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Histological analysis of the nasal roof cartilage in a neonate sperm whale (*Physeter macrocephalus* – Mammalia, Odontoceti)

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Abstract

The nasal roof cartilage of a neonate sperm whale (*Physeter macrocephalus*) was examined by gross dissection and routine histology. This cartilage is part of the embryonic *Tectum nasi* and is a critical feature in the formation of the massive sperm whale forehead. In neonates as well as in adults, the blade-like nasal roof cartilage extends diagonally through the huge nasal complex from the bony nares to the blowhole on the left side of the rostral apex of the head. It accompanies the left nasal passage along its entire length, which may reach several meters in adult males. The tissue of the nasal roof cartilage in the neonate whale shows an intermediate state of development. For example, in embryos and fetuses, the nasal roof cartilage consists of hyaline cartilage, but in adult sperm whales, it also includes elastic fibers. In our neonate sperm whale, the nasal roof cartilage already consisted of adult-like elastic cartilage. In addition, the active or growing, layer of the perichondrium was relatively thick compared to that of fetuses, and a large number of straight elastic fibers that were arranged perpendicularly to the long axis of the nasal roof cartilage were present. These neonatal features can be interpreted as characteristics of immature and growing cartilaginous tissue. An important function of the nasal roof cartilage may be the stabilization of the left nasal passage, which is embedded within the soft tissue of the nasal complex. The nasal roof cartilage with its elastic fibers may keep the nasal passage open and prevent its collapse from Bernoulli forces during inhalation. Additionally, the intrinsic tension of the massive nasal musculature may be a source of compression on the nasal roof cartilage and could explain its hyaline character in the adult. In our neonate specimen, in contrast, the cartilaginous rostrum (i.e., mesorostral cartilage) consisted of hyaline cartilage with an ample blood supply. The cartilaginous rostrum does not change its histological characteristics during development, but its function in adults is still not understood.

Keywords: Cetacea; Odontoceti; Sperm whale; *Physeter macrocephalus*; Nasal roof cartilage; Nasal skeleton

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1. Introduction

Many of the specialized anatomical features of toothed whales (Odontoceti) can be interpreted as adaptations to their aquatic environment. In the nasal region, these adaptations are reflected in three marked evolutionary changes from the original condition found in land mammals, which can also be observed during embryogenesis of the odontocete nasal region. These changes include: (1) the loss of the sense of smell; (2) the translocation of the nostrils from the tip of the rostrum to the vertex of the head; and (3) the elongation of the facial region to form an elongated rostrum (Klima 1999). Morphogenetic processes play a decisive role in these developmental changes. The lateral parts of the embryonic nasal capsule, which encompass the nasal passages, change their orientation from horizontal to vertical. At the same time, the structures of the original nasal floor (i.e., *Solum nasi*) are shifted in front of the nasal passages towards the rostrum. The structures of the original nasal roof (i.e., *Tectum nasi* and *Paries nasi*) are translocated behind the nasal passages towards the neurocranium. For the most part, the medial nasal septum (i.e., the *Septum nasi*) loses its connection to the nasal passages and projects rostrally (Klima 1999). In general, these cartilaginous anlagen do not persist in adult toothed whales; only the rostral portion of the nasal septum is preserved as the cartilaginous rostrum (Klima 1999), which is rod-like and positioned between the paired premaxillary bones. It consists of hyaline cartilage in fetal and adult whales (Klima et al. 1986; Klima 1990). Some additional small cartilaginous structures are embedded in the soft tissues of the nasal complex, such as the so-called cartilages of the nostrils (Klima and Van Bree 1985) and the bursal cartilages (Cranford et al. 1996).

In adult sperm whales (*Physeter macrocephalus* Linnaeus, 1758), an additional large cartilaginous structure persists as a derivative of the *Tectum nasi* and accompanies the left nasal passage from the bony nares to the blowhole. This cartilage was first described by Behrmann and Klima (1985) and later termed the nasal roof cartilage (Klima 1999). As a result of the pronounced asymmetry of the sperm what nasal complex (see below), the position of the nasal roof cartilage has been shifted to the left. In the fetal sperm whale, the nasal roof cartilage consists of embryonic hyaline cartilage, but in adults, it consists of a special type of elastic cartilaginous tissue resembling hyaline cartilage (Klima 1990). The process of histogenetic transformation of the nasal roof cartilage from the fetal to the adult condition, however, could not be studied until now because of a lack of intermediate developmental stages. The present neonate sperm whale offers a unique opportunity to reconstruct the histogenesis of the nasal roof cartilage and to try to explain why a nasal roof cartilage exists only in sperm whales among odontocetes.

