Odobenocetops peruvianus, the Walrus-Convergent Delphinoid (Mammalia: Cetacea) from the Early Pliocene of Peru

Christian de Muizon, Daryl P. Domning, and Darlene R. Ketten

ABSTRACT

Odobenocetops peruvianus Muizon, 1993 (early Pliocene, southern Peru), is a bizarre cetacean that is convergent in its skull, general aspect, and presumably feeding habits with the modern walrus *Odobenus rosmarus* (Linnaeus). Its cranial specializations are unique among cetaceans and include loss of the elongated rostrum, development of large premaxillary processes housing asymmetrical tusks, forward migration of the bony nares, reversal of the typical cetacean telescoping of the skull, dorsal binocular vision, large vaulted palate, and an inferred upper lip. The structure of the basicranium (possession of palatine expansions of the pterygoid sinus and presence of a large cranial hiatus) and face (possession of a medial portion of the maxillae at the anterior border of the nares) indicates that it belongs to the odontocete infraorder Delphinida and to the superfamily Delphinoidea. Within this group *Odobenocetops* is related to the Monodontidae because of the lateral lamina of its palatine flooring the optic groove, the anteroposterior elongation of the temporal fossa, and the thickness of the alisphenoid and squamosal in the region of the foramen ovale. We hypothesize that *Odobenocetops,* like the walrus, fed upon shallow-water benthic invertebrates and probably used its tongue and upper lip jointly in extracting the soft parts of bivalves or other invertebrates by suction. The highly modified morphology of the rostrum indicates that there was no melon as in all other odontocetes, and therefore that *Odobenocetops* was probably unable to echolocate; binocular vision could have compensated for this inability. The most probable function of the tusks themselves was social, as in the living walrus, but we suggest that the historically primary function of both the premaxillary processes of *Odobenoc-* *etops* and the tusks of *Odobenus* was as orientation guides in feeding. This reopens the question of whether the tusks of walruses play a role in feeding, as it seems that these also may be useful as orientation guides for the mouth and vibrissal array.

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Introduction

Abundant remains of fossil odontocete cetaceans have been found in the rocks of the Pisco Formation near the southern coast of Peru. Although the occurrence of cetacean bones in this area has been known for more than one hundred years (Lisson, 1890), the first odontocete described from this formation was *Incacetus brogii* Colbert, 1944. Subsequently, Hoffstetter (1968) was the first to show the importance of the faunal assemblage (fish, reptiles, birds, and mammals) of the locality of Sacaco, in the southern outcrops of the Pisco Formation, 540 km south of Lima. Further studies by Muizon (1981, 1983a, 1983b, 1983c, 1984, 1986, 1988), Pilleri (1989, 1990), and Cheneval (1992) have described part of the vertebrate fauna of the Pisco Formation, but abundant material still remains unstudied (work in progress includes that of C. de Muizon and G. McDonald on mammals, and J. Cheneval on birds). As established by Marocco and Muizon (1988), the Sacaco vertebrate fauna was deposited under shallow waters in a littoral and beach environment. The preservation of the fossils is exceptional, and associated skeletons are not rare; both characteristics indicate calm waters.

In 1990, the skull of an unexpected walrus-like cetacean (Muizon, 1993a) was found in the locality called "Sud-Sacaco" by Muizon (1981). In the Sacaco area, Muizon (1981, 1984, 1988a), Muizon and DeVries (1985), and Muizon and Bellon (1986) recognized five vertebrate horizons, which range from the late Miocene to the late Pliocene (approximately 9 Ma to 3 Ma). The specimen came from the Sud-Sacaco (SAS) horizon, earliest Pliocene, which has yielded an abundant vertebrate fauna (Muizon, 1981, 1984). Cetaceans are represented there

by balaenopterids, cetotheriids, pontoporiids (*Pliopontos littoralis*), ziphiids (*Ninoziphius platirostris*), and phocoenids (*Piscolithax longirostris*). The walrus-like cetacean, named *Odobenocetops peruvianus,* was briefly described by Muizon (1993a, 1993b), who concluded that its feeding adaptations were convergent with those of the walrus. Herein we describe that specimen more thoroughly and present a more detailed study of its features as a foundation for observations on the paleobiology of this unique cetacean. Its phylogenetic relationships with delphinoid odontocetes are confirmed.

INSTITUTIONAL ABBREVIATIONS.—The following abbreviations for institutions have been used:

MNHN	Muséum National d'Histoire Naturelle, Paris
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
USNM	Collections of the NMNH, which include those of the former United States National Museum

Systematic Paleontology

Superfamily DELPHINOIDEA

Family ODOBENOCETOPSIDAE Muizon (1993a)

TYPE GENUS.—*Odobenocetops* Muizon (1993a).
DIAGNOSIS.—As for the single known species, *O. peruvianus* Muizon (1993a).

Genus *Odobenocetops* Muizon (1993a)

TYPE SPECIES.—*Odobenocetops peruvianus* Muizon (1993).
DIAGNOSIS.—As for the species.

Odobenocetops peruvianus Muizon (1993a)

FIGURES 1–18, TABLE 1

TYPE SPECIMEN.—USNM 488252 (originally numbered USNM 460306), an incomplete skull lacking much of the left side and all of the auditory bones.

REFERRED SPECIMENS.—MNHN SAS 1613, a left periotic and partial tympanic; and MNHN SAS 1614, a left periotic.

One other, recently discovered specimen (MNHN SAO 202) is relevant to this study but is not described herein in detail; it will be described in a separate report (Muizon and Domning, 2002). It is a badly weathered partial skeleton with a partial skull, including the left tympanic, periotic and asymmetrical tusk; the distal half of a humerus; a complete radius; several dorsal and caudal vertebrae; and rib fragments. It was found in the SAO horizon of the Pisco Formation (ca. 3.5 Ma), which is younger than the SAS horizon (ca. 5 Ma), and is provisionally referred herein to *Odobenocetops* sp. (see "Addendum," below; Muizon et al., 1999).

ETYMOLOGY.—From *odon,* tooth, and *baino,* walk (Greek); and from *cetus* (Latin, from Greek *ketos*), whale, and *ops* (Greek, masculine), like: "the cetacean that seems to walk on its teeth," to refer to its feeding position (see below) and also to its similarity to the walrus (*Odobenus*). Species: *peruvianus,* from Peru.

DIAGNOSIS.—Delphinoid cetacean characterized by loss of elongate cetacean rostrum and concomitant probable absence of melon; development of large, ventrally directed premaxillary alveolar processes housing straight tusks; right tusk longer than 55 cm, cylindrical, with oval section, with long, open pulp cavity 23 cm deep; left tusk probably unerupted and probably no longer than 20 cm, with short conical pulp cavity 1.5 cm deep; important muscular insertion and numerous neurovascular foramina on anterior side of premaxillae and on anterior extremity of palate, suggesting presence of strong upper lip and possible vibrissae; regression in telescoping of skull by forward migration of nares and anterior withdrawal of maxillae and frontals; nasal on vertex of skull, contacting occipital and right maxilla, lying upon frontals but separated from mesethmoid, which followed bony nares in their forward migration; large temporal fossa open dorsally; large dorsal exposure of parietals and concomitant development of temporalis muscle origin; large orbits facing dorsally and not laterally as in other odontocetes; large pre- and postorbital processes expanded anterolaterally; maxillae articulating behind nares; large, deep, and vaulted palate; maxillae excluded from palate but forming part of lateral wall of skull; no maxillary teeth; no jugal; vomer very large and lanceolate; lateral lamina of palatine flooring the anteroposteriorly oriented optic gutter; pterygoid with flattened

subhorizontal hamular process and large rounded lateral crest for origin of pterygoid muscle; ventral surface of zygomatic process of squamosal forming large and deep anteroposteriorly elongated, trough-like glenoid fossa; large cranial hiatus; alisphenoid and squamosal strongly thickened on anterolateral region of cranial hiatus. Periotic with relatively small pars cochlearis and long and thickened anterior process with small bullar facet; ventral process with relatively flattened ventral rim and large ventral tuberosity; very large dorsal aperture of aqueductus vestibuli; periotic tympanic with clearly sigmoid-shaped involucrum.

GEOLOGICAL FORMATION AND AGE.—Pisco Formation, SAS (Sud-Sacaco) level as defined by Muizon (1981) and Muizon and DeVries (1985). As stated by these authors, the age of the Sud-Sacaco beds is early Pliocene, probably basal Pliocene, approximately 5 Ma.

TYPE LOCALITY.—Sud-Sacaco, southern coast of Peru, on the west side of the Panamerican Highway at km 542.

DESCRIPTION

GENERAL FEATURES.—The general morphology of the skull of *Odobenocetops peruvianus* is far from that of a typical cetacean. The hyperspecialization of this species (within the cetaceans) has resulted in the modification of the characteristic telescoping of the cetacean skull. The skull is bilobate in dorsal view, with a large braincase posteriorly and an anterior part made up of the narial, orbital, and rostral regions. These are separated by a well-marked constriction situated behind the supraorbital processes of the frontals. Such a condition is not observed in the other Neogene odontocetes, where the posterior expansions of the frontals and maxillae cover the braincase and the temporal fossa. In some primitive odontocetes (*Xenorophus, Archaeodelphis,* and *Agorophius*) and in archaeocetes, a similar condition can be observed because of the slight telescoping of the skull; in *Odobenocetops,* the condition described above is the result of a character reversal that considerably reduces the telescoping. Related to this reversal is the anterior position of the nares and of the orbits. The nares are very large compared with those in the Holocene Delphinoidea. They are anteroposteriorly elongate, and their length is more than double their width. The left naris is slightly larger than the right. The dorsal openings of the nares are horizontal (contrary to other Delphinoidea, where they are anterodorsally oriented), and they are not partially overhung in their anterior part by the maxillae and the premaxillae. In *Odobenocetops* the anterior walls of the narial passages face posterodorsally (posteroventrally in other delphinoids) and their contact with the dorsal surface of the premaxillae is a gently rounded surface, whereas it is a sharp crest in the other delphinoids. In lateral view, the dorsal profile of the skull is markedly concave; the nuchal crest and the rounded anterior part of the snout clearly overhang the much lower narial fossae and the posterior portion of the maxillae. Another obvious characteristic of *Odobenocetops* is the

reduction of the rostrum and the development of large premaxillary alveolar processes housing the tusks that give the skull a strong, although superficial, resemblance to that of the modern walrus. As preserved, the skull is large, with an anteroposterior length of approximately 46 cm (the posterior part of the only condyle preserved is missing) and an estimated bizygomatic width of $18 \times 2 = 36$ cm (Figure 1).

Premaxilla: The premaxillae are certainly the most amazing bones of the skull of *O. peruvianus.* Compared with other odontocetes, the elongate rostrum has disappeared, and the premaxillae show long ventral processes just anterior to the preorbital notch that form an angle of approximately 60° with the horizontal plane of the skull (Figures 2, 3). This condition defines a small dorsal horizontal portion of the premaxillae, situated between the anterior edge of the naris and the apex of the snout, and a large subvertical portion, the alveolar process, located almost entirely on the ventral part of the skull (i.e., below the supraorbital process of the frontal). The ventral extremity of the alveolar process is posterior to its dorsal extremity and below the postorbital process of the frontal. It is hollowed by large alveoli housing the tusks (see below). The right premaxilla is almost complete, but the left is broken and lacks most of the alveolar process.

On the dorsal side of the skull (Figures 1, 2), the premaxillae form the anterolateral edges of the nares; in that region, the bones have a conspicuous posterolateral process that runs along the anterior half of the lateral border of the nares on the left side, and along nine-tenths of its length on the right side. The anterior border of each naris is formed medially by a small medial portion of the maxilla and laterally by the premaxilla. Anterior to the nares the premaxillae become narrower, being narrowest just behind the fairly large premaxillary foramina. In that region they are thick and each bears a dorsolateral rounded keel that runs anteriorly from the posterolateral process, passes lateral to the premaxillary foramen (forming its lateral border), and converges with the other keel in the anteriormost region of the snout.

These keels mark the limits of an elongate triangle just anterior to the bony nares; in this area, in other odontocetes, are located the premaxillary sacs (posterior to the premaxillary foramina) and the origins of the nasal plug muscles (medial and anterior to the premaxillary foramina). The premaxillary sacs of the other Delphinoidea are generally situated upon the part of the premaxilla posterior to the premaxillary foramina and anterior and lateral to the nares; in *Odobenocetops* there was very little space for such air sacs and, if present, they must have been extremely reduced. The origin of the nasal plug muscle on the premaxillae of other delphinoids is generally a rugose lozenge-shaped or triangular area located medial and mostly anterior to the premaxillary foramina; in *Odobenocetops,* this part of the premaxilla is small, suggesting that the nasal plug muscle, if present, would have been fairly weak.

Demarcating the lateral edges of the triangular surface, and anterior to the premaxillary foramina, the rounded keels men-
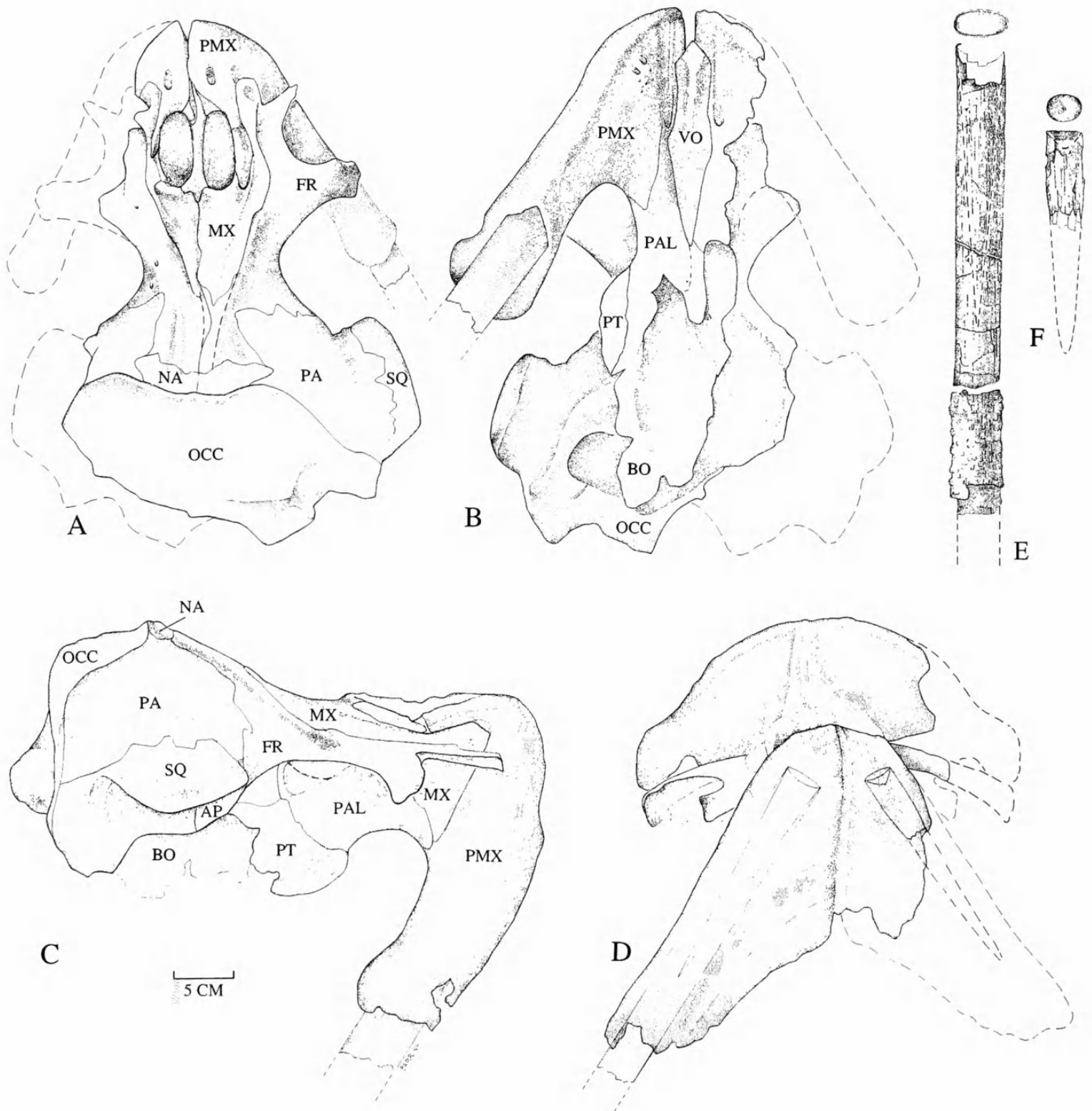
FIGURE 1.—*Odobenocetops peruvianus,* holotype (USNM 488252): skull in dorsal view (*a*), ventral view (*b*), lateral view (*c*), and anterior view (*d*); right premaxillary tusk (*e*) in lateral view (bottom) and proximal view (top); left premaxillary tusk (*f*) in lateral view (bottom) and proximal view (top).

tioned above are very thickened and most probably represent strong muscular attachments. These strong attachments are not in the position of the nasal plug muscle of other delphinoids, however, and consequently are not related to it. In fact, in the other delphinoids the two rounded keels of the premaxillae lat-eral to the origin of the nasal plug muscle receive fibers of the medial portion of the rostral muscle (Lawrence and Schevill, 1956; Mead, 1975). In *Odobenocetops,* they probably represent part of the rostral muscle modified for movements of a very strong upper lip (see below and "Discussion").
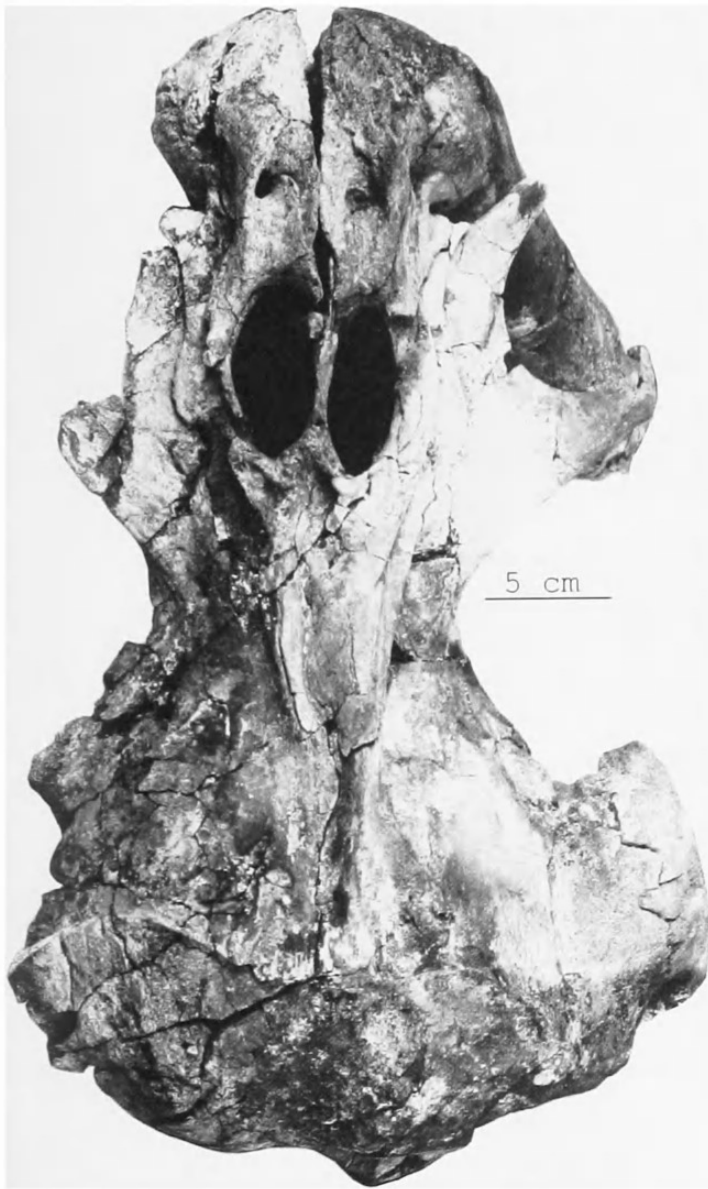
FIGURE 2.—*Odobenocetops peruvianus,* holotype (USNM 488252): dorsal view of the skull.

Anterior to the premaxillary foramina, the premaxillae are strongly expanded transversely; at the level of the preorbital process they are approximately twice as wide as at the level of the premaxillary foramina. On the dorsal portion, the right premaxilla is slightly wider and larger than the left, resulting in asymmetry of the skull. The two premaxillae are separated by a prominent premaxillary groove, which is partially filled in its posterior part by the mesethmoid. The anterior region of the snout is formed by the premaxillae only; it is very wide, massive, and rounded. In anterior view, the apex of the snout is a high and nearly vertical wall, fissured vertically by the premaxillary groove (Figures 4, 5). From that massive apex, two large alveolar processes are directed ventrolaterally and diverge at an angle of approximately 60°. In anterior view, the rounded apex of the snout shows an irregular and spongy surface that seems to indicate strong muscular attachments (Figure 4). The ante-

rior sides of the premaxillae show a very spongy structure and several large and small foramina (also seen on the anterior part of the palate), which indicate extensive vascularization and innervation.

The anterior edge of the alveolar process of the premaxilla presents a strong crest along its whole length (Figure 4). This crest is a long and irregular surface of bone, concave medially, 1–2 cm wide, which might have carried a long and narrow horny pad or, more likely, strong connective tissue for attachment of the upper lip. Several large vascular foramina are observable on the dorsomedial portion of this attachment area. Its morphology is very similar to what is observed on the dorsal side of the walrus mandible, between the first mandibular tooth and the apex of the symphysis. Fay (1982:167) mentioned that, in the walrus, "the incisive area is covered by an extraordinarily tough firm gingiva, unlike that on any other part of the mouth but closely resembling the skin on the palms and soles of the flippers." Furthermore, Howell (1927:21) mentioned the presence of a very hard horny tissue surrounding the lips of *Neophocaena phocaenoides,* and Kleinenberg et al. (1969:80) noted in the lips of *Delphinapterus leucas* a "many-layered keratinized epithelium" indicating that such structures are not uncommon in other delphinoids. Given the important modification of the superior edge of its mouth, however, it is likely that the keratinization was much more pronounced in *Odobenocetops* than in the other delphinoids.

