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DIVERGENT EVOLUTIONARY MORPHOLOGY OF THE AXIAL SKELETON AS A POTENTIAL KEY INNOVATION IN MODERN CETACEANS

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ABSTRACT

Cetaceans represent the most diverse clade of extant marine tetrapods. Although the restructuring of oceans could have contributed to their diversity, other factors might also be involved. Similar to ichthyosaurs and sharks, variation of morphological traits could have promoted the colonization of new ecological niches and supported their diversification. By combining morphological data describing the axial skeleton of 73 cetacean species with phylogenetic comparative methods, we demonstrate that the vertebral morphology of cetaceans is associated with their habitat. All riverine and coastal species possess a small body size, lengthened vertebrae and a low vertebral count compared with open ocean species. Extant cetaceans have followed two distinct evolutionary pathways relative to their ecology. Whereas most offshore species such as baleen whales evolved towards an increased body size while retaining a low vertebral count, small oceanic dolphins underwent deep modifications of their axial skeleton with an extremely high number of short vertebrae. Our comparative analyses provide evidence these vertebral modifications have potentially operated as key innovations. These novelties contributed to their explosive radiation, resulting in an efficient swimming style that provides energetic advantages to small-sized species.

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1. Introduction

Morphological disparity often supports various functional abilities, promoting the occupation of new ecological niches. Although many ecomorphological studies focused on external body shape or skull morphology, some have demonstrated correlations between vertebral morphology and species ecology in several vertebrate lineages [1–4]. For example, scansorial felids and arboreal marsupials have wider and/or shorter vertebral centra than their terrestrial counterparts [1,2]. In the aquatic ichthyosaurs and sharks, variation of body form and vertebral phenotypes has been linked to different lifestyles like the inhabitation of coastal or offshore habitats [5–7]. For instance, the disparification of body shape in ichthyosaurs is assumed to be linked to their adaptive radiation, with transitions from coastal habitats to open seas [6,7].

In terms of body shape, cetaceans exhibit a strong convergence with lamniform sharks and ichthyosaurs [8,9]. Cetaceans adapted to coastal or oceanic habitat differ in some phenotypic traits such as body proportions, fin shapes or inner ear morphology [10–12]. Slow swimming coastal species tend to have paddle-shaped fins and flukes and large bulbous heads compared to cruising species [10,11]. Cetaceans also exhibit a wide variation in their vertebral morphology which could support different swimming abilities [13–16]. Surprisingly, despite their large ecological diversity, no study has statistically investigated the relationship between the axial skeleton and the various habitats of cetaceans at a large phylogenetic scale. Previous studies have suggested that low vertebral count and spool-shaped vertebrae would be a primitive state in extant cetaceans typical of slow-swimming coastal species. In contrast, high vertebral count and discoidal vertebrae would be a derived condition corresponding to fast-swimming pelagic dolphins [13,16,17]. On the other hand, Viglino and colleagues did not find a correlation between vertebral morphology and habitat when using phylogenetic comparative methods on seven dolphin species [18]. This supports the need to further investigate the cetacean vertebral morphology by studying a large number of species and by using recently developed comparative methods to understand how the cetacean backbone diversified.

With 89 species [19], cetaceans are currently the most species-rich clade of extant marine tetrapods. In particular, 40% of cetacean species are Delphinidae, the family of oceanic dolphins. This high level of species diversity in Delphinidae results from increased rates of lineage diversification during the past 10 Ma [20–24]. This explosive radiation might be due to a combination of vicariant events and adaptation to scattered production areas caused by the restructuring of oceans that occurred during the middle-late Miocene [20,23]. However, it was later suggested that this shift might also be driven by the appearance of an unidentified key innovation [22]. As forward propulsion of cetaceans is achieved by oscillation of the backbone, the axial skeleton plays a central role in swimming and travelling capabilities. We might then expect that the disparity of the vertebral morphology in cetaceans to be linked to their ecological diversity [13,16,17]. Accordingly, variation of their axial skeleton could have acted as evolutionary innovations supporting their adaptive radiation.

In the present study, we hypothesize that the axial skeleton morphology of modern cetaceans is related to the species lifestyle and their diversification. We have thus compiled meristic and morphometric data on the axial skeleton of most cetacean species. Using various phylogenetic comparative methods, we demonstrate that the vertebral morphology is linked to the ecological diversity of cetaceans and that the explosive radiation of oceanic dolphins could be linked to sudden vertebral modifications that acted as key innovations.

2. Material and methods

(a) DATA SAMPLING

Vertebral count and shape data were collected from 217 specimens in nine museums, representing 73 extant species (specimen list in table S1). Every genus, except the monospecific *Indopacetus*, is represented in our dataset. We sampled at least two specimens per species although twelve species were represented by one specimen. Whenever possible, we measured specimens of different sex and/or from different populations. To estimate intraspecific variation, the morphological disparity was calculated for two species represented by numerous specimens (*Phocoena phocoena*: 17 specimens, *Tursiops truncatus*: 11 specimens) and was compared to the disparity level of the entire dataset (*morphol.disparity* function, R-package *geomorph* (v.3.0.7) [25]).

