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Trichechus manatus.

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Trichechus manatus Linnaeus, 1758

West Indian Manatee

Trichechus manatus Linnaeus, 1758:34. Type locality restricted to West Indies by Thomas (1911:132).
Manati Trichechus Boddaert, 1784:173. Type locality restricted to West Indies by Hatt (1934:535).
Trichechus antillarum Link, 1795:109. Type locality restricted to West Indies by Hatt (1934:535).
Trichechus americanus Link, 1795:109. Type locality restricted to West Indies by Hatt (1934:535).
Manatus Guyannensis Bechstein, 1800:732. Type locality unknown.
Manatus Oronocensis Bechstein, 1800:732. Type locality restricted to West Indies by Hatt (1934:535).
Trichechus Clusii Shaw, 1800:246. Type locality West Indies.
Trichechus Amazonius Shaw, 1800:246. Type locality restricted to West Indies by Hatt (1934:536).
Manatus minor Daudin, 1802:194. Type locality restricted to West Indies by Hatt (1934:536).
Manatus latirostris Harlan, 1824:394. Type locality eastern coast of Florida.
Manatus atlanticus Oken, 1842:1098. Type locality restricted to West Indies by Hatt (1934:536).
Manatus Koellikeri Kükenthal, 1897:40. Type locality Surinam.

CONTEXT AND CONTENT. Order Sirenia, Family Trichechidae. The single genus *Trichechus* includes three species, *T. manatus*, *T. inunguis* and *T. senegalensis*. Hatt (1934) recognized two subspecies as follows:

T. m. latirostris Harlan, 1824:394, see above.
T. m. manatus Linnaeus, 1758:34, see above.

Moore (1951*b*) and D. S. Hartman (personal communication) questioned recognition of two subspecies because the distinguishing characters provide little basis for separation. The subspecies are indistinguishable in the field (Hatt, 1934), and Gunter (1954) believed that the wandering habits of the manatees must result in the mingling of populations throughout the range.

DIAGNOSIS. A manatee with ventral color uniformly gray or with irregular pink patches, no distinct white markings on the abdomen or chest; nails present on the dorsal surface of the forelimbs; total length of adults 2.5 to more than 4.5 m, corresponding weights vary from 200 to more than 600 kg (Hartman, 1971; Jones and Johnson, 1967); tail horizontally flattened and spatulate in shape. Cranial bone smooth and dense; skull with large, wide nasal basin; medial zygomatic arches are directed approximately 35 to 40° laterally from the longitudinal skull axis; vomer extending to the posterior edge of the incisive foramen or beyond; upper border of the premaxilla lies below the lower border of the frontal; foramen incisivum partially divided; foramen magnum oval (Hatt, 1934). Symphyseal suture with a deep furrow along the anterior margin; sternum with a deep median notch in the anterior border; first phalanx approximately 25% of humerus length.

GENERAL CHARACTERS. Average adults are between 3 and 4 m in length and less than 500 kg in weight (Bertram and Bertram, 1964; Quiring and Harlan, 1953). Sexual dimorphism in size is not yet documented but females seem bulkier (Hartman, 1971). Skin is finely wrinkled throughout; color of calves blackish-gray (Phillips, 1964), which pales with maturation to variable shades of slate gray to brown; ground color often obscured by algal growth, barnacles or other incrustations on the skin. Fine, colorless hairs (30 to 45 mm in length) are sparsely distributed over the body; stiff, stout bristles are on the muscular, prehensile pads of the upper lip. There are two axillary mammae. The semicircular nostrils are about 1.5 cm in diameter, 5 cm apart, and positioned at the angle of the muzzle. The eyes are small, deeply set, and closeable with a sphincter action; eyelashes are absent. Ear openings are minute (about 4 mm in diameter) and have no external pinnae. Detailed anatomical descriptions and drawings appeared in Murie (1872) and Quiring and Harlan (1953). Excellent color photographs can be found in Hartman (1969, 1972), Vietmeyer (1974), and Cousteau (1972); numerous line drawings of manatees under natural conditions are in Hartman (1971).