The condition of the anterior face of the premaxilla suggests the presence of a well-developed upper lip, and given the vascularization of the bone, it is possible that it possessed strong vibrissae, as observed in the walrus. Hair is known to occur on the snouts of various fetal and newborn odontocetes (Yablokov and Klevezal, 1962; Tomilin, 1967; Brownell, 1989) and on the apex of the rostrum of the living Amazon dolphin *Inia geoffrensis* (Best and da Silva, 1989).

The rough and vascularized area mentioned above is restricted to the upper one-third of the alveolar process, except for the anterior crest, and may mark the limit of muscle origin and vibrissae.

In anterior view, the upper part of the mouth opening had a wide and elevated parabolic shape (Figure 5). In lateral view, the alveolar process of the right premaxilla is in sutural contact along the proximal one-half of its length with the maxilla, whereas its distal half is free. It is slightly concave posteriorly and widened at its apex; the posterior border of its free portion is rounded in cross section, differing therefore from the anterior crest, which received muscular and/or tendinous attachment of the upper lip. The lateral surface of the alveolar process is clearly convex and gently rounded, whereas its medial side is slightly convex at the apex and distinctly concave in its proximal portion, where it forms most of the anterior bony palate. The section of the alveolar process on its proximal two-thirds is teardrop-shaped, having a wide, convex, and rounded posterior edge and a thin, narrow, angular anterior edge. On the posterior side of the alveolar process, a small ridge runs from the poster-
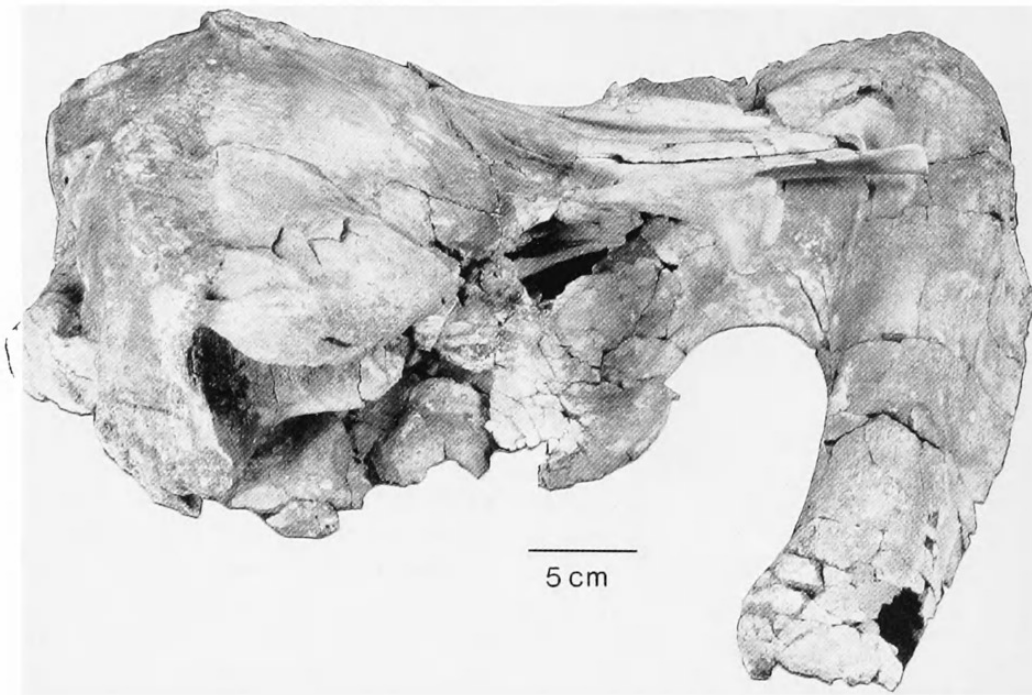
FIGURE 3.—*Odobenocetops peruvianus*, holotype (USNM 488252): lateral view of the skull.

omedial point of junction of the alveolar process with the palate (exactly at the anteroventral angle of the maxilla) to the posterolateral extremity of the process.

On the palate, the premaxilla is in contact with the vomer medially and with the palatine posteriorly. The maxilla does not participate in formation of the bony palate. Along its medial suture with the vomer, the premaxilla shows a deep, anteroposteriorly elongated fossa with a very large foramen (7–8 mm in diameter) posteriorly; this foramen, which opens in the palatine, is the anterior opening of a canal originating in the infraorbital canal and extending into the premaxillary fossa via a well-marked gutter. This greatly enlarged foramen corresponds to the palatine foramen that is commonly observed, but very reduced and sometimes nearly closed, in the other Delphinoidea (Figure 6). On the lateral edge of the premaxillary fossa and lateral to it, several other smaller (but still 2–4 mm in diameter) foramina perforate the premaxilla. There is little doubt that these particularly large foramina contained blood vessels for the abundant vascularization of the upper lip. The fossa is limited medially by the vomer, which forms its medial wall.

The significance of this fossa is not apparent, but in many other mammals, it is the location of a chemical sense organ (the vomeronasal organ). Chemoreception organs in living dolphins, however, are located on the tongue (Fried et al., 1990; Kuznetzov, 1990). Nothing definite can be said about the possibility of homology of the premaxillary fossae with the incisive foramina of terrestrial mammals (these foramina are absent in cetaceans), but the various pieces of evidence given below that *Odobenocetops* is a cetacean would favor the hypothesis that
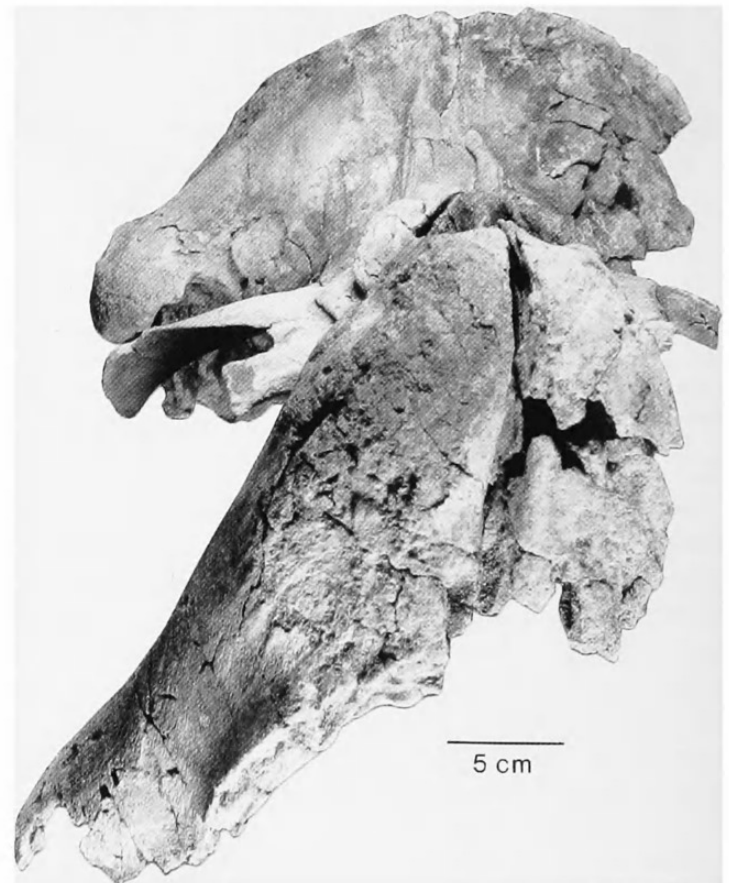

FIGURE 4.—*Odobenocetops peruvianus*, holotype (USNM 488252): anterior view of the skull approximately perpendicular to a horizontal swimming position.

FIGURE 5.—*Odobenocetops peruvianus*, holotype (USNM 488252): anterior view of the skull approximately parallel to the plane made by the alveolar processes (i.e., to the plane parallel to the bottom in a feeding position).

FIGURE 6.—*Odobenocetops peruvianus*, holotype (USNM 488252): ventral view of the skull.

these structures are not homologous.

The premaxilla extends onto the palate in a triangular posterior expansion that is in contact with the palatine; the contact between the two bones is flat and nearly horizontal, and the suture on the palate forms a large V-shape, opening anteriorly.

The alveolus of the right premaxilla is straight, transversely flattened (i.e., oval in section), and 30 cm deep; the left alveolus is not completely preserved, but it is clear that it had a much smaller diameter than the right.

Tusks: The right tusk (Figure 7) as preserved is not complete; however, a 39 cm long portion of it indicates that it was a straight cylindrical tooth with a transversely flattened section (at 10 cm from the base of the tusk, the two diameters are 38 mm and 30.5 mm). Its cross section is constant along the length of the whole fragment available, although it is possible that the section of the (badly crushed) anterior extremity of the fossil is slightly smaller than the intra-alveolar portion. The tusk is made of dentine only and does not show any enamel; its surface is regular and only shows fine and regular longitudinal striation. A 23 cm long pulp cavity indicates that the tooth had

continuous growth; at its base the tooth itself is only a thin layer of dentine surrounding the pulp cavity, whose diameter decreases toward the apex. A tentative reconstruction of the tooth shows that it could not have been shorter than 45 cm and possibly was no longer than 55 cm, 15–25 cm of the tusk thus being external to the alveolus.

The left tusk (Figure 8) is known from a small, 8 cm long fragment. It has a much smaller diameter than the right tusk (approximately 20% smaller); its section also is flattened transversely, and at its base the section is 30 mm long and 24 mm wide. Like the right tusk, it has no enamel and its surface shows very fine longitudinal striations. Unlike the right, its section is not constant and at its apex, as preserved, the diameters are 27 mm and 25 mm; in the middle part of the fragment the tooth is slightly inflated, and its diameters are 32 mm and 27 mm. Consequently, the tooth shows a slight but distinct taper-

b

2 cm

FIGURE 7 (left).—*Odobenocetops peruvianus*, holotype (USNM 488252), right tusk: *a*, lateral view; *b*, proximolateral view, showing the deep pulp cavity.

FIGURE 8 (right).—*Odobenocetops peruvianus*, holotype (USNM 488252), left tusk: *a*, lateral view; *b*, proximolateral view, showing the small pulp cavity.

a

b

2 cm
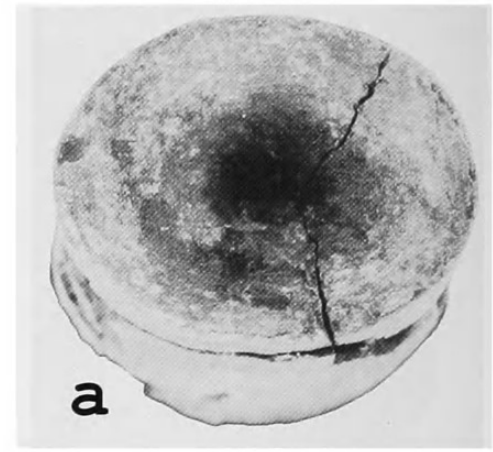
ing toward its apex. By projecting apically the edges of the fragment, it is possible to estimate the original length of the tusk to be between 15 cm and 20 cm. A wide-open but very short pulp cavity is present at the base of the tooth; it has a small conical opening, 15 mm deep, 30 mm long, and 24 mm wide at its base. This condition indicates that the tooth was still growing, although obviously much more slowly than the right tusk.

Evidence of continued growth does not prove that the tooth was erupted, as indicated by the presence of a deeper pulp cavity on an unerupted incisor of a 17-year-old female *Dugong dugon* (Marsh, 1980). The condition of the unerupted teeth of the narwhal, however, favors the hypothesis of an erupted tooth (Hay, 1980). In the newborn narwhal, the unerupted teeth (the right in the male and both in the female) have a long pulp cavity that occupies almost the entire length of the tooth; the cavity closes after deposition of approximately eight to nine dentine layers, which generally corresponds to an age younger than

sexual maturity. With the closure of the cavity, the root of the tooth develops a knot made of dentine and irregular cementum. Consequently, the narwhal's unerupted tusk stops growing before the animal has attained its full size and sexual maturity. In the skull of *Odobenocetops,* the pulp cavity is small but clearly

open, the knot at the root of the tooth is lacking, and the individual described herein is a relatively old adult, considering the state of fusion of its cranial bones. If the tusk was erupted, therefore, the premaxillae of *Odobenocetops* could have been strongly asymmetrical and the alveolar process of the left premaxilla should not have been longer than 18 cm, considering that a small portion of the tusk had to be external to the premaxilla; the alveolar process of the left premaxilla would therefore have been, at a minimum, almost 10 cm shorter than the right. Such asymmetry, which strongly modifies the external aspect of the head, is unknown in mammals, however; consequently we conclude that the left tusk of *Odobenocetops* was unerupted and that, as in the female dugong, it was still growing very slowly in the closed alveolus. The alveolar process of the left premaxilla could, therefore, have had a length similar to that of the right side (or only slightly smaller) and the ~20 cm long left tusk could still have grown for a long time in its 30 cm long alveolus.

Furthermore, it is noteworthy that the right tusk of *Odobenocetops* differs from all other tusks found among mammals in being straight and cylindrical.

Maxilla: The maxillae of *Odobenocetops peruvianus* are considerably reduced in comparison with those of other delphinoids; they do not cover the braincase posteriorly or the frontals laterally, and they do not participate in the construction of the bony palate. They form the posterolateral borders of the narial openings, and they are in contact behind the nares; between that region and the occipital crest they are reduced to a narrow strip of bone in the median area of the skull. The right maxilla is two to three times as wide as the left. They lie upon the frontals, and at their posterior ends they contact the nasals. On the specimen described herein, they are only preserved for two-thirds of the distance between the nares and the nasals, but their sutures with the frontals are clearly visible. Lateral to the nares, the maxilla forms a very narrow flange, no more than 2 cm wide, that is strongly withdrawn medially from the lateral edge of the frontal. Its lateral border is sigmoid and more or less follows the lateral profile of the frontal, being wider above the pre- and postorbital processes and narrower above the deep orbital notch. At the level of the preorbital process of the frontal, the maxilla shows a small lateral spine, which corresponds to the preorbital process of the maxilla in the other delphinoids, and which overhangs the jugolacrimal and is lateral to the antorbital notch. In *Odobenocetops* the jugolacrimal has disappeared. The maxillary rim, which forms the posterolateral border of the nares, continues posteriorly (4 cm behind the nares on the right side and 3 on the left side) and overhangs the flat lateral portion of the maxillae that overlaps the base of the supraorbital process of the frontal.

Three maxillary foramina are found on the right maxilla: (1) a small foramen at the level of the posterior edge of the nares, located between the maxilla and the frontal and opening posteriorly; (2) the anterodorsal opening of the infraorbital canal at the contact of the premaxilla and maxilla, which is preceded by a deep groove in the maxilla, communicating with the premaxillary foramen; and (3) a third small foramen anteromedial to the antorbital notch and distinctly pinched in the "folding" of the rostrum. On the left maxilla, the dorsal opening of the infraorbital canal is divided into four foramina, and through a broken portion of the lateral wall of the alveolus it is possible to see that one or two of these foramina gave passage to blood vessels for irrigation of the tusk pulp cavity.

The portion of the maxilla ventral to the supraorbital process of the frontal is a small triangle of bone bordered anteriorly by the premaxilla, posteriorly by the palatine, and dorsally by the frontal. A large posterior opening of the infraorbital canal is present in this ventral portion of the maxilla, just below the suture with the frontal. As mentioned above, the maxillae of *Odobenocetops* have been excluded from the palate and no maxillary teeth are present. The ventral portions of the maxillae are tightly fused to the premaxillae, thus indicating that the individual was not a young adult.

Mesethmoid: The mesethmoid is a large, relatively thick blade of bone separating the nares. In dorsal view its posterior extremity presents a Y-shaped relief that overhangs a lower portion, posterior to the nares and partially overlapped by the maxillae. This condition is unique among odontocetes and is related to important modifications of the skull, such as the long contact of the maxillae behind the nares, among others. The nares are large and anteroposteriorly elongated (almost three times longer than wide); the left naris is wider than the right and is located a little more anteriorly. The right naris is ~28 mm wide and ~62 mm long, and the left naris is ~31 mm wide and ~62 mm long.

On the dorsal face of the nasal passage, at the same level as the anteriormost point of the brain but slightly more lateral, is a group of small foramina that are directed posteromedially. Those foramina are most probably related to the small olfactory lobes of the brain (see below).

Frontal: The frontals have the typical cetacean trait of enlarged supraorbital processes, composed of the preorbital process and the postorbital process separated by a deep orbital notch. The preorbital process is an elongate, flat, and horizontal wing; its anterior extremity is square, and its lateral angle is distinctly twisted dorsally. It has a marked anterior orientation and runs along the posterolateral edge of the base of the alveolar process of the premaxilla. The antorbital notch is long (40 mm) and narrow (8 mm) and does not widen anteriorly as it does in most delphinoids. The postorbital process is large and much stouter than the preorbital process. It is a large triangular plate whose apex faces posterolaterally and not laterally as in other delphinoids. Like the preorbital process, it is markedly stretched anterolaterally. It is improbable that the masseter muscle, which arises partly from the postorbital process in the other odontocetes (Howell, 1927), originated on that process in *Odobenocetops* (see below for discussion). These two processes are separated by a deep and wide orbital notch that faces dorsally and not laterally as in other delphinoids, therefore in-

dicating very good dorsal binocular vision. The eyes were very large, probably the size of a tennis ball, and abutted the posterolateral side of the base of the alveolar process of the premaxilla.

In dorsal view, the posterior edge of the supraorbital process is almost straight and oblique, and it forms the anterior border of the temporal fossa. The supraorbital process does not cover the temporal fossa as it does (at least partially) in all Neogene and Holocene odontocetes. In those forms its posterior edge is anteroposteriorly oriented and not oblique as in *Odobenocetops*. As the supraorbital process is not (or only slightly) covered by the maxilla, it is widely exposed dorsally on the anterolateral region of the braincase. As a consequence of the reduction of the telescoping of the skull, the frontal of *Odobenocetops* does not cover the parietal posteriorly and does not participate in the formation of the roof of the temporal fossa as it does in all the other delphinoids. Consequently, this bone also is widely exposed on the posterolateral region of the braincase. The anterolateral portion of the suture with the parietal is transverse, but it shows two big indentations, which are clearly visible on the right side where it is completely preserved. Medially, each frontal is exposed, like the maxilla, in a long median strip that apparently joins the occipital posteriorly (sutures in the vertex are not easy to determine as the bones are badly encrusted with iron oxide). In that region, therefore, the classical relationships of the telescoped odontocete skull are preserved, as the maxillae overlap the frontals, which overlap the parietals.

On the right frontal, the narrow posterior portion is elevated medially and presents a strong keel that runs as far as the occipital; the strip formed by the right maxilla lies on the medial side of this frontal keel and reaches the nasals posteriorly. In fact, lateral to the maxilla-frontal suture there is a deep, elongate fossa located medial to the bottom of the temporal fossa and running from the posterior edge of the supraorbital process to approximately the middle of the braincase. This fossa is absent on the left side of the skull and could be interpreted as a pathological deformation. The keel mentioned above also could be a pathological structure related to the first one; in the middle region of the braincase, the right frontal appears to have been pinched transversely and thus elevated. It is possible that the animal suffered a minor skull trauma when young, the traces of which are still observable on the skull. Because of that deformation, the posterior median strip of the frontal clearly appears to be, in dorsal view, narrower than the left frontal at that level. In fact, however, if one "unfolds" the right frontal, both frontals have approximately the same width.

Another interpretation would be that the asymmetry of these structures is related to the asymmetry that characterizes the delphinoids. If this were the case, however, the asymmetry pattern observed in *Odobenocetops* would be unique among cetaceans. In delphinoids, the asymmetry is always manifested by larger size of the right maxilla and premaxilla and a displacement of the vertex to the left side of the skull. A possible interpretation

of that morphology would therefore be that the right elongated fossa and the crest serve as muscular attachments for part of the maxillonasolabialis. In odontocetes the pars nasalis of this muscle is the blowhole muscle, which arises from the maxilla and part of the frontal; the withdrawal of these bones from the roof of the braincase would have forced the fibers to concentrate in that fossa and on that crest. It would, however, be surprising if this phenomenon occurred only on the right side. Until new material is discovered, the first interpretation seems more reasonable. Consequently, it is likely that the maxillonasolabialis was relatively reduced in *Odobenocetops*. This muscle is related to the movements of the blowhole and of the nasal air sac complex, two structures related to ultrasonic sound production, so it is probable that *Odobenocetops* had a relatively reduced air sac system (already observed in the reduction of the premaxillary sacs) and consequently reduced ultrasonic sound production consistent with loss of echolocation. The posterior extremities of the frontals articulate with the nasals.

Ventrolaterally, the frontals contact the alisphenoid and the palatine posteriorly. In ventral view, the supraorbital process of the frontal is in a subhorizontal plane that meets the lateral wall of the palate at a right angle; along this angle, the frontals articulate successively with the orbitosphenoid (optic gutter), with the palatine, and anteriorly with the maxilla.

Nasal: The nasals are small plates of bone that have been pushed posteriorly; they articulate with the frontals anteriorly and with the occipital posteriorly. The nasals apparently lie upon the parietals, whereas in other odontocetes they always lie upon the frontals. The lateral half of the right nasal is preserved in situ, but its medial half, as well as the left nasal, have been lost during fossilization. The sutures, however, are clearly visible in numerous small anteroposteriorly directed grooves that mark the skull in that region. The nasals were more wide than long, and apparently the left nasal was larger than the right.

Parietal: The parietal forms most of the dorsal face of the braincase as a smooth bony plate that is covered only by the frontal medially. It contacts the squamosal by a very strong interdigitated suture, which differs from the squamous suture generally found in mammals. As seen below, this condition is probably related to the feeding adaptations of *Odobenocetops*. Ventrally, the parietal shows a small expansion in the anterior part of the glenoid cavity.

