

Occipital Ossification of Balaenopteroid Mysticetes

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ABSTRACT

The bones of the posterior portion of the mammalian skull often exhibit incomplete ossification of the joints between the bones at the time of birth, with complete ossification at some point after birth. The sequence of ossification of these joints in mysticetes can be used to characterize the relative age in the calf and early juvenile ontogenetic stages. This study examined occipital joints ossification of 38 dry prepared neonate specimens in four mysticete species from two families (Eschrichtiidae: *Eschrichtius robustus*; Balaenopteridae: *Balaenoptera acutorostrata*, *Balaenoptera physalus*, and *Megaptera novaeangliae*). Each of the joints responsible for the fusion of the occiput were examined and rated for degree of ossification. The cranial ossification analysis indicates that *E. robustus* calves have open occipital joints until ~6 months of age and are born at a less mature stage than closely related balaenopterids. All of the species followed the same sequence of ossification: basioccipital/exoccipital joint, followed by the basioccipital/basisphenoid joint, and completed by the supraoccipital/exoccipital joint. Anat Rec, 294:391–398, 2011. © 2011 Wiley-Liss, Inc.

Key words: mysticete; occiput; ossification

Mysticetes include some of the largest mammals in the world, especially some species within Balaenopteroidae, the clade consisting of Eschrichtiidae and Balaenopteridae (Deméré et al., 2008; Marx, 2010). This study focuses on the following balaenopteroid species (Fig. 1): Eschrichtiidae: *Eschrichtius robustus* (gray whale); Balaenopteridae: *Balaenoptera acutorostrata* (minke whale), *Balaenoptera physalus* (fin whale), and *Megaptera novaeangliae* (humpback whale). These species range in size from 8 m to 27 m in total body length at physical maturity (Omura, 1953; Blokhin and Vladimirov, 1983; Mizroch et al., 1984; Muranishi et al., 2004; Tetsuka et al., 2004). Growth to these large sizes requires alteration of nutrient allocation while adapting to lifestyle changes. Because of the range in body size in this group, it is possible that different balaenopteroids do not exhibit the same developmental patterns throughout life. The developmental patterns of closely related taxa should be similar, but the difference in body size requires a change in development. The similarities between the ontogenies of these balaenopteroid mysticetes can be studied to determine the influence of phylogeny on developmental patterns.

The sequence of mammalian cranial joint ossification can be used to characterize the relative age of young

animals. This method has been utilized to describe and estimate age in canids (Landon et al., 1998), phocids (Wyss, 1994), odontocetes (Besharse, 1971; Perrin, 1975; Christensen, 1981; Kato, 1983; Aguilar and Lockyer, 1987; Yoshida et al., 1994; Bisconti, 2001), and otariids (Brunner, 1998; Tedman, 2003; Brunner et al., 2004). These studies effectively described the degree of joint closure in relation to the age of the animal. The benefit of studying joint closure and using it as a tool to estimate age is that it can be used for cranial specimens of very young individuals, while other aging techniques such as ovarian corpus albicans and ear plug analysis

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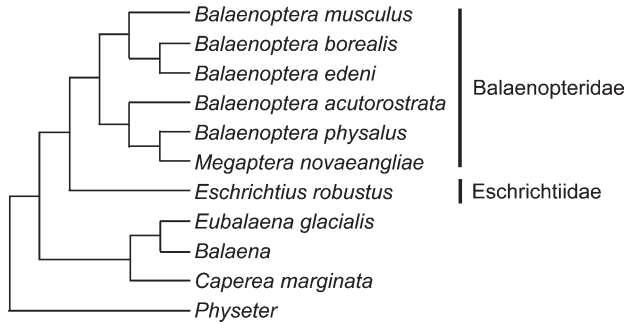


Fig. 1. Mysticete phylogeny (Adapted from Deméré et al., Syst Biol, 2008, 57, 15–37) combined morphological and molecular analysis using fossil and extant mysticetes (fossil taxa excluded from this phylogeny). *Physeter* is a basal odontocete used here as an outgroup.

(Besharse, 1971; Christensen, 1981; Kato, 1983; Aguilar and Lockyer, 1987; Bisconti, 2001; Deméré et al., 2008) are not useful for these age classes as they are either not found or not reliable in animals of this young age. This study characterizes the sequence of cranial joint ossification in terms of the replacement of cartilaginous synchondrosis joints with ossified synostosis joints and provides age estimates throughout the stages of ossification, which has never been described in mysticetes.

