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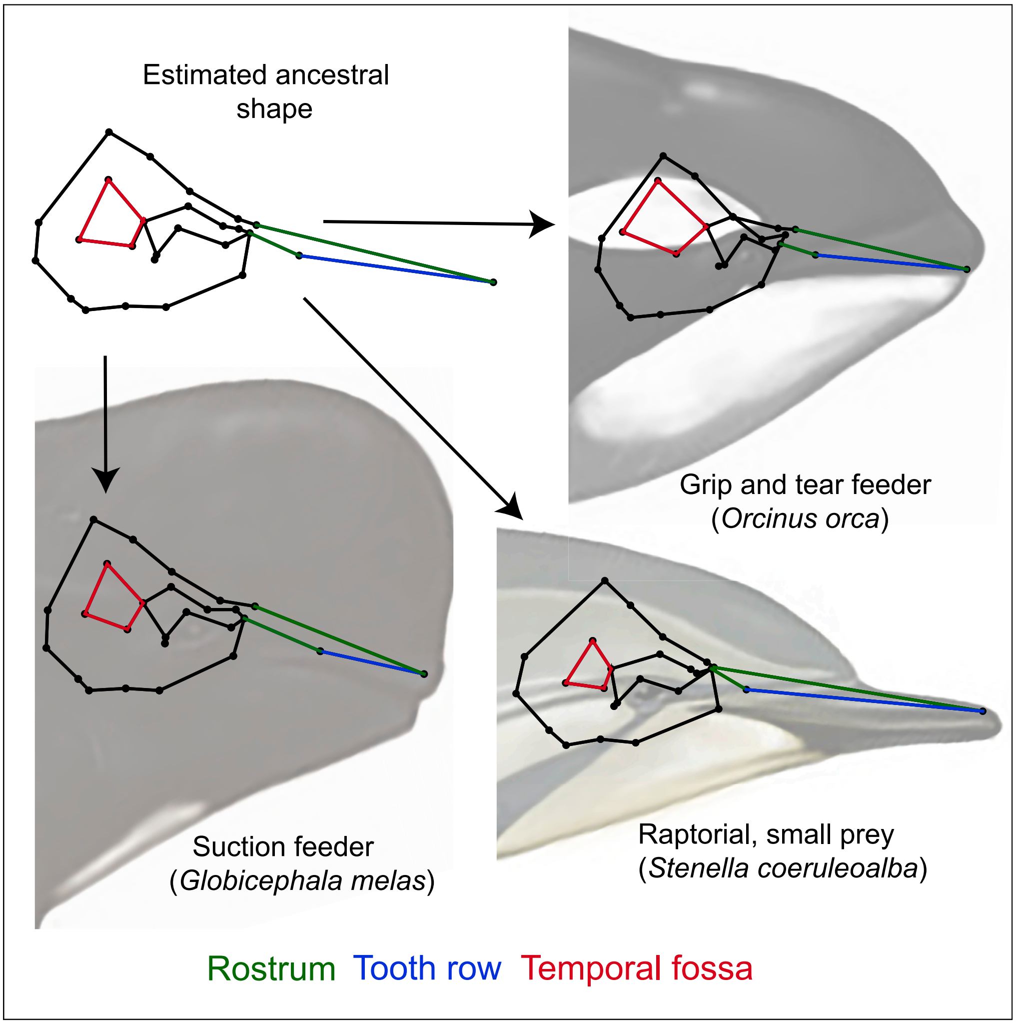

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HIGHLIGHTS

Dolphin skull shape is highly dependent on phylogeny

Feeding mode and prey size are primary drivers of the evolution of dolphin skull shapes

Adaptive radiation of skull shapes has been followed by evolutionary stability

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Evolution and Diversification of Delphinid Skull Shapes

Anders Galatius,[1,5,*] Rachel Racicot,[2] Michael McGowen,[3] and Morten Tange Olsen[4]

SUMMARY

The diversity of the dolphin family was established during a short window of time. We investigated delphinid skull shape evolution, mapping shapes on an up-to-date nuclear phylogeny. In this model, the common ancestor was similar to *Lagenorhynchus albirostris*. Initial diversification occurred in three directions: toward specialized raptorial feeders of small prey with longer, narrower beaks, e.g., *Delphinus*; toward wider skulls with downward-oriented rostra and reduced temporal fossae, exemplified by suction feeders, e.g., *Globicephala;* and toward shorter and wider skulls/rostra and enlarged temporal fossae, e.g., *Orcinus*. Skull shape diversity was established early, the greatest later developments being adaptation of *Steno* to raptorial feeding on large prey and the convergence of *Pseudorca* toward *Orcinus*, related to handling large prey. Delphinid skull shapes are related to feeding mode and prey size, whereas adaptation to habitat is not marked. Over a short period, delphinid skulls have evolved a diversity eclipsing other extant odontocete clades.

INTRODUCTION

In toothed whales, skull shape variation has been related to feeding and prey preferences (McCurry et al., 2017a; Werth, 2006a) as well as habitat (Galatius et al., 2011; Monteiro-Filho et al., 2002). Shape variation of skulls thus reflects the basic ecology of a species, making it a useful tool for studying macroevolutionary patterns. The family of oceanic dolphins (Delphinidae) consists of approximately 37 extant species that occur over a range of aquatic habitats from rivers to the open ocean and in climates ranging from the Arctic to the Tropics (Committee on Taxonomy, 2019; Jefferson and LeDuc, 2018). Prey preferences also show large variation, including benthic and pelagic fish in a large range of sizes, a diversity of cephalopods, and other marine mammals such as seals, dolphins, porpoises, and baleen whales (Slater et al., 2010). Unsurprisingly, this large ecological variation is reflected in a large diversity of skull shapes.

The odontocete family Delphinidae is an example of an explosive radiation with a rich diversity of species being established during a relatively short window of time approximately 10–15 mya (McGowen, 2011; McGowen et al., 2009, 2019; Steeman et al., 2009). This has been explained by physical restructuring of the oceans and temperature fluctuations during the late Miocene and early Pliocene epochs (Steeman et al., 2009). The rapid speciation and rich diversity also reflects a diversity of ecological niches where the basal, shared traits of delphinids such as large relative brain size, sophisticated echolocation, and sociality are presumed to have provided a competitive advantage (LeDuc, 2002). Some of these same traits are shared by the delphinoid relatives of delphinids to some degree, although, for example, sociality is low in phocoenids.

Several strategies for prey capture have evolved among aquatic tetrapods; usually these are divided into three or four classes: raptorial feeding, grip and tear feeding, suction feeding, and filter feeding (Kienle and Berta, 2016; McCurry et al., 2017b; Werth, 2000a). Except filter feeding, all of these strategies are seen in extant delphinids. Raptorial feeding is probably the plesiomorphic condition in odontocetes, as it requires few, if any, modifications relative to the feeding strategies of terrestrial ancestors (Werth, 2000a). Adaptations such as homodonty, polydonty, and longirostry have served to enhance raptorial capabilities (Werth, 2000a). Raptorial feeding, also called "pierce feeding," simply involves grasping prey items in the jaws following movements of the head, neck, and/or the whole body to swallow prey whole. Several odontocetes have long, specialized rostra with many pointed teeth for grasping prey, such as river dolphins and, to a lesser extent, many species of delphinids. Grip and tear feeding may be seen as a subset of raptorial feeding, where prey is held, torn, and ripped using large, interlocking teeth as seen in delphinids such

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as *Orcinus* and *Pseudorca* (McCurry et al., 2017b; Werth, 2000a). In suction feeding, prey is drawn into the mouth by a vacuum created by depressing or retracting the tongue (Heyning and Mead, 1996; Werth, 2000b). To increase effectiveness, suction feeding odontocetes tend to have smaller gapes; this may be accomplished by shorter rostra or increased tissue covering the lateral margins of the gape (Werth, 2006b). The dentition of suction feeders is generally reduced or absent (Werth, 2000b, 2006b). Among odontocetes, suction feeding may have evolved several times as a strategy for capturing cephalopods (MacLeod et al., 2006). Many delphinids may use suction and/or raptorial feeding, depending on the targeted prey and the circumstances (Werth, 2000a, 2006a). An alternative classification of aquatic mammalian feeding with emphasis on the process has been proposed (Hocking et al., 2017). In the current study, the former framework will be used, as we are directly investigating morphology.