2. Material and methods

A 3.41 m long, 546 kg, neonate male sperm whale (*P. macrocephalus*) was stranded alive near Sabine Pass, Texas, in 1989, but died after 8 days of unsuccessful rescue efforts in the Sea-Arama Marine World, Galveston, Texas (Ridgway and Carder 2001). Immediately following its death, the calf was perfused through the aorta with a 10% buffered formalin solution. After the hypodermal layers and superficial muscles had been dissected, the head was frozen and sectioned into 13 transverse slices of approximately 5 cm thickness using a band saw. The remaining caudal part of the head, including the caudal end of the nasal complex, was scanned by magnetic resonance imaging (MRI) and dissected macroscopically. Out of three transverse slices (black arrows in Fig. 1 corresponding to frontal surfaces of sections 4, 8 and 12), representing the rostral, middle and caudal parts of the sperm whale nasal complex,

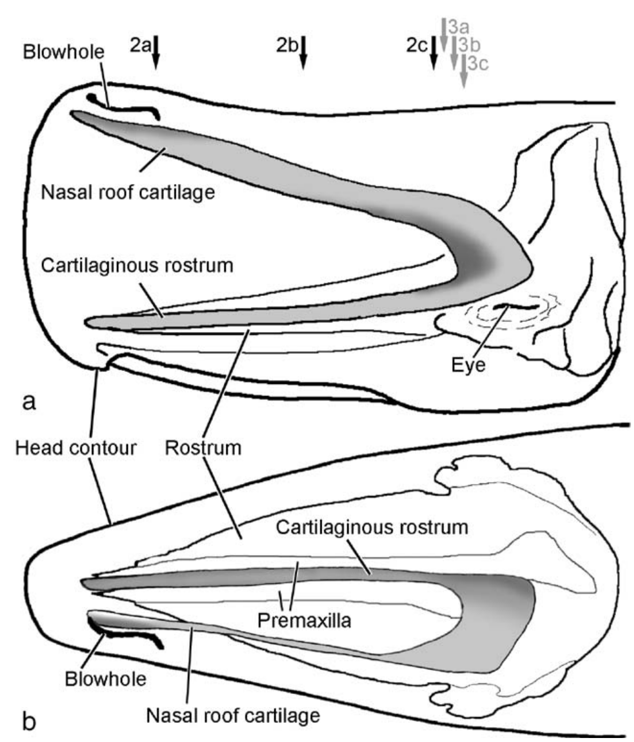

Fig. 1. Diagram drawing in left lateral view (a) and dorsal view (b) of the head of a neonate sperm whale showing the position of the nasal roof cartilage and the cartilaginous rostrum. The length of the head (from the rostral tip of the nose to the occipital condyles) is 77 cm. The black arrows indicate the location of the cryo-sections in Fig. 2, from which the tissue samples of both cartilaginous structures were taken, and the gray arrows point to location of the sections of the MRI scans shown in Fig. 3.

samples of the nasal roof cartilage and cartilaginous rostrum were taken for histological processing. These samples were embedded in paraffin, sectioned into transverse slices of 10 μm thickness, and stained with AZAN (azocarmine and aniline blue) or resorcin. Because the tissues were slightly decomposed before fixation, the cell substances could not be examined cytologically; however, the basic arrangement of the cells, their territories (i.e., chondrons), and the extra-cellular matrix, including the elastic fibers, were not affected by autolysis and could be analyzed.

3. Observations

3.1. Topography of the cartilaginous rostrum

In the neonate sperm whale, the cartilaginous rostrum is approximately 53 cm long. It is 3 cm in diameter at its frontal end, but approximately 2.5 cm wide and 4 cm high at its caudal end (Fig. 2). The massive rod-like cartilaginous rostrum fills the *Fossa mesorostralis*, which is situated dorsal to the vomer and between the paired premaxillary bones (Fig. 1) rostral to the bony nasal passages in the mediosagittal plane of the rostrum. The bony nares are situated in a deep facial depression of the skull, which is reminiscent of an amphitheater (Norris and Harvey 1972), at approximately the same level as that of the eyes.

3.2. Topography of the nasal roof cartilage

The nasal roof cartilage traverses the nasal complex nearly diagonally from the bony nares on the skull to the blowhole, which is situated at the rostral vertex of the head (Figs. 1 and 2). In the region of the bony nares, the nasal roof cartilage is continuous with the cartilaginous rostrum, i.e., the nasal roof cartilage arises from the caudodorsal free edge of the cartilaginous rostrum over a length of approximately 8 cm in our neonate specimen. From here, the nasal roof cartilage extends dorsally and laterally. After approximately 10 cm, it runs rostrally in a medial curve to the left nasal passage. At its caudal end, the nasal roof cartilage has no direct contact with the nasal passage, but is topographically related to it and separated from it by soft tissue. At its caudal base, the nasal roof cartilage appears irregular and undulating in cross-section (Fig. 3). On its rostral course, the nasal roof cartilage assumes a blade-like shape that is flattened in the sagittal plane and abuts laterally the left nasal passage (Fig. 2) and medially the connective tissue envelope of the spermaceti organ, which is a large body of oil that runs rostrocaudally through the entire nasal complex (Figs. 2 and 3; Norris and Harvey 1972; Clarke 1978; Møhl et al. 2003a). Over most of its length of approximately 55 cm in our neonate specimen, the nasal roof cartilage is approximately 4–5 cm high and 2–3 mm wide, but at the level of the blowhole, it is less high (3–4 cm) but slightly wider (ca. 4 mm). The dorsal edge of the rostral part of the nasal roof cartilage is bent slightly mediad at an angle of approximately 37° (Fig. 2).

