www.nature.com/scientificreports

scientific reports

Check for updates

OPEN

Evolution of accessory bones in cetacean skull coupled with decreasing rate of ossification of cranial sutures

Valeriia Telizhenko & Pavel Gol'din

The skulls of cetaceans (whales, dolphins and porpoises) are distinguished by incomplete ossification of cranial sutures during their lifetime. We suggested suture ossification may correlate with the evolution of rarely reported accessory bones and examine the evolutionary patterns of cranial suture ossification and the presence of accessory elements in the skulls of 47 cetacean species and, for comparison, 15 terrestrial artiodactyls (even-hoofed mammals). A strong phylogenetic signal was found for both suture ossification rate and accessory bone presence. Cetaceans were shown to have a lower ossification rate than most terrestrial artiodactyls, except deer (Cervidae) and mouse deer (Tragulidae), which showed somewhat similar patterns. There were also several types of accessory bony elements, some of them first reported in the skulls of cetaceans and in one case, a muntjac deer. These elements (bones and clefts) evolved in the crania with the least number of ossified sutures. They can be identified as novel elements or, some of them, as plesiomorphies rarely seen in mammals but existing in reptiles and other ancestral groups. This leads to breaking a general trend of mammalian evolution: a reversal of Williston's law (reduction in bone number) and the development of new accessory cranial bones. Slowing cranial development rates explain these trends, and feeding mechanics may be a driver of decreasing suture ossification in cetaceans.

Cetaceans (whales, dolphins and porpoises) are an important mammalian group. In their evolutionary origin they are nested within terrestrial even-hoofed mammals (artiodactyls)[1,2], but underwent deep transformations in anatomy aligned with their adaptations to life in water[3,4]. Cetaceans have a highly transformed skull[5,6], and are also known for heterochronies in their evolution[7–10] that certainly affect cranial development and ossification[9–14]. Cranial ossification patterns have been reported for prenatal and early postnatal stages for both major lineages of extant cetaceans, toothed whales[15–19] and baleen whales[20–23]. Less data is available on later stages of cetacean skull ossification, such as suture closure during the lifetime, and most existing data originates from several studies of small toothed whales[9,24–27]. Meanwhile, unusual details of cranial ontogeny have been reported for cetaceans, such as the open fontanelles in adult beluga whales *Dephinapterus leucas*[28]. Homology of cetacean cranial bones revealed through heterochrony has also been discussed in the evolutionary context of the extinct toothed whale *Olympicetus*[29]. Overall, significant attention in cetacean studies has been given to multiple manifestations of paedomorphosis, in its evolutionary sense[30], which may reflect delayed ossification[8,9]. However, disparity of cetacean heterochronies and their effects on cranial morphology is evident[7,10,11]. Also, the same evolutionary and developmental event, such as a prolonged growth, can be interpreted in different ways depending on the analytical framework[31]. Therefore, quantitative phylogenetically-based descriptions of such events are important for a full understanding of heterochronies.

The characteristics of suture ossification events is a good marker for evolutionary heterochronies[32–34]. The skull of modern mammals, with their morphological disparity, often shows a conservative pattern of ossification events, with a few general features[35]. However, some patterns of pre- and post-natal ossification of bones and skull sutures show differences across mammalian phylogenetic lineages[36–38]. Recent studies uncovered homologies of: the mammalian cranial ossifications[36]; developmental sequences of mammalian ossifications[39] and sutures development[40]; variation in suture ossification rate among terrestrial artiodactyls[41]; evolution of cranial suture ossification and its link to cranial morphology across marsupial and placental mammals[42]; or developmental aspects of cranial suture fusion[43]; as well as specific aspects of evolution of cetacean cranial sutures[13,29]; and,

Schmalhausen Institute of Zoology, Kyiv, Ukraine. email: valeriia.dccclxiv@gmail.com; pavelgoldin412@gmail.com

interestingly, the problem of homology of variable elements in the cetacean cranium that highlights the presence and evolutionary significance of such unusual ossifications in cetaceans[29].

Here, we analyze patterns of ossification of cranial sutures and presence of accessory bony elements for a broad sample of modern cetaceans and terrestrial artiodactyls. Specifically, we aim to track general evolutionary trends in cranial ossification and to examine the possible correlation between the total rate of ossification and the presence of accessory bones in the cranium. By comparing cetaceans and their closest evolutionarily related group - terrestrial artiodactyls, we first attempt to identify potential shifts in the rate of suture closure associated with cetacean evolution, and then assess whether significant evolutionary modifications has occured. Also, we briefly summarize available knowledge on accessory bony elements in cetartiodactyl cranium and report several of them for the first time.

Results

Postnatal suture ossification is low in cetaceans and shows strong phylogenetic signal

We assessed states and patterns of suture ossification of 25 suitably visible cranial sutures in skulls of physically mature or ontogenetically old specimens of 47 species of extant cetaceans (members of families Balaenidae, Neobalaenidae, Balaenopteridae, Physeteridae, Kogiidae, Platanistidae, Ziphiidae, Iniidae, Pontoporiidae, Monodontidae, Phocoenidae and Delphinidae) and 15 outgroup species of terrestrial even-toed ungulates (members of Hippopotamidae, Bovidae, Tragulidae, Cervidae, Giraffidae, Suidae and Camelidae) and calculated an average number and total rate of fully ossified sutures. The statistics on each suture for all studied species are shown (Supplementary Table S2).

In overall cetaceans showed fewer fully ossified sutures (2–17) than terrestrial artiodactyls (11–23). Significance of this difference was confirmed by independent samples t-test ($p < 0.01$). Also, the number of sutures ossifying in odontocetes (6–17) was, in overall, greater than in living mysticetes (2–4) (Mann–Whitney U test, $p < 0.01$). Among odontocetes, the most mature crania, in terms of ossification, were observed in beaked whales (Ziphiidae) (14–17), while the least mature were found in sperm whales (Physeteroidea) (6–8) and porpoises (Phocoenidae) (6–9). Among terrestrial artiodactyls, the most mature crania were found in hippopotamuses (Hippopotamidae) (19–23) while the least mature were in deer (Cervidae) (11–16), consistent with the findings of Bärmann and Sánchez-Villagra[41], but with different scores. Among the sutures which often ossify in cetaceans, there are occipital and basicranial sutures and later ossifying sutures of the cranial vault and, sometimes, of the maxilla and other bones (Supplementary Table S2). Both Bloomberg's K and Pagel's λ indicated consistently strong phylogenetic signal ($K = 2.1$, $\lambda = 1$, $p < 0.01$), thus showing more similarity in ossification patterns between closely related species.

Further evidence for delay in ossification: accessory bones, Fontanelles and clefts

There were a few accessory ossification centers in the cetacean skull vault situated between the parietal, interparietal (when it was separate), supraoccipital and exoccipital bones (Table 1). Overall, six types of accessory bones were identified, of which at most two can be hypothetically classified as wormian bones. In this work, we refer to wormian bones as typically small, often unilateral (or centrally situated) supernumerary bones formed along sutures or within fontanelles[44]. We also identified a bilateral *de novo* ossification in the skull of *Muntiacus muntjak*, which is, to our knowledge, the first recorded case of an accessory bone (other than a wormian bone) in non-cetacean artiodactyls (Table 1).

A short description of the accessory elements (full description, Supplementary Material S2).

Postparietal or anterior median interparietal (AMI) bone[29,36] is mostly found in foetuses or neonates of modern cetaceans; in snubfin dolphins *Orcaella* spp. (Fig. 1b); and argued to be a novel element for crown Cetacea[29].

