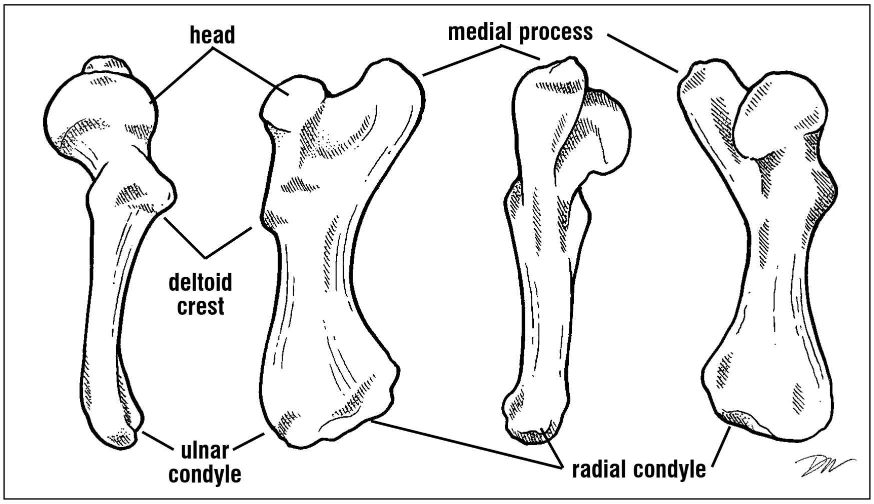
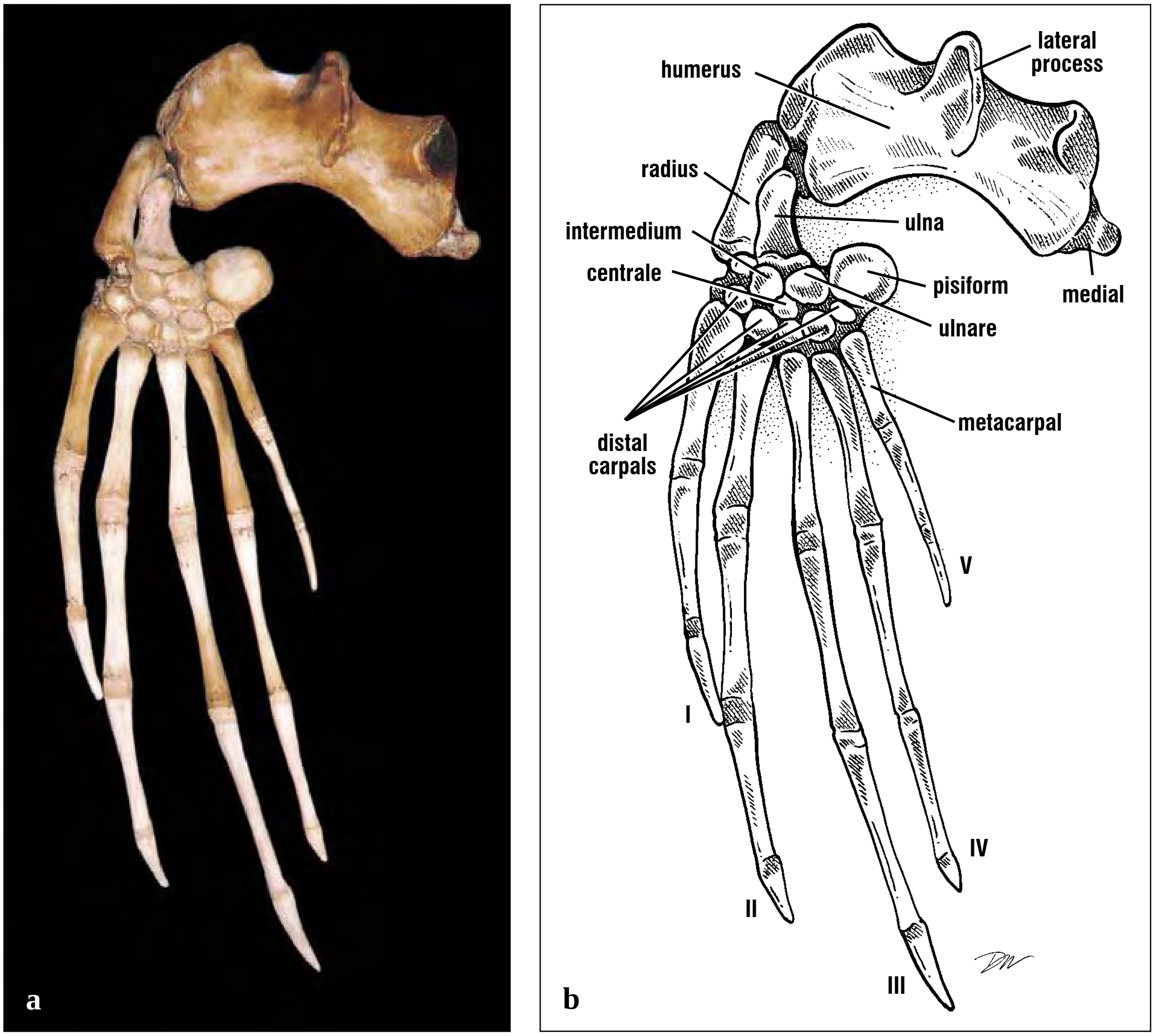
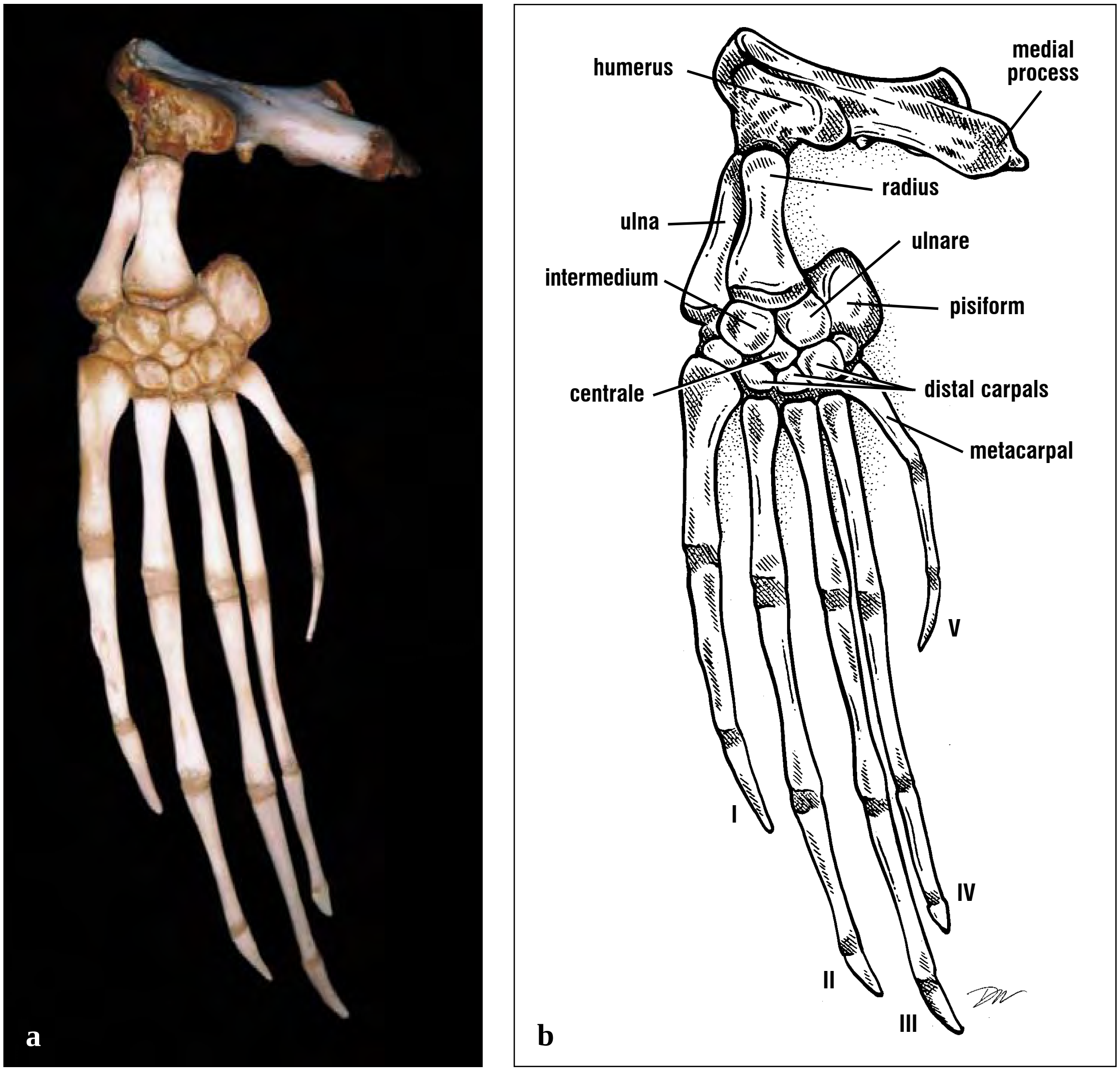


Fig. 101. *The cheloniid humerus is distinctive in its form with a slightly offset head and enlarged medial process. Almost opposite the medial process and just distal to the head is a U-shaped lateral process (deltoid crest) to which attaches the major ventral swimming muscles. (After Wyneken, 1988).*



Figs. 102a and 102b. *Dorsal view of a leatherback flipper.*

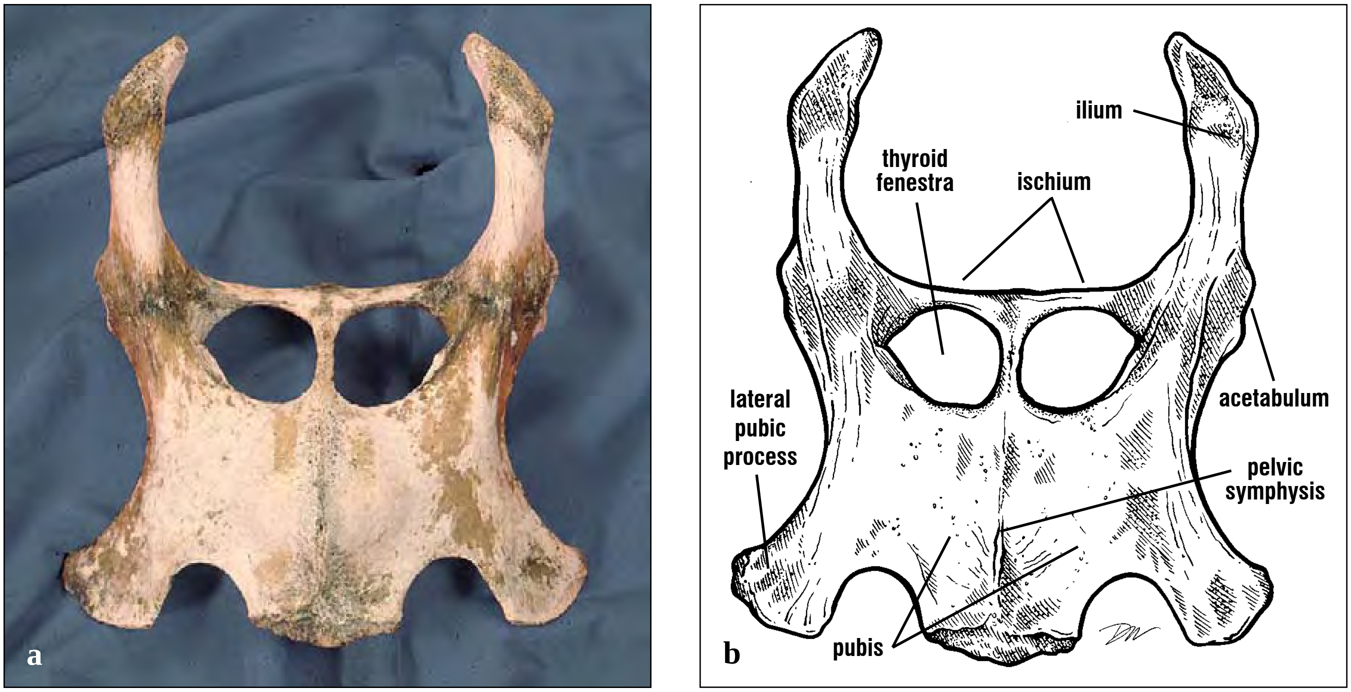


Figs. 103a and 103b. *Ventral view of the leatherback flipper. The articulated forelimbs of this leatherback shows some of the extensive cartilages at the bone ends and the extreme elongation of the digits. The large humerus has an almost primitive form with its flattened profile and extended medial process. The head and distal articulations to the radius and ulna are largely cartilaginous.*

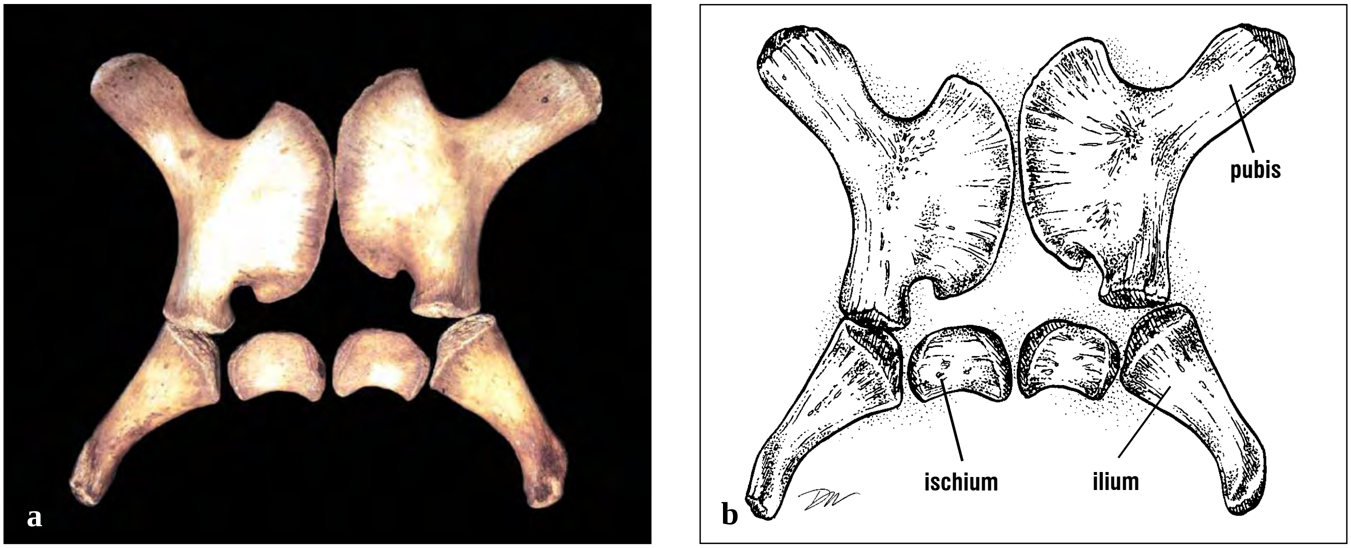
The pelvis is composed of 3 pairs of bones; **pubis, ischium,** and **ilium**. The pubic bones and the ischia form the ventrally positioned part of the pelvis (Fig. 106). The two ilia are oriented dorsoventrally, articulate with the sacral vertebrae, and attach the pelvis to the carapace via ligaments. All 3 bones form the **acetabulum** (hip socket) on each side. They are separate bones joined by cartilage in hatchlings but quickly ossify and fuse to form a single structure in older turtles. The pelvic bones of the leatherback, however, remain connected by cartilage throughout life (Fig. 107) and become separate elements when skeletons are prepared.

Fig. 104. *Chondro-osseus bone formation. Vascular channels are seen in this cut end of a leatherback humerus.*

Fig. 105. *Longitudinal sections through humerii. The loggerhead humerus (top) has relatively more lamellar bone (light color) than in the leatherback humerus (bottom). The lamellar bone is deposited in layers in some cheloniid species and populations; in others, layers are not distinct.*



Figs. 106a and 106b. *This loggerhead pelvis, dorsal view, shows the 3 bones fused (pubis, ischium, and ilium) that form each side. The epipubic cartilages that would form the anterior edge of the pelvis in life are missing from this preparation. The ilia articulate with the sacral vertebrae and carapace. Anterior is toward the bottom of the picture.*



Figs. 107a and 107b. *The pelvis of the leatherback is composed of both bone and cartilage throughout life. Hence, skeletal preparations of the pelvis usually result in 3 pairs of bones which do not retain their spatial relationships. Anterior is toward the top of the picture.*

The hind limb articulates with the pelvis via the head of the femur which fits in the acetabulum. The femur has a relatively straight shaft with a strongly offset head. There are **major** and **minor trochanters** distal to the head (Fig. 108); these are attachments for most of the thigh retractors and adductors, respectively. The distal femur articulates with the tibia and fibula. The short ankle consists of the **calcaneum, astragalus,** and **distal tarsals**. There are five digits. The 1st and 5th metatarsals are wide and flat and the phalanges are extended adding breadth to the distal hind limb area (Figs. 109 - 110).

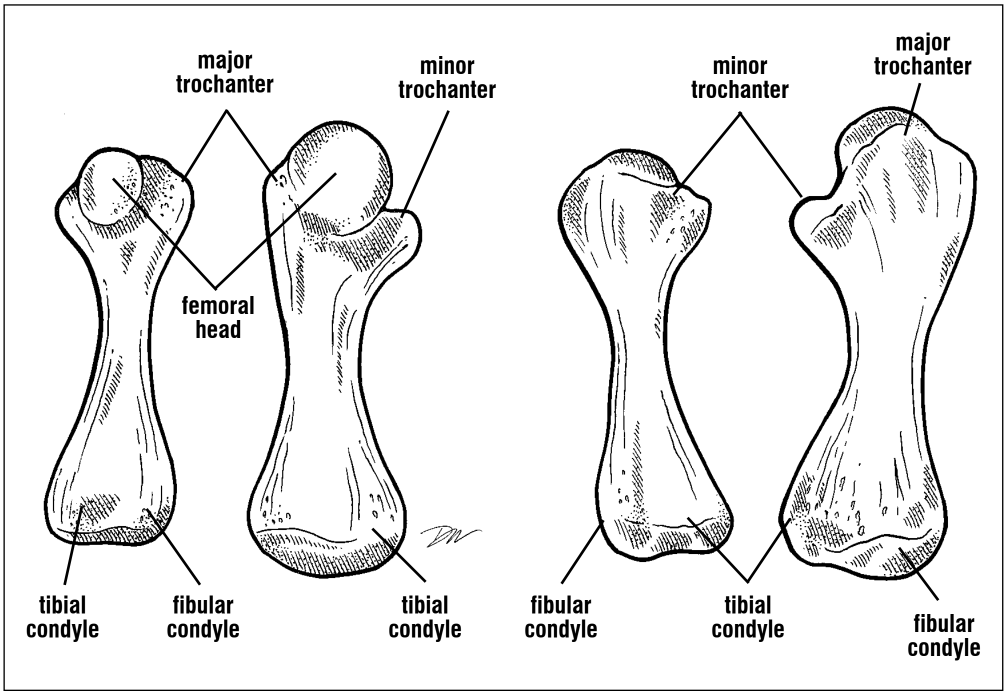
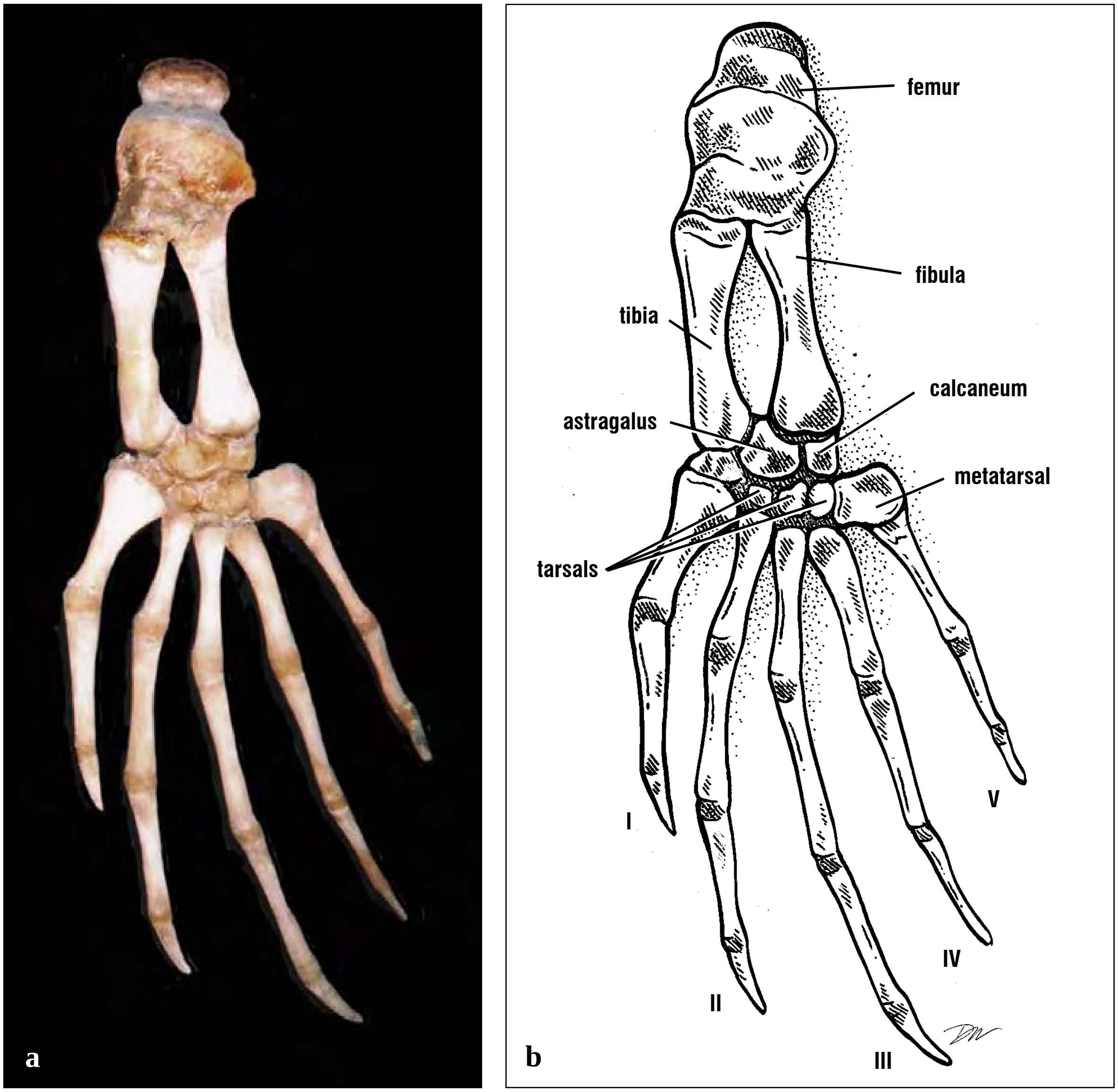
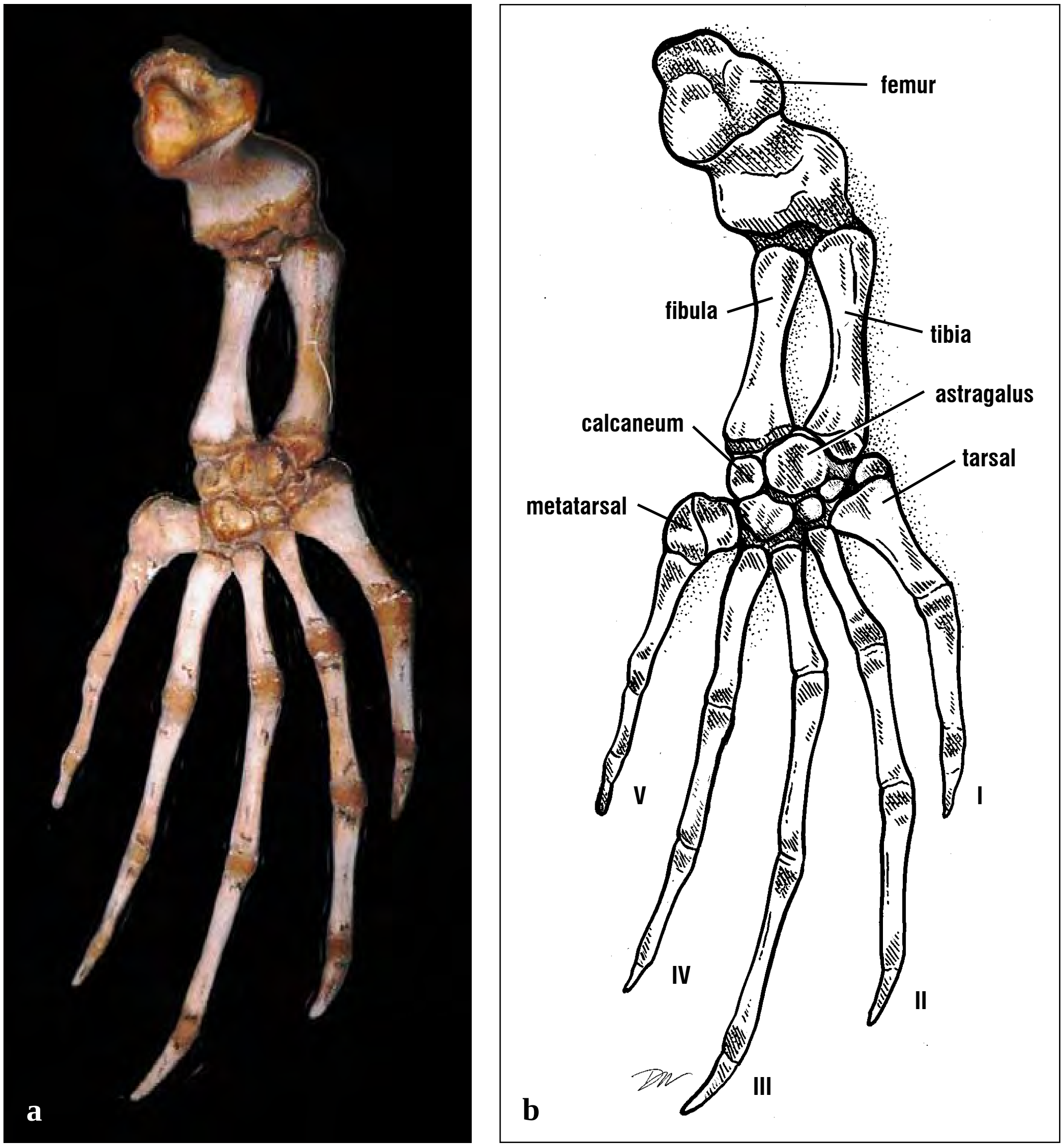


Fig. 108. *Left and right femurs anterior view (left) immature turtle, posterior view (right) mature turtle. The femur, an hour glass-shaped bone, has an offset head. The trochanters become more pronounced as the turtles age.*



Figs. 109a and 109b. *Dorsal view of a leatherback hind limb. The articulated hind limb shows the extensive cartilages between bones that are typical of the leatherback skeleton. The hind foot is wide and the digits somewhat elongated. Digits are designated by numbers, with **I** being the digit on the tibial side and **V** on the fibular side.*



Figs. 110a and 110b. *Ventral view of the leatherback hind limb. The femur is the bony element of the thigh, the tibia and fibula are the bony elements of the shank. The ends of these bones are cartilaginous. The ankle is somewhat flattened and laterally expanded, resulting in wide placement of the digits. This architecture contributes to the rudder-shape of the hind limb.*

Muscle Anatomy

The muscles are responsible for moving structures, modifying the function of other muscles, and stabilizing joints. Muscles originate and insert via tendons. The origin of a muscle is its fixed point while the insertion is typically the point that it moves. Muscles can attach via their tendons to bones, muscles, skin or eyes. Where known, the innervations of the muscles are reported. For reading ease, the designation of *M.*, prior to muscles names, has been omitted. Names and key concepts are given in bold the first time the muscle is discussed.

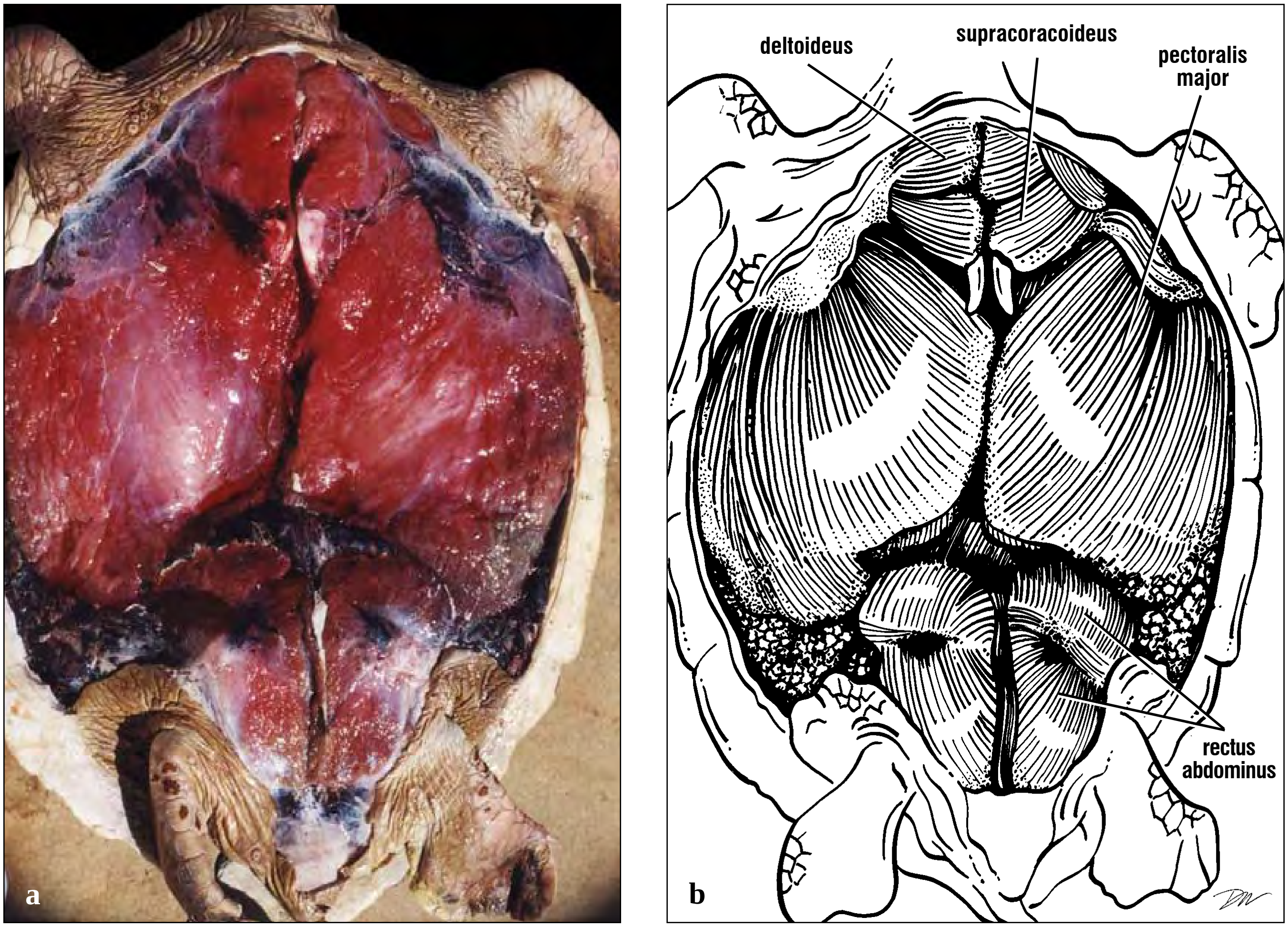
Muscle functions are described with each figure. As they apply to sea turtles, these functions are as follows. **Flexion** bends one part relative to another at a joint; **extension** straightens those parts. **Protraction** moves one part (usually a limb) out and forward; **retraction** moves that part in and back. **Abduction** moves a part away from the ventral surface; **adduction** brings the part toward the body's ventral surface. **Rotation** turns a structure. **Depressor** muscles open (a special form of abduction) a structure, jaws in this case, while **levators** close jaws (a kind of adduction).

Muscle groups. The muscles described here are the major or large muscles (detailed discussion of most muscles can be found in the primary literature). For convenience, muscles are grouped by region; **axial** muscles, include the head muscles; **ventral** muscles include both proximal pectoral and pelvic muscles that are associated with the plastron; **forelimb** and **respiratory** muscles are those found on the flippers, carapace, and scapula involved in flipper movements and breathing. **Posterior** muscles are the large muscles of the hip, thigh, and lower leg. Muscles of the flipper blade and hind foot are not discussed or illustrated in detail here because they are obscured by extensive connective tissue and are difficult for most to identify, even with special dissection equipment and techniques.

