A peer-reviewed version of this preprint was published in PeerJ on 21 November 2017.

View the peer-reviewed version (peerj.com/articles/4090), which is the preferred citable publication unless you specifically need to cite this preprint.

Morphological convergence in ‘river dolphin’ skulls: a disparate grouping justified

Charlotte E Page Corresponding Author, Natalie Cooper

1 Imperial College London, London, United Kingdom
2 Department of Life Sciences, Natural History Museum, London, London, United Kingdom

Convergent evolution can provide insights into the predictability of, and constraints on, the evolution of biodiversity. One striking example of convergence is seen in the ‘river dolphins’. The four dolphin genera that make up the ‘river dolphins’ (Inia geoffrensis, Pontoporia blainvillei, Platanista gangetica and Lipotes vexillifer) do not represent a monophyletic group, despite being very similar in morphology. This has led many to using the ‘river dolphins’ as an example of convergent evolution. However, these morphological similarities have never been quantified. We investigate whether the skulls of the four ‘river dolphin’ genera are convergent when compared to other toothed dolphin taxa. We use geometric morphometrics to uncover shape variation in the skulls of the ‘river dolphins’ and then apply a number of phylogenetic techniques to test for convergence. We find significant convergence in the skull morphology of the ‘river dolphins’. The four genera seem to have experienced evolution in the same direction, leading to a convergent morphotype characterised by elongation of skull features. The cause of this morphological convergence remains unclear, but our results support hypotheses of shared feeding mode or diet and thus provide the foundation for future work into convergence within the Odontoceti.
Morphological convergence in ‘river dolphin’ skulls: a disparate grouping justified

Charlotte E Page\textsuperscript{1,2} and Natalie Cooper\textsuperscript{2}

\textsuperscript{1}Imperial College London, Kensington, London, SW7 2AZ, UK.
\textsuperscript{2}Natural History Museum, London, Cromwell Road, London, SW7 5BD, UK.

Corresponding Author:

Charlotte E Page\textsuperscript{1,2}

Email address: charlotte.eve.page@gmail.com
Abstract

Convergent evolution can provide insights into the predictability of, and constraints on, the evolution of biodiversity. One striking example of convergence is seen in the ‘river dolphins’. The four dolphin genera that make up the ‘river dolphins’ (Inia geoffrensis, Pontoporia blainvillei, Platanista gangetica and Lipotes vexillifer) do not represent a monophyletic group, despite being very similar in morphology. This has led many to using the ‘river dolphins’ as an example of convergent evolution. However, these morphological similarities have never been quantified. We investigate whether the skulls of the four ‘river dolphin’ genera are convergent when compared to other toothed dolphin taxa. We use geometric morphometrics to uncover shape variation in the skulls of the ‘river dolphins’ and then apply a number of phylogenetic techniques to test for convergence. We find significant convergence in the skull morphology of the ‘river dolphins’. The four genera seem to have experienced evolution in the same direction, leading to a convergent morphotype characterised by elongation of skull features. The cause of this morphological convergence remains unclear, but our results support hypotheses of shared feeding mode or diet and thus provide the foundation for future work into convergence within the Odontoceti.

Keywords: Convergent evolution, Geometric Morphometrics, GMM, Inia geoffrensis, Pontoporia blainvillei, Platanista gangetica, Lipotes vexillifer, Skull, Mandible.
Introduction

Convergent evolution, or convergence, is the independent evolution of similar phenotypes in different lineages (Losos 2011), producing taxa that are more similar than expected given their phylogenetic relatedness (Morris 2008). Convergence is widespread over the Tree of Life (McGhee 2011; Morris 2003) and continues to be a central concept in evolutionary biology through both its role in describing evolutionary patterns and in providing strong evidence for natural selection (Donley et al. 2004; Foote et al. 2015; Losos 2011; Muschick et al. 2012).

