Title: Dual sound reception apparatus in protocetid whales

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Abstract

Modern cetaceans dwell in an underwater world of sound. Due to the specific physico-acoustic conditions inherent in the aquatic environment, sound reception pathway in modern whales drastically differs from that of land mammals and implies deep modification of their external acoustic apparatus. To fathom the implementation of this underwater hearing system, the rare data on the auditory region of early whales are paramount. Among them, previous studies on protocetid auditory region highlighted the presence of two potential acoustic portals on the lateral wall of the bulla: a tympanic ring and a tympanic plate. Through an anatomical survey, I explore the external sound reception apparatus of a protocetid whale and discuss the functionality of these two sound portals. The study of the tympanic ring, allow me to propose a reconstruction of the tympanic membrane of this early whale, suggesting that this structure was functional for aerial hearing. 3D investigation of the bone thickness of the bulla reveals the presence of homologous areas of reduced thickness within the tympanic plate of protocetid and modern cetaceans, highlighting a common functioning of this structure for underwater hearing. Thus, this detailed anatomical survey of the lateral wall of a protocetid tympanic bulla confirms

the functionality of the two contiguous acoustic portals and sheds new light on the sound transmission mechanism in these early whales.

Keywords: acoustic portals, auditory bulla, archaeocetes, bone thickness, μ CT-scan

Introduction

Extant cetaceans form a clade of fully aquatic artiodactyls (*i.e.* even-toed ungulates) that originates from terrestrial mammals. Dwelling in an ecological niche where light fades faster than in the air (Kröger 2008), the neocetes (*i.e.* extant whales) live principally in an underwater world of sound (Ketten 1994; Tyack 1999; Wartzok & Ketten 1999; Mooney *et al.* 2012; Yamato *et al.* 2014; Ary *et al.* 2016; Nummela & Yamato 2018) and possess complex acoustic communication systems (*e.g.* Payne & McVay 1971; Rendell & Whitehead 2003; Eriksen *et al.* 2005; King & Janik 2013; Gero *et al.* 2016; López-Marulanda *et al.* 2017; Allen *et al.* 2018; Rossi-Santos 2018; Stafford *et al.* 2018; Martin *et al.* 2019).

Since the underwater physico-acoustic conditions strongly differ from that of the air (Nummela *et al.* 2007; Nummela & Thewissen 2008), the adaptation of the cetacean auditory system to the aquatic soundtope implied drastic morpho-anatomical modifications. Among these, spectacular changes affect the external ear, which is deprived of pinna and mainly obstructed by a waxy ear-plug (*int. al.* Howes 1880; Lillie 1915; Yamada 1953; Ichihara 1959, 1964; Lockyer 1984; Tinker 1988; Ketten 1997; Rauschmann *et al.* 2006; Trumble *et al.* 2013, 2018; De Vreese *et al.* 2020). In addition, the tympanic membrane, located at the interface between the external and middle ears, that transmits sound from the air to the ossicular chain in terrestrial mammals, is highly modified (*e.g.* tympanic ligament), and is probably no longer

functional in an acoustic point of view (Lillie 1910; Fraser & Purves 1960a,b; McCormick *et al.* 1970; Fleischer 1978; Ekdale *et al.* 2011; Yamato *et al.* 2012; Rehorek *et al.* 2019). Thus, in extant cetacean, the sound reaches the middle ear by other pathways, that are, to date, not clearly understood (Popov & Supin 2007; Cranford *et al.* 2008a,b, 2010; Yamato *et al.* 2012; Mooney *et al.* 2012, 2015; Popov *et al.* 2016, 2019; Ryabov 2016; Cranford & Krysl 2018; Sysueva *et al.* 2018; Tubelli *et al.* 2018). One of the main underwater hearing pathways in odontocetes (*i.e.* tooth whales) is through fatty tissues surrounding the middle ear (*int. al.* Reysenbach de Haan 1957; Bullock *et al.* 1968; Norris 1968; McCormick *et al.* 1970; Varanasi & Malins 1971, 1972; Norris & Harvey 1974; Brill *et al.* 1988; Ketten 2000; Ryabov 2016). This could also be the case for mysticetes (*i.e.* baleen whales; Yamato *et al.* 2012, 2014; Yamato & Pyenson 2015; Nummela & Yamato 2018). Commonly referred as fat pad, this soft tissue contacts a very thin part of the auditory bulla named the tympanic plate. This bullar structure is a bony analogue of the tympanic membrane, and transmits sound vibrations collected by the outer sound reception apparatus to the malleus (*i.e.* the first link of the ossicular chain; Fleischer 1973; Hemilä *et al.* 1999; Nummela *et al.* 1999a, b).