Similar to other mammalian species, cetacean cranial ontogeny follows a consistent sequence of ossification. For example, the braincase joints complete closure prior to the closure of the rostral and palatal areas in odontocetes (Perrin, 1975, 1993). However, mysticete rostral joints remain open throughout the life of the animal (Oelschlager and Oelschlager, 2002), in contrast to odontocetes that complete fusion of the rostrum by sexual or physical maturity (Brunner, 1998). At the time of birth, all of the joints of the braincase with the exception of the occipital bones (Fig. 2) are ossified to some degree. The occiput joints (Fig. 3) are the only joints that can be described as being open or unfused. For this reason, only the joints of the occiput region will be examined in this study for the purpose of describing the sequence of joint ossification. Mysticete occipital joints remain open at birth and complete their development during the first stage of life. These joints unite four bones that comprise the occipital bone and include the supraoccipital, right and left exoccipitals, and the basioccipital. The joints between these bones are named for the bones that they join together (basioccipital/basisphenoid, basioccipital/exoccipital, and supraoccipital/exoccipital). These joints in the posterior region of the braincase are of particular interest in the development of the mysticete skull because they protect the rapidly growing brain (Sumich, 1986), and the closure of these joints is examined herein.

MATERIALS AND METHODS

The specimens in this study were studied and measured at the following institutions: California Academy of Sciences, San Francisco, California (CAS MAM); Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ); Humboldt State University Vertebrate Museum, Arcata, California (HSU); Natural History Museum of Los Angeles County, Los

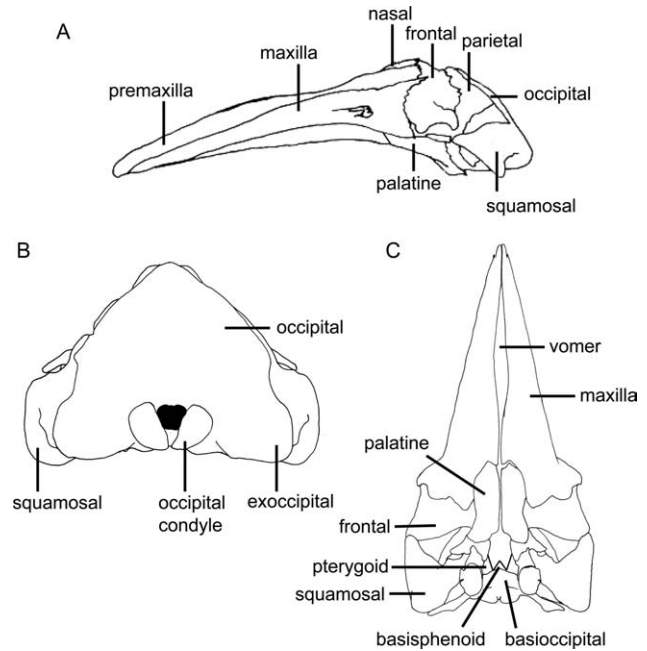


Fig. 2. Bones and landmarks of the mysticete skull in (A) lateral, (B) posterior, and (C) ventral views.

Angeles, California (LACM); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH); San Diego Natural History Museum, San Diego, California (SDSNH); San Diego State University, San Diego, California (SDSU); University of California, Berkeley Museum of Vertebrate Zoology, Berkeley, California (MVZ); University of Washington, Burke Museum of Natural History and Culture, Seattle, Washington (UWBM).

Complete skulls of *Eschrichtius robustus* (N = 20), *Balaenoptera acutorostrata* (N = 8), *Balaenoptera physalus* (N = 6), and *Megaptera novaeangliae* (N = 4) fetal and neonatal dry, prepared specimens were examined for degree of joint closure. Cranial joints of the braincase (Fig. 3) were given a joint rating (SR) using the following descriptions, adapted from the rating system described by Brunner (1998): SR1: joint open; SR2: joint partially closed; SR3: joint closed with observable joint; SR4: joint tightly closed with no observable joint (Fig. 4). All joints were observed through the SR4 stage to determine the order of joint closure and estimate age at which the joints are closed based on age/length estimates determined in previous studies.

RESULTS

The sample of *Eschrichtius robustus* specimens includes 18 calves under the age of 1 year. This sample indicates that calves are born at a state of open joints at SR1 and SR2 (Fig. 5). The basioccipital/basisphenoid joint is partially closed and is at the SR2 stage in most specimens. The closure of this joint appears to progress from the anterior–lateral edges toward the posterior–medial edges. This joint is the first to begin ossification, but the last joint to complete ossification between 7 months and 1 year of age. The basioccipital/exoccipital