Although convergent evolution has been studied since Darwin (1859), there has been a recent resurgence of interest in the field, partly fueled by the ongoing debate on its role in limiting biodiversity (Mahler et al., 2017; Speed & Arbuckle 2016). If the evolutionary forces that cause convergence are common, then phenotypes of organisms may be predictable, ultimately constraining the diversity of living species (Losos 2011; Morris 2003; Morris 2008).

Despite recent developments in methods for quantifying of convergence (e.g. Arbuckle et al. 2014; Ingram & Mahler 2013; Speed & Arbuckle 2016; Stayton 2015a), convergence is rarely rigorously quantified beyond some classical examples; such as *Anolis* lizards (e.g. Mahler et al. 2013) and cichlid fishes (e.g. Muschick et al. 2012). Quantitative analysis of convergence in more taxa will help us to gain further understanding of the concept and the mechanisms that underlie it. It will also allow exploration of whether qualitative human classifications of convergence using external morphology alone are quantitatively justified.

One iconic example of convergent evolution is in the ‘river dolphins’, a group of distantly-related cetaceans that secondarily entered river systems from the ocean, evolving riverine lifestyles and similar morphological characteristics (Hamilton et al. 2001). The river dolphins consist of four recent genera: the Amazon river dolphin (*Inia geoffrensis*), the La Plata dolphin
(Pontoporia blainvillei), the Yangtze river dolphin (Lipotes vexillifer), which is thought to be extinct (Turvey et al. 2007) and the Ganges river dolphin (Platanista gangetica), which contains two subspecies, Platanista gangetica spp. gangetica and Platanista gangetica spp. minor (Kasuya 1972) (Figure 1A). Based on their similar external morphology and shared riverine and estuarine habitats, taxonomists originally placed the four taxa into a single higher grouping, the Platanistoidea (Kasuya 1972; Simpson 1945). Molecular techniques have since clarified that the four taxa do not form a monophyletic group (Geisler et al. 2011; Hamilton et al. 2001; McGowen et al. 2009; Steeman et al. 2009). Convergent features of the river dolphins include a longirostral skull (i.e. a long narrow rostrum and mandible), an elongated and fused mandibular symphysis, relatively more teeth than in other dolphin lineages (up to 250 teeth in Pontoporia, compared to 100 in Tursiops (Werth 2006) an extended alveolar tooth row, long zygomatic process, nasal bones that lie at the same level as the squamosal processes, and a flexible neck due to unfused caudal vertebrae (Geisler & Sanders 2003) (Figure 1B). They also share a number of soft anatomical features such as broad forelimb flippers and reduced eyes (Cassens et al. 2000) (Figure 1B).

Here we present the first quantitative investigation of the morphological variation present in the skulls of river dolphins, and quantify whether the four river dolphin genera are convergent. We use geometric morphometric (GMM) techniques (Rohlf & Marcus 1993) to compare skull morphology of the river dolphins to extant Odontoceti (toothed whale and dolphin) genera. We then determine whether river dolphins are convergent using a range of methods. Our results reveal that the river dolphins show significant convergence in the shape of their crania and mandibles when compared to other the odontocete species.

Materials and methods

Data collection

One of us (CP) collected data from the Natural History Museum, London. We photographed all available, complete river dolphin specimens (four species, crania: 12 specimens, mandibles: 10 specimens; SI1 Table S1). To ensure we had representatives of all groups that were equally closely-related to river dolphins, we photographed specimens across all Odontoceti except sperm
whales (Physeteridae) which are more distantly-related, and too large to sample using our protocol. Sexual dimorphism varies among odontocete genera, being present in some species as differences in size, but with no differences in shape between sexes recorded (Amaral et al. 2009; Higa et al. 2002). We therefore chose males and females from different collection locations where possible to provide a representative sample of each species. Juveniles were not included because skull characters typically change during growth and development (Perrin & Heyning 1993). See Supplemental Information 1 for full details of the specimens used and their accession numbers (Table S1). All specimen data are available from the Natural History Museum’s Data Portal at http://dx.doi.org/10.5519/0082274 (Page & Cooper 2017a).