Total vertebral count was taken only on complete specimens or on specimens missing up to three vertebrae and for which the number of missing vertebrae could be estimated. When specimens of the same species had different vertebral counts, we retained the highest count for the species. To quantify vertebral shape, two angular and 12 linear measurements were taken on each vertebra with a protractor, digital calipers, and rulers (figure S1) [26]. Shape data were collected on thoracic, lumbar, and caudal vertebrae allowing the inclusion of specimens missing most of their fluke vertebrae. The first caudal vertebra was defined as the first vertebra possessing an articular facet for a chevron bone on its posterior face [27]. The first fluke vertebra was the first dorsoventrally compressed vertebrae.

The scarcity of undamaged fossilised backbones and phylogenetic uncertainties of some fossil taxa prevented us from reliably including extinct cetaceans in our analyses. However, length and height of vertebral centra from fossil taxa were obtained from the literature [28–37]. Their mean length/height (*L/H*) ratios were compared to extant species (Appendix I, Supplementary materials).

Prior to analysis, each species was classified into one of the following habitat categories based on synthetic bibliographic works; (*i*) rivers, bays, and estuaries; (*ii*) continental shelf; (*iii*) continental slope and offshore waters; and (*iv*) mixed lifestyle between continental shelf and offshore waters [38–40]. All phylogenetic analyses were based on the cetacean consensus time-tree published by Steeman [20]. The topology and divergence time estimations of this tree are congruent with other recently published phylogenies [21,41–43]. Although some uncertainties remain at shallow phylogenetic levels, relationships at the family levels are well established. Similarly to other recent comparative studies in cetaceans [22,24], we are confident that this phylogenetic uncertainty should not impair our results. Prior to analysis, *Orcaella heinsohni* which is not included in Steeman's tree was added to the tree (*add.species.to.genus* function, R-package *phytools* (v.0.6-44) [44,45]).

In order to highlight raw morphological variation without accounting for phylogenetic signal, all analyses described hereafter were repeated by using regular statistics (Appendix II, Supplementary materials).

(b) VERTEBRAL COUNT, BODY SIZE AND ECOLOGY

We first investigated variation in the number of vertebrae and tested its linear relationship with body length using a phylogenetically corrected generalized least squares regression (PGLS) in the *nlme* R-package (v.3.1-131) [46]. For this analysis, the average body length of each species was obtained by calculating the mean value of the body size range provided by Berta [39]. We also tested the effect of habitat on the vertebral count with a phylogenetic ANOVA (*aov.phylo* function, R-package *geiger* (v.2.0.6) [47]).

Due to an apparent difference in vertebral count among families (see Results), we tested whether Delphinidae and Phocoenidae (*i.e.* oceanic dolphins and porpoises) differ from other families in their vertebral count and body size by applying a phylogenetic MANOVA (*aov.phylo* function). According to the results from this MANOVA and those from evolutionary patterns analyses (see section *(d)*), we repeated the analysis testing the effect of habitat (phylo-ANOVA) and body size (PGLS) on four different subgroups of species: (*i*) Delphinidae and Phocoenidae; (*ii*) all species except Delphinidae and Phocoenidae; (*iii*) Delphinoidea; and (*iv*) non-Delphinoidea.

(c) MORPHOSPACE OF VERTEBRAE AND ECOLOGY

To compare vertebral shape among species with highly different vertebral counts, we calculated individual mean regional measurements (IMRMs) which correspond to the mean of each linear/angular measurement for each region of each individual (figure S1*e*). All linear IMRMs were $\log_{10}$-transformed and then phylogenetically size-corrected (*phyl.resid.intra* function [48]). Total centrum length (TCL) was calculated for each specimen by summing the length of the vertebral centrum of all measured vertebrae [26]. It was $\log_{10}$-transformed and used as a proxy of body length for IMRMs size-correction. Angular IMRMs were not correlated to body size and were thus transformed using a cosine function. Specimen residuals of each IMRM were then averaged for each species to obtain species mean regional measurements (SMRMs).

All SMRMs were implemented in a regular principal component analysis (PCA) based on the correlation matrix, using the *prcomp* function in R. Similarly to analyses on vertebral count, four additional PCAs were run separately for each species subgroup. According to the Jollife cut-off, only principal components (PCs) with an eigenvalue ≥ 0.7 were conserved. Thus the first eight PCs for the "all cetaceans" PCA and the first nine PCs for each subgroup PCA were used in the following analyses.

We first tested the effect of habitat on vertebral shape (PCs) for each PCA separately using phylogenetic MANOVAs. Then, we tested the effect of body size on vertebral shape with a multivariate phylogenetic linear regression (*procD.pgls* function, *geomorph* package). A multivariate PGLS was also used on the "all cetaceans" PCA to test the relationship between vertebral count and vertebral shape. Differences in vertebral shape between Delphinidae and Phocoenidae *versus* other species were tested with a phylogenetic MANOVA.

(d) EVOLUTIONARY SHIFTS OF PHENOTYPIC TRAITS

Analyses of vertebral count and morphospace point out to a marked divergence of oceanic dolphins and porpoises from other species (see Results). In order to test if this morphological divergence corresponds to evolutionary shifts, we applied two Bayesian statistical methods to our phenotypic data. BAMM (v.2.5.0) [22] uses a Bayesian multi-rate approach and allows the detection of variations in the rate of morphological evolution. Bayou (v.2.1.1) [49] is based on a Bayesian multi-regime Ornstein-Uhlenbeck approach and can identify changes in phenotypic optima over time. These two methods can identify the presence of one or several shifts without *a priori* information on the position of shifts along the phylogeny. Analyses were run independently for each PC of the "all cetaceans" PCA and on the $\log_{10}$-transformed vertebral count.

