Rostral densification in beaked whales: Diverse processes for a similar pattern

La densification du rostre des baleines à bec : des processus variés pour un résultat similaire

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Article history:
Received 24 September 2010
Accepted after revision 21 March 2011
Available online 31 May 2011

Written on invitation of the Editorial Board.

Keywords:
Odontoceti
Ziphiidae
Beaked whales
Pachyostosis
Osteosclerosis
Computed tomography
Bone histology

Abstract

As compared to other odontocetes (toothed whales), the rostrum of beaked whales (family Ziphiidae) often displays extensive changes in the shape, thickness, and density of its constituent bones. Previous morphological observations suggested that these modifications appeared in parallel in different ziphiid lineages. However, very few data were available on the compactness and histology of these rostral bones, which precluded the study of the processes at work for the development of such structures, as well as the interpretation of their functional implications. In this work we review the bibliographic data on the anatomy of the ziphiid rostrum and we add new observations on adults of several extinct and extant taxa. These observations are based on CT scans and transverse histological sections. Our results confirm that different bones (vomer, mesethmoid, premaxilla, maxilla) are involved in the various morphologies displayed by ziphiid rostra. Strong density contrasts are detected between bones and/or inside the bones themselves; for example, parts of the rostrum reach densities in the range of Neoceti ear bones, which are among the densest bones known hitherto. Furthermore, the histology of the pachyostotic and osteosclerotic bones proves to change from one taxon to the other; the degree of Haversian remodeling varies strongly between species: it can be absent (e.g. Aporotus recurvirostris), partial (e.g. aff. Ziphirostrum), or complete (e.g. Mesoplodon densirostris). The atypical secondary osteons known to be responsible for bone hypermineralization in the rostrum of M. densirostris occurred also in Choneziphius sp. Confronted with a phylogenetic framework, these anatomical and histological observations indicate that the acquisition of compact (osteosclerotic) and/or swollen (pachyostotic) bone is the result of a broad convergence between taxa, in response to common selective pressures. The functional dimension of this question is discussed with respect to what is known about extant ziphiid ecology.

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Résumé

Comparé aux autres odontocètes (cétacés à dents), le rostre des baleines à bec (famille des Ziphiidae) est souvent sujet à d’importantes modifications de la forme, de l’épaisseur, et de la densité des os qui le constituent. Des observations préliminaires ont suggéré que ces modifications se sont développées en parallèle dans plusieurs lignées de ziphiidés. Cependant, très peu de données étaient disponibles sur la compacité et l’histologie des os du
1. Introduction

Beaked whales (Ziphiidae) form a diversified family of odontocetes (toothed whales), including 21 extant species and six genera. Predominantly teuthophagous, most ziphids are considered as deep divers, with dive records at more than 1800 m for some species (Hooker and Baird, 1999; Schreer and Kovacs, 1997; Tyack et al., 2006), depths at which prey are detected by echolocation (Johnson et al., 2004). With exception for Tasmacetus shepherdi, all extant ziphids display an important reduction of their dentition related to suction feeding (Heyning and Mead, 1996; Werth, 2006): only one or two pairs of mandibular teeth are retained, modified in tusks that generally erupt in adult males only. Dental reduction is similarly observed in several of the extinct species known bitherto, whereas others (e.g., Messapicetus spp., Ninaziphius platyrostris) retain numerous homodont rostral and mandibular teeth (Bianucci et al., 2007, 2010; de Muizon, 1984; Lambert, 2005; Lambert et al., 2009).

In addition, the ziphid skull, and specially its rostral region, is often modified, as compared to the typical condition of other odontocetes (Bianucci et al., 2007; Heyning, 1989a; Lambert, 2005). Various changes in the general shape, thickness, and inner compactness of its constituent bones have been described in both extinct and extant taxa. The most common modification is a filling of the mesorostral groove by the thickened vomer (Bianucci et al., 2007; Fraser, 1942; Heyning, 1989b; Mead, 1989a). In the extant species Mesoplodon densirostris, the only ziphid to have been studied in detail from an osteohistological point of view, the filling of the groove is accompanied by a strong increase of the compactness and mineralization rate of all rostrum bones (maxillae, premaxillae, and vomer), with strong implications for their mechanical properties (de Buffrénil and Casinos, 1995; Zioupos et al., 1997; Zylberberg et al., 1998). In several extinct taxa, the mesorostral groove is dorsally closed by the thickened and compact premaxillae, which, in some cases, form elevated longitudinal crests (Lambert, 2005), whereas large rostral maxillary crests are observed at the rostrum base of the extant Hyperoodon spp. At least in Hyperoodon ampullatus the development of these crests is a sexually dimorphic character (Mead, 1989b).

The preliminary observation of the diverse morphological peculiarities of ziphid rostra leads to the assumption that pachyosteosclerosis, the combination of pachyostosis, or swollen, protuberant periosteal cortices, and osteosclerosis, an increase in bone inner compactness (de Buffrénil and Rage, 1993; de Ricqlès and de Buffrénil, 2001), was a common feature in ziphids, occurring independently in multiple lineages (Bianucci et al., 2007; Lambert, 2005). However, this assumption was based on a superficial observation of the skulls, lacking a detailed analysis of their inner organization and histological features. Furthermore, various potential function(s) of a pachyosteosclerotic rostrum in ziphids have been proposed in the past, in relationship with three different ecological or behavioral traits of extant taxa: echolocation, deep diving, and intraspecific fights between males (de Buffrénil et al., 2000; Heyning, 1984; Lambert et al., 2010a; MacLeod, 2002). Until now, none of these functional hypotheses can explain the full range of patterns observed.

