Breaking the mold: telescoping drives the evolution of more integrated and heterogeneous skulls in cetaceans (#67337)

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Breaking the mold: telescoping drives the evolution of more integrated and heterogeneous skulls in cetaceans

Mónica Buono Corresp., 1 , **Evangelos Vlachos** 2

1 Instituto Patagónico de Geología y Paleontología, CCT CONICET-CENPAT, Puerto Madryn, Chubut, Argentina
2 CONICET and Museo Paleontologico Egidio Feruglio,, Trelew, Chubut, Argentina

Corresponding Author: Mónica Buono
Email address: buono@cenpat-conicet.gob.ar

Background: Along with the transition to the aquatic environment, cetaceans experienced profound changes in their skeletal anatomy, especially in the skull, including the posterodorsal migrations of the external bony nares, the reorganization of skull bones (= telescoping) and the development of a remarkably cranial asymmetry (in odontocetes). Telescoping represents an important anatomical shift in the topological organization and sutural contact of cranial bones; however, the impact of these changes in the connectivity pattern and integration of the skull has never been addressed. **Methods:** Here, we apply the novel framework provided by the Anatomical Network Analysis to quantify the organization and integration of cetacean skulls, and the impact of the telescoping process in the connectivity pattern of the skull. We built the anatomical networks for 14 cetacean skulls and estimated network parameters related to their anatomical integration, complexity, heterogeneity, and modularity. This dataset was analyzed in the context of the broad tetrapod skull sample as well. **Results:** The skulls of crown cetaceans (Neoceti) occupy a new tetrapod skull morphospace, with better integrated, more heterogeneous and simpler skulls in comparison to other tetrapods. Telescoping adds connections and improves the integration of those bones involved in the telescoping process (e.g., maxilla, supraoccipital) as well as other ones (e.g., vomer) not directly affected by telescoping. Other underlying evolutionary processes (such as basicranium specializations linked with hearing adaptations) would also be responsible for the changes in the connectivity and integration of palatal bones. We also find prograde telescoped skulls of mysticetes distinct for an increased heterogeneity, modularity and integration, whereas retrograde telescoped skulls of odontocetes are characterized by higher complexity. In mysticetes, as expected, the supraoccipital gains relevance and centrality in comparison to odontocetes, increasing the heterogeneity of the skull network. In odontocetes, an increase in the numbers of connections and complexity is probably linked with the dominant movement of paired bones in retrograde telescoping~~, such as the maxilla~~. Extant mysticetes (*Eubalaena*,

Caperea and *Balaenoptera)* distinguish by having, comparatively, more integrated and modular skulls, whereas extinct baleen whales (*Aetiocetus, Yamatocetus* and *Piscobalaena*) have more heterogeneous and less integrated skulls. Odontocetes do not show a clear evolutionary trend that allows distinct living and fossil forms; this might relate to the broad range of skull specialization developed by this group. However, a better integration by clustering, probably enhanced by the main movement of paired bones, and a moderate heterogeneity (~~might be~~ promoted by the increased relevance of the vomer) are identified as the main evolutionary trend followed by the retrograde skull of extant odontocetes.

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Mónica Romina Buono[1], Evangelos Vlachos[2]

[1]Instituto Patagónico de Geología y Paleontología, CCT CONICET-CENPAT, Puerto Madryn, Chubut, Argentina.

[2]CONICET — Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina

Corresponding author: Mónica Romina Buono
Boulevard Brown 2915, Puerto Madryn, Chubut, 9120, Argentina
Email address: buono@cenpat-conicet.gob.ar

ABSTRACT

Background: Along with the transition to the aquatic environment, cetaceans experienced profound changes in their skeletal anatomy, especially in the skull, including the posterodorsal migrations of the external bony nares, the reorganization of skull bones (= telescoping) and the development of a remarkably cranial asymmetry (in odontocetes). Telescoping represents an important anatomical shift in the topological organization and sutural contact of cranial bones; however, the impact of these changes in the connectivity pattern and integration of the skull has never been addressed.

Methods: Here, we apply the novel framework provided by the Anatomical Network Analysis to quantify the organization and integration of cetacean skulls, and the impact of the telescoping process in the connectivity pattern of the skull. We built the anatomical networks for 14 cetacean skulls and estimated network parameters related to their anatomical integration, complexity, heterogeneity, and modularity. This dataset was analyzed in the context of the broad tetrapod skull sample as well.

Results: The skulls of crown cetaceans (Neoceti) occupy a new tetrapod skull morphospace, with better integrated, more heterogeneous and simpler skulls in comparison to other tetrapods. Telescoping adds connections and improves the integration of those bones involved in the telescoping process (e.g., maxilla, supraoccipital) as well as other ones (e.g., vomer) not directly affected by telescoping. Other underlying evolutionary processes (such as basicranium specializations linked with hearing adaptations) would also be responsible for the changes in the connectivity and integration of palatal bones. We also find prograde telescoped skulls of mysticetes distinct for an increased heterogeneity, modularity and integration, whereas retrograde telescoped skulls of odontocetes are characterized by higher complexity. In mysticetes, as expected, the supraoccipital gains relevance and centrality in comparison to odontocetes, increasing the heterogeneity of the skull network. In odontocetes, an increase in

the numbers of connections and complexity is probably linked with the dominant movement of paired bones in retrograde telescoping, such as the maxilla. Extant mysticetes (*Eubalaena*, *Caperea* and *Balaenoptera)* distinguish by having, comparatively, more integrated and modular skulls, whereas extinct baleen whales (*Aetiocetus, Yamatocetus* and *Piscobalaena*) have more heterogeneous and less integrated skulls. Odontocetes do not show a clear evolutionary trend that allows distinct living and fossil forms; this might relate to the broad range of skull specialization developed by this group. However, a better integration by clustering, probably enhanced by the main movement of paired bones, and a moderate heterogeneity (might be promoted by the increased relevance of the vomer) are identified as the main evolutionary trend followed by the retrograde skull of extant odontocetes.

INTRODUCTION

The skull of crown cetaceans (= Neoceti) experimented dramatic changes throughout its evolutionary history, related to the arrangement of cranial bones and the acquisition of a novel feature in mammalian skull configuration: the telescoping (i.e., skulls with a combination of extensive bones overlap and extreme proximity of anterior and posterior cranial elements; Miller, 1923; Roston & Roth, 2019). Cetacean telescoping is not only evident by the radical changes in the position of bones, but also promotes changes in the connections between bones and the arrangements of cranial sutures, with large areas of bone overlap (= horizontal sutures) (Roston & Roth, 2019). This represents a new level of bone-suture configurations, breaking the typical mammalian skull design and exploring new morphospaces which might bias the exploration of new ecological and behavioural strategies. Within neocetes, two types of telescoping are recognized (Fig. 1): one dominated by the posterior expansion of anterior bones (= retrograde cranial telescoping sensu Churchill et al., 2018) typical of odontocetes, and the other dominated by forwarding movement of posterior bones (= prograde cranial telescoping sensu Churchill et al., 2018) found in mysticetes (Miller, 1923; Kellog, 1928a,b).

A recent morphometric analysis of the skull of odontocetes suggested three phases in the evolution of facial morphology and cranial telescoping: the first phase, in which the lateral expansion of the maxilla is limited and the intertemporal region is broadly dorsally exposed, and premaxilla, nasal and external bony nares are anterior to the orbits (typical of Xenorophiidae and *Simocetus,* among other stem forms); the second phase, in which a further posterior displacement of the nares and surrounding bones (nasal, premaxilla and maxilla) is observed, intertemporal region is not evident in dorsal view (this condition is described for wapatiids and squalodontids);

and the final phase characterized by an increased overlap of frontal and maxilla (observed in crown odontocetes) (Churchill et al., 2018). Among mysticetes or baleen whales, different types of telescoping are described by Miller (1923; P:20-22) characterizing the main families of baleen whales; however, quantitative analys~~i~~s as those performed by Churchill et al. (2018) in odontocetes (which include a small sample of mysticetes) ~~is~~ still required.

