

Monachus tropicalis. By Peter J. Adam

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Monachus Fleming, 1822

- Phoca* Linnaeus, 1758:38. Type species *Phoca vitulina*.
Monachus Fleming, 1822:187 (footnote). Type species *Phoca monachus*.
Pelagios Cuvier, 1824:196. Type species not specified.
Pelagius Cuvier, 1826:550. Type species *Pelagius monachus*.
Pelagus McMurtrie, 1834:71. Erroneous spelling of *Pelagius* Cuvier.
Pelgias Gray, 1837:582. Type species not specified.
Pelagocyon Gloger, 1842:163. Type species *Pelagocyon monachus*.
Rigoon Gistel, 1848:X. New name for *Pelagius* Cuvier.
Cystophora Gray, 1849:93. In part.
Heliophoca Gray, 1854a:43. Type species *Heliophoca atlantica*.
Mammonachus Herrera, 1899:13. Type species not specified.

CONTEXT AND CONTENT. Order Carnivora, suborder Pinnipedia, family Phocidae, subfamily Monachinae, genus *Monachus*. Paraphyly of the genus has been suggested (Paulian 1959; Wyss 1988), although recent studies support its monophyly (Bininda-Emonds and Russell 1996; Bininda-Emonds et al. 1999). *Monachus* includes 3 allopatric species: *M. monachus* (Mediterranean Sea and northwest African coast), *M. schauinslandi* (Hawaii and its leeward chain of islands), and *M. tropicalis* (western tropical Atlantic Ocean). A dichotomous key to adults follows (from Bininda-Emonds and Russell 1996; Kenyon and Rice 1959; King 1956; King and Harrison 1961; and specimens listed in Remarks):

1. Pelage usually with conspicuous ventral white patch; upper incisors without marked cervical constriction; P2–4 and p2–4 with single cusp posterior to main cusp; antorbital process prominent; pterygoid processes poorly defined and not visible in dorsal view; anterior tips of nasals rounded; visibility through paired optic foramina in lateral view not blocked by bone; auditory bulla without distinct oblique ventral sulcus *M. monachus*
 Pelage without ventral white patch; upper incisors with marked cervical constriction; P2–4 and p2–4 with 2 cusps posterior to main cusp; antorbital process reduced; laterally curved pterygoid processes well developed and usually visible in dorsal view; anterior tips of nasals flat or incised; visibility through paired optic foramina in lateral view usually blocked by bone; auditory bulla with distinct oblique ventral sulcus 2
2. Extra bone encircling jugular foramen; postorbital constriction absent except in presence of Wormian bones on interorbital septum; frontomaxillary suture passes through antorbital process; posterior ends of nasals rounded *M. schauinslandi*
 Extra bone around jugular foramen absent; postorbital constriction present; antorbital process confined to maxilla; posterior ends of nasals pointed *M. tropicalis*

Monachus tropicalis (Gray, 1850)

West Indian Monk Seal

- Cystophora antillarum* Gray, 1849:93. Type locality “West Indies.” In part.
Phoca tropicalis Gray, 1850a:28. Type locality “Jamaica.” (Genus not specified) *wilkianus* Gosse, 1851:307–308 (footnote). Type locality “Pedro Kays off the south coast of Jamaica.”
Monachus tropicalis: Gray, 1866a:20. First use of current name combination.

CONTEXT AND CONTENT. Context as above. *Monachus tropicalis* is monotypic, although *M. schauinslandi* may be a subspecies of *M. tropicalis* (Kenyon and Rice 1959).

DIAGNOSIS. *Monachus tropicalis*, being limited to the western tropical Atlantic Ocean, is readily distinguished from congeners based on allopatry. It also differs from congeners by presence of a postorbital constriction of the skull and reduced antorbital process confined to maxilla. *M. tropicalis* is distinguished from other western Atlantic phocids in having smooth vibrissae; incisor formula of 2/2; a broad, parallel-sided interorbital region; nasal bones in broad contact with premaxilla; and large, obliquely positioned postcanine teeth with crenulate enamel surfaces (King 1956; Nowak 1995; Ray 1977).

GENERAL CHARACTERS. *Monachus tropicalis* (Fig. 1), now almost certainly extinct, has a typical seal-like appearance, with well-developed blubber layer, flipper-like limbs, short tail, and smooth body contour. External pinnae are absent, and fore- and hind limbs are enclosed within body contour to level of proximal humerus and knee, respectively (Gosse 1851; Hill 1843). Manual claws are well-developed (1.9–2.5 cm long), but pedal claws are reduced to horny points (Allen 1887a, 1887b; King 1956). Manus has either glabrous palms (Allen 1880; Gosse 1851) or palms with short hairs (True and Lucas 1886). Manual digit I is longest, with each successive digit being shorter. Pedal digits I and V are longest, others being successively shorter mesially (Gosse 1851; Hill 1843; King 1956). Penis is hidden within body contour and testes are inguinal (Gosse 1851). Females have 2 pairs of functional mammae (Ward 1887). Head is large and prominent. Eyes are large with dark brownish-red (Gaumer 1917), light reddish-brown (Ward 1887), or crimson (Hill 1846) irises; round pupils; and little sclera at iridial margins (King 1956). Nostrils are narrow fissures (Gosse 1851; Hill 1843).