Bone	Interpretation	Species (this study)	Species (previous studies, references in parentheses)
Postparietal or anterior median interparietal (AMI) (interparietal)	Postparietal or anterior median interparietal (AMI)	*Orcaella* spp.	*Orcaella* spp.[64], *Olimpicetus* spp.[29]
Tabular or bilateral posterior interparietal (PI) (lateral interparietal)	Tabular or posterior interparietal (PI)	*Lagenorphynchus albirostris*, *Tursiops truncatus*, *Phocoena phocoena*	*Phocoena phocoena* (foetus)[64], *Olimpicetus* spp.[29]
Unnamed bones posterior to the lambdoid suture	*De novo* ossification, tabular or wormian	*Neophocaena asiaeorientalis*, *Phocoena spinnipinnis*, *Phocoena sinus*, *Phocoena phocoena* (juv.), *Lagenorhynchus albirostris* (juv.), *Tursiops truncatus* (juv.)	
Occipital fontanellar bones	*De novo* ossification or posttemporal	Phocoenidae and Monodontidae, *Lagenorphynchus albirostris*, *Lissodelphis borealis*, *Tursiops truncatus*, *Grampus griseus*	Phocoenidae[25], Monodontidae[28]
Composite element including the unnamed bone and the fontanelle-replacing ossification center	*De novo* ossification	*Phocoena phocoena*, *Phocoena sinus*, *Grampus griseus*, *Neophocaena asiaeorientalis* *Muntiacus muntjak*	
Anterior fontanellar wormian bone	Preinterparietal	*Physeter catodon* (foetus)	*Orcaella* spp.[64], *Phocoena phocoena* (foetus)[65]
Cleft in the parietal bone	Posterior parietal (the same as postparietal)	*Phocoena spinnipinnis*, *Phocoena phocoena*, *Phocoena sinus*	
Squamosal cleft	Supratemporal	*Inia geoffrensis*, *Delphinapterus leucas*, *Orcinus orca*	Mysticeti[20,66]

Table 1. Accessory bones in a cetartiodactyl skull.

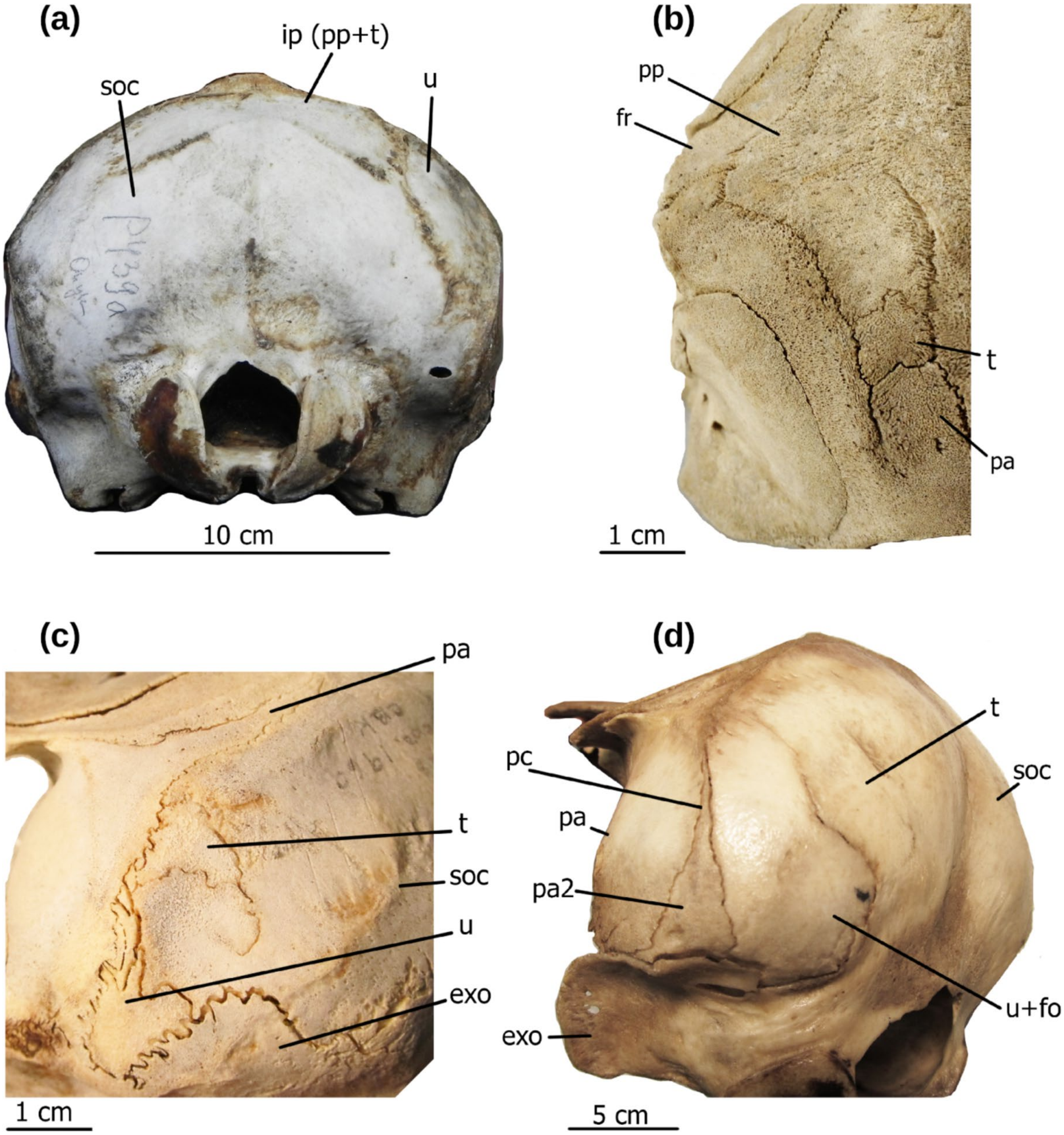

Fig. 1. **Accessory bones and clefts in cetacean cranium.** **(a)** Sutures of interparietal and unnamed bones, the bottlenose dolphin *Tursiops truncatus* TNU P-439a; **(b)** Postparietal (or anterior median interparietal) and tabular (or posterior interparietal) bones, *Orcaella brevirostris* MCZ 21,929; **(c)** Tabular and unnamed bones on the occiput, the Burmeister's porpoise *Phocoena spinnipinnis* MVZ 139,501; **(d)** novel combination of the skull vault bones and clefts (see ***Clefts in the skull vault bones***), vaquita *Phocoena sinus* MVZ 120,934. **Abbreviations**: exo, exoccipital; fo, fontanellar; fr, frontal; ip, interparietal; p.a., parietal; pa2, posterior parietal; pp, postparietal; soc, supraoccipital; t, tabular; u, unnamed bone.

Tabular or bilateral posterior interparietals (PIs)(lateral interparietal) bones[29,36]: paired bones lateral to the postparietal. In this study, found in adult *Orcaella* spp. (Fig. 1b), and their traces were also noted in other species (Fig. 1a, c), as well as previously reported[45] and argued to be homologous to the interparietal bones of terrestrial artiodactyls[29].

Unnamed bones posterior to the lambdoid suture (Fig. 1c), bilateral elements found in adult specimens of three species of porpoises (Phocoenidae) and in neonates of other taxa.

Occipital fontanelles and ossifications in them[15]: the bilaterally symmetrical fontanelles between the exoccipital and supraoccipital and *de novo* ossifying dermal bones in them were confirmed by our study in numerous species. The open fontanelles were found in adult dolphins, porpoises, belugas and narwhals. Also, in three species of porpoises, the Risso's dolphin and notably, in muntjac deer, we found a bilateral composite novel element that included unnamed bone and fontanelle-replacing ossification center (Fig. S2a-d).

Preinterparietal[46,47]: a single anterior fontanellar wormian bone within the frontal-frontal suture; was found only in a foetus of the sperm whale but reported for other taxa[45,48].

Clefts in the skull vault bones were noted in adult porpoises. Moreover, there is a case of *Phocoena sinus* MVZ 120,934 (Fig. 1d) having a combination of all the traits described above: it had traces of tabular bone sutures, an unnamed bone, ventral to it, and fused with the occipital fontanelle ossification center and a cleft in the parietal bone crossing the whole bone and, thus, delimiting an ossification center anterior to the lambdoid suture.

Similarly to the results for total rates of suture ossification, we obtained high phylogenetic signal estimates for the presence of accessory bones or clefts, with D = 0.115 and probability of E(D) resulting from Brownian phylogenetic structure = 0.408.

Ancestral state reconstructions

The **ancestral state reconstructions (ASR)** results for total suture closure rate and the presence of accessory bones were mapped on the phylogenetic tree and visualized (Fig. 2). When comparing two Mk models for accessory bones, we obtained higher weight for the all-rates-different (ARD) model in which the back-and-forth transitions between character states can differ (ARD = 0.737, ER = 0.263).

