Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 1: Paleogene Pinniped Remains; The Oldest Known Seal (Carnivora: Phocidae)

Irina A. Koretsky and Albert E. Sanders

ABSTRACT

The proximal halves of two femora from the Chandler Bridge and Ashley Formations (early Chattian, late Oligocene) near Charleston, South Carolina, provide the earliest evidence to date of true seals. They are clearly referable to the Phocidae and furnish information regarding osteological and myological features that had evolved in early phocids by early Chattian time. Although not determinate to the generic level, these specimens represent a taxon closely comparable to the most specialized phocid, the modern genus *Cystophora*.

Introduction

The long-standing question of phylogenetic relationships among the Odobenidae, Otariidae, and Phocidae is still open. The debates about the monophyletic or diphyletic origin of pinnipeds from a series of ancestors (mustelid- or ursid-like animals) are not yet resolved. The new material reported herein, the proximal parts of two femora from the late Oligocene of South Carolina, now in The Charleston Museum (ChM), helps little in solving the problems of phylogeny, but we have for investigation the earliest and most primitive remnants of Phocidae. Herein we refer to the two partial femora from the late Oligocene as the "Oligocene seal." The two new specimens appear to represent the same taxon, but they are so incomplete that any taxonomic assignment below the family level would be mere speculation. This material nonetheless does provide information concerning some derived (=apomorphic) and primitive (=plesiomorphic) characters of the Phocidae.

Irina A. Koretsky, Research Associate, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0121. Albert E. Sanders, Department of Natural Sciences, The Charleston Museum, 360 Meeting Street, Charleston, South Carolina 29430.

For comparisons we used postcranial material from several living and fossil representatives of aquatic and semiaquatic carnivores, including Mustelidae (the genera *Lutra, Enhydra,* and *Potamotherium*); Otariidae (the genera *Zalophus* and *Allodesmus,* the latter the most controversial eared seal (Berta and Wyss, 1994; Barnes and Hirota, 1994)); and Phocidae (for example, the genus *Cystophora* as the most specialized representative of the family).

ACKNOWLEDGMENTS.—The authors are grateful to James Mead and Charles Potter for access to modern comparative material, to Clayton E. Ray for access to fossil pinniped collections, to Victor Krantz and Steven Jabo for specimen photography (all National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.), and to Robert J. Emry (NMNH), Daryl Domning (Howard University, Washington, D.C.), and Mieczyslaw Wolsan (Institute of Paleobiology, Warsaw, Poland) for their helpful comments on several versions of this manuscript.

MATERIAL AND LOCALITY.—Proximal portion of right femur (ChM PV5712), from a ditch in the Irongate subdivision, approximately 3.9 km (2.4 mi.) SW of Summerville, Dorchester County, South Carolina, collected by Vance McCollum, summer 1978; cast of ChM PV5712 (USNM 299831) in the NMNH (which subsumed the collections of the former United States National Museum). Proximal portion of right femur (ChM PV5713), from a ditch on Trolley Road (County Road 199), approximately 3.0 mi. (4.8 km) SW of Summerville, Dorchester County, South Carolina, collected by Chris Kenney, 6 December 1978; cast of ChM PV5713 (USNM 306508).

FORMATION AND AGE.—ChM PV5712: Chandler Bridge Formation, early Chattian (late Oligocene). ChM PV5713: Ashley Formation, early Chattian (late Oligocene).

The Chandler Bridge Formation, an unconsolidated noncalcareous marine unit rich in vertebrate fossil remains, occurs at numerous disjunct localities in Berkeley, Charleston, and Dorchester Counties, South Carolina. It unconformably over-

