The anatomy of *Odobenocetops* (Delphinoidea, Mammalia), the walrus-like dolphin from the Pliocene of Peru and its palaeobiological implications

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The Pliocene Beds of the Pisco Formation on the southern coast of Peru have yielded three new skulls of the walrus-like odontocete, *Odobenocetops* (Delphinoidea, Cetacea). Two of the skulls are from a slightly younger horizon than the holotype of *O. peruvianus* and belong to a different species, *O. leptodon*. The holotype of *O. leptodon* bears a 135 cm long needle-like right tusk and a small 25 cm long left tusk, the apex of which was erupted. The third skull, referred to a female of *O. peruvianus*, bears two small tusks similar in size to the small left tusk of the holotype. The new specimens include periotic, tympanic and ear ossicles, which confirm referral to the Order Cetacea and the morphology of the humerus reinforces affinities of odobenocetopsids to monodontids. Because the anterodorsal edge of its orbit is slightly concave *O. leptodon* had reduced anterodorsal binocular vision, a condition compensated for by the probable presence of a small melon (and inferred echolocation). The head was bent ventrally when swimming in such a way that the long tusk was approximately parallel to the axis of the body. The extremely salient occipital condyles of *Odobenocetops* are indicative of great mobility of the neck, probably related to bottom-feeding. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **134**, 423–452.

ADDITIONAL KEY WORDS: *Odobenocetops* – Delphinoidea – Pliocene – Peru – asymmetric tusks – feeding adaptation – functional anatomy.

INTRODUCTION

The Neogene beds of the Pisco Formation (Peru) are well known for their marine mammal fauna and have yielded several hundred partial skulls and skeletons of cetaceans, phocid seals, and semiaquatic edentates (de Muizon, 1981; 1984; 1988a; 1993a; de Muizon & McDonald, 1995). This taxonomically diverse fauna includes more than 35 mammalian taxa, among them two species of the genus *Odobenocetops*, a bizarre odontocete cetacean which presents an astonishing convergence in feeding adaptations with the living walrus, *Odobenus rosmarus*. *Odobenocetops peruvianus*, the type-species of the genus, was first described from a single incomplete skull which shows unexpected characteristics for a cetacean (de Muizon, 1993a,b; de Muizon *et al*., 2002). The long cetacean rostrum has become considerably shortened, rounded and blunt, and the nares have migrated anteriorly. The premaxillae, which are almost absent from the ventral face of the skull in the other cetaceans, extend strongly ventrally in large alveolar sheaths which bear one tusk each. The right tusk is large and the preserved portion in the holotype of *O. peruvianus* is approximately 50 cm long; the left tusk is small, its diameter is half that of the right tusk, and its length was estimated at *c*. 20 cm. The palate of *Odobenocetops* is very wide and deep and its U-shaped and thickened anterior border probably carried a strong upper lip.

The deep palate and the inferred upper lip are convergences with the living walrus, which also has a

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deep and wide palate and a powerful upper lip. It feeds upon benthic invertebrates (see Fay, 1982: table 23 for a systematic list of organisms that have been identified as food for the Pacific walrus), mainly thin-shelled molluscs (e.g. *Natica*, *Clinocardium*, *Spisula*, *Macoma*, *Mya*, *Astarte*, *Mactra*, *Tellina*, *Hiatella*), and removes their feet and siphons by suction while holding the shell in its powerful lips, the tongue acting like a piston. The shells are not ingested, but rejected partly broken (Fay, 1982: 167–171). The palate and inferred muscular lip of *Odobenocetops* strongly recall the morphology of the walrus and, together with the tusk-like premaxillary sheaths, are the basis for our hypothesis of feeding convergence between these species. A significant implication of this hypothesis is that, contrary to the consensus of walrus biologists today, it suggests an important role in feeding for the tusks of true walruses: namely, as orientation guides for the vibrissal array (Muizon *et al.*, 2001; this paper was essentially complete by 1996 but publication was delayed).

Except for two periotics and partial tympanic referred by de Muizon *et al.* (2002) to *O. peruvianus*, no cranial remains other than the holotype had been reported until the preliminary description of three new partial skulls of *Odobenocetops* from the Pisco Formation in the Sacaco area (de Muizon *et al.*, 1999). Two of these three skulls are slightly younger geologically than the holotype of *O. peruvianus* and have been referred to the new species *O. leptodon* de Muizon *et al.* 1999, mainly because of some morphological differences in the rostrum and the palate, which imply different strategies in feeding adaptations and sensory systems (vision and echolocation). The third skull has been referred to *O. peruvianus,* but differs from the holotype in the size of its tusks, which are both small and approximately of the same size. Because of this characteristic it has been regarded as a female of *O. peruvianus*, the difference between the two specimens being attributed to sexual dimorphism.

The purpose of this work is to present a detailed description and interpretation of *O. leptodon* and to compare its adaptations to those inferred for *O. peruvianus*. The phylogenetic relationships of *Odobenocetops* will not be analysed in detail as they have already been discussed by de Muizon *et al.* (2002). Since the periotics and tympanics of the three new specimens are preserved *in situ* they will be considered with special care, given the importance of these bones in cetacean systematics when associated with skulls. However, the periotic and tympanic of one specimen only (the referred specimen MNHN SAO 202) could be removed from the skull and will be described in detail below. The ear bones of the holotype of *O. leptodon* (SMNK 2492), which could not be separated from the skull, will be CT-scanned and will be treated in a work

in progress. We also describe here some postcranial elements associated with MNHN SAO 202, which provide some new data on the affinities and functional anatomy of this dolphin.

Institutional abbreviations: MNHN, Muséum national d'Histoire naturelle, Paris, France; SMNK, Staatliche Museum für Naturkunde, Karlsruhe, Germany; USNM, United States National Museum of natural History, Smithsonian Institution, Washington DC, USA.

SYSTEMATIC PALAEONTOLOGY

ORDER CETACEA BRISSON, 1762
SUBORDER ODONTOCETI FLOWER, 1869
INFRAORDER DELPHINIDA HAECKEL, 1866
SUPERFAMILY DELPHINOIDEA GRAY, 1821
FAMILY ODOBENOCETOPSIDAE MUIZON, 1993

Type and only included genus: *Odobenocetops* Muizon, 1993.

Diagnosis of the family: As for the type genus.

ODOBENOCETOPS MUIZON, 1993

Type species: *Odobenocetops peruvianus* Muizon, 1993. *Emended diagnosis*: delphinoid cetacean which does not possess the elongated rostrum present in all other cetaceans. The rostrum is short, rounded, and blunt; it is formed by the premaxillae which are greatly enlarged and have large, asymmetrical ventral alveolar sheaths holding sexually dimorphic tusks. The right tusk of the male is large and can reach one metre or more in length. It is cylindrical and its section is mediolaterally compressed (the long axis measures *c*. 4–5 cm). The left tusk of the male was only between 20 and 25 cm long, of which a few cm were erupted. Its section is also mediolaterally compressed. Both tusks are straight. In the female, the right tusk is only slightly larger than the left and both protruded only a few cm from the gum. Premaxillary sheaths and tusks form an angle of approximately 60–70° with the dorsal plane of the skull. The bony nares have been displaced anteriorly and are anteroposteriorly elongated. The palate is very deep and arched, and its anterior border (which is formed by the anterior edges of the alveolar sheaths) is U- to V-shaped. On the palate the vomer is very large and the premaxillae and the pterygoids are in contact with it. The maxillae have been excluded from the palate and relegated to a small triangular area on the lateral side of the rostrum and an elongated strip on the dorsal face of the skull. The postorbital processes are large and lateral to the posterior end of the nares. The orbits face anterolaterally and dorsally. The portions of the frontals and maxillae

which cover the temporal fossae in the other odontocetes have been reduced and narrowed in such a way that the temporal fossae are opened dorsally. Ventrally, the crest of the hamular process of the pterygoid is strong and rounded and the choanae are very wide. The basioccipital is extremely wide and long. The glenoid cavity of the squamosal is an anteroposteriorly elongated groove. The occipital condyles are very salient and more convex than in any other Pliocene or living cetacean.

ODOBENOCETOPS LEPTODON MUIZON, DOMNING & PARRISH, 1999
(FIGS 1–12, TABLES 1 AND 2)

Holotype: SMNK PAL 2492, an incomplete skull (lacking most of the dorsal and right sides of the braincase, right orbit, and right side of the right alveolar sheath), with the right ear bones and the atlas.

Referred specimen: MNHN SAO 202, partial skeleton with partial skull lacking the right tusk and with the alveolar sheaths very damaged. Most of the braincase has been weathered away but the left periotic and a partial tympanic are preserved *in situ*. The postcranial skeleton is very poorly preserved, comprising only a few hyoid fragments, 26 partial vertebrae, several rib fragments, the distal half of the left humerus, most of the left radius, a proximal portion of the ulna lacking the olecranon, and fragments of carpals and metacarpals. MNHN PPI 249, a right periotic is referred to *O.* cf. *leptodon*.

Etymology of the species name: from Greek: *leptos* (thin) and *odon* (tooth), in reference to the needle-like morphology of the large right tusk.

Diagnosis: *Odobenocetops leptodon* differs from *O. peruvianus* in the morphology of the snout, which is more rounded and wider in dorsal view; in the lack of large premaxillary foramina; in the presence of small depressions for premaxillary sacs in the premaxillae, anterior to the bony nares; in the presence of supplementary rostral bones at the anterodorsal apex of the snout; in the broader, deeper, and longer palate; in the anterior border of the palate, which is more U-shaped, while it is more V-shaped in *O. peruvianus*; and in the straight (or slightly concave) anterodorsal border of the orbit, which is deeply concave in *O. peruvianus*.

Locality, Horizon and Age: the holotype and MNHN SAO 202 are from the SAO level of the Pisco Formation in Peru (at approximately km 540 of the Panamerican Highway south of Lima). The SAO horizon has been defined by de Muizon & Bellon (1980) but see also de Muizon (1981), de Muizon & DeVries (1985), and de Muizon & Bellon (1986). Its age spans approximately from 4 to 3 Ma; therefore, the specimens are early Pliocene in age. The SAO level of the Pisco Formation

Table 1. Measurements of the holotype of *Odobenocetops leptodon* (SMNK PAL 2492) in mm. (e = estimated)

Skull
    Basicondylar length: 415e
    Bizygomatic width: $150 \times 2 = 300e$
    Minimum width of the skull posterior to the postorbital
        processes: $70 \times 2 = 140e$
    Maximum width between the postorbital processes:
        $130 \times 2 = 260$
    Maximum width of both nares: 59e
    Maximum length of the left naris: 53.5e
    Width of the choanae: 104
    Maximum width of the skull at the level of the
        exoccipitals: $123.5 \times 2 = 257e$
    Maximum width between the pterygoid crests: 142
    Width between the apices of the hamular processes:
        112
Tympanic
    Length of the lateral lobe of the left tympanic: 54.2
Atlas
    Maximum width of the atlas: 174
    Maximum height of the atlas at sagittal plane: 106
    Maximum vertical diameter of neural canal: 64.5
    Maximum horizontal diameter of neural canal: 56.5
Limb
    Maximum length of the radius: 117
    Anteroposterior length of distal end of humerus: 60.1
    Mediolateral width of distal end of humerus: 43

Table 2. Measurments of the ear bones of *Obobenocetops leptodon* (referred specimen, MNHN SAO 202) in mm (e = estimated)

Periotic
    Anteroposterior length: 77.5e
    Maximum width (measured ventrally, approximately
        perpendicular to anteroposterior length: 42e
    Length of pars cochlearis from contact with anterior
        process anteriorly to medial edge of aqueductus
        cochleae (measured dorsally): 29.5
    Maximum width of the pars cochlearis in medial view:
        30.8
    Length of internal auditory meatus: 14.3
Tympanic
    Length of the involucrum (measured medially): 58.8
Malleus
    Maximum length in posteromedial view (cf. Fig. 10A):
        11.4
    Maximum width in posteromedial view (cf. Fig. 10A):
        6.05

is slightly younger than the SAS level (5–4 Ma), which yielded the holotype of *O. peruvianus* and the third specimen referred to here as a female of *O. peruvianus*. MNHN PPI 249, an isolated periotic, is from beds of the Pisco Formation located at *c*. 3 km east of Yauca (these beds may be slightly younger than those of the SAO horizon and may belong to the late Pliocene).

DESCRIPTION

The following description focuses on the differences between the two species of *Odobenocetops*. We refer to de Muizon *et al*. (2002) for the aspects of the cranial anatomy common to the two species.

GENERAL FEATURES

The general morphology of the skull of *Odobenocetops leptodon* is similar to that of *O. peruvianus* in its basic pattern (Figs 1–4). However, in dorsal view, the former differs from the latter in the morphology of the snout, which is much wider and more blunt. In anterior view the snout was more massive. Furthermore, if a melon was actually present, as hypothesized below, it is likely that the head of *O. leptodon* was more rounded than that of *O. peruvianus*. The skull of *O. leptodon* has the same bilobate outline as is observed in *O. peruvianus,* which is unique in a Neogene odontocete (de Muizon *et al*., 2002). This condition, where the frontals and maxillae do not overhang the temporal fossa, is found in primitive odontocetes such as *Xenorophus*, *Agorophius* and *Archaeodelphis* and in archaeocetes because of the lesser telescoping of the skull (Kellogg, 1936; Fordyce, 1981). In *Odobenocetops* it is regarded as a reversal of this typically cetacean telescoping.

In general, the skull of *O. leptodon* is very heavily built and the bone is much denser, thicker, and more solid than in other delphinoids, being almost osteosclerotic in its posteroventrolateral angle.

PREMAXILLA

The premaxillae of *O. leptodon* are built on the same pattern as those of *O. peruvianus* (de Muizon *et al*., 2002). They both present a large alveolar process housing one tusk, the right tusk (of the presumed male, which is the only sex represented) being much larger than the left. Since the left alveolar process is not preserved on the holotype of *O. peruvianus* (the only specimen known when this species was first described) and because there are no other mammals which exhibit pronounced cranial asymmetry, it was hypothesized that the processes sheathing the tusks were both of the same size and that, consequently, the
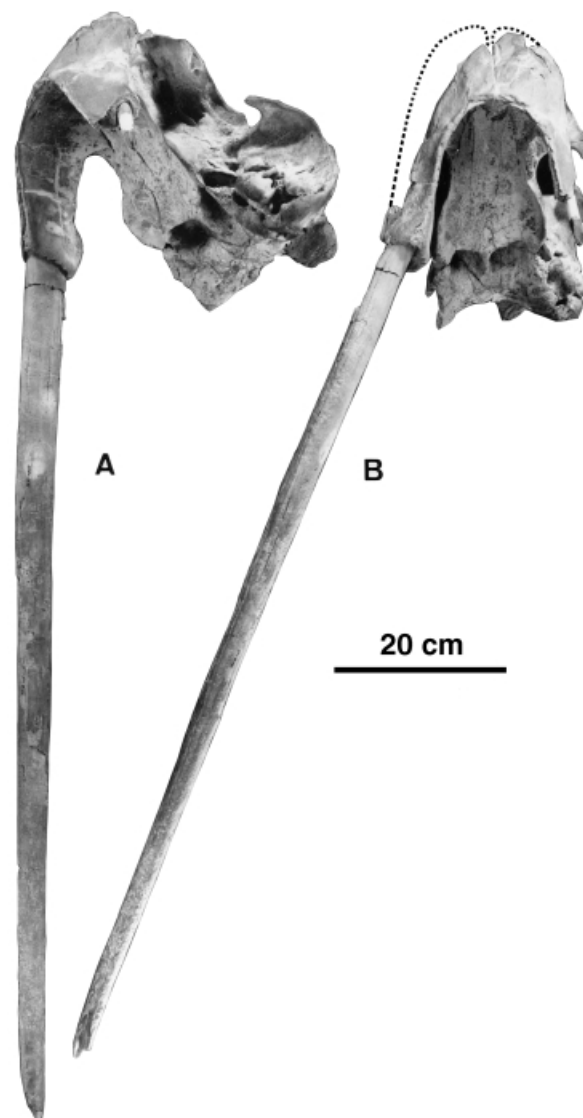

Figure 1. *Odobenocetops leptodon*, holotype (SMNK PAL 2492). Skull: left ventrolateral view (A), anterior view (approximately parallel to the feeding plane) (B).

