UNIVERSIDADE DE ÉVORA

ESCOLA DE CIÊNCIAS E TECNOLOGIA

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Orientação:

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Function, sexual dimorphism and intraspecific variation of the bizarre rostral structures of the extinct beaked whale, *Globicetus hiberus*

Abstract

Ziphiids (commonly known as beaked whales) are deep-diving, echolocation-user odontocetes. The recently named Pliocene *Globicetus hiberus* bears a peculiar large bony sphere in the rostrum, the *mesorostral process of the premaxillae* or MPP. The origin and function of MPP is mysterious, but hypotheses are addressed: 1. malformation, deformity or disease; 2. ballast; 3. intraspecific fighting; 4. reflection and directional aim of the sound beam; 5. increasing the velocity of sound waves; 6. sound barrier; and 7. secondary sexual organ. Some hypotheses are rejected (1, 2, 6), others may play a secondary role (3, 4, 5) and we suggest the secondary sexual organ (7) as the most likely explanation. The MPP varies in size in the six specimens studied. During life, MPP grows allometrically in a subgroup but not in the other, suggesting that one subgroup corresponds to males and the other to females (sexual dimorphism). Beaked whales are able to perceive bones as distinctive echoic images with their sonar; therefore the MPP may work as a secondary sexual organ, the so-called “antlers inside” hypothesis.

Key words: Ziphiid cetaceans; beaked-whales; sexual dimorphism; secondary sexual organ; echolocation; skull anatomy

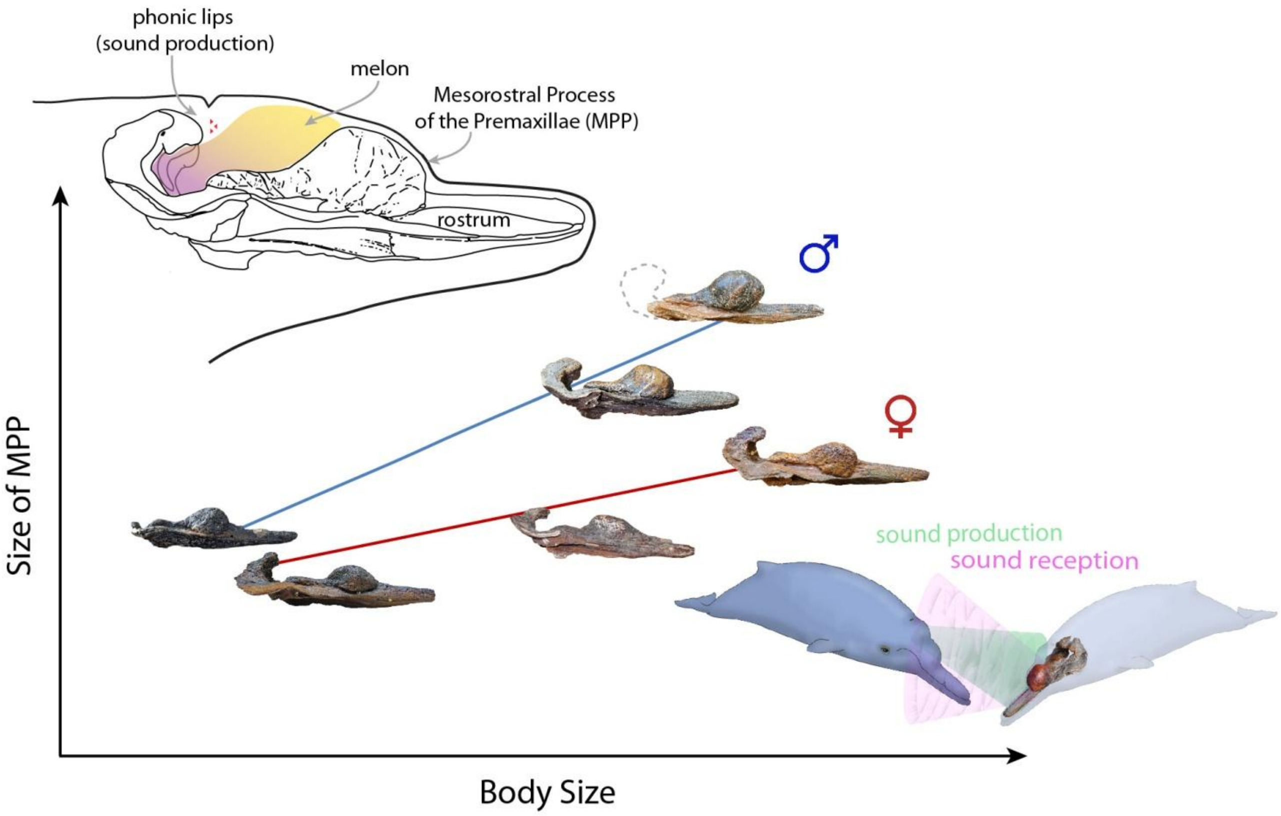
Função, dimorfismo sexual e variação intraespecífica das estruturas rostrais bizarras na baleia-de-bico extinta *Globicetus hiberus*

Resumo

Zifídeos (vulgarmente conhecidos como baleias de bico) são odontocetes ecolocalizadores capazes de efetuar mergulhos de grande profundidade. O recentemente nomeado *Globicetus hiberus* do Plioceno, exibe uma peculiar e grande esfera óssea no rostro, o *processo mesorostral da pré-maxila* ou MPP. A origem e função do MPP é misterioso, mas algumas hipóteses são abordadas: 1. malformação, doença ou deformidade; 2. lastro; 3. luta intraespecífica; 4. reflexão e orientação do feixe de som; 5. aumento da velocidade das ondas sonoras; 6. barreira sonora; e 7. órgão sexual secundário. Algumas hipóteses são rejeitadas (1, 2, 6), outros podem desempenhar um papel secundário (3, 4, 5) e sugerimos o órgão sexual secundário (7) como a melhor hipótese. O MPP varia de tamanho nos seis espécimes estudados. Durante a vida, o MPP cresce alométricamente apenas em um subgrupo, sugerindo que um deles corresponde a machos e o outro a fêmeas (dimorfismo sexual). Estas baleias seriam capazes de detetar ossos como imagens ecóicas distintas com o seu sonar, portanto, o MPP poderia funcionar como um órgão sexual secundário, a chamado hipótese das “hastes internas”.

Palavras-chave: Cetáceos zifídeos; baleia-de-bico; dimorfismo sexual; órgão sexual secundário; ecolocalização*;* anatomia craniana

Graphical abstract



Abbreviation List

Institutional

- **DGAOT** Departamento de Geociências Ambiente e Ordenamento do Território of **FCUP**, Porto, Portugal;
- **FCUP** Faculdade de Ciências da Universidade do Porto, Porto, Portugal;
- **PAL/UE** Paleontologia da Universidade de Évora, Évora, Portugal;
- **IEO** Instituto Español de Oceanografía, Gijón, Spain;
- **MHNUSC** Museo de Historia Natural Luis Iglesias, Universidad de Santiago de Compostela, Santiago de Compostela, Spain;
- **ML** Museu da Lourinhã, Lourinhã, Portugal;
- **MNHN** Muséum National d'Histoire Naturelle, Paris, France;
- **NMB** Natuurhistorisch Museum Boekenberg, Antwerp, Belgium;
- **IRSNB** Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium;
- **SGHN** Museo da Natureza da Sociedade Galega de Historial Natural, Ferrol, Spain;
- **NMR** Natuurhistorish Museum Rotterdam, Rotterdam, Nederland;
- **CRAM-Q** Centro de Recuperação de Animais Marinhos, Figueira da Foz (Quiaios), Portugal;
- **LARC** Laboratório de Arqueociências, Lisboa, Portugal.

Nomenclatural

- **MPP** Mesorostral Process of the Premaxillae
- **ICI** Inter-click-intervals
- **BL** Body Length
- **BW** Body Weight
- **PW** Postorbital Width of the Skull
- **WOC** Width across Occipital Condyles
- **EPB** Extant Phylogenetic Bracket

Table of contents

Table of figures

1. Introduction

The objective of the present work is to understand the function, development, osteology and evolution of the sphere-like structure (the *mesorostral process of the premaxillae*, MPP) in the skull of a poorly-known extinct species of beaked whale, *Globicetus hiberus*.

1.1. Beaked Whales (Ziphiidae; Cetacea)

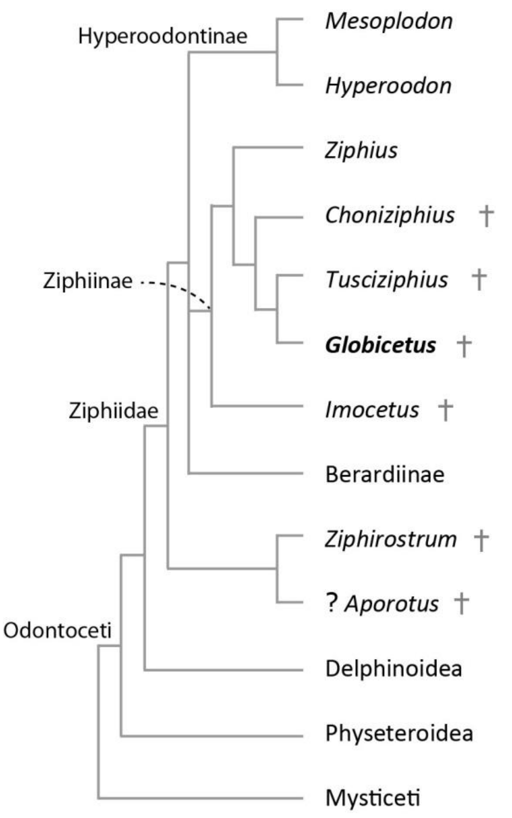


Fig. 1.1: Ziphiid phylogeny based on Lambert (2005), Bianucci et al. (2013) and Gol'din (2014); †, strictly fossil taxa.

Cetacea comprises three suborders, the extinct and paraphyletic Archeoceti, the Mysticeti or baleen whales and the Odontoceti or toothed whales. Beaked whales (family Ziphiidae Gray, 1850, within the Odontoceti) are the second most species-rich modern cetacean family, following the Delphinidae Gray, 1821. Ziphiidae includes at least 21 extant species (Dalebout *et al.,* 2002; Lambert, 2005; Bianucci *et al.*, 2007; Bianucci *et al.*, 2013) and a diverse fossil record (see cladogram in fig. 1.1). Beaked whales are widespread throughout the world's oceans, but remain one of the most poorly-known groups of cetaceans. Almost nothing is known about many of the species, and some have never been positively identified in the wild, largely due to their cryptic behaviors and deep-water habits (Mead, 1989; Hardy, 2005; Soldevilla *et al.,* 2005; Rommel *et al.,* 2005; Bianucci *et al.,* 2007; Lambert *et al.,* 2011; Bianucci *et al.,* 2013; Gol'din 2014). They are capable of staying submerged for long periods of time, with apnea durations over one hour (Tyack *et al*., 2006; Schorr *et al*., 2014) and diving to incredible depths. Down to more than 1800 meters have been documented in some species: individuals of Blainville's beaked whale (*Mesoplodon densirostris*) and Cuvier's beaked whales (*Ziphius cavirostris*) have been recorded at depths up to 1251 and 1888 meters (Tyack *et al*., 2006; Lambert *et al*., 2011; Schorr *et al*., 2014), with average foraging dives durations of 47 and 58 minutes, respectively (Tyack *et al*., 2006). A recent study by Schorr *et al*. (2014), reported a new mammalian dive record, setting it at a depth of 2992 meters and lasting 137.5 minutes by Cuvier's beaked whales.

In addition to their deep-diving habits, they exhibit dental reduction, being generally teuthophagous (squid-eating) suction-feeders (MacLeod & Herman, 2004; Soldevilla *et al.,* 2005; Rommel *et al*., 2005; Lambert *et al.,* 2011; Bianucci *et al.,* 2013) and are characterized by various skull specializations, some being considerably sexually dimorphic; these specializations place them as one of the most peculiar odontocete groups and lead to contrasted functional interpretations (Buffrénil *et al*., 2000; MacLeod, 2002; Lambert *et al.*, 2011). Jaws and facial skulls (rostra) of many living and extinct ziphiids contain various 'bizarre' bone structures (in the sense broadly introduced by Gould in his 1974 work on the evolutionary significance of antler and skull size in *Megaloceros giganteus*). Examples include a rod-shaped mesorostral ossification formed by the vomer, exaggerated premaxillae and premaxillary crests on the rostrum and vertex, dome-shaped and bulbous maxillary crests, thickened nasals of irregular shape and enlarged lower teeth (tusks); high compactness extending to a part or to all rostral bones is common to adult male specimens from many taxa of ziphiids along with occasional hyperplasia of the premaxillae (*Buffrénil et al.*, in review), resulting in highly species-specific morphological patterns of crests and associated structures, many demonstrating age variation and sexual dimorphism, providing evidence of evolution under sexual selection (Cranford *et al*., 2008a). Dentition is often reduced, generally developed in extant males only and used in combats (Hardy, 2005).The *Mesoplodon* genus is a good example of the sexual dimorphism in these animals: tusks grow only in sexually mature males, while females are effectively toothless (see, for instance Hardy, 2005 and Dalebout *et al*., 2008). Heavy scarring throughout the body of many beaked whales suggesting that the large teeth of the lower jaw are used aggressively (Mead, 1989; MacLeod & Herman, 2004; Hardy, 2005; Souza *et al*., 2005). Those species that accumulate scars are predominantly cetaceans that exhibit largely cephalopod-based diets and do not require complex teeth to capture their prey (Heyning & Mead, 1996).

Most odontocetes (toothed whales, dolphins and porpoises) spend the majority of their lives in an underwater world where light barely penetrates the surface layers and where vision is of limited value, for which they have to rely heavily on echolocation (Heyning, 1989a). They hunt and navigate through dark and turbid aquatic environments; the cephalic anatomy is marked by structural complexes that have long been recognized as components of a sophisticated biosonar system. The nasal apparatus in all odontocetes, as compared to all other mammals, is greatly enlarged, fitted with specialized lipid organs with complex surrounding muscles (Heyning, 1989a). It is equipped with rostral bones that sometimes form an amphitheater-like shape (Cranford *et al*., 2008b), perfect for accommodation of the soft tissues. The echolocation uses mainly the phonic lips for the production of sound, and the melon and connective tissues to guide the sound waves.

Members of the beaked whale family are characterized by a prominent beak and wide rostrum base, providing a broad surface area for muscle attachments and sometimes a bulging forehead. Some of their skull bones suffer from a condition called pachyosteosclerosis (MacLeod, 2002; Buffrénil *et al*., 2000; Buffrénil & Lambert, 2011; Lambert *et al*., 2011), an increase in bone inner compactness and thickening (Zioupos *et al*., 1997; Cranford *et al*., 2008a; Lambert *et al*., 2011; Li & Pasteris, 2014). The facial and rostral bones in ziphiid *Mesoplodon densirostris* (the maxillae, premaxillae, vomer, palatine, mesethmoid) exhibit the densest, most compact, mineralized and rigid osseous tissue described so far (Zylberberg *et al*., 1998; Zioupos *et al*., 1997; Lambert *et al*., 2011; Li & Pasteris, 2014; Buffrénil *et al*., in review). Other ziphiids can sometimes display protruding structural specializations of facial and rostral bones, exhibited by excrescences, rugosities or crests (Bianucci *et al*., 2007 & 2013; Gol'din, 2014; Buffrénil *et al*., in review).

Many of the spectacular diversity of anatomical solutions displayed by beaked whales are not only functional but also presumed to be a result of sexual selection. In the animal kingdom, secondary sexual traits are often easy to spot and characterize, but in cetaceans, little research has been conducted. Some whales do show impressive and very developed sexual traits, which can include the highly developed melon (*Globicephala* spp.), the spermaceti organ (sperm whale, *Physeter macrocephalus*) and the development of specialized tusks in a variety of beaked whales, such as the *Mesoplodon* genus (Mead, 1989; Dalebout *et al*., 2008).

In the skeleton of extant whales, some sexual dimorphism is easy to identify, since teeth, which are highly diagnostic, are only present in the lower jaw of males of certain species; in fossilized beaked whales it´s harder, since most of the recovered fossils are simply rostra, probably because of the high mesorostral ossification some of them suffer; unfortunately, this makes tooth identification impossible, since they are normally only present in the lower jaw, and do not appear very often in the fossil record. Size can be considerably sexually dimorphic: among aquatic mammals, it is normal for males to be larger than females (Berta *et al*., 2005), and in odontocetes this is usually also the case, such as in the killer whale and the sperm whale; but this is actually reversed when referring to the Mysticeti, and in some ziphiid species (Berta *et al*., 2005).

Lastly, it is important to be aware that beaked whales are elusive creatures and that there is still a lot to learn about their behavior, since some species actually have never been observed alive. A major limitation of this type of study is the scarce availability of both fossil and extant specimens impairing more accurate comparisons with fewer speculations. An additional problem is the inaccuracy of the data regarding the localities where many of the fossils were found, mostly because of the secrecy kept by some trawling fisherman about their fishing grounds. In the case of this study, this was not a major concern, but in future works dedicated to evolutionary studies and habitat reconstitutions it could be a considerable obstacle.

Record of marine mammals of Portugal through time

The worldwide fossil record of ziphiids is scarce compared to the widespread presence and diversity of extant species. Even now, the number of fossil species based on specimens originating from inland deposits remains small (Muizon, 1984; Lambert, 2005; Lambert & Louwye 2006; Bianucci *et al.*, 2010; Bianucci *et al*., 2013). However, specimens recovered from the ocean floor proved to be an essential source of information. These fossils, generally isolated skulls or fragmentary rostra, have been recovered from trawling and long fishing activities on the ocean bottom at depths up to 1000 m (Bianucci *et al*., 2007 & 2013; Antunes *et al.*, 2015).

Marine mammals from the Neogene of Portugal, occurring mostly in the Miocene, comprise 28 taxa: 24 Cetacea (16 Odontoceti and 7 Mysticeti), 3 Sirenia and 1 Pinnipedia (Estevens, 2006a), and could be used to distinguish four major evolutionary intervals, which according to Estevens (2006a), can be "correlated to local paleoenvironmental changes and global evolutionary and oceanographic events".

Excluding the fossils fished from the bottom of the Portuguese coastal waters, the Neogene marine mammals from inland deposits were still poorly studied until recently (Estevens, 2006b), although several occurrences were previously published; as pointed by Estevens (2000), in older fossil collections there are problems of systematic assignment of the specimens and of definition of their provenance. Published records of marine mammals for the Early Miocene of Lisbon include sirenians by Cotter (1956) and Choffat (1950a) (cited by Estevens, 2000: p. 324) and the work by Antunes (Antunes, 1959, 1969-70, 1984), who allocated several fragmentary fossils from the Early Miocene as belonging to sirenians (Estevens, 2000: p. 324). Estevens (2000: p. 324), also refers to work by Zbyszewski (1965 & 1967) of the fossil record for the Burdigalian of Foz da Fonte, originally reported to Cetacea and later reassigned to Sirenia. Zbyszewski (1954) also allocated a lower jaw collected in Melides in southern Portugal to a new ziphiid species, which he named *Palaeoziphius melidensis* (fig. 1.2). The genus *Palaeoziphius* was founded in 1905 by O. Abel, based on an incomplete mandible found in the Boldérien (Miocene) of the Old Fort (Antwerp) that had been classified by du Bus in 1872 as *Champsodelphis scaldensis* and by O. Abel in 1899 as *Acrodelphis scaldensis* (Zbyszewski, 1954); however, due to the fragmentary nature of the holotype material, the genus *Palaeoziphius* Abel (1905), has been considered *incertae sedis* Odontoceti by Lambert (2005: p. 445). The species *"Palaeoziphius" melidensis*, in particular, was regarded as a probable kentriodontid dolphin of uncertain affinities (Estevens, 2006b).

Fig. 1.2: Lower jaw of "*Palaeoziphius" melidensis* Zbyszewski (1954), currently on display in the Museu Geológico de Lisboa, Portugal. Original photograph by Octávio Mateus. Scale bar: 10 cm.

Besides some fragmentary fossil material from the Miocene assigned to a variety of genera and families of toothed cetaceans (Estevens & Antunes, 2004), one other important fossil discovery in mainland Portugal was the nearly complete skull, a partial left scapula, five lumbar vertebrae, and some fragments of ribs of a medium−sized kentriodontid dolphin, *Tagicetus joneti*; it was discovered in the middle Miocene of the Setúbal Peninsula, Lower Tagus Basin, and constitutes the first record of the subfamily from the east coast of the North Atlantic, and was assigned to a new genus and species (Lambert *et al*., 2005). The importance of the find relates to the reassertion of the Kentriodontinae as the best−known subfamily within the Kentriodontidae, since it was based on a nearly complete skull (Lambert *et al*., 2005). More recently, an anterior axial skeleton and a partial anterior limb of another kentriodontid dolphin (Cetacea; Delphinoidea) was discovered in the Tortonian sediments of Caparica, Portugal, by an FCT-UNL research team.

An overall review of the marine mammals from the Neogene of Portugal was carried out during PhD studies (Estevens, 2006b), which focused mainly on odontocetes and sirenians (although also referring mysticetes and phocids) and reviewed most of the previously published records.

Around the Portuguese Atlantic islands of the Azores archipelago, there is a rich living cetaceans fauna and the archipelago has also produced records of Late Neogene fossils of whales in Santa Maria Island, the only island in this volcanic archipelago with a significant sedimentary record (Estevens & Ávila, 2007). Estevens & Ávila (2007) reviewed the scarce fossil record of cetaceans from Santa Maria, including both the historical occurrences long cited in the literature and more recent ones. The most significant fossil occurrences belong to groups whose living representatives are mostly pelagic, such as large baleen and beaked whales (mostly Balaenopteridae and Ziphiidae).

Among these, there is one of the few beaked whale fossils described for Portugal, which was assigned to *Mesoplodon* sp. by Estevens & Avila (2007); they were able to identify the fossil as a portion of rostrum as belonging to Ziphiidae, due to "the cylindrical to laterally compressed shape of the rostrum, together with the lack of dental alveoli and the strong mesorostral ossification of the vomer" (Estevens & Ávila, 2007). There is only another beaked whale fossil record from Portugal, corresponding to a rostral fragment from the Miocene of Algarve, tentatively assigned to *Messapicetus* sp. (Estevens, 2006b).

Many modern species of cetacean live, visit and strand along Portuguese waters; on a side note, next are given some additional reports about strandings of beaked whales in Portuguese shores: in continental Portugal it has been reported the stranding of *Mesoplodon densirostris, Mesoplodon mirus* (namely male specimen Cram-Q figured in section 1.2.), *Ziphius cavirostris* and *Mesoplodon europaeus* (Reiner, 1979, Freitas, 2004, Santos-Reis & Mathias, 1996; and unpublished data). In Madeira archipelago, it has been reported the presence of *Ziphius cavirostris*, *M. densirostris*, and *Mesoplodon bidens* (Freitas, 2004, Santos-Reis & Mathias, 1996), while in Azores, *Hyperoodon ampullatus, M. densirostris,* and *M. bidens* (Santos-Reis & Mathias, 1996).

1.2. Production, transmission and reception of sound

The cephalic anatomy of toothed whales, Odontoceti, has long been recognized by its sophisticated biosonar system (Cranford et al., 2008a, 2008b). The nasal apparatus of odontocetes is greatly enlarged and fitted with specialized fat lipidic organs, connective tissues and a set of skull bones that form an hyperbolic paraboloid shape in the posterior part of the rostrum, compared by Cranford et al. (2008b: p. 1), to an amphitheater-like shape. Dense, thick and downturned rostrum, air sac fossae, cranial asymmetry and exceptionally broad maxillae (Geisler et al., 2014) are also features shared by all sonar-using whales.

The biosonar apparatus includes structures for sound generation and transmission, located on the dorsal part of the head (see, for example, Cranford et al., 1996, 2008a), but also components for the reception of the sound waves (fig. 1.3). These are associated to the mandibles and the presumed hearing apparatus located in two large furrows that run between the mandible on each side of the ventral aspect of the head (Cranford et al., 2008a) to the highly specialized and mineralized tympanic bulla (Buffrénil et al., 2000). The soft tissues used in the echolocation are mainly the phonic lips, melon and connective tissues.

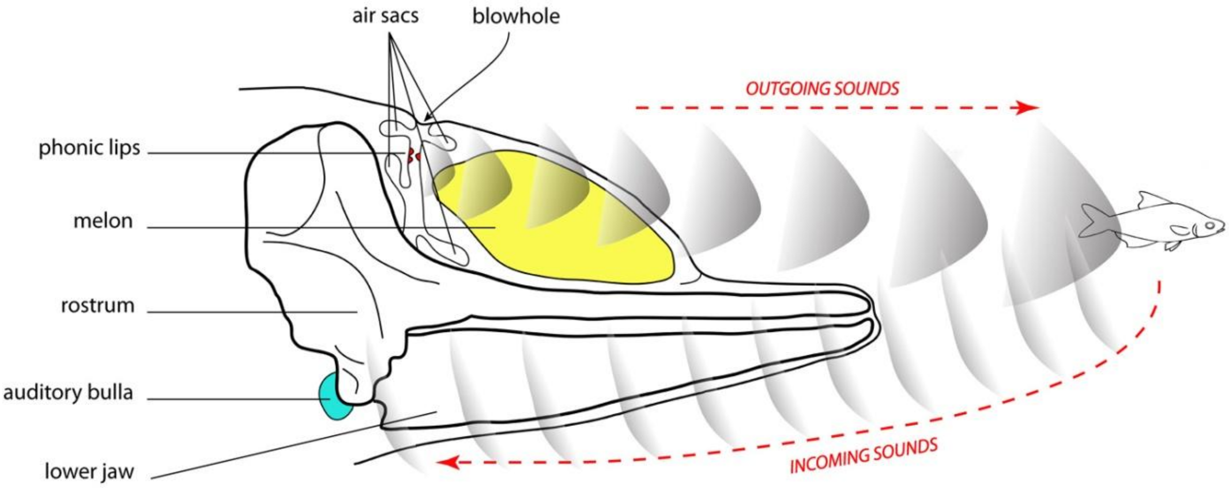


Fig. 1.3: Model of the production and reception of sound waves in *Delphinus*, and valid for all other Odontoceti.

The phonic lips, also called "museau de singe" (Pouchet & Beauregard, 1885 in Cranford et al., 2008a: p. 354), are composed of two separate sets of dense connective tissue which account for two separate virtual sound sources and produced beams that converged just outside the head (Cranford et al., 2008b). The phonic lips are connected to the nasal passage and the distal air sacs (Cranford, 1999) and to the prenarial basin air sacs. The fat bodies extend from the phonic lips, underneath the overhanging vertex of the skull to approximately halfway along the anterior portion of the rostrum. According to Soldevilla (2005: p. 2320), it was Norris (1968) who introduced the term "acoustic fats" to describe the mandibular fat bodies due to their supposed role in the sound propagation of the sonar beam. The melon , normally being the dorsal-most fat body (Cranford et al., 2008a), is a fat and connective adipose tissue with varying amount of connective tissue within it (Heyning, 1989a); it conducts the sound beam out of the head (Cranford et al., 2008b), which begins in the phonic lips, and is the most important acoustic fat of the head. From a structural point of view, the melon is composed of a graduation of tissues with a central core of acoustic lipids grading into more complex musculature, like dense connective tissue (theca) and blubber (Heyning, 1989a; Cranford et al., 1996 in Soldevilla et al., 2005: p. 2321), the last one different from other types of adipose tissue, being adapted to serve as a thermal insulator. It is typically set asymmetrically, slightly off to the right side and can be divided into two parts: one region represents the 'low density' section of the melon theorized to be the 'functional' portion of the melon organ that is homologous to the 'spermaceti organ' of the sperm whale, Physeter macrocephalus; the other part, represents the 'denser' region of the melon organ (Hardy, 2005). The lower density part sits next to important rostral bones that help redirect some of the sound, and the denser part is responsible for transmitting the sound from the head into the aquatic environment. The main distinction between the lipid fats, the melon and the anterior spermaceti organ in odontocetes can be tricky and is based primarily upon their position in the skull, their geometry and density differences (Heyning, 1989a; Cranford *et al.,* 2008a). The melon and the spermaceti organ have been considered to be homologous by some authors (Hardy, 2005; Cranford *et al.,* 2008a), however Heyning (1989a) disagrees and argues that "the only structure that even vaguely resembles the spermaceti organ is the adipose structure found in the prenarial basin of adult males of *Ziphius cavirostris*". In the present study, following the work by Cranford *et al*. (2008a), the ´low density´ section of the melon is referred as ´spermaceti organ´ or ´spermaceti-like organ´ and the ´denser´ region of the melon will just be called melon.

