

Icaphoca choristodon n. gen., n. sp.,
a new monachine seal (Carnivora, Mammalia)
from the Neogene of Peru

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Icaphoca choristodon n. gen., n. sp., a new monachine seal (Carnivora, Mammalia) from the Neogene of Peru

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ABSTRACT

Icaphoca choristodon n. gen., n. sp., described in the present study, represents the sixth monachine seal from the Neogene Pisco Formation of Peru. The species is solely known from the holotype, including a cranium with both mandibles, as well as five cervical vertebrae including the atlas and axis. This holotype was collected at the Cerro La Bruja locality, the type locality of *Magophoca brevirostris*, in the Ica Desert after which *Icaphoca* has been named. Stratigraphically, the holotype was recovered from strata underlying those of the Cerro La Bruja level (CLB level), from which *Magophoca* was recovered. These beds likely correspond with the P1-2 unit of the P1 sequence within the Pisco Formation. Assumed to be as old as 9 Ma (middle Tortonian), *Icaphoca* may be the oldest described monachine seal from the southeast Pacific. Following *Magophoca* and *Noriphoca*, *Icaphoca* is the third extinct monachine seal known to have six upper incisors. This plesiomorphic character is absent in all other extant and extinct Monachinae which have only four upper incisors. The elongation of the snout, as well as the presence of profound diastemas between the postcanine teeth, suggests that *Icaphoca* is closely related to *Acrophoca* from the upper Tortonian and Messinian of the Pisco Formation in the Sacaco area (Arequipa Department), c. 200 km southeast to Cerro La Bruja. The specific name *choristodon* refers to this spacing between the post-canine teeth. The close phylogenetic relationship between *Icaphoca* and *Acrophoca* is confirmed by the phylogenetic analysis, which retrieves both genera as sister taxa.

RÉSUMÉ

Icaphoca choristodon n. gen., n. sp., un nouveau phoque monachiné (Carnivora, Mammalia) du Néogène du Pérou. *Icaphoca choristodon* n. gen., n. sp., décrit dans cette étude constitue le sixième phoque monachiné provenant de la Formation Pisco du Néogène du Pérou. Cette espèce n'est connue que par son holotype qui inclut un crâne avec les deux mandibules ainsi que cinq vertèbres cervicales dont l'atlas et

KEY WORDS
Lobodontini,
Monachinae,
Phocidae,
Peru,
Pisco Formation,
Cerro La Bruja,
Tortonian,
new genus,
new species.

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

l'axis. L'holotype a été récolté dans la localité de Cerro La Bruja (département d'Ica), localité type de *Magophoca brevirostris*, dans le désert d'Ica qui a donné son nom à *Icaphoca*. Sur le plan stratigraphique, l'holotype provient de strates sous-jacentes à celles du niveau de Cerro La Bruja (Niveau CLB) dans lequel ont été récoltés les restes de *Magophoca brevirostris*. Ces couches correspondent très probablement à l'unité P1-2 de la séquence P1 au sein de la Formation Pisco. Avec un âge probable de 9 Ma (Tortonien moyen), *Icaphoca* est probablement le plus ancien phoque monachiné décrit dans le Pacifique du Sud-Est. Avec *Magophoca* et *Noriphoca*, *Icaphoca* est le troisième monachiné fossile connu à posséder six incisives supérieures. Ce caractère plésiomorphe est absent chez les autres monachinés, fossiles et actuels qui n'ont que quatre incisives supérieures. L'allongement du rostre ainsi que la présence de longs diastèmes séparant les dents post-canines suggèrent une relation étroite avec le genre *Acrophoca* du Tortonien supérieur et Messinien de la Formation Pisco dans la région de Sacaco (département d'Arequipa), environ 200 km au Sud-Est de Cerro La Bruja. Le nom d'espèce *choristodon* se réfère à cet espacement entre les dents post-canines. La relation étroite entre *Icaphoca* et *Acrophoca* est confirmée par l'analyse phylogénétique présentée dans ce travail, qui indique que les deux genres sont des taxons frères.

INTRODUCTION

Although the origin of pinnipeds has been traced to the late Oligocene or early Miocene of the eastern North Pacific, the earliest records of Phocidae Gray, 1821, or true seals, come from the North Atlantic and Mediterranean (e.g., Deméré *et al.* 2003; Koretsky & Domning 2014; Berta *et al.* 2018; Dewaele *et al.* 2018; Rule *et al.* 2020a; Park *et al.* 2024; and references therein). At the time, the Central American Seaway (CAS) separated North and South America, allowing Miocene phocids to easily migrate from the North Pacific to the North Atlantic. Indeed, the – confirmed – oldest known 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, but have also shown to be uncertain (Koretsky & Sanders 2002; Diedrich 2011; Dewaele *et al.* 2018; vs Peredo & Uhen 2016; Dewaele *et al.* 2017; Pickford & Muizon 2024). For the evolution of Phocidae, the North Atlantic Ocean was the place where phocid seals diversified into the two subfamilies, Monachinae Gray, 1869 and Phocinae Gray, 1821, and thrived during the Miocene (e.g., Ray 1976; Muizon 1982; Deméré *et al.* 2003; Berta *et al.* 2018). 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.* 2020a, 2021).

Since the early 1980s, five extinct species of the monachine subfamily have been described from the Neogene of Peru: *Acrophoca longirostris*, *Piscophoca pacifica*, *Hadrokirus martini*, *Australophoca changorum*, and *Magophoca brevirostris* (Muizon 1981; Amson & Muizon 2014; Valenzuela-Toro *et al.* 2016; Dewaele & Muizon 2024), showing that a diverse monachine seal fauna thrived in the Neogene eastern South Pacific as well. Considering the dichotomy between the long-presumed North

Atlantic origin of monachines and the recent hypothesis of a South Pacific origin of monachines (Muizon 1982; Deméré *et al.* 2003; Berta *et al.* 2018; vs Rule *et al.* 2020a), the study of new fossil phocid material from the Neogene of Peru is indispensable to bring more clarity. To date, the exact taxonomic and phylogenetic relationships between these 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 these fossil monachine seals from Peru and the four Antarctic phocids in the subfamily of Monachinae (Muizon 1981; Amson & Muizon 2014; Govender 2015; Dewaele & Muizon 2024), but others consider them to be stem monachines (Berta *et al.* 2015; Rule *et al.* 2020a, b). The former hypothesis suggests that the Neogene Peruvian seals may lie at the origin of the evolution of the present-day Antarctic seals of the tribe Lobodontini Gray, 1869 (e.g., Muizon 1981, 1982; Deméré *et al.* 2003; Dewaele & Muizon 2024), warranting the importance of understanding their evolutionary history from the point of view of ongoing climate change. In the present study, new fossil material from the Cerro La Bruja locality in Peru is examined, representing a new phocid seal species, providing clues to evolutionary and temporal pathways of the Neogene conquest of the Southern Hemisphere by Monachinae.

MATERIAL AND METHODS

PALEONTOLOGICAL AND BIOLOGICAL SAMPLE

Fossil phocid specimens housed at the Muséum national d'Histoire naturelle, Paris, France (MNHN) form the nucleus of the present study, with the holotype (and only referred specimen) of the newly described taxon being housed at the MNHN. Comparison material includes specimens of all extant phocid genera. *Phoca largha* was the sole extant species of seal unavailable to include as comparison material in this study; but it is represented by the congeneric *Phoca vitulina*.

The extinct taxa used as comparison material in the present study include all published South American taxa from Chile and Peru: the monachines *Acrophoca longirostris*, *Australophoca changorum*, *Hadrokirus martini*, *Magophoca brevirostris*, and *Piscophoca pacifica*; and *Kawas benegasorum* and *Properiptychus argentinus* from Argentina. Following the description of *Magophoca* by Dewaele & Muizon (2024), *Kawas* has been reconsidered to be a monachine, contradicting Cozzuol (2001) who originally identified the species as a phocine. Previously, Rule *et al.* (2020a) returned *Kawas* as a stem phocid. In addition, Dewaele & Muizon (2024) also limit the name *Properiptychus argentinus* to the type specimen, a right maxillary fragment with the P3 preserved. As done by Dewaele & Muizon (2024), other referred specimens are considered for comparative purposes, but their identification as *Properiptychus* should be considered with extreme care. Other extinct Monachinae included in the present study include the (fairly) completely known South African *Homiphoca capensis*, the equally well-known Mediterranean *Pliophoca etrusca*; and *Eomonachus belegaerensis* from New Zealand and *Sarcodectes magnus* from the east coast of North America, primarily known from cranial material. Other extinct Phocidae are generally very incompletely known: they are considered in this study, but their value as comparison material remains generally limited because if the limited diagnostic value of isolated (long) bones for phocid identification and comparison (Churchill & Uhen 2019; Rule *et al.* 2024).

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 remain consistent with other recent systematic paleontological descriptions of extinct Monachinae, the osteological anatomical nomenclature follows the nomenclature used by Amson & Muizon (2014) for the description of *Hadrokirus martini*, by Berta *et al.* (2015) for the redescription of *Pliophoca etrusca*, and by Dewaele & Muizon (2024) for the description of *Magophoca brevirostris*. Anatomical terminology used in the present study that have not been used by these studies, draws from Evans & De Lahunta (2013).

PHYLOGENETIC ANALYSIS

Similar to aiming to preserve consistent use of the anatomical nomenclature among different studies, the phylogenetic analysis of *Magophoca brevirostris* from Dewaele & Muizon (2024) forms the basis of the phylogenetic analysis in the present study. The present phylogenetic data matrix includes all 93 characters as used by Dewaele & Muizon (2024). All characters are equally weighted and all but two are unordered (char. 50, 53). 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 the 25 taxa, including the 24 taxa used by Dewaele & Muizon (2024). These include three outgroup species, outside Phocidae. These include the extinct non-pinniped pinnipedimorph *Pteronarcos goedertae*,

and three representatives of the Odobenidae Allen, 1881 and Otariidae Gray, 1825, the two extant pinniped clades outside Phocidae. The extinct *Pteronarcos 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: *Odobenus rosmarus* represents Odobenidae, and *Arctocephalus pusillus*, and *Otaria byronia* represent Otariidae.

Twenty-one phocid taxa are included in the phylogenetic analysis. Phocinae are represented by the extant *Erignathus barbatus*, *Halichoerus grypus*, *Pagophilus groenlandicus*, and *Phoca vitulina*. Seven extant and nine extinct taxa represent Monachinae. The extant taxa represent all three monachine tribes: Lobodontini are represented by *Hydrurga leptonyx*, *Lep-tonychotes weddellii*, *Lobodon carcinophaga*, and *Ommatophoca rossii*; Miroungini Muizon, 1982 by *Mirounga leonina*; and Monachini Gray, 1869 by *Monachus monachus* and *Neomonachus schauinslandi*. *Acrophoca longirostris*, *Eomonachus belegaerensis*, *Hadrokirus martini*, *Homiphoca pacifica*, *Kawas benegasorum*, *Magophoca brevirostris*, *Piscophoca pacifica*, *Pliophoca etrusca*, and *Sarcodectes magnus* are the extinct Monachinae included in the current phylogenetic analysis, in addition to *Icaphoca choristodon* n. gen., n. sp., the new taxon described in the present study.

The phylogenetic matrix is built using Mesquite 3.51 (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 has been adapted from Rule *et al.* (2020a; corrected phylogeny) and Dewaele & Muizon (2024). Character states are optimized using the accelerated transformation criterion (ACCTRAN). Homoplasy is downweighted 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/10.7934/P5967>

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

INSTITUTIONAL ABBREVIATIONS

IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium;
MEF	Museo paleontológico “Edigio Feruglio”, Trelew, Chubut, 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.

SYSTEMATIC PALEONTOLOGY

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

Genus *Icaphoca* n. gen.

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TYPE AND ONLY SPECIES INCLUDED. — *Icaphoca choristodon* n. gen., n. sp.

ETYMOLOGY. — from the city of Ica (Peru), which gave its name to the Department where the specimen was discovered, and *phoca* (seal, in Greek).

DIAGNOSIS. — As for the type species, *Icaphoca choristodon* n. gen., n. sp.

Icaphoca choristodon n. gen., n. sp.
(Figs 2-6; Tables 1-5)

urn:lsid:zoobank.org:act:D62656C2-2C7D-4C7C-87F9-2F892F941620

TYPE MATERIAL (HOLOTYPE BY MONOTYPY). — Peru • 1 specimen (original specimen; subcomplete skull with associated left and right mandibles, atlas, axis, third, fourth, and fifth cervical vertebrae); Ica Department, Cerro La Bruja; Pisco Formation, P1 sequence, unit P1-2; Cenozoic, Neogene, Tortonian; c. 14°32'08.13"S, 75°39'39.45"W; 1981; Muizon leg.; MNHN.F.PP1270.

DIAGNOSIS. — Small to medium-sized lobodontin monachine, having an elongated rostrum, similar to, but not to the same extent as *Acrophoca longirostris*. *Icaphoca choristodon* n. gen., n. sp. is a lobodontin, based on the following unambiguous synapomorphies, as detailed by the phylogenetic analysis, below: a parasagittal orientation of the medial margins of the tympanic bullae; the presence of a lip in the anteromedial region of the mastoid, abutting the posteromedial edge of the tympanic bulla; and the transverse foramen of the atlas is at least partially visible in dorsal view. *Icaphoca choristodon* n. gen., n. sp. differs from all other monachine except *Acrophoca longirostris* in the presence of well-developed diastemata between all post-canine teeth, the diastema between P4 and M1 being distinctly larger. *Icaphoca* also shares with *Acrophoca* the anterior end of the maxillary process of the jugal reaching above or dorsomedially to the infraorbital foramen. It differs from *Acrophoca* in having six upper incisors as in *Magophoca brevirostris*, and *Noriphoca gaudini* (a condition, absent in all other monachines), in having a moderately inflated ectotympanic, and an atlas in which the transverse foramen is visible in posterior view only.

ETYMOLOGY. — from the Greek *choristos* (separated) and *odontos* (tooth) referring to the wide separation between the upper and lower postcanine teeth, to enhance this major difference with the stratigraphically close *Magophoca brevirostris*.

TYPE LOCALITY. — The holotype of *Icaphoca choristodon* n. gen., n. sp. was discovered in 1981 by one of us (CM) at the base of the slopes of the Cerro La Bruja in the Ica Desert on the west side of the road from Ocucaje to Lomitas, west to the area named "Pampa Los Pescadores" (Carta Nacional 1/100 000,

Hoja 30-1, Lomitas; Instituto Geografico militar Lima-Peru 1977; Ica Department) (Fig. 1). Since no GPS coordinates were available in 1981, an approximate collecting area of the specimen described here is outlined as a red oval on the west side of the road on Figure 1.

TYPE HORIZON AND AGE. — The holotype of *Icaphoca choristodon* n. gen., n. sp., has been extracted from beds slightly older than those of the CLB level. The latter correspond to the base (unit P2-1) of the P2 sequence of the Pisco Formation, and the beds which have yielded the holotype of *I. choristodon* n. gen., n. sp. therefore likely proceed from the younger beds (unit P1-2) of the P1 sequence of the Pisco Formation. The age of the specimen should therefore be slightly older than that of the CLB level (in which *Magophoca brevirostris* remains have been discovered). According to Di Celma *et al.* (2017) the strata of the P1 sequence of the Pisco formation were deposited between 9.5 and 8.9 Ma. Therefore, *I. choristodon* n. gen., n. sp. could be as old as 9 Ma, which corresponds to the middle part of the Tortonian.

DESCRIPTION AND COMPARISON

CRANIUM (Figs 2-6; Tables 1-5)

General

The holotype (MNHN.F.PP1270) specimen of *Icaphoca choristodon* n. gen., n. sp. is also the only known specimen of the species. The skull is fractured and notably deformed. However, the overall morphology is well preserved, allowing a detailed description of most visible bones.

The dental formula of *Icaphoca* is I3/2 C1/1 4/4P 1/1M (char. 39[0], 42[0], 51[1]). The presence of six upper incisors (three per upper quadrant) and four lower incisors (two per lower quadrant) has been considered a plesiomorphy, present in most terrestrial and aquatic Carnivora and Phocinae, whereas Monachinae are traditionally characterized by two upper incisors and two lower incisors (e.g., Muizon 1981; Berta & Wyss 1994; Bininda-Emonds & Russell 1996). Notable exceptions are the monachine genus *Mirounga*, and the phocine species *Cystophora cristata*, having two upper incisors and one lower incisor. Although all extant and most extinct Monachinae have two upper and two lower incisors, two extinct Monachinae conform the plesiomorphic condition of having three upper incisors, besides *Icaphoca*. These are *Noriphoca gaudini* from the early (?) Miocene of the Abruzzo region in Italy (Guiscardi 1871; Dewaele *et al.* 2018), and *Magophoca brevirostris* from the late Miocene of the Cerro La Bruja locality in Peru (Dewaele & Muizon 2024).

