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A Review

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The evolutional pathway of communication sounds (i.e., whistles) in odontocetes is reviewed using recent acoustic and phylogenetic studies. The common ancestor of Ziphiidae, Inioidea, and Delphinoidea acquired the ability to whistle in the early Oligocene. Subsequently, Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus* lost the ability to whistle and evolved narrow-band high-frequency (NBHF) clicks. I hypothesize that sexual selection based on acoustic signaling contributed to the evolution of whistle. However, group size cannot be excluded as the reason for whistle emergence. The event of whistle loss and replacement with NBHF clicks occurred on three independent occasions after killer whale divergence, through the reconstruction of sound-producing organs. Species with whistle loss may use alternative methods to compensate for whistle information, such as tactile communication. Further research on acoustic communication by Ziphiidae, Inioidea, Monodontidae, and the genus *Cephalorhynchus* is essential to clarify the evolutionary pathway of odontocete whistles.

Researchers have paid less attention to the evolution of communication sounds in odontocetes, or toothed whales, compared with that in songbirds (e.g., Kroodsma & Miller, 1996), anurans, and insects (e.g., Gerhardt & Huber, 2002). This is due to the paucity of detailed studies on the acoustic characteristics produced by each of the odontocete species, as well as ambiguity in the phylogenetic relationship among species. Over the last decade, an increasing number of studies have reported the acoustic characteristics of many species, which has been facilitated by the technological development of devices that can record odontocete sounds more easily and at a lower cost. Molecular analysis has also been subject to technical development, which has provided a more reliable foundation for delineating the phylogenic relationships among odontocete species. Recently, several papers related to the sound evolution in odontocetes have been published (e.g., for echolocation clicks, Kyhn et al., 2010; Madsen, Carder, Bedholm, & Ridgway, 2005; Morisaka & Connor, 2007; Morisaka et al., 2011; Tougaard & Kyhn, 2010; for communication sounds, May-Collado, Agnarsson, & Wartzok, 2007; Morisaka & Connor, 2007; Podos, da Silva, & Rossi-Santos, 2002). Here, I review the evolution of communication sounds in odontocetes, and discuss two conspicuous changes in this trait, i.e., emergence and loss, to provide future directions towards revealing the evolution of communication sound in odontocetes.

Basics of Odontocete Sound

Odontocete sounds have been traditionally classified into three categories: tonal whistles, clicks, and burst-pulse sounds (Janik, 2009; Richardson, Greene, Malme, & Thomson, 1995). A whistle is represented by narrowband pure-tonal sounds of longer durations (>20 ms; May-Collado & Wartzok, 2007), with fundamental frequencies ranging from several hundred hertz in bottlenose dolphins (*Tursiops truncatus*) (Schultz & Corkeron, 1994) to 75 kHz in killer whales (*Orcinus orca*) (Samarra et al., 2010) (Figure 1A). Group cohesion with individual identity might be an important function for whistles in delphinids (e.g., Janik & Slater, 1998), while few studies were conducted to reveal whistle function in non-delphinid species. Clicks are short broadband sounds, the dominant frequency of which usually reaches ultrasonic range (Figure 1B). It has been confirmed that several individual species use clicks for echolocation and this is thought to be true of odontocetes as a whole (Richardson et al., 1995). Burst-pulse sounds are pulsed sounds that have a very short inter-pulse interval (<20 ms; Lammers, Au, Aubauer, & Nachtigall, 2004; Madsen, Johnson, de Soto, Zimmer, & Tyack, 2005; Morisaka et al., 2011) and usually have relatively lower frequencies (Lammers et al., 2004) (Figure 1C). Burst-pulse sounds are categorized as sounds that are not clicks or whistles (for review, see Janik, 2009); hence, this sound category should be used with caution.
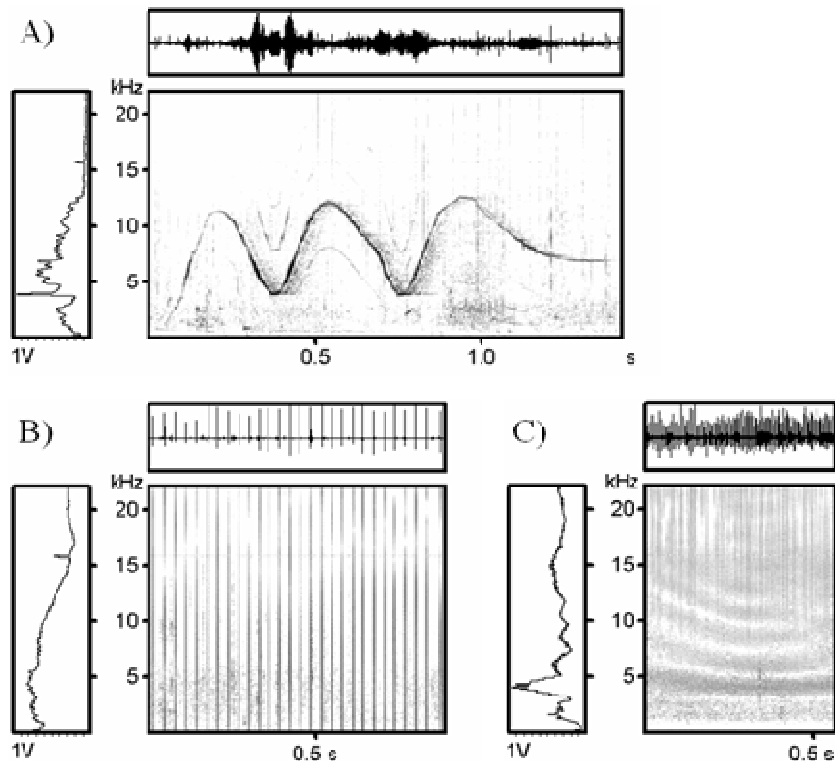