Cranford *et al.* (2008a) describes connective tissue theca as a bond of connective tissue that arches over the fat bodies of the forehead composed of fibers oriented in several directions, anchored to the vertex and the maxilla; they also point out that the melon in extant ziphiid *Ziphius cavirostris*, projects out through the arch, suggesting the pathway for sound transmission accepted for odontocetes and that the concave cavity on the posterior part of the rostrum (or prenarial basin) may have been formed as the fat body intruded into the region, ‘pushing aside’ the various bony elements; this would result in the extremely dense pachyosteosclerotic condition of the bones of the basin and be counterintuitive to the notion of bone absorption in the region.

The phonic lips are the primary source of sound and particularly of sonar signals in odontocetes (Cranford, 1999; Cranford *et al*., 2008a, 2008b). Cranford *et al*. (2008a) hypothesizes that “the phonic lips probably represent the ancient external closure of the nasal openings that have invaginated over evolutionary time so that the phonic lips are now located just inside the external nasal closure, the blowhole (K.S. Norris, personal communication)”; they have ridges and grooves (for visual aid, see Cranford *et al*., 2008a: p. 366) that vibrate by compression of the air sacs that surround them, and are believed to perhaps play a role, not just in producing the sound, but also in directing the flow of air.

The mechanism for producing the sound waves and beam is complex and is the result of several interactions between soft tissues and the bony anatomic components of the rostrum, as noted by Cranford *et al*. (2008b); they performed simulated sound beam direction by placing a sound source at the phonic lips, one to the right of the nasal septum and one to the left, of a recent dead *Ziphius cavirostris*. The beam produced overlapped in front of the head along its horizontal axis and some of the energy (wave forms) refracted ventrally around the tip of the mandibles. This gives clues on how the sound is formed in the phonic lips and how the sound beam may be directed forwardly through the soft tissue and reflected off the head.

1.2.1. Clicks and buzzes

The echolocating sounds have been described as short broad-band pulses of high frequency (Heyning, 1989a) and the main vocalizations used by the Odontoceti are called clicks and buzzes (Heyning, 1989a; Johnson *et al.,* 2004, 2008). Johnson *et al*. (2004) did extensive work recording high frequency vocalizations from the genera *Ziphius* and *Mesoplodon*, showing the production of ultrasonic clicks and echoes from prey; they were able to assess that no vocalizations were detected from the tagged whales within 200 m of the surface, but that they all clicked almost continuously in deep waters. The recorded trains of clicks often ended in a rapid increase in click rate (250 clicks per second), which could be an indication of the final approach on prey (Johnson *et al*., 2008) or aggressive behavior (Dunn, 2015). This increase in click production is commonly called “buzz”, terminology used for odontocetes and bats (Griffin, 1958; Johnson *et al.,* 2004). Dunn (2015) also refers sounds in porpoises where slow repetition rates followed by a sudden increase were deduced to be contact calls between a mother and her calf (Clausen *et al*., 2010; Dunn, 2015). Before the buzz, which is associated with an increase in the dynamic acceleration of the whale, there are clicks with sound production intervals called inter-click-intervals (ICI). These ICIs can be the result of the time needed for the sound to be reflected on prey or conspecific whales, and be detected by the sound producing whale (Johnson *et al.,* 2004).

However, sound categorization should be used with caution, since authors like Morisaka (2012) refer to odontocete sounds as classified into three categories rather than two: tonal whistles, clicks, and burst-pulse sounds. The work by Dunn (2015), also refers other forms of echo-communication, such as patterns of clicks called codas that function as communicative signals, described by Watkins & Schevill (1977), and slow clicks, distinguished from usual clicks by their slower repetition rate or interclick interval, which are usually correlated with sexual advertisement by mature male sperm whales (Weilgart & Whitehead, 1988). The same study also mentions the existence of distinctive acoustic signals called signature whistles, produced by bottlenose dolphins. Dunn (2015), reports that male *Mesoplodon densirostris* produce more sounds than their female counterparts, acknowledging the possibility of sexually distinctive signals of communication and social interaction for *Mesoplodon densirostris*. Dunn (2015) concludes that “the sexually distinctive sounds produced by both males and females may be important cues for the more likely scenario of males choosing which group of females to join”. However, although they dive to great depths for long durations, they still spend enough time at or near the surface between foraging dives to provide opportunity to choose their associates using visual cues. However, Dunn (2015) admits the whales may be able to maintain group cohesion simply through their echolocation clicks, functioning as a group cohesion cue.

By studying extant whale behavior and vocalizations, data can be applied to virtual experiments using acoustic models to mimic the effects in extinct ziphiids skulls.

1.2.2. Sound reception

The idea of an "acoustic window" and/or "jaw hearing" to refer to the sound reception pathway in odontocetes was according to Cranford *et al.* (2008b: p. 2), first introduced by Norris in 1968 in his work "The evolution of acoustic mechanisms in odontocete cetaceans*"*. He proposed that sound entered the head through a fatty pad which lies between the skin and the thin posterior portion of mandible, commonly called "pan bone" (Cranford *et al.,* 2008b). Odontocete mandibles are filled with pellucid fat bodies, and according to Norris, the sound would pass through a channel of these fatty tissues to the ear complexes, propagating the sound through the thin external bony lamina of the pan bone along the internal mandibular fat body to the dense bony ear tympanoperiotic complex. This complex is the primary component of the hearing apparatus and can be viewed as the fusion between the tympanic and periotic bones (Cranford *et al.*, 2008a). There have been several attempts to explain which pathway does sound "use" to reach the hearing apparatus in odontocetes. Cranford *et al*. (2008b), conducted studies on this subject and suggested a new way of sound reception, which he called "the gular pathway"; it proposes that the acoustic pressure wave encounters the core of soft tissues surrounding the head and refracts below and in between the mandibles, entering through the internal mandibular fat bodies via the opening created by the absence of the medial bony wall of the mandible. This produces a series of small amplitude waves that flex specific regions of the pan of the mandible ("flexural wave mechanism") that propagates to the ear complex, where the tympanic bulla is situated.

1.3. Recycling of the air: aid in deep diving

Ziphiids possess a series of air sacs associated with the sound production system: vestibular, accessory, nasofrontal and premaxillary (Heyning, 1989a). Muscles surrounding them, like the palatopharyngeal muscle, contract the nasopharyngeal airspace forcing the air up through the bony nares into the distal nasal passages (Heyning, 1989a); these and other muscles, could therefore be responsible for allowing the air sacs to be a reservoir for air to be recycled, possibly exchanging air, after entering through the blowhole, between the upper air sacs (that surround the phonic lips) and lower air sacs situated near the premaxillary crests and the base of the premaxillary bones. There are plugs located in the nasal premaxillary sac fossae that help transfer this air up and down through the nasal track, forcing the air passage by contracting and relaxing the tissues (Heyning, 1989a). As mentioned before, beaked whales are deep divers and perform long deep dives, so this recycling of air, which could be compared to a bagpipe that swells and deflates using the same air, could be hypothesized in helping the dives, avoiding the necessity of carrying a large amount of air in their lungs, thus leaving them free to be compressed.

1.4. Cranial asymmetry in odontocetes

Unlike most mammals, cranial and facial asymmetry is found in most modern odontocete whales (Physeteridae, Ziphidae, Delphinidae, Monodontidae, Phocoenidae, Iniidae and Platanistidae), being regarded as a synapomorphy of the group: both the rostrum bones and some soft tissues lack bilateral symmetry (Heyning, 1989a; Cranford, 1999); within the living Ziphidae, the genus *Berardius* exhibits the least degree of cranial asymmetry (Heyning & Mead, 1990). Heyning (1989a) defines cranial asymmetry as "any deviation from the symmetrical pattern visible in the bones of the skull" and facial asymmetry for the same deviation in facial soft anatomy. The terms are separate since it is possible to have facial but not cranial asymmetry (Heyning, 1989a). For this reason, we cannot separate cranial asymmetry from facial and soft anatomy: cranial bones may have developed asymmetry in response to facial asymmetry (Heyning, 1989a), which would have evolved for several functional purposes. The work of Heyning (1989a) also points out that the asymmetry of the head is related to some aspect of sound production.

Fossil evidence indicates that cranial asymmetry is less pronounced or even absent in some extinct groups of ziphiids which may be indicative that the soft tissues may have developed an earlier asymmetry, modifying the bony cranial structures along the way (Heyning, 1989a). In *Globicetus*, asymmetry can be seen in the premaxillary crests and nasals (fig. 1.4), but also in the premaxillary shelf, which is significantly different from one side to the other: the left sided soft tissues would probably have a different morphology with different muscles and tissue attachments, hence the contrast in symmetry. However, like *Globicetus* (ML 1361), there are several examples of extreme asymmetry in fossil beaked whales, such as *Tusciziphius atlanticus*, which also has a very pronounced asymmetry of the premaxillary sac fossa, premaxillary crests and bony nares (Bianucci *et al*., 2013). This could be related, once more, to the right side apparatus hypothesis of Heyning, since the major development is on the right side (Heyning, 1989a). Reidenberg, & Laitman (1994), suggest that the position and shape of the odontocete hyoid apparatus (the collective term used to refer to the bones of the tongue), which has a tilted placement, allowing for an asymmetrical enlargement of the piriform sinuses, may have "evolved to subserve several specialized upper respiratory/digestive tract functions, such as simultaneous feeding (suction and swallowing) and sound production".

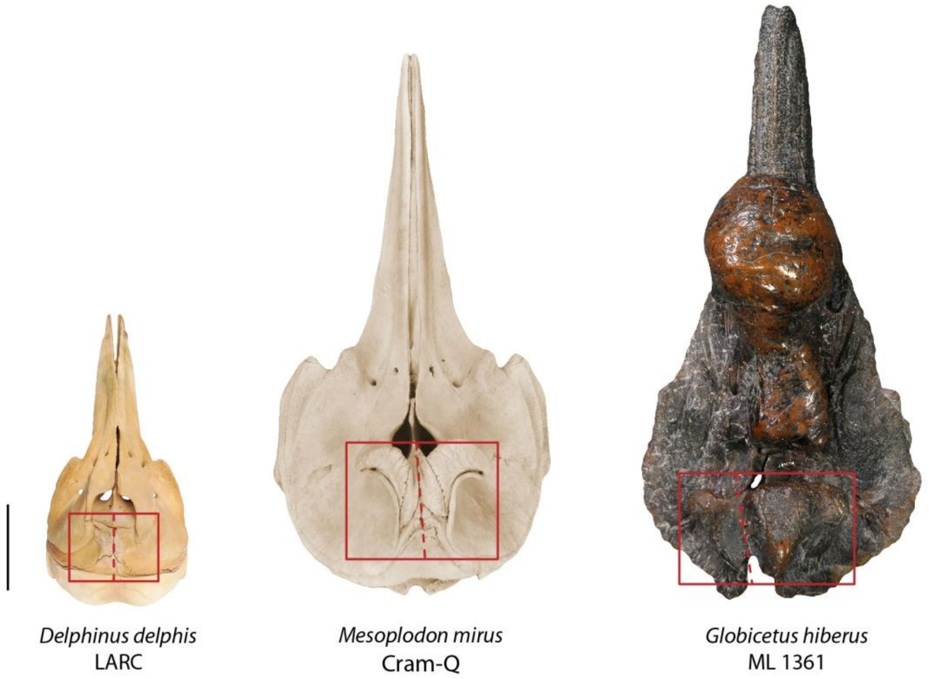


Fig. 1.4: Skull of *Delphinus delphis* (LARC), *Mesoplodon mirus* (Cram-Q) and *Globicetus hiberus* (ML 1361) in dorsal view: size and cranial asymmetry between the different skulls; the red boxes and dashed lines draw attention to the most notorious asymmetry in the vertex: the development between left and right nasals and premaxillary crests. Scale bar: 10 cm.

Finally, cranial asymmetry is usually related to the biosonar apparatus, intraspecific fights and tissue anchoring, but also to bottom suction feeding (Muizon *et al*., 1999). It is noted by Muizon *et al.* (1999), that some cetaceans like *Eschrichtius* and *Tursiops* are known to feed preferentially on the right side, but their skulls are not as dimorphic as the ones found in other extinct and extant ziphiids.

If we consider that in ziphiids the bony structures are usually less developed on the left side, then we could hypothesize that the left side would be used for bottom feeding in other ziphiids too (as it happened with the extinct walrus-like cetacean *Odobenocetops* (Muizon *et al*., 1999; Muizon & Domning, 2002; Nweeia *et al*., 2009), which had a posteroventrally-oriented right premaxillary tooth (Muizon *et al*., 1999; Muizon & Domning, 2002); this could be the case in *Globicetus*, but this is still hypothetical, since feeding habits in deep diving ziphiids are still fairly unknown. Skull asymmetry may also be related with differential timing of sound reception which helps to target prey and better judge distances, as reported for dolphins. A skull of a short-beaked common dolphin, *Delphinus delphis* (Linnaeus, 1758) is used in figure 1.4 to illustrate and compare size and asymmetric dimorphism found in the majority of odontocetes.

1.5. Geological and environmental framework

Overall, Middle-Late Miocene was proposed by Bianucci *et al*. (2008), as a possible age for the fossils of beaked whales recovered from the ocean floor, based on phosphogenic episodes, which could be correlated with the fossil ziphiids trawled off the South African coastal waters (Bianucci *et al*., 2008, 2013). In the work by Antunes *et al.* (2015), additional data is used to advance more accurate paleobiogeographic and paleoecological hypotheses for the sites of the Iberian fossil beaked whale finds, since comparison with ziphiids from other localities proves to be insufficient.

The fossils here described were collected by trawlers off the Portuguese western coast, but most of the time fishermen do not disclose accurate information about the findings; *Globicetus* fossils have been found in several localities, but in closely similar conditions. Their matrix is phosphatized and iron-rich with small quantities of manganese and zinc and even less copper (Antunes *et al.,* 2015). Cetacean bones, often with a dark brown patina and "porcellaneous" look, also mentioned by Buffrénil & Lambert (2011) and Bianucci *et al*. (2013), are dominant among the vertebrate fossils recovered in trawling nets. It is noted by Antunes *et al*. (2015), that the remnants of the beaked whales deposited at the sea floor stay there for long and may act as a substrate for other organisms for which the study of their foraminiferal assemblages may indicate a more accurate age span. The studied cetacean skull cavities contents analyzed in Antunes *et al*. (2015), had evidence of planktonic foraminifera which pointed to a late Messinian - Zanclean age (late Miocene-early Pliocene, from 6.1 to 4.4 Ma., see fig. 1.5), indicative of a subtropical to temperate province (Antunes *et al*., 2015). According to Buffrénil *et al*. (in review), the time interval matches the late Miocene-Pliocene phosphogenesis episod TB3. The fact that benthic foraminifera were extremely scarce in the sample provides evidence of a more or less deep environment (Antunes *et al*., 2015). It is important to note that *Choneziphius* sp. has been found in Portuguese coastal waters (Bianucci *et al.,* 2013), and similar rostrums have been described by Lambert (2005) from the Deurne Sands Member of the Diest Formation (Antwerp, Belgium) as being from the Tortonian (late Miocene) (Lambert, 2005; Antunes *et al*., 2015).

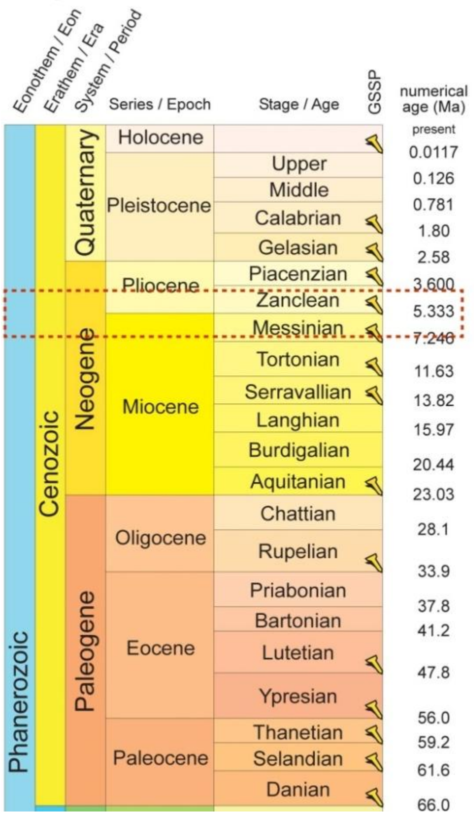


Fig. 1.5: Detail of the International Chronostrat Chart 2015 (Cohen *et al*., 2013, updated); red dashed box marks the late Messinian - Zanclean age.

Bianucci *et al*. (2008: p. 141) make reference to periods of intensified upwelling during the Late Miocene and the Early to early Late Pliocene, which may also find an expression in extant ziphiid habitats, since there seems to be evidence of a connection between feeding areas and the interaction of submarine topography (submarine canyons) with marine currents (Waring *et al*., 2001; Bianucci *et al*., 2008). This nutrient-rich water stimulates the development and reproduction of primary producers, such as phytoplankton.

Survey of fishermen with fossil ziphiids

Globicetus and other phosphatized ziphiid skulls have been collected by fishermen during their fishing activities near the coast of Peniche, Portugal. Paleontologist Octávio Mateus and I visited three of these boat-owner fishermen from Ribamar and Casais de Porto Dinheiro (Lourinhã, Portugal), who all have fragments or complete phosphatized rostra of extinct beaked whales in their homes. Several genus of extinct beaked whale were identified: *Caviziphius*, *Imocetus* and *Aporotus*. The fishermen were using long-line fishing techniques ("*Palangre*") with numerous hooks in which the fossils were unintentionally collected: the fishing hooks got stuck on the natural structures of the rostra, such as the ascending process of the premaxillae, and would be "fished" out the sea floor, as well as some of the original phosphatized matrix. Two of the men had been the masters of their fishing vessels; Master ("*Mestre*" in Portuguese) Daniel Vieira Pinto from Porto Dinheiro has a *Caviziphius* specimen caught "more than 20 years ago". Mestre Ramiro Francisco Aguiar, known as "Ti Ramiro", and his daughter, Nélia Aguiar, loathed the times her father would go to sea and bring this bizarre creature's home and explained how some neighbors had suggested the broken rostra were pterosaurid fossilized beaks. Their private possessions account for two fragmentary anterior-most part of the rostrum of *Caviziphius* and an almost complete rostrum of *Caviziphius* or possibly *Tusciziphius*, but this needs further analysis. He reported, from memory, the collecting coordinates around 39.21 to 22°N and 10.23 to 24°W. Hélder Pinto, a fisherman also from Porto Dinheiro, accounts for several rostra being dragged of the sea floor, sometimes two in the same day. His collection has spectacular specimens, of *Caviziphius* and two complete rostra: one of *Imocetus* and one that shows similarities with a fragmentarily preserved specimen Ziphiidae aff. *Aporotus dicyrtus* (*Ziphirostrum tumidum* sensu du Bus, 1868), IRSNB 3807-M.1889, figured in Lambert (2005), p. 489.

The account for the finds are all very similar and consistent: all the ziphiids skulls were collected from a sea bottom, south of Nazaré Canyon at a depth of about 900 to 1500m (most commonly reported around 1000m) southwest to west of the Farilhões Islands, at Berlengas archipelago, at the latitude of Peniche, about 30 miles from the coast. Taking into account the bathymetry of the region where the ziphiids were collected, they should have been collected from the sea floor at 9.8 to 10.1°W and 39.3 to 39.4°N, around the 1000m of depth. In this survey, there are no reports of ziphiid skulls collecting outside this area and there are no accounts for occurrences of *Megaselachus megalodon* teeth for that location. In the geological map "Carta Geológica de Portugal 1:1 000 000" of 2010 with the offshore geology, republished in the "Mapa Geológico de España y Portugal 1:1 000 000" of 2015, the provenance area is reported as Pliocene "Areias e Argilas – Depósito de Transporte de Massa" (fig. 1.6). At the current state of knowledge, the age is consistent with the work by Antunes *et al*. (2015).

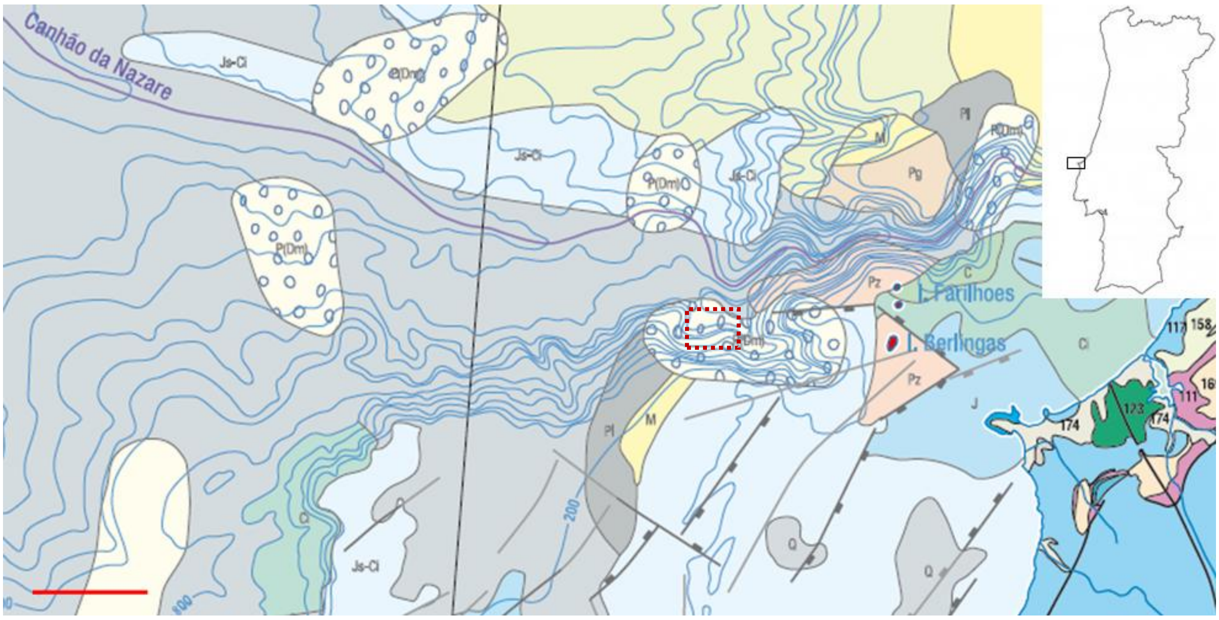


Fig. 1.6: Extract of *Mapa Geológico de España y Portugal 1:1 000 000* (2015) of the coast at the latitude of Peniche; the dotted rectangle refers to the area of 9.8 to 10.1°W and 39.3 to 39.4°N, around the 900-1000m of depth. Scale bar (in red): 10 km.

2. Materials and Methods

2.1. Specimens

The spectacular spherical bone structure seen in *Globicetus hiberus* has been reported to be very similar in several specimens recovered from the sea floor, some of which cannot be fully described here, since they are kept in private collections. Half of the specimens of *Globicetus* described or redescribed in this work are from the collection of the Museu da Lourinhã; in total, five fossilized skulls were personally analyzed and a sixth one (IEO DR26 026) was compared only based on literature by Bianucci *et al*. (2013) and Buffrénil *et al*. (in review). Four skulls have never been figured and studied before (ML 1850, ML 2023, DGAOT-a, 100/PAL/UE), see fig. 2.1. Other fossil and extant beaked whale rostrums were also analyzed for determining association of bone structures and intraspecific variation.

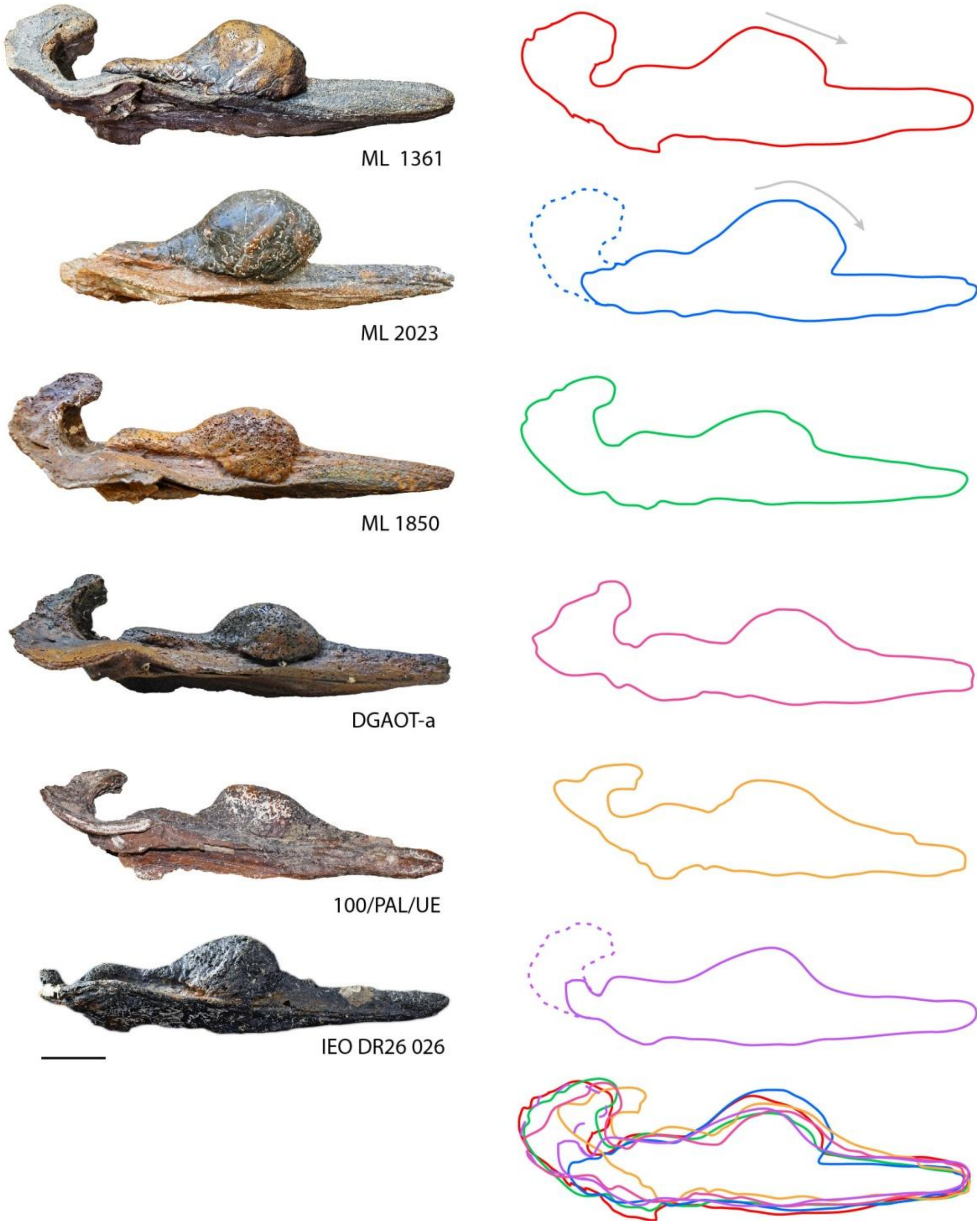


Fig. 2.1: Skulls of *Globicetus hiberus* and respective outlines. On the bottom, an overlay of the outlines is provided to illustrate the intraspecific variation within the skulls; the grey arrows show the proposed growth direction of the MPP. Scale bar: 10 cm.

The fossilized skulls were recovered from the Atlantic Ocean floor during fishing activities based on longline fishing. The holotype, ML 1361, was found in deep waters off central Portugal (at the latitude of Lourinhã, or Peniche) south of the Nazaré Canyon, likely around 39°18'N, 9°47'W; the other rostrums belonging to the Museum of Lourinhã (ML 1850 and ML 2023) share a similar location; 100/PAL/UE was collected at about 600 meters of depth, from an unknown location based at the Setúbal harbor (central Portugal); the fossil designated as unnumbered DGAOT-a (it belongs to FCUP, which has a major part of its collection yet to be catalogued, so it is a provisional designation; the same happens with specimen DGAOT-b, see below) was found in deep waters of Porto, north Portugal, around 41°12'N, 9°30'W; IEO DR26 026 was recovered off the Galician coast (42°27'N, 11°59'W), from a depth of approximately 1500 m. For the horizon and age, see section 1.5.

Extant whales *Ziphius cavirostris* and *Mesoplodon mirus* skulls were described as a comparative measure of some structures in living ziphiids (see section 3.1.2. and 3.1.3.). The male Cuvier´s beaked whale, *Ziphius cavirostris* (MNHN 395775, from the National Museum of Natural History, Washington DC, USA) is used in this work for osteological comparison with *Globicetus*. The specimen of True's beaked whale, *Mesoplodon mirus* (Cram-Q), washed up at a beach in central Portugal and was considerate an immature male, based on size and genitalia. The body of the animal was collected and dissected by the Portuguese Society of Wildlife (Sociedade Portuguesa de Vida Selvagem – SPVS), in their headquarters at Quiaios, Figueira da Foz (Portugal), where they operate a center for marine animals rehabilitation (CRAM-Q). The skull was lent to Museu da Lourinhã for study purposes and further examination of the anatomical features of the extant beaked whale.