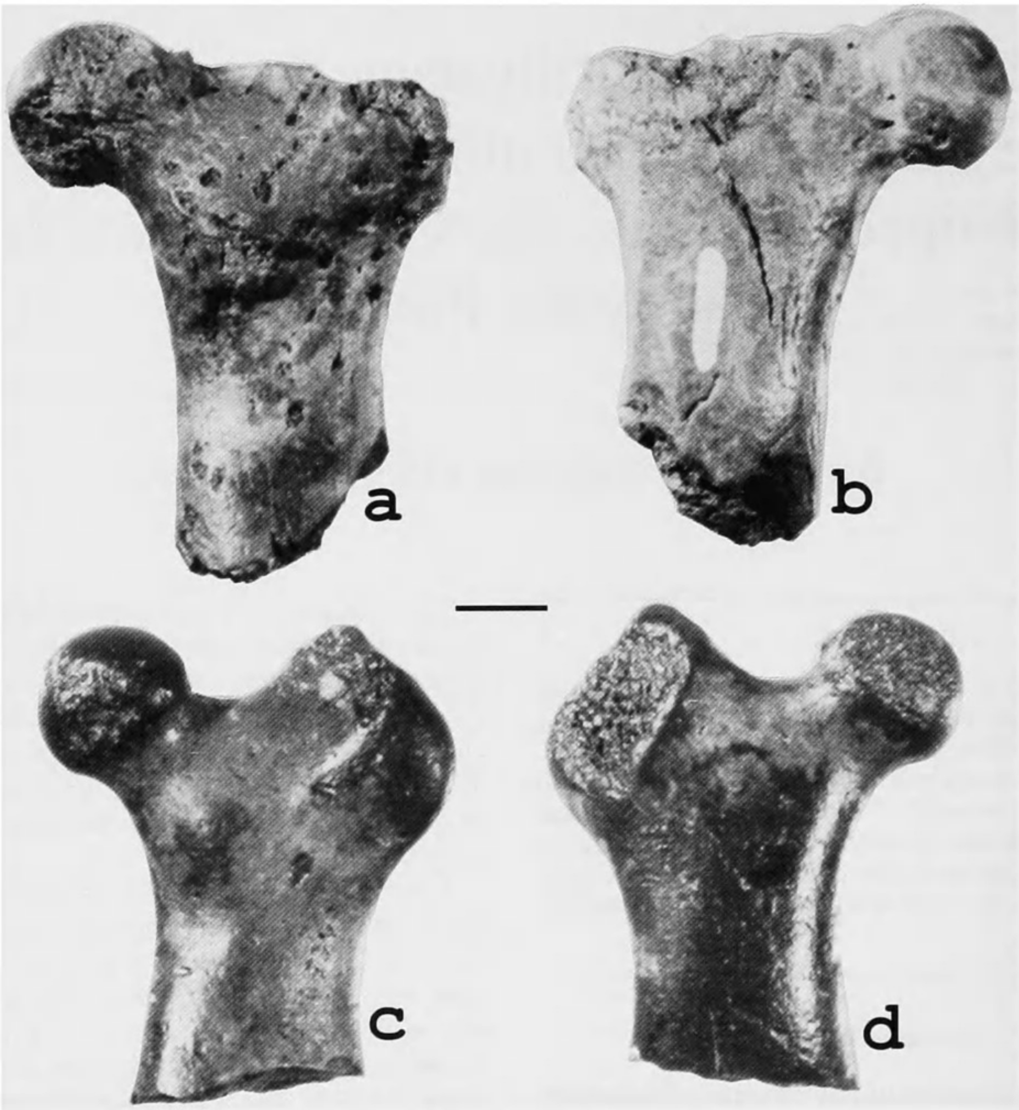

FIGURE 1.—Femora of Oligocene seals (×1). Right femur, original ChM PV 5712, cast USNM 299831, from Chandler Bridge Formation, early Chattian, late Oligocene: *a*, caudal view; *b*, cranial view. Right femur, original ChM PV 5713, cast USNM 306508, from Ashley Formation, lower Chattian, late Oligocene: *c*, caudal view; *d*, cranial view.

lies the Ashley Formation, a highly indurated calcarenite underlying most of the area encompassed by the aforementioned counties (Sanders, 1980; Sanders et al., 1982). E. Martini has found the nannoplankton of the Ashley Formation to be referable to zone NP24 (Sanders and Barnes, 2002). Sanders et al. (1982) have estimated the Chandler Bridge Formation to be approximately 28 million years old and the Ashley Formation to be about 30 million years in age. Both units have yielded abundant remains of sharks; bony fishes; sea turtles (*Carolinachelys, Procolpochelys, Syllomus,* two dermochelyids); three nonmarine turtle taxa; a large, newly described estuarine crocodile, *Gavialosuchus carolinensis* Erickson and Sawyer (1996); marine birds (including a large pseudodontorn with a wingspan of about six meters); sirenians; and more than 20 taxa of primitive cetaceans. Now a pinniped is added to the impressive faunas of marine vertebrates from these two formations.

