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Evolution of orbit size in toothed whales (Artiodactyla: Odontoceti)

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Abstract

For many marine tetrapods, vision is important for finding food and navigating underwater, and eye size has increased to improve the capture of light in dim ocean depths. Odontocete whales, in contrast, rely instead on echolocation for navigation and prey capture. We tested whether the evolution of echolocation has influenced the orbit size, a proxy for eye size, and examined how orbit size evolved over time. We also assessed variation in orbit size amongst whales and tested how body size, diving ability, sound production, foraging habitat, and prey capture strategy influenced the orbit size using phylogenetic independent contrasts and phylogenetic ANOVAs. Using measurements of orbit length and bizygomatic width, we calculated proportional orbit size for 70 extant and 29 extinct whale taxa, with an emphasis on Odontoceti. We then performed ancestral character state reconstruction on a time-calibrated composite phylogeny. Our analysis revealed that there was no shift in proportional orbit size from archaeocetes through stem odontocetes, indicating that the evolution of echolocation did not influence the orbit size. Proportional orbit size increased in Ziphiidae, Phocoenidae, and *Cephalorhynchus*. Proportional orbit size decreased in Balaenidae, Physeteridae, Platanistidae, and Lipotidae. Body size, diving ability, foraging environment, and prey capture strategy had a significant influence on orbit size, but only without phylogenetic correction. An increase in orbit size is associated with deep diving behavior in beaked whales, while progenesis and retention of juvenile features into adulthood explain the pattern observed in Phocoenidae and *Cephalorhynchus*. Decrease in proportional orbit size is associated with adaptation toward murky freshwater environments in odontocetes and skim feeding in balaenids. Our study reveals that the evolution of echolocation had little effect on orbit size, which is variable in whales, and that adaptation for different feeding modes and habitat explains some of this variance.

1 | INTRODUCTION

During the transition from terrestrial to aquatic environments, tetrapods developed numerous adaptations to live underwater. In adapting, they underwent major changes in methods of locomotion, reproduction, and prey capture (Kelley & Pyenson, 2015; Mazin & de Buffrénil, 2001). Major changes to sensory organs also occurred.

Many marine tetrapods rely upon vision as a primary sense for navigating their environment. However, the physical properties of

water require changes to the eye to allow animals to see underwater effectively. Water absorbs, refracts, and scatters light to a higher degree than air (Webb, 2019). Due to this, light is unable to penetrate deeper than the photic zone, which may be as deep as 200 meters but can be much shallower depending on nutrient load (Webb, 2019). Turbidity can further reduce vision, due to the mixing of sediment into the water column. Below the photic zone, the only illumination comes from light produced by bioluminescent organisms. Different wavelengths of light travel through water at varying speeds, with shorter wavelength light in the blue spectrum penetrating much deeper than other wavelengths (Jerlov, 1976). Some tetrapods may also need to balance adaptations for underwater vision with the ability to see above water, especially if they still return to land for reproduction (Hanke et al., 2009; Supin et al., 2001).

To adapt to the challenges of seeing underwater, many marine tetrapods have increased the size of the eye, specifically orbit diameter (Debey & Pyenson, 2012; Fitzgerald, 2006; Humphries & Ruxton, 2002; Marx, 2011; Motani et al., 1999; Thewissen & Nummela, 2008). Size of eyes is a good proxy for the importance of vision in animals as it allows for the packing of a greater number of photoreceptors as well as reception of light from a larger number of angles (Hughes, 1977; Martin, 1983; Walls, 1942). An increase in eye size also increases visual acuity, improving the ability to see fine details (Humphries & Ruxton, 2002; Land, 1981). Increases in proportional eye size are documented in many marine tetrapod clades, including ichthyosaurs (Humphries & Ruxton, 2002; Motani et al., 1999), pliosaurs (Taylor & Cruickshank, 1993), metriorhynchid crocodiles (Young et al., 2010), mosasaurs (Konishi et al., 2016), pinnipeds (Debey & Pyenson, 2012), later-diverging archaeocetes (Thewissen & Nummela, 2008), and stem mysticetes (Fitzgerald, 2006; Marx, 2011). Within these different lineages, increased eye size has been correlated with deep diving (Motani et al., 1999) or macropredatory behavior (Fitzgerald, 2006; Marx, 2011).

Although other senses aid marine tetrapods in navigating or finding prey (Wartzok & Ketten, 1999), in only odontocete whales has echolocation evolved to become an important means of sensing their environment (Au, 1993). In echolocation, odontocetes use a unique set of facial muscles and air sacs to produce ultrasonic sounds, which propagate through the water column ahead of the whale (Cranford et al., 1996). When the sound wave produced contacts an object, echoes propagate back toward the whale. The acoustically isolated specialized ear then receives these vibrations (Nummela et al., 2004; Oelschläger, 1986), and the whale is able to use this sound information to produce 3D maps of the environment. Echolocation evolved very early in odontocete whales (Churchill et al., 2016; Geisler et al., 2014) and possibly evolved twice within the clade (Racicot et al., 2019). Echolocation potentially has reduced the importance of vision in odontocetes. For instance, whales such as *Platanista* have a significantly reduced eye size and are nearly blind (Dral & Beumer, 1974; Herald et al., 1969). One suggested reason to explain the evolution of echolocation in odontocetes was to help find prey at night or at depth (Lindberg & Pyenson, 2007); this same behavior has been associated with increases in eye size in other marine tetrapod clades

(Debey & Pyenson, 2012; Motani et al., 1999). It is unknown how the evolution of echolocation by odontocete whales affected the evolution of vision in this clade.

The evolution of the eye remains poorly known in whales. Extant whales are generally considered to have large eyes compared to many mammals, both proportionally and absolutely (Ulrike & Peichl, 2003), with the exception of the paraphyletic "river dolphins." Whales possess large corneas with correspondingly large pupils to increase the amount of light entering the eye (Meredith et al., 2013; Ulrike & Peichl, 2003), while a spherical lens increases refractive power (Dral, 1972; Mass & Supin, 2007; Wartzok & Ketten, 1999). Whales also possess a prominent tapetum lucidum, increasing light absorption (Dawson, 1980; Mass & Supin, 2007; Ulrike & Peichl, 2003; Walls, 1942; Wartzok & Ketten, 1999). Rods dominate the retina, with cones making up 1% or less of the total photoreceptors (Mass & Supin, 2007; Ulrike & Peichl, 2003). Rods, specialized for light gathering, show a shift in sensitivity toward light in the blue spectrum (Bischoff et al., 2012; McFarland, 1971; Meredith et al., 2013; Ulrike & Peichl, 2003). Genes associated with short wavelength-sensitive rod opsins deactivate early in whale evolution (Meredith et al., 2013; Peichl et al., 2001; Ulrike & Peichl, 2003). Some species have even deactivated color opsin genes completely; this has evolved independently in mysticetes, ziphiids, and physeteroids (McGowen et al., 2020b; Meredith et al., 2013). Although odontocete whales rely upon echolocation for navigation, behavioral studies still suggest an important role for vision in prey capture and intraspecies communication (Ulrike & Peichl, 2003).

The anatomical structure of the eye in odontocete whales is far better known than its actual evolution, with most research focused on eye evolution in archaeocetes and stem-mysticetes. Thewissen and Nummela (2008) examined the eye size in archaeocete whales. They found that proportional orbit size in pakicetids and the later diverging *Ambulocetus* was comparable to that of closely related terrestrial mammals. *Remingtonocetus*, however, had unusually small eyes. Increases in eye size occurred in later diverging archaeocetes such as protocetids and dorudontines. Thewissen et al. (2009) elaborated on this discussion, expanding it to include orbit position. They showed an overall trend of eyes changing their position through archaeocete evolution, shifting toward the dorsal surface of the skull in pakicetids and later toward the lateral side of the skull in *Ambulocetus* and later-diverging whales.

Within mysticetes, proportionally large eyes are present in stem taxa including *Janjucetus*, *Mammalodon*, and aetiocetids (Fitzgerald, 2006; Marx, 2011). Fitzgerald (2006) argued that the unusually large eyes of *Janjucetus* indicated specialization toward macropredation, consistent with other anatomical features of the skull. Marx (2011) extended these observations to aetiocetids and argued that reduction in orbit size in later mysticetes was a result of specialization toward bulk feeding and a reduced need for vision.

Given the unique evolution of echolocation, it is worth considering what if any effect the evolution of this sensory capability had on eye evolution, as compared to other taxa. In this study, we reconstruct the evolutionary history of orbit size in a large sample of both

extinct and extant odontocetes. We predict that a diminished need for vision as a primary sense will result in proportional reductions in orbit size. Furthermore, we predict that taxa foraging in environments with limited visibility (deep-sea depths and turbid freshwater rivers) will also have reduced orbit size.

2 | METHODS

2.1 | Sampling and measurements

To assess how the evolution of echolocation influenced orbit size within whales, we collected 3D scan data from a phylogenetically diverse assortment of extant and fossil taxa, with an emphasis on odontocetes. Overall, 171 adult specimens representing 70 extant taxa and 34 fossil specimens representing 29 extinct taxa were measured (Appendix S1). At least one member of every extant whale family was included. Amongst the fossil taxa sampled, we examined four archaeocete whales, five mysticetes, and twenty odontocetes. Fossil odontocetes sampled included representatives of Xenorophidae as well as various other stem odontocetes, platanistoids, lipotids (*Parapontoporia*), kentriodontids, and phocoenids (*Semirostrum*). Scan data used in this study is available on Phenome10k (www.phenome10k.org).