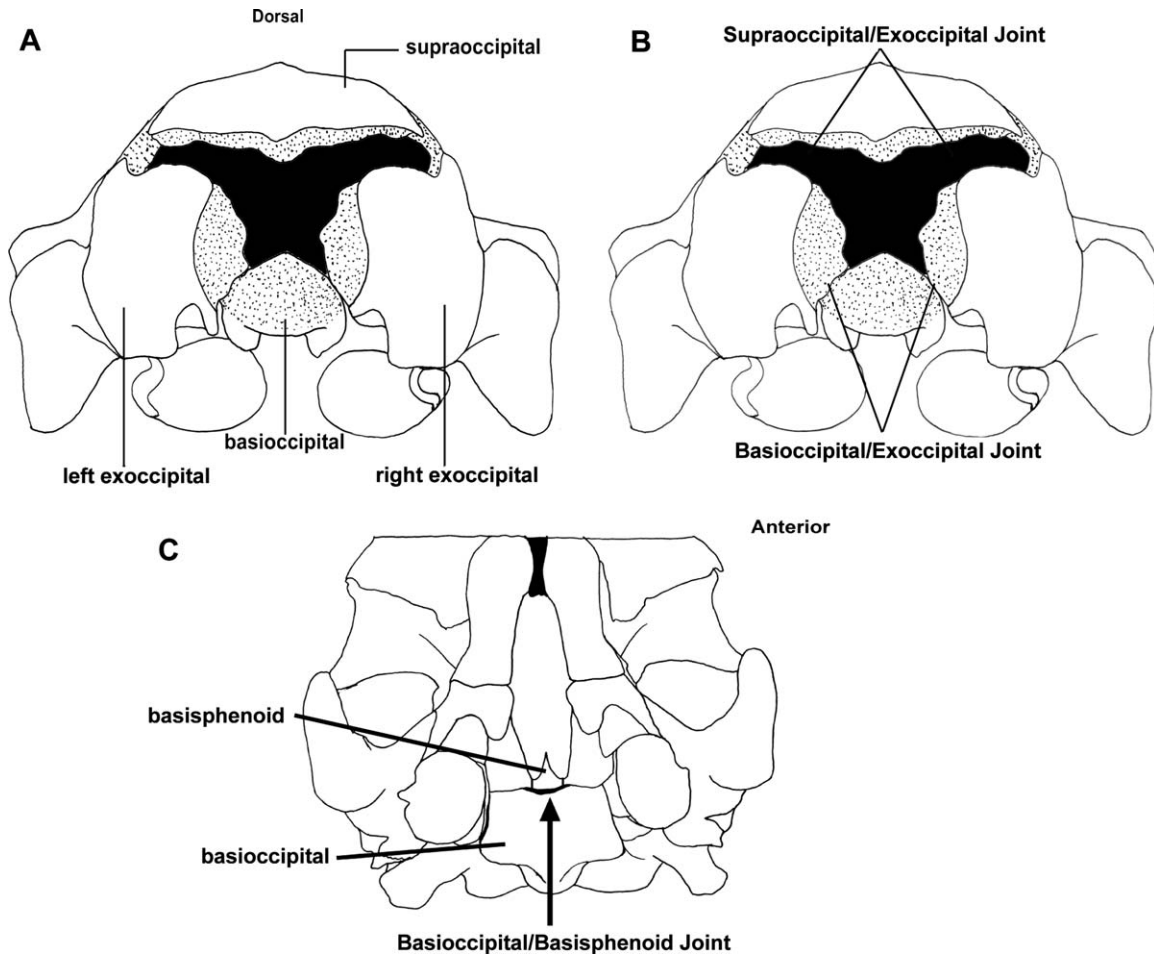


Fig. 3. Bones and joints of the mysticete occiput. Black areas signify open fontanelles. (A) posterior view of occipital bones; (B) posterior view of occiput sutures; (C) ventral view of braincase region.

joints are also partially closed by the time of birth and are at the SR2 stage until total body length reaches a range of 590–660 cm. It is at this size-range that this joint completes its ossification and can be classified at the SR4 stage, soon before the age of 7 months (TL = 700 cm) (Ohsumi et al., 1958). The supraoccipital/exoccipital joints are at the SR1 stage at the time of birth and do not progress until total body length reaches a range of 575–600 cm, when the joints ossify very rapidly to the SR4 stage by the age of 7 months. These joints begin ossification at the lateral edges where the occiput contacts the parietal bones. The medial edge then ossifies at the dorsal edge of the foramen magnum (Fig. 6). The joint then ossifies in a medial direction from the lateral edges. The *E. robustus* cranial joints described here are all closed (SR3 or SR4) by the age of 7 months with the following order of ossification: basioccipital/exoccipital, supraoccipital/exoccipital, basioccipital/basisphenoid.