Despite telescoping was investigated in the last years ~~from~~ different methodologies and approaches (e.g., Churchill et al., 2018, Roston & Roth, 2019), the impact of the novel suture configurations in the topographical organization and integration of the cetacean skull has never been addressed. Anatomical Network Analysis (AnNA) has recently emerged as a new tool to quantify the complexity of anatomical structures as a function of their pattern of organization, in which bones and suture joints are modeled as the nodes and links of a network (Raskin-Gutman & Esteve-Altava, 2014). This methodology allows studying a level of morphological information that has been seldom analyzed, the level of connections, complementing an integral morphological approach (Esteve-Altava, 2013). The solid theoretical foundations of the AnNA (Esteve-Altava, 2013; 2014; Raskin-Gutman & Esteve-Altava, 2014) allowed its successful application in various anatomical structures, like the mammalian skeleton (Powell et al., 2018), tetrapod skull (e.g. Esteve-Altava et al., 2013a, b; Esteve-Altava & Rasskin-Gutman, 2014; Lee, Esteve-Altava & Abzhanov, 2020) and tetrapod limbs (Molnar et al., 2017; Esteve-Altava et al., 2018, 2019; Fernández et al., 2020), among many other studies.

This work is placed within the context of the broad tetrapod skull sample of Esteve-Altava et al. (2013a), which revealed that the reduction in the number of skull bones during tetrapod evolution has increased the complexity of the connectivity pattern under a regime of important structural constraints. In this study, we expand this framework and apply Anatomical

Network Analysis to examine the organization and integration of archaeocetes, odontocetes and mysticetes skulls. In addition, we would like to assess if telescoping has also affected the connectivity pattern of the skulls of these animals that have re-conquered the pelagic marine environment. Additionally, we look for significant differences in the connectivity pattern between the two types of cetacean telescoping at the skull and individual bone level, which would add meaningful interpretations applicable to ongoing neontological and paleontological discussions.

MATERIALS & METHODS

Sample

We constructed networks of 14 cetacean skulls covering the main lineages of cetaceans, three stem cetacea or archaeocetes (*Pakicetus*, Protocetidae, *Dorudon)*, six mysticetes (*Aetiocetus*, *Yamatocetus*, *Piscobalaena*, *Eubalaena*, *Caperea*, and *Balaenoptera)*, and five odontocetes (*Albertocetus, Waipatia, Notocetus, Physeter* and *Tursiops*) based on the most complete published skulls and/or first-hand examinations (see supplemental Table S1 and Data S1). For Protocetidae, due to the lack of complete skulls in known taxa, we constructed an average protocetid skull network based on specimens of different species. In the case of *Tursiops* — the only cetacean included in the Esteve-Altava et al. (2013a) dataset — the anatomical network is new and based on our own observations. Even though the telescoped sutures of cetaceans present a different pattern in comparison to other mammals (Roston & Roth, 2019), they were modeled in the anatomical networks as links with the same weight.

Anatomical Network analysis

The cetacean networks were included in the dataset of Esteve-Altava and collaborators (2013a), expanding the tetrapod~~´s~~ sample. The anatomical networks were digitized in Gephi (Bastian, Heymann & Jacomy, 2009) and five main descriptors were used to characterize the networks: *Density* (D, the complexity of the anatomical structure), *Heterogeneity* (H; the differentiation of the connected parts), *Average Clustering Coefficient* (C; the anatomical integration of the various bones with their surroundings), *Parcellation* (P, the degree of anatomical modularity of the network); *Average path length* (L; the anatomical integration of the various bones related to their effective proximity), based on Esteve-Altava et al. (2013a; b; 2014; 2018, 2019), and Esteve-Altava & Rasskin-Gutman (2014); Parcellation was calculated as in Fernández et al., (2020). Our data are summarized in Table 1; see supplemental information as well. For the analysis at the individual bone level, we used the *Clustering Coefficient* of each bone, and the three main centrality measures: the *Degree Centrality* (how many connections a bone has), *Closeness Centrality* (the average of the shortest path of a node with any other node of the network), and *Betweenness Centrality* (how many times a node is included in the shortest path of any other pair of nodes) (Esteve-Altava 2013). The various graphs, Principal Component Analysis (PCA) under correlation (normalized var-covar), and PERMANOVA were performed in PAST v. 4.0 (Hammer et al., 2001).

Phylogeny

For the analysis of network descriptors within a phylogenetic context, we constructed a composite~~d~~ phylogeny following Martinez Cáceres et al., (2017) for archaeocetes, Marx et al., (2019) for mysticetes and Viglino et al., (2021) and Boessenecker et al., (2017) for odontocetes.

The network descriptors were optimized and mapped under maximum parsimony in the TNT 1.5 software (Goloboff & Catalano, 2016).

RESULTS

Cetaceans skull networks within tetrapod morphospace

The first two PCAs explained ~~the~~ 80 % of the variation of the tetrapod skull (PC1: 69,21%; PC2:20,06%; Fig. 2). PC1 represents a variable of overall integration (based on higher clustering, lower path length) and complexity (higher density) (Fig. 2, inset), and all cetacean skulls score positive along the PC1, being clearly more integrated in comparison with other tetrapod groups (dinosaurs, sauropsids, turtles, synapsids, squamates), but less integrated than some mammals and some amphibians. PC2 mostly sorts the skulls according to their heterogeneity vs. their complexity (Fig. 2, inset), and most derived cetaceans are placed in the morphospace with higher heterogeneity values. Thus, the skulls of neocetes occupy a previously unoccupied place in the tetrapod skull morphospace, with better integrated and more heterogeneous skulls in comparison with other tetrapods (except some birds). Besides, cetaceans explore quite different morphospace in comparison with other mammals, mostly because ~~of~~ they have more heterogeneous skulls. *Pakicetus* and protocetids are placed close to the region of the morphospace occupied by amphibious/semiaquatic forms, with skulls that are less integrated and simpler in comparison with most crown cetaceans. These results reflect not only the increase in the numbers of connections of skull bones (increased integration) in crown cetaceans but also the acquisition of more irregularly distributed connections of some of these bones (increased heterogeneity) within the network, suggesting a new level of organization of the cetacean skull in their transition to the modern lineages. PERMANOVA analysis supports this conclusion, showing a statistically significant difference between the skulls of aquatic and terrestrial tetrapods (p= 0.0069) and between cetaceans and non-cetacean mammals (p=0.0001), suggesting a unique network specialization of cetaceans skull even within mammals (Table S2).

Skull networks specializations of cetaceans

A more detailed PCA analysis focused only on cetaceans (and including an additional variable of modularity, Parcellation) showed that the first two PCs explain nearly ~~the~~ 70% of the recorded variation (PC1: 48,53%%; PC2:22,58%; Fig. 3; Table 1). In this case, the skull of crown cetaceans explores two different and mostly well-separated morphospaces, based on heterogeneity, integration, complexity and modularity. Mysticetes form a group of points that are mostly distinct from odontocetes (with a small overlap) and archaeocetes are segregated by having simpler, more heterogeneous and modular skulls (Fig. 3b-c). Extant baleen whales *Eubalaena*, *Caperea* and *Balaenoptera* ~~separately~~ plot from the remaining mysticetes by having, comparatively, more integrated and modular skulls, whereas extinct baleen whales (*Yamatocetus* and *Piscobalaena*) and toothed ~~whales~~ (*Aetiocetus*) have more heterogeneous and less integrated skulls. On the other hand, odontocetes explore a broader morphospace, forming a group of points from negative to positive values along PC1 (between -3 and 1,5) reflecting a great variation of skull network organization. As a general pattern, the skull of odontocetes is more complex in comparison with mysticetes (Fig. 3b); however, both groups show a similar (and remarkable) increase in the integration of several bones with their immediate surroundings, more evident in the extant forms of both groups. The enlargement of odontocetes morphospace is expected as this group exhibits great anatomical variability in the facial skull configurations, with *Physeter* plotting far apart from the remaining odontocetes (on the I quadrant; Fig. 3a) and the opposite position for the stem odontocete *Albertocetus* on the II quadrant. Therefore, three groups of odontocetes can be identified: i) one comprising *Physeter* and *Notocetus* with more complex and homogeneous skulls; ii) ~~other~~ only occupied by *Waipatia*, with a more heterogeneous but less integrated and modular skull; iii) and finally a group of points including *Tursiops* and *Albertocetus* (~~overlapping in this point with~~ the morphospace of mysticetes), with more modularized, heterogeneous and less integrated skulls.