left tusk (which was judged to be shorter than the right sheath) was not erupted. The holotype of *O. leptodon,* however, indicates that the left sheath was clearly smaller than the right and that the left tusk was actually erupted. It is therefore probable that the condition of *O. leptodon* was also present in *O. peruvianus*. In the holotype of *O. leptodon*, the left sheath is transversely flattened and lies almost in a parasagittal plane (it diverges only slightly laterally). The right sheath is thicker because of the larger size of the tusk and diverges more markedly laterally. The region of the sheaths anterior to the tusks is strongly flattened and forms a posteriorly bent U-shaped lamina which borders the palate anteriorly. The
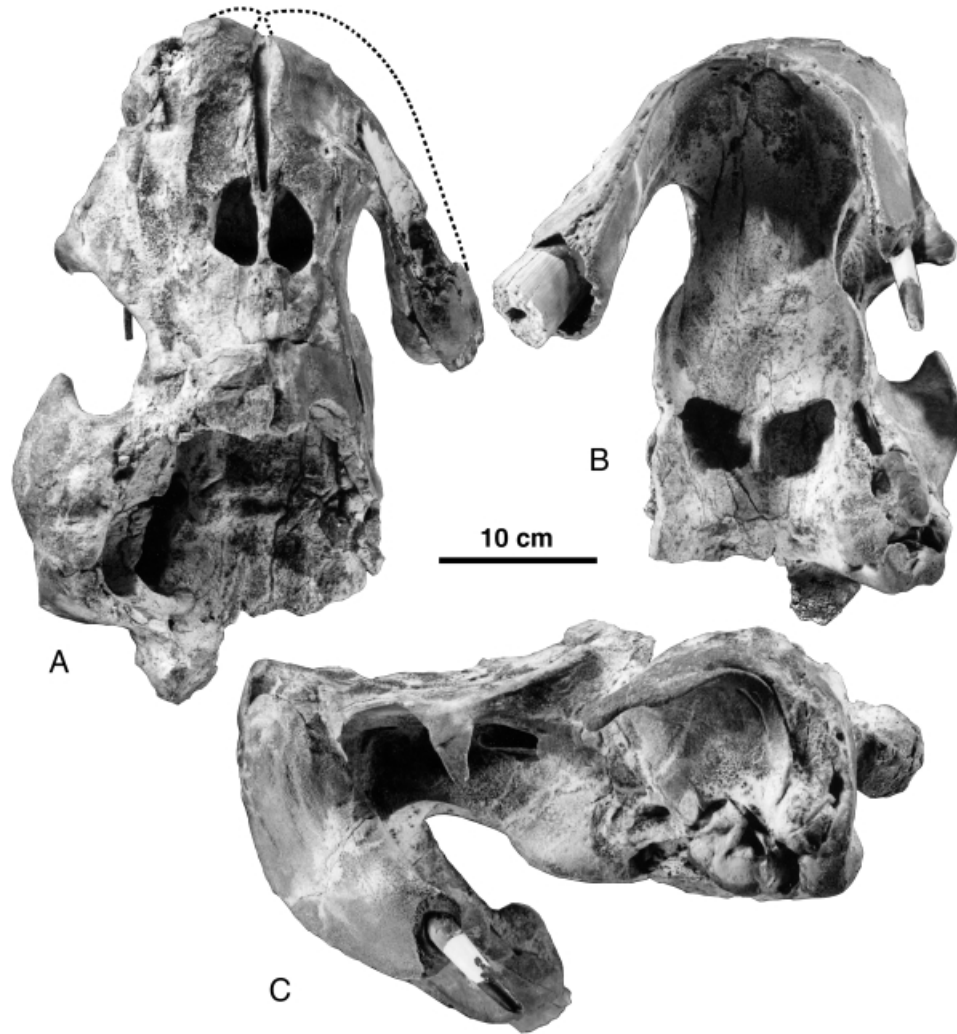
Figure 2. *Odobenocetops leptodon*, holotype (SMNK PAL 2492). Skull: dorsal (A), ventral (B), and lateral (left side) (C) views.

anteroventral edge of this lamina is 0.5–1 cm thick, and presents longitudinal irregular ridges of bone to which was firmly attached the strong upper lip that was very probably present in *O. leptodon* as in *O. peruvianus*. The anterior and anterolateral side of each premaxillary sheath is a broad convex surface bearing several large grooves and foramina. These structures indicate an extensive vascularization of the anterior region of the skull, which is regarded here as related to the presence of a thick, muscular upper lip. In anterior view, in the sagittal plane, the snout is more elevated than in *O. peruvianus* and the surface of attachment of the upper lip is larger. Furthermore, the snout is wider in anterior view, and the anterior edge of the palate is grossly U-shaped rather than more V-shaped as in *O. peruvianus*. Therefore it is clear that the upper lip of *O. leptodon* was much larger than in

O. peruvianus, indicating a larger vibrissal array and/or better suction ability in the former than in the latter.

Dorsally, the morphology of the premaxillae of *O. leptodon* presents the major characters which differentiate this species from *O. peruvianus*. These bones are much wider than in *O. peruvianus,* and the right premaxilla is more expanded laterally because of the greater size of the tusk (Figs 2A and 3A). There are no enlarged premaxillary foramina as are observed in the other odontocetes, including *O. peruvianus*. This absence is regarded as a loss in *O. leptodon* which, in this respect, is more derived than *O. peruvianus*. The premaxillary foramina transmit branches of the internal maxillary artery and maxillary nerve from the infraorbital foramen (internal to the orbit) to parts of the nasofacial muscles anteriorly and posteriorly on
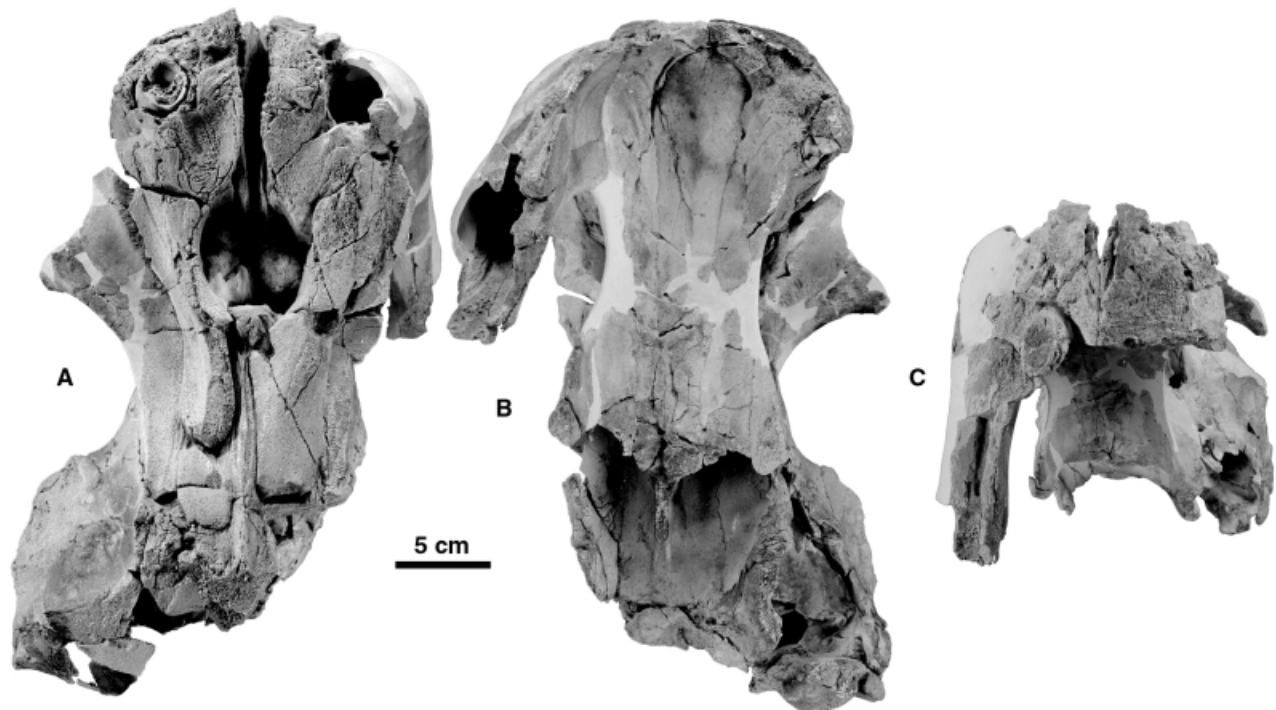
Figure 3. *Odobenocetops leptodon,* referred specimen (MNHN SAO 202). Skull in dorsal (A), ventral (B), and anteroventral (C) views.

the rostrum (see e.g. Schenkkan, 1973: fig. 5, on *Mesoplodon bidens*). In *Odobenocetops* these vessels and nerves are probably related to the irrigation and innervation of the strong upper lips and associated musculature as well as the possible vibrissae. In *O. leptodon* the canals conducting the nerves and vessels do not open dorsally but are clearly present. This is observed on the referred skull MNHN SAO 202 (Fig. 3A), in which the apex of the snout is eroded above the pulp cavity of the tusks. The canals passed above the proximal extremities of the tusks and apparently (clearly observable on the right side) divided into several smaller canals perforating the premaxillae to reach the upper lip anteriorly. Ramifications of the premaxillary canals are also observable on the lateral side of the premaxilla at the level of the antorbital notch, where several large foramina are present. It is likely that irrigation and innervation for the pulp cavities of the tusks were also transported by the premaxillary canals.

The premaxillae of *O. leptodon* bear a small concave area, anterior to the bony nares, where lay the premaxillary sacs of the air sac system (Mead, 1975). These fossae for the premaxillary sacs are limited medially by the medial border of the premaxilla which overhangs the vomerian gutter; they are limited anteromedially by the suture with the rostral supplementary bone (see below); and anterolaterally they are

medial to the posterior edge of each tusk alveolus (Figs 2A, 3A and 5). Fossae for premaxillary sacs are absent in *O. peruvianus,* where the space between the large premaxillary foramina and the anterior edge of the nares is so reduced that it was supposed that the premaxillary sacs were either very reduced or absent in this species (de Muizon *et al.*, 2002).

On the dorsal face of the skull the premaxillae of *O. leptodon* extend further posteriorly than in *O. peruvianus*. The posterior extremity of the left premaxilla is damaged on MNHN SAO 202, but it is clear that it lay slightly posterior to the posterior border of the nares. The posterior extremity of the right premaxilla lies about 5 cm posterior to the nares. On the holotype of *O. peruvianus,* the posterior extremity of the left premaxilla is located half-way between the anterior and posterior limits of the naris and on the right side (as well as on both sides of SMNK PAL 2491) it reaches the posterior edge of the naris.

The Pmx-Mx suture is external to the nares, the border of which is formed by the maxillae only, in contrast to the condition of *O. peruvianus* in which the Pmx-Mx suture is internal to the nares in the anterior two-thirds of their length. In their dorsal portions the premaxillae of *O. leptodon* are relatively flat and not as salient as is observed in *O. peruvianus*. This feature is clearly observed on the lateral edges of the nares and at the level of the antorbital notch, where the
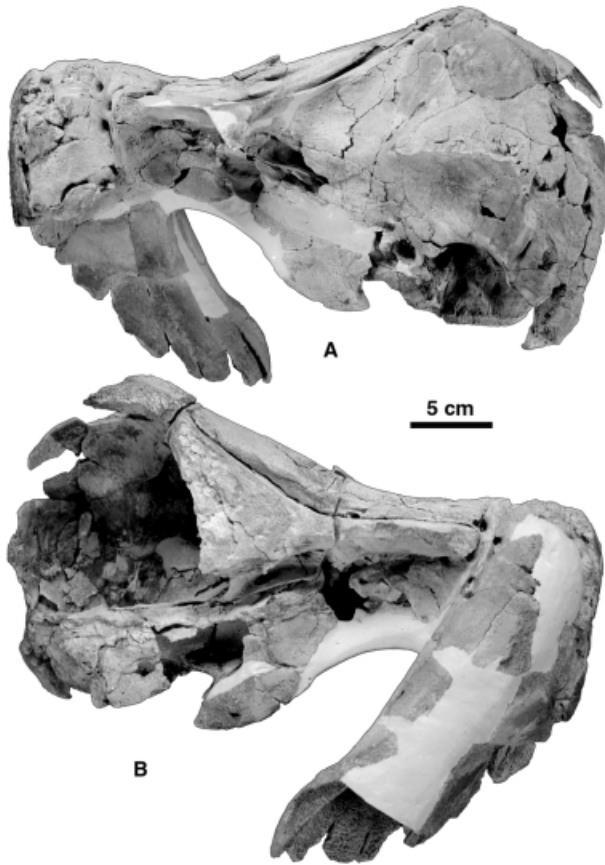
Figure 4. *Odobenocetops leptodon,* referred specimen (MNHN SAO 202). Skull in lateral left (A) and lateral right (B) views.

premaxillae markedly overhang the maxillae in *O. peruvianus*, whereas the relief of these regions is much smoother in *O. leptodon*.

The anterior sides of the premaxillae of *O. leptodon* (SMNK PAL 2492) bear strong foramina and grooves, which indicates an abundant vascularization related to the development of the upper lip. The premaxillae are much broader and much more elevated than in *O. peruvianus*, again indicating a larger and stronger upper lip (Figs 1B and 3C). The premaxillary sheaths, which house the tusks, are partly preserved on SMNK PAL 2492. The right is complete and the left is broken, apparently no more than 2 or 3 cm from the apex. Contrary to what was hypothesized in the case of *O. peruvianus,* the sheaths are not identical in size; the left one is clearly smaller and shorter than the right and reflects the size difference between the tusks. In lateral view, the right alveolar process forms an angle of *c*. 60° with the dorsal plane of the skull (from the vertex to the anterodorsal tip of the rostrum). The anteroventral edges of the sheaths (which include the anterior edge of the palate) are

thickened and corrugated, as is observed in *O. peruvianus*, which indicates attachments for strong, possibly horny, connective tissue for the attachment of the upper lip. This narrow edge also bears (in both species) a series of foramina, which could have been related to a fringe of vibrissae. In the style of feeding we have hypothesized, these could have allowed the animal to detect when the front edges of the sheaths were in contact with the sea floor.

The anteroventral crest of the premaxillae (Figs 1B and 3C) has a very wide U-shape whereas it is more V-shaped in *O. peruvianus*. This morphology is the result of the widening of the snout and is possibly related to the presence of the supplementary bones described below. The U-shaped anterior border of the palate is not perpendicular to the sagittal plane. In other words, in anterior view, if the sagittal plane is positioned vertically (based on pterygoids, basioccipital and vomerian groove), the plane of the anterior crest of the palate dips towards the right side of the skull. This is because the anteroventral edge of the smaller and less laterally divergent left sheath is dorsal to (more elevated than) that of the right sheath. This condition implies that when the animal was feeding (i.e. with the anterior border of the palate parallel to the sea floor; see de Muizon, 1993b and de Muizon *et al.*, 2002), the sagittal plane was inclined toward the left side of the animal (i.e. dipping toward the right side). Therefore, because of the asymmetry of the premaxillae, *O. leptodon* was feeding slightly inclined on left side.

The premaxillae form the anterior region of the palate as is observed in *O. peruvianus*. Although the palate of *O. leptodon* is much broader than in *O. peruvianus*, the area occupied by the premaxillae in this part of the skull is only slightly larger than in *O. peruvianus* (see below).

ROSTRAL BONES

One of the most striking differentiating characters of *O. leptodon* is the presence of two supplementary bones (one on each side) anterior to the premaxillae at the anterodorsal apex of the snout. These bones are apparently appressed against the medial edges of the premaxillae and lie partly on the dorsal part of the skull and partly on the anterior slope of the snout. The dorsal portion is narrower than long but broadens anteriorly. It is limited posteriorly by the fossa for the premaxillary sac of the premaxilla, while medially it has a small contact with the medial portion of the maxilla on the dorsal face of the rostrum (Figs 1B, 2A, 3A and 5). Within the vomerian groove, the rostral supplementary bone is bordered by the medial portion of the maxilla, but the edge of the groove is formed by the rostral bone itself. The lateral suture is directed
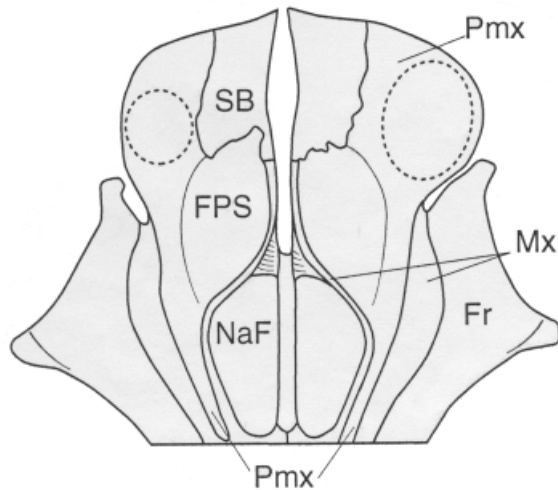
Figure 5. Reconstruction of the dorsal view of the rostrum of *Odobenocetops leptodon*. Abbreviations: Fps, fossa for the premaxillary sac; Fr, frontal; Mx, maxilla; NaF, narial fossa; Pmx, premaxilla; Sb, supplementary bone.

anteroposteriorly and is located just medial to the tusk alveoli. The anterior portion is not observable on MNHN SAO 202 but it is in relatively good condition on the left side of SMNK PAL 2492. It is also relatively narrow and forms a strip of bone overlying the premaxilla, tapering ventrally, and reaching (or almost reaching) the ventromedial border of the premaxilla at the anterior edge of the palate. Its medial suture is with the vomer. These supplementary bones are in fact wedged (as far as the dorsal portion is concerned) between the tusks laterally and the vomer and maxilla medially. They are partly responsible for the breadth of the snout in *O. leptodon* and tend to separate the proximal extremities of the tusks and alveoli (i.e. the premaxillae). As a probable consequence of their presence, the tusks are less divergent distally than in *O. peruvianus* and the anterior border of the palate is U-shaped in *O. leptodon* rather than more V-shaped as in *O. peruvianus*. Apparently, as is observed on the left premaxilla of SMNK PAL 2492, the rostral bones were anterodorsally protruding, forming an elevated prominence at the apex of the snout. This condition is not observable on MNHN SAO 202 since the bones have been partly eroded in their apical portions.