In addition to prey preference and feeding strategy, habitat may also shape skull morphology. The most well-known examples are more ventrally inclined rostra and occipital condyles in bottom feeders (Galatius et al., 2011; Monteiro-Filho et al., 2002). Another aspect of habitat influencing skull shape may be the climate. Colder climates may favor stouter morphologies to facilitate a smaller surface-to-volume ratio. As an example, *Lagenorhynchus cruciger,* inhabiting Antarctic and subantarctic waters, has a more robust skull than the other members of the subfamily Lissodelphininae living in warmer waters (Galatius and Goodall, 2016).

In the current study, we investigate the diversity and radiation of delphinid skull shapes using the species richness of the North Atlantic, as these species cover all extremes of delphinid skull morphology. We use three-dimensional geometric morphometrics to describe skull shape across the 18 species occurring in the North Atlantic and map these shapes on a phylogenetic tree generated from nuclear genome data to reconstruct a model of the evolution of delphinid skull shapes and investigate the role of skull morphology with respect to habitat, niche partitioning, and feeding strategy. This study underlines the importance of investigating extant morphology and genome-based phylogenetic reconstruction in examining the origins and possible drivers of modern delphinid skull morphologies while supporting our model with evidence from the fossil record.

RESULTS

Shape Is Dependent on Phylogeny

Skull shape was defined by a suite of 48 cranial landmarks (Figure S1; Table S2). A large proportion of the skull shape variation (62.6%) of the North Atlantic delphinids was represented by principal components 1 and 2 of the PCA at 45.6% and 17.0%, respectively. All subsequent components each accounted for less than 7% of the variance. PC1 describes a lengthening of the rostrum with a longer toothrow and a general lateral compression and dorsoventral expansion of the skull with increasing scores. PC2 describes a more ventral orientation of the rostrum and an anterior tilt of the foramen magnum with increasing scores. Furthermore, the temporal fossa is dramatically enlarged, whereas the orbit and its surrounding structures are displaced anteriorly and the braincase is expanded posteriorly.

Mapping of the phylogeny on the PCs (see Transparent Methods) shows two of the phylogenetically earliest-diverging species, *Lagenorhynchus albirostris* and *Leucopleurus acutus*, to maintain a shape proximate to the modeled ancestral shape at the root of the tree (Figure 1). Early branching shows the three subfamilies Orcininae, Globicephalinae, and Delphininae to evolve in different directions in terms of skull shape. The modeled evolution of Orcininae is toward a lower score along PC1 and a higher score along PC2. Globicephalinae have evolved toward lower scores along both PC1 and PC2, whereas Delphininae have evolved toward higher scores along PC1 and somewhat lower scores along PC2. The Delphininae species occupy the lower right part of the plot, with the exception of *Tursiops truncatus*, which retains a position close to the modeled ancestral shape of this subfamily. Among the Globicephalinae, *Pseudorca crassidens* is highly divergent from other members of the subfamily along PC2 and approaches convergence in skull shape with *Orcinus*. In our analysis, the affiliation of *Steno* with Globicephalinae entails the most dramatic adaptation of skull shape within Delphinidae, with a much higher PC1 score, and a higher PC2 score, than its closest relatives. A permutation test with 10,000 iterations of the null hypothesis of no phylogenetic signal in the skull shapes (Klingenberg and Gidaszewski, 2010) gave a significant result ($P < 0.0001$). Figure S2 shows the mean skull shape of each species compared with the grand mean shape of all species.

Feeding Mode and Prey Size Are Primary Drivers of Skull Shape Evolution

Feeding mode appears to be a strong driver of skull shape variation in delphinids (Figure 2). Along the first two PCs, the feeding modes were well separated: grip and tear feeders occupied the upper left quadrant,

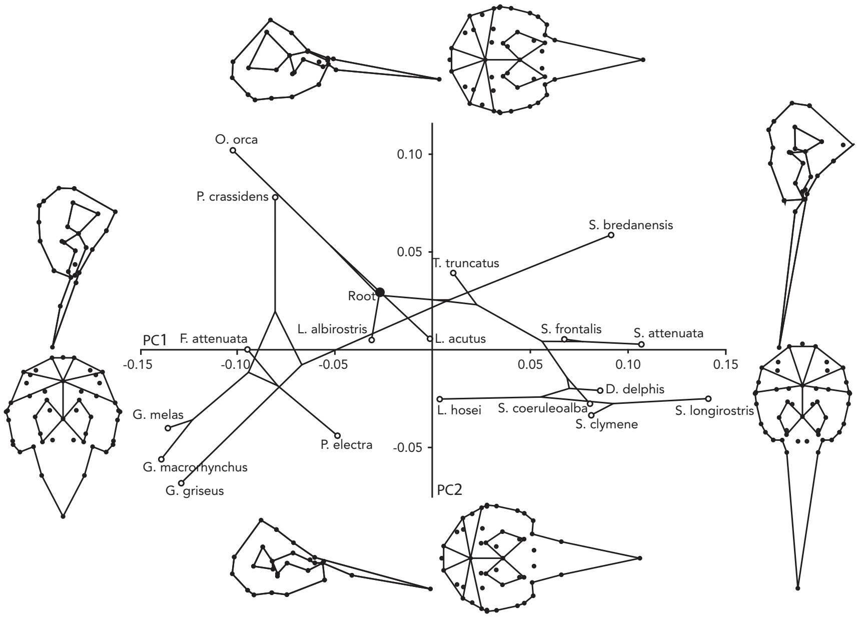

Figure 1. Modeled Evolution of Delphinid Skull Shapes

PC1 (x axis) versus PC2 (y axis) scores of mean skull shapes of the 18 delphinid species of the North Atlantic and the reconstructed scores for nodes and root of the mitogenome phylogeny. Shape changes along the PCs are illustrated at the margins of the plot. Above and below the plot are skull shapes (dorsal and lateral views) representing the highest and lowest scores among the species along PC2, with PC1 scores kept neutral (at zero). Right and left are skull shapes (dorsal and lateral views) representing the highest and lowest scores among the species along PC1, with PC2 scores kept neutral (at zero). See also Figure S2 for species-specific shapes.

suction feeders occupied the lower left quadrant, and raptorial feeders mostly occupied the lower right quadrant and extended into the lower left with more robust species such as *Lagenorhynchus albirostris*, *Peponocephala electra*, and *Feresa attenuata* (Figure 2A). In terms of maximum prey size (see Transparent Methods), the species with "small" maximum prey size (<0.2% of body weight) were mostly isolated in the lower right quadrant. Species with "medium" maximum prey size (>0.2% < 1% of body weight) were distributed in a band of the morphospace running from the lower left quadrant to the upper right quadrant. Species with "large" maximum prey size (>1% of body weight) were positioned in the upper and lower left quadrants (Figure 2B). Phylogenetic generalized least squares regressions of predator-prey size ratios on PCs 1–3 for all species did not yield significant results. Following the example of McCurry et al. (2017b), who removed suction feeders from their analysis, we removed Globicephalinae from the analyses and achieved a significant association for PC2 (see Table 1 for results of PGLS analyses). In terms of climate, species occurring in the "warm temperate-tropical" zone were found throughout the morphospace. Species from the "arctic-cold temperate" zone were only found in the left half of the morphospace along PC1 (Figure 2C). In terms of habitat, species occurring in the "continental slope-oceanic" habitat were found in most of the morphospace. Species occurring in the "continental shelf" habitat were not found in the lower left quadrant. Species occurring in the "coastal" habitat were only found in a narrow band running from the upper left to the lower right quadrant (Figure 2D). To further analyze habitat use, we conducted PGLS regressions of dive depth on PCs 1–3. These did not yield significant results (Table 1). To investigate relationships of shape with size, we conducted PGLS regressions of centroid size on PCs 1–3. These analyses yielded a significant result for PC1, indicating that species relying on suction or grip and tear feeding tend to be larger than raptorial species, irrespective of phylogeny.