Adult pelage, which lacks underfur, is dark dorsally and grades into a lighter countershade ventrally. Dorsal fur is variable in color, being brown, sepia, black, dark blackish-brown, or dark gray, and often appears grizzled due to distal tips of hair shafts being gray or yellow. Ventral fur ranges from pale yellow to yellowish-gray or yellowish-brown and is sometimes mottled with darker patches. Front and sides of muzzle and edge of full and fleshy lips are yellowish-white. Limbs are of a similar color to the dorsum (Allen 1887a; Fernández de Oviedo 1944; Gaumer 1917; Goodwin 1946; Gosse 1851; Hill 1843; King 1956; True and Lucas 1886;



FIG. 1. Captive *Monachus tropicalis* of unknown sex at the New York Aquarium in ca. 1910. Photograph reproduced with permission of the Department of Mammalogy Archives, American Museum of Natural History. Specimen originally captured from either Arrecifés Triángulos (Campeche) or Arrecife Alacrán (Yucatan) in Mexico (Townsend 1909).



FIG. 2. Dorsal, ventral, and lateral view of skull and lateral view of mandible of an adult female *Monachus tropicalis* collected at the Arrecifés Triángulos (Campeche, Mexico) on 23 June 1900 by E. A. Goldman and E. W. Nelson (National Museum of Natural History, USNM 102536). Right P2 is missing. Condylbasal length is 258 mm.

Ward 1887). Older adults tend to be lighter in color, with more gray, and sometimes a dusky-colored muzzle (Allen 1887a). Females are reported to be more uniform than males in color, with less white or yellow ventrally (Gauger 1917; King 1956), but Allen (1887a) notes no perceptible sexual differences.

Few marks of combat were visible in ca. 50 specimens (Ward 1887), although a large male with many scars was observed (Gosse 1851). Individual body hairs are short (maximum length 6–10 mm), stiff, and closely appressed to the skin (Gosse 1851; Hill 1843; King 1956). Alga in the fur occasionally makes some individuals appear green on the back and hind flippers (Ward 1887). The ventrum may have ochre (Allen 1887a) or red discoloration (Fernández de Oviedo 1944; Gaumer 1917). Near-term fetuses and suckling pups lack dorsoventral countershading and instead have a pure black pelage of long, soft, and wooly hairs (Ward 1887). An intermediate juvenile pelage is yellowish-gray dorsally (Gauger 1917).

Smooth, flexible, and tapering mystacial vibrissae are arranged in 6 rows. Longest shafts are ca. 7.6 cm in adults and 11.4 cm in young specimens (Allen 1887a). Individual shafts are oval in cross section (King 1956). Vibrissae are variable in color, from black to yellow-white, and sometimes have dusky colored bases, transverse bars of gray, or dark or light colored tips (Allen 1887a, 1887b; Gosse 1851; Hill 1843; King 1956; True and Lucas 1886). Vibrissae of individual animals also vary in color (Gosse 1851). Vibrissae

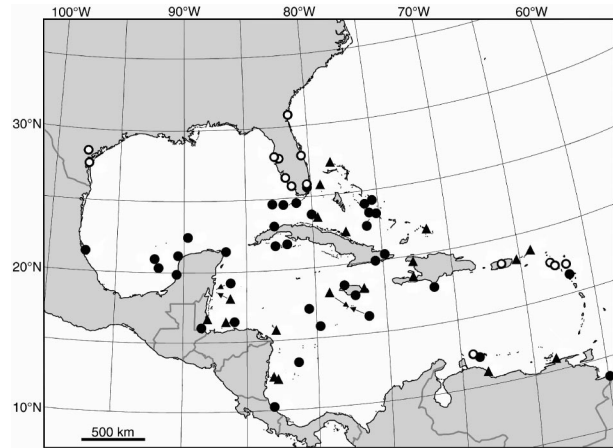


FIG. 3. Distribution of *Monachus tropicalis* in the western tropical Atlantic region based on historical records (closed circles), archaeological and fossil records (open circles), and localities with names suggestive of occurrence (triangles). Details provided in Adam and Garcia (2003). Adapted with permission from Timm et al. (1997).

of newborn pups are completely black and longer and thicker than those of adults (Allen 1887a, 1887b; King 1956; Ward 1887). Vibrissae become shorter, thinner, more tapered, and lighter in color with age (Allen 1887a).

Females are slightly smaller than males (Allen 1887a; Allen 1942; Boulva 1979; King 1956). Standard measurements (Anonymous 1967) of length (nose to tail) are 226 cm for 1 adult male, 199, 214, 216, and 224 cm for 4 pregnant females, and 89 cm for 1 near-term fetus (Allen 1887a; Ward 1887). Standard lengths of 3 adult males estimated from skeletons are: 216, 226, and 229 cm (Allen 1887c; Ward 1887). A standard length range of 213–244 cm is reported for adult male *M. tropicalis*, although the source of this estimate is unclear (Allen 1887a). Nose to tail lengths on preserved skins range from 131 to 145 cm for 3 immature individuals and up to 217 cm for 9 adults. The pelt of a pup assumed to be only a few days old is 107 cm (Ward 1887).

Tail lengths of adults range from 5.1 to 7.6 cm (Allen 1887b; Gosse 1851; Hill 1846; Ward 1887). Manus and pes lengths of a mature (214 cm) female are 30.0 and 32.0 cm, respectively (Allen 1887a). Other detailed, nonstandard measures of *M. tropicalis* are available (Allen 1887a; Gosse 1851; Hill 1843, 1846). Estimates of 305 cm for length of a male (Gosse 1851) and >457 cm length and 244 cm in maximum girth for adults (Fernández de Oviedo 1944; Nesbitt 1836) are probably exaggerated. Body mass, available for a captive female that was fed liberally and had little room to exercise, is 163 kg (Anonymous 1903).

