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

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17 Short title: **Inner ear of *Caperea marginata***

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

25 **ABSTRACT**

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

39 **KEY WORDS**

40 Cetacea; Mysticeti; Plicogulae; hearing; tympanal recess; *Caperea*

41 **INTRODUCTION**

42 The pygmy right whale, *Caperea marginata* (Gray, 1846), is the most bizarre and least
43 known of all extant baleen whales. Its basic anatomy and ecology are poorly understood, with
44 limited data on distribution and behaviour (Kemper, 2009; 2014; Kemper et al., 2012; Ross et
45 al., 1975; Sekiguchi et al., 1992). The phylogenetic position of *Caperea* is the most
46 contentious problem in mysticete systematics, with morphological analyses traditionally
47 advocating a close relationship with right whales (Balaenidae) (Bisconti, 2015; Churchill et
48 al., 2012; Steeman, 2007), whereas molecular data routinely place *Caperea* as sister to

49 rorquals and grey whales (Balaenopteroidea) (Deméré et al., 2008; McGowen et al., 2009;
50 Steeman et al., 2009). A third hypothesis, also consistent with the molecular data, groups
51 *Caperea* with the otherwise extinct family Cetotheriidae (Fordyce and Marx, 2013; Gol'din
52 and Steeman, 2015; Marx and Fordyce, 2016), but remains a matter of ongoing debate among
53 morphologists (Berta et al., 2016; Bisconti, 2015; El Adli et al., 2014).

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

63 New insights might arise from further studies on functional morphology (e.g.
64 swimming style) and sensory capabilities. In particular, considerable progress has been made
65 in recording the anatomy of the cetacean cochlea, which is one of the few sensory structures
66 whose detailed shape can be studied in both extant and extinct species (Ekdale, 2016; Ekdale
67 and Racicot, 2015; Fleischer, 1976; Geisler and Luo, 1996; Luo and Eastman, 1995; Luo and
68 Marsh, 1996; Park et al., 2017; Park et al., 2016). However, the inner ear anatomy of the
69 pygmy right whale is currently undocumented. Here, we describe for the first time, the
70 cochlea of *Caperea marginata* and compare it to that of other modern and fossil mysticetes.

71 **MATERIALS AND METHODS**

72 **Specimens examined**

73 We scanned the right cochlea of *Caperea marginata* (NMV C28531), previously
74 figured by Ekdale et al. (2011: fig. 11), as well as four isolated and hitherto undescribed
75 periotics of the cetotheriid *Herpetocetus*, one of its putative fossil relatives (Fordyce and
76 Marx, 2013). The specimens were scanned by two of the authors (TP and ARE) and Rob
77 Williams at the Melbourne Brain Centre Imaging Unit. All four specimens clearly represent
78 *Herpetocetus* based on the presence of (i) a shelf-like, anteriorly projected lateral tuberosity;
79 (ii) a well-developed ridge for the attachment of the tensor tympani on the anterior process;
80 (iii) a medially projecting anteromedial corner of the pars cochlearis; and (iv), in IRSNB
81 V00377, a distally enlarged compound posterior process with a deep facial sulcus bordered
82 by well-developed anterior and posterior ridges (Fordyce and Marx, 2013; Geisler and Luo,
83 1996; Whitmore and Barnes, 2008) (Fig. S1).

84 Two of the *Herpetocetus* periotics (IRSNB V00372 and V00373) come from the Lee
85 Creek Mine exposure of the Yorktown Formation (Aurora, North Carolina, USA; Early
86 Pliocene) (Browning et al., 2009), whereas the remainder (IRSNB V00376, V00377) are
87 from the Kattendijk Formation as exposed in the Deurganckdok of Antwerp, Belgium (Early
88 Pliocene) (De Schepper et al., 2009). The species-level taxonomy of *Herpetocetus* remains
89 problematic, owing to the lack of mature, well-preserved type specimens for most species.
90 Nevertheless, IRSNB V00372 and V00373 come from the same locality and, presumably,
91 horizon as *H. transatlanticus*, and furthermore resemble this species in having a triangular
92 (rather than rounded) lateral tuberosity. We therefore here tentatively refer the North
93 American specimens to *H. cf. transatlanticus*. For detailed comparisons, only IRSNB
94 V00372 and V00377 were segmented and measured. Additional comparative data for other
95 cetotheriid species were taken from Geisler & Luo (1996), Churchill et al. (2016) and Ekdale
96 (2016).