Due to the delicate nature of this thin tympanic plate, the lateral wall of the tympanic bulla of early amphibious whales is often broken and rarely preserved in the fossil record. Yet, recent studies highlighted the presence of two contiguous sound portals (a tympanic membrane and a tympanic plate) on the lateral wall of the well preserved tympanic bulla of an indeterminate species of protocetid (early semi-aquatic whale) from Togo (Mourlam & Orliac 2018, 2019). Here, through a detailed anatomical survey of the lateral wall of the bulla of this specimen, I discuss the functionality of these two potential sound reception apparatus in protocetids and bring new insights on their sound transmission mechanism (Nummela *et al.* 2004, 2007; Mourlam & Orliac 2019).

Material and methods

The tympanic bulla investigated in this study is part of the skull fragment UM-KPG-M 73 belonging to an indeterminate genus of protocetid, phylogenetically close to *Protocetus* (Kassegne *et al.* 2021), and referred to as “morphotype γ ” by Mourlam and Orliac (2018). This specimen was collected in Togo and comes from the Lutetian phosphate deposits (*ca.* 46-44 Ma) of Kpogamé (Cappetta & Traverse 1988; Gingerich & Cappetta 2014). UM-KPG-M 73 was scanned using the General Electric Phoenix Nanotom S at the AniRA-ImmOs (SFR Biosciences Gerland-Lyon) microtomography facility with a resolution of 70 μ m. The 3D model of the bulla is available at MorphoMuseum.com under the number M3#134_UM KPG-M 73. Detailed descriptions of the bony labyrinth, petrotympanic complex and ossicular chain of protocetid indeterminate γ were provided by Mourlam and Orliac (2017, 2018, 2019).

Quantification of the bone thickness of the tympanic bulla was computed using the “Surface Distance” tools of AVIZO 9.0 (Visualization Sciences Group – an FEI Company 2018), following the protocol described by Mourlam and Orliac (2019), based on Guy *et al.* (2013; see also Lazzari & Guy 2014; Thiery *et al.* 2017). 3D chromatic and isopleth bone thickness maps were generated following Lazzari *et al.* (2008). As comparison material, a tympanic ring model, along with 3D chromatic and isopleth bone thickness maps were also computed for the tympanic bulla of the odontocete *Delphinus capensis* (NOAA-cet 436B-KXD0307), the mysticete *Balaena mysticetus* (UM-430 N) and the ruminant (land artiodactyl) *Capra ibex* (UM-N74). Technical parameters of these specimens are presented in Table 1.

Institutional Abbreviations

GSP-UM, Geological Survey of Pakistan – University of Michigan collection, Michigan, USA;
NOAA, National Oceanic and Atmospheric Administration, Southwest Fisheries Science
Center, Washington, D.C., USA; **SNMS**, Staatliches Museum für Naturkunde, Stuttgart,
Germany; **UM**, Université de Montpellier, France.

Table 1. Technical parameters related to the specimens investigated.