Palatine: The palatine forms an important part of the palate; it is located posterior to the premaxilla, medial to the pterygoid, and lateral to the vomer. As mentioned above, a very large palatine foramen opens anteriorly in a deep elongate fossa on the anteromedial border of the premaxilla. The palate is very large and deeply arched transversely, as well as longitudinally. Very wide anteriorly, at the level of the premaxillae, it narrows posteriorly at the level of the palatines and widens again at its posterior extremity at the level of the pterygoids. The anterior portion of the palatines is located in the narrowest part of the palate, and consequently the anterior part of the palatine (on the palate) is much narrower than the posterior. On

the lateral side of the skull, below the supraorbital process, the palatine forms a subvertical wall with a deeply concave ventral border. The suture with the maxilla is markedly concave posteroventrally. Above the lateral edge of the palate and just anterior to the suture with the pterygoid, the palatine presents an elongate fossa that also extends onto the pterygoid. That fossa is deeper on the palatine and gradually shallows and disappears on the pterygoid posteriorly. It follows the lateral edge of the palate and consequently is oriented anterodorsally–posteroventrally. Boenninghaus (1904), referring to *Phocoena,* and Fraser and Purves (1960), referring to *Delphinus,* mentioned that the origin of the internal pterygoid muscle was on the lateral edge of the maxilla, palatine, pterygoid, and (in the case of *Phocoena*) basioccipital. The elongated fossa observed on the lateral edge of the palatine, therefore, probably corresponds to a strong attachment of the internal pterygoid muscle, which also attaches on the pterygoid hamulus and on the medial lamina of the pterygoid (see below).

Although the palatine is partially broken in its dorsal portion, it clearly had an important contact with the frontal. Ventral to the optic gutter of the orbitosphenoid, the dorsal edge of the palatine shows a small curvature (concave dorsally), which we regard herein as the medial part of the lateral lamina that was covering the optic gutter and contacting the frontal dorsally. Posterodorsally, the palatine also contacts the anterior edge of the alisphenoid.

Pterygoid: The pterygoid is excavated by a relatively small pterygoid sinus and, therefore, is divided into lateral and medial laminae. On the palate, its suture with the palatine is an anteroposterior line observable at the posterolateral corner of the palate. The suture between the two bones on the palate is actually a horizontal plane, as the large backward expansion of the palatine covers the pterygoid posteriorly. Because of this morphology of the palatine, the pterygoids are laterally displaced and widely separated, and the palatine must have formed the major part of the posterior edge of the bony palate. Widely separated pterygoids are known in the Holocene Monodontidae and Phocoenidae and in some living Delphinidae.

The pterygoid hamulus is only partially excavated by the pterygoid sinus and possesses a large ventrolateral crest, probably for the insertion of the pars lateralis of the pterygoid muscle. The outline of the crest is strongly convex in ventral view, in contrast to the markedly concave lateral border of the palatine anteriorly. The anteriormost extremity of the palatine-pterygoid suture is on the lateral edge of the palate at the inflexion point of the curve.

Although the apex of the pterygoid hamulus is broken on the specimen, it is probable that only a small part is missing. The medial lamina of the pterygoid, posterior to the hamulus, is strongly thickened relative to other odontocetes. Its lateral edge shows a sort of semicylindrical crest, which delimits a semicircular cupule. Probably an extremely strong pterygoid muscle originated partly on this structure. On its medial side and ventral to this muscle attachment is an anteroposteriorly directed notch excavated in a very thickened and dense bony wall. This structure is in the location of the passage of the eustachian tube observed in the other odontocetes, although it is never as conspicuous in the latter. The pterygoid forms the dorsal wall of the choanae and partially overlaps the vomer medially, contrary to the condition in other odontocetes, where the vomer generally overlaps the medial border of the medial lamina of the pterygoid. The lateral lamina of the pterygoid contacts the palatine anteriorly and the alisphenoid posteriorly. It is large and smooth and participates in the formation of a continuous bony bridge between the palate and the frontal, a condition that strongly recalls that observed in the Monodontidae.

Vomer: The vomer is very large, and its participation in the palate is much more extensive than in any other odontocete. On the palate the vomer has the characteristic lanceolate shape observed in those odontocetes in which the vomer participates in the formation of the palate. It is long and occupies approximately two-thirds of the midline of the palate. Its maximum width is at the level of the anteriormost point of the palatine-premaxillary suture; its anterior half contacts the premaxilla, and its posterior half contacts the palatine. The posterior part of the bone, in the basicranial basin, is relatively narrow but much thicker than in the other delphinoids.

Orbitosphenoid: The orbitosphenoid has a long and wide optic canal, whose anterior opening is situated below the posterior edge of the supraorbital process and above the inflexion point of the sigmoid lateral border of the palate. It has an almost anteroposterior orientation and faces laterally, whereas in the other odontocetes it faces ventrally and forms an angle of approximately 45° with the anteroposterior axis of the skull. A large optic foramen opens in the optic canal just below the narrowest part of the temporal fossa; lateral to it, the large sphenorbital fissure (anterior lacerate foramen) is walled laterally by the lateral laminae of the palatine and pterygoid. The morphology of this region of the skull is related to the strong anterior displacement of the nares and the orbits, which have dragged the optic canal anteriorly (above the palatine-pterygoid suture); in most delphinids and phocoenids, the optic canal lies posterior to the lateral lamina of the pterygoid. It is noteworthy, however, that a condition intermediate between that of *Odobenocetops* and that of most of the other Delphinoidea is observed in *Delphinapterus,* in which the orbits are located fairly far anteriorly.

Alisphenoid: The alisphenoid is a very thick bone located just anterior to the large squamosal gutter. It contacts the frontal dorsally, the squamosal and parietal posteriorly, and the pterygoid ventrally. On its ventral edge can be observed the dorsal border of an enormous foramen ovale. This foramen was not closed and was confluent with the cranial hiatus of the auditory region, contrary to what is observed in the other delphinoids. Apart from this feature, the major characteristic of the alisphenoid is its thickness, which, among the delphinoids, also is found in the Monodontidae (Muizon, 1988b).

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Basioccipital: The basioccipital is almost totally broken away, and only the anterior portion of the right side is preserved. On its ventrolateral side, a small and shallow gutter very probably represents the passage for the internal carotid. The carotid foramen was, therefore, confluent with the foramen ovale and with the cranial hiatus. On the dorsal side of the basioccipital, the carotid gutter reaches the lateral edge of the sella turcica, as in the other delphinoids. The carotid gutter has a strong anteroposterior orientation, however, and the internal carotid entered the skull at a point well posterior to the sella turcica. In the other delphinoids the carotid foramen is located approximately at the same level as the sella turcica.

Squamosal: The squamosal is a relatively small bone whose entire morphology is conditioned by a wide, deep, and anteroposteriorly elongate gutter, which is formed mainly by the highly modified zygomatic process. The gutter is open anteriorly and posteriorly and is approximately cylindrical. It corresponds in other delphinoids to the depression observed between the lateral wall of the zygomatic process and the crest that joins the falcate process to the posteromedial origin of the fossa for the middle sinus. The lateral edge of the squamosal gutter of *Odobenocetops* is very thick, and its anterior extremity represents the greatly shortened zygomatic process. It is likely that the glenoid cavity did not occupy the whole volume of the gutter. A comparison with the position of the glenoid fossa in a beluga or narwhal shows that in *Odobenocetops* it probably occupied the posterolateral quarter of the squamosal gutter. The articulation of the condyle was therefore on the posterior half of the medial side of the lateral wall of the gutter. The posterior region of the gutter bears a posterodorsally extroverted saddle-like crest, which strongly suggests the presence, anterior to it, of a very mobile articulation. The prominence of this saddle-shaped crest also indicates the mature development of the articulation, in agreement with the extensive fusion of the bones of the skull, and indicates a relatively old animal. It is therefore likely that the condyle articulated only with the posterolateral extremity of the squamosal gutter.

The squamosal gutter (and consequently the glenoid fossa) is located in a much higher position than in the other delphinoids. It is well above the lateral wall of the cranial hiatus, and its bottom is approximately at the same level as the posterior edge of the postorbital process of the frontal. In the other delphinoids, the glenoid cavity is at the same level as the lateral wall of the cranial hiatus and well below the posterior edge of the postorbital process of the frontal.

The ventral edge of the medial wall of the gutter is rounded, very thick, and dense, and it forms the lateral edge of the enormous cranial hiatus; it is related anteriorly to the extremely thickened medial edge of the alisphenoid. Immediately behind the suture with the alisphenoid, on the thickened medial wall of the squamosal gutter, a small crest probably represents the very reduced falciform process of the squamosal. At the posterior extremity of the medial wall of the squamosal is the medial extremity of the middle sinus fossa; the sinus was probably fairly

well developed and may have extended onto most of the medial wall of the squamosal gutter. At the posteromedial corner of the bone, on the suture with the occipital, there is no articulation area for the periotic but rather some squamous and spongy bone for attachment of the ligament that, as in the other Delphinida, held the periotic in place.

Behind the saddle-shaped posterior extremity of the squamosal gutter, and squeezed between it and the exoccipital, the passage for the external auditory meatus is long but very reduced; it opens dorsolaterally in the ventral part of the very small sternomastoid fossa. The latter is reduced and occupies the posterodorsal corner of the zygomatic process (or of the lateral wall of the squamosal gutter). It is limited dorsally by a small crest, which is much more reduced than its homologue in other delphinoids. The lateral side of the zygomatic process is wide and elongated anteroposteriorly. In other delphinoids this surface gives rise to the masseter muscle; therefore, the condition observed in *Odobenocetops* suggests a strong masseter (for a cetacean).

On the lateral wall of the braincase, the suture of the squamosal with the parietal is very unusual. In most other mammals, and certainly in all the other odontocetes, the squamosal-parietal suture is mainly a subvertical plane facing laterally, and the part of the squamosal contacting the parietal is a squamous lamina, which gives its name to the bone. In *Odobenocetops,* the articulation is a rough zigzag line, and the joint surface faces dorsally. This articulation, together with the general stoutness of the squamosal, suggests that large muscular tensions were applied to the bone. In the posterolateral region of the squamosal, just anterior to the paroccipital process, the entire region of the external auditory meatus is tremendously thickened, further exemplifying the exceptional stoutness of this bone in *Odobenocetops peruvianus.*

Periotic: One isolated left periotic (MNHN SAS 1614) and one partial tympanic associated with another left periotic (MNHN SAS 1613) are referred to *Odobenocetops peruvianus* (Figures 9, 10). The taxonomic assignment of these isolated elements is clearly confirmed by the recent discovery of a partial skeleton of *Odobenocetops* sp. (MNHN SAO 202) that includes, associated in situ with the skull, a tympanic and periotic like those described herein. In the following description the tympanic side of the periotic will be called ventral; the cerebral side, dorsal; the cochlear promontory side, medial; and the side opposite to the cochlear side, lateral. The nomenclature of the external anatomy of odontocete periotics follows Fordyce (1994). Both periotics are morphologically as unusual as the skull and do not closely resemble those of any other cetacean. The periotic of *Odobenocetops* is a large and stout bone whose proportions are in agreement with the very large cranial hiatus of the skull. It has a large, long, and robust anterior process with a blunt rounded apex. On the ventral side of the anterior process, a large lateral tuberosity is located lateral to the mallear fossa. From the tuberosity, a wide and flat ventral rim extends anteriorly as far as the apex of the anterior process. It is
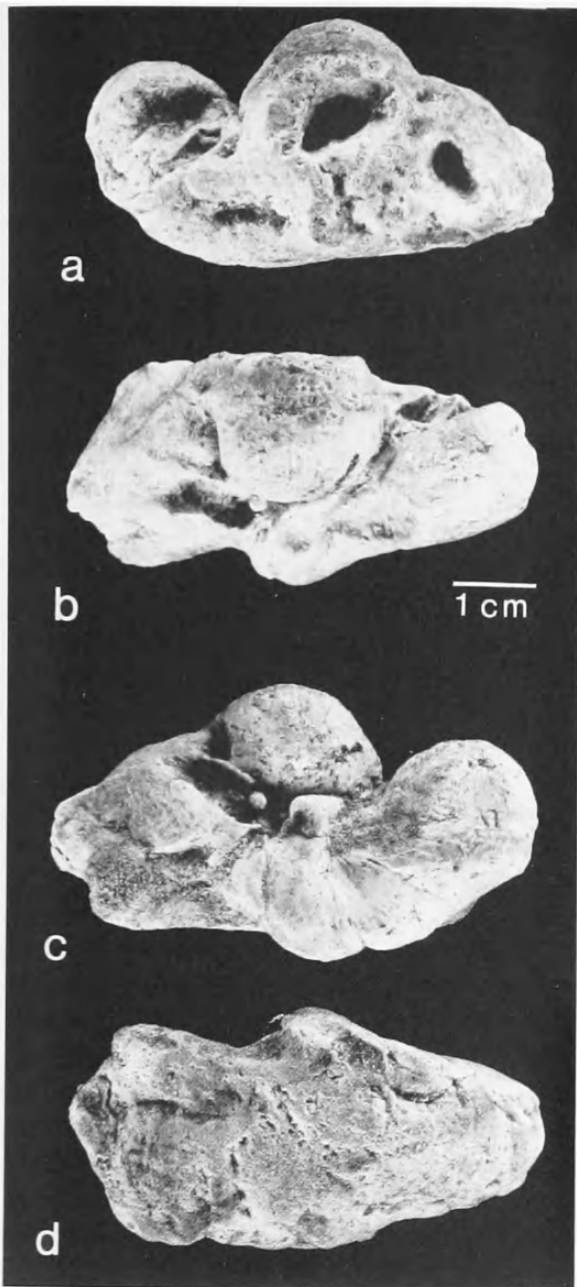
FIGURE 9.—*Odobenocetops peruvianus,* left periotic (referred specimen, MNHN 1613): *a,* dorsal view; *b,* medial view; *c,* ventral view; *d,* lateral view.

FIGURE 10.—*Odobenocetops peruvianus,* left periotic (referred specimen, MNHN 1614): *a,* dorsal view; *b,* medial view; *c,* ventral view; *d,* lateral view.

wider and flatter than in other delphinoids, especially in its anterior portion. This rim bears numerous fine parallel wrinkles, which are slightly concave anteriorly and oblique to the axis of the bone. This structure, although flattened, corresponds to the "bourrelet ventral" defined by Muizon (1988b), which is a synapomorphy of the Delphinida.

Three small fossae are observed on the ventral face of the anterior process, medial to the ventral rim. They are, from rear to front, the mallear fossa (or fossa capitis mallei), the epitubarian fossa, and the bullar facet. The mallear fossa receives the head of the malleus; it is oriented more ventrally than in the other Delphinoidea, especially the Monodontidae where the orienta-

tion is almost medial. The epitubarian fossa receives the processus tubarius of the tympanic, also called the accessory ossicle, unciform process, or uncinate process. When compared with that in other delphinoids, the epitubarian fossa is small relative to the size of the bone, but it is more concave. The third and most anterior fossa is the bullar facet, as defined by Fordyce (1994), and erroneously termed epitubarian fossa by Muizon (1987, 1988a, 1988b, 1988c, 1991). The bullar facet is a shallow fossa, slightly longer than it is wide, which occupies approximately the anterior one-third of the ventral face of the process.

The bullar facet is surprisingly well developed for a delphinoid; however, it is noteworthy that a small bullar facet also is

observed in some Kentriodontidae (Muizon, 1988b:172), such as *Liolithax*. The bullar facet is a common structure in several groups of odontocetes (Squalodontidae, Squalodelphidae, Platanistidae, Waipatiidae, Ziphiidae, Physeteridae, and Lipotidae). The loss of the bullar facet (=epitubarian fossa sensu Muizon, 1987, 1988a, 1988b, 1988c, 1991) has been considered a synapomorphy of the monophyletic clade Delphinoidea +Inioidea (Muizon, 1988b). This clade is defined by three other synapomorphies (Muizon, 1988b:165), so it is possible that loss of the bullar facet occurred several times in the evolution of the Delphinida. It also is possible that the presence of a bullar facet in *Odobenocetops* is related to the increase in length and thickness of the anterior process of the periotic, which is as highly specialized as the rest of the skull.

In dorsal view, the anterior process shows several slits, foramina, and fissures, as is often the case in the Monodontidae. The fossa incudis (or fossa crus breve incudis) is located just posterior to the mallear fossa and anterior to the anterior extremity of the tympanic articular facet of the posterior process. It is small and shallow, and it faces more anteroventrally than in other delphinoids.

Anterolateral to the fossa incudis is the ventral (or tympanic) opening of the facial canal, which transmits the facial nerve (VII). This foramen is small, approximating the size of that observed in *Delphinapterus*, although the periotic of *Odobenocetops* is almost twice the size of that of *Delphinapterus*. Between the mallear fossa, the fossa incudis, and the ventral opening of the facial canal is a small elongate fossa that faces posteriorly. Such a fossa is not present in all Delphinoidea; among the Holocene species, we have observed it in *Pseudorca*. In some periotics of an undescribed fossil delphinapterid and of a fossil kogiine (Luo and Marsh, 1996) from Lee Creek Mine (North Carolina), a very small pit is observed ventrolateral to the ventral opening of the facial canal.

The fossa for the stapedial muscle is large but shallow and faces almost ventrally. It differs in this respect from the condition in *Delphinapterus* and most other odontocetes, where the fossa faces laterally or ventrolaterally. The groove for the facial nerve is not well separated from the stapedial muscle fossa as is generally observed in other Delphinoidea. Posteromedial to the ventral opening of the facial canal is the fenestra ovalis. Contrary to what is observed in *Delphinapterus, Monodon,* and generally in the Delphinoidea, where the fenestra ovalis is oval-shaped, in *Odobenocetops* it is almost circular, and the stapes (preserved in MNHN SAS 1613) is a small conical bone, inflated at its ventral extremity for articulation with the incus (Figure 12). It is not flattened as in most other odontocetes.

Posteromedial to the fenestra ovalis is the fenestra rotunda, which is clearly reniform in MNHN SAS 1613. The posterolateral wall of the fenestra rotunda is thickened and shows a conspicuous elevation responsible for its oval shape. That morphology is not observed in the other Delphinoidea, but it is common in *Squalodon* and in the Eurhinodelphidae (Muizon, 1988c, 1991). In MNHN SAS 1614, the fenestra rotunda is wider than in MNHN SAS 1613, a condition that could be pathologic or related to erosion.

The pars cochlearis is extremely small considering the large size of the periotic. It is very low and somewhat recalls that of *Squalodon,* although it is not as compressed dorsoventrally in medial view, is not ventrally shifted, and has a rounded overall shape in ventral view. It differs strongly from the much higher profile (in dorsal or ventral view) pars cochlearis of other Delphinoidea and especially that of the Monodontidae. The posterior process is relatively slender and bears a narrow, anteroposteriorly elongate articular facet for the tympanic. Lateral to the tympanic facet is a conspicuous anteroposteriorly oriented crest that bordered the external auditory meatus dorsally.

On the dorsal face of the bone is the internal auditory window, composed of the tractus spiralis foraminosus (or fundus of the internal auditory meatus) (posteromedially), the foramen singulare, and the dorsal aperture of the facial canal for the facial nerve (anterolaterally). The window is large but relatively smaller than in the other Delphinoidea. It is approximately the size of that of *Delphinapterus,* although the periotic of *Odobenocetops* is twice as large. In particular, the tractus spiralis foraminosus is smaller than that of most large delphinoids. The window in *Odobenocetops,* however, differs from that of the other delphinoids in being much deeper, probably because of the thicker (in medial view) pars cochlearis. The same can be said concerning the aperture for the endolymphatic duct (dorsal opening of the vestibular aqueduct), which is a large conical pit posterolateral to the window. It is larger than that of *Delphinapterus* but resembles it in being widely open. The aperture for the cochlear aqueduct is a small pit facing dorsally, anteromedial to the aperture for the endolymphatic duct. The dorsal face of the periotic has an irregular aspect and presents numerous exostoses made of dense bone; it does not show the smooth and regular morphology generally observed in the other Delphinoidea. In this respect, it resembles the periotics of Physeteridae. In lateral view, the periotic of *Odobenocetops* shows a very large and relatively flat surface.

CT Scans of the Periotics

METHODS.—The two periotics of *Odobenocetops peruvianus* were scanned with an ultra-high resolution protocol developed for analysis of fossil material. The technique provides fine-level differentiation of mineralization characteristics, which in turn provides good delineation of inner-ear structures in CT images. Simple surface reconstruction algorithms were used to obtain three-dimensional reconstructions of the periotic shell. Segmentation algorithms were used to visualize particular features, e.g., the cochlear canal, vestibular aqueduct, facial nerve, and auditory nerve. In live ears, these algorithms utilize the attenuation coefficients for cochlear fluids and neural tis-
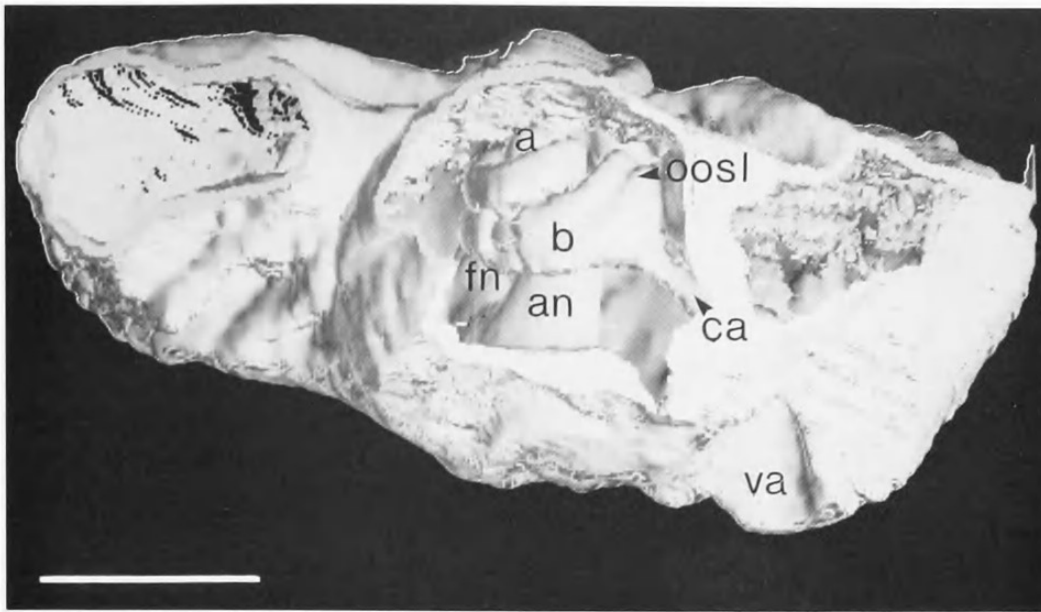
FIGURE 11.—*Odobenocetops peruvianus,* left periotic (referred specimen, MNHN SAS 1613): reconstruction of inner ear spaces from CT data. (Scale bar=1 cm; a=apex of cochlea; an=auditory nerve canal; b=basal turn; ca= cochlear aqueduct; fn=facial nerve canal; oosl=outer osseous spiral laminar ridge; va=vestibular aqueduct.)

sues to produce three-dimensional representations of inner-ear anatomy; in fossils, the differences in X-ray attenuations of sediments or mineralization of bone versus neural and inner ear areas are used for the reconstructions.