3.3. Histology of the cartilaginous rostrum

The cartilaginous rostrum is formed by hyaline cartilage that shows nearly the same composition in all three transverse sections examined. The cartilaginous cells and their territories occur individually or in groups. In the center of the cartilaginous rostrum, the cells appear rounded, but at the periphery, they are slightly flattened (Figs. 4a and b). Furthermore, the cartilaginous cells are arranged concentrically around the blood vessels and lacunae. The extra-cellular matrix, which fills approximately 50% of the volume of the cartilaginous rostrum, appears homogeneous, and fibers were not observed (Fig. 4). The balanced ratio between cartilaginous cells and matrix is an indication of immature and growing tissue (Benninghoff 1925; Kummer 1985). The perichondrium is only slightly developed. This points to interstitial growth of the cartilage, which is also demonstrated by the robust vascularization of the cartilaginous tissue (not shown in figures). Blood vessels, including their typical wall structures (Fig. 4d), and lacunae, which appear to lack wall structures, are present (Fig. 4c). Delicate elastic fibers are seen in some layers of the walls of the blood vessels, which probably belong to the *Tunica intima* (not shown in figures). There are no distinct differences between the arterial and venous blood supply. There are no elastic fibers in the hyaline cartilage besides those in the walls of the blood vessels (Fig. 4).

3.4. Histology of the nasal roof cartilage

The nasal roof cartilage appears to be more complex than the cartilaginous rostrum in tissue composition as well as in structure and shows some peculiarities. In the neonate sperm whale, it consists of a special type of elastic cartilaginous tissue, as was observed in all three sections that were examined: the chondrocytes and their territories are arranged individually and only occasionally in groups. At the periphery of the nasal roof cartilage, the chondrocytes are small and flattened but, in the center they are relatively large and rounded. More than 50% of the volume of the nasal roof cartilage consists of extra-cellular matrix. Interestingly, this composition differs from typical elastic cartilage of terrestrial mammals, in which cellular components predominate within the extra-cellular matrix (Kummer

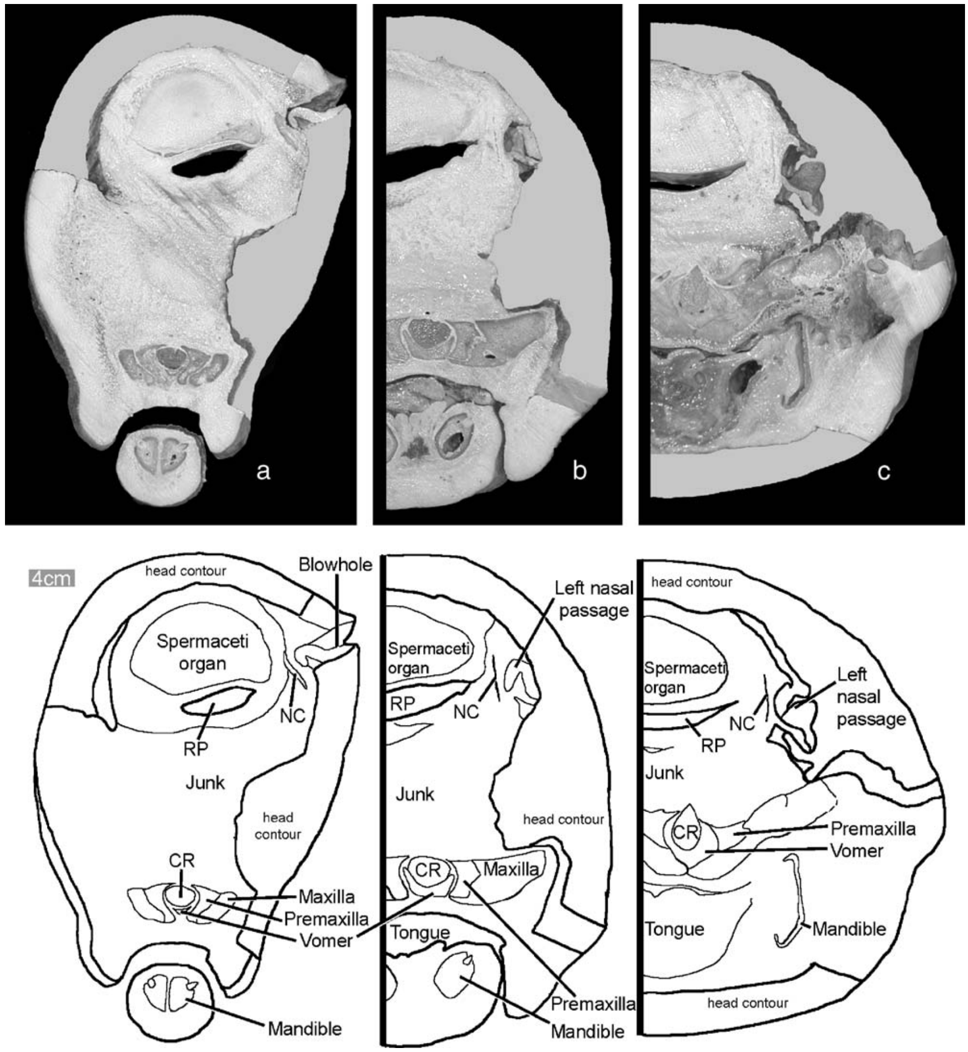

Fig. 2. Transverse cryo-sections through the head of a neonate sperm whale in frontal view from rostral (a) to caudal (c) showing the position of the nasal roof cartilage (NC) and the cartilaginous rostrum (CR). The positions of the particular sections within the head are indicated in Fig. 1. The superficial layers of the nasal complex were removed so that the original head contours were reconstructed graphically. Only the left side of the section is shown in (b) and (c). RP, right nasal passage.