In general, there was an uncertainty in character states observed closer to the root, which can be improved by incorporation of fossil taxa. However, we can clearly observe several key features. Firstly, the pattern of similarity between related species for both continuous and binary traits confirms the strong phylogenetic signal shown above. There is a possibility that accessory bones or clefts evolved at the base of the crown cetacean clade (in agreement with Roston et al.[29]), and we can confidently assign them to the ancestral nodes of Mysticeti and Delphinoidea. No accessory bones/clefts were found in Balaenidae, Kogiidae, Platanistidae, Ziphiidae and a part of Delphinidae, although in Ziphiidae and Platanistidae the "secondary loss" may be plausible because of the high uncertainties in their basal nodes.

The rate of evolution of ossification slows down

The best fitted model of evolution was the simple BM model (~ 58%) with EB and OU getting almost equal weights (23% and 19%). The evorates model suggests the general slowing of evolution of rates of total sutures

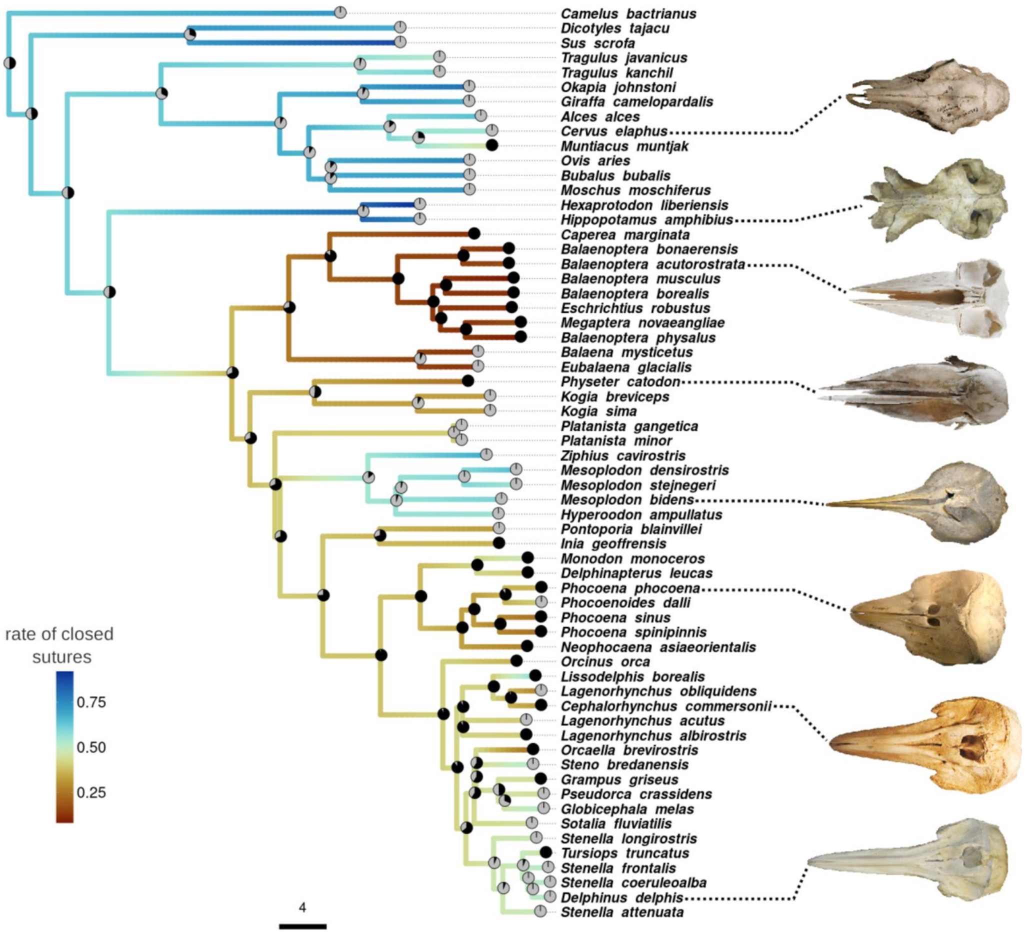

Fig. 2. Ancestral state reconstructions for the rates of ossification and presence of accessory bones or clefts. Continuous trait (ossification rates) is represented as a colour gradient along the branches. The probabilities for presence of accessory bones or clefts are mapped on the tree nodes as pie charts.

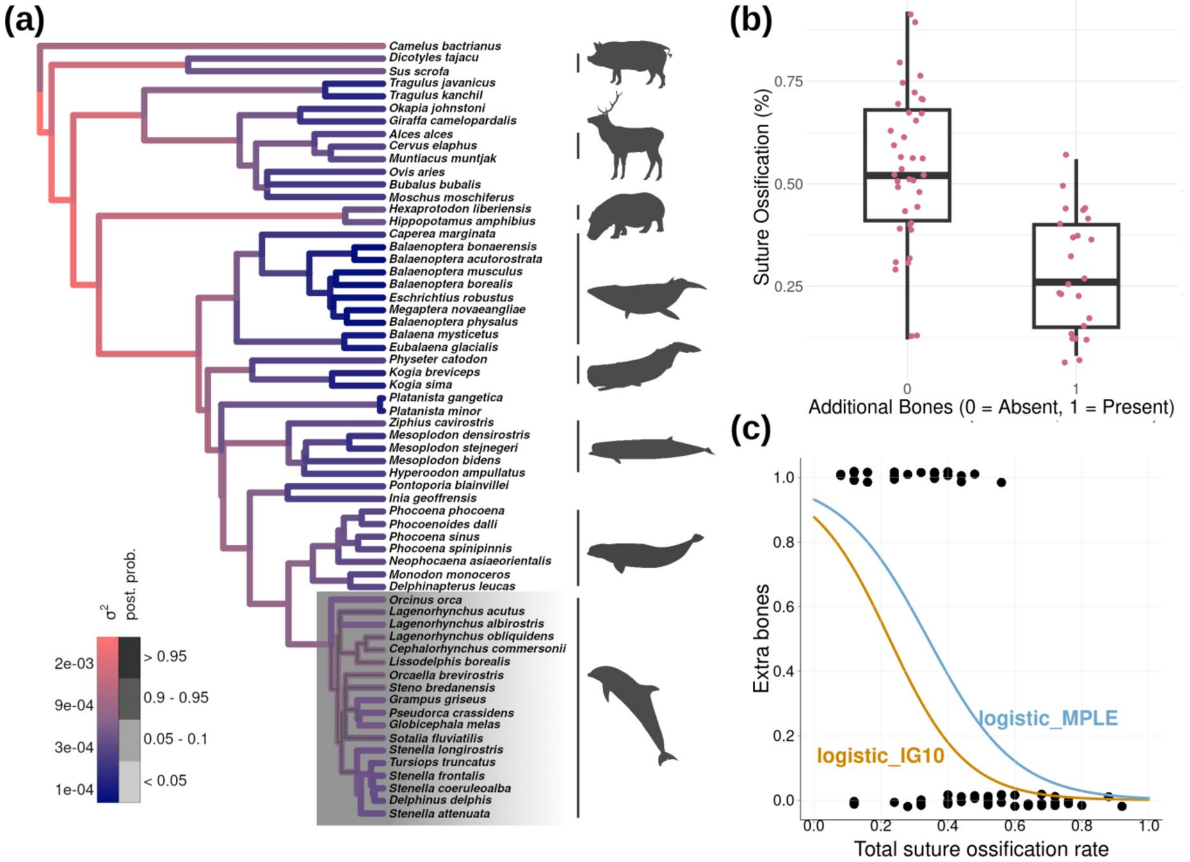

Fig. 3. **The results of evolutionary rates analysis and correlation of accessory bones with the total rate of ossified sutures.** **(a)** The results of evorates model for the rates of evolution of suture ossification. Branch colors represent median posterior estimates of lineagewise rates. The inset colors ranging from light to dark grey represent the PP that rate is anomalously fast according to its rate deviation; **(b)** boxplots, showing the distribution of suture ossification values for species having and lacking accessory bones or clefts; **(c)** phylogenetic logistic regression curves predicting the presence or absence of accessory bones or clefts as a function of the total rate of suture ossification. Two methods (logistic_MPLE and logistic_IG10) were used.

ossification (two-tailed p-value = 0.01). The calculated rates are declining by approximately 6% every million years. The average rate variance was approximately 0.04 per million years (CI: 0.002–0.27; SD = 1.11).