Pakicetus presents the most typical mammal skull network, with less integrated and more homogeneous skull~~s~~. Conspicuously, *Pakicetus* plots close to *Dorudon* based on having skulls with a similar integration (close values of clustering and parcellation; Fig. 3c-d), but separately of protocetids when the same descriptors are considered. PERMANOVA test only show a statistically significant difference between the skulls of mysticetes and archaeocetes (Fig. 3, inset).

Integration of bones within the networks

Overall, all the bones of cetacean skulls show a similar number of connections (Degree; Fig 4a; Fig. S1); however, mysticetes and odontocetes have one or two more connections (i.e., some bones in mysticetes and odontocetes could reach 14 connections) in comparison with archaeocetes, suggesting an increase in the complexity of integration of the bones within the skull networks. Whereas the median of connections is roughly similar between the groups, the distribution of the connections is different between the two Neoceti clades. Mysticetes show more bones with low (2–4) and intermediate (5–7) number of connections, compared to odontocetes with a more intermediate and high number of connections (Fig. 4a). The frontals are, in both groups, th~~os~~e bones with the higher number of connections (13–14), whereas the most connected vomer of odontocetes could have more connections compared to the most connected vomer of the mysticetes (14 over 12) (Fig. S1). The integration of the bones with their surroundings (Clustering Coefficient) shows (Fig. 4b; Fig.S2) that both mysticetes and odontocetes have bones in their skulls that are better or less integrated compared to those in archaeocetes skulls. Closeness centrality (i.e. how close the bones are to each other) does not show significant differences between the groups, although odontocetes have, comparatively, more bones that are closer to each other compared to mysticetes (Fig. 4c). Bones with high Closeness Centrality are the frontals, the vomer and the supraoccipital. Betweenness Centrality values (Fig. 4d; Fig. S3) indicate bones that hold central positions in the skull networks, suggesting that the skulls of both odontocetes and mysticetes have bones with more central positions compared to those in archaeocetes. Among these groups, some odontocete bones achieve the highest betweenness centrality value (172.87, the vomer in *Albertocetus*). Again, the vomer and the frontals are by far the most important bones in terms of Betweenness Centrality (Supplemental data S2; Fig. S4).

When we compare the individual metrics of the bones that are mainly involved (both directly and indirectly) in the telescoping process (supraoccipital, frontal, vomer, maxilla, premaxilla, and nasal) some interesting observations emerge. These allow tracing the different types of telescoping in odontocetes and mysticetes to the connectivity pattern of the individual bones. The clearest, and statistically significant, separation between the two groups is found in the vomer (Fig. 4e–g). The vomer of odontocetes has more connections (12–14) compared with the vomer of mysticetes (10–12), and it is also much more integrated with its surroundings (Fig. S1). On the other hand, the vomer is the most central bone in the odontocete *Albertocetus*, although the vomer of the mysticete *Piscobalaena* is quite close as well. The greater integration of the vomer in odontocetes reflects the retrograde type of telescoping: as pairs of bones that are directly connected to the vomer (e.g., premaxillae and maxillae) retrocede and gain connections, the integration of the vomer increases. Similarly and as expected, the retrograde telescoping causes increased integration in the maxillae and premaxillae of most odontocetes.

The supraoccipital, which is the main bone involved in the prograde telescoping of the mysticetes, gains importance reflected in the higher values of Closeness and Betweenness Centralities in most derived mysticetes (Fig. 4e–g). With the exception of the outlier odontocete *Physeter*, the supraoccipital of the mysticetes has a more central position compared to the supraoccipital of the odontocetes with the same number of connections (Fig. 4e–g).

The frontals are bones that receive additional connections under both types of telescoping. However, the reception of additional connections of pairs of anterior bones in retrograde telescoping slightly increases the integration of the frontals in odontocetes, while they assume a similar central position in both odontocetes and mysticetes (Fig. 4e–g).

Organizational modularity of skull cetacean networks

The detection of modules in anatomical networks is a matter of ongoing debate (see Esteve-Altava, 2020 and references therein). In general, the skulls of modern cetaceans are more modular (higher parcellation) compared with archaeocetes (Table 1). Extant mysticete skulls are more modularized in comparison with extant odontocetes; with increased modularity in *Balaenoptera* and *Eubalaena* (P=0,797; P= 0,795 respectively) and a remarkable decrease in *Physeter* (P=0,666). The best modularity solutions consistently recover four main modules: 2 dorsolateral, 1 palatal and another in the posterodorsal region in ~~both~~ archaeocetes (e.g., *Dorudon*), mysticetes (e.g., *Yamatocetus*), and odontocetes (e.g., *Notocetus*) in both symmetric and asymmetric reconstructions (Fig. 5). In some cases, the posterodorsal module could be divided into ~~a~~ left and right portion (e.g., *Eubalaena* and *Caperea*; Fig. 5). Given the various issues in the reconstruction of the modules, we refrain from discussing their boundaries in detail.

DISCUSSION

Telescoping promotes a new path in the connectivity of cetacean skull

During their transition to the aquatic environment, cetaceans experienced profound changes in their skeletal anatomy, especially in the skull. Among the most remarkable changes are the posterodorsal migration of the external bony nares, the reorganization of the skull bones (= telescoping) and the development of a remarkabl~~y~~ cranial asymmetry (characteristic of odontocetes) (Miller, 1923; Fordyce & Muizon, 2001; Berta et al., 2014; Marx et al., 2016). Cranial telescoping represents an important key innovation in the evolution of Neoceti and might be linked to facilitating breathing while they are submerged, structural reinforcement of the vertex to avoiding fractures during the air-breathing movements, the development of filter-feeding in mysticetes and/or echolocation in odontocetes (Miller, 1923; Fleischer, 1976, Heyning & Mead,1990; Oelschlager, 1990; Churchill et al., 2018; Roston & Roth, 2019). Besides, it represents an important anatomical shift in the topological organization and sutural contact of cranial bones (Miller, 1923; Roston & Roth, 2019), and thus in the connectivity of the skull elements. Our study is the first attempt to analyze the patterns of skull connectivity in cetaceans captured through the lens of anatomical networks.

Our results show that, along with the transition to ~~the~~ fully aquatic lifestyle, the cetacean skull underwent a remarkable reorganization of the connectivity pattern that allowed the exploration of a new tetrapod morphospace. While archaeocetes (specially *Pakicetus* and protocetids) still remain in the known morphospace for other non-cetaceans mammals, with comparatively less integrated and more complex skulls, modern cetaceans (Neoceti) follow the path towards more heterogeneous, better integrated and simpler skulls (Fig.5; Fig. S5-11). Telescoping, as well as the other modifications of the skull linked to feeding (e.g. filter-feeding in mysticetes) and hearing (e.g. echolocation in odontocetes), are important key innovations that drive the evolution of modern cetaceans (Cranford, Amundin, & Norris,1996; Fordyce & Muizon, 2001; Marx et al 2016; Bouetel, 2005). Telescoping caused a profound reorganization of skull bones and changes in the configurations of the sutures (Miller, 1923; Kellog, 1928a,b; Churchill et al., 2018; Roston & Roth, 2019;), reaching a new level of topological organization which breaks the molds of mammalian skull. Besides, telescoping promotes contact between bones that otherwise would not be possible (e.g. occipital and rostral bones), and the increase of the numbers of connections ~~are~~ more evident in the crown Mysticeti and Odontoceti (87–92 and 98–101 respectively; Fig. 5; Fig. S6) where telescoping reaches its full development (in terms of the degree of overlaps of facial bones). The bones that reach the widest range of variation~~s~~ in the number of connections are the supraoccipital (5–11), frontals (6–14), maxillae (5–11), but also the pterygoids (4–9), presphenoid (3–9), basisphenoid (3–9), alisphenoid (2–6) and ethmoid (2–9) (). These results suggest that the rearrangement of facial and occipital bones impacts not only the numbers of connections of those bones directly involved in telescoping (e.g., maxilla, supraoccipital) but also ~~in~~ other ones (e.g., palatal) not directly affected by telescoping (see further discussion below).