1959, 1985). The high proportion of extra-cellular matrix in the nasal roof cartilage points to slow interstitial growth in spite of the large size of the nasal roof cartilage in the neonate sperm whale.

The nasal roof cartilage is interwoven by a number of more or less straight elastic fibers (Fig. 5). A wave-like or spiral structure, otherwise typical for elastic fibers (Roux 1895; Benninghoff 1925; Kummer 1985), is nearly absent; instead the elastic fibers vary in diameter. A greater number of elastic fibers are found at the periphery of the nasal roof cartilage near the perichondrium than in the center (Fig 5). Here, the elastic fibers are relatively thick, but ramify into thinner strands and extend into the center of the cartilage more or less perpendicularly to the surface. The perichondrium consists of a thick connective tissue layer with a number of collagen fibers, a network of elastic fibers (Fig. 5a), and some blood vessels (not shown in figures). The connection between the elastic network in the perichondrium and the elastic fibers of the cartilage is a sign of intensive proliferation of elastic fibers from the perichondrium into the deeper cartilaginous tissue (Fig. 5a). It appears, therefore, that peripheral, or appositional, growth at the perichondrium is more prominent than interstitial growth. This interpretation also correlates with the lack of blood vessels within the nasal roof cartilage.

4. Discussion

In the embryonic cetacean, the *Septum nasi* of the nasal capsule forms a wall in the median plane, dividing

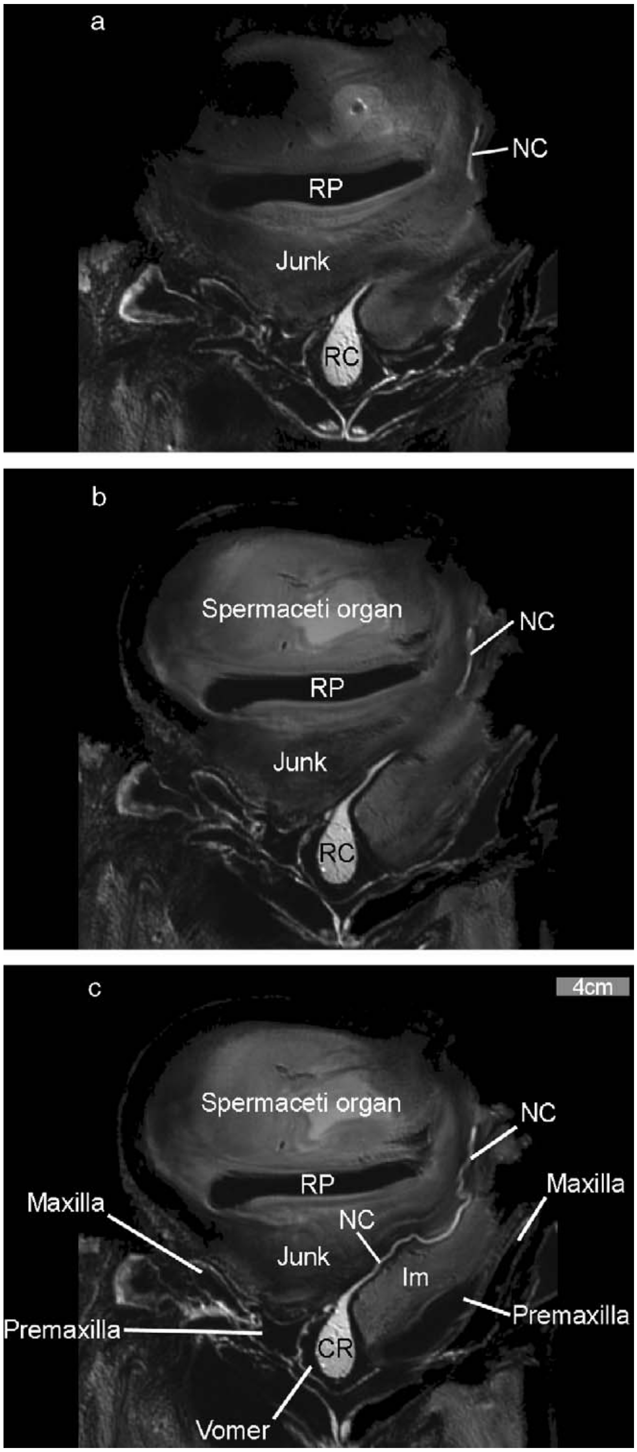

Fig. 3. Transverse MRI scans of the head of a neonate sperm whale from rostral (a) to caudal (c) showing the branching of the nasal roof cartilage (NC) and the cartilaginous rostrum (CR). The position of the sections within the head are indicated in Fig. 1. The superficial layers of the nasal complex were removed. lm, left nasal plug muscle; RP, right nasal passage.