Three separate measurements, modified from Marx (2011), were collected from each skull (Figure 1): bizygomatic width, a proxy for body size in whales (Pyenson & Sponberg, 2011), and the length of the left and right orbits, as measured as the distance between the preorbital and postorbital processes of the frontal. Although orbit length is not a precise match for eyeball size (Thewissen & Nummela,

2008), it is generally considered a decent approximation (Debey & Pyenson, 2012; Fitzgerald, 2006). Sampling focused on specimens with at least one intact orbital region and from which we could measure bizygomatic width. For a few incomplete fossil specimens (e.g. *Aetiocetus* and *Diorocetus*), the latter measurement was estimated, taking the width of the skull from the lateral edge of the zygomatic processes to the midline and multiplying it by two. We made every measurement three times in the program Artec Studio 12 using the linear measure tool. We then calculated an average based on the three measurements. Before we performed any further analysis, we first verified that the size of the orbit reflected actual eye size. Within the orbit, there is large amount of fatty padding and other tissues, and it is possible that the orbit ratio is not a true measure of eye size. While other studies have confirmed the strong correlation between orbit length and eye size in mammals (Pihlström, 2012), we wanted to be certain that this relationship held for whales specifically.

We tested correlation of eye size with orbit size by using least squares linear regression and comparing the log orbit ratio to log eye mass data from Burton (2006). Actual measurements of eyeball size are scarce in the literature, so we are limited to nine species, although these nine species were phylogenetically diverse and spanned a range of body sizes.

If multiple individuals were available for a given species, we averaged measurements for the entire species. This was performed as it is not possible to perform ACSR with multiple specimens from the same taxon. We also averaged, when applicable, the left and right orbit lengths. Before doing this, we tested for cranial asymmetry. Odontocetes possess extreme bilateral facial asymmetry, with bony elements of the right side of the skull typically larger than bony elements on the left side of the skull (Coombs et al., 2020; Ness, 1967). If such asymmetry was present in the orbit morphology, then the averaging of the left and right orbit lengths would not be appropriate. If we did not detect asymmetry, we would average right and left sides for each specimen. To test for asymmetry in orbit size, we performed a paired T-test comparing average left and right orbits lengths for each specimen. If we detected statistically significant ($p \leq 0.05$) differences, we would only use measurements from the right side of the skull.

We standardized orbit measurements to account for differences in body size by dividing the final averaged orbit length by bizygomatic width and multiplied by 100 to produce a ratio. We used these ratios, hereafter referred to as orbit ratios, for all further analyses of orbit size. We tested for significant differences in orbit ratio between clades using Kruskal-Wallis and Wilcoxon paired rank sum tests. For these statistical tests, we placed whales into 13 categories: archaeocetes, stem mysticetes, crown mysticetes, stem odontocetes, physeteroids, platanistoids, ziphiids, lipotids, kentriodontids, inoids, phocoenids, monodontids, and delphinids.

2.2 | Ancestral character state analysis

To determine how orbit size evolved within whales, we performed ancestral character state reconstruction (ACSR) to map
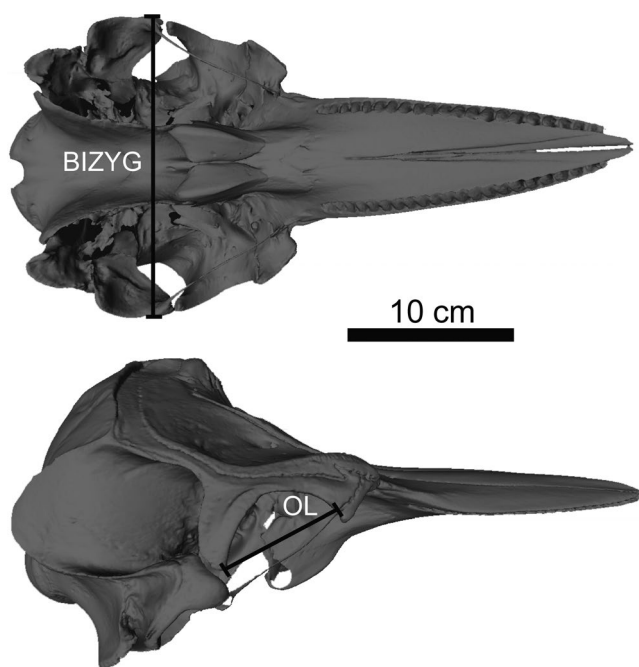

FIGURE 1 Measurements of bizygomatic width (BIZYG) and orbit length (OL) used in study, on an isosurface produced from 3D surface scan of a *Tursiops truncatus* (USNM 571698) skull

orbit ratios onto a time-scaled phylogeny of whales. This was a composite phylogeny based on the tree used in Churchill et al. (2018), pruning taxa for which orbit ratios were unavailable. As this phylogeny lacked several important extant taxa, we incorporated the results of McGowen et al. (2020a) overall and McGowen (2011) for delphinids specifically. The position of archaeocetes largely followed Martínez-Cáceres et al. (2017), *Berardius minimus* followed Yamada et al. (2019), *Mesoplodon hotaula* followed Dalebout et al. (2014), and *"Argyrocetus" joaquinensis* followed Lambert et al. (2015).

To generate branch lengths for the tree, we time-scaled the tree using the R package Paleotree (Bapst, 2012). Time-scaling was based on binned first (FAD) and last (LAD) occurrence data (Appendix S2). We gathered age information from Churchill et al. (2016) and supplemented this dataset with age data from the Paleobiology Database (www.paleobiodb.org). We considered extant taxa with no fossil record to be of Holocene age for time scaling.

We then tested for phylogenetic signal (Pagel's λ; Pagel, 1999) in orbit ratios, using the tree generated above. If we detected no phylogenetic signal, it would be pointless to attempt an ACSR. Phylogenetic signal was estimated using the APE (Paradis et al., 2004) and GEIGER (Harmon et al., 2008) packages in R and simulated 10,000 times. We then calculated an average λ value, with a λ equal or greater than 0.5 considered indicative of strong phylogenetic signal.

If strong phylogenetic signal was confirmed, ACSR was implemented using the composite tree and the R package Phytools (Revell, 2012), treating orbit ratio as a continuous character. We used a maximum likelihood approach and the Contmap function to generate ancestral character state tracings as well as phenograms of orbit ratio change through the phylogeny.

2.3 | Analysis of quantitative life history traits

Knowing the evolutionary history of orbit size is important, but we also sought to test what environmental or biological factors may explain variation in proportional orbit size across different clades. To determine potential drivers of orbit size change, we carried out general least squares (GLS) linear regression as well as phylogenetic independent contrasts (PIC) to test for correlations with quantitative variables. We excluded extinct taxa other than *Lipotes* from these analyses as they typically lacked information on the variables of interest; we also excluded any taxa that we could not find data for analyses relevant to that variable. We logged all orbit ratios for GLS and PIC.

We examined three major hypotheses. First, we tested whether changes in orbit size are largely a function of allometry. As body size changes, does orbit ratio change in a consistent manner? We used both log body mass and log total length as variables, with these data collected from Jefferson et al. (2008). For taxa with strong sexual dimorphism, body mass and total length were averaged across both sexes.

Second, we tested whether changes in orbit size correlated to changes in diving ability. Do species that spend more time hunting in the dark depths of the ocean show a decrease in orbit size compared to species that largely hunt near the well-lit surface? We examined two metrics for diving ability, maximum dive depth and maximum known dive duration. These data were mostly collected from Schreer and Kovacs (1997) and supplemented by Tyack et al. (2006) and Edwards and Schnell (2001). We logged both dive depth and dive duration.

Finally, we tested the role that echolocation played in the evolution of eye size. As echolocation became more important, was there a diminished role for the eyes, resulting in smaller proportional orbits? To assess this hypothesis, we relied upon two potential proxies for echolocation: bilateral facial asymmetry and highest frequency of sound produced. Bilateral facial asymmetry may play a role in echolocation (Coombs et al., 2020; Heyning, 1989; Heyning & Mead, 1990), and thus, it is reasonable to imagine that increases in this variable may correlate with decreased orbit size. To quantify facial asymmetry, we used sum radii data from Coombs et al., (2020). Sum radii represent a measure of overall differences between positioning of cranial landmarks on an actual skull versus a generated map of landmarks created by mirroring one half of the skull; the larger the sum radii, the more asymmetrical the skull.

High frequency sound production is a prerequisite for echolocation and found in all odontocetes (Au, 1993). In contrast, mysticetes are specialized for low frequency sound production and presumably hearing (Cummings & Thompson, 1971; Park et al., 2017). Based on the relationship of sound production frequency and echolocation, we might assume that taxa that produce higher frequency sounds may thus have smaller orbits due to less need for vision and more reliance on echolocation. We collected sound frequency data from Ketten (1994) and Morisaka and Connor (2007). When available, the sound frequency used was the highest peak frequency, produced as part of the clicks used in echolocation. When available info was insufficient to determine if sound values represented clicks, we went with the highest frequency recorded. Mysticetes do not echolocate at all and hence do not produce clicks. Instead, we used the highest frequency sound produced via vocalization, excluding other forms of sound production such as fluke slapping.

We determined the strength of the correlations first using least squares regression, with p and R^2 values used as a measure of fit. We then carried out PIC using the composite tree produced for the ancestral character state analysis with only modern taxa included. PIC was carried out because orbit ratios for given taxa are not independent from one another, due to shared ancestry. Factoring out the influence of phylogeny is thus important. We carried out PIC analyses using the APE and GEIGER packages in R. We carried out separate analyses for each variable, with any taxa missing data for that variable removed from the specific analysis. We generated branch lengths 10,000 times, resulting in 60,000 analyses total. We calculated R^2 and p values for the correlation for each analysis. For each variable, we then averaged R^2 and p value across the analyses. We considered correlations significant if they had p values equal to or less than 0.05.