The present study investigates, from morphological and structural points of view, the diversity of forms displayed by the ziphid rostrum bones. The aim is to elucidate the growth processes at work in the different lineages, and to bring new data that could enrich the discussion of functional hypotheses. In addition to a review of published data, we bring new information on bone compactness and histology in several extinct and extant taxa thanks to two techniques: computed tomography (or CT scans) and ground sections.
2. Material and methods

2.1. Remarks on information sources

Two information sources were exploited, bibliographic data and first hand observations.

2.1.1. Bibliographical data

A rich set of bibliographic information dealing with rostrum anatomy in various extant and extinct ziphiids, and specially stressing the relationships between the modified rostral bones (premaxillae, maxillae, vomer, and mesethmoid), was considered (Besharse, 1971; Bianucci et al., 2007, 2008, 2010; Fraser, 1942; Glaessner, 1947; Hardy, 2005; Heyning, 1984, 1989a, 1989b; Lambert, 2005; Lambert et al., 2010a, 2010b; Leidy, 1877; MacCann, 1965; MacLeod and Herman, 2004; Mead, 1975a, 1989a, 1989b; Miyazaki and Hasegawa, 1992; Moore, 1968; Post et al., 2008; Raven, 1942; Reyes et al., 1991; True, 1910). A second set of published works focusing on the histology and mechanical properties of the rostrum of the extant M. denirostris was also considered (de Buffrénil and Casinos, 1995; de Buffrénil et al., 2000; Rogers and Zioupos, 1999; Zioupos et al., 1997; Zylberberg et al., 1998). Finally, a few recent works investigating the anatomy of some extant ziphiid skulls by means of X-ray analyses were also taken into account (Cozzi et al., 2010; Cranford et al., 2008).

2.1.2. First hand observation

New information, mainly dealing with the inner structure of the rostral region of ziphiid skulls, was collected along two main axes:

- three-dimensional mapping of bone density using computed tomography;
- histological examinations based on ground sections.

2.2. Biological sample and analyses performed

2.2.1. Extinct ziphiids

New observations of fossil material were made on the five taxa listed below. Aporotus recurvirostris (Neogene of Antwerp area, Belgium) IRSNB 3810-M.2012 a–b, right part of the rostrum, including the subcomplete premaxilla and adjacent remnants of the maxilla, ground sections; Choneziphius planirostris (Late Miocene of Antwerp area, Belgium) IRSNB 3775-M.1883, partial skull including rostrum and facial area, figured in Lambert, 2005, CT scan; Choneziphius sp. (Neogene of Antwerp area, Belgium) MB CR-15, apex of rostrum, ground sections; aff. “Mesoplodon” longirostris (Neogene of Antwerp area, Belgium) IRSNB 3804, partial skull including rostrum and facial area, ground sections; aff. “M.” longirostris (Neogene of Antwerp area, Belgium) MB CR-9, left part of the rostrum, ground sections; aff. “M.” longirostris (Neogene of Antwerp area, Belgium) MB CR-10, anterior part of the rostrum, ground sections; Ziphirostrum marginatum (Neogene of Antwerp area, Belgium) MB CR-13, rostrum base fragment, right side, ground sections; Z. recurvus (Neogene of Antwerp area, Belgium) IRSNB 3805-M.544, rostrum, figured in Lambert, 2005, CT scan; aff. Ziphirostrum (Neogene of Antwerp area, Belgium), rostrum base fragment, right side, ground sections. Based on the complete closure of the sutures between rostral bones, we estimate that all the specimens examined were adult.

The stratigraphic context is unfortunately not known precisely for many of the fossil specimens discussed here. Either they have been reworked and found in basal gravel layers, or they were dredged from the bottom of the sea (Bianucci et al., 2007; Lambert, 2005). Therefore, for most of them we can give only an approximate geological age.

Even if the extinct species “M.” longirostris and “M.” tumidirostris have been described from isolated rostrum elements (Cuvier, 1823; Miyazaki and Hasegawa, 1992) that were shown to be of low diagnostic value (Bianucci et al., 2007), we choose to maintain the original attribution to the genus Mesoplodon (between quoting marks) to stress their obvious affinities with this genus. We agree that the final genus and species attribution of the specimens displaying similarities with the original material of these taxa will depend of the description of more complete skulls, from the same stratigraphic levels.

2.2.2. Extant ziphiids

Hyperoodon ampullatus MNHN 1881-1149, juvenile, CT scan; M. bidens MNHN 1975-112, adult female, CT scan; M. layardii MNHN 1984-038, adult male, CT scan; Ziphius cavirostris MNHN 1934-253, adult male, CT scan.

2.2.3. Non-ziphiid extant odontocetes

Delphinus delphis MNHN 1934-367, adult, CT scan; Kogia breviceps MNHN 1976-37, adult, CT scan; Monodon monoceros MNHN 1983-103, adult female, CT scan.

2.3. Techniques implemented

2.3.1. Computed tomography

Each skull was scanned with a standard medical X-ray tomograph (Siemens AS + 128 slices), producing transverse slices of 0.6 mm thickness. For all specimens, the scanner was operated at 120 kV, 350 mAs. Mimics software (version 13.1) allowed the extraction of transverse sections and three-dimensional reconstructions of the skulls based on the sections.

In addition to the identification of sutures between bones (when not fused), CT scans provide access to bone mineral density (BMD), a morphometric parameter commonly used in medicine, combining local bone compactness (or trabecular volume) and mineral content of the osseous tissue (Meunier and Boivin, 1997). This parameter was not quantified in the present study (not calibrated with rods of known density), but considered in qualitative terms only, through a visual assessment of the local variation of X-ray opacity (white or grey values). For example, a roughly similar X-ray opacity could be noted between the ear bones and some portions of the rostrum in ziphiids. Neoceti (Odontoceti + Mysticeti) ear bones are made of one of the densest bone tissues described hitherto (Currey, 2002; de Buffrénil et al., 2004; Nummel et al., 1999). Using the threshold algorithm in Mimics we isolated parts of the skull displaying a given density range and produced three-
dimensional reconstructions of these high-density parts, in a way similar to Cranford et al. (2008).

