

Gross and Microscopic Anatomy

Sentiel A. Rommel and Linda J. Lowenstine

Introduction

The California sea lion (*Zalophus californianus*) (Figure 1), Florida manatee (*Trichechus manatus latirostris*) (Figure 2), harbor seal (*Phoca vitulina*) (Figure 3), and bottlenose dolphin (*Tursiops truncatus*) (Figure 4) are used in this chapter to illustrate gross anatomy. These species were selected because of their availability and the knowledge base associated with them.* Gross anatomy of the sea otter (*Enhydra lutra*) is presented in Chapter 44 covering medical aspects of that species. Illustrations of the (A) external features, (B) superficial skeletal muscles, (C) relatively superficial viscera with skeletal landmarks, (D) circulation, body cavities, and some deeper viscera, and (E) skeleton are presented as five separate "layers" on the same page for each of the four species. These illustrations, based on dissections by one of the authors (S.A.R.), are of intact carcasses and thus help show the relative positions of organs in the live animals. The major lymph nodes are illustrated, but to simplify the illustrations, most are not labeled. The drawings represent size, shape, and position of organs in a healthy animal; the skeleton is accurately placed within the soft tissues and body outline. The scale of the drawings is the same for each species so that vertical lines can be used to compare features on all five; a photocopy onto a transparency would allow the reader to compare layers directly. Names of structures are labeled with three-letter abbreviations.** A brief figure legend helps the reader apply basic veterinary anatomical knowledge to the marine mammals illustrated. The style found in *Miller's Anatomy of the Dog* (Evans, 1993) is followed as much as possible. Most technical terms follow the *Illustrated Veterinary Anatomical Nomenclature* by Schaller (1992).

Recent comparative work on anatomy of marine mammals is found in Pabst et al. (1999), Rommel and Reynolds (2000; in press), and Reynolds et al. (in press). Older but valuable anatomical works include Murie (1872; 1874), Schulte (1916), Howell (1930), Fraser (1952), Slijper (1962), Green (1972), St. Pierre (1974), Bonde et al. (1983), King (1983), and Herbert (1987).

* A set of illustrations of a mysticete would be valuable, but as space is limited and they are less likely to be under veterinary care, we chose an odontocete; the skeletal anatomy of the right whale (*Eubalaena glacialis*) is compared with that of other marine mammals in Rommel and Reynolds (in press).

** Abbreviations in the text use capital letters to refer to the label on the structure. The first letter refers to the layer (A being external features at the top and E the skeleton) followed by a hyphen and then the abbreviation of the structure. For example, D-HAR refers to the heart on layer D.

FIGURE 1 Left lateral illustrations of a healthy California sea lion (*Zalophus californianus*). Based on dissections by S.A.R., with details and nomenclatures from the literature: Murie, 1874; Howell, 1930; English, 1976a. Thanks to Rebecca Duerr for many helpful suggestions. (© Copyright S.A. Rommel. Used with permission of the illustrator.)

(Layer A) External features. The following abbreviations are used as labels: ANG = angle of mouth; ANS = anus; AXL = axilla, flipperpit; CAL = calcaneus, palpable bony feature; EAR = external auditory opening, ear; EYE = eye; INS = cranial insertion of the extremity; flipper, fin, and/or fluke; NAR = naris; OLC = olecranon, palpable bony feature; PAT = patella, palpable bony feature; PEC = pectoral limb, fore flipper; PEL = pelvic limb, hind flipper; PIN = pinna, external ear (as opposed to external ear opening); SCA = dorsal border of the scapula, palpable (sometimes grossly visible) bony feature; TAI = tail; UMB = umbilicus; UNG = unguis, finger and toe nails; U/G = urogenital opening; VIB = vibrissae.

(Layer B) The superficial skeletal muscles. The layer of skeletal muscles just deep to the blubber and panniculus muscles. The following abbreviations are used as labels: ANS = anus; BIF = femoral biceps; BRC = brachiocephalic; DEL = deltoid; DIG = digastric; EAM = external auditory meatus; EXT = external oblique; FAS = fascia; FS,B&P = fur, skin, blubber, and panniculus muscle (where present) cut along midline; GLU = gluteals; LAT = latissimus dorsi; MAM = mammary gland; MAS = masseter; PECp = deep (profound) pectoral; PECs = superficial pectoral; REC = rectus abdominis; SAL = salivary gland; SER = serratus; nipple; STC = sternocephalic; TFL = tensor fascia lata; TMP = temporalis; TRAc = trapezius, cervical portion; TRAt = trapezius, thoracic portion; TRI = triceps brachii; UMB = umbilicus.

(Layer C) The superficial internal structures with "anatomical landmarks." This perspective focuses on relatively superficial internal structures; the other important bony or soft "landmarks" are not necessarily visible from a left lateral view, but they are useful for orientation. The relative size of the lung represents partial inflation—full inflation would extend the lung margins to the distal tips of ribs. The female is illustrated because there is greater variation in uterine anatomy than in testicular and penile anatomy; note, however, that only the sea lion (of the illustrated species) is scrotal (actually the sea lion testes migrate into the scrotum in response to environmental temperature). The following abbreviations are used as labels (structures in midline are in type, those off-midline are in italics): ANS = anus; AXL *ln* = axillary lymph nodes; BLD = urinary bladder; FS&B = fur, skin, blubber (cut at midline); HAR = heart; HYO = hyoid apparatus; INT = intestines; ILC = iliac crest; KID = left kidney; LIV = liver; LUN = lung (note that the lung extends under the scapula); MAN = manubrium of the sternum; OVR = left ovary; PAN = pancreas; PAT = patella; PSC *ln* = prescapular lymph nodes; RAD = radius; REC = rectum; SAL = salivary glands; SCA = scapula; SIG *ln* = superficial inguinal lymph node; SPL = spleen; STM = stomach; TIB = tibia; TMP = temporalis; TRA = trachea; TYR = thyroid gland; TYM = thymus gland; ULN = ulna; VAG = vagina.

(Layer D) A view slightly to the left of the midsagittal plane illustrating the circulation, body cavities, and selected organs. Note that the diaphragm separates the heart and lungs from the liver and other abdominal organs. The following abbreviations are used as labels (structures on the midline are in normal type, those off-midline are in italics): AAR = aortic arch; ADR = adrenal gland; ANS = anus; AOR = aorta; ARH = aortic hiatus; AXL = axillary artery; BIF = tracheobronchial bifurcation; BLD = urinary bladder; BRC = bronchus; BRN = brain; CAF = caval foramen; CAR = carotid artery; caMESa = caudal mesenteric artery; CEL = celiac artery; CRZ = crus of the diaphragm; crMESa = cranial mesenteric artery; CVC = vena cava, between diaphragm and heart; DIA = diaphragm, cut at midline, extends from crura dorsally to sternum ventrally; ESO = esophagus (to the left of the midline cranially, on the midline caudally); ESH = esophageal hiatus; FS&B = fur, skin, blubber (cut at midline); HAR = heart; HYO = hyoid bones; KID = right kidney; LIV = liver, cut at midline; LUN = right lung between heart and diaphragm; MAN = manubrium of sternum; OVR = left ovary; PAN = pancreas; PUB = pubic symphysis; PULa = pulmonary artery, cut at hilus of lung; PULv = pulmonary vein, cut at hilus of lung; REC = rectum; REN = renal artery; SPL = spleen; STM = stomach; STR = sternum, sternabrae; TNG = tongue; TRA = trachea; TYM = thymus gland; TYR = thyroid gland; UMB = umbilicus; UTR = uterus; VAG = vagina; VRT = vertebral artery; XIP = xyphoid process of the sternum.

(Layer E) The skeleton. Regions of the vertebral column (cervical, thoracic, lumbar, sacral, and caudal) are abbreviated (in lower case) as cer, tho, lum, sac, and cau, respectively, and are used as modifiers after an abbreviation in caps and a comma. If a specific vertebra is labeled, it will be represented by a capitalized first letter (for caudal, Ca will be used) and the vertebral number, i.e., first cervical = C1. The following abbreviations are used as labels: CAL = calcaneus; CAN = canine tooth (not present in cetaceans or manatees); DIG = digits; FEM = femur; FIB = fibula; HUM = humerus; HYO = hyoid bones; ILC = iliac crest of the pelvis; LRB = last, or caudalmost, rib; MAN = mandible; MNB = manubrium, the cranialmost bony part of the sternum; NSP = neural spine (spinous process), e.g., thoracic neural spines = NSP, tho; OLC = olecranon; ORB = orbit; PAT = patella; RAD = radius; SCA = scapula; STN = sternum, composed of individual sternabrae; SRB = sternal ribs, costal cartilages; TIB = tibia; TMF = temporal fossa; TPR = transverse process, e.g., TPR, C1 = transverse process of the first cervical vertebra; ULN = ulna; VBR = vertebral ribs; ZYG = zygomatic arch.

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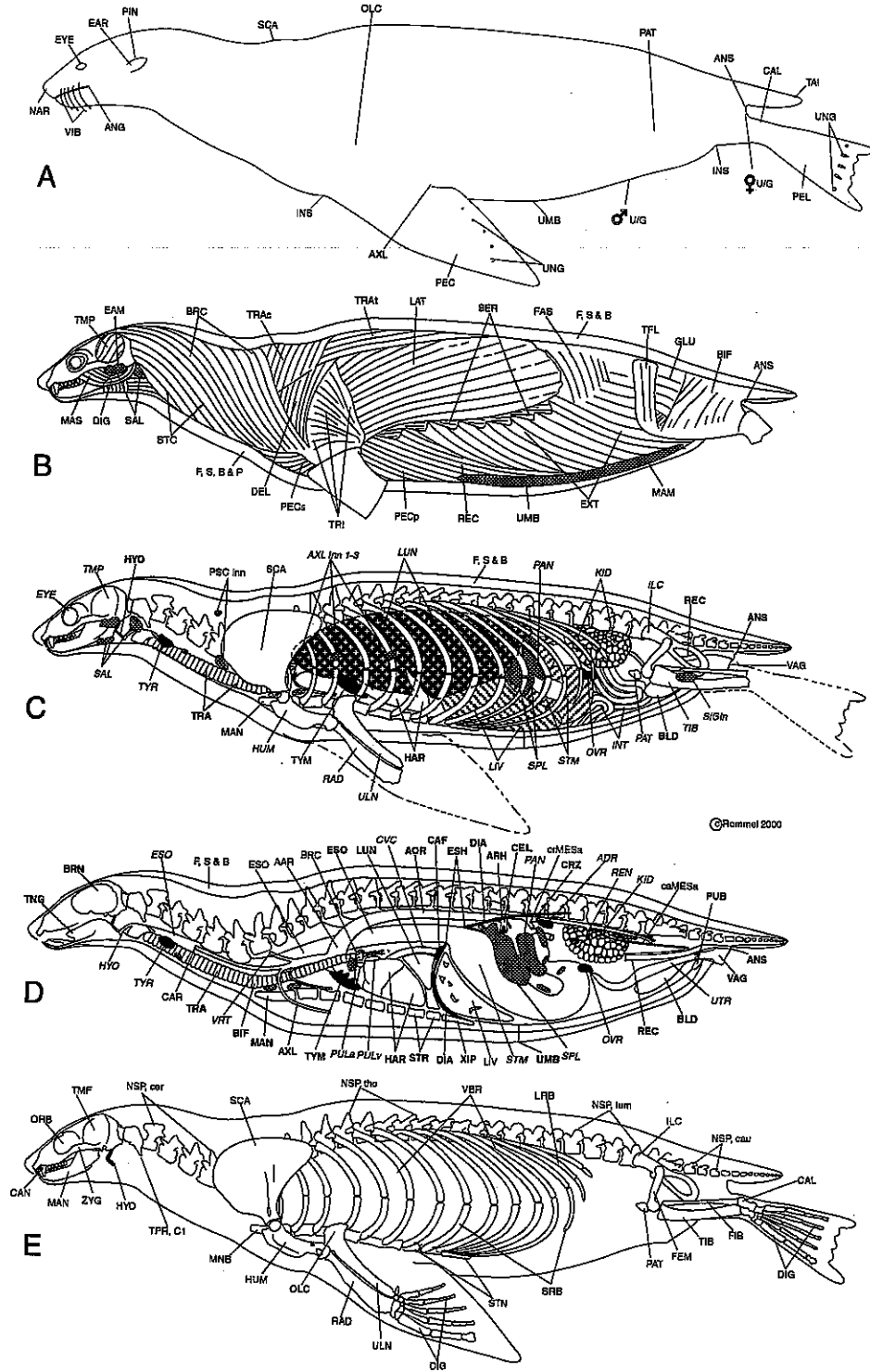


FIGURE 2 Left lateral illustrations of a healthy Florida manatee (*Trichechus manatus latirostris*). Based on dissections by S.A.R., with details and nomenclatures from the literature: Murie, 1872; Domning, 1977; 1978; Rommel and Reynolds, 2000. Thanks to D. Domning for suggestions on the muscle illustration. (© S. A. Rommel. Used with permission of the illustrator.)