For BAMM, priors were automatically generated in the R-package *BAMMtools* (v.2.1.6) [50]. Analyses were run using a Metropolis-coupled Markov chain Monte Carlo (MCMC) with 5,000,000 generations for each univariate trait. Parameters were sampled every 1,000 iterations, with the first 10% deleted as burn-in.

For Bayou, several independent MCMC chains with different priors were run and their respective marginal likelihoods were computed to select the most appropriate ones. Priors retained for analyses are listed in table S2. For each univariate dataset, five MCMC chains of 1,000,000 generations were run independently and the first 20% of each chain were deleted as burn-in. Chains convergence was assessed using Gelman and Rubin's *R* and the chains were then combined as a single chain from which results were computed.

(e) DIVERSIFICATION AND MORPHOLOGICAL EVOLUTIONARY RATES

Here, we explored the relationship between lineage diversification rate and phenotypic evolution rate to test the key innovation hypothesis. The linear relationship between speciation rate and the vertebral count and shape evolutionary rates were tested with the ES-sim test under a Brownian motion model [51]. We used the $\log_{10}$-transformed number of vertebrae for vertebral count analysis and we ran the ES-sim test for each PC independently for vertebral shape analysis. Each analysis was run with 1,000 iterations.

3. Results

Hereafter, we present the results of statistical analyses accounting for phylogenetic information. Results from regular statistics, which are congruent with phylogenetic comparative methods, are detailed in the Appendix II of the Supplementary materials. The morphological variance at the species level (*P. phocoena* and *T. truncatus*) is relatively low compared to the disparity of all cetaceans for vertebral shape and count (table S3). Intraspecific variability should not impair our results.

(a) VERTEBRAL COUNT, BODY SIZE AND ECOLOGY

While most mammals possess fewer than 70 vertebrae [52], the number of vertebrae constituting the axial skeleton of cetaceans greatly varies, ranging from 42 (*Caperea marginata* and *Inia geoffrensis*) to 97 units (*Phocoenoides dalli*) (figure 1*b*). Habitat has no significant effect on the number of vertebrae across all cetaceans (phylo-ANOVA: $p = 0.39$, $\eta^2 = 0.08$) but it has a significant effect in oceanic dolphins and porpoises (phylo-ANOVA: $p = 0.01$, $\eta^2 = 0.3$).

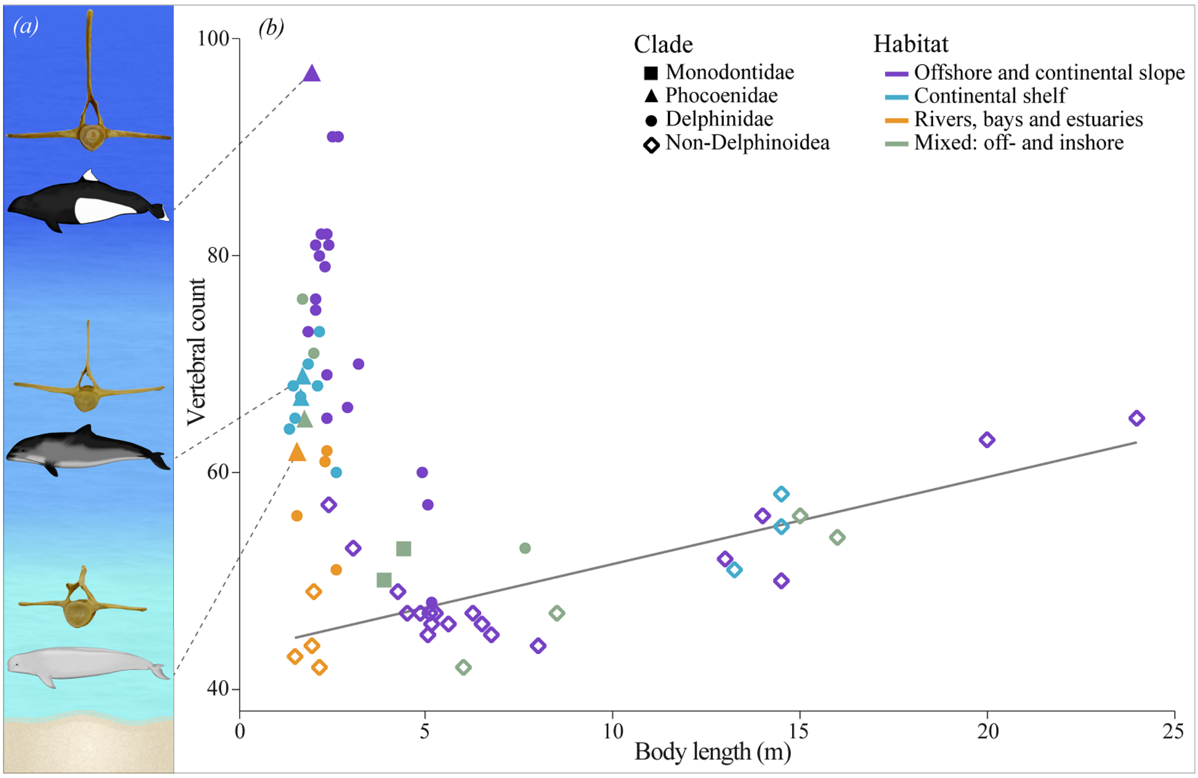

Figure 1. Relationship between vertebral count and body size according to habitat. (*a*) Correspondence between vertebral shape and count for three species of porpoises (from top to bottom: *P. dalli*, *P. phocoena*, *Neophocaena phocaenoides*). (*b*) Vertebral count according to body length for all cetacean species. Symbol shapes correspond to different phylogenetic groups and colours correspond to different habitats. The statistically significant relationship between vertebral count and body length for non-Delphinoidea and Monodontidae based on phylogenetically corrected linear regression (pgls) is represented by the solid grey line.