One of the network descriptors that better define the evolution of the cetaceans skull is ~~the~~ heterogeneity, which shows an important increase at the base of the Pelagiceti, and even further in the Neoceti clade (Fig. 5 and Fig. S6). In terms of anatomical networks, heterogeneity reflects a disparity in the number of connections among the skull bones, indicating different hierarchy levels of the parts of a network (i.e. anisomerism; Esteve-Altava et al., 2013a; Rasskin-Gutman & Esteve-Altava, 2014). In tetrapods, the increase of the specialization of individual bones has been linked to the appearance of new unpaired bones by fusion of paired ones (Esteve-Altava et al., 2013a). Cetaceans do not present variations in the numbers of bones by loss or fusion in the different groups analyzed (except *Dorudon* and *Physeter;* Fig S7); however, our results show that the unpaired bones ratio (a measure of anisomerim; Esteve-Altava et al., 2013a) is higher in cetaceans in comparison with other tetrapods that have the same bone number (Fig. S12), suggesting an increase in the specialization of individual bones. We hypothesize that telescoping, otherwise, bone loss or fusion, provides an alternative mechanism to increase the connectivity pattern of unpaired bones and thus increase the heterogeneity of the skull networks.

Another hallmark path that marks the evolution of the connectivity pattern of modern cetaceans is the increase of the integration of the skull (Fig.5 and Fig. S9-S10) Our results show that average path length, along with clustering, appears to be good descriptor of telescoped skulls, both reflecting an increasing morphological complexity and integration of the bone elements of the skull in this new level of organization. The bone overlap and the proximity of occipital-rostral elements affect directly the connectivity of those bones involved in the telescoping process, but indirectly also affect the sutural relationship of other ones. There is an important increase in the integration by clustering of maxilla, premaxilla, supraoccipital, parietal and nasals, but also in palatal bones, such as palatine, pterygoid and vomer, and the alisphenoid (the latter reaches the higher values of clustering in some mysticetes). The topological reorganization of palatal bones during telescoping, mainly the covering of the palatine and alisphenoid by the pterygoid, has been suggested in the pioneering work of Miller (1923) but not extensively studied in modern analyses (e.g. Churchill et al., 2018; Roston & Roth, 2019).

Besides, changes in the distribution and sutural contacts of these bones along with the evolution of different groups, but not directly linked with the telescoping process, have also been reported (Muller, 1954; Fraser & Purves, 1960; Boutel & Muizon, 2006). In addition to the telescoping process, the skull of neocetes has experienced profound changes associated with the developments of air and vascular sinus systems and ~~the~~ modifications in the ear region (Fraser & Purves, 1960; Reidenberg & Laitman, 2008; Mead & Fordyce, 2009). In particular, the air sinus system develops in the basicranium and orbital region, extending mainly over the surface of pterygoids, palatines, basisphenoid, and alisphenoids, with variations in their development and configurations of their bone-correlates among the different groups of neocetes (see Fraser & Purves, 1960 for a detailed analysis). We speculate that the increase in the integration of neocete~~s~~ skull was achieved not only with the changes associated with the telescoping process but also with all the morphological modifications that occur in the basicranium linked with the specialization to underwater hearing and deep diving.

Telescoped skulls, especially in crown mysticetes and odontocetes (Fig. S9), reach the shortest average path length, suggesting that bones of the skull are more integrated by proximity. One of the main obvious anatomical changes coupled with telescoping is the extreme reduction or loss of the intertemporal region— by the reduction of the dorsal exposition of frontal and parietal in the roof of the skull— contributing to the “shortening” of the occipital-rostrum distance (Miller, 1923; Kellogg, 1928a; Roston & Roth, 2019). The better integration of the skull by proximity results in a better speed of the information within the skull network, especially between two key regions traditionally associated with important functional correlates —feeding and brain support respectively~~—~~.

Moreover to the increase in the integration and heterogeneity in neocetes, there is a marked shift toward an increment of modularity from non-telescoped to telescoped skulls (Fig. 5; Fig.S11). Connectivity modules differ from variational modules — sensu Esteve-Altava, 2017— in that they reflect the topological arrangement of anatomical units, not their shapes; thus information of connectivity modules should be presented as a complement of the information generated with the variational modules (Raskin- Gutman & Esteve-Altava, 2014; Esteve-Altava, 2017). Unfortunately, studies on the variational modules in cetacean skulls are very scarce and only focus on odontocetes (del Castillo et al., 2017; Churchill et al., 2018). The amount of modules identified depends if the models of modularity identified a development correlation (in which case they identified 3 modules; del Castillo et al., 2017) or a functional correlation (between 5–10 modules; Churchill et al., 2018). Our analysis shows a mean of four connectivity modules for neocetes, with a variable number in odontocetes (between 3–5) and a more constant number in mysticetes (most with 5 modules), associated with the rostr~~um~~ and orbital (recovered in symmetric modules), basicrani~~um~~ (including in a variable array of the bones of the floor of the cranium as well as palatal bones) and crani~~um~~ regions (including the bones that form the cranial vault and the squamosals). These organizational modules are more closely related to the basicranium, neurocranium and rostrum modules reported by del Castillo et al., (2017), and suggest a basic connectivity modularity pattern of the neocete skull. Due to sutures representing the physical link between the elements of the networks, and in neocetes telescoped sutures acquired a novel configuration—being points of contact, growth but also of extensive bone overlap; Roston & Roth, 2019—, it is likely that the sutures more than bones itself, mark an important constraint in the topological arrangement of the anatomical units and, thus, in their connectivity. Underlying developmental processes, growth and/or biomechanical functions are, in the end, the main responsible for the origin of connectivity modules (Klingenberg, 2008).

Mysticetes and odontocetes skull networks specializations

Two main patterns of telescoping can be traced in mysticetes and odontocetes, with important differences in the topographical organization of the skull bones. In mysticetes, telescoping is dominated by the forward movement of the supraoccipital and parietal until the orbit level, while only a narrow medial part of maxilla extends posteriorly interlocking with the frontal (but not covering at all). In odontocetes, rostral elements, maxilla and premaxilla, extend backwards approaching the supraoccipital; in this case, maxilla spread over almost all the surface of the frontal, including the supraorbital process (Miller, 1923; Fig. 1). Different development sequences of bone ossification and sutures closure have been identified as the underlying process that influences the skull anatomy of both groups (Perrin, 1975; Lanzetti, 2019). What is the impact of these disparate skull anatomical organizations of odontocetes and mysticetes in the network organization?

Within an evolutive framework, prograde telescoped skulls of mysticetes distinct for increased heterogeneity, modularity and integration (especially by clustering) while retrograde telescoped skulls of odontocetes follow the path of increasing complexity, reaching the higher number of total connections (Fig 5; Figs S5–S11). Both lineages show a similar integration by path length, at least at the base of mysticetes and odontocetes as well as at the point of diversification of crown lineages. This suggests that one of the main characteristics of the telescoping process, — shortening of the occipital-rostrum distance— impacts the integration by the proximity of the skull network in a similar way, independently of the telescoping specialization followed by each group. In mysticetes, heterogeneity is mainly driven by the increased role of unpaired bones within the network. As expected, the supraoccipital gains relevance and centrality in the networks in comparison to odontocetes and also achieves a high number of connections if we compare it with an archetypal odontocete skull as *Tursiops* (*Physeter* reaches 11 connections however the morphology of this skull is quite disparate from other odontocetes due to the extreme posterior extension of the maxillae and the lack of one nasal; see further discussion below) (Supplemental data S2). On the other hand, the increased connections and, thus, complexity in the skull network of odontocetes, are probably linked to the dominant movement of paired bones in retrograde telescoping, such as the maxilla, which gains connections and integration not only in its own node but also in its surroundings. No remarkable differences are observed between odontocetes and mysticetes in the connections/integration/centrality of other bones also affected by telescoping, such as premaxillae, frontals, nasals and parietals (Fig 4e-g; Table X SOI). On the contrary, the vomer, alisphenoid, and pterygoids show conspicuous differences between both groups in the numbers of connections, centrality and integration. This result provides evidence that, again, even though telescoping defines the quite distinct anatomical configuration of the skull of mysticetes and odontocetes, there is not a broad effect in the connectivity pattern of all the bones directly involved in these processes. Besides, our results invite us to re-evaluate the role of palatal and sphenoid bones in the evolution of the skull of modern cetaceans and might consider them as the “hidden hands" that play a key role in the improvement of connection and integration of the different elements of the skull. Future works should focus on analyzing with more detail the anatomical reorganization of these regions, and their correlation (or lack of it) either with the telescoping or with the evolution of air sinus systems, or both.