RESULTS.—*Inner Ear:* Both specimens are left periotics with well-preserved inner ears. Small differences in cochlear dimensions and turn number (Table 2) between these specimens are within the range of normal interindividual variability for modern odontocete inner ears (Ketten and Wartzok, 1990). The cochleae have approximately 2.5 turns with the three classic hallmarks of odontocete cochleae: a ventrolateral apical orientation, a substantial outer osseous lamina in the basal turn, and an exceptionally large cochlear aqueduct (Figure 11). The cochlear canal follows a conventional odontocete type II format (Ketten, 1984; Ketten and Wartzok, 1990), with closest morphometric affinities to *Delphinapterus leucas* and *Monodon monoceros.* The three-dimensional cochlear canal length for each specimen is approximately 44.4 mm, implying an animal length of 360–400 cm, assuming that the ratio of canal length to body mass follows the same allometry as extant odontocetes (Table 1). A substantial outer osseous lamina (as indicated by the laminar indentation in Figure 11) is present throughout the first 16 mm of the lower basal turn in both specimens and is a clear indication of some ultrasonic hearing in *Odobenocetops.* The outer lamina covers approximately 35% of the cochlear length, again consistent with a type II odontocete cochlear format. Cochleae of this type have maximum peak ultrasonic sensitivities below 80 kHz. In fact, the cochlear profile of these *Odobenocetops* cochleae is best approximated

by species at the lower end of the type II group of odontocete ears, which have a peak frequency of 35–50 kHz.

Although *Odobenocetops,* judging from its cochlear configuration, could (like most mammals) perceive frequencies above 20 kHz, it is important to note that having ultrasonic hearing abilities is not synonymous with echolocation. Echolocation per se requires not only perception but also synchronized production of ultrasonic signals coupled with the ability to analyze target features from the returning echoes.

A notable deviation from typical extant odontocete inner ear configuration is the presence of well-defined semicircular canals (Figure 12), a large, reniform vestibular aqueduct, and, judging from the diameter of the residual VIIIth nerve canal (Table 3), relatively large vestibular and facial nerve fiber counts (Figure 13). Extant Odontoceti have vestibular volumes that are substantially less than their cochlear canal volumes. In

TABLE 1.—Measurements (in cm) of holotype of *Odobenocetops peruvianus* (USNM 488252).

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Total length of skull from anteriormost extremity of premaxillae to posterior border of occipital condyle	45.7
Width of postorbital constriction	11.6
Width of orbit from apex of antorbital process to apex of postorbital process	10.5
Length of right premaxillary sheath from its apex to antero-dorsal hump of premaxilla	31.7
Depth of right alveolus	30.7
Bizygomatic width (estimated)	15.4×2=30.8
Anteroposterior length of braincase	18.3
Width of braincase (estimated)	10.2×2=20.4
Length of mandibular gutter	10.2
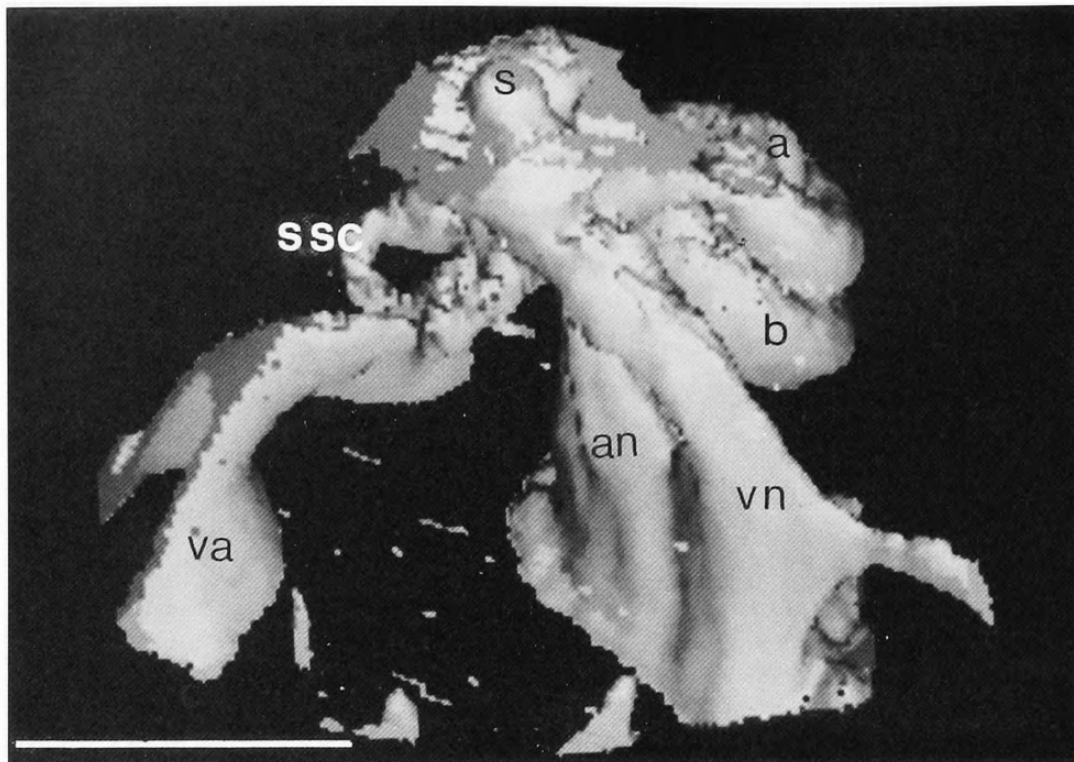
FIGURE 12.—*Odobenocetops peruvianus*, left periotic (referred specimen, MNHN SAS 1613): reconstruction of inner ear spaces from CT data. (Scale bar=1 cm; a=apex of cochlea; an=auditory nerve canal; b=basal turn; s= head of stapes; ssc=semicircular canal; va=vestibular aqueduct; vn=vestibular nerve bundle.)

many species, the semicircular canals are sufficiently small and thread-like that the complete canal system cannot be traced in periodic histologic sections, much less detected by high-resolution CT (Gray, 1951; Ketten, 1992). This contrasts sharply with the condition in land mammals, in which vestibular canal volumes rival cochlear volumes and are readily imaged by even conventional CT (Gray, 1951; Spoor, 1993). Although size is not a criterion for vestibular function, the majority of cetaceans appear to have uniquely small semicircular canals that are significantly shorter and narrower than their cochlear canals (Gray 1951; Jansen and Jansen, 1969). This anomalous vestibular de-

velopment is underscored by the fiber distributions of cetacean acoustovestibular nerves. Recent data show that the majority of odontocetes have 3%–5% of the total of VIIIth nerve fibers devoted to vestibular components, as compared with an average of 45% in land mammals—percentage ranges from about 20% in bats to about 60% in brachiating primates (Gao and Zhou, 1995).

The three readily imaged semicircular canals and the well-defined vestibule of *Odobenocetops* are similar in dimensions to those of the beluga (*Delphinapterus leucas*) (Figure 12). *Delphinapterus leucas* has the highest semicircular canal ratio of any extant odontocete studied. In all mammals, cochlear size is best correlated with body mass, but the exact correlates of the semicircular-canal size in most mammals remain unclear. For primates, a positive relationship to locomotory behavior appears relatively robust (Spoor, 1993). It has been suggested that fusion of the cervical vertebrae in Cetacea resulted in limited head movements and substantially fewer inputs to the vestibular system, leading to a loss of related receptors (Ketten, 1992). Better-developed semicircular canals in *D. leucas* are consistent with this species having a well-defined neck and greater rotational and lateral head movements (a full right angle) than other living odontocetes. The diameters of the auditory and vestibular canals in *Delphinapterus*, *Monodon*, and *Odobenocetops* are very close but not substantially different from those of other odontocetes. Cross-sectional areas of the canals for the vestibular component versus the auditory compo-

TABLE 2.—Cochlear morphometry of cetaceans. Measurement are in millimeters. (e=estimated.)

| Species	Turns	Scalae length	Basal diameter	Axial height	Body length
Delphinapterus leucas	1.75	41.99	10	4.21	325
Grampus griseus	2.5	40.5	8.73	5.35	228
Lagenorhynchus albirostris	2.5	34.9	8.74	5.28	207
Monodon monoceros	2.5	45.12	11.6	5.3	425
Phocoena phocoena	1.5	25.93	5.25	1.47	133
Physeter catodon	1.75	72.21	14.3	3.12	1361
Stenella attenuata	2.5	36.9	8.61	4.36	185
Tursiops truncatus	2.25	40.65	9.45	5.03	259
Odobenocetops peruvianus (MNHN SAS 1613)	2.5	44.37	10.1	4.31	380e
Odobenocetops peruvianus (MNHN SAS 1614)	2.25	44.41	10	4.5	380e
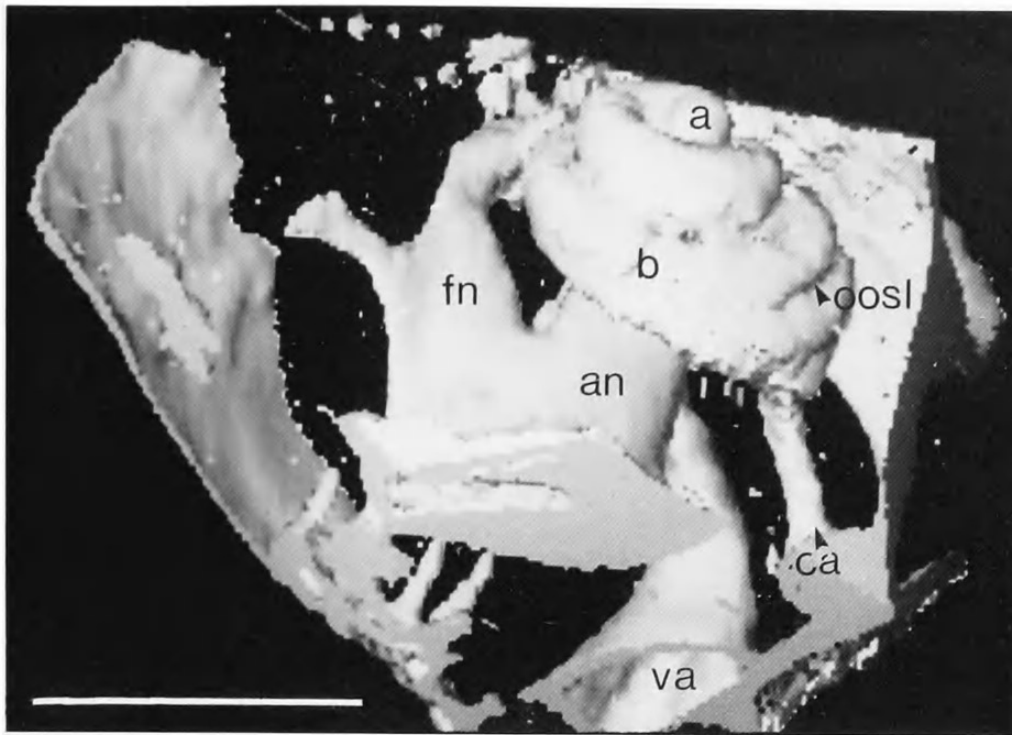
FIGURE 13.—*Odobenocetops peruvianus,* left periotic (referred specimen, MNHN SAS 1613): reconstruction of inner ear spaces from CT data. (Scale bar=1 cm; abbreviations as in Figure 11.)

nent of the VIIIth nerve are somewhat higher for both *Delphinapterus* (7%) and *Odobenocetops* (6%–9%) than for most delphinids. Assuming that the diameters of neural fibers occupying those cross sections were equivalent in extinct and extant species, we speculate that *Odobenocetops* had a vestibular-ganglion cell population between 4500 and 7000 neurons, with an average auditory ganglion population of approximately 75,000 to 80,000. There are, however, a great many caveats to this speculation, chief among them being that the available database is too small for explicit conclusions about exact neuronal levels. At this point, the most appropriate interpretation is that the exceptionally close morphometric resemblance between the *Delphinapterus* and *Odobenocetops* vestibular systems is striking and consistent with the idea that *Odobenoce-*

tops also may have had substantially greater head motions than most modern cetaceans. This motility could be related to the benthic feeding adaptations proposed herein.

The significance of an enlarged vestibular aqueduct and presumably equally large endolymphatic duct is unclear. Large reniform aqueducts are found in some baleen whales, e.g., *Balaena mysticetus*. No detailed comparative studies of the aqueduct across a variety of species are currently available for aquatic mammals, however.

Equally striking is the relative size of the facial nerve canal in *Odobenocetops* compared with that of most odontocetes. With the exception of *Monodon monoceros,* the facial nerve is typically less than 1.5 mm in diameter. The facial nerve of the specimen of *M. monoceros* examined for this study, an adult

TABLE 3.—Neural canal morphometry of cetaceans. Measurements are in millimeters.

| Species	Vestibular nerve diameter	Facial nerve diameter	Internal auditory canal diameter	Auditory nerve diameter
Delphinapterus leucas	1.20	1.47	5.6	4.4
Grampus griseus	–	–	4.7	3.7
Lagenorhynchus albirostris	–	–	4.6	3.6
Monodon monoceros	1.50	3.04	6.22	4.92
Phocoena phocoena	0.52	1.09	3.7	2.78
Physeter catodon	–	–	11.3	–
Stenella attenuata	–	–	4.9	–
Tursiops truncatus	1.00	1.41	5.6	4.5
Odobenocetops peruvianus (MNHN SAS 1613)	1.15	2.7	5	3.85
Odobenocetops peruvianus (MNHN SAS 1614)	1.00	2.5	5	4.0
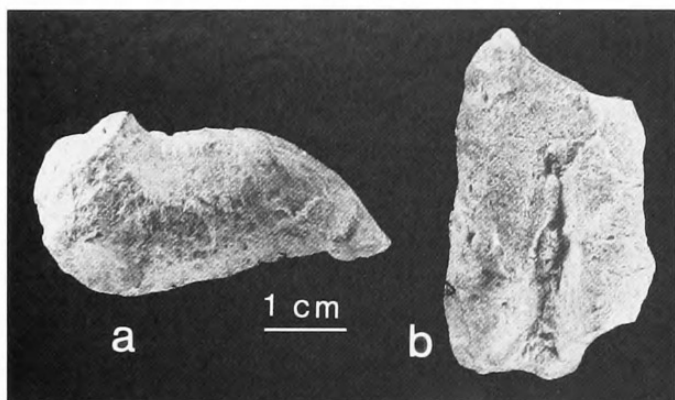
FIGURE 14.—*Odobenocetops peruvianus*, left tympanic (referred specimen, MNHN 1613): *a*, medial view; *b*, ventral view.

male, measured 3.1 mm, or approximately double the odontocete average. The *Odobenocetops* facial nerve canals averaged 2.6 mm at mid-periotic level. Once again, it is not possible to draw definitive neural conclusions from the anatomy of one or two animals; however, it is noteworthy that in each of these species the tusks coincide with an unusually large volume of facial nerves.

Middle Ear: Little can be said about the middle ear because of the lack of complete tympanics. One stapes remains in situ. It is monocrural with a large head and footplate, a configuration common among both Odontoceti and Sirenia. The distal facet has a surface area that is large in comparison with the

stapes footplate and is more ventrally directed in this specimen than in other odontocetes.

Tympanic: The tympanic is incomplete, as only the involucrum and a small portion of the ventral side are preserved (Figure 14). It shows, however, a typical feature of the Delphinida (Muizon, 1988b), namely the sigmoid morphology of the involucrum in medial view. This feature is very clear in the Lipotidae, Inioidea, and Delphinoidea. It is absent in the Platanistoidea (sensu Muizon 1987, 1991) and in the Physeterida. The involucrum is much more robust and stout in *Odobenocetops* than in any other Delphinoidea. It is not dorsoventrally flattened as in the Holocene Delphinoidea, even in the most robust forms such as *Orcinus*. In some Kentriodontidae, such as *Atocetus*, the involucrum is relatively robust but much smaller.

Occipital: The occipital is relatively lower than in other Delphinoidea but is very wide and convex (Figure 15). It has undergone some slight postmortem deformation, but this apparently had little effect on the overall shape of the bone. The portion of the bone lateral to the occipital condyle is much wider and lower than in the Delphinidae and Phocoenidae and is strongly expanded laterally. It somewhat resembles the condition in the Monodontidae, where the posterior crest of the temporal fossa (the lambdoid crest) is oblique and not vertical. In *Odobenocetops* the lambdoid crest is assimilated into the nuchal crest as a consequence of the strong modification of the temporal fossa. The paroccipital process, although partially broken, seems to have been very well developed, robust, and
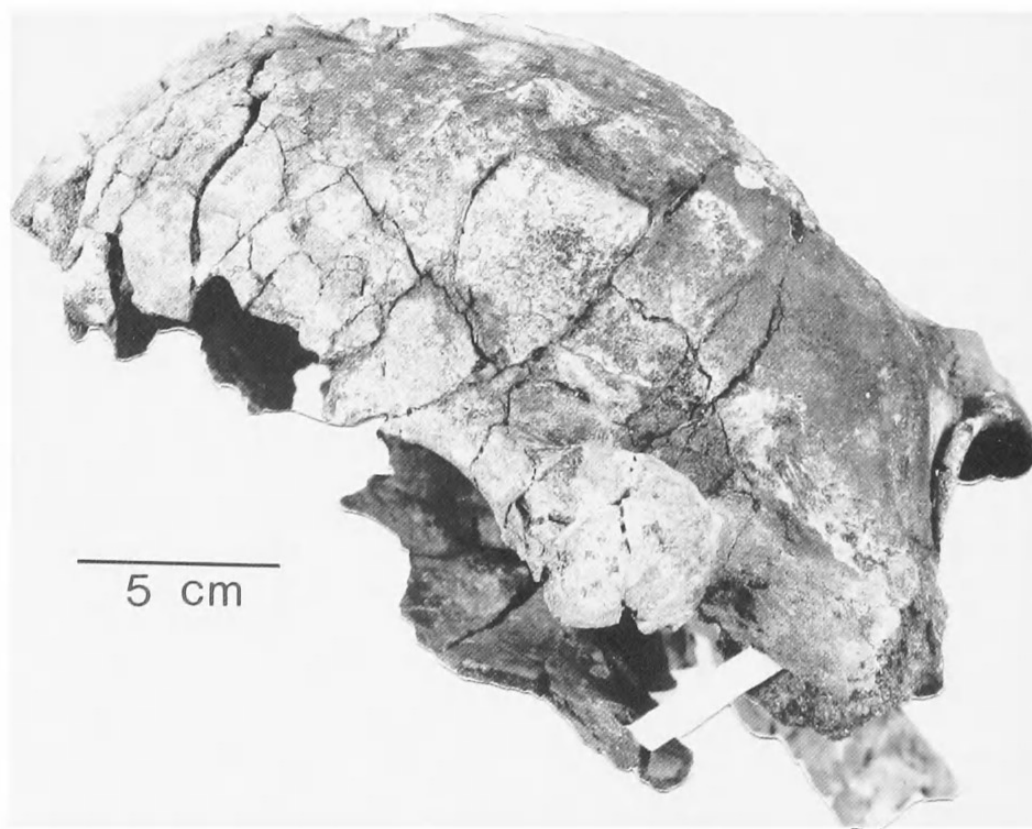

FIGURE 15.—*Odobenocetops peruvianus*, holotype (USNM 488252): occipital view of the skull.

markedly expanded laterally. Its anterior face very probably received a posterior sinus. It is thickened and fused to the posterior thickened region of the squamosal. The very stout morphology of this squamoso-paroccipital angle of the skull, as well as the robustness of the zygomatic process of the squamosal, seems to indicate very strong musculature inserted on this region of the skull: the scalenus ventralis and scalenus dorsalis, which insert on the anteroventral and posteroventral regions of the paroccipital process respectively, and possibly the costohumeralis and sternomastoideus, which insert in part on the posterolateral border of the process. In its dorsal region, the occipital crest does not seem to have been more prominent than in other delphinoids, and the muscle insertions are not as marked as in some Monodontidae (in some males of *Monodon*). The occipital shield is strongly convex, much more so than in other Delphinoidea. It differs from the somewhat flattened condition observed in the Monodontidae and is closer to the more convex condition of the Delphinidae and Phocoenidae.

The right condyle only is preserved, and that not totally. It is much more convex and salient than in any Holocene delphinoid and adjoins a very deep supracondylar fossa. These structures are much more developed than in *Delphinapterus*, which is well known for having a very well-defined and flexible neck for a cetacean. Consequently, the morphology of the occipital condyle of *Odobenocetops* obviously indicates that it was capable of very ample movements of its head, which was certainly much more mobile and flexible than in *Delphinapterus*.

Endocranial Cavity: The endocranial cavity is widely opened, as major parts of the posterolateral and ventrolateral regions of the left side of the skull are missing, allowing observation of the internal morphology of the braincase (Figure 16). Its major characteristic is the presence of ethmoidal fossae for a pair of small olfactory bulbs, separated by a small bony wall. The fossae are horizontal, slightly higher than they are wide, and approximately 4 mm wide, 6 mm high, and 8 mm deep. Such structures are very uncommon in the living odontocetes but have been mentioned in the Delphinidae (Sinclair, 1966) and Eoplatanistidae (sensu Pilleri and Ghir, 1981, 1982; Muizon, 1988c), and Muizon observed them in the Eurhinodelphidae, in the Platanistidae (cf. *Pomatodelphis* sp., USNM 214759), and in the Squalodontidae (*Squalodon tiedemani*). Kellogg (1926) observed, in the posterior wall of the bony nares of the platanistid *Zarhachis flagellator,* two crescentic foramina that represent the exits of the olfactory nerves. Furthermore, Oelschläger and Buhl (1985a, 1985b) noted, in early ontogenetic stages of *Phocoena phocoena,* an olfactory bulb that becomes reduced in later growth stages.