These supplementary bones could be ossa prenasalia, cartilage bones which appear late in development (mainly in postnatal life) and which are not uncommon in mammals. They are paired or unpaired bones which articulate with the nasals or premaxillae and which are always related to the presence of a rhinarium (*Rhynchocyon*, *Sus*, *Talpa*, Chiroptera) or a proboscis (Starck, 1967). In the case of *O. leptodon* the supplementary bones present at the anterodorsal apex

of the snout could be related to the thick and powerful upper lip used by *Odobenocetops* to forage on the bottom in search of food (de Muizon, 1993a;b; de Muizon *et al.*, 2002). They could also indicate of the presence of a very sensitive tactile organ, with or without vibrissae (see de Muizon, 1993a), much more developed in *O. leptodon* than in *O. peruvianus*. It is likely that strong muscles for the upper lip of *O. leptodon* were attaching on the (?)prenasalia. However, it is noteworthy that the prenasalia of other mammals are generally not tightly articulated with the premaxillae and/or the nasals, and not distinctly paired.

If these supplementary bones are not prenasalia, another alternative which could explain the condition of *O. leptodon* is the presence of septomaxillae. These bones are present in crossopterygians, lissamphibians, squamates, in all nonmammalian therapsids, and in all the nontherian mammals except multituberculates. The septomaxilla is absent in marsupials and placentals except in Xenarthra (Wible, 1990; Zeller *et al.*, 1993). However, we are reluctant to interpret the supplementary bones of *O. leptodon* as septomaxillae, since the study of the development of the nasal capsule of odontocetes (Klima & Van Bree, 1985; Klima *et al.*, 1986; Klima, 1987) does not show any indication that such bones are present at any developmental stage in this group.

A third alternative is to regard the supplementary bones of *O. leptodon* as neomorphic elements different from prenasalia and septomaxillae, possibly related to the muscle attachment of the lip, which was probably much stronger than in *O. peruvianus*.

TUSKS

The tusks of *O. leptodon* are similar to those of *O. peruvianus* (Figs 1A,B). They are much better preserved in SMNH PAL 2492 than in the holotype of *O. peruvianus*. The large right tusk is a straight, cylindrical, needle-like tooth. Its erupted portion (broken and worn during life) is 107 cm long and its alveolar portion (as preserved) is approximately 28 cm long. Before the loss of its original tip, it could easily have been 30 cm longer. Therefore, the right tusk of *O. leptodon* is much longer than what was estimated for *O. peruvianus*, in which we suggested that it was possibly no longer than 55 cm with a 15–20 cm long erupted portion. It is therefore probable that the long tusk of *O. peruvianus* was longer than previously suspected (but see below). In *O. leptodon* as in *O. peruvianus,* the section of the tusk is elliptical and the diameters diminish towards the apex. At the alveolar border the diameters are 50 mm and *c.* 36 mm, whereas at 8 cm from the broken and worn apex the diameters are 30 mm and 25 mm. The large tusk of *O. leptodon* is made of dentine only (it has no enamel) and bears lon-

gitudinal striae as in *O. peruvianus*. At the apex of the tusk is a long wear facet which faces ventrally. It is 8 cm long and convex ventrally. The facet is strongly oblique and its posterior edge does not present a marked limit with the ventral border of the tusk. The pulp cavity is wide open at the proximal extremity of the tooth, which indicates continuous growth. At the proximal extremity of the erupted portion (2 cm distal to the alveolar border) the diameters of the pulp cavity are 24 mm and 13 mm. Considering that the pulp cavity is almost as wide as the tooth itself at the proximal extremity of the tusk, and if (as in *O. peruvianus*) the cavity was conical, the pulp cavity of *O. leptodon* should have been approximately 60 cm long, which is more than twice the length measured in *O. peruvianus* (23 cm). Hay & Mansfield (1989) stated that the pulp cavity of the narwhal tusk is conical at the root. However, '10–20 cm from the base it narrows to a canal 0.5 cm in diameter which passes nearly to the tip of the tusk' (Hay & Mansfield, 1989: 160). These authors, citing Porsild (1922), also stated that in very old males the pulp canal is nearly occluded. Therefore, if the age of the animal is unknown, the length of the pulp cavity is probably not a good criterion to estimate the length of the right tusk of *O. peruvianus*. The apex of the tusk of the holotype of *O. leptodon* shows an open cavity. Since the wear facet clearly indicates the apex of the tooth, this canal had to be separated from the pulp cavity. In fact, a radiograph of the tusk shows that 35 cm from the apex, this apical canal is probably closed by dentine. It is likely that when the tooth was unworn the pulp cavity extended almost to the apex, as is observed in the living narwhal.

The small tusk is not complete in either specimen of *O. leptodon,* but its apex is preserved on SMNK PAL 2492, although separated from the intra-alveolar portion of the tooth. Therefore, on the specimen (Figs 2B,C) the reconstructed length of the tusk is an estimate, although probably relatively close to the actual length. The total length of the tusk was approximately 25 cm and the intra-alveolar portion approximately 20 cm. It is unlikely that more than 5 cm of the tusk were erupted. The eruption of the small tusk is corroborated by the presence, at the apex, of a small wear facet, which is grossly parallel to the anterior U-shaped border of the palate and therefore to the sea bottom in feeding position. The section of the small tusk is also oval and the diameters at its proximal extremity are 22 mm and 18 mm. At the extremity of the preserved portion of the alveolar part of the tusk (which is close to the alveolar border) the diameters are 18 mm and 14.5 mm. At the level of the proximal extremity of the wear facet (approximately 1 cm from the apex of the tusk), the diameters are 10 mm and 11 mm. The pulp cavity of the tusk is similar to that observed in *O. peruvianus*:

it is small, conical, and approximately 1 cm deep, partially filled with a knot of irregular dentine on MNHN SAO 202. In the narwhal such a knot on the unerupted small tusk (right in the male, and both in the female) is produced when the growth of the tooth stops, generally prior to sexual maturity.

MAXILLA

The maxilla is reduced as in *O. peruvianus,* and is basically similar to that of this species. It does not participate in the construction of the bony palate, which has no teeth other than the tusks. In MNHN SAO 202, as is observed in *O. peruvianus*, the portions of the maxillae posterior to the nares are narrow strips of bone and the right is wider than the left. A slight asymmetry of the bones of the face (especially the maxillae) is characteristic of odontocetes, in which the right bones are more developed than the left.

FRONTALS

The frontals of *O. leptodon* also have the same basic pattern observed in *O. peruvianus*. The supraorbital process is a large triangular plate overhanging an anterolaterally orientated orbit. The dorsal border of the orbit differs from that of *O. peruvianus* in being only slightly concave instead of deeply notched. The condition of *O. leptodon* probably precluded (certainly reduced) the dorsal binocular vision that was hypothesized by de Muizon *et al*. (2002) for *O. peruvianus*.

PALATINES AND VOMER

On the palate the vomer of *O. leptodon* is more developed than in *O. peruvianus*, in which it is already much larger than in the other odontocetes. It extends further posteriorly on the palate than in *O. peruvianus,* and as a consequence the palate is wider in its median region and its lateral edges are not so deeply notched. In the posterior region of the palate of the holotype, the palatines are not in contact medially (as is observed in *O. peruvianus*); as a result, the vomer is visible continuously in the middle of the palate from the anterior crest to the basisphenoid. However, on the referred specimen MNHN SAO 202 the palatines are almost in contact and the condition of the holotype may be an individual variation. The palate of *O. leptodon* is longer than in *O. peruvianus*. This condition is mainly due to the fact that the posterior edge of the palate (between the apices of the pterygoid hamuli) is convex posteriorly in the former while it is deeply concave in the latter. Consequently, the palate in *O. leptodon* is much larger than in *O. peruvianus* in both length and width.

PTERYGOIDS

The pterygoids have a large ventrolateral crest as in *O. peruvianus*, probably for attachment of the pars lateralis of the pterygoid muscle. However, the apex of the pterygoid hamulus is smaller and not as salient posteriorly as in *O. peruvianus* (see below). The apex of the pterygoid hamulus contacts the medial lamina of the pterygoid. The latter is greatly thickened and incorporated into the basioccipital crest as in *O. peruvianus* (see below, the description of SMNK PAL 2491, referred to *O. peruvianus*). This contact of the pterygoid hamulus with the enlarged medial lamina of the pterygoid forms a large foramen through which passes the eustachian tube.

The pterygoid sinus is extremely reduced when compared to most other odontocetes. It is about one-tenth the size observed in *Delphinapterus,* and if a functional sinus was actually present it was obviously vestigial. In fact, the lateral side of the *Odobenocetops* skull between the apex of the tympanic and the pterygoid hamulus is considerably shortened.

A small lateral lamina of the pterygoid is present. However, contrary to the condition in other odontocetes it does not articulate with the squamosal but with the alisphenoid. It forms the anterior border of the foramen ovale on the lateral wall of the skull. This condition is only superficial since internally the foramen ovale is fully enclosed in the alisphenoid as in the other eutherians.

ALISPHENOID

As in *O. peruvianus*, the alisphenoid is a very thick bone, which contrasts with the condition observed in the other delphinoids. The foramen ovale is well separated from the cranial hiatus and not confluent with it as in the holotype of *O. peruvianus*, in which it is probably broken (see, below, the description of SMNK PAL 2491, a specimen referred to *O. peruvianus*, in which the alisphenoid region is much better preserved than in the holotype, USNM 488257). The foramen ovale is enormous (two to three times the size observed in *Delphinapterus*), as is observed in *O. peruvianus*. The mandibular nerve, which exits the skull through the foramen ovale, has eight branches in the dog (Miller *et al.*, 1964): the pterygoid nerve, the buccal nerve, the deep temporal nerve, the masseteric nerve, the auriculotemporal nerve, the mylohyoid nerve, the mandibular alveolar nerve, and the lingual nerve. It is a mixed nerve, sensory and motor. Of course the condition in *Odobenocetops* was not necessarily similar to that in the dog. However, it is noteworthy that these branches totally or partially innervate the tongue, the masticatory and digastricus muscles, the hyoid muscles, the cheeks, and the lips. Therefore, the size of the foramen ovale and the inferred large size of the mandibular nerve are consistent with the large size of the tongue, the upper lip and the jaw muscles as well as with their function as hypothesized by de Muizon (1993a,b) and de Muizon *et al.* (1999; 2002).

SQUAMOSAL

The major characteristic of the squamosal of *Odobenocetops* is the highly modified glenoid cavity and zygomatic process, described by de Muizon *et al.* (2002), which forms a large, anteroposteriorly orientated gutter-like cavity (Figs 1B and 6). This region, although following the same basic pattern in the two species, shows some differences in *O. leptodon*. In the latter, the glenoid cavity is approximately 15% shorter anteroposteriorly. Furthermore, in lateral view, the posterior border of the glenoid cavity lies 3–4 cm from the lambdoid crest of the exoccipital, whereas in *O. peruvianus* the posterior edge of the cavity is at the level of the crest. The lateral wall of the glenoid cavity (or gutter), although concave ventrolaterally, is almost horizontal and not strongly recurved ventrally as is observed in *O. peruvianus*. Furthermore, the zygomatic process of the squamosal is apparently located in a higher and more anterior position on the skull. This condition is not easy to observe on the available specimens of *O. leptodon,* since the roof of the braincase is almost totally lacking in SMNK PAL 2492 and the process is broken in MNHN SAO 202. It is clear, however, that the anterior notch of the glenoid cavity of *O. leptodon* is closer to the lateral ridge of the frontal (the posterior extension of the posterior edge of the supraorbital process) than in *O. peruvianus*. This separation measures *c.* 5.1 cm in SMNK PAL 2492 and *c.* 6.3 cm in MNHN SAO 202 (*O. leptodon*); *c.* 9.5 cm in USNM 488257 and *c.* 9.2 cm in SMNK PAL 2491 (*O. peruvianus*). The squamosal-parietal suture is especially clear on MNHN SAO 202. It is similar to that described for *O. peruvianus*, having the same unusual zig-zag shape. This is likely to represent an adaptation to strong muscular tensions applied to the bones during the suction feeding of *Odobenocetops*.

EAR BONES

The ear bones have relatively tight osseous contacts with the squamosal, alisphenoid, and basioccipital, contrary to the condition observed in the other delphinoids in which the petrotympanic is loose and almost totally surrounded by a well-developed peribullary sinus. In *O. leptodon* the sinus was certainly less extensive than in the other delphinoids.

The periotic has been removed from the skull of MNHN SAO 202 (Fig. 7), and an isolated periotic (PPI 249) from the SAO horizon at Yauca (approximately
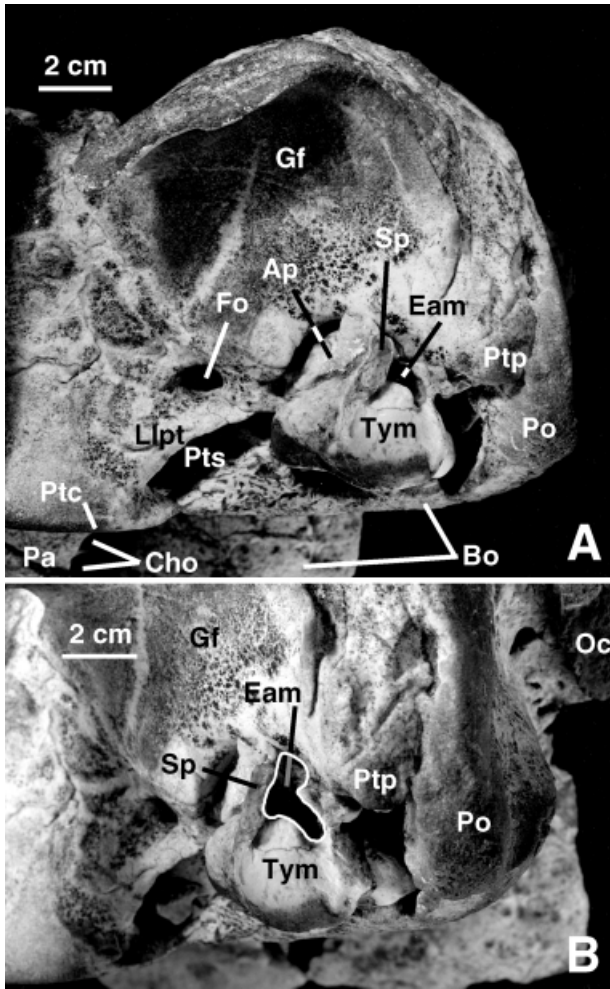
Figure 6. Auditory region of *Odobenocetops leptodon*, holotype (SMNK PAL 2492). Lateral view (A) and postero-lateral view showing the tympanic aperture (B). On B, the outline of the tympanic aperture has been enhanced with a white line. Abbreviations: Ap, anterior process of the periotic; Bo, basioccipital; Cho, choanae; Eam, external auditory meatus; Fo, foramen ovale; Gf, glenoid fossa; Llpt, lateral lamina of the pterygoid; Oc, occipital condyle; Pa, palatine; Ptc, pterygoid crest; Ptp, post-tympanic process of the squamosal; po, paroccipital process of the exoccipital; Pts, pterygoid sinus; Sp, sigmoid process of the tympanic; Tym, tympanic.

