REVIEW

Determinants of echolocation click frequency characteristics in small toothed whales — recent advances from anatomical information

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ABSTRACT

1. The pulse-like clicking sounds made by odontocetes for echolocation (biosonar) can be roughly classified by their frequency characteristics into narrow-band high-frequency (NBHF) clicks with a sharp peak at around 130 kHz, and wide-band (WB) clicks with a moderate peak at 30–100 kHz. Structural differences in the sound-producing organs between NBHF species and WB species have not been

comprehensively discussed, nor has the formation of NBHF and WB clicks.

2. A review of the sound-producing organs, including the latest findings, could lead to a new hypothesis about the sound production mechanisms. In the current review, data on echolocation click characteristics and on the anatomical structure of the sound-producing organs were compared in 33 species (14 NBHF species and 19 WB species).

3. We review interspecific information on the characteristics of click frequencies and data from computed tomography (CT) scans and morphology of the sound-producing organs, accumulated in conventional studies. The morphology of several characteristic structures, such as the melon, the dense connective tissue over the melon (the 'porpoise capsule'), and the vestibular sacs, were compared interspecifically.

4. Interspecific comparisons suggest that the presence or absence of the porpoise capsule is unlikely to affect echolocation frequency. Folded structures in the vestibular sacs, features that have been overlooked until now, are present in most species with NBHF sound production and not in WB species; the vestibular sacs are therefore likely to be important in determining echolocation click frequency characteristics. The acoustical properties of the shape of the melon and vestibular

sacs are important topics for future investigations about the relationship between anatomical structure and sound-producing mechanisms for echolocation clicks.

Keywords: anatomy, CT scan, dolphin, echolocation clicks, Odontoceti (toothed whales), porpoise, vestibular sacs

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INTRODUCTION

Click sounds of extant odontocetes

Odontocetes recognise their surrounding environment using the echoes of high-frequency ultrasonic pulses called clicks. This method of environmental recognition is called echolocation (Au 1993) or biosonar. Clicks for echolocation are often at high frequencies, above 50 kHz, and usually inaudible to humans. The clicks of extant odontocetes can be roughly classified into two groups: narrow-band high-frequency clicks (NBHF clicks) with a sharp peak around 130 kHz (Au et al. 1999), and wide-band clicks (WB clicks) with a moderate peak at 30–100 kHz (Au & Herzing 2003). NBHF clicks (used by NBHF species; Fig. 1a) have relatively long duration (>120μs) with one peak above 100 kHz, and a relatively weak signal. WB clicks (used by WB species; Fig. 1b) are stronger signals of shorter duration (40-70 μs; Au 2002). Focusing on the difference in amplitude, NBHF clicks show a waveform called 'polycyclic', which gradually increases in amplitude for up to five or six wave cycles, and then decays exponentially, while WB clicks show a waveform called 'oligocyclic', which consists of approximately three to five wave cycles in each burst, and has the largest amplitude in the first cycle (Nakamura 1999, Madsen et al. 2004b).

Sound-production mechanisms and click frequency formation

The organs of odontocetes used for sound production and radiation are concentrated in the forehead. In this review, all organs in the forehead composed of soft tissues, such as the melon, air sacs and dense connective tissue, are collectively called the sound-producing organs. The structure of the sound-producing organs was studied even before the existence of echolocation was confirmed. In the 19th Century, Karl-Ernst von Baer demonstrated that the blowhole of *Phocoena phocoena* is a nostril for respiration, which triggered the discovery that dolphins have a unique nasal structure, comprising a blowhole (nasal passage), one or more air sacs, and a nasal plug at the opening of each air sac (Sibson 1848). Norris (1969) discovered that the nasal plugs of dolphins vibrate while they are emitting clicks. This observation led to the idea that the source of the click sounds might be in the vicinity of the nasal plugs.

Cranford et al. (1996) observed the nasal passage of *Phocoena phocoena* using an endoscope, and confirmed that click emissions could be matched to the vibration of lip-like structures named ‘monkey lips’ on the inner wall of the nasal passage. Furthermore, a pair of anterior and posterior small elliptical fat bodies, the dorsal bursae, embedded in the monkey lips, were described (Fig. 2). Thus, Cranford et al. (1996) described the monkey lips/dorsal bursae complex (MLDB complex), and concluded that

it is the sound source of clicks (Cranford et al. 1996, Cranford 2000, Cranford & Amundin 2004). Monkey lips are now referred to as 'phonic lips' (Cranford et al. 1996, Cranford, 2000, Cranford & Amundin, 2004), and have been confirmed to exist in other odontocetes (Aroyan et al. 2000, Au et al. 2006, Cranford et al. 2008). All odontocetes are now understood to produce clicks using the MLDB complex.

Cranford et al. (1996) further revealed the mechanics of air moving through the MLDB complex. High-pressure air, sent from the lungs to the nasal passage, causes the dorsal bursae to vibrate as it passes between the phonic lips. The air rises toward the nasal passage and is stored in the vestibular sacs (the largest air sacs branch from the nasal passage), then passes through the phonic lips and back into the lungs. This makes it possible for odontocetes to produce clicks continuously without opening and closing the blowhole to take in fresh air.

The vibration of the dorsal bursae propagates to the melon, a spindle-shaped mass of fatty tissue covered with dense collagenous connective tissue in the forehead (Fig. 2). The melon is considered to function as an acoustic lens that concentrates sound as a beam (Harper et al. 2008, McKenna et al. 2012). An elliptical surface on the front of the head, where the melon is not covered by fibrous tissue, is called the emitting surface (Fig. 2; Kuroda et al. 2016). Clicks are believed to be emitted from the emitting

surface into the water (Norris & Hervey 1974, Kuroda et al. 2016).