2.4 | Analysis of qualitative life history traits

We cannot easily quantify all of the behavioral and ecological variables that may influence orbit size into a format appropriate for PIC. Two qualitative life history characters that we were interested in that fall under this categorization were foraging habitat and prey capture method. To test how these two variables influenced orbit size, we used permutation ANOVAs with one million permutations in the R package permuco (Kherad-Pajouh & Renaud, 2015) and Wilcoxon paired sum rank tests. To remove the confounding factor of phylogeny from our comparisons, we also performed phylogenetic ANOVAs, using the phylANOVA function in the R package Phytools. For these analyses, we used the same phylogeny as was used in our ancestral character state analysis, pruning all taxa known only from fossils from the tree. We need to interpret the results of the phylogenetic ANOVAS with caution, as the orbit ratio data we used in this study violated normality. Failure to account for normality increases the chances of Type I error. We included only extant taxa in these analyses. All variables described below are included in Appendix S3.

We classified foraging habitat for each extant whale into one of three categories: freshwater, nearshore, and offshore. Amount of sediment is likely to vary between these different habitats, and so we might assume that taxa in silt-laden rivers and coastal waters may be less reliant on vision, and so have smaller proportional orbits than more pelagic species. While we binned foraging habitat into one of three discrete categories, many species show a degree of flexibility in the habitats they occupy. We classified only four taxa as freshwater in this study: *Platanista*, *Lipotes*, *Inia*, and *Sotalia fluviatilis*. The Yangtze population of *N. asiaeorientalis* is freshwater;however, we did not sample this population, and so we treated *Neophocaena* as nearshore for the purpose of this study. We classified taxa as nearshore if the majority of their distribution was in shallow marine environments on the continental shelf, or if the majority of their population inhabited these waters. We classified taxa as offshore if the majority of their distribution was away from the continental shelf and they possessed a pelagic distribution. We treated taxa that inhabited areas of pack ice (*Balaena* and *Monodon*) as nearshore taxa. Some species have relatively strict habitat preferences and only occur in nearshore (e.g. *Pontoporia*, *Neophocoena*) or offshore environments (physeteroids and ziphiids). Many taxa are more generalist, with some populations inhabiting nearshore waters, while other populations are pelagic. In such cases, unless nearshore populations made up the majority of the population, we generally categorized the species as offshore. Other species may migrate through more offshore environments but largely forage in nearshore waters, such as *Delphinapterus*. We treated these species as nearshore. To classify taxa by habitat, we used distribution information from Jefferson et al. (2008).

We also expected that prey capture strategy would influence orbit size, with species targeting bulk prey items that require less precision in capturing, such as filter feeders, having less need for vision than those actively pursuing their prey, such as most raptorial feeders. For prey capture method, we recognized six major categories of feeding: skim, engulfment, suction, ram, snap, and grip-and-tear. Categorization of prey capture method follows Johnston and Berta (2011), Galatius et al. (2020), and Martins et al. (2020). When feeding behavior was unknown for a given species, we used the behavior of closely related species for the assignment of prey capture strategy.

Hocking et al. (2017) have suggested an alternative framework for looking at prey capture and handling, in which they treat different methods of filter-feeding as well as grip-and-tear feeding as alternative methods of prey processing, versus capture, and that prey capture itself for these taxa would involve elements of raptorial or suction feeding. While we do recognize that there is overlap between the categorizations of prey capture as defined by Johnston and Berta (2011), Galatius et al. (2020), and Martins et al. (2020), we nonetheless find that the classification used by these latter authors to be helpful when sorting whales into different ecological categories relevant to this study.

3 | RESULTS

3.1 | Variation in orbit size

When we compared the left and right orbits, no asymmetry was detected ($p = 0.38$, T value = 0.88, DF = 154). Because there were no significant differences, we averaged left and right orbit measurements for all specimens. Orbit and eye size were found to be significantly correlated (Figure 2; $p < 0.001$, $R^2 = 0.93$). We thus consider orbit size to be a good proxy of eye size in whales.

Even with body size taken into account, there was substantial variation in orbit ratio across whales (Figure 3, Table 1). Orbit size ratios varied from 8% through 44.04%, with the smallest orbit ratio possessed by *Platanista* and the largest by *Cephalorhynchus commersoni*. Generally, most cetaceans had an orbit ratio within the range of ~17–28%. We saw this range in orbit ratio in archaeocetes through extant odontocetes, with a slight trend toward increased orbit ratios in Ziphiidae, Phocoenidae, and Delphinidae. A tendency toward decreased orbit ratio was evident in mysticetes. Taxa with unusually large orbit ratios compared to the typical range included *Aetiocetus* (29.33%), *Indopacetus* (30.79%), *Mesoplodon* (up to 34.41%), *Parapontoporia* (34.12%), Kentriodontidae (up to 31.23%), Phocoenidae (up to 35.47%), Lissodelphininae (up to 44.04%), *Steno* (32.2%), *Stenella frontalis* (29.08%), and *S. attenuata* (30.63%). Taxa with unusually small orbit ratios included Balaenidae (as low as 8.04%), Balaenopteridae (as low as 12.28%), *Physeter* (10.43%), *Platanista* (8%), and *Lipotes* (12.65%).

Kruskal-Wallis tests found significant differences in orbit ratio between major clades ($p < 0.001$, H = 47.60). Wilcoxon paired rank sum tests found that there were no significant differences between most clades of whale. In particular, we found no difference between archaeocetes and all other later whale clades. Significant differences in orbit ratio were identified however between crown mysticetes versus Delphinidae ($p = 0.002$, T = 6.73).

3.2 | Ancestral character state reconstruction

Strong phylogenetic signal ($\lambda = 0.84$) was found in orbit ratio data, warranting ancestral character state analysis. Mapping the evolution of orbit ratio onto the phylogeny revealed that orbit size remained consistent through cetacean evolution (Figures 4 and 5), with a very slight trend toward increased orbit size in crown odontocetes (Figure 5). Deviations from the ancestral condition can are shown on the phenogram (Figure 6).

The ACSR and phenogram identified reduced orbit ratios as having evolved in Balaenidae, with stem mysticetes having larger orbit ratios overall than crown taxa. Within Odontoceti,
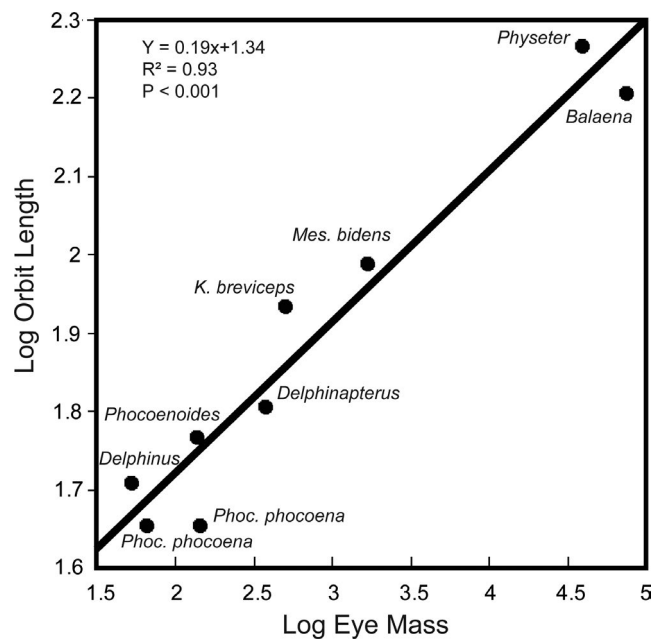
reductions in overall orbit ratio were relatively rare and limited. Major reductions in orbit size evolved four times within odontocetes, within Physeteridae, Platanistidae, Lipotidae, and *Berardius*. The pattern within Lipotidae was complex, with the extinct *Parapontoporia* possessing proportionally large orbits, while *Lipotes* possessed proportionally small orbits. *Berardius bairdi* also separately evolved reduced orbit size, although the recently described and closely related *B. minimus* had an orbit ratio within the typical odontocete range; the pattern in *B. bairdi* contrasts to the overall pattern in other ziphiids, which evolved larger orbit ratios.

Large orbit ratios evolved at least three times. It evolved at least once within the clade including *Indopacetus* and *Mesoplodon*; however, the large degree of intrageneric variation in orbit size within this genus may suggest that increased orbit size evolved multiple times within this clade. Large orbit size also evolved within Phocoenidae, with the large orbits of the extinct porpoise *Semirostrum* indicating that the increased orbit size may have evolved early in this group. Large orbit ratios also evolved within Lissodelphininae, especially *Cephalorhynchus*. *Cephalorhynchus commersoni* possessed the largest orbit ratio of any whale in our study.