(Layer A) External features. The following abbreviations are used as labels: ANG = angle of mouth; ANS = anus; AXL = axilla; EAR = external auditory opening, ear; EYE = eye; FLK = fluke entire caudal extremity in manatees; flukes = entire caudal extremity in dugongs; INS = cranial insertion of the extremity, flipper and/or fluke; NAR = naris; OLC = olecranon, palpable bony feature; PEC = pectoral limb, flipper; PED = peduncle, base of tail, between anus and fluke; SCA = dorsal border of the scapula, palpable bony feature in emaciated individuals; UMB = umbilicus; UNG = unguis, fingernails; U/G = urogenital opening; VIB = vibrissae.

(Layer B) The superficial skeletal muscles. The layer of skeletal muscles just deep to the blubber and panniculus muscles. The following abbreviations are used as labels: ANS = anus; CEP = cephalohumeralis; DEL = deltoid; EXT = external oblique; FAS = fascia; S,B&P = skin, blubber, and panniculus muscle (where present) cut along midline; IIN = internal intercostals; ILC = iliocostalis; ITT = intertransversarius; LAT = latissimus dorsi; LEN = levator nasolabialis; LON = longissimus; MAM = mammary gland, in axillary region, thus partly hidden under the flipper; MEN = mentalis; MND = mandibularis; PAN = panniculus, illustrated using dotted lines, is a robust and dominant superficial muscle; a layer of blubber is found on both the medial and lateral aspects of this muscle; REC = rectus abdominis; SLT = mammary slit, nipple; SPC = sphincter colli; SVL = sarcoccygeus ventralis lateralis; TER = teres major; TMP = temporalis; TRA = trapezius; TRI = triceps brachii; UMB = umbilicus; XIN = external intercostals.

(Layer C) The superficial internal structures with "anatomical landmarks." This perspective focuses on relatively superficial internal structures. Skeletal elements are included for reference, but not all are labeled. The left kidney (not visible from this vantage in the manatee) is illustrated. The relative size of the lung represents partial inflation. The following abbreviations are used as labels: ANS = anus; BLD = urinary bladder (dotted, not really visible in this view); BVB = brachial vascular bundle; CHV = chevrons, chevron bones; EYE = the eye (note how small it is); HAR = heart; HUM = humerus; INT = intestines; note the large diameter of the large intestines; KID = left kidney, not visible from this vantage in the manatee; LIV = liver; LUN = lung (note lung extends under scapula, and over heart); OVR = left ovary; PEL = pelvic vestige; RAD = radius; SAL = salivary gland; S&B = skin and blubber; SCA = scapula; SIG ln = superficial inguinal lymph node; S,B&P = skin, blubber, and panniculus muscle, cut at midline; STM = stomach; TMJ = temporomandibular joint; TYM = thymus gland; ULN = ulna; UMB = umbilical scar; UTR = uterine horn; VAG = vagina.

(Layer D) A view slightly to the left of the midsagittal plane illustrates the circulation, body cavities, and selected organs. Note that the diaphragm of the manatee is unique and that the distribution of organs and the separation of thoracic structures from abdominal structures requires special consideration. The following abbreviations are used as labels (structures on the midline are in normal type, those off-midline are in italics): AAR = aortic arch; ADR = left adrenal gland; ANS = anus; AOR = aorta; AXL = axillary artery; BLD = urinary bladder; BRN = brain; BVB = brachial vascular bundle (cut); CAF = caval foramen; CAR = carotid artery; CDG = cardiac gland; CEL = celiac artery; CER = cervix; CHV = chevron bones; CRG = cardiac gland; CVB = caudal vascular bundle; DUO = duodenum; ESO = esophagus (to the left of the midline cranially, on the midline caudally); EXI = external iliac artery; HAR = heart; KID = right kidney; LIV = liver, cut at midline; OVR = right ovary; PAN = pancreas; PULa = pulmonary artery, cut at hilus of lung; PULv = pulmonary vein, cut at hilus of lung; REC = rectum; REN = renal artery; S&B = skin and blubber; SKM = skeletal muscle; SM&B = skin, muscle, and blubber (cut at midline); SPL = spleen; STM = stomach; STR = sternum; TNG = tongue; TRA = trachea; TRS = transverse septum; TYM = thymus gland; TYR = thyroid gland; UMB = umbilical scar; UTR = uterus; VAG = vagina.

(Layer E) The skeleton. Regions of the vertebral column (cervical, thoracic, lumbar, sacral, and caudal), are abbreviated (in lowercase) as cer, tho, lum, sac, and cau, respectively, and are used as modifiers after an abbreviation in caps and a comma. If a specific vertebra is labeled, it will be represented by a capitalized first letter (for caudal, Ca will be used) and the vertebral number, i.e., first cervical = C1. The following abbreviations are used as labels: CHV = chevrons, chevron bones; DIG = digits, columns of finger bones; HUM = humerus; HYO = hyoid apparatus; HYP = hypapophysis, ventral midline vertebral process; LRB = last, or caudalmost, rib; LVR = last, or caudalmost, vertebra; MAN = mandible; NSP = neural spine (spinous process), e.g., thoracic neural spines = NSP, tho; OLC = olecranon; ORB = orbit; PEL = pelvic bone; RAD = radius; SCA = scapula; STN = sternum, if sternabrae are commonly fused; SBR = sternal ribs, costal cartilages; TMF = temporal fossa; TPR = transverse process, C1; ULN = ulna; VBR = vertebral ribs; XNR = external (bony) nares; XIP = xyphoid process, cartilaginous caudal extension of the sternum; ZYG = zygomatic process of the squamosal.

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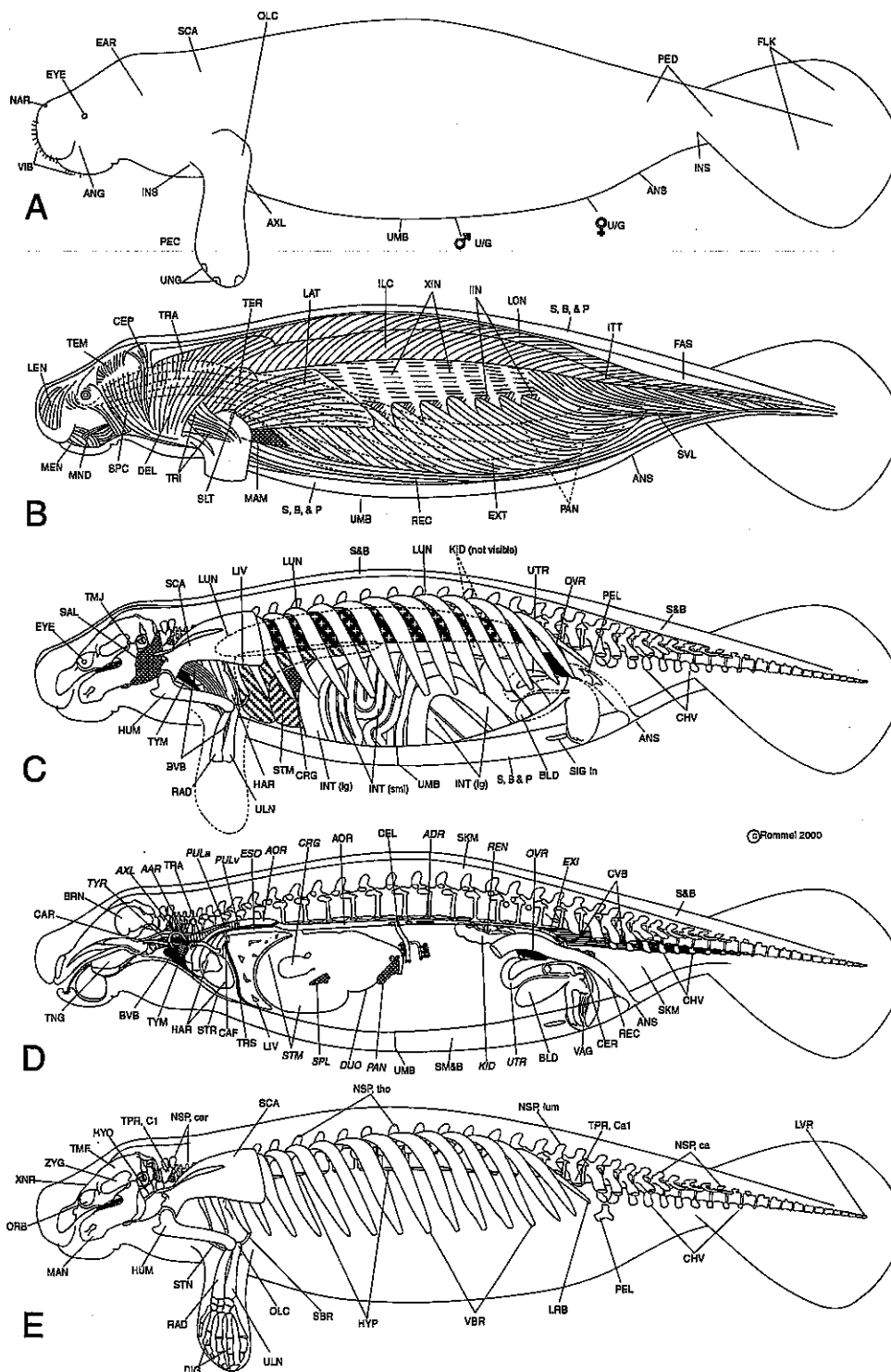


FIGURE 3 Left lateral illustrations of a healthy harbor seal (*Phoca vitulina*). Based on dissections by S.A.R., with details and nomenclatures from the literature: Howell, 1930; Huber, 1934; Bryden, 1971; Tedman and Bryden, 1981; Rommel et al., 1998; Pabst et al., 1999. (© Copyright S. A. Rommel. Used with permission of the illustrator.)

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in, 1971; Tedman and
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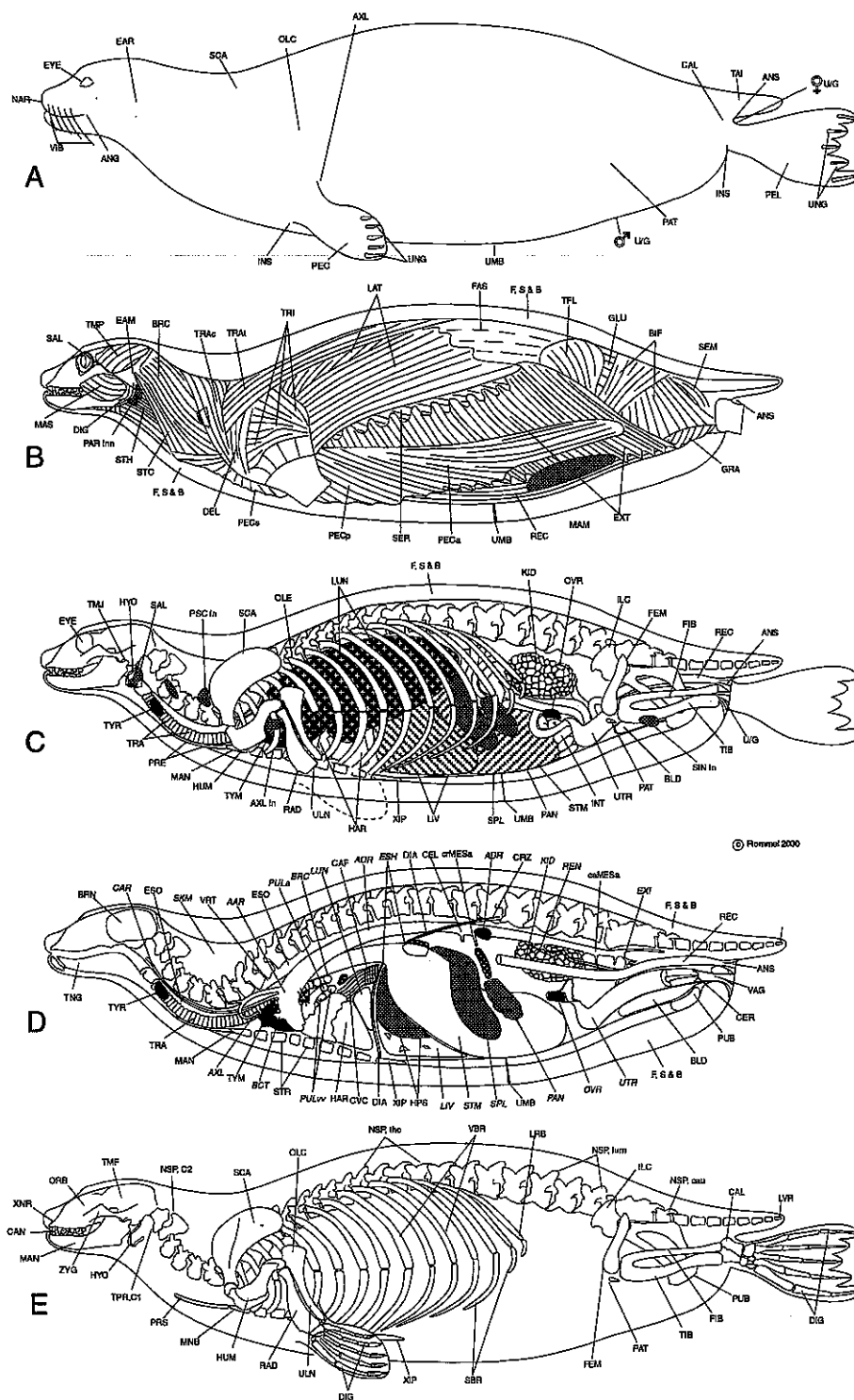


FIGURE 4 Left lateral illustrations of a healthy bottlenose dolphin (*Tursiops truncatus*). Based on dissections by S.A.R. with details and nomenclatures from the literature: Howell, 1930; Huber, 1934; Fraser, 1952; Slijper, 1962; Mead, 1975; Strickler, 1978; Klima et al., 1980; Pabst, 1990; Rommel et al., 1998; Pabst et al., 1999. Thanks to T. Yamada for suggestions on the muscle illustration. (© S. A. Rommel. Used with permission of the illustrator.)