97 **Scanning technique**

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

104 **Cochlear measurements**

105 Basic measurements of the internal structures of the cochlea were taken using the
106 Measure, Slice and Spline Probe tools in Avizo, following the protocols of Park et al. (2016).
107 These measurements include: (i) cochlear height; (ii) cochlear width; (iii) number of turns;
108 (iv) cochlear canal length (measured along the midline); (v) extent of the secondary spiral
109 lamina; (vi) cochlear volume; (vii) basal radius; and (viii) apical radius (Fig. 1). The extent of
110 the spiral laminae is a proxy for the stiffness of the basilar membrane (Ekdale and Racicot,
111 2015), which supports the organ of Corti. The extension (%) of the secondary spiral lamina
112 (SSL) was measured by dividing the length of the cochlear canal at the apical-most point of
113 the SSL by the total length of the cochlear canal, then multiplying by 100. Our approach
114 slightly differs from that of Ekdale and Racicot (2015), who instead measured the length of
115 the SSL directly along the outer edge of the cochlea. We amended their method because the
116 outer edge of the cochlea follows an inherently larger spiral than the midline of the cochlear
117 canal (where the length of the canal is measured), leading to an overestimate of relative SSL
118 extension.

119 From our initial measurements, we calculated several previously established ratios,
120 which together form a quantitative description of cochlear morphology (Ketten and Wartzok,
121 1990). First, the axial pitch, which is the height of the cochlea divided by the number of turns
122 and, in odontocetes, is negatively proportional to frequency (Ketten and Wartzok, 1990);

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

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

$$135 \quad f = 1507 \exp(-0.578[\rho-1])$$

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

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

146 scala tympani extending beyond the basal quarter turn of the cochlea in vestibular (or ventral)
147 view.

148 **Ancestral state reconstruction**

149 We investigated the phylogenetic significance of the tympanal recess by reconstructing it
150 along two alternative versions of the phylogeny by Marx and Fordyce (2016: S2 fig), pruned
151 to match the combined mysticete taxon sample of our study and those of Ekdale and Racicot
152 (2015), Ekdale (2016), and Park et al. (2017). The first version the phylogeny retained the
153 topology of Marx and Fordyce (2016), which groups *Caperea* with cetotheriids, whereas the
154 alternative version places *Caperea* as sister to balaenids (e.g. Bisconti, 2015; El Adli et al.,
155 2014). Parsimony-based ancestral state reconstructions of the tympanal recess along both
156 phylogenies were then carried out in Mesquite, v. 3.11 (Maddison and Maddison, 2016).

157 **Institutional abbreviations**

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

161 **RESULTS**

162 *Caperea marginata*, NMV C28531: The cochlea completes approximately 2 turns (Fig. 2A).
163 There is a distinct tympanal recess, with the scala tympani being inflated radially along the
164 first half turn and the greatest point of inflation being located at the half turn mark. In
165 vestibular view, the first quarter of the basal turn and the apical turns are close to each other,
166 as in other modern mysticetes and fossil cetotheriids. The apical turn is tightly coiled and
167 encloses a small open space, rather than being fully closed like in more primitive taxa (e.g.
168 *Zygorhiza*). Approximately three quarters of the apical turn overlap the section of the

169 cochlear canal immediately below. In cross section, the bone separating the basal turn from
170 the apical turn is thin, as in other modern mysticetes (Fig. 3).

171 The cochlea is large in absolute terms, with a height of 10.41 mm, a width of 18.7
172 mm, a volume of 874.38 mm³ and a cochlear canal length of 60.97 mm (Table 2). The
173 secondary spiral lamina extends along the radial wall of the cochlear canal for approximately
174 half of the basal turn (approximately 37% of the total length of the cochlear canal). The basal
175 ratio of *Caperea* is 0.56, indicating that the cochlea is approximately twice as wide as it is
176 high. The axial pitch, cochlear slope and radii ratio values are 5.20, 0.085 and 6.43,
177 respectively, resulting in an estimated low frequency hearing limit of 65 Hz.

178 ***Herpetocetus cf. transatlanticus*, IRSNB V00372:** The cochlea completes approximately
179 2.75 turns (Fig. 2B), slightly fewer than in the indeterminate *Herpetocetus* specimen
180 examined by Geisler & Luo (3 turns; 1996) and *Herpetocetus morrowi* (3.3 turns; Ekdale,
181 2016). There is a small amount of radial inflation in the first quarter of the basal turn, similar
182 to most cetaceans, but no distinct tympanal recess. The apical turn is tightly coiled and
183 encloses a small open space. The entire apical turn overlaps the section of the cochlear canal
184 immediately below.