Figure 1. Spectrogram of **(A)** clicks, **(B)** a burst-pulse sound, and **(C)** whistle from wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). The left panel of each spectrogram indicates the power spectrum of the sound, and the upper panel of each spectrogram shows the waveform of the sound.

Whistles

The definition of "whistle" is controversial, and this issue has been addressed by several authors (Janik, 2009; May-Collado et al., 2007; Morisaka & Connor, 2007; Podos et al., 2002). That is because no study shows that the whistles of all whistling-odontocetes are produced by the same mechanism. In this review, pure-tonal sounds with narrowband, frequency modulation and longer durations, sometimes with harmonics are considered as whistles, similar to the description of Morisaka and Connor (2007). The production of whistles has been reported in some Ziphiidae species (Figure 2A), as well as species of the Lipotidae (Figure 2B), Iniidae, Monodontidae, and Delphinidae families, except for the genus *Cephalorhynchus* and the species *Lagenorhynchus australis* and *L. cruciger*. In contrast, the Physeteridae, Kogiidae, Platanistidae, Pontoporiidae, and Phocoenidae (Figure 2C) families, as well as the genus *Cephalorhynchus* (Figure 2D) and the species *L. australis* and *L. cruciger* (Tougaard & Kyhn, 2010) have been reported not to produce whistles (for review, see May-Collado et al., 2007; Morisaka & Connor, 2007). Few reports have been published on the sounds produced by Ziphiidae, with contradictory reports of the presence (Dawson, Barlow, & Ljungblad, 1998; Rankin & Barlow, 2007; Rogers & Brown, 1999) and absence of whistles (e.g., Hooker & Whitehead, 2002). Hence, further research is required to resolve these differences. In this review, I treat Ziphiidae as a whistling group because several species in the Ziphiidae family have been reported to produce whistles.

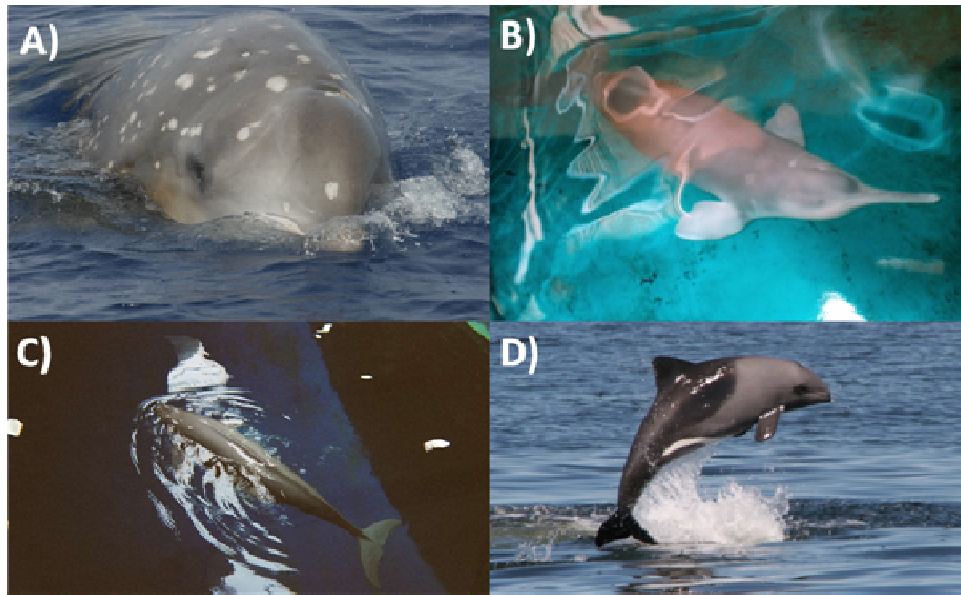*Figure 2.* **A)** Ziphiidae; *Ziphius cavirostris* Image courtesy of Mai Sakai, photo taken under NMFS Scientific Research Permit No.731-1774. **B)** Lipotidae; *Lipotes vexillifer* at Baiji Aquarium, Institute of hydrobiology, Chinese Academy of Sciences, China. **C)** Phocoenidae; *Neophocaena phocaenoides* at Toba Aquarium, Japan. **D)** the genus *Cephalorhynchus*; *C. heavisidii* off Cape Town, South Africa).

Clicks. The click sounds of odontocetes can be divided roughly into two types. Broadband clicks are short (<50 μs) and intense (often >200 dB re 1 μPa) pulses with broader bandwidths (>10 kHz for -3 dB bandwidth). Narrow-band high-frequency (NBHF) clicks are longer (>125 μs) and weaker sounds, with one peak above 100 kHz and a narrower bandwidth (<10 kHz for -3 dB bandwidth) (Au, 1997, 2002).