Taxon	Specimen	Side	Voxel size (μm)	X-Ray Microtomograph	CT scan institution
Protocetid indet. γ	UM-KPG-M 73	Left	70	General Electric Phoenix Nanotom S	AniRA-ImmOs (SFR Biosciences Gerland-Lyon)
<i>Balaena mysticetus</i>	UM-430 N	Right	154	EasyTom 150	MRI - ISEM (Montpellier)
<i>Capra ibex</i>	UM-N74	Left	180	EasyTom 150	MRI - ISEM (Montpellier)
<i>Delphinus capensis</i>	NOAA-cet 436B-KXD0307	Left	34.69	EasyTom 150	MRI - ISEM (Montpellier)

Description and comparisons

The lateral wall of the tympanic bulla of UM-KPG-M 73 bears two contiguous acoustic portals,
responsible for sound transmission to the ossicular chain (Mourlam & Orliac 2018): i) the
tympanic ring, bony support of the tympanic membrane that allows for airborne sound
transmission (*int. al.* Fleischer 1978; Luo 1998; Mead and Fordyce 2009; Ekdale 2016), and ii)
the tympanic plate that receives sound under water via a fatty tissue (see Discussion and also
Fleischer 1973; Hemilä *et al.* 1999; Nummela *et al.* 1999a, b).

Tympanic ring (Fig. 1). - Among the two acoustic portals located on the lateral wall of the tympanic bulla of UM-KPG-M 73, there is the free inner edge of the meatal tube (Luo 1998; Mead & Fordyce 2009) that bears the tympanic ring, bony support of the tympanic membrane. As described by Mourlam and Orliac (2018), the tympanic ring of protocetid indeterminate γ resembles that of terrestrial artiodactyls. In that sense, its tympanic ring joins the posterior process to the sigmoid process forming a “left-leaning italic U-shaped” septum, nearly perpendicular to the lateral wall of the bulla (Fig. 1A). At the base of the posterior process, the shallow sulcus of the tympanic membrane, about 0.4 mm wide, goes all along the lateral side of the tympanic ring (Supplementary Fig. S1). This sulcus widens at the base of the conical process and reaches about 1.5 mm wide. The tympanic ring of the steinbock *Capra ibex* (Fig. 1B) is morphologically close to that of protocetid indeterminate γ and also consists in a continuous bony septum. This suggests that the tympanic membrane of UM-KPG-M 73 was functional for aerial hearing (see Discussion). The main difference between the external auditory meatus of the UM-KPG-M 73 and the steinbock lies in the absence of the conical process in the latter. It is interesting to note that the centre of the lateral wall between the two bullar crura of *C. ibex* is bulged (Fig. 1B: “ba”). In addition, the protocete also presents a different orientation of the bony septum: the tympanic ring of *C. ibex* faces medially while that of UM-KPG-M 73 faces more anteriorly.

The tympanic membrane of modern cetaceans highly differs from that of land mammals. Partially attached to the lateral wall of the tympanic bulla (distally) and to the reduced manubrium of the malleus (proximally), it forms a conical ligament pointing medially towards the inside of the tympanic cavity (Lillie 1910; Fraser & Purves 1960a, b; Fleischer 1973, 1978; Lancaster 1990; Nummela *et al.* 1999b; Ekdale *et al.* 2011; Rehorek *et al.* 2019). Thus, the conformation of the tympanic membrane area in mysticetes, such as *Balaena mysticetus*,

Figure 1. Left tympanic ring in medial view. (A) protocetid indeterminate γ (UM-KPG-M 73); (B) *Capra ibex* (UM-N74); (C) *Delphinus capensis* (NOAA-cet 436B-KXD0307); (D) *Balaena mysticetus* (mirror image from the right specimen UM-430 N). Abbreviations: **ace**, anterior crus of ectotympanic; **ba**, bulged area; **cp**, conical process; **eam**, external auditory meatus; **pce**, posterior crus of ectotympanic; **pp**, posterior process of ectotympanic; **sp**, sigmoid process; **stm**, sulcus of tympanic membrane *sensu lato*; **team**, tube for external auditory meatus; **tr**, tympanic ring. Dark grey regions represent broken or virtually cut bone. Scale bars = 5 mm. Illustrations by R. Mourlam.

