NOTE

Comparison of the musculoskeletal forelimb anatomy of the Saimaa (*Pusa hispida saimensis*) and Baltic ringed seals (*Pusa hispida botnica*)

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Species or subspecies that are difficult to distinguish based on morphological characters are common in all major marine groups and habitats (Churchill & Uhen, 2019; Knowlton, 1993). Ringed seals form a particularly interesting group in this respect, consisting of both widespread marine populations as well as small local populations inhabiting fresh or brackish water environments. The unique evolutionary history of the Saimaa ringed seal offers an excellent opportunity for comparative anatomical studies with other ringed seal subspecies adapted to different habitats, but such studies are also challenging due to the endangered status of the Saimaa ringed seal. The population consisted of less than 200 individuals from the 1950s to 1980s, but the estimated population size is now circa 400 individuals (Metsähallitus, 2019).

Low-to-moderate genetic differentiation between ringed seals from the Baltic Sea and from the Arctic Seas are reported in contrast to the high differentiation between these populations and the Saimaa ringed seal population (Martinez-Bakker et al., 2013; Savriama et al., 2018; Valtonen et al., 2012), which became landlocked about 9,500 years ago (Ukkonen et al., 2014; Valtonen et al., 2012). Subtle but distinct morphological differences between the ringed seal subspecies have been reported mainly from the skull and jaw muscles (Amano et al., 2002; Endo et al., 1998, 2002; Hyvärinen & Nieminen, 1990; Laakkonen & Jernvall, 2020; Nordqvist, 1899) but also from the lungs (Laakkonen & Jernvall, 2016). Most of these studies, however, compare only a few individuals of each subspecies, which prevents elimination of intraspecific and age-specific variation between subspecies. Furthermore, a recent study cautions against the use of postcranial anatomy below the level of subfamily taxonomy due to intraspecific variation in seals (Churchill & Uhen, 2019).

Phocids have retained archaic features like mobile phalanges and sizeable claws allowing prey processing with forelimbs (Böhmer et al., 2019; Hocking et al., 2018; Quakenbush, 1991). Besides steering during swimming forelimbs are also used when moving on ice or land during molting and breeding (Backhouse, 1961; Berta et al., 2015). Quakenbush (1991) observed a captive ringed seal holding a large fish between its teeth and slapping it with a flipper until a piece small enough to swallow had been torn off, but the relatively small-sized prey of the Baltic and Saimaa ringed seals (Auttila et al., 2015; Kunnasranta et al., 1999; Sinisalo et al., 2008) do not require manual handling or oral

food processing (Jernvall 2000; Jones et al., 2013; Kienle & Berta, 2016; Laakkonen & Jernvall, 2020). Both subspecies studied here, however, routinely use their forelimbs for digging, to excavate lairs in ice for breeding (Helle et al., 1984; McLaren, 1958; Smith, 1987), and for scraping ice to form breathing holes (Stirling, 1977).

There are several reports in the literature describing the form of limb bones and muscles of seals (Bryden, 1971; Bryden & Felts, 1974), including members of the genus *Pusa* (Howell, 1929; King, 1969; Miller, 1888; Murie, 1870, 1872, 1874; Piérard, 1971; Quakenbush, 1991; Turner, 1888) but the limb muscle anatomy of the freshwater ringed seals has not been studied apart from the examination of the thoracic anatomy of the Baikal seal, *Pusa sibirica* (Koster et al., 1990). As part of our research aiming to understand the morphological variation in ringed seals, we studied with cadaver dissections the forelimb anatomy of the Saimaa (*Pusa hispida saimensis*) and Baltic ringed seals (*Pusa hispida botnica*).

All Saimaa ringed seals that are found dead are collected by the staff of Parks & Wildlife Finland, a unit of Metsähallitus (a state enterprise that administers state-owned land and water areas), and stored at −20°C until necropsy. Specimens are usually in various stages of decomposition, but in both 2018 and 2019 one individual was in relatively good condition, enabling a more detailed morphological examination. These were shipped frozen to the Veterinary Faculty of the University of Helsinki for dissection in June 2019 and 2020. The seals examined were bycaught in gill nets. One of the seals was a subadult (30–42 kg) and the other a pup (≤30 kg). In addition, two Baltic ringed seals that were legally shot by a hunter (outside the research community) in the Bothnian Bay (the northernmost part of the brackish water Baltic Sea) were shipped frozen via the University of Oulu to the Veterinary Faculty of the University of Helsinki for dissection that was carried out in summer 2020. Both seals were adults (≥42 kg). We weighed the seals just prior to the dissection (Table 1). After removal from the body, we soaked the forelimbs with the intrinsic muscles (the muscles located within the forelimb itself) attached for 24 hr to remove blood from the muscle tissues (Figure 1). We dissected both forelimbs from each of the four seal specimens, with 26 specific, intrinsic muscle–tendon units (see Table 1 for muscle names) being identified and systematically removed. The anatomical terminology is in accordance with the International Committee on Veterinary Gross Anatomical Nomenclature (ICVGAN, 2017). Of architectural measurements, we measured the muscle mass (tendon removed) on an electronic balance (Pesola PTS3000, division 0.1 g). After removal of the muscles, we studied the joint architecture for possible differences in ligaments between subspecies. Finally, we boiled and cleaned the bones for examination of the general bone anatomy, especially the joint surfaces and the attachment sites of the muscles (Figures 2–5; specimen number 846 was chosen as the model for the bone architecture figures because it represents an adult). The muscle insertions to metacarpal bones and phalanxes were not visualized with figures because there was considerable individual variation in the exact muscle attachments. Koster et al. (1990) reported differences in the extrinsic muscles (the muscles joining the forelimb to the trunk) between *Pusa hispida* and *P. sibirica* but we did not examine these muscles due to the damage caused by hunting (the Baltic ringed seals) or sampling for other studies (the Saimaa ringed seals).