Skull is dorsoventrally depressed and wide (Fig. 2). Sagittal crests are poorly developed in both sexes, and dorsal surface is convex in profile except for naso-maxillary region, which is flat (Allen 1887a; King 1956; True and Lucas 1886). Condylbasal lengths (in mm; $\pm SD$) in adult males (255.6 ± 26.0 , range 208.6–282.0, $n = 14$) and females (256.3 ± 16.2 , range 213.9–281.6, $n = 30$) do not differ. Cranial measurements (in mm; sexes combined; $\bar{X} \pm SD$, range, n) are: condylbasal length, 256.1 ± 19.6 , 208.6–282.0, 44; zygomatic width, 157.6 ± 13.4 , 108.6–180.3, 46; mastoid breadth, 146.8 ± 8.3 , 122.9–157.3, 45; least interorbital width, 27.7 ± 2.3 , 23.1–34.9, 46; width of rostrum at canines, 53.5 ± 4.4 , 43.5–62.1, 45; length of palate, 103.1 ± 8.5 , 79.6–114.6, 46; length of nasals, 62.3 ± 4.8 , 51.7–74.7, 46; length of dentary, 173.6 ± 15.6 , 137.4–197.2, 48 (Adam and Garcia 2003).

DISTRIBUTION. Historic distribution of *Monachus tropicalis* is unknown, but a minimum range (Fig. 3) has been interpolated from historical and archeological records and from geographical features bearing names suggestive of its presence (e.g., various Seal Cays and Seal Rocks in the western tropical Atlantic Ocean—Adam and Garcia 2003). West Indian monk seals are recorded from numerous isolated islands, cays, and reefs throughout southern, western, and northeastern portions of the Gulf of Mexico, along the southern coastline of the Caribbean Sea bordering Central

and South America as far east as Guyana, and throughout the Greater and Lesser Antilles. Extremes of known occurrence are Cumberland Island to the north (Georgia, United States; 30°52'N, 81°27'W), Islas de Lobos to the west (Veracruz, Mexico; 21°27'N, 97°13'W), and the coast of Guyana to the south and east (ca. 7°00'N, 60°00'W—Adam and Garcia 2003).

West Indian monk seals have not been confirmed for the northwestern Gulf of Mexico. Unconfirmed sightings along the Texas coast in the mid-1900s (Gunter 1947, 1954) were probably feral California sea lions (*Zalophus californianus*—Caldwell and Caldwell 1978; Gunter 1968; Rice 1973, 1998). Canines of *M. tropicalis* from Nuestra Señora del Espíritu Santo de Zuniga (Goliad County, ca. 1749) and Rancho Diemo (Nueces County, age not known) sites in Texas are known, but may represent trade items of North American aboriginals or colonial Spaniards (Raun 1964).

FOSSIL RECORD. *Monachus tropicalis* is represented in the fauna of Late Pleistocene (0.7–0.01 million years ago) Florida sites, including Melbourne (Ray 1958) and Lake Hellen Blazes (Neill 1957) in Brevard County as well as the Irvingtonian (1.77–1.07 million years ago) Leisey and Rigby Shell Pits in Hillsborough County (Berta 1995). It is absent from younger strata of Florida (Morgan 1994). Occurrence of *M. tropicalis* fossils in Pleistocene deposits of South Carolina (Ray 1961) is erroneous (Cumbaa 1980), and no pre-Holocene records of the species occur outside of Florida (Adam and Garcia 2003).

Subfossil Holocene remains are known from numerous archeological sites, including Long Bayou (Saint Petersburg, Pinellas County, Quaternary Period, ca. 4,500–2,800 years ago—Ray 1961), South Indian Field (Brevard County, Orange Period, ca. 4,000 years ago—Rouse 1951), Wightman Site (Sanibel Island, Lee County, ca. 2,300–1,900 years ago—Fradkin 1976; Wing 1992), Marco Island (Collier County, Glades I Period, 2,000–1,500 years ago—Cockrell 1970; Cumbaa 1980), Granada (Miami, Dade County, Glades I, III Periods, 2,000–500 years ago—Wing and Loucks 1984), Miami Circle (Miami, Glades I–II Periods, 2,500–1,250 years ago—I. Quitmyer and R. Carr, pers. comm.) in Florida, and Table Point in Georgia (Cumberland Island, Camden County, Depford Phase, 2,600–1,300 years ago—Milanich 1971). In the Greater Antilles, archeological remains of *M. tropicalis* are known only from the Taino Indian Caracoles Midden in Ponce, Puerto Rico (700–510 years ago—Y. Narganes, pers. comm.; Wing 1992). In the Lesser Antilles, remains are known from Cinnamon Bay (Saint John, U.S. Virgin Islands, 1,000–510 years ago—I. Quitmyer and K. Wild, pers. comm.), Sint Eustatius (Netherlands Antilles, 1,400–1,100 years ago—van der Klift 1992), as well as Hichman's Site (1,660 years ago) and Hichman's Shell Heap (2,550 years ago) on Nevis (Saint Christopher-Nevis—Wing 1992, 2001a). Two additional records at Santa Barbara (Ceramic Age, 400–1,600 years ago—Haviser 1994) and Sint Michiel (Archaic Age, 3,790–3,820 years ago—Debrot 2000; Haviser 1987) occur on Curaçao. *M. tropicalis* is the only species of its genus with a pre-Quaternary fossil history, and by this criterion is the oldest known record of *Monachus* (Deméré et al. 2003).

FORM AND FUNCTION. Blubber, especially on the abdomen, is thick. Blubber from a young male specimen (127 cm long) that had fasted 4 months was 10 cm thick and yielded 15 l of oil (Gosse 1851). Blubber in healthy adults is ca. 11 cm thick (Fernández de Oviedo 1944) and yields 76–114 l of oil. Individuals taken by sealers in November and December are fattest (Campbell 1978; Nesbitt 1836).

