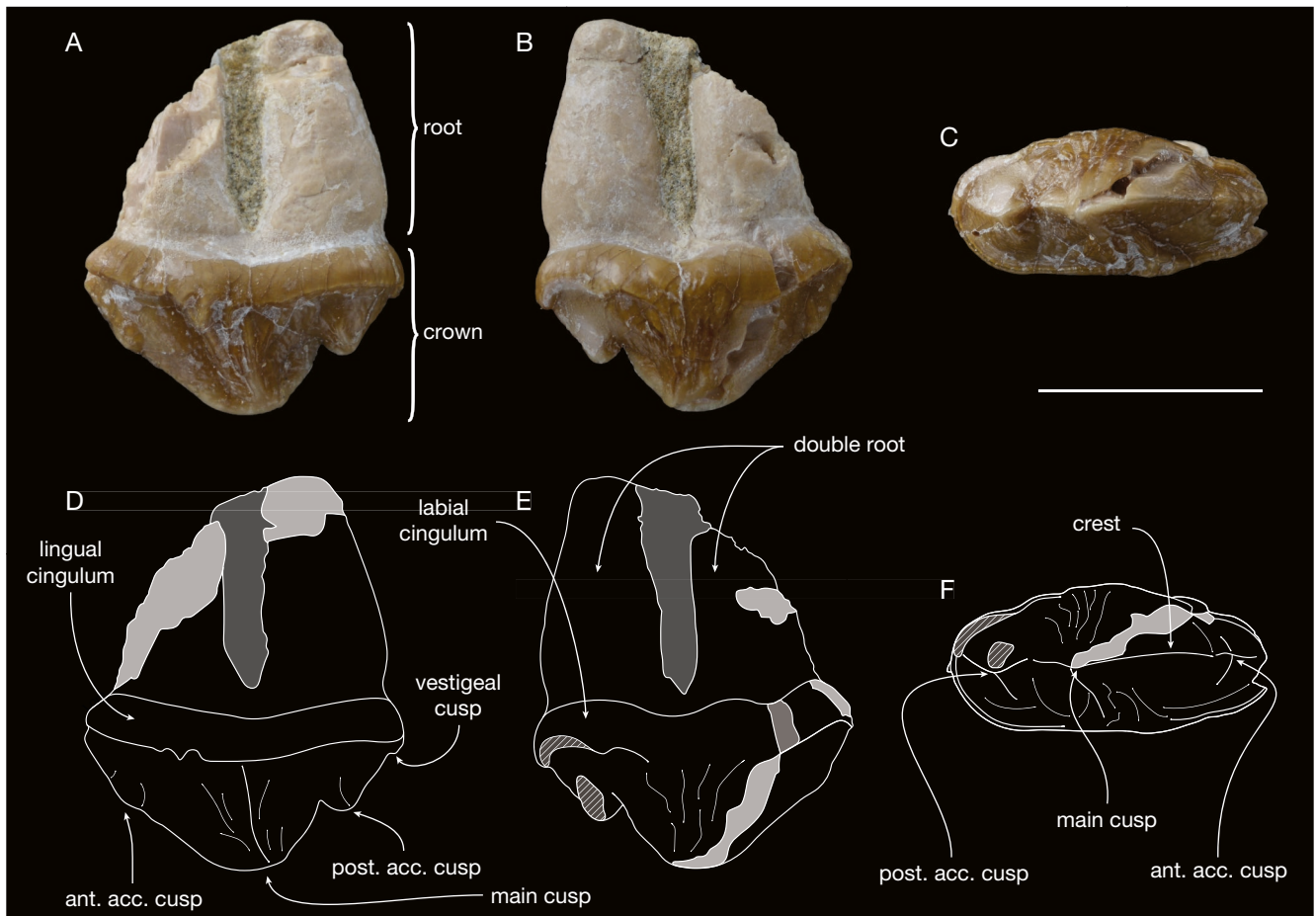


FIG. 14. — Isolated postcanine tooth of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, postcanine tooth in lingual view; **B**, same tooth in labial view; **C**, same tooth in occlusal view; **D–F**, corresponding labelled line drawings. Areas in light gray in the line drawings are fractured; areas in dark gray are obscured from view by sediment matrix; and dashed areas are abraded or worn. Abbreviations: **ant.**, anterior; **acc.**, accessory; **post.**, posterior. Scale bar: 1 cm.

dae, maybe apart from the extant monachines *Hydrurga* and *Lobodon* which, although they do not have a double-rooted P1, feature a bilobed single root for P1. With the exception of the extant monachine genus *Mirounga*, and the extant phocine species *Cystophora*, and *Halichoerus*, P2, P3, P4, and M1 are double-rooted in all Phocidae.

The crowns of the postcanine teeth in *Magophoca* n. gen. are relatively low. With the exception of the comparatively short P1, the crown is twice as long as it is high in the postcanine teeth. This corresponds with the general condition observed in other Monachinae with little specialized postcanine teeth. M1 is comparable in size to the preceding premolars. Among other Monachinae, M1 is always smaller than P4, but the degree of the size discrepancy varies: for example, M1 is only marginally smaller in the extant *Hydrurga* and in the extinct *Acrophoca*, *Hadrokirus*, and *Homiphoca*; it is considerably smaller in the extant *Leptonychotes* and in the extinct *Piscophoca*. All postcanine teeth of *Magophoca* n. gen. have slightly wrinkled enamel with apicobasal ridges.

Except for the posterior portion of P1 that is slightly anterolabial to the anterior portion of P2, the postcanine toothrow is straight and the teeth are parallel to the toothrow, with no imbrication or crowding (char. 46[0]), as in most Monachinae,

except for *Hadrokirus*, *Monachus*, *Neomonachus*, and *Pliophoca*. The single alveolus of P1 is larger than one of the two alveoli of the other postcanine teeth. P4 is separated from M1, by a small diastema, 3–4 mm in length (char. 48[1]). In the paratype specimens MNHN.F.PPI269 and MNHN.F.PPI277, there is also a small diastema between P3, and P4.

In occlusal view, P1 appears as a semi-circle, with an almost straight labial margin and a semi-circular lingual margin. The lingual margin of P1 is marked by a narrow yet prominent cingulum. The cingulum continues on the labial side, where it forms a narrow labial cingulum. An anteroposteriorly elongate central cusp, appears semi-circular in outline in lateral view. It is flanked posteriorly by an accessory cusp and anteriorly by another tiny anterior accessory cusp (char. 44[1]). The latter is located on the cingulum.

The other upper premolars, P2, P3, and P4, are anteroposteriorly elongate and the crowns are approximately twice as long as they are high. P2, P3, and P4 bear a prominent lingual cingulum. This cingulum is widest posterolingually, creating a distinct shelf-like platform (char. 45[1]). As in P1, the cingulum continues on the labial side, but the labial cingulum remains much smaller than the lingual cingulum. The main cusp is slightly elongated anteroposteriorly, bearing slightly

TABLE 7. — Measurements (in mm) of the lower dentition of the *Magophoca brevirostris* n. gen., n. sp. paratype (MNHN.F.PPI269). Abbreviations: >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured.

Character	MNHN.F.PPI269 (paratype)	
	left	right
i2, crown height	n/a	n/a
i2, crown length	n/a	n/a
i2, crown width	n/a	n/a
c, crown height	>10.3	>10.7
c, crown length	8.8	8.5
c, crown width	5.8	6.1
p1, crown height	4.1	4.3
p1, crown length	7.6	7.3
p1, crown width	4.7	4.5
p2, crown height	n/a	6.2
p2, crown length	n/a	11.0
p2, crown width	n/a	6.1
p3, crown height	6.9	7.3
p3, crown length	12.5	12.2
p3, crown width	6.1	6.1
p4, crown height	7.0	7.3
p4, crown length	13.3	13.9
p4, crown width	6.2	6.5
m1, crown height	7.2	7.4
m1, crown length	14.8	14.5
m1, crown width	6.6	6.6

angular crests on the anterior and posterior margin, and is flanked anteriorly and posteriorly by accessory cusps. M1, of the same size as the preceding double-rooted premolars (char. 49[0], 50[0]), is also anteroposteriorly elongate, with a well-developed lingual cingulum and a labial cingulum that is weakly-developed, as in the premolars. In contrast to the premolars, there is no posterolingual shelf-like projection of the lingual cingulum in M1. The main cusp and the flanking anterior and posterior accessory cusps are less raised than in P2-4. In particular, the prominence of the anterior accessory cusp is low, compared to the condition in P2-4. The main cusp is slanted posteriorly, resulting in a smoothly-sloping anterior margin and a strongly-sloping to almost vertical posterior margin.

Lower teeth and alveoli (Figs 11-13; 15; Tables 4; 7)

With the exception of the incisors and the left p2, all lower teeth are present in the mandibles of MNHN.F.PPI269.

The alveoli of i1 and i2 show that i1 is located posteromedial to i2, and that the roots of i1 and i2 are strongly transversely compressed (char. 43[0]). In MNHN.F.PPI269, the alveolus of i1 is distinctly larger than that of i2; whereas on MNHN.F.PPI278 the diameter of i1 and i2 are similar in length (i.e. labiolingually) but the alveolus of i1 is distinctly narrower (i.e. mesiodistally) than that of i2.

The lower canine of *Magophoca brevirostris* n. gen., n. sp. is slightly everted laterally. The tooth is rather small, slightly compressed transversely, and with slightly posteriorly recurring apex. There is a distinct lingual carina on the posteromedial surface of the canine. The apex of the lower canine is flattened as a result of tooth wear. Interestingly, the postcanine teeth of MNHN.F.PPI269 shows very little to no wear.

The first lower premolar is the only lower postcanine tooth that is single-rooted, in contrast to the other postcanines (p2-4, m1) which are all double-rooted (char. 47[1]). This corresponds with the general condition among Phocidae, again, except for *Cystophora* (bilobed P2), *Halichoerus* (all single-rooted), and *Mirounga* ssp. (all single-rooted). On the paratype MNHN.F.PPI269, the first and second premolar are implanted obliquely, whereas p3, p4, and m1 are implanted parallel to the long axis of the tooth row. However, this condition is prone to intraspecific, e.g. ontogenetic and/or sexual, variation since it is absent in the holotype and the referred specimen MNHN.F.PPI278. The lower postcanine teeth increase in size posteriorly with p1 having the smallest crown and m1 the largest one. The enamel of the mandibular postcanine teeth is slightly wrinkled and bears few apicobasal ridges, as observed on the upper teeth.

In occlusal view, p1 is oval, with the lingual margin being more convex than the labial margin. This contrasts with the upper P1, which has a virtually straight labial margin. The lower p1 has a well-developed lingual cingulum forming a distinct shelf. The labial cingulum is thin, but clearly present. The labial cingulum is highest but also thinnest at mid-length of p1. The anteroposteriorly elongate and transversely compressed main conid dominates the crown. The crown is not highly raised; it is lower than long. Anterior and posterior to the main cuspid, are much smaller accessory cusps. Especially the anterior accessory cuspid is minute.

The p2, p3, and p4 are anteroposteriorly elongate. Although they present a well-outlined lingual cingulum, these cingula lack the well-developed posterolingual projection in p3 and p4, observed in their upper premolar correspondents. Due to the weaker development of this posterolingual projection, the discrepancy in the degree of development between the lingual and labial cingula is small and the main and accessory cusps align with the long axis of each premolar. For p2, p3, and p4, the crowns are low: almost twice as long anteroposteriorly as high. The central main conid has prominent angular (i.e., anterodorsally and posterodorsally bowed) anterior and posterior crests and is flanked by a accessory cusps anteriorly and posteriorly.

The lower m1 is the largest postcanine tooth. The crown is proportionally higher in m1 than in the preceding premolars, but, as in the premolars, it is at least twice as long as it is high. The lingual cingulum is moderately well developed, but lacking the posterolingual shelf-like projection. The labial cingulum is narrow. This corresponds with the lower premolars, as well as with the upper first molar. The main conid dominates the crown. Its anterior and posterior crests are somewhat rounded, in contrast to the lower premolars, in which these crests are angular. Notably, the anterior margin is profoundly sloping, forming the base for a weakly-developed anterior accessory cuspid. In contrast, the posterior accessory cuspid is relatively well developed, compared to the anterior accessory cuspid. Posterior to the posterior accessory cuspid, the vestigial cuspid forms a small but distinct protuberance on the posterior margin of the tooth, as large as in p4.

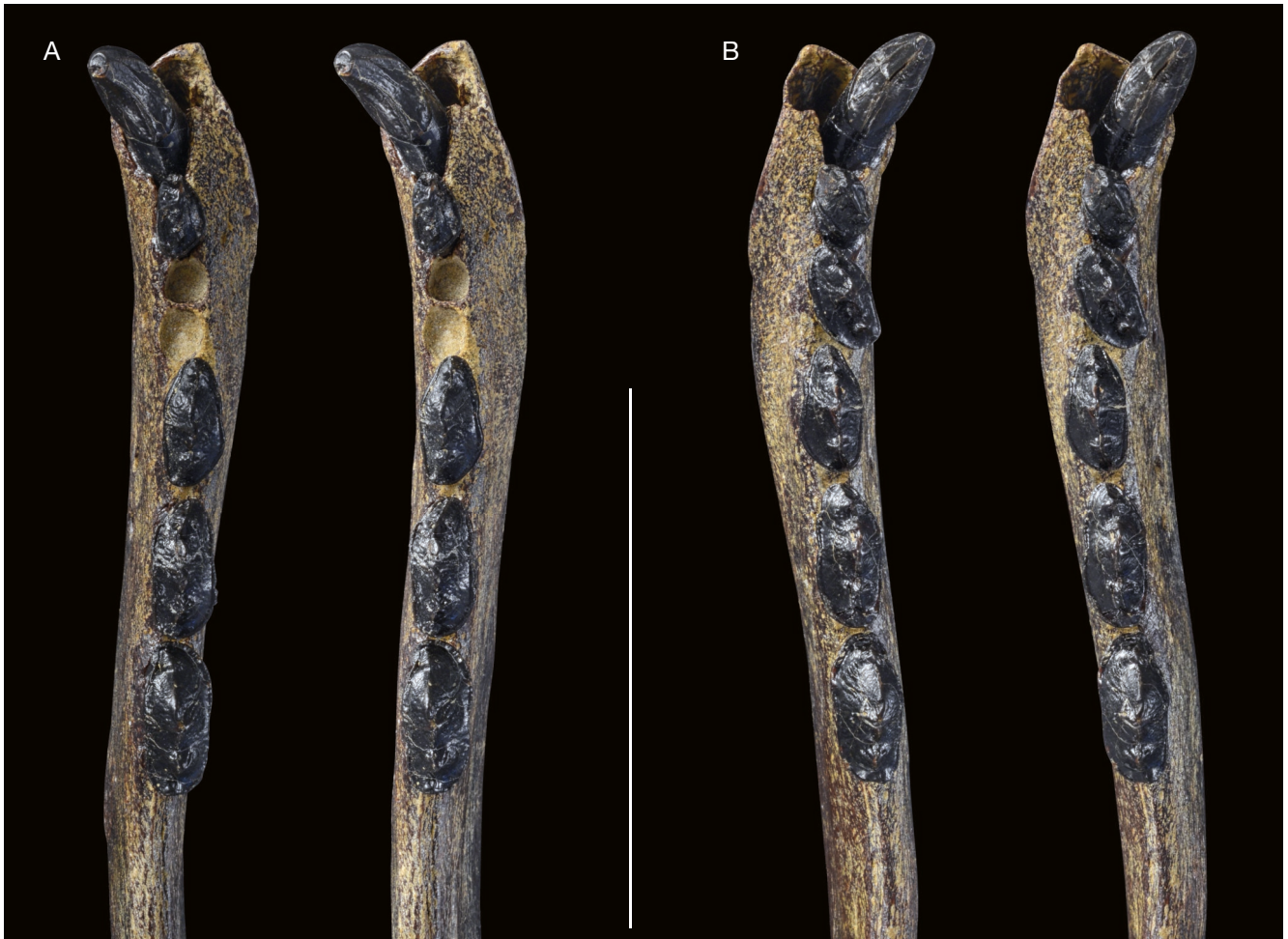


FIG. 15. — Stereoscopic view of the mandibular dentition of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, left mandible in occlusal view; **B**, right mandible in occlusal view. Scale bar: 5 cm.

AXIAL SKELETON

Cervical vertebrae

Atlas (Fig. 16; Table 8). Two atlases are known for *Magophoca brevirostris* n. gen., n. sp.: the atlas of the holotype, MNHN.F.PPI276, and the atlas associated with the paratype skull, MNHN.F.PPI269.

The atlas of *Magophoca* n. gen. is gracile. Overall, the shape of the atlas of *Magophoca* n. gen. does not depart starkly from the condition in most other Monachinae, except for *Acrophoca* and *Hadrokirus*. The former has a uniquely anteroposteriorly elongate atlas and the latter has a particularly robust atlas.

The transverse process of the atlas expands only moderately, laterally. The process has a roughly semi-circular convex lateral outline with a distinct anterior limit forming a hook-like tip, which forms the posterior margin of the alar notch. This lateral expansion of the transverse process conforms with most other Monachinae. Exceptions are *Hadrokirus*, *Monachus*, and *Piscophoca*, in which the transverse process of the atlas projects more strongly laterally. The convex curvature of the lateral margin of the transverse process of the atlas is also a character shared with most Monachinae, with the notable exception of *Acrophoca* and *Piscophoca*. In *Acrophoca*, this pro-

cess is flared distally and has a straight, posteriorly expanding lateral margin. In lateral view, the transverse process of the atlas is straight and oriented anterodorsally-posteroventrally oblique, in *Magophoca* n. gen. (char. 53[0]). Among Phocidae, the oblique orientation of this process is a character shared with Phocinae, *Acrophoca*, *Hadrokirus*, *Leptonychotes*, and *Neomonachus*. This process is implanted rather subvertically in other Monachinae. The transverse process is curved, in lateral view, in *Hadrokirus*.

The transverse foramen is smaller than in extant Monachinae, comparable in proportions *Piscophoca*, but slightly larger than in *Acrophoca* and *Hadrokirus*. On the anteroventral side of the wing, the transverse foramen opens in a wide and open atlantal fossa. The posterior opening of the transverse foramen is visible in dorsal view, as in all other extant and extinct Lobodontini, except for *Ommatophoca* (char. 52[1]). The cranial articular foveae are oval but strongly concave-cylindrical. The caudal articular foveae for articulation with the axis are rounded and both left and right are in an almost right angle to one another. The neural canal of the atlas of *Magophoca* n. gen. is round with prominent internal processes. The dorsal tubercle is raised high and marked laterally by deep fossae for

TABLE 8. — Measurements (in mm) of the atlas of *Magophoca brevirostris* n. gen., n. sp. Abbreviations: **e**, estimate for a character due to minor damage; **>**, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; **n/a**, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)		MNHN.F.PPI269 (paratype)	
	left	right	left	right
Overall, height	> 46.8		50.2e	
Overall, width	115.8		114.2e	
Wings, transverse length	32.2	n/a	29.8	28.1
Wings, least width	32.6	n/a	28.7	28.7
Wings, maximum width	38.0e	n/a	> 33.5	35.3
Articular facet for axis, height	n/a	18.1	19.8	20.3
Articular facet for axis, width	n/a	18.9	21.8	21.7
Neural arch, length	26.9		27.1	
Ventral bar, length	n/a		15.7	
Neural canal, width	27.1		27.6	
Neural canal, height	30.7		27.8	

m. rectus capitis dorsalis minor (char. 54[1]). Amson & Muizon (2014), previously described this as a unique character for the extinct monachine *Hadrokirus*. However, we also observed these fossae in *Monachus*. The intervertebral foramen on the lateral surface of the dorsal arch is large and round.

Axis (Fig. 17; Table 9). Two axes are known for *Magophoca brevirostris* n. gen., n. sp. As for the atlases, described above: one as part of the holotype, MNHN.F.PPI276, and one as part of the paratype skull, MNHN.F.PPI269.

The shape of the dens differs between both specimens, being exceptionally thick and stubby in the holotype specimen: even more than the dens of *Hadrokirus*, which has been considered to be thick by Amson & Muizon (2014). The dens is circular in cross-section in both specimens. The cranial articular surfaces are subcircular to subtriangular in outline and at a 90° angle to one another. The shape of the thin spinous process differs between both specimens: it does not reach anterior to the dens in either of both, but it has a distinct anterior ‘knob’ in MNHN.F.PPI276. The posterior tip forms a small ‘knob’ in both specimens. The spinous process of the holotype (MNHN.F.PPI276) project further posteriorly than that of the paratype (MNHN.F.PPI269). In the former it projects, well posterior to the postzygapophyses and posterior articular facet of the centrum. In the latter it is slightly anterior to the posterior articular facet of the centrum (although the epiphysis of the centrum is missing the spinous process is dorsal to the posterior end of the centrum asd preserved) and well anterior to the postzygapophyses. This notable difference in size and stoutness of the dens and spinous process of the two specimens is likely to be related to sexual dimorphism since the holotype is a male and the paratype is probably a female. In its overall size, the spinous process of *Magophoca* n. gen. is proportionally as large as in other extinct Monachinae, but notably larger than in extant Monachinae. The centrum is incompletely preserved in both. The dorsal surface of the body appears semi-cylindrical in MNHN.F.PPI269 and the ventral surface is strongly excavated with a distinct, sharp ventral keel, which is strongly prominent posteriorly and which

TABLE 9. — Measurements (in mm) of the axis of *Magophoca brevirostris* n. gen., n. sp.. Abbreviations: **e**, estimate for a character due to minor damage; **>**, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; **n/a**, a character could not be measured.

Character	MNHN.F. PPI276 (holotype)		MNHN.F. PPI269 (paratype)	
	left	right	left	right
Overall, length	67.4		68.7	
Overall, height	n/a		> 64.7	
Overall, width	30.1 × 2 = 60.2e		n/a	
Body, length	50.9		> 53.8	
Body, height (posterior)	n/a		> 23.4	
Body, width (posterior)	n/a		27.3e	
Dens, length	12.3		15.5	
Articular facet for atlas, height	18.9	n/a	n/a	20.8
Articular facet for atlas, width	16.6	n/a	n/a	19.3
Spinous process, horizontal length	66.3		56.8	
Neural canal, length	17.4		20.5	
Neural canal, height	19.4		22.1	
Neural canal, width	14.4		18.5	

separates two deep fossae. The development of this keel, and the depth of the fossae adjacent to it, are similar to the condition in *Acrophoca*; better developed than in either *Hadrokirus* or *Piscophoca*. The neural canal is distinctly higher than wide with a concave ventral margin. The postzygapophysis on the posterior margin of the neural arch is simple, bearing a flat, teardrop-shaped postzygapophyseal articular facet. Both left and right facets are facing ventrolaterally, perpendicular to one another. The transverse foramen is oval and transversely elongate. It is dorsally and ventrally covered by thin laminae of the transverse process. The transverse process forms a gracile stub, running parallel with, but posterior to the anterior articular surface. This process is oriented posterolaterally and almost reaches the same posterior level as the centrum.

Other cervical vertebrae (Figs 18; 19; Table 10). All cervical vertebrae, Ce3–7 are known for the holotype MNHN.F.PPI276, whereas only Ce3 is known for MNHN.F.PPI269, in addition to the atlas and axis.

The centrum is dorsoventrally slightly flattened. Its dorsal aspect is roughly flat on Ce3 of MNHN.F.PPI276 to slightly concave on Ce3 of MNHN.F.PPI269. The dorsal part of the centrum is slanted anteriorly. As a consequence, the posterior articular surface of the centra is strongly oblique being anterodorsally-posteroventrally oriented. This oblique orientation decreases from Ce3 to Ce7 and is almost absent on the anterior thoracic vertebrae. The anterior articular surfaces are roughly oval in outline, whereas the posterior surface is roughly triangular due to the development of a strong posteroventral tubercle. The length of the centra varies from Ce3 to Ce7. It increases from Ce3 to Ce6 (38.8 mm; 39.4 mm; 41.1 mm; 44.5 mm). Then, it decreases in Ce7 (43.0 mm) and decreases again on the anterior thoracic vertebrae. The ventral aspect of the centrum bears a prominent ventral keel which exhibits a strong posterior tubercle. The keel is deeply concave from Ce3 to Ce5; the concavity decreases on Ce6 and the keel is straight on Ce7. The ventral keel separates two deep ventral

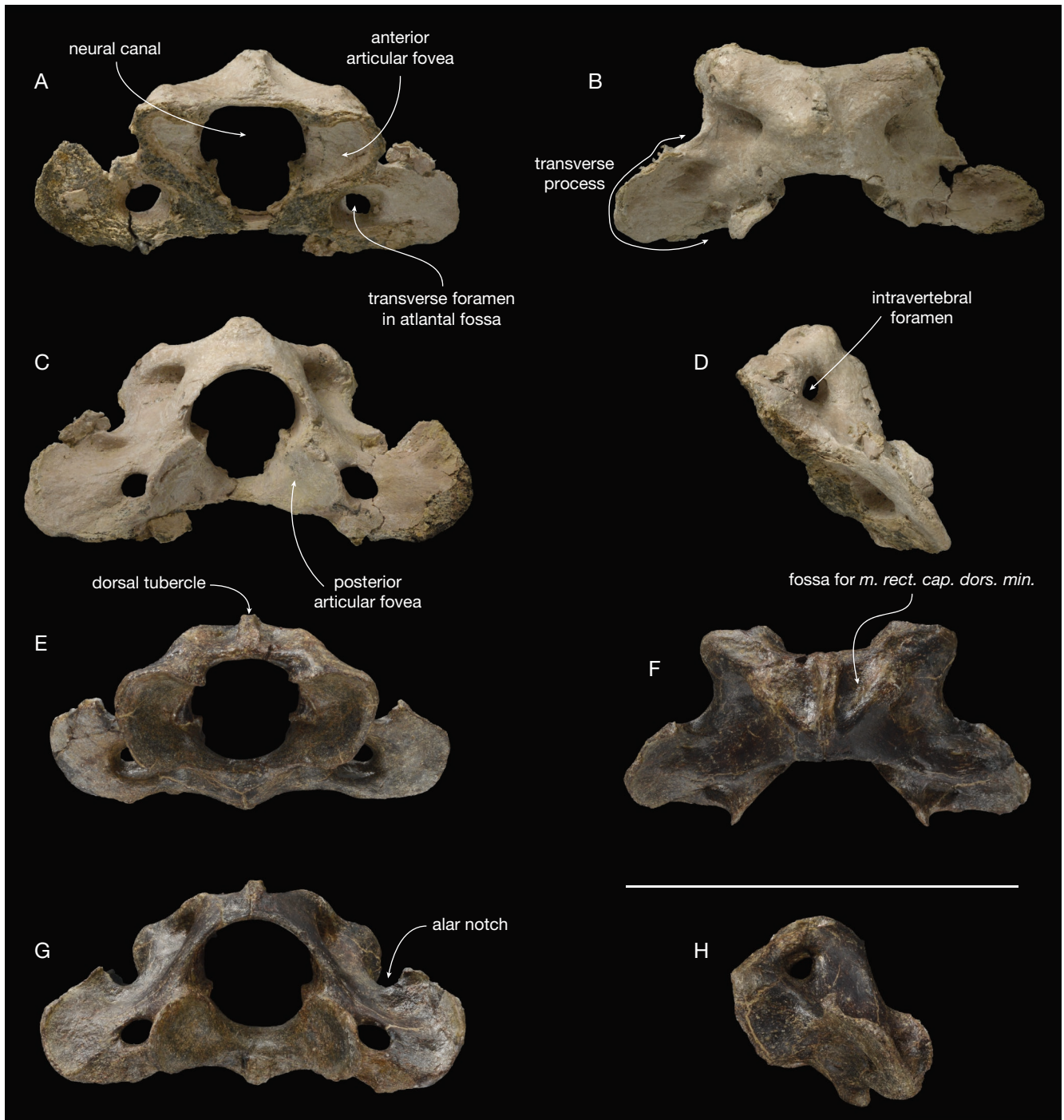


FIG. 16. — Atlases of *Magophoca brevirostris* n. gen., n. sp. (A–D, holotype, MNHN.F.PPI276; E–H, paratype MNHN.F.PPI269): A, E, atlases in anterior view; B, F, same atlases in dorsal view; C, G, same atlases in posterior view; D, H, same atlases in left lateral view. Abbreviation: *m. rect. cap. dors. min.*, *musculus rectus capitis dorsalis minor*. Scale bar: 10 cm.

fossae, which receive the insertion of the cervical fascia the *m. longus coli*, originating on the transverse processes of the anterior vertebra. The shape of the neural arch varies along the series of vertebrae: crescent-shaped or semi-circular in the anterior vertebrae, and subtriangular in the posterior cervical vertebrae. The gradually more prominent dorsal tapering of the neural canal into a triangle corresponds with the development of the spinous process. Whereas the spinous

process is small in the anterior vertebrae, it is much higher in the posterior vertebrae. In addition, the spinous process is slanted anteriorly in Ce4–6 and extends anterodorsal to the neural arch. It is subvertical in Ce7. The prezygapophysis is simple, forming a flattened spatula-like process that projects anterodorsally. The prezygapophyseal articular facet is oval and flat, facing mediodorsally. The postzygapophysis bears a small, flattened knob-like prominence on its dorsal surface.

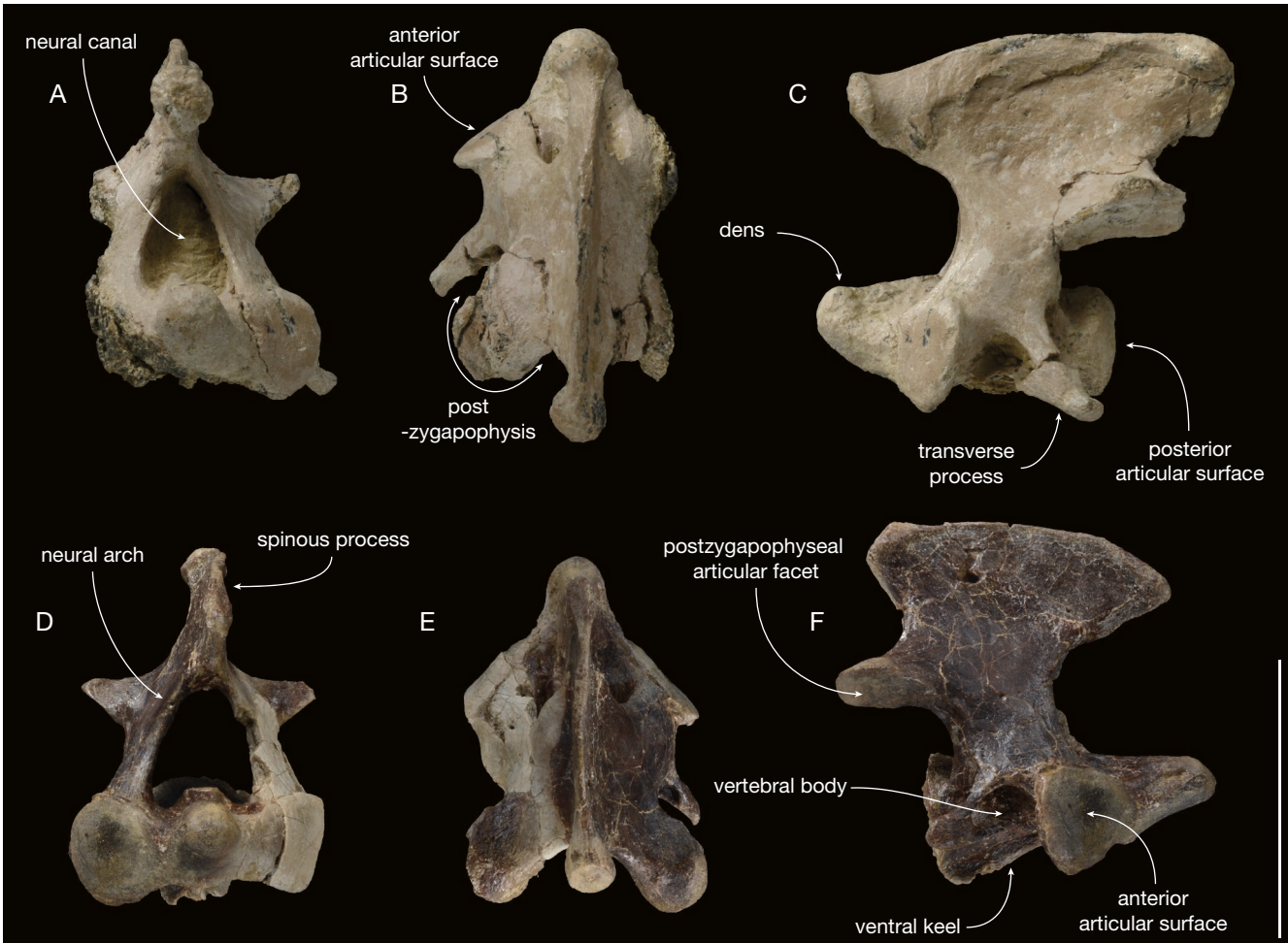


FIG. 17. — Axes of the *Magophoca brevirostris* n. gen., n. sp. (A–C, holotype, MNHN.F.PPI276; D–F, paratype, MNHN.F.PPI269): A, D, axes in anterior view; B, E, same axes in dorsal view; C, left lateral view of MNHN.F.PPI276; F, right lateral view of MNHN.F.PPI269. Scale bar: 5 cm.

TABLE 10. — Measurements (in mm) of the cervical vertebrae of *Magophoca brevirostris* n. gen., n. sp. (excluding atlas and axis). Abbreviations: e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured; DEF, the character is deformed.