The specimens did not display any pathology. The muscle architecture of the two subspecies was similar, with no major differences in the corresponding muscle attachments. Statistical muscle weight comparisons were not possible due to the small sample sizes and the age/body size difference between the specimens. Individual muscles were grouped as functional units of the corresponding joint, and any noted differences to those of previously reported findings are briefly discussed.

A protuberance in the spina scapulae, similar to the one reported for *P. sibirica* by Koster et al. (1990), was visible in both *Pusa hispida botnica* specimens (Figure 2) but only a minor protuberance was seen in the specimens of the *Pusa hispida saimensis*, probably due to their young age. Interestingly, the *P. hispida* specimen studied by Koster et al. (1990) lacked this protuberance. In relation to the size of the infraspinous fossa, the supraspinous fossa is considerably reduced in phocids (Wyss, 1988; Figure 2). In both subspecies, a low caudal ridge (infraspinous ridge in Quakenbush, 1991) separated the musculus infraspinatus and musculus teres major, which was located almost entirely on the lateral side of the bone (Figure 2). The articular surface of the scapula was concave, and the humeral side of the joint surface was spheroidal.

TABLE 1 Weights of the forelimb muscles of two Baltic and two Saimaa ringed seal specimens.

|	Baltic ringed seal		Saimaa ringed seal	
Specimen number	845	846	2704	2744
Body weight (kg)	49.5	54.5	35.0	18.5
Muscle weight (g)	left/right	left/right	left/right	left/right
musculus deltoideus	30.7/32.2	45.8/37.1	21.8/22.4	13.5/13.5
musculus infraspinatus	16.0/15.4	21.0/17.2	15.2/14.1	7.5/7.6
musculus supraspinatus	70.2/71.3	67.6/66.2	54.6/52.9	26.3/25.6
musculus teres major	73.8/71.2	51.3/56.5	53.3/55.2	24.6/25.0
musculus teres minor	2.8/2.9	4.0/2.0	2.6/2.7	2.9/2.7
musculus subscapularis	129.2/130.7	168.7/187.5	71.3/73.1	59.0/65.6
musculus triceps brachii pars longus	82.3/82.7	54.3/55.2	72.4/77.1	12.3/11.6
musculus triceps brachii pars lateralis	81.3/82.3	66.5/78.9	34.2/36.2	13.3/15.8
musculus triceps brachii pars medialis	37.0/41.3	44.9/46.1	24.4/21.4	9.9/11.1
musculus anconeus	4.7/5.0	5.6/5.2	4.7/4.3	1.7/2.1
musculus biceps brachii	18.6/22.0	21.2/21.2	8.4/10.7	10.4/12.7
musculus brachialis	11.2/12.4	13.3/12.0	8.4/9.8	10.4/12.7
musculus coracobrachialis	3.3/3.7	2.8/3.8	3.0/2.8	2.3/1.9
musculus extensor digitorum communis	10.1/11.1	12.3/13.5	6.8/8.8	4.3/4.1
musculus extensor digitorum lateralis	4.8/4.9	10.3/8.5	4.1/3.3	—[a]/3.9
musculus extensor carpi ulnaris	5.6/5.7	5.1/5.2	4.8/4.1	1.9/1.7
musculus abductor digiti pollicis I	9.1/9.8	7.9/7.0	4.3/3.0	2.3/2.3
musculus abductor digitorum longus	4.4/4.8	7.2/6.8	4.3/ 4.0	2.3/1.8
musculus flexor carpi radialis	3.3/3.5	15.1/12.3	3.3/3.3	—[a]/—
musculus flexor carpi ulnaris	7.0/7.7	7.4/7.9	6.7/7.7	6.5/6.9
musculus flexor digitorum superficialis	31.9/32.3	31.0/38.2	28.1/29.3	10.8/10.6
musculus flexor digitorum profundus	33.9/34.1	55.6/59.9	31.6/32.1	13.9/13.1
musculus pronator teres	6.7/7.1	8.5/5.5	5.4/5.9	4.2/4.9
musculus supinator	4.5/3.9	3.4/4.0	2.5/2.9	1.5/1.3
musculus brachioradialis	6.3/ 6.7	6.6/8.9	—[a]/—	2.7/2.0

[a]Muscle weight is missing due to damage to the specimen.