When considering all cetaceans, species living in rivers, bays, or estuaries are small body sized and possess a relatively low vertebral count, similar to the range observed in terrestrial mammals (figures 1, S2 and S3). On the other hand, species living on and off the continental shelf follow two distinct morphological patterns. The first pattern corresponds to large species with a low vertebral count (up to 65), while the second is made of small species (less than 4 meters) with an extremely high number of vertebrae.

All species following the second pattern belong to the closely related families of Delphinidae (oceanic dolphins) and Phocoenidae (porpoises) [20,21], both of which significantly differ in body size and vertebral count from the remaining families (phylo-MANOVA: $p = 0.03$, $\eta^2 = 0.69$) (figures 1 and S3*a*). In this group, the vertebral count is weakly related to body size (PGLS: $p = 0.04$, $R^2 = 0.14$, slope ± *s.e.* = -4.36 ± 2.00) but is habitat-related. Offshore species have significantly more vertebrae than species living closer to shore (figures 1 and S3*c* and tables S4 and S5). On the other hand, the vertebral count is not associated with habitat variation in the remaining families (phylo-ANOVA: $p = 0.52$, $\eta^2 = 0.17$), but it is correlated to body size, with approximately eight additional vertebrae per ten metres increase in body length (PGLS: $p < 0.001$, $R^2 = 0.56$, slope ± *s.e.* = 0.80 ± 0.18) (figures 1 and S3*d* and tables S4 and S5).

(b) MORPHOSPACE OF VERTEBRAE AND ECOLOGY

In the morphospace approach including all studied cetaceans PC1 accounts for 41% of the total variance. PC1 is mainly associated with the relative length of vertebral centra, width of vertebral processes, and inclination of neural spines (figure 2). PC2 explains almost 21% of the variation and is primarily associated with the length of transverse processes and the height of vertebral centra (figures 2 & S4). When considering all cetaceans, vertebral shape is strongly associated with habitat (phylo-MANOVA: $p = 0.001$, $\eta^2 = 0.35$, table S5) and the number of vertebrae (PGLS: $p = 0.001$, $R^2 = 0.31$, figure. 1*a*) but not with body size (PGLS: $p = 0.06$, $R^2 = 0.11$, table S4).

As shown in figure 2, the vertebrae of Delphinidae and Phocoenidae differ in shape from those of the other families (phylo-MANOVA: $p = 0.02$, $\eta^2 = 0.87$). Species from these families have shorter vertebral centra, narrower processes, and neural spines with an anterior inclination (figures 2 and S4). Based on PC scores of the "Delphinidae and Phocoenidae" PCA, vertebral shape is not correlated to body size (PGLS: $p = 0.13$, $R^2 = 0.05$, table S4) but it is strongly associated with the habitat within this group (phylo-MANOVA: $p = 0.001$, $\eta^2 = 0.46$, table S5). In addition to a higher vertebral count, offshore species have shorter vertebral centra and narrower processes than riverine and coastal species (figure S5*a*).

Based on the PCA on the remaining families (*i.e.* all cetaceans except Phocoenidae and Delphinidae), their vertebral shape is related to the habitat (phylo-MANOVA: $p = 0.001$, $\eta^2 = 0.62$, table S5) and is weakly related to body size (PGLS: $p = 0.03$, $R^2 = 0.11$, table S4). However, their habitat-associated shape variation is different from the pattern seen in dolphins and porpoises. Whereas riverine species still differs from other species by having more elongated vertebrae, coastal and offshore species tend to have vertebrae of similar length. Coastal species differs from offshore ones by having higher and wider centra and larger metapophyses (figure S5*b*).

Extant delphinoids have lower *L/H* ratio (mean ± S.D. = 0.73 ± 0.15), *i.e.* more discoidal centra, than non-delphinoid odontocetes (1.14 ± 0.18), although there is some overlap. Extant mysticetes cover a range of ratio (0.88 ± 0.20) overlapping with delphinoid and non-delphinoid odontocetes (figure S6). Regarding fossil taxa, mysticetes and stem cetaceans, except *Basilosaurus cetoides,* have ratios between 0.92 and 1.05 and fall in the range of extant non-delphinoids. *Basilosaurus cetoides* has a ratio higher than any other cetacean

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(*L*/*H* = 1.72). Extinct non-delphinoid odontocetes have ratios extending from 1.08 to 1.38 and are similar to extant non-delphinoid odontocetes. *Kentriodon pernix* has a ratio of 1.13, similar to non-delphinoids. The stem delphinoid, *Atocetus iquensis* has a ratio (*L*/*H* = 0.88) similar to delphinoids (*e.g. Sotalia fluviatilis L*/*H* = 0.84, *Tursiops* spp. *L*/*H* = 0.83). Only one non-delphinoid has a lower ratio than *Atocetus* (*Physeter macrocephalus L*/*H* = 0.68). *Albireo whistleri* has a ratio (*L*/*H* = 0.63) equivalent to most delphinoids (*e.g. Stenella coeruleoalba L*/*H* = 0.62, *Lagenorhynchus australis L*/*H* = 0.65).