PHOCIDAE

Genus and Species Indeterminate

DESCRIPTION.—The femora (Figure 1, Table 1) are similar in size to those of the modern harp seal, *Pagophilus groenlandicus*. The shaft of the bone is flattened in the cranial-caudal direction. The greater trochanter extends proximally slightly higher than the head and is slender, although not well developed. The trochanteric fossa is shallow and wide open, actually not reaching the middle of the greater trochanter. The intertrochanteric crest is not expanded. The lesser trochanter is very well developed and is located on the posteromedial side of the bone at the same level as the distal border of the greater trochanter. The cervix is short but narrow relative to the bone's mass. The head is damaged, but it clearly has an indentation for attachment of the ligamentum teres in the center of the head.

TABLE 1.—Measurements (in mm) of the late Oligocene seal femora from the Chandler Bridge Formation (ChM PV5712) and the Ashley Formation (ChM PV5713), Dorchester County, South Carolina.

Character	Measurements	
	ChM PV5712	ChM PV5713
Length of greater trochanter	29.5	-
Intertrochanteric length	42.0	-
Height of head	20.5	21.5
Width of proximal epiphysis	54.0	56.5
Width of head	18.0	19.0
Narrowest part of diaphysis	27.0	28.0
Maximum thickness of greater trochanter	13.5	-
Anteroposterior thickness of diaphysis	16.0	18.0
Diameter of cervix	17.0	20.0

This insertion of the ligamentum teres is not a completely developed fovea as it is in most terrestrial mammals. In phocids this fovea is absent.

The slight difference in bone morphology of the two Oligocene femora perhaps could be ascribed to sexual dimorphism (Koretsky, 1987), but the limitations of the material preclude a more precise interpretation.

According to authors who have studied the functional morphology and myology of the limbs of different carnivores (Howell, 1928, 1930; Savage, 1957; Mori, 1958; Mitchell, 1966; Piérard, 1971; Tarasoff, 1972; Sokolov et al., 1974), the lesser trochanter is the point of insertion of the iliopsoas muscle. These authors also noted, however, that if the lesser trochanter is absent, then the pectineus and adductor muscles insert on this place; that is true for all comparatively aquatic and semiaquatic mammals. The iliopsoas muscle is a large, heavy muscle connecting the lumbar spine and ilium with the femur. The actions of this muscle are to flex and laterally rotate the femur, tilt the pelvis forward, flex the thigh upon the pelvis, and adduct the femur (working as a synergist with the adductor brevis) (Gordon, 1983).

The quadratus femoris muscle is absent in extant phocids. In the otter, this reduced and weakened muscle inserts on the distal part of the greater trochanter, on the caudal border of the femur (Sokolov et al., 1974). In sea lions (otariids), the insertion of the m. quadratus femoris is along the entire laterocaudal border of the femur (Howell, 1928). The action of the quadratus femoris muscle is to extend the hip joint.

Howell (1928, 1930), Piérard (1971), and other researchers described the trochanteric fossa as a place of attachment of the obturator internus and externus muscles, together with the two gemelli muscles, the superior and inferior. The gemelli and obturator externus muscles arise from the lateral border of the obturator foramen and its membrane. The two gemelli join with the obturator internus muscle to form a common tendon for insertion. (Piérard at the same time (1971:68) mistakenly stated that the origin of the tendon of the obturator internus muscle is a shallow groove in the middle one-third of the pubic edge.) The action of the obturator externus muscle is to rotate the femur laterally. The actions of the gemelli and obturator internus are to abduct the femur and also to rotate it laterally.

COMPARISONS.—The Oligocene seal differs from other carnivores we examined (except for *Cystophora* and *Zalophus*) in its shallow and poorly defined trochanteric fossa, from all except *Cystophora* by its slight extension of the greater trochanter above the head, and from all except *Lutra* and *Potamotherium* in having a pit for attachment of the ligamentum teres.