(Layer A) External features. The following abbreviations are used as labels: ANG = angle of mouth; ANS = anus; AXL = axilla; BLO = blowhole, external naris in dolphin; EAR = external auditory opening, ear; EYE = eye; FIN = dorsal fin; FLK = flukes (entire caudal extremity in cetaceans); INS = cranial insertion of the extremity; flipper, fin, and/or fluke; NOC = fluke notch in dugongs and in most cetaceans; PEC = pectoral limb, flipper; PED = peduncle, base of tail, between anus and flukes; MEL = melon; SCA = dorsal border of the scapula, palpable bony feature in emaciated dolphins; SNO = snout, cranial tip of upper jaw; UMB = umbilicus; U/G = urogenital opening.

(Layer B) The superficial skeletal muscles. The layer of skeletal muscles just deep to the blubber and panniculus muscles. Note that the large muscles ventral to the dorsal fin are surrounded by a tough connective tissue sheath (Pabst, 1990). The following abbreviations are used as labels: ANS = anus; BLO = blowhole; DEL = deltoid; DIG = digastric; EAM = external auditory meatus; EPX = epaxial muscles, upstroke muscles; EXT = external oblique; HYP = hypaxialis; HPX = hypaxial muscles, downstroke muscles; ILI = iliocostalis; INT = internal oblique; ISC = oschium; ITTd = intertransversarius caudae dorsalis; ITTv = intertransversarius caudae ventralis; LAT = latissimus dorsi; LEV = levator ani; LON = longissimus; MAM = mammary gland; MAS = masseter; MUL = multifidus; PECp = deep (profund) pectoral; PSC In = prescapular lymph node; REC = rectus abdominis; RHO = rhomboid; ROS = rostral muscles; S,B,&P = skin, blubber, and panniculus muscle (where present) cut along midline; SER = serratus; SLT = mammary slit, nipple; SPL = splenius; STE = sternohyoid; STM = sternomastoid; TER = teres major; TMP = temporalis; TRAd = trapezius dorsalis; TRAc = trapezius cranialis; TRI = triceps brachii; UMB = umbilicus.

(Layer C) The superficial internal structures with "anatomical landmarks." The relative size of the lung represents partial inflation—full inflation would extend margins to distal tips of ribs. The following abbreviations are used as labels: ANS = anus; BLD = urinary bladder; BLO = blowhole; EYE = eye; HAR = heart; HPX = hypaxial muscles; HUM = humerus; HYO = hyoid apparatus; INT = intestines; KID = left kidney; LIV = liver; LUN = lung (note that it extends beneath the scapula); MEL = melon; OVR = left ovary; PEL = pelvic vestige; PSC In = prescapular lymph node; PUL In = pulmonary lymph node, unique to cetaceans; RAD = radius; REC = rectum; ROS = rostral muscles, to manipulate the melon; SAC = lateral diverticulae, air sacs in dolphin; S&B = skin and blubber; SCA = scapula; SKM = skeletal muscle; SPL = spleen; STM = stomachs; TMJ = temporomandibular joint; TRA = trachea; TYR = thyroid gland; ULN = ulna; UMB = umbilical scar; UOP = uterovarian plexus; URE = ureter; UTR = uterine horn; VAG = vagina.

(Layer D) A view slightly to the left of the midsagittal plane illustrates the circulation, body cavities, and selected organs. Note that the diaphragm separates the heart and lungs from the liver and other abdominal organs. The following abbreviations are used as labels (structures on the midline are in normal type, those off-midline are in italics): AAR = aortic arch; ADR = left adrenal gland; ANS = anus; AOR = aorta; AXL = axillary artery; BLD = urinary bladder; BLO = blowhole; BRC = bronchus; BRN = brain; CAR = carotid artery; CEL = celiac artery; CER = cervix; CRZ = left crus of the diaphragm; CVB = caudal vascular bundle; DIA = diaphragm, cut at midline, extends from crura dorsally to sternum ventrally; ESO = esophagus (to the left of the midline cranially, on the midline caudally); ESH = esophageal hiatus; EXI = external iliac artery; FINaa = arteries arrayed along the midline of the dorsal fin; FLKaa = arterial plexus on dorsal and ventral aspects of each fluke; HAR = heart; KID = right kidney; LAR = larynx or goosebeak; LIV = liver, cut at midline; MEL = melon; OVR = right ovary; PAN = pancreas (hidden behind first stomach); PMX = premaxillary sac; PULa = pulmonary artery, cut at hilus of lung; PULv = pulmonary vein, cut at hilus of lung; REC = rectum; REN = renal artery; S&B = skin and blubber, panniculus where appropriate cut at midline; SKM = skeletal muscle; SPL = spleen; STM1 = forestomach; STM2 = main stomach; STM3 = pyloric stomach; STR = sternum, sternabrae; TNG = tongue; TRA = trachea; TYM = thymus gland; TYR = thyroid gland; UMB = umbilicus; UOP = right uterovarian vascular plexus in dolphin; URE = right ureter; UTR = uterus; VAG = vagina.

(Layer E) The skeleton. Regions of the vertebral column (cervical, thoracic, lumbar, sacral, and caudal), are abbreviated (in lower case) as cer, tho, lum, sac, and cau, respectively, and are used as modifiers after an abbreviation in caps and a comma. If a specific vertebra is labeled, it will be represented by a capitalized first letter (for caudal, Ca will be used) and the vertebral number, i.e., first cervical = C1. The following abbreviations are used as labels: CHV = chevrons, chevron bones; DIG = digits; HUM = humerus; HYO = hyoid apparatus; LRB = last, or caudalmost, rib; LVR = last, or caudalmost, vertebra; MAN = mandible; NSP = neural spine; e.g., thoracic neural spines = NSP, tho; OLC = olecranon; ORB = orbit; PEL = pelvic vestige; RAD = radius; SCA = scapula; STR = sternum; SBR = sternal ribs, costal ribs; TMF = temporal fossa; ULN = ulna; VBR = vertebral ribs; XNR = external (bony) nares, nasal aperture of the skull; ZYG = zygomatic arch.

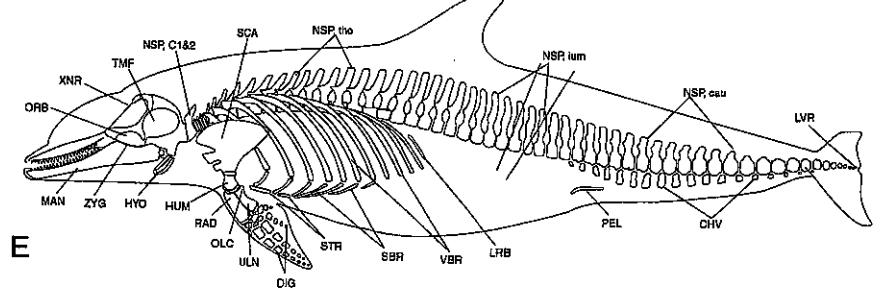
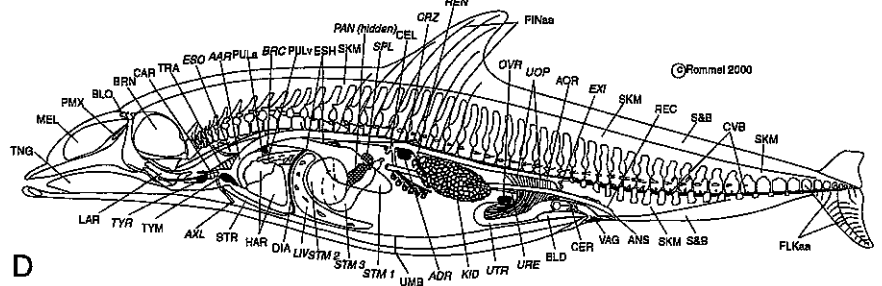
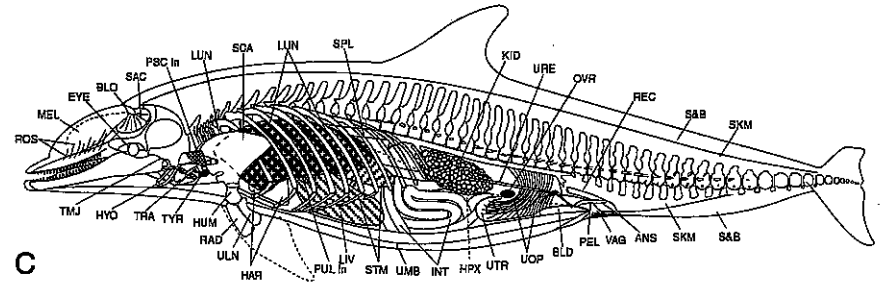
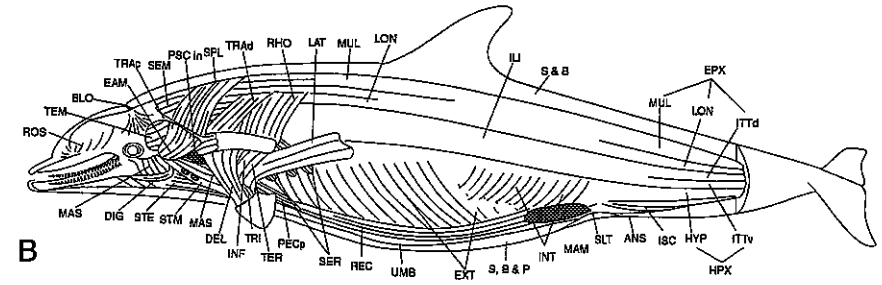
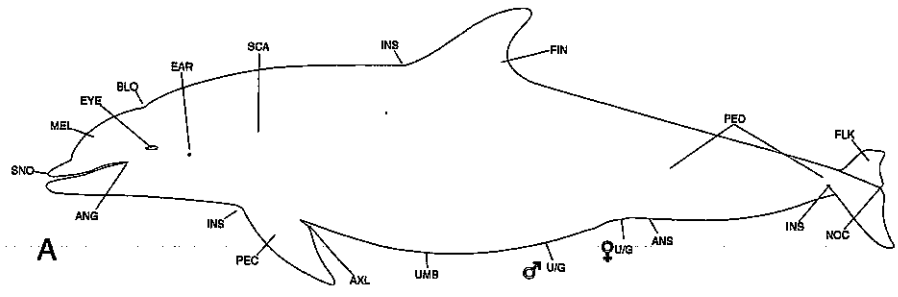
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Included is a section on microanatomy to introduce the microanatomical peculiarities of marine mammals to pathologists and thus aid them in performing routine histopathological examination of marine mammal tissues. The microscopic appearance of organs and tissues is presented following the gross anatomical descriptions. This information has been gathered from the examination of tissues submitted to the University of California Veterinary Medical Teaching Hospital Pathology Service over the last 20 years. These tissues were acquired from stranded marine mammals, such as California sea lions, harbor seals, northern elephant seals (*Mirounga angustirostris*), southern sea otters (*Enhydra lutris nereis*), and a few small odontocetes and gray whales (*Eschrichtius robustus*). Anatomical observations from the literature are also included and referenced. Previous reviews of microanatomy include Simpson and Gardner (1972), Britt and Howard (1983), and Lowenstine and Osborne (1990).

Histological recognition of organs and tissues from marine mammals poses little problem for individuals acquainted with the microanatomy of terrestrial mammals. The patterns of degenerative, inflammatory, and proliferative changes observed in marine mammal tissues are also similar to those observed in domestic mammalian species. Knowledge of specific microanatomy is necessary, however, for subtle changes to be recognized.

