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Macroscopic Anatomy of the Saimaa Ringed Seal (*Phoca hispida saimensis*) Lower Respiratory Tract

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ABSTRACT

We studied the macroscopic anatomy of the lower respiratory tract of the endangered Saimaa ringed seal (*Phoca hispida saimensis*). Examination of one adult and one young individual found dead showed that trachea had 85 and 86 complete cartilage rings. The adjacent cartilages exhibited very few random anastomoses. There was variation in the confirmation of the trachea between the cranial and caudal part of the trachea. The right lung was divided by partly incomplete inter-lobar fissures into cranial, middle, caudal, and accessory lobes. The left lung consisted of cranial, middle, and caudal lobes. The lungs were characterized by a high amount of interlobular connective tissue. Silicone casts were prepared of the two specimens to visualize the tracheobronchial branching which was similar to that of marine ringed seals but in the Saimaa ringed seal the right middle lobar bronchus originated at the same level as the accessory lobar bronchus. Anat Rec, 299:538–543, 2016. © 2016 Wiley Periodicals, Inc.

Key words: Phoca hispida; pulmonary anatomy; Saimaa; silicone casts

INTRODUCTION

The Saimaa ringed seal (*Phoca hispida saimensis*) has a population size of approximately 300 individuals that inhabit the highly fragmented Lake Saimaa in southeastern Finland. The long isolation period (due to the most recent glaciation period at the end of the Pleistocene) of the small landlocked populations has greatly reduced genetic variation of the Saimaa ringed seal (Valtonen, 2014). This genetic bottleneck in combination with derived morphological traits, such as large orbits, dark pelage, and unique tooth shapes (Hyvärinen and Nieminen, 1990; Amano et al., 2002; Berta and Churchill, 2012) makes the Saimaa ringed seal an important model species to uncover the genetic underpinnings of phenotypic traits. As part of our ongoing research on the genotypic and phenotypic characteristics of the Saimaa ringed seal, we documented the macroscopic anatomical features of its' lower respiratory tract, and compared that to those of other phocid species. Marine mammals have unique distribution of cartilage in the trachea and bronchi. Cartilaginous rings act to reinforce the airways in order to receive air expelled from the compliant alveolar space (Scholander, 1940; Kooyman and Sinnett, 1979). This kind of morphology allows alveolar compression and collapse, resulting in cessation of gas exchange as pressure increases during deep dives (Bostrom et al., 2008). The tracheal rigidity of marine mammals facilitates the rapid and more complete emptying of lungs as

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compared to terrestrial mammals (Denison et al., 1971; Bostrom et al., 2008). Recent theoretical models suggest that the compliance of the trachea plays a role in determining the lung collapse depth and subsequent levels of gas exchange at pressure (Bostrom et al., 2008; Fahlman, 2008). Thus, structural differences of tracheas may correlate with diving ability and life history (Moore et al., 2014). Ultimately, we may be able to understand the genetic basis of the variation in the morphological traits of various seal species that enable us to compare phenotypic adaptations of seals to other marine mammals (Foote et al., 2015) in detail.

MATERIALS AND METHODS

The Saimaa ringed seal tissue bank is maintained by the University of Eastern Finland and the Parks & Wildlife of Metsähallitus (a state enterprise that administers state-owned land and water areas) which collects all Saimaa ringed seals found dead and stores them in −20°C. Once a year all the specimens recovered are examined at the Oulu unit of the Finnish Food Safety Authority (Evira) where various tissue samples are collected for the long-term monitoring on the health of the seals. Most specimens are in various stages of decomposition preventing any detailed morphological studies.

During October 2013, two by-caught seals (by gill nets) were necropsied and were found to be in a good condition, allowing detailed morphological examination. One specimen was a young female (36 kg, specimen number 2563) found in Pihlajavesi in January 2013, and the other an approximately 4-month old female (21 kg; specimen number 2585) found in Haukivesi in July 2013. The larynx, trachea, and lungs were cut off as whole and transported in cold storage box to the Faculty of Veterinary Medicine in Helsinki where the lower respiratory tract was examined macroscopically for basic morphology.

