ANATOMY OF THE RIVER OTTER, SEA OTTER AND HARP SEAL.

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Thesis title - Anatomical observations on the river otter, sea otter and harp seal with reference to those structures that are of known significance in thermal regulation and diving.

Department of Biology

Doctor of Philosophy

ABSTRACT

This thesis contributes new knowledge towards the understanding of specific anatomical adaptations in aquatic mammals. The research is based on the anatomy of the Canadian river otter, Lutra canadensis, the northern sea otter, Enhydra lutris and the harp seal, Pagophilus groenlandicus with respect to thermal regulatory and diving adaptations. These species range from a lacustrine (Lutra) to a maritime (Enhydra and Pagophilus) habitat and represent varying degrees of specialization to an aquatic medium.

The regulation of body temperature is of major concern for diving mammals, especially those in higher latitudes. The animals are exposed not only to the daily and seasonal temperature fluctuations while on land, but also to the often extreme land-water-air temperature gradients and the high thermal conductivity of water. The species in this study are usually exposed tollow temperatures and mechanisms of heat retention are enhanced. Heat retention mechanisms take the form of variations in body insulation (pelage and subcutaneous fat), in size of body regions with a high surface area-to-volume ratio, in regional differences and specializations in the vascular, and behavioral patterns. In each species, the feet (with their reduced pelage and fat content, thin skin, and relatively large surface area-to-volume ratio) appear to be the primary regions of heat release.

The study of diving adaptations includes terrestrial and aquatic locomotory patterns and limb anatomy, lung topography and bronchial patterns, tracheal anatomy, and the anatomy of the caval sphincter and vascular reservoirs. The results show both species variation and general trends from *Lutra* to *Enhydra* to *Pagophilus* towards increased aquatic specialization.

ANATOMICAL OBSERVATIONS ON THE RIVER OTTER, SEA OTTER AND HARP SEAL WITH REFERENCE TO THOSE STRUCTURES THAT ARE OF KNOWN SIGNIFICANCE IN THERMAL REGULATION AND DIVING.

by

Frederick John Tarasoff

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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August, 1972.

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SUMMARY

This thesis contributes new knowledge towards the understanding of specific anatomical adaptations in aquatic mammals. The research is based on the anatomy of the Canadian river otter, *Lutra canadensis*, the northern sea otter, *Enhydra lutris* and the harp seal, *Pagophilus groenlandicus* with respect to thermal regulatory and diving adaptations.

As the thesis title implies, the presence of specific anatomical structures have been described and their role interpreted in some mammals. However, the contribution to new knowledge in this work lies in the description and functional significance of these structures as they directly apply to mammals that show increased aquatic specialization. Each anatomical feature that is documented in the summary of each section of this work is original and as such adds to a more thorough understanding of the species concerned.

The contributions to new knowledge are as follows:

Thermal regulation:

1. The feet are comparatively poorly insulated and have a high surface area-to-volume ratio, and thus are areas of a potentially high heat loss. For these three species there is a trend for the combined feet surface areas to decrease from *Pagophilus* to *Lutra* to *Enhydra*. The tail surface area decreases from *Lutra* to *Enhydra* to *Pagophilus*.

2. Body insulation in the from of pelage plays a more important role in *Lutra* and *Enhydra* than in *Pagophilus*. In the former two species, the pelage prevents water-to-skin contact, whereas in *Pagophilus* the skin

is wettable. Pelage density and length contribute to the number of dead air spaces and the depth of insulation. These parameters decrease from *Enhydra* to *Lutra* to *Pagophilus*, and regionally from the tail to midback to tarsus to foot. Also contributing to the insulative role of the pelage is the presence of a well-developed medulla found in the guard hairs of *Lutra* and *Enhydra*, but absent in *Pagophilus*. The pelage of each species is composed of caudally sloping, straight-shafted, dorso-ventrally flattened guard hairs and wavy underhairs. Pelage morphology is similar in *Lutra* and *Enhydra* with all guard hairs having a lanceolate outline and spike or leaf-like cuticular scales on the hair shaft. The cuticular scales contribute to the integrity and protection of the more delicate underhairs, and the maintenance of entrapped air.

3. Renewal of air within the pelage of *Lutra* may occur by pilo-erection of the hairs, by a pleating of the skin by means of the *m. cutaneous trunci*, or by shaking the body upon emergence from the water. *Enhydra* may blow air into its fur or pleat the skin to renew the entrapped air. Comparable adaptations are not found in *Pagophilus*.

4. Subcutaneous fat is most abundant in *Pagophilus* (37.9% of the total body weight) and provides the principal means of insulation. It is less abundant in *Lutra* (12.6%) and of secondary importance to the pelage in thermal regulation. *Enhydra* has little or no subcutaneous fat.

5. Interdigital webs are present in the hind feet of all three species. This skin is thinner than that of the body and, in the cases of *Enhydra* and *Pagophilus*, may be highly vascularized. Heat loss may be reduced from these areas by a counter-current heat exchange principle in *Pagophilus*, or by retaining a relatively dense pelage in this region, as in *Enhydra*.

The feet of Enhydra may also serve as an avenue for thermal absorption by direct solar radiation. Characteristics that contribute to this latter function are the dark hairs and skin, the presence of a highly developed superficial venous circulation on the dorsal surface of the foot, and the behavioral pattern of expanding the foot and fanning during warm periods.

Locomotory patterns and species topography:

1. Terrestrial locomotion

Lutra and Enhydra have the typical carnivore limb sequences during walking, with alternate movements of opposite fore foot and hind foot. On land, Lutra walks, runs, and bounds; Enhydra has been observed only to walk and bound. Papophilus, during terrestrial locomation, does not differ from that described previously for hair seals. Terrestrial locomotion is more awkward from Lutra to Enhydra to Papophilus.

2. Aquatic locomotion

Lutra moves by two methods:
1. vertical undulations of the tail and caudal regions of the body.
2. cranio-caudal thrust and recovery movements of the limbs.

Enhydra moves by three methods:
1. cranio-caudal sweeps of the pelvic limbs often involving bending of the lumbar, sacral and caudal regions.
2. horizontal thrust and recovery movements of the pelvic limbs while on its back at the surface of the water.
3. horizontal sweeps of the dorso-ventrally flattened tail while at the surface of the water.

Pagophilus moves by two methods: 1. alternate horizontal sweeps of its pelvic limbs (feet).
2. thrust and recovery movements of its fore limbs (short distances).

Lutra actively maintains itself at the surface of the water. As does *Pagophilus* during the spring and early summer months. *Enhydra* can remain at the surface for long periods of time with no movements. These differences can be attributed to differences in pelage density, quantities of subcutaneous fat and the differential buoyancy of the aquatic medium.

3. There is an increased tendency from *Lutra* to *Enhydra* to *Pagophilus* to have the area of aquatic locomotion assigned to one body region.

4. Convergent evolution towards a highly efficient carangiform mode of swimming with a graded increased approximation of a "perfect" lunate border of the propulsive organ is seen from *Lutra* to *Enhydra* to *Pagophilus*. The feet of *Lutra* and *Enhydra* have not become as highly specialized as in *Pagophilus*, and they retain distinct carnivore-type limbs for terrestrial locomotion.

5. There is an increased foot surface area and increased importance of this area as a means of aquatic propulsion *Lutra* to *Enhydra* to *Pagophilus*.

The tail surface area decreases in the above order, and with it a decreased importance of this region for aquatic propulsion.

The foot has a reduced density and length of hairs compared with the midback and tarsal regions, with the hair density decreasing from *Lutra* to *Enhydra* to *Pagophilus*.

Syndesmology of the pelvic limb

1. The coxal joint of *Lutra* and *Enhydra* permits maximum movement of the femur in a cranio-caudal direction during terrestrial and aquatic locomotion.

In Enhydra, increased lateral rotation of the pelvic limb is made possible by the absence of the femoral ligament of an increased articulatory facet on the dorsal surface of the femur. This lateral rotation of the limb is used when the animal swims on its back at the surface of the water. In these two otters, the increased thickened one-half of the capsular membrane, acetabular lip and acetabular ridge indicate that these regions receive most of the force of the head of the femur during locomotion. The coxal joint of Pagophilus appears well-adapted for movements of the head of the femur in a cranio-caudal direction as reflected in the equal development of these regions of the acetabular lip.

A femoral ligament is present in Lutra and absent in Enhydra and Pagophilus. Its absense may reflect the decreased amount of weight supported by the pelvic limbs. Enhydra is less agile on land than is Lutra, and Pagophilus does not use the pelvic limbs to support the caudal regions of the body.

2. The stifle joint of Lutra and Enhydra permits flexion and extension movements of the shank and little rotation. In Pagophilus, the anatomical evidence suggests that there is much lateral rotation of the leg during aquatic locomotion. This evidence is seen in the laterally directed patella fossa, the absence of a fibular collateral ligament and enlargement of ligaments associated with the femoral-tibial junction, differential sizes of the lateral and medial meniscus, and the laterally sloping articulatory facets of the femur, tibia and fibula.

3. The tarsal joint in all three sepcies is held in place by the tibial and fibular collateral ligaments, and articulatory surfaces seem best adapted for flexion and extension movements of the foot, with little or no lateral rotation. In each species, the bones of the plantar surface of the foot are more rigidly bound together than on the dorsal surface.

The lungs (topography, weights and measurements)

1. The lungs of the river otter and sea otter are semi-conical shaped, being narrowest cranially and broadening caudally. The lungs of the sea otter are broader overall than in the river otter. The lungs of the harp seal are oblong-shaped in width cranially and caudally. The topography of the lungs corresponds closely to the shape of the thoracic cage of each species.

2. There is a trend toward a reduced lobulation of the lungs from the river otter to sea otter to harp seal. The lungs of the river otter and sea otter are asymmetrical with the left having cranial and caudal lobes, and the right composed of cranial, medial, caudal and accessory lobes. The lungs of the harp seal are symmetrical, with divisions not apparent in the right lung, and a shallow, incomplete division of the left lung into cranial and caudal lobes.

3. Lung tissue depth is maximum in the dorsal and lateral regions in each species, with the sea otter having the greater depth laterally and the harp seal having a proportionally greater amount of tissue dorsally.

4. The hilus region is located more cranially in the harp sean than in the otters.

5. The mean ratio of lung weight/100 grams of body weight is 1.39 in the river otter, 3.86 in the sea otter and 1.31 in the harp seal. In the river otter, the mean percentage difference between the right and left lungs is 19.9% and in the sea otter 9.8%, with the right lung being the larger. In the harp seal the difference is 6.4%, with the left lung being the larger.

The trachea and bronchial tree

1. The trachea, as a percentage of body length, is 23.2% in Lutra, 19.0% in Enhydra and 17.6% in Pagophilus. The width of the trachea relative to its length is least in Lutra and greatest in Pagophilus.

2. The mean number of tracheal rings is 71 in Lutra, 48 in Enhydra and 43 in Pagophilus. The ventral widths of the rings in Lutra and Enhydra vary in a non-uniform pattern, whereas in Pagophilus they are widest cranially and narrowest caudally. A dorsal gap between the arms is present throughout the length of the trachea in Lutra and Enhydra, and appears only in the caudal one-third of the trachea in Pagophilus. In Lutra and Enhydra there is a dorsal overlapping of the rings, whereas in Pagophilus there is dorsal, lateral and ventral overlapping. The tracheal rings of Lutra and Enhydra are partially clacified, but in Pagophilus there is no evidence of calcification. In each species, the cartilaginous rings are replaced by irregular plates prior to the entry of the principal bronchi into the lungs.

3. The lamina propria of Pagophilus is thicker than in Lutra and Enhydra.

4. A pennate-like branching of the lobar bronchi are found in Lutra and Enhydra, whereas in Pagophilus this branching has a more dicotomous pattern.

5. The bronchial patterns in the right and left lungs of Lutra and Enhydra are asymmetrical and correspond to the differences in lobulation of the lungs. In Pagophilus there is close symmetry between the two lungs and bronichial patterns.

6. The numbers of subsegmental bronchioles increases from Lutra to Enhydra to Pagophilus.

The caval sphincter and hepatic sinus

1. *Ondatra* and *Lutra* lack both the caval sphincter and the hepatic sinus.
2. *Enhydra* has a simplified caval sphincter composed of slips of muscle surrounding the intrathoracic portion of the inferior vena cava. These sphincter muscle slips are not separable from the diaphrahm at their base. Extensive hepatic sinuses are not present.
3. *Pagophilus* has a well-developed caval sphincter and hepatic sinus, and these correspond closely to those found in other phocid seals.
4. *Zalophus* has a well-developed caval sphincter and hepatic sinus.
5. *Delphinapterus* has a sphincter in the form of a 'sling-like' arrangement of muscle fibers surrounding the vena cava, that are not easily spearated from the diaphragm at their base. An extensive hepatic sinus is not present.

The research for this thesis was carried out at the following institutions: Redpath Museum, McGill University; Department of Zoology, University of Alberta; B. C. Fish and Game Department; and the Arctic Biological Station of the Fisheries Research Board of Canada. Financial assistance was from personal funds and Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada (research grant of Dr. A. W. Cameron) and McGill University.

In keeping with the newly-accepted regulations for thesis style which have been authorized by the Graduate Training Committee of the Biology Department at McGill University, the main body of this thesis has been written in a form suitable for publication. Use is made of the style recommended by the Canadian Journal of Zoology and sections have been submitted to this journal for publication.

The following sections of this thesis have been accepted for publication-

1. Tarasoff, F.J. Thermal regulatory adaptations in the river otter, sea otter and harp seal. Contribution to - The Functional Anatomy of Marine Mammals. Edited by R.J. Harrison. Academic Press (London). (in press)
2. Tarasoff, F.J., A. Bisaillon, J. Piérard and A.P. Whitt. 1972. Locomotory patterns and external morphology of the river otter, sea otter and harp seal (Mammalia). Can. J. Zool. 50- 915-929.
3. Tarasoff, F.J. Comparative aspects of the hind limbs of the river otter, sea otter and seals. Contribution to - The Functional Anatomy of Marine Mammals. Edited by R.J. Harrison. Academic Press (London). (in press)
4. Tarasoff, F.J. and G.L. Kooyman. Comparative aspects of the respiratory system in the river otter, sea otter and harp seal. Part I. The topography, weights and measurements of the lungs. (resubmitted to Canadian Journal of Zoology after minor corrections)
5. Tarasoff, F.J. and G.L. Kooyman. Comparative aspects of the respiratory system of the river otter, sea otter and harp seal. Part II. The trachea and bronchial tree. (resubmitted to the Canadian Journal of Zoology after minor corrections)
6. Tarasoff, F.J. The anatomy of the caval sphincter and hepatic sinus in diving mammals. Contribution to - The Functional Anatomy of Marine Mammals. Edited by - R.J. Harrison. Academic Press (London). (text accepted by the editor but will not be submitted until more species are examined)

Sections in this thesis dealing with locomotion and the anatomical basis of locomotion are parts of a four part study worked on jointly by Drs. A. Bisaillon and J. Piérard (Ecole de Médecine vétérinaire, Université de Montréal). This study deals with the locomotory patterns and species topography, and osteology, myology and syndesmology of the caudal regions of these three species as related to locomotion. I am the major contributor to the sections on locomotory patterns and species topography, and syndesmology, whereas the research on the osteology and myology has been more equally shared and has not been included in this thesis.

Two sections of this thesis have dealt with comparative aspects of the respiratory system of the three species. These are part of a three part series of which Part III - Lung histology - has not been included. Although many of the more functional aspects of the respiratory system can be interpreted only after histological examination, it was not possible to obtain fresh-fixed material. A small quantity of material has now been collected and is being processed.

B. Anatomical adaptations in the river otter, sea otter and harp seal with reference to thermal regulation.

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Introduction

For the most part, studies of the thermal regulatory adaptations of aquatic mammals have been confined to the cetaceans and pinnipeds, with little reference to aquatic carnivores, such as the river otter and sea otter. Literature pertaining to the former two groups has been reviewed recently by Kanwisher and Sundnes (1966), Harrison and Kooyman (1968), Irving (1966) and Tarasoff (1972). The latter two species and the pinnipeds have been dealt with briefly by Tarasoff (opp cit.).

The pinnipeds, in particular, have been studied extensively, principally because of the availability and ease of handling. Our knowledge of these mammals has come from a combination of studies dealing with their anatomy, behavior and physiology, and, as is often the case, much of the physiological adaptations are predictable from anatomical and behavioral studies.

The sea otter, *Enhydra lutris*, has been neglected principally because of a lack of availability and a limited knowledge of proper handling techniques. Recently, the Alaskan sea otter population has become sufficiently large to permit selective harvesting, thereby making carcasses available for anatomical research. Sea otters have been maintained in captivity and information from this source and from recently published field observations (Kenyon, 1969) permit some evaluation of thermal regulatory adaptations based on the animal's behavior. Results of transplantation projects and the relative difficulties of keeping these animals in captivity indicate that handling procedures have not been understood well enough to permit extensive physiological studies. However, it is anticipated that, as for pinnipeds, some evaluation of the sea otter's thermal regulatory adaptations

It is the purpose of this report to document anatomical and behavioral thermal regulatory adaptations in the sea otter. To help emphasize its position relative to other aquatic mammals, direct comparisons have been made with the river otter and harp seal wherever possible. This approach will contribute to the understanding of how each species is adapted to its particular habitat and demonstrate varying degrees of aquatic adaptation.

Materials and Methods

External features

The external features were examined on the unskinned carcasses of 7 river otters (*Lutra canadensis*) from Quebec, Canada and Maine, U.S.A.; 11 sea otters (*Enhydra lutris*) from Alaska, U.S.A.; and 15 harp seals (*Pagophilus groenlandicus*) from Quebec. The sea otters were collected during the summer months (April to September) and the river otters and harp seals from January to March. From each carcass, the body weight, standard length, total surface area, and surface areas of the tail and feet were determined. The river otters and sea otters were skinned and the surface areas calculated by dividing the skins into 5 cm. strips and summing the areas of the thus formed rectangles. The surface areas of the harp seals were computed using the formula: $S\ (m^2) = 0.083 \sqrt[3]{\text{Wt. (Kg)}^2}$ (Irving, et al., 1935). The surface areas of four harp seals were calculated by the method used for the otters before skinning to determine if the above formula approximated the actual surface area for seals greater than 30 kilograms. The tail and feet surface areas were calculated using the procedures outlined in the section on locomotion (Part I. Locomotory patterns and species topography).

Pelage and skin

Hair and skin samples were removed from the base of the tail, midback, tarsus, and interdigital web of the foot of 3 river otters, 12 sea otters and 7 harp seals, and preserved in 5 % formalin, or Bouin's fluid. In all cases, the animals were either juveniles or adults. From these samples, the morphology, length, diameter, density and slope of the hairs, and the skin thickness were determined. Hairs were examined by scanning electron and light microscopy to determine the external features (topography) and characteristics of the medulla. The average hair length (mm) was determined from 15 hairs of each type (primary and secondary guard and underhairs) in the four regions. Hair diameters from each region were determined using the procedures of Hardy (1935). Paraffin embedded sections containing cross-sections of hairs were examined under a compound microscope and the diameter measured to the nearest 0.001 mm. Subepidermal hair diameter, and hair density (hairs/cm^2) were calculated from histological preparations stained routinely with Harris' hematoxylin and eosin. Vertical skin sections were prepared from the three species and hair slope, skin thickness and arrector pili muscles were examined. Hair slope is that angle formed between the skin surface and the hair shaft at its emergence from the hair canal. Skin thickness includes both the epidermis and dermis.

Subcutaneous fat

Subcutaneous fat distribution was noted in all specimens. The contribution to the body weight (%) made up of this fat or blubber was determined in 3 river otters, 1 sea otter and 4 harp seals. In the harp seals, the blubber depth was recorded every 10cm. along the mid-dorsal surface from the head to the tip of the tail.

Myology and angiology

The distribution of the *M. cutaneous trunci* was recorded in 3 river otters, 3 sea otters and 3 harp seals.

Latex injected arteries and veins of the pelvic limb were dissected in

2 specimens of each of the three species.

Observations on captive otters and seals

Four captive sea otters were observed in August, 1971 at the Woodland Park Zoo, Tacoma, Washington. Particular attention was given to grooming activities and movements of the pelvic limbs and feet during quiescent periods. Less extensive observations were made on captive river otters and harp seals.

RESULTS

A. Surface area

Table I shows the percentages of the total surface area of the tail and feet in each of the three species. For the tail, *Lutra* has the highest value (8.1%). This percentage decreases from *Enhydra* (2.2%) and *Pagophilus* (0.4%). The combined surface areas of the feet are greatest in *Pagophilus*. (18.0%) and decreases from *Lutra* (10.2%) to *Enhydra* (5.8%). The fore feet always have a smaller area than the hind feet, with *Enhydra* having the smallest value (0.8%).

The surface areas of four harp seals were determined prior to skinning and these values were compared to those determined using the formula:

$$S(m^2) = 0.083 \sqrt[3]{wt.\ (Kg)^2}$$

These values were within 5% of each other, indicating that this formula is acceptable for estimating the surface area of harp seals weighing up to 113Kg.

B. Hair morphology

The basic characteristics of the pelage of *Enhydra* have been described by Scheffer, and Ling (in Kenyon, 1969) and readers are referred to this work for details in addition to those presented here.

The pelage of the tail, midback, tarsal regions and the interdigital web of the foot of Enhydra contain primary and secondary guard hairs and

Table I. Surface areas of the tail and feet of *Lutra*, *Enhydra* and *Pagophilus* expressed as a percentage of total body surface area.

	surface area (cm)	body weight (Kg)	$\frac{\text{tail area}}{\text{surface area}}$ (6/o)	$\frac{\text{forefeet area}}{\text{surface area}}$ (o/o)	$\frac{\text{hindfeet}}{\text{sfc. area}}$ (o/o)	$\frac{\text{all feet}}{\text{sfc. area}}$ (o/o)
Lutra						
$\overline{X}$	2,757	6.7	8.1	3.1	7.1	10.2
R	2,511-3,172	4.9-8.0	6.7-9.5	2.9-3.9	6.5-8.3	9.2-11.9
N = 7						
Enhydra						
$\overline{X}$	10,856	21.2	2.2.2	0.8	5.0	5.8
R	5,206-16,380	10.0-34.1	1.6-3.0	0.6=1.0	3.2-7.8	4.0-8.8
N = 11						
Pagophilus						
$\overline{X}$	1.5 (m^2)	8080.4	0.4	4.1	13.9	18.0
R	1.1-1.9 (m^2)	49.0-113.2	0.3-0.6	2.1-5.6	9.7-17.0	12.5-21.1
N = 15						

underhairs (Fig 1). Primary and secondary guard hairs are straight-shafted and morphologically similar to each other, with the principal differences being diameter and length. Both are oval in cross-section at their emergence from the hair canal. Halfway up the shaft, the width gradually increases laterally until it is about two times the diameter of the lower shaft. The shaft then narrows to a fine point. Underhairs are wavy, and shorter than the guard hairs. These hairs are of more equal cross-sectional diameter throughout their length and increase in width slightly before tapering to a fine point (Fig 2). The diameters of the various hairs at the skin surface and at maximum width are shown in Table II. A medulla is present in all guard hairs and near the base of some of the underhairs (Fig 3). In the guard hairs, the medulla is continuous in the proximal 2/3 of the hair shaft. It then becomes discontinuous and disappears at the level of the lateral broadening of the shaft.

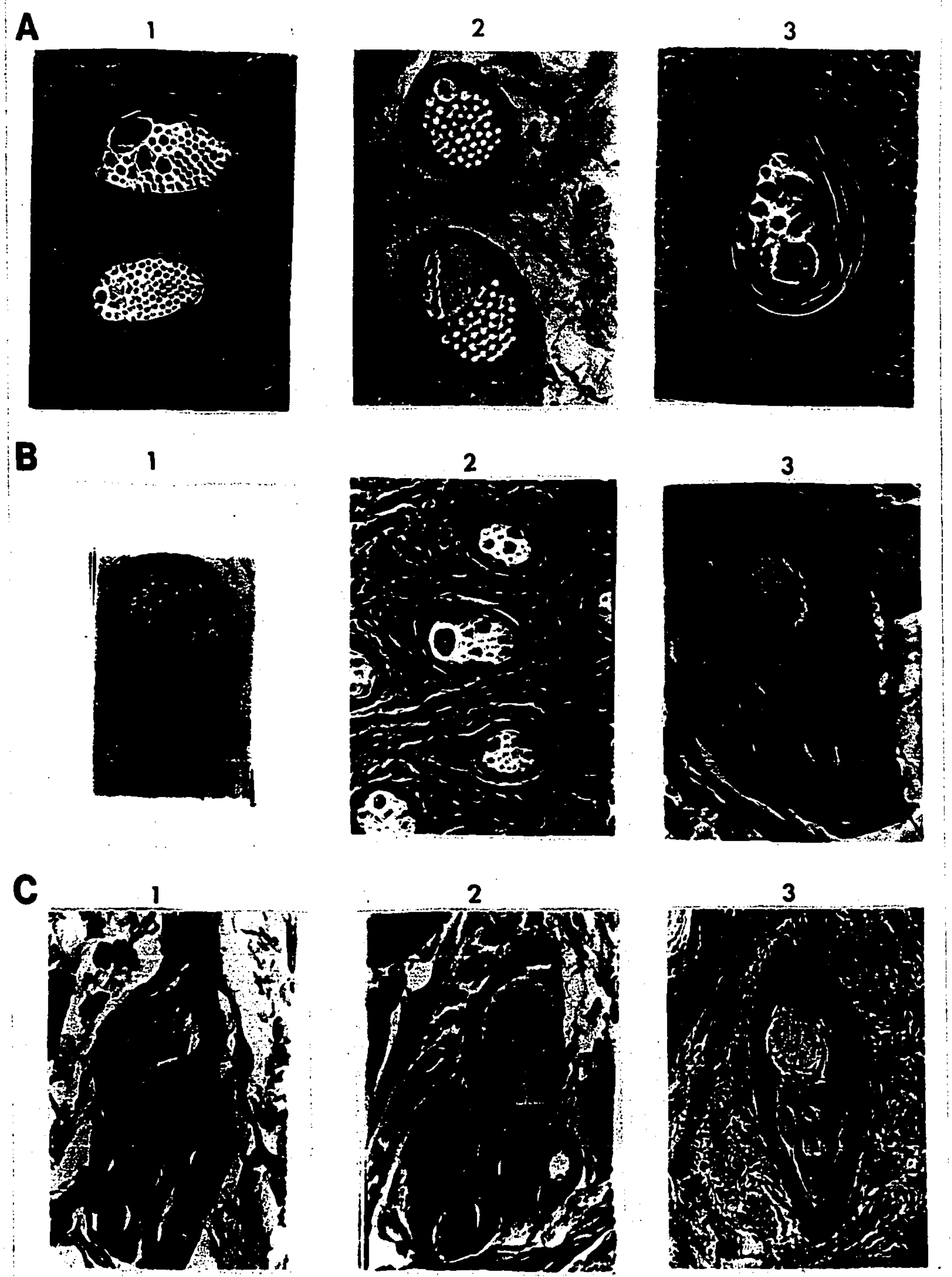
The pelage of the tail, midback and tarsal regions of *Lutra* contains primary and secondary guard hairs and underhairs, while the interdigital web of the foot lacks secondary hairs (Fig 1). Guard hairs are shaped similar to those of *Enhydra* (Fig 2). Lateral expansion of the shaft is greater than in *Enhydra*, being about three times that of the base. The underhairs are wavy and increase slightly in diameter near their distal ends. A well-developed medulla is present in the guard hairs, but absent in the underhairs (Fig 3). In the guard hairs, the medulla is maximally developed in the proximal and distal one-third of the expanded hair and interrupted in the central regions.

The guard hairs of *Pagophilus* are dorsoventrally flattened at their emergence from the skin. They increase in diameter very gradually in the

Table II. Mean diameter of hairs (μ) from the tail, midback, tarsus and interdigital web of the foot of *Lutra*, *Enhydra* and *Pagophilus*.

		tail	midback	tarsus	foot
Lutra					
-primary guard hair	base	72	50	60	45
	max.	220	198	180	162
-secondary guard hair	base	50	45	22	--
	max.	150	115	90	--
-underhair	base	10	10	10	18
	max.	12	12	12	21
Enhydra					
-primary guard hair	base	59	60	52	98
	max.	105	97	110	130
-secondary guard hair	base	23	20	35	40
	max.	45	45	60	48
-underhairs	base	10	13	15	22
	max.	14	16	18	30
Pagophilus					
-primary guard hair	base	175	190	168	150
	max.	185	210	185	170
-secondary hairs	base	68	65	68	65
	max.	85	85	85	85

Figure I. Horizontal sections of hair bundles from the midback (1),tarsus(2), and interdigital web of the foot (3) of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (magnification X100)


A
1
2
3
B
1
2
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C
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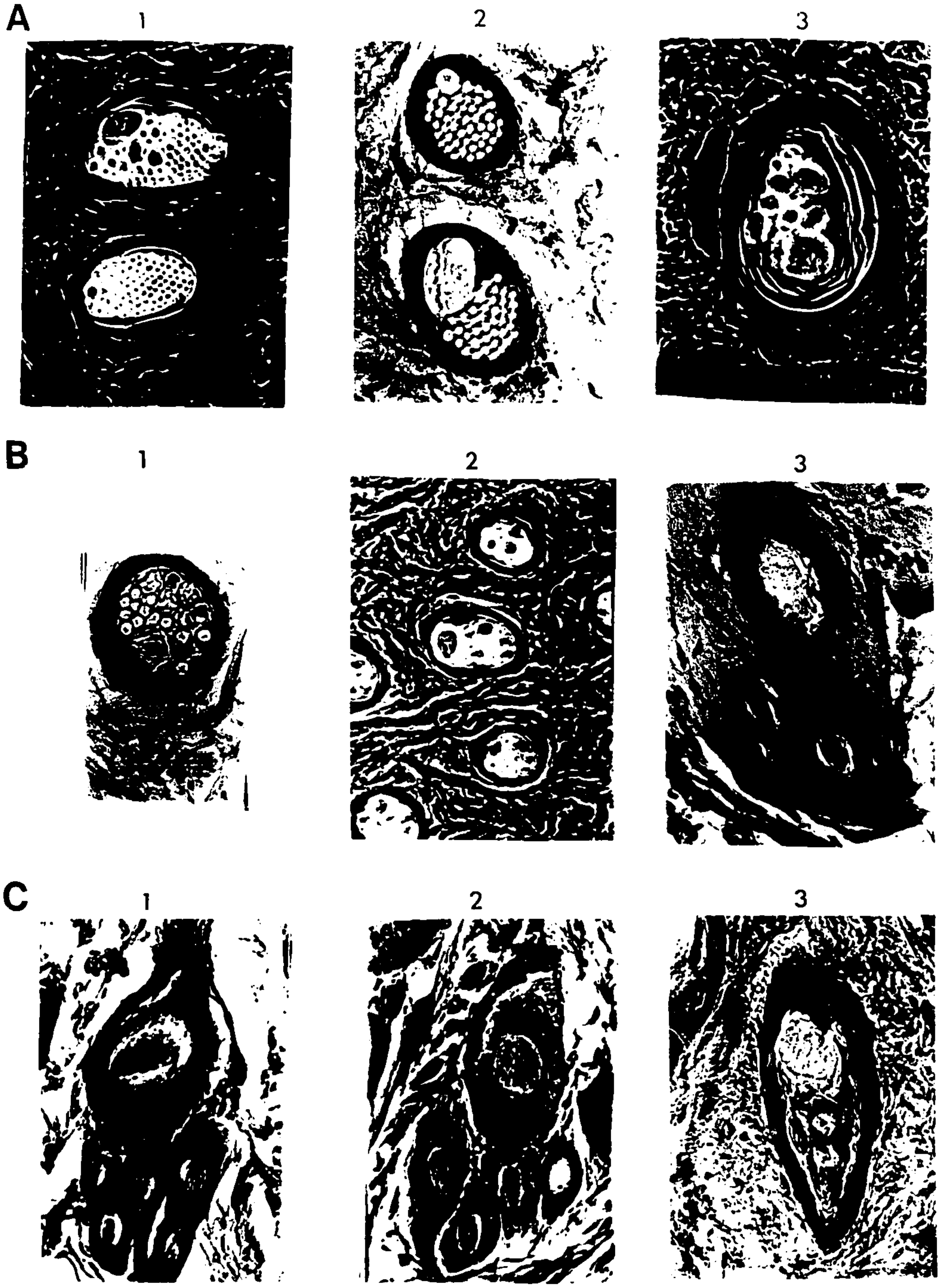
2
3


A
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C
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2
3

Figure 2. Drawings illustrating the outline and cross-sections of primary guard hairs (a), secondary guard hairs (b), underhairs (c) and secondary hairs (d) in *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

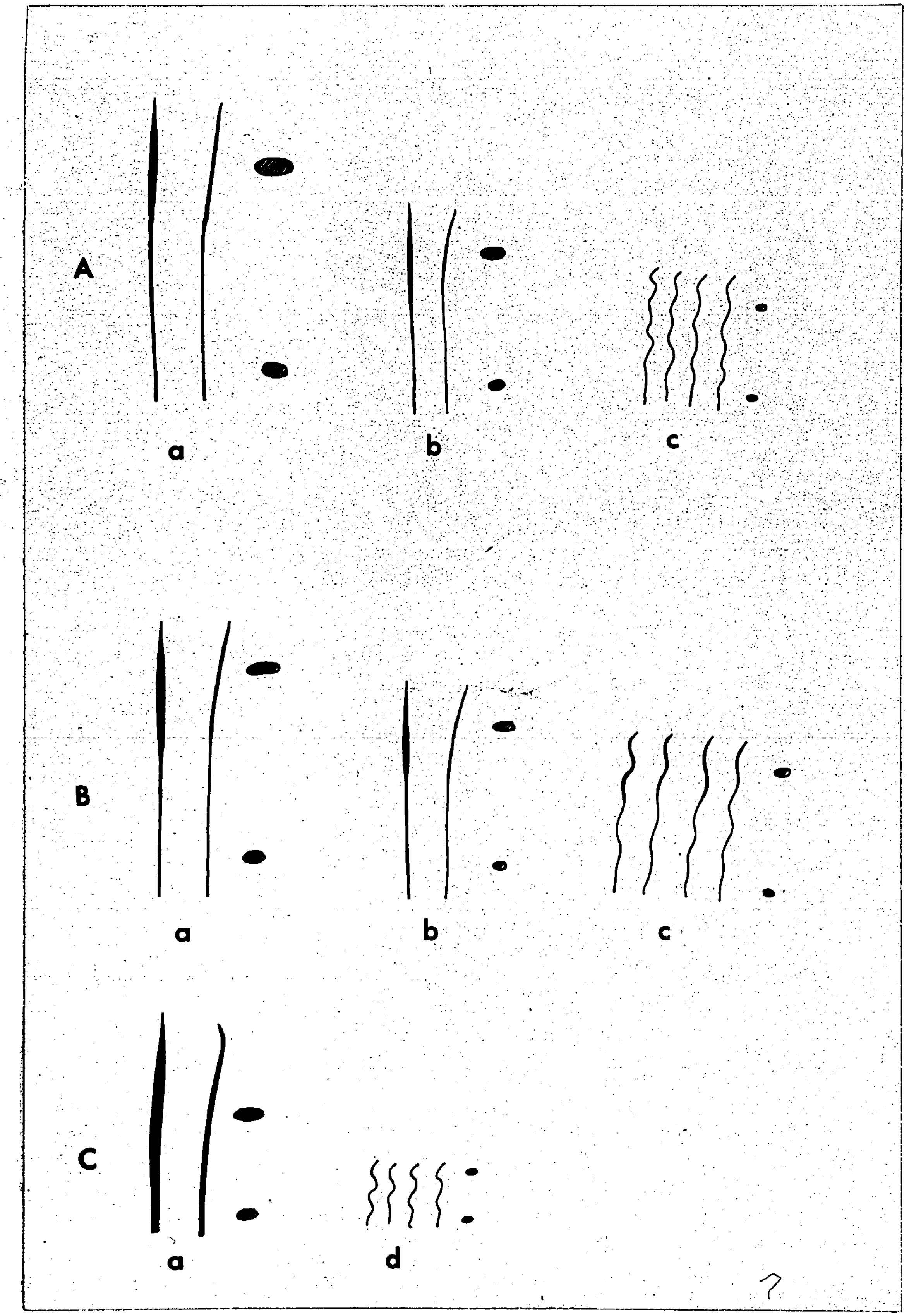

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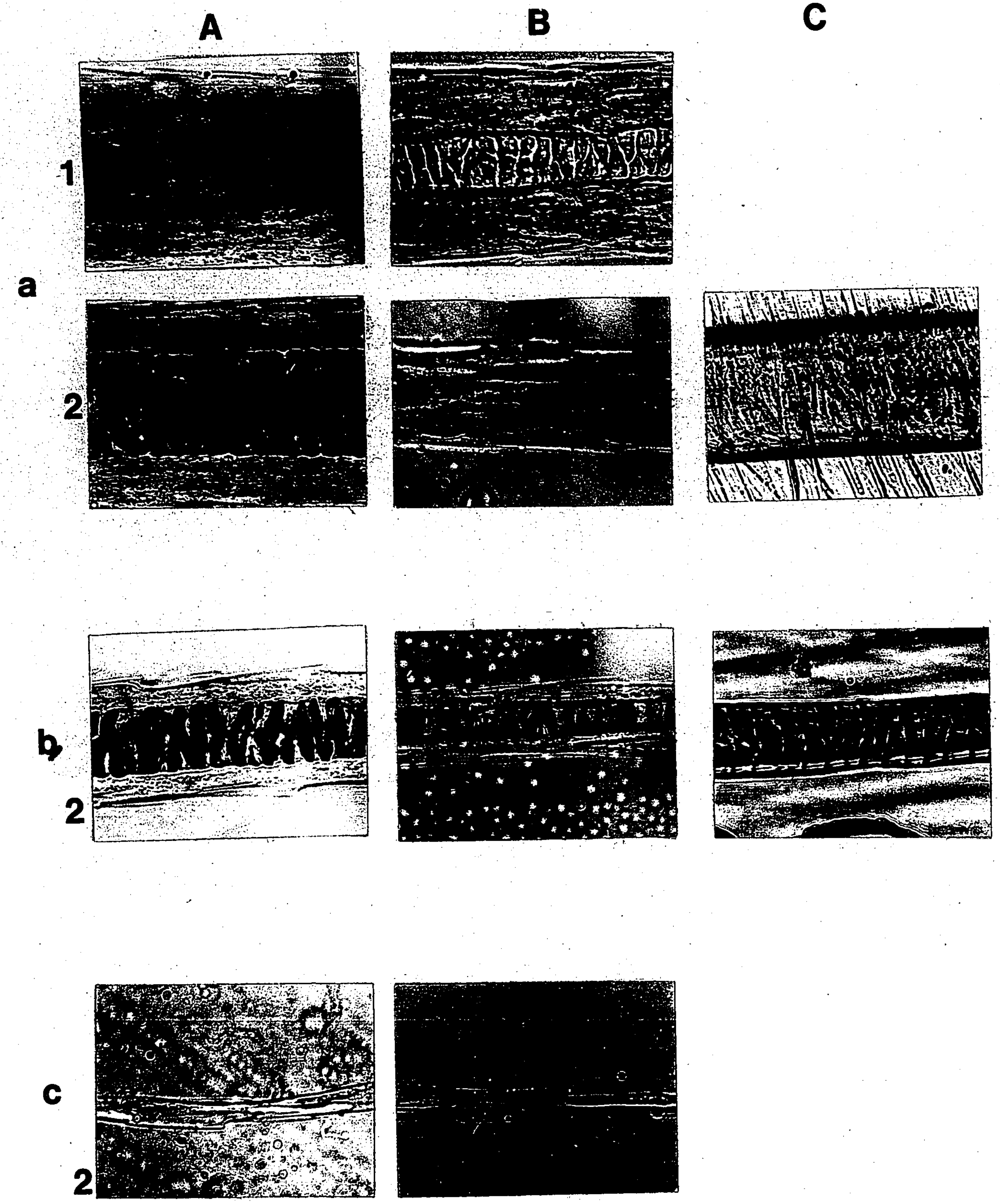
Figure 3. The medulla in representative hairs from the midback region of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (magnification X 420).

a. primary guard hair
b. secondary guard hair
c. underhair

1. midway up hairsshaft
2. base of hair shaft


A
B
C
1
a
2
b
2
c
2

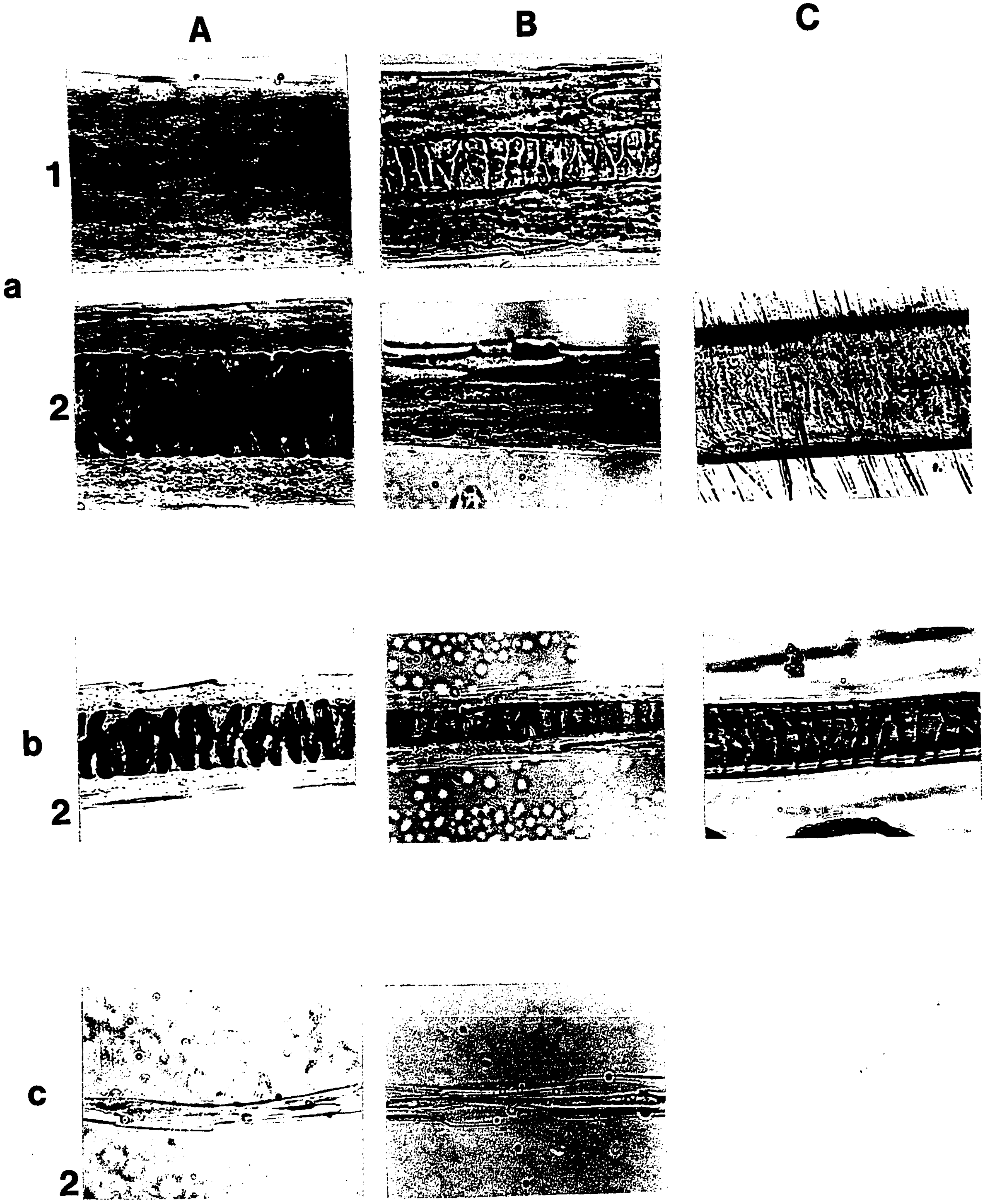

A
B
C
1
a
2
b
2
c
2

Table III. Mean hair lengths (mm) from the tail, midback, tarsus and interdigital web of the foot of *Lutra*, *Enhydra* and *Pagophilus*.

	tail	midback	tarsus	foot
Lutra				
-primary guard hairs	20.0	20.0	10.0	4.0
-secondary guard hairs	14.0	14.0	5.0	---
-underhairs	10.0	10.0	6.0	2.5
Enhydra				
-primary guard hairs	30.0	30.0	21.0	10.0
-secondary guard hairs	22.0	23.5	20.0	8.0
-underhairs	19.0	12.0	15.5	4.5
Pagophilus				
-primary guard hairs	9.0	16.0	9.4	4.0
-secondary hairs	4.5	7.0	5.2	2.0

Figure 4. Scale patterns on hairs from the midback region of *Lutra*(A), *Enhydra* (B) and *Pagophilus* (C). (magnification X 350)

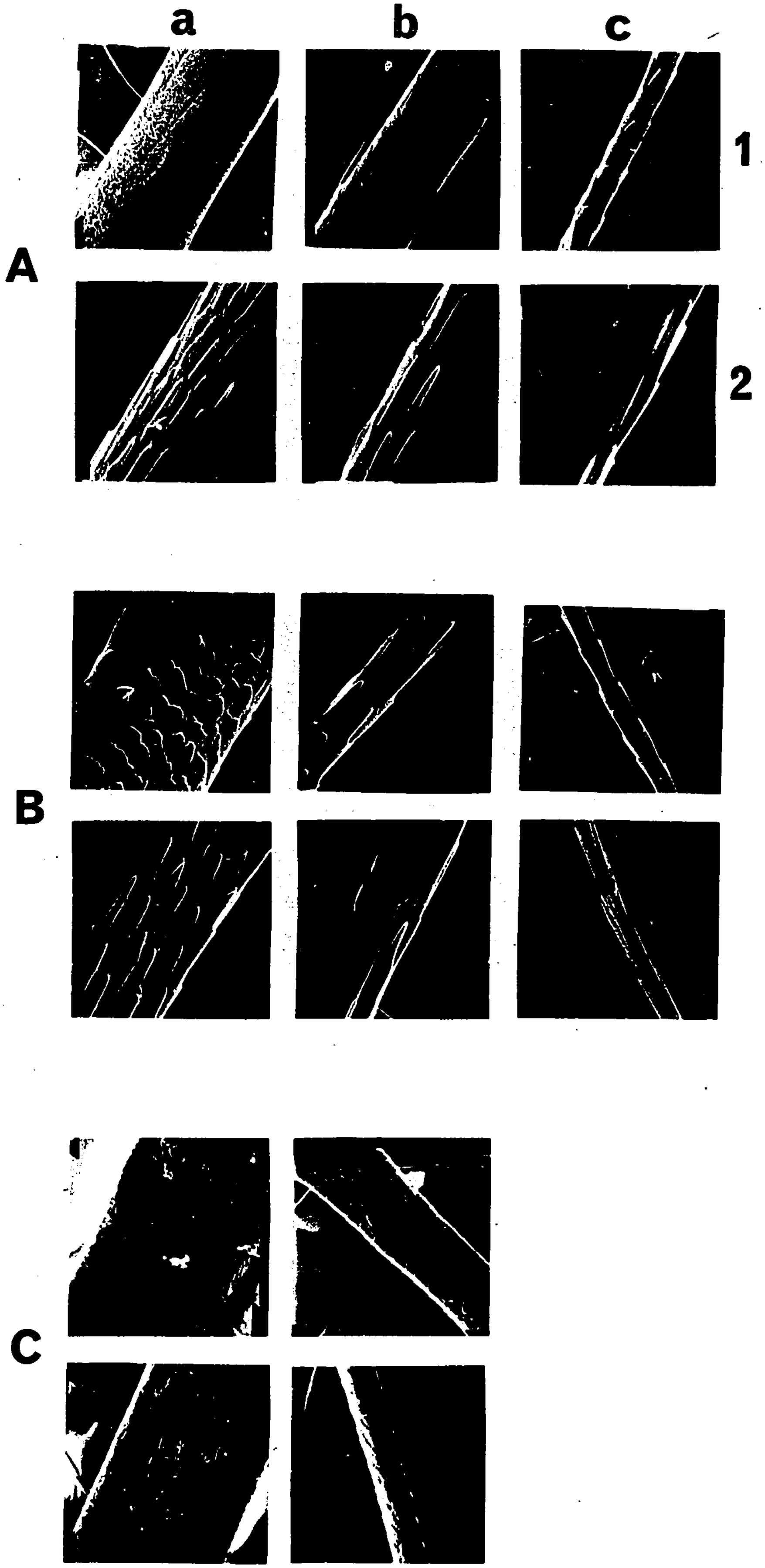
a. primary guard hair

b. secondary guard hair

c. underhair

1. maximally expanded region of hair shaft

2. base of hair shaft


a
b
c
1
2
A
B
C

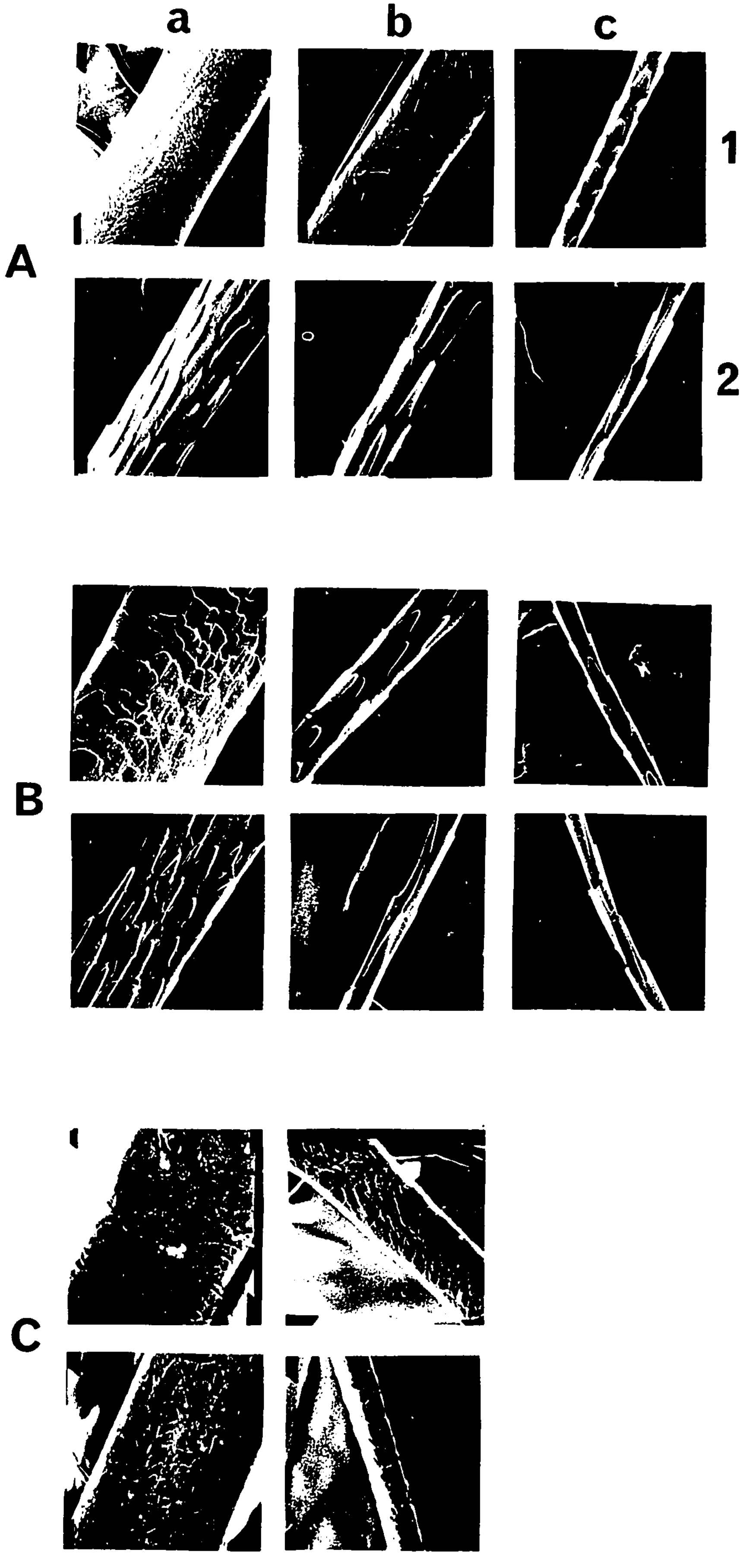
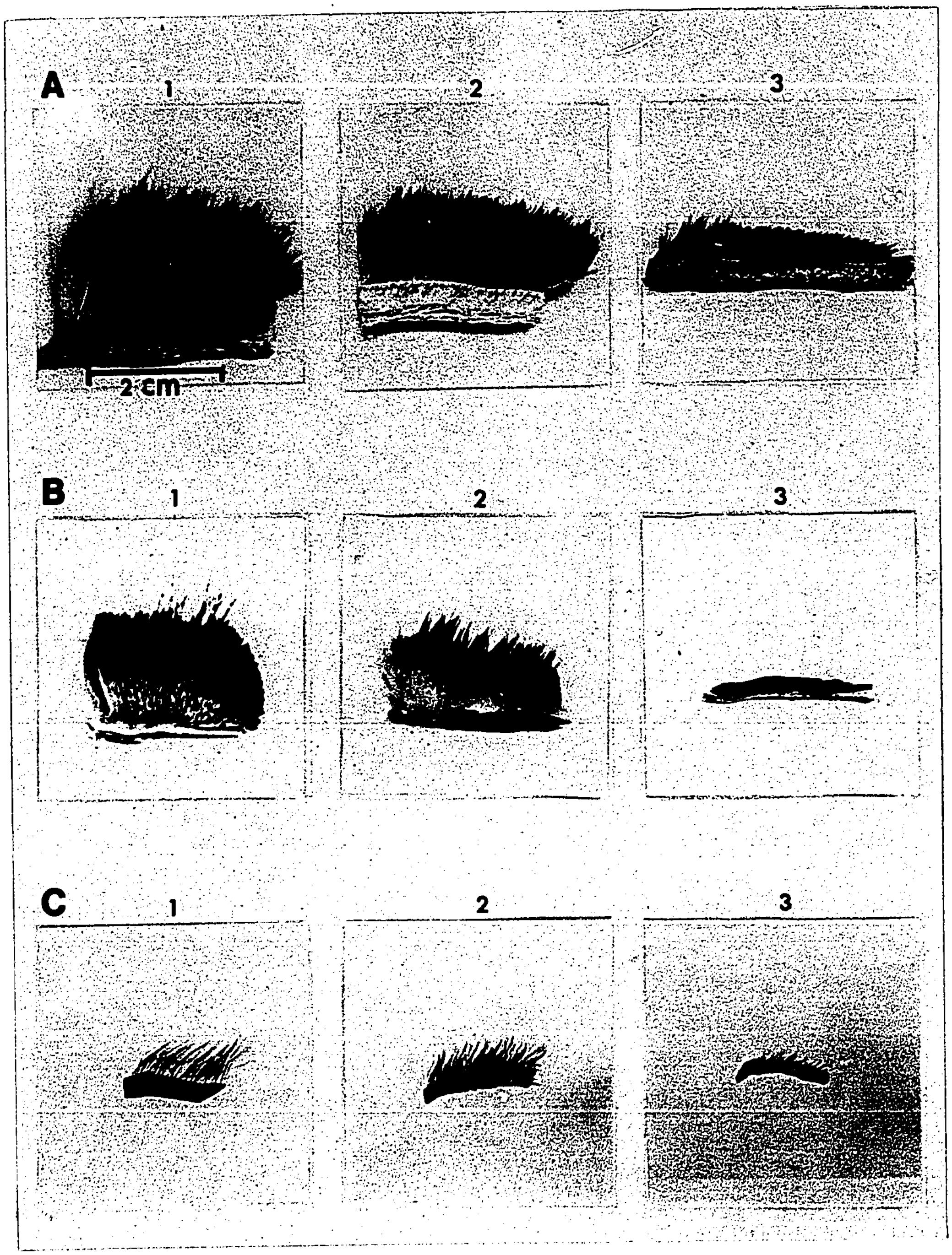

a
b
c
1
A
2
B
C

Figure 5. Skin and pelage samples from the midback (1), tarsus (2) and interdigital web of the foot (3) of *Lutra*(A), *Enhydra* (B) and *Pagophilus* (C).