2.3.2. Ground sections

Ground sections were made from rostrum fragments from extinct taxa (see list above), according to the classic technique for this kind of preparations (de Buffrénil and Mazin, 1989). All sections were made transversely, i.e., perpendicular to the longitudinal axis of the rostrum. They were observed at low (25×) and medium (200×) power magnification of a microscope, in natural and polarized light. The quantification of bone compactness, or parameter C, was performed on sketches of the sections made with a camera lucida (magnification 40–50×: minimum size of cavities: 20 μm), using the software Bone Profiler (Girondot and Laurin, 2003). Because all the sections were relatively large (at least 8–12 cm²) and displayed a very homogeneous compactness, measurements were made for each section in six to nine fields 2.5 × 2.5 mm, evenly distributed within the sectional area, and finally averaged to give a mean indication.

The terminology used in this study for describing bone structure and histology refers to Francillon-Vieillot et al. (1990).

2.3.3. Phylogeny

The phylogenetic background of the discussion is a composite phylogeny based on several phylogenetic analyses available in literature (Bianucci et al., 2007, 2010; Lambert, 2005). It must be noted that the phylogenies taken into account refer to morphological characters only, including those related to the closure or filling of the mesorostral groove by rostral bones. The main features discussed in the text can be summarized as four characters:

- **char. 1**, filling of the mesorostral groove: vomer (0) – absent (1) – mesethmoid (2);
- **char. 2**, dorsal closure of the mesorostral groove by the thickened premaxillae: absent (0) – present (1);
- **char. 3**, degree of remodeling of the compact rostrum bones: absent (0); partial (1); complete (2);
- **char. 4**, atypical osteons in remodeled compact rostrum bones: absent (0); present (1).

Character states are given in Table 1. Using MacClade 4 (Maddison and Maddison, 2005), we optimized the characters 1–3 on the composite tree under linear parsimony (see Swafford and Maddison, 1987). The derived state for character 4 is for now observed only in two taxa. Finally, with Mesquite (Maddison and Maddison, 2010) we used random taxon reshuffling on the reference phylogeny to assess the presence of a phylogenetic signal for each of the characters above (Laurin, 2004), a method that can also be used for discrete characters (Laurin, 2005). Ten thousands trees were randomly generated, and the number of steps for the given character has been compared between the reference phylogeny and the random trees. If the number of steps is lower in the reference tree than in at least 95% of the generated trees, it can be concluded that a phylogenetic signal is detected for the studied character (Laurin, 2004).

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Data-matrix for the four characters discussed in the text.</th>
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<tr>
<td>char. 1</td>
<td>1 2 3 4</td>
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<tr>
<td>char. 2</td>
<td>0 0 2 2</td>
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<tr>
<td>char. 3</td>
<td>0 0 0 0</td>
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<tr>
<td>char. 4</td>
<td>0 0 0 0</td>
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0: primitive state; 1, 2: derived states; ?: no data; –: not applicable; †: extinct taxa.

2.4. Institutional abbreviations


3. Results

By far the most common (and much likely pleiomorphic) condition of the rostrum in odontocetes is a mesorostral groove void of bone or other mineralized tissue (Fig. 1a, b) and only filled with the mesorostral cartilage, an anterior extension of the nasal septum (Cozzi et al., 2009). The groove is laterally and ventrally bordered by the vomer, which is usually thin on the lateral walls of the groove (Fig. 1a, b). Dorsally, the groove is often partly overhung by the dorsal portion of the premaxillae that forms a thin plate with a transversely convex, smooth and hard dorsal surface (i.e., porcelaneous part in Mead and Fordyce, 2009). This porcelaneous part is often made of compact, intensely remodeled bone (de Buffrénil and Lambert, 2011), contrasting with the more spongy aspect of the ventral part of the premaxilla and of the maxilla, with exception for the palatal cortex of this bone (e.g. Delphinus delphis).

3.1. Different bones, different shapes

A synthesis of previous works (Bianucci et al., 2007; Lambert, 2005), new external observations of the skull anatomy, and CT scans altogether suggest that the diverse modifications of the rostrum shape in ziphiids can be classified in several distinct groups. However, we acknowledge...
that the limits of these groups are not always sharply defined. For example, in some cases where the premaxillae dorsally close the mesorostral groove (e.g., *Choneziphius*), the vomer is significantly thickened in the groove, and the maxillae display an increased width lateral and dorsolateral to the groove. In other cases the inner sutures are fused and the degree of involvement of each rostral bone is difficult to establish (e.g., *M. densirostris*; De Buffrénil and Casinos, 1995). The classification proposed here is the following.

3.1.1. Filling of the mesorostral groove by the vomer

*Africanacetus* †, *Ihlengesi* †, *Izikoziphius* †, *Khoi khoicetus* †, *Mesoplodon*, “M.” *longirostris* †, “M.” *tumidirostris* †, *Microberardius* †, *Pterocetus* †, *Xhosacetus* †, *Ziphius* (Fig. 2; char. 1, state 0). Sexual dimorphism has been demonstrated for this character in *Ziphius cavirostris* and at least some species of *Mesoplodon*, in which the filling is more advanced in adult males than in young males and females (Heyning, 1984, 1989b; MacLeod and Herman, 2004; Mead, 1989a). Nevertheless, it should be noted that some degree of filling has been observed in adult females of some species (Reyes et al., 1991). An incipient development of this condition is observed in a sexually mature female *Tasmacetus shepherdi* USNM 484878 in anterodorsal view, in which the filling is more advanced in adult males than in young males and females (Heyning, 1984, 1989b; MacLeod and Herman, 2004; Mead, 1989a). 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groove (e.g. the extant *Mesoplodon carlhubbsi*, Heyning, 1984). The high elevation of the vomer above the mesorostral groove at the rostrum base is associated with a distinct bulge in the extinct species "M." *tumidirostris* (Miyazaki and Hasegawa, 1992).