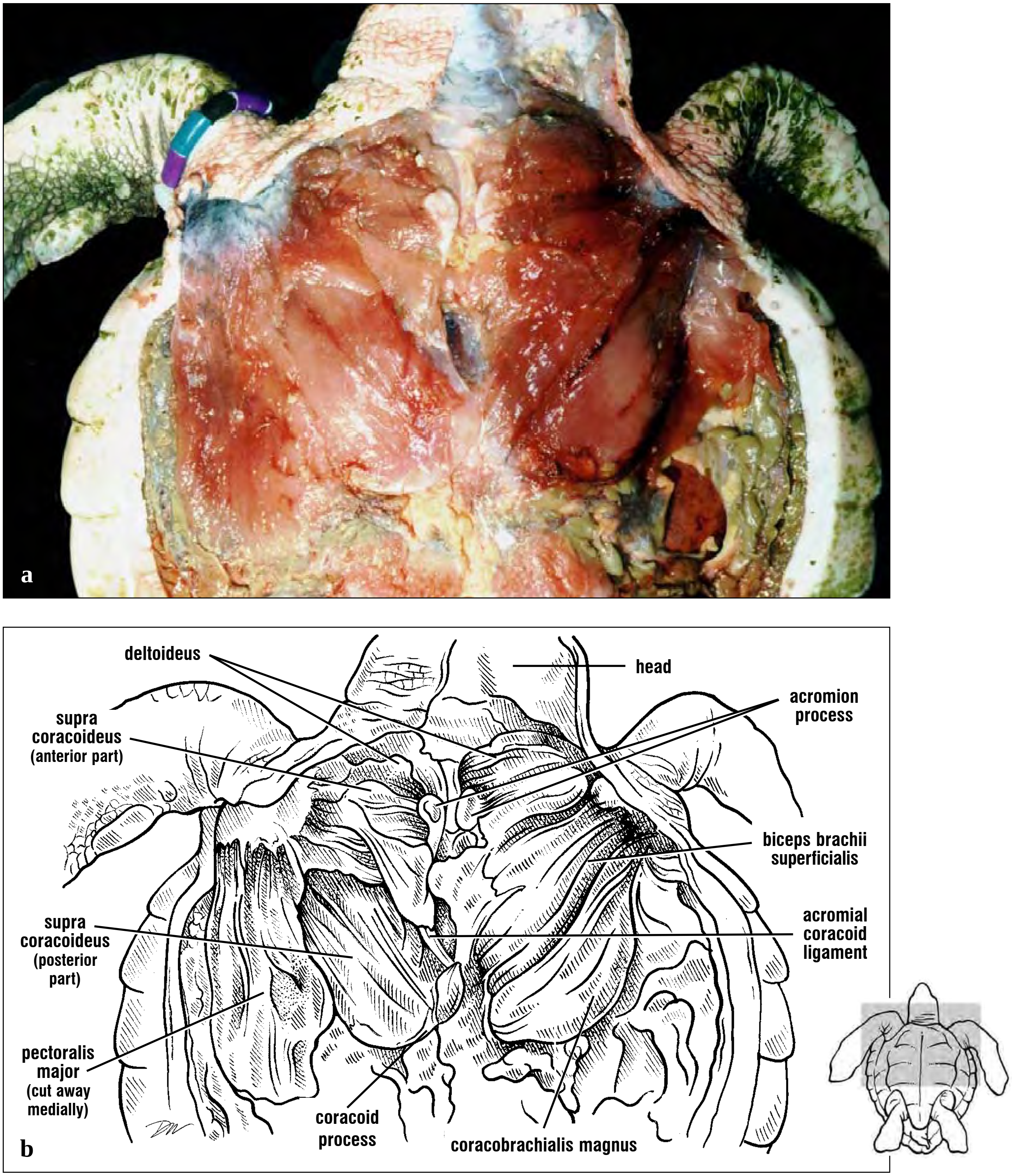
Ventral Muscles. The massive ventral musculature is found after removing the plastron (Fig. 111). This musculature is dominated by a superficial muscle, the **pectoralis major**, which originates on the plastron and inserts on the lateral process and shaft of the humerus. Anterior to the pectoralis and ventral to the acromion processes are two muscles: the **deltoideus** (ventral part), which originates on the ventral scapula, acromion, and anterior plastron bones and the **supracoracoideus,** which has several subdivisions. Its anterior part originates on the acromion (Figs. 112-114). Both the deltoideus and the anterior part of the supracoracoideus insert on the lateral process of the humerus. These 3 ventral muscles function in swimming and respiration (by movement of the shoulders and plastron). Their innervations are via the supracoracoid nerve from the ventral portion of the **brachial plexus** (see Nervous System, Figs. 204-206).

After removing the pectoralis major, deep locomotor muscles are found associated with the pectoral girdle (Figs. 112-114). The **biceps brachii** has several subdivisions, or heads, in sea turtles. The superficial head (Figs. 112-114) originates on the coracoid and extends via a long tendon to insert on the radius and ulna; the profundus head inserts on the humerus and radius. Innervation is via the inferior brachial flexor and median nerves. The **coracobrachialis magnus** originates on the dorsal side of coracoid process and inserts on the medial process of the humerus. The posterior part of the **supracoracoideus** (Fig. 112) originates on the coracoid and its cartilage and inserts in the lateral process of the humerus. These muscles are innervated by the supracoracoid nerve. There is an extensive series of arteries and veins running within and between these very active muscles (Fig. 114).

A pair of superficial posterior muscles, the left and right **rectus abdominis** (Fig. 111) are found ventrally. Each originates on the lateral pubis and inserts on the plastron. They stabilize the pelvis and may function in compressing the plastron during breathing.



Figs. 111a and 111b. *Superficial ventral muscles of the pectoral and pelvic girdles. The large pectoralis major is a forelimb retractor and adductor. Both the deltoideus and the supracoracoideus protract and abduct the humerus. The rectus abdominus is a pelvic stabilizer. Anterior is toward the top of the picture.*



Figs. 112a and 112b. *The deep pectoral muscles are exposed after removal of the pectoralis major. These forelimb retractors, separated on the animal's left (right in picture), are the biceps brachii superficialis and coracobrachialis magnus. The posterior part of the supracoracoideus both adducts and retracts the flipper.*

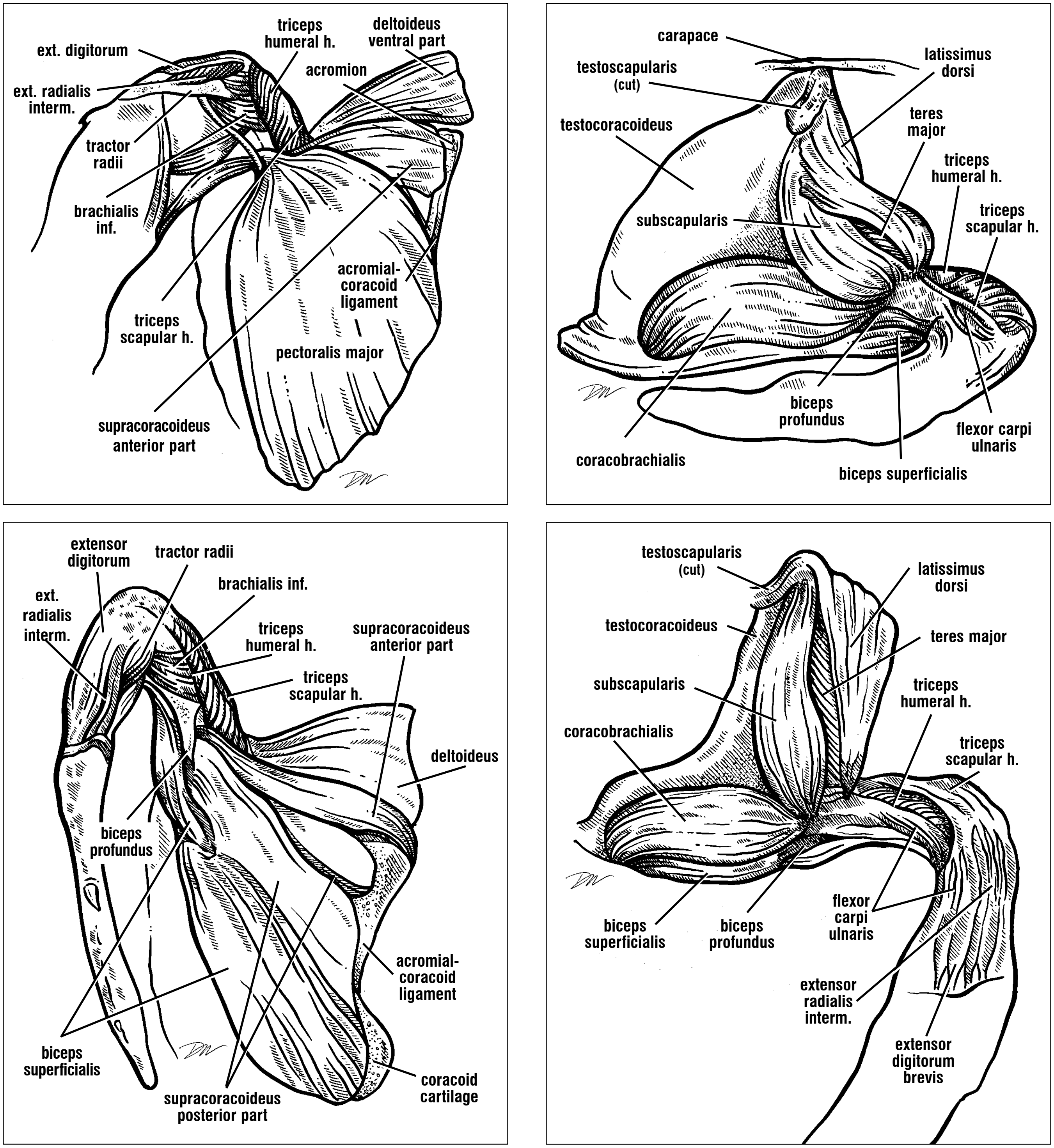
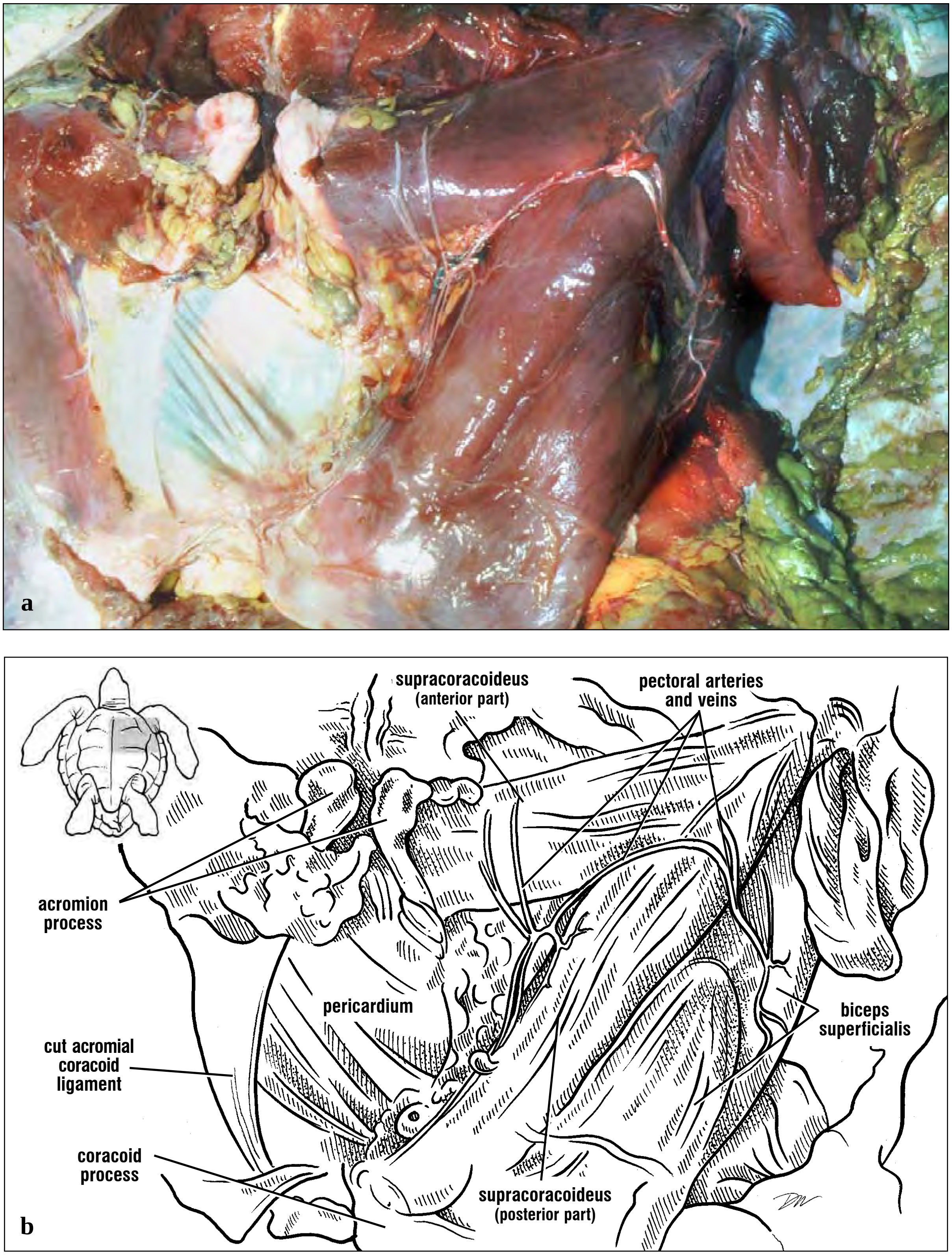


Fig. 113. *Diagrams of cheloniid right shoulder muscles including locomotor and respiratory muscles. Superficial ventral muscles (top left), deep ventral muscles (bottom left), posterior muscles (bottom right), and lateral muscles (top right). The extensor digitorum, extensor radialis intermedius, tractor radii, and flexor carpi all control the extension and flexion of the flipper blade. Ext.= extensor, h.= head, Inf.= inferior, Interm.= intermedialis. (After Wyneken, 1988)*

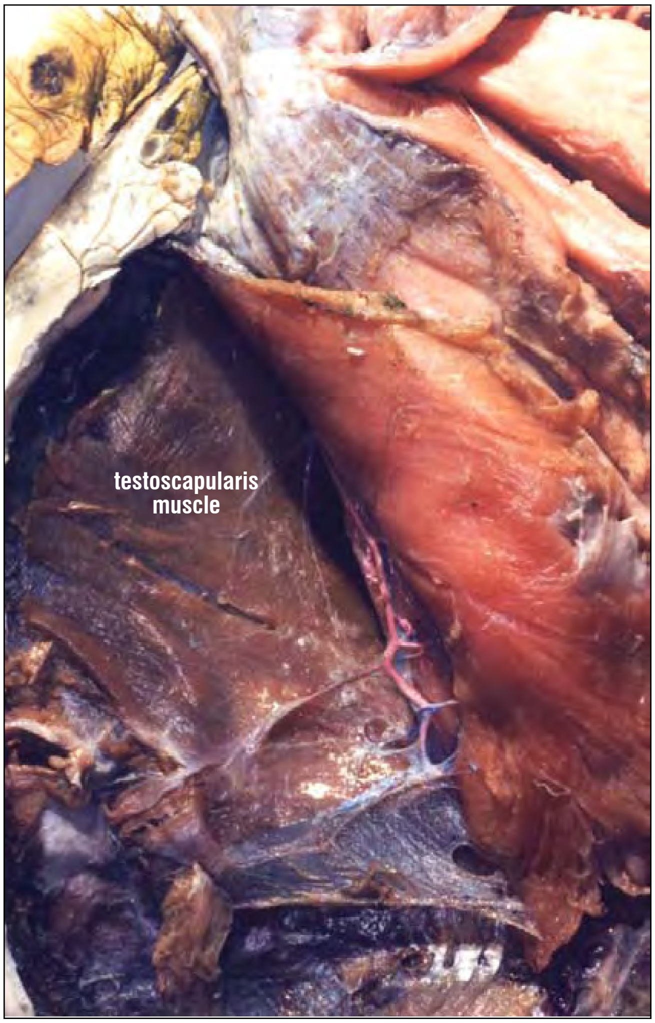


Figs. 114a and 114b. *The deep pectoral muscles of the animal's right side are shown in detail. The supracoracoideus has two parts: posterior, which protracts and anterior, which retracts the forelimb.*

Forelimb and Respiratory Muscles. The **latissimus dorsi/teres major complex**, the scapular head of the **deltoideus**, and the **subscapularis** originate on the carapace and/or shoulder girdle and insert on the proximal humerus (Fig. 113). The latissimus dorsi and teres major together originate on the scapula and the carapace from the attachment point of the scapula, along the first pleural bone to the anterior peripheral bones. They insert via a common tendon just distal to the head of the humerus. The scapular head of the deltoideus arises from the anterior scapula and inserts on the lateral process and shaft of the humerus. The subscapularis muscle is very large, originates on the medial and posterior scapula, and inserts on the large medial process and the shaft of the humerus. These muscles are innervated by the deltoid nerve (a branch of the brachial plexus).

There are two sheet-like respiratory muscles located dorsally, which are often destroyed when removing the pectoral girdles (Figs. 113 and 115). These are the **testocoracoideus** (origin: carapace near the anterior inframarginals; insertion: dorsal coracoid) and **testoscapularis** (origin: carapace posterior to the latissimus dorsi; insertion: dorsal scapula and the scapular attachment to the carapace). They are innervated by cervical spinal nerves.

The remaining dorsal shoulder muscle, the **triceps brachii** (= triceps superficialis) has two heads in cheloniid sea turtles (Figs. 113-116). The humeral head arises from the humerus, and the scapular head arises from the scapula. Both converge to form a common tendon inserting on the proximal ulna. This muscle may have only a humeral head in *Dermochelys*. The triceps is innervated by the superficial radial nerve (a branch from the superior brachial nerve of the brachial plexus).



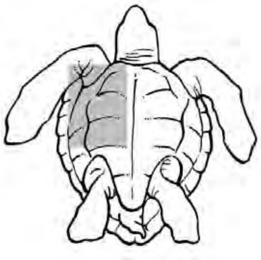


Fig. 115. *Ventral pectoral muscles with arteries and veins. The pectoral artery is found running along the deep muscles of the shoulder. The testoscapularis, a respiratory muscle, is deep to the pectoralis. Other pectoral muscles originating on the coracoid are reflected medially (to the right) in this picture.*

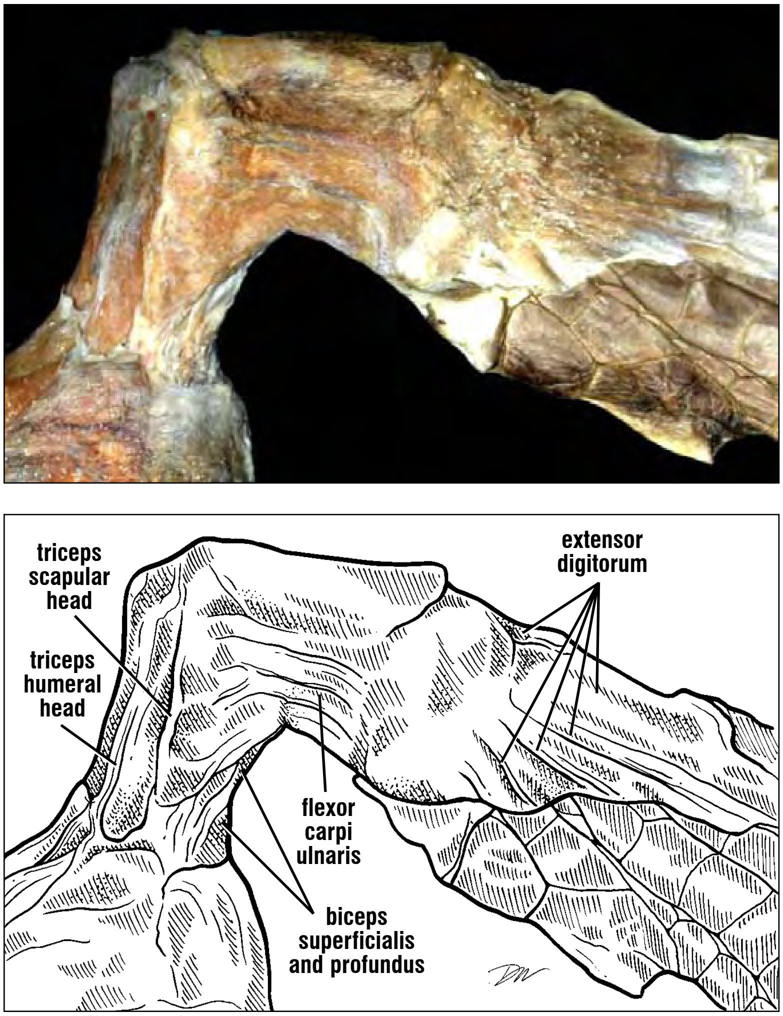


Fig. 116. *Superficial dorsal forelimb muscles (right). The two heads of the triceps brachii, (triceps scapular head and triceps humeral head) are forelimb adductors, which twist the flipper. The more medial biceps and flexor carpi ulnaris muscles flex the flipper blade. The extensor digitorum muscle becomes diffuse in adults as fibrous connective tissue stiffens the flipper blade. Young turtles can extend the digits, somewhat mature turtles cannot.*

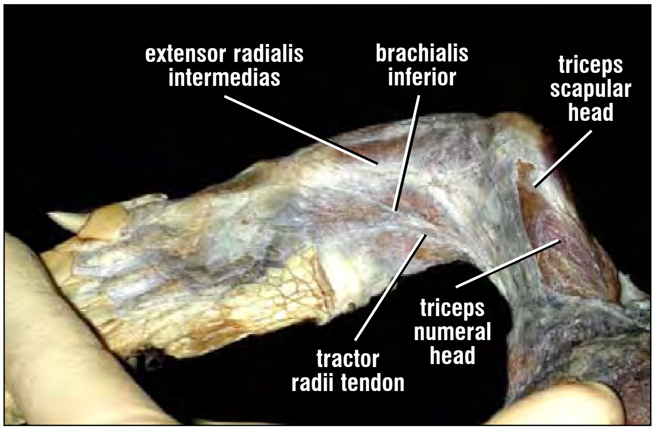


Fig. 117. *Ventral forelimb muscles (right). Most of the ventral muscles flex the flipper blade relative to the upper arm. The extensor radialis extends the flipper. The scapular head of the triceps may twist the flipper blade along its axis, or abduct the forearm.*

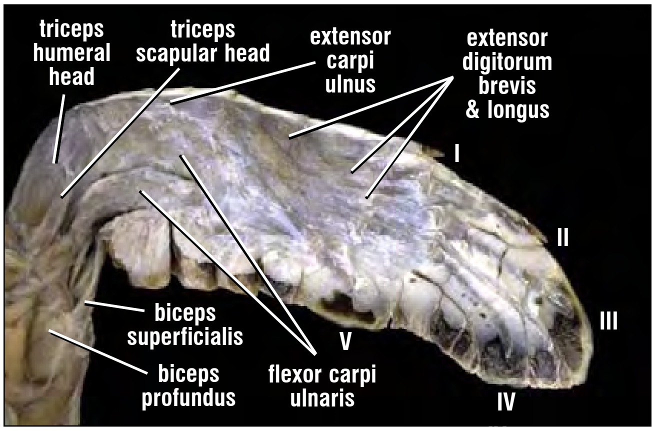
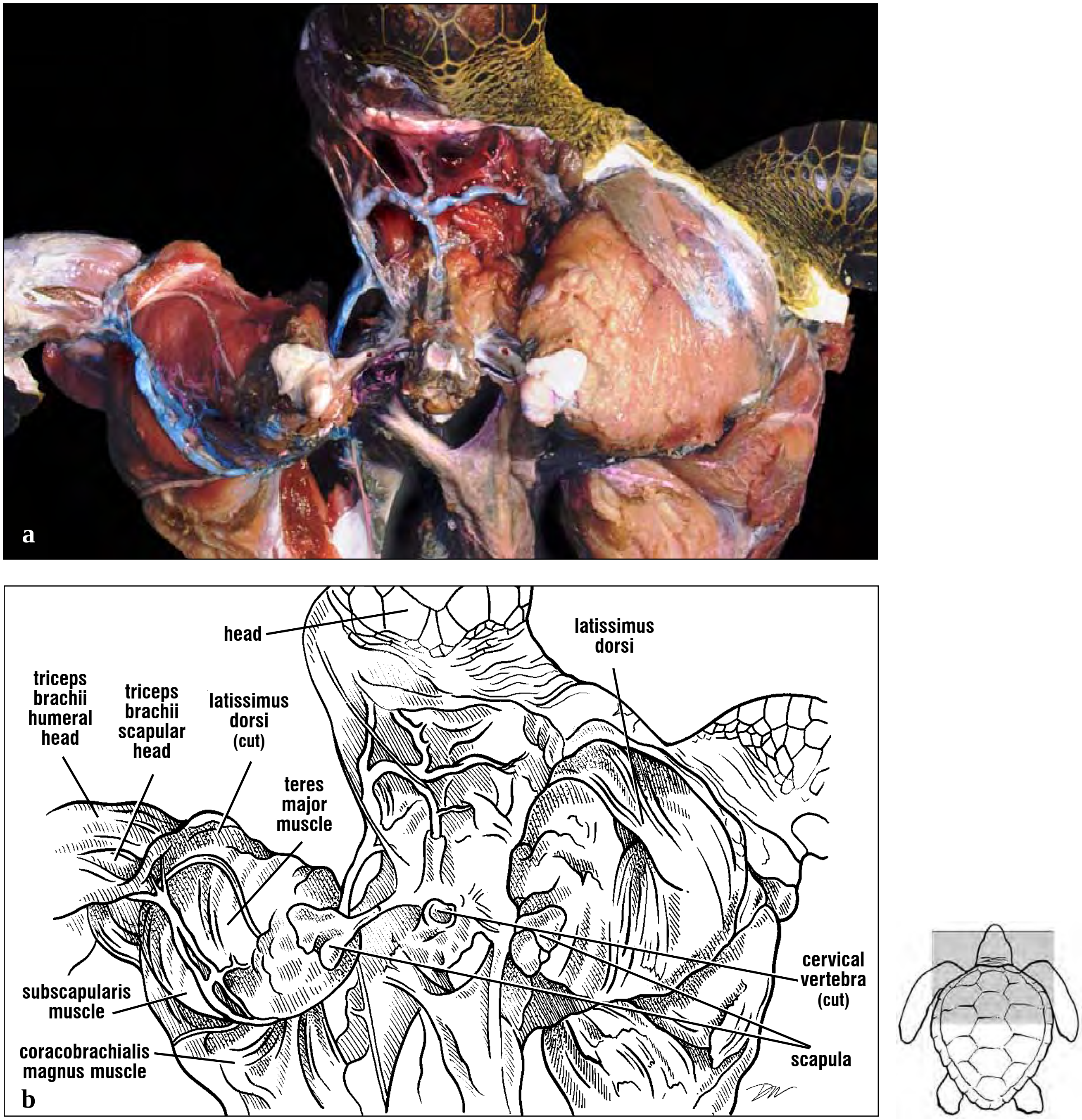
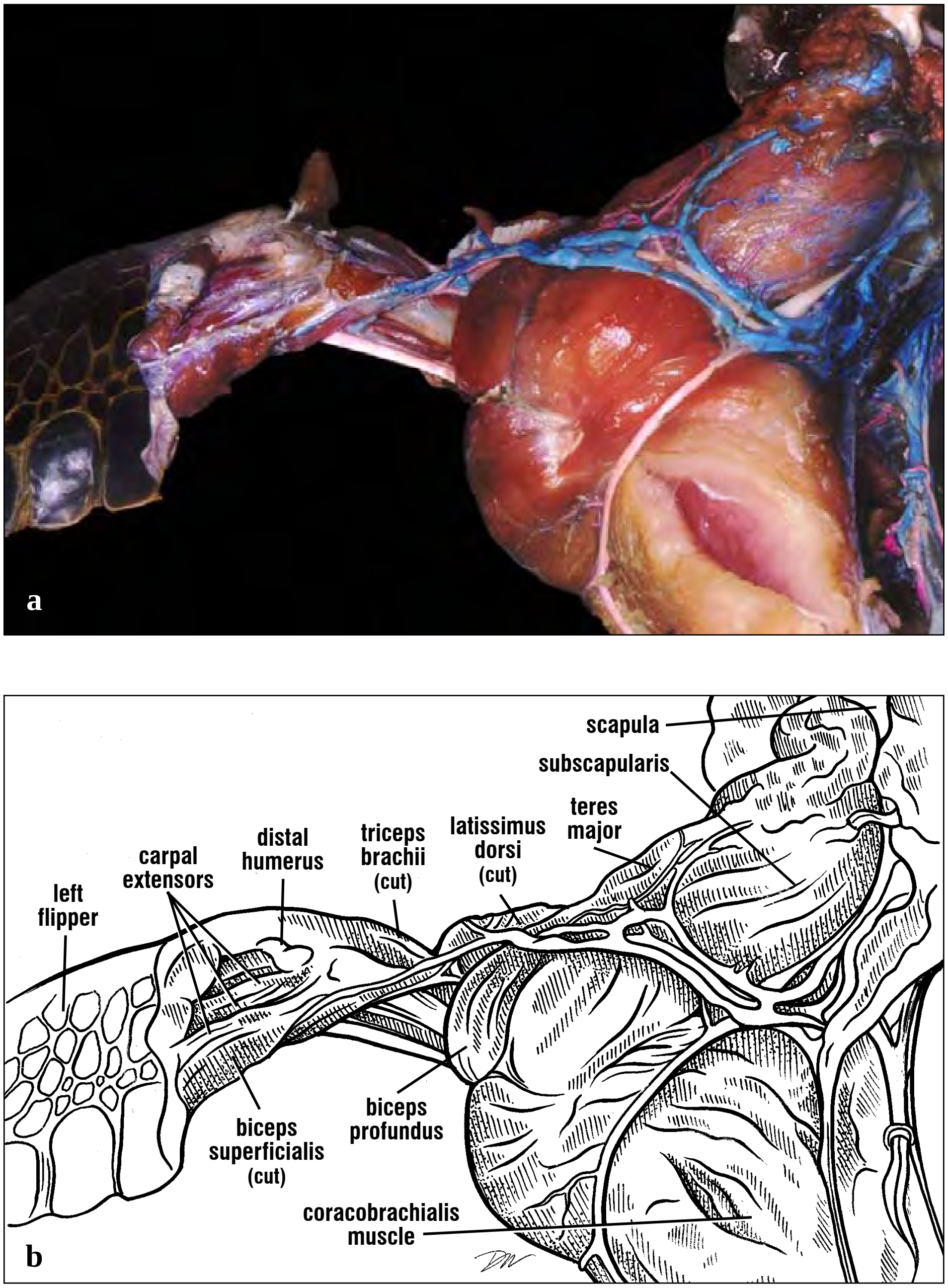


Fig. 118. *Dorsal forelimb muscles of an immature hawksbill. In young animals, the muscle divisions of the forearm and the flipper, particularly, are more obvious than in older animals. Less connective tissue is present and the digits can flex and extend to a limited extent.*

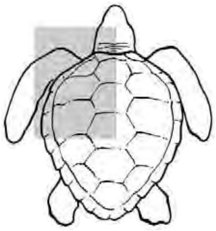


Figs. 119a and 119b. *Dorsal view of the pectoral musculature. The carapace, skin and fat have been removed (from left). The head, cut cervical vertebra, and scapular ends provide landmarks for orientation. The latissimus dorsi, a large sheet-like muscle, is shown intact (animal's right) and cut (animal's left). It, plus the teres major and deltoideus (scapular head, not shown), abduct and sometimes protract the flipper. The large subscapularis is a strong flipper protractor. The coracobrachialis, a ventral muscle, is seen extending from the shoulder posteriorly, toward its origin, the coracoid.*

The biceps muscle may have one or two parts (Figs. 112 and 114). When two heads are present, the **biceps superficialis** arises from the coracoid and inserts on the pisiform of the wrist. The muscle has two bellies in series, with a short tendon in the middle. The second and most prominent head, the **biceps profundus**, also originates on the posterior coracoid, but ventral to the biceps superficialis and inserts via a tendon with the **brachialis** on the ulna (Fig. 114). In *Dermochelys* and *Lepidochelys*, often there is just a single head inserting on the radius and ulna.