DISTRIBUTION. The range of *T. manatus* generally includes rivers, estuaries, and coastal areas of the tropical and sub-tropical regions of the New World Atlantic (figure 2). An extremely detailed and well-documented distribution of *T. manatus* within the United States is presented in Hartman (1974), who concluded that this population is increasing due to the proliferation of aquatic weeds. The United States range is largely confined to peninsular Florida and the coast of Georgia. A few records exist for Louisiana and the mouth of the Rio Grande (Alvarez, 1963; Gunter, 1954; Lowery, 1943). Manatees have been reported from as far north as Currituck Sound, Virginia (Tomkins, 1956), but these reports have been rare and probably represent stray wanderers (D. S. Hartman, personal communication). Recent records exist from the coasts of Mexico from Vera Cruz to Quintana Roo; however, manatee numbers are much reduced there (Philip and Fisher, 1970; Lluch, 1965; Alvarez, 1963). Substantial breeding populations were reported from British Honduras (Charnock-Wilson, 1970), and although manatees were once abundant in both Honduras and Nicaragua (Allen, 1910; Peary, 1889; Brown, 1878), recent information on their status is lacking. They were formerly numerous in Costa Rica (Goodwin, 1946; Frantzius, 1869), but are now rare or absent (D. E. Wilson, personal communication). Numbers currently are low in Panama, due primarily to hunting (Anon., 1973*a*). *T. manatus* occurs along the northern

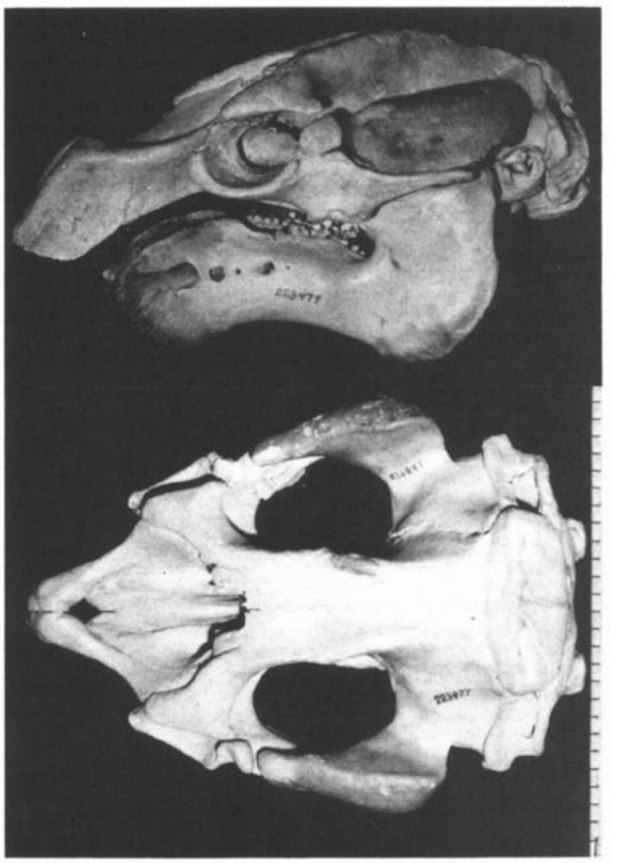

FIGURE 1. Photographs of the skull and lower jaw of *Trichechus manatus*, USNM 228479. Top, lateral view; bottom, dorsal view. Scale in centimeters.

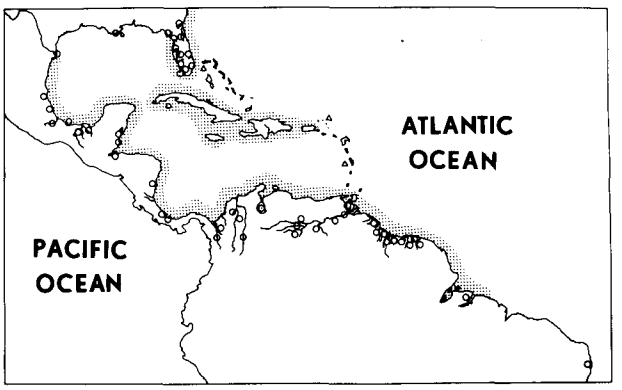

FIGURE 2. *T. manatus* coastal distribution is indicated by hatched areas. The species also is known to occur in all rivers shown on this map.

