A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seals phylogeny

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Here we describe a new phocid, Hadrokirus martini gen. et sp. nov., from the Pisco Formation, in the locality of Sud-Sacaco (Late Miocene to Early Pliocene of Peru). This taxon is the third true seal described from this locality. It is characterized by strong dentition paired with a powerful masticatory musculature and a peculiar atlas. No precise diet is inferred here, but a propensity for durophagy and predation on large prey (such as the extant leopard seal, Hydrurga leptonyx) can be considered. A cladistic analysis including characters from the literature as well as original ones places Hadrokirus among lobodontines in a clade with Piscophoca pacifica, another phocid from the Pisco Formation. In addition, this analysis supports the monophyly of both Phocinae and Monachinae and recognizes a clade consisting of the four extant species of lobodontines, with Acrophoca longirostris (the third phocid from the Pisco Formation) as sister-group of this clade. All clades are supported by unambiguous non-homoplastic synapomorphies. Following the optimization, our analysis recognizes aquatic innovations as phocine reversions at the scale of Carnivora, or as convergences of monachines with non-phocid pinnipeds.

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Introduction

The Pisco Formation (Peru) has been exceptionally prolific for Neogene vertebrate palaeontology, delivering numerous and often complete specimens of marine vertebrates, especially mammals and birds. Two phocid species endemic to this region of the world have already been described, namely Piscophoca pacifica and Acrophoca longirostris (Muizon 1981), although they may have been present on the north-central coast of Chile in the Bahía Inglesa Formation (Walsh & Naish 2002). Here we describe a new species of Phocidae from the Sud-Sacaco locality, Late Miocene to Early Pliocene, which is peculiar in the robustness of its skull, mandible and teeth. A reappraisal of the phylogeny of Phocidae has also been carried out, with special consideration for monachine seals. The ‘classical’ systematics of phocids recognizes two subfamilies, the northern Phocinae and the southern Monachinae (Trouessart 1897). This classification was subsequently modified with, for instance, the inclusion of the elephant seal Mirounga in monachines (King 1966), and supported by cladistic analysis (Muizon 1982). Thereafter, the monophyly of monachines was challenged by cladistic analyses based on morphological characters (Wyss 1988; Cozzuol 2001). In contrast, molecular analyses generally support the monachine–phocine dichotomy (Arnason et al. 2006; Fulton & Strobeck 2010).

Our study examined the existing morphological coding of phocids as well as studying the collections of living and fossil pinnipeds in Paris (MNHN) and Brussels (IRSNB). This work represents the first cladistic analysis known to the authors including extant and extinct taxa and treating the four extant species of lobodontines independently as least inclusive taxonomic units, sensu Pleijel & Rouse (2000).

Institutional abbreviations

MNHN: Muséum national d’Histoire naturelle, Paris, France; MUSM: Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru; MP: Museo di Storia Naturale e del Territorio Certoso di Calci dell’Università di Pisa, Italy; IRSNB: Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium.

Systematic palaeontology

| Phocidae Gray, 1821 |
|-------------------|
| Monachinae Gray, 1869 |
| Lobodontini Gray, 1869 |

Definition. All taxa that are more closely related to Lobodon carcinophaga than to Mirounga leonina are

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here considered as pertaining to the Lobodontini. The apomorphic states of characters defining the Lobodontini are: parasagittal medial margin of the tympanic bulla; presence of a mastoid lip abutting the posteromedial edge of the tympanic; presence of a well-developed articular surface for the fibula on the calcaneum.

**Hadrokirus gen. nov.**

**Type species.** *Hadrokirus martini*, by monotypy.

**Diagnosis.** As for the type species.

**Etymology.** From the Greek word *hadros*, stout and robust and the quechua word *kirus*, tooth.

**Hadrokirus martini** sp. nov. (Figs 1–14)

**Diagnosis.** A lobodontine diagnosed by: long skull (but not as long as that of *Acrophoca longirostris*); extremely robust dentition; an alveolar process of maxilla anteroventrally oriented for its part posterior to P1, forming a conspicuous angulation at the level of the latter; nasals strongly inclined anteroventrally; tympanic bulla extending posteri- orly but not covering the petrosal totally, incipient mastoid lip appressed against the posterior wall of the bulla, no external cochlear foramen; robust mandible; atlas featuring a very deep fossa for the *m. rectus capitis dorsalis* and an oblique wing, i.e. its dorsal plane faces dorsocaudally.

**Etymology.** In honour of Carlos Martin (deceased March 1999), the former owner of the Sacaco hacienda, who found the holotype as well as an impressive amount of other vertebrate fossils from the Pisco Formation in the Sacaco area.

**Types.** Holotype: MNHN.F.SAS 1627, a sub-complete skull on which the right zygomatic arch, parietal, entocuneiform and mesocuneiform; a sub-complete diaphysis of tibia; partial right calcaneum, astragalus, navicular, entocuneiform and mesocuneiform; a sub-complete right metatarsal I and a distal fragment of the left one; a fragmentary right metatarsal V; a sub-complete sesamoid; sub-complete posterior first, second and distal phalanges and another fragmentary phalanx. The closed sutures and dental wear suggest a fully mature individual. Paratype: MUSM 1662, same locality and horizon as the holotype, a sub-complete skull lacking the dorsal half as well as the incisors, canines, P1, P2 and M1 on both sides for all these teeth. This skull is bigger than the types but it is here considered that it can be referred to the same taxon because it bears extremely massive teeth characterizing the holotype and paratype.

**Type locality and horizon.** The holotype and the paratype are from the locality of Sud-Sacaco and were discovered in the SAS level of the Pisco Formation (as defined by Muizon & DeVries 1985; Muizon 1988). According to these authors the age of this level is Early Pliocene. In a recent recalibration of the late Neogene beds of the Pisco Formation, Ehret et al. (2012) referred the SAS level to the Late Miocene. This reassessment is related to a new dating of a tuff at Sacaco in a level (SAO level) stratigraphically younger than that of SAS. This tuff was dated by Muizon & Bellon (1980) at 3.9 ± 0.2 million years ago. The new age provided by Ehret et al. (2012) is 5.75 ± 0.5, indicating latest Miocene to earliest Pliocene. It is therefore likely that the SAS level, which is located below this tuff, should be attributed a latest Miocene age.

**Description and comparison**

The cranial material of *Hadrokirus* is well represented because two sub-complete skulls are available for study (holotype and paratype). Little postcranial material was recovered, but thanks to the good preservation of the skull of the types and to numerous cranial characters bearing phylogenetic information, a precise assessment of the affinities of *Hadrokirus* is possible.

The skull, mandible and postcranial elements are remarkably robust. The overall size must have been close to that of the extant monk seal, *Monachus monachus* (see online supplemental material, Appendix 1 for selected measurements of the holotype). Unless stated otherwise, the following description is based on the holotype. In the following description and discussion, the myological inferences are based on published dissections of the extant phocids (Howell 1928; Bryden 1971, 1974; Piérad 1971) and to a lesser extent on the anatomy of other carnivorans (Reighard & Jennings 1951; Davis 1964; Miller et al. 1964; Barone 1968, 1999). Pinniped anatomy is also based on dissections by CM of two specimens of *Halichoerus grypus* and one specimen of *Arctocephalus pusillus*.

**Upper teeth and alveoli.** The entire upper dentition is preserved and peculiarly massive (Figs 1, 2, 3A), i.e. the teeth are linguolabially broad when compared with their mesiodistal length. Moreover, the postcanines feature blunt carinae and apex. Such massiveness is not found in any other phocids, although the condition of *M. monachus* approaches that of *Hadrokirus*. Four upper incisors are present (as in all described monachines) and almost perfectly lined up transversely. The lateral incisor is slightly longer than the mesial. The incisors’ alveoli are both oval.
but that of the mesial one is more compressed mesiodistally. Although damaged, the mesial incisor seems to have been single cusped and without cingulum. Both lateral incisors show a wear facet that affects the mesial and distal margins of the tooth. They bear a well-developed distal cingulum.