For further anatomical comparison, two fragmented *Caviziphius* sp. fossil rostra and a partial rostrum of *Tusciziphius atlanticus*, were also analyzed and described (see section 3.1.4. and 3.1.5.). *Caviziphius* sp. (ML 2022; DGAOT-b) and the rostra of *Tusciziphius atlanticus* (ML 1819) were also recovered by trawling and are believed to be of the same age as the other fossils found in the coastal waters of the Portuguese western coast. ML 2022 from the same locality as ML 2023, DGAOT-b probably from the coastal waters of Porto, and ML 1819 was recovered by a fisherman from Ribamar, Miguel Fonseca Lourenço, 500m southwest of the Farilhões Islands, at Berlengas archipelago, at a depth of around 275m. The specimens have never been figured and formally studied before.

Five different fossil beaked whales from the Neogene inland deposits of Antwerp (Belgium) kept in the collection of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) in Brussels were also analyzed. The purpose of using specimens from Antwerp is to discuss some of the features of the rostral bones, not repeating original work by Lambert (2005), but simply comparing them with homologous structures observed in *Globicetus*. New information on the fossils of IRSNB is not added (see section 3.2.).

A skull of a short-beaked common dolphin *Delphinus delphis*, is used in figure 1.4 to illustrate and compare size and asymmetric dimorphism. The skull is part of the collection of the Laboratory of Arqueosciences (Laboratório de Arqueociências – LARC) in Lisbon (Portugal), with collections accessible to students and to the scientific community in general.

Preservation and taphonomy

The fossils analyzed have different degrees of preservation. Some *Globicetus* rostra are not complete: some are missing the posterior part (ML 2023; IEO DR26 026) or part of the ascending process of the premaxilla (100/PAL/UE); *Caviziphius* sp. specimens (ML 2022; DGAOT-b) are missing most of its posterior process and *Tusciziphius atlanticus* (ML 1819) the most anterior part of the telescoping rostrum.

The *Globicetus* fossils studied show signs of bioturbation by lithophagous animals, which create borings in the fossil. These borings seem similar to the ones made by *Petroxestes pera* known from Ordovician to Miocene; however, their slit-like aperture seems a bit wider and slightly elongated in one of the extremities. These trace fossils are described by Taylor & Wilson (2003: p.11) as "pouch-shaped borings", and are produced by acrothoracican barnacles, and are called *Rogerella* (Lambers &

Boekschoten, 1986). Without further tests, which could involve making a silicone internal cast of the borings, both possibilities (*Petroxestes* and *Rogerella*) should be considered.
Associated to the fossils are also incrustations by polychaets, bryozoans, corals and sponges. Some non-phosphatized sediment filling the natural cavities of the rostra and *Rogerella* borings is present, with evidence of extant foraminifers (planktonic forms) and pteropods (*Cavoplinia inflexa* Lesueur, 1813) (fig. 2.2).

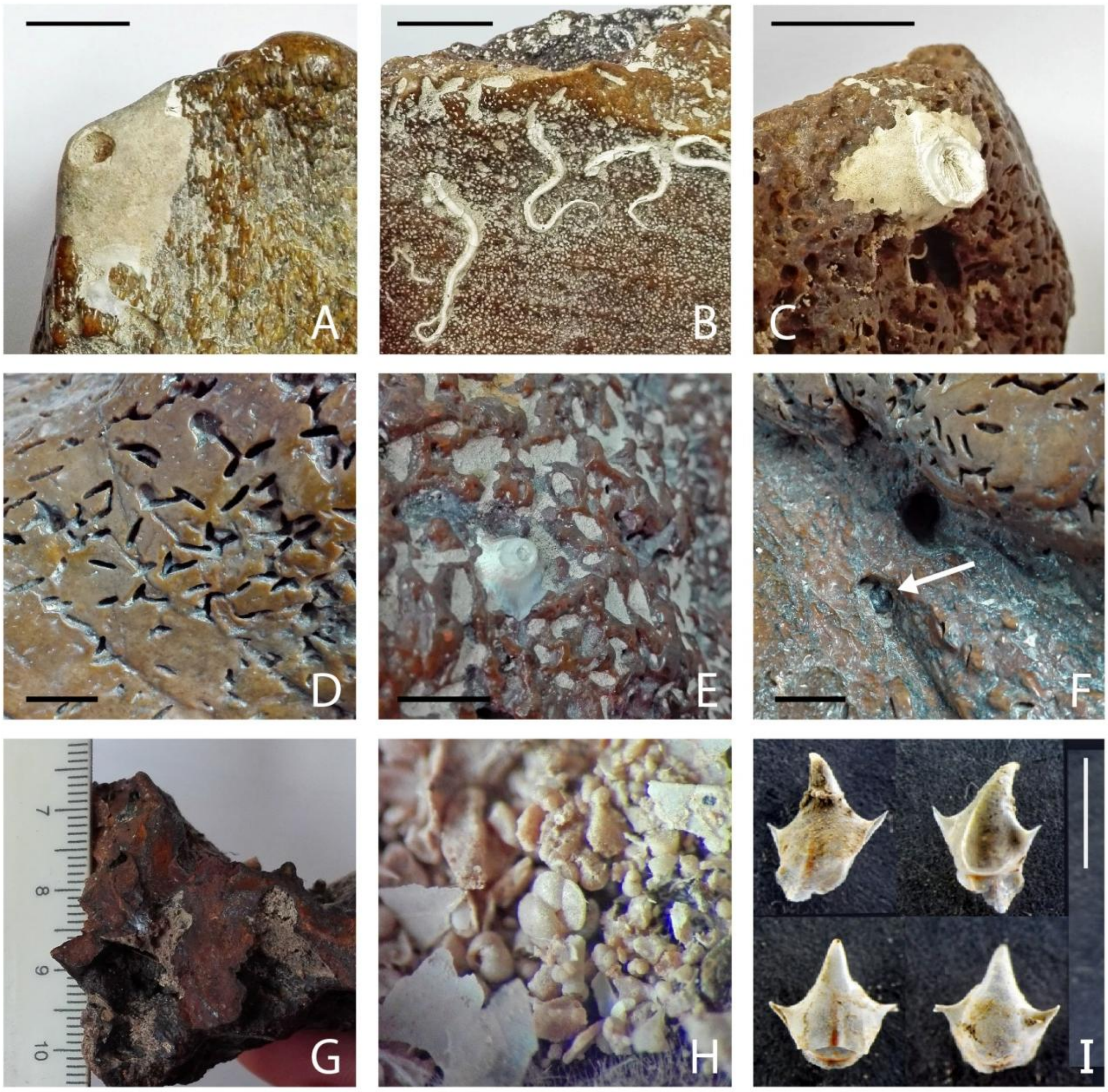


Fig. 2.2: Associated fauna and taphonomy in ziphiid skulls and other phosphorites samples from the same area: **A**, sponge over *Globicetus* skull ML 2023; **B**, polychaet calcium carbonate tubes over skull ML 2023: **C**, coral over skull ML 1850; **D**, cf. *Rogerella* borings (trace fossil attributed to cirripeds); **E**, cf. *Rogerella* borings filled with sediment with posterior coral incrustation; **F**, phosphate-coated pebble (white arrow) in dorsal infraorbital foramen of skull ML 1850. Black scale bars: 1 cm; **G**, phosphatized matrix with pockets filled with sediment containing foraminifers and modern(?) pteropoda (next insets); **H**, sediments of sample G with foraminifers, pteropoda, and sponge spicules, amplified 10x; **I**, pteropod gastropods *Cavoplinia inflexa* from sediment over ML 1850, scale bar: 5 mm.

2.2. 3D prototyping

Using photographs of the holotype of *Globicetus* specimen ML 1361, it was possible to generate a digital version of the fossilized rostrum with the software *Agisoft PhotoScan Professional Edition* (version 0.9.0), creating a model fit for 3D printing. The model was then generated using a ceramic-polymer composite, strong yet very light, and was printed in a scale 1:10 (fig. 2.3). The printer used was a Z Printer 650, which uses a selective laser sintering (SLS) to precisely control local polymerization. Using printed models gives an easier opportunity for the modeling of soft tissues of the rostrum, allowing the study of the fossil without the specimen being physically present, and makes it a great future teaching tool. The impossibility of not having permanent access to the *Globicetus* skulls was minimized by having a 3D model of ML 1361, allowing to better hypothesize on the soft tissue anatomy placement and to formulate some structure comparison.

Fig. 2.3: 3D model of skull of *Globicetus hiberus* (ML 1361) printed by Tridaxis at the scale: 1:10.

2.3. Skull measurements

The only skulls measured in the present study were the *Globicetus* specimens. The trades selected were chosen because of their value for MPP sizes comparison and inference of an approximate size of the animals when alive. The medial pad of premaxillae described in some of the specimens was not measured, since it is not a common feature to all the rostra. Figure 2.4 represents the characteristic/structures measured and Table 2.1 the actual measurements.

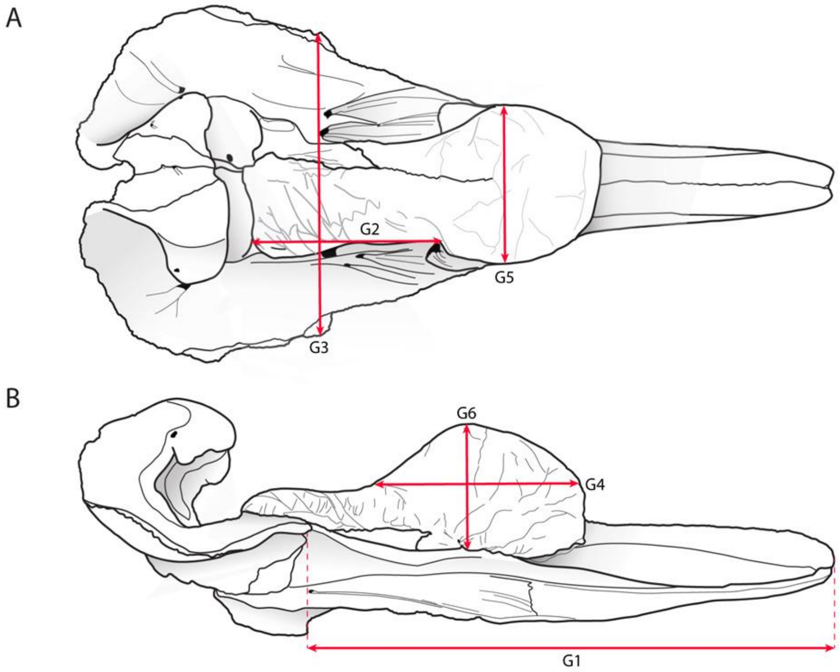


Fig. 2.4: Description of the measurements taken from the skull of *Globicetus*: A, dorsal view; B, lateral view Outline: ML 1361, adapted from Bianucci *et al.* (2013).

Table 2.1: Measurements of *Globicetus* skulls (in mm). *estimated.

	ML 1361 (holotype)	ML 1850	ML 2023	100/PAL/UE	DGAOT-a	IEO DR26 026
Rostrum length (G1)	530	506	530	507	470	552
Maximum premaxillary shelf length (G2)	130	125	150	230	175	138
Preorbital width of the skull (G3)	306	320	>250 (310*)	256	270	260
MPP length (G4)	200	180	220	250	195	200
MPP width (G5)	185	180	195	155	130	135
MPP maximum height (G6)	125	110	140	100	90	100
G5×G6	23125	19800	27300	15500	11700	13500

2.4. Histology

The work by Buffrénil *et al*. (in review) gives the only insight on the histology of *Globicetus* and how the MPP may have been formed. Buffrénil *et al*. (in review) cutted *Globicetus hiberus* rostrum IEO DR26 026 into eight slices; the four main slices (fig. 2.5) some 15 mm thick were sampled in transversal planes from the most interesting sites of the rostrum: the middle of the MPP (plane A, fig. 2.6), the middle of the medial pad of premaxillae (plane B), the middle of the premaxillary shelf (plane C) and finally the middle of the non-swollen distal part of the rostrum (plane D). Transversal and/or sagittal plane sections of different thicknesses were also made for additional information. It is only figured (in detail) plane A, since it is the most important for the specifications of this study.

A summary of the most important morphological and structural peculiarities of the bones that make out the rostrum are given, based on the work by Buffrénil *et al*. (in review):

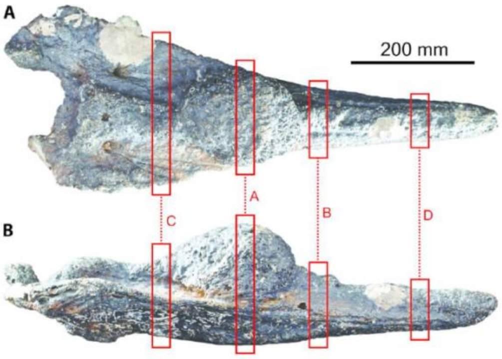


Fig. 2.5: Skull of *Globicetus hiberus* IEO DR26 026: A: right lateral view, used in the study by de Buffrénil *et al*. (in review); B: dorsal view. A-D: red rectangles represent the place of the four slices made. Original image from Buffrénil *et al.* (in review).

- The bone tissue forming the MPP displays extreme compactness (98% to *ca*. 100%);
- Five pairs of large neurovascular canals (1 to 5.5 mm in diameter), symmetrically distributed, occur in the ventral part of the rostrum, an anatomical region corresponding to the vomer and maxillae; there is also a pair of larger canals (diameters 5 and 5.5 mm, respectively) that perforate the rostrum on its whole length;
- The core of the prominence shows a uniform whitish coloration and a vitreous aspect similar to those displayed by sections from very compact extant bones such as the rostrum of *Mesoplodon densirostris*;
- No suture visible between the structures; however, in naked eye observation, two territories are clearly distinct by some characteristics of their structural organization;
- The ventral region of the rostrum, corresponding to the maxilla and the vomer, is occupied by a greyish translucent Haversian tissue, densely remodeled with exceptional size secondary osteons with convoluted orientations, and with walls often made of non-lamellar, poorly

birefringent tissue; however, the premaxillae remains untouched by this process, a situation also encountered, for example, in *Aporotus recurvirostris* (Buffrénil & Lambert 2011);

- The dorsal part of the rostrum, corresponding to the premaxillae and the MPP, is composed of a very homogeneous succession of thin white and grey strata that extend up to the peripheral margins of the bone forming a regularly stratified structure similar to the geometrical organization of the laminar bone tissue;
- The micro-anatomical and histological features of bone from the medial pad of premaxillae and the premaxillary shelf are also similar to those previously of the MPP;
- Bone structure may turn into plexiform or reticular patterns in the basal part of the MPP.

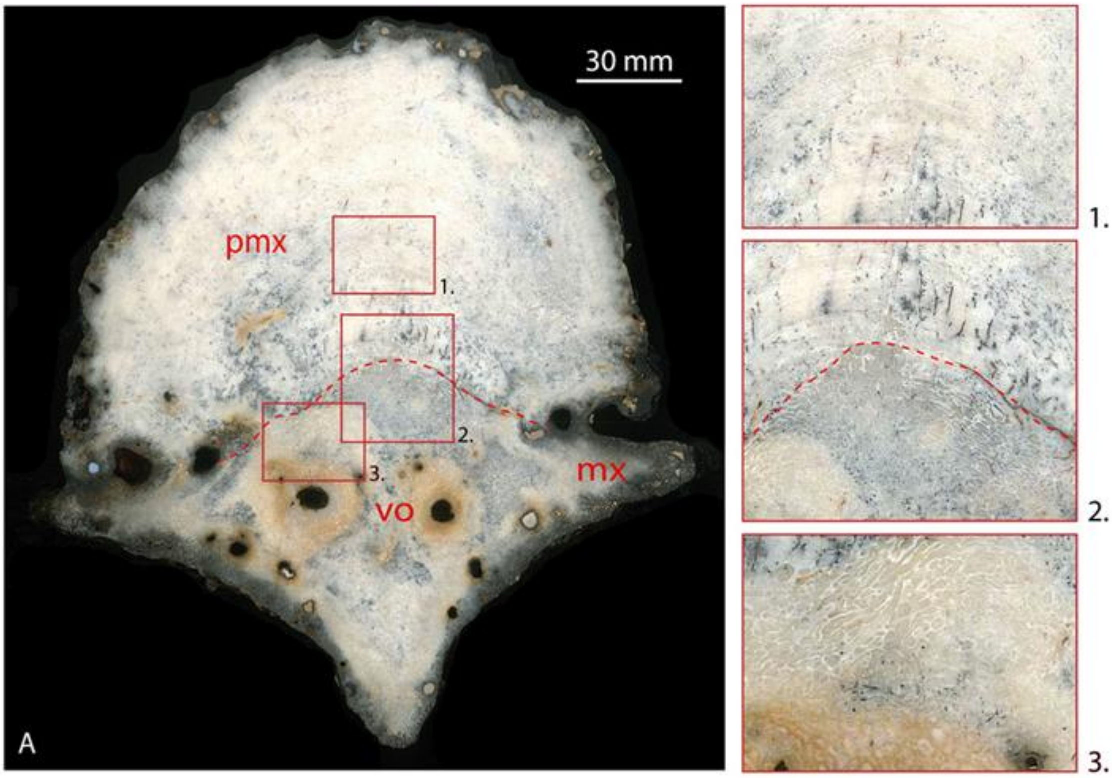


Fig. 2.6: Section of skull of *Globicetus hiberus* IEO DR26 026: A, transverse section of slice A with enlarged fields of different aspects of the bone (red squares numbered 1 – 3): 1. – laminar-like bone tissue in the deep region of the prominence with clear strata altering with darker ones; 2. – laminar-like formation of the MPP contrasting with the remodeled area of the vomer, easily observed at the naked eye; 3. – dense Haversian tissue with very big secondary osteons in the ventral region of the rostrum. pmx: putative area occupied by the premaxillae; mx: putative area occupied by the maxillae; vo: putative area occupied the vomer. Original images by Olivier Lambert.

3. Description and comparisons

3.1. Extinct and extant ziphiids

In this section, fossil and extant ziphiid skulls are described with the purpose of highlighting and understanding anatomical aspects relevant in this work. For complete and extensive anatomical descriptions see Bianucci *et al*. (2013) for *Globicetus hiberus* ML 1361 and IEO DR26 026 plus *Caviziphius* sp. ML 2022, as well as Lambert (2005), for descriptions of the specimens from the Neogene of Antwerp, Belgium. Throughout the course of this work, *Globicetus hiberus* will most of the times be referred to just as *Globicetus*, for a simpler, easier read.

Anatomical terminology

Anatomical terminology used to refer and describe the distinctive rostral structures in *Globicetus* has been given different names in literature. As such, we hereby propose standardizing this terminology. I have tried to avoid, as much as possible, the creation of new terms, and for each term listed below, synonymies in parentheses and the author who coined the term first are referred.

Mesorostral Process of the Premaxillae (MPP) – Refers to the sphere-like structure only found in this particular species of beaked whale, also known as "spherical medial premaxillary prominence" (Bianucci *et al*., 2013), "voluminous premaxillary spheroid" (Bianucci *et al*., 2013), "premaxillary prominence" (Buffrénil *et al*., in review), "hemispherical prominence" (Buffrénil *et al*., in review) or "protuberance" (Buffrénil *et al*., in review). The terms "medial premaxillary bulge" or simply "bulge" have been used to refer to similar ontogenetic structures in extinct beaked whales such as *Caviziphius* sp. and *Tusciziphius atlanticus* (Bianucci *et al*., 2013) and in *Choneziphius planirostris* (Lambert, 2005). For a more practical reason, we will refer to the medial rostral premaxillary bone developments found in *T. atlanticus*, *Caviziphius* sp. and *C. planirostris* as MPP also, since the structure seem to have a very similar ontogenetic origin.

Maxillary rugosity – Refers to several rugosities found on the dorsal surface of the maxilla on the posterior half of the rostrum in several species of beaked whales, also known as "excrescences on maxilla" (Lambert, 2005; Bianucci *et al*., 2013), "excrescences and irregularities" (Lambert, 2005) or simply as "excrescences" (Lambert, 2005; Bianucci *et al*., 2013).

3.1.1. ***Globicetus hiberus*** Bianucci *et al*., 2013

Globicetus hiberus was first described by Bianucci *et al*. (2013), based on three fossilized skulls: ML 1361, holotype (Fig. 3.2; 3.3), IEO DR26 026, and MHNUSC 3958. The present work does not intend to repeat the extensive work presented by the previous authors, since they made an excellent work in describing the different rostral bones of *Globicetus*; for the purpose of this work, only some skull bones and specific characteristics will be discussed and approached in detail.

Globicetus exhibits one of the most striking and strange cases of rostrum specialization; it is characterized by the extreme thickening of the premaxillae, forming a large spherical premaxillary prominence in the middle of the snout, possibly cradling the anteriorly soft tissues and sound production mechanisms: the **mesorostral process of the premaxillae** (MPP). According to Buffrénil *et al*. (in review), its development resulted from a mere protraction of periosteal accretion over the premaxillae made of an atypical fibro-lamellar complex displaying an irregular laminar organization and extreme compactness called osteosclerosis. The MPP is preserved in all the specimens studied, but has different sizes and sometimes shapes, normally with an anteriorly directional growth. Specimen ML 1850 and DGAOT-a have similar MPP sizes, lower than ML 2023 and ML 1361; the latter ones have the vertex of the premaxillary crests on a similar height as the top of the MPP.

Posteriorly, it is followed by a thick shelf predominantly constituted by the right premaxillae, the **premaxillary shelf**; both their surfaces are similarly compact and covered with sulci and the two structures are fused together, being somehow part of one single structure, but differentiated in this work for a better osteological comprehension. The abrupt posterior margin of the shelf corresponds to the anterior limit of the right premaxillary sac fossa, which is considerably wider than the left fossa. The shelf is slightly asymmetrical and on the left side is marked by parallel lines attributed to muscle and tissue attachment related to the protection and positioning of the melon and other soft tissues. A wide subhorizontal surface margins the premaxillary shelf on both sides of the rostrum base, which is pierced by several dorsal infraorbital foramina.

In specimens ML 1361 and ML 2023 (fig. 3.2, 3.3, 3.4), the anterior and anterolateral margins of the MPP does not contact the underlying premaxilla and maxilla, leaving an open space, whereas in the other analyzed rostrums, a high **medial pad of premaxillae** (term mentioned by Bianucci *et al.*, 2013 and de Buffrénil *et al.*, in review) frames and joins the MPP to the dorsal surface of the telescoping rostrum. The pad can have different elongation and is only present in individuals with lower MPPs and premaxillary crests, such as IEO DR26 026, ML 1850 and DGAOT-a (fig. 3.6); fossil 100/PAL/UE (fig. 3.5) exhibits a longer anteriorly projected pad of premaxillae than the other specimens.

As for the **maxilla**, it slightly widens along the distal half of the skull, with a somewhat medially convex maxilla-premaxilla suture, similar to the one in *Mesoplodon mirus* specimens. From the level of the MPP, it sends a thin lateral plate whose lateral margin reaches the pre-orbital process in a nearly rectilinear line, forming a wide rostrum base.

A large longitudinal sulcus passes between the MPP and the maxilla, exiting on the anterior margin of the spheroid: the MPPs lateral margins only slightly contact the underlying maxilla, leaving what is seen as innervations passages or canals (fig. 3.1); these ventral gaps could be interpreted as places for the attachment and as a gateway for vital soft tissues (nerves, vessels, tendons, muscles, et cetera), allowing for a good vascularization of innervations responsible for important irrigation of bones and tissue of the apex of the rostrum or be related with acoustics and the echolocation signal reception. The gaps may also be a sign of historical evolutionary legacy, where the MPP evolved at faster rate and the rest of the structures could not keep up, leaving these vestigial grooves on its sides.

Fig. 3.1: Skull of *Globicetus hiberus* ML 2023 in posterior view: detail of left inner passage between the maxillary bone and the MPP.

The **vomer**, contrary to extant ziphiid *Ziphius cavirostris* and some species of *Mesoplodon*, is hidden dorsally by the development of the premaxillae. It is only visible ventrally between the premaxillae and maxillae. In some cases, the vomer fills the mesorostral canal of the rostrum.

The **nasals** in the medial margin of the right maxilla are more erected than the margin of the left maxilla. The facial area is short with the low and wide vertex overhanging it, hiding the bony nares and most of the premaxillary sac fossae in dorsal view.

The ascending process of the premaxilla is steeper and more anteriorly pronounced than in other genera such as *Choneziphius* and *Ziphius.* The top of the vertex is formed by the right premaxilla which is higher than the left. The anterior margin of the right premaxillary crests is posterolaterally directed, whereas the anterior margin of the left premaxillary crest is roughly anterolaterally directed, similar to *Imocetus piscatus* (Bianucci *et al.*, 2013: fig. 14A-B). In *Tusciziphius* both crests are usually anterolaterally directed. The crests cause extreme cramping of the soft tissues of the head in their most posterior part. When comparing *Globicetus* with *Ziphius* and *Hyperoodon*, it is important to refer that the MPP in *Globicetus* is only slightly more anterior than the position of the melon in *Ziphius*, and it is nearly as high (Bianucci *et al*., 2013). *Globicetus* does not have a prenarial basin, which is very characteristic of *Ziphius cavirostris*, so the premaxillary shelf and deep premaxillary sac fossa should be a substitute for that absence. The term prenarial basin should therefore not be used when referring to *Globicetus*, since it is not present in the latter; when referring to the facial bones that hold the lower density part of the melon in *Globicetus* the correct term should be "*concave ascending process of the premaxilla"* (Bianucci *et al*., 2013). As previously referred, other fossilized beaked whales from around the world show different degrees and MPP-like structures on the anterior part of the rostrum, which could lead to some speculation on the purpose of the bone compactness. The development of the medial pad of premaxillae in some of the rostrum is also discussed in section 4.4.

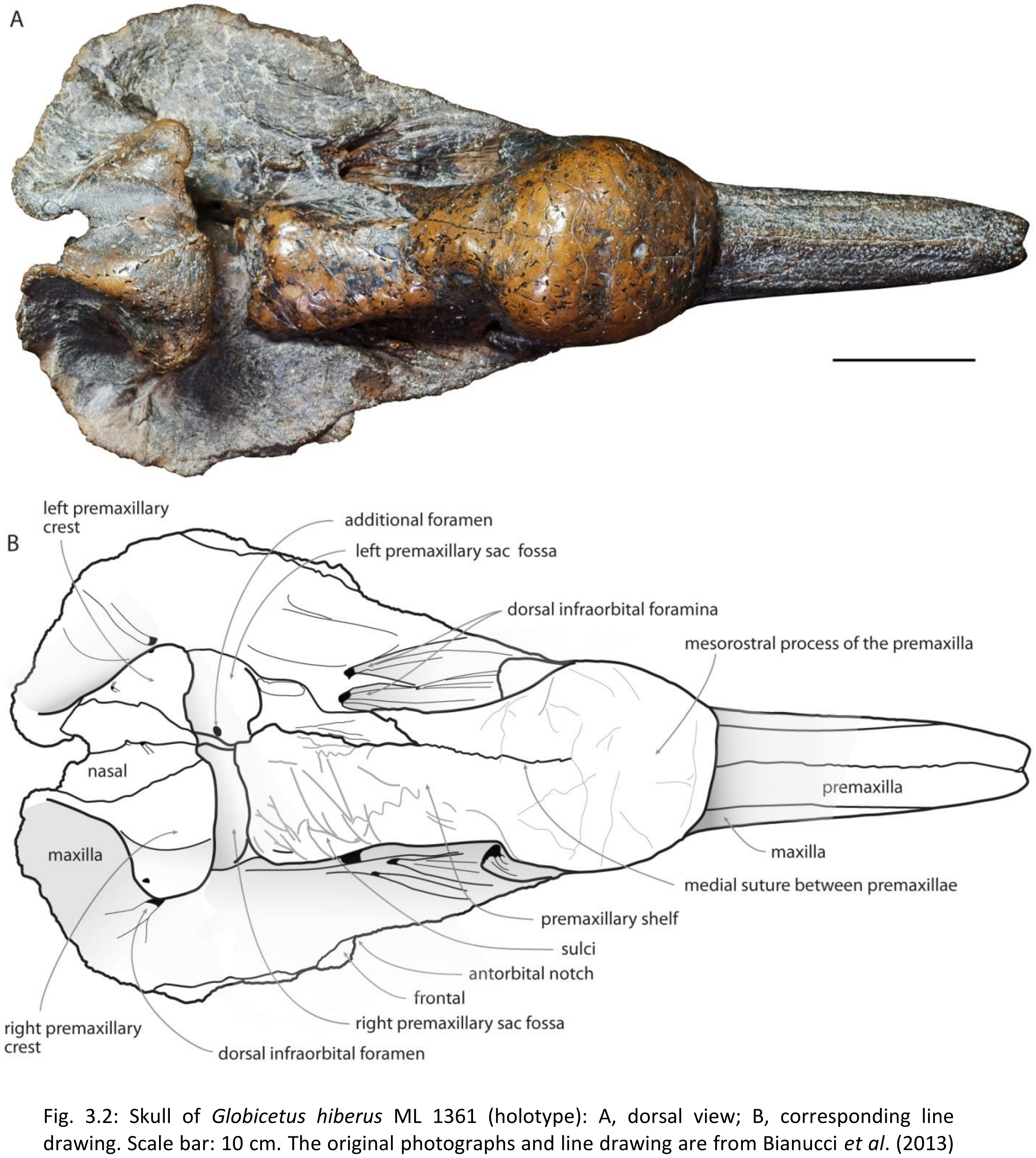


Fig. 3.2: Skull of *Globicetus hiberus* ML 1361 (holotype): A, dorsal view; B, corresponding line drawing. Scale bar: 10 cm. The original photographs and line drawing are from Bianucci *et al*. (2013) by courtesy of this author.