Figs. 120a and 120b. *The pectoral muscles of the left shoulder, arm and flipper. The large subscapularis covers most of the scapula. The large coracobrachialis is seen ventrally, covering much of the coracoid. The biceps muscle has one or two heads (varying among species and among individuals). The biceps superficialis extends from the shoulder (mostly the coracoid) to the pisiform bone of the wrist, and probably helps control the twist or rotation of the flipper blade. The biceps profundus (seen only as a partial separation here) acts as a flipper retractor and a flexor of the flipper blade at the elbow.*



Axial Muscles. Most axial muscles are associated with the neck and tail of sea turtles. The majority of the neck muscles are illustrated with the neck circulation (Figs. 131, 141, 143-153). These include the transverse cervical muscles, and the biventer cervical muscle. Here, the superficial muscles of the throat and the jaw muscles are described. The tail musculature is not discussed because it has not been studied in any detail.

The major deep muscles of the neck are the **longus colli** and **retrahens colli**. The longus colli muscles are short, segmentally arranged, and travel obliquely between successive cervical vertebrae; they serve to extend the neck. The retrahens colli originate on the cervical vertebrae and extend posteriorly to insert on the dorsal vertebral elements of the carapace. They are neck flexors and retractors, to the extent that marine turtles extend and retract the neck.

Head Muscles. Just beneath the skin of the throat is a thin layer of muscle, the **intermandibularis**, which has fibers running between the two dentary bones. It inserts on a flat midline tendon (raphe) that runs the length of the throat (Fig. 121). The intermandibularis becomes the **constrictor colli** posterior to the jaw joint (Fig. 121), originating on a dorsolateral cervical tendon. Just deep to the intermandibularis are muscles running obliquely between the jaws and inserting on the hyoid, the **geniohyoideus**. Posterior to the geniohyoideus is a pair of strap-like muscles, the **coracohyoideus** that extend to the hyoid apparatus from the coracoid (Figs. 122-123). These muscles assist in depressing the jaw, swallowing, and pumping the throat (gular flutter). They are innervated by the facial nerve. Muscles of the tongue, innervated by the hypoglossal nerve, and the glossopharyngeal nerve are not described here.

The jaw muscles of turtles are mostly located inside the skull. Because of these deep positions, most are described but not illustrated. Unlike mammals, turtles lack a **mandibularis** muscle; instead they have an **adductor mandibulae** with several heads. The heads originate on the parietal, supraoccipital, quadrate, prootic, and opisthotic bones (Fig. 31) and converge on a tendon that inserts primarily on the lower jaw (dentary, with small insertions on the squamosal bone posterior to the jaw joint). Medial to the adductor mandibulae complex is a pair of connected muscles. The intermandibularis muscle runs from the lower jaw to the tendon of the **pseudotemporalis** muscle which itself continues to the parietal bone. These jaw closing muscles are all innervated by the **trigeminal nerve**. The jaws

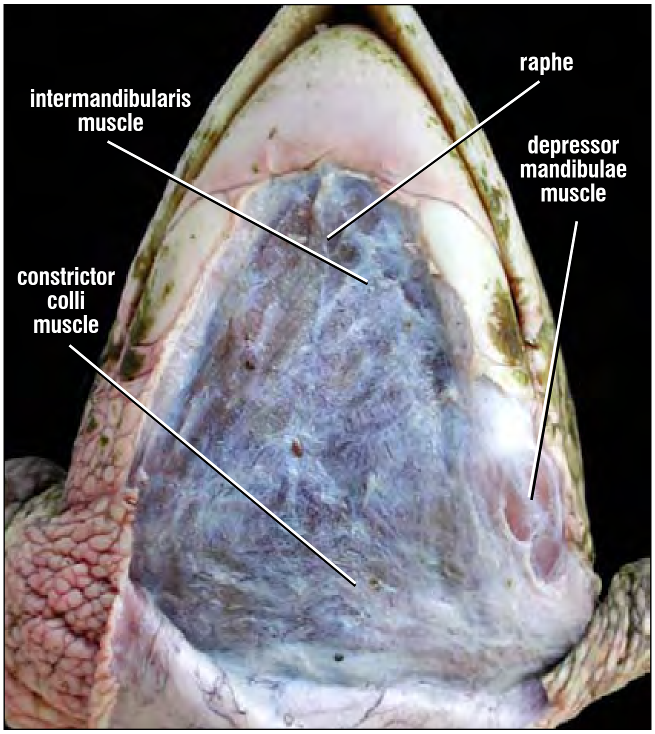
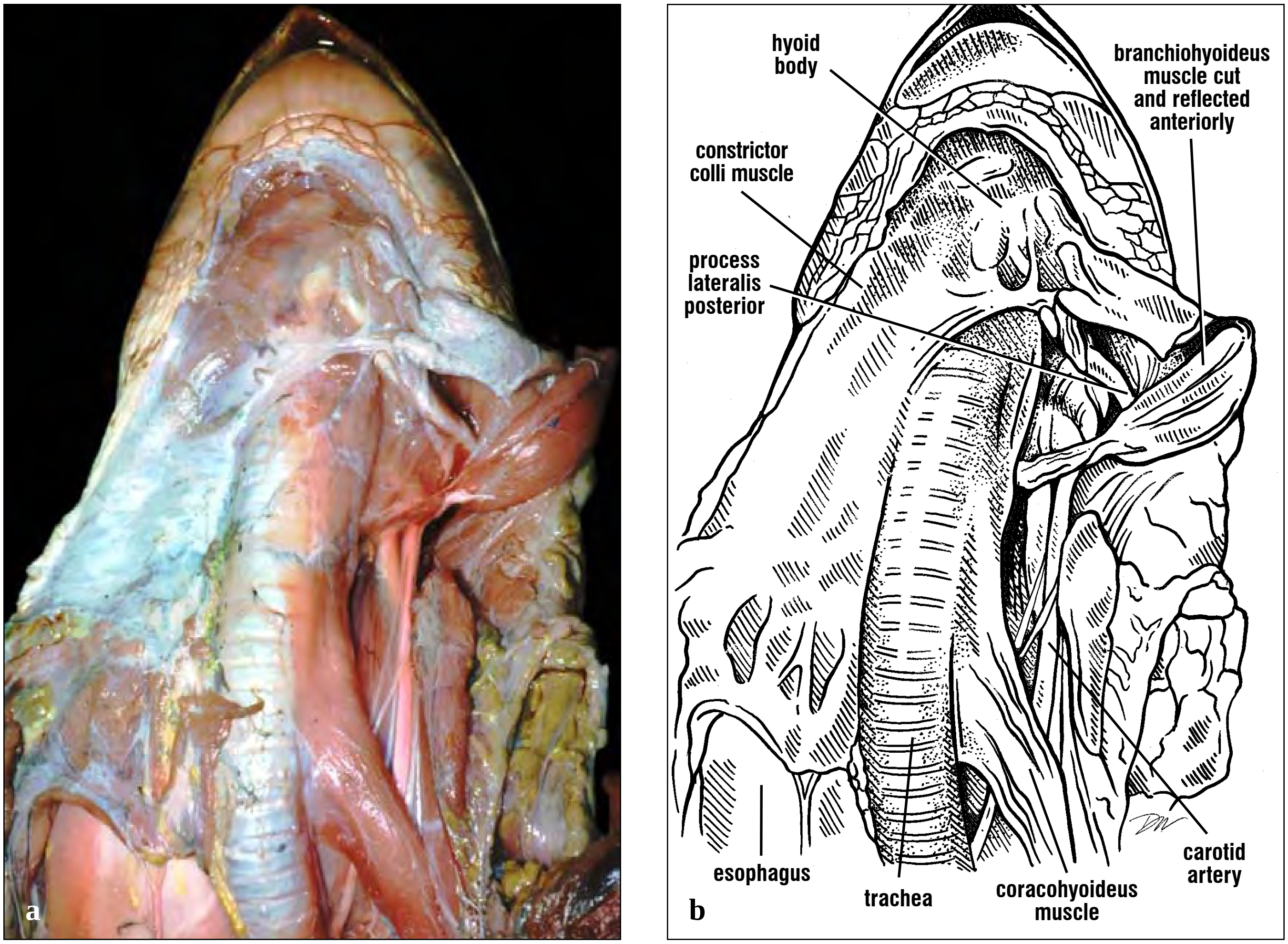
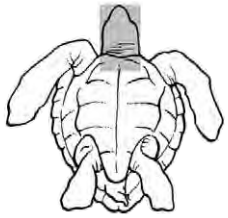


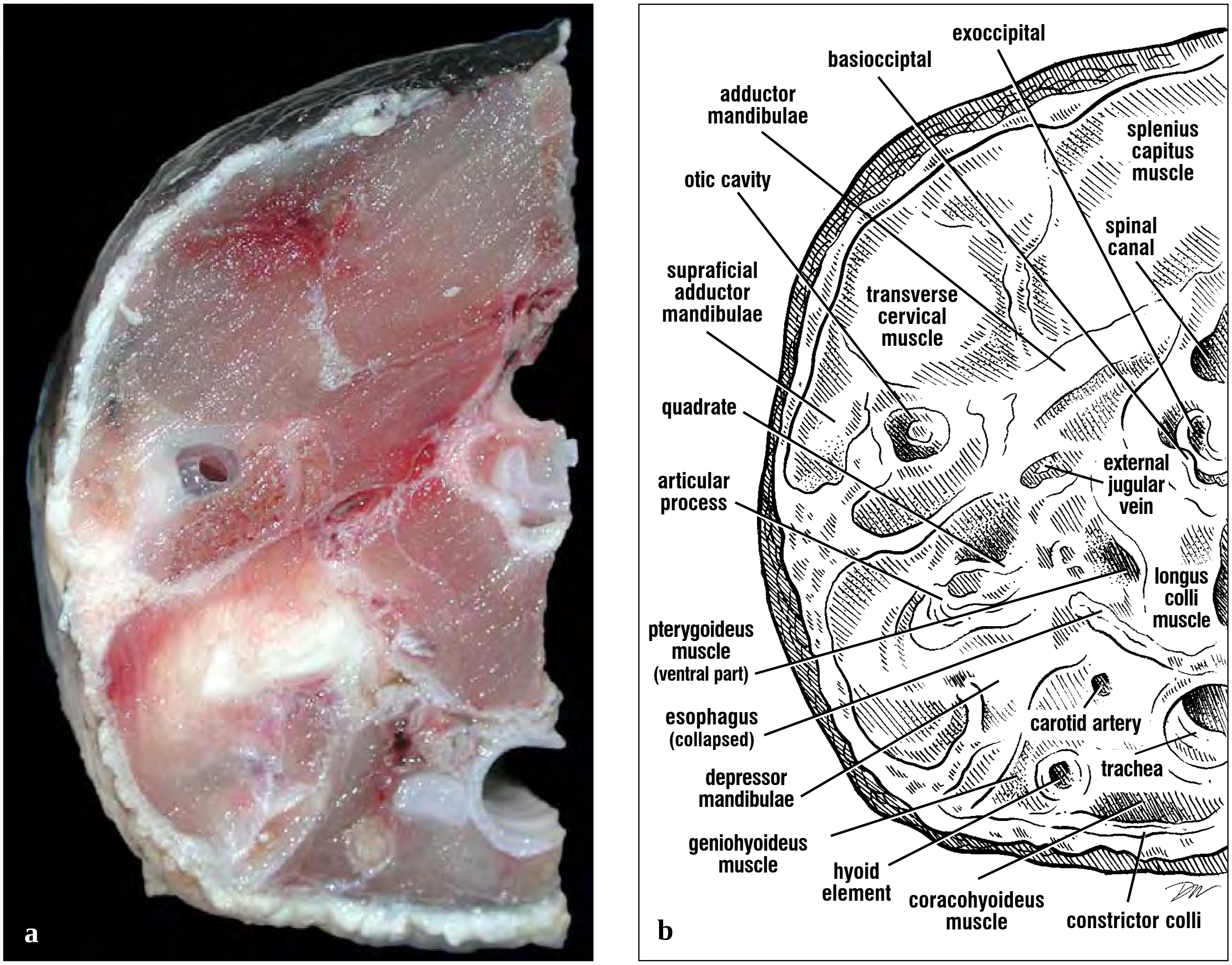
Fig. 121. *Ventral and superficial neck muscles. The constrictor colli muscle of the ventral neck is exposed lateral to and overlying the trachea. Connective tissue that loosely attached the muscle to the skin is still present on the turtle's anterior neck. The midline raphe (tendon) is visible along the anterior half of the muscle.*

are opened by the **depressor mandibulae** muscle, which has several parts. The depressor mandibulae arises from the quadrate, quadratojugal, and squamosal bones and inserts on the articular of the lower jaw; in *Dermochelys* a portion also inserts on the auditory tube. These parts are innervated by the facial nerve.

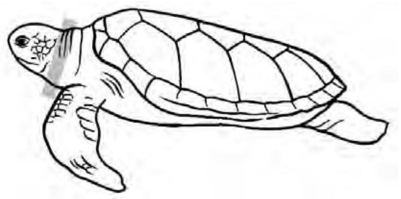


Figs. 122a and 122b. *Dissection of the ventral neck muscles, showing the deep muscles (right in picture) and superficial muscles (left). The parallel fibers of the intermandibularis arise from the lower jaw, and terminate in the cut raphe (found overlying the hyoid body and anterior trachea). The branchiohyoideus is cut between the hyoid body and the hyoid process (process lateralis posterior) on the turtle's left. The coracohyoideus travels along the trachea to the hyoid. The carotid artery lies deep to these muscles.*





Figs. 123a and 123b. *This oblique axial section through the neck of a hawksbill, is just posterior to the jaw joint ventrally and supraoccipital crest dorsally. The muscles, major blood vessels, trachea, and esophagus can be identified. Their relative positions and extent are seen in this dissection.*



Posterior Muscles. The major posterior muscles can be identified after removing the rectus abdominus and the skin covering the hind legs and tail. Ventrally, these are the **puboischiofemoralis externus** and **internus**, the **pubotibialis**, the **flexor tibialis** complex and the **ambiens** (Figs. 125-126; see also Nervous System). These ventral hip muscles are innervated by the obturator and tibial nerves of the sacral (=lumbosacral) plexus. The puboischiofemoralis externus, a thigh adductor, covers much of the ventral pelvis, and arises from the ventral pubis, ischium, and membrane covering the thyroid fenestrae (Fig. 106); it inserts on the femur's minor trochantor. Different parts of this muscle can either protract or retract the leg. The puboishiofemoralis internus is large in cheloniids and has both superficial and deep components. It may be absent in *Dermochelys* and replaced in function and position by the **iliofemoralis**. When present, it originates on the dorsolateral pubis, ilium, and the sacral vertebrae. It inserts on the femur's major trochanter.

The **pubotibialis**, part of the flexor tibialis complex, is found in cheloniids but is absent in *Dermochelys*. This muscle originates on the pubic symphysis and lateral pubis; it inserts on the tibia with the **flexor tibialis internus**. The flexor tibialis internus, a Y-shaped muscle, originates on the sacral and postsacral vertebrae dorsally, and ventrally on the pelvic symphysis and lateral pubis. It passes distally and wraps around the **gastrocnemius** muscle to insert on the tibia. The **flexor tibialis externus** has two heads (Figs. 125-126) and is somewhat medial to the internus. The dorsal head arises from the ilium and the ventral head from the posterior ischium. Both converge to insert, via a single tendon, on the tibia and the gastrocnemius muscle of the shank; some fibers insert on the skin and connective tissues of the shank.

The **adductor femoris** (Fig. 126) originates on the lateral ischium and inserts on the posterior femoral shaft. The **ischiotrochantericus** (not shown), a leg retractor, originates on the anterior pubis and pubic symphysis. It inserts on the major trochanter of the femur. The dorsal hip and thigh muscles (illustrated in Circulatory Anatomy; Figs. 156-157 and Nervous System; Fig. 207), include the hip abductors: **iliotibialis**, **femorotibialis**, and **ambiens**. The ventrally positioned ambiens (Fig. 125) originates on the pubioischiadic ligament, and inserts on the "patellar" tendon across the knee to the anterior tibia. The **iliotibialis** originates on the dorsal ilium and inserts with the ambiens on the patellar tendon. Deep to these two muscles, the **femorotibialis** (see Nervous System, Fig. 207), arises from the dorsal and anteroventral surfaces of the femur, and inserts with the iliotibialis and ambiens. The **peroneal** and **femoral** nerves of the **sacral plexus** innervate most of these dorsal hip muscles.

The hind foot extensors (Fig. 124) are large sheet-like muscles originating on the dorsal and lateral femur and inserting on the dorsal and anterior fibula and digits. They flex the lower leg or extend the digits.

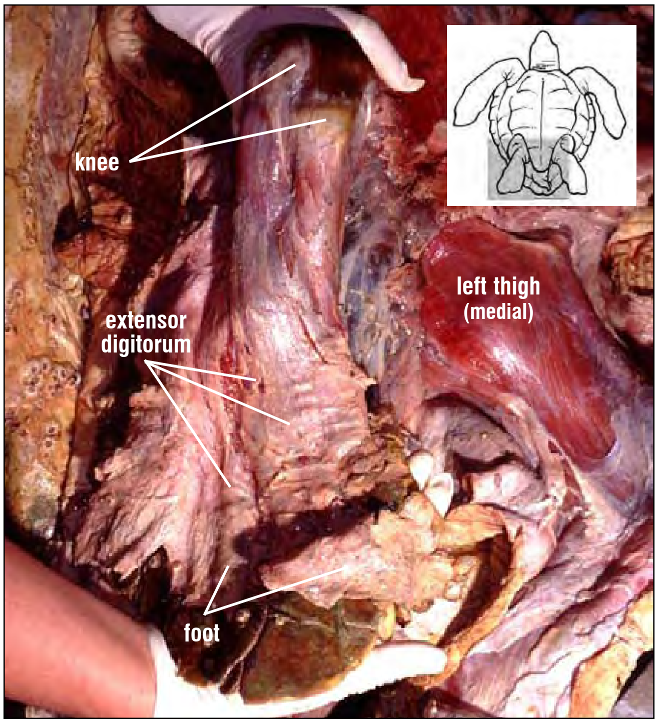
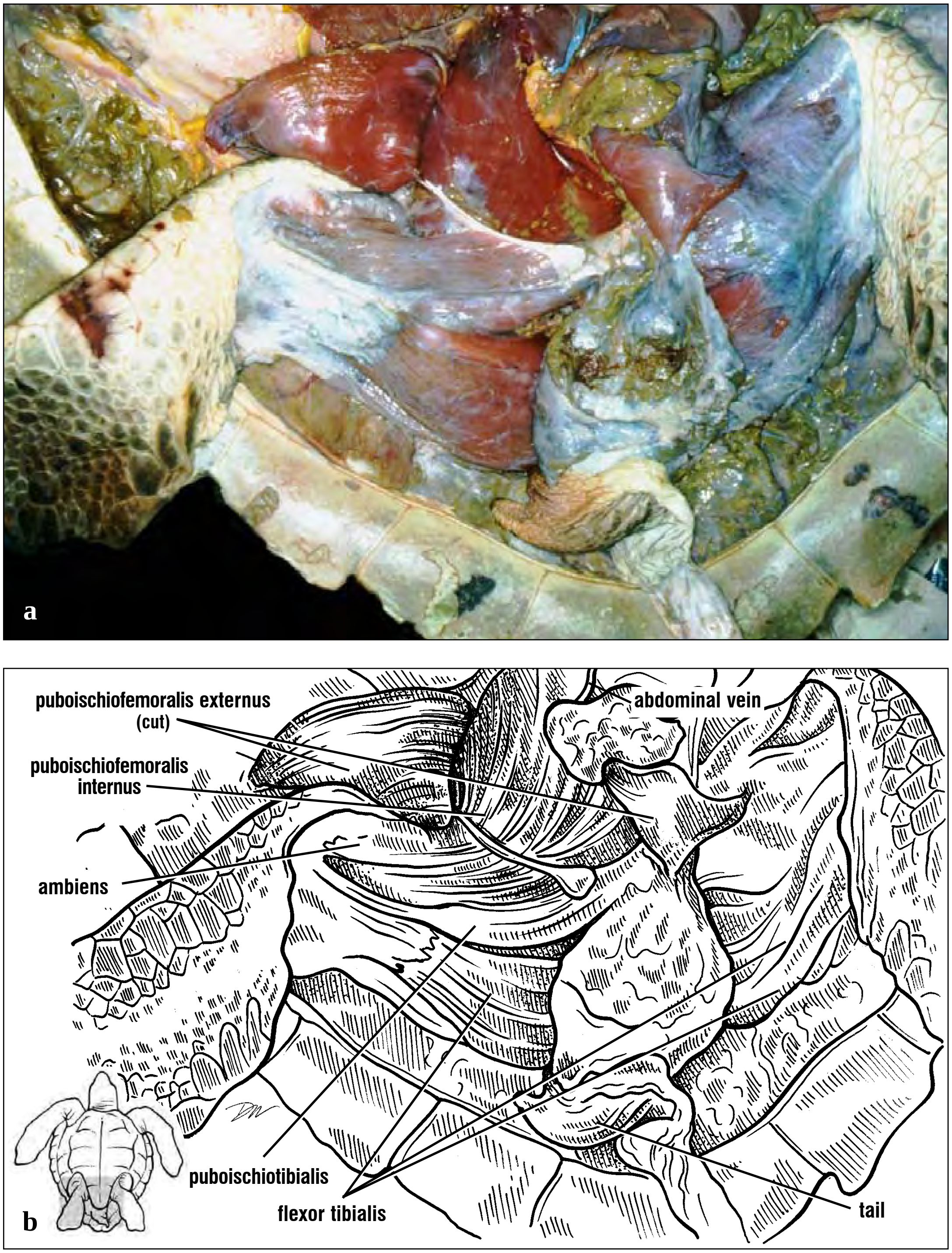
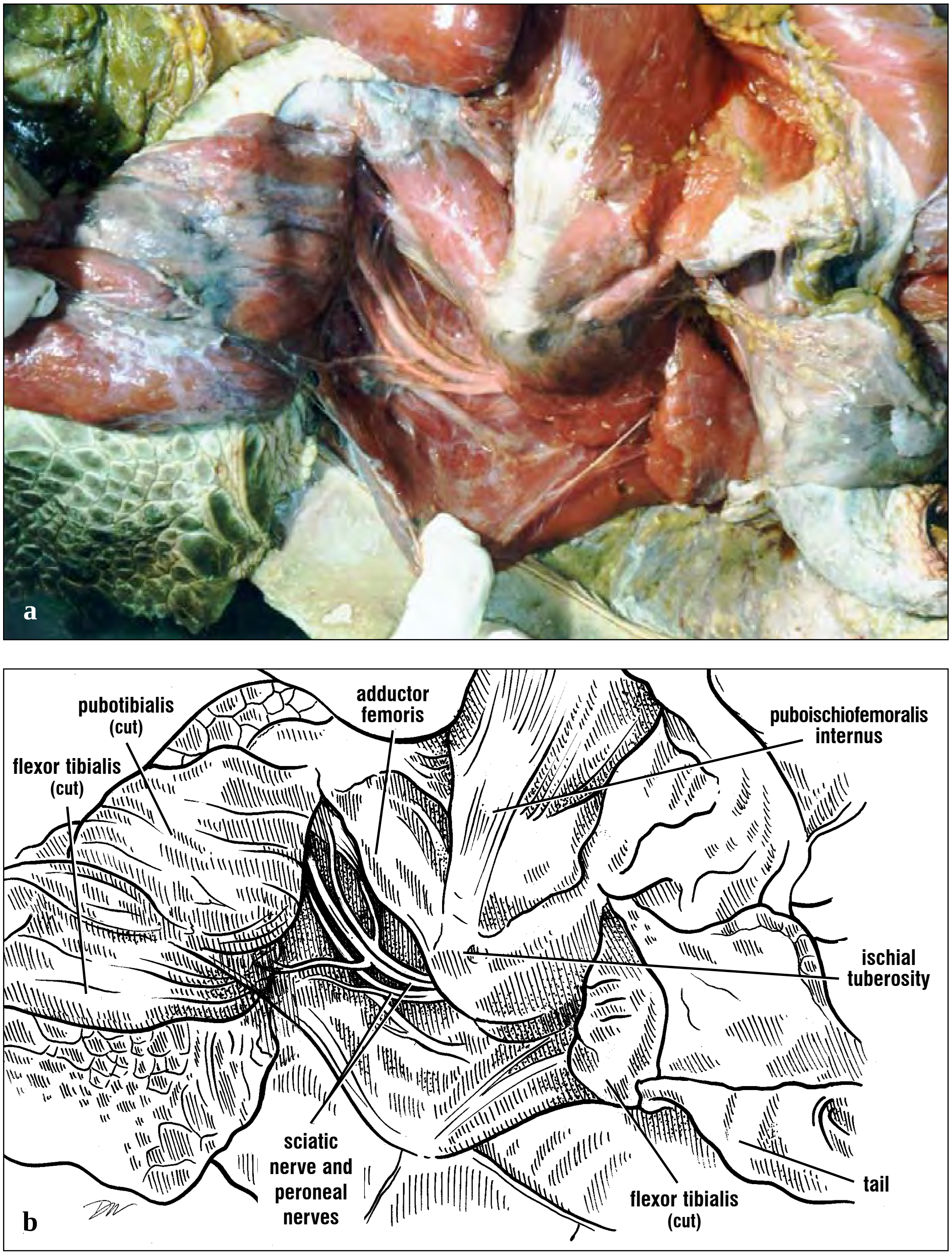
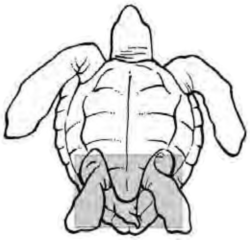


Fig. 124. *Anterior and dorsal foot extensors of a loggerhead right hind limb. The leg is abducted and flexed at the knee. The foot extensors flex the lower leg or extend and spread the digits.*



Figs. 125a and 125b. *The superficial ventral hip muscles. The puboischiofemoralis externus is an adductor of the leg. The puboishiofemoralis internus (the anterior ventral portion is seen here) is a protractor and abductor of the leg. The flexor tibialis complex, including the pubotibialis, flexes and retracts the leg and controls the shape of the trailing edge of the foot, perhaps during steering. More anteriorly, the ambiens is a weak adductor and protractor of the hind leg and can extend the shank.*





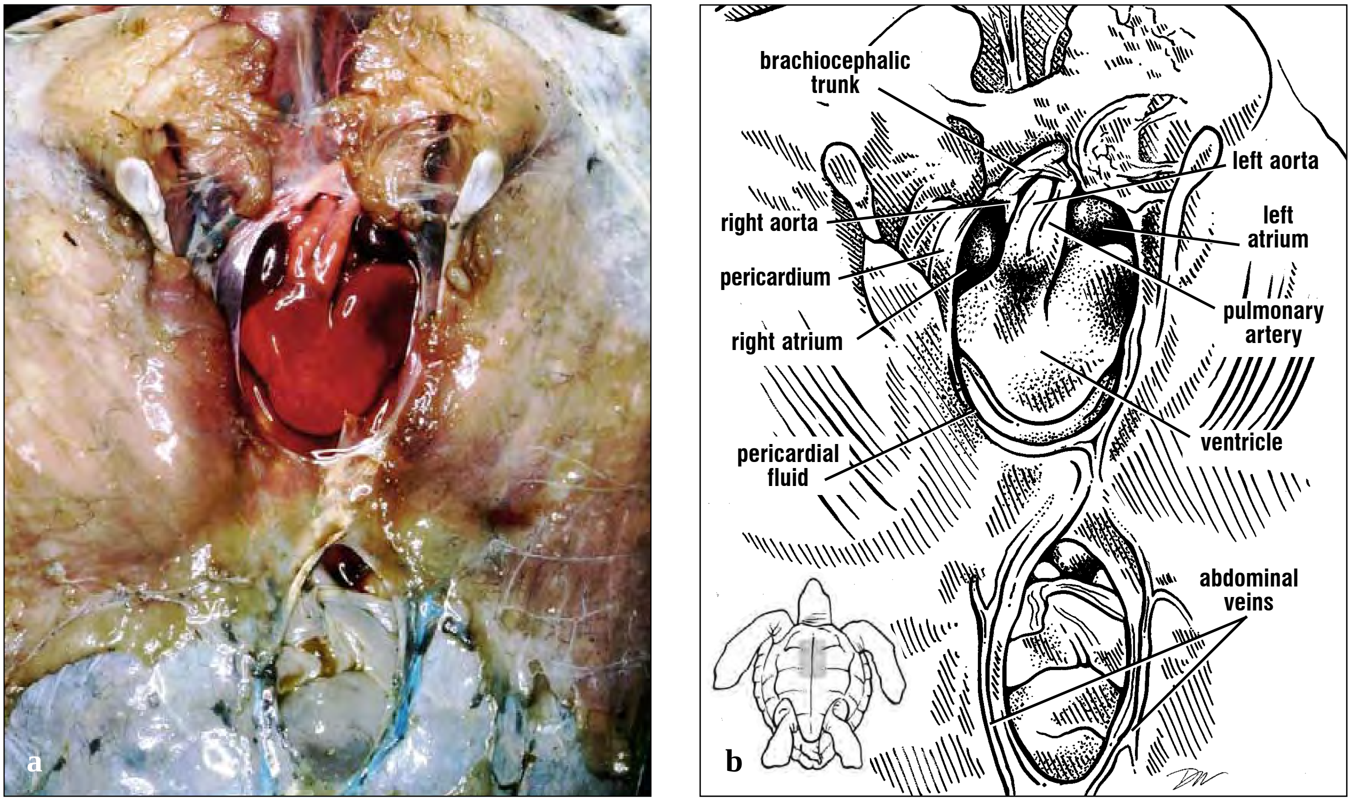
Figs. 126a and 126b. *The deeper ventral hip muscles are shown after removing the superficial limb retractors. The adductor femoris and puboishiofemoralis internus are antagonistic muscles, with the former adducting the thigh and the later abducting it.*

Circulatory Anatomy

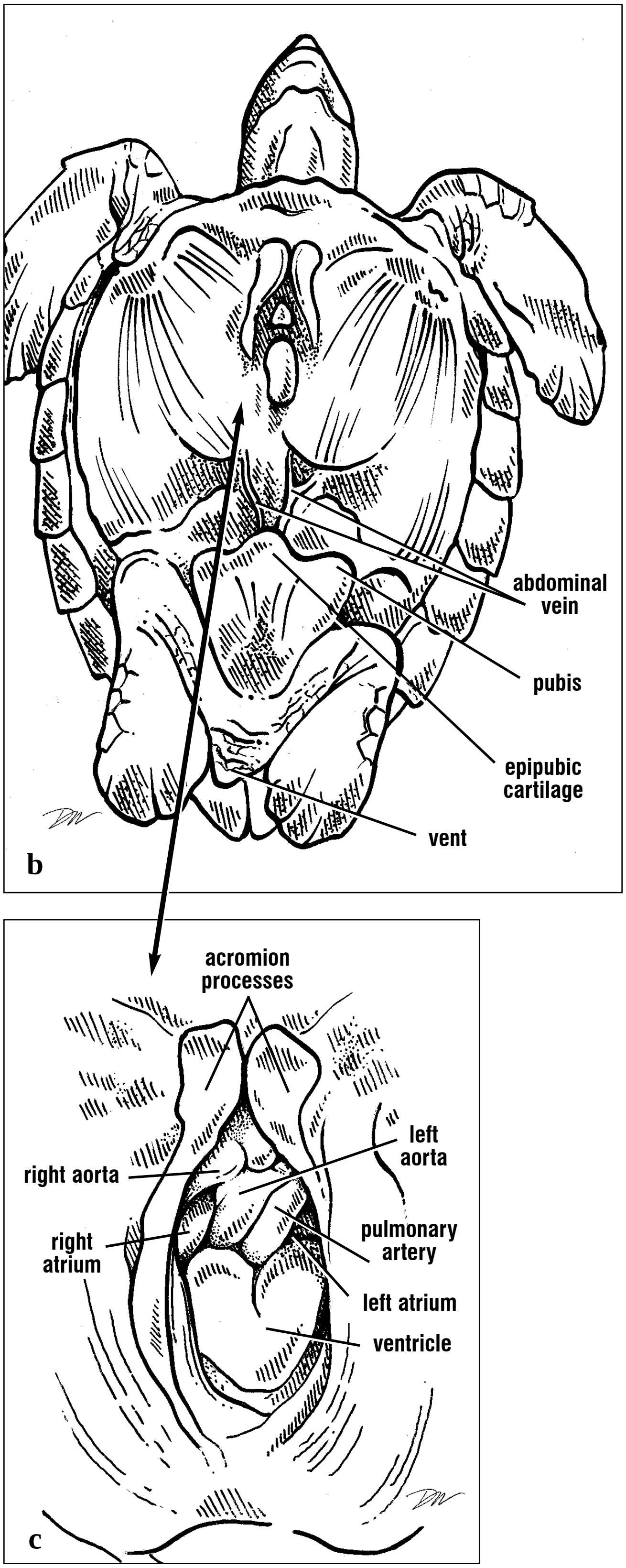
The circulatory anatomy includes the heart, arteries, veins, and lymphatic vessels. The heart is multichambered and serves as the main pump. Arteries have thick walls of muscles and elastic fibers; they carry blood away from the heart. Veins carry blood to the heart; they have thinner layers of muscle and elastic tissues and tend to collapse in dead animals. Most veins contain valves. The lymphatic vessels transport tissue fluid from outside the circulatory system back to the blood. The lymphatic vessels are very thin walled and difficult to photograph. They surround the arteries and veins like sheaths.

