

## RESEARCH ARTICLE

# The cochlea of the enigmatic pygmy right whale *Caperea marginata* informs mysticete phylogeny

Travis Park<sup>1,2</sup>  | Felix G. Marx<sup>1,2,3</sup> | Erich M. G. Fitzgerald<sup>2,4,5</sup> | Alistair R. Evans<sup>1,2</sup>

<sup>1</sup>School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

<sup>2</sup>Geosciences, Museum Victoria, Melbourne, Victoria, Australia

<sup>3</sup>Directorate of Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

<sup>4</sup>National Museum of Natural History, Smithsonian Institution, Washington, DC

<sup>5</sup>Department of Vertebrate Zoology, Department of Life Sciences, Natural History Museum, London, United Kingdom

## Correspondence

Travis Park, 18 Innovation Walk, Melbourne, Victoria 3800, Australia.  
Email: travis.park@monash.edu

## Abstract

The pygmy right whale, *Caperea marginata*, is the least understood extant baleen whale (Cetacea, Mysticeti). Knowledge on its basic anatomy, ecology, and fossil record is limited, even though its singular position outside both balaenids (right whales) and balaenopteroids (rorquals + grey whales) gives *Caperea* a pivotal role in mysticete evolution. Recent investigations of the cetacean cochlea have provided new insights into sensory capabilities and phylogeny. Here, we extend this advance to *Caperea* by describing, for the first time, the inner ear of this enigmatic species. The cochlea is large and appears to be sensitive to low-frequency sounds, but its hearing limit is relatively high. The presence of a well-developed tympanal recess links *Caperea* with cetotheriids and balaenopteroids, rather than balaenids, contrary to the traditional morphological view of a close *Caperea*-balaenid relationship. Nevertheless, a broader sample of the cetotheriid *Herpetocetus* demonstrates that the presence of a tympanal recess can be variable at the specific and possibly even the intraspecific level.

## KEYWORDS

Cetacea, hearing, Plicogulæ, tympanal recess

## RESEARCH HIGHLIGHTS

We describe the cochlea of the pygmy right whale. The cochlea is large and sensitive to low-frequency sounds. Possession of a tympanal recess links *Caperea* with Plicogulæ (cetotheriids and balaenopteroids). However, this feature may be more variable than previously thought.

## 1 | INTRODUCTION

The pygmy right whale, *Caperea marginata* (Gray, 1846), is the most bizarre and least known of all extant baleen whales. Its basic anatomy and ecology are poorly understood, with limited data on distribution and behaviour (Kemper, 2009, 2014; Kemper, Middleton, & van Ruth, 2012; Ross, Best, & Donnelly, 1975; Sekiguchi, Best, & Kaczmaruk, 1992). The phylogenetic position of *Caperea* is the most contentious problem in mysticete systematics, with morphological analyses traditionally advocating a close relationship with right whales, Balaenidae (Bisconti, 2015; Churchill, Berta, & Deméré, 2012; Steeman, 2007), whereas molecular data routinely place *Caperea* as sister to rorquals and grey whales, Balaenopteroidea (Deméré, McGowen, Berta, & Gatesy, 2008; McGowen, Spaulding, & Gatesy, 2009; Steeman et al.,

2009). A third hypothesis, also consistent with the molecular data, groups *Caperea* with the otherwise extinct family Cetotheriidae (Fordyce & Marx, 2013; Gol'din & Steeman, 2015; Marx & Fordyce, 2016), but remains a matter of ongoing debate among morphologists (Berta, Lanzetti, Ekdale, & Deméré, 2016; Bisconti, 2015; El Adli, Deméré, & Boessenecker, 2014).

Much of the uncertainty about the ecology and evolution of the pygmy right whale stems from a lack of data on its disparate morphology, which combines a right whale-like, arched rostrum with traits more typical of cetotheriids and/or balaenopteroids, such as a narrow, tetradactyl flipper, an elongate scapula, the presence of a squamosal cleft, and an enlarged posterior process of the tympanoperiotic (Kemper, 2009; Marx & Fordyce, 2016). Even more strikingly, *Caperea* stands out for a range of unique features, such as the partial detachment of the anterior process from the remainder of the periotic, as little as one or two lumbar vertebrae, and its armour-like, supernumerary and partially overlapping ribs (Beddard, 1901; Buchholtz, 2011).

New insights might arise from further studies on functional morphology (e.g., swimming style) and sensory capabilities. In particular, considerable progress has been made in recording the anatomy of the cetacean cochlea, which is one of the few sensory structures whose

TABLE 1 Parameters of CT scans of cetacean periotics in this study

Taxon	Specimen number	Scan power (kV)	No of slices	Section thickness ( $\mu\text{m}$ )	Voxel/Pixel size ( $\mu\text{m}$ )
<i>Caperea marginata</i>	NMV C28531	140	1,831	100	236
<i>Herpetocetus cf. transatlanticus</i>	IRSNB V00372	140	1,601	58.77	58.77
<i>Herpetocetus cf. transatlanticus</i>	IRNSB V00373	140	1,601	37.17	37.17
<i>Herpetocetus sp.</i>	IRNSB V00376	140	1,601	37.17	37.17
<i>Herpetocetus sp.</i>	IRNSB V00377	140	1,601	37.17	37.17

kV = kilovolt;  $\mu\text{m}$  = micrometres.

detailed shape can be studied in both extant and extinct species (Ekdale, 2016; Ekdale & Racicot, 2015; Fleischer, 1976; Geisler & Luo, 1996; Luo & Eastman, 1995; Luo & Marsh, 1996; Park, Evans, Gallagher, & Fitzgerald, 2017; Park, Fitzgerald, & Evans, 2016). However, the inner ear anatomy of the pygmy right whale is currently undocumented. Here, we describe, for the first time, the cochlea of *Caperea marginata*, and compare it to that of other modern and fossil mysticetes.

## 2 | MATERIALS AND METHODS

### 2.1 | Specimens examined

We scanned the right cochlea of *Caperea marginata* (Gray, 1846) (NMV C28531), previously figured by Ekdale, Berta, and Demere (2011: figure 11), as well as four isolated and hitherto undescribed periotics of the cetotheriid *Herpetocetus*, one of its putative fossil relatives (Fordyce & Marx, 2013). The specimens were scanned by two of the authors (TP and ARE) and Rob Williams at the Melbourne Brain Centre Imaging Unit. All four specimens clearly represent *Herpetocetus*, based on the presence of (i) a shelf-like, anteriorly projected lateral tuberosity; (ii) a well-developed ridge for the attachment of the tensor tympani on the anterior process; (iii) a medially projecting anteromedial corner of the pars cochlearis; and (iv), in IRSNB V00377, a distally enlarged compound posterior process with a deep facial sulcus bordered by well-developed anterior and posterior ridges (Fordyce & Marx, 2013; Geisler & Luo, 1996; Whitmore & Barnes, 2008) (Supporting Information Figure S1).