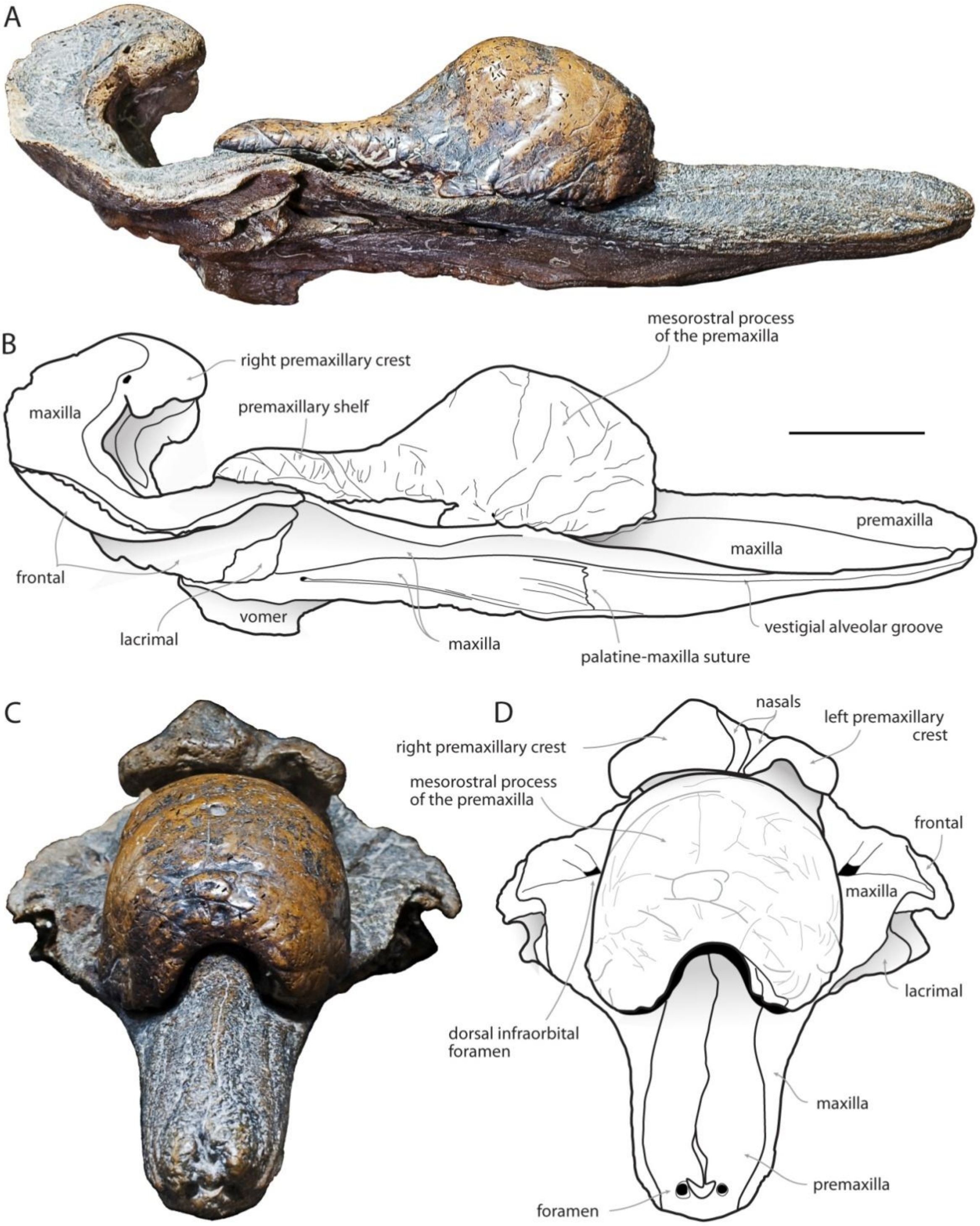


Fig. 3.3: Skull of *Globicetus hiberus* ML 1361 (holotype): A, lateral view; B, corresponding line drawing; C, anterodorsal view; D, corresponding line drawing. Scale bar: 10 cm. The original photographs and line drawing are from Bianucci *et al*. (2013) by courtesy of this author.

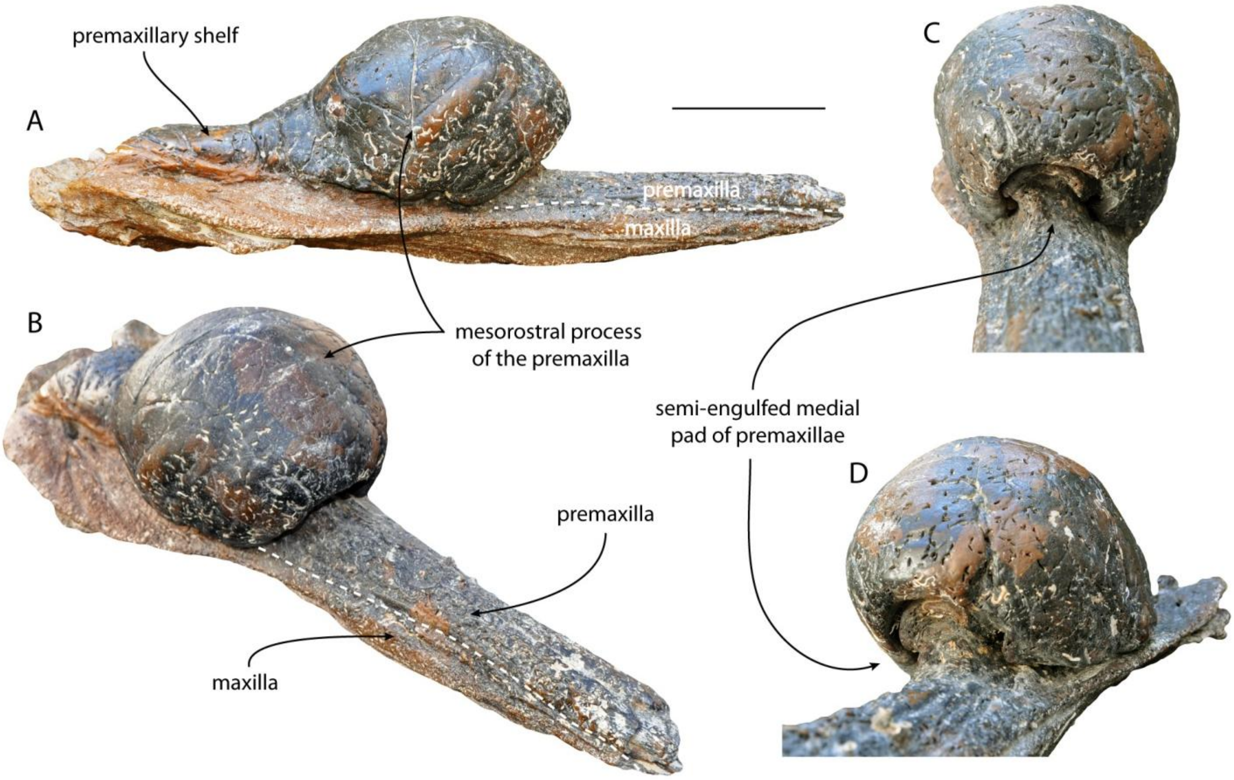


Fig. 3.4: Skull of *Globicetus hiberus* ML 2023: A, lateral view; B, anterolateral view; C, anterior view; D, detail of anterolateral view. Scale bar: 10 cm.

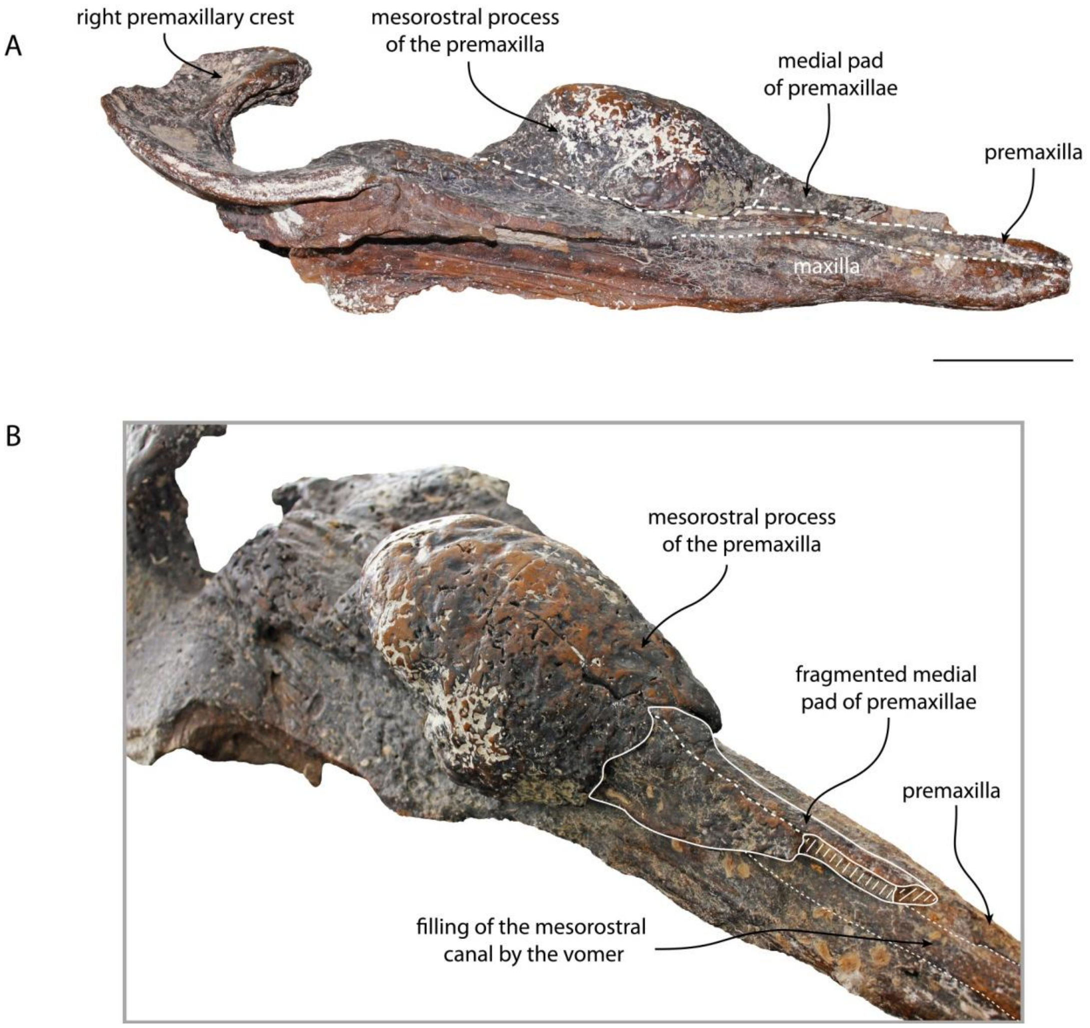


Fig. 3.5: Skull of *Globicetus hiberus* 100/PAL/UE: A, lateral view; B, detail of anterolateral view, the white lines delimitate the fragmented pad of premaxillae. Scale bar: 10 cm.

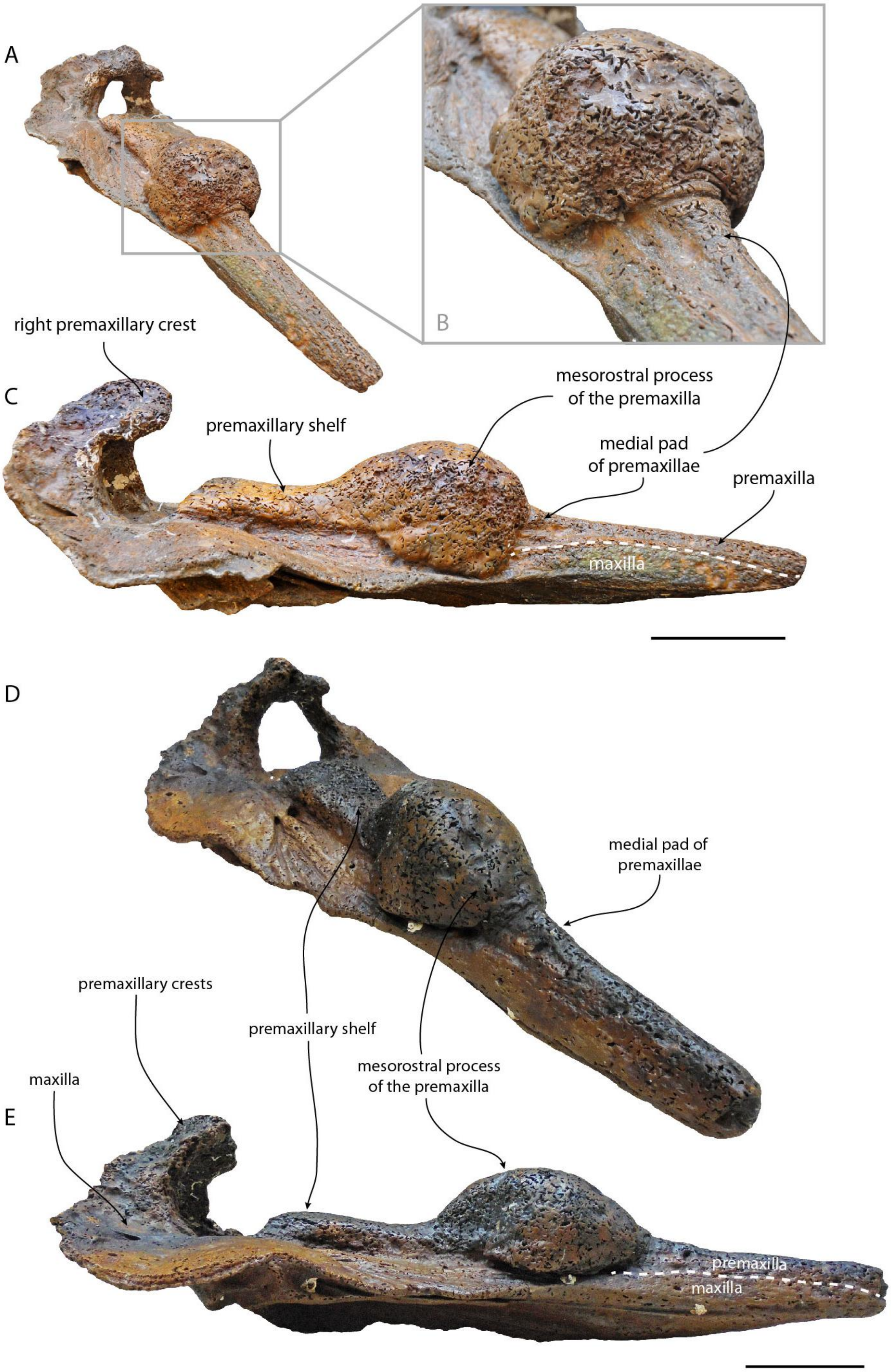


Fig. 3.6: Skull of *Globicetus hiberus* ML 1850, A-C: A, anterolateral view; B, detail of A, showing the pad of premaxillae; C, lateral view; D-E, DGAOT-a: D, anterolateral view; E, lateral view. DGAOT´s crests and nasals show a high degree of wear, the shape is nearly gone, but the asymmetry of the skull is still perceptible. The premaxillary shelf is also partially eroded and pad of premaxillae and the MPP are very similar in shape and height as in ML 1850 and IEO DR26 026. Scale bar: 10 cm.

3.1.2. ***Ziphius cavirostris*** Cuvier, 1823

Cuvier's beaked whale, *Ziphius cavirostris* (fig. 3.8), is mentioned due to its hard bone composition and to the very characteristic prenarial basin, which could be related to the very concave ascending process of the premaxilla in *Globicetus*. In a cladistic analysis of extinct and extant ziphiids based on morphological characters, authors such as Bianucci *et al*. (2013) place *Globicetus* in the subfamily Ziphiinae, making it more closely related to *Ziphius cavirostris* than to any of the 21 other extant ziphiid species. It is also essential when hypothesizing and inferring on the soft-tissue in *Globicetus*, based on the work by Cranford *et al*. (2008a).

Cuvier (1823) was the first to describe the species from a partial cranium and, according to Heyning (1989b), he, supposedly, first thought the skull was a fossil due to its "petrified" appearance. *Z. cavirostris*, indeed represents a ziphiid where the ossification of the rostrum happens to a significant degree (Zylberberg *et al*., 1998; Currey *et al*., 2001; MacLeod, 2002).

The ascending process of the **premaxilla** forms the very characteristic **prenarial basin**. It is a "bowl-shaped" cavity in the center of the dorsal surface of the skull just anterior to the external bony nares (Fig. 3.8). This region of secondary resorption of bone anterior to the external bony nares appears with presumably advancing age in males and results from the reabsorption of bone from the nasal passage, specifically from the vomer, premaxilla and maxilla (Heyning, 1989a; Heyning, 1989b; Hardy 2005). Fossil beaked whales such as *Choneziphius* and *Ziphirostrum* also possess a prenarial basin, but this sexually dimorphic anatomical feature is only present in *Z. cavirostris* males among extant ziphiids (Heyning, 1989a).

The floor of the basin is made of the **vomer**, which sends thin dorsomedial plates partially closing dorsally the mesorostral groove in the basin. There is also a dorsal intrusion of the vomer and to a less extent from the premaxillae that fills, with age, the mesorostral canal (Heyning, 1989a). This intrusion is called **mesorostral ossification** and is a deposition of bone usually found in adult males of the genera *Mesoplodon*, *Ziphius* and to a lesser extent *Berardius* (Heyning, 1984; Heyning, 1989a). Posterior to the mesorostral ossification in males, is a deeper part of the prenarial basin which houses a series of connective tissue sheaths which, according to Heyning (1989a), originate from "the dorsal anterior rim of the premaxillae bounding the basin"; these connective tissue supposedly corresponds to a fatty organ that may be homologous to the spermaceti organ of the sperm whale and occupies the excavation of the surface of the rostrum (Heyning, 1989a; Hardy, 2005), communicating with the enlarged oily right nasal plug (Heyning, 1989a), also housed in the prenarial basin. Part of the fatty organ should also correspond to the melon (Hardy, 2005) as expected for odontocetes. The prenarial basin is surrounded on its anterior, posterior, lateral, and ventral surfaces by the basin walls (see fig. 3.7). The connective tissues and dermal shield cushion the dorsal surface of the melon/spermaceti organ from potentially severe blows inflicted upon the forehead in 'jousting' contests.

The anterior part of the **maxilla** is not very wide and *Z. cavirostris* **nasals** are approximately the same size and are not cramped between the premaxillary crest bones as seen in beaked whales such as *Mesoplodon* and *Globicetus*: on the vertex of the skull, the nasal bones protrude and extends forward of the premaxillae and frontal bones. The enlarged nasals are separated from the premaxilla bones by thick bands of cartilage that fill the clefts between the structures (Heyning, 1989a).

The skulls are extremely sexually dimorphic in the facial region: sexual differences include the presence of a prenarial basin, mesorostral ossification and more massive and compact rostrum in adult males and longer and leaner rostra in females.

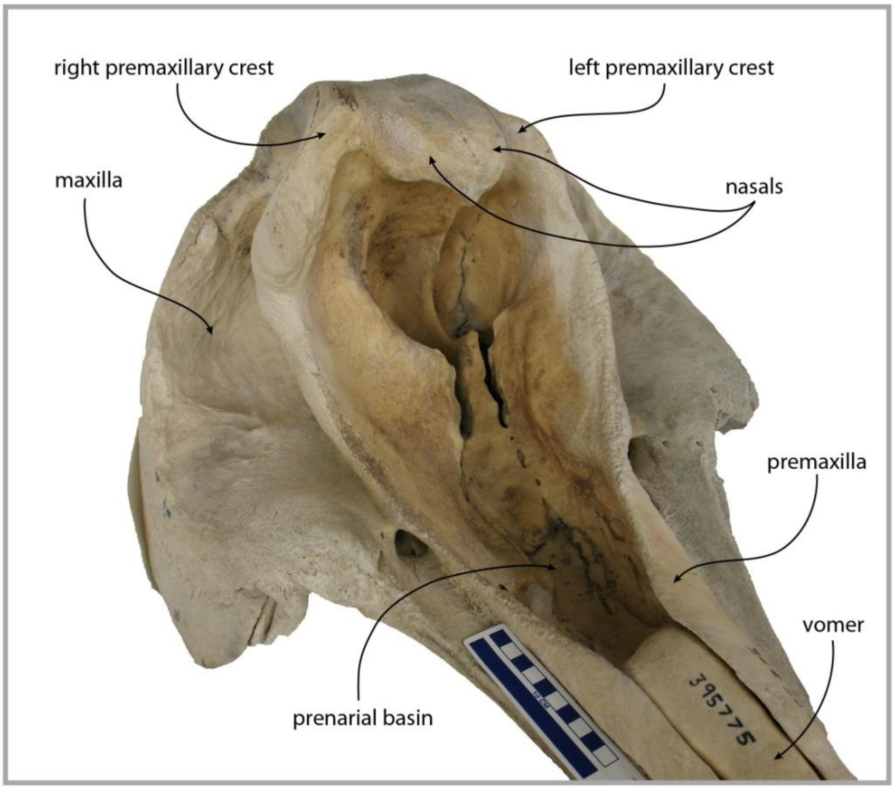


Fig. 3.7: Skull of male *Ziphius cavirostris* (USNM 395775), from the National Museum of Natural History, Washington DC, USA. Detail of the middle/posterior part of the skull. Original photograph by Olivier Lambert.

3.1.3. ***Mesoplodon mirus*** True, 1913

Beaked whales of the genus *Mesoplodon* (Cetacea; Odontoceti; Ziphiidae) are the least known group among extant cetaceans and the few data about them primarily come from analysis of skeletons and carcasses of stranded animals (Souza *et al*., 2005). The *Mesoplodon* genus, particularly *Mesoplodon mirus* (fig. 3.8) is used, mainly for osteological comparisons and to aid in size and weight estimates for *Globicetus*. The analyzed skull of True´s beaked whale, *Mesoplodon mirus* Cram-Q (fig. 3.9, 3.10), belonged to an animal considered an immature male, due to the overall size (when recovered, it measured 4600 mm) and gonads development.

In the **premaxilla**, an important feature that can be observed is a premaxillary basin, which in *M. mirus* is not very wide or excavated like the homologous prenarial basin in *Z. cavirostris*. On the vertex of the skull, the premaxillary bone extends forward of the nasal and frontal bones, separating this genus from *Berardius* and *Ziphius*.

The dorsal exposure of the **maxilla** widens posteriorly and displays a steeper slope along the premaxillary basin. There is a thickening of the maxilla on the supraorbital process (the lateral flange of bone that dorsally covers the orbit (Heyning, 1989a), which is more pronounced than in other beaked whale species analyzed; its ventral surface is formed by the frontal and its dorsal surface consists primarily of the maxilla.

As for the **nasals**, they are not pushed forward as seen in the skulls of *Z. cavirostris* and are not leveled and pushed together: a sulcus runs along the middle of the nasal bones depressing their combined medial region. As in all the beaked whale family, *M. mirus* also shows the characteristic telescoping of the rostrum, characterized by having the maxilla extending onto the top of the head.

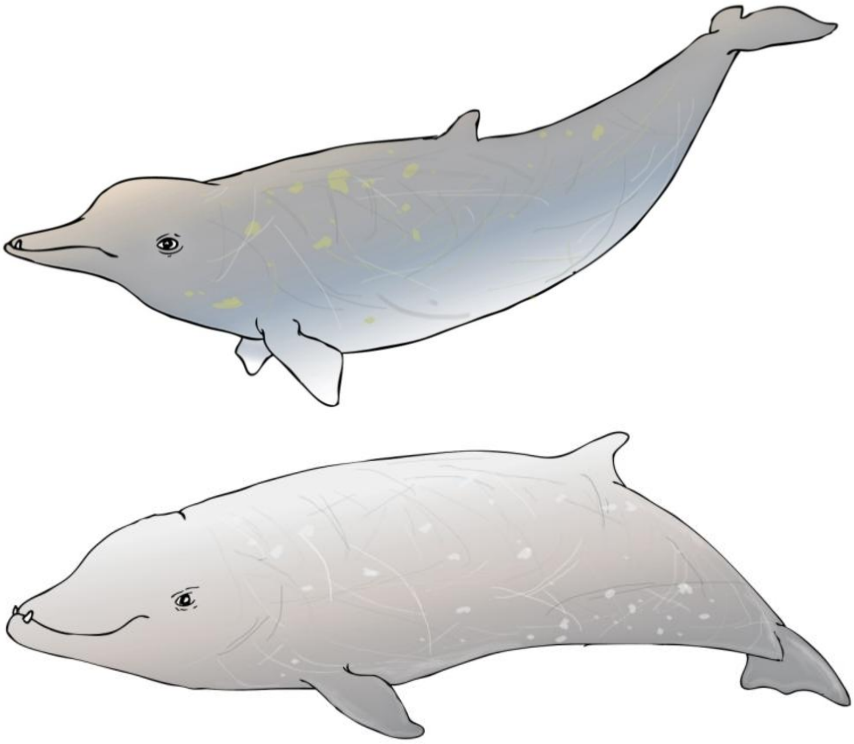


Fig. 3.8: Artistic life reconstruction of True´s beaked whale, *Mesoplodon mirus* (top) and Cuvier´s beaked whale, *Ziphius cavirostris* (bottom). Illustrations not to scale.