We adjusted a protocol described by Báez-Molgado and colleagues (2013) and photographed specimens using a Canon EOS 550D fitted with a EFS 18–55mm lens. To account for variations in lighting, we used a white card to set the custom white-balance function on the camera at the start of each session. We included a 25 cm scale bar and specimen accession number in every photograph. We placed the specimens directly under the camera lens and used foam board to make sure the specimen was level. A problem with imaging is the phenomenon of parallax, which occurs when a camera lens is placed too close to a specimen, thereby producing a slightly warped or distorted image. However, the error produced by this phenomenon is constant among samples when the same lens orientation and positioning is used (Mullin & Taylor 2002). For this reason, the same photographing setup was replicated at every photographing session.

For each specimen we photographed (1) ventral view of the cranium (77 specimens; 24 species) and (2) dorsal view of the mandible (67 specimens; 23 species). The numbers of specimens in the two analyses varied because specimen had damaged mandibles. After photographing in raw file format, we converted the photographs to grey-scale to help with structure identification, and exported them as TIFFs. We then converted these files into import TPS files using the tpsUtil (Rohlf 2010) ‘build TPS files from images’ function.

Geometric morphometric analyses (GMM)

We used GMM to capture the shape of the dolphin skulls (Mitteroecker & Gunz 2009) We used a combination of landmarks and semi-landmarks. Where possible, we used landmarks that had
been previously used in the cetacean literature, but we primarily chose landmarks based on the objective of this study, i.e. placing emphasis on putatively convergent features of the river dolphins (Geisler et al. 2011; Geisler & Sanders 2003). To remove errors associated with using a 2D image, we chose landmarks that were in the same plane. One of us (CP) digitised all landmarks shown in Figure 2 using tpsDig (Rohlf 2006), on separate data files for each view. We set the scale on each image individually. Detailed descriptions of the landmarks can be found in the Supplemental Information 2 (Tables S2 and S3). We digitised 12 landmarks onto the images depicting the ventral view of the cranium (Figure 2A, Table S2). These were based on GMM studies of odontocete and river dolphin genera (Amaral et al. 2009; Higa et al. 2002). We digitised eight landmarks onto the images depicting the dorsal view of the mandible (Figure 2B, Table S3). These were adapted from the only current GMM study that considers the dorsal mandibular view of Odontoceti (although this used 3D images; Table S4) (Barroso et al. 2012).

We also drew curves on each specimen before resampling them with a specified (Figure 2, Tables S2-5) number of equally spaced semi-landmarks. The semi-landmark approach can introduce error into GMM analyses through oversampling curves, because simpler structures, such as the rostrum, will require fewer semi-landmarks to accurately represent their shape (MacLeod 2012), compared to more complex structures. To overcome this, we followed a resampling method described by MacLeod (2012) to determine the minimum number of semi-landmarks needed to measure an outline to at least 95% accuracy of the true length of the curve. We resampled cranial curves A and B with five points, and curves C and D with three points. We resampled mandibular curves A and B with three points. See Figure 2 and Supplemental Information 2 for more details.

We saved the landmark coordinates as a TPS file, and downloaded them into R package version 3.0.4 to carry out all further analyses (R Core Development Team 2017) We carried out separate analyses on both the cranial and mandibular datasets at all stages. We used the ‘gpagen’ function in geomorph (Adams et al. 2017) to run a Generalised Procrustes alignment (GPA). This converts the digitised, raw landmark configurations into shape variables by removing non-shape (i.e. scale, rotation and size) variation (Rohlf & Marcus 1993). Because we are interested in convergence among species, we then calculated the mean GPA coordinates for each odontocete
species, and used these for all further analysis. We also repeated the analyses using the specimen-level GPA coordinates and report these results in the Supplemental Information 3. We used the phylogeny of Steeman et al. (2009) in all phylogenetic analyses (Figure 1A).