Character	MNHN.F.PPI276 (holotype)					MNHN.F.PPI269 (paratype)
	Ce3	Ce4	Ce5	Ce6	Ce7	Ce3
Overall, height	66	> 75	76	84.5	76	50.5
Overall, width	39.5 × 2 = 79.0e	41.1 × 2 = 82.2e	42.9 × 2 = 85.8e	39 × 2 = 78	47 × 2 = 94	80.8
Body, length	40.0	39.6	41.4	45.5	44.2	38.4
Body, height (anterior)	n/a	n/a	24.0e	25	28.4	21.5
Body, width (anterior)	n/a	29.2	28.8	29	28.7	27.4
Body, height (posterior)	n/a	n/a	28e	29e	28.1	24.8
Body, width (posterior)	27.7	31	32.6	n/a	33.2	26.2
Neural arch, canal, length	18.7	19.2	17.4	20.3	25.7	14.1
Neural canal, height	14.8DEF	15.6DEF	15.9DEF	20.2	20.5	15.3
Neural canal, width	18.4DEF	23.2DEF	23.5DEF	23.3	23.0	23.1
Spinous process, height	5.9	15.7e	15.2	22.2	25.5	10.4

The postzygapophyseal articular facet is round to oval and faces lateroventrally. Both left and right facets are perpendicular to one another. The prezygapophysis and postzygapophysis extend anterior to the anterior articular surface and posterior to the posterior articular surface, of the centrum, respectively. The shape of the transverse process varies along the series of

cervical vertebrae. It gradually changes along Ce3–6, but starkly differs in Ce7. For Ce3–6, the transverse process is oriented posterolaterally and bifurcates distally. In Ce3, this process is transversely flattened with a superior branch projecting dorsally and a wider inferior branch projecting ventrally. The superior branch of the transverse process is tubular in Ce4

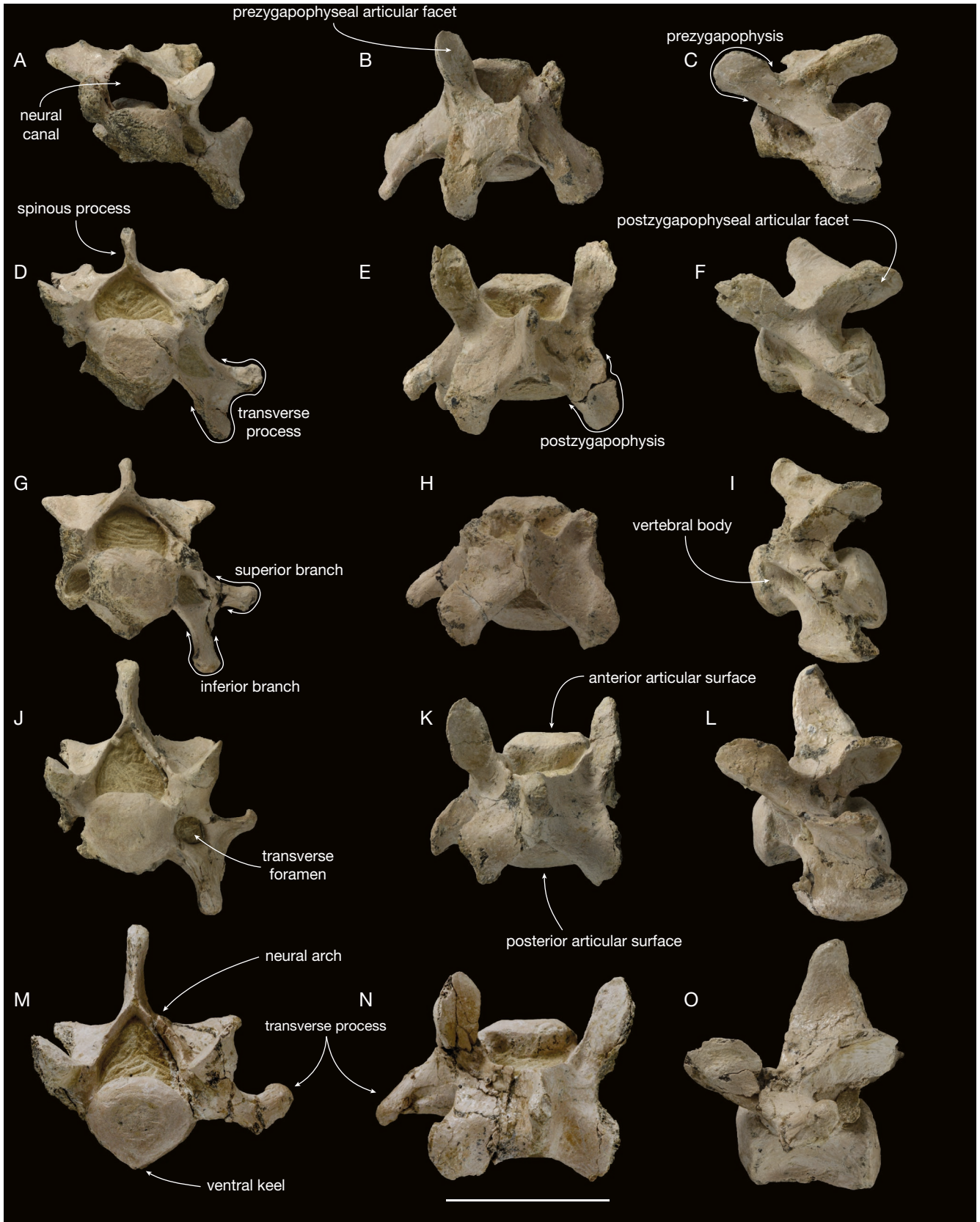


FIG. 18. — Cervical vertebrae of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, Ce3 in anterior view; **B**, Ce3 in dorsal view; **C**, Ce3 in left lateral view; **D**, Ce4 in anterior view; **E**, Ce4 in dorsal view; **F**, Ce4 in left lateral view; **G**, Ce5 in anterior view; **H**, Ce5 in dorsal view; **I**, Ce5 in left lateral view; **J**, Ce6 in anterior view; **K**, Ce6 in dorsal view; **L**, Ce6 in left lateral view; **M**, Ce7 in anterior view; **N**, Ce7 in dorsal view; **O**, Ce7 in left lateral view. Scale bar: 5 cm.

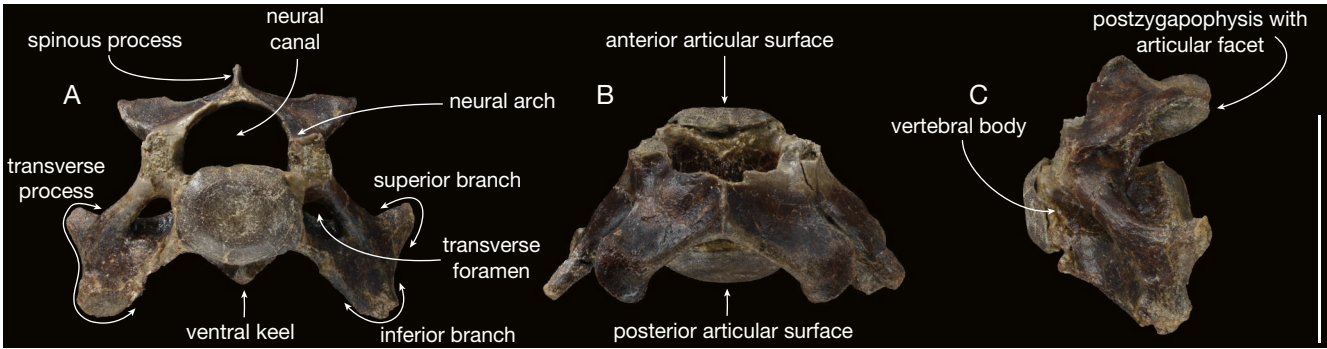


FIG. 19. — Third cervical vertebra of *Magophoca brevirostris* n. gen., n. sp. (paratype, MNHN.F.PPI269): **A**, cervical vertebra in anterior view; **B**, same vertebra in dorsal view; **C**, same vertebra in left lateral view. Scale bar: 5 cm.

TABLE 11. — Measurements (in mm) of the thoracic, lumbar, and caudal vertebrae of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured.

Character	thoracic				lumbar			caudal
	Anterior thoracics	Posterior thoracics			L3	L4	L5	Ca2
Overall, height	n/a	n/a	76.3	> 90.0	75.5	n/a	n/a	n/a
Overall, width	n/a	n/a	46.9	47.2	45 × 2 = 90e	n/a	n/a	n/a
Body, length	38.0e	39.0e	43.3	37.3e	58.7	58.4	52.3	32.5
Body, height (anterior)	>28.6	n/a	28.2	n/a	34e	33.4	n/a	n/a
Body, width (anterior)	n/a	n/a	21.2	n/a	41.6	n/a	39.9	n/a
Body, height (posterior)	n/a	27.5	27.8	28.8e	33e	n/a	35.6	17.6
Body, width (posterior)	28.1	n/a	n/a	31.7e	29.9	39.9	n/a	22.4
Neural arch, canal, length	31.0	n/a	27.4	30.3	39.8	28.2	21.2	n/a
Neural canal, height	19.8	20.2	26.0	22.6	n/a	n/a	15.9	n/a
Neural canal, width	24.1	27.0	24.1	26.8	25.9	n/a	29.2	n/a
Spinous process, height	39.5	n/a	26.7	40.0	21	n/a	n/a	n/a

and Ce5, and transversely flattened again in Ce6. The inferior branch of the transverse process forms a transversely flattened wedge in Ce4-6, gradually expanding anteroposteriorly along the series of vertebrae. The inferior branch of the transverse process reaches ventral to the centrum. A transverse foramen is present at the base of the transverse process, just lateral to the centrum. This foramen is oval in Ce3-5, but round in Ce6. As usual in most mammals, the transverse process of Ce6 is the largest of the cervical series featuring a large plate, on which insert the thoracic part of the *m. longus coli* and originates the Ce6-Ce5 fascia of the cervical part of the muscle. In Ce7, there is no transverse foramen, the transverse process projects laterally instead of ventrolaterally, and it is not transversely flattened but forms a tubular prominence.

Overall, there are little significant characteristics setting these cervical vertebrae of *Magophoca* n. gen. apart from other Monachinae, with the notable exception of *Acrophoca*, in which the cervical vertebrae are strongly elongated anteroposteriorly.

Thoracic vertebrae (Figs 20; 21; Table 11)

Five thoracic vertebrae have been recovered for *Magophoca brevirostris* n. gen., n. sp. All belong to the holotype, MNHN.F.PPI276. Two are still in articulation after preparation and for one, only a small portion of the centrum is preserved. As has been suggested by Dewaele *et al.* (2017b), the thoracic vertebrae can arbitrarily be separated in anterior,

middle and posterior series. The anterior and posterior series are characterized by the fact that each vertebra articulates with one rib, i.e., each vertebra has only one costal fovea on each side. The middle thoracic vertebrae articulate with two ribs each, one rib at the contact with the anterior vertebra and one rib at the contact with the posterior vertebra. The shape of the transverse process has been noted to change dramatically along the series of thoracic vertebrae. Of the preserved thoracic vertebrae, two are anterior thoracic vertebrae and the two articulating vertebrae are middle thoracic vertebrae. Evans & Lahunta (2013, for the domesticated dog) and Rule *et al.* (2020d) employ another separator for the series of thoracic vertebrae: the distinction between preantclinal vertebrae, the antclinal vertebra (T11), and the postantclinal vertebrae. The antclinal vertebra has a distinct contact between the prezygapophysis and the anterior costal fovea. Furthermore, post-antclinal vertebrae lack the postzygapophysis. As shown in the description below, these characteristics confirm that the preserved thoracic vertebrae of *Magophoca* n. gen. are indeed from positions anterior to T11.

The vertebral bodies are subcylindrical, with a slightly convexly curving dorsal margin in the two anterior thoracic vertebrae and flat dorsal margin in the two middle thoracic vertebrae. The anterior and posterior articular surfaces are oval in the former two, and semicircular in the latter two vertebrae. A ventral keel runs along the ventral margin of the centrum in all specimens. This

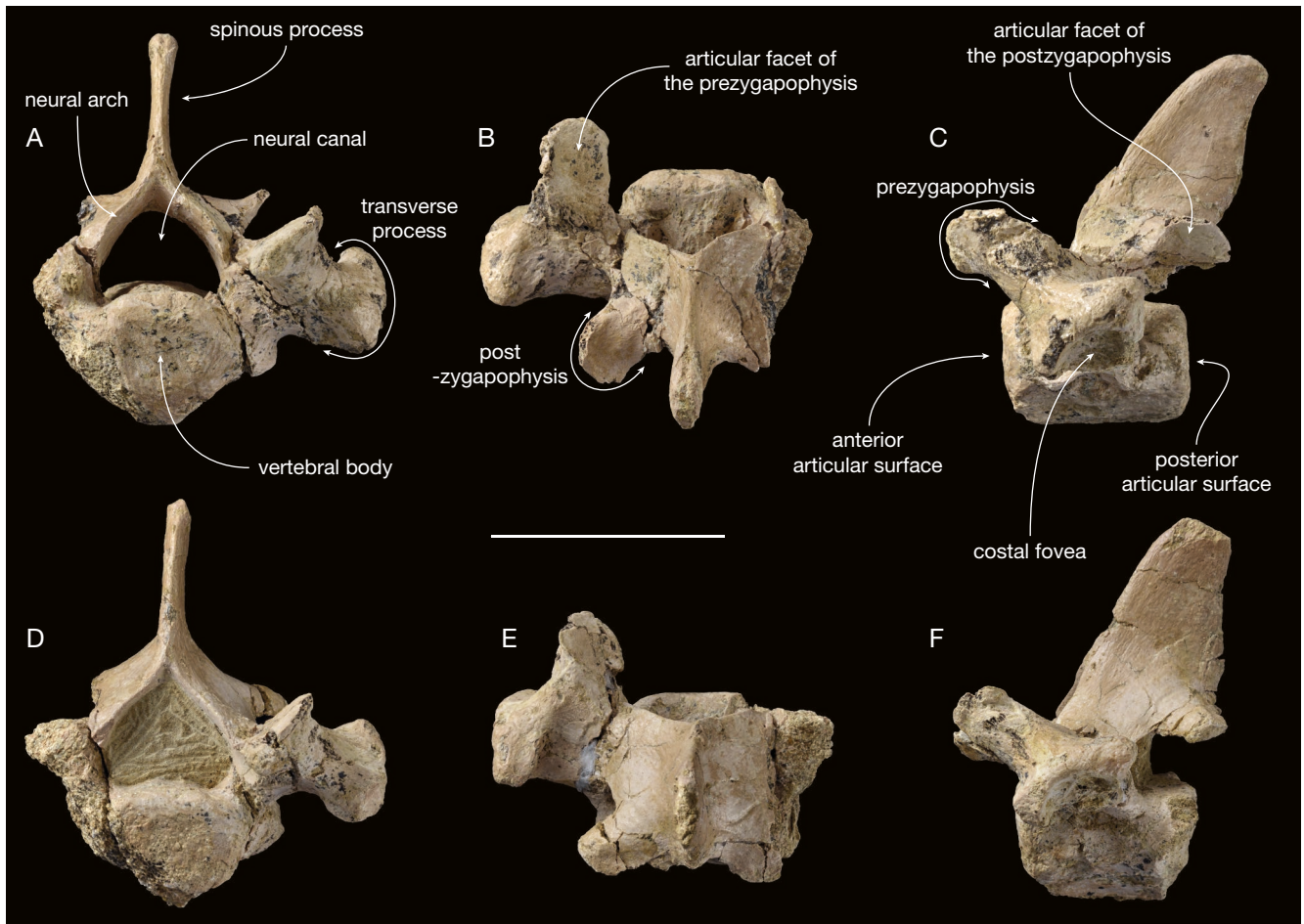


FIG. 20. — Anterior thoracic vertebrae of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A, D**, thoracic vertebrae in anterior view; **B, E**, same vertebrae in dorsal view; **C, F**, same vertebrae in left lateral view. Scale bar: 5 cm.

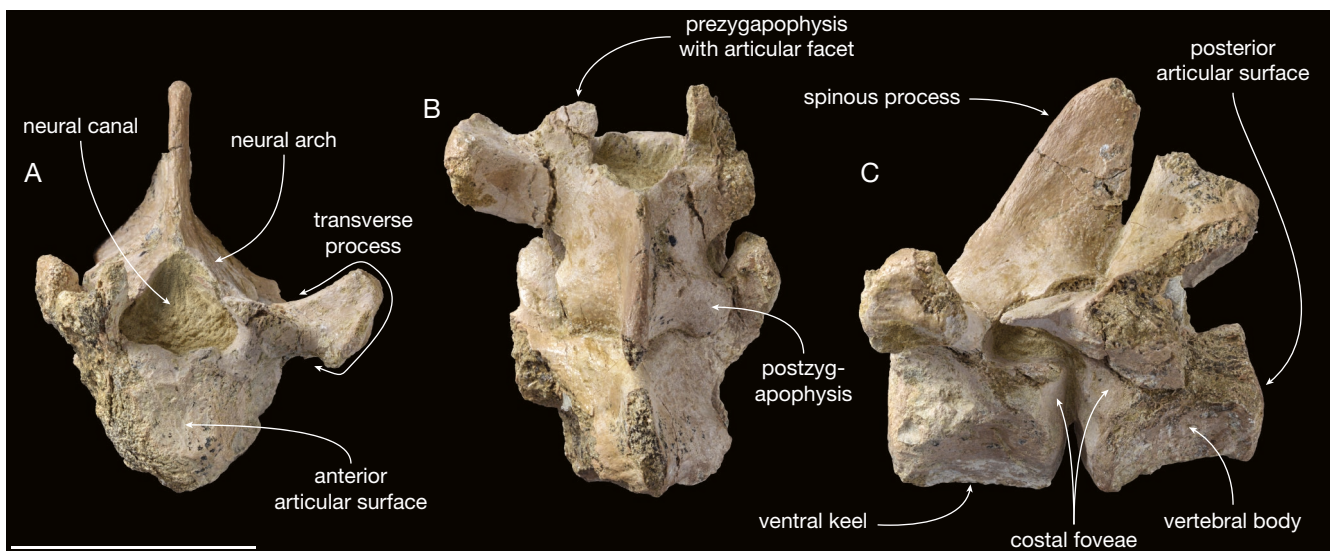


FIG. 21. — Middle thoracic vertebrae of the *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, middle thoracic vertebrae in anterior view; **B**, the same vertebra in dorsal view; **C**, the same vertebra in left lateral view. Scale bar: 5 cm.

keel is equally developed along its entire length in each vertebra. In the anterior thoracic vertebrae, a circular and concave costal fovea is located centrally on the lateral surface of the centrum,

facing rather ventrally to ventrolaterally. In the middle thoracic vertebrae, there is a small, lens-shaped and concave costal fovea on the centrum, anterodorsal and posterodorsal on the lateral

TABLE 12. — Measurements (in mm) of the sacrum of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: e, estimate for a character due to minor damage; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)	
	left	right
Overall, length	111.6	
Anterior portion, total width across	61.4 × 2 = 122.8e	
Anterior articular facet, height	34.9	
Anterior articular facet, width	35.7	
Wings, width across	n/a	45.7
Wings, height of the lateral margin	n/a	28.7
Wings, height at the medial margin	n/a	36.6e

surface of the centrum. The neural canal is triangular in cross-section. The neural arch is large and wide, with the transverse process located on the arch. The transverse process is a robust knob projecting laterally, with a well-developed concave costal fovea on the ventrolateral margin. The prezygapophysis is located at the horizontal level of the transverse process, but projecting anteriorly. The prezygapophysis is located anterolateral to the anterior articular surface of the body in the anterior thoracic vertebrae, having prezygapophyseal articular facets facing dorsomedially. In contrast, in the middle thoracic vertebrae, the prezygapophysis is located anterior to the anterior articular surface of the body, and the prezygapophyseal articular facet faces dorsally. The postzygapophysis is slim and simple, facing ventrally to lateroventrally in different specimens. The postzygapophysis extends posterior to posterior articular surface. The spinous process is long, slightly tapering dorsally, and slightly slanted posteriorly.

In addition, multiple rib fragments have been preserved for *Magophoca* n. gen., but they are too incompletely preserved to allow an adequate description and comparison.

Lumbar vertebrae (Figs 22; Table 11)

For the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, a succession of three lumbar vertebrae have been preserved and the two posterior ones are still in articulation. Phocids have five lumbar vertebrae and the last one has a centrum distinctly shorter than the anterior ones. Because the posterior vertebra of the series has a centrum conspicuously shorter than the anterior one, we interpret it as the L5. Therefore, the other two are L4 and L3.

The centra of the lumbar vertebrae are subcylindrical, with a slightly flattened dorsal surface. The anterior and posterior articular surfaces are shaped accordingly: oval, with a (slightly) flatter dorsal margin. The anterior one of the two articulating lumbar vertebrae has two hemal processes on the posterior portion of the ventral margin of the body.

The neural canal is triangular in cross-section. The neural arch is anteroposteriorly elongate. The prezygapophysis is large, curving dorsolaterally. The prezygapophysis extends anterior to the anterior articular surface of the centrum. The prezygapophyseal articular facet is teardrop-shaped and concave, positioned anteriorly on the medial surface of the prezygapophysis. Dorsolateral to the prezygapophyseal articular facet is a thick, robust mammillary process.

The postzygapophysis is simple, slim, and flattened. It projects posteriorly. The postzygapophyseal articular facet is teardrop-shaped and faces ventrolaterally.

The dorsoventrally flattened transverse processes are strongly anterolaterally projecting, with only a slight ventral aspect. Two transverse processes are completely preserved in two incomplete lumbar vertebrae of strongly differ in length and anteroposterior breadth.

The only completely preserved spinous process of a lumbar vertebra of *Magophoca* n. gen. is that of L3. It is low and projects straight dorsally. It is much lower than in *Monachus* and, in lateral view, it is broader at its base. The apex of the spinous process is remarkably flattened dorsally and strongly widened transversely and forms a characteristic plateau. This robustness indicates a strong attachment of the supraspinous ligament, which is therefore likely to have been very powerful. On the whole, this morphology is very similar to that of the lumbar of *Acrophoca*.

Sacrum (Fig. 23; Table 12)

The sacrum of the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, remains in articulation with both innominates after preparation. The dorsal and left lateral portions of the sacrum are strongly abraded.

The sacrum consists of three fused sacral vertebrae (char. 56[1]). This strongly conforms with other Monachinae: among Phocidae, Monachinae have three fused sacral vertebrae and Phocinae four fused sacral vertebrae. The only known exception may be the extinct phocine *Nanophoca vitulinoides* having a notable record of individuals with only three fused sacral vertebrae. The promontory, the anterior articular surface of the first sacral vertebra, is small and subrounded. The sacral wings are proportionally large, and the width across the entire anterior portion of the sacrum (both wings + promontory) is well over three times as large as the width across the promontory. In addition, the sacral wing is ventrally curving, and the ventrolateral tip of the wing extends conspicuously ventral to the ventral margin of the promontory. Such a strong ventral deflection of the sacral wings is a characteristic that has been observed in Phocinae, but not in other Monachinae.

The state of preservation of the specimen precludes further detailed description. However, it can be noted that the prezygapophyseal articular facet of S1 is slightly concave and oriented rather dorsally than dorsomedially, the preserved sacral foramina are large and oval, and the lateral sacral crest is thin.

Caudal vertebrae (Figs 23; 24; Table 11)

Fragments of six caudal vertebrae of the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, are preserved. The first caudal vertebra is currently still in articulation to the sacrum via sediment (Fig. 23). The state of preservation does not allow a more detailed description. The other preserved caudal vertebrae are simple in their overall morphology. They are elongate, approximately twice as long as they are high and with stubby protuberances as the relics of a strongly reduced neural arch and transverse apophyses, resulting in a sub-square appearance of the anterior and posterior articular surfaces.

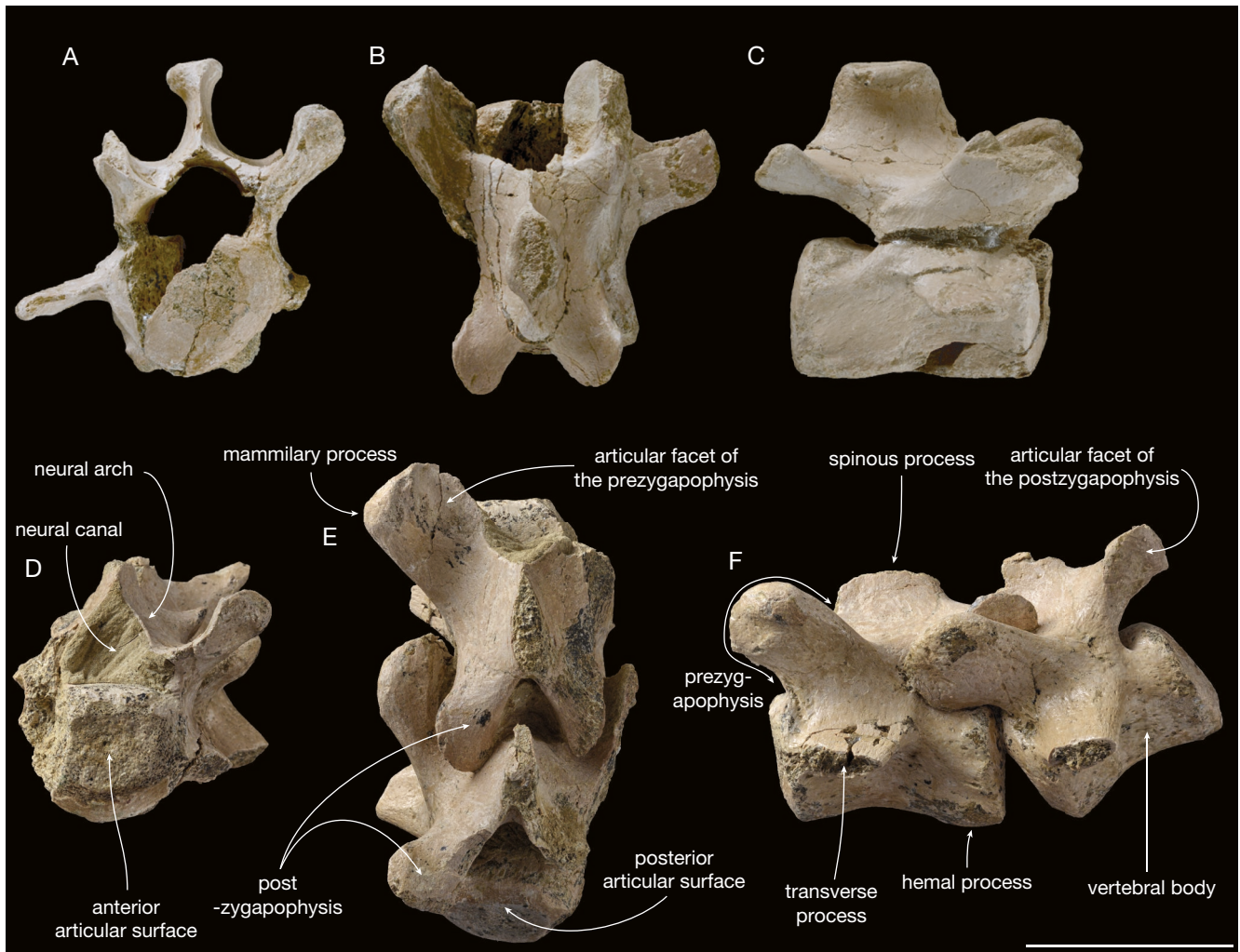


FIG. 22. — Lumbar vertebrae of *Magophoca brevirostris* n. gen., n. sp. (holotype MNHN.F.PPI276): **A–C**, L3 in anterior, dorsal and right lateral views respectively; **D**, L4 in anterior view; **E, F**, articulated L4 and L5 in dorsal and left lateral views respectively. Scale bar: 5 cm.

PECTORAL GIRDLE AND FORELIMB

Scapula (Fig. 25; Table 13)

The left scapula of the holotype of *Magophoca brevirostris* n. gen., n. sp. is well preserved and virtually complete. Only the distal articular part of the right scapula is preserved.

The glenoid cavity is incompletely preserved, but roughly teardrop-shaped or sub-triangular and with thin and gracile lateral and ventral margins. It is moderately concave: not as strongly concave as in *Acrophoca*, but more so than in *Piscophoca*. The supraglenoid tubercle, the origin area of *m. biceps brachii*, is moderately developed as well, resembling the condition in the extant *Hydrurga*, *Leptonychotes* and Monachini; it is more prominent than in the extinct *Piscophoca*, but less so than in the other extant Monachinae and the extinct *Acrophoca*. The neck is well-delineated and moderately long, conforming with most other Monachinae. The neck is shorter than in *Acrophoca* and *Ommatophoca*, but longer than in *Homiphoca*, *Lobodon*, Monachini, and *Piscophoca*. The posterolateral portion of the neck is only weakly developed, showing a rather weak development of the origin area of *m. triceps brachii caput longus*.

The scapular spine, dividing the lateral surface of the scapula, is very low along most of the length of the spine (char. 59[1]), but, on its distal end, the acromion forms a small but prominent anteriorly facing hook-like process, which features a teardrop shape (char. 58[1]). Whereas the scapular spine is elevated along the entire length and doesn't terminate anteriorly in a well-developed acromion in Phocinae, it is generally lowly-raised in Monachinae, raised anteriorly, and terminating in a well-developed acromion anteriorly. Nevertheless, it rarely forms a hook-like spine, as is observed only in *Magophoca* n. gen. and *Hydrurga*, Monachini, and *Piscophoca*. The scapular spine of *Magophoca* n. gen. runs roughly perpendicular to the long axis of the scapula (char. 60[0]), as in most Monachinae, except for *Mirounga*, Monachini, and *Piscophoca*, in which it is oriented obliquely.

The scapular spine separates the supraspinous fossa (origin *m. supraspinatus*) from the infraspinous fossa (origin *m. infraspinatus* and *m. teres major*). Both parts are approximately of equal size in *Magophoca* n. gen. (char. 61[2]). The supraspinous fossa is roughly semi-circular, with a vertically straight posterior border along the scapular spine, and a convex semi-circular anterior border. It is laterally convex

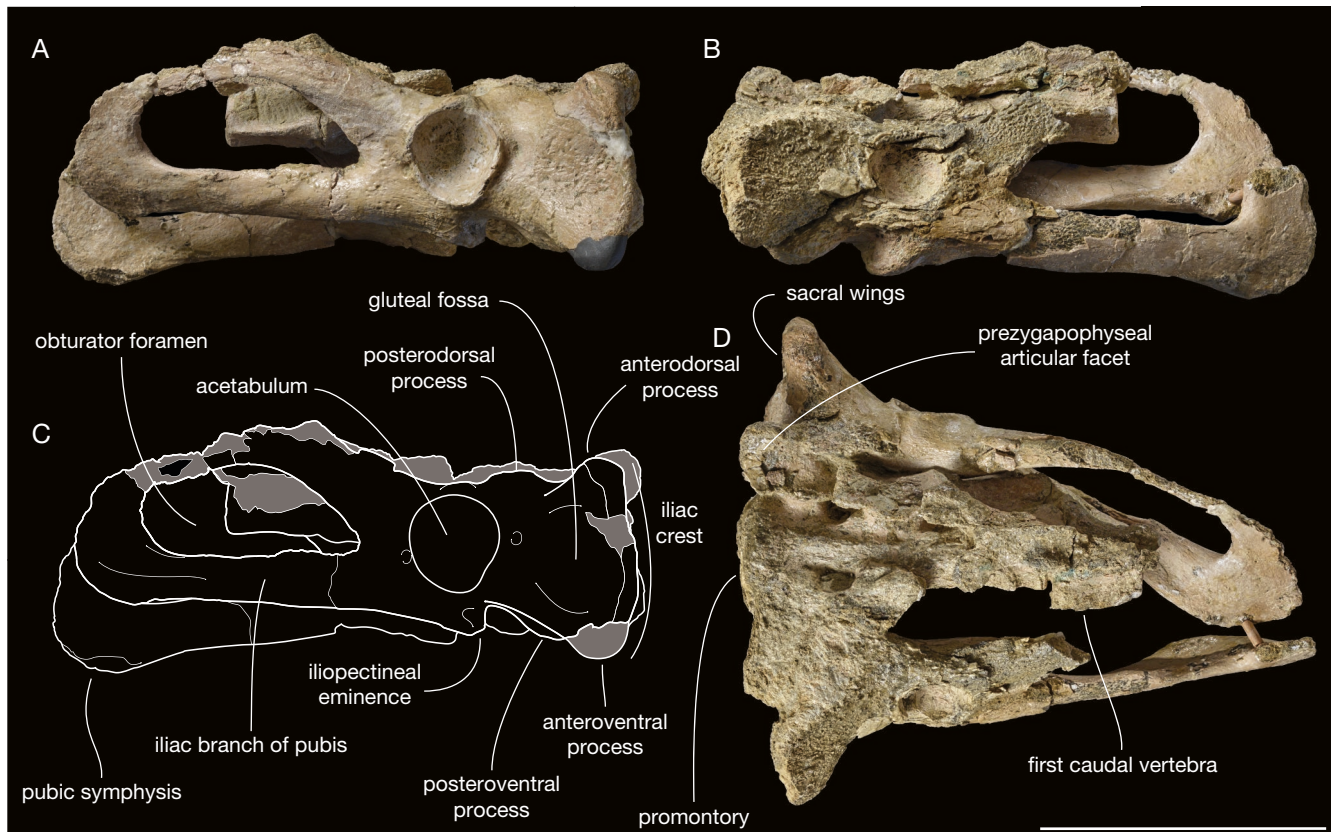


FIG. 23. — Pelvis (innominates cemented to the sacrum) of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, pelvis in right lateral view; **B**, the same pelvis in left lateral view; **C**, corresponding line drawing for **A**; **D**, the same pelvis in dorsal view. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Scale bar: 10 cm.