Clarke (2003) and Thornton et al. (2015) introduced that the sound radiation process in the Kogiidae differs from that in *Phocoena phocoena* and other odontocetes . Kogiid whales have phonic lips wrapped in sponge-like fibrous tissue called ‘cushion’, and also have a spermaceti organ in common with the Physeteridae (Rice 1998), but it is curved at right angles and differs in shape from that of the Physeteridae. When a click sound is generated by the phonic lips in the Kogiidae, the cushion catches and reflects the click, diffusing it to the right side of the head. Click sounds are believed to be transmitted from the phonic lips to the core of the spermaceti, to be emitted at the front of the melon into the water.

For all odontocetes, the process of click radiation and the functions of each soft tissue have been deduced based on the available anatomical information. However, the sound-producing organs have additional obscure functions in producing and propagating clicks. While it is possible to infer the mechanical movements of sound-producing organs from their form, it has not been possible to verify the acoustical validity of the presumed sound production and sound-propagating mechanisms. The frequency-determining mechanism that is used to form NBHF and WB clicks has never been investigated acoustically.

118

119 **Evolution of echolocation clicks**

120 Distance attenuation is proportional to the frequency of sound: the higher the frequency,
121 the shorter the propagation distance. Therefore, WB clicks have the advantage of
122 allowing a longer detectable distance than NBHF clicks. However, the range resolution
123 of the acoustic signal used in echolocation is generally improved by using higher
124 frequency clicks (Masters & Harley 2004); therefore, using NBHF clicks allows
125 odontocetes to identify smaller objects.

126 About 20% of the 72 extant species of odontocetes produce NBHF clicks and
127 do not use whistles (Morisaka & Connor 2007); they are relatively small, exist in small
128 groups, and include both river and marine species (Galatius et al. 2019). The NBHF
129 species comprise several different families, including Kogiidae, Phocoenidae and
130 Delphinidae. Only the Delphinidae has both NBHF and WB species. In the genus
131 *Cephalorhynchus*, all four species *Cephalorhynchus hectori*, *Cephalorhynchus*
132 *commersonii*, *Cephalorhynchus heavisidii*, *Cephalorhynchus eutropia* are NBHF
133 (Dawson & Thorpe 1990, Au 1993, Kyhn et al. 2009, Götz et al. 2010, Kyhn et al.
134 2010). In the genus *Lagenorhynchus*, of the six species, only *Lagenorhynchus australis*
135 and *Lagenorhynchus cruciger* are NBHF (Kyhn et al. 2009, 2010).

NBHF clicks are much higher than the maximum frequency that is audible to *Orcinus orca* (Szymanski et al. 1999, Branstetter et al. 2017), a natural predator of most small odontocetes. The 'predator hypothesis' suggests that NBHF clicks evolved as a strategy to escape detection and predation by *Orcinus orca* (Andersen & Amundin 1976, Morisaka & Connor 2007, Miller & Wahlberg, 2013). The alternative 'environmental hypothesis' suggests that NBHF clicks evolved to increase the signal to noise ratio (i.e. the information content) of echoes in the scattered environment of the ocean (Mellen 1952, Madsen et al. 2005, Miller & Wahlberg 2013, Madsen & Surlykke 2014).

Galatius et al. (2019) summarised and reconsidered the two hypotheses using anatomical and paleoclimatological methods, showing that the emergence of NBHF species was much earlier than emergence of the extant *Orcinus orca.* Ocean ambient noise was considered to promote the evolution of NBHF clicks, but was not found to be the primary factor; instead, an extinct predator sharing an ecological niche with extant *Orcinus orca*, such as *Acrophyseter*, may have driven the evolution of NBHF clicks (Galatius et al. 2019).

The frequency-determining process

The structure and mechanism of the differentiation between NBHF and WB clicks is a

154 significant topic from an acoustical, anatomical, and evolutionary point of view. If the
155 turning point of NBHF and WB differentiation can be found in extant odontocetes by
156 comparing the available anatomical information of all available species, the
157 evolutionary process may be revealed one step further.

158 Skull asymmetry was believed to be involved in the production of NBHF clicks,
159 but Galatius and Goodall (2016) and Huggenberger et al. (2017) did not support this
160 hypothesis based on investigation of the skulls of 10 and 12 species, respectively.
161 Although the skulls of odontocetes differ in their morphology, the basic parabolic
162 structure that supports the soft tissue from below is the same for all species. Therefore,
163 soft tissue morphology is likely to be important in the frequency-determining
164 mechanism, as the acoustic properties of clicks may be influenced by the morphology of
165 the soft tissues of the sound-producing organs (Cranford et al. 1996, Aroyan et al. 2000).
166 Interspecific differences in the melon terminal branch (Amundin 1991, Cranford et al.
167 1996, Frainer et al. 2019) and the dense connective tissue that covers the posterior end
168 of the melon observed in Phocoenidae, called the ‘porpoise capsule’ (Huggenberger et
169 al. 2009), might be involved in the click frequency-determining mechanism. In addition,
170 vestibular sacs with many plicae (folds), observed in *Phocoena phocoena*,
171 *Phocoenoides dalli* and *Neophocoena phocaenoides,* are considered to be involved in