10 km south of Sacaco) has been referred to *O.* cf. *leptodon* (Fig. 8). The periotic of *O. leptodon* is larger than in *O. peruvianus*, and much more massive. The anterior process is almost as wide as it is long and bears on MNHN SAO 202 numerous independent nodular ossicles of variable size. On the dorsal side of the process, two or three larger nodules occupy a pronounced excavation in the bone. A similar condition is observed on MNHN PPI 249, in which the ossicles

have been lost. In fact, the preparation of the brain-case of MNHN SAO 202 revealed a great abundance of these ossicles surrounding the cerebral face of the periotic. The ventrolateral rim of the anterior process is enormous and extremely salient, to a much greater extent than in *O. peruvianus*. On the dorsal (cerebral) face of the bone the lateral edge of the dorsal opening of the vestibular aqueduct is markedly thickened and strongly projects dorsally relative to the condition in *O. peruvianus*. The posterior process does not project posteriorly as in *O. peruvianus* and its posterior edge is wider and more transverse. The pars cochlearis is also much larger (longer and wider) and more massive in *O. leptodon* than in the two periotics referred to *O. peruvianus* by de Muizon *et al.* (2002).

The tympanic has the classical delphinoid morphology (Figs 6 and 9). It does not present the lateral groove generally observed in many primitive taxa (kentriodontids, iniids, pontoporiids, platanistoids, eurhinodelphinoids, physeteroids, ziphioids, agorophiids). The lateral groove is absent in all Recent delphinoids. The sigmoid process is very large and dorsoventrally elongated. It is much more transverse than in any other delphinoid and not shifted posteriorly. Posterior to the sigmoid process is a long, low, and rounded conical process. Posterior to the conical process is a well-developed anterior crest of the posterior process of the tympanic. These three structures are formed in such a way that they surround a much larger external auditory meatus than in any other delphinoid (Fig. 6B). This indicates a larger surface of the tympanic membrane, which would indicate that sound transmission via the middle ear could have been more important in *O. leptodon* than in the Recent delphinoids.

In lateral view, the tympanic of *O. leptodon* is similar to that of *O. peruvianus* but larger. The tympanic of SMNK PAL 2492 has not been removed from the skull, while in SAO 202 the disarticulation of the bone allows observation of the internal side of the involucrum (Fig. 9). This region of the tympanic is significantly different from that of *O. peruvianus* from Sud-Sacaco described by de Muizon *et al.* (2002). It is much wider and more massive, especially the postero-medial lobe of the tympanic (Fig. 9). The involucrum is markedly concavo-convex ventromedially because of the development of the medial lobe, while it is roughly straight in *O. peruvianus*.

Auditory ossicles are preserved in SAO 202 and have been isolated (Fig. 10). The malleus is quite unusual for a delphinoid. When viewed posteromedially (on its articular face with the incus) with the articular head being positioned below the tuberculum, the manubrium is clearly higher than the muscular insertion for the tensor tympani muscle. In the other Delphinida (de Muizon, 1988b), the muscular process
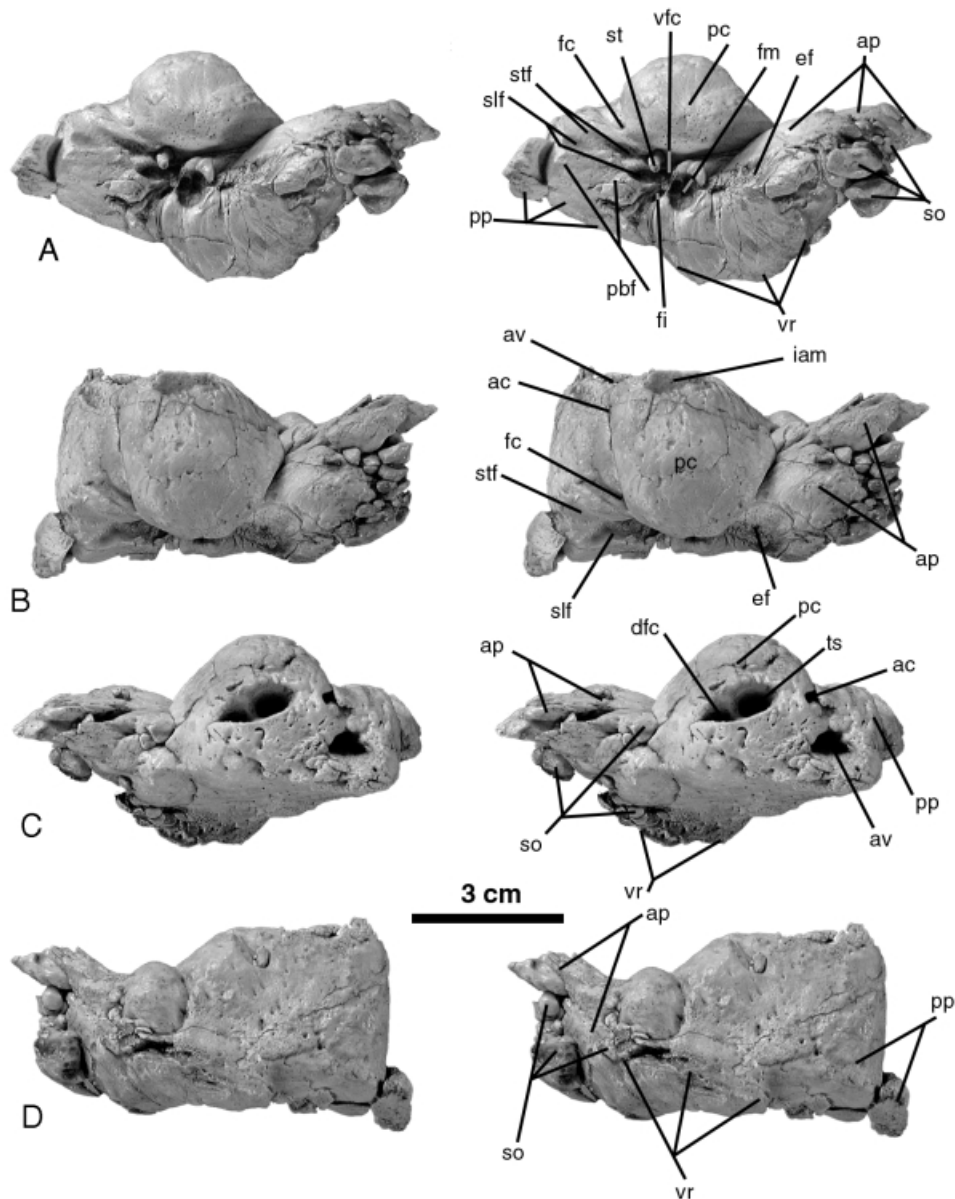
Figure 7. *Odobenocetops leptodon*, referred specimen (MNHN SAO 202). Periotic in dorsal (A), lateral (B), ventral (C), and medial (D) views. Abbreviations: ac, aqueductus cochleae; ap, anterior process; av, aqueductus vestibuli; dfc, dorsal opening of the facial canal; ef, fovea epitubaria; fc, fenestra cochleae; fi, fossa incudis; fm, fossa mallei (= epitympanic recess); iam, internal auditory meatus; pbf, posterior bullar facet; pc, pars cochlearis (= promontorium); pp, posterior process; slf, sulcus facialis; so, supernumerary ossicles; st, stapes; stf, fossa for stapedial muscle; ts, tractus spiralis; vfc, ventral opening of the facial canal; vr, ventral rim of the anterior process.

is always above the manubrium, this condition being extremely pronounced in the iniids, pontoporiids, and some kentriodontids (e.g. *Atocetus*). The tuberculum is massive and shifted dorsally. In these respects, the malleus of *O. leptodon* more resembles that of *Squalodon* than those of the other delphinoids. The incus is also very massive and the base of the crus breve is robust. Its major characteristic is the shape of the articular facet for the stapes on the crus longum. It is oval-shaped, but close to circular (W/L = 1.22/1.52 mm = 0.80). It differs from that of the other delphinoids, in which the oval is much more flattened (W/L in *Tursiops* (a Recent delphinid) = 0.36/1.1 mm = 0.32; *Atocetus* (a middle Miocene Kentriodontid) = 0.47/0.97 mm = 0.48). The stapes is massive and almost cylindrical with no stapedial foramen. In this
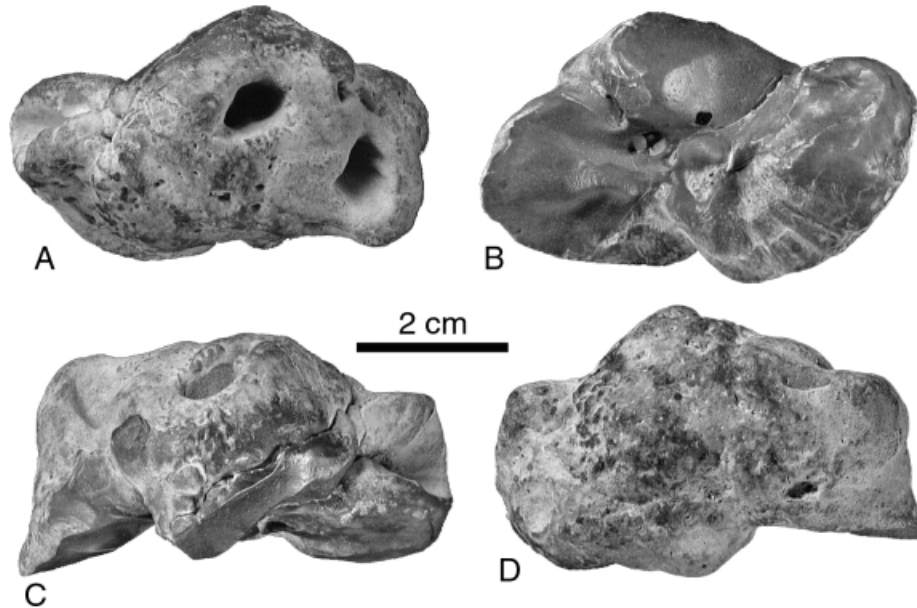
Figure 8. *Odobenocetops* cf. *leptodon*, referred specimen (MNHN PPI 249). Periotic in dorsal (A), lateral (B), ventral (C), and medial (D) views.
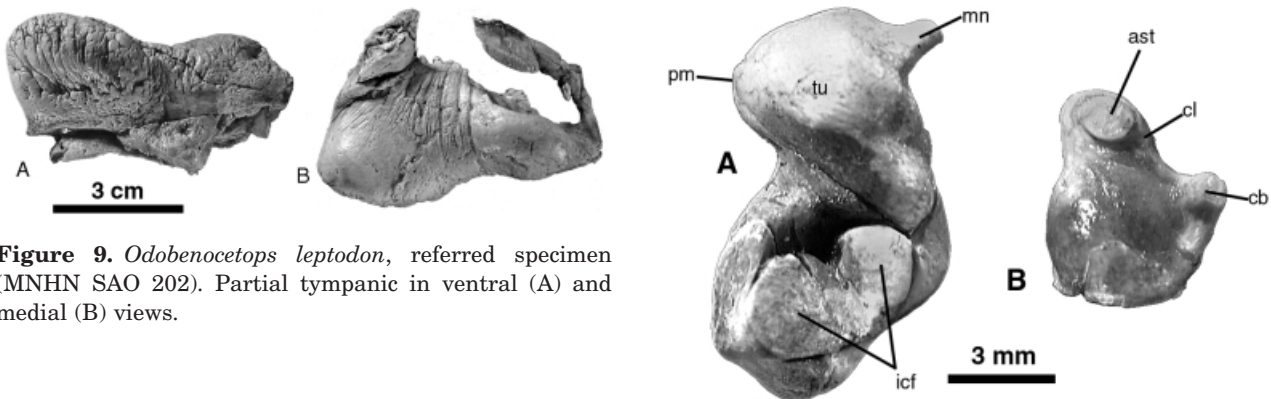

Figure 9. *Odobenocetops leptodon*, referred specimen (MNHN SAO 202). Partial tympanic in ventral (A) and medial (B) views.
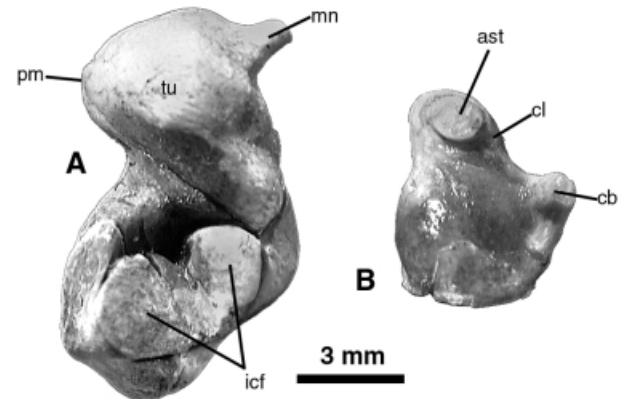

Figure 10 *Odobenocetops leptodon*, referred specimen (MNHN SAO 202). Malleus in posteromedial view (A); incus in ventral view (B). Abbreviations: ast, articular facet for the stapes; cb, crus breve; cl, crus longum; icf, articular facets for the incus; mn, manubrium; pm, processus muscularis; tu, tuberculum.

respect *O. leptodon* resembles the monodontids but differs from the other delphinoids, in which this bone has a minute foramen and is anteroposteriorly compressed. The stapes is also imperforate in ziphiids and *Squalodon*, although in these forms the bone is also anteroposteriorly compressed. In eurhinodelphinids the stapes is perforated by a larger foramen than in delphinids. On its posterior edge, almost adjacent to the articular surface for the incus, is a strong process for the stapedial muscle. This process is absent or very reduced in the other delphinoids. The stapedial footplate is almost circular, thus differing from that in the other delphinoids, in which it is oval.

BASIOCCIPITAL

This bone in *O. leptodon* is extremely wide and deep, as was already observed on the holotype of *O. peru-*

vianus, in which it is very incomplete. As mentioned above, the basioccipital crests are formed by the medial laminae of the pterygoid anteriorly and the basioccipitals posteriorly. They are roughly parallel because of the breadth of the posterior region of the palate and choanae, which widens the anterior region of the basioccipital. Therefore, the basioccipital does not have the trapezoidal morphology observed in the other odontocetes. The basioccipital crests are

extremely thick and laterally overlap a large portion of the medial lobe of the tympanic. In *Kogia*, according to von Schulte & Forest Smith, 1918), and in *Monodon*, according to Howell (1930), the medial side of the basioccipital crest receives the insertion of the scalenus medius muscle, which draws the head downward. This muscle was probably inserted (at least in part) on the large and deeply excavated circular to elliptical muscle scars which are visible here. The posteroventral angle of the basioccipital crest contacts the ventromedial angle of the paroccipital process in such a way that the jugular notch of the other odontocetes becomes, in both *Odobenocetops* species, a large jugular window. The suture between the vomer and the basioccipital is not clear because of the preservation of the specimen.

EXOCCIPITAL AND SUPRAOCCIPITAL

The occipital region is very incomplete on both specimens of *O. leptodon*. On SMNK PAL 2492 the left exoccipital only is preserved. The paroccipital process is larger and stouter than in the other delphinoids, as is observed in *O. peruvianus*. The ventromedial edge of the paroccipital process, which laterally borders the jugular window mentioned above, is a thick posteriorly projecting bony crest. The posterior face of the paroccipital process receives the insertion of the rectus capitis lateralis in *Kogia* (von Schulte & Forest Smith, 1918) and part of the apparently undivided rectus capitis in *Monodon* (Howell, 1930). The ventrolateral region of the paroccipital process also receives the sternomastoideus, another muscle which draws the head downward. In fact, the whole region, reinforced by the tight contact between the paroccipital process of the exoccipital and the posterior angle of the basioccipital crest, presents very strong muscle attachments

and clearly indicates a very strong musculature of the neck involved in head movements. Furthermore, the single preserved occipital condyle is extremely convex and salient, to a greater extent than in any other odontocete. The condyle is relatively damaged on SMNK PAL 2492 but it is obvious that it allowed a greater amplitude of movement of the head than in any other odontocetes (see below, description of the occipital of *O. peruvianus*).

ENDOCRANIAL CAVITY

The endocranial cavity (essentially its anterior and basal parts) is partially preserved in both specimens. The major difference between the two species of *Odobenocetpos* is the size of the olfactory lobes, which are slightly larger in *O. leptodon* than in *O. peruvianus*. Numerous bony nodules were found in the cranial cavity of MNHN SAO 202. These elements vary in size from 1 to 15 mm and sometimes agglutinate to form a 4 cm long and 2 cm wide element. The latter was lying above the dorsal process of the periotic. Apparently these bony nodules were concentrated in the auditory region and they seem to have allowed a tight contact of the periotic with the rest of the skull (see discussion below).