In preparation of tracheobronchial cast (Laakkonen and Kivalo, 2013), the airways were washed twice with tap water to remove blood and debris. The lungs were dripped dry. A two component (portioned in a singular package) silicone (3M Express© 2 Light Body Standard Quick) was injected into the trachea using a gun-like silicone dispenser (Garant, with a 3M mixing tip), which mixed the two components during injection. For the injection, the lungs were positioned horizontally (to allow adequate flow into all lobes) on a table, and silicone mix was applied separately into each bronchus (the correct position of the mixing tip was checked by palpation). The dispenser was hooked tightly into the bronchus by forceps. The low viscosity mix flowed distally freely through the wet tracheobronchial lumina via digital pressure provided by the dispenser. When silicone material started to flow out around the applicator tip, the injection was deemed finished, and the bronchi were closed with digital pressure for 3 min. At this point, the surface of the lungs was examined for the pink silicone-mix to be seen through the serosa and parenchyma of the lung that confirmed adequate airway flow of silicone. The silicone hardened in 2 min–3 min (as indicated by the manufacturer's instruction manual) but all specimens were allowed to harden for 15 min to make sure that all parts of the cast were hardened. After hardening, the specimens were placed into a bucket of sodium hypochlorite solution (14%, Sigma-Aldrich, Switzerland) in a horizontal position for the removal of lung tissue. During maceration the specimens were rotated daily and the sodium hypochlorite solution was changed two to three times a week depending on how well the maceration proceeded. The finished casts were stored in room temperature and examined for branching of the bronchi and smaller airways. The trachea was first examined fresh and then placed in sodium hypochlorite solution for 2 days for removal of the soft tissue. Anatomical terminology used is in accordance with the International Committee on Veterinary Gross Anatomical Nomenclature (2012).

RESULTS

Trachea

The trachea began immediately caudal to the cricoid cartilage of the larynx and extended caudally to tracheal bifurcation. The trachea of the adult Saimaa seal contained 85 cartilages and that of the young seal 86 cartilages. The adjacent cartilages exhibited very few random anastomoses. In both specimens, all tracheal cartilages were complete rings but especially the most caudal ones were very thin on the dorsal aspect. During the sodium hypochlorite treatment most of the cartilages broke from the dorsal aspect indicating that the dorsal aspect of rings was weaker than the ventral aspect. In the cranial part of the trachea, the rings were wider and thicker than those in the caudal part. There was also very little soft tissue between the adjacent cartilages in the cranial part of the trachea. From larynx until approximately midway of the trachea, the tracheal lumen was round on cross section (diameter 12 mm–15 mm) but in the latter part of the trachea the lumen was slightly dorsoventrally, and in the most caudal part, laterally compressed. This caused the caudal half of the trachea to be less rigid than the cranial part when pressure was applied from the dorsal side.

Lung Lobation and Lobulation

The lungs were dark and swollen, but the lobulation became more readily visible after the lungs had been injected with silicone that made the lungs more rigid (Fig. 1). The natriumhypoclorite bath for a few days further enhanced the external lines and shapes of the lung lobulation (Fig. 1), and illustrated the marked separation of the lung parenchyma by connective tissue septa into segments and lobules visible on the lung surface (Fig. 1).

The right lung of the Saimaa ringed seal was divided by partly incomplete inter-lobar fissures into cranial, middle, caudal, and accessory lobes (Figs. 1 and 2). In the right cranial lobe a notch or incomplete accessory fissure was visible along the free edge of the lobe. During the maceration process this presented itself as a distinct fissure (Fig. 2). The apex of the right cranial lobe was rounded but less so than the cranial left lobe (Fig. 2). The accessory lobe exhibited two distinct segments separated by a pleural band (Fig. 1).