Skull dimensions of *Icaphoca* are comparable to most other extinct Monachinae, but smaller than extant Monachinae (Tables 1; 2). A notable exception is *Australophoca*, which does not have any published skull specimens, but is the smallest monachine based on postcranial remains. Churchill *et al.* (2014) presented two equations to estimate overall body length of pinnipeds based on cranial measurements. The equation used for Phocidae is:

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

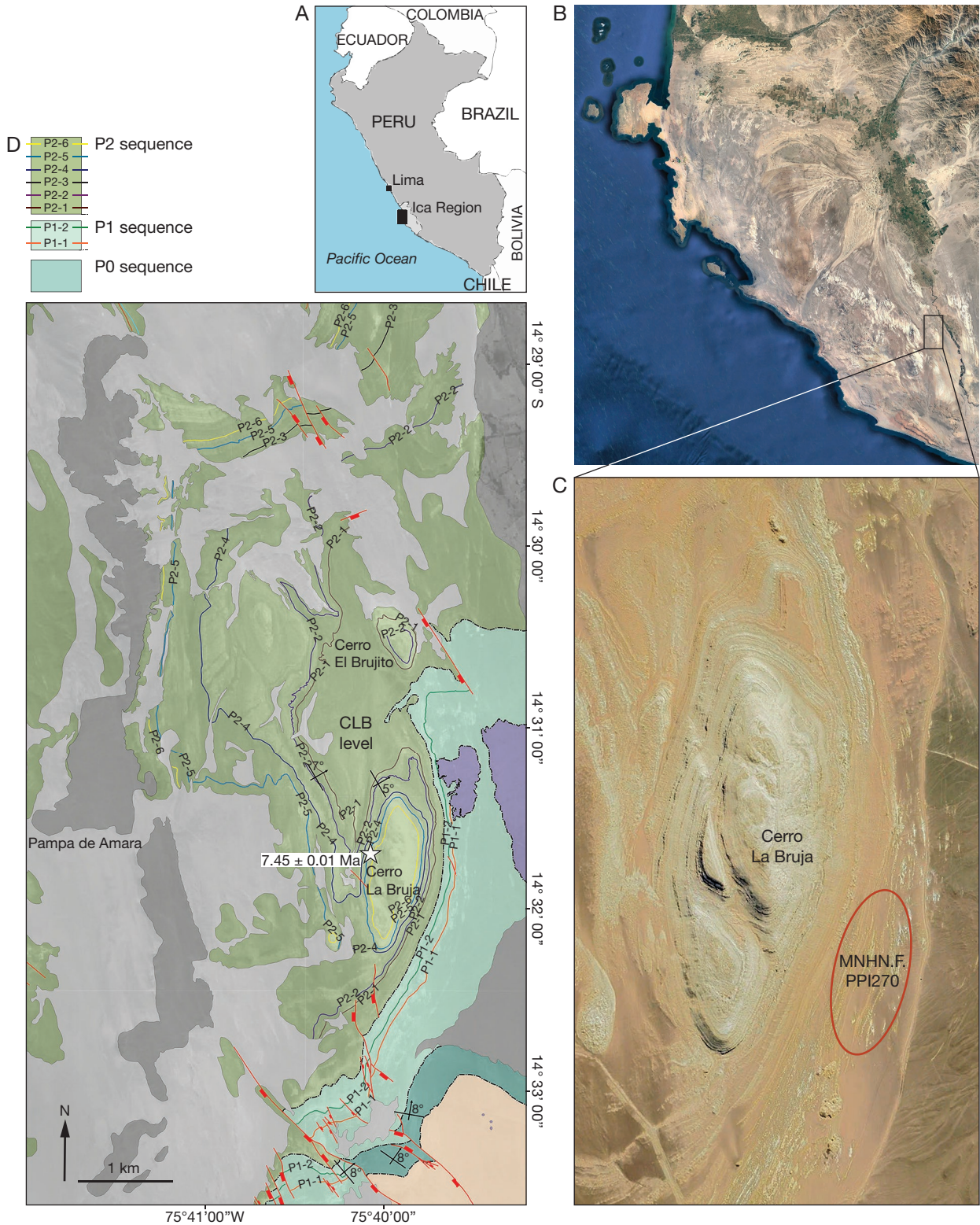


FIG. 1. — Geography and geology of the Cerro La Bruja Locality. **A**, Geographic location of the study area of Cerro La Bruja; **B**, **C**, photos of the locality (red oval indicates the place where the holotype of *Icaphoca choristodon* n. gen., n. sp. was extracted); **D**, geological map indicating the CLB level in the Cerro La Bruja locality; white star indicates a radioisotopic age obtained from a volcanic ash layer (Di Celma *et al.* 2017). Credits: A, D, modified from Di Celma *et al.* (2017); B, C, Google Earth.

With a width of 43.4 mm and a width of 59.2 mm across the canines and across the occipital condyles respectively, the individual to which the holotype skull belongs, had an

estimated body length of *c.* 224 cm. This is roughly similar to the size of *Magophoca* as calculated by Dewaele & Muizon (2024).

TABLE 1. — Comparative measurements of the holotype cranium (MNHN.F.PPI 270a) of *Icaphoca choristodon* n. gen., n. sp. in comparison with other Monachinae and selected Phocinae. Abbreviations: **BCW**, bicondylar width; **BZW**, bizygomatic width; **e**, estimate; **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; **WRPP**, width of rostrum at preorbital processes. Measurements in mm.

Specimen	BZW	MPW	WRPP	PLWM1	BCW	GLFW
<i>Icaphoca choristodon</i> n. gen., n. sp. (MNHN.F.PPI270a)	–	70.3 × 2 = 140.6e	–	31.1 × 2 = 62.2e	29.6 × 2 = 59.2e	–
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>Magophoca brevirostris</i> (MNHN.F.PPI276; male)	–	–	–	31.9 × 2 = 63.8	–	–
<i>Magophoca brevirostris</i> (MNHN.F.PPI277; female?)	132e	120.7	–	–	58.3	122.6
<i>Magophoca brevirostris</i> (MNHN.F.PPI269; female?)	136	129.5	49e	63e	60.3	130
<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
<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	148.2
<i>Neomonachus tropicalis</i> (USNM 100363; male)	167	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	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	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> (USNM 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	43.7	58	105.4
<i>Pagophilus groenlandicus</i> (USNM 188791; female)	102.8	109.7	27	45	57.6	101.2
<i>Phoca vitulina concolor</i> (USNM 504298; male)	130.4	125.1	34.3	54.5	56.1	114
<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

ROSTRUM

The rostrum of *Icaphoca choristodon* n. gen., n. sp. is elongate (Figs 2-4). As measured from the anterior edge of the orbit to the apex of the premaxilla it is 93.5 mm long. In the paratype of *Magophoca* (MNHN.F.PPI269) the length of the rostrum is 79.5 mm, therefore the rostrum of *Icaphoca choristodon* n. gen., n. sp. is 5 % longer than that of *Magophoca brevirostris*. This difference is regarded as significant since the two specimens have the same estimated body length 224 cm vs 223 cm respectively.

The premaxilla lines the medial wall of the nasal cavity. The ascending ramus of the premaxilla largely remains within the nasal cavity, with only the posterodorsal triangular shaped portion of the ascending ramus of the premaxilla extending outward and being visible in lateral view (char. 2[1]). Consequently, the maxilla-premaxilla suture follows the dorsal edge of the nasal cavity in its median portion and is not visible in lateral view in the anteroventral and median portions of the rostrum.

When compared to other Phocidae, this condition conforms with Monachinae. In Phocinae, on the other hand, the ascending ramus of the premaxilla is visible in lateral view

along the entire length of the nasal cavity. Notable exceptions are the phocine Histriophocini, in which this ascending ramus is marginally visible in lateral view at the middle part of the nasal cavity. In the phocine *Cystophora cristata* and the monachine *Mirounga*, the premaxilla is only visible in lateral view in the anterior portion of the nasal cavity. This condition can be considered an osteological adaptation to accommodate the “hood” of *Cystophora* and the proboscis of *Mirounga*.

The premaxilla of *Icaphoca* bears small dorsally pointing tuberosities at the anteromedial end of the nasal cavity. The premaxillary tuberosities are generally absent or at least very weak in extant Monachinae, except for *Hydrurga*. Within fossil monachines, premaxillary tuberosities are weak in *Eomonachus* and *Sarcodectes*, whereas they are conspicuous in *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Magophoca*, and *Piscophoca*. Furthermore, *Homiphoca*, and to a lesser extent *Piscophoca*, are characterized by a strong anterior projection of the tuberosities.

The lateral margin of the nasal cavity in *Icaphoca* appears to be strongly concave dorsally (char. 4[1]), with the opening of the nasal cavity oriented more dorsally than anteriorly (char. 3[1]).

Both conditions vary among Monachinae. Whereas most Monachinae have a nasal cavity with a rather strongly curving lateral margin and an opening that faces dorsally rather than anteriorly, this curvature is gentle in *Lobodon*, and the nasal cavity faces rather anteriorly in *Ommatophoca*.

The posterodorsal extremity of the ascending ramus of the premaxilla contacts the nasal (char. 1[0]). This contact is extensive, a plesiomorphic character shared with Phocinae, except *Cystophora* and *Mirounga*, in which the posterior part of the ascending process is lost. Among Monachinae, this character varies and appears to largely split between extant and extinct taxa, with *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Magophoca*, and *Sarcodectes* also exhibiting an extensive contact between the premaxilla and the nasal. This contact is reduced in *Leptophoca*, *Piscophoca*, and the tribe Monachini (not preserved in *Pliophoca*). In *Hydrurga*, *Lobodon*, *Mirounga* and *Ommatophoca* the premaxilla and the nasal do not contact.

The left and right palatal processes of the premaxilla form an acute triangle, with the incisors arranged in a curved arch. The incisive foramen forms a deep groove, located within the premaxillary portion of the palate, but aligning the premaxilla-maxilla suture. Both left and right incisive foramina are well separated by a thick septum. Among other Monachinae, this aligns with the extinct *Eomonachus*, *Hadrokirus*, *Magophoca*, *Piscophoca*, and *Sarcodectes* and the extant *Hydrurga*, and *Ommatophoca*. Among other Monachinae, the incisive foramina are shallow or absent.

The nasals form a long V-shaped wedge between the frontals.

The anterior margin of the right nasal over the external naris is U-shaped to V-shaped with the lateral branch being distinctly longer than the medial one. Therefore, the anterior edge of the nasals is distinctly W-shaped. This condition is similar to that observed in *Magophoca* and *Neomonachus schauinslandi*, *Hydrurga*, *Leptonychotes*, and *Lobodon*, but differs from that in *Homiphoca*, *Ommatophoca*, and *Neomonachus tropicalis*, in which it is U-shaped to concave anteriorly or from that of *Monachus*, in which the nasals are protruding anteriorly. The condition in *Acrophoca* and *Piscophoca* is unknown because this region of the skull is not preserved on the specimens available during this study.

The posterior end of the nasal of *Icaphoca* reaches at least midway between the level of the anterior margin of the orbit and the superior squamosal process of the jugal, which correspond to the posterior edge of the orbit (char. 5[1], 6[1]). Except for *Erignathus* and *Neomonachus schauinslandi*, this character agrees with other Phocidae: in *Erignathus* and *N. schauinslandi*, the nasals still form a V-shaped wedge between the frontals but have a more rounded distal termination. The posterior extension of the nasals between the frontals varies strongly among Monachinae; even intraspecifically (LD, pers. obs). Generally, the nasals terminate posterior to the anterior margin of the orbit, but do not reach the level of the superior squamosal process of the jugal posteriorly. In *Acrophoca* it extends more posteriorly than in *Icaphoca* and *Magophoca*, whereas in *Hadrokirus*, *Homiphoca*, *Sarcodectes*, *Mirounga*, Monachini, and *Ommatophoca*, it is clearly more anterior.

The ventral margin, or palatal process, of the maxilla of *Icaphoca* is horizontal, resulting in a horizontal maxillary tooth row, or alveolar process. This condition conforms with Phocidae, except

TABLE 2. — Measurements of the holotype cranium (MNHN.F.PPI270a) of *Icaphoca choristodon* n. gen., n. sp. Abbreviations and symbols: e, estimate for a character due to minor damage; n/a, a character could not be measured; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value; *, the resulting value is based on a multiplication of a measurement with factor two, particularly for characters that are ideally measured across the sagittal plane but for which only one half is incomplete. Measurements in mm.

Character	Left	Right
Overall, length	277.8	
Overall, bizygomatic width	n/a	
Rostrum, width across canines	43.4*	
Rostrum, width across maximum constriction	33.4*	
Rostrum, width across widest portion	62.2*	
I1, alveolus length	n/a	n/a
I1, alveolus width	n/a	n/a
I2, alveolus length	n/a	n/a
I2, alveolus width	n/a	n/a
I3, alveolus length	n/a	n/a
I3, alveolus width	n/a	n/a
C, alveolus length	n/a	n/a
C, alveolus width	n/a	n/a
P1, alveolus length	8.9	8.6
P1, alveolus width	7.8	7.7
P2, alveolus length	11.9	11.7
P2, alveolus width	5.6	5.7
P3, alveolus length	11.9	11.7
P3, alveolus width	6.2	5.9
P4, alveolus length	12.6	11.7
P4, alveolus width	5.1	6.1
M1, alveolus length	10.0	9.9
M1, alveolus width	4.8	5.0
Postcanine toothrow, length	74.8	72.6
Postcanine toothrow, diastema P1-P2	3.3	4.6
Postcanine toothrow, diastema P2-P3	6.1	3.5
Postcanine toothrow, diastema P3-P4	3.1	3.4
Postcanine toothrow, diastema P4-M1	9.8	8.7
Infraorbital foramen, width	8.4	7.5
Premaxilla, length ventral portion at sagittal suture	41.1	
Maxilla, length of palatine process at sagittal suture	n/a	
Tympanic bulla, width	38.1	37.9
Tympanic bulla, length	46.2	45.5
Tympanic bullae, width between	n/a	
Naris, horizontal length	54.7e	
Interorbital bridge, least width	19.0e	
Glenoid fossae, width	31.6	30.0
Glenoid fossae, length	n/a	18.3
Braincase, length	100.5e	
Braincase, width	108.6e*	
Mastoids, width across	140.6*	
Occipital condyles, width across	59.2*	
Occipital condyles, height	32.8	
Foramen magnum, width	28.0*	
Foramen magnum, height	22.4	

for the extant monachine *Ommatophoca*, and the extinct monachines *Hadrokirus* and, to a lesser extent, *Piscophoca*, in which the ventral margin of the maxilla is upturned, facing anteroventrally (char. 18[1]) (Muizon & Hendey 1980; Muizon 1981; Amson & Muizon 2014; Govender 2015). The alveolar process is reduced, with the base of the tooth row raised only little over the palate. In cross-section, the palate is flat, as in other Monachinae, but unlike Phocinae, which have a more arching palate.

The maxillary tooth row is constricted at the level of P2 (char. 19[1]), with the palate widening posteriorly being almost twice as wide at the level of M1, as at the level of P2 (Table 2). The condition of *Icaphoca* differs from that in *Magophoca*, in which the palate constriction is at the level

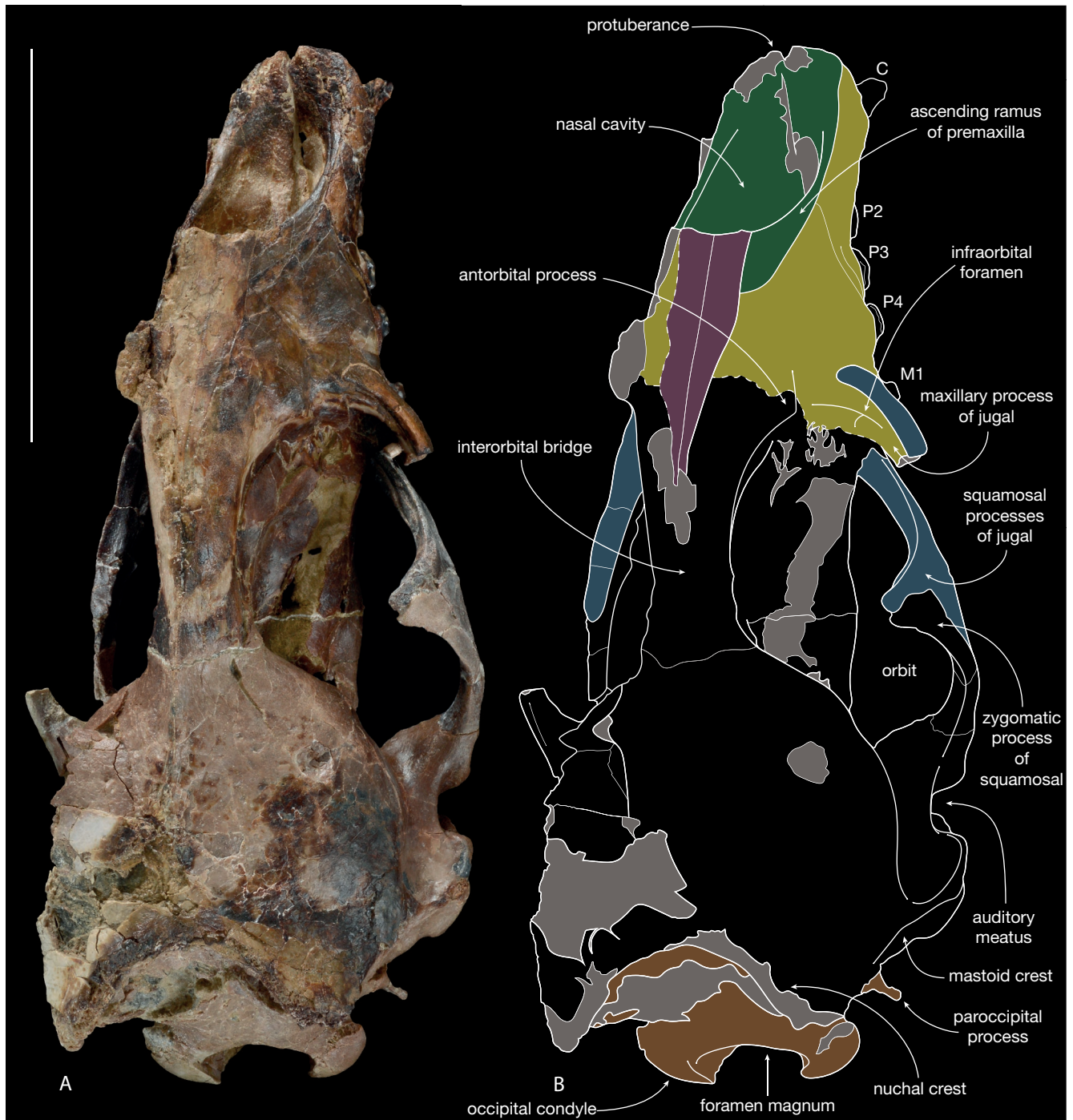


FIG. 2. — Cranium of *Icapthoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270). A, Cranium in dorsal view; B, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, nasals in purple, maxillae in yellow, jugal in blue, basioccipital in brown. 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 nasals, maxillae and frontals. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm. Photo by L. Cazes & P. Loubry (CR2P); drawing by L. Dewaele.

of P1. Among other Monachinae, the tooth row is mostly constricted at the level of P1 or P2, and the palate also significantly widens posteriorly. Notable exceptions are *Hydrurga*, and *Mirounga*, and to a lesser extent *Lobodon*, which have maxillary tooth rows that do not diverge posteriorly, or only slightly, respectively.

The palate is incompletely preserved but appears largely flat. The alveolar process is strongly reduced, with the base of the toothrow only very little elevated over the palate.