The sample of *Balaenoptera acutorostrata* specimens includes seven calves under the age of 1 year old, which display considerable individual variation in the degree of closure of the occipital joints. Nonetheless, the occipital joints are at some degree of closure soon after birth (SR2, SR3, SR4) (Fig. 7). The basioccipital/basisphenoid

joint is at an SR2 stage in the youngest calves and progresses to a consistent SR3 stage by the total body length of 350 cm. The basioccipital/exoccipital joints of this dataset are at the SR3 stage by the total body length of ~314 cm. This joint then progresses to the SR4 stage before the total body length reaches 420 cm. Although this joint is closed, it remains at the SR3 stage throughout the life of the animal. The basioccipital/exoccipital joint begin their ossification at the medial edge of the joint and progress in the lateral direction. The supraoccipital/exoccipital joint are consistently at the SR2 stage by the total length of 350 cm and progress rapidly to the SR4 stage by the total body length of 420 cm. The supraoccipital/exoccipital joints begin ossification at the medial edge and continue laterally (Fig. 8A). There is some ossification that occurs at the lateral edge prior to the medial ossification reaching the lateral-most portion. The deeper portion of these joints, positioned along the inside wall of the braincase, appears to ossify before the superficial portion of the joints. The last remaining portion of the joint to ossify is a small opening in the middle of the joint that is closed on the deep portion (Fig. 8B). *Balaenoptera acutorostrata* occipital joints described here all close before the age of 1 year

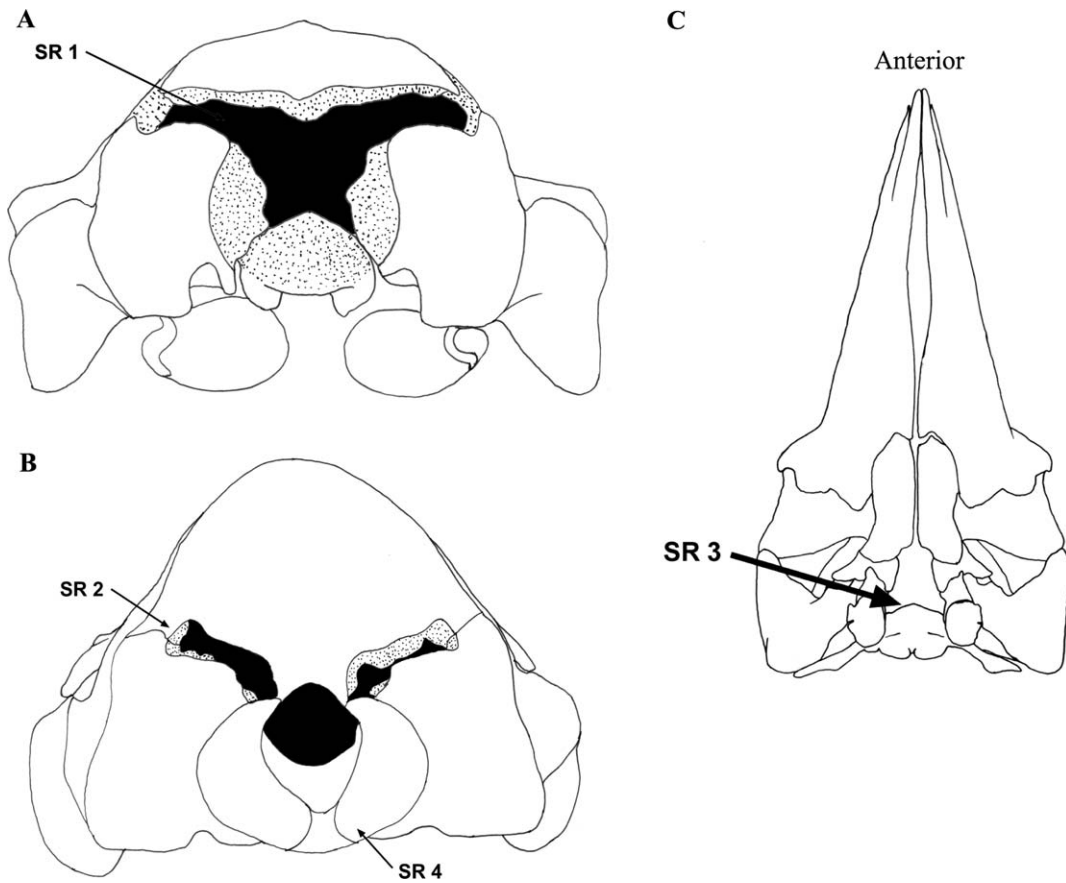


Fig. 4. Schematic of occiput joint closure ratings (SR). SR1: open; SR2: partial closure; SR3: closed with observable joint; SR4: closed with no observable joint. (A) posterior view; (B) posterior view; (C) ventral view.

