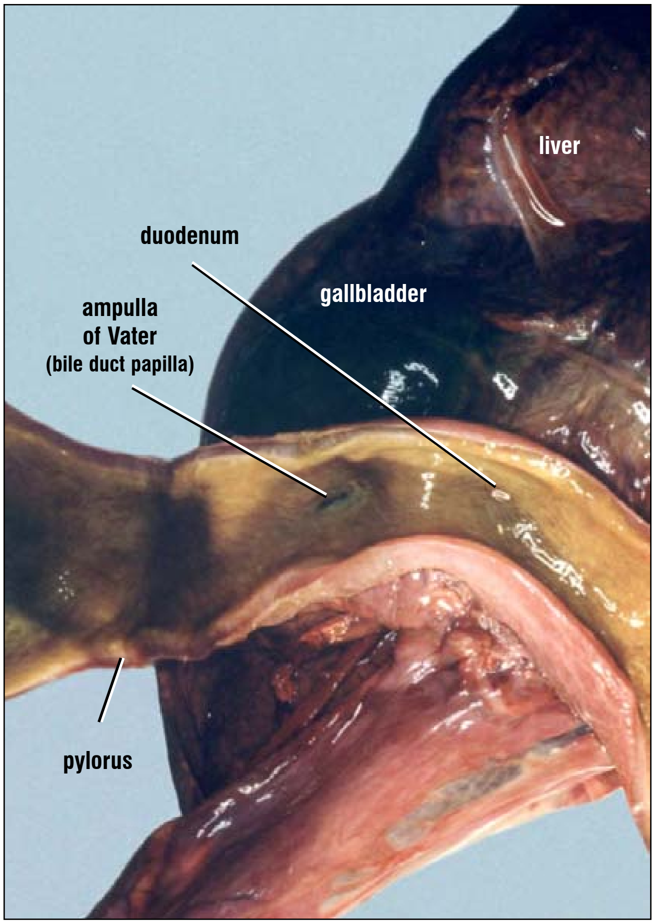


Fig. 170. *Longitudinal section of the duodenum. The common bile duct opens into the duodenum at a papilla (termed the Ampulla of Vater). The common bile duct extends from the gallbladder to the duodenum.*

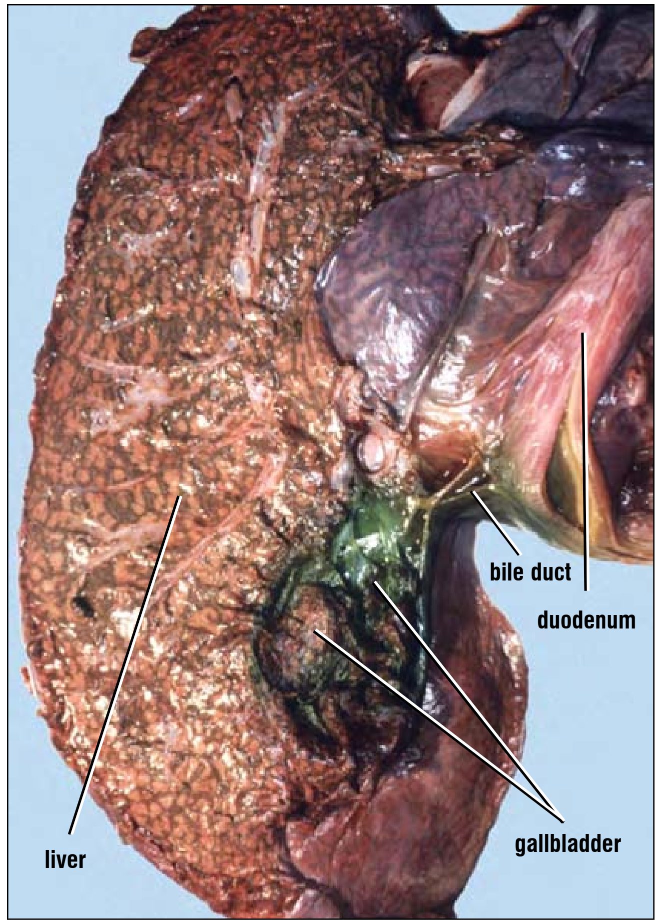
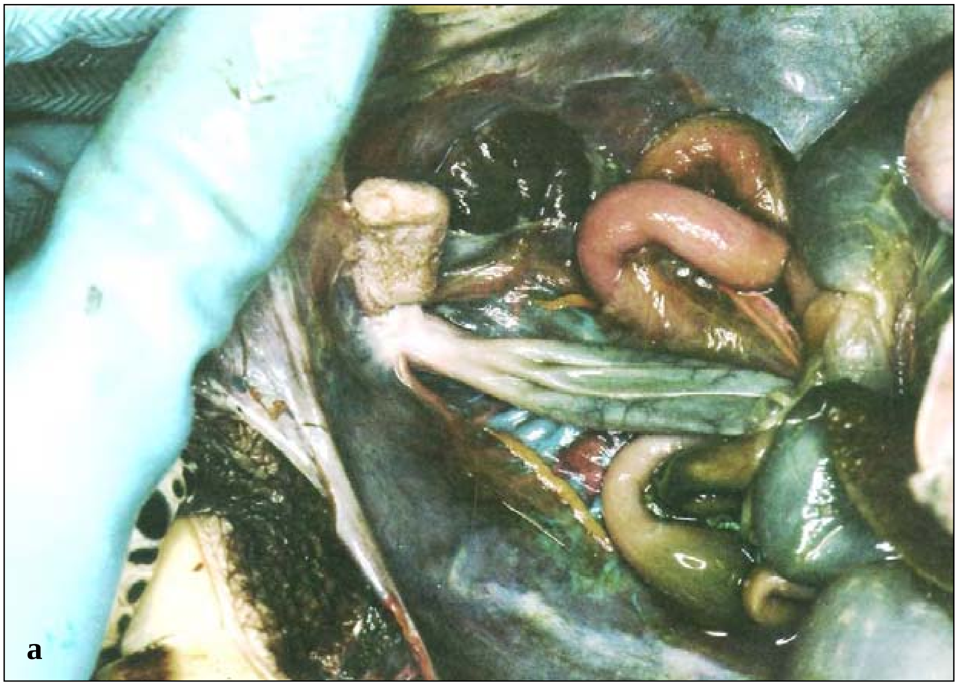
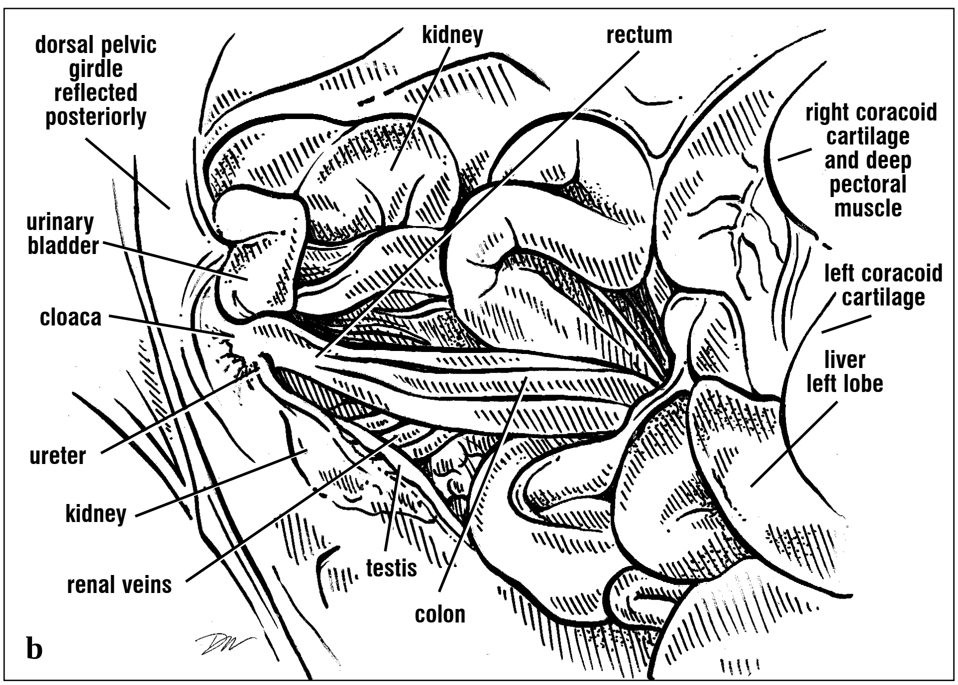
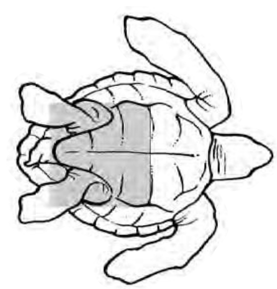


Fig. 171. *Longitudinal section through the liver and gallbladder. The walls of the gallbladder are removed dorsally to expose the common bile duct to the duodenum.*



Figs. 172a and 172b. *Ventral view of the posterior viscera. The rectum (collapsed here) narrows as it joins the cloaca. The urinary bladder, seen just above the rectum, enters the cloaca ventrally. The dorsally-located kidneys produce urine that travels though the ureters to enter the dorsal cloaca. Several renal veins are exposed medial to the kidney. The testis of this immature male is still attached to the peritoneum (and is located anatomically ventral to the kidneys).*





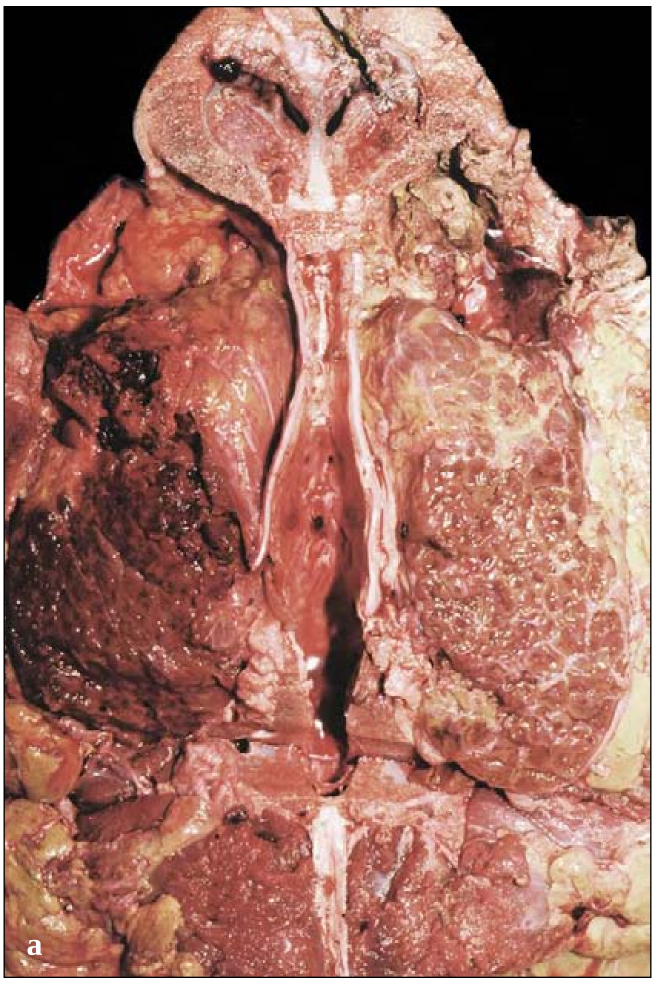
The rectum empties into the cloaca (Fig. 171), a chamber that also receives the urine from the kidneys, eggs or sperm, and connects ventrally into the urinary bladder. The cloaca empties to the outside via the cloacal opening or vent. Each function of the cloaca is associated with a region into which the products empty. The **coprodeum** received feces from the rectum. The **urodeum** is associated with the **urinary papillae** and the opening of the urinary bladder. The **proctodeum** is the most distal region and is associated functionally with copulation and structurally with proximity to the genital ducts.

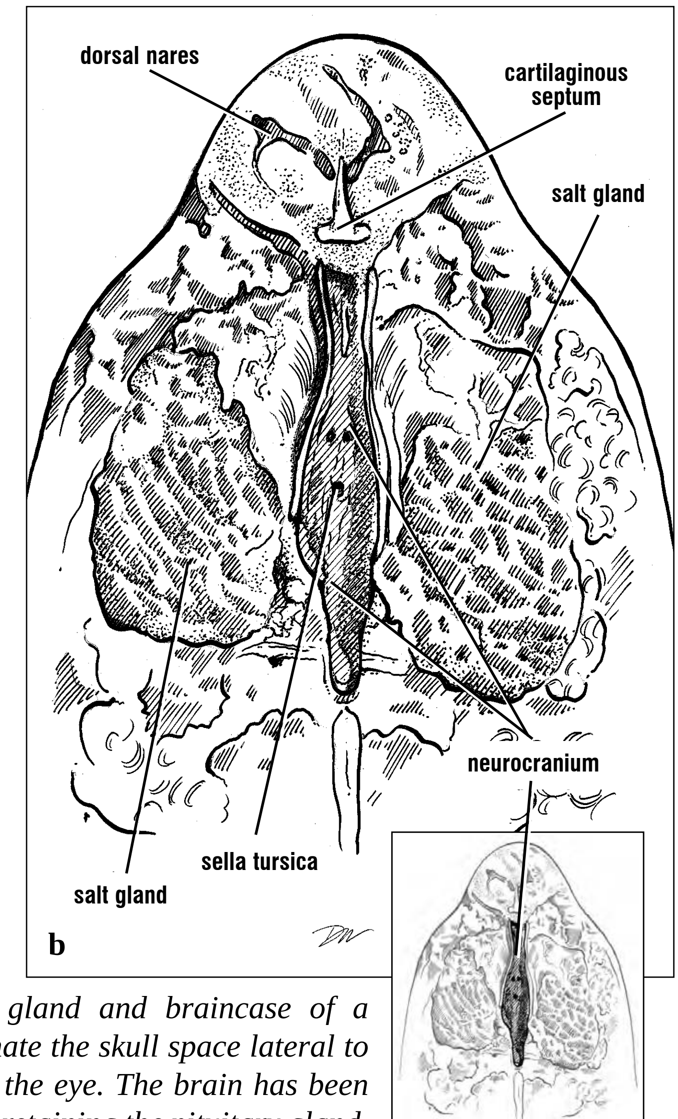
Glands

Glands are often lobular and may have ducts or are ductless. They are involved the in production of peptides and steroids, which can form skin coatings (waxes), enzymes, or hormones. Glands are either formed in the skin and its related structures (ectodermal in origin) or from deeper within the body (mesodermal in origin). Glands are discussed below by region and function, when known.

The **salt** (lacrimal) **gland** (Figs. 81 and 172) is the largest gland in the head and is found dorsal and medial to the eye. These glands are large in all sea turtles, but are especially hypertrophied in *Dermochelys* (Fig. 172). The salt gland is responsible for removal of excess salt from the body. Anterior to the eye, there is a small **Harderian gland**, associated with lubricating the eye.

Sea turtles, like most aquatic lower vertebrates, appear to lack oral glands.





Figs. 172a and 172b. *Dorsal view of the salt gland and braincase of a leatherback. The extremely large salt glands dominate the skull space lateral to the braincase and dorsal, medial, and posterior to the eye. The brain has been removed leaving the braincase with the sella tursica retaining the pituitary gland.*

The ductless **pineal gland** (epiphysis) is a dorsal extension of the brain; it connects indirectly to the dorsal surface of the braincase, it is located deep to the frontoparietal scale in cheloniids and the "pink spot" in *Dermochelys* (illustrated in the Nervous System, Figs. 193-194, 196, 198-201). It is responsible for modulating biological rhythms.

The **pituitary gland** (hypophysis) is found in a cavity, the **sella tursica** in the floor of the braincase (Nervous System, Fig. 190). The pituitary is composed of two parts, the **neurohypophysis** (infundibulum) and the **adenohypophysis**. The neurohypophysis produces releasing hormones (e.g. oxytocin) and release-inhibiting hormones (e.g. antidiuretic hormone), while the adenohypophysis produces growth hormone, prolactin, thyroid-stimulating hormone, gonadotropins, adrenocortacoids, and melanophore-stimulating hormone.

More posteriorly are several glands derived from pharyngeal pouches of the embryo. These ductless glands are the **thyroid, thymus, parathyroid**, and **ultimobranchial bodies**. All are located in the ventral neck and upper body. The thyroid gland can be located medially to the the acromion processes (Figs. 75 and 173) by tracing along the brachiocephalic trunk where it gives rise to thyroid arteries (soon after its bifurcation to form the subclavian arteries). The thyroid arteries "frame" the single thyroid gland that is encased in connective tissue (Fig. 173). The thyroid is round and is often coated with a thin layer of fat. In fresh specimens, it is bright red. However, in turtles that have been frozen, then thawed, or that have started decomposing, it may become brown. It is gelatinous in texture in fresh and fresh-frozen animals. In decomposing carcasses, it liquifies. The thyroid is involved with increasing oxygen consumption when reptiles exceed their preferred body temperatures, and it functions in gonadal maturation.

The thymus glands can be located by tracing along the subclavian arteries and palpating for a dense, laterally elongated structure (Figs. 174-175). There is a gray to pink thymus gland on each side of the body that is composed of small lobes. It is usually associated with fat. The thymus glands are more dense and compact than the fat. They are often easiest to find by palpating. The thymus glands play a role in immune responses. In chronically ill animals this gland is frequently thin and diffuse.

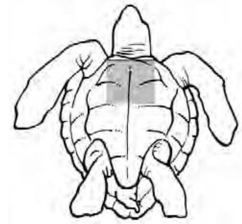


Fig. 173. *Thyroid gland in ventral view, medial to the acromion processes. The thyroid is the dark, round structure at the tip of the pointer. The heart has not been exposed yet. Anterior is toward the top of the figure. The two acromio-coracoid ligaments extend posteriorly from the acromion process.*

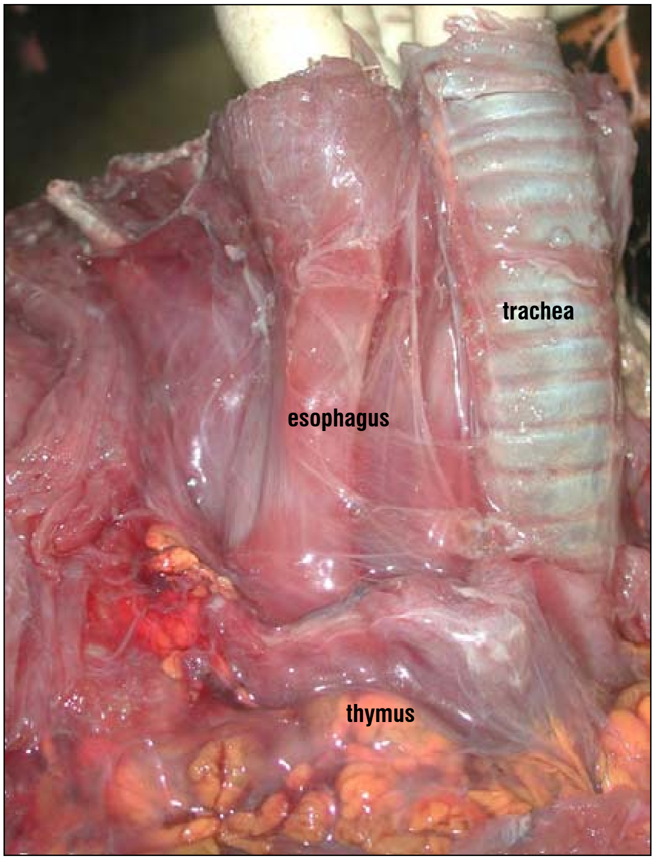


Fig. 174. *Ventrolateral view of the neck structures. Positions of the trachea (with cartilaginous rings) and esophagus to the animal's right provide landmarks. The head is removed; anterior is toward the top of the picture. The lobular right thymus gland is at the bottom of the picture.*

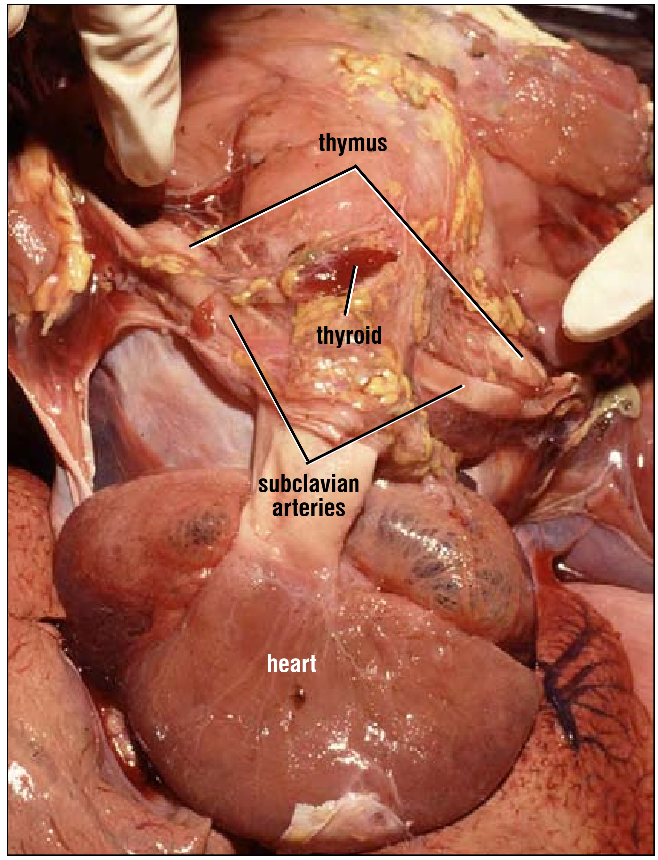
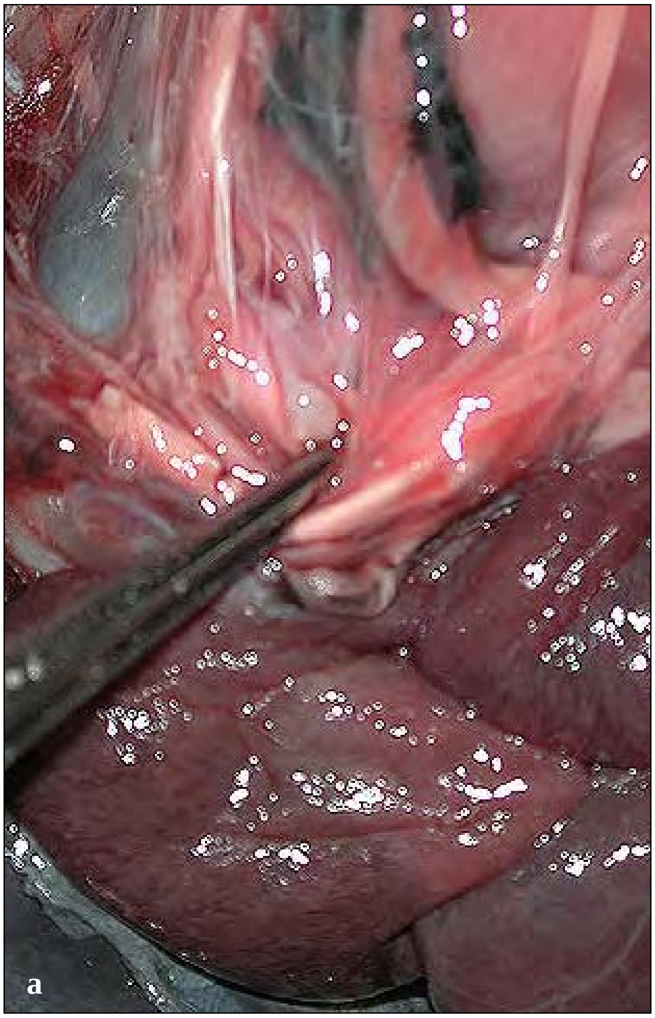
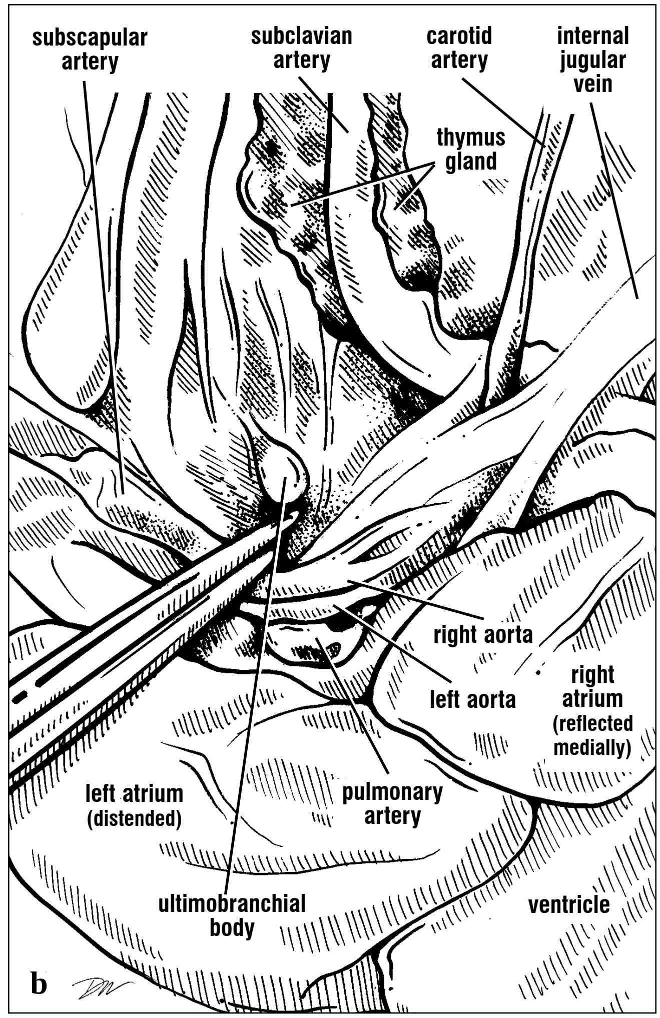


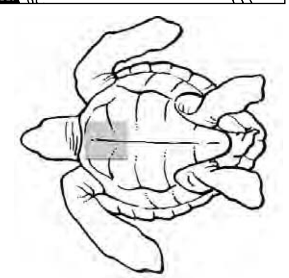
Fig. 175. *Ventral view of the two thymus glands, just below the fingertips, are located adjacent to the subclavian arteries. They are anterior to the heart and lateral to the thyroid gland (seen as the smooth oval tissue anterior to the great vessels).*

The **parathyroid** and **ultimobranchial bodies** are difficult to identify and can only be distinguished from one another histologically (Fig. 176). They are very small and located along the carotid and ventral cervical arteries. Generally, the parathyroid glands are the more anterior glands and the ultimobranchial bodies are more posterior. They are brown or dark pink in color. They are best located by feeling for the round, dense glands, then using careful dissection. The two kinds of glands have antagonistic functions. The parathyroid gland releases parathormone, which stimulates the mobilization of calcium and phosphorus from storage (usually bones). The ultimobranchial body releases calcitonin, which lowers blood levels of calcium and phosphorus.





