



## ORIGINAL RESEARCH

**Feeding mode drives mandibular shape in extant Delphinidae**D. Vicari<sup>1</sup> , G. Boccone<sup>2</sup> & L. Pandolfi<sup>3</sup> <sup>1</sup>Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK<sup>2</sup>Dipartimento di Scienze della Terra, Università di Pisa, Pisa, Italy<sup>3</sup>Dipartimento di Scienze, Università degli Studi della Basilicata, Potenza, Italy**Keywords**

mandible; Delphinidae; geometric morphometrics; ecology; macroevolution; precoronoid crest; biosonar mode; feeding mode.

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Editor: Andrew Kitchener

Received 11 January 2024; revised 5 July 2024; accepted 9 August 2024

doi:10.1111/jzo.13214

**Introduction**

Delphinidae is the most diversified group of Odontoceti (toothed whales), and it includes 38 extant species (Committee on Taxonomy, 2023) that inhabit oceanic, coastal and river environments. Adaptations in delphinid mandibles have been the subject of several studies in the past decades, and they have been a central part of functional morphological studies due to their functional duality: feeding and hearing.

Delphinids display a wide range of feeding strategies, from biting (raptorial) to suction feeding (Berta & Lanzetti, 2020; Bianucci et al., 2022; Kienle et al., 2017). Feeding is a basic need for animal survival and the aquatic environment imparts strong selective pressures on delphinid feeding adaptations, which can be seen in the mandible (Werth, 2006a). Deductions from the structure of mandibles can be used to predict feeding techniques. They can indirectly provide ecological, trophic

**Abstract**

Delphinidae is the most diverse family within the toothed whale clade, displaying two biosonar modes, different feeding strategies, and diving and habitat adaptations. This work examines the delphinid mandible to determine the association between shape, size and ecological variables in extant species. Geometric morphometric analysis on 95 mandibles belonging to 30 (out of 38) extant species, representatives of all 17 extant genera, was performed in occlusal (or dorsal) and lateral (or labial) view. The results reveal that feeding mode and climate primarily drive mandibular shape in extant species. Biosonar mode is an evolutionary driver in mandibular shape in occlusal view, while diet and maximum prey size play a significant role in size only in both views. By contrast, Diving Ecology, Superficial Temperature and Rostral index do not play a significant role in driving delphinid mandibular shape and size.

information and the ability of delphinids to exploit the resources of their environment (Marshall, 2009). In many delphinids, the mandible becomes long and narrow, and the elevation of the posterior portion relative to the dental alveoli (coronoid process) varies depending on the number of teeth. In species with reduced dentition, the mandibular ramus extends from the mandibular condyle to the very anterior end of the coronoid crest at the level of the last tooth.

In addition, the mandible is specialized to receive sound waves through a fat body in the mandibular canal, which opens posteriorly (mandibular foramen). The lateral wall of the mandible is thin at the level of the mandibular foramen (pan bone or acoustic window), and it appears to represent a compromise between a solid structure for grabbing prey and a low-thickness structure for hearing (Nummela et al., 2004). In the whole clade, the mandibular foramen has become extremely wide compared to other mammals to host fatty tissues (fat pad) to channel sound through the

ears (Koopman, 2018; Koopman et al., 2006; Mead & Fordyce, 2009). Over a short period across the Plio-Pleistocene, delphinids evolved a diversity of skull forms, increased their encephalization quotient, and faced climate and sea level changes eclipsing other extant odontocete clades (Belluzzo & Lambert, 2021; Bianucci & Landini, 2006; Fordyce & de Mui-zon, 2001; Geisler et al., 2011; Marino et al., 2004; Steeman et al., 2009).

The cranial shape of Delphinidae has been previously investigated with traditional morphometry in a few delphinid species (Perrin, 1975; Yao et al., 2008), and more recently, studies have focused on the whole toothed whale clade (Coombs et al., 2022; Vicari et al., 2023) using 3D Geometric Morphometric Methods (GMM). In particular, McCurry, Fitzgerald, et al. (2017) analysed both the cranium and mandible within toothed whales including 28 species while other studies (del Castillo et al., 2014, 2017; Galatius et al., 2020; Guidarelli et al., 2014; Vicari, Lorenzen, et al., 2022; Vicari, Sabin, et al., 2022) were focused on one or a few species to analyse intraspecific variation. However, all the published GMM studies have mainly focused on the cranium (Coombs et al., 2022; Galatius et al., 2020; Vicari et al., 2023). Galatius et al. (2020) state that delphinid cranial shapes are related to feeding mode and prey size but not to their habitat while accounting for phylogeny. That is also in line with that found for the whole toothed whale clade (Vicari et al., 2023). To investigate and elucidate the adaptive significance of mandible morphological variation in response to ecological pressures in Delphinidae, we examined 67 mandibles in occlusal and 88 in lateral view, covering 30 (out of 38) extant species and all 17 genera. We used a comparative framework integrating phylogenetic and geometric morphometric analyses to test for the association between the evolution and diversification of the delphinid mandible shape and size and ecological variables including two different diet variables (Diet: Galatius et al., 2020; Gaskin, 1982; Vicari et al., 2023; and Diet2), biosonar mode (Jensen et al., 2018), diving ecology (Noren & Williams, 2000; Werth, 2006a; Würsig, 2009), prey size (minimum, maximum and average) (MacLeod et al., 2006), surface temperature (ST; Vicari et al., 2023), climate (Climate) and rostral index (RI; McCurry & Pyenson, 2019). Maximum/minimum peak auditory frequencies (kHz) used in Vicari et al. (2023) were only available for 16 species, thus not covering all the genera and, therefore, were not included in this study.

## Materials and methods

### Samples

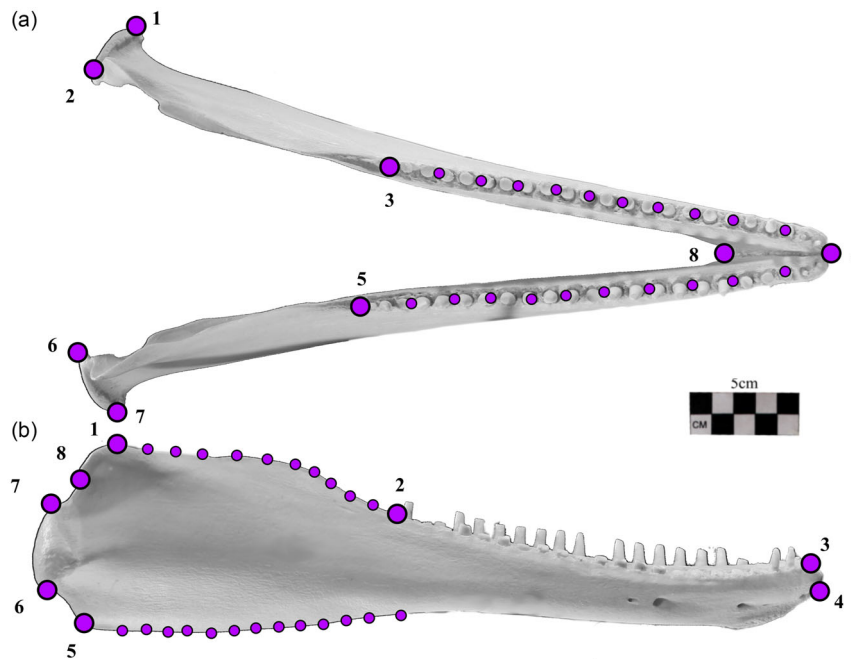
We used the classification of delphinid species recently accepted by the Committee on Taxonomy, 2023 ([www.marinemammalscience.org](http://www.marinemammalscience.org)), recognizing 38 extant species and 17 genera of Delphinidae. Ninety-five mandibles of 30 adult delphinid species, representatives of all 17 extant genera, are considered in this work. The specimens were collected from the following institutions: Royal Belgian Institute of Natural Sciences (RBINS; Brussel, Belgium), Muséum National d'Histoire Naturelle (MNHN; Paris, France), Natural History Museum of the University of Pisa (MSNUP; Pisa, Italy), Museo de Historia

Natural de la Universidad Nacional Mayor de San Marcos (MUSM; Lima, Peru), National Museum of Natural History Naturalis (NNML; The Netherlands), National Museum of Natural History (USNM; Washington, United States), Zoologisch Museum Amsterdam (ZMA; Amsterdam, The Netherlands) and Museo di Zoologia, La Specola, Università di Firenze (MZUF; Firenze, Italy). They are listed in Table S1.