The groove for the optic chiasma is located just below the ethmoidal fossae, and the optic nerves exited the skull at the very front of the brain, as in the living Monodontidae but unlike the condition in the other odontocetes. The exits of the optic nerves are located more medially (much closer to the midsagittal plane of the skull) and the chiasmatic groove is much narrower than in the other delphinoids, however. In *Delphi-*

napterus the distance between the exits of the optic nerves is generally two to three times greater in absolute value than in *Odobenocetops*.

Posterolateral to the optic canal are the sphenorbital fissure and the foramen rotundum. They are large and the latter is superposed to the former. They are separated by a bony wall (partially broken) where they exit the skull. Among the Delphinoidea this morphology is present in *Monodon*. In the Delphinidae and Phocoenidae, the sphenorbital fissure and the foramen rotundum are most commonly confluent with the optic foramen. In *Delphinapterus* the optic foramen is isolated, but the sphenorbital fissure and foramen rotundum are confluent.

The sphenorbital fissure of *Odobenocetops* is much larger than in *Delphinapterus* and approaches the size observed in the much larger *Monodon,* although in that genus the foramen rotundum is smaller than in *Odobenocetops*. The sphenorbital fissure is the passage for the nerves and blood vessels that provide innervation and blood supply to the anterior part of the skull, including the oculomotor nerve (III), trochlear nerve (IV), ophthalmic branch of the trigeminal nerve (V1), abducens nerve (VI), anastomotic artery, and cavernous sinus. The foramen rotundum is the passage for the maxillary branch of the trigeminal nerve (V2). The large size of these apertures in the skull of *Odobenocetops* is certainly related to the major modifications of the rostrum (large mobile eyes, premaxillary tusks, and inferred large upper lip), which would have required extensive blood and nerve supplies. The very large sphenorbital fissure in the walrus and the narwhal is very probably related to the growth of the tusks (and to the large upper lip, in the case of the walrus).

The remainder of the internal view of the braincase shows mainly the cavities for the cerebral hemispheres, which appear to be proportionally shorter and wider than in the other Delphinoidea. Immediately dorsal to the lateral border of the foramen ovale, on the internal side of the braincase, is a longitudinal groove that seems to reach the foramen rotundum; it is absent from the other Delphinoidea, and its function is not clear.

COMPARISONS AND AFFINITIES

Comparing *Odobenocetops peruvianus* with other taxa is not easy, as most of the typical odontocete characters have been strongly modified. As already stated (Muizon, 1993a, 1993b), *Odobenocetops* is a delphinoid odontocete cetacean. Within the Delphinoidea, comparisons are not very productive because *Odobenocetops* differs from the other Delphinoidea in almost all the features observed. The exceptional morphology of the cetacean described herein, however, requires a statement of which characters allow a precise taxonomic definition of *Odobenocetops*. Five major features allow assignment of *Odobenocetops* to the Cetacea:

1. The presence of large air sinuses in the auditory region, connected to well-developed pterygoid sinuses. All cetaceans have a peribullary sinus, but pterygoid sinuses are not found in all members of the order. Although they are absent in *Pakicetus*
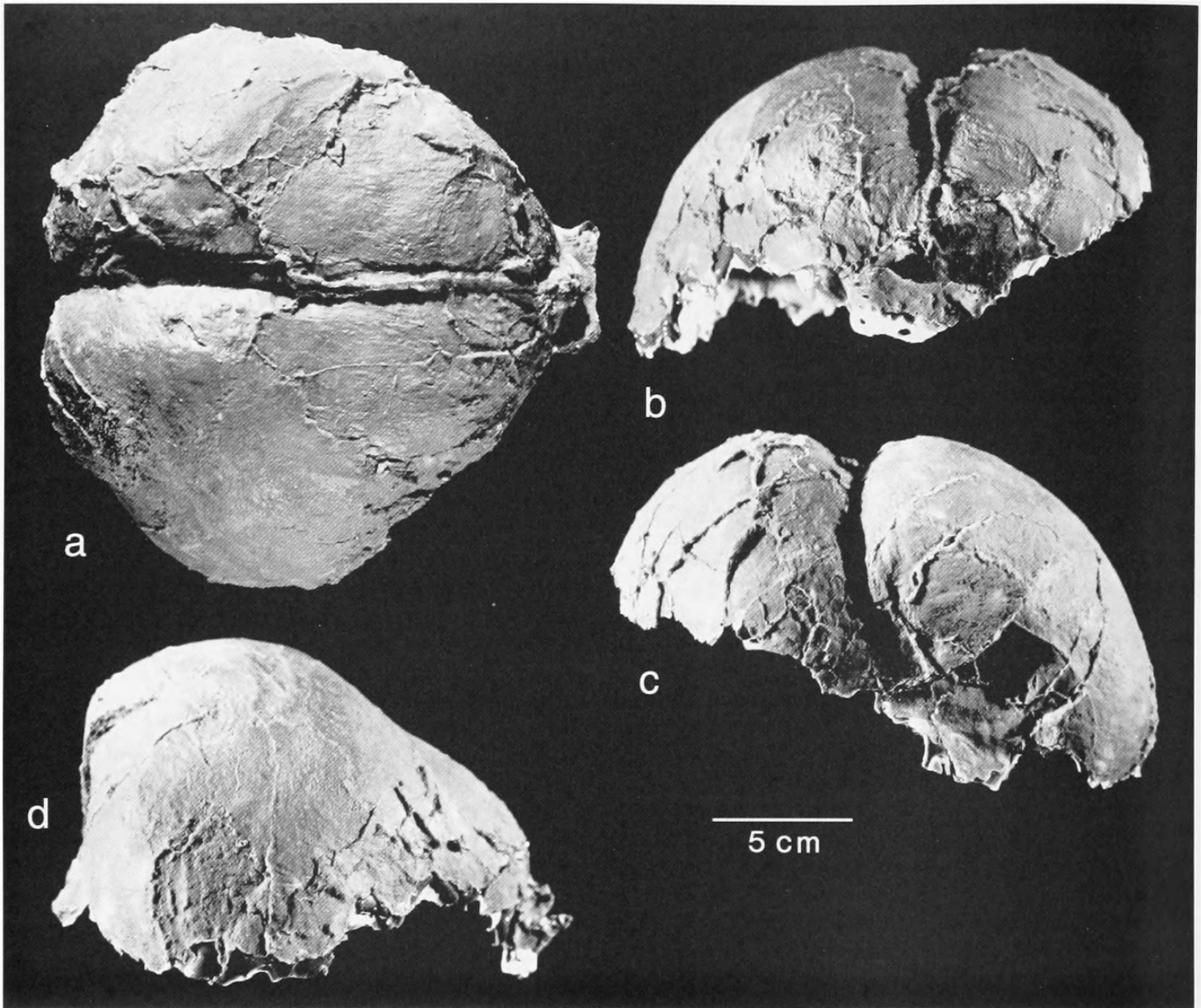
FIGURE 16.—Endocranial cast of the holotype of *Odobenocetops peruvianus* (USNM 488252): *a*, dorsal view; *b*, anterior view; *c*, posterior view; *d*, lateral view.

and in *Protocetus,* they are present in all other cetaceans. Air sinuses surrounding the auditory region and invading the pterygoid are not known in any other mammals. A pterygoid duplicated into two laminae also is found in the Erinaceidae, the Macroscelidae, and the Tupaiidae. In these families, however, the fossa is always opened anteriorly, unlike what is observed in all cetaceans, and there are no peribullary sinuses.

2. The large supraorbital process of the frontal, which widely overhangs the orbital region. This feature is present in all adequately known cetaceans; however, it has not been observed in *Pakicetus* because that part of the skull is unknown in this genus.

3. The narial fossae of *Odobenocetops,* which open dorsally and are not located at the apex of the skull. In the Sirenia the

condition of the bony nares is significantly different from that in the cetaceans; the nares open anteriorly in a wide narial basin that opens dorsally and is located in the anterodorsal region of the skull. In the proboscideans, the narial fossae are not located at the anterior end of the skull but they open anteriorly. A condition convergent with that of the cetaceans is found, however, in *Macrauchenia,* a Pleistocene South American litoptern. The cetacean condition is not found in any carnivores.

4. The absence of a true cribriform plate. This structure is located in the mesethmoid, at the anterior region of the cranial cavity, and gives passage to the olfactory nerves. The olfactory nerves have not totally disappeared in the cetaceans, however; small olfactory bulbs have been observed in several cetaceans, and *Odobenocetops* still retains small ethmoidal fossae (see

above). The loss of the cribriform plate is obviously related to the aquatic life habits of the cetaceans. A well-developed cribriform plate is present in all the aquatic carnivores, but it is reduced in the Sirenia.

5. An immobile elbow. Although archaeocetes do not have an immobile elbow, this feature is constant in mysticetes and odontocetes. The partial forelimb illustrated in Figure 17 was found associated with a partial skull of *Odobenocetops* (as mentioned above) and shows the characteristic immobility of the elbow seen in the modern cetacean forelimb.

Several other features allow us to classify *Odobenocetops* among the odontocetes, although the hyperspecialization of the skull partially hides the key character of the suborder. It has been noted elsewhere (Muizon, 1994) that the odontocetes are diagnosed by a posterior projection of the maxilla that covers the supraorbital process of the frontal totally or partially. In *Odobenocetops,* the maxillae have withdrawn medially and the supraorbital process is almost totally uncovered dorsally. Nonetheless, this key character of the odontocetes is still observable in *Odobenocetops*. The following features allow the assignment of *Odobenocetops* to the odontocetes.

1. Although strongly withdrawn, the maxillae still cover part of the medial part of the supraorbital processes medially, are expanded far backwards behind the nares, and are in contact with each other medially in that region. This condition is found neither in the Archaeoceti nor in the Mysticeti.

2. The fossa for the pterygoid sinus of *Odobenocetops* is greatly expanded dorsoventrally, and its dorsal limit is dorsal to the floor of the braincase. This condition is never found in any Archaeoceti or Mysticeti but is common in the odontocetes. In some very early taxa, such as agorophiids and *Waipatia,* the pterygoid fossa is not as developed as in the Holocene forms, but it is still clearly more developed than in the archaeocetes and mysticetes.

3. The premaxillary foramina are large. The premaxillary foramen of odontocetes is a supplementary passage for branches of the external carotid artery and for the maxillary division of the trigeminal nerve. This need for supplementary blood supply and innervation is related to the major specializations of the odontocete head, namely the melon and the air sac system. Enlarged premaxillary foramina are observed neither in the archaeocetes nor in the mysticetes.

4. The bones of the skull in the facial region are asymmetrical, especially the premaxillae and the maxillae; the right bone is always more developed than the left. Although this asymmetry is lacking or extremely reduced in several fossil groups (among others, Squalodontidae, Eurhinodelphidae, and Agorophiidae), this pattern of asymmetry is known among mammals only in the odontocetes. Furthermore, *Odobenocetops* presents a strong asymmetry of the tusks, as in the narwhal.

5. The narial passages are more vertical than those of archaeocetes and mysticetes. In *Odobenocetops,* because of the forward migration of the nares, this feature is not so well marked as in the other odontocetes. This is not a very satisfac-
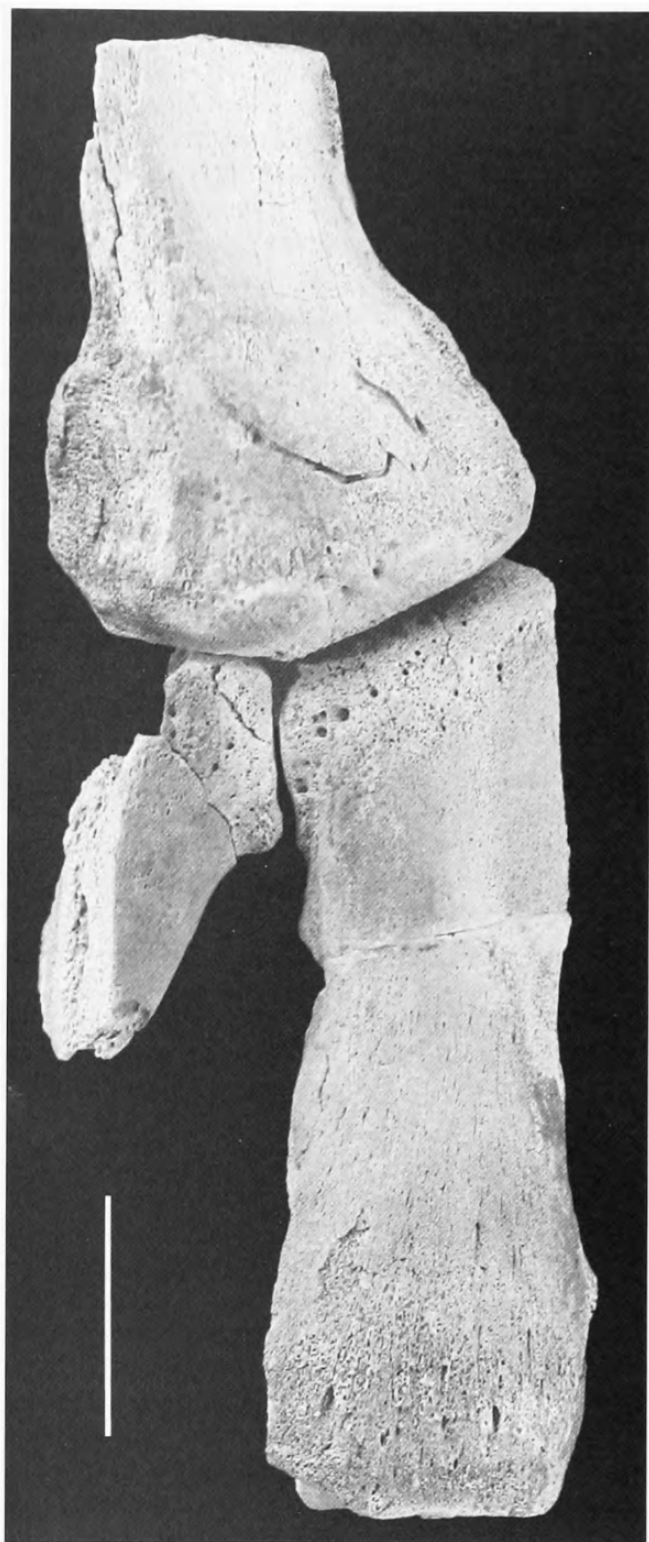
FIGURE 17.—*Odobenocetops* sp. (MNHN SAO 202): left forelimb, with partial humerus, partial ulna, and complete radius, in medial view. (Scale bar=3 cm.)

tory character, however; in the early-diverging odontocetes it also is little developed, because the telescoping of the skull has not yet proceeded very far.

As to the position of *Odobenocetops* within the odontocetes, some features allow its classification within the infraorder Delphinida (sensu Muizon, 1988c). The major synapomorphy of

the Delphinida is the protrusion of the pterygoid sinus within the palatine, which is thereby divided into a medial and a lateral lamina. Such a structure is present in all eight families of the group (Lipotidae, Iniidae, Pontoporiidae, Kentriodontidae, Albireonidae, Monodontidae, Phocoenidae, and Delphinidae). The Delphinida also share the presence of a cranial hiatus that greatly enlarges the posterior lacerate foramen, which in turn is coalescent with the median lacerate foramen; in the Delphinida the periotic hangs in the hiatus, because it is connected to the skull by ligaments only. As mentioned above, *Odobenocetops* has a very large cranial hiatus. Furthermore, if the tympanic described above actually belongs to *Odobenocetops*, the sigmoid morphology of its involucrum in medial view leaves little doubt that the walrus-like dolphin belongs to the Delphinida (see Muizon, 1988c:163, fig. 3). The sigmoid involucrum of the tympanic of the Delphinida contrasts with the olive shape observed in the Platanistoidea (sensu Muizon 1987, 1991) and with the indented involucrum of the Eurhinodelphoidea and Ziphiidae.

Odobenocetops peruvianus is a delphinoid because it bears a medial maxilla-premaxilla suture in the anterolateral edge of each narial fossa, which is formed by the maxilla. This character, which was analyzed by Muizon (1988c:199), is present in all the living Delphinoidea (with some individual variation), but it is not constant in the fossil groups, such as the Kentriodontidae. This feature is found only in the Delphinoidea, however, so its presence in *Odobenocetops* is evidence for its classification in that superfamily.

Among the Delphinoidea, *Odobenocetops* is related to the Monodontidae by three derived features that have been regarded as synapomorphies of the Monodontidae (Muizon, 1988b:191):

1. A lateral lamina of the palatine that passes below the optic gutter and joins the frontal laterally.

2. An alisphenoid and adjacent portions of the squamosal that are very thickened lateral to the foramen ovale and medial to the zygomatic process.

3. The presence of a very long and low temporal fossa (contrary to what Muizon (1988b:207) stated, it is clearly present in *Denebola* (Barnes, 1984, fig. 6)). This morphology corresponds to an anteroposterior elongation of the middle region of the skull. Related to this modification are the anterior stretching of the supraorbital process of the frontal, the less transverse orientation of the optic gutter than in the other delphinoids, and the position of the exits of the optic nerves at the most anterior region of the brain and not posteroventral to the apex of the brain as in the other delphinoids. In fact, the transformation in the Monodontidae seems to be the consequence of the anterior migration of the eyes. That original modification is present to an extreme degree in *Odobenocetops,* where the supraorbital process of the frontal is tremendously stretched anteriorly, the optic gutter is oriented almost anteroposteriorly, the exits of the optic nerves are located at the anterior extremity of the brain,

and the temporal fossa is greatly elongated anteroposteriorly. The morphology of *Odobenocetops* is obviously a much more derived stage of the condition observed in the Monodontidae.

The Monodontidae also were diagnosed by two additional features: the extension of the maxilla-premaxilla suture on the lateral side of the nares (in the other Delphinoidea, the suture always remains on the anterior edge of the nares) and the reduction of the lateral lamina of the hamular process of the pterygoid (all the other delphinoids have well-developed lateral laminae) (Muizon, pers. obs.). These characters are not observed in *Odobenocetops,* which is therefore less derived than the living Monodontidae for those features.

The Monodontidae are further characterized by widely separated pterygoid hamuli. This monodontid condition is greatly accentuated in *Odobenocetops,* where the pterygoids are very widely separated. This feature, however, also is known in some Delphinidae (generally as an individual variation) and in the Holocene Phocoenidae (it is absent in *Piscolithax,* a Tertiary phocoenid).

In addition to the above evidence, the discovery of a partial skeleton (including skull and forelimb) of *Odobenocetops* sp. (MNHN SAO 202) in a slightly younger level at Sacaco confirms both that *O. peruvianus* is a cetacean and that its affinities lie with the Monodontidae. The forelimb shows the typical cetacean modifications (immobility of the elbow), and its overall morphology recalls that of the Monodontidae (Muizon and Domning, 2002) (Figure 17). The monodontid affinities of *Odobenocetops* are clearly reinforced by the morphology of the inner ear, as shown above.

In view of the exceptional specializations of *Odobenocetops peruvianus,* it was referred (Muizon, 1993a) to a new family, the Odobenocetopsidae, regarded as the sister group of the Monodontidae. *Odobenocetops peruvianus* shows obvious autapomorphies, the most important of which are (1) loss of the typical cetacean rostrum and enormous thickening of the premaxillae at the anterior region of the skull, (2) development on the premaxillae of large, downturned alveolar processes housing one large erupted right tusk and a small, probably unerupted left tusk, (3) extreme anterior position of the enlarged nares and the dorsally facing orbit, (4) withdrawal of the frontal and maxilla from the posterodorsal angle of the skull, a condition that opens the temporal fossa dorsally, (5) reduction of the maxillae, which are excluded from the bony palate and only form part of the lateral wall of the skull, (6) extensive modification of the zygomatic process of the squamosal into the thick lateral wall of a large, anteroposteriorly elongated squamosal gutter, part of which houses the glenoid cavity and the middle sinus, (7) great reduction or absence of the premaxillary sacs, and (8) a strongly thickened posteroventral region of the squamosal and a very solid, interdigitated parietal-squamosal suture.

The occurrence of tusks in *Odobenocetops* is a convergence with *Monodon;* in the latter genus the large tusk of the male is

implanted in the left maxilla, whereas in *Odobenocetops* the large tusk is implanted in the right premaxilla. Consequently, the tusk of *Monodon* and that of *Odobenocetops* are not homologous.

Enlarged apical teeth or tusks are known in some other cetaceans. Enlargement of apical teeth is common in squalodonts, where the anteriormost tooth of the premaxilla and of the dentary are enlarged and protrude anteriorly, being almost horizontal (Dal Piaz, 1916; Kellogg, 1923). A similar condition is found in *Kentriodon pernix* from the middle Miocene of the Calvert Formation of Maryland. These teeth, in squalodonts and *Kentriodon,* do not show asymmetry. *Kharthlidelphis diceros* from the Oligocene of Georgian Republic (Mchedlidze and Pilleri, 1988) also possesses one pair of enlarged apical upper teeth that protrude anteriorly and horizontally. In this case the left tooth has a diameter approximately twice that of the right one, and the teeth are implanted in the maxillae. This condition is basically similar to that of the narwhal, but the size difference between the teeth is much less and the right tusk is erupted. *Kharthlidelphis* is therefore very different from *Odobenocetops,* where the tusks are implanted in the premaxillae and the right tusk is much larger than the left one. Furthermore, the downturned tusks of *Odobenocetops* are unique among cetaceans.

Functional Anatomy

When compared with the other delphinoids, *Odobenocetops* shows drastic modifications of the skull that have been mentioned in the description above. These can be classified in three groups: (1) those related to the nasal sacs, basicranial sinuses, and auditory region, and consequently to sound production and reception; (2) those related to feeding; and (3) the tusks. In the following sections we analyze each of these groups of specializations.