presents some sizeable changes compared to that of land mammals and protocetid indeterminate γ . In the bowhead whale, the tympanic ring is reduced to a short and delicate bony rim that lingers continuously from the posterior process of the bulla to the sigmoid process (Fig. 1D; see also “glove finger scar” in [Ekdale et al. 2011](#)). This bony rim is nearly parallel to the lateral wall of the bulla and delimits a gutter-like sulcus that support the glove finger, a convex membrane probably derived from the *pars flaccida* of the tympanic membrane in mysticetes. This thimble-shaped structure is oriented towards the inside of the external auditory meatus ([Lillie 1910, 1915](#); [Ridewood 1922](#); [Reysenbach de Haan 1957](#); [Ichihara 1959](#); [Fraser & Purves 1960a, b](#); [Fleischer 1978](#); [Ketten 1997](#); [Luo 1998](#); [Luo & Gingerich 1999](#); [Ekdale et al. 2011](#);

Tubelli *et al.* 2018; Rehorek *et al.* 2019). In comparison, the tympanic ring of the odontocetes, such as *Delphinus capensis*, appears even more derived. It consists of a thick and smooth bony rim at the base of a hollow conical process (Fig. 1C). This bony rim does not extend on the posterior process of the bulla. Furthermore, with the exception of a slight notch anteroventrally, there is no sign of the tympanic membrane's sulcus lingering along the vestigial tympanic ring.

Tympanic plate (Fig. 2). - The other acoustic portal located on the lateral wall of the tympanic bulla of UM-KPG-M 73 is the tympanic plate (Fleischer 1973; Hemilä *et al.* 1999; Nummela *et al.* 1999a, b). The bone thickness of this structure is not homogeneous and the 3D chromatic map highlights three areas composed of particularly thin bone within the lateral wall. The first one is located at the base of the free inner edge of the meatal tube and corresponds roughly to the anterior half of the plate supporting the thick conical process (Fig. 2A1: "TP1"). The bone thickness of this sub-rectangular area, covering about 90 mm², is mainly comprised between 0.5 and 1 mm. The second area forms a thin bony channel where bone thickness is under 0.5 mm. It is located anterior to the sigmoid process and follows mainly the lateral furrow (Fig. 2A2: "TP2"). Due to breakages on the lateral wall, it is not possible to observe the dorsal limit of this thin bony channel. Finally, a third area covers a hemicircular surface of about 50 mm² located anterior to the tubarius process on the dorsolateral part of the bulla. This area, where bone thickness is also below 0.5 mm, extends dorsally and is continuous with the thin bony plate that contacts the falciform process of the squamosal (Fig. 2A3: "TP3"). In addition, adjacent to the area located anterior to the sigmoid process (TP2), there is a small notch at the base of the tubarius process (Fig. 2A: "sct") where bone thickness is under 0.5 mm. According to the morphology of the bulla of other protocetids such as *Artiocetus* (GSP-UM 3458) and *Protocetus* (SMNS 11084), it is likely that this notch is a subtle remain of the broken

Figure 2. 3D chromatic bone thickness maps of the left tympanic bulla in lateral view. (A) protocetid indeterminate γ (UM-KPG-M 73); (B) *Capra ibex* (UM-N74); (C) *Delphinus capensis* (NOAA-cet 436B-KXD0307); (D) *Balaena mysticetus* (mirror image from the right specimen UM-430 N). (A1-3) details of the three areas composed of particularly thin bone of protocetid indeterminate γ . Thickness indications on isopleth are in millimetre. Abbreviations: **cp**, conical process; **eam**, external auditory meatus; **lf**, lateral furrow; **msmr**, medial sulcus of the malleolar ridge; **pp**, posterior process of ectotympanic; **sct**, sulcus for chorda tympani; **sp**, sigmoid process; **TP 1-3**, areas of the tympanic plate composed of particularly thin bone (see text for more details); **tub**, tubarius process. Scale bars = 1 cm. Illustrations by R. Mourlam.