DISCUSSION

Skull Shapes Radiated from a Central Position of the Morphospace

According to our reconstruction of the radiation of delphinid skull shapes, the ancestral shape of delphinid skulls was similar to those of the extant species *Lagenorhynchus albirostris*, *Leucopleurus acutus*, or *Tursiops truncatus*. This entailed a moderately long and robust rostrum, a temporal fossa of intermediate size, a toothrow running most of the length of the rostrum, and a general shape that is intermediate relative

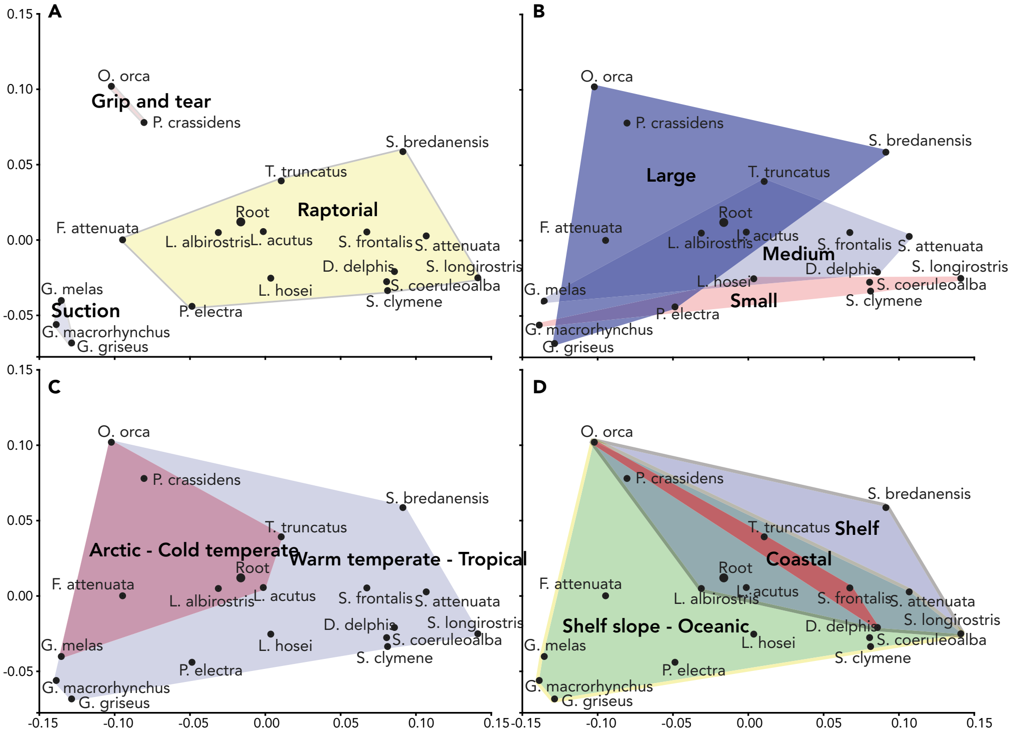

Figure 2. Skull Shape Morphospace in Relation to Feeding Mode, Prey Size, Climate, and Habitat

Plots of average shapes of species along PCs 1 and 2 with polygons defining sub-morphospaces for categories based on feeding strategy (A), maximum prey size (B), occurrence in climate zones (C) and occurrence in habitat type (D).

to the extremes shown by the current variation. The earliest known delphinid fossil is *Eodelphinus kabatensis,* dating to the late Miocene, 13–8.5 mya (Murakami et al., 2014a, 2014b). The width of its premaxillae at the base of the rostrum and relatively robust teeth point to a rostrum of intermediate length and width, similar to our estimated ancestor.

When compared with the range of skull shapes within extant and extinct odontocetes, the diversity within Delphinidae is rather low. The earliest known odontocetes (Oligocene, 33.9–24 mya) possessed the greatest disparity and diversity in facial region morphologies associated with telescoping of the skull, compared with any later lineage including modern clades (Churchill et al., 2018). Diversity in rostral length peaked in the early Miocene (~20–16 mya) (Boessenecker et al., 2017); however, bizarre forms that greatly deviated from a generalized odontocete rostrum existed into the Pliocene (5.3–2.6 mya), such as the walrus-like delphinoid *Odobenocetops* and the strange porpoise with an elongate mandible, *Semirostrum ceruttii* (Benites-Palomino et al., 2020; Boessenecker et al., 2017; Churchill et al., 2018; de Muizon, 1993; Lambert, 2005; McCurry and Pyenson, 2019; Racicot et al., 2014). Thus, the relatively low diversity of modern and fossil delphinid skull morphology may result from the relative age of the taxon; however, facial asymmetry, telescoping of the skull, and loss of tooth replacement, all of which emerged in the Oligocene, undoubtedly constrain facial morphologies (Boessenecker et al., 2017; Churchill et al., 2018, 2019).

Although "kentriodontids" (Odontoceti: Kentriodontidae), an extinct paraphyletic group of small odontocetes with relatively symmetrical skulls that were present from the late Oligocene to late Miocene (Ichishima et al., 1994), have been suggested as potential ancestors to modern delphinoids, only a clade of six kentriodontids have been reconstructed phylogenetically as sister to Albireonidae + Iniodea + Delphinoidea (Lambert et al., 2017; Racicot, 2018). The group thus requires further study in the context of relationships with Delphinoidea before we can make inferences regarding delphinid ancestry.

From the ancestral condition reconstructed in our analysis, our model shows a development in two opposite directions: (1) toward blunter and wider rostra with shorter toothrows, accompanied by a generally wider and dorsoventrally compressed skull, as seen in the subfamilies Orcininae and Globicephalinae,

	Coefficient	Standard Error	t Value	p Value
Predator-prey size ratio				
PC1	−238.89	251.52	−0.95	0.36
PC2	551.98	347.12	1.59	0.13
PC3	−157.67	456.62	−0.35	0.73
Predator-prey size ratio, without Globicephalinae				
PC1	−297.76	80.69	1.13	0.28
PC2	1,812.12	751.34	2.41	**0.03**
PC3	−206.38	534.81	−0.39	0.71
Dive depth				
PC1	−1,306.97	902.51	−1.45	0.17
PC2	137.25	1,386.51	0.10	0.92
PC3	1,358.20	1,667.50	0.81	0.42
Centroid size				
PC1	−1,782.17	734.22	−2.43	**0.03**
PC2	562.62	1,232.98	0.46	0.65
PC3	99.27	1,522.44	0.07	0.95

Table 1. Explorations of the Relationships of Prey Size and Dive Depth with Shape

Coefficients, standard errors, and t and p values of phylogenetic generalized least squares regressions of predator-prey size ratios and dive depths on principal components 1–3. significant p values are given with bold numerals.

or (2) toward the extended, narrow rostrum with longer toothrow, and laterally compressed skull of the Delphininae and *Steno*. These two opposite trends are each further divided on both sides of the described spectrum into (1) forms with enlarged temporal fossae and an anteriorly displaced orbit (*O. orca* and *P. crassidens*) or a reduced postorbital process (*S. bredanensis*) and (2) an opposite trend toward diminished temporal fossae, exemplified by Globicephalinae other than *P. crassidens* and Delphininae other than *T. truncatus*.