NASAL SACS, BASICRANIAL SINUSES, AND AUDITORY REGION

Several authors have stated that the nasal sacs are at least partially implicated in sound production (Lawrence and Schevill, 1956; Lilly, 1961; Lilly and Miller, 1961; Evans and Prescott, 1962; Norris, 1964, 1968, 1969; Norris and Evans, 1967). Mead (1975) critically reviewed the literature on the relations between the nasal diverticula and sound production and reached the conclusion that "the structures more likely to be involved in sound production are those in the vicinity of the nasal plugs." Mead (1975) also stated that the premaxillary sacs could be used as sources for air during phonation.

The role of the basicranial air sinus has been debated. Fraser and Purves (1960) stated that their function is the phonic isolation of the periotic from bone-conducted sounds. The sound waves transmitted by bone conduction are reflected on the in-

terfaces between bone and soft tissues (which behave like liquid in sound transmission) and the foamy filling of the air sinus (which behaves like air in sound transmission). The sound waves are therefore forced to enter the cochlea through the external auditory meatus, thus providing good directional hearing. McCormick et al. (1970) rejected this idea, however, stating that the acoustic vibrations reach the ear through the tissues of the head, and Norris (1964, 1968, 1969) and Brill et al. (1988) proposed that the echolocation sounds may return to the body "by the way of the intramandibular fat body which acts as a passive wave guide and enter the middle ear via the tympanic bulla which transmits sounds directly to the ossicular chain and cochlea through the processus gracilis," which attaches the malleus to the tympanic.

The melon is a fatty organ located on the dorsal side the rostrum anterior to the nasal complex. In some species, the melon reaches the apex of the rostrum; this is generally true, for example, in the Globicephalinae. The melon is embraced by the medial portion of the rostral muscle (Mead, 1975), also called the pars labialis of the maxillonasolabialis (Lawrence and Schevill, 1956) and the nasolabialis profundus pars lateralis (Rodinov and Markov, 1992). Below the posterior part of the melon are the nasal plug muscle and the premaxillary sacs (Mead, 1975), in which it is partially imbricated. The most commonly suggested function of the melon is as an acoustic lens (Lilly, 1961; Norris, 1964, 1968, 1969; Wood, 1964). Although it seems clear that the melon is involved in sound reception and transmission (Norris and Harvey, 1974; Mead, 1975), its function remains unclear.

On the skull of *Odobenocetops,* three features can be observed that denote lesser ability in sound production and/or transmission than in the other delphinoids: (1) the premaxillary sacs and nasal plug muscles were either absent or very reduced; (2) the melon was vestigial or absent; and (3) apparently the nasal diverticula of the nasal passages were very reduced or absent. The latter statement requires explanation.

The nasal diverticula of the Delphinidae have been well described by Lawrence and Schevill (1956) and Mead (1975). The nasal sacs and the communication between them are controlled by the various layers of the pars nasalis of the maxillonasolabialis muscle. Most of that muscle is attached to the dorsal side of the skull, lateral to the nasal opening and to the premaxilla, and posterior to the antorbital notch and the nuchal crest. It is divided into six layers according to Lawrence and Schevill (1956), and five layers according to Mead (1975). Rodinov and Markov (1992) recognized nine muscles, four in their nasolabialis group (which includes the nasal plug muscle, their nasolabialis profundus pars anterior medialis) and five in their maxillonasalis group. None of these layers or muscles is attached to the parietal. In *Odobenocetops,* the anterior withdrawal of the frontal and maxilla and the loss of the roof of the temporal fossa are supposed to have considerably reduced the attachment area of the pars nasalis of the maxillonasolabialis.

This statement assumes that very few or no muscle fibers would have migrated onto the broadly uncovered parietal, posteriorly. The five layers recognized by Mead (1975) are the pars posteroexternus (PE), the pars intermedius (I), the pars anteroexternus (AE), the pars posterointernus (PI), and the pars anterointernus (AI). The first four layers (PE, I, AE, PI) attach to the lateral edge of the supraorbital process and to the temporal crest. The pars AI attaches mainly to the ascending process of the maxilla and to the lateral border of the premaxilla.

Consequently, we can assume that the great reduction of the maxilla would have resulted in an extreme reduction (or loss) of AI. Furthermore, the disappearance of the temporal crest and the reduction of the lateral edge of the supraorbital process (which is very thin and strongly notched in dorsal view) also suggest a great reduction of the four layers PE, I, AE, and PI. Even if all the nasal diverticula totally disappeared, however, it is obvious that at least part of the maxillonasolabialis (pars anteroexternus) must have been retained, as this layer is involved in opening the blowhole.

Furthermore, *Odobenocetops* has large nasal apertures, and the problem is to determine whether it had nasal plugs or not. Given the size of the bony nasal passages, if nasal plugs were present, they would have been very large and consequently would have been moved by equally developed muscles. We observed, however, that the nasal plug muscle, if present, was very small. Furthermore, Mead (1975:53) stated that the "PI and AI also serve to seat the nasal plugs in the orifice of the bony nasal passage." The AI originates on the posterior border of the supraorbital process and on the temporal crest, and the PI originates on the ascending process of the maxilla. As stated above, these layers were probably very reduced in *Odobenocetops*, a condition that would be in agreement with the absence of nasal plugs. Furthermore, Lawrence and Schevill (1956) and Mead (1975) have shown that the nasal plugs are tightly imbricated with the dorsal surface of the premaxillary sacs and with the melon and that there is a sort of histological continuity among these organs. Consequently, the absence or great reduction of the premaxillary sacs and the absence of a melon would be consistent with the absence or reduction of the nasal plugs. If the nasal plugs were actually present and well developed, there would be an inconsistency between their large size on the one hand and the reduction of the nasal plug muscle, premaxillary sacs, and melon on the other. From this discussion it therefore follows that the nasal plugs were very probably absent or vestigial in *Odobenocetops*.

There seems to be a consensus that the nasal plugs and the nasal diverticula are related to sound production (Lilly, 1961; Lilly and Miller, 1961; Norris, 1964, 1968, 1969; Norris and Evans, 1967; Kleinenberg et al., 1969; Diercks et al., 1971; Norris et al., 1971; Evans and Maderson, 1973; Mead 1975; Dormer, 1979; Ridgway et al., 1980). It also is possible that sound could be produced by the larynx (Lawrence and Schevill, 1956; Purves, 1967; Schenkkan, 1973). Some authors have suggested that both the nasal sac system and the larynx are implicated in sound production (Lilly and Miller, 1961; Evans and Prescott, 1962; Schevill, 1964; Evans, 1967). Ridgway et al. (1980), however, clearly rejected the possibility of any sound production in the larynx and stated that sounds are produced by the nasal system only.

Consequently, *Odobenocetops* probably had no (or vestigial) nasal plugs, no (or vestigial) melon, and very reduced premaxillary sacs, if any; and, as the maxillonasolabialis was apparently very reduced in comparison to the other delphinoids, it also is likely that the other nasal diverticula were either reduced or totally absent. If so, then *Odobenocetops* had little (or no) ability to produce sounds (in the usual cetacean way) and therefore to echolocate.

As indicated earlier, the inner-ear structure implies that *Odobenocetops*, like most mammals, was capable of perceiving ultrasonic sounds (frequencies >20 kHz), but whether *Odobenocetops* could echolocate cannot be determined from ears alone. High-frequency facility is not synonymous with echolocation. The ability to echolocate implies the production of self-generated, beamed, gated signals and analysis of the corresponding echoes. Analysis of ambient sound is passive listening and is common to all mammals. Passive listening clearly provides considerable information about the immediate environment (e.g., directionality or the relative distance of two sound sources), but it does not provide spatial or textural information with the level of resolution commonly obtained through biosonar. Biosonar is an extraordinarily sophisticated acoustic imaging system that conventionally uses very high frequencies because the level of detail that can be transduced is related to the wavelength of the ensonifying signal. The stronger the evidence against the presence of a melon, which is directly implicated in outgoing signal generation and control, the less support there is for functional echolocation by *Odobenocetops*. The absence of nasal plugs would be critical evidence against echolation, as that structure and the diagonal membrane seem to represent the major sound producers in odontocetes, although it is not possible to refute definitively the hypothesis that *Odobenocetops* had a reduced air sac system and nasal plugs.

Whatever the morphology was, it is very probable that *Odobenocetops* had little echolocational ability, if any—a condition that may have been compensated for by good binocular vision. The orbit of *Odobenocetops* is proportionally much larger than in any other cetacean. The distance between the apices of the postorbital and antorbital processes is close to that in *Monodon* even though *Odobenocetops* is an animal approximately 15% smaller. Furthermore, the dorsal shifting of the process and the depth of the orbital notch clearly indicate that dorsal or anterior binocular vision was possible. Furthermore, good dorsal or anterior binocular vision is in agreement with the probable feeding posture of *Odobenocetops* (see "Scenario for the Feeding Mode of *Odobenocetops peruvianus*," below).

FEEDING ADAPTATIONS

The modifications of the skull of *Odobenocetops* are correlated with major modifications of its musculature. Four aspects should be considered: mandibular movements, head movements, morphology of the palate, and inferred presence of an upper lip and vibrissae.

MANDIBULAR MOVEMENTS.—In *Odobenocetops,* the withdrawal of the maxillae and frontals from the dorsal side of the braincase has opened dorsally the temporal fossa, which in most odontocetes is roofed. The parietals are widely uncovered dorsally and secondarily increased in size so that they occupy most of the dorsal surface of the braincase. In the other delphinoids, the temporal fossa is roofed by a lateral expansion of the frontal and the maxilla. The parietals are small bones restricted to the lateral sides of the skull and do not contact each other. The temporalis is a small weak muscle whose origin is located on the parietal, on the lateral side of the skull, and whose insertion is on the coronoid process of the dentary. Its action is to raise the mandible to close the mouth. If muscle insertions and origins are at least partially related to particular bones (which is known to be not always true), the great development of the parietal of *Odobenocetops* might have led to a great extension of the temporalis on the dorsal side of the skull. Consequently, *Odobenocetops* probably was capable of much stronger adduction of the mandible than are other odontocetes.

Another important elevator of the mandible is the masseter. In the dog, the masseter is divided into three layers. The superficial and middle layers originate on the lateral side of the zygomatic arch (on the jugal and squamosal), and the deep layer originates on its medial side (Miller et al., 1964). As for the odontocetes, Howell (1927) described two layers in *Neophocaena,* superficialis and profundus, but only the former had a bony origin, on the zygomatic process of the squamosal and on the postorbital process of the frontal. The superficial layer inserts on the posteroventral angle of the mandible and the deep layer on the dorsal edge of the dentary in front of the insertion of the temporalis. In *Odobenocetops,* the large distance existing between the postorbital process of the frontal and the zygomatic process might indicate that the masseter was divided into two clearly defined elements. Several features suggest, however, that the masseter did not originate on the postorbital process, but rather that it was attached only on the strong zygomatic process of the squamosal. This structure is the very stout lateral wall of the squamosal gutter described above. It is a thick bony wall strongly attached to the skull all along its length. Furthermore, the squamosal-parietal contact is not squamous and vertical as in most other mammals; it is a very solid, transversely oriented, interdigitated suture apparently capable of resistance to strong anteroposterior stresses. Consequently, the architecture of the areas of origin of the masseter indicates a muscle much stronger than in the other delphinoids.

On the ventral side of the skull the pterygoid muscles also are mandibular adductors. In a terrestrial mammal (the dog, cf. Miller et al., 1964), both pterygoideus muscles (lateralis and medialis) originate on the lateral side of the skull, on the pterygoid but also on the orbitosphenoid. In *Neophocaena,* Howell (1927) observed a very reduced muscle originating on the pterygoid membrane and on the lateral edge of the pterygoid bone adjacent to it. The "insertion is not upon the mandible but on the tough tissue near the ear bone" (Howell, 1927:23). In *Kogia,* however, Schulte and Forest Smith (1918) observed two relatively strong pterygoid muscles (internus and externus) that insert upon the medial side of the dentary. Seagars (1982) found that in long-jawed delphinids with numerous teeth, the pterygoideus internus (=medialis) is in fact the dominant adductor muscle, followed in importance by the temporalis, masseter, and pterygoideus externus (=lateralis). In species with fewer teeth and broader jaws (*Globicephala, Grampus*), the temporalis is more powerful relative to the pterygoideus internus, and in *Orcinus* the temporalis is actually the dominant muscle (Murie, 1870, 1973). In *Odobenocetops,* the pterygoid shows a very strong laterally convex crest in the position of the pterygoideus medialis of the dog and *Kogia,* and of part of the undivided pterygoid of *Neophocaena.* This crest is more developed than any structure observed in the other odontocetes and indicates, in *Odobenocetops,* a pterygoid muscle much stronger than in the other delphinoids. Together with the evidence of a large temporalis cited above, this seems consistent with the pattern documented by Seagars (1982) in delphinids, which would lead us to expect a large temporalis and internal pterygoid in connection with the presumably short, toothless mandible of *Odobenocetops.*

The main mandibular depressor muscle in terrestrial mammals is the digastricus. In the dog it originates on the anterior side of the paroccipital process of the occipital and inserts upon the ventral border of the mandible (Miller et al., 1964). In the odontocetes, Howell (1927, 1930) termed it monogastricus, and the origin is on the anterolateral border of the thyrohyal and/or basihyal. Apparently there is no attachment to the skull. The tremendous thickening of the squamosal and, to a degree, of the occipital at the posterolateral angle of the skull in *Odobenocetops,* however, seems to indicate considerable muscular stress in that region. Although it is therefore possible that part or all of the digastricus muscle was attached to the posterolateral angle of the skull, a condition that would have to be regarded as a reversal, the neck muscles (see below) are more probably responsible (at least partially) for the strong development of that region of the skull.

The masticatory musculature of *Odobenocetops* thus seems to have been much more powerful than in any other odontocetes. Considering the lack of maxillary teeth, it indicates a very peculiar mode of feeding involving powerful movements of the lower jaw and perhaps of the tongue, gular, and hyoid musculature. Although there is no direct evidence of these latter muscle groups, the very deep and arched palate suggests a very large tongue and a consequently strong throat musculature (see below).

HEAD MOVEMENTS.—The muscles involved in head movements are numerous and strong. In odontocetes, the most important are the semispinalis, rectus capitis, splenius, multifidus, sternomastoideus, longissimus, and scaleni. The first four muscles insert on the occipital shield, and not much can be said about their morphology in *Odobenocetops*. The three latter muscles insert on the posterior border of the paroccipital process of the occipital and/or on the zygomatic process of the squamosal. The sternomastoideus and the longissimus insert on the posterior region of the sternomastoid fossa and the lateral edge of the paroccipital process. In *Odobenocetops* this region is greatly expanded ventrally and forms the tremendously thickened posterolateral angle of the squamosal. The enlargement of the area of insertion of these muscles and the stoutness of the bone in this region suggest that the sternomastoideus and longissimus of *Odobenocetops* were very powerful muscles. The same could be said about the scaleni, which insert on the posterior surface of the paroccipital process and basioccipital crests. The bony origin of the sternomastoideus is on the anterolateral edge of the sternum; the bony origin of the longissimus is on the transverse process of the anterior thoracic vertebrae (Pabst, 1990); origin of the scaleni (dorsalis and ventralis) is on the first ribs. These three muscles, if acting bilaterally, are depressors of the head, and if acting unilaterally, are lateral rotators of the head. The region of the nuchal crest located behind the sternomastoid fossa also is extremely thickened. In *Neophocaena* and *Monodon* the splenius and semispinalis capitis insert in this area. The lateral extremity of the insertion of these muscles also is on the posterior part of the upper part of the sternomastoid fossa. If acting bilaterally these muscles are levators of the head.

Consequently, the assumed strength of the sternomastoideus, longissimus, and scalenus in *Odobenocetops* would indicate strong and active vertical and transverse movements of the head or at least a need for a strong control of these movements. This conclusion is in agreement with the morphology of the condyles and of the supracondylar fossa, which would allow significant vertical movements of the head (see above). It is further corroborated by the relatively large size of the semicircular and vestibular canals, in *Odobenocetops* as in *Delphinapterus,* which are apparently related to the mobility of the neck (see above).

PALATE MORPHOLOGY.—The palate of *Odobenocetops* is very wide, very deep, and arched. The morphology of its anterior part is dominated by the exceptionally developed premaxillae and the large vomer. The palate is very wide posteriorly because of the lateral expansion of the pterygoid, which forms a ventrolaterally oriented wing. The palatines also are very enlarged in the posterior region of the palate. Between the alveolar process of the premaxilla and the pterygoid wing, a deep, rounded notch forms the narrowest (middle) portion of the palate. This notch lies exactly in the path of a prolongation of the squamosal gutter and was obviously for the passage of the mandible. Seen ventrally, the notch is wide and almost semicircular; viewed along the axis of the squamosal gutter, though, it

is much narrower, as the lateral plane of the palate is oblique in relation to a line joining the squamosal gutter to the apex of the rostrum, the supposed axis of the dentary. If the dentary of *Odobenocetops* was straight as it is in all the other odontocetes, then the dentary in its middle portion was only slightly thicker than in the other delphinoids; however, it was probably very high, as it needed to be strong to bear the stresses of the powerful musculature. The anterior part of the mandible probably was greatly thickened to partially fill the anterior region of the palate. Another possibility is that at their anterior ends, the dentaries were as high as the concave portion of the medial side of the premaxillary process (i.e., its proximal two-thirds, approximately 15 cm) and formed two divergent processes or expansions complementary to those of the premaxillae. This mandibular morphology would somewhat resemble that observed in the borhyaenoid marsupial *Thylacosmilus* from the Pliocene of Argentina. Such a morphology would allow the apex of the lower jaw to fit perfectly in the anterior region of the palate, thereby allowing a perfect closing of the mouth.

An even slightly deep, wide, and/or vaulted palate is unknown among other cetaceans, so the morphology of *Odobenocetops* is unprecedented. In non-cetacean mammals, a deep, arched palate is known in the Odobenidae (*Odobenus rosmarus, Valenictus chulavistensis*) and in the Otariidae (*Otaria flavescens* and to a lesser extent *Phocarctos hookeri*). As mentioned above, the deep palate of *Odobenocetops* is consistent with a large tongue and consequently strong tongue muscles. Also, the gular musculature must have been fairly powerful, as it is related to the tongue and mandible movements.

UPPER LIP AND VIBRISSAE.—Muizon (1993a, 1993b) has suggested the presence in *Odobenocetops* of a strong upper lip. That hypothesis is maintained herein. Lips are known in several other odontocetes and are especially well developed in the beluga (Kleinenberg et al., 1969:80). Although these authors state that the lips of the beluga are devoid of musculature and not movable, figure 5 of Brodie (1989:132) seems to demonstrate considerable mobility of the beluga's lips. Furthermore, Mead (1975:39) mentioned that part of the lateral rostral muscle of the delphinoids is associated with the upper lip and stated that "[t]he lips of Cetacea are generally considered to be immobile, but in view of the great expanse of lip surface in animals such as *Globicephala* and *Grampus* and the relatively large mass of muscle inserting into the connective tissue of the lips in these forms, a certain amount of mobility may be present and may be important in feeding." A strongly developed, mobile upper lip in *Odobenocetops* could therefore result from the enlargement of a structure already existing in the other delphinoids.

We mentioned above the strong muscle attachments on the dorsal and anterior face of the apex of the rostrum. Given that the medial rostral muscle is inserted into the melon (Mead, 1975:10), which *Odobenocetops* lacks, both the medial and lateral portions of the rostral muscle might be implicated in upper lip movements in *Odobenocetops*. Consequently, the muscle arising from the subapical rims described above (passing laterally to the premaxillary foramina, converging at the apex of the

rostrum, and enclosing the triangular area where, in other delphinoids, the nasal plug muscle is attached) would represent part of the medial portion of the rostral muscle. The remaining part of the medial portion of the rostral muscle, together with the lateral portion, would create the strong muscle attachments observed on the anterodorsal sides of the alveolar processes of the premaxillae. The whole rostral musculature of *Odobenocetops* would therefore be related to upper lip movements.

The occurrence of a large upper lip in *Odobenocetops* is consistent with the presence of the large neurovascular foramina observed on the anterior and ventral borders of the alveolar process and with the presence of the very large palatine foramen, which could have provided extensive blood and nerve supply to the ventral region of the lip. The dorsal region of the lip was irrigated and innervated via the very large maxillary (and probably premaxillary) foramina, which also were related to the blood and nerve supply of the pulp cavities of the tusks.

As noted above, the facial nerve of *Odobenocetops* is significantly larger than in the other delphinoids except *Monodon* (Table 3). The large diameter of the facial nerve canal in the periotic is consistent with the presence of a large upper lip and vibrissae.

Muizon (1993a, 1993b) suggested that the upper lip of *Odobenocetops* could have carried vibrissae, evolved convergently with those of the walrus. The extensive vascularization and innervation of the upper lip and the very spongy nature of the bone of the anterior side of the rostrum suggest that such structures could possibly have been present. Furthermore, vestigial vibrissae are well known in some adult cetaceans (mysticetes, *Inia*) and have been observed in several newborn or fetal delphinoids and *Pontoporia* (Bourdelle and Grassé, 1955; Yablokov and Klevezal, 1962; Tomilin, 1967; Best and da Silva, 1989). The vascularization of the anterior side of the rostrum of *Odobenocetops* also could be related to the lip only, however, so the presence of vibrissae remains undemonstrated.

COMPARISON WITH *Odobenus*.—Several features of *Odobenocetops* are convergent with the morphology of the walrus. They are (1) the large, deep, vaulted palate; (2) the presence of tusks; (3) the wide and low occipital, in posterior view, and the ventrolateral expansion of the ventrolateral angle of the skull; (4) the thickness and the extreme stoutness of the bone forming the ventrolateral angle of the skull and of the alisphenoid; (5) the well-developed upper lip and the presence of vibrissae (not certain in *Odobenocetops*); and (6) the presence of a rough, irregular, and expanded area for attachment of tough or horny tissue on the edges of the mouth (inferred for *Odobenocetops*).