Eyes are described as expressionless or lusterless and opaque, with corneas protected by a fibromuscular membrane (Gauger 1917; Ward 1887), but the membrane and opacity probably represents a pathological condition, such as cataracts (Ridgway et al. 1975). Eyesight on land was poor, as *M. tropicalis* is unable to distinguish men from distances of ca. 27–37 m (Adam and Garcia 2003). External ear openings and nostrils can be closed and flared (Gosse 1851; Hill 1843).

Sides of wide rostrum of skull are subparallel, as are sides of the broad interorbital region. A slight postorbital constriction is present. Nasals are long, narrow, and typically separated anteriorly by external emergence of the nasal septum between them. Infra-orbital canals are large, usually with a longer dorsal border compared to the ventral border. Orbits are large. Tympanic bullae are enlarged and pachyostotic, with concave anterior margins and

oblique ventral sulci. Malleus and incus meet in a single, confluent saddle-shaped articulation. Mandibular symphysis is thick, but not fused except in old individuals. Ventral dentary margins are straight, and a low mandibular condyle is situated at the approximate alveolar plane. Dental formula is $i\ 2/2, c\ 1/1, p\ 4/4, m\ 1/1$, total 32. Lateral incisors are larger than medial incisors. Canines are large. Homodont postcanine teeth are large, have well developed cingula, and are set obliquely relative to the sagittal plane. Left and right upper tooththrows diverge from each other posteriorly. Postcanines are double-rooted except for P1 and p1, which have only 1 root, and M1 which has 1 or 2 roots. Enamel surfaces of newly erupted postcanine teeth are rugose, most bearing a large central cusp bordered anteriorly by a single accessory cusp and posteriorly by 2 cusps. M1 has 1 cusp on either side of central cusp, p1 has indistinct cusps, and m1 has only a single cusp posterior to central cusp. In older animals, both enamel and cusps are usually obliterated by wear (Adam 2001; Allen 1887a, 1887b, 1887c; Daneri and de Santis 2002; Goodwin 1946; King 1956; King and Harrison 1961; Repenning and Ray 1977; True and Lucas 1886; Wyss 1988).

Vertebral formula of *M. tropicalis* is 7 C, 15 T, 5 L, 3 S, 11–13 Cd, total 41–43 (Allen 1887a; King 1956; Thomson 1909). Skull and cervical, thoracic, lumbar, sacral, and caudal regions of the spine account for 12.4, 12.4, 36.4, 16.8, 5.0, and 16.8% of body length, respectively. Neural arches of cervical vertebrae may fail to meet dorsally. Only the first 2–3 caudal vertebrae have a neural arch. Ribs 1–13 have distinct capitulae and tuberculae, but 14–15 have capitulae only. Ribs 1–10 are vertebrosteral, 11 and 12 are vertebrocostal, and 13–15 are vertebral. Sternum has 9 sternbrae. Triangular scapulae have poorly developed spines but well-developed acromion processes. Humeri are short and robust, lack supracondylar foramina, and have strong detopectoral ridges that extend almost the entire shaft length. Radii are distally expanded. Manus has 7 bones: scapholunar, trapezium, trapezoid, os magnum, unciform, cuneiform, and pisiform. Manual and pedal formulae are 2-3-3-3-3 each. Os coxae have short, recurved ilia and strongly developed ischia and pubes. Pubic symphysis is unfused and probably cartilagenous in life. Femora are short, flattened, and distally expanded. Tibiae and fibulae fuse proximally. Pedes have 7 bones: astragalus, calcaneum, navicular, cuboid, and 3 cuneiforms. Pedal digits decrease in length as follows: I>V>II>IV>III. Baculum is well developed; baculum length is 16.7 cm in 1 adult (Allen 1887a; King 1956).

Bones are covered with thick musculature (Gauger 1917; Ward 1887). Brain has a well-developed cerebrum, cerebellum, olfactory lobe, numerous shallow fissures, an indistinct subsurface postica, and well-represented collateral fissure (Fish 1898). Brain mass is estimated at 460.0 g from an adult male skull (Bininda-Emonds 2000). *M. tropicalis* is commonly reported to have anterior notching of the tongue to facilitate nursing (Gosse 1851), although whether the original description (Hill 1843) referred specifically to *M. tropicalis* or to phocids in general is unclear.

ONTOGENY AND REPRODUCTION. Pregnant females are known only from the Triangle Keys of Mexico, where a newborn suckling pup and 5 females with fetuses were collected in early December (Ward 1887) in addition to a single pregnant seal from late June (Adam and Garcia 2003). *M. tropicalis* had low pupping synchrony due to the lack of seasonal climate changes and little seasonal variation in prey abundance (Adam and Garcia 2003). The smallest known sexually mature female was 199 cm long. Pregnant females did not completely leave the water when hauling out (Ward 1887). Although early natural historians reported that *M. tropicalis* commonly gave birth to paired young (Fernández de Oviedo 1944; López de Gómara 1932; Nesbitt 1836), only single fetuses were found in pregnant specimens (Adam and Garcia 2003; Ward 1887). A near-term fetus had a standard length of 89 cm and mass of ca. 17 kg and kicked and squirmed 1–2 min after being removed from the mother. One female lay on her side to allow a pup to suckle. This ca. 3–4-day-old pup lacked deciduous teeth and had no permanent teeth erupted beyond the gum, although all permanent teeth had begun to penetrate the bone (Allen 1887a; Ward 1887). An annual birth rate of 15% has been estimated (Rice 1973), but this estimate is probably low (Adam and Garcia 2003). Females rarely bore young in successive years (Rice 1973). The male : female ratio of specimens collected during a single 1900 expedition in Mexico was 24:76, with subadults (ca. 0.5–2.5 years old) comprising 21%

of this sample (Rice 1973). Weaning occurred 2 weeks after parturition. Young developed quickly, becoming as active as adults by 9 months of age (Nesbitt 1836).