The canine is conical, linguually curved and a fine carina runs along the entire length of the lingual side of its crown. Its alveolus is slightly oval. The left canine displays a small wear facet on its apex that reaches its distal surface. On the other hand, the right canine has suffered breakage and shows at the level of the second third of the estimated length of its crown a large wear facet that extends on its labial surface and that is slightly oriented distally.

As shown by Muizon (1981), the phocid postcanine dentition is composed of four premolars and one molar; this interpretation is based on the fact that the fourth postcanine is always preceded by a deciduous tooth while the fifth postcanine is not. We suppose that the condition of Hadrokirus does not depart from this disposition. The premolars are extremely massive compared with those of other lobodontines. Their enamel is thick and wrinkled. P1 and P2 are obliquely implanted, their mesiodistal length forming angles of 20° and 30° with the tooth row, a condition observed in M. monachus as well. P1 is small and single-rooted. In occlusal view, its labial margin is straight and its lingual margin is convex. P2–P4 are double-rooted. Furthermore, these teeth are reniform in occlusal view, because of the slight convexity of their lingual margin and the strong concavity of their labial margin. The premolars consist of a developed central cusp flanked by a mesial accessory cusp and one or two distal accessory cusp(s), the latter not being well individualized. In fact these accessory cusps are not independent from the main cusp but simply represent a swelling of the anterior and posterior crests of the main cusp. The premolars feature a well-marked lingual cingulum particularly inflated distolingually, where
a platform is present and displays a small cusp isolated from the main cusp of the crown. This particular trait is found in most lobodontines. The mesiolingual area of the cingulum is, in a lesser proportion, inflated as well, and bears a small accessory triangular cusp pointing toward the apex of the tooth. This accessory cusp is well individualized on P2. P2 and P3 show an important wear facet at the level of the distolingual inflation of the cingulum. The labial side of the premolars shows a cingulum extended at its mid-length by a carina joining the base and the apex of the crown, as observed in the extinct *Piscophoca, Homiphoca capensis* and the extant *Ommatophoca rossii*. Two great distal wear facets affect both P4.

The molar (M1) is reduced compared with other postcanines but is nonetheless noticeably massive, being low and bulky. This globular tooth features a single cusp, curved
distally, hence giving a ‘hook’ shape to the crown. The labial crest observed on the premolars is present but weaker. Like the premolars, M1 has a rugose labial surface. On both molars, a distal wear facet is visible on the bottom three-quarters of the height of their crowns.

The superior part of the roots of P2–M1 protrudes from the alveoli, being clearly visible in lateral view. The jugal teeth are almost concomitant, excepted for the molar, which is isolated from the premolars by a small 4 mm long diastema.

The tooth rows slightly diverge posteriorly (as in other Phocomorpha sensu Deméré et al. 2003) and displays, at the level of the two first premolars, a constriction that also concerns the palate.

**Skull.** The holotype features an almost complete but slightly deformed skull (Figs 1, 2, 4), whereas the paratype lacks most of the teeth but includes a better-preserved skull (Fig. 5). A specimen referred to the species herein described was also recovered that consists of a skull lacking the entire dorsal side (Fig. 6). A reconstruction of the skull and mandible based on both types is provided in Fig. 10. The skull is long and heavily built. The premaxilla shows on its anterior edge a developed tuberosity that protrudes dorsally in front of the nasal cavity (as is the case for almost all lobodontines). This tuberosity does not protrude anteriorly and the anterior alveolar plane of the premaxilla is vertical, as is observed in *Piscophoca*, but differing from the condition in *Homiphoca*, in which the plane faces anteroventrally. The premaxilla–maxilla suture is located, for the anterior two-thirds of the premaxilla, within the nasal cavity. As a consequence, only the posterior part of the ascending ramus is visible in lateral view (as in all other monachines). The ascending ramus, anteroposteriorly dilated, has a long contact along all the width of its apex with the anterolateral edge of the nasal. The opening of the nasal cavity is distinctly lengthened anteroposteriorly, and features a clear change of its curve where the ascending ramus of the premaxilla exits the nasal cavity (i.e. at the base of the dilated ascending process). This results in a strongly concave lateral border for the nasal cavity in lateral view. On the palate, the posterior edge of the incisive foramina is located posterior to the anterior margin of P2, as can be observed on the paratype (Fig. 5B).

The nasal is narrow and relatively short, as its posterior edge is anterior to the jugal–squamosal suture. Its anterior edge displays a medial notch that does not extend much posteriorly. The nasal is distinctively sloping anteriorly, forming an obtuse angle with the horizontal plane of the skull in lateral view. The nasal–frontal suture is slightly shorter than half the length of the nasal.

The maxilla of *Hadrokirus* differs from that of all other phocids in the great elevation of its anterior third. As a consequence, the posterior two-thirds of the snout, bearing P3–M1, are strongly inclined posteroventrally. Because of this condition, in lateral view, the tooth row is clearly

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**Figure 3.** Stereophotographs of the dentition of *Hadrokirus martini* gen et sp. nov. (holotype, MNHN.F.SAS 1627) in occlusal view. **A,** upper dentition (minus the mesial incisor); **B,** lower dentition. Scale bars: 5 cm.
The lateral margin of the tooth row. The elongated maxilla contributes to the length of the snout of Hadrokirus (a long snout being observed in most lobodontines). The palate is deep and shows a well-marked palatine sulcus that extends posteriorly almost as far as the posterior margin of P4 (as featured by the paratype, Fig. 5B). On the lateral face of the maxilla, the anterior opening of the infraorbital canal is subcircular, and the lamina forming its ventral and lateral

oblique, being depressed posteriorly and uplifted anteriorly and the palate is oriented anterodorsally. The only living phocid that displays a similar trait is Ommatophoca, but to a much lesser extent; extinct phocids sharing this feature are Piscophoca and Homiphoca, but their condition is never as pronounced as in Hadrokirus. A transverse constriction affects the maxilla at the level of the P1 and P2. The lateral surface of the maxilla is strongly convex and juts out above

Figure 4. Drawing and photograph of the skull of Hadrokirus martini gen. et sp. nov. (holotype, MNHN.FSAS 1627) in dorsal view. Abbreviations: fr, frontal; ju, jugal; mx, maxilla; na, nasal; ncr, nuchal crest; onc, opening of nasal cavity; or, orbit; pmx, premaxilla; porp, preorbital process; zpsq, zygomatic process of squamosal. Teeth abbreviations: as in text, capitalized. Scale bar: 5 cm.
walls is particularly thick. This canal is located above M1. The preorbital process is small but prominent. As in all phocids, there is no crest joining it to the ventral border of the orbit. The maxilla is inflated at the anterior root of the zygomatic arch. The anteroventral edge of the orbit is made of an imbrication of the maxillar process of the jugal anterodorsally and the zygomatic process of the maxilla anteroventrally and medially. It forms an elevated vertical wall as is observed in *Acrophoca*, but differing from the laterally tilted condition of other monachines. As a consequence, the suture between the zygomatic process of the maxilla and the jugal is largely visible in lateral view. In the orbit, the maxilla–jugal suture forms a deep groove that becomes more shallow posteriorly. The posterior end of

Figure 5. Skull of the paratype of *Hadrokirus martini* gen. et sp. nov. (MUSM 1662) in A, dorsal view; B, ventral view; C, lateral view. Scale bar: 5 cm.
the zygomatic process of the maxilla almost reaches the level of the anterior margin of the zygomatic process of the squamosal, ventral to it.