Figs. 176a and 176b. *Ventral view of an ultimobranchial body (or parathyroid) and thymus gland. The carotid and ventral cervical arteries are the best landmarks for locating the parathyroid and ultimobranchial glands. The glands tend to be associated with the connective tissue on the dorsal surfaces of the arteries. Typically, 2-4 glands are present on each side. The large thymus gland, deep to the subclavian artery, is seen near the top of the picture.*



The **liver** is the largest visceral organ and is located ventrally, but deep to the pectoral skeleton and peritoneum (Fig. 177). It is dark brown to reddish brown and composed of two lobes joined by one or more connecting strips of hepatic tissues. The right lobe houses the gallbladder on its ventral surface and is typically larger than the left lobe (Fig. 177). The liver is highly vascular; it receives blood from the hepatic portal vein and the hepatic artery. Blood from the body drains from the liver via the hepatic veins to the sinus venosus.

The liver contains many bile ductules and hepatocyte cords. The hepatocytes manufacture bile which drains via bile ductules into the gallbladder.

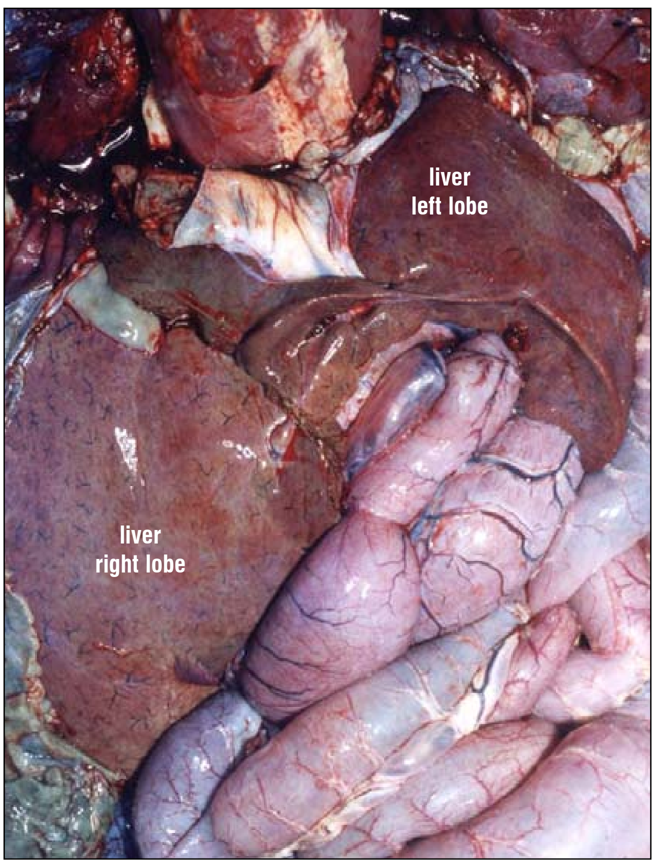


Fig. 177. *The liver is exposed in a green turtle. The left and right lobes are located lateral and slightly dorsal to the heart. Both lobes receive blood from the hepatic portal system.*

The gallbladder stores bile which is then transported via the common bile duct to the duodenum in response to the presence of fats. Bile contains the enzymes involved with fatty acid breakdown.

The liver plays a major role in carbohydrate and protein metabolism as well as in removal of toxins from the blood. Blood from the stomach and intestines percolates through hepatic tissues where carbohydrates, amino acids, and peptides are broken down. Other liver cells make serum albumin and a number of clotting factors.

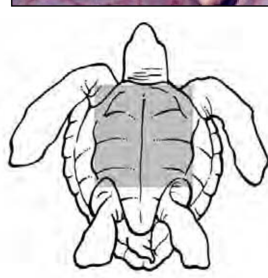


Fig. 178. *Dorsal view of the duodenum (at top) with the pancreas, spleen (at arrow), and a portion of the liver's right lobe.*

Pancreas. The pancreas is located along the duodenum just past the stomach (Fig. 178-179). It is a smooth and thick tissue that extends as an irregular strip past the common bile duct and often ends at or just past the spleen. It is pink to yellow orange in color. The pancreas is a digestive gland as well as an endocrine gland and produces pancreatic polypeptides which stimulate flow of gastric juices in the stomach. Other pancreatic cells produce insulin which assists in the metabolism of glucose. Some pancreatic cells produce glucagon which stimulates the breakdown of glycogen to increase blood glucose levels.

Rathke's glands are located deep to the inframarginal scutes in *Lepidochelys* (Figs. 180-181) and in the posterior axilla and anterior-most inguinal regions in *Eretmochelys* and *Chelonia* (Figs. 182-183). Rathke's glands have not been identified in *Caretta* and *Dermochelys*. While prominent, they show no change with reproductive condition or season. Their function is unknown. The secretions of the glands have been hypothesized to play various roles including intraspecific communication, anti-fouling, and/or anti-microbial function.

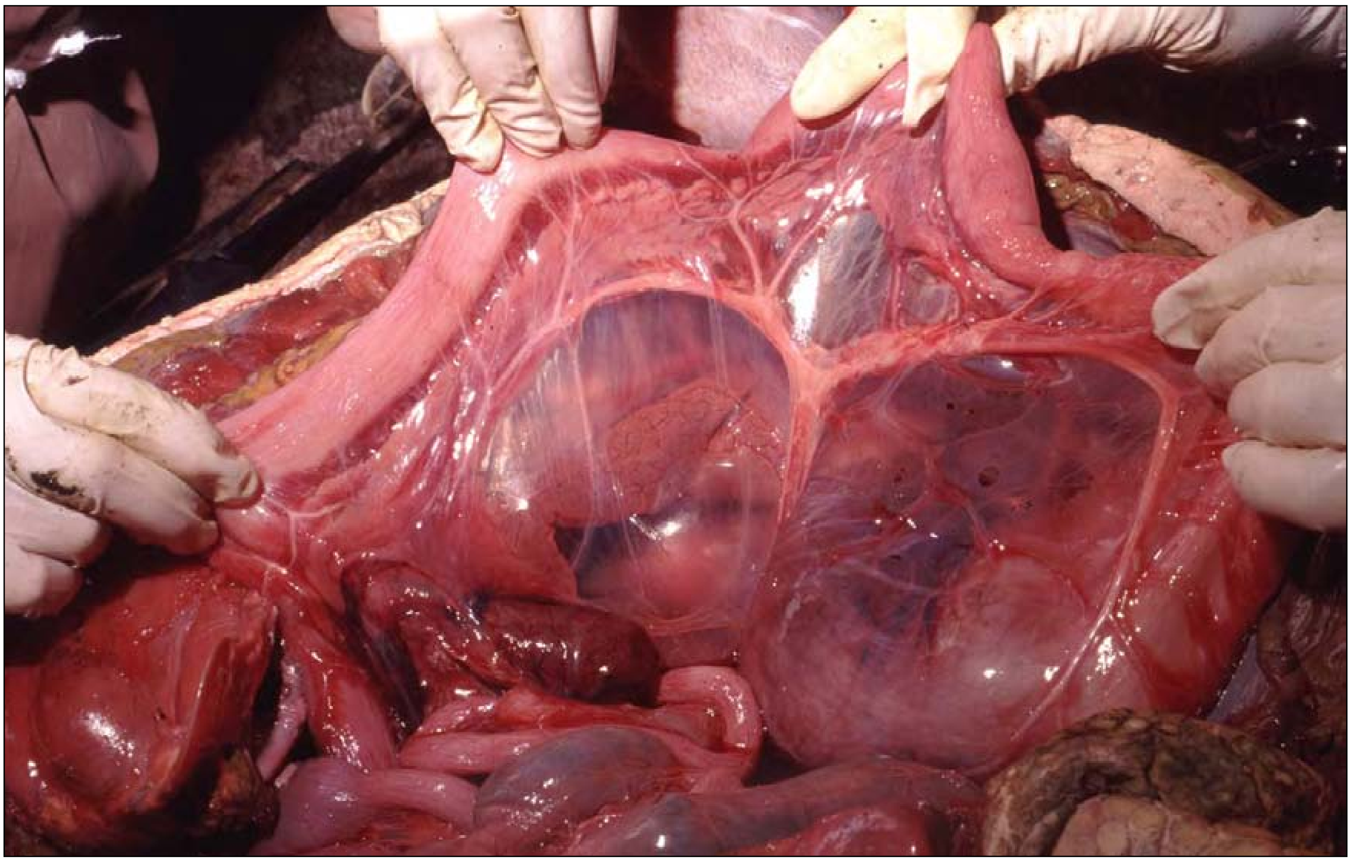
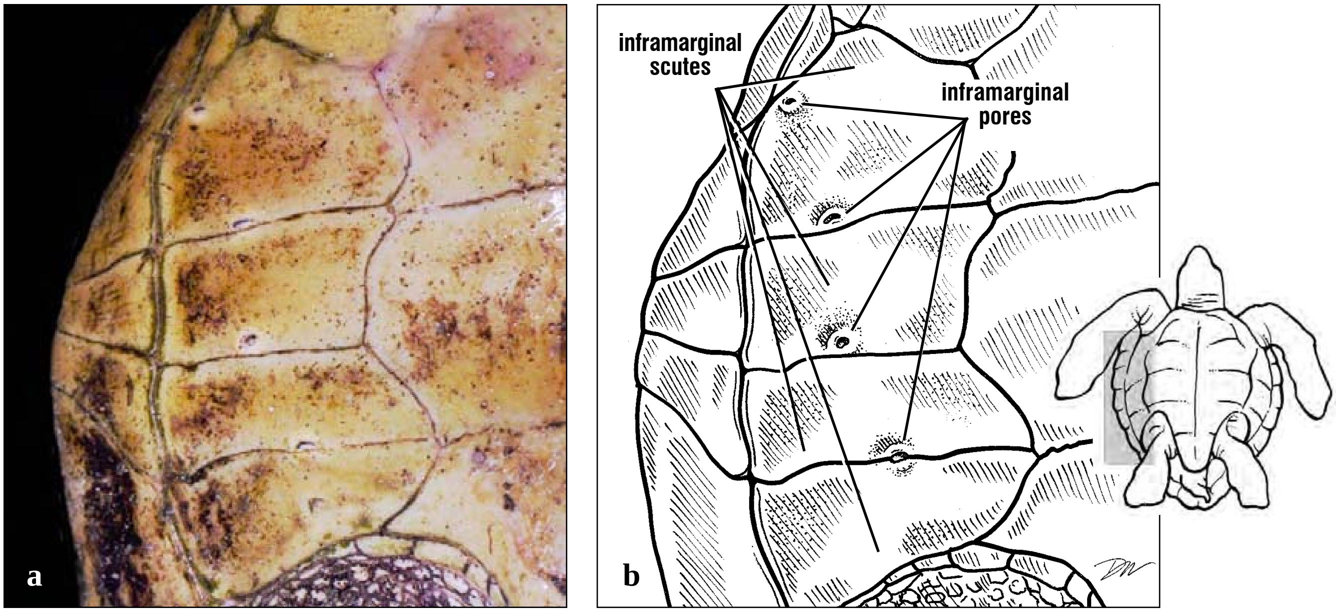
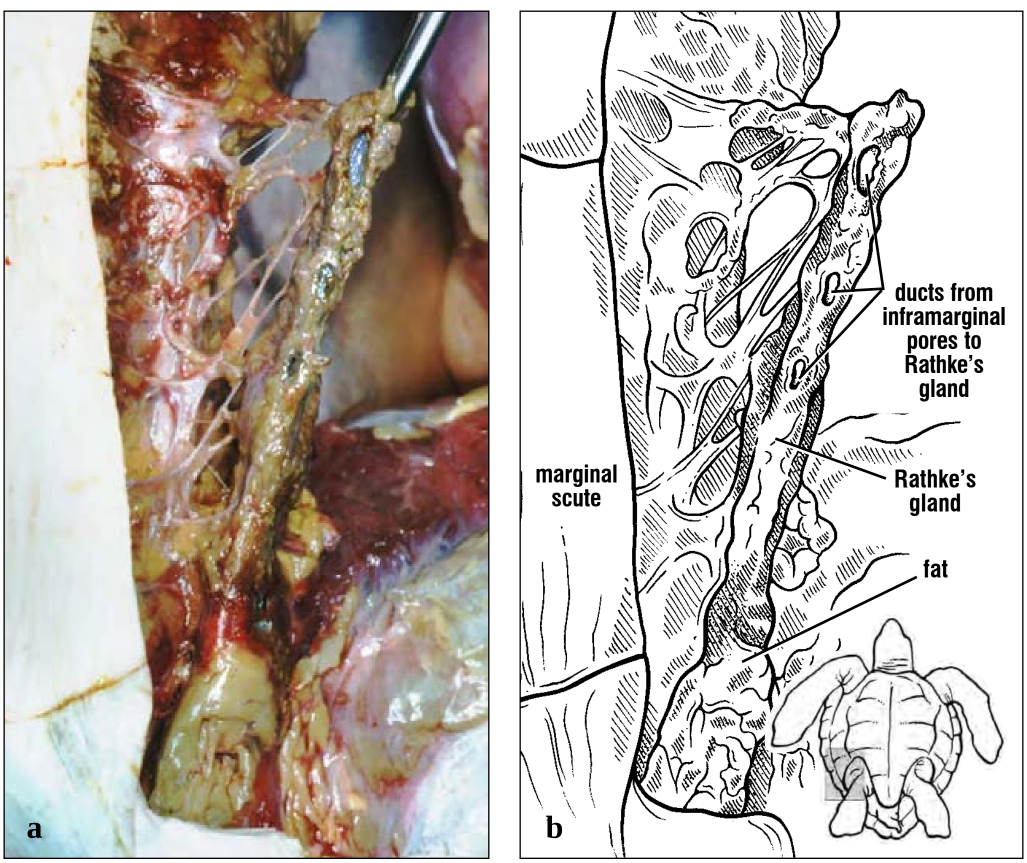


Fig. 177. *The long narrow pancreas is seen just below the duodenum (at arrow) in this loggerhead dissection. It is encased in the mesentery. A large artery in the mesentery is seen supplying branches to the proximal and distal pancreas. The dark, oval spleen is seen below the pancreas, above the loops of small intestines.*

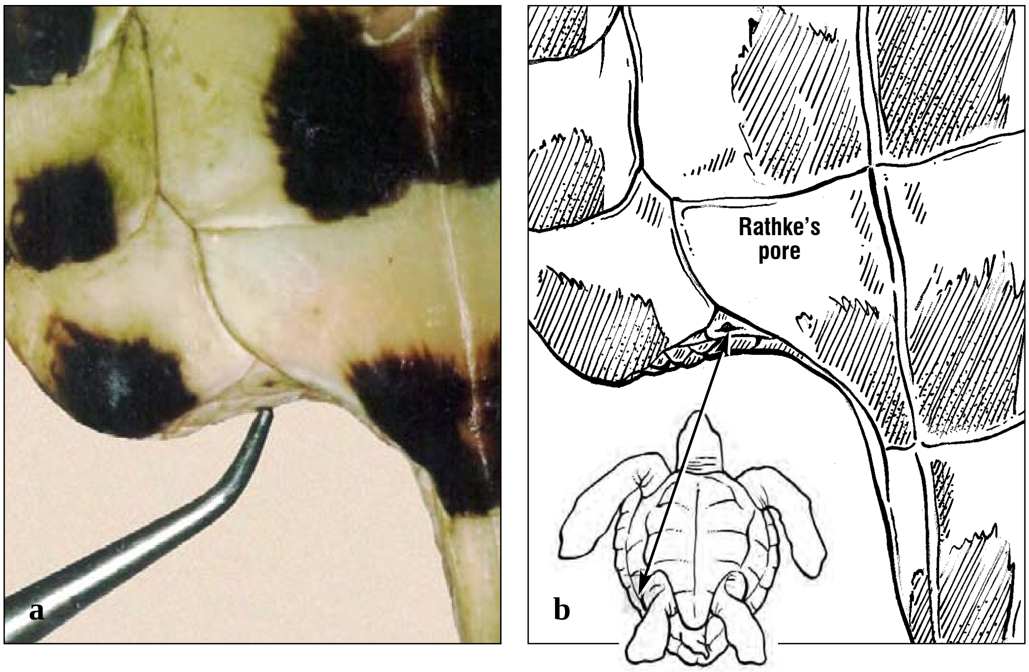


Figs. 180a and 180b. *Inframarginal Pores. Ridley turtles have pronounced inframarginal or Rathke's pores associated with each inframarginal scute. The pores lead to the Rathke's gland. In mature turtles, with fully developed plastron bones, the ducts from these pores are surrounded by bone. They leave foramina (holes) in the hyoplastron and hypoplastron bones.*

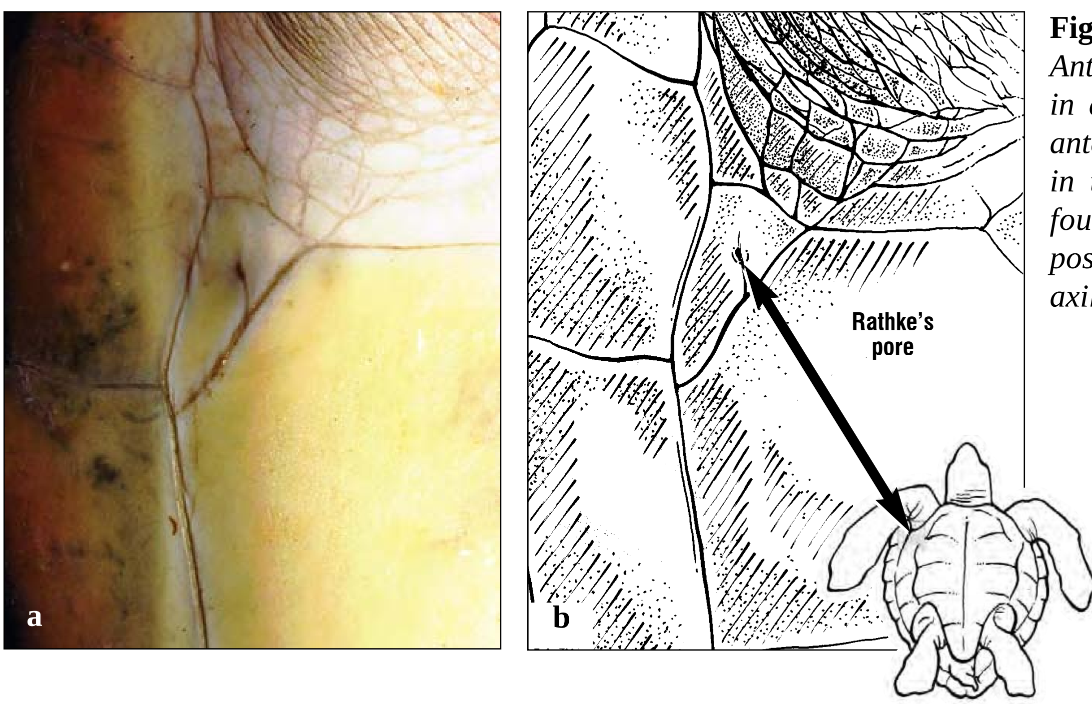


Figs. 181a and 181b. *When the plastron is removed, the gray-green Rathke's gland and its ducts are exposed. Each duct leads to an inframarginal (Rathke's) pore. The gland is typically embedded in fat. It extends the length of the inframarginal scutes from the axilla to the anterior extent of the inguinal region.*

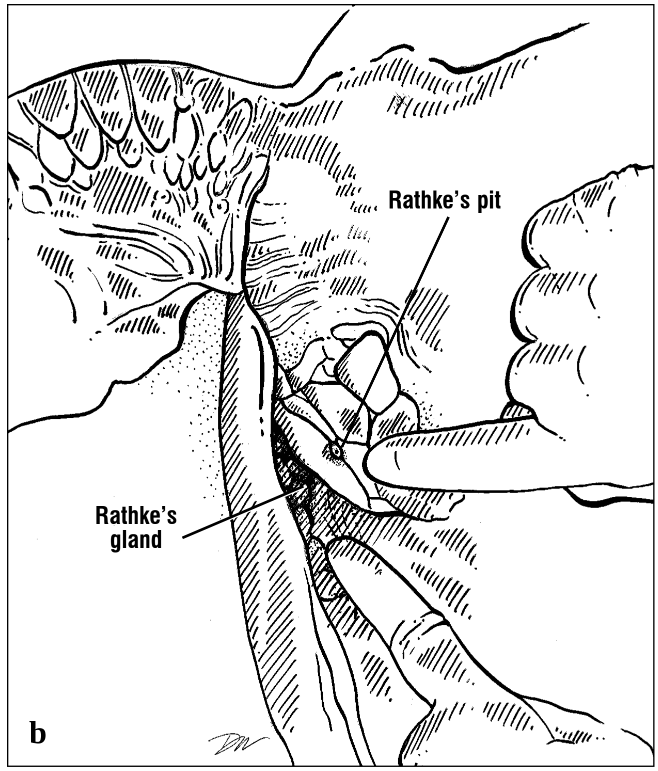
Rathke's pores and Rathke's glands are also found in *Chelonia mydas* and *Eretmochelys imbricata*. They are restricted to the posterior axilla and the anterior-most inguinal scales. The pores typically do not extend to the inframarginal scutes (Figs. 182-185).