172 the generation of NBHF clicks (Curry 1992, Nakamura et al. 1999). However, the soft
173 tissues in the head have been compared morphologically only among NBHF species
174 (Curry 1992, Kuroda et al. 2016, 2018) and in a few NBHF and WB species (McKenna
175 et al. 2012, Arribart et al. 2017). The authors of these morphological studies did not
176 discuss the frequency-determining organs or their acoustical validity.
177
178 **Aim of the current review**
179 To summarise the important morphological information relating to the sound-producing
180 organs in odontocetes, and to stimulate new discussions about the
181 frequency-determining process, it is necessary to compare in detail the morphology of
182 as many NBHF species and WB species as possible. So far, anatomical information
183 about soft tissue morphology has been published separately from the latest information
184 on click frequency characteristics, so our aim is to connect both sources of information
185 and to set new research goals and tasks.
186 In recent years, a research environment that enables extensive morphological
187 comparison and review has been developed. Galatius et al. (2019) provided the latest
188 comprehensive information on the classification and evolution of NBHF and WB
189 species and made new suggestions based on detailed anatomical and

paleoclimatological investigations. The development of open databases such as the Computerised Scanning and Imaging Facility of the Woods Hole Oceanographic Institution (https://csi.whoi.edu/) also makes interspecific comparison of head anatomical structure easier. In addition, various stranded and bycaught odontocete specimens have been collected and included in the review, mainly from the north Pacific Japanese coast (Table 1).

The purpose of this review is to summarise the available morphological information from BNHF and WB species, in order to provide new comparative perspectives on the organs involved in the click frequency-determining mechanism of odontocete echolocation.

METHODS

Morphological descriptions of the sound-producing organs, mainly in the odontocete species summarised by Galatius et al. (2019), were collected, compiled and updated as much as possible with the latest anatomical information on head structure. A particular focus was on anatomical differences in the sound-producing organs between NBHF and WB species. Interspecies comparisons of characteristic structures described in anatomical studies, such as the melon terminal branch, the porpoise capsule and the

208 folded vestibular sac, were performed. We added to the data by including stranded and
209 bycaught specimens (Table 1).
210 We collected data on echolocation clicks (lower peak, higher peak, and central
211 frequency) for 32 species of odontocete in a literature survey. Species were identified as
212 WB or NBHF based on the description in each reference.
213
214

215 **Table 1.** Stranded and bycaught odontocete specimens used in the current comparative
216 study of echolocation click frequency characteristics, examined by computed
217 tomography scan (CT) and dissection (D). All locations are in Japan.

Scientific name	Specimen no.	Sex	Body length (cm)	Status	Date found	Location	Examination
Kogia breviceps	SNH14045	M	245.2	Stranded	26 Aug 2014	Toyokoro	CT, D
Phocoena Phocoena	SNH12009-1	F	129.0	Bycatch	19 Apr 2012	Hakodate	CT, D
Phocoenoides dalli	SNH14026-2	M	219.5	Bycatch	25 Jun 2014	Rausu	CT, D
Neophocoena phocaenoides	EW05784	F	130.2	Stranded	8 Jan 2015	Saijo	CT
Stenella coeruleoalba	NSMTM42137	F	227.3	Stranded	26 Apr 2013	Kasasa	CT, D
Peponocephala electra	EW05720	F	248.6	Stranded	10 Apr 2015	Hokota	CT, D
Grampus griseus	EW05782	M	253.1	Stranded	11 Mar 2015	Ainan	CT
Lagenorhynchus obliquidens	SNH15020	F	167.8	Stranded	19 Jun 2015	Noboribetsu	CT

218

219

220 **RESULTS**

221 The lower peak, higher peak, and central frequencies of NBHF and WB clicks for 32
222 species of odontocete are summarised in Table 2. Anatomical data on the folded
223 structure of the vestibular sacs, the porpoise capsule, the size of the melon's emitting
224 surface, the shape of the melon, and the terminal branches are summarised in Table 3.
225 Stranded and bycaught specimens are included (Table 1).

226

227 **The emitting surface and melon morphology**

228 Three-dimensional computed tomography (CT) images of *Phocoena phocoena*,
229 *Phocoenoides dalli*, *Peponocephala electra*, *Stenella coeruleoalba* and *Kogia breviceps*
230 (Fig. 3) show that the first two species have a relatively wide round emitting surface at
231 the centre of the forehead. Only *Peponocephala electra* has a donut-shaped emitting
232 surface, with a circular area of fibrous tissue at the centre of the emitting surface (Fig. 3).
233 In *Kogia breviceps*, almost all the surface area at the front of the cylindrical head is an
234 emitting surface. *Stenella coeruleoalba* has only a small, radiating elliptical surface in
235 front of the blowhole, close to the top of the head; its anatomy is quite different from the
236 anatomy of the other four species.

237 *Lagenorhynchus* includes both WB and NBHF species. The WB species

238 *Lagenorhynchus obliquidens* and *Lagenorhynchus albirostris* have a characteristic
239 peanut-shaped melon with a larger front part and smaller rear part. However, it was not
240 possible to compare the sound-producing organs in these WB *Lagenorhynchus* with
241 NBHF congeners, because anatomical information is lacking on the NBHF species
242 *Lagenorhynchus australis* and *Lagenorhynchus cruciger*. Inferring the mechanism by
243 which this characteristic melon shape can affect click frequency determination suggests
244 the possibility of resonance between the front part and the rear part. If the lengths of the
245 front and rear parts of the melon were measured, the resonance frequency of the two
246 parts could be calculated. Assuming that the length of the front and rear parts differs
247 between the NBHF and WB *Lagenorhynchus*, the resulting difference in resonance
248 frequency might influence the frequency and bandwidth of their clicks. To investigate
249 these ideas, it is necessary to measure the acoustic impedance of the peanut-shaped
250 melon and the muscle tissue that covers and surrounds the melon. This would clarify the
251 propagation process of clicks in and between the two parts of the melon, and enable the
252 resonance frequency of the melon to be calculated.