As in other phocids, the tuberculum minus was elevated above the head of the humerus (Figure 3), providing a wide insertion area for the large musculus subscapularis (Bryden & Felts, 1974; this study). By lying above the proximal joint surface of the bone head, this insertion point provides a greater moment arm for the rotator cuff musculature acting as protractors and humeral rotators than in animals with smaller humeral tubercles (English, 1974, cited in Berta et al., 2015).

At the distal end, the humerus possessed a large supracondylar foramen on the medial side in all specimens. There were no discernible ligaments on the shoulder joint but a slight thickening on the lateral side of the capsule was observed in all specimens. A visible thickening also on the medial side of the joint capsule was noted in one of the Baltic ringed seal specimens.

Seven muscles act on the shoulder joint. The musculus deltoideus originated from the spina scapulae with fascial attachments to adjacent muscles. It continued distally approximately along the caudal edge of the musculus

FIGURE 1 Overview of the Saimaa ringed seal forelimb musculature (specimen 2744) after soaking in water for 24 hr. MTMa = musculus teres major; MS = musculus supraspinatus; MTBlo = musculus triceps brachii caput longum; MTBla = musculus triceps brachii caput laterale; MECR = musculus extensor carpi radialis; MEDC = musculus extensor digitorum communis; MEDL = musculus extensor digitorum lateralis; MEP = musculus extensor pollicis; MFCU = musculus flexor carpi ulnaris; MECU = musculus extensor carpi ulnaris. Right limb, lateral view. Scale bar = 5 cm.
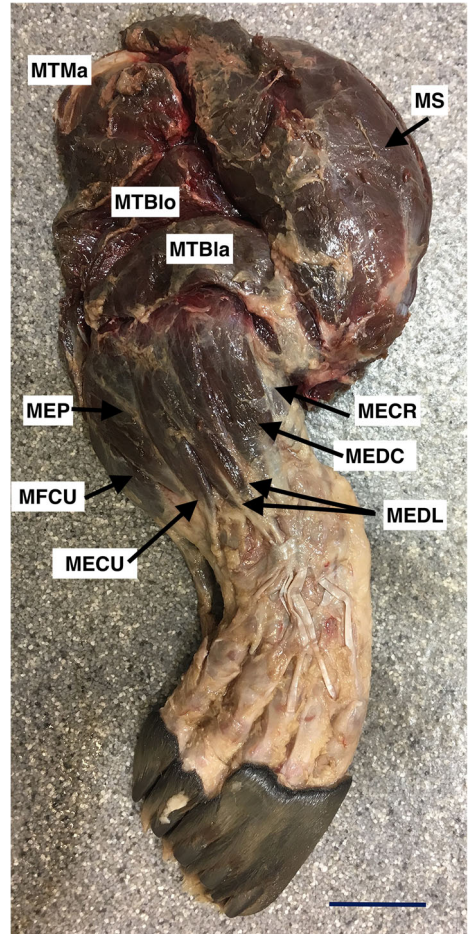
infraspinatus, which the former muscle partly covered before insertion on the deltoid crest (Figure 2). We did not find the accessory part described by Quakenbush (1991) in any of our specimens. The musculus supraspinatus covered the entire fossa supraspinatus, also extending over the cranial edge of the scapula. At the distal end, this muscle showed a varying degree of partition (also in Howell, 1929) before inserting widely on the lateral side of the humerus, including the tuberculum majus and the joint capsule (Figure 2). The musculus infraspinatus occupied the fossa infraspinata, including the caudal aspect of the spina scapulae (Figure 2). Its insertion fused with that of the musculus supraspinatus on the tuberculum majus and also on the joint capsule. Although mostly laterally located (Figure 2), the musculus teres major acts on the medial side of the shoulder joint due to its medial insertion (Figure 3). The muscle was attached to the entire length of the caudal edge of the scapula and also partly to the subscapularis and infraspinatus muscles. It inserted with a strong tendon on the tuberculum minus and slightly distally to this tuberosity on the medial side of the humerus (Figure 3). The tiny musculus teres minor followed the caudal edge of the musculus infraspinatus at its origin (scapula) and insertion (humerus) points (Figure 2). This muscle had a wide attachment to the joint capsule distal to the articular surface. Similar insertion points in *P. hispida* were reported by Quakenbush (1991) but Howell (1929) described insertion fibers fusing with the musculus deltoideus before insertion to humerus.