The mandibles were photographed in occlusal (or dorsal) and lateral (or labial) views at a standard 1-metre distance. We used photos rather than 3D models as the hemi-mandible is predominantly planar. However, crucial morphological information can still be seen only in the occlusal plane, notably in the orientation of the two hemi-mandibles to one another. This makes the delphinids mandible ideal for arranging landmarks on a 2D surface.

### Geometric morphometrics and statistical analysis

Geometric Morphometric Methods were used to investigate size and shape variation. The 2D coordinates of eight landmarks and two curves of semi-landmarks were recorded on 59 complete mandibles in occlusal (or dorsal) and on 84 hemi-mandibles in right lateral (or labial) view using the software tpsDig2 v2.17 software (Rohlf, 2015) (Fig. 1; see Table 1 for landmark descriptions; see Table S1 for the list of specimens considered per each view). Because odontocete mandibles are generally considered symmetrical (Barroso et al., 2012), only the right side was captured in lateral view, while the full occlusal shape was captured in dorsal view only for the available joined mandibles. Semi-landmark curves were used to capture the morphology of complex outlines where anatomical homology was difficult to recognize. The landmark configuration was defined following previously published research (Guidarelli et al., 2014; Vicari, Lorenzen, et al., 2022; Vicari, Sabin, et al., 2022) and adjusted accordingly for our research questions. Semi-landmarks were placed in occlusal view between landmarks 4–5 and 4–3, and in lateral view between landmarks 1–2, 5 and the projection of landmark two on the basal side of the mandible as no fixed landmark was possible to define. TPS algorithm was used to keep the semi-landmarks at the same distance to describe effectively: (i) the alveolar portion of the mandible in occlusal view and (ii) the acoustic window, coronoid crest and masseteric line in lateral view. To eliminate inter-observer error, the same operator (GBo) recorded the entire landmark configuration using the photographs of the mandibles in both views. A 5 cm scale bar next to the specimen ensured the correct scaling for each digital image. In addition, the total mandibular length (from the tip of the mandible to the coronoid tip) was measured and compared with the length obtained in the software after scaling. Subsequently, the slider file indicating the semi-landmarks was prepared with TPSUtil, and a Generalized Procrustes Analysis (GPA), with sliding of semi-landmarks (Bookstein, 1997) was performed in R (R Core Team, 2018). Generalized Procrustes Analysis was used to rotate, translate and scale landmark configurations to unit centroid size (CS). The specimens were aligned in R using a function developed in the library 'geomorph' (Adams &



**Figure 1** Landmark location. Landmark configuration of the eight anatomical homologous landmarks and semi-landmarks on the 2D specimen of a bottlenose dolphin (*Tursiops truncatus* NHM), in occlusal (top) and lateral (bottom) view. Scale bar 5 cm. See Table 1 for landmark description.

Otárola-Castillo, 2013) for subsequent analyses. Mean shape and size were calculated for each species and used for the following analyses. After GPA, a Principal Components Analysis (PCA) was performed to visualize orthogonal axes of morphological variation, and wireframe and deformation grid were used to visualize shape changes in ordination plots.

Extant species were also grouped within different ecological categories following Vicari et al., 2023 (Table S2). More specifically, we examined eight categorical ecological variables (superficial temperature, diet, diet2, biosonar, diving ecology, climate regions, feeding strategies and rostral morphologies) and five continuous variables (adult average body mass, adult average body length, minimum, mean and maximum prey size). Superficial temperature (ST) is defined as the surface temperature at the area of the maximum abundance for each species. It includes the following categories: warm, temperate, cold and cold-temperate, as defined in Perrin et al. (2009). Diet was defined following Slater et al. (2010) and then grouped into three categories: fish, squid and fish/mammal eaters. Dietary habits and preferences of the species were considered in Diet2. Biosonar mode was defined following Surlykke et al. (2014) and Jensen et al. (2018) as broad-band (BB) covering frequency ranges from tens to 150–170 kHz and narrow-band high-frequency (NBHF) with peak frequencies being at 125–140 kHz and bandwidths of 11–20 kHz. Diving ecology was defined following Perrin et al. (2009) and Vicari et al. (2023) as deep, semipelagic and shallow. Body mass (kg) and length (m) were average measures for mature adults. In addition to Vicari et al. (2023), species were also grouped in climate regions, feeding strategies and rostral

morphologies. Regarding the climate regions, the extant delphinid species were divided into arctic-cold temperate and warm temperate-tropical (Galatius et al., 2020). The feeding strategies were pierce, grip and tear (both part of the biting strategy) and suction feeders (Berta & Lanzetti, 2020; Bianucci et al., 2022; Kienle et al., 2017). The rostral morphology, concerning the crania associated with the examined mandibles, was used to divide the species into brevirostrine, mesorostrine and longirostrine depending on their Rostral Index (RI = rostral length/condylobasal length calculated from 106 crania; Lambert & Goolaerts, 2022, McCurry & Pyenson, 2019, Werth, 2006a, 2006b) (Table S3). We use the `procD.lm` function from `geomorph` to test for the presence of allometry in mandibular mean shape variation in both views. The UPGMA (Unweighted Pair Group Method with Arithmetic mean) algorithm performed on the averaged Procrustes distances was used to assess similarities among taxa in PAST 2.17 (Hammer et al., 2001). We tested for significant phylogenetic signals in size (CS) and shape using the function `physignal` in `geomorph`. We used phylogenetic generalized least squares (PGLS) regressions (Adams & Collyer, 2015) from `geomorph` to evaluate the relationship between size and shape of the mandible mean per each species incorporating the phylogenetic covariance matrix as an error term (Mundry, 2014; Rohlf, 2001).

## Phylogeny

We used the phylogenetic reconstruction provided by McGowen et al. (2009) and modified by Vicari et al. (2023) in order to test for phylogenetic signal in shape within the study taxa (Fig. 2).

