

New discoveries of fossil toothed whales from Peru: our changing perspective of beaked whale and sperm whale evolution

OLIVIER LAMBERT¹

SUMMARY: Following the preliminary description of a first fossil odontocete (toothed whale) from the Miocene of the Pisco Formation, southern coast of Peru, in 1944, many new taxa from Miocene and Pliocene levels of this formation were described during the 80's and 90's, (families Kentriodontidae, Odobenocetopsidae, Phocoenidae, and Pontoporiidae). Only one Pliocene Ziphiidae (beaked whale) and one late Miocene Kogiidae (dwarf sperm whale) were defined. Modern beaked whales and sperm whales (Physeteroidea = Kogiidae + Physeteridae) share several ecological features: most are predominantly teuthophagous, suction feeders, and deep divers. They further display a highly modified cranial and mandibular morphology, including tooth reduction in both groups, high vertex and sexually dimorphic mandibular tusks in ziphiids, and development of a vast supracranial basin in physeteroids. New discoveries from the Miocene of the Pisco Formation enrich the fossil record of ziphiids and physeteroids and shed light on various aspects of their evolution. From Cerro Colorado, a new species of the ziphiid *Messapicetus* lead to the description of features previously unknown in fossil members of the family: association of complete upper and lower tooth series with tusks, hypothetical sexual dimorphism in the development of the tusks, skull anatomy of a calf... A new small ziphiid from Cerro los Quesos, *Nazcacetus urbinai*, is characterized by the reduction of the dentition: a pair of apical mandibular tusks associated to vestigial postapical teeth, likely hold in the gum.

Two new stem-physeteroids, one yet unnamed from the late middle Miocene of Cerro la Bruja, and the other, *Acrophyseter deinodon*, from the latest Miocene of Sud-Sacaco, display enlarged upper and lower teeth associated to a large temporal fossa, suggesting a raptorial rather than suction feeding technique.

Key words: Cetacea, Cetacean fossils, Pisco Formation, Kogiidae, Odontoceti, Perú, Physeteridae, Physeteroidea.

RIASSUNTO: A partire dalla descrizione preliminare di un primo odontocete fossile (cetaceo dotato di denti) dal Miocene della Formazione Pisco dalla costa meridionale del Perú nel 1944, molti nuovi taxa sono stati descritti negli anni '80 e '90 da livelli miocenici e pliocenici di questa formazione. Solo un Ziphiidae pliocenico e un Kogiidae (capodoglio nano) tardo miocenico sono stati altresì definiti attraverso nuove scoperte nella Formazione Pisco che arricchiscono la documentazione fossile e gettano luce su vari aspetti dell'evoluzione delle rispettive famiglie. Una nuova specie dello zifide *Messapicetus* da Cerro Colorado conduce alla descrizione di caratteri precedentemente sconosciuti nei membri fossili della famiglia. Un nuovo piccolo zifide da Cerro los Quesos, *Nazcacetus urbinai*, è caratterizzato dalla riduzione della dentizione. Due nuovi fiseteroidi basali, uno ancora non denominato e proveniente dal Miocene medio di Cerro la Bruja, e l'altro, *Acrophyseter deinodon*, dal Miocene terminale di Sud-Sacaco mostrano denti superiori e inferiori molto grandi e associati ad un'ampia fossa temporale lasciando supporre una tecnica di alimentazione raptoria.

Parole chiave: Cetacea, Cetacei fossili, Formazione Pisco, Kogiidae, Odontoceti, Perú, Physeteridae, Physeteroidea.

Introduction

Study of fossil odontocetes (toothed whales) from Peru

The history of the study of fossil toothed whales from Peru started with the description of *Inzacetus broggii* by Colbert (1944). The holotype, a

partial skeleton discovered close to the mouth of the Ica River, along the south coast of Peru, comes from the lowest levels of the Pisco Formation and is dated from the middle Miocene (Muizon, 1988). Colbert (1944) first attributed the specimen to a beaked whale (Ziphiidae) but a new preparation

1. Département de Paléontologie, Institut royal des Sciences naturelles de Belgique, rue Vautier, 29, B-1000 Brussels, Belgium and Département Histoire de la Terre, Muséum national d'Histoire naturelle, rue Buffon, 8, F-75005, Paris, France. e-mail: olambert@mnhn.fr.