The musculus subscapularis covered almost the entire medial aspect of the scapula except for narrow parts near the edges of the bone especially on the proximal part of the bone. This muscle had a wide insertion point on the tuberculum minus (Figure 3). Many of the muscle tendons surrounding the shoulder joint had an insertion point on
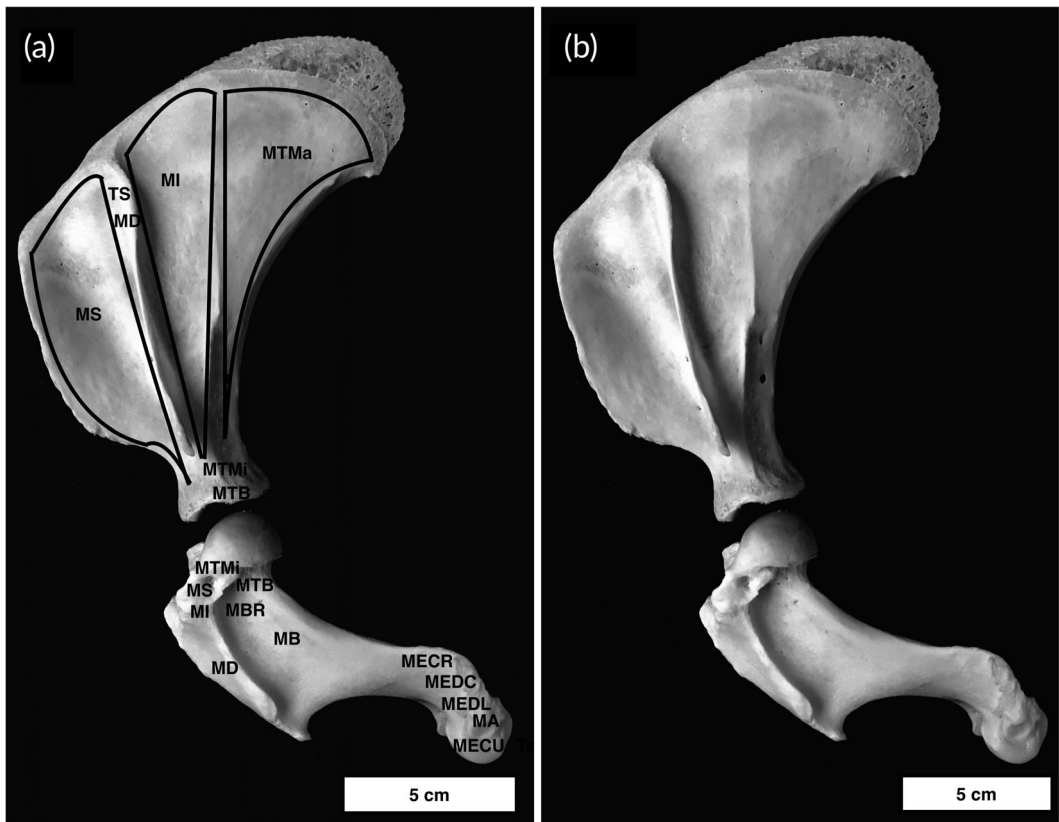
FIGURE 2 (a) Muscle attachments of the Baltic ringed seal, lateral aspect of the scapula and humerus of the left forelimb. MA = musculus anconeus; MB = musculus brachialis; MBR = musculus brachioradialis; MECR = musculus extensor carpi radialis; MD = musculus deltoideus; musculus extensor digitorum communis; musculus extensor digitorum lateralis; MI = musculus infraspinatus; MS = musculus supraspinatus; MTMa = musculus teres major; MTMi = musculus teres minor; MTB = musculus triceps brachii. The origin of the musculus supinator was on the lateral epicondyle of the humerus near the musculus anconeus. TS = Tuber spinae of the scapula. (b) Lateral aspect of the scapula and humerus of the left forelimb showing the bone morphology.

the capsule but the subscapularis muscle had a particularly wide attachment to the capsule in all specimens. Also on the medial side, the musculus coracobrachialis had its origin caudal to that of musculus biceps brachii, with insertion on the caudal side of the tuberculum minus (Figure 3). Quakenbush (1991) described a muscle with similar attachments as musculus subscapulo-capsularis. Musculus coracobrachialis was not reported in *P. hispida* or *P. sibirica* by Koster et al. (1990).

The olecranon process of the ulna which provides an insertion point to many muscles associated with the elbow joint, was laterally flattened (Figures 4 and 5) and very enlarged as in all pinnipeds (Berta et al., 2015). The hinge-like distal end of the humerus articulated with the concave joint surface of the ulna (Figure 4). The joint surface between the ulna and humerus was relatively wide in contrast to the narrow, partly laterally oriented articulation between the ulna and radius (Figure 4). A lateral collateral ligament was visible in all specimens. No separate medial collateral ligament could be distinguished but there was a thicker part on the capsule on the medial side at the corresponding site.