185 The cochlea has a height of 7.97 mm, a width of 10.88 mm, a volume of 274.99 mm³
186 and a cochlear canal length of 35.08 mm (Table 2). This is smaller than in all extant
187 mysticetes, but comparable to several small-sized fossil species (Ekdale, 2016), and may
188 hence – at least in part – reflect the relatively small body size of cetotheriids. The secondary
189 spiral lamina extends along the radial wall of the cochlear canal for approximately half of the
190 basal turn (approximately 42% of the total length of the cochlear canal). The basal ratio of
191 IRSNB V00372 is 0.73. The axial pitch, cochlear slope and radii ratio values are 2.90, 0.082
192 and 6.43, respectively, resulting in an estimated low frequency hearing limit of 65 Hz.

193 *Herpetocetus* sp., IRSNB V00377: The cochlea completes approximately 2.5 turns (Fig. 2C),
194 slightly fewer than in IRSNB V00372. There is a distinct tympanal recess resembling that of
195 *Caperea*. The apical turn is tightly coiled and encloses a small open space. The entire apical
196 turn overlaps the section of the cochlear canal immediately below. The cochlea has a height
197 of 8.17 mm, a width of 12.45 mm, a volume of 279.64 mm³ and a cochlear canal length of
198 42.20 mm, similar to IRNSB V00372 (Table 2). The secondary spiral lamina extends along
199 the radial wall of the cochlear canal for approximately half of the basal turn (approximately
200 40% of the total length of the cochlear canal). The basal ratio of IRNSB V00377 is 0.64. The
201 axial pitch, cochlear slope and radii ratio values are 3.27, 0.077 and 6.70, respectively,
202 resulting in an estimated low frequency hearing limit of 56 Hz.

203 **DISCUSSION**

204 **Possible effects of ontogeny**

205 All of the scanned specimens represent juveniles at various stages of development, with
206 NMV C28531 (*Caperea*) representing a 3.30 m long individual with open skull sutures.
207 Nevertheless, its periotic resembles that of adults in having an elongate compound posterior
208 process, a sharply defined promontorial groove, a cranially elongated anterior portion of the
209 pars cochlearis, and a relatively massive bone surface texture (see photos in Ekdale et al.,
210 2011: fig. 11). The age of the fossils is harder to gauge. Of the North American specimens,
211 IRSNB V00372 is likely the older given its larger size, better defined attachment for the
212 tensor tympani, and larger and more anteriorly positioned lateral tuberosity. The periotics
213 from Belgium are comparable in size, but IRSNB V00376 appears to older based on its
214 larger, more anteriorly projected lateral tuberosity and the pronounced hypertrophy of its
215 suprameatal area. In mysticetes, a certain degree of ontogenetic change affects the
216 tympanoperiotic (Bisconti, 2001), and could hence plausibly also influence cochlear shape.
217 Observations on other mammals, however, suggest that the cochlea remains relatively stable

218 after initial ossification, enabling comparisons that are largely independent of age class
219 (Ekdale, 2010; Hoyte, 1961; Jeffery and Spoor, 2004).

220 **Comparisons of *Caperea* with other taxa**

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

228 The high degree of overlap of the basal and apical turns also resembles the condition
229 found in archaeocetes and modern mysticetes, but not odontocetes (Ekdale, 2016; Ekdale and
230 Racicot, 2015). In mysticetes, the apical turn is shifted posteriorly towards the fenestra
231 rotunda, whereas in odontocetes and archaeocetes it tends to be located further anteriorly.
232 The tightness of apical coiling in *Caperea* is most similar to that of fossil cetotheriids and
233 balaenids, and contrasts with the much more loosely coiled apices of balaenopterids (Yamada
234 and Yoshizaki, 1959).

235 *Caperea* shares with nearly all other members of Plicogulae – balaenopterids and
236 cetotheriids – the presence of a tympanal recess (Churchill et al., 2016: fig. 3; Ekdale, 2016;
237 Ekdale and Racicot, 2015). Among cetotheriids, a similar structure is present in one of the
238 *Herpetocetus* specimens examined here (IRSNB V00377), as well as *Herpetocetus morrowi*,
239 *Metopocetus durinasus*, *Piscobalaena nana* and, to a lesser extent, *Cephalotropis coronatus*
240 (Churchill et al., 2016: fig. 3; Ekdale, 2016). IRSNB V00377 furthermore shares with
241 *Caperea* and an undescribed fossil balaenopterid (Ekdale and Racicot, 2015: fig. 6H) a
242 similar morphology of the tympanal recess, with a distinct distal expansion forming a blunt

243 point (Fig. 2). Strikingly, however, a tympanal recess is entirely absent in the other three
244 *Herpetocetus* cochleae examined here (e.g. IRSNB V00372; Fig. 2).