The jugal is extremely high and thick. Its dorsal edge is thin, and forms a sharp crest on the ventral border of the orbit. Its anterodorsal extremity climbs on the maxilla and reaches a level dorsal to the posterior edge of the infraorbital canal but well ventral to the preorbital process of the maxilla. The anterior suture with the maxilla is subvertical above the infraorbital canal and oblique posterior to the canal. The lateral and medial surfaces of the jugal are subvertical along their entire length. The lateral plane of the jugal is slightly but distinctly concave. The ventral edge of the bone is relatively wide and flat especially at the level of the inferior squamosal process; it bears a sharp crest on the ventrolateral edge of the bone. The superior squamosal process of the jugal is remarkably slender. Its posterior extremity covers the anterodorsal end of the zygomatic process of the squamosal and is bent posteriorly. The inferior squamosal process is, in contrast, very robust. It is very high in its anterior part, thinned out posteriorly and almost reaches the glenoid fossa.

The frontal shows a weak tuberosity on the anterodorsal edge of the orbit. This corresponds to the supraorbital process usually well developed and prominent in non-phocid pinnipeds. The interorbital bridge is long, narrow, and its dorsal surface is distinctly domed in lateral view. In dorsal view, its margins moderately flare anteriorly and its posterior end narrows anterior to the braincase. Hence the least interorbital width occurs on the posteriormost portion of interorbital bridge, as in most pinnipeds but phocines, in which it occurs on the anterior half.

The squamosal shows a particularly upward oriented zygomatic process that contributes, with the inferior squamosal process of the jugal, to the massiveness of the zygomatic arch. Its anterior end is spatulate and is anterior to the limit between the braincase and the ethmoid region. It is slightly tilted medially; therefore its extremity juts out above the temporal fossa. The glenoid fossa is deep and cylindrical and its major axis slightly dips dorsomedially. The preglenoid process (which forms the anterior wall of the glenoid fossa) is well developed and forms a triangular prism that tapers medially. The postglenoid process is quite thick but thins out ventrally. It has an important ventral extension reaching well ventral to the level of the preglenoid process. A small postglenoid foramen is present on the posterior edge of the postglenoid process just anterior and ventral to the external auditory meatus.

The tympanic bulla has a triangular outline, its margins being roughly rectilinear (Fig. 7). Its medial margin is parasaagittal, as in extant and extinct lobodontines. The ectotympanic is not unusually inflated, although it marks a low bulge where the suture with the entotympanic is located. On the other hand, the entotympanic is distinctly inflated in its medial part. The ectotympanic lip that partially covers the postglenoid process in some pinnipeds seems to be absent, or extremely reduced. The lateral angle of the bulla is located near the postglenoid process and forms the thick ventral wall of the external auditory meatus. It extends laterally beyond the level of the mid-width of the glenoid fossa but does not protrude laterally from the lateral edge of the braincase. An anterolateral tuberosity confers to this angle the shape of an anteriorly oriented hook. The carotid foramen is located at the posterior angle of the bulla. It is visible in ventral view, as it opens posteromedioventrally and not mediadly as in phocines. It is isolated from the basioccipital by a narrow lamina of the tympanic bulla. The posterodorsal margin of this foramen is a sharp and angular blade of bone, which protrudes posteromedially and which forms almost a right angle on the border of the bulla. The posterior lacerate foramen was slightly distorted during preservation of the holotype, but it appears to have been reniform (and approximately semicircular on the paratype). On the posterior wall of the ectotympanic, the pit for the tympanohyal is wide and limited mediadly and laterally by thin laminae protruding from the tympanic bulla. The medial lamina is more developed and ventrally covers the median part of the
pit. Anterolateral to the tympanohyal pit and at the junction between the ectotympanic and the pars mastoidea is a large stylomastoid foramen with an anterolaterally oriented opening and groove. Posterior to the stylomastoid foramen, and posterolateral to the tympanohyal pit is a large triangular swelling of the mastoid, which seems to penetrate below the bulla. This swelling, however, does not contact the tympanic bulla and therefore the auricular foramen (located posterior to the swelling) is not fully separated from the stylomastoid foramen. The two foramina, however, are not fully coalescent, as is observed in non-phocid Pinnipedimorpha sensu Deméré et al. (2003). There is no external cochlear foramen and the tympanic does not cover the pars petrosa of the petrosal totally posteriorly as in Recent lobodontines. Therefore, as is observed in M. monachus, a small triangular portion of the pars petrosa is visible at the posterior angle of the bulla, although smaller and not ‘dome-shaped’ as in this taxon. Hadrokirus also differs from M. monachus in having a mastoid lip, although it is incipiently developed, almost reduced to a simple crest, appressed against the posteromedial border of the bulla. In all other lobodontines the tympanic fully covers the pars petrosa posteriorly and a well-developed mastoid lip closes the external cochlear foramen. The posterolateral surface of the pars mastoidea bears a shallow concavity on its posterior part. As in all other monachines except Ommatophoca, the pars mastoidea is not widely visible in dorsal view because the lambdoid crest of the occipital is not inflected medially as is observed in phocines. On the lateral edge of the pars mastoidea is a large, massive, and laterally salient mastoid process, which is relatively stouter than in the other lobodontines.

Ventrally, the basioccipital is a roughly rectangular bone, which occupies the space between the tympanic bullae. This correlates with the parallel medial borders of the tympanic bullae, also found in other lobodontines. Its anterior suture with the basisphenoid is obliterated but on the paratype, a light transverse ridge indicates that it was located approximately mid-way on the medial edge of the bulla. The lateral borders of the basioccipital are roughly parallel. On the exoccipital, the hypoglossal foramen is located posterior and lateral to the posterior lacerate foramen. The exoccipital bears a remarkably robust triangular paroccipital process. Its posterior crest extends dorsally and joins the ventrolateral end of the nuchal crest. The occipital condyles are strongly convex and show a lateral bulge on the dorsal half of their height. They are salient posteriorly, however, in lateral view, they do not protrude further posteriorly than the nuchal crest. This condition is unclear on the holotype because of the distortion of the specimen but is distinct on the paratype (Fig. 5C). The articular surfaces of the occipital condyles are fused ventrally. In dorsal view, the nuchal crest is V-shaped and weakly opened posteriorly, forming an angle of approximately 100°. In lateral view, it forms a simple arc anteriorly opened. The nuchal crest is relatively thin in its dorsomedial region, but it greatly thickens in its ventrolateral part to reach approximately 1 cm width. Its posterolateral extremity is inflated in a massive protuberance. This condition is more pronounced on the holotype.
than on the paratype and could be related to sexual dimorphism. The massiveness of the nuchal crest of *Hadrokrinus* is doubtlessly related to a powerful neck musculature.

The parietal of the holotype shows a well-developed sagittal crest. The surface of the parietal is irregular on both sides of this crest, indicating a powerful origin for the *m. temporalis* (inferred from Howell 1928; Piérard 1971). As for the nuchal crest, the sagittal crest is much lower on the paratype, suggesting that the power of the *m. temporalis* is subject to intraspecific polymorphism (i.e. sexual dimorphism), as is the case in most extant carnivorans.

On the ventral side of the skull, the palatine extends anteriorly up to the posterior border of P4. The anterior edge of the choanae is semicircular and positioned, as in most phocids, anterior to the mid-length of the skull, but slightly posterior to the anterior end of the temporal fossa. The horizontal lamina of the palatine is perforated by a minor palatine foramen communicating with the lateral surface of the vertical lamina. The sphenopalatine vacuity is completely included in the palatine and probably confluent with the pterygopalatine vacuity. The former vacuity is clearly oval, its major axis being anteroposteriorly oriented.

The pterygoid contacts medially the posterior part of the vertical lamina of the palate and is relatively vertical in its posterior portion. The hamulus is reduced because it only forms a small knob on the ventral and medial surface of the perpendicular lamina of the palatine, as is observed in most monachines, but not *Mirounga* in which it forms a ‘hook-like’ process.

The vomer and presphenoid are prepared (and therefore visible) only on the paratype (Fig. 5B). They form a small lamina tapering and becoming a slender median ridge to support the cartilaginous nasal septum.