The palatine sulcus is shallow and overall weakly outlined, being more pronounced posteriorly, where it terminates into the palatine foramen. This small, rounded palatine foramen

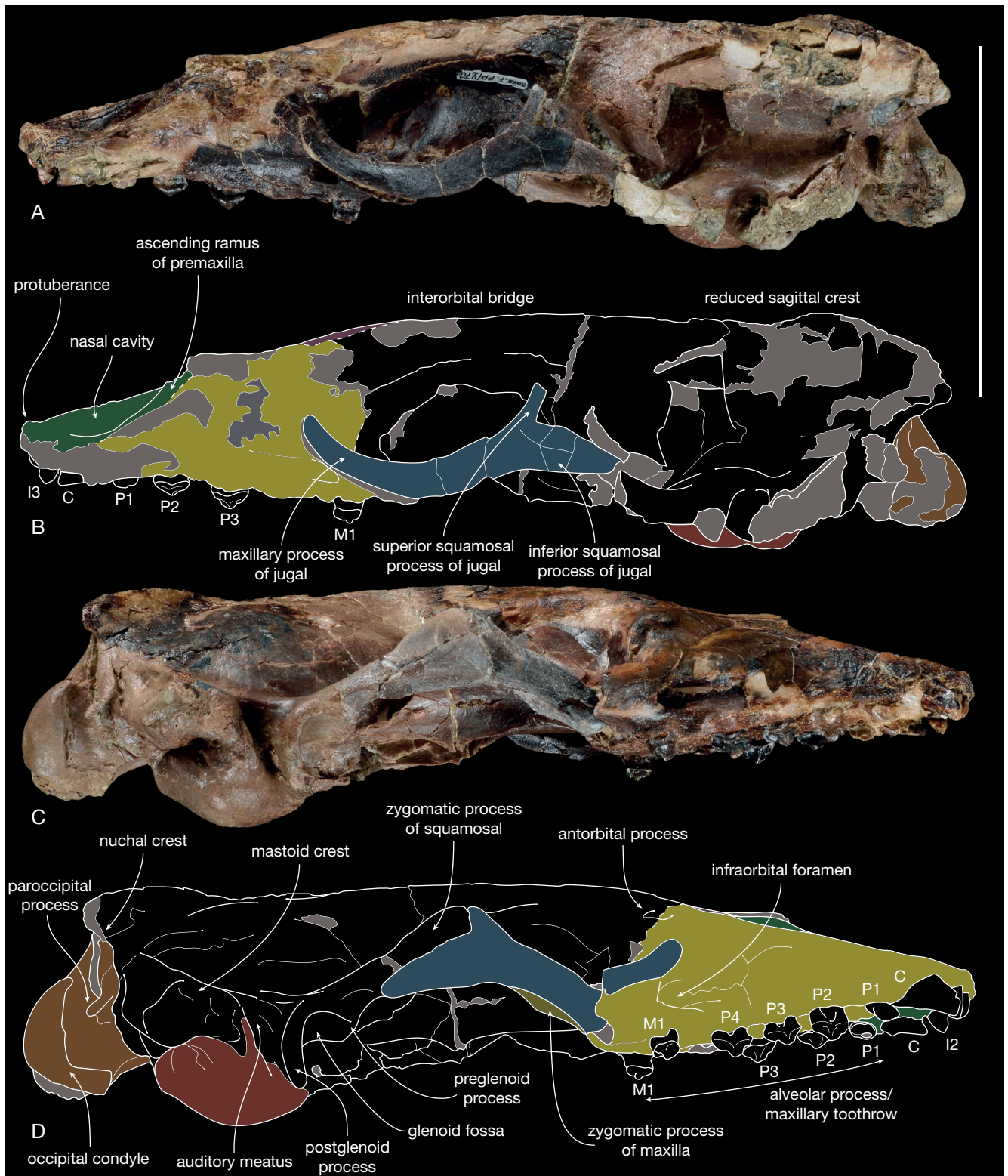


FIG. 3. — Cranium of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270). **A**, cranium in left lateral view; **B**, corresponding labelled line drawing; **C**, same cranium in right lateral view; **D**, corresponding labelled line drawing. Areas in gray in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, nasal in purple, maxilla in yellow, jugal in blue, tympanic bulla 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. Photos by L. Cazes & P. Loubry (CR2P); drawings by L. Dewaele.

is located at the level of the diastema between P4 and M1, and within the palatomaxillary suture. The position of this

foramen, with respect to the postcanine teeth, as well as the palatomaxillary suture, differs notably among Phocidae.

In Phocinae, this foramen is located well posterior to the level of M1, and on the palatamaxillary suture or on the palatine bone. An exception is the genus *Phoca*, in which it is anterior to the suture. Among Monachinae, this condition varies widely. In most fossil species, the foramen is located in the palatamaxillary suture in *Piscophoca*, *Acrophoca*, and *Homiphoca* as in *Icaphoca*. In *Hadrokirus* the foramen is anterior to the suture and in *Magophoca* its position is variable (anterior to the suture in the holotype and on the suture in the paratype). In extant monachine the foramen is anterior to the suture in *Monachus*, *Neomonachus*, *Mirounga*, *Leptonychotes*, *Lobodon*, and *Hydrurga*, but it is on the suture in *Ommatophoca*. In most extant monachines the foramen is at the level or slightly anterior to M1 except in *Hydrurga* in which it is positioned more anteriorly, at the level of P3.

ORBIT AND ZYGOMA

The antorbital process forms a distinct prominence, which is rather uncommon among Phocidae, only shared with the extant monachine *Hydrurga*, and the extinct monachines *Acrophoca*, *Hadrokirus*, *Homiphoca*, and *Piscophoca*. *Icaphoca choristodon* n. gen., n. sp. differs in this respect from *Magophoca*, in which the antorbital process is weak and low, being barely present in the holotype.

On the lateral surface of the maxilla, is the anterior opening of the infraorbital foramen, which pierces the antorbital wall. This foramen is located at the base of the zygomatic process of the maxilla, dorsal to M1. It is subcircular and large in *Icaphoca* (char. 11[1]). It is however distinctly smaller than in the paratype of *Magophoca brevirostris*, an individual which is similar in size to the holotype of *Icaphoca choristodon* n. gen., n. sp. (diameter of the left foramen is 9.8 mm in the former and 7 mm in the latter). Among other Monachinae, the infraorbital foramen is subcircular in *Acrophoca*, *Hadrokirus*, *Leptonychotes*, *Magophoca*, and Monachini; whereas it is oval in cross-section in other Monachinae. Also, among other Monachinae, the infraorbital foramen is located dorsal to M1 in most taxa, apart from extant Lobodontini, in which it is located slightly anterodorsal to M1, and *Mirounga*, in which it is located posterodorsal to M1.

The zygomatic process of the maxilla is perforated by the infraorbital canal. It extends posteriorly in a thin blade appressed against the ventromedial aspect of the maxillary process of the jugal almost reaching the base of the superior squamosal process of the jugal. On its dorsolateral side, the jugular process of the maxilla has a long, oblique, and sigmoid suture with the ventromedial side of the maxillary process of the jugal. This agrees with the condition in most other Monachinae (char. 12[0]). In Phocinae, as well as in the monachines *Hadrokirus* and *Mirounga*, the jugo-maxillary suture is rather subvertical and both the jugular process of the maxilla and the maxillary process of the jugal are stout.

The maxillary process of the jugal tapers anteromedially and forms the anterior wall of the orbit. As observed in anterior view, the anterior limit of this process terminates dorsal to the medial wall of the infraorbital foramen, a condition shared with *Acrophoca* and *Magophoca*. This condition differs from that of

Homiphoca, *Piscophoca*, *Hadrokirus* and extant Monachini, in which it is slightly lateral to or dorsal to the lateral wall of the foramen) and (char. 13[1]). In other Phocidae, the anterior tip of the maxillary process terminates lateral to the level of the infraorbital foramen.

Posteriorly, the jugal splits into a superior and an inferior squamosal process, forming a mortized jugosquamosal contact (char. 15 [1]). In addition, the superior squamosal process is more slender than the inferior squamosal process. All this agrees with other Phocidae. In *Icaphoca*, the angle between the inferior and superior squamosal branches of the jugal is roughly 90°.

Although the cranium of the holotype of *Icaphoca choristodon* n. gen., n. sp. is severely distorted, in lateral view, the lowest point of the ventral margin of the zygomatic arch is dorsal to the level tooth row (char. 14[0]). This condition agrees with other extinct Monachinae (except *Acrophoca*, *Eomonachus*, and *Homiphoca*) and the extant *Hydrurga* and *Monachini*.

The zygomatic process of the squamosal projects anterodorsally, like the condition in *Acrophoca*, *Homiphoca*, and *Magophoca*. In other extant and extinct Monachinae, this process is oriented more dorsally (i.e. with a greater dorsal component), as is the case in *Eomonachus*, *Hadrokirus*, *Mirounga*, *Monachus*, *Neomonachus tropicalis*, *Ommatophoca*, and *Piscophoca*, or anteriorly (i.e. with a greater horizontal component), as in *Hydrurga*, *Leptonychotes*, *Lobodon*, *Neomonachus schauinslandi*, and *Sarcodectes*. The zygomatic process of *Icaphoca* is very slender as in *Magophoca*, being strongly expanded at the apex differing, in this respect, from the condition observed in *Magophoca*. In other extinct monachines the process is more massive. In *Icaphoca*, the ventral edge is straight, as is observed in *Hadrokirus*, *Homiphoca*, and *Magophoca*, and differs from the conspicuously sigmoid ventral edge observed in *Acrophoca* and *Piscophoca*.

The glenoid fossa is deep and strongly semi-circular in cross-section, with a moderately well-developed preglenoid process and a strongly developed postglenoid process. Among other Monachinae, this condition corresponds most with *Hadrokirus*, *Hydrurga*, *Piscophoca*, and *Sarcodectes*. In this respect, *Icaphoca* differs from *Magophoca*, in which the glenoid fossa is shorter transversely and distinctly shallower.

The orientation of the long axes of the glenoid fossae remains difficult to ascertain, due to the fractured nature of the skull. However, as it appears, the long axes are parallel to one another, a condition shared with other Monachinae, contrasting with Phocinae, in which these axes converge posteriorly (char. 20[0]).

The interorbital bridge, formed by the frontals, is long and narrow (Table 2), and at its narrowest in the posterior portion of the bridge slightly anterior to the level of the apex of the superior squamosal process of the jugal (char. 16[0], and char. 17[1]). In other Phocidae, the location of the narrowest portion of the interorbital bridge varies between Monachinae (except *Ommatophoca*) and Phocinae. The condition in *Icaphoca* follows that in other Monachinae (except *Ommatophoca*) in which it is close to the posterior region of the orbit, whereas in Phocinae and *Ommatophoca*, it is narrowest anteriorly (in the anterior region of the orbit), gradually broadening posteriorly towards the braincase. Among other Phocidae, the width of

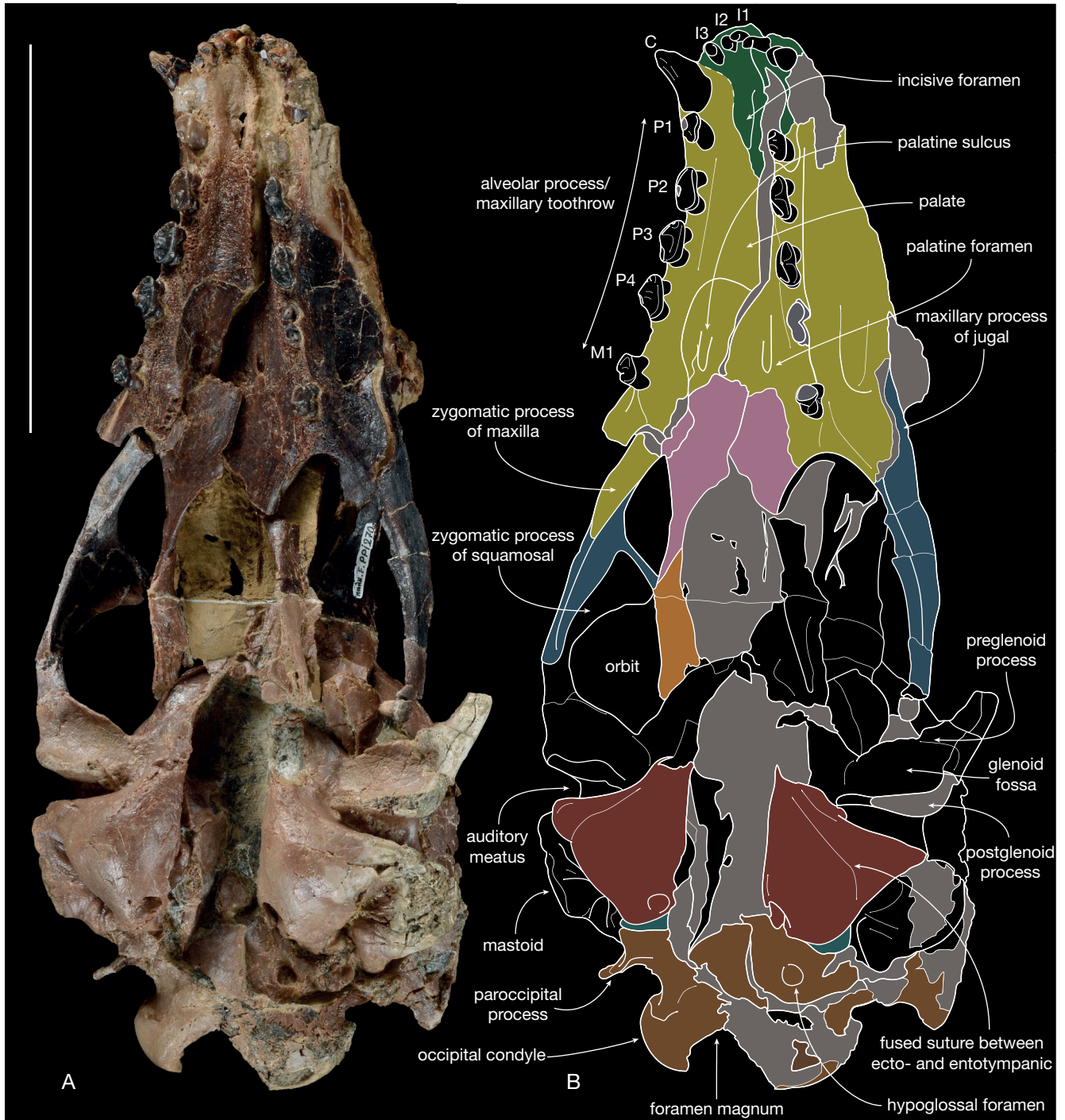


FIG. 4. — Cranium of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270). **A**, cranium in ventral view; **B**, corresponding labelled line drawing. Areas in grey in the line drawings are incompletely preserved, either severely abraded or fractured, or obscured from view by sediment matrix. Premaxillae in green, maxillae in yellow, jugals in blue, palatine in pink, pterygoids in orange, tympanic bullae in red, petrosals in teal, basioccipital in brown. Other bones are 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. Dashed lines represent the presumed sutures between the premaxillae, nasal, maxillae and frontals. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm. Photo by L. Cazes & P. Loubry (CR2P); drawing by L. Dewaele.

the interorbital bridge is similar, proportionally to the bizygomatic width, in most taxa, with the exception of the phocines *Histrophoca*, *Pagophilus*, and *Pusa*, in which it is extremely narrow, and *Cystophora*, *Erignathus*, *Homiphoca*, *Lobodon*, and *Ommatophoca*, in which this it is proportionally broad.

BASICRANIUM AND BRAINCASE (Figs 5, 6)

The braincase of *Icaphoca* is sub-rounded in dorsal view. Posterior to the interorbital bridge, the sagittal crest is only weakly developed. The nuchal crest on the posterodorsal margin of the braincase is semi-circular in outline (in dorsal

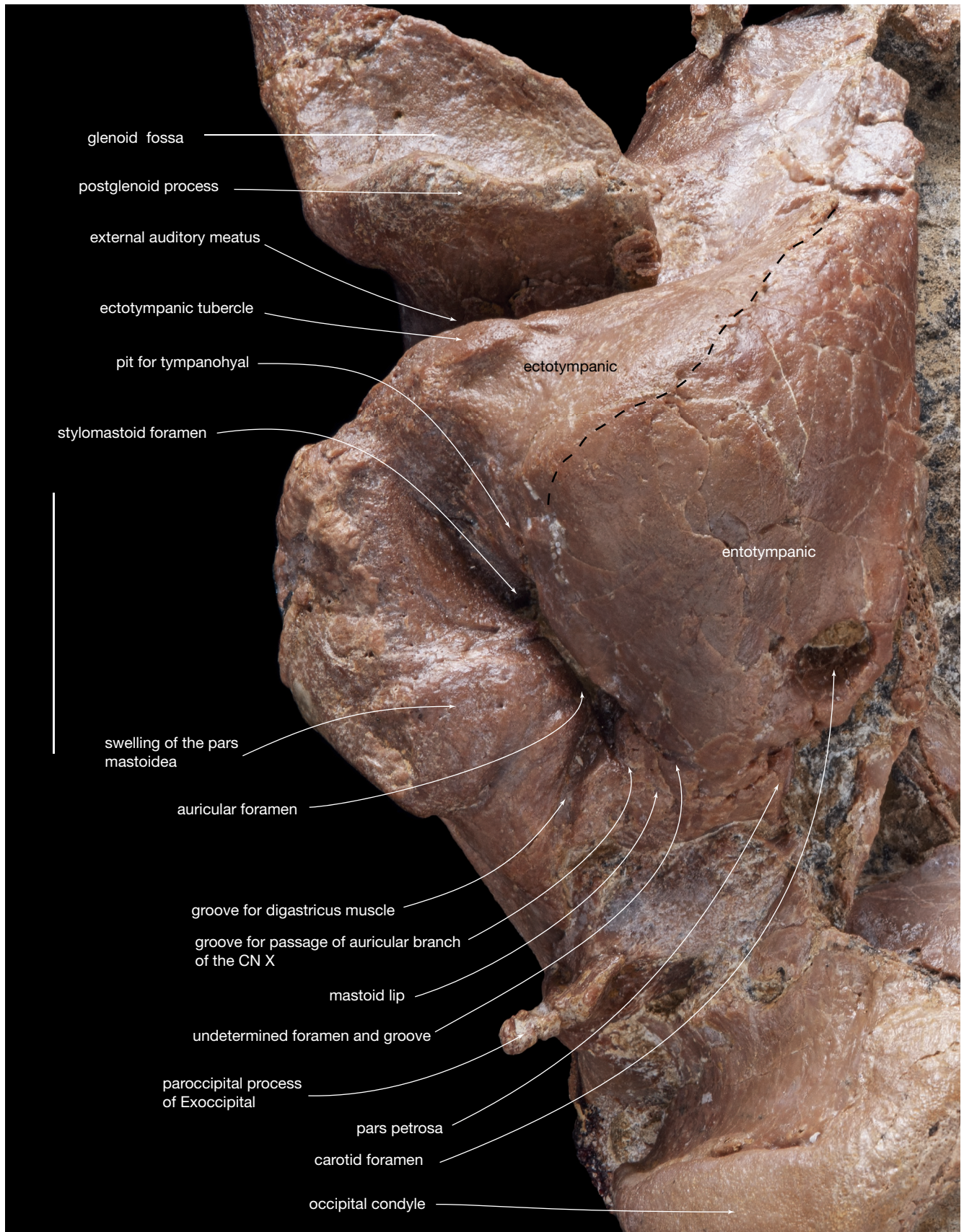


FIG. 5. — Basicranium of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270a); right auditory region in ventral view. Scale bar: 3 cm. Photo by L. Cazes & P. Loubry (CR2P).