Additionally to the different paths identified in odontocetes and mysticetes, some particular evolutionary trends distinguish the different lineages of both groups (Fig. S5-S11). Among mysticetes, the toothed whale *Aetiocetus* presents the smallest number of connections of the whole mysticete sample and the simpler and less integrated by proximity skull. This pattern of skull connectivity is consistent with the poorly telescoped skull of this taxon, reflected in a non-telescoped supraoccipital, and a broadly exposed parietal and frontal in the skull roof (e.g. Deméré & Berta, 2008). Furthermore, the skull of the toothless mysticetes *Yamatocetus* distinguish by, comparatively with *Aetiocetus*, a more pronounced telescoped supraoccipital, but still retaining a long intertemporal region. These small anatomical changes might explain the slight increase in the complexity, integration by proximity, and heterogeneity observed in *Yamatocetus* in comparison with *Aetiocetus*.

Within crown mysticetes, outstanding differences can be observed in the anatomical networks of balaenids (*Eubalaena*), neobalaenines (*Caperea*), and balaenopterids (*Balaenoptera*). The skull of *Eubalaena* and *Caperea* distinct by high heterogeneity, complexity and modularity (in all the cases the higher values among the extant taxa), and also by reaching the better integration by proximity —the “shorter skulls" considering the average path length— and with their surrounding (especially in *Eubalaena*) (Figs. S6-S11). Balaenids and neobalaenines have a conspicuous telescoping process, dominated by the pronounced anterior expansion of the supraoccipital, which extends beyond the level of the orbit excluding the parietal from the vertex of the skull. Besides, the nasal and ascending process of the premaxilla and maxilla do not protrude into the occipital region, defining a sub-rectilinear suture between occipital-rostral bones (Miller, 1923 pl: 8; Bouetel, 2005). The increase of the structural disparity (=heterogeneity) of the skull networks of *Eubalaena* and *Caperea* is probably related to the leading role that some unpaired bones —i.e. supraoccipital, the bone that reaches the higher closeness centrality and clustering values; Fig. 4f— achieved during its characteristic telescoping process. Besides, the "shortening" of the skull evident by the shorter path length is extreme in these taxa and correlates with the pronounced proximity of the occipital-rostral elements observed in balaenids and neobalaenines. This, together with the high complexity of the skull, suggest a network system with strong functional and developmental codependence between the parts, but also with important structural constraints that might be driven by the very specialized skim feeding method of these whales (Werth, 2004; Bouetel, 2005).

Within an evolutionary context, the skull of *Balaenoptera* is the most homogeneous, less complex and better-integrated with their surroundings in comparison with the other extant mysticetes analyzed (Fig. S6-S11). Balaenopterids display a more extreme telescoped skull, with both rostral and occipital elements moving in similar proportions: maxilla, premaxilla and nasals project backwards, until the half level of the orbit, while the supraoccipital extends forward meeting the rostral bones almost the same level (Miller, 1923; pl 8,5). This configuration determines a strong interdigitation of occipital-rostral bones, which has an important biomechanical function supporting the forces induced during the lunge feeding (Lambertsen, Ulrich & Straley, 1995; Bouetel, 2005). We hypothesized that balaenopterids telescoping promotes skull networks with similar structural connections, since there is no specialization of some elements over others, but reaching a better integration of the surrounding elements of the network. Conversely, balaenopterids exhibit variations in the shape and contacts of some bones in the vertex, which has been used as a taxonomic source to diagnose species (see for example Wada, Oishi & Yamada 2003; Yamada, 2006). We speculate that, as expected for anatomical systems with low density (Rasskin-Gutman & Esteve-Altava 2014), variation and phenotypic plasticity enhance the evolution of less complex skulls in balaenopterids.

Odontocetes also exhibit some particular evolutionary trends within the different lineages, even though there is no clear differentiation between network specialization followed by extinct and extant forms (Fig. 5; Fig. S5-S11). The skull network of *Albertocetus*, a stem Odontoceti (e.g., Uhen, 2008; Churchill et al., 2016), shows the small number~~s~~ of connections ~~of~~ all the odontocete sample, together with the less complex and less integrated by proximity skull. This is probably related to~~, comparatively~~, the less advanced stage of telescoping observed in *Albertocetus* ~~evidencing in the little~~ posterior projection of the ascending process of the premaxillae, poor~~ly~~ lateral expansion of maxillae and the broad ~~exposition~~ of the parietals and frontal in the roof of the skull (phase one sensu Churchill et al., 2018). Within crown odontocetes, ~~P~~lastanistoids (sensu Muizon, 1987) represented by the extinct forms *Waipatia* and *Notocetus*, exhibit a mosaic in their network~~s~~ skull descriptors, with density and integration by proximity being close to the values of extant odontocetes, while integration by clustering, heterogeneity and modularity represent extreme and unique values —i.e., *Waipatia* is the most heterogeneous and the least modular skull of all the odontocetes sample while *Notocetus*, on the opposite~~,~~ side represents the most homogeneous and one of the most modular skulls~~—~~. A more advanced stage of telescoping is patent in platanistoids, with an almost absent intertemporal region and a more pronounced posterior expansion of maxilla, premaxilla and nasal~~s~~ (phase II of Churchill et al., 2018). This progress in telescoping is reflected in the increase of the number of connections, complexity and integration of the skull in comparison to stem odontocete~~s~~. Nevertheless, our results suggest that the connectivity pattern of platanistoids does not follow a clear evolutionary trend; rather, it reflects an experimentation phase that matches those proposed for the evolution of skull eco-morphological strategies of the group (Viglino et al., 2021).

Finally, extant odontocetes (Delphinidae and Physeteridae) show disparate patterns of skull connectivity, especially ~~by the bizarre morphology of~~ *Physeter* (Fig. S5-S11). While *Tursiops* represents a more archetypical stage of retrograde telescoping (i.e with a broad overlap of the maxilla and frontal bones; Fig. 1), *Physeter* has an extreme telescoped skull, with a highly asymmetrical facial region, and the loss of ~~a~~ skull bone (Flower, 1868, figs.1-2). The highe~~r~~ density and integration by proximity and with the surrounding of all the odontocete sample is reached by *Physeter*. This is not unexpected due to the pronounced shortening of occipital-rostral distance and, thus, the gain of bone~~s~~ contacts —in for example the maxillae and supraoccipital (supplemental data S2)—, as well as for the increase of complexity ~~by~~ the loss of one nasal bone (as suggested by Esteve-Altava et al., 2013a for the evolution of tetrapod skulls). Leaving aside this outlier skull morphology, a better integration of the bones with their surroundings, probably enhanced by the main movement of paired bones, as well as a moderate heterogeneity (might be promoted by the increased relevance of the vomer in the skull network) can be traced as a distinct connectivity evolutionary pattern of the retrograde skull of extant odontocetes.

Conclusions

Telescoping is one of the most remarkable changes in the anatomy of the cetacean skull, and has been associated with a plethora of morpho-functional explanations. Along with changes in the shape of bones and sutures, our studies show that telescoping also promotes profound changes in the topographical organization of the skull, and thus in its connectivity and integration. ~~M~~odern cetaceans explore a new morphospace in comparison to other tetrapods (and even ~~with~~ other mammals), with better integrated, slightly simpler, and mainly more heterogeneous skulls. This represents a break in the mammalian skull mold, triggering the exploration of new morphospaces. Telescoping increases the anisomerism of the skull by specialization of unpaired bones, as those directly involved in the telescoping process (e.g. supraoccipital) or other ones (i.e. vomer) are not obviously affected by telescoping. It is also possible that telescoping together with all basicranium specializations linked with hearing adaptations are the main responsible for the changes in the connectivity and integration of neocetes skull. Our findings also support a distinct connectivity pattern in mysticetes and odontocetes, with prograde telescoped skulls of mysticetes distinct for an increased heterogeneity, modularity and integration while retrograde telescoped skull of odontocetes characterized ~~for~~ being more complex. Besides, retrograde telescoping causes increased integration in the maxillae and premaxillae of most odontocetes while prograde telescoping of mysticetes promotes a greater relevance and centrality of unpaired bones (i.e. the supraoccipital). Additionally, particular evolutionary trends in the connectivity pattern of the skull were identified within the different groups of odontocetes and mysticetes, many of them coupled with the different stages of the advance of the telescoping (for example between extinct and extant forms) but also with feeding, hearing and other ecological specializations acquired for different lineages throughout their evolutionary history. Finally, our results show that not all shape variations observed along the evolution of cetaceans skull have a direct impact on the topological organization and connectivity of the elements of this complex structure; this reinforces the idea that Anatomical Networks are a complementary tool to the other areas of morphological research which need to be further explored.