195 sulcus for the chorda tympani that extends between the sigmoid and tubarius processes. This
196 suggests the presence of a possible fourth area of very thin bone (see below).

197 In comparison, the tympanic plate of *Delphinus capensis* occupies a wider area of the
198 lateral wall and is mainly composed of bone less than 0.7 mm thick (Fig. 2C). Furthermore, the
199 three areas of thin bone retrieved on the tympanic plate of protocetid indeterminate γ are also
200 present. The one at the base of the free inner edge of the meatal tube (Fig. 2C: “TP1”) has a
201 similar shape and extends dorsally towards the top of the conical process and also spreads
202 towards the notch at the junction between this process and the sigmoid process. This area is
203 even thinner than that of the tympanic bulla UM-KPG-M 73 with a thickness inferior to 0.5
204 mm. The second area (Fig. 2C: “TP2”) also forms a bony channel that follows the course of the
205 lateral furrow, at the base of the anterior rim of the sigmoid process, but does not extend to the
206 sulcus for the chorda tympani due to the thicker malleal ridge (*sensu* Fordyce 1994). The third
207 and anteriormost area (Fig. 2C: “TP3”) is wider than that of protocetid indeterminate γ and
208 extends all along the anterodorsal crest of the bulla. In addition, the medial sulcus of the malleal
209 ridge (*sensu* Cranford *et al.* 2010) of *Delphinus capensis* is also very thin. This bony area,
210 crossed by the sulcus for the chorda tympani, corresponds to the floor of the bony funnel
211 (Cranford *et al.* 2010) and is in direct connection with the gonial of the malleus. The general
212 bony thickness of the medial sulcus of the malleal ridge is under 0.6 mm and some small areas
213 near the malleus are extremely thin with bone comprised between 0.2 and 0.3 mm thick
214 (Supplementary Fig. S2).

215 The lateral wall of the mysticetes *Balaena mysticetus* is about ten times thicker than that
216 of *Delphinus capensis* (Fig. 2D and Supplementary Fig. S3). Nevertheless, two of the three
217 areas of very thin bone (TP1-2) can also be observed, with a thickness of up to 3 mm. The first
218 area (TP1) mainly corresponds to the notch at the junction between the conical and the sigmoid
219 processes and is composed of bone that can be thinner than 1.5 mm. This notch is perforated

by two foramina with a diameter of about 1.3 and 2 mm. This area of thin bone also slightly extends on the anterior half part of the conical process and spreads ventrally along the sigmoid fissure (Ekdale *et al.* 2011) to form an adjacent sub-circular area at the base of the sigmoid process. It is noteworthy that a thin zone of thicker bone (between 3 and 3.5 mm thick) crosses this area and corresponds to the position of the tympanic ring. In a similar way than that observed for protocetid indeterminate γ and *Delphinus capensis*, the second area (TP2) forms a bony channel that follows the lateral furrow. It is between 2.5 and 3 mm thick and extends towards the bony funnel. *Balaena mysticetus* lacks the anteriormost area (TP3) as seen for protocetid indeterminate γ and *Delphinus capensis* anterior to the tubarius process. In addition, another area of thin bone is retrieved between the base of the anterior pedicle and the sigmoid process and forms a U-shaped valley (Supplementary Fig. S4). This valley corresponds to the floor of the bony funnel and is composed of bone that can be thinner than 1mm. It is so delicate that some parts appear broken on the 3D model while being intact on the physical specimen. This area narrows anteriorly to form a small canyon, about 15 mm long and 2.5 mm wide, following the flanks of the anterior pedicle. The floor of this canyon is composed of bone thinner than 2.7 mm.