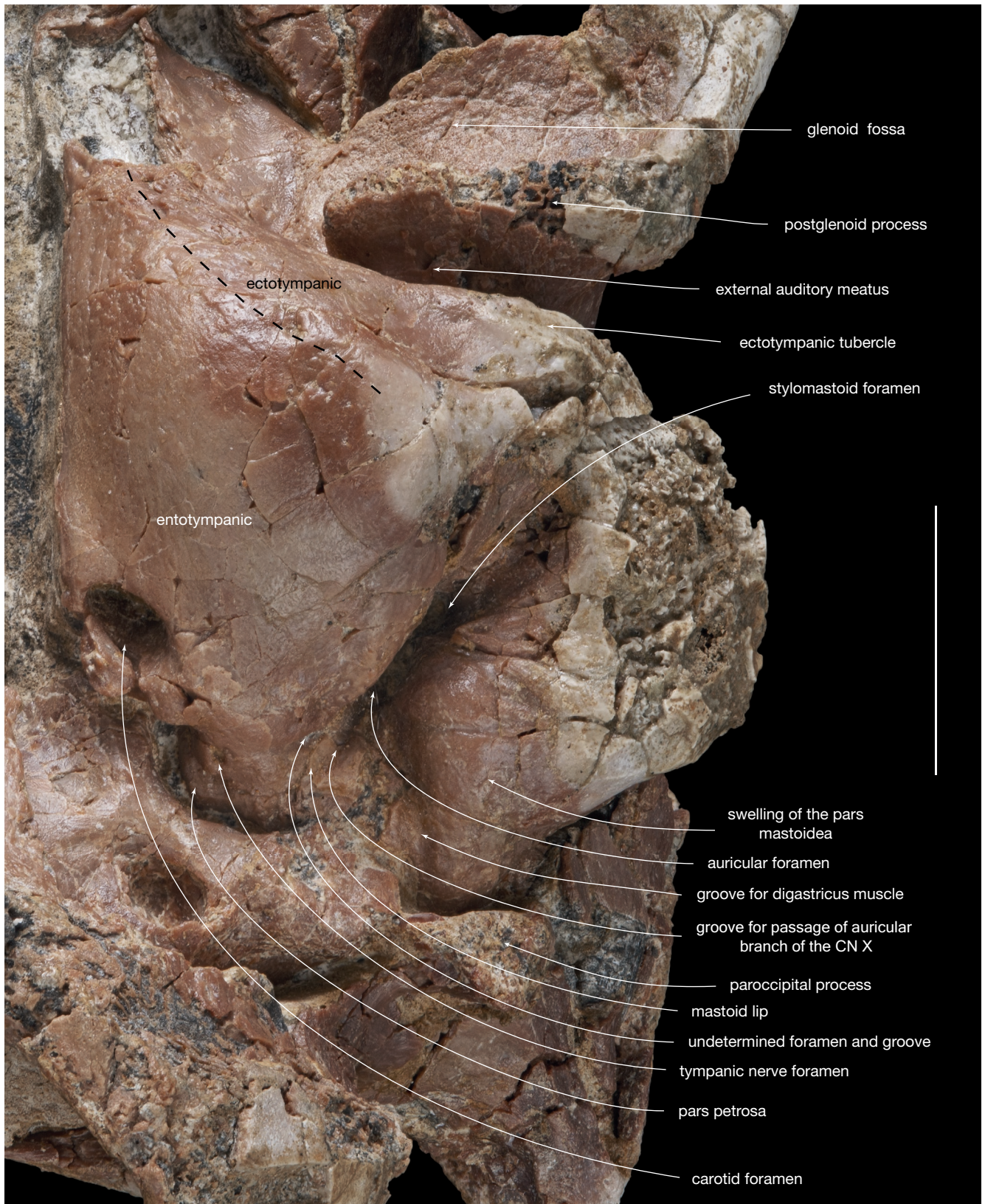


FIG. 6. — Basicranium of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270a); Left auditory region in ventral view. Scale bar: 3 cm. Photo by L. Cazes & P. Loubry (CR2P).

view) and moderately well developed, projecting slightly over the posterior portion of the braincase.

The tympanic bulla of *Icaphoca* is isosceles triangular in ventral outline. It is slightly more inflated than in the other Pisco monachines, although it approaches in this respect the condition observed in *Magophoca brevirostris* (especially on the holotype). This triangular outline, which corresponds with the condition in other Monachinae, is in part attributed to the moderate inflation of the entotympanic and ectotympanic as compared to Phocinae. In the latter, the tympanic bulla is strongly inflated, resulting in a rather sub-rounded outline in ventral view.

The straight medial margins of the left and right tympanic bullae appear parasagittal and parallel (char. 21[1]), which it shares with other Lobodontini. In other Phocidae, the medial margins of the tympanic bullae diverge posteriorly. However, it should be noted that this part of the holotype cranium of *Icaphoca* is severely fractured, and this condition cannot be ascertained unambiguously.

The bulla is constituted by the ectotympanic and entotympanic. The two bones are fused on the holotype of *Icaphoca choristodon* n. gen., n. sp. but a discrete uneven line can be observed from the anteromedial angle of the bulla, extending posterolaterally towards an anterolateral swelling of the bulla and from there turning anterolaterally toward the groove for the facial nerve (CN VII) leading to the stylomastoid foramen (Figs 5, 6).

The moderately-inflated ectotympanic forms the anterolateral portion of the tympanic bulla. It bears a gentle swelling, as mentioned above at the posterolateral portion of its suture with the entotympanic. Posteromedial to the ectotympanic the bulla is formed by the entotympanic. The inflation of the entotympanic is strongest in the central portion of the tympanic bulla, in the anterolateral portion of the entotympanic. The ectotympanic is triangular to club-shaped in ventral view, with the long “handle” along the anterolateral region of the entotympanic and the “head” projecting anterolaterally as a prominent ectotympanic lip, covering the external auditory meatus (char. 22[1]). The lateral tip of the ectotympanic reaches lateral to the center of the glenoid fossa and bears a moderately developed ectotympanic tubercle.

The entotympanic is subtriangular in outline as well, with the anterolateral and posterolateral margins forming a right angle. At the anteromedial tip of the bulla, the anterior lacerate foramen and the opening for the musculotubal canal coalesce and open anteriorly. The posterior tip of the entotympanic—and of the tympanic bulla—is blunt. It almost totally covers the posterior region of the pars petrosa of the petrosal and almost borders the anterior edge of the posterior lacerate foramen.

The posterior carotid foramen forms a large, circular, and posteriorly oriented opening on the posteromedial region of the entotympanic. This foramen opens posteroventrally and is visible in ventral view (char. 29[0]). This condition in *Icaphoca* follows other Monachinae. It differs from that in Phocinae, in which the posterior carotid foramen opens totally medially (thus facing its counterpart) and is not visible in ventral view, due to the inflation of the tympanic bulla.

The posterior carotid foramen of Phocinae opens directly below and is coalescent with the posterior lacerate foramen.

In *Icaphoca* and other monachines the posterior carotid foramen is located entirely in the tympanic bulla and does not open directly on the posterior lacerate foramen from which it is separated by a thin lamina of the tympanic bulla (char. 30[0]).

The posterior lacerate foramen is inadequately preserved to allow a detailed description and comparison with other Phocidae.

On the anterior edge of the posterior lacerate foramen, the entotympanic extends posteriorly; it almost totally covers the pars petrosa of the petrosal but a narrow strip of petrosal is visible ventrally. A similar condition with the entotympanic almost totally covering the petrosal is also observed in *Acrophoca*, *Hadrokirus*, *Magophoca*, and *Piscophoca*. This condition differs from that in Monachini and Phocinae in which the pars petrosa is widely exposed ventrally at the anterior edge of the posterior lacerate foramen.

On the lateral edge of the posterior region of the tympanic bulla, the entotympanic interlocks with the anteromedial edge of the canal for the auricular branch of the CN X, which is excavated in the mastoid. In this region, the mastoid features a thin lip which overlaps the posterolateral edge of the entotympanic. This mastoid lip is approximately 9 mm long on the holotype of *Icaphoca choristodon* n. gen., n. sp. Such a structure has been observed in the four genera of extant lobodontines, and among fossil monachines, in *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Magophoca*, *Piscophoca*, and *Sarcodectes*, as well as the tympanic bulla attributed to the *nomen dubium* *Monotherium? wymani* (Muizon & Hende 1980; Muizon 1981, 1982; Amson & Muizon 2014; Rule *et al.* 2021; Dewaele & Muizon 2024). It is noteworthy however that in *Icaphoca* and *Magophoca* this lip is less developed than in the other fossil and extant lobodontins. This structure was observed for the first time by Repenning & Ray (1977) and has been regarded as a synapomorphy of the Lobodontini. (Muizon 1981, 1982; Amson & Muizon 2014; Dewaele & Muizon 2024).

In the Phocinae and Monachini, a large portion of the pars petrosa of the petrosal is visible at the anterior edge of the posterior lacerate foramen and the posterior edge of the entotympanic is more anterior than in the extant and fossil Lobodontini, *Sarcodectes*, *Monotherium? wymani*, and Miroungini. In contrast in the latter taxa, the entotympanic totally (or almost totally) covers the petrosal posteriorly (char. 33[0]) and the petrosal is not inflated, as is the case in most Phocinae and Monachini.

On the medial edge of the posterior apex of the entotympanic, facing posteromedially is a small foramen overhanging (in ventral view) the posterior lacerate foramen. We interpret this foramen as the passage of the tympanic nerve, which connects the CN IX to the minor petrosal nerve within the tympanic cavity. Such a foramen is present in *Acrophoca*, *Hadrokirus*, *Homiphoca*, and *Piscophoca* (pers. obs.) as well as in the four extant Lobodontini. Although not mentioned by Dewaele & Muizon (2024), it is also present in *Magophoca*.

On the posterolateral edge of the entotympanic, just antero-medial to the mastoid lip is a small foramen, which is the opening of a small anterolaterally oriented canal. We have no interpretation for this foramen, which is clearly distinct from the tympanic nerve foramen (Figs 5, 6), although it could simply be a nutrient foramen.

On the posterolateral margin of the tympanic bulla, the contact between the bulla and the swollen mastoid is invaginated. At the posterolateral surface of the ectotympanic, the pit for the tympanohyal descends into this contact. The pit for the tympanohyal is a small and shallow groove. Among other Monachinae, the pit for the tympanohyal is bordered by elevated lips, which partially cover it as is observed in *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Leptonychotes*, *Lobodon*, and *Monachus*. In contrast, in *Magophoca*, the edges of the stylomastoid groove are smoothly rounded, a condition that is probably also present in *Icaphoca* but not possible to ascertain due to the preservation of the specimen.

The stylomastoid foramen is located at the contact between the ectotympanic and the mastoid. It is a large and circular foramen, which opens anterolaterally into a semi-cylindrical groove. The latter extends anterolaterally at approximately 45° to the sagittal plane and conveys the facial nerve (CN VII), which 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. Posterior to the stylomastoid foramen, the mastoid is notably swollen along the posterior half of the posterolateral margin of the tympanic bulla. This swelling largely separates the stylomastoid foramen anteriorly from the auricular foramen posteriorly. However, this swelling remains separated from the tympanic bulla, thus separating both foramina only incompletely. Such a swelling separating the stylomastoid foramen from the auricular foramen is present in all Phocidae (Deméré *et al.* 2003). Bordering the swelling medially is a deep groove oriented posterolaterally for the origin of the digastric muscle (Piérard 1971). Anteromedial to the digastric groove, and at approximately 45° to it, is a narrow groove leading to the auricular foramen. The auricular foramen conveys the auricular branch of the vagus nerve (CN X), which runs in a groove along posterolateral edge of the entotympanic, from the posterior lacerate foramen (where the vagus nerve exits) to the facial nerve (CN VII) laterally.

The robust mastoid aligns and abuts the posterolateral margin of the tympanic bulla. As in other Monachinae (except *Ommatophoca*), the mastoid is not visible in dorsal view (char. 25 [0]). This condition contrasts with that observed in Phocinae and *Ommatophoca*, in which the mastoid is visible in dorsal view of the skull due to the medial inflexion of the lambdoid crest.

The paroccipital process on the exoccipital forms a slender hook-like process (char. 32[1]), comparable to other Monachinae. However, it is noteworthy that it is considerably more gracile in *Icaphoca* than in any other Monachinae.

A large hypoglossal foramen is observed distal to the posterior lacerate foramen. Although this region of the skull is strongly fractured, it seems clear that it was closer to the posterior edge of the posterior lacerate foramen than to the occipital condyle.

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. The fossa in *Icaphoca* is deeper and wider than in *Magophoca*. Dorsally, the occipital condyles are strongly diverging (char. 35[1]). The articular surfaces of the occipital condyles are ventrally fused, and the ventral margin of the foramen magnum is roughly parabolic. Among other Monachinae, a similar condition is observed in *Hadrokirus*, *Homiphoca*, *Hydrurga*, *Magophoca*, *Monachini*, and *Piscophoca*. In lateral view, the occipital condyles strongly protrude distally more so than in *Magophoca* probably because of the larger condyloid fossa. This condition in *Icaphoca* is also probably enhanced because of the more anterior position of the nuchal crest (in lateral view) as compared to that of *Magophoca*.

The nuchal crest of *Icaphoca* protrudes distal to the paroccipital process. Both left and right halves form a parabolic crest in dorsal view, with both halves at slightly less than 90° at one another. The crest is moderately raised. The parabolic shape of the nuchal crest resembles the condition in *Magophoca*, and *Piscophoca*, but differs from the V-shaped nuchal crest of *Acrophoca*, *Eomonachus*, *Homiphoca* and *Hadrokirus*. 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* (with some variation in the former two genera).

The sagittal crest is only lowly-raised where the interorbital bridge transitions into the braincase, but dissipates onto the braincase. This condition resembles that of *Magophoca* but differs from that in *Acrophoca*, *Hadrokirus* and *Piscophoca*, in which the sagittal crest extends up to the nuchal crest posteriorly. A sagittal crest is absent in *Homiphoca*. Among extant monachines, a well-developed sagittal crest contacting the nuchal crest posteriorly is present in *Hydrurga* and *Monachus*; a weak sagittal crest is observed in *Neomonachus* and it is absent in *Leptonychotes*, *Lobodon*, and *Ommatophoca*.

MANDIBLE (Fig. 7; Table 3)

Both left and right mandibles are well preserved for the holotype specimen, MNHN.F.PPI270. The anterolateral portion of the chin is damaged in both mandibles, as well as the vertical ramus of the left mandible.

The mandible is gracile and mediolaterally thin, comparable to the condition in most other Lobodontini, with the notable exceptions of the extinct *Acrophoca* and *Hadrokirus*, in which the mandible is even more gracile and slender, or very robust, respectively. The right mandible of the holotype of *Icaphoca choristodon* n. gen., n. sp. is almost complete and misses probably no more than a few mm. As preserved it is 191.2 mm long being distinctly longer than that of the paratype of *Magophoca brevirostris* (MNHN.F.PPI269) which is 168.3 mm long, when both specimens have been estimated to be of similar body length. This comparison confirms one of the major differences between both taxa which is the relative length of the snout, much longer in *Icaphoca* than in *Magophoca*.