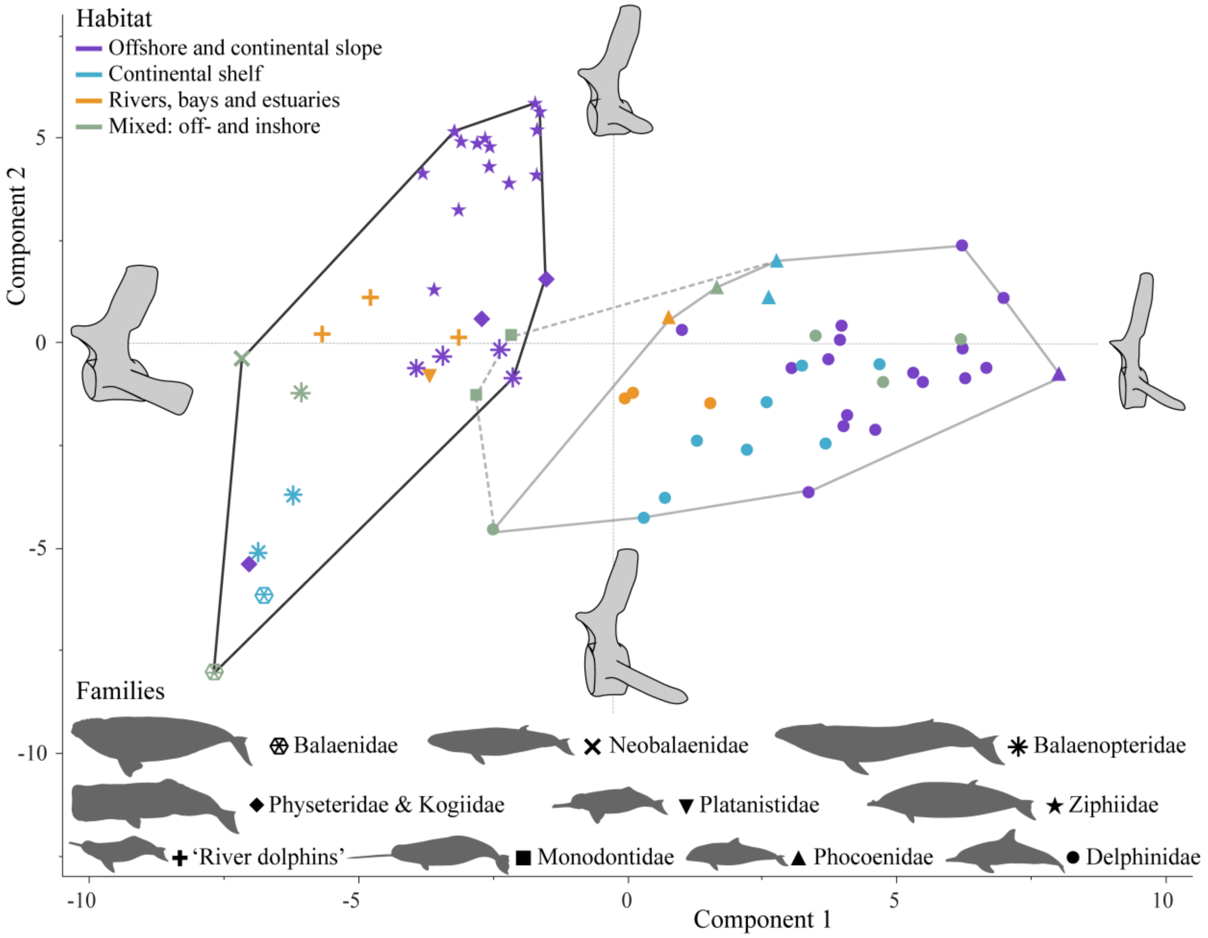

Figure 2. Effect of the habitat on the vertebral shape. Principal components analysis plot of PC1 versus PC2 of the PCA calculated on all cetacean species. PC1 accounts for 41% of the total variance and is associated with the relative length of vertebral centra, the width of vertebral processes and the inclination of neural spines. PC2 explains 21% of the variation and is primarily associated with the length of transverse processes and the height of the vertebral centra. Typical vertebral shapes are shown on each extremity of the axes. Symbol shapes correspond to phylogenetic groups and symbol colours correspond to habitats. Convex hulls represent (i) Delphinidae and Phocoenidae (grey lines), and (ii) non-delphinoidean cetaceans (black lines). Dotted grey lines show the inclusion of Monodontidae with Phocoenidae and Delphinidae.

(c) EVOLUTIONARY SHIFTS OF PHENOTYPIC TRAITS

The consistent segregation of oceanic dolphins and porpoises from other cetaceans suggests that they might follow a distinct evolutionary pattern. Evolutionary mode and tempo of vertebral count and shape were then investigated using Bayesian multi-rate (BAMM) and multi-regime (Bayou) approaches.

