

**Sea Otter Systematics and Conservation: Which are Critical Subspecies?**

C. Gregory Anderson, John L. Gittleman, Klaus-Peter Koepfli, and Robert K. Wayne

The sea otter (*Enhydra* sp.) is a charismatic carnivore. As an aquatic, crustacean feeder possessing four incisors in the lower jaw, having webbed feet, and spending most of its life on its back, this is not your typical carnivore! Although all otters have adaptations for living in an aquatic environment, sea otters have carried this approach to an extreme and are unique in many respects. Indeed, in tracing the history of sea otter taxonomy some early authorities confused the many aquatic adaptations of the sea otter with its phylogenetic heritage. As a result, the sea otter was even misplaced with the pinnipeds, which include seals and sea lions, rather than with the mustelids, which include river otters, weasels, and badgers. Nevertheless, species designation and much of the phylogenetic history of the sea otter have been remarkably consistent and accurate (see Table 1). The main systematic difficulties rest with whether subspecific units are meaningful evolutionarily and how to manage these units from a conservation standpoint. In this paper, we review the history of sea otter systematics, summarize morphological and molecular studies of subspecies, comment on the implications systematics have for conservation efforts, and provide suggestions for future areas of study.

**Historical ranges and extirpations**

Table 1. History of the taxonomy of the sea otter, *Enhydra lutris*.

Name	Author	Comments
<i>Lutra marina</i>	Steller (1751)	Binomial but pre-Linnaean and therefore considered to be unacceptable according to the International Commission of Zoological Nomenclature (ICZN)
<i>Mustela lutris</i>	Linnaeus (1758)	Partially based on Steller's account (1751), <i>Mustela</i> was used for all members of the Mustelidae recognized at that time.
<i>Phoca lutris</i>	Pallas (1811)	An attempt to ally <i>Enhydra</i> with the Pinnipeds
<i>Pusa orientaliis</i>	Oken (1816)	An attempt to give <i>Enhydra</i> its own generic appellation but Oken's names are not available according to the ICZN (and has been synonymized with <i>Phoca</i> )
<i>Enhydra marina</i>	Fleming (1822)	Oldest available valid Genus name
<i>Latax lutris</i>	Gloger (1827)	Renaming of <i>Pusa</i> Oken, which was preoccupied
<i>Endris marina</i>	Lichtenstein (1827)	Emmendation of <i>Enhydra</i>
<i>Enchydris</i>	Lesson (1842)	Emmendation of <i>Enhydra</i>
<i>Enhydris lutris</i>	Lesson (1842)	Emmendation of <i>Enhydra</i>
<i>Enhydra</i>	Gray (1843)	First use of current name combination

*lutris*

*Sutra  
marina*

Elliot (1874) Junior synonym of *Enhydra*

Like many carnivores, the history of sea otter distribution is one of an initial contiguous range followed by periodic extirpations, leaving present-day population ranges patchily distributed (see Figure 1).

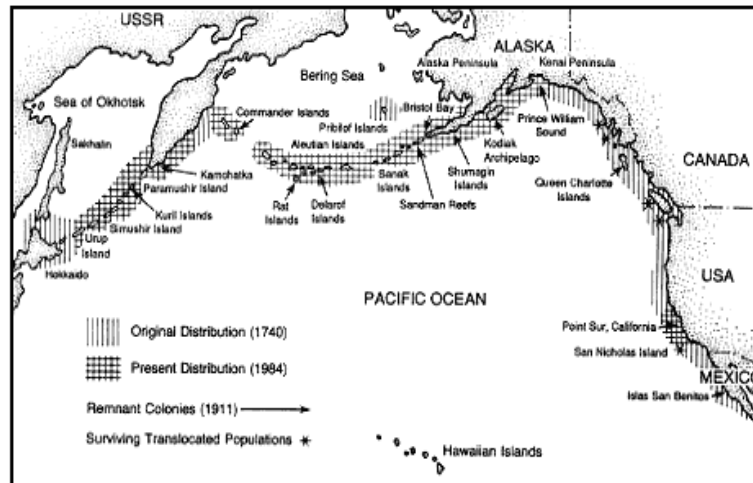


Figure 1. Present distribution of the sea otter.