Two of the *Herpetocetus* periotics (IRSNB V00372 and V00373) come from the Lee Creek Mine exposure of the Yorktown Formation (Aurora, North Carolina; Early Pliocene; Browning et al., 2009), whereas the remainder (IRSNB V00376, V00377) are from the Kattendijk Formation as exposed in the Deurganckdok of Antwerp, Belgium (Early Pliocene; De Schepper, Head, & Louwye, 2009). The species-level taxonomy of *Herpetocetus* remains problematic, owing to the lack of mature, well-preserved type specimens for most species. Nevertheless, IRSNB V00372 and V00373 come from the same locality and, presumably, horizon as *H. transatlanticus*, and furthermore resemble this species in having a triangular (rather than rounded) lateral tuberosity. We, therefore, here tentatively refer the North American specimens to *H. cf. transatlanticus*. For detailed comparisons, only IRSNB V00372 and

V00377 were segmented and measured. Additional comparative data for other cetotheriid species were taken from Geisler and Luo (1996), Churchill, Martínez Cáceres, de Muizon, Mnieckowski, and Geisler (2016), and Ekdale (2016).

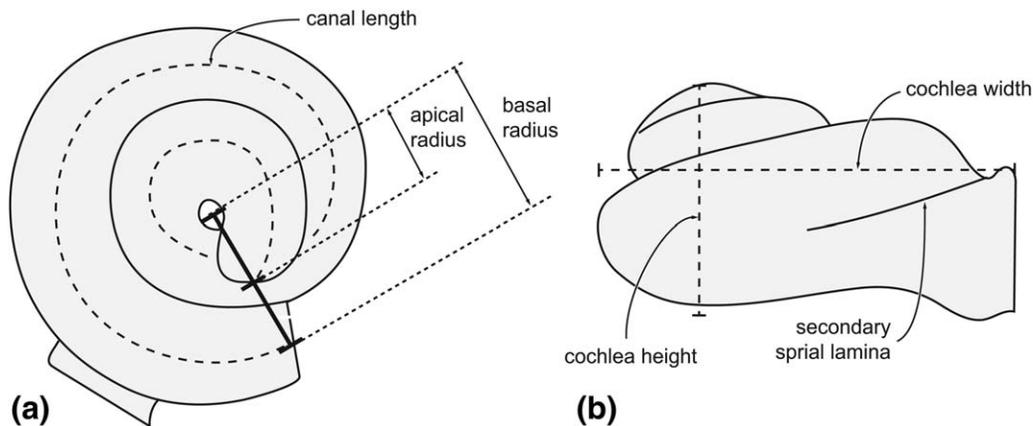
### 2.2 | Scanning technique

The periotics were scanned using either the Zeiss Xradia 520 Versa at the Monash University X-ray Microscopy Facility for Imaging Geomaterials (XMFIG) or, in the case of the extant mysticetes, the Siemens 128-slice PET-CT scanner at the Melbourne Brain Centre Imaging Unit (see Table 1 for scan parameters). The raw CT-data were then compiled into three-dimensional models, and digital endocasts of the cochlea were segmented using the visualisation software package Avizo (Version 9.1.0 Standard; FEI).

### 2.3 | Cochlear measurements

Basic measurements of the internal structures of the cochlea were taken using the Measure, Slice and Spline Probe tools in Avizo, following the protocols of Park et al. (2016). These measurements include: (i) cochlear height; (ii) cochlear width; (iii) number of turns; (iv) cochlear canal length (measured along the midline); (v) extent of the secondary spiral lamina; (vi) cochlear volume; (vii) basal radius; and (viii) apical radius (Figure 1). The extent of the spiral laminae is a proxy for the stiffness of the basilar membrane (Ekdale & Racicot, 2015), which supports the organ of Corti. The extension (%) of the secondary spiral lamina (SSL) was measured by dividing the length of the cochlear canal at the apical-most point of the SSL by the total length of the cochlear canal, then multiplying by 100. Our approach slightly differs from that of Ekdale and Racicot (2015), who instead measured the length of the SSL directly along the outer edge of the cochlea. We amended their method because the outer edge of the cochlea follows an inherently larger spiral than the midline of the cochlear canal (where the length of the canal is measured), leading to an overestimate of relative SSL extension.

From our initial measurements, we calculated several previously established ratios, which together form a quantitative description of cochlear morphology (Ketten & Wartzok, 1990). First, the axial pitch, which is the height of the cochlea divided by the number of turns and, in odontocetes, is negatively proportional to frequency (Ketten & Wartzok, 1990); second, the basal ratio, which is the height of the



**FIGURE 1** Line drawing of a cochlea in (a) vestibular and (b) posterior view, illustrating key measurements. Redrawn from Ekdale (2013), under a CC-BY licence

cochlea divided by its basal diameter, here measured following the method of Ekdale (2013) (Figure 1), and is negatively proportional to frequency (Ketten & Wartzok, 1990); third, the cochlear slope, which is the height of the cochlea divided by the length of the cochlear canal divided by the number of turns (Ketten & Wartzok, 1990); and, finally, the radii ratio, or graded curvature, which is the radius of the cochlea at its base divided by the radius at its apex, and is strongly correlated with low frequency hearing limits (Manoussaki et al., 2008). For the radii ratio, radius measurements were taken using the Slice tool in Avizo, with the apical radius measured to the outer wall of the cochlea (as in Ekdale & Racicot, 2015), rather than the midpoint of the basilar membrane (as in Ketten, Arruda, Cramer, & Yamato, 2016).

Finally, we estimated the low frequency hearing limit for all specimens following Manoussaki et al. (2008):

$$f = 1507 \exp(-0.578[\rho - 1])$$

where  $f$  = low frequency hearing limit at 60 dB re 20  $\mu$ Pa in air and 120 dB re 1  $\mu$ Pa in water, and  $\rho$  = radii ratio value. However, this equation was derived mainly from terrestrial mammals in air, and should therefore be considered tentative until audiograms of mysticetes become available (Ekdale & Racicot, 2015).