Heart. The heart is located within the pericardium and bordered ventrally by the acromion and coracoid processes (Figs. 127-129). Dorsally it is bordered by the lungs and laterally by the lobes of the liver. Within the pericardial sac, the heart is bathed with clear, colorless to slightly yellow pericardial fluid. All turtle hearts have four parts or chambers (Fig. 127): a **sinus venosus**, two large **atria** and a **ventricle**. The ventricle is thick-walled and internally subdivided into three compartments, the **cavum venosum, cavum arteriosum** and **cavum pulmonae** (not shown). These three ventricular compartments are separated only partially from one another.

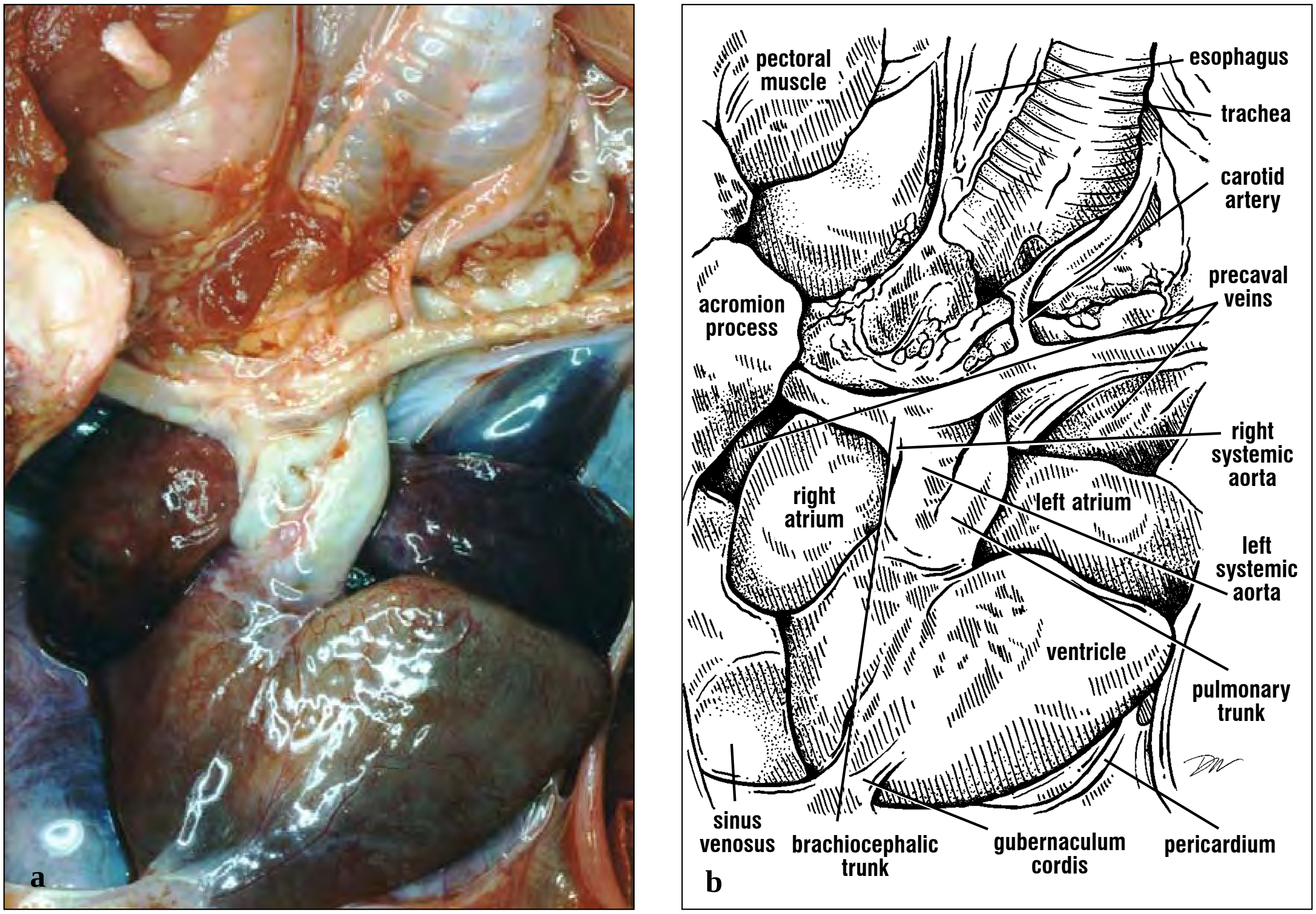
The posterior part of the pericardium and ventricle apex are attached to the peritoneum by the gubernaculum cordis (Fig. 129). This structure anchors the heart during ventricular contraction.



Figs. 127a and 127b. *Ventral heart. The heart is exposed after removing the pericardium. The more dorsal sinus venosus is not visible. Both aortas turn dorsally and are obscured partially by the brachiocephalic trunk. The pulmonary arteries arise from a common base, the pulmonary trunk. The abdominal veins from the posterior muscles are exposed posterior to the heart.*



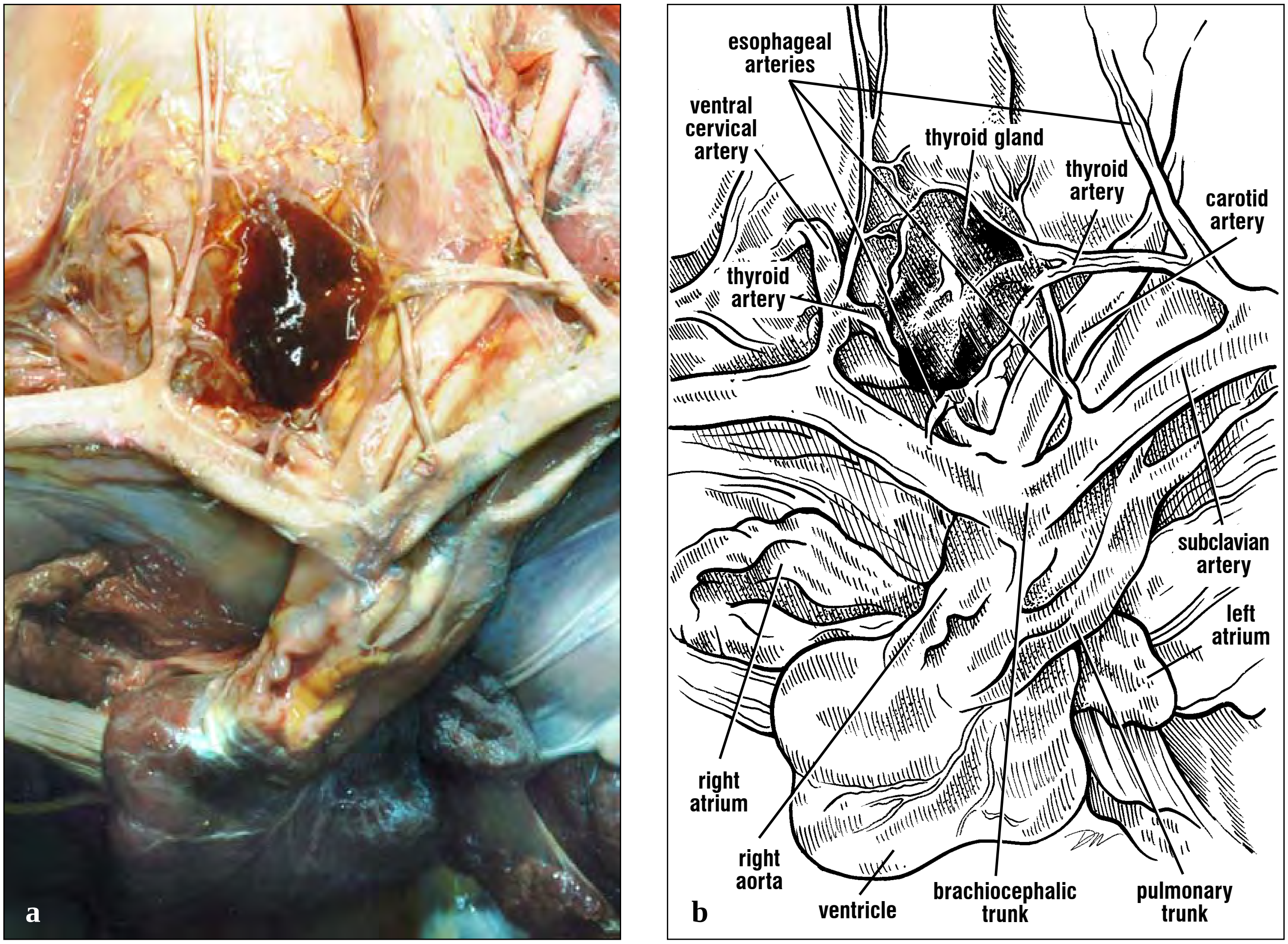
Figs. 128a, 128b, and 128c. *Landmarks for location of the heart after removal of the plastron. The two acromion processes and acromial-coracoid ligaments frame the pericardium ventrally. When the plastron is removed carefully, the paired abdominal veins are preserved. They drain the ventral pelvic muscles; blood flows anteriorly returning toward the two lobes of the liver. View c shows a close-up of the heart after removal of the ventral pericardium.*



Figs. 129a and 129b. *The four chambers of the heart can be identified in this ventral view. The ventral pericardium has been trimmed away to show both the heart and its great vessels. The apex of the ventricle is anchored to the pericardium and peritoneum posteriorly. The venous drainage from the anterior body to the precaval veins can just be seen lateral and anterior to the left atrium.*

Arteries. Arising from the anterior and ventral part of the heart are the **great vessels:** two aortas and a pulmonary trunk (Fig. 129). The **right aorta** supplies blood to the head, limbs, and lower body, the **left aorta** to the viscera. The pulmonary trunk divides into the right and left **pulmonary arteries** taking the blood to the right and left lungs, respectively.

The branches of the major vessels are good landmarks for locating organs and hence can serve like a map to locate specific structures. The right aorta gives off a branch right away called the **brachiocephalic trunk** and then continues posteriorly to the lower body where it joins the left aorta. The brachiocephalic trunk bifurcates; each branch produces a small **thyroid artery** to the thyroid gland anteromedially (Fig. 130). The branches of the brachiocephalic continue laterally as **subclavian arteries** (Figs. 129-130). The brachiocephalic trunk acts as a landmark for locating the thyroid and thymus glands (Glands; Figs. 159-160).



Figs. 130a and 130b. *Anterodorsal view of the heart and its major arteries. The great vessels emerge as three large vessels. The right aorta gives rise to the brachiocephalic trunk before it bends posteriorly. The thyroid arteries arise from the brachiocephalic trunk shortly after it bifurcates, (or, in this case, from the carotid arteries). It then gives rise to the left and right subclavian arteries. The right carotid is not dissected free of its connective tissue.*

The **carotid** arteries (Figs. 129-130), then the **ventral cervical arteries**, arise from either the brachiocephalic trunk or the subclavian arteries lateral to the thyroid arteries (Fig. 130). The carotids (often termed common carotids) supply blood to the head. They bifurcate near the skull to form the **external** and **internal carotid arteries.** The **ventral cervical arteries** travel anteriorly then bifurcate to supply branches to the esophagus. The subclavian arteries continue laterally towards the flippers; near the junction of the scapula and coracoid they become the **axillary arteries.** There, branches to the scapular musculature arise (**anterior subscapular artery**). The axillary artery gives off both a branch to the carapace just prior to entering the forelimb, the **marginocostal artery** which travels posteriorly along the lateral aspect of the shell, and a branch to the ventral pectoral muscles, the **pectoral artery** (Fig. 131). As the axillary artery crosses the humerus, it becomes the **brachial artery** supplying radial, ulnar, then distally the digital arteries of the flipper.

The major arterial and venous paths are summarized diagrammatically in Figs. 131-132. These diagrams show the most common routes taken by vessels. However, the circulatory system is among the most variable of all organ systems and hence, sometimes vessels branch in unique and unexpected manners.

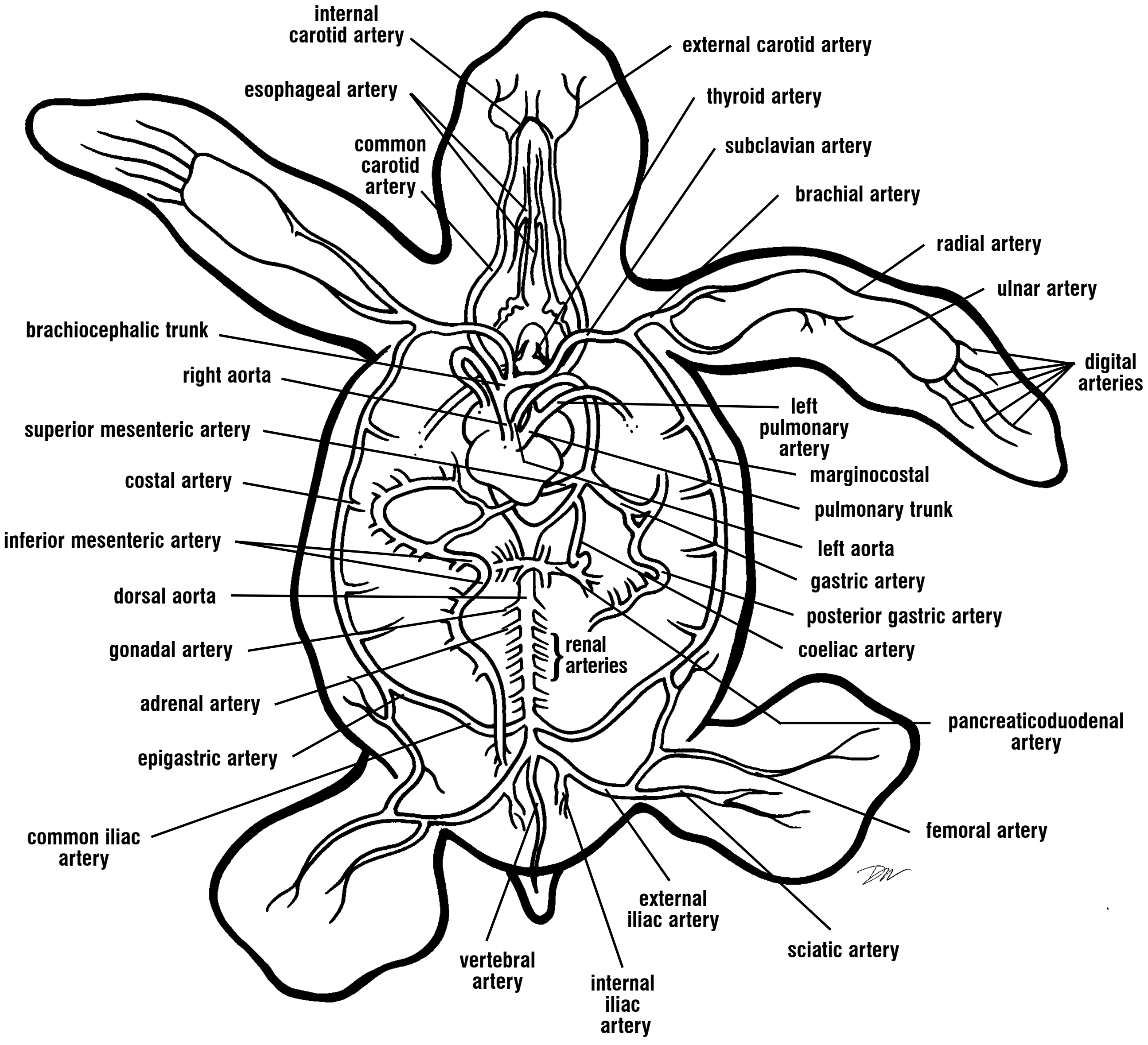


Fig. 131. *Major arteries, ventral view. The major arteries are shown diagrammatically. Some subdivisions are not labeled for diagram clarity. These include the ventral cervical, axillary, anterior scapular, pectoral, anterior pancreaticoduodenal, and haemorrhoidal arteries.*

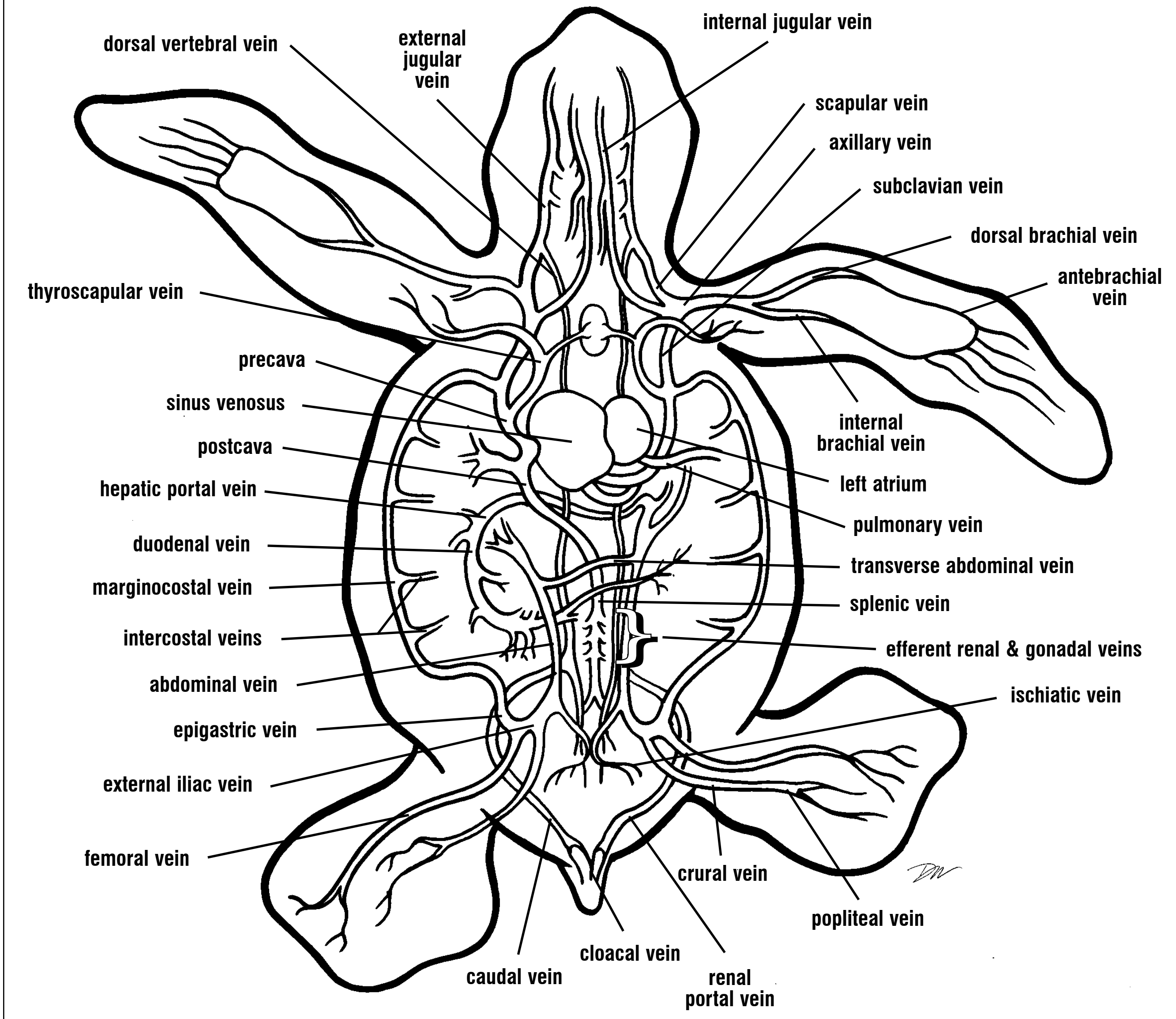


Fig. 132. *Major veins, ventral view. Note that all branches are not shown or labeled to minimize diagram complexity. These include the azygos, transverse and central vertebral, eosophageal, hepatic, pectoral, pericardial, vesicular, pelvic, lipoidal, hypogastric, gastric, anterior and posterior pancreatic, mesenteric, common mesenteric, and inferior mesenteric.*

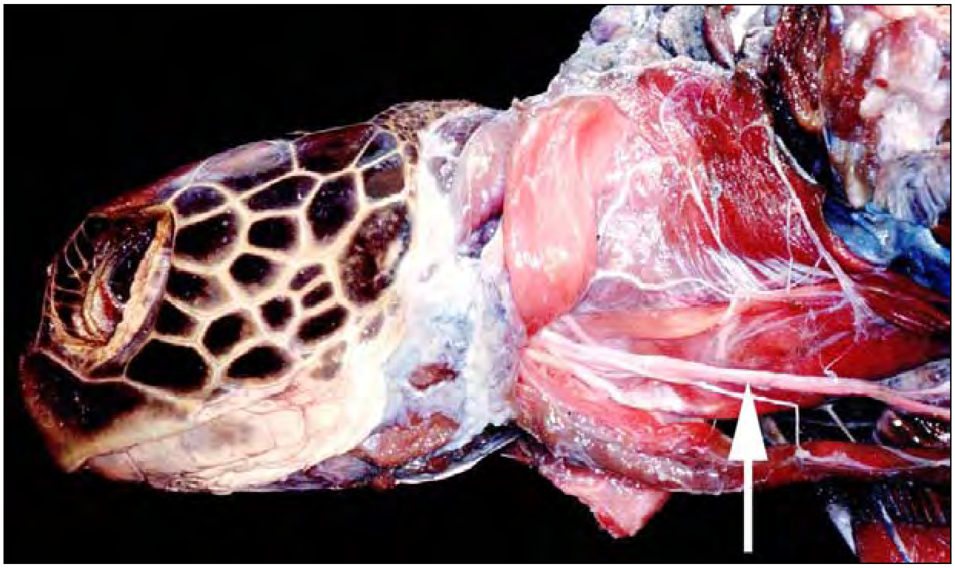


Fig. 133. *This lateral view of a green turtle has all superficial neck muscles cut and reflected dorsally. The arteries and veins were injected with latex to provide contrast. The carotid artery (at arrow) is deep and lies adjacent to the longus colli muscles of the cervical vertebrae.*

The left aorta, the middle of the three great vessels, turns dorsolaterally and passes the level of the stomach before producing three branches: the **gastric artery**, the **coeliac artery** and the **superior mesenteric artery**. The gastric artery bifurcates quickly and sends branches to the greater (lateral aspect) and lesser (medial aspect) curvatures of the stomach (Figs. 135-136). The coeliac artery branches shortly after leaving the left aorta and forms the **anterior pancreaticoduodenal artery** to the pancreas, duodenum and stomach and the **posterior pancreaticoduodenal artery** to the distal pancreas, duodenum, liver, and gallbladder (Fig. 136). The superior (or anterior) mesenteric artery gives off many branches that fan out through the intestinal mesenteries and supply the small intestines. After giving off the superior mesenteric artery, the left aorta continues posteriorly where it joins the right aorta (typically) to form a single dorsal aorta. The position where the two join is variable, but generally is within the middle third of the body.

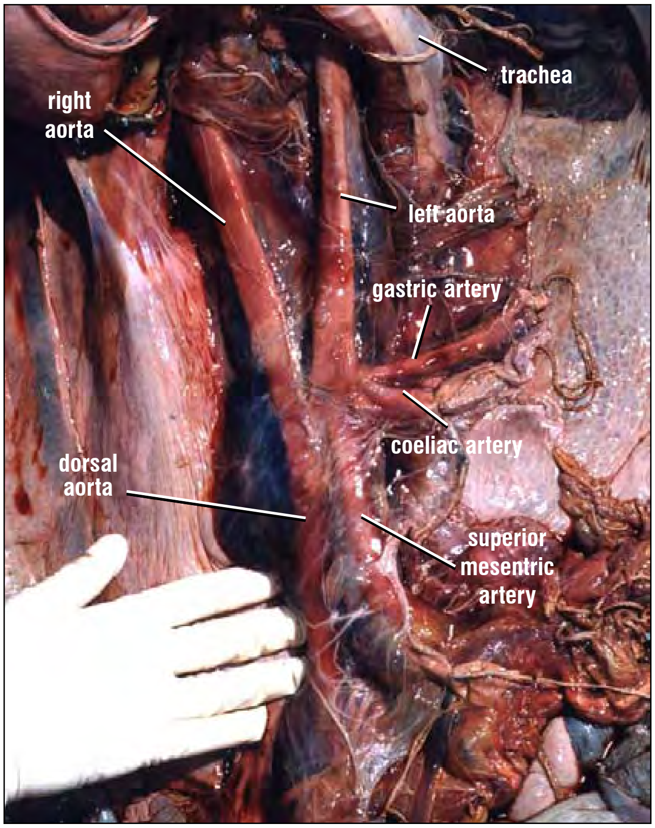
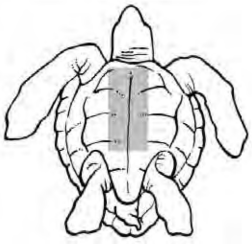
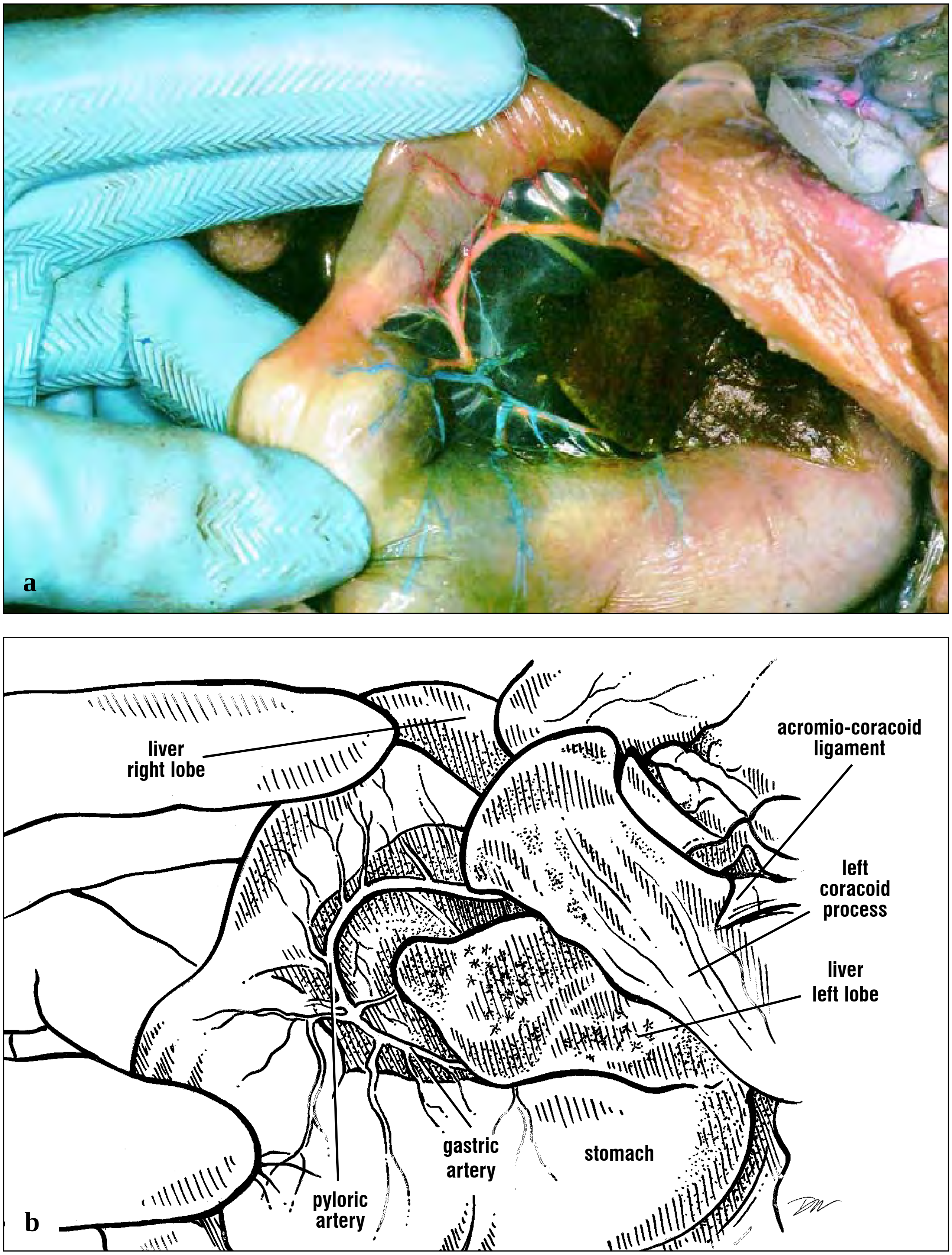
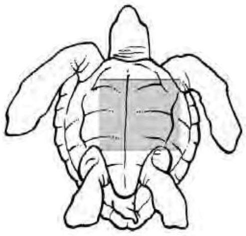


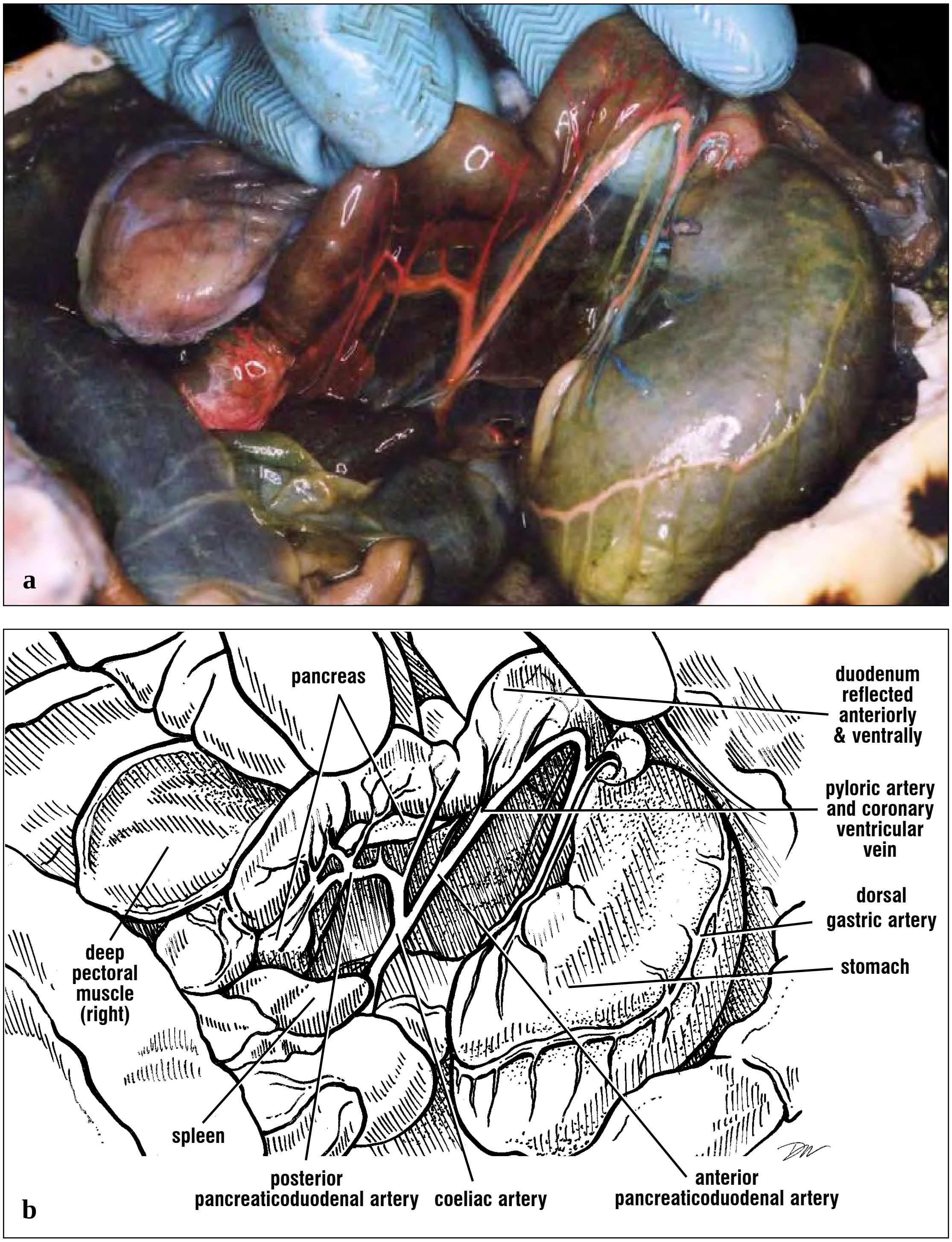
Fig. 134. *The ventral view of the left aorta and its major branches in a loggerhead after removal of the heart and viscera. Anterior is toward the top of the picture. The right aorta joins the left aorta very early in this loggerhead, just posterior to the origin of the superior mesenteric artery.*