Described delphinid fossils besides *Eodelphinus* further support our model of morphospace evolution from a generalized morphology similar to *Lagenorhynchus albirostris* and *Tursiops*. As expected from a rapid radiation, they are preserved from the Pliocene (5.3–2.6 mya) onward and include globicephalines such as *Protoglobicephala mexicana* (Aguirre-Fernández et al., 2009; Boessenecker et al., 2015), possible relatives of *Orcinus* such as *Orcinus citonensis* (Bianucci, 1996), and delphinines such as *Septidelphis morii* (Bianucci, 2013) and *Hemisyntrachelus*, which share skull shape similarities and possible transitional morphologies among their extant relatives. *Protoglobicephala* has a slightly longer rostrum than many of the extant globicephalines and was described as ''intermediate'' in morphology between *Tursiops* and extant globicephalines (Aguirre-Fernández et al., 2009), a transitional morphology that is supported by our model. *Atadelphis gastaldi* is described as sharing affinities with *Steno bredanensis*, while also possessing plesiomorphic characters similar to kentriodontids (Bianucci, 1996). *Armidelphis sorbinii* shares skull shape similarities with *Peponocephala* and *Feresa*, with antorbital processes similar to *Orcinus orca*, and probably had a strong bite for seizing large prey (Bianucci, 2005). The skull proportions of *Stenella giulli* are within the range of extant *Stenella* species, with a relative rostral length between that of *S. coeruleoalba* and *S. longirostris*, and with a relatively antero-posteriorly elongated neurocranium distinguishing it from the short and broad neurocranium of *S. clymene* (Bianucci, 1996). *Septidelphis morii* is reconstructed as sister to delphinines in a phylogenetic analysis and has an elongate, narrow rostrum similar to *Stenella* species and *Astadelphis* (Bianucci, 2013). *Hemisyntrachelus* is interpreted as having intermediate features between *Tursiops* and *Pseudorca* and *Orcinus*; for example, the skull size of *Hemisyntrachelus cortesii* is much larger (60 cm condylobasal length) than that of *Tursiops*, but the premaxillae do not narrow at the apical portion of the rostrum and fewer (14–15), larger teeth are present, which is more similar to *Orcinus* and *Pseudorca* (Bianucci, 1996). Similarly, *Hemisyntrachelus oligodon* has a lower tooth count (11–12) than is typical for extant *Tursiops* and is even larger than *Hemisyntrachelus cortesii* (62.5 cm condylobasal length). Dorsal views of the skull of *Hemisyntrachelus oligodon* show transversely narrow neurocranium and preorbital region compared with extant *Tursiops* (Pilleri and Silber, 1989). The vertex of the skull forms a more concave surface than that of *Hemisyntrachelus cortesii*, which has a shallow angle reaching the vertex (Pilleri and Silber, 1989). The rostra of both *Hemisyntrachelus* species are more elongate than in *Orcinus* and *Pseudorca*, reflecting their similarities with *Tursiops*, and they have deeper and narrower antorbital notches. *Tursiops osennae* possesses intermediate features between *Hemisyntrachelus* and extant *Tursiops* (Bianucci, 1996). *Orcinus citonensis* is distinguishable from extant *Orcinus orca* in its smaller size and larger number of smaller teeth (Bianucci, 1996), which seems intermediate between delphinines and globicephalines or *Orcinus*. All of these extinct delphinids appear to be transitional among extant species and are thus supported within the framework of our model of morphospace evolution. Some more bizarre extinct delphinids existed, however, including the toothless ziphiid-like *Australodelphis mirus* and a "hammerhead" globicephaline *Platalearostrum hoekmani* (Fordyce et al., 2002; Post and Kompanje, 2010). If the phylogenetic relationships of the extinct taxa were reconstructed, we might have a better understanding and ability to include them in similar morphometric analyses. One difficulty is the convergence in skull shapes between *Orcinus* and *Pseudorca* leading to possible confusion on the affinities of certain extinct taxa. Inclusion of the fossils with our extant dataset could not only inform on possible feeding mode and prey type, but also provide data on the transitional forms leading to the more extreme or convergent morphologies.

Feeding Mode Drives Skull Shape Evolution

Feeding mode is a major driver of delphinid skull radiation, as raptorial feeders, suction feeders, and grip and tear feeders each form discrete sub-spaces within the larger morphospace (Figure 2A). This is in agreement with the overall trends in skull diversity of odontocetes, which encompasses long narrow beaks in archaeocetes, river dolphins, and some delphinids and blunt beaks in some delphinids, phocoenids, and monodontids (Boessenecker et al., 2017; Norris and Møhl, 1983). Second, the teeth of ancient forms were typically numerous and prominent, whereas many modern genera show marked tooth reduction or outright loss. Norris and Møhl (1983) related the blunt-beaked forms with reduced dentition to suction feeding, whereas longer, narrower rostra and a long tooth row were related to feeding by grasping prey with the interlocking teeth. This axis of variation has been further investigated by Werth (2006a) and Werth (2006b), who found that wider and shorter beaks in delphinids provided superior suction. Thus, there is no sharp distinction between suction feeders and raptorial feeders, but our study underlines and quantifies this axis as the source of most of the skull shape variation among Delphinidae (Figure 2A).

Werth (2006a) further found that dentition was reduced as rostra became wider and shorter. Our study reveals two exceptions to this rule: *O. orca* and *P. crassidens*. Although their teeth are numerically reduced, they are very large and the relative extent of the toothrow is not shorter than in species with long, narrow rostra (Figure S1). As mentioned, these two species diverge on the second axis of delphinid skull shape variation, characterized by a large temporal fossa. Among the species included here, only *O. orca*, *P. crassidens*, *S. bredanensis*, and *T. truncatus* have evolved in this direction from the estimated shape root of the delphinid tree. All other species have evolved in the opposite direction, toward a smaller temporal fossa and a more posteriorly placed orbit.

As previously alluded to, delphinid feeding strategies and their associated morphological adaptations likely form a continuum, so delineations between feeding strategies are somewhat arbitrary. It could be argued that all delphinid species rely on some combination of raptorial and suction feeding, seeing that even long-beaked forms have suction capability, albeit at a much lower level than short-beaked forms (Johnston and Berta, 2011; Werth, 2006a).

Species with low PC1 scores, i.e., suction and/or grip and tear feeders were significantly larger than species tending to the raptorial side of the shape spectrum. Grip and tear feeders may need to be large to cope with attractive prey. The delphinid suction feeders included here tend to dive more deeply and for longer durations, for which larger size is an advantage (Noren and Williams, 2000). On the other hand, we did not see a significant relationship between dive depth and PC1. It should be noted that a relationship between suction feeding and size is not a general trend across Odontoceti, as phocoenids seem to largely rely on suction feeding.

Prey Size Drives Skull Shape Evolution

The first axis of variation is associated with suction feeding versus raptorial feeding, whereas the second axis seems to be associated with prey size. The two grip and tear feeders, *O. orca* and *P. crassidens*, display the two highest scores along this axis and there is an association between maximum prey size and this axis, particularly for species on the raptorial side of the suction-raptorial spectrum (Figure 3B). The development of larger temporalis muscle mass indicated by the larger temporal fossa associated with this axis is a logical adaptation for larger prey items, and the association of a larger temporal fossa with larger prey has been proposed previously (Perrin, 1975). Other authors have suggested that the size of the temporal fossa (in *Delphinus delphis*) is largely constrained by asymmetry of the facial region of the skull, an ancient feature of odontocetes (Churchill et al., 2019). The ability of species with shorter and wider rostra to handle larger prey than those with longer and narrower rostra is unsurprising; McCurry et al. (2017c) have demonstrated the intuitive consequence of less mechanical strain with shorter and wider rostra. Thus, the evolution of grip and tear feeding in *O. orca* and *P. crassidens* may have progressed from the ancestral delphinid skull shape via an initial adaptation toward suction feeding. This is almost certainly the case for *P. crassidens*, phylogenetically nested deep within Globicephalinae, a subfamily otherwise consisting of members with extreme to moderate morphological adaptations for suction feeding. *O. orca* is also capable of suction when feeding on, e.g., schooling fish such as herring and mackerel (Werth, 2000a). Interestingly, for *F. attenuata*, the closest morphospace neighbor of *O. orca* and *P. crassidens* among the Globicephalinae, there are reports of killing and eating of *D. delphis* and *Stenella* spp. in relation to tuna fisheries in the eastern tropical Pacific (Perryman and Foster, 1980), providing further evidence that the short, wide rostrum related to suction feeding among delphinids may be a preadaptation for handling large prey items. Compared with *Globicephala*, however, *F. attenuata* is more adapted to large prey in terms of skull shape.