In addition to quantitative measurements, we scored the presence of a radial expansion of the scala tympani, or tympanal recess (Fleischer, 1976). An incipient expansion occurs in all cetaceans, but usually disappears by the first quarter of the basal turn. By contrast, the expansion is much more pronounced in several mysticetes, as well as *Physeter* and ziphiids (Ekdale, 2016; Ekdale & Racicot, 2015; Park et al., 2016). To reflect this situation, we therefore here redefine the tympanal recess as a radial inflation of the scala tympani extending beyond the basal quarter turn of the cochlea in vestibular (or ventral) view.

## 2.4 | Ancestral state reconstruction

We investigated the phylogenetic significance of the tympanal recess by reconstructing it along two alternative versions of the phylogeny by Marx and Fordyce (2016: S2 figure), pruned to match the combined

mysticete taxon sample of our study and those of Ekdale and Racicot (2015), Ekdale (2016), and Park et al. (2017). The first version the phylogeny retained the topology of Marx and Fordyce (2016), which groups *Caperea* with cetotheriids, whereas the alternative version placed *Caperea* as sister to balaenids (e.g., Biscconti, 2015; El Adli et al., 2014). Parsimony-based ancestral state reconstructions of the tympanal recess along both phylogenies were then carried out in Mesquite, v. 3.11 (Maddison & Maddison, 2016).

## 2.5 | Institutional abbreviations

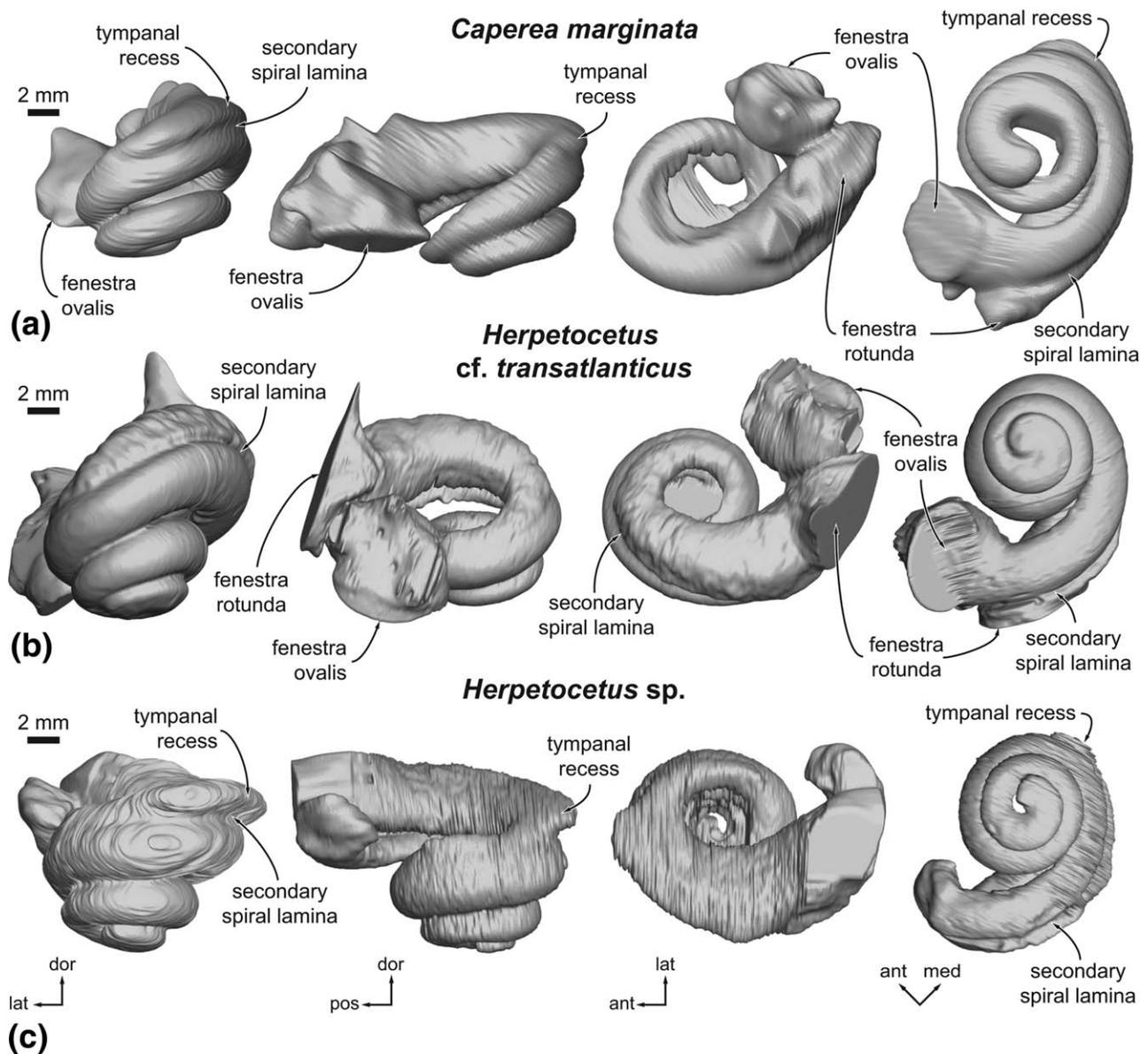
IRSNB = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NMV = Museum Victoria, Melbourne, Australia; USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

## 3 | RESULTS

### 3.1 | *Caperea marginata*, NMV C28531

The cochlea completes approximately two turns (Figure 2a). There is a distinct tympanal recess, with the scala tympani being inflated radially along the first half turn, and the greatest point of inflation being located at the half turn mark. In vestibular view, the first quarter of the basal turn and the apical turn are close to each other, as in other modern mysticetes and fossil cetotheriids. The apical turn is tightly coiled and encloses a small open space, rather than being fully closed like in more primitive taxa (e.g., *Zygorhiza*). Approximately three quarters of the apical turn overlap the section of the cochlear canal immediately below. In cross section, the bone separating the basal turn from the apical turn is thin, as in other modern mysticetes (Figure 3).