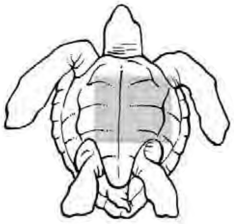






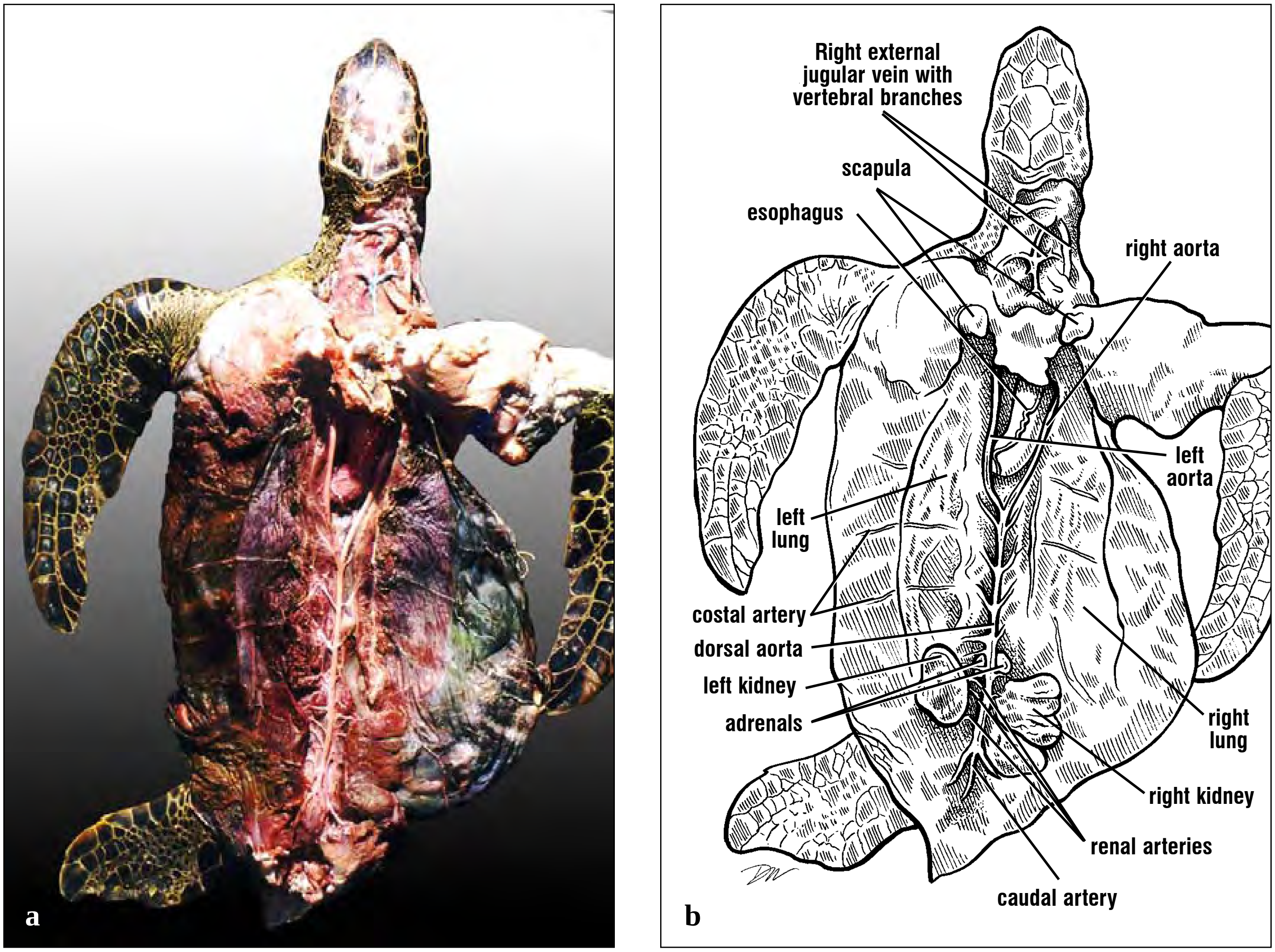
Figs. 135a and 135b. *Circulation of the stomach. The ventral gastric artery drains to the lesser curvature of the stomach. It becomes the pyloric artery at the level of the pyloric sphincter.*



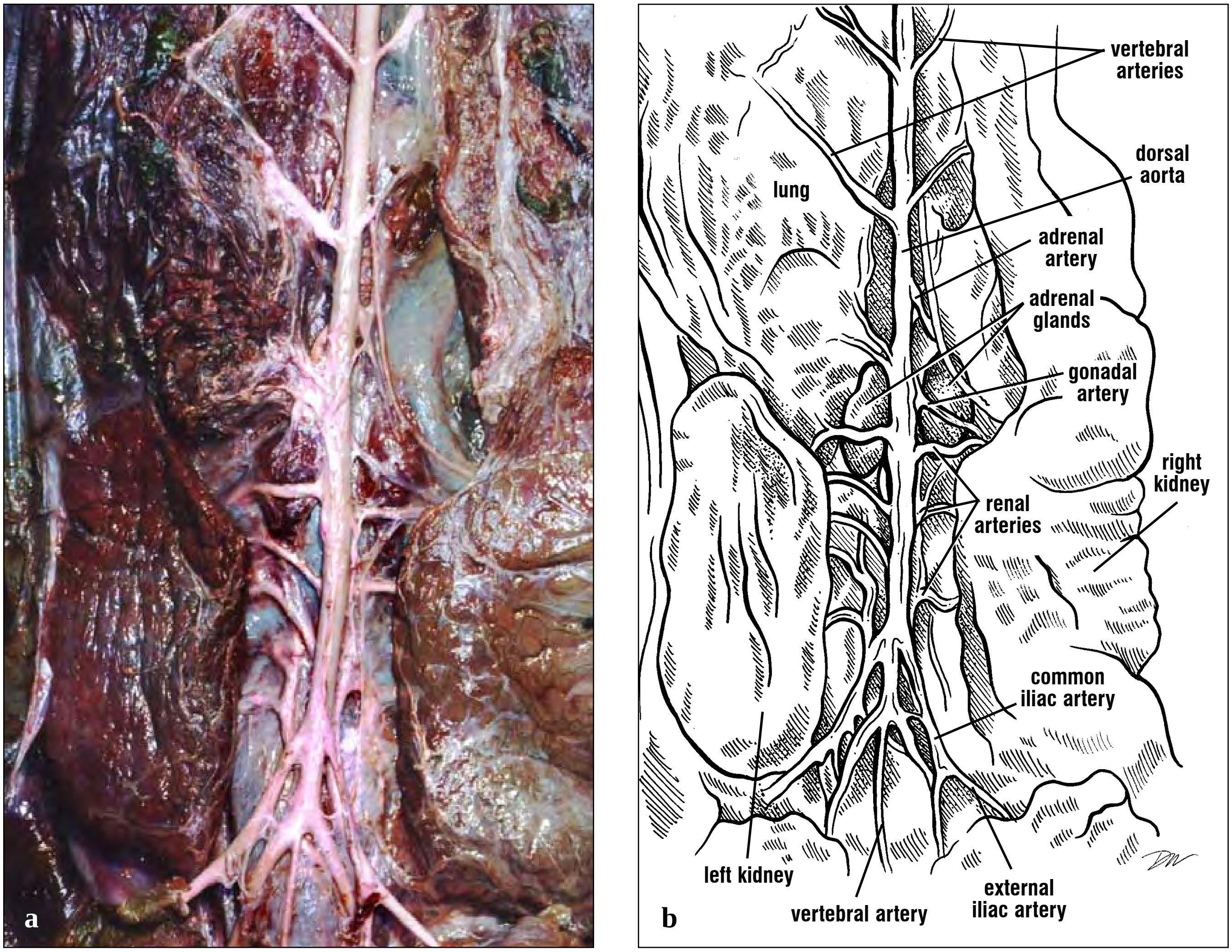


Figs. 136a and 136b. *Arteries and veins of the stomach, pancreas, and duodenum. The dorsal gastric artery drains to the greater curvature of the stomach. The coeliac artery, the second artery arising from the left aorta, supplies these branches to the duodenum, the stomach near the pyloris, and to the pancreas.*

The **dorsal aorta** (Figs. 134, 137-138) continues posteriorly and gives off paired branches, the **costal arteries** of the carapace, **gonadal arteries** to the ovaries or testes (there may be more than one per gonad), a pair of **adrenal arteries**, and three or more **renal arteries** to each kidney (Figs. 137-138). A pair of **epigastric arteries** branches off the dorsal aorta at the level of the kidneys; they travel laterally to join the marginocostal artery of the carapace.



Figs. 137a and 137b. *The carapace has been removed from this green turtle and the arteries injected with latex. The right and left aortas join along the middle third of the body. Costal (intercostal) branches extend anteriorly and across the body. Branches to the gonads, adrenals, kidneys, and hind limbs arise, then the caudal artery continues posteriorly along the midline to the tail and cloaca. This animal was missing its right hind limb.*



Figs. 138a and 138b. *The carapace has been removed from this green turtle. The arteries are injected with latex to show the arterial branches to the gonads, adrenal glands, and kidneys. Variability is common in the circulatory system and is shown here. In this animal, the right gonadal artery is long and crosses dorsal and to the right adrenal gland, rather than extending lateral or anterior to it. There are 3 asymmetric (rather than symmetric) pairs of renal arteries supplying the kidneys. The epigastric arteries do not arise in the typical manner from the dorsal aorta, but instead from the left common iliac. The common iliacs continue as the external iliacs then divide to form the femoral and sciatic arteries. The internal iliacs arise directly from the dorsal aorta, in this case, turn ventrally, and supply blood to the bladder and large intestine. The caudal (vertebral) artery continues posteriorly along the midline.*

The arteries to the pelvic limbs, the **external** and **internal iliac arteries**, may leave the dorsal aorta on each side via paired trunks (common iliacs), or they may branch off separately (Figs. 138-139). The external iliac supplies the **femoral** and **sciatic arteries** to the hind leg (Fig. 130). The internal iliac provides branches to the bladder and gonadal ducts, and the **haemorrhoidal artery** to the large intestine. The dorsal aorta then extends to the tail as the **vertebral** (caudal) **artery** (Figs. 131, 138-139).

Pulmonary Trunk. The pulmonary trunk divides shortly after leaving the heart and supplies the right and left pulmonary arteries to the lungs (Figs. 129-130). The pulmonary arteries enter the lungs along the dorsal side of the bronchus, and travel posteriorly with the bronchi giving off multiple branches throughout the lung. The pulmonary artery walls are thickened as a muscular sphincter near the lungs. The lumen of each of the great vessels near the heart should be roughly uniform in thickness, except for the pulmonary arteries as they approach the lungs.

Pulmonary Veins. Capillaries, venules (small veins), and veins within the lung coalesce into branches that drain into the **pulmonary veins** (not shown). The pulmonary veins travel along the ventral surface of each bronchus, then exit the lung anteriorly and arch medially. They enter the left atrium dorsolaterally.

Systemic Veins. The venous circulation is described by tracing the veins away from the heart. However, it should be remembered that venous blood typically flows toward the heart. (It is noteworthy that flow direction can reverse in some veins.) Multiple terms are used to describe the major veins. The synonyms are given to clarify terminology. Venous blood from the body drains into the **sinus venosus** from 4 major veins: the **left precava** (= left common cardinal, = left superior vena cava), the **right precava** (= right common cardinal, = right superior vena cava), the **left hepatic vein**, and the **postcava** (= posterior vena cava, = right hepatic vein; Fig. 132). The left and right precaval veins each drain the anterior body. Each precava receives branches from the **subclavian** and **azygos veins** and anteriorly from the internal and external jugular veins. The azygos vein is narrow and supplies the deep pectoral muscles (Fig. 140). The subclavian vein extends laterally. It receives the **thyroscapular vein** with thyroid branches from the thyroid gland and the scapular musculature, the **scapular, transverse scapular**, and **subscapular veins.** The transverse scapular vein supplies drainage for the **cephalic vein** from the dorsal arm and the posterior and ventral flipper (Fig. 132). After receiving the thyroscapular branch, the subclavian vein extends laterally and forms the **axillary vein** in the axilla (armpit). Many branches arise in the axillary as the venous component of the rete system. The axillary components rejoin as the **brachial vein** in the upper arm, and then bifurcate as the **internal brachial vein** to the posterior flipper and the **dorsal brachial vein** to the anterodorsal flipper. As in the arterial system, a vascular circumflex forms near or just distal to the wrist, and receives drainage from the interdigital veins found medial to each digit. Because of the extensive connective tissue layers in the forearm and flipper blade, these vessels were traced by destructive dissection and so are illustrated diagrammatically (Fig. 132).

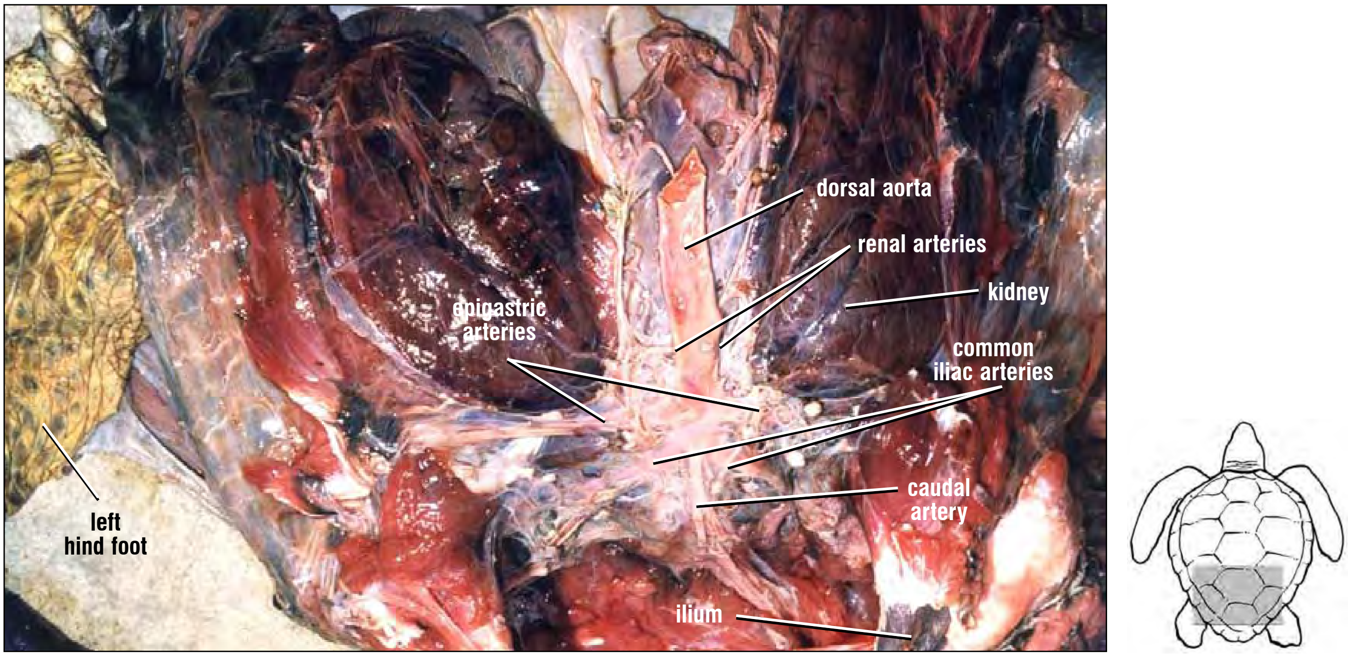
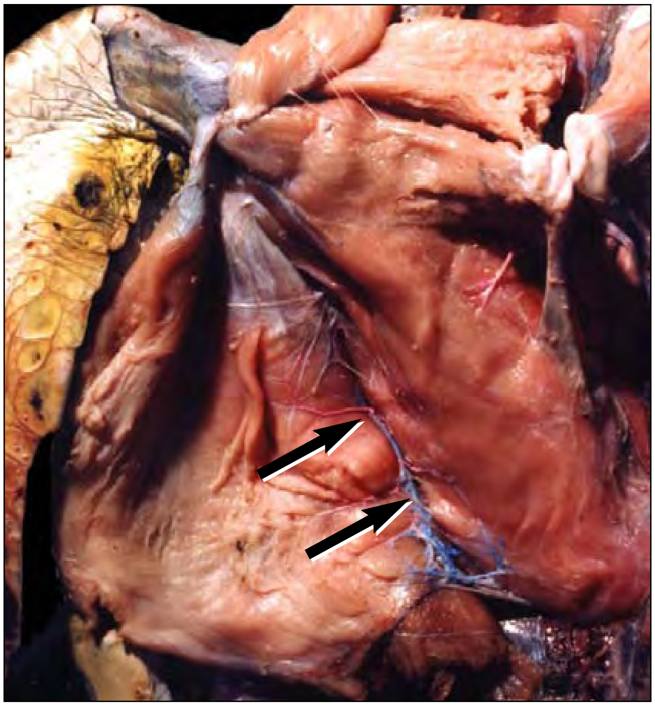


Fig. 139. *Dorsal arteries to the posterior musculature and kidneys of a loggerhead.*



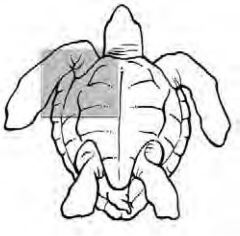
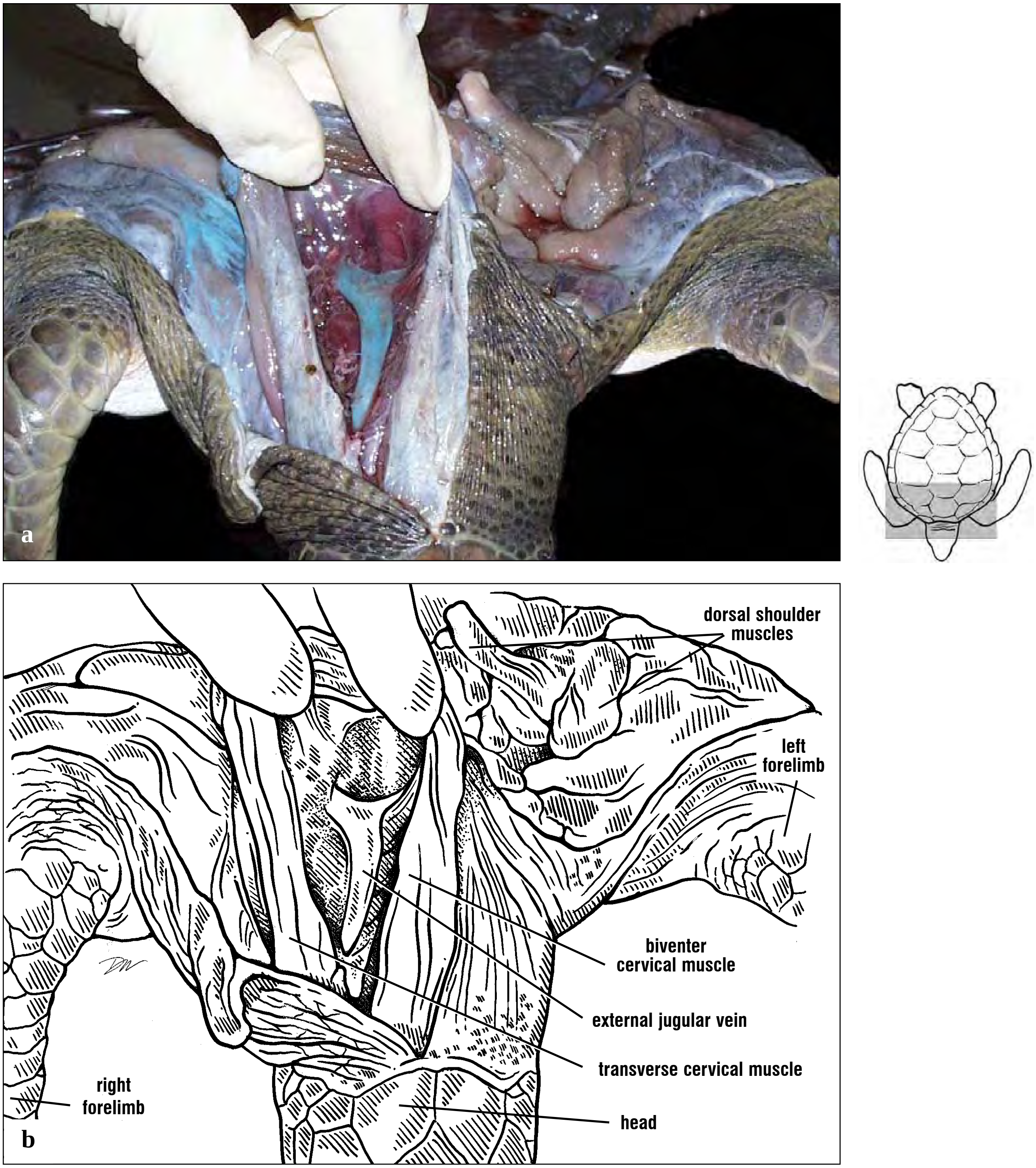
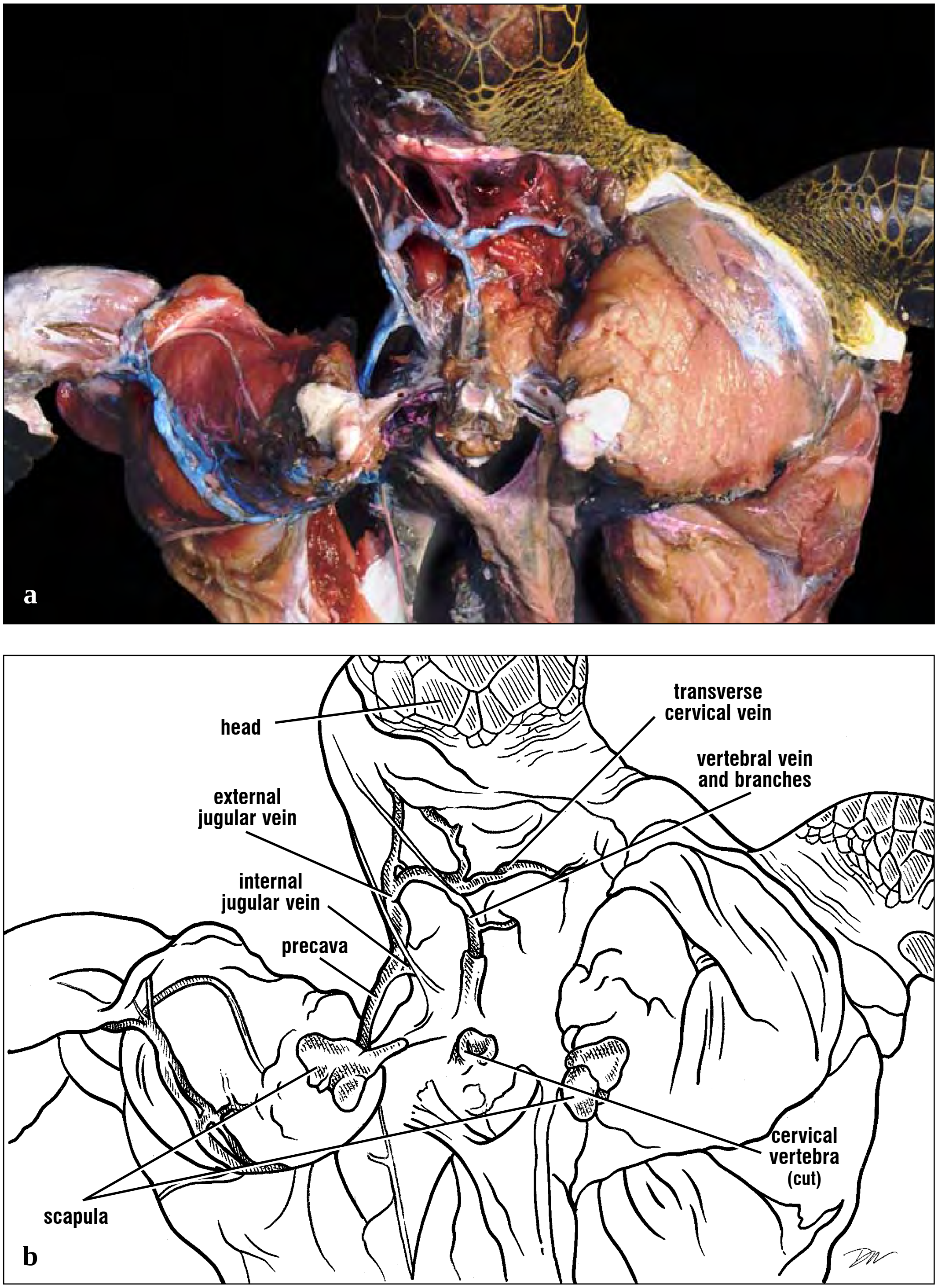


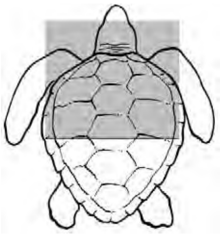
Fig. 140. *The azygos artery and veins and branches of the pectoral vein supply the deep pectoral musculature. Here the pectoralis major has been reflected anteriorly to expose the azygos vessels (at arrows) supplying the coracobrachialis-anterior and -posterior parts, as well as branches to the biceps profundus.*

The external jugular vein is located relatively dorsal and superficial in the neck. The **biventer cervical** (= splenius capitus) and **transverse cervical** muscles are good dorsal landmarks for the external jugular. These muscles are obvious from the exterior and are to either side of the vessels; the external jugular is located deep and between them (Figs. 141-142), and medial to the transverse cervical muscle.

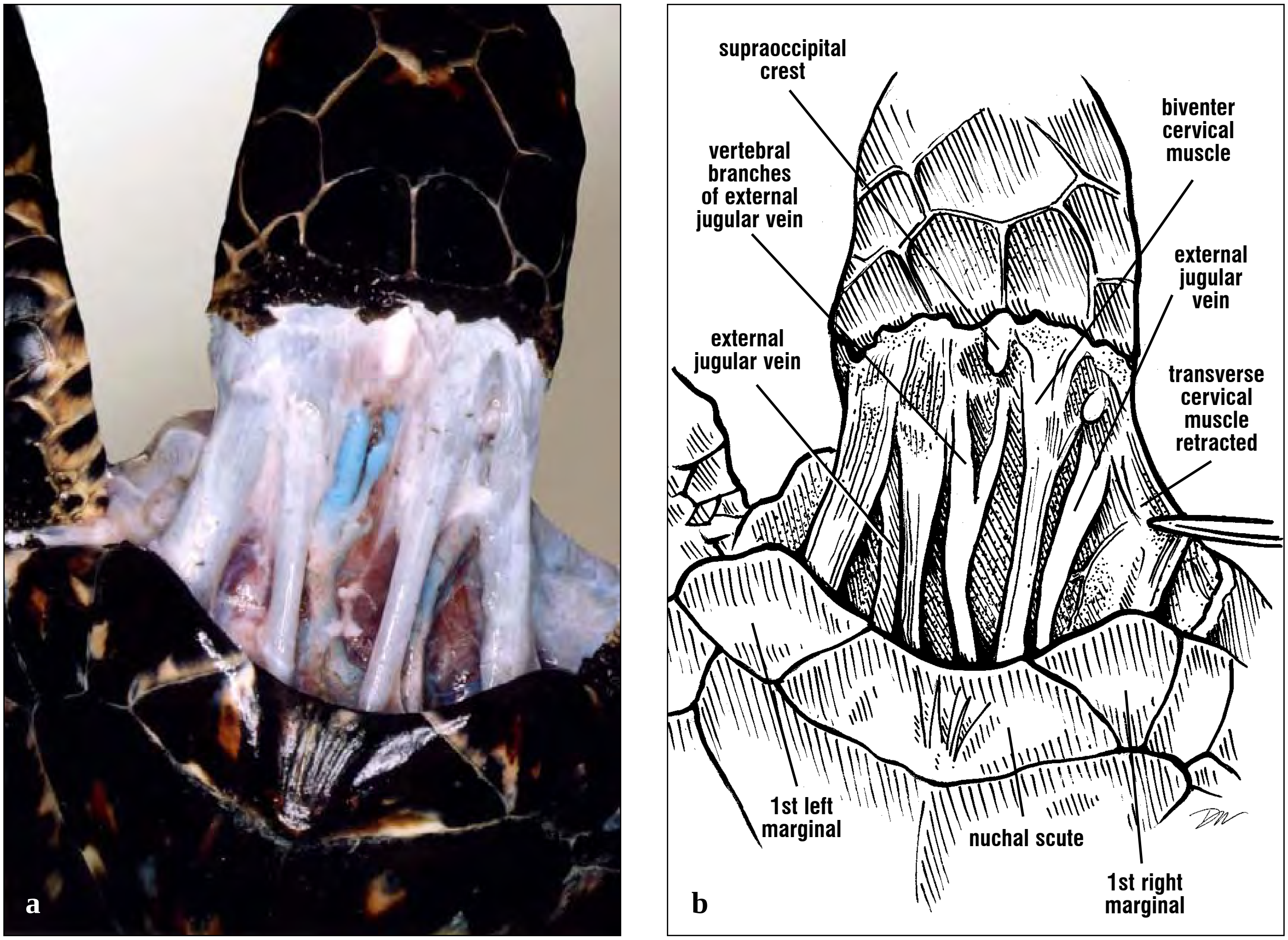


Figs. 141a and 141b. *Green turtle cervical circulation. The external jugular vein was dissected free on the turtle's right and injected to provide contrast. It shows the transverse cervical branch extending medially into the muscle.*