3.1.2. No thickening or filling (char. 1, state 1; char. 2, state 0)

*Indopacetus, Nazcacetus* †, *Ninoziphius* †. Among the six described specimens of the extant *Indopacetus pacificus*, including only one possible adult male, none displays an extensive filling of the mesorostral groove (Dalebout et al., 2003). Only one specimen of *Nazcacetus urbinai* and two specimens of *Ninoziphius platyrostris* were observed. The small samples available for these two extinct species leave open the question of sexual dimorphism; it is possible that only females were discovered until now.

3.1.3. Partial filling of the mesorostral groove by the mesethmoid

*Berardius, Microberardius* †, *Nenga* † (Fig. 4; char. 1, state 2). In the specimens of *Berardius arnuxii* in which this feature has been observed, the outer surface of the mesethmoid is made of spongy bone.

3.1.4. Dorsal closure of the mesorostral groove by the thickened premaxillae

*Aporotus* †, *Beneziphius* †, *Choneziphius* †, *Messapicetus* †, *Tusciziphius* †, *Ziphirostrum* † (Fig. 5; char. 2, state 1). A mesorostral canal remains open, although its diameter varies from one species, or one specimen, to another. Above the canal, the premaxillae either remain separated (e.g. *Aporotus*), or more often display a sutural contact, with a varying degree of fusion between the premaxillae (Fuller and Godfrey, 2007, fig. 4). In some cases the premaxillae either form joined high longitudinal crests, in contact with (but not fused to) each other, as exemplified by *Aporotus*, or a single medial crest on the rostrum (e.g., *Tusciziphius*). In both cases, the volume of the premaxillae is significantly increased.

3.1.5. Combination of filling of the mesorostral groove by the vomer and dorsal closure by the thickened premaxillae (char. 1, state 0; char. 2, state 1)

*Z. recurvus* †. In this case the mesorostral groove is completely closed and the rostrum is massive and much higher than wide (see description of growth marks farther in the text and Lambert, 2005, fig. 15).

3.1.6. Development of high rostral maxillary crests, at the rostrum base

*Hyperoodon* (Fig. 6). Sexual dimorphism has been demonstrated for this character in at least *H. ampullatus*; adult males bear much higher crests (Hardy, 2005;
Fig. 7. CT scan of the skull of an adult male *Mesoplodon layardii* MNHN 1984-038. (a) 3D reconstruction in right lateral view. The densest areas, mostly on the rostrum and part of the vertex, are highlighted in red. (b–d) transverse sections displaying the variation of compactness, at the rostrum base (b), three quarters of the rostrum length (c), and mid-rostrum length (d). Scale bar = 100 mm.

Fig. 7. CT scan du crâne d’un mâle adulte de *Mesoplodon layardii* MNHN 1984-038. (a) reconstruction 3D en vue latérale droite. Les zones les plus denses, principalement sur le rostre et une partie du vertex, sont colorées en rouge. (b–d) coupes transversales montrant la variation de compacité, à la base du rostre (b), aux trois quarts de la longueur du rostre (c), et à mi-longueur (d). Barre d’échelle = 100 mm.

Mead, 1989b). Here again, the increase in bone volume is very important. Considerably lower crests medial or lateral to the antorbital notch have been described in various extinct and extant ziphiids (Mead and Fordyce, 2009, Diagram 2); the most conspicuous dome-like crests, in the extinct *Africanacetus ceratopsis*, are much less developed than in *Hyperoodon* spp. (Bianucci et al., 2007).

3.2. Bone compactness

Based on the one hand, on CT scans of specimens of extant species and, on the other hand, on ground sections of fossil specimens, we obtained, respectively, qualitative and quantitative compactness assessments for the different bones constituting the rostrum.

Fig. 8. CT scan of the skull of adult male *Ziphius cavirostris* MNHN 1934-253. (a) 3D reconstruction in left anterodorsolateral view. The densest areas, mostly the premaxillae, the vomer, and the left periotic, are highlighted in red. (b–e) transverse sections at mid-rostrum length (b), three quarters of the rostrum length (c), the rostrum base (d), and across the left periotic (e). Scale bar = 100 mm.

Fig. 8. CT scan du crâne d’un mâle adulte de *Ziphius cavirostris* MNHN 1934-253. (a) reconstruction 3D en vue antérodorsolatérale. Les zones les plus denses, principalement les prémâxillaires, le vomer, et le périotique gauche, sont colorées en rouge. (b–e) coupes transversales à mi-longueur du rostre (b), aux trois quarts (c), à la base du rostre (d), et travers le périotique gauche (e). Barre d’échelle = 100 mm.
As mentioned above, for rostrum bones in non-ziphiid odontocetes (e.g., *Delphinus*, *Monodon*) and in ziphiid specimens devoid of conspicuous local specialization of skull bones (e.g., female *M. bidens* MNHN 1975–112), compact bone is often observed at the level of the thin premaxillae above the mesorostral groove and on the palatal portion of the maxillae (Fig. 1b).