Other distinct differences between this seal and other genera also exist. It differs from *Cystophora* (the hooded seal) in having a lesser trochanter (but this is always absent in females of *Cystophora*); a narrower and less prominent greater trochanter; and a more delicate, not massive, overall bone structure. So far as they can be determined, the muscle attachments for the Oligocene seal are in general the same as for *Cystophora,* but with one exception: in female hooded seals, which lack a lesser trochanter, the tendons of the pectineus and adductor cranialis muscles are inserted on the same spot on the bone, and the iliopsoas muscle inserts upon the medial tuberosity of the tibia (Howell, 1928).

From *Lutra* this seal differs in the presence of a well-developed and distinct lesser trochanter and a much broader shaft. In general, there are no differences between these two taxa in insertion of the described muscles; gemelli, obturator externus, and internus muscles all insert into the trochanteric fossa, and the iliopsoas muscle inserts onto the lesser trochanter (Sokolov et al., 1974).

The Oligocene seal differs from *Enhydra* in the shorter cervix and smaller size of the head compared with the rest of the bone. Insertions of the muscles into the fossa trochanterica are almost the same in *Enhydra* and *Lutra,* but the mass of these muscles is apparently greater in *Enhydra*. In contrast to the Oligocene seal, *Enhydra* lacks the ligamentum teres (Sokolov et al., 1974; Howard, 1975).

Its differences from *Potamotherium* are the more medial location of the lesser trochanter and the absence of the intertrochanteric crest. In *Potamotherium* the tendon of the obturator internus did not merge with the common tendon of the obturator externus and gemelli; the quadratus femoris was located on the intertrochanteric crest (Savage, 1957).

The Oligocene seal differs from *Zalophus* in having a more medially located lesser trochanter and in lacking an intertrochanteric crest. Presumably the insertion of the obturator externus in the Oligocene seal is located distal to the trochanteric fossa on the posteromedial side of the greater trochanter; the tendons of the two gemelli muscles were not joined together. In *Zalophus,* the tendon of the gemellus superior muscle does not join with the tendon of the obturator internus muscle; the tendon of the adductor brevis muscle inserts into the intertrochanteric crest (Howell, 1928; Lyon, 1937); and the ligamentum teres is absent.

From *Allodesmus,* the Oligocene seal differs in its smaller and thinner greater trochanter and its lack of the intertrochanteric crest. By analogy to the living otariids, the adductor brevis

TABLE 2.—Comparative diagnostic characters of the femora of the Oligocene seal and some other members of Carnivora. (+=character present; –=character absent; +/–=character variable.)

Character	Olig. seal	*Cystophora*	*Lutra*	*Enhydra*	*Potamotherium*	*Zalophus*	*Allodesmus*
1. Shallow and open trochanteric fossa	+	+	–	–	–	+	–
2. Greater trochanter slightly extended over head	+	+	–	–	–	–	–
3. Lesser trochanter present	+	+/–	–	–	+	+	+
4. Location of lesser trochanter on posteromedial side	+	+	–	+	+	–	+
5. Cervix short and narrow	+	–	+	+	+	–	+
6. Intertrochanteric ridge absent	+	+	+	+	–	–	–
7. Fovea for ligamentum teres present	+	–	+	–	+	–	–

muscle in *Allodesmus* inserted on the intertrochanteric crest (Mitchell, 1966; Hirota, 1983), which is not present in the Oligocene seal. The fovea capitis, and hence presumably the ligamentum teres, is absent also in *Allodesmus*.

Discussion

The osteology and interpreted myology of these proximal femora indicate that these remains are definitely more closely related to the Phocidae than to other carnivores (Table 2). In addition, the functional morphology of even these proximal femora can suggest whether this Oligocene seal used its hind limb predominantly for propulsion in water or to some degree for terrestrial movement as well.

For example, the diaphysis of the femur of *Lutra* is almost circular in cross-section and is better prepared for terrestrial locomotion than for aquatic movement. Increasing the surface area for insertion of the adductor muscle makes the shaft of the femur broader. The enlarged adductor muscle also helps prevent rotation and movement of the femur. The diaphysis in the Oligocene seal is flatter and wider than in *Lutra, Potamotherium,* and *Enhydra;* similar to that of *Allodesmus;* and narrower than in *Cystophora* and *Zalophus*.