External Features

Consider the morphological features of the selected marine mammals. Streamlining and thermoregulation have caused changes in the appearance of marine mammals; these adaptations include the modification of appendages and other extremities for swimming, an increase in blubber for insulation, the development of axial locomotion, and the development of ascrotal testes (Pabst et al., 1999).

Sea Lions

The otariids (fur seals and sea lions), represented by the California sea lion, are also called eared seals because they have distinct pinnae (A-PIN) associated with their external ear openings (A-EAR). Like other pinnipeds, sea lions have robust vibrissae (A-VIB) on their snouts. Fur and/or blubber help streamline and insulate their bodies. Otariids (and walruses) can assume distinctly different postures on land by rotating their pelvis to position their pelvic (or hind) flippers (A-PEL) under their bodies. Note the presence of nails (unguis; A-UNG) on the extremities. Eared seals propel themselves with their pectoral (or fore) flippers (A-PEC) when swimming. The adult males of the sexually dimorphic California sea lion (and most other otariids) are much larger than the females. The teeth of sea lions are often stained dark brown or black in the absence of significant dental calculus. As in other carnivora, the nasal turbinates are well developed (Mills and Christmas, 1990).

Manatees

The sirenians are represented by the Florida manatee. They lack hind limbs and have a dorsoventrally flattened fluke (A-FLK; note that it is *flukes* in cetaceans and dugongs and *fluke* in manatees). There is no dorsal fin, and the pectoral limbs or flippers are much more mobile than those of cetaceans—it is common to see manatees with their flippers folded across their chests or manipulating food into the mouth. The skin is rough and relatively thick and massive when compared with that of terrestrial mammals of the same body size. The skin is denser than water and contributes significantly to negative buoyancy (Nill et al., 2000). The vibrissae are robust but short (from wear), and the body hairs are fine but sparse, and give a nude

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appearance to the skin of the manatee. Although body hairs are sparse, they are uniquely innervated and might provide vibrational and other tactile sensations (Reep et al., 1999). The eyes (A-EYE) of manatees are small and, unlike the eyes of other mammals, close using a sphincter rather than distinct upper and lower eyelids.

Seals

The phocids, or earless seals (also called hair seals), are represented by the harbor seal. They have vibrissae similar to those of a dog. Their nares (A-NAR) are located at the dorsal aspects of their snouts. Phocid eyes are typically large (C-EYE) when compared with those of other marine mammals. Note that the appearance of phocids is generally the same, whether they are in the water or on land. Phocids commonly tuck their heads back against the thoraxes, making the neck look shorter than it really is, and they locomote in the water by lateral undulation of their pelvic flippers (A-PEL). Their flippers have long curved nails (A-UNG). Some phocids have multiple cusps on the caudal teeth, which in some species are quite complex and ornate.

Dolphins

The odontocetes are represented by the bottlenose dolphin. The cetaceans are characterized by the absence of pelvic limbs but are graced with large caudal structures called flukes (A-FLK). The melon (A-MEL) is a rostral fat pad that, together with elongated premaxillae and maxillae, gives the dolphin its "bottlenose." The external nares are joined as a single respiratory opening at the blowhole (A-BLO), located at or near the apex of the skull. The externally smooth skin of dolphins has a thickened dermis, referred to as blubber. Some cetaceans also have dorsal fins (A-FIN), which are midline, nonmuscular, fleshy structures that may help stabilize them hydrodynamically. The keel of the peduncle (A-PED) provides streamlining and acts as a mechanical spring (Pabst et al., 1999). Cetaceans also have a pair of pectoral flippers that help them steer. Dolphins have facial hairs *in utero* but lose them at or near the time of birth (Brecht et al. 1997). Drawings contrasting features of the head and teeth of a representative porpoise and a representative dolphin appear in Reynolds et al. (1999). The unusual head of the sperm whale (*Physeter macrocephalus*) is described in detail by Cranford (1999). Dolphins have conical, pointed (when young and unworn) teeth. In contrast to dolphins, porpoises have flattened spade-shaped teeth and the lower, cranial margin of the melon extends all the way to the margin of the upper jaw or beak—there is no "bottle-shaped nose." As dolphins age, their teeth wear down, as they are abraded by ingested material and each other; the name *truncatus* is derived from the truncated appearance of the teeth in the original specimen. The tongues of the bottlenose dolphin and some other odontocetes have elaborate cranial and lateral marginal papillae, which are important for nursing (Donaldson, 1977).

Microanatomy of the Integument

The cetacean integument differs significantly from that of terrestrial mammals in that there are no hair follicles (save for a few on the snouts of some species) and no sebaceous or apocrine glands (Greenwood et al., 1974; Ling, 1974). The thick epidermis is nonkeratinizing, lacks a granular layer, and is composed primarily of stratum spinosum (stratum intermedium) with deep rete pegs. The basal layer has continuous mitoses. Continuous desquamation caused by water friction may account for the absence of a keratinized stratum corneum and the continuous cell replication in the basal layer. The papillary dermis is extremely well vascularized (Elsner et al., 1974). The reticular dermis grades into the fat-filled panniculus adiposus, creating a fatty

layer referred to as the blubber layer. The blubber contains many collagen (fibrous) bundles and elastic fibers, and adipocytes are interspersed so that blubber thickness may not diminish significantly during catabolism of fat. The blubber layer is connected to the underlying musculature by loose connective tissue (subcutis).

Pinnipeds, sea otters, and sirenians are haired (although hair density varies enormously from sea otters to walruses and sirenians), and therefore their skin is more similar to domestic mammals than is cetacean skin. The epidermis of these species is partially or entirely keratinizing. The stratum corneum is thickest on weight-bearing surfaces, such as the relatively glabrous ventral surfaces of fore and hind flippers, where the entire epidermis is quite thick. A stratum granulosum is present in phocids. Compound hair follicles consisting of a single guard hair follicle and several intermediate and underfur follicles are common, especially in fur seals and sea otters. Elephant seals, monk seals, and walruses, which lack underfur, all have simple hair follicles consisting of a single guard hair. Like terrestrial mammals, hair follicles of sea otters and pinnipeds are associated with well-developed sebaceous and apocrine (sweat) glands. Apocrine sweat glands are relatively large in the otariid seals, whereas the sebaceous glands are more prominent in the phocids. In densely haired regions of fur seals, the sweat glands enter the hair follicle above (distal) the sebaceous gland duct, but in sparsely haired species (such as the harp seal) and in sparsely haired areas of densely haired species, the pattern is reversed (Ling, 1974). Concentrations of glands vary with location on the animal, and patterns of gland distribution have not been fully described for all species. In some pinniped species, apocrine gland secretion may be more evolved for scent and olfactory communication than for thermoregulation (Greenwood et al., 1974). Hair follicles in all species are said to lack arrector pili muscles and have a fairly fixed angle relative to the skin surface. Vibrissae may be selectively heated by changes in blood flow (Mauck et al., 2000).

The blubber layer is relatively thin in fur seals and sea otters; in these species, the pelage is presumed to provide primary insulation. The connective tissue in the pinniped dermis contains many elastic fibers. The reticular layer is thicker than the papillary layer. The lower portions of hair follicles extend into the deep reticular dermis and are often surrounded by adipose tissue in those species with a thick blubber layer.

An interesting physiological phenomenon involving the marine mammal integument is the catastrophic cyclic molting that occurs in some phocids (Ling, 1974). Domestic mammals also tend to shed hair cyclically, but the stratum corneum is desquamated continuously, accompanied by continuous proliferation of the basal cell layer. In some phocids, basilar mitosis is seasonal, and the lipid-rich stratum corneum is parakeratotic and persists as a protective, presumably waterproof, sheet from one molt to the next. Prior to molt, a granular cell layer develops, and during molt, the surface epithelium is shed in great sheets along with the hair. In harp seals, this process is manifest grossly as small circular lesions that open and become confluent, leading to a drying-out and sloughing of the entire epidermal surface. Catastrophic molt has been best described histologically in the southern elephant seal (*M. leonina*) and is also evident in the northern elephant seal. Cyclic shedding or molt has also been seen in otariids but occurs more slowly, with shedding of the hair over several weeks or months.

Mammary glands (B-MAM) are ventral, medial, and relatively caudal in most marine mammals, but they are axillary in sirenians. Cetaceans and some phocids have a single pair of nipples (B-SLT), but otariids and polar bears have two pairs of nipples. In cetaceans, the nipples are within mammary slits located lateral to the urogenital opening (note that some male cetaceans have distinct mammary slits). Detailed anatomy of the phocid mammary gland is described by Bryden and Tedman (1974) and Tedman and Bryden (1981).

The Superficial Skeletal Muscles

The skeletal muscles that are encountered when the skin, blubber,* and panniculus muscles are removed are illustrated in layer B of each figure. Note that the panniculus (B-PAN) is represented as dotted lines in the manatee because it is such a robust muscle, bordered on its lateral and medial aspects by "blubber." The skeletal muscle of most marine mammals is very dark red, almost black, because of the relatively high myoglobin concentration.

The design of the musculoskeletal system profoundly influences any mammal's power output because it affects both thrust and propulsive efficiency (Pabst et al., 1999). Thrust forces depend on muscle morphology and the mechanical design of the skeletal system. The propulsive efficiency of the animal depends on the size, shape, position, and behavior of the appendage(s) used to produce thrust. Terrestrial mammals usually use their appendicular musculoskeletal system to swim using the proverbial dog paddle—alternate strokes of the forelimbs (and sometimes hind limbs). Pinnipeds use their more-derived appendicular musculoskeletal systems to swim. Unlike the other marine mammals, the fully aquatic sirenians and cetaceans swim using only their vertebral or axial musculoskeletal systems.

Thus, in mammals that use their appendicular musculoskeletal systems to swim, two morphological "solutions" to increase thrust production are observed (Pabst et al., 1999). Proximal locomotor muscles tend to have large cross-sectional areas and so would have the potential to generate large in-forces. Proximal limb bones (i.e., humerus and femur) tend to be shorter than more distal bones (i.e., radius, ulna, tibia, and fibula), which increases the mechanical advantage of the lever system. The short proximal limb bones have an added hydromechanical benefit. These bones tend to be partially or completely enveloped in the body, which helps reduce drag on the appendage and increased body streamlining (Tarasoff, 1972; English, 1977; King, 1983).

Contrast the distribution of muscle mass in the four species. Note that adaptations to each locomotory specialization have enlarged or reduced the corresponding muscles found in terrestrial mammals. Contrast the massiveness of the pectoral muscles (B-PEC) of the sea lion with those in the seal. The triceps (B-TRI) and deltoids (B-DEL) are also enlarged in both pinnipeds to increase thrust, and the olecranon (C,E-OLC) of both the seal and sea lion are enlarged to increase the mechanical advantage of these muscles. Note that the harbor seal has a unique component of the pectoral—an ascending pectoral muscle (B-PECa)—that extends over the humerus (also described for another phocid, the southern elephant seal; see Bryden, 1971). A dramatic change in thickness of the abdominal wall muscles (B-INT, EXT) occurs in young seals as they make the transition from a more terrestrial to a more aquatic lifestyle.

Cetaceans and sirenians use their axial musculoskeletal systems to swim. Epaxial muscles (B-EPX) bend the vertebral column dorsally in upstroke; hypaxial muscles (B-HPX) and abdominal muscles bend the vertebral column ventrally in downstroke. Because there is no "recovery" phase, efficiency is increased. These muscles generate thrust forces that are delivered to the fluid medium via their flukes (Domning, 1977; 1978; Strickler, 1980; Pabst, 1990).

The elongated neural spines (E-NSP) and transverse processes (E-TPR) of cetaceans also increase the mechanical advantage of the axial-muscle lever system, relative to that system in terrestrial mammals. By inserting far from the point of rotation, the lever arm-in is increased and, thus, force output is increased. A novel interaction between the tendons of the epaxial muscles and a connective tissue sheath that envelops those muscles also increases the work output of the axial musculoskeletal system in cetaceans (Pabst, 1993; Pabst et al., 1999). The

*The term *blubber* is used differently in different species. In sea lions, seals, and manatees, it is subcutaneous fat in one or two layers, and resembles that found in terrestrial mammals. Blubber in cetaceans is fat—"inflated" dermis (Pabst et al., 1999).

sirenian axial skeleton does not display elongated processes, which would increase the lever arm-in for dorsoventral flexion. Instead, the lumbar and cranialmost caudal vertebrae have elongated transverse processes (Domning, 1977; 1978).

The Diaphragm as a Separator of the Body Cavities

The orientation of the diaphragm (C,D-DIA) in most marine mammals is very similar to the orientation of the diaphragm in the dog. Visualizing size, shape, and extent of the diaphragm will help one visualize the dynamics of respiration and diving. The diaphragm lies in a transverse plane and provides a musculotendinous sheet to separate the major organs of the digestive, excretory, and reproductive systems (all typically caudal to the diaphragm) from the heart with its major vessels; the lungs (C-LUN) and associated vessels and airways; the thyroid (C,D-THY), thymus (C,D-TYM), and a variety of lymph nodes, all located cranial to the diaphragm. The diaphragm is generally confluent with the transverse septum, so it attaches medially at its ventral extremity to the sternum.