ATLAS

The atlas of SMNK PAL 2492 was found lying in the palatal region of the skull, which leaves no doubt about its belonging to the same individual (Fig. 11). This vertebra is free (i.e. not fused to the axis) as in the Recent monodontids but in contrast to the other Recent delphinoids, in which the first two to five cervical vertebrae are synostosed in a compact synarcual. The atlas of *O. leptodon* is extremely massive and
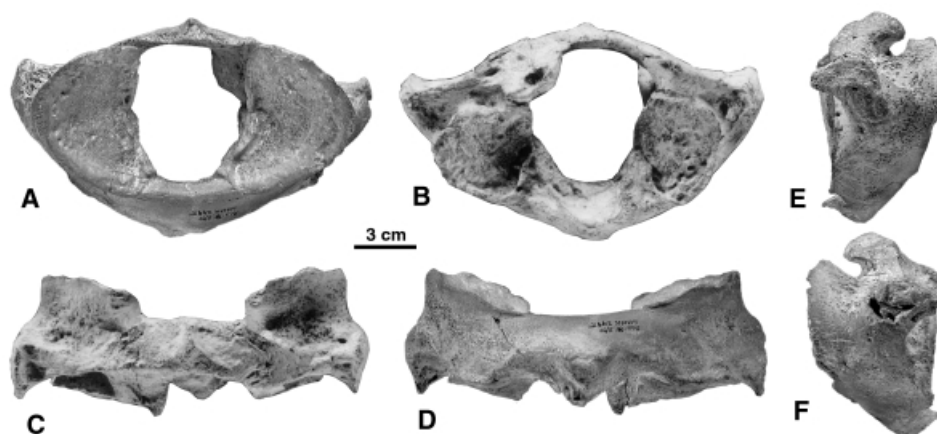

Figure 11. *Odobenocetops leptodon*, holotype (SMNK PAL 2492). Atlas in anterior (A), posterior (B), dorsal (C), ventral (D), lateral right (E), and lateral left (F) views.

longer anteroposteriorly than in *Monodon* or *Delphinapterus*, although more resembling the latter than the former in this respect. The articular surfaces for the cranial condyles are much deeper than in the living monodontids and their dorsal edges form a large crest, which strongly projects anteriorly. This morphology denotes a great amplitude of movement of the head and corroborates the conclusion drawn from the morphology of the occipital condyles. Furthermore, in lateral view, the anteroposterior length of the vertebra at the level of the dorsal edge of the articular surfaces is almost twice the length at the level of the ventral edge. In other words, the vertebra is almost twice as long dorsally as ventrally. This condition tends to orientate the skull slightly downward, rather than anteriorly as in the other cetaceans. A similar condition is found in *Delphinapterus*, but it is less pronounced than in *Odobenocetops*. As a matter of fact, *Delphinapterus* is the living odontocete which presents the greatest mobility of the neck.

The transverse process of terrestrial mammals and archaeocetes presents a transverse foramen, which totally encloses the vertebral artery. In the other cetaceans, the transverse 'foramen' is an open notch and the transverse process is divided into a dorsal and a ventral branch. As stated by de Muizon (1988a; b), the ventral process is enlarged in delphinoids and the dorsal process is reduced to a simple knob on the posterolateral region of the neural arch. In *O. leptodon*, the ventral branch of the transverse process is located higher on the vertebra than in the Recent monodontids. Its apex is sharp and turned upward and backward. In the Recent monodontids the ventral transverse process is slightly orientated backward, but its apex is rounded and not sharply orientated posteriorly. Furthermore, the ventral transverse process of the Recent monodontids and other odontocetes is not orientated dorsally, but laterally or slightly ventrally. It is noteworthy that the transverse process of the sirenians (e.g. *Trichechus*) is located high on the atlas and is turned upward and backward as is observed in *O. leptodon*. However, in sirenians this process is the dorsal portion of the transverse process because the vertebral artery passes ventral to it.

The dorsal knob of the transverse process of delphinoids is almost absent on the right side of the atlas of *O. leptodon*. However, on the left side, in the position of the dorsal knob of the transverse process, the neural arch presents a salient crest which joins the posterior border of the ventral transverse process. At this level, the posterior edge of the neural arch also develops a long (*c*. 27 mm), thick (maximum 15 mm) and wide (*c*. 32 mm) posterior process which contacts the dorsomedial angle of the left articular facet for the axis. The dorsal knob of the transverse process receives the insertion of the obliquus capitis caudalis, a muscle which is here apparently much stronger on the left side than on the right. The left ventral transverse process of the atlas is also larger and stronger than the right. This process receives the origin of the rectus capitis lateralis on its apex. On its posterior side are the insertions of the scalenus, the longissimus dorsi, and the semispinalis capitis, and on its anterior side is the origin of the obliquus capitis cranialis. This condition could be related to the size of the right tusk, since the strength of the muscles cited above might compensate for the weight of the tusk and/or the asymmetry of the snout during feeding. In Recent monodontids, the dorsal knob of the transverse process is a relatively well developed transverse crest in *Monodon* and is very large and points dorsolaterally in *Delphinapterus*.

In accordance with the greater strength of the left atlas musculature, in dorsal view, the left half of the atlas of *O. leptodon* is longer anteroposteriorly, wider transversely, and stronger than the right. Furthermore, on the posterior side of the vertebra, the articular facets for the axis are not similar in shape as is generally observed in the other odontocetes. The left cotyle is transversely wider and dorsoventrally lower than the right. These conditions are also probably related to the asymmetry of the tusks.

OTHER VERTEBRAE

The other known vertebrae of *O. leptodon* (MNHN SAO 202) are all very damaged and, at best, only the centrum is preserved. However, in spite of their poor preservation they can give an estimate of the length of the body in relation to the skull. The cervical vertebrae are known from fragments of the atlas and axis and three centra of posterior cervicals. The posterior cervical vertebrae are easily recognized because of the reduced anteroposterior length of their centra compared to the thoracic vertebrae. As in the Recent monodontids, they are articulated and do not present the synostosis observed in the Recent delphinids and phocoenids. An estimate of their length falls close to 20 cm. The Recent monodontids have 11 thoracic vertebrae (while their number varies from 12 to 15 in the delphinids and phocoenids) and it is hypothesized that the same number was present in *Odobenocetops*. The 11 centra following the cervicals are estimated to have a total maximum length of *c*. 60 cm. The Recent monodontids have 9–10 lumbar vertebrae, while their number varies from 10 to 20 in the Recent delphinids and phocoenids. In MNHN SAO 202 (*Odobenocetops leptodon*) ten centra are preserved posterior to the thoracic vertebrae. Since the last centrum does not seem to have possessed articular facets for the chevrons (a characteristic of the caudal vertebrae), the number of lumbar vertebrae is at least ten. The preserved

lumbar vertebrae of *Odobenocetops leptodon* have an approximate length of 80 cm. The centra of these lumbar vertebrae are longer than wide, as is observed in Recent monodontids but in contrast to the condition of the Recent delphinids and phocoenids. No caudal vertebrae are preserved in MNHN SAO 202. In *Delphinapterus* the caudal portion of the vertebral column is approximately 30% longer than the lumbar portion. If the number of lumbar vertebrae was similar in *Odobenocetops* and *Delphinapterus* then the caudal portion of the vertebral column should be close to 105 cm in length. Hence, the total vertebral column of *Odobenocetops leptodon* could have approached a length of 265 cm for a skull which is estimated to have been 40 cm long from the tip of the rostrum to the occipital condyles; i.e. the animal was *c*. 3 m long. Therefore, the length of the skull of *Odobenocetops* was *c*. 13% of the total length of the animal, while in *Delphinapterus* (MNHN A 3246) it represents 16.5% of the length of the body (skull: 62 cm, vertebral column: 375 cm). The difference between the relative lengths of

the skulls of *Odobenocetops* and *Delphinapterus* is explained by the reduction of the rostrum, which characterizes the former.

FORELIMB

Partial humerus, ulna, radius, and one carpal are associated with the specimen MNHN SAO 202 (Fig. 12). The distal half of the right humerus shows a characteristic narrowing of the diaphysis (anteroposteriorly and transversely) at the level of the fossa for insertion of the infraspinatus muscle (de Muizon, 1988b). This condition is also present in the Recent monodontids, but not to such an extent in the other delphinoids. The deltopectoral tuberosity is located at the apex of the anterior edge of the humerus, as is observed in Recent delphinids and phocoenids but in contrast to the condition of the Recent monodontids in which the tuberosity is more proximal on the diaphysis and does not reach the anterior edge of the distal epiphysis. This condition is also present in several
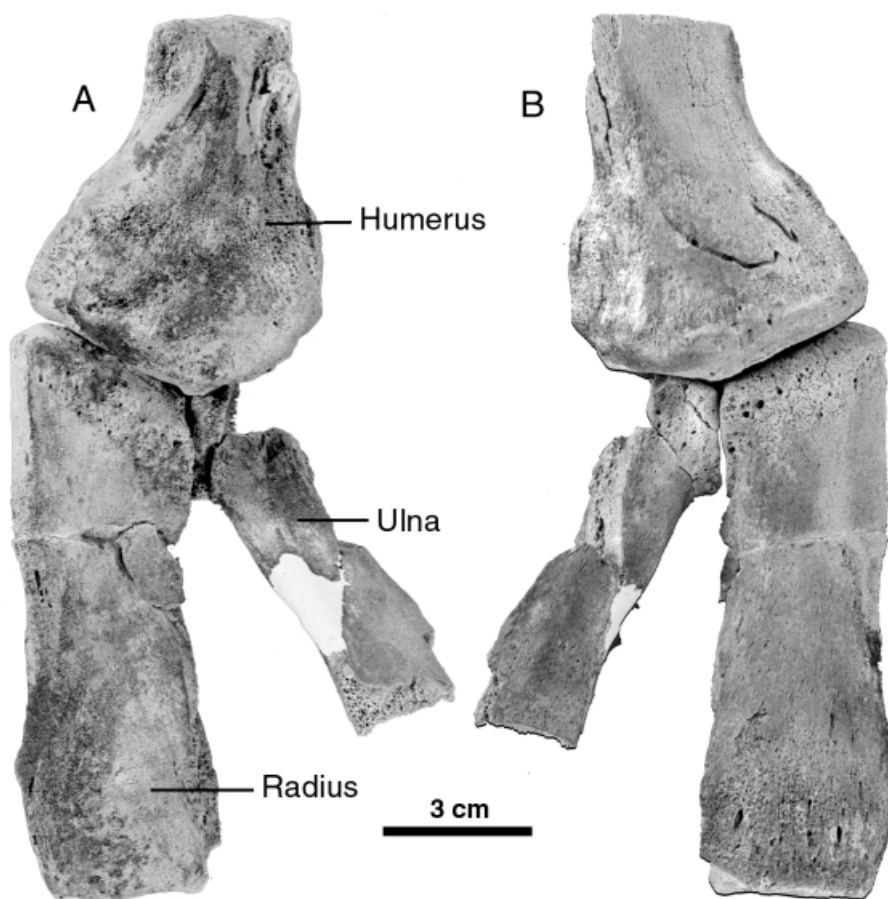
Figure 12. *Odobenocetops leptodon,* referred specimen (MNHN SAO 202). Left forelimb in lateral (A) and medial (B) views.

fossil (kentriodontids, eurhinodelphinids) and Recent (iniids, ziphiids, physeterids) families of odontocetes and is a plesiomorphic character state. The distal epiphysis for articulation with the ulna and radius is transversely wider than in the Recent delphinids and phocoenids but resembles the morphology of the Recent monodontids.

As is observed in *Monodon (*and less so in *Delphinapterus*), the radius is longer and apparently narrower distally than that of the Recent delphinids and phocoenids. Since the posterior region of the proximal epiphysis of the ulna is broken, it is not possible to observe the condition of the olecranon, which is almost lacking in the monodontids while it is reduced but still present in the other delphinoids.

ODOBENOCETOPS PERUVIANUS MUIZON 1993
(FIGURES 13–15, TABLE 3)

A second skull of *Odobenocetops peruvianus* has been discovered in the earliest Pliocene beds of the Pisco Formation at Sud-Sacaco. This specimen is of special interest because it is more complete than the holotype and especially because it bears two small tusks similar in size to the small tusk of the holotype (USNM 488252) and has therefore been regarded as a female of *O. peruvianus* (de Muizon *et al.*, 1999). In the following discussion, we do not exhaustively describe the new skull, but simply describe the new features *O. peruvianus* provided by the new specimen.

Holotype: USNM 488252, an incomplete skull lacking much of the left side and all of the auditory bones.

Referred specimens: SMNK PAL 2491, a relatively complete skull which lacks only the posterodorsal roof

Table 3. Measurements of the skull of *Odobenocetops peruvianus* (SMNK PAL 2491) in mm. (e = estimated).

Basicondylar length: 412
Bizygomatic width: 158 × 2 = 316e
Minimum width of the skull posterior to the postorbital processes: 116
Minimum width between the dorsal edges of the orbits: 123
Maximum width between the postorbital processes: 226
Width of the snout between the antorbital notches: 87
Maximum width of both nares: 60
Maximum length of the right naris: 51.5
Width of the choanae: 96
Maximum width of the skull at the level of the exoccipitals: 250
Bicondylar width: 143
Width between the apices of the hamular processes: 128
Length of the lateral lobe of the left tympanic: 48.5

of the braincase, and which still retains the ear bones *in situ*; MNHN SAS 1613, a left periotic and partial tympanic; and MNHN SAS 1614, a left periotic.

Emended diagnosis: *Odobenocetops peruvianus* differs from *O. leptodon* in its snout, which is narrower at its apex and tapers dorsally (although the apex is still rounded); in the presence of large premaxillary foramina, anterior to the nares; in the absence of depressions for premaxillary sacs; in the shorter and shallower palate (especially in the anterior region); in the anterior border of the palate which is more V-shaped whereas it is more U-shaped in *O. leptodon*; and in the deeply notched anterodorsal edge of the orbit, which is slightly concave in *O. leptodon*.

DESCRIPTION

TUSKS AND PREMAXILLAE

The major differences between the new specimen and the holotype are in the size of the tusks and morphology of the premaxillae. Both tusks are small and the left tusk is slightly smaller in diameter than the right. Neither of the tusks is complete. The left tusk is broken inside the sheath; however, the right tusk is only lacking its apex and, as preserved, is 23 cm long and is probably missing a few cm only. Therefore, the right tusk was very close to the length as well as the diameter of the small left tusk of *O. leptodon*. Although the tusk is not complete, given the length of the tusk (as preserved) and the sheath, it is certain that it was erupted. The premaxillary sheaths are small, and, in agreement with the sizes of the tusks, the left one is smaller than the right. Because of this slight asymmetry and although the apices of the left sheath and tusk are not preserved, it is likely that the left tusk was also erupted. Furthermore, the walls of the left sheath at its apex are very thin, which suggests that very little of the bone is missing. The apex of the right sheath is not completely preserved either, but given the thickness of the bone at the broken extremity, it is probable that no more than a few centimeters are lacking.