the nasal capsule bilaterally into symmetrical halves (Fig. 6; Klima 1999). It consists of a vertical, triangular cartilaginous plate. Its ventral portion projects rostrally as the long cartilaginous rostrum (Fig. 6; Klima 1999), which is typical for adult cetaceans in general. In the sperm whale, however, the dorsal edge of the embryonic *Septum nasi* and the left *Tectum nasi* project dorsorostrally to form the nasal roof cartilage (Fig. 6; Klima 1999). The growth of this prominent structure extending diagonally through the forehead may be an important process for the formation of the soft nasal complex and, therefore, for the development of the typical shape of the sperm whale head (Klima et al. 1986; Klima 1999). A nasal roof cartilage was also found during the anatomical dissection of a 18 m long male sperm whale that was found stranded near Bremerhaven (Germany) in 1984 (Behrmann and Klima 1985). A comparison of the histological pattern of the nasal roof cartilage in the fetal and adult specimens revealed substantial differences (Klima 1990). In the fetus, the nasal roof cartilage consists of embryonic hyaline cartilage, which is well suited for morphogenetic processes and fast growth. In the adult sperm whale, however, the nasal roof cartilage consists of a special kind of elastic cartilage closely resembling hyaline cartilage (Klima 1990).

In our neonate sperm whale, as in the adult (Klima 1990), the cartilaginous rostrum and nasal roof cartilage differ greatly. Both cartilages are similar in length, but differ significantly in volume: The nasal roof cartilage is thin and blade-like, but the cartilaginous rostrum is conical, so that the estimated volume of the nasal roof cartilage is approximately 1% of the rostrum cartilage. However, the volumes of these two cartilages are similar in embryos and early fetuses. In fetuses of 10–90 cm total length, the nasal roof cartilage is as massive as the cartilaginous rostrum (Klima et al. 1986). The considerable sizes of these fetal cartilages may reflect their important role during the developmental arrangement and the fast growth of the sperm whale forehead (Klima et al. 1986; Klima 1999).

In the neonate sperm whale of 3.41 m total length examined in this study, the structure of the nasal roof cartilage is similar to that in the adult sperm whale with respect to the presence of elastic fibers. However, the histological analysis revealed some differences between the neonate and the adult. First, the perichondrium of the neonate nasal roof cartilage is thicker than in the adult (Klima 1990). This is an indication that cartilage growth is completed in the adult and that cartilage may be replaced only by regeneration. Second, there are differences in the accumulation, structure, and arrangement of the elastic fibers. The neonate sperm whale has more elastic fibers in the nasal roof cartilage than the adult (Klima 1990). This difference is probably caused by the perichondrium, which seems to lose its capacity to generate elastic fibers in the mature stage. The

