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Biological Synopsis of the Manatee

K. Ronald, L. J. Selley, and E. C. Amoroso

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Postal Address: Box 8500, Ottawa, Canada K1G 3H9
Head Office: 60 Queen Street, Ottawa

Ronald, K.
Selley, L.J.
Amoroso, E.C.
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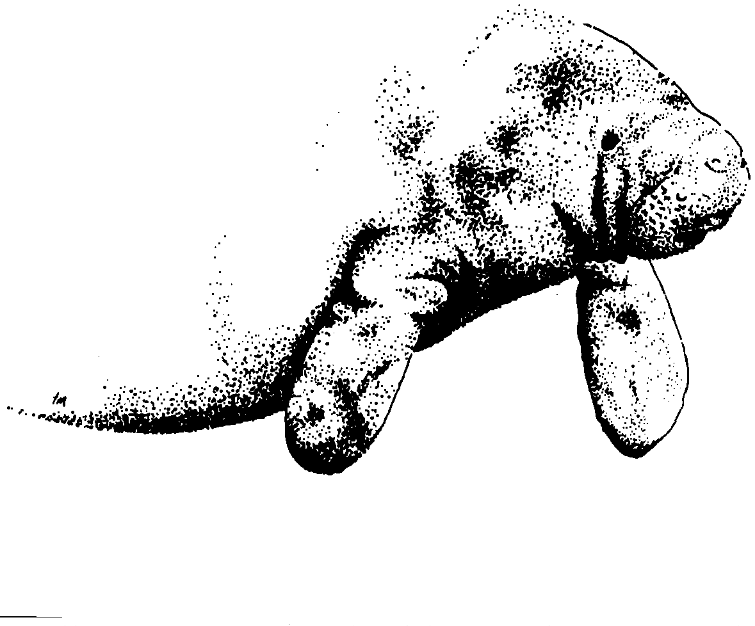
Biological Synopsis of the Manatee

K. Ronald, L.J. Selley, and E.C. Amoroso[1]

College of Biological Science, University of Guelph, Guelph, Ontario



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[1] Present address: Agricultural Research Council, Institute of Animal Physiology, Babraham, Cambridge, England.

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Contents

Preface

The *Biological Synopsis of the Manatee* has been written in response to increasing interest in the species, which (as an herbivore) has potential for aquatic weed control and as a source of protein for human consumption. The synopsis is based on a bibliographical summary begun in 1960 and requested, then, by the Food and Agriculture Organization as a part of the FAO series on aquatic animals. The objective of this work has been to gather together all that has been written about the manatee and to summarize the information on its anatomy, structure, function, environment, distribution, etc. Research such as this is critical to the survival and effective use of the manatee, and much more investigation is needed into the animal's physiology, ecology, behaviour, and conservation.

A small international centre for manatee research was recommended at a workshop of scientists from 23 interested research institutions in eight countries held in Guyana in 1974. An interim steering committee, acting under the auspices of the National Research Council of Guyana, was appointed to consider the institutional structure and actions necessary to establish and operate such a centre. Meanwhile, research is continuing in various institutions in Manaus (Brazil), Florida, western Africa, and Guyana. This synopsis is offered as a contribution to this research in hopes that it will advance the current interest in the potential uses of the manatee.

W.H. Allsopp
International Development
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Introduction

Manatees are aquatic mammals of the order Sirenia whose two living genera — *Trichechus* and *Dugong* — have maintained a biphyletic history since the middle Eocene epoch. They are herbivores living in subtemperate and tropical coastal waters, rivers, and estuaries of the Atlantic Basin between the tropics of Cancer and Capricorn.

At present, the manatee is threatened with extinction, and its future, ironically, lies in the hands of its major predator — man. For years, it has been hunted relentlessly in all its habitats, for hide, oil, and meat. Although there is legal protection for manatees in many areas, the laws in most are poorly enforced and ineffective.

Protecting the manatee is a political task; it is also an economically beneficial one. The overgrowth of tropical vegetation in waterways and irrigation canals imposes many adverse health and economic conditions on man. Because the manatee will eat almost any form of aquatic vegetation, it represents a natural biological control agent. In Guyana, for example, it has been keeping canals vegetation-free for many years.

Little is known about the biology of the manatee. At one time because of its voracious appetite, pachyostotic bones, cyclic tooth formation, and hind gut digestion, the animal was thought to have evolved from a line similar to elephants. The dearth of information available is underlined by the fact that the anatomical works of the 19th century remain the definitive papers on this animal. (The plates of Dr James Murie, 1872, Zool. Soc. Lond., Trans., 8: pl. 17-26 — bound in 1874 — appear as an appendix in this monograph.)

There is an especial need for investigations about the African manatee, *T. senegalensis*, and the South American species, *T. inunguis*. Almost no information is recorded about the former and the status of the latter is virtually unknown except that its numbers have rapidly diminished in the last few years.

What is written here is a summary of what little we do know and, therefore by implication, demonstrates what we need to know. As authors, we hope the information presented will provide incentive and directions for future research and would welcome corrections to our interpretations as well as expansion of the material recorded.

Chapter 1.
Nomenclature and Classification

Oldest available name for classification of the species, genus *Trichechi*, is documented in 1802 by Ozertskovsky, N.: *De Specibus Systematicum Genus Trichechi* (Nova Acta Petropolitana, 13: 371–375). The existing classification (Hatt 1934; Scholander 1941; IUCN 1966; Bertram and Bertram 1973) is:

Order: Sirenia (Illiger 1811)
Suborder: Trichechiformes
Family: Trichechidae (Gill 1872[2]), replacing Manatidae (Gray 1821)
Family: Dugongidae
Genus: *Trichechus* Linnaeus 1758, replacing *Manatus* (Horr 1780)
Species: *Trichechus manatus*
Subspecies: *Trichechus manatus manatus* Linnaeus 1758
Subspecies: *Trichechus manatus latirostris* (Harlan 1824)
Species: *Trichechus senegalensis* Link 1795
Species: *Trichechus inunguis* (Natterer 1883)

Common Names

An early record of manatees in the New World was by Columbus, who noted three off the coast of Hispaniola. Later, Spanish and Portuguese explorers reported seeing them in the West Indies. The name was believed to be a derivative of "manatui" or "manatoui" (Simpson 1930). Pereira (1945) referred to the manatee as the Amazon *peixe-boi*, or steer-fish.

Type Locality

T. m. manatus is found in the West Indies, central American coasts, northern South America (Guyana, Surinam, Venezuela, and Trinidad); *T. m. latirostris* is found mainly off the Florida peninsula; *T. senegalensis* frequents West African rivers and coastal regions from Senegal to Angola; and *T. inunguis* is found in the Amazon and Orinoco rivers (Bertram and Bertram 1973).

Objective synonyms[3]

Order: Sirenia (Illiger 1811)
Family: Dugongidae
    Trichechidae (Gill 1872)
Genus: *Trichechus* Linnaeus 1758
  Synonyms:
    Manatus Brunnich 1772
    Oxystomus G. Fischer 1803
    Halipaedisea Gistel 1848
    Monatus D'orbigny, date unknown
Species: *Trichechus manatus* Linnaeus 1758
  Synonyms:
    Manati Trichechus Boddaert 1784
    Trichechus manatus australis Gmelin 1788
    Trichechus antillarum Link 1795
    Trichechus americanus Link 1795
    Manatus Orinocensis Bechstein 1800
    Manatus Guyannensis Bechstein 1800
    Manatus stroggylonurus Bechstein 1800
    Trichechus clusii Shaw 1800
    Trichechus Amazonius Shaw 1800
    Manatus minor Daudin 1802
    Manatus latirostris Harlan 1824
    Manatus atlanticus Oken 1838
Subspecies: *Trichechus manatus manatus* (Linnaeus 1758)
Subspecies: *Trichechus manatus latirostris* (Harlan 1823)
Species: *Trichechus senegalensis* Link 1795
  Synonyms:
    Phoca manatus Brisson 1762
    Manati Trichechus Boddaert 1784

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[2] Although the Library of Congress does not list a paper by Gill in 1872, it does list: Gill, T. 1873. On the affinities of the sirenians. Acad. Nat. Sci., Philadelphia, Proc., 262–273.

[3] The objective synonyms have been taken from Hatt (1934).

Trichechus manatus australis Gmelin 1788
Manatus australis Retziuz 1794
Trichechus aequatorialis Lacépède 1799
Trichechus Australis Shaw 1800
Manatus stroggylonurus Bechstein 1800
Trichechus senegalensis Daudin 1802
Manatus sphaerurus Illiger 1815
Trichechus, Manatus, africanus Oken 1816
Manatus senegalensis Desmarest 1817
Manatus atlanticus Oken 1838
Manatus nasutus Wyman 1848
Manatus Vogelii Owen 1856
Manatus Oweni Du Chaillu 1861
Species: *Trichechus inunguis* (Natterer 1883)

Chapter 2.
Criteria for the Classification of Manatees[4]

Gross Anatomy

T. senegalensis and *T. manatus* are indistinguishable in appearance. *T. inunguis* can be identified by absence of nails, a white breast patch, slender proportions, and elongated flippers.

In the vertebral column, the number of vertebrae varies, but there are no other interspecific characteristics of enough definition to separate the species. Thoracic variations are *T. m. latirostris*, 17–19; *T. m. manatus* (Puerto Rico) 17; *T. senegalensis* 17; *T. inunguis* 15, and lumbocaudal differences are *T. m. latirostris*, 27–29; *T. m. manutus* (Puerto Rico) 25; *T. senegalensis* (Congo) 25; *T. inunguis* 25 (older), 22 (younger).

The sternum of *T. manatus* has a deep median notch and no incision in the margin of the caudal prolongation, whereas the sternum in *T. senegalensis* has no single deep median notch in the anterior border of the bone. It may have two light notches flanking a median prominence, and the margin of the caudal prolongation is incised. In *T. inunguis*, the sternum is smaller in relation to the size of the animal than in the others and may be recognized by its slender proportions and backwardly directed lateral processes.

The scapula in *T. senegalensis* resembles more closely that of *T. inunguis* than that of *T. manatus*, but it differs from both, being comparatively long and narrow. Its coracoid border is gently curved, without a pronounced angle at either the coraco-vertebral juncture or above the incisura. The spine in *T. senegalensis* is a little higher than in the others, the tuberosity less pronounced, and the acromion thinner. *T. inunguis*' scapula is intermediate in width but otherwise can hardly be distinguished from *T. manatus*. *T. m. manatus* and *T. m. latirostris* show no constant peculiarities of the scapulae.

The humerus of *T. senegalensis* is thinner than that found in comparably sized *T. m. latirostris* and is half the weight, resembling very closely the size of the humerus in *T. inunguis*.

The relative proportions of the humerus in the three species are also reflected in the radius and ulna. In *T. senegalensis* and *T. inunguis* the diameters of the radius and ulna are half those found in *T. manatus*.

The lengths of the metacarpals differ markedly in the three species.The fourth metacarpal in *T. manatus* is 45% of radial length, in *T. inunguis*, 65%, and in *T. senegalensis*, 62%. Because the fourth digit, the longest, grows more rapidly, or for a longer period, than does the radius, it is proportionately longer in older animals.

In length, the first carpal in *T. senegalensis* is not intermediate between *T. manatus* and *T. inunguis* but is within the limits of variation of its counterpart in *T. manatus*.

The first phalanx of the fourth digit in both *T. manatus* and *T. senegalensis* is 25% of the humerus length or 40% of the metacarpal length; in *T. m. latirostris*, it is longer than in *T. m. manatus*. In *T. inunguis* the corresponding percentages are 40 and 60. *T. inunguis* may be dubbed "long-fingered," and *T. manatus* and *T. senegalensis*, "short-fingered."

Innominate bones are present in the pelvic girdle but are rudimentary in *T. manatus* and *T. senegalensis* and absent in *T. inunguis*.

In general, the skull in *T. inunguis* is elongated with a long snout and is readily distinguished from the broad and compact skull of *T. senegalensis* and *T. manatus*. Ventrally, the posterior nares are shaped differently in all three species (see Table 1).

Twelve skulls of *T. m. latirostris*, from youth to full maturity, measured from 255 to 375 mm in length (Quiring and Harlan 1953), whereas skulls of *T. inunguis* ranged from 200 to 360 mm (Hatt 1934).

The charateristics of individual bones that constitute the skull are shown in Table 1 and are based on extensive verification of morphological data in the literature.

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[4] This section is a summary based on Hatt (1934).

Table 1. Bones of skull and jaw.

	T. inunguis	*T. senegalensis*	*T. manatus*
Skull			
Bones	Soft consistency, chalky and elaborately roughened; lighter than *T. senegalensis* and *T. manatus*	Dense and smooth	Dense and smooth
Shape	Elongated with a long snout	Broad, compact, short snout (shorter than *T. manatus*)	Broad, compact, short snout
Nasal basin	Long and narrow; very distinct from *T. senegalensis* and *T. manatus* even in immature skulls	In adults, much broader than in *T. inunguis* but narrower than in *T. manatus* (Kaiser 1974); cannot distinguish *T. manatus* from *T. senegalensis* in immature animals.	Broader than in other two species; *T. m. manatus* longer snouted than *T. m. latirostris* but not conclusively
Posterior nares (basal view)	Ventrally, presents the form of a double, symmetrically notched circle	Almost circular	Deltoid
Nasal process of premaxilla	Upper border of premaxilla lies below lower border of frontal	Overlies the orbital process of frontal to some extent; the suture between the bones is shorter than in other species	As in *T. inunguis*, upper border of premaxilla lies below border of frontal
Anterior frontal margin		Between roots of orbital process, typically smooth, unserrated[a]	Slightly jagged; breadth is greater than in *T. senegalensis*[a]
Nasalia	Not always present as separate bones; when present, surface of frontals slightly concave to accommodate the modified lozenge-shaped bones (triangular or quadrangular — greatest diameters: 25–13 mm, smallest: 15–11 mm, thickness 6–3 mm)	Extremely varied in their development; right more frequently absent than left; left when present usually small, spongy, and fixed in the small pit of the frontal	Typically thick, almond-shaped bodies but range from apparent absence to well-developed peglike bones, lying in deep sockets of the frontal and uniting in a loose suture with the ascending rami of maxillae and/or premaxillae
Lacrimal bone	Often missing in prepared specimens		
	Scalelike, unlike *T. manatus*.	Intermediate in size and shape between *T. inunguis* and *T. manatus*; broadest point 3 mm in thickness, tapers to groove between 2 laminae of maxillae; upper border nearly in contact with orbital process of frontal; lower edge touches edge of jugal; triangular surface freely exposed laterally and forms part of the anterior-medial wall of orbital ring	Large, thick; closely resembles *T. senegalensis*

(con't.)

(Table 1 con't.)

	T. inunguis	*T. senegalensis*	*T. manatus*
Vomer	Intermediate in length between *T. senegalensis* and *T. manatus*; in newborn nearly as short as in *T. senegalensis*; in old, occasionally reach to within 25 mm of incisive foramen	Short; extending approximately to level of the middle of orbit	Long (except in newborn); reach to foramen incisivum or beyond
Floor of nasal chamber	Ledges present but lightly developed; farther to rear than in *T. senegalensis*	Ledges on sides of floor; consistently present	No ledges
Circumorbital region	Orbital process of frontal diverges most strongly in lateral direction; upper orbital borders, strongly convergent; when line of outer border of orbital process is extended forward, will cross median line within limits of skull; feature is well marked in newborn	Similar to *T. inunguis*	Unlike *T. inunguis* and *T. senegalensis* if line of outer border of orbital process is extended forward, will cross median line anterior to end of skull
Infra-orbital foramen	Usually simple	Usually simple	May be divided
Temporal bone	Muscular ridges; laterally directed and not rising above general level of skull roof		
Zygomatic arch		Thicker at its base than in *T. inunguis*	Similar to *T. senegalensis*
Malar process	Narrow, sharply tipped, and backwardly directed	Broad and sharply truncated	Same basic shape as *T. senegalensis*, but backwardly directed as in *T. inunguis*
Supraoccipital bone	Differs markedly from other species, surface roughened; lambdoidal ridge, seen from above, is yoke-shaped	Surface smooth and very nearly flat in transverse plane	Shares common pattern with *T. senegalensis*
Exoccipitals	Similar to *T. senegalensis*	Outer borders are knotty, pitted, and rough	Not as roughened as in other species
Foramen magnum	Narrowest, with vertical diameter 75% of the horizontal diameter	Intermediate between *T. inunguis* and *T. manatus* in transverse diameter	Ratio of the greatest vertical diameter to the greatest horizontal diameter is the least in this species *T. m. latirostris*: Flat dorsal rims; this may be one of constant features to justify subspecies; notching of basioccipital fairly constant and distinctive mark of this subspecies

(con't.)

(Table 1 con't.)

<table>
<tr><th></th><th><i>T. inunguis</i></th><th><i>T. senegalensis</i></th><th><i>T. manatus</i></th></tr>
<tr><td colspan="4">Postero-Ventral View of Skull</td></tr>
<tr><td>Pterygoid process</td><td>Formed by wing of alisphenoid, palatine, and pterygoid bone; long and narrow, palatal point highest of 3 species</td><td>Long and narrow, palatine and pterygoid points coequal and longer than alisphenoid</td><td>No general rule for all subspecies. <i>T. m. latirostris</i>' pterygoid similar to <i>T. senegalensis</i> except thicker. <i>T. m. manatus</i>' pterygoid, short and very broad and either pterygoid or palatine point, is highest</td></tr>
<tr><td>Foramen incisivum</td><td>Completely or incompletely divided</td><td>Always simple</td><td>Partial division into anterior and posterior incisive foramina</td></tr>
<tr><td>Palate</td><td colspan="3">Anterior end broadest at junction of maxilla and premaxilla and constricted just anterior to the level of the premolars</td></tr>
<tr><td></td><td>Constriction pronounced, width being about half that at the maxillary-premaxillary suture</td><td>Same as in <i>T. manatus</i></td><td>Constriction variable, but never pronounced</td></tr>
<tr><td>Molars</td><td>Differ markedly from other species; smaller diameter, with anterior and posterior transverse ridges present and strongly furrowed even in unerupted teeth; the primary cones of these ridges broken into a series of smaller cones</td><td>Transverse ridges present and divided into 3 primary cones or sectors; ridges smooth in unerupted teeth</td><td>Indistinguishable from <i>T. senegalensis</i></td></tr>
<tr><td colspan="4">Mandible</td></tr>
<tr><td>Interramal interval</td><td>Rami lie more nearly in parallel planes than in other two species; likewise, angular process wider and more in line with ramus</td><td>Less constriction in diameter of ventral border between the body and angular process than in <i>T. manatus</i></td><td>As broad as in <i>T. senegalensis</i></td></tr>
<tr><td>Symphysial suture</td><td>Furrowed but less conspicuous than in <i>T. manatus</i></td><td>Closes early, no deep furrow along anterior margin</td><td>Furrow most conspicuous in this species but best developed at maturity and not well marked in newborn</td></tr>
<tr><td>Anterior end of mandible</td><td>Truncated as with other species and spine on anterior part of symphysis sometimes present</td><td>Truncated and spine invariably absent</td><td>Truncated; sharp median cone of compact bone (spine) extends forward from anterior part of the symphysis as a constant postnatal feature in this species</td></tr>
<tr><td>Mandibular ramus — ventral border</td><td colspan="2">Slightly curved in longitudinal plane</td><td>More greatly curved in the horizontal plane than in other species; results from deepening of mandibular symphysis and is one of the most pronounced features of this species</td></tr>
</table>

(con't.)

(Table 1 concluded)

	T. inunguis	*T. senegalensis*	*T. manatus*
Coronoid process	Highly variable in shape and cannot be relied on as taxonomic feature		
Mandibular foramen	No septum; rarely, converging processes occur that nearly touch to form a partial septum	Septum well developed	Similar to *T. inunguis*
Mental foramina	11–15	3–4	4–7
Tooth rows	Never closely approach mandibular symphysis in old age as in other 2 species		

[a] According to Kaiser's (1974) plates, the anterior frontal margin is smooth and narrow in *T. inunguis*; jagged and broad in *T. manatus*; and *T. senegalensis* is intermediate in both respects.

Chapter 3.
Evolution and Distribution

Sirenia is a mammalian order comprising only two living genera, the manatee (*Trichechus*) and the dugong (*Dugong*) and, until recent times, the Steller's sea cow (*Hydrodamalis*) (Savage 1977). The earliest known sirenians appeared in the Eocene epoch (Savage 1977), with Trichechids forming a separate phyletic line from the dugongs (Reinhardt 1959). After the Eocene, Oligocene, Miocene, and Pliocene ages, eight sirenian genera (*Prorastomus, Trichechus, Protosiren, Eotheroides, Halitherium, Anomotherium, Metaxytherium, Dugong*) appeared and all but two (*Eotheroides* and *Halitherium*) were monospecific. Fossil remains have been found in America, Europe, and North Africa, and recently major discoveries have been made in Middle-Upper Eocene marine deposits of southeast France (Savage 1977).

The sirenians evolved from a four-footed terrestrial mammal into an aquatic animal. Their hind limbs degenerated, the tail became flattened, and the hairy body covering disappeared except for a few scattered bristles. In some, the teeth were reduced in number or lost completely; in others they were replaced in a cyclic pattern (Hopwood 1927; Prater 1928), and the jaw became deflected downward to varying degrees (Prater 1928; Simpson 1930; Savage 1977).

According to Savage (1977), the structures common to early sirenians included pachyostosis especially in the ribs, zygoma, postorbital processes, and premaxilla, and a distinctive periotic system. All of these features are maintained in the known manatees. Others have evolved and are discussed in the relevant sections of this text.

Distribution

Historically, *T. manatus* ranged from North Carolina to southern Texas in the U.S., from the Bahamas and Greater Antilles to southern Mexico, along the Caribbean and Atlantic coasts of Central and South America to central Brazil (Bertram and Bertram 1973; Heinsohn 1976; Campbell 1976). At present, the species is extremely rare, and population estimates should be regarded as tenuous (Heinsohn 1976).

A small colony of approximately 1000 individuals of the subspecies *T. m. latirostris* resides along the Florida peninsula (Heinsohn 1976), and another 60 on the west coast in the Crystal River (Hartman 1971). The population of *T. manatus* in Mexico is estimated to be 5000 (Heinsohn 1976), and in Guyana, which has the largest numbers, between 1000 and 10 000 (Bertram 1974; FAO 1976; Heinsohn 1976). In Guyana, the species has been sighted along the sea coast, in all the main rivers, but, primarily, in the estuaries (Bertram and Bertram 1973). In Surinam, there is thought to be a moderate number (±1000) of animals living in the rivers, creeks, and in the swamp areas of the west. The status of this species in Central America is unknown and should be investigated (Bertram and Bertram 1973; FAO 1976; Heinsohn 1976). In 1968 Charnock-Wilson reported moderate numbers in Honduras, where they are relatively safe because their alligator predators are rare and they are not hunted by man. *T. manatus* is rare in Puerto Rico and absent from the Virgin Islands (Evermann 1900; Erdman 1970). In 1975, a single manatee was sighted at the west end of the Grand Bahamas for the first time since 1904 (Odell 1976, personal communication). The Brazilian coast population is estimated to be about 200 (Heinsohn 1976).

T. inunguis was once abundant in the Amazon basin, including Brazil, Peru, Colombia, and Venezuela. The animals frequented the Putumayo, Napo Tigre, Maranon, and Ucayali rivers and possibly the Rio Huallaga in Peru, and the Orinoco River in Venezuela (Bertram and Bertram 1973; Heinsohn 1976). According to Pereira (1945), the numbers at that time were small in the Amapa (Rio Branco), Mearim, and Marapanim river mouths, and the lower Amazon. The species was more frequently seen in the Faro lakes area, which was sparsely inhabited by human beings. Pereira reported thriving colonies in the Lago Grande de Vila France, Lago do Periquito, Parintino, Lago de Macurincana, and the Uruli River. In the lakes surrounding the towns of Itacoatiara, Urucara,

Table 2. Worldwide distribution of manatee.

Trichechus inunguis		*Trichechus manatus*		*Trichechus senegalensis*	
Country	Site	Country	Site	Country	Site
Colombia	Putumayo-Leticia regions	USA	Florida peninsula	Senegal	Marigots from Senegal River south to the Casamance region on coastal areas between Dakar and Banjul
Peru	Putumayo, Napo Tigre, Maranon, and Ucayali Samiria, Pacaya Maniti, Autumayo Amazon rivers	Mexico	Yucatan peninsula	Gambia	Gambia River
Venezuela	Orinoco headwaters	Belize	Rivers, e.g., Belize River	Portuguese Guinea	
Guyana	Rupununi and Essequibo headwaters (not confirmed)	Guatemala	Peten region	Guinea	
Brazil	Lower reaches of Amazon main tributaries (e.g., Nhamunda, Tapajos rivers) and its lower lake	Honduras	Caribbean coast	Sierra Leone	Mangrove swamps
		Nicaragua	Caribbean coast, Bluefield River	Liberia	
		Costa Rica	Limon Province	Ghana	Volta River (above and below the dam), probably lower reaches of other rivers
		Panama		Ivory Coast	Cavally River, probably lower reaches of other rivers
		Colombia	Caribbean coast	Togo	
		Venezuela	Lake Maracaibo, lower Orinoco	Benin	
		Guyana	Coastal region, all main rivers	Mali	Segou, Lac Debo, Timbuktu Ansongo, Gao
		Surinam	Coastal region, rivers, swamps of west	Nigeria	Mouth of the Niger River, Calabar; coastal rivers in western and midwestern regions: Benue River, e.g., at Numan
		French Guiana	Coastal region	Chad	Lake Lere, Benue River
		Brazil	Coastal rivers in the northeast	Cameroon	Mangrove regions
		Curacao		Rio Muni	
		Cuba		Gabon	Lower reaches of Gabon and Ogooue rivers
		Jamaica		Congo	Kouilou River
		Haiti		Zaire	Lower Zaire from Banana to Chaudron d'Enfer, especially around Boma
		Dominican Republic		Cabinda	
		Puerto Rico		Angola	Coastal rivers north of the Cuanza
		Other Caribbean			
		Bahamas	West Grand Bahamas		

Source: National Science Research Council, Guyana, 1974.