Morisaka and Connor (2007) reviewed click types for each species and reported that Kogiidae, Phocoenidae, Pontoporiidae, and the genus *Cephalorhynchus* produce NBHF clicks, whereas all other odontocetes produce broadband clicks. After the publication of this paper, two *Cephalorhynchus* species (specifically, *C. eutropia,* Götz, Antunes, & Heinrich, 2010; *C. heavisidii,* Morisaka et al., 2011) and two *Lagenorhynchus* species (specifically, *L. cruciger,* Tougaard & Kyhn, 2010; *L. australis,* Kyhn et al., 2010) were found to produce NBHF clicks.

Phylogeny and Evolution of Whistles and NBHF Clicks

To understand the evolution of whistles and NBHF clicks, the distribution of these sounds against recently established phylogenies are examined (Figure 3). Physeteroidea (including Physeteridae and Kogiidae) is an ancient sister group of all other extant odontocetes (Agnarsson & May-Collado, 2008; Arnason, Gullberg, & Janke, 2004; Cassens et al., 2000; Hamilton, Caballero, Collins, & Brownell, 2001; May-Collado & Agnarsson, 2006; McGowen, Spaulding, & Gatesy, 2009; Nikaido et al., 2001; Steeman et al., 2009). The phylogenic position of Ziphiidae is controversial (e.g., Agnarsson & May-Collado, 2008; Arnason et al., 2004); however, it is generally accepted that Platanistidae diverged after the Physeteroidea and that Ziphiidae and the other families (Inioidea and Delphinoidea) diverged after Platanistidae (Hamilton et al., 2001; McGowen et al., 2009; Nikaido et al., 2001; Steeman et al., 2009). After Ziphiidae, Inioidea (including Iniidae, Lipotidae, and Pontoporiidae) diverged, followed by the Delphinoidea (including Monodontidae, Phocoenidae, and Delphinidae) (Agnarsson & May-Collado, 2008; May-Collado & Agnarsson, 2006; McGowen et al., 2009; Slater, Price, Santini, & Alfaro, 2010; Steeman et al., 2009).

Because of the recent radiation of the family Delphinidae, it is difficult to establish phylogenetic relationships within this group. Recent studies have suggested that the killer whale (*Orcinus orca*) is the most basal species within Delphinidae (McGowen et al., 2009; Steeman et al., 2009), which diverged about 10 million years ago. The phylogenic relationships within the subfamily Lissodelphininae (including *Cephalorhynchus*, *Lissodelphis*, and four species within *Lagenorhynchus* or *Sagmatias*, specifically, *L. obliquidens*, *L. obscurus*, *L. australis*, and *L. cruciger*) were suggested to be monophyletic by LeDuc, Perrin, and Dizon (1999). However, several papers have since discussed these relationships, whereby *Lagenorhynchus* is now considered a polyphyletic group (Harlin-Cognato & Honeycutt, 2006; May-Collado & Agnarsson, 2006; McGowen et al., 2009; Steeman et al., 2009). Several papers have grouped two *Lagenorhynchus* species (*L. australis* and *L. cruciger*) within the *Cephalorhynchus* clade (May-Collado & Agnarsson, 2006; McGowen et al., 2009). Both these two

Lagenorhynchus and *Cephalorhynchus* species produce NBHF clicks. Therefore, it has been suggested that these two *Lagenorhynchus* species should be transferred to the genus *Cephalorhynchus* (Tougaard & Kyhn, 2010). In this review, I treat *L. australis* and *L. cruciger* as species within *Cephalorhynchus*.
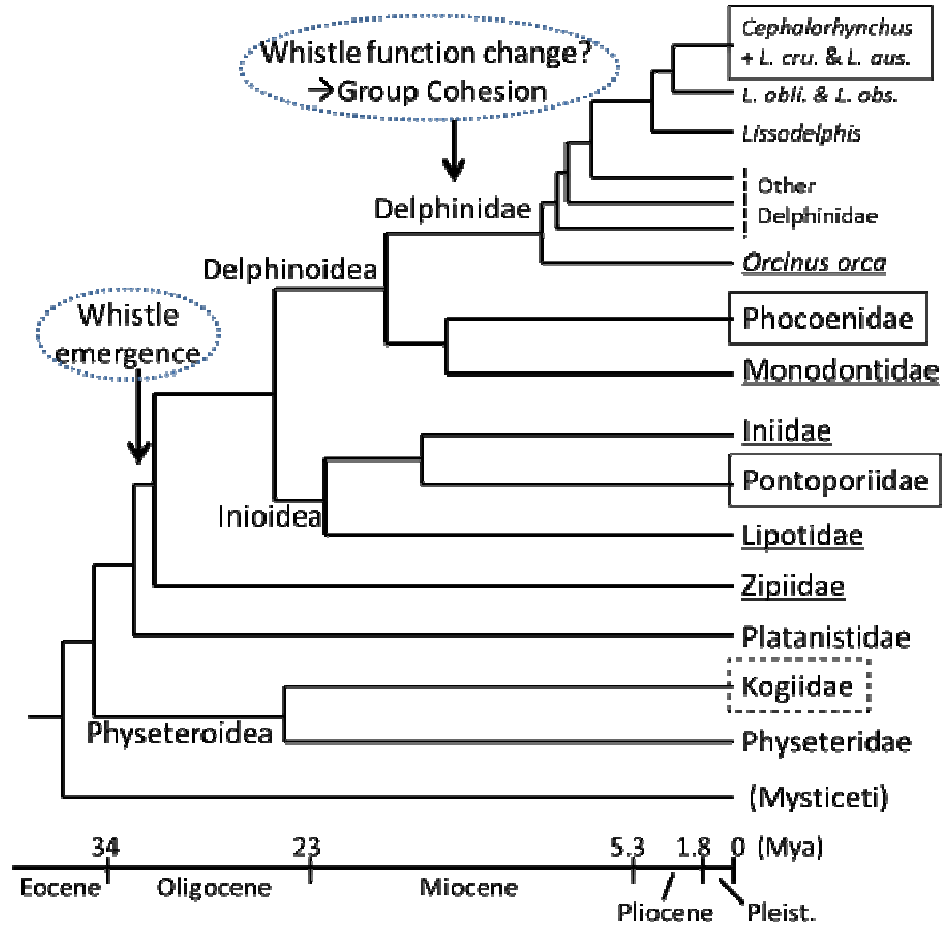
Figure 3. Phylogenetic relationships among cetaceans reconstructed from McGowan et al. (2009).The names of groups containing whistling species are underlined, species with narrow-band high-frequency (NBHF) are enclosed inside a broken rectangle, and species with whistle loss & NBHF are enclosed inside a solid rectangle. Arrows indicate the timing of whistle emergence and of whistle function change. Abbreviations: Pleist. = Pleistocene, Mya = million years, *L. obli.* = *Lagenorhynchus obliquidens*, *L. obs.* = *L. obscurus*, *L. cru.* = *L. cruciger*, *L. aus.* = *L. australis*