In adult males of *M. layardi* and *Z. cavirostris*, the mesorostral groove is filled by the vomer, and the dorsal part of the vomer and the dorsomedial part of the premaxillae are much more compact than the surrounding bones (Figs. 7 and 8). In both cases, the limits of the bones do not match the marked changes in compactness. Compact bone extends on the posterior part of the premaxilla, until the vertex, as observed in *Z. cavirostris* by Cranford et al. (2008). However, compact bone is predominantly concentrated in the rostrum, becoming thinner towards the vertex. An in situ periotic (ear bone) in the scanned skull of *Z. cavirostris* fits the range of compactness of the most compact rostrum bones of this specimen.

As already suggested by Hardy (2005), the maxillary crests of the young *H. ampullatus* are much less compact than the thin plate of premaxilla overhanging the mesorostral groove and than the ear bones (Fig. 9). Unfortunately, due to size constraints we could not scan the skull of a large adult male of this species (MNHN 1872–491), but the external surface of its crests is distinctly spongy (Fig. 6b), corroborating the scans of the young specimen.

A previous study based on ground sections of *M. densirostris* (de Buffrénil and Casinos, 1995) yielded an extremely high value of compactness (99%) for all the bones of the rostrum, with completely fused sutures. Compactness is similarly high in rostrum fragments from *Chonezuphius* sp. and aff. *Ziphirostrum*, and in the whole rostrum of two specimens of the extinct aff. "M." *longirostris*, where only some of the sutures can be distinguished on the sections. In the rostrum of *A. recurvirostris*, a different condition is observed: the hyperplasic premaxilla (i.e. the cortex of this bone is much more developed than in other taxa, which induces a swollen aspect) is very compact (96.8–98.8%), whereas the maxilla is made of cancellous bone (C: 40–65%; de Buffrénil and Lambert, 2011).

Skull parts that are most commonly preserved in fossil ziphiids are the rostrum and the dorsal part of the cranium, sometimes including the vertex (Bianucci et al., 2007, 2008; Lambert, 2005; Leidy, 1877). This typical preservation is much more frequent than in any other extinct odontocete group, and much likely results from the high compactness of these areas of the skull. More spongy bones simply disappear in the course of deposition, burial, and fossilization.

### 3.3. Bone histology

In the compact rostrum of the extant *M. densirostris*, all hypermineralized bones consist of a dense Haversian tissue, the secondary osteons of which display atypical features intermediate between parallel-fibered and woven-fibered bone (this tissue is monorefringent in transverse sections). This structure is very different from that of the lamellar bone usually observed in the walls of secondary osteons in adult mammals (de Buffrénil et al., 2000; Fig. 10e,f). In *M. densirostris*, the osseous tissue forming the walls of the osteons is characterized by a drastic reduction of its collagenous network, a feature that could explain the extremely high mineralization rate and physical density of the rostrum (2.612 to 2.686 g/cm³; de Buffrénil and Casinos, 1995; Zylberberg et al., 1998). In addition to its exceptional mineralization rate, this kind of bone proved to be the stiffest and hardest ever observed, with a corresponding high brittleness (Zioupos et al., 1997).

Similar histological features are observed in a transverse section from the anterior part of the rostrum of *Chonezuphius* sp. Here again the bone is completely remodeled, with the same type of atypical, longitudinally oriented secondary osteons made of monorefringent, non-lamellar osseous tissue (Fig. 10).

In the extinct aff. "M." *longirostris*, a part of the sutures between rostral bones (vomer–maxilla and vomer–premaxilla) is not fused (Fig. 11). The dorsal portion of the vomer in the mesorostral groove is distinctly less remodeled than the ventral portion, the maxilla, and the premaxilla. This upper part of the vomer is mostly made of a fibrolamellar complex with a predominantly vertical orientation of the primary osteons (equivalent to a radial orientation in a tubular long bone). The secondary osteons observed in the rest of the rostral bones are more often longitudinally or obliquely oriented. They differ strikingly from the secondary osteons observed in *M. densirostris* and *Chonezuphius* sp. because they display an alternate birefringence in polarized light, indicative of a true lamellar bone tissue characterized by an orthogonal alternation of lamellae (Fig. 11 g).

The association of non-remodeled and strongly remodeled compact bone is similarly observed in a dorsal fragment of the rostrum base of aff. *Ziphirostrum*. The location of these two types of tissue roughly corresponds to the premaxilla and the maxilla, respectively (Fig. 12). The clear alternate birefringence of the numerous longitudinally oriented secondary osteons forming the dense Haversian tissue indicates that osteon walls are made of typical lamellar bone.
Fig. 10. (a) Outline of the partial skull of *Choneziphius planirostris* IRSNB 3774-M.1881 in right lateral view, with the location of the transverse section performed in the rostrum fragment *Choneziphius* sp. MB CR-15. (b–d) details of the ground section in *Choneziphius* sp. MB CR-15. (b) numerous secondary osteons, some of them with a subcomplete closure of the vascular canal. Small rectangle = area enlarged in c–d. (c–d) atypical secondary osteons made of parallel-fibered to woven-fibered bone, in natural (c) and polarized (d) light. (e–f) details of a transverse ground section in the rostrum of *Mesoplodon densirostris* MNHN 1922-143, in polarized light, displaying similar atypical secondary osteons, lacking an alternate birefringence. Scale bars = 100 mm for a, 2 mm for b, 200 μm for c–f.