**Table 1** Description of the eight homologous landmarks used in the 2D geometric morphometric analysis of 95 delphinids mandibles in occlusal and lateral view

Landmark and semilandmark description	
Occlusal view	
1	Lateral tip of the left mandibular condyle
2	Medial tip of the left mandibular condyle
3	Posterior tip of the left tooth-row
4	<i>Pogonion</i> ; Tip of the mandible
5	Posterior tip of the right tooth-row
6	Lateral tip of the mandibular condyle
7	Medial tip of the mandibular condyle
8	Posterior tip of the mandibular symphysis
3–	Curve describing the length of the left tooth-row from
4	landmark 3 to 4
5–	Curve describing the length of the right tooth-row from
4	landmark 5 to 4
Lateral view	
1	Tip of the coronoid process
2	Posterior tip of the tooth-row
3	Anterior tip of the tooth-row
4	<i>Pogonion</i> : Tip of the mandible
5	Postero-ventral tip of the angular process
6	Ventral tip of the mandibular condyle
7	Dorsal tip of the mandibular condyle
8	Maximal concavity of the mandibular incisurae
1–	Curve describing the dorsal profile of the mandible from the
2	coronoid process to the posterior tip of the tooth-row
5–	Curve describing the ventral profile of the mandible from the
2	postero-ventral tip of the angular process to the projection of the posterior tip of the tooth-row on the ventral side of the mandible

## Results

### Overall mandible shape

The first two components explained 77.01% and 12.28% of the total variance, respectively, in occlusal view (Fig. 3a) and 83.92% and 9.72% in the lateral view (Fig. 3b). In occlusal view, all species show relative displacement of all the landmarks in the occlusal region and at the condyles. Negative scores represent a more V-shaped and long mandible, while positive scores represent a shortening and widening of the mandible. The most extreme deformation is observable between landmarks 3–5, representing the extent of the dental groove and the symphysis (LM 8). In the lateral (labial) view, negative scores represent a longer and more gracile mandible. In contrast, positive scores represent a more robust structure and a reduction in teeth. Species on the left side of the PCA show a precoronoid crest (see Fig. 2). This is a distinct elevation between the coronoid process (LM 1) and the end of the alveolar groove (LM 2). This is not displayed in *Orcinus orca*, *Globicephala melas*, *G. macrorhynchus*, *Orcaella brevirostris*, *Feresa attenuata* and *Grampus griseus*. The precoronoid crest represents the pterygoid muscle attachment in labial view for closing the mandible (Seagars, 1982).

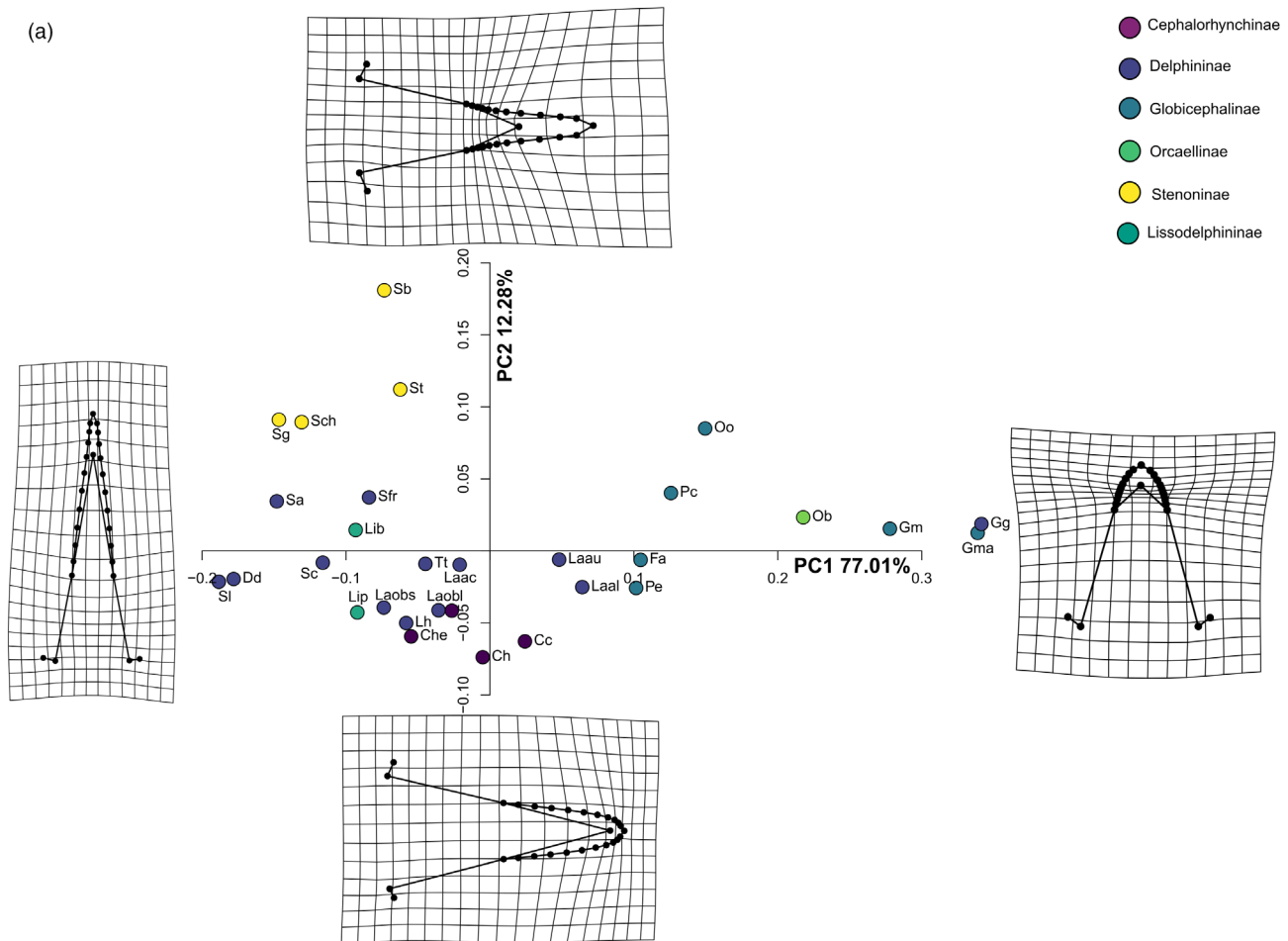
When the categorical variables were mapped onto the morphospace for both views (Fig. 4a,b), the PCA in occlusal view shows the different feeding strategies related to mandibular shape. Negative PC1 values show pierce and longirostrine species with a narrow mandible, longer symphysis and longer tooth rows that are raptorial-ichthyophagous. Positive PC1 values represent brevirostrine species with a massive and broad mandible and tooth rows orientation. Grip and tear feeders occupy the central part of the scatterplot together with mesorostrines. PC2 positive values show species with an intermediate mandibular shape with a relatively elongated symphysis. PCA in lateral view shows the posteroalveolar mandibular shape well. Specifically, the coronoid process is elevated, and a precoronoid crest is also present in the (macro) raptorial species (PC2 positive values). In contrast, the coronoid process is not that elevated, and the precoronoid crest is absent in the teutophagous species with the pterygoid muscle not attached in the labial view (PC1 positive values). The precoronoid process is present in the species that use a combination of raptorial and suction feeding (PC1 and PC2 negative values). UPGMA on Procrustes distance calculated on mean occlusal and lateral shape (Figure S1) grouped the suction feeders and grip and tear species together in both views. Specifically, it showed a group formed by the grip and tear feeders (*Orcinus*, *Pseudorca* and *Orcaella*), a second group with suction feeders (*Globicephala*, *Grampus*), and a larger group composed of several pierce species, with *Sousa* belonging to an isolated group in lateral view only.