The literature and observation of living animals both indicate that terrestrial locomotion in *Lutra* (and presumably in *Potamotherium*) is only slightly impaired. The increased surface area of the femur suggests that *Enhydra, Zalophus,* and the Oligocene seal have more limitations on land. *Cystophora* has lost the ability to turn its hind limbs forward on solid ground, as have other modern Phocidae, in contrast to the Otariidae and Odobenidae. When the animal is on land, the ligamentum teres allows rotational movement of the femur and helps to fix the head of the femur to the acetabular fossa. This ligament disappears when the animal spends less time on land (Tarasoff, 1972) and has greater freedom of movement of the femur. In the Oligocene seal there is morphological evidence for a higher degree of terrestriality than in *Cystophora* and *Zalophus* but much less than in *Lutra* and *Potamotherium*.

The distribution among carnivore taxa of osteological features associated with lower-limb propulsion can assist in interpreting the specific method of locomotion in both aquatic and terrestrial movement. The main effect of the flattening and expansion of the greater trochanter is thus to increase the area of insertion of the muscles that rotate the femur (Howell, 1928; Tarasoff, 1972; Gordon, 1983). The Oligocene seal, with its greater trochanter only slightly expanded, used its hind limb in lateral movement and with some flexion and adduction (similar to *Cystophora*) for aquatic movement. This involved little rotation of the femur, suggesting that these Oligocene animals were not as good swimmers as later phocids.

As the antagonistic muscle to those lateral rotators, the iliopsoas muscle, located on the caudal side of the femur, becomes very much reduced and weakened. In parallel to the decrease in its stress on the lesser trochanter, the latter is reduced and finally disappears. In those mammals that do not bring their hind limbs forward, the lesser trochanter is less and less developed. We can observe this progressive reduction from *Lutra,* to the Oligocene seal, to *Cystophora* (where it is small in males and absent in females), and finally to *Phoca,* where it is completely absent. The lateral rotation of the lower limb results in turning the hind foot so that it can move in a horizontal plane.

The anatomy of *Enhydra* and *Zalophus* shows that the feet of these animals are adapted predominantly for lateral movement, but that vertical and horizontal movement also is possible for body support and locomotor activity on land. On the other hand, the anatomy of the pelvic limb of *Lutra* is similar to that of completely terrestrial carnivores. Phocids have undergone major morphological changes that are closely correlated with their specialized methods of aquatic locomotion. In its patterns of aquatic locomotion, *Enhydra* shows analogy to both *Lutra* and *Cystophora* and to the Oligocene seal. Moreover, *Enhydra* has a convergent similarity to the seal in its elongated hind limb as the major organ of propulsion.

The primary result of this study is that, from the viewpoint of adaptation to the water, the numerous modifications of the Oligocene seal correspond most closely with *Cystophora*. From a taxonomic viewpoint, the relationship between the Oligocene seal and other phocids is supported both osteologically and, by inference, myologically.

Within the range of taxa compared herein, the Oligocene seal is closer in several characters (see Table 2) to the semiaquatic Mustelidae than to the representative of the eared seals. These characters are primitive (e.g., the lesser trochanter), indicating its derivation from land carnivores. At the same time, the Oligocene seal has derived characters (for example, the much enlarged greater trochanter) that place it within the Phocidae rather than as an ancestor of this taxon. The morphology of these partial femora, and the functional myology interpreted from the osteology, shows that the locomotor adaptations of the Oligocene seal were much closer to the pinniped type (especially the phocids) than to that of the semiaquatic mustelids. This, along with its occurrence in marine deposits, associated with other fully marine vertebrates, suggests that the Oligocene seal was well adapted to a marine environment.

Savage (1957:235) concluded that the Phocidae "evolved from a lutra-like mustelid in the Oligocene. The Otariidae and Odobenidae may have had a separate origin." The material of this Oligocene seal is not sufficient to either support or falsify the hypothesis of mustelid ancestry, but it is sufficient to conclude that the ancestor of Phocidae must be sought in deposits older than the late Oligocene.

Literature Cited

Barnes, L.G., and K. Hirota
1994. Miocene Pinnipeds of the Otariid Subfamily Allodesminae in the North Pacific Ocean: Systematics and Relationships. *Island Arc,* 3(4):329–360, 13 figures.

Berta, A., and A.R. Wyss
1994. Pinniped Phylogeny. *In* A. Berta and T.A. Deméré, editors, Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr., *Proceedings of the San Diego Society of Natural History,* 29:33–57, 6 figures, 3 tables, 2 appendices.