The palate of *Odobenocetops*, however, differs strongly from that of *Odobenus*. It is much wider and deeper. It is composed of the premaxillae, palatines, vomer, and pterygoid, but the maxillae do not crop out on the palate as in most other mammals. There are no maxillary teeth in *Odobenocetops*, although it is known that some fossil odobenine walruses (*Valenictus chulavistensis*) also lacked maxillary teeth (Deméré, 1994). The vomer is very large and lozenge-shaped, as (but much larger than) in most other odontocetes. The tusks of *Odobenoc-*

etops are premaxillary and strongly asymmetrical, whereas they are maxillary and symmetrical in *Odobenus*. The posteroventral angle of the skull is made up of the paroccipital process and the squamosal, whereas in *Odobenus* it is formed by the tremendously enlarged mastoid process of the periotic. The attachment area of tough tissue is located on the anterior edge of the premaxilla; in the walrus it is on the dorsal side of the mandibular symphysis.

Muizon (1993a, 1993b) regarded *Odobenocetops peruvianus* as a walrus-convergent bottom feeder. We have noted above that *Odobenocetops* and *Odobenus* share several strong similarities in their skull morphology. Functional comparisons will help determine whether the adaptations of *Odobenocetops* could fit with the walrus's mode of feeding.

The living walrus feeds mainly upon benthic invertebrates, such as thin-shelled bivalves (*Mya,* other clams, and mussels), gastropods, molting crustaceans, holothurians, and tunicates, but rarely upon cephalopods, fish, or other vertebrates. Prey buried in the substrate, such as clams, are excavated by jetting water from the mouth (Kastelein and Mosterd, 1989; Kastelein et al., 1991). As suggested by Vibe (1950) and clearly expressed by Fay (1982), the walrus does not crush the shells of the mollusks it ingests; rather, it holds them between its lips and jaws at the front of the mouth and sucks out their siphons, using its mouth as a vacuum pump. Fay (1982:171) described the walrus mouth as follows: "The extraordinary vacuum pump of the walrus ... is powered by very large lingual retractors and depressors (M. styloglossus, hyoglossus, and genioglossus), complemented by the highly vaulted palate, the long firmly ankylosed mandibular symphysis, and the unusually powerful m. tensores veli palatini and m. buccinatorius, which provide rigidity to the walls of the 'cylinder.' The tongue is the 'piston.' The small rigid oral aperture, complemented by ample muscular lips, insure that the full effect of the vacuum is exerted only on objects held in the incisive area at the front of the mouth." Gordon (1984) confirmed that the vacuum is created by movement of the tongue directly rearward. Fay (1982:167) also stated, concerning the tough tissue covering the dorsal surface of the mandibular symphysis: "The rough cornified surface seems admirably suited for grasping and holding slippery prey; I believe that it functions also to hold molluscan shells while their contents are removed by suction."

When searching for food, the walrus moves along the bottom with its head down and its body at an angle to the bottom of about 10°–45° (Fay, 1982:164). The vibrissae are the sensitive organs that are constantly in contact with the bottom and transmit information to the animal. As mentioned by Fay (1982), the walrus feeds in darkness and "the eyes are comparatively smaller than those of other pinnipeds;" "they may be the least important as sensors" and "the animals probably locate their prey by vibrissal contact." Fay (1982:164) also mentioned that excavation of buried animals may be achieved by "rooting" with the snout: "the pattern of vibrissal abrasion, the greater cornification of the upper edge of the snout..., and the powerful cephalo-cervical musculature of the walrus are unlike those of
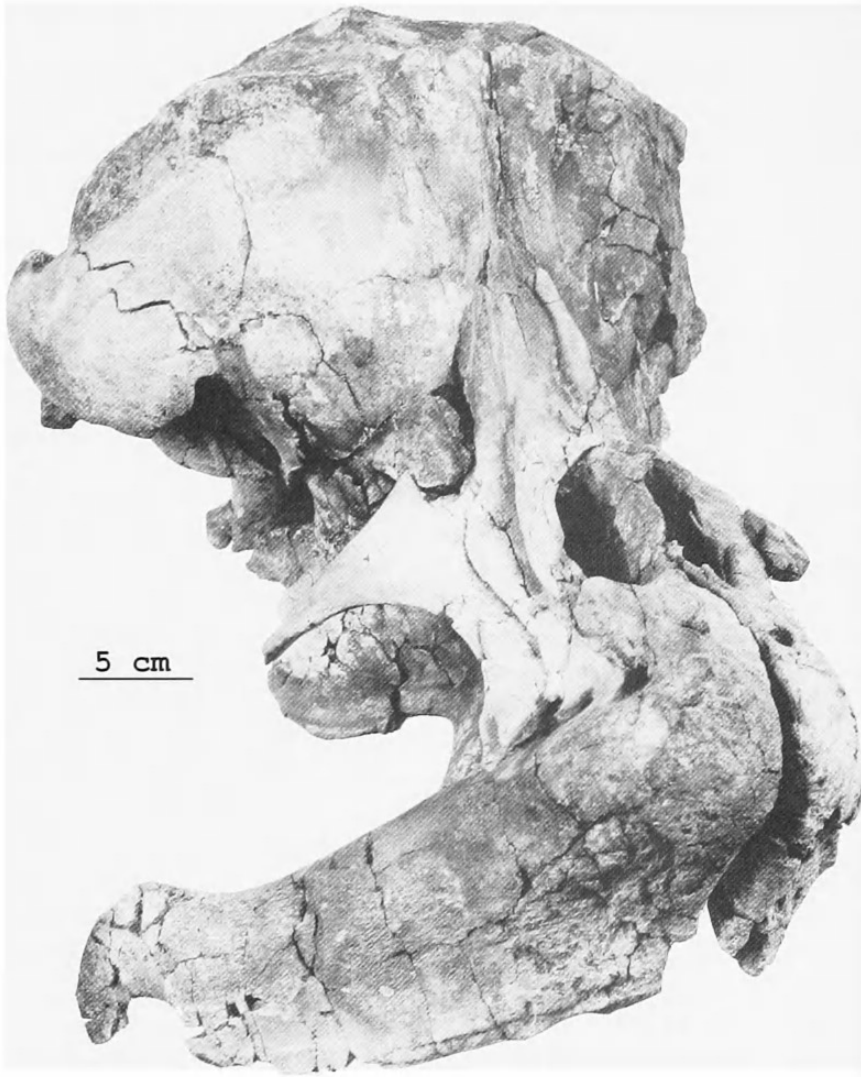
FIGURE 18 (left).—*Odobenocetops peruvianus*, holotype (USNM 488252): anterolateral view of the skull in a feeding position.

any other pinnipeds. Each points to frequent use of the snout as a digging organ." This mode of feeding creates long, sinuous furrows in the seafloor (Nelson and Johnson, 1987), each presumably representing a single bout of feeding by a walrus on a single dive.

In *Odobenocetops,* although the mandible is unknown, several aspects of the skull morphology are in perfect agreement with suction bottom feeding (see Figures 18, 20): The very large vaulted palate (even larger than in the walrus); the inferred cornified (or strongly fibrous) edge of the upper lip; the fairly well-developed masticatory musculature (for a cetacean), close, in strength, to that of the walrus; the powerful occipital musculature (at least the scalenus, sternomastoideus, and longissimus); and the significant atlanto-occipital movements denoted by the very convex and salient occipital condyles and the large supracondylar fossae. Contrary to walrus morphology, though, the eyes of *Odobenocetops* were large, and good binocular vision compensated for the probably poor echolocational ability. Even walruses have good anterodorsal binocular vision and seem to forage visually when water clarity permits, however (Kastelein and Wiepkema, 1989; Kastelein et al., 1993).

Odobenocetops had no maxillary teeth; like the living walrus, it was a sucking feeder that did not have the masticatory apparatus necessary to crush any hard exoskeleton of its prey. Fay (1982:166) has shown that the teeth of the living walrus are not used for crushing, and it is noteworthy that some fossil odobenids (Deméré, 1994) had lost the postcanine teeth altogether.

Another noteworthy feature of *Odobenocetops* is the strongly modified zygomatic process with a large squamosal gutter and a tremendously resistant parieto-squamosal suture. As it has no equivalent in any living mammal, this structure is difficult to interpret. If, however, this structure is related to the very strong masticatory musculature mentioned above, it likely permitted very powerful (though probably not very extensive) movements of the lower jaw. The exceptional strength of the mouth of *Odobenocetops* would thus have allowed it to maintain its prey extremely firmly in its mouth. The extreme development of the squamosal gutter and its high position are difficult to explain because the mandible is unknown.

Odobenocetops also shares with *Odobenus* the possession of tusks, but the large premaxillary alveolar processes of *Odobenocetops* are absent in the walrus. Fay (1982:136) stated that the tusks of the walrus are not related to feeding but instead

play a social role. The same has been stated for the narwhal (Nishiwaki, 1972; Hay and Mansfield, 1989). Consequently, we assume that the tusks of *Odobenocetops* were used more as social organs than as feeding implements (see below for further discussion of the tusks). The deep premaxillary fossae bordering the anterior extremity of the vomer on the palate are absent in all the other odontocetes, and nothing similar is observed in the walrus. Their function has not been elucidated.

COMPARISONS WITH MARINE MAMMALS OTHER THAN *Odobenus*.—*Delphinapterus leucas:* Kleinenberg et al. (1969: 89–90) presented an interesting interpretation of the functions of the tongue of the beluga for feeding. According to these authors, the tongue is a very mobile and strong organ that has three functions. First the tongue orients the prey in the mouth. Second, the animal "draws its tongue back, pressing the prey to the palate and forcing it to the entrance of the pharynx." Third, "the tongue forces the water out of the mouth, preventing its entrance into the intestinal tract." The tongue thus appears to be a powerful and extremely specialized organ for food ingestion. It is therefore very probable that *Odobenocetops*, like all living odontocetes, had a powerful, enlarged (given the size of the palate) tongue, and that it could have been involved in a pumping feeding action as is observed in the walrus.

Bottom feeding is well established for belugas; worms and benthic animals are often found in their stomachs (Matthews, 1978). Belugas also are capable of powerful water-jetting similar to that observed in the walrus (D.P. Domning, pers. obs., and J.G. Mead, pers. comm., 1992). Bottom feeding also is known in *Globicephala,* and water-jetting in *Orcinus* and *Globicephala* (Werth, 1992).

Kolponomos clallamensis and K. newportensis: Tedford et al. (1994) described the skull of *Kolponomos,* an aquatic ursid from the early Miocene of Washington and Oregon. Among the most peculiar modifications of the skull of *Kolponomos* are the extremely enlarged mastoid processes, which are oriented ventrolaterally as is observed in the walrus. According to Tedford et al., *Kolponomos* could have fed upon benthic hard-shelled invertebrates, mainly mollusks but also echinoids. Consequently, the substantial and strong movements of the head must have necessitated strong neck musculature.

Furthermore, *Kolponomos* had anterior binocular vision, which assisted its search for food, as in *Odobenocetops* and *Odobenus* (Kastelein et al., 1993). Tedford et al. (1994) also suggested that *Kolponomos* could have had enhanced tactile sensitivity of the lips and the muzzle, possibly possessing a large upper lip and tactile vibrissae like the walrus. If that was actually the case, then *Odobenocetops* also would resemble *Kolponomos,* in having both good binocular vision and an enlarged, highly tactile upper lip. That bottom feeders could rely upon binocular vision and/or tactile sensibility of the upper lip and vibrissae is in agreement with the apparent lack (or reduction) of echolocational ability in *Odobenocetops. Kolponomos,* however, was very different from *Odobenocetops* in its mode of ingestion of prey. *Kolponomos* had very strong sea-otter-like

crushing teeth, which were used to break the hard shells of benthic invertebrates (Tedford et al., 1994).

Desmostylians and Sirenians: Like *Odobenocetops,* most marine mammals that are believed to have dug for food in the seafloor possess large ventrolateral expansions of the posteroventral angle of the skull, which presumably reinforced the neck when the animal was searching for its food, with its head down and the body in an oblique position in the water. Desmostylians provide another example of this; they were evidently substrate-feeding herbivores (Domning et al., 1986) and all shared an enlarged paroccipital process (Ray et al., 1994). Furthermore, the peculiar sirenian *Miosiren,* which has been suspected of molluscivory on the basis of its dentition and reinforced palatal region, also has enlarged post-tympanic processes (Sickenberg, 1934). Other tusked sirenians, however, do not, and at least the most specialized of them may have used their jaw muscles instead of their neck muscles for digging (Domning, 1989).

The Holocene sirenian *Dugong dugon* (Müller) superficially resembles *Odobenocetops* in having a pair of slender, relatively straight, and open-rooted upper incisor tusks that are largely enclosed in prominent, downward-directed premaxillae. In the dugong, however, these tusks are symmetrical, are not strongly divergent, project at most a few centimeters outside the gum, and are directed anteroventrad rather than posteroventrad. Although tusks of fossil dugongids were surely used in feeding (probably to excavate sea grass rhizomes; Domning, 1989), those of the living species seem to have lost this function and have become relegated to purely social uses, such as fighting between males (Preen, 1989; Domning, unpubl. data). Evidently as a result of this restriction in function, tusks of *D. dugon* (uniquely among sirenians) have become sexually dimorphic, normally erupting only in the males (Marsh, 1980). It thus appears that the tusks of the herbivorous dugong can shed no additional useful light on the biology of the presumably carnivorous *Odobenocetops.*

Scenario for the Feeding Mode of Odobenocetops peruvianus: *Odobenocetops* lived in the early Pliocene on the coast of Peru, in the shallow waters of the bay of Sud-Sacaco, probably close to the shore (Marocco and Muizon, 1988). It was a sucking feeder preying upon benthic invertebrates such as thin-shelled mollusks and/or molting crustaceans, which were abundant in the Pisco Formation (Muizon 1981; Muizon and DeVries, 1985; Carriol et al., 1986). It searched for food using a position similar to that of the walrus. The head maintained contact with the bottom while the body was at an angle to the bottom, probably close to the angle of the premaxillary process with the anteroposterior axis of the skull (~45°). The tail helped in keeping that position and, as in other cetaceans, provided propulsion (as mentioned by Fay (1982:164), the walrus also uses the posterior part of the body to move forward, but by means of the hind limbs). The forelimbs probably had a stabilizing role, as in the walrus, and would have helped to maintain the upper lip and vibrissae in contact with the bottom. It used its very good dorsal binocular vision and its large and
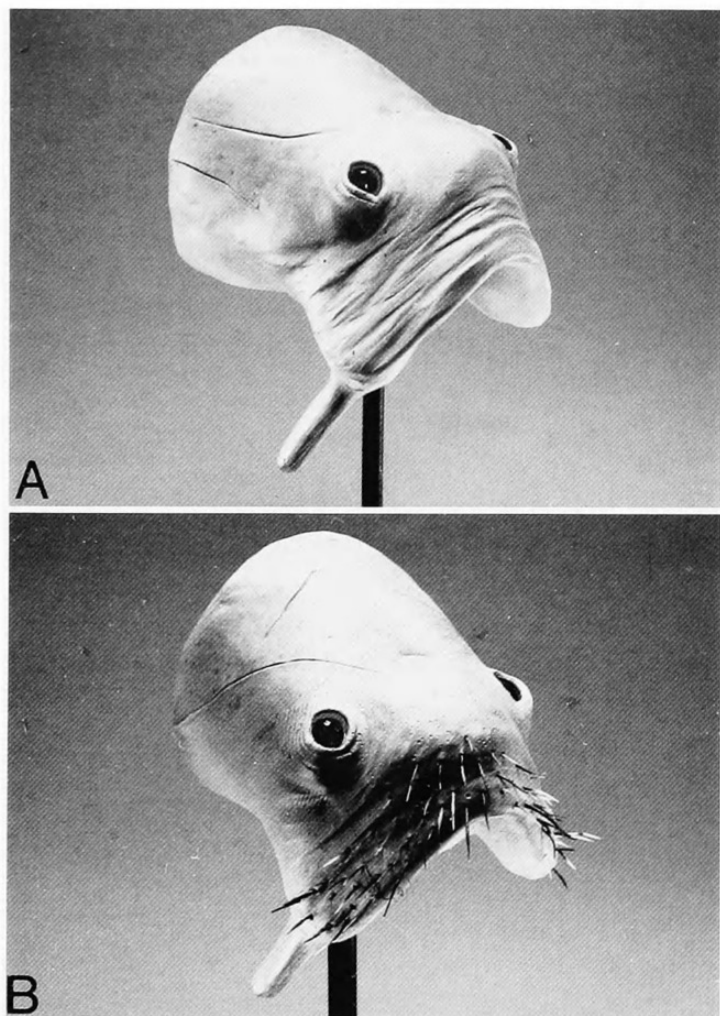
FIGURE 19.—*Odobenocetops peruvianus*, two possible reconstructions of the head: *a*, hypothesis without vibrissae, a "cetacean-like" interpretation; *b*, hypothesis with vibrissae, a "walrus-like" and more speculative interpretation (sculptures by Mary Parrish, Department of Paleobiology, NMNH).

FIGURE 20.—Artist's reconstruction of *Odobenocetops peruvianus* in feeding position (original painting by Mary Parrish, Department of Paleobiology, NMNH).

highly sensitive upper lip, possibly assisted by strong vibrissae, to search for food (Figures 18–20). Most probably, little or no echolocation was involved. Once found, buried prey, such as clams, was probably excavated by water-jetting, as in the walrus, then caught in the anterior part of the mouth and strongly held in this position by the powerful lips and jaws. Then dorsoventral and/or anteroposterior movements of the tongue would have transformed the mouth into a sort of vacuum pump, and part of the prey was sucked out of its shell and ingested.

Consequently, *Odobenocetops* was a highly specialized cetacean that combined adaptations of both *Odobenus* (water-jetting and sucking) and *Kolponomos* (good binocular vision), and therefore was probably the best-adapted known bottom-feeding marine carnivore.

This proposed feeding scenario is not unexpected for an odontocete. Suction feeding has been reported many times in odontocetes (Kleinenberg, 1938; Wilke et al., 1953; Ray, 1966; Rae, 1973; Matthews, 1978; Crawford, 1981; Seaman et al.,

1982; Martin, 1990; Heyning and Mead, 1996). An excellent review of the topic was presented by Werth (1992). According to Werth, it is in fact the absence of suction feeding that is unusual among odontocetes. Werth reported suction feeding in a number of species, both through direct observation: *Delphinapterus leucas* and *Globicephala melaena;* and inferred from anatomical or ecological evidence: *Berardius bairdi, Mesoplodon layardi, Monodon monoceros, Phocoena phocoena, Phocoenoides dalli, Physeter macrocephalus,* and *Tursiops truncatus.* Werth (1992:37) also reported a personal communication of W. Walker describing "a *Tursiops* stomach full of fresh, undigested siphons removed from clams; this type of diet (and inferred feeding method) is strikingly similar to that of suction-feeding walruses." The observations made by Werth and others make the feeding adaptation inferred for *Odobenocetops peruvianus* much more likely than could be suspected at first glance.

Possible Functions of the Tusks and Alveolar Processes

The most striking and unexpected features of *Odobenocetops* are its tusks and the massive alveolar processes of the premaxillae that support them—features paralleled in no other ceta-

cean. These structures, in our opinion, embody the twofold importance of *Odobenocetops:* Not only does the discovery of this new taxon dramatically extend the known morphological and ecological diversity of the Cetacea, but it also reopens the question of the function of tusks in true walruses.

After centuries of speculation and study, a consensus appears to have emerged that walruses use their tusks primarily in social (mostly agonistic) interactions, and secondarily for a variety of other purposes, but not to any significant extent in the course of their normal bottom-feeding (Fay, 1982; Nelson and Johnson, 1987; Kastelein and Mosterd, 1989; Kastelein et al., 1991). In other words, according to this view, walrus tusks are not feeding adaptations and do not form an integral part of the functional complex of feeding adaptations.

All who have examined the skull of *Odobenocetops* have been immediately struck by its gross resemblance to that of a walrus, most obviously in regard to the tusks. Moreover, this study has confirmed that the feeding behavior of *Odobenocetops* was walrus-like in that it consisted mainly of water-jetting and suction. This, however, raises a paradox: If walrus tusks are not feeding adaptations, then why should an animal whose feeding adaptations converge on those of a walrus be expected to have walrus-like tusks?

Fay (1982:137–138) proposed a plausible explanation of how walruses evolved large tusks. He hypothesized that "positive selective pressures and the potential for tusk development probably have existed in all polygynous pinnipeds from the beginning," but that the functional demands of pelagic piscivory, which required an unobstructed gape, precluded enlargement of the tusks beyond a certain point until odobenids took up feeding on benthic mollusks. Freed from the opposing selective pressure for a large gape, the animals were then able to respond to the preexisting social selection for hypertrophied tusks.

This explanation, however, would probably not apply to *Odobenocetops.* Early odontocete cetaceans, unlike pinnipeds, did not have enlarged caniniform teeth with obvious "potential for tusk development." Moreover, although some odontocetes that have become specialized for suction feeding have developed tusk-like upper or lower teeth (narwhals, ziphiids), others have developed similar specializations without any enlargement of teeth (belugas); "selective pressures for tusk development" thus seem not to have existed in all odontocetes. Furthermore, if any of the suction-feeding specializations in belugas, narwhals, and *Odobenocetops* were inherited from a common ancestor, they obviously did not coincide in time of evolution with any enlargements of teeth, because tusks are absent in the first and nonhomologous in the other two. It appears, then, that any net social selection for tusk enlargement in odobenocetopsids did not result directly from, nor was it correlated with, a shift from primitive piscivory to suction feeding.

This also may have been true in walruses. *Protodobenus japonicus,* a new odobenine from the early Pliocene of Japan, seems to have been principally a piscivore with incipient adaptations for suction feeding, but its upper canine is not nearly so enlarged as in *Odobenus* (Horikawa, 1995). At least the beginnings of the evolution of suction feeding thus apparently preceded tusk enlargement. The tusk of *Protodobenus* is open-rooted, however, and apparently ever-growing, so it could be argued that this taxon also fulfills the prediction of Fay's hypothesis that tusk enlargement should have followed immediately upon a shift away from piscivory.

In *Odobenocetops,* tusk enlargement appears to have been correlated with the adoption of specifically *Odobenus*-like suction feeding, i.e., benthic suction feeding that involved continuous direct contact of the snout with the substrate, possibly with major dependence on tactile vibrissae. If, as believed by students of living walruses, this mode of feeding does not involve any use of, nor necessitate any enlargement of, the tusks, then the co-occurrence of benthic suction feeding and large tusks in both walruses and *Odobenocetops* is purely coincidental. If, on the other hand, this "explanation" is deemed unparsimonious, then we should look more closely for a functional connection between feeding and tusk enlargement in the modern walrus.