Suspected and known breeding areas encompass the southwestern Gulf of Mexico, western Caribbean Sea, southern Bahamas, and Greater Antilles (Campbell 1978; Timm et al. 1997) and Gulf Islands of Florida (Cumbaa 1980). Pregnant specimens are known only from the Triangle Keys (Adam and Garcia 2003; Townsend 1923; Ward 1887). West Indian monk seals were present on the Triangle Keys in all seasons (Adam and Garcia 2003).

ECOLOGY. West Indian monk seals were found on isolated islands, keys, and atolls surrounded by shallow, reef-protected waters. They were most often hauled out on sandy beaches that remained exposed at high tide (Gaumer 1917; Hill 1843; Kerr 1824; Ward 1887), but also hauled out on near shore rocks and rocky islets (Allen 1880; duTertre 1978; Gaumer 1917). Hauling sites typically had sparse or no vegetation and no fresh water (Goldman 1951; Lewis 1948; Ward 1887).

The West Indian monk seal was allopatric with respect to the normal ranges of other pinnipeds. On some islands, *M. tropicalis* occurred with magnificent frigatebirds (*Fregata magnificens*), royal terns (*Sterna maxima*), boobies (*Sula*), columbids, and other unidentified seabirds (Dampier 1729; Kerr 1824; Ward 1887). Rats, probably introduced by humans, were also found with West Indian monk seals at Alacrán Reef (Dampier 1729). Apart from humans, the only known natural predator of *M. tropicalis* is an unidentified shark (Fernández de Oviedo 1944; Sloane 1707). Attacks typically involved multiple sharks (Fernández de Oviedo 1944). Fossil (Irvingtonian) West Indian monk seals associated with several large carnivores, including canids (*Aenocyon*, *Canis ambrusteri*, and *C. eduardii*), felids (*Homotherium*, *Miracinonyx*, *Panthera onca*, and *Smilodon*), a hyena (*Chasmaporthetes*), and ursids (*Arctodus* and *Ursus*—Berta 1995; Ray 1958). Historically, West Indian monk seals rarely occurred on the mainland.

All stomachs of wild *M. tropicalis* have been empty and the natural diet is unknown (Adam and Garcia 2003; Gosse 1851; Ward 1887). Dental and osteological skull features are consistent with a generalist feeding strategy (Adam and Berta 2002). Captive animals ate fish and crabs (Adam and Garcia 2003; Ward 1887).

The only parasite identified from *M. tropicalis* is the nasal mite *Halarachne americana* (Acari, Halarachnidae = Gamasidae, Dermanyssidae), recovered in great numbers and in all stages of its life cycle from the respiratory passages of a single captive specimen (Banks 1899; Dailey and Brownell 1972; Ferris 1925; Furman and Dailey 1980; Newell 1947). *H. americana* is only known from *M. tropicalis*. *M. tropicalis* carried heavy parasitic helminth loads (Adam and Garcia 2003; Grant 1911; Ward 1887), but the identity of these worms described only as being “several inches in length” (Ward 1887:262), is not known. The observation that worms swarmed out of the vagina in freshly killed West Indian monk seals (Ward 1887) is probably erroneous (Rice 1973). Unidentified, minute algae grew on fur (Ward 1887; incorrectly cited as fungus by Rice 1973).

In archeological excavations, *M. tropicalis* remains have been found in middens and in association with remains of deer (*Odocoileus virginianus*), fish, and marine invertebrates. Nomadic aboriginals of the Orange Period (Cumbaa 1980; Rouse 1951) and Depford Phase (Milanich 1971) and Glades I–III Period Tequesta Indians (Cumbaa 1980; Wing and Loucks 1984) are the only aboriginal peoples of the southeastern mainland United States known to have taken West Indian monk seals for food. Historical records indicate that for Calusa Indians of the Florida Keys, West Indian monk seal meat was eaten only by tribal chiefs and other members of high rank (Larson 1980; True 1945). Subsistence records are also known from Sint Eustatius (van der Klift 1992) and Nevis (Wing 2001a) in the Lesser Antilles, as well as Archaic Age hunter-gatherer-fishing folk and Ceramic Age horticultural peoples of Curaçao (Debrot 2000; Haviser 1987, 1994). Arowak Indians of Curaçao hunted West Indian monk seals at Klein Curaçao within historic times (Debrot 2000; van Grol 1934). Archeological excavations of Taino Indian sites with West Indian monk seal remains occur at St. John (U.S. Virgin Islands) and Puerto Rico (Y. Narganes, pers. comm.; I. Quitmyer and K. Wild pers. comm.; Wing 1992, 2001a), but seals are notably absent from most archeological sites in the Lesser Antilles (Pregill et al. 1994). The low number of individual West Indian monk seals (when present) in archeolog-

ical contexts indicates that they were never used as a major source of subsistence. When killed, carcasses were distributed to the community (Wing 2001a, 2001b; Wing and Wing 2001). West Indian monk seals were too agile to capture in open water (Cumbaa 1980; Milanich 1971). Within historic times, sealers dispatched West Indian monk seals sleeping on the beach with a hand-spike (Fernández de Oviedo 1944; Nesbitt 1836). Shooting *M. tropicalis* proved inadequate, as the sound would scare away any remaining individuals (Adam and Garcia 2003; Nesbitt 1836).