The left lung was divided by inter-lobar fissures into cranial, middle and caudal lobes (Figs. 1 and 2). The interlobar fissure separating the middle and caudal lobes extended from the dorsal border of the lung to the

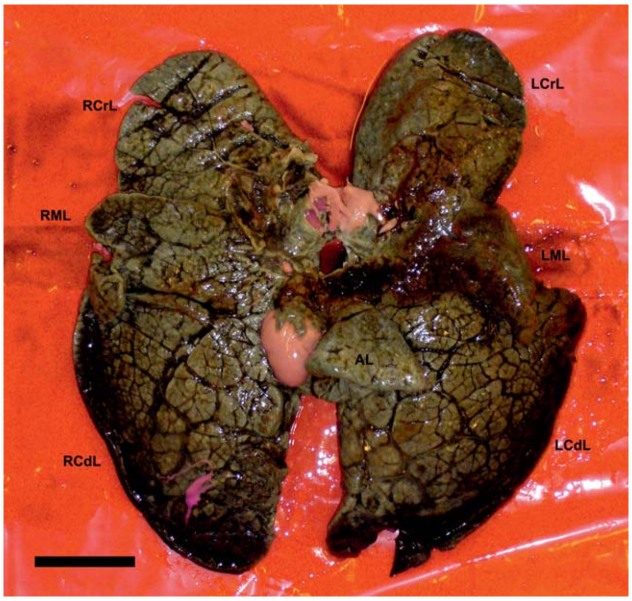

Fig. 1. Lungs of the adult Saimaa ringed seal injected with silicone (visible in places where the pink silicone has escaped through broken pulmonary pleura) and subjected to natriumhypoclorite bath for 2 days to enhance the external lines and shapes of the lung lobulation. Note the marked separation of the lung parenchyma by connective tissue septa into segments and lobules visible on the lung surface. Ventral view. Right cranial (RCrL), middle (RML), caudal (RCdL), and accessory (AL) lobes. Left cranial (LCrL), middle (LML), and caudal (LCdL) lobes. Scale bar = 5 cm.

Fig. 2. Lungs of the adult Saimaa ringed seal injected with silicone and subjected to natriumhypoclorite bath for 7 days. Dorsal view. Right cranial (RCrL), middle (RML), caudal (RCdL), and accessory (AL) lobes. Left cranial (LCrL), middle (LML), and caudal (LCdL) lobes. Scale bar = 6 cm.

ventral margin only on the edge of the lobe, Fig. 2). The caudal lobe had an incomplete accessory fissure visible along the free caudal edge of the lobe (Fig. 2). The apex of the left cranial lobe was round.

Tracheobronchial Tree

The bifurcation of the trachea gave rise to two caudodorsally directed principal bronchi (Fig. 3) which were at a 90-degree angle from each other. In the young seal, the diameter of the bronchi was 11 mm, and in the adult seal was 14 mm. The principal bronchi were divided into lobar bronchi upon entering the lung parenchyma.

Right Lung Bronchial Tree

The craniodorsally directed right cranial lobar bronchus (6 mm and 9 mm in diameter in the young and adult seal, respectively) arose 7 mm–8 mm caudal to the tracheal bifurcation (Fig. 3). The right cranial lobar bronchus divided into three segmental bronchi of which one divided immediately further into two, producing four clearly distinguished segments. The first one (diameter 3 mm in both specimens), was directed dorsally at a 90-degree angle from the lobar bronchus, and the other two craniodorsally (diameter 3 mm–4 mm) at a 45-degree angle from each other. Of these two, the more cranial one was subsequently divided irregularly into 6–7 smaller airways. The more caudal of these two, first divided further into two larger airways (diameter 2 mm) before each dividing irregularly into 6–7 smaller airways.

At the level of the middle lobar bronchus, the right principal bronchus gave rise (at an angle of 90-degree) to the accessory lobar bronchus (diameter 3 mm–4 mm) that emerged from the ventromedial aspect but curved into dorsomedial direction (Fig. 3). The accessory lobar bronchus gave rise to 5 segmental bronchi (ca. 1.5 mm) which arose from all aspects of the accessory lobar bronchus but almost all showed a tendency to project dorsally.