Similar to our results, McCurry et al. (2017b) also found an association between prey size and skull shape in odontocetes. However, McCurry et al. (2017b) only included landmarks on the mandible and the anterior skull and did not detect a clear pattern in the analysis of prey size in relation to skull shape among odontocetes and had to exclude suction feeders from the analysis to obtain a signal. Similarly, we only obtained significant results when we excluded Globicephalinae from the analysis. This subfamily contained some outliers relative to the other species; for example, *G. griseus* and *P. electra* had much larger maximum prey sizes than expected from the analyses. Thus, the blunter rostra of these species may allow for larger prey sizes despite a reduced temporal fossa. The analysis of McCurry et al. (2017b) only included aspects of shape related to the rostrum and mandible, thus leaving out information found to be relevant to prey size in our analyses, namely, the size of the temporal fossa and the associated displacement of the orbit. Of the species with high PC2 scores, *S. bredanensis* is noteworthy as being the only species in this study to be a raptorial feeder on larger prey, as *S. bredanensis* is known to take large prey items, such as Mahi-Mahi (*Coryphaena hippurus*) (Pitman and Stinchcomb, 2002). The most specialized suction feeders, *G. griseus*, *G. melas*, and *G. macrorhynchus*, all have small temporal fossae, indicating a weaker *temporalis* muscle, an adaptation opposed to that of the dedicated grip and tear feeders, *O. orca* and *P. crassidens*. Given the reduced temporal fossa and teeth and the limited maximum gape (Werth, 2000b), morphological evidence indicates specialization toward small to moderate prey sizes for both *Globicephala* species. *G. griseus* is morphologically very similar to *Globicephala*, but much smaller, and has been recorded to take relatively large *Octopus* prey up to about 7 kg (Cockcroft et al., 1993).

Habitat and Climate Are Less Important Drivers of Evolution

Delphinids are found in a wide range of habitats, ranging from rivers to the open ocean, and in another odontocete family (Phocoenidae), the primary axis of shape variation among extant species was related to habitat (Galatius et al., 2011). In the current study, however, no clear links of morphology to habitat were detected. The current study focuses on the macroevolutionary trends of delphinid skull shape evolution, and it is very probable that adaptations for specific habitats do occur in this family. Such adaptations have been reported for the genus *Sotalia* (Monteiro-Filho et al., 2002) and in the subfamily Lissodelphininae (Galatius and Goodall, 2016). In the current dataset, detection of this is hampered by the fact that the four species included in the coastal category, *O. orca*, *D. delphis*, *S. frontalis*, and *T. truncatus* all are found in shelf habitats as well, and most also in oceanic habitats.

Species spanning the entire morphospace occur in tropical and warm temperate waters, but in the temperate and arctic zones, there is a conspicuous lack of longirostrine forms. These colder environments also have small pelagic prey suitable for longirostrine forms, evidenced by large colonies of sea birds foraging in pelagic waters of these climate zones. Thus, thermoregulation could explain the lack of longirostrine delphinids in colder waters. Alternatively, McCurry et al. (2017a) suggested that potentially faster swimming speeds in fish (von Herbing, 2002) could have initiated predator-prey escalation, driving evolution of longer rostra in warmer climates.

Adaptive Radiation Followed by Evolutionary Stability

Our model indicates a phylogenetically stable morphospace distribution with most taxa remaining within a narrow range of shapes after the initial adaptive radiation. The primary exception to this rule is *S. bredanensis*, which is phylogenetically affiliated with the globicephalines but has made the most dramatic adaptation from an ancestral shape recorded in our analysis to become a raptorial feeder of large prey. However, the phylogenetic relationship of the genus *Steno* is unclear with some analyses based on mitogenomes or a small set of nuclear genes indicate affiliation with Delphininae (Steeman et al., 2009; Galatius et al., 2019), whereas several other analyses based on nuclear DNA—including the most comprehensive genomic analysis conducted to date—indicate affiliation with Globicephalinae (McGowen, 2011; McGowen et al., 2009, 2019). Thus, future work is needed to address the evolution of *S. bredanensis.* A more minor exception is *P. crassidens*, which is phylogenetically nested deep within the Globicephalinae but shows convergent evolution with *O. orca*, having a similar skull shape to this species. Another species that has adapted its skull morphology after the initial radiation is *L. hosei* with adaptation to a greater reliance on suction than other members of the subfamily Delphininae. This subfamily is otherwise specialized in raptorial feeding on small prey items, with the exception of *T. truncatus*, which has retained a morphology closer to the ancestral shape of the subfamily, apparently with greater reliance on suction and adaptation for larger prey items. The early-diverging *Lagenorhynchus* and *Leucopleurus* lineages have most likely occupied morphospace spheres close to the ancestral shape throughout their evolutionary history.

As the primary axes of variation relate to foraging strategy and prey size, it is most likely that adaptation in these regards has been the major evolutionary driver of diversification of delphinid species and skull shapes. This is not a new idea but something that has been suggested for Odontoceti in general (Boessenecker et al., 2017; McCurry et al., 2017a; Norris and Møhl, 1983; Werth, 2006a). However, it is interesting in light of the fact that other extant odontocete clades have much less variation now than some of their extinct relatives. This is obvious for the modern oligotypic clades Pontoporiidae, Physeteridae, Kogiidae, Lipotidae, Platanistidae, Iniidae, and Monodontidae but is also true for the more speciose extant Phocoenidae and Ziphiidae. Extinct members of all modern odontocete clades were more morphologically diverse throughout the Miocene and Pliocene than they are in the present day, with the exception of the Delphinidae, which (in terms of species richness) currently rival that of the entire remaining Odontoceti. In this context, an interesting question is: did diversity within non-delphinid odontocete clades decline as a result of global environmental change toward the end of the Pliocene? In this scenario, evolutionary radiation in the Delphinidae may have been in response to the availability of resources and the opening of free ecospace. Alternatively, did the explosive radiation of delphinids in part drive this diversity decline via resource competition and evolutionary replacement? Future analyses integrating geochronological, paleoenvironmental, and palaeontological (including paleoecological and phylogenetic) data, combined with an analysis of past and current morphospace, could be used to test these hypotheses.

CONCLUSIONS

Delphinids are the result of a rapid radiation that has resulted in the most species-rich and morphologically diverse extant cetacean family in terms of skull shape. This diversity is primarily related to feeding strategy, where delphinids are unique among cetaceans in encompassing specialized raptorial, suction, and grip and tear feeders. Secondary features of the skull are associated with feeding on prey items of different size. Climate may have also shaped the phylogeography of delphinids as none of the species specialized for raptorial feeding are found in colder climates. This remarkable radiation of skull shapes seems to have occurred in a simple radiation, mostly driven by feeding strategy and prey size, with few major events after initial diversification.

Limitations of the Study

The results of this study come with a few caveats. By focusing on the delphinid species inhabiting the North Atlantic, we do not comprehensively cover this family's ~37 species. The bulk of the species not covered are represented by the subfamily Lissodelphininae, which occurs in the Southern Hemisphere and the North Pacific. Galatius and Goodall (2016) found a primary axis of variation within Lissodelphininae very similar to the one found here for the Delphinidae of the North Atlantic. All 10 lissodelphinine species were positioned between *L. albirostris* and *D. delphis* (included for comparative reasons) along this axis, indicating that we are not missing major variations of shape by the exclusion of this taxon. The same can be said for the missing species of the mostly tropical genera *Sousa* and *Sotalia*, which, from a visual inspection, have similar skull shapes to *S. bredanensis*, including large temporal fossae. Another species not included in the current study, *Orcaella brevirostris*, is indicated to be sister to the Globicephalinae subfamily (McGowen et al., 2019), in line with its gross skull morphology. Another part of delphinid diversity that we did not include was fossils. These were omitted because of the lack of firm knowledge regarding phylogenetic relationships and the rather few skulls that are sufficiently complete to record most landmarks. Given rigorous phylogenetic analysis of delphinid fossils, they can be included in a future study.

Resource Availability

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Anders Galatius (agj@bios.au.dk).

Materials Availability

No materials were newly generated for this paper.

Data and Code Availability

The specimens included in the study are listed in Table S1. Variable values of size, feeding mode, max weight, max prey weight, climate, habitat, and dive depth are in Table S3. Morphometric data used for this paper have been deposited to Mendeley Data: https://doi.org/10.17632/x4kfyfzyc6.1.

METHODS

All methods can be found in the accompanying Transparent Methods supplemental file.