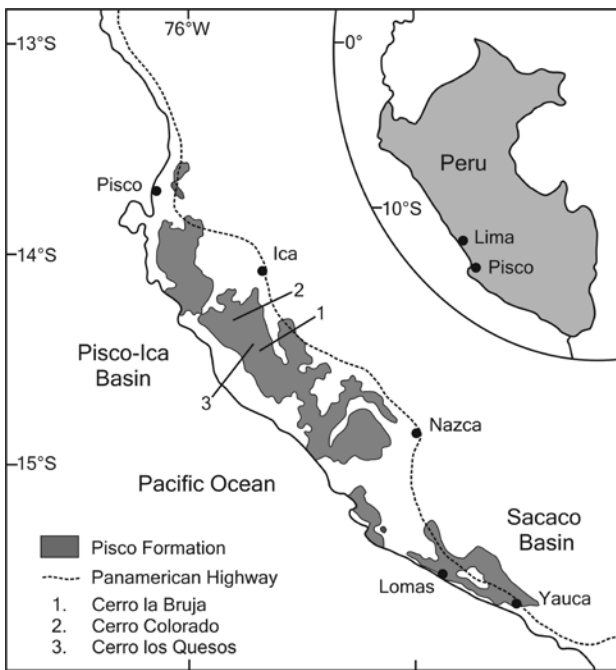


Fig. 1 - Map of the southern coast of Peru in the area of Pisco, showing the extent of the Mio-Pliocene Pisco Formation in the Pisco-Ica and Sacaco basins, and highlighting the main localities discussed in the text: Cerro la Bruja, Cerro Colorado, and Cerro los Quesos (modified from Muizon, 1988).
 Fig. 1 - Mappa della costa meridionale del Perù nell'area di Pisco che mostra l'estensione della Formazione Pisco di età mio-pliocenica nei bacini Pisco-Ica e Sacaco e individua le principali località discusse nel testo: Cerro la Bruja, Cerro Colorado e Cerro los Quesos (da Muizon, 1988 modif.)

and the re-description of the holotype lead to its placement in the paraphyletic fossil delphinoid family Kentriodontidae (Muizon, 1988).

More than thirty years later, extended fieldwork in the Pisco-Ica Basin and Sacaco Basin undertaken by Christian de Muizon yielded an impressive amount of fossil marine mammal material from different localities and levels of the Pisco Formation (Fig. 1), ranging from middle Miocene to Pliocene and displaying a high preservation quality. Besides pinnipeds (seals) and mysticetes (baleen whales), a large part of the specimens were referred to various families of odontocetes (Muizon, 1981, 1983a,b,c, 1984, 1986, 1988; Muizon, DeVries, 1985), revealing high toothed whale diversity and the early radiation of several modern groups. In the Miocene layers Muizon (1986, 1988) described two new porpoises (Phocoenidae): *Australithax intermedia* and *Lomacetus ginsburgi*, two kentriodontids in addition to *Incacetus broggi*: *Atocetus iquensis* and *Belonodelphis peruanus*, one pontoporiid *Bra-*

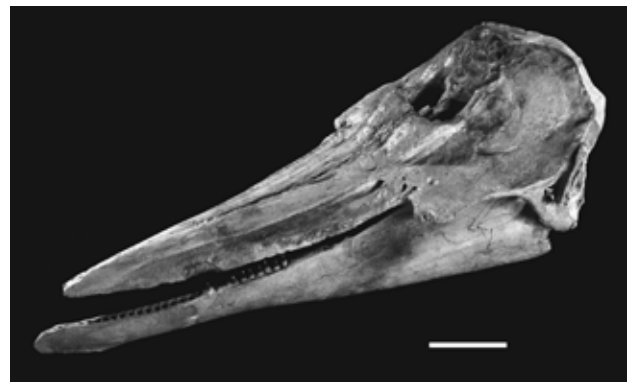


Fig. 2 - Skull and mandible of the Pliocene phocoenid *Piscalithax longirostris* (holotype), in anterolateral view. Scale bar = 5 cm. Photo: D. Serrette (Muséum National d'Histoire Naturelle, Paris).

Fig. 2 - Cranio e mandibola del focenide *Piscalithax longirostris* (olotipo) in norma anterolaterale. Barra di riferimento = 5 cm. Foto: D. Serrette (Muséum National d'Histoire Naturelle, Paris).

chydelfhis mazeasi (related to the Recent estuarine to coastal dolphin *Pontoporia blainvillei*), and one unusual kogiid (dwarf sperm whale) *Scaphokogia cochlearis*, for which a new subfamily Scaphokogiinae was erected. Apart from the latter, only one fragment of dentary of a physeteroid from Cerro la Bruja was mentioned (Muizon, 1988). From the Pliocene part of the Pisco Formation, Muizon (1983a,b,c, 1984) further described an additional porpoise, *Piscalithax longirostris* (Fig. 2), a new pontoporiid, *Pliopontos littoralis*, and the beaked whale (Ziphiidae) *Ninoziphius platyrostris*.

Following these major and detailed works on the fossil odontocete faunas of Peru, Pilleri and colleagues published preliminary notes on some cetaceans from the Pisco Formation. Among these, they described the new Pliocene delphinid (true dolphin) *Tursiops oligodon* Pilleri and Siber, 1989a. They tentatively referred to the family Pontoporiidae a late Miocene odontocete from the Aguada de Lomas locality that they named *Piscorhynchus aenigmaticus* Pilleri and Siber, 1989b. The holotype is much likely a phocoenid. Finally Pilleri (1989) also proposed the presence of a eurhinodelphinid (long-snouted dolphin family) in the same locality of Aguada de Lomas, based on a skull fragment and a humerus. However, no diagnostic character of the family Eurhinodelphinidae could be detected on these elements.

Later, in addition to works on aquatic sloths (Xenarthra) from Pliocene layers of the Pisco



Fig. 3 - Skull of the walrus-like Pliocene delphinoid *Odobenocetops peruvianus* (holotype), in anterolateral view, displaying the truncated rostrum and the base of the right premaxillary tusk. Scale bar = 5 cm. Photo: V. Krantz (National Museum of Natural History, Smithsonian Institution, Washington D.C.).