Uricurituba, and Maues, there were a few animals. The Antazes River had many individuals, but they were relentlessly hunted. *T. inunguis* was considered to be rare in the Madeira River and its tributaries. Groups of 10–30 animals were often seen traveling in the Purus River and the Solimoes River and its tributaries (Pereira 1945).

At present, the population of *T. inunguis* is greatly reduced and is in danger of extinction (Bertram 1974; FAO 1976) because it is still hunted for its meat (Heinsohn 1976). It is found in the sluggish tributaries of the lower Amazon and in their interconnecting systems of lagoons, oxbows, and creeks. The animal probably does not exist south of latitude 7°S. Till 1957 they were still known in the Orinoco River, and when Lago Callac dried out in 1963, a few were discovered. In 1968, a survey yielded no evidence of *T. inunguis* in the upper limits of the Xingu River, and by 1972 the species was considered rare in the Tocantins and Tapajos rivers. As late as 1973, manatees were fairly common in the lower part of the Nhamunda River and in the lakes of the lower Tapajos. A stable colony of *T. inunguis* is concentrated in the central and northeast lower jungle of Peru. Although not present in the basin of the Madre de Dios River, manatees are present in the Samiria, Pacaya, Maniti, Autumayo, Napo, Ucayali, and Amazon rivers. Within Peru there is an urgent need for effective legal protection for the manatees. At present, the laws are not respected by the public industries, official representatives, or by the people, and hunting is encouraged by the local government. If the Pacaya Samiria National Reserve were to be sanctioned as an international refuge for *T. inunguis* as an endangered species, recuperation of the species might be possible (Brack 1977, personal communication). In Guyana, *T. inunguis* was not known after 1970 in any rivers south of latitude 4°N. Although the species is legally protected in Brazil, the law is not enforced.

At one time, *T. senegalensis* was widely distributed along the coastal lagoons and far up the African rivers from Senegal in the north to the Cuanza River, Angola, in the south (Bertram 1974; Heinsohn 1976). Occasionally, the animal has been seen in the lake drainage areas of Lake Chad and the Gulf of Guinea (Bertram and Bertram 1973).

In 1969, *T. senegalensis* was placed in Class A of the African Convention but in reality it has not been protected (Bertram and Bertram 1973). It is extinct in many of its former habitats (Bertram 1974; FAO 1976), such as the Niger River (Poche 1973). Until 1973, it was familiar to the Parc National of the Casamance, Senegal (Dupuy 1973), and was known in rivers several kilometres inland and in marine areas (Heinsohn 1976). It is probably still present above the Volta dam in the Kete Drachi area but is still hunted there. It may still exist in the rivers of Ghana where protection is superficial but this has not been confirmed. The Benue River has local stocks and in its adjacent lakes conservation is being attempted. Until 1957 there were reports of abundant manatees between Dakar and Banjul (formerly Bathurst). In 1973, Bertram and Bertram concluded "knowledge inadequate and prospects gloomy" for *T. senegalensis*.

Chapter 4.
Structure and Function: Part 1

To date, the only work done on the cytogenetics of manatees was carried out on a 1-m male specimen of *T. inunguis*, probably less than age 6 months (Loughman et al. 1970), and several adults and one young of *T. m. latirostris* (White et al. 1976). Biopsies of the skin and the supporting tissues of the caudal peduncle in *T. inunguis* gave 37 karotypes, each having the same pattern and varying in length from 0.5 to 5 μm. Based on length and arm ratio, six distinct groups, plus X and Y chromosomes were determined.

Group A (1–3) consisted of three pairs of large submetacentrics; the X chromosome is easily confused with members of this group. In group B (4–5), two pairs of large subacrocentrics were easily identified. Three pairs of medium acrocentrics were found in group C (6–8). Group D (9–10) consisted of two pairs of medium acrocentrics or telocentrics and group E (11–17), of seven pairs of medium to small metacentrics and submetacentrics, continuously graded in size. In group F (18–27), 10 pairs, probably acrocentrics, small and continuously graded in size, were present; the shortest pair, being separate, could be compared with the Y chromosome.

X and Y chromosomes were shown separately, with the X not being clearly distinguishable. After pairing group A in each karotype, X, a single large submetacentric, remained unpaired. Its appearance in each karotype was highly variable, in length, arm ratio, or both. Measurements of absolute length and arm ratio were therefore subjected to statistical analysis. With 95% confidence, the X chromosome was reliably identified in 7.5% of the karotypes that could be constructed. The Y chromosome was identified in 40%. It was assumed that in the female manatee, like in other mammals, the X chromosome would be a large submetacentric and the Y, a small acrocentric.

The size and number of chromosomes are the same as those from karotypes of Asian and African elephants (*Elephas maximus* and *Loxodonta africana*), but the metacentric and submetacentric chromosomes, exclusive of X and Y, differ in that *Trichechus* has 10 pairs, *Elephas* 3, and *Loxodonta* 2. *Trichechus* has 2 pairs of the subacrocentrics, *Elephas* 3, and *Loxodonta* 1. The *Trichechus* Y chromosome is the shortest with the centromere poorly defined and ''probably nearly terminal'' (Loughman et al. 1970). There are chromosomes with satellites in *Elephas* but none in *Loxodonta* or *Trichechus*. The number of satellite arms in the female are: *Trichechus* 82, *Elephas* 70, and *Loxodonta* 64. The overall karotype of the manatee is therefore unlike that of the elephant; any evolutionary connection is distant (Loughman et al. 1970).

In *T. m. latirostris* the chromosome number is constant at $2n = 48$ in all metaphases. White et al (1976) noted that *T. m. latirostris* has fewer acrocentric chromosomes than *T. inunguis*, which has a diploid number of 56. They suggested that a comparison of the karotypes of the two using banding techniques would yield more precise correlations and reveal any evolutionary variations.

Biochemistry

Tissue fats of an immature 1.6-m male of *T. senegalensis* were taken from the cervical, dorsal, and thoracic regions and from the thoracic muscles. Tables 3 and 4, adapted from Itoh and Tsuyuki (1974), show respectively, the complete values of the fatty acid components and the properties of different tissue fats. In fatty acid composition, the manatee resembles the Halicore dugong except that $C_{20:0}$ and $C_{20:4}$ were the only fatty acids with more than 20 carbon atoms observed in Dugong fat. The fats in both deviated from most marine and freshwater mammalian fats. Four main fatty acids were isolated: $C_{14:0}$, $C_{16:0}$, $C_{16:1}$, and $C_{18:1}$. These accounted for 90% of the total fatty acids; 26 others were observed in low quantities (Itoh and Tsuyuki 1974).

Integument and Derivatives

The skin of the manatee is corrugated and wrinkled like the hide of an elephant (Lucas 1916) with deep folds around the head, at the juncture of the flippers, and at the base of the tail (Phillips

Table 3. Fatty acid component of different tissue fats of Senegal manatee.

	Fatty tissues			
Fatty acids	Cervical	Dorsal	Thoracic[a]	Thoracic[a] muscle tissue
		Saturated		
6:0	0.81	trace	0.72	–
8:0	0.31	0.19	0.27	0.16
10:0	3.14	1.59	2.52	2.09
12:0	1.65	1.30	1.54	1.70
Iso 14:0	0.04	trace	trace	0.05
14:0	15.98	14.97	18.66	15.72
15:0	0.50	0.28	0.42	0.33
Iso 16:0	0.31	0.37	0.35	0.08
16:0	24.82	27.78	24.57	26.12
17:0	0.54	0.47	0.36	0.55
18:0	2.73	2.53	2.77	2.84
19:0	0.09	0.05	0.04	0.02
20:0	0.74	0.63	0.70	0.54
% Total	51.66	50.16	52.93	50.21
		Monounsaturated		
12:1	0.14	trace	0.09	0.11
14:1	0.41	0.28	0.36	0.33
16:1	7.18	7.30	6.69	7.32
18:1	37.60	39.75	36.86	39.17
20:1	0.33	0.21	0.25	0.21
22:1	0.26	0.20	0.19	0.24
% Total	45.92	47.74	44.71	47.38
		Polyunsaturated		
14:2	0.36	0.27	0.35	0.33
16:2	0.24	0.42	0.28	0.30
16:3	0.49	0.42	0.43	0.46
18:2	0.32	0.22	0.34	0.41
18:3	0.41	0.28	0.40	0.51
20:2	0.20	0.22	0.24	0.13
20:3	0.04	0.05	0.03	0.02
20:4	0.06	0.04	0.04	0.02
22:2	0.06	0.05	0.04	0.05
22:3	0.04	trace	0.02	0.01
22:5	0.09	0.06	0.08	0.07
22:6	0.11	0.07	0.11	0.10
% Total	2.42	2.10	2.36	2.41

Source: Itoh and Tsuyuki 1974.

[a]The columns of thoracic and thoracic muscle tissue do not total 100.00; this is likely a *lapsis calami*.

Table 4. Properties of different tissue fats of the Senegal manatee.

	Fatty tissues			
Appearance (at 30°C)	Cervical: whitish semisolid	Dorsal: whitish semisolid	Thoracic: whitish semisolid	Thoracic muscle tissue: yellowish semisolid
Oil content (%)	78.0	69.1	71.8	5.8
Refractive index (at 50°C)	1.4527	1.4531	1.4532	1.4536
Acid value	0.21	0.29	0.24	0.32
Iodine value	48.1	47.3	46.9	47.4
Saponification value	209.1	210.8	209.2	207.7
Unsaponifiables (%)	0.34	0.38	0.35	0.51

Source: Itoh and Tsuyuki 1974.

1964). Nail-like structures are found at the end of each digit (Quiring and Harlan 1953), except in *T. inunguis* (Pereira 1945). The integument is from 8 to 16 mm thick and sparsely covered with fine, colourless hairs, which are most numerous on the flippers (Barrett 1935). They are usually 3.0–4.5 cm in length, although those on the flippers and top of the head are slightly shorter (Murie 1872). The skin of the upper lip-pads is coarse in texture and covered with numerous keratinized, colourless bristles. In the area surrounding the mouth and on the inner surfaces of the lips, the bristles are stiffer and more ventrally directed than on the outer surface of the pads (Quiring and Harlan 1953; Pereira 1945). The skin of newborn calves is soft and dark gray but roughens and becomes pebbly in texture within a few days (Phillips 1964).

The skin of *T. m. latirostris* lightens with age to a dull gray, varing from dirty, whitish gray to an uneven, almost mottled, bluish-brown gray (Hartman 1969; Barrett 1935). Some have uniform pigmentation, whereas others have irregular pale pink patches on the abdomen. Ventral colour is often obscured by algal growths, barnacles, and incrustations of the skin (Hartman 1969).

T. inunguis has been described as lead-coloured with several marble-white blotches on the abdomen. Some white manatees have been seen, possibly albinos, but scientific documentation is lacking. South American fishermen generally distinguish four types of manatees according to size and colour: carapanauba (spotted chest), camuti (small and thick), mati de azeite (reddish, colour of clay), and prête (black, and very rare) (Pereira 1945).

The epidermis is sloughed continuously, and dark patches of new epidermis appear. Many manatees are scarred from accidents with motor boats and other objects, such as harpoons (Magor 1976, personal communication). The scar tissue is pale and has been found useful for identification (Moore 1956; Hartman 1971).

Thermoregulation

Manatees cannot tolerate low temperatures, but their threshold has not been definitively established (Bangs 1895; Cahn 1940; Moore 1951; Moore 1951a; Husar 1973). It is generally assumed that a sudden drop in temperature will kill manatees, but Hartman (1971) has disagreed. He quoted Allsopp (1961) as saying that "the manatee does not appear to be able to live at ease in temperature below 21°C" and Sguros (1966) as asserting "the minimum tolerable water temperature is frequently stated as about 16° to 18°C," but he himself suggested (1971) that *T. m. latirostris* can endure water temperatures below 15°C and acclimatize to cold water as winter progresses. Although a drop in T_A (ambient temperature) to below 10°C in November caused a group of manatees to congregate into warmer spring-fed waters, the same group did not move in March until the T_A dropped to 5°C.

The manatee has almost no subcutaneous fat (Murie 1872a; Nishiwaki 1972), and the rectal temperature is probably among the lowest recorded for mammals. During an 18-day period, *T. senegalensis* immersed in water at 20.5–23.0°C had a rectal temperature that varied from 25 to 28.5°C (Dekeyser 1952).

Skeleton

Some bones of the axial and appendicular skeleton have been used for classification (Chapter 2). Peculiarities include the extremely dense and pachyostotic bones (Prater 1928; Fawcett 1942; Harrison and King 1965), which add to the manatee's specific gravity and may facilitate browsing on the bottom when the animal is submerged (Prater 1928).

The skull of *Trichechus* is generally broad with a relatively short and slightly deflected snout (Harrison and King 1965). In both the details of the facial bones and in the view from above, it resembles that of the elephant (Agassiz 1849). The large, expanded nasal basin, the floor of which is formed by the maxilla and vomer, is located in the anterior portion of the skull, extending posteriorly beyond the borders of the orbits and is perhaps one of the most obvious features of the skull (Harrison and King 1965). The orbits are almost closed posteriorly (Kaiser 1974) by a postorbital bar (Harrison and King 1965). The vomer is most prominent in *T. manatus* (Kaiser 1974). Small, ovoid nasal bones are present. The zygomatic arches are thick and deep and the braincase is characteristically small (Harrison and King 1965).

The walls of the braincase vary in thickness. the length and breadth of the cranial cavity are nearly equal, but the height is rather less than either (Murie 1872a). In one animal, the frontal bones near the point of union in the mid-dorsal line were 3.0 cm thick, whereas the occipital bone was 2.6 cm thick and portions of the temporal bone were less than 1.0 mm in thickness (Quiring and Harlan 1953). The mandibles are massive with the roughened dorsal surface of the symphysis sloping and extended slightly downward (Prater 1928; Harrison and King 1965). This feature is more pronounced in the dugong and is presumed to be an adaptation for feeding (Prater 1928; Domning 1977). The coronoid process is short and directed anteriorly (Harrison and King 1965).

The premaxillae are less prominent in *Trichechus* than in the dugong, in which there is a strong (~70°) deflection of the rostrum and mandibular symphysis from the palatal plane. In *Trichechus*, the deflection is relatively slight (~40°) (Domning 1977). The bodies of both premaxillae in *T. inunguis* are almost parallel; those of *T. senegalensis* present a wider angle, and those of *T. manatus* the widest of all. The differences in the direction of the orbital openings are equally remarkable as species-specific characteristics (Kaiser 1974).

There are some significant structural differences found in the skulls of *T. senegalensis*, *T. inunguis*, and *T. manatus* (Kaiser 1974). An emissary parietal foramen is not found in *Trichechus*, although it is present in the dugong. In *T. senegalensis*, the exoccipitals extend laterally further than in dugong or *Hydrodamalis*. The sagittal suture is not prominent in either dugong or *Trichechus* and is less developed in *T. inunguis* than in *T. senegalensis* or *T. manatus*. The other principal sutures are very late in closing, thus accounting for the looseness of the temporal bones sometimes seen in prepared specimens of adult skulls (Harrison and King 1965).

Ventrally, the skulls differ in width. *T. inunguis*' skull appears elongated but the occipital region is rectangular in form; *T. manatus*' skull is the broadest and is robust in appearance. The foramen magnum is narrow in *T. inunguis*, wider in *T. senegalensis*, and widest in *T. manatus*.

The auditory ossicles of the sea cows resemble each other but can be readily differentiated from the homologous bones of all other mammals by their pachyostotic structure (Kaiser 1974; Robineau 1965); *T. m. latirostris* has the largest malleus found in extant mammals (Kaiser 1974). Doran (1884, plate 63, Fig. 21–25) illustrated the malleus and incus in *T. manatus* and the stapes of *T. senegalensis* and also commented on their position and large size.

Variations in the number of vertebrae have been reported. Hatt (1934) and Jones (1967) both reported between 48 and 54 vertebrae (C 6, T 17–19, L 0, Ca 27–29), but Quiring and Harlan (1953) and more recently Kaiser (1974) recorded 47–50 vertebrae. Quiring and Harlan recorded the vertebral formula as C 6, T 17, L 3, Ca 24, making a total of 50 vertebrae, and the formula given by Kaiser was C 6, D 17, L 1–2, S 1, and Ca 22–24. Cervical vertebrae are compressed, disclike bones and are rarely fused. An odontoid process is present on the axis, and according to Harrison and King (1965) the third cervical vertebra seems to have been lost. To each of the thoracic vertebrae, which increase in size from the first to the last, is articulated a pair of ribs; when present, the lumbar vertebrae have wide transverse processes. One vertebra provides the locus for the ligamentous attachment of the vestigial pelvic bones (Quiring and Harlan 1953). Because the caudal vertebrae do not unite to form a sacrum, the manatee has great flexibility in the lower spinal region, which presumably is an aid in swimming (Prater 1928).

The ribs of the manatee are broad and massive and are arranged so that a line joining their distal free ends lies almost parallel to the vertebral column (Quiring and Harlan 1953).

The sternum of *Trichechus* consists of a single bone, the manubrium, that is broad and flat with a handle-shaped extension at the caudal end. Three pairs of ribs are attached to it (Quiring and Harlan 1953).

The bony ridge or crest of the manatee scapula rises near the centre of the blade and runs downward toward the glenoid articulation for the humerus. Its free edge turns slightly forward and continues beyond the neck of the bone. A long, rodlike acromion is produced projecting considerably beyond the coracoid and the anterior edge of the glenoid and lying outside the notch that separates the two (Pocock 1940). A clavicle represented by a thin ligamentous band was described by Quiring and Harlan (1953) as extending from the manubrium sterni to the coracoid process of the scapula.

The humerus is extremely heavy and characteristic of pachyostotic bones. The head of the humerus is prominent and the lesser tuberosity is separated from the greater tuberosity by a bicipital groove of variable dimensions (Quiring and Harlan 1953). The radius curves forward (Kaiser 1974) and is approximately the same size as the ulna (Quiring and Harlan 1953). The ulna is a short, straight bone fused with the radius both proximally and distally (Quiring and Harlan 1953) to form a wide, oval-shaped interosseous space (Kaiser 1974).

The carpal bones of *Trichechus* are arranged in a proximal and a distal row. Those of the proximal row are the radiale, the intermedium, and the ulnare, the first two of which are invariably fused into one element that articulates with the radius; the remaining element articulates with the ulna. The distal row comprises the first, second, third, and fourth carpal bones; the first and the second are usually fused, facing and articulating with the radiale-intermedium (Quiring and Harlan 1953). Of the remaining two bones in the distal row, carpal three articulates with the intermedium, and carpal four with the intermedium and ulnare (Kaiser 1974, pl. 63E). Of the five metacarpals, the first two articulate with fused carpals one and two. Metacarpals three and four articulate with carpals three and four, respectively, and the fifth metacarpal with the ulnare (Quiring and Harlan 1953).

Quiring and Harlan (1953) gave the formula of the phalanges as 1,2,2,2,2; however, the formula derived from their diagram of *T. m. latirostris* is 1,3,3,3,2, and that obtained from Kaiser (1974) in an illustration of *T. senegalensis* is 1,3,3,3,3.

The pelvic bones are vestigial or absent (Barrett 1935; Quiring and Harlan 1953; Kaiser 1974). When vestigial, the girdle consists of a small bone on each side of the vertebral column (Quiring and Harlan 1953; Harrison and King 1965).

Skeletal Microscopic Anatomy

Gebhardt (1901) concluded that the bones of Sirenia are heavy and dense as a result of a partial suppression of bone resorption, and Fawcett (1942) elaborated, detailing the microscopic anatomy of the fetal skeleton and adult long bones in *T. m. latirostris*. The fetuses measured 44.0 cm and 95.0 cm respectively, and the adult male weighed 340 kg.

According to Fawcett, the ribs are fusiform and taper toward each extremity. In the middle of the shaft, they measure 5.0 cm in thickness and 8.0 cm in width, but at the costochondral junction the largest diameter does not exceed 2.0 cm. The ribs are asymmetrical and oval in cross-section. The pleural edge is curved slightly, and the contour of the outer edge is almost semicircular.

The ribs are remarkably dense and heavy, largely due to the lack of a medullary cavity and the absence of cancellous bone in the shaft. Though not evident in X rays, a porous central area of small intercommunicating cavities is apparent in a cross-section near the chondral end and is separated by heavy anastomosing bony trabeculae. This porous area is structurally similar to, but denser than, spongy bone.

In most mammals, the compact bone of the ribs has a lamellar structure throughout whereas in the manatee, a considerable portion is nonlamellar. In the shape and distribution of its cells and in its spongy texture, this nonlamellar bone is identical to the primary perichondral spongiosa of the fetal rib. The osteocytes are oval or round and their branching processes radiate in all directions. A network of primary nonlamellar bone persists as a framework of adult compact bone. Spaces in the primary, trabeculated framework are filled with secondary lamellar bone, deposited in irregular layers, containing flattened osteocytes with processes oriented in definite planes. However, this secondary bone lacks the sharp definition of lamellae as well as the definite concentric arrangement of the Haversian systems ordinarily found in mammalian compact bone.

Histologically, adult manatee ribs resemble fetal bones of other mammals. The continuity of persisting primary and secondary bone is interspersed with the interjection of the typical Haversian systems of adults. These systems have probably replaced resorbed primary and secondary bone, as evidenced by the refractile cement lines that bind them. The compact bone is therefore composed of primary and secondary bones, that are only partially replaced by mature tertiary concentric systems. Hence, though manatee ribs are much denser and heavier than the bones of most other mammals, their structure is less differentiated.

Because of the predominance of Haversian systems, the inner third of a cross-section resembles ordinary compact bone. With the diminution of the Haversian systems at the outer edge of the section, the trabeculated framework of the nonlamellar bone increases and strongly exhibits the fetal arrangement of primary and secondary bone. The pattern of the trabeculae of nonlamellar bone varies to produce a number of concentric zones, or alternating rows, in the outer part of the rib. The rows have slightly different trabecular architecture and account for the macroscopic appearance of stratification in the outer two-thirds of the ribs. Near the pleural edge, the lamination is less apparent because the pattern of primary and secondary bone is largely replaced by a great number of closely approximated Haversian systems. This arrangement of periosteal bone suggests that osteogenic activity is periodic or seasonal. There is also a certain amount of modeling resorption between bouts of periosteal activity.

The periosteum of the adult rib is unusually thick and adheres closely to the underlying bone, the surface of which consists of anastomosing, spongy trabeculae. Between the trabeculae are connective tissue and blood vessels from the deep layer of the periosteum. A feature of this recently formed, primary spongiosa is the occurrence of numerous osteoblasts and the secondary bone deposits on the surfaces of the trabeculae. The manatee is exceptional in this regard, because in other adult mammals, under normal conditions, the periosteum has no osteogenic function.

Similarly, the eccentric deposition of periosteal bone is apparently unique. Old and new bones coexist in cross-sections of adult manatee ribs, and the number of Haversian systems in any given area of a cross-section indicates the extent of the area's internal reconstruction and its chronological age. The most advanced structural differentiation found in the adult manatee rib corresponds to the histogenesis found in the human bone in the 1st year of its life. Therefore, although internal reorganization by resorption and replacement occurs in Sirenia, it is much less extensive and occurs at a much slower rate than in the bones of other mammals.

The manatee humerus, like the rib, is dense and very radio-opaque, containing no marrow cavity. A longitudinal section reveals both compact and cancellous components. The cancellous tissue at the extremities of the bone is vastly denser than the spongy bone at the articular ends of ordinary mammalian long bones. The interstices are very small, and the trabeculae so massive that the spongiosa can scarcely be distinguished from the cortical bone. The interstitial spaces are richly vascularized, whereas the compact bone contains no interstitial cavities or blood vessels visible to the naked eye. Both ends of the humerus consist of heavy cancellous bone covered with a thin cortex of compact bone. The cortex increases in thickness from the ends to the middle, while the core of cancellous bone diminishes, and this accounts for the radio-opacity at the ends of the bone. The thickness of the cortex increases more gradually from the proximal end than from the distal end so that the core of cancellous bone is narrowest at the lower and middle third of the shaft. Here the cortices of the opposite sides are only separated by a slender central canal occupied by the nutrient artery.

The unusual distribution of cancellous and compact bone in the adult can be better understood by examination of the structure of the fetal humerus. In other mammals, the diaphyseo-epiphyseal junction of normal fetal bones consists of a richly vascularized zone of one-cell wide columns of swollen and degenerating cartilage that run parallel across the width of the bones as well-defined bands. In the humerus of the fetal manatee, the zone is deeper and contains columns that are two or three cells wide and not uniformly parallel.

Blood vessels penetrate the cartilage columns to varying depths, and the trabeculae of the metaphysis interdigitate with the jagged border of the epiphyseal cartilage so there is no orderly epiphyseal "line." The trabeculae in the metaphysis are coarse, irregularly shaped, uneven in size, and inconstant in their orientation. The region of endochondral ossification is highly vascular, forming a rich plexus among the trabeculae. There are few islets of hemopoietic activity and the quantity of blood cells formed in the fetal humerus is insignificant. In adult long bones, no blood elements appear to be formed, and no true marrow cavity ever develops. In other mammals, connective tissue, virtually devoid of blood-forming elements, is found in the marrow of the perivascular spaces.

In sirenian long bones, internal reorganization due to resorption and replacement is far less extensive than in the bones of other mammals and is further advanced at the centre of the long bones and ribs than at the periphery. It may be assumed that the sequence of events in the histogenesis of bone is the same in the manatee as in other mammals, but the rate of the resorption and reorganization is very much slower. As a consequence of this inability to absorb bone and calcified cartilage at the usual rate, endochondral ossification, which depends upon excavation of the epiphyseal cartilage, is seriously retarded — a circumstance consistent with the presence of few osteoclasts at the diaphyseo-epiphyseal junction and their complete absence in the endochondral bone near the middle of the shaft. Growth in width of the epiphysis and the deposition of periosteal bone are relatively unimpaired, thus accounting for the short, thick proportions of sirenian bones and the unusual thickness of the cortices.