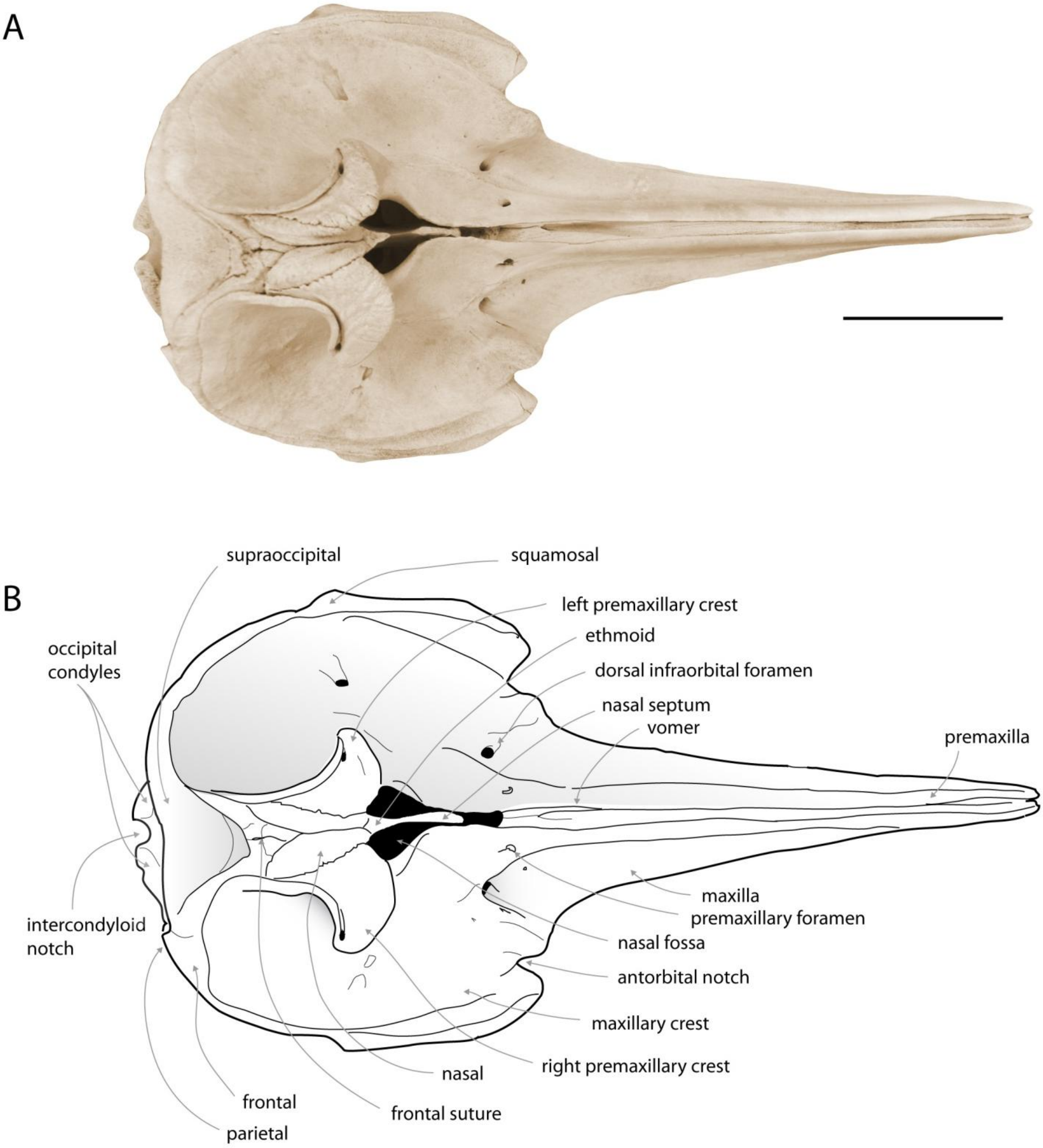


Fig. 3.9: Skull of *Mesoplodon mirus* Cram-Q: A, dorsal view; B, corresponding line drawing. Scale bar: 10 cm.

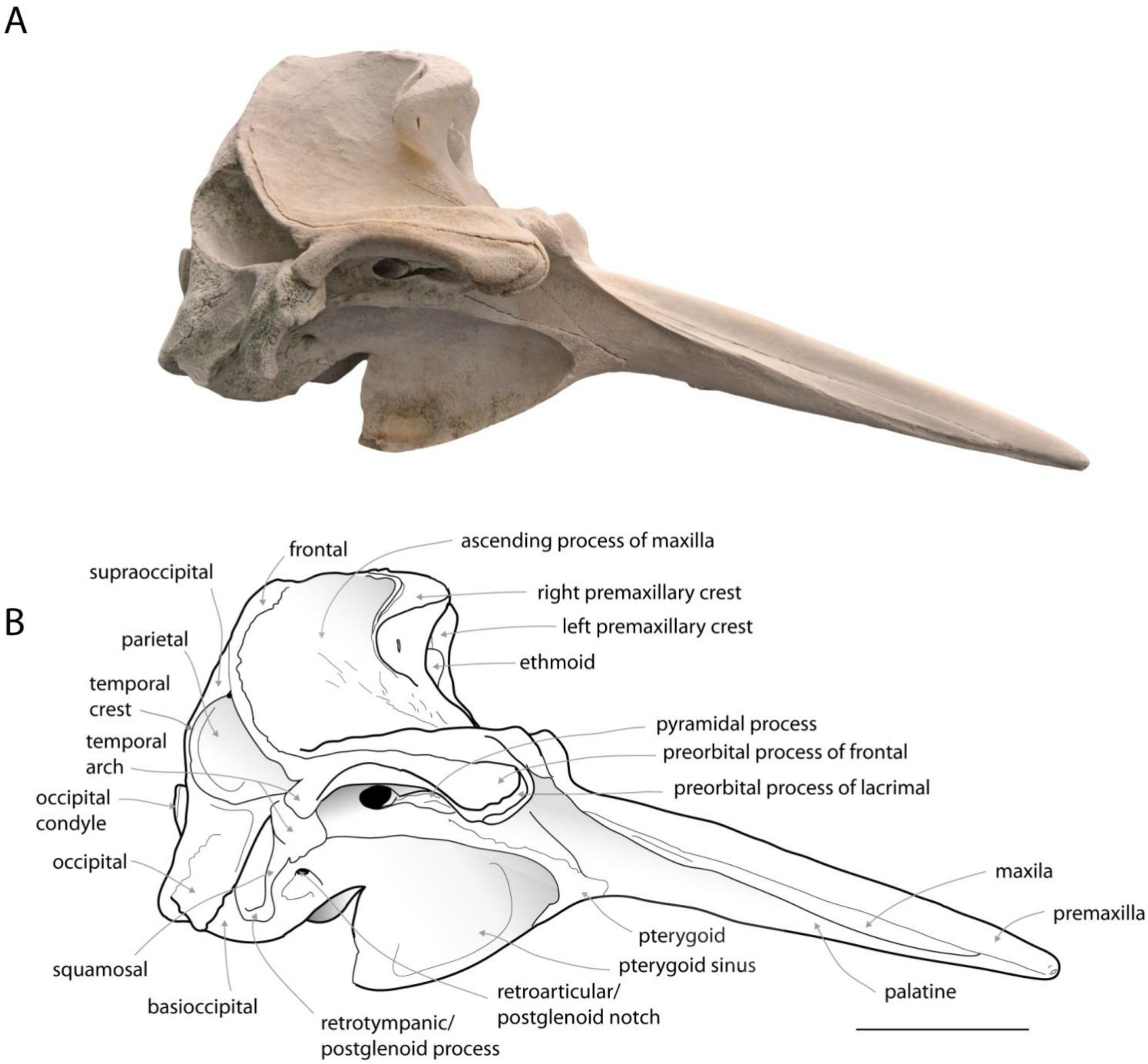


Fig. 3.10: Skull of *Mesoplodon* mirus Cram-Q: A, lateral view; B, corresponding line drawing. Scale bar: 10 cm.

3.1.4. ***Tusciziphius atlanticus*** Bianucci *et al*., 2013

Bianucci *et al*. (2013) were the first to describe another very interesting species of extinct beaked whale: *Tusciziphius atlanticus*. The extinct whale has a rostral maxillary eminence and fused premaxillae forming a protuberant MPP-like structure (which will be referred also as MPP), which can assume a variety of positions and heights. It also exhibits rostral maxillary eminences, located posteriorly above the maxilla just anterior to the antorbital notches.

In the **premaxilla**, the MPP is positioned anteriorly in the rostrum facial area, showing that the bone development was not exclusive to *Globicetus*, even if the latter had a much extreme MPP. In terms of shape, *T. atlanticus* MPP does not become a spheroid, resembling more the sail of a sailboat.

The anterior part of the right **premaxillary sac fossa** is completely filled by compact bone, forming a thick semicircular shelf, absent in the left premaxillary fossa, which is severely concave; Bianucci *et al.* (2013) propose that the partial filling of the right premaxillary fossa may be homologous with the rectangular premaxillary shelf of *Globicetus.* However, in the species *Tusciziphius crispus*, both premaxillary sac fossae are excavated (Bianucci *et al.*, 2013).

The **right premaxillary crest** of *T. atlanticus* shows the extreme transverse widening typical for *Tusciziphius*: the right premaxillary crest is larger, higher and more anteriorly projected than the left. In this character, *Tusciziphius* differs from *Globicetus,* in which both crests have approximately the same anterior extent.

The **nasals** are anteroposteriorly elongated and, as in *Globicetus*, the lateral margin of the nasal is in contact with the premaxillary crest for all its extent. The dorsal surface of the joined nasals forms a shallow depression between the premaxillary crests, but due to the extreme ossification observed, their sutures are hard to detect.

A high and voluminous **rostral maxillary eminence**, slightly medially curved can also be observed in specimen ML 1819 (fig. 3.11). This maxillary characteristic is present on the right side and is less developed on the left side, exhibiting lower rostral maxillary eminences, more anteriorly positioned than the one present on the right side. This different development could be the result of erosion of the fossil surface. However, fossils analyzed by Bianucci *et al*. (2013), sometimes exhibit a more developed rostral maxillary eminence on the left side. The structures would, probably, serve as anchors for muscles and attachment of connective tissue (Bianucci *et al.*, 2013).

In what regards the fossilized rostra of *T. atlanticus*, Bianucci *et al*. (2013), based on the development of the MPP and the rostral maxillary eminences, proposed a differentiation between male and female rostra. Their analysis was made by analogy with extant ziphiids, especially *Hyperoodon ampullatus*, whose development of the rostral maxillary crests reach its peak in mature adult males (Hardy 2005; Bianucci *et al*., 2013). The intraspecific variation considered as possibly related to sexual dimorphism that can be observed at the level of the MPP within the species *T. atlanticus* is considered by Bianucci *et al*. (2013), as “the most significant found until now in a fossil ziphiid considering the range of sizes for the concerned element”. The same analogy will be used in this work for the evaluation of size and shape variation of structures in the rostra of the *Globicetus* specimens.

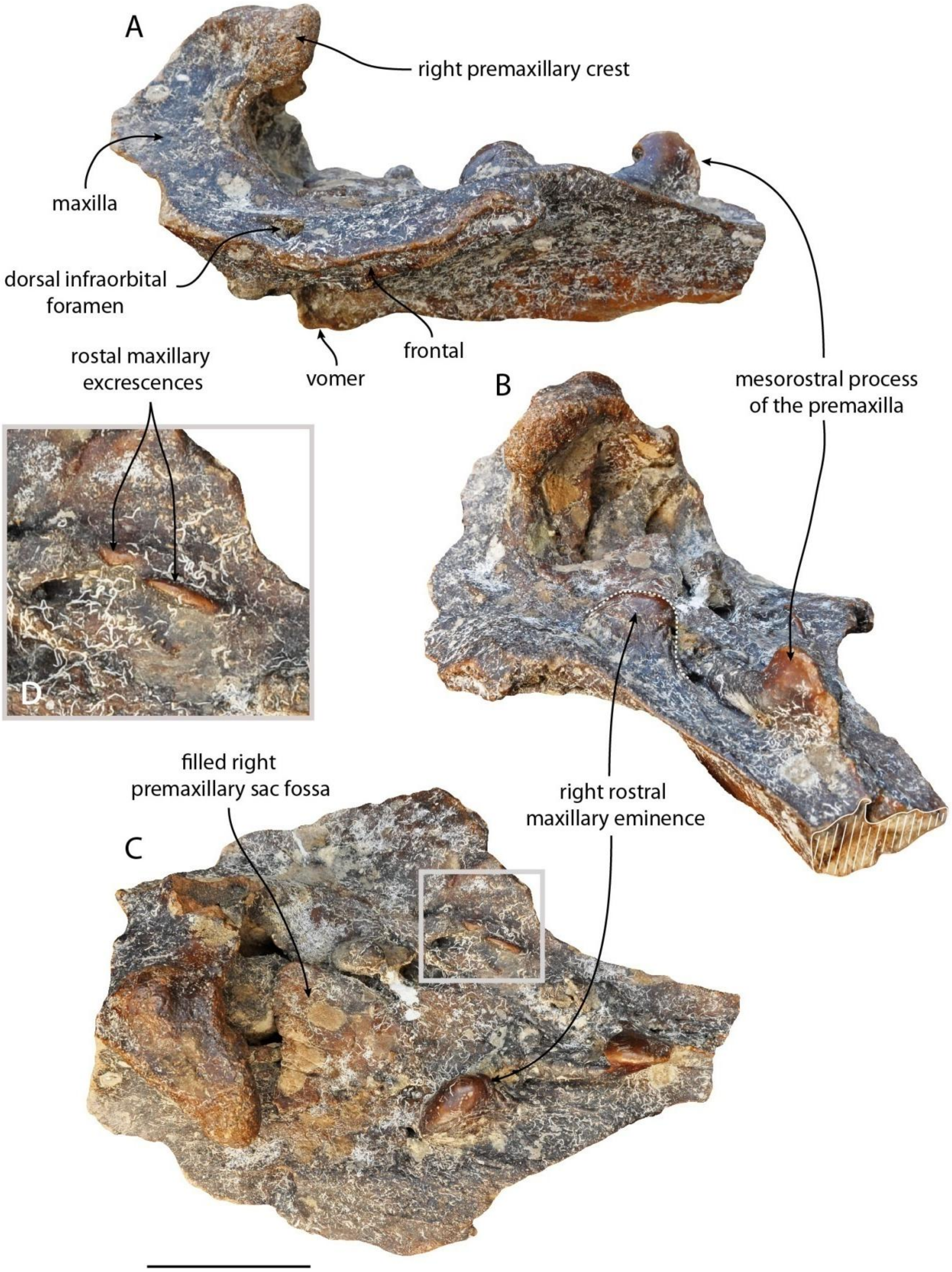


Fig. 3.11: Fragmented skull of *Tusciziphius atlanticus* ML 1819, A – D: A, lateral view; B, anterolateral view; C, dorsal view; D, detail of C showing maxillary eminences. Parallel lines indicate worn portion of the rostrum. Scale bar: 10 cm.

3.1.5. ***Caviziphius* sp.** Bianucci & Post, 2005

The genus *Caviziphius* was first described by Bianucci & Post (2005), based on the single specimen know at the time. A second aff. *Caviziphius* sp., SGHN MA0920, was later described by Bianucci *et al.* (2013: fig. 18 A-B). The importance of this particular beaked whale is the medial rostral premaxillary, structure also supposed to be analogous to the MPP of *Globicetus* and *T. atlanticus*. The very characteristic sail-like MPP allows for a quick and easy identification of the genus, even if only a fragment of the rostrum is preserved.

In lateral view, there is a progressive increase in height of the **premaxillae** starting from the tip of the rostrum, forming a protuberant MPP, and an abrupt decrease posteriorly, generating a clear step on the dorsal outline of the rostrum. The MPP is slightly curved to the right side of the rostrum. A similar anterior MPP is present in a partial skull from the Neogene of Antwerp, Belgium (NMB 002), referred by Lambert (2005: fig. 27 A-C).

In the analyzed fossil specimens described here (fig. 3.12), both ascending processes of the premaxilla are not preserved, and the premaxillary sac fossae are incomplete: they are only posteriorly distinguishable by their semicircular deep excavation. The deep excavation and depression of the rostral area could be compared with the one observed in specimens of *Imocetus piscatus* described by Bianucci *et al*. (2013: fig. 14, 15, 17).

No significant features can be inferred for the **maxilla** of ML 2022 and DGAOT-b, with the exception of a slightly worn left rostral maxillary eminence, located at the rostrum base, and a medially right premaxillary eminence. Two parallel maxillary eminences can be observed in SGHN MA0920 (Bianucci *et al.*, 2013: fig. 18A-B) and DGAOT-b, which allows for supposition that ML 2022 would also possess a right rostral maxillary eminence if complete. The rostral maxillary eminences are tilted medially to the center of the maxilla and could have helped anchor the melon; they can be further compared to the maxillary crests observed in *Hyperoodon*, since they would probably also confine (slightly) part of the lower melon and with *Imocetus piscatus* (Bianucci *et al.*, 2013: fig. 16A-C), because of its maxillary crests, which may have served a similar purpose in aff. *Caviziphius* sp.; despite similarities of *Imocetus* with hyperoodontines, it is interpreted as a member of the subfamily Ziphiinae (Bianucci *et al*., 2013).

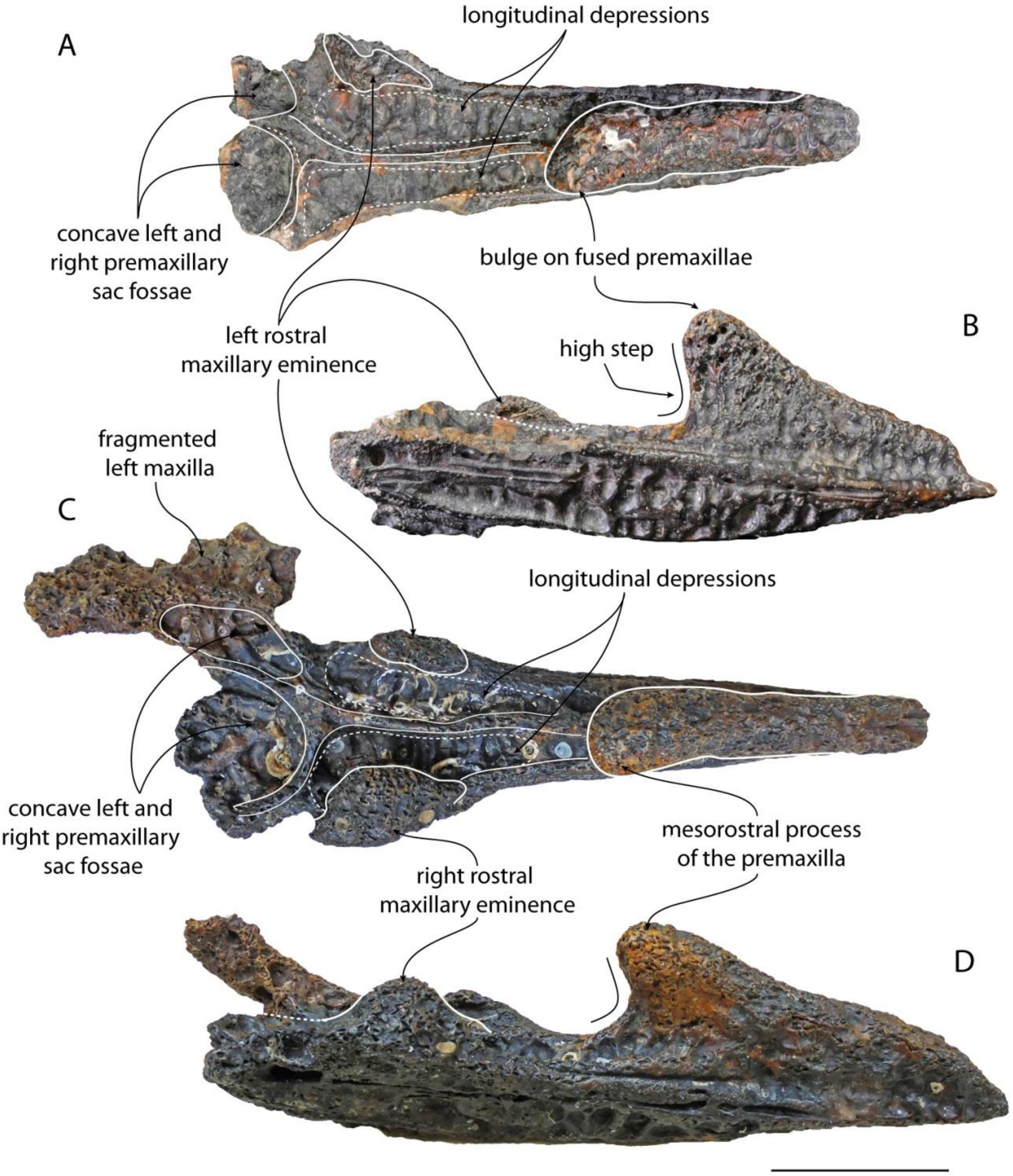


Fig. 3.12: Partial rostrum of aff. *Caviziphius* sp. ML 2022: A, dorsal view; B, lateral view; fragmented skull of *Caviziphius* sp. DGAOT-b: C, dorsal view; D, lateral view. Scale bar: 10 cm.

3.2. Description of structures in extinct beaked whales from Antwerp

Unusual ossification of the rostrum bones in beaked whales is not as rare and unique as one may think: development of crests, rostrum densification and eminences are also evident in the fossil record of Antwerp. The Neogene (Tortonian, late Miocene) of the Deurne Sands Member of the Diest Formation, Antwerp (North of Belgium, southern part of the North Sea Basin) are, according to Lambert (2005), probably the richest location where diagnostic specimens of ziphiids have been discovered, with several genera based on species originating from the sequence. The present work does not intend to repeat the extensive systematic work done by Lambert (2005), but to draw attention to structures of specimens from the collection of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) of Brussels, that can somehow be homologous to other fossil beaked whales analyzed in the present work.

Specimen IRSNB 3781-M.543 (fig. 3.13), is a partial rostrum with the left premaxillary sac fossa still partially preserved. Its most striking feature is the very developed maxillary rugosities on the dorsal surface of the maxillae at the base of the rostrum (some of them longer than 8 mm); they are hock-like in shape, a feature that would be very efficient in muscle and tissue anchoring. Similar rugosities can also be found in the triangular maxillary surface of *Ziphirostrum* sp., SGHN MA0936 (Bianucci *et al.*, 2013: fig. 19, page 141).

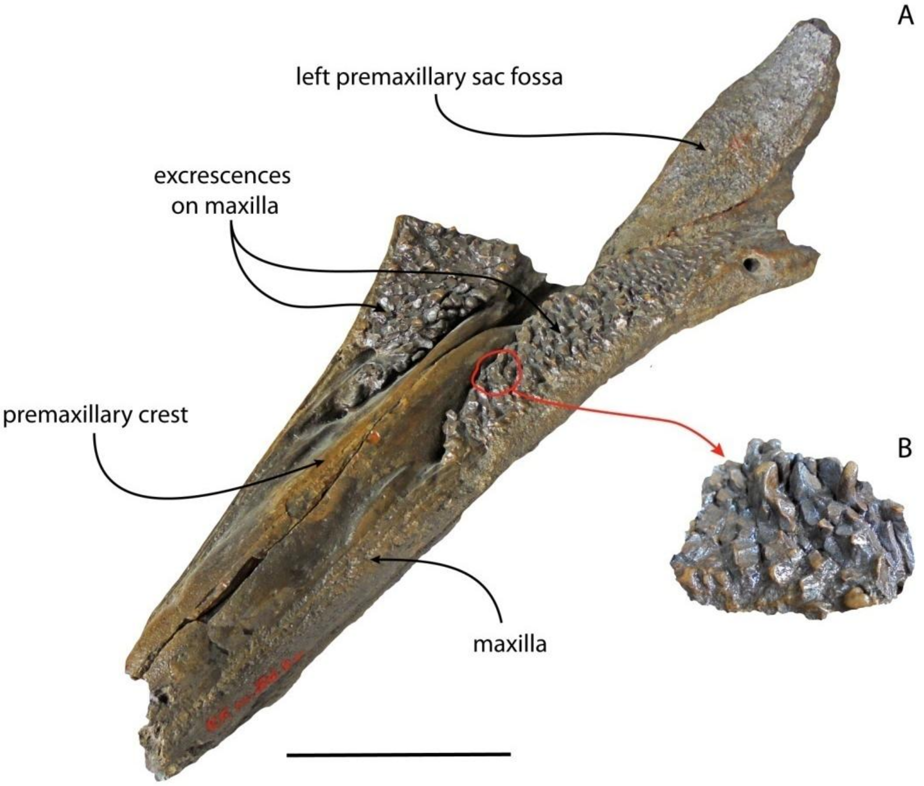


Fig. 3.13: Rostrum and left premaxillary sac fossa of Ziphiidae *indet.* (*sensu* Lambert, 2005, but seen as *Ziphiopsis phymatodes* by du Bus, 1868), IRSNB 3781-M.543; A, anterolateral view; B, detail of the hock-like maxillary rugosities. Scale bar: 10 cm, but may change due to perspective.

However, the development of rugosities with the same hock-like shape is not exclusive of the previous beaked whale species, and can also be observed in the posterior part of the rostrum of *Globicetus* ML 1361, near the dorsal infraorbital foramen, just on the right side of the premaxillary shelf (fig. 3.14).

Fig. 3.14: Skull of *Globicetus hiberus* ML 1861 in anterodorsal view with detail of maxillary rugosities for the attachment of tissue and muscle, marked by two white arrows.

But maxillary rugosities are not always so developed; *Choneziphius planirostris* Cuvier (1823) IRSNB 3775-M.1883 also exhibits covering of its surface by series of dorsal anteriorly directed prominent rugosities and irregularities (fig. 3.15). Lambert (2005) draws awareness to the fact that "In extant ziphiids, such as *Ziphius* and *Mesoplodon*, the dorsal surface of the maxilla on the rostrum corresponds to the main area of insertion for the rostral muscles, extending partially dorsally and medially onto the melon", which could mean that the rugosities in *Choneziphius planirostris* may serve as an efficient anchoring area for muscles to the surface of the rostrum.

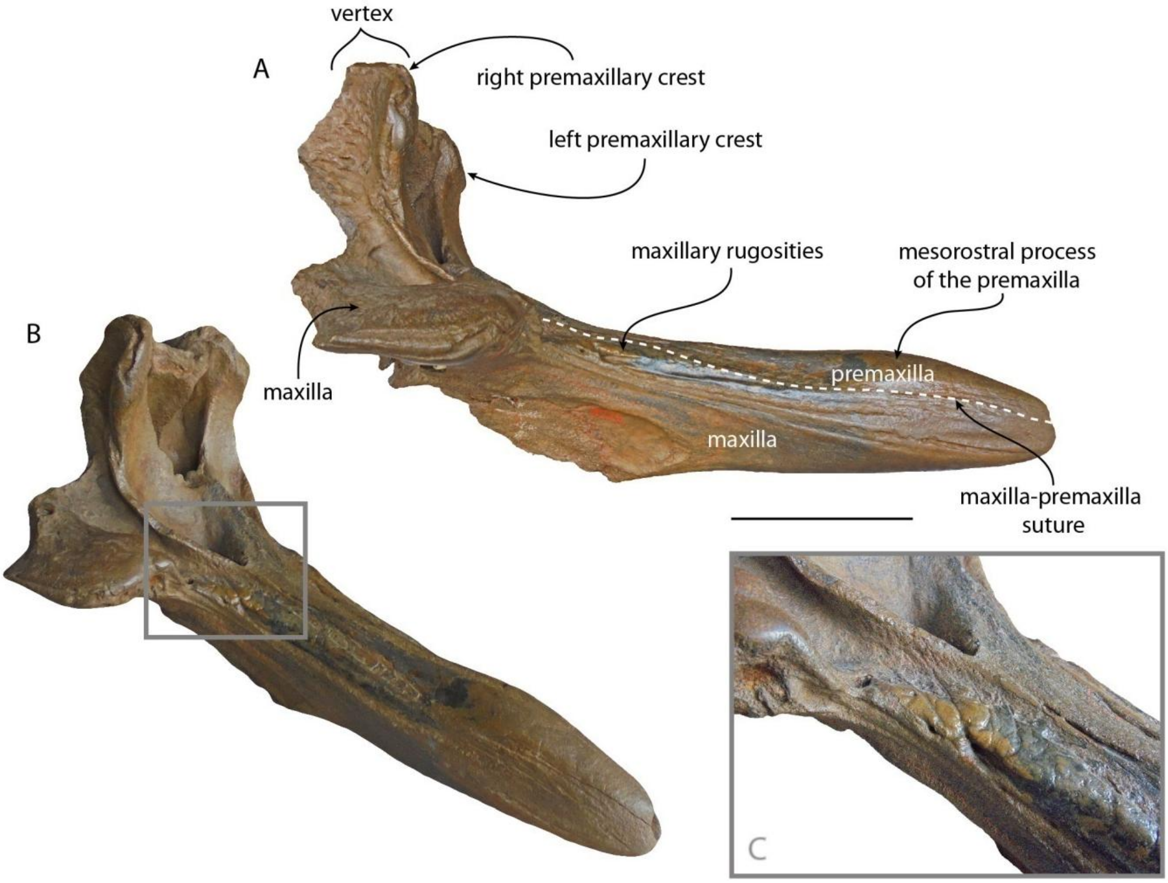


Fig. 3.15: Skull of *Choneziphius planirostris* Cuvier, 1823 (IRSNB 3775-M.1883), A - C: A, lateral view; B, anterolateral view; C, detail of B: rugosity of the maxilla for anchoring of rostral muscle and tissue. Scale bar: 10 cm.

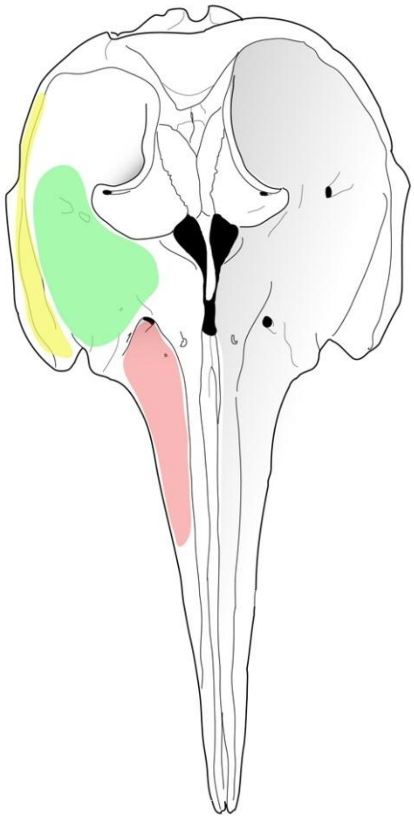


Fig. 3.16 – Outline of skull of *Mesoplodon mirus* with the origin of some of the facial maxillary muscles: yellow, *pars anteroexternus*; green, *pars anterointernus*; red, rostral muscles. The placement of the muscles are based on illustration of muscles in *M. carlhubbsi* by Heyning (1989a).