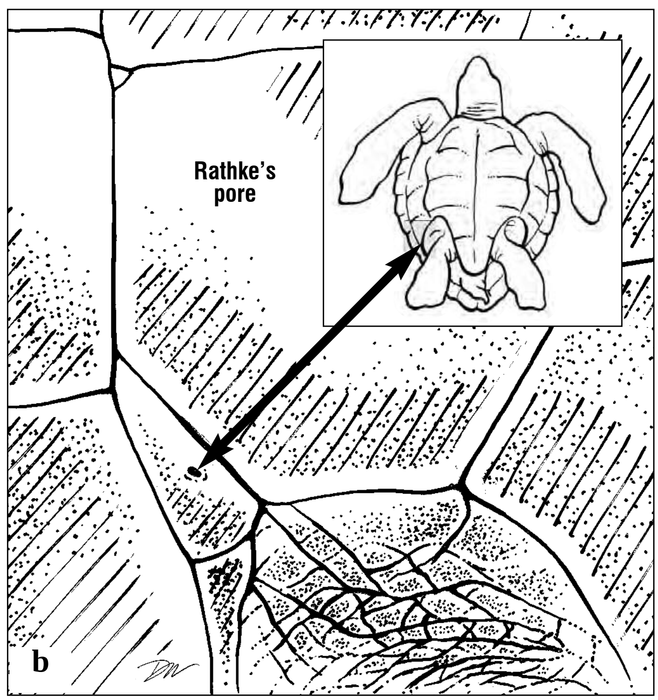
Figs. 182a and 182b. *Rathke's pores in a hawksbill. The posterior Rathke's pore in this hawksbill is found in the anterior-most inguinal scale.*



Figs. 183a and 183b. *Anterior Rathke's pore in a green turtle. The anterior Rathke's pore in this green turtle is found in the most posterior and lateral axillary scale.*

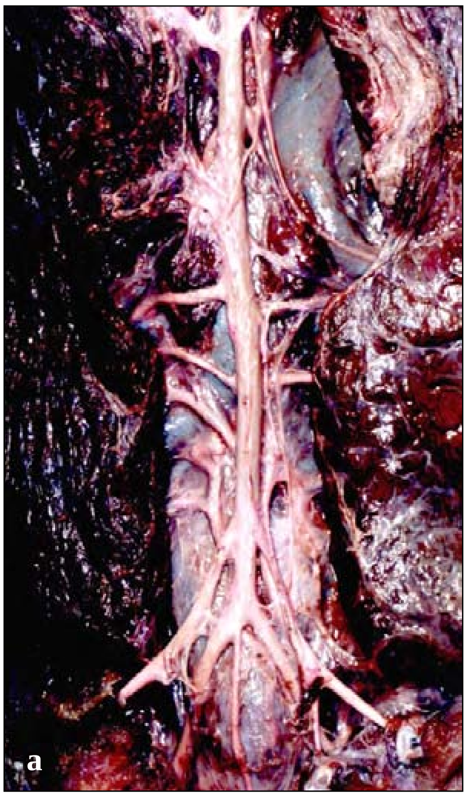


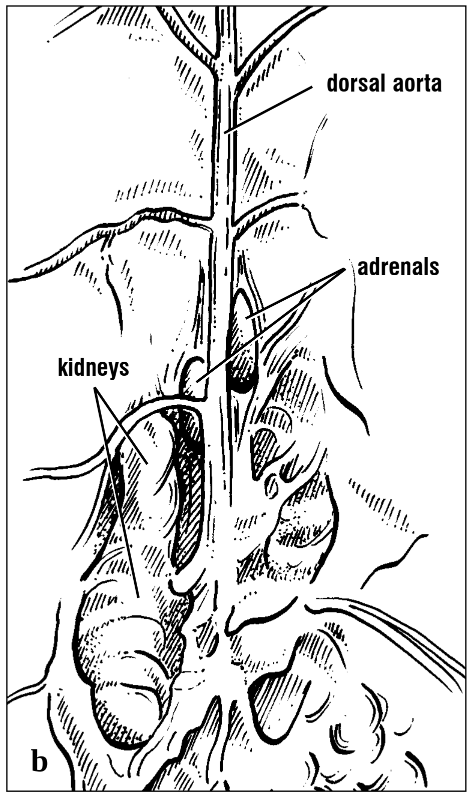
Figs. 184a and 184b. *Rathke's gland and pore in a green turtle. As the plastron is removed, the gray Rathke's gland can be found embedded in fat just deep to the Rathke's pore.*

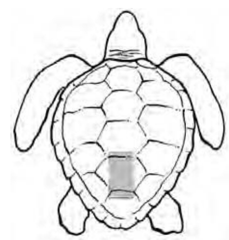


Figs. 185a and 185b. *Posterior Rathke's pore in a green turtle. The posterior Rathke's pore in this green turtle is found in the most anterior and lateral inguinal scale.*

The **adrenal glands** (Fig. 186) are paired, tan to pink in color and are located lateral to the dorsal aorta, usually anterior to the renal arteries. They are usually medial to, and just anterior to, the kidneys. The adrenal glands develop from the anterior (cranial) poles of the embryonic kidneys. The paired adrenals are elongated along the anterior-posterior axis and oval in cross section. They are composed of two intermingling tissue types: interrenal bodies, that produce steroids (corticosterone) and chromaffin bodies that produce catecholamines such as adrenaline (epinephrine and norepinepherine). Unlike mammals, these tissues are not organized into a distinct cortex and medulla.





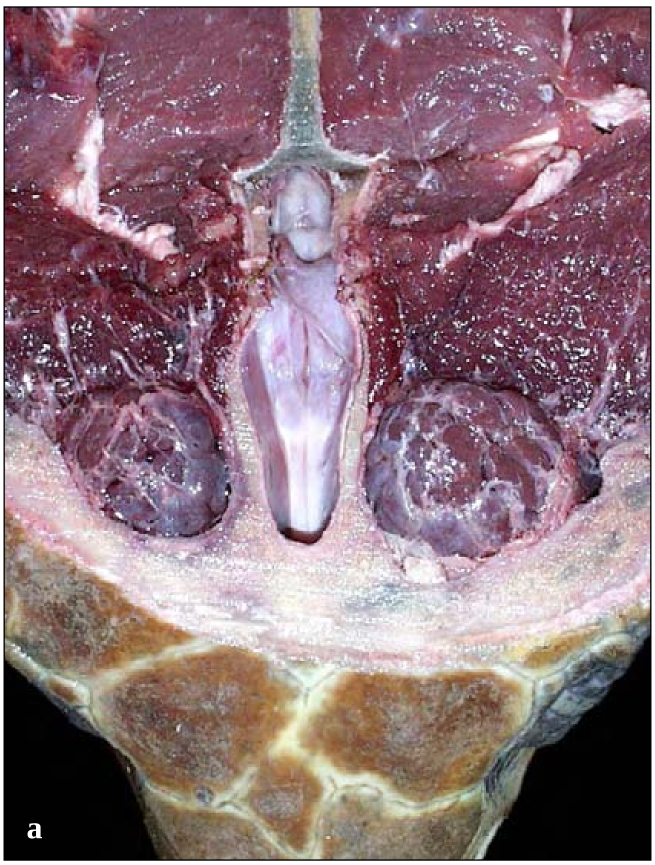


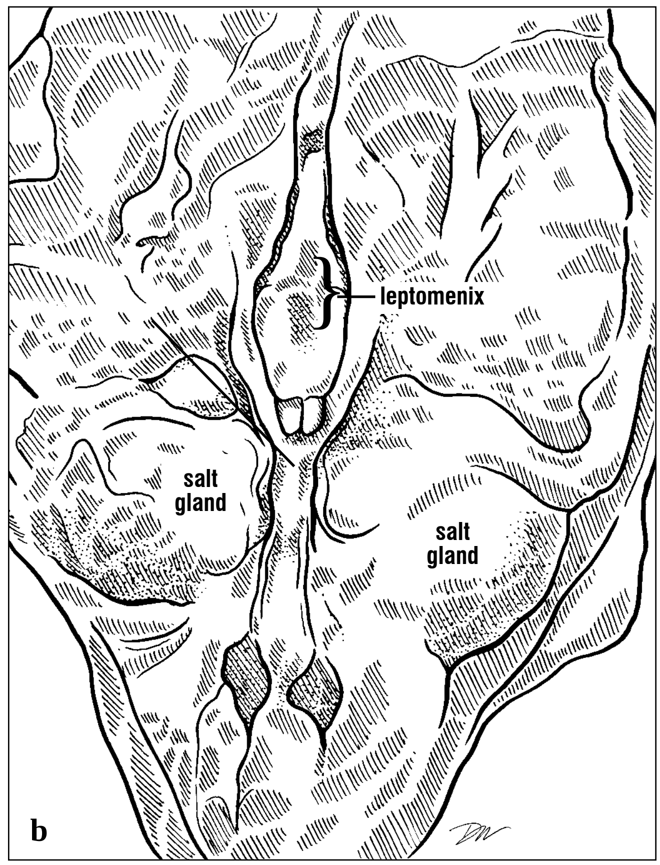
Figs. 186a and 186b. *Adrenal glands. This dorsal view of the adrenal glands shows their elongate shape and their position just anterior and medial to the kidneys. The adrenal arteries are not clear in this dissection. The left adrenal is crossed by a costal artery.*

Nervous System

The **brain** or **central nervous system** (**CNS**) of sea turtles is longitudinally arranged along the midline of the skull (Fig. 187). The brain is housed in a tubular braincase, composed anteriorly of the following bones: ethmoid, epiotic, prootic, opisthotic, basisphenoid, laterosphenoid, and otic (Figs. 26 and 30). Posteriorly it is completed by the basioccipital, exoccipital, and supraoccipital. It is roofed by the parietal and frontal bones (Fig. 25).

Two tissue layers, the **meninges**, cover the brain. The outer menix (singular) is the tough **dura mater**. A more delicate leptomenix (sometimes termed the pia mater) lies directly on the brain's surface (Fig. 187). There are both subdural (beneath the dura mater) and epidural (above the dura mater) spaces within the brain case. **Epimeningeal veins** occupy some of the epidural space. The brain is bathed in clear **cerebral spinal fluid** produced by the **tela choroidea**, a vascular region of the brain (Fig. 187).





Figs. 187a and 187b. *Exposed brain and cut meninges. The anterior and posterior extent of the dura mater and a vascular portion of the leptomenix (= pia mater) are seen in this exposed loggerhead brain. In life, both meninges would envelop the brain.*

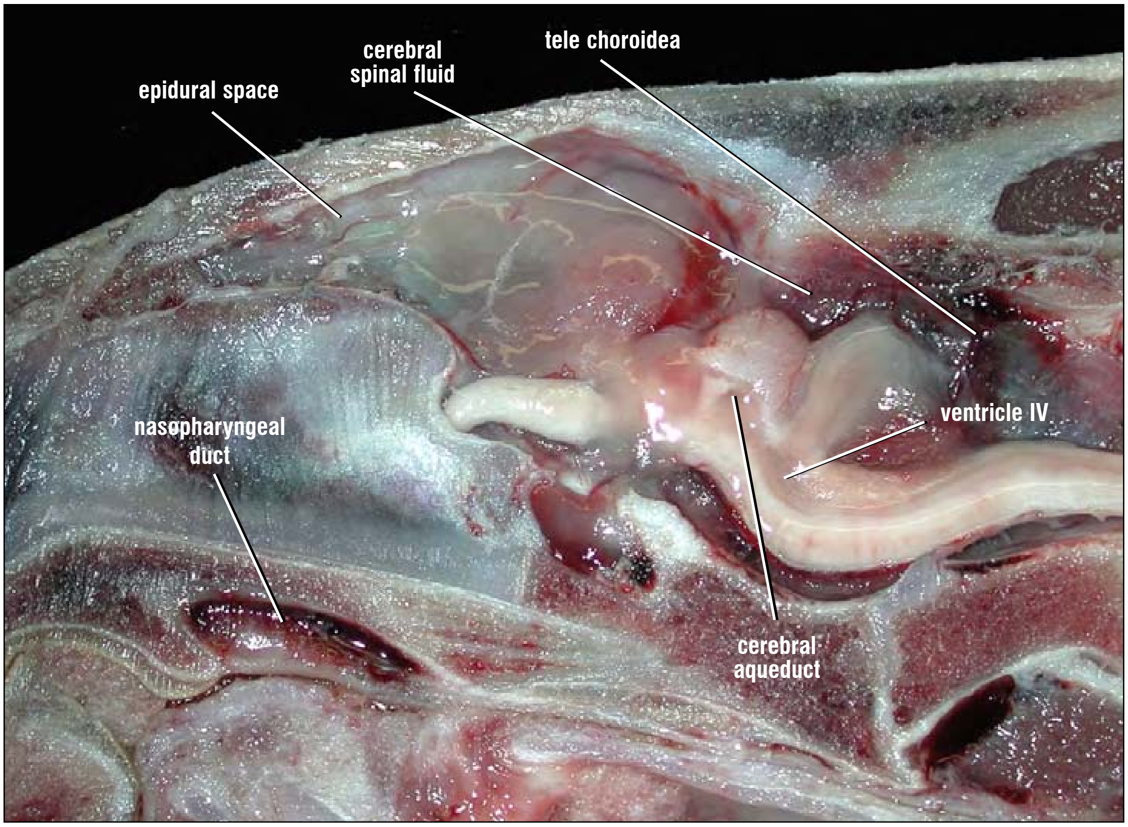
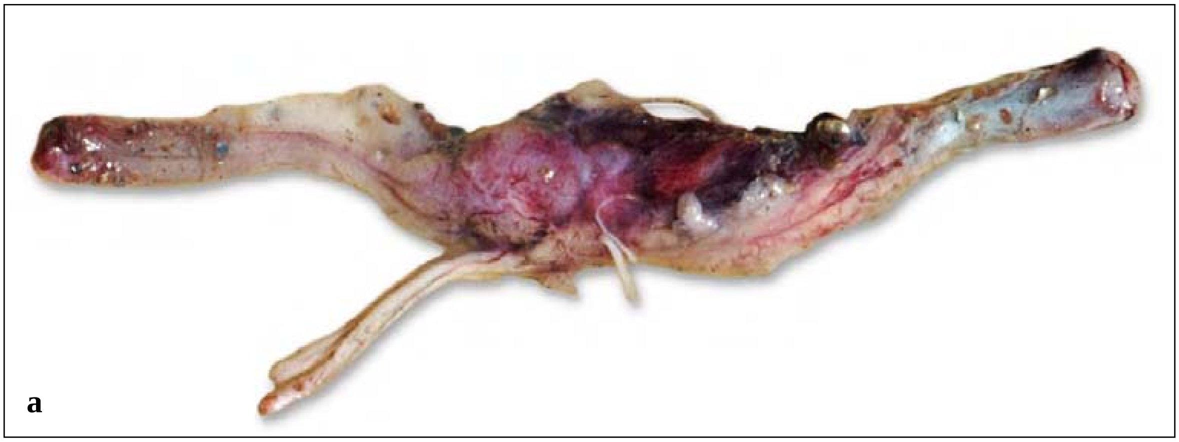
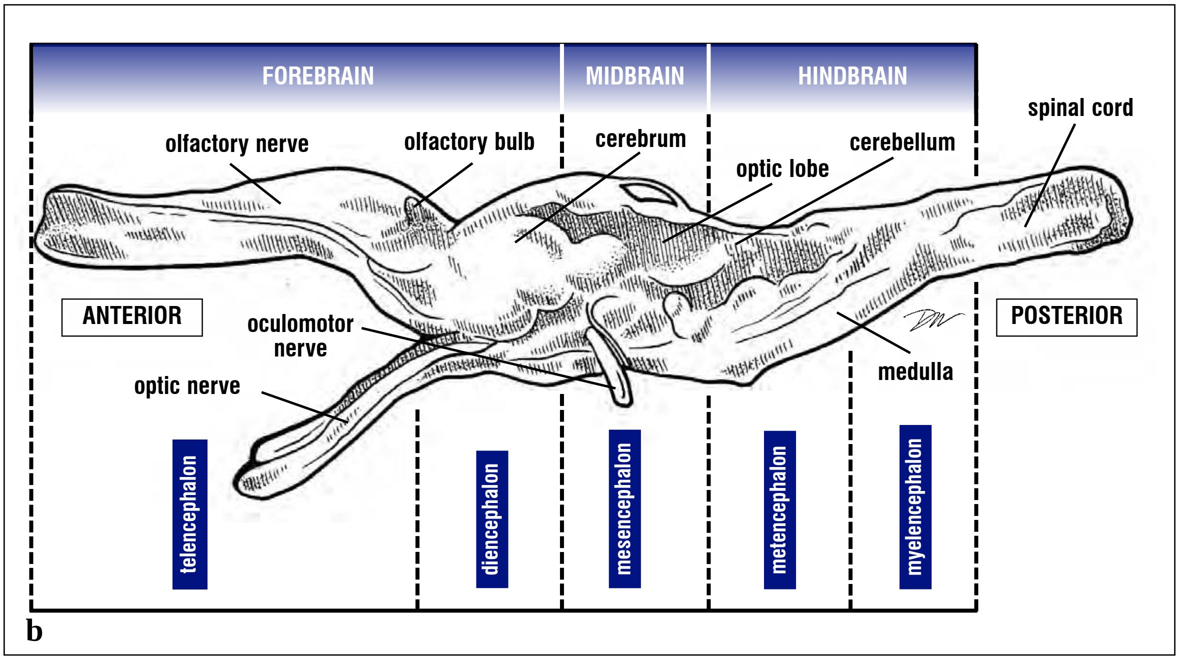


Fig. 188. *Parasagittal section of the brain and airways. The section though this green turtle head shows the tight epidural space and the more voluminous subdural space surrounding the brain. Because this cut is to the right of the midline, the cerebral ventricles and part of the cerebellar ventricle can be seen. The nasopharyngeal duct, part of the respiratory system, can be seen passing from the olfactory sacs to the internal choane.*

Traditionally, the brain (Fig 189) is described by three regions that are initially demarked during development: the **forebrain**, **midbrain**, and **hindbrain**. The following combinations of external and internal landmarks roughly identify these divisions. The forebrain extends from the nose to the posterior cerebrum. The midbrain extends from the eye to the posterior aspect of the optic lobes. The hindbrain extends from the ear to the posterior cerebellum. These regions, in turn, are subdivided topographically and/or histochemically into principal divisions: **telencephalon** and **diencephalon** of the forebrain, **mesencephalon** of the midbrain, **metencephalon** and **myelencephalon** of the hindbrain (Fig. 189).





Figs. 189a and 189b. *Leatherback brain showing major regions and landmark structures. The brain is demarcated into its major regions and principal divisions.*

The divisions of the brain and their major components are as follows.

Telencephalon: cranial nerve I, (olfactory nerve), olfactory bulbs, cerebral hemispheres, lateral ventricles.

Diencephalon: hypothalamus, thalamus, infundibulum and pituitary, pineal, optic chiasma, cranial nerves II-III (optic and oculomotor nerves).

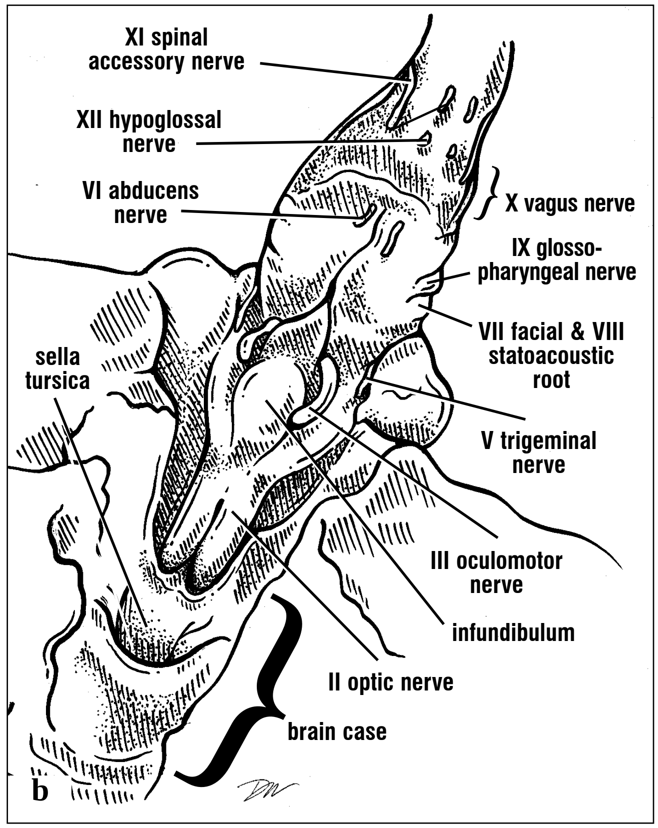
Mesencephalon: optic lobes, third ventricle, cerebral aqueduct, cranial nerve IV (trochlear nerve).

Metencephalon: cerebellum, anterior part of medulla, fourth ventricle, cranial nerves V-X (trigeminal, abducens, facial, statoaccoustic, glossopharyngeal, and vagus, respectively).

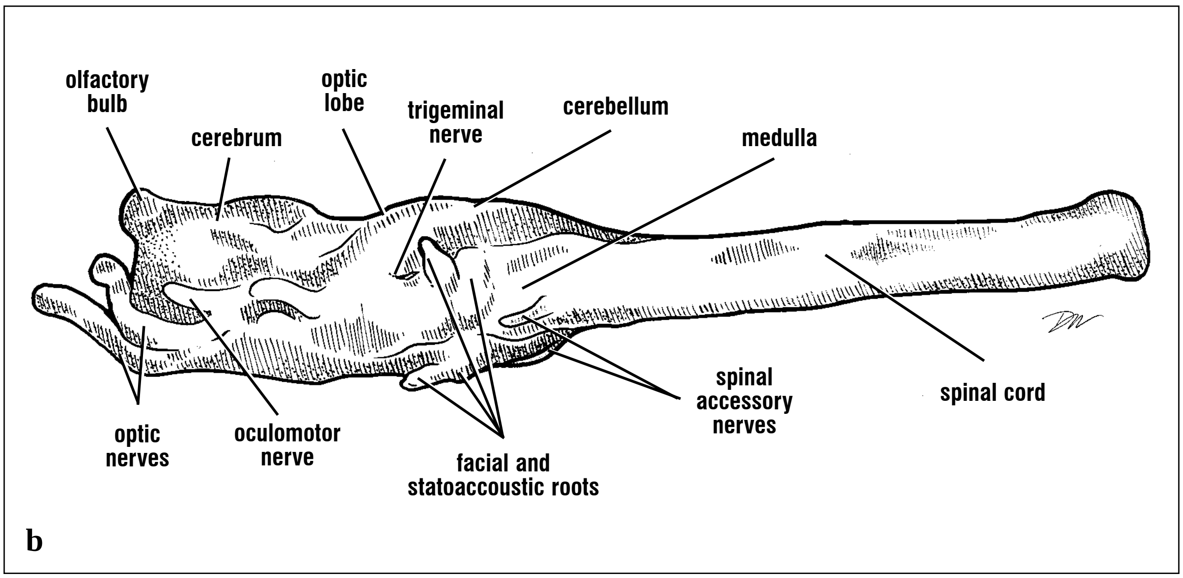
Myelencephalon: most of medulla, cranial nerves XI-XII (spinal accessory and hypoglossal).

The brain forms as a tube during sea turtle development. It then undergoes considerable regional specialization, torsion, and expansion to form the structures found in adult turtles. Remnants of the nerve tube cavity persist as the **lateral ventricles** of the cerebral hemispheres, the **third ventricle** and **cerebral aqueduct**, and the **fourth ventricle** of the cerebellum and medulla (Fig. 188).

Most of the cranial nerves arise ventrally and laterally, and are easiest to observe when the brain is removed (Figs. 189-191).



Figs. 190a and 190b. *Ventral surface of a ridley brain. This brain is viewed from the posterior aspect of the skull and is reflected anteriorly and dorsally. Only the optic and olfactory nerves are still attached to the head. The cut pituitary can be seen in the sella tursica in the floor of the brain case, while the infundibulum is removed with the rest of the brain.*



Figs. 191a and 191b. *Ventrolateral view of a loggerhead brain without the olfactory nerves. The size of the brain of mature and maturing turtles is remarkably small for the body size. This brain from a 72 cm SCL loggerhead is just less than 10 cm long.*

Specific landmarks identifying the parts of the brain differ slightly across cheloniids and, even more when compared with *Dermochelys* (Figs. 192-202). Among the cheloniids, the brain is closest to the skull roof in *Lepidochelys kempii*. It is furthest from the skull roof in adult *Caretta caretta* and *Eretmochelys imbricata*.