253 *Pontoporia blainvillei* is the only NBHF species that has a melon with two
254 terminal branches (Table 3); this feature also occurs in WB species but is not confined
255 to them, as has been stated by other authors (Madsen et al. 2010, McKenna et al., 2012).

256 The presence of terminal branches in the melon seems unlikely to determine click
257 characteristics.
258
259 **The porpoise capsule**
260 Fig. 4 shows two-dimensional CT images in a coronal plane around the end of the
261 melon in five species: *Phocoena phocoena*, *Phocoenoides dalli*, *Stenella coeruleoalba*,
262 *Peponocephala electra*, and *Kogia breviceps*. The porpoise capsule is clearly visible
263 above the melon in *Phocoena phocoena* and *Phocoenoides dalli*. This structure is not
264 seen in other families (e.g., Delphinidae, Kogiidae; Clarke 2003, Thornton et al., 2015,
265 Dawson et al. 2017; Fig. 4), and no authors have reported the porpoise capsule outside
266 of the family Phocoenidae (Table 3). It is difficult to conclude whether or not the
267 porpoise capsule is involved in determining click characteristics.
268
269 **The cushion and the vestibular sacs**
270 Although members of the Kogiidae are NBHF species, the structure of their
271 sound-producing organs and the acoustic pathway of their clicks are quite different from
272 that of many other NBHF species. The Kogiidae have reticulated collagenous
273 connective tissue forming a cushion around the phonic lips (Clarke 2003, Thornton et al.

2015). The cushion is not found in *Physeter macrocephalus* (Møhl 2001), a WB species closely related to the Kogiidae. Hence, this structure might affect the sound-producing process and the frequency of the clicks.

Phocoena phocoena, *Phocoenoides dalli*, and *Neophocoena phocaenoides* (Phocoenidae) have thick and hypertrophied vestibular sacs with many folds on the ventral side (Curry 1992, Huggenberger et al. 2009, Kuroda et al., 2016, Kuroda et al. 2018; Table 3, Fig. 5). This specific fold-like structure could influence the generation of clicks, but the mechanism has not yet been analysed, and acoustic verification has not been performed. The shape of the vestibular sacs has not been described in other *Phocoena* species, such as *Phocoena sinus*, *Phocoena spinipinnis*, and *Phocoena dioptrica,* but folded vestibular sacs have been reported in NBHF species in other families. *Pontoporia blainvillei* has highly asymmetrical vestibular sacs (Huggenberger et al. 2010, Frainer et al. 2015); the right vestibular sac occupies about half the volume of the head, and the interior of the vestibular capsule has a structure resembling a wall partition. This species is believed to use only the right dorsal bursae for generating clicks; its asymmetrical vestibular sacs might influence the frequency characteristics of the clicks.

Cephalorhinchus hectori and *Cephalorhinchus commersonii*, both NBHF

292 Delphinid species, do not have any folded structure in their vestibular sacs; their overall
293 head structure resembles that of other delphinids (Dawson et al. 2017). However, no
294 information on head anatomy is available for the NBHF *Lagenorhynchus* spp., namely
295 *Lagenorhynchus australis* and *Lagenorhynchus cruciger*. The WB species
296 *Lagenorhynchus obliquidens* has small, thin vestibular sacs (Hashimoto et al. 2015),
297 like most delphinids. At this stage, based on the available literature, it is not possible to
298 discuss commonalities in the sound-producing organs of all NBHF and WB species.
299

300 **Table 2.** Echolocation click frequencies of odontocete species included in the review, divided into narrow-band high-frequency (NBHF)
301 species and wide-band (WB) species by the authors ('Reference'). LPF = lower peak frequency, HPF = higher peak frequency, CF =
302 central frequency.

Scientific name	Common name	Click frequency (kHz)			Clicks	Reference
		LPF	HPF	CF		
Kogia breviceps	pygmy sperm whale		130	129	NBHF	Madsen et al. (2005)
Kogia sima	dwarf sperm whale		126		NBHF	Merkens et al. (2016)
Pontoporia blainvillei	Franciscana dolphin		130		NBHF	Von Fersen et al. (2000)
Phocoena phocoena	harbour porpoise		123.9		NBHF	Au et al. (1999)
Phocoena sinus	Vaquita		132.9		NBHF	Silber (1991)
Phocoena spinipinnis	Burmeister's porpoise		120		NBHF	Reyes Reyes et al. (2018)
Phocoenoides dalli	Dall's porpoise		133		NBHF	Kamminga et al. (1996)
Neophocoena phocaenoides	finless porpoise		125		NBHF	Kamminga et al. (1986)
Lagenorhynchus australis	Peale's dolphin		126	129	NBHF	Kyhn et al. (2010)
Lagenorhynchus cruciger	hourglass dolphin		125		NBHF	Kyhn et al. (2009)
Cephalorhinchus hectori	Hector's dolphin		125		NBHF	Dawson & Thorpe (1990)
Cephalorhinchus commersonii	Commerson's dolphin		125.4		NBHF	Nakamura (1999)
Cephalorhinchus heavisidii	Heaviside's dolphin		122-130		NBHF	Morisaka et al. (2011)
Cephalorhinchus eutropia	Chilean Dolphin		126		NBHF	Götz et al. (2010)
Physeter macrocephalus	sperm whale			15	WB	Madsen et al. (2002)