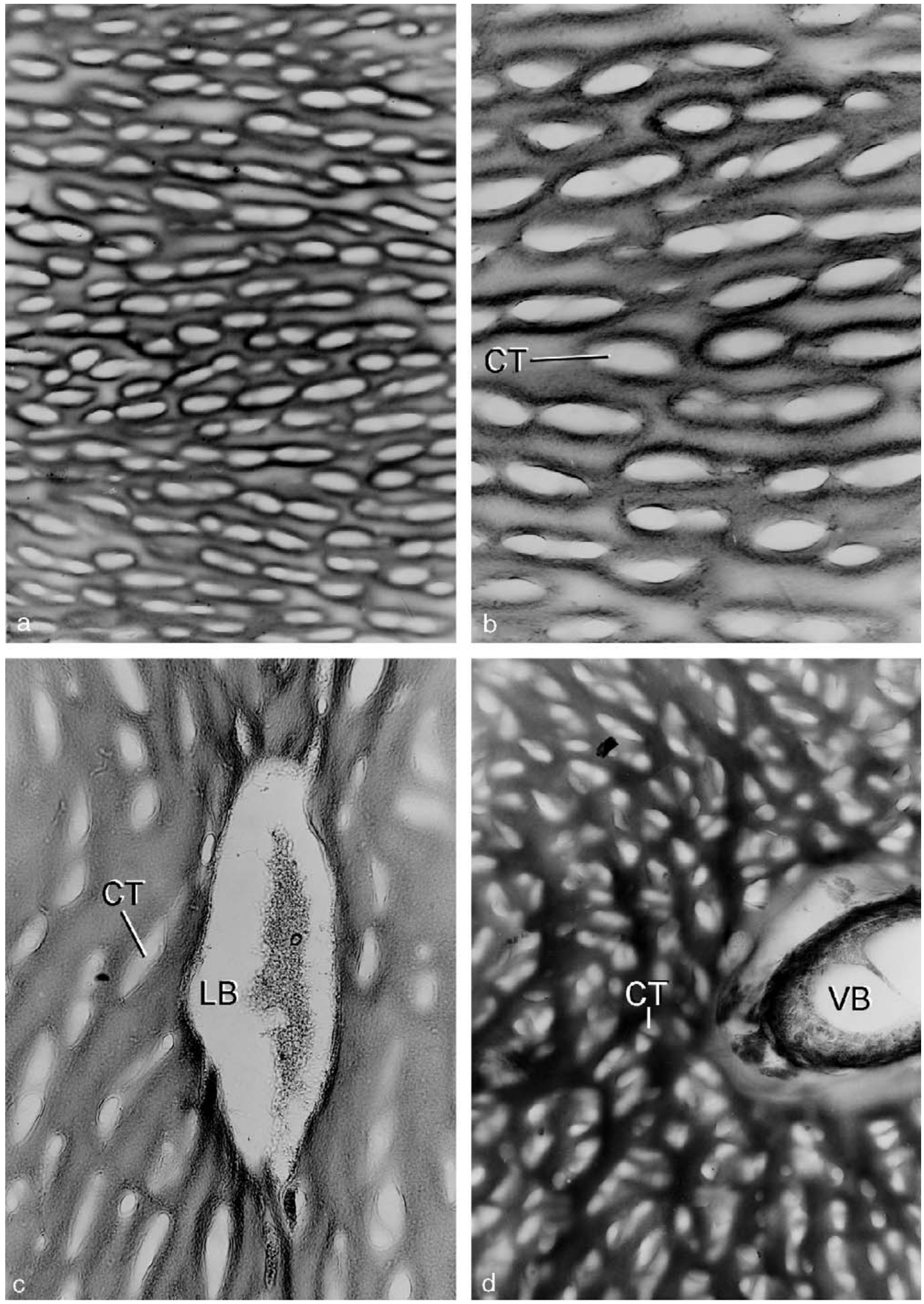

Fig. 4. Transverse sections of hyaline cartilaginous tissue of the cartilaginous rostrum of the neonate sperm whale. (a) Arrangement of peripheral cartilage cells and their territories (CT) within the extra-cellular matrix in overall view. (b) Detail of (a). (c) Blood lacuna (LB). (d) Blood vessel (VB) within the cartilaginous tissue. Stained with AZAN, approximate scale 1:180 (a, c, d) and 1:400 (b).

straight or slightly undulating course of the elastic fibers, as well as their parallel arrangement near the center of the cartilage in the neonate sperm whale could be caused by a lack of the mechanical stress that is characteristic for adults. Thus, the postnatal use of the head and jaw may lead to the adult-stage mature configuration of the nasal roof cartilage in which the elastic fibers become arranged and oriented in various directions according to their function.

After birth, the nasal roof cartilage seems to be reduced to a supporting structure of the left nasal passage. Its volume is reduced in relation to the tissues of the huge epicranial complex, while the relative volume of the cartilaginous rostrum is constant