The cochlea is large in absolute terms, with a height of 10.41 mm, a width of 18.7 mm, a volume of 874.38 mm<sup>3</sup>, and a cochlear canal length of 60.97 mm (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for approximately half of the basal turn (approximately 37% of the total length of the cochlear canal). The basal ratio of *Caperea* is 0.56, indicating that the cochlea is



**FIGURE 2** Digital endocasts of the cochlea of (a) *Caperea marginata*, NMV C28531, (b) *Herpetocetus cf. transatlanticus*, IRSNB V00372, and (c) *Herpetocetus sp.*, IRSNB V00377. Starting from the left, specimens are shown in anterior, lateral, dorsal, and vestibular views. All specimens are shown as right cochlea with specimens from the left side reversed. Abbreviations: ant = anterior; dor = dorsal; med = medial; pos = posterior

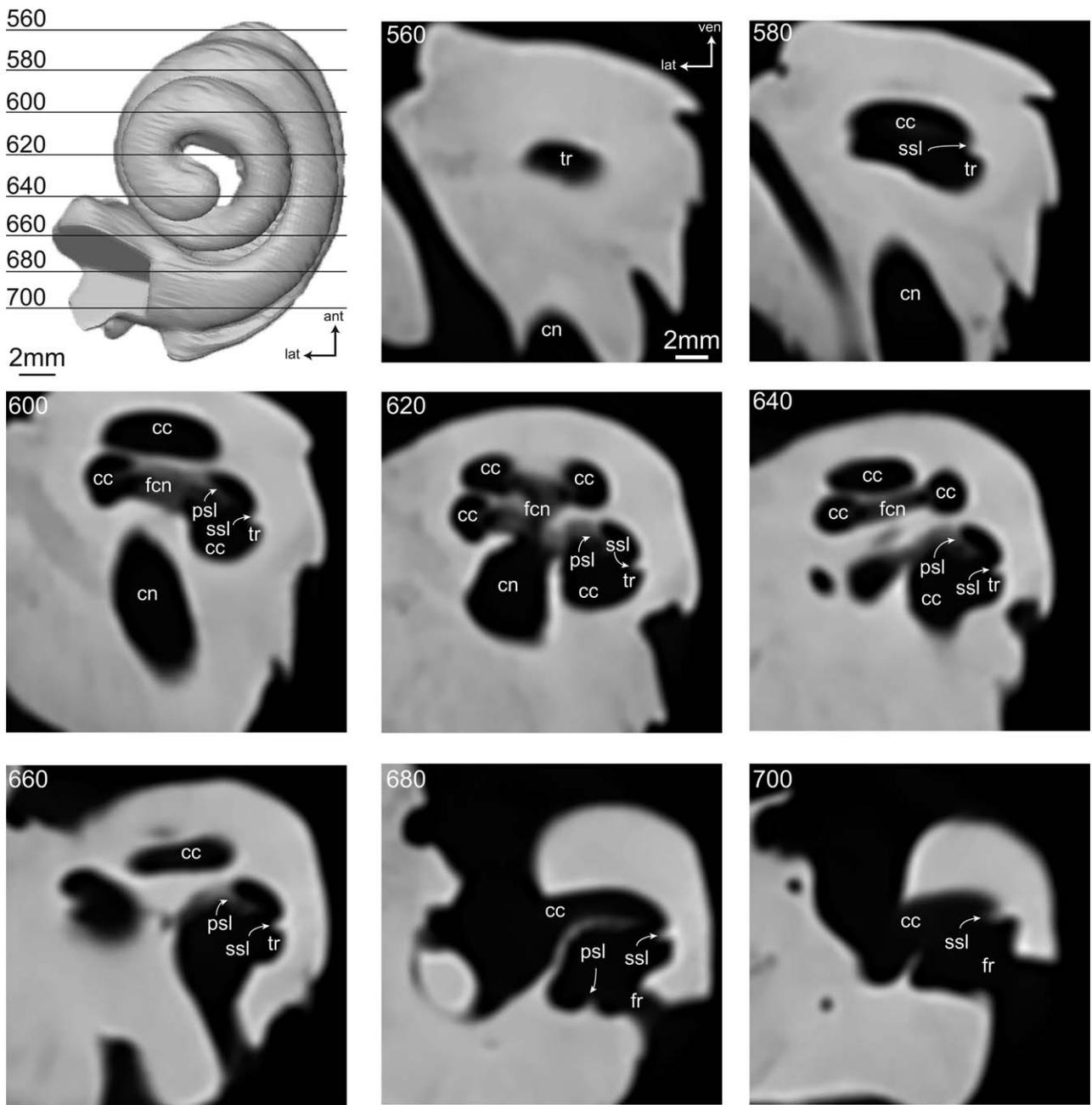
approximately twice as wide as it is high. The axial pitch, cochlear slope and radii ratio values are 5.20, .085, and 6.43, respectively, resulting in an estimated low frequency hearing limit of 65 Hz.

### 3.2 | *Herpetocetus cf. transatlanticus*, IRSNB V00372

The cochlea completes approximately 2.75 turns (Figure 2b), slightly fewer than in the indeterminate *Herpetocetus* specimen (three turns) examined by Geisler and Luo (1996) and *Herpetocetus morrowi* (3.3 turns; Ekdale, 2016). There is a small amount of radial inflation in the first quarter of the basal turn, similar to most cetaceans, but no distinct tympanal recess. The apical turn is tightly coiled and encloses a small

open space. The entire apical turn overlaps the section of the cochlear canal immediately below.

The cochlea has a height of 7.97 mm, a width of 10.88 mm, a volume of 274.99 mm<sup>3</sup>, and a cochlear canal length of 35.08 mm (Table 2). This is smaller than in all extant mysticetes, but comparable to several small-sized fossil species (Ekdale, 2016), and may hence, at least in part, reflect the relatively small body size of cetotheriids. The secondary spiral lamina extends along the radial wall of the cochlear canal for approximately half of the basal turn (approximately 42% of the total length of the cochlear canal). The basal ratio of IRSNB V00372 is 0.73. The axial pitch, cochlear slope and radii ratio values are 2.90, .082, and 6.43, respectively, resulting in an estimated low frequency hearing limit of 65 Hz.