Ziphius cavirostris	Cuvier's beaked whale		40	42	WB	Zimmer et al. (2005)
Platanista gangatica	Ganges river dolphin		58.8	61.4	WB	Jensen et al. (2013)
Lipotes vexilifer	Chinese river dolphin	71	112.1	78.9	WB	Nakamura (1999)
Inia geoffrensis	Amazon river dolphin			94.4	WB	Yamamoto et al. (2015)
Monodon monoceros	narwhal			53	WB	Miller et al. (1995)
Orcaella brevirostris	Irrawaddy dolphin			94.6	WB	Jensen et al. (2013)
Orcinus orca	killer whale	20-30	40-60	50	WB	Au et al. (2004)
Pseudorca crassidens	false killer whale	45.7	110	62.3	WB	Au et al. (1995)
Fellesa attenuate	pygmy killer whale	40	100	70-85	WB	Madsen et al. (2004a)
Peponocephala electra	melon-headed whale			21.7	WB	Baumann-Pickering et al. (2015)
Grampus griseus	Risso's dolphin	30-50	80-100	47.9	WB	Philips et al. (2003)
Sotalia fluviatilis	Tucuxi			99.2	WB	Yamamoto et al. (2015)
Stenella attenuata	pantropical spotted dolphin	40-60	120-140	69.4	WB	Schotten et al. (2004)
Stenella coeruleoalba	striped dolphin	no numerical information			WB	Rankin et al. (2017)
Tursiops truncates	bottlenose dolphin	67.3	114.3	94.1	WB	Nakamura (1999)
Delphinus delphis	common dolphin	81.4	114.8	112.1	WB	Nakamura (1999)
Lagenorhynchus obliquidens	Pacific white-sided dolphin	22	39		WB	Soldevilla et al. (2008)
Lagenorhynchus albirostris	white-beaked dolphin	115	250	82	WB	Rasmussen & Miller (2002)

303

304

305 **Table 3.** Structural data on the sound-producing organs of odontocete species included in the review, divided into narrow-band
306 high-frequency (NBHF) species and wide-band (WB) species. The species are the same as in Table 2, except that *Stenella coeruleoalba*
307 was added. 'Anatomical structure' records the presence (Y = yes; N = no) of the folded structure in the vestibular sacs (Fold) and of the
308 the porpoise capsule (PC). For the melon, the emitting surface (ES) was described as large = L or small = S, and NB = no branch, TB =
309 two branches, P = peanut-shaped melon. In 'Reference', CSI indicates the Computerised Scanning and Imaging Facility of the Woods
310 Hole Oceanographic Institution (https://csi.whoi.edu/), and stranded and bycaught specimens are indicated by the specimen number
311 (Table 1).

Scientific name	Clicks	Anatomical structure				Reference
		Fold	PC	ES	Melon	
Kogia breviceps	NBHF	Y		L	NB	SNH14045
Kogia sima	NBHF	Y		L	NB	Thornton et al. (2015)
Pontoporia blainvillei	NBHF	Y		L	TB	Frainer et al. (2019)
Phocoena phocoena	NBHF	Y	Y	L	NB	SNH12009-1
Phocoena sinus	NBHF					No anatomical info
Phocoena spinipinnis	NBHF					No anatomical info
Phocoenoides dalli	NBHF	Y	Y	L	NB	SNH14026-2

Neophocoena phocaenoides	NBHF	Y	Y	L	NB	EW05784
Lagenorhynchus australis	NBHF					No anatomical info
Lagenorhynchus cruciger	NBHF					No anatomical info
Cephalorhinchus hectori	NBHF	N	N			Galatius & Goodall (2016)
Cephalorhinchus commersonii	NBHF	N	N			Huggenberger et al. (2017)
Cephalorhinchus heavisidii	NBHF		N			Galatius & Goodall (2016)
Cephalorhinchus eutropia	NBHF		N			Galatius & Goodall (2016)
Physeter macrocephalus	WB	N	N			Huggenberger et al. (2016)
Ziphius cavirostris	WB	N	N		TB	Cranford et al. (2008)
Platanista gangatica	WB	N				Purves & Pilleri (1973)
Lipotes vexilifer	WB	N				Zhou (2009)
Inia geoffrensis	WB	N				Huggenberger et al. (2017)
Monodon monoceros	WB	N				Nweeia et al. (2012)
Orcaella brevirostris	WB	N	N			Stacey & Arnold (1999)
Orcinus orca	WB	N	N			Cozzi et al. (2017)
Pseudorca crassidens	WB	N	N		TB	Cozzi et al. (2017), CSI
Fellesa attenuate	WB	N	N			Huggenberger et al. (2017)
Peponocephala electra	WB	N	N	L	TB	EW05720
Grampus griseus	WB	N	N	L	TB	EW05782
Sotalia fluviatilis	WB	N	N			Fettuccia et al. (2009)
Stenella attenuata	WB	N	N			Huggenberger et al. (2017)
Stenella coeruleoalba	WB	N	N	L	TB	NSMTM42137
Tursiops truncates	WB	N	N	S	TB	Huggenberger et al. (2017), CSI

Delphinus delphis	WB	N	N		TB	Huggenberger et al. (2017)
Lagenorhynchus obliquidens	WB	N	N	S	P	SNH15020
Lagenorhynchus albirostris	WB	N	N		P	Galatius & Goodall (2016)

DISCUSSION

The number of fundamental studies of the head anatomy of odontocetes is still not enough, but has been increasing steadily. Our review of the available information suggests that folded structures in the vestibular sacs and morphological differences in the melon may determine click frequency characteristics in odontocetes.