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.isci.2020.101543.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.G.; Methodology, A.G.; Investigation, A.G., Writing – Original Draft, A.G., R.R., M.T.O.; Writing – Review & Editing, A.G., R.A.R., M.M., M.T.O.; Funding Acquisition, A.G.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental Information

Evolution and Diversification of Delphinid Skull Shapes

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Supplemental material

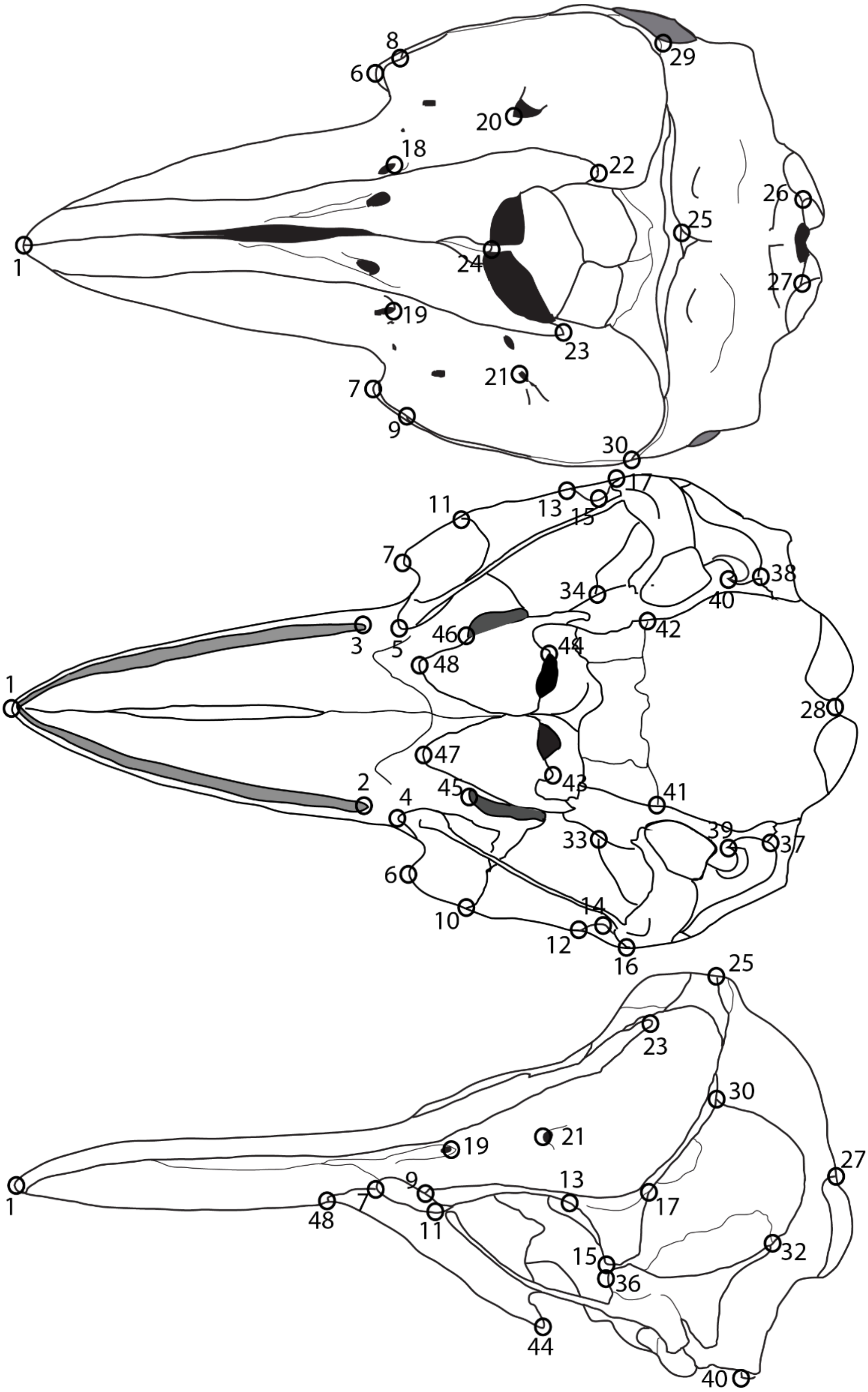

Figure S1. Three-dimensional cranial landmarks, Related to Figure 1 and Transparent Methods. Landmarks used for shape analysis defined for dorsal, ventral and lateral views of the skull, exemplified by a *Lagenorhynchus albirostris*. See Supplementary Table 2 for definitions of landmarks.

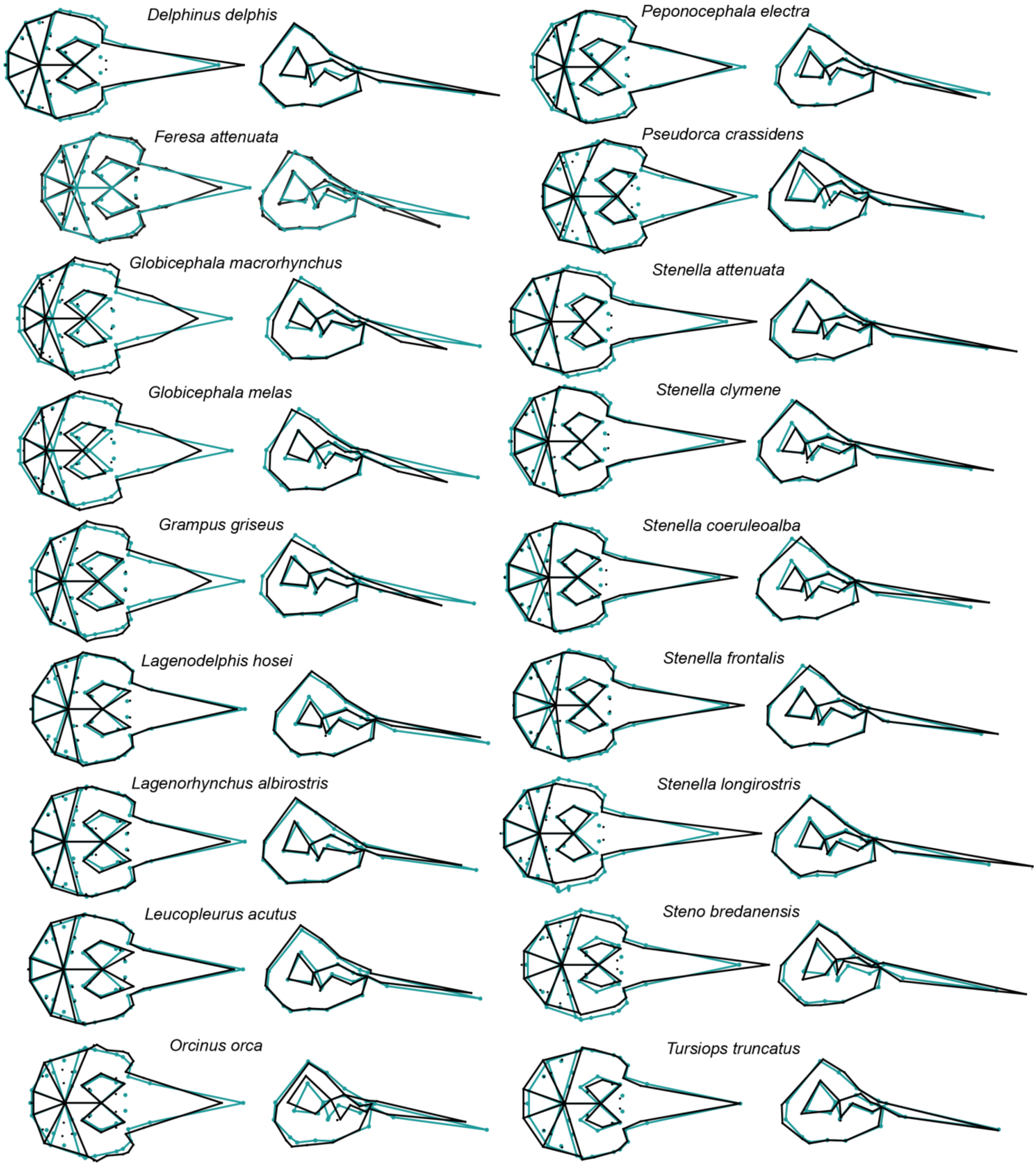

Figure S2. Mean species-specific shapes of each North Atlantic delphinid species, Related to Figures 1 and 2. Left panel: dorsal aspect, right panel: lateral aspect. Black outline and markers are species specific shapes, gray outline and markes are grand mean shape of all species.