A
1
2
3
2 cm
B
1
2
3
C
1
2
3

lateral plane until near their distal end where they taper to a point (Fig 2 and Table II). The secondary hairs are smaller in diameter, curly and shorter. A medulla is absent in all hairs (Fig 3).

Details of the cuticular scales on hairs from the midback region of each species are seen in figure 4. Three types of scales are characterized: 1. spike-like 2. leaf-like 3. irregular scales. Spike-like scales are found in *Lutra* and *Enhydra* at the base of the shaft of guard hairs and underhairs. They are relatively long and narrow, with the points directed toward the distal end of the hair shaft. Their sides are concave and the top is flat. Leaf-like scales are found in *Lutra* and *Enhydra* at the laterally expanded region of the underhairs and in *Enhydra* in the expanded region of the secondary guard hairs. These scales are shorter, broader and terminate more bluntly than the spike-like scales. Irregular scales are found at the laterally expanded regions of the primary and secondary guard hairs of *Lutra*, the expanded region of the primary guard hairs of *Enhydra*, and throughout the length of the guard and secondary hairs of *Pagophilus*. These cuticular scales have an overlapping pattern with an irregular distal border. As with the other scale types, the free margin is directed distally along the hair shaft.

C. Hair length

The mean hair lengths from the tail, midback, tarsus and interdigital web of the foot of *Lutra*, *Enhydra* and *Pagophilus* are shown in Table III. The overall trends in the three species are for the primary guard hairs to be longer than the secondary guard hairs and both of these to be longer than the underhairs. In each region examined, *Enhydra* has the longest hairs of any type, with *Lutra* next, and *Pagophilus* having the shortest hair (Fig 5).

Hair length decreases from the tail to midback to tarsus to foot.

D. Hair density

The mean hair densities (hairs/cm^2) for the three species are shown in Table IV. Hair density follows a trend similar to that of hair length with *Enhydra* > *Lutra* > *Pagophilus* and the tail > midback > tarsus > interdigital web of the foot.

E. Hair slope and errector pili muscles

The angle of hair slope (degrees from the horizontal plane at emergence of the hair from the hair canal) is shown in Table V. In all the species, the hairs are directed caudally. Individual animals have about the same hair slope in the tail, midback and tarsal regions, with the hairs on the foot forming a more acute angle. The hairs of *Enhydra* and *Lutra* slope less than those of *Pagophilus*.

In *Lutra*, the errector pili muscles are present in all four regions examined. These muscles are absent in *Enhydra* and *Pagophilus*.

F. Skin thickness

In each animal, the skin is of about equal thickness in the tail, midback and tarsal regions, and much thinner in the interdigital web region of the foot (Table VI). *Enhydra* and *Pagophilus* have the thickest skin in all regions.

Table IV. Hair density (hairs/cm2) from the tail, midback, tarsus and interdigital web of the foot of *Lutra*, *Enhydra* and *Pagophilus*.

	tail	midback	tarsus	foot
Lutra				
$\bar{X}$	62,144	57,833	58,667	1,648
R	71,342-59,631	62,021-52,309	65,701-52,801	1,785-1,528
N = 3				
Enhydra				
$\bar{X}$	131,094	125,333	107,301	3,375
R	142,011-125,937	129,632-115,617	118,721-98,848	5,298-2,980
N = 12				
Pagophilus				
$\bar{X}$	1,697	1,798	1,715	450
R	1,807-1,500	1,894-1,460	1,875-1,609	582-407
N = 7				

Table V. Hair slope at emergence from hair canal in *Lutra*, *Enhydra* and *Pagophilus*. (degrees from the horizontal)

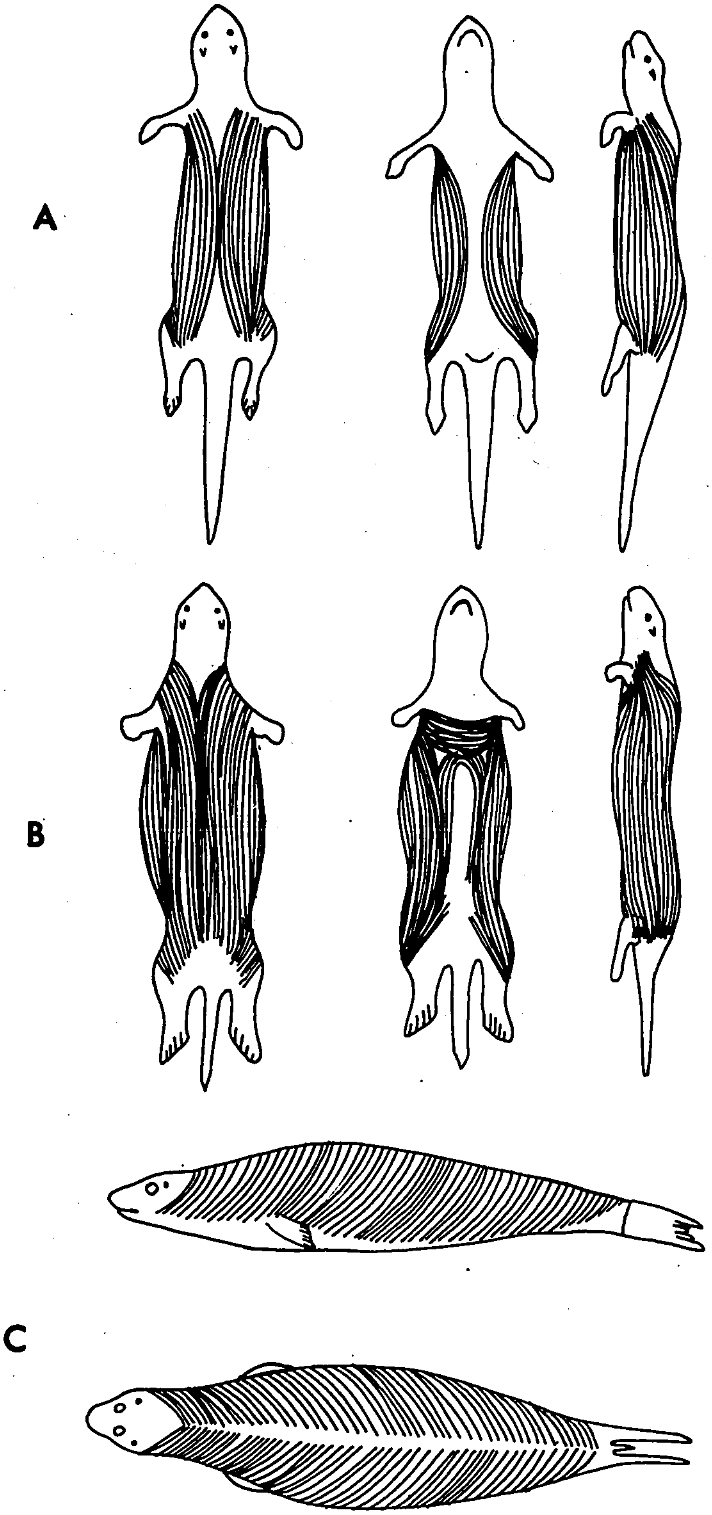
	tail	midback	tarsus	foot
Lutra	61	63	60	40
Enhydra	72	68	68	51
Pagophilus	42	45	45	42

Table VI. Skin thickness (mm) in the tail, midback, tarsus and interdigital web of the foot of *Lutra*, *Enhydra* and *Pagophilus*.

		tail	midback	tarsus	foot
Lutra	$\bar{X}$	2.0	2.0	1.9	0.9
	R	2.0-2.1	1.9-2.0	1.9-2.0	0.9-1.0
	N = 3				
Enhydra	$\bar{X}$	3.5	3.4	3.4	1.3
	R	3.5-3.6	3.4-3.5	3.3-3.5	1.2-1.5
	N = 6				
Pagophilus					
	$\bar{X}$	3.0	3.3	3.4	1.5
	R	2.9-3.2	2.5-3.4	3.0-3.7	1.5-1.6
	N = 6				

Figure 6. Distribution of the *M. cutaneous trunci* on the dorsal, lateral and ventral surfaces of *Lutra*(A), *Enhydra* (B) and *Pagophilus* (C).

(C is redrawn from Howell, 1929)


A
B
C

G. M. cutaneous trunci

In all three species, the cutaneous trunci muscle is located in the superficial trunk fascia immediately ventral to the skin and the subcutaneous fat. This muscle is thin, sheet-like, composed of fleshy fibers, and envelopes the dorsal and lateral sides of the trunk (Fig 6). The major differences are in the points of origin and insertion, and direction of the fibers.

Lutra

Origin and insertion: (Fig 6A): This muscle almost completely covers the body, except the head, forearm and hand, lower leg and foot, and tail (Fisher, 1942). Origin is by tendinous fobers in the dorsal and lateral gluteal fascia. The fibers become fleshy almost immediately and pass cranially. The muscle spreads out over the dorsal, lateral and ventral surfaces of the abdomen and thorax. From their origin, the dorsal-most fibers converge, meet in a raphe, and run in straight lines parallel to the neural spines of the lumbar and thoracic vertebrae. At the scapular region, some of the fibers pass ventrally to the axillary region and the medial brachial fascia, while the rest continue cranially to meet those of the *M. platysma*. These latter fibers are directed cranioventrally. Lateral fibers pass cranially over the sides of the abdomen and thorax to their insertion in the medial brachial fascia. The ventrally located fibers pass over the cranial surface of the thigh and converge ventrally to run parallel to the *M. rectus abdominis* over the central one-half of the body. Fibers from each side do not meet in the midline. Near the mid-part of the thorax, the fibers diverge and pass to their insertion in the medial brachial fascia. This muscle is equally developed in all regions and the fibers are united by tendinous fibers, so it would seem that the muscle can act as a whole upon stimulation.

Functions: Shivering reflex and flexion of the skin upon emergence from the water.

Enhydra

Origin and insertion:(Fig 6B): Origin is by tendinous fibers over a wide area in the dorsal and lateral gluteal fascia. The dorsal-most fibers meet along the dorsal midline and are not separated by a raphe. These fibers are parallel to the neural spines of the lumbar and thoracic vertebrae. Cranially,the fibers meet the *M. platysma* and are directed cranio-ventrally. Along the lateral abdominal and thoracic regions, the fibers of the cutaneous trunci run in straight lines to their insertion either on the medial brachial fascia or on the *M. platysma*. The ventral fibers of this muscle run cranio-ventrally over the cranial surface of the thigh and remain well-separated from the midline. Some of the more medial fibers insert on the mid-ventral fascia forming an angle of about 45 degrees. The cranial fibers divide in the proximal part of the thorax and insert in the medial brachial fascia. Fibers of this muscle also have their origin on the ventral surface of the animal. These strap-like fibers run cranially and many are seen to intermingle and cross each other. This portion of the muscle is most highly developed in the proximal thoracic region and completely covers the pectoralis musculature. Fibers converge laterally and insert on the medial brachial fascia.

In *Enhydra*, the cutaneous trunci muscle is most highly developed on the dorsal and lateral surfaces, and the proximal thoracic region of the ventral surface of the body. The midventral fibers are weak, strap-like and well-separated from each other.

Functions: Shivering reflex and pleating the skin on the dorsal and lateral surfaces of the body prior to quiescent periods in the water.

Pagophilus

Origin and insertion: (Fig 6C): Howell (1929) accurately describes the cutaneous trunci muscle in *Phoca hispida*, and as there is no observable differences in this muscle between that seal and *Pagophilus*, his description is restated here.

> "There was no converging of the fibers to the axilla, but origin was somewhat laterad of the middorsal line and all fibers were uniformly directed ventro-craniad at an angle from the vertical of about 35 degrees; covering the knee and extending almost to the base of the tail, in which vicinity the line of origin extended somewhat more dorsad. Insertion of the portion over the scapula was onto the fascia of the middle forearm, and of the remainder upon the fascia of the ventral surface slightly laterad of the midventral line." (from Howell, 1929, p. 51).

Functions: Shivering reflex and possibly assisting during terrestrial locomotion.

H. Subcutaneous fat

All of the river otters were obtained during the winter season. In these animals, fat is most abundant in the proximo-lateral regions of the tail and the dorso-medial axillary regions of the limbs. On the trunk, the fat increases from the middorsal to midventral surface. The head, and cranial and lateral sides of the limbs have little or no fat deposits. From three adult animals, the mean percentage of fat to total body weight is 12.6% (Table VII).

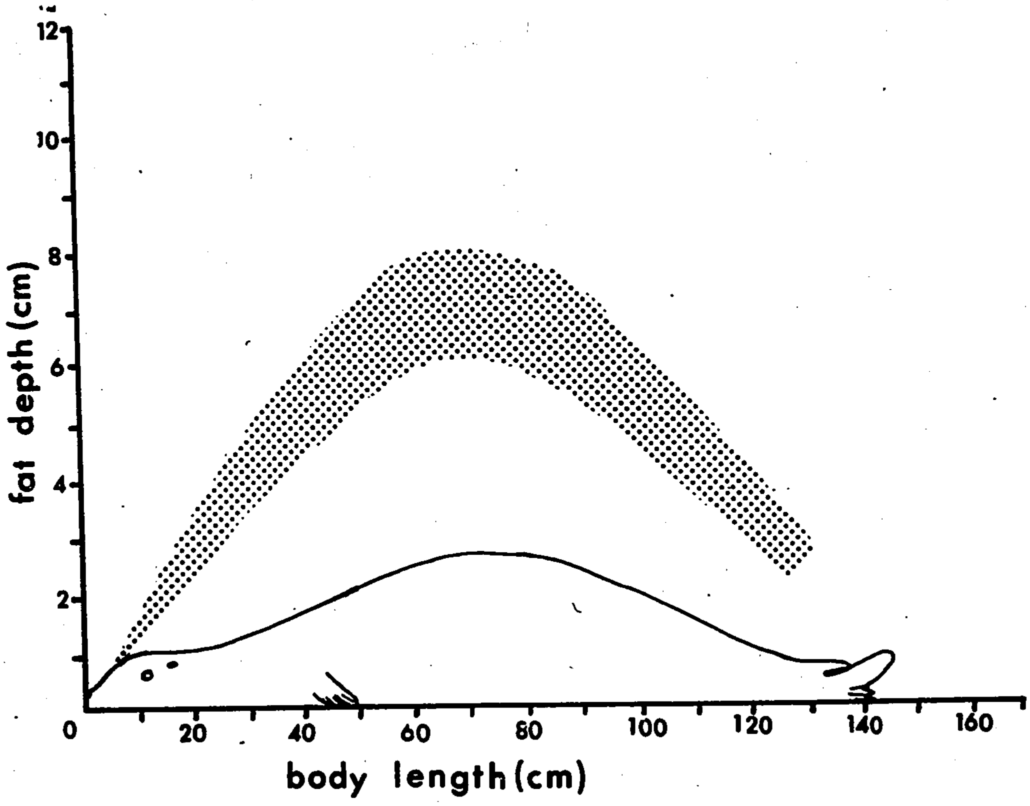
Sea otter specimens were obtained during each season, and have little abdominal or subcutaneous fat at any time. When subcutaneous fat is present, it is most abundant along the lateral and ventral sides of the abdomen, the external genitalia and anus, the medial sides of the pelvic limb axilla, and the lateral sides of the tail. Fat weight was recorded in one adult female and is 1.8% of the total body weight.

Harp seal carcasses were obtained during March when the animals are feeding in the St. Lawrence River. The depth of fat along the middorsal line in four specimens is shown in figure 7. The depth is least in the procranial and tail regions, and on thellimbs (distal from where they protrude from the body). Fat depth increases progressively toward the c central body region and reaches a maximum depth of 8.0cm. Depth measurements were not recorded on the lateral and ventral surfaces, but it appears that there is not a drastic change in depth from the middorsal to midventral surface at a given position. The mean percentage of subcutaneous fat to total body weight in four animals is 37.9%.

Table VII. Subcutaneous fat as a percentage of total body weight in *Lutra*, *Enhydra* and *Pagophilus*.

Lutra	$\bar{X}$	12.6
	R	10.9-14.0
	N = 3	
Enhydra	$\bar{X}$	1.8
	N = 1	
Pagophilus		
	$\bar{X}$	37.9
	R	33.3-42.5
	N = 4	

Figure 7. Depth of subcutaneous fat along the middorsal line in four specimens of *Pagophilus*.


12
10
8
6
4
2
fat depth (cm)
0
20
40
60
80
100
120
140
160
body length (cm)

I. Angiology of the pelvic limb

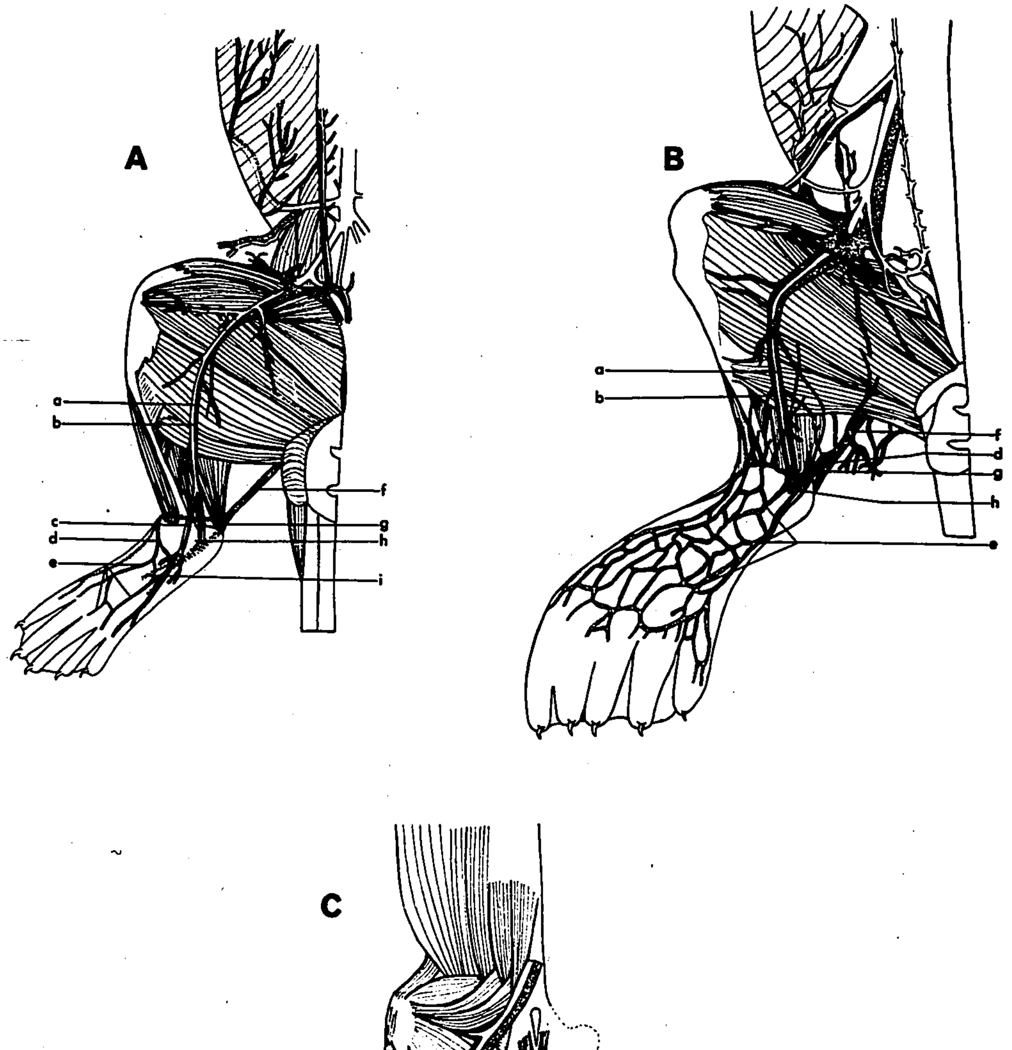
Immediately ventral to the skin and embedded in the superficial fascia on the dorsal surface of the foot of *Enhydra* is located an extensive venous circulation that drains into the caudal gluteal vein (Fig 8B). No comparable arrangement of blood vessels is present on the dorsal surface of the feet of *Lutra* (Fig 8A) and *Pagophilus* (Fig 8C). The blood to the superficial plantar surface of the foot of *Enhydra* is supplied by the saphenous artery and drained primarily by the saphenous vein. These two vessels are very closely associated throughout their lengths as is the femoral artery and the iliac vein. A deep plantar circulation is present and of a simple plan. Other than the absence of the superficial venous plexus, the vascular anatomy of the pelvic limb of *Lutra* is similar to that of *Enhydra*.

Pagophilus has a relatively poorly developed circulation on the dorsal surface of the foot, but the plantar surface appears to be more highly vascularized than in the other two species (Fig 8C). The superficial plantar surface is supplied principally by the superficial branches of the saphenous artery and drained by the medial saphenous or caudal gluteal vein, and the lateral saphenous vein. During its course over the medial surface of the leg, the saphenous artery and vein give off fewer muscular branches than in *Lutra* and *Enhydra*, the main circulation to the musculature being from the deep vessels of the leg.

Blood vessel distribution in the plantar region of the foot is very

Figure 8. Superficial arteries and veins on the medial surface of the leg, and dorsal surface (*Lutra* -A and *Enhydra* -B) and the plantar surface (*Pagophilus* -C) of the foot.

a. saphenous artery
b. saphenous vein
c. dorsal branch of saphenous artery and vein
d. dorsal branch of medial saphenous vein
e. dorsal superficial metatarsal, digital and interdigital veins
f. medial saphenous vein (caudal gluteal vein)
g. plantar branch of medial saphenous vein
h. plantar branch of saphenous vein
i. plantar superficial metatarsal, digital and interdigital veins


A
a
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c
h
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i

similar to that of *Phoca vitulina*, as described and figured by Tarasoff and Fisher (1970).

J. Grooming and digital expansion

Captive sea otters groom the fur vigorously on all parts of the body after feeding and prior to quiescent periods. The characteristics of this behavior are described by Kenyon (1969). The animals roll over frequently and expose their dorsal surface above the water. While in this position, the skin on the dorsal surface is pleated rapidly several times along the long axis of the body. When the animal again comes to rest on its back at the surface, it rides higher in the water and air trapped in the fur is seen as a visible silvery layer. If grooming continues in this position, the animal sinks lower in the water until its ventral surface is nearly awash. Then, the rolling over and pleating of the skin is repeated. This pattern is also observed prior to the onset of quiescent periods.

During periods of rest, or when sleeping, the sea otter may expose its feet above the surface of the water (Figs 9 and 10). When in this position, the digits are frequently expanded and the foot moved slowly in a direction along the long axis of the body. Although extensive data were not recorded, foot expansions during the summer and winter conditions indicate that the frequency of expansions may increase with increased air temperature (Table VII (Table VIII).

The behavior patterns of river otters and harp seals relating to possible thermal stress were not studied systematically. However, from brief observations, they appear to spend little or no time grooming, and foot expansions were not observed. On a hot day, one captive river otter was observed to sleep in a sprawling position while on land (Fig 11).

Table VIII. Foot expansions of captive sea otters.

Animal	water temp.(°F)	air temp.(°F)	time observed	expansions/ min.
adult male	53	65-66	61	5.0
adult female	53	65-66	30	7.0
adult male	53	70	14	9.5
adult female	53	70	14	8.3
subadult female (a)	53	70	14	10.0
subadult female(b)	53	70	14	11.0
adult female	53	78	26	10.8

Foot expansions and limb waving were not observed during times when the air temperature was less than the water temperature (Mr. A.P. Whitt, personal communication).

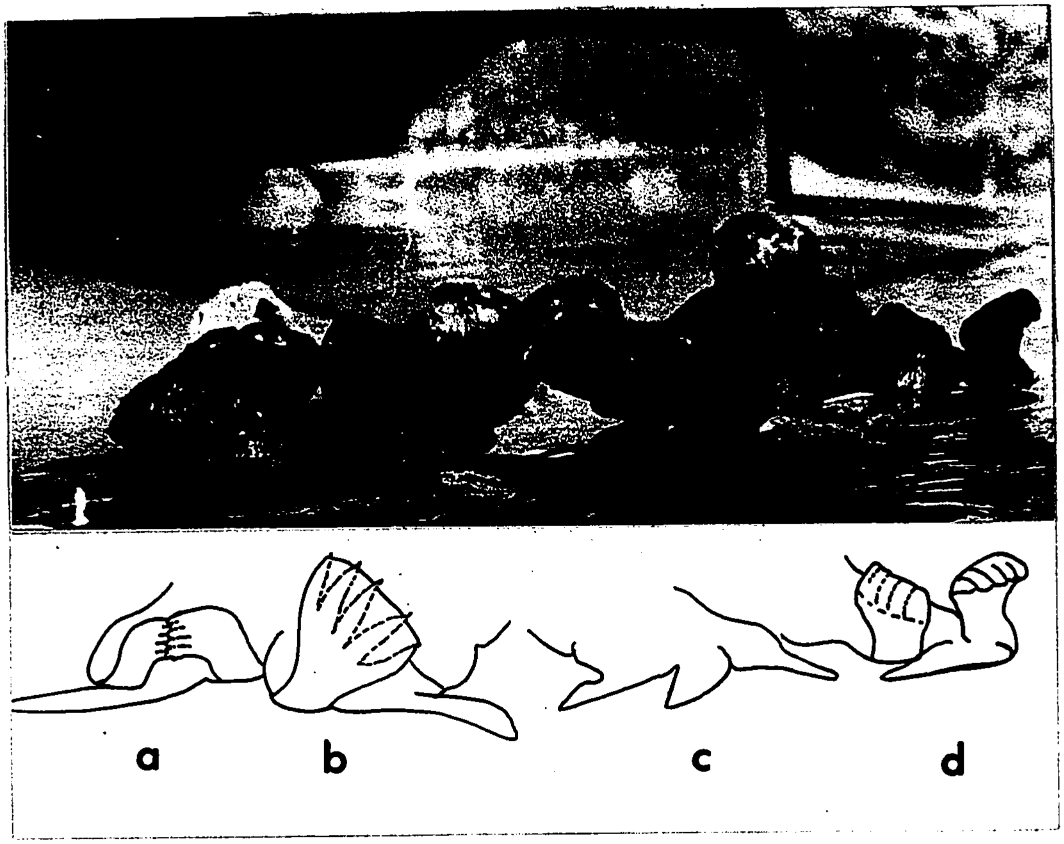
Figure 9. Four captive sea otters, illustrating foot positions when the animals are quiescent at the surface of the water.

a. feet overlapping and lying on the abdomen

b. both feet maximally expanded

c. feet immersed and used for orientation of the body

d. feet exposed but not expanded


a
b
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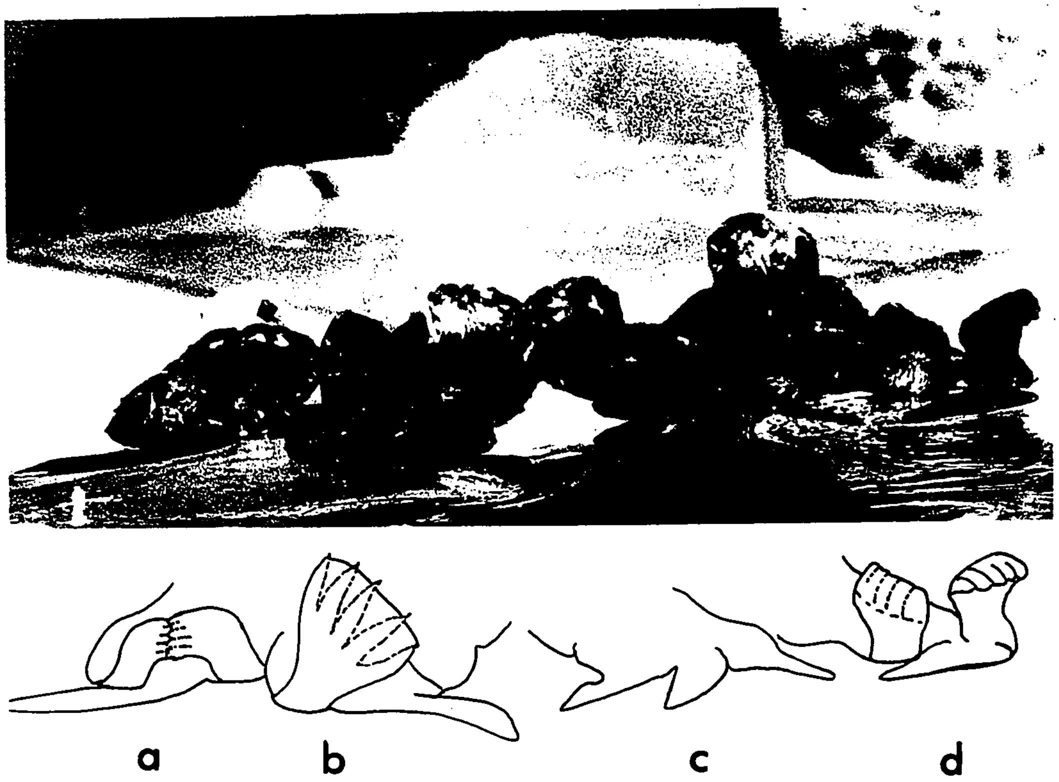
a
b
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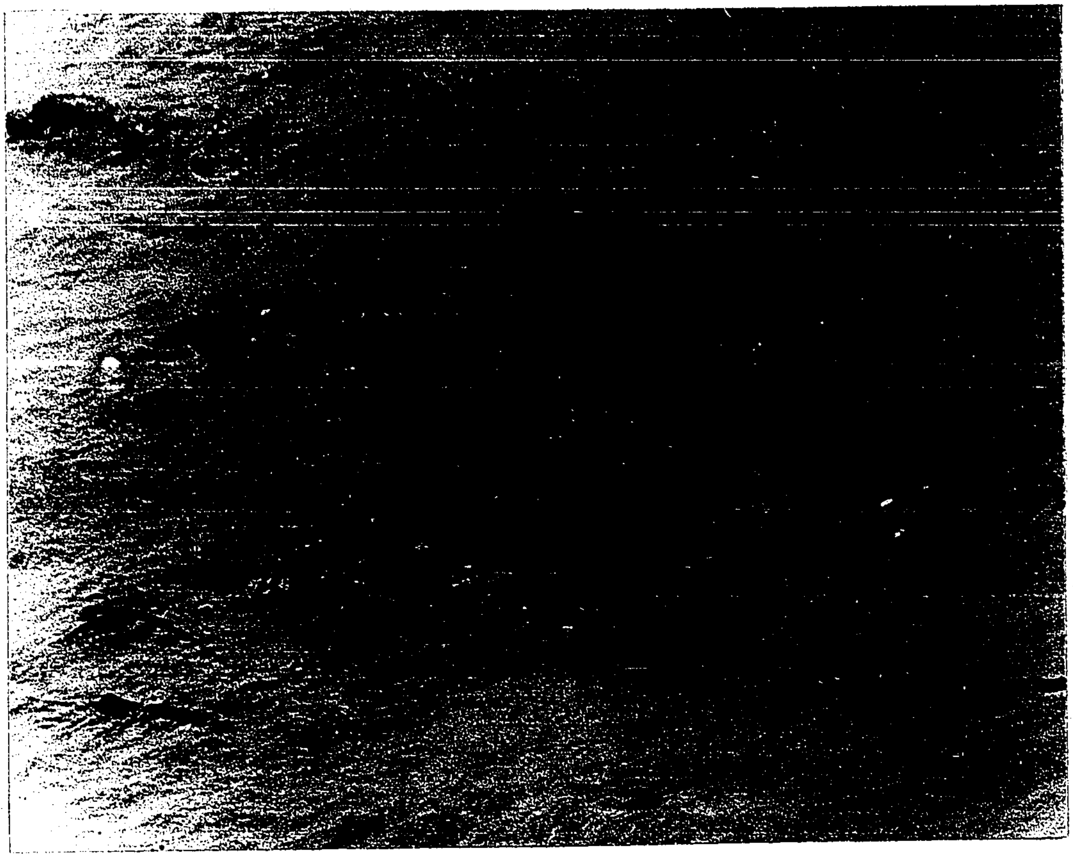
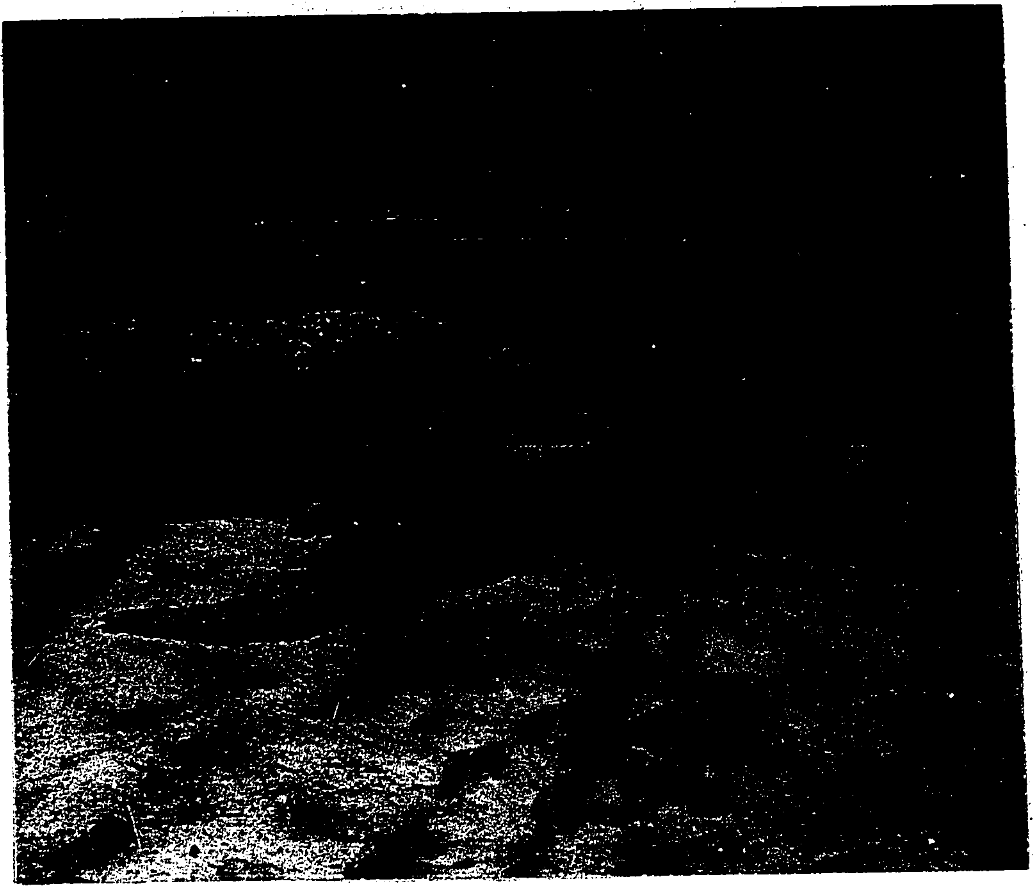
d

Figure 10. Sea otter raft in California waters, showing 69 sea otters, 49 of which have their feet above the surface. (photographed by Wm. L. Morgan, Monterey, California)

Figure 11. Sprawling position of a captive river otter on a hot day.





DISCUSSION

The habitat ranges and diving habits of the river otter, sea otter and harp seal are such that these animals are frequently exposed not only to extreme and rapidly changing temperature gradients, but also to an environment of a high thermal conductance when they are in water. As the environmental temperatures are usually below the mammalian body core temperature, it may be expected that heat conserving mechanisms would be enhanced. Anatomical adaptations for heat conservation are principally in the form of body insulation (pelage and/or subcutaneous fat), whereas, behavioral adaptations are to be found in the adjustment of surface areas and/or habitat selection during adverse times.

To be an effective insulator, the pelage must function to reduce or prevent air-to-skin contact while the animal is on land and water-to-skin contact while in water. As insulation varies with the numbers and sizes of dead air spaces formed between the skin surface and the medium, these characteristics of the pelage that may contribute to its insulative qualities are density, length, morphology and slope.

Enhydra has the most dense pelage of any mammal thus far described. The mean hair density in the midback region is about 125,000 hairs/cm^2. This is more than two times that of the northern fur seal, *Callorhinus* (Scheffer, 1962) and the river otter, *Lutra*; four times more than the mink, *Mustela* (Kaszowski, *et al.*, 1970); and more than eight times greater than in the muskrat, *Ondatra* (Wussow, 1968); and more than 60 times greater than in hair seals (Scheffer, 1964). Hair length in *Enhydra* varies from 30mm for the guard hairs to 12mm for the underhairs, thereby adding to the depth of the covering and to its insulative properties. This barrier, plus the waterproofing secretions from well-developed sebaceous glands found in all regions, assist in preventing water-to-skin contact and heat loss by conduction.

The guard hairs of *Enhydra* are sparse compared to the quantity of underhairs and probably have little direct insulative value. Their main function may be one of protecting the integrity of the underhairs when the animal is immersed in the water. These hairs would form an overlapping pattern similar to that found in *Callorhinus* (Scheffer, 1962), thereby minimizing disruption of the more delicate underfur fibers. The guard hairs give some rigidity and protection to the underpile against mechanical damage while the animal is on land. Also, their relatively stout shaft and springiness may assist in elevating the underhairs to renew entrapped air when the animal emerges from the water. Further insulation and buoyancy may be afforded by the presence of a medulla.

In *Enhydra*, the wavy underhairs are shorter and of a more uniform diameter than the guard hairs. Their waviness contributes to reducing the size of the air spaces in the longitudinal plane. Thus, when the animal is immersed, the underhairs overlap and interlock to a certain extent, instead of a flat overlapping of each other. The spike-like and leaf-like scale patterns on the hair shafts may contribute to the interlocking of the hairs and add to the maintenance of entrapped air. The waviness of the underhairs produces dead air spaces that have a small diameter, further decreasing heat loss by convection currents.

All of the hairs slope caudally, and this, plus the absence of erector pili muscles, are believed to enhance the ability of the hairs to lie flat during submersion (Ling, 1970) contributing to streamlining and reducing disruption of the overlapping pattern.

The importance of the pelage for insulation is supported by the efforts of the sea otter to keep its fur well-groomed and aerated. Grooming behavior has been reported by Kirkpatrick, *et al.* (1955), Vincenzi (1961), Kenyon (1969), and others. Kenyon (1969) compared grooming times between a wild and a captive sea otter; these values were 11 and 48%, respectively. Despite the fact the values are very different and are probably related to food seeking and feeding requirements, they do emphasize the necessity of coat care. During grooming, the entire body, limbs, tail and head receive attention, and the looseness of the skin seems particularly well-adapted for this purpose. Snarled or soiled hair quickly loses its waterproofness and insulative properties. The mechanical action of grooming would also spread the waterproofing sebaceous gland secretions over the hairs. Vincenzi (1961) also emphasizes the care of the pelage and its probable importance in thermal regulation. Air bubbles are seen escaping from the fur during diving (captive animals) and, if the insulative qualities are to be preserved, a renewal of this air in the fur is essential. The predominantly aquatic or maritime habits of the sea otter make the reaeration of the coat a difficult problem, as the animal is unable to dry out completely if it is at sea for long periods of time or closely associated with damp areas while ashore. The function of grooming, at least in part, seems to be aeration of the fur. Evidence of aeration is seen by the animals blowing into the fur, beating the water to a froth (Kenyon, 1969), and by pleating the skin on the dorsal and lateral sides of the body while these areas are exposed above the water. The cutaneous trunci muscle of the sea otter is well-developed and the observed rapid contractions of the skin along the dorsal and lateral sides of the body in a cranio-caudal direction are indicative of this function. Similar observations have been documented by Fisher (1939) and Kirkpatrick, *et al.* (1955). Grooming time may be related to the ratio of guard hairs to underhairs. If more guard hairs were present they could elevate the underhairs more readily for aeration and keep the latter free of snarls. Grooming time is also related to the eating habits of the animal, that is, using its chest as a table for preparing its food. This area must be thoroughly cleaned after every feeding if the pelage is to retain its insulative properties.

The tail and feet of *Enhydra* are regions with a high surface area-to-volume ratio and therefore are areas of a potentially high heat loss. There appears to be a reduction in the surface area of these parts in the more aquatic mammals such as *Enhydra* (Mertens, 1935). The tail of *Enhydra* has a reduced surface area compared with *Lutra*, and an increased hair length and density compared with hair on the other body regions. This increased hair density and length was noted by Stellar (1751) and Snow (1910). Similar characteristics are present in *Lutra*, and are reported in the mink (Kaswalski, *et al.*, 1970). Subcutaneous fat deposits are found on the lateral sides of the tail and are important not only for insulation, but also for broadening the tail for locomotion (see Locomotion and External Features section). Skin thickness of the tail is slightly increased over that of the body proper and may serve to further reduce heat loss.

The feet of *Enhydra* have a reduced surface area, representing about 5.8% of the total body surface area, compared with 10.2% in *Lutra* and 18.0% in *Pagophilus*. The interdigital webs have a short, sparse pelage and a thinner skin than the rest of the body. However, the hair density is greater than that found in the other species, and may reduce or prevent water from contacting the skin surface. The relative stoutness of the hairs may in part reduce this function as there would be less integrity of the air spaces. This function may also be reduced by the action of the feet during locomotion on land and in water. Because the feet are the primary source of aquatic locomotion, their movements would tend to increase heat loss by conduction. As there is a reduced insulation in these areas in the forms of pelage and subcutaneous fat, prevention or reduction of heat loss must be related to the decreased surface area and the arterial-venous circulation, tissue tolerance and behavioral patterns. The angiology described, shows a circulation somewhat similar to that of terrestrial mammals. There may be some adaptation for heat retention in the arterial-venous associations in the upper leg regions, especially related to the saphenous artery and veins. In this region, the arteries are closely associated with two large, thin-walled collateral veins. Based on the counter-current heat exchange principle, it is possible that there is some heat transfer between these vessels when the animal dives. During diving, bradycardia and peripheral vasoconstriction may result in a reduced blood flow and heat loss from the feet. The behavior pattern of taking the feet out of the water during quiescent periods undoubtedly serves a function of reducing heat loss by conduction, and may increase the body heat by direct solar radiation. Digital expansions and fanning movements, a black skin with dark brown and overlapping hairs, and a well-developed venous plexus appear to be important adaptations for increasing body heat by direct radiation.

In *Enhydra*, the feet may be of some value for heat dissipation because of their size, reduced insulation and superficial venous circulation. Unlike the fur seal, which has naked feet with a large surface area and often fans them during warm periods on land (Bartholomew and Wilke, 1956), the sea otter has not been observed to fan its feet while on land, and its primary mechanisms seem to be avoidance of heat, conduction on damp surfaces and respiratory heat loss. Kenyon (1969) states that the sea otter on land remains within a meter or two of the water, and, although their behavior has not been documented during warm days on land, it may be expected that they would seek shade and cool, damp places.

In the wild, sea otters spend much of their time feeding or in persuit of food, and in captivity their food consumption may equal from 1/4 to 1/3 of their body weight per day (Kenyon, 1969). Under both conditions, there is little deposition of fat. These facts suggest that such large quantities of food are required because of the low caloric content of the food and/or a high metabolic rate compensating for the inefficiency of the pelage to maintain the normal body temperature. Food caloric composition and metabolic rate have not been investigated and their relationships to thermal regulation must remain unanswered.

The harp seal, *Pagophilus*, regulates its body temperature along somewhat different lines than *Enhydra*. The short, sparse, non-medullated pelage with its irregular scale pattern probably has little insulative value when the animal is immersed in water, as the water can come in direct contact with the skin and much of the body heat could be lost by conduction (Irving and Krog, 1955). However, the pelage may serve some thermal regulatory functio while the animal is on land. In this case, the pelage may act as a baffel by interrupting air currents near the skin thereby reducing heat loss by convection. The 'greenhouse' effect involving the broad guard hairs, curly underhairs and dark skin may also be functioning to increase body heat by direct solar radiation. These two functions have been described for the Weddell seal (Ray and Smith, 1968) and, as the pelage characteristics are similar for these two hair seals, they may serve similar roles. Irving and Hart (1957), Davydov and Makarova (1965) and Øritsland (1968) found that the skin temperatures of harp seals fluctuate at varying atmospheric temperatures and at times approximate that of the air temperature. This further emphasizes the relative inefficiency of the pelage as a major source of insulation. Grooming has not been observed in these animals and the sparsity and shortness of the hairs probably require little care.

The skin is slightly thinner than in *Enhydra*, but may contribute to heat retention, especially when relatively inert as when peripheral vasoconstriction occurs during diving. The skin is not as thick as in the walrus, *Odobenus*, where it evidently serves an important role in reducing heat loss (Fay and Ray, 1968).