On the anterolateral region of the braincase, the alisphenoid develops a singularly angular and sharp tubercle, which forms a salient crest, which was probably receiving part of the *m. temporalis*. This process is generally reduced to a simple rugose area in other phocids.

**Lower teeth.** The incisors are not preserved on the holotype and paratype (Figs 3B, 9). The right canine of the holotype is complete; the left is missing the crown. The canine is distinctly everted laterally and the crown is slightly bent lingually. It displays a fine lingual carina observable at the apex of the crown. It bears an important wear facet on its lingual margin. A vertical carina joining the cingulum to the apex of the main cusp is present. The apex of the tooth bears an oval wear facet anterolaterally oriented.

The lower premolars show, as on the uppers, on the labial side of the tooth, a vertical carina joining the cingulum to the apex of the main cusp. This carina is especially developed on p3. It is wide at its contact with the labial cingulum and strongly narrows toward the apex of the tooth. The enamel of the labial surface of the jugal teeth is strongly wrinkled. Except for p4, all lower jugal teeth are double-rooted, hence mesiodistally elongated. The premolars feature a large central cusp slightly convex on its lingual and labial margins flanked by a mesial and a distal accessory cusp, both located at approximately half to two-thirds of the height of the crown. These cusps are not well individualized from the main cusp as in some Recent lobodontines (e.g.*Hydrurga, Lobodon carcinophaga*), but are somehow integrated to the anterior and posterior crests of the main cusp. The anterior accessory cusp is larger than the posterior one. On p1–p3, another accessory cusp is present at the bottom of the distal cingulum; it is also present on p4, albeit extremely reduced. The molar bears only one main cusp, very convex labially, and a distal accessory cusp notably well developed. The carina joining the base of the labial cingulum to the apex is also present but reduced and more distally located. The roots of the postcanines protrude a few millimetres off their alveoli; this condition is probably related to the relatively old ontogenetic age of the specimen. The premolars are obliquely implanted, especially p2 and p3, for which their mesiodistal lengths form angles of approximately 30° and 20° with the tooth row. Correlatively, the tooth row is short and the horizontal ramus of the dentary is anteriorly widened (Fig. 3B). Small wear facets are present on p2 and p3; they affect the apex of the mesial crest leading to the main cusp as well as the apex of the latter.

**Dentary.** The dentary of the holotype is very well preserved, although it lacks the anterior end (Fig. 8); the dentary of the paratype on the other hand lacks the coronoid process, but its anterior end is preserved (Fig. 9). See Fig. 10 for a reconstruction of the skull and mandible. The dentary is extremely robust and stout and broadly resembles that of *M. monachus* and *Pliophoca etrusca*; this condition differs from the more slender bone usually found in other phocids. The dentary of the holotype is slightly larger and more massive than that of the paratype, a condition probably related to sexual dimorphism, as is found in the extant lobodontines, *Hydrurga* for instance. On the holotype, most of the alveoli of the incisors are not preserved except for a small portion of the alveolus of the lateral incisor on the right hemimandible. This alveolus is anteromedial to the canine. The horizontal ramus of the paratype on the other hand is entirely preserved, and shows a subcircular alveolus for the lower canine. In both specimens the dentary is very thick anteriorly (in dorsal view) but thins out posterior to the tooth row on the vertical ramus. The horizontal ramus is long and elevated especially on the holotype. On this specimen the height of the body increases anteriorly while on the paratype it is roughly constant and slightly decreases at the level of the symphysis. The short and vertical mandibular symphysis extends posteriorly as far as the level of p2 on the
paratype and up to the anterior edge of p3 on the left hemimandible of the holotype. The symphysis of the paratype is roughly oval-shaped but only slightly longer than wide. Three large mental foramina are lined up at mid-height of the horizontal ramus of the holotype below p1–p3. On its medial surface, the horizontal ramus shows a shallow but distinct fossa for the insertion of the m. digastricus below p4 and m1 that fades posteriorly at the level of the retromolar space. The insertion of the m. digastricus probably extends posteriorly on the ventral edge of the vertical ramus where a line of rough bone is present just anterior to the angle of the dentary (inferred from Piérard 1971). The retromolar space is short, since the dorsal edge of the mandible begins to rise less than 1 cm posterior to m1.

The vertical ramus is very high, long and transversely thin. The coronoid process is large, wide and flat and also resembles that of M. monachus. It clearly differs from that of Piscophoca, which is narrow and deeply excavated. Its anterior edge is strongly sharpened on c. 3–4 cm and thickens again posterodorsally toward the apex of the process. This peculiarity is observed in Acrophoca, Ommatophoca and some specimens of Piscophoca (MNHN.F.SAS 501). The

Figure 8. Mandible of Hadrokirus martini gen. et sp. nov. (holotype, MNHN.F.SAS 1627) in A, lateral view; B, dorsal view. Abbreviations: ag, angular process; cp, coronoid process; mc, mandibular condyle; mf, mental foramina; ms, mandibular symphysis. Teeth abbreviations: as in text, capitalized. Scale bar: 5 cm.
Figure 9. Mandible of the paratype of *Hadrokirus martini* gen. et sp. nov. (MUSM 1662) in A, medial view; B, dorsal view; C, lateral view. Scale bar: 5 cm.

The medial surface of the coronoid process displays a deep semicircular fossa limited anteroventrally by a powerful crest. The apex of the coronoid process is rounded and slightly bent laterally. Its posterior edge is distinctly concave and forms a posterodorsally oriented notch.

The masseteric fossa is shallow but wide, which denotes a vast insertion for the *m. masseter*. The bone is particularly thin at the level of the insertion of the *m. masseter profundus* (inferred from Howell 1928; Piérad 1971). The masseteric fossa of *Hadrokirus* resembles that of *M. monachus* and differs from the deep fossa observed in *Piscophoca*.

The condyloid process is elevated, well above the level of the tooth row. The condyle is laterally tilted. Its lateral end displays an anterior projection of the articular surface. This condition was also observed in *Acrophoca, Piscophoca, Homiphoca* and on some specimens of *Odobenus rosmarus* (the extant walrus). The angular process forms a large tuberosity, developed on the posterior margin and the medial surface of the mandible, for the insertion of the *m. pterygoideus medialis* (inferred from Howell 1928; Piérad 1971). This tuberosity extends distally as far as the level of the anterior edge of the condyle. Although a roughened surface is present and probably denotes the insertion of the *m. masseter superficialis* (inferred from Howell 1928; Piérad 1971), the ventral margin of this angular region is not medially or laterally bent as observed in most pinnipeds.

On the medial side of the dentary, the mandibular foramen is located posterior to the apex of the coronoid process. The foramen and the canal are both weakly developed.

**Hyoid apparatus.** Some elements of the hyoid apparatus have been recovered (Fig. 11), namely the basihyal, both thyrohyals and two fragments of another hyoid bone, possibly the ceratohyal (too fragmentary to be informative,
Figure 10. Reconstruction of the skull and mandible of *Hadrokirus martini* gen. et sp. nov. Skull in A, dorsal view; B, ventral view. C, skull and mandible in lateral view. Scale bar: 5 cm.
The atlas is extremely robust. The transverse process is a fossa for the m. obliquus capitis caudalis (inferred from Howell 1928; Piérard 1971). These fossae are not as deep as in Ommatophoca and wide resembling that of Piscophoca. It clearly differs from that of Acrophoca, which is much longer and narrower. On its ventral surface, the body shows a thin median crest that separates two fossae for the insertion of the m. longus colli (inferred from Howell 1928; Piérard 1971). These fossae are not as deep as in Acrophoca. The posterior end of the ventral crest is caudally broadened, forming a massive posterior tubercle. The crest disappears just anterior to the caudal edge of the ventral surface of the dens. The transverse foramen is transversely narrow on the left side, but almost circular on the right and more than three times larger than the left foramen. The transverse process is complete on the left side of the axis. By contrast with the massiveness of the remaining vertebrae, it is extremely slender.