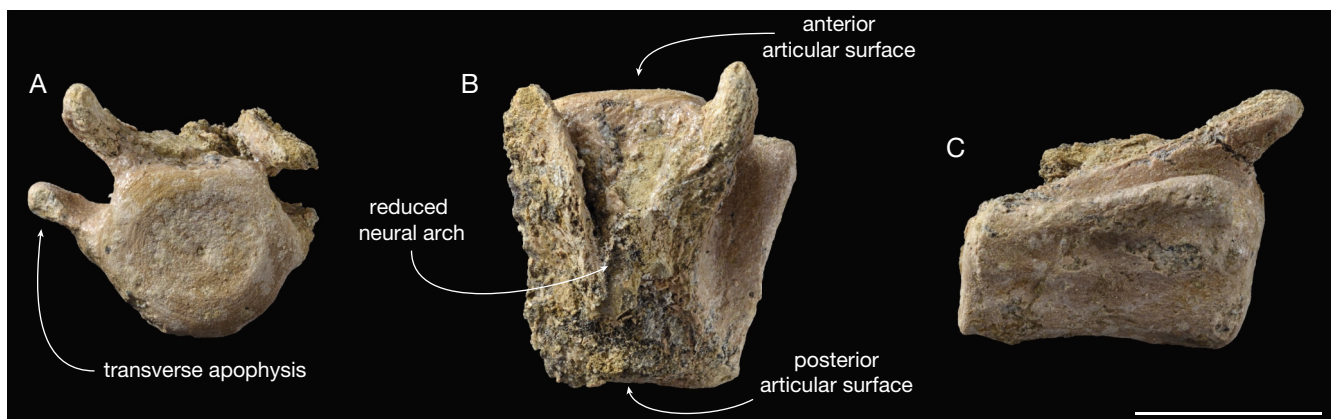


FIG. 24. — Caudal vertebra of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, second caudal vertebra in anterior view; **B**, the same vertebra in dorsal view; **C**, the same vertebra in right lateral view. Scale bar: 2 cm.

with an irregular “wavy” surface. The infraspinous fossa is subtriangular, with the origin of *m. Infraspinatus* roughly forming a right triangle, and the origin of *m. teres major* forming a narrow triangular wedged just posteroventral to the former. The dorsal border of the scapular blade is gently convex, whereas the posterior border is slightly concave and strongly oriented posteroventrally, the ventral component being greater than the posterior one (char. 57[1]). This morphology corresponds with observations in most Monachinae,

with the notable exception of *Leptonychotes*, *Lobodon*, and *Ommatophoca*, in which the posterior component is either equal to the ventral one, or distinctly greater. In Phocinae, the origin area for *m. teres major* is proportionally larger. In addition, in Phocinae, the relative size of the surface area of the supraspinatus fossa is smaller than in Monachinae, thus reducing the size differences between the origins of *m. Infraspinatus*, *m. supraspinatus*, and *m. teres major*. Also, in extant Lobodontini, the supraspinous fossa does not project

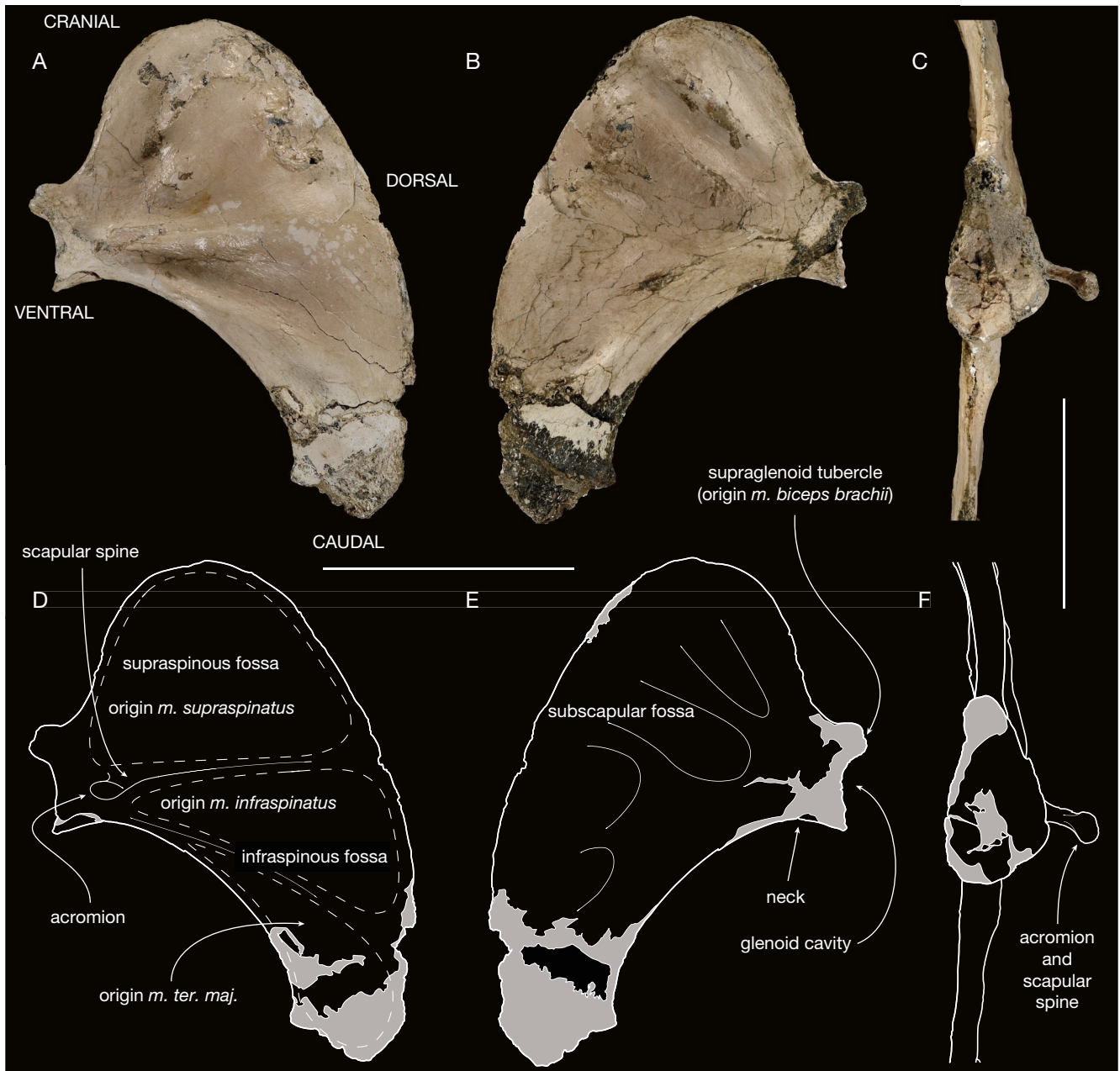


FIG. 25. — Left scapula of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, left scapula in lateral view; **B**, the same scapula in medial view; **C**, articular area of the same scapula in ventral view; **D-F**, corresponding labelled line drawings. Areas marked by dashed lines in (**D**) indicate origin areas of *musculus infraspinatus*, *musculus supraspinatus*, and *musculus teres major* (abbreviated as *m. infraspinatus*, *m. supraspinatus*, and *m. ter. maj.*, respectively). Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured. Scale bars: A, B, D, E, 10 cm; C, F, 5 cm.

anteriorly as much as in *Piscophoca*, *Acrophoca*, *Magophoca* n. gen., and Monachini and its anterior border is less convex than in these latter taxa, giving the scapula a rather trapezoidal appearance. In *Mirounga*, the cranial border of the scapula is angular and pointed, instead of rounded.

The medial surface (subscapular fossa) of the scapular blade is subdivided into four fossae, in which the two median fossae are the largest. The small ridge separating the cranial subscapular fossa from the second is low, as in Monachini, but in contrast to Lobodontini, in which this ridge is prominent.

Humerus (Figs 26; 27; Table 14)

Both left and right humeri are preserved for the holotype MNHN.F.PPI276. The right humerus is significantly abraded on its medial side (medial region of the head and lesser tubercle, medial epicondyle and medial region of the trochlea). The left humerus shows only little abrasion, confined to the lesser tubercle and the medial epicondyle. Another referred specimen, MNHN.F.PPI279, also includes a relatively well-preserved right humerus.

The diaphysis of the humerus of *Magophoca brevirostris* n. gen., n. sp. is rather slender and gracile, as compared to other extinct

TABLE 13. — Measurements (in mm) of the scapula of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: e, estimate for a character due to minor damage; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype, left)
Overall, anteroposterior length	218.8
Acromion, height	20.2
Acromion, dorsoventral length of the base of the acromion	24.5
Acromion, dorsoventral length of the apex	15.0
Glenoid, height	n/a
Glenoid, height of articular surface	33.3e
Glenoid, width	22.8
Glenoid, height neck	41.3

and extant Monachinae, except for the Argentinean *Properiptychus argentinus*, as presented by Muizon & Bond (1982). However, as Echarri *et al.* (2021) pointed out, ICZN Article 72.4 states that all type specimens are required to appear in the original description. Consequently, with only the holotype mandible fragment presented originally by Ameghino (1897), other specimens later referred to this species have been done so tentatively because they are not associated to the type mandible. However, keeping this in mind, we treat Muizon & Bond’s (1982) humerus of *Properiptychus* as a “referred” specimen for simplicity’s sake. Similarly, *Callophoca obscura* has long been used as a wastebin taxon, but it is currently treated as a *nomen dubium* with the name strictly referring to its lectotype (Rule *et al.* 2020a). Although we agree with Rule *et al.* (2020a), to transition gradually away, we consider *Callophoca*, as treated by Koretsky & Ray (2008) and Dewaele *et al.* (2018b) but highlight it with quotation marks to reflect its new identification as a *nomen dubium*. In addition, the humerus of *Magophoca* n. gen. is overall comparable in morphology and size to the humerus of *Frisiphoca aberrata* from the North Sea Basin. The latter has been identified as either a monachine or a phocine by different authors (e.g., Van Beneden 1877; Kellogg 1922; versus Dewaele *et al.* 2018a).

The humeral head of *Magophoca* n. gen. is hemispherical and of proportions similar to other Monachinae, with the exception of extant Lobodontini, and the genus *Neomonachus*, which appear to have proportionally larger humeral head. In *Magophoca* n. gen., the head is oriented posteroproximally (with roughly equal posterior and proximal components) as in most Monachinae, except for *Acrophoca*, *Hydrurga*, and *Sarcodectes*, in which it faces more proximally than posteriorly.

The lesser tubercle is weakly developed and, although its apex is slightly abraded on the two specimens described, it is likely to have been slightly lower than the head (char. 62[0]). Among other Phocidae, the development of the lesser tubercle varies. A small lesser tubercle, not exceeding the proximal level of the humeral head, as in *Magophoca* n. gen., is a characteristic shared with most extinct Phocidae, with the notable exceptions of the extinct monachines *Australophoca*, “*Callophoca*”, *Homiphoca*, and *Pliophoca*, which have a lesser tubercle that exceeds the proximal level of the humeral head. Among extant Phocidae, the lesser tubercle reaches proximal to the

TABLE 14. — Measurements (in mm) of the humerus of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: e, estimate for a character due to minor damage; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)	
	left	right
Overall, length	142.7	143.2e
Deltpectoral crest, length	102.7	102.2
Deltpectoral crest, proximal length to deltoid tuberosity	69.8	66.8
Deltpectoral crest, maximum anteroposterior breadth	47.9	47.0
Proximal epiphysis, width	50.1e	n/a
Distal epiphysis, width	n/a	n/a
Head, width	35.9	n/a
Head, height	35.0	33.4
Diaphysis, minimum width	22.6	21.9
Trochlea, anterior width	n/a	n/a
Trochlea, posterior width	24.0e	n/a

level of the humeral head in most taxa except *Leptonychotes*, *Mirounga*, and Monachini.

The greater tubercle reaches the same proximal level as the humeral head in *Magophoca* n. gen. (char. 63[1]), and extends only slightly proximal to the level of the lesser tubercle. A greater tubercle reaching the level of the head proximally, is a condition shared with most other extinct Monachinae. Exceptions are the extinct “*Callophoca*” (greater tubercle reaching at or proximal to the level of the head), *Acrophoca*, the referred *Properiptychus* from Muizon & Bond (1982) (MER 685), and *Sarcodectes* (greater tubercle not reaching the level of the head). Among extant Monachinae, most have a greater tubercle that does not reach the level of the head, with the notable exception of *Monachus* (greater tubercle reaching the proximal level of the head).

In *Magophoca* n. gen., the lesser and greater tubercles are separated anteriorly by a narrow and deep bicipital groove. The bicipital groove is generally much wider and open in other Monachinae, possibly except for *Frisiphoca aberrata*. Although the deltopectoral crest is incompletely preserved in *F. aberrata*, the preserved portions suggest that the bicipital groove of its humerus is rather narrow and deep too.

The bicipital groove of *Magophoca* n. gen. lacks a bicipital bar (char. 64[0]), a character that varies among Monachinae. A bicipital bar is absent in *Acrophoca*, *Homiphoca*, *Hydrurga*, *Leptonychotes*, and *Virginiaphoca*, whereas all other extant and extinct Monachinae (with a completely known humerus) have a transverse bar in the bicipital groove. Considering the genus *Frisiphoca* to be monachine (contra Dewaele *et al.* 2018a), *F. affinis* lacks a bicipital bar and *F. aberrata* has a bicipital bar. *Magophoca* n. gen. has a deep dimple at the top of the bicipital groove, just anterior to the humeral head. Such a dimple has also been observed in *Acrophoca*, *F. affinis*, Monachini, and *Piscophoca*.

In lateral view, the deltopectoral crest curves gently, smoothly tapering towards the distal epiphysis. It is long, extending distally to the anterior level of the epicondylar crest, and the insertion for *m. pectoralis* reaches well distal to the mid-

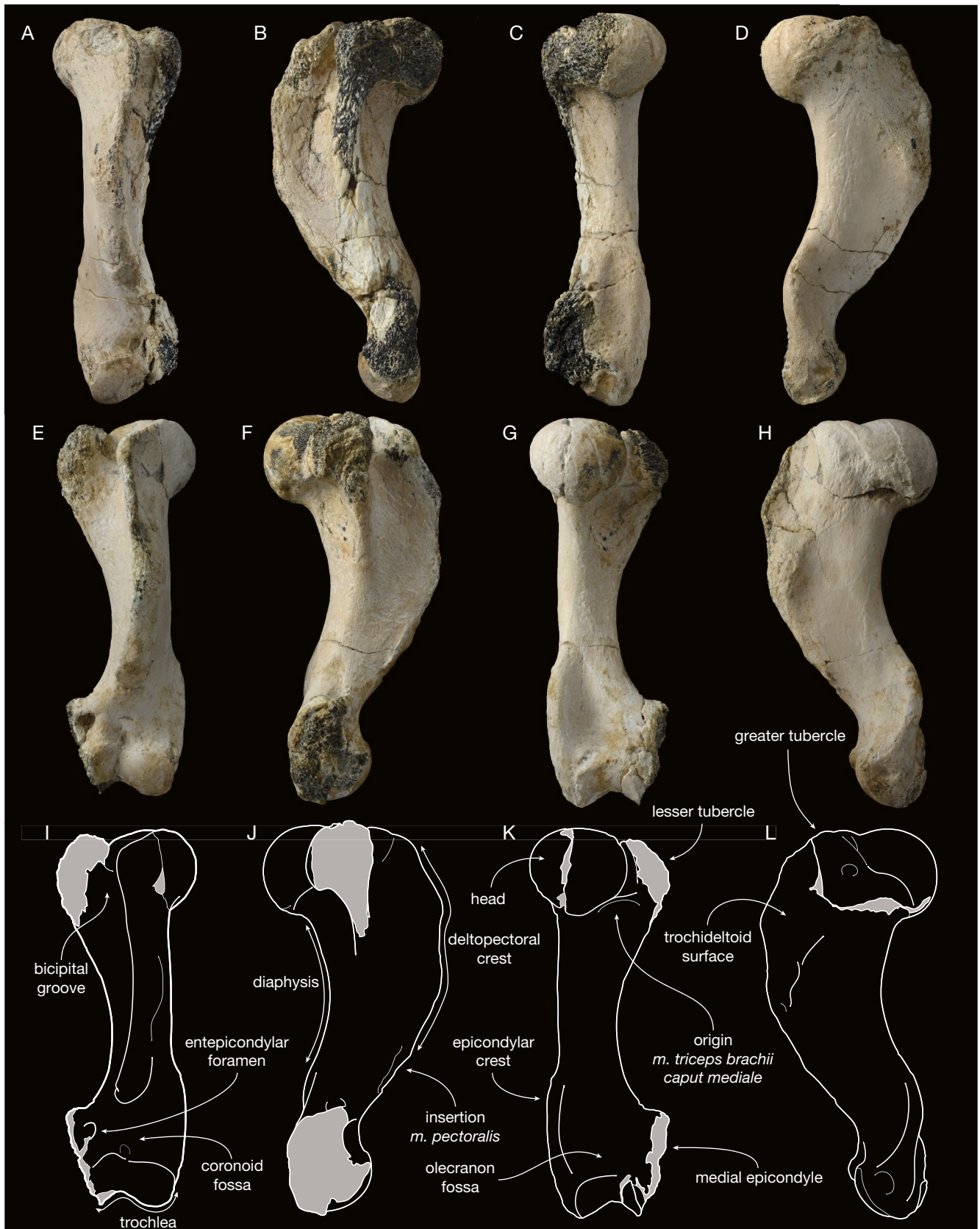


FIG. 26. — Humeri of *Magophoca brevirostris* n. gen., n. sp. (holotype, [MNHN.F.PPI276](#)): **A**, right humerus in anterior view; **B**, the same humerus in medial view; **C**, the same humerus in posterior view; **D**, the same humerus in lateral view; **E**, left humerus in anterior view; **F**, the same humerus in medial view; **G**, the same humerus in posterior view; **H**, the same humerus in lateral view; **I-L**, corresponding labelled line drawings of **E-H**. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured. Scale bar: 10 cm.

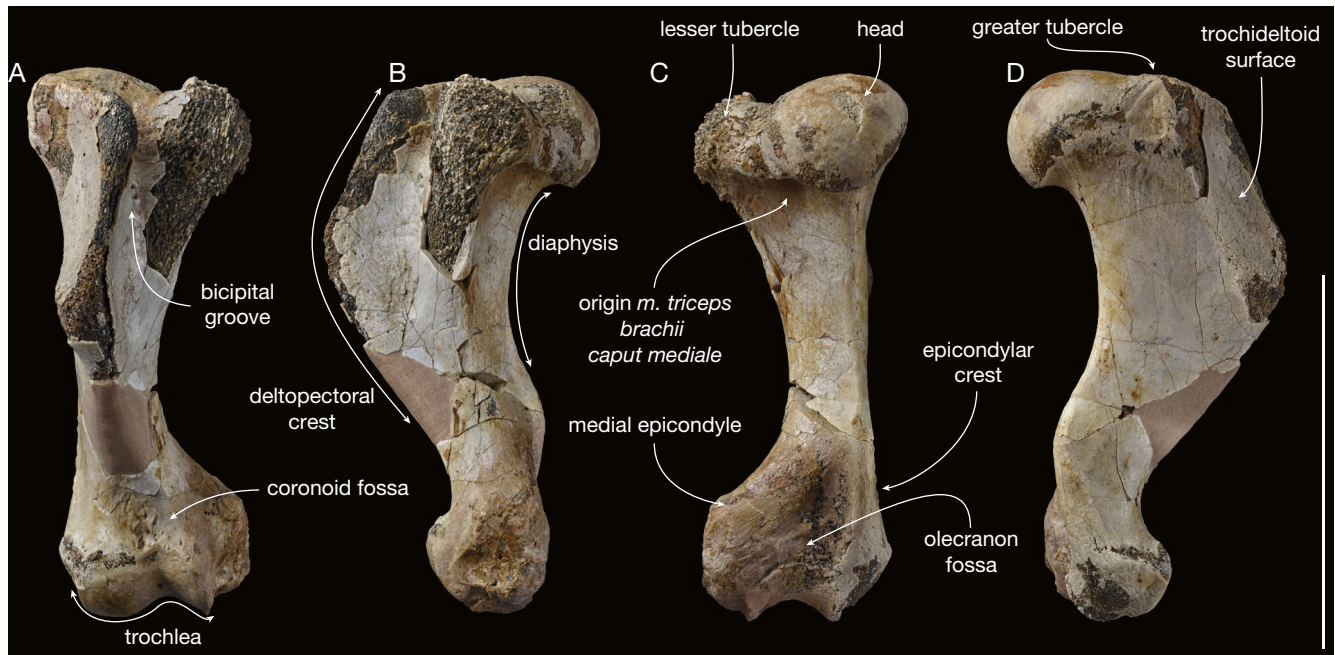


FIG. 27. — Right humerus referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI279): **A**, right humerus in anterior view; **B**, the same humerus in medial view; **C**, the same humerus in posterior view; **D**, the same humerus in lateral view. Scale bar: 10 cm.

point of the bone (char. 66[0]). This condition conforms with other extinct Monachinae and Monachini. Extant Monachinae (except Monachini) and Phocinae differ in one or more characteristic: the deltopectoral crest is limited to the anterior half of the humerus and/or it sharply terminates distally. This may be less evident in extant Monachinae and certain extinct Phocinae, in which the distal termination of the deltopectoral crest may be less abrupt (see, e.g., Koretsky 2001; Koretsky & Grigorescu 2002). However, in all extant and extinct Phocinae, the insertion for *m. pectoralis* does not extend as far distal as in extinct Monachinae.

The proximal portion of the deltopectoral crest of *Magophoca* n. gen. is remarkably thin being thinner than in other Monachinae. Only *Acrophoca*, *Frisiphoca* spp., and extant Monachini tend to approach this condition. The trochideltoid surface is slightly concave, appearing as if it folds over the bicipital groove. Among Monachinae, a similar morphology for the trochideltoid surface has only been observed in *Acrophoca* and the unnamed taxon from the late Pliocene of the North Sea Basin, described by Dewaele *et al.* (2018c). However, the deltopectoral crest is notably thicker, transversely, in these later two taxa.

On the posterior surface of the diaphysis, just distal to the humeral head and the lesser tubercle, there is well-developed fossa for the origin of the *m. triceps brachii caput mediale* (char. 65[1]). This fossa is also well developed in *Frisiphoca* and *Piscophoca*; its development is not notable in other Monachinae.

On the distal extremity, the lateral epicondylar crest (= supinator crest) is well developed and strongly projects posteriorly (char. 67[0]). This is a plesiomorphic characteristic present in all Phocinae, but which varies among Monachinae: the epicondylar crest is well developed in *Frisiphoca*, *Homiphoca*,

Leptonychotes, *Lobodon*, and *Piscophoca*; but not in others. Consequently, the humerus appears rather strongly curving in lateral view in taxa with a well-developed epicondylar crest.

Interestingly, the fossil record for *Magophoca* n. gen. includes humeri with (MNHN.F.PPI276) and without (MNHN.F.PPI279) an entepicondylar foramen on the medial epicondyle (char. 68[0&1]). The presence of an entepicondylar foramen is considered a plesiomorphy present in Phocinae, but also retained in a few extinct Monachinae: *Frisiphoca*, *Homiphoca*, and *Kawas* (this taxon is included here in the Monachinae, see below in the phylogeny section). However, the absence of an entepicondylar foramen has been observed in specimens of different Phocinae. We observed variation within an *Erignathus* individual, having an entepicondylar foramen in one humerus but not in the other (LD and CM, personal observation). It is not unlikely that this condition may vary in *Magophoca* n. gen. too. Unfortunately, the small sample size inhibits elucidating the default condition in the species. The absence or presence of an entepicondylar foramen impacts the overall morphology of the medial epicondyle in MNHN.F.PPI279.

The medial margin of the medial epicondyle on MNHN.F.PPI279 is straight and vertical (i.e., proximodistally oriented) in anterior view, but it does not extend high, proximally. Among other Monachinae, these conditions vary between different taxa. The morphology of the medial epicondyle in *Magophoca* n. gen. conforms with that of *Acrophoca*, and *Piscophoca*. The medial epicondyle is rounded in anterior view, or widest proximally and tapering distally in other extant and extinct Monachinae.

As in other Phocidae, the coronoid and olecranon fossae are shallow in *Magophoca brevirostris* n. gen., n. sp. The dis-

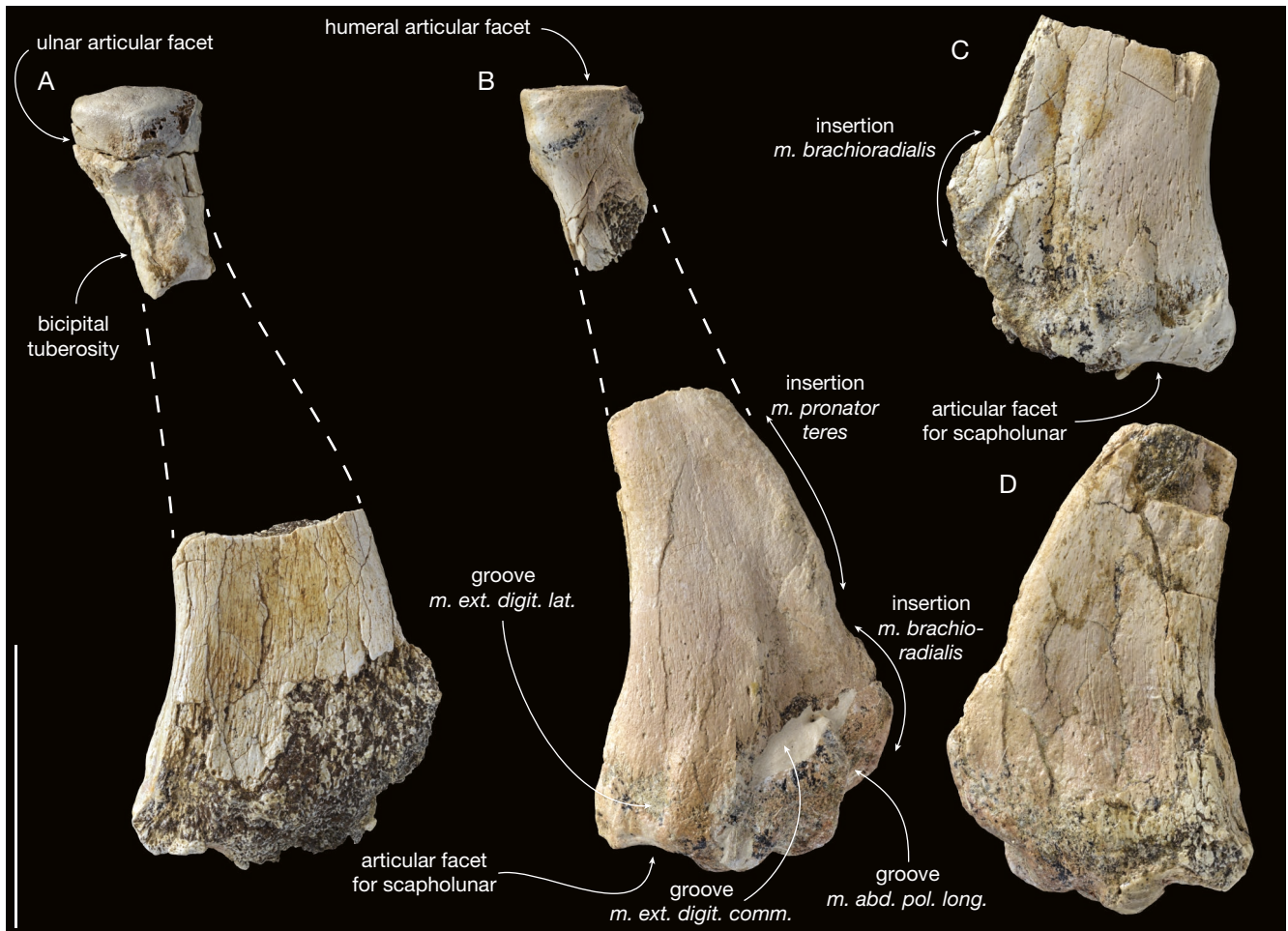


FIG. 28. — Radii of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, left radius in medial view; **B**, right radius in lateral view (both missing part of their diaphysis); **C**, distal portion of the left radius in lateral view; **D**, distal portion of the right radius in medial view. Dashed lines aid in visualizing the overall shape of the radius. Abbreviations: *m. abd. pol. long.*, musculus abductor pollicis longus; *m. ext. digit comm.*, musculus extensor digitorum communis; *m. ext. digit lat.*, musculus extensor digitorum lateralis. Scale bar: 5 cm.

tal margin of the trochlea is slightly more strongly concave in *Magophoca* n. gen. than in other Monachinae. The distal margin of the trochlea, at the junction between the anterior and the posterior parts of the trochlea, features a right angle, in distal view. Among other Monachinae, this angle is right in *Callophoca*, *Frisiphoca aberrata* and *Monachus*; it is acute in *Ommatophoca*, and obtuse in all other Monachinae except *Homiphoca*, in which it is variable, being either acute, obtuse, or right (observations based on 10 specimens: MNHN.F.AFS29, AFS30, AFS31, AFS32, AFS34, three MNHN.F.AFS uncatalogued specimens; SAM-PQ-L 4638, 30235, 40969).

Radius (Figs 28; 29; Table 15)

For the holotype specimen MNHN.F.PPI276, the left and right radii are preserved but incompletely: the proximal epiphyses and distal halves are physically separated and the proximal part of the diaphysis lacks for both. Another referred, left, radius has been assigned to *Magophoca brevirostris* n. gen., n. sp.: MNHN.F.PPI280 (Fig. 29). The latter is subcomplete, only missing its posterior extremity. In addition to the humerus MNHN.F.PPI278, this specimen also includes two fragments

of the radius: a fragment of the proximal epiphysis of the right radius, and a pathologically deformed left distal epiphysis.

The articular facet for the humerus is rounded, medially and posteriorly smoothly curving into the articular facet for the ulna. This facet is lens-shaped and wrapped around the posteromedial margin of the proximal epiphysis. The lateral part of the ulnar facet contacts the humeral facet, thus differing from the condition in *Acrophoca* and *Piscophoca* in which a deep sub-horizontal notch separates the two facets laterally. In contrast, a condition like that of *Magophoca* n. gen. is present in *Homiphoca*.

The bicipital tuberosity is only little elevated and clearly separated from the proximal epiphysis. This tuberosity is located on the medial surface of the diaphysis (char. 69[0]). The latter condition varies among Monachinae: it is also located medially in other extinct Monachinae, such as *Acrophoca*, *Homiphoca*, *Messiphoca*, *Piscophoca*, *Pliophoca*, *Sarcodectes*; but it differs from extant Monachinae, in which this tuberosity is located posteromedially on the diaphysis of the radius.

The diaphysis of the radius of *Magophoca* n. gen. is transversely flattened. In lateral view, the diaphysis appears to widen

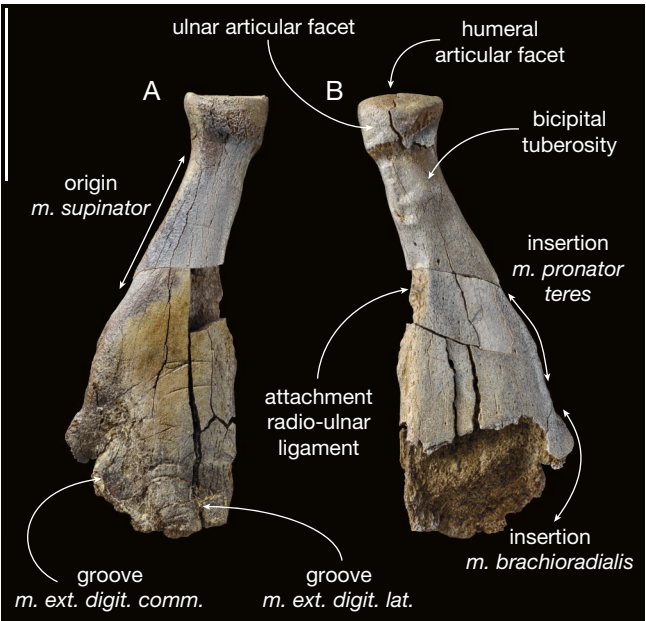


FIG. 29. — Right radius referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI280): **A**, lateral view; **B**, medial view. Abbreviations: **m. ext. digit comm.**, *musculus extensor digitorum communis*; **m. ext. digit lat.**, *musculus extensor digitorum lateralis*. Scale bar: 5 cm.

TABLE 15. — Measurements (in mm) of the radius of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: **n/a**, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)	
	left	right
Proximal epiphysis, height	n/a	12.5
Distal epiphysis, length	n/a	49.6
Distal epiphysis, length articular facet	n/a	22.0
Distal epiphysis, width articular facet	n/a	17.1
Diaphysis, least width	n/a	10.9

TABLE 16. — Measurements (in mm) of the ulna of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: **e**, estimate for a character due to minor damage; **n/a**, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)	
	left	right
Overall, total length	n/a	160.9
Overall, length from proximal tip to oblong rugosity	38.4e	37.3
Sigmoid facet, length	n/a	106.9
Greater sigmoid cavity, height	n/a	n/a
Greater sigmoid cavity, width	n/a	n/a
Lesser sigmoid cavity, height	n/a	16.7
Lesser sigmoid cavity, width	n/a	13.7
Oblong rugosity, width of diaphysis at the level of the oblong rugosity	n/a	12.8e
Oblong rugosity, breadth of the diaphysis at the level of the oblong rugosity	n/a	27.0e
Olecranon, length of the crest	57.3e	n/a
Anconeal tuberosity, width across	17.6	n/a

very gradually. On the posterior margin of the diaphysis, is the attachment area for the radio-ulnar ligament. This insertion area is slightly concave just distal to the bicipital tuberosity, but transitions into a faintly convex rugosity more distally.