The subcutaneous fat or blubber of *Pagophilus* accounts for about 40% of the total body weight. This value is slightly more than that of the Weddell seal (Bruce, 1913) and the harbour seal (Slijper, 1956; Dorofeev and Freiman, 1935, cited by Slijper) and the southern elephant seal (Angot, 1953). The harp seal is feeding in mid-spring and reaches its near-maximum point of fat deposition (D.E. Sergeant, personal communication). This fat appears to play an important role in thermal regulation. Work on the southern elephant seal, *Mirounga*, indicates that this fat layer is an efficient and flexible means of regulating heat loss (Bryden, 1964). In *Pagophilus*, the fat appears to be well-vascularized and, when inert, as when vasoconstriction occurs during diving, it undoubtedly forms an important barrier for preventing heat loss. The metabolism of this fat reserve also serves as a source of body heat.

The tail and limbs of *Pagophilus* have less subcutaneous fat than on the body proper, and together with a high surface area-to-volume ratio, could be sources of much heat loss. The tail is greatly reduced in size and this may compensate for its relative lack of insulation. The fore flippers also have a small surface area and this area is further reduced when the animal is swimming by the characteristic placing of them in hollows of the skin. The hind flippers have a well-vascularized plantar surface, a large surface area, a reduced pelage and a thin skin. Circulatory arrangements are present in the plantar tarso-metatarsal region of the feet that may function on a counter-current heat exchanging principle to reduce heat loss. Similar arterial-venous arrangements have been described in *Phoca* and *Callorhinus* and may also be functional in *Pagophilus*. A further compensation against excessive heat loss may be in the relatively poorly vascularized dorsal surface of the foot.

Behavioral mechanisms such as fanning, panting or avoidance of adverse conditions, such as is seen in *Callorhinus* (Bartholomew and Wilke, 1956; Irving, *et al.*, 1962) and *Odobenus* (Fay and Ray, 1968), *Phoca* (Tarasoff and Fisher, 1970), and other seals (see review by Fay and Ray, 1968) have not been documented for *Pagophilus*.

Comparisons of those anatomical features that may serve an insulatory function in the sea otter and harp seal, indicate that the river otter occupies a somewhat intermediate position. This is seen in the pelage and subcutaneous fat, both of which are moderately developed. The river otter's pelage is shorter and less dense than that of the sea otter, but its quality and quantity compared with the harp seal and terrestrial mammals leads one to conclude that it serves as the primary source of insulation. The pelage density in the midback region is comparable to that of the northern fur seal. This density, plus the secretions from the well-developed sebaceous glands, would help waterproof and prevent water-to-skin contact, thereby reducing heat loss by conduction. The pelage has long, wavy caudally sloping underhairs that form dead air spaces in a vertical and horizontal direction similar to *Enhydra*. Errector pili muscles are present and serve to adjust the pelage during varying climatic conditions and assist aeration of the fur. Guard hairs are more numerous than in *Enhydra* and are useful for erection of the pelage for renewal of the air in the pelage when the otter surfaces or comes on land. Extensive grooming has not been observed. Excess water is shaken from the coat, and this fluffing of the fur when the animal is on land may also help renew entrapped air. The cutaneous trunci muscle may also serve this function. A well-developed medulla is present in all guard hairs and this may serve to increase buoyancy as well as aid in thermal regulation. There is a reduction in medulla size and length from *Lutra* to *Enhydra* to *Pagophilus*, and this may be related to the positive buoyancy of the marine habitat frequented by *Enhydra* and *Pagophilus*.

Subcutaneous fat deposits are less extensive than in the harp seal, and they may serve for insulation, buoyancy and food reserves.

The hair density on the tail is slightly greater than on the body proper and the the tail subcutaneous fat content is greater than in any other region. Other less extensive fat deposits are found in the axillae and around the external genitalia, with the least fat on the body proper. The fat differences found on the tail may be an important adaptation to reduce heat loss from the tail with its proportionately larger surface area than in the other two species examined. These fat deposits also serve a function for increasing the tail bulk and surface area for locomotion.

Foot size is intermediate between *Enhydra* and *Pagophilus*, representing about 12% of the total surface area. The foot has a reduced pelage length and density, a thin skin, and a sparse subcutaneous fat content. If heat retention from this area does occur it must depend on circulatory adjustments during diving. Counter current heat exchange mechanisms comparable to those of *Pagophilus* are not found, but the arterial-venous associations in the upper limb are similar to those observed in *Enhydra*. The circulation on the dorsal surface of the foot is not as extensive as in *Enhydra*, and this may be important in terms of reducing the blood volume to the foot and keeping it away from the exterior where heat could most easily be lost to the environment. As there is little evidence that the feet of *Lutra* are particularly well-adapted for heat retention, they may be important regions for heat escape. A comparable situation is seen in *Callorhinus* in which the body has a dense pelage and the feet are naked. In this case, the feet undoubtedly serve as the primary areas of rapid thermal adjustment (Irving, *et al.*, 1962). *Lutra* has a pelage density similar to *Callorhinus* and inhabits a wide geographical range (Harris, 1968) with daily and seasonal temperature fluctuations (aquatic, terrestrial and atmospheric). Under such conditions, the river otter would require sites, such as the feet, for rapid adjustments of body heat.

Summary

Anatomical features contributing to a stability of the body temperature have been examined in the river otter (*Lutra canadensis*), the sea otter (*Enhydra lutris*) and the harp seal (*Pagophilus groenlandicus*). As these species are usually associated with cold environmental temperatures, it may be assumed that features to combat excessive loss of body heat would be enhanced. The parameters chosen for this study include differences in regional surface areas, pelage qualities, subcutaneous fat quantity, and circulatory and behavioral patterns.

The feet are comparatively poorly insulated and have a high surface area-to-volume ratio , and thus are areas of a potentially high heat loss. For these three species there is a trend for the combined feet surface areas to decrease from *Pagophilus* to *Lutra* to *Enhydra*. The tail surface area decreases from *Lutra* to *Enhydra* to *Pagophilus*.

Body insulation in the form of pelage plays a more important role in *Lutra* and *Enhydra* than in *Pagophilus*. In the former two species, the pelage prevents water-to-skin contact, whereas in *Pagophilus* the skin is wettable. Pelage density and length contribute to the number of dead air spaces and the depth of insulation. These parameters decrease from *Enhydra* to *Lutra* to *Pagophilus*, and regionally from the tail to midback to tarsus to foot. Also contributing to the insulative role of the pelage is the presence of a well-developed medulla found in the guard hairs of *Lutra* and *Enhydra*, but absent in *Pagophilus*. The pelage of each species is composed of caudally sloping, straight-shafted, dorso-ventrally flattened guard hairs and wavy underhairs. Pelage morphology is similar in *Lutra* and *Enhydra* with all guard hairs having a lanceolate outline and spike or leaf-

like cuticular scales on the hair shaft. The cuticular scales contribute to the integrity and protection of the more delicate underhairs, and the maintenance of entrapped air.

Renewal of air within the pelage of *Lutra* may occur by pilo-erection of the hairs, by a pleating of the skin by means of the *m. cutaneous trunci*, or by shaking the body upon emergence from the water. *Enhydra* may blow air into its fur or pleat the skin to renew the entrapped air. Comparable adaptations are not found in *Pagophilus*.

Subcutaneous fat is most abundant in *Pagophilus* (37.9% of the total body weight) and provides the principal means of insulation. It is less abundant in *Lutra* (12.6%) and of secondary importance to the pelage in thermal regulation. *Enhydra* has little or no subcutaneous fat.

Interdigital webs are present in the hind feet of all three species. This skin is thinner than that of the body and, in the cases of *Enhydra* and *Pagophilus*, may be highly vascularized. Heat loss may be reduced from these areas by a counter-current heat exchange principle in *Pagophilus*, or by retaining a relatively dense pelage in this region, as in *Enhydra*. The feet of *Enhydra* may also serve as an avenue for thermal absorption by direct solar radiation. Characteristics that contribute to this latter function are the dark hairs, and skin, the presence of a highly developed superficial venous circulation on the dorsal surface of the foot, and the behavioral pattern of expanding the foot and fanning during warm periods.

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Acknowledgments

The assistance of the following persons and institutions are most gratefully acknowledged: Mr. Karl Kenyon (U.S. Fish and Wildlife Service, Seattle, Washington); Mr. Karl Schneider (Department of Fish and Game, Alaska); Mr. Ian Smith and Mr. Denis Wilder (B.C. Fish and Game Department, Nanaimo, B.C.); Mr. Charles Guiguet (B.C. Provincial Museum, Victoria, B.C.); Dr. John Holmes and Mr. T. Nerassen (University of Alberta, Edmonton, Alberta); Dr. D.E. Sergeant and Mr. W. Hoek (Arctic Biological Station of the Fisheries Research Board of Canada, Ste Anne de Bellevue, Quebec); Mr. A.P, Whitt (Tacoma, Washington); Mr. D. More and Miss B. Hyams (Montreal, Quebec); Mr. Paul Montreuil (Montreal Public Aquarium, Montreal, Quebec); Dr, S.H, Ridgway (U,S. Naval Missile Center, Point Mugu, California:; Mr. G, Seibel (Pulp and Paper Research Institute of Canada, Montreal, Quebec); and the Audio-visual Aids Department (Cambridge University, Cambridge, England).

This research was supported by Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada and McGill University.

C. ANATOMICAL ADAPTATIONS FOR DIVING IN THE RIVER OTTER, SEA OTTER AND HARP SEAL.

Part I. Locomotory patterns and species topography

Part II. Syndesmology of the pelvic limb

Appendix to Parts I and II. Additional data on the hind limbs as related to locomotion

Part III. The lungs

Part IV. The trachea and bronchial tree

Part V. The caval sphincter and hepatic sinus

Part I. Locomotory patterns and species topography

Table of Contents

Introduction

The movements and dynamics of aquatic locomotion in pinnipeds have been studied by many authors, including Duvernoy (1822), Murie (1870), Howell (1929 and 1930), Slijper (1961), Ray (1963), Mordvinov (1968) and Lighthill (1969). Most of these studies were based strictly on morphology and more detailed analyses of the relationships of locomotory patterns to body form and structure are needed to further the understanding of terrestrial and aquatic adaptation. This could be achieved in part by comparing and contrasting the amphibious and the more aquatic mammals. For purposes of this study, the latter are considered more specialized in aquatic locomotion. It is the purpose of this paper to describe the terrestrial and aquatic locomotory patterns of the river otter, *Lutra canadensis* Schreber, 1776, the sea otter, *Enhydra lutris* Linnaeus, 1758, and the harp seal, *Pagophilus groenlandicus* (Erxleben, 1777) and to evaluate and discuss topographical differences associated with changes in these patterns.

This study is one example of changes that may have occurred during the evolution and adaptation of mammals from an amphibious, lacustrine habitat to a more aquatic, marine habitat. It also serves to demonstrate how locomotory patterns are related to the habits and habitats of individual species.

Materials and Methods

a. Locomotion

Studies of locomotory patterns were made on: a. four Canadian river otters (*Lutra canadensis*), one at the Granby Zoo, Granby, Quebec, and three at Stanley Park, Vancouver, B.C. b. 10 Northern sea otters (*Enhydra lutris*), four at the Tacoma Zoo, Tacoma, Washington, five at the Woodland Park Zoo, Seattle, Washington, and one at the Vancouver Public Aquarium, Vancouver, B.C. and c. four harp seals (*Pagophilus groenlandicus*),two at the Montreal Public Aquarium, Montreal, Quebec and two at the Quebec Aquarium. Moving films (8mm) were made of each representative animal, to show terrestrial and aquatic movements. The films concentrated on the sequence of limb movements during walking, running and bounding on land, and on the use of the body, limbs and tail during forward propulsion and turning patterns in the water.

Carangiform movements are defined as those movements in which only a rather small caudal fraction of the body length is capable of a high degree of flexure (Breder, 1926 and Lighthill, 1969).

Inactive periods for all three species are defined as those times when animals are at the surface of the water and not moving forward appreciably. At these times the animals may be resting, sleeping, grooming or feeding.

b. External features

The external features of the body, pelvic limbs and tail were examined on the carcasses of four Canadian river otters from Maine, U.S.A. and Quebec, 33 sea otters from Alaska, U.S.A. and 10 harp seals from the Gulf of the St. Lawrence River and four live seals at the Montreal and Quebec aquaria.

For each specimen, the total body length, and detailed measurements of the pelvic limbs and tail were recorded. Foot length was measured as that distance from the *tuber calcanei* to the distal end of digit III. Total body length was the distance between the nose pad (*nasus externus*) to the distal end of the tail. Tail length was measured between the root of the tail (*radix caudae*) and its distal extremity. The proportions of foot length versus total body length, tail length versus total body length, and the ratio of foot surface area to tail surface area were calculated and the mean determined for each species.

Foot surface area was calculated as that region from the *tuber calcanei* to the distal end of the digits. For *Lutra*, this was determined by treating the maximally expanded foot as two triangles with their bases together at the level of the distal ends of digits I and V and the apices on the *tuber calcanei*.and digit III. For *Enhydra* and *Pagophilus* , this area was calculated as a triangle with its base along the maximally expanded distal border of the foot web with the apex at the *tuber calcanei*. The area of the tail was determined as that area distal to the root of the tail. The tail of *Lutra* was treated as two triangles and not as a cone because of its slight dorso-ventral flatness. The difference between this value and the actual surface area was 8%, and this correction is made in the results. The tails of *Enhydra* and *Pagophilus* were treated as rectangles because of the slight degree of tapering until near their distal end. These tails were flatter than in *Lutra* and the calculated error was 4%. These two percentages were determined by skinning the tail on three specimens of each species and comparing this surface area with the measurements of the intact tail.

Skin and hair samples were taken from the midback, tarsus and interdigital web of the foot of three (adult) river otters, nine (juvenile and adult) sea otters, and eight (juvenile and adult) harp seals. The skin samples were prepared for histological examination, sectioned parallel to the skin surface, and stained with Harris' hematoxylin and eosin. Hair follicles from each body region were counted in 75 to 100 hair bundles and the number of hairs calculated per square centimeter. Hair samples were cut off at the skin surface and hair length measured to the nearest millimeter. The hairs of *Lutra* and *Enhydra* were classified into primary and secondary guard hairs and underhairs (Kenyon, 1969), and in *Pagophilus* into primary and secondary hairs (Scheffer, 1964). An average of 15 hairs of each type were measured from each area in each species.

Anatomical terms used in this study are those listed in the Nomina Anatomica Veterinaria (Vienna, 1968).

Results

a. Terrestrial locomotion

Lutra

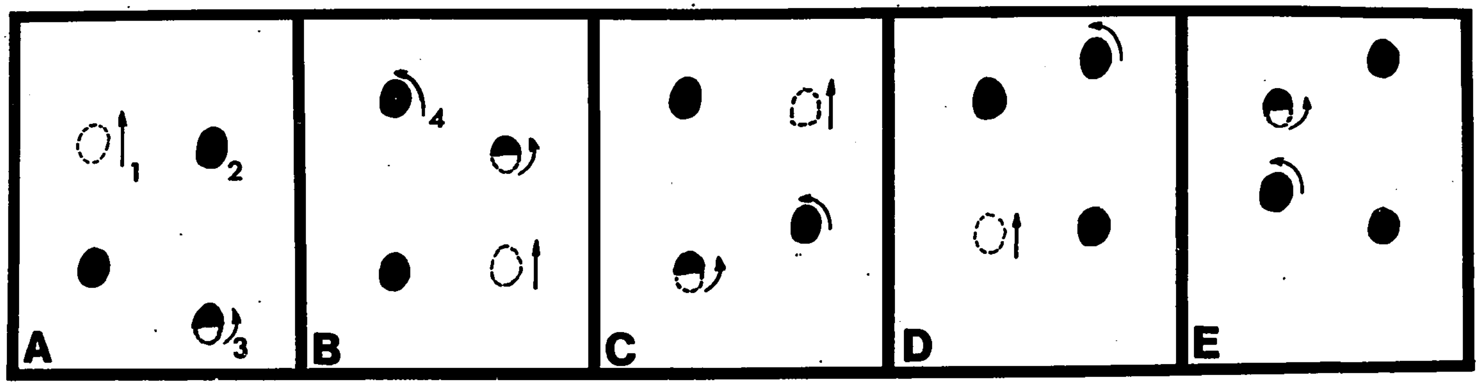
The patterns of terrestrial locomotion used by *Lutra* are walking, running and bounding.

Walking and running

For walking, the general pattern is one of forward movement of alternate limbs, one at a time. The limb sequence for one complete cycle is illustrated in Figure 1. At first (Fig 1A), the palmar region of the right hand and plantar region of the left foot are positioned firmly on the ground. The left hand is lifted off the ground and moved forward past the right hand, parallel with the long axis of the body, with the palmar surface perpendicular to the ground and facing caudad. At the same time as the left hand moves forward, the tarso-metatarsal region of the right foot is lifted off the ground. As the digits of the left hand touch the ground (Fig 1B), the caudal digital (*torulus digitalis*) and palmar pads (*torus metacarpalis*) of the right hand lift off the ground. At this moment, the right foot, with its plantar surface facing caudad at a 60 degree angle, is moving forward past the left foot, which is still firmly planted on the digital and plantar pads (*torus metatarsalis*). As the right hand lifts off the ground and moves forward (Fig 1C), the left foot begins lifting off the ground. At this time, most of the weight of the animal is on the right foot and left hand, which are on the ground. The right hand

Figure 1. Foot sequence of *Lutra* and *Enhydra* walking.

1. foot advancing above the ground
2. foot on the ground
3. tarso-metatarsal region being lifted
4. foot being placed on the ground


A
1
2
3
B
4
C
D
E

moves to a leading position and the left foot begins to move forward (Fig 1D). As the left foot becomes stationary (Fig 1E), the left hand is beginning to lift off the ground and the right hand is firmly replaced. When the left foot is resting on the ground (Fig 1A), the sequence begins again with the left hand advancing and the right foot beginning to lift off the ground. In general, the pattern is one of alternating the four limbs: left hand, right foot, right hand and left foot in a continuous manner. During walking, the limbs are moved in a plane parallel to the long axis of the body. The body as a whole, is held rigidly with the head and neck outstretched (Fig 2A). The body is inclined slightly forward since the hind limbs are longer than the front ones. The long axis of the body is more-or-less horizontal and the distal third of the tail may drag on the ground. The digital regions of the limbs are the first to make contact with the ground.

During rapid forward movement (running) the same limb pattern is followed, but the movements are faster and the tail is held above the ground with its distal one-quarter forming a slight arc.

Bounding

The limb pattern for bounding is shown in figure 3. In the initial stage (Fig 3A),all four limbs are planted firmly on the ground, parallel with the long axis of the body. In this position, the back is arched and the tail is lifted off the ground. Then, both hands are lifted off the ground simutaneously (Fig 3B). As they move forward, one hand advances faster than the other; in this case, the right hand is ahead of the left (Fig 3C). At the same time as the left hand touches the ground (Fig 3D), the metatarsal regions of both feet are lifted off the ground so that the caudal regions

Figure 2. Position of body, limbs and tail of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C) while on land.

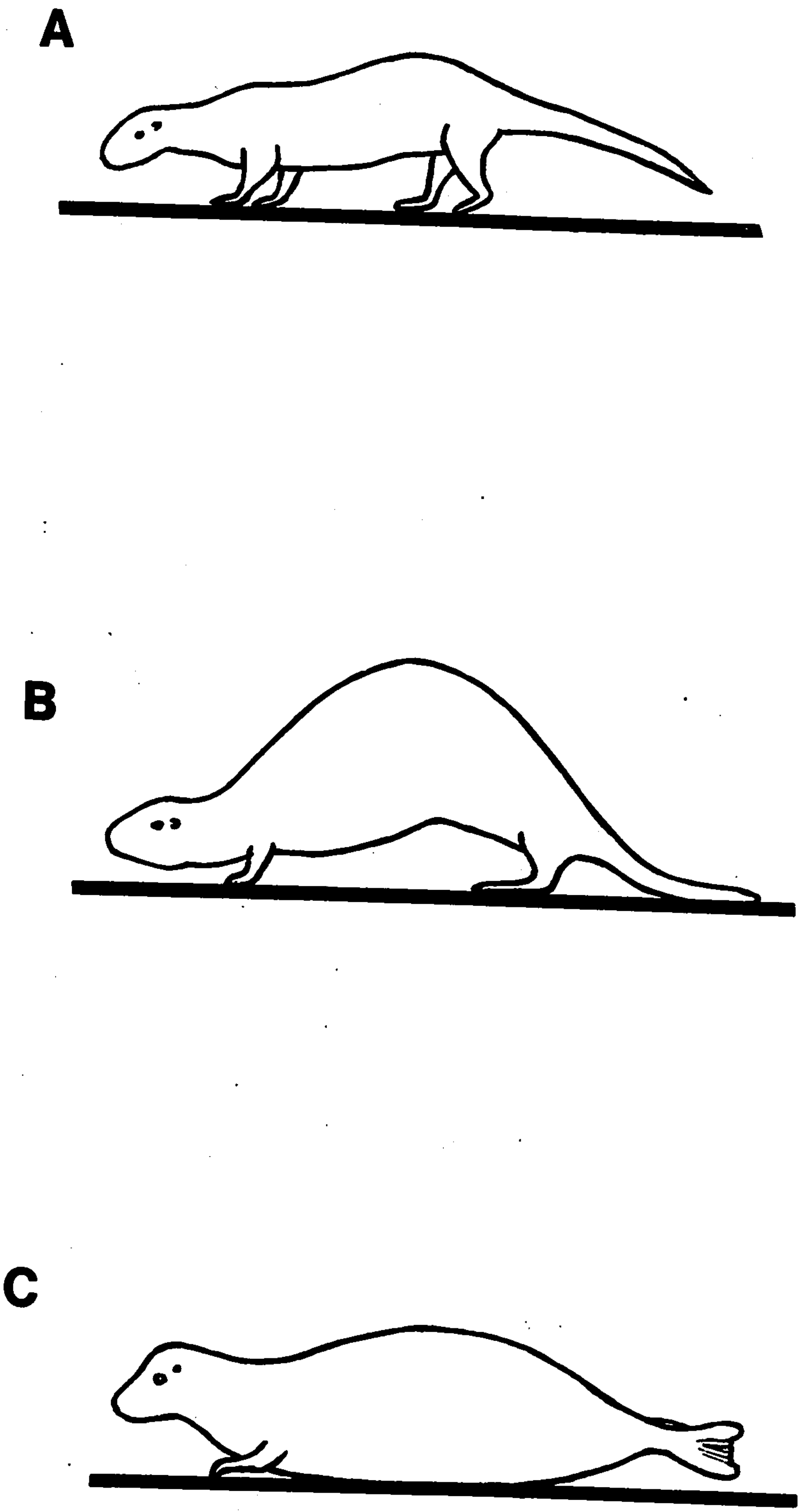
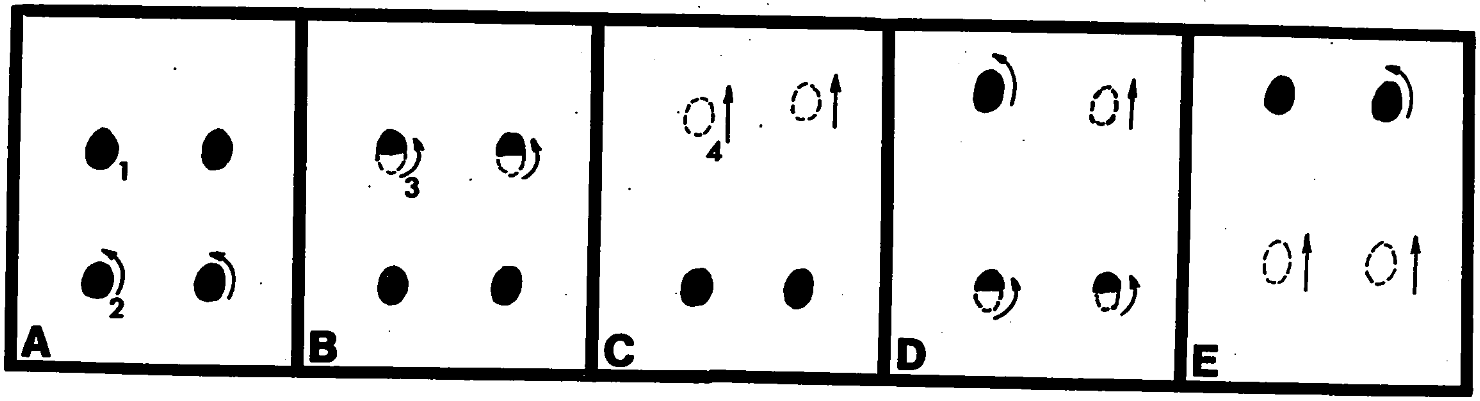

A
B
C

Figure 3. Foot sequence of *Lutra* and *Enhydra* bounding.

1. foot on the ground
2. foot being placed on the ground
3. tarso-metatarsal region being lifted
4. foot advancing above the ground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body or straight forward. The feet rest on the ground over the distal tarsal, metatarsal and digital areas of the foot. When the foot is moved forward, the first region to make contact with the ground is the tarso-metatarsal region. This is then followed by the digital region which can often be heard to strike the ground with an audible slap. Usually the distal third to half of the tail drags on the ground.

Limb positions during bounding movements in *Enhydra* are the same as in *Lutra* (Fig 3). The back is more highly arched in *Enhydra* with maximum height reached in the caudal thoracic and cranial lumbar regions, with the tail usually not held above the ground.

Pagophilus

Pagophilus has three basic patterns of terrestrial locomotion: (a) a forward hitching of the trunk without use of the forelimbs; (b) a dragging forward of the body using the forelimbs; and (c) a sinuous movement of the body. In the second type of locomotion (b), the forelimbs are held lateral to the body and moved simultaneously in a cranio-caudal direction with a certain amount of hitching forward of the trunk at the same time (Fig 2C). Further descriptions of the terrestrial locomotion of *Pagophilus* are found in the works of Murie (1872 and 1878), O'Gorman (1963) and Mordvinov (1968). It is important to state at this point that the hind limbs are not involved to a great extent in terrestrial movement and that this region is dragged forward passively.

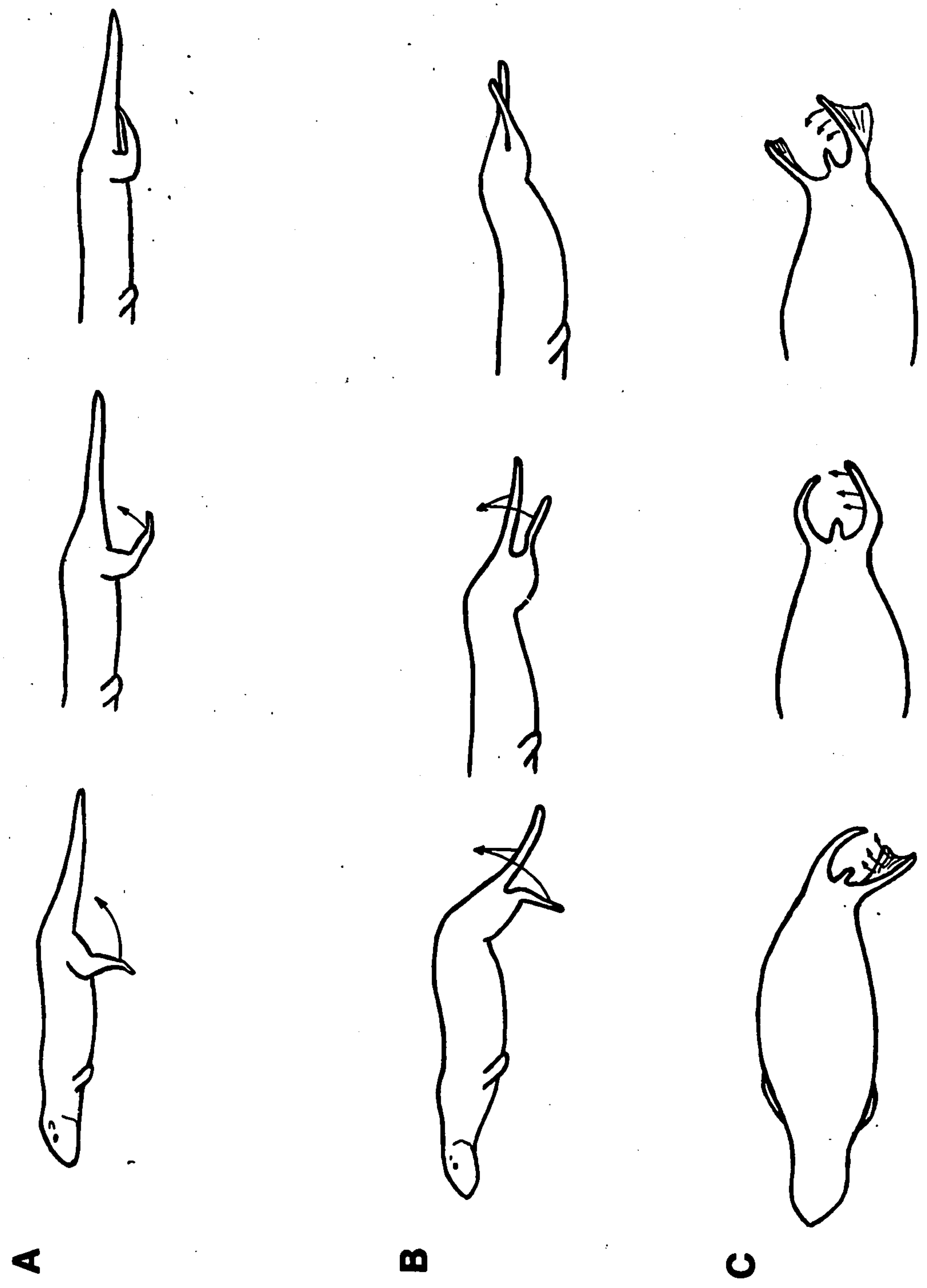
b. Aquatic locomotion

Lutra

Lutra has two methods by which it moves forward in the water: (a) a thrust-recovery movement of the limbs and (b) a carangiform movement of the tail in a vertical direction.

The thrust-recovery action (a) is the principal means of aquatic locomotion and is a unilateral or bilateral movement of the hind limbs in an cranio-caudal direction (Fig 4A). The basic movement can be described as a cranio-caudal power stroke through an arc of 120 degrees, followed by a recovery phase in the opposite direction. The limbs, at the beginning of a stroke, are positioned cranially and are flexed with the digits compressed. During caudal movement, the legs are moved parallel to the long axis of the body and the foot is maximally expanded with its plantar surface pushing the water caudad. The foot was not observed to rise above the back or the water surface. At the end of the stroke, the digits are compressed. During the recovery phase, the hind limbs move craniad and parallel to the long axis of the body with the foot flexed. During hind limb movement, the fore limbs may move in an identical manner. For turning, the fore limbs are displaced laterally from the body and are moved unilaterally away from the direction of the turn. There may also be an increased activity of the hind limb that is opposite the direction of the turn. No recurring pattern of limb movement has been observed while the animal is swimming. The limbs are moved unilaterally, bilaterally, or all four simultaneously. The paddling may be sustained for varying lengths of time, followed by a glide in which the limbs are held caudad and close to the body with the digits compressed.

Figure 4. Sequence of body, limb and tail movements of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C) during aquatic locomotion.


A
B
C

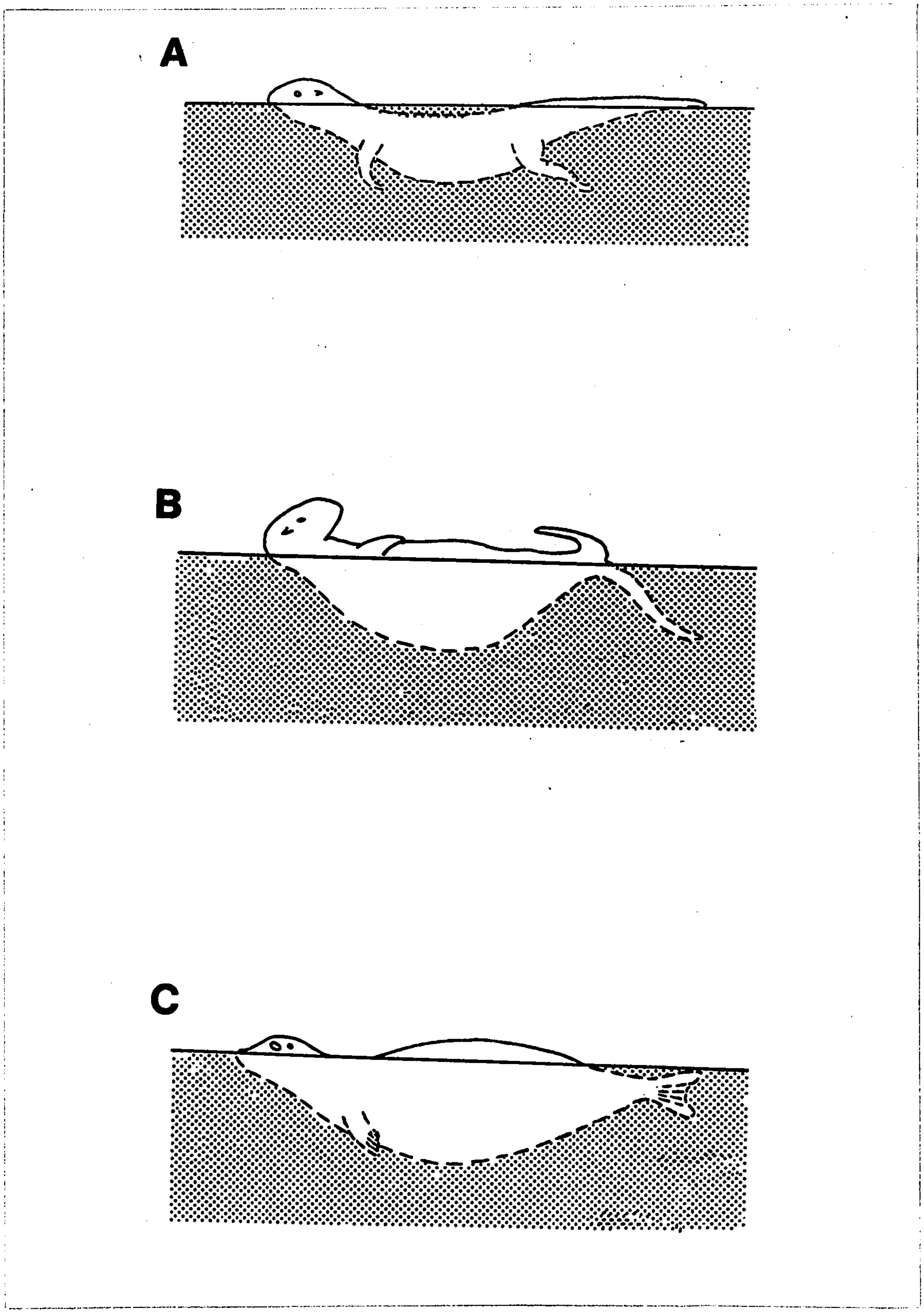
Lutra moves its feet, tail, and lumbosacral regions in a dorso-ventral carangiform manner during rapid swimming. The feet are usually fixed laterally and held parallel to the long axis of the body with the plantar surfaces facing upwards, but may also move to assist in balancing the body. The cranial part of the body, with the fore limbs held close to the chest, remains relatively rigid. The dorso-ventral movements originate from the lumbar region, with the sacrum moving through a 90 degree arc. The main power stroke may be during the dorsal and/or the ventral sweep. The dorso-ventral stroke and recovery is repeated for varying lengths of time and may be followed either by a gliding period or by paddling movements of the limbs. In general, rapid swimming is used for shorter periods of time than the paddling ones described previously.

When the hind limb is not moving, it is held caudad and parallel to the surface of the water with the plantar surface oriented dorsally. When the forelimbs are inactive, they are usually held in a position perpendicular to the long axis of the body. At the surface of the water, the dorsal surface of the head, including the nostrils, ears and eyes, is exposed, the dorsal cranial two-thirds of the thorax, and the dorsal distal half of the tail are seen above the water surface, while the remainder of the dorsum of the animal is submerged (Fig 5A).

Enhydra

The predominant underwater locomotory movement of *Enhydra* is a dorso-ventral displacement of the caudal parts of the body, similar to those described for *Lutra* during rapid swimming. For intermediate speeds, only the hind limbs and tail are moved, whereas at high speeds the lumbo-sacral region as well as the hind limbs and tail are involved. When *Enhydra* first

Figure 5. Body, limb and tail position of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C) when the animals are inactive at the surface of the water.


A
B
C

submerges (head first), the body receives a forward thrust by a vertical to horizontal displacement of the limbs and the lumbo-sacral region of the body (Fig 4B). This thrust at the beginning of the dive increases the arch in the back and increases the angle of the sea otter's body at the water surface. The overall result is a downward positioning of the body and an accelerated motion. The dive begins with the head dipping below the water surface with the animal's body arched. At this time the hind limbs are brought under the body almost perpendicular to the long axis of the body. In this position, the feet are parallel to or slightly overlapping each other. As the feet, with their plantar surfaces facing caudad, move to a hindward horizontal position, they are maximally expanded and moved laterally. The amount of lateral displacement from the side of the tail by the feet varies between 25 and 30 degrees. The movement to the horizontal position (power stroke) is accomplished mainly by extension of the tarsal joint and extension of the vertebral column. At the final horizontal position, the back is curved slightly upwards in the lumbo-sacral region and the feet are parallel with the surface of the water and dorsal to the level of the back and tail. To bring the feet under the body again, the feet are flexed and rotated to lie perpendicular to the water surface. In this position they are moved ventrad and craniad mainly by a flexion of the tarsal joint and lumbo-sacral flexion. At the end of the recovery phase, the hindlimbs are in a vertical position perpendicular to the body axis. For forward movement underwater, the above sequence is repeated. The tail moves in sequence with the limbs but does not appear to contribute directly to the production of acceleration.

For a very rapid forward motion underwater, there is a 90 degree flexion followed by extension. This extreme bending occurs two or three times, after which the animal maintains speed by flexing the caudal regions of the body in a 45 degree arc. These flexing movements may be followed by gliding periods of variable duration. During the glide, the feet may be trailed passively, moved independently up and down for turning, or extended laterally at varying degrees from the tail for planing. Although the sea otter is usually submerged when using these movements, similar motions may occur when the animal is lying on its front at the surface of the water.

When *Enhydra* is lying inactive on its back at the surface of the water, over two-thirds of the animal may be below the surface (Fig 5B). Various parts of the animal appear above the surface of the water depending on how long it has remained inactive. Before periods of inactivity, the animal rolls over several times in the water and pleats its skin when its dorsal parts are above the water.

When the hind limbs of *Enhydra* are not used for forward movements and orientation, the tail may become the primary source of propulsion. This occurs when the animal is on its back feeding, grooming or resting. The hind limbs are either held clear of the water or lie flat on the water surface, and the tail is moved in a carangiform manner just below the surface of the water. The distal two-thirds of the tail appear to twist laterally so that the flattened ventral side is brought perpendicular to the direction of movement. Occasionally the tail is lifted clear of the water and moves to one side of the body. The tail has only been observed to move laterally from one side to the other.

For *Enhydra*, the feet provide the one means of propulsion when the animal is moving slowly on its back. Occasionally both feet may be lifted out of the water together and used as oars. Usually, the feet move alternately to propel the animal in a straight line. The propelling stroke occurs cranio-caudally, with a recovery phase in the opposite direction. At the beginning of the stroke, the foot is maximally expanded and moved by extension of the stifle and tarsal joints caudally and at right angles to the long axis of the body. At the end of the stroke, the hind limb is moved cranially by a flexing of these joints. During this phase, the foot is also flexed in the metatarsal region. During hind limb movement, the fore limbs do not contribute to locomotion.

For turning or orientation, one foot is either more active or more forceful than the other. Also the tail, if necessary, may assist the one limb in turning the body. During all of these movements, the trunk is held rigid and the ventral part of the body is above the water surface.

Pagophilus

Pagophilus employs a "sculling" action of the feet as the principal means of aquatic propulsion (Fig 4C). Although both feet, with their plantar surfaces facing medially, are moved from side to side, only one flipper is extended at a time. Thus, the feet alternately provide the power strokes. Consider, for example, one stroke from left to right. The sequence begins with the right foot moving laterally in a flexed state, while the left foot is extended and moving medially. The latter is maximally spread with its plantar surface at about a 25 degree angle to the body axis. During the initial phases of medial movement, the ventral edge of the plantar surface is leading. As the extended foot reaches the maximum medial position, it tilts so that the dorsal edge of the plantar surface now becomes the leading one. When the extended foot reaches the end of the stroke, it flexes, and at the same time, the right foot reaches its maximum lateral position, is extended and spread maximally, and begins its medial movement. The left foot, now flexed, moves laterally and the stroke is repeated in the opposite direction. There is seen an alternation of the leading edges of the feet which results in body movement either up or down. When the most dorsal digit (digit V) is leading, the action of the body is one of downward thrust and the opposite occurs when the ventral digit (digit I) is leading. The combined effort of both feet acting equally results in a forward movement. During "sculling" the cranial regions of the body are held relatively rigid with the hands held close to the body and directed slightly ventrad. At moderate speeds, the vertebral column is held relatively rigid and movement of the feet originates from the tarsal region. During rapid movement, the lumbar, sacral and coccygeal regions of the body are also in motion, moving in the direction and in time with the active foot.

The fore limbs are used for slow forward propulsion. The caudal regions are held relatively rigid with the feet trailing, while the fore limbs are used as paddles and moved in a cranial to caudal direction. During the power stroke, the digits are maximally spread and strike the water with their palmar surfaces as they move caudad. The fore limbs flex while moving cranio-dorsad and ventrad during the recovery phase. The fore limbs are used as the primary source of turning movements. They are projected laterally and serve as hydrofoils. Usually the head points in the direction of the turn, with the foot extended on the opposite side.

During inactive periods at the surface of the water, *Pagophilus* may use its fore and/or hind limbs to maintain its position. The hands are moved either uni- or bilaterally in a cranio-caudal direction. The feet are used in the "sculling" manner described above. When at the surface, *Pagophilus* has two main poses: (a) one is that of exposing the head above the surface while the body is upright in the water. The other (b) is a prone position with the dorsal parts of the head, including the nose, eyes and ears, and the dorsal region of the back exposed (Fig 5C). The former position is accompanied by movements of the limbs, while during the latter pose there may or may not be limb activity.

b. External features

Body shapes and dimensions

The river otter (Fig 6A) has a cylindrical neck and body, with the thorax having a larger diameter than the rest of the body. The tail is slightly dorso-ventrally flattened near its base. The tail tapers gradually and comprises more than one-third of the animal's length (Table I). The sea otter (Fig 6B) has a somewhat bulkier body outline than the river otter. The major differences are a broader thorax relative to its length, a larger foot surface area and a shorter, more dorsoventrally flattened tail. The tail is oval in cross-section at its base, less robust than in the river otter, and tapers very little until near its extremity, where it narrows rapidly. The tail is about one-sixth of the total length of the animal (Table I). The harp seal (Fig 6C) has a smoothly tapering body, with the thoracic region being rounder and greater in girth than in the sea otter. The tail is greatly shortened (Table I), slightly dorso-ventrally flattened, and tapers gradually until near its distal extremity.

Pelvic limb shapes and dimensions

Table I.

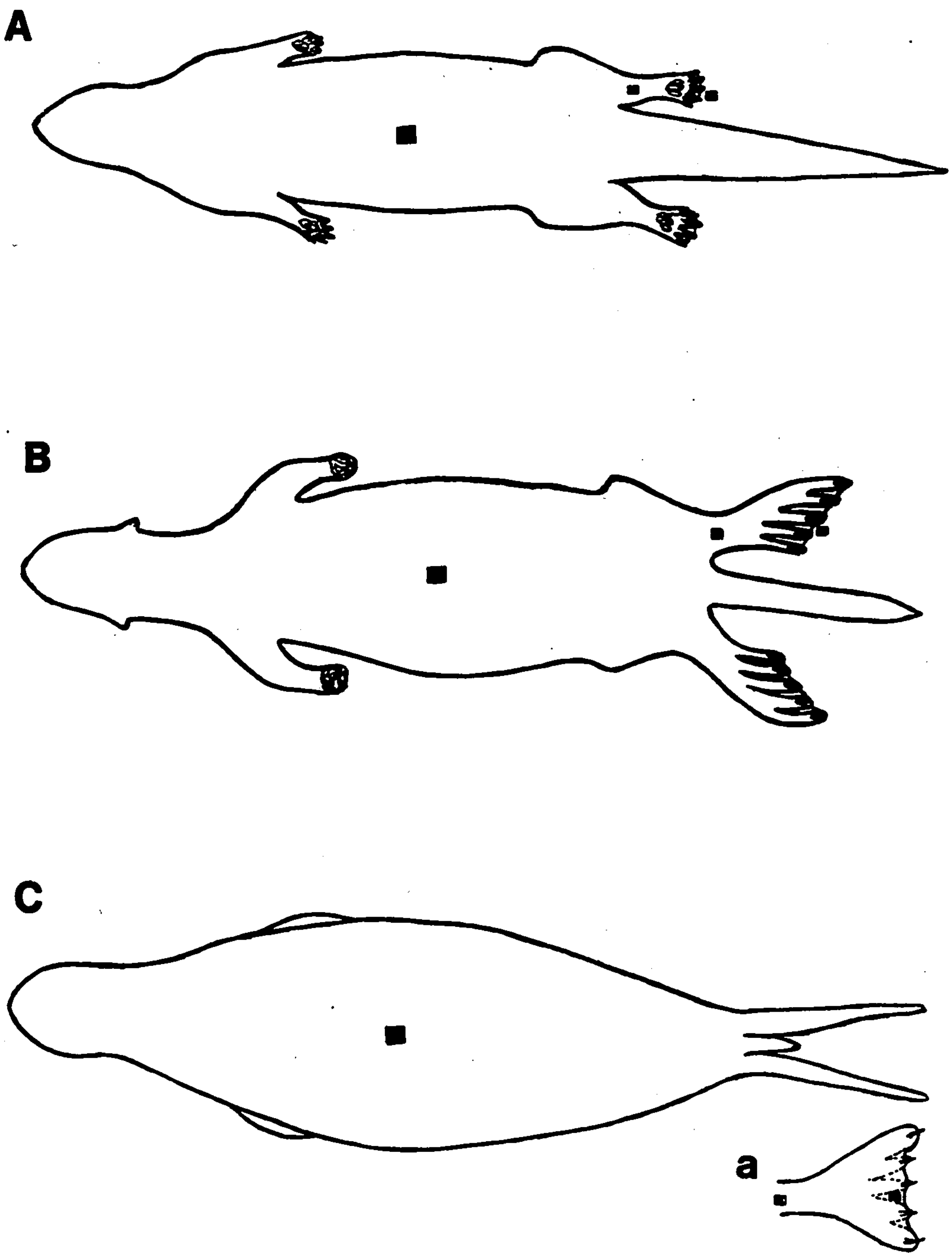
A. Percentage of tail length to body length(a) and foot length to body length (b).

a.	*Lutra*	*Enhydra*	*Pagophilus*
a.	42.1	22.4	6.3
b.	10.5	18.4	13.6

B. Ratio of plantar surface area of feet to tail surface area.

Eutra	*Enhydra*	*Pagophilus*
0.27	1.87	11.70

Figure 6. Body outline of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C), illustrating streamlined shape, incorporation of the hind limbs into the body outline, differential limb and tail sizes, foot shape, and skin and hair sample localization. (a. lateral view of foot of *Pagophilus*; ■ regions from which skin and hair samples were taken)


A
B
C
a

The parts of the pelvic limb that project free from the skin of the body proper vary in the three species. In the river otter, the cranial proximal half of the femur is located within the body skin, leaving exposed the distal half of the femur and the rest of the limb. Caudally, the limb, up to the middle of the leg, is included within the body skin. In the sea otter, the cranial face of the femur, except the distal epiphysis, is enveloped in the loose body skin. On the caudal face, the limb is not distinct from the body until the tarsal region. In the harp seal, both cranial and caudal surfaces of the femur, and the tibia and the fibula, are located within the body skin. Distally, the limb becomes distinct only from the tarsus.

The feet of all three species have their five digits united by an interdigital web. In the river otter, the foot, when fully expanded, has a diamond-shape (digital length sequence: IV=III>V=II>I). The web begins in the metatarsal region and stops just proximal to the extremities of the digits. The sea otter has toes of unequal length (digital length sequence: V>IV>III>II>I)giving the foot a square, paddle-shape. The fourth and fifth digits are closely bound together, with the web beginning at the distal end of the proximal phalanx. Between the fourth and third digits the web begins at the proximal end of the proximal phalanx. The remaining digits are connected by more extensive webbing beginning in the distal metatarsal region and extending to the distal extremities of the digits. The foot of the harp seal when expanded, forms a triangle (digital length sequence: I≥V>II≥IV>III). The interdigital web between digits I and II, and IV and V begins in the distal metatarsal region and is somewhat reduced. The web connecting the three central digits begins in the central metatarsal region and extends to the distal ends of the digits.

The ratio of the plantar surface area of the foot to the surface area of the tail, for each species (Table I), shows an increase in foot area and a decrease in tail area from *Lutra* to *Enhydra* to *Pagophilus*.

Hair density and length

The mean density of hair in the midback, tarsus and the interdigital web regionsof the foot of the three species is given in Table II. The river otter has primary and secondary guard hairs and underhairs in the midback and tarsus regions, whereas in the interdigital web of the foot, secondary hairs are absent. The sea otter has all three classes of hairs in these regions, and the harp seal has primary guard and secondary hairs. The densities of hairs in the midback, tarsus and foot regions are similar for each individual species, but decrease from sea otter to river otter to harp seal. In all three species, the hair density decreases greatly from the tarsus to the interdigital web of the foot. Hair lengths decrease from the midback to tarsus to interdigital web, and from sea otter to river otter to harp seal (Table III).

Table II. Mean hair density in the midback, tarsus and interdigital web of the foot (hairs/cm2).

	midback	tarsus	foot
Lutra	57,833	58,667	1,520
Enhydra	125,333	107,301	3,327
Pagophilus	1,798	1,715	450

Table III. Mean hair length from the midback, tarsus and interdigital web of the foot. (mm)

		guard (primary)	guard (secondary)	underhairs
Lutra		23.8	18.6	14.0
Enhydra	midback	28.5	25.3	11.5
Pagophilus		16.0	7.0	---
Lutra		11.0	6.8	5.5
Enhydra	tarsus	13.2	15.2	13.3
Pagophilus		9.4	5.2	---
Lytra		3.3	---	2.6
Enhydra	foot	9.7	7.6	5.5
Pagophilus		4.0	2.0	---

Discussion

a. terrestrial locomotion

Some mammals are restricted to the aquatic medium and cannot venture onto land. This is exemplified by the Cetacea and Sirenia, both of which have highly specialized tails for aquatic locomotion and have completely lost the use of their pelvic limbs for terrestrial support. The hair seals (Phocidae), also specialized for aquatic locomotion, cannot bring their pelvic limbs forward for supporting the caudal regions of the body. Less aquatically specialized mammals, such as the river otter and sea otter, have retained the ability to support their bodies on land and may frequent either medium, but with decreased facility on land as compared to an almost exclusively terrestrial mammal, such as the dog.