FIGURE 2 Relationship between log length of orbit and log eye weight, for nine species of whale. Eye weight data from Burton (2006)

3.3 | Orbit size and quantitative life history characters

When phylogeny was not taken into account, orbit ratios were found to be significantly correlated with several variables (Table 2), including body mass ($p < 0.001$; $R^2 = 0.4$), total body length ($p < 0.001$; $R^2 = 0.38$), and peak sound frequency produced ($p = 0.001$; $R^2 = 0.21$). Maximum dive duration ($p = 0.04$; $R^2 = 0.1$) was weakly but significantly correlated with orbit ratio. There was no significant correlation for either maximum dive depth or bilateral cranial asymmetry with orbit ratio.
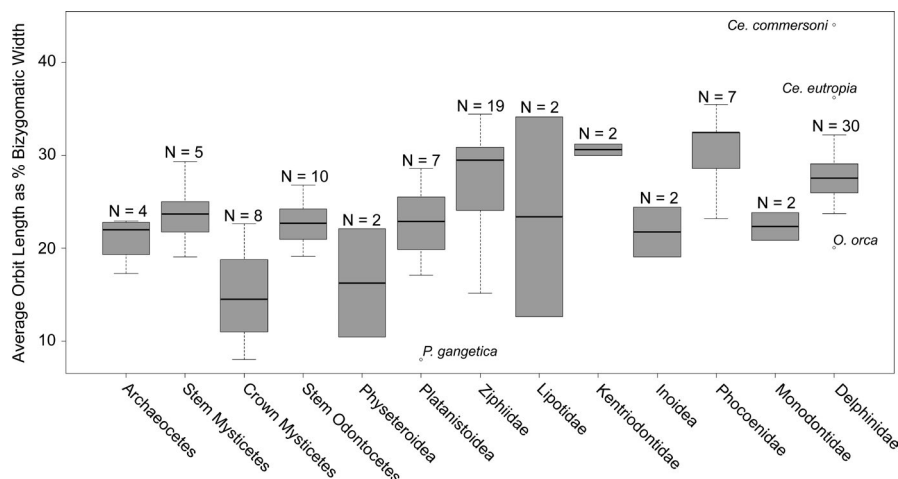

FIGURE 3 Variation in orbit length as a percentage of bizygomatic width of the skull, for different taxonomic groups of whale. Both fossil and extant taxa included. Numbers above boxplots represent number of species sampled for each group. Outliers indicated by taxon name

TABLE 1 Summary statistics for orbit length as a percentage of bizygomatic width (orbit ratio), for major whale clades included in this study

|	N	Min	Max	Mean	Median	Std. Deviation
Archaeocetes	4	17.27	22.92	21.05	22.02	2.61
Stem Mysticetes	5	19.07	29.33	23.78	23.67	3.83
Crown Mysticetes	8	8.04	22.65	14.9	14.52	5.28
Stem Odontocetes	9	19.15	28.2	23.2	22.22	3.25
Physeteroidea	2	11.56	22.1	16.83	16.83	7.45
Platanistoidea	7	8	28.58	21.46	22.88	7.03
Ziphiidae	17	16.1	34.53	28.51	30.05	5.05
Lipotidae	2	12.65	34.12	23.38	23.38	15.18
Kentriodontidae	2	29.99	31.23	30.61	30.61	0.88
Inoidea	2	19.1	23.25	21.18	21.18	2.93
Phocoenidae	7	23.18	35.47	30.46	32.46	4.36
Monodontidae	2	20.85	23.81	22.33	22.33	2.09
Delphinidae	30	20.09	44.04	28.06	27.58	4.26
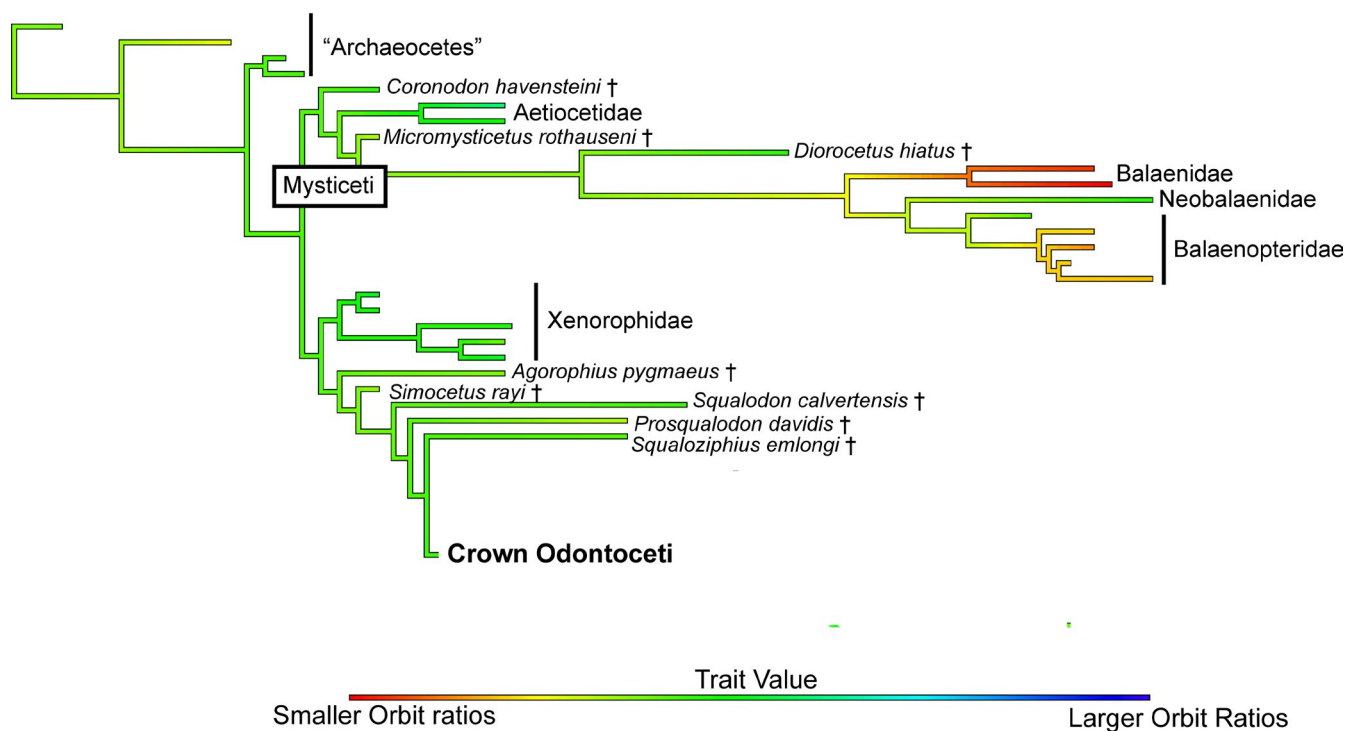
FIGURE 4 Ancestral character state reconstruction of orbit length as a ratio to bizygomatic width in whales, focused on archaeocetes, mysticetes, and stem odontocetes. Ancestral character state reconstruction for crown odontocetes continues in Figure 5. Warmer colors represent smaller orbit ratios, while cooler colors represent larger orbit ratios. Phylogeny based on Churchill et al. (2016). We position archaeocetes not included in that phylogeny based on Martinez-Cáceres et al. (2017). Branch lengths generated by time scaling the tree using fossil age data and the R package Paleotree

Looking at overall trends (Figure 7), body mass and total length showed the same pattern: as body size increased, the orbit ratio decreased. Outliers to this general pattern included *Cephalorhynchus commersoni*, *Mesoplodon*, and *Indopacetus*, which had unusually large orbits compared to the overall allometric trend. Taxa with unusually small orbits for their size included Balaenidae, Physeteridae, Platanistidae, Lipotidae, and Iniidae.

Orbit ratio did not vary with dive depth (Figure 8a). For dive duration, as dive duration increased, orbit size decreased (Figure 8b). Taxa that violated this trend include *M. densirostris*, *M. bidens*, *Ziphius*, *P. phocoena*, and *Steno*, all possessing unusually large orbit ratios for their recorded dive duration. Balaenopteridae (except *B. acutorostrata*), Physeteridae, Platanistidae, and Lipotidae had unusually small orbit ratios for their recorded maximum dive duration.
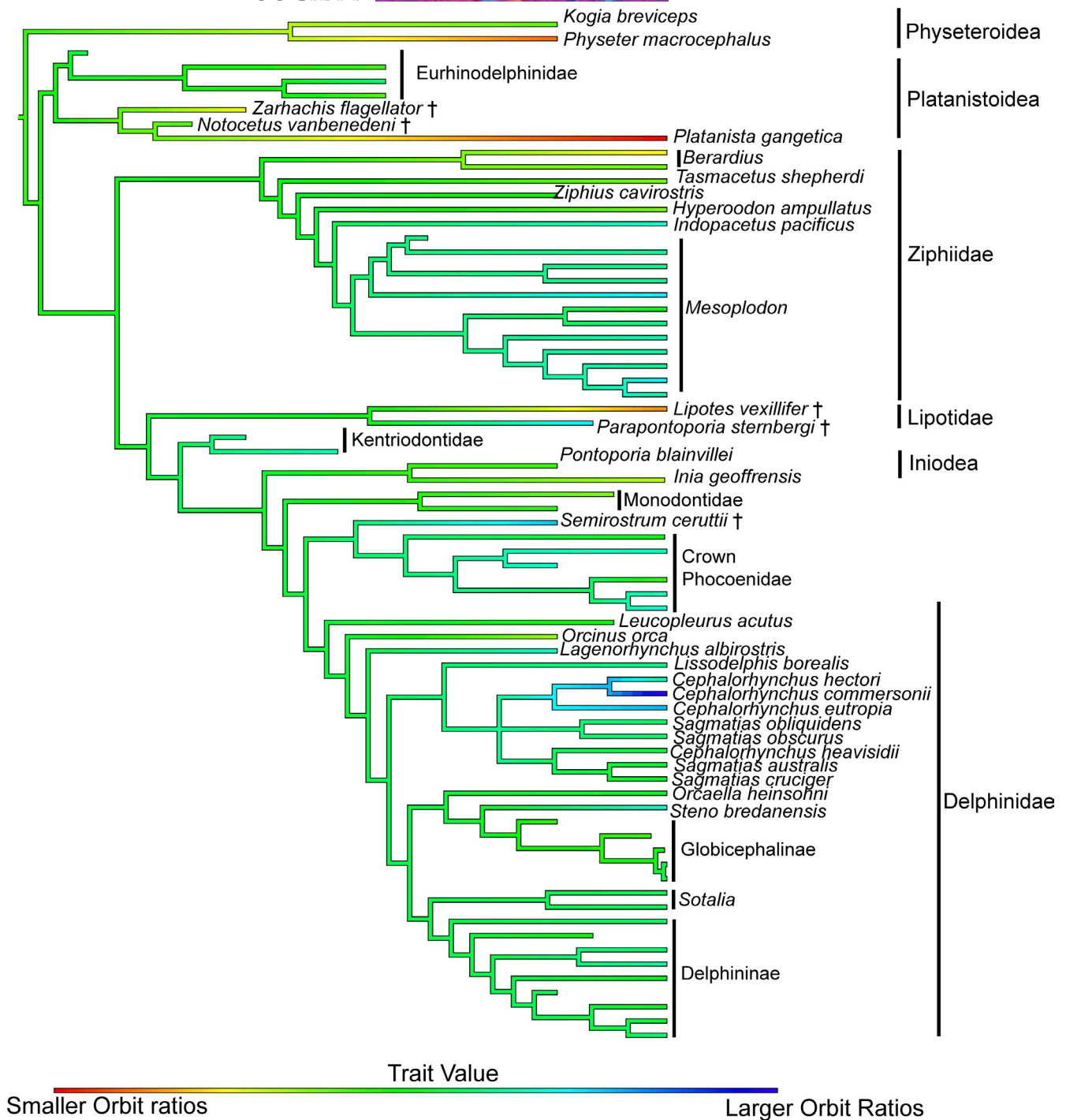
FIGURE 5 Ancestral character state reconstruction of orbit length as a ratio to bizygomatic width in whales, focused on crown odontocetes. Relationships and ACSR of archaeocetes, mysticetes, and stem odontocetes are shown in Figure 4. Warmer colors represent smaller orbit ratios, while cooler colors represent larger orbit ratios. Phylogeny based on Churchill et al. (2016) We place taxa not included in that phylogeny based on McGowen et al. 2020 for delphinoids, Yamada et al. (2019) for *Berardius minimus*, Dalebout et al. (2014) for ziphiids, and Lambert et al. (2015) for "*Argyrocetus*" *joaquinensis*. Branch lengths generated by time scaling the tree using fossil age data and the R package Paleotree