245 A lack of data on total body size (e.g. for *Herpetocetus*) currently prevents
246 comparisons of relative cochlear size. Nevertheless, at 952 mm³, *Caperea* has one of the
247 largest reported cochlear volumes of any cetacean, surpassing *Balaena mysticetus* (618 mm³),
248 *Eubalaena glacialis* (559 mm³) and *Eschrichtius robustus* (783 mm³), and exceeded only by
249 an indeterminate species of extinct balaenopterid (974 mm³) (Ekdale, 2016: s-table 2).
250 Likewise, its cochlear height and width are within the upper range of values for mysticetes
251 (Ekdale, 2016: s-table 2), notwithstanding the status of *Caperea* as the smallest extant
252 mysticete (Kemper, 2009).

253 A basal ratio of 0.56 is comparable with that of balaenopterids, but below that of
254 balaenids and extinct cetotheriids (Table 2) (Ekdale, 2016). The radii ratio of *Caperea* is also
255 comparatively low, with only *Herpetocetus* (Table 2), *Cephalotropis coronatus*, *Cophocetus*
256 *oregonensis* and *Balaena mysticetus* reaching similar or lower values (Ekdale, 2016). By
257 contrast, its axial pitch (5.20) and slope (0.085) are among the highest of any mysticete
258 studied so far (Table 2) (Ekdale, 2016).

259

260 **Hearing abilities of *Caperea***

261 The cochlea of *Caperea* is unambiguously of the mysticete type or “Type M” of Ketten &
262 Wartzok (1990), and thus specialised for detecting low frequency sounds. Nevertheless, its
263 low radii ratio give *Caperea* one the highest low frequency hearing limits (65 Hz) of any
264 mysticete, apparently matched or exceeded only by one of the specimens of *Herpetocetus*
265 (IRSNB V00372; 65 Hz), *Balaena mysticetus* (106 Hz) and *Cophocetus oregonensis* (112
266 Hz) (Table 2) (Ekdale, 2016). Notably, the hearing limit of *Caperea* approximately
267 corresponds to the lowest frequency sound (ca 60 Hz) previously recorded from a juvenile

268 individual of the same species (Dawbin and Cato, 1992). The functional implications of the
269 large size of the *Caperea* cochlea currently remain unclear. Nevertheless, our findings add to
270 the impression that *Caperea* stands out from other mysticetes not only in terms of its external
271 and skeletal morphology, but also in its sensory capabilities (Bischoff et al., 2012; Meredith
272 et al., 2013).

273

274 **Phylogenetic implications**

275 Besides its large size, one the most striking features of the cochlea of *Caperea* is the presence
276 of a well-developed tympanal recess. The same structure occurs in a variety of other
277 mysticetes, including most balaenopteroids and cetotheriids, but is absent in balaenids and
278 stem mysticetes, as well as the archaic balaenopterid '*Megaptera*' *miocaena* and some
279 individuals of *Herpetocetus* (Fig. 2) (Churchill et al., 2016; Ekdale, 2016; Ekdale and
280 Racicot, 2015; Park et al., 2017). *Herpetocetus* in particular demonstrates that the tympanal
281 recess can be variable with a single genus and, potentially, even within a single species.

282 Further, much broader sampling of neocete species is required to assess the prevalence of this
283 phenomenon. Nevertheless, the frequent occurrence of the tympanal recess among the more
284 than 20 species of living and fossil mysticete sampled so far appears to follow a pattern,
285 which suggests the existence of a phylogenetic signal irrespective of intraspecific variation.

286 Specifically, ancestral state reconstruction recovers the presence of a tympanal recess
287 as a synapomorphy of the clade uniting *Caperea* with cetotheriids and balaenopteroids (3
288 steps; Fig. 4), as supported by molecular and recent morphological evidence (Marx and
289 Fordyce, 2016; McGowen et al., 2009). By contrast, placing *Caperea* as sister to balaenids,
290 the traditional position suggested by several morphological studies (e.g. Bisconti, 2015; El
291 Adli et al., 2014), increases the number of steps to four (Fig. 4). Thus, the tympanic recess
292 offers strong, independent morphological support for the monophyly of Plicogulae.

293 Apart from suggesting a placement inside Plicogulae, the cochlear anatomy of
294 *Caperea* does not provide specific evidence for or against a close relationship with
295 cetotheriids. While the similar shape of the tympanal recess in *Caperea* and IRSNB V00377
296 is striking, the cochlea of *Herpetocetus* in general appears more archaic. One exception to
297 this is the large number of turns (≥ 2.75) shown by it and certain other cetotheriids, which
298 appears to be a derived feature and may point to specialised hearing abilities (Ekdale, 2016;
299 Geisler and Luo, 1996). These differences in morphology either imply that *Caperea* and
300 balaenopteroids show a certain degree of convergent evolution (e.g. via a secondary reduction
301 of the number of turns in *Caperea*), or that *Caperea* is not as deeply nested within
302 Cetotheriidae as previously suggested.