Erickson, B.R., and G.T. Sawyer
1996. The Estuarine Crocodile *Gavialosuchus carolinensis* n. sp. (Crocodylia: Eusuchia) from the Late Oligocene of South Carolina, North America. *Monograph of the Science Museum of Minnesota* (St. Paul), 3: 47 pages, 30 figures.

Gordon, K.R.
1983. Mechanics of the Limbs of the Walrus (*Odobenus rosmarus*) and the California Sea Lion (*Zalophus californianus*). *Journal of Morphology,* 175:73–90, 7 figures, 2 appendices.

Hirota, K.M.
1983. Notes on the Miocene Sea-Lion *Allodesmus.* 128 pages. Masters thesis, Department of Geology and Mineralogy, Faculty of Sciences, Kyoto University, Japan.

Howard, L.D.
1975. Muscular Anatomy of the Hind Limb of the Sea Otter (*Enhydra lutris*). *Proceedings of the California Academy of Sciences,* 40(12): 335–416, 59 figures.

Howell, A.B.
1928. Contribution to the Comparative Anatomy of the Eared and Earless Seals (Genera *Zalophus* and *Phoca*). *Proceedings of the United States National Museum,* 73(15):1–42, 1 plate.
1930. *Aquatic Mammals: Their Adaptations to Life in the Water.* vii + 338 pages, 54 figures. Springfield, Illinois, and Baltimore, Maryland: Charles C. Thomas.

Koretsky, I.A.
1987. [Sexual Dimorphism in the Structure of the Humerus and Femur of *Monachopsis pontica* (Pinnipedia: Phocinae).] *Vestnik Zoologii,* 4: 77–82. [In Russian.]

Lyon, G.M.
1937. Pinnipeds and a Sea Otter from the Point Mugu Shell Mound of California. *Publications of the University of California at Los Angeles in Biological Sciences,* 1(8):133–168, 11 figures.

Mitchell, E.D.
1966. The Miocene Pinniped *Allodesmus. University of California Publications in Geological Sciences,* 61:1–46, 29 plates.

Mori, Masaru
1958. The Skeleton and Musculature of *Zalophus. Folia Anatomica Japonica,* 31(3–4):203–284, 54 figures, 4 plates.

Piérard, Jean
1971. Osteology and Myology of the Weddell Seal *Leptonychotes weddelli* (Lesson, 1826). *In* W.H. Burt, editor, Antarctic Pinnipedia. *Antarctic Research Series,* 18:53–108, 59 figures.

Sanders, A.E.
1980. Excavation of Oligocene Marine Fossil Beds near Charleston, South Carolina. *National Geographic Society Research Reports,* 12: 601–621.

Sanders, A.E., and L.G. Barnes
2002. Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 2: *Micromysticetus rothauseni,* a Primitive Cetotheriid Mysticete (Mammalia: Cetacea). *In* R. Emry, editor, Cenozoic Mammals of Land and Sea: Tributes to the Career of Clayton E. Ray *Smithsonian Contributions to Paleobiology,* 93:271–293.

Sanders, A.E., R.E. Weems, and E.M. Lemon, Jr.
1982. Chandler Bridge Formation: A New Oligocene Stratigraphic Unit in the Lower Coastal Plain of South Carolina. *U.S. Geological Survey Bulletin,* 1529-H:105–124, figures 24–27.

Savage, R.J.G.
1957. The Anatomy of *Potamotherium,* an Oligocene Lutrine. *Proceedings of the Zoological Society of London,* 129(2):151–244, 38 figures, 3 plates, 8 tables.

Sokolov, I.I., A.S. Sokolov, and E.A. Klebanov
1974. [The Morphological Specialization of the Organs of Movement of Some Mustelidae, in Connection with Their Life-Style.] *In* [Functional Morphology of the Mammals.] *Trudy Zoologicheskogo Instituta, Akademii Nauk SSSR* (Leningrad), 54:4–103, 24 figures, 13 tables. [In Russian.]

Tarasoff, F.J.
1972. Comparative Aspect of the Hind Limbs of the River Otter, Sea Otter and Seals. *In* R.J. Harrison, editor, *Functional Anatomy of Marine Mammals,* pages 333–359. London and New York: Academic Press.