Ziphiids exhibit strong head muscles that aid in the closure and opening of the blowhole and in the air exchange between air sacs. These muscles also have an important role in the soft tissue reinforcement and placement. Most superficial is the *pars posteroexternus* that originates from the supraorbital process and sweeps dorsally to the vertex and the connective tissue surrounding the blowhole; deep to these muscles is the *pars intermedius* that has a similar origin just medial to the *pars posteroexternus*, but with fibers that extend over the facial region farther anteriorly to insert into the connective tissue melon (Heyning, 1989a). According to Heyning (1989a), the most anterior fibers of this muscle originate anteriorly along the rostrum and are termed the rostral muscle, which can usually be subdivided into a lateral and a medial rostral muscle. Rostral muscles originate off the dorsal surface of the mandibles (along the lateral aspect of the rostrum) and radiate laterally and dorsally (Bianucci, 2005). The lateral muscle originates on the lateral surface of the maxillae, inserting in the connective tissue mass around the blowhole (Heyning, 1989a); the medial originates primarily on the dorsal surface of the premaxillae and inserts on the ventrolateral aspect of the melon, whose tissue grades into the connective tissue just below the epidermis (Heyning, 1989a). Heyning (1989a) concluded that the muscles do not pass over the top of the melon, but that there are some fibers that sweep over the top, completely encircling it, having extreme importance in the lateral confinement of the melon and other oily tissues and a role in the blowhole and nasal plug closure and opening. It is these rostral muscles that are anchored along the maxillae by the maxillary rugosities, so developed in some fossil ziphiids, such as IRSNB 3781-M.543 and IRSNB 3775-M.1883 (Lambert, 2005). Activity in the *pars anterointernus*, *pars posterointernus*, nasal plug muscles and diagonal membrane muscles has been associated with phonations (Heyning, 1989a) and in having an important role during submersion, since it is important that a tight seal be maintained in order to prevent the entrance of water into the lungs. Facial maxillary muscles *pars anteroexternus*, *pars anterointernus* and the rostral muscles placement is exemplified in figure 3.16.

The development of maxillary rugosities in some ziphiids is higher on the right side of the skull, indicating that probably more powerful muscles would be found on the right side. This can be explained due to the usual asymmetry of the melon: in extant odontocetes, the melon is set asymmetrically, slightly off to the right side (Heyning, 1989a; Lambert, 2005) and extends posteriorly into the right nasal plug, which in adult males of *Ziphius* – the closest extant genus to *Choneziphius*, is much enlarged (Heyning 1989a; Lambert, 2005) when compared with the left one. Heyning (1989a) describes that in some species of *Mesoplodon*, such as *Mesoplodon carlhubbsi*, on the right side of the skull, the melon takes up some of the space occupied by the lateral rostral muscle, making the lateral rostral muscle to appear slightly larger on the left side.

For further information on ziphiids rostral muscles, connective tissues and soft anatomy, readers should refer to the work of Heyning (1989a) and Cranford *et al*. (2008a).

Some other fossilized specimens exhibit crest like structures that can be compared to the ones found in extant *Hyperoodon,* but are very different in bone density. *Aporotus recurvirostris* du Bus (1868)**,** IRSNB 3812-M.1887 (holotype), is partially fragmentary, but gives a clear overall view of the skull anatomy (fig. 3.17): it includes an almost complete rostrum and the anterior part of the vertex, exhibiting elevated longitudinal premaxillary crests; the surfaces of the crests exhibit numerous anastomosed vascular sulci, which, even though the rostrum is split/broken in two, are evidence that there was no fused suture between the crests, since innervations canals would not be found in the interior surface if they were fused. The lateral surface of the crest is also covered by sulci and the expansion of these canals can be observed quite easily.

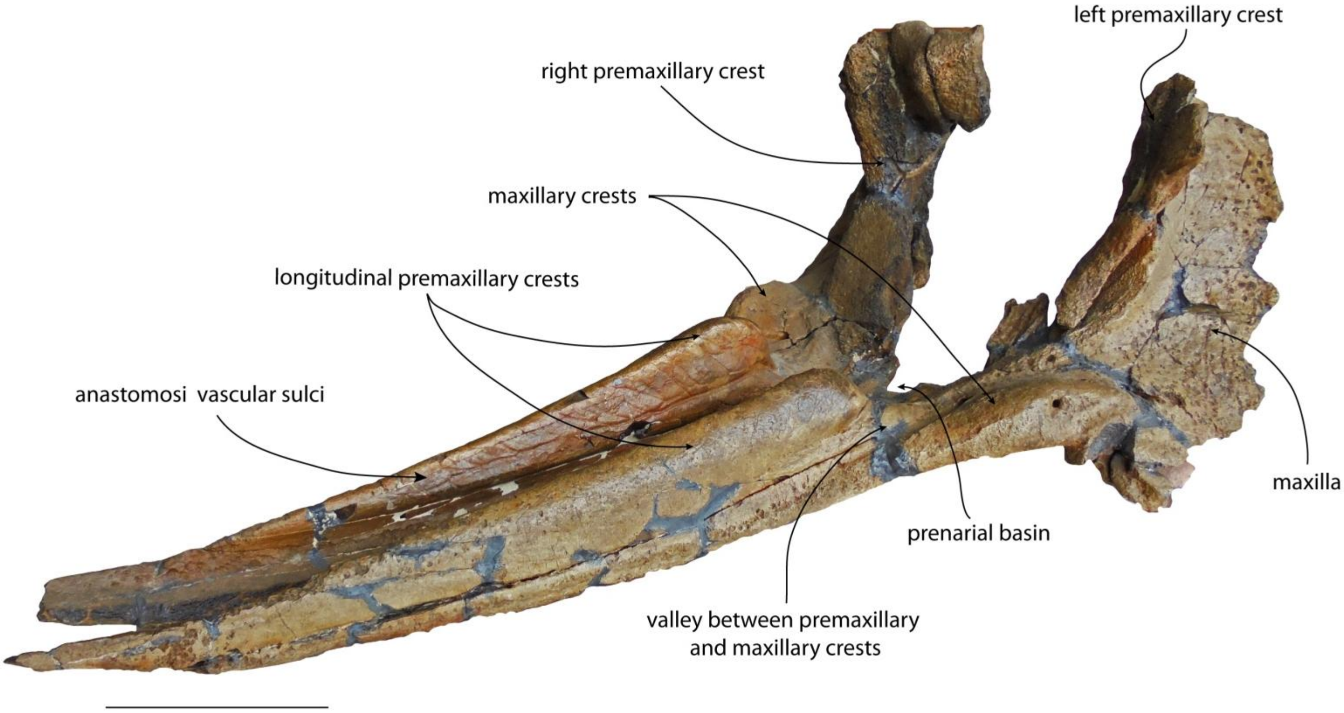


Fig. 3.17: Skull of *Aporotus recurvirostris* du Bus (1868), IRSNB 3812-M.1887 (holotype) in anterolateral view. Notice that the right and left crests would not contact, since vascular sulci are seen preserved between their supposed contact surfaces. Scale bar: 10 cm, but may change due to perspective.

Rostrum IRSNB 3807-M.1889 (fig. 3.18), also exhibits numerous small vascular sulci on its very smooth premaxillary surface. This fragment of rostrum is just a part of the premaxillae and is extremely developed to form a massive elongated dome, hiding the maxillae from dorsal view. The premaxillae are only partly fused along their dorsal medial contact above the reduced mesorostral groove and there is a clear break on the ventral part of the contact surface between the two crests; they have a maximum height of 92 mm and a maximum width of 82 mm, both roughly at mid rostrum length. These vast innervations canals and the partial fusion of the premaxillae above the mesorostral groove are similar to the ones found in *Globicetus*, even though in IRSNB 3807-M.1889 the structure initially developed as independent premaxillary crests.

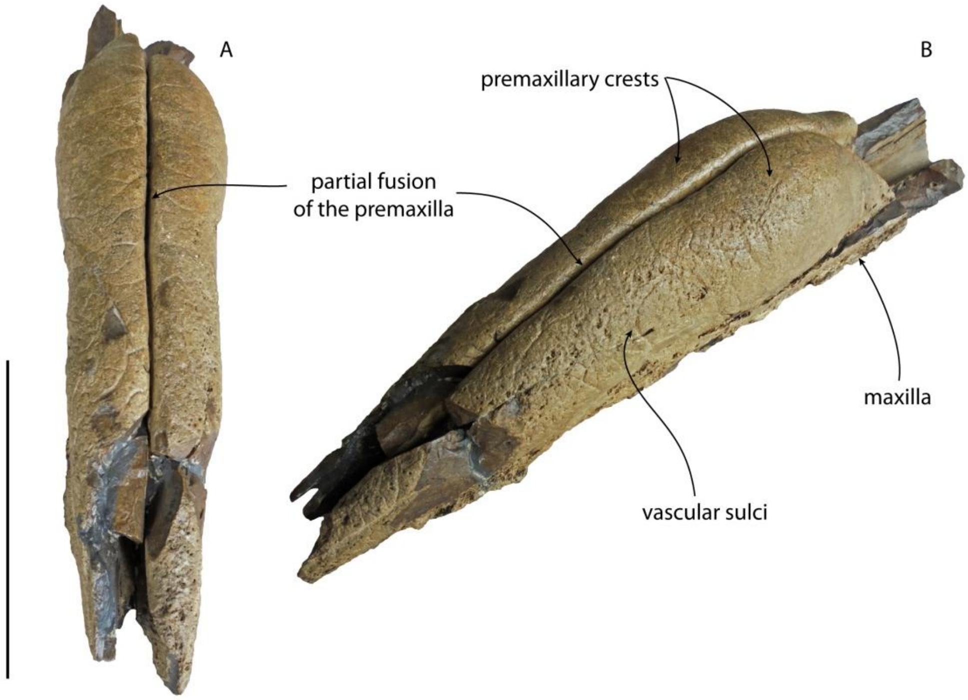


Fig. 3.18: Rostrum of *Aporotus* dicyrtus (sensu Lambert, 2005, but seen as *Ziphirostrum timidum* by du Bus, 1868), IRSNB 3807-M.1889; A, anterior view; B, anterodorsal view. Scale bar: 10 cm, but may change due to perspective.

Specimen IRSNB 3845-M.538 (fig. 3.19) is a good example of a prenarial basin, similar to the one found in extant *Ziphius cavirostris*, formed by nearly complete reabsorption of the premaxillae, and limited, laterally, by the maxillae. The premaxillae are thick and dense and appear at the anterior limit of the prenarial basin (Lambert, 2005).

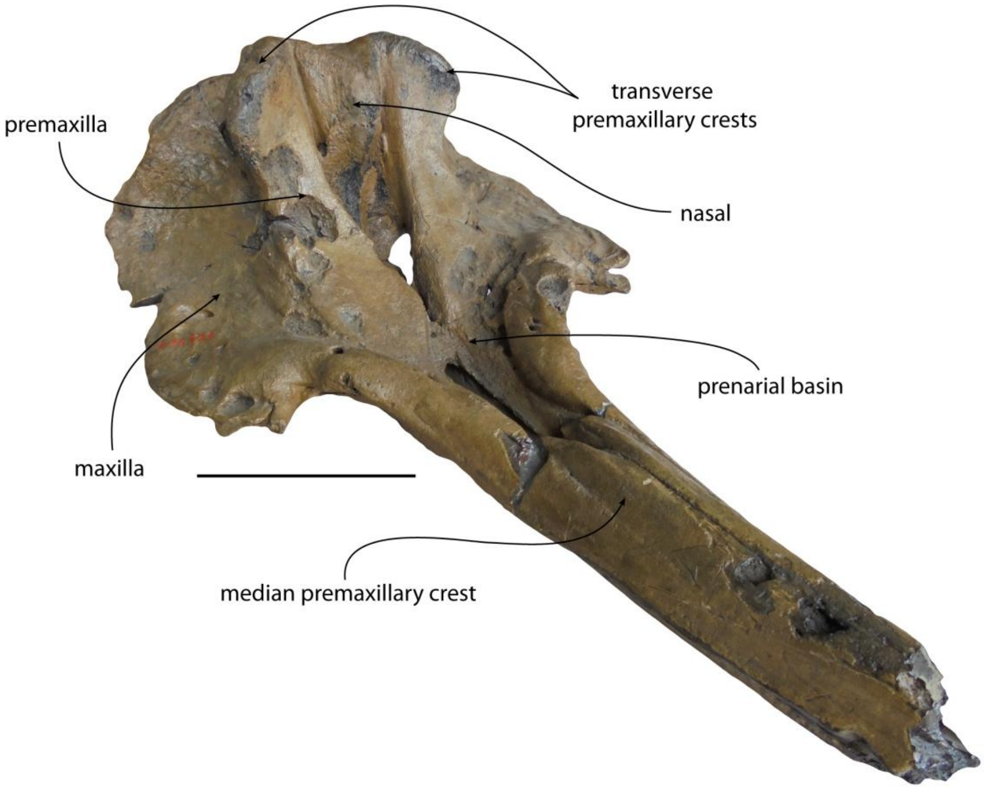


Fig. 3.19: Skull of *Ziphirostrum marginatum* du Bus, 1868 (IRSNB 3845-M.536) in anterodorsal view. Scale bar: 10 cm, but may change due to perspective.

4. Discussion

4.1. Dimorphic variation and sexual crest development in *Hyperoodon*

There are two known species of *Hyperoodon* Forster, 1770: *Hyperoodon ampullatus* and *Hyperoodon planifrons*. Their skulls are fairly easy to identify because they are very different from the skulls of other ziphiids: they have maxillary bone eruptions (different from *Globicetus* in which the major bone development is observed in the premaxilla that forms the MPP), usually referred as maxillary crests, that become ossified and enlarged, increasing in size allometrically with age (Heyning, 1989a) in adult males (Gray & Flower, 1882; Heyning, 1989a; Gowans & Rendell, 1999; Hardy, 2005). As far as fossil ziphiids, *Hyperoodon´s* crests could be better compared to *Imocetus pisctatus*, which also shows unusual maxillary development (Bianucci *et al.*, 2013, page 131 to 136), but both placement and overall compactness is different. The skull of *H. planifrons* differs from *H. ampullatus* in crest size and development, which Hardy (2005) describes as having maxillary “bumps” or “mounds”, instead of crests, when comparing them with the structures in *H. ampullatus*. *Hyperoodon* is one of the best examples of crest development being both sexually dimorphic and age related. Age/sex of *H. ampullatus*, based on their skulls is usually not hard to determine (see figure 4.1), through crest development and shape. Males exhibit a bigger crest development than females, accentuated with maturity. Females have smaller crests and the space between them is wider than in males.

The term “latifron” to describe the more developed crests is used in honor of Gray as mentioned by Hardy (2005: p. 8); what Gray (1863) described as a new species (*Lagenoctus latifrons*) was actually just older *H. ampullatus* males, but the term “latifrons-type” maxillary development stuck, and is still used today to describe older male crest maturity. Hardy (2005) refers that this structures are “perfectly suited for storing vast amounts of fluid (blood, oil, et cetera) that, in turn, would make them excellent morphological adaptations for absorbing violent impacts”: they are both dense and strong at the same time, able to absorb and dissipate the impacts of head-butting encounters.

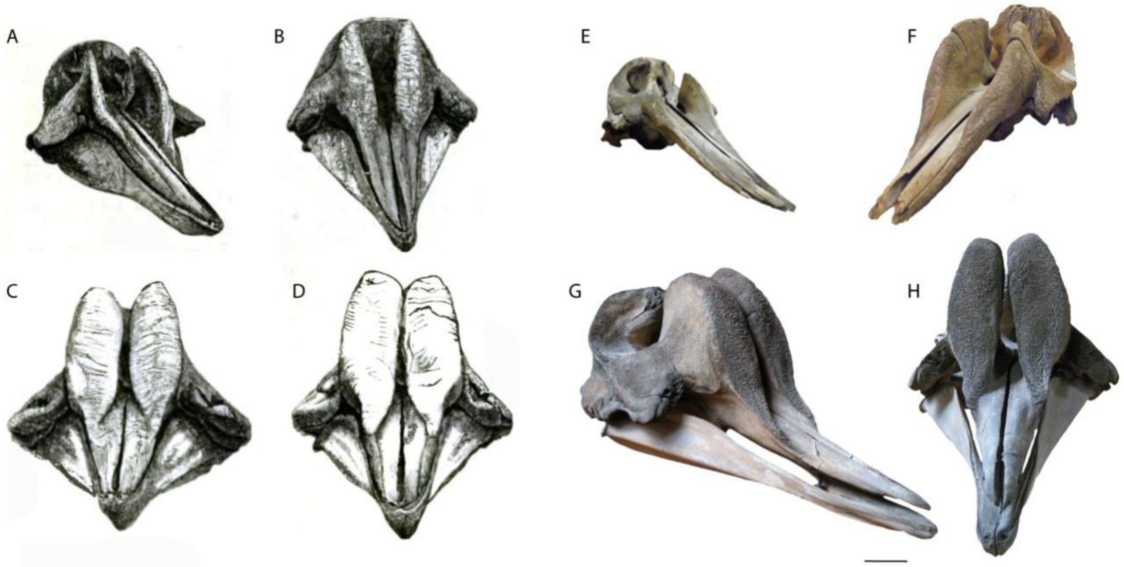


Fig. 4.1: Age and sexually dimorphic development and differences of the maxillary crest region in the skull of *Hyperoodon ampullatus*. A-D: A, young male; B, older male, but still young; C, mature male; D, older male, exhibiting the “latifrons-type” maxillary development. Drawings originally from Gray & Flower (1882), adapted from Hardy (2005); E-H: E, juvenile, anterolateral view (IRSNB 1503B); F, juvenile/ possibly female, anterolateral view (IRSNB 18027); G & H, adult male, anterolateral & anterodorsal view (same skull, MNHN 1872-491, on display in the National Museum of Natural History of Paris, France), photographs by Olivier Lambert. Scale bar: 10 cm, but may change due to perspective.

The melon is described as sitting between the crests (Heyning, 1989a; Hardy, 2005; pers. comm. Lambert) and then shrinking as the gap between them narrows as the "latifrons-type" develops in males (Hardy, 2005). According to Hardy (2005), this tube-like structures allows the semi-plastic melon to move while the animal grows, moving "downward and forward into and ahead of the crests". It is this bone structure that protects the soft tissue from impacts in head-butting activities by other males. Other functions, aside from fighting, for the extreme maxillary development have been proposed. Hardy (2005) proposed that the narrow and convex region between the crest would also be a "channel" which could enhance sound transmission along its length.

Hyperoodontines are imperative when trying to hypothesize how bone structures could have been used in extinct whales and how they might have affected their behavior and have developed with age. A few hypotheses for how the melon in *Globicetus* would develop and how it could be cramped by the MPP can be inferred by studying the extreme crest development in *Hyperoodon*, although neither the position nor the constitution of the bone is the same in *Globicetus.*

4.2. Soft-tissue inference in *Globicetus*

"Obviously, living organisms are more than collections of bones and teeth. As a result, the evolutionary interpretation of the paleobiology of extinct organisms often requires explicit reference to anatomical systems other than the skeleton, that is, to those portions of the organism not normally preserved in the fossil record."
Witmer, L. M. (1995)

In modern paleontology, the reconstruction of extinct animals does not rely only on the assemblage of the fossilized bones, but tries to actually bring the animal "back to life". Soft-tissue reconstruction is important for paleobiological inferences as functional morphology, behavior and mode of life. According to Witmer (1995), taking soft tissues into account, allows the formulation of causal hypotheses of character correlation, since skeletal tissues are largely responsive to the influence of their soft-tissue functional matrices and thus may be only subjected indirectly to natural selection.

Trades exhibited by extant descendents are the starting point to formulating hypotheses about the tissues attributes on the common ancestor of the extant phylogenetic bracket. The Extant Phylogenetic Bracket (EPB) is a methodology for reconstructing soft anatomy in fossils which references at least the first two extant outgroups of the fossil taxon of interest, correlation involving the application of basic cladistic principles (Witmer, 1995). Witmer (1995: p. 25) proposes that "all similarities in soft tissues (and correlated osteological features) between the two extant taxa can be hypothesized to have been present (minimally at least) in their common ancestor and all its descendants, including the fossil taxon of interest".

The proposed method requires and makes explicit use of extant taxa as these are the only organisms for which we can obtain precise information about the soft tissues and their relations to the bones and the phylogenetic relationships of the fossil and extant taxa (Witmer, 1995). The soft tissue modeling for *Globicetus* may be labeled, according to the hierarchy of inference proposed by Witmer, as a level I inference: "almost no speculation in situations where the EPB approach yields a decisive positive assessment at the outgroup node". A level II inference is not the case here since it refers to "soft tissue suspected to occur in a fossil taxon is found in its extant sister group but not in any other outgroups" (Witmer, 1995). Witmer (1995: p. 30) warns that "the EPB approach does not bar the recognition of the novelties of extinct taxa; rather, it allows us to assess critically the empirical basis of the inference"; this means that, in the case of *Globicetus* and other fossil ziphiids, structures not exactly present in extant taxa have to be treated with some prudence.

Bryant & Russell (1992: p. 406) refer to the work of Bock (1989) about the transferal of known attributes from extant taxa to fossil specimens based on phylogenetic relationships; given this, basic evolutionary assumptions justify for inferring features of organisms closely related to the fossil taxa. According to Bryant & Russell (1992), "fossil taxa are predicted to share the synapomorphies that diagnose the clades to which they belong". In the case of fossil ziphiids, the echolocating apparatus has several features suggestive of echolocation, such as dense, thick and downturned rostrum, the air sac fossae, cranial asymmetry and exceptionally broad maxillae (Geisler *et al.,* 2014). Based on the sound apparatus commonly associated with ziphiids, we can hypothesize how the sound transmission and pathway may have been in *Globicetus*: the direction of the vibrations produced in the phonic lips would first travel through the air sacs that surround them and then go to the spermaceti-like organ, which, with the help of the high-density bony boundaries of the bones where it is normally cradled (the concave ascending process of the premaxilla), would reflect the beam through the rest of the melon, being then transmitted into the water which has a bigger mean sound speed, emanating the transmitted sonar at a higher velocity; this cradling of the melon may be similar to the function of the dense connective tissue case that bounds the spermaceti organ in sperm whales (Cranford, 1999). Part of the high frequency sounds would indeed probably propagate in a posteroventral direction through the lower density part of the melon, but a large part of the beam would be directly transmitted through the lower denser density part, and focused anteriorly by a low density pathway inside the melon (as is proposed for many extant odontocetes). Functionally the best suited sounds would probably be the ones that leave the head without major reflections. Clearer sounds would be more advantageous for the echolocating activities, since fewer reflections would produce a sound with less noise. *Globicetus* strange osteological structure leaves an open door for conjecture on how the sound would be propagated and how the soft tissue and sound production apparatus would be cradled in the posterior portion of the rostrum.

The exercise of soft-tissue inference is partially based on the work by Cranford *et al*. (2008a), which uses remote imaging technology to quantify, compare, and contrast the cephalic anatomy between a neonate female and a young adult male Cuvier's beaked whale (*Ziphius cavirostris*). His work provides clues to infer and compare traits that lack osteological correlates. However, such inferences must require additional theorizing (Witmer, 1995), and two main examples as far as the anatomical soft tissue traits and placement in the rostrum of *Globicetus* are presented next. When trying to figure out how the soft tissues would be positioned inside the head of *Globicetus*, there are a couple of things to consider: how high up were the phonic lips positioned in relation to the premaxillary crests vertex and how high would the melon sit on the rostrum. Important note: we will refer to the "melon" as a single organ, but in figure 4.2, the melon in divided into two colors referring to the different densities it exhibits: purple, lower density; yellow, higher density.

In extant beaked whale anatomy, the phonic lips and the melon have a close relationship when it comes to the placement inside the head (Fig. 4.2). If the phonic lips are high, the melon is also high up in the rostrum, and in direct line with

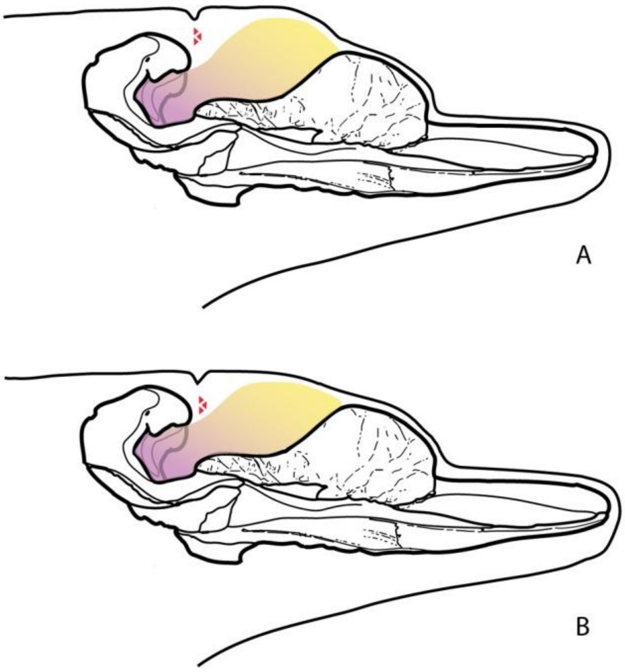


Fig. 4.2: Representations of *Globicetus hiberus* with hypothesis for the placement of the melon (low density part in purple and the higher density portion in yellow) and the phonic lips (red triangles); A, higher positioned melon and phonic lips; B, lower positioned MPP and phonic lips, allowing for a better anchoring of the muscles and tissues that involve and keep them in place. Rostrum outline from specimen ML 1361.

them, since the sound waves have a specific way of being transmitted through the soft tissues, and the melon is a crucial part of the transmission mechanism. If the location of the phonic lips was above the premaxillary crests vertex, the melon would reduce the hydrodynamic shape characteristic to almost all beaked whales, with the exception of *Hyperodoon* and to the Delphinidae family (e.g. *Globicephala*), which have very big bulbous foreheads and are still able to deep dive efficiently. Furthermore, having a melon too high could bring another complication: the connective tissues that secure the soft structures of the head and maintain the phonic lips in place would have little bone structures to anchor all the soft tissues of the head, since almost all bony eminences are located at the base of the maxilla or on the premaxillary crest and premaxillary shelf. This is not a problem in *Hyperodoon* or *Globicephala*, since the first has very developed maxillary crests surrounding the melon and therefore, allow for a big area of connective tissue placement on the crests and the latter has a small excavated prenarial basin enough to hold and anchor the soft tissues as well as a moderately wide rostrum base (Van Bree, 1971). The fact that *Globicetus* exhibits such a low and curved ascending process of the premaxilla, may indicate that the soft structures would be cramped inside or just anteriorly to these structures, suggesting that by having lower positioned phonic lips (in direct line with the highest part of the premaxillary crests) and melon, it would be easier to find a way of anchoring the connective tissues around them. However, Bianucci *et al*. (2013) argues that the sounds must have been produced at a level high enough above the level of the dorsal surface of the spheroid as they consider the MPP an unsurpassable obstacle. Although further studies on the acoustics and anatomy of *Globicetus* are needed to better characterize the soft tissue arrangement in this ziphiid (acoustic tests should be performed for a more accurate influence of the sphere in regard to the sound transition), it seems most likely that it may have resulted from an evolutionary compromise between a barrier (if the phonic lips were placed too ventrally) and a hydrodynamic cost (if placed too dorsally).

4.3. Size estimates for *Globicetus*

The distance between the posterior limit of the symphysis to the mandibular condyle (S-C length) can be used to determine adulthood in whales. As an example, according to MacLeod & Herman (2004), the majority of sexual dimorphic features in *Mesoplodon bidens*, become noticeable at a S-C length of around 441 and 444 mm, suggesting that males mature around a S-C length of 444 mm. Unfortunately, there has not been found any fossilized lower jaw of *Globicetus*, so the only way to estimate its size is by measuring the postorbital width of the skull.