Error checking

Error can be introduced at two main points of a GMM analysis: 1) photographing, and 2) digitising (Zelditch et al. 2012). Error present in GMM datasets can affect later analyses by inflating the amount of variance among samples, and obscuring biological signal (Fruciano 2016). To assess the measurement error in our data, we followed a method outlined by Zelditch et al. (2012) on replicate attempts to calculate the intraclass correlation coefficient (Fisher 1925), often termed ‘repeatability’ (Fruciano 2016). See the Supplemental Information 2 for more detail.

Exploring shape variation in dolphin skulls

To uncover the shape variation present in the skulls of the river dolphins, we conducted a principal component analysis (PCA) on the mean species GPA coordinates for both the cranium and mandible datasets using the geomorph function, ‘plotTangentSpace’ (Adams et al. 2017). We then visualized patterns of cranial and mandibular shape evolution in phylomorphospace by plotting PC axes 1-3 against each other and projected phylogeny onto the morphological trait space (Sidlauskas 2008) using the function ‘plotGMPhyloMorphoSpace’ in geomorph (Adams et al. 2017). In these plots, each data point represents a shape, and species close to each other in the morphospace are more similar in shape. Shape changes along the PC axes correspond to landmark eigenvectors, which we visualised using wire frame deformation grids, using the function ‘plotRefToTarget’ in geomorph (Adams et al. 2017). It is important to note that we did not use a phylogenetic PCA (pPCA) to plot the phylomorphospaces. This is because pPCA scores are correlated across axes, unlike PC axes (Polly et al. 2013), so cannot be used for further analysis.

Testing for convergence

We first estimated phylogenetic signal in the mean species cranial and mandibular GPA landmarks using $K_{sav}$ (Adams 2014), the multivariate version of Blomberg’s $K$ (Blomberg et al.
Phylogenetic signal was present in both our datasets (cranium: $K_{mult} = 1.14$, $p = 0.001$; mandible: $K_{mult} = 1.17$, $p = 0.001$), so we used analytical methods that account for phylogeny in our tests for convergence.

To determine whether river dolphins have significantly different skull shapes compared to other odontocetes, we performed a Procrustes ANOVA while accounting for phylogenetic relatedness, on the mean species GPA coordinates for both cranial and mandibular datasets using the function ‘procD.pgl’ in geomorph (Adams et al. 2017) with 1000 iterations. This analysis tells us about the overall shape variation present. Therefore, to identify which specific shape axes are important, we performed multiple phylogenetic ANOVAs for each dataset on the PC axes which accounted for >95% of the variation present in both the cranium and mandible (PC1-PC4 for crania and PC1-PC3 for mandibles), using the ‘aov.phylo’ function in the geiger R package (Harmon et al. 2007).

Next we constructed phenograms for the crania and mandible datasets and compared these to the phylogeny. We used Ward’s hierarchical clustering agglomerative method (Ward Jr 1963) on a distance matrix generated using the PCs accounting for >95% of the variance in shape (PC1-PC4 for crania and PC1-PC3 for mandibles) to build the phenetic trees. Ward’s method considers all possible species pairs of clusters, and merges those that result in the minimum increase in the error sum of squares (Ward Jr 1963). Species that cluster together will therefore have the most similar morphology.

Finally, we quantified the amount of convergence in both cranium and mandible datasets using a distance-based approach (Stayton 2015a). This method is based on the idea that convergence occurs when two taxa evolve to be more similar than their ancestors were to one another (Losos 2011; Stayton 2015a) and produces an index of convergence ($C_1$). We calculated $C_1$ for both the cranium and mandible datasets using the PCs accounting for >95% of the variance in shape (PC1-PC4 for crania and PC1-PC3 for mandibles) whilst also meeting the statistical requirement of fewer shape variables than putatively convergent taxa ($n = 4$) using the R package convevol (Stayton 2015b). The function ‘convrat’ infers ancestral states using weighted means of extant species data and also scales $C_1$ to permit comparisons among different taxa (Stayton 2015b).
tested the significance of each C1 calculated using the function ‘convratsig’ (Stayton 2015b). R
code for all analyses is available from http://dx.doi.org/10.5281/zenodo.846278 (Page & Cooper
2017b).