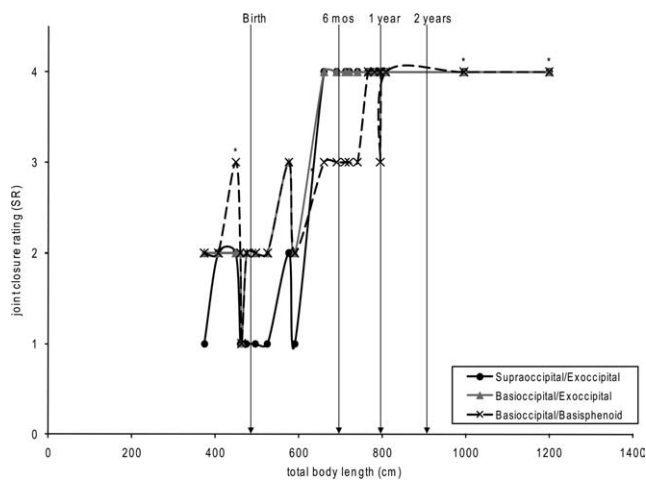


Fig. 5. Joint closure of *Eschrichtius robustus* occiput. * denotes estimated total body length.

with the following order of ossification: basioccipital/basisphenoid (SR3), basioccipital/exoccipital (SR4), supraoccipital/exoccipital (SR4).

The sample of *Balaenoptera physalus* specimens includes three fetuses and three neonates under the age

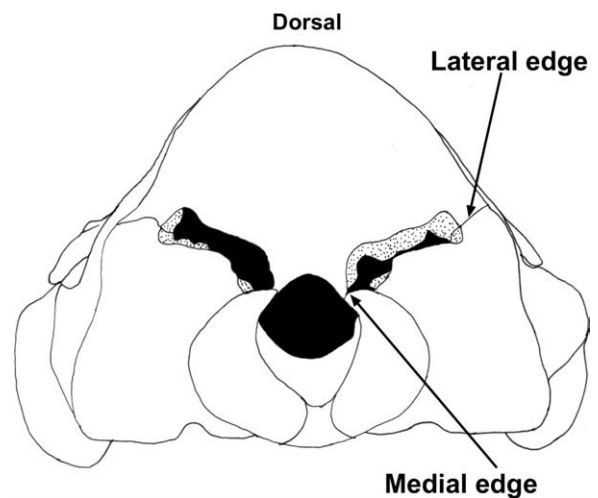


Fig. 6. Schematic of *Eschrichtius robustus* supraoccipital/exoccipital joint in posterior view. Joint begins ossification at the lateral edge and then begins to ossify at the medial edge.

of 1 year. The basioccipital/basisphenoid joint is the first to exhibit ossification at the SR2 stage, demonstrated in the fetal stage by ~155 cm total body length (Fig. 9). At some time between birth and the early calf stage, as our

746 cm TL specimen represents, this joint closes to an SR3 stage (visible joint) and remains at this state for the life of the animal. The basioccipital/exoccipital joints are between SR1 and SR2 stages in the fetal specimens, but rapidly progress to the SR4 stage by and the early calf stage. The supraoccipital/exoccipital joints are open at an SR1 stage during the fetal stage, but quickly progress to the SR4 stage and the early calf stage. The *B. physalus* cranial joints described here all close soon after birth with the following order of ossification: basioccipital/basisphenoid (SR3), basioccipital/exoccipital (SR4), supraoccipital/exoccipital (SR4).

The sample of *Megaptera novaeangliae* specimens consists of four neonates all of which have closed occipital joints (Fig. 10). The basioccipital/basisphenoid joint is closed at SR3 by the total body length of 800 cm and remains visible throughout the life of the animal. Both the supraoccipital/exoccipital and basioccipital/exoccipital joints are closed at SR4 by the total body length of 800 cm. It is not possible to determine the order of joint ossification in this species because of the lack of fetal

and early neonate specimens, but the occipital joints are closed at SR3 or SR4 before the age of 1 year.

DISCUSSION

Cranial Ossification Within Balaenopteroids

The occipital joints of the sampled balaenopteroid mysticetes are closed before the age of 1 year. *Eschrichtius robustus* joints are all open at birth and closed before the animal reaches 7 months of age. The approximate total body length for *E. robustus* at the age of 7 months old (700 cm) (Muranishi et al., 2004; Tetsuka et al., 2004) and that for *B. physalus* at the age of 6 months old (1,100 cm) (Ohsumi et al., 1958; Mizroch et al., 1984) are available in the literature, but age/length estimates less than 1 year old have not been established for the other two species. All of the joints in *B. acutorostrata* and *M. novaeangliae* are closed by the age of 1 year and are at a stable joint ossification stage that does not progress further during the life of the animal. Most of the ossification for *B. acutorostrata* occurs after birth, but the joints of *B. physalus* are closed relatively early in the growth of the first 6 months. This might be attributable to the larger size of *B. physalus* calves at the time of birth. *Balaenoptera acutorostrata* is a small balaenopterid, giving birth to calves ~280 cm in length (Fish, 1996). *Balaenoptera physalus* is one of the largest whales of this group, giving birth to calves that are ~600 cm in length (Oelschlager and Oelschlager, 2002). The advanced state of occiput ossification in *B. physalus* could be correlated with the size difference between the two species. Unfortunately, it was not possible to discriminate the phylogenetic signal from allometric size constraints between *B. acutorostrata* and *B. physalus* because *M. novaeangliae* calves at a state close to birth were unavailable. It was only possible to determine that the occipital joints of *M. novaeangliae* are closed by the age of 1 year. This dataset presents individual variation in the timing of joint closure, but the order and final joint closure is reliable.