Eight muscles were described for the action on the elbow joint. The main extensors of the forearm are the four parts of the musculus triceps brachii. The caput longum of this muscle originated from the caudal edge of the scapula (Figure 2). The muscle also appeared to attach with a fascia to the musculus teres major and musculus deltoideus
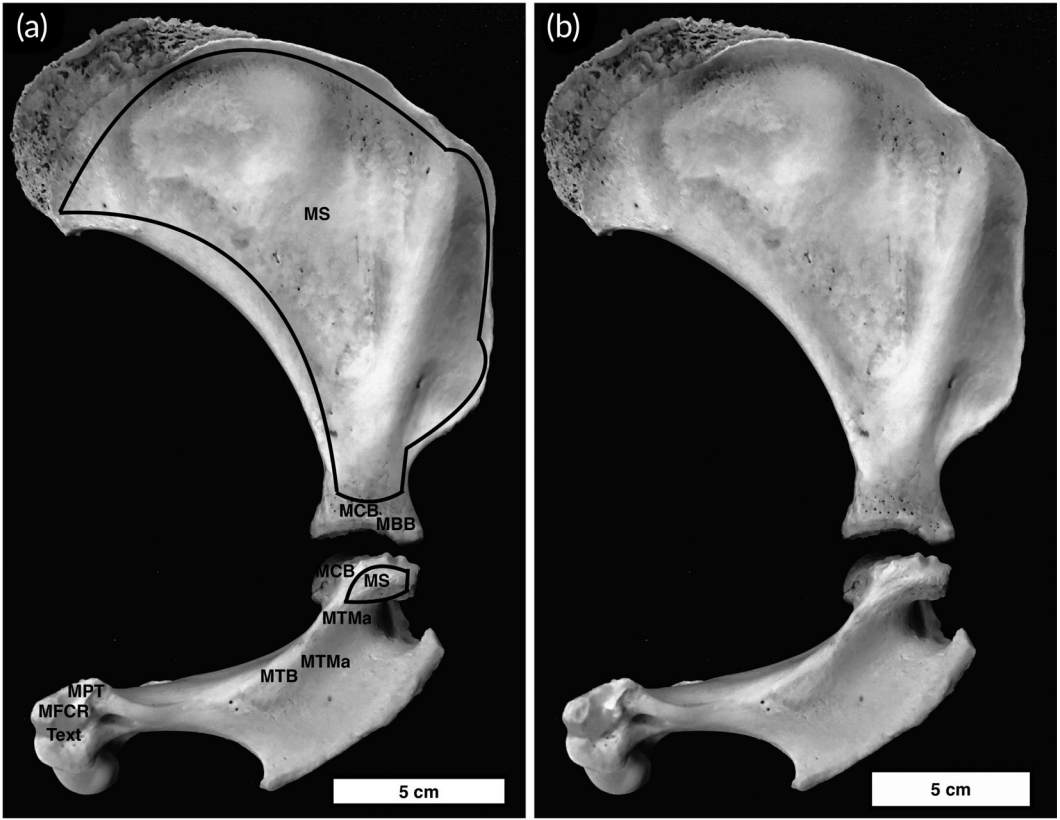
FIGURE 3 (a) Muscle attachments of the Baltic ringed seal, medial aspect of the scapula and humerus of the left forelimb. MCB = musculus coracobrachialis; MFCR = musculus flexor carpi radialis; MFDP = musculus flexor digitorum profundus; MS = musculus subscapularis; MBB = musculus biceps brachii; MPT = musculus pronator teres; MTB = musculus triceps brachii; MTMa = Musculus teres major. (b) Medial aspect of the scapula and humerus of the left forelimb showing the bone morphology.

before insertion on the caudal part of the olecranon (Figures 4 and 5). The small caput accessorium of the musculus triceps brachii had a similar orientation and attachment points to those of the caput longum but the former was located very close to the joint at both ends of its attachment. The caput accessorium was not weighed because it was not possible to keep the muscle intact upon its removal. The caput mediale originated from the mediocaudal part of the humerus shaft including the base of the bone, with insertion on the craniomedial part of the olecranon (Figure 5). The caput laterale originated from the proximal end of the humerus (base of the caput humeri) on the lateral side (Figure 4), with insertion on the dorsocranial part of the olecranon very close to the joint capsule (Figure 4). The musculus anconeus originated from the lateral crest of the humeral epicondyle with insertion points both on the caudomedial side of the humerus and beneath the cranial end of the olecranon on the lateral side (Figure 4). Koster et al. (1990) also described a medial part of the musculus anconeus in *Pusa sibirica*. The musculus tensor fasciae antebrachii was not examined in this study due to the damage caused by hunting (the Baltic ringed seals) or by severing and sampling for other studies (the Saimaa ringed seals). Koster et al. (1990) do not report musculus tensor fasciae antebrachii from *Pusa sibirica* or *Pusa hispida*, and some authors discuss it as part of the triceps brachii complex (Bryden, 1971; Piérard, 1971; Quakenbush, 1991).