A Tequesta Indian plummet fashioned from the tooth of a whale to resemble a West Indian monk seal was recovered from the Granada site of Florida (Richardson and Pohl 1984). Additionally, an upper third *M. tropicalis* incisor tooth drilled in the root to form a plummet is known from Cinnamon Bay, Antigua (I. Quitmyer and K. Wild, pers. comm.) and a drilled lower second premolar has been recovered from the Caracoles Midden of the Taino Indians in Puerto Rico (Y. Narganes, pers. comm.). Prehistoric Arowak Indian petroglyphs on Aruba resembling West Indian monk seals are also known (Coomans 1997; Debrot 2000). In Puerto Rico, West Indian monk seals (“sea wolves”) were blamed by fishermen for beheading stray dogs in the night, leaving the bodies to be discovered on the beach in the morning (Mignucci-Giannoni 1989). West Indian monk seals were also blamed for devouring sailors that fell overboard (de Herrera y Tordesillas 1726).

The first known encounter between West Indian monk seals and Europeans occurred in late July 1494, when Christopher Columbus on his second voyage anchored for 3 days at Alto Velo (a small island south of the Dominican Republic) and killed at least 8 seals (Adam and Garcia 2003; Kerr 1824). West Indian monk seals were the most easily exploited source of oil in the tropical west Atlantic Ocean and were vigorously hunted to near extinction for their blubber until the early 1900s (Adam and Garcia 2003; King 1956; Rice 1973). West Indian monk seal oil was worth U.S. \$0.16/l in the late 1800s (Adam and Garcia 2003) and cured skins were worth U.S. \$1.00 each in the early 1800s (Nesbitt 1836). Blubber was processed and used for lubrication, coating the bottom of boats, and as lamp and cooking oil (Campbell 1978; Fernández de Oviedo 1944; Kellogg 1941–1943; Nesbitt 1836; Roberts 1976). West Indian monk seal skins were sought to make such items as trunk coverings, caps, belts, straps, and bags (Fernández de Oviedo 1944; Nesbitt 1836). In the early 1700s, a girdle fashioned from a *M. tropicalis* pelt was believed to relieve lower back pain, and its fur was prized by sailors who claimed that hairs became erect during rough seas but remained flat in calm seas (Fernández de Oviedo 1944). Guano gatherers visiting the Triangle Keys in ca. 1856 made a bonfire of ca. 100 barrels of *M. tropicalis* skins and skeletons left behind by sealers, indicating that oil was the primary objective of slaughter (Ward 1887). Fishermen sometimes hunted *M. tropicalis* for meat as late as 1885 (Gaumer 1917). Some European sailors were averse to eating *M. tropicalis* meat (Dampier 1729), although others claimed it tasted good but spoiled quickly (Fernández de Oviedo 1944). West Indian monk seals were taken for food by sailors stranded on the Arricifés Viboras (Cuba) in ca. 1520 (Díaz del Castillo 1912), Islas de Lobos (Veracruz, Mexico) in 1524 (Timm et al. 1997), Dry Tortugas (Florida) in 1742 (Swanson 2000), and the Triangle Keys in ca. 1846 (Ward 1887). Live specimens of *M. tropicalis* were eagerly sought by zoos following the discovery of remnant populations (Mann 1930). In 1897, 2 live specimens sold for U.S. \$50.00 each (Adam and Garcia 2003). *M. tropicalis* specimens were also sold to museums for high prices (van Bree 1994). Two scientific expeditions to the Triangle Keys (Adam and Garcia 2003; Ward 1887) contributed to extinction of the species. Fishermen killed West Indian monk seals as competitors (Rice 1973), and seals occasionally become entangled in turtle and shrimp nets (Knudtson 1977; Villa-Ramírez et al. 1985). In at least 1 instance, 2 *M. tropicalis* were killed simply “for fun” (Allen 1880:721).

ANIMAL HUSBANDRY. Within historic times, 18 West Indian monk seals have been held in captivity on 8 separate occasions (Boulva 1979; Moore 1953; Rice 1973). None bred in captivity (Boulva 1979). Captive West Indian monk seals were fed fish cut into small pieces and crabs (Adam and Garcia 2003; Ward 1887). Survival in captivity was low, with most animals living from 1 week (Gosse 1851) to 2 years (Anonymous 1903, 1910; Gilmore 1959; Mann 1946; Townsend 1909). A female that lived 5.5 years in captivity died of fatty degeneration of the heart, liver, and kid-

neys and pneumonia of the left lung (Anonymous 1903). Two specimens died of pneumonia after ca. 6 months captivity (Grant 1911). One female died after 2.5 months captivity from purulent bronchitis and meningitis (Adam and Garcia 2003). A young male became blind and died 4 months after capture, during which time it refused to eat. The specimen displayed symptoms of an unknown “disease of the head” in its last month of life (Gosse 1851; Hill 1843). Two instances of histiocytosis X, carcinoma, or other pathology of the hard palate in *M. tropicalis* are known (Adam and Garcia 2003).

BEHAVIOR. *Monachus tropicalis* was oblivious to humans (Allen 1880; Rice 1973; Ward 1887; Würsig et al. 2000). When approached on land, West Indian monk seals often examined, but did not appear to fear, distant humans or boats, simply shifting uneasily and going back to sleep (Gauger 1917; Ward 1887). West Indian monk seals entered water after being closely approached by men (0.9–1.8 m distance) or boats (Adam and Garcia 2003; Allen 1880; Gauger 1917). When scared into the water, individuals did not haul out again until the men left (Adam and Garcia 2003; Allen 1880; Gosse 1851). Unmolested, hauled-out West Indian monk seals were inactive and remained on land for days at a time (Adam and Garcia 2003; Ward 1887). When abundant, *M. tropicalis* hauled out in groups of up to 500 individuals (Nesbitt 1836). On land, seals typically huddled closely together (Gosse 1851). Live West Indian monk seals hauled out among skinned carcasses of other seals. West Indian monk seals showed no curiosity for boats (Ward 1887).