Scalation patterns on the lateral head and the position of the ear provide species-specific landmarks for some structures (Fig. 192). The brain of the leatherback is housed deeply, except for the pineal, which extends dorsally in a cartilaginous cone-like chamber adjacent to the pink spot on the middorsal surface of the head (Figs. 201-202).

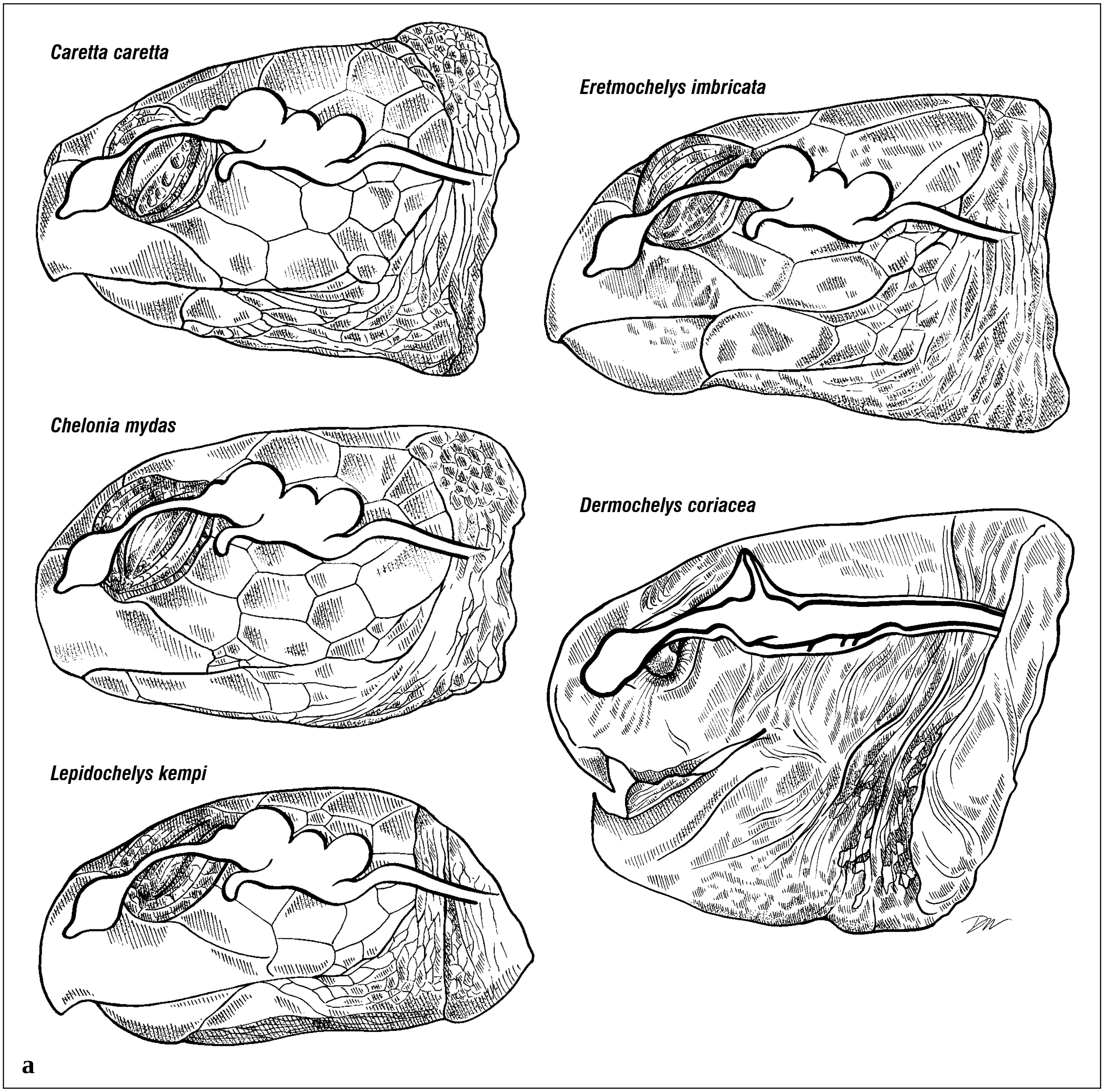
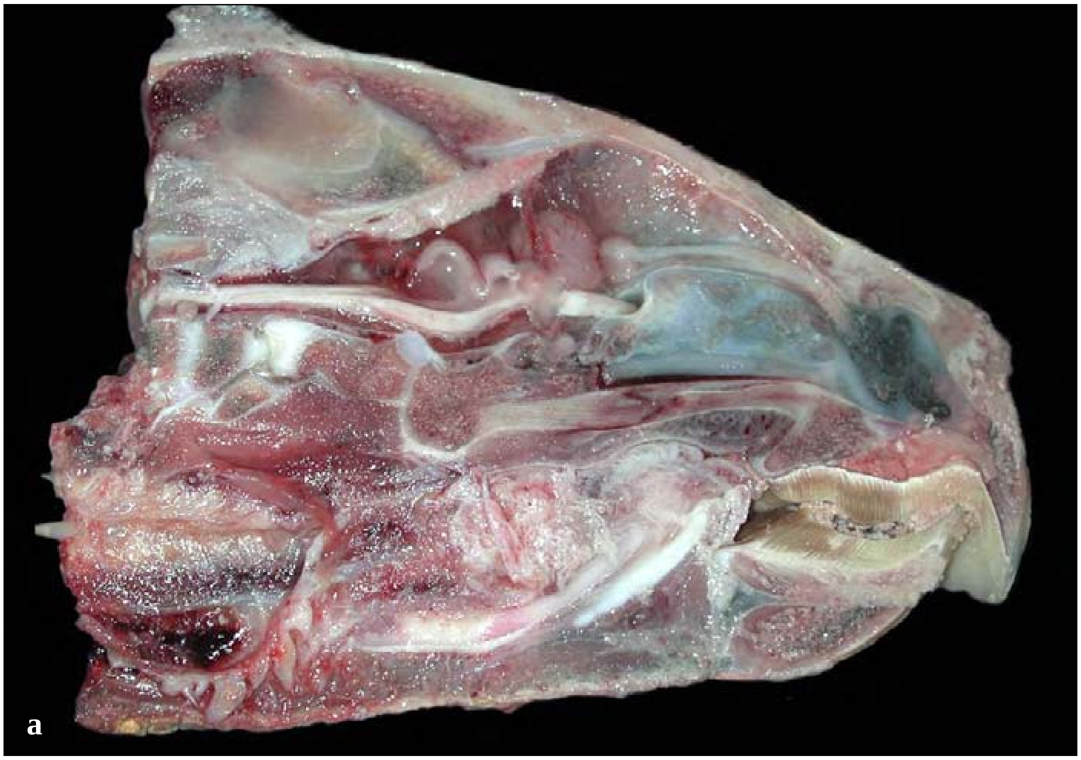


Fig. 192. *Brain landmarks for marine turtles. Overlays of brain positions are shown for 5 species. The position of the head scales, the eye, and the ear provide some reference points for identifying the position of the brain, which varies in dorsal-ventral position with species. The brain position of the leatherback, in this drawing, is based more upon the shape of the braincase because of the poor condition of all leatherback brains examined. The landmarks shown are accurate for large turtles, however the brains of hatchlings and juveniles are disproportionately larger.*



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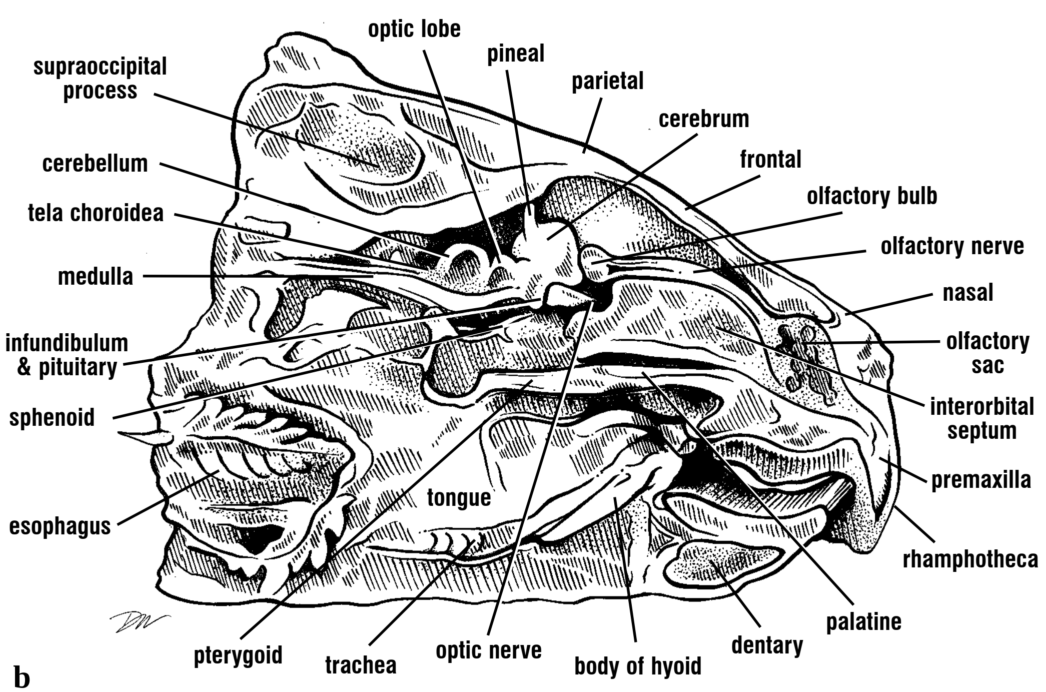
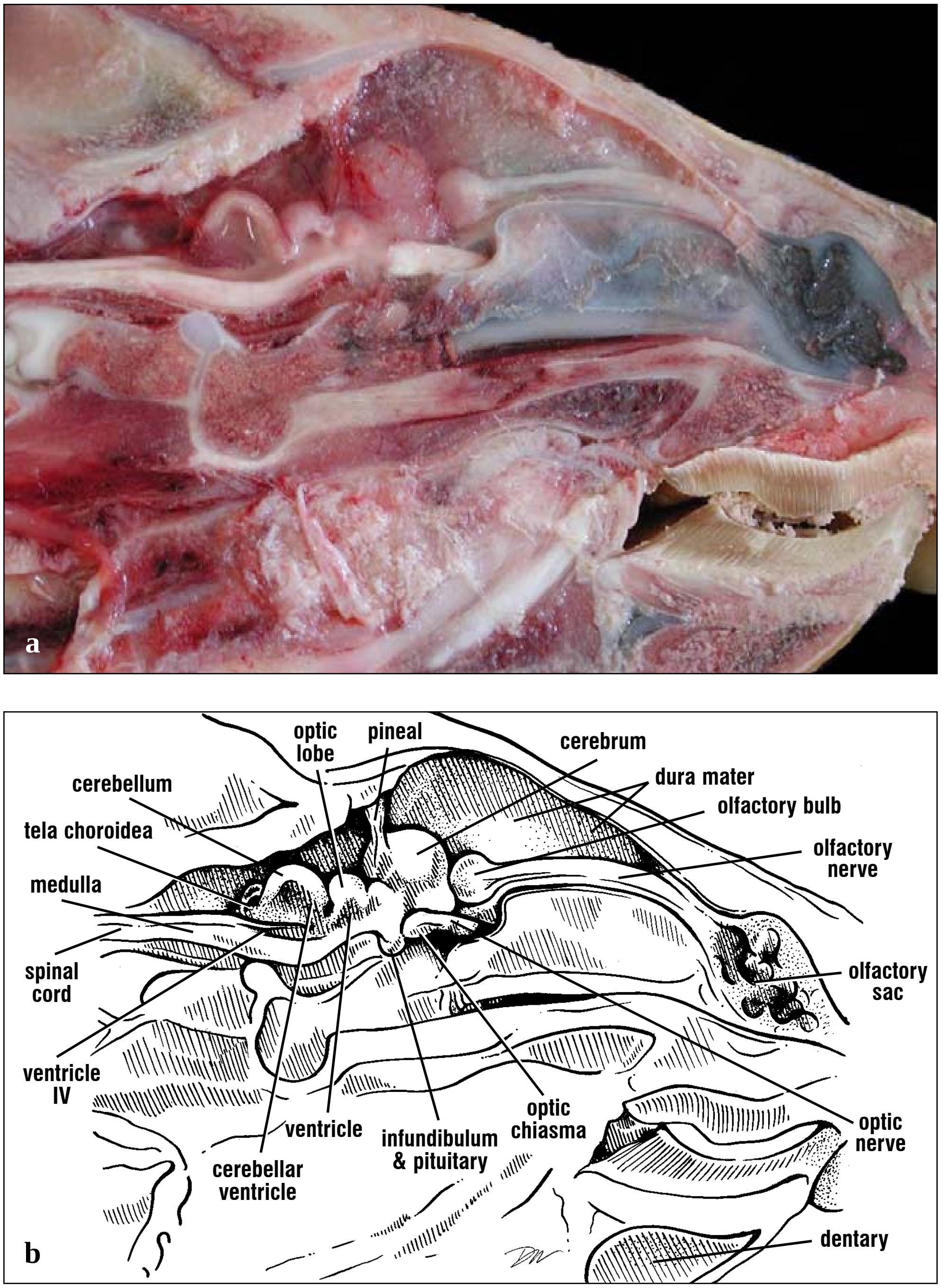
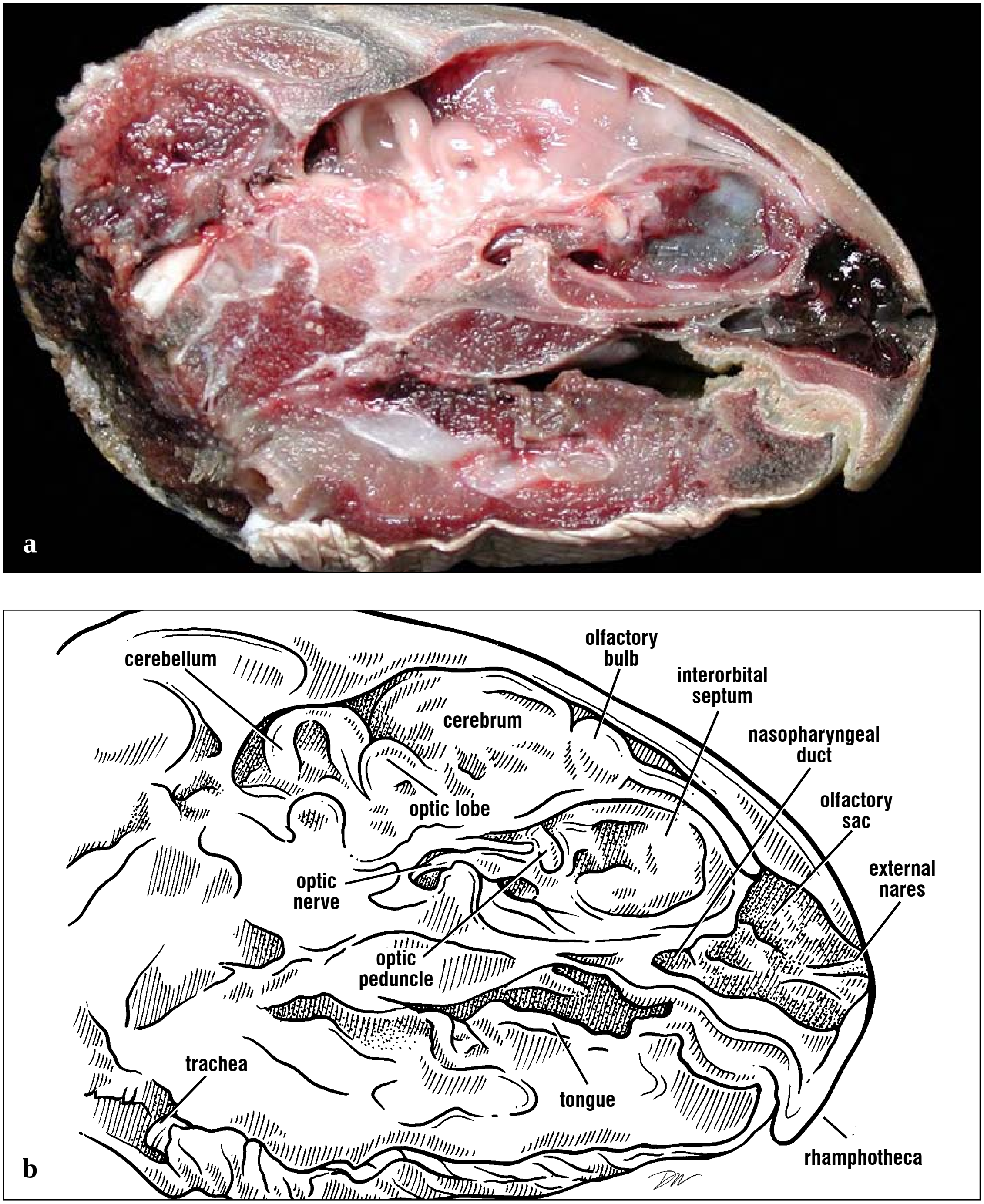


b

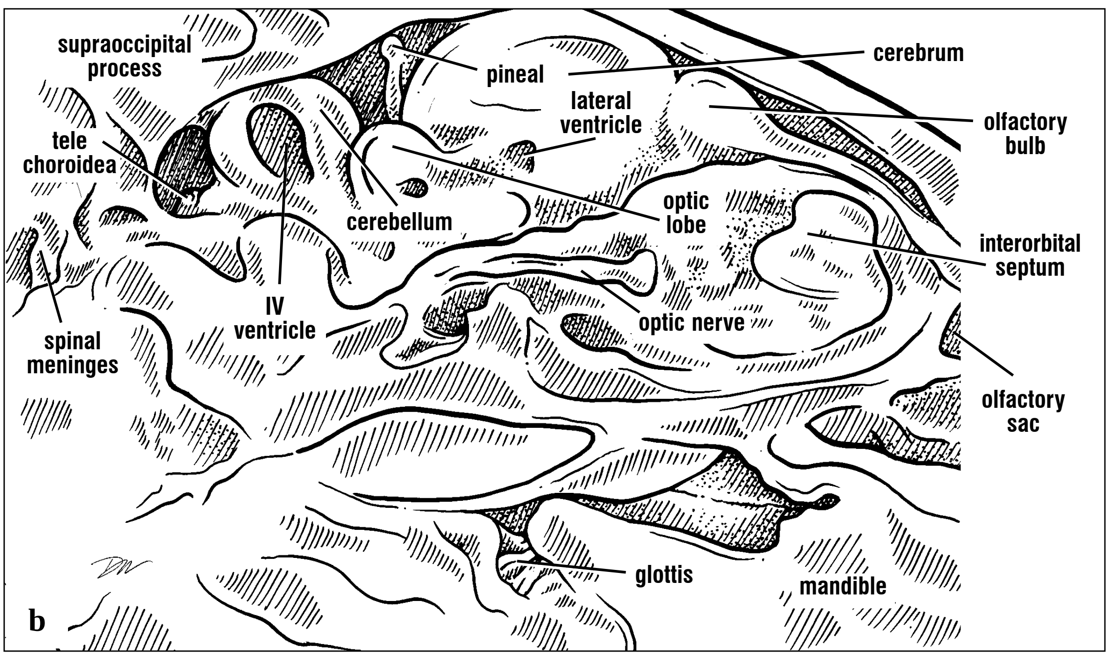
Figs. 193a and 193b. *Parasagittal view of a loggerhead head. The brain, airways, oral cavity, and esophagus are exposed. The interorbital septum is intact and the optic nerve is seen passing through its foramen. There is a large subdural space, above the cerebrum and olfactory nerve, in loggerheads.*



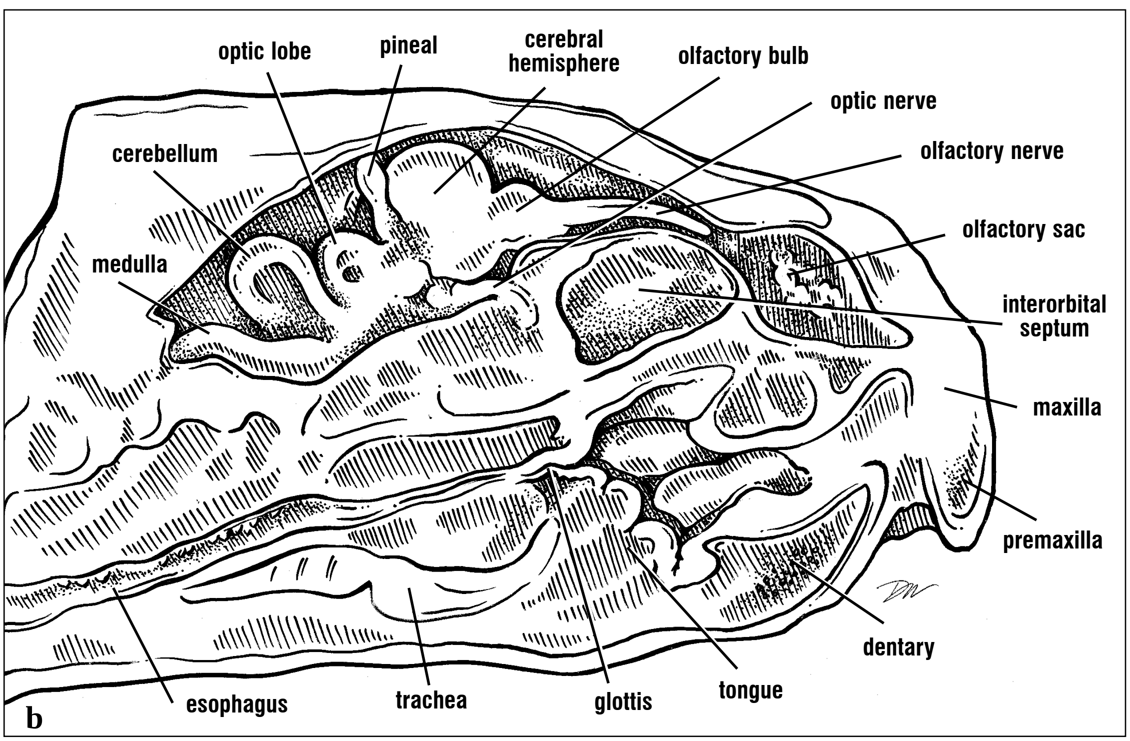
Figs. 194a and 194b. *Parasagittal cut through the head of a subadult loggerhead, close up. The positions of the brain, its parts, and the large subdural space containing cerebral spinal fluid relative to the dorsal skull are clear. The lateral ventricles are not exposed by this cut; the third ventricle and cerebral aqueduct are seen ventral to the optic lobe. The cerebellar ventricle is part of the 4th ventricle. Ventrally, the infundibulum leads to the pituitary (dorsal to the palate). The pituitary is housed in a bony socket, the sella tursica.*