Supplemental data items

Table S1. Specimens included in the study; Related to Figure 1, Figure 2 and Transparent methods. Abbreviations: NHMDK: Natural History Museum of Denmark. USNM: Smithsonian National Museum of Natural History, Division of Mammals.

ID	Species	Collection	ID	Species	Collection
1165a	*Orcinus orca*	NHMDK	USNM504508	*Peponocephala electra*	USNM
CN1	*Pseudorca crassidens*	NHMDK	USNM504514	*Peponocephala electra*	USNM
CN10	*Orcinus orca*	NHMDK	USNM504785	*Stenella attenuata*	USNM
CN24	*Orcinus orca*	NHMDK	USNM504802	*Stenella attenuata*	USNM
CN30	*Stenella coeruleoalba*	NHMDK	USNM504804	*Stenella attenuata*	USNM
CN425	*Globicephala melas*	NHMDK	USNM504901	*Stenella attenuata*	USNM
CN7	*Pseudorca crassidens*	NHMDK	USNM504948	*Peponocephala electra*	USNM
CN906	*Pseudorca crassidens*	NHMDK	USNM550022	*Lagenodelphis hosei*	USNM
M1098	*Globicephala melas*	NHMDK	USNM550024	*Stenella frontalis*	USNM
MCE1260	*Lagenorhynchus albirostris*	NHMDK	USNM550025	*Stenella frontalis*	USNM
MCE1575	*Globicephala melas*	NHMDK	USNM550129	*Stenella frontalis*	USNM
MCE1598	*Globicephala melas*	NHMDK	USNM550389	*Feresa attenuata*	USNM
ZSS1981	*Orcinus orca*	NHMDK	USNM550399	*Peponocephala electra*	USNM
USNM14246	*Leucopleurus acutus*	USNM	USNM550514	*Stenella clymene*	USNM
USNM14279	*Leucopleurus acutus*	USNM	USNM550516	*Stenella clymene*	USNM
USNM14281	*Leucopleurus acutus*	USNM	USNM550530	*Stenella clymene*	USNM
USNM267573	*Lagenorhynchus albirostris*	USNM	USNM550531	*Stenella clymene*	USNM
USNM292071	*Stenella frontalis*	USNM	USNM550823	*Stenella coeruleoalba*	USNM
USNM35156	*Lagenorhynchus albirostris*	USNM	USNM552312	*Stenella longirostris*	USNM
USNM482836	*Stenella longirostris*	USNM	USNM571219	*Delphinus delphis*	USNM
USNM487185	*Stenella longirostris*	USNM	USNM571260	*Stenella coeruleoalba*	USNM
USNM49753	*Lagenorhynchus albirostris*	USNM	USNM571268	*Feresa attenuata*	USNM
USNM500232	*Globicephala macrorhynchus*	USNM	USNM571351	*Grampus griseus*	USNM
USNM500233	*Globicephala macrorhynchus*	USNM	USNM571599	*Delphinus delphis*	USNM
USNM500343	*Globicephala macrorhynchus*	USNM	USNM571619	*Lagenodelphis hosei*	USNM
USNM501200	*Pseudorca crassidens*	USNM	USNM572129	*Delphinus delphis*	USNM
USNM502313	*Stenella longirostris*	USNM	USNM572313	*Grampus griseus*	USNM
USNM504196	*Leucopleurus acutus*	USNM	USNM572339	*Delphinus delphis*	USNM
USNM504295	*Tursiops truncatus*	USNM	USNM572790	*Steno bredanensis*	USNM
USNM504310	*Tursiops truncatus*	USNM	USNM572791	*Steno bredanensis*	USNM
USNM504325	*Tursiops truncatus*	USNM	USNM572794	*Steno bredanensis*	USNM
USNM504326	*Tursiops truncatus*	USNM	USNM572801	*Steno bredanensis*	USNM
USNM504411	*Lagenodelphis hosei*	USNM	USNM572921	*Grampus griseus*	USNM

Table S2. Landmark definitions; Related to Figure 1, Figure 2 and Transparent Methods.

1	Anterior tip of right premaxilla
2 and 3	The caudalmost alveoli, left and right
4 and 5	Anterior point of lacrimal, right and left
6 and 7	Anterior point of the maxilla, right and left
8 and 9	Anterior point of frontal, right and left
10 and 11	Tip of the antorbital process, right and left
12 and 13	Anterior base of the postorbital process of the frontal, right and left
14 and 15	Ventral point of the postorbital process of the frontal, right and left
16 and 17	Posterior base of the postorbital process of the frontal, right and left
18 and 19	Posterior margin of anterior dorsal infraorbital foramen, right and left
20 and 21	Anterior margin of the posterior dorsal infraorbital foramen, right and left
22 and 23	Posterior tip of premaxilla, right and left
24	Nasal septum at the anterior end of the nasal apertures
25	Anteriormost point of the sutures between the frontal and interparietal bones
26 and 27	Dorsal tip of occipital condyle, right and left
28	Medial point of the intercondylar notch of the basioccipital in ventral aspect
29 and 30	Lateral corner of the supraoccipital, meeting the maxilla, left and right
31 and 32	Junction of exoccipital, parietal and squamosal, right and left
33 and 34	Junction of the parietal, frontal and sphenoid, right and left
35 and 36	Tip of the zygomatic process of the squamosal
37 and 38	Deep point of the jugular notch, right and left
39 and 40	Medial tip of the paraoccipital process, right and left
41 and 42	Suture of pterygoid and basioccipital at the lateral margin of the bones, right and left
43 and 44	Posterior tip of the pterygoid hamulus, right and left
45 and 46	Anterior tip of the pterygoid, right and left
47 and 48	Anterior margin of the ventral infraorbital foramen, right and left

Table S3. Variables used in figures and statistical analyses; Related to Figure 2, Table 1 and Transparent Methods. Categorizations of species in terms of feeding mode, climate and habitat as well as values used in analyses for centroid size, maximum prey size and dive depth, and the references for those values. PPSR: Predator-prey size ratio percentage.

Species	Mean centroid size	Feeding mode	Max weight (kg)	Max prey weight (kg)	PPSR	Prey weight reference	Conversion of prey length to weight	Climate	Habitat	Dive depth	Dive depth references
D. delphis	686.2	Raptorial	136	0.38	0.28	Melo et al. (2010)	Costa (2010)	Warm	Shelf, Coast	280	Leatherwood et al. (1982)
*F. attenuata**	716.4	Raptorial	225	100.00	44.44	Perryman and Foster (1980)	-	Warm	Ocean	364	Pulis et al. (2018)
G. macrorhynchus	1338.5	Suction	3200	1.10	0.03	Hernández-García and Martín (1994)	-	Warm	Ocean	1.019	Aguilar Soto et al. (2008)
G. melas	1266.8	Suction	2300	4.94	0.22	Beasley et al. (2019)	-	Cold	Ocean	828	Heide-Jørgensen et al. (2002)
G. griseus	1020.2	Suction	400	7.00	1.75	Cockcroft et al. (1993)	Smith et al. (2006)	Warm	Ocean	566	Arranz et al. (2016)
L. hosei♦	665.3	Raptorial	210	0.02	0.01	Dolar et al. (2003)	Froese and Pauly (2019)	Warm	Ocean	≈600	Dolar et al. (2003)
L. albirostris	820.6	Raptorial	354	2.30	0.65	Jansen et al. (2010)	Arnason et al. (2009)	Cold	Shelf	<200	Rasmussen et al. (2013); Galatius and Kinze (2016)
L. acutus	754.8	Raptorial	230	1.12	0.49	Hernandez-Milian et al. (2016)	-	Cold	Ocean, Shelf	≈100	Hamran (2014); Winn (1982)
*O. orca**	1894.2	Grip & Tear	6600	30000.00	454.55	Ford (2018)	-	Warm, Cold	Ocean, Shelf, Coast	≈767.5	Reisinger et al. (2015)
P. electra	845.5	Raptorial	200	2.25	1.13	West et al. (2018)	-	Warm	Ocean	471.5	Joyce et al. (2017); West et al. (2018)
P. crassidens	1136.0	Grip & Tear	1500	29.00	1.93	Sekiguchi et al. (1992)	-	Warm	Ocean	927.5	Baird et al. (2014)
S. attenuata	590.2	Raptorial	119	0.57	0.48	Wang et al. (2003)	-	Warm	Ocean	213	Baird et al. (2001)
S. clymene♦	599.5	Raptorial	79	0.01	0.01	Perrin et al. (1981)	-	Warm	Ocean	<700	Mullin et al. (1994); Weir et al. (2014)
S. coeruleoalba♦	693.4	Raptorial	156	0.84	0.54	Spitz et al. 2006	-	Warm	Ocean	≈700	Archer and Perrin (1999)
S. frontalis	686.1	Raptorial	143	0.20	0.14	Melo et al. (2010)	-	Warm	Coast	≈60	Davis et al. (1996)
S. longirostris♦	553.9	Raptorial	80	0.01	0.01	Dolar et al. (2003)	Froese and Pauly (2019)	Warm	Ocean, Shelf	≈600	Dolar et al. (2003); Perrin (2018)
S. bredanensis	791.6	Raptorial	155	8.00	5.16	West et al. (2011)	-	Warm	Shelf	≤300	Wells et al. (2008)
T. truncatus	767.2	Raptorial	650	1.77	0.27	Milmann et al. (2016)	-	Warm, Cold	Ocean, Shelf, Coast	≈500	Klatsky et al. (2007)