**FIGURE 3** Raw CT-slices through right inner ear of NMV C28531. Slice number is indicated in the top left corner. Abbreviations: ant = anterior; cc = cochlear canal; cn = canal for cranial nerve VIII (auditory nerve); fcn = foramina for the cochlear nerves; fr = fenestra rotunda; lat = lateral; psl = primary spiral lamina; ssl = secondary spiral lamina; tr = tympanal recess; ven = ventral

**TABLE 2** Measurements for the cochleae of *Caperea* and *Herpetocetus*

Taxon	Specimen No	Number of turns	Canal length (mm)	Radii ratio	SSL length (mm)	% extent of SSL	Basal ratio	Axial pitch	Slope	Volume (mm <sup>3</sup> )	Estd. LFL (Hz)
<i>Caperea marginata</i>	NMV C28531	2.00	60.97	6.43	22.74	37.29	0.56	5.21	.085	952.06	65
<i>Herpetocetus cf. transatlanticus</i>	IRNSB V00372	2.75	35.08	6.43	14.75	42.06	0.73	2.90	.082	274.99	65
<i>Herpetocetus sp.</i>	IRNSB V00377	2.50	42.20	6.70	16.69	39.55	0.64	3.27	.077	279.64	56

Estd. LFL = estimated low frequency limit; Hz = Hertz (rounded to the nearest integer); SSL = secondary spiral lamina.

### 3.3 | *Herpetocetus* sp., IRSNB V00377

The cochlea completes approximately 2.5 turns (Figure 2c), slightly fewer than in IRSNB V00372. There is a distinct tympanal recess resembling that of *Caperea*. The apical turn is tightly coiled and encloses a small open space. The entire apical turn overlaps the section of the cochlear canal immediately below. The cochlea has a height of 8.17 mm, a width of 12.45 mm, a volume of 279.64 mm<sup>3</sup>, and a cochlear canal length of 42.20 mm, similar to IRSNB V00372 (Table 2). The secondary spiral lamina extends along the radial wall of the cochlear canal for approximately half of the basal turn (approximately 40% of the total length of the cochlear canal). The basal ratio of IRSNB V00377 is 0.64. The axial pitch, cochlear slope and radii ratio values are 3.27, .077, and 6.70, respectively, resulting in an estimated low frequency hearing limit of 56 Hz.

## 4 | DISCUSSION

### 4.1 | Possible effects of ontogeny

All of the scanned specimens represent juveniles at various stages of development, with NMV C28531 (*Caperea*) representing a 3.30 m long individual with open skull sutures. Nevertheless, its periotic resembles that of adults in having an elongate compound posterior process, a sharply defined promontorial groove, a cranially elongated anterior portion of the pars cochlearis, and a relatively massive bone surface texture (see photos in Ekdale et al., 2011: figure 11). The age of the fossils is harder to gauge. Of the North American specimens, IRSNB V00372 is likely the older given its larger size, better defined attachment for the tensor tympani, and larger and more anteriorly positioned lateral tuberosity. The periotics from Belgium are comparable in size, but IRSNB V00376 appears to be older based on its larger, more anteriorly projected lateral tuberosity and the pronounced hypertrophy of its suprameatal area. In mysticetes, a certain degree of ontogenetic change affects the tympanoperiotic (Bisconti, 2001), and could hence plausibly also influence cochlear shape. Observations on other mammals, however, suggest that the cochlea remains relatively stable after initial ossification, enabling comparisons that are largely independent of age class (Ekdale, 2010; Hoyte, 1961; Jeffery & Spoor, 2004).

### 4.2 | Comparisons of *Caperea* with other taxa

The two turns completed by the cochlea of *Caperea* fall at the lower end of values reported for other mysticetes (Ekdale, 2016; Ekdale & Racicot, 2015; Fleischer, 1976; Geisler & Luo, 1996) (Table 2). The fenestra rotunda is large and separated from the cochlear aqueduct, as in archaeocetes and the majority of modern mysticetes. The extension of the secondary spiral lamina (~37% of cochlear canal length) falls into the range of other living and fossil mysticetes (15–69%), but is considerably shorter than in odontocetes (Ekdale, 2016; Park et al., 2016).

The high degree of overlap of the basal and apical turns also resembles the condition found in archaeocetes and modern mysticetes, but not odontocetes (Ekdale, 2016; Ekdale & Racicot, 2015). In mysti-

cetes, the apical turn is shifted posteriorly towards the fenestra rotunda, whereas in odontocetes and archaeocetes it tends to be located further anteriorly. The tightness of apical coiling in *Caperea* is most similar to that of fossil cetotheriids and balaenids, and contrasts with the much more loosely coiled apices of balaenopterids (Yamada & Yoshizaki, 1959).