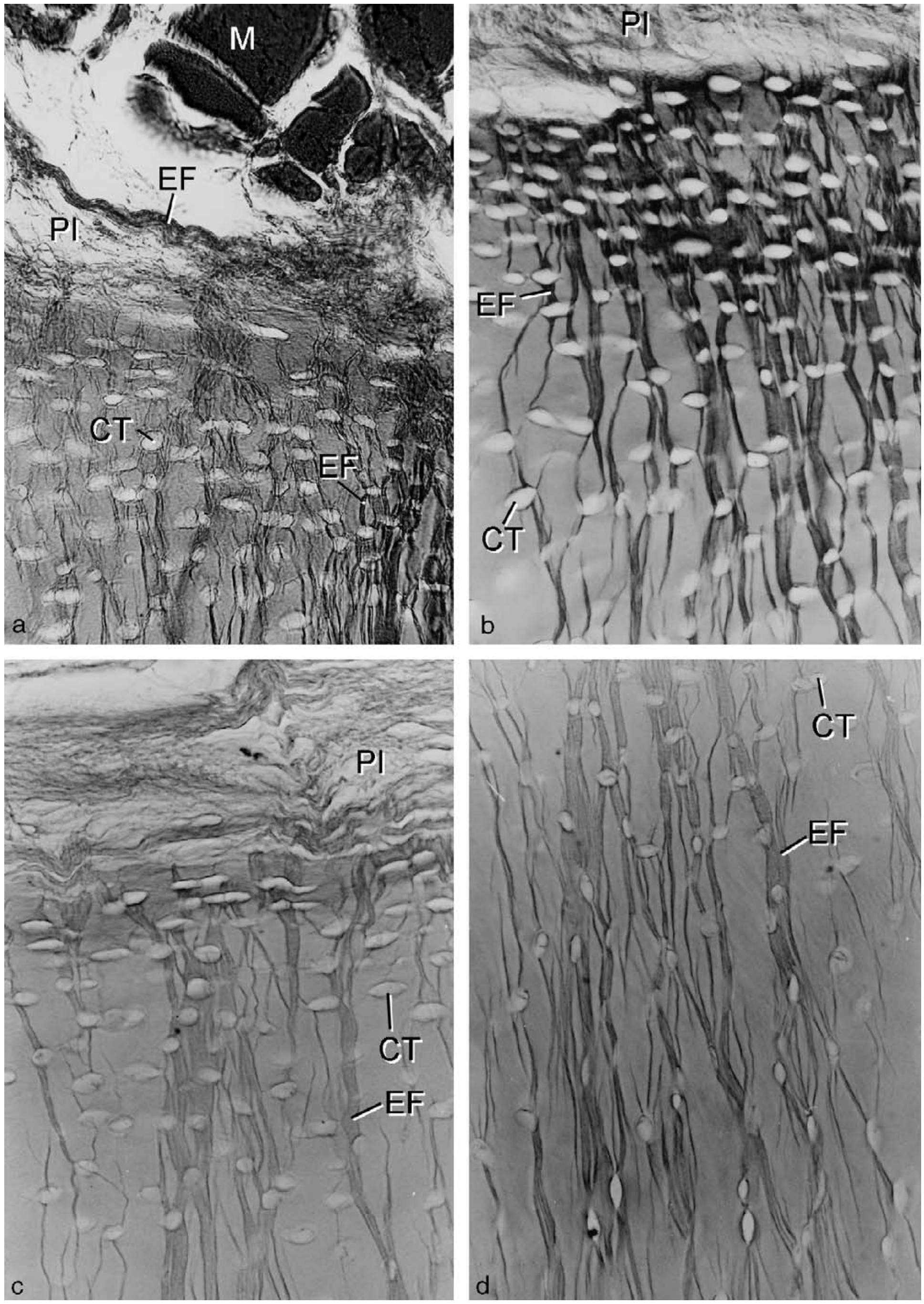

Fig. 5. Transverse sections of elastic cartilaginous tissue of the nasal roof cartilage in the neonate sperm whale. (a) Perichondrium (PI) and periphery of cartilage. (b) Arrangement, proliferation, and ramification of elastic fibers (EF) in the periphery of the nasal roof cartilage. (c) Penetration of the elastic fibers from the periphery to the center of the nasal roof cartilage. (d) Parallel and straight elastic fibers in the center of the nasal roof cartilage. Stained with AZAN (a, b) and resorcin (c, d), approximate scale 1:180. CT, territory of cartilage cell (chondron); M, muscle fibers.

throughout the entire developmental process (Klima 1999). This fact may be explained by the role of the cartilaginous rostrum as one of the main components of the elongated upper jaw, but the functional reason why it does not ossify during development and persists as such a prominent cartilaginous structure is still unknown. The high water content, the purported resistance to compression, and the elasticity and resilience of the cartilaginous tissue seems to be advantageous for an aquatic lifestyle (Felts and Spurrell 1965; Felts 1966; Klima 1999), but it is not clear how and why these mechanical properties are relevant for the cartilaginous

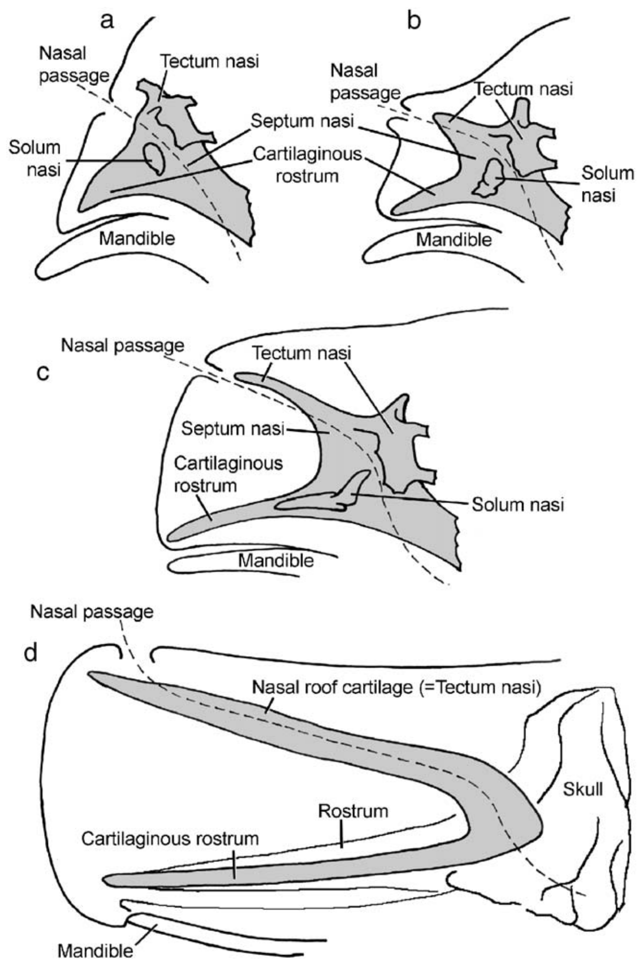

Fig. 6. Diagram drawings in left lateral view of a sequence of four stages in the developmental changes of the cartilaginous structures of the sperm whale (not to scale; a, b, c modified from Klima et al. 1986). (a) Small fetus, 40 mm crown-rump-length (CRL). (b) Medium-sized fetus, 90 mm CRL. (c) Larger fetus, 170 mm CBL. (d) Neonate, 340 cm total length.

rostrum, which is embedded in dense and stable bones. An acoustic function of the cartilaginous rostrum, as suggested by Pilleri and co-workers (Pilleri et al. 1983; Purves and Pilleri 1983; Pilleri 1990), is unlikely because of the poor acoustic coupling between the proposed sound, or click, generator (i.e., the phonic lips) at the rostral end of the spermaceti organ (Cranford et al. 1996; Cranford 1999; Møhl 2001) and the cartilaginous rostrum. The cartilaginous rostrum of the neonate sperm whale examined here consists of mature hyaline cartilage. There are no indications of embryonic hyaline cartilage, except the relatively robust blood supply. However, in the present context, the vascularization may not be interpreted as an embryonic character but as an allometric phenomenon of the mature cartilaginous rostrum, since such a massive structure cannot be supplied with nutrients through the superficial perichondrium alone. An internal blood supply seems necessary as is typical for large cartilaginous structures (Wilsman and van Sickle 1972).