Bianucci *et al.* (2008) did extensive comparisons of size of extinct and extant South African beaked whales that allow us to estimate the size of an adult *Globicetus*. To estimate the body length (BL) was used the following regression equation (Lambert *et al*., 2015), $BL = (9.464 * PW) + 1137$, where: PW = postorbital width of the skull (in millimeters). The holotype (ML 1361) was used as the subject; it has a PW of 372 mm, therefore its body length is proposed to fall in the range of *Mesoplodon bowdoinii* and *Mesoplodon densirostris*, between about 4.5 and 4.7 meters (Bianucci *et al*., 2008; Lambert *et al*., 2015; Lambert pers. comm.), since $BL = (9.464 * PW) + 1137 = 4{,}65$. A size comparison between *Globicetus* and an adult human male is illustrated in figure 4.3. For further information on beaked whale size, Bianucci *et al.* (2008) is recommended.

Weight may also be estimated for some fossil ziphiids. For estimating the body weight (BW), a regression equation proposed by Pyenson & Lindberg (2003) in Lambert *et al*. (2015: p. 4), is used: $BW = 0.4628 * (WOC)^{3.2087}$, where WOC = width across occipital condyles. Unfortunately, for the fossil specimens analyzed, the occipital condyles did not fossilize; however, since its body size seems to fall in the range of those of extant *Mesoplodon*, it is possible that the extinct whale could weigh as much as extant *Mesoplodon densirostris*: up to 1033 kg (Ross, 1984). Even though *Globicetus* had such a heavy rostrum bony structure, when considering the probable overall size and weight of the animal, the mass of the MPP would most likely not be as influential as expected, so the comparison with a specimen of *M. densirostris* can be made.

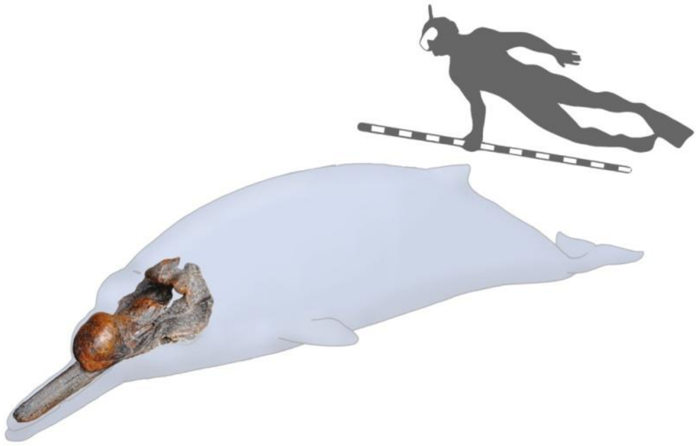


Fig. 4.3: Size comparison between *Globicetus hiberus* and an adult human male. Illustration by Simão Mateus.

4.4. Skull variation and sexual dimorphism in *Globicetus*

The MPP shows a ring-like growth. As mentioned before, the MPP increases continuously after the rest of the other bones have stopped their growth, with the final steps of the growth of the spheroid occurring in fully adult and mature animals. The pad-like structure is made of the same non-remodeled bone as the MPP and the premaxillary shelf and the structures are intrinsically connected. In Bianucci *et al*. (2013), it appears designated as “medial pad of premaxillae”; for an easier read, it will only be referred next as “bony pad” or simply “pad”.

Fossil specimens, such as ML 1859, IEO DR26 026, 100/PAL/UE and DGAOT-a exhibit a bony pad, which connects the MPP to the dorsal surface of the rostrum and in others the pad is missing (ML 1361) or shows, what appears to be, a progressive reabsorption of the structure by the overlaying MPP (ML 2023). Assuming the MPP continues growing after the rest of the bones have finished developing, it is not unexpected that the spheroid continuous growing dorsally and anteriorly and that it would in fact, eventually, end up covering the bony pad.

The intraspecific variation of possessing a pad or not seems to be a sign of sexual dimorphism. Ziphiids have various degrees of skull sexual dimorphism and crest development in *T. atlanticus* has been explained as being sexual dimorphic by Bianucci *et al*. (2013). Specimen ML 2023 shows a degree of transition between having and not having a pad, unlike ML 1361. In ML 1361, the anterior margin of the spheroid does not contact with the underlying premaxillae, leaving an open space of about 10 mm (Bianucci *et al.,* 2013), whereas in ML 2023, the margin between the bony structures is much wider and it can be observed, what looks like, an engulfed pad inside the margin left between the bones.

ML 2023 can lead to some new hypothesis as for the way the MPP would develop: not only could the different sized MPPs be related to sex but also with the different stages of the natural development of the animal. Even though there seems to be a morphological link between MPP growth and the engulfing of the pad, it is still hypothetical, since a larger sample of skulls and further comparison has to be done in order to provide more solid evidence of this deduction; the problem with this analysis is that the bigger specimen has a still visible pad, which could be a sign of being in an earlier development stage than ML 1361. However, this does not seem to be the case, as demonstrated by the graph in figure 4.5. The sexing of the specimens and size is further discussed in section 4.5. and for further information on the relation between the medial pad of premaxillae, MPP and premaxillary shelf and the velocity of the deposition of the bone, see section 4.6.

Ratio between body size and MPP size

Genitalia rarely fossilize, so determining the sex in fossil can be problematic. To tackle such challenge, the work by Motani *et al*. (2015) provides examples of allometric techniques used for differentiation of sex in fossil specimens, in particular, *Keichousaurus hui* (a Middle Triassic sauropterygian), dividing the sample into two independent phenotypes suspected to suffer from sexual shape dimorphism (fig. 4.4). The same theoretical model is used next for *Globicetus*.

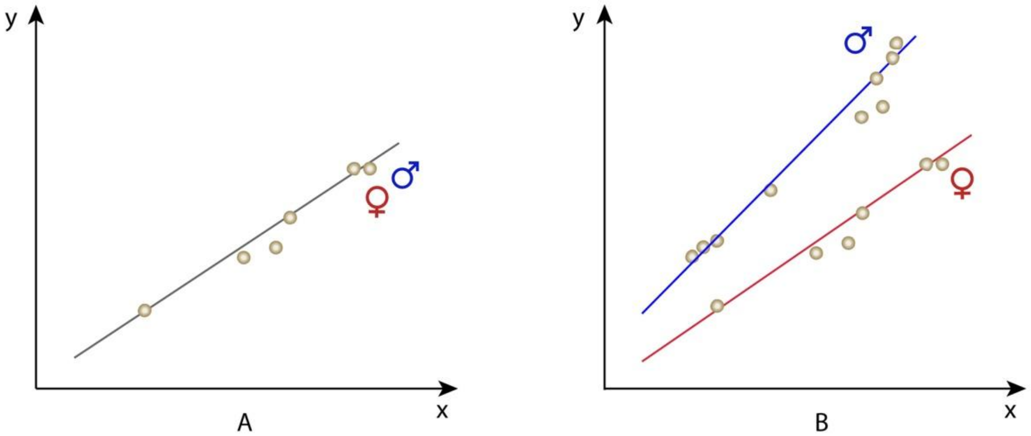


Fig. 4.4: Examples, based o the work by Motani *et al*. (2015), of the expected regression lines representations of gender relationships; A: sample of specimen growth and development with non-dimorphic character between gender; B: sample of specimens with a dimorphic character present and visible sex segregation; x: body size or age; y: expression of secondary sex character.

For *Globicetus*, we postulated that the MPP is a dimorphic structure and we use proxies and estimations to correlate body and MPP size. The measurement of the postorbital width of the skull usually provides the best proxy for body-size and maturity in ziphiids. However, due to the fragmentary state of some of the specimens where the postorbital is missing, the preorbital (better preserved in all the fossils) is used here as an alternative, since both widths of the orbital structures are usually related. The size of the MPP was given by the width multiplied by maximum height of MPP, given in measurements G5 and G6 (table 2.1), respectively.

All six *Globicetus* specimens studied were plotted (fig. 4.5) which allowed the recognition of two morphotypes: i) voluminous and thick MPPs seen in two specimens (ML 1361, ML 2023), additionally this feature seems related to an obliteration of the medial pad of the premaxillae, either through effective absence or complete engulfment by the MPP, and ii) lower MPP and medial pad seen in the other three specimens (ML 1850, DGAOT-a, and 100/PAL/UE). Because in dimorphic secondary sexual traits, the most conspicuous traits are seen in males and this being also valid for ziphiids, the two morphotypes are interpreted as male and female, respectively. For each correlation, is given the basic linear equation (y = ax + b) where y is the trait size (MPP is this case) and x is the body size (G3 measurement in this case). In fig. 4.5, sexual dimorphism is evidenced, with two clear lines: one representing alleged males (y = 248,15x - 51153) and the other (y = 146,43x - 26798), the females. Positive allometry means that the trait in question increases more than proportionally with body size: larger animals have proportionally larger traits than smaller ones (Hone *et al*., 2016). In *Globicetus* males, the MPP grows more and after the rest of the body growth halts, but females have an isometric growth, where the MPP grows in proportion with the body. The specimen IEO DR26 026 is in direct line with the previous male specimens, but reveals different anatomical features than the other males: lower MPP and an elongated medial pad of premaxillae. These are considered female attributes but the analysis suggests it to be a male (maybe subadult or immature); this is justified by two characteristics exhibit by the specimen: the MPP growth shows a similar pattern of anterior projection and exhibited complete mesorostral ossification of the mesorostral canal (Buffrénil et al., in review), a dimorphic trait discussed next.

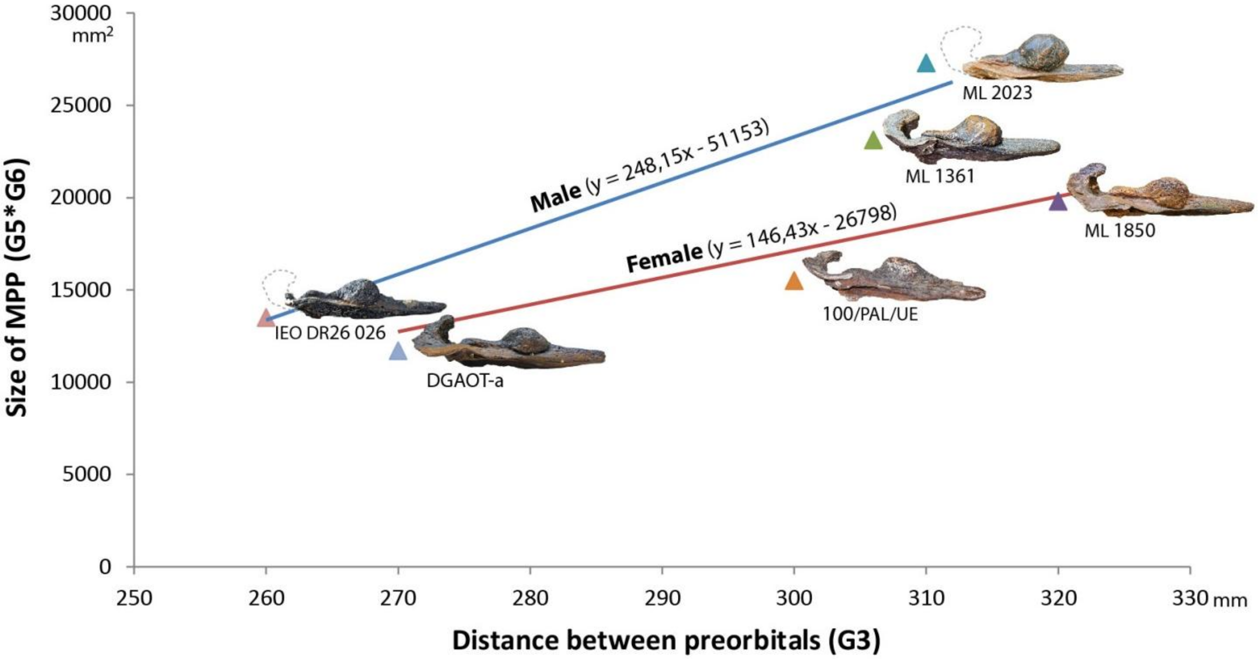


Fig. 4.5: Relationships between body size (given by the distance between the preorbitals, in mm) and the MPP size (in mm^2) of the analyzed specimens of *Globicetus hiberus*. Different color triangle points represent different specimens, which are represented next to them; the blue and red lines represent male and female individuals, respectively.

Note: the preorbital width of the skull in specimen ML 2023 was estimated. The fossil is fragmented and its posterior part, right after the orbital notch, is missing; it measures around 250 mm of width between preorbitals, which show signs of erosion. By analyzing the crest around the orbits in other specimens and similar development of structures and rostrum length in ML 1361 in particular, we estimated a minimum size of 306 (as in ML 1361) and a maximum of around 310 mm for ML 2023. The maximum approximation (310 mm) will be used in the graph of figure 4.5 because some structures are bigger in ML 2023 (premaxillary shelf length and overall MPP size) than in ML 1361.

Filling of the mesorostral canal by the vomer as a male condition

In ziphiids, and more visible in *Ziphius cavirostris* and *Mesoplodon* spp., the filling of the mesorostral groove and canal by a pachyostosed vomer and/or mesethmoid is considered an intraspecific variation of sex and age (Besharse, 1971; Bianucci *et al*., 2008; Lambert *et al*., 2009) also described as an hyperossification of the premaxilla, maxilla and vomer eventually fusing into a massive rostral bone unit (Allen *et al*., 2011), usually seen from both the top and bottom of the skull (Tinker, 1988). According to Tinker (1988), the vomer is greatly extended in a lengthwise direction, forming the bony septum which divides the nasal cavity, and extends forward to end between the two maxillary bones of the upper jaw, resulting in a gradual replacement of mesethoid cartilage by secondary bone during maturation (McLeod, 2002). In ziphiid adult males the mesorostral canal tends to be filled by the vomer, while females still retain the tubular canal condition. This sexual dimorphism character is much more developed in adult males of the genus *Mesoplodon* spp. and *Ziphius cavirostris* than in females (Besharse, 1971; MacLeod, 2002; MacLeod & Herman, 2004; Bianucci *et al*., 2013). *Z. cavirostris* is probably the most extreme case of vomer ossification of the mesorostral canal, where the male exhibits a big intrusion and robustness, which the female lacks.

This sexual dimorphism in ziphiids is anatomically independent from the MPP, thus provides an important confirmation of the gender identification of *Globicetus* seen in the trend of fig. 4.5. Male *Globicetus* rostra show compact filling of the mesorostral canal to the tip of the upper jaw, while female show an open canal with little evidence of such a compact ossification. Admitting a similar pattern for *Globicetus* as observed in *Mesoplodon*, the ossification of the canal can therefore be another character used for attributing sex to the specimens. Fossil specimen ML 1361 and ML 2023 show ossification of the mesorostral canal and are figured in figure 4.6, which corroborates with the sex distinction approach demonstrated in figure 4.5. Mesorostral ossification in IEO DR26 026 is not figured since the specimen was used for an histological analysis reported in section 2.4, but the slices made, revealed a total ossification of the mesorostral canal (Buffrénil *et al*., in review).

However, this ossification of the canal by the vomer can also happen to some degree in female ziphiids; 100/PAL/UE also shows signs of mesorostral ossification (see fig. 3.5-B), but the rostrum does not seem complete.

Bianucci *et al.* (2013) divided a sample of *Tusciziphius atlanticus* skulls as male and female, but their analyses did not account for mesorostral groove or canal filling by the vomer. In the case of *Globicetus*, a bigger sample of specimens would probably allow for a more accurate interpretation of the mesorostral canal filling as being sexually dimorphic.

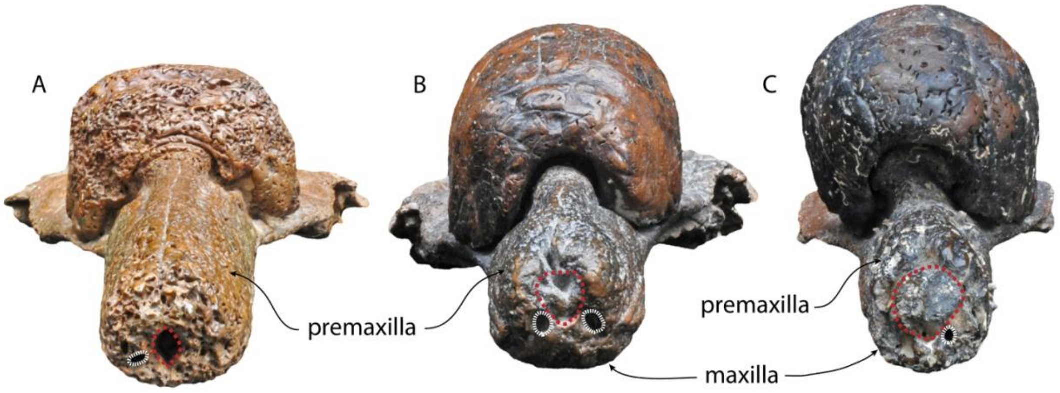


Fig. 4.6: Skulls of *Globicetus hiberus* in anterior view: ML 1850 showing no signs of mesorostral canal/tunnel filling by the vomer; ML 1361 and ML 2023 showing complete filling of the mesorostral canal by the vomer (red dashed lines); the white dashed lines delimitate the foramina.

4.5. Ontogeny and histology

Perrin & Reilly (1984) and Reidenberg & Laitman (2009) say that odontocetes reach sexual maturity at ages of 10 years or more and live for four or more decades. The biology of beaked whales, including the age, remains largely unknown, even in modern living taxa. In a global study for ziphiids, Mead (1984) gives the mean sexual maturity varying between 8 and 11 years. Age at attainment of sexual maturity was known only for *H. ampullatus* and *Berardius bairdii* and ranges between 7 and 11 years. The maximum reported age of a ziphiid is 71 years for a male *B. bairdii*. Buffrénil & Lambert (2011) studies on histology of ziphiids, namely *Aporotus recurvirostris,* are congruent to these dates of sexual maturity in beaked whales.

For *Globicetus*, the exact age is unknown. However, Buffrénil *et al*. (in review) made histology studies on the specimen IEO DR26 026 and estimate an age of no less than 9 years old, but likely a few years older than that. It is therefore clear that the holotype specimen and the other large individuals (ML 2023, ML 1850) are mature adults with definitively more than a decade of age. The surface bone rugosity and the obliteration of bone sutures also agrees with the assumption of an advanced ontogenetical age.

When comparing histology of *Globicetus*, Buffrénil *et al*. (in review) conclude that the speed of bone apposition over the MPP was steady during growth and similar to that over the premaxillary shelf. Buffrénil *et al*. (in review) also points out that the MPP must have grown after the adult size was reached, and that the MPP must have had more than one functional purpose. The extreme osteosclerotic-like condition in *Globicetus* MPP, described by Buffrénil *et al*. (in review), is associated with prolonged growth specializations of some rostrum structures of extant and extinct ziphiids, characteristic of adult males individuals (Buffrénil *et al*., in review). As mentioned before, *Globicetus* is not the only ziphiid displaying different remodeling of the bones. This remodeling pattern was observed in the rostral bones of other ziphiid whales: the extant *Mesoplodon densirostris* (Li *et al*., 2013), the extinct *Mesoplodon longirostris* (Lambert *et al*., 2011) and *Choneziphius planirostris* (Lambert *et al*., 2011), where it results in extremely compact, dense and (at least in *M. densirostris*) hypermineralized bone tissue.

4.6. Hypotheses for the origin and function of the MPP

"(…) a given structure may have several purposes and even in living animals it is often difficult to determine the uses of particular structures, their evolutionary histories, and even how the animals are communicating."
Padian & Horner (2011)

The local hyperplasia and/or densification of the bones in *Globicetus* rostra is still puzzling, since there is no morphological equivalent of ziphiid rostral peculiarities in other extant tetrapods (Buffrénil *et al.*, in review) and the ecology of ziphiids is poorly documented.

In this work, seven hypotheses are proposed and discussed: 1. malformation/deformity or some kind of disease; 2. ballast in deep-diving; 3. intraspecific fighting; 4. reflection and directional aim of the sound beam; 5. increasing the velocity of sound waves; 6. sound barrier and 7. secondary sexual organ ("antlers inside" hypothesis).

4.6.1. Malformation/deformity or some kind of disease

It could be hypothesized that the bizarre formation of bone in *Globicetus* be the result of deviations from normal bone growth, such as malformations/deformities or caused by some kind of disease.

There are several arguments against this interpretation in the work by Bianucci *et al*. (2013): unlikely pathological bone growths, the MPP is nearly symmetrical with smooth surfaces and has vascular and innervations canals at the base of the spheroid that are not interrupted, which excludes the fact that it could be of cancer origin (a tumor tissue growth). Kim *et al.* (1993), states that "the development of new blood vessels (angiogenesis) is required for many physiological processes including embryogenesis, wound healing and *corpus luteum* formation. Blood vessel neoformation is also important in the pathogenesis of many disorders, particularly rapid growth and metastasis of solid tumors", being angiogenesis the physiological process through which new blood vessels form from pre-existing vessels (Folkman, 1990); if it is not visible, a tumors origin may be excluded. It could be suggested to be a traumatic condition, but these are usually characterized by a bony growth called a callus (fractured bone replaced by zonal lamellar bone) during the healing process. Works by Claes & Heigele (1999) and Hanna (2002), are good examples of callus healing in extant species and in the fossil record, and they both concur that callus surrounding the healthy bone is localized, and usually has a different texture in comparison to normal segments of the bone. The MPP and the rest of the adjacent maxillary bones do not show signs of the stress and strain characteristic on cells in a fracture callus tissue. De Buffrénil *et al*. (in review) also addresses this hypothesis, dismissing considerations made by Gerholdt & Godfrey (2010), which believe some of the structures could be symptoms of periostitis, a cortical hyperplasy due to periosteum inflammation, with supposed lesions limited to the premaxillae that became progressively swollen as evidenced by the onion-like layering within the "deformity" (Gerholdt & Godfrey, 2010), observed in some specimens of fossil beaked whales; it is dismissed because osteosclerosis or pachyosteosclerosis is a highly species-specific morphological characteristic in ziphiids and because sexual dimorphism displayed by such structures is unexplainable by a pathological context (Buffrénil *et al*., in review).

Based on the grounds exposed above, and the obvious sexual dimorphism of the MPP, this hypothesize seems highly unlikely and can be excluded.

4.6.2. Ballast in deep-diving

It has been proposed that the MPP could have a hydrostatic role. According to this hypothesis, some of the rostral structures could serve as ballast during deep diving (Buffrénil & Casinos, 1995; Buffrénil *et al.*, 2000; MacLeod, 2002; Lambert *et al.*, 2011).

Reducing buoyancy and passively maintaining a vertical, head-down orientation of the body (Buffrénil *et al.*, 2000), would be an advantage for the animal, reducing the energy cost of diving. However, the main purpose would be lost when the animal returned to the surface to breath (MacLeod, 2002; Lambert *et al.*, 2011). MacLeod (2002), objects that “a structure that only aids the whale in diving to depth and has to be worked against when it returns to the surface would be counterproductive, requiring an increased output of energy at a time when much of the whale’s oxygen stores have already been used up”, losing the energetic saving benefit in the descend. Lambert *et al.* (2011), also refers that a group of studied animals (*M. densirostris* and *Z. cavirostris*) would more frequently perform passive and metabolically cheap gliding during the descent, with more active swimming during the ascent (Tyack *et al.,* 2006; Lambert *et al.,* 2011) and do not need a structure to aid in deep diving. Furthermore, there is no data showing that both female and juvenile whales dive more shallowly than adult males (MacLeod, 2002; Lambert *et al.*, 2011; Gol’din, 2014, Dunn, 2015), assuming that the MPP would be preferentially more developed in adult males, since mesorostral ossification is usually more developed in extant males than in females (MacLeod, 2002).

Mesorostral ossification has been referred as an important attribute for deep-diving. However, *Mesoplodon* species display different levels of mesorostral ossification (MacLeod, 2002), and all of the species are thought to occupy similar ecological niches. Even *Hyperoodon*, which lack mesorostral ossification, is capable of diving repeatedly to great depths (Gowans & Rendell, 1999; MacLeod, 2002; Hardy, 2005), so the existence of the MPP could help in diving more quickly, but should not be the primary function of the structure.

Lastly, it is important to acknowledge that the weight hypothesized for an adult *Globicetus* (see section 4.3.) would not be greatly influenced by a structure such as the MPP, since it probably would not have a significant effect on the overall weight; however, further work is needed to evaluate the effect of the MPP on the weight of the rostrum.

4.6.3. Intraspecific fighting

Male-male aggression is a common aspect of many terrestrial mating behaviors, especially amongst the even-toed ungulates of the Cervidae and Bovidae families (order Artiodactyla), as well as in many of the phylogenetically related Cetacea (Gowans & Rendell, 1999; Hardy, 2005). Aggressive interactions between male artiodactyls (order that comprises both the Cetacea family, Cervidae, Bovidae and many others) involve some form of head-to-head interaction, and the morphology of the head is often specifically adapted for these contests, which play an important role in the social structure of a species (Gowans & Rendell, 1999).

Scarring in cetaceans has been recorded for a wide range of species with many of these scars attributed to inter-male aggression (Heyning, 1984; Visser, 1998). Bumping has also been observed and may, according to research conducted by Visser (1998), be one of the causes why some killer whales (*Orcinus orca*) shown some kind of deformation of the fins. Visser (1998: p. 79) quotes Bigg (1982), who mentions that in adult males the dorsal fins “seem to develop structural weakness eventually, which result in curling at the tip, less rigidity of the dorsal fin and (…) complete collapse of the dorsal fin to lie flat along the side of the body” which suggests that collapsing or collapsed fin may be attributed to age; nonetheless, he points out that it is possible that the collapsing of some fins may have been caused by the same agent as the body scars. Cetaceans such as *Globicephala* (Gowans & Rendell, 1999; Hardy, 2005) and some delphinids (Gowans & Rendell, 1999) have been described to bump with their melon. In whales such as the sperm whale, the bumping is made with the junk, which is derived from the odontocete melon, and is reinforced with collagenous partitions and is directly in line with the cervical vertebrae (Carrier *et al.*, 2002); Carrier *et al.* (2002), suggests that the size and structural reinforcement of the sperm whale nose, may represent the result of selection for being used as a "battering ram", which is still believed to be the cause of the shipwreck of the whaling ship *Essex* in 1821, documented by Chase (1821) (please see Carrier *et al*., 2002: p. 1755).

In beaked whales, skull structures are believed to be used as male weapons (Heyning, 1984; MacLeod, 2002; Lambert *et al*., 2011; Gol'din, 2014), admitting bone densification as a mechanical reinforcement of the rostrum in mature males, avoiding fracture during intraspecific fights between adult males (Heyning, 1984). Heyning (1984) and MacLeod (2002) confirm that mesorostral ossification in adult males correlates with the presence of scars along the body, which could be the traces of aggressive teeth interactions as described in detail in MacLeod (2002); his work points out that scars occur mostly in males by intraspecific fights in the species of *Mesoplodon* (the largest genus of Ziphiidae) and are characterized by a number of morphological features, including the development of large sexual dimorphic tusks in the lower jaw and secondary ossification of the rostrum (Heyning, 1984 in MacLeod, 2002: p. 178). But, densification of the rostrum could increase its brittleness (Buffrénil *et al.,* 2000), since dense and compact bones, if hypermineralized, are prone to fast fracture propagation and are poorly resistant to shock (Zioupos *et al.,* 1997; Currey *et al.*, 2001; Buffrénil & Lambert, 2011).