The sequence of joint closure among the sampled balaenopteroid mysticetes is to a great extent conserved.

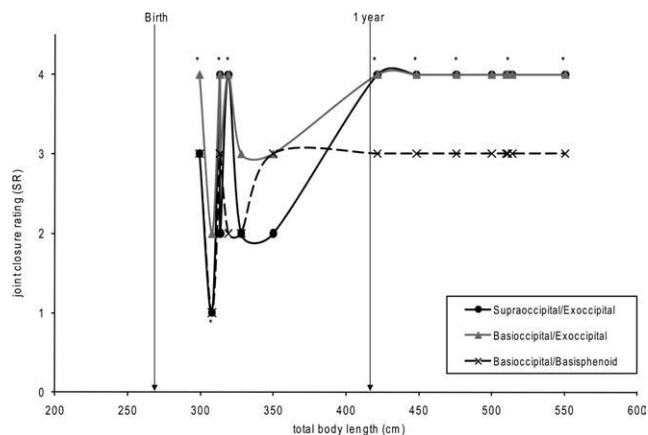


Fig. 7. Joint closure of *Balaenoptera acutorostrata* occiput. * denotes estimated total body length.

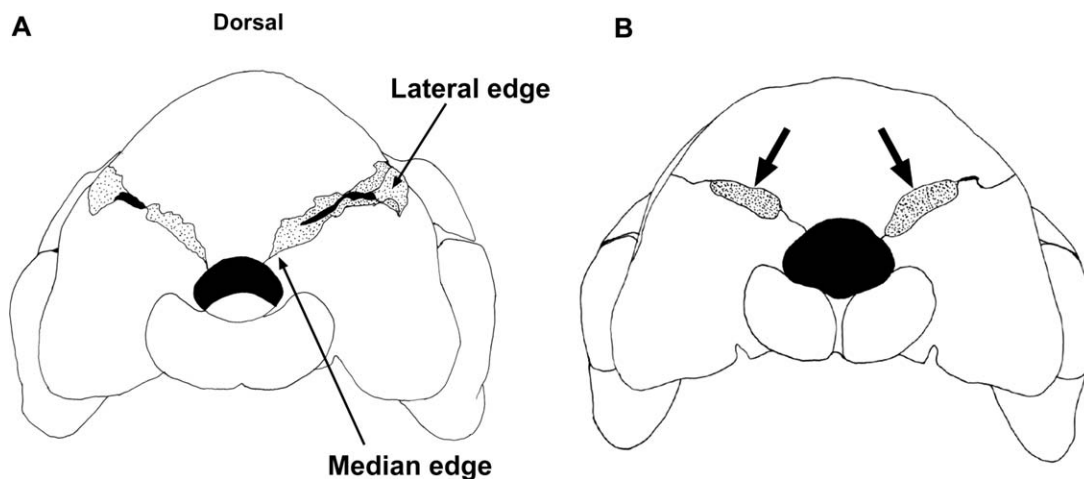


Fig. 8. Schematic of *Balaenoptera acutorostrata* skull in posterior view depicting supraoccipital/exoccipital joint closure. (A) from medial edge toward lateral edge. (B) final portion to close in middle of joint with deeper portion of joint ossified.

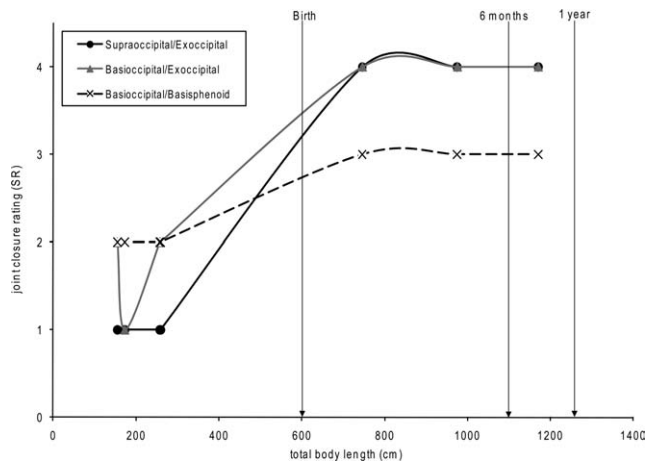


Fig. 9. Joint closure of *Balaenoptera physalus* occiput.