Historical records of distribution are reasonably reliable, as *Enhydra* was known to the indigenous peoples who hunted them, and trade in sea otter pelts to the Spanish began in California at least by and probably prior to 1733 (Ogden 1941). The historical range of the sea otter extended across the Pacific rim in a wide arc from Morro Hermoso in Baja California to the island of Hokkaido in northern Japan (Ogden 1941; Barabash-Nikiforov 1947). Population estimates for this historical range vary from between 100,000-150,000 (Kenyon 1969) to 300,000 (Johnson 1982).

According to Barabash-Nikiforov (1947), intensive hunting of the sea otter in the northern part of its range began almost immediately upon the return of Steller from the Bering Expedition (1741-1742), which collected over 700 pelts. This expedition provided one of the first detailed descriptions of the sea otter from Bering Island, but ironically also led to its extirpation there. By 1762, after thousands of pelts were exported from Bering Island by commercial hunters, there were too few sea otters in the area to justify commercial expenses in hunting them. This pattern was repeated throughout the range of the sea otter, exterminating population after population around the Pacific rim from Kamchatka to Alaska, British Columbia, Washington, Oregon, California, and Baja California. Estimates for the total number of sea otters killed from 1740 to 1911 range from 500,000 (Kenyon 1969) to well over 800,000 (Lensink 1960). The result of such unregulated hunting was a patchwork of roughly 11-13 isolated populations from what was once a continuous distribution (Kenyon 1969). It is estimated that only about 1,000 individuals survived the onslaught of commercial hunting (Kenyon 1969), between 1 and 2 percent of the original estimated population.

In California, estimates of historical population numbers range from 16-20,000 (Ralls et al. 1983; see DeMaster et al., this issue). Commercial hunting began in 1784 and ended in 1840 when it became unprofitable due to the low number of available sea otters (Ogden 1941). The population was thought to be extinct by the turn of the century, but a small group of between 32-50 were observed in 1914 (Bryant 1915). Subsequent rediscoveries of sea otters in California elicited much excitement. When a rancher and his wife found a small population off the coast of Big Sur in 1938 (Bolin 1938), one marine biologist remarked that reporting dinosaurs would not have caused more surprise (Wolkomir 1995)!

Under protection of the International Fur Trade Treaty of 1911, sea otter populations around the Pacific began to recover, slowly at first and mainly in areas with little human disturbance. Today, it is estimated that sea otters inhabit most of their historic range west of Prince William Sound (Riedman and Estes 1988, 1990; Estes 1990), but populations have not yet fully recovered in Southeast Alaska and British Columbia and are very limited south of British Columbia.

### Subspecific status

Subspecies are defined as a geographical or ecological population within a species which differs from any other such population within the same species. The difficulty arises in what we mean by "differs." Variation within a species often differs among individuals, varieties and subspecies; the problem lies in determining how much of this variation represents a legitimate subspecies. Subspecific delineations involve a continuous process of refinement with a subspecies proposed, then reanalyzed and refined, until relative stability is reached. Recently emphasis has been placed on taxonomically identifying subspecies by concordant characters which are consistent with explicit phylogenetic partitioning (Avice and Ball 1990; O'Brien and Mayr 1991). The following is a review of how the above subspecific delineations for *Enhydra* have been refined over the years and provide a consistent phylogenetic picture.

#### *Morphological data*

Barabash-Nikiforov (1947) was the first to suggest that the Commander Island subspecies was not sufficiently different from the Aleutian Island form and so designated the Northern American form as *E.I. lutris*, the Kuril-Kamchatkan race as *E.I. gracilis*, and the Southern Californian group as *E.I. nereis*. Barabash-Nikiforov based these findings on measurements from 5 specimens from the Aleutian Islands and Alaska, 3 specimens from the Commander Islands, 7 from Mednyi Island, 5 from the southern tip of the Kamchatka Peninsula, and 1 from Bering Island. No specimens were available from either the Kuril Islands or California. The separation of *E.I. gracilis* was based primarily on pelage differences described from pelt scraps (Barabash-Nikiforov 1947) and the description of this form was later refuted by Stroganov (1962) because it is a composite of other subspecies (but see below).

The subspecific taxonomy of the southern sea otter (*E.I. nereis*) was not contested until Scheffer and Wilke (1950) reexamined the specimen used by both Merriam (1904) and Grinnell et al. (1937) as well as new material from western (n=46) and southeastern (n=2) Alaska, Washington (n=1), Oregon (n=2), and California (n=5, including the type-specimen). They concluded that several of Merriam's characters were flawed and there was insufficient evidence to support the existence of a southern subspecies of sea otter. Despite these assertions, most authors were not convinced because of small sample sizes and therefore continued to recognize the southern subspecies (e.g., Murie 1959).