Young animals played in pools of water isolated from the ocean. Presence of only young animals in pools indicates segregation of age classes (Adam and Garcia 2003). A female suckled a pup in an isolated, shallow pool of water (Ward 1887). Parents accompanied young in the water to teach them how to swim and hunt, and carried young on their backs if they tired (Nesbitt 1836). Play behavior of young *M. tropicalis* included blowing and snorting under water and swimming with only the muzzle exposed to the air (Gosse 1851; Hill 1843; Ward 1887). A young captive West Indian monk seal was playful when left unmolested and was very sensitive to touch, responding by jerking the body forward (Gosse 1851; Hill 1843).

Although West Indian monk seals usually hauled out in the early morning or were at rest on beaches during the day (Adam and Garcia 2003; Gauger 1917; Ward 1887), some hauled out in the evening to rest overnight (Díaz del Castillo 1912; Ximénez 1967). Subadult *M. tropicalis* foraged nocturnally in shallow, near-shore waters to avoid direct competition with adults which fed during the day (Adam and Garcia 2003).

Vocal repertoire of *M. tropicalis* was varied, consisting of harsh roaring; pig-like snorting; moaning; dog-like barks; growls; and snarls (Anonymous 1910; Gosse 1851; Hill 1843; Nesbitt 1836; Townsend 1909). Undisturbed males intermittently uttered a hoarse, guttural roar on land and more rarely in the water (Adam and Garcia 2003). Molested West Indian monk seals woke and uttered a bark described as a hoarse, gurgling, death-rattle tone before moving to water. Suckling infants gave a long, drawn out, guttural “ah” with a series of vocal hitches during enunciation (Ward 1887). *M. tropicalis* often emitted loud snorts that carried long distances (Fernández de Oviedo 1944; López de Gómar 1932).

Terrestrial locomotion was accomplished by hitching forward of the body with dorsoventral spinal undulations characteristic of most phocids (Adam and Garcia 2003; Ward 1887). Each undulation moved a West Indian monk seal ca. 0.3 m forward. In one instance, an excited *M. tropicalis* attempted “to scull through the sand with its hind flippers as though it were in water” (Ward 1887: 262) indicating that swimming in *M. tropicalis* was accomplished by typical phocid lateral undulations of the spine coupled with alternating flexion and extension of the coupled hind flippers. West Indian monk seals were agile in water (Fernández de Oviedo 1944) and capable divers (Nesbitt 1836).

Unmolested *M. tropicalis* are not known to have exhibited intraspecific fighting (Adam and Garcia 2003; Ward 1887), although a large male had numerous scars (Gosse 1851; Neill 1957). While being killed, West Indian monk seals rushed at their attackers for distances of 0.3–0.6 m, occasionally tried to bite men, and bit and shook dead seals or engaged other live seals with biting (Adam and Garcia 2003; Nesbitt 1836; Ward 1887). A lone West Indian monk seal under attack by sharks bit at the sharks with

considerable ferocity before succumbing (Fernández de Oviedo 1944).

Captive animals were easy to train and could learn to eat from a trainer's hand (Adam and Garcia 2003). A large male was known to splash water at zoo patrons and another learned to spray water at people from the mouth (Anonymous 1903, 1910; Townsend 1909).

GENETICS. The genetics of *M. tropicalis* are not known.

CONSERVATION STATUS. *Monachus tropicalis* was first discovered in 1494 (Kerr 1824) and received occasional, non-descriptive acknowledgement by some naturalists (Halle 1757–1760: 581,593; Olafsen 1774:284). *M. tropicalis* was not officially described until 1849 (Gray 1849). In the interim, West Indian monk seals were slaughtered for oil at a rapid rate (Dampier 1729; Sloane 1707). Although reported abundant in the early 1700s (e.g., Fernández de Oviedo 1944; Ximénez 1967), *M. tropicalis* was considered rare by the late 1800s (Allen 1887b; Elliott 1884; Gratacap 1900; Lucas 1891, 1892) and virtually extinct by the early to mid-1900s (Mann 1930, 1946; Townsend 1906, 1923). The last record of *M. tropicalis* in U.S. waters is from 23 March 1922 when a single individual was killed near Key West, Florida (Townsend 1923). The last reliable sighting of *M. tropicalis* was at Serranilla Bank (Columbia) in 1952 (Adam and Garcia 2003; Rice 1973). One potential record of an individual seal at Isla Mujeres (Yucatan, Mexico—Goodwin and Goodwin 1973) in 1962 is insufficiently documented. Most sightings of seals since 1950 and within the former range of *M. tropicalis* can be attributed to feral California sea lions (*Zalophus californianus*), endemic manatees (*Trichechus manatus*), and young vagrant hooded (*Cystophora cristata*) and harbor seals (*Phoca vitulina*—Gunter 1968; Knudtson 1977; Mignucci-Giannoni and Haddow 2001; Mignucci-Giannoni and Odell 2001; Rice 1973; Schmidly 1981). Although fishermen and lighthouse keepers occasionally report sightings, aerial and boat surveys within the former range of *M. tropicalis* in 1949, 1959, 1969, 1973, 1980, 1984, 1995, 1996, and 1997 failed to locate living West Indian monk seals (Boyd and Stanfield 1998; Charnock-Wilson 1970; Dougan 1988; Gilmore 1959; Kenyon 1977; King 1956; Knudtson 1977; LeBoeuf et al. 1986; Sergeant et al. 1980; Villa-Ramírez et al. 1985; Westerman 1953). Statistical analyses of sighting data have been used to evidence the extinction of *M. tropicalis* (Burgman et al. 1995; Solow 1993), although exclusion of many data has led to criticism of these methods (Boyd and Stanfield 1998). The 50-year threshold for declaring a species extinct due to lack of sightings under current convention has now passed (Burgman et al. 1995).