In this study, varying degrees of terrestrial locomotor facility could be related to the structure of the limbs and tail. The river otter, with its robust and proportionately large tail, which appears to function as a balancing organ, probably has less speed and agility on land than terrestrial carnivores. Its webbed feet and somewhat reduced limb length could contribute to a decreased agility on land. The sea otter, although it has the same foot patterns as the river otter during walking and bounding, appears to be even more awkward on land. Its fore limbs are very reduced in length and surface area. Its hind feet move laterally to the sides of the body giving the animal a somewhat rolling gait, similar to that of the California sea lion, *Zalophus californianus* (Peterson and Bartholomew, 1967). The reduced tail size probably also contributes to the relative lack of balance as compared to the river otter. At times, the chest strikes the ground or the animal may be unable to raise its chest above the ground (Kenyon, 1969), and its back is usually more arched than in the river otter. The sea otter has not been observed to run and its terrestrial movements are limited to walking and bounding. As these observations were made on captive sea otters, it may very well be that running does occur in wild animals, although this has not been reported. The story of the exaggerated awkwardness of the sea otter on land with its toes curled under the feet, has been refuted many times (zur Strassen, 1914; Pocock, 1928; Murie, 1940; Kenyon, 1969).

In the three species studied, the most highly specialized adaptations are found in the harp seal. The terrestrial patterns of this seal have been dealt with by Murie (1870) and Mordvinov (1968). The basic patterns are either a hitching forward action, unilateral cranio-caudal movement of the fore limbs with a sinusoidal movement of the caudal regions, or a sweeping by the fore limbs in a cranio-caudal direction. The hind limbs and tail are not involved in any of these actions.

Although maximum speed and endurance tests for these species on land have not been determined, each, using its own method of movement, appears to be able to move as quickly as a man running (19kph, used by O'Gorman, 1963). In the case of the river otter (Liers, 1951) and the sea otter (Kenyon, 1969), maximum speed was by bounding, and the case of the harp seal, by alternate use of the fore limbs (O'Gorman, 1963, citing H.D. Fisher). It is quite likely that the river otter could move for a longer period of time on land than the sea otter and harp seal. This is inferred from the relative depth and density of the insulative covering of hair in the sea otter and the insulative qualities of fat or blubber in seals (Bryden, 1964). Both of these parameters are related to heat retention, and thus, the latter two mammals may be more liable to heat prostration than the river otter with its its relatively sparse pelage and fat deposits. Pelage and its relationship to heat prostration resulting from terrestrial locomotion has been documented for another highly insulated aquatic mammal, the northern fur seal (Bartholomew and Wilke, 1956).

b/ aquatic locomotion

The aquatic locomotory patterns of the river otter have been described briefly in the literature. Liers (1951) noted body undulations during rapid swimming, and Howell (1930) mentions various motions of the limbs, body and tail. Savage (1957) commented on the leg movements of the river otter, reporting movements similar to those described here. The basic pattern for rapid locomotion is a vertical movement of the tail. The tail is robust, long and slightly dorso-ventrally flattened, and appears well adapted for sinusoidal movements. Routine swimming is by cranio-caudal thrusts of the hind limbs, with the webbed feet striking the water with the plantar surface.

The patterns of aquatic locomotion of the sea otter have been described by zur Strassen (1914), Howell (1930), Fisher (1939), Barabash-Nikiforov (1947), Kirkpatrick, *et al.* (1955) and Kenyon (1969). Zur Strassen was the first to describe correctly the basic pattern of underwater swimming - that of having the legs extended caudally and moved horizontally. Howell predicted this type of movement from the animal's myology, and Barabash-Nikiforov confirmed the predictions of Howell from observations on wild and captive animals. Kirkpatrick, *et al.*, Kenyon and Fisher described the use of the feet and tail when the animal is on its back at the surface of the water, and reconfirmed previous accounts of its terrestrial and aquatic movements.

The aquatic locomotory patterns of the harp seal have not been documented, but accounts of other hair seals by Duvernoy (1822), Howell (1929), Backhouse (1961), Gambarjan and Karapetjan (1961), Ray (1963), and Mordvinov (1968) cover all of the observed patterns and variations. The basic pattern is one of alternate lateral-medial sweeps of the hind flippers, or rapid strokes of the feet in the lateral-medial plane, with the plantar surfaces of the feet pressed together.

The necessity of sustained activity of the river otter while at the surface of the water appears to be closely related to the relative lack of buoyancy offered by the medium and the quantity of air entrapped in the underhairs. The reduced pelage of the harp seal may be compensated for by the thick layer of blubber, giving the animal a positive buoyancy from July to February, whereas at other times the buoyancy is negative (Dr. D.E. Sergeant, personal communication). At these latter times, the animal must actively maintain itself at the surface. Apparently, harbour seals in British Columbia do not have a positive buoyancy, since they often sink rapidly when shot. Those that do not sink rapidly are supposedly those that have inhaled just prior to death. Similar reports for the river otter are not available because of the usual method of trapping the animals instead of shooting them. However, based on their activity at the surface and the relative lack of buoyancy offered by fresh water, it may be anticipated that they would sink within a short period of time. The sea otter can float at all times of the year with little movement. This ability to float is probably due to the dense pelage and its entrapped air, and the buoyant effect of sea water. One can assume that the sea otter renews its air supply in the fur periodically by pleating the skin on its back while it is exposed above the water surface. Repeated pleating of the skin is observed to occur prior to any extended resting period at the surface, and probably ensures an increased buoyancy during inactive periods. Activity, such as grooming, reduces this air supply and gradually the animal sinks lower in the water.

Lighthill (1969) recently reviewed the hydrodynamics of aquatic animal propulsion. A major feature of his review is a discussion of the convergent evolution of a carangiform mode of propulsion by those animals that require and display speed in the water. The species discussed here have this basic undulatory mode of progression. They have the requirements for minimizing both recoil (narrowing of the body cranial to the feet and an extension in breadth and depth of the body) and body resistance (streamlined shape). Although the otters and hair seals show variations in their hind limb and tail topographies, their aquatic propulsion can be compared closely with that of the Cetacea, which, according to Lighthill, have a truly lunate form of tail. The cetaceans move by means of vertical undulations (oscillations) of an expanded, lunate-shaped tail. The river otter also has a motion similar to this, the main difference being an absence of the 'flukes' region and the narrowing of the regions immediately cranial to the tail. In the river otter, as in the cetaceans, the limbs are used for balancing functions when the tail is the main source of propulsion. On the basis of these similarities, Howell (1930) pointed out that the river otter may represent a stage through which cetaceans may have passed during their evolution from terrestrial ancestory.

The shapes and movements of the hind limbs of the river otter and the sea otter are considered to have a lunate border and the requirements for the carangiform mode of propulsion, Compared with the cetaceans, the main sources of inefficiency are in the resistance and turbulence created on the recovery stroke, and the leakage of water between the hind limbs and the tail.

Lighthill (1969) briefly mentions hair seals and concludes that their mode of progression (alternate horizontal sweeps of the hind limbs) is a "crude approximation to carangiform propulsion". This may be the case during this method of propulsion, but seals may also move their feet as a unit with the plantar surfaces pressed together (Howell, 1930 and Backhouse, 1961). The feet in this position have a lunate outline similar to the caudal fin of many fishes, and, a combination of the flexibility of the feet, the undulations of the lumbo-sacral region, and a relatively large body followed by a narrowing of the tarsal regions, suggest that the seals have the requirements for efficient carangiform propulsion. Furthermore, the work of Mordvinov (1968) has shown that on the recovery sweep (lateral movement) a certain amount of forward thrust may be derived from the dorsal surface of the flipper, thereby ascribing some use to this phase other than just causing turbulence. This latter point may also be possible in the sea otter, but is unlikely in the river otter. This comparison suggests a graded efficiency of aquatic propulsion between these three species with *Pagophilus* > *Enhydra* > *Lutra*, and as the propulsive organ approximates a lunate border.

The modes of progression appear to be closely related to the mammal's habits. The river otter has little need of sustained high speed, except when it is persuing fish or escaping from enemies. The sea otter usually dives in relatively shallow water for sessile prey, and the harp seal, although a deep diver and a migratory mammal, has little need for adaptations that ensure sustained speed. All three species are capable of relatively high speeds for short periods of time in the water, and the need of a 'perfect' lunate border for sustained high speed and activity would appear unnecessary.

Locomotor facility in an aquatic medium requires a large surface area that may be used to displace a maximum volume of water while at the same time retaining its manouverability. In the case of the most highly specialized aquatic mammals, either the limbs (fore and/or hind) or the tail have developed into the principal means of aquatic propulsion. The otariids use mainly their fore limbs, and the phocid seals their hind limbs (Howell, 1929; Backhouse, 1961; Ray, 1963; Mordvinov, 1968). The Cetacea (Slijper, 1961) and Sirenia (Pettigrew, 1867) primarily use their expanded tail flukes. Whereas, the more amphibious mammals often use two body regions for locomotion. In general, each region used alone appears less efficient than the corresponding body region of the more specialized aquatic mammals. Comparing locomotory organs of the individual species, it is seen that in the river otter, the four limbs, moved in a thrust-recovery fashion, are the principal means of sustained aquatic progression. The tail, which is stout and larger in surface area than the limbs, is used for short bursts of rapid locomotion. This observation is contradictory to Howell (1930) who states that the hind limbs are mainly balancing organs and the tail is the principal driving force. Hair seals, usually considered highly specialized aquatic mammals, have evolved feet that are of a relatively larger surface area than those of the river otter. The feet are used as the major propelling force and the tail is reduced to a vestige and considered non-functional. The sea otter is intermediate between the lacustrine mammal (*Lutra*) and the marine mammals (cetaceans, sirenians and pinnipeds). The sea otter is similar to the river otter in that it may use its hind limbs and tail for aquatic propulsion, and similar to the harp seal in that its hind limbs are the primary means of propulsion.

Numerous authors have stated the characteristics of the fore and hind limbs of the river otter (Baird, 1857; Pocock, 1921; Burton, 1962; Harris, 1968; Kenyon, 1969), the sea otter (Home and Menzies, 1796; Snow, 1910; Pocock, 1928; Fisher, 1939; Murie, 1940; Barabash-Nikiforov, 1947; Kenyon, 1969) and hair seals (Duvernoy, 1822; Scammon, 1874; Allen, 1880; Howell, 1929 and 1930; Scheffer, 1958; King, 1964). These authors have described the limbs principally for diagnostic and systematic purposes. Here the animal's morphology is considered in relation to locomotion.

The overall morphological trends are an increased hind limb surface area and a decreased tail surface area as the animal becomes more aquatically adapted. In the species studied, an increased digital length and the presence of an interdigital web are the two topographical means for increasing foot surface area. The ratio of limb surface area/tail surface area increases from *Lutra* to *Enhydra* to *Pagophilus*, whereas the total tail surface area decreases from *Lutra* to *Enhydra* to *Pagophilus*. These trends reflect the change in emphasis from a tail and foot motion to a foot action only, which appears indicative of the more accomplished divers and swimmers. Hair density and length in the midback and tarsal regions of these species are greater than on the feet. This adaptation may be one to reduce the drag effect of water on the pelage. The feet are, for the most part, areas that must remain smooth and light for rapid movement both on land and in the water. Longer hairs would tend to interrupt the flow patterns of the water and cause turbulence that could result in inefficiency.

Taylor (1914) and Kenyon (1969) emphasize that the fifth toe of the sea otter is more closely bound to the fourth than are the other digits to each other, and state that this may be useful for increasing foot strength in swimming. This seems plausible and is somewhat analagous to the foot of hair seals. The harp seal has the first and fifth digits more closely united to the second and fourth than are these to number three. Also in the harp seal, the first and fifth digits are considerably thicker than the three central ones and may offer more lateral support. This is also seen in the northern fur seal (Scheffer, 1962, plate 110). This support in hair seals may be necessary when considering the shape of the foot as it is actively moved against the water. During the active phase of movement, the plantar surface of the foot is cup-shaped and is thus directing the water caudad from the central region, and the strengthened lateral edges would help prevent leakage over the lateral and medial edges of the foot, thereby increasing the effective surface area. The manner in which the leading edge of the foot changes direction may also be related to this increased thickening. The leading edge is that surface which is most active, passing through the largest arc in advance of the other digits. In the harp seal, the dorsal and ventral edges alternate with each stroke and one finds that these edges are equally well developed. In the sea otter, the fifth digit is the leading edge of the foot during aquatic locomotion, and it is longer and stronger than the other digits. The river otter does not exhibit this apparent adaptation, but does form a cup-shaped foot. Here again, the topographical differences of these three species suggest relationships indicative of the locomotory patterns and efficiency, and aquatic versus terrestrial adaptation.

Summary

1. Terrestrial locomotion

Lutra and *Enhydra* have the typical carnivore limb sequences during walking, with alternate movements of opposite fore foot and hind foot. On land, *Lutra* walks, runs and bounds; *Enhydra* has been observed only to walk and bound. *Pagophilus*, during terrestrial locomotion,does not differ from that described previously for hair seals. Terrestrial locomotion is more awkward from *Lutra* to *Enhydra* to *Pagophilus*.

2. Aquatic locomotion

Lutra moves by two methods:

1. vertical undulations of the tail and caudal regions of the body.
2. cranio-caudal thrust and recovery movements of the limbs.

Enhydra moves by three methods:

1. cranio-caudal sweeps of the pelvic limbs, often involving bending of the lumbar, sacral and caudal regions.
2. horizontal thrust and recovery movements of the pelvic limbs while on its back at the surface of the water.
3. horizontal sweeps of the dorso-ventrally flattened tail while at the surface of the water.

Pagophilus moves by two methods: 1. alternate horizontal sweeps of its pelvic limbs (feet).
2. thrust and recovery movements of its fore limbs (short distances).

Lutra actively maintains itself at the surface of the water. As does *Pagophilus* during the spring and early summer months. *Enhydra* can remain at the surface for long periods of time with no movement. These differences can be attributed to differences in pelage density, quantities of subcutaneous fat and the differential buoyancy of the aquatic medium.

3. There is an increased tendency from *Lutra* to *Enhydra* to *Pagophilus* to have the area of aquatic locomotion assigned to one body region.

4. Convergent evolution towards a highly efficient carangiform mode of swimming with a graded increased approximation of a "perfect" lunate border of the propulsive organ is seen from *Lutra* to *Enhydra* to *Pagophilus*. The feet of *Lutra* and *Enhydra* have not become as highly speciaized as in *Pagophilus*, and they retain distinct carnivore-type limbs for terrestrial locomotion.

5. There is an increased foot surface area and increased importance of this area as a means of aquatic propulsion from *Lutra* to *Enhydra* to *Pagophilus*.

6. The tail surface area decreases in the above order, and with it, a decreased importance of this region for aquatic propulsion. The foot has a reduced

The foot has a reduced density and length of hairs compared with the midback and tarsal regions, with the hair density decreasing from *Lutra* to *Enhydra* to *Pagophilus*.

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Acknowledgments

I wish to express my appreciation to the following people for specimens and assistance during the preparation of this report: Mr. Karl Kenyon (U.S. Fish and Wildlife Service, Seattle, Washington); Mr. Karl Schneider (Alaska Fish and Game Department); Mr. A.P. Whitt (Tacoma, Washington); Mr. Ian Smith and Mr. Denis Wilder (B.C. Fish and Game Department); Dr. Charles Guiguet (B.C. Provincial Museum); Dr. J.C. Holmes and Mr. T.C. Neraasen (Department of Zoology, University of Alberta); Mr. H. Killian (Canadian Wildlife Service, Ottawa); Mr. V. Penfold (Vancouver Public Aquarium); Mr. Paul Montreuil (Montreal Public Aquarium, Montreal); Mr. Karl H. Krumke (Quebec Aquarium); Mr. Gilles Charbonneau (Granby Zoo), and Mr. David More, Miss B. Hyams and Mr. A. Klingner (Montreal). I also thank Drs. A.W. Mansfield and D.E. Sergeant (Fisheries Research Board of Canada) and Dr. K.M. Backhouse (Royal College of Surgeons, London) for reviewing earlier drafts of this report.

The research was financed by Canadian Wildlife Service scholarships and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada and McGill University.

Parts of the final draft of this report were written in consultation with Drs. A. Bisaillon and J.Piérard, École de Médecine vétérinaire, Université de Montréal.

Part II. Syndesmology of the pelvic limb

Table of Contents

Introduction

Studies on the anatomical basis of locomotion have tended to concentrate on the differences in the osteology and myology of individual species and few studies have investigated or compared the syndesmology of aquatic mammals as related to locomotion. Presented here is a comparative study of the syndesmology of the pelvic limbs of three aquatic mammals: the river otter (*Lutra canadensis*), the sea otter (*Enhydra lutris*) and the harp seal (*Pagophilus groenlandicus*). The pelvic limb was chosen as this region serves as the primary source of propulsion in each species. Where possible, the results have been related to the terrestrial and aquatic locomotory patterns described in the previous section of this thesis.

Materials and Methods

The syndesmology of the coxal, stifle and tarsal joints of the pelvic limbs were examined in 3 Canadian river otters (*Lutra canadensis*), 3 Northern sea otters (*Enhydra lutris*) and 3 harp seals (*Pagophilus groenlandicus*).

Anatomical terms used in this study follow those listed in the Nomina Anatomica Veterinaria (Vienna, 1968).

Results and discussion

A. Coxal joint (*articulatio coxae*)

In each of the species, a ball-and-socket joint is formed between the head of the femur and the acetabulum of the innominate. This arrangement permits movement in all directions, and based on the locomotory patterns (see Part I Section C of this thesis), it may be expected that adaptations may be present to restrict movement in some planes and facilitate movement in others during terrestrial and aquatic locomotion.

Lutra canadensis

In the river otter, the coxal joint is enclosed in an articular capsule (*capsula articularis*) that extends from the distal portion of the neck of the femur and the greater trochanter (Fig 1Ac) to the lip of the acetabulum (Fig 2Ab). The capsular membrane encircles and unites with the cranio-ventral surface of the head and neck of the femur, and the dorso-cranial side of the greater trochanter. The capsular membrane does not attach directly to the articular surface of the acetabulum and the lip of this fossa, but external to it, merging as a sheet with the periosteum covering this region of the innominate. The tough articular membrane, composed of connective and elastic tissue, is thickest in the dorso-caudal regions, becoming thinner cranially and caudally, and is thinnest mid-ventrally.

The transverse acetabular ligament (*Lig. transversum acetabuli*) (Fig2Ae) is intimately bound to the capsular membrane. This ligament is located on the caudo-ventral surface of the acetabulum and spans the gap in the lunate border of the acetabulum just ventral to the acetabular bone.

The femoral ligament (*Lig. capitis femoris*) attaches to the dorso-caudal side of the acetabular fossa (Figs 2Aa and 3Ab) and inserts on the cranio-ventral side of the head of the femur (Fig 1Ab).

On the dorsal side of the acetabulum there is a ring of fibrocartilage, the acetabular lip (*labrum acetabulare*) (Fig 3Aa). This lip is well-developed and extends from the dorsal to ventral surface on the cranial aspect of the acetabulum. In one river otter, at its maximum height it is 0.35 cm., giving the acetabulum a total depth of 0.85 cm. at this point. The acetabulum varies in depth. If the lateral face of the innominate is held horizontally, the cranial and caudal edges of the acetabulum are of equal height, and both are slightly higher than the dorsal and ventral edges (Fig4A).

Enhydra lutris

As in the river otter, the articular capsule membrane in the sea otter has the same insertions on the greater trochanter and neck of the femur (Fig 1Bc), and acetabulum (Fig 2Bb). It also merges with the periosteal covering around the lip of the acetabulum. This tough membrane is thickest dorso-cranially, becomes thinner cranially and caudally, and is thinnest ventrally.

The transverse acetabular ligament has the same position as in the river otter (Fig 2Be).

The acetabular lip is more extensive than in the river otter, extending

Figure 1. Proximal end of the femur of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (medial surface)

a. greater trochanter

b. fovea of femoral ligament

c. line of attachment of articular capsule membrane

d. lesser trochanter

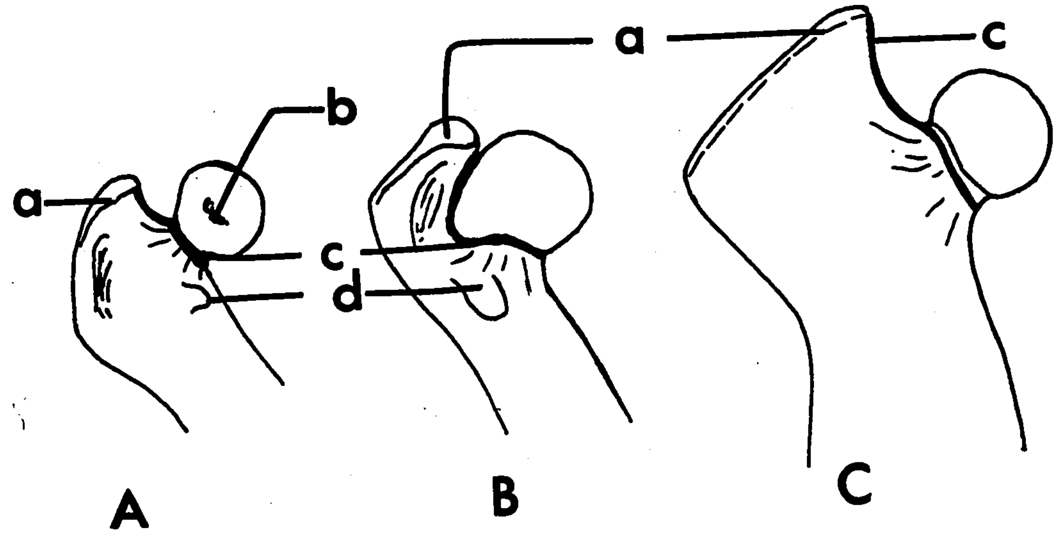
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Figure 1. Proximal end of the femur of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (medial surface)

a. greater trochanter

b. fovea of femoral ligament

c. line of attachment of articular capsule membrane

d. lesser trochanter

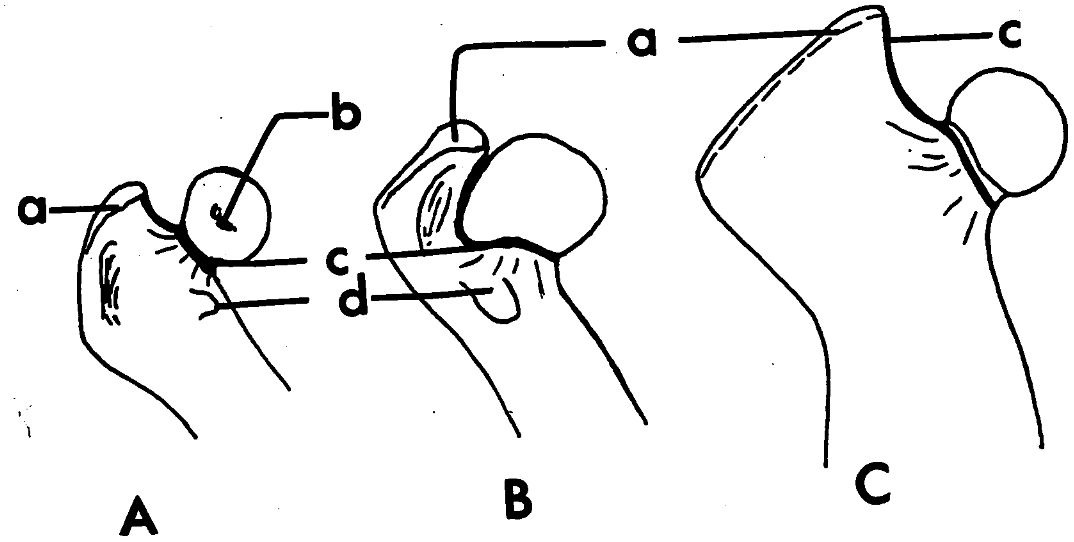
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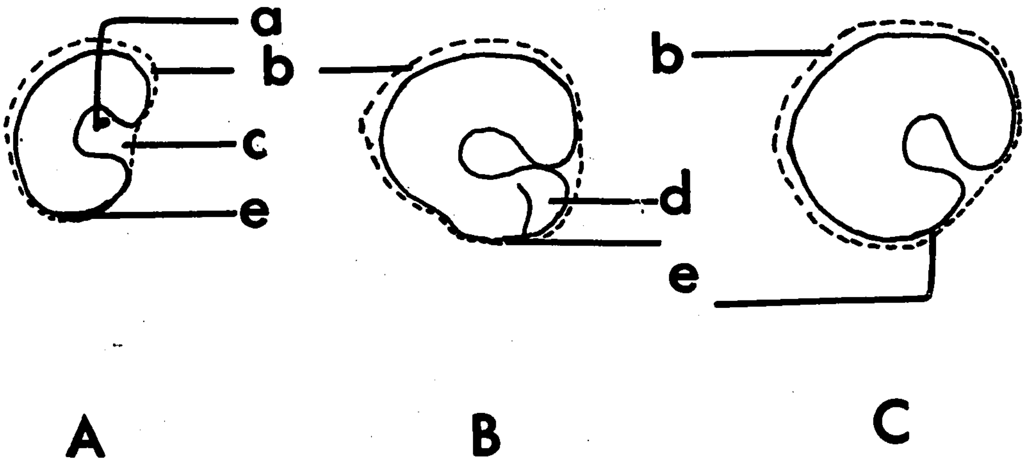
Figure 2. Articular capsule of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

a. femoral ligament
b. articular capsule membrane
c. acetabular incisura
d. acetabular bone
e. transverse acetabular ligament

Figure 3. Articular capsule of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

a. lip of the acetabulum
b. femoral ligament
c. acetabular incisura
d. acetabular bone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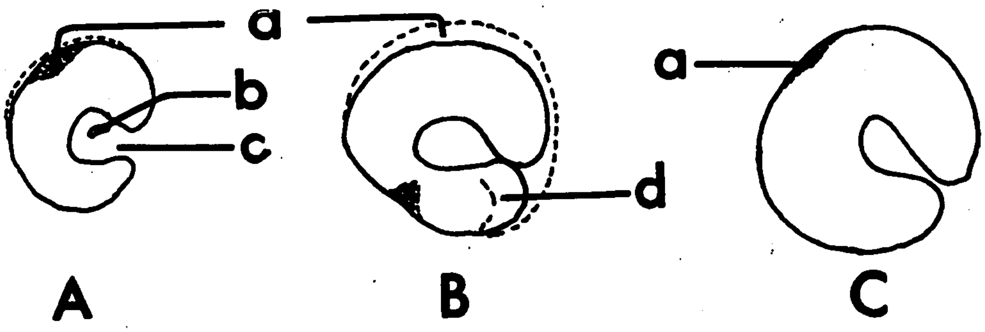
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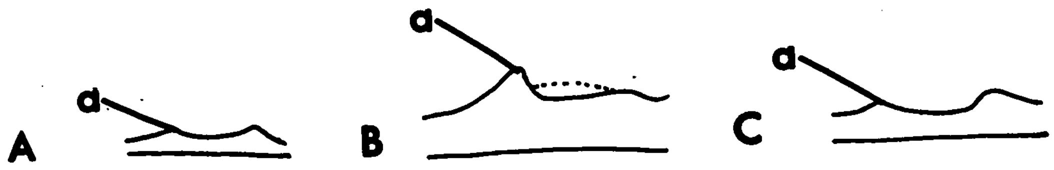
Figure 4. Horizontal view of the lips of the acetabulum in *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

(a. cranial lip of the acetabulum)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more caudally, and ventrally as far as the transverse acetabular ligament (Fig 3Ba). Maximum height in one animal was 0.35 cm. giving the acetabulum a depth of 1.1 cm. at that point. The femoral ligament is absent, and there is no remnant or evidence in the acetabular fossa or on the head of the femur to indicate its former position.

Fat deposits in the acetabulum (*fossa acetabuli* and *incisura acetabuli*) are less extensive in the sea otter than in the river otter.

When the innominate is held horizontally, the cranial and dorsal edges of the acetabulum are much higher than the other edges (Fig 4B). In one case they were 0.40 cm. higher.

Pagophilus groenlandicus

In the harp seal, the articular capsule membrane attaches to the femur most strongly on the cranio-medial face of the greater trochanter and less strongly to the neck and medial rim of the head of the femur (Fig 1Cc). This membrane encircles the coxal joint and inserts on the periphery of the acetabular fossa (Fig 2Cb). Unlike in the river otter and sea otter, this membrane is well-developed on its dorsal, cranial and ventral sides, and poorly developed on the caudal side.

The transverse acetabular ligament cannot be easily differentiated from the capsular membrane (Fig 2Ce).

The femoral ligament is absent, as in the sea otter.

As in the river otter, the acetabular lip is found on the dorso-cranial side of the acetabular fossa (Fig 3Ca) and is exceedingly short and narrow compared with the river otter and sea otter. The maximum height is 0.15 cm. giving the acetabulum a depth of 1.4 cm. at this point.

When the innominate is held horizontally, the dorso-caudal lip of the acetabulum is slightly higher than the cranio-dorsal lip (Fig 4C).

Terrestrial support and movement

The river otter has the most terrestrial habits of the three species described, and the characteristics of the coxal joint are similar to those of a terrestrial carnivore,such as the dog (Miller, *et al.*, 1964). These anatomical characteristics are related to terrestrial mobility and counteracting gravitational effects while the pelvic limbs support the caudal regions of the body. Movement on land is by extension and flexion movements of the limbs, and one sees that all of the above characteristics are related to facilitate these movements in a cranio-caudal direction along the long axis of the body. During each movement, the force of the head of the femur is directed cranially and caudally, together with constant gravitational effects directed against the dorsal rim of the acetabulum. Force is directed both cranially and caudally by the head of the femur during forward mo locomotion. That support is least required ventrally is seen in the relatively weak ventral regions of the capsular membrane. Counteracting the effects of gravity and guarding against luxation of the head of the femur from the acetabular fossa are seen in the heightened lips of the acetabulum in the cranial, dorsal and caudal regions, the ball-and-socket construction of the joint, the femoral ligament, and the transverse ligament. The resulting action of the hip muscles on the femur is a cranio-dorsal pull. This is admitted in terrestrial quadrapeds and illustrated by a usual dorso-cranial dislocation of the *caput femoris* in hip dysplasia of the dog. The raised cranial and caudal lips of the acetabulum in the river otter would allow more extensive movements in a cranio-caudal plane. In a vertical adduction-abduction plane, the femoral ligament prevents over-abduction. Facilitating flexion and extension is the ball-and-socket construction of the hip joint and the relatively loose capsular membrane.

The sea otter spends less time on land, and observations indicate that it is less agile on land than the river otter (see Part I, Section C of this thesis). The sea otter retains all of the adaptations for body support and terrestrial movement as are seen in the river otter. The only major difference is the absence of the femoral ligament.

The harp seal is not adapted for body support and terrestrial movement by extension and flexion movements of the pelvic limbs. This is seen in the absence of the femoral ligament, the reduced acetabular lip, and the less-developed dorsal ridge of the acetabulum.

Aquatic locomotion

During forward propulsion and maintenance at the surface of the water, the river otter employs flexion and extension movements of the limbs similar to those for terrestrial locomotion. It is to be expected, therefore, that those adaptations for terrestrial locomotion would also be of importance during aquatic locomotion, with the main difference being one of the buoyant support given by the water. The active propulsive phase of locomotion is during the extension of the limb. During this arc of extension, most forces within the acetabulum are directed principally toward the dorsal half of the acetabulum. Lateral movement of the limb is restricted by the capsular membrane and femoral ligament, as well as the opposing muscular attachments. Some lateral movement is possible, and this may be used during turning movements.

The sea otter uses its pelvic limbs in flexion and extension movements during forward propulsion in the water, although perhaps with more force and frequency than the river otter because of the decreased use of the tail. Most of the force on the coxal joint during aquatic locomotion is directed against the cranial edge of the acetabulum. In the sea otter, this edge is greatly enlarged and much higher than the rest of the acetabulum. The craniodorsal region of the capsular membrane is also stronger than in the other regions, indicating perhaps the necessity of more strength in this region to prevent dislocation of the head of the femur when force is applied caudally. The dorsal and caudal edges of the acetabulum is strengthened to resist the forces during extension and flexion and to premit more extensive movement in the cranio-caudal plane. The femoral ligament is absent and this would impart more flexibility in the range of possible movements. The lack of support offered by the femoral ligament may be compensated by the buoyant effects of sea water and the increased development of the acetabular lip. The lateral positioning of the pelvic limb is assisted by the absence of the femoral ligament and perhaps also by the relatively thin capsular membrane located ventrally. When the animal is on its back, the limbs are moved laterally in flexion and extension movements along the long axis of the body. The absence of the femoral ligament is probably the most significant feature of the coxal joint that makes this movement possible. As this movement is a form of flexion and extension, the adaptations for maintaining the head of the femur in the acetabulum would also apply.

The harp seal moves its feet horizontally in alternating flexion and extension movements, with the thigh and leg having reduced flexion and extension compared with the river otter and sea otter. There is also a reduced movement within the coxal joint. Forces are directed dorsally, cranially,and ventrally , and the capsular membrane is more highly developed in these regions than caudally. Little caudal movement occurs because of the inability of the seal to bring its limbs forward. There is also little enlargement of the acetabular lip and the edge of the acetabulum compared with these features in the river otter and sea otter. This also reflects the relatively decreased extension and flexion movements within the coxal joint. The absence of the femoral ligament is due to the lack of support required to counteract the forces of gravity. The seal moves its limbs in a variety of directions, but as will be seen, most of these movements center around the stifle joint.

In connection with the lateral movements of the limbs, there is seen in the sea-otter, an extension on the dorsal side of the head of the femur, for most of the neck of the same (Fig 1B). This surface perhaps indicates that the limb is held caudally and horizontally (as seen by the locomotory patterns) and the cartilaginous covering permits easy rotational movements cranially and caudally, and laterally and medially.

B. Sesamoid bones and their ligaments

a. Patella and patellar ligament (*ligamentum patellae*)

b. Patella. A large sesamoid bone articulating with the patellar surface of the femur.

Lutra canadensis

In the river otter, the patella is narrow distally and increases in dimensions proximally (Fig 5A). The bone is slightly concave along its cranio-caudal axis on its caudal surface and convex on its cranial surface. Along its lateral and medial borders the patella blends with the stifle capsular ligaments and at its proximal end it is intercalated with the tendon of insertion of the *M. quadriceps femoris.*

Length = 2.2cm. Width = 1.0cm. Height = 0.5cm.

Enhydra lutris

The patella of the sea otter lies in a similar position as that of the river otter, and is held similarly in position of the patellar surface of the femur by heavy lateral and medial femoral capsular ligaments (*retinaculum patellae laterale, mediale*). It is concave caudally and convex cranially and does not taper distally as much as in the river otter. From figure 5B, it is seen that the patella of the sea otter is slightly thicker than in the river otter.

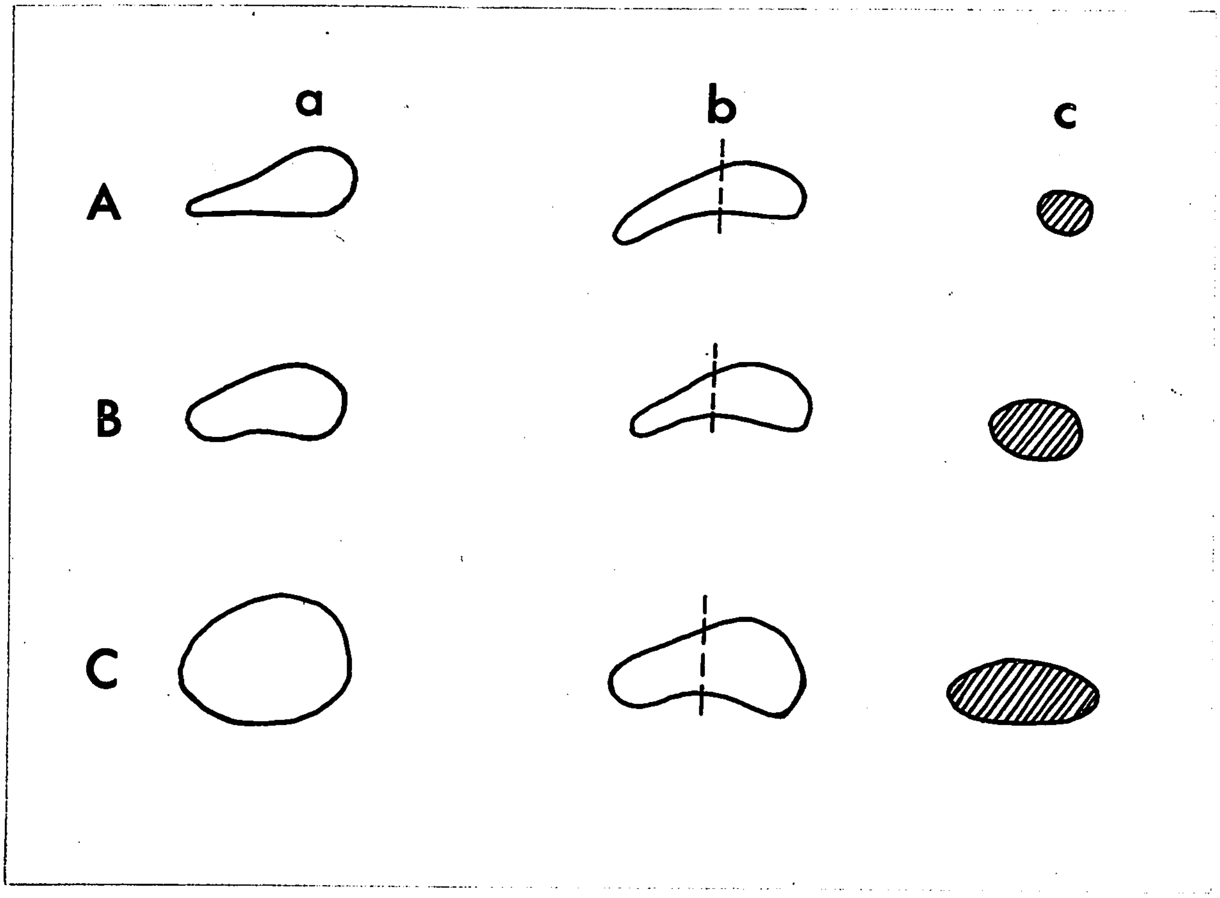
Length = 2.2cm. Width = 1.1cm. Height = 0.75cm.

Pagophilus groenlandicus

In the harp seal, the patella is located in the same position on the femur and covers the stifle joint as seen in the above two species. There is an increase in thickness and width proximally, however, unlike in the other species, the bone is more circular in outline, relatively shorter,

Figure 5. Patellar sesamoid of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

a. dorsal view b. lateral view c. cross-section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and less concave on its caudal surface (Fig 5C). This caudal face corresponds to the articular surface of the femur,which is flat; unlike the rounded, concave surface in the other species. The conspicuously keeled caudal surface of the patella is flatter in the harp seal. The concave caudal face is thicker on the lateral side and the lateral border is longer than the medial one. Along the lateral and medial borders, the patella and patellar ligament are held to the femur by lateral and medial capsular retinaqula.

Length = 2.3cm. Width = 1.9cm. Height = 1.2cm.

In these three species, there is seen a decreasing depth of the concavity on the caudal surface of the patella, and a shortened, more circular outline from the river otter to sea otter to harp seal. Differences are also seen in the depth and angle of the patellar articular surface of the femur. In the river otter, the articular surface is directed caudally, it is straight and concave, with high lateral and medial edges. This surface reflects the predominant extension and flexion movements of the limb in a plane parallel with the long axis of the body. In the sea otter, the patellar surface of the femur is less deeply grooved and the patella less keeled. Flexion and extension are the predominant movements of the limbs, but the less rigidly confined patella may permit more lateral and medial rotation. The flattened and reduced, and shallow patellar surface of the femur of the harp seal indicates there may be more movement of the shank with the femur. The patellar articulatory surface on the femur is deflected laterally, and this is an adaptation for facilitating lateral rotation of the leg during aquatic locomotion. The patella of the harp seal is thicker medially than laterally; a 'thinner' lateral side would be easier to insituate and slide laterally on the femur in rotational movements of the leg. Or possibly, this could be more of a reshaping of the bone to correspond to the medial concavity of the femoral patellar surface.

ii. Patellar ligament

Lutra canadensis (Figs 6Ad, 7Af)

In the river otter, the patellar ligament extends from the cranial surface of the tibial tuberosity as a broad ligament (0.95cm in width) and inserts one-third of the way up the cranial surface and sides of the patellar sesamoid. The ligament blends with the connective tissue of the lateral and medial stifle capsular ligaments. Beneath the patellar sesamoid and its ligaments is located a large bursa almost entirely filled with fatty tissue (*corpus adiposum infrapatellare*).

Length of patellar ligament = 2.5cm.
Width of patellar ligament = 0.4cm.

Enhydra lutris (Figs 6Bd, 7Bf)

The origin and insertion of the patellar ligament in the sea otter is identical with that of the river otter. The only difference is that the ligament is wider in the sea otter.

Length of patellar ligament = 2.4cm.
Width of patellar ligament = 1.1cm.

Pagophilus groenlandicus (Figs 6Cd, 7Cf)

Figure 6. Superficial ligaments of the pelvic limb of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (lateral aspect)

a. patellar sesamoid
b. lateral condyle of femur
c. tendon of *M. extensor digitorum longus*
d. patellar ligament
e. tibial tuberosity
f. tibial crest
g. cranial ligament of sesamoid of *M. gastrocnemius lateralis*
h. shaft of femur
i. sesamoid of *M. gastrocnemius lateralis*
j. fibular collateral ligament of the stifle joint
k. lateral capsular ligament
l. cranial tibiofibular ligament
m. caudal capsular ligament
n. *M. popliteus*
o. caudal tibiofibular ligament
p. head of fibula

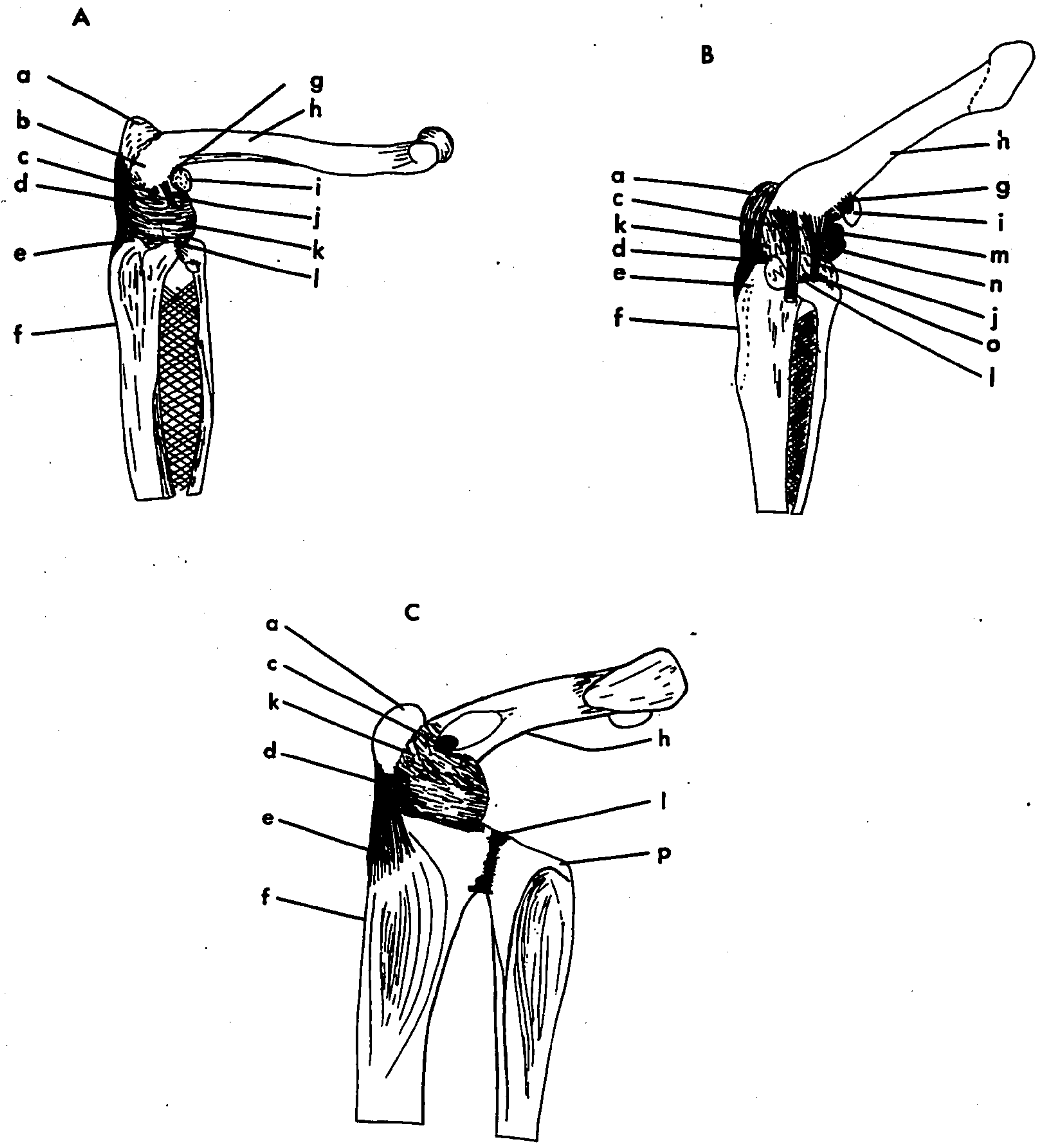

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Figure 7. Superficial ligaments of the pelvic limb of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (medial aspect)

a. fovea for femoral ligament

b. lateral sesamoid of the *M. gastrocnemius lateralis*

c. caudal tibiofibular ligament

d. fibula

e. patellar sesamoid

f. patellar ligament

g. ligament of sesamoid of *M. gastrocnemius medialis*

h. medial capsular ligament

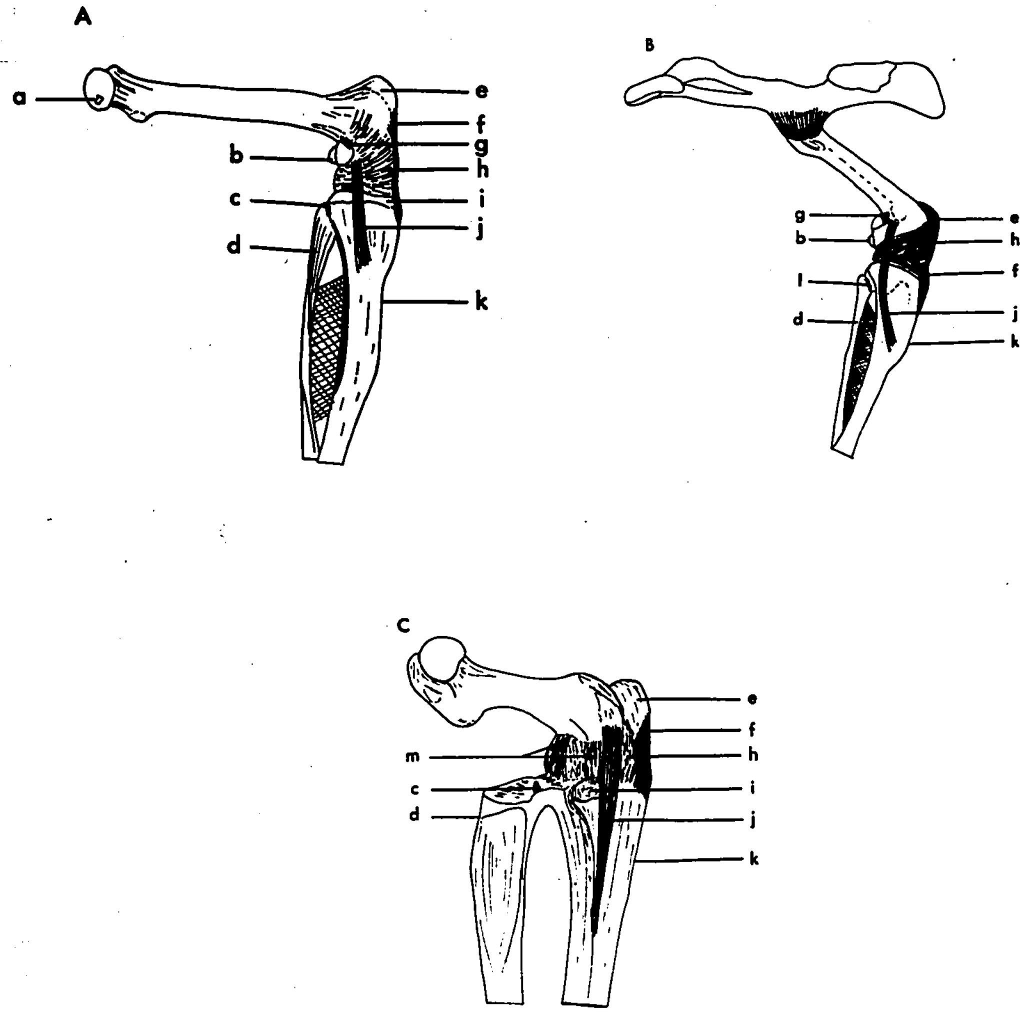
i. medial condyle of tibia

j. tibial collateral ligament of stifle joint

k. tibial crest

l. caudal tibiofibular ligament

m. thickened regions of caudal capsular ligaments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In the harp seal, the patellar ligament extends from the tibial tuberosity as a broad ligament and inserts on the distal and cranial surface of the patellar sésamoid as a flat ligament. As in the river otter and the sea otter, an extensive fat deposit is located in the bursa beneath the patella and the patellar ligament.

Length of patellarlligament = 2.7cm.
Width of patellar ligament = 1.4cm.

iii. Lateral and medial sesamoid bones (*osse sesamoidea M. gastrocnemii*)

Lutra canadensis

Lateral sésamoid (Fig 6Ai)

The large lateral sésamoid bone in the river otter lies in the angle between the proximal surface of the lateral condyle of the femur and the shaft of the femur. Two strong ligaments connect this sésamoid firmly with the femur.

1. The lateral sésamoid ligament is most highly developed and extends along the lateral surface of the femur between the lateral condyle and the diaphisis of the bone.