Cartilaginous tissue can adapt to various mechanical forces by developing into different types of cartilage. Pressure stress causes the development of hyaline cartilage, whereas shearing stress induces the formation of elastic cartilage (Roux 1895; Benninghoff 1925; Kummer 1959, 1985). In the adult sperm whale, the arrangement of the cells, their territories, and the extracellular matrix of the nasal roof cartilage corresponds to that in hyaline cartilaginous tissue (Klima 1990). The occurrence and arrangement of elastic fibers in this cartilage correspond to elastic cartilaginous tissue. The combination of hyaline cartilage with elastic fibers indicates that both pressure and shearing influence the structure of the nasal roof cartilage (Klima 1990, 1999). In the following paragraphs, we propose possible causes that may have led to the typical histological arrangement of the nasal roof cartilage in adult sperm whales.

The nasal roof cartilage does not serve as a true skull strut given the huge proportions of the nose in the sperm whale (Raven and Gregory 1933; Klima 1990, 1999). After losing its important function in the formation of the nasal complex during early prenatal development (Klima et al. 1986; Klima 1999), the nasal roof cartilage seems to be partly reduced in postnatal animals but supports the left nasal passage throughout its entire length. Since the left nasal passage probably serves mainly in respiration (Norris and Harvey 1972), it is likely that the close association of the nasal roof cartilage and the left nasal passage benefits rapid air exchange during ventilation. One of us (SHR) has palpated the left side of the head while the neonate was still alive during the respiratory cycle and felt a lateral movement of the side of the head presumably due to the airflow in the nasal passage. The left nasal passage is embedded in the soft tissue of the nasal complex. It is plausible, therefore, that the nasal roof cartilage may stabilize this long passage during respiration. A muscle that inserts onto the lateroventral wall of the left nasal passage and originates in the connective tissue and the skull ventral of this passage (i.e., the nasal plug muscle; Fig. 3; Schenkkan and Purves 1973; Clarke 1978) may open it for inhalation, while the medial wall of the passage facing the dorsal roof cartilage remains stationary. Consequently, the nasal roof cartilage may prevent the nasal passage from collapsing during the high negative pressure event of inhalation, yet, the cartilage would slightly deform due to shearing stress during this event, since it is not supported by rigid tissue and since Bernoulli forces probably would deform the medial wall of the left nasal passage.

Klima (1990) interpreted the presence of elastic fibers in the dorsal roof cartilage as a possible adaptation to resist deformation by hydrostatic pressure during dives. This hypothesis cannot be rejected here, but from a functional point of view, it is plausible that the left nasal passage, which is probably not involved in phonation in contrast to the right nasal passage (Norris and Harvey 1972; Cranford et al. 1996; Cranford 1999), would be collapsed by the increased pressure during a dive so that the hydrostatic pressure would not deform the adjacent soft tissues of the sperm whale nose.

The entire nasal complex of sperm whales is covered dorsolaterally by the very strong maxillonasolabialis muscle which stretches from the dorsal crest of the frontal bone rostrally (Norris and Harvey 1972; Schenkkan and Purves 1973; Clarke 1978). Contraction of this muscle may pull the rostrodorsal area of the nasal complex, i.e., the phonic lips, caudally (Norris and Harvey 1972). This muscle action could compress and deform the nasal roof cartilage over its entire length and could be another source of stress possibly explaining the presence of both the hyaline and elastic components of the dorsal roof cartilage in neonates and adults (Klima 1990).

Among Cetacea, the sperm whale is distinguished by extremes: it is the largest toothed whale and possibly the mammal that can dive into the greatest depth (Kooyman 2002). Adult male sperm whales have the ‘‘biggest nose on record’’ (Raven and Gregory 1933). The whale’s head may be as much as 7 m in length in the largest males (Nishiwaki et al. 1963; Berzin 1972), and the nasal passages could reach more than 4 m in length (Behrmann and Klima 1985) in such specimens. Norris and Harvey (1972) proposed an acoustic function for the sperm whale nose, and most recent examinations of this immense nasal apparatus interpret it as a bio-acoustic machine (Cranford et al. 1996; Cranford 1999; Ridgway and Carder 2001; Møhl 2001; Møhl et al. 2003a, b) that is capable of generating the highest biological source level recorded to date (Møhl et al. 2000, 2003b; Møhl 2001). According to theoretical considerations (Norris and Harvey 1972; Møhl 2001), the click sounds are generated by clapping events of the so-called phonic lips, which are part of the right nasal passage (Cranford et al. 1996). Due to the hypertrophied size of the acoustic structures associated with the right nasal passage (Cranford et al. 1996; Cranford 1999), the nasal components of the left side appear to be reduced although the left nasal passage is still quite robust. The hyaline character of the nasal roof cartilage accompanying the left nasal passage medially may be explained by stress caused by compression of the massive nasal musculature associated with structures of the right nasal passage (i.e., the spermaceti organ and phonic lips) and the blowhole. The left nasal passage primarily functions in respiration and is probably not involved in sound production (Norris and Harvey 1972; Cranford 1999; Møhl 2001). This condition is in contrast to that in non-physeterid toothed whales, in which both nasal passages serve both respiration and phonation (Cranford et al. 1996). The nasal roof cartilage of sperm whales may stabilize the left nasal passage during inhalation over its extreme length. The elastic fibers may develop in reaction to the deformation of this cartilage for the period of the high negative pressure during inhalation.

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