The presence or absence of a porpoise capsule was not considered to contribute to click frequency characteristics, because it is present only in Phocoenidae. Morphological characteristics of the melon, including the number of terminal branches and the size of the emitting surface, may be involved in click frequency determination. Both NBHF and WB species have both large and small emitting surfaces. It is difficult to compare melon terminal branch morphology and the size of the emitting surface, due to potential differences in the appearance of the photographs and the settings of the CT scanner in each study. For this reason, we cannot rule out melon morphology or size of emitting surface as a factor in click frequency determination.

Folding in the vestibular sacs is found in the Phocoenidae (Curry 1992, Kuroda et al. 2016, 2018), but not confirmed in other families. The ventral side of the vestibular sac, the folded side, is located just above the musculature tissue between the dorsal bursae to the melon (Fig. 2). This indicates that the folded vestibular sac might be just

330 on the acoustic pathway. However, the cushion found in the Kogiidae (Clarke 2003,
331 Thornton et al., 2015) had numerous deep cuts just on the side facing the phonic lips. It
332 is possible that these folds or cuts are somehow responsible for narrowing the sound.
333 Perhaps, these folds or cuts could control or assist to change WB clicks into NBHF.
334
335 **Conclusions and future research directions**
336 It is still difficult to narrow down the physical structures involved in determining click
337 frequency characteristics, but this review could have a guiding role, allowing future
338 researchers to accumulate anatomical and acoustic information more efficiently.
339 Acoustical investigations of how NBHF and WB clicks are produced, alongside a
340 morphological focus on the folded structure of the vestibular sacs, would be worthwhile.
341 Research is also needed on the physical properties of the tissues of the melon's terminal
342 branch. The ideal method would be to measure physical properties such as the acoustic
343 impedance at the end of the melon, and define the branch more quantitatively.
344 Verification of the presence of the folded structure in vestibular sacs should be
345 conducted, as the folds may be directly involved in the production of NBHF clicks.
346 Identification of which species do not have folded vestibular sacs is equally required.
347 Specifically, three-dimensional CT data or visual reports of macroscopic dissection of

348 *Cephalorhynchus* species (*Cephalorhynchus hectori*, *Cephalorhynchus commersonii*,
349 *Cephalorhynchus eutropia* and *Cephalorhynchus heavisidii*) and of the NBHF species
350 of *Lagenorhynchus* (*Lagenorhynchus australis* and *Lagenorhynchus cruciger*) are
351 strongly desired, since filling those gaps would allow a complete investigation of the
352 frequency-determining process. For *Cephalorhynchus* dolphins, the process of sound
353 production cannot be proposed, because information on the anatomical structure of the
354 sound-producing organs is lacking. The lack of information on head anatomy, especially
355 in several rare species, makes it difficult for researchers to narrow down the structures
356 involved in frequency determination. For example, information on the anatomy of three
357 rare Phocoenidae (*Phocoena sinus*, *Phocoena spinipinnis*, and *Phocoena dioptrica*)
358 might confirm that the porpoise capsule is found only in phocoenids. To understand the
359 morphological commonalities and differences between species, three-dimensional CT
360 data and acoustic from more species is needed.
361
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373

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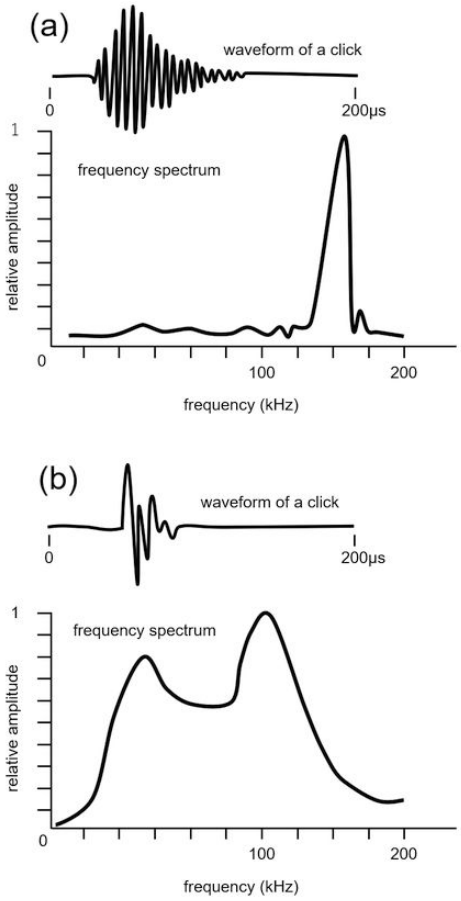
596