There were also several lineages for which rate of evolution was higher than average with marginally significant posterior probability of 0.9 (Fig. 3a). These lineages include ancestral branches of subfamilies Delphininae, Lissodelphininae and Globicephalinae and species *Orcaella brevirostris*, *Steno bredanensis*, *Sotalia fluviatilis*, *Lissodelphis borealis*, *Lagenorhynchus obliquidens* and *Cephalorhynchus commersonii.*

Although analyses using PhylogeneticEM and BAMM did not find any significant shifts in the rates of suture ossification evolution, BAMM highlighted several species with relatively accelerated rates (Fig. S2). These species, *Orcaella brevirostris* and members of subfamily Lissodelphininae (*Lissodelphis borealis*, *Lagenorhynchus obliquidens* and *Cephalorhynchus commersonii*) were also identified by the evorates method, which provides additional confidence in recognizing them as lineages with increased rates of suture ossification evolution.

Orcaella brevirostris was also shown to be among the species with the least developed suture fusion but most accelerated evolutionary rate of total suture ossification. Lissodelphininae also exhibited relatively accelerated rates of evolution, with its members showing contrasting states. The number of ossified sutures varied from 7 in *Lagenorhynchus obliquidens* and 8 in *Cephalorhynchus commersonii* to 14 in *Lissodelphis borealis*. What we observe here is the disparity in ontogeny trajectories, as *Lissodelphis borealis* has a larger skull with a longer rostrum, while the cranium of *C. commersonii* is smaller with a shorter and caudally displaced rostrum[49].

Correlation between the total rate of ossification and presence of accessory elements

The presence of accessory bones mostly coincides with lower values for the rate of suture ossification (Figs. 2 and 3b). Phylogenetic logistic regression was used to check possible correlations (Fig. 3c). The analysis showed significant associations between total rates of ossification and presence of accessory bones or clefts (logistic_MPLE: $p = 0.0007$, logistic_IG10: $p = 0.0001$). Thus, species with less ossified skulls are more likely to have accessory bones or clefts than those with a greater proportion of fully ossified sutures.

The results for clefts alone were also significant, with similar statistics (logistic_MPLE: $p = 0.0007$; logistic_IG10: $p = 0.0004$). However, the analysis that focused on the counts of accessory bones did not yield statistically significant values, with only the logistic_MPLE method providing a marginally significant result (logistic_MPLE: $p = 0.084$, logistic_IG10: $p = 0.13$).

Discussion

Interpretation of homology of newly identified accessory bones and clefts

Unnamed bones posterior to the lambdoid suture could represent a *de novo* ossification center, similar to intrasutural wormian bones, best studied in humans[44]. However, the unnamed bones are not exactly situated within the suture and, thus, cannot be identified as wormian. Also, they are larger than a typical wormian bone. Moreover, consistent presence of large bilateral bones in the same position across several taxa requires an evolutionary explanation. Also, they could be possibly interpreted as two or more **tabular bones**, which can be presented at each side[29]. Third, a posterolateral element bordering the parietal and squamosal can be the bone homologous to the supratemporal of reptiles. However, in cetaceans there are other structures in the temporal region better matching the position of the supratemporal (see ***The supratemporal bone and squamosal cleft***).

The most consistent interpretation of the ***occipital fontanellar ossification*** is that it is a *de novo* ossification center which ossifies latterly as a dermal bone and replaces the fontanelle. This fontanelle is not homologous to mastoid fontanelle of mammals, although it is confluent with the latter one during the foetal development[15,19]. However, it corresponds to the posttemporal fenestra of early amniotes[50], a structure which is reduced and present as the posttemporal foramen in such mammals as *Vintana* and modern Xenarthra[51]. In this case, a separate ossification center replacing this fenestra hypothetically may be the **posttemporal bone**, which is largely lost among the tetrapods.

The ***Parietal cleft*** shows that two ossification centers are found for each parietal bone, and the second center is **the posterior parietal (postparietal) bone**. Dual ossification for the parietal is a rare state for amniotes, and it refers to the discussion on interpretations of their skull development: at least, it can be found in several lineages of extinct reptiles, in some of which it could be secondarily acquired[52]. Therefore, co-existence of two ossification centers of the parietal bone in cetaceans can be suggested as a plesiomorphy.

The supratemporal bone and squamosal cleft. The squamosal cleft, a deep fissure dividing the anterior portion of the squamous area, is a characteristic feature of a few mysticete lineages (Fig. S3b, d,e): rorquals Balaenopteridae, gray whales Eschrichtiidae, pygmy right whales Neobalaenidae, and a few extinct Neogene groups[20,53]. However, the squamosal cleft develops not only in mysticetes: the short bilaterally symmetrical clefts are rarely found in odontocetes – juvenile and adult specimens of the *Inia geoffrensis*, *Delphinapterus leucas* and the killer whale *Orcinus orca* (Fig. S2c, S3c). Moreover, in mysticetes, the clefts vary in extension, and in foetal skulls of the gray whale, *Eschrictius robustus*, the squamosal cleft clearly divides the temporal region into two bones, bordering a separate ossification center in the dorsal part of the squama (Fig. S3d-e).

Dual origin of the squamosal bone in cetaceans can be suggested from published embryological studies: two ossification centers are found in the squamosal of the humpback whale, *Megaptera novaeangliae*, after the Carnegie stage 23[22] and the spotted dolphin, *Stenella attenuata*, at the Carnegie stage 21/22[19]. This is unusual for mammals; however, the dual nature of the developing squamosal is common in amphibians[54] suggesting that the bone dorsal to the squamosal *s.s.* is the **supratemporal bone**, seen also in extinct reptiles[55].

Therefore, among the accessory elements in the skull of whales, dolphins and terrestrial even-hoofed mammals there may be bones which can normally be found in living or extinct reptiles, present in other mammals as an anomaly.

It is also worth noting the absence of accessory elements in members of the Ziphiidae and Kogiidae families, although a fontanellar wormian bone is present in fetal P. macrocephalus. This absence may indicate a secondary loss, but tracing its occurrence in the past remains challenging. At least, no evidence of accessory bones has been found in extinct ziphiids and physeteroids known to date[56,57].

Dual origins of skull ossification in cetaceans

The dual origin of the mammalian skull vault was found in embryological studies[58–60]: occipital, parietal and tabular bones derive from mesoderm, whereas the postparietal, frontal and squamosal derive from the neural crest cells (NCC). The decrease in activity of the NCC has been suggested as a mechanism causing numerous effects delaying the development of the facial skull and, thus, underlying the evolutionary heterochrony. It could contribute to the evolution of various paedomorphic phenotypes retaining juvenile traits at adult age[61,62], and, with some reservations, to the overall diversity of mammalian facial skulls[63]. In fact, slowing development rate can explain many aberrant features of cetacean skulls. Therefore, both the presence of accessory bones and low rate of cranial sutures' ossification can be interpreted as manifestations of paedomorphosis.

In fact, most of the sutures between the bones, which derive from the NCC (except a few sutures of frontals and maxillae), do not complete ossification in cetaceans (Fig. S1), as well as in the least cranially mature terrestrial artiodactyls - deer. However, the cetacean-specific traits in the decreased skull ossification are not limited to the NCC-derived skull region, in baleen whales they involve all the cranial regions and, therefore, cannot be explained solely by the neural crest development. Moreover, many morphological innovations found here derive from mesoderm rather than the neural crest[60]. Thus, the heterochronies in evolution of the cetacean skull are likely caused by a more complex mechanism than sole changes in the neural crest development.

Delayed ossification of sutures as a key to cetacean skull flexibility and feeding mechanisms

A possible function of the delayed suture ossification in cetaceans is the prolonged growth which is accompanied with skull telescoping and rostral elongation and is associated with feeding adaptations[11,13,23]. Another important function of the delay or stop in cranial sutures' ossification is the cranial kinesis (bone movement) for suction or gulp feeding[64], common for many vertebrates but rare for mammals[65,66]. Importantly, all the extant and most of the extinct baleen whales, including the earliest ones, have some evidence for cranial kinesis[67–69]. For odontocetes, cranial kinesis has not been reported before but can be hypothetically suggested. For example, porpoises (Phocoenidae) and pygmy sperm whales (Kogiidae) have unusually shaped or reduced teeth, the short and wide rostrum and blunt mandibles associated with suction feeding[70]. Their cranial and, especially, rostral sutures are retarded in fusion, and the latter ones usually do not fuse during their lifetime (Yoshida et al.[25]; Galatius[9]: Supplemental data S3). Functionally, the delayed fusion is partly explained by prolonged widening of the rostrum in porpoises[71]. This is also the precondition for kinesis of rostral elements during the feeding act: loose fusion of rostral elements with each other and with frontal bones, especially in early life, enables cranial kinesis and allows the encircling gape needed for suction feeding[67]. Moreover, the cranial adaptations for suction feeding hypothetically evolved before divergence of cetaceans into mysticete and odontocete lineages and, possibly, were exaptations resulting from other evolutionary processes[72,73]. Also, paedomorphic phenotypes evolving during the history of toothed whales are mostly associated with suction feeding[74]. In this regard, the suction feeding mammalian phenotype is obviously paedomorphic, since the milk suckling mammals by definition are obligate suction feeders in their early postnatal ontogeny that indirectly implies some cranial or rostral kinesis[75].