The regression of occlusal mandible mean shape on mean size ( $n = 30$ ) indicated that overall, allometry explains 18% of mandible shape variation in occlusal view, and it is significant ( $P = 0.007$ ; Fig. 5a). The lower part of the regression (Fig. 5a) is occupied by small species belonging to Cephalorhynchinae together with *Lagenorhynchus australis* that also displayed an NBHF biosonar type. In contrast, the right side is occupied by larger species belonging to Globicephalinae. Delphininae occupies a range of sizes from small, such as *Lagenorhynchus* spp., to large, such as *Tursiops truncatus*. In contrast, the regression on mean lateral shape was not significant ( $n = 30$ :  $P = 0.06$ ;  $R = 10\%$ ; Fig. 5b), and the CS for occlusal and lateral view was not statistically different between longirostrine and mesorostrine (Occl:  $P = 0.57$ ; Lat:  $P = 0.32$ ), brevirostrine and mesorostrine (Occl:  $P = 0.96$ ; Lat:  $P = 0.72$ ) and longirostrine and brevirostrine ( $P = 0.67$ ;  $P = 0.78$ ) species. The CS values of brevirostrine include the ranges of both meso- and longirostrine, suggesting a high variability in the size of brevirostrine species. In both views, brevirostrine taxa are well-differentiated from longi- and mesorostrine taxa by shape in the PCA but not by size.

### Phylogenetic generalized least squares (PGLS)

Phylogenetic signal was strong in both mandibular shape (Occl: K mult 1.086;  $P = 0.001$ ; Lat: K mult 0.97;  $P = 0.001$ ) and size (Occl: K mult 1.076;  $P = 0.001$ ; Lat: K mult 0.859;  $P = 0.001$ ) in both views. When the phylogenetic tree was used as an error matrix (Table 2), mandibular shape was found





**Figure 3** Principal component analysis of mean shape delphinids mandible in (a) occlusal and (b) lateral view for 30 species. Shape changes on the axes are shown by 2D wireframe and deformation grid. Letters indicate species abbreviations: Cc, *Cephalorhynchus commersoni*; Ce, *Cephalorhynchus eutropia*; Ch, *Cephalorhynchus heavisidii*; Che, *Cephalorhynchus Hector*; Dd, *Delphinus delphis*; Fa, *Feresa attenuata*; Gg, *Grampus griseus*; Gma, *Globicephala macrorhynchus*; Gm, *Globicephala melas*; Lh, *Lagenodelphis hosei*; Laac, *Lagenorhynchus acutus*; Laal, *Lagenorhynchus albirostris*; Laau, *Lagenorhynchus australis*; Laobl, *Lagenorhynchus obliquidens*; Laobs, *Lagenorhynchus obscurus*; Lib, *Lissodelphis borealis*; Lip, *Lissodelphis peronii*; Ob, *Orcaella brevirostris*; Oo, *Orcinus orca*; Pe, *Peponocephala electra*; Pc, *Pseudorca crassidens*; Sg, *Sotalia guianensis*; Sch, *Sousa chinensis*; St, *Sousa teuszii*; Sa, *Stenellattenuata*; Sc, *Stenella clymene*; Sfr, *Stenella frontalis*; Sl, *Stenella longirostris*; Sb, *Steno bredanensis*; Tt, *Tursiops truncatus*.

Werth, 2006a, 2006b) with feeding mode. The MBI is a descriptive index of amblygnathy (*amblos* = blunt; *gnathos* = jaw): bluntest mandibles or brevirostrines have the highest MBI, which corresponds to a reduction in the length of the tooth row indirectly related to a decrease of tooth count and a tendency to use suction feeding. Conversely, the longest mandibles or longirostrines have the lowest MBI, corresponding to an increased number of teeth (longer tooth row) and a pierce feeding mode. Brevirostrine species have a wider symphyseal area and higher mandibular bluntness index, which makes them specialized for suction feeding. This is true for most delphinids, but we have some exceptions for toothed whales (Monodontidae, Ziphiidae, Physiteridae; Werth, 2006a, 2006b). Subsequently, other experimental works demonstrated different suction abilities in three toothed whales with different skull

morphology: common dolphin (*Delphinus delphis*) and Atlantic white-sided dolphin (*Leucopleurus acutus*) (Werth, 2006b). However, amblygnathy (shorter and broader mandibles) improves water flow for suction feeding, creating the optimal circular mouth opening shape for prey ingestion. It also frees the teeth from their grasping function. These observations agree with the recently published study on delphinid crania (Galatius et al., 2020) and the extant toothed whale clade (Vicari et al., 2023).

### Feeding mode and precoronoid crest

Our results show that the absence and presence of the precoronoid crest (see Fig. 2) is an important feature related to feeding mode as it represents an external pterygoid muscle attachment