Orbit ratio did not vary with cranial asymmetry (Figure 9a). For frequency spectrum, we observed that, as the highest frequency of sound produced increased, orbit ratio also increased (Figure 9b). Taxa that had unusually large orbit ratios relative to the highest sound frequency produced include *Indopacetus*, *Mesoplodon*, and

C. commersoni. Taxa with unusually small orbit ratios in comparison to the produced spectrum frequency of sound include Balaenidae, Physeteridae, Platanistidae, *Berardius*, and Lipotidae.

When we corrected for phylogeny, we did not find any correlation between orbit ratio and the above variables. *p*-values generally
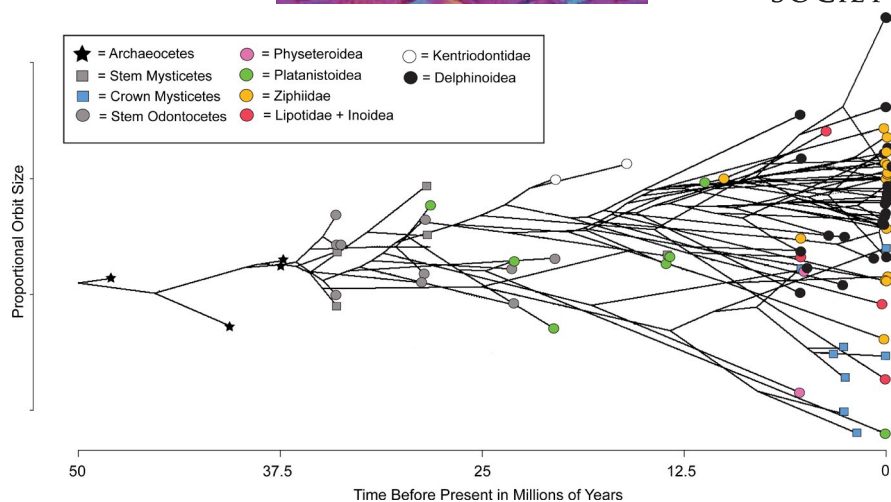
FIGURE 6 Phenogram depicting change in the size of the orbit through time. Orbit size is a ratio of orbit length to bizygomatic width of the skull

TABLE 2 Results of generalized least-squares (GLS) and phylogenetic independent contrast (PIC) regressions of orbit ratio and life history relevant variables

| Variables | GLS | | PIC |
	Equation	p and R^2 values	p and R^2 values
Log body mass	**Y = −0.1x + 1.67**	**$p < 0.001 R^2 = 0.40$**	$p = 0.21$ $R^2 = 0.05$
Log total length	**Y = −0.30x + 1.57**	**$p < 0.001 R^2 = 0.38$**	$p = 0.19$ $R^2 = 0.05$
Log maximum dive depth	Y = −0.10x + 1.59	$p = 0.16$ $R^2 = 0.04$	$p = 0.29$ $R^2 = 0.03$
Log maximum dive duration	**Y = −0.13x + 1.46**	**$p = 0.04$** **$R^2 = 0.10$**	$p = 0.48$ $R^2 = 0.009$
Asymmetry index (Sum radii)	Y = 0.08x + 1.36	$p = 0.71$ $R^2 = 0.01$	$p = 0.15$ $R^2 = 0.04$
Peak frequency (KHz)	**Y = 0.001x + 1.23**	**$p = 0.001$** **$R^2 = 0.21$**	$p = 0.61$ $R^2 = 0.009$

Significant correlations indicated in bold.

ranged from 0.15 at their lowest to 0.61 at their highest, with R^2 values all below 0.05.

3.4 | Orbit Size and qualitative life history characters

We found significant differences (F = 3.54, Df = 2, $p = 0.036$) in average orbit ratios among the three habitat categories (Figure 10a) in the permutation ANOVA; however. no significant differences were found between the three habitat categories using Wilcoxon paired rank sum tests. Freshwater taxa had the smallest average orbit ratios (mean = 16.97%) when compared with either nearshore (mean = 26.76%) and offshore (mean = 25.44%) taxa. For nearshore taxa, *Cephalorhynchus commersoni* had an unusually large orbit ratio, while *Balaena* and *Eschrichtius* had unusually small orbit ratios. *Physeter* and *Eubalaena* had unusually small orbit ratios for offshore taxa. When phylogeny is removed, no significant differences

can be found in orbit ratio in relation to foraging habitat (F = 7.11, $p = 0.47$).

Significant differences (F = 10.71, Df = 5, $p < 0.001$) were also found in average orbit ratios between taxa with different prey capture strategies (Figure 10b). Snap (mean = 16.05%), engulfment (mean = 15.88%), and skim (mean = 13.45%) feeders had the smallest orbit ratios, while ram (mean = 29.29%) and suction (mean = 26.04%) feeders had the largest orbit ratios. Grip-and-tear (mean = 22.47%) feeders had orbit ratios intermediate in size. *Cephalorhynchus commersoni* and *Ce. eutropia* had unusually large orbit ratios for ram feeders, while *Physeter* had an unusually small orbit ratio for a suction feeder. Wilcoxon paired rank sum tests revealed significant differences between ram feeders versus snap ($p = 0.002$), engulfment ($p < 0.001$), and skim ($p = 0.002$) feeders; and suction feeders versus skim ($p = 0.012$) feeders. Significant differences were also found between engulfment and suction feeders ($p = 0.049$), although barely. When the data is corrected for phylogeny, no significant differences (F = 12.22, $p = 0.1$) were found between the different prey capture strategies.
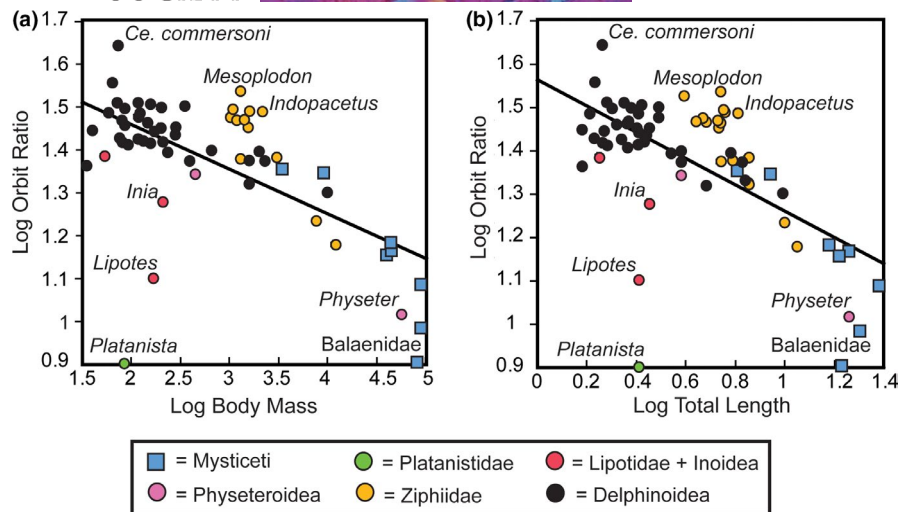
FIGURE 7 Relationships between body mass (a) and total body length (b) and proportional orbit size. Different taxonomic groups represented by different colors, with mysticetes indicated by square symbols and odontocetes indicated by round symbols. Orbit size is a ratio of orbit length to bizygomatic width of the skull. Body size information from Jefferson et al., 2008 [viewed at wileyonlinelibrary.com]
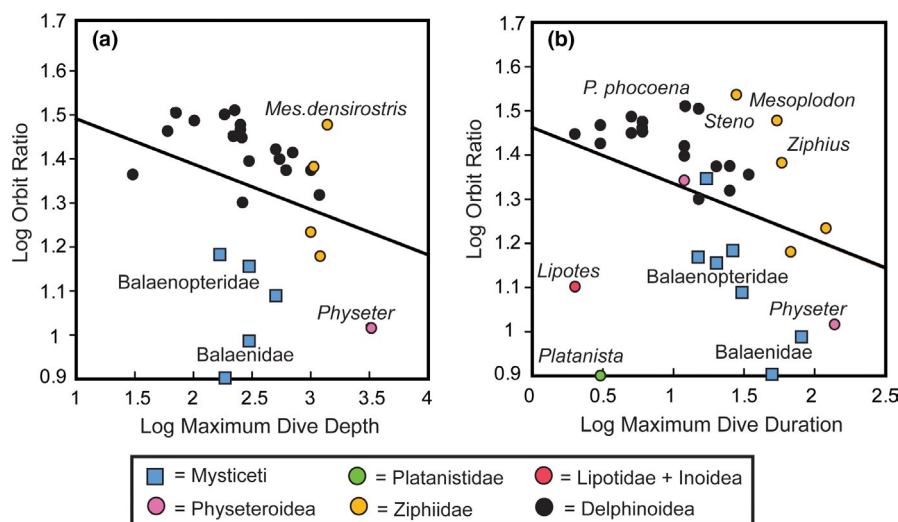