In 1969, Kenyon critically reviewed the southern subspecies question, specifically in regard to Scheffer and Wilke's (1950) analysis. Kenyon summarized his position as follows: "...it is not possible, without further study, to distinguish racially distinct populations which might exist" (Kenyon 1969, p. 5). Later, Kenyon (1982) reiterated the conclusion of Roest: "...all sea otters from the Pacific coast of North America represent a single clinally varying population, *Enhydra lutris lutris*" (Roest 1979, p. 14). The precise study called for by Kenyon was performed by Wilson et al. (1991), with one ironic result being an accepted subspecies designation bearing Kenyon's name, *Enhydra lutris kenyoni*. This study examined 236 specimens from the former Soviet Union, 84 from northwestern North America and Alaska, and 48 specimens from California (total n=368), using a sequential discriminant function analysis. They found clear support for the recognition of three subspecies of sea otter, with the greatest distinction existing between the two extreme populations in the USSR and California, and mandibular length generally being the best morphological character for subspecific recognition. Currently there are three recognized subspecies of *Enhydra lutris* (Reeves et al. 1992; Wozencraft 1993), as shown in Table 2.

Table 2. Commonly recognized subspecies of sea otter.

Subspecies	Author	Common name	Status
------------	--------	-------------	--------

Name			
E. I. lutris	(Linnaeus 1758)	Asian sea otter	CITES Appendix 2
E. I. kenyoni	(Wilson, 1991)	Alaskan sea otter	CITES Appendix 2
E. I. nereis	(Merriam, 1904)	California sea otter	CITES Appendix 1 U.S. ESA Threatened

In summary, morphological analyses have consistently supported subspecies designations. However, further phylogenetic studies of these subspecies are needed to clarify the systematics at the subspecific level. What new analyses would improve our understanding? As stated, most phylogenies across species have been morphological, with major emphasis on cranial and dental characters. Consistency among studies is hampered by selection of different characters, subjective evaluations of characters, variation in phylogenetic methods, and non-representation of some taxa (see Table 1). We are now correcting some of these problems (Anderson and Gittleman, in preparation) by analyzing across all lutrines a broader suite of morphological and other characters (e.g., behavioral and life history traits) than has been previously used. In addition, as many complications of phylogenetic study undoubtedly rest with convergence due to the effects of aquatic living, molecular analyses will play a critical role in better understanding systematic relationships.

#### *Molecular data*

Molecular analyses will serve as an independent test of the results obtained from morphological analyses. Most molecular studies to date have only examined higher level relationships among carnivore families (Wayne et al. 1989; Vrana et al. 1994; Ledje and Arnason 1996); few have dealt with relationships within the Mustelidae (but see Masuda and Yoshida 1994). However, a project examining the phylogenetic relationships among otter species using DNA sequences of the mitochondrial DNA cytochrome b gene is currently underway (Koeplli and Wayne, in preparation).

Molecular techniques are quite useful for delineating systematic relationships among populations and subspecies (Avice 1994). Much molecular work is ongoing with the sea otter, particularly in evaluating the subspecific question (Scribner et al., in press).

Lidicker and McCollum (1981, cited in Riedman and Estes 1990, and Scribner et al., in press) used allozymes to determine levels of heterozygosity and genetic differentiation between the Californian and Alaskan populations. Their findings indicated that five of 30 loci were variable and no alleles were site specific; they hypothesized that the absence of rare alleles in the California population was due to population bottleneck effects, although this is not completely accepted.

Rotterman (1992) also used allozymes to assess genetic variability between three Alaskan populations and the California population. Of 41 loci examined, only three were variable, and only two of these were sufficiently variable to be informative. Genetic distances for these populations were also small (0.001-0.006), revealing a high degree of genetic similarity (Nei 1978) that would not confirm subspecific status for the California population. An intriguing result from the genetic distance analysis was that the California population showed a higher genetic affinity to several of the Alaskan populations than among the Alaskan populations themselves.

Recent analyses of mitochondrial DNA (mtDNA) employing restriction fragment-length polymorphisms (RFLPs) assessed relationships among populations in Prince William Sound, the Kuril Islands, and central California (Sanchez 1992). The California population was most divergent from the Prince William Sound population, followed by the Kuril Island and Prince William Sound populations, and lastly the Kuril

Island and California populations, revealing total genetic divergences of 0.0008-0.0060. Sanchez concluded that the mtDNA haplotype distribution generally supported the morphological classification of Wilson et al. (1991), although there was also indication of recent common ancestry, high gene flow and reduced effective population sizes. To date, analyses of mitochondrial DNA (mtDNA) have only approximated divergences among otters and other mustelids using linear fragments from different parts of the mtDNA molecule without mapping restriction sites (Cronin et al. 1996); therefore, caution must be taken because single-locus phylogenies may not be accurate.