The dorsal aspect of the premaxillae is very similar to that of the holotype although slightly more symmetrical. The posterior extension of the right premaxilla behind the nares is only slightly greater than that of the left, contrary to the condition of the holotype, in which the posterolateral process of the left premaxilla reaches the middle of the lateral edge of the left naris, whereas the right process almost reaches the posterior edge of the right naris. Since the premaxillae of SMNK PAL 2491 project posteriorly slightly behind the bony naris, this feature shows some variation within the species. The asymmetry of the tusks and alveolar processes may thus be reflected
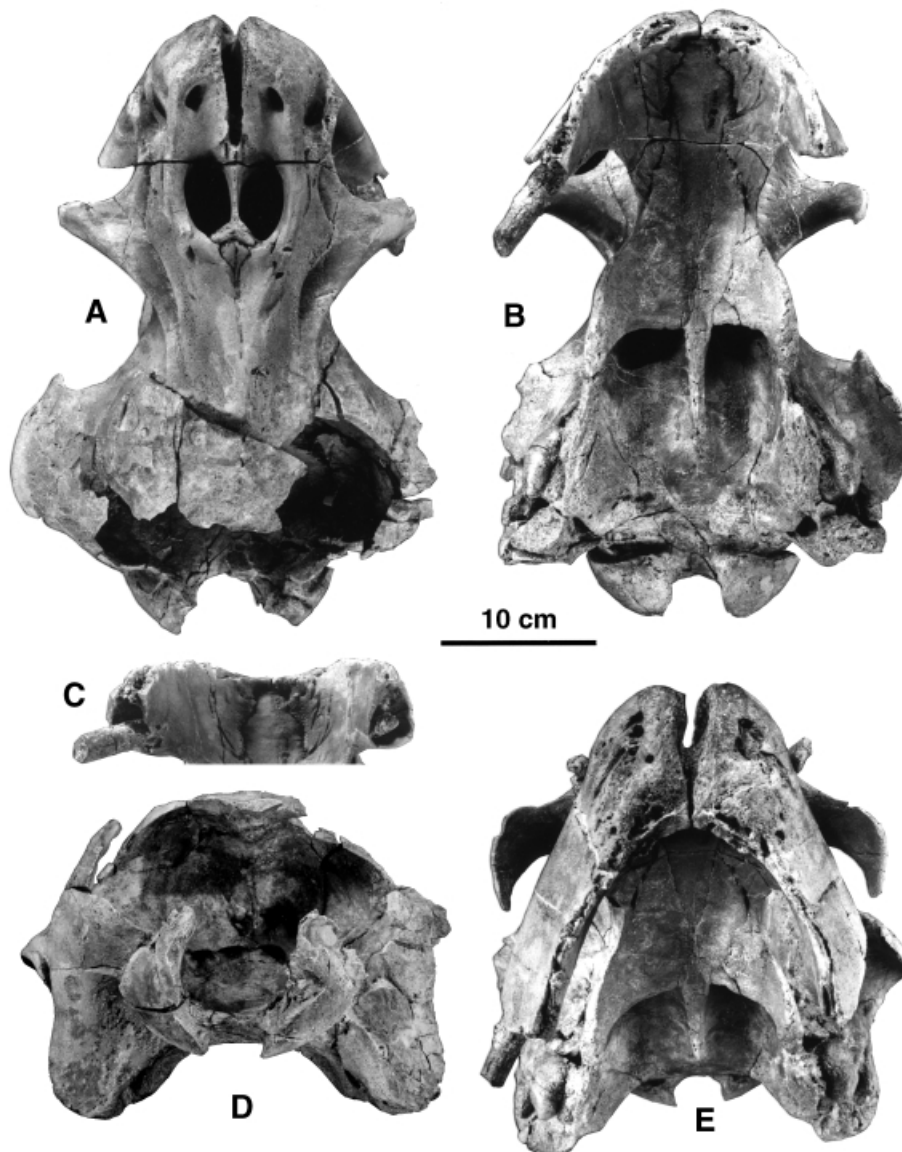
Figure 13. *Odobenocetops peruvianus*, referred specimen (SMNK PAL 2491). Skull of a probable female in dorsal (A), ventral (B), occipital (D), and anteroventral (E) views; posteroventral view of the anterior region of the palate showing the two small tusks (C).

in the asymmetry of the posterior processes of the premaxillae. However, this inference must be made cautiously since most odontocetes (including monodontids) present an asymmetry of the dorsal bones of the skull, the right premaxilla and maxilla extending farther posteriorly than the left and slightly displacing the vertex on the left side of the skull. Nevertheless, the asymmetry of the male narwhal does not reflect the tusk asymmetry since the right maxilla is slightly more expanded posteriorly than the left, which carries the large tusk.

In SMNK PAL 2491 the snout is very complete and the structure of the bone is perfectly preserved. There-fore, muscle scars and foramina are clearly observable and provide important data. Anterior to the large premaxillary foramina is a rough, triangular surface, distinct on each bone, which reaches the apex of the snout. This area corresponds to the attachment scar for the nasal plug muscle in the other odontocetes. These muscle scars are so well marked that it is unlikely that there was no nasal plug muscle in *O. peruvianus*. It is therefore very probable that *O. peru-vianus* had nasal plugs, which is to be expected in an odontocete, but was not clear on the holotype (de Muizon *et al*., 2002). Posterior to the premaxillary foramina are two short saddle-shaped grooves, which

form the anterior edges of the bony nares. The morphology of the new specimen confirms the conclusions of de Muizon *et al.* (2002) that, if premaxillary sacs (which are located between the premaxillary foramina and the anterior edge of the nares) were present in *Odobenocetops peruvianus*, they were very reduced, probably vestigial. Therefore, and considering the reduced space on the dorsal face of the rostrum, it is highly probable that *O. peruvianus* had no (or only a vestigial) melon. Although the nasal plugs, premaxillary sacs and melon are tightly related organs, the well-developed muscle scars for the insertion of the nasal plug muscle force us to conclude that *O. peruvianus* exhibited a strong reduction of the two latter organs but little reduction of the former.

On the anterior face of the snout the premaxillae bear several large foramina indicative of an extensive vascularization of the snout related to the inferred presence of a large and strong upper lip. The irregular surface of the bone in this region corresponds to the attachment of a very robust musculature of the lip. The morphology of the much better preserved female specimen of *O. peruvianus* (SMNK PAL 2491) confirms the hypotheses based on the holotype of the species.

MAXILLAE AND FRONTALS

Posterior to the nares, between the mesethmoid and the maxillae, are two small triangular medial portions of the frontals, which have the same condition as the maxillae in relation to the premaxillae at the anterior region of the nares. In other words, the maxillae, which lay on the frontals, have withdrawn posterior to the nares, uncovering the frontals. Posteriorly, the medial portions of the frontals become thin and progressively disappear after the maxillae become joined. Further posteriorly, the medial edges of the maxillae separate again and uncover a thin strip of the frontals

which widens posteriorly. On the holotype it is probable that the lower portion of the mesethmoid posterior to (and overhung by) the Y-shaped portion which separates the nares (see de Muizon *et al.*, 2002) is in fact the medial portion of the frontal observed on the female skull fused to the mesethmoid. A medial portion of the frontal is clearly present in *O. leptodon* (MNHN SAO 202). The extensions of the maxillae posterior to the nares narrow posteriorly but are, like the premaxillae and tusks, relatively symmetrical, whereas in the male the right maxilla is wider and extends further posteriorly than the left.

The preorbital process of the frontal of the female skull is anteriorly elongated and blade-like, as in the holotype. However, in this specimen it is clear that both the maxilla medially and the frontal laterally are components of the process. Therefore, although highly modified, the preorbital process of *O. peruvianus* resembles that of the other odontocetes in the combined participation of the maxilla and frontal. The postorbital process is similar in shape to that of the holotype but is larger and longer, indicating some individual variation of this character. A clear asymmetry of the frontal is present, as is observed in the other odontocetes, in which the right supraorbital process of the frontal is distinctly larger than the left.

PALATINE, PTERYGOID AND VOMER

The vomer is very wide, the maxillae do not participate in the construction of the palate, and the premaxillae and the palatines have a large V-shaped suture on both sides as is observed in the holotype. The posterior region of the palate is perfectly preserved and adds to the knowledge of the species. In the posterior region of the palate, the medial edges of the palatines are in contact, hiding the vomer for a few centimetres of its length. Further posteriorly the palatines separate again, uncovering the vomer ven-
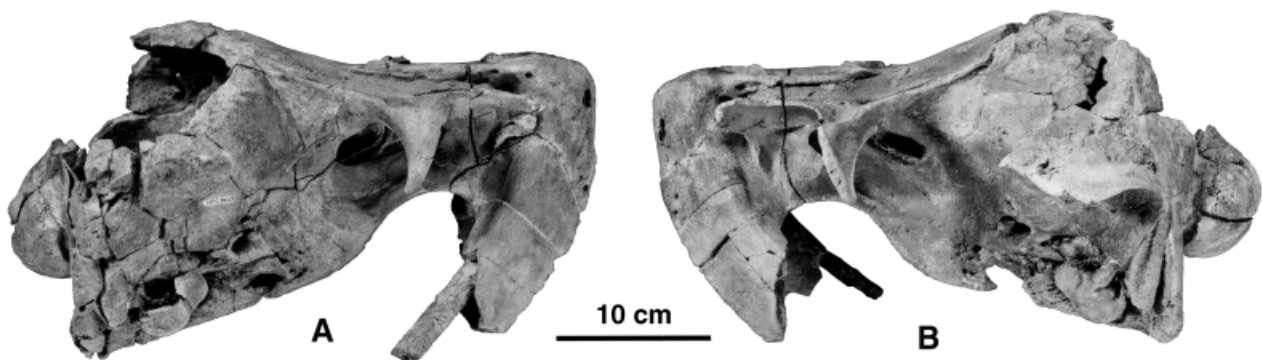

Figure 14. *Odobenocetops peruvianus*, referred specimen (SMNK PAL 2491). Skull of a probable female in lateral right (A) and lateral left (B) views.

trally. The median ridge of the vomer projects about 7 cm posterior to the posterior edges of the palatines. The sutures with the pterygoids are widely separated. The apices of the pterygoid hamuli are sharply pointed and extend toward the anterior angle of the basioccipital crests formed by the medial laminae of the pterygoids. They are almost in contact on the right side and the anterior end of the left medial lamina is apparently broken. Because of this projection and the long nonpalatal ridge of the vomer, the palate of *O. peruvianus* is clearly shorter than in *O. leptodon* and its posterior border is strongly concave. The pterygoid hamulus is transversely compressed and the lateral lamina of the pterygoid almost contacts the medial lamina. Therefore, the fossa for the pterygoid sinus is extremely reduced (as observed by de Muizon *et al.*, 2002 on the holotype) and hardly present in *O. peruvianus*. It is clearly more reduced than in *O. leptodon*, in which the fossa is very small but conspicuous. As in *O. leptodon*, there is a short but continuous lateral lamina of the pterygoid, which contacts the alisphenoid, contrary to the condition in Recent delphinoids. However, in Recent monodontids, a continuous lateral lamina of the pterygoid, although almost absent from the pterygoid hamulus, is sometimes present and contacts the squamosal dorsally.

ALISPHENOID

The alisphenoid is similar to that of *O. leptodon*. It is very thick and bears an enormous foramen ovale not confluent with the cranial hiatus. de Muizon *et al.* (2002) stated that in the holotype of *O. peruvianus* the foramen ovale was confluent with the cranial hiatus. Because this is not the case in the three other skulls referred to *Odobenocetops*, it is possible that the condition observed in the holotype is due to a postmortem breakage of the alisphenoid. As in *O. leptodon* the external opening of the foramen ovale is formed anteriorly by the pterygoid and posteriorly by the alisphenoid. Internally, the foramen ovale is fully enclosed in the alisphenoid. It is noteworthy, however, that this condition is not easy to observe because of the partial fusion of the bones.

SQUAMOSAL AND EAR BONES

The squamosal of SMNK PAL 2491 is basically similar to that of the holotype. The tympanic and the periotic are preserved *in situ* on both sides of the specimen (Fig. 15). Since the bones could not be removed from the skull it is not possible to describe them thoroughly. However, it is clear that they are extremely similar to those referred to the species by de Muizon *et al.* (2002). The lateral face of the tympanic bears a large sigmoid process which is grossly perpendicular to the antero-
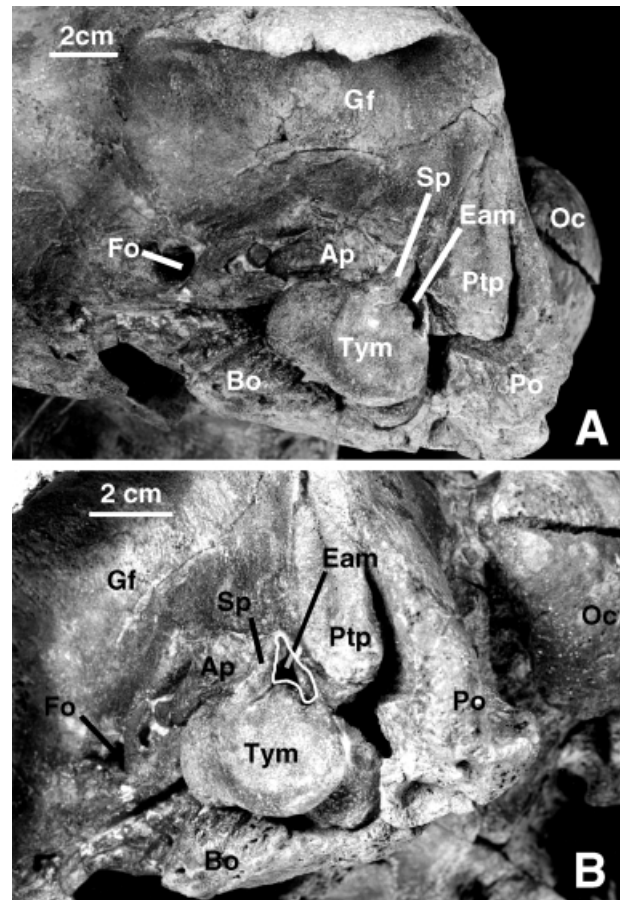

Figure 15. Auditory region of *Odobenocetops peruvianus*, holotype (SMNK PAL 2491). Lateral view (A) and posterolateral view showing the tympanic aperture (B). On B, the outline of the tympanic aperture has been enhanced with a white line. Abbreviations: Ap, anterior process of the periotic; Bo, basioccipital; Eam, external auditory meatus; Fo, foramen ovale; Gf, glenoid fossa; Oc, occipital condyle; Po, paroccipital process of the exoccipital; Ptp, post-tympanic process of the squamosal; Sp, sigmoid process of the tympanic; Tym, tympanic.

posterior axis of the bone and not shifted posteriorly as in the classical (i.e. non-odobenocetopsid) delphinoids. The apex of the process is straight, rounded, and not strongly recurved anteriorly as is observed in the classical delphinoids. Posterior to it is a low conical process and a relatively large anterior border of the posterior process. These three elements surround the external auditory meatus and, as a consequence of their morphology, the meatus is much larger than in the classical delphinoids. It is slightly smaller than in *O. leptodon* (SMNK PAL 2492). This condition would indicate a more efficient (effective) tympanic membrane in the Odobenocetopsidae and therefore possibly

better sound perception via the middle ear than in the other odontocetes.

The lateral wall of the tympanic is high, as is observed in *O. leptodon*. This condition indicates that the middle ear cavity was larger than in the classical delphinoids. It resembles the condition of most early diverging odontocetes (Squalodontidae, Squalodelphinidae, Platanistidae, Eurhinodelphinidae), and could represent a plesiomorphic condition or, more likely, a reversal corresponding to a need for enlargement of the middle ear cavity. The anterior extremity of the tympanic is blunt and rounded, as is observed in the other delphinoids.

The ventral lobes are well separated by a deep median groove which is well-marked on the posterior two-thirds of the bone. Their posterior extremities are rounded and wide and the medial lobe is slightly posterior to the lateral. This condition is similar to that of *O. leptodon* but clearly differs from that of the Recent monodontids, in which the posterior extremity of the medial lobe is narrower and more anterior than that of the lateral lobe. This feature is especially obvious in *Monodon*. It is also present to a lesser extent in the delphinids and phocoenids. Again, the odobenocetopsid condition is found in the early diverging odontocetes mentioned above, but is regarded here as a reversal (rather than a plesiomorphy).

Not much can be said about the periotic, which is preserved *in situ*, except that it has the massive morphology observed on the referred specimens described by de Muizon *et al*. (2002). Contrary to what is observed in the classical delphinoids, the lateral portion of the bone is closely appressed against the squamosal, in this respect resembling the condition observed in the platanistoids (*sensu* de Muizon, 1987; 1991; 1994; Fordyce & Barnes, 1994; Fordyce *et al*., 1994; Fordyce, 1994; not sensu McKenna & Bell, 1997). Furthermore, the posterior process of the periotic is deeply wedged between the squamosal and the exoccipital, which is in agreement with the long posterior process observed on MNHN SAS 1614 (an isolated periotic from the same horizon as the holotype of *O. peruvianus* and referred to this species). A similar condition is present in *Delphinapterus* (Kasuya, 1973) and *Monodon*. The delphinids and phocoenids are characterized by a petrotympanic completely isolated from the skull and maintained *in situ* by ligaments only (Fraser & Purves, 1960). Early derived odontocetes such as platanistoids have a tympanic and a periotic still articulated with the squamosal, which is regarded as a plesiomophic character state (de Muizon, 1987; 1991; 1994). Therefore, the condition of *Odobenocetops* and the Monodontidae could be regarded as plesiomorphic. However, because they have synapomorphies of the Delphinoidea absent in the Platanistoidea, we rather consider the condition of *Odobenocetops* as a reversal due to its hyperspecialization. The fact that a condition approaching this one is also found in monodontids could represent a synapomorphy of the two families, possibly related to sound transmission.

In general, the periotic and tympanic of *Odobenocetops* have relatively tight and extensive contacts with the surrounding bones: basioccipital and squamosal for the tympanic, and squamosal and exoccipital for the periotic. The lateral tuberosity and rim of the anterior process of the periotic are closely appressed against the squamosal in a similar pattern to that observed in the platanistoids. The squamosal in this region is greatly thickened and forms the medial border of the trough-like glenoid cavity.