Although the diaphragm acts as a separator between the heart and lungs and the other organs of the body, the diaphragm is traversed by nerves and other structures, such as the aorta (D-AOR) (crossing in a dorsal and central position), the vena cava (D-CVC) (crossing more ventrally than the aorta, and often slightly left of the midline, although appearing to approximate the center of the liver), and the esophagus (D-EOS) (crossing slightly right of the midline, at roughly a midhorizontal level). This transverse orientation exists in most marine mammals, although the orientation of the diaphragm may be slightly diagonal, with the ventral portion more cranial than the dorsal portion.

The West Indian manatee's diaphragm differs from this general pattern of orientation and attachment. The manatee diaphragm and the transverse septum (D-TRS) are separate, with the latter occupying approximately the "typical" position of the diaphragm, and the diaphragm itself occupying a horizontal plane extending virtually the entire length of the body cavity. This apparently unique orientation presumably relates to buoyancy control (Rommel and Reynolds, 2000). There are two separate hemidiaphragms in the manatee. The central tendons firmly attach to hypapophyses (E-HYP) on the ventral aspects of the thoracic vertebrae, thereby producing the two pleural cavities.

Gross Anatomy of Structures Cranial to the Diaphragm

Heart and Pericardium

The pericardium is a fluid-filled sac surrounding the heart; in manatees, it often contains more fluid than is found in the typical mammal or in other marine mammals. The heart occupies a ventral position in the thorax (immediately dorsal to the sternum; D-STR). The heart lies immediately cranial to the central portion of the diaphragm (D-DIA; or the transverse septum in the manatee, D-TRS). In some species, the lungs (D-LUN) may embrace the caudal aspect of the heart, separating the caudal aspect of the heart from the diaphragm. As in all other mammals, marine mammal hearts have four chambers, separate routes for pulmonary and systemic circulation, and the usual arrangements of great vessels (venae cavae, D-CVC; aorta, D-AOR; coronary arteries; pulmonary arteries, PULaa; pulmonary veins, PULvv). Many marine mammal hearts are flattened from front to back (ventral to dorsal), are relatively squat from top to bottom, and have a rounded apex, giving them a shape quite different from the hearts of most terrestrial mammals (Drabek, 1975). Most pinnipeds and some cetaceans also have a distinctive dilatation of the aortic arch (Drabek, 1977). Cardiac fat occurs, but is rapidly lost in debilitated animals.

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Pleura and Lungs

The pleural cavities and lungs (C-LUN) are generally found dorsal and lateral to the heart; in the manatee, the lungs are unusual in that they extend virtually the length of the body cavity and remain dorsal to the heart (Rommel and Reynolds, 2000). Lungs of some marine mammals (cetaceans and sirenians) are unlobed. The cranial ventral portion of the left lung in the bottlenose dolphin and other small odontocetes is very thin, almost veil-like, where it overlies the heart. Lobation in the pinnipeds is generally similar to that in the dog, that is, two lobes on the left (the cranial lobe has cranial and caudal parts) and three (including the accessory lobe) on the right. Reduction of lobation occurs in some phocids (Boyd, 1975; King, 1983). The terminal airways in all marine mammals are reinforced with either cartilage or muscle (Pabst et al., 1999). Apical (tracheal) bronchi are present in dolphins. In otariids, it is important to note that the bifurcation (D-BIF) of the trachea into the main-stem bronchi takes place at the thoracic inlet, not at the pulmonary hilus as is the case in phocids and cetaceans (McGrath et al., 1981; Nakakuki, 1993a,b; Wessels and Chase, 1998). The lungs of cetaceans are grossly smooth, but those of many pinnipeds are divided into distinct lobules in the ventral fields. Interestingly, sea otter lungs have distinct interlobular septa. The size of marine mammal lungs depends upon each species' diving proficiency. Marine mammals that make deep and prolonged dives (e.g., elephant seals) tend to have smaller lungs than expected (based on allometric relationships), whereas shallow divers (e.g., sea otters) tend to have larger than expected lungs (Pabst et al., 1999).

Mediastinum

The mediastinum is an artifact of the downward expansion of the lungs on either side of the heart in the typical mammal (Romer and Parsons, 1977); thus, the traditional definition of the mammalian mediastinum does not apply to manatees. The positions of the aortic hiatus, caval foramen (D-CAF), and esophageal hiatus (D-ESH) are unusual because of the configuration of the diaphragm. The manatee mediastinum (see manatee, layer D) is the midline region dorsal to where the pericardium attaches to the heart and ventral to the diaphragm, cranial to the transverse septum up to approximately the level of the first cervical vertebra. This is essentially what constitutes the cranial mediastinum of other mammals. The thyroid, thymus, tracheobronchial lymph nodes, and the tracheobronchial bifurcation are in the region defined as mediastinal in the manatee (Rommel and Reynolds, 2000). The mediastinum is thin and generally complete in the pinnipeds.

Thymus

The thymus (C,D-TYM), which typically is relatively larger in young than in old individuals of any species, is found on the cranial aspect of the pericardium (sometimes extending caudally to embrace almost the entire heart) and may extend into the neck in otariids, the bottlenose dolphin (Cowan and Smith, 1999), and some other species.

Thyroids

The thyroid glands (C,D-TYR) of the bottlenose dolphin and the manatee are located in the cranial part of the mediastinum along either side of the distal part of the trachea (C,D-TRA), prior to its bifurcation (D-BIF) into the bronchi. The paired, large, oval, dark-brown thyroid glands of pinnipeds, however, lie along the trachea just caudal to the larynx outside of the thoracic inlet (similar to the position in dogs).

Parathyroids

The parathyroid glands have been described in small cetaceans, and their location relative to the thyroid gland varies among species examined to date (Hayakawa et al., 1998). In Risso's dolphins (*Grampus griseus*) they are dorsal to the thyroids or embedded within them, whereas in bottlenose dolphins they are on the surface of the thyroids and in the connective tissue surrounding the dorsal side of the thyroids. Little is known about the parathyroids of pinnipeds and sirenians.

Larynx

The cetacean respiratory system has undergone several modifications that are associated with the production of sound. Immediately ventral and lateral to the blowhole (B,C,D-BLO) are small sacs or lateral diverticulae (C-SAC). Medial to the diverticulae are the paired internal nares that extend on the cranial aspect of the braincase (D-BRN). The larynx (C-LAR), a spout-shaped structure referred to as the goosebeak, is composed of an elongated epiglottis and corniculate cartilage (Reidenberg and Laitman, 1987). The goosebeak extends through a small opening in the esophagus (supported laterally by an enlarged thyroid cartilage) into the relatively vertical narial passage; food can pass to either side of the goosebeak. Cetaceans have a robust hyoid apparatus (C,E-HYO) to support movements of the larynx. A palatopharyngeal sphincter muscle can keep the goosebeak firmly sealed (Pabst et al., 1999). For a detailed description of sound-producing anatomy, see Cranford et al. (1996).

Caval Sphincter

One additional structure that is associated with the circulatory system, located on the cranial aspect of the diaphragm in seals and sea lions, is a feature atypical in mammals. This is the muscular caval sphincter (D-CAS), which can regulate the flow of oxygenated* blood in the large venous hepatic sinus (D-HPS) to the heart during dives (Elsner, 1969).

Microscopic Anatomy of Structures Cranial to the Diaphragm

Respiratory System

In cetaceans and otariids, cartilage extends around small bronchioles to the periphery of the lungs. In most phocids, cartilage is present around bronchi and bronchioles (Tarasoff and Kooyman, 1973; Boshier, 1974; Boyd, 1975). Bronchial glands are especially numerous in larger-caliber bronchi and bronchioles of phocids. The configuration of terminal airways branching into alveoli varies among marine mammals, but, in general, respiratory ducts with small alveolar sacs make up the functional parenchyma. Myoelastic sphincters are present in the terminal bronchioles, presumably as an adaptation to diving (Boshier, 1974; Wessels and Chase, 1998). The number of alveolar duct units per lobule varies with species. The interalveolar septa have double rows of capillaries in most cetaceans and some otariids (e.g., in Steller but not California sea lions) but a single row of capillaries in phocids.

*In diving mammals with abundant arteriovenous anastomoses (shunts between arteries and veins before capillary beds), one can find high blood pressure and highly oxygenated blood in veins. One such venous reservoir of oxygenated venous blood is the hepatic sinus of seals (King, 1983).

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Thymus

The thymus of marine mammals is composed of lobules, each with a distinct lymphocyte-rich cortex and a less cellular medulla. In many stranded immature marine mammals, there is profound thymic atrophy, with lymphoid depletion, and mineralization and keratinization of Hassell's corpuscles.

Thyroids

The thyroids of neonatal California sea lions, harbor seals, and elephant seals have plump cuboidal epithelium and little colloid (Little, 1991; Schumacher et al., 1993). In adults of the former two species, the epithelium also remains cuboidal, and the follicles remain fairly uniform in size. The thyroids of cetaceans are often distinctly lobulated, and the follicles of both young and adults are often small and lined with cuboidal epithelium similar to that of pinnipeds (Harrison, 1969b).

Parathyroids

The parathyroids of Risso's dolphins are divided into lobules by connective tissue, and have parenchymal cells consisting of chief cells with intracellular lipid droplets (Hayakawa et al., 1998).

Gross Anatomy of Structures Caudal to the Diaphragm

Easy-to-find landmarks caudal to the diaphragm include a massive liver (C,D-LIV) and the various components of the gastrointestinal (GI) tract. The gonads and most other parts of the reproductive tracts are found only after the removal of the GI tract, except in a pregnant uterus.

Liver

Typically, the liver is located immediately caudal to the diaphragm. It is a large, brownish, multi-lobed organ that tends to have most of its volume or mass positioned to the left of the body midline. Marine mammal livers are generally not too different from those of other mammals, although the manatee liver is a little more to the right and dorsal than are the livers of most other mammals. The number of lobes and the fissures in the lobes may vary, particularly in the sea lion's liver, in which deep fissures give the lobes a deeply scalloped appearance. Bile may be stored in a gall bladder (often greenish in color) located ventrally, between lobes of the liver, although some mammals (e.g., cetaceans, horses, and rats) lack a gall bladder. Bile enters the duodenum (D-DUO) to facilitate chemical digestion of fats.

Digestive System

Most of the volume of the cavity caudal to the diaphragm (the abdominal cavity) is occupied by the various components of the GI tract: the stomach, the small intestine (C-INTsml; duodenum, jejunum, ileum), and the large intestine (C-INTlg; cecum, colon, and rectum; C,D-REC). A strong sphincter marks the distal end of the stomach (the pylorus) before it connects with the small intestine (duodenal ampulla in cetaceans and sirenians). The separation between jejunum and ileum of the small intestine is difficult to distinguish grossly, although the two sections differ microscopically.

The junction of the small and large intestines may be marked by the presence of a midgut cecum (homologous to the human appendix). The cecum is absent in most toothed whales, but present in some baleen whales (not the bowhead whale), vestigial but present in pinnipeds, and

absent in sea otters. In manatees, the cecum is large, globular, and has two blind pouches called cecal horns. The large intestine, as its name implies, has a larger diameter than the small intestine in some marine mammals. In the sea lion, seal, and dolphin there is little difference in gross appearance between the small and large intestines. The cecum of sea lions and seals is about a meter from the anus, whereas the small intestines are about 20 times as long; in adult manatees, both the large and small intestines may approach or even exceed 20 m (Reynolds and Rommel, 1996). The proportions and functions of these components reflect feeding habits and trophic levels of the different marine mammals.

Accessory organs of digestion include the salivary glands (C-SAL; absent in cetaceans, present in pinnipeds, very large in the manatee), pancreas (D-PAN), and liver. The pancreas is sometimes a little difficult to locate, because it can be a rather diffuse organ and decomposes rapidly; however, a clue to its location is its proximity to the initial part of the duodenum into which pancreatic enzymes flow (Erasmus and Van Aswegen, 1997). Another organ that is structurally, but not functionally, associated with the GI tract is the spleen (D-SPL), which is suspended by a ligament, generally from the greater curvature of the stomach in simple-stomached species, or from the first stomach in cetaceans). It is usually on the right side, but may have its greatest extent along the left side of the body. The spleen is usually a single organ, but in some species (mainly cetaceans), accessory spleens (occasionally referred to as hemal lymph nodes) may accompany it. It varies considerably in size among species; in manatees and cetaceans it is relatively small, but the spleen is relatively massive in some deep-diving pinnipeds (Zapol et al., 1979; Ponganis et al., 1992), where it acts to store red blood cells temporarily.