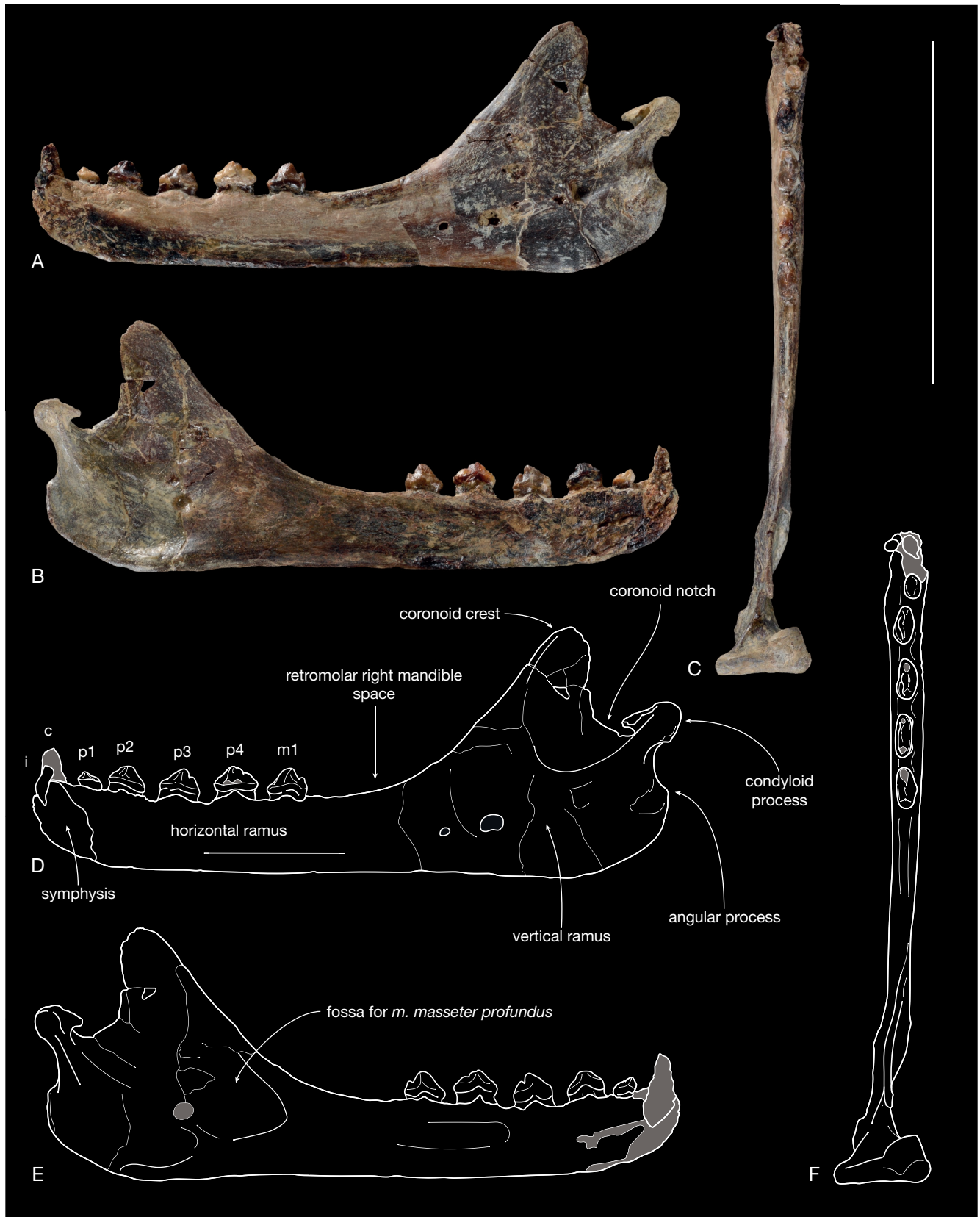


FIG. 7. — Right mandible of *Icapoca choristodon* n. gen., n. sp. (holotype, MNHN.FPPI270). **A**, mandible in lingual view; **B**, the same mandible in labial view; **C**, the same mandible in occlusal view; **D-F**, corresponding labelled line drawings. Areas in gray are abraded or obscured from view by sediment matrix. Abbreviations of the teeth follow the convention used in the main text. Scale bar: 10 cm. Photos by L. Cazes & P. Loubry (CR2P); drawings by L. Dewaele.

TABLE 3. — Measurements of the holotype mandibles (MNHN.F.PPI270a) of *Icaphoca choristodon* n. gen., n. sp. Abbreviations: e, estimate for a character due to minor damage; n/a, a character could not be measured; abbreviations of the teeth follow the convention used in the main text. Measurements in mm.

Character	Left	Right
Overall, total length	190.9e	191.2e
Overall, length from anterior tip to angular process	188.0e	189.0e
Overall, total height	76.3	73.6
Symphysis, length	n/a	28.1
Symphysis, height mandible at the distal tip of the symphysis	21.9	22.1
i1, alveolus length	n/a	n/a
i1, alveolus width	n/a	n/a
i2, alveolus length	n/a	n/a
i2, alveolus width	n/a	n/a
c, alveolus length	n/a	n/a
c, alveolus width	n/a	n/a
p1, alveolus length	7.0	n/a
p1, alveolus width	4.9	n/a
p2, alveolus length	11.4	11.8
p2, alveolus width	4.7	4.3
p3, alveolus length	12.9	12.7
p3, alveolus width	4.5	4.6
p4, alveolus length	12.5	12.4
p4, alveolus width	4.8	4.8
m1, alveolus length	12.2	12.1
m1, alveolus width	4.4	4.6
Horizontal ramus, height at level just posterior to m1	23.3	22.1
Horizontal ramus, width at level just posterior to m1	7.5	7.5
Postcanine toothrow, length	68.0	67.4
Coronoid, vertical height from the lowest point of the coronoid notch to the apex of the coronoid process	29.9	31.0
Condylar process, width	27.4	27.6

The length of the mandibular tooth row on the right mandible is 81.8 mm, which represents 42.7 % of the dentary's total length. Similar proportions are observed in *Magophoca* in which the length of the tooth row is 71.3 mm which represent 42.3 % of the dentary's overall length. This condition is comparable with most other Monachinae, except for *Hydrurga* and *Lobodon*, in which the tooth row is either approximately half the total length of the mandible, or more than half the total length of the mandible, respectively.

In dorsal view the dentary of *Icaphoca* is almost straight (very smooth medial bending), whereas the bending is distinctly more pronounced in *Magophoca*, possibly because of the shorter rostrum of this genus.

In lateral view, the horizontal ramus (*corpus mandibularis*) is roughly equally high throughout, with a smoothly convex chin running from the anterior extremity to p2. The horizontal ramus is slightly upturned dorsally, anteriorly, resulting in the incisor(s), the canine, p1, and p2 being located higher than p3-m1 in lateral view. In 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. Transversely, the horizontal ramus of the mandible of *Icaphoca* becomes gradually more slender, posteriorly.

The symphysis has an ovale-shaped outline. It is short and small, terminating just ventral to the anterior edge 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 which it extends further posteriorly.

Two mental foramina have been identified on the lateral margin of the horizontal ramus: one sub-circular mental fora-

men ventral to the anterior root of p2, and one deep and horizontally elongate foramen ventral to the posterior root of p3.

The retromolar space is long, much longer than in *Magophoca*. Just distal to m1, the horizontal ramus initially widens very gently, in lateral view; widening gradually more strongly toward the vertical ramus (*ramus mandibularis*). Among other Monachinae, the retromolar space is short in *Hadrokirus*, *Hydrurga*, *Lobodon*, *Magophoca*, and tribe Monachini. The retromolar space is moderately long in the extinct monachines *Homiphoca*, *Piscophoca*, and *Pliophoca*, and long in all other Monachinae: *Acrophoca*, *Leptonychotes*, *Mirounga*, and *Ommatophoca*.

Overall, the ventral margin of the dentary is straight, only deflecting slightly ventrally at the posterior end of the mandible, vertically at the level of the coronoid process, before rising to the angular process.

The vertical ramus is approximately three times as high as the horizontal ramus, at the level of the maximum elevation of the coronoid process.

Compared with other Monachinae, a similarly proportionally high vertical ramus is also present in extinct Monachinae (e.g., *Acrophoca*, *Hadrokirus*, *Homiphoca*, *Magophoca*, 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 crest is rather straight, terminating posterodorsally in the coronoid process. Transversely, the coronoid process is thin. The coronoid process is a blunt, rounded apex, a condition that varies among other monachines, ranging from a concave “hook” in *Hydrurga*, *Leptonychotes*, and *Neo-*

monachus; a straight posterior margin in *Lobodon*, *Magophoca*, *Mirounga*, and *Monachus*, to an anterodorsal-posteroventrally slanted ridge in *Ommatophoca*. Among fossil monachines, it is wide and stout in *Acrophoca*, *Hadrokirus*, and *Magophoca*; it is relatively narrow and slender in *Homiphoca* and very thin, narrow, and strongly oriented posteriorly in *Piscophoca*. The coronoid process of *Icaphoca* more resembles that of *Acrophoca* than any other extinct monachines.

The lateral aspect of the of the vertical ramus of the mandible receives the masseter muscle ventrally and part of the temporalis muscle dorsally. The insertion of the masseter is weakly outlined but clearly separated into two elongate insertion areas by the condyloid crest. Ventral to the condyloid crest is an elongated fossa for the masseter superficialis (on the ventral edge of the fossa) and for the larger masseter intermedius. Dorsal to the condyloid crest and ventral to the coronoid process is a roughly oval-shaped fossa for the masseter profundus. Dorsal to this latter fossa is the insertion area for the temporalis lateralis muscle, on the lateral aspect of the coronoid process.

On the medial surface of the mandible, a shallow, roughly reniform fossa along the coronoid notch was receiving the insertion of the temporalis medialis muscle.

The mandibular foramen on the medial surface is located horizontally at the level of the tooth row, but vertically at the level of the posterior margin of the coronoid process.

The condyloid process (condyle) is tilted anterolaterally-posteromedially, as in *Hadrokirus* and *Magophoca*. The condyloid process roughly forms a horizontal, cylindrical bar. The articular facet on the condyloid process is contorted: at the lateral tip, it projects more anterior than at the medial tip, but at the medial tip, it projects more ventral than at the lateral tip. It remains uncertain whether the latter is a diagnostic characteristic for *Icaphoca* or may be attributed to intraspecific variation and only present in the holotype specimen. The condyloid process is seated on a slender and long root.

The angular process is strongly reduced, forming a blunt projection, just posterior to the body of the mandible (char. 36[1]). This condition follows the general condition among Monachinae, with few exceptions: there is no –or only a weakly–discernible angular process in *Hydrurga*, *Leptonychotes*, and *Magophoca*. It is large (for a phocid) and strongly projecting posteriorly in *Homiphoca*. The angular process is small in most other Monachinae.

DENTITION

Upper teeth and alveoli (Figs 3, 4, 8; Tables 2, 4)

In the holotype specimen of *Icaphoca choristodon* n. gen., n. sp., most of the upper teeth are preserved except the left canine and P4. However, the state of preservation of the incisors and canines is poor, as well as the left M1, which is missing a part of the labial side of its main cusp. The incisors and right canine are worn (especially the canine) and the left I2 is broken. The left canine is broken at the base of the crown and only the roots are preserved for the left P4.

The upper dental formula for *Icaphoca* is 3I 1C 4P 1M. Except for the number of incisors, the upper dental formula

is consistent among all Phocidae. The number of incisors is often quoted as a characteristic separating both subfamilies, Monachinae and Phocinae: monachines have two upper incisors, and phocines have three upper incisors. However, the extant phocine *Cystophora* has two instead of three upper incisors and the extinct monachine *Magophoca* has three instead of two upper incisors (Dewaele & Muizon 2024).

The upper incisors are notably compressed transversely (especially I1 and I2), with peg-like crowns, like the condition in Phocinae, and in contrast to other Monachinae, in which this transverse compression is less pronounced (char. 40[0]). The incisors increase in size from I1 to I3. The third incisor is incisiform, yet, distinctly larger than the other inner incisors, being 5.3 mm in labio-lingual length, whereas this length is 3.7 mm on I2 and 2.8 mm on I1 (char. 41[0]). A flat facet, oblique on the lingual side of the right second incisor represents an occlusal tooth wear facet.

The canines are too incompletely preserved to allow description, other than that they appear to have a strong anteroventral orientation.

The postcanine teeth are little specialized, compared with the highly specialized postcanine teeth in extant Monachinae (except *Monachus* and *Neomonachus*). Among other extinct Monachinae, the degree of specialization varies. The postcanine teeth of *Icaphoca* trend to homodonty, as in other Monachinae. Similar to most other Phocidae, the postcanine teeth of *Icaphoca* are double-rooted, with the exception of P1, which is single-rooted (char. 47[1], 50[0]). Exceptions are *Hydrurga* and *Lobodon* which, although they do not have a double-rooted P1, feature a bilobed single root for P1. Furthermore, *Mirounga*, and the phocine species *Cystophora*, and *Halichoerus*, have single-rooted P1-M1.

All postcanine teeth are widely separated by diastemas. These range from three millimeters to six millimeters between the premolars (Table 2). In contrast, the diastema separating M1 from P4 is approaches one centimeter, or approximately one postcanine tooth length in length. This condition is notable, because among other Monachinae, only *Acrophoca* has large diastemata between all the postcanine teeth. The condition of *Icaphoca* strongly differs from that of *Magophoca*, in which postcanines are not separated by diastemata. *Sarcodectes* also presents an enlarged diastema between P4 and M1, but no diastema is observed between the premolars. All postcanine teeth of *Icaphoca* are oriented parallel to the tooth row axis and no tooth imbrication or tooth crowding has been observed (char. 46[0]).

The notable spacing of the postcanine teeth of *Icaphoca* is a unique condition among monachines that foreshadows the spectacular lengthening of the rostrum of *Acrophoca* (see below, phylogenetic analysis section).

In occlusal view, the first upper premolar has a semi-circular lingual margin and a weakly convex labial margin. The well-developed lingual margin sports a prominent, broad, lingual cingulum. There is no labial cingulum on P1. The apex of the main cusp bears a flat wear facet, oblique on the lingual side of the cusp. Tooth wear on the enamel is also present down from this wear facet, towards the lingual cingulum. Anteriorly



FIG. 8. —Upper dentition of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270). **A**, stereoscopic view of the upper right cheek teeth in occlusal view; **B**, upper right cheek teeth in lateral view in occlusal view. Scale bar: 3 cm. Photos by L. Cazes & P. Loubry (CR2P).

TABLE 4. — Measurements of the upper dentition of the holotype MNHN.F.PPI270 of *Icaphoca choristodon* n. gen., n. sp. Abbreviation and symbol: *n/a*, a character could not be measured; *>*, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value. Measurements in mm.

Character	Left	Right
I1, crown height	n/a	4.4
I1, crown length	n/a	3.0
I1, crown width	2.0	2.2
I2, crown height	n/a	>4.6
I2, crown length	n/a	4.0
I2, crown width	n/a	3.2
I3, crown height	n/a	5.9
I3, crown length	5.3	5.6
I3, crown width	4.6	n/a
C, crown height	n/a	n/a
C, crown length	n/a	n/a
C, crown width	n/a	n/a
P1, crown height	>4.2	>5.0
P1, crown length	7.8	7.9
P1, crown width	5.0	4.8
P2, crown height	>5.8	>6.2
P2, crown length	11.5	11.4
P2, crown width	5.8	6.0
P3, crown height	5.6	>6.2
P3, crown length	11.5	11.6
P3, crown width	5.9	6.3
P4, crown height	n/a	6.5
P4, crown length	n/a	>11.5
P4, crown width	n/a	6.2
M1, crown height	>5.7	>5.2
M1, crown length	>7.9	8.4
M1, crown width	4.9	4.9

and posteriorly, the main cusp is flanked by accessory cusps. Whereas the anterior accessory cusp is miniscule and barely visible, the posterior accessory cusp has a little prominence.

The double-rooted premolars P2–4 are anteroposteriorly elongate. The crowns are approximately twice as long as they are high. The lingual cingulum is well-developed overall, forming a prominent posterolingual shelf. The labial cingulum is narrow, but disappears just below the main cusp. The crown is dominated by a large and anteroposteriorly elongate main cusp, anteriorly and posteriorly bound by sharp crests. Anterior and posterior to the main cusp, there are the small anterior and posterior accessory cusps. Tooth wear is moderate, but wear facets are present on the apices of the main and accessory cusps some of them being significantly shortened. Moreover, on the right P4 the wear is prominent, since it almost totally obliterates the posterior accessory cusp and extends onto the posterolabial margin of the tooth. It remains questionable whether tooth wear as profound as the tooth wear observed in the right P4 of MNHN.F.PPI 270 is common for the species of *Icaphoca choristodon* n. gen., n. sp. or intraspecifically variable.

M1 is noticeably smaller than P4. Among other Monachinae, M1 is generally smaller than P4, but the degree of the size discrepancy varies: for example, M1 is comparable or only marginally smaller in the extant *Hydrurga* and in the extinct *Acrophoca*, *Hadrokirus*, *Homiphoca*, and *Magophoca*; it is considerably smaller in the extant *Leptonychotes* and in the extinct *Piscophoca*.

The labial and lingual cingula are strongly reduced and the main cusp is comparatively large, in relation to the entire tooth crown, when compared to premolars. Towards its apex, the main cusp tends to curve posteriorly and has a small and flat wear facet. The accessory cusps of M1 are vestigial.

Lower teeth and alveoli (Figs 7, 9; Tables 2, 5)

For the holotype mandibles, only the postcanine teeth are preserved adequately complete, allowing a detailed description. One right incisor and the right canine are preserved as well, but too poorly to allow a detailed description and comparison. A well-preserved and isolated lower incisor has been associated with the holotype too.

Each mandible sports two incisors, one canine, four premolars, and one molar. Although none of the mandible preserves all its incisors it is likely that the holotype specimen bears two incisors in each lower quadrant, since two alveoli are observed on the left mandible. They are anteroposteriorly disposed and the smaller anterior alveolus is anteroventral to the larger one. The larger posterior alveolus is medial to the anterior edge of the canine. Another cavity, below the incisors' alveoli, most likely represents the anterior mental foramen. Phocidae generally have two lower incisors per quadrant, except for the extant monachine genus *Mirounga* and the extant phocine *Cystophora*. A dental formula with 3I/2i is shared with all Phocinae (except *Cystophora*) and the sympatric monachine *Magophoca brevirostris*.

For the (isolated) incisor, it appears that the root is slightly flattened transversely. The crown forms a stubby peg in anterior view. The tooth crown is slightly recurved lingually, and it has a small lingual cingulum. Assuming that there is not enough space in the right mandible to accommodate the isolated incisor with the other incisor already in place, this isolated incisor can be assumed to be a left incisor. This incisor has a large wear facet mesiolabially, again, considering this incisor to be a left incisor. This tooth wear facet is long and deep, cutting through the entire thickness of the enamel.

The lower canine appears to be oriented almost straight vertical, compared to the horizontal ramus.

As for other Monachinae, p1 is single-rooted and p2–m1 are all double-rooted (char. 47[1]). Apart from the smaller p1, the lower postcanine teeth are all of comparable size, with low crowns, approximately half as high as they are long. The lower postcanine dentition of *Icaphoca* is marked by wide diastemas between p2, p3, p4, and m1 (Table 5), otherwise only known in *Acrophoca*. The diastema between p1 and p2 is smaller. The lower postcanine teeth of *Icaphoca* are implanted parallel to the long axis of the tooth row.

The first premolar, p1 is roughly oval in occlusal view, with a slightly straighter labial surface than the lingual surface. The main cusp dominates the crown. However, it is not high, less than half as high as the tooth is long (Table 5). It does not point straight vertical but is instead slanted anteriorly. Posteriorly, the main cusp is flanked by a small accessory cusp. Both are aligned labial to the long axis of p1, thus creating a prominent lingual cingulum forming a relatively wide plateau. The labial cingulum is strongly reduced.