Bones usually adapted for shock loading like the ones found in deer antlers have the opposite structural characteristics of the ones found in most ziphiids (Currey, 1990; Buffrénil *et al.,* 2000; Price *et al.,* 2005). *H. ampullatus*, the only species of beaked whales in which head-butting has actually been observed (Gowans and Rendell, 1999; Lambert *et al.,* 2011), has crests made of spongy bone, in strong contrast with the compact bone of many other ziphiid rostra. However, highlighting this weakness of the rostrum itself (the premaxilla and the telescoping part of the rostrum) is the damage noted on a large male specimen (ZD.1992.2.4.2.), designated 'individual 62' and described in Hardy (2005: p. 77). This skull exhibited severe damage (fig. 4.7) that would indicate an impact to the rostrum from ahead and above. Whatever the cause of this impact may have been (possibly a misaligned head-butt or collision with a boat), is evidence of the weakness of the rest of the rostrum bones; even though there is evidence of healing and callus formation on the damage section, consequent torsion probably did not allow for a full recovery, causing a pseudarthrosis hypertrophic non union or commonly called nonunion or false joint, eventually leading to the death of the animal.
In the specific case of *Globicetus*, the shape of the MPP can also be taken into account. The fact that spheres dissipate energy, could make them able to absorb the impact energy caused by head-butting fights and therefore enable the whale to use the structure as a weapon to some extent. The sphere itself would be protected by a thin layer of blubber, popularly and commercial used to denote the superficial tissues of whales and seals, which comprises the animal's epidermis, dermis, and hypodermal tissues (Parry, 1949). However, the regular and somehow smooth surface of the MPP in *Globicetus* could have been a problem if fighting would occur. In *Hyperoodon*, the crests have a very irregular contact surface, perfect for the attachment of connective tissue layers, blubber, muscles and skin. This characteristic is useful when the animal engages in fighting activities with other male competitors, since it is an excellent place for the anchoring of the tissues, protecting them from tearing. While *Hyperoodon* have irregular crests surface, *Globicetus* does not; the smooth surface would probably not be able to withstand the traction between some head-butting action,

Fig. 4.7: Lateral (skull positioned at a 45° angle on its rear) and dorsal views of severe rostral damage and related bone growth in a large mature male, *Hyperoodon ampullatus*. Specimen held at British Museum, Natural History (ZD.1992.2.4.2.). Image adapted from Hardy (2005).

increasing the danger of the tearing of some of the soft tissue that involve the MPP, a friction compared to a sandpaper effect between the skulls of the animals. Certainly some of the smoothness observed in the fossil specimens is the result of erosion, but compact bone would not have the same grip as the spongier bone which characterizes the crest in the *Hyperoodon* genus. Lastly, the MPP could be hypothesized of having a similar origin to the dome like structure in the dinosaur genus *Pachycephalosaurus*, which had squamosal horns and nodes that, according to Horner & Goodwin (2009), originated ontogenetically as node-like structures, some of which expanded into horns and bony spikes and then became modified as blunt, nodal structures in later stages of ontogeny. From a structural point of view, marginocephalian dinosaurs employ metaplasia to grow their horns, cranial ornaments, domes and shields as they rapidly remodel their skulls. However, according to Padian & Horner (2011), "histological studies have shown that the columnar cell structure of these domes would not have deflected the forces incurred in battering", since skulls of adults have compact bone in their external cortices.

The position, size and sphericity of the MPP, would apparently make it an ideal head-butting tool and, since odontocetes have been recorded bumping and fighting, this hypothesis cannot be excluded. However, other head-butting odontocetes, such as *Gobicephala* and orcas, bump with their melon but their rostrum projection is inferior to the one seen in ziphiids, where the beaks are much more projected, making it and disadvantage if the bumping were to occur.

Nevertheless, additional tests on shock resistance are needed.

4.6.4. Reflection and directional aim of the sound beam

It can be hypothesized that the enormous MPP on *Globicetus* head could be a way of reflection and directional aim of the sound beam. Because all ziphiids are deep-divers and are obliged to use a non-compressive tissue (Lambert *et al.*, 2011), it was noted by Buffrénil & Lambert (2011), that hard and stiff skull bones could be involved in reflection of the echolocation vibrating waves, since toothed whales cannot use air-filled ducts as acoustic reflectors.

High-density bones that encase rostrum fat tissues have been described by Buffrénil & Lambert (2011) and Cranford *et al.* (2008b), as being able to act as "waveguides", focalizing the vibration waves emitted by the animals. In this case, the geometry of the rostrum bones and tissues is very important. However, Cranford *et al.* (2008a) did some tests in an adult male *Ziphius cavirostris* and realized that the geometry of the tissue structures and their interfaces were more important factors in the beam formation than the actual hardness of the bone; they conducted tests where the stiffen of the bones was changed up or down by 10% and there was no change in the resultant beam shape and direction. But not only hardness is of importance, shape plays a big role as well. Vercammen (2008) work on reflections of sound from concave surfaces confirmed that the focusing effect of a spherical reflector is much stronger than the focusing effect of (for example) a cylindrical shape, since the amplification at the focal point can be quite dramatic, especially for spherically-curved structures. Finally, it is important to refer that a sphere shape not only reflects and amplifies sound, but sound waves can bend around it, a phenomenon known as diffraction (Wiener, 1947). Based on these studies, it may be inferred that even if the sound waves coming from the phonic lips would encounter the MPP in its pathway, they may be able to still be projected into the environment with less acoustic noise than expected. However, as hypothesized in section 4.2. (see figure 4.2), the phonic lips would probably be in a position high enough for the transmission of sound not to be affected by the MPP. This hypothesis is not confirmed nor excluded, pending further studies on the acoustics of *Globicetus*.

4.6.5. Increasing the velocity of sound waves

The MPP could be hypothesized as being a mechanism for increasing the velocity of the sound waves, as they passed through it and then into the column of water.

As referred before, rostral bones may be involved in signal conduction (Pilleri *et al.,* 1986 in Buffrénil *et al*., 2000: p.64) and can easily be related to improvement of the ultrasonic signal condition on account of reduced signal attenuation (Ashman *et al*., 1984 in Buffrénil *et al.,* 2000), but Buffrénil *et al.* (2000) objects that the difference in ultrasonic conductivity or impedance mismatch between the rostrum and the sea water would cancel out the benefit of the high density rostrum bones conductivity. Zioupos *et al.* (1997) stated that there is a considerable impedance mismatch between a high density material such as rostral bones and sea water, and because of that, the rostrum may not act as an efficient radiator of high velocity sound waves.

Soldevilla *et al*. (2005), conducted tests on the physical properties of head tissue of *Z. cavirostris* and realized that the fatty tissues were significantly less dense than seawater, while muscle was not significantly different, and that only the connective tissue was denser than seawater. Impedance matching occurs when the acoustic impedances (the product of density and sound speed) of two adjacent materials are similar, resulting in greater transmission of acoustic energy at the boundary between the two materials. The theory for sound production in odontocetes states that the sound waves speed increase between the melon and the blubber, producing an impedance match with the water, maximizing the acoustic energy transferred out of the forehead (Soldevilla *et al.*, 2005). This corroborates with statements by Buffrénil *et al*. (2000), that if the sound would go from soft tissue to bone and then to water, the increase of sound gained would be lost with the impedance mismatching between dense bone/water, so probably, sound, instead of penetrating the bony MPP, would bend around or above it, which corroborates with works by Vercammen (2008).

This hypothesis still needs further work, and will not be excluded, but seems highly unlikely.

4.6.6. Sound barrier

The hypothesis for the MPP as a sound barrier between the emitted sound waves from the phonic lips and the sounds being received, at the same time, by the sound-reception acoustic fats in the lower jaw is discussed next.

Cranford *et al*. (2008a) describes the pterygoid sinuses from the hearing apparatus as "confluent with a complex of sheet-like and finger-like projections of air spaces (peribullary sinuses), forming acoustics shields or reflective boundaries along the medial and posterodorsal aspects of the bony ear complexes". These complex structures have been referred as exquisite sound mirrors that provide acoustic isolation and protection from self-made sounds originating in the nasal complexes (Cranford *et al*., 2008a), so these structures, if present in *Globicetus,* would be enough to block any sound produced by the phonic lips, and therefore the MPP would have no, or minimal influence in blocking sound waves. Despite this, directional sound reflectivity of the spherical body could be valid in selecting different pitch frequencies produced by the animal, and helping with the acoustic isolation of the rostrum and therefore leaving the pan bone and the ear complex able to process sound better. However, this hypothesis seems highly unlikely.

4.6.7. Secondary sexual organ

"Beautiful and irresistible features have evolved numerous times in plants and animals due to sexual selection, and such preferences and beauty standards provide evidence for the claim that human beauty and obsession with bodily beauty are mirrored in analogous traits and tendencies throughout the plant and animal kingdoms."
Grammer *et al*. (2003)

In his "antlers inside" hypothesis, Gol'din (2014) suggested that the bony structures in ziphiids could be a case of sexual dimorphism perceived through echolocating by members of the same species, playing a role of secondary sexual organ, comparable to antlers in artiodactyls.

Echolocation allows cetaceans to form and recognize three-dimensional acoustic images, so they might be able to recognize and perceive massive bone structures, as MPP, in a body of another whale (Gol'din, 2014). Since the peculiar structures of the rostrum are highly diagnostic for ziphiids taxa

(Lambert *et al*., 2011; Bianucci *et al*., 2013), echoic perception gains importance at depth (Gol'din, 2014) for an individual and species recognition (Johnson *et al*., 2004). These authors concluded that beaked whales use their echolocation capability not only on prey but on conspecifics, pointing their sonar beam towards other whales. In addition, Kamminga & Van Der Ree (1976) showed that hollow spheres used in the trials by dolphin, complicated the echo perception while compact ones where more successful. Buffrénil *et al*. (in review) also agree that the function of ziphiid rostral peculiarities is likely to be linked to ecological specializations, such as feeding activity at great depths using highly specialized sonar but do not dismiss Gol'din (2014) hypothesis of ziphiids acoustic recognition via the echolocation system. Due to high density contrast using high frequency sounds, Gol'din (2014) hypothesizes that the detection of the compact spheroid through soft tissue can make the spheroid not a sound transmitter, but a display object, perceived as complex echoic image of the differential impedance contrast and echo reflectivity between bone and the adjacent soft tissues.

As a linguistic side note one can propose that the "antlers inside" hypothesis could also be called "horns inside" because unlike keratinized antlers, bony horns are never branched, are never shed, are also used in antagonistic fights between males and in many species horns never stop growing throughout an animal's life (Goss, 2012); horns serve as a better analogue on its structure and origin.

This hypothesis involves many aspects and discussions; therefore, to facilitate reading, it is developed in the following section on its own.

4.7. MPP as a secondary sexual organ

Fig. 4.8: Peacock courtship: female on the left and male on the right of the picture. Photograph by Joana Muchagata.

The antlers hypothesis first suggested for *Globicetus* by Gol'din (2014) is the one that gathers more strength and is discussed in more detail below. A secondary sexual organ can be defined as an accessory display structure of mating. It usually has a high sexual dimorphism and generally correlates with the fitness of the individual. Horns, antlers and other displays structures are intertwined with dominance: males that bear it enjoy reproductive advantage, since size is supposed to carry a priori dominance status and gene quality. The animal world is full of examples of males displaying dimorphic structures to attract females and repel opponents. Display structures can be subtle, such as face features in human beings (for example, strong square jaws in man) or more exuberant, like the antlers in deers, colored skin in lizards, and the spectacular tail of peacocks (fig. 4.8), which are just some of many extraordinary examples available of visual display. Already Darwin (1871) hypothesizes that male ornaments are favored by mates and probably evolve as a result of female preference, which he describes as "taste for the beautiful" (Larson, 2013). But not all dimorphisms are visible to the eye: songs and sound by birds, fishes, frogs, land mammals and cetaceans also form an acoustic display that shows the virility and power of its bearer. The case of sexual display in peafowl is well documented (see, for instance Louchart, 2003; Petrie *et al*., 1991 and Zahavi, 1991) and is an iconic example.

Features of secondary sexual organs

A secondary sexual organ is a sexually dimorphic biological ornament related with sexual display by males to influence choice by females into what is also called a "Fisherian runaway". According to the Fisherian runaway hypothesis, male ornamentation results from the preference by females, for exaggerated trades. This leads to an extreme degree of exaggeration in the male ornament, proportional to female preference and resulting in a cost that surpasses the benefits of possessing such trade (Pomiankowski & Iwasa, 1998). For more information on this topic, please refer to Fisher (1915), *The evolution of sexual preference*.

Secondary sexual organs have the following features:

1. Exaggerated male ornamentation
2. Perceptible (visual in most cases)
3. Dimorphic
4. Handicap for survival
5. Unique and different from species to species
6. Enhances through ontogeny (mostly conspicuous in mature males)
7. Not essential for reproduction (i.e., excludes genitalia)
8. Are related with better fitness
9. Preference or attraction of females for ornamented male mates

1. Exaggerated male ornamentation: the MPP occupies close to 1/3 of the skull, being clearly exaggerated. This extreme condition is not seen in any other ziphiid, although comparable with the crests in *Hyperoodon and Tusciziphius*, but the structure being quite different.

2. Perceptible (visual in most cases): this is a key point of a secondary sexual organ because it has to be perceived by females. *Globicetus* does not fill this requisite in the visual sense (through eye sight), but the echoic perception of the MPP is the equivalent and replaces visual capability. This replacement is unique in the animal kingdom as far as we know.

3. Dimorphic: *Globicetus* is interpreted here as dimorphic concerning sexes. See figure 4.5.

4. Handicap for survival: quite often the secondary sexual organ is a strong handicap for survival. The tail of peacock is a good example, where such an exuberant trade may be a burden in a rain forest with predators, such as tigers. Zahavi (1975) proposed, in his handicap theory, that these exaggerated feather displays acted as honest signals of the males' fitness. The handicap theory seems quite evident for *Globicetus*, where the MPP occupies a major part of the skull and in a critical central position that almost certainly effects echolocation, which is essential to the survival of beaked whales; as a result, the sheer existence of a large MPP in a male *Globicetus* is a display of its virility and, therefore, corresponds to a potentially good mating partner.

5. Unique and different from species to species: the shape and size of secondary sexual organs are very variable from species to species and rostral variation among beaked whales may contribute to the species recognition and prevent unwanted hybridization. This is very obvious in antlers in Cervids (each species has a unique and peculiar antler shape), paradise birds (males have conspicuous behaviors and feathers, also different and unique from species to species), and many other taxa. Also in beaked whales, the region of the rostrum where the MPP lays is different and unique in each species, and that condition also supports the sexual dimorphism and secondary sexual organ “antlers inside” hypothesis and can be related to species recognition, since both males and females possess the spherical MPP.

Curiously, some artiodactyls have modified canine or incisor teeth modified into enlarged tusks (Janis, 1990), a condition similar to some ziphiid species.

6. Enhances through ontogeny (mostly conspicuous in mature males): in most dimorphic species, the secondary sexual organs only become evident after puberty and enhances in mature

males through age. This trend is also proposed for *Globicetus*. The graph of figure 4.5 shows that the MPP seems to become more conspicuous in males through ontogenetical development.

7. Not essential for reproduction (i.e., excludes genitalia): the structure is not essential/required for the insemination of the female. Therefore, it should only be accessory when it comes to the actual copulation itself. Unlike cutting a peacocks tail feathers or a lion´s mane, removing the MPP of *Globicetus* would affect the animal to some degree, but would not really affect its capacity in mating.

8. Related with better fitness: more exuberant/bigger structures/features are usually correlated to better fitness of the bearer, such as the nose in the male sperm whale, and muscle development in humans. However, these are behavioral aspects that cannot be accessed in fossils at the current stage of knowledge.

9. Preference or attraction of females for ornamented male mates: the desirability of a male is always correlated to its overall appeal and capability of showing of its attributes. In the animal kingdom, females gravitate towards males with the most exuberant features. However, these are behavioral aspects that cannot be accessed in fossils at the current stage of knowledge.

We tackle all nine common denominator characteristics of the secondary sexual organs, and confirm seven of them in *Globicetus*, despite the fact that one (visual accessibility) being replaced by echoic accessibility is the only reported case to date, as far as we know. Two features (“Related with better fitness” and “Preference or attraction of females for ornamented male mates”) cannot be tackled in fossils.

Secondary sexual organs may have a supplementary non-reproductive function. This requires modeling, simulation and further studies that lay beyond the scope of this work. Future work will be to simulate the acoustic propagation inside *Globicetus* head and rostrum using digital 3D models (fig. 4.9). 3D reconstructions gain increasing importance for paleontological research at the anatomical level (Kolb *et al.*, 2015) and models of sound propagation within beaked whales’ skulls may provide insight on their response to sound exposure, echolocation production and sound reception. When simulating the acoustic wave interaction in the skull of the whale, measurements of the various extant bone morphology, an approximation of the soft tissue, physical attributes of the various tissues, the position of the phonic lips, an approximation of the oral cavity and internal path of the airway, and click frequency range and patterns of ziphiid vocalizations are needed. The MPP was, most likely, covered by layers of fat tissues, such as the acoustic fats and blubber, as well as layers of muscle and several connective tissues; so the most important impedance mismatch would probably be between the soft tissues that cover the MPP of *Globicetus* and the bones of the rostrum.

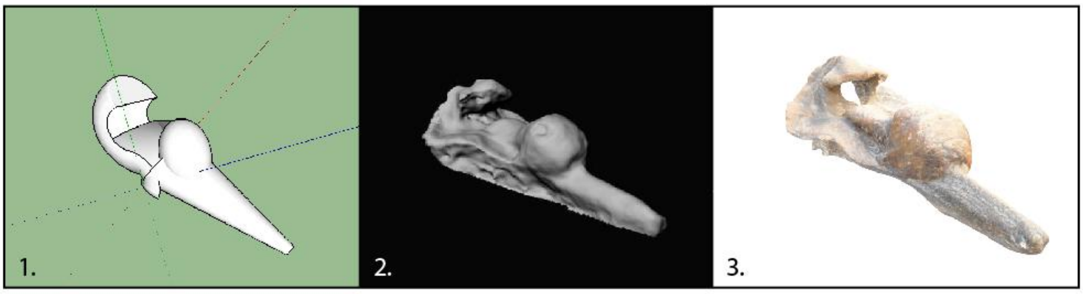


Fig. 4.9: *Globicetus hiberus* specimen ML 1361: digital 3D models of the rostrum; software used: 1. – SketchUp; 2. – Autodesk 3ds Max 9; 3. – Agisoft PhotoScan.

Other curiosities about acoustics and sexual selection

Acoustics is common in many vertebrates, being birds the most famous, but fishes are the largest vertebrate group with vocalizations, which use the contraction of intrinsic and extrinsic sonic muscles that excite the swim bladder, or the rubbing of certain body parts (called “stridulation”) to produce vibration and create complex sound patterns (Fine *at al*., 2001).

Vocalizations can assume different forms in the animal world. Odontocetes, such as the sperm whale (*Physeter macrocephalus*) possess hidden echo display-structures for attraction of mates. The male sperm whales has relatively larger facial regions than females and it is proposed that males signal their size and therefore, virility and fitness using signal pulses called “interpulse intervals”. Sperm whales are well-known for their monotonous clicking behavior and the pulses or amplitude peaks that comprise a burst are most often separated by a relatively constant time interval. The acoustic mechanism in the sperm whale is a result of air entering the blowhole, passing throughout the phonic lips, reflecting the sounds off the frontal air sac and propagating them into the spermaceti organ, which are then redirected into the junk via the low-density pathway, where they are transmitted as sound waves, or “interpulse intervals” (regularly spaced pulses), projected into the environment through a series of lens-like structures in the anterior region of the structure (Cranford, 1999), representing the effects of reverberation within the spermaceti organ**.** This results in a signal “signature” (Norris & Harvey, 1972; Cranford, 1999), flaunting the size of the signaler (male), or more specifically, the size of the signaling apparatus (its nose), since bigger interpulse intervals between clicks flaunt a bigger size of the nasal apparatus, attracting possible female partners or drive off potential mates and threaten males (Cranford, 1999). Figure 4.10 represents the sperm whale cranial soft tissue anatomy.

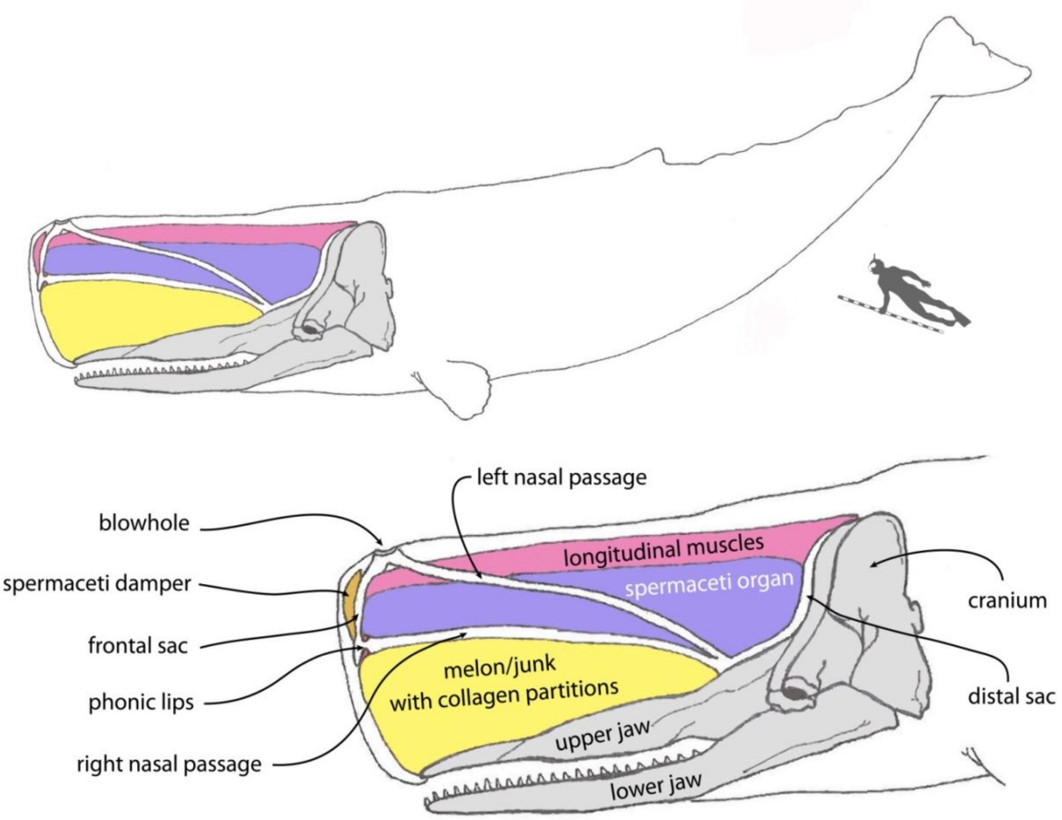


Fig. 4.10: Illustration of sperm whale (*Physeter macrocephalus*): top, comparison with average male human; bottom, detail of cranial soft tissue anatomy and the sound apparatus.

Other animals, however, can announce their presence without sound, simply using acoustic flags. “Acoustic flags” are here defined as mute structures (normally acoustically conspicuous) in one species that are evolved to be perceived through echolocation by other individual, of the same species or other. The idea that the spherical MPP in *Globicetus* could be a unique case of a structure in the animal kingdom capable of acting as an acoustic flag giving information about its shape is actually not true. Other species show mutualistic relationships between animals, where echolocation detection and some kind of shapes are interpreted as acoustic flags. Schöner *et al*. (2015) work on the mutualistic relationship between the carnivorous pitcher plant, *Nepenthes hemsleyana* (family Nepenthaceae) and the insectivorous bat, *Kerivoula hardwickii* (Vespertilionidae) concluded that the pitchers´ orifice features a prolonged concave structure, which exploits the bats’ perceptual bias to attract them echo-acoustically reflecting its echolocation calls, helps the bats to quickly find and enter suitable day roosts and the plants to benefit from higher nitrogen intakes (Schöner *et al*., 2015).

5. Conclusions

Globicetus hiberus is an early Pliocene beaked whale that lived along the Iberian coast. Six specimens, recovered from the bottom of the sea, were analyzed in the present work: two had been described by Bianucci *et al.* (2007) before (ML 1361-holotype, IEO DR26 026) and four were identified and referred herein for the first time (ML 2023, ML 1850, DGAOT-a, 100/PAL/UE).

All the fossil specimens exhibit a bizarre derived structure named here the mesorostral process of the premaxillae (MPP), corresponding to the large hemispheric expansion of the premaxillae along the proximal portion of the rostrum. Associated to the MPP, there is a premaxillary shelf and, usually, a medial pad of premaxillae. Investigation of bone inner structure of the MPP indicates compact bone, with concentric LAGS and cumulative growth; there are also evident differences on the degree of bone remodeling between the main structure (MPP) and the rest of the rostrum, with MPP bone not remodeled or only partially remodeled.

Our study also demonstrates that larger animals bear larger MPPs; however, there is also a trend associated to the medial pad of premaxillae and the MPP form: when the pad is present, the MPP is lower and leaner. There is an allometric growth of the structures and body size, which can be graphically represented by two linear lines, proposed to be associated to sexual dimorphism, differentiating male and female individuals. By analogy with extant ziphiids (especially with *Hyperoodon)*, the different degrees of development of the medial premaxillary structures in *Globicetus* and other extinct beaked whales, like *Tusciziphius atlanticus,* might be explained by sexual dimorphism with adult males displaying a higher MPP. Lower MPPs and the presence of medial pads of premaxillary bone may be indicative of, not immature animals, but female individuals, if we admit bigger, more robust MPPs, and the reabsorption or absence of the medial pad of premaxillae to be associated with male individuals.

Specimens ML 1850, DGAOT-a and 100/PAL/UE are considerate females and ML 1361 and ML 2023 are males. Specimen IEO IR 26 026 could be considerate a subadult male, since it displays both female traits (long lower MPP with associated medial pad of premaxillae) and total ossification of the mesorostral canal, which can be exclusive or more developed in males of some extant ziphiid species.

This filling of the mesorostral groove or canal by the vomer can in some species of ziphiids display intraspecific variation depending on sex and age, and specimen ML 1361, ML 2023 and IEO IR 26 026 show ossification of the mesorostral canal which corroborates with the sex distinction approach demonstrated by associating body size and MPP size. This sexual dimorphism is anatomically independent from the MPP, and may provide an important confirmation of the gender identification of *Globicetus*. However, rostrum 100/PAL/UE also shows signs of ossification to a degree not so easily quantified for which this characteristic may be somewhat variable among males and females of different ages.

Hyperoodon spp. is a good example of modern beaked whales exhibiting unusual rostral anatomy and related soft tissue changes, showing the plasticity of the soft tissues, and can be used as a tool for the hypothesizing on how soft tissue would have been fitted inside the head of *Globicetus*. The melon would probably surpass the highest point of the MPP and the phonic lips (origin of the sound) would be in line with the highest part of the premaxillary crests. Such a condition would allow for the sounds to be reflected on the ascending premaxillary process and be focused through the melon and above the MPP. Based on cranial dimension, *Globicetus* is proposed to fall in the range of *Mesoplodon bowdoinii* and *Mesoplodon densirostris*, between about 4.5 and 4.7 meters, and weight up to 1033 kg, as much as the extant *Mesoplodon densirostris*.

Hypothesizing about the function of the MPP and its associated bony structures (premaxillary self and medial pad of premaxillae) is an interesting yet complex process, and multiple views and parameters should be accounted for. Some hypotheses for the function of the MPP are rejected: result of disease/malformation, ballast for deep diving, and sound barrier between the emitted sound waves from the phonic lips and the sounds being received. Other hypotheses cannot be excluded, such as the MPP being used as a mechanism for better acoustic performance, for instance, speed increase of sound waves and helping in the reflection and directional aim of the sound beam, but further experimental acoustic simulations are recommended; however, these seem relatively unlikely due to impedance mismatch between rostral bones and sea water. Help in intraspecific fights is a hypothesis consistent with the head-butting behaviour known in some ziphiids and cannot be totally discarded. The characteristics of MPP, namely its position in the skull, size and sphericity would make the structure seemingly ideal as a head-butting tool. The comparable bony structure in the bottlenose whales *Hyperoodon* is age and sex related and is known to be used as a weapon by males; however, *Hyperoodon* crests are made of spongy bone, whereas *Globicetus* MPP exhibits a much higher structural compactness.

Because ziphiids possess a highly specialized echolocation system, and because sound travels through bodies, *Globicetus* individuals would be able to perceive the MPP with their sonar even in darkness. So, it is hypothesized that the MPP could be not only associated with the transmission of sound, but worked as a visual display object, perceived as a complex echoic-visual image by other whales for mating and individual recognition purposes, as proposed by Gol'din (2014) with his “antlers inside” hypothesis. The sphere can then be used as a secondary sexual trait, indicative of the fitness of males, detected via echolocation in deep, dark waters by conspecifics.

Globicetus possesses the 7 characteristics of secondary sexual organs that can be tested in fossil species: exaggerated male ornamentation, perceptible (visual in most cases), dimorphic, handicap for survival, unique and different from species to species, enhances through ontogeny (mostly conspicuous in mature males) and not essential for reproduction. Therefore, we can confidently assume that MPP´s main function in *Globicetus* was a secondary sexual organ used for acoustic display. *Globicetus* is also the first case of acoustic flag among cetaceans, using the MPP as a mute structure to be perceived through echolocation by other individuals.

As a final note, bizarre structures are not uncommon in extinct beaked whales, which suggest they must have played an important role in the animal´s life, such as social hierarchy and other intraspecific interactions. By studying living animals we get the foundation for inference of traits, otherwise impossible to reconstruct in related fossil specimens, such as soft tissues and hypothetical behaviors. *Globicetus* strange cranial osteological structures leave an open door for further discussion on how the sound would be propagated and how the sound production apparatus would be cradled in the skull. Sexual dimorphism is also a topic that needs further work; a larger sample of specimens is needed for a future, more consistent interpretation.

Beaked whales are fascinating whales to study and having access to such amazing fossil specimens was an absolute privilege. Finally, one other question persists: if the bearers of such specialized structures are extinct, did these structures become an issue at some point (not benefiting the animal) or did the environmental conditions change? We may never know for sure, but we will certainly try to find out in the future.

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