Whistle Evolution in Odontocetes

As suggested by Morisaka and Connor (2007) and May-Collado et al. (2007), whistles are likely to have emerged after the divergence of Platanistidae (Figure 3). Hence, Physeteridae, Kogiidae, and Platanistidae never derived whistles evolutionarily. Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus* lost whistles independently, based on the most parsimonious

explanation for the distribution of whistling groups after Ziphiidae (Figure 3). Several papers have reported the differences in whistle characteristics among individuals, populations, and species, proposing several factors that may explain these differences. Such factors include context, coded information, vocal learning, environment, sociality, etc. (e.g., Janik, 2009; Janik, Sayigh, & Wells, 2006; Janik & Slater, 1998; May-Collado et al., 2007; Morisaka, Shinohara, Nakahara, & Akamatsu, 2005a, 2005b; Rendell, Matthews, Gill, Gordon, & Macdonald, 1999; Steiner, 1981; Tyack & Sayigh, 1997; Wang, Würsig, & Evans, 1995). The change in whistle characteristics during odontocete evolution is also an important topic from the evolutionary perspective. However, I do not review this aspect here because of the volume and complexity of topics. For more information, Janik (2009) provides an excellent review of this topic.

Whistle Emergence

The common ancestor of Ziphiidae, Inioidea (including Lipotidae, Iniidae, and Pontoporiidae), and Delphinoidea (including Monodontidae, Phocoenidae, and Delphinidae) acquired whistling capabilities in the early Oligocene, which was about 30 million years ago (Figure 3; McGowen et al., 2009; Nikaido et al., 2001; Steeman et al., 2009). Unfortunately, the reasons for the emergence of such acoustic communication is difficult to explore because (1) it is not well known that the organs involved in whistle production leave traces either on the fossils or on the genes of odontocetes, and (2) studies describing the function of whistle use by possible direct descendants of the first whistling ancestors are apparently absent. In addition, such studies do not exist for Ziphiidae, and there are limited studies on whistle production in Inioidea, specifically *Lipotes vexillifer* (baiji; Yangtze river dolphin) and *Inia geoffrensis* (boto; Amazon river dolphin) (Jing, Xiao, & Jing, 1981; May-Collado & Wartzok, 2007). Here, I propose several possible reasons for whistle emergence, based on the comparison of several viewpoints about Physeteroidea, Platanistidae, Ziphiidae, and Inioidea (particularly Platanistidae and Ziphiidae).

Group Size and Whistle Emergence

Herman and Tavolga (1980) suggested that whistles may have evolved for a special function in large groups, such as maintaining vocal communication during foraging, because species living in large groups tend to produce whistles, and vice versa. Information suggesting that the direct descendants of the first whistling ancestors (Ziphiidae and Inioidea) did not form larger groups indicates that whistles may not have evolved to facilitate large group living at first but may have played a role in the acoustic communication of solitary or small-group living species (May-Collado et al., 2007; Morisaka & Connor, 2007). After whistle emergence, delphinids with larger groups might divert whistles to maintain group cohesion (discussed below).