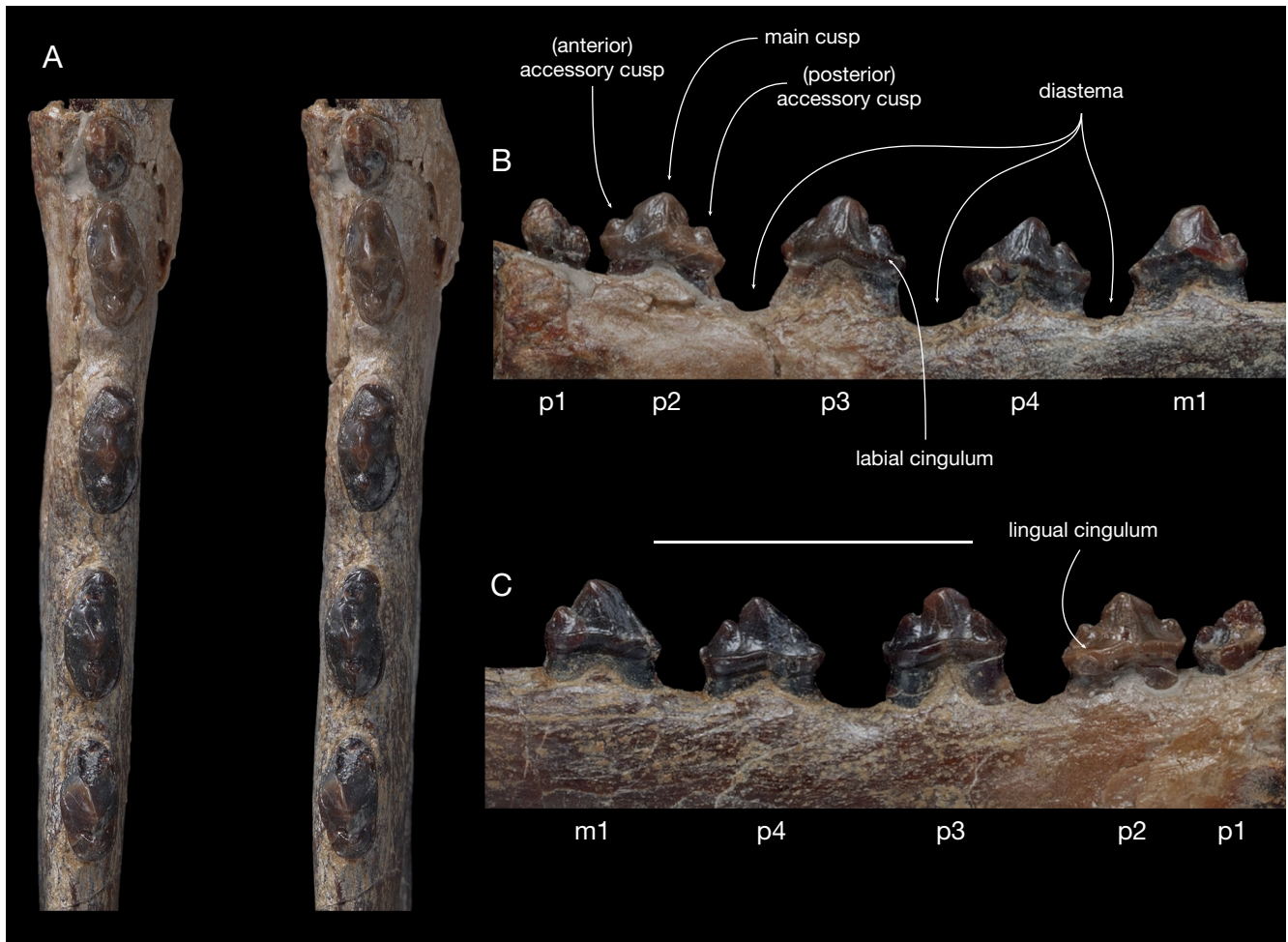


FIG. 9. —Lower dentition of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.F.PPI270). **A**, Stereoscopic view of the left lower cheek teeth in occlusal view; **B**, right lower cheek teeth in lateral view; **C**, right lower cheek teeth in medial view. Scale bar: 3 cm. Photos by L. Cazes & P. Loubry (CR2P).

The other lower premolars, p2, p3, and p4 are morphologically comparable to one another. The crown forms an elongate oval in occlusal view, and is approximately twice as long as it is high. A prominent main cusp is located centrally on the crown and has sharp, angular anterior and posterior ridges descending to an anterior and posterior accessory cusp. These accessory cusps are roughly similar in size, but much smaller than the main cusp. Whereas the labial cingulum is strongly reduced, the lingual cingulum is well-developed. The distolingual portion of the lingual cingulum is most prominent in p2, and gradually smaller in p3 and p4. The tooth crowns of p2, p3 and p4 are affected by slight tooth wear. The apex of the main cusp is worn in all p3 and p4. In p3 and, especially, p4, the anterior half of the tooth crown is significantly worn down.

The lower first molar, m1, differs notably from the premolars. The main cusp is slightly inflated, thus reducing the labial and lingual cingula. This cusp is slightly turned posteriorly, giving the anterior portion of the main cusp a markedly convex appearance in lateral view. The posterior accessory cusp is similar in size to the posterior accessory cusps in the premolars. The anterior portion of the tooth is worn to the extent that

it is impossible to determine whether there was an anterior accessory cusp present or not before being worn down.

AXIAL SKELETON

The known axial skeleton of *Icaphoca choristodon* n. gen., n. sp. is limited to the cervical vertebrae, which were recovered articulated to the skull of the holotype specimen, MNHN.F.PPI 270, comprising the atlas, axis, and Ce3-5.

Atlas (Fig. 10A-C; Table 6)

The atlas is incompletely preserved, missing its left wing; however, the right wing is almost complete and allows a complete description of the atlas.

The atlas of *Icaphoca* is not particularly distinctive from the average monachine in its overall dimensions. Exceptions among Monachinae are *Acrophoca* and *Hadrokirus*, with the former having an anteroposteriorly elongate atlas with posteriorly projecting wings, and the latter having a large and very stout atlas.

The transverse process of the atlas is roughly quadrate and projects only moderately, laterally. The lateral margin of the transverse process flares posteriorly, with a slightly convex

TABLE 5. — Measurements of the lower dentition of the holotype MNHN.F.PPI270 of *Icaphoca choristodon* n. gen., n. sp. Abbreviations and symbols: n/a, a character could not be measured; ~, estimate for a character due to minor damage or deformation; >, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value. Measurements in mm, taken with an analog caliper.

Character	Left	Right
p1, crown height	4.6	n/a
p1, crown length	~7.1	~7.2
p1, crown width	4.6	4.6
p2, crown height	6.5	>5.9
p2, crown length	12.0	>11.8
p2, crown width	5.4	>5.5
p3, crown height	6.7	6.8
p3, crown length	11.8	11.8
p3, crown width	5.6	5.7
p4, crown height	6.7	>6.3
p4, crown length	12.2	12.9
p4, crown width	5.5	5.7
m1, crown height	6.9	6.8
m1, crown length	>11.2	>12.1
m1, crown width	5.5	5.8

anteromedially-posterolaterally oriented lateral margin and a rather transverse posterior margin, which bears a small, pointed process on its lateral half. On the posterior edge of the transverse process is a deep triangular fossa, which extends from the posterior articular facet for the axis to the small pointed process. The fossa forms an isosceles triangle whose base is along the articular facet.

Although the anterolateral angle of the transverse process is damaged it overhangs the alar notch. Because of this slight breakage of the transverse process, it is not possible to evaluate the depth of the alar notch.

This morphology of the margin of the transverse process in the atlas of *Icaphoca* differs from the posteriorly projecting processes of *Acrophoca* and from the rather triangular ones of *Piscophoca*. In contrast, it resembles the rather convex and rounded to quadrate processes of other Monachinae.

The degree of the lateral eversion of the transverse process in *Icaphoca* is moderate as observed in *Magophoca* and conforms with the genera condition in Monachinae. However, in a few taxa, i.e. *Hadrokirus*, *Monachus*, and *Piscophoca*, the transverse process projects more strongly laterally.

In lateral view, the transverse process of the atlas of *Icaphoca* is straight and oriented obliquely (char. 53[0]). Compared to other Phocidae, this corresponds with the condition in Phocinae and the monachine taxa *Acrophoca*, *Hadrokirus*, *Leptonychotes*, *Magophoca*, and *Neomonachus*; whereas this process is oriented subvertically in other Monachinae.

The transverse foramen at the base of the transverse process is small, comparable in dimensions to *Acrophoca* and *Hadrokirus*, and slightly smaller than in *Magophoca* and *Piscophoca*; it is much smaller than in extant Monachinae. On the anteroventral surface of the transverse process, the transverse foramen opens in a large and wide atlantal fossa, which is larger than in *Acrophoca*, *Hadrokirus*, and *Magophoca*, resembling in this respect to the condition of *Piscophoca*. It is transversely elongate rather than roughly circular as in *Acrophoca*, *Hadrokirus*, and *Magophoca*. The posterior opening of the transverse foramen

is visible in dorsal view, as in other Monachinae, with the notable exception of *Mirounga*, and *Lobodon* (char. 52[1]).

The anterior articular fovea for articulation with the cranial condyles is reniform and strongly concave. The posterior articular fovea for articulation with the axis is weakly concave and has a roughly rectangular outline, and both left and right posterior articular foveae are at a slightly obtuse angle to each other.

The neural canal of the atlas of *Icaphoca* is vertically oval-shaped, being conspicuously higher than wide. The internal processes are smaller than in *Magophoca* but distinctly present.

The dorsal tubercle is low and is not bordered laterally by deep fossae for the *m. rectus capitis dorsalis minor* as observed in *Hadrokirus*, and *Magophoca*. In contrast, this condition resembles that of *Acrophoca*, and *Piscophoca*.

The ventral bar is thin and slender compares favorably with that of *Magophoca* and *Piscophoca*, differing from the stronger morphology observed in *Acrophoca*, and *Hadrokirus*.

Axis (Fig. 10D-F; Table 7)

The axis of the holotype of *Icaphoca* is missing the left transverse process and the apex of the right one. Nonetheless, the right transverse process is preserved, allowing a nearly full description of the axis.

The dens forms a thick and stubby peg, round in cross-section, with a horizontally flat dorsal margin and an anteriorly ascending ventral margin. The robustness of the dens is comparable to that of *Magophoca*, and thicker than the dens of the axis of *Hadrokirus*, which already has a dens more robust than other Monachinae (Amson & Muizon 2014).

The cranial articular surfaces are subcircular in outline and at an obtuse angle to each other of 107°. This condition resembles that observed on the holotype of *Piscophoca pacifica* MNHN.F.SAS564 (107°). It is conspicuously wider than in the paratype of *Magophoca brevirostris* MNHN.F.PPI269 (87°), the holotype of *Acrophoca longirostris* MNHN.F.SAS563 (93°), and *Homiphoca* (100°, mean of three specimens; MNHN.F.AFS 38, 40, and 41), but narrower than in the holotype of *Hadrokirus martini* MNHN.F.SAS1627 (115°).

The dorsal margin of the spinous process is slightly abraded but its anterior and posterior extremities are preserved. The dorsal margin of the spinous process is roughly straight resembling the condition in *Acrophoca*, but differing from *Magophoca* and *Piscophoca*, in which it is convex. The posterior angle of the spinous process forms a narrow and elongated process, which projects dorsally and posteriorly to a greater extent than in *Magophoca*, and *Piscophoca*, a condition, which clearly resembles that of *Acrophoca*. The posterior projection extends well posterior to the postzygapophyses, whereas in *Magophoca brevirostris*, it is anterior in the paratype (MNHN.F.PPI269) and it is only slightly posterior in the holotype (MNHN.F.PPI276). In the holotype of *Piscophoca pacifica* it is also only slightly posterior to the postzygapophyses. The anterior angle of the spinous process is sharp and extends anteriorly almost above the apex of the dens as is observed in *Acrophoca*, *Hadrokirus*, *Magophoca*, and *Piscophoca*. The spinous process remains

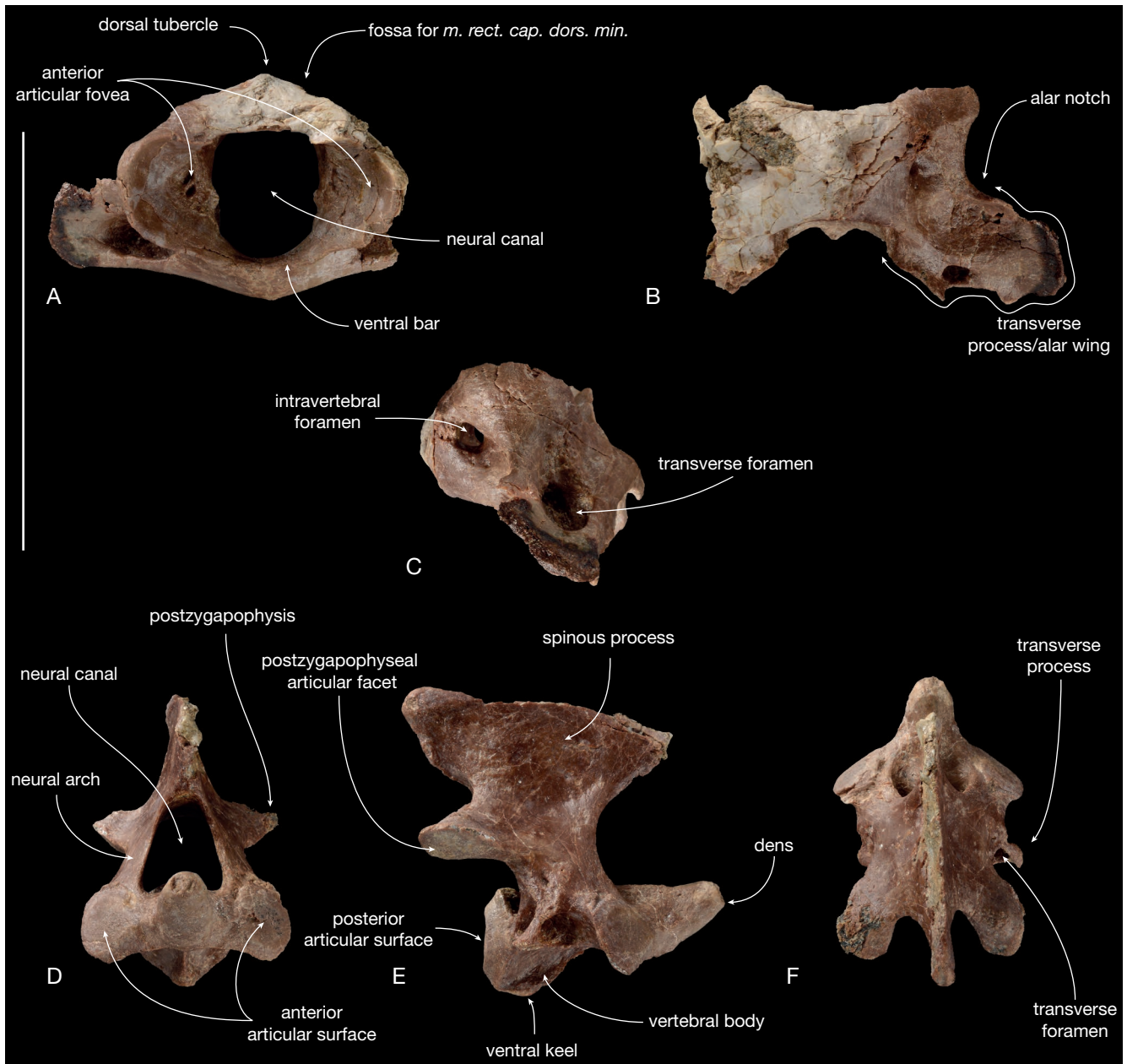


FIG. 10. — Atlas and axis of *Icaphoca choristodon* n. gen., n. sp. (A–C, holotype atlas, MNHN.F.PPI270; D–F, holotype axis, MNHN.F.PPI 270): A, atlas in anterior view; B, atlas in dorsal view; C, atlas in left lateral view; D, axis in anterior view; E, axis in right lateral view; F, axis in dorsal view. Abbreviation: *m. rect. cap. dors. min.*, *musculus rectus capitis dorsalis minor*. Scale bar: 10 cm. Photos by L. Cazes & P. Loubry (CR2P).

equally thin along its entire length. The spinous process of the axis of *Icaphoca* is morphologically comparable to that of the extinct *Acrophoca*, but notably shorter anteroposteriorly. It is proportionally longer than that in the other extinct monachines *Hadrokirus*, *Magophoca*, and *Piscophoca*, and slightly larger than in extant Monachinae, in which the posterior projection of the spinous process is never as pronounced as in *Icaphoca*.

The centrum is comparable in length to that of *Magophoca*; it is apparently slightly longer, but comparative measurements are difficult by the absence of the posterior epiphysis of the axis of the paratype of *Magophoca brevirostris* (MNHN.F.PPI269).

The centrum is much shorter than in *Acrophoca*, and conspicuously longer than in *Homiphoca*, and *Piscophoca*. It has a semi-cylindrical dorsal surface; whereas the ventral surface is strongly excavated into two deep fossae on both sides of the ventral keel. This is similar to the condition in *Acrophoca*, and *Magophoca*, but unlike *Hadrokirus*, and *Piscophoca*, in which the fossae are shallower.

The neural canal is higher than it is wide, subtriangular in outline in anterior view. The dorsal surface of the centrum bears an elevated square (in section) carina, which divides it into two deep fossae. In posterior view the neural canal is U-shaped.

TABLE 6. — Measurements of the atlas of the holotype MNHN.F.PPI270 of *Icaphoca choristodon* n. gen., n. sp. Abbreviations and symbols: **e**, estimate for a character due to minor damage or deformation; **n/a**, the character could not be measured; *****, the resulting value is based on a multiplication of a measurement with factor two, particularly for characters that are ideally measured across the sagittal plane but for which only one half is incomplete. Measurements in mm.