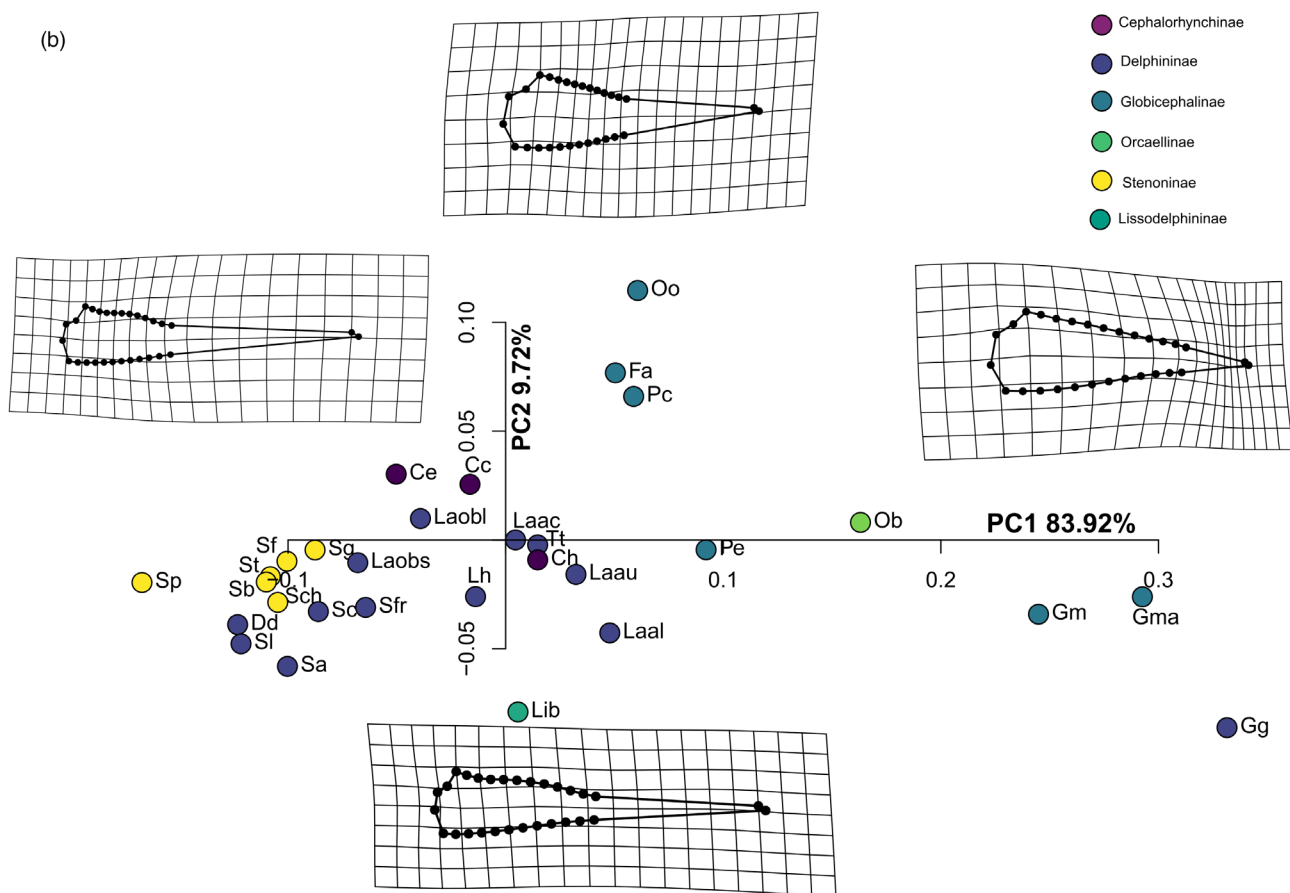
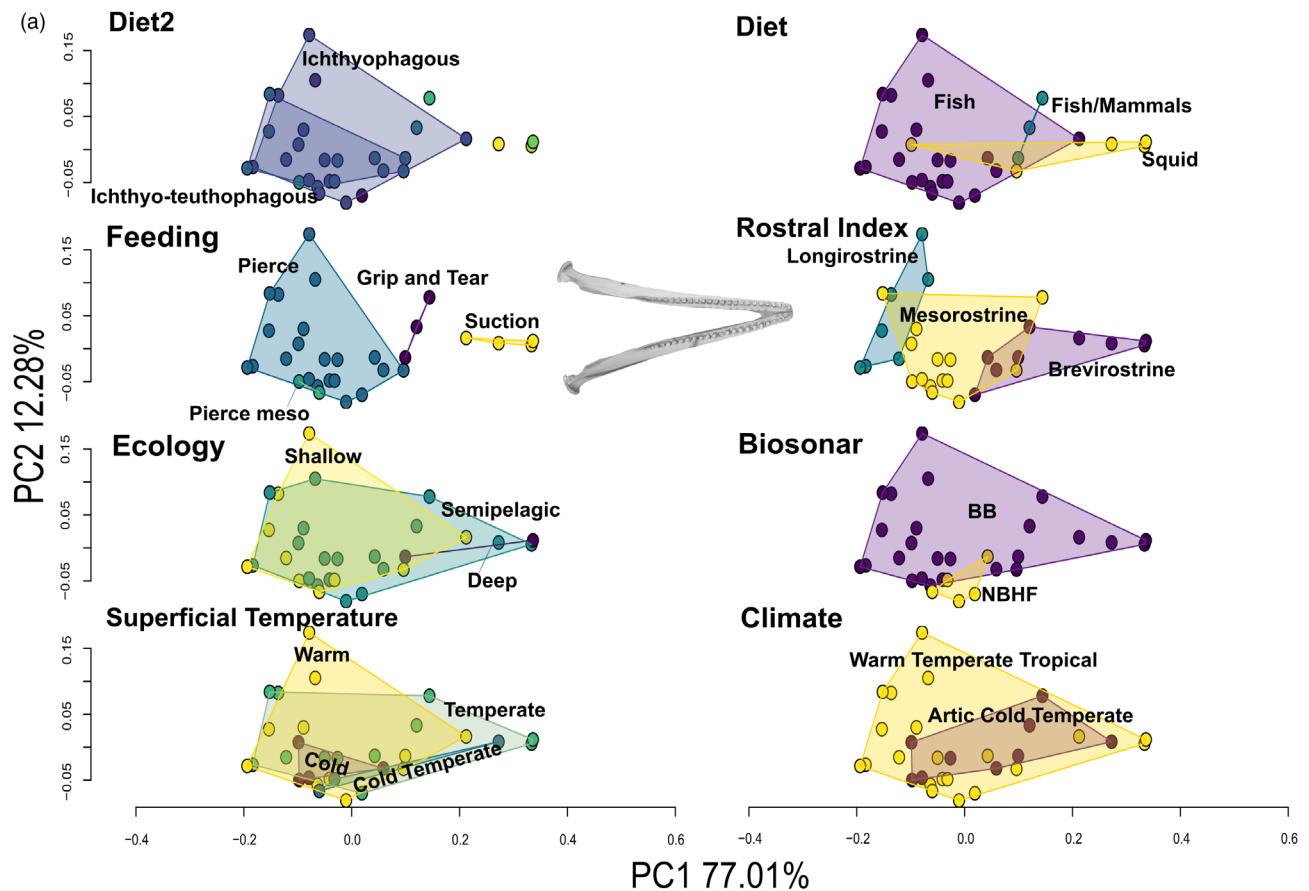


Figure 3 Continued

(Seagers, 1982) and supports the coronoid process. The overall mandible shape is essential for the attachment of masticatory muscles (masseter, temporalis and pterygoideus) and the depressor (digastric) muscle. The attachments on the mandible can be better appreciated and described in lateral view by the two curves of semilandmarks. The masseter muscle is attached to the lower part of the mandible and the zygomatic arch on the cranium, helping with the elevation of the mandible. The temporalis is connected to the temporal fossa on the cranium and the coronoid process of the mandible, contributing to the closing of the jaw. Its strength is also directly related to the extent of the temporal fossa on the cranium and the robustness of the posterior region of the mandible. For example, killer whales have a sizeable temporal fossa (Vicari et al., 2023) and a robust mandible that can be translated into a strong bite force for crushing. The pterygoid muscle (internal and external) is instead a paired muscle composed of two parts that originate from the pterygoid area on the cranium (Seagers, 1982): pterygoideus internus (pi) and external (pe). Both insert on the mandible: pe inserts on the coronoid process in lingual view ventrally. At the same time, the pi surrounds the mandibular foramen in lingual view and is inserted on the precoronoid crest in species that display this morphology (Seagers, 1982).

Since 1871 (Murie, 1871), the pterygoids have been described as the most powerful muscular structure influencing the lower jaw's upward, forward and sideways movements (Seagers, 1982). Specifically, the pi is important for snapping movements (Seagers, 1982). The last muscle involved in feeding is the depressor or digastric muscle. This muscle can be a single or double-bellied within toothed whales (Ito & Aida, 2005). While having a single-bellied muscle plays a minor role in jaw opening (Ito & Aida, 2005), a double-bellied digastric can allow a better gular expansion. The digastric muscle attaches beneath the mandible, and it has an anterior part or belly that originates from the digastric fossa on the mandible connected with the hyoid. In contrast, the posterior part arises from the mastoid notch on the temporal bone on the cranium and inserts into the mandible condyle. While the anterior part is important for pulling down the mandible, the posterior part stabilizes the hyoids. This duality is crucial while feeding: while the anterior contracts, the mandible is pulled down rapidly, essential for prey capture. Our morphospace shows that fish/mammal eaters and squid feeders do not have a precoronoid crest for the attachment of the pterygoid muscle on the labial view of the mandible. Here, we present two hypotheses that can explain the presence and absence of the precoronoid crest: (i) species



**Figure 4** Principal component analysis (PCA) on (a) occlusal and (b) lateral view plot representing Diet and Diet2 (fish, fish/mammals and squid) groups; Feeding mode (Suction, Pierce and Grip and Tear); Rostral Index (Longirostrine, mesorostrine and Brevirostrine); their Diving ecology (deep, semipelagic and shallow); Biosonar mode groups (broadband BB and narrow-band-high-frequency NBHF); four Superficial water Temperature (Warm, Cold, Cold Temperate and Temperate) and Climate (Artic Cold Temperate and Warm Temperate Tropical). Letters indicate species abbreviations listed in Fig. 3 and Table S2.