FIGURE 8 Relationships between log maximum dive depth (a) and log maximum dive duration (b) and proportional orbit size. Different taxonomic groups represented by different colors, with mysticetes indicated by square symbols and odontocetes indicated by round symbols. Orbit size is a ratio of orbit length to bizygomatic width of the skull. Diving depth and duration data from Schreer & Kovacs, 1997, Edwards & Schnell, 2001, and Tyack et al., 2006

4 | DISCUSSION

4.1 | Orbit size and the evolution of echolocation

We predicted that proportional orbit size would decrease concomitant with the evolution of echolocation in odontocete whales, as vision would have reduced importance. Eyes are energetically costly to maintain (Moran et al., 2015), and thus, it would make sense for the size of these organs to diminish in time with reduced need. This prediction was wrong, and we found no overall shift in proportional orbit size corresponding to the evolution of echolocation. Proportional orbit size in early-diverging stem odontocetes (including xenorophids and simocetids) was not significantly different from either archaeocete

whales or later diverging crown odontocetes. Instead, a tendency toward increased orbit size is present in some clades of echolocating whales, such as ziphiids and certain delphinoids. Vision is important for social interactions as well as the capture of prey (Madsen & Herman, 1980; Mass & Supin, 2017; Mobley & Helweg, 1990). For most clades of odontocete whale, echolocation has not been able to replace vision for these functions fully.

For some whales, it is clear that possession of biosonar has compensated for the decrease in utility of vision in certain environments (Zhou et al., 1980). This is the case for the "river dolphins" *Platanista* and *Lipotes*. Both species inhabit riverine environments with high sediment loads, reducing the utility of vision underwater for navigation and foraging. Both species had unusually small orbits, with
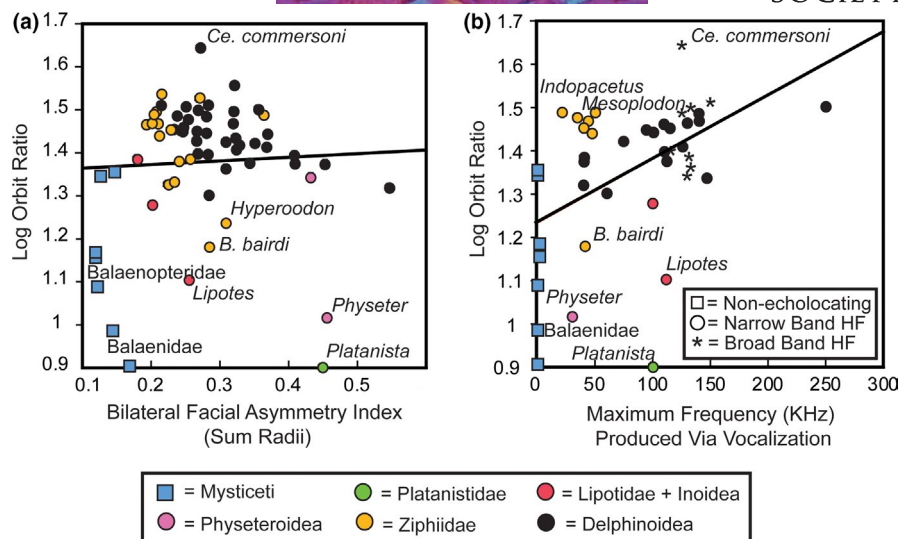
FIGURE 9 Relationships between facial asymmetry (a) and maximum frequency of sound produced (b) and proportional orbit size. Different taxonomic groups represented by different colors, with mysticetes indicated by square symbols and odontocetes indicated by round symbols. In plot b, non-echolocating taxa (mysticetes) are indicated by square symbols, taxa that are narrow-band high frequency producers are indicated by round symbols, and broad-band high frequency producers are indicated by stars. Orbit size is a ratio of orbit length to bizygomatic width of the skull. Facial asymmetry index from Coombs et al. (2020) and maximum frequency of sound produced from Ketten (1994) and Morisaka and Connor (2007)

Platanista having the smallest proportional orbit (8%) of any whale included in this study. Beyond reduction in orbit size, *Platanista* also shows degeneration of the lens of the eye (Pilleri, 1974; Purves & Pilleri, 1975), and it is likely that the eye is only capable of distinguishing light from dark (Herald et al., 1969; Kelkar et al., 2018). In this way, vision may play an important role in orientation while swimming (Herald et al., 1969; Kelkar et al., 2018; Pilleri, 1974), but may not play much a role in social interaction or prey capture. *Lipotes* also possessed a proportionally small eye (12.65%), although it appears to remain fully functional despite some degree of atrophication of the eye muscles and nerves (Zhou et al., 1980). In these two lineages, we can thus clearly see that the possession of echolocation has allowed species to adapt to new environments where vision is of limited use.

4.2 | Orbit size and allometry

In examining variables related to different aspects of life history and their relationship to orbit size, we found that a strong allometric relationship existed between orbit size and body size. As body size increased, proportional orbit size decreased. While we did not recover this relationship when phylogeny was considered, it still provided the best overall explanation to the pattern we observed in orbit ratio variation.

Deviations in this overall pattern were evident, with some taxa having proportionally smaller or larger orbits than expected for their body sizes. Differences in ecology explain many of these deviations, but variation in allometry and development may explain others.

Taxa with unusually small orbit sizes in relation to body size included the river dolphins *Platanista* and *Lipotes*, right whales

(Balaenidae), and the sperm whale *Physeter*. The reason for the unusually small orbits in rivers dolphins is probably ecological and is discussed later in this paper.

For the remainder, all large taxa, one explanation for these unusually small orbits could be due to allometry. Within mammals, there is a tendency for very large species within a taxonomic group to have smaller eyes than expected (Kiltie, 2000; Pihlström, 2012; Ritland, 1982). The relationship between proportional orbit size and body size breaks down, and eye size no longer keeps pace with increases in mass and total length in the same way as it does in smaller taxa. Eyes are expensive organs to maintain, and at some point, increasing eye size may provide little further benefit to vision while requiring more resources. This could then result in proportionally smaller eyes than expected in very large whales.

The pattern observed in balaenopteroids would seemingly dispute this hypothesis for mysticetes. Balaenopterids attain great body sizes and include the largest animal to have ever evolved, the blue whale *Balaenoptera musculus*. Most balaenopteroids plotted fairly close to the regression line, suggesting that they follow the allometric relationship we described. Although we did not include *B. musculus* in our initial study, we calculated proportional orbit size using data from the literature (Miller, 1924). Using data for specimen USNM 49757, we found that *B. musculus* had a proportional orbit ratio of ~10%, and given a total length of 22.86 m and logging of these measurements, this individual plotted where we would expect it based on allometry and did not possess an unusually small orbit for its body size. This suggests that the deviation found in balaenids is due to ecology, not allometry.

Another enormous whale with relatively small orbits is the sperm whale *Physeter*. *Physeter* makes a stronger case for allometry being
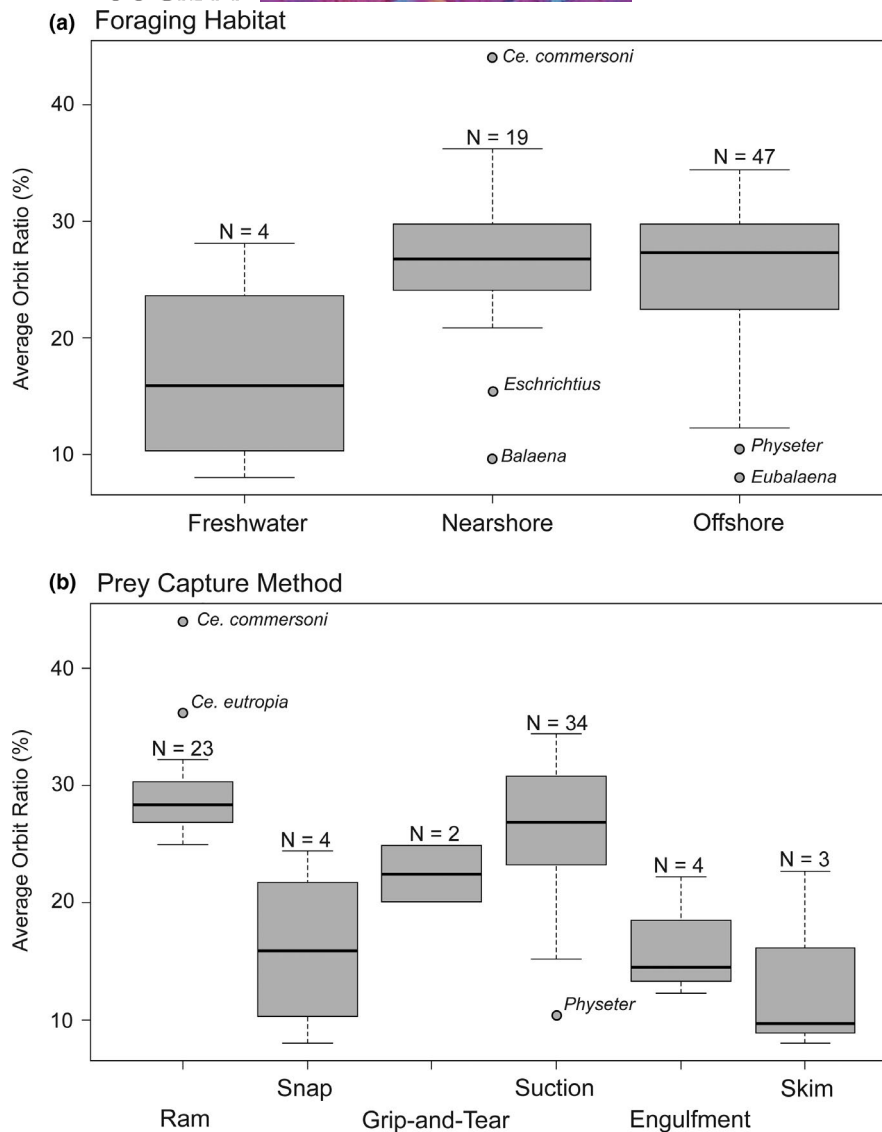
FIGURE 10 Variation in proportional orbit size by foraging habitat (a) and method of prey capture (b). Orbit size is a ratio of orbit length to bizygomatic width of the skull. Habitat classifications based on Jefferson et al. (2008) and prey capture method based upon Johnston and Berta (2011), Galatius et al. (2020), and Martins et al. (2020). Numbers above box plots represent sample size of species. Outliers labeled by scientific name