Fig. 3 - Cranio del delfinoide pliocenico *Odobenocetops peruvianus* (olotipo) in norma anterolaterale; si noti la somiglianza con il cranio di un leone marino, il rostro tronco e la base della zanna premaxillare destra. Barra di riferimento = 5 cm. Foto: V. Krantz (National Museum of Natural History, Smithsonian Institution, Washington D.C.).

Formation, Muizon (1993), Muizon *et al.* (1999), Muizon and Domning (2002), and Muizon *et al.* (2002) described two species of *Odobenocetops*, an extraordinary tusk-bearing Pliocene delphinoid having convergently evolved the feeding adaptations of the walrus *Odobenus* (Fig. 3).

New localities of the Pisco Formation

In addition to several localities in the Sacaco Basin (Sacaco, Sud-Sacaco, Montemar, Aguada de Lomas), Muizon prospected one rich locality in the Pisco-Ica Basin, Cerro la Bruja. Since the nineties new promising localities were discovered in the Pisco-Ica Basin, most of them by Mario Urbina. In June 2006, our Belgian-Dutch-Italian-Peruvian team visited the locality of Cerro Colorado (Figs. 4-5), 35 km south-west to the city of Ica. Part of us came back there several times in 2007 and 2008. In November 2008, we prospected Cerro los Quesos, a rich locality 5.5 km west to Cerro la Bruja that we only briefly visited in 2006 (Fig. 1).

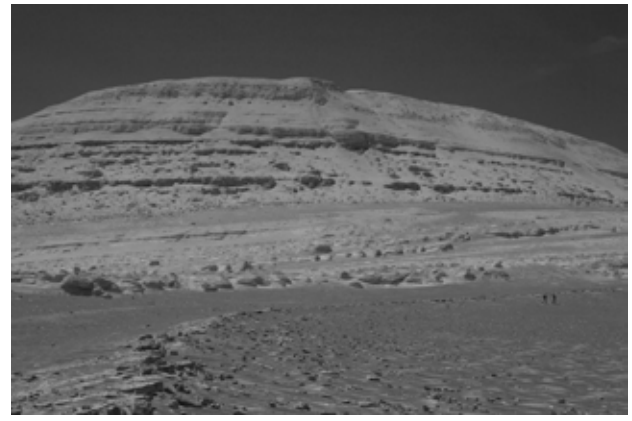


Fig. 4 - Prospection in the locality of Cerro Colorado, in November 2008. The hill is made of Miocene layers of the Pisco Formation. Silhouettes on the right bottom give the scale. Photo: J. Reumer (Natuurhistorisch Museum, Rotterdam).

Fig. 4 - Prospezione nella località di Cerro Colorado nel novembre 2008. La collina è formata da strati miocenici della Formazione Pisco. Le silhouette a destra sullo sfondo danno la scala di riferimento. Foto: J. Reumer (Natuurhistorisch Museum, Rotterdam).



Fig. 5 - Field work in the locality of Cerro Colorado, in June 2006. Excavation of a skull and mandible of the late middle Miocene beaked whale *Messapicetus* n. sp. Photo: G. Bianucci (Università di Pisa).

Fig. 5 - Missione sul campo nella località di Cerro Colorado nel giugno 2006. Scavo di un cranio e mandibola dello bifide *Messapicetus* sp. nov. del tardo Miocene medio. Foto: G. Bianucci (Università di Pisa).

Preliminary geological and palaeontological work suggests that Cerro Colorado is one of the oldest localities of the Pisco Formation, just above the disconformity with the underlying Chilcatay Formation. Cetacean remains and molluscs indicate an age similar to or slightly older than Cerro la Bruja, around 12 Ma, late middle Miocene. The cetacean fauna of the top of the section in Cerro los Quesos is clearly younger, most probably belonging to the late Miocene. But the base of the section also shows similarities with the Cerro la Bruja locality; especially the presence of the short-beaked pontoporiid *Brachydelphis mazeasi* was recorded in both areas. In any case, new data including radiometric dating of ash layers and microfossil biostratigraphy (diatoms, radiolarians, etc.) should allow a better age determination of these Miocene levels of the Pisco Formation.

Cerro Colorado yielded a diversified fauna of cetaceans, seabirds, turtles, and fish, whereas only one fragment of pinniped limb was found. Among the cetaceans, at least two baleen whales (Cetotheriidae *s. l.*) were identified, as well as several small pontoporiids, one kentriodontine, two physeteroids, and one ziphiid (Fig. 5). In Cerro los Quesos we discovered in various levels one small cetotheriid, at least one large baleen whale (possibly a rorqual), small delphinoids, one pontoporiid, one phocoenid, at least one small physeteroid, and a new ziphiid. Finally, a short visit of several outcrops around Cerro la Bruja lead to the identification of one delphinoid and one ziphiid, in addition to the excavation of physeteroid remains.

In the next paragraphs we will focus on the new physeteroids and ziphiids from the Pisco Formation, providing preliminary systematic, phylogenetic and palaeoecological discussions. But first we will briefly present the ecology and skull morphology of modern beaked whales and sperm whales, followed by a summary of their respective fossil record.