coast of South America from Colombia to Brazil and populations have been reported from river drainages up to 800 km from the coast. More complete distributional information is in Mondolfi (1973) for Venezuela, and Bertram and Bertram (1973) for Guyana and Surinam. No information was found for the northern coast of Brazil, except for a single record from Goiana (Da Rocha, 1971). Manatees have been extirpated from the Virgin Islands (Erdman, 1970) and are now rare around Puerto Rico (Barrett, 1935). They occur along the coasts of Cuba, Haiti, and Jamaica (Lewis, 1949; Miller, 1929; Gundlach, 1877), but the current status is unknown. Manatees are presently found along the southwestern coast and the entire northern coast of the Dominican Republic, with concentrations located in the Bay of Neiba and in the vicinity of Las Terranas; unfortunately, the animals are taken by fisherman when possible (Husar, unpublished). A single record exists for Bimini in the Bahama Islands (Allen, 1942).

FOSSIL RECORD. Although the geographic origin of the Trichechidae remains unknown, the family apparently had a relatively long evolution in the Caribbean (Reinhart, 1959). *Potamosiren*, the earliest fossil manatee, was present in Colombia during the early Miocene (Reinhart, 1951), and it appears to be derived from the oldest Eocene Sirenia (Reinhart, 1959). *Sirenotherium*, also from the early Miocene, was taken from Para, Brazil (Couto, 1967). *Ribodon*, earlier believed to be of Miocene-Pliocene origin from Argentina (Pascual, 1953), is now thought to be referable to *Trichechus*, from the Pleistocene (Reinhart, 1959). Other Pleistocene *Trichechus* remains have been discovered along the United States coast from Florida to Maryland (Simpson, 1932; Keferstein, 1834). This early manatee apparently displaced the dugongids, which had occupied that region since the Tertiary (Simpson, 1932).

FORM. The tough skin is rugose and the epidermis is in a continual state of sloughing, resulting in noticeably dark patches of new epidermis. Scar tissue, frequently present, is distinctively pale. The nails on the dorsal surface of the flippers may be worn to variable sizes due to scraping of the substrate. Notches and tears often are present in the tail.

The skeleton is of extremely dense (pachyostotic) bone. The skull is broad and has a relatively short and slightly deflected snout. The expanded nasal basin extends posteriorly beyond the borders of the orbits. Small nasal bones are present. Zygomatic arches are thick and deep, and the braincase is small. Each jaw has two vestigial incisors, which are later resorbed (Harrison and King, 1965). Functional cheekteeth (five to seven in each jaw) are brachyodont and without cement; each has two cuspidate crosscrests. Roots are closed and divided. Replacement is from the rear by newly erupting teeth, and was once believed to continue throughout the life of the manatee (Thomas and Lydekker, 1897), but P. van Bree (personal communication) has recently examined a single skull in which the replacement had apparently ceased. The age of that animal is unknown. Thomas and Lydekker (1897) estimated up to 20 teeth per jaw and Mohr (1957) claimed that 30 per jaw may erupt.

Vertebrae number 48 to 54 (cervical 6, thoracic 17 to 19, lumbo-caudal 27 to 29) (Hatt, 1934; Jones and Johnson, 1967). The manubrium is the only element of the sternum. Ribs and long bones are especially dense with few osteoclasts present; resorption of bone is minimal. No marrow cavities are formed. Adult ribs continue to grow in thickness by the apposition of new bone to their outer surfaces (Fawcett, 1942*b*). Ilium and ischium are present but much reduced. Further discussion of the skeleton is available in Murie (1872), Hatt (1934) and Fawcett (1942*b*).