Results

Error checking

The level of error in our results was negligible. Repeatability was 91.3% in the cranial dataset
and 93.1% in the mandibular dataset (Supplemental Information 2).

Exploring shape variation in dolphin skulls

River dolphins cluster together in morphospace, but there was considerable shape variation
across the odontocetes (Figure 3). More than 95% of the variation in shape is explained by the
first four PC axes for odontocete crania, and the first three PC axes for odontocete mandibles.
The variance explained by each major PC (>95% variation) and the loadings of the landmarks on
each PC axis (eigenvectors) are in the Supplemental Information 3 (Table S6-8).

Shape changes associated with these PC axes are depicted by wireframe deformation grids at the
minimum and maximum extent of each PC axis in Figure 4. Cranial PC1 describes variation in
the shape of the rostrum and the cranium (Figure 4A). This represents the relative changes in the
positions of the tip of the rostrum, and the rest of the cranium (Figure 4A) resulting in the
elongation and narrowing of the rostrum, and narrowing of the cranium. PC2 describes variation
in the shape of the rostrum and zygomatic arches (Figure 4B). PC3 and PC4 describe variation in
the shape of the lacrimojugal bones, in addition to small changes in the shape of the rostrum
(Figure 4C). Mandibular PC1 describes variation in the elongation of the mandible resulting in
an elongation of the rostrum, symphysis and alveolar tooth row (Figure 4D). PC2 describes
decreases in the length of the symphysis and increases in the alveolar tooth row length (Figure
4E) PC3 describes variation in the length of the symphysis and slight changes in jaw flare
(Figure 4F).

Testing for convergence
Overall, river dolphins have significantly different skull shapes compared to other odontocetes for both the cranium (phylogenetic Procrustes ANOVA: $F_{1,22} = 3.96$, $p < 0.001$) and mandible (phylogenetic Procrustes ANOVA: $F_{1,21} = 3.89$, $p < 0.001$) datasets. When considering individual PC axes, the four river dolphin genera occupy significantly different positions on mandibular PC1 (phylogenetic ANOVA: $F_{1,22} = 19.268$, $p < 0.05$) compared with other odontocetes, but there are no significant differences for the other PC axes in either the crania or mandible datasets (Table S9). The specimen-level, rather species-level, results show a similar pattern (Supplemental Information 3, Table S10).

Phenetic trees based on cranium (Figure 5) and mandible (Figure 6) major PCs cluster the river dolphins together. Within the river dolphins, the analysis pairs Lipotes with Inia, then Platanista and finally Pontoporia, based on skull morphology; and pairs Lipotes with Inia, and Pontoporia with Platanista, based on mandible morphology.

C1 values (Stayton 2015b) indicate that the river dolphins evolved to be more similar to each other than would be expected under a null model of Brownian motion evolution (crania: $C1 = 0.521$, $p < 0.001$; mandibles $C1 = 0.622$, $p < 0.001$).