Character	Left	Right
Overall, height	53.9	
Overall, width	106.0*	
Alar wings, transverse length	30.2	n/a
Alar wings, least width	25.4	25.2
Alar wings, maximum width	32.8e	n/a
Articular facet for axis, height	21.7	n/a
Articular facet for axis, width	22.7	n/a
Neural arch, length	23.9	
Ventral bar, length	14.6	
Neural canal, width	25.0	
Neural canal, height	30.2	

The neural arch, overarchng the neural canal, sports postzygapophyses on both lateral sides of the spinous process. The postzygapophysis is robust, bearing a flat and rounded postzygapophyseal articular facet that faces ventrolaterally. The postzygapophyses reach well posterior to the posterior articular surface of the centrum, yet not as far posterior as the spinous process.

The transverse process is simple, long, and slender, projecting posterolateroventrally, posteriorly almost reaching the level of posterior articular surface of the centrum. It bears a large, triangular transverse foramen.

Other cervical vertebrae (Fig. 11; Table 8)

In addition to the atlas and axis, three other cervical vertebrae have been recovered articulated to the skull of the holotype of *Icaphoca choristodon* n. gen., n. sp.: Ce3, Ce4, and Ce5. Just as the atlas and axis, these cervical vertebrae are overall well preserved.

The centrum of Ce3 is slightly longer (40.3 mm) than that of Ce3 of the paratype of *Magophoca brevirostris* (38.2 mm). as for the axis, the centrum is proportionally much shorter than in *Acrophoca*. The centrum is smaller, compared to the neural arch and the transverse processes than in the paratype of *Magophoca brevirostris*. On the three cervical vertebrae described, the anterior articular surface of the centrum is roughly rectangular, wider horizontally than it is high vertically and the posterior articular facet is slightly oval-shaped to sub-circular. On the ventral aspect of the centrum, a narrow and sharp ventral keel is present. It is low and thin anteriorly but gradually becomes prominent and blunt at the posterior margin, where it forms a thick posterior tubercle. Overall, the vertebral body appears roughly parallelepiped, with the posterior articular surface offset ventrally compared to the anterior articular surface, in lateral view. As a consequence, in lateral view with the length of the centrum horizontal, the articular surfaces appear strongly oblique the anterior one being anteroven-trally and the posterior one posterodorsally oriented. The length of the centra increases posteriorly from Ce3 to Ce5 (39.2 mm; 41.2 mm; 44.7 mm).

TABLE 7. — Measurements of the axis of the holotype MNHN.F.PPI270 of *Icaphoca choristodon* n. gen., n. sp. Abbreviation: **n/a**, the character could not be measured. Measurements in mm.

Character	Left	Right
Overall, length	63.0	
Overall, height	73.0	
Overall, width	n/a	
Body, length	51.0	
Posterior articular facet, height	23.3	
Posterior articular facet, width	25.0	
Dens, length	12.0	
Articular facet for atlas, height	19.1	18.8
Articular facet for atlas, width	17.1	18.3
Spinous process, horizontal length	62.8	
Neural canal, length	19.9	
Neural canal, height	20.8	
Neural canal, width	18.2	

In anterior view, the neural canal is roughly U-shaped in the anterior cervical vertebra (Ce3), but becomes more triangular in the posterior cervical vertebrae (Ce4-Ce5): the ventral margin of the neural canal remains slightly convex, but the dorsal margin becomes rather angular.

The prezygapophyses are simple. The prezygapophyseal articular facet is elongated, oval-shaped on Ce3 and becomes more semi-circular and flat on Ce3-4. They face dorsomedially approximately at a 90° angle in Ce3, and slightly more open in the more posterior cervical vertebrae. Also, in Ce3, the medioventral portion of the prezygapophyseal articular facet is slightly curving around the long axis of the vertebra being distinctly concave. On the lateroventral surface, the prezygapophysis bears a faint mammillary tuberosity. The postzygapophysis is dorsoventrally thicker than the prezygapophysis. On the lateroventral surface, the postzygapophyseal articular facet is flat and elongate semi-circular. Whereas the dorsomedial surface of the postzygapophysis is marked by a prominent but blunt mammillary process in Ce3, the dorsomedial surfaces on the postzygapophyses of the more posterior cervical vertebrae bear small anteroposteriorly oriented ridges. The spinous process is insignificant in Ce3, but is more prominent in more posterior cervical vertebrae and increases in height posteriorly. In the more posterior cervical vertebrae (Ce4-5), the spinous process is slanted anteriorly: the blunt apex of the spinous process is located anterior to the level of the anterior opening of the neural canal. The posterior margin of the spinous process is more strongly slanted anteriorly than the anterior margin of the spinous process.

The transverse process is completely preserved in only Ce3 and Ce4. All the preserved cervical vertebrae, with the exception of the atlas and axis, have large, oval, and anteroposteriorly oriented transverse foramina. The transverse processes are oriented lateroventrally with the ventral component being much more pronounced than the lateral one. In lateral view the transverse processes are oriented almost fully ventrally differing from the condition in *Acrophoca*, and *Magophoca*, in which they are strongly slanted posteriorly. In anterior view, the transverse processes slightly diverge ventrally. In anterolateral view, they, widen distally and bifurcate, being divided into a small and

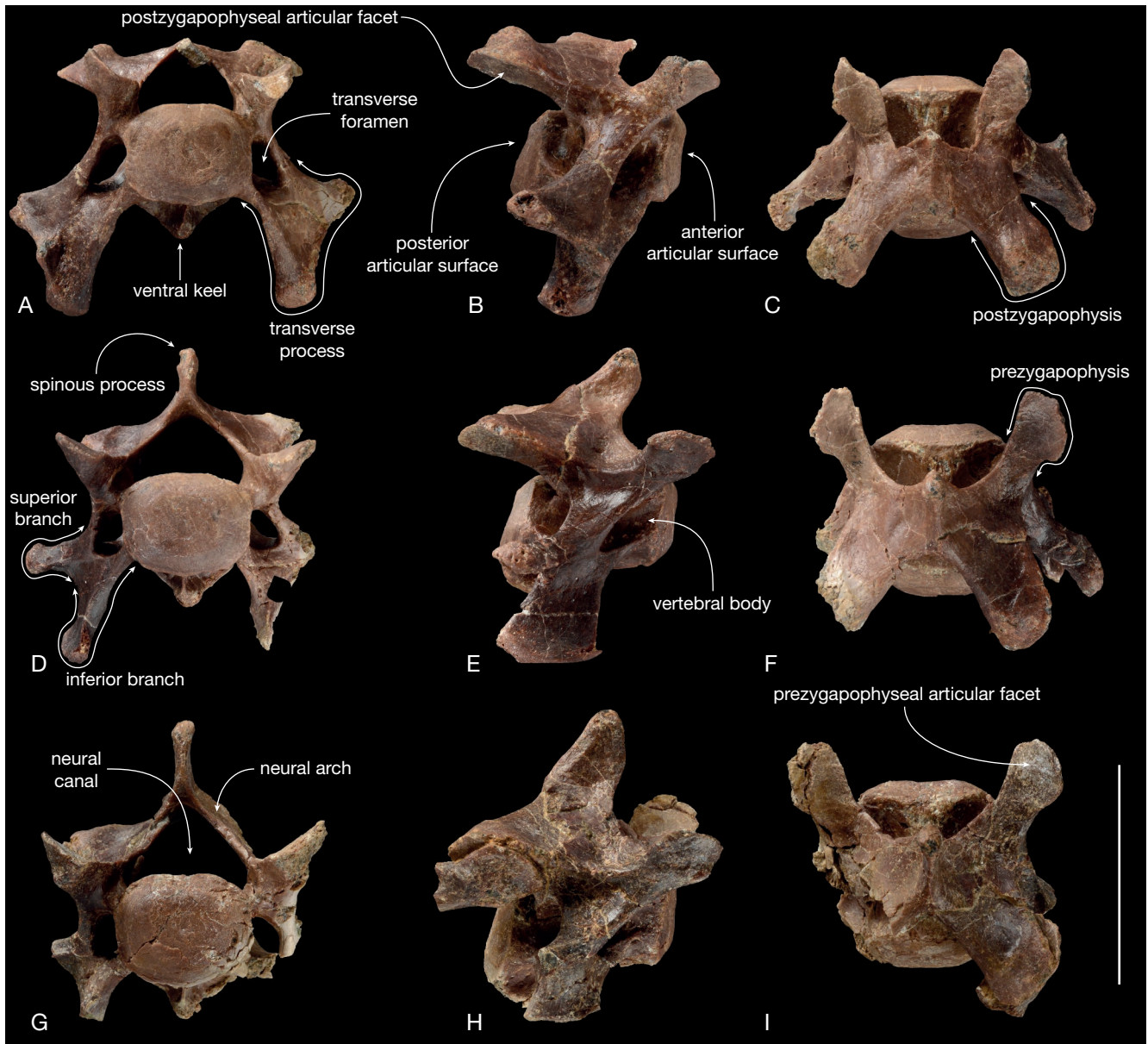


FIG. 11. — Cervical vertebrae of *Icaphoca choristodon* n. gen., n. sp. (holotype, MNHN.FPPI270). **A**, Ce3 in anterior view; **B**, Ce3 in right lateral view; **C**, Ce3 in dorsal view; **D**, Ce4 in anterior view; **E**, Ce4 in right lateral view; **F**, Ce4 in dorsal view; **G**, Ce5 in anterior view; **H**, Ce5 in right lateral view; **I**, Ce5 in dorsal view. Scale bar: 5 cm. Photos by L. Cazes & P. Loubry (GR2P).

more slender superior branch and a larger and wider inferior branch. The medial aspect of the transverse processes is almost oriented ventrally. The bifurcation is less prominent in Ce3, than it is in Ce4-5. In Ce3, the ventrally-oriented inferior and lateroposteriorly-oriented superior branches end as blunt processes, with the former being larger. In Ce3 the inferior branch is a thick process, whereas in the more posterior cervical vertebra, the inferior branch is transversely flattened and anteroposteriorly elongate. In Ce3-5 the superior branch forms a tubular process. The inferior branch of Ce3 resemble that of *Magophoca* but differs from the blade-like branch observed in *Acrophoca*. Although well-developed, the blade-like inferior branch of Ce4-5 are much smaller than in *Acrophoca* being approximately 50 % shorter than it is in this genus.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis using PAUP*4.0a169 yields fifty most parsimonious trees, with a tree length of 257 after 415 965 tried rearrangements. The strict consensus tree (Fig. 12) highlights that the topology of Monachinae is unresolved. Consequently, we performed a second analysis, downweighing homoplasy via implied weighing (Goloboff criterion, with $k = 3$). The heuristic analysis resulted eight most parsimonious trees with a best score of 258 and Goloboff fit -71.33016 after 44 527 tried rearrangements (Fig. 13). The consistency index is 0.4380, and the retention index is 0.6902.

The topology of the outgroup taxa, i.e. the stem pinnipedimorph *Pteronarctos goedertae*, the otariids *Arctocephalus*

TABLE 8. — Measurements of the cervical vertebrae of the holotype MNHN.FPPI270 of *Icaphoca choristodon* n. gen., n. sp., excluding the atlas and axis. Abbreviations and symbol: **e**, estimate for a character due to minor damage or deformation; **n/a**, the character could not be measured; **>**, the character is larger than the provided measure, on the condition that the measure is not too far off the actual value. Measurements in mm, taken with an analog caliper.

Character	C3	C4	C5
Overall, height	47.0	61.6	>71.5
Overall, width	82.4	81.0*	n/a
Body, length	38.5	39.7	42.8
Body, height (anterior)	22.8	23.4	24.7
Body, width (anterior)	28.1	29.3	31.0
Body, height (posterior)	24.3	25.3	>28.6
Body, width (posterior)	27.4	28.4	29.8e
Neural arch, canal, length	16.4	15.8	17.3
Neural canal, height	16.6	17.2	20.5
Neural canal, width	16.4	15.8	17.3
Spinous process, height	4.7	15.7	20.5

pusillus, and *Otaria byronia*, and the odobenid *Odobenus rosmarus* is as expected, with the former branching off first, followed by the otariids, followed by *Odobenus*. Phocidae form a monophyletic clade, with 23 synapomorphies, including 17 unambiguous ones. The unambiguous synapomorphies of Phocidae are: the strongly concave anterior border of the nasal cavity in anterior view (char. 4[0 > 1]); 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 > 0]); the pterygoids are laterally tilted and flaring posteriorly (char. 34[0 > 1]); the occipital condyles diverging dorsally (char. 35[0 > 1]); an intermediately large, posteriorly and medially protruding angular process on the mandible (char. 36[0 > 1]); all premolars are double-rooted (char. 47[2 > 1]); a reduced acromion process on the scapula (char. 58[0 > 1]); an unreduced intermediate phalanx on digit V (char. 74[1 > 0]); a moderately well developed iliopectineal eminence on the innominate (char. 80[0 > 1]); and no lesser trochanter on the femur (char. 83[0 > 1]). Ambiguous synapomorphies are characters 23, 62, 66, 81, 90, and 91 (further details, see Appendices 3, 4).

The topology of the four species representing Phocinae correspond well with that in previous studies (e.g., Bininda-Emonds & Russell 1996; Higdon *et al.* 2007; Fulton & Strobeck 2010; Rule *et al.* 2020a, b). In the current phylogenetic analysis, which focuses on Monachinae, Monachinae are supported as a monophyletic group by 17 synapomorphies, with no contact between the premaxilla and nasal (char. 1[0 > 2]); the nasal cavity opens more dorsally than anteriorly (char. 3[0 > 1]); there are two upper incisors per

quadrant (char. 39 [0 > 1]); an anterior orientation of the posterior border of the scapula in lateral view (char. 57[0 > 1]); a reduced scapular spine (char. 59[0 > 1]); a humerus with a greater tubercle below the level of the head (char. 63[2 > 0]); the presence of a transverse bar in the bicipital groove of the humerus (char. 64[0 > 1]); a flattened distal end of the styloid process of the ulna (char. 71[0 > 1]); a femur with a long epicondylar crest (char. 85[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 MtIII approximately 50 % (or more) shorter than MtI (char. 93[0 > 1]) as unambiguous synapomorphies. Apart from these twelve unambiguous synapomorphies, five others are ambiguous: characters 2, 14, 60, 69, and 91 (further details in Appendices 3, 4).

The resulting topology of the clades in this phylogenetic analysis clearly return the Miroungini and Monachini tribes. The Lobodontini tribe forms a polytomy at its base, with a clade of extant Lobodontini, most extinct Lobodontini, *Sarcodectes*, and *Acrophoca* + *Icaphoca*.

Unlike the previous study by Dewaele & Muizon (2024), Miroungini are the first to branch off, with Lobodontini and Monachini being sister groups to each other. Following previous studies, *Eomonachus* and *Pliophoca* are returned as Monachini, together with *Monachus* and *Neomonachus* (Tavani 1941; Berta *et al.* 2015; Berta *et al.* 2018; Rule *et al.* 2020a, b; Dewaele & Muizon 2024).

Within the polytomy, the four extant Lobodontini, *Hydrurga*, *Leptonychotes*, *Lobodon*, and *Ommatophoca*, group together as crown lobodontins. No extinct lobodontin included in this analysis falls within this crown group.

The polytomy of Lobodontini in the strict consensus tree underlines that a detailed phylogenetic analysis of extant and extinct Monachinae, with a special focus on Lobodontini is much needed. Such an analysis should include *Magophoca* and *Icaphoca* (which analyses of Rule *et al.* 2020a, b do not) as well as some specimens of the collection of the MUSM referable to new taxa and remarkable material (partial skulls and a sub-complete skeleton) of *Australophoca changorum*, whose holotype is a severely weathered incomplete humerus, partial radius and ulna. Such an analysis is currently beyond the scope of this study (which focusses on the description of a new monachine genus and species from the Pisco Formation) and will be undertaken in a work in progress by the authors.