The *rectus abdominis*, and *pectoralis major* and *minor* are red, as are the shoulder muscles and diaphragm; all other muscles are the pale color of pork. The heart is large (1.24 kg in a 557-kg animal), globular, and with a characteristic interventricular cleft (Quiring and Harlan, 1953). Fawcett (1942*a*) described the posterior vena caval system as double, similar to that of the Cetacea and Edentata. Unusual vascular bundles (not *rete mirabile*) in a broomlike arrangement are especially developed in the flippers; similar bundles occur in the face and jaw regions, body walls, tail, and spinal canal (Fawcett, 1942*a*). Some red blood cells are small (4 to 7 microns in diameter) while about 10% are large (8 to 12 microns), this size is found also in elephants, edentates, walrus, and aardvark (Knoll, 1958; Garrod, 1877).

The brain (about 370 g) of an adult manatee is quadrangular in shape and has a deep longitudinal fissure separating the cerebral hemispheres, which are relatively smooth except for the well-defined Sylvian fissures (Murie, 1872). The rounded occipital lobe is concave ventrally over the somewhat convoluted cerebellum (Murie, 1872). The *corpus callosum* is short and thick, whereas the *corpus striatum* and *thalamus* are large (Harrison and King, 1965). Mammillary bodies are present (Wislocki, 1940). The *trigeminus* is the largest of the cranial nerves, and the spinal cord ends at the last lumbar or first caudal vertebra (Quiring and Harlan, 1953).

The trachea, supported by eight to 12 tracheal rings, divides into two bronchi which run parallel for some distance before entering the lungs, which are unlobed, extremely elongate and enclosed in a heavy vascularized pleura (Quiring and Harlan, 1953). They extend posteriorly to the level of the vestigial pelvis (Wislocki, 1935*b*). Numerous cartilaginous rings extend to the smallest bronchioles, which are reduced in length and numbers (Kooyman and Andersen, 1969). Alveolar sacs are large, heavy-walled, and composed of unusually large amounts of fibro-elastic and smooth muscle tissue. These sacs are well supplied with blood through double layers of capillaries in the alveolar walls (Wislocki, 1935*b*).

Submaxillary salivary glands are prominent (Quiring and Harlan, 1953) but sublingual glands are small (Murie, 1872). A narrow esophagus leads to the compound stomach. The cardiac chamber has extremely thick muscular walls and an associated large cardiac gland (Murie, 1872). Two coiled caeca are located at the pyloric end of this section. A thinner-walled second chamber leads directly to the muscularized small intestine (18.88 m long and 57 mm in diameter in a 2.96-m animal). Low squamous cells line the intestine (Harrison and King, 1965). The large intestine, about the same length as the small intestine and roughly twice the diameter, has numerous mucous glands in its lining of squamous epithelium (Harrison and King, 1965). The liver is trilobed and the gall bladder is large. Pancreatic ducts and the bile duct open separately into the duodenum (Harrison and King, 1965).

The kidneys (1316 g in a 570-kg adult) are located retropleurally. Lobulation appears to develop with age (Beddard, 1897). The ureters, uniform in diameter, enter the relatively small semi-globular bladder. Testes are abdominal and seminal vesicles are large; the prostate gland is composed of erectile muscular tissue rather than normal glandular tissue (Harrison and King, 1965). Ovaries are large masses of beadlike spherules without a heavy capsular coat; oviducts are short and fused distally. The bicornuate uterus narrows distally to a rounded cervix. The placenta is of the hemochorial, deciduate type, like that of the Proboscidea and Hyracoidea (Wislocki, 1935*a*).

Both anterior and posterior lobes of the oval-shaped hypophysis are well developed; however, the *pars tuberalis* and *pars intermedia* are reduced (Wislocki, 1940). The thyroid gland is bilobed, there is no evidence of an isthmus. Glands removed from three individuals ranged from .11 to .13 g per kg of body weight. The thyroid is not lobulated and follicles are largest near the periphery, decreasing in size toward the center (Harrison, 1969). Cuboidal epithelium lines the follicles; a basement membrane is absent. Interfollicular tissue is abundant and some areas are extremely compact (Harrison, 1969). The colloid is profuse, suggesting low activity (Fawcett, 1942*b*). Four parathyroids are imbedded in the thyroid surface. The cortex of the thymus is prominent, consisting largely of lymphocytes; the medulla is small and pale. Adrenals are elongate and positioned retropleurally between the carotid artery and the bronchus. They are atypical in apparently having no cortical zones. A small spleen is present (Chapman, 1875).