From the medial area to the peripheral dorsolateral region of the swollen, hyperplasic premaxilla of *A. recurvirostris*, bone tissue type changes, within the general frame of fibrolamellar complexes, from reticular to laminar, and finally radiating bone, according to vascular orientation (Fig. 13). This succession likely reflects changes in the accretion rates of the bone tissue, with an initial high rate (reticular bone), an intermediate lower rate (laminar bone), and a final increase of the accretion rate (radiating bone). In the laminar bone, growth marks are conspicuous. The thickness of the growth layer groups (GLG) tends to increase from deep to superficial layers in the dor-
sal and dorsolateral parts of the bone. This indicates that sub-periosteal accretion rate was particularly fast in these directions, with a tendency to get still faster in time (de Margerie et al., 2002, 2004). The premaxilla of *Aporotus* is entirely made of primary bone devoid of any kind of inner (especially Haversian) remodeling, with exception for a narrow zone along the medial wall of the bone. Conversely, the spongy maxilla of the same specimen was intensely remodeled (Fig. 13e), as is the general condition for this bone in mammals. Remodeling of the maxilla in *A. recurvirostris* is a first argument against the hypothesis of an age-related non-remodeling of the premaxilla. A second argument is the observation of 8 to 9 GLGs in this specimen, each of them supposed to represent one year in the life of the animal (de Buffrénil and Lambert, 2011). Therefore, this specimen must have died in its 9th or 10th year. Among extant ziphiids, the few data available indicate that sexual maturity is reached at 7–11 dental GLGs in *Hyperoodon ampullatus* (Benjaminsen and Christensen, 1979), and occurred at 9 GLGs in one female *M. densirostris* (Ross, 1984). These comparative elements suggest that the studied specimen of *A. recurvirostris* was a young adult or, at least, a late subadult. Furthermore, an absence or a low degree of remodeling is commonly observed in the lamellar bone tissue of adults in other mammals, for example artiodactyls (Currey, 2002).

The macroscopic examination of fracture surfaces in the hyperplasic premaxillae of aff. *Aporotus dicyrurus* and *Choneziphius planirostris* (Fig. 14a–c; Lambert, 2005, fig. 18), and the examination of CT scan sections of the premaxilla of *Z. recurvus* (Fig. 14d) reveal clear growth marks in complete sequences. Therefore, it must be concluded that these bones were not remodeled, like those of *A. recurvirostris*.

To summarize, the degree of remodeling in ziphiid rostra strongly differs between taxa: secondary osteons can be developed in the whole rostrum (*M. densirostris*), or only in some bones (aff. “*M.* longirostris, aff. *Ziphirostrum*). They...
Fig. 12. (a) Outline of the partial skull of Ziphirostrum marginatum IRSNB 3847-M.537 in right lateral view (reversed), with the location of the transverse section performed in the rostrum fragment aff. Ziphirostrum. (b) ground section in the maxilla and premaxilla. (c–d) detail of the maxilla-premaxilla suture area displaying the non-remodeled premaxilla (upper left) and the strongly remodeled maxilla (lower right), in natural (c) and polarized (d) light. (e–f) secondary osteons in the maxilla, in natural (e) and polarized (f) light, displaying the subcomplete closure of the vascular canals and the alternate birefringence typical of lamellar tissue. Scale bars = 100 mm for a, 1 mm for c–d, 500 μm for e–f.

Fig. 12. (a) Contour d’une partie du crâne de Ziphirostrum marginatum IRSNB 3847-M.537 en vue latérale droite (inversée), montrant la position de la coupe transversale réalisée dans le fragment de rostre aff. Ziphirostrum. (b) lame mince dans le maxillaire et le prémaxillaire. (c–d) détail de la région de la suture maxillaire-prémaxillaire montrant le prémaxillaire non remanié (en haut à gauche) et le maxillaire fortement remanié (en bas à droite), en lumière naturelle (c) et polarisée (d). (e–f) ostéones secondaires dans le maxillaire, en lumière naturelle (e) et polarisée (f), montrant la fermeture subcomplète des canaux vasculaires et la biréfringence alternée typique du tissu lamellaire. Barres d’échelle = 100 mm pour a, 1 mm pour c–d, 500 μm pour e–f.

can also be absent from the bones (otherwise pachyostotic and osteosclerotic) of other species (A. recurvirostris). Remodeling can also be restricted to a part only of a bone (e.g., vomer of aff. “M.” longirostris that is only remodeled in its ventral portion). With the exception of the atypical osteons of Choneziphius sp. and M. densirostris, secondary osteons in ziphiid rostra display a normal lamellar organization in transverse section. In all rostra for which ground sections of compact bone were available, a complete or subcomplete occlusion of vascular canals occurs. Since the precursor cells of the osteoclasts, the monocytes, are brought in situ via blood vessels, this observation would mean that the remodeling process of ziphiid rostral bones, though potentially intense, cannot proceed after canal closure and is thus limited in time (there is a trend to self-blockage of remodeling). This inference is confirmed by the lack or great sparseness of open erosion bays in all the taxa investigated.

3.4. Confrontation with phylogenetic framework

The data compiled here are summarized in a composite phylogenetic tree in Fig. 15. The optimization of the ancestral state for the characters 1–4 gave the following results. The ancestral state for char. 1 (filling of the mesorostral groove) is equivocal, depending on the choice of the Accelerated Transformation (AccTran) or Deleted Transformation (DelTran) hypothesis; either the filling by the vomer is ancestral (DelTran), subsequently lost in several clades and re-appearing in the clade Izikoziphius + Ziphius, or it appeared independently (AccTran) in numerous clades (Z. recurvus but not the other species of the genus Ziphirostrum, Tasmacetus, Izikoziphius + Ziphius, Xhosacetus, Pterocetus, Africanaetus + Ihlengezi + Mesoplodon + aff. “M.” longirostris). The derived filling of the groove by the mesethmoid appears in the clade Berardius + Microberardius (unknown in Archaeoziphius). However, it should be noted that when assessing the phylogenetic signal for char. 1, the number of steps in the reference tree is lower than in 94.61% of the randomly generated trees (probability 0.0539, Table 2), which is at the very limit of reliability for this character optimization. For char. 2 (dorsal closure of the groove by the thickened premaxillae) the ancestral state is similarly equivocal; either the closure occurs in the common ancestor of all ziphiids (AccTran) and is lost in several clades, or it appears independently (DelTran) in three clades (Aporotus + Benezhiphus + Messapicetus + Ziphirostrum, Aporotus + Benezhiphus + Messapicetus + Ziphirostrum,
Table 2