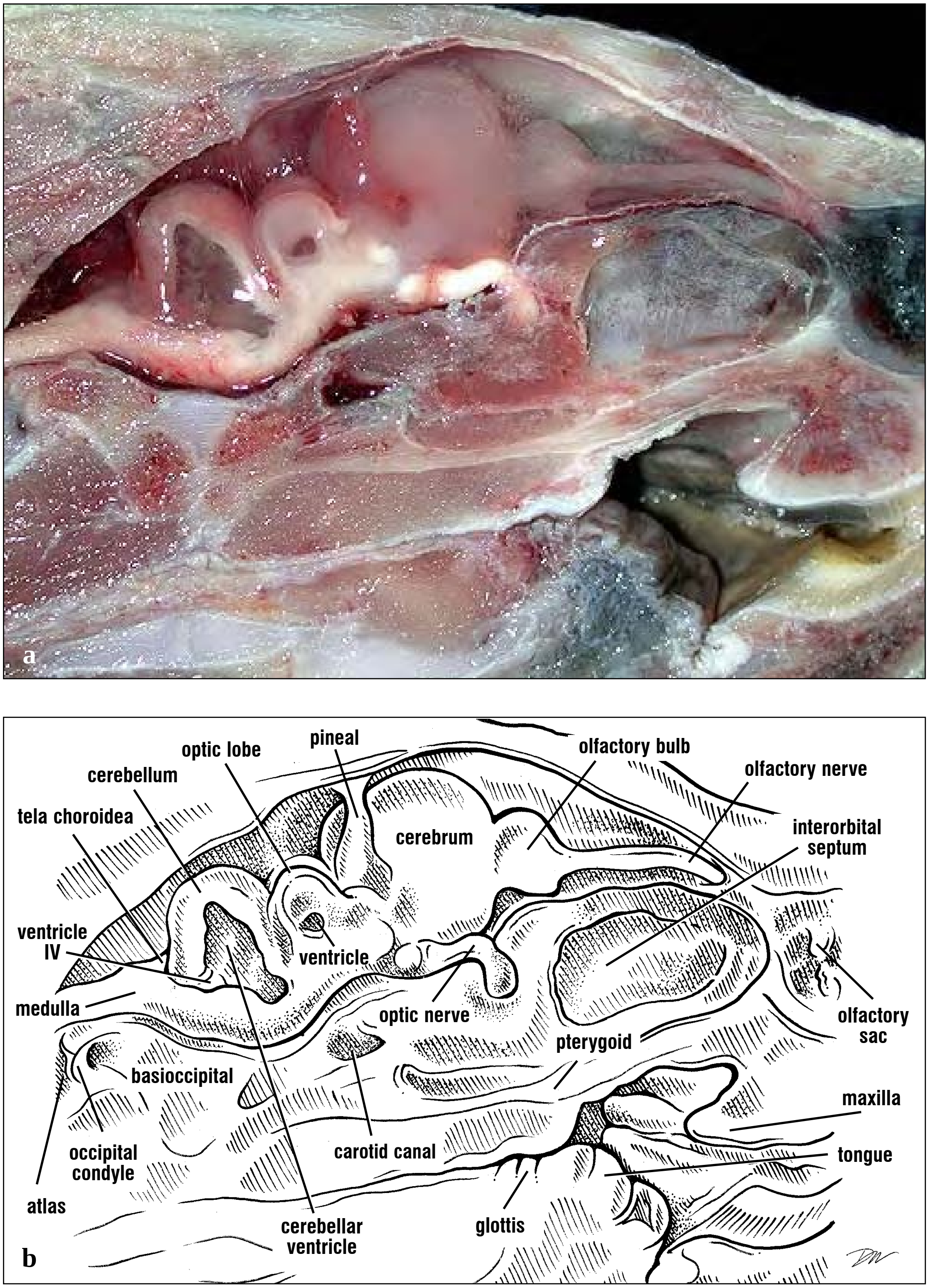
Figs. 195a and 195b. *Parasagittal cut through an immature green turtle head. This view shows the spatial relationships of the CNS to other head structures. The brain is located close to the dorsal skull. The cut removed part of the interorbital septum so that the eye muscles are exposed dorsal to the palate and posterior to the olfactory sac. The intact olfactory nerve can be seen extending to the olfactory sac.*



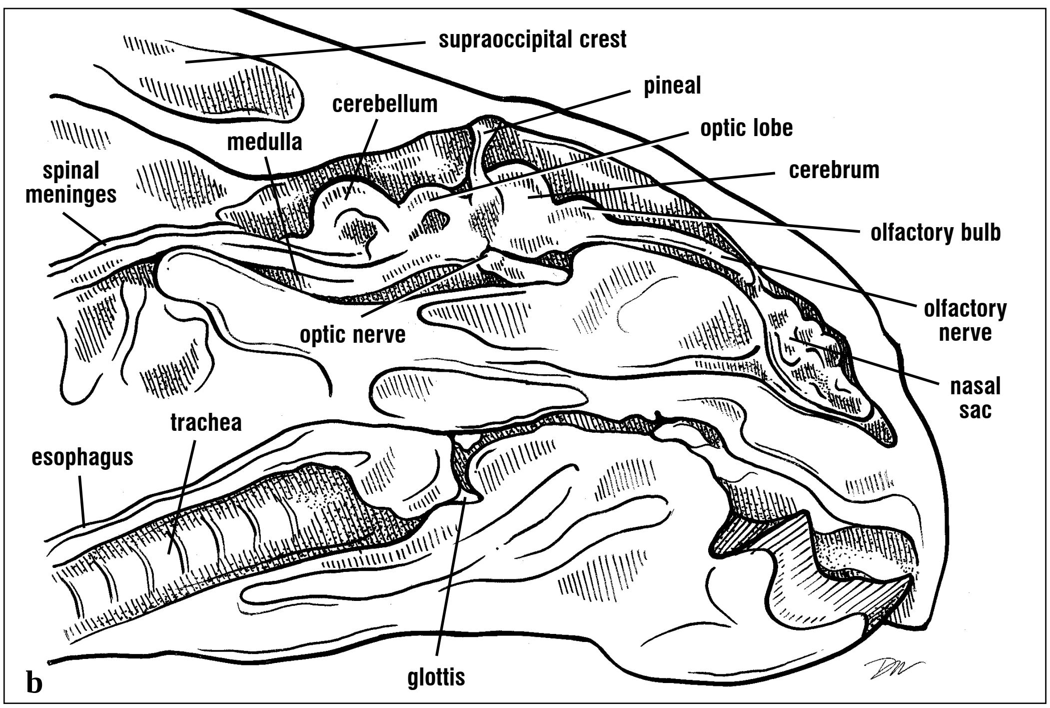
Figs. 196a and 196b. *Parasagittal cut through a subadult green turtle head (close up). The brain is located very close to the dorsal skull in green turtles. The lateral ventricles are just exposed by the parasagittal cut; part of the cerebral aqueduct is seen within and ventral to the optic lobe. The cerebellar ventricle, part of the fourth ventricle, is exposed.*



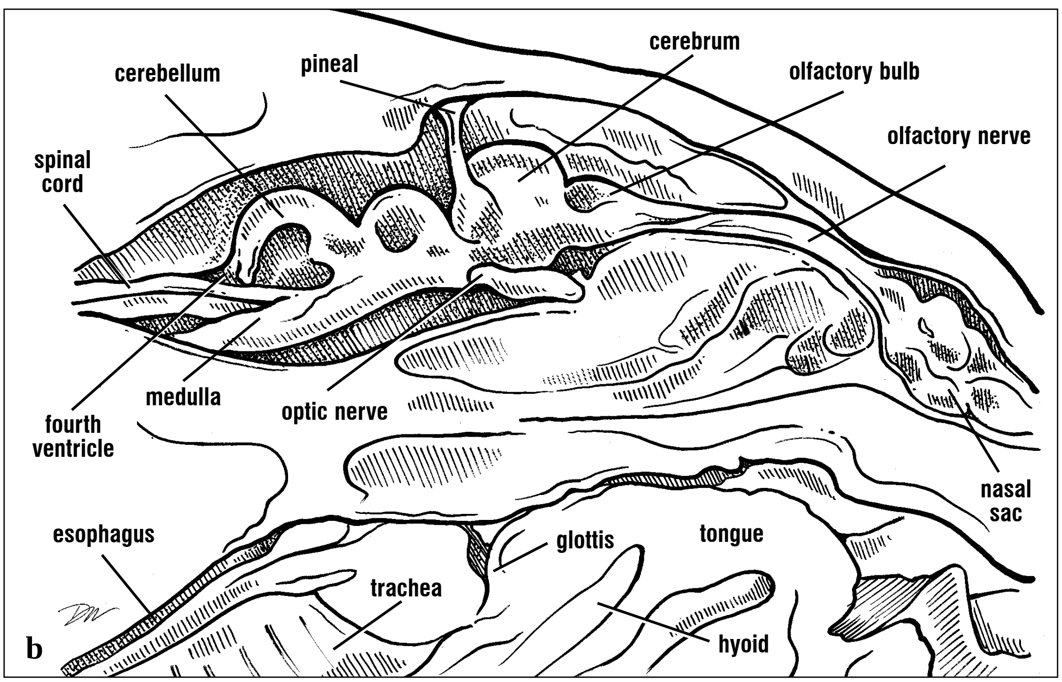
Figs. 197a and 197b. *Parasagittal cut through the head of an immature Kemp's ridley. The anterior half of the brain is flexed slightly dorsally in this species.*



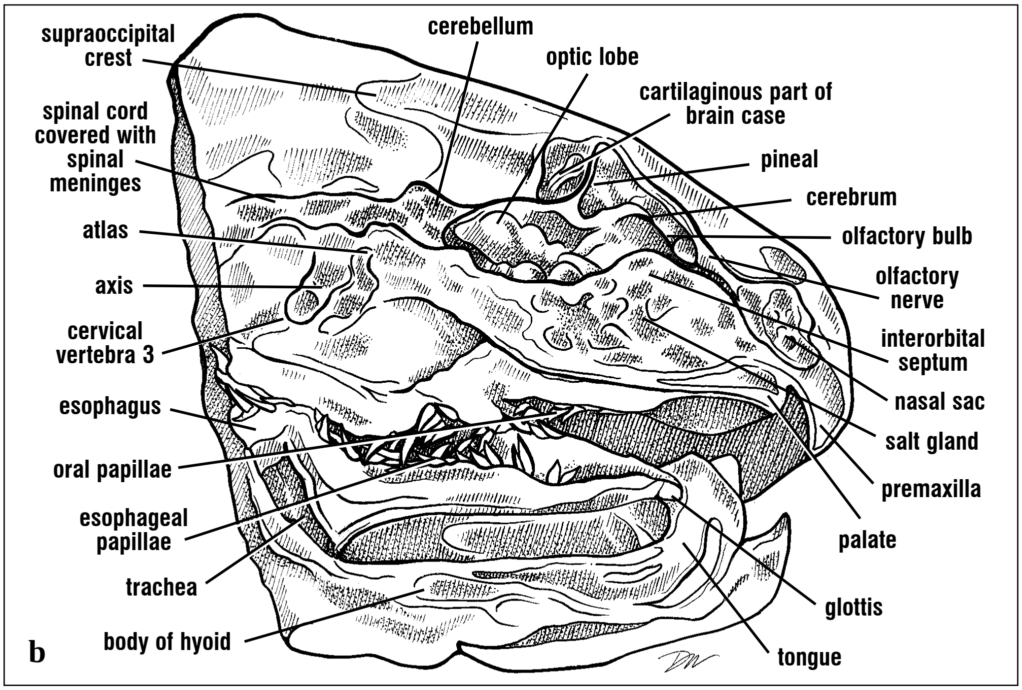
Figs. 198a and 198b. *Parasagittal cut near the midline of a juvenile Kemp's ridley turtle (close up). The cerebral hemispheres are closer to the skull roof bones in ridleys than in the other cheloniid species. The cut was positioned so that the optic chiasma (at the posterior end of the optic nerve) was bifurcated. The pituitary is not seen in this section.*



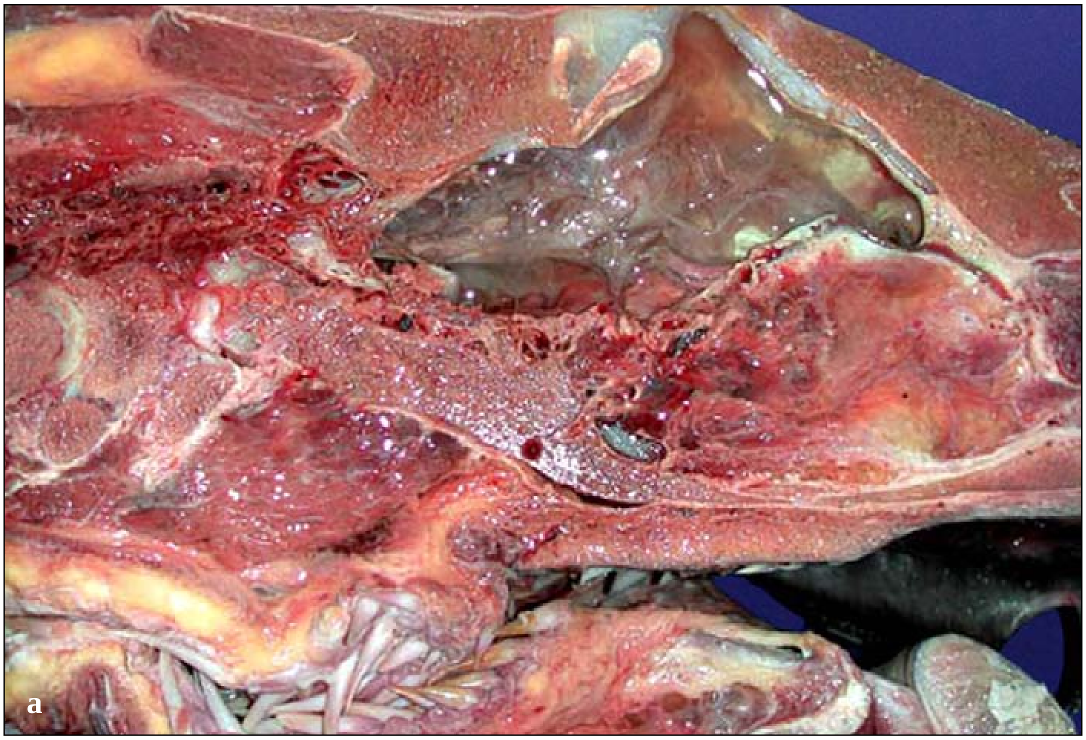
Figs. 199a and 199b. *Parasagittal section through a hawksbill head. The brain is not as closely positioned to the skull roof in hawksbills as in other cheloniids. The pineal gland is clearly exposed in this dissection. Other parts of the brain are partially decomposed so their structure is slightly collapsed. The partial collapse makes the spinal meninges more distinct. The trachea and oral cavities are clearly exposed. The esophagus is collapsed in this specimen.*

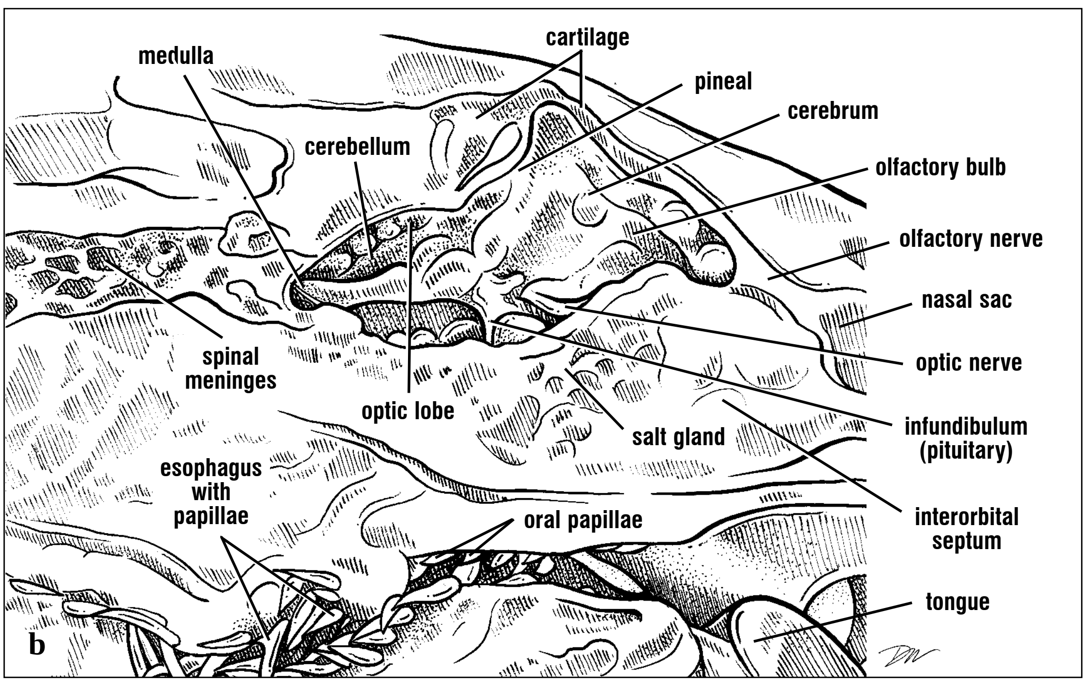


Figs. 200a and 200b. *Parasagittal cut near the midline of a subadult hawksbill turtle (close up). The subdural space is relatively large in the hawksbills. In this dissection, the medulla was sliced so a portion is displaced ventrally to an abnormal position. Structures from other systems are clearly exposed in this dissection. The tongue, glottis, and trachea are shown with the supporting hyoid skeletal structure.*



Figs. 201a and 201b. *Midsagittal section of an adult leatherback head. The braincase is largely cartilaginous around the dorsal and anterior aspects of the forebrain and midbrain. The parietal and frontal skull bones cover this cartilaginous portion of the braincase. The brain is partially decomposed and has collapsed. The extremely hypertrophied salt gland is visible where a portion extends medial to the eye.*





Figs. 202a and 202b. *A midsagittal cut of an adult leatherback head (close up). The brain is partially decomposed, however the pineal is still attached to the skull roof dorsally and the infundibulum remains attached to the pituitary ventrally. The largely cartilaginous positions of the braincase are typical of leatherbacks.*

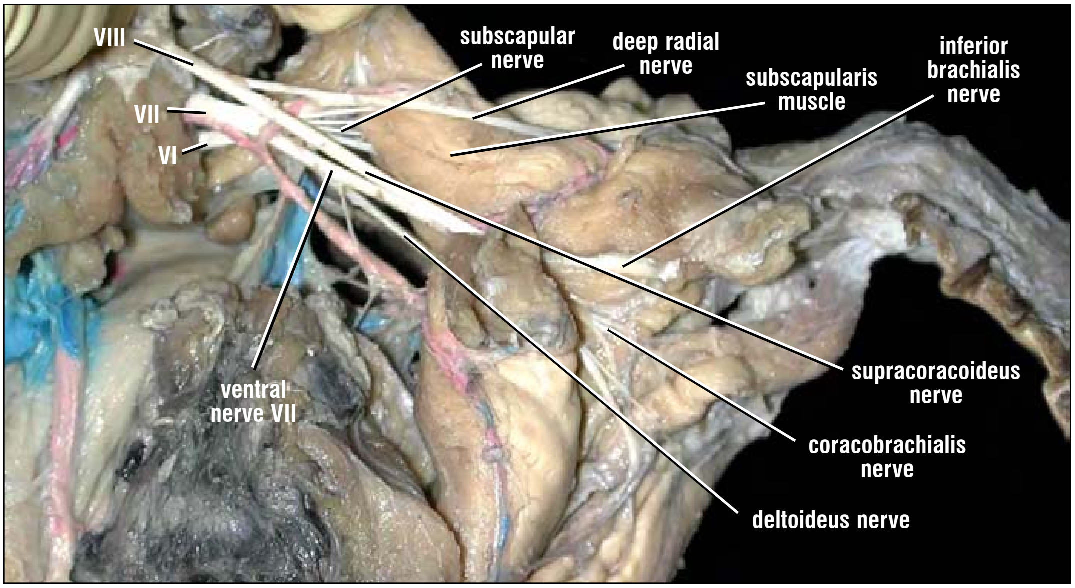
Fig. 203. *Dorsal views of the brains of hatchling and juvenile turtles shows the negative allometric growth of the brain relative to the size of the head. Hatchlings have disproportionately large brains.*

The relative sizes of parts of the brain vary through ontogeny. The brain is proportionately larger in hatchlings and juveniles than in subadults and adults (Fig. 203). The olfactory nerves become proportionately longer and the cerebral hemispheres, optic lobes, and cerebellum are proportionately smaller in subadult and adult turtles.

Peripheral Nerves -- The **spinal nerves** form the **peripheral nervous system**. They leave the spinal cord as paired dorsal and ventral nerve roots and exit the vertebrae via **intervertebral foramina**. The dorsal nerves are composed of **somatic** and **visceral sensory** nerve fibers and may contain motor fibers as well; the ventral roots are generally composed of both **somatic** and **visceral motor** nerve fibers. These nerves function as the autonomic nervous system. The autonomic nervous system of turtles has both **sympathetic** and **parasympathetic** components. However, these are not anatomically segregated as "thoracolumbar" sympathetic and "craniosacral" parasympathetic regions as in mammals. Hence, nerves arising along the length of the spinal cord may have both sympathetic and parasympathetic components.

Two networks of interconnected spinal nerves, the **brachial plexus** and **sacral** (= lumbosacral) **plexus**, are associated with control of the limbs. They are poorly described in the literature on sea turtles. In cheloniids they are formed by ventral nerve roots and their branches. The brachial plexus (Figs. 204-206) arises at the level of cervical vertebrae VI-VIII in sea turtles. These cervical nerves form a complex network innervating the pectoral, arm (humerus), and flipper muscles (Table 1) as well as sending branches to the respiratory muscles. Most muscles receive innervation from more than one branch of the plexus. A ventral branch of nerve VI makes a large contribution to the **median** nerve. Nerves VII & VIII give rise to the **inferior brachial** nerve, which immediately divides to form the **superficial radial** nerve and the **deep radial** nerve to the anterior shoulder and dorsal flipper. Next, the **supracoracoideus**, **subscapular**, and **ulnar** nerves arise and travel to those pectoral muscles and the ventral side of the flipper. The **deltoideus** nerve arises primarily from nerves (VI and VII).

There are no descriptions available for the brachial and sacral plexuses of *Dermochelys*.