Among aquatic mammals, Sirenia alone exhibit solid bones, and they alone eat sea algae, rich in iodine. Because clinical observations of cretins showed evidence of disturbances in ossification that mimic the structure of sirenian bones, it was postulated that the high iodine content of their aquatic diet resulted in a hypofunctioning of the thyroid (Nopsca 1923). Sickenberg (1931) elaborated on the theory, stating that the evolution of amedullary bones was probably caused by anoxia. However, anoxia affects the thyroid rather than the bone marrow; therefore, he reasoned that the heavy bones of Sirenia were secondary to an inherent hypothyroidism that arose in a period of imperfect adaptation to the aquatic environment as a consequence of the combined effects of high iodine intake and chronic anoxia. Fawcett (1942) stated that the histological structure of the manatee thyroid is consistent with hypothyroidism and Harrison and King (1965) have confirmed the inactive, storage state of the gland.

Scholander and Irving (1941) showed that resting oxygen consumption is lower in the manatee than in any other aquatic mammal so far investigated, and they regarded the unusually low basal metabolic rate as convincing evidence of hypothyroidism. Given the diminished thyroid function, it is not surprising that sirenian bones resemble those found in mammals with either natural or induced athyroidism or so-called marble-bones or osteopetrosis. The latter is a rare, hereditary abnormality in human bones. The conditions have in common: delayed growth in length of bones accompanied by relatively normal growth in width; incomplete differentiation of periosteal bone into Haversian systems; retardation of endochondral ossification with disorderly arrangement at the diaphyseo-epiphyseal junction; a diminution of osteoclasts, both in number and in activity; an unusual persistence of unabsorbed calcified cartilage and primary nonlamellar bone; and a reduction in the amount of functional bone marrow. The evidence strongly indicates that the peculiarities of the Sirenian bones are related to an inherent hypofunctioning of the thyroid gland (Fawcett 1942).

Skeletal Muscles and Connective Tissues

The colour of the skeletal muscles of the manatee varies from pink to deep red. Probably due to high myoglobin levels, the rectus abdominis muscle, heavily ensheathed in a deep fascia, is elongated and red, whereas the remaining abdominal muscles, namely the external and internal obliques and transverse abdominis, are pink. The pectoralis major and minor muscles of the thorax are a rich red colour as are the shoulder muscles and the diaphragm. The remaining body musculature is light and pink (Garrod 1877; Quiring and Harlan 1953).

The central tendinous portion of the diaphragm is attached to the vertebral bodies (Murie 1872a) and extends almost the entire length of the abdominal cavity from the level of the third rib to the region of the pelvis (Murie 1872a; Quiring and Harlan 1953; Harrison and King 1965). The fleshy portion of the muscle is fastened to the foreshortened, forwardly directed costal cartilages, forming together with the external oblique muscle, a small pocket into which the flattened, elongated lungs taper (Murie 1872a; Barrett 1935). The lungs and heart thus lie in a dorsal thoracic compartment separated from the abdominal viscera lying ventrally (Murie 1872a). Hence, Quiring and Harlan (1953) have incorrectly described the kidneys and adrenals, like the lungs, as retropleural, occupying the upper chamber.

In the manatee, the panniculus carnosus muscle, which all aquatic mammals have developed to an unusual degree (Murie 1872a, Fawcett 1942b) extends from the pelvic region to just below the eye, with some fibres running to the forelimb and some beneath the neck to form a sphincter colli. In some places it is 38.1 mm thick. Broad and powerful, it helps strengthen the abdomen and substitutes for the missing costal cartilages. Together with the rectus abdominis, the panniculus carnosus aids in swimming (Harrison and King 1965).

The peritoneum is composed of dense, white connective tissue; the omentum does not extend the whole length of the abdominal cavity and is not very fatty (Quiring and Harlan 1953).

Myoglobin values were obtained from two specimens of both the shallow-diving manatee, *T. inunguis*, and the harbour porpoise, *Phocoena phocoena*. Of all the muscles examined in the manatee, the diaphragm had the highest myoglobin values, namely 3.64 and 3.78 g/100 ml, whereas in the porpoise the muscles with the highest myoglobin concentration were the psoas (15.77 and 15.94 g/100 ml) and the back muscles (15.20 and 17.06 g/100 ml). Values of myoglobin content of cardiac and psoas muscles in the manatee were respectively, one-half and one-tenth of those of the porpoise, whereas corresponding human values are less than one-half and one-fifth those of the porpoise. The myoglobin content of manatee skeletal muscles other than the diaphragm seems to be of the same order as humans, but the cardiac muscle contains more myoglobin and may correlate with the manatees' shallow-diving, sluggish behaviour (Blessing 1972).

Chapter 5.
Structure and Function: Part 2

The manatee has a large, globular heart; for example, the heart of a 557-kg female *T. m. latirostris* weighed 1.24 kg (Quiring and Harlan 1953). A deep interventricular cleft characterizes this organ (Murie 1872a; Quiring and Harlan 1953; Beddard 1897). The heart is situated ventrally from the apex of the lung, loosely enclosed in the parietal pericardium allowing the twin-pointing apex to move freely in this area of the common cardiopleural cavity (Quiring and Harlan 1953).

Variations are present in the hearts of adult specimens of *T. inunguis* and *T. m. latirostris*. In both species, the right ventricle is less well defined than the left. The moderator band is distinct in both. More marked in *T. inunguis*, it continues forward from its attachment to the interventricular septum to the base of the semilunar valve of the pulmonary artery. *T. m. latirostris* exhibits a moderator band that adheres for a greater extent to the heart wall and does not extend to the base of the valve. There is no difference in the origin of the major coronary arteries in either species (Beddard 1897).

There are two superior venae cavae (Fawcett 1942b; Harrison and King 1965), the right one opening into the right auricle above, the left one below (Chapman 1875). The two pulmonary veins unite to enter the left atrium at a single opening (Harrison and King 1965). There are two abdominal venae cavae as in dugongs and a small hepatic sinus, which is absent in dugongs (Harrison and Tomlinson 1964). Communicating with the post-caval system are a pair of extradural veins lying ventral to the spinal cord for movement of blood from the trunk and tail (Fawcett 1942b). There is no caval sphincter, but there is a diaphragmatic muscle in the form of a muscle sling (Harrison and Tomlinson 1964).

The vasculature of the manatee is highly developed. The vascular bundles (Wislocki and Straus 1932; Fawcett 1942b; Harrison and King 1965), which are uniquely arranged, have been referred to as a rete mirabile (Murie 1872a), a term that does not describe them accurately. The larger arteries are completely subdivided near their sources into small arteries that travel for considerable distances together, in a broomlike arrangement, not branching into the usual mammalian vascular network (Fawcett 1942b). Present in almost every muscle in the body (Quiring and Harlan 1953), the feature is most extensive in the vascularization of the forelimbs (Fawcett 1942b) and head, the rostrum and inner angle of the jaw particularly. The size of the vascular spaces varies in the muscle and surrounding fascia. Many retial bundles unite to form a large blood vessel, probably the internal jugular vein, which runs along the ramus of the jaw (Quiring and Harlan 1953). Retial bundles are also found elsewhere in the face, body wall, tail, and spinal cord. The extensive network enveloping the spinal canal together with the large intraspinal venous pathways is probably an aquatic adaptation. During diving and the resulting hydrostatic compression of the abdominal cavity, the network offers the path of least resistance (Fawcett 1942b), for blood shunted to the so-called vertebral system (Batson 1940). The fanlike formation of arteries is not conspicuous in the abdominal viscera.

The blood supply to the muscles and subcutaneous tissue and skin is peculiar. Normally, in mammals, the artery enters the muscle and breaks up within it; branches do not emerge from its undersurface to enter and supply the adjacent structures. In the manatee, however, the arteries accompanied by two veins perforate the muscle at right angles to the long axis of the muscle fibres. These triad groups penetrate the internal surface of the panniculus and other flat muscles of the trunk and emerge from the external surface, undiminished in calibre to pass into the fat and fascia beneath the skin. When the skin is reflected, many blackened pores are disclosed through which the vessels have passed. This arrangement rarely occurs in other mammals (Fawcett 1942b).

The majority of the circulating red corpuscles of *Trichechus*, like those of other mammals, are circular, nonnucleated discs, 4–7 μm in diameter (Garrod 1877; Gulliver 1878; Knoll 1958). A minority (1:300) are immature, nucleated forms that are slightly larger (normoblasts). The white cells, the majority of which are monocytes and lymphocytes, all have spherical nuclei and measure 8–12 μm in diameter. The manatee has no evidence of eosinophils, has comparatively fewer granulocytes than do humans, and a lower ratio of neutrophils to basophils (Knoll 1958).

Recent data on *T. m. latirostris* indicate that the red cells are larger than those of dolphins or humans, and that the serum electrolytes, blood chemistry, and serum enzyme activities are similar to those of man. White et al. (1976) reported low levels of glutathione reductase activity and did not corroborate earlier findings that eosinophils are absent except in small numbers (5.2%) associated with low-level infections in captive animals. The whole blood P_{50} values for the young manatee were higher than for the adult female (20 and 16.5 mm Hg, respectively), differing unusually from values in other fetal mammals (White et al. 1976).

A noteworthy feature of the plasma of *T. inunguis* is its ability to clump staphylococci (Lewis and Wilson 1973).

Nervous System

The brain of the manatee is small and quadrangular in shape (Murie 1872a; Quiring and Harlan 1953; Harrison and King 1965) with rounded poles (Chapman 1875) and is invested by relatively thin leptomeninges (Harrison and King 1965). The cerebral hemispheres, though longer in proportion to their breadth (65:30 mm) in *T. inunguis* (Beddard 1897), are smaller in relation to body size than in other mammals (Verhaart 1972). The weight of the brain in an adult female weighing 557 kg was 380 g (Quiring and Harlan 1953), and Harrison and King (1963) gave an average brain weight of 300 g. The cerebrum is quite smooth, having only the Sylvian fissure with no signs of opercularization (Murie 1872a; Quiring and Harlan 1953; Harrison and King 1965). Thus the fetal-like brain ranks at a very low level of mammalian neurological development (Verhaart 1972). The reduction in size of the hemispheres was attributed by Jelgersma (1934) to the slowness of the manatee's movements in contrast to Cetacea and Pinnipedia (Verhaart 1972).

The rounded occipital lobe is concave ventrally to accommodate the large parafloccular lobe of the cerebellum (Murie 1872a; Harrison and King 1965) from which it is separated by a rather extensive, membranous tentorium cerebelli. The cerebellum is broad, flat, and partially convoluted (Quiring and Harlan 1953). As early as 1875, Chapman was able to identify the fissure of Rolando, the hippocampus, and the corpus callosum, which is short, but thick (Harrison and King 1965).

Other features of the manatee central nervous system are a large corpus striatum and thalamus (Harrison and King 1965) and an extremely small fourth ventricle. In one specimen, the hypophysis measured 2.0 by 1.2 cm and was oval in shape. A median body partition, the homologue of the crista galli, seems to separate the olfactory nerves as in other mammals (Quiring and Harlan 1953).

The oculomotor nerve is comparatively large. The trochlear nerve is a delicate filament (Chapman 1875), and the trigeminal, the largest cranial nerve (Quiring and Harlan 1953), is small compared to that of pinnipeds (Verhaart 1972); distal to its ganglion and prior to its division into ophthalmic, maxillary, mandibular, and lingual branches, it consists of a broad band of nervous tissue (Quiring and Harlan 1953). Murie (1872a) described an abducens nerve, but Chapman (1875), noting the origin and direction of this nerve, suggested that the abducens was absent and the nerve Murie described was in fact the facial nerve. It is likely that Chapman was incorrect and that he did not trace out the nerves in his specimen.

More recently, Verhaart (1972) redescribed the architecture of the brain. He stated that the acoustical apparatus is fairly well developed in agreement with Hartman's conclusion (1971) that hearing is the most important sense. In fact, the apparatus is no less well developed than in cetaceans, in which it has an acoustic function. The eyes, optic nerve, lateral geniculate body, and superior colliculus are small in contrast to most other acquatic mammals. Verhaart suggested, therefore, that vision is not important, supporting Chapman's (1875) findings.

The medial lemniscus compares in size with that in cetaceans, is larger than in Insectivora and Chiroptera, but is less well developed than in humans. The trigeminal contribution to the medial lemniscus is large compared to that of pinnipeds. As with other aquatic mammals, the mesencephalic component of Darkschewitch's nucleus is distinct. Typically also there is a small magnocellular red nucleus associated with a reduced rubrospinal tract, as is found in primates and humans. In the latter, however, a very large pyramidal tract is also a feature, whereas in the manatee and the cetaceans, the corticospinal projection is greatly reduced. A distinctive morphologic feature of the decussation of the pyramidal tract is its extreme rostral position, a characteristic that the manatee shares only with bats and the pangolin or scaly anteater. The main olivary nucleus is better developed than in other mammals with the exception of higher primates and humans (Verhaart 1972).

The basal ganglia are characterized by a small globus pallidus, the absence of an interpeduncular nucleus, and a large putamen and caudate nucleus divided by a compact internal capsule (Verhaart 1972). Despite the manatees' primitive brain form, Gorry (1963) stated that the extent and structural differentiation of Meynert's basal nucleus is between that of rodents, ungulates, and carnivores on the one hand, and Cetacea and primates on the other; however, the nerve cells of the nucleus are scattered diffusely in the caudal part of the globus pallidus, differing from the Cetacea and primates. The cells in *T. inunguis*, like those of *Tursiops truncatus*, were larger than any of the ungulates, carnivores, cetaceans, and primates examined. (Cell and nuclear size have been shown to relate to body size among the species within an order and to a certain extent to the whole phylogenetic series.) According to Verhaart (1972), a central tegmental tract was not distinguishable and the compact zone of the substantia nigra was as small as in any other mammal. The medial longitudinal bundle within the lower medulla oblongata was larger than in the higher apes but smaller than in monotremes. Verhaart (1972) placed the manatee on a level below *Saimiri*, a low, middle-level primate and regarded the unusually small cerebrum to be a result of retarded development and not degeneration as suggested by Jelgersma (1934).

Vision

The spherical, deep-set eyes of the manatee are laterally situated and are small in relation to the size of its body (Walls 1942) and the orbital cavity (Harrison and King 1965). The dugong's eyes are about the size of a human's, the manatee's somewhat smaller. The manatee's pupils are horizontally oval (Duke-Elder 1957) and the irises, dark brown. As in cetaceans, the sclera is dense and thick at the back of the eye (Harrison and King 1965) and visible only when the eye moves laterally (Quiring and Harlan 1953). The lenticular-shaped lens, in keeping with the aquatic environment, is closely approximated to the cornea so the anterior chamber is small (Duke-Elder 1957). The horizontally oval cornea is more suited to the grazing manatee than is the ellipsoid cornea of other aquatic mammals. The quotient of horizontal and axial diameters of the lens has been calculated at 1.40–1.24 (Walls 1942). The very minute retinal vessels extend only a short distance from the disc (Duke-Elder 1957), suggesting a low retinal metabolism, a pure rod condition, or the presence of only a few cones (Walls 1942). The tapida lucida shine pink in reflected light (Hartman 1971).

Eyelashes are present but scanty (Dollman 1933; Walls 1942; Duke-Elder 1957). There is a well-developed retractor-bulbi muscle (Duke-Elder 1957). Scientists generally disagree on the presence of eyelids, Harrison and King (1965) reporting that upper and lower lids are not really discernible but both Walls (1942) and Duke-Elder (1957) describing freely moving lids that almost close completely when the globe is retracted. There is also disagreement about the presence of a nictitating membrane, with Walls (1942) denying its existence and Dexler and Freund (1906) as well as Harrison and King (1965) describing it as well developed, functional, possessing a cartilage as in elephants, and situated at the medial aspect.

A lacrimal gland and nasolacrimal duct are absent (Walls 1942; Duke-Elder 1957; Harrison and King 1965), but there is a well-developed, Harderian gland that secretes copious amounts of a thick mucus, augmented by products of special oil glands lining the eyelids (Walls 1942; Duke-Elder 1957). Similar to terrestrial mammals, manatees secrete their aqueous humour with the few rugose ciliary processes on the small ciliary body. The optic nerve, although thick, is composed mostly of sheath (Walls 1942).

Bertram and Bertram (1964) suggested that the small size and upward direction of the eyes preclude binocular vision, and Walls (1942) supported them, claiming that the manatees' vision is "wretched." He stated that the sirenian eye has lost the globe organization for air vision and has not taken on any features that would make it useful underwater. Here Hartman (1971) disagreed; his observations have suggested that the manatee has fully functional binocular and even stereoscopic vision; typically, he said, a manatee investigates unfamiliar sound, head-on, because it cannot turn its head, not because it cannot see. According to him, the manatees' underwater vision may be considerable, though hypermetropic, so that the manatee can see 35 m away but bumps into inanimate objects at close range (Hartman 1971). He has never observed them raising their heads above water to investigate surface stimuli; therefore he reported that they are probably unable to see patterns and activities in the air.

Professor D.J. Piggins, Department of Psychology, University of Guelph (personal communication, 1977) reported that the underwater refraction of nine eyes of five *T. inunguis*, aged 0.5–4 years, showed low hyperopia within a narrow range. The presence of atropine cycloplegia appeared to make little difference. The refractive findings indicate that a well-focused retinal image is possible underwater. All animals appear to possess some degree of binocular overlap of monocular visual fields, estimated by casual inspection to be approximately 15°. The presence of a nictitating membrane operating in an anterior-posterior manner was confirmed. The ocular aperture is more sphincterlike than lidlike, and a narrow beam of moderately intense light caused total closure under general darkened conditions. Ocular aperture opening occurs regularly upon respiration and may also be elicited by an arousing stimulus, e.g., tactile stimulation of the back or face, especially the muzzle and mouth. The comea and pupil are both circular, the irises appearing brown. The presence of a tapetum has not been confirmed.

Hearing

The manatee lacks a pinna to the ear and the external auditory meatus is very narrow, being sometimes occluded in its s-shaped course. It expands when it reaches the relatively large tympanic membrane (Harrison and King 1965). The openings are behind and somewhat below the eyes (Quiring and Harlan 1953). According to Bertram and Bertram (1964, 118) the external auditory meatus in a 1.9-m specimen was described to them by Harrison and Tomlinson in a personal communication as "a very narrow tube that scarcely admits a seeker. It is about 40 mm in length and at the surface only 2 mm in diameter. The meatus is a fairly straight tube, narrowing to almost occlusion point where it obliquely meets the tympanic membrane. The inside of the meatus is a pigmented greyish colour and there is no sign whatever of any wax plug . . . The tube is embedded in semifluid mucoid tissue and as it approaches the tympanic membrane becomes almost undissectable."

Morphologic evidence, namely the unusually large and bulky ear ossicles (Robineau 1965), supports observations that the manatee has exceptional hearing (Robineau 1965; Hartman 1971; Bertram and Bertram 1964) and Verhaart's (1972) work on the CNS also lends them credence.

By crystallography and transmission electron microscope, Giraud-Sauveur and Miloche (1968) have shown that the crystals of hydroxyapatite (the essential mineral constituent of the bones) are somewhat larger in the ear ossicles than in the other cranial bones of *T. senegalensis*. They compared this finding to the situation in Odontocetes, where the crystals are much larger in the ossicles than in the cranium, suggesting an echolocation function.

Hartman (1971) concluded that manatees have exceptional acoustic sensitivities and that sound is a major directional cue to social interactions. The animal can immediately locate surface disturbances, responding to the banging of an oar on the side of a boat 40 m away. Although the underwater auditory range is unknown, some approximations are possible from earlier investigations. A female responded to the squeals of her young from 60 m away and some manatees have responded to sounds such as the clicking of a camera shutter. On the other hand, Hartman (1971) reported that a high frequency transmitter held at 70 kHz next to the external ear openings did not elicit any reaction. In Guyana, according to Bertram and Bertram (1964), tongue clicking, motion picture-taking, and whistling, had no effect, but the sound of the human voice, no matter how soft, evoked an immediate response of submersion. This, they suggested is because man is the chief enemy of the manatee.

Phonation

The Sirenia have no vocal cords, and any sounds emitted from the manatee result from vibrations of the laryngeal cartilages (Dexler and Freund 1906). Phonation in *T. m. latirostris* was studied by Schevill and Watkins (1965). The sounds emitted by the animals were only 10–12 dB at 3–4 m distance above ambient. Most calls lasted 0.15–0.50 sec and were composed of two or more frequencies, resulting in a ragged disharmonic sound. Occasionally, harmonics were exhibited, and phonation began and ended at different times accounting for the general ragged quality. The beginning and final sounds may be complex with intercalated frequencies. The fundamental tones were 2.5–5.0 kHz but might be as low as 600 Hz. Calls lacking harmonics were generally of higher frequency (4 or 5 kHz), the highest harmonic being 16 kHz. The second harmonic was often much more intense than the fundamental.

In *T. inunguis*, phonation was studied by Evans and Herald (1970). The majority of the sounds were similar to, but louder than, those recorded by Schevill and Watkins (1965) for *T. m. latirostris*, reaching 15–22 dB above the background. The main difference between species was in the fundamental frequency, and no evidence has been found for the navigational or echolocational function of phonation (Schevill and Watkins 1965; Evans and Herald 1970).

Olfaction and Taste

Murie (1872a) described a well-developed, olfactory nerve and bulb and regarded the sense of smell as far from deficient. Chapman (1875) also claimed that the large olfactory organs indicated a keen sense of smell. He observed that captive animals seemed to orient to food thrown into the tank by smell. As was pointed out by Boenninghaus as early as 1903, however, it is difficult to assess the function of the organ of smell, because the nasal tract is hermetically sealed under water (Dexler and Freund 1906; Hartman 1971). Nevertheless, Dexler and Freund (1906) noted the large size of the olfactory organs together with the atrophic condition of the ethmoids and suggested that the manatee alone among mammals has a partially adapted olfactory nerve that allows it to perceive chemical stimuli using water, not air, as a conducting medium. They, therefore, assumed that, because the chemical stimuli "cannot reach the olfactory membrane in the usual way," they must take another course, perhaps by way of the mouth, pharynx, and choanes (Dexler and Freund (1906, 60).

More recently, Hartman (1971) commented that he had never seen manatees trying to scent airborne odours. The prevalence of "mouthing" in social encounters suggested to him the existence of functional sense receptors on the tongue. Such a taste organ, the so-called papilla foliata, was described in the manatee by Gmelin (1892). The care shown in the selection of food, likewise, points to a certain taste function (Dexler and Freund 1906). Whether or not sirenians possess a chemical sense of "smell-taste" whereby they can recognize odour gradients in the water is uncertain (Hartman 1971).

Touch

As evidenced by social bodily contact, rubbing on inanimate objects, and apparently soliciting "caresses" from divers, manatees are highly sensitive to tactile stimulation. The hairs on the dorsum are sensitive to water currents (Hartman 1971), and the sensitive upper lip (Dexler and Freund 1906) as well as its bristles are used during feeding, mouthing and exploring (Hartman 1971). The vibrissae of *T. m. latirostris* resemble superficially those of the walrus. Histologically, they are typical sinus hairs (Woodward, personal communication to Hartman 1971). The manatee's vibrissae may have a tactile sensory function (Caldwell and Caldwell 1972) in that sinus hairs are thought to be tactile (Trautman and Fiebiger 1952). It appears that one manatee can follow another by reacting to the currents produced by the other's movements (Hartman 1971).

Excretory System

The kidneys of the manatee rest upon the tendinous surface of the diaphragm close to the spine, the posterior ends reaching the last ribs (Murie 1872a). In a 557-kg female adult, a kidney weighed 1316 g (Quiring and Harlan 1953), and each renal organ in a 2-m adult male measured 15.24 cm in length by 7.62 cm in breadth (Beddard 1897; see also Murie 1872a).

The kidney of the manatee fetus or very young is externally smooth in all species (Beddard 1897; Petit 1924a). Petit reported (1924a) that a section through the organ of a young *T. senegalensis* showed distinct internal lobation, characterized by invasions of cortical substance completely surrounding the pyramids.

In adults, Murie (1872a) described superficial lobulation in a 12.7-cm long kidney of *T. manatus*, and in *T. m. latirostris*, Beddard (1897) noted a 15.3-cm long kidney that was distinctly lobulated externally and internally. Renal lobulation or lobation developing from a smooth fetal kidney is an exceptional process, by which the fetal condition is accentuated externally as the animal grows, perhaps at the same time as the kidney lengthens. Chapman observed no lobulation in a 15.3-cm long kidney of *T. manatus*, suggesting that lobulation is specific or an individual characteristic (Petit 1924a, b).

The hilus in a young *T. m. latirostris* was "as nearly as possible on the edge of the gland," whereas in the adult it was on the "side." On the other hand in *T. inunguis* the hilus in a young animal was on the side as in the adult *T. m. latirostris* (Beddard 1897, 51). In *T. manatus* the hilus was described as shallow (Murie 1872a) and in *T. senegalensis* as an elongated deep sinus (Petit 1924b).

The ureters are uniform in diameter (Murie 1872a; Chapman 1875; Quiring and Harlan 1953), and in females they hook around the uterine horn, pass beneath the hypogastric artery (Murie 1872a), and then enter a small semiglobular bladder (Murie 1872a; Quiring and Harlan 1953). In a 1.8-m male, the ureters measured 25.4 cm in length from bladder to pelvis (Chapman 1875).

Respiratory System

The manatee's epiglottis is rudimentary, unlike that of the cetaceans (Murie 1872a), and its vocal cords, which do not exist according to Dexler and Freund (1906), are probably represented by fleshy, prominent cushions of ligamentous and fibroelastic tissue (Murie 1872a; Harrison and King 1965). Thyroid, cricoid, and arytenoid cartilages are all present (Murie 1872a). There are 8–12 tracheal rings that are not continuously spiral in shape as in the Halicore dugong and that, at times, are bifurcated at the tips and obliquely cross the long axis of the tube (Stannius 1846; Murie 1872a). In

Steller's sea cow and in the dugong, the spiral shape of the cartilages was believed to facilitate the lengthening and shortening of the lungs (Owen 1838). The trachea divides into two bronchi that run parallel for about 12.7 cm and enter the lungs almost at their summit (Murie 1872a; see also Harrison and King's fig. 11a, 1965, 198).