<table>
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<th>Character</th>
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<td>Char. 4</td>
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4. Discussion

Although occurring in most ziihids, be they extinct or extant, the morphological specialization of rostral bones is expressed in distinct ways among the various lineages.
Fig. 14. Growth marks in the premaxilla, on dorsal surface of the rostrum of *Choneziphius planirostris* IRSNB 3777-M.1882 (a), on transverse fracture surface at the rostrum base of aff. *Aporotus dicyrthus* IRSNB 3807-M.1889 (b–c), shown in dorsal view (b), in posterior view of the fracture surface (c), and on virtual transverse section at mid-length of the rostrum of *Ziphirostrum recurvus* IRSNB 3805-M.544 (d). Arrows indicate the most conspicuous growth marks. Scale bars = 50 mm for a–b, 10 mm for d.

Fig. 14. Marques de croissance dans le prémaxillaire, en surface dorsale du rostre de *Choneziphius planirostris* IRSNB 3777-M.1882 (a), sur une surface de fracture transversale à la base du rostre de aff. *Aporotus dicyrthus* IRSNB 3807-M.1889 (b–c), en vue dorsale (b) et en vue postérieure de la surface de fracture (c), et en coupe transversale virtuelle à mi-longueur du rostre de *Ziphirostrum recurvus* IRSNB 3805-M.544 (d). Les flèches indiquent les marques de croissance les plus manifestes. Barres d’échelle = 50 mm pour a–b, 10 mm pour d.

From an anatomical point of view, the bones involved in the changes of shape of the rostrum (vomer, mesethmoid, maxilla, premaxilla) differ considerably from one taxon to another. Furthermore, the optimization of ancestral states indicates a complex history with several convergences and reversions (Fig. 15). From a histological point of view, the limited sample of adult specimens studied hitherto suggests that the remodeling pattern of compact cortices also varies among taxa (no remodeling, partial remodeling, complete remodeling). In a same lineage, the extent of bone remodeling may deeply change from one taxon to another (Fig. 15; *Aporotus and Zhiphirostrum, M. densirostris* and aff. “M.” *longirostris*). Furthermore, similar, atypical (monorefringent) secondary osteons can be observed in two taxa belonging to distantly related lineages (*Choneziphius* sp. and *M. densirostris*). Due to the preservation state of fossil specimens and the difficulty to gain access to samples of extant species, hypermineralization could be demon-

Fig. 15. Composite phylogenetic tree of the ziphiids based on several cladistic analyses (Bianucci et al., 2007, 2010; Lambert, 2005). †, extinct taxa. Specimens referred to the extinct “*Mesoplodon*” *longirostris* probably do not belong to the genus *Mesoplodon*, even if they are closely related. Optimization of the ancestral state is shown for characters 1–2. Char. 1 (filling of the mesorostral groove) on the left mirror-tree. Light grey, filling by the vomer (0); dark grey, absence of filling (1); black, filling by the mesethmoid (2). Char. 2 (dorsal closure of the groove by the thickened premaxillae) on the right mirror-tree. Light grey, absence (0); black, presence (1). Only the DelTran hypothesis is illustrated for both characters.

Fig. 15. Arbre phylogénétique composite des ziphidiens, basé sur plusieurs analyses cladistiques (Bianucci et al., 2007, 2010; Lambert, 2005). †, taxons éteints. Les spécimens attribués au taxon éteint “*Mesoplodon*” *longirostris* n’appartiennent vraisemblablement pas au genre *Mesoplodon*, même s’ils en sont proches. L’optimisation de l’état ancestral est montrée pour les caractères 1–2. Car. 1 (remplissage de la gouttière mésorostrale) sur l’arbre-miroir de gauche. Gris clair, remplissage par le vomer (0) ; gris foncé, absence de remplissage (1) ; noir, remplissage par le mésethmoïde (2). Car. 2 (fermeture dorsale de la gouttière par les prémaxillaires épaissis) sur l’arbre-miroir de droite. Gris clair, absence (0) ; noir, présence (1). Seule l’hypothèse DelTran est illustrée pour les deux caractères.
strated for now only in *M. densirostris* (Zylberberg et al., 1998). With the exception of *Chonezuphius* sp., the other taxa studied display osteons made of typical lamellar bone, a tissue known to have a high collagen content and a relatively low mineralization rate (Boivin and Meunier, 2002). However, further investigation of the mineral and collagen content of extant zibihiid rostra would be necessary to confirm this potentially important difference.

The high variation, at different levels of bone organization (at least anatomical and histological), of the detailed phenotypical expressions of rostrum specializations in the Zibihiidae strongly suggests that distinct processes were at work for the acquisition of such features in the various zibihiid lineages. Indeed, even if, as proposed by character optimization, the ancestral condition might be a mesorostral groove filled by the vomer or dorsally closed by the thickened premaxillae (both results equivocal), a great diversity of anatomical and histological specializations appears within this clade. These features do not simply represent a plesiomorphic feature inherited from stem-zibihiids; they would rather reflect a broad convergence between most zibihiid taxa (but not all taxa; cf. the cases of *Indopacetus*, *Nazzacetus*, and *Ninozuphius*), in response to (a) common selective pressure(s) arising from similar, but possibly not fully identical, ecological specializations (Bianucci et al., 2008).

This consideration raises, of course, the question of the functional implication(s) of the rostral specializations. A basic observation is that, beyond the diversity of processes, there is an obvious, factual result: increasing bone mass, stiffness, and physical density in the rostral region of the skull.