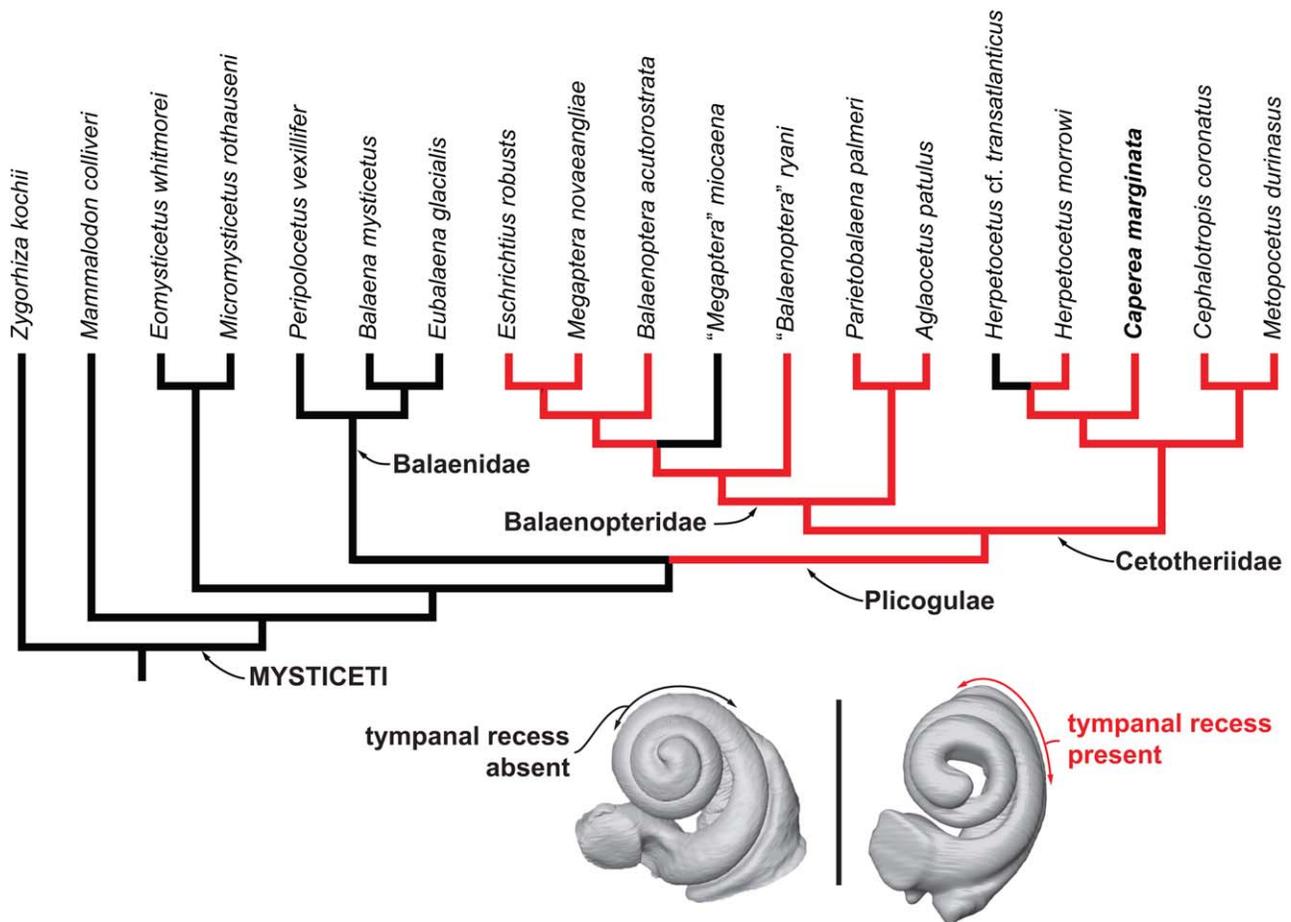
*Caperea* shares with nearly all other members of Plicogulae–balaenopterids and cetotheriids—the presence of a tympanal recess (Churchill et al., 2016: figure 3; Ekdale, 2016; Ekdale & Racicot, 2015). Among cetotheriids, a similar structure is present in one of the *Herpetocetus* specimens examined here (IRSNB V00377), as well as *Herpetocetus morrowi*, *Metopocetus durinasus*, *Piscobalaena nana* and, to a lesser extent, *Cephalotropis coronatus* (Churchill et al., 2016: figure 3; Ekdale, 2016). IRSNB V00377 furthermore shares with *Caperea* and an undescribed fossil balaenopterid (Ekdale & Racicot, 2015: figure 6H) a similar morphology of the tympanal recess, with a distinct distal expansion forming a blunt point (Figure 2). Strikingly, however, a tympanal recess is entirely absent in the other three *Herpetocetus* cochleae examined here (e.g., IRSNB V00372; Figure 2).

A lack of data on total body size (e.g., for *Herpetocetus*) currently prevents comparisons of relative cochlear size. Nevertheless, at 952 mm<sup>3</sup>, *Caperea* has one of the largest reported cochlear volumes of any cetacean, surpassing *Balaena mysticetus* (618 mm<sup>3</sup>), *Eubalaena glacialis* (559 mm<sup>3</sup>), and *Eschrichtius robustus* (783 mm<sup>3</sup>), and exceeded only by an indeterminate species of extinct balaenopterid (974 mm<sup>3</sup>) (Ekdale, 2016: s-table 2). Likewise, its cochlear height and width are within the upper range of values for mysticetes (Ekdale, 2016: s-table 2), notwithstanding the status of *Caperea* as the smallest extant baleen whale (Kemper, 2009).

A basal ratio of 0.56 is comparable with that of balaenopterids, but below that of balaenids and extinct cetotheriids (Table 2) (Ekdale, 2016). The radii ratio of *Caperea* is also comparatively low, with only *Herpetocetus* (Table 2), *Cephalotropis coronatus*, *Cophocetus oregonensis*, and *Balaena mysticetus* reaching similar or lower values (Ekdale, 2016). By contrast, its axial pitch (5.20) and slope (.085) are among the highest of any mysticete studied so far (Table 2) (Ekdale, 2016).

### 4.3 | Hearing abilities of *Caperea*

The cochlea of *Caperea* is unambiguously of the mysticete type or “Type M” of Ketten and Wartzok (1990), and thus specialised for detecting low frequency sounds. Nevertheless, its low radii ratio give *Caperea* one of the highest low frequency hearing limits (65 Hz) of any mysticete, apparently matched or exceeded only by one of the specimens of *Herpetocetus* (IRSNB V00372; 65 Hz), *Balaena mysticetus* (106 Hz), and *Cophocetus oregonensis* (112 Hz) (Table 2) (Ekdale, 2016). Notably, the hearing limit of *Caperea* approximately corresponds to the lowest frequency sound (ca. 60 Hz) previously recorded from a juvenile individual of the same species (Dawbin & Cato, 1992). The functional implications of the large size of the *Caperea* cochlea currently remain unclear. Nevertheless, our findings add to the impression that *Caperea* stands out from other mysticetes not only in terms of its external and skeletal morphology, but also in its sensory capabilities (Bischoff,



**FIGURE 4** Mysticete phylogeny showing the distribution of the tympanal recess. Topology based on Marx and Fordyce (2016: S2 figure). Ancestral states were reconstructed using parsimony. Red and black indicate the presence and absence of a tympanal recess, respectively. The current topology requires three steps: acquisition of a tympanal recess at the base of Plicogulae, followed by losses in *Herpetocetus* cf. *transatlanticus* and "*Megaptera*" *miocaena*. Placing *Caperea* as sister to balaenids, as traditionally advocated by morphological studies (e.g., Bisconti 2015), increases the number of steps to four

Nickle, Cronin, Velasquez, & Fasick, 2012; Meredith, Gatesy, Emerling, York, & Springer, 2013).

#### 4.4 | Phylogenetic implications

Besides its large size, one of the most striking features of the cochlea of *Caperea* is the presence of a well-developed tympanal recess. The same structure occurs in a variety of other mysticetes, including most balaenopteroids and cetotheriids, but is absent in balaenids and stem mysticetes, as well as the archaic balaenopterid "*Megaptera*" *miocaena* and some individuals of *Herpetocetus* (Figure 2) (Churchill et al., 2016; Ekdale, 2016; Ekdale & Racicot, 2015; Park et al., 2017). *Herpetocetus* in particular demonstrates that the tympanal recess can be variable within a single genus and, potentially, even within a single species. Further, much broader sampling of neocete species is required to assess the prevalence of this phenomenon. Nevertheless, the frequent occurrence of the tympanal recess among the more than 20 species of living and fossil mysticete sampled so far appears to follow a pattern, which suggests the existence of a phylogenetic signal irrespective of intraspecific variation.