FUNCTION. Few physiological data are available for *T. manatus*. Hematology and blood chemistry have been studied (White, 1970). Oxygen capacity of the blood is about 17.2 per cent by volume (Scholander and Irving, 1941). Blood vessels are especially numerous within the spinal canal, a possible adaptation to the aquatic existence of the manatee. Blood may be shunted from the abdominal cavity to this vertebral system during a dive, undergoing less resistance within the vertebral column than would be present in the body cavity (Fawcett, 1942*a*).

Sensory capacities of manatees have been studied by observations of animals under natural conditions (Hartman, 1971). Acoustical ability appears to be exceptional, and the available evidence suggests they are far-sighted; a "smell-taste," whereby odor gradients in the water are recognizable, is probable.

Large quantities of muscle within the lungs may function by compressing air, thereby increasing the manatee's density and allowing it to sink. Diving experiments with manatees, conducted by Scholander and Irving (1941), provided the following picture. Bradycardia develops slowly during diving, and the heart rate decreases from about 50 or 60 beats per minute, to about 30 during an eight-minute dive; CO_2 blood content increases without a corresponding increase in lactic acid, suggesting that muscles are isolated from circulation during the dive. With early recovery, lactic acid levels in the blood rise immediately. The CO_2 tension of the alveolar air rises less than the O_2 tension decreases throughout the dive. Manatees were also found to have an extremely low resting consumption of oxygen (300 mm^3 O_2/g/min); however, the utilization of oxygen from the inspired air was high (7 to 10%).

The pachyostotic condition of manatee bone, the sluggish behavior of manatees, and their extremely low rate of oxygen consumption have been suggestively linked to the unusual structure of the thyroid gland and to possible hypothyroidism (Harrison and King, 1965; Fawcett, 1942*b*; Sickenberg, 1931; Nopsca, 1923).

ONTOGENY AND REPRODUCTION. Breeding of *T. manatus* apparently occurs throughout the year (Hartman, 1971; Betram, 1963; Moore, 1956; Charnock-Wilson, 1968). A detailed description of underwater mating was presented by Hartman (1971). Females seem to pass through proestrus, estrus, and metestrus periods throughout which they are attractive to bulls, but receptivity is confined to a short estrus period. When receptive, the cow is promiscuous. The gestation period is at least 152 days (Moore, 1951*a*), and is probably about 385 to 400 days (Hartman, 1971). Parturition has not been observed. Hartman (1971) believed that cows choose secluded backwaters for giving birth. Usually one calf is produced; however, twins have been reported (Hartman, 1971), as have cases of foster parenthood (Hartman, 1971; Phillips, 1964). Newborns weigh from 11 to 27 kg and may measure over 1 m in length (Phillips, 1964; Moore, 1957). Immediately after birth calves swim with the flippers only, not learning the use of the tail for several days (Moore, 1957; Barbour, 1937). Suckling occurs underwater in a horizontal position, and the cow makes no special efforts to feed her young (Hartman, 1971). A 38-day-old captive ate lettuce (Moore, 1957), and another nibbled algae at only a few weeks of age (Phillips, 1964). Calves may nurse for a period of one to two years, and Moore (1956) observed a dependent calf that was at least 1.8 m long. Hartman (1971) classified three age groups in relation to behavior. These are: calves, any young associating with a cow; juveniles, independent but not yet sexually mature; and adults, animals taking part in reproduction. Transition to adulthood is gradual and sexual maturity probably is not attained until four to six years of age and 2.5 to 2.7 m in length (Hartman, 1971). Longevity in the wild is unknown. Baby Snooks, a captive at the South Florida Museum, was 23 years old in March, 1973 (Anon., 1973*b*).