On the anterior region of the anterior process of the periotic are several independent bony nodules which are appressed against the anterior process and apparently part of it. Such a condition has been observed in *O. leptodon* and is also present sometimes in *Platanista*.

BASIOCCIPITAL

The basioccipital is extremely wide and basically similar to that of *O. leptodon* although slightly wider. The basioccipital crests are large and undergird the tympanics, which are partially imbedded in their lateral face. The posteromedial faces of the basioccipital crests bear very large and deep muscular scars for insertion of the scalenus, at least as strong as in *O. leptodon*.

EXOCCIPITAL

The paroccipital process is very large and stout. It differs from that of the holotype in being orientated ventrally and not ventrolaterally. Its ventromedial angle contacts the posteroventral angle of the basioccipital crest and encloses the jugular notch to form a relatively large window, as is observed in *O. leptodon*. The exoccipital border of the window is very thick and forms an elevated crest. This indicates a strong scalenus dorsalis, which is inserted on the posteroventral face of the paroccipital process. This part of the occipital indicates an exceptionally strong musculature of the neck as was noted in regard to the holotype of *Odobenocetops peruvianus* (de Muizon *et al*., 2002). The anterior face of the paroccipital process does not present any fossa for the posterior sinus such as is observed in many other delphinoids. Fraser & Purves (1960) have stated that the absence of a fossa is not equivalent to absence of a posterior sinus. As a matter of fact, in the Recent monodontids the anterior face of the paroccipital process is not excavated by a fossa and a small posterior sinus is present. However,

the presence of a large sinus is related to a deep fossa. In SMNK PAL 2491 the anterior face of the paroccipital process has a reduced area and is not indicative of a large posterior sinus. This statement contrasts with the observations made on the holotype of *O. peruvianus* (de Muizon *et al.*, 2002).

The occipital condyles are more convex and salient than in any recent delphinoid and confirm the great mobility of the neck which was noted with regard to the holotype. In fact, the occipital condyles form a quarter of a sphere (Figs 13B,D and 14) and are proportionally larger and more convex than in any other cetacean (Recent or fossil) or in the walrus. The morphology of the condyles of SMNK PAL 2491 therefore indicates an exceptional mobility of the neck in *Odobenocetops*; certainly much greater than that of any other odontocete.

AFFINITIES

AFFINITIES OF THE GENUS ODOBENOCETOPS

The morphology of the associated ear bones, atlas, and forelimb clearly confirms, if it was necessary, the referral of *Odobenocetops* to the Order Cetacea. Therefore, we will not further discuss the cetacean affinities of *Odobenocetops* in this paper.

The new skulls of *Odobenocetops* do not provide new data reinforcing the infraordinal (Delphinida) and superfamilial (Delphinoidea) affinities proposed by de Muizon (1993a,b) and de Muizon *et al.* (2002). However, all the characters cited by de Muizon *et al.* (2002) to relate *O. peruvianus* to the Delphinida and Delphinoidea have been confirmed in *O. leptodon*, except the presence of large premaxillary foramina, which are not present as such in *O. leptodon*. The lack of this character is regarded here as a derived character state in *O. leptodon* and therefore a reversal within the odontocetes. One character which has been regarded as a synapomorphy of the Monodontidae (de Muizon, 1988b) is present in *O. leptodon*, but absent in *O. peruvianus* (de Muizon *et al.*, 2002): the medial Mx-Pmx suture, which is a characteristic feature of the Delphinoidea, is totally external to the nares in the Monodontidae (i.e. the lateral edge of the naris is formed by the maxilla only, with no participation of the premaxilla, in contrast to the condition observed in the other delphinoids where the medial Mx-Pmx suture is generally located at the anteromedial angle of the naris). In *O. leptodon* the Mx-Pmx suture is completely external to the naris and therefore resembles the condition of the Recent monodontids, differing in this respect from the condition of *O. peruvianus*.

It is noteworthy that, as in monodontids, the stapes of *Odobenocetops leptodon* has no stapedial foramen. Since such a foramen is present in the other delphinoids, the loss of this structure could represent a synapomorphy of the Odobenocetopsidae and Monodontidae. The fact that eurhinodelphinids have a larger stapedial foramen than in delphinids, phocoenids, and kentriodontids is an indication that the loss of this foramen is probably the derived character state within odontocetes.

Another important similarity between *Odobenocetops* and the Recent Monodontidae is the great mobility of the atlantooccipital articulation. The Monodontidae are the Recent delphinoids which display the greatest mobility of the neck; this is especially well-known in *Delphinapterus,* as has been abundantly observed in captivity. On the basis of the convexity of the condyles, in *Odobenocetops*, not only was the mobility of the neck greater than in the Recent monodontids but it is likely to have been more developed than in any other odontocete.

The new postcranial elements of *O. leptodon* provide some data which confirm the relationships hypothesized by de Muizon (1993a,b) and de Muizon *et al.* (2002). The morphology of the transverse process of the atlas is clearly a delphinoid character state: as mentioned by de Muizon (1988b), the reduction of the dorsal branch of the transverse process and the enlargement of its ventral branch is a synapomorphy of the Delphinoidea. Therefore, the morphology of the transverse process of the atlas of *O. leptodon* confirms the inclusion of the genus in this superfamily. In the forelimb, the humerus of *O. leptodon* presents a characteristic narrowing of the diaphysis, which forms a neck as in the Recent monodontids. This character is regarded here as a synapomorphy of the Monodontidae and Odobenocetopsidae and reinforces the sistergroup relationship of the two families suggested by de Muizon (1993a,b) and de Muizon *et al.* (2002).

RELATIONSHIPS OF THE TWO SPECIES OF *ODOBENOCETOPS*

O. peruvianus and *O. leptodon* have well-defined stratigraphic relationships, since the former is from the SAS horizon of the Pisco Formation, which is earliest Pliocene in age, and the latter is from the SAO horizon which is stratigraphically younger in the early Pliocene. All four specimens were found in an area no larger than 5 km^2. Since *Odobenocetops* is, apparently, endemic to the Pacific coast of South America, one could expect an ancestor–descendant relationship between the two species.

Several features of *O. leptodon* are indeed more derived than in *O. peruvianus*. *O. leptodon* is more specialized than *O. peruvianus* in its larger, longer and wider palate, in the elevation and breadth of the snout, in the loss of the premaxillary foramina, and in the presence of rostral supplementary bones.

Furthermore, a comparison of the sizes of the tusks in the holotypes of the two species seems to corroborate this hypothesis. The holotype of *O. peruvianus* is 46 cm long in the sagittal plane from the anterior edge of the palate to the occipital condyle, and that of *O. leptodon* is 41.5 cm. In the holotype of *O. peruvianus*, the diameters of the large tusk at the alveolar border are 38 mm and 31 mm. In the holotype of *O. leptodon*, which is slightly smaller, these diameters are 50 mm and 36 mm. If the length of the tusk relative to the diameters is the same in the two species, and considering that the total length of the long tusk of the holotype of *O. leptodon* is 135 cm, then the long tusk of the holotype of *O. peruvianus* should have been 102 cm long (based on the larger diameter). If a correction is made because of the smaller size of the holotype of *O. leptodon*, then the long tusk of *O. peruvianus* for a skull of the size of that of the holotype of *O. leptodon* would be 92 cm long. In other words, the long tusk of *O. peruvianus* was proportionally *c*. 30% shorter than in *O. leptodon*. A similar comparison can be made on the diameter of the small tusk. In the holotype of *O. peruvianus* the diameters of the small tusk at base are 24 mm and 30 mm, while in *O. leptodon* they are 18 mm and 22 mm. The estimated total length of the small tusk (partly reconstructed) of the holotype of *O. leptodon* is 25 cm. Therefore an estimate (based on the larger diameters) of the small tusk of the holotype of *O. peruvianus* would approach 34 cm. If a correction is made relative to the length of the skull, then the length of the small tusk of *O. peruvianus* should approach 31 cm (for a skull of the size of the holotype of *O. leptodon*). The small tusk of *O. peruvianus* was therefore approximately 24% longer than that of *O. leptodon*. Furthermore, these comparisons indicate that the small tusk was approximately 18% the size of the long tusk in *O. leptodon* and approximately 33% in *O. peruvianus*. Therefore, assuming that the plesiomorphic condition was represented by smaller tusks subequal in size, then *O. peruvianus* is clearly more plesiomorphic than *O. leptodon* for these character states. If the approximations made above are correct, then an ancestor–descendant relationship between the two species is consistent with these characters.

In other respects, however, the earlier species appears to be more derived than the younger. de Muizon *et al*. (2002) have regarded the absence of fossae for the premaxillary sacs on the premaxillae anterior to the nares and the inferred lack (or extreme reduction) of the melon as derived conditions in *O. peruvianus* since such structures are present in all the other delphinoids. In *O. leptodon*, anterior to the nares, the premaxillae present distinct shallow oval fossae which are very probably homologous to the fossae for premaxillary sacs in the other odontocetes.

Since the presence of premaxillary sacs is closely related to the presence of a melon (Mead, 1975), it is probable that *O. leptodon* had a melon. This hypothesis is reinforced by the fact that the dorsal surface of the snout (between the nares and the apex) is much wider and larger in *O. leptodon* than in *O. peruvianus* in which there is just no space for a melon. Therefore, *O. leptodon*, which probably still retained a melon and premaxillary sacs, is more primitive than *O. peruvianus*, which had no melon or premaxillary sacs or only vestigial ones.

Furthermore, the deeply notched anterodorsal border of the orbit is a very specialized feature allowing good dorsal binocular vision, which probably compensated for the lack of echolocation ability (a consequence of the probable absence of a melon). In *O. leptodon*, the anterodorsal border of the orbit is slightly concave and is regarded as less derived than in *O. peruvianus*. Therefore, because of the probable presence of a melon and premaxillary sacs and because of the morphology of the anterodorsal edge of the orbit, *O. leptodon* is more primitive than *O. peruvianus* for this character. An ancestor–descendant relationship seems ruled out and the two species must be viewed as sister taxa.

FUNCTIONAL ANATOMY

VISION VS. ECHOLOCATION

The feeding strategies of *Odobenocetops peruvianus* and their anatomical bases have been discussed in detail by de Muizon *et al*. (2002). Like the walrus (*Odobenus rosmarus*), *O. peruvianus* probably fed upon benthic invertebrates such as thin-shelled bivalves or crustaceans. The living walrus does not crush the shells, and *O. peruvianus*, which had no cheek teeth, was certainly incapable of crushing or chewing. As in the walrus, the deep palate and the tongue of *O. peruvianus* acted as a piston to suck out the siphon and foot of bivalves. It is likely that the inferred strong upper lip of *O. peruvianus* firmly held the shell, which was ejected after the soft parts had been ingested, as is observed in the walrus (Fay, 1982; Kastelein & Mosterd, 1989; Kastelein & Wiepkema, 1989).

In *Odobenocetops leptodon* the basic pattern of the skull is similar to that of *O. peruvianus* and the morphology of the snout and palate leads us to hypothesize an almost identical feeding adaptation. However, since the palate of the former is longer, wider, and deeper, it is likely that it had greater suction power than the latter.

However, the morphology of the dorsal face of the snout of *O. leptodon* is clearly different from that of *O. peruvianus*. As described above, it is much wider and

larger, and presents small depressions in the premaxillae anterior to the nares which are likely to have contained premaxillary sacs. As shown by Mead (1975), these diverticulae of the nasal air sac system of odontocetes are in histological continuity with the melon and are closely related functionally. It is therefore very probable that a small melon was present in *O. leptodon*. This interpretation contrasts with the probable condition of *O. peruvianus*, in which the melon was regarded as vestigial or absent (de Muizon *et al.*, 2002). Since the melon is likely to play a role in echolocation, it is probable that *O. leptodon* was capable of echolocating (though perhaps only to a limited degree) while *O. peruvianus* was not.

In *O. peruvianus*, the anterodorsal edge of the orbit was deeply notched, which allowed good anterodorsal binocular vision (de Muizon *et al.*, 2002). This condition probably compensated for the absence of echolocation abilities in *O. peruvianus*, since in feeding position as well as in swimming position (see de Muizon *et al.*, 1999 and below), the animal had anterior stereoscopic vision. Furthermore, given the size of the eye (which was approximately 20–30% larger than in the living delphinoids), it is likely that vision was also better in *Odobenocetops* than in the other delphinoids. It is noteworthy that the walrus also has anterodorsal binocular vision, and Fig. 29(D) in Kastelein *et al.* (1993), showing the overlapping of the visual fields of a walrus in feeding position, could very well apply to *Odobenocetops peruvianus*.

In *O. leptodon*, the anterodorsal edge of the orbit is only slightly concave and the visual fields probably had little or no overlap in feeding position. Therefore, the area of stereoscopic vision was minimal and probably precluded an efficient visual search for food on the bottom. However, the presence of a melon in *O. leptodon* indicates echolocation ability, which probably compensated for the lack (or reduction) of anterodorsal binocular vision in the search for food. Therefore, in *O. leptodon* the strategy of localization in the environment was probably more similar to that of the classical delphinoids than was that of *O. peruvianus*, in which the probable loss of the echolocation ability is regarded here as a reversal and therefore an autapomorphy of this species. In this respect *O. peruvianus* is more derived than the later *O. leptodon*.

POSITION AND MOBILITY OF THE HEAD

The length of the large (right) tusk of the holotype of *Odobenocetops leptodon* is a major novelty in our knowledge of the odobenocetopsid family. Judging from the condition of the tusk observed in this species we hypothesize here that the large tusk of *O. peruvianus* was much longer than initially suggested (de Muizon, 1993a; de Muizon *et al.*, 2002) and probably

similar in length to that of *O. leptodon*. The length of the tusk of *O. leptodon* raises the problem of its position when the animal was swimming. As reconstructed for *O. peruvianus* (de Muizon, 1993b; de Muizon *et al.*, 2002), the large tusk was regarded as being no longer than 50–60 cm (including the alveolar portion). Moreover, de Muizon *et al.* (2002) presented a reconstruction of the animal in a walrus-like position of the head, with the tusk directed ventrally to posteroventrally. Given its length and relatively small diameter, however, the large tusk of *O. leptodon* was probably relatively fragile (in the holotype its distal part was broken off during life), and it is unlikely that the animal swam with the tusk at an angle greater than 20° to the axis of the body.

In seeking to determine the position of the tusks in swimming and feeding, as well as the dorsoventral amplitude of movements of the head, several planes, axes, and angles need to be considered (see Fig. 16)

1 The dorsal plane of the skull, which intersects the tip of the snout and the vertex, is perpendicular to the sagittal plane. The vertex is not preserved in the three new specimens but an estimation can be obtained by comparison with the holotype of *O. peruvianus*.

2 The plane of the palate, which intersects the anterior apex of the vomer on the palate and the posteroventral tip of the vomerian crest which separates the choanae.

3 The orientation plane of the condyles, which is perpendicular to the sagittal plane of the skull and which intersects the anterodorsal and anteroventral borders of the articular surface of one condyle.

4 The anterior articular plane of the atlas, which is perpendicular to the sagittal plane and intersects the anterodorsal and anteroventral borders of the anterior articular surfaces of the atlas.

5 The posterior articular plane of the atlas, which is perpendicular to the sagittal plane and intersects the posterodorsal and posteroventral borders of the posterior articular surfaces of the atlas.

6 The (long) axis of the body, which is approximated by a perpendicular to the posterior articular plane of the atlas. Although this approximation does not have to be exact, it provides a good reference, especially in discussing the orientation of the long tusk.

7 The axis of the long tusk.

8 The angle between the projection of the axis of the tusk onto the sagittal plane and the dorsal plane of the skull (*c.* 60° in *Odobenocetops leptodon*).

9 The angle between the orientation plane of the condyles and the dorsal plane of the skull (*c.* 56° in *Odobenocetops peruvianus*).