that use the pierce feeding mechanism need a fast closure of the mouth to catch their prey and an attachment of the pterygoid muscle on the labial view of the mandible can significantly help in exerting this function. The attachment of this muscle on the precoronoid crest has been observed in *D. delphis*, *L. obliquidens* and *T. truncatus* but not in *G. macrohynchus*, *G. griseus* and *O. orca* (Seagers, 1982). Seagers (1982) also observed that the pterygoideus internus muscle is more massive than the masseter and temporal groups in *Tursiops*. This would also support our hypothesis on the presence of the precoronoid crest in these species to give more space for the attachment of the pterygoideus, which is important for fast snapping movements. Then, the absence of a precoronoid crest in delphinid species with tooth count reduction might be due to a complete lack of teeth on the maxillary teeth or a reduced number of teeth in general caused by the shortening of the mandible. Consequently, these species exhibit a less developed pi and the absence of a precoronoid crest (Seagers, 1982). Mandible stability is crucial for suction feeding,

and they compensate with a larger digastric muscle, which, based on its morphology, enhances the efficiency of the suction feeding mechanism (Ito & Aida, 2005). In our morphospace, species that do not display the precoronoid crest are brevirostrines such as *Orcaella brevirostris*, *Globicephala* spp, *Grampus griseus*, *Pseudorca crassidens* and *Feresa attenuata*. (ii) Our second hypothesis is that as the ramus is reduced in toothed whales, the precoronoid process might be a structure that can support the coronoid process as the temporal muscle is smaller in this species compared to grip and tier and suction feeders (Seagers, 1982). This way, when using pierce feeding, the precoronoid process might increase strength along the delphinid mandible's reduced ramus and significantly support the coronoid process where the temporalis is attached. To test these hypotheses, finite element analysis and more dissections on stranded delphinid species are needed to compare anatomically the pterygoid muscle attachments between species with and without precoronoid crest and the efficiency of having a single or double bellied digastric muscle in suction feeder species.