responsible for the unusually small eyes of this taxon. *Physeter* is largest odontocete whale alive today, and the largest to have ever evolved (Boersma & Pyenson, 2015). Much like ziphiids, *Physeter* is a deep-diving hunter that mostly feeds on squid. Sperm whales are believed to primarily use echolocation to find prey (Aoki et al., 2012; Madsen et al., 2007; Møhl et al., 2000; Norris & Harvey, 1972), although some have hypothesized that vision may be important (Fristrup & Harbison, 2002). Ziphiids share many similarities in ecology, and some taxa showed increased orbit size, consistent with adaptations toward increased light gathering at depth. The closest living relatives of *Physeter*, the dwarf and pygmy sperm whales *Kogia*, possess proportionally larger orbits (22.1%) that matched expectations of orbit size for their body size. Basal physeteroids even showed a propensity for increased orbit size, with some extinct taxa having orbit ratios as high as 28% (Lambert et al., 2016; Lambert et al.,

2010). Given these comparisons, why should the orbits of *Physeter* be so small relative to the body size of the animal? While the orbit is smaller than expected for the size of the animal, the eye shows no major anatomical differences from other whales (Bjerager et al., 2003), other than loss of functional rod opsin genes (McGowen et al., 2020b; Meredith et al., 2013). Perhaps, the simplest explanation is that while *Physeter* orbits are proportionally small, the absolute size of the eye is still enormous. It may be that further investment of resources into producing larger eyes is simply not necessary, and that eyes at this size, especially when working in coordination with echolocation, are more than sufficient, and *Physeter* follow allometric trends seen in other unusually large mammal taxa (Kiltie, 2000; Pihlström, 2012; Ritland, 1982).

At the other extreme, Phocoenidae and *Cephalorhynchus* all had unusually large orbits for their body size. The best explanation for

the unusually large orbit size in phocoenids and *Cephalorhynchus* may be paedomorphosis. Both clades largely inhabit coastal temperate waters and share many similarities in morphology and ecology due to convergent evolution, including a small body size, possession of a stocky body with blunt head, and production of similar vocalizations (Galatius, 2010; Morisaka & Connor, 2007; Read, 2002). Both clades show evidence of paedomorphosis (Galatius, 2010; Galatius et al., 2011), which can be described as the retention of juvenile characteristics into adulthood (Gould, 1977), the result of changes in the timing of development, (heterochrony). Two major forms of heterochrony can accomplish paedomorphosis: neoteny, which is a slowing of the rate of development, or progenesis, the early onset of sexual maturity. In phocoenids and *Cephalorhynchus*, paedomorphosis is a result of progenesis (Galatius, 2010; Galatius et al., 2011). Paedomorphic features found in the skull of these taxa include delayed cranial suture fusion, short rostra, a proportionally large braincase, reduction in the size of orbital processes, reduction in size of the zygomatic processes, and poorly developed lambdoidal and occipital crests (Galatius, 2010; Galatius et al., 2011). Not explicitly cited by Galatius et al., (2011), although correlated with reduction in size of postorbital and preorbital processes, it has increased orbit size. It thus seems reasonable to conclude that the proportionally large orbits of these taxa are not a result of ecological adaptation, but rather a consequence of retention of juvenile features of the skull due to paedomorphosis.

Paedomorphosis may also help explain the large orbits present within the fossil porpoise *Semirostrum*. This bizarre porpoise is unique amongst whales in possessing an extremely elongated and prognathous mandible (Racicot et al., 2014; Racicot & Rowe, 2014). Features of the mandible in addition to tooth wear have been used as evidence for benthic foraging, *Semirostrum* using its elongated mandible to probe the muddy sea bottom to detect and capture prey (Racicot et al., 2014). This foraging strategy would no doubt increase turbidity and reduce visibility, and *Semirostrum* may have relied more upon a sense of touch than vision while hunting (Racicot et al., 2014; Racicot & Rowe, 2014). A reduced use of vision is supported by a decrease in the size of the optic chiasm and optic groove compared to extant porpoises (Racicot & Rowe, 2014). Based on the suggested ecology and the above anatomical features, we would suspect that the eye and thus the orbit would also be reduced in size. We found the opposite, however, with *Semirostrum* possessing a comparably large orbit ratio (35.47%). Further work, including further characterization of other vision-related features, is needed to clarify the ecology of this species and its visual ability.

Alternatively, the unusually large eyes of these species could simply reflect a common trend in scaling of the eye, with taxa that are very small having unusually large eyes for their body size (Kiltie, 2000; Pihlström, 2012; Ritland, 1982). Porpoises and *Cephalorhynchus* rank amongst the smallest of all living whales. The extinct *Parapontoporia* and kentriodontid dolphins included in this study are also very small and possessed proportionally large orbits for their body size. This tendency, alongside paedomorphosis in

Phocoenidae and *Cephalorhynchus*, provides the best explanation for the unusually large orbits of the small taxa discussed here.

4.3 | Orbit size and ecology

4.3.1 | Orbit size and diving ability

Correlations of proportional eye size with ecological variables produced mixed results. Only when we did not consider phylogeny did we recover any significant relationships for dive depth, highest sound frequency produced, foraging habitat, and prey capture strategy. Much of the reason for this comes from the inextricable entanglement of allometry and life history with phylogeny. Phylogenetic conservatism is known to bias analyses that use phylogenetic correction (de Bello et al., 2015), with the removal of phylogeny also breaking any association of the trait of interest with different life history variables. Examples of phylogenetic conservatism can be seen in body size, prey capture, and habitat, with very large body size, snap, skim, and engulfment feeding, and occupation of freshwater environments limited to a very small number of often closely related and highly divergent taxa. Further complicating the situation, some of the variables selected will also interact with other life history parameters. For instance, increases in eye size may enhance vision while feeding at depth, but diving ability is also related to body size (Noren & Williams, 2000), which, in turn, influences proportional orbit size. Thus, even though our PIC analyses did not find significant relationships between some of the variables we examined and orbit size, it is premature to rule out the role of these life history traits in explaining orbit size variation for some taxa.

Large orbit size correlates with deep diving behavior in marine tetrapods (Debey & Pyenson, 2012; Humphries & Ruxton, 2002; Motani et al., 1999). On that note, we see a pattern of increased orbit size in *Mesoplodon* and *Indopacetus*. Beaked whales, including *Mesoplodon*, are champion deep divers that almost entirely rely upon echolocation to locate and capture prey (Johnson et al., 2008). It may thus be reasonable to suspect that proportional orbit size would decrease or at least not change, rather than increase in these whales, consistent with what we observed in *Physeter*. Results from our study suggest that vision continues to play an important role in beaked whale behavior. Although light may be absent when diving below the photic zone, many marine organisms create bioluminescence in the abysmal depths, and *Mesoplodon* may use that light to find prey (Fristrup & Harbison, 2002). Vision may also be important for social interactions. Male beaked whales possess elaborate tusks, which vary in shape and position amongst species. These tusks are used for fighting (Macleod, 2000), but fighting alone does not explain the morphological variation inherent in these structures. Instead, these tusks may be important for species recognition, preventing hybridization between sympatric taxa (Macleod, 2000). Eyesight may thus play a very important role in mate selection for members of this

genus, allowing females to identify males of their species by their unique tusk morphology.

4.3.2 | Orbit size and macropredation

Orbit size is sometimes linked to macropredatory behavior and specialization toward hunting large vertebrate prey (Fitzgerald, 2006). This may have been especially important in stem mysticetes that lack echolocation or adaptations for filter feeding. We did not focus our study on examining orbit size evolution in mysticetes, although we did include several stem mysticetes. *Coronodon havensteini* had an orbit ratio of 23.67%, similar to that observed in the archaeocetes *Zygorhiza* and *Dorudon*. In contrast, the later diverging *Chonecetus* and *Aetiocetus cotylalveus* had orbit ratios of 25.02% and 29.33% respectively, an increase over their archaeocete ancestors. Gathering data from the literature (Deméré & Berta, 2008; Fitzgerald, 2006; Peredo et al., 2018), we also calculated proportional orbit size for several other reasonably complete extinct stem mysticetes. *Janjucetus* had the largest orbit ratio of any mysticete (36.1%), and indeed one of the largest orbit ratios of any whale. Although we calculated proportional orbit size differently than Fitzgerald (2006), we nonetheless confirmed the unusually large orbits possessed by this taxon. We found proportionally large orbits in other extinct mysticete taxa including *Aetiocetus weltoni* (29%) and *Maiabalaena nesbittae* (31.7%). This would seem to confirm that stem mysticetes went through a phase of evolution where they were active pursuit predators relying on vision, preceding a shift toward filter feeding in later-diverging lineages (Fitzgerald, 2006; Marx, 2011). Caution is warranted for these conclusions, as some of the mysticete taxa with the largest proportional orbit sizes are also the smallest known mysticetes (Marx et al., 2015), and small taxa often have unusually large eyes (Kiltie, 2000; Pihlström, 2012; Ritland, 1982). The increased orbit size seen in some of these taxa could be a result of paedomorphic processes and dwarfing, as seen in phocoenids and *Cephalorhynchus*. Paedomorphosis may have played a significant role in mysticete evolution (Tsai & Fordyce, 2014a; Tsai & Fordyce, 2014b). However, many cranial features linked to paedomorphosis in delphinoids, other than possession of a short rostrum, were absent in *Janjucetus* and other stem mysticetes. These features include reduced orbital processes, proportionally large braincases, reduced zygomatic processes, and poorly developed lambdoidal and occipital crests. This would provide further credence to the idea that the large orbits of *Janjucetus* and possibly other toothed mysticetes were an adaptation to predatory behavior, but further work is needed to assess the role of heterochrony in toothed mysticete evolution.