The length and mass of the GI tract may be very impressive and create three-dimensional relationships that can be complex. Tough connective tissue sheets called mesenteries suspend the organs from the dorsal part of the abdominal cavity, and shorter connective tissue bands (ligaments*) hold organs close to one another in predictable arrangements (e.g., the spleen is almost always found along the greater curvature of the stomach and is connected to the stomach by the gastrosplenic ligament). Numerous lymph nodes and fat are also suspended in the mesenteries.

The GI tracts of pinnipeds and other marine mammal carnivores follow the general patterns outlined above, although the intestines can be very long in some species (Schumacher et al., 1995; Stewardson et al., 1999). Cetaceans, however, have some unique specializations (Gaskin, 1978). In these animals, there are three or more compartments to the stomach, depending on the species. Functionally, the multiple compartments of cetacean stomachs correspond well to regions of the single stomach of most other mammals. Most cetaceans have three compartments; the first, called the forestomach (D-STM1; essentially an enlargement of the esophagus), is muscular and very distensible; it acts much like a bird crop (i.e., as a receiving chamber). The second (D-STM2), or glandular compartment, is the primary site of chemical breakdown among the stomach compartments; it contains the same types of enzymes and hydrochloric acid that characterize the "typical" mammalian stomach. Finally, the "U-shaped" third compartment, or pyloric stomach (D-STM3), ends in a strong sphincteric muscle that regulates flow of digesta into the duodenum of the small intestine. The initial part of the cetacean duodenum is expanded into a small saclike ampulla (occasionally mistaken for a fourth stomach).

*Ligament has several meanings in anatomy: a musculoskeletal element (e.g., the anterior cruciate ligament), a vestige of a fetal artery or vein (e.g., the round ligament of the bladder), the margin of a fold in a mesentery (e.g., broad ligament), and a serosal fold between organs (e.g., the gastrosplenic ligament). *Note:* In human terminology *anterior* and *posterior* are used; in comparative and veterinary terminology *cranial* and *caudal* are used when relating to the head and tail, respectively.

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Among the marine mammals, sirenians have the most remarkable development of the GI tract. Sirenians are herbivores and hindgut digesters (similar to horses and elephants), so the large intestine (specifically the colon) is extremely enlarged, enabling it to act as a fermentation vat (see Marsh et al., 1977; Reynolds and Rommel, 1996). The sirenian stomach is single chambered and has a prominent accessory secretory gland (the cardiac gland) extending prominently from the greater curvature. The duodenum is capacious and has two obvious diverticulae projecting from it. The GI tract of the manatee, with its contents, can account for more than 20% of an individual's weight.

Urinary Tract

The kidneys (C,D-KID) typically lie against the musculature of the back (B-HPX, hypaxial muscles), at or near the dorsal midline attachment of the diaphragm (crus, D-CRZ). In the manatee, the unusual placement of the diaphragm means that the kidneys lie against the diaphragm, not against hypaxial muscles. In many marine mammals, the kidneys are specialized as reniculate (multilobed) kidneys, where each lobe (renule) has all the components of a metanephric kidney. The reason that marine mammals possess reniculate kidneys is uncertain, but the fact that some large terrestrial mammals also possess reniculate kidneys has led to speculation that they are an adaptation associated simply with large body size (Vardy and Bryden, 1981), rather than for a marine lifestyle. Large body size may be important as the proximal convoluted tubules cannot be overlengthy and still conduct urine (Maluf and Gassmann, 1998).

The kidneys are drained by separate ureters (D-URE), which carry urine to a medially and relatively ventrally positioned urinary bladder (C,D-BLD). The urinary bladder lies on the floor of the caudal abdominal cavity and, when distended, may extend as far forward as the umbilicus (A,B,C,D-UMB) in some species. The pelvic landmarks are less prominent in the fully aquatic mammals. In the manatee the bladder can be obscured by abdominal fat. Note that the renal arteries (D-REN) of cetaceans enter the cranial pole of the organ, and the ureters exit near the caudal pole, whereas in other marine mammals they enter and exit the hilus (typical of most mammals). Additionally, in manatees, there are accessory arteries on the surface of the kidney (Maluf, 1989).

Genital Tract

Pabst et al. (1999) noted that the reproductive organs tend to reflect phylogeny more than adaptations to a particular niche. If one were to examine the ventral aspect prior to removal of the skin and other layers, one would discover that, especially in the sirenians and some cetaceans, positions of male and female genital openings are obviously different, permitting easy determination of sex without dissection. In all cases, the female urogenital opening (A-U/G) is relatively caudal, compared with the opening for the penis in males. One way to approach dissection of the reproductive tracts is to follow structures into the abdomen from the external openings.

The position and general form of the female reproductive tracts are similar to those of terrestrial mammals (Boyd et al., 1999). The vagina (C,D-VAG) opens cranial to the anus (A,B,C,D-ANS) and leads to the uterus (C,D-UTR), which is bicornuate in marine mammal species. The body of the uterus is found on the midline and is located dorsal to the urinary bladder (the ventral aspect of the uterus rests against the bladder). The uterine horns (cornua) extend from the uterine body toward the lateral aspects of the abdominal cavity. Implantation of the fertilized egg and subsequent placental development take place in the walls of the uterine horns, usually in the ipsilateral horn to ovulation (see Chapter 11, Reproduction). Dimensions of uterine horns vary with reproductive history and age. Often the fetus may expand the pregnant horn to occupy a substantial portion of the abdominal cavity. The horns terminate

distally in an abrupt reduction in diameter and extend as uterine tubes (fallopian tubes) to paired ovaries (C,D-OVR). The uterus and ovaries are suspended from the dorsal abdominal wall by the broad ligaments. Uterine scars and ovarian structures may provide information about the reproductive history of the individual (Boyd et al., 1999; see Chapter 11, Reproduction).

The ovaries of mature females may have one or more white or yellow-brown scars, called corpora albicantia and corpora lutea, respectively (see Chapter 11, Reproduction). Although ovaries are usually small solid organs, in sirenians they are relatively diffuse, with many follicles and more than one corpus albicans.

The male reproductive tracts of marine mammals have the same fundamental components as those of "typical" mammals, but positional relationships may be significantly different. These differences are due to the testicond (ascrotal) position of the testes in many species (sea lion testes become scrotal when temperatures are elevated). The testes of some marine mammals are intra-abdominal* (DeSmet, 1977), whereas in phocids they are in the inguinal canal, covered by the oblique muscles and blubber (see Figure 2-20 in Pabst et al., 1999). The position of marine mammal testes creates certain thermal problems because spermatozoa do not survive well at body (core) temperatures; in some species, these problems are solved by circulatory adaptations mentioned below. The penis of marine mammals is retractable, and it normally lies within the body wall. General structure of the penis relates to phylogeny (Pabst et al., 1999). In cetaceans, it is fibroelastic type with a sigmoid flexure that is lost during erection, as seen in ruminants. Pinnipeds, sea otters and polar bears have a baculum within the penis, as do domestic dogs; in manatees it is muscular (see Chapter 11, Reproduction, and see Sexual Dimorphisms, below).

Adrenal Glands

In marine mammals, adrenal glands (D-ADR) lie cranial to the kidneys and caudal to the diaphragm, as in terrestrial mammals. Adrenal glands can be confused with lymph nodes, but if one slices the organ in half, an adrenal gland is easy to distinguish grossly by its distinct cortex and medulla. In contrast, lymph nodes are more uniform in appearance.

Microscopic Anatomy of Structures Caudal to the Diaphragm

Liver

The histology of the liver of pinnipeds is quite similar to that of terrestrial mammals. In cetaceans, however, portal triads may have very thick-walled vessels (Hilton and Gaskin, 1978). Smooth muscle may also be found around some central veins (throttling veins) (Arey, 1941). Stainable iron (hemosiderosis) is common in neonatal harbor and northern elephant seals and in older otariids in captivity. Ito cells may be quite prominent in marine mammals, compatible with the presence of high vitamin A levels found in these livers (Rhodahl and Moore, 1943).

Digestive System

The oropharynx of pinnipeds and odontocetes, and the caudal part of the odontocete tongue, are richly endowed with minor mucous glands, which enter out onto the mucosal surface via ducts that are visible grossly as small pits. Microscopically, the nonglandular and glandular stomachs resemble the analogous structures in terrestrial mammals. Parietal cells are exception-

*The position of the testes in sea otters is scrotal, and the testes of polar bears are seasonally scrotal (Reynolds et al., in press).

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ally prominent in odontocetes. In sirenians, the cardiac gland is a submucosal mass that protrudes cranially from the greater curvature of the stomach; it has a complicated folded lumen lined by mucous surface cells overlying long gastric glands lined with mucous and parietal cells. The glands of the main sac are lined by mucous cells and a lesser number of parietal cells (Marsh et al., 1977; Reynolds and Rommel, 1996). Histologically, the intestines of marine mammals are also similar to those of domestic mammals with the following exceptions (Schumacher et al., 1995). The villi are said to be absent in the proximal duodenum in some cetaceans, and Brunner's glands are variably present. Plicae rather than villi are often present, creating chevron shapes on cross sections of cetacean intestine. The light and electron microscopic appearance of the small intestine of small odontocetes has been described in detail (Harrison et al., 1977). Gut-associated lymphoid aggregates are present throughout the intestines and may be diffuse or nodular. They are especially numerous in the distal colon of odontocetes and baleen whales, where they form the anal tonsil (Cowan and Brownell, 1974; Romano et al., 1993).

Urinary Tract

Each reniculus has a histologically distinct cortex and medulla. Since cortex completely surrounds the medulla in the reniculi, ascending inflammation in one reniculus may spill over into the interstitium of an adjacent reniculus, giving the pattern of interstitial (hematogenous) nephritis. Thus, it is important to sample several reniculi from each kidney to assess pathological processes. In cetaceans there is normally a fibromuscular band at the corticomedullary junctions surrounding the medullary pyramid. Glomeruli of all species examined are of remarkably similar size (about one half the width of a 40 \times high dry field).

Genital Tract

The morphology of the reproductive tract of the female varies with the stages of estrus and gestation (see Chapter 11, Reproduction). A description of cyclic changes in some of the cetaceans is given in Harrison (1969a) and in some sirenians in Boyd et al. (1999). Morphological changes of the genital mucosa associated with the estrous cycle have not been studied in detail in marine mammals, other than the harbor seal (Bigg and Fisher, 1974). In this species (described here to illustrate the variation in appearance through the estrous cycle), during follicular development then regression, the uterine mucosa increases in height and pseudostratification and then decreases to simple cuboidal. Uterine gland epithelium increases in height and secretory activity, and glands become increasingly coiled. Vaginal epithelium "destratifies" to become a "transitional-type" epithelium only a few cells thick, with vaginal pits (glands) lined by columnar epithelium with apical secretory product (goblet cell-like). The endometrial luminal and glandular epithelium of the nongravid horn is secretory and declines to cuboidal by parturition. During this luteal phase, there are subnuclear lipid vacuoles in the glandular epithelium. The vaginal epithelium is transitional during early placentation, but increases in secretory activity to become lined with tall columnar mucous cells with fingerlike projections of the lamina propria replacing the mucosal pits. During lactation, the morphology of both uterine and vaginal epithelium changes again. In the first part of lactation, the surface and glandular uterine epithelium is cuboidal, then undergoes hypertrophy and hyperplasia during the latter half of lactation. Luminal epithelium is occasionally pseudostratified, and the uterine stroma of both horns is edematous. The patchy hyperplasia and pseudostratification might be mistaken for dysplasia. Vaginal epithelium is almost transitional during the first part of lactation but proliferates to stratified squamous nonkeratinizing cells covered by sloughing mucous cells by the end of lactation.

The endometrium of the gray seal prior to implantation is described by Boshier (1979; 1981).

The placenta of pinnipeds is zonary, endotheliochorial, similar to that of domestic carnivores. In late gestation, it is often deep orange because of the marginal hematoma from which the fetus gains its iron stores *in utero*. After parturition and involution, old implantation sites may be visible grossly as dark areas in the mucosa, which are represented histologically by stromal hemosiderosis and arterial hyalinization. The placenta of cetaceans is diffuse epitheliochorial. The structure of the phocid corpus luteum is described by Sinha et al. (1972; 1977a).

The prostate is the only accessory sex gland in pinnipeds and cetaceans (Harrison, 1969a). It is tubuloalveolar and has cuboidal to low-columnar to pseudostratified lining cells with basilar nuclei and pale apical cytoplasm. The fine structure of phocid testes and seminiferous tubules are described by Leatherland and Ronald (1979) and Sinha et al. (1977b), respectively.

Adrenals

Pinniped adrenals may have an undulating or pseudolobulated cortex. In cetaceans, however, pseudolobulation is extensive and is created by connective tissue septae extending from the capsule. Large nerves, ganglia, and many blood vessels are associated with the hilus and capsular surface of pinniped adrenals.