It is noteworthy that, proportionally to the size of the skull, the atlas and axis of Hadrokirus are much larger than those of Piscophoca, which confirms the powerful neck of the former.

Tibia–Fibula. In the holotype, the right tibia is preserved lacking posterior and anterior fragments of the proximal epiphysis and most of the distal epiphysis (Fig. 13A, B). It is proximally fused to the fibula. Starting from approximately the middle of its length, the diaphysis is slightly bent laterally. A deep intercondylar fossa is located between the two articular condyles for the femur. This condition is enhanced by the fact that both the lateral margin of the medial condyle and the medial margin of the lateral condyle form distinct eminences on the proximal surface of the bone. The anterior tibial fossa is well marked (but a proximolateral portion is missing); the posterior tibial fossa is deeper but does not extend much medially, leaving a wide surface medial to it for the origin of the m. flexor digitorum longus and insertion of the m. popliteus (both muscular attachments inferred from Howell 1928;
Figure 12. Drawing and photographs the two first cervical vertebrae of *Hadrokirus martini* gen. et sp. nov. (holotype, MNHN.F.SAS 1627): photographs of the atlas in A, cranial view; B, caudal view. C, D, drawing and photograph of the atlas in lateral view. E, axis in lateral view. Abbreviations: cas, caudal articular surface; frc, fossa for *m. rectus capitis dorsalis minor*; if, intervertebral foramen; tf, transverse foramen; tp, transverse process. Scale bars: 3 cm.
Piérard 1971). The posterior tibial fossa is not as deep as in phocines. The medial side of the diaphysis shows a broad roughened surface for the *m. biceps femoris* (inferred from Howell 1928; Piérard 1971) that extends distally as far as the second third of the length of the bone. This surface, concerning proximally all the medial side, is limited to its anterior half for the second third of the length of the bone, leaving space posteriorly for the insertion of the *mm. gracilis, semimembranosus* and *semitendinosus* (muscular attachments inferred from Howell 1928; Piérard 1971). The anteromedial surface of the bone is sharpened and forms a clear carina extending along almost the entire length of the diaphysis.

Only the anterior half of the proximal epiphysis and a portion of the diaphysis (Fig. 13A, B) of the fibula were recovered. The proximal epiphysis features a very marked
cresid extending the width of the origin of the extensor m. hallucis longus (inferred from Howell 1928; Piéard 1971).

Foot. Several bones of the foot, mostly fragmentary, were recovered. A partial right calcaneum is preserved (Fig. 13D) missing the calcaneal tuber, a medial fragment and a lateral fragment. A well-developed articular facet for the astragalus is visible on its medial side. However, the facet for the fibula is extremely reduced. The facet for the cuboid is distally oriented.

A sub-complete right astragalus is preserved (Fig. 13C). The body is narrow. The proximal trochlea features a long but narrow articular surface for the tibia; the one for the fibula is transversely expanded, being clearly wider than long. Compared with other lobodontines, the medial end of the trochlea, articulating with the medial malleolus, is wide and very long. The distal articular surface shows facets for the calcaneum, the cuboid (there is no clear distinction between the two facets) and for the navicular.

A small part of the navicular is preserved, but it is too fragmentary to be described.

A right entocuneiform was recovered but lacks a plantar half (Fig. 13E). Its articular facet for the mesocuneiform is narrow and unusual in being dorsally oriented. The dorso-lateral and dorsomedial margins of its articular facet for the metatarsal I are strengthened by the presence of small tubercles. The dorsal surface of the entocuneiform on the contrary does not display, as in many phocids, a lateral tubercle, but a simple tuberosity.

A right mesocuneiform is preserved but lacks a medi-plantar fragment (Fig. 13F). It does not bear any noticeable feature, resembling that of Hydrurga.

Both metatarsals I are preserved; the right one is sub-complete (Fig. 14A, B) and the left one is only represented by a distal fragment. This robust bone has an overall rod-like shape. It is weakly bent medially and dorsally and its diameter reduces distally. The articular surface for the entocuneiform is shallow. The other proximal articular surface, for the metatarsal II, is not entirely preserved but seems to have been dorsolaterally oriented like in all monachines. The plantar surface of the proximal half of the diaphysis is flat. On the plantar side of the distal extremity, the two fossae for the sesamoids are especially deep.

A right metatarsal V is preserved but very fragmentary, consisting only of the distodorsal quarter of the bone (Fig. 14F). It bears no noticeable feature.

A sesamoid (probably from the right foot) is preserved (Fig. 14H, I). It is sub-complete and bears a concave articular facet on two-thirds of its length on one side, and is convex on the other.

A sub-complete posterior first phalanx is preserved (Fig. 14C, D). Its plantar surface is medially grooved on the proximal third of its length but becomes flat distally. Its dorsal surface is irregular. The plantar side of the head shows a deep fossa for the insertion of the ligament. Another phalanx (possibly first) is preserved, but too fragmentary to be described.

A sub-complete second phalanx was recovered (Fig. 14E); it lacks the proximal epiphysis. Its plantar surface is flat along all the length of the bone.

The distal half of a distal phalanx is preserved (Fig. 14G). Like in all monachines, it features a reduced insertion for the claw.

Functional interpretations

The dentition featured by Hadrokirus is the most robust of all extant and extinct phocids. This peculiarity paired with powerful insertions of masticatory and craniocervical muscles challenge inference of a ‘classical’ phocid diet consisting essentially of actinopterygians, chondrichthians and cephalopods. As for the preceding description, myological references are based on dissections of extant carnivores (see earlier in the text for cited literature).

Masticatory musculature and dentition

It should be emphasized that both adductor and abduc- tor masticatory muscles of Hadrokirus were powerful. The scars of the mm. temporalis, pterygoideus lateralis and medialis on the skull and dentary testify to the strength of the adductor musculature. The origin of the m. temporalis is marked by a broad temporal fossa (heightened by a well-developed sagittal crest on the holotype) and an irreg- ular surface of the parietals (Fig. 1). Its insertion on the coronoid process is marked as well, but is peculiar because it is especially conspicuous on its medial side. In addition, the large size and width of the coronoid process is an indication of the size of the m. temporalis, one of the main adductors of the mandible. The massteric fossa on the other hand is not especially deep (although a small depression is visible in the middle of the lateral surface of the coronoid process); however, the large size of the ramus denotes a large area of insertion of the muscle and therefore a powerful m. massetter. Furthermore, the widened ventral surface of the zygomatic arch and the large size (high and thick) of the jugal suggest an equally important origin of the m. massetter, hence confirming the power of the adduc- tor musculature and stroke. Similarly, a large size jugal is present in Hyaena or large felids (Panthera tigris, Panthera leo) and correlates to a very powerful adduction of the mandible. Moreover, the protruding alisphenoid process denotes (as in Crocuta crocuta for instance) two powerful adductor masticatory muscles, mm. pterygoideus lateralis and medialis (both muscular attachments inferred from Howell 1928; Piéard 1971). Furthermore, the developed angular process of the mandible also vouches for a strong m. pterygoideus lateralis (inferred from Howell 1928; Piéard 1971).
The abductor musculature of *Hadrokirus* is also powerful, as shown by the deep and anterior insertion of the *m. digastricus* on the medial and ventral sides of the dentary.