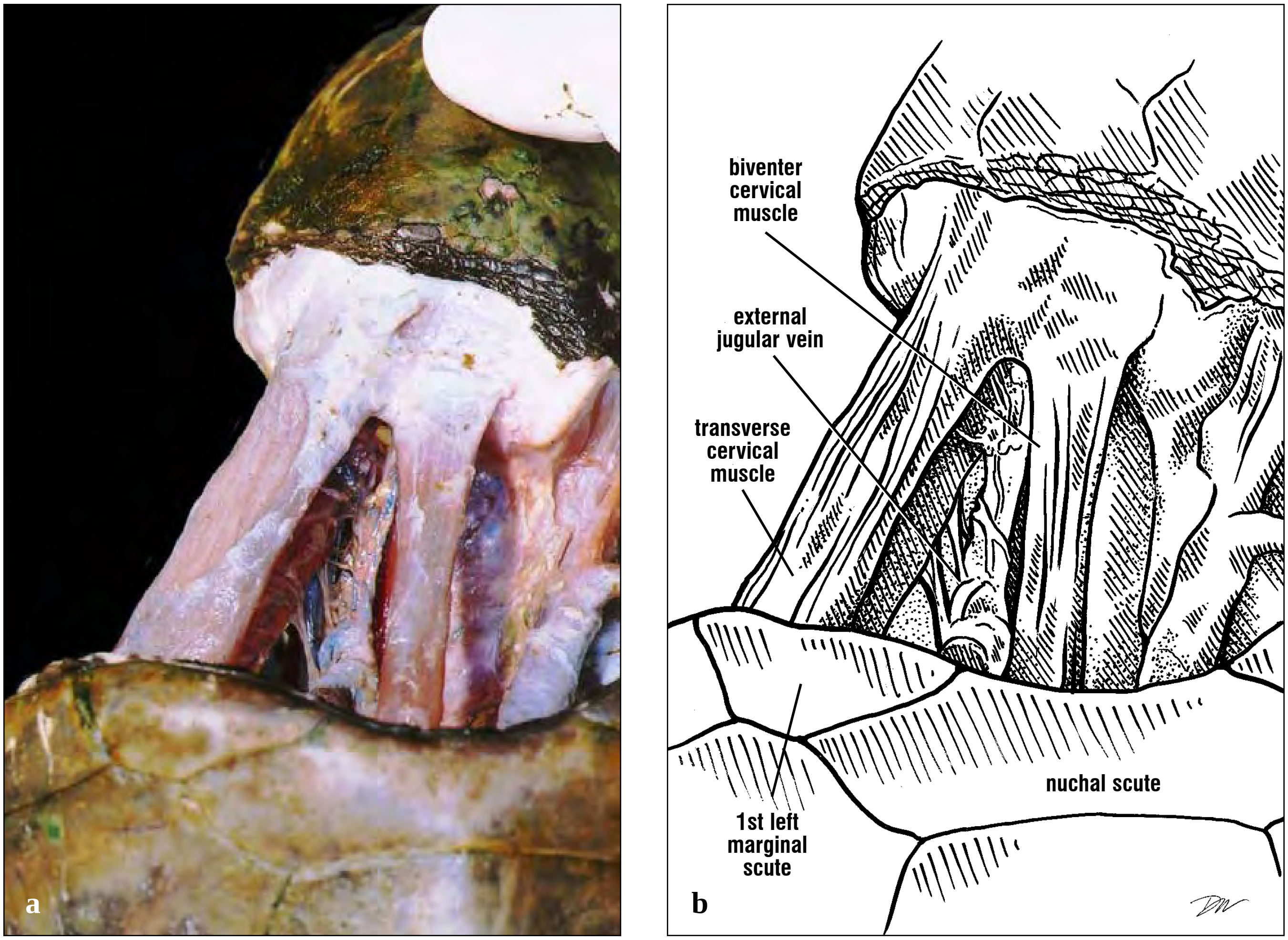




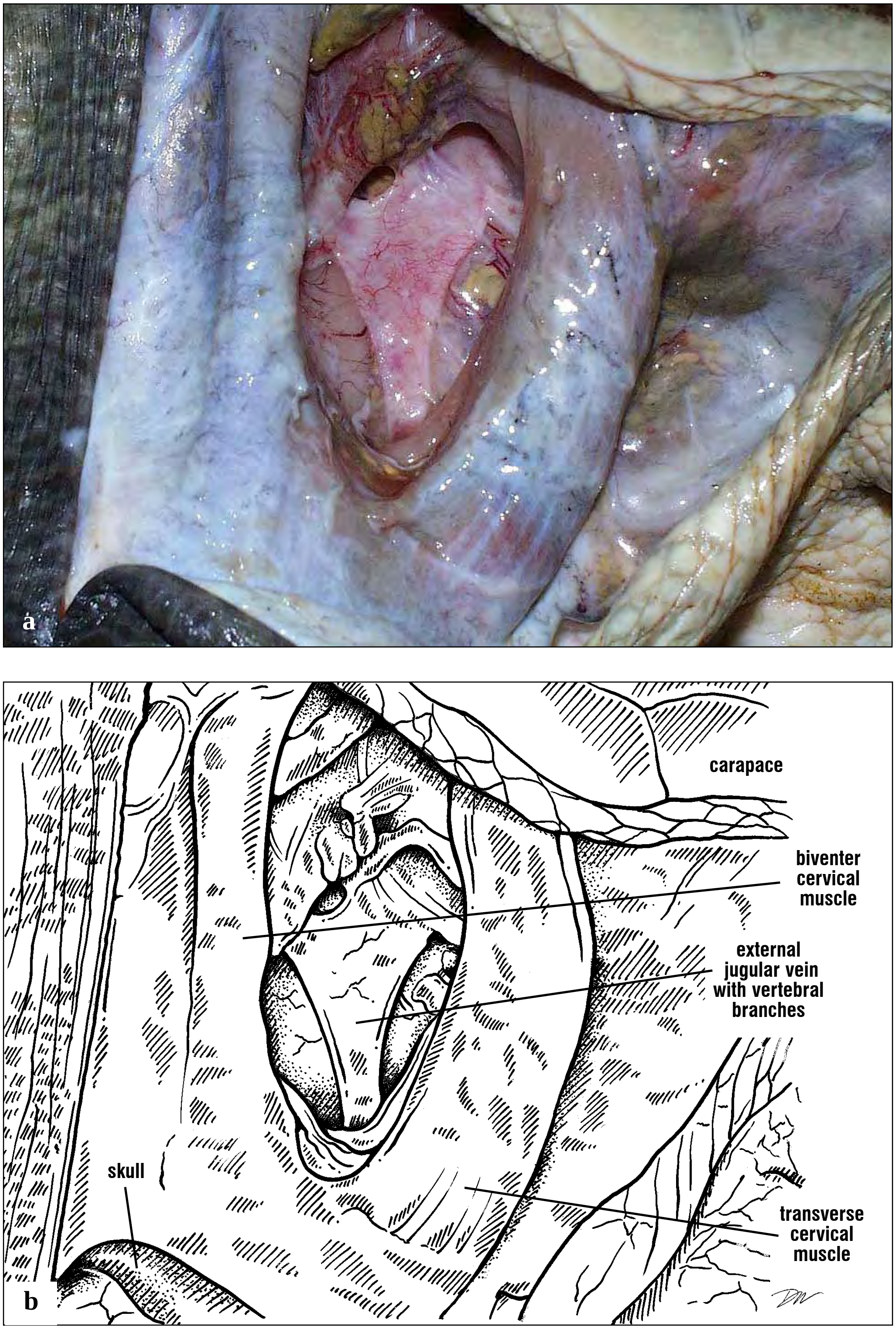
Figs. 142a and 142b. *Dorsal view of the neck of a green turtle with the carapace removed. The precava (superior vena cava) receives blood from the subclavian veins. The relatively small external jugular vein of green turtles receives relatively few branches when compared with the anatomy in other cheloniids.*

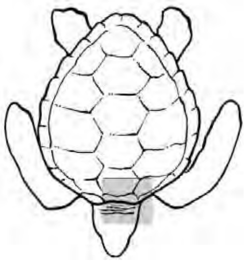


Figs. 143a and 143b. *Dorsal view of the external jugular veins and the vertebral vein. In this turtle the transverse veins are not obvious. There is an anterior bifurcation of the vertebral vein at the level of the neck rather than at the skull in this individual. The external jugular vein of this hawksbill receives dorsal and ventral vertebral branches from the cervical musculature proximally and distally. However, there are no branches along most of the intervening length.*

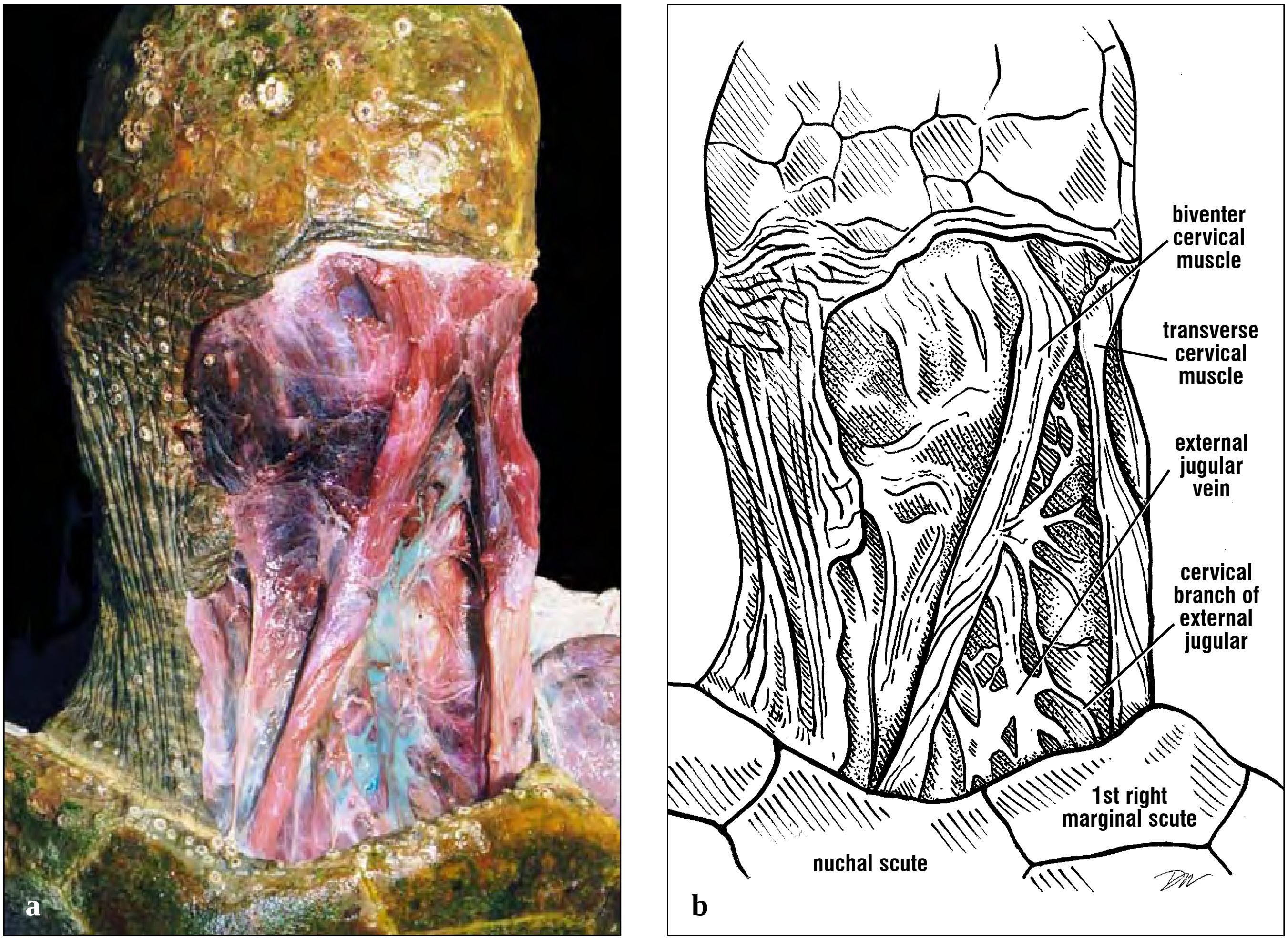


Figs. 144a and 144b. *The external jugular vein and its network of vertebral branches are obvious in this Kemp's ridley. Multiple vertebral branches are common in this species between the prominent dorsal neck muscles.*

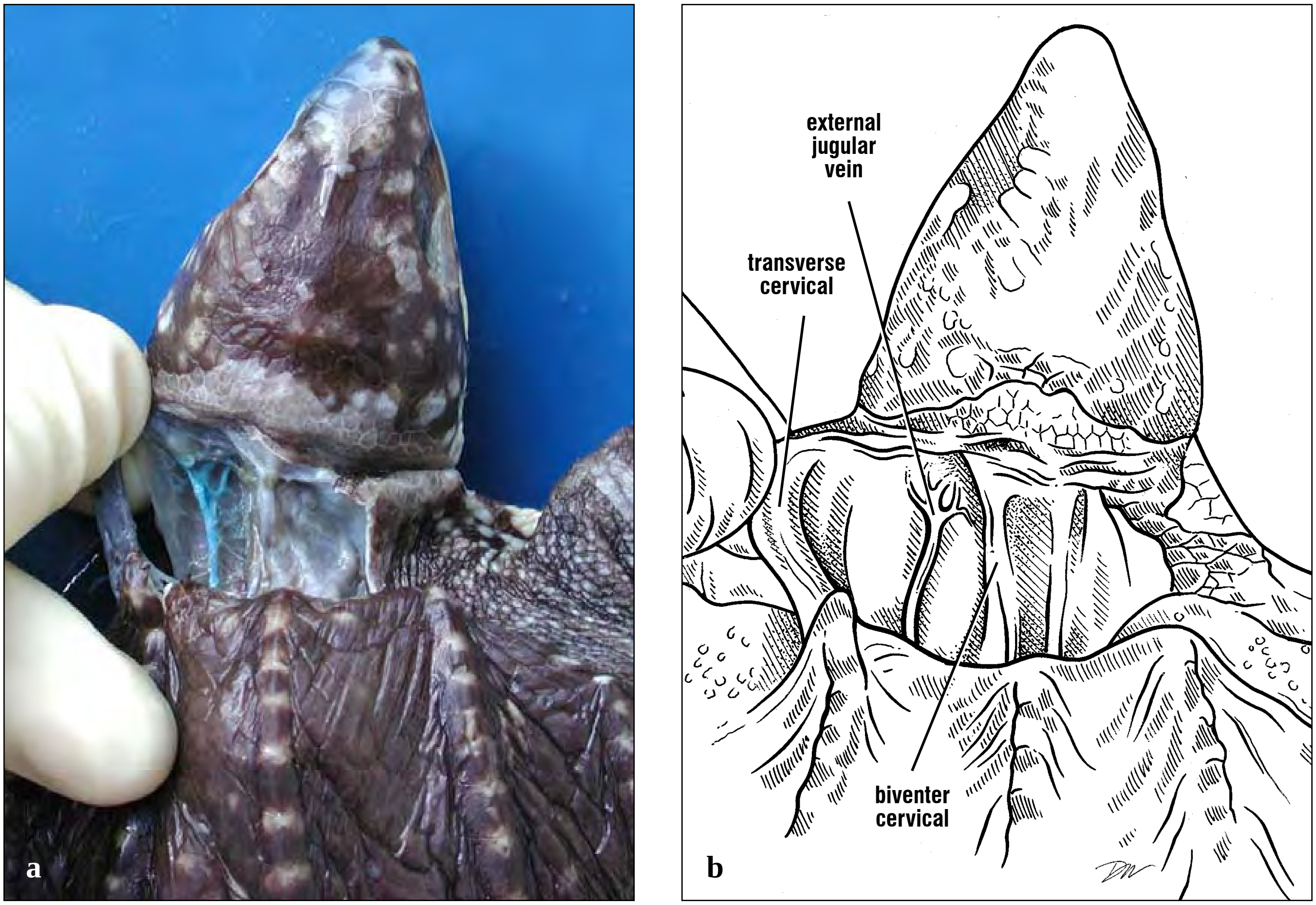




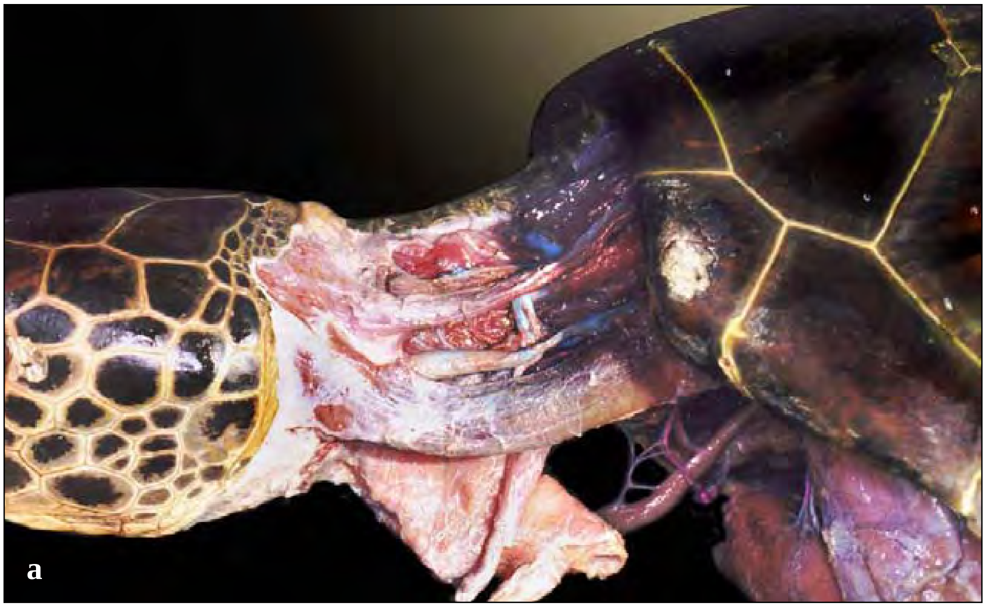
Figs. 145a and 145b. *Dorsal view close-up of a Kemp's ridley external jugular vein, and its transverse branch arises medially (toward the left in this picture).*

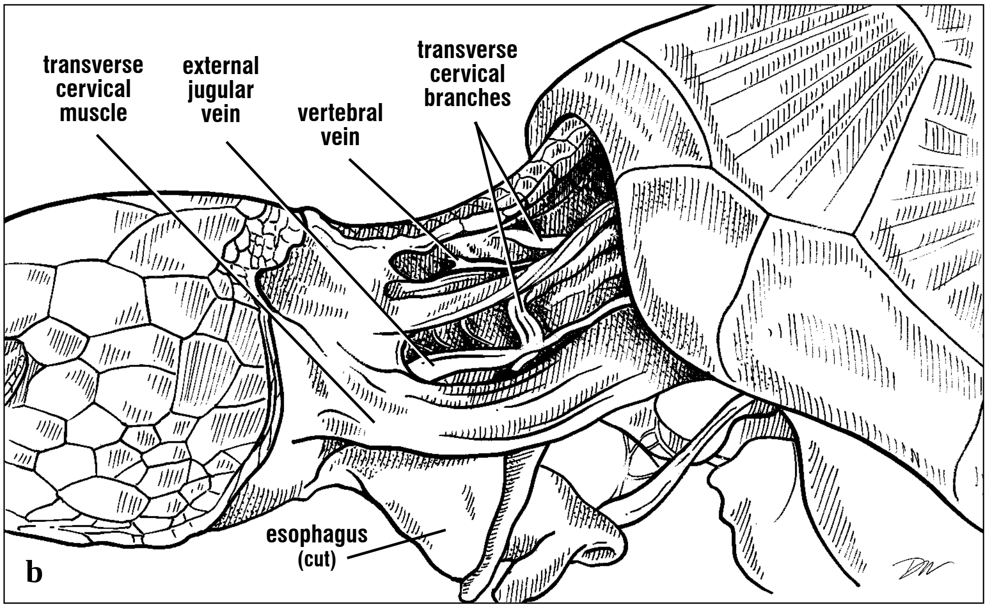


Figs. 146a and 146b. *The external jugular vein is large and is associated with many anastomoses (networks of interconnected blood vessels) as well as cervical (vertebral) branches to the neck muscles of loggerheads.*



Figs. 147a and 147b. *Dorsal neck circulation in a leatherback. The external jugular vein is large and is associated with many small cervical (vertebral) branches to the neck muscles. The vessel is located deep between the transverse cervical and biventer cervical muscles.*





Figs. 148a and 148b. *Lateral view of the external jugular vein and both right and left transverse cervical branches in a green turtle. The vertebral vein is visible for part of its length, and is medial and deep to the cut skin of the dorsal neck.*

The external jugular vein (often termed the dorsal cervical sinus) is a commonly used venipuncture (blood collection) site in sea turtles. The external jugulars are large and extend from the base of the neck into the head where they drain the structures of the head. Each gives off at least one transverse branch that joins the other medially (Figs. 141-147). Often a small central **vertebral vein** extends along the midline from the junction of the transverse cervical veins and provides drainage to the dorsal cervical muscles, cervical vertebrae, and the spinal meninges. In *Chelonia mydas* and *Eretmochelys imbricata*, the external jugular is smaller in diameter and branches little (Figs. 141-143, 148-149). This vessel branches frequently in the dorsal cervical region of *Caretta caretta* and *Lepidochelys kempii* (Figs. 144-146). In *Dermochelys*, it branches near the head (Fig. 147). All species have vertebral branches from the external jugular draining the cervical structures.

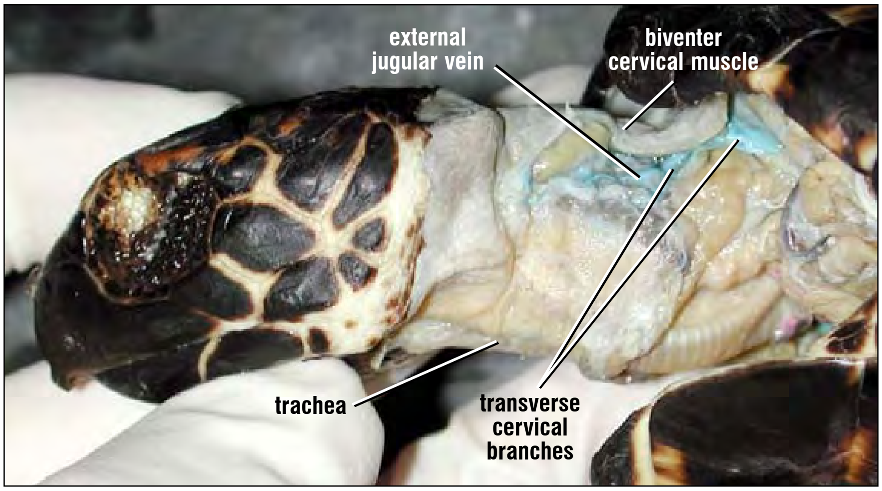
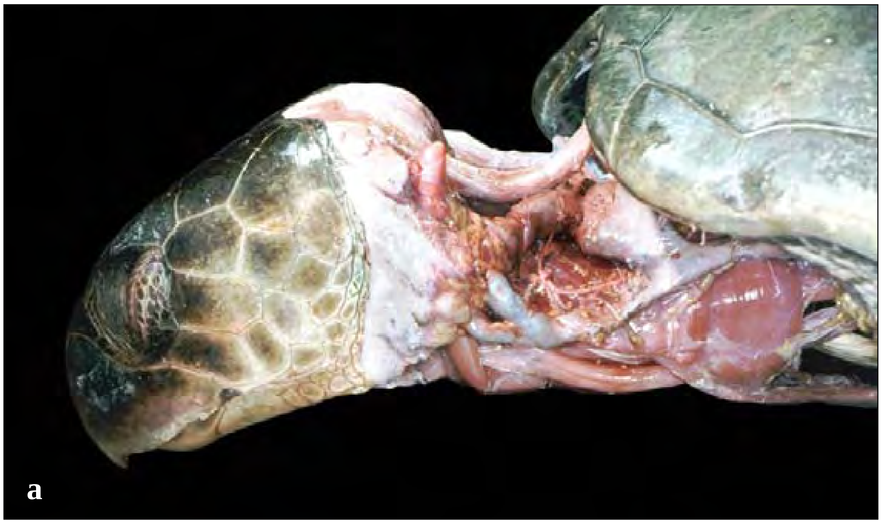
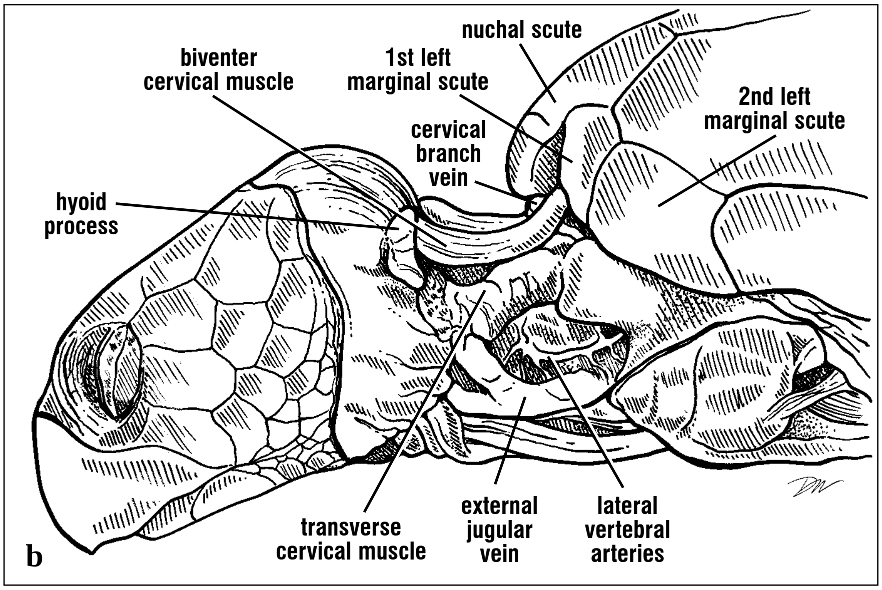
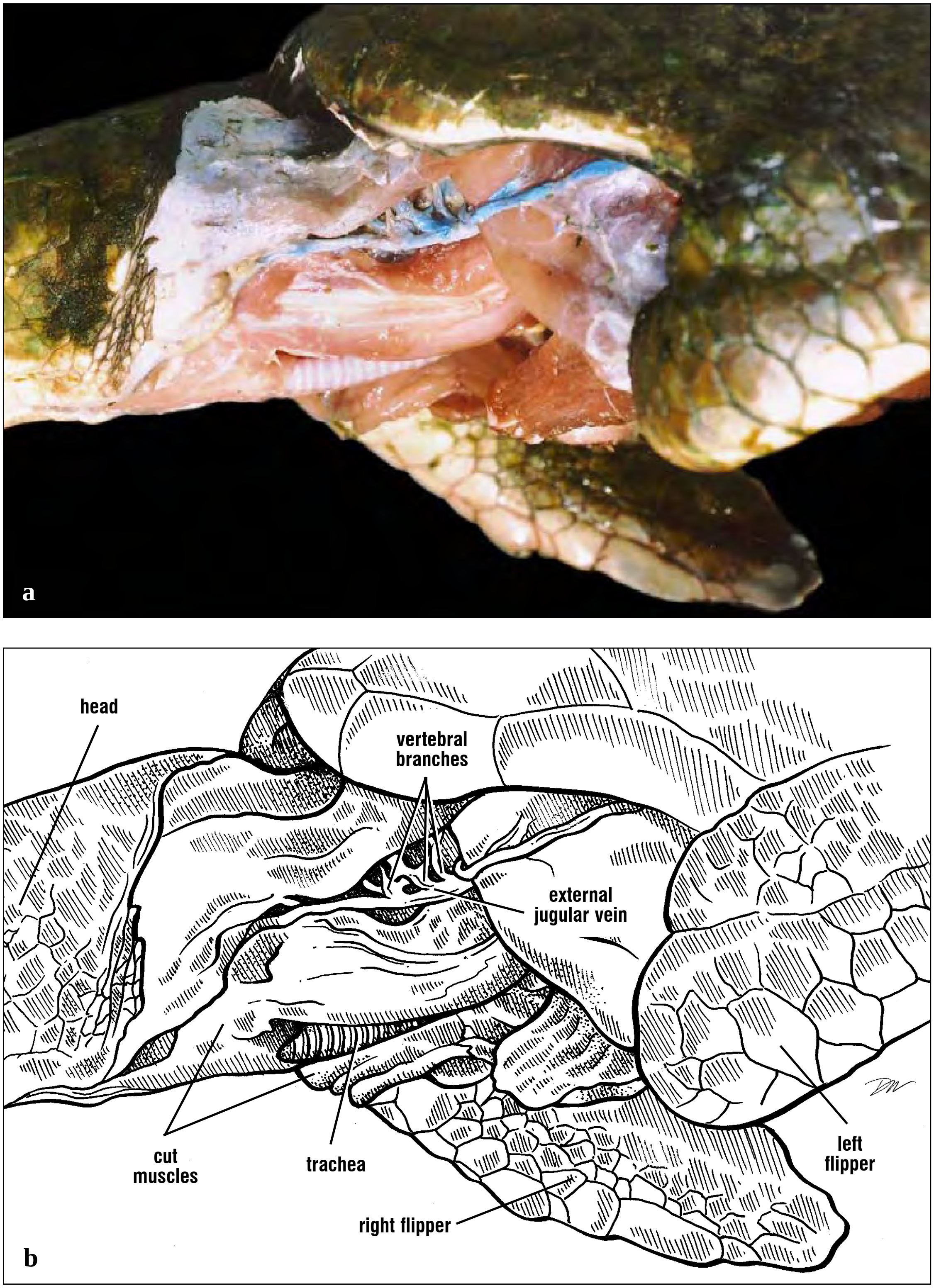


Fig. 149. *Lateral view of hawksbill cervical circulation. The external jugular vein in hawksbills has few branches along most of its length. The vessel branches proximally to receive vertebral branches (near the nuchal scute) and ventrally, draining the ventrolateral neck muscles. Ventral cervical arteries are exposed adjacent to the trachea near the plastron.*

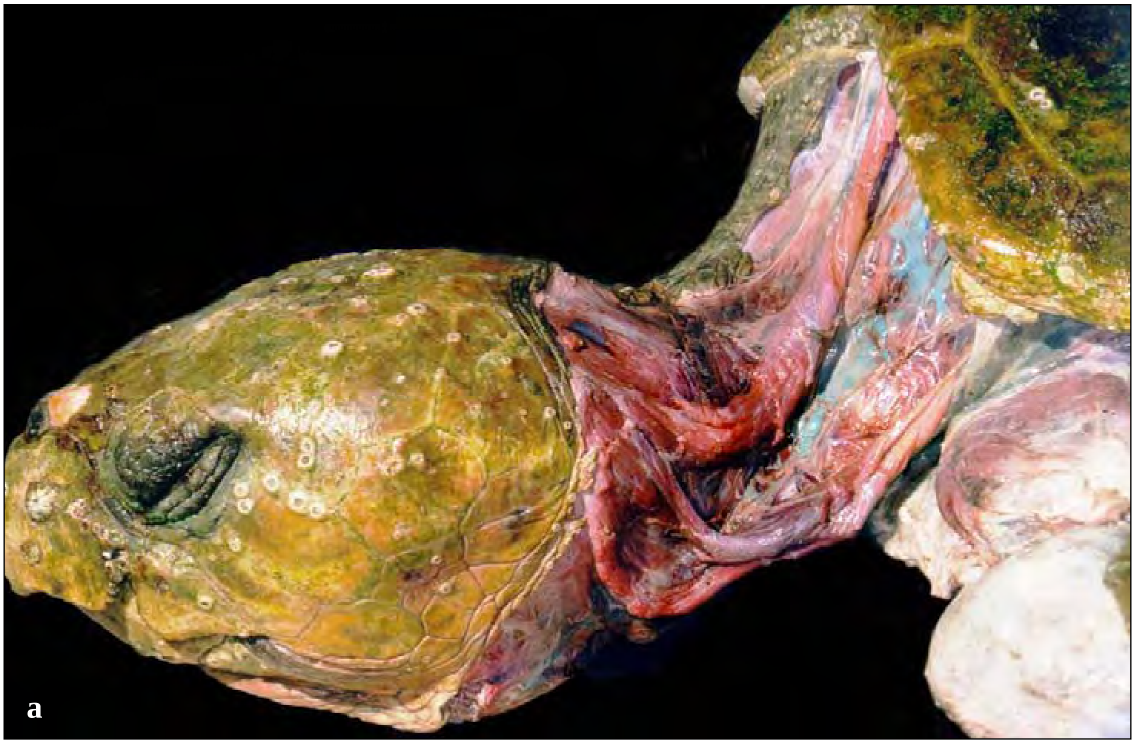


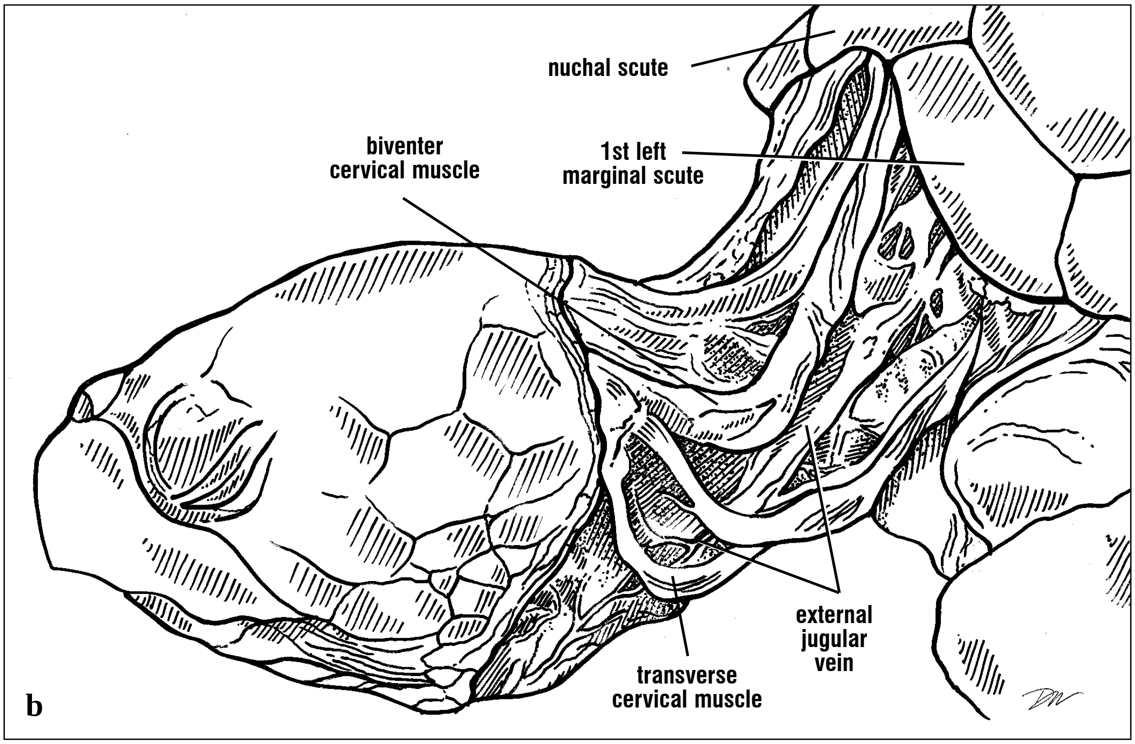


Figs. 150a and 150b. *The external jugular, injected with latex to provide contrast, is very large in this Kemp's ridley. After removing the connective tissue, the external jugular dropped to a more ventral position than would be found in life. Lateral vertebral arteries from the carotid are seen in this deep dissection.*



Figs. 151a and 151b. *This lateral view of a Kemp's ridley shows the many vertebral branches off the external jugular going to the deep cervical musculature.*





Figs. 152a and 152b. *This lateral dissection of a loggerhead's external jugular shows the extensive branching that is typical of this species. The transverse cervical muscle has been split along its length to expose the vein. Both the muscles and veins are displaced ventrally because their supporting connective tissues have been removed.*

The internal jugular vein is smaller in diameter than the external jugular and is found more deeply adjacent to the longus colli muscles. It receives multiple branches from the esophagus (**esophageal veins**) before it drains into the precava (Fig. 153).