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Table 1(on next page)

Main descriptors of the cetacean sample analyzed.

C, average clustering coefficient; D, density; H, heterogeneity; K=connections; N, nodes; P, parcellation; PL, average path Length; UBR, unpaired bone ratio.

Taxon	**Group**	**Category**	**N**	**K**	**D**	**PL**	**C**	**H**	**P**	**UBR**
Pakicetus	“Archaeoceti”	Extinct	35	99	0.166	2.334	0.391	0.404	0.731	0.2
Protocetidae	“Archaeoceti”	Extinct	35	102	0.171	2.366	0.540	0.435	0.744	0.2
Dorudon	“Archaeoceti”	Extinct	33	88	0.167	2.333	0.408	0.497	0.722	0.21
Aetiocetus	Mysticeti	Extinct	35	82	0.138	2.464	0.501	0.568	0.789	0.2
Yamatocetus	Mysticeti	Extinct	35	86	0.145	2.370	0.428	0.578	0.746	0.17
Piscobalaena	Mysticeti	Extinct	35	85	0.143	2.450	0.478	0.533	0.738	0.17
Caperea	Mysticeti	Extant	35	92	0.155	2.338	0.474	0.561	0.790	0.2
Eubalaena	Mysticeti	Extant	35	99	0.166	2.292	0.490	0.563	0.795	0.2
Balaenoptera	Mysticeti	Extant	35	87	0.146	2.447	0.494	0.514	0.748	0.2
Albertocetus	Odontoceti	Extinct	35	88	0.148	2.536	0.476	0.476	0.761	0.2
Waipatia	Odontoceti	Extinct	35	101	0.170	2.382	0.401	0.552	0.650	0.2
Notocetus	Odontoceti	Extinct	35	109	0.183	2.321	0.461	0.424	0.744	0.2
Tursiops	Odontoceti	Extant	35	98	0.165	2.418	0.477	0.543	0.738	0.2
Physeter	Odontoceti	Extant	34	107	0.191	2.196	0.493	0.501	0.666	0.2

Figure 1

The two different types of telescoping in modern cetaceans, from skull to network.

Although superficially (dorsally) the connectivity pattern of the two different types of telescoping is rather similar (see the simplified drawings), under the hood the bones are connected in a quite different way. In the prograde telescoping seen in mysticetes (here represented by *Balaenoptera* spp) additional connections are seen in the supraoccipital and the ventro-lateral parts of the skull. In the retrograde telescoping seen in the odontocetes (illustrated by *Tursiops*), numerous new connections are modeled in the internal (e.g. vomer) and ventral parts of the skull (corresponding to the palatal region).

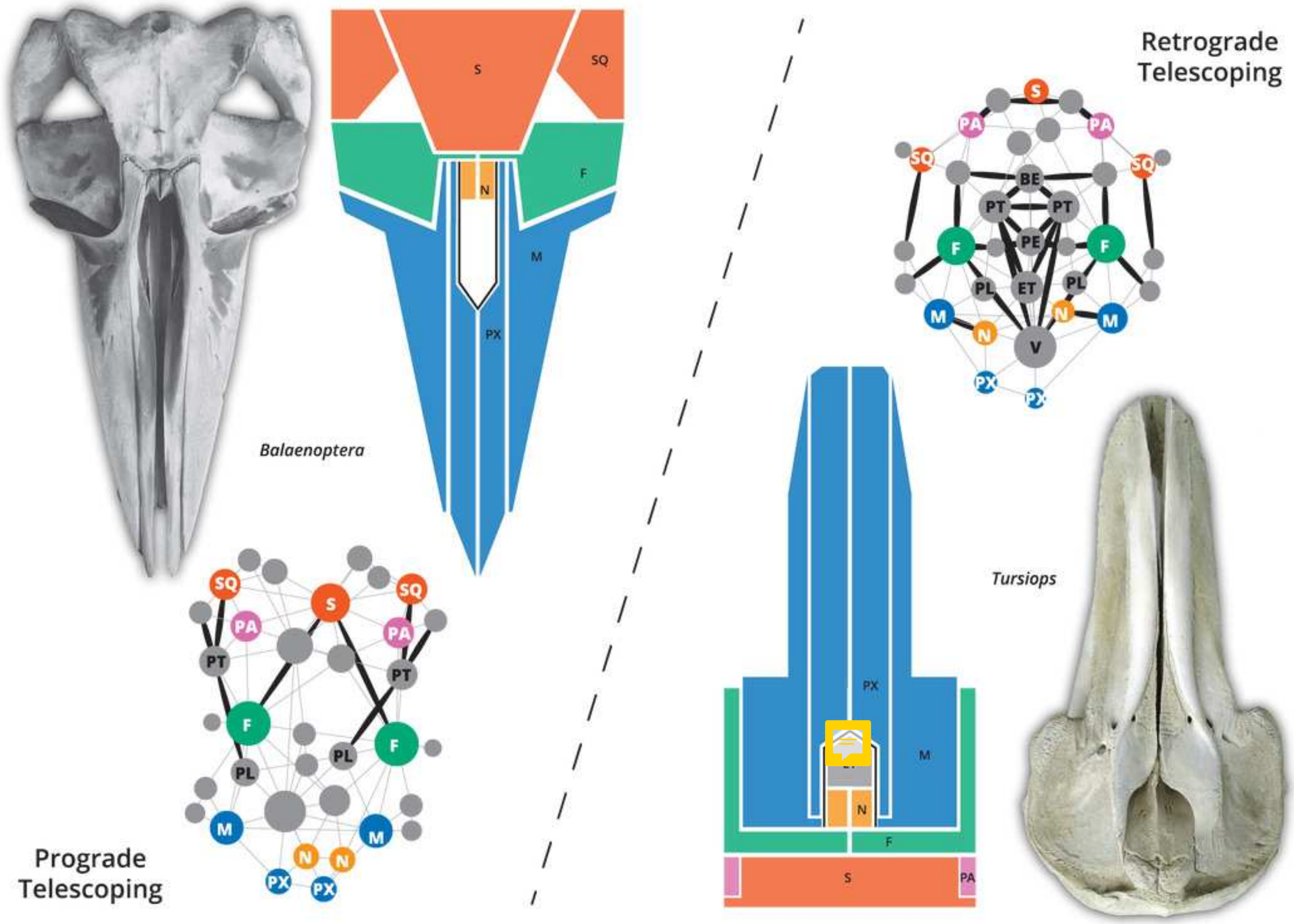
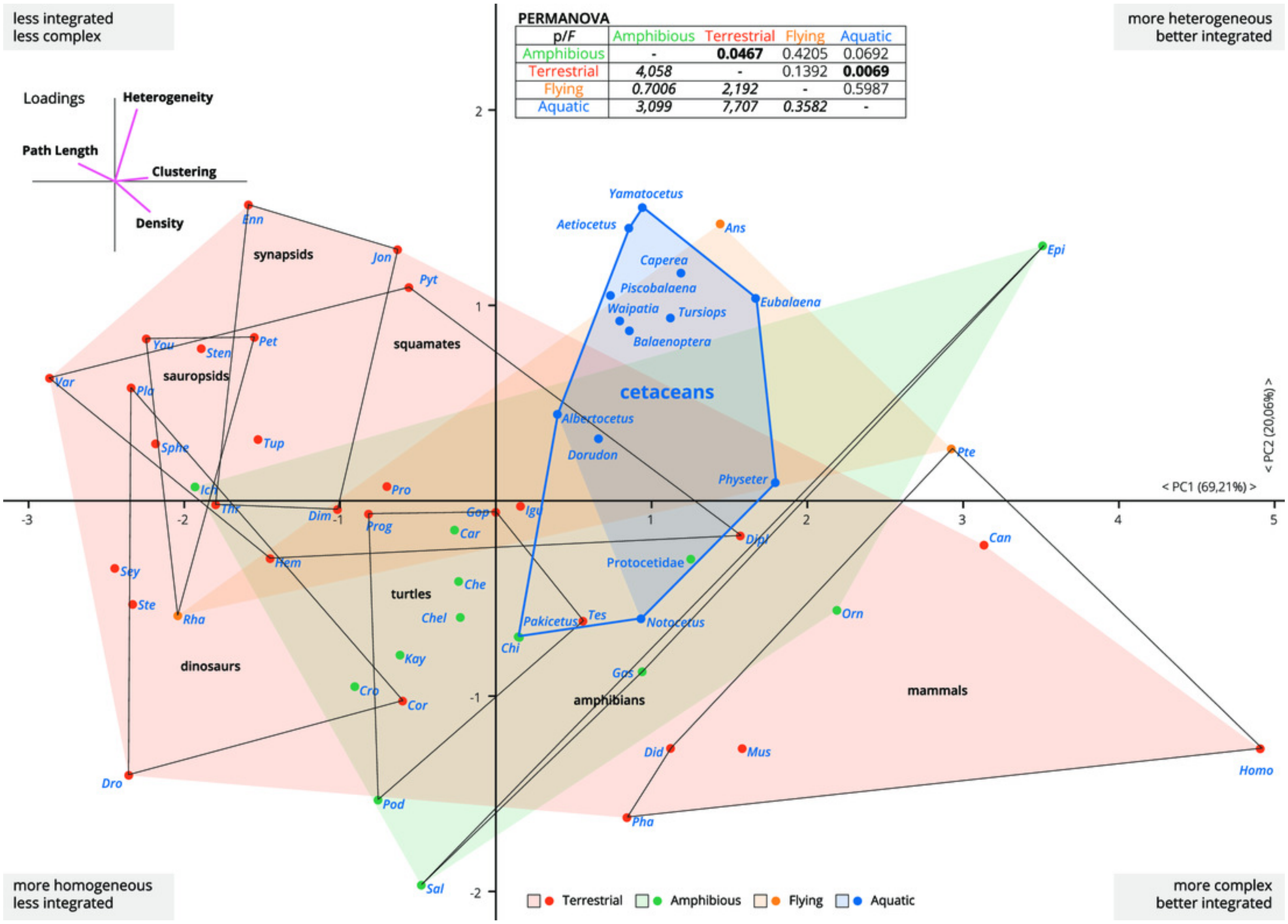