In contrast to what we saw in extinct mysticetes, the extant odontocete that pursues the most macropredatory lifestyle, *Orcinus orca*, had an orbit ratio of 20.09%. This was within the normal range of variation for other delphinids. This could suggest that macropredatory odontocetes do not need to rely on vision to the same extent as non-echolocating predators. *Orcinus* is a relatively young

taxon and lacks a fossil record from prior to the Pliocene (Heyning & Dahlheim, 1988). The earliest known member of this genus, *O. citoniensis*, was much smaller and possessed a morphology intermediate between *O. orca* and typical delphinids (Pilleri & Pilleri, 1982). The lack of enlarged orbits in this taxon could be a result of there being insufficient time for this feature to evolve, or perhaps more likely, that the unique style of cooperative hunting carried out by this species may have reduced the need for further increases in eye size.

Two groups of extinct odontocete have been proposed to pursue macropredatory lifestyles, the paraphyletic "squalodont" whales (Loch et al., 2015; Marx et al., 2016) and some physeteroid whales (Bianucci & Landini, 2006; Lambert et al., 2010). Only two squalodont-like whales were included in our study, *Squalodon* and *Prosqualodon*. Both have moderate orbit ratios within the range of variation typical of most modern odontocetes of their size (23.13% and 19.16% respectively). Thus, we cannot use orbit size as evidence for macropredatory behavior in these taxa.

We did not initially include any extinct physeteroids in our study; however, we were able to calculate proportional orbit size for three physeteroids with proposed macropredatory habits based on measurements from the literature (Bianucci & Landini, 2006; Lambert et al., 2016; Lambert et al., 2010). Two of the three species sampled possessed unusually large orbit ratios, including *Livyatan* (25.63%) and *Acrophyseter* (28%). *Zygophyseter* possessed a much smaller orbit ratio (18.79%). Although the proportional orbits for *Livyatan* and *Acrophyseter* did not reach the size seen in some stem mysticetes, they are nonetheless much larger than those of many odontocetes. Furthermore, unlike the stem mysticetes, these extinct physeteroids attained large body sizes, ruling out allometry or paedomorphosis as a probable explanation for orbit size. Macropredatory behavior has been suggested in these sperm whales based on the presence of large body size, enormous temporal fossae, robust teeth, and possession of short and wide rostra (Bianucci & Landini, 2006; Lambert et al., 2010). In addition to the above characters, we can add possession of a large proportional orbit as potential evidence of macropredatory behavior in some extinct sperm whales.

4.3.3 | Orbit size and "river dolphins"

On the other end of the orbit ratio spectrum, some taxa had unusually small orbits, with "river dolphins" the most obvious example. Small eye size is obvious for these species and taken to the extreme in *Platanista*. This reduction in eye size is unique to *Platanista* amongst platanistoids: most extinct platanistoids had orbit ratios between 17 and 28%. Some taxa, such as *"Argyrocetus" joaquinensis* and *Schizodelphis*, had even larger orbits. This suggests that vision was still important in extinct platanistoids.

Lipotes had the second smallest proportional orbit of any river dolphin. The fossil record for Lipotidae is much more limited, with only *Parapontoporia* considered a close relative (Geisler et al., 2012; Geisler & Sanders, 2003). In contrast to *Lipotes*, *Parapontoporia* had unusually large orbits (34%). *Parapontoporia* was a very small

odontocete, much like *Phocoena* and *Cephalorhynchus*. It is likely the increase in orbit size in this extinct taxon may simply be due to the very small body size of this species and allometry, as discussed above.

Inia had an orbit somewhat smaller than is typical for an odontocete of its body size (19.1%), but not as small as *Lipotes* or *Platanista*. This is consistent with the previous studies that have found the eye of this species to be larger than *Platanista* and *Lipotes*, but smaller than most marine dolphins (Mass & Supin, 1989; Pilleri, 1977). It is unclear when *Inia* first entered freshwater, as this species has no close extant marine relatives. Iniids are known from the Late Miocene of South and North America (Cozzuol, 2010; Geisler et al., 2012). Evidence of members of this family inhabiting freshwater environments is almost as old, with fossils from freshwater deposits dating to the Late Miocene of Argentina (Gutstein et al., 2014), although this taxon was likely not ancestral to *Inia*. Beyond an orbit showing minor reduction in size, *Inia* also lacks a tapetum lucidum and displays a yellowing of the lens (Mass & Supin, 2017).

Although habitat may help explain the reason for why these species have small orbits, not all freshwater species show the same decrease in orbit size. No reduction in orbit size was evident in *Sotalia fluviatilus* (28.12%). *Neophocoena asiorientalis* has a freshwater population in the Yangtze River. Although we did not directly sample individuals belonging to this population, morphologically similar and closely related marine populations of the same species showed no reduction in orbit size (25.69%). Lack of orbit reduction in *Sotalia* and *Neophocoena* may reflect the relatively recent invasion of these taxa into freshwater environments. *Sotalia fluviatilus* only diverged from its marine sister taxon 1–1.2 mya (Caballero et al., 2007), while *Neophocoena* may have colonized the Yangtze River 100,000 years ago (Zhou et al., 2018). There simply may have not been enough time for the diminished need for vision to result in changes in eye anatomy in these taxa.

Even though the phylogenetic ANOVA did not find significant differences between freshwater taxa and whales inhabiting other environments, habitat is still the best explanation for diminished orbit size in river dolphins. As dolphins adapted to living in muddy, turbid rivers, vision became less important and echolocation more important; consequently, eyes became smaller and less developed. That there is variation in the degree of degeneration and reduction in the size of the eye may simply be a matter of when the ancestors of each of these taxa entered freshwater or at least estuarine environments.

4.3.4 | Orbit size and skim-feeding

Balaenopterids possessed the proportionally largest orbits of modern mysticetes and specialize in suction and engulfment feeding, targeting larger prey items (Kawamura, 1980; Werth, 2000) than balaenids. Balaenopterids employ a variety of different hunting strategies to corral and capture their food (Hain et al., 1982). Vision is likely to be important in prey capture for balaenopterids, explaining the proportionally larger orbits of these species when compared to balaenids.

Balaenids, in contrast, had the proportionally smallest orbits of any mysticete, extinct, or extant. Balaenids are the only large mysticetes to specialize in skim feeding. In skim feeding, balaenids passively swim through large aggregations of zooplankton with their mouths open, straining tiny prey from the water column (Werth, 2000; Werth & Potvin, 2016). Given the size of the prey and strategy used, vision is of probably limited use in foraging. Balaenids may instead rely upon a sense of smell to track plankton concentrations (Baumgartner et al., 2007). Unlike odontocetes, mysticetes retain functional olfactory bulbs (Berta et al., 2016; Cave, 1988; Pihlström, 2008), and right whales specifically have an excellent sense of smell (Kishida & Thewissen, 2012; Thewissen et al., 2011). Aggregations of plankton may produce their own distinct chemical trails that allow the whales to find them at distance (Baumgartner et al., 2007). With a reduced need for vision, there may have been no selective pressure for eye size to track body size to the same degree as seen in balaenopteroids, leading to a diminishment of eye size.

5 | CONCLUSIONS

Ancestral character state analysis of proportional orbit size revealed that, while echolocation plays a major role in how odontocete whales perceive their environment, the evolution of this sense does not seem to have influenced orbit size. Our study found that proportional orbit size varied little during the transition from non-echolocating to echolocating whales. When we examined the correlation between various life history variables and orbit size, we received mixed results, with correction for phylogeny removing most significant differences. Our failure to find significant results may be a result of the inability to fully separate out the influences of phylogeny, allometry, and ecology given that variation in life history traits corresponds to taxonomic differences. Allometry appeared to explain most variation in orbit size, with proportional orbit size decreasing with body size. Taxa that violated this trend included *Cephalorhynchus* and Phocoenidae, likely due to their unusually small body size and through paedomorphic retention of unusually large orbits. Members of the genus *Mesoplodon* also showed unusually large orbits for their body sizes, which may have helped them with finding prey at deep ocean depths and for recognition of conspecifics during social interactions. River dolphins, *Physeter*, and balaenids possessed unusually small orbits for their body size. Small orbit size in river dolphins is related to increased reliance on echolocation for foraging in sediment-laden waters, while reduction in orbit size in balaenids may be a result of decreased importance for vision during skim feeding. The proportionally small eyes of *Physeter* may relate to eye size not keeping up with body size at the same rate as other taxa in the largest known odontocete.

AUTHOR CONTRIBUTIONS

M.C.: designed the study. M.C. and C.B. carried out the analyses and wrote the paper. C.B. collected the data.

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