Advances in the study of the evolutionary history of beaked whales and sperm whales

Brief overview of the ecology and morphology of modern beaked whales and sperm whales

Modern beaked whales (family Ziphiidae) and sperm whales (superfamily Physeteroidea) are

contrasted in terms of their diversity. 21 modern species of beaked whales are described in six genera, with sizes ranging from 3.7 to 12.8 meters (Balcomb, 1989; Dalebout *et al.*, 2002; Heyning, 1989a; Mead, 1989a,b,c), whereas only three species of sperm whales are known: the large *Physeter macrocephalus* with adult males reaching a length of 18 meters and two species in the much smaller genus *Kogia* (Caldwell, Caldwell, 1989; Rice, 1989).

These two groups share a series of ecological and morphological features, which sometimes lead to their phylogenetic grouping in a single clade (e.g., Fordyce, 1994; Muizon, 1991; for different relationships, see Cassens *et al.*, 2000; Geisler, Sanders, 2003; Lambert, 2005a). Both beaked whales and sperm whales are deep divers, feeding in deep oceanic water on the continental slopes and submarine canyons. At least part of the beaked whale species routinely dive at depths exceeding 1000 meters and *Physeter macrocephalus* has been recorded at an extraordinary depth of 3000 meters (e.g., Schreer, Kovacs, 1997; Tyack *et al.*, 2006). Their main (but not exclusive) prey items are cephalopods, which they catch by suction (Heyning, Mead, 1996; Werth, 2004).

The skull and mandibular morphology is highly modified compared to other modern odontocetes. In both groups the dentition is strongly reduced. Most modern beaked whales only retain one or two pairs of lower teeth, modified in tusks in adult males. These tusks are thought to be used in intraspecific fights; even if this phenomenon could not be observed yet, numerous linear scars on the body of animals suggest frequent violent tusk-body contacts (Heyning, 1984; MacLeod, 1998, 2002; Mead *et al.*, 1982). In sperm whales only the lower teeth are functional; upper teeth are sometimes present but they do not erupt. Furthermore, in beaked whales the vertex of the skull is elevated and bears premaxillary crests (Heyning, 1989b). The mesorostral groove on the rostrum is often filled with dense and thick bone, especially in adult males, differing on that point from all other modern odontocetes (Heyning, 1984). The most striking facial structure of the sperm whales is the vast supracranial basin excavating the dorsal surface of the skull. This basin contains the spermaceti organ and other structures associated to the production and transmission of echolocation sounds (Cranford

et al., 1996; Cranford, 1999; Madsen *et al.*, 2002; Mead, 1975a). The basin is associated to a marked asymmetry of the bony nares and surrounding bones, reflecting the asymmetry of the nasal passages and sound producing elements. Fossil specimens mostly give us information about the bony elements, which, can provide clues about the non-preserved associated soft tissues and, by comparison with modern members of the lineages and other groups of marine mammals, elements of the ecology of these extinct animals.

Fossil record of beaked whales and sperm whales

Except for non-diagnostic rostrum fragments (*e.g.*, Glaessner, 1947; Mead, 1975b; Miyazaki, Hasegawa, 1992; Whitmore *et al.*, 1986), the fossil record of beaked whales has long been limited to Western Europe (Abel, 1905; Capellini, 1885; Cuvier, 1823; du Bus, 1868) and the east coast of USA (Cope, 1895; Leidy, 1876, 1877).

The Peruvian south coast was the first area to yield a new beaked whale based on diagnostic material: as mentioned above, *Ninziphius platyrostris* originates from early Pliocene layers of the Pisco Formation (Muizon, 1983b, 1984). The holotype displays a partial skull with the ventral area especially well preserved and, even more interestingly, an associated mandible with a complete series of robust teeth, ear bones, and several post-cranial elements of the skeleton. Later, Muizon (1991) referred to the family Ziphiidae a skull from much older early Miocene strata of Washington State, west coast of USA, which he named *Squaloziphius emlongi*. The affinities of the latter are however still debated (Fordyce, Barnes, 1994; Geisler, Sanders, 2003; Lambert, Louwye, 2006).

In Europe, the new beaked whale *Messapicetus longirostris* was described from late Miocene beds of a quarry of Pietra leccese, in the south of Italy (Bianucci *et al.*, 1992, 1994), and *Tusciziphius crispus* Bianucci, 1997 was erected based on a Pliocene partial skull from Tuscany previously referred to the common species *Choneziphius planirostris*. It should be noted that *Tusciziphius* is now also recorded on the east coast of USA (Post *et al.*, 2008). More recently the large collection of partial skulls from the Neogene of the area of Antwerp, north of Belgium, attributed by Abel (1905) to the genera *Choneziphius* Duvernoy, 1851 and *Mioziphius* Abel, 1905 was reviewed (Lam-

bert, 2005b). This systematic revision lead to the definition or redefinition of species in the genera *Aporotus* du Bus, 1868, *Beneziphius* Lambert, 2005, *Choneziphius*, and *Ziphirostrum*. An additional new species known from a single partial skull, *Caviziphius altirostris*, was added to this faunal list by Bianucci and Post (2005). Also from the southern margin of the North Sea, the new middle Miocene taxon *Archaeoziphius microglenoideus* Lambert and Louwye, 2006 was described based on three partial skulls. One of these skulls could be dated by means of dinoflagellates as late Langhian to early Serravalian, constituting the oldest reported beaked whale known by cranial material (Lambert, Louwye, 2006).