The musculus biceps brachii originated from the processus coracoideus and also partly the craniomedial shoulder joint area (Figure 3). The muscle lay under a strong ligament in the wide intertubercular groove of the humerus, but
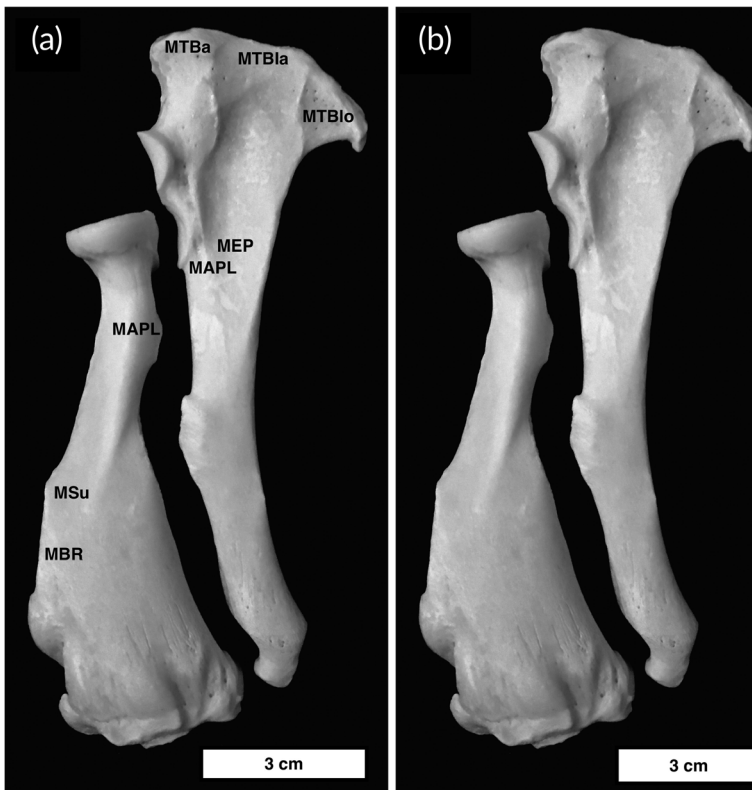
FIGURE 4 (a) Muscle attachments of the Baltic ringed seal, lateral aspect of the radius and ulna of the left forelimb. MAPL = musculus abductor pollicis longus; MEP = musculus extensor pollicis; MBR = musculus brachioradialis; MSu = musculus supinator; MTB = musculus triceps brachii. (b) Lateral aspect of the radius and ulna of the left forelimb showing the bone morphology.

the muscle was not attached to it. The biceps muscle inserted on the medial side of the radius with an aponeurosis-like tendon one to two centimeters distal to the elbow joint in close proximity to the insertion of the brachialis muscle (Figure 5). The musculus brachialis originated from the lateral side of the humerus (Figure 2), distally from the base of the caput humeri, before passing at the proximal third of the humerus to the medial side with insertion on the proximal part of the radius and ulna near the radioulnar joint surface (Figure 5). The origins of both elbow flexors were similar to those reported by Quakenbush (1991) and Koster et al. (1990) but there seems to be variation on the insertion areas (radius, ulna or both).

The origin of the musculus supinator was on the epicondylus lateralis of the humerus (Figure 2). The muscle extended to cover part of the joint capsule on the proximal part of the radius, while the musculus pronator teres originated from the medial epicondyle of the humerus (Figure 3). Both muscles inserted dorsally on the radius, the latter also on the medial side, and its insertion was more distal than the one of the supinator (Figure 5). Howell (1929) described a more proximal insertion for musculus pronator teres. The musculus brachioradialis had its origin on the lateral side of the humerus distally to the articular surface. It attached into the insertion tendon of the supinator muscle with eventual insertion on the dorsal edge of the radius distal to the insertion point of the supinator (Figure 4). In all specimens, the distal end of the articular capsule of the elbow joint was thickened, but no distinct annular ligament was visible.