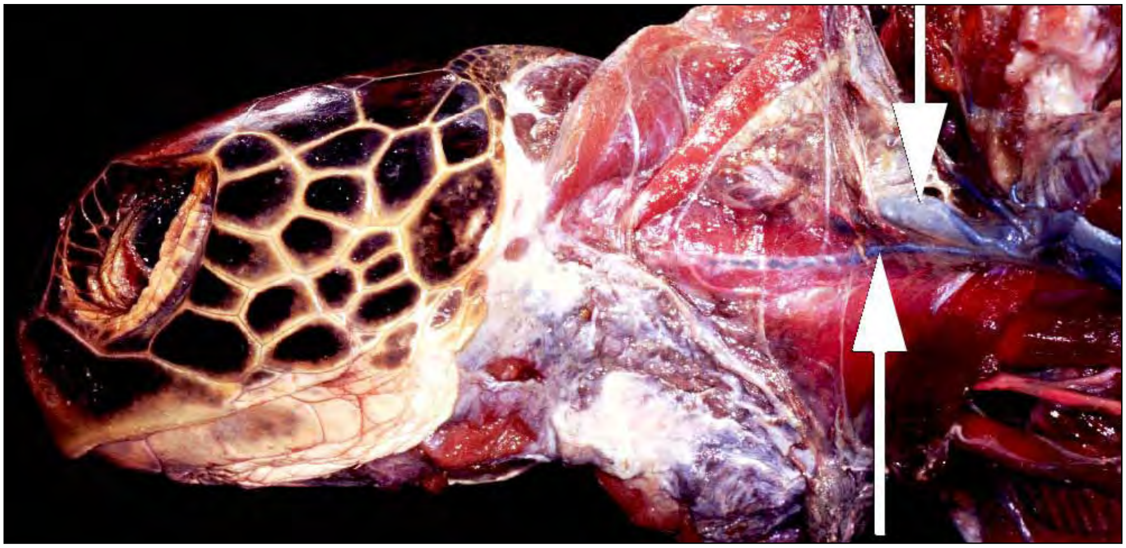
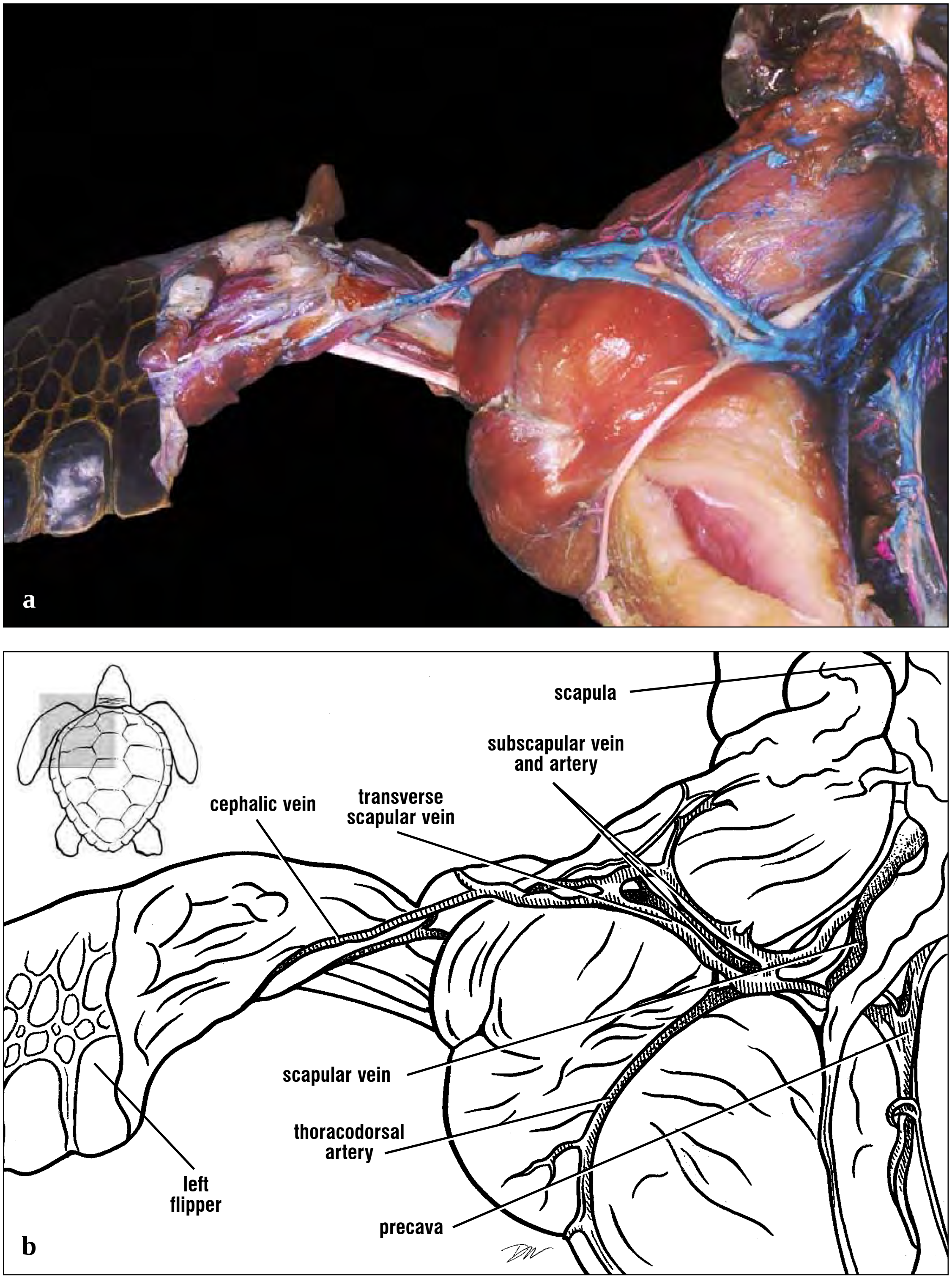


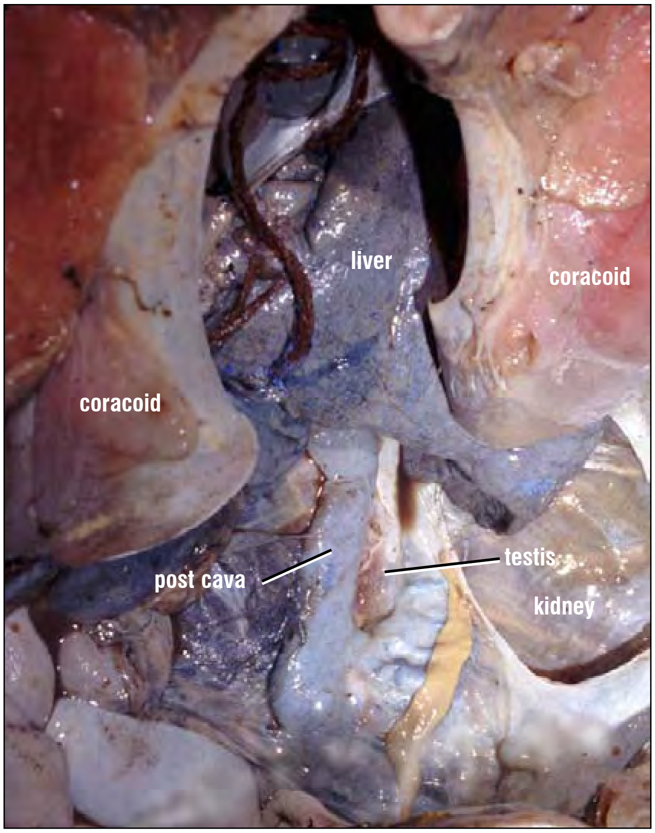
Fig. 153. *The internal and external jugular veins from the precava are exposed in this dissection of a green turtle. The external jugular vein (downward pointing arrow) is mostly covered by the cut neck musculature which has been reflected dorsally. The internal jugular (upward pointing arrow) is partially injected with latex. The internal jugular vein is usually accompanied by the vagus nerve, however it is not distinct in this photo.*



Figs. 154a and 154b. *Venous and arterial branches of the posterior aspect of the flipper. The cephalic vein from the flipper drains into the transverse scapular vein along the scapular musculature, then to the scapular vein, which then joins the precava. The thoracodorsal artery is a branch from the subclavian or the brachial in most turtles.*

Venous return from the posterior body is by both direct routes (to the postcava and the left hepatic vein) and indirect routes (via the **renal portal** and **hepatic portal** systems). Portal systems are those that start and end in capillaries. The renal portal system consists of veins draining into the **postcava, abdominal, renal portal,** and **external iliac veins.** The hepatic portal system includes the veins draining into the **hepatic portal, common mesenteric, mesenteric,** and **duodenal veins.** These will be discussed separately.

The postcava runs anteriorly from the capillaries of kidneys through the right lobe of the liver (Fig. 132). It emerges from the right lobe of the liver and enters the right side of the sinus venosus. Posteriorly, the postcava receives multiple pairs of **renal veins** from the ventral surface of the kidneys. **Gonadal veins** also pass from gonads, through the kidneys, and to the postcava. Branches from the **iliac veins** drain the pelvic musculature, and the **costal veins** from the carapace occasionally drain into the postcava. Anteriorly it receives multiple **hepatic veins** from throughout the liver. The postcava is part of the renal portal system. The **left hepatic vein** drains blood through the liver and from the paired **abdominal veins**, (Fig. 132) which are located just anterior to the pelvis and in the peritoneum. There is usually a **transverse abdominal vein** connecting the abdominal veins. Blood can flow in either direction through this vein. The abdominal veins receive **pectoral veins** (Fig. 127) descending from the pectoral muscles. **Pericardial veins** usually enter the abdominals near the pectoral veins and posterior to these, a pair of vesicular veins enters from the bladder. The abdominals extend along the dorsal pelvic musculature and receive **pelvic veins** from the left and right sides.



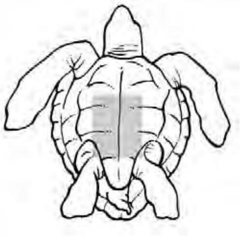
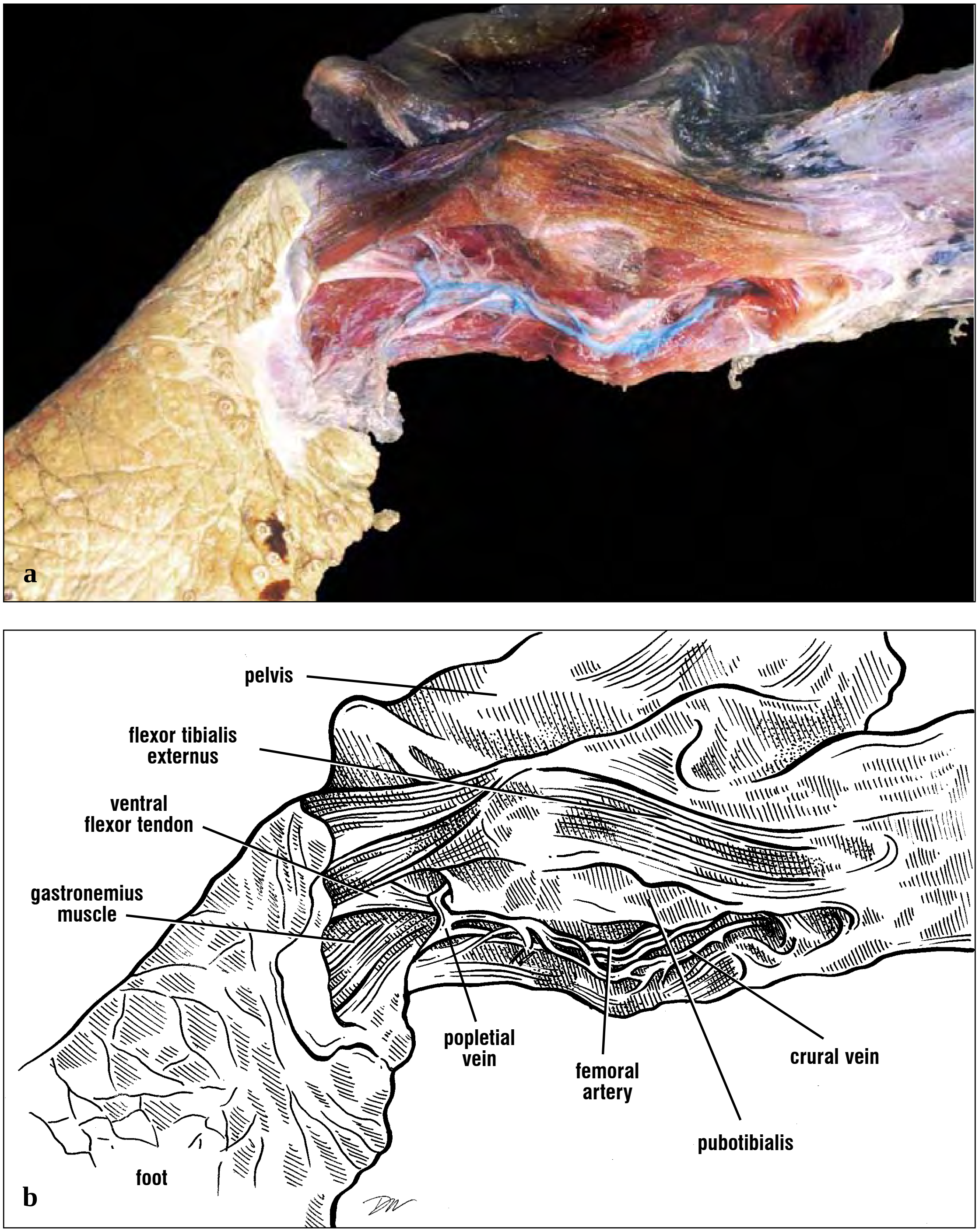
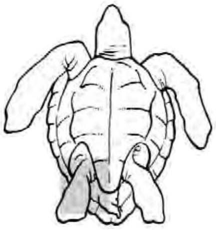


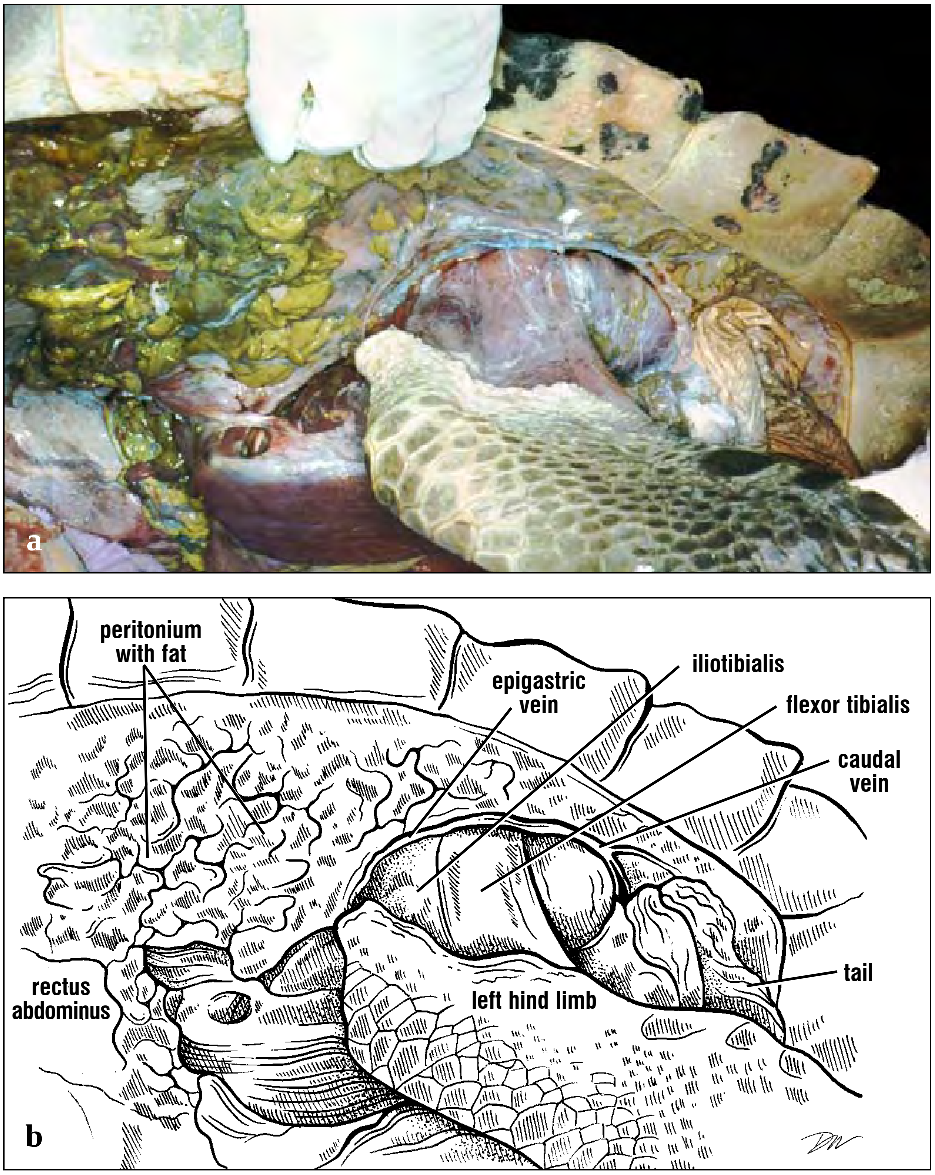
Fig. 155. *Ventral view of the postcava. The postcava emerges from the liver and passes to the kidneys. Blood is drained from the kidneys and posterior body to the liver.*

In the hind limb, **crural veins** extend from the medial to the posterior thigh and shank. Crural branches from the shank, the **tibial** and **popletial veins**, plus the **femoral veins** (from the dorsolateral thigh and shank; Figs. 132 and 156) drain to enter the abdominals, usually just posterior to the pelvic veins. Paired **lipoidal veins** from the left and right inguinal fat pads, enter the abdominal veins from near the crural veins. **External iliac veins** drain into the abdominals at or near the junction of the femoral and crural veins with the abdominal veins. The **epigastric vein** (Fig. 157) extends from the marginocostal vein on each side and travels with the epigastric artery along the posterolateral margin of the carapace. It runs along the upper thigh, and drains into the external iliac vein.



Figs. 156a and 156b. *The right hind limb of this loggerhead shows the positions of the femoral artery, crural, and popletial veins. These arteries and veins travel with the sciatic nerve.*





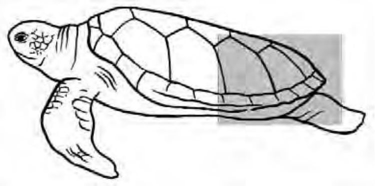


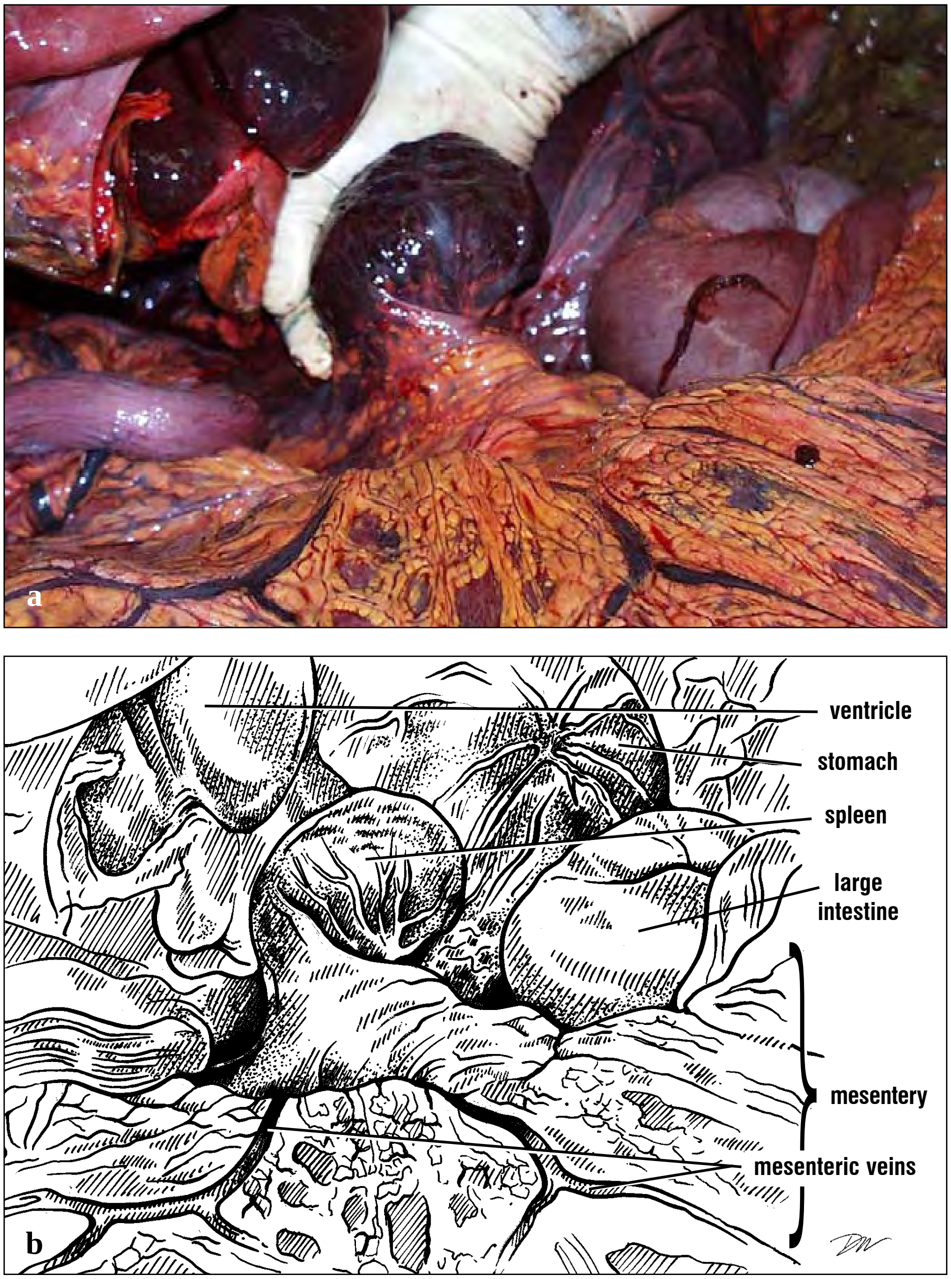
Fig. 157. *Lateral and posterior view. The epigastric vein travels dorsally to the dorsal hind leg extensors (iliotibialis) and flexors (flexor tibialis). This vein is medial to the marginal scutes and just ventral to the dorsal fat layer. It receives drainage from into the caudal veins just dorsal to the tail.*

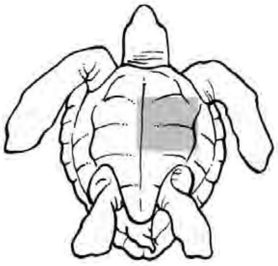
The paired **renal portal veins** receive the **ischiadic veins** from the posterior hip muscles. The **caudal veins** (Fig. 157) extend along the lateral tail and receive the **cloacal veins**, medially from the cloaca and rectum. The caudal veins drain into the ischiadic veins, as well as the epigastric vein in sea turtles. The renal portal vein also receives drainage from the narrow **vertebral veins**, which are found lateral to the vertebral column and enter the kidneys anteriorly and dorsally. The vertebrals receive costal veins from the shell, which are connected laterally with the **marginocostal vein** (Fig. 132). From the cloaca, bladder, rectum, and in males, the penis, blood drains to the **hypogastric vein**, which enters the kidneys posteriorly and ventrally. The renal portal veins drain from the dorsal kidney capillaries into the external iliacs at the level of the epigastric veins, or into the posterior extent of the abdominal veins.

The **hepatic portal** vein receives drainage from the abdominal veins. It passes dorsally between the right and left lobes of the liver. Anteriorly, it receives several branches from the stomach, the **gastric veins**, with several branches forming the **anterior**

pancreatic veins (along the left half of the pancreas), the **posterior pancreatic veins** (from the right half of the pancreas), and the long **duodenal vein** (Figs. 134 and 136). The spleen, found near the posterior end of the pancreas, is highly vascular and is drained by several **splenic veins** to the hepatic portal vein (Fig. 158).

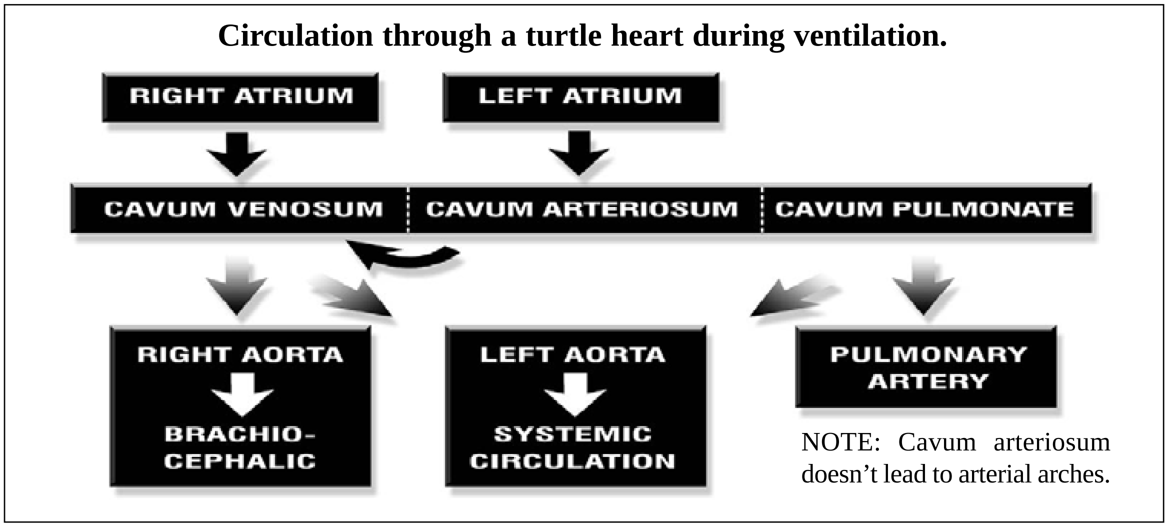
More posteriorly, multiple **mesenteric veins** travel with the mesenteric arteries radiating from the small intestines and through the fan-shaped mesentery (Fig. 158). The mesenteric veins converge on the **common mesenteric vein**, which drains into the hepatic portal vein. The **inferior mesenteric vein** drains branches from the large intestine up to the iliocaecal junction (where the large intestine meets the ileum), then itself enters the common mesenteric vein leading to the hepatic portal vein.





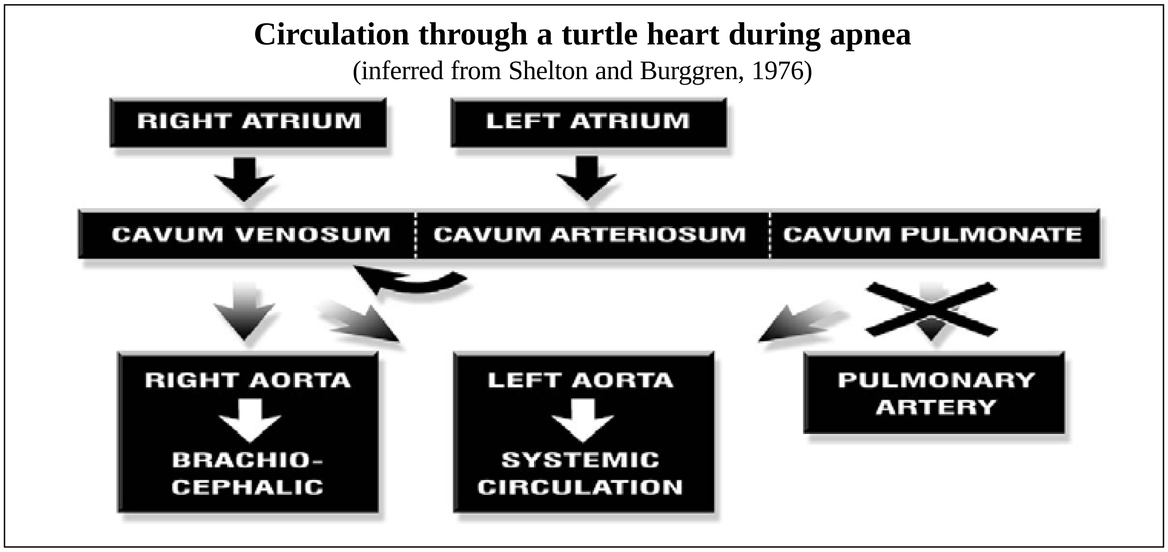
Figs. 158a and 158b. *The spleen is exposed to the left of the stomach and distal to the pancreas (covered by mesentery). Several splenic veins cover the spleen's surface. Mesenteric veins, in the fat-rich mesentery, drain blood returning from the small intestines.*

Circulation Through the Heart. The route blood takes though the heart differs depending upon whether blood is shunted toward the lungs and the body, or primarily toward the body. Unlike mammalian cardiopulmonary systems, the pulmonary and systemic blood flows are not always separate. The extent of separation between the pulmonary and systemic circuits of flow differs somewhat between *Dermochelys* and the cheloniids. There is a nearly complete separation of systemic (body) and pulmonary (lung) circulation in the leatherback heart, but the intra-cardiac flow is less well separated into pulmonary and systemic outflows in the cheloniid species. Studies of turtles generally show that whether blood is shunted to or away from the lungs is a function of arterial blood gas levels. Venous blood returning from the head, limbs, and body enters the sinus venosus, then flows to the right atrium. From the right atrium, blood enters the ventricle where it flows along at least two possible routes. The diagram below (Fig. 159) summarizes the route blood takes through the heart. Blood from the kidneys returns to the left atrium via the pulmonary veins. It then flows from the left atrium to the ventricle and usually out through the aortas to the body.



Circulation through a turtle heart during ventilation.

NOTE: Cavum arteriosum doesn't lead to arterial arches.



Circulation through a turtle heart during apnea

(inferred from Shelton and Burggren, 1976)

Fig. 159. *Circulation through a turtle heart during breathing and during breath-holding (apnea).*

Lungs and Airways

The **pulmonary system** is composed of the **glottis**, **trachea**, a **bronchus** to each lung, and the left and right **lungs**. The airways begin at the glottis, which is located in the middle to posterior portion of the tongue (Fig 160). The glottis and its muscles are supported ventrally by the hyoid apparatus. The glottis opens during air passage and is closed during breath-holding. The glottis leads directly into the trachea, which is supported by complete cartilaginous rings that are usually white, except in decomposing animals or some turtles with pulmonary disease. The trachea is long and bifurcates into two bronchi dorsal and anterior to the heart. These then enter the anterior part of the lungs next to the pulmonary arteries. The bifurcation begins internally, anterior to the external division to form the bronchi. The bronchi extend for virtually the length of the lungs and have many openings into the complex internal lobes of the lungs (Fig. 161). Unlike the bronchi of mammalian lungs, these openings lead to chambers that are not supported by cartilage. There are no secondary bronchi in sea turtles.