Most recently, Cronin et al. (1996) used RFLPs of several large segments of mtDNA, amplified using the polymerase chain reaction (PCR) technique, to investigate genetic differentiation within and among subspecies. Results indicate that only *E.I. nereis* has monophyletic mtDNA, not found in either populations of *E.I. lutris* or *E.I. kenyonii*. Cronin et al. (1996) propose an explanation that there was pre-exploitation divergence between the following four groups: California, Prince William Sound, Kodiak-Adak-Amchitka-Attu-Medney islands, and Kuril island populations. In examining these results it appears that these divergent populations correspond to the four most frequently proposed subspecies (*E.I. nereis*, *E.I. kenyonii*, *E.I. lutris*, and *E.I. gracilis*, respectively).

### **Conclusion and recommendations**

Molecular studies consistently support differentiation among populations along subspecific lines. The California subspecies (*E.I. nereis*) appears to have monophyletic haplotypes of mtDNA, which do not overlap with other populations; in contrast, *E.I. lutris* and *E.I. kenyonii* have frequencies of haplotypes which are similar to some extent. Four problems should receive future molecular work.

(1) The California haplotypes, though monophyletic, are not unequivocal and therefore phylogenetic analysis should be performed alongside other genetic and morphological studies (Cronin et al. 1996).

(2) Genetic sequence analysis using the mitochondrial DNA control region and nuclear microsatellites should be used to distinguish populations within subspecies which may be important for identifying populations that may be managed as independent units (currently being carried out by Koepfli and Wayne).

(3) Much of the studies using mtDNA (e.g., Cronin et al. 1996; Sanchez 1992; Koepfli and Wayne, in preparation) have shared samples. An independent analysis is needed to assess whether some concordance among molecular results is affected by sampling biases.

(4) Although allozymes have been used previously (see review in Scribner et al., in press), additional nuclear markers with higher variability need to be employed to assess concordance with mitochondrial DNA results. Koepfli and Wayne are currently conducting such a study using hypervariable nuclear microsatellite markers.

Without question, bad taxonomy is detrimental to conservation efforts. An increasing number of studies show that endangered and threatened species must be rigorously defined by explicit phylogenetic units (Avice and Ball 1990; O'Brien and Mayr 1991). Present data indicate validity of named subspecies for the sea otter and therefore current protection measures should remain in place to ensure the survival of threatened populations. (*E.I. nereis* is listed as threatened under the Endangered Species Act and under CITES Appendix 1, all other subspecies are listed under CITES Appendix 2; see Baur et al.; Clark, this issue). Further systematic work is needed, however, to bring into line subspecific recognition with regard to phylogenetic units. First, phylogenetic analyses of different phenotypic characters and molecular gene markers should resolve the history of natural population distinctions. Second, phylogenetic population clusters should then be identified in relation to phylogeographic boundaries. Conservation efforts involving captive management and breeding programs as well as reintroduction plans must demand such results from systematics.