The bones forming the carpal joint were attached with short but wide ligaments. The digits of both subspecies were distinct with trochleated phalangeal articulations enabling considerable mobility of the digits. As reported previously for *P. hispida* (Quakenbush, 1991), the first digit had no phalanx media in either subspecies examined here. This arrangement probably contributes to the haulage grip of ringed seals (discussed below). The reduction of the fifth intermediate phalanx of the manus reported in all pinnipeds (Berta et al., 2015) was seen in all specimens of this study. Unlike otariids, phocids including the subspecies studied here, have retained a webbed paw bearing sharp
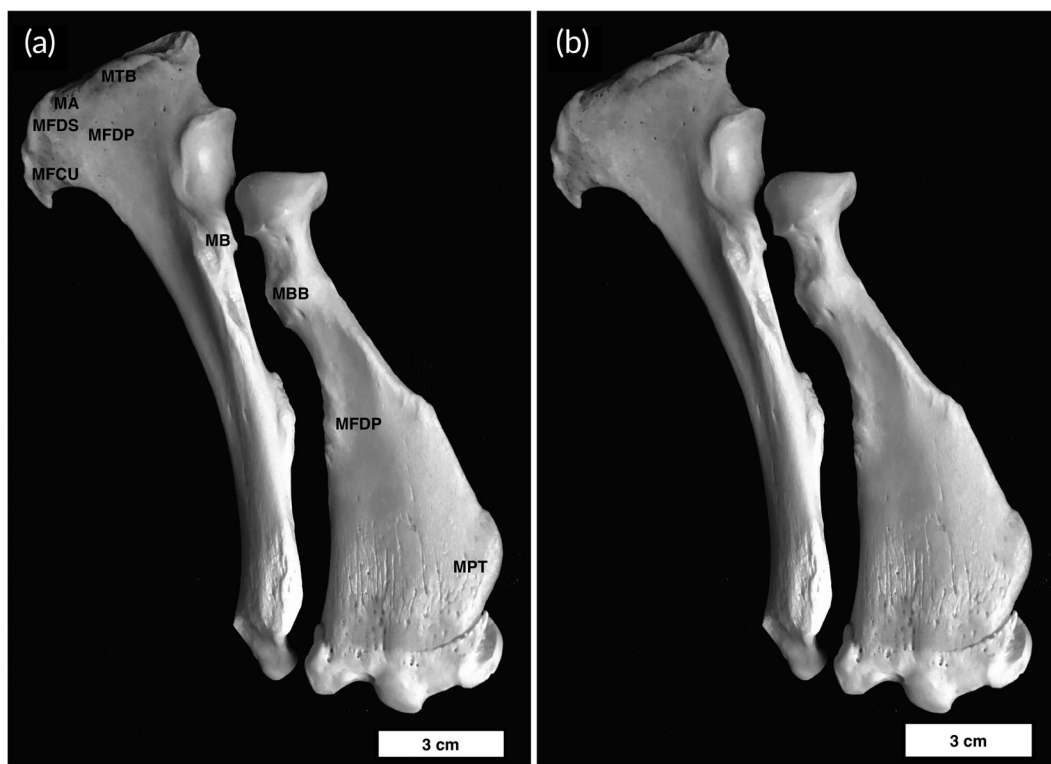
FIGURE 5 (a) Muscle attachments of the Baltic ringed seal, medial aspect of the radius and ulna of the left forelimb. MA = musculus anconeus; MB = musculus brachialis; MBB = musculus biceps brachii; MFCU = musculus flexor carpi ulnaris; MFDP = musculus flexor digitorum profundus; MFDS = musculus flexor digitorum superficialis; MPT = musculus pronator teres; MTB = musculus triceps brachii. (b) Medial aspect of the radius and ulna of the left forelimb showing the bone morphology.

claws supported internally by distinct ungual processes, closely resembling that of the terrestrial carnivores, which employ their clawed forelimbs for a variety of tasks (Hocking et al., 2018).

The musculus extensor digitorum communis originated from the lateral epicondyle of the humerus, caudal to the origin of the musculus extensor carpi radialis, the most proximal muscle on the lateral epicondyle (Figure 4). The musculus extensor digitorum communis went under the transverse ligament of the carpus before insertion on the distal phalanxes of all fingers except the thumb. The musculus extensor digitorum lateralis also originated from the distal end of the humerus caudal to the musculus extensor digitorum communis (Figure 4), and the former attached to the ulna with a strong tendon on the distal side of the joint. The musculus extensor digitorum lateralis inserted with two tendons, one on the proximal phalanxes of the third and fourth digits, the other attached to the phalanx proximalis of the fifth digit with two tendons. The musculus extensor carpi radialis originated from the lateral end of the humerus (Figure 4), and it inserted with two tendons of which the thinner attached to the lateral side of the first carpal bone. The other insertion tendon attached to the ossa metacarpalia II and III. The most distal muscle originating from the lateral epicondyle of the humerus (Figure 4), the musculus extensor carpi ulnaris, inserted with a thin tendon on the accessory bone before terminating on the os metacarpale V. There appeared to be another insertion branch between the radius and ulna. The musculus abductor pollicis longus originated from the radius with a wide attachment to the bone's laterocaudal side (Figure 4). There was also an attachment point on the lateral side of the proximal ulna. This muscle inserted with a tendon crossing under the other distal extensors on the medial side of the first metacarpal bone. The musculus abductor pollicis longus was also attached to the fascia in the area. The

musculus extensor pollicis (the musculus abductor digiti I longus, or m. extensor metacarpi pollicis in Quakenbush, 1991) appeared to originate together with the previous muscle (Figure 4) but after that the musculus extensor pollicis remained separate from the other muscles before insertion at the distal end of the first metacarpal bone. In the specimen of *Pusa sibirica* examined by Koster et al. (1990), these two muscles were already separate at the origin point of the muscles.