Figure 2

PCA of the skull networks of various tetrapods, based on the initial dataset of Esteve-Altava et al. (2013a) and the ~~added~~ cetacean sampling herein.

Sampling includes taxa adapted to terrestrial, aquatic, amphibious and flying lifestyles and from many important tetrapod clades. The first two PCs explain nearly 80% of the variation (PC1: 69,21%; PC2:20,06%) and permit separating the skulls of tetrapods based on their heterogeneity, integration (based on clustering and path length) and complexity (based on density). Those placed in the first and second quadrants show skulls that are better integrated, further divided into those with more heterogeneous (first quadrant) or more complex (fourth quadrant) skulls. Those ~~tetrapods~~ placed in the second and third quadrants show skulls that are less integrated, further divided into those with more homogeneous (third quadrant) or simpler (second quadrant) skulls. Most derived cetaceans explore a previously unoccupied region for other non-flying tetrapods, with integrated skulls that are quite heterogeneous. Also, the morphological variation that ~~the~~ cetaceans exhibit is significantly different from the variation of all other sampled mammals. Abbreviations: *Ans*, *Anser*; *Can*, *Canis*; *Car*, *Carettochelys*; *Che*, *Chelodina*; *Chel*, *Chelydra*; *Chi*, *Chisternon*; *Cor*, *Corythosaurus*; *Cro*, *Crocodylus*; *Did*, *Didelphis*; *Dim*, *Dimetrodon*; *Dipl*, *Diplometopon*; *Dro*, *Dromaeosaurus*; *Enn*, *Ennantosaurus*; *Epi*, *Epicrionops*; *Gas*, *Gastrotheca*; *Gop*, *Gopherus*; *Hem*, *Hemitheconyx*; *Ich*, *Ichthyostega*; *Igu*, *Iguana*; *Jon*, *Jonkeria*; *Kay*, *Kayentachelys*; *Orn*, *Ornithorhynchus*; *Pet*, *Petrolacosaurus*; *Pha*, *Phascolarctos*; *Pla*, *Plateosaurus*; *Pod*, *Podocnemis*; *Pro*, *Procolophon*; *Prog*, *Proganochelys*; *Pte*, *Pteropus*; *Pyt*, *Python*; *Rha*, *Rhamphorhynchus*; *Sal*, *Salamandra*; *Sey*, *Seymouria*; *Sphe*, *Sphenodon*; *Ste*, *Stegosaurus*; *Sten*, *Stenocercus*; *Tes*, *Testudo*; *Thr*, *Thrinaxodon*; *Tup*, *Tupinambis*; *Var*, *Varanus*; *You*, *Younginia*.

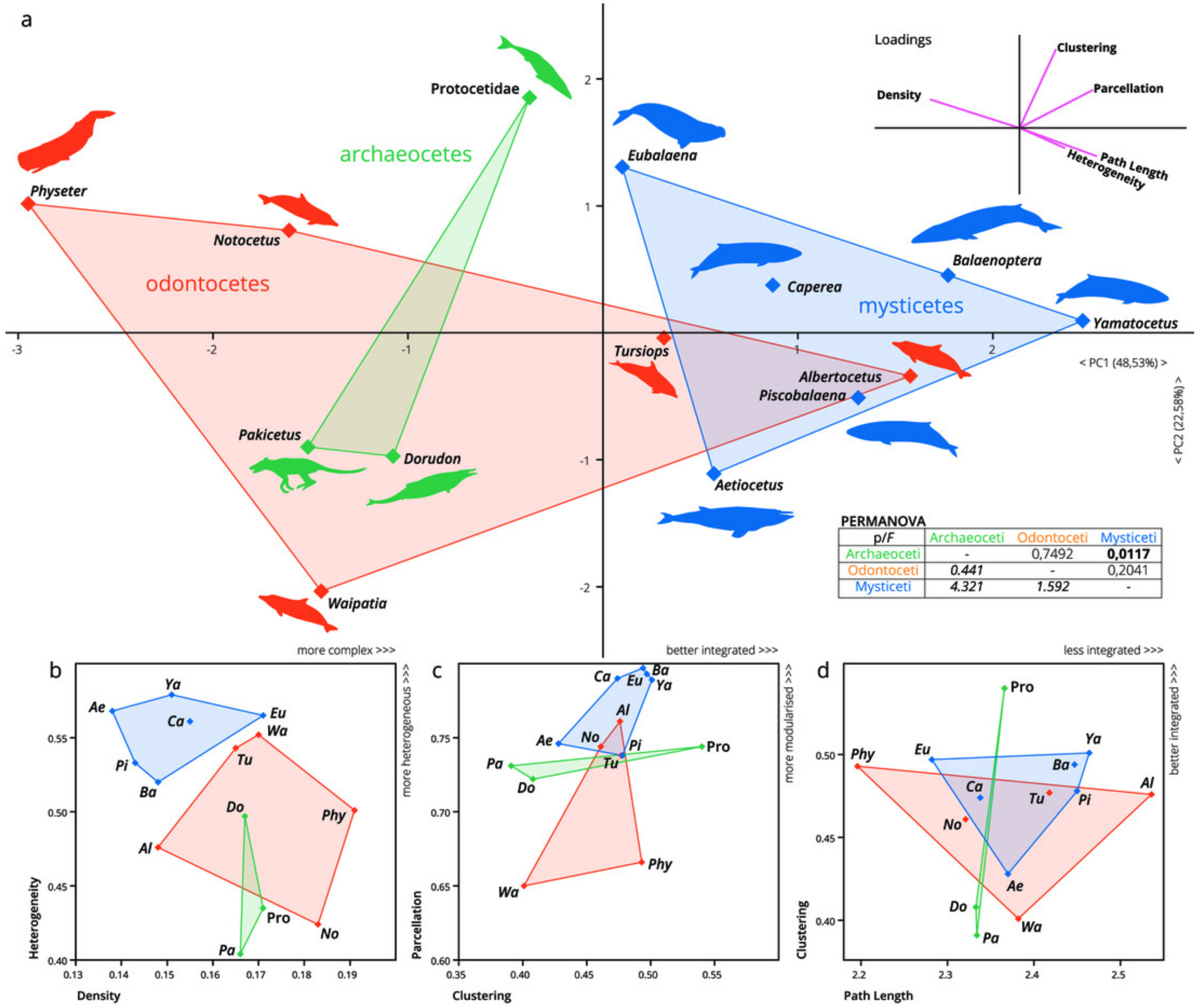

PERMANOVA

p/*F*	Amphibious	Terrestrial	Flying	Aquatic
Amphibious	-	**0.0467**	0.4205	0.0692
Terrestrial	*4,058*	-	0.1392	**0.0069**
Flying	*0.7006*	*2,192*	-	0.5987
Aquatic	*3,099*	*7,707*	*0.3582*	-