As an illustration of fully terrestrial artiodactyl, the pattern of bone thickness distribution of *Capra ibex* is markedly different (Fig. 2B). Indeed, despite some similarities, such as a bony channel with a thickness inferior than 0.5 mm that lingers on the anterior crus, anterior to the tympanic ring (Fig. 2B: “TP2?”), the ectotympanic contribution to the external auditory meatus tube clearly brings a different pattern of bone thickness distribution.

Thus, homologous areas of reduced thickness within the tympanic plate of protocetid indeterminate γ are only found, without ambiguity, in modern cetaceans (Figure 2C-D). From a mechanical standpoint, a thin bony area corresponds to a preferential vibration zone of the tympanic plate and participates to the sound transduction mechanism (Cranford *et al.* 2010: 25).

The location of the thinner areas of our two modern cetacean specimens matches the vibrational patterns highlighted by motion maps retrieved in previous works (odontocetes, [Cranford et al. 2010](#) and [Ary et al. 2016, fig. 7.1](#); mysticetes, [Cranford & Krysl 2015, SI fig. 16-17](#)). Consequently, since the lateral wall of the bulla of UM-KPG-M 73 presents a bone thickness pattern similar to that of modern cetaceans, it is very likely that its tympanic plate was also functional.

Discussion

Morphology and Function of the Tympanic Membrane in UM-KPG-M 73

The tympanic bulla of UM-KPG-M 73 bears a tympanic ring morphologically very similar to that of terrestrial artiodactyls, which suggests the presence of a terrestrial-like tympanic membrane in this protocete (Fig. 1, see also Supplementary Fig. S1; [Mourlam & Orliac 2018](#)). Yet, like other protocetids, it also bears a developed conical process. This bullar structure is traditionally associated to the derived “cetacean type” tympanic membrane, which consists of an elongated tympanic ligament (*e.g.* [Lillie 1910](#); [Fraser & Purves 1960a, b](#); [Fleischer 1973](#); [Lancaster 1990](#); [Luo 1998](#); [Ekdale et al. 2011](#); [Rehorek et al. 2019](#)). The presence of the conical process on protocetids’ tympanic bullae led some authors to conclude that their tympanic membranes were of modern cetacean type, which hindered their aerial sound perception ([Luo & Gingerich 1999](#); [Nummela & Yamato 2018](#)). Nevertheless, this inference is essentially based on the fact that, during ontogeny, the emergence of the tympanic ligament is correlated with that of the conical process along with the degeneration of the tympanic ring (*e.g.* [Hanke 1914](#); [Ridewood 1922](#); [Luo 1998](#)). This suggests that the conical process and the tympanic ring cannot simultaneously be present on a tympanic bulla. Yet, this is the case in UM-KPG-M 73, highlighting a more complex evolutionary history of that part of the auditory region.

Furthermore, in extant neocetes, the location of the attachment area of the lateral end of the tympanic ligament varies and is not always related to the conical process (*e.g.* [Lillie 1910](#); [Hanke 1914](#); [Fraser & Purves 1960b](#)). Therefore, the presence of the conical process among protocetids cannot be reliably used as a proxy to infer the morphology of their tympanic membrane.