The development of the origin and insertion areas for *m. supinator*, *m. pronator teres*, and *m. brachioradialis* on the anterior margin of the diaphysis corresponds with the condition in other Phocidae, with the exception of the extant Lobodontini (see Muizon 1981): the insertion area for *m. pronator teres* forms a low prominence, in accordance with other Phocidae, except extant Lobodontini. The prominence for the insertion of *m. brachioradialis* forms a distinctly convex tuberosity in lateral view, in *Magophoca* n. gen. Compared to other extinct and extant Monachinae, the insertion area for *m. brachioradialis* is located rather distally on the diaphysis.

On the lateral surface of the distal part of the diaphysis, the grooves for the passage of tendons are easily discernible. The grooves for the tendons of *m. extensor digitorum lateralis* and *m. extensor digitorum communis* are wide, shallow for the former and well-outlined and moderately deep for the latter. A strong development of the groove for *m. extensor digitorum communis* unites *Magophoca* n. gen. with *Acrophoca* and *Piscophoca* (char. 69[1]). The groove for the tendon of *m. abductor pollicis longus* at the anterior margin of the diaphysis is deep and laterally covered by a bony lip. The condition of the latter follows the condition of the extinct *Acrophoca* and extant Lobodontini. The distal extremity of the radius bears a strongly concavoconvex articular facet for the scapholunar.

Ulna (Figs 30; 31; Table 16)

A partial left and right ulna are preserved for the holotype MNHN.F.PPI276 of *Magophoca brevirostris* n. gen., n. sp. For the left ulna, only a severely abraded proximal portion is preserved. For the right ulna, only the diaphysis with proximal and distal epiphyses is preserved, lacking the distolateral and distal portions. Associated with the referred radius MNHN.F.PPI280, there is also a right ulna. For the latter ulna, only the anterior half of the bone is preserved.

The ulna is fairly straight, only faintly curving posteriorly. This corresponds with most other Monachinae, with the exception of *Piscophoca* in which this curvature is more pronounced.

The transversely flattened olecranon process is strongly protruding. The proximal margin of the olecranon process is markedly concave. This results in an apparently less posterodistally slanting posterior part of the olecranon process than in other Phocidae. The only other phocids with such a strong concavity on the proximal margin of the olecranon process are *Homiphoca* and *Messiphoca*, and to a lesser extent *Piscophoca*. The anconeal process on the medial margin of the proximal tip of the olecranon process is prominent and little sloping distally in *Magophoca* n. gen. A prominent anconeal process is a characteristic shared with Phocinae and several other extinct Monachinae, such as *Acrophoca*, *Homiphoca*, *Messiphoca*, *Piscophoca*, and *Pliphoca*, but not with extant Monachinae in which the anconeal process is generally reduced. The trochlear notch terminates proximally in a distinct coronoid process. In the trochlear notch, the greater sigmoid cavity for articulation with the humerus forms a hori-

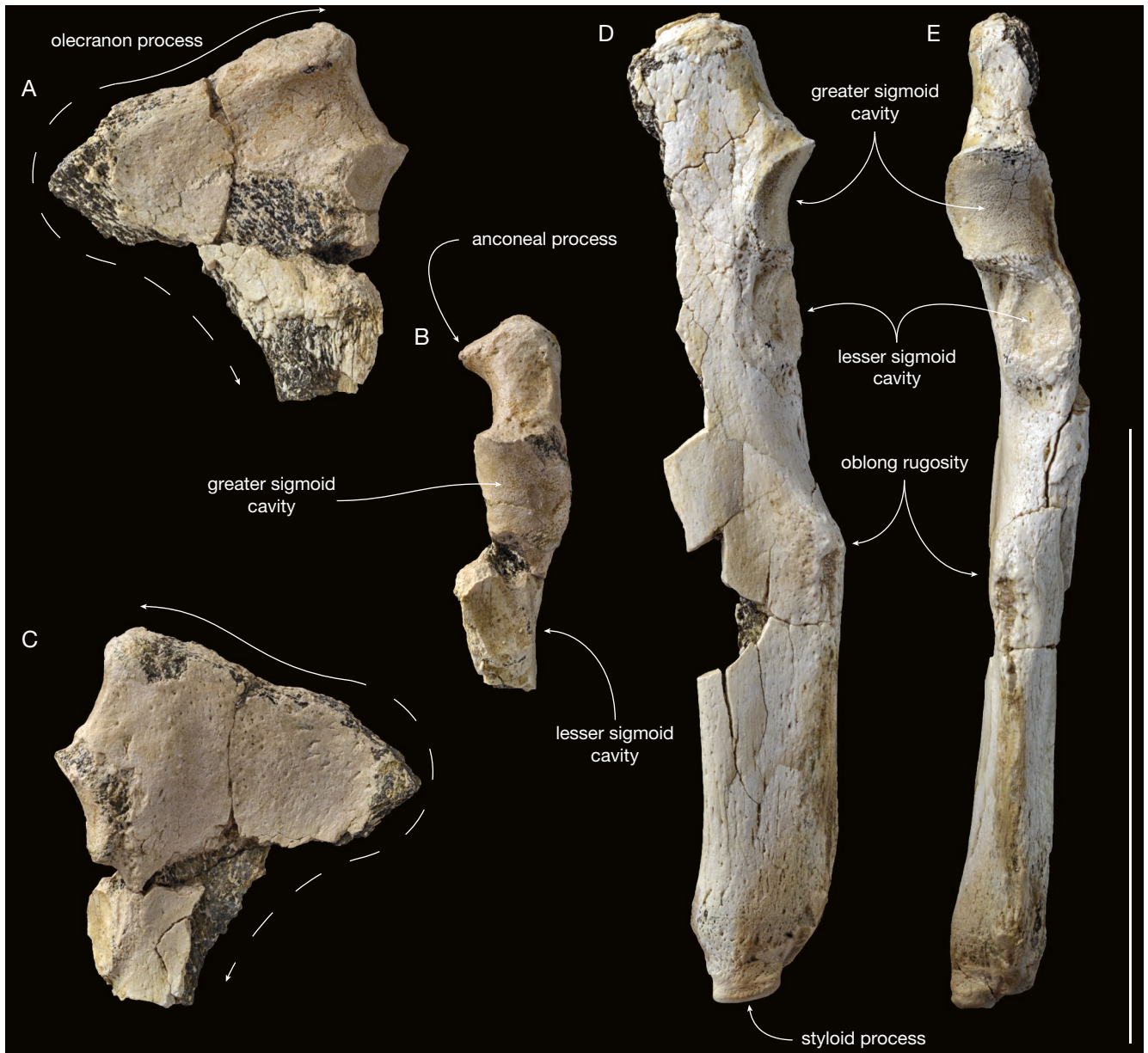


FIG. 30. — Ulnae of *Magophoca brevirostris* n. gen., n. sp. (holotype MNHN.F.PPI276): **A**, left ulna, with only the proximal half incompletely preserved, in medial view; **B**, the same ulna in anterior view; **C**, the same ulna in lateral view; **D**, right ulna, missing the olecranon process in lateral view; **E**, the same ulna in anterior view. Dashed lines in **A** and **C** aid in visualizing the overall shape of the olecranon process. Scale bar: 10 cm.

zontal saddle-shaped concavity that curves medially, distally, around the lesser sigmoid cavity. The lesser sigmoid cavity is flat and sub-circular, facing anterolaterally.

The diaphysis is transversely strongly flattened. On the anterior margin of the diaphysis, a prominent oblong rugosity for the interosseous ligament is located just distal to mid-length of the bone. At the distal extremity of the ulna, the styloid process is flattened, as in other Monachinae (char. 71[1]). This condition varies among Phocinae, between being either flattened or pointed in different taxa.

The flattened articular facet for the pyramidal, at the apex of the styloid process, is bean-shaped in distal view. This process is shifted posteriorly in relation to the long axis of the bone.

On the lateral margin of the styloid process, a laterally-facing concavity marks the articular facet for the cuneiform.

Carpus (Fig. 32)

Several bones of the carpus are known for *Magophoca brevirostris* n. gen., n. sp. Paratype MNHN.F.PPI269 includes a left scapholunar and MNHN.F.PPI295 includes the right scapholunar, trapezium, trapezoid and magnum.

Scapholunar

The bone bears the typical concavo-convex proximal articular surface for the radius as observed in Phocidae. As observed by Muizon (1981) the concave part of the articular surface

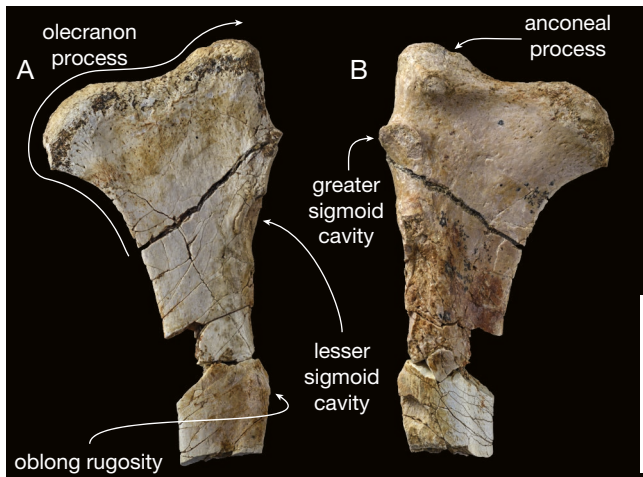


FIG. 31. — Right ulna referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI279): **A**, lateral view; **B**, medial view. Note the strong concavity of the proximal margin of the olecranon process. Scale bar: 5 cm.

is separated from the convex one by a distinct constriction in phocines whereas no constriction exists in monachines. In this respect, the condition of *Magophoca* n. gen. resembles that of other monachines. Furthermore, in phocines, the concave part is medial to the convex part; whereas it is anterior in monachines. In *Magophoca* n. gen., the concave part is anteromedial to the convex one, being intermediate between phocines and monachines. As observed in phocines the anterior tuberosity for ligament attachment is salient and pointed, but not wide and round as in monachines. Therefore, *Magophoca* n. gen. differs from *Acrophoca* since in the latter the condition of the last two features mentioned above is clearly monachine.

Distally the scapholunar bears four facets, from anterior to posterior: 1) a circular facet for the styloid process of the trapezium; this facet is separated by a faint ridge from the 2) oval-shaped trapezoid facet; 3) the small transversely elongated facet for the magnum, which is distinctly wider palmarly than dorsally and facing distally; and 4) the facet for the hamate, which is triangular, wider dorsally than palmarly and distinctly facing posteriorly. A pronounced carina separates the facets for the hamate and magnum.

In extant phocines, the trapezium facet is medial to the trapezoid one whereas in extant monachine it is anterior to it. In *Magophoca* n. gen., the facet is anterolateral to the trapezium facet is anteromedial to that for the trapezoid, as is observed in *Acrophoca*, being intermediate between the condition in extant phocines and monachines. In the latter the four distal facets of the scapholunar are anteroposteriorly disposed.

Trapezoid

This bone is triangular in proximal view and proximodistally short (proximodistal length is roughly half of the dorsal anteroposterior width) in *Magophoca brevirostris* n. gen., n. sp. The proximal articular facet is concavo-convex, triangular, and articulates with the scapholunar, posteriorly to the trapezium facet. Two facets are observed on the distal aspect of the bone.

Anteriorly, a saddle-shaped facet roughly ovoid to rectangular articulating with the trapezium; and posteriorly, a much smaller elongated roughly rectangular facet articulating with the anterodistal facet of the McII. Both facets are separated by an elevated crest and are approximately at a right angle.

Trapezium. The proximal part of the bone bears two facets. An anterior one strongly convex, and subvertical for the scapholunar; and a posterior one, smoothly concave and gently sloping posteriorly for the trapezoid. The contact of the two facets is a sharp carina, which forms a strongly elevated styloid process, the apex of which is located in the anterior region of the bone (in dorsal view). As noted by Muizon (1981), in extant monachines, the styloid process is very low and more resembles a crest, whereas in extant phocines it is strongly elevated as is observed on *Magophoca brevirostris* n. gen., n. sp. The condition of *Magophoca* n. gen. resembles that observed in *Acrophoca*. In extant monachines, the trapezoid facet is as deeply excavated as in *Magophoca* n. gen., whereas in extant phocines this facet is only slightly concave. Posterior to the trapezoid facet is a small circular facet that articulates with the small anterior circular facet of the McII, distal to that for the trapezoid. Both facets for the trapezoid and McII on the trapezium are approximately at a right angle. The McII facet of *Magophoca* n. gen. is much smaller than in *Acrophoca*, being at least twice as small.

In lateral view, the body of the bone is relatively longer (proximodistally) in extant monachines than in extant phocines. The condition of *Magophoca* n. gen. resemble that of phocines; it differs from that of *Acrophoca* and *Piscophoca*, which are intermediate between phocines and extant monachines.

The distal articular facet for McI in *Magophoca* n. gen. is trifoliate with deep lateral and medial notches. It differs from the cordiform facet observed in phocines and from the triangular one with rounded angles of extant monachines. It also differs from the condition in *Acrophoca* and *Piscophoca*, which feature a phocine-like cordiform facet.

Magnum. This bone is markedly triangular in anterior or posterior view in *Magophoca brevirostris* n. gen., n. sp. Its dorsal part is proximodistally very short whereas its palmar edge is much longer, a condition which resembles that observed in extant phocines and fossil monachines *Acrophoca*, and *Piscophoca*. As observed in the latter two, the articular facet for the scapholunar is strongly oblique, facing proximodorsally and anteriorly. However, in these two taxa, the condition is less pronounced since the lateral side of the magnum is higher than in *Magophoca* n. gen. and phocines, and the facet for the scapholunar is less oblique. In extant lobodontins, the magnum is roughly rectangular in anterior and posterior view (the lateral side being roughly as high as the medial one) and the scapholunar facet is roughly parallel to the distal facet for the McIII. In *Monachus* and *Pliophoca* the condition is intermediate between extant phocines and lobodontin monachines. The distal facet for the McIII of the magnum of *Magophoca* n. gen. is rectangular and smoothly concave.

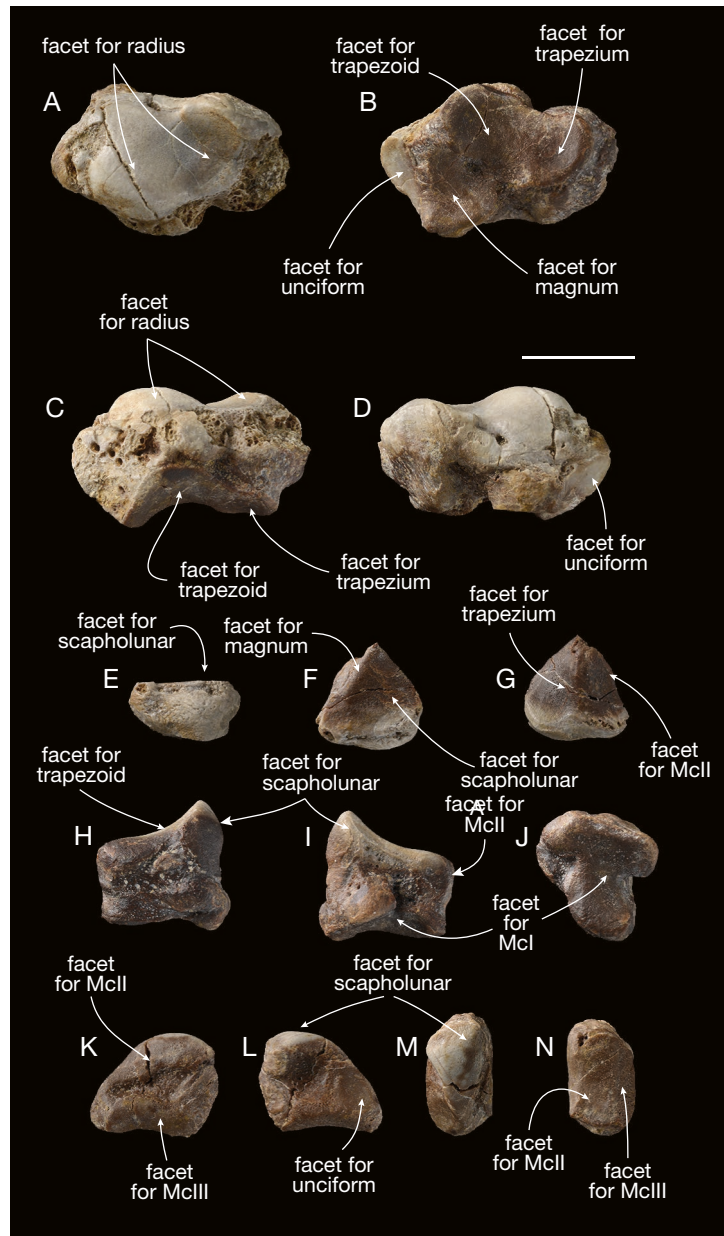


FIG. 32. — Carpals referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI295): **A**, right scapholunar in proximal view; **B**, the same scapholunar in distal view; **C**, the same scapholunar in lateral view; **D**, the same scapholunar in medial view; **E**, right trapezoid in dorsal view; **F**, the same trapezoid in proximal view; **G**, the same trapezoid in distal view; **H**, right trapezium in dorsal view; **I**, the same trapezium in palmar view; **J**, the same trapezium in mediolateral view; **K**, right magnum medial view; **L**, the same magnum in lateral view; **M**, the same magnum in proximal view; **N**, the same magnum in distal view. Scale bar: 1 cm.

Metacarpus (Fig. 33; Tables 17; 18)

Besides several carpal bones, MNHN.F.PPI295 includes the five metacarpals, four of them being complete or almost complete. Only McI is missing its distal end.

Metacarpal I (McI). Because this metacarpal is incomplete, its length cannot be compared to that of other phocids. However, as preserved it is roughly as long as the complete McII; the complete McI was therefore significantly longer than McII. Furthermore, an isolated McI (MNHN.F.PPI297, referred to *Magophoca brevirostris* n. gen., n. sp.) lacking its proximal epiphysis is 66 mm long. The length of the proximal epiphysis

(including the styloid process) of the McI of MNHN.F.PPI295 is approximately 11.5 mm. Therefore, because the two bones appear to be roughly of the same size, a reasonable estimation of the McI of *Magophoca* n. gen. could be $66 + 11.5 = 77.5$ mm. This metapodial was therefore approximately 29.7% longer than the McII (54.5 mm, see Table 17). An McI clearly longer than the McII is present in all monachines, both extant and extinct. This condition contrasts with that in phocines, in which the McI is roughly as long as, or only slightly longer than McII.

The proximal end of the McI of *Magophoca* n. gen. is well preserved and is clearly more quadrate than in *Piscophoca*

TABLE 17. — Relative lengths of Mcl and McII in fossil and extant Phocidae. The length of the incomplete Mcl of *Magophoca brevirostris* n. gen., n. sp., which lacks its distal extremity has been estimated by comparison with the Mcl of MNHN.F.PPI297 that is lacking the proximal epiphysis; addition of the length of the proximal epiphysis of MNHN.F.PPI295 to the length of the diaphysis and distal epiphysis of MNHN.F.PPI297; provides an estimate of the total length of Mcl. Furthermore, the distal epiphysis of MNHN.F.PPI295 is slightly eroded probably missing very little of the bone; therefore, the length of the McII of *Magophoca* n. gen. is also slightly estimated. e, estimate for a character due to minor damage. Measurements in mm.

	L Mcl	L McII	L McII/L Mcl
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI295)	77.5e	54.5e	0.703e
Other extinct Monachinae			
<i>Acrophoca</i> (MNHN.F.PPI273)	89.2	66.1	0.74
<i>Piscophoca pacifica</i> (MNHN.F.SAS564)	92.4	70.2	0.76
Extant Monachini			
<i>Monachus monachus</i> (MNHN-ZM-AC-A7953)	83.7	59.7	0.71
<i>Neomonachus tropicalis</i> (BMNH 1887.8.5.1)	90.7	65.5	0.73
Extant Lobodontini			
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1970-325)	161.2	105.5	0.645
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1884-1152)	144.4	99	0.685
<i>Leptonychotes weddellii</i> (IRSNB 15390)	100.5	65	0.646
<i>Leptonychotes weddellii</i> (IRSNB 1163)	89.5	61	0.681
<i>Lobodon carcinophaga</i> (IRSNB 1161)	93	58	0.623
<i>Lobodon carcinophaga</i> (MNHN-ZM-AC-A7951)	108.5	74.3	0.684
<i>Ommatophoca rossii</i> (IRSNB 15389)	93	58	0.623
<i>Ommatophoca rossii</i> (IRSNB 1164G)	103	63	0.611
Extant Phocinae			
<i>Erignathus barbatus</i> (MNHN-ZM-AC-A7949)	55	52.1	0.94
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1981-165)	47.9	47.5	0.991
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1978-48)	55	53.5	0.972
<i>Phoca vitulina</i> (MNHN-ZM-AC-1894-524)	49.5	48	0.970
<i>Phoca vitulina</i> (MNHN-ZM-AC-1983-792)	47.3	46.3	0.979
<i>Pusa hispida</i> (MNHN-ZM-AC-17951)	44.8	41.5	0.926

in which it is rectangular, being longer anteroposteriorly than wide dorsopalmarly. The condition in *Homiphoca* is intermediate between that of *Magophoca* n. gen. and *Piscophoca*. In contrast, the condition of *Magophoca* n. gen. resembles the quadrate morphology observed in *Hydrurga*. At the anterodorsal angle of the Mcl is a prominent styloid process for insertion of the *m. abductor pollicis longus* muscle. This process is more developed than in *Piscophoca* and much more than in *Acrophoca* (MNHN.F.PPI273), *Homiphoca*, *Monachus*, and *Neomonachus* (it is barely present in the latter). The larger styloid process of the Mcl of *Magophoca* n. gen. would indicate a stronger and more active muscle. Because the contraction of the *m. abductor pollicis longus* stretches the flipper, this movement should be more efficient in *Magophoca* n. gen. than in other monachines, fossil and extant. In extant lobodontins, the styloid process is very reduced; it is almost absent in *Hydrurga*.

Metacarpal II (McII). This metacarpal is almost complete in MNHN.F.PPI295, only missing some fragments of the diaphysis and being slightly eroded at its proximal articulation. However, these deteriorations do not prevent from measuring the length and distal width of the bone.

On the proximal extremity of the bone, the articular facet for the trapezoid is sloping anterodistally and is at an angle of approximately 51° to the length of the bone. This angle is 45° in *Piscophoca* (MNHN.F.SAS501), 57° in *Acrophoca* (MNHN.F.SAS563). In *Homiphoca* the angle is 88° and the sloping of the facet is more reduced than in the Peruvian monachines; whereas in *Monachus* the angle is 28° and the facet is subvertical.

On the anterodorsal region of the proximal extremity of McII is a strong tubercle, just distal to the facet for the trapezium; this tubercle probably received the insertion of one of the two radial tendons of the *m. extensor digitorum lateralis* muscle (Howell 1929; Piérard 1971). Posteroproximally to this tubercle is a rugose area, which could also receive part of this tendon or simply an interosseous ligament between McII and McIII. The distal extremity of the McII is dorsopalmarly flattened as is observed in all monachines, thus differing from the roughly quadrate morphology observed in phocines. On MNHN.F.PPI295 the palmar keel is poorly preserved but was more salient distally than in the other monachines extant and fossil (e.g., *Acrophoca*, *Homiphoca*, and *Piscophoca*).

Metacarpal III (McIII). This metacarpal is distinctly shorter than McII as observed in all Phocidae. However, the length difference between McII and McIII greatly varies among phocines. Table 18 shows that the ratio L McIII/ L McII in *Magophoca* n. gen. is similar to that observed in *Monachus*, higher (i.e., McIII is proportionally shorter as compared to McII) than in *Piscophoca*, most extant lobodontins and extant phocines except *Erignathus* in which it is lower (i.e., McIII is proportionally longer as compared to McII).

On the anterior and dorsal angle of the proximal end of the McIII is a circular facet which articulates with the postero-dorsal facet of the proximal end of the McII. Posterior and distal to this facet, on McIII is a salient rugose area probably for insertion of the posterior radial tendon of the extensor digitorum lateralis muscle as observed in *Phoca* (Howell 1929) and *Leptonychotes* (Piérard 1971). On the distal extremity, the palmar keel is slightly damaged but appears to be more prominent than in *Piscophoca* and much more than in *Homiphoca*. As is observed in *Piscophoca*, the distal extremity is less flattened dorsopalmarly than in *Homiphoca* and extant monachines. In distal view, its morphology is intermediate between the sub-circular contour of phocines and the planar shape of other monachines.

Metacarpal IV (McIV). This metacarpal is slightly shorter than the McIII, and slightly recurved anteriorly. It articulates with the Mc III with a circular antero-proximo-dorsal facet and posteriorly with an elongated oval-shapes facet with the McV. The proximal articular facet for the with the unciform, is

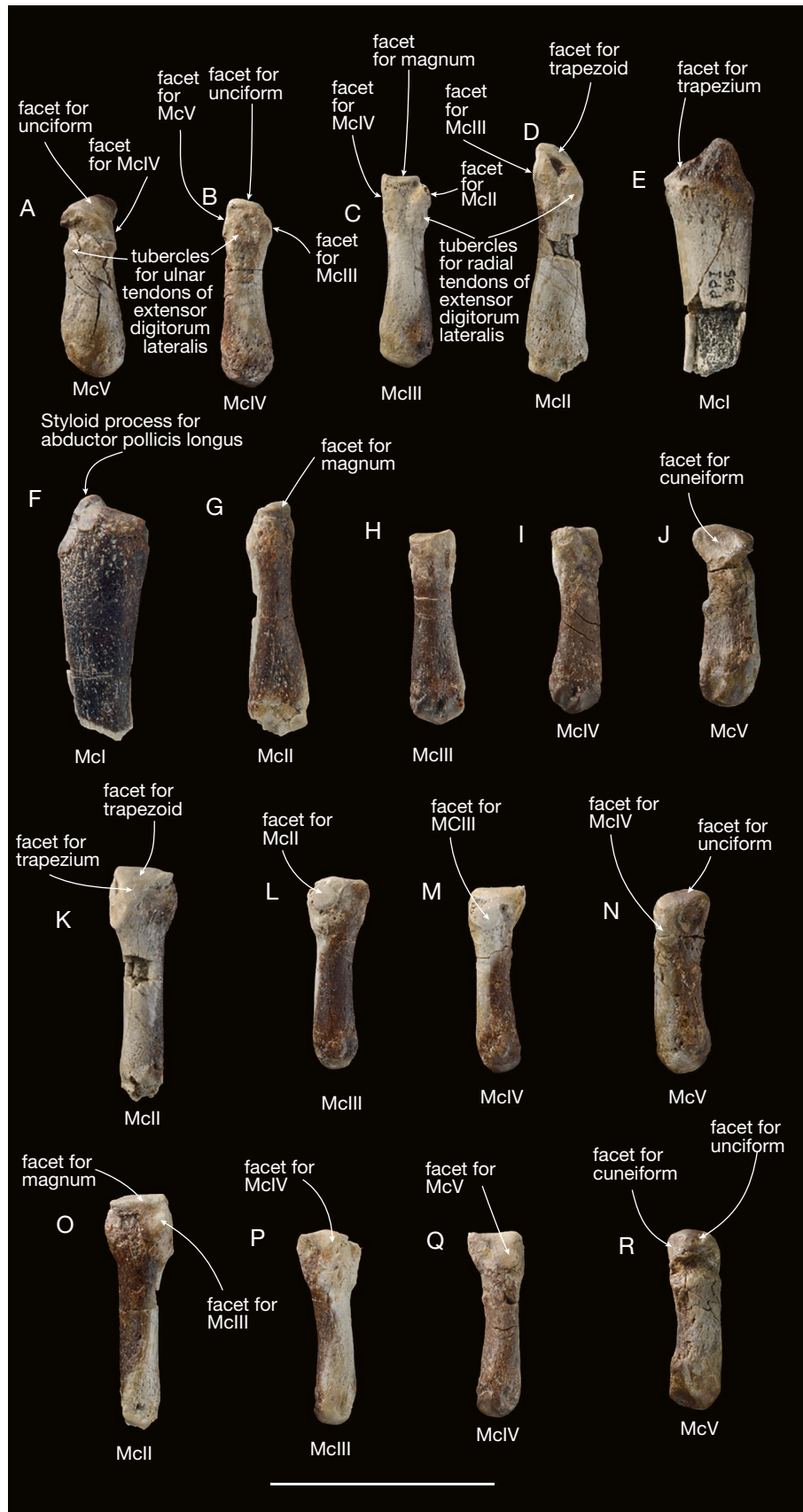


FIG. 33. — Metacarpals referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI295): **A–E**, right McV to McII and left MCI in dorsal view (the latter is reversed on the figure in order to fit the other metacarpals which are all from the right manus; **F–J**, the same metacarpals, but inverted, in ventral view; **K–N**, right McII to McV in medial view; **O–R**, the same in lateral view. Abbreviations: **m. ext. digit. lat.**, *musculus extensor digitorum lateralis*; **tubs.**, tubercles Scale bar: 5 cm.

TABLE 18. — Relative lengths of McII and McIII in some extant and extinct phocids. Measurements in mm.

	L McII	L McIII	L McIII/L McII
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI295)	53.8	44.5	0.827
Other extinct Monachinae			
<i>Piscophoca pacifica</i> (MNHN.F.SAS501)	75	56.4	0.75
Extant Monachini			
<i>Monachus monachus</i> (MNHN-ZM-AC-A7953)	59.61	49.1	0.823
<i>Neomonachus tropicalis</i> (BMNH 1887.8.5.1)	65.5	50.9	0.777
Extant Lobodontini			
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1970-325)	105.5	71.2	0.674
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1884-1152)	99	69	0.696
<i>Leptonychotes weddellii</i> (IRSNB 15390)	65	47	0.723
<i>Leptonychotes weddellii</i> (IRSNB 1163)	61	44	0.721
<i>Lobodon carcinophaga</i> (MNHN-ZM-AC-A7951)	74.3	59.8	0.804
<i>Lobodon carcinophaga</i> (IRSNB 1161)	58	41	0.706
<i>Ommatophoca rossii</i> (IRSNB 15389)	58	47	0.746
<i>Ommatophoca rossii</i> (IRSNB 1164G)	63	53	0.841
Phocinae			
<i>Erignathus barbatus</i> (MNHN-ZM-AC-A7949)	51.94	48.6	0.935
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1981-165)	47.5	35.6	0.749
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1978-48)	53.5	38.6	0.721
<i>Phoca vitulina</i> (MNHN-ZM-AC-1894-524)	47.5	36.9	0.776
<i>Phoca vitulina</i> (MNHN-ZM-AC-1983-792)	46.3	35.6	0.768
<i>Pusa hispida</i> (MNHN-ZM-AC-17951)	41.5	32.2	0.776

elongated and rectangular, being twice as long dorsopalmarly than wide anteroposteriorly. On the posterodorsal angle of the proximal end of the bone is a rugose area, almost a tubercle probably for insertion of the one of the two ulnar tendons of the *extensor digitorum lateralis* muscle. The distal extremity of McIV is almost quadrate and its palmar keel is very salient distally and palmarly.

Metacarpal V (McV). This metacarpal is the shorter of the hand, although only slightly shorter than McIV. As usual in phocids it is more massive than the other metacarpals. Its proximal extremity bears, anteriorly an elongated facet for articulation to the McIV. Proximal to this facet is a dorso-palmarly elongated facet for articulation with the unciform, and posterior to the latter is a strongly concave facet for the cuneiform. This latter facet clearly differs from that in *Acrophoca* and *Piscophoca*, in which it is very slightly convave or even, in some specimens, slightly convex. In contrast, it closely resembles the condition observed in *Homiphoca*, in which the facet is also markedly concave. On the posterior angle of the dorsal aspect of the proximal extremity of the McV, is a

salient rugose area probably for insertion of the second ulnar tendon of the *m. extensor digitorum lateralis* muscle. In distal view, the distal extremity is roughly quadrate to circular and not dorsopalmarly flattened as is observed in *Acrophoca*, *Homiphoca*, *Piscophoca* and extant monachines. The palmar keel is significantly developed and more resembles that observed in phocines than in other monachines, extant and extinct.

Anterior phalanges (Fig. 34)

Seven complete and partial anterior phalanges of MNHN.FPPI295 are associated to the carpus and metacarpus described above. One complete proximal phalanx is possibly referable to digit II since it appears to be slightly too short to belong to digit I and slightly too long to be referred to digits II or IV. It is slightly bent posteriorly as is observed on extant *Monachus*. Its proximal articulation bears a distinct median fossa for the palmar keel, which fits well the distal articulation with palmar keel of McII. The distal extremity of a proximal phalanx is referred to digit I (the largest digit of the hand) since it is slightly larger than the distal extremity of the proximal phalanx referred to digit II (the second largest digit of the hand). One partial proximal phalanx (missing its distal extremity) is probably referable to digit V. As the latter, it features a small anterior curvature. Its proximal articulation is deeply concave and do not present a median fossa for the palmar keel as observed on the proximal phalanx referred to digit II. This condition fits with McV, the distal articulation of which is very globular with a palmar keel located more palmarly and proximally than on the other metacarpals. Two complete middle phalanges could belong to digit III (for the longer) and IV (for the shorter). Their proximal articulations are slightly bi-concave, a morphology compatible with the bi-lobated distal articulation of the corresponding proximal phalanx. Two ungual phalanges are known, both missing the distal extremity of the bony claw. The dorsal wall of the sheath in which the horny claw inserts is interrupted and the dorsal aspect of the bony claw is visible dorsally up to the proximal end of the phalanx. A dorsally open bony sheath is also present in *Monachus* and extant lobodontins, whereas it is continuously closed in *Erignathus* and *Phoca*, although in the latter some variation exists since the sheath may in some cases be slightly open dorsally. On the only anterior ungual phalanx known in the holotype of *Acrophoca* the bony sheath is continuously closed around the bony claw. A similar condition is also observed in *Homiphoca*. In all phocines the bony sheath is also continuously closed (with some possible variation as mentioned above).