The origin of the *m. digastricus* of *Hadrokirus* requires some comment. In phocids the location of the origin of the *m. digastricus* is variable. In *Pusa hispida*, it is on “the depression upon the mastoid directly caudal to the center of the bulla” (Howell 1928, p. 46). In *Leptonychotes* it is “on the mastoid part of the temporal bone, caudolateral to the bulla tympanica, and the caudal fourth of the bulla” (Pièrard 1971, p. 84). In *Mirounga leonina*, it is on the “rudimentary jugular process of the exoccipital bone” (Bryden 1971, p. 121). In fact, it is noteworthy that the morphology and size of the paroccipital process varies among phocids. It is very small or absent in most Recent phocines, which have a medium-sized to reduced dentition.
It is a low crest in *Leptonychotes* and *Mirounga*, genera that have small jugal teeth. It is very large and robust in *M. monachus* and *Hydrurga*, two genera that have powerful jugal teeth. In land mammals bearing a conspicuous paroccipital process of the exoccipital, the origin of the *m. digastricus* is generally on the apex of the process (Reighard & Jennings 1951; Davis 1964; Miller et al. 1964; Barone 1968, 1999). This condition is therefore likely to be plesiomorphic for carnivorans and it is likely that the origin of the *m. digastricus* of *Hadrokirus* was on the apex of the paroccipital process. Therefore, the thickness and massiveness of this structure support the hypothesis of a strong *m. digastricus*, which corroborates the observations made on the dentary.

The inferred powerful masticatory musculature of *Hadrokirus* is paired with large and globular teeth and robust dentary. The tooth row is short (correlatively to the oblique implantation of the first premolars), allowing a small area of application for the bite force and therefore greater pressure is obtained.

Even if the diet of *Hadrokirus* is difficult to infer, because seals are generally very eclectic, an interesting comparison can be made with the diets of the recent Monk seals. Furthermore, an analogy with the robust dentition of durophagous carnivorans like *Enhydra lutris* (which also shows robust jugal teeth) can be made. Monk seals have the most robust teeth among Recent phocids. They mainly prey on actinopterygians and chondrichthyans but also on squids, octopuses, brachyurans and lobsters (Gilmartin & Forcada 2009). *Monachus schauinslandi* is recorded to feed upon *Panulirus marginatus* (banded spiny lobster; Kenyon 1981a) and *M. monachus* on *Panulirus regius* (royal spiny lobster; Marchessaux 1989). Both are relatively large lobsters, and so feature a thick carapace, the crushing of which requires robust teeth. Even if lobsters are not the most common prey of monk seals, it is clear that these seals can eat them. However, the teeth of *Hadrokirus* are clearly more robust than those of *M. monachus* and *M. schauinslandi*, which suggests that it may have been able to feed upon invertebrates with stronger shells, such as thin-shelled bivalves or sea urchins.

Among aquatic carnivorans, *Enhydra lutris* (sea otters) is the most durophagous. In a sample of 309 stomachs of sea otters from Amchitka Island (Alaska), Kenyon (1969) mentions that 37% of the total items found are echinoderms and 21% of the total items belonged to the green sea urchin (*Strongylocentrotus drobachiensis*). Molluscs represented 31% of the total items and 17% belonged to three species of thin-shelled bivalves (mussels: *Musculus vernicosa* and *Volsella volsella*; pearly monia: the anomiid *Pododesmus mariscochisma*). The sea urchins and thin-shelled molluscs were crushed with the teeth (but not always) and sometimes an abundance of shell fragments was ingested. Therefore, sea otters clearly use their teeth to break the shell of their food if necessary (Kenyon 1981b). It is noteworthy that according to the sample analysed by Kenyon (1969), fishes only represent 22% of the sea otters’ diet. The postcanine teeth are described by Estes (1980, p. 3) and other authors cited therein as bunodont and adapted for crushing. The dentition of *Hadrokirus* is to a certain degree reminiscent of that of *Enhydra*. It is also reminiscent in terms of massiveness of the premolars (P2, P3; p2, p3, p4) of *Hyaena* and *Crocuta*.

Given the robustness of the teeth of *Hadrokirus* and given the fact that monk seals with weaker teeth are capable of crushing the carapace of large lobsters, it is plausible that at least part of the diet of *Hadrokirus* included molluscs and/or echinoderms. Moreover, the extensive degree of wear (and even fracture) of the dentition featured by both holotype and paratype also vouches for durophagous habits (Barnes & Raschke 1991; Tedford et al. 1994). The wear facets are on the whole sub-horizontal, which denotes a more crushing than cutting function. As a matter of fact, large mytilids (cf. *Choromytilus*) have been discovered by one of us (CM) in the beds of the Pisco Formation at Sud-Sacaco. Furthermore, Muizon & DeVries (1985) mention the presence of *Anomia* sp. (a thin-shelled anomid) in the *Acanthinunocella* zone, which includes the SAS level at Sud-Sacaco. Furthermore, the warmth of the Early Pliocene waters at Sud-Sacaco, which was greater than at present (Muizon & DeVries 1985), suggests that lobsters, which today are abundant in northern Peru, may have been present in the Sud-Sacaco waters although no remains of such crustaceans have been recovered. Although this hypothesis is still clearly speculative it is noteworthy that warm water crustaceans (decapods) are widely represented in the Mio-Pliocene beds of the Pisco Formation (Carriol et al. 1987).

Another aquatic carnivore bearing large and robust crushing teeth is the arctoid *Kolponomos* represented by two species, *Kolponomos clallamensis* and *Kolponomos newportensis*, from the Early Miocene respectively of Washington and Oregon (USA) (Tedford et al. 1994). *Kolponomos* bears strongly inflated bunodont teeth and is thought to have fed upon hard-shelled to very hard-shelled marine invertebrates (Tedford et al. 1994, p. 31). In fact the robust teeth of *Kolponomos* are concomitant with a robust zygomatic arch, a stout and short rostrum and a massive dentary. These conditions are also observed in *Hadrokirus* and are especially conspicuous on MUSM 430, as far as the zygomatic arch and rostrum are concerned (Fig. 6). They are regarded here as an eloquent indication of durophagy and support the hypothesis that *Hadrokirus* was likely to have fed (at least partly) upon hard-shelled invertebrates.

**Neck musculature**

The distinctive atlas of *Hadrokirus* deserves some consideration. One feature of interest concerns the wing of the atlas. In most terrestrial carnivorans the plane of the wing is roughly cranio-caudally oriented. In other words, the plane of the wing is almost parallel to the axis of the neural canal.
In some taxa (Hyaena hyaena for instance), the wing is slightly inclined. In other words, the plane of the wing is oblique in comparison with the axis of the neural canal: the anterior edge of the wing is slightly above the canal and the posterior edge below. In monachines and Odobenus, the wing is dorsoventrally oriented, being almost perpendicular to the axis of the neural canal. In Hadrokirus (Fig. 12C, D), Acrophoca and phocines, the wing is oblique (with a craniodorsal–ventrocaudal orientation) being intermediate between the conditions of terrestrial carnivorans and that of the other Lobodontini; otariids also show this intermediate condition.

This difference can probably be interpreted as an aquatic adaptation of phocids, namely the more streamlined body allowed by a smaller angle between the head and the neck (Williams & Kooyman 1985). The terrestrial condition is an erect position for the head, a position allowed by the action of muscles dorsally inserted on the wing of the atlas as the mm. longissimus capitis (inferred from Pierard 1971) and intertransversarii (inferred from Miller et al. 1964). The different orientation of the wing found in most monachines may consequently be interpreted to have facilitated a streamlined position of the head. This adaptation, which is not found in Hadrokirus, may suggest more terrestrial habits than in other monachines, except for Acrophoca for which such an inference was already suggested (Muizon 1981). In other words, Hadrokirus probably had greater ability to move on land than living Lobodontini and may have spent more time on the shore.

Another remarkable feature of the atlas of Hadrokirus is the deep fossa for the m. rectus capitis dorsalis minor (extensor of the atlanto-occipital joint) on the anterodorsal edge of the neural arch (Fig. 12B–D). The rectus capitis fossae are medially separated by a very high tubercle. It should be noted that M. monachus also shows a conspicuous medial tubercle on the dorsal side of the atlas, but the fossae are not as deep as those observed in Hadrokirus. The unusual inferred size of the m. rectus capitis dorsalis minor, when compared with that of other phocids, may corroborate the previous hypothesis, because one can argue that it allows the head to be kept in an upward position. This feature is exclusive to Hadrokirus, and could embody more terrestrial habits than Recent lobodontines.