For the vertebral count, both BAMM and Bayou showed an evolutionary shift occurring on the branch leading to Delphinoidea, the clade grouping Delphinidae, Phocoenidae and Monodontidae (BAMM marginal shift probability = 0.95, Bayou posterior probability = 0.52) (figures 3*a* and 3*c*). BAMM showed a 10-fold increase of the evolutionary rate on this branch while Bayou found optima of 50 vertebrae for non-Delphinoidea and 67 vertebrae for Delphinoidea. Interestingly, the main shift detected by BAMM for the vertebral shape is on the same branch and correspond to a 5-fold rate increase (PC1: marginal shift probability = 0.68) (figure 3*b,* see figure S7 for PC2 to PC8). Bayou detected the presence of two shifts rather than one for PC1 (figures 3*b* and 3*d*). One shift is on the branch leading to all Delphinidae except killer whales (*Orcinus orca*) (posterior probability = 0.73) while the second is on the branch supporting Phocoenidae (posterior probability = 0.63). Nonetheless, the respective optimum of Delphinidae and Phocoenidae fall in the same posterior distribution peak reflecting that the two families probably follow a similar evolutionary regime (figure 3*d*).

This supports the hypothesis that Delphinidae and Phocoenidae differ substantially from other cetaceans. They also suggest some similarities between Monodontidae, Delphinidae, and Phocoenidae, at least concerning their tempo of morphological diversification. Accordingly, we repeated our comparative analyses on the effect of habitat and body size on vertebral count and shape by including monodontids with delphinids and phocoenids (figure S8). The inclusion of these two species did not alter previous statistical results (tables S4 and S5). Cetaceans could thus be divided into two groups in accordance with their distinct mode and tempo of morphological evolution: Delphinoidea and non-Delphinoidea.

(d) DIVERSIFICATION AND MORPHOLOGICAL EVOLUTIONARY RATES

The ES-sim analyses found evidence for a correlation between the rate of lineage diversification and the rates of morphological evolution of the axial skeleton (Vertebral count: p = 0.03, R² = 0.37, slope ± *s.e.* = 5.02 ± 0.79; Vertebral shape: p = 0.002, R² = 0.55, slope ± *s.e.* = 0.14 ± 0.02) (figure S9 and table S6).