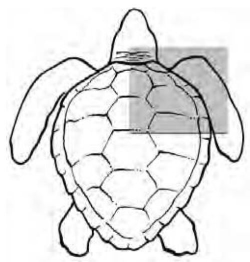
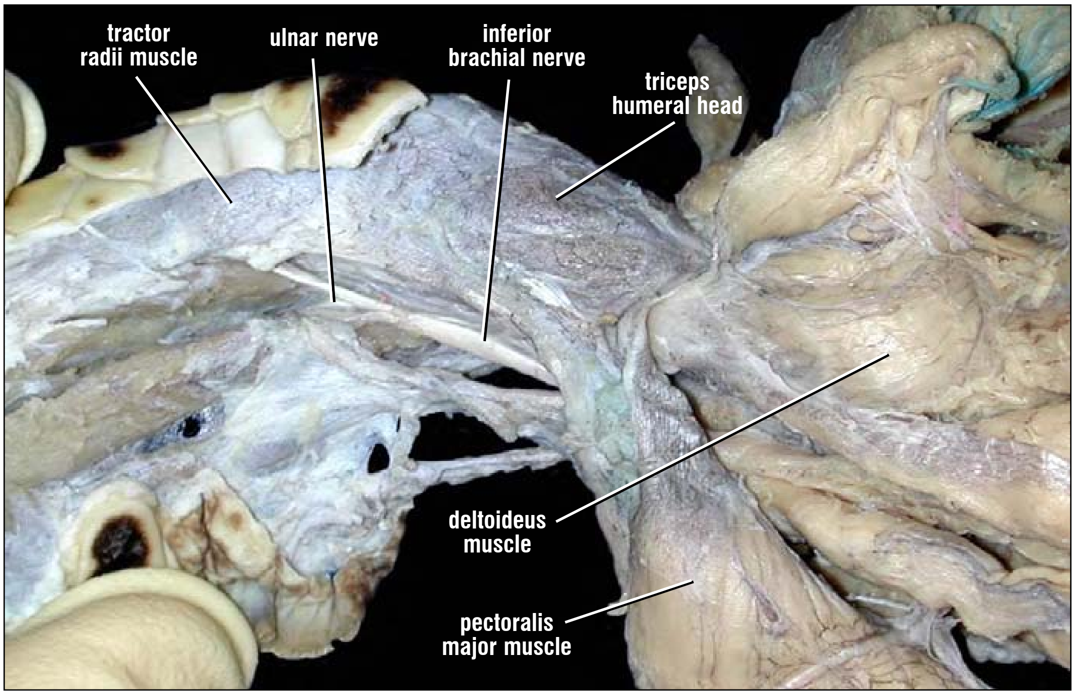


Fig. 204. *The brachial plexus of a hawksbill. The brachial plexus arises from the most posterior cervical vertebrae. Its nerves innervate the pectoral muscles and flippers. The carapace and connective tissues have been removed to provide this posterodorsal view of the brachial plexus. Its 3 rami arise from the intervertebral foramina and immediately undergo a series of divisions and interconnections to form the nerves of the brachial plexus.*



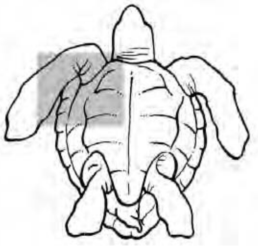


Fig. 205. *Branch of the brachial plexus of a hawksbill (ventral view). The inferior brachial nerve of the brachial plexus travels along the ventral and anterior aspect of the flipper. The ulnar nerve is seen branching off. The other main nerve of the arm, the median nerve, is deep to the inferior brachial nerve and cannot be seen.*

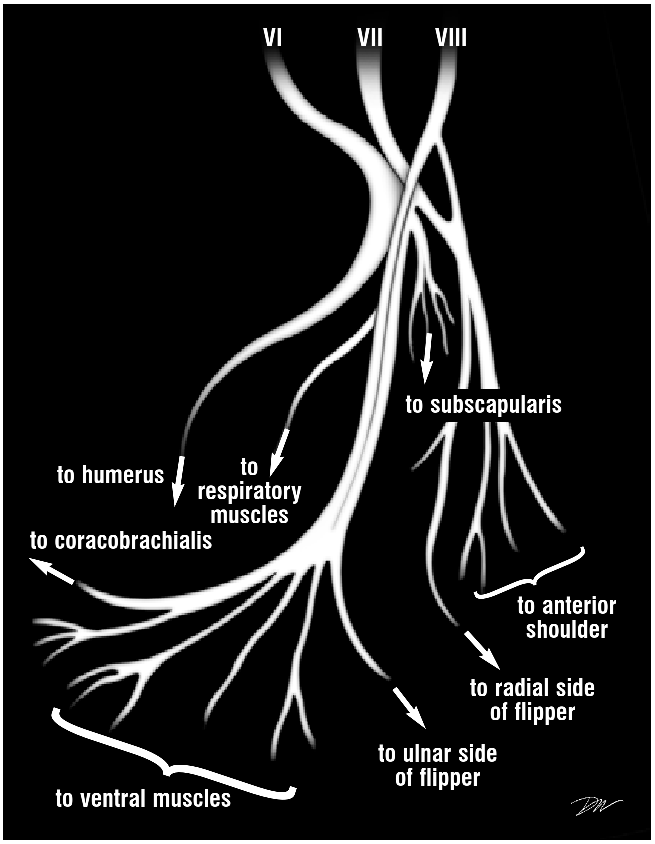


Fig. 206. *Diagram of the right brachial plexus based upon cheloniids. The three roots of the brachial plexus and their interconnections to the flipper and shoulder musculature are shown. Branches to ventral muscles go to the pectoralis, biceps superficialis, biceps profundus, and the deltoideus Larger branches are shown as thicker lines. The most distal branches are not shown.*

The sacral plexus (Figs. 207-208) arises as 4 (sometimes 5-6) rami (branches) from spinal nerves XVII-XXI, located on the last dorsal and sacral vertebrae. These nerves interconnect and subdivide several times as they send nerves to the inguinal, pelvic, and hind leg muscles (Table 1). Many muscles receive multiple innervations. The more posterior nerves roots give rise to the **obturator** nerve, going to the ventral pelvic muscles, and the **ichiadicus** nerve, which runs medial to the ilium and then divides to form the **peroneal** and **sciatic** nerves. The anterior two nerve roots interconnect provide major innervations (via **crural**, **femoral**, and **tibial** nerves) to the inguinal muscles, thigh adductors, and leg extensors.

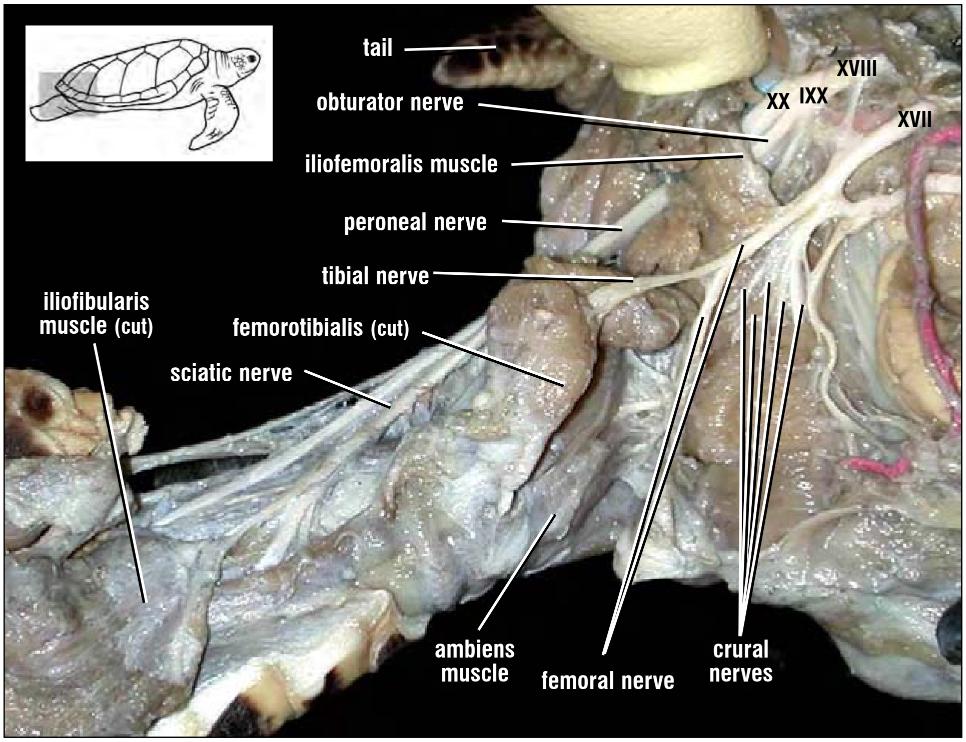


Fig. 207. *The sacral plexus of a hawksbill. This lateral view of the sacral plexus shows four roots giving rise to the interconnecting nerves that innervate the hind limb and respiratory muscles of the inguinal region. The most posterior branch of the sacral plexus extends posteriorly, medial to the ilium, and then travels along the posterior hind limb. It gives rise to the sciatic, tibial and peroneal nerves that innervate many of the distal hind limb muscles.*

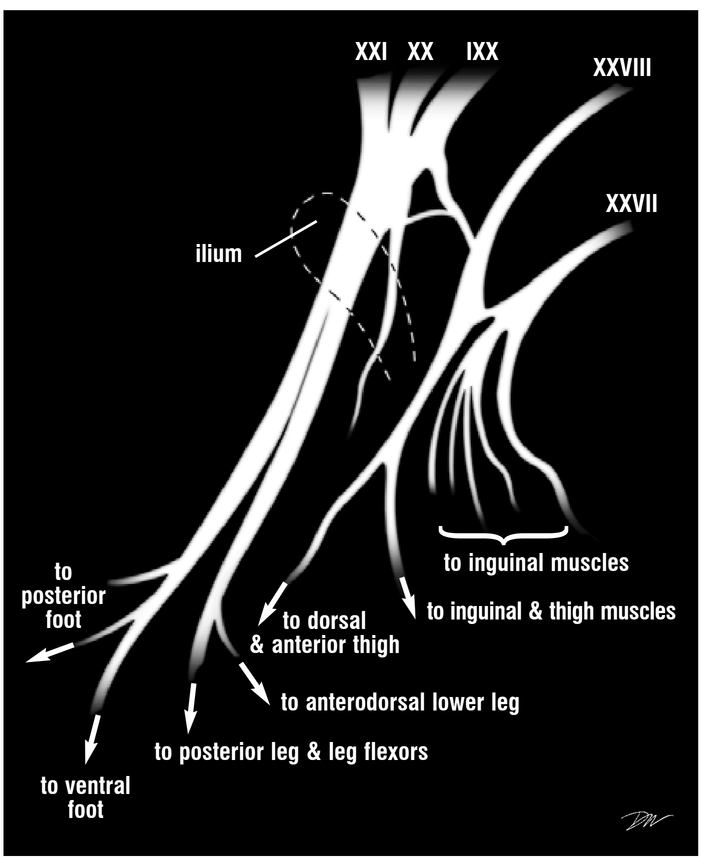


Fig. 208. *Diagram of the right sacral plexus (lateral view) based upon cheloniids. The roots of the sacral plexus and their interconnections to the pelvic, inguinal, and hind limb musculature are diagrammed. Thicker lines represent larger branches. The most distal branches are not shown. The lone branch medial to the ilium is the oburator nerve to the ventral pelvic muscles.*

Brachial Plexus	Innervations
Inferior brachial nerve	Tractor radii
Superficial radial nerve	Latissimus dorsi
Deep radial nerve	Latissimus dorsi Supracoracoideus Testoscapularis
Supracoracoideus nerve	Supracoracoideus Pectoralis major Biceps brachii (profundus and superficialis)
Subscapular nerve	Subscapularis
Axillary (= Deltoideus) nerve	Deltoideus (ventral parts) Brachialis
Radial nerve	Latissimus dorsi Teres major Tractor radii Triceps brachii (humeral head) Respiratory muscles
Ulnar nerve	Deltoideus (dorsal head) Latissimus dorsi Subscapularis Extensor radialis Medial flipper muscles Extensors of digits
Median nerve	Coracobrachialis Flexor carpi ulnaris Flexors of digits
Sacral Plexus	**Innervations**
Crural nerve	Inguinal muscles Thigh protractors (Triceps femoris complex)
Femoral nerve	Puboischiofemoralis Dorsal hip muscles
Obturator nerve	Ventral hip muscles Caudi-ilioformoralis Ischiotrocantericus Adductor femoris Flexor tibialis (internus & externus) Pubotibialis complex
Ischiadicus nerve	Posterodorsal hip muscles
Sciatic nerve	Gastrocnemius Iliofemoralis Ventrolateral foot extensors
Peroneal nerve	Triceps femoris (ambiens, femorotibialis, Iliotibialis) Gastrocnemius Foot flexors
Tibial nerve	Flexor tibialis (internus & externus) Ambiens Pubotibialis Inguinal muscles Foot extensors

Table 1. *Major innervations by the nerves of the brachial and sacral plexuses. Nerves are named using mammalian nerve terminology.*

Sense Organs

Chemical, visual, acoustic, and vestibular senses of sea turtles are concentrated in the head.

The **tongue** (Fig. 209) is a muscular organ covered by a mucous membrane. Taste buds are present but are poorly characterized. The tongue lacks obvious lymphoid tissue at its posterior, as is seen in mammals.

The **nose** includes **external nares** leading to an **olfactory (nasal) sacs**. The olfactory sac communicates via the nasopharyngeal duct to the internal choanae (internal nares; Figs. 195 and 210). The olfactory sacs and **choanal folds** are covered with a ciliated sensory epithelium. The olfactory epithelium, located posterodorsally in the nasal cavity, is innervated by the olfactory nerve leading to the olfactory bulb (Figs. 189, 193-201). The **vomeronasal organ** (Jacobsen's organ) of turtles is not typical in its structure. This specialized sense organ, usually associated with detection of airborne and substrate-borne odor molecules, is not recessed in a separate pit as in snakes and some lizards. It is widely distributed anterolaterally and ventrally in the olfactory sac. The vomeronasal organ is distinguished from olfactory epithelium by region and histological characteristics rather than gross appearance. It is innervated by nerves running to

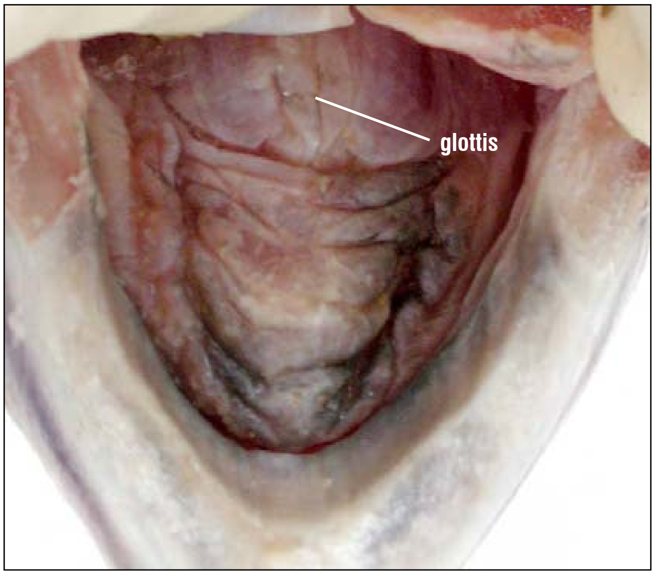


Fig. 209. *Dorsal view of the tongue of the Kemp's ridley. The tongue is muscular and attached to the floor of the mouth. The surface is grossly smooth. The epithelium is covered in small, short, flat papillae.*

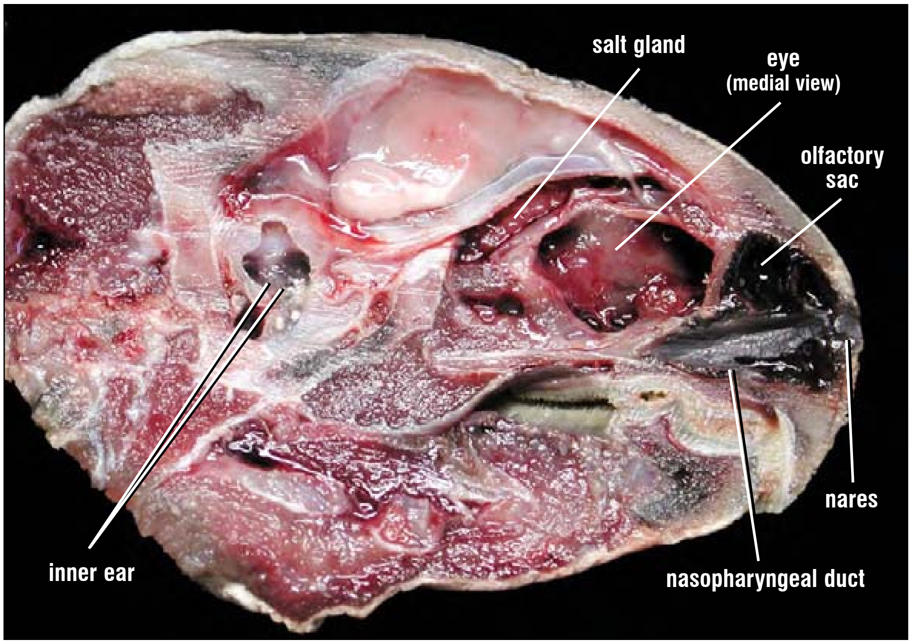


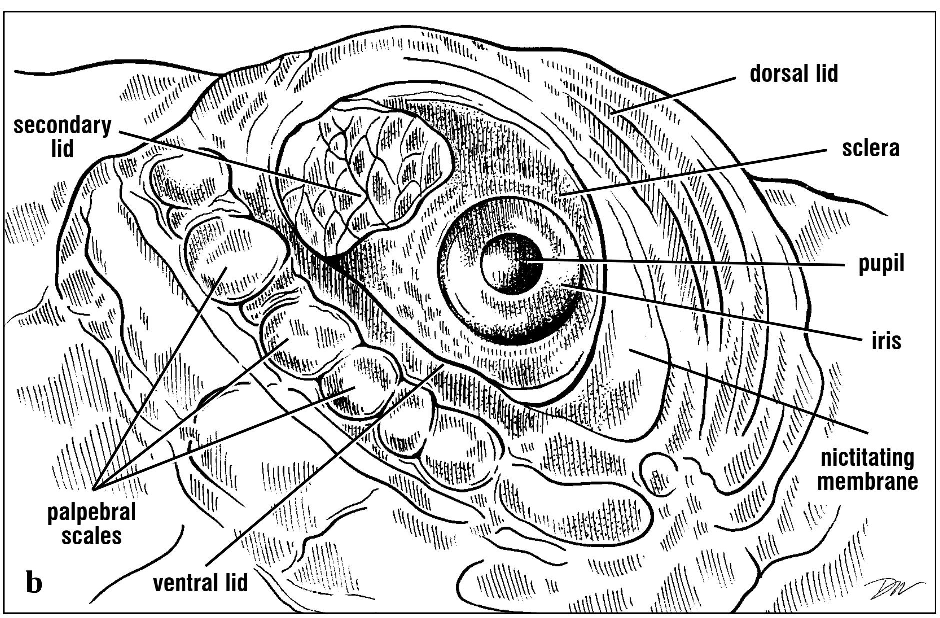
Fig. 210. *The sense organs of a green turtle. The nares lead to large pigmented olfactory sacks. There are several choanal folds on the walls of the olfactory sac, which lack bony supports. The olfactory sac leads, via the nasopharyngeal duct to the internal choanae. The olfactory nerve is cut in this dissection and has fallen ventrally. The inner cavity is cut ventral to the brain; the cochlea is also cut and part is exposed at the ends of the inner ear pointers. The middle ear is located more laterally and hence is not seen in this view.*

the accessory olfactory bulb (effectively the dorsal part of what is grossly called the olfactory bulb).

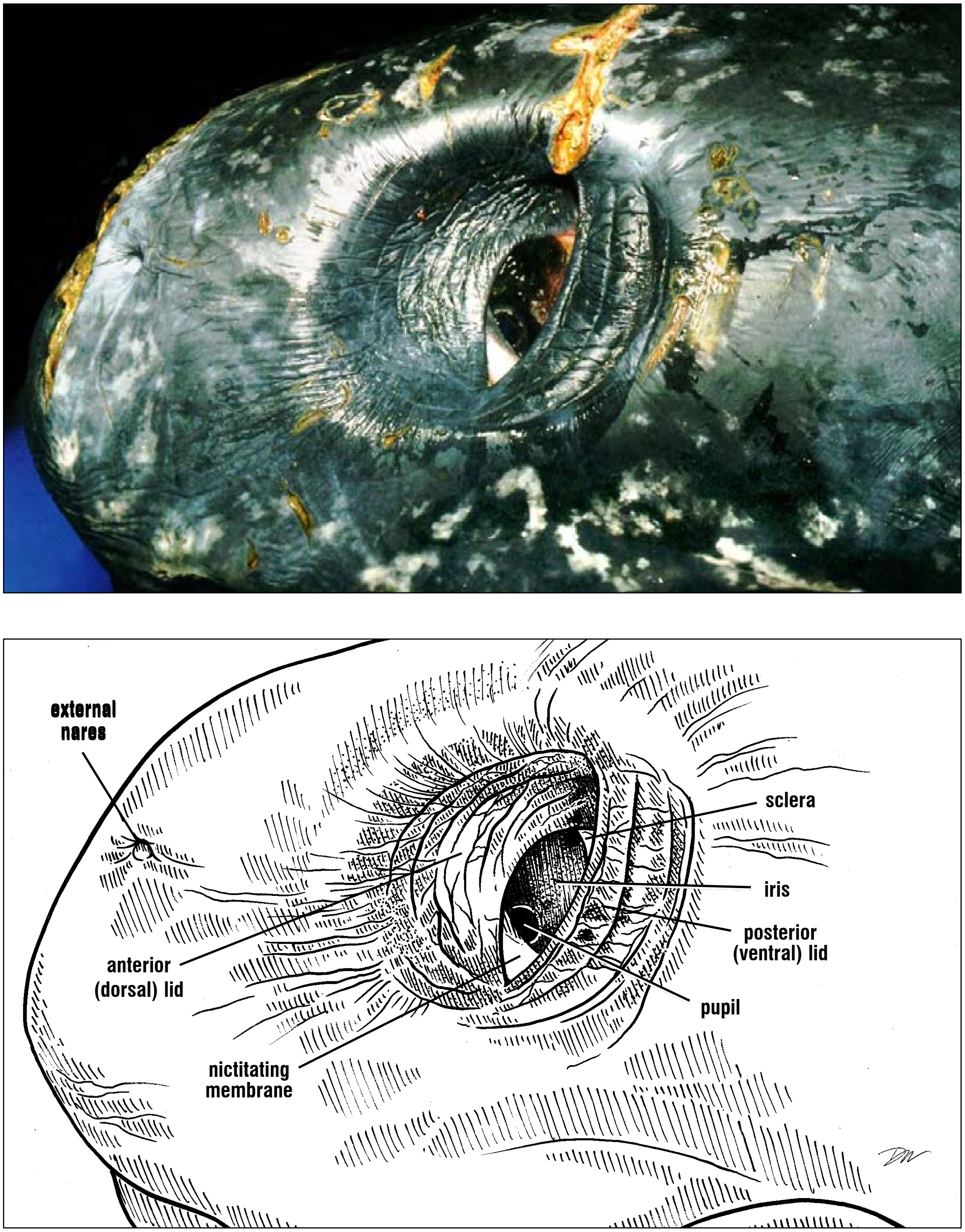
A series of small spike-like papillae line the lateral margin of the internal choane in *C. mydas*. These papillae are absent or poorly developed in other species.

The anterior tissue lining the nares is highly vascular and erectile in adult sea turtles. It appears not to have a sensory function but instead has the ability to seal the nostrils when the turtles are submerged.

The **eyes** of sea turtles are round and housed in bony orbits. The eye is protected by **dorsal** and **ventral lids**. The ventral lid is continuous with the **conjunctiva**, which forms its inner surface. The **nictitating membrane**, at the anterior and ventral corner of the eye, also is continuous with the conjunctiva (Figs. 198-200).



Figs. 211a and 211b. *Eye and lids of a loggerhead. The eyes are located dorsally and anterolaterally. They have overlapping fields of view (hence, binocular vision). The dorsal and ventral lids are keratinized and mobile. The secondary lid is also keratinized but not mobile. The cornea, not labeled, is a clear portion of the sclera that overlies the iris and pupil. Palpebral scales are found in the margins of the ventral lid in cheloniids, but not in Dermochelys.*



Figs. 212a and 212b. *Leatherback eye. The lids of the leatherback eyes are positioned as more anterior and posterior lids than dorsal and ventral lids.*

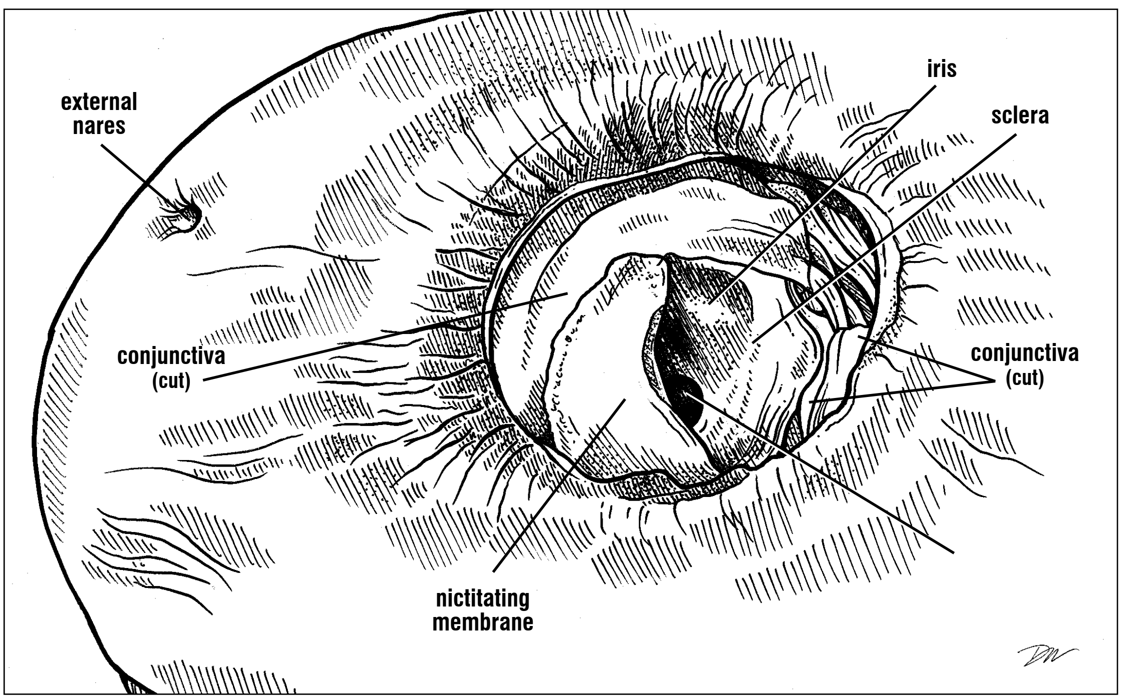


Fig. 213. *Leatherback eye dissection. The lids of this leatherback eye were removed to show the extent and position of the nictitating membrane.*

The wall of the eye (or globe) is composed of 3 major layers: the **sclera, uvea,** and **retina**, surrounding the viscous **vitreous body**. The eye is supported medially by cartilage and laterally by **scleral ossicles** (Figs. 82-84). The outer-most layer is the **sclera**. The eye muscles attach to the sclera (Figs. 215-216). The **superior oblique muscle** inserts dorsally and it is innervated by the **trochlear nerve**. The **superior rectus** muscle attaches posteriorly. Ventral to these muscles is the attachment of the **internal rectus** muscle. Anteriorly, the **pyramidalis** muscle extends from the eye to the eyelids and nictitating membrane. Deep and ventral to the pyramidalis muscle are the **inferior oblique** and **inferior rectus** muscles. The **external rectus** muscle is located posteriorly and ventrally and is innervated by the **abducens nerve**. The superior rectus, inferior rectus, inferior oblique and internal rectus muscles are all innervated by the **oculomotor nerve**.