However, the possibility that the group living in a slightly-larger (but still "small") group of ancient Ziphiidae with its divergence enhanced whistle evolution cannot be ruled out at present. A high concentration of ziphiids identified from the

middle Miocene, which are similar to extant ziphiid species (for extant Ziphiidae, see Hooker, Whitehead, Gowans, & Baird, 2002), indicates site fidelity (Bianucci, Lambert, & Post, 2010) and group living of these species. On the other hand, although information is not available about the group size of ancient Platanistidae, such as *Pomatodelphis*, there are examples of solitary and a few groups of extant Platanistidae (for extant Platanistidae, see Smith, Braulik, Strindberg, Ahmed, & Mansur, 2006). Thus, the group size of ancient Ziphiidae may have become slightly larger when it diverged.

Some non-whistling species have similar ecological niches as whistling species. For example, the non-whistling *Physeter macrocephalus* (sperm whale) forms a large group and dives in deep waters, similar to the whistling Ziphiidae. The non-whistling *Platanista gangetica* (susu; Ganges river dolphin) lives in muddy rivers as a solitary individual or in small groups, similar to the whistling *L. vexillifer* or *I. geoffrensis*. These observations imply that whistles might not have evolved to support large group living or specific ecological niches but to fulfill an alternative, but strong, requirement.

Ecological Conditions when Whistles Emerged

Several studies imply that the first whistling ancestors experienced different ecological conditions compared to their extant descendants. Ancient Platanistidae (such as *Zarhachis* or *Pomatodelphis*) were abundant in the marine environment, especially in the epeiric (i.e., shallow) seas of the United States and of Europe to south Asia (Bianucci & Landini, 2002; Gottfried, Bohaska, & Whitmore, 1994; Hamilton et al., 2001), and started to invade freshwater environments about 10 million years ago (Fordyce, 1998; Morgan, 1994). Some fossil Ziphiidae have been found in worldwide geological formations of shallower seas (Bianucci et al., 2010; Bianucci, Post, & Lambert, 2008; Dooley, 2010; Fuller & Godfrey, 2007) or freshwater environments (Mead, 1975). Small-sized primitive ziphiids, *Archaeoziphius microglenoideus*, were also found in the shallow-water formations of northern Belgium (Lambert & Louwye, 2006; Louwye, Marquet, Bosselaers, & Lambert, 2010). These findings imply that whistles evolved in the marine environment, possibly in shallow waters (but see Bianucci et al., 2010, which stated that "fossil ziphiids had a pelagic habitat and a wide geographical distribution" p. 1093). As the early Physeteroidea were found at the Pisco Formation, Peru, which was deposited in shallow and lagoonal waters, they were living in shallower water and were not deep-sea animals (Bianucci et al., 2010; Lambert, Bianucci, Post, et al., 2010; Mchedlidze, 2002). The early Inioidea also being found in the formations of shallow waters worldwide (for review, see Hamilton et al., 2001). Thus, whistle emergence may not correlate with major habitat shifts, such as river living or deep diving, but occurred in shallow waters.

Sexual Selection and Sound Evolution

One of the most conspicuous characteristics of the Ziphiidae is the sexual dimorphism in their mandible tusks and surrounding structures (Dalebout, Steel, & Baker, 2008). These characteristics suggest the occurrence of intraspecific fights

between adult males to mate with females. Interestingly, ancient Ziphiidae also showed sexual dimorphism in their tusks and surrounding structures (Dooley, 2010; Lambert, Bianucci, & Post, 2010). In extant Iniidae, males are pinker than females and more heavily scarred by the tooth rakes of conspecifics (Martin & da Silva, 2006). In addition, adult males of this species have a sexual display (object carrying behavior), which suggests strong sexual selection in this species (Martin, da Silva, & Rothery, 2008). Iniidae exhibit obvious sexual dimorphism in body size (larger males and smaller females; Martin & Da Silva, 2006), in spite of the "reversal" in body size sexual dimorphism in the other "river dolphins," which are within Platanistidae and Inioidea (smaller males and larger males; Connor, Read, & Wrangham, 2000). This also implies that strong male-male competition may exist in Iniidae. Interestingly, May-Collado and Wartzok (2007) discussed the function of whistles for *I. geoffrensis geoffrensis*, whereby even solitary animals of this species may use whistles in the context of maintaining distances among animals, rather than to promote group cohesion. Maintaining distances among animals (usually males) by sounds occurs in territorial birds, which suggests the presence of acoustic sexual selection (Catchpole & Slater, 1995). Although further research on the function of *Inia* whistles is needed, the possibility exists that *Inia* use whistles for reproductive displays.

Based on these findings, I hypothesized that sexual selection (including mate finding, male-male competition, and female choice) may be one of the important factors influencing the evolution of whistles in odontocetes. Numerous publications have reported that sexual selection may have a dramatic influence on the use of acoustic signals in animals, especially birds (Catchpole & Slater, 1995). In marine mammals, there are also some reports of the effect of sexual selection on acoustic signals. For example, humpback whales (*Megaptera novaeangliae*) produce long and complex songs, which might have been formed through sexual selection (for review, see Tyack & Clark, 2000). In phocid seals, the size of the acoustic repertoire positively correlates to the gregariousness of females and was related to the mating system (higher polygamous species than monogamous and promiscuous species), which indicates that sexual selection may favor large repertoire size in phocid seals (Stirling & Thomas, 2003). Interestingly, predation pressure was thought to decrease repertoire size in those seals (Stirling & Thomas, 2003). Hence, it is possible that the first whistling odontocetes evolved the whistle for acoustic display in the context of sexual selection. Further research is therefore needed to confirm this hypothesis on the whistle usage in Ziphiidae and Iniidae. Unfortunately, it is now difficult to complete acoustic studies on Lipotidae because of their functional extinction (Turvey et al., 2007).