PELVIC GIRDLE AND HIND LIMB

Innominate (Fig. 23; Table 19)

For the holotype of *Magophoca brevirostris* n. gen., n. sp., both left and right innominates are preserved, diagenetically fused with the sacrum. For both innominates, the dorsal portion of the post-acetabular area is either incompletely preserved (right) or missing (left). The acetabular area and ilium of the right innominate is fairly completely preserved. For the left innominate, only the anteroventral portion of the innominate is not completely abraded.

TABLE 19. — Measurements (in mm) of the innominate of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). e, estimate for a character due to minor damage.

Character	MNHN.F.PPI276 (holotype, left)
Acetabulum, height	28.1
Acetabulum, length	26.8
Acetabulum, depth	15.0e
Acetabulum, height of innominate across	52.4
Obturator foramen, length	80.9
Obturator foramen, height	34.8e
Ilium, length of iliac crest between anterodorsal and anteroventral processes	63.7
Ilium, length of lateral surface between acetabulum to middle of iliac crest	48.2

The ilium is anteroposteriorly short, less than 40% of the length of the postacetabular region. Among other Monachinae, the relative length of the ilium is comparable to that of *Magophoca* n. gen. in most other taxa, with the notable exception of Monachini and *Piscophoca*.

The degree of the lateral eversion of the ilium of the holotype of *Magophoca* n. gen. is estimated to be approximately 65°. Because the innominates are still in contact with the sacrum, and slightly displaced, measuring the exact angle of the lateral eversion of the ilium is difficult. The estimated angle of 65° corresponds with the general condition in Monachinae. Qualitatively observed by Muizon (1981), Dewaele *et al.* (2017b) provide a preliminary quantitative analysis showing that the lateral eversion of the ilium is statistically significantly more pronounced in Phocinae than in Monachinae, despite the slight overlap in ranges. With a lateral eversion of approximately 65°, the lateral eversion of the ilium of *Magophoca brevirostris* n. gen., n. sp. falls well within the 95% confidence range for Monachinae, and just within the lower limits of the 95% confidence range for Phocinae, as presented by Dewaele *et al.* (2017b).

On the ilium, the gluteal fossa is weakly excavated (char. 76 [0]). The overall weak development of the gluteal fossa is a characteristic shared with other extinct Phocidae. Among extant Phocidae, a true gluteal fossa is absent in the phocine *Erignathus* and the monachine *Monachus*. The gluteal fossa is weakly excavated in other extant Monachinae and the phocine *Pusa sibirica*. The gluteal fossa is deep in all extant Phocinae, with the aforementioned exceptions of *Erignathus* and *Pusa sibirica*.

The iliac crest is roughly straight and the anterodorsal process prominently projects more dorsally than anteriorly. Although incomplete on the right ilium and abraded on the left, it is possible to observe that the anteroventral process prominently projects ventrally with respect to the acetabulum, giving the ilium a faint wedge-shaped appearance. Many Phocidae exhibit such a wedge-shaped ilium. However, certain monachine taxa have an ilium that can be considered to be ‘slanted ventrally’ or ‘slanted dorsally’. The ilium is ‘slanted ventrally’ if the anterodorsal process is directed rather anteriorly than anterodorsally. This is the case for *Acrophoca*, *Homiphoca*, and



FIG. 34. — Anterior phalanges referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI295): **A**, proximal phalanx of right digit I in dorsal view; **B**, **C**, intermediate phalanges of digit II, II or IV; **D**, ungual phalanx of digit I (?) missing the apex of the claw. Scale bar: 2 cm.

Monachini. The ilium is ‘slanted dorsally’ if the anteroventral process is directed rather anteriorly than anteroventrally, as in *Ommatophoca*. The ilium of *Magophoca* n. gen. is slanted neither ventrally nor dorsally.

On the ilium of *Magophoca* n. gen., the anteroventral process only slightly project anteriorly as compared to the anterodorsal process (char. 78 [1]). This condition is intermediate between the condition in other Monachinae and Phocinae: in other Monachinae, with the exception of *Mirounga* and *Ommatophoca*, the anteroventral and anterodorsal processes are almost at the same level, anteriorly; in Phocinae, and *Mirounga* and *Ommatophoca*, the anteroventral process is located well anterior to the level of the anterodorsal process.

The anterodorsal process on the ilium of *Magophoca* n. gen. forms an acute angle in lateral view. Among other Phocidae, this angle varies from an acute angle in Phocinae and in *Mirounga* and extant Lobodontini, a right angle in *Acrophoca*, and an obtuse angle in other extant Monachinae, and the extinct monachines *Homiphoca* and *Piscophoca*.

The posterodorsal process is anteroposteriorly broad, located posterior to the level of the blunt posteroventral process. Both are fairly well developed. Among Monachinae, a well-developed posterodorsal process is a characteristic shared with Phocinae, the extant monachines *Mirounga*, Monachini, and the extinct monachine *Piscophoca*. A well-developed posteroventral process is a characteristic also present in Phocinae, *Kauas*, and Monachini (char. 79).

The iliopectineal eminence forms a distinct and prominent anteriorly-oriented hook for the origin of *m. psoas minor* (char. 80[0]). Combined with the posteroventral process of the ilium, this results in a strongly concave ventral margin of the ilium, for the origin of *m. psoas major*. This eminence is located ventral to the anterior half of the acetabulum. Among Monachinae, a (moderately) well-developed iliopectineal eminence is a characteristic shared with *Acrophoca*, *Mirounga*, Monachini and *Piscophoca*. In *Homiphoca*, the development of the iliopectineal eminence is variable. Extant Lobodontini



Fig. 35. — Baculum of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): partial baculum, missing the proximal portion, in left lateral view, with the distal apex on the left. Scale bar: 10 cm.

and other extinct Monachinae, lack an iliopectineal eminence, or have an iliopectineal eminence that is strongly reduced.

The acetabulum is large: the dorsal margin of the acetabulum contributes to the dorsal margin of the innominate. The acetabulum is deep and the margins are raised over the bone. The iliac branch of the pubis is slightly transversely flattened. Posteriorly, the ventral margin of the pubis flattens, i.e., expands slightly, transversely towards the pubic symphysis.

Baculum (Fig. 35)

A partial baculum is preserved for the holotype, confirming that the holotype represents a male individual. The preserved portion is long (+130.1 mm), slender and sub-triangular in cross-section and slightly curving dorsally. Given the scarcity of fossil seal bacula, comparisons are only possible with bacula from extant Phocidae. Unfortunately, the incompleteness of this specimen precludes any detailed comparison, especially considering that the baculum is subject to important ontogenetic changes (e.g. Morejohn 2001).

Femur (Fig. 36; Table 20)

Both left and right femora are preserved for the holotype, MNHN.F.PPI276. The holotype also includes one preserved patella. In addition, MNHN.F.PPI281, MNHN.F.PPI284, and MNHN.F.PPI289 are also referred to *Magophoca brevirostris* n. gen., n. sp. As in other Phocidae, the femur of *Magophoca* n. gen. is anteroposteriorly flattened.

The femoral head is markedly globular, as is observed in phocines contrasting with the condition in extant monachines. However, as compared to fossil monachines the head of *Magophoca* n. gen. is clearly more globulous than in *Homiphoca*, *Kawas*, and *Pliophoca*, and slightly more than in *Acrophoca*. The neck is moderately well-defined as is observed in *Acrophoca*, and *Kawas* but contrasting with the condition in *Homiphoca*, and extant Monachini which have a better-defined neck than in *Magophoca* n. gen. The neck of *Magophoca* n. gen. is distinctly less defined than in phocines except *Cystophora*) but much better pronounced than in extant Lobodontini and Miroungini.

The femoral head and neck are oriented proximomedially, as in other Phocidae, except for extant Lobodontini and the genus *Mirounga*, in which the head and neck are more proximally oriented. This may also be the case for the extinct monachine *Callophoca*, if the isolated femora assigned to the taxon in the past indeed represent *Callophoca* (Van Beneden 1877; Koretsky & Ray 2008; contra Dewaele *et al.* 2018b; Rule *et al.* 2020a; see comments on the humerus above in the

TABLE 20. — Measurements (in mm) of the femur of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276).

Character	MNHN.F.PPI276 (holotype)	
	left	right
Overall, length	107.9	109.1
Proximal epiphysis, width	60.2	57.7
Distal epiphysis, width	60.7	61.2
Head, width	23.4	22.6
Head, height	25.0	25.4
Neck, height	23.8	23.3
Greater trochanter, width	34.2	33.6
Greater trochanter, breadth	21.4	21.7
Diaphysis, minimum width	33.2	32.3
Diaphysis, minimum breadth	15.1	16.8
Distal condyles, width across	55.7	56.1
Intercondylar groove, width	11.6	12.0
Lateral condyle, width	22.9	23.6
Lateral condyle, height	24.7	25.7
Medial condyle, width	19.0	19.7
Medial condyle, height	22.7	22.5
Patellar facet, height	20.9	21.3
Patellar facet, width	23.7	23.3

present study). In extant Phocinae, the medial component of the orientation of the femoral head and neck is always greater than in fossil and extant monachines. In *Magophoca* n. gen., the fovea capitis is not defined on the femoral head.

The greater trochanter is roughly rectangular in anterior and posterior view, and oval in proximolateral view. Proximally, the greater trochanter extends more proximally than the femoral head. This has also been observed in Phocinae and extinct Monachinae (char. 81[2]). Among extant Monachinae, the greater trochanter is higher than the femoral head, only in *Monachus* and *Ommatophoca*. From the previously published literature, the exact orientation of the femur needed to assess this character remains unclear, thus, allowing interpretation. It remains difficult to find the exact orientation of the long axis of the femur independently. Therefore, we consider the long axis to be perpendicular to the line of the least transverse width of the diaphysis (Fig. 36).

On the posterior surface, the greater trochanter bears a deep trochanteric fossa (char. 82[0]). This fossa opens posteromedially and is covered proximally by a bony lip. Such a deep trochanteric fossa is a characteristic shared with Phocinae and extinct Monachinae (except for *Acrophoca* and *Pliophoca*). Apart from *Lobodon*, all extant Monachinae have no, or a strongly reduced, trochanteric fossa.

The narrowest part of the diaphysis is slightly proximal to mid-length of the bone.

The epicondylar crest on the medial margin of the femur has a sub-vertical and distinctly straight medial margin in posterior view. Proximally, this crest terminates near mid-length of the bone, and just distal to a nutrient foramen (char. 85[1]). This foramen is observed on both femora of the holotype (MNHN.F.PPI276) and on MNHN.F.PPI289; it is apparently absent in MNHN.F.PPI281 but could not be observed on the two other isolated femora available for this study (MNHN.F.PPI284 and 296) since this region of the bone

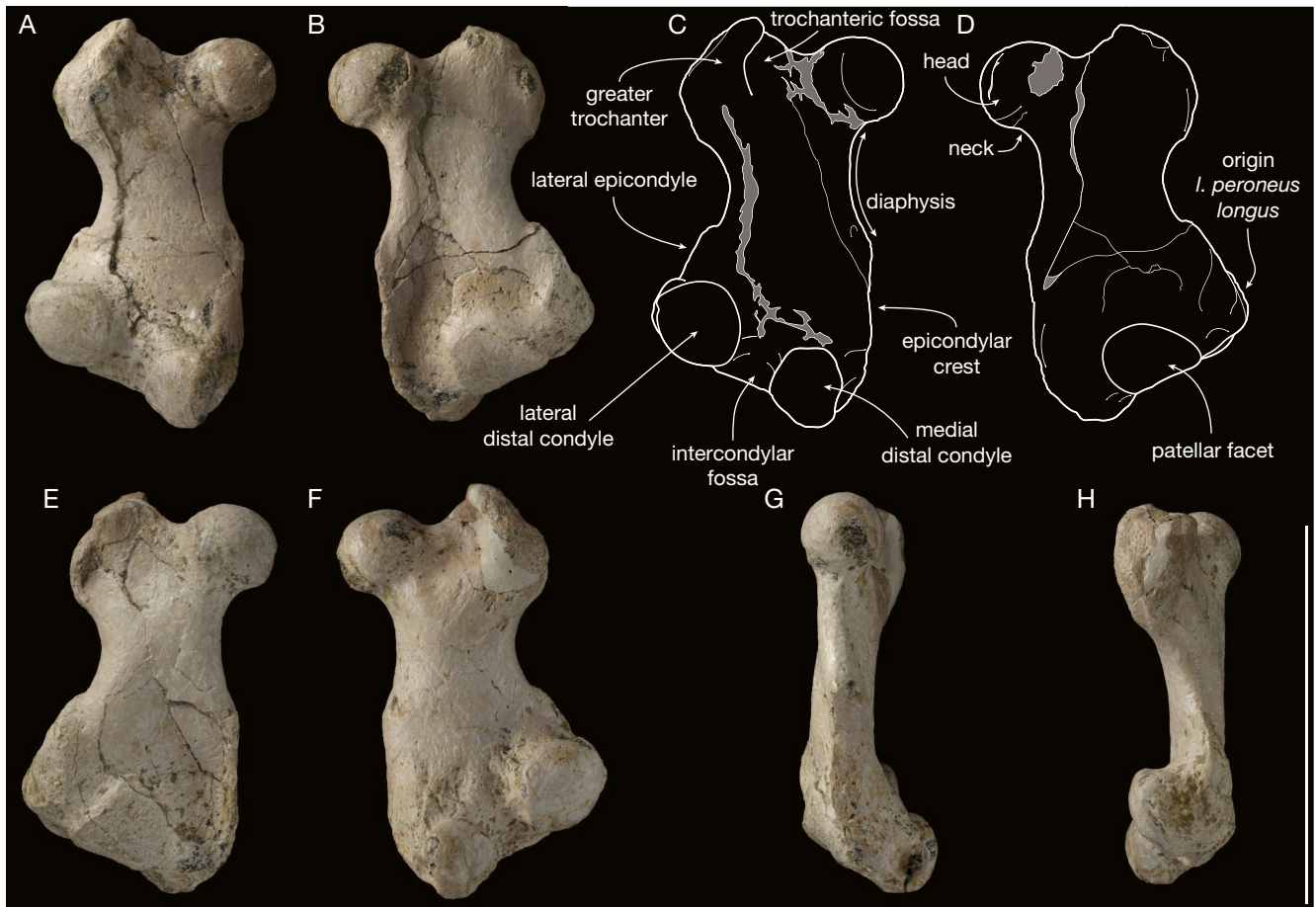


FIG. 36. — Femora of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, left femur in posterior view; **B**, the same femur in anterior view; **C**, labelled line drawing corresponding with **A**; **D**, labelled line drawing corresponding with **B**; **E**, right femur in anterior view; **F**, the same femur in posterior view; **G**, the same femur in medial view; **H**, the same femur in lateral view. Areas in gray in the line drawings indicate incompletely preserved parts, either abraded or fractured. Scale bar: 10 cm.

was damaged on these specimens. It is therefore not possible to determinate if this structure is a variation in *Magophoca* n. gen. or a specific feature of this taxon. A similar foramen is also present in *Kawas* (on the only known femur for this genus) but absent in *Homiphoca*. Distally, the epicondylar crest extends prominently, resulting in a lateral contortion of the distal epiphysis. This condition is not different from that in other Monachinae. By contrast, the development of the epicondylar crest is not as strong in Phocinae, resulting in the lack of such a distolateral distortion of the distal epiphysis in the latter subfamily.

The lateral epicondyle forms a short but distinct crest, proximally almost reaching just below the proximal tip of the epicondylar crest. As for the medial epicondyle, a strongly developed lateral epicondyle is a characteristic of Monachinae, separating the subfamily from Phocinae. A rugosity on the anterolateral margin of the distal epiphysis marks the origin surface for *m. peroneus longus* (char. 86[1]). This condition is like that in other Monachinae, except for the extinct *Callophoca obscura*, in which this surface is located laterally.

The patellar facet on the anterior surface of the distal epiphysis is raised and marginally wider than it is high. With

the exception of *Acrophoca*, this corresponds to the condition in other Monachinae. In *Acrophoca*, the patellar facet is as high as it is wide. In Phocinae, the patellar facet is higher than it is wide.

The distal condyles strongly differ in size, with the lateral condyle being significantly larger than the medial condyle (char. 84[1]). This condition has been observed in many extinct and extant Phocidae, across both subfamilies. Whereas the lateral condyle is gently convex, the convexity of the medial condyle is faint. In posterior view, the medial condyle is also contorted distally and laterally, due to the strong development and distal projection of the epicondylar crest.

Patella (Fig. 37; Table 21)

The patella (probably right) is notably higher (25.6 mm) than it is wide (23.1 mm), slightly tapering proximally (Fig. 37; Table 21). It is roughly symmetrical in anterior view. The articular facet for the femur is equally wide as high (19.7 mm), but also tapering proximally. The articular facet is slightly concave, and the anterior surface is strongly convex, giving the patella a crescent appearance in lateral view; with the maximum thickness of the patella (15.9 mm) offset distally.

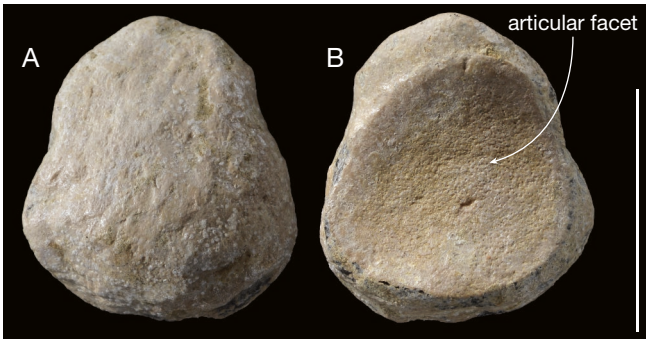


FIG. 37. — Right (?) patella of *Magophoca brevirostris* n. gen., n. sp. (holotype MNHN.F.PPI276): **A**, right patella in anterior view; **B**, the same patella in articular or posterior view. Scale bar: 2 cm.

Tibia-Fibula (Fig. 38; Table 22)

For the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, both left and right tibiae and fibulae are preserved. Notwithstanding fracturing, which is locally profound, both are complete. Both tibia and fibula are described together, because they are proximally fused (char. 88[1]). This is a characteristic uniting all Phocidae, with the exception of the extant monachine *Neomonachus schauinslandi*.

The proximal epiphysis of the fibula, fused to the proximal epiphysis of the tibia, bears no prominent features. The proximal epiphysis of the tibia is complex. It has two articular condyles for the femur, separated by the intercondyloid area. The latter is divided into an anterior and posterior pit. The two pits are separated by the intercondylar eminence, which is divided into lateral and medial intercondylar tubercles. These structures are distinctly elevated to a degree observed in phocines in contrast to the condition in extant monachines in which they are very low. The anterior pit forms a round concavity, anteriorly buttressed by the tibial tuberosity and the tibial crest. This tibial tuberosity on the anterior margin of the proximal epiphysis is triangular in outline and slightly higher than it is wide. This triangular shape conforms with *Acrophoca* and the extinct phocine *Nanophoca*. Other Phocidae have a rather transversely elongate oval tibial tuberosity. The posterior pit slopes into well-defined popliteal notch, which contrast with the very shallow structure observed in *Monachus*. The condyles are relatively concave more resembling the condition observed in phocine than in monachines. The lateral condyle is the larger of the two and faintly saddle-shaped: weakly concave in anterior view and weakly convex in lateral view. The smaller medial condyle is markedly saddle-shaped. Laterally, the medial condyle presents a distinct slope which forms the medial edge of the elevated intercondylar eminence

The diaphyses of the tibia and the fibula are relatively straight: the laterally sigmoidal curvature of the distal half of the diaphysis of the tibia is weak. This corresponds with the condition observed in other Monachinae, with the exception of *Acrophoca*, and Monachini in which this lateral curvature is more profound. In Phocinae, this curvature is also more prominent. The diaphyses of the tibia and fibula of *Magophoca* n. gen. are slender, compared to other Monachinae, and more conforming Phocinae.

TABLE 21. — Measurements (in mm) of the patella of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276).

Character	MNHN.F.PPI276 (holotype)
Overall, height	25.5
Overall, width	22.6
Articular facet, height	20.3
Articular facet, width	19.5

The diaphysis of the tibia of *Magophoca brevirostris* n. gen., n. sp. bears deep anterior and posterior tibial fossae. These fossae are typically monachine in being approximately equally developed. In Phocinae, the anterior tibial fossa is reduced or even absent and the posterior tibial fossa is extremely deep.

The distal extremity of the tibia, which bears the medial malleolus, has a smooth triangular articulation with the distal extremity of the fibula, which bears the lateral malleolus. The latter is notably thicker and wider than the diaphysis of the fibula. The articular facet for the astragalus on the medial malleolus is sub-triangular to sub-rounded in distal view and slightly concave. A medial lip and an anterior lip extend distal to the articular surface for the astragalus. The tendon grooves on the anterior and medial margins of the medial malleolus are strongly reduced. Muizon (1981) already noted this character in other extinct Monachinae, in contrast to extant Monachinae, in which these grooves are generally better developed.

On the lateral surface of the lateral malleolus, a thin but strongly-raised longitudinal ridge separates the tendon grooves for *m. peroneus brevis* and *m. peroneus longus*. Such a strong development of this ridge has been observed in Phocinae and the extinct Monachinae *Acrophoca*, *Homiphoca*, and *Piscophoca*, but not in other extinct and extant Monachinae.

Distally, the medial malleolus extends slightly more distal than the lateral malleolus.

The articular facet for the astragalus on the fibula is semi-circular to sub-oval and slightly concave.

Tarsus

Astragalus (Figs 39A-C; 40A, B; Table 23). For the holotype specimen of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, both left and right astragali are preserved. With the exception of slight abrasion of the caudal processes, both astragali are complete. Another well preserved right astragalus is known in MNHN.F.PPI282, only missing the lateral apex of the fibular facet.

The body (talus) bears the articular facets for the tibia and fibula. It is prominent and high. The tibial facet, medially, is sub-rectangular and strongly convex. On the medial margin of the tibial facet a deep fossa marks the medioventral margin of the facet. Such a fossa is also present in *Piscophoca* and to a minor extent in *Homiphoca*, but not in *Acrophoca*. The fibular facet, laterally, is sub-triangular and moderately concave. It extends laterally in a rounded and slightly upturned process. On the plantar aspect of the astragalus, the ectal facet is located ventral to the posterior part of the fibular facet. It is strongly concave and forms an elongated and oval-shaped facet. In distal view, the angle between the tibial and fibular

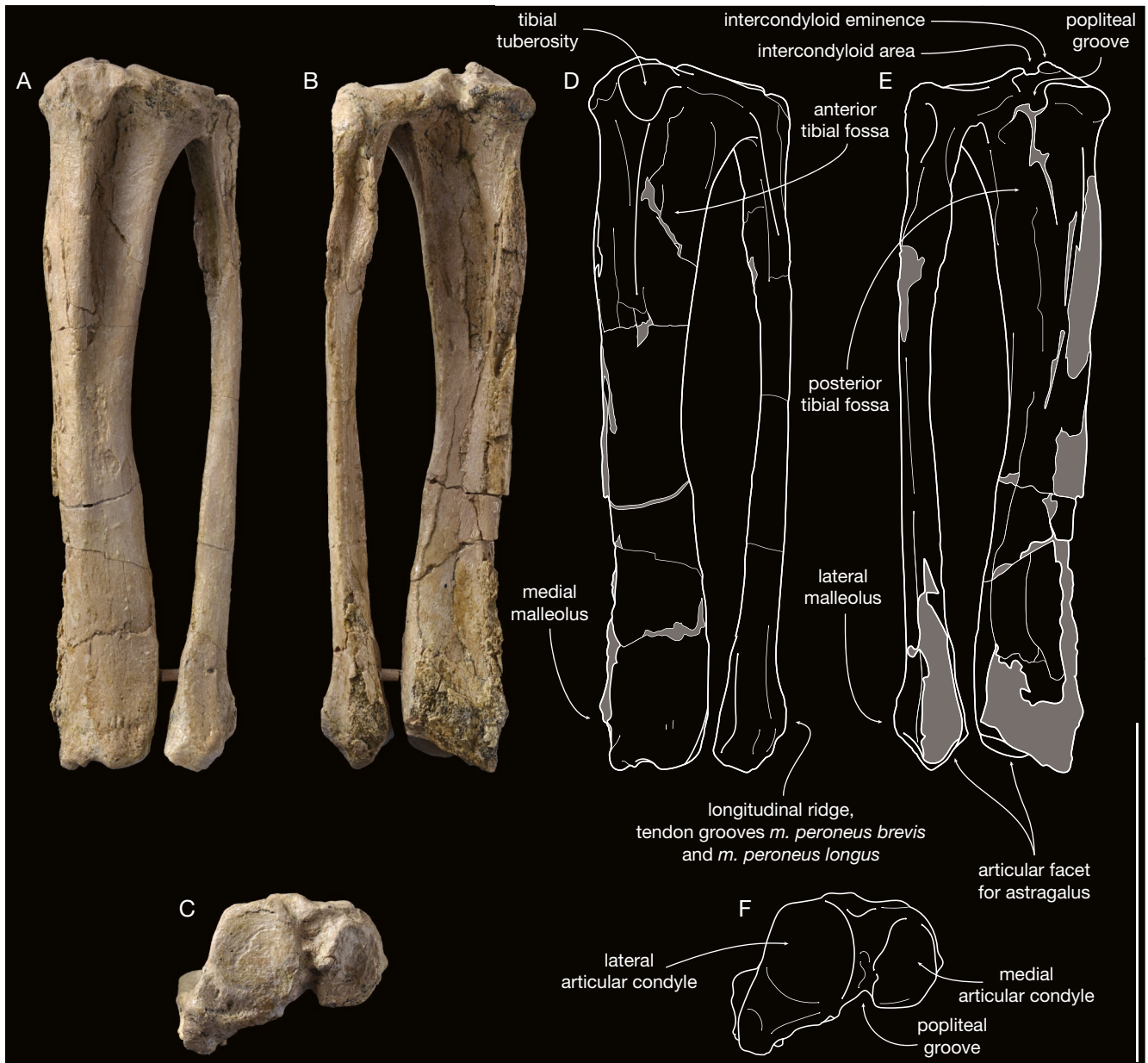


FIG. 38. — Left tibia and fibula of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, left tibia and fibula in anterior view; **B**, the same tibia and fibula in posterior view; **C**, proximal view of the same tibia and fibula; **D–F**, corresponding labelled line drawings. Areas in gray in the line drawings indicate incompletely preserved areas, either abraded or fractured. Scale bar: 10 cm.

facets is approximately right. This corresponds with many other extant and extinct Monachinae, with the exception of the extant Lobodontini and the extinct *Homiphoca*, in which this angle is obtuse, up to 120°. The neck is strongly reduced. It separates the talus from the head.

On the plantar aspect of the head, laterally, the sustentacular facet is elongate and narrow, widening distally, merging into the articular facets for the navicular and cuboid (char. 91[1]). This corresponds with Phocinae, most extinct Monachinae (e.g., *Homiphoca*, *Piscophoca*), and Monachini. In extant Lobodontini and *Mirounga*, as well as in *Acrophoca* and *Pliophoca*, the sustentacular facet is wide and short. The medial interarticular sulcus, which separates the sustentacular

facet from the proximal part of the navicular facet, is deep and wide. As in other Monachinae, with the exception of *Acrophoca*, a noticeable angulation marks the contact between the articular facets for the cuboid and the navicular. The articular facet for the navicular curves proximodorsally on the medial surface of the astragalus, terminating on a medial prominence at the ventral margin of the fossa below the tibial facet described above.

The caudal process is incompletely preserved on both astragali of the holotype but is perfectly preserved on MNHN.F.PPI.282. It is notably short compared to other Monachinae, except for *Acrophoca*, *Homiphoca*, *Lobodon*, and Monachini (char. 90[2]).

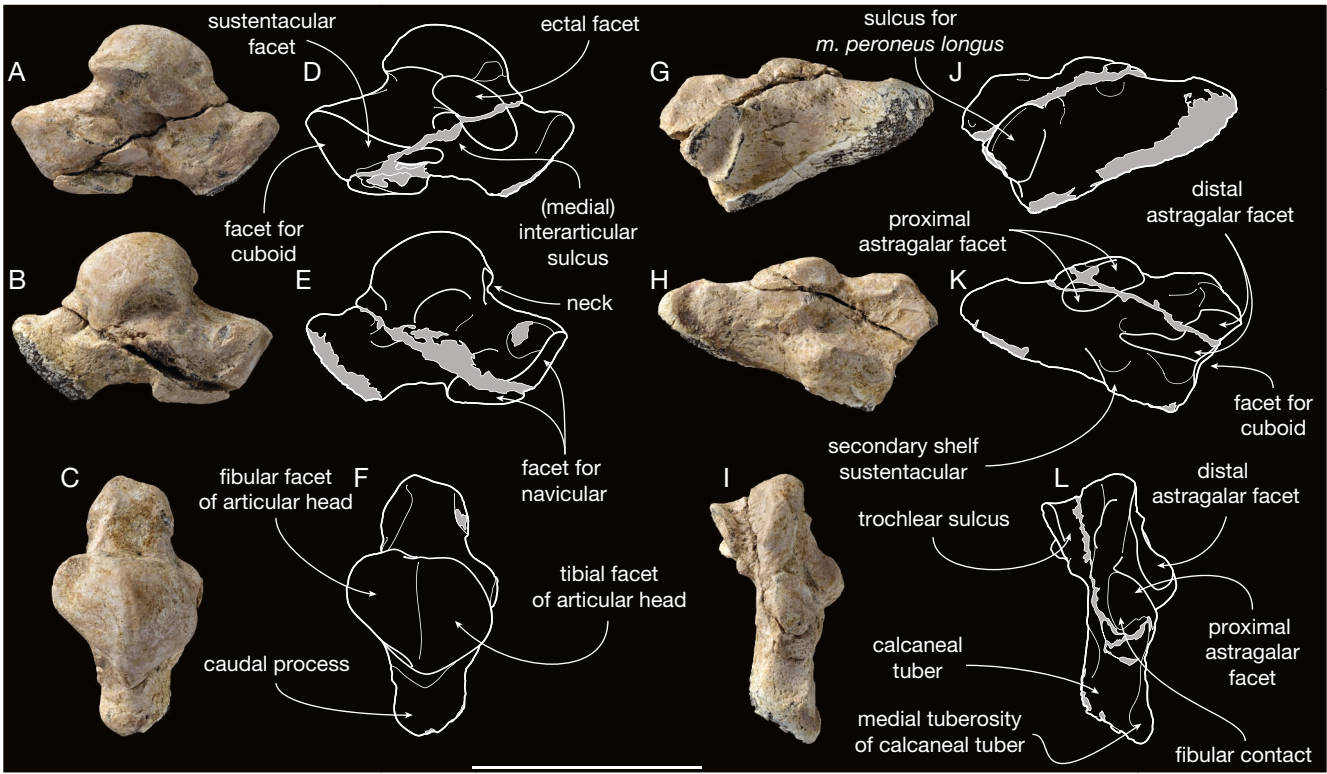


FIG. 39. — Left astragalus and calcaneum of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, astragalus in lateral view; **B**, the same astragalus in medial view; **C**, the same astragalus in proximal view; **D–F**, corresponding labelled line drawings; **G**, left calcaneum in lateral view; **H**, the same calcaneum in medial view; **I**, the same calcaneum in proximal view; **J–L**, corresponding labelled line drawings. Areas in gray in the line drawings indicate incompletely preserved areas, either abraded or fractured. Scale bar: 5 cm.

TABLE 22. — Measurements (in mm) of the tibia and fibula of *Magophoca brevirostris* n. gen., n. sp. Abbreviations: **e**, estimate for a character due to minor damage; **n/a**, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)		MNHN.F. PPI282
	left	right	right
Overall, length	224.4	237.2e	n/a
Proximal epiphysis, max. width	62.7	65.5e	n/a
Tibial plateau, width	51.7	51.7e	n/a
Diaphysis of the tibia, min. width	22.4	n/a	n/a
Diaphysis of the tibia, min. breadth	n/a	n/a	n/a
Diaphysis of the fibula, min. width	8.8	n/a	n/a
Diaphysis of the fibula, min. breadth	11.4	n/a	n/a
Medial proximal articular facet, width	19.9	n/a	n/a
Medial proximal articular facet, length	24.6	25.3	n/a
Lateral proximal articular facet, width	25.0	23.9	n/a
Lateral proximal articular facet, width	33.4	33.4	n/a
Intercondylar groove, min. width	5.8	7.4	n/a
Tibial tuberosity, width	15.7	17.1	n/a
Tibial tuberosity, length	17.1	17.7	n/a
Distal epiphysis of the tibia, width	34.9	33.2	36.0
Distal epiphysis of the tibia, breadth	28.7	26.0	30.6
Distal epiphysis of the fibula, width	22.5	19.8	n/a
Distal epiphysis of the fibula, breadth	26.7	27.3	23.4
Distal articular facet of tibia, width	20.3	20.1	25.1
Distal articular facet of tibia, breadth	20.0	21.3	29.4
Distal articular facet of fibula, width	16.9	15.3	n/a
Distal articular facet of fibula, breadth	21.9	21.3	22.0

Calcaneum (Figs 39G–I; 40C; Table 24). The left and right calcanea are both preserved for the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276. For the left calcaneum, the ventral portion is slightly abraded. The right calcaneum is missing its ventromedial half. A relatively well preserved right calcaneum is known in MNHN.F.PPI282.