The lungs, which are symmetrical, single-lobed, flattened, and extremely elongated, are enveloped in a heavily vascularized pleura (Wislocki 1935; Barrett 1935; Quiring and Harlan 1953). In a 1.7-m long female *T. manatus*, the lungs measured 58.4 cm in length, and in their uninflated state, the greatest thickness was 2.54 cm. In width their measurements were 7.0 cm at their rostral end, 8.9 cm at their midpoint, and 3.8 cm at their caudal extremity (Murie 1872a).

Beginning at the bifurcation of the trachea, the lungs extend laterally in the pleural cavity and caudally to the level of the vestigial pelvis (Quiring and Harlan 1953), thereby occupying most of the dorsal cardiopleural cavity (Barrett 1935; Quiring and Harlan 1953). They taper into a pocket at the lumbovertebral end of the diaphragm (Murie 1872a; Barrett 1935).

Within the lung, each main stem bronchus passes to the caudal extremity of the organ (Murie 1872a) and lies on its medial aspect immediately beneath the visceral pleura. Each main bronchus divides into at least 12 secondary bronchi (Murie 1872a; Harrison and King 1965), which in turn subdivide in the pulmonary substance into a number of smaller branches (Murie 1872a). Although these bronchioles exhibit a moderate amount of smooth and elastic tissue, a specialized system of myoelastic sphincters such as is seen in the porpoise is totally lacking in the manatee. As with all aquatic mammals, numerous cartilaginous rings extend into the walls of the smallest bronchi, but nowhere are they calcified (Wislocki 1935) as they sometimes are in the dugong (Pick 1907)

The sirenian air sacs are many times the size of those of any terrestrial mammal. Both the manatee and dugong have extremely large tubular-shaped air sacs — as much as 6 mm in length by 1–2 mm in diameter — at the dorsum border of their lungs immediately beneath the pleura. The alveolar sacs underlying the pleura on the ventral surface, however, are not elongated. Wislocki (1935) believed that the difference in air sacs might be related to the distribution of the bronchial tree, which is ventrally located and which sends off short, stout bronchioles toward the dorsum of the lung. Wislocki (1935) also speculated that the epithelial cells on the subpleural surface of the dilated sacs are respiratory in function. This was later confirmed by Belanger (1940). The large alveolar sacs are composed of unusual amounts of fibroelastic and smooth muscle tissue (Wislocki 1935) and the interalveolar septa are thick (Belanger 1940). Each septum has a double layer of capillaries contrasting with the single layer found in the seal (*Phoca vitulina*) (Wislocki 1935; Belanger 1940).

The lungs in the manatee, the *Phoca vitulina*, and the large Cetacea are notable in that a heavy cartilaginous armature extends to the respiratory sacs and produces a more rigid bronchial tree than in terrestrial mammals; the three groups have eliminated to some degree the bronchiolus (Bronchiolus respiratorius) and have enlarged the ductus alveolaris and sacculus. The musculature of the ductus alveolaris and sacculus has hypertrophied, favouring the occlusion of the air sacs and stabilization of intrapulmonary pressure (Belanger 1940).

When breathing, the manatee rises slowly to the surface, sticks only its nostrils out of the water, and inspires and expires two or three times for 30–60 sec each (Moore 1951a). It normally breathes six to eight times every 10 min (Scholander and Irving 1941) but may stay submerged for 10–30 min if frightened (Barrett 1935). Breathing is very quiet and can easily go unnoticed from above (Scholander and Irving 1941). A wild manatee was observed to breathe 68 times in 1 h, with the intervals averaging 50.2 sec and breathing periods lasting 2–5 sec. One breath was taken per period (Moore 1951a). Another observation was that an adult Guyanese manatee, shortly after being released from captivity, breathed every 90 sec while swimming rapidly (Ronald, personal communication 1975).

The lung volume-to-body weight ratio of the manatee is of the same order as that for an adult human or seal, whereas the ratio of tidal air-to-body weight is three times that of humans and half that of porpoises. At rest, the manatee renews 50% of its pulmonary lung air with each breath compared to a 10–20% renewal in humans and 80–90% in the porpoise. The resting consumption of 0_2/min/kg is low, equalling 10–20% of that in humans, and ventilation/min/kg is comparatively small. Oxygen utilization from inspired air and $C0_2$ concentration in expired air are high. High concentrations of $C0_2$ in the alveolar air together with rebreathing experiments suggest that the manatee has a low sensitivity to $C0_2$ in inspired air. During an 8-min dive, bradycardia slowly develops from a resting heart beat of 50–60 down to 30 beats/min but is not accompanied by any increase in lactic acid in the blood. The absence of lactic acid increase indicates that the muscles are completely isolated from the general circulation.

Oxygen stores are small for the animal's size but because of its low metabolism are sufficient for prolonged diving (Scholander and Irving 1941).

Teeth

Like the elephant, the manatee has a peculiar tooth pattern (Heuvelmans 1941a and 1943), and estimates of the total number of teeth in a lifetime range from 44 (Prater 1928) to 180 (Hopwood 1927; Thomas 1897). Manatees have a cyclic tooth replacement pattern, which offsets the excessive wear on the teeth caused by the grit in their food. New teeth emerge as needed from the back half of the jaw replacing old ones at the front, and the entire row of teeth moves forward (Hopwood 1927; Prater 1928; Heuvelmans 1941, 1941a, 1943). New teeth are continually being formed in the alveolar bulb at the posterior of the tooth row. Horizontal succession of teeth occurs as does bone resorption on the mesial surface and deposition on the distal surface of the alveoli (Harrison and King 1965). The septa between the teeth are very porous enabling the teeth to move easily guided by the dense bony walls of the jaw bone (Prater 1928). Anterior molars are shed when their roots are absorbed (Harrison and King 1965).

The two upper and two lower vestigial incisors are buried beneath horny plates that cover the anterior palate and lower jaw (Prater 1928; Quiring and Harlan 1953; Harrison and King 1965). In the adult manatee, there are no canines (Prater 1928), and, thus, the rudimentary incisors are separated from the molars by a large gap (Prater 1928).

Although premolar germs are present at birth, they never develop (Andrews 1924), and there are never more than five or six teeth/jaw at any one time (Prater 1928). (Quiring and Harlan, 1953, have given the female dental formula as $\frac{0,0,0,6}{0\ 0\ 0\ 6}$.) The anterior teeth are shed before new posterior teeth come into position, and the size of newly formed teeth progressively increases with age. Thus, by studying the jaws of animals at various ages, an investigator may deduce the number of teeth produced in a lifetime (Prater 1928).

Andrews (1924) has said the manatee's teeth are bilophodont with a tendency in adulthood to form a third ridge. In new teeth, the ridges on the crowns are surmounted by a few small cusps that are worn down with use (Harrison and King 1965). The polyphyodont dentition has a total of 60 transverse ridges, but no individual tooth develops more than two ridges with a small talon. And all the teeth are low crowned. The teeth have been described as selenodont (Quiring and Harlan 1953), and Thomas (1897) has asserted that each tooth possesses two cuspidate crosscrests and roots that are closed and divided. The prisms of enamel are straight and parallel with each other. Sirenia, like Odontocetes, some Insectivora, and some Chiroptera, lacks prism decussation and exhibits round enamel prisms, separated by an abundance of interprismatic substance, which is usually surrounded by complete prism sheaths (Harrison and King 1965). Harrison and King (1965) suggest that the so-called vascular channels in the manatee dentine are simply prominent interglobular spaces.

Alimentary System

A deep cleft characteristically divides the prehensile upper lip of the manatee into two lobes that are strikingly studded with stiff bristles (Prater 1928). The lower lip, also bristle-clad, protrudes slightly forward (Murie 1872a). Within the mouth, hardened, horny, dental plates, not unlike the single, upper dental pad of ruminants, overlie the symphysial areas of the upper and lower jaws and are separated from the lips by deep furrows. The rugose lower mandibular cushion has an extremely rough inner surface and a moderately rough outer segment due to large conical and smaller filiform papillae. The horny plate of the premaxillary pad is covered by a thick, v-shaped zone of backwardly directed papillae, the longest being about 5 mm in length (Murie 1872a).

The short, firm tongue is fixed, incapable of being protruded (Murie 1872a; Sonntag 1922; Harrison and King 1965), and its surface is covered with various filiform, fungiform, and circumvallate papillae (Murie 1872a; Beddard 1897; Harrison and King 1965). It differs considerably from that of cetaceans and more closely resembles that of ungulates, thickening progressively anteroposterially with a distinct internal moundlike eminence. The papillae immediately behind the apex consist of a cluster of retroverted cuticular spines, used in cropping vegetation. Beyond the spines, the dorsum is relatively smooth (Sonntag 1922). Mayer's organs (Beddard 1897), consisting of two conspicuous, fissured cushions of well-developed circumvallate papillae, are situated on the posterolateral surfaces of the tongue. These organs (Sonntag 1922), one on each side of the tongue, are a little closer to each other and farther back in *T. inunguis* than in *T. m. latirostris* (Beddard 1897). The inferior surface of the tongue of *T. manatus* has many pits; and in all the species the frenum is slight, and there is no foramen cecum or any comblike structures (Sonntag 1922). Lateral organs are said to be absent in the dugong (Sonntag 1922), but the two nipplelike processes at the base of the tongue, described by Home (1820), may be the counterpart of Mayer's organs.

The submaxillary glands are prominent, a single gland from a 557-kg female (*T. m. latirostris*) weighing 567 g (Quiring and Harlan 1953). The parotids are especially large (Harrison and King 1965), but the sublinguals are small (Murie 1872a).

The narrow, muscular esophagus (Murie 1872a; Harrison and King 1965; Lemire 1968) has a strong cardiac sphincter at its lower end (Murie 1872a; Harrison and King 1965) and contains many mucous glands where it enters the stomach (Harrison and King 1965; Lemire 1968).

There are several interesting features in the structure of the manatee stomach, some no doubt, functionally significant. The main compartment, the cardiac stomach, is shaped like that of a human stomach (Harrison and King 1965) and is the only true stomach (Lemire 1968). Along its greater curvature, just caudad to the entry of the esophagus, it has a fundic, secretory diverticulum, the cardiac gland (Murie 1872a; Barrett 1935; Harrison and King 1965; Lemire 1968). In *T. manatus*, a prominent left-sided, retroesophageal recess occasionally occurs just cranial to the entrance of the cardiac gland (Murie 1872a; Harrison and King 1965).

The cardiac gland is often referred to as Owen's glandular appendage, and it is the only true gastric diverticulum in the manatee (Lemire 1968). Internally, its appearance contrasts with that of the principal stomach. It is almost solid, with complex, leaflike folds of glandular tissue (Harrison and King 1965), which are so hypertrophic that the glandular septa are not as distinct as in the dugong (Lemire 1968, illustrated in Dorst 1973, 296). The mucous membrane is thick and full of typical fundic glands, containing numerous oxyntic cells. The cardiac gland is not to be regarded as a special gland but rather as an auxiliary organ capable of providing additional gastric secretion (Harrison and King 1965; Lemire 1968).

The main compartment of the stomach, the cardiac stomach, has few rugae and communicates with the dilated duodenum through a well-developed pyloric sphincter (Harrison and King 1965), which Lemire (1968) regarded as not a true constricting muscle as in other mammals. The mucous membrane is divisible into two regions, fundic and pyloric. The fundic area occupies the region of the lesser curvature and contains many glands that are slightly branched. Beyond the entrance of the cardiac gland, along the greater curvature, is the pyloric zone, whose glands are longer and more branched, especially at their base, than are those in the fundic region (Lemire 1968).

The tubular duodenal pocket (second stomach pocket) or pyloric stomach of Owen (1838), Murie (1872a), Pilliet (1890), Meinertz (1965) (see also Dorst 1973, fig. 243), with longitudinal folds in its walls, is beset with villi and covered with columnar intestinal epithelium and mucous goblet cells. Elongated crypts of Lieberkühn open at the base of the villi (Lemire 1968, pl. XXVII D), and Brunner's glands, typical of the duodenum, lie below the muscularis mucosae (Lemire 1968). This part of the intestinal tract cannot, therefore, be regarded as a second stomach (Harrison and King 1965; Lemire 1968).

Beyond the pylorus, there are two elongated, slightly coiled (Harrison and King 1965), ceca which in *T. manatus* and *T. senegalensis* (Harrison and King 1965; Lemire 1968) are directly opposite, in contrast to their position in *T. inunguis* (Husar 1973b); they open into the tubular duodenal pocket, and a slight narrowing delimits the duodenal extension (Lemire 1968). Barrett (1935) found only one cecum in *T. m. manatus*.

The ceca are essentially hollow organs with wide openings that communicate freely with the cavity of the principal pocket; only the longitudinal folds of the duodenum penetrate into the interior of the blind sac (Lemire 1968). There is some disagreement between Harrison and King (1965) and Lemire (1968) about the nature of the mucous membrane. The former stated that in the manatee it "is the gastric type with both oxyntic and peptic cells" (Harrison and King 1965, 162), whereas the latter considered that in *T. senegalensis* it is identical to that of the duodenum and is composed of crypts of Lieberkühn and Brunner's glands.[5]

The length of the intestinal canal from pylorus to anus in *T. manatus* has ranged from about 13. m in a 1.7-m long female to 18.5 m in a 1.8-m long male (Table 5). The diameters of the small intestine in these same animals were 2.54 cm and 1.3 cm respectively. Comparative diameters of the large intestine are available, but Barrett (1935) stated that the tract is of even diameter from pylorus to anus in *T. m. manatus*. The most remarkable feature of the intestinal tract is the great length of the large intestine, which in *T. inunguis* is almost as long as the small intestine (Beddard 1897).

Quiring and Harlan (1953) describing the very muscular small intestine in *T. m. latirostris* gave its length as 18.8 m and its diameter as 5.7 cm in a

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[5] "La muqueuse, strictement identique à celle du duodénum, renferme des glandes de Lieberkühn, elles-memes doublées par les glandes de Brunner de la sous-muqueuse. Les diverticules postérieurs appartiennent donc à la portion duodénale contre laquelle ils sonts appendus (Owen 1838) et ne représentent qu'une sacculisation du tube digestif." (Lemire 1968, 490).

Table 5. Comparison of external measurements of intestinal tract in male and female manatee.

Author	Species	Length of animal (m)	Sex	Small intestine Length (m)	Small intestine Diameter (cm)	Large intestine Length (m)	Large intestine Diameter (cm)	Total length from pylorus to anus (m)
Murie 1872a	*T. manatus*	1.7	F	7.6	+1.3	5.4		13.
	T. manatus	1.2	M	7.4	+1.3	5.5		12.9
Chapman 1875	*T. manatus*	1.8	M	10.2	2.54	8.3	3.2	18.5
Barrett 1935	*T. m. manatus*	2.8	M	Of even diameter from pylorus to anus				15.2
Quiring & Harlan 1953	*T. m. latirostris*	2.9	M	18.28	5.7	18.58	11.4	37.0
		3.25	F	23.68	7.2	17.7	11.4	41.4
Harrison & King 1965	*Trichechus* sp.	2.4	M	+7.6		+5.5		13.1

2.9-m long male; they also stated that the large intestine is about the same length and about twice the diameter. Comparing these figures with those in Table 5 suggests that in *T. m. latirostris* the intestinal tract in both males and females is about twice the length and about three times the diameter of that in *T. manatus*.

The small intestine has an uncommonly thick muscular coat (Murie 1872a; Harrison and King 1965); valvulae conniventes (plicae circulares) are absent, but commencing near the duodenal loop are five or six longitudinal mucous ridges that continue as far as the ileum (Murie 1872a). Harrison and King (1965) appear to be the only investigators to give histological details of the structure of the intestinal mucosa. They stated that the small intestine lacks villi and crypts, but Murie (1872a) recorded the presence of Lieberkühn glands in the ileum (but see also Murie 1872a). The epithelial lining has an interesting structure; it is not the usual single layer of columnar epithelium with goblet cells but consists instead of a double layer of squamous cells (Harrison and King 1965).

In the manatee, Peyer's patches, which are usually elongated, are numerous, especially in the last 30.0 cm of the ileum (Beddard 1897). From 12.7 to 25.4 mm apart, they are arranged in zigzag formation, as well as in the furrows between the longitudinal mucous folds (Murie 1872a). At the ileocecal orifice, which is guarded by a powerful sphincter (Murie 1872a; Harrison and King 1965), there is a Peyer's patch of exceptional size (Beddard 1897). Murie (1872a) described, and Beddard (1897) illustrated, a pouched ileocolic lymphatic node resembling that in the giraffe and hippopotamus.

The general shape of the cecum in all species of the manatee is similar, and two conical, teatlike appendages are attached to it, 25.4 mm from the ileocecal valve (Murie 1872a); in *T. m. latirostris* the two orifices are closer to each other and to the ileocecal orifice than in *T. inunguis* (Beddard 1897). The cecal appendages are thick-walled, ridged, and glandular within (Murie 1872a). In a 1.8-m male of *T. manatus*, they measured 12.7 cm in length (Chapman 1875). Murie (1872a) describing a 3.8-cm long cecal appendage set the diameter at approximately 1.6 cm.

Harrison and King (1965) stated that the large intestine lies peripheral to the small intestine within the abdomen and possesses no tenia coli. The lining epithelium, with many mucous glands, consists of a stratified, superficial layer of squamous epithelial cells, instead of the columnar cells found in other mammals. Harrison and King (1965) believed this modification of the intestinal epithelium may be related to the need to restrict water absorption.[6]

Murie (1872a) described two dilatations of the colon beyond the cecum, the first being very glandular with convoluted rugae, the second thinner-walled and similar in structure to the remainder of the large intestine. This modification of the colon is not mentioned by others. However, Beddard (1897) has also called attention to the presence on either side of the mesentery supporting the ileum, near the cecum, of two discrete avascular, peritoneal folds that are connected over the front of the ileum. These are present and similarly situated in *T. m. latirostris* and *T. inunguis*.

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[6] The modification may, in fact, aid absorption of high concentrations of fatty acids.

The manatee has a large gall bladder, with biliary and pancreatic ducts opening separately into the duodenum (Murie 1872a; Chapman 1875; Beddard 1897; Harrison and King 1965). The relative positions of the openings of these ducts may be a mark of specific distinction (Beddard 1897). The papillae are prominent and further apart in *T. m. latirostris* than in *T. inunguis* (Beddard 1897), and in the former, the pancreatic duct is more rostral to the orifice of the ductus choledochus (Murie 1872a; Beddard 1897) and in the latter the ductus choledochus is "behind but markedly below" the pancreatic duct (Beddard 1897, 49). Chapman (1875) stated: "Ductus communis choledochus in both of my specimens [*T. manatus*] opened into intestine close to the pylorus, while the pancreatic duct opened 1½ inches from the ductus communis" (p. 457). The cystic duct in *T. manatus* is of considerable calibre (Murie 1872a); the pancreas is pale, firm, and very lobulated (Murie 1872a; Chapman 1875), measuring 16.5 cm in length in a 1.8-m male (Chapman 1875).

The liver has three main lobes (Murie 1872a; Chapman 1875; Beddard 1897; Quiring and Harlan 1953; Harrison and King 1965) and is flattened against the diaphragm. The quadrate lobe is diminutive. All the hepatic fissures are shallow, the most distinctive being the longitudinal fissure and that of the ductus venosus (Murie 1872a). In shape it is said to resemble the inflated lungs of terrestrial mammals (Murie 1872a; Chapman 1873) and *in situ* extends completely across the abdominal cavity. In a 1.8-m specimen of *T. manatus*, it measured 35.6 cm from the edge of the right lobe to that of the left; the breadth of the right and left lobes being respectively 19.1 cm and 16.5 cm; it weighed approximately 1.4 kg (Chapman 1875). In a 2.96-m male (424 kg) and a 3.25-m female (557 kg) of *T. m. latirostris*, the liver weighed 5.50 kg and 6.24 kg respectively (Quiring and Harlan 1953).

The spleen is small, occupying its usual position along the greater curvature of the stomach (Chapman 1875). It is oval and of the usual colour. In a 1.8-m male, it measured 6.35 cm by 2.54 cm.

Digestion and Absorption

Details of the physiology of digestion in manatees are entirely lacking, although Lemire (1968) has offered some speculations. Some information is available on the dugong, which has a similar digestive system. It is almost certain that the manatee, like the dugong, has a postgastric fermentative digestive system similar to that in many terrestrial herbivores, such as the horse.

The manatee, like the dugong and the horse, has a small stomach and a greatly enlarged hindgut and midgut cecum with a rich microflora (Lemire 1968; Hill 1970; Murray et al. 1977). The species of Sirenia also resemble each other in that the digesta are quite gelatinous and spongy throughout the digestive tract, the spongy texture being due, in part at least, to gelatinous compounds present in the marine grasses (Lemire 1968; Murray et al. 1977). Because the short-chain volatile fatty acids (VFA) (acetic, propionic, and butyric acids) are among the most important fermentation products absorbed from the cecum and colon of the horse, it is of some interest to find that VFA concentrations in the stomach and small intestine of the dugong are low (16 and 18 mM/litre respectively), whereas the mean concentrations within the cecum and large intestines are very high (193 and 236 mM/litre respectively) (Murray et al. 1977), suggesting that these acids, especially butyric, result from the fermentative processes in this part of the alimentary tract.

The process by which the volatile fatty acids (VFA), the final end products of microbial digestion of carbohydrates, are transported across the epithelium of the large intestine of the Sirenia is not known. It must be remembered, however, that Phillipson and McAnally (1942) showed that short-chain fatty acids are absorbed through the heavily keratinized epithelium of the rumen into the portal blood. In ruminants, this stratified epithelium consists of a basal layer of columnar cells, superimposed by cuboidal cells, which, in turn, give way to flattened cells in which keratinization occurs. Similarly Harrison and King (1965) described the epithelium that lines the large intestine in sirenians as consisting of "a stratified superficial layer of squamous epithelial cells instead of the columnar cells found in other mammals." It may be presumed, therefore, that these animals are well equipped to absorb the high VFA concentrations in the hindgut.

Pituitary

In the manatee, the pituitary gland is almost vertical in the sella turcica, a disposition shared only with the lion and some primates (Herlant 1973, 307). In an adult female *T. m. latirostris* weighing 557 kg, the gland measured 2 cm in length and 1.2 cm in width (Quiring and Harlan 1953). Anterior and posterior (neural) lobes are well developed, the two being separated by a thick layer of dense connective tissue (Oldham et al. 1938). The neural lobe or pars nervosa is incompletely subdivided by prominent strands of connective tissue containing numerous blood vessels. Nuclei of pituicytes in the pars nervosa of *T. inunguis* are fairly abundant, but Herring bodies are relatively scarce (Oldham et al. 1938). In *T. m. latirostris*, the pars nervosa, represented by hyaline material — in appearance not unlike the colloidal material of the thyroid gland — is fairly compact (Quiring and Harlan 1953). A pars intermedia was not distinguishable in *T. inunguis* (Oldham et al. 1938) nor in *T. m. latirostris* (Maximov and Bloom 1942; Quiring and Harlan 1953).

In *T. inunguis* (Oldham et al. 1938), the anterior lobe is divided by thin strands of connective tissue into lobules in which cells are arranged in closely packed cords. A large cleft, presumably a remnant of Rathke's pouch, is lined with low columnar or squamous epithelium, extending along the entire posterior margin of the lobe. A single layer of cells separate the cleft from the connective tissue lying between the two lobes. Nowhere do the epithelial cells invade the neural lobe. Toward the anterior margin of the pars distalis, there are several cystlike structures, which are lined with low epithelium and filled with a blue-staining colloid material. The pars tuberalis is represented by a group of nonglandular epithelial cells underlying the hypothalamus just in front of the pituitary stalk. Its cells are separated from the brain by the very vascular leptomeninges.

In *T. inunguis*, four main types of cells have been distinguished (Oldham et al. 1938). The acidophils and chromophobes are similar to those found in other species, and the cytoplasm of the chromophobes is sparse and stains palely. The other two types of cells are basophilic in their staining properties. Acidophils are more numerous at the periphery of the lobe and chromophobes more numerous in the centre of the individual lobules (Oldham et al. 1938). In *T. m. latirostris*, no basophilic cells have been identified, but the presence of acidophils and chromophobes has been confirmed. The chromophobes are larger than the acidophil cells, irregular in shape, and have large spherical nuclei surrounded by cytoplasmic margins of varying thickness (Quiring and Harlan 1953).

In *T. inunguis*, extracts of the posterior lobe revealed oxytocic, pressor, and antidiuretic properties but only a doubtful trace of melanophore-expanding activity. In contrast, anterior lobe extracts had a very marked melanophore-expanding activity on the frog (Oldham et al. 1938). Because it is generally agreed that the melanophore-dilating hormone is a product of the intermediate lobe, which in the manatee is said to be absent (Oldham et al. 1938; Maximov and Bloom 1942; Quiring and Harlan 1953; Herlant 1973), it may be that the hormone has come from cells bordering the remnant of Rathke's pouch, attesting to the laggard remains of the pars intermedia.

Wislocki's (1940) description of the pituitary of a nearly full-grown *T. manatus* differs from that of Oldham et al. (1938). Most notably, he found a series of nodular protuberances on the ventricular surface of the shallow infundibular recess, something he had not seen in any other mammal. Arterioles and venules penetrated into the interior of the infundibular stalk as isolated vascular tufts, the ends of which, with the surrounding tissue, produced the protuberances. He also found what he considered to be an attenuated pars intermedia, and the vessels of the neural lobe were arranged in such a way that the tissue formed a curious mosaic.

Thyroid

Very little is known about the thyroid gland of the manatee. In *T. m. latirostris*, the two lobes of the gland are situated about 10.0 cm caudal to the anterior extremity of the larynx (Quiring and Harlan 1953). Weights range from 0.11 to 0.13 g/kg of body weight reaching 78.87 g in a 557-kg female animal (Quiring and Harlan 1953). The gland is not invaded from the periphery by macroscopically visible connective tissue septa (Fawcett 1942) and hence is not lobulated (Harrison 1969). Quiring and Harlan (1953) found what appeared to be four parathyroid bodies imbedded in the gland.