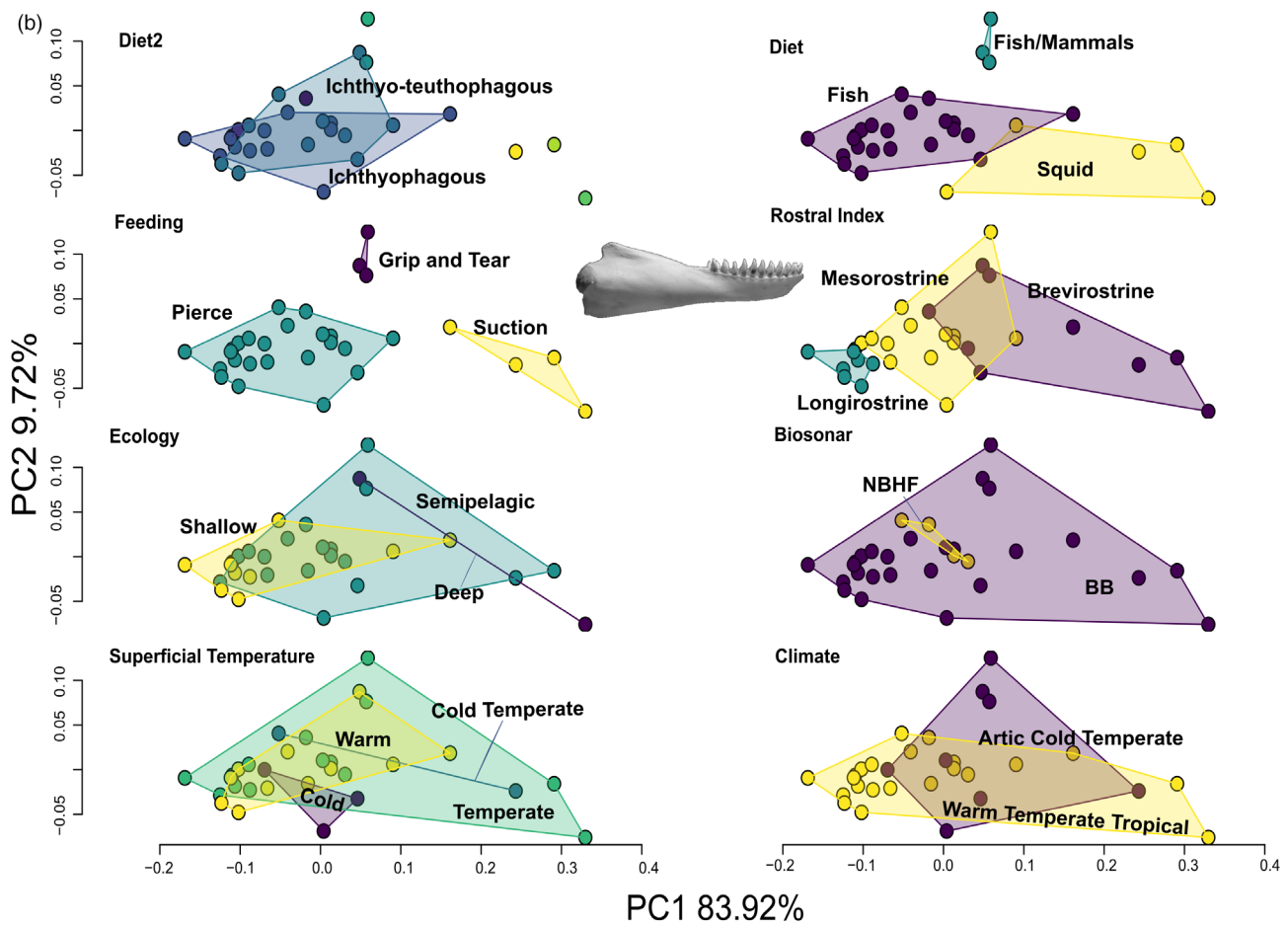


Figure 4 Continued

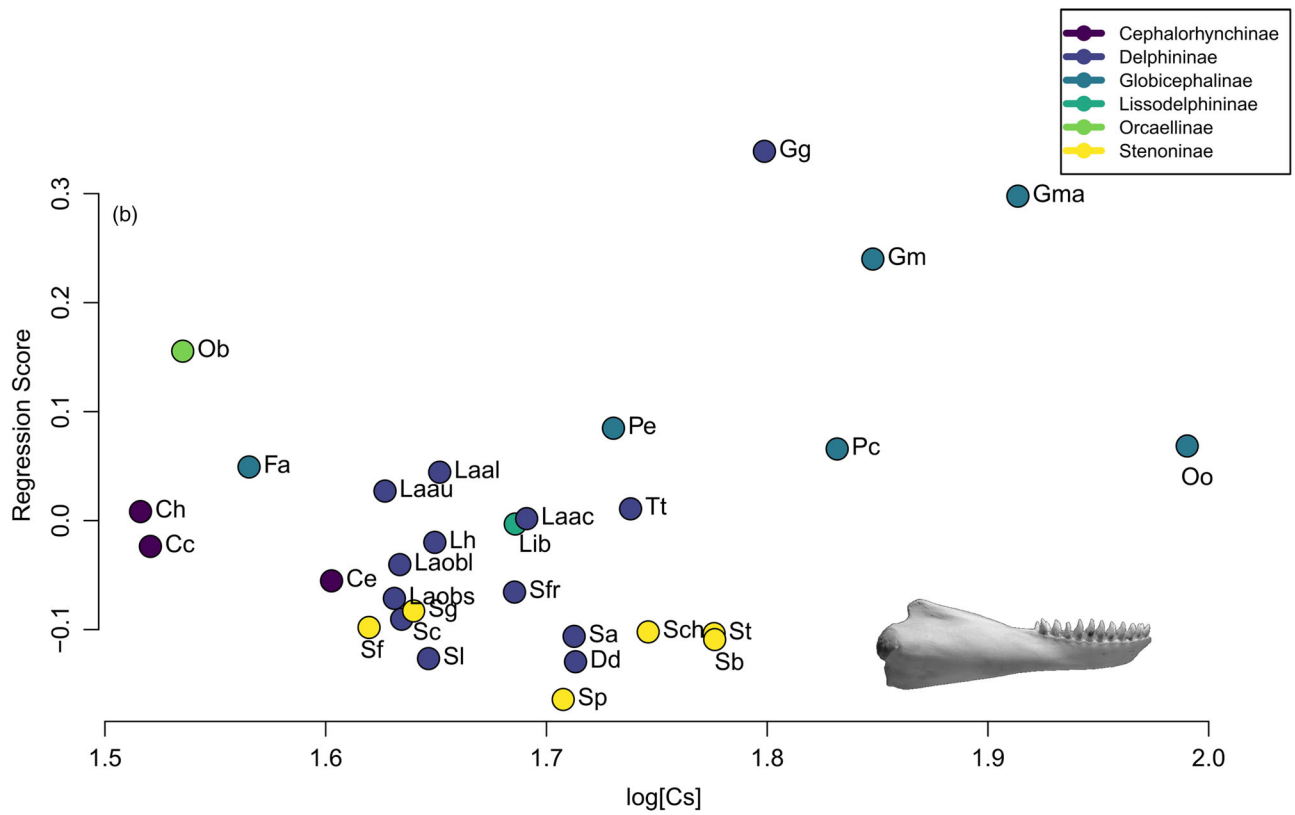
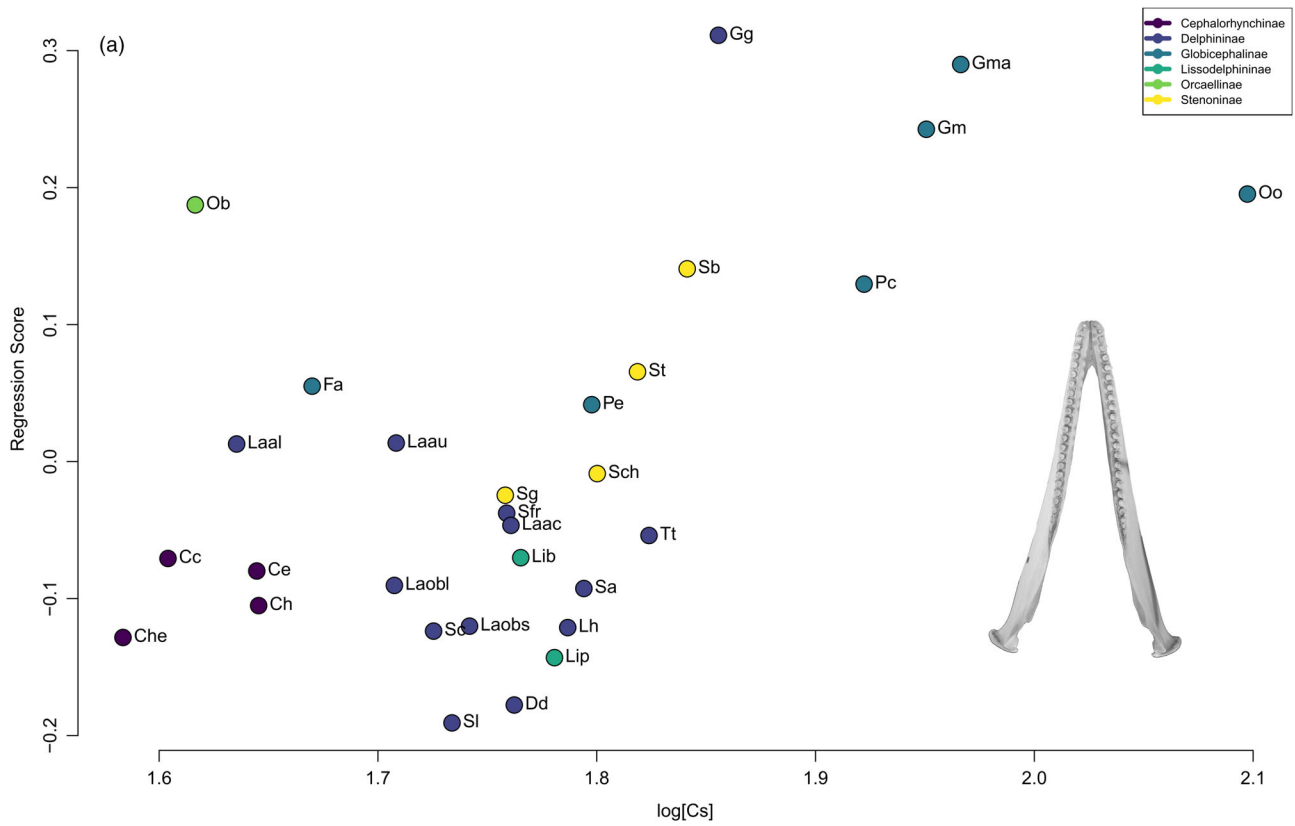
### Diet and maximum prey size drive mandibular size

Our results show that diet varies within species in relation to their size, and they prey on a selected maximum prey size. The giant killer whale is the most basal species (Fig. 2) having a diet that includes mammals and larger prey. A first branch with the smallest species that eats fish; another branch that eats squid (*Grampus griseus*, *Peponocephala electra*, *Globicephala* spp) and fish/mammals (*Pseudorca crassidens* and *Feresa attenuata*) and again medium to smaller-size range of fish eaters. Larger size provides greater energy and strength required to hunt larger prey, while small dolphin species find more accessible smaller prey (MacLeod et al., 2006). Moreover, unlike the cranium (Vicari et al., 2023), the mandible will dictate the maximum possible prey size as the muscle attachments and mandible size limit the mouth opening. While the cranium will dictate the mean and minimum commonest prey size available (Vicari et al., 2023) due to its role in supporting the position and function of the melon essential for prey detention, the mandible will act on the maximum prey size as it determines the maximum width of the mouth opening

during feeding. The size-diet relationship, together with the maximum prey size hunted by this group, is determined by multiple selective pressures. The size of the cranium (Vicari et al., 2023) of the toothed whales and dolphins has developed to maximize the prey hunt efficiency, and the size of the mandible will act on the maximum prey size that can be hunted.

### Biosonar mode drives mandibular occlusal shape evolution

Our study confirms the biosonar as a driver of mandibular occlusal shape within Delphinidae. This further confirms the dual role of the mandible: feeding and sound reception. NBHF species are mesorostrine with similar mandibular width (distance between the two hemi-mandibles measured at the condyles), a shorter mandible than long-snouted species, and the tooth row runs half of the total length of the mandible. Following the phylogenetic tree and the distribution of species in our morphospace, the first branching of delphinid species is the BB and brevirostrine *Orcinus orca*, together with the mesorostrines *Lagenorhynchus acutus* and *L. albirostris*. This is followed by NBHF species such as *Cephalorhynchus* spp



**Figure 5** Regression of mandible means (a) occlusal and (b) lateral shape against mean centroid size. Colours indicate subfamilies, and letters indicate species abbreviation, as in Fig. 3.