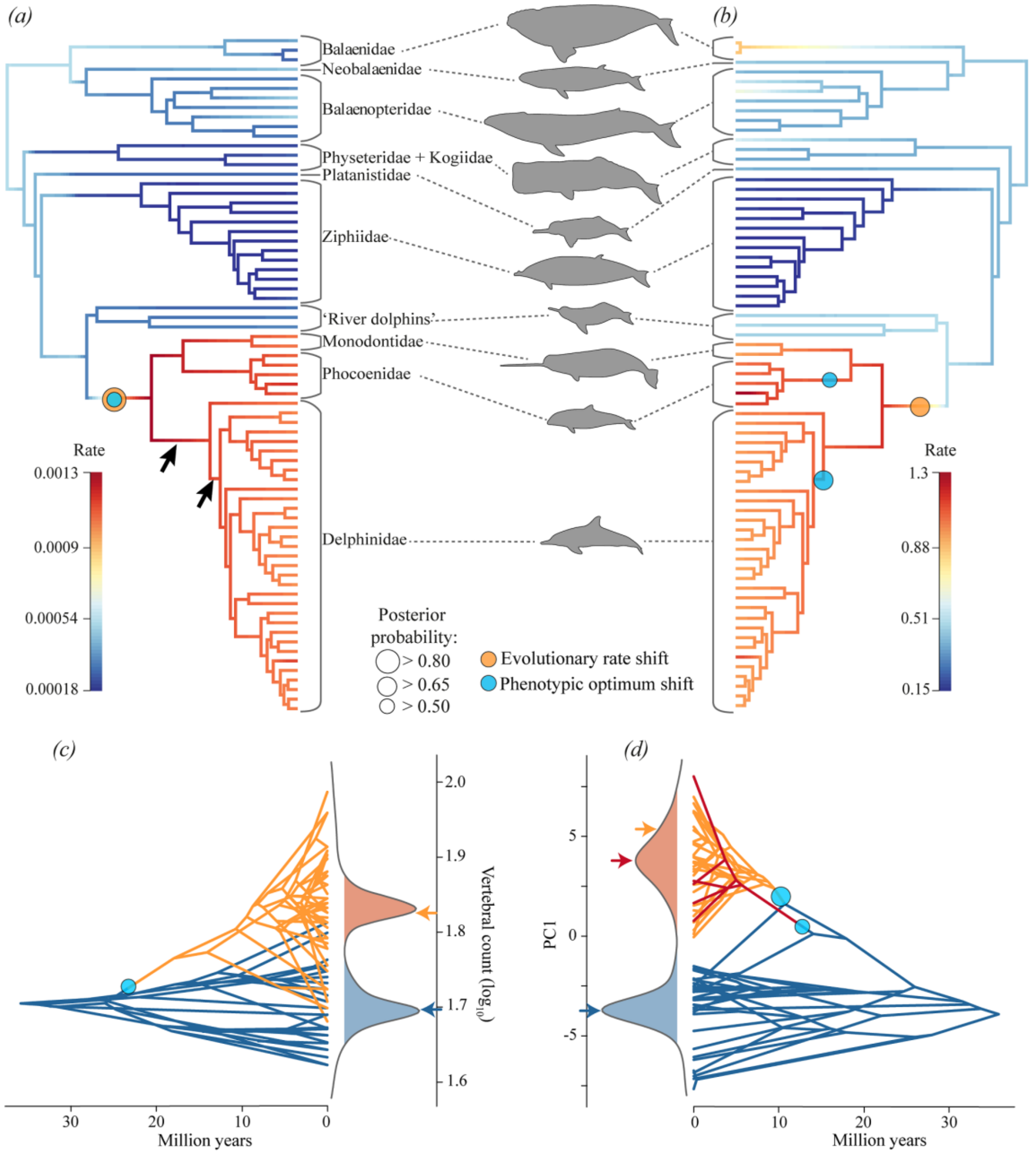

Figure 3. Evolutionary patterns of vertebral count and shape. (*a,b*) Phylogenetic tree of cetaceans showing the tempo of phenotypic trait evolution. Branches are coloured according to the evolutionary rates of phenotypic traits calculated from a Bayesian multi-rate approach (BAMM): (*a*) $\log_{10}$-transformed vertebral count; (*b*) PC1 from the PCA on vertebral shape for all extant cetacean in our dataset. Higher PC1 values correspond to more discoidal vertebrae. Red shades correspond to higher evolutionary rates. (*c,d*) Traitgrams showing the mode of phenotypic optimum evolution calculated from a Bayesian multi-regime Ornstein–Uhlenbeck approach (Bayou): (*c*) $\log_{10}$-transformed vertebral count; (*d*) PC1 from the PCA on the vertebral shape of all cetaceans. Phylogenetic tree tips are plotted according to their phenotypic score and internal nodes according to their estimated state. Branches colours show clades with different evolutionary regimes and coloured arrows correspond to their respective phenotypic optima. Density curves show the posterior distribution of traits optima sampled from 4 000 000 simulations. Orange and blue circles in each panel indicate significant shifts of the evolutionary rate (BAMM) and the phenotypic optima (Bayou), respectively. Circles relative sizes correspond to the posterior probability of the shift. Probable positions of speciation rate increase identified by previous studies [20–24] are shown by black arrows on (*a*).

4. Discussion

Our results show the existence of two distinct evolutionary patterns in modern cetaceans: Delphinoidea and non-Delphinoidea. Vertebral shape varies with habitat in both groups but vertebral count is associated to habitat only in delphinoids. Non-delphinoids retained a low vertebral count similar to terrestrial mammals but exhibit large variation in body sizes, offshore species being larger than estuarine and riverine species (figure 1) [52]. On the other hand, Delphinoidea retained a small body size but coastal and offshore species have an extremely increased vertebral count associated with shortening of all vertebrae.

(a) VERTEBRAL MORPHOLOGY AND BIOMECHANICAL ADVANTAGES

Whilst the small body length of riverine non-Delphinoidea allows swimming in shallow and complex habitats, the large body size of their oceanic counterparts might provide various advantages in pelagic habitats [21,53–57]. For example, the large body size of mysticetes has been linked to higher feeding performances in scattered high density prey patches and better resistance to long travelling distances [57]. Large body size of sperm whales and beaked whales might also be an adaptation to their deep-diving behaviour [55]. As the ancestor of crown cetaceans had an estimated body weight comparable to extant dolphins, small body size is likely the ancestral condition and gigantism is a derived state [58]. Within non-Delphinoidea, the number of vertebrae increases with body size (figure 1). Although pleomerism has been reported in teleosts and snakes, body size is usually unrelated to vertebral count in mammals (figure S2) [59–61]. As baleen whales reach body sizes greater than any other terrestrial mammal, their pleomerism might reflect functional or developmental limits to vertebral elongation. From a biomechanical point of view, the addition of a few more vertebrae while increasing body length could improve the backbone flexibility needed for foraging, provided that vertebrae remain globally spool-shaped [62]. Stem cetaceans of the genus *Basilosaurus* reached body sizes comparable to extant mysticetes and possessed 58 to 67 extremely elongated vertebrae (figure S6) [15,30,63]. Their vertebral morphology is clearly atypical among cetaceans and could reflect a specialised ecology.

Conversely, the axial skeleton of Delphinoidea has undergone deep modifications with an extreme increase of the vertebral count in offshore species (figure 1) resulting in vertebrae with a discoidal shape (figures 2 and S8*a*). Such a vertebral shortening provides a stiffer body and restricts swimming oscillations to the posterior third of the body whereas species possessing elongated vertebral centra display undulations of almost the entire body [14,15]. Body rigidity enhances stability and swimming efficiency and is thus adapted for sustained high-speed swimming styles in opposition to a more flexible body providing higher manoeuvrability [7,16,54,64,65]. Vertebral modifications of small delphinoids provide energetic advantages allowing them to cover long distances between scattered production areas in offshore environments [66,67]. Manoeuvrability, *i.e.* turning performances, in marine mammals is not only dependent on body flexibility but also on body size and the use of control surfaces [54]. Given their small size, offshore dolphins are more manoeuvrable than most large pelagic non-delphinoids likely allowing the exploitation of the same habitat in a different manner.