The follicles vary in size from about 1 cm in diameter near the periphery in *T. manatus* (Harrison 1969) to 2–3 mm in the centre of the gland in *T. m. latirostris* (Fawcett 1942). The interfollicular connective tissue, for the most part quite delicate, is present in unusually large amounts (Fawcett 1942). Histologically, the follicular epithelium in *T. manatus* is low and flattened in all but the smallest follicles, where it is slightly columnar (Harrison 1969). In *T. m. latirostris*, however, the epithelium is for the most part low and cuboidal, being in some instances quite flattened (Fawcett 1942; Quiring and Harlan 1953). A basement membrane is said to be absent (Quiring and Harlan 1953). The colloid in both Caribbean and Florida manatees is relatively abundant (Fawcett 1942; Harrison 1969). Scattered interfollicular cells, as well as the aggregates of such cells observed by Quiring and Harlan (1953), may correspond to thyroid "c" cells (Pearce 1966; Pearce and Carvalheira 1967).

Although it is now generally thought that the historical appearance and functional activity of the thyroid are not as closely correlated as was formerly believed, Fawcett (1942) considered that the general appearance of the gland is consistent with a hypothyroid state and that the lack of a marrow cavity in either ribs or long bones, together with their heaviness and density, may be due to underactivity of the thyroid. It has been suggested that an underactive thyroid is also responsible for the manatee's sluggish behaviour and very low rate of O_2 consumption (Harrison and King 1965).

Adrenals

Only Quiring and Harlan (1953) have described the adrenal glands in manatees. The structures they described are situated retropleurally between the carotid artery and the bronchus, measuring 3.8 cm in length and having adrenal/body weight of 0.02 g/kg. The histological features are atypical and no definite cortical zones are evident, the cortical pattern having the appearance of an extensive zona glomerulosa. The medulla of the gland, consisting chiefly of a reticular network invested with elastic connective tissue, may have undergone considerable degeneration. Nerve fibres have not been observed in this part of the gland.

Thymus

Quiring and Harlan (1953) have described the thymus in the Florida manatee *T. m. latirostris*. It consists characteristically of clusters of lymphocytes (thymocytes) with an occasional connective tissue septum separating the clusters. In contrast, the medulla is small and contains a few thymic corpuscles.

Chapter 6.
Reproduction and Reproductive Organs

In the male manatee, the genital aperture is located on the abdomen, halfway between the anus and the umbilicus (Harrison and King 1965; Hartman 1971). The testes are abdominal, bluish-grey in colour, and are unusually flattened dorsoventrally (Barrett 1935). In a 2.74-m animal (*T. manatus*), they measured approximately 15.0 cm long, 10.2 cm wide, and 5.1 cm thick. The epididymides are comparatively large (Barrett 1935), as are the seminal vesicles (Harrison and King 1965). The "prostate" gland is not glandular but is composed of erectile muscular tissue (Harrison and King 1965). The penis, when extruded, measures more than 50 cm (Hartman 1971). From the pelvic muscle mass, it extends about 6.1 cm along the floor of the abdomen to the sheath pouch. The sheath pouch is about 10 cm long and nearly filled by the glans. The length from the sheath opening to the firm cartilage "beak" is about 10 cm and about 7.6 cm in diameter. The penis is held fixed except in the sheath; therefore it can only be protruded 10 or 11 cm. There is a cartilaginous rodlike structure, corresponding to the baculum, which extends along the dorsal side of the penis from the base to the tip of the glans. In repose, the glans measures about 7.6 cm; it is deeply excavated, the conical cavity extending back about 5 cm and concealing the meatus on the ventral aspect. A tough fold of skin barely covers its apex. There is a large amount of aponeurosis on the dorsal and lateral surfaces of the penis, which prevents the organ from altering its size, shape, or position to any extent; hence, copulation must depend upon the glans alone. There is no trace of a corona glandis (Barrett 1935).

Reproductive Anatomy of the Female

The genital aperture of the female manatee is in close proximity to the anus. The ovaries are located at the extreme lower limit of the body cavity, approximately at the same level as the inguinal canal. Quiring and Harlan (1953) described the ovaries of a *T. m. latirostris* as large masses of beadlike follicles having no heavy capsular coat. They noted that all the follicles are at approximately the same stages of development, and in some, the stratum granulosum is well defined, and occasionally thecae are discernible (Quiring and Harlan 1953).

The uterus is a bilobed organ, consisting of two short, stout cornua continuous with equally short oviducts (Wislocki 1935). Nongravid, it presents transverse rugae extending well into the oviducts (Quiring and Harlan 1953).

The duration of the estrus cycle in manatees is unknown. Hence, its division by Hartman (1971) into proestrus, estrus, and metestrus is arbitrary. According to Hartman, the females, though receptive only during estrus proper, engage the attention of the males during the other phases of the cycle and may undergo a number of sterile estrus cycles like the elephant before becoming pregnant (Short 1966).

Reproductive Behaviour

So little is known about the biology of the manatee that even the most basic features of the animal's reproduction, including age of sexual maturity, length of reproductive cycle, calving interval, gestation period, and life expectancy remain undetermined. The animals rarely breed in captivity, are reported to have an extremely slow reproductive rate, and a long period between gestations.

Male manatees are sexually very active and do not confine their sexual overtures to estrus females. Although the anestrus female defends her venter and turns her dorsum to a sexually aggressive male, he persists for hours and his sexual activity may incite surrounding males to join in the pursuit (Hartman 1971; Moore 1956).

Acknowledging that *T. inunguis* in the Amazon shows a preference for winter breeding, Pereira (1945) has suggested that there is no definite breeding season, and the relative sizes of the young accompanying their mothers support the view (Moore 1951, 1956). Hartman (1971) in his Crystal River studies also found evidence that *T. m.*

latirostris breeds throughout the year, showing preference for the spring or summer; in 1 year, four manatees gave birth, three in the spring or summer and one in the winter. Birth dates for captive animals suggest year-round breeding (Moore 1951). It has been suggested that the Honduras *T. m. manatus* mates in the driest months, especially in April but also in August because the young are seen with their mothers most often from September to March (the wet months) (Charnock-Wilson 1968).

It has been suggested that the manatee is monogamous (Beal 1939) but in fact the females and males are both promiscuous (Hartman 1971; Natl. Sci. Res. Counc., Guyana, 1974). The temperatures and surroundings during mating have not been thoroughly investigated but may prove important for breeding in captivity (Bertram and Bertram 1964). The Florida manatee is said to mate in water about 2.5 m deep (Hartman 1971; Natl. Sci. Res. Counc., Guyana, 1974), although one report described the animals copulating on a river bank in Guyana in 15 cm of water while the river was in flood (Bertram and Bertram 1964). Pereira's studies (1945) indicated that *T. inunguis* mates more often during the winter months, a time of high tides and temperatures in the Amazon.

For about 2–4 weeks, an estrus female is followed by many males, but she is only receptive for a restricted period (Hartman 1971; Natl. Sci. Res. Counc., Guyana, 1974). It may be that her reproductive responses are stimulated by the presence of several males (Natl. Sci. Res. Counc., Guyana, 1974). One estrus herd may consist of 1 female and 17 males — a nucleus of males residing nearby and others coming and going (Hartman 1971). Courtship is said to be most urgent when the female moves around, the males constantly nuzzling and mouthing her back. When unreceptive, she dislodges them with a jackknife motion as they try to mouth her undersides and genitals, or she may seek out a shoal where the males cannot reach her venter. The males often transfer their attention to a passing estrus female or revert to homosexual encounters. Pereira (1945) reported that the males strike violently at the abdomen of the females with their tails. The encounters are noisy and protracted, becoming more violent as dominance is established. Male aggression is evident only during courtship, according to Hartman (1971).

It has been reported that the manatee assumes a variety of positions during copulation. Bertram and Bertram (1964) described the animals mating on their sides in shallow water, whereas Pereira (1945) said they copulate face to face, then vertically with their heads out of the water, and then again with one on top of the other. According to Pereira, the male beats the female's genitals with his tail to relax her muscles and permit intromission. Hartman (1971) said copulation occurs only underwater and receptive females are polyandrous. The male lies on the bottom on his back during copulation, which lasts 15–30 seconds. There are less than 1-minute intervals between matings, and, postcoital behaviour is similar to courtship, the male in pursuit.

The males are sexually very aggressive, often pursuing anestrus females, subadults, and females with calves. The sexual encounters are vigorous and exhausting. In fact, Pereira (1945) stated that it is not rare for the female to die during copulation from the effort.

Mutual masturbation among male manatees is common, although there is no evidence of female homosexuality. Often during courtship, frenzied males will transfer their attention to homosexual encounters, the sexual embraces of which do not in any way resemble those during copulation. Juvenile males do not compete with the adult males but they engage in play that is suggestive of sexual activity. They rub bellies and mouth the mouth and genitals of the females. Any mature males that arrive during play disrupt all activity (Hartman 1971).

Gestation

The duration of pregnancy is not known with accuracy. Pereira (1945) reported that *T. inunguis* carries its young for 9 months like humans and domestic cows, whereas Moore (1951) gave a period of 152 days for *T. manatus*. The latter, which was based entirely on an account of a captive manatee, is likely an underestimate. Harrison and King (1965) placed the time as closer to 12 months, as did Kenneth and Ritchie (1953), and Hartman (1971) suggested approximately 13 months from observations of an estrus herd of *T. m. latirostris*. According to Hartman, mating and fertilization of one female took place between 20 October and 5 November 1967, and birth occurred between 20 November and 2 December 1968, a gestation of 385–400 days. Pereira (1945) has commented on the ponderous increase in the pregnant Amazonian manatee, remarking that not only the abdomen but the entire trunk appears to be abnormally enlarged.

Less is known about the placentation of the Sirenia than of any other group of mammals. Harting's (1879) and Turner's (1889) early accounts of the dugong placenta are not entirely reliable. Wislocki's (1935a) examination of the chorioallantoic hemochorial placenta and membranes of a 44-cm fetus of *T. m. latirostris* provides some insights.

Wislocki noted that the placenta is zonary, located along with the fetus entirely in the right horn of the uterus. Both chorionic poles are completely membranous. The voluminous allantois, which almost completely fills the chorionic sac, comprises four saccular compartments. These communicate with a common allantoic antrum that is bordered by four diverging pairs of allantoic vessels constituting the umbilical pedicle. The placenta is formed of fused chorionic and uterine tissues that form a fine-meshed hemochorial labyrinth of the deciduate variety. At the fetal surface of the labyrinth, there is a superficial zone consisting of arcades of columnar trophoblasts enclosing spaces in which stagnant maternal blood has accumulated. The maternal corpuscles are phagocytosed by the trophoblastic cells and provide histiotrophic nourishment for the fetus. The labyrinth consists of moderately distinct trabeculae of syncytial trophoblast bordering the maternal blood channels, which are arranged vertically. At the base of the placenta, tonguelike masses of fetal tissue are covered externally by cytotrophoblast unlike the trophoblast of the placental labyrinth. The membranous chorion is covered by palisadelike columnar cells. The endometrium, except for the placental site, is fully covered by uterine epithelial cells. The uterine glands are not very prominent and play no conspicuous role in the formation of the placenta. The quadri-lobular allantoic sac found in the manatee is characteristic of placentation of the Hyracoidea and Proboscidea, as are the many protruding mesenchymal appendages (postules) that cover the allantoic sac. The amnion, like that of the elephant and hyrax, is provided with extremely minute caruncles (Wislocki 1935).

Parturition

The birth of a manatee has not yet been observed, but Hartman (1971) suggested that a breech presentation like that of the cetaceans is likely. He based his belief on Slipjer's (1962) comment: "The distribution of the foetus's mass would favour the heavier and bulkier head settling in the lower front of the uterus, while the tail would be forced toward the cervix." Barbour (1937) published the first description, based on a personal communication after a birth at the Miami Aquarium in 1930. The neonate weighed 28.6 kg, measured 1 m long, and its tail was folded up on its back, and remained thus for 4.5 h. The presentation appears to have been cephalic. Pereira (1945) claimed that in *T. inunguis* the male assists the female during birth and that the female howls during her delivery.

The manatee is born in the water, and the mother pushes it to the surface to take its first breath (Jones and Johnson 1967; Natl. Sci. Res. Counc., Guyana, 1974). According to one report, an infant kept out of water 45 min was slowly submerged, the submergent periods being gradually increased (Moore 1951a). By the second half of the day after birth, the young swims and surfaces alone (Moore 1957; Hartman 1971) but does not swim with its tail until it is some days old (Harrison 1969). Parturition under natural conditions probably has not been witnessed to date because females seek quiet, secluded shallows in which to give birth (Hartman 1971).

Usually one manatee is born at a time, twins being a rare occurrence (Pereira 1945; Natl. Sci. Res. Coun., Guyana, 1974). Hartman (1971) described a twin birth and an apparent adoption in the Crystal River population. In November 1971, a manatee gave birth to twins and the next month she was seen with three young. The orphan — a yearling — mimicked the twins' relationship with their mother, behaviour that suggests it was probably being nursed as well. Jones and Johnson (1967) reported that one calf born in captivity was cared for by both parents until it was approximately half grown.

Lactation, Suckling, and Postpartum Behaviour

Two functional teats are located adjacent to the ventral insertion of the limbs, and in a parous female of *T. manatus* they measured 3.8 cm and 8.9 cm in length, respectively (Moore 1951a). In nonparous, pubertal females, there are one or two slight mammiform thickenings of the integument with no underlying glandular development (Murie 1872a; Garrod 1877; Pereira 1945; Moore 1951a).

Manatees are usually, but not invariably, suckled underwater, while the mother is idling. Approaching the cow from behind or from the side, the young draws the nipple into its mouth unassisted by the mother. Each spell lasts for about 2 minutes, during which both the mother and calf can submerge (Moore 1957; Hartman 1971a).

After 1–2 months, the young manatee begins to graze (Barbour 1937; Pereira 1945; Hartman 1971) but continues to suckle for as long as 2 years (Jones and Johnson 1967; Hartman 1971; Natl. Sci. Res. Counc., Guyana, 1974), staying close to its mother (Moore 1957; Hartman 1971). The time of weaning varies widely — for example, a yearling (~ 20 months old), 35 cm shorter than the mother, may be less independent than another animal 6–8 months old (Hartman 1971).

Sometimes, if the mother is resting on the bottom, the young manatee will engage in play with others. The young animal seems to reinforce the bond with its mother by mouthing and "kissing," but, when the female is in estrus, the offspring's position by its mother is usurped by courting males (Hartman 1971). There is evidence that mother-offspring communication occurs across distances as great as 60 m, the mother squealing to warn her young that danger is imminent. The female does not, however, show antagonistic behaviour when her young is threatened by man (Hartman 1971).

Chapter 7.
Life History

A neonatal *T. m. latirostris* is reported to weigh approximately 27 kg and to measure approximately 1 m in length (Moore 1951a, cited by Jones and Johnson 1967). These measurements correspond to those of Odell (personal communication, 1977) who gives the birth weight as 18–22 kg; the length as approximately 1 m. The figures also agree with a recently recorded birth weight of 19.1 kg in *T. m. latirostris* (Anonymous 1977) and with the length of *T. inunguis* given by Pereira (1945). The carcass of a bloated female calf, alleged to be 5–17 days old, weighed 42 kg and was 1.4 m long (Hartman 1971). The foregoing measurements, recorded some time after the birth of the young, represent but a few animals and hence, should be accepted with caution; more reliable data should be forthcoming from Odell (personal communication, 1977).

The age of sexual maturity is not known with any accuracy but has been estimated to be about age 3–5 years (Moore 1957; Walker 1964; Harrison and King 1965; Natl. Sci. Res. Counc., Guyana, 1974). Using size, growth rate, and behaviour as criteria for judging the Crystal River population, Hartman (1971) has commented that some manatees reach puberty as late as age 6 years. To date, figures are based on a relatively limited number of animals and, according to Odell (personal communication, 1977), may represent an underestimate of the reproductively active age.

The Adult

The early literature includes several accounts of animals attaining enormous proportions (Bertram and Bertram 1973). The largest manatee was reputedly more than 6.0 m long (Mohr 1957, cited by Bertram and Bertram 1973). In general, manatees grow to an average 2.5–3.0 m long (Quiring and Harlan 1953; Harrison and King 1965) weighing 362–590 kg (Quiring and Harlan 1953), but they may attain lengths as great as 4 or 5 m and weights of 540–550 kg (Campbell 1976).

Measurements of length, weight, and other external characteristics have not always been taken by biologists and are not necessarily reliable. Thus, standard measurements of adult male and female manatees of known ages in all species are urgently needed. Although females are believed to be bulkier, but not longer, than males (Hartman 1971), weight/length relationships are to be viewed with reservation.

T. inunguis averages 2.0–2.3 m long (Pereira 1945), and one account stated that *T. senegalensis* measures 3.0–6.0 m long and weighs 299.4–748.4 kg (Menegaux 1918 cited by Beal 1939). Moore (1951a) gave the average length of *T. m. latirostris* as 1.8–2.6 m, but greater lengths for this species were given by both Quiring and Harlan (1953) and Hartman (1971). Quiring and Harlan recorded a 2.96-m male weighing 424 kg and a 3.25-m female weighing 557 kg, and Hartman listed the lengths of two males and one female as 2.9, 3.0, and 2.7 m respectively. The larger figures are more in accord with those of Bangs (1895) who said the Florida manatee averages approximately 3.4 m long, two of his largest animals having measured 3.6 and 4.1 m.

Early 19th century travelers in Guyana reported manatees of enormous sizes ranging from 5.5 to 6.1 m long, although measurements taken by Bertram and Bertram (1964) showed that *T. m. manatus* does not exceed 3.7 m long, the average being between 2.1 and 2.7 m. Table 6 summarizes data collected by Dr Frank Mongul (National Co-ordinator, International Manatee Project, Georgetown, Guyana) of captive *T. m. manatus*.

Little information exists on the life span of the manatee although Betz (1968) thought it may exceed 50 years in the wild. In captivity, animals have lived for upwards of 26 years (Anonymous 1917; Hartman 1971).

At present, the extent of, and reasons for, perinatal mortality are little known, although extreme temperatures may in part be responsible for high rates. For example, the harsh freeze prevailing in Florida in the winter of 1976–77 caused widespread deaths of the young, and the full toll of casualties and effect of the disaster on the manatee population have not yet been assessed.

Table 6. **External measurements of 17 adults and 1 young male[a] of *T. m. manatus* presently held in captivity in Guyana.**

			Nose to					Flipper			Fluke			
Animal no.	Sex[b]	Length: nose to fluke (m)	Anterior origin of flipper (cm)	Umbilicus (m)	Genital aperture (m)	Anus (m)	Eye to eye (cm)	Anterior insertion to tip (cm)	Axilla to tip (cm)	Maximum width (cm)	Length (cm)	Width (cm)	Widest girth (m)	Narrowest girth (m)
1	F	2.77	50.8	1.04	1.73	1.90	20.3	48.3	38.1	15.2	81.3	66.0	1.80	–
2	M	2.62	55.8	1.01	1.17	1.80	25.4	48.3	46.0	30.5	71.1	56.0	–	–
3	F	2.46	55.8	.91	1.50	1.70	20.3	35.6	30.5	56.0	71.1	–	–	–
4	M	2.54	48.3	.91	1.09	1.73	20.3	35.6	33.0	15.2	66.0	56.0	1.70	0.76
5	F	2.51	40.6	.94	1.58	1.73	20.3	33.0	33.0	15.2	74.0	61.0	1.80	0.84
6	M[a]	1.70	35.6	.69	.74	1.17	15.2	25.4	22.9	10.2	48.3	40.6	1.21	0.56
7	F	2.89	55.8	1.04	1.80	1.91	20.3	33.0	35.6	15.2	67.3	55.8	1.83	0.97
8	M	2.49	55.8	.91	1.01	1.70	17.8	33.0	28.0	15.2	68.6	55.8	1.70	0.84
9	F	2.64	55.8	.91	1.52	1.70	17.8	40.6	33.0	13.0	68.6	58.4	1.70	0.94
10	M	3.02	55.8	1.14	1.30	2.10	17.8	30.1	41.0	17.0	84.0	64.0	1.78	0.97
11	F	2.57	50.8	1.00	1.60	1.73	20.3	43.2	33.0	15.2	66.0	61.0	1.58	0.89
12	M	2.89	55.8	1.04	1.19	1.91	20.3	46.0	38.1	17.8	74.0	66.0	1.78	1.07
13	M	2.51	50.8	1.04	1.14	1.73	20.3	48.3	38.1	15.2	58.4	43.2	1.37	0.69
14	F	1.98	40.6	.69	1.22	1.32	15.2	30.5	25.4	13.0	53.3	46.0	1.27	0.61
15	F	2.62	50.8	1.04	1.16	1.83	22.9	40.6	40.6	20.3	76.2	64.0	1.70	0.91
16	F	2.92	43.2	1.17	1.90	2.01	22.9	43.3	38.1	15.2	86.4	66.0	1.83	0.99
17	M	2.89	48.3	1.09	1.25	2.00	20.3	46.0	46.0	19.1	76.2	66.0	1.90	1.04
18	M	2.77	61.0	1.07	1.25	1.90	22.9	46.0	40.6	17.8	79.0	61.0	1.63	0.51

[a] This 3-year-old is the only animal of known age.

[b] Females averaged 2.60 m long, and males averaged 2.60 m. The average length of all animals was 2.60 m.

Social Behaviour

With the exception of the mother–young unit (Jones and Johnson 1967; Hartman 1971), manatees are essentially solitary animals. Adults do occasionally gather in small groups of two or three animals, especially in winter (Hartman 1971) for both sexual and nonsexual activities. The latter is a pastime indulged in by all animals irrespective of age or sex. Males are more social than females, which tend to be passive particularly when gravid (Hartman 1971).

Play takes the form of swimming together, mouthing, and wrestling (Hartman 1971), the predominant form being mouthing, which Moore (1957) suggested is a sign of mutual identification and which Hartman (1971) regarded as an indication of the presence of gustatory sense receptors in the tongue. When in groups, the manatees may follow one member's initiative in feeding, resting, or playing but do not usually react to alarm as a group. There is no evidence of manatees' assisting or defending other manatees in danger, and aggression is shown by males only when escorting females in an estrus herd (Hartman 1971).

Although Moore (1957) stated that the young do not take interest in other young, Hartman (1971) thought that they often play together in a manner suggestive of a social bond. Juvenile males play with older females in a manner resembling sexual activity without penis extrusion or aggressions.

Migration and Habitat

Young manatees often travel in groups of 15–20 (Jones and Johnson 1967), but each manatee appears to have an independent range. No individual, with the exception of the mother and her young, remains with another for any significant time (Moore 1957). The range seems to be dependent on seasonal migration so that summer and winter ranges may be different (Moore 1957). In the summer, the animal appears to move casually and unpredictably, pausing for varying lengths of time in suitable habitats and probably not returning the next year (Hartman 1971).

In the winter months, Florida manatees, *T. m. latirostris*, respond to a drop in the TA (several degrees blow 10°C in November, approximately 5°C by March) by congregating loosely in groups for the duration of the cold spell (Moore 1957; Hartman 1975). They gather on sites of constant temperature springs and warm outflow waters, the principal congregating site on the central west coast of Florida being the headwaters of the Crystal River (Hartman 1971). Based on observations of the cold-snap aggregations, it now seems possible that adult manatees have a home range to which they return for successive winters (Moore 1957; Hartman 1971).

Until recently, manatee migration was spoken of in vague terms, for there was insufficient evidence to support more than speculation. Hartman's (1971) Crystal River, Florida, studies have greatly increased our knowledge of migration, suggesting that manatees are moderately vagrant and that they routinely migrate tens of kilometres. In Florida, the habitat of the east coast manatee, *T. m. latirostris*, extends from the north of the peninsula to the south. Manatees have been observed in the north only during the summer months; therefore, a corresponding winter migration to the south was assumed to take place to avoid the cold (Moore 1951). On the west Florida coast, *T. m. latirostris*, influenced by the temperature gradient in the Gulf and Kings Bay, also migrates seasonally, seeming to ply familiar routes by way of deep channels; only channels and waterways over 1 m deep are regarded as potential thoroughfares for manatees (Hartman 1971).

Manatees are resident on the Gulf coast of Florida in relatively isolated populations. They concentrate in accessible rivers and estuaries that are of suitable depth and that provide an adequate source of food. They tend to remain in areas of prime habitat, migrating from time to time to other areas. In each new area, they reside temporarily before returning to their original surroundings or moving on. They have been known to migrate into salt water and stay long enough to become barnacle encrusted (Hartman 1971). According to Bertram and Bertram (1964), *T. m. manatus* is often found along the Guyana coast, in transit from one river estuary to another, presumably in quest of new feeding grounds.

Because they feed on plants growing in the euphotic zone, they essentially frequent shallow waters near shore, and they do not seem to dive to great depths. Although they may cross areas of deep water, they do not normally venture far from shore. With the exception of *Hydrodamalis*, all known fossil and living sirenians have been confined to tropical or subtropical waters, being acutely sensitive to low temperatures (Domning 1977).

The manatee is essentially a fluvial rather than a marine mammal (Phillips 1927), with most sightings occurring in fresh or brackish waters (Pereira 1945; Hartman 1971; Bertram and Bertram 1973). The animal can survive, however, in water that is fresh or salt, turbid or clear, acidic or alkaline (Phillips 1927), using salt-water habitats primarily for migratory purposes (Hartman 1971). A recent listing of manatee habitats as given by the International Union for the Conservation of Nature and Natural Resources (1972) is: *T. manatus* — shallow coastal water, bays, estuaries, lagoons, and rivers; *T. inunguis* — confined to "black water" (slow moving) and is unknown in "white water" regions; *T. senegalensis* — marine bays and sluggish rivers in warm, humid climates. *T. inunguis* is exclusively fluvial, being confined to the Amazon and Orinoco drainages (Jones and Johnson 1967).

The minimum tolerable (water) temperature is frequently stated as about 16–18°C (Sguros 1966), but Allsopp (1961) said "the manatee does not appear to be able to live at ease in a temperature below 21°C." These estimates Hartman (1971) regarded as high, because on a number of occasions he tracked animals in waters 15°C or even lower.

Temperature change strongly influences the manatee's activity (Hartman 1971). Generally, when the sun and air temperature are low, manatees tend to aggregate in quiet groups. As the sun comes up and the air temperature increases, manatees become more active and show more of their bodies above the water. In strong sunlight, they again become tranquil (Moore 1956). They cannot withstand extended periods of cold or sudden drops in water temperature (Cahn 1940; Odell, personal communication, 1977). Wind and rain seem to have no effect on their activity and currents as strong as 6 km/h have not affected them (Hartman 1971).