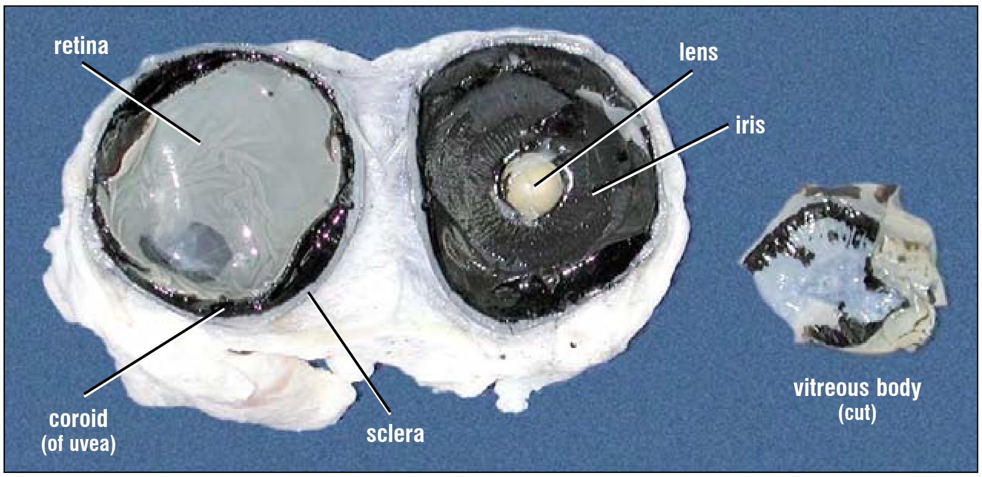


Fig. 214. *Sagittal section of a loggerhead eye. The eye is cut into medial and lateral halves. The retina and back of the eye are on the left. The inside of the iris, lens, and pupil are in the middle of the photo. Part of the vitreous body was removed and placed on the right.*

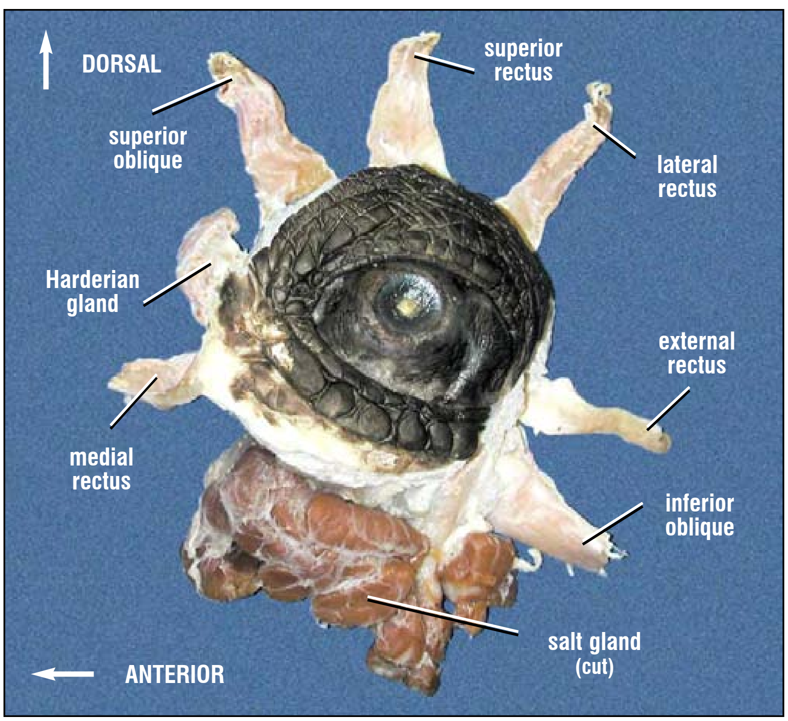


Fig. 215. *Lateral view of a loggerhead left eye. The extrinsic eye muscles are extended radially in this picture to show their relative insertion points. Normally their origins would converge on the interorbital septum.*

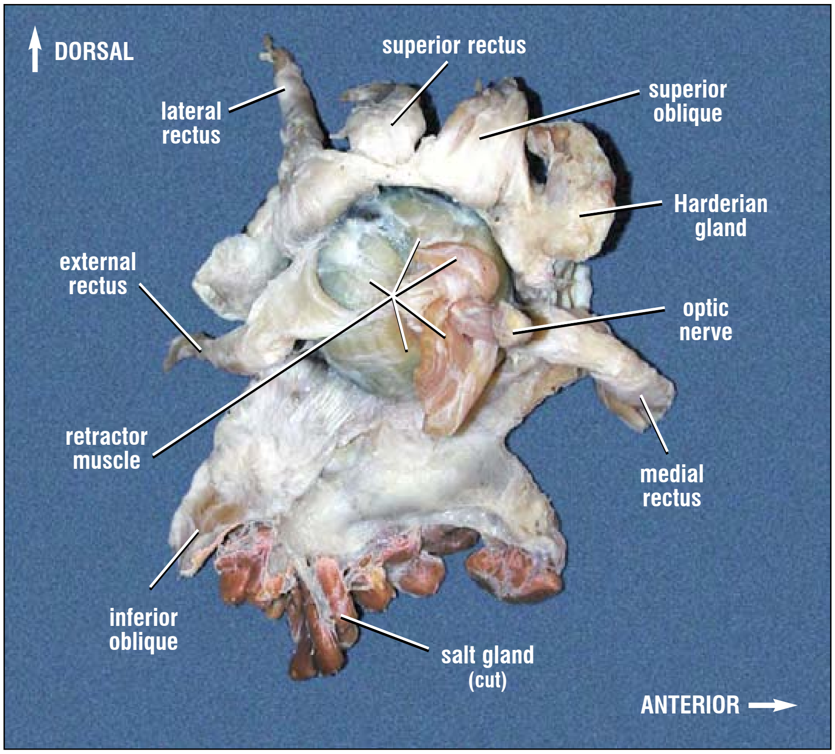


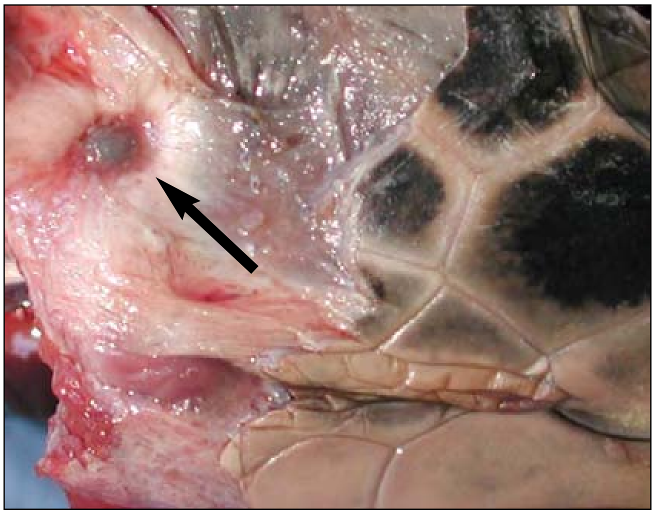
Fig. 216. *Loggerhead left eye (medial view) showing extrinsic eye muscles. The extrinsic eye muscles are responsible for eye movements. Also shown is the Harderian gland, which lubricates the eye and a portion of the salt gland (an organ primarily responsible for salt excretion and maintaining water balance). The retractor muscle surrounds the optic nerve and positions the eye deeply or shallowly in the orbit.*

The sclera, often termed the "white of the eye" in vertebrates, is partially pigmented in most sea turtles. The sclera is clear at the front of the eye; there it is termed the **cornea**. Internal to the sclera is the uvea, composed of the **choroid, tapetum lucidum, ciliary body**, and the **iris** (Fig. 199). The choroid is pigmented and extends from the iris to the retina. It includes the reflective material (tapetum lucidum) that is responsible for "eye-shine". The reflective material enhances the eye's sensitivity under low light conditions. The ciliary body (not shown), is responsible for changing lens shape during visual accommodation. It extends from the choroid near the front of the eye, to the attachments that suspend the lens. The iris is pigmented brown or black and extends from the choroid across the front of the eye. The **limbus** (= limbas) is the tissue between the cornea and the sclera. Because the cornea and sclera are continuous with one another, the limbus represents a transitional zone that is usually described histologically (not labeled in the figures). The free border of the iris forms the edge of the **pupil**. The **lens** is strongly curved in sea turtles (Fig. 214). It is suspended behind the pupil and iris by "ligaments" attached to striated muscles of the ciliary bodies. The chamber of the eye is filled with a clear viscous liquid, the **vitreous body**.

The eyes are photoreceptors that are capable of color and shape discrimination. The **retina** is the sensory layer of the eye; it detects color as well as brightness. The retina is composed of several cell layers and includes several types of rods and cones, each containing photopigments.

The **ears** of sea turtles are responsible for hearing and equilibrium. Each ear consists of an external **tympanum** covered by a tympanic scale that stretches across the **otic notch** (= auditory canal) formed by the quadrate, quadratojugal and squamosal bones (Fig. 28). There is middle and inner ear but no outer ear. The **middle ear** is involved in sound transduction while the **inner ear** functions in sound reception and the detection of position and acceleration. The middle ear contains a single ear bone, the **stapes** (= columella). The stapes extends from the tympanum via an **extrastapedial process** of cartilage (Fig. 217), through the **tympanic cavity** and **recessus cavi tympani**, to articulate via an expanded footplate (also cartilage) on the **vestibular window** of the **cochlea** (Fig. 218). A Eustachian tube extends to each middle ear from the mouth near the jaw joints (Fig. 165).

The inner ear of turtles is composed of the cochlea and 3 semicircular canals, all of which are encased in bone. The cochlea is involved in sound transduction and is innervated by the auditory nerve; it transmits sound information to the brain. The semicircular canals sense the head's position and movement by detecting changes in acceleration in the three planes. One canal resides in each plane (sagittal, coronal, and axial) in each ear.



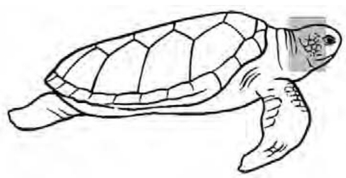
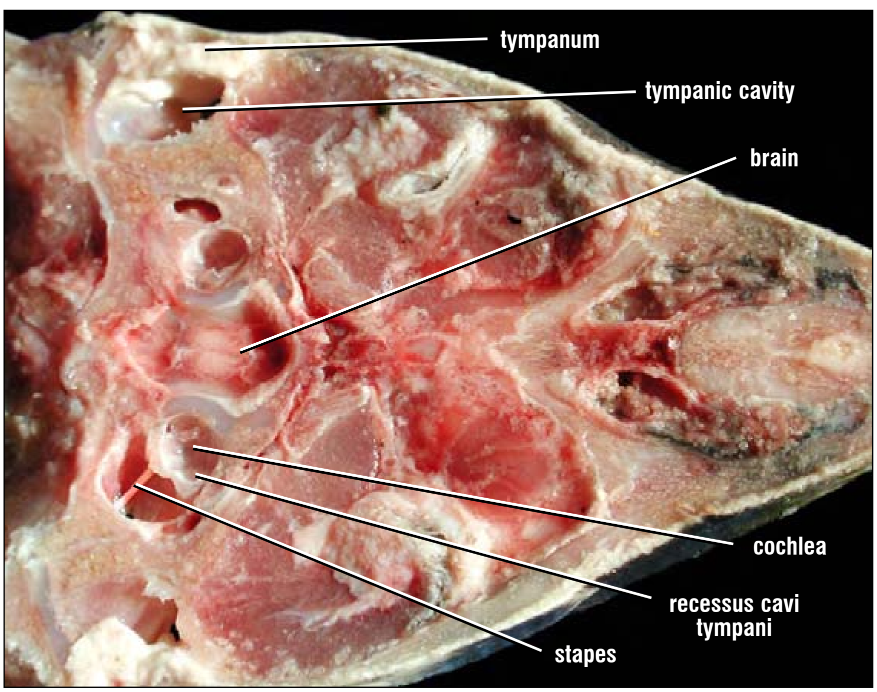


Fig. 217. *The tympanum of a ridley ear. The tympanic scale has been removed to expose the tympanum and the distal-most aspect of the extrastapedial process (at arrow).*



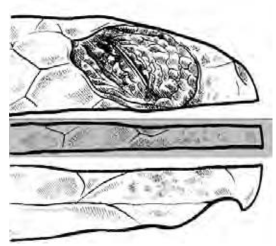


Fig. 218. *Ventral view of a ridley ear. The coronal section exposes the tympanic cavity (= the otic notch of a skull) and, more medially the recessus cavi tympani. The footplate of the stapes articulates with the vestibular window.*

Urogenital Anatomy

The **urogenital system** (UG) is made up of the **kidneys**, **ureters**, **gonads** and their ducts, the **urinary bladder**, and derivatives of the **genital papilla** (penis or clitoris) in the floor of the cloaca. The kidneys function in removal of nitrogenous wastes (excretion) and maintaining water and electrolyte balance (osmoregulation). The ureters transport nitrogenous wastes to the cloaca where it either drains into the urinary bladder or is eliminated. The gonads (**ovaries** or **testes**) produce gametes and their ducts transmit eggs or sperm to the cloaca. They are reproductive structures. The urinary bladder functions in water and urine storage. The cloaca is the common chamber into which the ureters, gonadal ducts, rectum, and bladder empty. The cloaca leads to the outside of the body via the vent.

Excretory System. The kidneys are paired, lobular, elliptical red structures that are located retroperitoneally (between the peritoneum and the shell). Sea turtle kidneys are **metanephric**, meaning (1) they arise from the posterior part of the nephric ridge in the embryo and (2) the kidney tubules are drained by ureters (metanephric ducts). The ureters extend from the kidney, through the peritoneum and empty into the dorsal cloaca on each side. Ureters are located on the ventral surface of each kidney. They drain uric acid, ammonia, and water to the cloaca. Each ureter enters the cloaca with a gonadal duct via a **urogenital papilla** in the **urodeum** portion of the cloaca (Figs. 219 - 220).

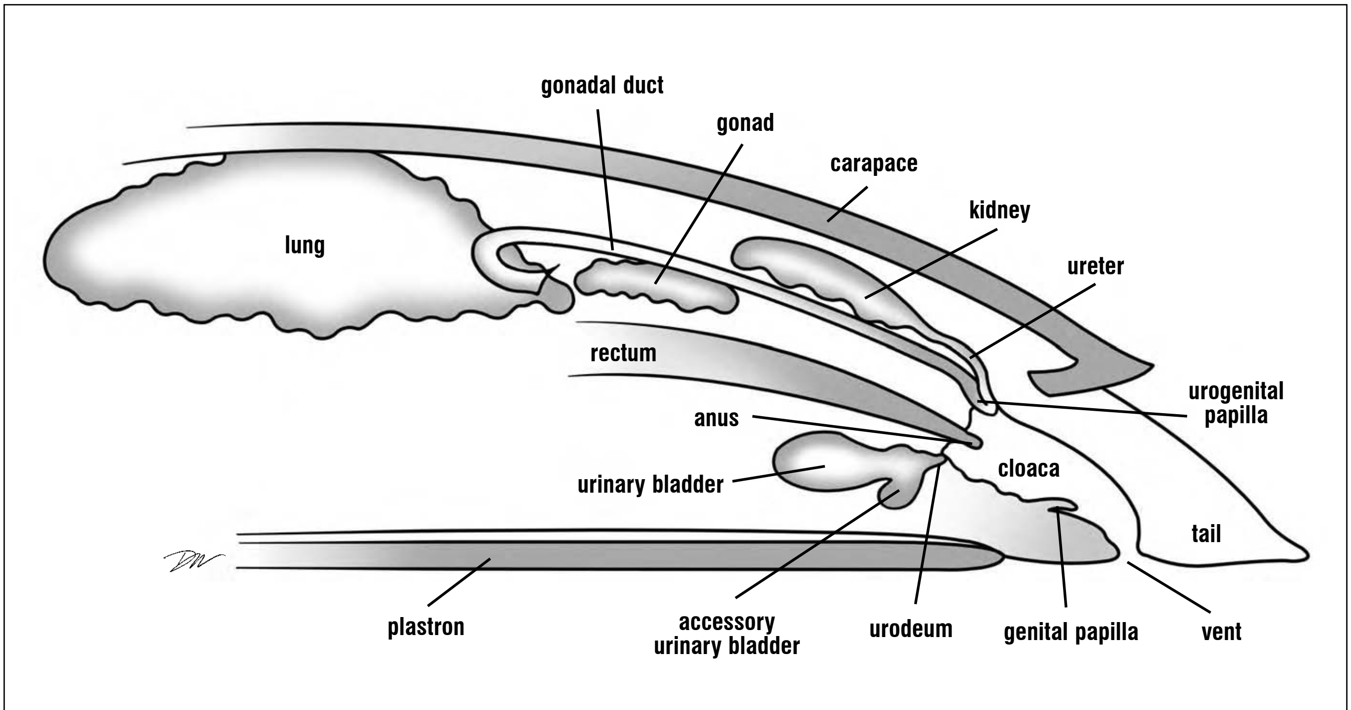
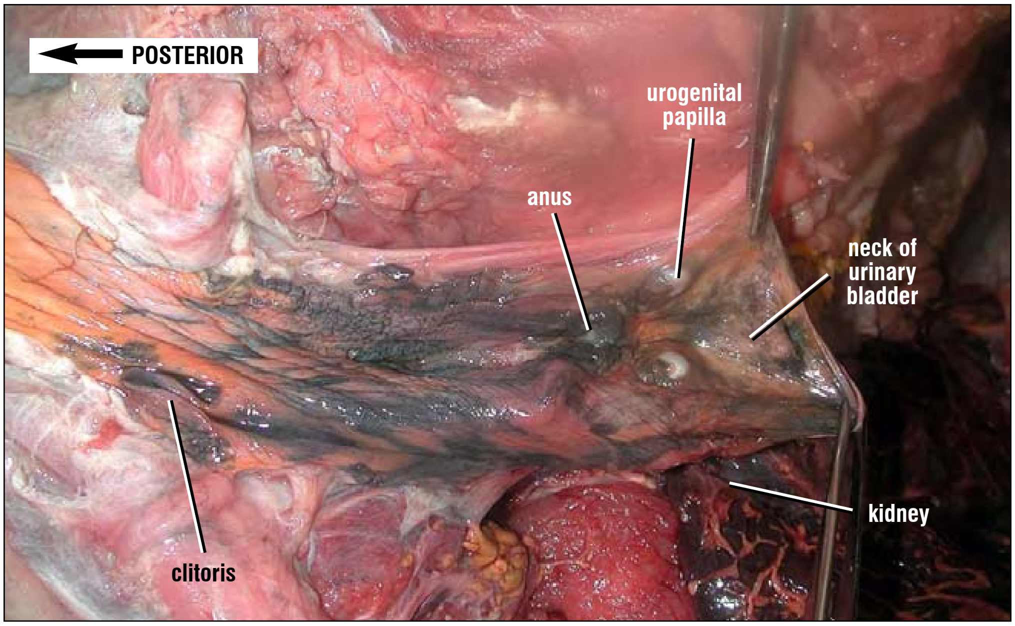


Fig. 219. *Diagram of the Urogenital System. The relative positions of the kidneys, gonads (undifferentieted for diagrammatic purposes), accessory ducts, urinary bladder, rectum and cloaca are shown. Anterior is to the left.*



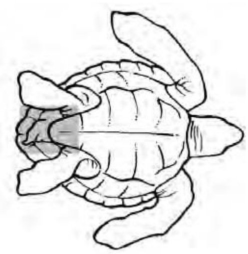


Fig. 220. *Lateral view of the cloaca of an immature hawksbill. The lateral wall of the cloaca has been cut away to show the urogenital papillae from the oviducts and ureters, the opening to the urinary bladder, and the dorsally positioned anus from the rectum. The urinary and genital ducts enter the cloaca adjacent to one another in females. They are small and located as the lateral walls of the urogenital papillae.*

The kidneys of sea turtles lack a distinct **cortex** and **medulla**. Sea turtle nephrons are composed of a **renal capsule**, **proximal tubule** (which is linked to water transport and protein synthesis), an **intermediate segment** (function unknown), **distal convoluted tubule** (responsible for fluid reabsorption) and **collecting tubule** (draining to the ureters). There is no loop of Henle as is found in mammalian nephrons. Unlike higher vertebrates, marine turtles retain the ability to form new functional nephrons as they mature (and perhaps throughout life).

Blood flows through the kidneys from afferent vessels entering (renal arteries and iliac veins), and efferent vessels leaving (renal portal and renal veins) the kidneys. Water and mineral waste (a filtrate) is removed from the blood at the renal corpuscle (glomerulus plus renal capsule).

The urinary bladder is a highly elastic, single, sack-like structure located along the midline of the pelvis. It opens via a single opening to the ventral floor of the cloaca (Figs. 219-221). The bladder is located ventrally and urine, water, and sometimes other waste products may enter it via the cloaca. This anatomical position and the connection of the cloaca to the outside sometimes allows materials other than urine (e.g., fecal material, parasites, or, in females, eggs) to enter opportunistically.

Sea turtles have two small **accessory urinary bladders** connected to the urinary bladder; each located lateral to the neck of the urinary bladder and dorsal to the pubis (Fig. 221). They are seldom filled and often are missed in dissections.

Gonads. The gonads of both species are located dorsally in the body cavity, posterior to the lungs, and ventral to the kidneys and peritoneal wall Figs. 222 and 223).