Discussion

Despite disparate phylogenetic histories, we find that the river dolphins exhibit similar variation in cranial and mandibular morphologies. The four genera seem to have experienced evolution in the same direction (i.e. towards higher scores of PC1 for the cranium and towards lower scores of PC1 for the mandible). Collectively, morphospace positions of the river dolphins define a morphotype characterised by the elongation of skull features (rostrum, zygomatic arches, mandibular symphysis and alveolar tooth row) and narrowing of the brain case. Our results suggest that this morphotype is significantly convergent. We find that the river dolphins cluster differently based on morphology than they do on a phylogeny based on molecular data (Steeman et al. 2009), and Stayton’s (Stayton 2015a) distance-based measure of convergence on both datasets, also suggests that the river dolphins are morphologically more similar to each other than their ancestors were.
The river dolphin morphotype uncovered is consistent with discrete characteristics that have been highlighted as convergent amongst the river dolphins (Geisler & Sanders 2003). In particular, elongation of morphological features, a character named ‘longirostral’ (Geisler & Sanders 2003) dominates shape changes associated with both the crania and mandibles. This shape change is also one that has been found by other studies on odontocete skulls ((Barroso et al. 2012; McCurry et al. 2017a; Werth 2006). The river dolphins represent a polyphyletic group (Geisler et al. 2011; Hamilton et al. 2001; McGowen et al. 2009; Steeman et al. 2009) indicating that this morphotype has evolved more than once within the odontocetes. There are several other possible evolutionary explanations for the shared morphological characteristics uncovered in this study: they could be plesiomorphic (an ancestral trait shared by two or more taxa), they could be due to reversals, or some combination of these. Several authors have suggested that the narrow and elongate rostrum shared by the river dolphin genera, is in fact plesiomorphic (Geisler & Sanders 2003; Messenger & McGuire 1998). If shared characters were plesiomorphic, we may expect to see the sister species Pontoporia and Inia cluster together based on morphology, but this is not what we find.

The cause of the convergence demonstrated here is still debated. Convergent evolution among other taxa has largely been attributed to adaptation to a similar niche (Losos 2011; Muschick et al. 2012). Among the river dolphins, this includes utilization of riverine systems, mode of feeding and prey size (Cassens et al. 2000; Geisler et al. 2011; Hamilton et al. 2001; Kelley & Motani 2015; Werth 2006). Convergent evolution can occur for other reasons that are unrelated to adaptive evolution in similar environments (Losos 2011; Stayton 2008). However, key features of the river dolphin skull morphotype described by this study could be related to prey capture, and therefore adaptive evolution, i.e. elongate rostrum, mandibular symphysis and zygomatic arches (Cassens et al. 2000). The river dolphins have been classified as raptorial feeders (Werth 2006), and have a diet consisting of small and agile riverine fish (Kelley & Motani 2015). Elongation of the skull significantly correlates with prey type (McCurry et al. 2017a; McCurry et al. 2017b; Werth 2006) and has also been hypothesised as morphologically optimal for raptorial feeding through reduction in drag (McHenry et al. 2006). Similarity in diet
has been shown to underlie the convergence seen amongst the river dolphins and gharials (a river
dwelling species of crocodile) (McCurry et al. 2017a).

There were several limitations in our approach. Availability of skull material for some species
was limited, with some species having only one specimen available i.e. for the now extinct
species, *Lipotes* (Turvey et al. 2007). This led to our sample sizes being limited in some cases.
The results presented here are also restricted to only cranial and mandibular skeletal s
morphology. Further work could look to corroborate this study through the analysis of other
skeletal and soft anatomy traits. This could provide further insights into the morphological
variation present amongst the river dolphin genera. Stayton’s (Stayton 2015a) distance-based
measure is a particularly novel method. For this reason, the interpretation of C1 values varies
among authors. The interpretation used in this study is conservative, following that used by
McLaughlin and Stayton (McLaughlin & Stayton 2016; Stayton 2015a). This metric also relies
upon accurate ancestral state reconstructions (Stayton 2015a), which are calculated using
weighted means of species data. This means that the phenotypes of ancestors are restricted to fall
between the sampled extant species values, when in reality ancestors may occur outside this
phenotypic space.

**Conclusions**

Here we have presented the first quantitative investigation into convergence in the river dolphins.
Our results show that overall skull morphology of the river dolphins is significantly convergent,
being more similar than expected given their phylogenetic relationships. The findings we present
provide the foundation for future work into convergence within the Odontoceti, in addition to
quantitatively justifying qualitative human classifications of the river dolphin grouping based on
morphology alone.