597

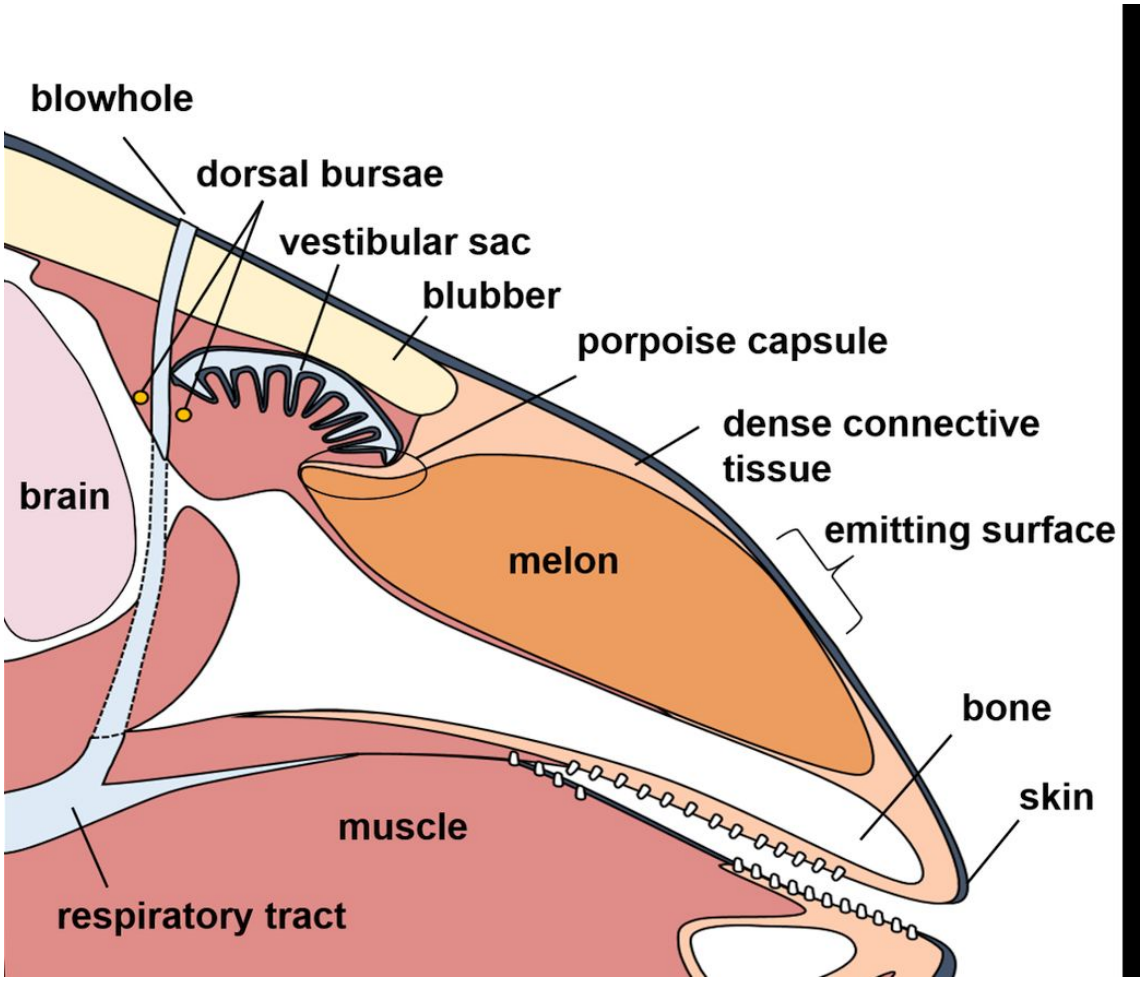
598 **Figures**



599

600 **Fig. 1.** Representative echolocation clicks of odontocetes, shown as waveforms and
601 frequency spectra: (a) a narrow-band high-frequency (NBHF) species *Phocoena*
602 *phocoena*, redrawn from (1993), and (b) a wide-band (WB) species *Stenella frontalis*,
603 redrawn from Au and Herzing (2003). NBHF clicks are longer in duration (> 120 µs)
604 and have a sharper frequency peak at >100 kHz; WB clicks are shorter (40-70 µs) and
605 have a moderate frequency peak at 30-100 kHz.