However, extant Physeteridae (or sperm whales), which are the largest odontocetes, show extreme sexual dimorphism in body size, whereby fully grown adult males are 1.5 times longer than females (Connor et al., 2000). In contrast, Kogiidae, which are the closest relatives of Physeteridae, show no obvious size dimorphism (Caldwell & Caldwell, 1989). Sexual dimorphism in the sound transmission organ (spermaceti organ) in relation to body size was also reported for extant sperm whales (see Cranford, 1999). It is proposed that the sexual dimorphism of the spermaceti organ may be explained by sexual selection. For example, male sperm whales with large spermaceti organs produce clicks with

longer inter-pulse intervals, which advertise their large body size (Cranford, 1999). However, it is also proposed that the size of the spermaceti organ has increased only in the lineage of recent *Physeter* (Lambert, 2008b). Hence, extreme sexual dimorphism may only have occurred recently. Several basal groups of sperm whales (*Acrophyseter*, *Brygmophyseter*, *Livyatan*, and *Zygophyseter*) were raptorial, with various body sizes (3-17.5 m) and are considered to have hunted warm-blooded animals, from seabirds to large baleen whales, similar to that recorded for extant killer whales (Bianucci & Landini, 2006; Kimura, Hasegawa, & Barnes, 2006; Lambert, Bianucci, & de Muizon, 2008; Lambert, Bianucci, Post, et al., 2010). Suction feeding in Physeteroidea would have emerged after the divergence of raptorial sperm whales (Lambert, 2008b), which may have led to the use of deeper ocean habitats.

In summary of sperm whale evolution, basal sperm whales may have lived in shallower waters and would not have extreme sexual dimorphism. During the evolution of Physeteridae, there may have been stronger sexual selection on the sound production organ (spermaceti organ), resulting in the change of click structures and consequent extreme sexual dimorphism in body size. Hence, the click characteristics of Physeteridae may have changed rather than the evolution of a whistle that corresponded to the strong pressure of sexual selection. Thus, sexual selection may change sound production organs in odontocetes; this may strengthen my hypothesis of whistle emergence.

Although first whistling ancestors with solitary or small groups had evolved whistles via sexual selection mechanism, ancient delphinids that lived in a larger group might divert whistles to maintain group cohesion because of their efficient transmission range. In other words, delphinids might be able to expand their group size because they had already evolved whistles which were convenient for maintaining large group cohesion. It is possible that whistle function is different between delphinids and the other whistling groups such as *Inia* and Monodontidae as May-Collado and Wartzok (2007) suggested.

Whistle Loss

Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus* independently lost the ability to whistle after the emergence of whistling species. All three groups produce NBHF clicks, which cut off frequencies below 100 kHz. Morisaka and Connor (2007) hypothesized that the convergent evolution of whistle loss and production of NBHF clicks in these groups is a form of adaptive evolution to evade predation risk from killer whales, which apparently cannot hear NBHF clicks. Kogiidae also adopted this anti-predatory strategy (Madsen et al., 2005). These four groups are thought to have adopted not only acoustic crypsis but also other anti-predatory strategies, such as small body size, coastal shallow water use (except deeper water for Kogiidae), small group size, body coloration pattern or appearance, and behavior (e.g., "shyness" in not coming close to boats [several Phocoenidae] and the production of "ink" clouds to hide [in Kogiidae]) (for review, see Morisaka & Connor, 2007). Here, I review the reliability of the acoustic crypsis hypothesis from the evolutionary standpoint, the possibility of whistle loss compensation, and other strategies of predator/prey interactions. I use

the term "whistle-loss species" for only three groups (Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus*), while I use the term "NBHF species" for four groups, comprising Kogiidae and the three whistle-loss species groups.

NBHF and Whistle Loss versus Killer Whale Divergence

It is difficult to answer why only these four groups adopted such anti-predatory strategies, but strong selective pressure by killer whale predation might have occurred within a certain time period after killer whales diverged, which was about 10 million years ago (for estimated divergence date, see McGowen et al., 2009). The genus *Kogia* might have evolved NBHF clicks between the time when the *Kogia* genus emerged and the time when *K. breviceps* and *K. sima* separated, which is estimated from the fossil record to have been about the middle of the late Miocene (Lambert, 2008b) and is supported by molecular data (McGowen et al., 2009). On the other hand, Pontoporiidae diverged from Iniidae in the middle Miocene (McGowen et al., 2009), which was before killer whales diverged. Extant Pontoporiidae have a symmetrical skull, which is thought to be related to the symmetrical sound production organ (dorsal bursae) that produces NBHF clicks (Cranford, Amundin, & Norris, 1996). However, the ancient Pontoporiidae genera, such as *Brachydelphis* and *Parapontoporia*, had an asymmetrical skull (Godfrey & Barnes, 2008), which might be evidence of the production of broadband clicks and whistles (for review, see Morisaka & Connor, 2007). The genera *Pontistes*, and *Plipontos* which diverged in the Pliocene, and the extant *Pontoporia* all have symmetrical skulls (Godfrey & Barnes, 2008), which suggests that whistle loss and the emission of NBHF clicks occurred during the Pliocene, or after killer whale divergence. Phocoenidae diverged from Monodontidae in the middle of the Miocene (McGowen et al., 2009). In the Pliocene, several basal Phocoenidae, such as *Haborophocoena* and *Septemtriocetus*, had asymmetrical skulls (Ichishima & Kimura, 2005, 2009; Lambert, 2008a). This observation suggests that whistle loss and the emergence of NBHF click emission for these groups occurred in the Pliocene, which was again after killer whale divergence. Fossils of *Cephalorhynchus* have not been found; however, molecular data suggests that this group diverged around 3 million years ago (McGowen et al., 2009), long after killer whales diverged. Therefore, the incidence of NBHF clicks and whistle loss in these four groups may have occurred after the emergence of killer whales.