The musculus flexor carpi ulnaris consisted of two parts which originated from the caudomedial edge of the proximal olecranon (Figure 5), and the muscle had a long insertion tendon that widened at the distal part of the carpal canal before insertion on the medial side of the fifth metacarpal bone via the os carpi accessorium. In one of the Baltic ringed seals it also inserted on the dorsal side of the fourth metacarpal bone. The musculus flexor carpi radialis originated from the medial epicondyle of the humerus (Figure 5) and it had a wide attachment to the distal part of the musculus pronator teres before insertion on the first metacarpal bone. Howell (1929) and Quakenbush (1991) reported numerous variations in the number of metacarpal insertion points with differences also between the right and left sides in individual seals. The musculus flexor digitorum superficialis originated from the caudal half of the olecranon on the medial side (Figure 4). The inserting tendons joined at the carpal level before insertion on the phalanx media of the digits. The musculus flexor digitorum profundus originated from the medial side of the humerus (Figure 3) and it had a wide attachment to the ulna but only a very narrow insertion to radius (Figure 5). The inserting tendon divided into two at the level of the carpus: the more lateral tendon inserted on the phalanx distalis of the first digit. The wider tendon attached to the fascia of the carpus on its way into the phalanx distalis of the rest of the digits (Figure 6). The muscle covered the carpal canal, and it appeared to have three parts which varied slightly between the examined specimens. Strong flexion of finger joints (Figure 6) results in the "haulage grip" (Backhouse, 1961) used by ringed seals whenever they use forelimbs in locomotion on the ice (Quakenbush, 1991).

FIGURE 6 Together with the bone architecture of the phalanxes, the strong musculus flexor digitorum profundus displayed by the wide insertion tendons (arrows) of ringed seals enables a powerful grip when moving on ice. Baltic ringed seal (specimen 846), palmar view. Scale bar = 4 cm.

Koster et al. (1990) and Quakenbush (1991) mention the musculus abductor digiti quinti longus, which is not verified by ICVGAN (2017), inserting on the proximal phalanx of the fifth digit. We described the corresponding pars muscularis as a second part of the musculus flexor carpi ulnaris inserting on the os carpi accessorium. Howell (1929) also suggested that this muscle part derived from the musculus flexor carpi ulnaris.

Comparison of the ringed seal muscle weight data with those of terrestrial mammals was not possible due to the small number of (adult) seal specimens (Bryden & Felts, 1974; Koster et al., 1990; this study). The muscle mass of the musculus subscapularis of all studied pinnipeds (Bryden & Felts, 1974; this study), however, appears to be considerable in comparison with that of the corresponding muscle in the well-studied felines (Cuff et al., 2016; Viranta et al., 2016). This muscle extends the shoulder joint, but it also has the potential to adduct the forelimb, which is likely important for seals when they stream-line their body during swimming. It should also be noted that in contrast to the terrestrial mammals, only the distal part of the forelimb of phocids is visible outside the body contour. As a result, the axilla in phocids falls at the wrist.

In conclusion, we found the musculoskeletal gross anatomy of the Saimaa ringed seal forelimb to be similar to that of other ringed seal subspecies (Howell, 1929; Koster et al., 1990; Quakenbush, 1991) and the forelimb intrinsic muscle anatomy of the *Pusa hispida botnica* to be similar to that previously reported from the arctic *Pusa hispida* (Howell, 1929; Koster et al., 1990; Quakenbush, 1991). Furthermore, it appears that there is considerable individual variation in the insertion of the extensors and flexors of the wrist and fingers (Howell, 1929; Quakenbush, 1991; this study). Because the wrist bones are tightly connected with ligaments and function as a unit (Quakenbush, 1991), the insertion of the distal extensors and flexors may be able to vary without significantly altering their function. The webbed paw of ringed seals may also render the function of individual fingers less important and reduce the selection pressure for specific muscle attachments. The matching of a specific phenotypic characteristic to particular biomechanical function, however, requires analyses beyond that of form alone.

AUTHOR CONTRIBUTIONS

Juha Laakkonen: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; visualization; writing-original draft; writing-review & editing. **Heini Nihtilä:** Conceptualization; investigation; methodology; writing-review & editing.

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