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311 **Author contributions**

312 TP, FGM and EMGF conceived the study. TP and ARE constructed three-dimensional
313 models of the periotic and cochleae. FGM photographed the *Herpetocetus* specimens. ARE
314 and EMGF guided the data analysis. TP and FGM analysed the data. TP, FGM, EMGF and
315 ARE wrote the manuscript. All authors approved the final draft of the manuscript. All authors

316 agree to be accountable for all aspects of the work in ensuring that questions related to the
317 accuracy or integrity of any part of the work are appropriately investigated and resolved.

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440 **Tables**

441 TABLE 1. Parameters of CT scans of cetacean periotics in this study. kV, kilovolt; μm ,
 442 micrometres

Taxon	Specimen number	Scan power (kV)	No of slices	Section thickness (μm)	Voxel/Pixel size (μm)
<i>Caperea marginata</i>	NMV C28531	140	1831	100	236
<i>Herpetocetus</i> cf. <i>transatlanticus</i>	IRNSV 00372	140	1601	58.77	58.77
<i>Herpetocetus</i> cf. <i>transatlanticus</i>	IRNSB V 00373	140	1601	37.17	37.17
<i>Herpetocetus</i> sp.	IRNSB V00376	140	1601	37.17	37.17
<i>Herpetocetus</i> sp.	IRNSB V00377	140	1601	37.17	37.17

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445 TABLE 2. Measurements for the cochleae of *Caperea* and *Herpetocetus*. AP, axial pitch; BR,
 446 basal ratio; CL, canal length; Est. LFL, estimated low frequency limit; Hz, hertz
 447 (rounded to the nearest integer); #T, number of turns; SSL, secondary spiral lamina;
 448 Vol, volume.

Taxon	Specimen No	Number of turns	Canal length (mm)	Radii ratio	SSL length (mm)	% extent of OSL	Basal ratio	Axial pitch	Slope	Volume (mm^3)	Est. LFL (Hz)
<i>Caperea marginata</i>	NMV C28531	2.00	60.97	6.43	22.74	37.29	0.56	5.21	0.085	952.06	65
<i>Herpetocetus</i> cf. <i>transatlanticus</i>	IRNSB V00372	2.75	35.08	6.43	14.75	42.06	0.73	2.90	0.082	274.99	65
<i>Herpetocetus</i> sp.	IRNSB V00377	2.50	42.20	6.70	16.69	39.55	0.64	3.27	0.077	279.64	56

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452 **Figure legends**

453 Fig. 1. Line drawing of a cochlea in (A) vestibular and (B) posterior view, illustrating key
454 measurements. Redrawn from Ekdale (2013), under a CC-BY licence.

455 Fig. 2. Digital endocasts of the cochlea of (A) *Caperea marginata*, NMV C28531, (B)
456 *Herpetocetus cf. transatlanticus*, IRNSB V00372, and (C) *Herpetocetus* sp., IRSNB
457 V00377. Starting from the left, specimens are shown in anterior, lateral, dorsal, and
458 vestibular views. All specimens are shown as right cochlea with specimens from the
459 left side reversed. Abbreviations: ant, anterior; dor, dorsal; med, medial; pos,
460 posterior.

461 Fig. 3. Raw CT slices through right inner ear of NMVC28531. Slice number is indicated in
462 the top left corner. Abbreviations: ant, anterior; cc, cochlear canal; cn, canal for
463 cranial nerve VIII (auditory nerve); fcn, foramina for the cochlear nerves; fr fenestra
464 rotunda; lat, lateral; psl, primary spiral lamina; ssl, secondary spiral lamina; tr,
465 tympanal recess; ven, ventral.

466 Fig. 4. Mysticete phylogeny showing the distribution of the tympanal recess. Topology based
467 on Marx and Fordyce (2016: S2 fig). Ancestral states were reconstructed using
468 parsimony. Red and black indicate the presence and absence of a tympanal recess,
469 respectively. The current topology requires three steps: acquisition of a tympanal
470 recess at the base of Plicogulae, followed by losses in *Herpetocetus cf. transatlanticus*
471 and “*Megaptera*” *miocaena*. Placing *Caperea* as sister to balaenids, as traditionally
472 advocated by morphological studies, increases the number of steps to four.

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