The ossicles of UM-KPG-M 73 provide additional information to determine the characteristics of the tympanic membrane in this protocete ([Mourlam & Orliac 2019](#)). Indeed, the morphology of the tympanic membrane and its function are directly related to the morphology and position of the malleus. The malleus of UM-KPG-M 73 bears a conspicuous, short, pointed, manubrium with a long, flat, surface on one side ([Mourlam & Orliac 2019: fig. 1j-k](#)). It suggests that the tympanic membrane was connected to the manubrium on a significant surface, as it is the case for terrestrial mammals ([Møller 2006](#); [Buytaert *et al.* 2011](#)). Besides, the orientation of the protocetid's incudal crura relative to the incudomalleolar articular surface is similar to that of *Pakicetus* ([Thewissen & Hussain 1993](#); [Luo 1998](#)) and implies a slight shift of the incudomalleolar complex when compared to the initial terrestrial position. This suggests that the manubrium of the malleus was close to the plane defined by the tympanic ring, as proposed for *Pakicetus* ([Nummela *et al.* 2004, 2007](#)). This is also consistent with the fact that the rotation of the sigmoid process of UM-KPG-M 73 is similar to that of pakicetids ([Luo 1998](#)) and that its medial edge lies in the plane defined by the tympanic ring. Based on these observations, it seems likely that the tympanic membrane of UM-KPG-M 73 consisted in a weakly stretched cone (Fig. 3). It was probably close to the last hypothetical stage of evolutionary development of the archaeocete middle ear proposed by Lancaster ([1990, fig. 8C](#)), but with a rounder shape and a larger surface of attachment on the malleus. From a functional point of view, compared to the terrestrial configuration, the augmentation of the cone's height increases the efficiency of sound transmission, especially the energy, to the ossicular chain

(Koike *et al.* 2001; Fay *et al.* 2006). The presence of a conical tympanic membrane, therefore, was probably not affecting terrestrial hearing in this semi-aquatic cetacean (contra Luo & Gingerich 1999; Nummela & Yamato 2018).

Morphology of the Fatty Tissue in UM-KPG-M 73

According to our anatomical investigation, the bulla of UM-KPG-M 73 also bears a tympanic plate fully functional for underwater hearing. Among modern cetaceans, the tympanic plate of both odontocetes (*e.g.* Bullock *et al.* 1968; McCormick *et al.* 1970; Cranford *et al.* 2010; Ryabov 2016) and mysticetes (Yamato *et al.* 2012, 2014; Yamato & Pyenson 2015; Nummela & Yamato 2018; Tubelli *et al.* 2018) are associated with fatty tissue. In detail, this fatty tissue is divided in several branches, among which, two connect the tympanic plate: a small and conical dorsal branch and a large ventral branch (Ketten 1994; Cranford *et al.* 2010; Yamato *et al.* 2012). As previously shown by Cranford *et al.* (2010), most of the sound probably reaches the ossicular chain via the small dorsal branch lodged on the medial sulcus of the malleolar ridge (Fig. 2C-D, see also Supplementary Figs. S2 and S4), a restricted area of the tympanic plate composed of extremely thin bone at the vicinity of the gonion of the malleus (see also Yamato *et al.* 2012; Yamato & Pyenson 2015; Nummela & Yamato 2018). Interestingly, as suggested by Yamato and Pyenson (2015) for most archaeocetes, this very thin bony surface, also called the floor of the bony funnel, is present in protocetid whales [*e.g.* *Artiocetus* (GSP-UM 3458) Supplementary Fig. S5 and *Protocetus* (SMNS 11084) pers. obs.] and part of this area is preserved on UM-KPG-M 73 (Fig. 2A: “sct”). This suggests that the fatty tissue surrounding UM-KPG-M 73 bulla likely presented two branches like in modern cetaceans. In the absence of mandibular remains associated to the taxon described here, and due to the broad interspecific variation in the size of the mandibular canal in protocetids [*e.g.* small in *Togocetus* (Gingerich

& Cappetta 2014) and large in *Carolinacetus* (Geisler *et al.* 2005)], no clue is available to determine the anterior extension of the fatty tissue, leaving the question open about underwater sound entrance in the protocetid head [*i.e.* whether sound was collected preferentially via the mandible (*e.g.* Nummela *et al.* 2004, 2007), the gular region (*e.g.* Cranford *et al.* 2008a, b), the lateral fatty channel (*e.g.* Ketten 1994; Yamato *et al.* 2012), and/or any other location (Cranford & Krysl 2018)].