There is a wide range of possible functions for the tusks of *Odobenocetops.* Because the alveolar processes that support them are even more prominent than the tusks themselves, and differ from them in probably having been more nearly symmetrical, it is worthwhile to consider their possible functions separately.

Use of Tusks in Feeding: PRO: Tusks are teeth and primitively serve for food-gathering. Even a single, asymmetrical tusk directed downward and backward could be used for stabbing prey, and walruses may kill seals on occasion (Fay, 1982:153). On the other hand, most, if not all, dental specializations for feeding are symmetrical, but the tusks are asymmetrical. Asymmetry of feeding structures may occur in cetaceans. Fin whales have asymmetrical color patterns around the mouth that are possibly associated with feeding (Gamble, 1985). *Tursiops* preferentially bottom-feed on the right side and have an asymmetrical larynx (with the piriform recess wider on the right) that may make it easier to swallow with that side down (Joy S. Reidenberg, pers. comm., 1995).

CON: The tusks are asymmetrical; most, if not all, dental specializations for feeding are symmetrical. Asymmetry of feeding structures in cetaceans is not yet conclusively demonstrated and is not known to include the dentition.

Tusks as Ballast: PRO: The relatively dense tusks, by adding extra weight to the front of the head, may have helped keep the snout against the bottom during feeding. Walrus tusks and their supporting bone also may serve this function.

CON: If this was the primary function of the tusks, it is hard to explain why they were not equal in size. Also, it seems unlikely that tusks as small as those of *Odobenocetops* would have had a significant ballast effect in an animal that could have approached the mass of a narwhal (between 800 and 1000 kg). The much larger tusk of a narwhal is not known to produce (either facultatively or obligately) a down-by-the-head attitude

in that animal, even though it has a much greater moment for doing so than would have been the case in *Odobenocetops*.

Use of Tusks for Hauling Out: PRO: This is an important function of tusks in walruses.

CON: Post-Eocene cetaceans do not haul out. Tusks used in hauling out would be most useful if they were symmetrical and stronger than observed in *Odobenocetops*.

Use of Tusks in Piercing, Abrading, or Anchoring to Ice: PRO: Both walruses and narwhals use their tusks to make breathing holes, and walruses use them to anchor to ice (Fay, 1982:137).

CON: Sea ice did not exist in Peru in the early Pliocene. Although *Odobenocetops* may have lived in the Antarctic, it has not yet been found there.

Social Role of Tusks: PRO: In many species tusks play social roles, such as in combat, in courting or mating, and in visual display. This is true both in walruses and in narwhals, the sister group of *Odobenocetops,* in which they also are asymmetrical. In walruses, they are used for ritualized dominance-threat displays by both males and females (Fay, 1982: 135–136). Use for combat would be consistent with the tusks' orientation, which is suitable for a slashing attack to an opponent's flank, using powerful muscles attached to the paroccipital processes. If the opponent were always approached head-on (right side to right side), this also would be consistent with the tusks' asymmetry. Use for social roles also would predict that the tusks would be larger in some individuals than in others.

CON: The sex of the available specimen and the degree of intrapopulational variation in the size of tusks are unknown. The tusks may have had a role in actual contact with other animals, but they seem rather slender to have been used for extremely forceful contact. Neither do their downward-and-backward direction, unilateral enlargement, and slenderness seem optimized for an impressive visual display, especially under water.

Tusks as Primitive Retentions: PRO: The tusks may not have been adaptive in *Odobenocetops* itself, but merely retained from an earlier evolutionary stage.

CON: The weight, location, and external form of the tusks would probably have had deleterious hydrostatic and hydrodynamic effects on the animal's behavior and locomotion. Presumably, they would therefore have been eliminated quickly by selection in the absence of some positive selective value.

Alveolar Processes as Support for the Tusks: PRO: Any use of the tusks would likely result in bending stresses, which supporting sheaths would help resist.

CON: The alveolar processes were probably relatively symmetrical, whereas the tusks are grossly asymmetrical. An unerupted tusk could not be used for anything and therefore would require no extra support. Walruses use their tusks very forcefully in a variety of ways and do not have such elongate bony sheaths to support them. Rather, they have been strengthened by being made thicker. In *Odobenocetops* they are relatively slender, implying relatively little selection pressure for resistance to bending.

Alveolar Processes as Hydrofoils or Diving Planes: PRO: The processes were prominent features of the head, at the very front end of the body where control surfaces would be most effective. Their oblique orientation resembles that of cetacean flippers. The bottom-feeding behavior of *Odobenocetops* might well have benefited from hydrofoils to keep the snout pressed against the substrate.

CON: The processes may have been too small to have much effect as normal hydrofoils, especially if *Odobenocetops* was a relatively slow-swimming cetacean. Their angle of attack was not easily adjustable, so they would not have been as effective as the flippers. Other cetaceans manage without such control surfaces on the head. In cross section, the processes are thinner in front and thicker behind, hence not like that of an airfoil, so they would not have generated significant lift, even if they could have been held in a transverse rather than an oblique position. In bottom feeding, the alveolar processes would have lain against and parallel to the bottom (and hence in the same plane as the direction of advance) and would have had minimal effectiveness as hydrofoils. Moreover, their cross-sectional shape would, in that position, have tended to lift the head off the bottom rather than the contrary. If muscles or skin inserted on their posterior edges (see below), the processes plus attached soft tissues might have had the size and shape necessary to function as hydrofoils, but the other objections would still apply.

Alveolar Processes as Ballast: PRO: The extra mass of bone in the process, by adding weight to the front of the head, may have helped keep the snout against the bottom during feeding. Walrus tusks and their supporting bones also may serve this function.

CON: The bone of the processes is not denser than the rest of the skull, unlike the bone in the rostrum of the walrus. Furthermore, as is true for the tusks, the mass of the alveolar processes was not great when compared with that of the animal.

Use of Alveolar Processes for Sediment Displacement: PRO: The backward divergence of the processes would tend to produce a plowshare effect during feeding, shoving sediment to the sides and increasing the effective width of the path searched for prey. Cornified skin on the leading edge of the processes would be consistent with such use.

CON: The dorsolaterad slope (in head-down position) of the lateral surface of the processes is unlike the ventrolaterad slope of a plowshare, and would press sediment downward rather than digging in and lifting it. Increasing by this means the area searched for prey would presuppose the presence of vibrissae along the whole length of each process, which is questionable (see below).

Use of Alveolar Processes for Muscle Attachment: PRO: The processes would have provided highly effective lever arms for muscles (such as a modified platysma and/or cutaneus trunci) that flexed the neck and/or turned the head, both important actions in bottom feeding and in most of the conceivable uses of the tusks. The faint ridge on the posterior edge of the

process might represent the insertion of a muscular aponeurosis.

CON: The large ventrolateral expansions of the occipital region would seem adequate for neck-muscle attachments, and such anterior muscle insertions are absent in walruses.

Use of Alveolar Processes for Skin Attachment: PRO: The faint ridge on the posterior side of each alveolar process could even more plausibly mark the attachment of a sheet of skin extending backward from the process. Such a sheet might have served as a barrier to keep churned-up mud and turbid water away from the eye during head-down bottom feeding. Although *Odobenus* lacks such a sheet of skin (and a bony strut to support it), it depends less upon vision during feeding, as suggested by its more lateral placement of the eyes compared with *Odobenocetops*. Walruses do sometimes use their vision in foraging, but they do not always do so (Kastelein et al., 1993).

CON: No contrary evidence is known.

Alveolar Processes as Restricting Size of Mouth Opening for Suction Feeding: PRO: In walruses, known suction feeders, the short bony sheaths of the tusks form rigid sides for the mouth opening and help concentrate the suctional force (see Fay, 1982:171, fig. 106).

CON: This also would be true for the most proximal parts of the alveolar processes of *Odobenocetops,* but not the distal parts, and so would not explain the great elongation of the processes. Both tusks of *Odobenocetops* seem large enough to have served this function even if supported only by short, walrus-like processes.

Alveolar Processes as Increasing Area and/or Breadth of Vibrissal Array: PRO: The symmetry and backward divergence of the processes increase the total width of the snout, which could, therefore, support an increased number of vibrissae. Cornified skin on the leading edge of the process would be consistent with such use.

CON: Large nutrient foramina are found only on the proximal, not the distal, portions of the alveolar processes (however, these foramina were not necessarily coextensive with the vibrissae). Moreover, it is not certain that vibrissae were in fact present.

Alveolar Processes as Orientation Guides and Stabilizers for the Mystacium: PRO: More-or-less symmetrical tusk-like bony processes could serve as guides, somewhat in the manner of sled runners, to maintain the proper orientation of the mystacium and vibrissal array to the substrate while the animal searched for food and to reduce the exertion of neck muscles. In *Odobenocetops,* the symmetry and backward divergence of the processes would have given them more leverage in countering roll and yaw, as well as pitch. The right tusk, at least, would have enhanced this leverage (but the advantage of this must have been small, or else both tusks would have been of similar length). The cross-sectional shape of each process would have caused it to ride over sediment rather than digging in, likewise stabilizing the head against roll. Cornified skin on the leading edge of the process would be consistent with such use. Odobe-

nids with "walrus-like" morphotypes have analogous structures, i.e., long, symmetrical tusks with oval cross sections.

CON: No contrary evidence is known.

Use of Alveolar Processes in Combat: PRO: The large alveolar processes might have served a function in combat between males. This would be consistent with a social role for the tusks. The downward, backward, and lateral slope of the processes would serve, in a head-on collision, to guide an opponent's alveolar process and tusk ventrolaterad and away from the eye and flank. Cornified skin on the leading edge of the process would be consistent with such use.

CON: The sex of the available specimen is unknown.

Use of Alveolar Processes in Visual Display: PRO: This, too, would be consistent with a social role for the tusks. The processes are bulkier than the tusks themselves, and they would have accentuated and called attention to the presence and orientation of the tusks. In head-on view, they also would have made the entire animal look larger. Use for display would predict that the processes would be larger in some individuals than in others.

CON: The sex of the available specimen and the degree of intrapopulational variation in the size of the processes are unknown.

Alveolar Processes as Primitive Retentions: PRO: Enlarged alveolar processes of the tusk-bearing bones are a necessity in animals with enlarged tusks. If tusks (however oriented) were present in the ancestors of *Odobenocetops,* enlarged alveolar processes also would have been present (as in narwhals); hence, enlargement of the processes may call for no special adaptive explanation.

CON: For the reasons stated above, support for the tusks alone seems inadequate to account for the size of the processes. In any case, the enlarged processes of *Odobenocetops* relative to the rest of the skull are derived with respect to all other cetaceans, and this enlargement calls for explanation.

We conclude that the most plausible and important uses of the tusks of *Odobenocetops* were social ones. The alveolar processes probably also played social roles, incidentally as a support for the erupted tusk and perhaps more directly as weapons and/or shields in agonistic encounters, or in visual displays. Other functions, such as restricting the mouth opening for suction feeding or supporting an array of vibrissae, cannot be entirely ruled out and may even have been important in the early stages of evolutionary enlargement of the processes. Likewise, attached sheets of skin might have been useful in keeping suspended sediment out of the field of vision in later stages of the processes' enlargement. At all stages of evolution, the increased skeletal mass represented by both tusks and processes also would have had an incidental value in keeping the snout against the substrate during feeding.

We suggest, however, that the single most important function of the alveolar processes, and the one that may have controlled their evolution, was that of orientation guides for the mystacium and vibrissal array. This is the only hypothesis that

seems to offer an explanation for the co-occurrence of benthic suction feeding and tusk-like structures in both *Odobenocetops* and walruses. Indeed, one of the most significant implications of the discovery of *Odobenocetops* is the fact that it reopens the question of whether the tusks of walruses are important in their feeding strategy.

As noted above, the work of Fay (1982) and others seemed to have answered this question in the negative, and the consensus today is that walrus tusks serve primarily in social behavior. In addition to their subsidiary functions, such as hauling out and opening holes in ice (Fay, 1982), perhaps walrus tusks also serve as orientation guides for the mystacium and vibrissae. An analogy can be drawn with sled-mounted undersea cameras that are designed to be dragged along the seafloor; the sled runners stabilize the sled in roll, pitch, and yaw, keeping the lights and cameras pointed in the right direction. Similarly, tusk-like structures would stabilize an animal's head and help maintain the mouth and vibrissal array in a fixed attitude relative to the bottom, increasing the efficiency of search by the sense organs and, possibly, the efficiency and accuracy of water-jetting and/or suction feeding.

If such orientation guides are important in the odobenine style of bottom feeding (and it should be possible to test this experimentally in living walruses), then we would expect both sexes to have them (as is the case with the tusks of *Odobenus*). The external form of such guides rather than their internal structure would be functionally important, however, so they would not necessarily have to be genuine tusks; for example, tusk-like bony structures would serve just as well, provided they were reasonably symmetrical and sufficiently long. Such structures would make real tusks redundant, and vice versa, so we would not expect to find both long, symmetrical tusks and bony equivalents of them in the same species. This is borne out by fossil odobenines such as *Valenictus* (Deméré, 1994), which resemble modern *Odobenus* in this regard—although this would of course be expected from their close relationship alone.

This hypothesis also is consistent with the ontogeny of walrus tusks. Weaning usually occurs in *Odobenus* at 14–27 months, and benthic feeding begins at 6–24 months (Fay, 1982:138–141). Tusk eruption also begins in the first year of life; the tusk begins to show signs of discoloration and wear by the age of two years, and at this time the tip of the crown extends below the ventral side of the mandible and usually 2–4 cm below the edge of the upper lip (Fay, 1982:105–107, fig. 71). It therefore seems possible that the tusks could be starting to function as guides even at this age.

What we find in *Odobenocetops* also is consistent with this interpretation. Although tusks are present, they are not symmetrical; indeed, only one of the pair may have erupted. Instead we find elongated, and probably much more symmetrical, alveolar processes of the premaxillae, which might very well have served as orientation guides for the snout. Their posterior divergence would have enhanced their effectiveness in this

role. In fact, it is difficult to explain them merely as sheaths for the tusks, because walruses manage to wield much larger tusks very forcefully without the support of such elongated sheaths, and relatively symmetrical sheaths should not be needed for the highly asymmetrical (and, in the case of the unerupted tusk, functionless) teeth of *Odobenocetops*. We therefore posit a functional role for the alveolar processes independent of the tusks themselves.

This still leaves unexplained the evolution of tusks in *Odobenocetops*. Given their asymmetry and the unlikelihood of functions such as hauling-out or ice-breaking in the case of a cetacean living in Peru, it is probably safe to make an analogy with narwhal tusks and attribute to them a primarily social function. It would not be surprising if sister groups such as monodontids and odobenocetopsids evolved such analogous structures in parallel, albeit developing the tusks from canines and incisors, respectively.

Conclusions

It appears, then, that the resemblance between *Odobenocetops* and walruses is not merely superficial, but a genuine case of functional convergence in feeding adaptations—specifically, adaptations for suction feeding on infaunal benthic prey. Furthermore, from the fact that structures resembling walrus tusks evolved in an animal clearly convergent on walruses in other characters that are unquestionably feeding adaptations, we can surmise that the tusk-like structures are probably associated with feeding in both animals. Otherwise, the correlation of benthic suction feeding with tusk-like structures in both animals is merely a striking coincidence—a conclusion we regard as unparsimonious.

Apart from the tusks and alveolar processes, the features in which *Odobenocetops* resembles a walrus are its hourglass-shaped skull, vaulted palate, enlarged paroccipital processes, possible vibrissae and sensitive upper lip, and possible horny covering of part of the upper lip. These features form a character complex apparently unique to odobenids and odobenocetopsids, and in the former are functionally related to a style of feeding documented in no other animals: powerful suction feeding on infaunal benthic prey. This character complex is wholly or partly absent in animals that prey on benthic invertebrates but are not suction feeders (e.g., sea otters), as well as in ones that are suction feeders but prey on animals that are free-swimming or merely rest upon the bottom (e.g., many odontocetes; A. Werth, pers. comm., 1992). It is thus only in association with this "benthic suction feeding" character complex that structures resembling walrus tusks are found—specifically in derived odobenines and in *Odobenocetops*.

If, instead, we attempt to explain the tusk-like structures in each case as having evolved mainly for social functions, we face an obvious problem. There is no apparent reason why fights or displays using such structures should occur always and only in benthic suction feeders. Moreover, it would be very

surprising if both an odontocete and a pinniped were to evolve closely similar social displays, rituals, or modes of fighting that were used in and out of water, respectively, by animals of such very different body form.

If Fay (1982:137) is correct in attributing a social selective pressure for tusk enlargement to all polygynous pinnipeds (and this may well be true), then we might expect to find convergences on the walrus morphotype among other pinnipeds if we found them anywhere—yet this is not the case. We think Fay is correct in arguing that benthic suction feeding was the key adaptive shift that led to the enlargement of tusks in walruses. In view of the similar morphology seen in *Odobenocetops*,

however, and the difficulty of applying the same social explanation to this otherwise very different animal, we propose that the utility of the tusk-like structures in both cases was primarily in feeding (as orientation guides for the mystacium) and only secondarily in social interactions. In other words, we consider the tusk-like structures to be an integral part of the "benthic suction-feeding" character complex, because we see no other plausible explanation for this striking correlation of characters.

Students of modern *Odobenus* should therefore reexamine its feeding behavior with the possibility in mind that the tusks may serve as orientation guides, as suggested herein. This hypothesis should be amenable to experimental tests.

Addendum

This paper was already in the editorial process when three new skulls of *Odobenocetops* were collected from the Pisco Formation, which justified the publication of a preliminary note (Muizon et al., 1999).

One of the skulls (SMNK 2491), referred to *O. peruvianus,* is from the Sud-Sacaco locality and from the SAS horizon (as was the holotype of *O. peruvianus*), which is earliest Pliocene in age. It is almost symmetrical and bears two small tusks; although the right is slightly larger than the left, it is still drastically smaller than the large tusk of the holotype. The alveolar sheaths are relatively small and of the same size. The two tusks are incomplete and their apices are missing. The right sheath is partly damaged at its apex, but because the preserved portion of the tusk is distinctly longer than the sheath as preserved, it is clear that the tusk was erupted. The left sheath and tusk also are incomplete, and the tusk is broken in the alveolus. It is therefore not possible to determine whether the left tusk was erupted. In the narwhal the unerupted tusks of the female are generally similar in size and definitely smaller than the large left tusk of the male, so this new skull of *Odobenocetops peruvianus* (SMNK 2491) was identified as a female.

The other two skulls (SMNK 2492 and MNHN SAO 202) come from the locality of Sacaco in the SAO horizon, which is slightly younger than the SAS horizon, in which the *O. peruvianus* specimens were found. They were referred by Muizon et al. (1999) to a different and new species, *O. leptodon*. The holotype (SMNK 2492) is a partially damaged skull that retains both tusks in situ. The right tusk is more than 1.35 m long as preserved (the apex was broken and worn during life), and its erupted portion measures 1.07 m. The left tusk is small and slender and was approximately 25 cm long. Its apex bears a distinct wear facet, which indicates that the tooth was erupted. The presence of a very long right tusk and of an erupted left tusk in *O. leptodon* is an indication (not a proof) that this condition also could be present in *O. peruvianus*. This has to be confirmed by the discovery of new specimens of *O. peruvianus*, however.

The morphology of the snout of *O. leptodon* differs from that of *O. peruvianus* in being more rounded and wider in dorsal view and in lacking large premaxillary foramina. Furthermore, the dorsal face of the premaxilla bears a fossa for a premaxillary sac, and a pair of supplementary rostral bones is present at the anterodorsal apex of the snout. The anterodorsal edge of the orbit is only slightly concave in *O. leptodon,* whereas it is deeply notched in *O. peruvianus*. The presence of premaxillary sacs (which were probably absent in *O. peruvianus*) is probably an indication of the presence of a melon in *O. leptodon*. This organ, related to echolocation, was probably absent or vestigial in *O. peruvianus*. As stated above in the text, the inferred absence of a melon in *O. peruvianus* was probably compensated for by good anterodorsal binocular vision. Muizon et al. (1999) concluded that binocular vision was either reduced or absent in *O. leptodon* and that this was compensated for by echolocation abilities inferred from the probable presence of a melon.

The three new skulls have at least one tympanic and one periotic in situ. The characteristic morphology of these bones (especially the massiveness of the anterior process of the periotic) definitely confirms the referral of the periotics and tympanic described above to *Odobenocetops peruvianus*.

The holotype skull of *Odobenocetops leptodon* was associated with its atlas. The only occipital condyle preserved on the skull is damaged, which makes it difficult (but not impossible) to evaluate the position of the head relative to the axis of the body. An extrapolation could be done using the new skull of *O. peruvianus* (SMNK 2491), which has well-preserved condyles. The position of the atlanto-occipital articulation of *Odobenocetops* indicates that in swimming position the head was bent ventrally, bringing the dorsal plane of the skull into an anterodorsal orientation. With the head in this position, the long tusk was almost parallel to the long axis of the body. This interpretation is compatible with the length of the large tusk, as it is unlikely that such a long appendage could be at an angle of about 45° to the body during swimming (Muizon et al., 1999, fig. 2). The head of *Odobenocetops peruvianus* in Figure 20 therefore

should probably be bent slightly ventrally to make the long tusk parallel to the axis of the body.

To conclude, the new specimens of *Odobenocetops* indicate the following:

1. The long right tusk of *O. peruvianus* was probably longer than initially thought, although this needs to be confirmed by the discovery of new specimens of this species.

2. The small left tusk was probably erupted, but this also has to be confirmed by the discovery of new specimens.

3. The female of *O. peruvianus* had two small tusks, the right being only slightly larger than the left. This condition is likely to have also occurred in *O. leptodon,* although this has to be confirmed by additional specimens.

4. The new specimens confirm referral to *O. peruvianus* of the periotics and tympanic described above.

5. During swimming, the head of both species was bent ventrally and, in such a position, the long tusk was almost parallel to the axis of the body. *Odobenocetops peruvianus* (which has a deeply notched anterodorsal edge of the orbit) therefore had good dorsal (anterior) binocular vision when swimming.

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