2. The medial sesamoid ligament is on the caudal surface of the diaphipis of the femur.

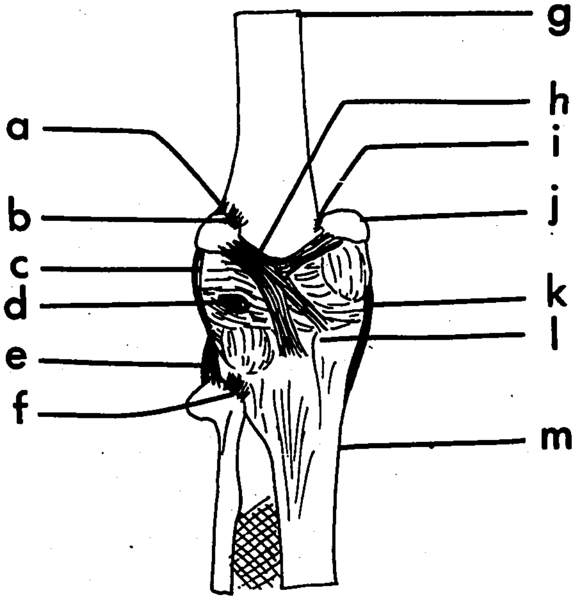
Medial sesamoid (Figs 7Ag, 8Aj)

This is a slightly narrower sesamoid bone lying in the same position

Figure 8. Superficial ligaments of the stifle joint of *Lutra* (A) and *Enhydra* (B). (caudal aspect)

a. cranial ligament of sesamoid of *M. gastrocnemius lateralis*
b. caudal ligament of sesamoid of *M. gastrocnemius lateralis*
c. fibular collateral ligament of stifle joint
d. *M. popliteus*
e. cranial tibiofibular ligament
f. caudal tibiofibular ligament
g. femur
h. caudal capsular ligament
i. ligament of sesamoid of *M. gastrocnemius medialis*
j. sesamoid of *M. gastrocnemius medialis*
k. tibial collateral ligament of the stifle joint
l. medial condyle of tibia
m. tibia

A



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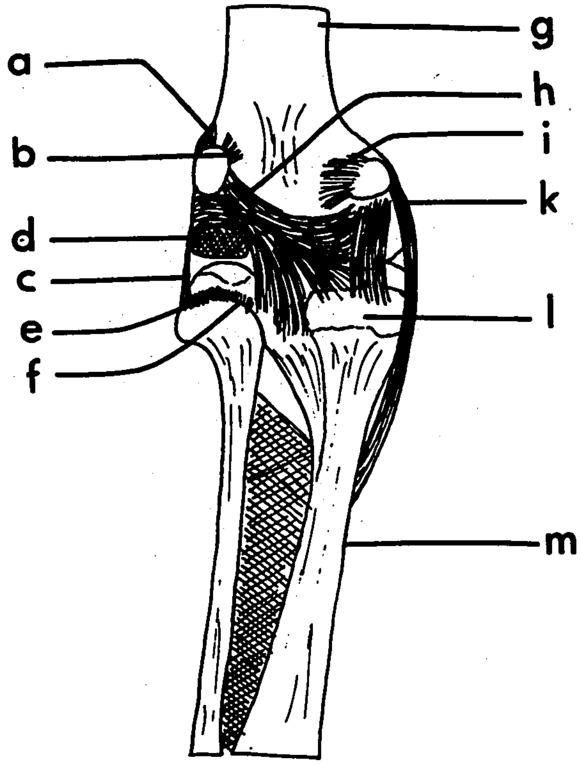


as the lateral bone, but on the medial surface of the femur and further distally. It has one distinct ligament to the femur, running from its entire proximal surface to the caudal medial face of the femur.

Enhydra lutris

Lateral sesamoid (Fig 6Bi) - as in the river otter

Medial sesamoid (Fig 7Bg)

The medial sesamoid has a ligament that extends in a semicircle along the lateral surface of the sesamoid and inserts on the caudo-medial face of the femur.

In both species the sesamoid ligaments are very short and stout.

Pagophilus groenlandicus

In the harp seal, lateral and medial sesamoid bones were not observed.

C. Stifle capsule (*capsula articularis articulatiorius genus*)

Lutra canadensis

1. Cranio-lateral surface (Fig 6Ak) The capsule in this region runs between the patellar ligament, under the stout tendon of the *M. extensor digitorum longus*, and the fibular collateral ligament (*Lig. collaterale laterale*). It is located ventral to the connective tissue of the femoral fascia and appears to be less thick than on the medial side. It attaches to the lateral condyle

of the femur and the lateral condyle and tibial tuberosity of the tibia.

2. Cranio-medial surface (Fig 7Ah) This part of the capsule attaches between the patellar ligament, medial collateral ligament, and the medial condyles of the femur and tibia. The strongest and thickest portions of this capsule are over the medial meniscus (*meniscus medialis*) with fibers in this region running parallel with the meniscus between the patellar ligament and the medial collateral ligament (*Lig. collaterale mediale*).

3. Caudal surface (Fig 8Ah) On the caudal surface of the stifle joint, the capsule runs distally from the lateral sesamoid to the medial sesamoid and head of the tibia. Distally from the lateral sesamoid, the capsule diverges into two bundles: one small bundle to the caudal edge of the median condyle of the tibia and the other to the caudo-proximal edge of the popliteal notch of the tibia. Several strands are also seen to insert on the medial edge of the lateral condyle of the tibia. Ventral to these bundles is a thin layer of loose connective tissue which conceals the bursa on the caudal side of the stifle joint. Laterally, these fibers blend and encircle the *M. popliteus* and its tendon. This loose layer of connective tissue is attached to the larger overlying bundles and connected between the condyles of the femur and tibia and the two collateral ligaments.

Enhydra lutris

1. Cranio-lateral surface (Fig 6Bk) - as in the river otter

2. Cranio-medial surface (Fig 7Bh) - as in the river otter

3. Caudal surface (Fig 8Bh) This part of the capsule extends from the lateral condyle of the femur, fibular collateral ligament and lateral condyle of the tibia, with all of the fibers passing over the *M. popliteus*. The fibers from these regions and the lateral sesamoid bone fuse and pass as a dense sheet to the popliteal notch of the tibia and the caudal surface of the medial condyle of the tibia. Into this sheet are also found fibers from the medial condyle of the femur and the medial condyle of the tibia. Many fibers attach to the medial sesamoid and a few to the medial collateral ligament.

Pagophilus groenlandicus

1. Cranio-lateral surface (Fig 6Ck) This capsule is not easily separable from the caudal part of the capsule because of the absence of the fibular collateral ligament. Its points of attachment to the patella, patellar ligament, femur and tibia are as in the river otter and sea otter.

2. Cranio-medial surface (Fig 7Ch) - as in the river otter and sea otter

3. Caudal surface (Fig 7Cm) On the caudal surface, the capsule is more simplified than in the other species. This surface has two enlarged bundles running distally from the femoral condyles to the caudal aspect of the tibial condyles. These ligamentous bundles are especially well-developed on the medial side.

The capsular ligaments of the harp seal are less rigidly separated than in the river otter and sea otter. In the river otter and sea otter, the capsular regions are similar to those described for the dog (Miller, *et al.*, 1965). A major difference is seen in the caudal surface of the harp seal, with the caudo-medial part of the capsule being greatly strengthened.

D. Ligaments of the stifle joint

1. Tibial collateral ligament (*Lig. collaterale mediale*)

Lutra canadensis (Figs 7Aj, 8Ak)

This ligament is relatively strong, flat, and narrow, and fibers extend from the ventral one-third of the medial condyle of the femur, pass cranially and distally, and insert on the medial surface of the tibial crest. The ligament begins on the femur immediately cranial to the medial sesamoid of the femur. Distally, it passes over the medial condyle of the tibia and spreads out slightly near its insertion. Connective tissue from the cranio-medial and caudal capsular ligaments of the stifle joint blend with the ligaments on its cranial and caudal sides, respectively.

Tibia (total length) = 9.4 cm. - ligament attaches from 1.4 to 2.2 cm. down the tibial shaft.
Total length of tibial collateral ligament = 2.4 to 3.1 cm.
Maximum width of ligament = 0.4 cm.

Enhydra lutris (Figs 7Bj, 8Bk)

The strong tibial collateral ligament extends from the midpoint and slightly to the cranial side of the medial condyle of the femur, and attaches to the medial surface of the tibial crest about two-fifths of the way down the shaft. It fuses with the stifle articular capsules as in the river otter.

The ligament fans out slightly near its insertion. During its course, it passes over the medial condyle of the tibia and then turns toward the tibial crest.

Tibial length = 8.5cm. - ligament attaches from 2.6 to 3.5 cm. down the tibial shaft.
Total length of tibial collateral ligament = 4.1 to 5.0 cm.
Maximum width of ligament = 0.4 cm.

Pagophilus groenlandicus (Fig 7Cj)

The tibial collateral ligament begins broadly on the dorsal cranial one-third of the medial condyle of the femur. The fibers pass distally over the articular surface of the medial condyles of the femur and tibia and insert on the medial redge of the shaft of the tibia in a narrow line. This ligament narrows distal to the medial condyle of the tibia and changes from a flat to a round-bodied ligament. Connective tissue from the medial and caudal capsular ligaments of the stifle joint blend with this ligament on its cranial and caudal sides, respectively. This ligament appears to be very strong and well-developed.

Tibial length (medial) = 19.8 - ligament attaches at 3.0 to 5.2 cm. down the shaft of the tibia.
Total length of tibial collateral ligament = 5.0 to 7.1 cm.
Maximum width of ligament = 1.1 cm.

2. Fibular collateral ligament (*Lig collaterale laterale*)

Lutra canadensis (Fig 6Aj, 8Ac)

This is an unusual ligament in that it is found in the same position on the femur as in the sea otter and dog, but does not connect with the fibula. It begins on the dorsal one-third of the lateral condyle of the femur and its fibers pass distally to blend with the lateral capsular ligament, and insert on the entire lateral side of the lateral meniscus. No fibers are seen to continue to the head of the fibula as is the usual case. This ligament is reduced in length compared with the tibial collateral ligament, but is equal in width and is slightly thicker. Origin is on the femur cranial to the lateral sesamoid of the femur and caudal to the tendon of the *M. extensor digitorum longus*. Fibers of the tendon of the *M. popliteus* pass under the mid-ventral region of the ligament. Connective tissue from the lateral sesamoid of the *M. gastrocnemius* and its lateral ligament, and the lateral capsular ligament blend with the cranial and caudal borders of the ligament.

Length = 1.2 cm. Width = 0.4 cm.

Enhydra lutris (Fig 6Bj, 8Be)

This ligament is very much reduced in size and length compared with the tibial collateral ligament. Its origin is on the mid-point of the lateral condyle of the femur. Fibers pass distally and insert on the head of the fibula, with a few fibers going to the adjacent lateral condyle of the tibia. As the ligament passes over the joint capsule, it passes over the tendon of origin of the *M. popliteus*. Just proximal to this muscle, fibers from the cranio-lateral and caudo-lateral capsular ligaments attach to the ligament.

Length = 2.5 cm.   Width = 0.35 cm.

Pagophilus groenlandicus

This ligament was not observed in the harp seal.

3. Tibiofibular ligaments

Lutra canadensis

a. cranial (Figs 6Al, 8Ae, 9Ak)

This ligament extends proximally from the lateral side of the tibial tuberosity to the midlateral side of the lateral condyle of the tibia. The fibers pass distally to insert along the dorsal ridge of the head of the fibula.

b. caudal (Figs 7Ac, 8Af, 10Ad)

This ligament extends from the caudal side of the lateral condyle of the tibia and its fibers pass directly distally and laterally to insert on the caudal one-fourth of the head of the fibula.

Enhydra lutris

a. cranial (Figs 6Bl, 8Be, 9Bk, 10Bd)

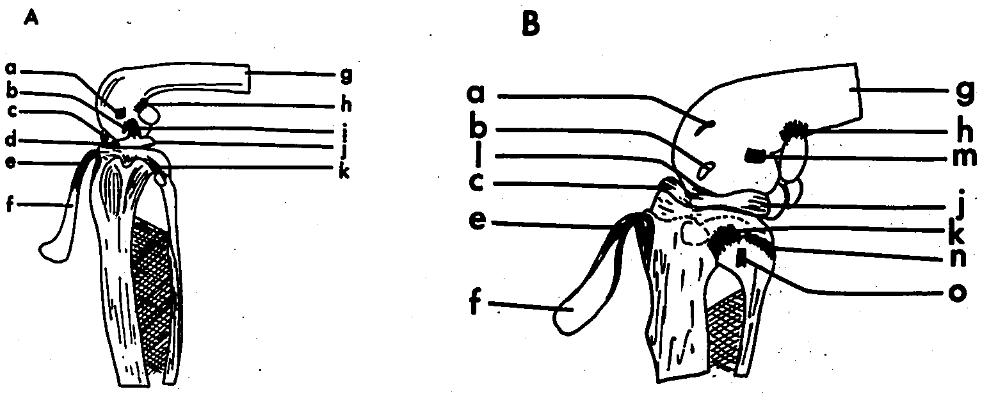
This ligament is distal to the capsular membrane and deep to the fibular collateral ligament. It extends from the lateral condyle of the tibia and inserts on the cranial regions of the head of the fibula. This ligament is short and thick; its fibers are directed slightly disto-caudally on going from the tibia to the fibula.

Figure 9. Ligaments of the stifle joint of *Lutra* (A) and *Enhydra* (B).
(lateral aspect)

a. tendon of *M. extensor digitorum longus*
b. tendon of *M. popliteus*
c. midial meniscus
d. cranial tibial ligament of medial meniscus
e. patellar ligament
f. patellar sesamoid
g. shaft of femur
h. ligament of sesamoid of *M. gastrocnemius lateralis*
i. fibular collateral ligament of stifle joint
j. lateral meniscus
k. cranial tibiofibular ligament
l. ligament from lateral meniscus to lateral condyle of femur
m. origin of fibular collateral ligament of stifle joint
n. caudal tibiofibular ligament
o. insertion of fibular collateral ligament of the stifle joint

Figure 10. Ligaments of the stifle joint of *Lutra* (A) and *Enhydra* (B).
(medial aspect)

a. shaft of femur
b. ligament of sesamoid of *M. gastrocnemius medialis*
c. tibial collateral ligament of stifle joint
d. caudal tibiofibular ligament
e. medial ligament of medial meniscus
f. patellar ligament
g. patellar sesamoid
h. medial cruciate ligament
i. ligament from medial meniscus to medial condyle of tibia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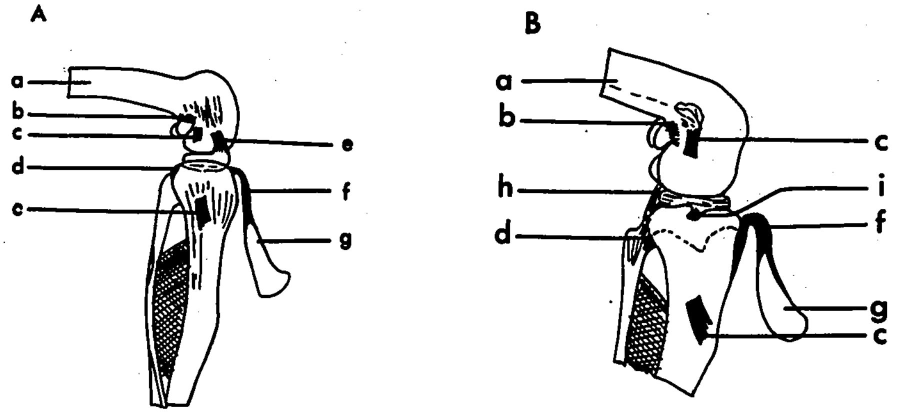
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b. caudal (Figs 6Bo, 7Bl, 8Bf, 9Bn, 10Bd)

This ligament is located directly caudal to the former ligament. It is more extensive and shorter. The fibers run from the tibia to the fibula perpendicular to the bones.

Pagophilus groenlandicus

a. cranial (Fig 6Cl)

This ligament extends from the lateral condyle of the tibia to the cranial surface of the head of the fibula. Its fibers pass at near right angles from the tibia to the fibula.

b. caudal (Fig 7Cc)

This ligament is very reduced in size compared with the cranial one. It unites the caudal edge of the lateral condyle of the tibia to the caudal edge of the head of the fibula.

In the harp seal, the proximal epiphysis of the tibia and fibula are intimately fused.

4. Cranial tibial ligaments of the medial meniscus

Lutra canadensis (Figs 9Ad, 11Am)

This ligament goes from the cranial, axial angle of the medial meniscus to the medial surface of the lateral condyle of the tibia, and the cranial intercondyloid area of the tibia. Its attachment is cranial to the attachment of the lateral meniscus (*meniscus laterale*) to the tibia,

Figure 11. Deep ligaments of the stifle joint of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (cranial aspect)

a. tendon of *M. extensor digitorum longus*

b. origin of fibular collateral ligament of the stifle joint

c. lateral cruciate ligament

d. lateral meniscus

e. cranial tibial ligament of the lateral meniscus

f. cranial tibiofibular ligament

g. head of fibula

h. tibial tuberosity

i. shaft of tibia

j. insertion of tibial collateral ligament of the stifle joint

k. distal end of patellar ligament

l. medial condyle of tibia

m. cranial tibial ligament of the medial mensicus

n. medial meniscus

o. medial ligament of the medial mensicus

p. medial cruciate ligament

q. medial condyle of the femur

r. sesamoid of the *M. gastrocnemius lateralis*

s. tendon of *M. extensor digitorum longus*

t. tibial crest

u. tibial tuberosity

v. ligament from medial meniscus to medial condyle of tibia

w. ligament from lateral meniscus to intercondyloid fossa of femur

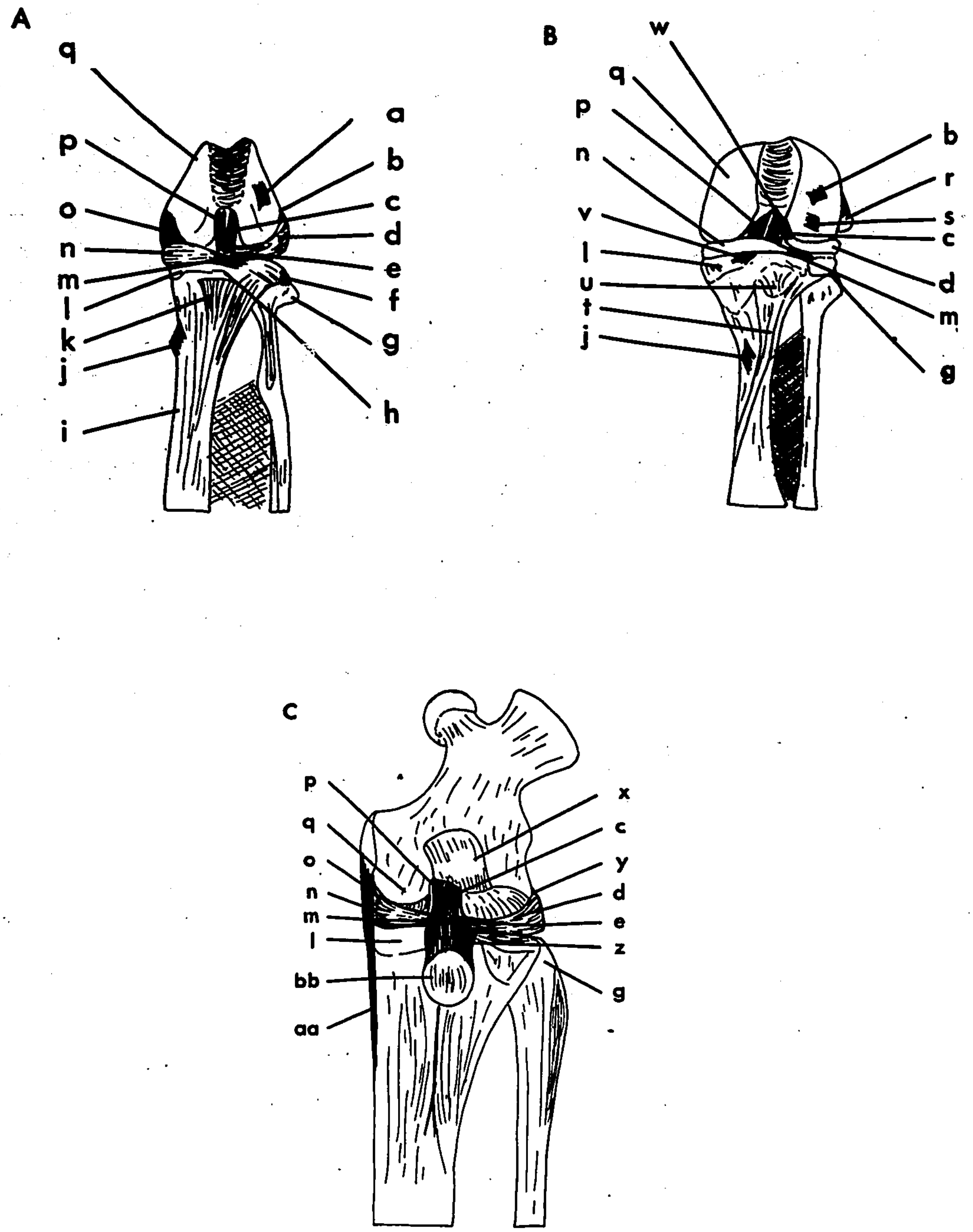
x. patellar fossa

y. lateral ligament of the lateral meniscus

z. patellar ligament

aa. tibial collateral ligament of the stifle joint

bb. patellar sesamoid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and immediately lateral to the tibial attachment of the lateral cruciate ligament on the tibia.

Enhydra lutris (Fig 11Bm) - as in the river otter

Pagophilus groenlandicus (Fig 11Cm) - as in the river otter and sea otter.

One difference is apparent in its insertion on the tibia in that it attaches to the intercondyloid area of the tibia immediately caudal to the patellar ligament.

5. Caudal tibial ligament of the medial mensicus

Lutra canadensis (Fig 12An)

This ligament passes from the caudal axial angle of the medial meniscus and spreads out over a wide area on the lateral border of the median condyle and intercondyloid area of the tibia. The insertion becomes more stout in the intercondyloid area. This attachment is just cranial to the tibial attachment of the medial cruciate ligament.

Enhydra lutris (Fig 12Bn) - as in the river otter

Pagophilus groenlandicus (Fig 12 Cn)

This ligament goes from the caudal axial angle of the medial meniscus and inserts on the lateral border of the median condyle and intercondyloid area of the tibia, just cranial to the tibial attachment of the medial cruciate ligament.

Figure 12. Deep ligaments of the stifle joint in *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (caudal aspect)

a. lateral cruciate ligament

b. caudal ligament of sesamoid of *M. gastrocnemius lateralis*

c. sesamoid of *M. gastrocnemius lateralis*

e. *M. popliteus*

f. lateral meniscus

g. caudal tibiofibular ligament

h. head of fibula

i. shaft of femur

j. ligament of sesamoid of *M. gastrocnemius medialis*

k. tibial collateral ligament of stifle joint

l. femoral ligament of lateral meniscus

m. medial cruciate ligament

n. caudal tibial ligament of medial meniscus

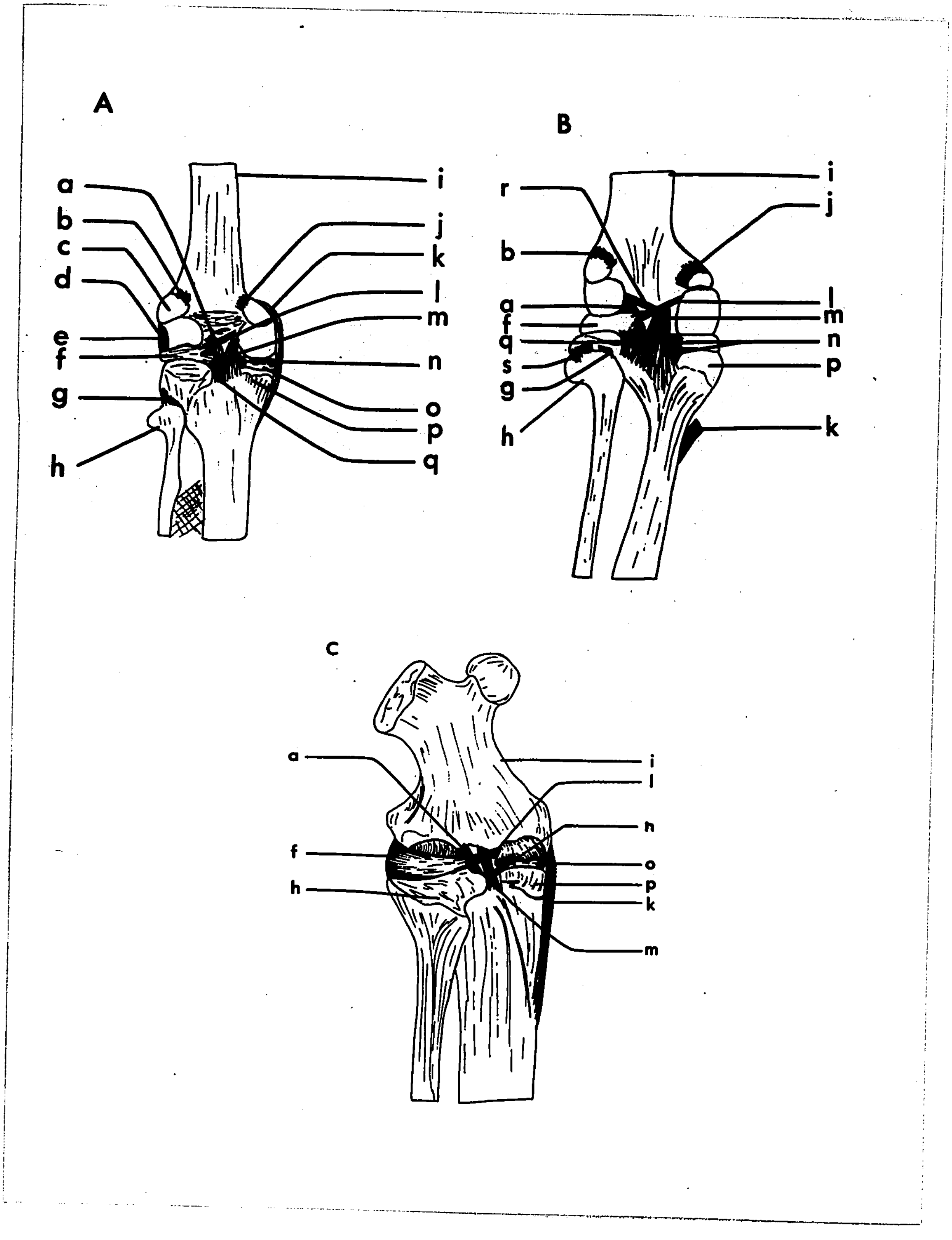
o. medial meniscus

p. medial condyle of tibia

q. caudal tibial ligament of lateral meniscus

r. ligament from lateral condyle of femur to medial cruciate ligament

s. cranial tibiofibular ligament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6. Medial ligament of the medial meniscus

Lutra canadensis (Figs 10Ae, 11Ao)

This ligament passes from the dorso-cranial surface of the medial meniscus as a thick band of connective tissue to the ventro-medial region of the medial condyle of the femur. Here it inserts cranial to and at the same level as the tibial collateral ligament.

Enhydra lutris (Figs 10Bi, 11Bv)

This ligament passes distally from the ventral-cranial surface of the medial meniscus to the medial side of the median condyle of the tibia.

Pagophilus groenlandicus (Fig 11C) - as in the river otter

7. Cranial tibial ligament of the lateral meniscus

Lutra canadensis (Fig 11Ae)

This ligament goes from the cranio-medial edge of the lateral meniscus to the middle of the intercondyloid area of the tibia. Here, it attaches more caudally on the tibia than does the cranial tibial attachment of the ligament of the medial meniscus and the lateral cruciate ligament.

Enhydra lutris (Fig 11Be) - as in the river otter

Pagophilus groenlandicus (Fig 11Ce)

This ligament goes from the cranial-medial edge of the lateral meniscus as a very broad, stout ligament, and attaches to the medial cranial edge of the lateral condyle of the tibia and the intercondyloid area of the tibia, immediately lateral to the lateral cruciate ligament.

8. Caudal tibial ligament of the lateral meniscus

Lutra canadensis (Fig 12 Aq)

This ligament goes from the caudal side of the lateral meniscus to the caudal and medial sides of the lateral condyle of the tibia. It attaches to the caudal tibial ligament of the medial meniscus and is directly opposite the insertion of the medial cruciate ligament on the tibia's intercondyloid area.

Enhydra lutris (Fig 12Bq) -as in the river otter

Pagophilus groenlandicus - not observed

9. Femoral ligament of the lateral meniscus

Lutra canadensis (Fig 12Al)

This ligament passes from the caudal axial angle of the lateral meniscus dorsally (at the same level as where the caudal tibial ligament of the lateral meniscus originates) to that part of the medial femoral condyle that faces the intercondyloid fossa.

Enhydra lutris (Fig 12Al) -as in the river otter

Pagophilus groenlandicus (fig 12Al)

This ligament is as in the river otter and sea otter and passes from the caudal axial angle of the lateral meniscus to the lateral side of the medial condyle of the femur. It is a very stout ligament that fans out near its insertion on the femur.

10. Transverse or intermeniscal ligament (*Lig. transversum genus*)

Not observed in any of the species.

11. Cranial or lateral cruciate ligament (*Lig. cruciatum craniale*)

Lutra canadensis (Figs 11Ac, 12Aa)

This ligament passes between the lateral, cranial border of the medial condyle of the tibia and cranial intercondyloid area of the tibia to the caudo-medial surface of the lateral condyle of the femur and adjacent parts of the intercondyloid fossa of the femur.

Enhydra lutris (Figs 11Bc, 12Ba) -as in the river otter

Pagophilus groenlandicus (Figs 11Cc, 12Ca) - as in the river otter and sea otter.

12. Caudal or medial cruciate ligament (*Lig. cruciatum caudale*)

Lutra canadensis (Figs 11Ap, 12Am)

This ligament passes from the lateral surface of the medial femoral condyle and adjacent part of the intercondyloid fossa of the femur, to the lateral, caudal edge of the medial condyle of the tibia, and the medial edge of the popliteal notch. This ligament is bulkier than the cranial cruciate ligament and lslightly longer. These two ligaments cross each other and prevent the femur and tibia from slipping both cranially and caudally.

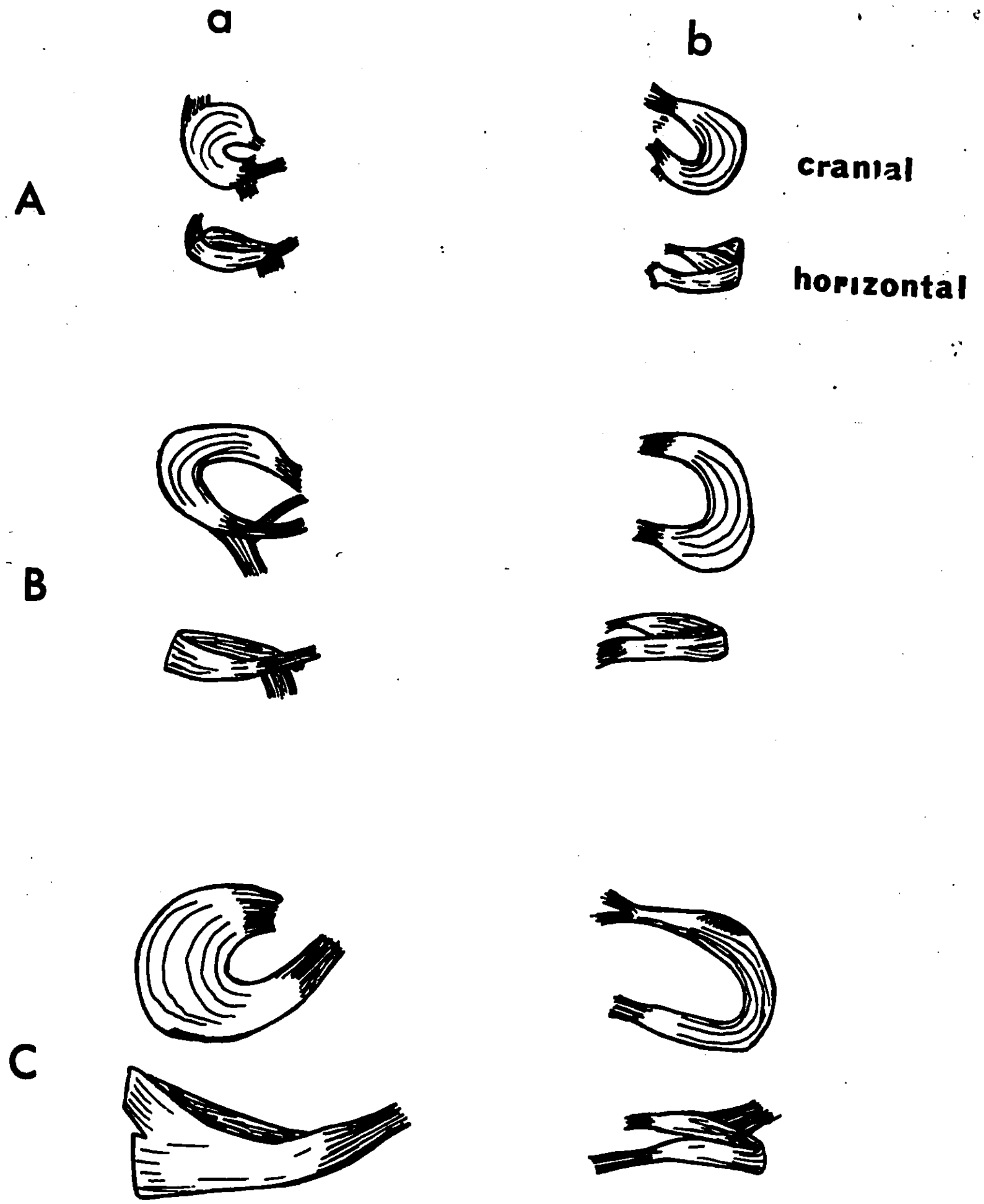
Enhydra lutris (Figs 10Bh, 11Bp, 12Bm) -as in the river otter

Pagophilus groenlandicus (Figs 11Cp, 12Cm) - as in the river otter and the sea otter

In the harp seal, there is a very great difference in size between the two cruciate ligaments, with the caudal one being the larger.

The ligaments of the stifle joint in the river otter and sea otter are positioned so as to give the joint maximum strength but allow free flexion and extension movements, and a minimum of lateral and medial rotation. The main difference between these two species is the absence of a fibular attachment of the fibular collateral ligament in the river otter. This absence of attachment should permit more lateral rotation of the leg than in the sea otter. Observations of the locomotory patterns do not show an obvious rotation of the leg and at present the functional significance of this difference is not known. Lateral rotation of the leg does occur in the harp seal during aquatic locomotion (see Part I, Section C of this thesis). Anatomical evidence indicates that there is a reduced movement between the medial femoral and tibial condyles, which acts as a pivot point, but much sliding movement of the leg around the lateral condyles. The anatomical evidence for this proposal is as follows: The medial meniscus of the harp seal is reduced in depth and width (Fig 13C). If the menisci serve the

Figure 13. Medial (a) and lateral (b) meniscus of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (X11)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function of a surface to facilitate gliding movements between bones, then if there is reduced gliding in one area, it may be expected that the meniscus would tend to be reduced in size. The medial meniscus is attached to the medial condyle of the femur, as in the river otter, thereby maintaining a closer union between the femur, medial meniscus and the tibia. The relatively larger lateral meniscus provides a larger surface area for ligamentous attachments to the femur to ensure that the lateral condyle stays in place. The only other mechanism for preventing dislocation is in the cranial or lateral cruciate ligament. The medial tibial condyle is concave and this shape would tend to confine and reduce the freedom of movement of the femur upon its surface. The lateral condyle of the tibia is enlarged and flat, and serves as a smooth surface for lateral and medial movements of the femur. The tibial collateral ligament is greatly enlarged and inserts on the medial face of the shaft of the tibia, unlike in the river otter and sea otter, where it inserts more toward the cranial edge of the tibial crest. A ligament passing directly distal from the femur to the tibia would tend to keep the bony elements more in a straight line and restrict movement in this area. The fibular collateral ligament is absent and this permits more freedom of rotation of the lateral regions. With this absence of the fibular collateral ligament there is an enlarged capsular region between the cranio-lateral and caudo-lateral capsular ligaments, and this may permit more freedom of movement laterally. The thickened medial capsular ligament is somewhat less well-developed. The caudal cruciate ligament appears stronger and shorter than the cranial cruciate ligament and this would tend to hold the medial regions of the stifle joint in a more fixed position. The cranial cruciate ligament probably acts also as a collateral ligament, functioning to hold the bones together, but with a minimum of interference in rotation movements. Finally, as described above, the patella and patellar articulatory surface on the femur also indicate that lateral rotation of the shank does occur, with the medial areas remaining relatively fixed.

E. Ligaments of the tarsal joint

1. Distal transverse ligament

Lutra canadensis (Figs 14Ah, 15Ai)

This ligament is located on the dorso-lateral side of the calcaneus directly opposite the neck of the talus. It is not connected with the proximal transverse ligament. It forms a loop from the central body region of the dorsal surface of the astragalus and encloses the tendon of the *M. extensor digitorum longus*.

Enhydra lutris (Figs 14Bh, 15Bi)

This ligament is located on the dorso-lateral surface of the tarsal area just caudal to the neck and head of the talus. Medially, it unites with the proximal transverse ligament. This ligament sends other smaller ligaments to the dorsal surface of the centrale and the fibula. Further strengthening of this ligament is by a proximal 'T' of fibers uniting it with the fibula and the proximal transverse ligament. It forms a loop from the central body region of the dorsal surface of the talus and encloses the tendon of the *M. extensor digitorum longus*.

Pagophilus groenlandicus - as in the river otter.

Figure 14. Ligaments of the tarsal joint in *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (dorsal aspect)

a. tibia

b. tibial collateral ligament of the tarsal joint (short part)

c. tibial collateral ligament of the tarsal joint (long part)

d. fibula

e. cranial tibiofibular ligament

f. talus-centrale ligament

g. astragalar-calcaneal ligament

h. distal transverse ligament

i. proximal transverse ligament from the tibia (part a)

j. proximal transverse ligament from the fibula (part b)

k. fibular collateral ligament of the tarsal joint

l. annular ligament

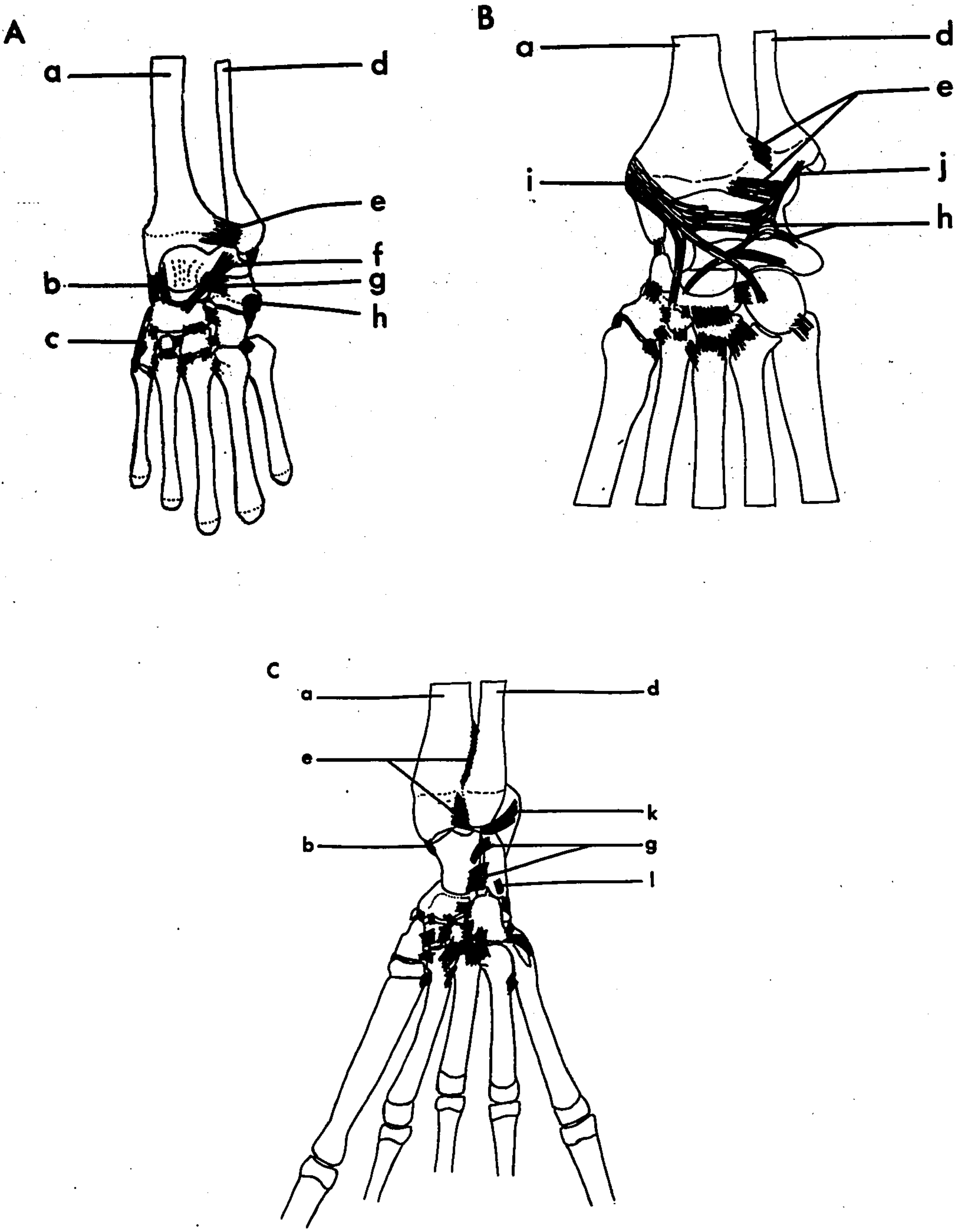
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Figure 15. Ligaments of the tarsal joint in *Lutra* (A),*Enhydra* (B) and *Pagophilus* (C). (caudal aspect)

a. fibula

b. tibia

c. caudal tibiofibular ligament

d. malleolus of astragalus

e. tibial collateral ligament of the tarsal joint

f. calcaneal-centrale ligament

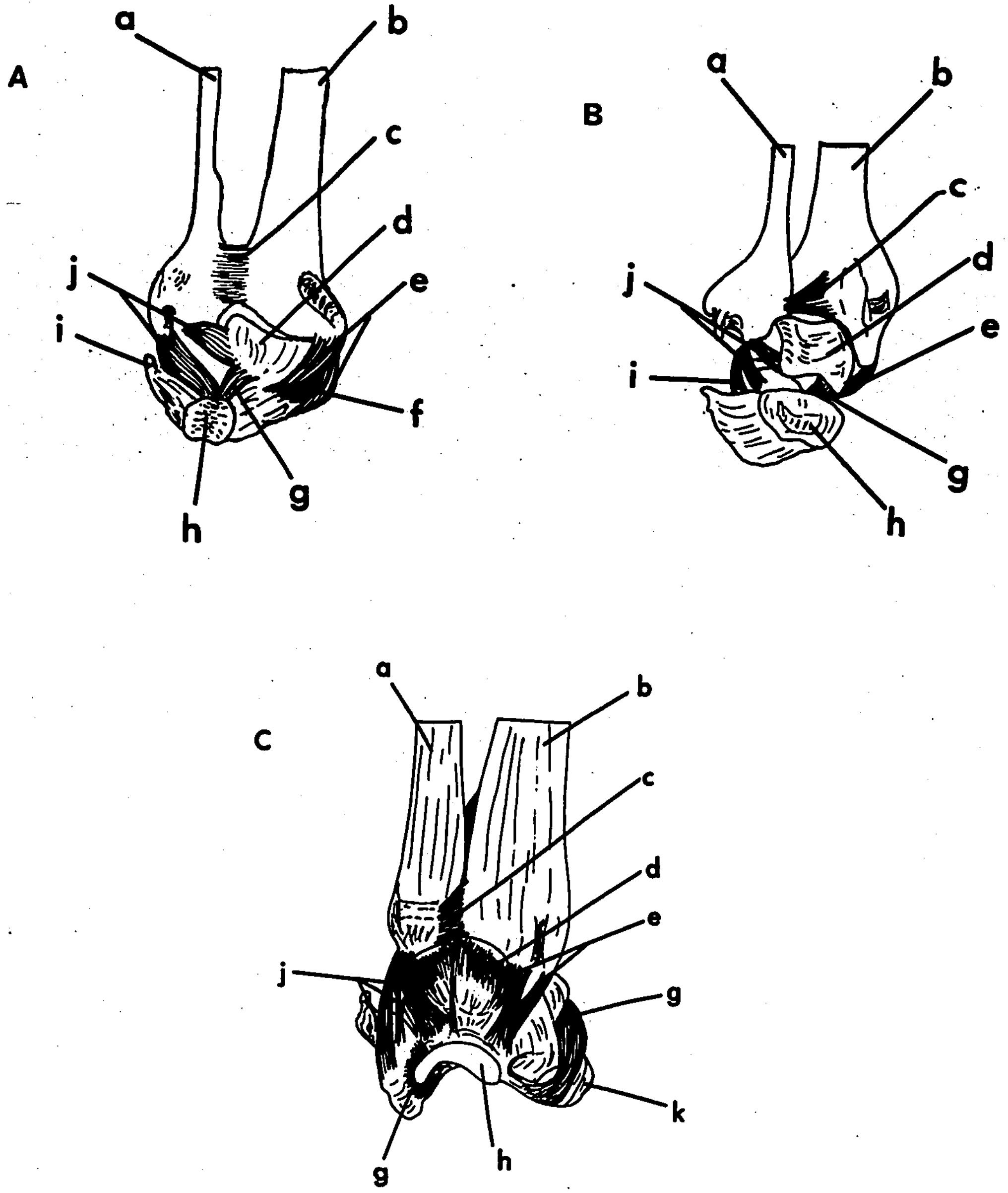
g. astragalar-calcaneal ligament

h. tuber calcus

i. distal transverse ligament

j. fibular collateral ligament of the tarsal joint

k. centrale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2. Proximal transverse ligament

Lutra canadensis (Fig 14Aij)

This ligament is a single, thick bundle of fibers passing from the lateral, dorsal side of the malleolus of the talus with fibers passing medially to the mid-dorsal surface of the centrales. No fibers are received either from the tibia or fibula.

Enhydra lutris (Fig 14Bij)

This ligament is located on the dorsal side of the lower limb and tarsal regions. It has its origin from the tibia (medial side) as a flat, thin sheet. As a sheet it branches in the region of the neck of the talus and sends narrow branches to the centrale, distal transverse ligament, cuboid, and lateral side of the head of the talus.

Pagophilus groenlandicus This ligament was not observed

3. Cranial tibiofibular ligament

Lutra canadensis (Fig 14Ae)

These tibiofibular ligaments are fused to form one mass that is 0.6cm wide at the tibia and 0.4cm. wide at the fibula. The ventro-laterally directed fibers extend between the tibia and fibula on the cranial side of the lower leg, and are located at a point where these bones converge at the termination of the interroseous membrane.

Enhydra lutris (Fig 14Be)

In this species, two separate ligaments can be identified. The proximal one extends between the tibia and fibula on the cranial side of the lower leg as in the river otter. The distal ligament is located more distally between the tibia and fibula. On the tibia, it starts in the central region as a band 0.7cm. wide and unites to the fibula on the dorsal surface of that surface that articulates with the malleolus of the talus. The gap formed between the articular surfaces of the tibia and fibula are covered by this ligament.

Pagophilus groenlandicus (Fig 14Ce)

The proximal tibiofibular ligament is located on the cranial surface of the distal regions of the tibia and fibula. Its fibers run obliquely from the tibia to the fibula in a lateral direction. It is composed of separate strands compared with the distal ligament which is for the most part a solid mass. The distal ligament starts on the tibia near the central cranial face and is directed laterally to the fibula where it inserts on the mid-cranial, distal surface, and on the proximo-medial side. The ligament tapers proximally. Where the tibia and fibula converge, this ligament narrows and the fibers run at a more oblique angle ventrally. The gap formed between the articular surfaces of the tibia and fibula are covered by this ligament, and the central part of the malleolus of the talus articulates on it.

4. Caudal tibiofibular ligament

Lutra canadensis (figs 15Ac, 16Ae)

This ligament is located at the distal ends of the tibia and fibula on their caudal side. Origin is directly over the lateral ridge of the malleolus of the talus and, on its ventral side, forms part of the articular surface of this ridge.

Width on tibia = 0.7cm	Width on fibula = 0.7cm

Enhydra lutris (Fig 15Bc) - as in the river otter

Width on tibia = 0.7cm	Width on fibula = 0.4cm

Pagophilus groenlandicus (Figs 15Cc, 16Ce)

This ligament is a distinct band that begins on the caudo-lateral surface of the tibia and is directed ventrally toward the fibula where it attaches on its caudo-medial surface.

Width = 1.0cm

5. Tibial collateral ligament of the tarsal joint

Lutra canadensis (Figs 14Ab,c; 15e; 16g,h)

This ligament is composed of two parts: A. From the tibia to the malleolus of the talus (on its medial surface).