ECOLOGY. To date, there is no documentation of predation upon manatees, although sharks (Lluch, 1965) and piranhas (Allsopp, 1961) have been suggested as potential predators. In Florida, heavy boat traffic is believed to be the major source of manatee mortality (Hartman, 1973). Propellors and keels of speeding boats strike manatees before they react to the oncoming noise. Resultant scarring is evident in the majority of the Florida population (D. S. Hartman, personal communication).

Many Florida manatees are coated with the freshwater alga, *Lyngbya martensiana*, and some have growths of the red alga, *Compsopogon coeruleus*. *Lyngbya* apparently harbors amphipods, isopods, dipteran larvae, nematodes, copepods, ostracods and microscopic protozoans (Hartman, 1971). Animals spending time in salt water become covered with marine diatoms (*Zygnema* or *Navicula*) or barnacles (Hartman, 1971). Macroscopic associates tend to be freeliving and ectophoretic rather than parasitic (Hartman, 1971). Internal parasites are *Chiorchis fabaceus* (Fischoeder, 1901), *Opisthotrema cochleotrema* (Travassos and Vogelsang, 1931), and *Plicalolabia hagenbecki* (Radhakrishnan and Bradley, 1970). A skin copepod, *Harpacticus pulex*, has also been reported (Humes, 1964).

Manatees appear to be highly susceptible to pneumonia and other bronchial disorders, and many carcasses have been reported following periods of cold (Sguros, 1966; Layne, 1965; Krumholz, 1943). Bloated manatees, unable to submerge, have been sighted. This possibly is due to trapped intestinal gas (D. S. Hartman and R. B. Brownell, personal communications).

Population structure and local sex ratios for the population of Crystal River, Florida, are presented in Hartman and Powell (1973).

FIGURE 3. Sketches of manatees by Wilma Martin, from photographs by the author.

T. manatus occupies both fresh and salt water, and neither salinity nor turbidity appear to affect their movements (D. S. Hartman, personal communication). Allsopp (1969) suggested 21° C as the minimum temperature tolerable to manatees; however, Hartman tracked animals in water at 15°C heading toward even cooler waters. Usual cruising depth is between 1 and 3 m below the surface; the deepest recorded dive is 10 m (Hartman, 1971).

In Florida, there is a predictable movement of manatees to warm-water springs or man-made warm-water refugia during cold spells of 10 to 15°C (Moore, 1951*b*). The likelihood of attendance at such congregation sites is inversely proportional to the time and energy expended by the individual to reach the site from its normal range (Hartman, 1971; Moore, 1956). There is also some evidence of north and south seasonal migration in the United States (Hartman, 1971; Moore, 1956; Hamilton, 1941). In the southern portion of the range, movements lack documentation, although Sanderson (1949) commented on movements in Surinam correlated with the rainy season.

Manatees are wholly herbivorous. Detailed dietary habits of the west Florida population were reported by Hartman (1971), and Allsopp (1969) compiled a list of food plant species in Guyana. When in salt water, *T. manatus* eats *Thalassia*, *Syringodium*, *Halophila*, and *Diplanthera* (D. S. Hartman, personal communication). Captive animals reportedly consume from 30 to 50 kg of food daily (Hartman, 1968).

T. manatus is currently considered an endangered species. Manatees have been widely hunted for their fine meat and oil, their bones, which were used as ivory, and for their skins. While *T. manatus* never has been commercially harvested, the hunting pressures exerted by individual fishermen are apparently responsible for the currently diminished numbers (Bertram and Bertram, 1973; Moore, 1956). These animals are now legally protected throughout most of their range; however, effective enforcement is virtually impossible. Poaching and vandalism remain a problem, probably contributing significantly to manatee mortality (Bertram and Bertram, 1964; D. Hartman, personal communication). Wounding of manatees by motor boats is also a major threat. In Florida, the Everglades National Park and the Blue Springs area have lowered boat limits specifically to protect manatees (O'Keefe, 1973), and efforts are now being made to establish a National Manatee Refuge in Florida (H. Campbell, personal communication). Possibly an aid in manatee conservation is their potential use in the control of aquatic weeds. Several experiments indicate that manatees could be effective for weed clearance only if large numbers of animals were available (Allsopp, 1969; MacLaren, 1967; Sguros, 1966). Unfortunately, there has been only minimal success in maintaining captives for long time periods (Hartman, 1968); no successful breeding has been reported in captives.