* prey size estimated as a small adult of cited prey species
♦ depth estimated according to prey distribution.

Transparent Methods

Skull samples

The specimens studied are in the collections of the Smithsonian National Museum of Natural History (USNM) and the Natural History Museum of Denmark in Copenhagen (NHMD). Only skulls that were deemed to be of adult size were included. The samples consisted of 3 to 4 skulls from each delphinid species occurring in the North Atlantic: *Orcinus orca, Lagenorhynchus acutus, Lagenorhynchus albirostris, Grampus griseus, Pseudorca crassidens, Feresa attenuata, Peponocephala electra, Globicephala macrorhynchus, Globicephala melas, Steno bredanensis, Stenella attenuata, Lagenodelphis hosei, Tursiops truncatus, Stenella frontalis, Stenella coeruleoalba, Stenella clymene, Stenella longirostris* and *Delphinus delphis*. As sex was not known for many of the specimens and marked sexual differences (except in size) are not described for any of these species, sexual dimorphism was not taken into account. A list of the specimens studied is available as supplementary material (Table S1).

Shape analysis

Skull shapes were analyzed using geometric morphometrics. Three-dimensional coordinates of 48 Type I and Type II (Bookstein, 1991) landmarks, spread throughout the skull and used in previous studies (Galatius and Gol'din, 2011; Galatius et al., 2012) were registered with a Microscribe® 3D digitizer (Figure S1, Table S2).

Analyses

Unless otherwise stated, all analyses were performed in MorphoJ (Klingenberg, 2011). A geometric measure of scale, centroid size (CS), was calculated for each individual, defined as the square root of the summed squared distances of each landmark to the centroid position, the averaged coordinates of the configuration.

The raw landmark coordinates were run through the generalized least-squares Procrustes superimposition (Rohlf and Slice, 1990). The Procrustes procedure includes translation of the centroids to a common position of origin, scaling of the configurations of landmarks to unit centroid size and rotation of the configurations of landmarks to obtain the smallest possible squared distances between homologous landmarks. In this procedure, differences among the individual configurations in size, location and orientation are removed, and the only variation remaining among the individual configurations is variation of shape. The Procrustes procedure used here was amended by the suggestions of Klingenberg et al. (2002) in order to deal with the redundancy of data points caused by the object symmetry of the vertebrate skull and to separate symmetric and asymmetric shape variation in separate components. After this amended Procrustes superimposition procedure, the shape data for each individual could be given in 2 * 4 (number of median landmarks in the sagittal plane of the skull) + 3 * 22 (number of pairs of bilaterally paired landmarks, e.g., landmarks 2 and 3) – 4 (number of dimensions lost through the superimposition) = 70 dimensions. This procedure excludes information on skull asymmetry, which was deemed to be of minor interest regarding the analysis of general skull shape. To assess measurement error, 18 specimens were measured twice independently. The mean Procrustes distance (Euclidian distance) between replicate configurations of the same skulls was 0.0061 (range 0.0039-0.0095) and small relative to the distances between taxa (range 0.0472-0.2898 – *S. coeruleoalba* and *S. clymene* are extremely similar, while the largest distance is between *S. longirostris* and *G. macrorhynchus*).

Skull Shape in Relation to Phylogeny

To analyze skull shape in relation to phylogeny, the potential effect of allometry in the sample was first investigated. This was done with multivariate regression of symmetric shape on the logarithmic of size (log[CS]) for analysis. The resulting vector described a pattern of shape change different to the usual pattern observed in Delphinoidea, where the relative size of the braincase decreases during ontogeny and the relative size of the rostrum increases (e.g., (Galatius, 2010; Galatius and Gol'din, 2011)). Here, the regression vector described an opposite trend with a relative decrease in the size of the rostrum and an increase in size of the posterior part of the skull. As the observed pattern was judged to represent interspecific differences disassociated from within-species patterns of allometry (e.g., generally rostra show positive allometry and are relatively longer in larger specimens/species, but the largest delphinids *O. orca*, *P crassidens*, *Globicephala* sp. all have short rostra), a general correction of the data for effects of allometry (e.g., Galatius and Goodall (2016) was not performed.

Correspondence between shape and phylogeny was assessed by mapping the average shape of each species onto the most recent phylogeny of McGowen et al. (2020). We pruned species from the tree which were not included in this study. A principal components analysis (PCA) was performed on the symmetric component of average species shapes. Because of the discrepancy in sample sizes, species averages were used to avoid the influence of intraspecific variation of the larger samples from obscuring the interspecific variation. Then ancestral and node shapes (as PC scores) of the phylogenetic relationships from the mitogenome phylogeny were constructed using squared-change parsimony (Maddison, 1991).

Drivers of skull shape evolution

To better understand the drivers of delphinid skull shape evolution we assessed putative associations with the feeding mode, prey size, climate, habitat, size and dive depth of each species and species groups. For feeding mode, species were divided into raptorial feeders and suction feeders according to McCurry et al. (2017), with the exception that *Pseudorca crassidens* and *Orcinus orca* were categorized as grip and tear feeders, a category not used by McCurry et al. (2017). These two species are known to handle prey items larger than what can be engulfed at one time, and we wanted to explore morphological adaptations in this regard. In terms of prey specialization, the species were divided into groups according to their maximum weight and maximum prey weight based on a literature search including species entries in Ridgway and Harrison (1994); Würsig et al. (2018) and (Ridgway and Harrison, 1999) for information on mass of each species and maximum prey mass retrieved from research papers. Dive depths were also extracted from a literature search. Information categorization in terms of climate and habitat, along with values of maximum size of prey items, dive depth and centroid size are listed in Table S3 along with references for the values. Where necessary, conversions of length to weight were conducted according to Arnason et al. (2009); Costa (2010); Froese and Pauly (2019) and Smith et al. (2006). Species were divided into three arbitrary predator-prey size ratio (PPSR) categories: small prey (<0.20% body mass), medium prey (0.20-1.0% body mass) and large prey (>1.0 body mass). Values for each species and references for these are in Table S3. For climate, species were divided into two groups: Arctic–Cold Temperate and Warm Temperate–Tropical based on species entries in Würsig et al. (2018). For habitat, species were divided into three groups: coastal, shelf and shelf slope – oceanic, based on species entries in Würsig et al. (2018). For climate and habitat, groupings were not treated as mutually exclusive, so the same species could be included in more than one group. Finally, maximum dive depth values for the species were retrieved from the literature, values and their references are in Table S3. For the variables with quantitative data, prey size, dive depth and centroid size, phylogenetic generalized least squares (PGLS) regression were used to investigate relationships with the PCs that accounted for > 5% of the variance in the dataset. PGLS analyses were performed in R (R Development Core Team, 2019), using the libraries ape (Paradis and Schliep, 2019) and nlme (Pinheiro et al., 2020), under the assumption of a Brownian motion scenario.

Data and software availability

Landmark data are accessible at https://data.mendeley.com/datasets/x4kfyfzyc6/draft?a=e458fdba-1fa6-457c-828f-3338b4d4a708.

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