## Literature Cited

- Avise, J.C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York, New York. 511 pp.
- Avise, J.C., and R.M. Ball Jr. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology* 7:45-67.
- Barabash-Nikiforov, I.I. 1947. Kalan. Pages 1-174 in Soviet Ministrov RSFSR. Glavnoe upravlenie po zapovednikam. [The sea otter. Translated from Russian by A. Birron and Z.S. Cole for the National Science Foundation by the Israel Program for Scientific Translations, Jerusalem, Israel. 1962. 227 pp.].
- Bolin, R.L. 1938. Reappearance of the southern sea otter along the California coast. *Journal of Mammalogy* 19:301-303.
- Bryant, H.C. 1915. Sea otter near Point Sur. *California Fish and Game* 1:134-135.
- Cheney, L.C. 1995. An assessment of genetic variation within and between sea otter (*Enhydra lutris*) populations off Alaska and California. M.S. thesis, San Jose State University, Moss Landing, California. 49 pp.
- Cronin, M. A., J. Bodkin, B. Ballachey, J. Estes, and J. C. Patton. 1996. Mitochondrial-DNA variation and populations of sea otters (*Enhydra lutris*). *Journal of Mammalogy* 77:546-557.
- Davis, J.A. 1978. A classification of the otters. Pages 14-33 in N. DuPlaix, editor. *Otters: proceedings of the first working meeting of the Otter Specialist Group*. Paramibo, Surinam, March, 1977. IUCN, Morges, Switzerland. Davis, J.D. and W.Z. Lidicker. 1975. The taxonomic status of the southern sea otter. *Proceedings of the California Academy of Sciences, Fourth Series* 40:429-437.
- Elliot, H.W. 1874. The sea otter and its hunting. Pages 54-62 in A report upon the condition of affairs in the Territory of Alaska. House Executive Document Number 83, 44th Congress, 1st session, Washington, D.C. 277 pp.
- Estes, J.A. 1990. Action plan for sea otters. Pages 22-28 in P. Foster-Turley, S. Macdonald, and C. Mason, editors. *Otters: an action plan for their conservation*. IUCN/SSC Publication, Kelyvn Press, Broadview, Illinois. 126 pp.
- Fleming. 1822. *The Philosophy of Zoology*. Archibald Constable, Edinburgh, Scotland. 2:187-188.
- Gittleman, J.L. and S.L. Pimm. 1991. Crying wolf in North America. *Nature* 351:524-525
- Gloger, C.W.L. and J.L.C. Gravenhorst. 1827. Bemerkungen über ein Paar schlesische Sœugethierarten. *Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorium* 13:479-512.
- Gray, J.E. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History) Publications, London, United Kingdom. 216 pp.
- Grinnell, J., J.S. Dixon, and J.M. Linsdale. 1937. *Fur-bearing mammals of California*. University of California Press, Berkeley, California. 375 pp.
- Harris, C.J. 1968. *Otters: a study of the recent Lutrinae*. Weidenfield and Nicolson, London, United Kingdom. 397 pp.

- Johnson, A.M. 1982. The sea otter, *Enhydra lutris*. Mammals in the seas: small cetaceans, seals, sireneans, and otters. Food and Agriculture Organization of the United Nations. Fisheries Series 5(4):525-531.
- Kenyon, K.W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna, Number 68. 352 pp. Kenyon, K.W. 1982. Sea otter. Pages 704-710 in J.A. Chapman and G.A. Feldhamme, editors. Wild mammals of North America: biology, management, and economics. Johns Hopkins University Press, Baltimore, Maryland. 1147 pp.
- Ledje, D. and U. Arnason. 1996. Phylogenetic analyses of complete cytochrome b genes of the Order Carnivora with particular emphasis on the Caniformia. *Journal of Molecular Evolution* 42:135-144.
- Lensink, C.J. 1960. Status and distribution of sea otters in Alaska. *Journal of Mammalogy* 41:172-182.
- Lesson, R.P. 1827. *Manuel de Mammalogie*. Roret, Paris, France. 441 pp.
- Lesson, R.P. 1842. *Nouveau Tableau du Règne Animal. Mammifères*. Paris, France.
- Lidicker, W.Z. and F.C. McCollum. 1981. Genetic differentiation of sea otter populations. Fourth Biennial Conference on the Biology of Marine Mammals, December 14-18, San Francisco, California.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10th edition Laurentii Salvii, Upsala 1:1-824.
- Masuda, R. and M.C. Yoshida. 1994. A molecular phylogeny of the Family Mustelidae (Mammalia, Carnivora), based on comparison of mitochondrial cytochrome b nucleotide sequences. *Zoological Science* 11:605-612.
- Merriam, C.H. 1904. A new sea otter from southern California. *Proceedings of the Biological Society of Washington* 17:159-160.
- Murie, O.J. 1959. Fauna of the Aleutian islands and Alaska peninsula. *North American Fauna* 61:1-406.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583-590.
- O'Brien, S.J. and E. Mayr. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. *Science* 251:1187-1188.
- Ogden, A. 1941. *The California sea otter trade 1784-1848*. University of California Press, Berkeley, California. 251 pp.
- Oken, L. 1816. *Lehrbuch der Natugeschichte. Zoologie*. August Schmidt und Comp., Jena 3:1-1270.
- Pallas, P.S. 1811. *Zoographia Rooso-Asiatica*. St. Petersburg 1:1-100.
- Ralls, K., J. Ballou, and R.L. Brownell. 1983. Genetic diversity in California sea otters: theoretical considerations and management implications. *Biological Conservation* 25:209-232.
- Reeves, R. R., B. S. Stewart, and S. Leatherwood. 1992. *The Sierra Club Handbook of Seals and Sirenians*. Sierra Club Books, San Francisco, California. 359 pp.