Specifically, ancestral state reconstruction recovers the presence of a tympanal recess as a synapomorphy of the clade uniting *Caperea* with cetotheriids and balaenopteroids (three steps; Figure 4), as supported by molecular and recent morphological evidence (Marx & Fordyce, 2016; McGowen et al., 2009). By contrast, placing *Caperea* as sister to balaenids, the traditional position suggested by several morphological studies (e.g., Bisconti, 2015; El Adli et al., 2014), increases the number of steps to four (Figure 4). Thus, the tympanal recess offers strong, independent morphological support for the monophyly of Plicogulae.

Apart from suggesting a placement inside Plicogulae, the cochlear anatomy of *Caperea* does not provide specific evidence for or against a close relationship with cetotheriids. While the similar shape of the tympanal recess in *Caperea* and IRSNB V00377 is striking, the cochlea of *Herpetocetus* in general appears more archaic. One exception to this is the large number of turns ( $\geq 2.75$ ) shown by it and certain other cetotheriids, which appears to be a derived feature and may point to specialised hearing abilities (Ekdale, 2016; Geisler & Luo, 1996). These differences in morphology either imply that *Caperea* and balaenopteroids show a certain degree of convergent evolution (e.g., via a

secondary reduction of the number of turns in *Caperea*), or that *Caperea* is not as deeply nested within Cetotheriidae as previously suggested.

## ACKNOWLEDGMENTS

We thank Mark Bosselaers for donating the *Herpetocetus* periotics, and both him and Olivier Lambert for making them available for study. We furthermore thank Karen Roberts, Katie Date, and David Pickering (Museum Victoria) for access to Museum Victoria collections, Will Gates (Monash University X-ray Microscopy Facility for Imaging Geo-materials) and Rob Williams (Melbourne Brain Centre Imaging Unit) for their help in digitizing the specimens, and Rachel Racicot and an anonymous reviewer for their constructive comments on the paper.

## AUTHOR CONTRIBUTIONS

TP, FGM, and EMGF conceived the study. TP and ARE constructed three-dimensional models of the periotic and cochleae. FGM photographed the *Herpetocetus* specimens. ARE and EMGF guided the data analysis. TP and FGM analysed the data. TP, FGM, EMGF, and ARE wrote the manuscript. All authors approved the final draft of the manuscript. All authors agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

## REFERENCES

- Beddard, F. E. (1901). Contribution towards a knowledge of the osteology of the pigmy whale (*Neobalaena marginata*). *Transactions of the Zoological Society of London*, 16, 87–115.
- Berta, A., Lanzetti, A., Ekdale, E. G., & Deméré, T. A. (2016). From teeth to baleen and raptorial to bulk filter feeding in mysticete cetaceans: The role of paleontological, genetic, and geochemical data in feeding evolution and ecology. *Integrative and Comparative Biology*, 56, 1271–1284.
- Bischoff, N., Nickle, B., Cronin, T. W., Velasquez, S., & Fasick, J. I. (2012). Deep-sea and pelagic rod visual pigments identified in the mysticete whales. *Visual Neuroscience*, 29, 95–103.
- Bisconti, M. (2001). Morphology and postnatal growth trajectory of roqual petrosal. *Italian Journal of Zoology*, 68, 87–93.
- Bisconti, M. (2015). Anatomy of a new cetotheriid genus and species from the Miocene of Herentals, Belgium, and the phylogenetic and palaeobiogeographical relationships of Cetotheriidae s.s. (Mammalia, Cetacea, Mysticeti). *Journal of Systematic Palaeontology*, 13, 377–395.
- Browning, J. V., Miller, K. G., McLaughlin, P. P., Edwards, L. E., Kulpecz, A. A., Powars, D. S., ... Wright, J. D. (2009). Integrated sequence stratigraphy of the postimpact sediments from the Eyreville core holes, Chesapeake Bay impact structure inner basin. *Geological Society of America Special Papers*, 458, 775–810.
- Buchholtz, E. A. (2011). Vertebral and rib anatomy in *Caperea marginata*: Implications for evolutionary patterning of the mammalian vertebral column. *Marine Mammal Science*, 27, 382–397.
- Churchill, M., Berta, A., & Deméré, T. A. (2012). The systematics of right whales (Mysticeti: Balaenidae). *Marine Mammal Science*, 28, 497–521.
- Churchill, M., Martínez Cáceres, M., de Muizon, C., Mnieckowski, J., & Geisler, J. H. (2016). The origin of high-frequency hearing in whales. *Current Biology*, 26, 2144–2149.
- Dawbin, W. H., & Cato, D. H. (1992). Sounds of a pygmy right whale (*Caperea marginata*). *Marine Mammal Science*, 8, 213–219.
- De Schepper, S., Head, M. J., & Louwye, S. (2009). Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geological Magazine*, 146, 92–112.
- Deméré, T. A., McGowen, M. R., Berta, A., & Gatesy, J. (2008). Morphological and molecular evidence for a stepwise evolutionary transition from teeth to baleen in mysticete whales. *Systematic Biology*, 57, 15–37.
- Ekdale, E. G. (2010). Ontogenetic variation in the bony labyrinth of *Monodelphis domestica* (Mammalia: Marsupialia) following ossification of the inner ear cavities. *The Anatomical Record*, 293, 1896–1912.
- Ekdale, E. G. (2013). Comparative anatomy of the bony labyrinth (inner ear) of placental mammals. *PLoS One*, 8, e66624.
- Ekdale, E. G. (2016). Morphological variation among the inner ears of extinct and extant baleen whales (Cetacea: Mysticeti). *Journal of Morphology*, 277, 1599–1615.
- Ekdale, E. G., Berta, A., & Demere, T. A. (2011). The comparative osteology of the petrotympanic complex (ear region) of extant baleen whales (Cetacea: Mysticeti). *PLoS One*, 6, e21311.
- Ekdale, E. G., & Racicot, R. A. (2015). Anatomical evidence for low frequency sensitivity in an archaeocete whale: Comparison of the inner ear of *Zygorhiza kochii* with that of crown Mysticeti. *Journal of Anatomy*, 226, 22–39.
- El Adli, J. J., Deméré, T. A., & Boessenecker, R. W. (2014). *Herpetocetus morrowi* (Cetacea: Mysticeti), a new species of diminutive baleen whale from the Upper Pliocene (Piacenzian) of California, USA, with observations on the evolution and relationships of the Cetotheriidae. *Zoological Journal of the Linnean Society London*, 170, 400–466.
- Fleischer, G. (1976). Hearing in extinct cetaceans as determined by cochlear structure. *Journal of Paleontology*, 50, 133–152.
- Fordyce, R. E., & Marx, F. G. (2013). The pygmy right whale *Caperea marginata*: The last of the cetotheres. *Proceedings of the Royal Society B*, 280, 20122645.
- Geisler, J. H., & Luo, Z. (1996). The petrosal and inner ear of *Herpetocetus* sp. (Mammalia; Cetacea) and their implications for the phylogeny and hearing of archaic mysticetes. *Journal of Paleontology*, 70, 1045–1066.
- Gol'din, P., & Steeman, M. E. (2015). From problem taxa to problem solver: A new Miocene family, Tranatocetidae, brings perspective on baleen whale evolution. *PLoS One*, 10, e0135500.
- Hoyte, D. A. N. (1961). The postnatal growth of the ear capsule in the rabbit. *The American Journal of Anatomy*, 108, 1–16.
- Jeffery, N., & Spoor, F. (2004). Prenatal growth and development of the modern human labyrinth. *Journal of Anatomy*, 204, 71–92.
- Kemper, C. M. (2009). Pygmy right whale *Caperea marginata*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 939–941). Burlington: Academic Press.
- Kemper, C. M. (2014). Family Neobalaenidae (pygmy right whale). In D. E. Wilson & R. A. Mittermeier (Eds.), *Handbook of the mammals of the world - volume 4, sea mammals* (pp. 214–220). Barcelona: Lynx Edicions.
- Kemper, C. M., Middleton, J. F., & van Ruth, P. D. (2012). Association between pygmy right whales (*Caperea marginata*) and areas of high marine productivity off Australia and New Zealand. *New Zealand Journal of Zoology*, 40, 102–128.