Finally, an unexpectedly high diversity of Neogene beaked whales was revealed through the study of a large collection of cranial remains dredged from the sea bottom off the coasts of South Africa (Bianucci *et al.*, 2007, 2008a); new species were described in the new genera *Africanacetes*, *Ihlangesi*, *Izikoziphius*, *Khoikhoicetus*, *Microberardius*, *Nenga*, *Pterocetus*, and *Xhosacetes*, and in the genera *Mesoplodon* and *Ziphius*, both including modern species.

The fossil record of the sperm whales is rather scanty; it goes back to the Late Oligocene of Caucasus, with the poorly known *Ferecetootherium kelloggi* (Mchedlidze, 1970). Among the oldest forms with more significant cranial material are the early Miocene species from Patagonia, Argentina *Diaphorocetus poucheti* (Moreno, 1892), *Idiorophus patagonicus* (Lydekker, 1893), and *Praeulophyseter gualichensis* Caviglia and Jorge, 1980. All these Patagonian fossil sperm whales already possess a well-formed supracranial basin.

On the west coast of USA, the large middle Miocene species *Aulophyseter morricei* Kellogg, 1927 is known by several specimens (Kellogg, 1927; Kimura *et al.*, 2006). A more fragmentary skull from the middle Miocene of California has been named *Idiophyseter merriami* Kellogg, 1925. Based on another fragmentary skull from the locality of Isla Cedros, Mexico, Barnes (1973, 1984) built the new taxon *Praekogia cedrosensis* Barnes, 1973, which was at that time the first fossil kogiid recorded. It is only some years later that, as seen above, Muizon (1988) published his work on *Scaphokogia*, from the late Miocene of Peru. The best known physeteroid species from the east

coast of USA is the middle Miocene *Orycterocetus crocodilinus* Cope, 1868, for which several nicely preserved skulls have been described and figured by Kellogg (1965). Recently, the description of the kogiid *Aprixokogia kelloggi*, from the Pliocene of North Carolina, was published by Whitmore and Kaltenbach (2008).

During the second part of the nineteenth century, the southern margin of the North Sea yielded various Miocene sperm whale remains displaying a wide range of sizes. Some of the largest fossils were placed in the species *Physeterula dubusi* Van Beneden, 1877. *Eudelphis mortezelensis* du Bus, 1872 and *Placoziphius duboisi* Van Beneden, 1869 are distinctly smaller, and the tiny *Thalassocetus antwerpiensis* Abel, 1905 had a size close to the Recent *Kogia breviceps*. The systematics and the phylogenetic affinities of all these North Sea species were recently reviewed (Lambert, 2008). In that study, *Thalassocetus* was confirmed as a kogiid, a referral already made by Bianucci and Landini (2006). From the Mediterranean (Tuscany), Bianucci and Landini (1999) referred to the genus *Kogia* the Pliocene species *Hyperoodon pusillus* Pilleri, 1987. Based on a well preserved specimen including the skull, the mandible, teeth, and a part of the post-cranial skeleton, the same authors recently erected the new genus and species of large late Miocene sperm whale *Zygophyseter varolai* Bianucci and Landini, 2006, from Apulia, southern Italy.

From the Middle Miocene of Austria, Kazár (2002) referred a partial skull to the North Sea species *Placoziphius duboisi*; this attribution has been temporarily questioned, pending new observations on the original material (Lambert, 2008).

A rather complete large skeleton with a damaged skull from early middle Miocene layers of Japan has been first assigned to the genus *Scaldicetus* by Hirota and Barnes (1995), but this genus being mostly defined with poorly diagnostic dental characters, Kimura *et al.*, (2006) later placed the Japanese taxon in the new genus *Brygmophyseter*.

These fossil taxa provide important clues about the evolution of the cranial and mandibular morphology of beaked whales and sperm whales, and therefore about the ecological changes in various lineages of these two diversified clades. However, a part of the species are based on fragmentary material, specially ziphiids dredged from the sea bottom, and skull-mandible associations are rare in the fossil record.

New beaked whales from the Miocene of Peru

Case study 1 - Cerro Colorado. All the ziphiid remains found in Cerro Colorado are referred to a new species of the genus *Messapicetus*. The latter was first described from the late Miocene of Italy, but also recorded on the east coast of USA (Fuller, Godfrey, 2007). In *Messapicetus* the rostrum is extremely elongated, more than in any other ziphiid, and it retains a complete series of upper teeth (Bianucci *et al.*, 1994). However, up to now, no mandible or teeth were found in association with the specimens from Italy and USA. In Cerro Colorado, several skulls were discovered with the mandible in situ (Figs. 5-6). Not surprisingly the alveoli of many lower teeth were identified, suggesting that *Messapicetus* was still able to firmly grasp its prey between its long upper and lower jaws. The striking feature of the lower jaw



Fig. 6 - Skull and mandible of the late middle Miocene beaked whale *Messapicetus* n. sp., from the locality of Cerro Colorado, in right lateral view. Scale bar = 10 cm. Photo: G. Bianucci (Università di Pisa).