The right principal bronchus then gave rise (at an angle of 45-degree) to a dorsolaterally directed middle lobar bronchus (diameter 6 mm–7 mm) 25 mm from the tracheal bifurcation (Fig. 3). This middle lobar bronchus divided into 12–13 segmental bronchi (diameter 1.5 mm–2.5 mm) most of which radiated cranio-laterally. All segmental bronchi divided further into multiple, very small airways (diameter < 1 mm).

From the point of origin of the accessory and middle lobar bronchi, the right principal bronchus continued caudally as the caudal lobar bronchus (diameter 9 mm–10 mm). Approximately 5 mm caudal to the origin of the accessory lobar bronchi, arose (at an angle of 45-degree) a segmental bronchi (diameter 4 mm–5 mm) from the dorsal aspect of the caudal lobar bronchus. These bronchi branched further irregularly into smaller airways. Approximately midway between the point of origin of the accessory and middle lobar bronchi and the origin of two segmental bronchi (diameter 5 mm) that run almost parallel, a small segmental bronchi (diameter 1.5 mm) arose (which branched into tiny airways) from the ventromedial aspect of the caudal lobar bronchus (Fig. 3). After giving off the two mentioned segmental bronchi, the caudal lobar bronchus continued caudally dividing into the two parallel segmental bronchi that subsequently branched into irregular divisions

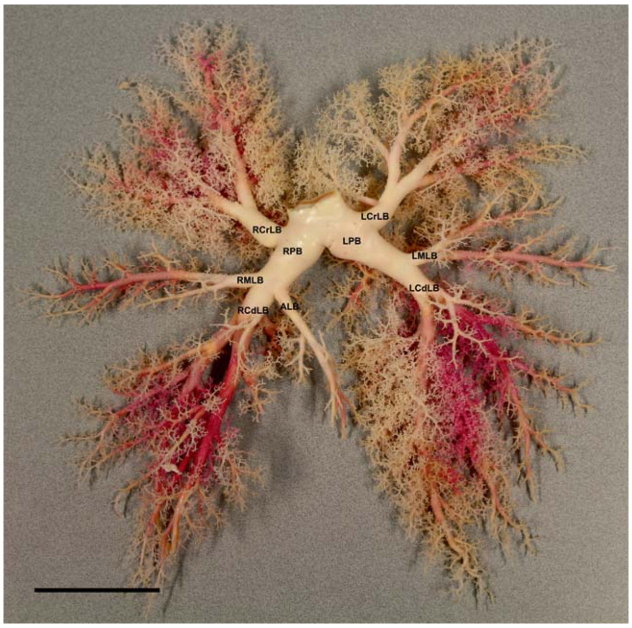

Fig. 3. Bronchial cast of the adult Saimaa ringed seal. Ventral view. The silicone compound accurately reproduced the branching and the size of the principal and segmental bronchi. Most of the smaller airways were also demonstrated but in some lung regions the silicone had not distributed equally well into the smaller airways. Right (RPB) and left (LPB) principal bronchus, right (RCrLB) and left (LCrLB) cranial lobar bronchus, right (RMLB) and left (LMLB) middle lobar bronchus, right (RCdLB) and left (LCdLB) caudal lobar bronchus, and accessory lobar bronchus (ALB). The darker pink indicates areas where the lung tissue was the thickest and the maceration process took the longest time. The complete maceration process took 6 weeks. Scale bar = 5 cm.

into multiple (7–9) smaller airways ranging in diameter <1 mm–2 mm.