Lymphoid and Hematopoietic Systems

The capsules and trabeculae of pinniped lymph nodes are quite thick, and there is often abundant hilar and medullary connective tissue as well (Welsch, 1997). The degree of fibrosis seems to increase with age, and may be a function of chronic drainage reactions. Pinniped lymph nodes are organized like those of canids, having a peripheral subcapsular sinus, cortical follicular and interfollicular (paracortical) regions, and medullary cords and sinuses. Although some authors report that marine mammal lymphoid tissue is usually quiescent and lacks follicular development, secondary follicles are common in both peripheral and visceral lymph nodes of stranded pinnipeds, probably due to the common presence of skin wounds and visceral parasitism. In many stranded pinnipeds, the lymph nodes are sparsely but diffusely populated by lymphocytes, and the ghosts of germinal centers can be seen. Since this morphology is most common when the interval from death to post-mortem is prolonged, it has been interpreted to be a "washing out" of lymphocytes due to autolysis.

The lymph nodes of some cetaceans are often deeply infolded or fused so that they appear to be organized similarly to the nodes of suids, whose follicular cortex is buried deep within the node and sinusoids and cords are located more toward the periphery. The correlation of anatomical location with nodal morphology has not been made for all species. The visceral nodes of the bottlenose dolphin have extensive smooth muscle in the capsule and trabeculae and have incomplete marginal sinuses (Cowan and Smith, 1999). The lymph nodes of the beluga are described by Romano et al. (1993).

The elongated spleen of pinnipeds has a thick fibromuscular capsule and trabeculae with a sinusoidal pattern similar to that of canids. Periarterial reticular sheaths are more prominent in phocids than in otariids. The spherical spleen of cetaceans also has a thick capsule, which is fibrous externally and muscular internally, with the muscle cells extending into the thick trabeculae (Cowan and Smith, 1999). Extramedullary hematopoiesis is common in the spleens of pinniped and sea otter pups, but it seems to be uncommon in cetaceans.

Nervous System

A detailed description of marine mammal neuroanatomy is beyond the scope of this chapter; for a comparison of some marine mammal brains (D-BRN), see Pabst et al. (1999). Suffice it

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to say that the brains of cetaceans and pinnipeds are large and well developed and have complex gyri in the cerebral and cerebellar cortices that are relatively larger than similarly sized brains of terrestrial mammals (Flanigan, 1972). The cetacean cerebrum is globoid and the rostral lobes extend ventrally. Like higher primates, cetaceans have well-developed temporal lobes (ventrolateral aspects of the cortices) that make brain removal a challenge. The pinniped brain is similar in orientation to the canine brain except for the larger cerebellum.

In pinnipeds, the pineal gland is very large (up to 1.5 cm in diameter), especially in neonates (Bryden et al., 1986) and the size varies seasonally (see Chapter 10, Endocrinology). The pineal gland is located on the dorsal aspect of the diencephalon between the thalami and may be attached to the falx cerebri when the calvarium is removed at necropsy. There are no published descriptions of the pineal in cetaceans, and whether or not it exists is unclear.

The pituitary gland is relatively large in both cetaceans and pinnipeds (Harrison, 1969b; Leatherland and Roland, 1976; 1978; Griffiths and Bryden, 1986). It is located within a shallow sella tunica in cetaceans and is surrounded by reams of blood vessels making it difficult to remove on necropsy. In pinnipeds, it is often sheared off during removal of the brain, so care should be taken to cut the lip of bone partially covering it to remove it intact.

The spinal cord of phocids is relatively shorter than that of otariids; only the cauda equina occupies the lumbar and sacral canal. The cauda equina of the harbor seal pup is similar to that of the dog, but as they grow older, the cord changes significantly. The cauda equina starts in the lumbocaudal region in manatees. The region surrounding the cord—the vertebral canal—is significantly enlarged in seals, cetaceans, and sirenians. The neural canal is filled mostly with vascular tissue in seals and cetaceans and mostly with venous and fatty tissue in manatees. Manatee brains have pronounced lissencephaly and large lateral ventricles (Reep et al., 1989).

Circulatory Structures

In general, blood vessels are named for the regions they feed or drain. Thus, the fully aquatic marine mammals (cetaceans and sirenians) lack femoral arteries, which supply the pelvic appendage. However, most organs in marine mammals are similar to those of terrestrial mammals, so their central blood supplies are also similar.

The aorta (D-AOR) leaves the heart (D-HAR) as the ascending aorta, then forms the aortic arch (D-AAR) and roughly follows the vertebral column dorsal to the diaphragm as the thoracic aorta, which gives off segmental intercostal arteries and, in the case of cetaceans and manatees, feeds to the thoracic retia. Some of the segmental arteries of the dolphin anastomose at the base of the dorsal fin to form the single arteries that are arranged along the centerline of the dorsal fin (D-DFNaa). The aorta continues into the abdomen as the abdominal aorta, which gives off several paired (e.g., renal, gonadal) and unpaired (e.g., celiac, mesenteric) arteries. The caudal aorta follows the ventral aspect of the vertebrae in the tail; in the permanently aquatic marine mammals the caudal vessels are large when compared with the vessels in species with small tails. In the dolphin, the caudal arteries branch into dorsal and ventral superficial arrays of arteries (D-FLKaa; Elsner et al., 1974). In the permanently aquatic marine mammals, there are robust ventral chevron bones that form a canal in which the caudal aorta, its branches, and some veins (the caudal vascular bundle, D-CVB) are protected. This site is convenient in some species for venipuncture; however, note that it is an arteriovenous plexus, so samples collected may be mixed arterial and venous blood.

Some of the diving mammals (e.g., seals, cetaceans, and sirenians) have few or no valves in their veins (Rommel et al., 1995); this adaptation simplifies blood collection because the blood can drain toward the site from both directions, although blood collection is complicated by the arteriovenous plexuses described above. Other exceptions to the general pattern of mammalian

circulation are associated with thermoregulation and diving. Countercurrent heat exchangers abound, and extensive arteriovenous anastomoses exist to permit two general objectives to be fulfilled: (1) regulating loss of heat to the external environment while keeping core temperatures high, and (2) permitting cool blood to reach specific organs (e.g., testes and epididymides, ovaries and uteri) that cannot sustain exposure to high body temperatures (see reviews by Rommel et al., 1998; Pabst et al., 1999).

Mammals have three options for blood supply to the brain: the internal carotid, the external carotid, and the vertebral arteries. Some species use only one and others two, but the manatees use all three pathways. Cetaceans have a unique blood supply to the brain (D-BRN); the blood to the brain first enters the thoracic retia, a plexus of convoluted arteries in the dorsal thorax. Blood leaves the thoracic retia and enters the spinal retia, where it surrounds the spinal cord and enters the foramen magnum (McFarland et al., 1979). There are two working hypotheses for this convoluted path to the brain: (1) the elasticity of the retial system allows mechanical damping of the blood pulse pressure wave (McFarland et al., 1979; Shadwick and Gosline, 1994), and (2) the juxtaposition of the thoracic retia to the dorsal aspect of the lungs may provide thermal control of blood entering the spinal retia (Rommel et al., 1993b). Combined with cooled blood in the epidural veins, the spinal retia may provide some temperature control of the central nervous system (Rommel et al., 1993b).

Carotid bodies, important in regulation of blood flow, have been documented in the harbor seal (Clarke et al., 1986).

The Potential for Thermal Insult to Reproductive Organs

Mammals maintain high and, in most species, relatively uniform core temperatures. Because they live in water, which conducts heat 25 times faster than air at the same temperature, many marine mammals have elevated metabolic rates and/or adaptations to reduce heat loss to the environment (Kooyman et al., 1981; Costa and Williams, 1999). Aquatic mammals with low metabolic rates must live in warm water or possess even more elaborate heat-conserving structures. Most mammalian tissues tolerate limited fluctuations in temperature, and some tissues, such as muscle, perform better at somewhat higher temperatures. However, reproductive tissues are particularly susceptible to thermal insult, and various mechanisms have evolved to protect them (VanDemark and Free, 1970; Blumberg and Moltz, 1988).

In terrestrial mammals, production and storage of viable sperm requires a relatively narrow range of temperatures. Temperatures between 35 and 38°C can effectively block spermatogenesis (Cowles, 1958; 1965). Abdominal temperatures can detrimentally affect long-term storage of spermatozoa in the epididymides in many species (Bedford, 1977). In many mammals, the scrotum provides a cooler environment by allowing the sperm-producing tissues to be positioned outside the abdominal cavity, away from relatively high core temperatures. Additionally, in scrotal mammals, the pampiniform plexus can, via countercurrent heat exchange, reduce the temperature of arterial blood from the core to the testes and help keep testicular temperature below that of the core (Evans, 1993). The skin of the scrotum is well vascularized, has an abundance of sweat glands, and is highly innervated with temperature receptors. Muscles in the scrotal wall involuntarily contract and relax in response to cold and hot temperatures, respectively. The exposed scrotum provides a thermal window through which heat may be transferred to the environment, thereby regulating the temperature of sperm-producing tissues.

Interestingly, the morphological adaptations for streamlining observed in some marine mammals create potentially threatening thermal conditions for the reproductive systems of diving mammals. The primary locomotory muscles of terrestrial mammals are appendicular,

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so much of the locomotory heat energy of the muscle is transferred to the environment rather than directed into the body cavities; this is not the case for ascrotal marine mammals, whose primary locomotory muscles surround the abdominal and pelvic cavities.

A factor that may increase core temperature of marine mammals is change in blood flow patterns during diving. Marine mammals can dramatically redistribute their cardiac output during dives, resulting in severely reduced blood flow to some body tissues, such as muscles and viscera (Elsner and Gooden, 1983; Kooyman, 1985). In terrestrial mammals, redistributions of cardiac output in response to physiological conditions such as exercise, feeding, thermoregulation, and pregnancy are relatively well known (Elsner, 1969; Baker and Chapman, 1977; Baker, 1982; Blumberg and Moltz, 1988). For example, in humans, large increases in muscle temperature (as high as 1°C/min) have been measured during the ischemia at the onset of exercise (Saltin et al., 1968). Surprisingly, the magnitude of routine cardiovascular adjustments undergone by marine mammals during prolonged dives (Elsner, 1999) is approached in terrestrial mammals only during pathological conditions such as hyperthermia and hypovolemic shock. The axial locomotion of pinnipeds, cetaceans, and manatees requires a relatively large thermogenic muscle mass around the vertebral column and abdominal organs. Blubber insulates these thermogenic muscles, suggesting the potential for elevated temperatures at the reproductive systems, particularly during the ischemia of prolonged dives. The temporary absence of cooling blood through locomotory muscles increases the probability of severe thermal consequences for the diving mammal. Abdominal, or partly descended, testes (cryptorchidism) result in sterility in many domestic mammals and humans. Ascrotal testes are typical for many marine mammals, such as phocid seals, dolphins, and manatees. There are vascular adaptations that prevent deep-body hyperthermic insult in cetaceans and phocids (Rommel et al., 1998). In dolphins, cooled venous blood is delivered to an inguinal counter-current heat exchanger to cool the testes and epididymides indirectly, whereas, in phocid seals, cooled venous blood is delivered to an inguinal venous plexus to cool the testes and epididymides directly. Similar structures prevent reproductive hyperthermic insult in females (Rommel et al., 1995).

One additional vascular adaptation that may have significant influence on diving is the presence of cooled blood in the large vascular structures within the vertebral canal, adjacent to the spinal cord. The large epidural veins (dolphins, seals, and manatees) and spinal retia (dolphins) may influence spinal cord temperature and, thus, influence dive capabilities, by modifying regional metabolic rates (Rommel et al., 1993b). The central nervous system is temperature sensitive, and lowering cord temperature influences global metabolic responses.

Skeleton

Knowledge of the skeleton offers landmarks for soft tissue collection and provides an estimate of body size from partial remains (Rommel and Reynolds, in press). Traditionally, the postcranial skeleton is subdivided into axial components (the vertebral column, ribs, and sternabrae, which are "on" the midline) and appendicular components (the forelimbs, hind limbs, and pelvic girdle, which are "off" the midline). The scapulae and humeri of the forelimbs are indirectly attached to the body, essentially by tensile elements (muscles and tendons); in contrast, the hind limbs are attached via a pelvis directly to the vertebral column and thus are able to transmit both tension and compression to the body.

The skeleton supports and protects soft tissues, controls modes of locomotion, and determines overall body size and shape; the marrow of some bones may generate the precursors of certain blood cells. While the animal is alive, bones are continuously remodeled in response to biochemical and biomechanical demands and, thus, offer information that can help

biologists interpret events in the life history of the animal after its death. Skeletal elements contribute to fat (particularly in the cetaceans) and calcium (particularly in the sirenians) storage and thus influence buoyancy.

The sea lion propels itself through the water by its forelimbs, and its skeletal components are relatively massive in that region. On land, its forelimbs can act as fulcrums for shifting the center of mass by changing the shape of its neck and the trunk (for more, see English, 1976a,b; 1977). The permanently aquatic species locomote with a dorsoventral motion of the trunk and elongated tail. This dorsoventral motion of the axial skeleton is characteristic of almost all mammalian locomotion. In contrast, the seal uses lateral undulations of its trunk and hind flippers when swimming (like a fish), yet it may locomote on land with dorsoventral undulations, like its terrestrial ancestors.