Fig. 6 - Cranio e mandibola dello zifide *Messapicetus* sp. nov. dal tardo Miocene medio della località di Cerro Colorado in norma laterale destra. Barra di riferimento = 10 cm. Foto: G. Bianucci (Università di Pisa).



Fig. 7 - Skull and mandible of the late Miocene beaked whale *Nazcacetus urbinai* Lambert, Bianucci & Post, 2009 (holotype), from the locality of Cerro los Quesos, in left lateral view. Scale bar = 10 cm. Photo: G. Bianucci (Università di Pisa).

Fig. 7 - Cranio e mandibola dello zifide miocenico *Nazcacetus urbinai* Lambert, Bianucci, Post, 2009 (olotipo) dalla località di Cerro los Quesos in norma laterale sinistra. Barra di riferimento = 10 cm. Foto: G. Bianucci (Università di Pisa).

is the presence of a pair of enlarged teeth at the anterior end of the robust symphyseal portion. Among modern ziphiids, such an association of complete upper and lower dentition with tusks is only seen in the rare *Tasmacetus shepherdi*. A similar condition was also described in the Pliocene ziphiid *Ninoziphius* (Muizon, 1984). On the rostrum of *Messapicetus*, the morphology of the premaxillae is modified compared to most other odontocetes: these bones are thick and contact each other medially, dorsally closing the mesorostral groove on a considerable length. A similar condition is observed, sometimes much more developed, in several other fossil beaked whales, for example *Choneziphius* or *Ziphirostrum*. Associated with the tusks, which are likely used as weapons during intraspecific fights in modern ziphiids, this unusual development of the premaxillae might correspond to a strengthening of the rostrum that would reduce the risk of fractures during fights (Lambert *et al.*, 2010a).

In Cerro Colorado, the size of the sample for *Messapicetus* was unusually high for a fossil odontocete: nine specimens were found, a majority of them corresponding to well-preserved skulls (Bianucci *et al.*, 2008b, 2010). Such a sample allows the investigation of two fields: ontogeny/sexual dimorphism and taphonomy. Anatomical observations, morphometric analyses, and comparison with modern ziphiid species lead to the identification of a calf of *Messapicetus* n. sp. The confrontation of the calf skull with adult speci-

mens allowed the discussion of ontogenetic trends in the development of the rostrum and vertex (elongation of the rostrum, fusion of the bones, changes in the size of the foramina; Bianucci *et al.*, 2010). In the adult sample, by comparison with Recent ziphiids (*e.g.*, MacLeod, Herman, 2004), differences observed at the level of the size of the tusk alveoli and robustness of the anterior portion of the mandible suggest some degree of sexual dimorphism; adult males would bear larger tusks surrounded by a more robust apex of the mandible (Lambert *et al.*, 2010a).

From a taphonomic point of view, none of the nine skulls of *Messapicetus* found in Cerro Colorado is associated to post-cranial remains, even cervical vertebrae. The only elements discovered with the skulls are mandible (for six of the nine specimens), ear bones, and hyoid bones. This condition contrasts highly with the numerous other cetacean remains (baleen whales, delphinoids) observed in Cerro Colorado: a vast majority of them are found as sub-complete skeletons. This observation suggests that the head of drifting carcasses of *Messapicetus* went quickly detached from the rest of the body, often before the loss of the mandible. The most obvious hypothesis to explain the difference with other cetaceans is that the head was more easily detached in *Messapicetus*, possibly because of the very long and heavy snout (Bianucci *et al.*, 2010).

Case study 2 - Cerro los Quesos. In the locality of Cerro los Quesos, M. Urbina discovered

one ziphiid specimen. This is a nicely preserved skull with the mandible in situ, loose tiny teeth, ear bones, and all the cervical vertebrae (Fig. 7). Based on this specimen the new genus and species *Nazcacetus urbinai* was erected (Lambert *et al.*, 2009a). This small ziphiid bears a rostrum considerably shorter than in *Messapicetus*. Upper and lower dentitions are strongly reduced: the absence of clear alveolar grooves and small teeth found in the matrix around the snout suggest that the teeth were held in gum, similar to the vestigial teeth of some Recent ziphiids (e.g., Boschma, 1951). Similarly to *Messapicetus*, a pair of apical mandibular tusks was likely originally present, but only an enlarged distal alveolus is preserved on the holotype. The premaxillae are slender on the rostrum and the mesorostral groove is not filled by the vomer. This new taxon indicates that the reduction of the dentition already occurred in some, but not all, late middle to early late Miocene ziphiids (Lambert *et al.*, 2009a). On the other hand, only the two first cervical vertebrae (atlas and axis) are fused, differing from all the modern ziphiids, which display three to seven fused cervical vertebrae.