Meanwhile, there are differences between living baleen and toothed whales in patterns of postnatal ossification of cranial sutures. In mysticetes, the occipital region early and rapidly ossifies[21,23] without forming accessory bones, and the rest of the sutures, including all the facial and rostral area, do not undergo postnatal ossification at all. Also, innovations in the mysticete skull, like the squamosal cleft, appear mostly in the temporal region. In odontocetes a greater number of sutures gradually ossify during their lifetime, and ossification is slower and lasts longer[9], with forming accessory bones in the skull vault.

Shared trend in suture ossification and accessory bones in cetaceans and terrestrial artiodactyls

Along with phylogenetic signals in suture ossification, several parallelisms are found among cetacean and terrestrial artiodactyl lineages. The general suture ossification pattern observed in cetaceans, and mostly manifesting itself in the occipital and basicranial region, is similar to that in deer[38,40,41]. Also, consistently low degree of ossification is equally found in cetaceans and deer. Interestingly, accessory cranial bones were found in a member of the deer family with the least ossified sutures, the muntjac deer, supporting the correlation between ossification patterns across the cetartiodactyl clade. It may be promising to additionally explore the presence of accessory bones in the other deer spp with the least ossified cranial sutures (e.g. *Capreolus* spp.) and the chevrotains (Tragulidae family), also distinguished by their relatively low cranial ossification. This shared trend between cetaceans and terrestrial artiodactyls further suggests common developmental pathways.

Moreover, the correlation between suture ossification and presence of accessory bones uncovers an interesting effect in mammalian evolution. The evolution of the mammalian skull generally follows Williston's law[76,77], which entails the reduction in the number of bones, partly driven by heterochrony—an earlier onset of ossification events and the fusion of ossification centers. So, in this study it is shown how this law can be reversed: decreasing the rate of cranial suture ossification may be coupled with the presence of accessory bones and clefts, the process that can be driven by another heterochrony. For example, *Orcaella* and *Neophocaena*, which exhibit some of the accessory bones described here, have been recognized as particularly paedomorphic morphotypes[7].

Importantly, the bone elements discussed here have different developmental histories. For example, the interparietal bone(s) in mammals form from multiple, at least four, ossification centers, which fuse over time. Thus, the median interparietals and lateral interparietals may be homologous to the postparietal and the tabular bones of ancestral forms[36]. In cetaceans these may be added by a single median novel element[29]. Independent from interpretations of homology of this bone complex, it can be concluded that its multiple elements reveal themselves in cetaceans. On the other hand, sutural bones such as wormian and bones forming in fontanelles are often treated as individual variations[78]. In humans they are often associated with increased cranial suture width due to conditions such as hydrocephaly or craniosynostosis[44]. Therefore, it is the opposite trend to what we observed in cetaceans and deer, and it also suggests that cetartiodactyl accessory bones are mostly not wormian and therefore may be considered as evolutionary innovations in a broader sense rather than developmental abnormalities.

Environmental influences may still also play a role in forming the wormian bones[79], and epigenetic factors, as well as complex congenital anomalies, cannot be fully ruled out in some of our cases (e.g., an inbred population of the vaquita *Phocoena sinus*). However, they cannot explain the whole diversity of correlated consistent morphological effects and phylogenetic signals across a broad range of evolutionary lineages.

In conclusion, these findings suggest a decrease in cranial suture ossification at the latest stages, an unusual effect found during the postnatal ontogeny in several cetartiodactyl lineages and peaking in some of cetaceans. This leads to breaking a general trend of mammalian evolution: the reversal of Williston's law and the development of multiple types of accessory cranial bones. Further studies may explore these innovations and their evolution, development and function, as well as functional aspects of decreasing cranial suture ossification in mammals. Investigating the patterns of suture ossification throughout ontogeny could provide important insights into the evolution of skull ossification and help clarify some questions about the origin and development of accessory elements posed in this study. This represents an intriguing direction for future research.

Materials and methods

Morphological dataset and phylogenetic tree Preparation

For this study, 395 skulls of 47 taxa of living cetaceans and 33 skulls of 15 species of terrestrial artiodactyls were visually examined for the state of postnatal cranial ossification in 25 sutures, best characterizing the cetacean skull (data on the sample and the list of sutures are provided in: Supplementary tables S1, S2, Supplementary material Fig. 1). Anatomical terminology for cranial osteology followed Mead and Fordyce[6]. The ontogenetically oldest specimens were chosen for measuring the maximum rates of cranial suture ossification, based on epiphyseal fusion of vertebral column, tooth wear, development of crests for muscle attachment and collection records on age and body size. Suture ossification was estimated, and the presence of full closure or obliteration at some part of a suture was used here as the indicator of full ossification. Such a criterion was chosen as the best reflection of the cetacean specific morphology, as far as even a partial obliteration means that the suture would be fully fixed, and the contacting bones would be immobile. This scoring differs from the protocol by Wilson and Sánchez-Villagra[80] (as well as the selected sutures) and results in consistently higher scores, as compared to Bärmann and Sánchez-Villagra[41]. The maximum values found per species were used for the quantitative analysis. To assess the total rate of ossification, the number of the fully ossified sutures were converted to decimals from 0 to 1, where the maximum possible number of closed sutures = 1 and opened sutures = 0. Presence of accessory bony elements and clefts, which potentially could indicate a trace from a partially fused element or show an innovation, was visually assessed and recorded for each specimen. For more information on such elements and their earlier developmental stages, in addition to the most adult specimens, we also analysed juvenile, neonate and foetal skulls of several species (Supplementary Table S1). Homology of bones, which have not been found in the other mammals, was assessed from their position in relation to adjoining bones, following general regularities found in vertebrates[50,52,54,81], considering reviews by Wegner[46] and Koyabu et al.[36]. We used a time-calibrated phylogeny downloaded from the TimeTree database v.5[82] for all our analyses.

Comparison of the number of fully ossified sutures between different taxa

The comparison was done for two cases - between cetaceans and terrestrial artiodactyls and between odontocetes and mysticetes.

To compare the number of closed sutures, we first made a normality assessment using the Shapiro-Wilk test on both groups' suture closure data. If the data in both groups were normally distributed we used an independent samples t-test to compare the mean number of closed sutures, otherwise we performed a Mann–Whitney U test.

Phylogenetic signal

Two measures, Blomberg's K[83] and Pagel's λ[84], were calculated using the phylosig function implemented in phytools library[85] in R.

To estimate phylogenetic signal for binary traits, the D statistic[86] was used. It was calculated in phylo.d function in R package *caper*[87]. A D-measure usually can take values between 0 (phylogenetically conserved under the Brownian model pattern) and 1 (phylogenetically random distribution).

Ancestral state reconstructions (ASRs)

To reconstruct the ancestral states for the total rate of sutures ossification (a continuous trait) we used fastAnc function in phytools[85]. For the presence of accessory bones (binary trait) we compared the equal rates model (ER) and the all-rates-different (ARD) model. Mk and extended Mk character transition models were fitted using the fitMk function. The best model was selected using the Akaike information criterion (AIC). ASRs were then constructed for the best models using 100 maps generated by stochastic character mapping (SIMMAP) in phytools. Posterior probabilities from stochastic mapping for binary traits were plotted on phylogenetic trees using the ggtree package[88].

Estimating the rates of evolution and rates shifts of total ossification

First, we used fitContinuous() function in R package geiger[89] to fit several macroevolutionary models to our data on the rate of suture ossification. We compared four models of character evolution - Brownian motion (BM), Early burst (EB) and Ornstein-Uhlenbeck (OU) and white noise (WN) using Akaike information criterion (AIC) values.