In South America, in the Amazon and Orinoco basins, *T. inunguis* has established its habitat, ranging about 100 000 km^2 and preferring muddy to clear waters. There are two ecological zones that are suited to its needs, namely *matupás-verdes* and *matupás-de-terra*. Both are floating masses of vegetation, the main difference being that the latter has more varied flora and fauna (Pereira 1945). A recent report describes the Peruvian habitat of *T. inunguis* as small water reservoirs and calm lakes with surface or floating vegetation and grassy shores (Brack, personal communication, 1977).

The chief predator of the manatee is man, although sharks periodically prey on manatee calves (Hartman 1971; Bertram and Bertram 1973), and jaguars occasionally attack *T. inunguis* (Pereira 1945). The alligator, reported to be the only predator of *T. m. manatus* in Honduras, is almost extinct and no longer poses a problem (Charnock-Wilson 1968).

Interspecies Relationships

Hartman (1971) gave the best account of interspecies relationships in his descriptions of Florida manatees. He said they do not pay attention to the indigenous fauna, which may include tarpon, sharp-nosed sharks, and dolphins, but that they are startled by surface splashing caused by jacks (*Caranx hippos*), coots, and pelicans. Although bacterial and fungal infections occur in captive manatees, they do not appear to occur in the wild (Hartman 1968 cited by Hartman 1971). Manatees do, however, harbour freshwater algae *Lyngbya martensiana*, suggesting infestation in estuaries and rivers. In general, the macroscopic associates of manatees seem to be free living and ectophoretic, rather than parasitic, whereas the microscopic inhabitats of its cutaneous surface apparently range from casual commensals to obligate parasites. Occasionally, manatees arriving in the headwaters of the Crystal River are covered with barnacles and marine diatoms of the general *Zygnema* and *Navicula*. These soon die in fresh water, but their presence provides evidence of the considerable time manatees spend outside the river.

The manatee is parasitized by digenetic trematodes and ascarid nematodes and in a marine environment frequently supports algae and barnacles externally (Jones and Johnson 1967; Hartman 1971). Specifically, the following parasites have been recorded:

- *T. m. manatus*: *Chiorchis fabaceus* in the large intestine; *Opisthotrema chochleatrema* in the esophagus, stomach, eustachian tubes, and nasal passages (Dailey and Brownell 1972);
- *T. senegalensis* and *T. inunguis*: *Chiorchis fabaceus* in the large intestine (Baylis 1936; Dailey and Brownell 1972);
- *T. m. latirostris*: *Harpacticus pulix*, a new species found on the sloughed skin of a manatee in captivity (Humes 1964).

The trematode *Schizamphistoma manati* in a manatee's intestine has been reported by Sokoloff and Caballero (1932, cited by Hartman 1971), and encrusted, ridged, and grooved patches on the hide of manatees have been recorded by Hartman (1971) and are believed to be of parasitic origin. Skin infections may attract copepods, which live in small numbers on the manatee under natural conditions and whose numbers may increase under captive conditions (Humes 1964).

Pereira (1945) held that manatees are the healthiest of all Amazonian aquatic animals. But in captivity it appears that they have an increased susceptibility to infection. Successful treatment of infections in manatees is relatively unrecorded, but Frye and Herald (1969) recounted the successful treatment of osteomyelitis in an immature *T. inunguis* male. Healing time was considerably shortened when the wound was kept in semidry isolation during treatment with antibiotics.

Feeding

The manatee spends one-quarter of its time feeding (Hartman 1971) and is said to consume as much as 20% of its body weight per day in wet vegetation (Natl. Sci. Res. Counc., Guyana, 1974). On the coasts of Central America and in the rivers of South America, the manatee has been reported to be primarily, but not exclusively, a nocturnal surface feeder (Barrett 1935; Pereira 1945). However, an extensive study by Hartman (1971, 50) in the Crystal River of Florida indicated that the Florida manatee feeds exclusively underwater and "is an essentially endogenous, arrhythmic species."

The longitudinal axis of the manatee's body is kept as nearly horizontal as possible; the distribution of its horizontal diaphragm, elongate lungs, and pachyostotic bones maximizes buoyancy (Hartman 1971; Domning 1977). Keeping its body horizontal, the manatee can feed on plants both on the bottom or the surface (Domning 1977). With only a slight deflection (~40°) of the rostrum and mandibular symphysis from the palatal plane, manatees are able to feed at any level from bottom to surface and are able to capture floating vegetation with ease (Hartman 1971). In contrast, the dugong with its strong deflection (~70°), causing its mouth to open almost straight downward, is an obligate bottom feeder (Heinsohn and Birch 1972; Domning 1977).

The manatee gathers up food with its upper lip, which is divided by a deep cleft. The two lobes of the lip, which can be narrowed and widened at will, allow a sideways motion during feeding, enabling the vegetation to be scooped and pushed backward to the teeth. When feeding on the surface, the manatee keeps its head well out of the water and its body nearly vertical, pushing the vegetation toward its mouth with its flippers (Barrett 1935). It tears soft plants with its muscular upper lips, which are strengthened by the lateral horny pads, hairs, bristles, and fibrous papillae. They grasp and tear much like the mandibles and the proboscis of some polychaetes (Bertram and Bertram 1964).

Manatees are remarkably unselective in their choice of food. Although they prefer succulent aquatics, they will consume almost any water plants (Natl. Sci. Res. Counc., Guyana, and Natl. Acad. Sci., USA, 1973; Domning 1977) that are soft enough to be torn by the upper lips (Bertram and Bertram 1968). They feed systematically on new, rather than old, growth (Allsopp 1961), texture being apparently more important than the type of plant (Allsopp 1961). Pereira (1945) stated that in South America, *T. inunguis* uses its front limbs to bend the low branches of the Brazilian guava and eats the leaves and fruits. The animals also consume slime and mud from the river banks or lake bottoms. He recorded that fishermen are able to track feeding manatees by the peculiar odour given off by the vegetation they eat. Hartman (1971) said that he is not convinced that the manatee feeds in salt water as is asserted by Bertram and Bertram (1968). Hartman (1971) stated that in Florida the manatee feeds exclusively underwater from just below the surface to 3–4 m, depending on the type of vegetation. It is indiscriminate when selecting a feeding site but may remain in a choice area, entirely stripping the vegetation. It feeds in sessions concentrating on one species of vegetation at a time. The adult manatees feed for 30–90 min and will feed for 2 h if hungry.

As they become sated, they rest periodically between mouthfuls and eventually quit eating altogether. They take two chews/sec, continuing to chew as they rise to the surface for air and resuming on their descent. The sound of grinding teeth can be heard underwater. Calves feed spasmodically for up to 30 min (Hartman 1971).

Manatees constantly eliminate waste and they produce a large quantity of gas because of the nature of their diet. While resting after a feed, they frequently regurgitate a yellow-green mash (Hartman 1971).

Although manatees will eat any type of plant, they prefer submerged, floating, rooted, and emergent growth, in that order (Allsopp 1969; Hartman 1971). In Guyana and Florida, they have been known to eat aquatic plants of the following genera:

- Submerged: *Cabomba, Elodea (Anacharis), Hydrilla, Utricularia, Najas, Myriophyllum, Potamogeton, Vallisneria, Ceratophyllum, Ruppia, Nitella, Syringodium, Thalassia, Chara, Ulva* (Natl. Sci. Res. Counc., Guyana, and Natl. Acad. Sci., USA, 1973). In areas where both *Myriophyllum* and *Ceratophyllum* grow, manatees favour the latter. In Florida *Ruppia* is the staple food of the manatee. *Ruppia* growing in brackish waters together with *Myriophyllum* is preferred when growing with *Potamogeton* and *Najas*. The animal consumes only the leaves of *Ruppia*, the young shoots, leaf bases, and root stalks of *Vallisneria*, the uppermost "coontails" of *Ceratophyllum*, the stalks, leaves, and flowers of *Myriophyllum*, and the entire *Hydrilla* plant, which grows from the water bottom to the surface (Hartman 1971).

- Floating: *Eichhornia, Salvinia, Azolla, Pistia, Victoria, Lemna, Paspalum, Neptunia, Hymenachne* (Natl. Sci. Res. Counc., Guyana, and Natl. Acad. Sci., USA, 1973). Hartman (1971), surprisingly, said that floating vegetation is virtually ignored as a food source by the animals he has observed.

- Rooted and emergent: *Montrichardia, Typha, Sagittaria, Spartina, Ipomoea, Panicum, Leersia, Althernantera, Nymphaea, Nelumbo, Nelumbium, Luziola, Mimosa* (Allsopp 1969; Natl. Sci. Res. Counc., Guyana, and Natl. Acad. Sci., USA, 1973). Manatees in the Crystal River have not been observed to eat rooted and emergent vegetation (Hartman 1971), although Moore (1951) stated that the Florida manatee consumes such vegetation.

Manatees also at times consume algae: *Enteromorpha, Oscillatoria, Navicula, Spirogyra, Cladophora, Gracilaria, Ectocarpus* (Hartman 1971).

Aquatic weeds are composed of as much as 95% water, and their chemical composition is markedly affected by the aquatic environment in which they grow; for instance, plants growing in sewage or industrial waste water are exceptionally high in mineral content. In general, 10–26% of the dry matter is crude protein; in the water hyacinth, water lettuce, and hydrilla, 80% of the total nitrogen is protein. Amounts of amino acids are similar to those found in terrestrial forages, but methionine and lysine are lower. Ash content depends on season and location such that minerals comprise from 8 to 60% of the dry weight, depending on the water's chemical content and turbidity. The water's silt, sand, and insoluble carbonates will be reflected in the plant's chemical makeup. The amounts of phosphorous, magnesium, sodium, sulfur, manganese, copper, and zinc compare to land vegetation; iron, calcium, and potassium levels are higher (Int. Dev. Comm. Int. Rel., Adv. Commu. 1976).

Other behaviour patterns have been observed by Hartman (1971) who said manatees probe the bottom rocks and surrounding territory with their mouth. According to Hartman, the manatee also engages in stretching (associated with resting and in males often with masturbation), scratching (using its flippers or rubbing against inanimate objects), mouth cleaning (an activity not restricted to feeding time and indulged in by young manatees as well as adults).

Chapter 8.
Population Ecology

Generally speaking, the manatee is sparsely distributed throughout its entire range and in many areas is regarded as very rare (Bertram and Bertram 1966, 1968). Up to 1974, the following statistics were available for individual species. *T. manatus* is vulnerable because it has been hunted excessively and has been destroyed and injured by power watercraft. In addition, its habitat is in danger of destruction from pollution, dredging, and filling. Manatees occur in moderate numbers in Honduras; they are said to be endangered in the United States and Guyana, rare in Costa Rica, and decreasing in Cuba and elsewhere. *T. inunguis* is endangered in the main Amazon tributaries and possibly in the Orinoco where the numbers have seriously declined as a result of hunting (IUCN 1972). In Peru, there are modest numbers of *T. inunguis* in the rivers of the Pacaya-Samiria National Reserve (Brack, personal communication, 1977).The population of *T. senegalensis* is seriously depleted throughout its range, being hunted for meat, hide, and oil (IUCN 1972).

Hartman's (1971) investigations in Crystal River, Florida, are the only current data published for *T.m. latirostris*. In the course of his study, 70 manatees were sighted, and of these, 63 were identified. The sex ratio was 31:32 male to female. Of the animals measured, juveniles averaged 2.3 m in length and adults, 2.9 m. Adult females tended to be bulkier than males, but there was no significant variation in length between females and males. In the absence of more precise aging criteria, Hartman divided the Crystal River population into calves, juveniles, and adults. A calf was defined as any animal associating with its mother, independent animals being considered juvenile or adult. Juveniles were distinguished from adults on the basis of size and sexual behaviour. Because the transition to adulthood is gradual, the assignment of animals to either class was subjective and arbitrary. Of the 63 individuals in the study, there were 13 calves, 15 juveniles, and 35 adults.

The population was in constant flux over the two winters. Citrus County manatees intermittently exchanged places with those of the Suwannee and more southerly populations, and there was a strong suggestion of population intermixing on the west coast, seasonal for some and nonseasonal for others. In the winters of 1967–68, and 1968–69, 54 manatees were identified in the Crystal River headwaters, and 33 of them were present for one of the two winters. Of the 21 remaining, 5 were seen the first winter, and 6 arrived for the second winter, suggesting that for some there was no permanent home.

In 1967, there were 6 mothers and 6 calves of a population of 19 females. In 1968, there were 7 mothers and 7 calves of a population of 13 females (one of the calves died 2 weeks after birth).

Because manatees generally live in areas where food is plentiful and predators few, and because they are relatively healthy, their rate of survival to puberty is good. They live in peril only of man and the climate, man contributing to pollution, slaughter, and injury. Hartman (1971) makes no reference to adult mortality. In captivity, the manatee is susceptible to pneumonia and pleurisy (Beddard 1897; Townsend 1904; and Sguros 1966, cited by Hartman 1971).

Chapter 9.

Management and Conservation

In 1945, Nunes Pereira wrote that from the first days of the conquest of the Amazon valley, reporters and naturalists had warned that hunting of the manatee by the interior peoples would eventually destroy the animal. He urged prompt, efficient legislation to control the killing and protect the existing populations. He proposed that the Ministry of Agriculture should set up projects to defend the manatee, because the animal could play a vital role in the economy. According to Pereira, Peru had been passing such legislation since 1902. He proposed a hunting restriction on the manatee for 10 years and the imposition of high fines and prison terms for offenders; he also called for laws prohibiting invasion and burning of the matupas (the manatee habitat), and lastly he suggested that shipping vessels be forbidden to carry any manatee products and businesses forbidden to stock them, with a penalty of a fine, 1 year in prison, and seizure of the goods.

In 1963, Bertram and Bertram suggested that the existing legislation in Guyana (then British Guiana) should be enforced, that a detailed biological study should be made, that both the public and government officials should be educated in the conservation of the manatee, and that wildlife reserves should be established. In 1964, Bertram and Bertram wrote that the Guyanan stock was vulnerable, and although there was legislation to protect the manatee, it was difficult to enforce because the country had poor communications as well as a shortage of meat.

In 1972, the IUCN Redbook listed that:

- *T. manatus* was legally protected throughout Florida, Cuba, Jamaica, Puerto Rico, Trinidad, Honduras, and Guyana.
- *T. inunguis* was legally protected in Brazil and Peru, but the legislation was difficult to enforce in isolated areas.
- *T. senegalensis* was placed in class A of the African Convention, 1969, which guaranteed protection but which has been reported to be ineffective.

Recommendations were made for regulation of power boats; elimination of pollution, siltation, dredging, and herbicides that destroy the food and habitat; and the establishment of wildlife reserves. In 1974, Fitter said that *T. inunguis* was one of the most acutely endangered mammals in the world because of the ruthless hunting for meat but that it was a hopeless situation to expect protection because of the poverty of the people of the Amazon. He, therefore, proposed immediate establishment of a reserve on the Rios Pacaya and Samiria in Peru; an urgent investigation of a suitable reserve or reserves in Brazil; a survey of manatees in the Rio Orinoco to establish the species' status there; and renewed attempts to enforce legal protection in Brazil and Peru.

Since 1974, progress has been made in attempts to establish an internationally coordinated manatee research centre based in Guyana. The objectives of the centre are to undertake basic research, especially into the fundamental questions on physiology, endocrinology, anatomy, reproductive biology, biochemistry, ethology, and ecology; to use the manatee as a research animal for basic life sciences; to assess the value and effectiveness of manatees for weed control; to develop a means of repopulating depleting stocks, promoting conservation, and fostering domestication; to provide guidance in planning and techniques of mammalian research, and to establish a closer research liaison between Guyana, the Caribbean, South America, and the rest of the developed world (Anonymous 1975a).

Furthermore, groups have been formed in Gainesville, Florida, under the direction of Dr H. Campbell of the U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory. In Manaus, Brazil, D. Magor initiated a project with *T. inunguis*, which has now been expanded with the help of D. Domning, University of California, and two recent graduates of the University of Guelph.

It is hoped that these groups indicate expanded interest that will lead to better knowledge and a secure future for this greatly endangered animal.

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Appendix

Plates 17–26, taken from Murie 1872a

Plate 17

Fig. 1. Lateral view of the body of a young male Surinam manatee (*Manatus americanus*, Cuv.) forwarded to the Society by Herr A. Kappler. Photographed from the dead body. The tail is seen, not in profile, but slightly tilted toward the observer. *n*, nasal orifice of the right side; *c*, tail-cleft.
Fig. 2. Abdominal surface of the same animal, also from a photograph: *u*, umbilical cicatrix; *p*, external orifice of the penis; *a*, anus.

Plate 18

Fig. 3. Dorsal aspect of the body, the pectoral limbs (as in Fig. 2) outstretched. *n*, nares; *e*, eye.
Fig. 4. Pectoral limb of the left side, seen on its external surface. *I*, *II*, *III*, first, second, and third digital nails.

Plate 19

Fig. 5. Head and neck, as far as the shoulder, of the same young male *Manatus*. *n*, left nose-opening; *ea*, ear-hole, or orifice of auditory canal.

Plate 20

Fig. 6. Front, and consequently foreshortened view of the head, body, and pectoral extremities of the specimen in plates 17–19. The body lying on a table while being photographed has necessarily slightly flattened the chest. *e*, eye; *n*, narial orifice.
Fig. 7. Muzzle with the mouth opened, from a photograph, of the natural size, showing: *nn*, narial orifices; also the upper and lower lips (=outer), the palatal or upper pad, and the mandibular or lower pad (=the additional labial masses, or inner, extra upper, and lower lips).

Plate 21

Fig. 8. Side view of the female manatee, with skin and subcutaneous fat removed, exposing the superficial muscular layers. The broad tail, consisting of fibroid and dermal tissues, is necessarily absent.

Muscles of the body and tail: *Sp.d.*, Spinalis dorsi and Levator caudae internus, *Lci*; *L.d.*, Longissimus dorsi and Levator caudae externus, *Lce.*; *Sp.*, Splenius; *Co.*, Complexus; *Tz.*, Trapezius; *Rh.*, Rhomboideus; *S.l*, *S.l**., Sacro-lumbalis; *Ei.*, External intercostals; *E.o.*, External oblique; *L.cd.*, Lumbo-caudalis; *Sc.*, Sacro-coccygeus; $P.c.^1$., $P.c.^2$., $P.c.^3$., *P.c.**, Different portions of the panniculus carnosus muscle, including the platysma myoides, or transverse nuchal portion of the panniculus; *La.d.*, Latissimus dorsi; *f.*, Dorsal layer of fat.

Muscles of the head: *Te.*, Temporalis; *ac.*, Auditory canal; *O.p.*, Orbicularis palpebarum; *L.l.s.a.n.*, Levator labii superioris alaequae nasi; *L.s.p.*, Levator labii superioris proprius; *D.l.i.*, *D.l.i.**, Depressor labii inferioris; *D.a.o.*, Depressor anguli oris; Pc^2., Mandibular portions of panniculus.

Muscles of the pectoral limb: *I.sp.*, Infraspinatus; *D.*, Deltoid; T^1, T^2., Triceps (first and second portions); *T.ma.*, Teres major; *B.a.*, Brachialis anticus; *E.md.*, Extensor minimi digiti; *Pl & c.*, Palmaris longus & c; *Sl. & E.c.r.l.*, Supinator longus and extensor carpi radialis longior; *E.c.d.*, Extensor communis digitorum; *E.c.u.*, Extensor carpi ulnaris; *E.p.i.p.*, Extensor primi internodii pollicis.

Fig. 9. Undersurface, showing the superficial muscular layer of the right half of the body, and dissected deeper parts of the left moiety. The letters used in Fig. 8 are applicable to similar parts exposed or cut short in the ventral aspect. The following muscles, vessels, etc., besides are seen partly uncovered: *R.ab.*, Rectus abdominis; *E.o.*, External oblique; *I.o.*, Internal oblique; *Tra.*, Transversalis; *Is.c.*, Ischio-coccygeus; *Ifc.*, Infracoccygeus; *P.ma.*, *Pma**., Pectoralis major; *Pmi.*, Pectoralis minor; *C.h.*, Cephalo-humeral; *St.m.*, Sterno-mastoid; *S.hy.*, Sterno-hyoid and Sterno-thyroid; *Thy.*, Thyro-hyoid; *S.*, Subscapularis; *Di.*, Digastric; *Ma.*, Masseter; *L.l.i.*, Levator labii inferioris; *A*, anus; *V*, vulva; *Pl*, pelvic bone; *Ab. Rete*, mammary arteries as a rete mirabile; *C* and *I*, carotid artery and jugular vein; *Ax. Rete*, axillary plexus of vessels; *tr*, trachea; *M.gl*, mammary gland; *P.gl*, parotid gland; *Sx.gl*, submaxillary gland.

Fig. 10. Second layer of the muscles of the head, with portions of the panniculus cut short to show their cranial insertions. *Te.*, Temporalis; *Di.*, Digastric, seen in part; Ma^1, Ma^2., Masseter, two layers; *L.l.s.a.n.*, The levator labii superioris alaeque nasi cut short & reflected; *L.s.p.*, Levator labii superioris proprius; *C.n.*, Compressor nasi & c.; *O.o.*, Orbicularis oris; *Bu.*, Buccinator; *D.a.o.*, Depressor anguli oris; *D.l.i.*, Depressor labii inferioris; Pc^1, Pc^2, Pc^3, Cheek and lip insertions of panniculus; *Px*, Vascular plexus emerging from skull behind the mandibular condyle.

Fig. 11. Third and deepest layer of cranial muscles as viewed in profile. The same lettering is used as in the preceding. *Z*, zygomaticus; *Md*, Mandibularis muscle; *Ty*, tympanic bulla.

Fig. 12. Muscles of face and muzzle seen from above. On the right side the levator labii superioris alaeque nasi has been entirely removed, the dotted line indicating its outline. On the left side the levator labii superioris proprius and maxillary portion of panniculus have been dissected, cut short, and thrown forward. Additional letters are: *Pn*, Pyramidalis nasi; and *Px*, infraorbital plexus of nerves, etc.

Plate 22

Fig. 13. Pectoral limb, inner view. The upper layer of the forearm muscles in place, and insertions into scapula and humerus of some of the thoracic ones displayed. *Rh*, rhomboideus; *S.mg*, serratus magnus; *T.ma & La.d*, teres major and latissimus dorsi; *P.ma & P.mi*, pectorales major and minor; *L.cl & C.h*, levator claviculae and cephalo-humeral; B^1 & B^2 biceps, first and second heads; T^1, T^2, T^3, triceps, three bellies; *B.a*, brachialis anticus; *P.r.t*, pronator radii teres; *F.c.r*, flexor carpi radialis; *F.c.d.*, belly and palmar distribution of the common flexor of the digits; *F.c.u*, flexor carpi ulnaris; *Pl*, palmaris longus; *Ab.m.d. & Fb.m.d.*, abductor and flexor brevis minimi digiti; Pc^3, aponeurosis from panniculus.

Fig. 14. Upper layer, short palmar muscles. Letters as in preceding. I^s, superficial interossei; 1 to 5, the digits.

Fig. 15. A similar view, but with the superficial muscular expanse hooked forward, exposing deep interossei: (I^s) deep interosseous series.

Fig. 16. Profile fetal skull of manatee in the Amsterdam Museum. *Fr*, frontal; *Mx*, maxillary; *Pmx*, premaxillary; *Pa*, parietal; *So*, supraoccipital; *Sq*, squamosal; *Ju*, jugal, and *S* an adjoining sesamoid bone; *Ty*, tympanic; *Md*, mandible. The dotted line indicates continuance of ascending contour, and 1, 2, 3, separate ossific centres; fo^1 & fo^2, the parietal and occipital fontanelles; *O*, orbit; *Mf*, mental foramen.

Fig. 17. Base of the same, additional lettering as follows: *Bs*, basisphenoid; *As*, alisphenoid; *Os*, orbito-sphenoid; *Pl*, palatine; *Bo*, basioccipital; *Eo*, exoccipital; *fm*, foramen magnum; *Eus*, Eustachian sac; *Sf*, sphenoidal foramen; *Iof*, infraorbital foramen; *An*, anterior palatine foramen; *I*, incisor-cavity; *Mo*, molars in dental sacs.

Fig. 18. Mouth view of the partially dissected lower jaw with tongue, larynx, hyoid, and muscles *in situ*. The dotted lines respectively show the approximate limits of the so-called outer lips (consult Fig. 7 etc.). *b*, bristles on *ll*, lower lip; *sp*, spines on *lp*, lower mandibular or symphysial pad; *T*, tongue; *id*, inferior dental foramen; *oe*, esophagus; *tr*, trachea; *Cs*, constrictor superior; *Cm*, constrictor medius; *S.ph*, stylo-pharyngeus; *Stg* + *h*, stylo-glossus and hyoid.

Fig. 19. The palate and portion of the upper lip of the same female manatee. The dotted lines indicate the contour of the muzzle etc. (Fig. 7). *ul*, upper lip partly in outline; *up*, upper callous pad = inner upper lip; *b*, bristles; *sp*, palatine spines; *bh*, buccal or inner labial hairs.

Plate 23

Fig. 20. Reduced sketch of the viscera *in situ* of the young male manatee. The lower left lobe of the liver is partially dragged out by a hook, the better to expose the natural foward tilt of the great curvature of the stomach. *I & IV*, first and fourth gastric cavities; and *III*, placed on liver, points to the third semispiral appendicular cavity; *gl*, cardiac gland; *sp*, spleen; *Cae*, at root of bifurcate cecum; *r*, right, and *l*, left, duplex lobes of liver; *Gb*, gallbladder; *pe*, pericardium; *II*, four cavities of heart; *pa*, pulmonary artery; *ao*, aorta; *u*, umbilicus; *p*, aperture for penis; *a*, anus.