New sperm whales from the Miocene of Peru

Case study 1 - *Acrophyseter deinodon*. Some years ago, the remains of a small fossil sperm whale were excavated in latest Miocene levels of the locality of Sud-Sacaco. The specimen, a nicely preserved skull with the associated mandible and teeth (Fig. 8), was only recently prepared at the Muséum national d'Histoire naturelle, Paris, and studied; it was placed in the new genus and species *Acrophyseter deinodon* Lambert *et al.*, 2008. The oral apparatus is characterized by a short and pointed rostrum, but more strikingly by 12 upper and 13 lower very robust teeth. In addition to this impressive dentition the temporal fossa is vast, extending far dorsally and posteriorly on the cranium and suggesting a powerful jaw musculature (temporal muscles). These features, contrasting with the absence of upper teeth and the proportionally small temporal fossa in the modern sperm whales *Kogia* and *Physeter*, support the interpretation of *Acrophyseter* as a raptorial flesh-eater. Not relying on suction for catching its prey, he grasped it with its powerful jaws and was possibly able to cut through the flesh with its posterior teeth. Considering an



Fig. 8 - Skull and mandible of the latest Miocene stem-physeteroid *Acrophyseter deinodon* Lambert, Bianucci & Muizon, 2008 (holotype), from the locality of Sud-Sacaco, in right lateral view. Scale bar = 10 cm. Photo: P. Loubry (Muséum National d'Histoire Naturelle, Paris).

Fig. 8 - Cranio e mandibola del fiseteride basale *Acrophyseter deinodon* Lambert, Bianucci, Muizon, 2008 (olotipo) dal Miocene terminale della località di Sud-Sacaco in norma laterale destra. Barra di riferimento = 10 cm. Foto: P. Loubry (Muséum National d'Histoire Naturelle, Paris).

estimated body size of 3.9-4.3 m, *Acrophyseter* might have preyed upon small odontocetes (pontoporiids, phocoenids), pinnipeds, or seabirds.

The supracranial basin is deep, posteriorly margined by a high nuchal crest. Contrary to *Physeter* the basin is limited to the cranium, not extending on the rostrum. The left bony naris is distinctly wider than the right naris and the right premaxilla is considerably widened. Similarly to the Mediterranean late Miocene *Zygophyseter* (see the reconstruction in Bianucci, Landini, 2006), this combination of primitive and derived features suggest that the nasal passages were already highly asymmetric, but that the spermaceti organ and other structures of the forehead did not extend on the rostrum, implying a posteriorly positioned blowhole differing from the modern *Physeter*.

In a preliminary phylogenetic analysis, *Acrophyseter* proved to be more basal than the clade grouping the last common ancestor of the modern *Kogia* and *Physeter*, and all the descendant of that ancestor. It must therefore be considered as a stem-physeteroid.

Case study 2 - new sperm whale from Cerro la Bruja. As mentioned above, only one physeteroid dentary fragment from Cerro la Bruja was described by Muizon (1988). Later, a skull and the associated mandible were collected in the same

locality, considerably older (late middle Miocene sensu Muizon, 1988) than Sud-Sacaco (latest Miocene) where *Acrophyseter deinodon* was found. In 2008, we came back to Cerro la Bruja to collect postcranial elements associated to the skull (some vertebrae, fragments of scapula, one phalanx). As in the skull of *Acrophyseter*, the supracranial basin is especially wide on the right side, overhanging the right orbit and antorbital notch, and ending at the rostrum base. However, the new skull from Cerro la Bruja is slightly larger, the rostrum was originally longer and less pointed, the mandible is less curved upwards, the temporal fossa is smaller and the coronoid process of the dentary is less erected and angled (Lambert *et al.*, 2009b). Some of these differences indicate a less powerful jaw musculature in the Cerro la Bruja specimen. Together with *Zygothyseter*, these new Peruvian physeteroids demonstrate that several lineages of raptorial sperm whales able to catch preys of a relatively large size persisted until the latest Miocene. It is only during the Pliocene that another odontocete lineage, large delphinids of the group of the killer whale *Orcinus orca*, will similarly acquire the ability to prey upon large preys, including pinnipeds, dolphins, but also baleen whales. Simultaneously, surviving Pliocene sperm whales will become efficient suction feeders and colonize new feeding areas in deeper oceanic regions.

Perspectives for future studies on fossil beaked whales and sperm whales in Peru

During the 2008 fieldtrip, several new fossil sperm whales from Miocene layers of the Pisco Formation were discovered in Cerro los Quesos (Fig. 9) and Cerro Colorado. One of them has already been excavated and its preparation is in progress. Others will be taken from the field in the near future. These new discoveries will help us to increase the knowledge of the evolutionary history of this highly specialized and diversified group, particularly focusing on the feeding and echolocation abilities and on the habitat.

The study of the beaked whales from Cerro Colorado is still in progress, and we hope that new investigations will provide clues to the ecology of *Messapicetus*. The analysis of the structure of the rostrum bones in various ziphiid taxa could



Fig. 9 - Discovery of remains of a small physeteroid in the late Miocene layers of the top of Cerro los Quesos, in November 2008. Photo: J. Reumer (Natuurhistorisch Museum, Rotterdam).

Fig. 9 - Scoperta dei resti di un piccolo fiseteroide negli strati tardo-miocenici sulla sommità di Cerro los Quesos nel novembre 2008. Foto: J. Reumer (Natuurhistorisch Museum, Rotterdam).

be especially informative. Different hypotheses have been proposed to explain the morphology of the pachyosteosclerotic rostrum of many ziphiids, and bone histology would certainly help to understand this phenomenon.