B. From the tibia to the centrale and tarso fibro-cartilage.

Figure 16. Ligaments of the tarsal joint in *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (plantar aspect)

a. fibular collateral ligament of the tarsal joint

b. tarsal fibrocartilages

c. tibia

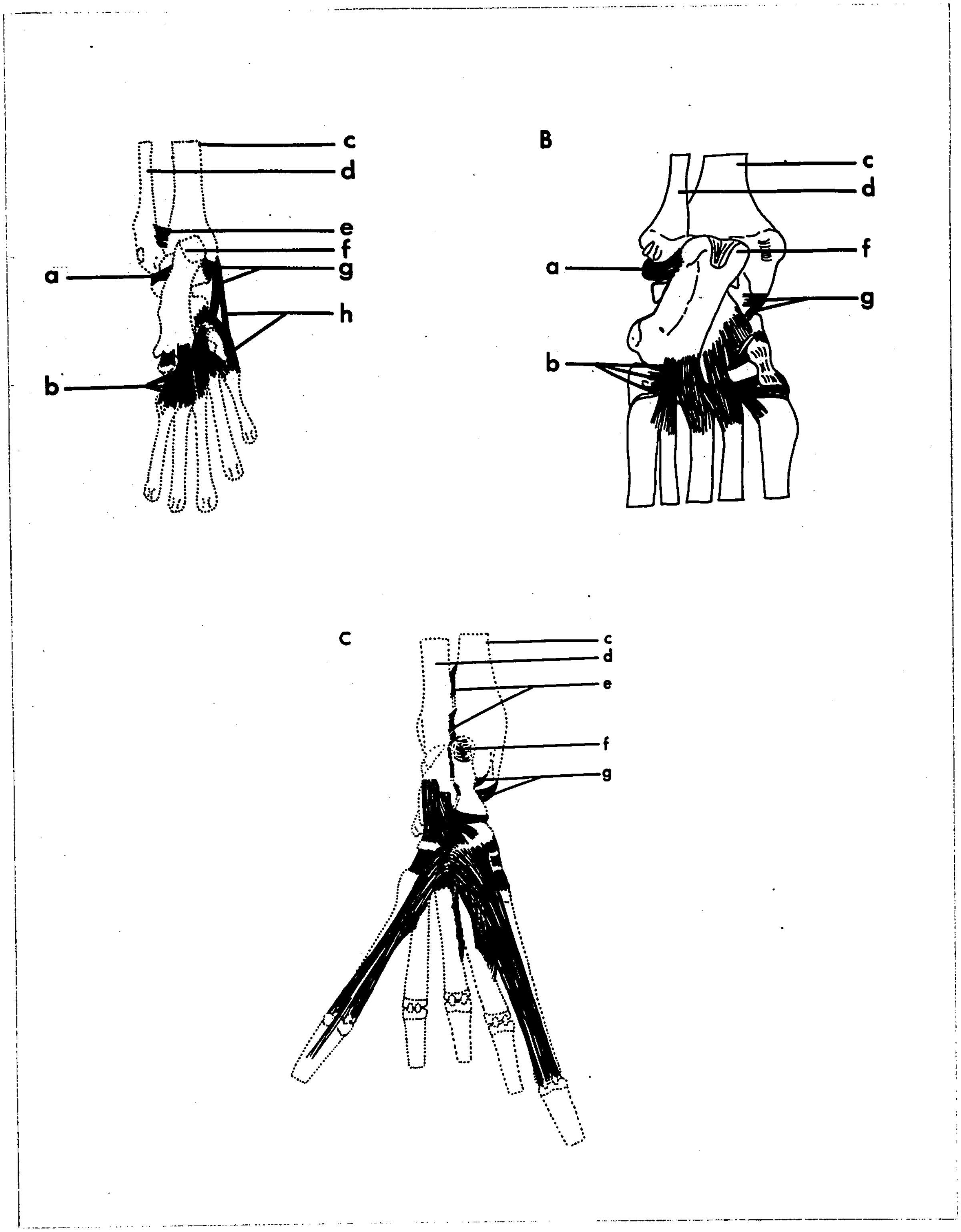
d. fibula

e. distal tibiofibular ligament

f. tuber calcus

g. tibial collateral ligament of the tarsal joint (short part)

h. tibial collateral ligament of the tarsal joint (long part)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This ligament starts as one unit on the cranial side of the medial malleolus of the tibia. It then divides, sending one short ligament to the ventro-medial side of the malleolus of the talus, and a longer branch to the mid-ventral surface of the centrale and the tarsal fibro-cartilage. These two parts are less stout than the two parts of the fibular collateral ligament.

Enhydra lutris (Figs 15Be, 16Bg) - as in the river otter. The only difference is that in the sea otter there is no connection to the 'centrale' part of the tarso fibro-cartilage.

Pagophilus groenlandicus (Figs 14Cb, 15e, 16g)

This ligament is composed of two parts: A. From the caudal surface of the tibia to the body of the talus.

B. From the medial side of the tibia to the disto-medial surface of the malleolus of the talus.

Part A is composed of a thin sheet of loose ligaments resembling dense connective tissue. Length = 2.0cm Width = 0.9cm. Part B is a thick ligament. Length = 2.0cm Width = 0.8cm.

6. Fibular collateral ligament of the tarsal joint

Lutra canadensis (Figs 15Aj, 16Aa)

This ligament is composed of two parts: A. From the fibula to the calcaneus.

B. From the fibula to the

malleolus of the talus.

Part A receives fibers from the tibiofibular ligament and from the distal lateral face of the fibula. Fibers pass ventro-caudally and insert on the body of the calcaneus just lateral and caudal to the articular facet of the calcaneus with the talus. There is also seen a thin, short branch passing to the ventro-lateral surface of the lateral malleolus of the talus.

Width = 0.45cm. Length = 1.1cm.

Part B is located ventral and medial to and more caudal to Part A. It is shorter (1/2 as long) and passes directly from the medial-caudal side of the articular surface of the fibula to the ventro-lateral side of the malleolus of the talus.

The long part of the fibular collateral ligament described in the dog (Miller, *et all*, 1965) was not observed.

Enhydra lutris (Figs 15Bj, 16Ba)

This ligament is located on the lateral side of the lower limb between:

A. the fibula and the calcaneus

B. the fibula and the talus

Both of these portions of the ligament are exceedingly thick and strong. Part A is the more lateral, and passes from the disto-lateral surface of the fibula (just medial to the distal cranial tibiofibular ligament) to the lateral ridge near the heel of the calcaneus. Part B is located more ventrally and medially to, and more caudal to Part A, and has a disposition similar to that in the river otter.

Pagophilus groenlandicus (Figs 14Ck, 15Cj)

This ligament is composed of two parts as in the river otter and the sea otter. Part A receives fibers from the tibiofibular ligament (distal) and from the lateral face of the fibula. The fibers pass ventro-caudally and insert on the body of the calcaneus just lateral and caudal to the articular facet of the calcaneus with the talus. Length = 3.5cm Width = 0.55cm. Part B is located more ventral, medial and caudal to Part A. It is shorter, but wider than Part A and passes from the lateral-caudal side of the articular surface of the fibula to the ventral-lateral side of the malleolus of the talus. A small branch is also given off to the body of the talus and a small strand goes to the body of the calcaneus.

Other intra-tarsal and digital ligaments are not described, but it is noted that those of the harp seal are especially strong, covering the entire area as a tough fibrous lining (Fig 16).

In each species, the morphology of the malleolus of the talus and the articulatory facets of the tibia and fibula are such that there is maximum freedom of flexion and extension movements of the foot, with only limited rotation possible. Maintenance of the malleolus within the distal condyles of the tibia and fibula is by the tibial and fibular collateral ligaments. These ligaments appear equally well-developed in each species and are perhaps stronger in the harp seal. The osteology and syndesmology of the tarsal joint gives further evidence for the necessity of lateral rotation at the stifle joint to produce the observed angling of the feet of the harp seal during active swimming.

The most significant adaptation is in the differences in the development of the fibro-cartilages on the dorsal and plantar surfaces of the foot of the harp seal. The bones of the plantar surface of the foot of the harp seal are closely bound by fibrocartilages. Many of the muscles on the plantar surface of this seal are present only as tendons. As the plantar surface receives or must provide the propulsive force to drive the body forward, it must be relatively rigidly structured. In the harp seal, the lateral digits appear to be the most highly strengthened by these tendons and ligaments. The central three digits are the least strengthened and are more easily displaced in both dorsal and plantar directions. These differential regions of strength assist in forming the cup-like shape of the foot during the propulsive phase and the collapsed-shape of the foot during the recovery phase of aquatic locomotion.

Summary

1. The coxal joint of *Lutra* and *Enhydra* permits maximum movement of the femur in a cranio-caudal direction during flexion and extension movements of the pelvic limb during terrestrial and aquatic locomotion. In *Enhydra*, increased lateral rotation of the pelvic limb is made possible by the absence of the femoral ligament and an increased articulatory facet on the dorsal surface of the femur. This lateral rotation of the limb is used when the animal swims on its back at the surface of the water. In these two otters, the increased thickened one-half of the capsular membrane, acetabular lip, and acetabular ridge indicate that these regions receive most of the force of the head of the femur during locomotion. The coxal joint of *Pagophilus* appears well-adapted for movements of the head of the femur in a cranio-caudal direction as reflected in the equal development of these regions of the acetabular lip.

   A femoral ligament is present in *Lutra* and absent in *Enhydra* and *Pagophilus*. Its absence may reflect the decreased amount of weight supported by the pelvic limbs. *Enhydra* is less agile on land than is *Lutra*, and *Pagophilus* does not use the pelvic limbs to support the caudal regions of the body.

2. The stifle joint of *Lutra* and *Enhydra* permits flexion and extension movements of the shank and little rotation. In *Pagophilus*, the anatomical evidence suggests that there is much lateral rotation of the leg during aquatic locomotion. This evidence is seen in the laterally directed patella and patellar fossa, the absence of a fibular collateral ligament and enlargement of ligaments associated with the femoral-tibial junction,

differential sizes of the lateral and medial meniscus, and the laterally sloping articulatory facets of the femur, tibia and fibula.

3. The tarsal joint in all three species is held in place by the tibial and fibular collateral ligaments, and articulatory surfaces seem best adapted for flexion and extension movements of the foot, with little or no lateral rotation. In each species, the bones of the plantar surface of the foot are more rigidly bound together than on the dorsal surface.

Literature cited

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Acknowledgments

For specimens and assistance during the preparation of this report, I wish to express my appreciation to the following: Mr. Ian Smith and Mr. Denis Wilder (B.C. Fish and Game Department); Dr. J.C. Holmes and Mr. T.C. Neraasen (Dept. of Zoology, University of Alberta); Dr. R.A. Green (Dept. of Veterinary Anatomy, University of Cambridge); and the Audio-visual Aids Department (University of Cambridge).

The research was financed by Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada and McGill University.

Parts of the final draft of this report were written in consultation with Drs. A. Bisaillon and J. Piérard (École de Médecine vétérinaire, Université de Montréal).

Appendix to Parts I and II.

Additional data on the hind limbs of otters and seals as related to locomotion.

Table of Contents

I. Introduction

It is generally accepted that the pinnipeds evolved from terrestrial carnivores through a series of ancestors which had morphological characteristics intermediate between the original prepinniped(s) and these present-day highly specialized seals, sea lions and walruses. The features and habits of the river otter (*Lutra*) and sea otter (*Enhydra*) appear to be similar to those of two proposed prepinniped carnivores: *Potamotherium* (Savage, 1957) and *Semantor* (Orlov, 1933) and, in terms of aquatic adaptation, they are intermediate between present-day terrestrial carnivores and pinnipeds. Therefore, a detailed comparative study of the anatomy, behavior and physiology of these aquatic and semi-aquatic mammals may very well indicate a stage through which the pinnipeds evolved, and also show how mammals may adapt to meet common habitat demands. Presented here is data in addition to that presented in Parts I and II on some aspects of the hind limbs of three major groups (Lutrinae, Enhydrinae and the Pinnipedia), with emphasis on locomotory adaptation. For simplicity, the discussion is directed toward a group representative from each of five Families (shown below), although other pinnipeds are noted where applicable.

Lutrinae: *Lutra canadensis* (the Canadian river otter)
Enhydrinae: *Enhydra lutris* (the sea otter)
Phocidae: *Pagophilus groenlandicus* (the harp seal)
Otariidae: *Zalophus californianus* (the California sea lion)
Odobenidae: *Odobenus rosmarus* (the walrus)

II Locomotion

Literature dealing with the terrestrial and aquatic locomotion of otters and seals can be divided into two groups: that dealing with the descriptive and analytical features of locomotion and that describing the anatomical bases of these movements (Tables I and II). To fully appreciate the adaptation of those mammals to both terrestrial and aquatic habitats, studies should be carried out relating both structure and function.

A. Locomotory patterns and mechanics

The aquatic and terrestrial movements of *Lutra, Enhydra, Pagophilus, Zalophus* and *Odobenus* resemble patterns displayed by all aquatic mammals, including the Cetacea and Sirenia. There is the use of the hind limbs, fore limbs or tail, or any combination of these three. The limbs may be moved unilaterally or bilaterally, and limbs and tail may be moved horizontally or vertically. The river otter (Table I) is more like a terrestrial mammal in its movements and, as the anatomical studies indicate, it is also more similar in its myology and osteology to this group than are the sea otter and seals. The seals have two principal aquatic locomotory patterns: Phocidae using the hind limbs laterally and Otariidae moving its fore limbs medially in cranial-caudal arcs (the odobenids having a combination of the two). The sea otter has locomotory patterns similar to both river otters and seals and appears to be intermediate between these two.

For forward movement, the following conditions should be met: an

Table I. Literature and summary of locomotory patterns of otters and seals.

Animal	Locomotory Characteristics	References
Lutra	aquatic- fore and hind limbs thrust anteriorly and posteriorly. -tail undulates horizontally with limbs used to stabilize the body. terrestrial-digitigrade -walks with back slightly arched. -walking, running and bounding observed.	Howell (1930) Severinghaus and Tanck (1948) Liers (1951) Savage (1957) Tarasoff (Part I-this thesis)
Enhydra	aquatic- hind limbs moved bilaterally and vertically. - tail moved vertically in time with the feet. -fore limbs not used actively. - paddles with hind limbs when on its back in the water. - may use tail for orientation movements when animal is on its back in the water.	zur Strassen (1914) Howell (1930) Fisher (1939) Barabash-Nikiforov (1947) Kenyon (1969) Tarasoff (Part I- this thesis)
	terrestrial -same foot patterns as in *Lutra*.. -back more highly arched than in *Lutra*.	Murie (1940) Barabash-Nikiforov (1947) Kirkpatrick *et al.*(1955)

(Table I. continued)

Enhydra	terrestrial (cont'd) -walking and bounding observed	Kenyon (1969) Tarasoff (Part I-this thesis)
Pagophilus	aquatic - hind feet moved laterally and medially with alternating flexion and extension. -fore limbs used in planing and for turns. -no use of tail	Tarasoff (Part I-this thesis)
	terrestrial - anterior-posterior sweeps of the fore limbs - unilateral movement of the fore limbs (sinusoidal) - hitching forward of the body -some assistance from hind limbs for climbing only - unable to turn hind limbs forward	Murie (1870) O'Gorman (1963) Mordvinov (1968) Tarasoff (Part I-this thesis)
Zalophus	aquatic- fore limbs moved laterally and medially in anterior-posterior direction	Howell (1929. 1930) Backhouse (1961) Gambarjan and Karapetjan (1961)

Table I (continued)

Zalophus	aquatic (cont'd).	- hind limbs usually trail, but may assist at high speeds	Ray (1963) Peterson and Bartholomew (1967)
	terrestrial	- hind feet turned forward and animal balances on tarsal region and fore limbs - walking and bounding observed	Murie (1870) Howell (1929) Tamino (1951) Gambarjan and Karapetjan (1961) Peterson and Bartholomew (1967)
Odobenus	aquatic	-uses both fore and hind limbs in a manner intermediate between *Zalophus* and *Pagophilus*.	Murie (1871) Ray (1963)
	terrestrial	- hind limbs may be brought under the body - moves in a manner similar to that of *Zalophus*.	Murie (1871)

Table II. Reference list of locomotory patterns of pinnipeds.

Duvernoy (1822)	- describes terrestrial and aquatic locomotory patterns of *Phoca vitulina*.
Pettigrew (1868)	- describes aquatic locomotion of seals, sea lions and walruses.
	- detailed description of *Neophoca hookeri*.
Murie (1870)	- describes terrestrial locomotion of *Pagophilus groenlandicus*, *Cystophora cristata* and *Phoca vitulina*.
	-refers to terrestrial locomotion of *Otaria jubata*.
Murie (1871)	- describes locomotory patterns of *Odobenus rosmarus* and mentions other pinnipeds in general.
Scammon (1874)	-describes terrestrial locomotion of *Phoca vitulina*.
	- mentions terrestrial locomotion of *Mirounga angustirostrus* and otariids.
Allen (1880)	- reviews locomotory patterns in general.
Wilson (1907)	- describes terrestrial locomotion of *Leptonychotes weddelli*.
Howell (1929, 1930)	- describes locomotion of *Phoca hispida* and *Zalophus californianus*.
Lindsey (1938)	- describes terrestrial locomotion of *Leptonychotes weddelli*.

Table II (continued)

Slijper (1946)	- brief description of otariid and phocid aquatic patterns.
Tamino (1951)	- describes terrestrial movements of *Zalophus californianus*.
Tamino (1952)	- compares terrestrial movements of otariids and phocids.
Scheffer (1958)	- reviews locomotory patterns in general.
Backhouse (1961)	- terrestrial locomotion of *Halichoerus grypus*. - reviews phocid and otariid locomotion in general.
Gambarjan and Karapetjan (1961)	- describes locomotion of *Zalophus californianus* and *Phoca sibirica*.
O'Gorman (1963)	- describes terrestrial locomotion of *Lobodon carcinophagus*, *Hydrurga leptonyx*, *Leptonychotes weddelli*. - comments on movements of *Mirounga leonina* and *Pagophilus groenlandicus* and probable movements of *Ommatophoca rossi*.
Ray (1963)	- describes locomotion of *Odobenus rosmarus*, *Zalophus californianus* and *Halichoerus grypus*.
Mordvinov (1968)	- describes aquatic and terrestrial movements of *Pagophilus groenlandicus*, *Arctocephalus pusillus* and *Phoca caspica*. - refers to movements of *Histriophoca fasciata*. - refers to the works of Smirnov (1929), Ognev (1935), Karpichnikov (1949), Arsen'ev (1957) on

Table II. (continued)

terrestrial movements of seals.

- refers to the work of Tikhomirov (1966) on movements of *Erignathus barbatus*, *Phoca hispida* and *Phoca vitulina* on ice.
- refers to the work of Tomilin (1965) on terrestrial speeds of *Hydrurga leptonyx* and *Lobodon carcinophagus*.

effective stroke coming from the feet and/or the tail; a coordination between strokes for straight line movement; and a streamlined body outline to reduce turbulence and resistance. The animal should also push the water past the body in a direction away from an advancing opposite limb so as to cause a minimum of disturbance. In *Lutra* and *Enhydra*, the hind limbs are moved in an arc dorsally and caudally. When the stroke finishes, the foot is in a dorsal position and the water moves away from the body in that direction and its turbulence produces little interference with the subsequent strokes. *Pagophilus* and other phocids usually change the angles of the leading hind flipper (sculling) so that the ventral edge is leading at first, pushing water dorsally, then the dorsal edge becomes the leading one near the end of the stroke and pushes water ventrally. This results not only in an alternating uplifting and descending effect on the body but also in the movement of water away from the opposite flipper. The latter moves medially with its leading ventral side pushing water into a relatively undisturbed area. Parry (1949) states that this changing of the angle of incidence during each half-cycle results in the greatest forward thrust. In *Zalophus*, the hind limbs trail for the most part and thus the water waves from the fore flippers are not interrupted. The relatively nonturbulent water around the hind limbs may assist the breaking function usually attributed to the hind limbs. The effect of moving these limbs to one side is to create turbulence and an increased resistance in the water. For aquatic movement, *Odobenus* may either use its fore limbs like *Zalophus* or its hind limbs like *Pagophilus*. The hydromechanics of propulsion would therefore be comparable to either of these two species depending on the method of propulsion used.

Lighthill (1969) has recently reviewed the hydromechanics of aquatic animal propulsion. His main emphasis is on the dynamics of the carangiform mode of propulsion found in strong swimming, active vertebrates. The requisites of this mode are an extension of depth and breadth of the body, a narrowing of the region cranial to the source of the drive, and good streamlining. These adaptations assist in minimizing the vertical and horizontal recoil of the body cranial to the propulsive organ(s) and reducing body resistance. Lighthill devotes most of his discussion to the fishes and the cetaceans with little emphasis on pinnipeds and no mention of otters. The variations of the carangiform mode with a lunate border found in the otters and the hair seals have been discussed in this thesis (Section C: part I). It is concluded that the river otter, sea otter and hair seals each have the requirements for a carangiform mode of propulsion and the individual puopulsive efficiency depends on the characteristics of the lunate border and their locomotory patterns. This Part (I) has also attempted to correlate swimming speeds with the animal's locomotory patterns and diving habits.

B. Myology and osteology

1. Pelvic girdle and limbs

The myology and osteology of the hind limbs of otters and seals have been extensively described (Table III). The relation of muscle and bone changes with increased aquatic adaptation has also been discussed (see

Table III. Principal contributors to the knowledge of the myology (M) and osteology (0) of the hind limbs of otters and seals.

Otters:

Lutra
- Lucae (1872, 1875) M,0
- Windle and Parsons (1898) M
- Taylor (1914) 0
- Pohle (1919) 0
- Luthe (1924) 0
- Fisher (1942) M,0

Enhydra
- Martin (1836) 0
- Lucae (1872, 1875) 0
- Taylor (1914) 0
- zur Strassen (1914) 0
- Pohle (1919) 0
- Howell (1930) M
- Jacobi (1938) 0
- Barabash-Nikiforov (1947) 0
- Gambarjan and Karapetjan (1961) M

Phocids:

Phoca vitulina
- Duvernoy (1822) M,0
- Humphry (1868) M
- Lucae (1872, 1875) M,0
- Miller (1888) M

Phoca hispida
- Howell (1929) M,0
- Miller (1888) M

Phoca sibirica
- Gambarjan and Karapetjan (1961) M

Erignathus barbatus
- Miller (1888) M

Mirounga leonina
- Miller (1888) M

Leptonychotes weddelli
- Piérard (1972) M,0

Otariids:

Zalophus californianus
- Howell (1929) M,0
- Mori (1958) M,0
- Gambarjan and Karapetjan (1961) M

Eumetopias jubata
- Murie (1872, 1874) M,0

Arctocephalus gazella
- Miller (1888) M

Odobenids:

Odobenus rosmarus
- Murie (1871) M

especially, Taylor (1914), Howell (1930), Smith and Savage (1956), Savage (1957) and Gambarjan and Karapetjan (1961). On reviewing this literature, it can be concluded that the anatomy of the hind limbs of *Lutra* is similar to that of terrestrial carnivores. Pinnipeds, on the other hand, have undergone extensive changes which are closely correlated with their specialized methods of aquatic locomotion. *Enhydra* shows similarities in its patterns of aquatic locomotion to both the river otter and hair seal, this being reflected also in its myology and osteology.

With reference to the principal changes in the muscles and bones of the hind limbs of otters and seals (Table IV), the major changes can now be briefly summarized along with the locomotory patterns.

The position of the hind limb bones of *Lutra* (Fig 1a) is adapted to support the hind regions of the body when the animal is on land and also to propel the animal in the water by means of repeated anterior-posterior arcs with the plantar surface of the foot being directed first posteriorly then dorsally. The movement of the hind limbs during swimming is similar to that of walking. The femur and the shank (tibia and fibula) are directed cranially and ventrally, nearly perpendicular to the long axis of the body. This positions the limbs under the body for better support. The muscles that produce flexion and extension of the limbs are similar in size and position to those of terrestrial carnivores (Fig 2a). The more aquatically adapted hair seal (Fig 1b) has the the shaft of the femur extending ventrally, almost at right angles to the long axis of the body. In addition, the pinniped shank is close to the body and nearly parallel to the vertebral column. The associated upper and lower limb muscles (*Mm. gracilis, biceps femoris* and *semitendinosus*) firmly secure the limb in this position by a

Table IV. Changes in the osteology and myology in *Canis*, *Lutra*, *Enhydra*, *Pagophilus* and *Zalophus* associated with increased flexion, elevations, and lateral rotation of the hind limb.

A. Innominate

1. Percent of ilium and pubo-ischiac to total innominate length

	ilium (o/o)	pubo-ischiac (o/o)
Canis	64	36
Lutra	53	47
Enhydra	50	50
Pagophilus	26	74
Zalophus	36	64

An increased pubo-ischiac permits greater surface area for origin of those muscles which insert on the femur and tibia and function to adduct these bones. The femur and tibia ultimately come to lie nearly parallel with the vertebral column. This also shifts the position of the acetabulum so that a relatively long lever arm is maintained for the adduction of the femur.

2. Sacro-pelvic angle (see Fig 1)

Canis	55°	94°
Lutra	35	70
Enhydra	25	68
Pagophilus	28	40
Zalophus	25	45

Table IV. (continued)

Along with the heightening of the ischiac spine, the principal result of these changes is that as the limb becomes more parallel with the vertebral column, the muscles which attach between the pubo-ischiac and the shank become short and lose much of their power. Therefore, to parallel the elevation of the limb, there has also been an elevation of the areas of muscle attachments on the pelvis to maintain relatively long moment arms.

3. Lateral flaring and flexion of the ilium.

	angle of lateral flexion
Canis	5°
Lutra	5
Enhydra	35
Pagophilus	65
Zalophus	30

The flaring results in an increased area for the origin of the *Mm. gluteus medius, minimus,* and *pyriformis*. These muscles attach to the greater trochanter of the femur, and upon contraction cause the femur to rotate. The lateral flexion serves mainly to increase the proximal (medial) surface of the ilium to provide an increased surface area for attachment of the *M. Iliocostalis* which becomes more important for lateral movements in phocid seals versus the vertical movements of the otters.

B. Femur

1. Loss of *ligamentum teres* from the head of the femur.

Table IV. (continued)

Canis	present
Lutra	present
Enhydra	absent
Pagophilus	absent
Zalophus	absent

This ligament is associated with rotational movements of the femur and is also of assistance for increasing fixation of the head of the femur to the pelvis when the animal is on land. In those species that spend less time on land, this ligament is not found.

2. Flattening and increased size of the greater trochanter.

The main result of these changes are to increase the area of insertion of muscles that rotate the femur (*Mm. gluteus medius, minimus* and *pyriformis*) and to shorten the distance between this trochanter and the ilium. The result is a reduced rotation of the femur upon contraction of these muscles.

3. Decrease and eventual loss of the lesser trochanter.

As the antagonistic muscles of those that rotate the femur caudally become very much reduced and weakened (*Mm. Iliacus* and *psoas major*) in those mammals that do not bring their pelvic limbs forward, there is seen a parallel decrease in their area of insertion (lesser trochanter).

4. Shortening of the shaft of the femur.

Table IV. (continued)

	femur	tibia and fibula	pes
Canis	31o/o	31o/o	38o/o
Lutra	30.0	33.0	37.0
Enhydra	27.0	32.0	47.0
Pagophilus	16.0	35.5	48.5
Zalophus	16.5	35.5	48.0

A shortened femur shaft enables the whole limb to be brought close to the body. It also reduced the length of the *M. vasti* and *rectus femoris* complex which attach to the patella and function in extension of the shank, giving more power and less speed as a result. In seals there is also a decrease in this muscle mass.

5. Broadening of the shaft of the femur.

With an increased adductor muscle mass, there is the need of an increased surface area for its insertion on the femur. This enlarged adductor mass also assists in preventing rotation and movement of the femur. Howell (1929) states three additional possible functions for this broadening of the femur, these include: lack of need for antero-posterior thickness; need for laterally placed greater trochanter with rotatory muscles; and need for broad distal extremity to the articular condyle of the tibia.

6. Increased angle of inclination of the femoral condyles* (medial condyle longer than the lateral condyle).

Table IV. (continued)

Canis	0°
Lutra	0
Enhydra	4
Pagophilus	15
Zalophus	8

This, plus a similar increased angle of slope on the articular surfaces of the tibia, has an unknown function. This increased difference in slope is compensated for by having a thicker lateral meniscus between the condyles of the femur and tibia (see Part II-this thesis).

*angle formed between condyles and a line perpendicular to the shaft of the femur.

C. Tibia and fibula

1. Increased proportional length of these lower limb components and the pes (see Femur: part 4).

A lengthening of the lower leg provides a large surface area for the origin of muscles for flexing and extending the foot. It also increases the area for the insertion of adductor muscles (*Mm. gracilis, biceps femoris, semitendinosus* and *semimembranosus*) for holding the limb close to the body. These muscles are located more caudally on the shank in the sea otter and seals than in the river otter and dog.

D. Tarsal joint

The tarsal joints of *Lutra, Enhydra* and *Zalophus* resemble those of

Table IV. (continued)

terrestrial carnivores and are adapted for movement in a horizontal plane with no lateral rotation. The tarsal joint of *Pagophilus* and other phocid seals has a more specialized astragalus, the head of which forms a ball-and-socket-like joint with the tibia and fibula and permits more lateral rotation.

E. Astragalus-calcaneum and centrale-cuboid articulation.

In phocids, this joint is more specialized than in the otariids and permits greater flexibility of the foot distal to the tarsal joint.

F. Foot.

1. Changes in muscle weights that:

i. Flex the foot*

	gastrocnemius	*flexor dig.* and *flexor hallucis longus*	*peroneus longus*
Lutra	8.4	3.0	0.6
Enhydra	9.3	1.8	0.8
Phoca	13.8	12.3	3.1
Zalophus	12.8	4.7	2.3

*from Gambarjan and Karapetjan, 1961. (percentage of the total weight of the flexor muscles of the foot)

Table IV. (continued)

ii. Spread the digits*

	extensor hallucis longus	*peroneus digiti quinti*
Lutra	1.9	3.3
Enhydra	6.7	14.0
Phoca	4.8	5.0
Zalophus	12.0	16.1

* from Gambarjan and Karapetjan, 1961. (percentage of those muscles that spread the digits)

Figure 1. Bones of the caudal regions of four aquatic mammals, illustrating spinal flexion, sacro-pelvic angle and relative bone lengths.

A. *Lutra canadensis*	C. *Enhydra lutris*
B. *Pagophilus groenlandicus*	D. *Zalophus californianus*

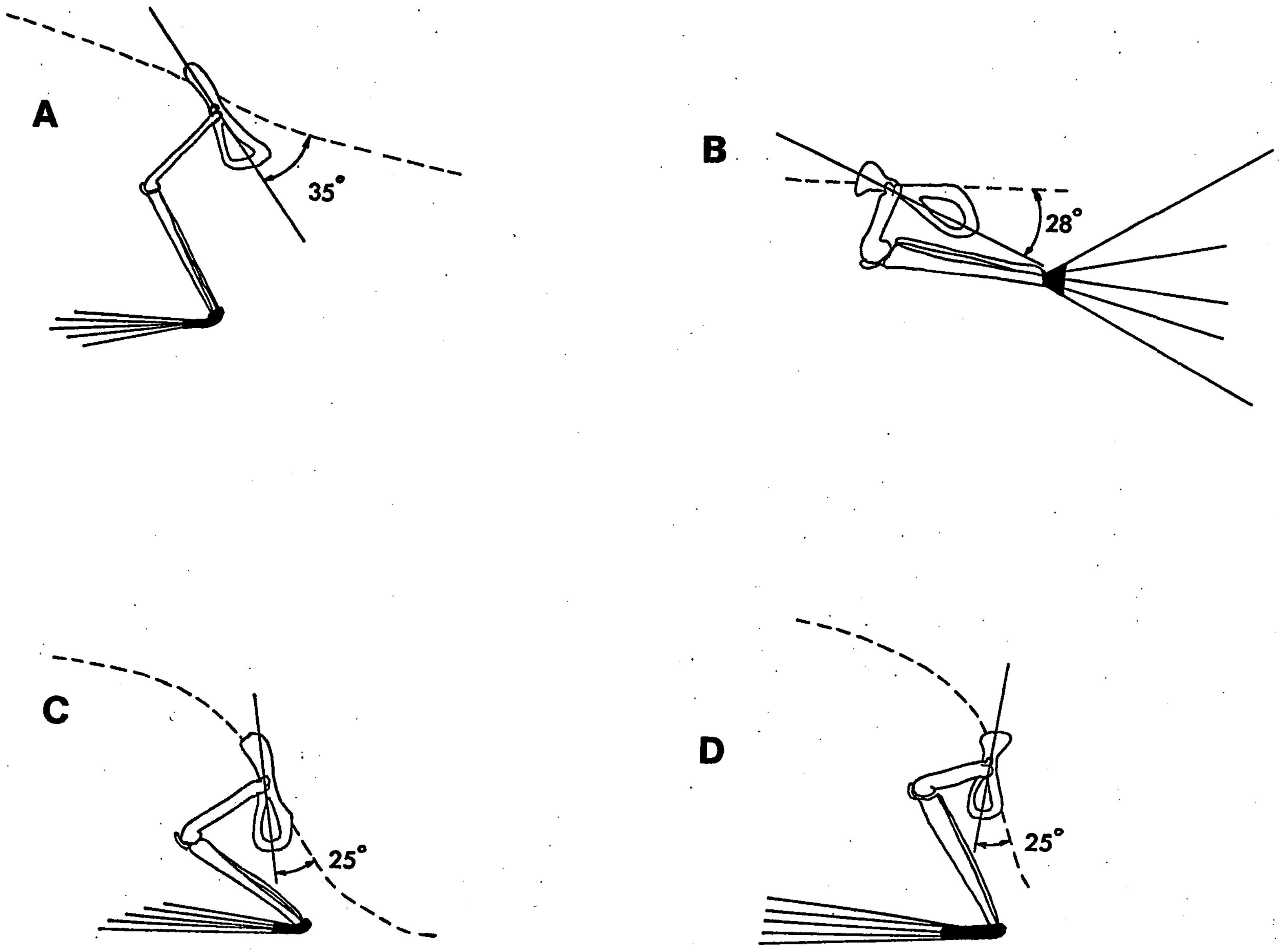
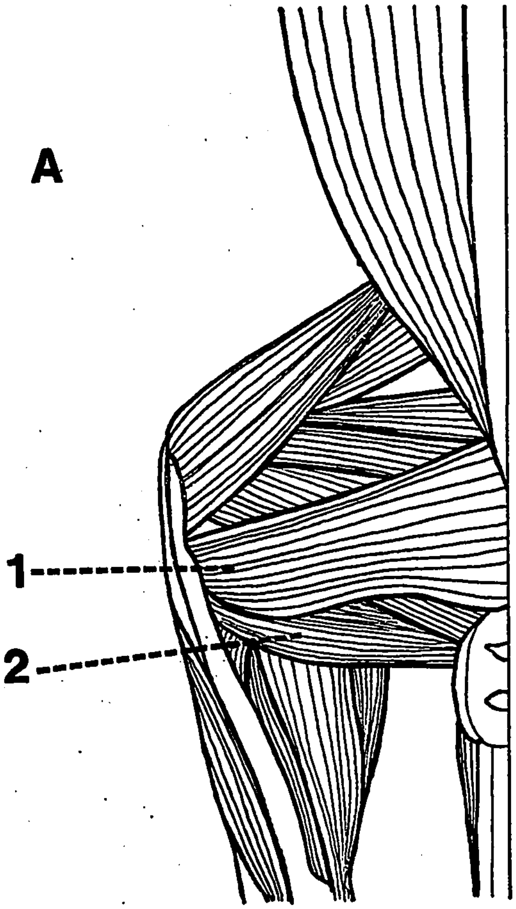

A
35°
B
28°
C
25°
D
25°

Figure 2. Superficial muscles (ventral aspect) of the upper portions of the pelvic limb of four aquatic mammals.

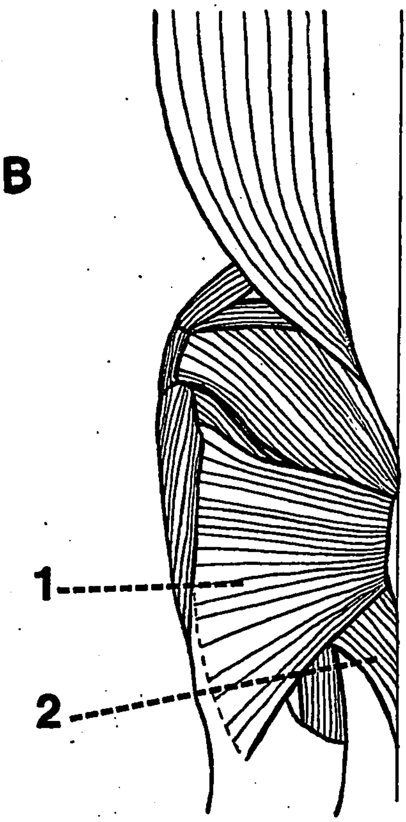
(1 = *M. gracilis*   2 = *M. semitendinosus*)

A. *Lutra canadensis*
B. *Pagophilus groenlandicus*
C. *Enhydra lutris*
D. *Zalophus californianus*

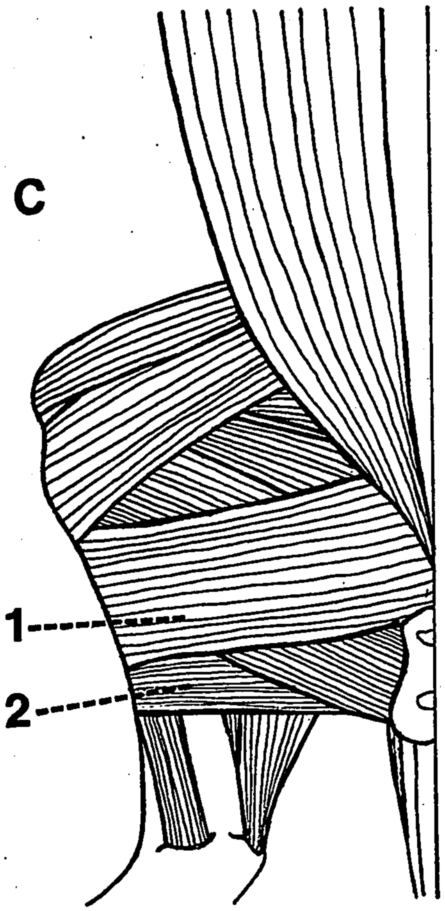
A



B



C



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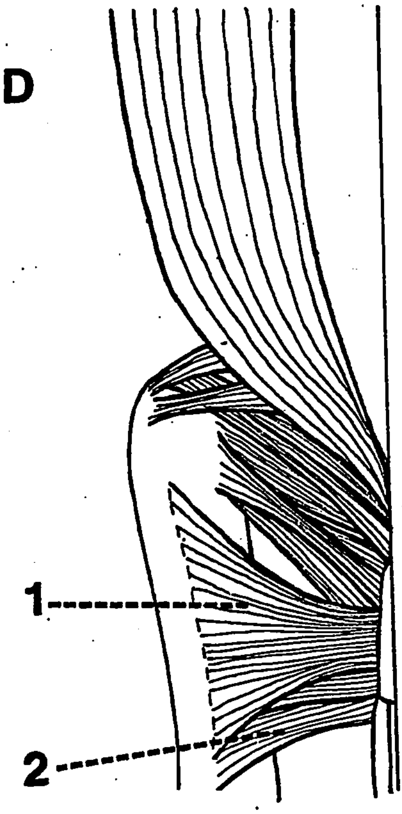


distal displacement of their insertions on the shank (Fig 2b). These muscles, in part, render the limb incapable of being turned forward (phocids). The rotation of the lower limb has assisted in positioning the hind foot so that the latter is now moved in an alternating flexion and extension pattern on a horizontal plane. The sea otter (Fig 1c and 2c) and the sea lion (Fig 1d and 2d) are intermediate between the above two animals. The hind limb of the sea otter is directed ventrally, similar to the river otter. However, the shank is more elevated and restricted in its flexion and extension movements, as in the case of phicids. The anatomy of *Enhydra* and *Zalophus* indicates that these animals are adapted for movements of the feet in vertical and horizontal planes as well as for body support and movement while on land.

Along with the restriction in flexion and extension of the hind limbs, there has been an increase in the size of the muscles used to move the foot. Since the power stroke is during extension, the muscles which one would expect to be increased in bulk are the extensors, namely the *Mm. extensor digitorum longus, gastrocnemius* and the *peroneus longus*. Gambarjan and Karapetjan (1961) have found that the relative weights of these extensors in the river otter, sea otter and seals increase in the following order: *Lutra* to *Enhydra* to seals. Their results indicate a change in emphasis from thrusting the whole limb (*Lutra*) to moving the hind foot only (seals). The necessity of actively spreading the foot has also been evaluated by comparing muscle weights of the *Mm. extensor hallucis longus* and *peroneus digiti quinti* (Gambarjan and Karapetjan, 1961). A similar pattern is seen in the foot flexors. Thus, there appears to be both an increased size in the flexors and extensors of the foot paralleling aquatic adaptation in these mammals.

2. Spinal column

During rapid aquatic locomotion, the lumbo-sacral region in *Lutra* and *Enhydra* is moved vertically, paralleling the activity of the tail and hind foot movements, respectively. As one wuold expect, there is increased development of these regions displayed by increased muscle mass of the epaxial musculature (*Mm. multifidus lumborum* and *longissimus*) (Gambarjan and Karapetjan, 1961) and increased height of the neural spines and transverse processes which provide attachment points for these muscles. Whereas, in the phocids, the hypaxial muscle mass (*Mm. quadratus lumborum, longissimus* and *iliocaudalis*) is increased in bulk. This is correlated with the horizontal movements of the caudal regions during swimming. The transverse processes are more elongated and peg-like. The epaxial spinal muscles are less developed than in the former two animals. *Zalophus* has moderately developed epaxial and hypaxial muscles in the lumbo-sacral region as would be expected since this area participates relatively less in active swimming. Paralleling the increased size of the hypaxial muscle mass there is a lateral deflection and broadening of the ilium providing an increased area for the attachment of this mass. The ilium increases its flaring and lateral flexion from *Lutra* to *Zalophus* to *Enhydra* to *Pagophilus* (Table IV). Either the epaxial or hypaxial muscles provide the power stroke in the mammals and their bulk reflects this (Table V). The *M. rectus abdominis* is not extensively developed in any of these mammals as it serves only to bend the hind regions ventrally, as in *Enhydra*, with little or no drive being derived from this action.

The tail muscles (*Mm. sacrococcygeus* and *intertransversarii*) and the vertebral processes of the coccygeal vertebrae decrease in size as the

Table V. Changes in spinal muscles*.(percentage of total spinal muscle weight)

	iliocostalis (a)	epaxial muscles (b)	a+b	*iliopsoas*	*psoas minor*
Lutra	---	---	38.50	0.97	0.61
Enhydra	4.05	36.20	40.25	3.04	1.31
Phoca	16.00	14.70	30.70	---	0.06
Zalophus	5.56	17.80	23.36	0.03	0.20

(*from Gambarjan and Karapetjan, 1961)

Table VI. Ratio of plantar surface area of hind feet to tail surface area for four aquatic mammals.*

	feet area (cm^2) (a)	tail area (cm^2) (b)	a/b
Lutra	40.1	262.5	0.15
Enhydra	212.5	206.3	0.97
Pagophilus	781.3	96.9	8.07
Zalophus	1062.5	68.75	15.45

(*Tarasoff, unpublished data)

tail becomes less important as a locomotory and/or balancing organ. All of the tail muscles found in *Lutra* and *Enhydra* are represented in *Pagophilus* and *Zalophus* although greatly reduced in size in the latter two.

C. Surface area

Lutra swims by a combination of limb and tail movements. Howell (1930) suggested that the tail is the primary source of forward propulsion and the limbs are used mainly for balancing functions. However, *Lutra* has been observed in captivity and in the wild to use its tail for rapid, non-sustained movement and the limbs for routine movement. Compared with the other mammals (*Enhydra* and the pinnipeds),*Lutra* has a much smaller foot to tail surface area ratio (Table VI). Although the limbs of the river otter are proportionately smaller than those of *Enhydra* and promote less speed, they still reflect an increased importance as aquatic locomotory organs in comparison to those of a terrestrial carnivore.

The most common method of locomotion for *Enhydra* is the vertical displacement of the hind limbs, with no function being attributed to the tail or fore limbs (Kenyon, 1969). However, the tail does function as a locomotory and orientation source while the animal floats on its back. As compared to *Lutra*, *Enhydra* has a larger foot/tail surface area ratio. This relative increase in foot area can be related to the increased use of mainly the hind feet and secondary use of the tail during aquatic locomotion. Since the sea otter frequents land much of the time, terrestrial agility is also imperative and the balancing and supporting functions of the tail and limbs are retained.

The tail of pinnipeds is reduced and considered nonfunctional, and the most extensive change is seen in the increased surface area of the hind limbs, as compared to tail surface area. The hind limbs (in the case of phocid seals) have taken over the locomotory function, and in otariids serve as an effective pair of rudders and breaking devices (Howell, 1929).

D. Limb exposure

With increasing adaptation to an aquatic habitat there is a relative decrease in exposed area of the hind limbs compared with terrestrial mammals. Thus, there is a general trend towards an enclosure of the femur and shank within the body proper, contributing to increased streamlining of the body. Disregarding the Cetacea and Sirenia, this trend reaches a peak in the Pinnipedia, in which only the tarsals and pes are exposed.

In *Lutra* (Fig 3a), there is seen the beginning of the incorporation of the limbs within the contours of the body skin. Compared with the dog or cat, the body skin of *Lutra* extends farther down the limb enclosing much of the femur and shank. The enclosure is to such a degree that the limbs can still move through a wide arc during both terrestrial and aquatic locomotion. During movement on land, the limbs must be capable of supporting the body and moving the animal by repeated flexion and extension movements. An increased fixation of the limb would impair these movements.

In *Enhydra* (Fig 3b), there is a further decrease in limb exposure. The femur is enclosed within the body skin, as is most of the shank, thereby obscuring the outline of the limb. However, the limb is still capable of being turned forward when the animal is on land because of the loose body

Figure 3. Outlines of the pelvic limbs and tail of four aquatic mammals,
Figure

illustrating increasing incorporation of the pelvic limbs into the body contour, foot shapes, foot pads, increasing foot size and decreasing tail size.

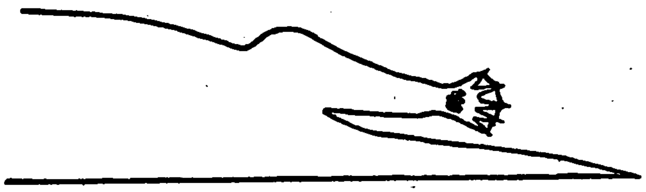
A. *Lutra canadensis*

B. *Enhydra lutris*

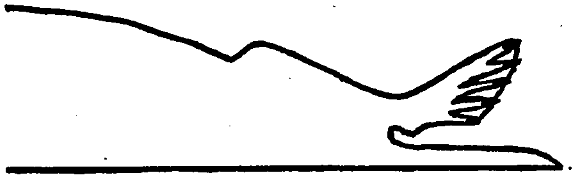
C. *Pagophilus groenlandicus*

D. *Zalophus californianus*

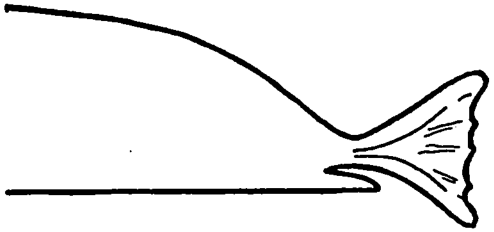
A



B



C



D

skin in this region and the assistance from an arching of the vertebral column. A comparable situation is seen in the Otariidae in which the limbs, except the pes, are enclosed within the body skin. In this case, the limbs can be turned forward, with with the major contribution being due to flexion of the spinal column and tarsal joint.

In Phocidae (Fig 3c), as in the Otariidae (Fig 3d), there is no external appearance of the femur, shank bones and the proximal tarsal bones. A tight skin, plus a thick blubber layer in this region creates a smooth contour. The hind limbs cannot be turned forward due to this tying down by the body skin and also to the differences in the myology (discussed previously).

With the gradual incorporation of the hind limbs within the body contour, there is created one major difficulty that is related to the animal's manouverability on land. As the limb becomes incorporated it also becomes "tied down" to the vertebral column, thereby preventing the limbs from being moved forward through as great an arc as is found in terrestrial carnivores. This decreased movement can be compensated for by having a loose skin in this region, increasing the arching of the back and flexion of the lumbo-sacral region of the vertebral column or by keeping the foot pointing backward.

Lutra appears to have only a slight impairment of movement on land which may be related to an increased incorporation of the limb into the body contour and a shortening of the limb elements. The skin is relatively loose in this region, and the usual carnivore movements of walking, running and bounding are observed. *Enhydra* and the otariid seals are slightly more handicapped on land. There is seen a more rolling type of gait (*Enhydra:* Kenyon, 1969; *Zalophus*: Peterson and Bartholomew, 1967), related to the tying down of the shank, a shortening of the exposed limb elements and the increased surface area of the hind limbs. Running has not been observed for *Enhydra* and otariids, and these groups break into a bounding or hitchinf forward of the caudal regions when rapid movement is necessary. In phocids, the shank bones are closely tied to the body and this contributes to the loss of the ability to turn the foot forward (Howell, 1929 and 1930). During terrestrial locomotion, the hind flippers of hair seals lie passively behind and play no role (Murie, 1870 and O'Gorman, 1963). However, the hind limbs may be used for climbing small prominences (Murie, 1870). Also, *Phoca vitulina* may use the hind limbs for climbing assistance by swinging them from side to side.

A result of the binding down of the shank and its elevation is the creation of a smooth body outline for increased streamlining. The smooth outline has been mentioned in terms of reducing turbulence. It also produces a compact unit to reduce limb movement proximal to the tarsal joint. Thus, there is produced a moveable lever arm (pes) and a stationary lever arm (upper limb) centered on a pivot point (tarsal joint). Because of the number of joints between the individual bones of the hind limbs, many of them have to be secured and rendered capable of only a minimum amount of movement. The securing of the shank in a near fixed position ensures that the maximum effort will come from the hind foot region. Finally, the elevation of the shank assists in rotating the foot to a position in which it can move in the horizontal plane (phocids).

E. Interdigital webs

With an increased use of the hind feet for aquatic propulsion there is seen an increase in length of the digits and in the area of the interdigital webs. These webs usually reach the tips of the digits and are capable of being stretched to increase the surface area contacting the water during propulsion. The foot must also be capable of flexing the web so as to reduce the water resistance when the limb is on its recovery phase.

Lutra, *Enhydra* and the pinnipeds have well-developed interdigital webs on their hind feet, compared with most terrestrial mammals. In *Lutra*, it appears to be less extensive than in the others, with the web terminating before the ends of the digits. In the others, the web extends to the end of each digit or even beyond the bony structures of the foot. The latter is observed especially in the otariids, where the digital length is greatly increased by cartilaginous extensions.

F. Symmetry and thickened areas of the foot

The shape of the foot varies with the species and often directly reflects not only the aquatic locomotory pattern but also the terrestrial manouverability of the animal. Also seen in certain aquatic mammals is a thickening or an increased strengthening of the leading edge of the foot.