The tribe of Lobodontini is supported by six synapomorphies, including five unambiguous synapomorphies: a parasagittal orientation of the medial margins of the tympanic bullae (char. 21[0 > 1]); the presence of a lip in the antero-medial region of the mastoid, abutting the posteromedial edge of the tympanic bulla (char. 27[0 > 1]); the transverse foramen of the atlas is at least partially visible in dorsal view (char. 52 [0 > 1]); a large size difference exists between the distal condyles of the femur (char. 84[0 > 1]); and a well-developed articular surface for the fibula on the calcaneum (char. 92[0 > 1]). A sixth character, 60, is an ambiguous synapomorphy (Appendices 3, 4). The extant, i.e. crown

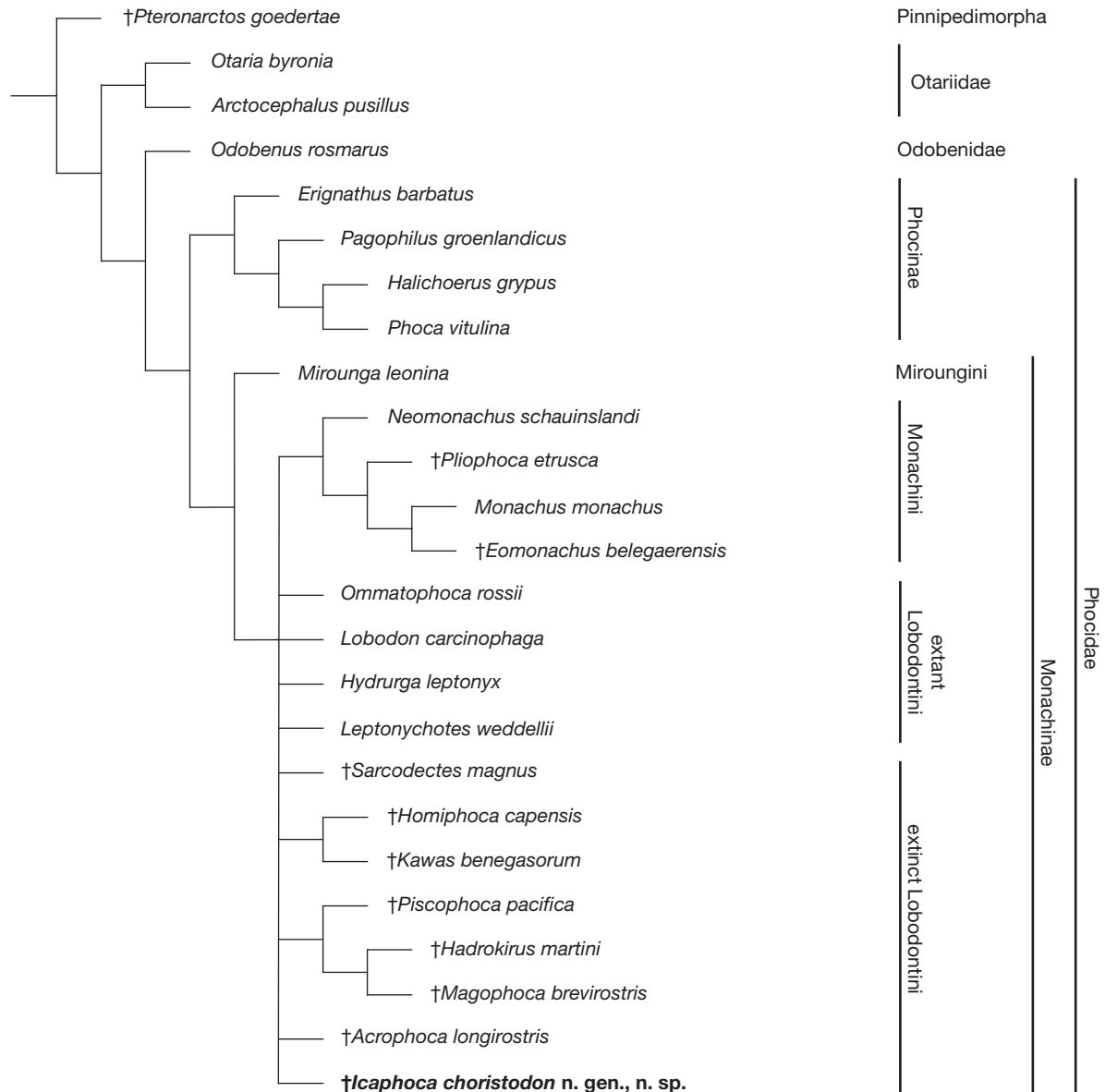


FIG. 12. — Phylogenetic relationships of *Icaphoca choristodon* n. gen., n. sp. among Phocidae. Strict consensus tree of the 50 most parsimonious trees of the phylogenetic analysis. Note the extremely poor resolution of the topology of Phocidae. Extinct species are preceded by a dagger.

lobodontins are supported by eight synapomorphies. Four are unambiguous: the anterior opening of the infraorbital foramen is located anterodorsal to M1 (char. 11 [1 > 0]); the posterior border of the scapula is oriented proximodistally in lateral view (char. 57 [1 > 0]); the radial tuberosity is located on the posteromedial side of the radius (char. 69[0 > 1]); and a manus with a strongly reduced intermediate phalanx on digit V (char. 74[0 > 1]). Four characters 17, 36, 62, and 66, are ambiguous. The extinct lobodontins are united by seven synapomorphies; all of which are ambiguous (characters 14, 53, 64, 70, 73, 75, and 80) (Appendices 3, 4).

Whereas *Sarcodectes* from the Northern hemisphere branches off before other extinct Lobodontini from the Southern hemisphere in the analysis by Dewaele & Muizon (2024), they form a polytomy with extant Lobodontini in the present study.

Of the seven extinct lobodontins of the Southern hemisphere included in the present analysis, *Hadrokirus*, *Homiphoca*, *Kawas*, *Magophoca*, and *Piscophoca*, form a clade that is retained in the strict consensus trees of both phylogenetic analyses with and without implied weighting. The analysis agrees with the previous analyses by Dewaele & Muizon (2024) that *Kawas* is a monachine and not a phocine, as stated by Cozzuol (2001) in the original description of the species.

Acrophoca and *Icaphoca* are sister taxa, united by five synapomorphies, of which two are unambiguous: the anterior end of the maxillary branch of the jugal reaches dorsal to dorso-medial to the infraorbital foramen (char. 13[0 > 1]), and the diastema between P4 and M1 is enlarged (char. 48[1 > 0]). Other synapomorphies are ambiguous. These are characters 40, 56, and 87 in the character list (Appendix 3).

Low bootstrap values (<50 %) for Monachinae, support the above statement that a detailed phylogenetic reassessment of extant and extinct Monachinae is much needed to create a more robust phylogenetic framework of the subfamily.

DISCUSSION AND CONCLUSIONS

Icaphoca choristodon n. gen., n. sp. is the sixth species of extinct Monachinae described from the Neogene of the southeastern Pacific realm, following *Acrophoca longirostris* and *Piscophoca pacifica* described by Muizon (1981), *Hadrokirus martini* by Amson & Muizon (2014), *Australophoca changorum* by Valenzuela-Toro *et al.* (2016), and by *Magophoca brevirostris* by Dewaele & Muizon (2024). Retrieved from stratigraphic beds below the CLB level (level P1-2 below P2), *Icaphoca choristodon* n. gen., n. sp. may be dated to the middle late Miocene (c. 9 Ma). This makes this taxon the oldest named phocid seal species from the Neogene of Peru. It enhances the exceptional diversity of the fossil phocid record on the Peruvian coast during the Neogene. However, it is noteworthy that these six taxa described so far were clearly not coeval since the Pisco Formation phocid record extends stratigraphically from the early late Miocene to the early Pliocene. As mentioned by Muizon & DeVries (1985), six faunistic levels can be identified in the Pisco Formation. The CLB level in the Ocucaje region, has yielded the all the specimens of *Magophoca brevirostris* and has been regarded as, as old as 8.4 Ma (i.e. middle Tortonian) by Dewaele & Muizon (2024), following Bosio *et al.* (2020). Since no remains of *Icaphoca choristodon* n. gen., n. sp. have been discovered in the CLB level beds, (although the latter has yielded abundant phocid remains, all referred to the single species, *Magophoca brevirostris*), it is therefore likely that *Icaphoca choristodon* n. gen., n. sp. was absent in the CLB level and that the two species were not coeval. In the Sacaco area, the late Miocene (c. 8-7 Ma) Aguada de Lomas level (AGL) has yielded remains referable to *Acrophoca* and *Australophoca*; and in the Latest Miocene to earliest Pliocene Sud-Sacaco level (SAS) have been retrieved specimens referred to *Acrophoca*, *Piscophoca*, *Hadrokirus* and *Australophoca*, four taxa that were therefore coeval. This suggests that Monachinae settled and spread along the Westcoast of South America possibly as early as nine million years ago. This starkly departs from the paleobiogeographic history of Monachinae, proposed by Rule *et al.* (2020a), who state that Monachinae originated in Australasia. However, their conclusion primarily relies on their phylogenetic analysis, despite the lack of a diverse (published) extinct monachine fauna from the region. Currently, only the late Pliocene monachin *Eomonachus* is known, yet, the fossil record doesn't extend much further in time, suggesting long ghost lineages. *Icaphoca choristodon* n. gen., n. sp. does not necessarily rule out an Australasian origin of Monachinae, but, by pushing back the earliest occurrence of Monachinae in the Southeast Pacific, it further lengthens these ghost lineages in the Southwest Pacific.

Furthermore, the presence of six upper incisors (three per quadrant) in *Icaphoca* is remarkable. Among monachines, this is shared with *Noriphoca gaudini*, possibly from the early Miocene, of Italy, and *Magophoca brevirostris* from the early late Tortonian of Peru. The presence of six upper incisors is common among Phocinae and other pinnipeds, suggesting that the presence of six upper incisors is a plesiomorphy. All three are also among the oldest known monachine seals. Certainly, *Icaphoca* and *Magophoca* are the oldest known monachine seals from the southern hemisphere.

Despite the lack of cranial material preserved for many extinct Monachinae from the northern hemisphere, and despite the varying topologies of phylogenetic analyses of Monachinae among different researchers, *Icaphoca* will help elucidating the paleogeographical history of Monachinae pending the discovery of more monachine fossil material.

Acrophoca and *Icaphoca* have been retrieved as sister taxa in the phylogenetic analysis presented above; they are united by five synapomorphies. Two of these are unambiguous, and easily visible: the anterior end of the maxillary branch of the jugal reaches dorsal to dorsomedial to the infraorbital foramen, and the diastema between P4 and M1 is enlarged. Despite the low bootstrap values, the latter character is striking: the diastema between P4 and M1, as well as the spacing between the other postcanine teeth contributes to the marked elongation of the skull of both species. This tooth spacing observed between all postcanine teeth, although clearly less pronounced than in *Acrophoca*, is unique among monachines. Adjoined by the fact that *Icaphoca* is geologically older than *Acrophoca*, this indicates that the former has already started to developed rostrum lengthening and forms an intermediate in the evolution from a monachine ancestor without an elongated rostrum, to the highly specialized condition in *Acrophoca* with a strongly elongated snout.

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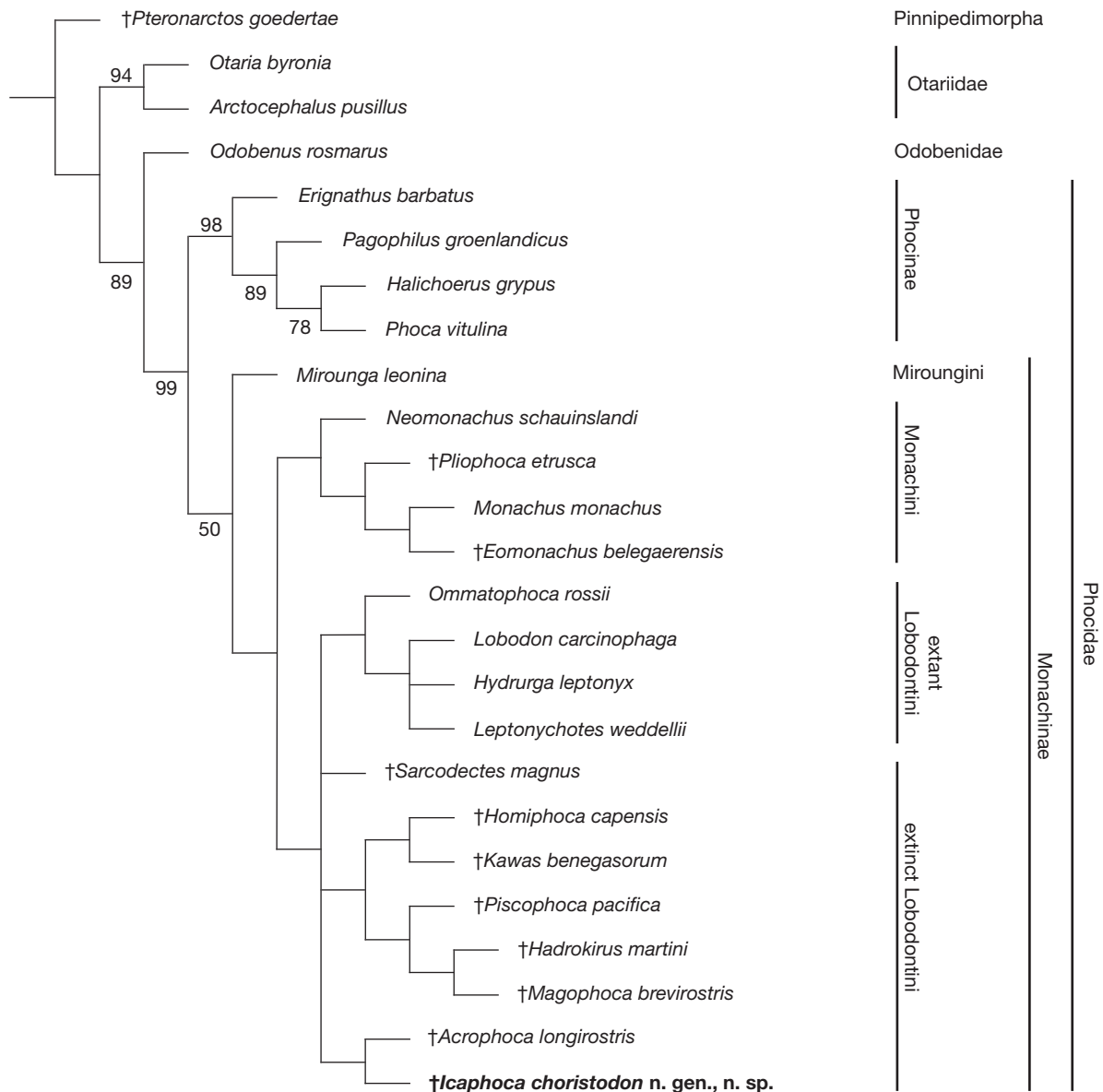


FIG. 13. — Phylogenetic relationships of *Icaphoca choristodon* n. gen., n. sp. among Phocidae, with Goloboff k-value set at three to downweigh homoplasy. Strict consensus tree of the eight most parsimonious trees of the phylogenetic analysis. *I. choristodon* groups with *Acrophoca longirostris*. Bootstrap values equal to or higher than fifty are shown. Extinct species are preceded by a dagger. Black bars represent the known age ranges of the different extinct taxa, clearly showing that *I. choristodon* is the oldest of the Peruvian seals. Abbreviations: **Ma**, million years; **Plioc.**, Pliocene; **Quat.**, Quaternary.

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APPENDICES

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
Arctocephalus pusillus (Schreber, 1775)
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, Tennyson, Scofield & Fitzgerald, 2020
Erignathus (Gill, 1886)
Erignathus barbatus Erxleben, 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)
Icaphoca n. gen.
Icaphoca choristodon n. gen., n. sp.
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 Dewaele & Muizon, 2024
Magophoca brevirostris Dewaele & Muizon, 2024
Mirounga Gray, 1827
Mirounga leonina (Linnaeus, 1758)
Monachus monachus Hermann, 1779
Monotherium Van Beneden, 1876
Monotherium delognii Van Beneden, 1876
Monotherium? wymani (Leidy, 1853)
Neomonachus Slater & Helgen, 2014
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)
Odobenus rosmarus (Linnaeus, 1758)
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
Properiptychus Ameghino, 1893
Properiptychus 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
Virginiaphoca magurai Dewaele, Peredo, Meyvisch & Louwye, 2018

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

PINNIPEDIFORMES

Pteronarctos goedertae: Barnes (1989, original description);

PINNIPEDIA

ODOBENIDAE

Odobenus rosmarus: IRSNB 1150B, IRSNB 1150D;

OTARIIDAE

Arctocephalus pusillus: USNM 484928;

Otaria byronia: USNM 95063, USNM 153568, USNM 153569, USNM 484888, USNM 484906, USNM 484912;

PHOCIDAE

Acrophoca longirostris: MNHN.F.SAS563 (holotype), MNHN.F.SAS1654, MNHN.F.SAS1654, MNHN.F.PPI265; *Australophoca changorum*: Valenzuela-Toro *et al.* (2016, original description);

Callophoca obscura: IRSNB 1156-M177 (lectotype);

Cystophora cristata: 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;

Devinophoca claytoni: Koretsky & Holec (2002, original description);

Devinophoca emryi: Koretsky & Rahmat (2015, original description);

Eomonachus belegaerensis: Rule *et al.* (2020a), original description);

Erignathus barbatus: (MNHN-ZM-AC-A795349), USNM 16116, USNM 269126, USNM 500249, USNM 500250, USNM 500251;

Frisiphoca aberrata: IRSNB 1191-M266 (lectotype);

Frisiphoca affinis: IRSNB 1118-M260 (lectotype);

Hadrokirus martini: MNHN.F.SAS1662 (holotype), MUSM 340 (paratype), MUSM 1662 (paratype), Amson & Muizon (2014, original description);

Halichoerus grypus: 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;

Histiophoca fasciata: USNM 16484, USNM 399449, USNM 504959, USNM 504960;

Homiphoca capensis: MNHN.F.AFS.1, MNHN.F.AFS.2, MNHN.F.AFS.23, MNHN.F.AFS.35, MNHN.F.AFS.36, SAM-PQ-L30080, Muizon & Hendey (1980);

Hydrurga leptonyx: MNHN-ZM-AC-1884-1152, MNHN-ZM-AC-1970-325, USNM 270326, USNM 275205, USNM 275208, USNM 396931, USNM 550359, USNM 550360, USNM 571676;

Kawas benegasorum: selected casts of MEF-PV 601 (holotype); Cozzuol (2001, original description);

Leptonychotes weddellii: IRSNB 1163, IRSNB 15390, USNM 269526, USNM 269528, USNM 395811, USNM 484886, USNM 504871, USNM 504875, USNM 550118;

Lobodon carcinophaga: IRSNB 1161, MNHN-ZM-AC-A7951, USNM 269526, USNM 269722, USNM 270325, USNM 310693, USNM 504740, USNM 504741, USNM 550080, USNM 550083;

Magophoca brevirostris: MNHN.F.PPI269 (paratype), MNHN.F.PPI276 (holotype), MNHN.F.PPI277 (paratype), MNHN.F.PPI278, MNHN.F.PPI294;

Mirounga leonina: IRSNB 3497, IRSNB 15642, IRSNB 17372;

Monachus monachus: MNHN-ZM-AC-A7953, USNM 219059;

Monotherium delognii: IRSNB 1153-M257;

Monotherium? sp.: IRSNB 1227;

Nanophoca vitulinoides: 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;

Neomonachus schaunslandi: USNM 243838, USNM 243839, USNM 334577, USNM 395996, USNM 395997, USNM 395999

Neomonachus tropicalis: BMNH.1887.8.5.1, USNM 100363, USNM 100371;

Noriphoca gaudini: Guiscard (1871, original description);

Ommatophoca rossii: IRSNB 1164, IRSNB 15389, USNM 275206, USNM 302975, USNM 339989;

Pagophilus groenlandicus: 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;

Phoca vitulina: 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;

Piscophoca pacifica: MNHN.F.SAS72, MNHN.F.SAS488, MNHN.F.SAS501, MNHN.F.SAS564 (holotype),

Pliophoca etrusca: MSNUP I-13993 (holotype), Berta *et al.* (2015);

Properiptychus argentinus: Muizon & Bond (1982);

Pusa capsica: USNM 341615, USNM 341616;

Pusa hispida: MNHN-ZM-AC-17951, USNM 225778, USNM 341617;

Pusa sibirica: IRSNB, 15264, IRSNB 21171;

Sarcodectes magnus: USNM PAL 475486 (holotype), USNM PAL 534034 (paratype), Rule *et al.* (2020b, original description);

Virginiaphoca magurai: USNM 639750.

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, ectotympanic 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)
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.

Appendix 3. — Continuation.

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. **Ina, 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, iliopectineal 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.
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.