Left Lung Bronchial Tree

The left principal bronchi gave rise to a craniodorsally directed cranial lobar bronchus approximately 10 mm–11 mm from the tracheal bifurcation at an angle of 90-degree (Fig. 3). The cranial lobar bronchus (diameter 6 mm) continued 9 mm before it gave off (at an angle of 90-degree) a dorsally directed segmental bronchus (diameter 2.5 mm–3 mm) which divided irregularly into smaller airways. The cranial lobar bronchus (diameter 4 mm–5 mm at this point) continued another 7 mm–8 mm before dividing into two dorso-cranially directed segmental bronchi. Of these, the minor, more cranial one (diameter 3 mm) branched at a 45-degree angle, and divided irregularly into smaller airways with diameters varying from 2 mm to < 1 mm. The major, more caudal segmental bronchi (diameter 4 mm) continued along the same axis as the left cranial lobar bronchus for 9 mm before giving off a craniodorsally directed segmental bronchi (diameter 2.5 mm) which quickly divided irregularly into 6–7 small airways (diameter <1.5 mm). The other branch also divided irregularly into 9–10 small airways (<1–2 mm in diameter).

Approximately 15 mm caudal to the origin of the cranial lobar bronchus, the left principal bronchus gave arise (45-degree) to the middle lobar bronchus (diameter 4 mm) from its ventrolateral surface. From that point, the principal left bronchus continued as the left caudal lobar bronchus. The middle lobar bronchus gave rise to four segmental bronchi (diameter 1.5–3 mm) which branched into smaller airways. One of the segmental bronchus originated from the ventral, one from the dorsal and two from the caudolateral surface of the middle lobar bronchus.

Almost immediately after the origin of the middle lobar bronchus, the left caudal lobar bronchus gave rise (45-degree) to its first segmental bronchus (diameter 3 mm) from its dorsal surface. From the point of origin of the middle lobar bronchus, the left caudal lobar bronchus continued for approximately 10 mm–11 mm before it gave rise to two dorso-laterally directed segmental bronchi (diameter 3.5 mm–4 mm at an 45-degree angle from each other) as well as one ventrally directed smaller segmental bronchi. All the segmental bronchi irregularly divided further into smaller airways.

DISCUSSION

The number of tracheal rings (85 and 86) in our Saimaa ringed seal specimen corresponded with those (an average of 87) of previous seal studies (Sokolov et al., 1971; cited in Smodlaka et al., 2009). Compared to some other phocid species, however (Boyd, 1975; Frost and Lowry, 1981; Smodlaka et al., 2009; Moore et al., 2014), the Saimaa ringed seal had no gaps or slips in any of their tracheal cartilage rings. However, the dorsal part of most of the rings was thin as it dissolved quickly, especially in the caudal part, after the trachea was placed in the hypochlorite treatment.

Similarly to that of ringed seal (Smodlaka et al., 2009), the tracheal diameter (11 mm–12 mm) of Saimaa ringed seal is small compared to its body size. Also, similarly to other pinnipeds (Boyd, 1975; Smodlaka et al., 2009), the trachea of the Saimaa ringed seals was partly flattened. Moore et al. (2014) recently summarized the discussion on the role of tracheal morphology on the diving ability of mammals. The maximum depth of the Lake Saimaa is 80 m, and the Saimaa ringed seals are known to dive also to those depths (Kunnasranta et al., 2002). The Saimaa ringed seal catches fish by rapid forward movements of the head and neck (M. Kunnasranta, personal communication). The dorsoventrally compressed, flexible caudal trachea may ensure that the neck of the Saimaa ringed seal can efficiently bend during the retraction phase despite the lack of incomplete caudal tracheal rings which add compliance to an overall rigid trachea in some other phocids (Smodlaka et al., 2009; Moore et al., 2014). Histological studies are needed to determine the type and amount of tissue present between rings lengthwise which may potentially indicate differences in flexibility between the bronchial regions. The feeding kinematics of Saimaa ringed seal has not been studied in detail but research on a closely related species, the harbor seal (*Phoca vitulina*) shows (Marshall et al., 2014) that seals have a wide repertoire of feeding strategies, some of which (suction, hydraulic jetting) relate partly to the anatomy of the respiratory apparatus.