New phylogenetic analyses including recently described species should also be undertaken, in a way to investigate the relationships within each group (Physeteroidea and Ziphiidae) and between them. For example, a preliminary analysis of the new Peruvian remains of *Messapicetus* and *Nazcacetus*, including the ear bones and basicranium, allowed the identification of several homoplasies between beaked whale and sperm whale lineages.

Finally it should be kept in mind that the earliest steps of the history of both beaked whales and sperm whales are still very poorly understood. Indeed the oldest well-preserved fossils already display the most diagnostic features of each group (elevated vertex with premaxillary crests and large hamular process for the beaked whales, supracranial basin for the sperm whales). This means that we still lack some crucial steps of this history. The Peruvian Pisco-Ica region is not only rich in middle Miocene to Pliocene fossil-bearing layers. Older sediments from the Paracas, Otuma, and Chilcatay formations, ranging from the middle Eocene to the early Miocene, already yielded interesting cetacean remains (Marocco,

Muizon, 1988; Uhen *et al.*, 2008). It is clear that such layers, especially the poorly known Chilcatay Formation, should be studied in detail to localize some of the earliest stem-physeteroids and stem-ziphiids.

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Addendum

After acceptance of this manuscript, an article about a new giant raptorial sperm whale from the locality of Cerro Colorado, *Livyatan melvillei*, has been published adding new important information about the ecology and evolution of these large odontocetes (Lambert *et al.*, 2010b).

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Riassunto

A seguito della descrizione preliminare del primo odontocete fossile dal Miocene della Formazione Pisco (costa meridionale del Perù) da parte di E. H. Colbert nel 1944, C. de Muizon (e in misura minore G. Pilleri) hanno descritto molti nuovi taxa di odontoceti negli anni '80 e '90 da livelli miocenici e pliocenici della formazione. I reperti così individuati sono stati assegnati alle famiglie Kentriodontidae, Odobenocetopsidae, Phocoenidae e Pontoporiidae. In questi studi, sono stati individuati soltanto uno Ziphiidae, *Ninoziphius platyrostris* e un Kogiidae (capodoglio nano) tardo-miocenico, *Scaphokogia cochlearis*. Dal 2006, nuovi studi sul campo nel bacino Pisco-Ica hanno portato alla scoperta e alla prospezione di nuove località con strati medio- e tardo-miocenici con un elevato contenuto in vertebrati marini fossili: Cerro Colorado e Cerro los Quesos.

Gli zifidi e i capodogli (Physeteroidea: Kogiidae + Physeteridae) condividono alcune caratteristiche ecologiche: la maggior parte delle specie di questi gruppi è teutofaga, si alimenta per suzione e si immerge a grandi profondità. Oltre a queste specializzazioni, questi cetacei mostrano morfologie craniche e mandibolari altamente modificate che includono la riduzione della dentatura in entrambi i gruppi, lo sviluppo di un vertex alto e di zanne mandibolari accoppiate e dimorfiche negli zifidi, e lo sviluppo di un vasto bacino supracranico nei fiseteroidi.

La documentazione fossile di zifidi e fiseteroidi basata su reperti che vanno dall'Oligocene superiore al Pliocene da varie regioni del mondo

fornisce importanti informazioni su vari momenti della storia di queste linee evolutive anche se le specie fossili sono basate in parte su reperti frammentari. Le nuove scoperte dal Miocene della Formazione Pisco gettano luce su vari aspetti dell'evoluzione di zifidi e fiseteroidi.

Molti reperti di una nuova specie di zifide da Cerro Colorado (*Messapicetus*) hanno permesso di descrivere caratteristiche precedentemente sconosciute nei membri fossili della famiglia: l'associazione tra serie dentarie complete superiori e inferiori con zanne particolarmente grandi, un ipotetico dimorfismo sessuale nello sviluppo delle zanne e, infine, l'anatomia di un neonato che permette di discutere modificazioni legate allo sviluppo ontogenetico etc.

Un nuovo zifide da Cerro los Quesos, *Nazcaceetus urbinai*, è caratterizzato da una notevole riduzione della dentatura. Insieme ad una coppia di zanne mandibolari apicali, questo piccolo zifide mantiene solo denti vestigiali che probabilmente erano trattenuti dalla gengiva.

Due nuovi fiseteroidi basali, uno dei quali non ancora denominato e proveniente dal tardo Miocene medio di Cerro la Bruja, e l'altro, *Acrophyseter deinodon*, dal Miocene terminale di Sud-Sacaco, mostrano, in aggiunta ad un bacino supracranio anteriormente accorciato, denti superiori e inferiori particolarmente grandi. Associati ad un'ampia fossa temporale, questi denti suggeriscono una tecnica di alimentazione raptoria piuttosto che basata sulla suzione. Quindi, queste caratteristiche portano a ritenere che questo capodoglio fosse probabilmente un predatore di altri odontoceti, pinnipedi (foche) e/o uccelli marini.

Nuove scoperte dal Miocene della Formazione Pisco e nuovi studi sul campo già in progetto in livelli inferiori della Formazione Chilcatay certamente illumineranno alcune altre fasi dell'evoluzione di queste due linee evolutive di odontoceti così altamente specializzate.

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