Fig. 21. The compound stomach, sliced open to show cavities and wallstructure. *oe*, esophagus; *I*, first gastric cavity (* and white arrow indicate its upper sacculus); *gl*, cardiac gland; *II*, second cornual cavity; *IV*, fourth cavity; *d*, duodenum; 1, esophageal opening into stomach; 2, stylet entering orifice of cardiac gland; 3, communication between *I & IV* stomachs; 4 & 5, two stylets passing respectively into the *II & III* cornual gastric divisions; 6, pyloric orifice; *dch* and *pd*, ductus communis choledochus and pancreatic duct, to the orifices of which arrows also point; *m*, gizzardlike thickening of muscular coat.

Fig. 22. Compound stomach, denuded of its serous coat, and exhibiting the direction of the external layer of muscular fibres. Lettering corresponds with Fig. 21.

Fig. 23. Semidiagramatic view of stomach as it appears on the esophageal or upper surface.

Fig. 24. A transverse section, about the middle of the cardiac glandular appendage, showing its irregular diverticulate central cavity and surrounding gland cells.

Fig. 25. Piece of the small intestine, toward the duodenal end, showing form of rugae and *P*, Peyer's glands.

Fig. 26. Piece of the small intestine, from the ileum, with glands (*L*) or crypts of Lieberkühn. *m*, muscular coat.

Fig. 27. Portion of gut from near the rectum: *L*, glands, as above.

Fig. 28. Ileocolic segment of the intestine, sliced open to show interior structure. *il*, ileum; *c*, colon, * its enlarged commencement; Coe^1, exterior, and Coe^2, interior of the cecal appendages; *gl*, compound and sacculate ileocolic valve-gland; *m*, thickening of muscular coat, the valve's wall.

Plate 24

Fig. 29. Short deep muscles of the ventral surface of the neck; intervertebral exit of the cervical and brachial plexus of nerves, and membranous chambers, postero-base of skull. Right side with upper layer and a partial outline of shoulder; left moiety, deeper view, and opened basicephalic chamber. *R.a.ma.*, Rectus capitis anticus major; *R.a.mi.*, Rectus capitis anticus minor; Lc^1, Lc^2, Lc^3, Longus colli, its three parts; *Rl.*, Rectus lateralis; *Sca.*, Scalenus; *Smg.*, Insertion of serratus magnus into atlas; *Ch.*, Cephalo-humeral; *St.m.*, Tendinous insertion, sterno-mastoid; *S.h.*, Stylo-hyoid cartilage, cut cranial origin; 1, 2, 3, 4, 5, 6, 7, & 8, anterior spinal cervical nerves issuing from the intervertebral foramina; *Ph*, phrenic nerve; *Fn*, facial nerve at exit; *na*, posterior nares; *ptp*, pterygoid process; *Eus*, Eustachian sac opened on left side.

Fig. 30. Anterior segment of the body, with the limbs cut short. Dissected so as to lay bare chiefly the heart, main vascular trunks, and complex rete mirabile of the neck and upper limb. The sternum has been dragged outward to the left side, showing the under surface of its left osseous moiety and trifid cartilages. The mammary gland and enlarged lymphatics partially occupy the right side of the chest. On the left side of the neck the jugular veins are intact, and the rete mirabile, cervical, and axillary superficially displayed. On the right side a deeper view is given. The large venous trunks and portion of the rete mirabile are removed, exposing the cervical and axillary plexus of nerves. The digastric muscle is cut away, and the parotid gland everted.

Heart and vessels, *v*, right, and *v**, left ventricles; *a*, right, and *a**, left auricle; *p.a*, pulmonary artery; *ao*, aortic arch, and *ao**, abdominal aorta; *l.c*, left common carotid artery; *ls*, left subclavian; *i*, innominata; *r.c*, right carotid; *th*, thoracic branch; *ic*, internal carotid; *ec*, external carotid; *im*, internal maxillary and plexus; *f*, facial; *rs*, right subclavian; *t.ax*, thyroid axis, and *ax*, axillary trunk splitting into retial divisions; *b.rete*, branchial retial plexus; *im*, internal mammary; *ve*, portion of vertebral artery under the pneumogastric nerve.

I.J, left internal jugular, and *E.J*, external jugular veins; *CO*, communicating branches of the same; *S.V.*, left subclavian vein, cut short; *BC*, ditto brachio-cephalic; *VCD & VCA*, vena cava ascendens and descendens severed.

Nerves: Nos. 2 to 8 numerically apply to the individual elements of the cervical and brachial plexus; *ph*, phrenic; *pn*, pneumogastric; *rl*, recurrent laryngeal; *sl*, superior laryngeal; *hy*, hypoglossal; *il*, inferior laryngeal; *fn*, facial nerve; *lt*, long thoracic; *mn*, median nerve; *ec*, external cutaneous; *un*, ulnar nerve.

Larynx, glands, etc.: *C*, cricoid, and *T*, thyroid cartilage; *bh*, basihyal; *sh*, stylo-hyal, and *, its cranial cartilage; *tr*, trachea; *Pgl*, parotid gland; *Mgl*, mammary gland; *r*, first rib; *st*, sternum reflected; c^3, the three sternal cartilages; *P*, pericardium opened; *oe*, esophagus, in part.

Muscles: *Ma*, masseter; *Stm*, sterno-mastoid; *Pc etc*., panniculus etc, reflected; *Pma & Pmi*, pectoralis major and minor; *Eo*, external oblique, a portion; *D*, diaphragm; *Cth*, crico-thyroid; *Th.h*, thyro-hyoid; *Sh*, stylo-hyoid; *Sph*, stylo-pharyngeus; *Mh*, mylo-hyoid.

Plate 25

Illustrations of the brain of the female, partly from rough sketches when fresh, and partly from the hardened brain, aided by a cast of the cranial cavity.

Fig. 31. Upper surface.

Fig. 32. View in profile.

Fig. 33. The base with origin of nerves.

Fig. 34. Longitudinal and vertical mesial section or inner face.

Fig. 35. Left hemisphere, exposing lateral ventricle; the horizontal section of the cerebellum is cut at a lower plate than is the cerebrum.

The following lettering applies throughout:

Nerves: 1, 2, 3, 4, 5, 6, 7, 8, 8*, 9; that to the olfactory is placed on the bulb.

Parts of base: *pi*, pineal gland; *al*, corpora albicantia; *cr*, crus, or peduncle; *pv*, pons Varolii; *ap*, anterior pyramid.

Interior horizontal and vertical sections: *ac*, anterior cornu; *dc*, descending cornu; *pc*, posterior cornu; *cs*, corpus striatum; *ts*, tenia semicircularis; *th*, thalamus opticus; *hmi*, hippocampus minor; *f*, fornix; *cc*, corpus callosum; *g*, its genu, and *sp*, splenium; *a*, anterior commissure; *c*, corpora quadrigemina; *v*, fourth ventricle; *v*, fifth ventricle.

Lobes of cerebrum: *F*, frontal; *P*, parietal; *T*, temporal; *O*, occipital.

Fissures, or sulci; *sy*, sy^1, sy^2, Sylvian; *if*, infero-frontal; *mf*, midfrontal; *sf*, supero-frontal; *ap*, antero-parietal; *ro*, Rolando, or postparietal; *op*, occipito-parietal; *ot*, occipito-temporal; *ca*, calcarine; *cm*, calloso-marginal.

Folds or gyri: *Io*, interorbital; *Mo*, midorbital; *Eo*, entorbital; *If*, infero-frontal; *Mf*, midfrontal; *Sf*, supero-frontal; *Ap*, antero-parietal (*premier pli ascendant*); *Pp*, postparietal (*second pli ascendant*); *Lob*, lobule of postparietal; *Ang*, angular; *At*, antero-temporal; *Mt*, midtemporal; *Pt*, posttemporal; *Soc*, Supraoccipital; *Moc*, midoccipital; *Ioc*, inferooccipital; *U*, uncinate; *Ma*, marginal; *C*, callosal.

Cerebellum: *av*, arbor vitae; *sv*, superior vermiform process or middle lobe; *fl*, flocculus; *ag*, amygdaloid lobe.

Fig. 36. Portion of skull of female manatee, with calvarium removed to show interior base. The dura mater is in place on the left moiety, but cleared away on the right.

Lettering applicable to the left half: 1, olfactory fossa; 2, foramen piercing membrane for optic nerve etc.; 3, perforation transmitting third and fourth nerves etc.; 5 & 7, foramina respectively for trigeminal and auditory nerves etc.; *ca*, carotid groove; *t*, temporo-sphenoidal fossa; *P*, pituitary fossa; *j*, jugular groove; *px*, plexus and lateral sinus; *px**, spinal plexus.

Lettering of right half: *Fr*, frontal bone; *Mx*, maxillary; *Os*, orbito-sphenoid; *As*, alisphenoid; *Bs*, basisphenoid; *Bo*, basioccipital; *Eo*, exoccipital; *Sq*. & *Pa*, squamo-parietal; *P*, periotic; *T*, tympanic; 2*, optic groove; 7, meatus auditorius internus; Sc^2, superior semicircular canals; *c*, *c**, condyles.

Plate 26

Fig. 37. Longitudinal and partly median section of the body, head, etc., of the young male manatee. The ribs are left in position but dissected so as to show the remarkable relations of the lungs, diaphragm, and viscera generally.

L, *L*, *L*, *L*, *L**, the lung resting on *D*, *D*, *D*, *D*, *D**, the lengthened horizontal diaphragm; *lsf*, ligamentum subflavum of dorsal vertebrae; *f*, coating fat and skin of the back; *H*, heart; *St*, sternum; *Li*, liver; *Sto*, stomach; *I*, folds of intestine; *B*, urinary bladder; *P*, penis within its sheath; *Rab*, rectus abdominis and cut fleshy wall; *B.c*, bulbous cavernosus muscle; *Icv*, ischio-cavernosus; *Sp.a*, sphincter ani; *a*, anus; *Is.c*, ischio-coccygeus; *Sc* + *If.c*, sacro-coccygeus and infra-coccygeus, obliquely cut through; *fc*, fibrous caudal expansion with a rim of the skin left; but on the opposite right side the skin has not been removed; *Pl*, pelvic bone; *Pf*, pelvic suspensory fasci; *C.Rete*, the rete mirabile, which proceeds to the end of the tail within the chevron bones; *L.Rete*, lumbar vascular rete shown in part; *Bc*, brain cavity; *n.ch*, nasal chamber leading by narrow canal to *n*, external narial orifice; *Pmx*, premaxillary bone in section, covered by the fleshy, fibrous snout; *sy*, mental symphysis; *ul*, upper lip (=outer); *up*, upper pad (=inner lip); *ll*, lower lip (=outer); *lp*, lower pad (=inner lip); *bh*, buccal hairs; *T*, tongue; *Eus*, orifice of Eustachian tube; *Sgh*, stylo-glossus and hyoid muscle; a double-headed arrow beneath leads from the fauces to the esophageal and laryngeal passages, each partially laid open; *la*, cut larynx; *oe*, esophagus; *Rete & c*, portion of rete cervicale; *J & C*, jugular vein and carotid artery severed; *M & F*, muscle and fat between the fore limbs; *cv*, cervical vertebrae.

Fig. 38. Front segment of the skull showing the nasal cartilage on the right side, and the open nares, diminutive nasal bone, etc., on the left. *Fr*, frontal bone; *Na*, left nasal; *Tu*, turbinals; *O*, right orbit; *nc*, nasal cartilage; *sp*, septal cartilage; *cf*, cartilaginous fissure; *Px*, infraorbital plexus of arteries.

Fig. 39. A transverse section of the tail behind the anal constriction, but in advance of the caudal expansion. It shows: *c*, centrum of a vertebra, its articulating surface surmounted by the neural arch (*a*) enclosing the spinal cord, which is surrounded by a vascular plexus; *t*, cut surface of transverse process, between which the centrum is another rete mirabile; *ch*, lamina of chevron bone enclosing subcaudal rete; *Lci*, *Lce*, levatores caudae internus and externus or continuation of the dorsal muscles; *L.c*, lumbo-caudalis; *Sc* and *If.c*, sacro-coccygeus and infra-coccygeus, lower tail-muscles; *Sk*, skin, fatty fibro-fatty layer, etc.

Fig. 40. A cross-section of the flat expanded tail: *vt*, vertebra; t^1, levator caudal tendons, and t^d, depressor caudal tendons surrounding the bone; *f*, fatty and fibrous tissue, containing the open mouths of nourishing vessels; *Sk*, skin, its fibroid subdermal layer, covered by a black line representing the derm and cuticular covering.

Fig. 41. A portion of the root end of the lung, with its vessels minutely injected: *B*, bronchus; *bb*, bronchia; *v*, plumonary vein, and *a*, artery; *l*, lobule.

Fig. 42. The right eyeball, mesially and vertically divided, and posteriorly other orbital contents. Parts about natural size and from the female manatee. *O.Rete*, orbital vessels; *m*, muscles; *on*, optic nerve; *ion*, infraorbital nerves; *ca*, ciliary artery; *sc*, sclerotic; *cp*, ciliary processes; *l*, lens.

Fig. 43. A transverse secton of the same eye behind the ciliary processes and iris.

Fig. 44. A ventral view of the female body eviscerated and dissected, chiefly to show the long tendinous diaphragm and kidney thereupon, the intercostal vascular plexuses, and the lumbo-caudal muscles. 1, 2, 3, 4, 5, 6, the cervical vertebrae; *cc*, costal cartilages of the sternal ribs; *ao*, arch of the aorta; *Ic*, *Rete*, intercostal rete; *Ii*, internal intercostal muscles; *D*, *D**, diaphragm of right side, *in situ*; *K*, kidney thereupon; *V*, renal vein; *u*, ureter; *Eo*, posterior termination of external oblique muscle; *Ql*, quadratus lumborum, internal to which portion of lumbar and caudal rete (*C. rete*) is seen; *Sc*, sacro-coccygeus entire on right side, and cut edge on left; *If.c*, infra-coccygeus; *L.cd*, partial view of lumbo-caudalis.

Fig. 45. The uterus, minus ovaries and fimbriae, seen deeply, or on its dorsal aspect. The parietes are cut open: *Ut*, uterus; *os*, os tincae; *lc*, left cornu; *R*, rectum; *Rete*, lumbar rete; *Px*, uterine plexus.

Fig. 46. A continuation of Fig. 45, displaying the pelvic parts from below the muscles, the retial vessels as they spread out, and part of that which runs under the tail. *L.Rete*, lumbar or hypogastric rete; *C.Rete*, caudal rete; *Pl*, pelvic bone; *Rab*, portions of rectus abdominis; *Isc*, ischio-coccygeus; *Pc*, termination of panniculus carnosus; *pn*, nerve piercing the tissues close to pelvis.

Fig. 47. The glans penis in its sheath, or male parts corresponding to those of the female shown in the succeeding figure: *s*, sheath slit open and dragged out; *g*, glans; *mu*, meatus urinarius.

Fig. 48. A reduced sketch of the vulva, the skin and superficial tissues having been removed: *cl*, clitoris; *mu & v*, vulva and meatus urinarius; *Spv*, sphincter vaginae.

Fig. 49. Sketch of the posterior abdominal region in the male, the parietes etc. being removed, and a deep dissection made on the left side. The penis has been cut away near its root; and what remains along with the bladder, is seen turned backward. *P*, penis, and *pa*, its artery; *B*, bladder; *vd*, vasa deferentia; *Te*, testicle; *H. Rete*, rete mirabile of loins and pelvo-generative region; *r*, tips of three hindmost ribs; *R*, rectum; *K*, kidney; *gl*, gland; *u*, ureter; *v*, vein; *a*, artery; *D*, diaphragm.

Fig. 50. A dissection of the left moiety of the pelvic region of the female, exhibiting the pelvic bone in place, its muscular attachments, the vast lumbar rete mirabile, and relation of the uterus, kidney, and bladder to each other. *D*, *D**, diaphragm; *K*, kidney; *v*, renal vein; *a*, artery; *u*, ureter; *B*, bladder; *V*, vulva; *A*, anus; *r*, rectum; *Pl*, pelvic bone; *c*, cornu; *f*, fimbria; *o*, ovary; *ha*, hypogastric artery; *H. Rete*, hypogastric or lumbar vascular plexus; *Pc*, *Pc*, panniculus, severed; *Rab*, *Rab**, rectus abdominis; *Eo*, external oblique; *L. cd*, lumbo-caudalis; *Sc*, sacro-coccygeus; *Is.c*, ischio-coccygeus; *Sp.a*, sphincter ani; *sp.v*, sphincter vaginae; *L.a*, levator ani; *Tp*, transversus perinaei; *E.c*, erector clitoridis.

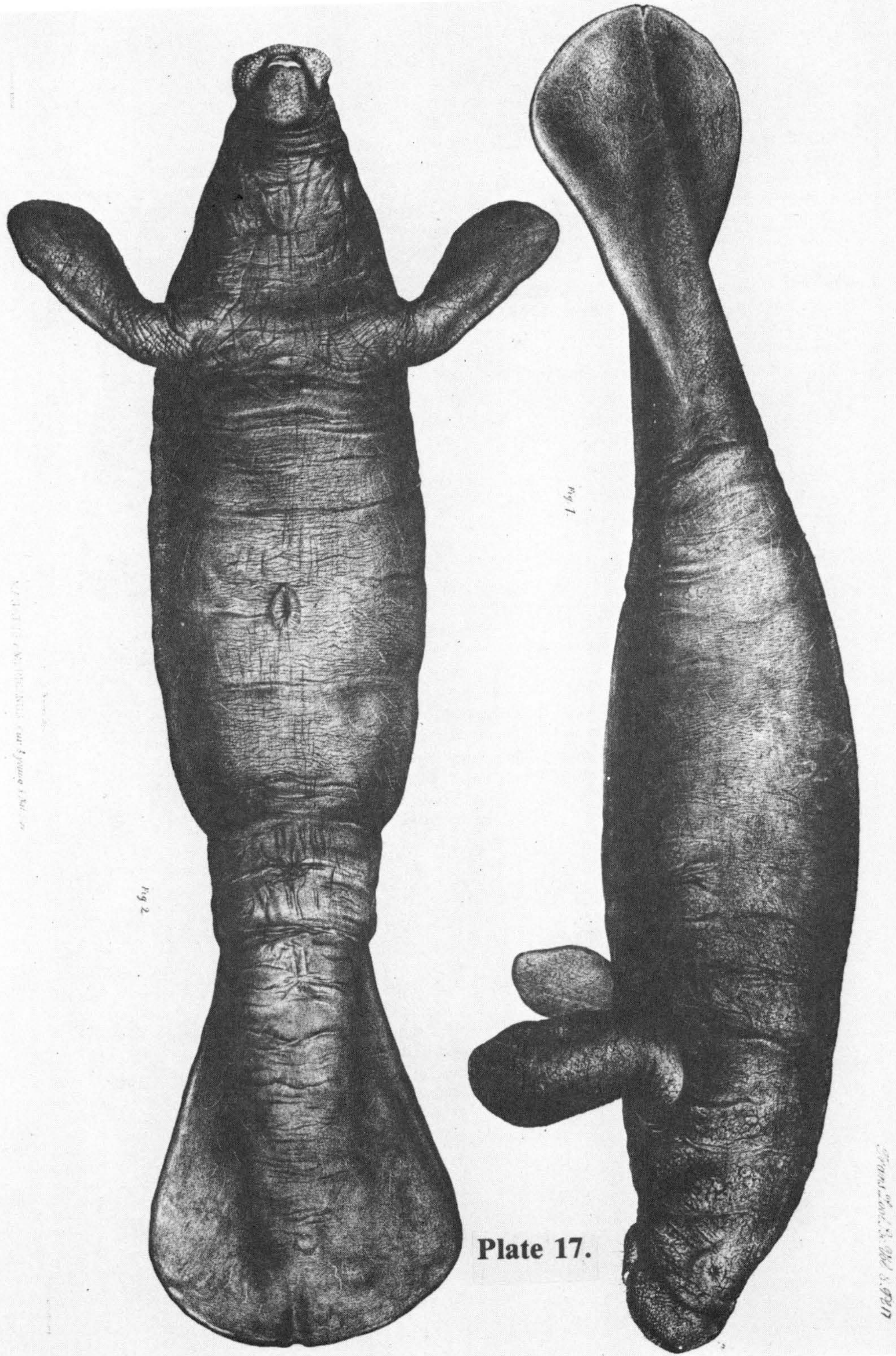


Plate 17.

Trans. Zool. Soc. Vol. 8 Pl. 18

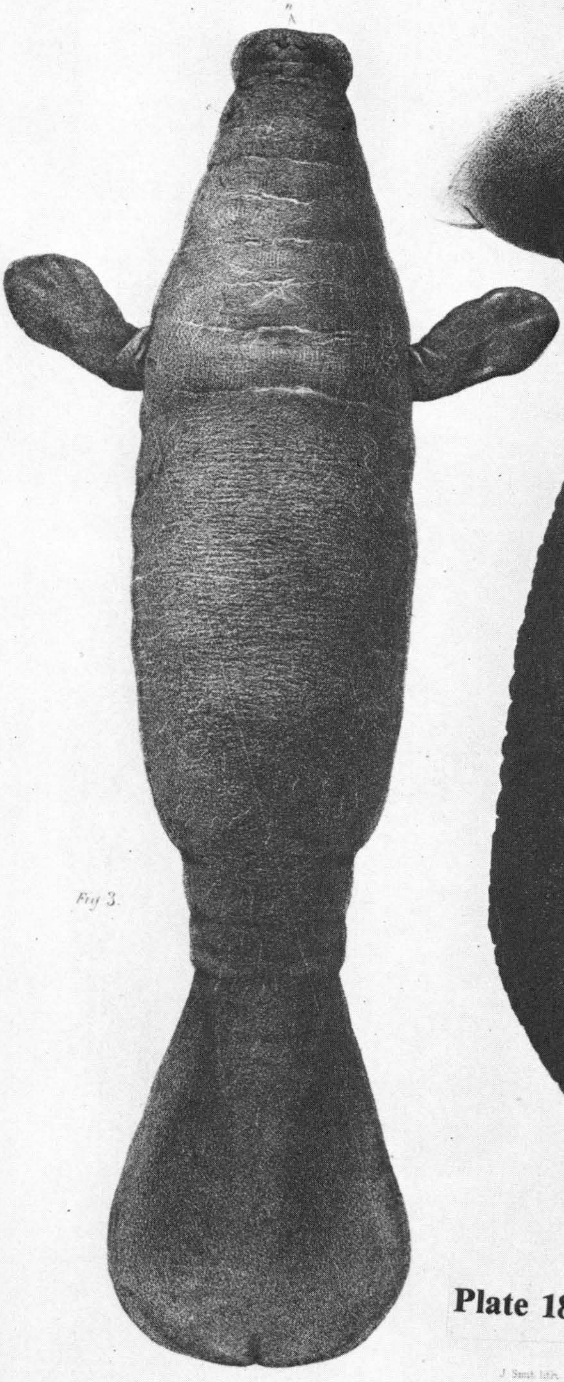


Fig. 3.

Fig. 4.

Plate 18.

J. Smit lith.

3 DORSAL VIEW [illegible] 4 LEFT PECTORAL LIMB, *Nat. Size* [illegible]

M & N Hanhart imp.

Trans. Zool. Soc. Vol. 8. Pl. 19

Fig. 5

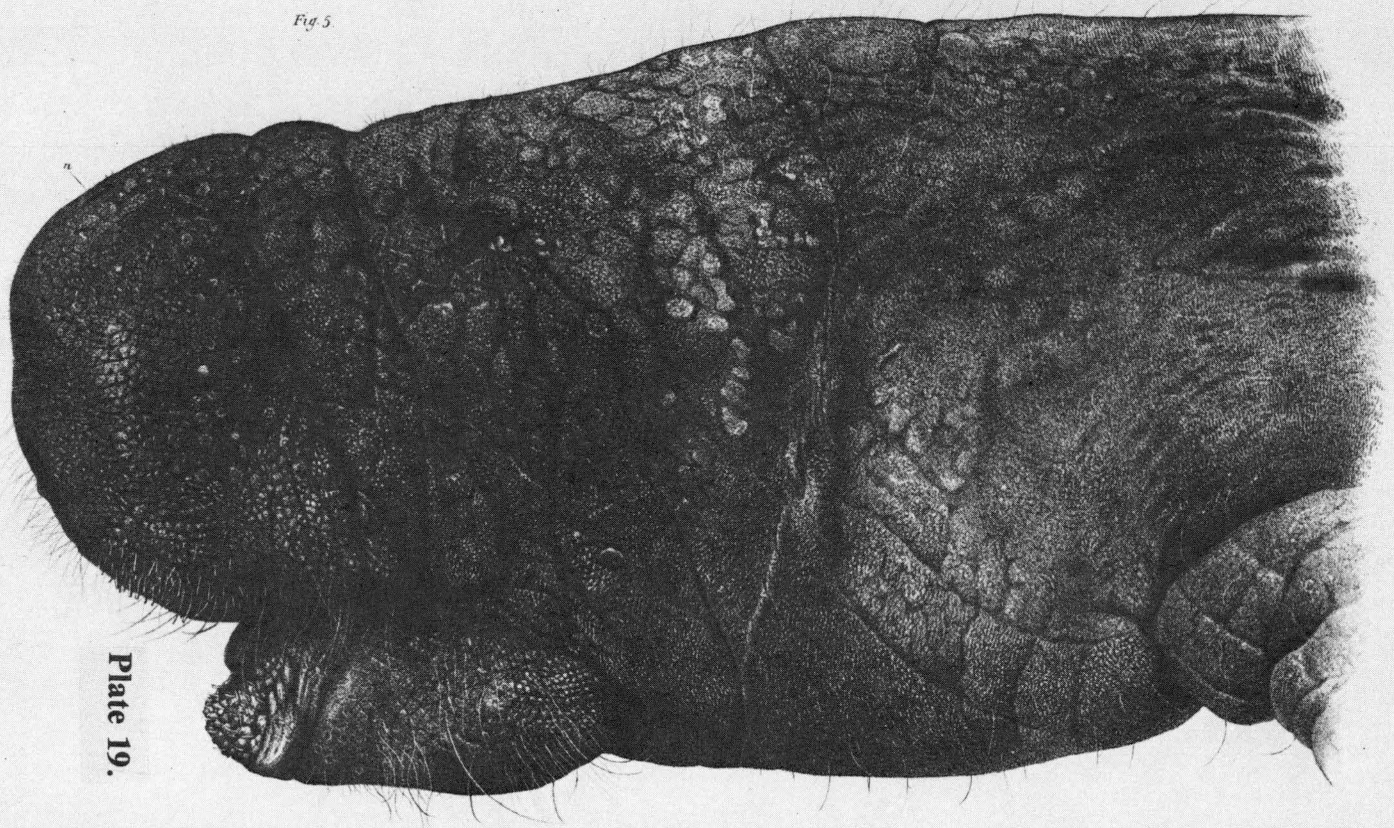


Plate 19.