10 The angle between the anterior and posterior articular planes of the atlas (*c.* 20° in *Odobenocetops leptodon*).
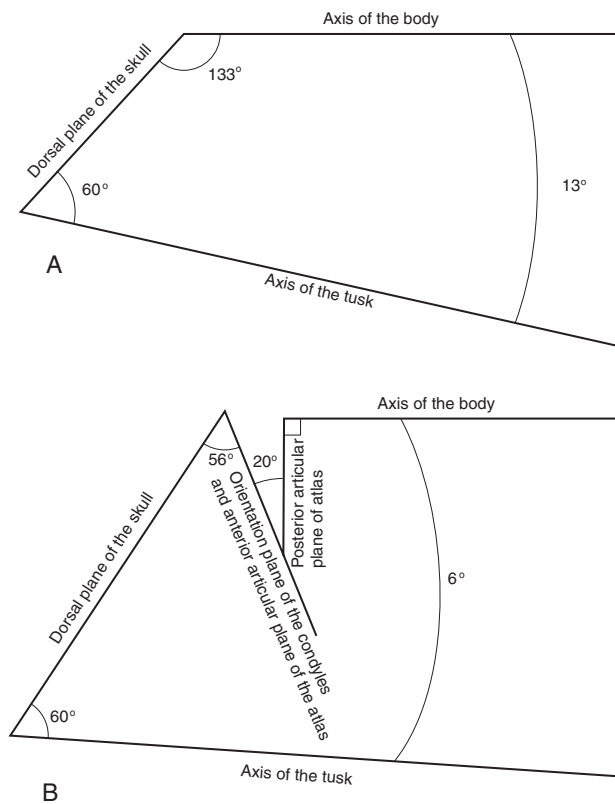
Figure 16. Estimation of the relative positions of various planes of the skull, atlas, and vertebral column of *Odobenocetops* in order to evaluate the position of the long right tusk relative to the axis of the body.

Since these referentials are sometimes difficult to measure and must often be estimated because of the incompleteness of the specimens, it is clear that all the angles and positions determined below are merely approximate. However, we believe that they provide a reasonable quantitative approach to some aspects of the biology of *Odobenocetops*.

The atlas of the holotype of *O. leptodon* allows an informative approximation regarding the orientation of the head. The articulations of the atlas have been compared to the occipital condyles of both skulls of *Odobenocetops* in which these articulations are preserved (SMNK 2491 and 2492). It should be kept in mind, however, that one of these two skulls (SMNK 2491) is referred to *O. peruvianus* while the other (SMNK 2492) is the holotype of *O. leptodon*. In SMNK 2491 (*O. peruvianus*) the occipital condyles are much better preserved than in the other skull (*O. leptodon*), and this is why the atlas of *O. leptodon* was first compared to this specimen. In comparing the atlas of *O. leptodon* to the occipital condyles of *O. peruvianus* it is assumed that this part of the skull and this vertebra do not differ substantially in the two species, although this cannot be demonstrated.

When the atlas is placed in the position of maximum congruence with the occipital condyles of SMNK 2491 (in other words, when the atlantooccipital joint is neither hyperextended nor flexed), the angle between the dorsal plane of the skull and the body axis (a perpendicular to the posterior articular plane of the atlas) is approximately 133°. In this position the large tusk, which is approximately at 60° to the dorsal plane of the skull, is grossly at 13° to the axis of the body (Fig. 16A). Therefore, given this anatomy it was easy for *Odobenocetops* to slightly flex the head when necessary in order to reduce the ventral divergence of the long tusk from the body. Hence, it is likely that in a swimming position the large tusk did not strongly diverge from the axis of the body in the sagittal plane, and could have been brought approximately parallel to the axis of the body without much effort, with the dorsal plane of the skull facing anterodorsally. The same comparison has been made with the holotype of *O. leptodon*. Although the only preserved condyle is relatively damaged, it seems that the position of the head could have been similar to that observed with the skull of *O. peruvianus*.

The orientation of the occipital condyle is also quite informative and allows an estimate of the orientation of the tusk relative to the axis of the body. The occipital condyles of *Odobenocetops peruvianus* are clearly tilted anteroventrally when compared to those of a classical delphinoid. In other words, the ventral sides of the condyles are more anterior relative to the dorsal sides than in the other odontocetes. This observation cannot be substantiated quantitatively, since the planes of reference in *Odobenocetops* are fundamentally different from those in the other delphinoids because of the drastic modifications of its skull. The angle between the dorsal plane of the skull and the orientation plane of the condyles is 56° in *O. peruvianus* (Fig. 16B). From this angle (which opens ventrally) must be subtracted the angle between the anterior and posterior articular planes of the atlas (*c.* 20°), which compensates for the first angle since it opens dorsally. Since the posterior articular surface of the atlas is estimated as perpendicular to the axis of the body (the orientation plane of the condyles is assumed to be parallel to the anterior articular plane of the atlas), then the angle between the dorsal plane of the skull and the axis of the body is 56 − 20 + 90 = 126°. Therefore, since the angle between the tusk and the dorsal plane of the skull is *c.* 60°, the angle between the tusk and the axis of the body is 186°. This approach results in a divergence of the tusk of *Odobenocetops* from the axis of the body of 6°, so the tusks lay almost parallel to the body (Fig. 16B).

The difference between these two estimates of the position of the tusk in swimming (13° vs. 6°; Figs 16A,B) could be due to the difficulty of estimating the

position of maximum congruence of the atlas (i.e. intermediate between the maximum extension and maximum flexion).

The weight of the long tusk probably required strong neck musculature, which is reflected in the very strong insertions of these muscles on the basioccipital.

As noted above, the skull of *Odobenocetops* is made of relatively dense bone and is massive in relation to the rest of the body. When feeding, the weight of the skull and tusks was certainly acting to pull the head of the animal towards the bottom while the body (which had greater buoyancy) was in an oblique position, as hypothesized by de Muizon (1993a; b) and de Muizon *et al.* (2002). In this position, the long tusk, which was dragged along the bottom, was diverging vertically from the axis of the body. Therefore, the head was in partial hyperextension, as is observed in the walrus (Figs 17 and 18). This feeding position differs from that often seen in sirenians (e.g. dugongs making feeding trails) which can more easily swim parallel to the bottom (Nishiwaki & Marsh, 1985) since the pachyosteosclerosis of their postcranial skeleton makes their body heavier than those of the walrus and *Odobenocetops*.

The condyles of *Odobenocetops* are extremely salient and the amplitude of the movements of the head approached 83°. This estimate was obtained by comparing the angles between the dorsal plane of the skull and the posterior articular plane of the atlas, the vertebra being in a totally hyperextended (*c.* 90°) or flexed (*c.* 7°) position of the head. In *Tursiops* this angle is *c.* 45°. In *Tursiops* the posterior articular plane of the atlas could not be used for measurements since the atlas is fused to the axis; however, it is likely that the posterior articular plane of the axis (which was used for measurement) has an orientation similar to that of the atlas. In *Delphinapterus*, this angle is *c.* 50° (average of three specimens). *Delphinapterus* is the living odontocete that has the greatest amplitude of movement of the atlantooccipital articulation. Therefore, the amplitude of the vertical movements of the head was much greater in *Odobenocetops* than in any other delphinoid.

Another quantification of the amplitude of the movements of the head can be obtained by comparing the convexity of the occipital condyles in the three genera. A dorsoventral section of the occipital condyle is presented in Figure 19 and includes the dorsal- and ventral-most extremities of the articular facet. This section is approximated to an arc of a circle. The convexity index (angle between the two radii drawn from the dorsal and ventral limits of the articular facet) quantifies the degree of convexity of the condyle. In *Delphinapterus* (the Recent odontocete with the most mobile head) the condyle has a convexity index of 117°, while it is 107° in *Tursiops*. This difference (9.3%) could be tentatively regarded as representing the difference in the amplitude of the movements of the head at the atlantooccipital joint in the two genera. In fact, actual measurements of the movements of the head in the two genera would perhaps show greater amplitudes, since the dorsal and ventral edges of the atlantal articular facets can probably extend slightly beyond the dorsal and ventral edges of the occipital articular facets, respectively. In *Odobenocetops* the angle between the two radii is 151°, which represents a difference from *Delphinapterus* of 29%; in other words, three times the difference between *Tursiops* and *Delphinapterus*. The difference between *Odobenocetops* and *Tursiops* is 41%. Therefore, the mobility of the atlantooccipital joint of *Odobenocetops* in the sagittal plane was at least 29% greater than that of a beluga. In *Odobenocetops*, the deep grooves which border the ventral and lateral edges of the occipital condyle are an indication that the ventral edge of the articular facet of the atlas could probably project beyond the ventral edge of the condyle. Similarly, the fossa present in the occipital above the condyle (observed in the holotype of *O. peruvianus*, de Muizon *et al.*, 2002) probably increased the amplitude of the extension of the head.

This significant mobility of the neck has also been argued by de Muizon *et al.* (2002) on the basis of the stoutness of the paroccipital processes and the thickness of the bones in the posteroventrolateral angle of the skull, which indicate very powerful musculature.
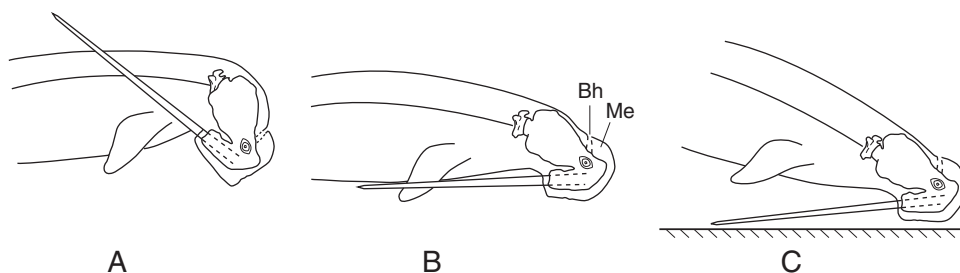

Figure 17. Positions of the head in *Odobenocetops leptodon*. Maximum flexion (occasional) (A); median position (swimming) (B); maximum extension (feeding) (C).

Figure 18. Reconstruction of *Odobenocetops leptodon* in its inferred environment (painting by Mary Parrish, Smithsonian Institution, Washington DC, USA).

The evidence for large neck muscles is now strengthened by the preservation on these new skulls of large insertion scars for massive scaleni. These observations on the atlantooccipital articulation further corroborate the earlier hypotheses suggesting that *Odobenocetops* had great mobility and strength of the neck related to its inferred feeding strategies.

As evidenced by the position and morphology of the occipital condyles and the occipital articular surfaces of the atlas of *O. leptodon*, the large tusk did not strongly diverge from the axis of the body when swimming. If there was some vertical divergence of the tusk, it was certainly no more than 10° and probably less. In feeding position (when the animal was rooting on the bottom), the tusk was at a greater angle to the axis of the body; this angle could have been close to 45° or more. In this position the atlantooccipital joint was in hyperextension. The tusks were dragged on or held parallel to the bottom. Given the potentially great amplitude of atlantooccipital movements, it is likely
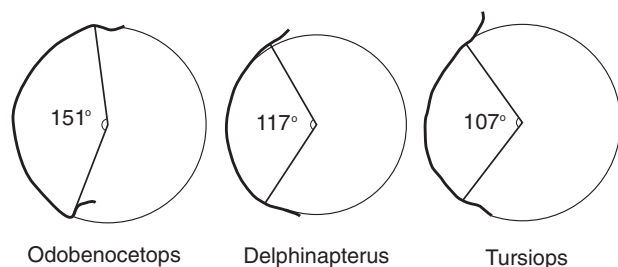
Figure 19. Approximate curvature radius of a vertical section of the occipital condyle in *Odobenocetops peruvianus*, *Tursiops truncatus* and *Delphinapterus leucas*.

that the head of *O. leptodon* could have been flexed to a greater extent than in any living cetacean. In this position the apex of the tusk was dorsal to its proximal extremity, and the tooth, which diverges laterally (*c*. 20°), was lateral to the flipper and the body.

The function of the tusk is even more unclear now that we know the tusks' full length. Because of its thinness it was certainly very fragile and it is hard to conceive that it could have played any kind of digging or fighting role. de Muizon *et al.* (2002) concluded that its major function was probably social, as is observed in the narwhal and walrus. In fact, even in the living narwhal the function of the tusk is not well established, but it is very probably at least partly social and the tusk could be used in nonviolent assessment of hierarchical display (Best, 1981) or in violent fights (Silverman & Dunbar, 1980; Gerson & Hickie, 1985). Whatever the role of the tusks is, it is likely that the length of the long tusk of the males played a major role in sexual selection and it is therefore probable that the increase in size of the tusk may have occurred rapidly in geological time.

The final point to be discussed is the function of the premaxillary (alveolar) sheaths. We previously concluded (de Muizon *et al.*, 2002) that these, as well as the analogously shaped tusks of walruses (Fay, 1981; 1982), served primarily as orientation guides and stabilisers (rather like sled runners) to keep the mouth and vibrissal array optimally positioned while searching for benthic prey. The new specimens described here do not necessitate a revision in our functional interpretation. The sheaths of the female *O. peruvianus* are very nearly symmetrical; the greater asymmetry seen in the male of both species may merely represent a compromise between selection for efficient use of the sheaths in feeding (which favoured symmetry) and selection for effective social use of the large male tusk (which favoured asymmetry). The lesser asymmetry of the sheaths of the male compared to the tusks themselves may constitute evidence of independent selection pressure on them. Because the sheaths

underlie and support the upper lip, they are selected for a feeding function and probably cannot become as asymmetric as the tusk without some loss or modification of this function. Certainly the asymmetry of the sheaths in the males is not so great as to prevent their use as orientation guides. In fact, the orientation guide hypothesis is strengthened by the finding that the anterior edge of each sheath consistently bears a row of foramina possibly corresponding to a row of vibrissae ideally positioned to sense contact with the substrate. Tactile organs arrayed in this particular manner would be a logical refinement of orientation guides such as we inferred the sheaths to be. They may even have rendered the tusk sheaths of *Odobenocetops* more efficient in this role than the tusks of *Odobenus*, possibly explaining why the sheaths need not approach walrus tusks more closely in length.

CONCLUSIONS

The cranial anatomy of the new specimens described herein confirms the hypothesis of feeding adaptation of *Odobenocetops peruvianus* proposed by de Muizon (1993a; b) and de Muizon *et al.* (1999; 2002). *O. leptodon* was a benthic suction feeder like *O. peruvianus*, and used its mouth cavity and tongue as a piston to extract the foot and siphon of molluscs. Given the depth and width of its strongly arched palate it is probable that it was a more efficient feeder than *O. peruvianus*. The elevation of the anterior face of the premaxillae indicates a huge upper lip, probably with an extensive array of tactile vibrissae. The upper lip of *Odobenocetops* could thus have been analogous, as a sensory organ, to the rostral disc of dugongs. This lip may also have played a role in gripping the molluscs or other thin-shelled benthic invertebrates on which the animal fed, although it is not likely that the lip was highly mobile or prehensile like the lips of sirenians.

The orientation strategies of *O. leptodon* were apparently different from those of *O. peruvianus*. Its field of binocular vision was probably smaller and the hypothesized presence of a small melon in the former (while it was probably absent or vestigial in the latter) is an indication of some retained echolocation ability, which could have compensated for the relatively poor (if any) binocular vision. Perhaps even more important for feeding in both species was the inferred vibrissal array, which was held in optimal position by the premaxillary sheaths sliding along the bottom like sled runners and serving as orientation guides for the mouth as well as the vibrissae. The tusks, in contrast, probably played no role in feeding but served only for social competition among the males.

The postcranial skeleton of *O. leptodon*, especially that of the flipper, shows the classical odontocete

pattern and confirms the close relationship of *Odobenocetops* to the Monodontidae.

One major unknown concerning *Odobenocetops* is the mandible. Although five skulls referable to this genus have been found (one skull of *O. leptodon* remains unprepared), none had the mandible associated.

Odobenocetops is the only mammal which displays obvious major external asymmetry, a condition which thus far remains unexplained. *Odobenocetops* has been found only in the Pisco Formation of Peru, and no transitional form between this aberrant cetacean and the classical odontocete pattern is hitherto known. Given the endemism of this genus and the stratigraphic proximity of the two species, it is surprising that no ancestor–descendant relationship could be established between *O. peruvianus* and *O. leptodon*. Instead, although several characters of *O. leptodon* appear to be more specialized than in the earlier species *O. peruvianus*, primitive characters of the former (the presence of a melon and the lack of a deeply notched anterodorsal edge of the orbit) appear to indicate a sister-group relationship between the two species.

Finally, we reiterate our belief (de Muizon *et al.*, 2002) that the orientation guide hypothesis as applied to *Odobenocetops* reopens the question of whether, in similar fashion, the tusks of walruses might have a hithero-undiscovered role in feeding. This explanation of the tusk-like premaxillary sheaths in *Odobenocetops* (as distinct from the tusks themselves) would seem to apply equally to the genuine tusks of walruses. Indeed, it seems inexplicable that these two very different marine mammals, convergent only in their specialization for benthic suction-feeding, should have such grossly similar tusk-like structures, unless these structures are somehow part of the benthic suction-feeding functional complex. We hope that students of walrus behaviour will soon put this hypothesis to the test.

ACKOWLEDGEMENTS

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