**Acknowledgements**
We thank Richard Sabin for assistance with accessing the cetacean collections at NHM, Ellen Coombs for help handling larger skulls and Dan Bell for use of his photos. We also thank Marcela Randau for helpful comments on earlier drafts of this work. Francesca Page also enriched our work with an illustration of *Inia geoffrensis*.

References


http://dx.doi.org/10.5519/0082274.


R Core Development Team. 2017. R: A language and environment for statistical computing [Internet]. Vienna, Austria; 2014.


Speed MP, and Arbuckle K. 2016. Quantification provides a conceptual basis for convergent evolution. *Biological Reviews* 92:815-829. 10.1111/brv.12257


10.1016/j.jtbi.2008.01.008


Figure 1

Phylogeny and convergent features of the ‘river dolphins’.

A) Molecular phylogeny of Odontoceti (adapted from Steeman et al. 2009) This topology places *Lipotes* as a sister-group to Iniidae + Pontoporidae. B) Convergent features (indicated by numbered circles) of two ‘river dolphin’ skulls, *Inia geoffrensis* (top, NHMUK_1169.b), and *Platanista gangetica* (bottom, NHMUK_1884.3.29.1). Soft anatomical features are shown on a photograph of *Inia geoffrensis* (top row). The views of the skull are: dorsal view of the cranium (left), ventral view of the cranium (centre) and dorsal view of the mandible (right). Features are as follows: 1) broad forelimb flippers, 2) reduced eyes, 3) flexible neck, 4) elongated and fused mandibular symphysis, 5) elongated rostrum, 6) extended alveolar tooth row, 7) long zygomatic arches and 8) nasals in line with zygomatic processes. Feature 8 is not visible on *Platanista* because the maxillary crests project anterially over the cranium and hide the nasals. Skulls are not to scale. Cetacean outlines by Chris huh licensed under CC BY-SA 3.0 (https://commons.wikimedia.org/wiki/File:Cetaceans.svg). River dolphin illustration by Francesca Page licensed under a CC attribution 4.0 international license.
Figure 2

Landmarks used on specimens.

Landmarks (numbered points) and curves (lettered blue outlines) for the A) ventral view of the cranium and B) dorsal view of the mandible. The top specimen is *Pontoporia blainvillei* (NHMUK_1925.11.21), the bottom specimen is *Tursiops truncatus* (NHMUK_1960.5.11.10). The line represents the 25 cm scale bar. Descriptions of the landmarks can be found in Supplemental Information 2, Tables S2 and S3.
Figure 3

Phylomorphospace plots for cranium (left) and mandible (right) morphology.

In both plots the river dolphin species are represented by blue points (n = 4), grey points represent other odontocetes (cranium: n = 20, mandible: n = 19), and black points represent internal ancestral nodes. Each point represents the average cranium or mandible shape of an individual species and lines represent the phylogenetic relationships.
Figure 4

Wireframe deformation grids showing shape changes.

Grids represent the shape changes associated with the minimum and maximum extents of PC1, PC2 and PC3 for crania (left) and mandibles (right) are shown (lettered A-F). Points represent landmarks and semi-landmarks digitised onto the cranium and mandible.
Figure 5

Tanglegram showing comparison in the position of the river dolphins on a phylogenetic tree and a phenetic tree based on cranial morphology.

Lines between trees link the same species and crossing lines indicate a lack of similarity in the two trees (e.g. where phenotype is more similar than implied by phylogeny, indicative of convergence). River dolphins are highlighted in blue.
Figure 6

Tanglegram showing comparison in the position of the river dolphins on a phylogenetic tree and a phenetic tree based on mandibular morphology.

Lines between trees link the same species and crossing lines indicate a lack of similarity in the two trees (e.g. where phenotype is more similar than implied by phylogeny, indicative of convergence). River dolphins are highlighted in blue.