606



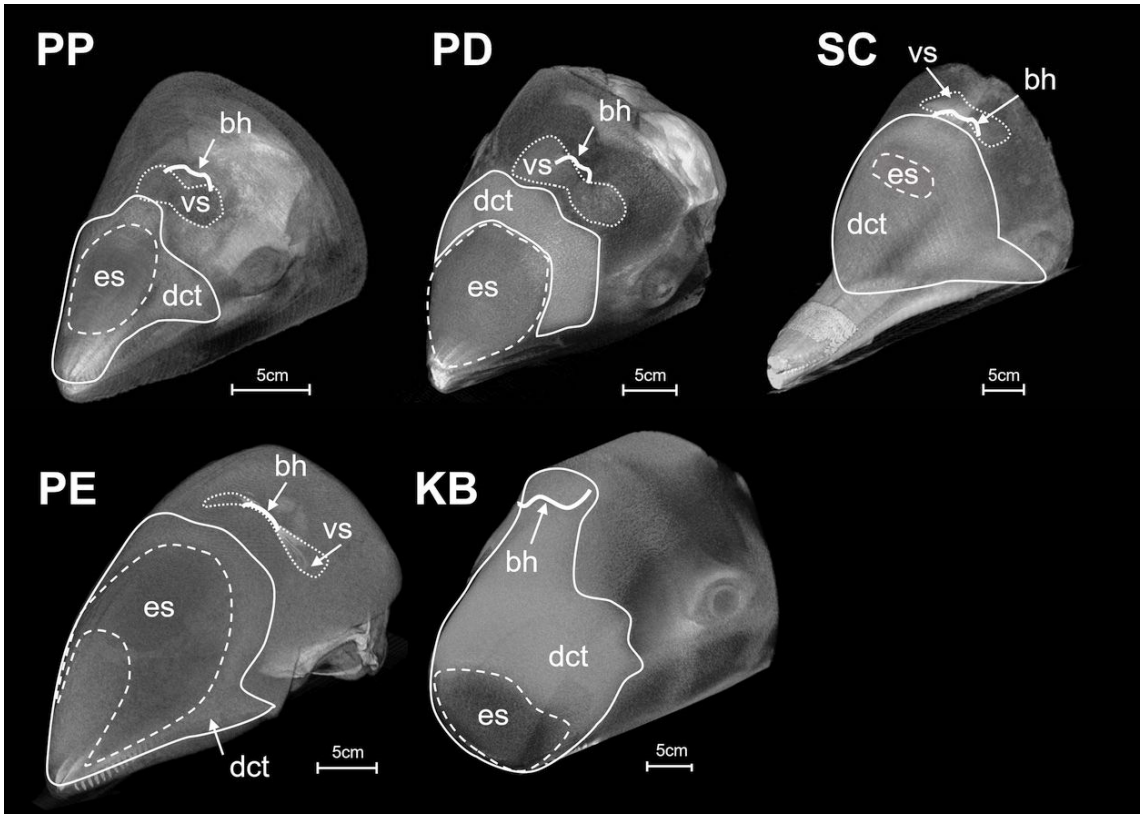
607

608 **Fig. 2.** Sagittal view of the head of *Phocoena phocoena*, showing the tissues; some of

609 the soft tissues are involved in the production of echolocation clicks. The dense

610 connective tissue above the melon is the 'porpoise capsule'.

611



612

613 **Fig. 3.** Reconstructed three-dimensional images of five species: *Phocoena phocoena*

614 (PP), *Phocoenoides dalli* (PD), *Stenella coeruleoalba* (SC), *Peponocephala electra* (PE)

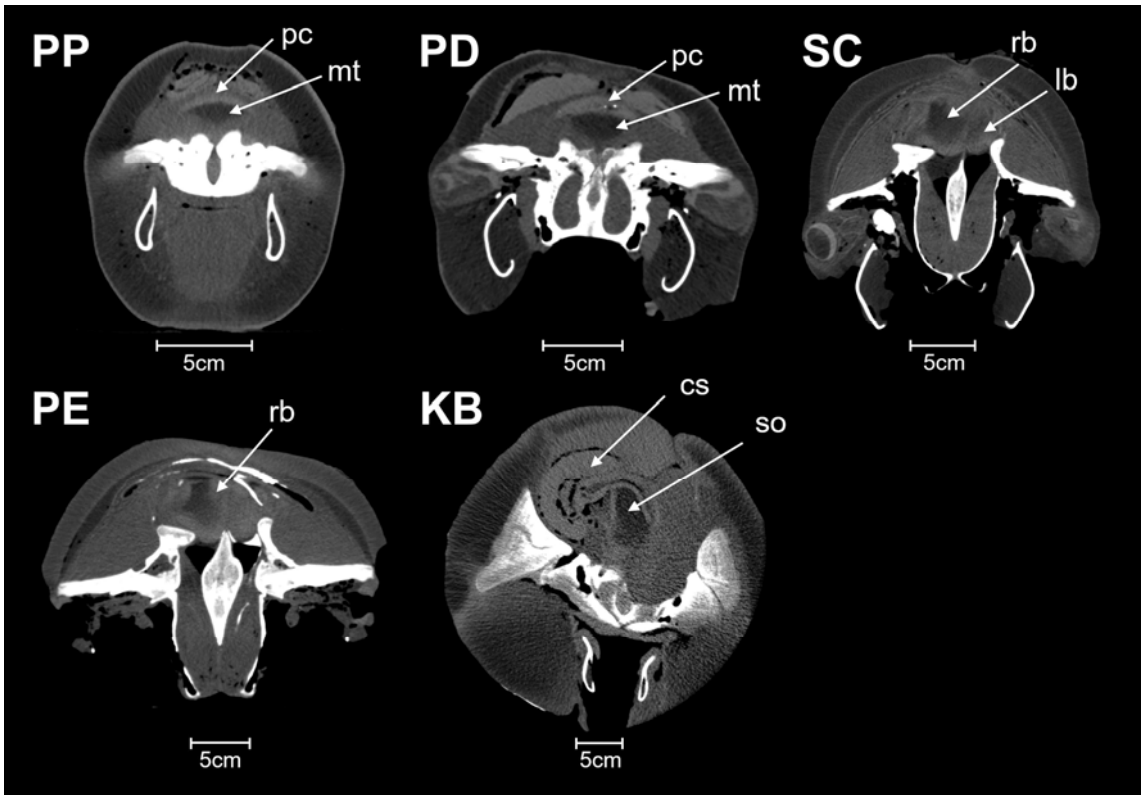
615 and *Kogia breviceps* (KB; see Table 1 for the list of specimens). In each species, the

616 area where dense connective tissue is particularly concentrated is surrounded by a white

617 line. A broken line marks the emitting surface (es), and a dotted line marks the

618 vestibular sacs (vs). Blowhole is indicated by broad line and an arrow (bh).

619



620

621 **Fig. 4.** Coronal CT scans for five species *Phocoena phocoena* (PP), *Phocoenoides dalli*

622 (PD), *Stenella coeruleoalba* (SC), *Peponocephala electra* (PE) and *Kogia breviceps*

623 (KB; see Table 1 for the list of specimens), with arrows indicating the melon terminal

624 (mt), porpoise capsule (pc), right branch of melon (rb), left branch of melon (lb),

625 cushion (cs), and spermaceti organ (so). Melon terminal branch of *Peponocephala*

626 *electra* in this figure could see only right one because of the positioning of cut, they

627 have both branches in ordinary.

628

Fig. 5. Sagittal view of the left vestibular sac of a *Phocoena phocoena* fixed in 10% formalin. R = rostral; C = caudal.