Do Species with Whistle Loss Compensate for its Absence?

Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus* lost the ability to whistle independently during evolution. Whistles, especially individual specific signature whistles, in delphinids (except for the genus *Cephalorhynchus*) are theorized to function as a cohesion call, by which individuals contact other members of the group (Janik & Slater, 1998; Quintana-Rizzo, Mann, & Wells, 2006), and to have caller identities (Janik et al., 2006). However, *Cephalorhynchus* lost the whistle function during its evolution. This raises the question of whether this species must compensate for whistle-related functions. The function of whistles produced by Iniidae, Lipotidae, and Monodontidae, which are the closest

extant relatives of Pontoporiidae and Phocoenidae, are not well known. Whatever the function of the whistles in these three related groups, the same question as for *Cephalorhynchus* occurs. Do these groups need to compensate for the functions that were facilitated by whistles? If so, how do these groups compensate for such whistle loss?

To answer these questions, further research on whistle function is required, especially on Inioidea, Monodontidae, and *Cephalorhynchus*. The group size of *Cephalorhynchus* is lower than that of other delphinids species (May-Collado et al., 2007). Hence, reduced group size might be one of the changes that occur as a result of whistle loss, because whistles in delphinids have the function of group cohesion. On the other hand, the group sizes of Pontoporiidae and Phocoenidae are similar to that of the closest relatives, which also form small groups (May-Collado et al., 2007). These observations imply that larger groups in delphinids need whistles for group cohesion, whereas smaller groups in whistling non-delphinids do not need whistles for group cohesion but for other purpose. Therefore, studies should focus on whistle function in smaller groups to identify how whistle loss has been compensated.

Several examples of possible compensation for whistle loss have been reported. For instance, Hector dolphins, *C. hectori*, may use clicks for communication by changing the repetition rate in the pattern of clicks when in different behavioral states (Dawson, 1991). The report showed a strong relationship between aerial behavior and very short inter-pulse intervals (i.e., "cry" sounds; Dawson, 1991). Furthermore, *P. phocoena* also produces a similarly high repetition rate of clicks to threaten other individuals (Clausen, Wahlberg, Beedholm, Deruiter, & Madsen, 2010; Nakamura, Akamatsu, & Shimazaki, 1998). Context-specific click repetition rate patterns have also been reported to function as contact calls (Clausen et al., 2010), which are similar to whistles in delphinids. The acoustic communication system by sperm whales that never have had whistles evolutionary would be a good model of pulsed communication. Sperm whales produce stereotyped sequences of 3-40 clicks, termed codas, usually lasting less than 3 s in total (Watkins & Schevill, 1977). It has been thought that the communicative function of the codas is the group membership recognition (Rendell & Whitehead, 2003), but Antunes, Schulz, Gero, Whitehead, Gordon,and Rendell (2011) recently reported the individually distinctive features in sperm whale codas, which imply the same function as signature whistle in coda usage. Thus, whistle-loss species may compensate for whistle loss by using other types of sound or clicks. Conversely, if dolphins communicate with each other in a group without whistles, the question naturally arises again: "why did ancestors evolve whistles?" However, the sexual selection hypothesis would resolve this question.

Other changes may occur to compensate for whistle loss, such as behavioral or physical changes. For example, three *Cephalorhynchus* species (*C. commersonii,* Goodall, Galeazzi, Sobral, & Cameron, 1988; *C. hectori* ,Slooten & Dawson, 1988; *C. heavisidii,* Best, 1988) have saw-toothed serrations on the leading edge of one (usually the left) or both pectoral fins. In addition, the males of Commerson's dolphins usually have serrations on the left fins, or sometimes both fins, while around 40% of the females do not have serrations on either fin (Goodall et al., 1988). The strong preference for the left pectoral fin during contact behavior

and a mechanically flexible left fin suggests that flipper serrations may be used in contact behavior to enhance tactile stimulation (Gómez-Campos, Aguilar, & Goodall, 2010; Johnson & Moewe, 1999). Similar observations have been made for *Neophocaena phocaenoides*, which have serration-like structures on the dorsal region (Pilleri & Chen, 1979), with the tubercles being used for tactile stimulation (Nakahara & Takemura, 1997). *P. spinipinnis* and *P. phocoena* also have "spine" or serration-like structures (Jefferson, Leatherwood, & Webber, 1993; Figure 4). Unlike delphinids that show frequent tactile behaviors (e.g., Sakai, Hishii, Takeda, & Kohshima, 2006), several species of *Cephalorhynchus* and Phocoenidae show both behavioral and physical changes for tactile communication. These observations imply that tactile communication may become important for species with whistle loss to compensate for whistle information, as Nakahara (1999) noted.