Relative motion between vertebrae is controlled, in part, by the size and shape of the intervertebral disks. The intervertebral disks resist the compression that skeletal muscles exert and tend to force vertebrae together. Intervertebral disks are composite structures, with a fibrous outer ring, the annulus fibrosus, and a semiliquid inner mass, the nucleus pulposus. The outermost fibers of the annulus are continuous with the fibers of the periosteum. The flexibility of the vertebral column depends, in part, on the thickness of the disks. Intervertebral disks are a substantial proportion (10 to 30%) of the length of the postcranial vertebral column. The intervertebral disks provide flexibility but are not "responsible" for the general curvature of the spine—the nonparallel vertebral body faces provide the spinal curvature.

For convenience, the vertebral column is separated into five regions, each of which is defined by what is or is not attached to the vertebrae. These regions are cervical, thoracic, lumbar, sacral, and caudal. In some species, the distinctions between vertebrae from each region are unambiguous. However, in some other species the distinctions between adjacent regions are less obvious. This is particularly true in the permanently aquatic species, where there is little or no direct connection between the pelvic vestiges and the vertebral column.

The vertebral formula varies within, as well as among, species. The number of vertebrae, excluding the caudal vertebrae, is surprisingly close to 30 in most mammals (Flower, 1885). Most mammals have seven cervical, or neck, vertebrae (sirenians and two-toed sloth have six and the three-toed sloth has nine), whereas the number of thoracic and lumbar vertebrae varies between species. The number of sacral vertebrae is commonly two to five, but there are exceptions. The number of caudal vertebrae varies widely—long tails usually have numerous caudal vertebrae.

The cervical vertebrae are located cranial to the rib-bearing vertebrae of the thorax. Some cervical vertebrae have movable lateral processes known as cervical ribs, none of which makes contact with the sternum. Typically, the permanently aquatic marine mammals have short necks, even if they have seven cervical vertebrae. However, the external appearance of a short neck in seals is misleading. Close comparison of the seal and sea lion skeletons reveals that they have quite similar neck lengths, although the distribution of body mass is different. Seals often hold their heads close to the thorax, which causes a deep "S" curve in the neck. This provides the seals with a "slingshot potential" for grasping prey (or careless handlers). The shapes of the seal neck vertebrae are complex to allow this curve. Serial fusion (ankylosis) of two or more cervical vertebrae is common in the cetaceans, although in some cetaceans (e.g., the narwhal, beluga, and river dolphins), all the cervical vertebrae are unfused and provide considerable neck mobility.

The rib-bearing vertebrae are the thoracic vertebrae, and the thoracic region is defined by the presence of movable ribs. The authors distinguish between vertebral ribs (E-VBR), which are associated with the vertebrae, and "sternal ribs" (E-SBR), which are associated with the sternum. This distinction is made because some odontocetes, unlike most other mammals,

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have bony rather than cartilaginous sternal ribs (bony "sternal ribs" are also found in the armadillo). "Costal cartilages" is an acceptable alternative term for sternal ribs if the sternal ribs are never ossified (calcification with old age does not count).

Some thoracic vertebrae have ventral vertebral projections called hypapophyses (see the manatee, E-HYP)—not to be confused with chevron bones, which are intervertebral and not part of the caudal vertebrae. In the manatee, the diaphragm is firmly attached along the midline of the central tendon to hypapophyses. Hypapophyses also occur in some cetaceans (e.g., the pygmy and dwarf sperm whales, *Kogia*) in the caudal thorax and cranial lumbar regions. It is assumed that these hypapophyses increase the mechanical advantage of the hypaxial muscles much as do the chevrons (Rommel, 1990).

The neural spines (E-NSP) of thoracic vertebrae of many mammals are often longer than those in any other region of the body. Long neural spines provide mechanical advantage to neck muscles that support a head cantilevered in front of the body. Terrestrial species with large heads tend to have long neural spines, but in aquatic mammals the buoyancy of water negates this reason for long neural spines.

Ribs

Embryologically, ribs and transverse processes develop from the same precursors. Thus, some aspects of ribs are similar to those of transverse processes (E-TPR). It is the formation of a movable joint that distinguishes a rib from a transverse process. An unfinished joint may be indicative of developmental age. In some species (i.e., the manatee) there may be a movable "rib" (pleurapophysis) on one side and an attached "transverse process" on the other side of the same (typically the last thoracic) vertebra (Rommel and Reynolds, 2000).

Ribs may attach to their respective vertebrae at one or more locations (e.g., centrum, transverse process). Typically, the cranialmost ribs have two distinct regions of articulation (capitulum and tuberculum) with juxtaposed vertebrae and are referred to as double headed. The caudalmost ribs have single attachments and are referred to as single headed. In most mammals, the single-headed ribs have lost their tubercula and are attached to their vertebrae at the capitulum on the centrum. In contrast, the single-headed ribs of cetaceans lose their capitula and are attached to their respective vertebrae by their tubercula on the transverse processes (Rommel, 1990). The last ribs (E-LRB) often "float" free from attachment at one or both ends; these ribs tend to be significantly smaller than the ones cranial to them, and they are often lost in preparation of the skeleton.

The ribs of some marine mammals are more flexible than those of their terrestrial counterparts; this flexibility is an adaptation to facilitate diving. Ribs are illustrated in layer E in the correct posture for a healthy animal. Note that all illustrated species but the manatees have oblique angles between the rib shaft and the long axis of the body. As the hydraulic pressures increase with depth, the ribs rotate to avoid bending with changes in thoracic cavity volume.

Sternum

The sternum (D,E-STR) is formed from bilaterally paired, serial elements called sternabrae. The paired elements fuse on the midline, occasionally imperfectly, leaving foramina in the sternum. The cranialmost sternal ribs (E-SRB, also called costal cartilages) extend from the vertebral ribs to articulate firmly with the sternum at the junctions between sternabrae. The first sternal rib articulates with the manubrium (C,D-MAN) cranial to the first intersternabral joint. The manubrium may have an elongate cartilaginous extension (e.g., in seals), and the first sternal rib is often different from the more caudal sternal ribs (typically larger and more robust). In some mysticetes, only the manubrium is formed, and only the first rib has a bony attachment to it. The subsequent ribs articulate with a massive cartilaginous structure that extends from the caudal

aspect of the manubrium (which may be referred to as a pseudosternum). The xiphoid process (E-XIP, last sternabra) is also different; it too may articulate with more than one (often many) sternal rib(s) and have a large cartilaginous extension.

Postthoracic Vertebrae

Some authors avoid the difficulties of defining the lumbar, sacral, and caudal regions in the permanently aquatic species by lumping them into one category—the postthoracic vertebrae; by “lumping,” these authors avoid some interesting comparisons. Generally, the lumbar vertebrae are trunk vertebrae that do not bear ribs, and the number of lumbar vertebrae is closely linked to the number of thoracic vertebrae, but not always. Note that the caudal vertebrae of cetaceans start with the start of the chevron bones, and extend to the tip of the tail (fluke notch, A-NOC), whereas manatee vertebrae stop 3 to 9% of the total body length (as much as 17 cm in a large specimen) from the fluke tip (E-LVR).

Sacral Vertebrae

There are at least two commonly accepted definitions for sacral vertebrae: (1) serial fusion of postlumbar vertebrae, only some of which may attach to the pelvis (the human os sacrum), and (2) only those that attach to the ilium, whether or not they are serially fused. Both definitions have merit. Within species, the number of serially ankylosed vertebrae may vary, particularly with age. Additional landmarks are the exit of spinal nerves from the neural canal and the foramina for segmental blood vessels. In species with a bony attachment between the vertebral column and the pelvis, the definition of sacral is easy. However, in the cetaceans and some sirenians (dugongs have a ligamentous attachment between the vertebral column and the pelvic vestiges), there are no sacral vertebrae by definition.

Chevron Bones

The chevron bones are ventral intervertebral ossifications in the caudal region. By definition, each is associated with the vertebra cranial to it (note that there is some controversy over which is the first caudal vertebra; see Rommel, 1990). Chevron bone pairs are juxtaposed (in manatees) or fused (in dolphins, but not always) at their ventral apexes and articulate dorsally with the vertebral column to form a triangular channel. Within the channel (hemal canal) are found the blood vessels to and from the tail. In some species, the ventral aspects of each chevron bone fuse and may continue as a robust ventral protection that can function to increase the mechanical advantage of the hypaxial muscles to ventroflex the tail. In some individuals, the first two or three chevrons may remain open ventrally but fuse serially on either side.

Pectoral Limb Complex

The forelimb skeleton includes the scapula, humerus, radius and ulna, and manus. The scapula is attached to the axial skeleton only by muscles. There is no functional clavicle in marine mammals (Strickler, 1978; Klima et al., 1980). The scapula consists of an essentially flat (slightly concave medially) blade with an elongate scapular spine extending laterally from it. The distal tip of the spine, if present, is the acromion. The scapular spine is roughly in the center of the scapular blade in most mammals. However, in cetaceans, the scapular spine is close to the cranial margin of the scapular blade, and both the acromion and coracoid extend beyond the leading edge of the blade.

The humerus (E-HUM) has a ball-and-socket articulation in the glenoid fossa of the scapula—this is a very flexible joint. The humerus articulates distally with the radius (E-RAD) and ulna (E-ULN); this is also a flexible joint in most other mammals, but it is constrained in cetaceans. The olecranon is a proximal extension of the ulna that increases the mechanical advantage of the

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The distal radius and ulna articulate with the proximal aspect of the manus. The manus includes the carpals, metacarpals, and phalanges (English, 1976). There are five "columns" of phalanges, each of which is called a digit. The digits are numbered starting from the cranial aspect (the thumb, which is digit one, associated with the radius).

In many of the marine mammals, the "long" bones of the pectoral limb (humerus, radius, and ulna) are relatively short, and the phalanges are elongated. Cetaceans are unique among mammals in that they have more than the maximum number of phalanges found in all other mammals; this condition is known as hyperphalangy (Howell, 1930). The number varies within each species—the bottlenose dolphin has a maximum number of nine digits.

Pelvic Limb Complex

The typical mammalian pelvis is made of bilaterally paired bones: ilium, ischium, pubis, and acetabular bone (the paired ossa coxarum), one to three caudal vertebrae, and the sacrum. Each of the halves of the pelvis attaches (via the ilium) to one or more sacral vertebrae. The crest of the ilium (C,E-ILC) is a prominent landmark that flares forward and outward beyond the region of attachment between the sacrum and the ilium. The ossa coxarum join ventrally along the midline at the pelvic symphysis, which incorporates the pubic bone cranially and the ischiatic bone caudally. In the permanently aquatic marine mammals, there is but a vestige of a pelvis (E-PEL) to which portions of the rectus abdominis muscles (B-REC) may attach. Additionally, the crura of the penis may be supported by these vestiges (Fagone et al., 2000). In some of the large whales, there is occasionally a vestige of a hind limb articulating with the pelvic vestige.

The hind limb, if present, articulates with the vertebral column via a ball-and-socket joint at the hip. The proximal limb bone is the femur (C,E-FEM). The socket of the pelvis, the acetabulum, receives the head of the femur. Distally, the femur articulates with the tibia and the fibula (as the stifle joint). The tibia and fibula distally articulate with the pes, or foot. The pes is composed of the tarsals proximally, the metatarsals, and the phalanges distally. Note that the digits of the sea lion terminate a significant distance from the tips of the flipper.

Sexual Dimorphisms

In many mammals, the adult males are larger than the adult females. In marine mammals, this size difference is at its extreme in otariids, elephant seals, and the sperm whales. In contrast, the adult females of the baleen whales and some other species are larger than the adult males. In the permanently aquatic marine mammals, there may be sexual dimorphisms in the pelvic vestiges (Fagone et al., 2000). The penises of mammals are supported by crura consisting of a tough outer component (tunica albuginea) and the cavernous erectile central component (corpus cavernosum), which attach to the ischiatic bones of the pelvis. The muscles that engorge the penis with blood are also attached to the pelvis. Presumably, the mechanical forces associated with these muscles influence pelvic vestige size and shape, particularly in manatees.

Males in some groups of mammals, particularly the carnivores, have a bone within the penis (the baculum) that helps support the penis. Growth rate of the os penis differs from that of the appendicular skeleton in some species (Miller et al., 1998).

Bone Marrow

Bone marrow of cetaceans is vertebral as well as costal. Because the marrow cavity of the bones of marine mammals generally retains abundant trabecular bone throughout life, it is best to examine the marrow histologically via impression smears of cut surface or in decalcified sections. Most manatee bones are amedullary (Fawcett, 1942), so usable marrow impression smears are restricted to vertebrae.

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