On the size of the underwater sound input area

The middle ear of tetrapods plays an essential role in transmitting the acoustic signal from the soundtope of an animal towards its inner ear, by adjusting the difference of acoustic impedance (Z ; *i.e.* intrinsic resistance of a medium to sound transmission) between these two media (Burda *et al.* 1992; Hemilä *et al.* 1995; Hetherington 2008; Koyabu *et al.* 2017). To match a high acoustic impedance soundtope, such as water ($Z=1500$ kPa s/m), with the fluid filled cochlea ($Z=150$ kPa s/m), the expected role of the middle ear is to decrease the sound pressure and increase the particle velocity (Nummela 2008; Nummela & Thewissen 2008; Hemilä *et al.* 2010; Nummela & Yamato 2018). The sound pressure can be decreased by reducing the size of the sound input area (Hemilä *et al.* 1995; Nummela *et al.* 2007; Nummela & Thewissen 2008; Nummela & Yamato 2018; Mourlam & Orliac 2019). Thus, it is projected that the sound input area of aquatic mammals would be smaller than that of land mammals. However, the area of the tympanic plate as defined by Nummela *et al.* (1999b) is larger than the surface of the tympanic membrane of land mammals, which increase the sound pressure. Interestingly, the floor of the bony funnel, present in protocetids and neocetes, is significantly smaller than the total area of the tympanic plate. The underwater sound input area could therefore be overestimated in cetaceans when this latter measure is considered. Indeed, considering the floor

of the bony funnel as underwater sound input area would be smaller than the sound input area of mammals (the tympanic membrane), *de facto* decreasing sound pressure and allowing impedance matching between external aquatic environment and the fluid filled cochlea. Thus, although this still need to be tested, it may well be that the bony analogue of the tympanic membrane is not the whole tympanic plate and that this designation would rather be limited to the floor of the bony funnel.

Figure 3. Schematic representation of the sound transmission pathways in protocetids (inspired from Hemilä *et al.* 2010). Based on the results of this study, protocetid indeterminate γ (UM-KPG-M 73) were able to hear efficiently in both air and underwater (for more details, see Summary and conclusion). In blue, pathway for sound collected underwater, in green for sound collected in air. Abbreviations: **bf**, bony funnel; **eam**, external auditory meatus; **i**, incus; **in**, involucrum; **m**, malleus; **pe**, petrosal; **s**, stapes; **sk**, skull; **tm**, tympanic membrane; **tp**, tympanic plate; **Z**, acoustic impedance in kPa s/m. Figure made by M.J. Orliac. Illustration of protocetid skull based on reconstruction from R. Mourlam.

Summary and conclusion

The anatomical survey of the lateral wall of the tympanic bulla of the protocetid confirms the presence of two contiguous acoustic portals that are both acoustically functional (see Mourlam

& Orliac 2018, 2019). Thus, this study completes the previous pictures of the sound transmission mechanism in protocetids (see Nummela *et al.* 2004, 2007; Mourlam & Orliac 2019). Indeed, the presence of two distinct acoustic portals on the tympanic bulla implies that sound reaches the middle ear from at least two sound reception apparatuses: i) via the ancestral terrestrial outer ear canal leading the sound to a conical, but no less functional, tympanic membrane (Fig. 3, green pathway) and ii), via a fatty tissue at the vicinity of the middle ear that contacts the functional tympanic plate and especially its bony funnel (Fig. 3: “bf”). However, the shape and extension of this fatty tissue remain mainly unknown, preventing to identify the primary underwater sound entrance in the protocetid head (Fig. 3, blue pathways). This dual sound transmission pathways, converging toward the ossicular chain (Fig. 3), allows to minimize the mismatch encountered from both a lower (air) and a higher (water) acoustic impedance soundtope compared to that of the fluid filled cochlea. Thus, this dual sound reception apparatus is a key element of the sound transmission mechanism in protocetid, allowing them to be in tune in both of their acoustic environments.

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