Another indication of a powerful neck musculature is the stoutness and size of the mastoid process of Hadrokirus. In Leptonychotes (Pierard 1971), the mastoid process receives the insertions of the splenius and the superficial layer of the sternoccephalicus. These muscles are involved in lateral movements of the head when acting individually and respectively in extension and flexion of the head when acting jointly. These muscles therefore also suggest a great mobility of the head with powerful movements.

A strong musculature of the neck is also observed in Hydrurga, a highly prédaçeous lobodontine. Bryden & Felts (1974) emphasized that the cervical muscles of Hydrurga are larger than those of other Antarctic seals, evoking, along with the mm. splenius and semispinalis, the m. rectus capitis dorsalis major. These authors correlated this feature with the large skull and powerful masticatory musculature to the predatory habits of Hydrurga. This is understandable because Hydrurga is known to prey upon large penguins or juvenile phocids or otarioids. A strong neck musculature is necessary to firmly hold the struggling prey in the mouth. Therefore, the inferred strong neck musculature of Hadrokirus could also be related to prédaçeous habits as in the case of Hydrurga. This hypothesis is in agreement with the abundance of marine birds, especially the large penguin (Spheniscus urbinal), that lived on the Peruvian coast during the Mio-Pliocene and that might have represented part of its diet. As a matter of fact, the robust teeth of Hadrokirus (see above for a discussion of the durophagous habits of Hadrokirus) could also be well adapted for crushing bird bones, which are especially thick in the case of penguins.

However, another hypothesis could be proposed. Tedford et al. (1994) have suggested that the inferred powerful neck of Kolponomos (based on the large size of the paroccipital and mastoid processes) could (in part) mean that this aquatic arctoid fed on epifaunal marine invertebrates living on rocky substrates. “Kolponomos probably obtained its food by leveraging tightly clinging animals off the substrate and twisting and prying with its head” (Tedford et al. 1994, p. 31). If such an interpretation can be extended to Hadrokirus, then the thin-shelled bivalves such as Choromytilus and Anomia (see above), which live attached to rocky substrates, could be easily removed and may have represented part of the diet. The breakages and the large wear facets observed on the upper and lower canines and upper incisors of the holotype, and on the upper canines of the paratype, as well as the powerful neck musculature, would also favour this interpretation.

Phylogeny of the Phocidae

A reappraisal of phocid phylogeny is proposed here. The study is focused on monachines, but the other family of phocids (i.e. phocines) was also included in the analyses, using least inclusive taxonomic units to represent its diversity. In the case of the phylogeny of Phocidae, it appears that the choice of the outgroup is critical. In this analysis, the outgroup comprises the other two groups of Recent pinnipeds (Otaridae and Odobenidae) and Potamotherium. A ‘classical’ choice would have been to root the tree only with other extant pinnipeds, given the fact that the monophyly of this taxon is now more widely accepted than its diphyle (see Wyss 1987, 1989) and clearly supported by molecular evidence (e.g. Arnason et al. 2006). But the character coding would not have been fully satisfactory in this ‘classical’ case because, for several characters,
autapomorphic states of members of the outgroup (i.e., Otariidae and Odobenidae) precluded a satisfactory polarization. This was probably because otariids and odobenids are, respectively, strongly specialized in their own direction, clearly different from that of phocids. The other taxa in the outgroup selected is Potamotherium. This small otter-like Oligo-Miocene arctoid has been regarded as closely related to the base of Pinnipedia (Rybczynski et al. 2009). Without acknowledging either the monophyly (Berta & Wyss 1994) or diphly (Tedford 1976) of pinnipeds, the use of such an outgroup allows the reconstruction of intra-phocid synapomorphies, in either case of an aquatic or terrestrial hypothetical ancestor.

Material and methods
A data matrix including 19 taxa and 91 characters was elaborated using characters existing in the literature (King 1966; Muizon 1982; Wyss 1987, 1988; Wozencraft 1989; Nojima 1990; Berta & Wyss 1994; Bininda-Emonds & Russell 1996; Cozzuol 2001; Koretsky & Holec 2002), as well as new ones. See online supplemental material, Appendix 2 for data matrix and Appendix 3 for the character coding. All the extant taxa were studied thanks to specimens from the collections of MNHN and IRSNB. All the character states are known for extant phocids included in the analysis. The coding of the following extinct taxa was based on direct observation of specimens (MNHN) and the literature: Piscophoca pacifica (Muizon 1981) (13% of character states unknown), Acrophoca longirostris (Muizon 1981) (4% of character states unknown), Homophoca capensis (Hendey & Repenning 1972; Muizon & Hendey 1980) (18% of character states unknown) and Potamotherium (Savage 1957) (5% of character states unknown). Enaliarctos and Pinnarctidion bishopi were coded thanks to observation of casts (MNHN) and to the literature (Mitchell & Tedford 1973 for the former and Barnes 1979 for both). Pliophoca etrusca (54% of character states unknown) was coded thanks to the observation of the holotype (MP by one of the authors (CM) and the literature (Tavani 1941). The coding of Callophoca obscura (44% of character states unknown) and Monotherium wymani is solely based on the literature (Van Benenden 1877; Koretsky & Ray 2008 for the former and Ray 1976 for both).

The ‘Branch and Bound’ algorithm of PAUP 3.1 (Swofford 1993) was used with no character weighting. Three characters coded with three states were ordered (see the list of characters hereafter), because in each case the transformation from one extreme state to the other logically implies the acquisition of the intermediary state. The support values (see Fig. 18) were obtained after a bootstrap analysis (1000 replicates) using a heuristic search (each with 10 random addition sequences). The rooting of the tree was performed by use of an outgroup comprising four taxa. Three of these represent the other extant families of pinnipeds, i.e. the Otariidae and Odobenidae, which in the analysis were represented by Arctocephalus pusillus and Otaria byronia (1% of character states unknown in both cases, because of a lack of data on ossicles) representing, respectively, Arctocephalinae and Otariinae, and the extant walrus Odobenus rosmarus. The other taxon included in the outgroup is Potamotherium (5% of character states unknown) considered by Rybczynski et al. (2009) as a ‘non-marine pinniped’.

Another outgroup consisting of Enaliarctos and Pinnarctidion bishopi, extinct taxa considered by some authors as the sister-group of all other Pinnipedimorpha sensu Demére et al. (2003), was also tested but the great amount of missing data precluded an informative analysis and hence this will not be discussed further. It is noteworthy that a complete preparation of the virtually complete skeleton of Enaliarctos mealsi USNM 374272 (Berta & Ray 1990) would have brought much insight to the analysis.

Results and discussion
The analysis results in one most parsimonious tree. The tree length is 162, the consistency index is 0.6 and retention index is 0.8. Each clade is supported by at least one unambiguous synapomorphy, whatever the optimization method used. Therefore no clade is artificially supported, because this topology does not depend on the collapse rule implemented in the program (see Coddington & Scharff 1994, for the ‘problems with zero-length branches’). Another analysis was performed without ordering any characters (for the three ordered characters, see online supplemental material, Appendix 3); the resulting topology is unchanged. The description of the synapomorphies will be divided into two sections. The first section will only describe the unambiguous non-homoplastic synapomorphies, synapomorphies for which the character consistency index is equal to one, that will be hereafter referred as ‘UNS’. The ambiguous synapomorphies vary depending on the optimization option chosen. Re-running the analysis with only Potamotherium as the outgroup or with only other extant pinnipeds does not affect the resulting topology, but recognizes more UNS either for phocines or for monachines. This embodies the different possible ancestral states reconstructed for the ingroup, the phocids (see Maddison et al. 1984 for details on the assessment of equivocal ancestral state). These synapomorphies will be described under two modalities, the first will consist of an aquatic ancestral state for phocids (given by the character states of the other extant pinnipeds); the second will recognize terrestrial character states as ancestral for the ingroup (given by the character states of Potamotherium).