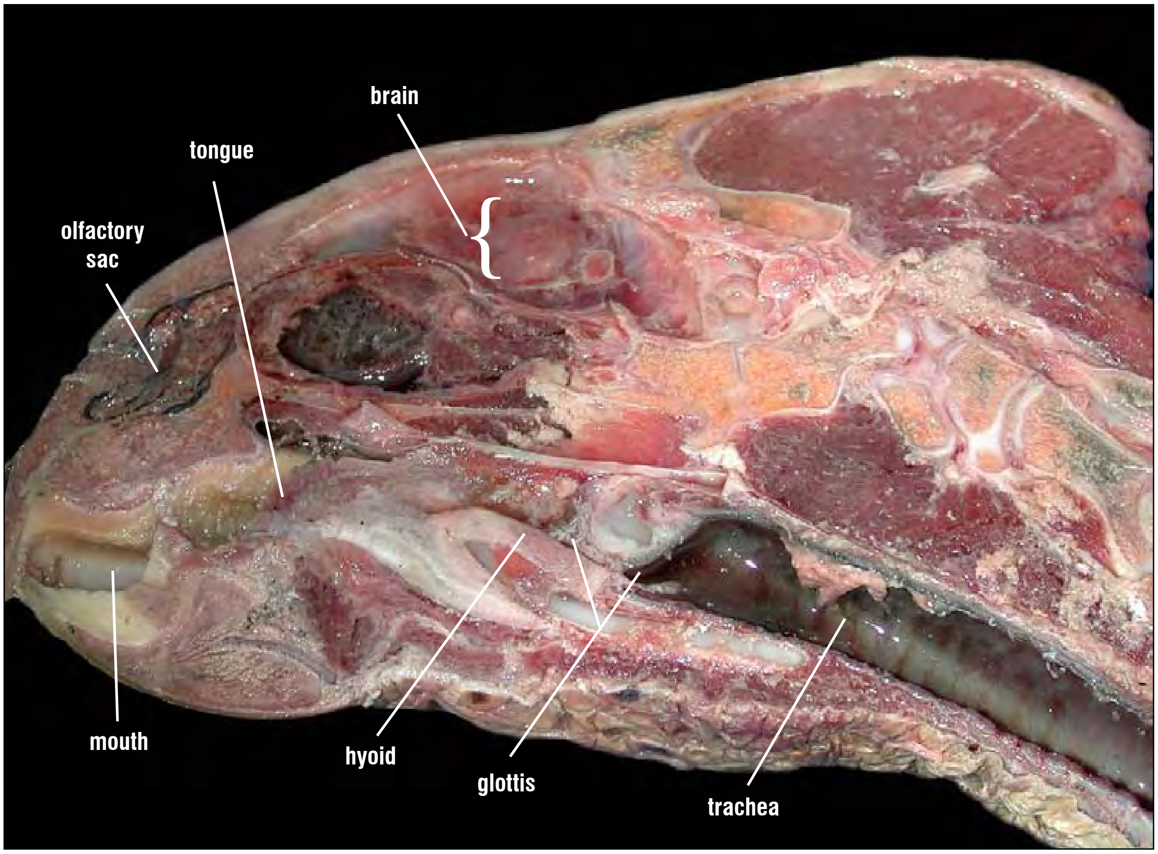


Fig. 160. *Parasagittal section of a hawksbill showing the airway. The hyoid apparatus, including both bony and cartilaginous portions, supports the glottis ventrally. The glottis, located between the hyoid and the surface of the tongue, is closed in this dissection.The large tracheal diameter is maintained by cartilaginous rings. The trachea is lined by smooth epithelium.*

Fig. 161. *Longitudinal section through a loggerhead bronchus. The lungs of cheloniids are spongy in construction and red in color. They also have a large surface area but are not as densely constructed as the lungs of leatherbacks. The large-bore trachea has many openings to the chambers of the lung along its length. These openings are not supported by cartilage once they leave the bronchus. The unsupported airways extend to the air exchange surfaces called faveoli and ascini. The trachea and bronchus are supported by cartilage, which resists collapse during ventilation and diving.*

The lungs are located dorsally and are attached dorsally to the carapace and vertebral column. In some species, (e.g., *L. kempii* and *C. caretta*) the lungs are more closely attached to the vertebral column than in other species. Ventrally, the left lung is attached to the stomach via the **gastropulmonary ligament**. The right lung is attached to the right lobe of the liver by the **hepatopulmonary ligament**. Posteriorly, the lungs attach to the peritoneum that overlies the kidneys and adrenal glands and are adjacent to the gonads. The medial border of each lung is firmly attached (Fig. 162) via fibrous connections to dorsolateral surfaces of the vertebral column.

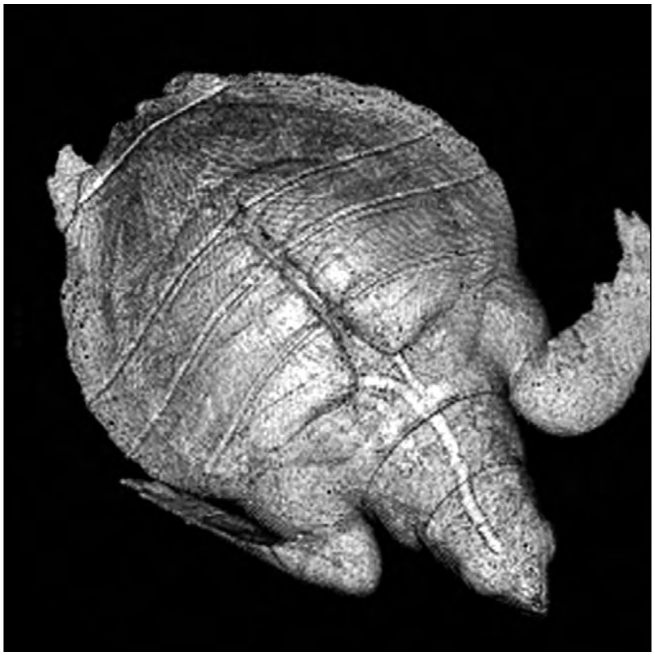


Fig. 162. *CT scan showing the lungs in a Kemp's ridley. This CT shows the position, form, and the extent of the lungs and airways in a living Kemp's ridley turtle. The medial surfaces of the lungs are attached tightly to the vertebral column.*

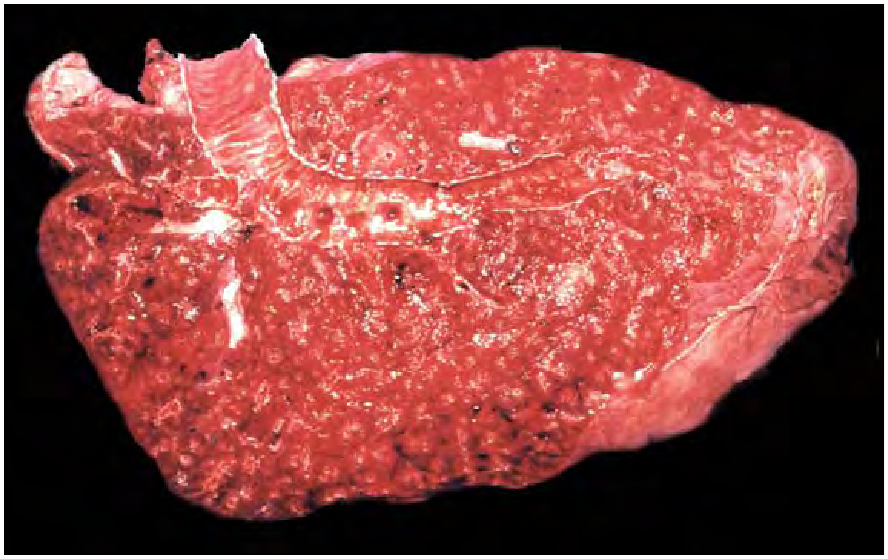


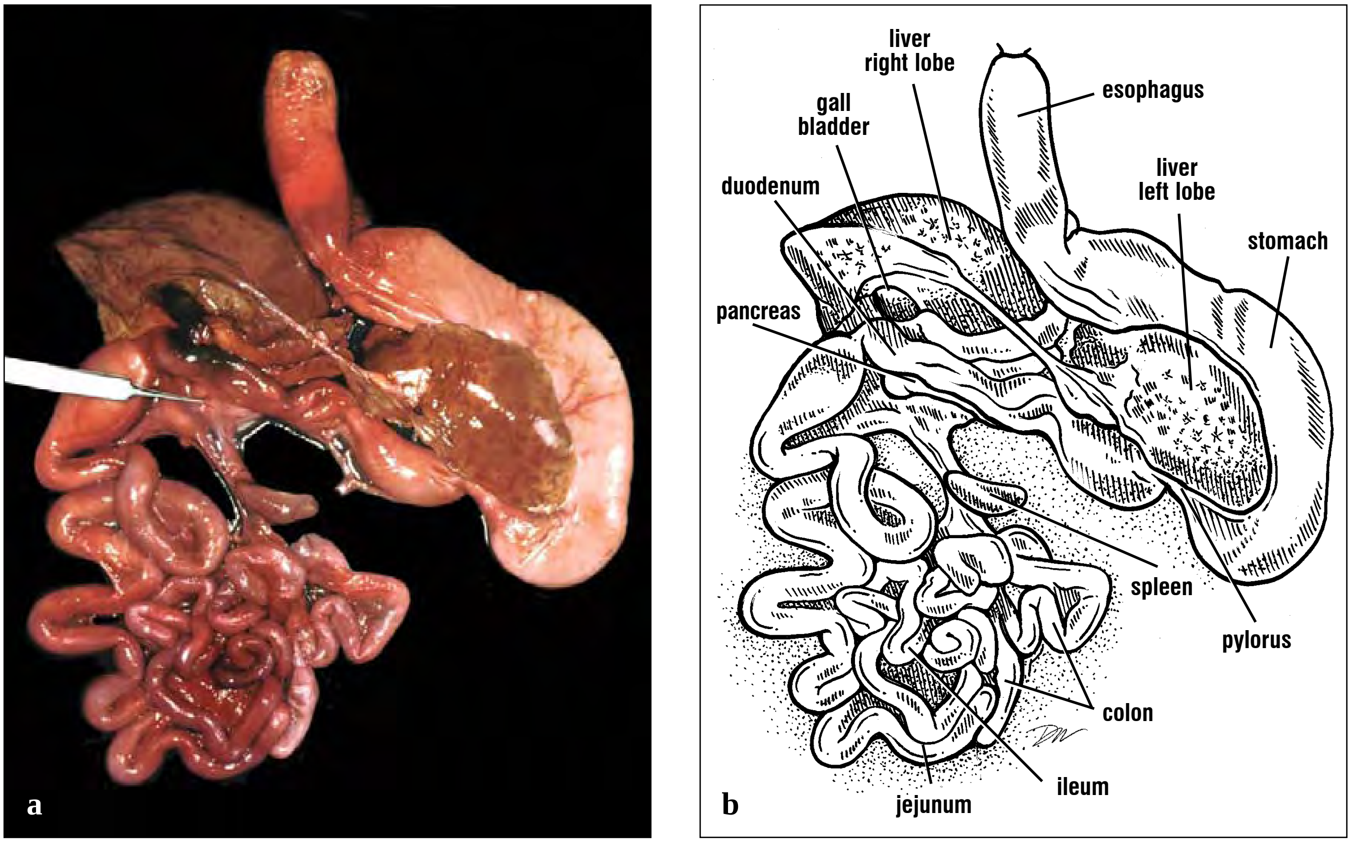
Fig. 163. *Longitudinal section through a leatherback lung. The lungs of leatherbacks are characterized by more dense construction. The high surface area, dense parenchyma, high levels of connective tissue, and extensive blood supply make leatherback lungs particularly spongy and deep red in color.*

All sea turtles have multichambered lungs (there are multiple lobes contained within the body of the lung). The lobes are not obvious externally. The lung tissue is spongy and highly elastic (Figs. 161 and 163) in sea turtles.

Ventilation of the lungs occurs without the assistance of a diaphragm. Marine turtles ventilate by movements of ventral muscles of the pelvic and pectoral girdles that attach to the plastron, compression of the inguinal region, and rocking of the shoulder muscle masses to change the pressure within the pleuroperitoneal cavity. Sea turtles have a large tidal volume. Under normal circumstances, they breath-hold until blood oxygen levels drop to low levels.

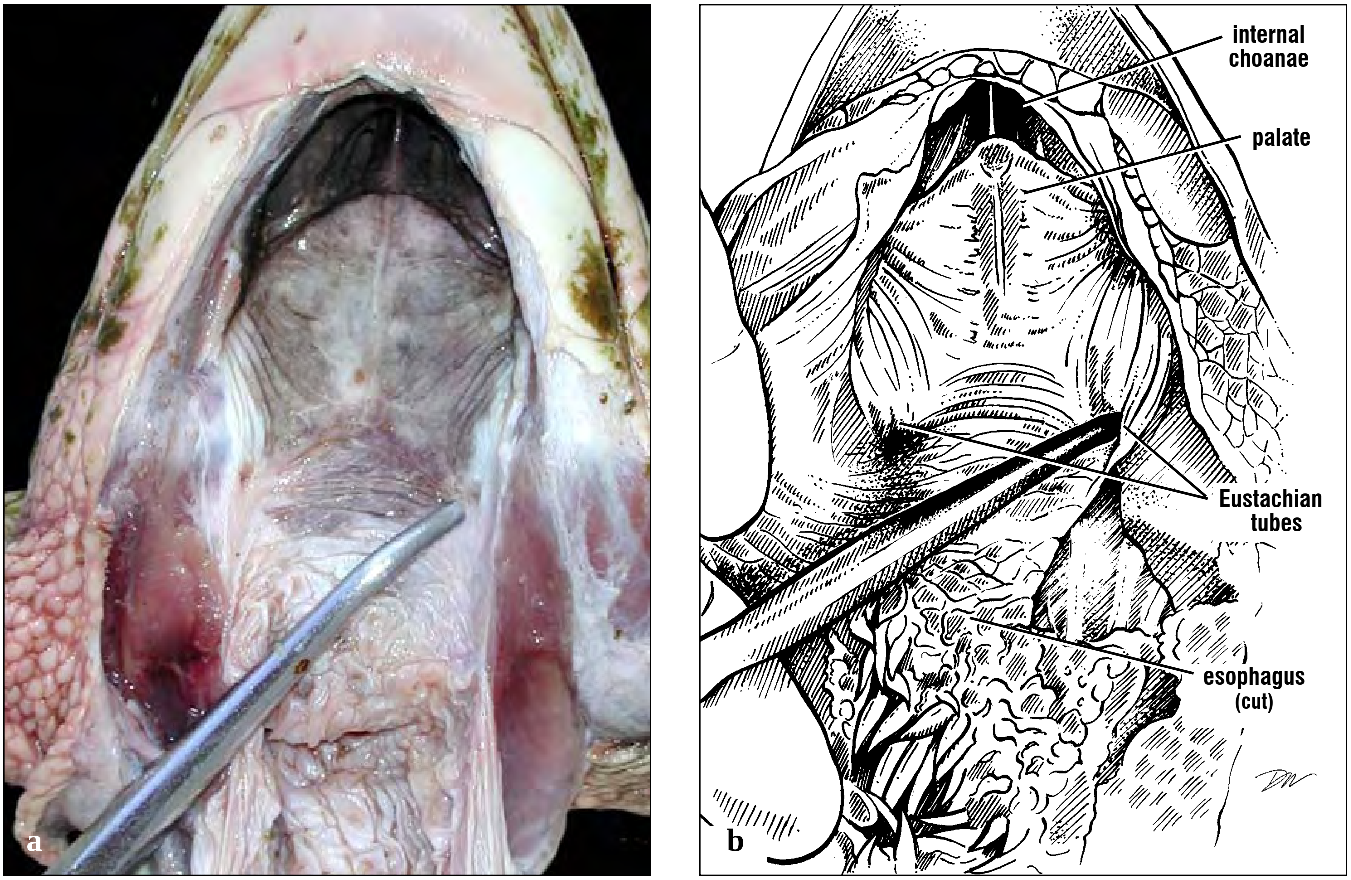
Gastrointestinal Tract

The **gastrointestinal tract** (GI tract or gut) extends from the mouth to the cloaca (Fig. 164). It is demarked by structural and functional divisions. The **mouth** captures and processes food. The **esophagus** conveys food to the stomach and expels excess water. It also works with the tongue in swallowing. The **stomach** starts the chemical and physical process of digestion. In the **small intestines**, digestive enzymes are added to food to break down proteins and complex carbohydrates. The small intestines are regionally specialized to absorb amino acids, carbohydrates, sugars, water, fatty acids, and minerals (particularly calcium and phosphorus). The **large intestine** (colon) typically reclaims water. The length of the gut is somewhat related to diet. It is proportionally longer in green and leatherback turtles than in loggerheads, ridleys, and hawksbills.

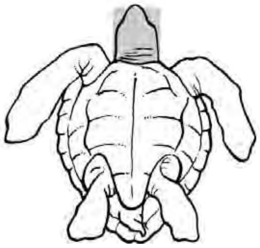


Figs. 164a and 164b. *The gastrointestinal tract with digestive glands and the spleen. The GI tract from the esophagus to the rectum from a Kemp's ridley turtle shows the different regions as well as the associated digestive glands, the liver and pancreas. The gall bladder stores bile, produced by the liver, and releases it through the common bile duct when food enters the duodenum. The spleen, located at the distal end of the pancreas, is not a digestive gland; rather it is a lymphoid organ in turtles involved in immunological activity.*

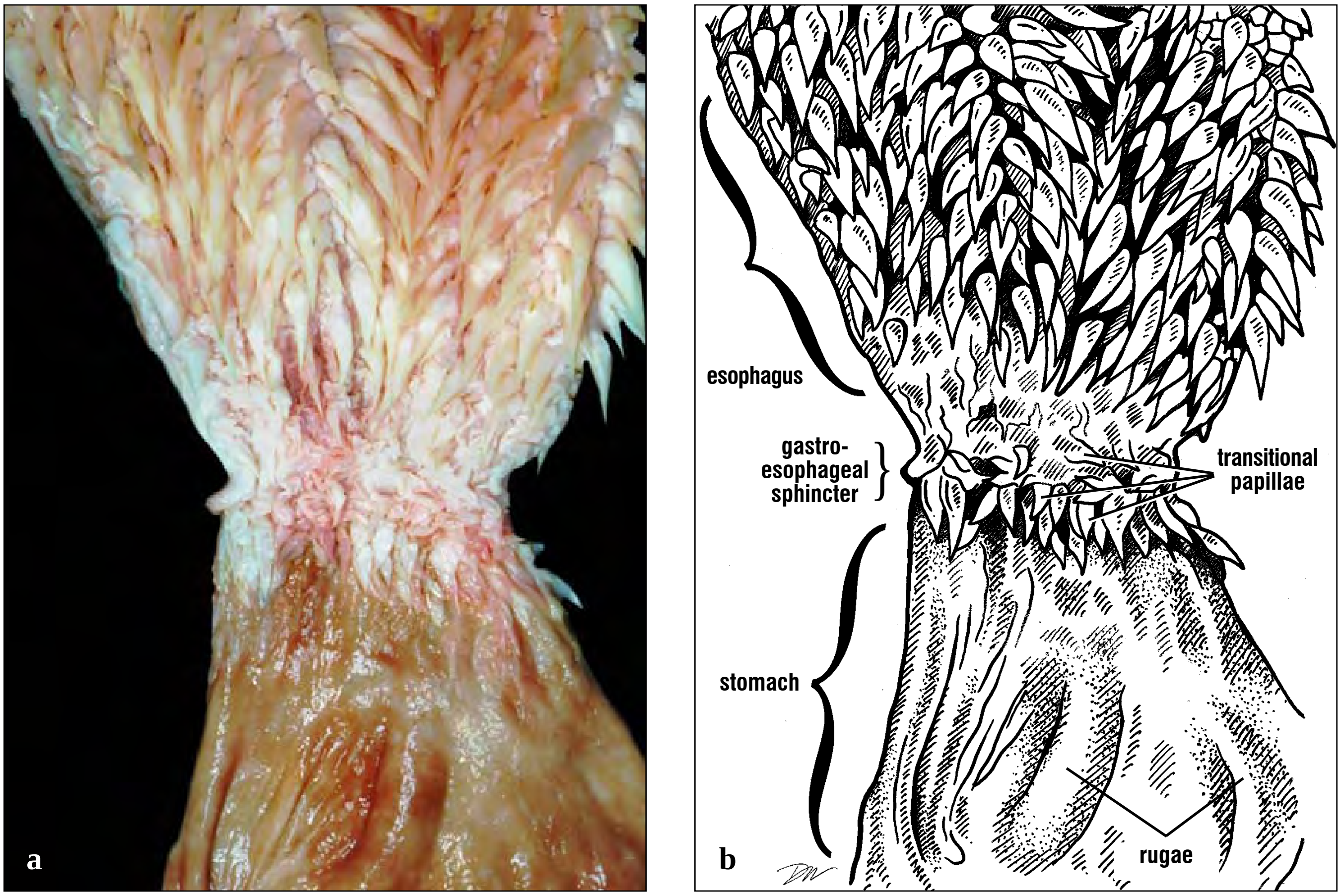
The mouth includes several GI, respiratory, and ear structures: the **mandibles** and the **pharynx** includes the **palate, esophagus, glottis, Eustachian tubes,** and **internal choanae** (Fig. 165). For convenience, these structures will be described together here. The glottis and internal choanae are part of the respiratory system and the Eustation tube connects the pharynx with the middle ear cavity. The tongue is fixed to the floor of the mouth and is not protrusible. The glottis is located on the middle part of the tongue (see Sense Organs, Fig. 209), just posterior and ventral to the internal choanae (internal nares); it acts as a valve to open and close the airway. The esophagus starts at the back of the tongue; it is a muscular tube that leads to the stomach. It passes slightly dorsal and to the right of the trachea. The Eustachian tubes (one on each side), are found in the posterolateral aspects of the mouth, medial to the jaw joint; they function in maintaining normal pressure in the middle ear (Fig. 165).



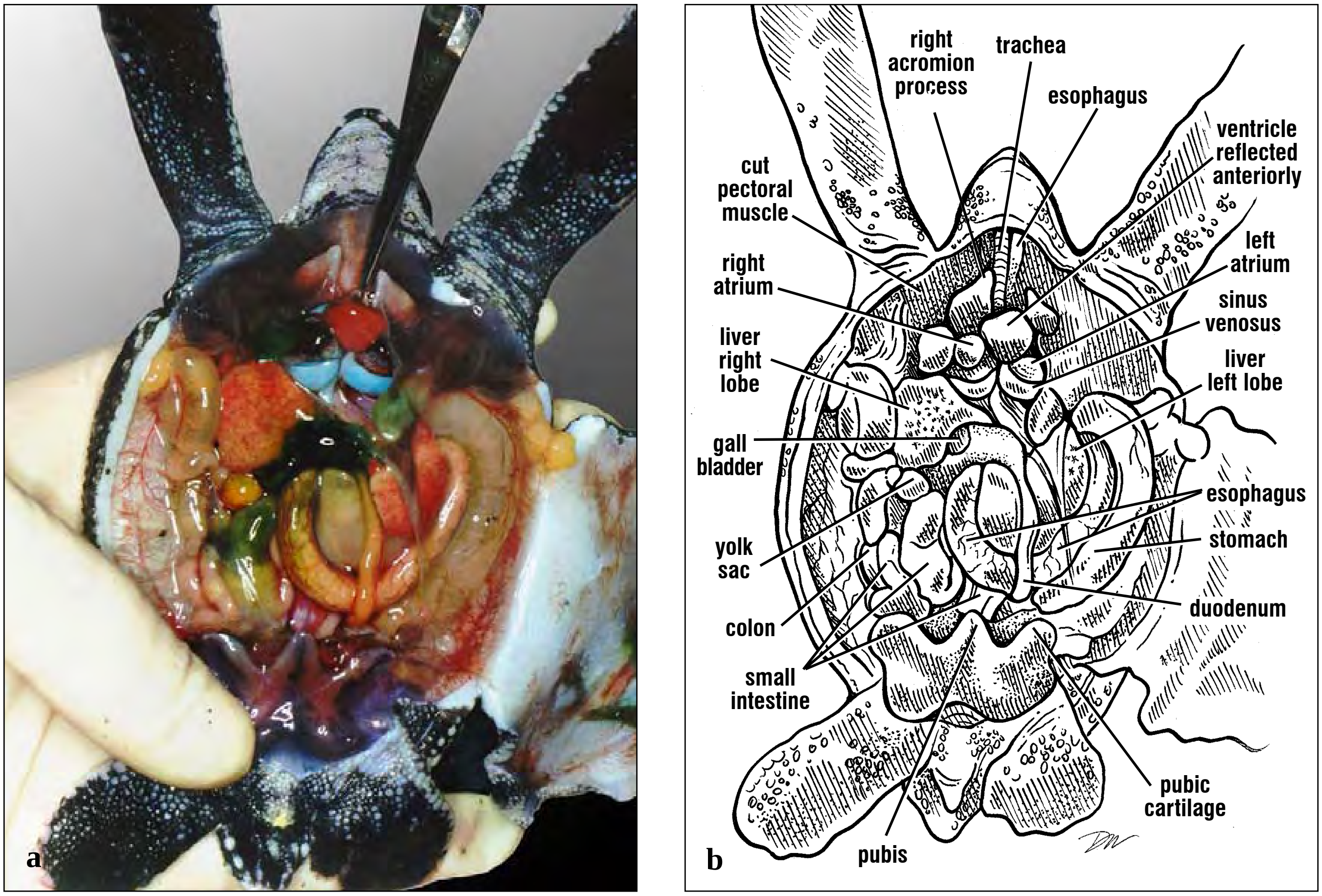
Figs. 165a and 165b. *Ventral view of the palate with the tongue and hyoid apparatus cut away. The roof of the mouth has internal choanae (internal nares) that open above the glottis (removed in this picture). In the posterior lateral parts of the palate, near the jaw joint, are the openings to the Eustachian tubes, which lead to the middle ear cavity.*



The esophagus (Fig. 166) is lined with **papillae** that are sharp and keratinized; they point inward towards the stomach. The papillae end where the esophagus joins the stomach (Fig. 166). The papillae are presumed to trap food while excess water is expelled prior to swallowing. In Atlantic green turtles, the esophagus enters the stomach in a smooth transition. However, in Pacific green turtles, there is a muscular specialization at the base of the esophagus called a **crop**. Its function is unclear. In cheloniids, the esophagus descends to a position just inside the plastron and bends to the left in an S-shaped curve to join the stomach. In *Dermochelys*, the esophagus is exceptionally long and extends almost half the length of the body before looping to the left, and returning anteriorly almost to the level of the axilla. There, the esophagus bends left again and joins the stomach (Fig. 167).



Figs. 166a and 166b. *The esophagus and anterior stomach lining. The papillae that line the esophagus are keratinized for most of the length of the esophagus. They end abruptly; several flat, transitional papillae, lacking keratin line the esophageal wall at the level of the gastroesophageal sphincter. Posterior to this sphincter, the stomach lining is very smooth and has no papillae.*

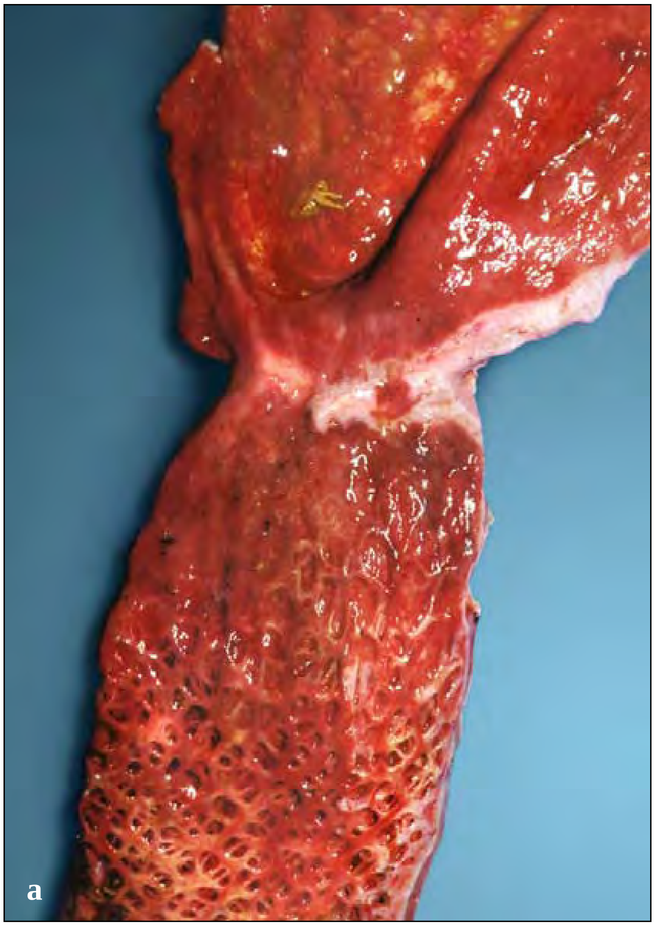


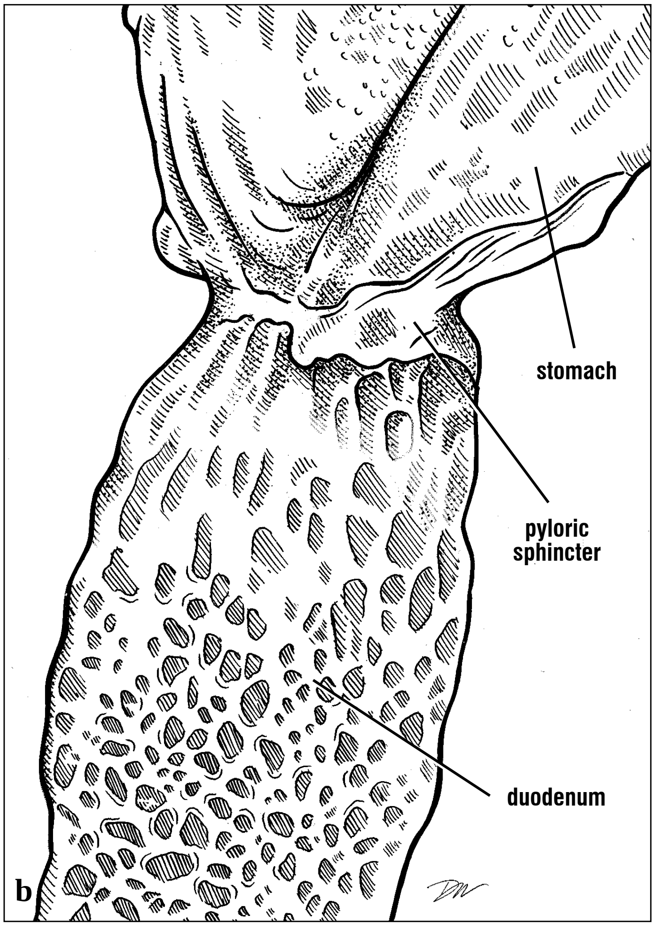
Figs. 167a and 167b. *Ventral view of a leatherback hatchling's viscera and heart. This dissection of a leatherback posthatchling shows the extremely long esophagus, large stomach, and small intestines. On the animal's right is the remaining yolk sac. The yolk sac can persist well after the time that the animal has begun feeding. In this animal, the coracoid processes were cut away and the acromion processes reflected anteriorly to provide a clear view of the heart and liver. The ventricle is pushed anteriorly exposing the sinus venosus, which was injected with latex to provide contrast.*

The **stomach** is on the animals left side and curves around the more medially located liver and pericardium. It is attached to the liver's left lobe by a **gastrohepatic ligament** and the left lung by a **gastropulmonary ligament**. The stomach is smooth-walled along its length. It ends in a short muscular region, the **pylorus** (= **pyloric sphincter** or **valve**). The pylorus is usually constricted and the intestinal lining on the **duodenal** side of the sphincter differs from that of the stomach (Fig. 169).

The pancreas runs distally along the duodenum from the pylorus to just past the **common bile duct** (Fig. 170). Both the pancreas and the common bile duct (from the gall bladder) deliver digestive enzymes to the duodenum. The common bile duct enters the duodenum via a small papilla, the **ampulla of Vater**, on the duodenum’s internal surface. Its location can be identified from the green bile stain (Figs. 170-171). The pancreatic duct (not shown) is difficult to locate in all but the largest turtles; it enters the duodenum near or in common with the common bile duct. The duodenum's lining is textured and, in some species, it is "honey-combed" in appearance (Fig. 171). This textured lining is associated with increased surface area and is well-developed in green turtles and leatherbacks. It is not as pronounced in the carnivorous/omnivorous species (e.g., loggerheads, ridleys, and hawksbills).

The transitions from one type of small intestine to the next (**duodenum** to **jejunum** to **ileum**) are often difficult to identify. Gross differences are often not obvious and are best confirmed by histological examination for the functional characteristics of the tissues. The transition from ileum to **colon** is clear. The ileum ends in a muscular sphincter, the **iliocaecal valve**. The proximal end of the colon is a **caecum** (pouch) that bulges somewhat more than the remaining large intestine (Fig. 77). It is more prominent in green turtles than other species. The colon narrows somewhat past the caecum; it is constricted weakly by segmentally arranged bands of muscle. Distally, the colon tapers to form a muscular rectum, which is often pigmented; its muscular walls are thickened and folded (Fig. 172).





Figs. 169a and 169b. *Linings of the stomach and duodenum. The stomach and duodenum are separated by a short muscular sphincter, the pylorus. While stomach lining is generally smooth, that of the duodenum is often textured. In the leatherback and green turtle, there are the overlapping crypts containing mucus found along the length of the duodenum and into the jejunum.*