We then used the *evorates* package[90] in R to model the evolution of rates of suture ossification and assess possible heterogeneity in rates. Four Hamiltonian Monte Carlo (HMC) chains consisting of 4000 iterations were run and the first 2000 iterations were discarded as burn-in. After check for convergence using *evorates* functions "check.ess" and "check.mix", chains were combined for a total of 8000 HMC samples.

We also implemented two additional methods to check if there are any shifts of evolutionary rates of ossification.

First, we used BAMM (Bayesian analysis of macroevolutionary mixtures)[91] that detects distinct shift configurations and their frequencies. We estimated betaInitPrior and betaShiftPrior parameters using the setBAMMpriors function of BAMMtools v2.1.6, and ran our model for 5 000 000 generations of MCMC (Markov chain Monte Carlo) sampling. The outputs of BAMM were then post-processed by BAMMtools, with the convergence, evolutionary rates of ossification and the best shift configuration extracted and visualised.

Another method used was PhylogeneticEM[92], that utilises an Expectation–Maximization (EM) algorithm for a maximum likelihood estimation of the shift positions. This method is available as an R package PhylogeneticEM and mostly used for multiple correlated traits, although it also can be applied to the single continuous trait as in our case.

Correlation between the total rate of ossification and presence of accessory bones or clefts

To test whether the presence of accessory elements correlates with the rates of suture ossification we performed phylogenetic logistic regression implemented as a phyloglm function in the R package phylolm[93,94]. The presence or absence of accessory elements was coded as 1 or 0 and used as a binary response variable. We used both logistic MPLE and logistic_IG10 methods to estimate the model and performed 1000 independent bootstrap replicates. We also examined three scenarios: one that combined the numbers of accessory bones and clefts, another that analysed only the presence of accessory bones but not clefts, and, finally, the presence of clefts only.

Data availability

The dataset used in the study is available in the Supplementary Material.

Received: 16 September 2024; Accepted: 21 March 2025

References

1. McGowen, M. R. et al. Phylogenomic resolution of the cetacean tree of life using target sequence capture. *Syst. Biol.* **69** (3), 479–501. https://doi.org/10.1093/sysbio/syz068 (2020).
2. Thewissen, J. G. M., Williams, E. M., Roe, L. J. & Hussain, S. T. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature* **413**, 277–281. https://doi.org/10.1038/35095005 (2001).
3. Geisler, J. H. & Sanders, A. E. Morphological evidence for the phylogeny of cetacea. *J. Mamm. Evol.* **10**, 23–129. https://doi.org/10.1023/A:1025552007291 (2003).
4. Gatesy, J. et al. A phylogenetic blueprint for a modern Whale. *Mol. Phylogenet Evol.* **66** (2), 479–506. https://doi.org/10.1016/j.ympev.2012.10.012 (2013).
5. Miller, G. S. The telescoping of the cetacean skull (with eight plates). *Smithson. Misc Coll.* **76** (5), 1–70 (1923).
6. Mead, J. G. & Fordyce, R. E. The Therian skull: a lexicon with emphasis on the odontocetes. *Smithson. Contrib. Zool.* **627**, 1–249. https://doi.org/10.5479/si.00810282.627 (2009).
7. Fordyce, E. & de Muizon, C. Evolutionary history of cetaceans: a review in *Secondary adaptation of tetrapods to life in water* (eds, Mazin J.-M.& de Buffrenil V.) 169–233Proc. Int. Meeting, Poitiers, (2001).
8. Mellor, L., Cooper, L. N., Torre, J. & Brownell, R. L. Paedomorphic ossification in porpoises with an emphasis on the vaquita *Phocoena sinus*. *Aquat. Mamm.* **35**, 193–202. https://doi.org/10.1578/AM.35.2.2009.193 (2009).
9. Galatius, A. Paedomorphosis in two small species of toothed whales (Odontoceti): how and why? *Biol. J. Linn. Soc.* **99** (2), 278–295. https://doi.org/10.1111/j.1095-8312.2009.01357.x (2010).
10. Lanzetti, A., Portela-Miguez, R., Fernandez, V. & Goswami, A. Testing heterochrony: connecting skull shape ontogeny and evolution of feeding adaptations in baleen whales. *Evol. Dev.* **25** (4–5), 257–273. https://doi.org/10.1111/ede.12447 (2023).
11. Tsai, C. H. & Fordyce, R. E. Disparate heterochronic processes in Baleen Whale evolution. *Evol. Biol.* **41**, 299–307. https://doi.org/10.1007/s11692-014-9269-4 (2014).
12. Tsai, C. H. & Fordyce, R. E. Juvenile morphology in baleen whale phylogeny. *Naturwissenschaften* **101**, 765–769. https://doi.org/10.1007/s00114-014-1216-9 (2014).
13. Roston, R. A. & Roth, V. L. Cetacean skull telescoping brings evolution of cranial sutures into focus. *Anat. Rec.* **302** (7), 1055–1073. https://doi.org/10.1002/ar.24079 (2019).
14. Coombs, E. J. et al. The tempo of cetacean cranial evolution. *Curr. Biol.* 32 (10), e4, 2233–2247; (2022). https://doi.org/10.1016/j.cub.2022.04.060
15. Eales, N. B. The skull of the foetal Narwhal, *Monodon monoceros* L. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **235** (621), 1–33. https://doi.org/10.1098/rstb.1950.0013 (1950).
16. Kuzmin, A. A. Embryogenesis of the osseous skull of the sperm whale (*Physeter macrocephalus* Linnaeus, 1758). *Investig Cetacea.* **7**, 187–202 (1976).
17. Klima, M. Cetacean phylogeny and systematics based on the morphogenesis of the cetacean skull. *Aquat. Mamm.* **21**, 79–89 (1995).
18. Rauschmann, M. A., Huggenberger, S., Kossatz, L. S. & Oelschläger, H. H. A. Head morphology in perinatal dolphins: A window into phylogeny and ontogeny. *J. Morphol.* **267** (11), 1295–1315. https://doi.org/10.1002/jmor.10477 (2006).
19. Moran, M. M., Nummela, S. & Thewissen, J. G. M. Development of the skull of the Pantropical spotted dolphin (*Stenella attenuata*). *Anat. Rec.* **294** (10), 1743–1756 (2011).
20. Ridewood, W. G. Observations on the skull in fœtal specimens of whales of the genera megaptera and balænoptera. *Philos. Trans. R Soc. Lond. Ser. B Contain Pap Biol. Character.* **211**, 209–272. https://doi.org/10.1098/rstb.1923.0005 (1923).
21. Walsh, B. M. & Berta, A. Occipital ossification of balaenopteroid Mysticetes. *Anat. Rec.* **294** (3), 391–398. https://doi.org/10.1002/ar.21340 (2011).
22. Hampe, O., Franke, H., Hipsley, C. A., Kardjilov, N. & Müller, J. Prenatal cranial ossification of the humpback whale (*Megaptera novaeangliae*). *J. Morphol.* **276** (5), 564–582. https://doi.org/10.1002/jmor.20367 (2015).
23. Lanzetti, A. Prenatal developmental sequence of the skull of minke whales and its implications for the evolution of Mysticetes and the teeth-to-baleen transition. *J. Anat.* **235** (4), 725–748. https://doi.org/10.1111/joa.13029 (2019).
24. Perrin, W. F. Variation of spotted and spinner porpoise (genus *Stenella*) in the Eastern Pacific and Hawaii. *Bull. Scripps Institution Oceanogr.* **21**, 1–206 (1975).
25. Yoshida, H., Shirakihara, M., Takemura, A. & Shirakihara, K. Development, sexual dimorphism, and individual variation in the skeleton of the finless porpoise, *Neophocaena phocaenoides*, in the coastal waters of Western Kyushu, Japan. *Mar. Mammal Sci.* **10** (3), 266–282. https://doi.org/10.1111/j.1748-7692.1994.tb00482.x (1994).
26. Castillo del, D. L., Flores, D. A. & Cappozzo, H. L. Cranial suture closure in the franciscana dolphin, *Pontoporia blainvillei* (Gervais and D'Orbigny, 1844). *Mastozoología Neotropical.* **22** (1), 144–148 (2015).
27. Chen, I., Chou, L. S., Chen, Y. J. & Watson, A. The maturation of skulls in postnatal Risso's dolphins (*Grampus griseus*) from Taiwanese waters. *Taiwania* **56** (3), 177. https://doi.org/10.6165/tai.2011.56 (2011).
28. Kleinenberg, S. E., Yablokov, A. V., Bel'kovich, B. M. & Tarasevich, M. N. Beluga (*Delphinapterus leucas*): Investigation of the species. Israel Program for Scientific Translations (1969).
29. Roston, R. A., Boessenecker, R. W. & Geisler, J. H. Evolution and development of the cetacean skull roof: a case study in novelty and homology. *Philos. Trans. R Soc. B Biol. Sci.* **378**, 20220086. https://doi.org/10.1098/rstb.2022.0086 (2023).
30. Alberch, P., Gould, S. J., Oster, G. F. & Wake, D. B. Size and shape in ontogeny and phylogeny. *Paleobiology* **5**, 296–317 (1979).
31. Klingenberg, C. P. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biol. Rev. Camb. Philos. Soc.* **73**, 79–123 (1998).
32. Sánchez-Villagra, M. & Maier, W. Ontogenetic data and the evolutionary origin of the mammalian scapula. *Naturwissenschaften* **89** (10), 459–461. https://doi.org/10.1007/s00114-002-0362-7 (2002).