Figure 3

A detailed PCA of the skull networks of cetaceans, based on the sampling herein

(a) Sampling includes “Archaeoceti”, Odontoceti, and Mysticeti. The first two PCs explain nearly 70% of the variation (PC1: 48,53%%; PC2:22,58%) and permit separating the skulls of cetaceans based on their heterogeneity, integration (based on clustering and path length), complexity (based on density), and modularity (based on parcellation). All sampled mysticetes are placed in the morphospace defined generally by simpler skulls (first and fourth quadrants), further divided into those also having integrated and more modular skulls (e.g., *Eubalaena* and *Balaenoptera*) or those with more heterogeneous and less integrated skulls (e.g., *Piscobalaena* and *Aetiocetus*). All archaeocetes and most odontocetes are placed in the morphospace defined by skulls that are, comparatively, more complex (second and third quadrants), further divided into those with better integrated and more homogeneous skulls (e.g., *Physeter* and Protocetidae) and those with less integrated and less modular skulls (e.g., *Waipatia* and *Dorudon*). However, odontocetes display the greatest morphological variation. **(b–d)** Whereas both odontocetes and mysticetes have similar integration (albeit odontocetes display a broader spectrum), mysticetes are clearly distinguished by more heterogeneity and modular skulls, compared to the more complex skulls of odontocetes. Silhouettes have been downloaded by phylopic.org under the following credits: *Pakicetus* (Conty, CC-BY), *Dorudon*, *Aetiocetus* (M. Keesey, public domain), Protocetidae (N. Tamura, vectorized by M. Keesey, CC-BY), *Physeter* (M. Michaud, public domain), general Odontoceti, *Tursiops*, general Mysticeti, *Eubalaena*, *Balaenoptera*, *Caperea* (C. Huh, CC-BY-SA). Abbreviations: *Ae*, *Aetiocetus*; *Al*, *Albertocetus*; *Ba*, *Balaenoptera*; *Ca*, *Caperea*; *Do*, *Dorudon*; *Eu*, *Eubalaena*; *No*, *Notocetus*; *Pa*, *Pakicetus*; *Phy*, *Physeter*; *Pi*, *Piscobalaena*; Pro, Protocetidae; *Tu*, *Tursiops*; *Wa*, *Waipatia*; *Ya*, *Yamatocetus*.



PERMANOVA

p/F	Archaeoceti	Odontoceti	Mysticeti
Archaeoceti	-	0,7492	**0,0117**
Odontoceti	*0.441*	-	0,2041
Mysticeti	*4.321*	*1.592*	-

Figure 4

Network analysis of the cetacean skull at the individual bone level, based on selected network descriptors of the individual bones.

a–d, Violin plots with included box plots of the Degree (**a**), Clustering Coefficient (**b**), Harmonic Closeness Centrality (**c**), and Betweeness Centrality (**d**) of all skull bones of archaeocetes (green), odontocetes (orange), and mysticetes (blue). **e–g**, scatter plot of the Clustering Coefficient (**e**), Harmonic Closeness Centrality (**f**), and Betweeness Centrality (**g**) vs. the Degree of the main bones involved ~~at~~ the two types of telescoping in odontocetes (orange) and mysticetes (blue).

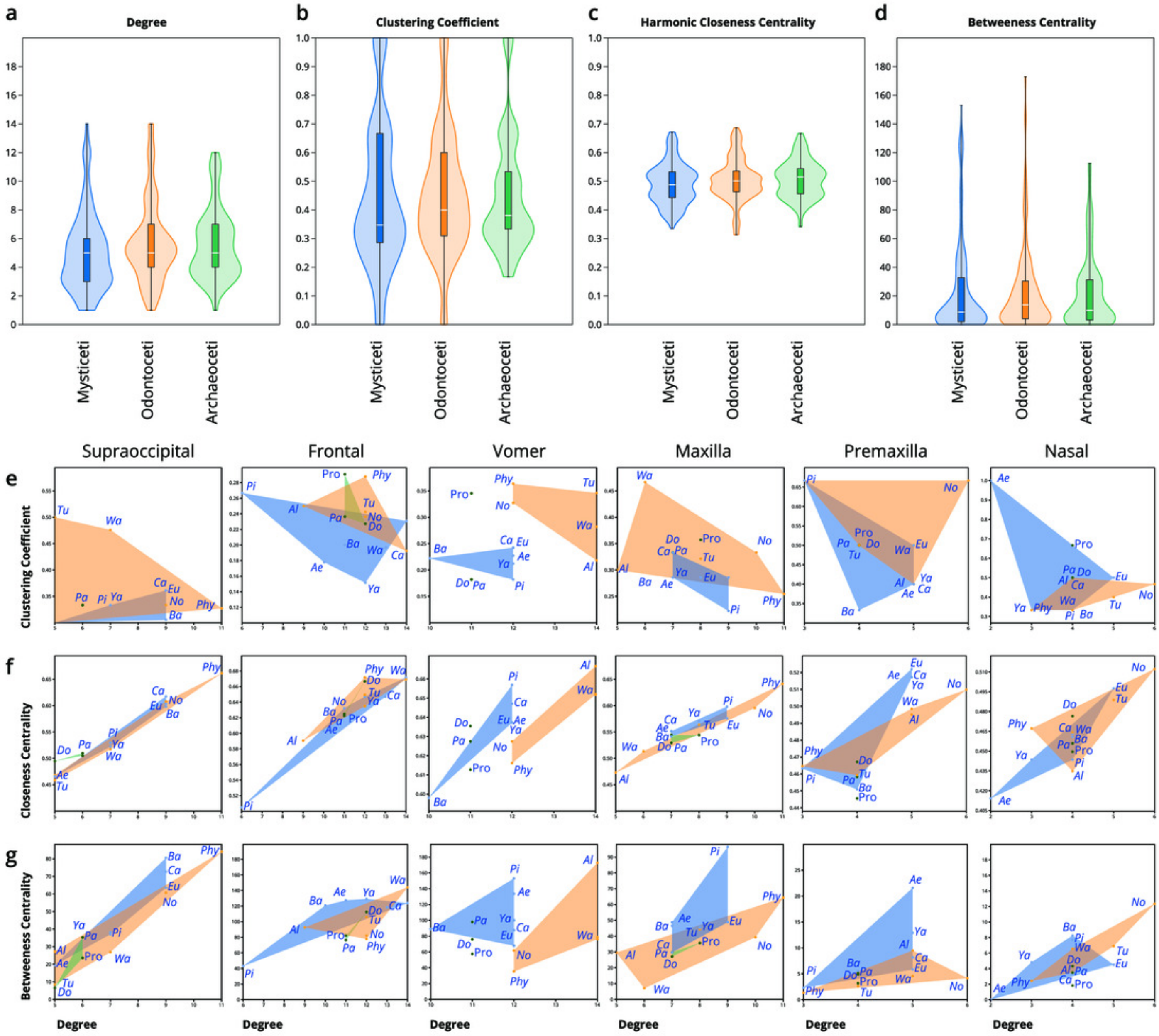

a
Degree
b
Clustering Coefficient
c
Harmonic Closeness Centrality
d
Betweeness Centrality
Mysticeti
Odontoceti
Archaeoceti
Supraoccipital
Frontal
Vomer
Maxilla
Premaxilla
Nasal
e
Clustering Coefficient
f
Closeness Centrality
g
Betweeness Centrality
Degree
Tu
Wa
Pa
Pi
Ya
Ca
Eu
No
Ba
Phy
Pro
Do
Al
Ae

Figure 5

Anatomical networks, recovered network modules and the evolution of the main network descriptors under parsimony in a phylogenetic framework

The phylogeny is based on Martinez Cáceres et al., (2017) for archaeocetes, Marx et al., (2019) for mysticetes and Viglino et al., (2021) and Boessenecker et al., (2017) for odontocetes. See supplemental figures for detailed mapping.