The calcaneum is elongated and slightly longer than the astragalus (Table 23 vs Table 24). Among Monachinae, this is a character uniting *Magophoca* n. gen. with *Acrophoca* and *Piscophoca*. The astragalus and the calcaneum are of equal length in the other extinct monachines, *Homiphoca* and *Pliophoca*, and the astragalus is longer than the calcaneum in extant Monachinae. The height/length ratio of the calcaneum of *Magophoca* n. gen. is approximately 34.3 mm/62.6 mm = 0.548 and is within range of ratios observed in other extinct Monachinae, *Mirounga*, and Monachini (0.509–0.548). In extant Lobodontini, the calcanea are proportionally shorter and higher (0.583–0.633) (Muizon 1981: table 8)

On the medial surface, for the contact with the astragalus, the proximal astragalar facet is divisible in a discorectangular medial facet for articulation with the astragalus or ectal facet and a sub-triangular dorsal facet for articulation with the fibula or fibular facet (char. 92[1]). Both facets are at an obtuse angle of approximately 120°. This angle varies among Monachinae, ranging from an acute angle or closed parabolic shape, such

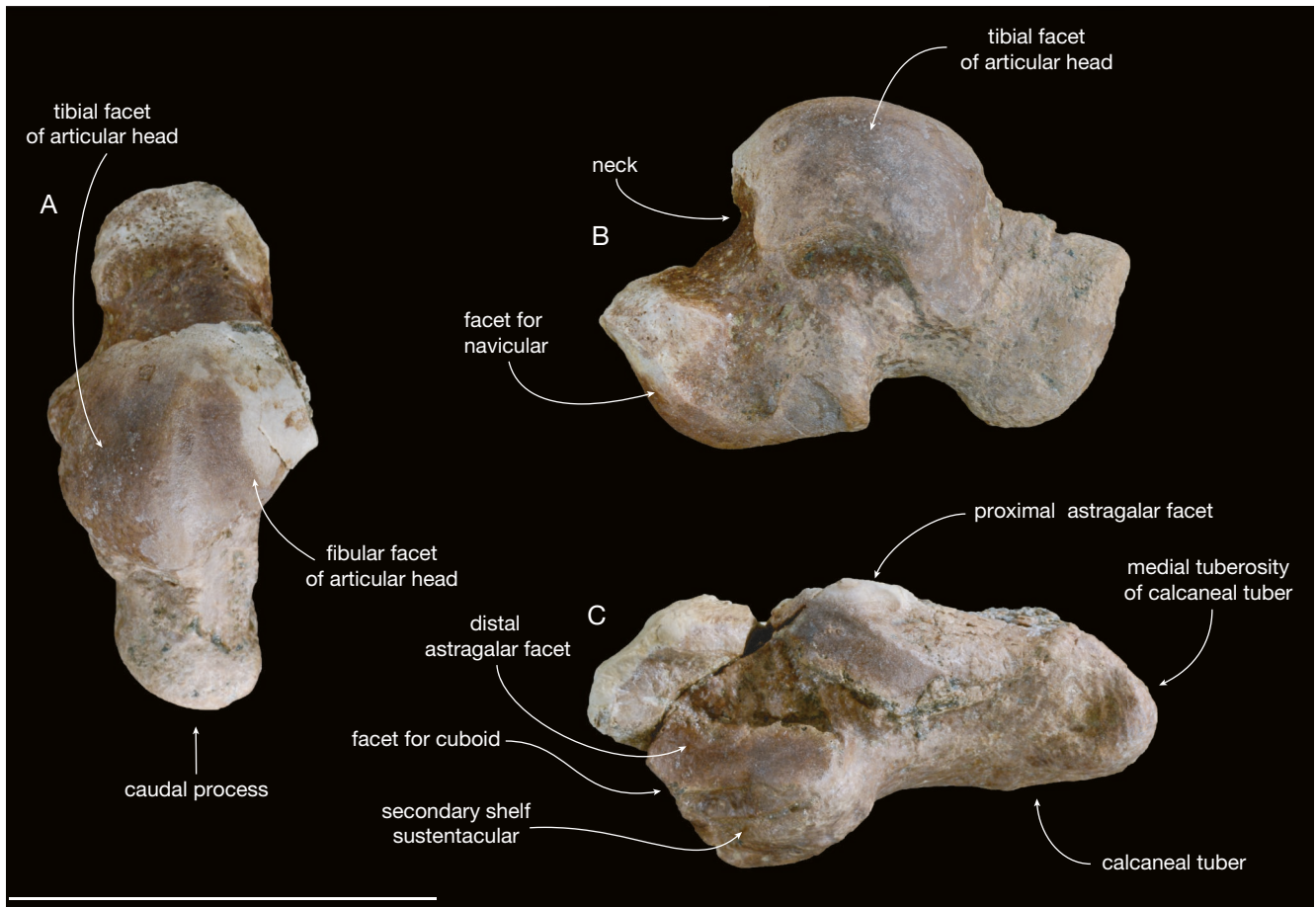


FIG. 40. — Right astragalus and calcaneum referred to *Magophoca brevirostris* n. gen., n. sp. (MNHN.F.PPI282): **A**, astragalus in proximal view; **B**, the same astragalus in medial view; **C**, calcaneum in medial view. Scale bar: 5 cm.

as, for instance, in *Acrophoca*, to a wide obtuse angle, such, as for instance, in *Homiphoca* and extant Lobodontini. The angle is obtuse (c. 120°) in *Magophoca* n. gen., but the fibular contact is also strongly reduced, in other extinct Monachinae and in the extant *Mirounga* and Monachini.

The sustentacular facet is long and strongly concave in *Magophoca* n. gen. It is proportionally as long as in *Homiphoca*, *Kawas*, and *Piscophoca*, and phocines and differs from the very short facet of *Acrophoca*, *Pliophoca*, and extant monachines. It significantly widens distally and its contact with the cuboid facet is proportionally longer than in other fossil monachines (e.g., *Acrophoca*, *Homiphoca*, and *Piscophoca*). Among extant lobodontins, the distal edge of the sustentacular facet is slightly shorter than the medial edge of the cuboid facet in *Leptonychotes*, whereas in *Hydrurga* both edges have the same length. The distal tip of the distal astragalar facet runs dorsally on the medial surface of the bone in *Magophoca* n. gen., as is observed in *Homiphoca* and *Piscophoca*, while it does not extend as far dorsal in *Acrophoca*, *Pliophoca* and extant Monachinae. The proximal portion of the distal astragalar facet is horizontal, resting on the blunt secondary shelf of the sustentaculum.

The sulcus for *m. peroneus longus* and the trochlear sulcus are well-outlined and prominent, as in other Monachinae. The sulcus for *m. peroneus longus* extends distal to the

TABLE 23. — Measurements (in mm) of the astragalus of *Magophoca brevirostris* n. gen., n. sp. Abbreviations: e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)		MNHN.F. PPI282
	left	right	right
Overall, length	59.8	59.9e	63.2
Overall, height	38.4	36.4	41.1
Caudal process, length	17.4	16.6e	17.3
Caudal process, width	15.7	n/a	17.5
Head, length	21.9	20.8	22.0
Head, width	20.3	20.6	21.1
Tibio-fibular head, length	31.9	32.8	30.0
Tibio-fibular head, width	27.8	28.1	n/a
Navicular facet, length	28.8	26.1	32.3
Sustentacular facet, length	n/a	25.0	25.5
Ectal facet, length	20.5	21.4	> 21.0
Ectal facet, width	9.7	8.9	9.0

cuboid facet and is proximally marked by a small laterally pointing tuberosity. The cuboid facet is semi-circular to weakly crescent shaped. The medial tuberosity of the calcaneal tuber is weakly pointed, extending further than the lateral margin.

TABLE 24. — Measurements (in mm) of the calcaneum of *Magophoca brevirostris* n. gen., n. sp. Abbreviations: e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured.

Character	MNHN.F.PPI276 (holotype)		MNHN.F. PPI282
	left	right	right
Overall, length	62.4	> 59.6	66.6
Overall, height	33.3e	n/a	n/a
Overall, maximum transverse width	30.4	n/a	n/a
Calcaneal tuber, length	21.9e	> 18.2	25.0
Calcaneal tuber, width	13.6	n/a	13.9
Cuboid facet, height	20.1	n/a	22.4e
Cuboid facet, width	15.5e	n/a	18.9e
Proximal astragalar facet, length	20.0	20.1	21.2
Proximal astragalar facet, width	8.8	8.9	8.5
Distal astragalar facet, length	26.0	26.9	—

Other tarsals (Fig. 41). For the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, left and right cuboids, naviculars and ectocuneiforms are preserved. Whereas the left cuboid and navicular are virtually complete, the plantar portions their right counterparts, are strongly abraded. Both ectocuneiforms are preserved but the medial portion of the left and the plantar portion of the right are missing. On MNHN.F.PPI282; the right navicular and cuboid are preserved, the latter being incomplete in its distolateral region.

Cuboid. The cuboid has a prominent convex facet for articulation with the calcaneum, proximally. This facet is transversely elongate, with a smoothly indented dorsal margin. This facet is roughly equidimensional in *Acrophoca*. Transition between the articular facet for the calcaneum and the navicular, medially, is smooth, whereas the facets are separated by a ridge in *Acrophoca*. Further medially, is an ovoid articular facet for the ectocuneiform, dorsally contacting the articular facet for the navicular. This facet does not extend onto the lateroplantar apophysis, as observed in other Monachinae, and in contrast to Phocinae. This lateroplantar apophysis is transversely elongate and is separated from the main bone by a deep groove. This groove conveys the tendon of *m. peroneus longus*. The distal tip of this apophysis is smooth, as in other Monachinae. In Phocinae, the distal tip of the apophysis of the cuboid bears a facet for articulation with the ventral portion of the proximal epiphysis of MtV. Distally, the articular facets for MtIV and MtV are merged into one large facet. This large facet is sub-rounded but medially invaginated.

Ectocuneiform. In its overall dimensions, the ectocuneiform is clearly monachine: with a height/length ratio of 0.62, the ectocuneiform of *Magophoca* n. gen. is proportionally elongate, as in other Monachinae (0.560-0.625), contrasting with Phocinae (0.694-0.714). In addition, the strong development of the plantar process follows the condition in other Monachinae too, while this process is less developed in Phocinae (Muizon 1981). On the distal margin, the concavity observed just dorsal to the plantar process in *Acrophoca* and *Piscophoca* is not observed in the ectocuneiform of *Magophoca* n. gen.

Navicular. The navicular articulates proximally with the astragalus, distally with the cuneiforms and laterally with the cuboid. In proximal view, the navicular forms a scalene right triangle with a vertical lateral margin and a horizontal plantar margin. The articular facet for the astragalus is smoothly curving, L-shaped, and slightly concave. The medial tip of the articular facet is raised proximally. The lateral articular facet is vertically elongate. The distal portion is slightly damaged.

Metatarsus (Fig. 42; Tables 25; 26)

All left metatarsals of the holotype of *Magophoca brevirostris* n. gen., n. sp., MNHN.F.PPI276, are preserved but in diverse conditions. Whereas MtI is virtually complete, MtIII largely misses its proximal epiphysis. In addition, the proximal portion of the right MtII is preserved too. Overall, the dimensions of the metatarsals of *Magophoca* n. gen. follow the conditions observed in other Monachinae, with MtI being by far the longest metatarsal, followed by MtV, then MtII, and MtIV; and MtIII being the shortest metatarsal and half the length of MtI (Table 25).

Metatarsal I (MtI). The first metatarsal is the longest of the pes, as usual in phocids. The MtI of *Magophoca brevirostris* n. gen., n. sp. is long and slender, to an extent greater than in most fossil and extant phocids. As shown on Table 26 below, it is proportionally much longer than in *Acrophoca*, *Homiphoca*, *Monachus*, *Neomonachus*, and *Pliophoca*. It is even proportionally slightly longer than in *Piscophoca* and than an isolated MtI from Antwerp Basin referred by Van Beneden (1877) to *Monotherium delognii*, a referral which is not ascertainable since this bone does not belong to the same individual as the holotype of that species (see Dewaele *et al.* 2018a). Besides of having similar proportions, this metatarsal is only 7% shorter than that of *Magophoca* n. gen. Among Monachinae, the MtI of Monachini (*Monachus*, *Neomonachus*, and *Pliophoca*) is shorter than in Lobodontini. Among Fossil Lobodontini, the shortest MtI are observed in *Acrophoca* and *Homiphoca*. Within extant Lobodontini the MtI of *Hydrurga* and *Leptonychotes* are relatively long, but in *Lobodon* and *Ommatophoca* individual variation exists (Table 26). Phocinae have relatively long MtI, except in *Erignathus*.

The MtI of *Magophoca* n. gen. is slightly arched laterally and only slightly flattened dorsoplantarly. The proximal facet for articulation with the entocuneiform is transversely elongated and slightly concave. Laterally, this facet transitions into the articular facet for MtII. In contrast to other extinct Monachinae, there is no clear ridge separating both and the transition is rather smooth, as in extant Monachinae. Although this margin is smooth, lacking a clear ridge, the proximal epiphysis of the MtI of *Magophoca* n. gen. has a distinct, proximally pointed, styloid apophysis, medioventrally, at the margin between the articular facets for the entocuneiform and the MtII. This apophysis is more prominent than in other Monachinae (except *Homiphoca*) and rather comparable to Phocinae and *Homiphoca*. The articular facet for MtII is convex and semi-cylindrical around the lateral margin of the proximal epiphysis. The articular facet for MtII is dorsoplantarly elongate.

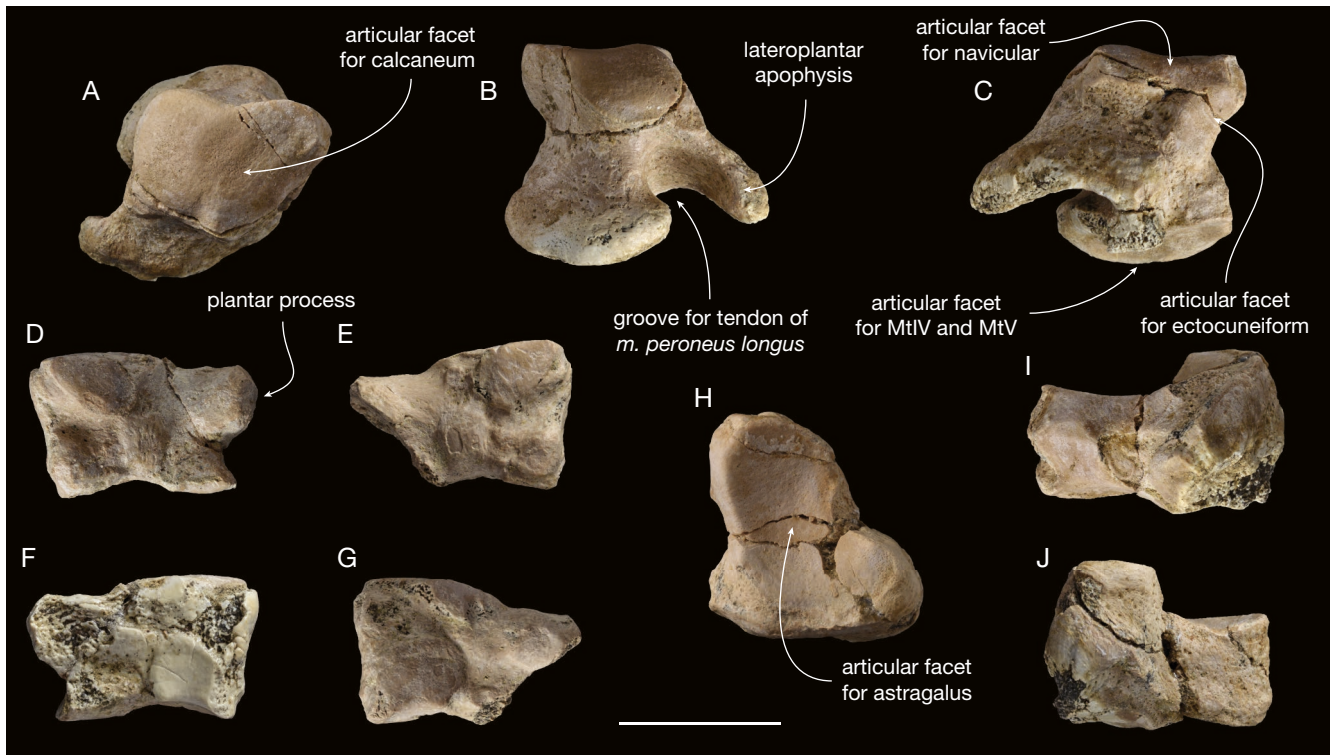


FIG. 41. — Tarsals of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A**, left cuboid in proximal view; **B**, the same cuboid in lateral view; **C**, the same cuboid in medial view; **D**, left ectocuneiform in lateral view; **E**, right ectocuneiform in lateral view; **F**, left ectocuneiform in medial view; **G**, right ectocuneiform in medial view; **H**, left navicular in proximal view; **I**, the same navicular in lateral view; **J**, the same navicular in medial view. Scale bar: 2 cm.

The distal articular facet for the corresponding phalanx is morphologically similar to that of the *Acrophoca* and *Piscophoca* and Phocinae in that it bears a prominent articular keel. Among extant Phocidae, such a keel and a strong convexity of the phalangeal articular facets separates Phocinae from Monachinae; the latter have flatter and simpler phalangeal articular facets.

Metatarsal II (MtII). The proximal epiphysis of MtII articulates with MtI medially, the mesocuneiform proximally and MtIII laterally. The articular facet for MtI is reniform in medial view, and weakly concave around the vertical axis. The proximal articular facet for the mesocuneiform is strongly concave. This corresponds with the condition in Phocinae, rather than in Monachinae, in which this facet is generally less concave. The lateral facet for articulation with MtIII is a weakly concave (laterally) to convex (proximolaterally) sub-triangular facet. The diaphysis of MtII is strongly slanted medially, as in other Monachinae. In Phocinae, MtII is generally straighter. The distal extremity is smooth and weakly-convex, with a small plantar keel. This conforms with other Monachinae and contrasts with Phocinae, in which the articular facet for the phalanx is more convex with a more developed plantar keel.

Metatarsal (MtIII). This metatarsal is by far the shortest metatarsal in the pes, as in other Phocidae. The state of preservation of the only preserved MtIII for *Magophoca* n. gen. does not allow a detailed description of the specimen, except for the distal epiphysis. As for MtII, the distal epiphysis is

smooth and weakly-convex, with a reduced plantar keel. This corresponds with the condition observed in other Monachinae, but differs from the condition in Phocinae. Although incomplete, the diaphysis appears circular in cross-section.

Metatarsal (MtIV). The articular facet for MtIII is abraded, precluding description. On the lateral margin, there is the articulation facet for MtV. This facet forms a curving but straight angle, consisting of a horizontal dorsal leg and a vertical proximal leg. Although incomplete, the vertical leg appears longer than the horizontal leg. The dimensions of this articular facet match other monachines: this facet is proximodistally longer in Phocinae. The diaphysis is circular in cross-section, and slightly slanted laterally relative to the proximal epiphysis. The shape of the distal epiphysis follows the general shape in Monachinae, as presented above for MtII and MtIII.

Metatarsal (MtV). The fifth metatarsal is the second largest bone, after MtI. MtV is slightly transversely compressed. The proximal epiphysis is dorsoplantarly expanded. The proximal epiphysis is transversely as robust as in other Monachinae. It is generally more gracile in Phocinae. Dorsomedially, the proximal epiphysis sports a slightly convex articular facet corresponding in shape to the angular shape of the articular facet for MtV, laterally on MtIV. Proximally and laterally, this facet transitions in a facet for the articulation with the cuboid. This facet is slightly convex, has a convex proximodorsal margin, and an undulating distaloplantar margin.

TABLE 25. — Measurements (in mm) of the metatarsals of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276). Abbreviations: e, estimate for a character due to minor damage; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; n/a, a character could not be measured; —, the character doesn't apply to a given metatarsal. All measurements taken on left specimens, except when marked with "r".

Character	MNHN.F.PPI276 (holotype, left)				
	I	II	III	IV	V
Overall, length	114.9	80.4e	> 57.5	66.1	93.4
Proximal epiphysis, height	> 22.1	21.9er	n/a	23.6	> 31.2
Proximal epiphysis, width	27.5	16.9r	n/a	n/a	17.6
Diaphysis, height	12.9	11.3	11.5e	11.5	16.6
Diaphysis, width	16.0	10.6	11.4	11.7	13.0
Distal epiphysis, height	18.6	18.8	n/a	16.8	20.2
Distal epiphysis, width	17.8	14.2	15.3	15.6	n/a
Mtl, navicular facet, height	14.9e	—	—	—	—
Mtl, navicular facet, width	17.6	—	—	—	—
Mtl, facet for MtlI, height	> 17.2	—	—	—	—
Mtl, facet for MtlI, width	9.1	—	—	—	—
MtlI, facet for Mtl, height	—	19.9e	—	—	—
MtlI, facet for Mtl, width	—	12.0	—	—	—
MtlIV, facet for MtlV, height	—	—	—	19.3	—
MtlIV, facet for MtlV, width	—	—	—	18.3	—
MtlV, facet for MtlIV, length	—	—	—	—	17.5
MtlV, facet for MtlIV, width	—	—	—	—	15.9
MtlV, cuboid facet, length	—	—	—	—	20.0
MtlV, cuboid facet, width	—	—	—	—	10.5

As in other Monachinae, and in contrast to Phocinae, the insertion for *m. peroneus brevis* is well-developed. Though incomplete, it appears to be proximodistally slightly elongate and slightly saddle-shaped.

Posterior phalanges (Fig. 43; Table 27). Three complete phalanges; and a proximal and distal fragment belonging to one or two phalanges of the holotype MNHN.F.PPI276 constitute all the posterior phalangeal material that is known for *Magophoca brevirostris* n. gen., n. sp.

The diaphysis of each phalanx is slightly dorsoventrally flattened and the shapes of the distal and proximal epiphyses are strongly simplified. The proximal articular surface is roughly reniform and only slightly concave, and the distal articular surface is saddle-shaped. This corresponds with the condition in other Monachinae, rather than with Phocinae, in which the articular surfaces are generally much better developed, with keeled distal articular surfaces for a higher mobility of the fore- and hindflippers. In Phocinae, the diaphyses of the phalanges are also more rounded in cross-section.

PHYLOGENETIC ANALYSIS

In the analysis performed here, the topology of the outgroup taxa, i.e. the stem-pinnipedimorph *Pteronarctos goedertae*, Otariidae (*Arctocephalus pusillus*, and *Otaria byronia*), and the odobenid *Odobenus rosmarus* has been constrained by the backbone constraint tree adapted from Rule *et al.* (2020b), with Odobenidae + Otariidae forming the clade Otarioidea as a sister group to Phocidae.

TABLE 26. — Proportions of the Mtl in extant and extinct Phocidae. Color code: **light orange**, fossil taxa with relatively long Mtl; **dark orange**, extant taxa with relatively long Mtl; **light green**, fossil taxa with short Mtl; **dark green**, extant taxa with short Mtl. Abbreviations: L, length; PW, proximal width; e, estimate for a character due to minor damage. Measurements in mm.

Specimen	L	PW	PW/L
<i>Magophoca brevirostris</i> n. gen., n. sp. (MNHN.F.PPI276)	115	27.7	0.24
Other extinct Monachinae			
<i>Acrophoca longirostris</i> (MNHN.F.SAS563)	109.9	30.0	0.272
<i>Hadrokirus martini</i> (MNHN.F.SAS1627)	138.9	35.4e	0.254
<i>Homiphoca capensis</i> (MNHN.F.AFS23)	102.1	29.3	0.287
<i>Monotherium?</i> sp. (IRSNB 1227)	122.9	30.6	0.249
<i>Piscophoca pacifica</i> (MNHN.F.SAS564)	126.9	31.9	0.251
<i>Pliphoca etrusca</i> (MSNUP I-13993)	103.0	32.0	0.31
Extinct Monachini			
<i>Monachus monachus</i> (MNHN-ZM-AC-A7953)	93.5	31.4	0.335
<i>Neomonachus tropicalis</i> (BMNH.1887.8.5.1)	107.5	34.9	0.32
Extant Lobodontini			
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1970-325)	158.0	40.0	0.253
<i>Hydrurga leptonyx</i> (MNHN-ZM-AC-1884-1152)	146.2	37.8	0.258
<i>Leptonychotes weddellii</i> (IRSNB 15390)	128.5	31	0.241
<i>Leptonychotes weddellii</i> (IRSNB 1163)	116	28.5	0.245
<i>Lobodon carcinophaga</i> (MNHN-ZM-AC-A7951)	128.8	33.2	0.257
<i>Lobodon carcinophaga</i> (IRSNB 1161)	113	34	0.300
<i>Ommatophoca rossii</i> (IRSNB 15389)	117	33	0.282
<i>Ommatophoca rossii</i> (IRSNB 1164)	133	33	0.248
Extant Phocinae			
<i>Erignathus barbatus</i> (MNHN-ZM-AC-A7949)	107.1	31.3	0.292
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1981-165)	90.8	23.6	0.256
<i>Halichoerus grypus</i> (MNHN-ZM-AC-1978-48)	102.2	23.9	0.234
<i>Phoca vitulina</i> (MNHN-ZM-AC-1894-524)	84.9	21.0	0.243
<i>Phoca vitulina</i> (MNHN-ZM-AC-1983-792)	80.3	19.8	0.246
<i>Pusa hispida</i> (MNHN-ZM-AC-17951)	75.5	18.9	0.250

In these conditions, the phylogenetic analysis using PAUP*4.0a169 yields 10 most parsimonious trees with a tree length of 261 after 14373 tried rearrangements. The strict consensus tree (Fig. 44) shows that the topology of Monachinae is poorly resolved, with a large polytomy at the subfamily level. Most notably, Extant Monachini are collapsed. However, interestingly, the clade composed of *Hadrokirus*, *Homiphoca*, *Kawas*, *Magophoca* n. gen., and *Piscophoca* is resolved, *Kawas* being sister genus to *Homiphoca* and *Magophoca* n. gen. sister genus to *Hadrokirus*. Nevertheless, because of the poor resolution of the strict consensus tree at higher phylogenetic levels, we performed a second analysis, downweighing homoplasy through implied weighing using the Goloboff criterion, with the k-value set at three. This resulted in one most parsimonious tree (score of best tree found = -70.75714) after 2654 tried rearrangements (Fig. 45). The consistency index is 0.4280, and retention index is 0.6739.

In the literature, the higher-level topology of the three crown pinniped families (Odobenidae, Otariidae and Phocidae) (and the extinct family Desmatophocidae) varies, with

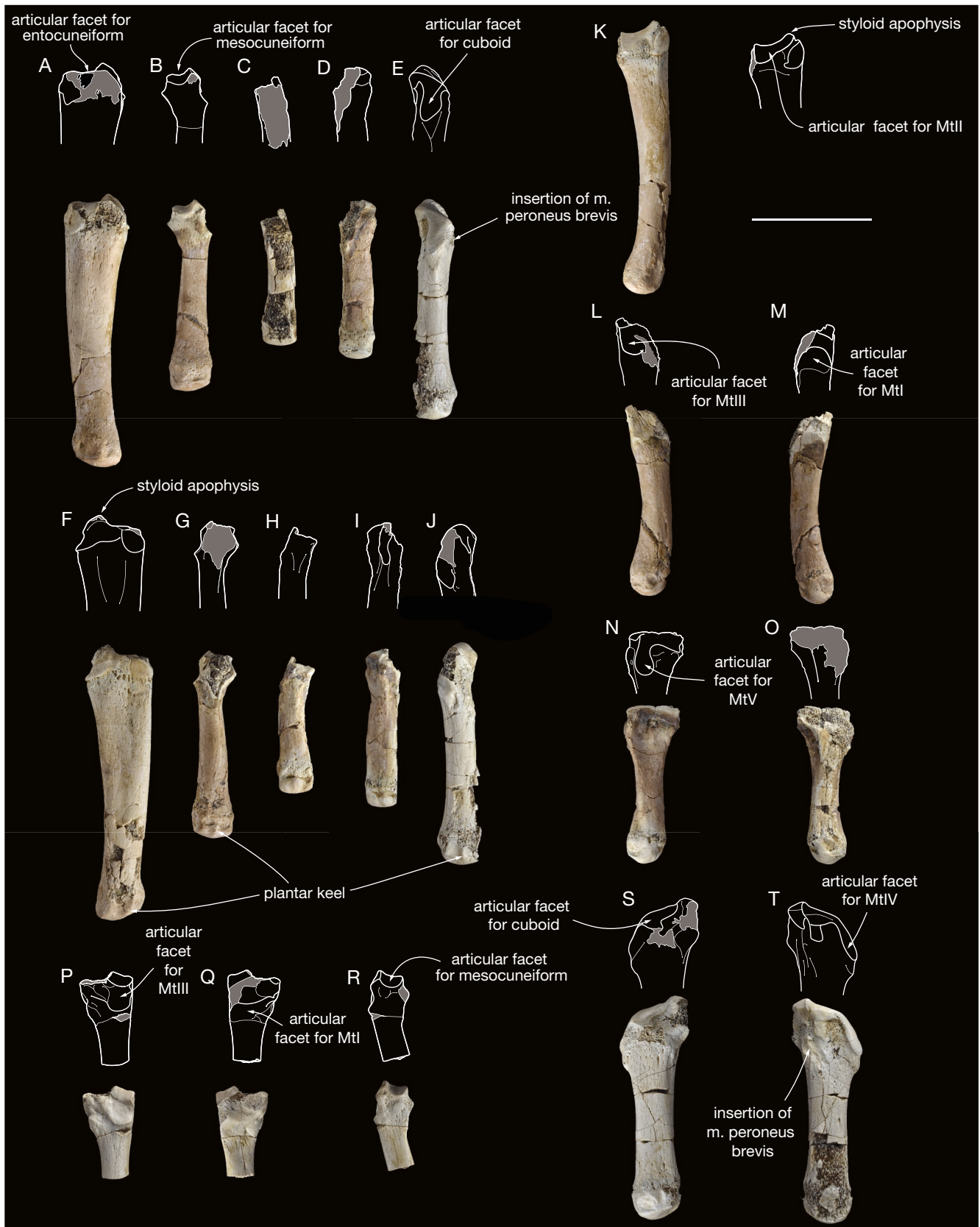


FIG. 42. — Metatarsals of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): all photographs are accompanied by a line drawing of the proximal part of the bone: **A**, left MtI in dorsal view; **B**, left MtII in dorsal view; **C**, left MtIII in dorsal view; **D**, left MtIV in dorsal view; **E**, left MtV in dorsal view; **F**, left MtI in plantar view; **G**, left MtII in plantar view; **H**, left MtIII in plantar view; **I**, left MtIV in plantar view; **J**, left MtV in plantar view; **K**, left MtI in lateral view; **L**, left MtII in lateral view; **M**, left MtII in medial view; **N**, left MtIV in lateral view; **O**, left MtIV in medial view; **P**, right partial MTII in lateral view; **Q**, right partial MTII in medial view; **R**, right partial MTII in dorsal view; **S**, left MtV in medial view; **T**, left MtV in lateral view. Scale bar: 5 cm.

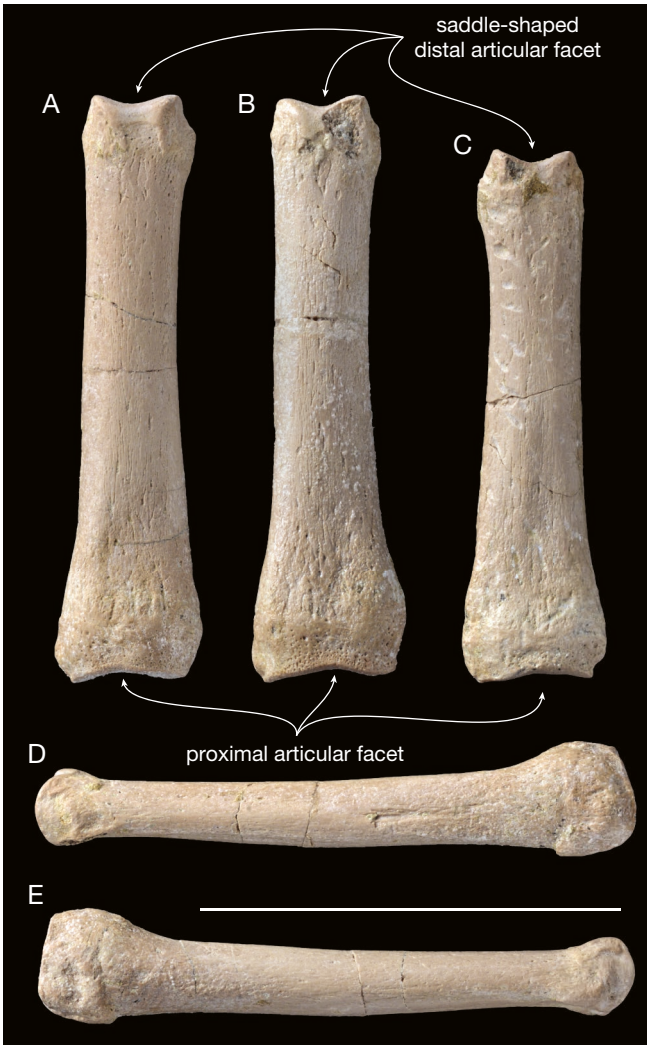


FIG. 43. — Phalanges of *Magophoca brevirostris* n. gen., n. sp. (holotype, MNHN.F.PPI276): **A-C**, proximal tarsal phalanges in dorsal view; **D**, medial and lateral views of phalanx **A**. Scale bar: 5 cm.

Odobenidae either under Otarioidea (Odobenidae+Otariidae) or under Phocomorpha (Odobenidae+Phocoidea) (e.g., Berta 1994; Deméré & Berta 2002; Berta *et al.* 2018). The former topology corresponds with the resulting phylogenetic tree retrieved in the current study.