Several functions have been proposed for the compact rostrum bones of extant and extinct zibihiids. The most convincing hypotheses can be classified into three categories, related to three main functional and ecological features: acoustics, deep diving, and intraspecific fights between males (de Buffrénil et al., 2000; Cozzi et al., 2010; Heyning, 1984; MacLeod, 2002).

In odontocetes, the production of echolocation sounds occurs in the forehead and the transmission is made through the melon (Cranford et al., 1996; Mead, 1975b). Air sacs surrounding the phonic lips, the sound-producing organs in the forehead, may act as acoustic mirrors for echolocation and communication sounds. In the case of deep-diving zibihiids (for example, individuals of *M. densirostris* and *Z. cavirostris* have been recorded at depths up to 1251 and 1888 m, with dive durations reaching 57 and 85 min, respectively; Tyack et al., 2006), hydrostatic pressure strongly reduces the volume of air spaces. Density disparity between forehead tissues and highly compact bone could therefore constitute an alternative acoustic reflector (Cranford et al., 2008). This model is in agreement with the geometry of compact bone elements in the skull of several extant and extinct zibihiids, even if compact bone is preferentially located in the anterior part of the skull. However, unusual shapes of hyperplastic bones in various extinct zibihiid taxa are in poor agreement with this acoustic model alone. For example, the elevated medial crests of “*M.* tumidirostris” and *Tusciuphius* sp. are located anterior to the area of production of the echolocation sounds, and may therefore be considered more as an obstacle than as a reflector for the sounds to be transmitted forwards via soft tissues. Another even more problematic issue is the preferential development of compact bone in adult males of extant zibihiids. Indeed, the few data available hitherto do not allow the distinction of different echolocation or diving abilities between adult males and females/juveniles in a same zibihiid species (Hooker and Baird, 1999; Johnson et al., 2004, 2008; Madsen et al., 2005; MacLeod, 2002; Tyack et al., 2006).

As mentioned above, the most obvious physical effect of developing pachyosteosclerotic rostrum bones (irrespective of their external shape and histology) is a local increase in mass. As deep divers, zibihiids might find a benefit in such a ballast, positioned at the anterior extremity of the body, even if it is of minor importance, as compared to the total weight of the animals. This ballast could indeed help them maintaining a vertical position in the water column during descent (dynamic ballast; de Buffrénil et al., 2000). The most obvious criticism to this hypothesis is that the energetic benefit during the descent would be lost during the way back to the surface (MacLeod, 2002). However, preliminary observations on diving zibihiids showed that, at least in some of the few dives recorded for *M. densirostris* and *Z. cavirostris*, the locomotion type changes from the descent to the ascent; the studied animals more frequently performed passive and metabolically cheap gliding during the descent, whereas swimming was more active, with more frequent tail strokes during the ascent (Tyack et al., 2006), a behaviour similarly observed in several other groups of diving marine mammals (Williams et al., 2000). Nevertheless, as mentioned above, no significant infraspecific difference could be observed for now between the swimming style and diving depths of adult males, adult females, and juveniles.

With their sexually dimorphic tusks, adult males of many extant zibihiid species are supposed to engage in intraspecific fights. Based on indirect observations (accumulation of unpigmented linear scars on the body, likely made by the tusks), this putative behaviour leads to the hypothesis that thicker and heavier rostrum bones (especially the filling of the mesorostral groove by the vomer) may limit the risks of fractures caused by impacts (Heyning, 1984; MacLeod, 2002). However, the extremely high mineral content of the hyperdense rostrum of *M. densirostris*, the only species on which mechanical tests have been applied, results in a very brittle material, certainly unsuited to impact loading (de Buffrénil et al., 2000; Ziopoulos et al., 1997). Interestingly, a preliminary analysis of the bone organization in the maxillary crests of *H. ampullatus*, the only species for which head-butting has been actually observed (Gowans and Rendell, 1999), indicates that, as proposed by Hardy (2005), the crests are made of spongy bone, in strong contrast with the compact bone of many other zibihiid rostra. Such a condition would actually be reminiscent of the spongy aspect of the antlers and other skull elements of head-butting terrestrial ungulates (Currey, 2002). It nevertheless remains that changes in the thickness and shape of the rostrum bones, leading to the dorsal closure or the filling of the mesorostral groove, could have a positive effect on the mechanical strength of this...
part of the skull, especially in long-nosed species with apical lower tusks (Bianucci et al., 2008; Lambert et al., 2010a). However, unusual shapes of the rostral bones, as exemplified by the medial crest in "M." tumidirostris and Tuscziphius sp., are more difficult to understand in the framework of this hypothesis.

To conclude, the striking diversity of morphological and histological features documented here in the rostrum of extinct and extant ziphiids suggests a complex evolutionary history for these characters within the family, and poorly matches a single, univoque functional explanation for now. Several behavioural/ecological factors may have played a role in the development of pachyosteosclerotic bone, and the latter could possibly be a relevant solution for more than one selective pressure. A broader sampling for histological analyses, including new extinct species and juveniles, adult females, and adult males of extinct species, will certainly provide additional arguments to the discussion, as well as more detailed data about the ecology of extinct ziphiids (recognition of different feeding and diving habits for males and females, observation of intraspecific fights . . .).

Acknowledgements

We wish to thank A. Abourachid, M. Bosselaers, A. Folie, C. Lefèvre, E. Pellé, and E. Steurbaut for the loan or gift of specimens, L. Cazes and J.L. Lemoine for the production of CT scans, D. Germain for his assistance with Mimics, and three anonymous reviewers and the editor M. Laurin for their constructive comments about our manuscript.

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