**Table 2** PGLS analyses performed on delphinids mandible in Occlusal and Lateral View to test covariation between mandible size (CS = centroid size), shape, and ecological (ST = surface temperature) and metric variables (L = Length)

Variables	Species no.	d.f.	procD.pgls											
			Occlusal view						Lateral view					
			Shape			Centroid size			Shape			Centroid size		
			Rsq	F	P*	Rsq	F	P*	Rsq	F	P*	Rsq	F	P*
Biosonar	30	1	0.11	3.43	<b>0.038</b>	0.08	2.45	0.106	0.11	3.41	0.061	0.05	1.56	0.224
Diet	30	2	0.09	1.43	0.219	0.06	0.94	0.372	0.14	2.23	0.056	0.16	2.59	0.086
Diet2	30	9	0.42	1.62	0.058	0.63	3.85	<b>0.013</b>	0.41	1.81	0.055	0.63	4.54	<b>0.003</b>
Feeding mode	30	3	0.25	2.85	<b>0.008</b>	0.10	1.01	0.41	0.22	3.91	<b>0.006</b>	0.09	1.28	0.3
Diving ecology	30	2	0.06	0.83	0.519	0.18	2.98	0.087	0.07	1.09	0.36	0.14	2.22	0.133
ST	30	3	0.09	0.89	0.529	0.11	1.09	0.367	0.11	1.07	0.411	0.12	1.24	0.289
Climate	30	1	0.12	3.96	<b>0.038</b>	0.01	0.33	0.536	0.14	4.75	<b>0.032</b>	0.01	0.19	0.634
Rostral index	30	2	0.13	2.01	0.06	0.01	0.17	0.85	0.12	1.81	0.108	0.01	0.19	0.832
L	30	1	0.96	2.09	0.145	0.96	2.04	0.409	0.94	1.89	0.181	0.97	4.46	0.153
BodyMass	30	1	0.96	2.09	0.145	0.96	2.04	0.409	0.95	1.55	0.341	0.98	4.09	0.251
BodyMass~Diet	30	2	0.16	2.64	0.101				0.15	2.45	0.1			
BodyMass~Diet2	30	9	0.67	4.52	<b>0.002</b>				0.66	5.06	<b>0.002</b>			
PreyMin	30	1	0.05	1.55	0.164	0.14	4.46	0.051	0.03	0.91	0.389	0.09	2.93	0.103
PreyMean	30	1	0.05	1.60	0.216	0.03	0.78	0.397	0.07	2.23	0.174	0.03	0.88	0.35
PreyMax	30	1	0.09	2.90	0.093	0.31	12.76	<b>0.004</b>	0.07	2.16	0.174	0.13	4.44	<b>0.04</b>

\*P-values are in bold when significant ( $P < 0.05$ ).

and *Lagenorhynchus australis*, and the most recent long-snouted species are BB longirostrines (e.g. *Delphinus delphis*). Predation pressures may have driven the evolutionary emergence of NBHF species before or after the appearance of ancient killer whales, as they have poor hearing above 100 kHz (Galatius et al., 2019). This distinct biosonar type makes these species cryptic, allowing them to avoid detection by giant predators (Galatius et al., 2019). These evolutionary pressures and adaptations are also reflected in delphinid anatomical structure. The development of the pterygoideus and reduction of the masseter contributed to the fatty tissue occupation of the mandibular foramen (Seagars, 1982). This anatomical adaptation is evident in the posterior part of the lateral wall of the odontocete mandible, where variation in thickness has been observed (Nummela et al., 2004), representing an excellent reasonable compromise that further confirms the dual role of the mandible. Unlike Vicari et al. (2023), our study fails to detect the relationship between mandible size and biosonar type. Still, it confirms a relationship between the mandible shape and biosonar type in BB and NBHF species. This indicates a possible relationship between muscular attachment and sound detection. Seagars (1982) hypothesized on the potential involvement of the pterygoideus contraction to alter the mandibular fat bodies in the mandible. The mandible opens in a channel that hosts a complex 3D distribution of lipids (Koopman, 2018), making the mandible six times more sensitive than the external auditory canal (Berta et al., 2005) and a well-designed structure for a specialized sound reception (Koopman, 2018; Norris, 1964, 1968). More studies are

needed to understand the muscle involvement as a ‘waveguide’ for sound in species displaying different biosonar types.

### Climate drives mandibular shape evolution

Taxa grouped within two different climatic zones, Warm Temperate-Tropical and Arctic-Cold Temperate, displayed a significant difference in mandibular shape. This implies that the Delphinidae evolved different shapes of the mandible within the two climatic zones, and these shapes were probably driven by different selective pressures associated with climate. In contrast to shape, size was not significantly related to climate. This result does not agree with that obtained on toothed whale and delphinid crania, where no links between shape and habitat have been detected after accounting for phylogeny (Galatius et al., 2020; Vicari et al., 2023). Even if the species are well distributed in the morphospace and overlap, mandibular shape and size are affected by phylogeny, suggesting that distantly related species adapted their mandible shape primarily to an Arctic and cold climate (brevirostrines) and successively to a warm, temperate and tropical environment (longirostrines). This might be due to thermoregulation as suggested by Galatius et al. (2020), or by a prey (mostly fish) swimming speed increase that could have driven the evolution of arctic species into tropical areas developing a longer rostrum (McCurry, Evans, et al., 2017). Species with a lower mandibular bluntness index could, in some cases, also be associated with hydrodynamics, with the fastest species presumably displaying longer mandibles to facilitate underwater movements during

tropical storms; alternatively, amblygnathus could be a good adaptation for breathing through ice openings in polar species (Werth, 2006a).

## Conclusions

The family Delphinidae is a group of successful mammals represented by many extant species. Geometric morphometric analysis of delphinid mandibles reveals that their feeding mode primarily drives shape in extant species. Climate influences the overall mandible shape and biosonar mode based only on occlusal view. Diet and maximum prey size played a significant role in affecting the mandibular size in both views. Accordingly, it is possible to estimate the feeding mode by investigating the position of their mandible within the morphospace, thus confirming an evolutionary trend in delphinids already observed by previous authors: a shortening of the mandible often corresponds to a reduction in the number of teeth, most likely in relation with a specialization for suction feeding. Our study also confirms the importance of the precoronoid crest and its relation to masticatory muscles with a specific focus on the pterygoideus attachment related to feeding mode. Thus, the modern delphinid mandible structure is the result of multiple modifications driven both by feeding and hearing needs. Further studies will aim to introduce extinct taxa to better investigate the hypothesis of a rapid radiation of Delphinidae due to a feeding mode specialization in a reach-prey species environment in the Pliocene.

## Acknowledgements

This project was possible thanks to the Campus World 2014-UNIVPM scholarship awarded to D. Vicari to study the shape of toothed whale mandibles at RBINS. We thank Giovanni Bianucci for providing the dataset and G. Bianucci, C. Fruciano and O. Lambert for providing feedback on the first draft of the manuscript. Open access publishing facilitated by Università degli Studi della Basilicata, as part of the Wiley - CRUI-CARE agreement.

## Conflict of interest

The authors declare no conflict of interest.

## Author contributions

DV and LP conceived the ideas and designed the methodology; GB collected the data; DV analysed the data with the support of LP; DV and LP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** (a) UPGMA-Mandible occlusal view. (b) UPGMA-Mandible lateral view.

**Table S1.** List of specimens used for the analysis.

**Table S2.** Variables used for the analysis.

**Table S3.** Rostral index calculation.