The Phocidae form a monophyletic clade, supported by 24 synapomorphies, of which 12 are unambiguous (with consistency index = 1). The unambiguous synapomorphies of Phocidae are: the position of the posterior end of the nasals posterior to the level of the maxilla-frontal suture (char. 5 [0 > 1]); the absence of the alisphenoid canal (char. 10[0 > 1]); a mortised jugal-squamosal contact (char. 15[0 > 1]); the lateral extremity of the tympanic bulla reaching lateral to mid-width of the glenoid fossa (char. 22[0 > 1]); the pit for the stylohyal oriented ventrally and anteriorly (char. 24[0 > 1]); a heavily pachyosteosclerotic mastoid (char. 26[0 > 1]); a paroccipital that is well separated from the mastoid (char. 28[0 > 1]); the posterior opening of the carotid canal and posterior lacerate foramen are separated (char. 30[1 >

TABLE 27. — Measurements (in mm) of the posterior phalanges of the *Magophoca brevirostris* n. gen., n. sp. holotype (MNHN.F.PPI276).

Character	MNHN.F.PPI276 (holotype, left)		
Overall, length	70.2	69.8	63.7
Proximal epiphysis, height	13.5	13.1	11.4
Proximal epiphysis, width	17.6	18.5	17.3
Diaphysis, height	6.6	6.6	6.4
Diaphysis, width	11.1	11.3	11.0
Distal epiphysis, height	9.0	8.5	8.4
Distal epiphysis, width	13.8	13.4	13.1

0]); the pterygoids are laterally tilted and flaring posteriorly (char. 34[0 > 1]); the occipital condyles diverging dorsally (char. 35[0 > 1]); a femur lacking a lesser trochanter (char. 83[0 > 1]); and a well-developed calcaneal process on the astragalus (char. 90[1 > 2]). Ambiguous synapomorphies are characters 4, 6, 11, 23, 36, 58, 61, 62, 66, 80, 81, and 91 (further details, see Appendices 3, 4).

The topology of the four species of Phocinae agrees with the general topologies in other morphological and molecular phylogenetic studies (e.g., Bininda-Emonds & Russell 1996; Higdon *et al.* 2007; Fulton & Strobeck 2010; Rule *et al.* 2020b). The subfamily Phocinae is supported by 18 synapomorphies, of which three are unambiguous. These are: the major axes of the glenoid fossa are slightly convergent posteriorly (char. 20[0 > 1]); the posterior opening of the carotid canal is visible in dorsal view (char. 29[0 > 1]); a sacrum composed of four fused sacral vertebrae (char. 56[1 > 2]). Ambiguous synapomorphies are characters 16, 23, 25, 55, 61, 65, 67, 68, 69, 72, 73, 75, 79, 82, and 84.

This phylogenetic analysis focuses on extant and extinct Monachinae, and especially the phylogenetic relationships of extinct Monachinae among extant taxa. The subfamily Monachinae is supported by 23 synapomorphies, of which five unambiguous: a reduced scapular spine (char. 59[0 > 1]); a flattened distal end of the styloid process of the ulna (char. 71[0 > 1]); an anterolaterally-oriented fossa for *m. peroneus longus* on the femur (char. 86[0 > 1]); a strongly developed anterior tibial fossa (char. 89[0 > 1]); and MtlIII approximately 50% (or more) shorter than Mtl (char. 93[0 > 1]). Ambiguous synapomorphies are characters 1, 2, 3, 12, 14, 37, 39, 49, 53, 57, 60, 63, 64, 77, 78, 85, and 91.

The topology of the phylogenetic relationships of Monachinae confirm the well-established separation of Monachinae in three tribes: Lobodontini, Miroungini, and Monachini. In the present study, as constrained by the constraint tree, Monachini are the first to branch off, with Miroungini, represented by *Mirounga leonina* forming a sister clade with Lobodontini.

Eomonachus and *Pliophoca* are confirmed as Monachini, together with *Monachus* and *Neomonachus* (Tavani 1941; Berta *et al.* 2015; Berta *et al.* 2018; Rule *et al.* 2020b). All four extant Lobodontini (*Hydrurga*, *Leptonychotes*, *Lobodon*, and *Ommatophoca*) group together as crown Lobodontini. All extinct Lobodontini included in this study fall outside the crown group. Extant and extinct Lobodontini form two sister monophyletic sister clades. This is a strong indicator

that a detailed phylogenetic analysis of extant and extinct Monachinae, and Lobodontini in particular, is much needed. However, this is beyond the scope of the current study. The clade composed of extant and extinct Lobodontini is supported by seven synapomorphies, of which three are unambiguous. These are: a parasagittal orientation of the medial margins of the tympanic bullae (char. 21[0 > 1]); the presence of a lip in the anteromedial region of the mastoid, abutting the posteromedial edge of the tympanic bulla (char. 27[0 > 1]); and a well-developed articular surface for the fibula on the calcaneum (char. 92[0 > 1]). Ambiguous synapomorphies are characters 52, 60, 80, and 84. Crown lobodontins are supported by five synapomorphies, all ambiguous (characters 11, 57, 69, 74, 80).

The first of the extinct lineage of Lobodontini to branch off, is *Sarcodectes* from the western North Atlantic, followed by *Acrophoca* from the southeast Pacific. The remaining five extinct lobodontins, the clade composed of *Hadrokirus*, *Homiphoca*, *Kawas*, *Magophoca* n. gen., and *Piscophoca*, branches in two groups, interestingly along paleobiogeographic lines: the South Atlantic taxa *Homiphoca* and *Kawas* are retrieved as sister species, which is coherent as far as biogeography is concerned and gives credit to the hypothesis of Hende (1972) to place the geographic origin of the south African monachine *Homiphoca* in the eastern seaboard of South America. The Southeastern Pacific *Hadrokirus*, *Magophoca* n. gen., and *Piscophoca* form a sister clade to the clade composed of *Homiphoca* and *Kawas*.

Bootstrap values (<50%) for the tree are shown in Fig. 45. Whereas there is absolute support for the phocid monophyly and moderate to high support for the phylogenetic relationships of phocines included in this study, bootstrap support for the Monachinae is low, yet at 53% above the 50% threshold.

DISCUSSION AND CONCLUSIONS

Magophoca brevirostris n. gen., n. sp. is the fifth species of extinct Monachinae to be described from the Neogene of Peru and Chile, after *Acrophoca longirostris* and *Piscophoca pacifica* by Muizon (1981), *Hadrokirus martini* by Amson & Muizon (2014), and *Australophoca changorum* by Valenzuela-Toro *et al.* (2016).

Collected at the CLB level of the Pisco Formation, as defined by Muizon & DeVries (1985), all specimens of *Magophoca* n. gen. have been recovered from the base of the P2 sequence of the Pisco Formation, dated to 8.4 Ma, i.e., late Tortonian, by Bosio *et al.* (2020). This makes *Magophoca* n. gen. the geologically oldest known phocid from the west coast of South America, with *Acrophoca*, *Hadrokirus*, and *Piscophoca* having been recovered from overlying, younger fossiliferous levels (SAO and SAO levels) within the Pisco Formation, dated to the latest Miocene and/or early Pliocene. For *Australophoca*, Valenzuela-Toro *et al.* (2016) presented a late Tortonian, c. 7.6 Ma, age. Thus, the present study pushes back the earliest occurrence of Monachinae in the southeast Pacific Ocean with 0.8 Ma, from 7.6 to 8.4 Ma.

Magophoca n. gen. is slightly smaller than extant and most extinct Monachinae, with the notable exception of the significantly smaller *Australophoca*. A most remarkable diagnostic character distinguishing *Magophoca* n. gen. from other Monachinae is the presence of six upper incisors, three in each quadrant. This character is considered a plesiomorphy, shared with Phocinae. Otherwise, *Magophoca* n. gen. shares most skeletal similarities with *Hadrokirus* and *Piscophoca*, as shown throughout the description and phylogenetic analysis.

NOTES ON *KAWAS* FROM ARGENTINA

Interestingly, *Kawas benegasorum* is well-nested among Monachinae. This departs starkly from the original description of and phylogenetic analysis for *Kawas* (Cozzuol 2001), as well as other, more recent phylogenetic analyses including the species (Dewaele *et al.* 2017a; Rule *et al.* 2020b). This follows a much more detailed phylogenetic analysis, comprising more taxa and more characters. A number of characters used by Cozzuol (2001) to group *Kawas* with Phocinae have shown to be present among (extinct) Monachinae as well. Most notably among them, the presence of an entepicondylar foramen on the humerus (also in *Frisiphoca*, *Homiphoca*, and *Magophoca* n. gen.), and the presence of a trochanteric fossa on the femur (also in *Homiphoca*, *Lobodon*, *Magophoca* n. gen., *Piscophoca*, and the referred *Properiptychus* from Muizon & Bond 1982 (MACN 3677). Other characters present in the skeleton of *Kawas*, are common among (extinct) Monachinae, setting it apart from Phocinae. These include the medial location of the bicipital tuberosity on the diaphysis of the radius (also in other Monachinae, except extant Lobodontini) the flattened distal end of the styloid process of the ulna, a shallow gluteal fossa on the ilium (also in *Erignathus*), and the anterodorsal iliac process is located dorsal to the anteroventral process (also in other Monachinae, except *Magophoca* n. gen., *Mirounga*, and *Ommatophoca*).

Despite the weak bootstrap support for the phylogenetic topology within the monachine subfamily, *Kawas* is nested well within this subfamily, and not within the Phocinae. The phylogenetic tree presented in the present study (Fig. 45) also places *Kawas* as a sister taxon to *Homiphoca*, suggesting that both form a South Atlantic branch, branching off of other extinct Lobodontini. However, the geologic age of *Kawas* is dated to the middle Miocene (12 to 14 Ma). If this age is correct, it -unfortunately- suggests long ghost lineages among extinct Lobodontini.

NOTES ON *MONOTHERIUM* AND *FRISIPHOCIA* FROM BELGIUM

The holotype humerus of *Magophoca brevirostris* n. gen., n. sp. strongly resembles the lectotype humerus of *Frisiphoca aberrata*. Characters grouping both include the overall slenderness, the small lesser tubercle, the deep fossa for the origin of the *m. triceps brachii caput mediale* just below the head, the slender deltopectoral crest, and the presence of an entepicondylar foramen. Individual characteristics are shared with multiple different other taxa. For instance, among Monachinae, the presence of an entepicondylar foramen

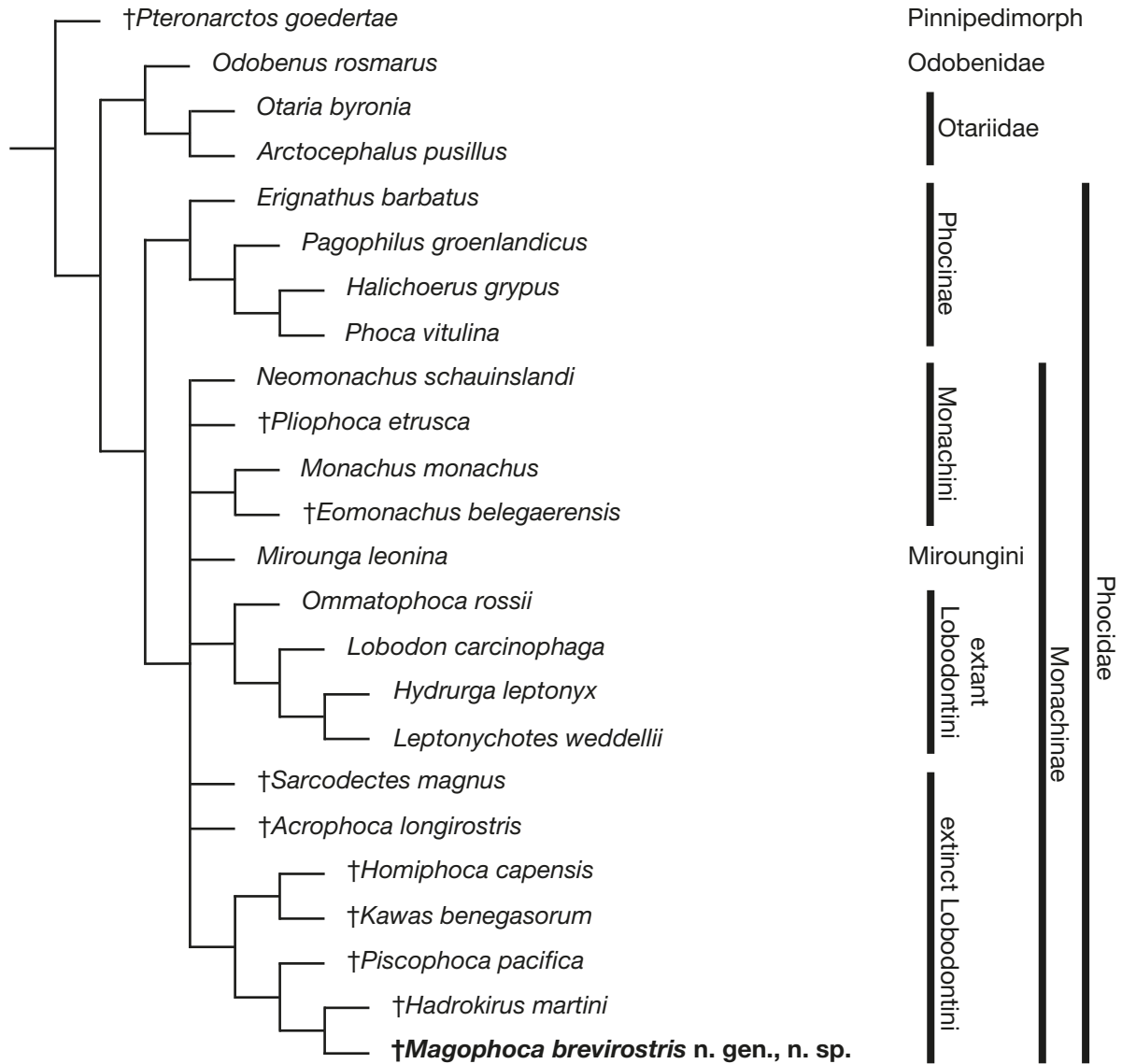


FIG. 44. — Phylogenetic relationships of *Magophoca brevirostris* n. gen., n. sp. among Phocidae. Strict consensus tree of ten most parsimonious tree of the phylogenetic analysis. *M. brevirostris* n. gen., n. sp. nests among stem-lobodontines and is closest related to *Hadrokirus martini* and *Piscophoca pacifica*, also from Peru. Extinct species are preceded by a dagger.

men is also shared with *Homiphoca* and the deep fossa for the origin of the *m. triceps brachii caput mediale* just below the head has also been observed in *Piscophoca*. However, this combination of characters is unique for *F. aberrata* and *Magophoca* n. gen.

This sheds new light on *F. aberrata*, spurring a note on the genera *Frisiphoca* and *Monotherium* from Belgium, partly in response to the review of the genus *Monotherium* and the establishment of the genus *Frisiphoca* (including *F. aberrata* and *F. affinis*) by Dewaele *et al.* (2018a).

Status of *Monotherium*

Kellogg (1922) selected *Monotherium delognii* as the type species of the genus. Subsequently, Dewaele *et al.* (2018a) selected specimen IRSNB 1153-M257a,b as the lectotype specimen for *M. delognii*, and, thus, the name-bearing speci-

men for the genus *Monotherium*. This specimen constitutes a partial left innominate with a partial sacrum.

Dewaele *et al.* (2018a) consider *M. delognii* to be an indeterminate Phocidae. However, selected characteristics of the lectotype innominate are shared with Phocinae: the strong development of the posteroventral process of the ilium and the anteroventral process extending anterior to the level of the anterodorsal process of the ilium.

Apart from similarities with other Phocinae, Dewaele *et al.* (2018a) also presented predominantly monachine characters to support the statement that it remains impossible to assign the lectotype of *M. delognii* to either Monachinae or Phocinae. These characters are the relatively weak lateral eversion of the iliac wing, with a lateral eversion well within the range for Monachinae but at the lower end of the range for Phocinae, and the poor excavation of the

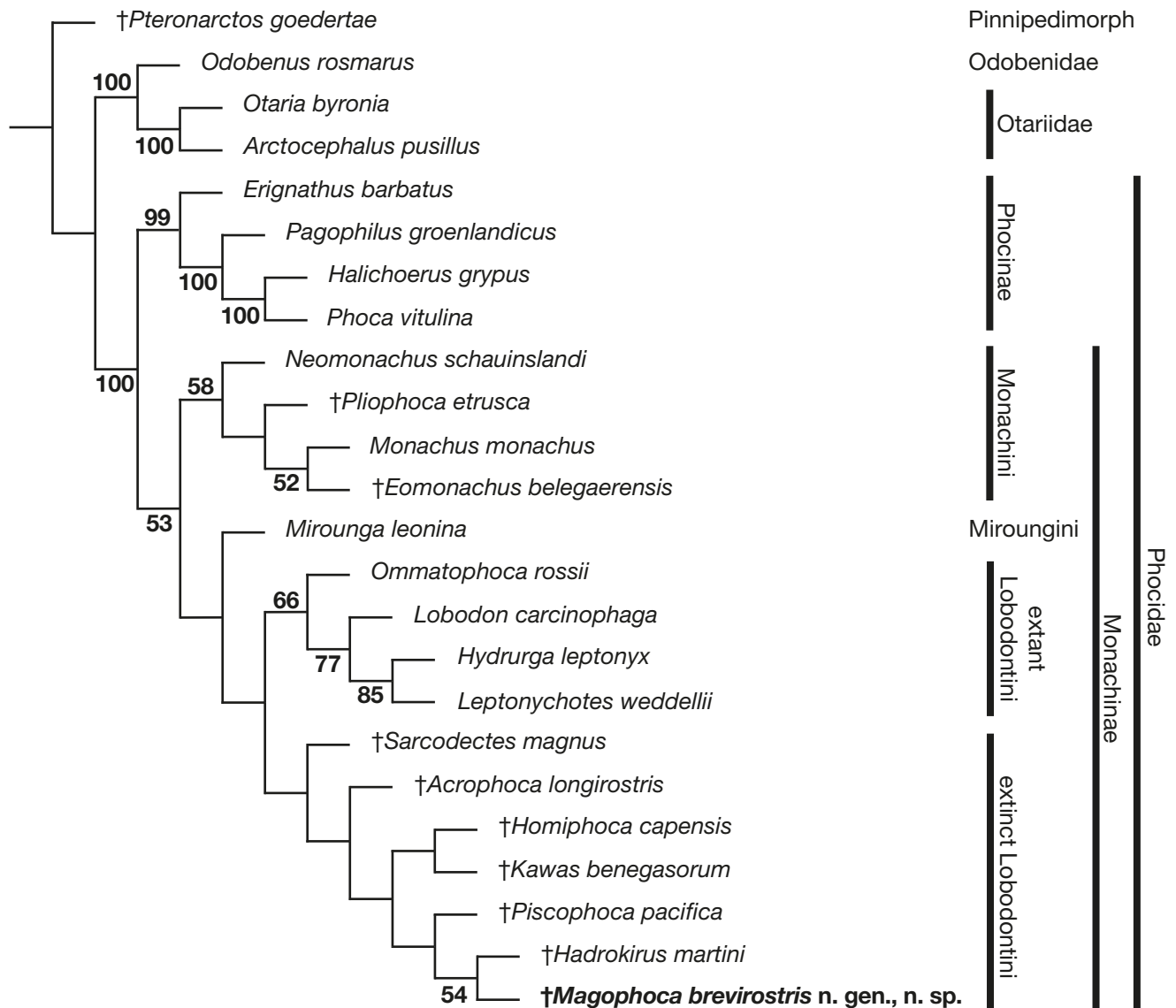


FIG. 45. — Phylogenetic relationships of *Magophoca brevirostris* n. gen., n. sp. among Phocidae, with Goloboff k-value set at three to downweigh homoplasy. Single most parsimonious tree of the phylogenetic analysis. *M. brevirostris* n. gen., n. sp. nests among stem-lobodontines and is closest related to *Hadrokirus martini* and *Piscophoca pacifica*, also from Peru. Bootstrap values higher than fifty are shown. Extinct species are preceded by a dagger.

gluteal fossa. However, it can be argued that both characters and character states in IRSNB 1153-M257a,b do not prohibit that the specimen can be considered a phocine. Although the relatively lateral eversion of the ilium of IRSNB 1153-M257a,b is at the lower part of the range in Phocinae, following the dataset of Dewaele *et al.* (2017b), it still falls within the observed range. In addition, the weak excavation of the gluteal fossa on the ilium has also been observed in two extant Phocinae: *Erignathus* and *Pusa sibirica*. Lastly, both the strong lateral eversion of the ilium and the strong excavation of the gluteal fossa on the ilium, observed in most extant Phocinae are apomorphies. In light of the —presumed— Tortonian age of the lectotype of *M. delognii*, it can be argued that this specimen is indeed phocine but not yet exhibiting certain derived characters shared among most extant Phocinae.

Consequently, we argue the genus *Monotherium* is monotypic, solely represented by *M. delognii*, which in turn has a fossil record limited to the lectotype innominate and sacrum. *M. delognii* is an extinct phocine seal of unknown intra-subfamilial affinities.

Status of *Frisiphoca*

The genus *Frisiphoca* was established to isolate *Monotherium aberratum* (*aberrata*) and *Monotherium affine* (*affinis*) from *Monotherium delognii*, the type species of the genus *Monotherium*, which is limited to a fragmentary innominate and fragmentary sacrum as lectotype. *Frisiphoca aberrata* and *Frisiphoca affinis* are both known solely based on their isolated lectotype humeri respectively IRSNB 1191-M266 and IRSNB 1118-M260.

Dewaele *et al.* (2018a) assigned the genus to the subfamily Phocinae, largely based on the presence of an entepicondylar

foramen in both and the presence of a well-developed supinator crest in *F. affinis*. This grouping among Phocinae was further supported by the phylogenetic analysis of Dewaele *et al.* (2018a).

However, the presence of an entepicondylar foramen has been observed among multiple extinct Monachinae: *Homiphoca*, *Kawas*, and *Magophoca* n. gen. in the present study. In addition, *Homiphoca* is also a monachine that possesses a well-developed supinator crest. Thus, the characters used by Dewaele *et al.* (2018a) to assign *Frisiphoca* to the subfamily Phocinae have also been observed in certain Monachinae.

In addition, Dewaele *et al.* (2018a) failed to highlight the distal termination of the insertion area for *m. pectoralis* on the deltopectoral crest. Muizon (1981) and Dewaele *et al.* (2018a) noted this character as an important character distinguishing Monachinae from Phocinae. Whereas this insertion area reaches consistently much more distal, towards the coronoid fossa, in Monachinae, it stays much more proximal in Phocinae. In the lectotypes of *F. aberrata* and *F. affinis*, the insertion of *m. pectoralis* on the deltopectoral crest is distal, as in Monachinae. This allows suggesting that *Frisiphoca* is indeed a monachine genus, *contra* Dewaele *et al.* (2018a), who included this genus among Phocinae.

The nesting of *Frisiphoca* among Phocinae in the phylogenetic analysis of Dewaele *et al.* (2018a) can be attributed to the small number of characters that could be scored for both species in the genus, thus, severely limiting the validity of the results of the analysis regarding the genus *Frisiphoca*. For that reason, we did not include neither *F. aberrata* nor *F. affinis* in our phylogenetic analysis. Furthermore, *Frisiphoca aberrata* has been designated as the type species of *Frisiphoca* by Dewaele *et al.* (2017a). Because no other specimens can be referred securely to the holotype of *F. aberrata*, this species is represented exclusively by the humerus IRSNB 1191-M266. Although this specimen may belong to the Monachinae, we regard this specimen as inadequate to define a phocid taxon and suggest to restrict the taxon *Frisiphoca* to the lectotype of *F. aberrata*, and that both genus and species name should be regarded as a Phocidae incertae sedis restricted to the lectotype specimen. Indeed, this practice would conform the recent trend, shown by Churchill & Uhen (2019) and Rule *et al.* (2020b), in which isolated humeri are no longer considered suitable as type specimens. Geometric analysis of humeri and femora by Churchill & Uhen (2019) showed that certain characters on phocid humeri and femora are still useful for taxon identification to an extent, but that their utility as – isolated – type specimens and for diagnosis has been exaggerated. They conclude by advising to move away from assigning taxon names to isolated phocid long bones.

Rule *et al.* (2020b) applied this by reconsidering previously described monachine species from the east coast of North America as nomina dubia, including the well-known large monachine *Callophoca obscura*.

However, the similarities between both the lectotype humerus of *F. aberrata* and the holotype humerus of *Magophoca*

n. gen. are remarkable and a close taxonomic relationship may be suggested. In addition, an isolated Mtl from the Neogene of Belgium, that has been attributed to the genus *Monotherium* shows marked similarities in size and proportions to the Mtl of *Magophoca* n. gen. presented in this study. However, the highly incomplete fossil record of *F. aberrata* is limited to the lectotype humerus, thus precludes a detailed in-depth comparison with *Magophoca brevirostris* n. gen., n. sp. If both are closely related, this may suggest that *Magophoca brevirostris* n. gen., n. sp. or its direct ancestors were among the first Monachinae to cross the equator and pass the Central American Seaway during the middle or early late Miocene from the North Atlantic into the Southeast Pacific.

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REFERENCES

- AMEGHINO F. 1897. — Mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à *Pyrotherium*. *Boletín Instituto Geográfico Argentino* 18: 406-521. <https://www.biodiversitylibrary.org/page/62504710>
- AMSON E. & MUIZON C. DE 2014. — A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seal phylogeny. *Journal of Systematic Paleontology* 12: 523-548. <https://doi.org/10.1080/14772019.2013.799610>

- BARNES L. G. 1989. — A new enaliarctine pinniped from the Astoria Formation, Oregon, and a classification of the Otariidae (Mammalia, carnivora). *Contribution in Science of the Natural History Museum of Los Angeles County* 403: 1-26. <https://doi.org/10.5962/p.241288>
- BERTA A. 1994. — New specimens of the pinnipediform *Pteronarctos* from the Miocene of Oregon. *Smithsonian Contributions to Paleobiology* 78: 1-30. <https://doi.org/10.5479/si.00810266.78.1>
- BERTA A., CHURCHILL M. & BOESSENECKER R. W. 2018. — The origin and evolutionary biology of pinnipeds: Seals, sea lions, and walruses. *Annual Review of Earth and Planetary Sciences* 46: 203-228. <https://doi.org/10.1146/annurev-earth-082517-010009>
- BERTA A., KIENLE S., BIANUCCI G. & SORBI S. 2015. — A reevaluation of *Pliophoca etrusca* (Pinnipedia, Phocidae) from the Pliocene of Italy: phylogenetic and biogeographic implications. *Journal of Vertebrate Paleontology* 35: e889144. <https://doi.org/10.1080/02724634.2014.889144>
- BERTA A. & WYSS A. R. 1994. — Pinniped phylogeny. *Proceedings of San Diego Society of Natural History* 29: 33-56.
- BIANUCCI G., DI CELMA C., LANDINI W., POST K., TINELLI C., MUIZON C. DE, GARIBOLDI K., MALINVERNO E., CANTALAMESSA G., GIONCADA A., COLLARETA A., SALAS-GISMONDI R., VARAS-MALCA R., URBINA M. & LAMBERT O. 2016a. — Distribution of fossil marine vertebrates in Cerro Colorado, the type locality of the giant raptorial sperm whale *Liopytan melvillei* (Miocene, Pisco Formation, Peru). *Journal of Maps* 12: 543-557. <https://doi.org/10.1080/17445647.2015.1048315>
- BIANUCCI G., DI CELMA C., COLLARETA A., LANDINI W., POST K., TINELLI C., DE MUIZON C., BOSIO G., GARIBOLDI K., GIONCADA A., MALINVERNO E., CANTALAMESSA G., ALTAMIRANO-SIERRA A., SALAS-GISMONDI R., URBINA M. & LAMBERT O. 2016b. — Fossil marine vertebrates of Cerro Los Quesos: Distribution of cetaceans, seals, crocodiles, seabirds, sharks, and bony fish in a late Miocene locality of the Pisco Basin, Peru. *Journal of Maps* 12: 1037-1046. <https://doi.org/10.1080/17445647.2015.1115785>
- BININDA-EMONDS O. R. P. & RUSSELL A. P. 1996. — A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonner Zoologische Monographien* 41: 1-256. <https://www.biodiversitylibrary.org/page/44795135>
- BOSIO G., MALINVERNO E., VILLA I. M., DI CELMA C., GARIBOLDI K., GIONCADA A., BARBERINI V., URBINA M. & BIANUCCI G. 2020. — Tephrochronology and chronostratigraphy of the Miocene Chilcatay and Pisco formations (East Pisco basin, Peru). *Newsletters on Stratigraphy* 53: 213-247. <https://doi.org/10.1127/nos/2019/0525>
- BRAND L., URBINA M., CHADWICK A., DEVRIES T. J. & ESPERANTE R. 2011. — A high resolution stratigraphic framework for the remarkable fossil cetacean assemblage of the Miocene/Pliocene Pisco Formation, Peru. *Journal of South American Earth Sciences* 31: 414-425. <https://doi.org/10.1016/j.jsames.2011.02.015>
- BRYDEN M. M. 1971. — Myology of the Southern elephant seal *Mirounga leonina* (L.). *Antarctic Research Series* 18:109-140. <https://doi.org/10.1029/AR018p0109>
- CHURCHILL M., CLEMENTZ M. T. & KOHNO N. 2014. — Predictive equations for the sedimation of body size in seals and sea lions (Carnivora: Pinnipedia). *Journal of Anatomy* 225: 232-245. <https://doi.org/10.1111/joa.12199>
- CHURCHILL M. & UHEN M. D. 2019. — Taxonomic implications of morphometric analysis of earless seal limb bones. *Acta Palaeontologica Polonica* 64: 213-230. <https://doi.org/10.4202/app.00607.2019>
- COZZUOL M. A. 2001. — A “Northern” seal from the Miocene of Argentina: Implications for phocid phylogeny and biogeography. *Journal of Vertebrate Paleontology* 21: 415-421. [https://doi.org/10.1671/0272-4634\(2001\)021\[0415:ANSFTM\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2001)021[0415:ANSFTM]2.0.CO;2)
- DEMÉRÉ T. A. & BERTA A. 2002. — The Miocene pinniped *Desmatophoca oregonensis* Condon, 1906 (Mammalia: Carnivora) from the Astoria Formation, Oregon. *Smithsonian Contributions to Paleobiology* 93: 113-147.
- DEMÉRÉ T. A., BERTA A. & ADAM P. J. 2003. — Pinnipedimorph evolutionary biogeography. *Bulletin of the American Museum of Natural History* 279: 32-76. [http://dx.doi.org/10.1206/0003-0090\(2003\)279<0032:C>2.0.CO;2](http://dx.doi.org/10.1206/0003-0090(2003)279<0032:C>2.0.CO;2)
- DEWAELE L., LAMBERT O. & LOUWY S. 2017a. — On *Prophoca* and *Leptophoca* (Pinnipedia, Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic affinities and paleobiogeographic implications. *PeerJ* 5: e3024. <https://doi.org/10.7717/peerj.3024>
- DEWAELE L., AMSON E., LAMBERT O. & LOUWY S. 2017b. — Reappraisal of the extinct seal ‘*Phoca*’ *vitulinoides* from the Neogene of the North Sea Basin, with bearings on its geological age, phylogenetic affinities, and locomotion. *PeerJ* 5: e3316. <https://doi.org/10.7717/peerj.3316>
- DEWAELE L., LAMBERT O. & LOUWY S. 2018a. — A critical revision of the fossil record, stratigraphy and diversity of the Neogene seal genus *Monotherium* (Carnivora, Phocidae). *Royal Society Open Science* 5: Article 171669. <https://doi.org/10.1098/rsos.171669>
- DEWAELE L., PEREDO C. M., MEYVISCH P. & LOUWY S. 2018b. — Diversity of late Neogene Monachinae (Carnivora, Phocidae) from the North Atlantic, with the description of two new species. *Royal Society Open Science* 5: Article 172437. <https://doi.org/10.1098/rsos.172437>
- DEWAELE L., LAMBERT O. & LOUWY S. 2018c. — A late surviving Pliocene seal from high latitudes of the North Atlantic realm: the latest monachine seal on the southern margin of the North Sea. *PeerJ* 6:e5734. <https://doi.org/10.7717/peerj.5734>
- DI CELMA C., MALINVERNO E., BOSIO G., COLLARETA A., GARIBOLDI K., GIONCADA A., MOLLI G., BASSO D., VARAS-MALCA R. M., PIERANTONI P. P., VILLA I. M., LAMBERT O., LANDINI W., SARTI G., CANTALAMESSA G., URBINA M. & BIANUCCI G. 2017. — Sequence stratigraphy and paleontology of the Upper Miocene Pisco Formation along the western side of the lower Ica Valley (Ica Desert, Peru). *Rivista Italiana di Paleontologia e Stratigrafia* 123 (2): 255-273. <https://doi.org/10.13130/2039-4942/8373>
- DIEDRICH C. G. 2011. — The world’s oldest fossil seal record. *Natural Science* 3: 914-920. <https://doi.org/10.4236/ns.2011.31117>
- DOMNING D. P. 1994. — A phylogenetic analysis of Sirenia. *Proceedings of the San Diego Society of Natural History* 29: 177-189.
- EHRET D. J., MACFADDEN B. J., JONES D. S., DEVRIES T. J., FOSTER D. A. & SALAS-GISMONDI R. 2012. — Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology* 55: 1139-1153. <https://doi.org/10.1111/j.1475-4983.2012.01201.x>
- ECHARRI S., PEREZ D. E., MINNA M. & LUCERO S. O. 2021. — New Record of a Phocid (Mammalia, Carnivora, Phocidae) in the Late Miocene of Patagonia, Argentina. *Ameghiniana* 58: 369-375. <https://doi.org/10.5710/AMGH.04.06.2021/3403>
- EVANS H. E. & DE LAHUNTA A. 2013. — *Miller’s Anatomy of the Dog, Fourth Edition*. Elsevier Saunders, St. Louis, 850 p.
- FULTON T. L. & STROBECK C. 2010. — Multiple markers and multiple individuals refine true seal phylogeny and bring molecules and morphology back in line. *Proceedings of the Royal Society B* 277: 1065-1070. <https://doi.org/10.1098/rspb.2009.1783>
- GOVENDER R. 2015. — Preliminary phylogenetics and biogeographic history of the Pliocene seal, *Homiphoca capensis* from Langebaanweg, South Africa. *Transactions of the Royal Society of South Africa* 70: 25-39. <https://doi.org/10.1080/0035919X.2014.984258>
- GUISCARDI G. 1871. — Sopra un teschio fossile di foca. *Rendiconti dell’Accademia delle Scienze Fisiche e Matematiche* 5: 1-8.
- HENDEY Q. B. 1972. — The evolution and dispersal of the Monachinae (Mammalia: Pinnipedia). *Annals of the South African Museum* 59: 99-113. <https://www.biodiversitylibrary.org/page/40938908>