Unambiguous non-homoplastic synapomorphies
The phocines (see clade Ph in Fig. 18) are composed of Phoca vitulina and Halichoerus grypus, representing the Phocini, and Erignathus barbatus as their sister-group. Phocines are supported by 10 to 21 synapomorphies depending on the optimization, see online supplemental
Figure 15. Drawings and photographs of the palate in ventral view of A, *Hydrurga leptonyx* (MNHN 1926-72); B, *Piscophoca pacifica* (MNHN.F.SAS 564); C, *Hadrokirus martini* gen. et sp. nov. (holotype, MNHN.F.SAS 1627). Abbreviations: a-, alveolus of the abbreviated teeth; if, incisive foramen; mx, maxilla; pa, palatine; pas, palatine sulcus; pmx, premaxilla. Teeth abbreviations: Il, lateral incisor; Im, medial incisor; others as in text and capitalized. The arrows point anteriorly. Scale bar: 1 cm.

Figure 16. Drawings and photographs of the rostrum in lateral view of A, *Hydrurga leptonyx* (MNHN 1926-72); B, *Piscophoca pacifica* (MNHN.F.SAS 564); C, *Hadrokirus martini* gen. et sp. nov. (inverted left side, holotype, MNHN.F.SAS 1627). Abbreviations: mx, maxilla; na, nasal; pmx, premaxilla. Teeth abbreviations: Il, lateral incisor; Im, medial incisor; others as in text and capitalized. The arrows point anteriorly. Scale bar: 1 cm.

The monachines form a clade supported by 10 to 22 synapomorphies. The seven UNS characterizing this clade are: only four upper incisors (character 3, state ‘0’ to ‘1’, Fig. 15A–C); the premaxilla–maxilla suture is at least partially included in the nasal cavity (character 12, state ‘0’ to ‘1’, Fig. 16A–C); a scapular spine that is tilted posteriorly (character 62, state ‘0’ to ‘1’); a femur with a long epicondyle crest (character 81, state ‘0’ to ‘1’); the articular facet between the metatarsals I and II is oriented dorsolaterally (character 88, state ‘0’ to ‘1’); a short metatarsal III (character 89, state ‘0’ to ‘1’); and reduced pes claws (character 90, state ‘0’ to ‘1’).

*Monachus monachus* and *Pliophoca* form a clade sister-group of all other monachines. This clade (*Monachini sensu* Muizon 1982) is supported by one UNS, a dome-like elevation of the uncovered part of the petrosal posterior to the posterior edge of the tympanic (character 39, state ‘0’ to ‘1’, Fig. 17B). Although this clade is not supported by numerous synapomorphies, the geographic distribution of
\textit{M. monachus} (mainly Mediterranean) and \textit{Pliophoca} (holotype from the Pliocene of Italy) seems to corroborate its recognition.

\textit{Mirounga} and \textit{Callophoca} form a clade sister-group of Lobodontini. This clade was already supported by Muizon (1982) and called Miroungini therein. One UNS can be mentioned: a low collo-diaphyseal angle of the femur (character 80, state ‘0’ to ‘1’). While these two taxa are the only ones included in the analysis that feature a well-marked sexual dimorphism (character 91, ‘1’), it is not recognized as a UNS because the state is unknown in \textit{Potamotherium} (and hence coded as a question mark). Together with the lobodontines, the Miroungini form a clade supported by two UNS: the tympanic is well extended posteriorly, almost contacting the exoccipital (character 37, state ‘1’ to ‘2’, Fig. 17C) and a short and wide femur (character 83, state ‘0’ to ‘1’).

The Lobodontini (see clade Lo in Fig. 18) are composed of a clade of extinct taxa, namely \textit{Hadrokirus}, \textit{Piscophoca} (one of the other phocid of the Pisco Formation) and \textit{Homiphoca} (phocid represented by South African fossils). The remaining taxa form a clade comprising the four extant Lobodontini, with \textit{Acrophoca} as sister-group of this clade. The three UNS of the Lobodontini are: the medial margin of the tympanic bulla is parasagittal (character 30, state ‘0’ to ‘1’, see Fig. 17C), the presence of a mastoid lip abutting the postero-medial edge of the tympanic (character 38, state ‘0’ to ‘1’, Fig. 17C), and the presence of a well-developed articular surface for the fibula on the calcaneum (character 87, state ‘0’ to ‘1’). The placement of \textit{Acrophoca} as the sister-group of the extant Lobodontini is not well supported (the morphology of this taxon departing conspicuously from the others), although there is an apomorphy shared by these taxa, i.e. a reduced scapular spine (character 61, state ‘0’ to ‘1’). The clade consisting of the four extant lobodontines is formed by two clades, one comprising \textit{Leptonychotes} and \textit{Ommatophoca}, the other \textit{Lobodon} and \textit{Hydrurga}.

\textit{Monotherium}? \textit{wymani} was tentatively included in this study but, while no precise position could be attributed...
Some details can be mentioned about character 37. As coded by the states ‘1’ and ‘2’, the tympanic is withdrawn anteriorly in phocids under two modalities. As in the outgroup the tympanic is fused to the mastoid and exoccipital, a ‘direct’ assessment of the plesiomorphic condition for phocids is difficult. It should be emphasized that the tympanic of phocids except for the Miroungini and Lobodontini has a strong anterior withdrawn, and that an undescribed specimen MNHN.F.PPI 269 from the Cerro la Bruja locality, dating from the late Middle to early Late Miocene of Peru (representing an undescribed taxon, personal observations), shows the posterior part of tympanic only slightly covering the petrosal. We therefore consider that the primitive state for phocids is a tympanic well withdrawn anteriorly, and that Miroungini and Lobodontini share the apomorphy of secondarily posterior expansion of the tympanic.

As coded with the character 57, a deep fossa for m. rectus capitis dorsalis minor is present on the atlas in Hadrokirus and M. monachus. It should be emphasized that, although we coded the same character states for these two taxa, we doubt its homology. In both cases, these fossae reach such a depth thanks to the development of a median tubercle on the dorsal surface of the atlas. But in Hadrokirus this tubercle is located caudally, and not on the craniodorsal margin of the atlas as in M. monachus. On the other hand, the condition of Hadrokirus is observed on the undescribed specimen from the Cerro la Bruja locality.

**Ambiguous non-homoplastic synapomorphies**

As stated earlier in the text, several apomorphies are ambiguous because of the impossibility for the software, given the composition of the outgroup, to reconstruct unequivocal ancestral states of character for the ingroup. To describe such apomorphies, one must choose between the different possible optimizations.

Considering the hypothetical ancestor of phocids to be aquatic (which in this case would be equivalent to rooting the tree only with other extant pinnipeds and hence excluding *Potamotherium* from the analysis) would have the consequence of acknowledging the reversions generally accepted for phocines at the scale of the carnivoran clade (see Wyss 1987; Berta & Wyss 1994). These reversions are: head of metapodials keeled with trocheiated phalangeal articulations (character 72, state ‘1’ to ‘0’); short metacarpal I (character 73, state ‘1’ to ‘0’); and large manus claws (character 75, state ‘1’ to ‘0’).

The other reversions generally recognized for phocines with respect to the carnivorans (Wyss 1987; Berta & Wyss 1994) are a large supraspinous fossa (a character not included in this study because we consider that discrimina-
Berta & Wyss (1994) are found in our analysis as ambiguous synapomorphies, either reversions of phocines or convergences with other pinnipeds, with the opposite character state as the apomorphic one. Although not more parsimonious, we prefer to acknowledge the latter contingency.

Concerning inferences about the palaeoecology of Hadrokinus, a propensity for durophagy and predation of large prey can be considered. The fragmentary postcranial elements of the types preclude us from proposing any well-sustained hypothesis concerning its habitat. More specimens that can be referred to this new taxon are required to do so.

Supplemental material

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