Interestingly, varied degrees of lobation in lungs of northern pinnipeds has been reported including the ringed seals (Sokolov et al., 1971; Frost and Lowry,

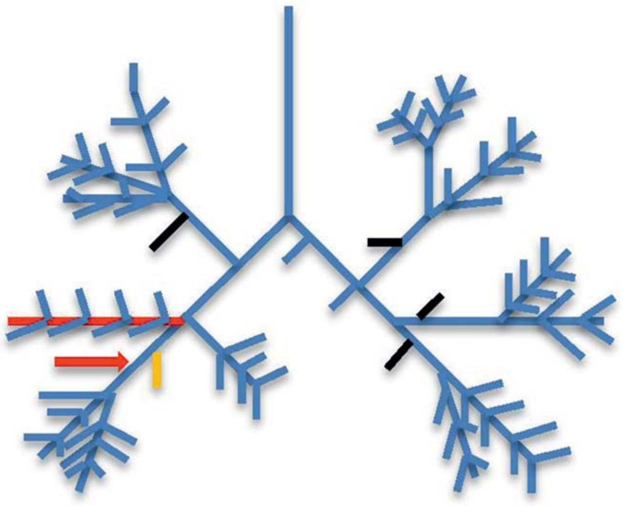

Fig. 4. Schematic presentation of the bronchial tree of the Saimaa ringed seal (ventral view). Branches with dorsal orientation are shown in black. Minor difference between the specimens was found in the origination point of the first segmental bronchus (which also had a dorsal orientation) from the right caudal lobar bronchus (marked in orange). The right middle lobar bronchus (marked in red) of the Saimaa ringed seal originated at the same level as the accessory lobar bronchus but in the ringed seal the right lobar bronchus is reported (Smodlaka et al., 2009) to emerge from the principal bronchus approximately 10 mm caudal to the origin of the accessory lobar bronchus (arrow).

1981; Koster et al., 1990; Smodlaka et al., 2009). In this study, the lobation became more readily visible during the natriumhypoclorite bath (Fig. 2), and showed that the Saimaa ringed seal, similarly to the marine ringed seal (Smodlaka et al., 2009) had clearly lobulated lungs. The functional explanation for the lobation pattern of mammalian lungs is not entirely clear (Tarasoff and Kooyman, 1973; Boyd, 1975) but it has been suggested that the unlobed, uniformly shaped lungs may facilitate the exchange of most of the lung capacity with each ventilation (cetaceans, see Boyd, 1975). In our study, the apex of the left cranial lobe of the Saimaa ringed seal was round (Fig. 1) but in the magnetic resonance imaging study of a dead Saimaa ringed seal (Usenius et al., 2007) the left cranial lobe appeared relatively pointed. Whether this discrepancy is due to post mortem changes remains to be investigated.

The tracheobronchial tree of the Saimaa ringed seal showed irregular mode of division (Schlesinger and McFadden, 1981) in some parts of lung, with the daughter branches differing with respect to the branch diameter. The general branching was similar to that of the marine ringed seal (Smodlaka et al., 2009) but one significant difference was also found. The right middle lobar bronchus of the Saimaa ringed seal originated (in both specimens) at the same level as the accessory lobar bronchus (Figs. 3 and 4) but in the ringed seal the right lobar bronchus emerged from the principal bronchus approximately 10 mm caudal to the origin of the accessory lobar bronchus (Smodlaka et al., 2009). In the two Saimaa ringed seal specimens, there was minor variation in the origin of the first segmental bronchus from the right caudal lobar bronchus. In the adult Saimaa ringed seal, the first segmental bronchus to the right caudal lobar bronchus rose from the dorsal side 6 mm, and in the young Saimaa ringed seal 9 mm, distal to the middle lobar bronchi. In the marine ringed seal, the corresponding segmental bronchus arose from the dorsal side approximately 5 mm caudal to middle lobar bronchi (Smodlaka et al., 2009). More Saimaa ringed seal specimens need to be examined to determine whether the difference in branching compared to that of marine ringed seal is due to variation within the former species or a consistent finding. The long isolation period and fragmented populations of the Saimaa ringed seal make it an intriguing species for studies on lung morphogenesis and bronchial tree branching (Metzger et al., 2008).

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