33. Depew, M. J., Compagnucci, C. & Griffin, J. Suture neontology and paleontology: the bases for where, when and how boundaries between bones have been established and have evolved. In Frontiers of Oral Biology (ed Rice, D. P.) 57–78, (Basel: KARGER, (2008).
34. Goswami, A., Foley, L. & Weisbecker, V. Patterns and implications of extensive heterochrony in carnivoran cranial suture closure. *J. Evol. Biol.* **26**, 1294–1306. https://doi.org/10.1111/jeb.12127 (2013).
35. Sánchez-Villagra, M. R., Goswami, A., Weisbecker, V., Mock, O. & Kuratani, S. Conserved relative timing of cranial ossification patterns in early mammalian evolution. *Evol. Dev.* **10**, 519–530. https://doi.org/10.1111/j.1525-142X.2008.00267.x (2008).
36. Koyabu, D., Maier, W. & Sánchez-Villagra, M. R. Paleontological and developmental evidence resolve the homology and dual embryonic origin of a mammalian skull bone, the interparietal. *Proc. Natl. Acad. Sci.* 109, 14075–14080; (2012). https://doi.org/10.1073/pnas.1208693109
37. Koyabu, D. et al. Mammalian skull heterochrony reveals modular evolution and a link between cranial development and brain size. *Nat. Commun.* **5**, 3625. https://doi.org/10.1038/ncomms4625 (2014).
38. Oh, J., Kim, Y. K., Yasuda, M., Koyabu, D. & Kimura, J. Cranial suture closure pattern in water deer and implications of suture evolution in cervids. *Mamm. Biol.* **86**, 17–20. https://doi.org/10.1016/j.mambio.2017.03.004 (2017).
39. Hautier, L. et al. Patterns of ossification in Southern versus Northern placental mammals: mammal skeletogenesis. *Evolution* **67**, 1994–2010. https://doi.org/10.1111/evo.12071 (2013).
40. Rager, L., Hautier, L., Forasiepi, A., Goswami, A. & Sánchez-Villagra, M. R. Timing of cranial suture closure in placental mammals: phylogenetic patterns, intraspecific variation, and comparison with marsupials. *J. Morphol.* **275**, 125–140. https://doi.org/10.1002/jmor.20203 (2014).
41. Bärmann, E. V. & Sánchez-Villagra, M. R. A phylogenetic study of late growth events in a mammalian evolutionary radiation — the cranial sutures of terrestrial artiodactyl mammals. *J. Mamm. Evol.* **19**, 43–56. https://doi.org/10.1007/s10914-011-9176-8 (2012).
42. White, H. E., Goswami, A. & Tucker, A. S. The intertwined evolution and development of sutures and cranial morphology. *Front. Cell. Dev. Biol.* **9**, 653579. https://doi.org/10.3389/fcell.2021.653579 (2021).
43. White, H. E., Tucker, A. S. & Goswami, A. Divergent patterns of cranial suture fusion in marsupial and placental mammals. *Zool. J. Linn. Soc.* zlae060. https://doi.org/10.1093/zoolinnean/zlae060 (2024).
44. Bellary, S. S. et al. Wormian bones: A review. *Clin. Anat.* **26**, 922–927 (2013).
45. Sleptsov, M. M. Development of osseous skull of Odontoceti in ontogeny and phylogeny. *Doklady AN SSSR*. **28**, 364–366 (1940).
46. Wegner, R. N. Das Os interparietale Als integrierender bestandteil der Säuger-und Theromorphenschädel. *Gegenbaurs Morphol. Jahrb*. **100**, 375–419 (1960).
47. De Beer, G. *The Development of the Vertebrate Skull* (Clarendon, 1937).
48. Beasley, I., Robertson, K. M. & Arnold, P. Description of a new dolphin, the Australian snubfin dolphin *Orcaella heinsohni* sp. n. *Mar. Mammal Sci.* **21**, 365–400. https://doi.org/10.1111/j.1748-7692.2005.tb01239.x (2005). N. (Cetacea, Delphinidae).
49. Galatius, A. & Goodall, R. N. P. Skull shapes of the lissodelphininae: radiation, adaptation and asymmetry. *J. Morphol.* **277**, 776–785 (2016).
50. Jarvik, E. On the dermal bones, sensory canals and pitlines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. (Almqvist & Wiksell, (1944).
51. Krause, D. W. et al. First cranial remains of a gondwanatherian mammal reveal remarkable mosaicism. *Nature* **515**, 512–517. https://doi.org/10.1038/nature13922 (2014).
52. Fabbri, M. et al. The skull roof tracks the brain during the evolution and development of reptiles including birds. *Nat. Ecol. Evol.* **1**, 1543–1550. https://doi.org/10.1038/s41559-017-0288-2 (2017).
53. Marx, F. G. The more the merrier? A large cladistic analysis of Mysticetes, and comments on the transition from teeth to Baleen. *J. Mamm. Evol.* **18**, 77–100 (2011).
54. Lebedkina, N. S. *Evolution of Amphibian Skull: on the Problem of Morphological Integration* (Nauka, 1979).
55. Parrington, F. R. A note on the supratemporal and tabular bones in reptiles. *J. Nat. Hist.* **20**, 69–76 (1937).
56. Lambert, O. et al. A new platyrostrine sperm whale from the early miocene of the southeastern Pacific (East Pisco basin, Peru) supports affinities with the Southwestern Atlantic cetacean fauna. *Geodiversitas* **45** (22), 659–679. https://doi.org/10.5252/geodiversitas2023v45a22 (2023).
57. Bianucci, G., Lambert, O. & Post, K. High concentration of long-snouted beaked whales (genus *Messapicetus*) from the miocene of Peru. *Palaeontology* **53** (5), 1077–1098. https://doi.org/10.1111/j.1475-4983.2010.00995.x (2010).
58. Morriss-Kay, G. M. Derivation of the mammalian skull vault. *J. Anat.* **199**, 143–151 (2001).
59. Morriss-Kay, G. M. & Wilkie, A. O. M. Growth of the normal skull vault and its alteration in craniosynostosis: insights from human genetics and experimental studies. *J. Anat.* **207** (5), 637–653. https://doi.org/10.1111/j.1469-7580.2005.00475.x (2005).
60. Gross, J. B. & Hanken, J. Review of fate-mapping studies of osteogenic cranial neural crest in vertebrates. *Dev. Biol.* **317** (2), 389–400. https://doi.org/10.1016/j.ydbio.2008.02.046 (2008).
61. Wilkins, A. S., Wrangham, R. W. & Fitch, W. T. The domestication syndrome in mammals: a unified explanation based on neural crest cell behavior and genetics. *Genetics* **197** (3), 795–808. https://doi.org/10.1534/genetics.114.165423 (2014).
62. Sánchez-Villagra, M. R., Geiger, M. & Schneider, R. A. The taming of the neural crest: a developmental perspective on the origins of morphological covariation in domesticated mammals. *R Soc. Open. Sci.* **3**, 160107. https://doi.org/10.1098/rsos.160107 (2016).
63. Usui, K. & Tokita, M. Creating diversity in mammalian facial morphology: a review of potential developmental mechanisms. *EvoDevo* **9**, 15. https://doi.org/10.1186/s13227-018-0103-4 (2018).
64. Sanderson, S. L. & Wassersug, R. Convergent and alternative designs for vertebrate suspension feeding in *The Skull, Volume 3: Functional and Evolutionary Mechanisms* (eds. Hanken, J. & Hall B.K.) 37–112University of Chicago Press, (1993).
65. Bramble, D. M. Cranial specialization and locomotor habit in the Lagomorpha. *Am. Zool.* **29**, 303–317 (1989).
66. Maier, W. On the evolutionary biology of early mammals -with methodological remarks on the interaction between ontogenetic adaptation and phylogenetic transformation. *Zool. Anz.* **238**, 55–74 (1999).
67. Deméré, T. A. & Berta, A. Skull anatomy of the oligocene toothed Mysticete *Aetioceus Weltoni* (Mammalia; Cetacea): implications for Mysticete evolution and functional anatomy. *Zool. J. Linn. Soc.* **154** (2), 308–352. https://doi.org/10.1111/j.1096-3642.2008.00414.x (2008).
68. Gol'din, P., Startsev, D. & Krakhmalnaya, T. The anatomy of a late miocene baleen whale from Ukraine. *Acta Palaeontol. Pol.* **59**, 795–814 (2013).
69. Lambert, O. et al. Earliest Mysticete from the late eocene of Peru sheds new light on the origin of baleen whales. *Curr. Biol.* **27**, 1535–1541. https://doi.org/10.1016/j.cub.2017.04.026 (2017). .e2.
70. Werth, A. J. Mandibular and dental variation and the evolution of suction feeding in Odontoceti. *J. Mammal.* **87**, 579–588 (2006).
71. Gol'din, P. E. Growth, proportions and variation of the skull of harbour porpoises (*Phocoena phocoena*) from the sea of Azov. *J. Mar. Biol. Assoc. U K*. **87**, 271–292 (2007).
72. Johnston, C. & Berta, A. Comparative anatomy and evolutionary history of suction feeding in cetaceans. *Mar. Mammal Sci.* **27** (3), 493–513. https://doi.org/10.1111/j.1748-7692.2010.00420.x (2011).
73. Marx, F. G. et al. Suction feeding preceded filtering in baleen whale evolution. *Mem. Mus. Vic.* **75**, 71–82. https://doi.org/10.24199/j.mmv.2016.75.04 (2016).
74. Boessenecker, R. W., Fraser, D., Churchill, M. & Geisler, J. H. A toothless dwarf dolphin (Odontoceti: Xenorophidae) points to explosive feeding diversification of modern whales (Neoceti). *Proc. R Soc. B Biol. Sci.* **284**, 20170531. https://doi.org/10.1098/rspb.2017.0531 (2017).