- Ketten, D. R., Arruda, J., Cramer, S. R., & Yamato, M. (2016). Great ears: Low-frequency sensitivity correlates in land and marine leviathans. *Advances in Experimental Medicine and Biology*, 875, 529–538.
- Ketten, D. R., & Wartzok, D. (1990). Three-dimensional reconstructions of the dolphin ear. *Nato ASI Series—Advanced Science Institutes Series Series A: Life Sciences*, 196, 81–105.
- Luo, Z.-X., & Eastman, E. R. (1995). Petrosal and inner ear of a squalodontoid whale: Implications for evolution of hearing in odontocetes. *Journal of Vertebrate Paleontology*, 15, 431–442.
- Luo, Z. X., & Marsh, K. (1996). Petrosal (periotic) and inner ear of a Pliocene kogiine whale (Kogiinae, Odontoceti): Implications on relationships and hearing evolution of toothed whales. *Journal of Vertebrate Paleontology*, 16, 328–348.
- Maddison, W. P., & Maddison, D. R. (2016). *Mesquite: A modular system for evolutionary analysis*. Version 3.11. Available at: <http://mesquite-project.org>.
- Manoussaki, D., Chadwick, R. S., Ketten, D. R., Arruda, J., Dimitriadis, E. K., & O'Malley, J. T. (2008). The influence of cochlear shape on low-frequency hearing. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 6162–6166.
- Marx, F. G., & Fordyce, R. E. (2016). A link no longer missing: New evidence for the cetotheriid affinities of *Caperea*. *PLoS One*, 11, e0164059.
- McGowen, M. R., Spaulding, M., & Gatesy, J. (2009). Divergence date estimation and a comprehensive molecular tree of extant cetaceans. *Molecular Phylogenetics and Evolution*, 53, 891–906.
- Meredith, R. W., Gatesy, J., Emerling, C. A., York, V. M., & Springer, M. S. (2013). Rod monochromacy and the coevolution of cetacean retinal opsins. *PLOS Genetics*, 9, e1003432.
- Park, T., Evans, A. R., Gallagher, S. J., & Fitzgerald, E. M. G. (2017). Low-frequency hearing preceded the evolution of giant body size and filter feeding in baleen whales. *Proceedings of the Royal Society B*, 284, 20162528.
- Park, T., Fitzgerald, E. M. G., & Evans, A. R. (2016). Ultrasonic hearing and echolocation in the earliest toothed whales. *Biology Letters*, 12, 20160060.
- Ross, G. J. B., Best, P. B., & Donnelly, B. G. (1975). New records of the pygmy right whale (*Caperea marginata*) from South Africa, with comments on distribution, migration, appearance, and behavior. *Journal of the Fisheries Research Board of Canada*, 32, 1005–1017.
- Sekiguchi, K., Best, P. B., & Kaczmaruk, B. Z. (1992). New information on the feeding habits and baleen morphology of the pygmy right whale *Caperea marginata*. *Marine Mammal Science*, 8, 288–293.
- Steehan, M. E. (2007). Cladistic analysis and a revised classification of fossil and recent mysticetes. *Zoological Journal of the Linnean Society London*, 150, 875–894.
- Steehan, M. E., Hebsgaard, M. B., Fordyce, R. E., Ho, S. Y. W., Rabosky, D. L., Nielsen, R., . . . Willerslev, E. (2009). Radiation of extant cetaceans driven by restructuring of the oceans. *Systematic Biology*, 58, 573–585.
- Whitmore, F. C., Jr., & Barnes, L. G. (2008). The *Herpetocetinae*, a new subfamily of extinct baleen whales (Mammalia, Cetacea, Cetotheriidae). *Virginia Museum of Natural History Special Publication*, 14, 141–180.
- Yamada, M., & Yoshizaki, F. (1959). Osseous labyrinth of Cetacea. *The Scientific Reports of the Whales Research Institute Tokyo*, 14, 291–304.

### SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1 Periotics of *Herpetocetus* scanned for this study, all in medial view. (a) *Herpetocetus* cf. *transatlanticus*, IRSNB V00373; (b) *Herpetocetus* cf. *transatlanticus*, IRSNB V00372; (c) *Herpetocetus* sp., IRSNB V00376 (photograph mirrored to facilitate comparisons); (d) *Herpetocetus* sp., IRSNB V00377.

**How to cite this article:** Park T, Marx FG, Fitzgerald EMG, Evans AR. The cochlea of the enigmatic pygmy right whale *Caperea marginata* informs mysticete phylogeny. *Journal of Morphology*. 2017;00:000–000. <https://doi.org/10.1002/jmor.20674>