J. Morse photo. J. Smit lith.

MANATUS AMERICANUS *Cur & young. Nat Size.*

M & N Hanhart imp.

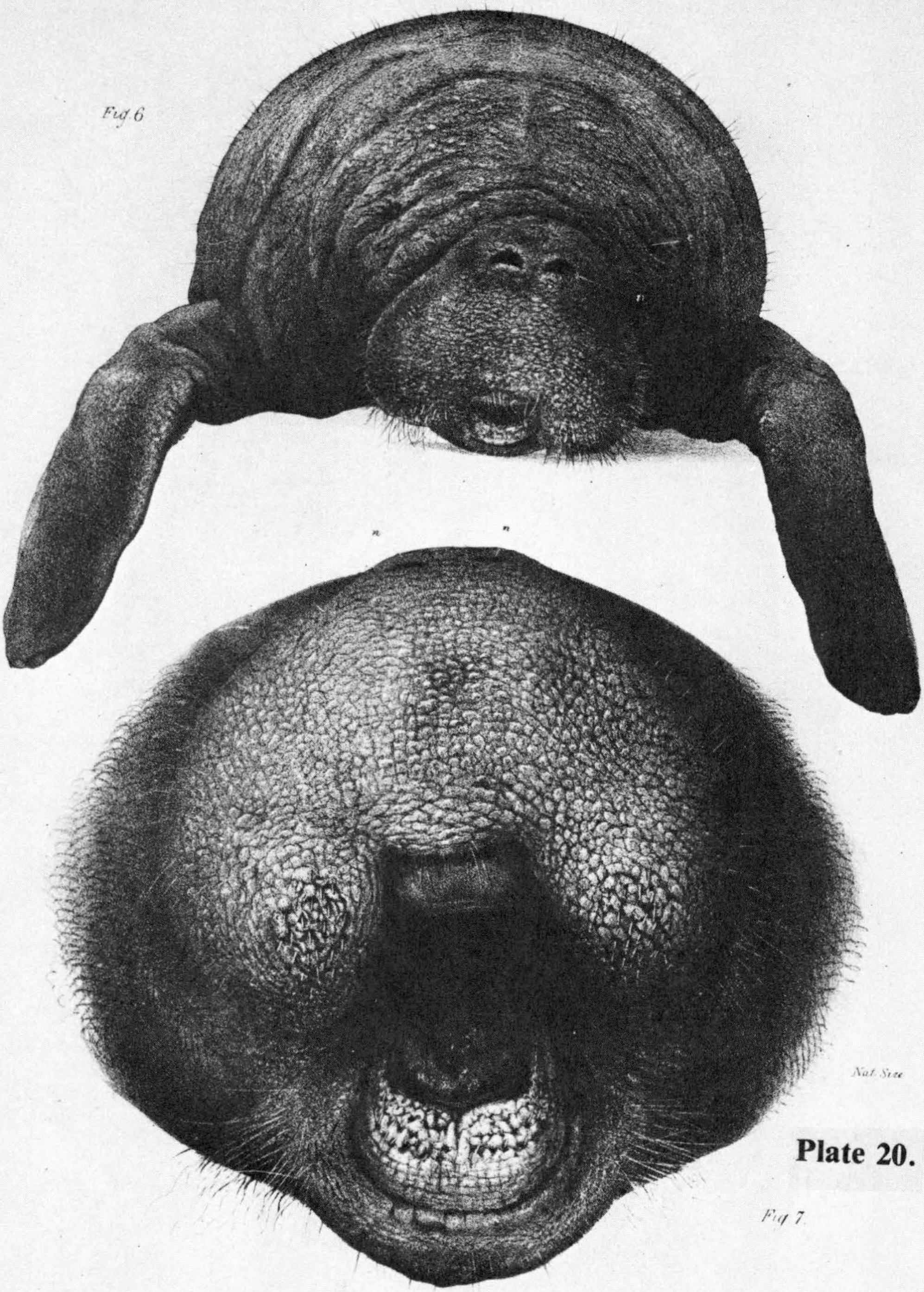
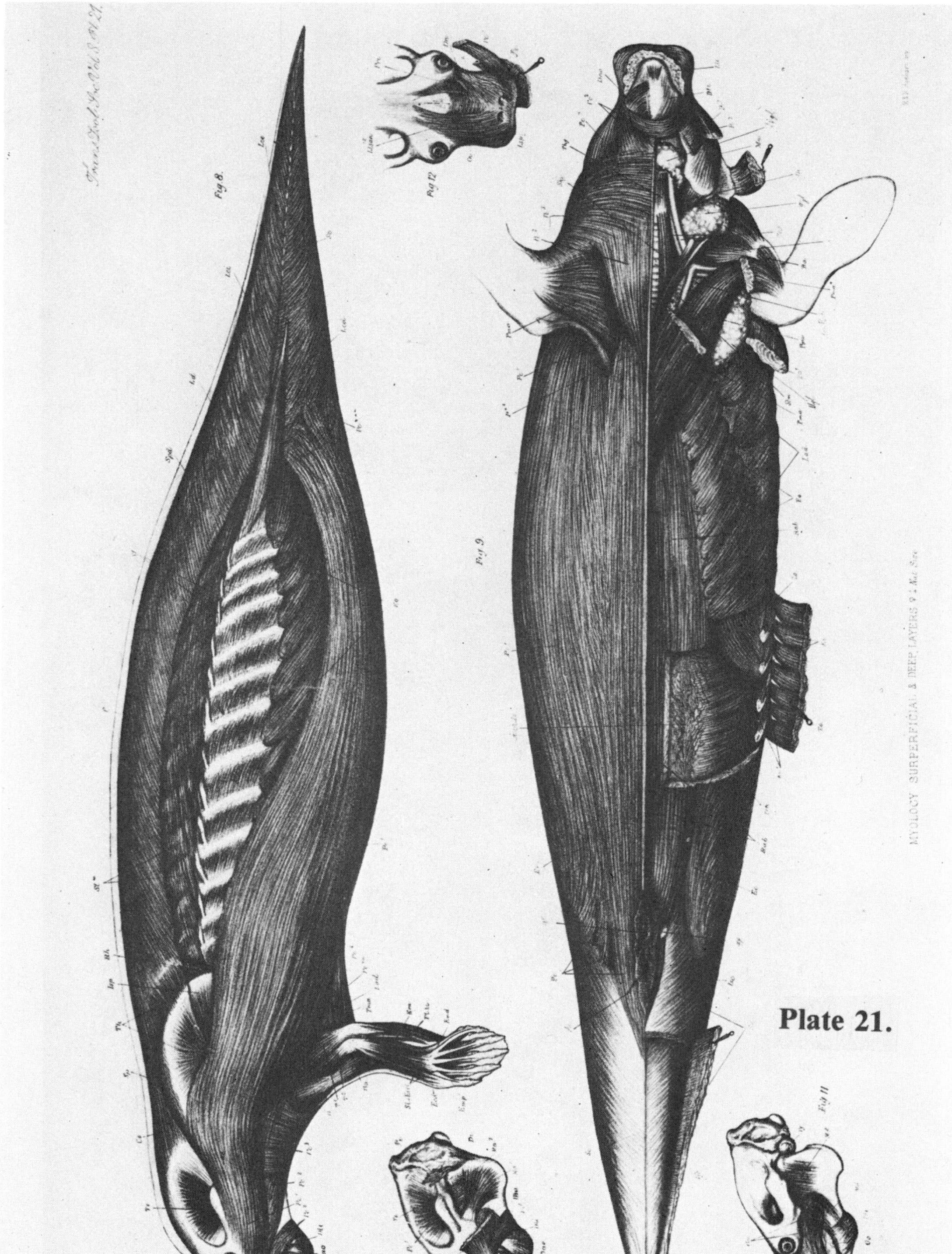


Plate 20.

J Murie photo, J Smit lith.

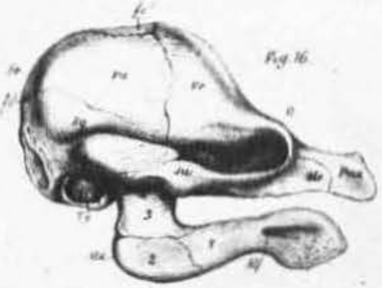
M&N Hanhart imp.

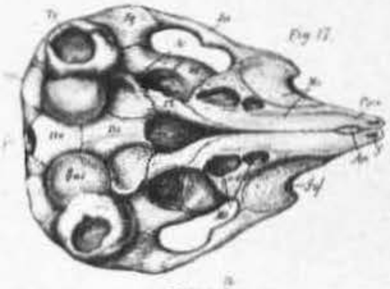
FORESHORTENED VIEWS MUZZLE, HEAD, &c.

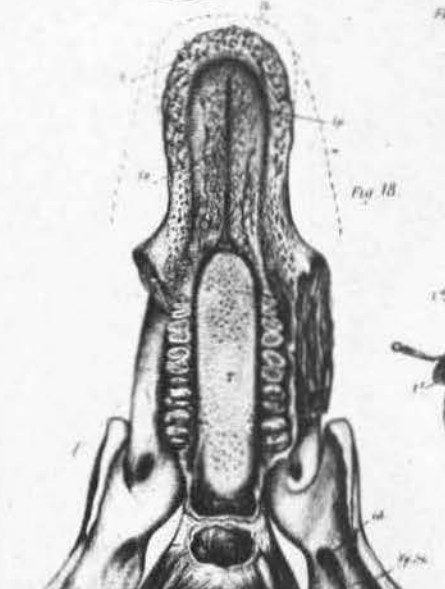


MYOLOGY SURPERFICIAL & DEEP LAYERS ⅔ Nat. Size

Plate 21.







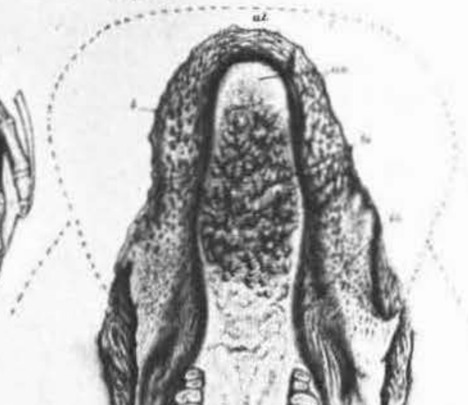


Plate 22.

J. Murie

LIMB MUSCLES MOUTH & FOETAL SKULL

Trans. Zool. Soc. Vol. 8. Pl. 23

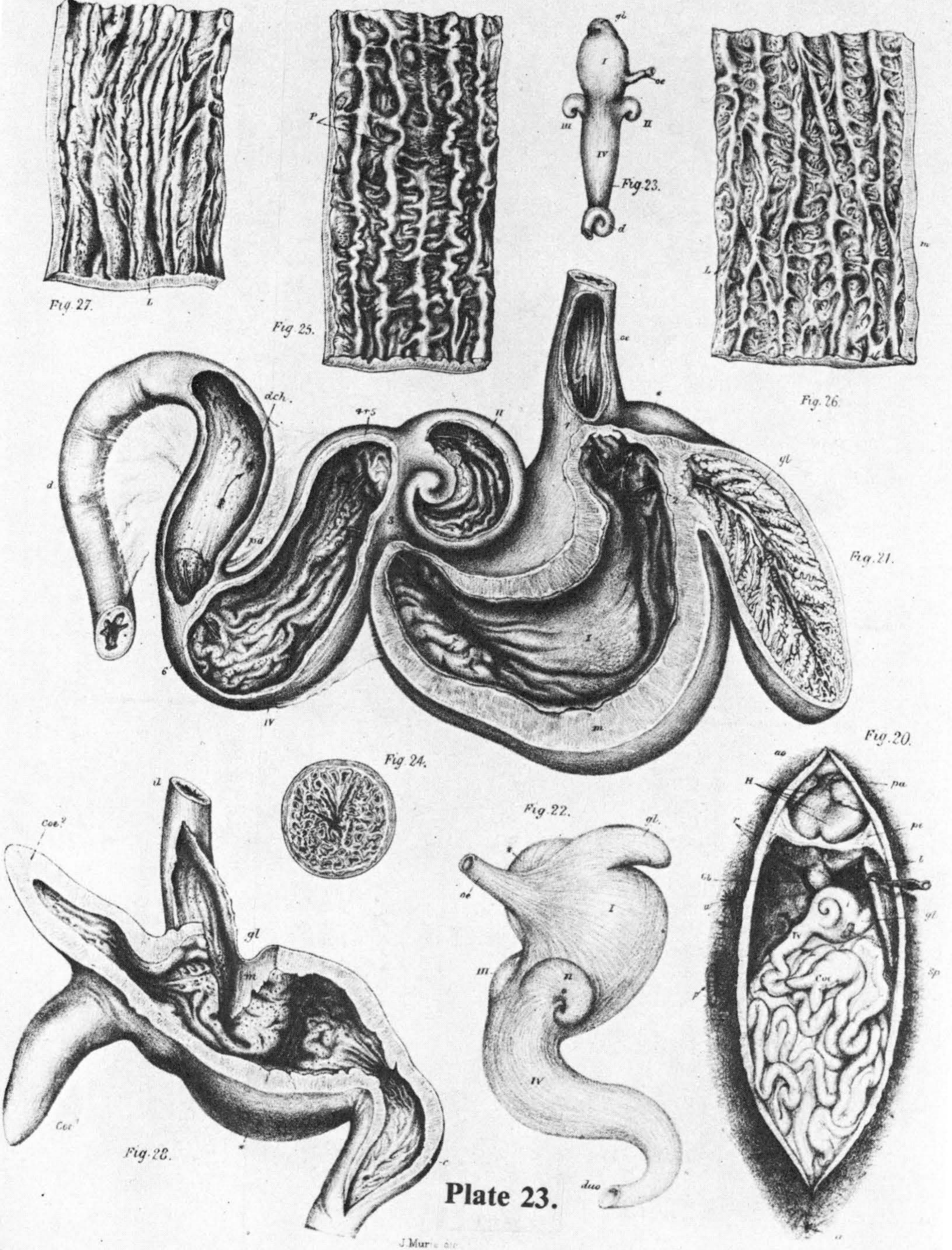


Plate 23.

C. Berjeau lith ad nat.

J. Murie dir.

ALIMENTARY CANAL.

M & N Hanhart imp.

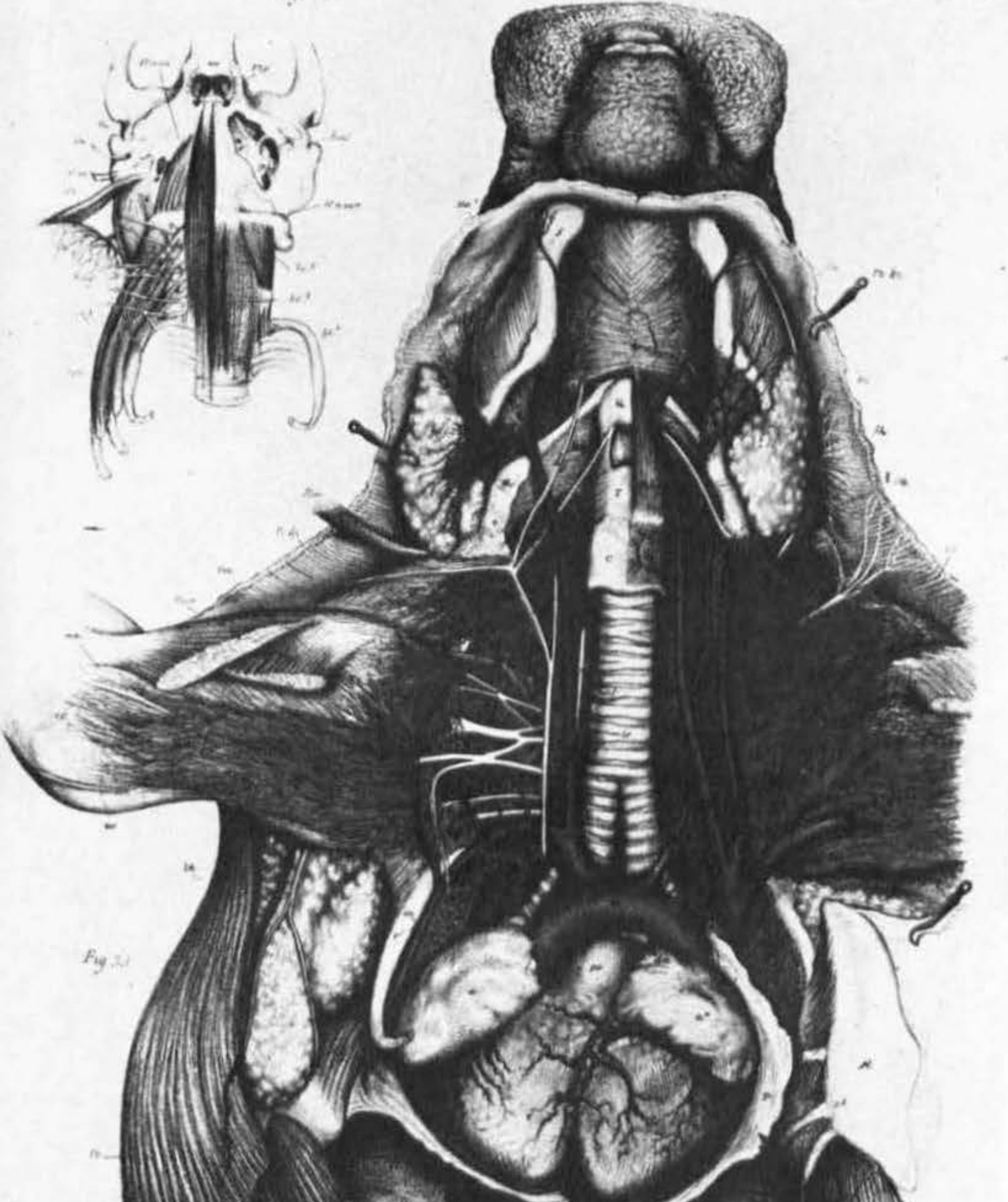


Plate 24.

HEART, PLEXUSES, NECK & AXILLARY REGIONS &c.

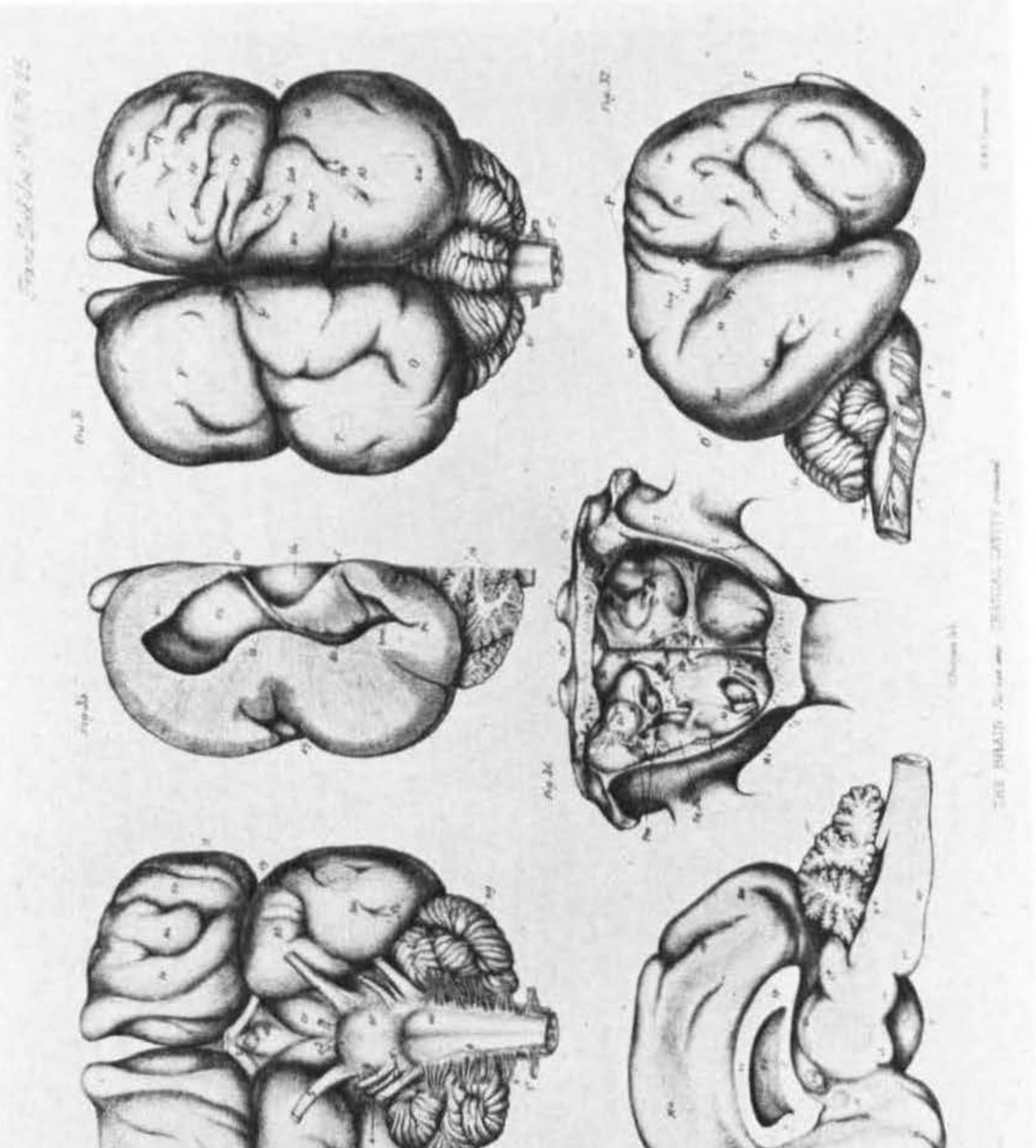


Plate 25.

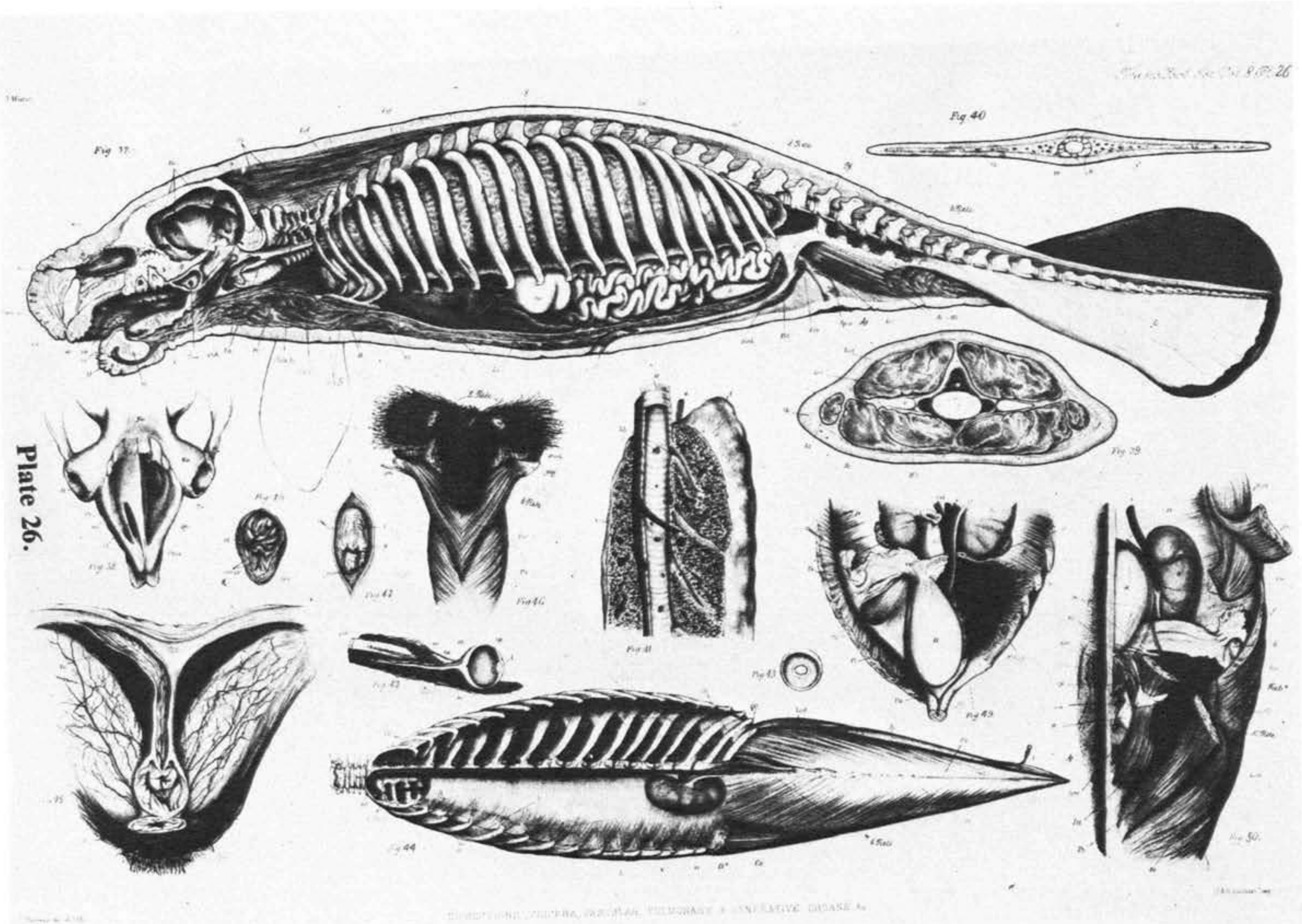


Fig 37
Fig 40
Fig 39
Fig 41
Fig 42
Fig 43
Fig 44
Fig 46
Fig 49
Fig 50
26

Plate 26.

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