75. Herring, S. W., Rafferty, K. L., Liu, Z. J. & Marshall, C. D. Jaw muscles and the skull in mammals: the biomechanics of mastication. *Comp. Biochem. Physiol. Mol. Integr. Physiol.* **131**, 207–219 (2001).
76. Gregory, W. K. Williston's law' relating to the evolution of skull bones in the vertebrates. *Am. J. Phys. Anthropol.* **20**, 123–152 (1935).
77. Esteve-Altava, B., Marugán-Lobón, J., Botella, H. & Rasskin-Gutman, D. Structural constraints in the evolution of the tetrapod skull complexity: Williston's law revisited using network models. *Evol. Biol.* **40**, 209–219. https://doi.org/10.1007/s11692-012-9200-9 (2013).
78. Koyabu, D. Evolution, conservatism and overlooked homologies of the mammalian skull. *Philos. Trans. R Soc. B Biol. Sci.* **378**, 20220081. https://doi.org/10.1098/rstb.2022.0081 (2023).
79. Sanchez-Lara, P. A., Graham, J. M., Hing, A. V., Lee, J. & Cunningham, M. The morphogenesis of Wormian bones: A study of craniosynostosis and purposeful cranial deformation. *Am. J. Med. Genet. A.* **143A**, 3243–3251. https://doi.org/10.1002/ajmg.a.32073 (2007).
80. Wilson, L. A. B. & Sánchez-Villagra, M. R. Heterochrony and patterns of cranial suture closure in hystricognath rodents. *J. Anat.* **214** (3), 339–354. https://doi.org/10.1111/j.1469-7580.2008.01031.x (2009).
81. Carroll, R. L. *Vertebrate Paleontology and Evolution* (Freeman, 1988).
82. Kumar, S. et al. TimeTree 5: an expanded resource for species divergence times. *Mol. Biol. Evol.* **39**, msac174. https://doi.org/10.1093/molbev/msac174 (2022).
83. Blomberg, S. P., Garland, T. & Ives, A. R. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57** (4), 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x (2003).
84. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. https://doi.org/10.1038/44766 (1999).
85. Revell, L. J. Phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* **12**, e16505. https://doi.org/10.7717/peerj.16505 (2024).
86. Fritz, S. A. Purvis & A. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24** (4), 1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x (2010).
87. Orme, D. et al. Pearse, W. caper: comparative analyses of phylogenetics and evolution in R. (2018). https://CRAN.R-project.org/package=caper
88. Yu, G., Smith, D. K., Zhu, H., Guan, Y. & Lam, T. T. Ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol. Evol.* **8** (1), 28–36. https://doi.org/10.1111/2041-210X.12628 (2017).
89. Pennell, M. W. et al. Geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* **30** (15), 2216–2218. https://doi.org/10.1093/bioinformatics/btu181 (2014).
90. Martin, B. S., Bradburd, G. S., Harmon, L. J. & Weber, M. G. Modeling the evolution of rates of continuous trait evolution. *Syst. Biol.* **72** (3), 590–605. https://doi.org/10.1093/sysbio/syac068 (2023).
91. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE.* **9** (2), e89543. https://doi.org/10.1371/journal.pone.0089543 (2014).
92. Bastide, P., Ané, C., Robin, S. & Mariadassou, M. Inference of adaptive shifts for multivariate correlated traits. *Syst. Biol.* **67** (4), 662–680. https://doi.org/10.1093/sysbio/syy005 (2018).
93. Tung Ho, L. S. & Ané, C. A linear-time algorithm for Gaussian and non-gaussian trait evolution models. *Syst. Biol.* **63** (3), 397–408. https://doi.org/10.1093/sysbio/syu005 (2014).
94. Ives, A. R. & Garland, T. Phylogenetic logistic regression for binary dependent variables. *Syst. Biol.* **59** (1), 9–26. https://doi.org/10.1093/sysbio/syp074 (2010).

Acknowledgements

Our sincere thanks to Igor Dzeverin and Anders Galatius for inspiration and valuable input into initial discussions on cranial suture ossifications and heterochrony in cetaceans; Elena Gladilina, Karina Vishnyakova, Pavlo Otriazhyi and Svitozar Davydenko for help in collecting primary morphological information; Carolin Kosiol and Maria Ghazali for their warm discussion of statistics; Annalisa Berta for overall discussion of results; David Paterson for reviewing the manuscript and providing helpful feedback on language and style; Jean Demouthe, Iryna Tkebuchava, Oleksandr Zinenko, Ihor Shydlovsky, Ihor Dykyi, Christian de Muizon, Mette Elstrup, Giovanni Bianucci, Alberto Collareta, Chris Conroy, Pat Holroyd, Mark Omura, Daniela Kalthoff, Volodymyr Peskov, Yevheniia Uliura, Andrew Kitchener, Oleh Melnyk, Volodymyr Lobkov, Tamar Dayan, Dan Kerem, Oz Goffman, Willy Dabin, Carl Kinze, Mogens Andersen, Daniel Johansson, Gearóid Mac a' Ghobhainn, Andrew Kitchener and especially Morten Tange Olsen for help in work with collections and access to collections under their care. Our special thanks to Mette Elstrup and the Museum of the Southern Jutland, Gill Braulik, Oscar Gaggiotti and the University of St Andrews for their hospitality and to the Ukrainian Army that made it possible to finish this research.

Author contributions

V.T. and P.G. conceived and designed the study, conducted data search and analysis and wrote the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-95566-x.

Correspondence and requests for materials should be addressed to V.T. or P.G.