In *Lutra*, the digital lengths are 4=3>5=2>1, giving the foot a diamond-shape, with the apices on the fourth digit and the calcaneum (Fig. 3a). There is no evidence of thickened regions at the edges and the foot appears adapted to moving through a cranial-caudal arc in a direction parallel with the long axis of the body. *Enhydra* has a digital sequence of 5>4>3>2>1, with the hind foot shaped like a scalene triangle (Fig. 3b). When the foot is moved vertically with the soles facing dorsally and somewhat caudally, the leading edge of the foot is along the fifth digit. Prevention of spillage over the lateral side of the foot is possibly prevented or reduced by having this edge particularly well-developed and strengthened both by an increase in thickness and a reduction in the area of the web between the fourth and fifth digits. These two digits are united up until the level of the second phalanges, as opposed to the other digits in which the web begins in the metatarsal region. Odobenids and phocids (Murie, 1871) have a hind flipper that is shaped like an isosceles triangle (Fig 3c) with the digital sequence being 1>5>2>4>3. One point not mentioned by those authors who have described the locomotory patterns of seals (phocids) is that of the change in angle of the flippers as the active flipper is moved medially. At the initial stages, the ventral or first digit is leading, pushing water dorsal to the tail. When nearing the midpoint of its arc, the angle of the flipper is changed so that the fifth digit is leading, thereby pushing water ventrally. It can be seen that both edges of the flipper are thickened to provide support against pressure and to assist in preventing spillage over the sides. The hind flipper of otariids are nearly rectangular in outline with the web terminating before the end of the digits (Fig 3d). *Zalophus* has a digital sequence of 5=1>4=3=2. Savage (1957) gives the sequence of *Otaria* as 1>5>2>4=3, while that of *Otaria jubata* is 1>2=3>4=5 (Murie, 1872) and for *Callorhinus* it is 1>2=3=4=5 (Scheffer, 1962). The flippers appear capable of little expansion (Howell, 1929). The digital lengths including the cartilaginous parts are of nearly equal length and there is some evidence of specialized thickening of digits one and five. The foot is also thicker on the proximal plantar surface where most of the contact occurs when these animals are on land. These lateral supports could be related to the fact that the hind feet of otariids play a role during breaking movements and turns, when some rigidity of the foot is necessary. The overall flexibility of the foot compared with phocid seals is perhaps indicative of their observable lack of participation during forward movements in the water.

G. Foot pads

In some terrestrial carnivores there are found plantar, metatarsal and digital foot pads. These pads appear to be an adaptation for terrestrial locomotion as a protective device for preventing abrasions and as a means of attaining more traction. Loss or reduction of the pads of the hind feet of mammals appears to be closely related to increased aquatic adaptation among the Carnivora. As the mammals become more aquatically adapted, the pads no longer have a selective advantage for protection and traction. Another important consideration is that the turbulence created by these pads could disrupt the laminar flow of water during aquatic locomotion. In *Lutra* (Fig 3a) there is loss of the metatarsal pads (Pocock, 1921), whereas in *Enhydra* (Fig 3b) plantar pads are never found and the metatarsal pads are usually absent, while the digital pads are retained (Pocock, 1928 and Kenyon, 1969). The pinnipeds (Fig 3c)and 3d) show no sign of foot pads.

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Part III. The lungs (topography, weights and measurements)

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Introduction

No studies have compared lung features in deep diving mammals with shallow diving forms. The lungs of marine mammals vary considerably in shape and relative weight, and these features appear to be related to swimming and diving facility (Kleinenberg, 1956, cited by Slijper, 1962).

Presented here is a comparative study of the topography and weights and measurements of the lungs of the shallow diving river otter, *Lutra canadensis* and sea otter, *Enhydra lutris*, and the deep diving harp seal, *Pagophilus groenlandicus*.

Materials and Methods

Lung topography, and weights and measurements were examined and recorded in 7 river otters, *Lutra canadensis* (Schreber), 20 sea otters, *Enhydra lutris* Linn. and 13 harp seals, *Pagophilus groenlandicus* Erxleben.

The topography includes the features of the lobes of each lung, the position of the lungs in the thoracic cavity, and the relationships of the lungs to the heart and diaphragm.

Right and left lungs were weighed (gms) without any attempts to exsanguinate them. Combined lung weights were compared to each other and the combined lung weights were expressed in terms of their percentage of the total body weight. Total length (to the nearest millimeter) is from the apex to the base of each lung and maximum width is from the medial border to the tip of the median lobe. All observations, weights, and measurements were made on collapsed lungs.

Terminology in this report follows that of the Nomina Anatomica Veterinaria, Vienna (1968).

Results

Lutra canadensis (Figs 1A and 2A)

In *Lutra* the left lung has two lobes: a cranial lobe and a caudal lobe. The right lung has four lobes: a cranial lobe, a central, medial lobe, a caudal lobe and an accessory lobe. In the thoracic cavity, the apex of the right lobe lies slightly more cranial than that of the left. The apex of the left lung begins cranially between the third and fourth thoracic vertebrae, and has its base at the level of the ninth thoracic vertebra and the diaphragm. The right lung begins cranially in the region of the third thoracic vertebra and extends caudally to the midpoint of the ninth thoracic vertebra. Both lungs decrease in depth from the vertebral to the mediastinal edges. The hilus is located in the central region of each lung on their medial surface.

Left lung a. cranial lobe

The cranial lobe of the left lung is semi-conical in shape. Cranially, it begins as a rounded apex and gradually increases in width dorso-ventrally to end at the cranial end of the hilus. There is also a slight tapering on the mediastinal border near the base. Maximum width is in the central one-half of the lobe. The costal surface is convex, with the vertebral border being the thickest and the lobe narrowing to a thin mediastinal border. Tapering also occurs from the thickened hilus region to the cranial and caudal ends. The medial surface of this lobe is flat cranially and concave caudally, where the latter overlies the apex of the caudal lobe. On the dorso-medial surface is a depression for the thoracic portion of the heart, aorta and oesophagus. Cranially, the aortic

Figure 1. Lateral and medial surfaces of the left lung of *Lutra* (A), *Enhydra* (B)and *Pagophilus* (C).

L.= lateral surface

M = medial surface

a. cranial lobe

b. aortic impression

c. hilus

d. caudal lobe

e. diaphragmatic impression

f. median lobe

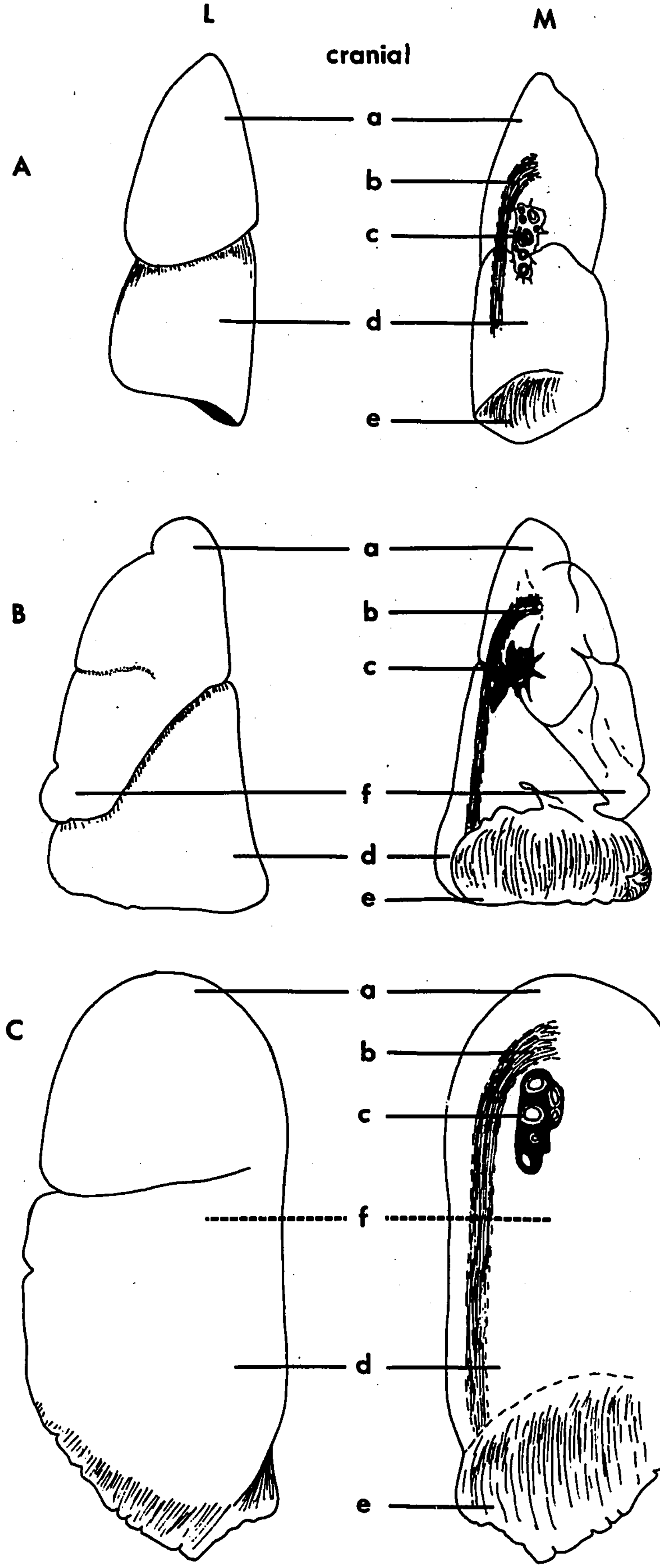
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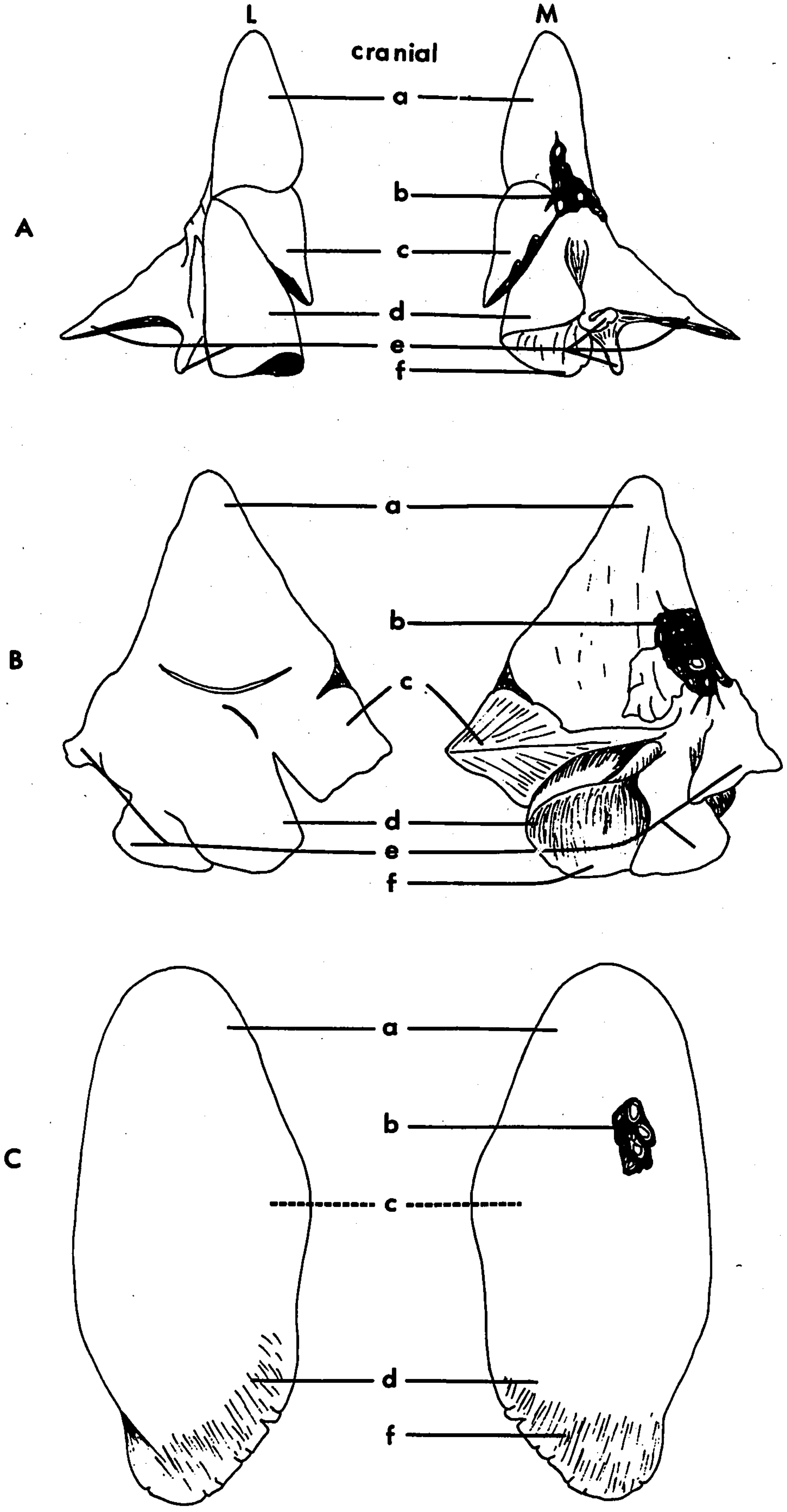
Figure 2. Lateral and medial surfaces of the right lung of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C).

L = lateral surface

M = medial surface

a. cranial lobe
b. hilus
c. median lobe
d. caudal lobe
e. accessory lobe
f. diaphragmatic impression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impression is noticeable over the cranial border of the hilus and marks the position of the aortic arch. The cranial lobe is completely separable from the caudal lobe except where they join at the hilus.

b. caudal lobe

This lobe is oval in outline, with the hilus located at the cranial end of the medial surface, and narrows at the cranial and caudal ends. The lobe is thickest on the vertebral side and tapers to the mediastinal edge. The costal surface is convex and medial surface is concave over most of its cranial area. On the medial surface, the caudal region (one-third) is curved to fit against the diaphragm and the cranial edge of the accessory lobe of the right lung. The cranial two-thirds of this lobe are concave to fit against the heart. On the medial surface, and dorsal to the hilus, is the continuation of the depression marking the region of the thoracic part of the aorta. A serous membrane on the medial edge of the lobe connects this lobe to the oesophagus.

Right lung a. cranial lobe.

This lobe is smaller, but its external characters are identical to the corresponding lobe of the left lung.

b. medial lobe.

This lobe is triangular in outline and located immediately caudal to the cranial lobe, with its main bulk visible on the mediastinal side of the lung. Its cranial border passes from beneath the caudal border of the cranial lobe and extends caudo-ventrally over the cranial one-half of the mediastinal surface of the caudal lobe. The thickest and broadest region of this lobe is at the hilus and decreases toward its tip. Depth decreases from the midline to the cranial and caudal borders, forming two concave areas on the medial surface. The cranio-medial surface is concave to fit against the costal side of the caudal lobe, and the caudo-medial side fits against the right side of the heart. The costal surface of the lobe is flat. This lobe is attached to the rest of the lung only at the hilus region.

c. caudal lobe

The caudal lobe is the largest and most caudal lobe of the right lung. The lobe begins cranially at the hilus as a narrow, but relatively thick apex. It passes caudally and progressively widens to form a broad, concave base, which lies against the diaphragm. The ventro-medial border overlies part of the ventral tip of the accessory lobe. The costal surface is convex, and the medial surface is narrow and concave to fit against the right side of the heart. The lobe is deepest along its dorso-medial edge and becomes thinner in all directions. The medial edge of the mid-dorsal surface is closely bound by connective tissue to the accessory lobe. A thin peritoneum extends from the dorso-medial edge of this lobe to the lateral edge of the oesophagus.

d. accessory lobe.

The accessory lobe is located between the diaphragm and the diaphragmatic surface of the heart. This lobe is irregular in shape and has three arms: one ventral, one dorsal and one medial. The ventral arm is located on the ventro-lateral surface. Its ventral surface narrows laterally while its caudal surface is circular and slightly concave, and fits against the diaphragm. The dorsal arm is characterized by a long, narrow projection that is directed caudally as far as the diaphragmatic edge of the caudal lobe. Its ventral edge is flat and fits against the diaphragm. The medial arm is a long, tapering projection that is concave on its ventral side and convex dorsally. It is triangular in cross-section with each side being slightly concave. It encircles the apex of the heart and lies between the apex and the diaphragm. The accessory lobe is located medially to the caudal lobe, close to the midline of the body. Its cranial origin at the hilus is continuous with that of the caudal lobe. The lobe has a narrow origin at the hilus, but increases rapidly in width and depth. Cranially, the dorsal surface is flat, but becomes convex where the medial arm begins. The mediastinal surface is concave over much of its area, and fits against the apex of the heart. Along the costal edge, passing between the dorsal and ventral arms, is a groove for the thoracic portion of the inferior vena cava.

Enhydra lutris (Figs 1B and 2B)

In *Enhydra* the lungs are similar to those of *Lutra*. Both lungs have a narrow apex and a broad, slightly concave base that lies against the diaphragm. As in *Lutra*, the lungs are asymmetrical with respect to lobulation, with the left lung having cranial and caudal lobes, and the right lung having cranial, medial, caudal and accessory lobes. The lobulation of the lungs is distinct, and each separation can be clearly defined. The right lung is larger than the left, with both beginning cranially at the level of the first thoracic vertebra and extending caudally to the twelfth or thirteenth thoracic vertebra.

Left lung a. cranial lobe.

This lobe is oblong-shaped and extends from T_1 to T_{10}, with maximum width occuring on the costal side at its point of junction with the caudal lobe. The apex, diaphragmatic and mediastinal borders are relatively thin, with increasing thickness occurring towards the center of the lobe and its vertebral margin. The vertebral edge increases in thickness from the apex to the hilus. This lobe is convex on its costal surface and slightly slightly concave on its medial surface, where the latter fits around the heart, and its associated vessels, and the oesophagus. The outline is not as smooth as that of *Lutra*, with ridges and indentations occurring on its mediastinal margin and medial face. On the mediastinal margin, a small notch divides the cranial tip from the caudal portion. This notch extends more deeply on the medial surface than on the costal surface. The caudal half of the lobe is incompletely divided from the cranial half by a shallow groove on the medial surface. As in *Lutra*, there are impressions on the dorso-medial surface which indicate the heart, aorta and oesophagus.

b. caudal lobe

This lobe is semiconical in shape with apex at the hilus, with a concave, broad base just cranial and parallel to the diaphragm. It is located caudal and ventral to the cranial lobe and extends between T_5 and T_{12} and is about the same size as the cranial lobe. Unlike the cranial lobe, the central and peripheral areas are thick, with a thinner region located along the caudal one-half of the vertebral border. The costal surface is convex, while the medial face is concave.

Right lung a. cranial lobe.

This lobe is semiconcial, with the apex directed cranially. From the apex, the lobe increases in width and thickness, to reach a maximum in the hilus region. It has a thick vertebral border; tapering, thin mediastinal and caudal borders, and in this regard is similar to the cranial lobe of the left lung. Along its caudal border, it is not completely separable from the hilus, as is the case in *Lutra*. The base of its ventral margin is indented and bound by serous membrane to the cranial border of the medial lobe. This indentation closes, and the caudal border of the lobe has a shallow groove on its costal surface which ends just prior to the vertebral margin of the lung. As in *Lutra*, the cranial lobe is convex on its costal surface and concave medially.

b. medial lobe.

The medial lobe is located on the ventral side of the right lung and is closely bound on its cranio-ventral side to the caudal margin of the cranial lobe, and is somewhat freer along its caudal margin. Its costal face is convex and square-shaped, whereas its medial face is concave and triangular. The cranio-medial surface is concave and overlies the right side of the heart, and also concave on its caudal side where it fits over the cranio-lateral side of the caudal lobe. This lobe is a less distinct entity, is not as large in relation to the other lobes, and is directed more laterally and less caudally than in *Lutra*.

c. caudal lobe.

This lobe is the largest and most caudal lobe of the right lung. It is immediately caudal to the medial lobe and, although it fuses with the medial lobe near the hilus, it is not united to it by a membrane. Its costal surface is convex laterally and concave medially, where the latter surface faces the diaphragm. It is very thick in its central regions and becomes thinner along its diaphragmatic, mediastinal and cranio-medial borders.

d. accessory lobe.

The accessory lobe has two divisions: one ventral and one dorsal. These divisions are most easily distinguishable on the medial surface of the lng lung. The ventral division has its cranio-lateral regions closely bound to the rest of the lobe as far cranial as the hilus, and is free on its ventral, dorsal and caudal borders on the medial surface. The division of the accessory lobe starts cranially at the hilus and becomes broader, but thinner, caudally. The lateral surface of the dorsal division of the accessory lobe is closely bound to the caudal lobe, and has its main bulk on the medial surface of the caudal lobe. This latter surface is clearly defined on the mediastinal, vertebral and diaphragmatic edges. It starts from the hilus and increases in width caudally and has thinner edges. This lobe lies between the apex of the heart and the diaphragm and has a groove between the arms for passage of the inferior vena cava.

In *Enhydra*, there is a less clearly defined dorso-lateral separation of the caudal lobe from the accessory lobe than in *Lutra*. The accessory lobe lacks a medial projection, and is more compact (with its ventral portion larger and the dorsal portion larger and shorter) than in *Lutra*.

Pagophilus groenlandicus (Figs 1C and 2C)

In *Pagophilus*, the lungs are oval-shaped and each is imperfectly divided into three lobes. In a cranial to caudal direction, the lobes are: cranial, medial and caudal. Both lungs start cranially at the level of T_3 and extend caudally to T_{12}, with the left lung being slightly longer than the right. The lungs are longer than they are wide. Maximum depth is in the hilus region and along the vertebral border. Maximum width is in the midline with narrowing toward the cranial and caudal extremities. The costal surface is convex, while the medial surface is for the most part flat, with the caudal extremity slightly concave to fit against the heart and diaphragm. The hilus is in the cranial half of each lung, unlike in *Lutra* and *Enhydra*, where it is more towards the center. The left lung has a depression on its medial surface for the aorta and oesophagus.

a. cranial lobe.

The cranial lobe of the right lung is not marked off from the rest of the lung by a constriction. The line of demarcation is apparent on the left lung where it extends nearly to the hilus on the costal surface. There is no indication of such a division on the thicker vertebral border of the left lung.

b. medial lobe.

Based on the surface topography of each lung, the medial lobe is not easily distinguishable, contrary to that in the right lungs of *Lutra* and *Enhydra*. However, based on bronchiograms, there is a separate lobar bronchus that supplies the central regions of each lung that warrants the classification of a medial lobe. This lobe is located immediately caudal to the cranial lobe in the central region of each lung, and at the region of maximum width. As in the other regions, it is deep in the vertebral areas and narrows to the mediastinal border.

c. caudal lobe.

In *Pagophilus*, this lobe makes up the caudal one-half of each lung. Starting from the wide and deep cranial regions, it tapers gradually along the mediastinal border, and more abruptly dorsally, to end in a thin, narrow base. Unlike *Lutra* and *Enhydra*, an accessory lobe is not distinguishable topographically, and no portion of the lung comes between the diaphragm and the apex of the heart. As in *Lutra* and *Enhydra*. the medial edge of the caudal lobe is loosely bound to the oesophagus by a thin, serous membrane.

Comparison of total lung weight and body weight (grams/100 grams of body weight) are summarized in Table I. The mean lung weights in *Lutra* and *Pagophilus* are 1.39 and 1.31, respectively, whereas in *Enhydra*, this value is 3.86. In *Lutra* and *Enhydra* the right lung is always the largest and heaviest, while in *Pagophilus*, the left lung has the larger dimensions. The percentage difference in weight between the right and left lungs is greater in *Lutra* and *Enhydra* (19.3% and 9.8%, respectively) than in *Pagophilus* (6.4%).

Table I. Lung weights and body weights in *Lutra*, *Enhydra* and *Pagophilus*.

		lung weight (a) (gms)	body weight (b) (Kg)	o/oof body weight (a/b x 100)
Lutra	$\overline{X}$	85.3	6.5	1.4
	R	66.6-115.4	4.8-7.4	1.04-2.3
	N = 7			
Enhydra	$\overline{X}$	716.1	18.3	3.9
	R	201.0-1400.0	5.5-34.2	2.44-6.9
	N = 20			
Pagophilus	$\overline{X}$	1133.3	86.6	1.3
	R	772.0-1948.3	70.5-113.3	0.9-1.6
	N = 13			

Discussion

In general, the lungs of each species have topographic characteristics corresponding to the shape of the thoracic cage. In the river otter, the thoracic cage is round in cross-section, and conical, widening from the cranial extremity to a broader caudal region. The lungs of the river otter are also long and tapering, beginning with a narrow apex (cranial lobe) and terminating in a broad base (caudal lobe). The sea otter has a relatively long, oval-shaped thoracic cage that is somewhat dorsoventrally flattened. As in the river otter, the thorax and lungs are narrow cranially and broader caudally. However, the lungs of the sea otter are somewhat broader and thicker than in the river otter. The harp seal has a round thorax, the circumference of which varies less from ribs 14 to 14 than in the other two species. The lungs correspond closely to this shape, being long and relatively uniformly broad throughout their length, and tapering slightly near the apex and base. A similar feature is found in cetaceans.

All the species have the maximum tissue depth on the vertebral and costal areas, with the harp seal having a greater bulk of tissue positioned toward the vertebral area than in the otters. Slijper (1956, 1962) interprets this distribution of tissue and similarity of the lungs in seals and cetaceans as being of major importance for symmetry and stability of the animals when immersed in water. He points out that the high, light lungs and lower heart and liver increases the animal's stability in the water. Also, the position and morphology of the lungs in hair seals and cetaceans, plus their sloping diaphragm, might serve as an adaptation for lung collapse during diving. As the bulk of the lung tissue lies proximal to the osseous portion of the ribs, the increased thoracic pressure during a dive would tend to force the whole of the lungs against this solid wall and facilitate a more total collapse. A further adaptation of the lungs in the harp seal may be in the more cranially positioned hilus region which would reduce the size of the extra-pulmonary airspace.

Lobulation of the lungs of the river otter has been noted by Owen (1868). The lungs of the sea otter have been described briefly by Home and Menzies (1796), in which they mention the left lung has two lobes and the right has three lobes plus a smaller lobe passing between the pericardium and diaphragm. The lungs of the harp seal have been described briefly by Murie (1870) and he noted the lack of lobes in the right lung and partial separation of the left lung into tow lobes. In other pinnipeds, the lungs have been described for otariids: *Arctocephalus hookeri* (Beddard, 1890), *Zalophus californianus* (Forbes, 1882) and *Otaria jubata* (Murie, 1874), for phocid seals: *Phoca vitulina* (Owen, 1831) and *Halichoerus grypus* (Hepburn, 1896), and the walrus: *Odobenus rosmarus* (Daubenton, 1765; Owen, 1853, Murie, 1871). Recently, the lungs of six North Pacific pinnipeds have been described by Sokolov, et al. (1971). These include the sea lion (*Eumetopias jubata*), the walrus (*Odobenus rosmarus*), the bearded seal (*Erignathus barbatus*), the common seal (*Phoca vitulina*), the ribbon seal (*Histriophoca fasciata*) and the ringed seal (*Pusa hispida*). From the data presented by Sokolov, et al., the lungs of otters, otariids, the walrus, bearded and ringed seals resemble those of terrestrial carnivores with respect to lobulation, whereas in the harp, common and ribbon seals, the lungs have less distinct lobulations and are relatively similar to each other.

The observations of this report indicate that there is a less distinct lobulation of the lungs in marine mammals compared with a terrestrial mammal, such as the dog. This trend increases from dog to river otter to sea otter to harp seal. The dog has a medial lobe on the left lung, and the caudal and medial arms of the accessory lobe of the right lung are narrow and elongated (Miller, et al., 1964). In the river otter and sea otter, there is no medial lobe of the left lung, and this lobe cannot be distinguished topographically in the harp seal. The accessory lobe in the river otter has reduced caudal and cranial arms and an enlarged medial arm. The sea otter has a short, but expanded accessory lobe. The lungs of the harp seal are very compact and similar to each other in shape and weight; having a mean weight difference of about 7%, compared with 20% and 10% in the river otter and sea otter, respectively.

The reason for a reduction in lobulation of the lungs in many marine mammals is unknown. Cetaceans may exchange up to 80 to 90% of their lung capacity with each breath (Irving, et al., 1941), while this value is from 10 to 15% for terrestrial mammals. Slijper (1962) has suggested that decreased lobulation of the lungs may be related to efficiency and rapidity of gaseous exchange, with the less-lobulated lungs possibly acting more uniformly and changing shape less than in terrestrial mammals. Other interpretations are perhaps equally plausible. For example, there seems to be a relationship between the agility of a marine mammal on land and lobulation. The lungs of those cetaceans studied are all unlobed, except for a thin, membranous lobe found in some species, and as mentioned earlier, the lungs of many seals are indistinctly lobed. In contrast, the otariids are quite agile on land, spend much time there and have a marked lobulation of the lungs. It could be that lobulation is necessary for additional support to and/or distributing the weight of the lungs. Jolts and jars are common in terrestrial mammals whereas a mammal in water is essentially weightless and the stresses of sudden "g" forces are absent.

Summary

1. The lungs of the river otter and sea otter are semi-conical shaped, being narrowest cranially and broadening caudally. The lungs of the sea otter are broader overall than in the river otter. The lungs of the harp seal are oblong-shaped and more medio-laterally flattened than in the otters, and taper slightly in width cranially and caudally. The topography of the lungs corresponds closely to the shape of the thoracic cage of each species.

2. There is a trend toward a reduced lobulation of the lungs from the river otter to sea otter to harp seal. The lungs of the river otter and sea otter are asymmetrical with the left having cranial and caudal lobes. The and the right composed of cranial, medial, caudal and accessory lobes. The lungs of the harp seal are symmetrical, with divisions not apparent in the right lung, and a shallow, incomplete division of the left lung into cranial and caudal lobes.

3. Lung tissue depth is maximum in the dorsal and lateral regions in each species, with the sea otter having the greater depth laterally and the harp seal having a proportionally greater amount of tissue dorsally.

4. The hilus region is located more cranially in the harp seal than in the otters.

5. The mean ratio of lung weight/100 grams of body weight is 1.39 in the river otter, 3.86 in the sea otter and 1.31 in the harp seal. In the river otter, the mean percentage difference between the right and left lungs is 19.3% and in the sea otter 9.8%, with the right lung being the larger. In the harp seal the difference is 6.4%, with the left lung being

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Acknowledgments

I wish to express my appreciation to the following people for specimens and assistance during the preparation of this report: Mr. Karl Schneider (Alaska Fish and Game Department); Mr. Ian Smith and Mr. Denis Wilder (B.C. Fish and Game Department); Dr. Charles Guiguet (B.C. Provincial Museum, Victoria, B.C.); Dr. J.C. Holmes and Mr. T. Neraasen (Department of Zoology, University of Alberta); and Mr. W. Hoek and Mr. G. Slenoss (Fisheries Research Board of Canada).

The research was financed by Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Reaearch Board of Canada and McGill University.

Parts of the final draft of this report were written in consultation with Dr. G.L. Kooyman (Scripps Institution of Oceanography, La Jolla, California.

Part IV. The trachea and bronchial tree

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Introduction

Some seals and whales dive to depths of several hundred meters (Kooyman and Andersen, 1969) at which time the body experiences a tremendous compression. Furthermore, in some whales particularly, tidal volume may represent nearly 90% of total lung volume and the expiratory-inspiratory manouver occurs in a very short time when they surface briefly and dive (Olsen, et al. 1969). These unusual diving and varied breathing patterns of aquatic mammals suggest that there may be marked differences in the structure of the respiratory system.

As an air conducting system, the trachea and bronchial tree have a direct effect on lung ventilation. For diving mammals, important considerations of these conducting tubes are their length-width relationships, and degrees of support, compressibility and flexibility. However, detailed descriptions of both the trachea and bronchial tree in any diving mammal are either incomplete or lacking.

My purpose is to describe the trachea and bronchial trees of three diving mammals: the river otter, *Lutra canadensis*, the sea otter, *Enhydra lutris* and the harp seal, *Pagophilus groenlandicus*. The rationale for selecting these three species was to compare animals that have specialized in varying degrees to an aquatic habit. The habits of the species range from a shallow, fresh water diver to an open ocean, deep water diver. Structural differences of the respiratory system that may be related to diving ability are discussed.

Materials and Methods

The trachea and bronchi were examined in 9 river otters, 16 sea otters and 9 harp seals. River otter and harp seal specimens were obtained from animals killed for commercial purposes, and the sea otters were casualties from the 1970 sea otter transplant from Alaska to British Columbia.

Measurements of the excised trachea include total length,(from the base of the cricoid cartilage to the bifurcation), internal diameter at the top, middle and base of the trachea, number of cartilaginous rings and fused rings, and width of the rings on the ventral surface at 5, 10, 20 and 30mm and base of the trachea. Attention was also given to the extent of the trachealis muscle, the fibroelastic tracheal ligaments, and the lamina propia.

The bronchi in both lungs of formalin-fixed specimens of each species were dissected and the nature of branching, supporting structures and distribution were noted in the various lobes of each lung. The trachea and bronchi of a representative of each species were inflated with air, injected with a suspension of barium sulfate in water, and X-rayed to reveal their relative size and branching patterns.

Terminology in this report follows that of the Nomina Anatomica Veterinaria, Vienna (1968).

Results

Trachea

a. *Lutra canadensis*

The trachea of *Lutra* extends from the base of the cricoid cartilage (C_2) to the level of the fourth thoracic vertebra (T_4), where it bifurcates into two stem bronchi (Fig 1A). A tracheal carina is present at the point of bifurcation. The mean tracheal length is 15.3 cm or 23.2% of the body length (total length minus tail length) (Table I). The trachea is relatively narrow compared with its length, varying from 0.9 to 1.3 cm (Table I). The width is relatively uniform throughout. The circular, partially calcified tracheal rings (Fig 2A) extend throughout the length of the trachea. They vary in width from 1.0 to 2.5 mm. (mean = 1.4mm) (Table I). Their numbers are from 62 to 80 (mean = 71.3), with fusion occurring in from 3 to 12 of the rings (mean = 6.3). The rings are oval in cross-section, being wider than deep (Fig 3A). Maximum thickness is in the mid-ventral line with the arms of the rings tapering in thickness toward the dorsal surface. The arms increase in width dorsally and terminate in an blunt, rounded, spatula-shape. These expanded regions overlap (cranially to caudally) throughout the length of the trachea (Figs 1A and 3A). The rings are incomplete dorsally and the gap varies from 0.1 to 0.5 cm (Table I). This gap increases in width from the top to the base of the trachea. The rings are bound together by fibro-elastic tissue. The trachealis muscle is present on the dorsal surface and extends ventro-laterally to insert on the arms of the rings (Fig 4-1). The muscle fibers are oriented mainly in a transverse direction. The lining of the trachea has a smooth inner surface separated uniformly from the tracheal rings by a thin lamina propia.

Figure 1. Trachea of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C). (X 1/2)

a. ventral surface

b. dorsal surface

c. cartilaginous rings

d. cartilaginous plates

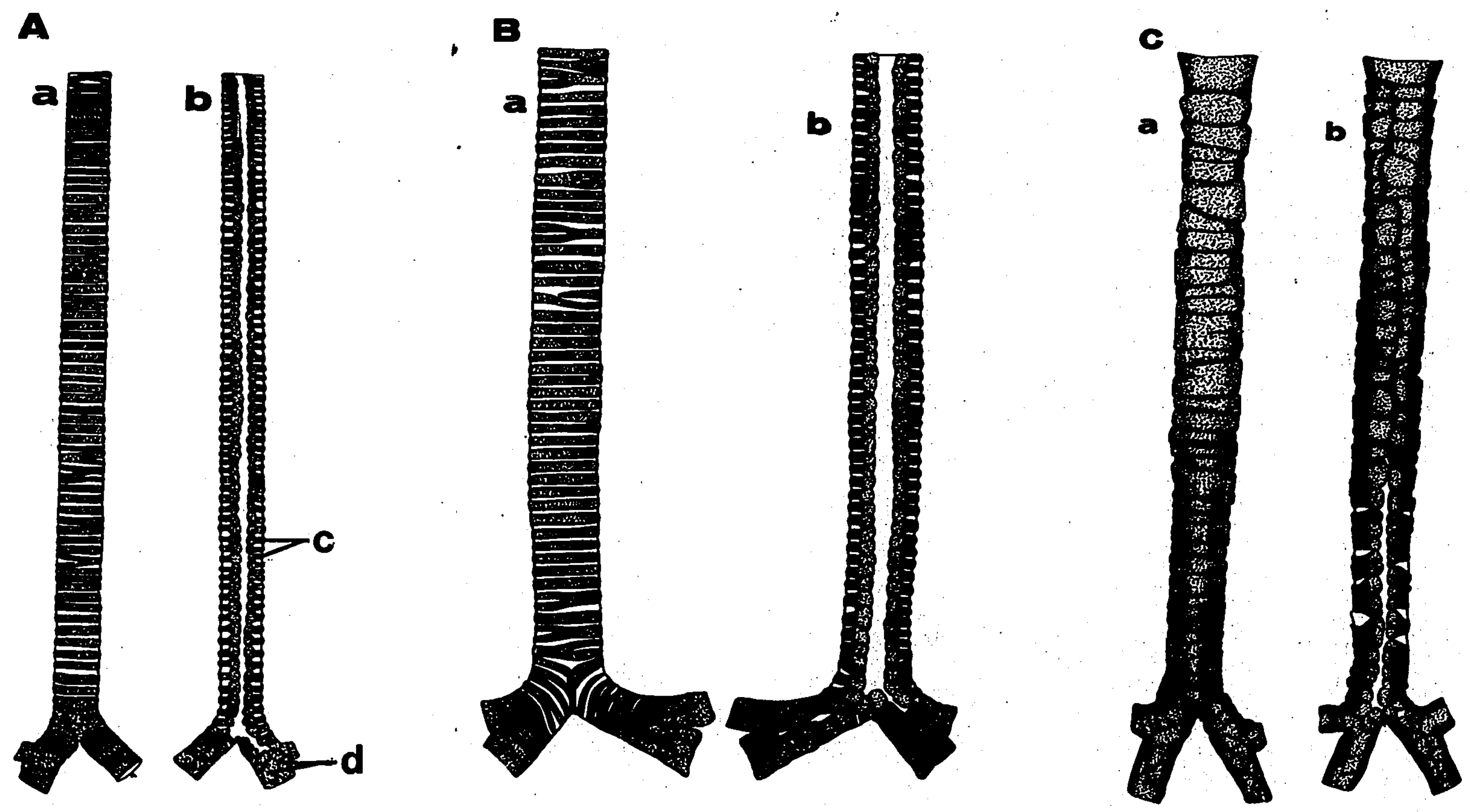
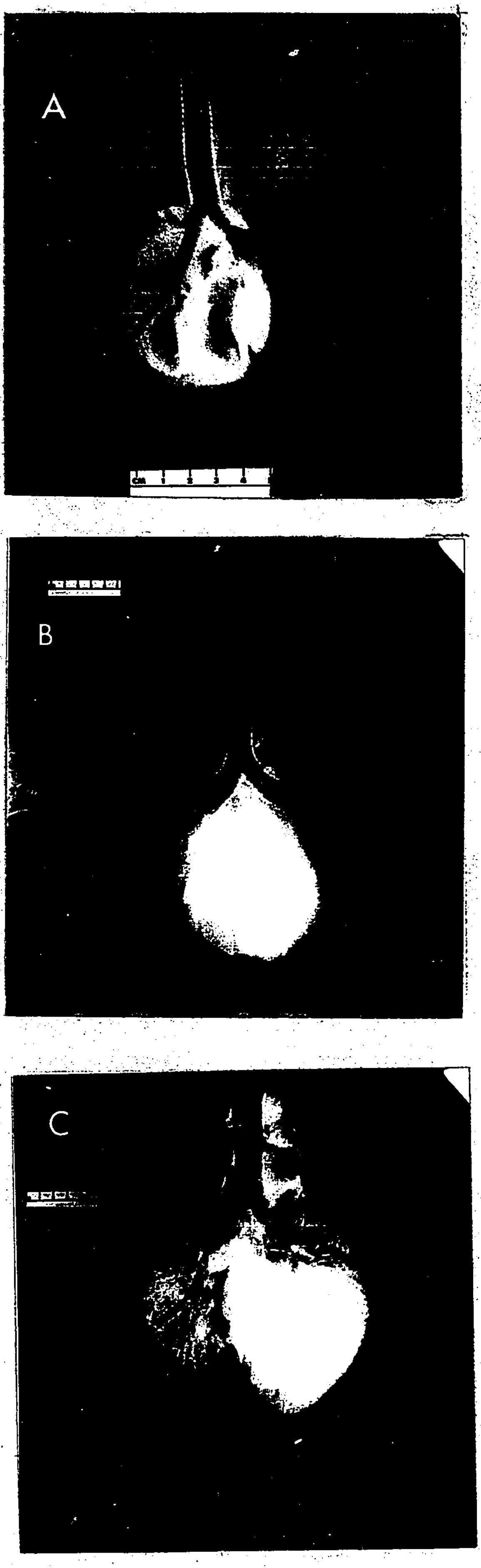

A
a
b
c
d
B
a
b
C
a
b

Figure 2. Roentgenograms of inflated trachea and bronchial tree, illustrating calcified tracheal rings and principal bronchi in *Lutra* (A) and *Enhydra* (B), and non-calcified tracheal rings and principal bronchi in *Pagophilus* (C).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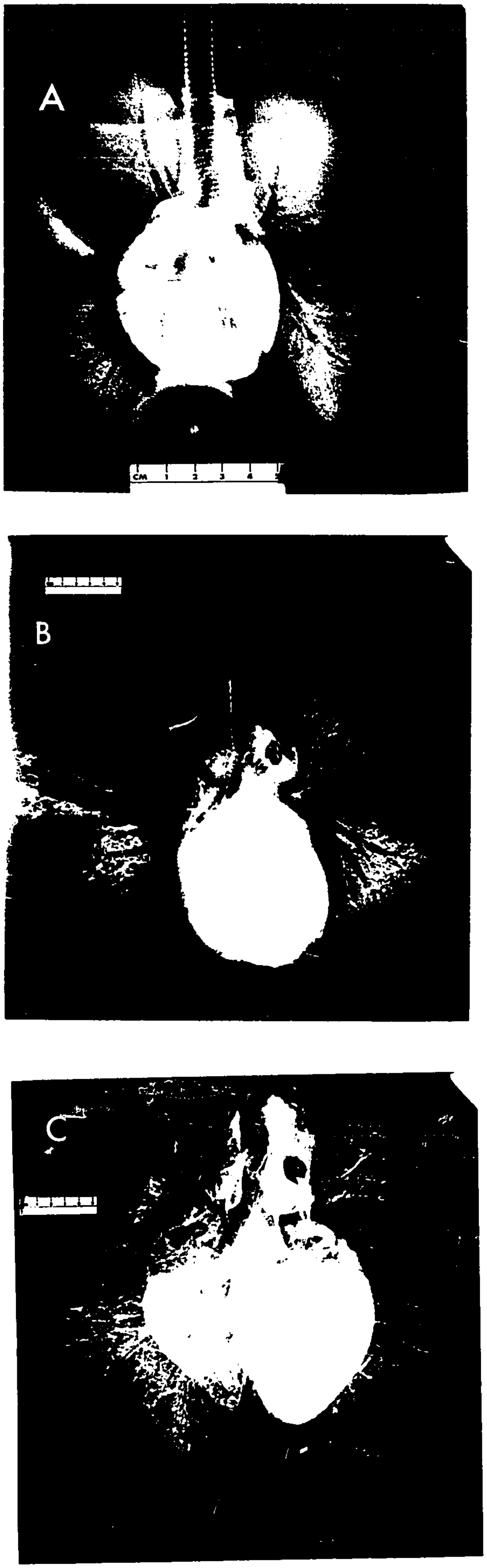
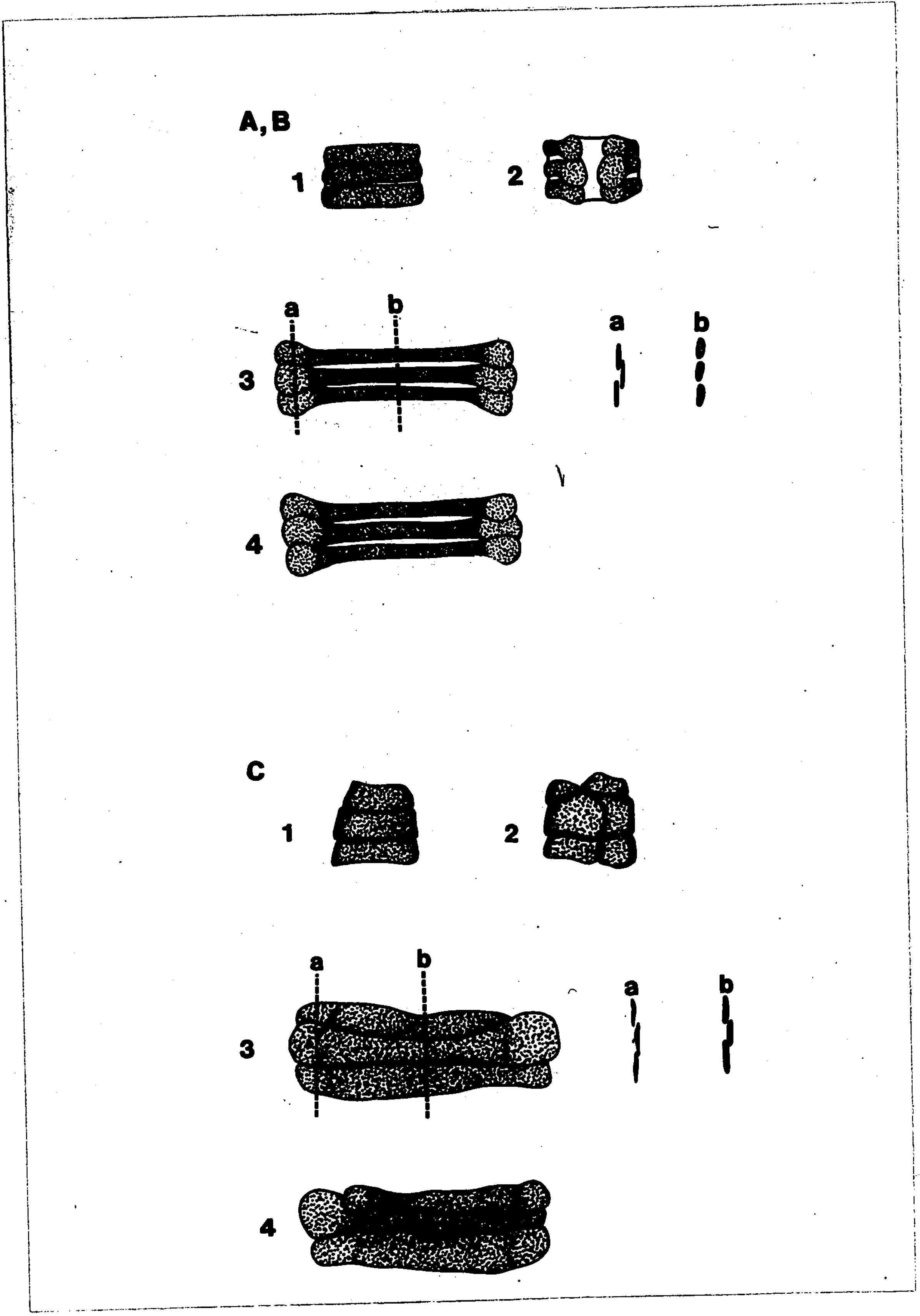

A
CM 1 2 3 4 5
B
C

Figure 3. Tracheal cartilages (cranial) of *Lutra* and *Enhydra* (A,B) and *Pagophilus* (C).

a and b = cross sections

1. ventral surface
2. dorsal surface
3. rings opened (exterior)
4. rings opened (interior)


A, B
1
2
a
b
3
a
b
4
C
1
2
a
b
3
a
b
4

The oesophagus passes to the left of the distal two-thirds of the trachea.

b. *Enhydra lutris*

In *Enhydra*, the trachea extends from the base of the larynx (C_3) to the level of the fifth or sixth thoracic vertebra (T_5-T_6), where it bifurcates into two stem bronchi (Fig 1B). A tracheal carina is present at the point of bifurcation. The mean tracheal length is 17.8 cm or 19.0% of the body length (Table I). Relative to its length, the trachea is somewhat wider than in *Lutra*. It varies from 1.2 to 2.3 cm (Table I), and in each specimen, the diameter is approximately uniform throughout. Circular, cartilaginous rings, with some calcification, extend throughout its length (Fig 2B). These rings are wider than in *Lutra* and vary in numbers from 45 to 54 (mean = 47.9) (Table I). Fusion of the rings occurs in from 0 to 8 rings (mean = 2.8). The rings are of maximum thickness in the mid-ventral line, and gradually decrease in thickness and increase in width dorsally, and are morphologically similar to those of *Lutra*.(Fig 3A). A gap between the arms appears on the dorsal surface and varies from 0.1 to 0.5 cm at the base (Table I). The annular ligaments of the trachea, the trachealis muscle, and the lamina propia are similar to *Lutra* (Fig 4-1).

c. *Pagophilus groenlandicus*

The trachea of *Pagophilus* extends from the third cervical (C_3) to the fifth thoracic (T_5) vertebra, where it bifurcates into two stem bronchi (Fig 1C). A morphologically distinct tracheal carina is present at the point of bifurcation. The mean tracheal length is 24.7 cm or 17.6% of the body length (Table I). The relationship between width and length is similar to that of *Enhydra* (Table I), with the width decreasing slightly

Table I. Measurements of the trachea and tracheal rings of 9 *Lutra*, 16 *Enhydra*, and 9 *Pagophilus*.