Riedman, M.L. and J.A. Estes. 1988. A review of the history, distribution, and foraging ecology of sea otters. Pages 4-21 in G.R. VanBlaricom and J.A. Estes, editors. The community ecology of sea otters. Springer-Verlag Publishing, New York, New York. 237 pp.

Riedman, M.L. and J.A. Estes. 1990. The sea otter (*Enhydra lutris*): behavior, ecology, and natural history. U.S. Department of the Interior, Fish and Wildlife Service. Biological Report 90(14). Washington, D.C. 126 pp.

Roest, A.I. 1971. A systematic study of the sea otter (*Enhydra lutris*). Pages 133-135 in Proceedings of the Eighth Annual Conference on the Biology of Sonar and Diving Mammals. Menlo Park, California.

Roest, A.I. 1973. Subspecies of the sea otter, (*Enhydra lutris*). Contributions in Science, Los Angeles County Museum 140(252):1-17.

Roest, A.I. 1976. Systematics and the status of sea otter *Enhydra lutris*. Bulletin of the California Academy of Sciences 75:267-270.

Roest, A.I. 1979. A reevaluation of sea otter taxonomy. Page 14 in Abstracts of the Sea Otter Workshop, August 23-25, 1979, Santa Barbara, California.

Rotterman, L.M. 1992. Patterns of genetic variability in sea otters after severe population subdivision and reduction. Ph.D. dissertation, University of Minnesota, Minneapolis, Minnesota. 227 pp.

Sanchez, M.S. 1992. Differentiation and variability of mitochondrial DNA in three sea otter, *Enhydra lutris*, populations. M.S. thesis, University of California, Santa Cruz, California. 101 pp.

Scheffer, V.B. and F. Wilke. 1950. Validity of the subspecies *Enhydra lutris nereis*, the southern sea otter. Journal of the Washington Academy of Science 75:269-272.

Scribner, K.T., J. Bodkin, B. Ballachey, S.R. Fain, M.A. Cronin, and M. Sanchez. In press. Population genetic studies of the sea otter (*Enhydra lutris*): a review and interpretation of available data. U.S. Department of Commerce, National Oceanic and Atmospheric Administration Technical Report.

Steller, G.W. 1751. De Bestiis Marinis. Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae 2:389-398, pls. 14-16.

Stroganov, S.U. 1962. Zveri Sibiri: khishchnye. Akademiya Nauk SSSR. Sibirskoe Otdelenie. Biologicheskii Institut, Moskow. [Carnivorous mammals of Siberia. Translated from Russian by A. Biron, published for the Smithsonian Institution and the National Science Foundation by the Israel Program for Scientific Translations, Jerusalem, Israel. 1969. 522 pp.].

van Zyll de Jong, C.G. 1972. A systematic review of the nearctic and neotropical river otters. Royal Ontario Museum 80:1-104.

Vrana, P.B., M.C. Milinkovitch, J.R. Powell, and W.C. Wheeler. 1994. Higher level relationships of the Arctoid Carnivora based on sequence data and "total evidence." Molecular Phylogenetics and Evolution 3:47-58.

Wayne, R.K., R.E. Benveniste, D.N. Janczewski, and S.J. O'Brien. 1989. Molecular and biochemical evolution of the Carnivora. Pages 465-494 in J. L. Gittleman, editor. Carnivore behavior, ecology and evolution. Cornell University Press, New York, New York. 620 pp.



Wilson, D.E., M.A. Bogan, R.L. Brownell, A.M. Burdin, and M.K. Maminov. 1991. Geographic variation in sea otters, *Enhydra lutris*. *Journal of Mammalogy* 72:22-36.

Wolkomir, R. 1995. The fragile recovery of California sea otters. *National Geographic*, 187:42-61.

Wozencraft, W.C. 1993. Order Carnivora. Pages 279-348 in D. E. Wilson and D. M. Reeder, editors. *Mammal species of the world: A taxonomic and geographic reference*. Smithsonian Institution Press, Washington, D.C. 1207 pp.

Greg Anderson and John Gittleman are with the Department of Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, TN 37996-1610. Klaus-Peter Koepfli and Robert Wayne are with the Department of Biology, The University of California, Los Angeles, CA, 90024-1606.

[back to index](#)