BEHAVIOR. Hartman's (1971) excellent dissertation on the behavior of *T. manatus* is based on hundreds of hours of detailed observation under natural conditions. Unless otherwise cited, all material in this section is taken from his work. Manatees appear to be arhythmical (Bertram and Bertram, 1964; Allsopp, 1961) and much of their time is spent eating or resting. Manatees feed from six to eight hours daily, usually in sessions of one to two hours and at depths of one to three meters. Different food plants are grazed differentially. The bristled upper lip pads are everted into the food source, then lateral pads are closed inward, pulling the vegetation into the cleft of the mouth.

Manatees rest from two to 12 hours daily, usually in sessions of two to four hours, and during cold spells rest may continue throughout the day. Animals rest suspended near the surface with the eyes closed, or they may lapse into the deeper sleep of bottom resting. The animal then lies on the substrate, with flippers held at the sides or tucked under the breast. Some individuals were observed on their backs or sides for short periods.

Breathing is through the nostrils, as manatees are apparently incapable of breathing through the mouth (Baughman, 1946). Only the tip of the snout is exposed during relaxed breathing, and surfacing occurs in two to four quick emergences in rapid succession. Exhalation-inhalation time ratios of resting animals range from 1:1 to 9:5 with a mean of 6:5. Average submergence time is 259 s; however, Parker (1922) reported a dive of 980 s. Both age and degree of activity influence breathing rates.

Dorso-ventral undulations of the tail propel manatees forward, and the tail is also used as a rudder for steering, banking, and rolling. Flippers are usually held loosely at the sides. Cruising animals were clocked at 4 to 10 km/hr, and for short distances (less than 100 m), 25 km/hr was attained. Detailed descriptions of locomotion, tail and flipper movement, with diagrams, are presented in Hartman (1971). Other maintenance behavior (surfacing, resting, feeding, comfort activities, and eliminative behavior) is also thoroughly described.

Although manatees are essentially solitary, they occasionally are mildly social. Groups of two to six animals are often reported (Layne, 1965; Charnock-Wilson, 1968; Moore, 1951*b*) and larger groups also have been noted, but these groupings are thought to be ephemeral. The only lasting relationship is between a cow and her calf. Several bulls may pursue an estrus cow for up to a month, but no bonds are formed.

Bulls are most active socially in initiating interactions. No displays have been observed; intraspecific contacts largely of mouthing, nuzzling, nudging, and embracing. Males often engage in homosexual activities, which may last for hours at a time. No agonistic contact or indication of communal defense was ever seen.

Manatees are usually silent whether alone or in a group, and vocalizations appear to be emitted primarily in contexts of fear, aggravation, play, and so forth. Schevill and Watkins (1965) presented a spectrographic analysis of *T. manatus* calls.

Much play has been observed in wintering congregations. Groups of two to three individuals involved in mouthing, bumping, and chasing were common. Both adults and calves, as well as lone individuals, have been observed at play.

Mating occurs throughout the year. Hartman (1971) described copulation occurring in water about 2.5 m in depth, although others have observed mating in extreme shallows (Caldwell and Caldwell, 1972; Bertram, 1963; Moore, 1956).

GENETICS. Nothing is known of the genetics of *T. manatus*.

REMARKS. The names *Manatus* and *Oxystomus* were introduced as a result of the vaguely defined species assigned by Linnaeus to *Trichechus*. The walrus was one of those associated with the genus *Trichechus*. Both *Manatus* and *Oxystomus* refer to Linnaeus' type *T. manatus*. In 1929, the International Commission on Zoological Nomenclature (Opinion 112) stated that *Trichechus manatus* is the correct name for the manatee.

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