The basioccipital/exoccipital joint is the first joint to completely ossify in all species, completing the occipital condyles. This early central development reflects the importance of the central axis to the undulatory propulsion mode of cetaceans. The central axis and occipital condyles are important because the muscles of the back that anchor to the central axis are responsible for the main propulsion of the animal (Yoshida et al., 1994). The basioccipital/basisphenoid joint reached the SR3 stage in all species before the supraoccipital/exoccipital joint completed its ossification. However, the order of complete closure is slightly different between *E. robustus* and balaenopterids because the basioccipital/basisphenoid joint continues its ossification in *E. robustus*, advancing to the SR4 stage to obliterate the visible joint that remains in the balaenopterid species. This joint remains at the SR3 stage in balaenopterids throughout their lives. The supraoccipital/exoccipital joint is the final joint to fully ossify, completing the bony plate covering the dorsal and posterior portion of the braincase referred to as the occipital shield. This pattern of the supraoccipital/exoccipital joints advancing to SR4, while the basioccipital/basisphenoid joint remains at SR3, is evident in the *M. novaeangliae* sample set.

The occiput ossification indicates a rapid development of the ventral surface of the braincase. Both the order of joint closure (basioccipital/exoccipital and basioccipital/basisphenoid) and the direction of ossification in the basioccipital/exoccipital joints (medial and partly ventral to lateral and more dorsal) follow a pattern of ventral surface development completing before dorsal development (i.e., supraoccipital/exoccipital joint). This may be related to the nervous system being supported by the ventral region of the braincase. Many mammals exhibit this ventral braincase development earlier than the supraoccipital development (Perrin, 1975; Yoshida et al., 1994). It has been suggested that this is due to the large amount of encephalization found in mammals, especially marine mammals (Yoshida et al., 1994).

It is possible that the closure of the ventral braincase prior to the dorsal development is related to the type of development responsible for each region of the braincase. The joints supporting the ventral braincase (basi-

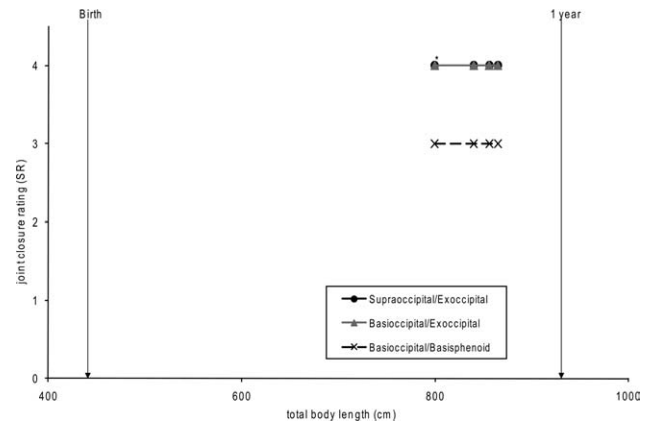


Fig. 10. Joint closure of *Megaptera novaeangliae* occiput. * denotes estimated total body length.

cipital/basisphenoid and basioccipital/exoccipital) are preformed in cartilage in early development and then replaced with bone, referred to as chondrocranial development. The dorsal portion of the braincase is derived from membranous bone, referred to as desmocranial development. It is possible that the chondrocranial development is a more rapid process than the replacement of membranous bone with ossified bone, as in desmocranial development.

The described sequence of joint closure in balaenopterids is different from that found in odontocetes. The first occipital joint to close in the finless porpoise is the basioccipital/basisphenoid, followed by the basioccipital/exoccipital joint and then the supraoccipital/exoccipital joint (Miller, 1923). The supraoccipital/exoccipital joint is the last joint to fully close in some described odontocetes, with fontanels (circular openings left by incomplete ossification of the supraoccipital/exoccipital joints) persisting at the lateral edge of the joint for many odontocete species (Perrin, 1975). Many researchers have described odontocete joints as being closed, despite the notation that the fontanels persist in the occipital shield, sometimes up to 4 years of age (Perrin, 1975). This is considered here an inaccuracy in the literature due to the fact that the fontanelles represent incomplete joint closure. Nonetheless, odontocete occipital joint closure begins with the basioccipital/basisphenoid joint, followed by the basioccipital/exoccipital joint, and concluded by the supraoccipital/exoccipital joint. In mysticetes, the basioccipital/exoccipital joint and basioccipital/basisphenoid joint reverse their order of closure compared to odontocetes. The differences in sequence of joint closure between mysticetes and odontocetes may be related to the differences in telescoping of the skull (Miller, 1923) or the fact that odontocetes exhibit more fusion of the bones throughout the skull than mysticetes (Perrin, 1975). In both groups, the chondrocranial development completes prior to the desmocranial development. Odontocetes develop the ventral surface of the braincase rapidly in the early calf stage, possibly in an attempt to develop the region related to the hearing apparatus lateral to the sphenoid bone (Ohsumi et al., 1958; Sumich, 1986), while mysticetes do not echolocate and are less dependent on the hearing apparatus.