The Jamaican Wild Life Law offered the first legal protection to the West Indian monk seal. Nonetheless, occasional individuals subsequently straying onto Jamaican shores were nearly always slaughtered (Lewis 1948). In 1949, the International Conference on the Protection of Nature (United Nations Scientific Conference on the Conservation and Utilization of Resources) included *M. tropicalis* in a list of 14 mammals whose survival was considered to be a matter of international concern and which required immediate protection (Westermann 1953). The International Union for the Conservation of Nature (IUCN) distributed circulars in both English and Spanish throughout the Caribbean region in 1973, offering U.S. \$500 for information on recent sightings of West Indian monk seals (Boulva 1979). The IUCN currently lists the species as extinct (Groombridge 1993). Although its probable extinction was acknowledged, a joint notice to give *M. tropicalis* Endangered status was filed in 1977 by the U.S. National Marine Fisheries Service and Fish and Wildlife Service (Anonymous 1977). Currently, *M. tropicalis* is listed as Endangered by the U.S. Department of the Interior and is afforded additional legal protection in the United States by the Marine Mammal Protection Act of 1972 and its subsequent amendments. *M. tropicalis* is currently listed under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES—Nowak 1995). *M. tropicalis* was included in the first edition of this appendix on 1 July 1975. LeBoeuf et al. (1986) recommended that *M. tropicalis* be removed from the Endangered Species list in recognition of its extinction.

Fishermen, shrimping boats, and abandoned camps are ubiquitous throughout the known hauling grounds of *M. tropicalis* (Anonymous 1977; Kenyon 1977; LeBoeuf et al. 1986). A shift in

habitat to secluded underwater and near-shore caves for parturition may be possible for *M. tropicalis* (Boyd and Stanfield 1998), but no evidence exists to support this (Mignucci-Giannoni and Odell 2001). Most authorities consider *M. tropicalis* extinct (e.g., Anderson 2001; Carlton et al. 1999; Mignucci-Giannoni and Odell 2001; Vermeij 1993; Villa-Ramirez 1978), and the species is often excluded from current guides to marine mammals of the western tropical Atlantic Ocean (Wynne and Schwartz 1999).

REMARKS. The genus name, *Monachus*, is derived from the Greek word for monk (monakhos), in reference to the smooth round head with rolls of skin about the neck, which reminded their original descriptor of a monk dressed in a robe (Lavigne and Johnson 2001; Würsig et al. 2000). The specific epithet, *tropicalis*, refers to the tropical habitat in which West Indian monk seals lived. Some workers erroneously report that the generic name refers to monk seals dwelling in solitude (Neill 1957). The first descriptions (Gray 1849, 1850a, 1850b) of the West Indian monk seal were based on the skin of *M. tropicalis* and a skull of *Cystophora cristata* (both specimens apparently from the West Indies). This error, coupled with a lack of additional specimens, caused considerable confusion in early taxonomic accounts of the species (Gill 1866). Gray's later descriptions were based on the skin only (Gray 1854a, 1854b, 1866a, 1866b), but Gray never explicitly resolved the error. Allen (1887a) clarified the error.

Monachus tropicalis is also known as the West Indian seal, Caribbean monk seal, and Caribbean seal. Early explorers of the western tropical Atlantic Ocean commonly called these animals sea wolves, hair seals, or simply seals (restriction to *M. tropicalis* based on allopatry with respect to other pinnipeds). In Spanish, *M. tropicalis* is known by many names, including: cabezas de frailes, foca Caribeña, foca del Caribe, foca monje Caribeña, foca monje de las Antillas, foca monje del Caribe, fraile marino, lobo del mar, lobo marino, and pez boto (Mignucci-Giannoni 1989). In Náhuatl, an ancient language of Mesoamerica, West Indian monk seals were known as ytzcuinatl (or itzcuinatl—Díaz del Castillo 1967).

A number of behaviors previously ascribed to *M. tropicalis* are the result of misinterpretation of Hill (1843). These include potentially erroneous statements that West Indian monk seals traveled in herds, were capable of sleeping at the surface of the water, and that adults were protective of their young (Neill 1957). These statements apply to a discussion of otariids and elephant seals (*Mirounga*) in Hill (1843). Larson (1930) suggested that *M. tropicalis* may have traveled between islands during the breeding season, but no data are available to support this assertion (Adam and Garcia 2003). Diet of *M. tropicalis* is reported to include algae, fish, bivalve mollusks, cephalopods, and hard-shelled crustaceans, but these assertions are speculative (Campbell 1978; Gosse 1851; Lewis 1948; Neill 1957; Nesbitt 1836; Ward 1887).

Specimens used in constructing the dichotomous key are as follows (AMNH = American Museum of Natural History [New York], USNM = National Museum of Natural History [Washington, DC]): *M. monachus*: AMNH 73607–73609, USNM 23250 and 219059; *M. schauinslandi*: USNM 24836, 181250, 181252, 239856, 243838–243846, 243849, 243853, 243854, 334573–334575, 334577, 395403, 395759–395761, 395786–395788, 395987, 395988, 395991–396001, 504892–504894, and 504926; *M. tropicalis*: AMNH 3820, 10421, 11988, 14441, 1566, 15896, 19600, 35354, 77741, USNM 18431, 20994a, 20994b, 22543, 49607, 49608, 100354–100373, 102523–102537.

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