Figure 4. Serration-like structure in *Phocoena phocoena*.

Strategy of Whistling Species for Predator/Prey Interactions

Some species adopt the acoustic crypsis strategy, while others produce whistles. If the strategy successfully allows whistle-loss species to avoid predation by killer whales, why do other species still produce whistles? Members of every cetacean family have been reported as victims of killer whales, including whistle-loss species (Kogiidae, Pontoporiidae, and Phocoenidae but excluding the genus *Cephalorhynchus*) (Jefferson, Stacey, & Baird, 1991; Ott & Danilewicz, 1996). Hence, the acoustic crypsis strategy is not perfect for avoiding predation by killer whales. However, killer whales have also adopted several strategies to hunt cetaceans, including whistle-loss species. For example, only after hunting or during surface-active behavior, mammal-eating killer whales produce isolated single or paired clicks (Barrett-Lennard, Ford, & Heise, 1996) and social pulsed

calls and whistles, and no sounds during other behavioral states (Deecke, Ford, & Slater, 2005; Riesch & Deecke, 2011); this is probably to avoid detection by potential prey. In addition, killer whales use passive listening to detect their prey and may even use surfacing and breathing sounds generated by NBHF species (Barrett-Lennard et al., 1996).

Such a "behavioral silence" strategy has been often observed in whistling species. For example, an effective counter-strategy by prey species against killer whales is to remain still and silent (Herman & Tavolga, 1980; Jefferson et al., 1991). Beluga whales become silent when killer whales swim nearby and even when killer whale sounds are played back (Fish & Vania, 1971; Schevill, 1964). In addition, Oswald, Rankin, and Barlow (2008) showed that dolphins in the eastern tropical Pacific Ocean produce whistles more frequently than those occupying the temperate US west coast. The possibility of predator avoidance against killer whales was considered because the predation risk from killer whales was greater in the temperate than the tropical study areas. Furthermore, two deep-diving beaked whale species did not produce clicks when they were in shallow water (<200 m), which again may be an adaptation to avoid acoustic detection by killer whales (Tyack, Johnson, Soto, Sturlese, & Madsen, 2006). However, this strategy is only effective before detection by the predator.

As stated earlier in this review, whistles have several benefits, especially for group living. If the cost of producing whistles (especially detection by killer whales) exceeds its evolutionary benefit, whistling species might cease producing whistles. As Iniidae and Lipotidae are adapted to riverine environments, in which killer whale predation is absent, the production of whistles must have a certain benefit. Although large groups may be easily detected by predators (i.e., the encounter effect; Acevedo-Gutiérrez, 2008), large groupings also provide an effective counter-strategy for predator avoidance and protection through increased vigilance and the dilution effect (Acevedo-Gutiérrez, 2008; Jefferson et al., 1991). Therefore, whistling species that live in larger groups benefit more by producing whistles than the cost of detection by killer whales, especially when maintaining larger groups. In comparison, whistling species that form smaller groups might preferentially adopt the behavioral silence strategy in response to predation pressure. If so, why has the loss of whistling ability occurred in whistle-loss species?

One hypothesis for the emergence of whistle-loss species is as follows. Ancestors of whistle-loss species that originally produced whistles may have adopted the behavioral silence strategy against predation pressure by killer whales. This predation pressure remained strong, or even increased, on these ancestors. As a result, there was strong selective pressure against the lower frequency in their clicks (<100 kHz), which is within the hearing range of killer whales, leading to the occurrence of NBHF clicks. As a consequence, the sound-producing organs required reconstruction to produce NBHF clicks, which dramatically affected the whistle-producing mechanism, because selection also acted against the production of whistles, leading to whistle loss (for further discussion, see Morisaka & Connor, 2007).

Dusky dolphins (*L. obscurus*), which are treated as whistling species, rarely produce whistles and are considered not to use whistles for important social

communications (Au, Lammers, & Yin, 2010). It is therefore possible that dusky dolphins are in the process of evolution towards becoming non-whistling and NBHF species because of strong predation pressure from killer whales.

Conclusions

Recent acoustic and phylogenetic studies have partly established the reasons for whistle evolution in odontocetes. The common ancestor of Ziphiidae, Inioidea, and Delphinoidea evolved whistle in the early Oligocene. Pontoporiidae, Phocoenidae, and the genus *Cephalorhynchus* lost the whistle trait in concordance with the emergence of NBHF clicks. I hypothesize that sexual selection was important for whistle emergence, but increasing group size cannot be excluded as a reason for whistle emergence. After the divergence of killer whales, whistle loss along with emergence of NBHF clicks occurred independently three times by reconstruction of sound-producing organs. Whistle-loss species may compensate for whistle information in other ways, including the use of other sounds (burst-pulse) or tactile communication. Further research on acoustic communication by Ziphiidae, Inioidea, Monodontidae, and the genus *Cephalorhynchus* would contribute towards improving our understanding about the evolution of whistles.

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