The direction of supraoccipital/exoccipital joint ossification is different in *E. robustus* and *B. acutorostrata* from that documented in odontocetes (McLeod et al., 1993). This joint in the observed balaenopteroids begins ossifying from the lateral and medial borders of the joint, progressing faster from the medial border than the lateral border. The ossification concludes by filling in a small opening in the middle of the joint. This method of closure is dissimilar to the closure in odontocetes in which the last remaining gap persists at the junction between the exoccipital, supraoccipital, and parietal bones at the lateral edge of the joint (Bisconti, 2000). In both groups, the medial border is the initial site on the joint for ossification, completing the boundaries of the foramen magnum.

Relationship Between Occipital Ossification and Age

The mysticete species in this study are born with varying stages of occipital joint ossification, but they all complete cranial ossification before the age of 1 year. *Eschrichtius robustus* and *B. physalus* are the only species for which age/length estimations are available in the literature for individuals less than 1 year old (Perrin, 1993; Yoshida et al., 1994). These results indicate that these species complete their occipital joint closure by the age of 7 and 6 months, respectively. The *B. acutorostrata* data is somewhat inconclusive in the young calves. Skull observations for which the total body length is known indicate that the occipital joints are at SR2 and SR3 at an early calf stage.

The joint closure trajectory seen in *B. physalus* mimics that of *B. acutorostrata* but seems to occur at an earlier ontogenetic stage (Figs. 7, 9). *Balaenoptera physalus* shows signs of early stages of joint closure in the fetus, with completion of ossification in young calves ~800 cm total body length. However, this may be explained by the difference in total body length at birth of this species (600 cm) compared to *B. acutorostrata* (280 cm). All of the occipital joints ossify in the same sequence in the balaenopterids. These results suggest that this sequence of joint closure is conserved in balaenopterids and that it is possible that the stage of closure is related to the relative size of the animal, not solely the ontogenetic stage. If this is true, one can hypothesize that the joint closure order and relative timing in *M. novaeangliae* may be similar to that found in *B. acutorostrata* and *B. physalus*.

CONCLUSIONS

Aging specimens based on the ossification sequence of occipital joints provides a valuable resource that can be used on calf specimens. The cranial development sequence for this age group has not been previously characterized. Being able to distinguish between neonate, weanling, and yearling is important because many researchers characterize skulls as juvenile based on the incomplete joint development in other groups of mammals. This is an inaccurate practice in balaenopteroid mysticetes because, as this research shows, the occipital joints are closed within the calf stage before the age of 1 year. There are a number of years after the calf stage (ranging from 3 to 6 years depending on the species)

before sexual maturity occurs, in which the animals are considered juveniles.

The new information with regard to classification of juvenile crania as having closed occipital joints would most likely impact the description of fossil taxa. Fossil mysticetes are described as smaller in size when compared to the extant taxa; however, it is possible that the assumptions of specimen maturity is biased and that the specimens may be younger than the researchers claim. For example, a description of the balaenid *Balaenula astensis* (Bisconti, 2000) notes that the specimen is a small adult individual. However, the dentary, supraoccipital, and squamosal surfaces show the spongy structure of the bone that is indicative of developing, not adult bone. This suggests that the specimen is from an early juvenile individual, not an adult. It is not stated in the description of this specimen how the determination of adult was given. It is possible that the specimen was not classified as a juvenile based on the closed occipital joints. The information provided by the present study would help prevent the overestimation of age of specimens.

This study both describes the pattern of occipital ossification and establishes a new technique for age estimation of young mysticete osteological specimens. Increasing the number of samples, especially in balaenopterids, and increasing the number of taxa across mysticetes would be useful to expand the present study. More cranial ossification studies need to be performed across all mysticetes and basal odontocetes to better determine the phylogenetic effect on development. Some previous research has described cranial ossification in members of Delphinidae (dolphins), a later diverging group of odontocetes, but little has been studied in Physeteridae and Ziphiidae, which are earlier diverging lineages of odontocetes. It is not appropriate to compare the ossification and growth of balaenopteroid mysticetes to delphinid taxa because of the great amount of phylogenetic distance between the two groups. Phocoenids (porpoises), a later diverging group of odontocetes for which there is a fair amount of information regarding growth, are recognized as being pedomorphic, exhibiting juvenile or young characteristics in the adult form (Galatius et al., 2010). To compare mysticete cranial ossification, it is more appropriate to use basal lineages that are not pedomorphic. Finally, growth of mysticetes is less explored than odontocetes because of their large size and fewer age diagnostic structures. It would be most useful to put a significant amount of effort into determining the developmental patterns of mysticetes to both fill the void of information and provide more accurate age estimates for population growth assessments.

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