Tracheal length (cm)	o/o of body length[1]	Tracheal width (cm)	Width of gap[2] (cm)	Number of rings	Ring widths (mm)
		Lutra canadensis			
$\bar{X}$ 15.3	23.2	1.1	0.32	71.3	1.4
R 13.1-18.0	20.0-29.5	0.9-1.3	0.1-0.5	62-80	1.0-2.5
		Enhydra lutris			
$\bar{X}$ 17.8	19.0	1.9	0.42Cephalad to 0.72 caudad	47.9	3.3
R 12.4-22.1	15.8-24.0	1.2-2.3	(0.2-0.7) + (0.4-1.3)	45-54	2.0-6.5
		Pagophilus groenlandicus			
$\bar{X}$ 24.7	17.6	2.5	0 cephalad to 0.9 caudad	42.6	6.0
R 22.1-25.9	16.3-20.2	2.0-2.9		40-49	3.0-14.0

1. Body length is less the tail

2. Width of gap is the dorsal separation between the two arms of the incomplete cartilaginous rings.

Figure 4. Cross-section of the trachea of *Lutra* and *Enhydra* (1) and *Pagophilus* (2a = cranial, 2b = caudal).

a. trachealis muscle

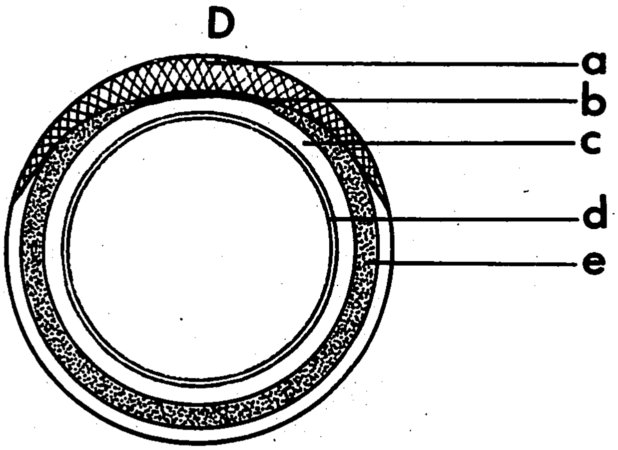
b. fibroelastic tissue

c. lamina propia

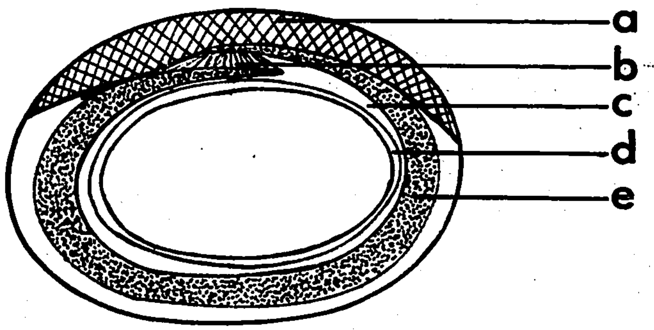
d. epithelium

e. tracheal ring

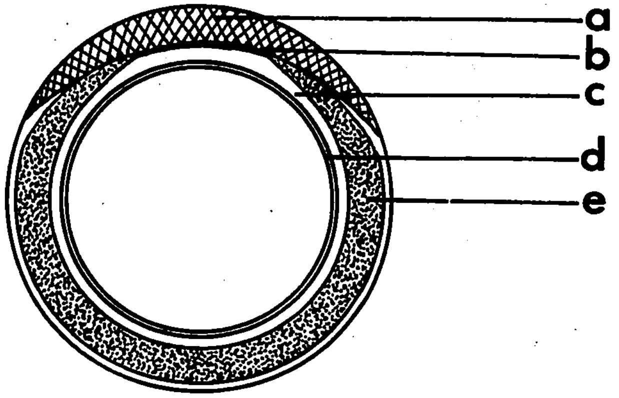
1



2a



2b



near the base (Fig 1C). The tracheal rings vary in number from 40 to 49 (mean = 42.6), are wider than those of *Lutra* and *Enhydra*, and overlap each other so that the uniform pattern seen in the other two species is lost. There is some fusion of tracheal rings, with an average of 4.8 rings having fused. The tracheal rings are cartilaginous throughout and evidence of calcification is not apparent from the roentgenograms (Fig 2C). The rings have their greatest depth midventrally and gradually taper dorsally (Fig 3B). The rings give the trachea an oval-shape cranially and a circular-shape caudally (Fig 4-2a, 2b). They are incomplete dorsally, and the arms overlap in the cranial two-thirds of the trachea and are bound together by fibroelastic tissue, whereas in the caudal one-third, there is a gap varying from 0.3 to 0.5 cm (Table I and Fig 1C). The width of the arms increase slightly on the dorsal surface, but not as regularly or abruptly as in *Lutra* and *Enhydra* (Fig 1C). The expanded portions overlap in the longitudinal plane. Overlapping of the rings also occurs on the ventral and lateral surfaces. Unlike *Lutra* and *Enhydra*, where the ligaments of the trachea extend from the caudal edge of one ring to the cranial edge of the adjacent ring, these ligaments in *Pagophilus* vary according to the overlapping of the rings. The mid-ventral regions usually are bound by the ligaments similar to those of the other two species, whereas, the lateral surfaces usually overlap. In these latter instances, the ligaments extend from the undersurface of the overlapping cartilage and insert on the cranial edge of the underlying ring. The trachealis muscle is well-developed and of uniform thickness (Fig 4-2a, 2b). The lamina propia is thicker in *Pagophilus* than in the other species.

Bronchial patterns

a. *Lutra canadensis*

The bronchial pattern in *Lutra* is shown in Figure 5A. Outside of the lung tissue the trachea bifurcates into two principal bronchi. These in turn divide to form four lobar bronchi on the right and two on the left. These bronchi correspond to the lobes of the lungs. On the right they are the cranial, medial, caudal and accessory lobar bronchi. The left is made up of cranial and caudal bronchi. The lobar bronchi in turn branch into segmental bronchi which leave the lobar bronchi at an angle of about 45 degrees and extend to the periphery of the lung tissue. Along their extent they in turn give off subsegmental bronchioles which in turn lead to respiratory bronchioles.

The lobar bronchi to the cranial lobe of each lung pass cranially on the medial sides of these lobes. These two bronchi have an equal number of segmental bronchi that branch in a similar, somewhat pennate fashion that extends cranially and tapers corresponding to the morphology of the lobes. The largest and longest segmental bronchi extends laterally in the cranial lobes. The other branches of the principal bronchi correspond to the lobes of the lungs on each side. The left lung has one lobar bronchus supplying the caudal lobe. This bronchus lies on the medial side of the lobe and has the longest and largest segmental bronchi positioned laterally. The base of the right lung has three lobes and each is supplied by a lobar bronchus. The lobar bronchus to the medial lobe is slightly smaller in diameter than the bronchi to the cranial lobes. This bronchus extends laterally in the middle of the medial lobe, and cranial and caudal segmental bronchi are of about equal lengths and diameters. Caudally, the principal bronchus divides into a larger lateral bronchus to the caudal lobe and a smaller, medially

Figure 5. Bronchiograms of *Lutra* (A), *Enhydra* (B) and *Pagophilus* (C), illustrating the bronchial pattern in the lobes of the lungs and the major subdivisions of the bronchial tree.

(Right lung: 1. cranial lobe; 2. medial lobe; 3. caudal lobe; 4. accessory lobe)

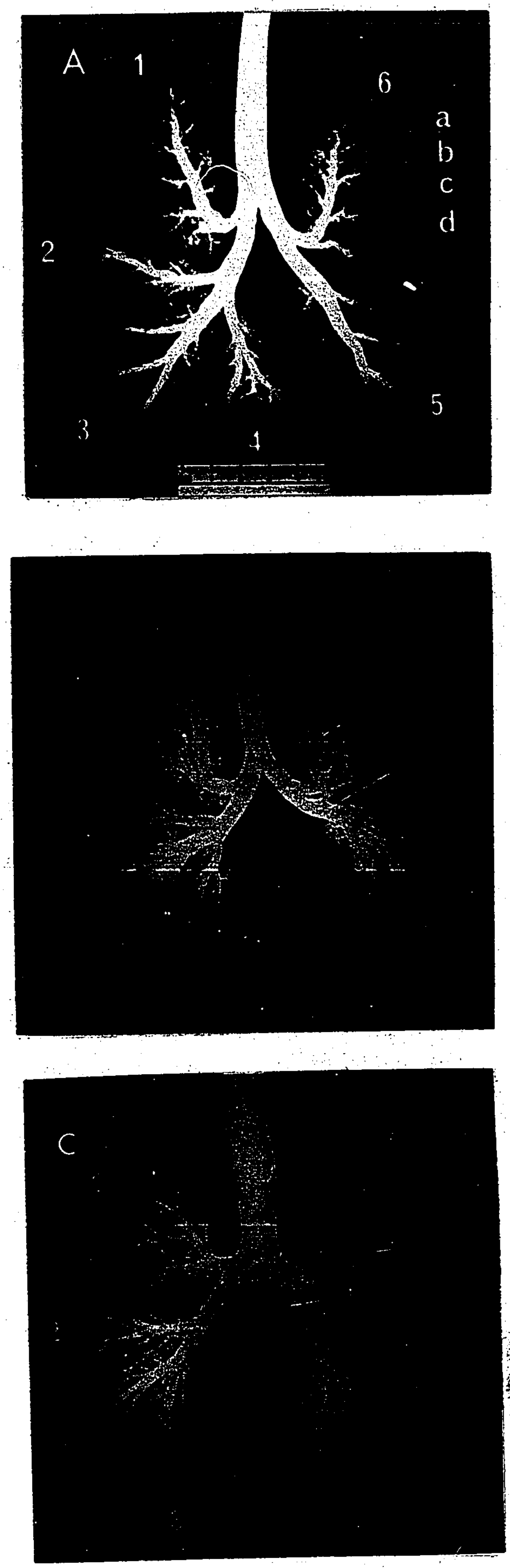
(Left lung: 5. caudal lobe; 6. cranial lobe; 7. medial lobe)

a. lobar bronchus

b. segmental bronchus

c. subsegmental bronchus

d. principal bronchus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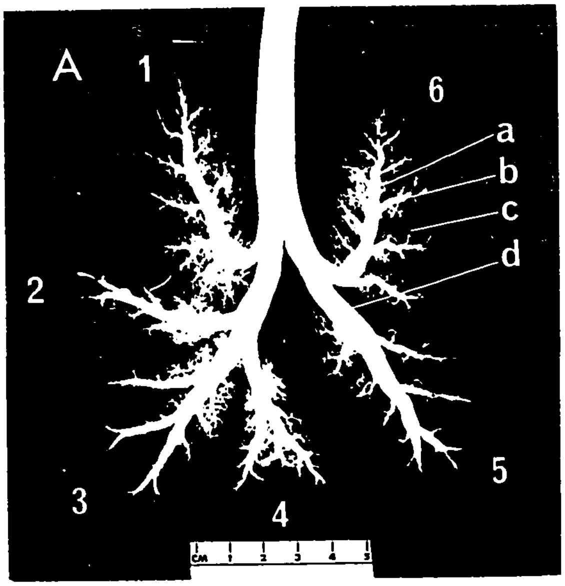
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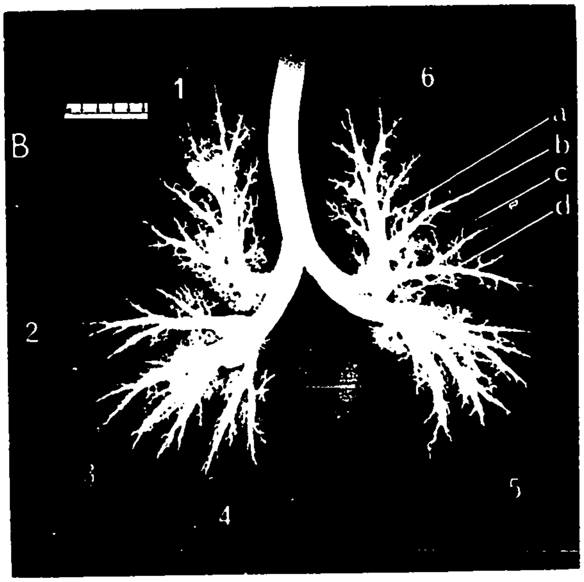
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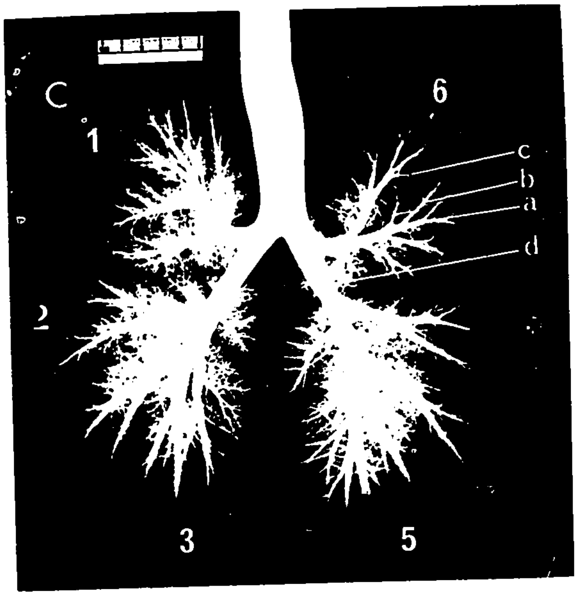
C
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a
d
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3
5

positioned bronchus to the accessory lobe. The caudal bronchus to the right lung is morphologically identical to that of the left caudal lobe. The lobar bronchus to the accessory lobe passes caudally and bifurcates into two segmental branches which pass to the lateral and medial sides of this lobe.

b. *Enhydra lutris*

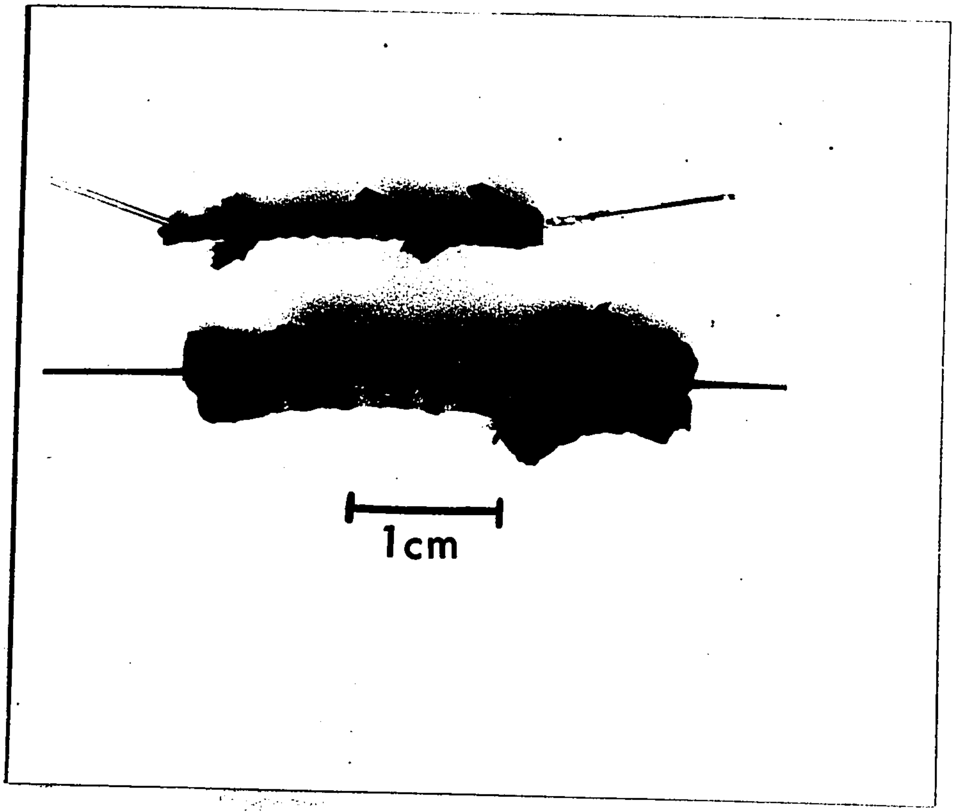
In *Enhydra*, as in *Lutra*, there is an asymmetry between the left and right lungs. The basic branching pattern of the bronchial system is also asymmetrical and is similar to that observed in *Lutra* (Fig 5B). There is little difference between the branching patterns in the cranial and medial lobes of these two animals. A difference is seen in the accessory lobe in *Enhydra*, in which the segmental bronchi are closer together, reflecting the reduced and compact nature of this lobe. From dissected specimens, the segmental branches of the lobar bronchi to the caudal lobe appear to be more numerous and have a more dicotomous branching pattern than is seen in *Lutra*. In *Enhydra*, the segmental bronchi to the caudal lobe are given off at a common point, whereas in *Lutra* the lobar bronchus extends the length of the lobe and the segmental bronchi are given off pennately.

c. *Pagophilus groenlandicus*

In *Pagophilus*, the bronchial patterns in the two lungs are symmetrical (Fig 5C). In each lung there are five lobar bronchi, supplying the cranial, medial and caudal lobes of each lung. Soon after the trachea bifurcates into two symmetrical principal bronchi, the cranial lobar bronchi arise prior to their entry into the lung tissue. These bronchi supply the cranial one-third of the lungs. After a very short base (o.5cm), each cranial lobar bronchus divides into three segmental bronchi, which in turn give off subsegmental bronchi. Caudally, from each principal bronchus there arises a branch that passes caudo-laterally. This in turn divides into three large segmental bronchi which supply the medial region of each lung. Caudally, each principal bronchi divides to form three lobar bronchi, each of which bifurcates to form segmental bronchi. Subsegmental bronchi may arise from the segmental bronchi either by bifurcation of the bronchi or in a pennate fashion. From the dissections and roentgenograms, there appears to be a greater number and a higher degree of branching in the segmental and subsegmental bronchi in *Pagophilus* and *Enhydra* than in *Lutra*.

In each of the three species, the rings of the principal bronchi are replaced by irregular, overlapping cartilaginous plates prior to the entry of these bronchi into the lung tissue (Fig 1A-C). On the segmental bronchi these cartilaginous supports fuse and are very irregular in shape and may completely surround a given area of the bronchus (Fig 6). These cartilaginous supports become less abundant in the subsegmental bronchi.

Figure 6. Bronchial cartilages in the segmental (a) and lobar (b) bronchi of *Pagophilus*.


1cm

Discussion

In the river otter and sea otter, the trachea is incomplete on the dorsal side. The arms are thickest ventrally and become thinner and wider laterally and dorsally. The expanded portions of the arms overlap longitudinally, and may provide more support through this increased surface area. In the harp seal there is a more extensive overlapping of the tracheal rings. The overlap occurs on all surfaces so that a double layer of cartilage may be present in portions of these places. The arms of the rings overlap in the cranial regions of the trachea so that an entire, circular ring is formed. This is similar to that described by Owen (1831) and Sokolov,et al. (1971) and figured by Kooyman and Andersen (1969) for *Phoca vitulina*, but in both species the rings are evidently not as firmly united as in the walrus, *Odobenus rosmarus* (Murie, 1871, Kooyman and Andersen, 1969, and Sokolov, et al., 1971) and the ringed seal, *Pusa hispida* (Sokolov, et al., 1971). In the caudal regions, the trachea conforms to the general pattern seen in the otters, *Otaria* (Murie, 1874), *Mirounga* (Murphy, 1913), *Monachus* and *Zalophus* (King, 1964), in which the rings are incomplete dorsally. In certain other seals the tracheal rings are very incomplete and are reduced to ventral bars. This is seen in *Ommatophoca rossi* (King, 1969, and Kooyman and Andersen, 1969), *Hydrurga leptonyx* (Murphy, 1913), *Leptonychotes weddelli* (Kooyman and Andersen, 1969),and *Erignathus barbatus* and *Histriophoca fasciata* (Sokolov, et al., 1971).

The relatively shallow diving river otter and sea otter have a circular trachea with the rings partially calcified. Calcification of the rings and the resultant rigidity could be a limiting factor to depth of dive in these animals. The tracheal rings of the harp seal show no signs of calcification, but may be equally rigid because of their increased width and thickness. However, lack of calcification may enable the rings to bend without breaking during compression which would permit the seals to dive deeply. The trachea of the harp seal appears to be intermediate in compressibility between the antarctic seals, *Hydrurga, Ommatophoca* and *Leptonychotes* and the arctic seals, *Erignathus* and *Histriophoca*, and the walrus, and *Phoca* and *Pusa*.

Also of importance in this discussion is the diameter of the trachea in relation to its length. Based on relative tracheal widths and lengths, the harp seal would appear to be able to be able to exchange a greater volume of air in a given time than would the otters with their relatively long, narrow tracheae. The relatively short trachea in cetaceans assists in an 80 to 90% exchange in one second compared to a 10 to 15% exchange in 4 seconds for terrestrial mammals (Slijper, 1962).

Bronchi and bronchioles are supported by cartilaginous, loosely bound plates rather than rings. These plates may be an adaptation for easier independent stretching as the lungs expand and contract during ventilation. The extent of cartilaginous support was not determined in this study. In the harbor seal, bronchiole cartilage has been reported to reach as far as the respiratory bronchiole, which is a short segment compared to many large terrestrial mammals (Belanger, 1940).

Summary

1. The trachea, as a percentage of body length, is 23.2% in *Lutra*, 19.0% in *Enhydra* and 17.6% in *Pagophilus*. The width of the trachea relative to its length is least in *Lutra* and greatest in *Pagophilus*.

2. The mean number of tracheal rings is 71 in *Lutra*, 48 in *Enhydra* and 43 in *Pagophilus*. The ventral widths of the rings in *Lutra* and *Enhydra* vary in a non-uniform pattern, whereas in *Pagophilus* they are widest cranially and narrowest caudally. A dorsal gap between the arms is present throughout the length of the trachea in *Lutra* and *Enhydra* , and appears only in the caudal one-third of the trachea in *Pagophilus*. In *Lutra* and *Enhydra* there is a dorsal overlapping of the rings, whereas in *Pagophilus* there is dorsal, lateral and ventral overlapping. The tracheal rings of *Lutra* and *Enhydra* are partially calcified, but in *Pagophilus* there is no evidence of calcification. In each species, the cartilaginous rings are replaced by irregular plates prior to the entry of the principal bronchi into the lungs.

3. The lamina propia of *Pagophilus* is thicker than in *Lutra* and *Enhydra*.

4. A pennate-like branching of the lobar bronchi are found in *Lutra* and *Enhydra*, whereas in *Pagophilus* this branching has a more dicotomous pattern.

5. The bronchial patterns in the right and left lungs of *Lutra* and *Enhydra* are asymmetrical and correspond to the differences in lobulation of the lungs. In *Pagophilus* there is close symmetry between the two lungs and their bronchial patter

bronchial patterns.

6. The numbers of subsegmental bronchioles increases from *Lutra* to *Enhydra* to *Pagophilus*.

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Acknowledgments

I wish to express my appreciation to the following people for specimens and assistance during the preparation of this report: Dr. M.B. Nogrady (Montreal Children's Hospital); Mr. Karl Schneider (Alaska Fish and Game Department); Mr. Ian Smith and Mr. Denis Wilder (B.C. Fish and Game Department); Dr. Charles Guiguet (B.C. Provincial Museum); Dr. J.C. Holmes and Mr. T. Neraasen (Department of Zoology, University of Alberta); and Mr. W. Hoek and Mr. G. Slenoas (Fisheries Research Board of Canada).

This research was financed by Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada and McGill University.

Parts of the final draft of this report were written in consultation with Dr. G.L. Kooyman (Scripps Institution of Oceanography, La Jolla, California).

Part V. The caval sphincter and hepatic sinus in aquatic mammals.

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Introduction

The morphology of the caval sphincter and inferior vena cava have been studied in the earless seals (Phocidae) by Burow (1838), Hepburn (1909), Burne (1910), Harrison and Tomlinson (1956; 1964), Barnett, *et al*. (1958), and others. The combined results of these studies indicate that in this Family there is a well-developed clearly defined caval sphincter surrounding the intrathoracic portion of the inferior vena cava, just cranial to the diaphragm, and easily separable from the muscles of the latter. These striated muscle fibers are innervated by a branch of the right phrenic nerve and are believed to play a role in regulating blood flow to the right atrium during diving and upon emergence (Murdaugh, *et al*., 1962). In these seals, there is also found an enlargement at the junction of the inferior vena cava and hepatic veins termed the hepatic sinus. These hepatic sinuses have been interpreted as playing a role in blood storage during diving.

In the eared seals (Otariidae), muscular bands, indicating a rudimentary caval sphincter, were found in a stillborn Calfironia sea lion (*Zalophus*) by Harrison and Tomlinson (1956), and in the walrus (Odobenidae), Owen (1853) and Burne (1909) describe a well-developed caval sphincter. In the Cetacea, a caval sphincter (caval sling) is found in the harbour porpoise (*Phocaena*), but is absent in *Tursiops* and the finback whale, *Balaenoptera* (Harrison and Tomlinson, 1956). In these taxonomic groups, the sphincter muscles are less well-developed than in earless seals, and at some point are continuous with the muscles of the diaphragm. However, the fibers do encircle the vena cava in such a way that their contractions could alter venous flow. Hepatic sinuses were not described in any of the above cetaceans, but are enlarged in *Odobenus* (Owen, 1853 and Murie, 1871), *Zalophus* (Forbes, 1882), and *Otaria* (Murie, 1874).

The semi-aquatic manatee (*Trichechus*) has a rudimentary sphincter and a small hepatic sinus, whereas the dugong (*Dugong*), river otter (*Lutra*) and the coypu rat (*Myocastor*) show no signs of a caval sphincter or hepatic sinuses (Harrison and Tomlinson, 1964).

In this report, the caval sphincter and hepatic sinus areas are examined in five diving mammals: the muskrat, the Canadian river otter, the Northern sea otter, the harp seal and the beluga whale. In the California sea lion, only the caval sphincter was examined.

Materials and Methods

The area of the diaphragm surrounding the post-caval hiatus and the intrathoracic and abdominal portions of the inferior vena cava were examined in 1 adult, female muskrat, *Ondatra zibethica*, 8 Canadian river otters, *Lutra canadensis*, 8 Northern sea otters, *Enhydra lutris*, 5 harp seals, *Pagophilus groenlandicus* and 1 calf, female beluga whale, *Delphinapterus leucas*. Only the caval sphincter was examined in 6 adult California sea lions, *Zalophus californianus*.

Prior to excising the veins and the diaphragmatic muscles, the lengths and diameters of the collapsed, relaxed prediaphragmatic and postdiaphragmatic portions of the inferior vena cava were measured to the nearest millimeter in *Ondatra, Lutra, Enhydra, Pagophilus* and *Delphinapterus*. To reveal the postdiaphragmatic venous distribution, the inferior vena cava of specimens of *Ondatra, Lutra* and *Enhydra* were injected with neoprene latex and dissected.

From each specimen, the diaphragmatic muscle containing the post-caval hiatus was fixed either in 10% formalin or Bouin's fluid. The muscle and nerves on the cranial side of the diaphragm were dissected and examined under low power magnification.

Results

A. Caval sphincter

Ondatra zibethica (Fig 1A)

In *Ondatra* there are no diaphragmatic muscle fibers associated with the inferior vena cava as the vein is completely surrounded by the central tendon of the diaphragm. The right phrenic nerve passes close to the inferior vena cava and branches enter the diaphragmatic musculature.

Lutra canadensis (Fig 1B)

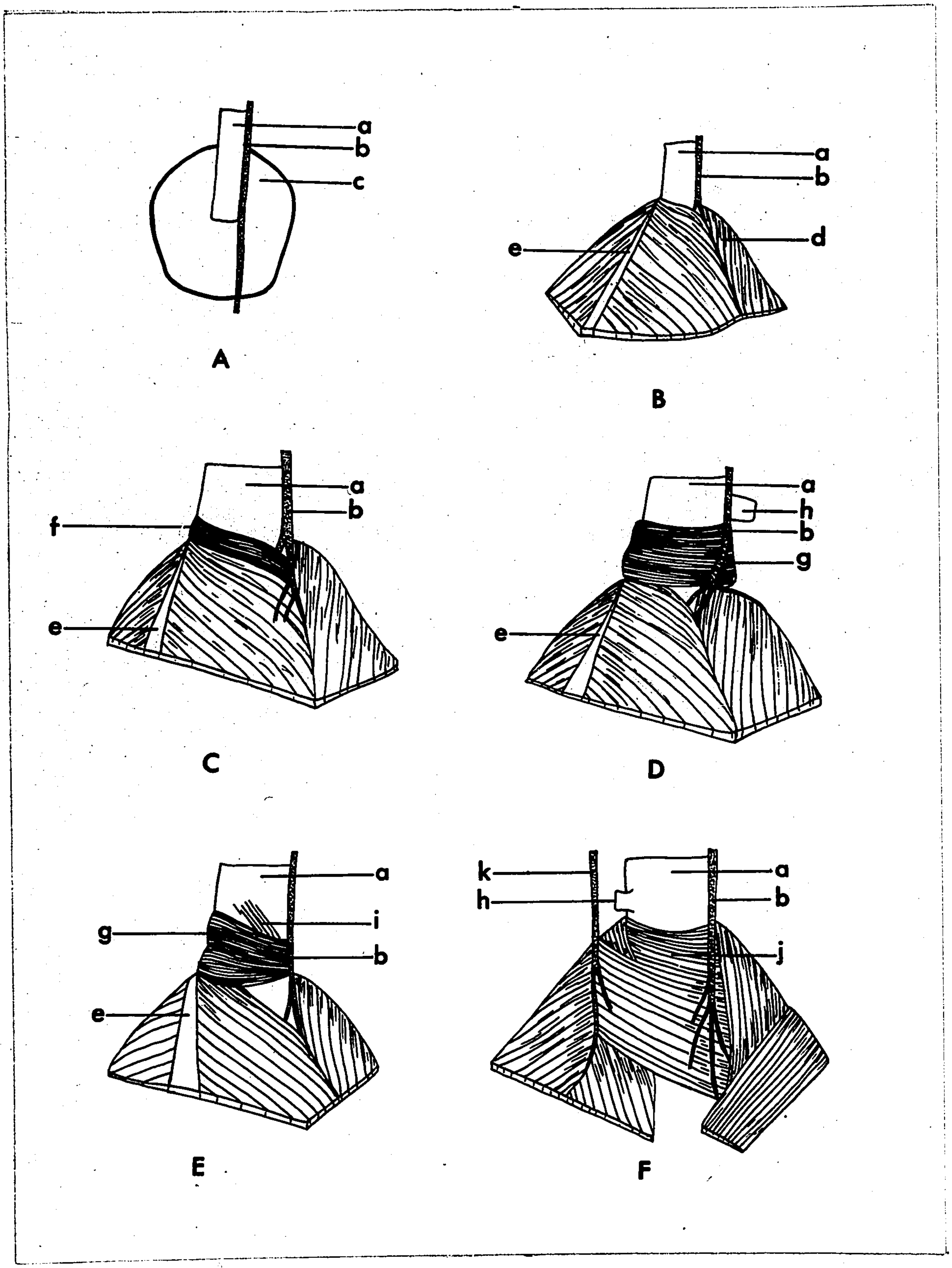
In *Lutra* the inferior vena cava passes through the diaphragmatic musculature on the right, cranio-lateral side of the central tendon. The vena cava at its entrance and exit from the diaphragm is tightly bound to this tendon by connective tissue. There is no sign of a sphincter-like arrangement of diaphragmatic muscles associated with the intrathoracic portion of the inferior vena cava. The diaphragmatic muscle associated with the postcaval hiatus is at right angles to the inferior vena cava and does not extend cranially along this venous trunk. The right phrenic nerve passes down the lateral side of the vena cava and enters the diaphragmatic musculature. A separate branch of the phrenic nerve is seen to enter the diaphragmatic musculature adjacent to the vena cava.

Enhydra lutris (Fig 1C)

In *Enhydra*, there are signs of a rudimentary caval sphincter. This

Figure 1. Cranial view of the inferior vena cava and surrounding diaphragmatic muscle in *Ondatra* (A), *Lutra* (B), *Enhydra* (C), *Pagophilus* (D), *Zalophus* (E) and *Delphinapterus* (F).

a. intrathoracic portion of the inferior vena cava
b. right phrenic nerve
c. central tendon of the diaphragm
d. diaphragmatic muscle
e. left arm of central tendon
f. 'rudimentary' caval sphincter
g. caval sphincter
h. vein from pericardial venous plexus
i. muscular slips on surface of inferior vena cava
j. caval 'sling'
k. left phrenic nerve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is in the form of two tendinous, closely packed muscle slips from the diaphragm, each of which intermingles on the ventral side and completely encircles the inferior vena cava. These muscles separate the vena cava from the medial side of the central tendon. The slips extend up the vena cava for about 6mm and are easily separable from this vein, but not from the diaphragm. This muscular band is most highly developed on the lateral side of the vena cava (0.4cm thick) and becomes progressively weaker medially (that side adjacent to the central tendon of the diaphragm). Diaphragmatic muscle fibers are oriented in a similar positional relationship to the central tendon as in *Lutra*, the main difference being that in *Enhydra* not all muscle fibers end on the central tendon. A separate branch of the right phrenic nerve passes into the sphincter region, similar to that of *Lutra*.

Pagophilus groenlandicus (Fig 1D)

All specimens of *Pagophilus* have a caval sphincter identical to that described in *Phoca vitulina* by Harrison and Tomlinson (1956). Their description is given below:

The thoracic part of the inferior vena cava " has disposed around it a muscular sphincter which surrounds the first 1.9cm to 5cm rostral to the diaphragm. The sphincter is 0.5 to 1.5cm thick, depending on the age of the animal, and is composed of a sheet of striated muscle fibers separated from the wall of the posterior vena cava by loose connective tissue ...... The sphincter ends abruptly with a well-defined edge at its cephalic end and caudally is almost completely separated from the diaphragmatic muscle by a circular, narrow tendinous band. The abdominal orifice is wider than the thoracic, thus the sphincter is funnel-shaped.

The sphincter is supplied by branches from the right phrenic nerve;

in several dissections there was one principal branch and a few fine filaments."

Zalophus californianus (Fig 1E)

The caval sphincters of the adult *Zalophus* specimens are in the form of striated muscle bands that completely encircle the inferior vena cava. On the lateral side, the muscle band extends cranially from 1.2 to 2.5cm and from 0.5 to 1.0cm medially, depending on the age of the animal. Most of the muscle fibers originate from the central tendon of the diaphragm, pass laterally and encircle the vena cava, with some fibers also originating from the right lateral column of the diaphragmatic tendon. Cranially, there are free muscle fibers that encircle, and fibers that are directed diagonally, becoming progressively thinner on the medial side. Superficially, the sphincter muscles are united to the diaphragmatic muscles by tough connective tissue. The inferior vena cava is larger in diameter at its base than at its emergence from the sphincter, giving the vein a funnel-shape. The right phrenic nerve passes down the lateral side of the vena cava and enters the diaphragmatic musculature with two separate branches entering the base of the sphincter.

Delphinapterus leucas (Fig 1F)

In *Delphinapterus*, there is a thin, distinct arrangement of muscle fibers encircling the intrathoracic portion of the inferior vena cava. On the dorsal surface these strap-like muscle fibers are not easily separable from the main diaphragmatic muscles. The sphincter is about 1.8cm wide and 0.2cm thick dorsally, and narrows to 0.9cm, and is about the same thickness ventrally (0.2cm). The left and right phrenic nerves pass close to the sphincter area and it was not possible to determine which nerve innervated this muscle mass.

B. Hepatic sinus (Fig 2)

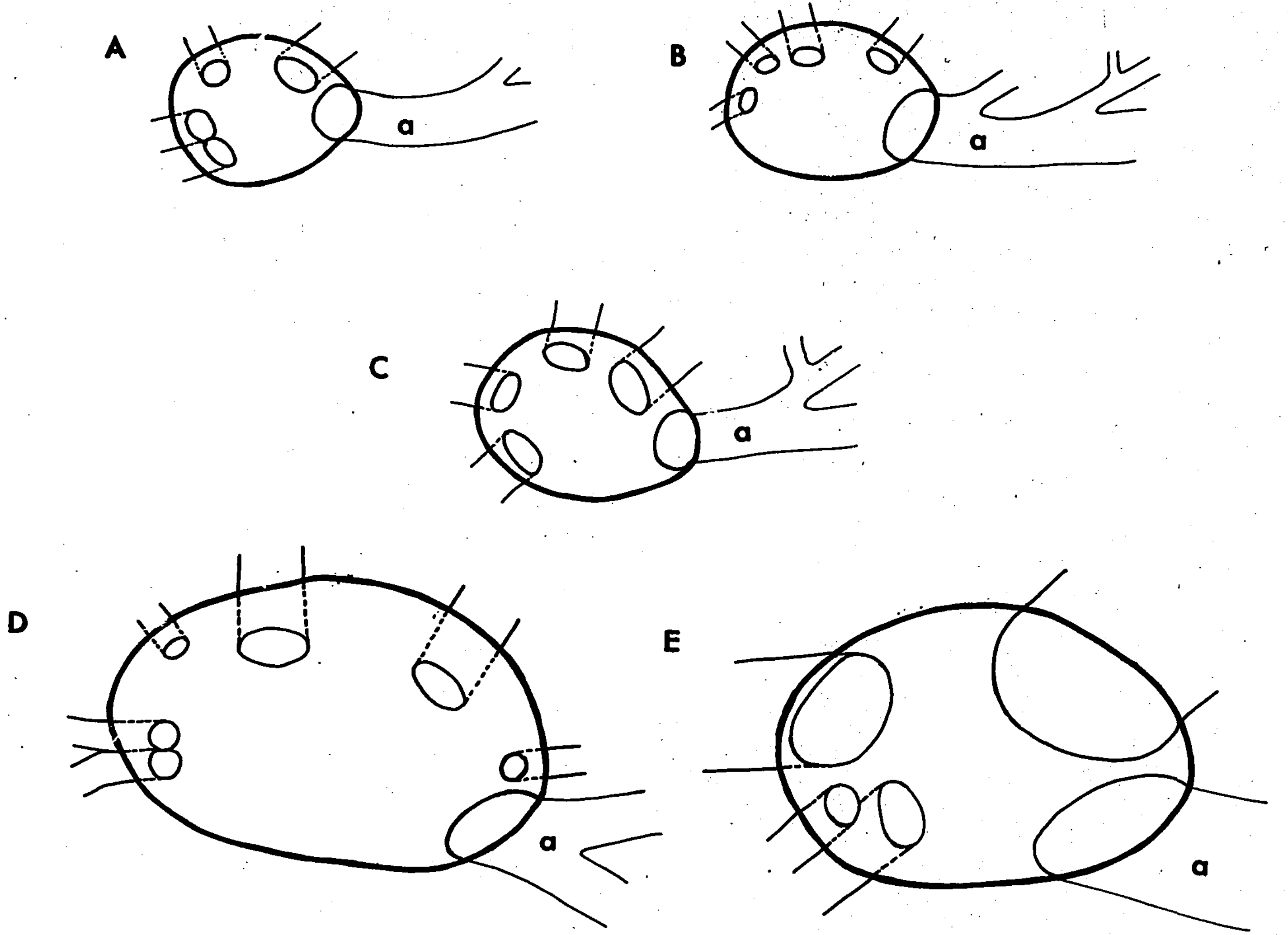
In each of the species examined, four major hepatic veins empty into the thoracic vena cava on the cranio-dorsal aspect of the liver, just caudal to the diaphragm (Fig 2 A to E). This region is not extensively enlarged in *Ondatra, Lutra, Enhydra* and *Delphinapterus*, but is greatly enlarged in *Pagophilus* and in *Zalophus* (Rowlatt, personal communication). In the former four species, this region is about 2 to 4 times as wide as the intrachoracic and abdominal regions of the inferior vena cava, whereas in *Pagophilus*, the sinus is from 7 to 9 times as large as the other regions of the vein (Table I).

Table I. Diameters of the inferior vena cava in six aquatic mammals.

	diameters (cm)		
	intrathoracic	thoracic	abdominal
Ondatra	0.2	0.6	0.4
Lutra	0.8	2.0	1.2
Enhydra	1.4	2.0	2.3
Pagophilus	3.5	27.0	4.2
Zalophus	2.5	----	----
Delphinapterus	3.0	5.2	----

Figure 2. Cranial view of hepatic sinus region in *Ondatra* (A), *Lutra* (B), *Enhydra* (C), *Pagophilus* (D) and *Delphinapterus* (E).

(all vessels are hepatic veins, except a = inferior vena cava)


A
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Discussion

The diving physiology of aquatic mammals has been studied extensively and much of the present day knowledge has been reviewed recently by Elsner (1969) and Harrison and Kooyman (1970).

During a dive, bradycardia occurs in the hippopotamus, *Hippopotamus* (Elsner, 1966), beaver, *Castor* (Irving and Orr, 1935), muskrat, *Ondatra* (Koppanyi and Dooyey, 1929), sea lion, *Zalophus* (Elsner, 1964), Northern fur seal, *Callorhinus* (Irving, *et al.*, 1963), earless seals (Irving, *et al.*, 1935; Scholander, 1940; and others), porpoise, *Tursiops* (Irving, *et al.*, 1941), and, as it is a wide-spread phenomenon among diving vertebrates, it may be assumed to operate during the submersion of each of the animals discussed here. Peripheral vasoconstriction is closely associated with bradycardia and results in an increased venous blood volume which has to be stored. It seems reasonable that the phylogenetic development of the hepatic sinus as a blood storage area may in part be dependent on increased venous blood volume which results from vasoconstriction during diving.

During a dive, earless seals exhibit a profound bradycardia. Associated with this change is a reduced venous return to the heart and an increased venous return to the body's central venous system. On examining the venous system for anatomical adaptations, workers have attached great importance to the hepatic sinuses to accommodate this increased venous return and to the caval sphincter to control its flow to the heart. According to Harrison and Tomlinson (1956), it is not possible to correlate the presence of a caval sphincter and hepatic sinus with the ability of an animal to dive deeply. This conclusion seems to be based on data from the Cetacea, in which some of these mammals are deep divers, but lack both of these structures (*Tursiops* and *Balaenoptera*). In others, the presence of a caval sphincter is not always associated with a large hepatic sinus, as in *Phocaena*. This latter difference has also been found here in *Delphinapterus*. Excluding the Cetacea for the time being, it appears that the presence of both a caval sphincter and hepatic sinus in seals is closely associated with the ability either to dive deeply and/or for a prolonged time. All of the eared and earless seals, and the walruses that have been examined have a well-developed caval sphincter and hepatic sinuses, and each can dive deeply and/or for relatively long periods of time. In a shallow and shorter duration diver, such as *Enhydra*, there is a rudimentary sphincter and a less well-developed hepatic sinus, and in very shallow divers, such as *Ondatra* and *Lutra*, there is an absence of both of these structures. Even a rudimentary caval sphincter in a diving mammal may be functionally significant in regulating venous blood flow to the heart during a dive and may prevent overloading of the right atrium upon emergence from a dive.

In *Ondatra* and *Lutra*, there is no check on venous return in the form of a caval sphincter, and no storage area in the form of a hepatic sinus. Both of these species are relatively shallow and brief divers. Thus, perhaps there is less need for oxygen conservation over a prolonged period. The presence of a dense pelage may contribute to less vasoconstriction than would occur in sparsely haired, deep diving mammals, such as the earless seals and cetaceans. If this is the case, there would not be the necessity of increased venous storage since the blood distribution in the body may remain relatively constant. Any blood storage that may be necessary could occur in the hepatic veins, epidural vein and vena cavae without the necessity of hepatic sinuses.

Based on feeding habits and direct observations, *Enhydra* (Slijper, 1962 and Kenyon, 1969) and porpoises and dolphins (Scholander, 1940) seldom dove for longer than 5 and 10 minutes, respectively. They are also relatively shallow divers compared with earless seals. During a dive, thee sea otter, as with the river otter and muskrat, would have less need for oxygen conservation over a long period. This may indicate that they may not have as marked a vasoconstriction and as great an increase in venous blood return upon surfacing as seals. Thus, a greatly enlarged hepatic sinus would not be necessary. Some loading of the veins may occur as reflected by the presence of a caval sphincter in the sea otter and some cetaceans. In *Delphinapterus*, the sphincter is relatively well-developed and may be related to the more prolonged dives of up to 15 minutes for this species (Vladykov, 1944, cited by Slijper, 1962).

In deep and/or prolonged divers, such as the earless seals (in *Phoca vitulina* a maximum time of 28 minutes has been recorded by Harrison, 1960), there is marked vasoconstriction (Bradley and Bing, 1942; Murdaugh, *et al.*, 1961; Elsner, *et al.*,1966) which plays an important role in terms of blood oxygen conservation. Vasoconstriction results in an increased volume of venous return to the heart upon surfacing, thereby necessitating storage and control of blood flow to the heart. As well as the hepatic sinuses, other venous adaptations for blood storage have been documented by Barnett, *et al.*, (1958), Harrison and Tomlinson (1956), and Tomlinson (1964), and include a large epidural intervertebral vein and large thin-walled inferior venae cavae.

The degree of venous return during diving may be related to total blood volume. Comparing the percentages of blood volume/body weight, the earless seals have a greater volume of blood than other mammals (*Ondatra* = 10%, Irving, 1934; *Enhydra* = 6.6 to 10%, Kenyon, 1969; *Phoca* = 10%, Irving, 1939; 11 to 18%, Harrison and Tomlinson, 1956, and Wasserman and Mackenzie, 1957; *Delphinapterus* = 5.5%, Slijper, 1962).

During exposure to low water temperatures, the insulation of the animals may be of some importance in determining the degree of peripheral vasoconstriction and hence the volume of blood return to the heart. Thus, in pinnipeds, during times of heat dissipation while on land, there may be a reduced blood volume in the body proper, much of the blood being in the highly vascular blubber. During submersion, when heat conservation is necessary, the blubber should be inert to serve as an effective insulator. Therefore, the blood flows to the body core, increasing the venous return. The Cetacea are constantly exposed to cold water temperatures and there may be less peripheral vasoconstriction since they have an extensive distribution of heat exchangers in the blubber and appendages (Parry, 1949 and Scholander and Schevill, 1954). The dense pelage and subcutaneous fat of *Ondatra, Lutra* and *Enhydra* may be sufficient insulation to account for a decrease in vasoconstriction during diving.

Suggested relationships between presence, absence and degree of development of the caval sphincter and hepatic sinus in diving mammals as related to diving habits and thermal regulation is outlined as follows:

Ondatra *Myocastor* *Lutra*	-shallow and short duration divers	--moderately cold aquatic environment -dense pelage and little subcutaneous fat	-little vasoconstriction with little increase in venous blood volume during diving	-no caval sphincter -no hepatic sinus
Enhydra	--intermediate depth and duration diver	-cold aquatic environment -very dense pelage and very little or no subcutaneous fat	-moderate vasoconstriction with moderate increase in venous blood volume during diving	-simple caval sphincter -no extensive hepatic sinus
Delphinapterus *Phocaena*	-intermediate depth and duration	-cold aquatic environment -no pelage and intermediate depth of subcutaneous fat	-increased vasoconstriction with increased venous blood volume during diving	-well-developed, specialized 'caval sling' -no extensive hepatic sinus, but greatly enlarged hepatic veins
Odobenus	-shallow depth and long duration diver	-cold aquatic environment -sparse or no pelage and much subcutaneous fat	-increased vasoconstriction with increased venous blood volume during diving	-well-developed caval sphincter -extensive hepatic sinus

Zalophus	-intermediate depth and duration diver	-cold aquatic environment -relatively sparse pelage and a moderate depth of subcutaneous fat	-increased vasoconstriction with increased venous blood volume during diving	-more highly developed caval sphincter -extensive hepatic sinus
Pagophilus *Phoca* *Halichoerus* *Monachus* *Leptonychotes* *Lobodon* *Hydrurga* *Ommatophoca* *Mirounga*	-deep and prolonged divers	-cold aquatic environment -sparse pelage and much subcutaneous fat	-increased vasoconstriction with increased venous blood volume during diving	-most highly developed caval sphincter -most extensive hepatic sinus

In this report, reference has been made to the hepatic veins of the liver as possible regions of blood storage during diving. Arey (1941) described the presence of spiral muscles in the hepatic tributaries in the liver of the seal (*Callorhinus*?). He interpreted these muscles as serving to retain blood in the liver and suggested that they may be of functional significance during submergence. These muscles were not present in *Ondatra*, and Arey unfortunately did not look for them in other diving mammals. Dilated hepatic veins have been described in the liver of Risso's dolphin (*Grampus grisseus*) by Richards and Neuville (1896) and have been interpreted as serving as a venous storage organ during diving. The sea otter has an unusually large liver (Kenyon, 1969) and, with its large hepatic veins, could serve as an important blood storage organ during diving.

Franklin and Janker (1936) noted in the rabbit that during inhalation there was increased hepatic blood flow into the vena cava and a restricted non-hepatic abdominal inflow into the thorax, with the reverse occuring during exhalation. In 1937, these same workers injected the inferior vena cava and hepatic portal vein of the cat and noted that there was backflow into the hepatic veins from the vena cava when the heart and breathing were arrested. Based on the evidence of these workers, plus what is known of the anatomy and physiology of diving mammals, the following hypothesis is presented to point out a possible function of thelliver during diving:

Prior to a dive, many mammals inhale and then, as the depth and/or duration of the dive increases, they gradually exhale, as witnessed by air bubbles escaping from the mouth. During inhalation there would be a compression of the liver as the diaphragm moves caudally and a flow of venous blood out of

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the liver into the vena cava would occur. As diving time increases, accompanied by a decreased heart rate and arrested breathing, the liver would be lifted by the inpushing of the diaphragm into the thoracic cage, and there would be a backflow of blood into the hepatic veins. The spiral-shaped sphincter muscles in the tributaries of the hepatic veins would help restrict blood flow from these regions into the hepatic veins and the vena cava. A sphincter arrangement at the orifice of the hepatic veins into the hepatic sinus area would be an asset for controlling blood flow from the liver.

SURFACED - prior to a dive

A. Inhalation
- diaphragm moves caudally
- liver moves dorsally and restricts flow from the vena cava
- compression of the hepatic veins and an increased flow into the vena cava
  int

SUBMERGED

B. Exhalation during a dive
- arrested breathing and decreased heart rate
- increased peripheral vasoconstriction and increased venous return
- diaphragm moves cranially and moves the liver ventrally thereby exposing and expanding the hepatic veins
- restricted blood flow through the vena cava because of contraction of the caval sphincter
- backflow of blood into the hepatic veins
- spiral muscles in the hepatic vein tributaries restrict blood flow into the hepatic veins
- outflow of blood in hepatic veins may be restricted by sphincter at their orifice

An arrangement as outlined above may be operating in diving mammals and may be especially important in those mammals, such as the Cetacea and Carnivora, that do not exhibit an enlarged hepatic sinus, and also in the Pinnipedia in which there is evidintly a profound peripheral vasoconstriction during diving.

Summary

1. *Ondatra* and *Lutra* lack both the caval sphincter and the hepatic sinus.

2. *Enhydra* has a simplified caval sphincter composed of slips of muscle surrounding the intrathoracic portion of the inferior vena cava. These sphincter muscle slips are not separable from the diaphragm at their base. Extensive hepatic sinuses are not present.

3. *Pagophilus* has a well-developed caval sphincter and hepatic sinus, and these correspond closely to those found in other phocid seals.

4. *Zalophus* has a well-developed caval sphincter and hepatic sinus.

5. *Delphinapterus* has a sphincter in the form of a 'sling-like' arrangement of muscle fibers surrounding the vena cava, that are not easily separated from the diaphragm at their base. An extensive hepatic sinus is not present.

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Acknowledgments

I wish to thank the following persons and institutions for assistance during the preparation of this report: Mr. Ian Smith (B.C. Fish and Game Department); Dr. J.C. Holmes (Department of Zoology, University of Alberta); Dr. D.E. Sergeant and Mr. W. Hoek and Mr. G. Sleno (Fisheries Research Board of Canada); Dr. Ursula Rowlatt (Pathology Department, University of Illinois Medical Center); Dr. S.H. Ridgway (U.S. Missile Center, Point Mügu, California); and the Audio-visual Aids Department (Cambridge University).

This research was supported by Canadian Wildlife Service scholarships, and grants-in-aid-of-research from the Canadian Wildlife Service, the National Research Council of Canada and McGill University.