- HIGDON J. W., BININDA-EMONDS O. R. P., BECK R. M. D & FERGUSON S. H. 2007. — Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology* 7: 216. <https://doi.org/10.1186/1471-2148-2-216>
- HOCKING D. P., MARX F. G., PARK T., FITZGERALD E. M. G. & EVANS A. R. 2017. — A behavioural framework for the evolution of feeding in predatory aquatic mammals. *Proceedings of the Royal Society B* 284: 20162750. <https://doi.org/10.1098/rspb.2016.2750>
- HOWELL A. B. 1929. — Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Proceedings of the United States National Museum* 73: 1-142. <https://doi.org/10.5479/si.00963801.73-2736.1>
- JEFFERSON T. A., WEBBER M. A. & PITMAN R. L. 2008. — *Marine Mammals of the World: a Comprehensive Guide to their Identification*. Elsevier/Academic Press, Amsterdam, 573 p.
- KELLOGG R. 1922. — Pinnipeds from Miocene and Pleistocene deposits of California. *University of California Publications in Geology* 13:23-132.
- KIENLE S. S., CUTHBERTSON R. D. & REIDENBERG J. S. 2022. — Comparative examination of pinniped craniofacial musculature and its role in aquatic feeding. *Journal of Anatomy* 240: 226-252. <https://doi.org/10.1111/joa.13557>
- KING J. E. 1966. — Relationships of the hooded and elephant seals (genera *Cystophora* and *Mirounga*). *Journal of Zoology* 148: 385-398. <https://doi.org/10.1111/j.1469-7998.1966.tb02958.x>
- KORETSKY I. A. & GRIGORESCU D. 2002. — The fossil monk seal *Pontophoca sarmatica* (Aleksiev) (Mammalia: Phocidae: Monachinae) from the Miocene of Eastern Europe. *Smithsonian Contributions to Paleobiology* 93: 149-162. <https://doi.org/10.5479/si.00810266.93.149>
- KORETSKY I. A. 2001. — Morphology and systematics of the Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic Region. *Geologica Hungarica Series Palaeontologica* 54: 1-109.
- KORETSKY I. A. & HOLEC P. 2002. — A primitive seal (Mammalia: Phocidae) from the early middle Miocene of Central Paratethys. *Smithsonian Contributions to Paleobiology* 93: 163-178. <https://doi.org/10.5479/si.00810266.93.163>
- KORETSKY I. A. & RAHMAT S. J. 2015. — A new species of the subfamily Devinophocinae (Carnivora, Phocidae) from the Central Paratethys. *Rivista Italiana di Paleontologia e Stratigrafia* 121: 31-47. <https://doi.org/10.13130/2039-4942/6399>
- KORETSKY I. A. & RAY C. E. 2008. — Phocidae of the Pliocene of Eastern North America, in RAY C. E., BOHASKA D. J., KORETSKY I. A., WARD L. W. & BARNES L. G. (eds), *Geology and Paleontology of the Lee Creek Mine, North Carolina. Volume IV. Virginia Museum of Natural History, Special Publication* 14: 81-140.
- KORETSKY I. A., RAY C. E. & PETERS N. 2012. — A new species of *Leptophoca* (Carnivora, Phocidae, Phocinae) from both sides of the North Atlantic Ocean (Miocene seals of the Netherlands, part I). *Deinsea* 15: 1-12.
- KORETSKY I. A. & SANDERS A. 2002. — Paleontology of the Late Oligocene Ashley and Chandler Bridge formations of South Carolina, 1: Paleogene pinniped remains; the oldest known seal (Carnivora: Phocidae). *Smithsonian Contributions to Paleobiology* 93: 179-183. <https://doi.org/10.5479/si.00810266.93.179>
- MADDISON W. P. & MADDISON D. R. 2019. — *Mesquite: a Modular System for Evolutionary Analysis*. Version 3.51. 2018.
- MAGALLANES I., PARHAM J. F., SANTOS G.-PH. & VELEZ-JUARBE J. 2018. — A new tuskless walrus from the Miocene of Orange County, California, with comments on the diversity and taxonomy of odobenids. *PeerJ* 6: e5708. <https://doi.org/10.7717/peerj.5708>
- MARX F. G., LAMBERT O. & DE MUIZON C. 2017. — A new Miocene baleen whale from Peru deciphers the dawn of cetotheriids. *Royal Society Open Science* 4: 170560. <https://doi.org/10.1098/rsos.170560>
- MOREJOHN G. V. 2001. — Baculum of the Weddell seal with comparisons to other phocid seals. *Journal of Mammalogy* 82: 877-881. [https://doi.org/10.1644/1545-1542\(2001\)082%3C0877:BOTWSW%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082%3C0877:BOTWSW%3E2.0.CO;2)
- MUIZON C. DE 1981. — *Les vertébrés fossils de la Formation Pisco (Pérou) Première partie: deux nouveaux Monachinae (Phocidae: Mammalia) du Pliocène de Sud Sacaco*. Institut français d'Études Andines, Mémoire 6: 20-161.
- MUIZON C. DE 1982. — Phocid phylogeny and dispersal. *Annals of the South African Museum* 89: 175-213. <https://www.biodiversitylibrary.org/page/40680570>
- MUIZON C. DE 1988. — Les vertébrés fossiles de la Formation Pisco (Pérou). Troisième partie: Les Odontocètes (Cetacea, Mammalia) du Miocène. *Travaux de l'Institut français d'Études andines* 42: 1-244.
- MUIZON C. DE & BELLON H. 1986. — Nouvelles données sur l'âge de la Formation Pisco (Pérou). *Comptes rendus de l'Académie des sciences. Série 2, Mécanique, Physique, Chimie, Sciences de l'univers, Sciences de la Terre* 303: 1401-1404. <https://gallica.bnf.fr/ark:/12148/bpt6k5664058j/f1407.item>
- MUIZON C. DE & BOND M. 1982. — Le Phocidae (Mammalia) Miocène de la formation Paraná (Entre Rios, Argentine). *Bulletin du Muséum National d'Histoire Naturelle, Paris, 4ème série* 3-4 : 165-207. <https://www.biodiversitylibrary.org/page/55651278>
- MUIZON C. DE & DEVRIES T. J. 1985. — Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74 (3): 547-563. <https://doi.org/10.1007/BF01821211>
- MUIZON C. DE & HENDEY Q. B. 1980. — Late Tertiary seals of the South Atlantic Ocean. *Annals of the South African Museum* 82: 91-128. <https://www.biodiversitylibrary.org/page/40752149>
- OCHOA D., DEVRIES T. J., QUISPE K., BARBOSA-ESPITIA A., SALAS-GISMONDI R., FOSTER D. A., GONZALES R., REVILLON S., BERROSPÍ R., PAIRAZAMÁN L. & CARDICH J. 2022. — Age and provenance of the Mio-Pleistocene sediments from the Sacaco area, Peruvian continental margin. *Journal of South American Earth Sciences* 116: 103799. <https://doi.org/10.1016/j.jsames.2022.103799>
- PARHAM J. F. & PYENSON N. D. 2010. — New sea turtle from the Miocene of Peru and the iterative evolution of feeding ecomorphologies since the Cretaceous. *Journal of Paleontology* 84: 231-247. <https://doi.org/10.1666/09-077R.1>
- PEREDO C. M. & UHEN M. D. 2016. — Exploration of marine mammal paleogeography in the Northern Hemisphere over the Cenozoic using beta diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology* 449: 227-235. <https://doi.org/10.1016/j.palaeo.2016.02.034>
- PIÉRARD J. 1971. — Osteology and Myology of the Weddell Seal *Leptonychotes weddelli* (Lesson 1826), in BURT W. H. (ed.), *Antarctic Pinnipedia. Antarctic Research Series* 18: 53-108. <https://doi.org/10.1029/AR018p0053>
- RAY C. E. 1976. — Geography of phocid evolution. *Systematic Zoology* 25: 391-406. <https://doi.org/10.2307/2412513>
- RULE J. P., ADAMS J. W., ROVISNKY D. S., HOCKING D. P., EVANS A. R. & FITZGERALD E. M. 2020a. — A new large-bodied Pliocene seal with unusual cutting teeth. *Royal Society Open Science* 7: 201591. <https://doi.org/10.1098/rsos.201591>
- RULE J. P., ADAMS J. W., MARX F. G., EVANS A. R., TENNYSON A. J. D., SCOFIELD R. P. & FITZGERALD E. M. G. 2020b. — First monk seal from the Southern Hemisphere rewrites the evolutionary history of true seals. *Proceedings of the Royal Society B* 287: 20202318. <https://doi.org/10.1098/rspb.2020.2318>
- RULE J. P., HOCKING D. P. & FITZGERALD E. M. G. 2020c. — Pliocene monachine seal (Pinnipedia: Phocidae) from Australia constrains timing of pinniped turnover in the Southern Hemisphere. *Journal of Vertebrate Paleontology* 39: e1734015. <https://doi.org/10.1080/02724634.2019.1734015>
- RULE J. P., ADAMS J. W. & FITZGERALD E. M. G. 2020d. — Colonization of the ancient southern oceans by small-sized Phocidae: new evidence from Australia. *Zoological Journal of the Linnean Society* 191: 1160-1180. <https://doi.org/10.1093/zoolinnean/zlaa075>

- RULE J. P., ADAMS J. W. & FITZGERALD E. M. G. 2021. — Early monk seals (Monachinae: Monachini) from the late Miocene-early Pliocene of Australia. *Journal of Systematic Palaeontology* 19: 441-459. <https://doi.org/10.1080/14772019.2021.1920639>
- STANTON C. 2014. — *Correlation and Paleoenvironments above West T9. 3 Tuff, Pisco Formation, Peru*. Loma Linda University, Master dissertation, 94 p.
- SWOFFORD D. L. 2002. — *PAUP*. Phylogenetic Analysis using Parsimony (*and other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- TAVANI G. 1941. — Revisione dei resti del pinnipede conservato nel museo di geologia di Pisa. *Palaeontographica Italica* 40: 97-112.
- TRUE F. W. 1906. — Description of a new genus and species of fossil seal from the Miocene of Maryland. *Proceedings of the United States National Museum* 30: 835-840. <https://doi.org/10.5479/si.00963801.30-1475.835>
- VALENZUELA-TORO A. M., PYENSON N. D., GUTSTEIN C. S. & SUÁREZ M. E. 2016. — A new dwarf seal from the late Neogene of South America and the evolution of pinnipeds in the southern hemisphere. *Papers in Palaeontology* 2: 101-115. <https://doi.org/10.1002/spp2.1033>
- VAN BENEDEN P.-J. 1877. — Description des ossements fossiles des environs d'Anvers, première partie. Pinnipèdes ou amphithériens. *Annales du Musée royal d'Histoire naturelle de Belgique* 1: 1-88.

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APPENDIX 1. — List of genus and species names cited in the text with authorship and date of publication

- Acrophoca* Muizon, 1981
Acrophoca longirostris Muizon, 1981
Australophoca Valenzuela-Toro, Pyenson, Gutstein & Suárez, 2016
Australophoca changorum Valenzuela-Toro, Pyenson, Gutstein & Suárez, 2016
Callophoca Van Beneden, 1876
Callophoca obscura Van Beneden, 1876
Cystophora (Nilsson, 1820)
Cystophora cristata (Erxleben, 1777)
Devinophoca Koretsky & Holec, 2002
Eomonachus belegaerensis Rule, Adams, Marx, Evans, Ten-nyson, Scofield & Fitzgerald, 2020
Erignathus (Gill, 1886)
Erignathus barbatus Erxleben, 1776
Eumetopias jubatus (Schreber, 1776)
Frisiphoca Dewaele, Lambert & Louwye, 2018
Frisiphoca aberrata (Van Beneden, 1876)
Frisiphoca affinis (Van Beneden, 1876)
Hadrokirus Amson & Muizon, 2014
Hadrokirus martini Amson & Muizon, 2014
Halichoerus (Nilsson, 1820)
Halichoerus grypus (Fabricius, 1791)
Histiophoca (Gill, 1873)
Histiophoca fasciata (Zimmerman, 1783)
Homiphoca Muizon & Hendey, 1980
Homiphoca capensis (Hendey & Repenning, 1972)
Hydrurga (Gistel, 1848)
Hydrurga leptonyx (Blainville, 1820)
Kawas Cozzuol, 2001
Kawas benegasorum Cozzuol, 2001
Leptonychotes (Gill, 1872)
Leptonychotes weddellii (Lesson, 1826)
Leptophoca True, 1906
Lobodon (Gray, 1844)
Lobodon carcinophaga (Hombron & Jacquinot, 1842)
Magophoca n. gen.
Magophoca brevirostris n. gen., n. sp.
- Mirounga* Gray, 1827
Mirounga leonina (Linnaeus, 1758)
Monachus monachus Hermann, 1779
Monotherium Van Beneden, 1876
Monotherium delognii Van Beneden, 1876
Neomonachus schauinslandi (Matschie, 1905)
Neomonachus tropicalis (Gray, 1850)
Nanophoca Dewaele, Amson, Lambert & Louwye, 2017
Nanophoca vitulinoides (Van Beneden, 1871)
Noriphoca Dewaele, Lambert & 2018
Noriphoca gaudini (Guiscardi, 1871)
Ommatophoca (Gray, 1844)
Ommatophoca rossii (Gray, 1844)
Otaria byronia Blainville, 1820
Pagophilus (Gray, 1844)
Pagophilus groenlandicus (Erxleben, 1777)
Phoca Linnaeus, 1758
Phoca largha (Pallas, 1811)
Phoca vitulina Linnaeus, 1758
Piscophoca Muizon, 1981
Piscophoca pacifica Muizon, 1981
Pliophoca Tavani, 1941
Pliophoca etrusca Tavani, 1941
Properitychus Ameghino, 1893
Properitychus argentinus (Ameghino, 1893)
Proterozetes Barnes, Ray & Koretsky, 2006
Proterozetes ulysses Barnes, Ray & Koretsky, 2006
Pteronarcos goedertae Barnes, 1989
Sarcodectes Rule, Adams, Rovinsky, Hocking, Evans & Fitzgerald, 2020
Sarcodectes magnus Rule, Adams, Rovinsky, Hocking, Evans & Fitzgerald, 2020
Titanotaria orangensis Magallanes, Parham, Santos & Velez-Juarbe, 2018
Virginiphoca magurai Dewaele, Peredo, Meyvisch & Louwye, 2018

APPENDIX 2. — Taxon list, specimens, and references used for comparisons.

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|--------------------------------|--|----------|
| Pinnipediformes | | |
| <i>Pteronarcos goedertae</i> | Barnes 1989 (original description); | |
| <i>Pinnipedia</i> | | |
| ODOBENIDAE | | |
| <i>Odobenus rosmarus</i> | IRSNB 1150B, IRSNB 1150D; | |
| OTARIIDAE | | |
| <i>Arctocephalus pusillus</i> | USNM 484928 | |
| <i>Otaria byronia</i> | USNM 95063, USNM 153568, USNM 153569, USNM 484888, USNM 484906, USNM 484912; | |
| | | PHOCIDAE |
| <i>Acrophoca longirostris</i> | MNHN.F.PPI60, MNHN.F.SAS563 (holotype), MNHN.F.SAS1654, MNHN.F.SAS1654, MNHN.F.PPI265; | |
| <i>Australophoca changorum</i> | Valenzuela-Toro <i>et al.</i> 2016 (original description); | |
| <i>Callophoca obscura</i> | IRSNB 1156-M177 (lectotype); | |
| <i>Cystophora cristata</i> | USNM 1745, USNM 16022, USNM 188931, USNM 188946, USNM 188962, USNM 241360, USNM 257030, USNM 269129, USNM 504888, USNM 504889, USNM 550317, USNM 550377, USNM 550411, USNM 550444, USNM 571678, USNM 572578, USNM 572579, USNM 593970; | |

Appendix 2. — Continuation.

<i>Devinophoca claytoni</i>	Koretsky & Holec 2002 (original description);	<i>Monotherium?</i> sp.	IRSNB 1227;
<i>Devinophoca emryi</i>	Koretsky & Rahmat 2015 (original description);	<i>Nanophoca vitulinoides</i>	IRSNB M2276a-q (neotype), IRSNB 1059-M240a-f, IRSNB 1066-M243a-c, IRSNB 1226-M244a,b, IRSNB M2268, IRSNB M2274, IRSNB M2270, IRSNB M2269, IRSNB 1075-M245, IRSNB M2273, IRSNB M2279, IRSNB 1073-M246, IRSNB 1092-M236, IRSNB M2277, IRSNB 1068-M241, IRSNB 1063-M242, IRSNB M2278, IRSNB M2272, IRSNB M2271, IRSNB 1049-M247, IRSNB 1051-M251, IRSNB 1102-M238, IRSNB 1069-M248, IRSNB 1070-M249, IRSNB 1090-M233, IRSNB 1105-M239, IRSNB 1300-M250, IRSNB M2275;
<i>Eomonachus belegaerensis</i>	Rule <i>et al.</i> 2021 (original description);	<i>Neomonachus schaunslandi</i>	USNM 243838, USNM 243839, USNM 334577, USNM 395996, USNM 395997, USNM 395999
<i>Erignathus barbatus</i>	MNHN-ZM-AC-A7949, USNM 16116, USNM 269126, USNM 500249, USNM 500250, USNM 500251;	<i>Neomonachus tropicalis</i>	BMNH.1887.8.5.1, USNM 100363, USNM 100371;
<i>Frisiphoca aberrata</i>	IRSNB 1191-M266 (lectotype);	<i>Noriphoca gaudini</i>	Guiscard 1871 (original description);
<i>Frisiphoca affinis</i>	IRSNB 1118-M260 (lectotype);	<i>Ommatophoca rossii</i>	IRSNB 1164, IRSNB 15389, USNM 275206, USNM 302975, USNM 339989;
<i>Hadrokirus martini</i>	MNHN.FSAS1662 (holotype), MUSM 340 (paratype), MUSM 1662 (paratype), Amson & Muizon 2014 (original description);	<i>Pagophilus groenlandicus</i>	USNM 3517, USNM 21535, USNM 188766, USNM 188790, USNM 188791, USNM 257031, USNM 504475, USNM 504476, USNM 550212, USNM 550332, USNM 572634, USNM 594013, USNM 594170, USNM 594206, USNM 594207;
<i>Halichoerus grypus</i>	MNHN-ZM-AC-1978-48, MNHN-ZM-AC-1981-165, USNM 36279, USNM 188839, USNM 218323, USNM 446405, USNM 446406, USNM 446408, USNM 446409, USNM 446414, USNM 504481, USNM 550367, USNM 593564, USNM 594174, USNM 494199, USNM 594203, USNM 594204, USNM 594208, USNM 594209;	<i>Phoca vitulina</i>	MNHN-ZM-AC-1983-792, MNHN-ZM-AC-1894-524, USNM 15276, USNM 21056, USNM 219876, USNM 283568, USNM 504298, USNM 550060, USNM 550330, USNM 593947, USNM 594137, USNM 594207;
<i>Histriophoca fasciata</i>	USNM 16484, USNM 399449, USNM 504959, USNM 504960;	<i>Piscophoca pacifica</i>	MNHN.FSAS72, MNHN.FSAS488, MNHN.FSAS501, MNHN.FSAS564 (holotype),
<i>Homiphoca capensis</i>	MNHN.F.AFS1, MNHN.F.AFS2, MNHN.F.AFS23, MNHN.F.AFS35, MNHN.F.AFS36, SAM-PQ-L30080, Muizon & Hendey (1980);	<i>Pliophoca etrusca</i>	MSNUP I-13993 (holotype), Berta <i>et al.</i> 2015;
<i>Hydrurga leptonyx</i>	MNHN-ZM-AC-1884-1152, MNHN-ZM-AC-1970-325, USNM 270326, USNM 275205, USNM 275208, USNM 396931, USNM 550359, USNM 550360, USNM 571676;	<i>Properiptychus argentinus</i>	Muizon & Bond (1982);
<i>Kawas benegasorum</i>	selected casts of MEF-PV 601 (holotype); Cozzuol 2001 (original description);	<i>Pusa capsica</i>	USNM 341615, USNM 341616;
<i>Leptonychotes weddellii</i>	IRSNB 1163, IRSNB 15390, USNM 269526, USNM 269528, USNM 395811, USNM 484886, USNM 504871, USNM 504875, USNM 550118;	<i>Pusa hispida</i>	MNHN-ZM-AC-17951, USNM 225778, USNM 341617;
<i>Lobodon carcinophaga</i>	IRSNB 1161, MNHN-ZM-AC-A7951, USNM 269526, USNM 269722, USNM 270325, USNM 310693, USNM 504740, USNM 504741, USNM 550080, USNM 550083;	<i>Pusa sibirica</i>	IRSNB, 15264, IRSNB 21171;
<i>Mirounga leonina</i>	IRSNB 3497, IRSNB 15642, IRSNB 17372;	<i>Sarcodectes magnus</i>	USNM PAL 475486 (holotype), USNM PAL 534034 (paratype), Rule <i>et al.</i> 2020a (original description);
<i>Monachus monachus</i>	MNHN-ZM-AC-A7953, USNM 219059;	<i>Virginiphoca magurai</i>	USNM 639750.
<i>Monotherium delognii</i>	IRSNB 1153-M257;		

APPENDIX 3. — Character list.

1. **Premaxilla, contact with the nasal:** (0) extensive; (1) reduced; (2) absent.
2. **Premaxilla, contact with the maxilla:** (0) lateral to the nasal cavity along the entire length of the contact; (1) central portion of the contact included in the nasal cavity; (2) dorsal (and central) portion of the contact included in the nasal cavity.
3. **Nasal cavity:** (0) short and opening more anteriorly than dorsally; (1) long and opening equally (more) dorsally as (than) anteriorly.
4. **Nasal cavity, lateral border in lateral view:** (0) rectilinear or weakly concave; (1) strongly concave.
5. **Nasals, position of the posterior end:** (0) anterior to or at the same level as the maxilla-frontal suture; (1) posterior to maxilla-frontal suture.
6. **Nasals, posterior extremity:** (0) flattened or frontals inserted between the nasals (1) pointed; (2) rounded.
7. **Nasals, fusion:** (0) absent; (1) present.
8. **Frontal, preorbital process:** (0) not present; (1) angular, connected to the anterior margin of the orbit by an uninterrupted crest; (2) separated from the ventral border of the orbit.
9. **Frontal, supraorbital process:** (0) absent; (1) present, but vestigial; (2) present and well developed.
10. **Alisphenoid canal:** (0) present; (1) absent.
11. **Infraorbital foramen, position of the anterior opening:** (0) anterodorsal to M1; (1) dorsal to M1; (2) posterodorsal to M1.
12. **Jugal, maxillary process in lateral view:** (0) thin process, progressively increasing in height posteriorly; (1) thick, high and widening abruptly posteriorly.
13. **Jugal, anterior end in dorsal view:** (0) lateral to, or just dorsal to the lateral margin of the infraorbital foramen; (1) above or reaching dorsomedially to the infraorbital foramen.
14. **Zygomatic arch, ventral edge in lateral view:** (0) higher than the alveolar plane; (1) at or near the level of the alveolar plane.
15. **Jugal-squamosal contact, mortised:** (0) no; (1) yes.
16. **Interorbital septum, least interorbital width:** (0) in the posterior portion of the interorbital septum; (1) in the anterior half of the interorbital septum.
17. **Interorbital septum, least interorbital width to bizygomatic width ratio:** (0) very low (0.10 or less); (1) low (between 0.10 and 0.25); (2) high (0.25 or more).
18. **Maxilla, orientation of the alveolar process:** (0) facing ventrally; (1) facing anteroventrally posterior to P1.
19. **Palate, constriction at the level of P1 and P2:** (0) absent; (1) present.
20. **Glenoid fossae, orientation of the major axes:** (0) sub-parallel; (1) slightly convergent posteriorly.
21. **Tympanic bullae, orientation of the medial margins:** (0) diverging posteriorly; (1) parasagittal.
22. **Tympanic bulla, lateral extremity:** (0) medial to, or level of the mid-width of the glenoid fossa; (1) reaching lateral to the level of mid-width of the glenoid fossa.
23. **Tympanic bulla, inflation:** (0) weak; (1) moderate, ecto-tympanic little inflated; (2) strong.
24. **Pit for the stylohyal, orientation:** (0) ventral and/or posterior; (1) ventral and anterior.
25. **Mastoid, visible in dorsal view:** (0) no; (1) yes.
26. **Mastoid, heavily pachyosteosclerotic:** (0) no; (1) yes.
27. **Mastoid, development of a lip of the anteromedial region of the mastoid, abutting the posteromedial edge of the tympanic bulla:** (0) absent; (1) present.
28. **Mastoid, relation to the paroccipital process:** (0) paroccipital process connected to the mastoid by a high and continuous ridge; (1) paroccipital process well separated from the mastoid.
29. **Carotid canal, posterior opening, visible in ventral view:** (0) yes, at least partially facing ventrally; (1) no.
30. **Carotid canal and posterior lacerate foramen, posterior opening:** (0) separated; (1) coalescent.
31. **Posterior lacerate foramen:** (0) small; (1) large and reaching medial to the tympanic bulla.
32. **Paroccipital process, size:** (0) small; (1) intermediate; (2) large.
33. **Petrosal, inflation of the uncovered part visible in the posterior lacerate foramen:** (0) no; (1) yes.
34. **Pterygoid, orientation:** (0) vertical; (1) laterally tilted and flaring posteriorly.
35. **Occipital condyles, direction in occipital view:** (0) vertical; (1) diverging dorsally.
36. **Mandible, angular process:** (0) large process protruding medially and posteriorly; (1) intermediate; (2) more a knob than a process and weakly protruding or not protruding medially.
37. **Mandible, angular process:** (0) located ventral to the level of the tooth row; (1) located at or dorsal to the level of the tooth row.
38. **Upper tooth row:** (0) parallel; (1) slightly diverging posteriorly; (2) strongly diverging posteriorly.
39. **Upper incisors, number (per quadrant):** (0) three; (1) two.
40. **Upper incisors, relative size of lateral incisors:** (0) incisiform; (1) intermediate shape; (2) caniniform.
41. **Upper incisors, roots:** (0) strongly transversely compressed; (1) moderately transversely compressed.
42. **Lower incisors, number (per quadrant):** (0) two; (1) one.
43. **Lower incisors, relative position:** (0) mesial incisor posterior to the lateral incisor; (1) mesial incisor at the same level or slightly anterior to the lateral incisor.
44. **Postcanine teeth, accessory cusps and cones:** (0) single-cusped; (1) very small or weakly-developed (longer than high); (2) well developed (higher than long).
45. **Upper premolars, distolingual projection of the cingulum:** (0) absent; (1) present. **Totally different scores compared to Amson & Muizon (2014)*

Appendix 3. — Continuation.

46. **Upper premolars:** (0) parallel to tooth row axis; (1) obliquely oriented in tooth row.
47. **P2-4 and p2-4, roots:** (0) at least one is triple-rooted; (1) all are double-rooted; (2) at least one is single-rooted.
48. **P4 and M1, diastema between P4 and M1:** (0) large; (1) reduced.
49. **P4, size comparison with M1:** (0) about equal in size; (1) P4 larger than M1.
50. **M1 and m1, roots:** (0) double-or triple-rooted; (1) single-rooted.
51. **M2:** (0) present; (1) absent.
52. **Atlas, transverse foramen:** (0) visible in posterior view; (1) at least partially visible in dorsal view.
53. **Atlas, direction of transverse process in lateral view:** (0) oblique; (1) sub-vertical.
54. **Atlas, deep fossa for *m. rectus capitis dorsalis minor*:** (0) absent; (1) present.
55. **Cervical vertebrae 3-6, tubercle and lamina of the transverse process:** (0) fused or poorly isolated from each other; (1) clearly isolated from each other.
56. **Sacrum, number of fused vertebrae:** (0) two, (1) three; (2) four.
57. **Scapula, major orientation of the posterior border in lateral view:** (0) proximodistal (dorsal component greater than posterior component; (1) anterior (posterior component greater than dorsal component).
58. **Scapula, acromion process:** (0) prominent; (1) reduced.
59. **Scapula, scapular spine:** (0) unreduced (i.e. the spine almost reaches the dorsal edge of the scapula); (1) reduced (i.e. the spine almost totally disappears and is reduced to its most proximal portion and the acromion).
60. **Scapula, scapular spine:** (0) vertical or slightly tilted posteriorly; (1) tilted posteriorly.
61. **Scapula, supraspinatus insertion area:** (0) considerably larger than infraspinatus plus teres major areas; (1) slightly larger than infraspinatus plus teres major areas; (2) equal to or smaller than infraspinatus plus teres major areas.
62. **Humerus, lesser tubercle and head:** (0) head higher or at the same level as the lesser tubercle; (1) tubercle higher.
63. **Humerus, greater tubercle and head:** (0) tubercle below the level of the head; (1) tubercle at the level of the head or slightly above; (2) tubercle above the level of the head.
64. **Humerus, transverse bar in the bicipital groove:** (0) absent; (1) present.
65. **Humerus, fossa for the origin of *m. triceps brachii caput mediale* below capitulum and lesser tubercle:** (0) shallow; (1) deep.
66. **Humerus, position of insertion of *m. pectoralis* and length deltopectoral crest:** (0) distal, long (continuous and almost reaches the distal epiphysis); (1) proximal to half length bone, short (stops abruptly approximately at mid-length of the diaphysis).
67. **Humerus, supinator ridge:** (0) well developed; (1) absent or poorly developed.
68. **Humerus, entepicondylar (=supracondylar) foramen:** (0) present; (1) absent.
69. **Radius, location of the radial tuberosity:** (0) on the medial side; (1) on the posteromedial side.
70. **Radius, deep groove for the *m. extensor digitorum communis* tendon:** (0) absent; (1) present.
71. **Ulna, distal end of the styloid process:** (0) distally pointed; (1) flattened.
72. **Metapodials, head:** (0) keeled with trochleated phalangeal articulation; (1) smooth, with flat phalanges, and articulations hinge-like.
73. **Metacarpal I, length:** (0) slightly longer than metacarpal II; (1) much longer.
74. **Manus, digit V, intermediate phalanx:** (0) unreduced; (1) strongly reduced.
75. **Manus claws:** (0) large; (1) small.
76. **Innominate, ilium:** (0) no or shallow gluteal fossa; (1) deep gluteal fossa.
77. **Innominate, proportions of the postacetabular region (width/length):** (0) long and narrow (ratio less than or equal to 0.5); (1) short and wide (ratio greater than 0.6).
78. **Innominate, location of anterodorsal iliac spine:** (0) dorsal to the anteroventral iliac spine; (1) posterodorsal to the anteroventral iliac spine.
79. **Innominate, posteroventral iliac spine (= iliac tuberosity):** (0) large and strongly protruding; (1) small or absent.
80. **Innominate, ilipectineal eminence:** (0) strongly developed; (1) moderately well developed; (2) small or absent.
81. **Femur, head and greater trochanter:** (0) head reaches higher than the greater trochanter; (1) both reach the same level; (2) greater trochanter reaches higher than the head.
82. **Femur, trochanteric fossa:** (0) little reduced; (1) strongly reduced or absent.
83. **Femur, lesser trochanter:** (0) present; (1) absent.
84. **Femur, distal condyle:** (0) roughly similar in size or slight size difference; (1) large size difference.
85. **Femur, epicondyle crest:** (0) inconspicuous or short; (1) long (reaching at least the mid-length of the diaphysis).
86. **Femur, orientation of fossa for *m. peroneus longus*:** (0) lateral; (1) anterolateral.
87. **Femur, diaphysis:** (0) width notably less than 2/3 of the width of the proximal epiphysis; (1) width approximately equal to or larger than 2/3 of the width of the proximal epiphysis.
88. **Tibial and fibula:** (0) proximal epiphyses not fused; (1) proximal epiphyses fused.
89. **Tibia, anterior tibial fossa:** (0) weak to moderately developed; (1) strong developed.
90. **Astragalus, calcaneal process:** (0) absent; (1) poorly developed; (2) well developed.
91. **Sustentacular facet of the astragalus:** (0) oval-shaped and narrowed at the contact with the cuboid facet; (1) long (at least twice longer than wide), slender and strongly bent medially; (2) short and tongue-like with no narrowing at the contact with the cuboid facet.

APPENDIX 3. — Continuation.

92. **Calcaneum, articular surface for the fibula:** (0) absent or very reduced; (1) well developed.
93. **Metatarsal III, length:** (0) less than 50% shorter than metatarsal I; (1) approximately 50% shorter (or more) than metatarsal I.

APPENDIX 4. — Phylogenetic matrix: https://doi.org/10.5852/geodiversitas2024v46a3_s1