The pattern of axial skeleton disparity in small delphinoids could be paralleled to sharks and ichthyosaurs. Anguilliform sharks and Early Triassic ichthyosaurs have a slender body and spool-shaped vertebrae whereas thunniform sharks and more derived oceanic ichthyosaurs are deep-bodied and possess more discoidal vertebrae [6–8,68]. Beyond strong convergences in body and fin shapes [8,9], cetaceans appear to follow similar vertebral modifications than sharks and ichthyosaurs in accordance with their ecology. Transitions between coastal and offshore waters are a recurrent evolutionary pattern that promoted diversification in various marine organisms such as fishes or cephalopods (*e.g.* [69,70]).

(b) KEY INNOVATION AND REFINING EVOLUTIONARY SHIFT WITH THE FOSSIL RECORD

An increase of the lineage diversification rate characterizes the evolutionary history of Delphinidae and, to a lesser extent, Phocoenidae [20–24]. Remarkably, we found that large changes in vertebral morphology also occurred in these clades (figure 3). Moreover, evolutionary rates of these morphological traits are significantly related to diversification rates in cetaceans. Accordingly, we suggest that dolphin backbone modifications acted as a key innovation that allowed small species to occupy a new adaptive zone in offshore waters and thus supported their explosive radiation.

The results of both multi-rate and multi-regime Bayesian methods highly suggest the morphology of Delphinoidea evolved under a different rate of phenotypic diversification and/or through a different phenotypic optimum. However, some uncertainty remains in the position of the morphological evolutionary shift between these two methods. There might either be a single shift on the branch supporting the clade of Delphinoidea, or two distinct shifts occurring later with one on the branch supporting Delphinidae (except *Orcinus orca*) and another on the branch of Phocoenidae (figure 3).

The *L/H* ratios analysis shows that all extinct non-delphinoids have higher ratios (*i.e.* more spool-shaped centra) than most extant delphinoids (figure S6). These data should be interpreted with caution as they rely on a limited number of mostly incomplete fossils and only capture a small portion of vertebral shape variation. Nevertheless, these results are in accordance with previous works that considered that stem cetaceans and extinct mysticetes had a vertebral morphology comparable to extant mysticetes [15]. At equivalent body size, stem cetaceans appear to have more vertebrae than extant mysticetes [30,35,37,63]. For example, *Dorudon atrox* had 65 vertebrae and had an estimated body length of 5.35 meters while most extant beaked whales (*Mesoplodon* spp.) have 45 to 49 vertebrae [35]. However, the vertebral count of stem cetaceans remains lower than 70 and support the hypothesis of an ancestral state with a low vertebral count.

Medium-sized extinct dolphins *Atocetus* and *Albireo* and the extinct porpoise *Piscolithax* possess a morphology comparable to modern delphinoids (figure S6) [15,34,71]. According to Barnes, the vertebral count and shape of *Atocetus nasalis* are comparable to those of the bottlenose dolphin (*Tursiops truncatus*) [71]. Similarly, *Albireo whistleri* has discoidal vertebrae and possesses more pre-caudal vertebrae than most non-delphinoids [36]. Although there is still some uncertainty on the precise phylogenetic position of *Albireo* and *Atocetus*, most phylogenetic analyses identify them as stem delphinoids [72–74]. Their morphology and their phylogenetic relatedness with Delphinoidea hence support the hypothesis of a single morphological shift for all delphinoids.

The single shift hypothesis implies that Monodontidae also experienced the morphological shift albeit their backbone is more similar to non-Delphinoidea. Their morphology might be associated to their specialized arctic habitat requiring manoeuvrability or to their large body size. Indeed, larger Delphinidae such as pilot whales (*Globicephala* spp.), killer whales (*O. orca*) and false killer whales (*P. crassidens*) possess vertebral count and shape more similar to non-Delphinoidea. Thus, we cannot rule out the possibility that body size could affect the vertebral morphology in Delphinoidea.

Our results highlight the presence of phenotypic evolutionary shift concordant with an increase in the rate of diversification of extant delphinoids. Data from fossil taxa suggest that some stem delphinoids at least also experienced this phenotypic change. Investigating diversity and disparity through time at the family level using total evidence phylogeny could help to infer the precise timing of the evolutionary shift but current morphological and phylogenetic data on fossils prevent such analysis. For example, *Kentriodon pernix* is represented by a well-preserved skeleton composed of approximately 48 spool-shaped vertebrae [29] but, depending on the analyses, it is either considered as a stem Delphinida or a stem Delphinoidea [42,72–74].

5. Conclusion

Our study reveals that the body size and morphology of the axial skeleton are linked to the ecology of cetaceans. While all species inhabiting rivers, bays, and estuaries are small body sized and have a low vertebral count, other species acquired a morphology adapted for open sea following two distinct evolutionary patterns. The evolution of most oceanic species tended towards an increased body size while retaining a low vertebral count. Conversely, small delphinoids experienced extreme modifications of their axial skeleton morphology. Such a variation in vertebral morphology has been linked to an increased stiffness of the backbone resulting in a more efficient swimming style and allowing small dolphins to maintain a high swimming speed over long distances in offshore waters [14,15,64]. Our results support the hypothesis that the exceptionally high vertebral count and associated vertebral morphology of Delphinoidea operated as key morphological innovations helping for the adaptation of oceanic dolphins to coastal and offshore environments and leading to their explosive radiation.

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