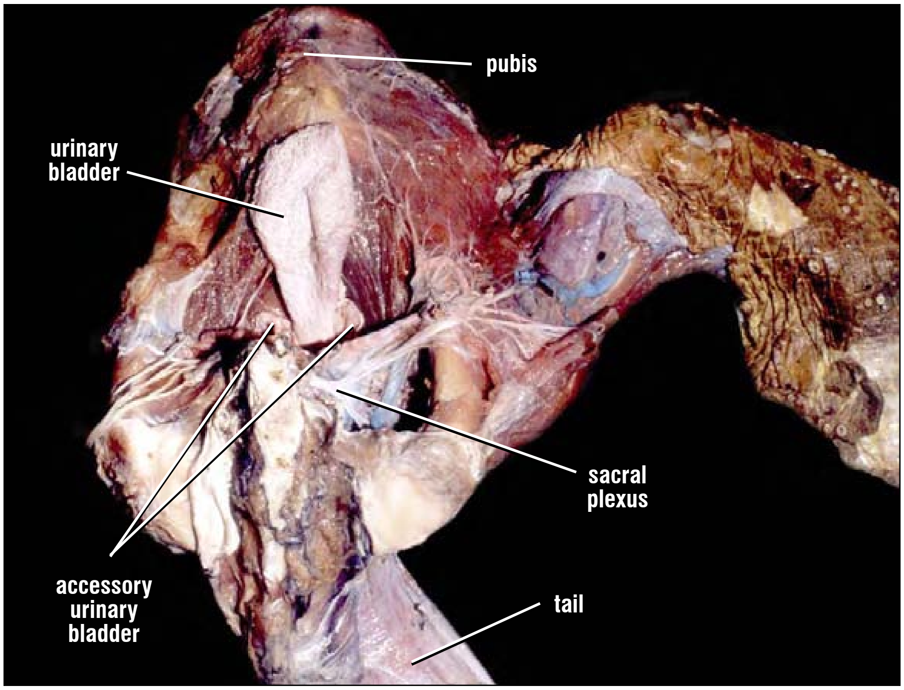
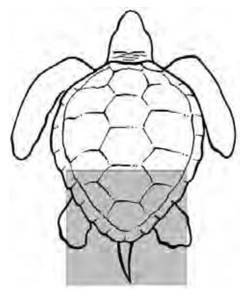
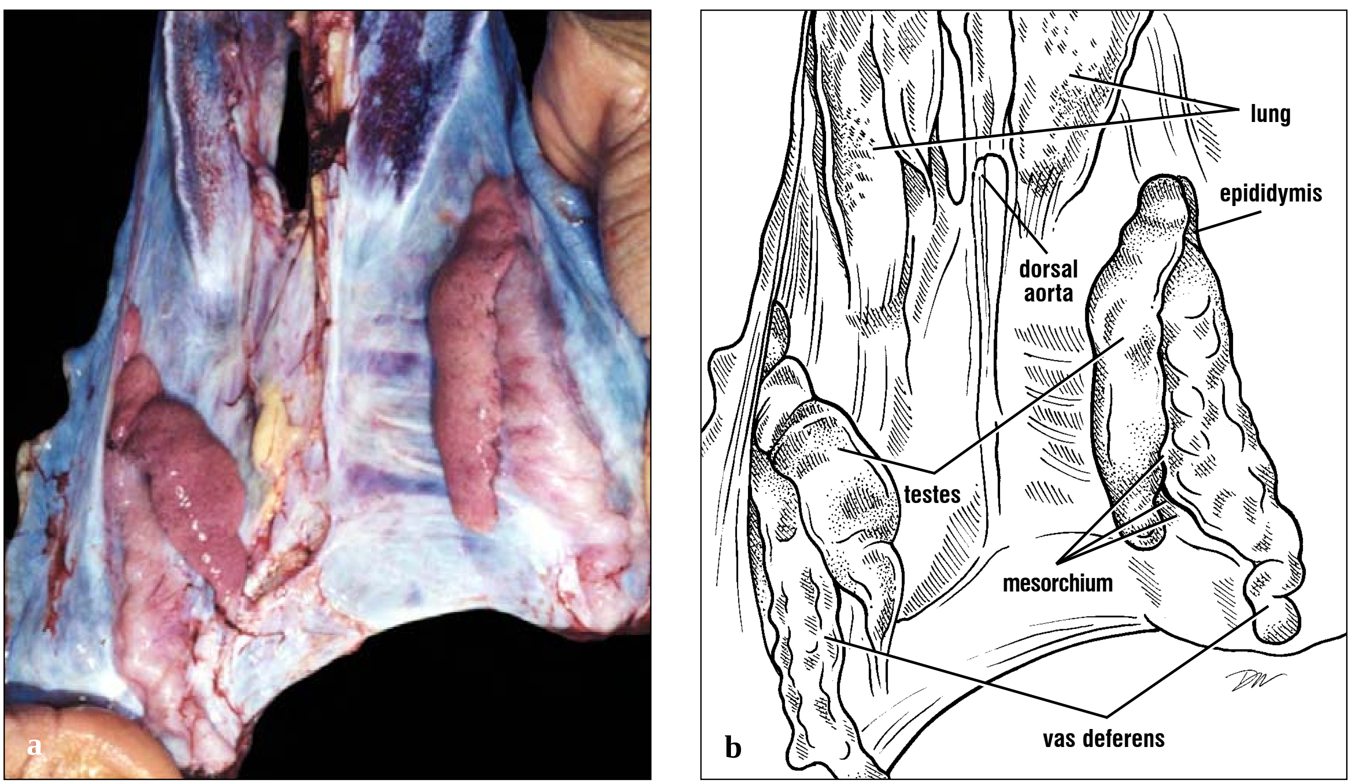
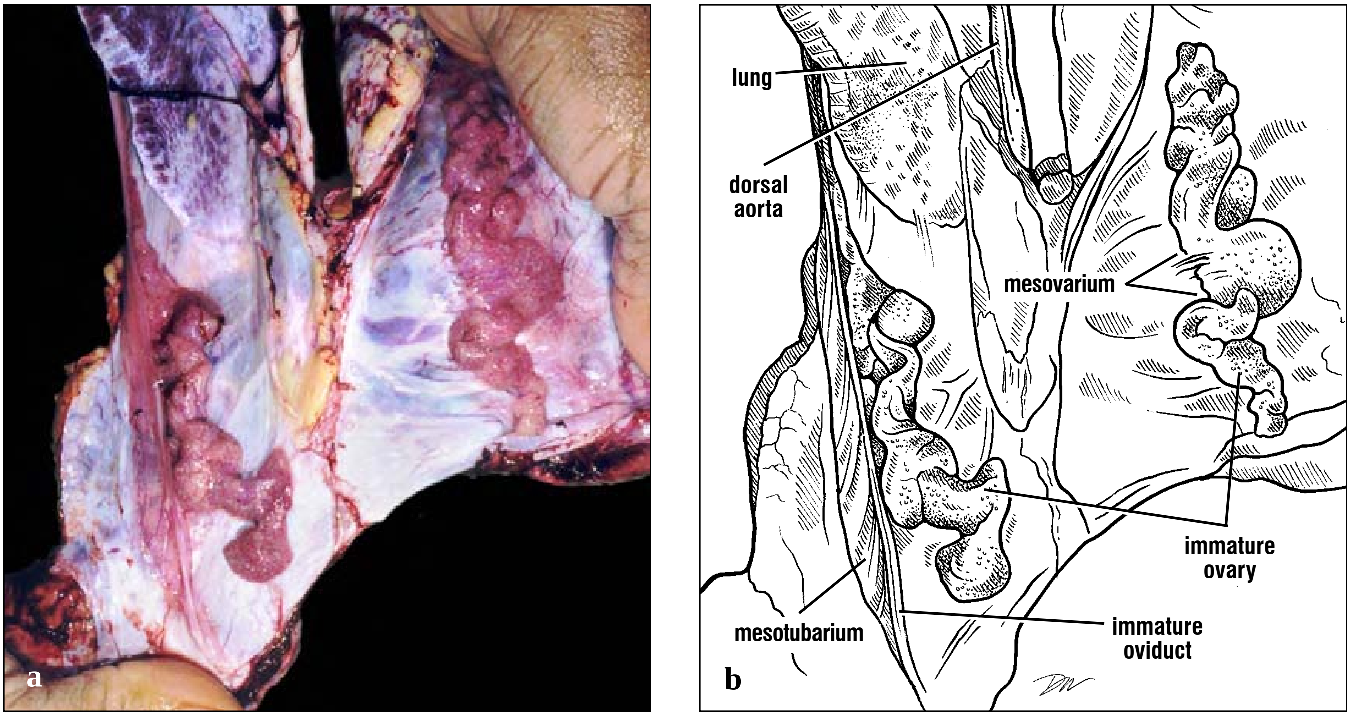


Fig. 221. *Dorsal view of the urinary bladder and dorsal pelvis of a male loggerhead. The empty urinary bladder and accessory bladders are shown free of connective tissues. The ilia are found laterally; the sacral and proximal caudal vertebrae are present dorsally. The sacral plexus is exposed in part.*





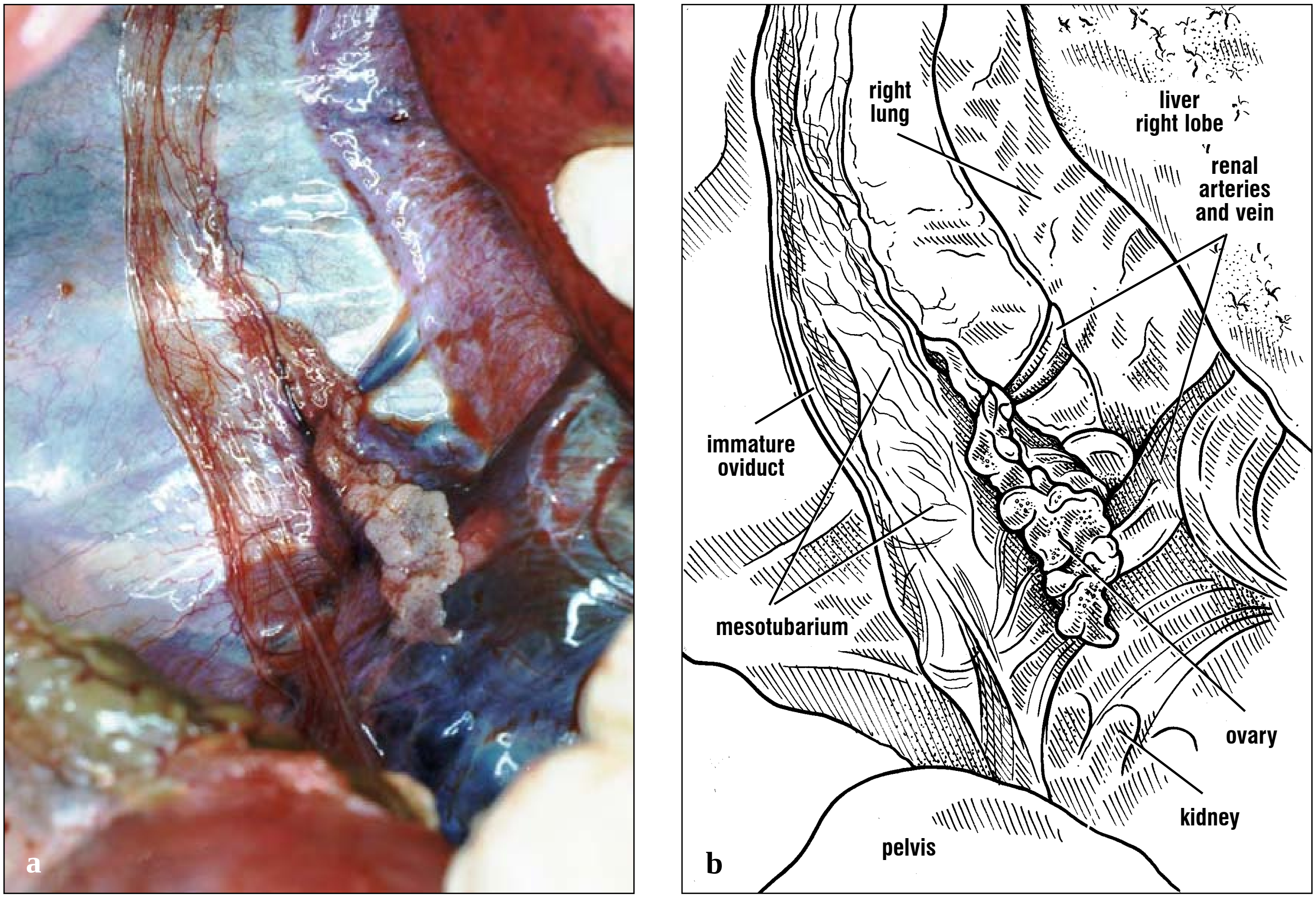
Figs. 222a and 222b. *Testes of an immature green turtle. The testes are attached to the peritoneal wall by their flat dorsal surface. Lateral and slightly dorsal to each testes is an epididymis, which leads to a vas deferens. The surface of the testis is smooth in immature turtles.*



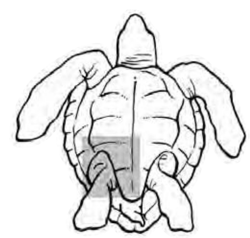
Figs. 223a and 223b. *Ovaries of an immature green turtle. The ovaries are attached to the peritoneal wall by their lateral edges. The surface of the ovary is granular. Lateral to the ovary is the immature oviduct, which is suspended by the mesotubarium.*

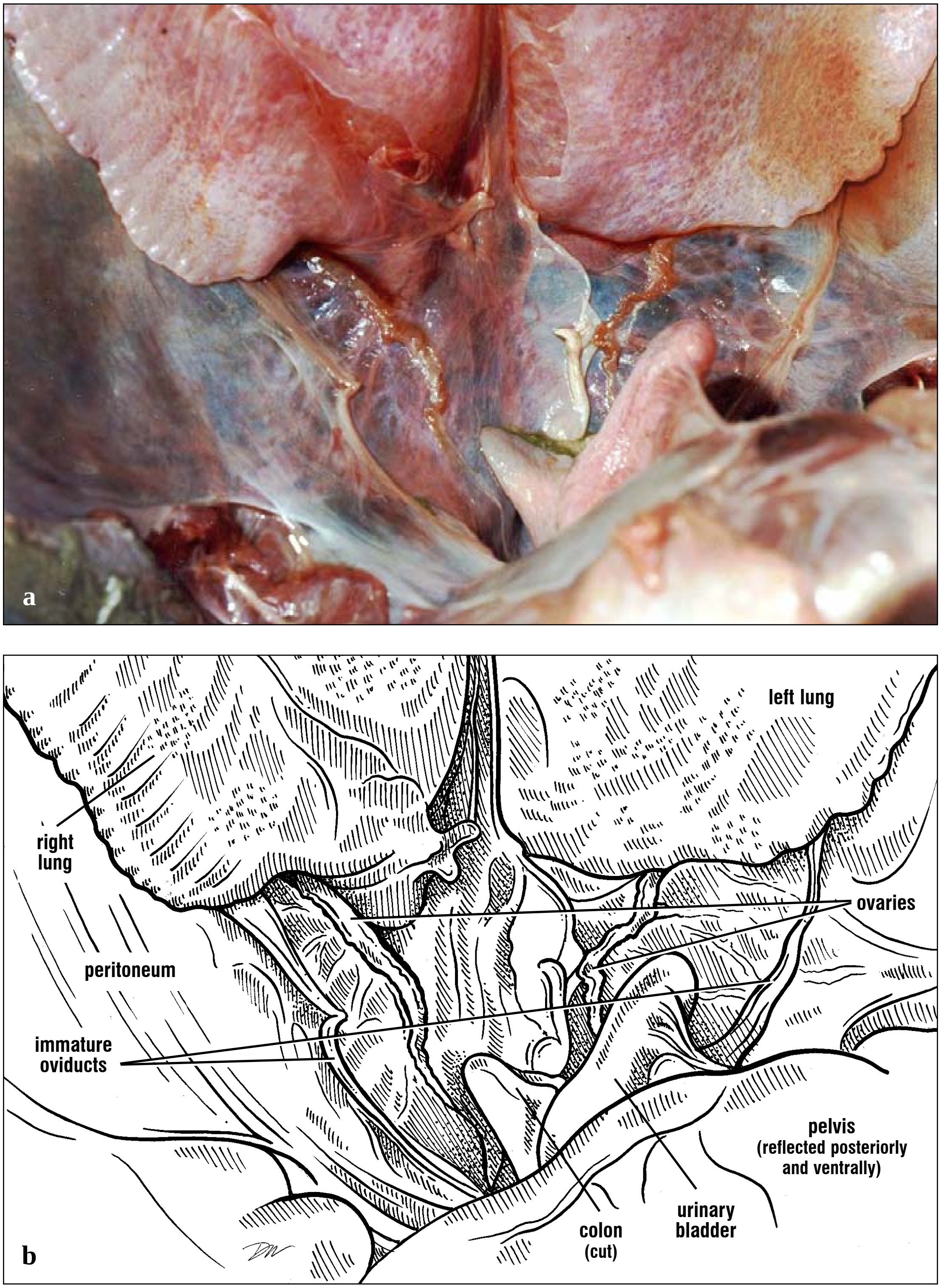
Female: The female reproductive tract consists of paired ovaries, oviducts (also called **Müllerian ducts**), and the suspensory ligaments or mesenteries (**mesovarium**, **mesosalpinx**, and **mesotubarium**). The ovary and oviduct change in size and composition with age and between breeding and nonbreeding seasons.

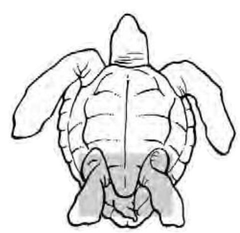
The cranial pole of the ovary is located just posterior to the lung and extends posteromedially toward the cloaca. Along its medial and dorsal surface, it is attached by the mesovarium to the peritoneum that overlies the kidney (Fig. 224) Another ligament, the mesotubarium, extends from the ovary to the oviduct. The oviduct lies lateral to the ovary and extends anteriorly, before curving medially and ending in a funnel shaped opening, the ostium. The ostium, which receives ovulated follicles, is supported by the mesosalpinx. There are no tubules connecting the ovary directly to the oviduct. The posterior end of each oviduct joins the urodeum of the cloaca (Fig. 225).



Figs. 224a and 224b. *Ovary and accessory ducts of a juvenile green turtle, (ventral view). This immature ovary has a granular surface. Its follicles have not yet added significant amounts of yolk. The immature oviduct is a thin, flat tube supported in the mesentery (mesotubarium). Engorged renal arteries and veins can be seen extending from the kidney, anatomically dorsal to the ovary, and toward the midline.*

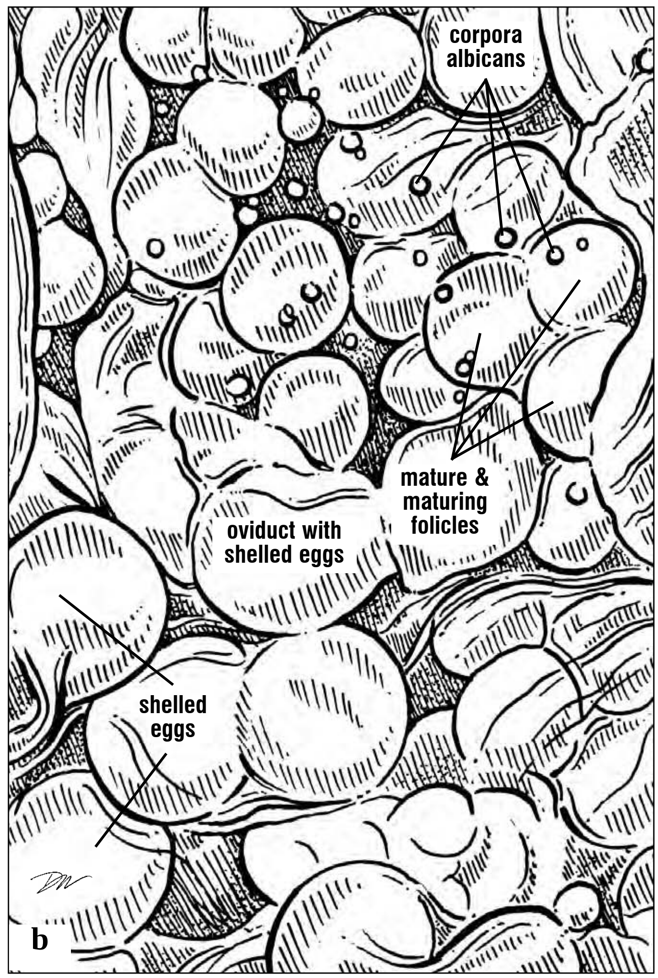






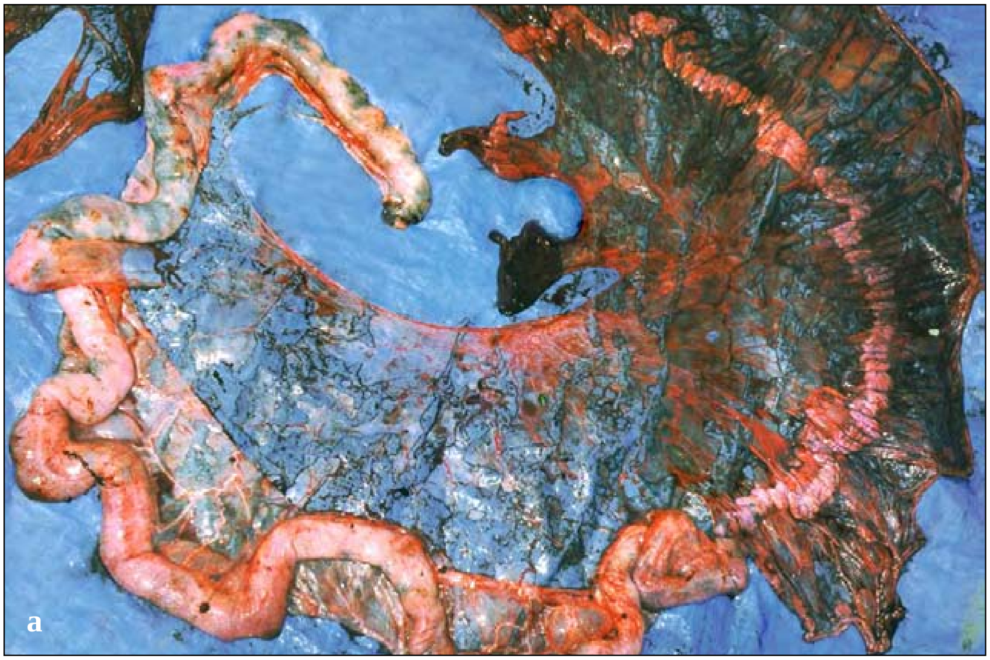
Figs. 225a and 225b. *Immature ovary and oviduct (ventral view). The immature ovary is thin and located more medially than the oviduct. The immature oviduct extends anteriorly then turns posteriorly. The ostium is formed at the expanded end. The oviduct, mesotubarium, and mesosalpinx are reflected laterally.*

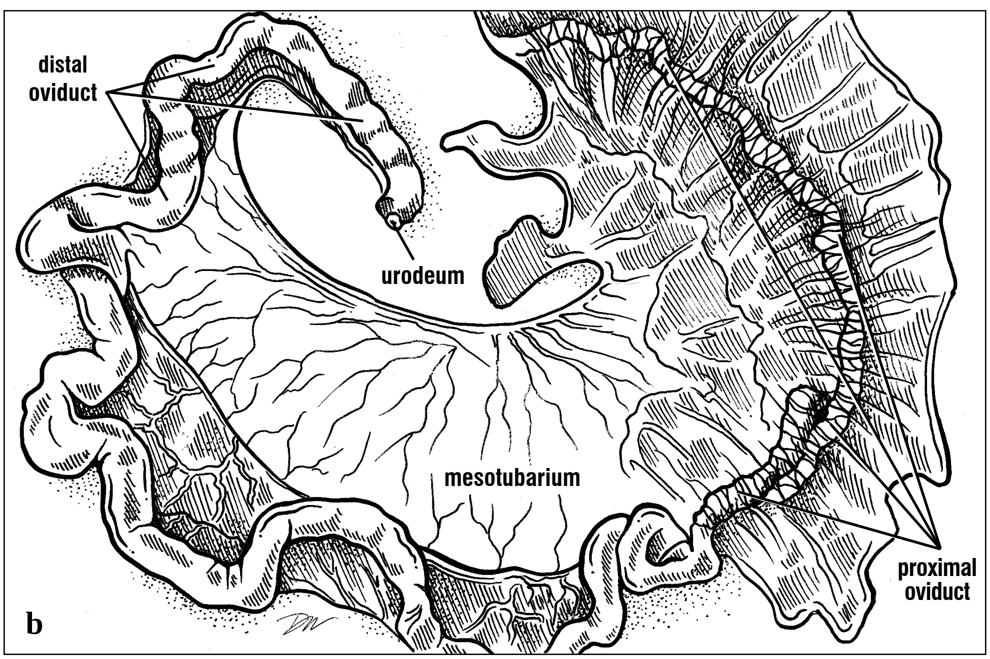
In hatchlings, the ovaries are difficult to distinguish from testes. If histology is unavailable, the attachment of the mesovarium to the ovary edge and the lack of a coiled vas deferens suggest that the gonad is an ovary. In older turtles, the gonad will be pink and will have a grainy texture as small follicles become more distinct. As turtles approach maturity, some follicles increase in size and start to accumulate bright yellow yolk. In sexually mature turtles, mature follicles tend to cluster along the cranial aspect of the ovaries. Immature follicles are most concentrated in the posterior third of the ovary. Mature turtles that have nested previously will have large follicles that are ~2-3cm in diameter and scars from previously ovulated follicles, **corpora albicans** (Fig. 226). Recently ovulated follicles leave active scars, each is called a **corpus luteum**. The corpus luteum becomes a corpus albicans after it ceases to produce the hormone progesterone. The ages of corpora albicans are difficult to judge, however larger ones are generally more recent than smaller ones. It is safest to use this information simply to determine if the turtle had nested previously or not.



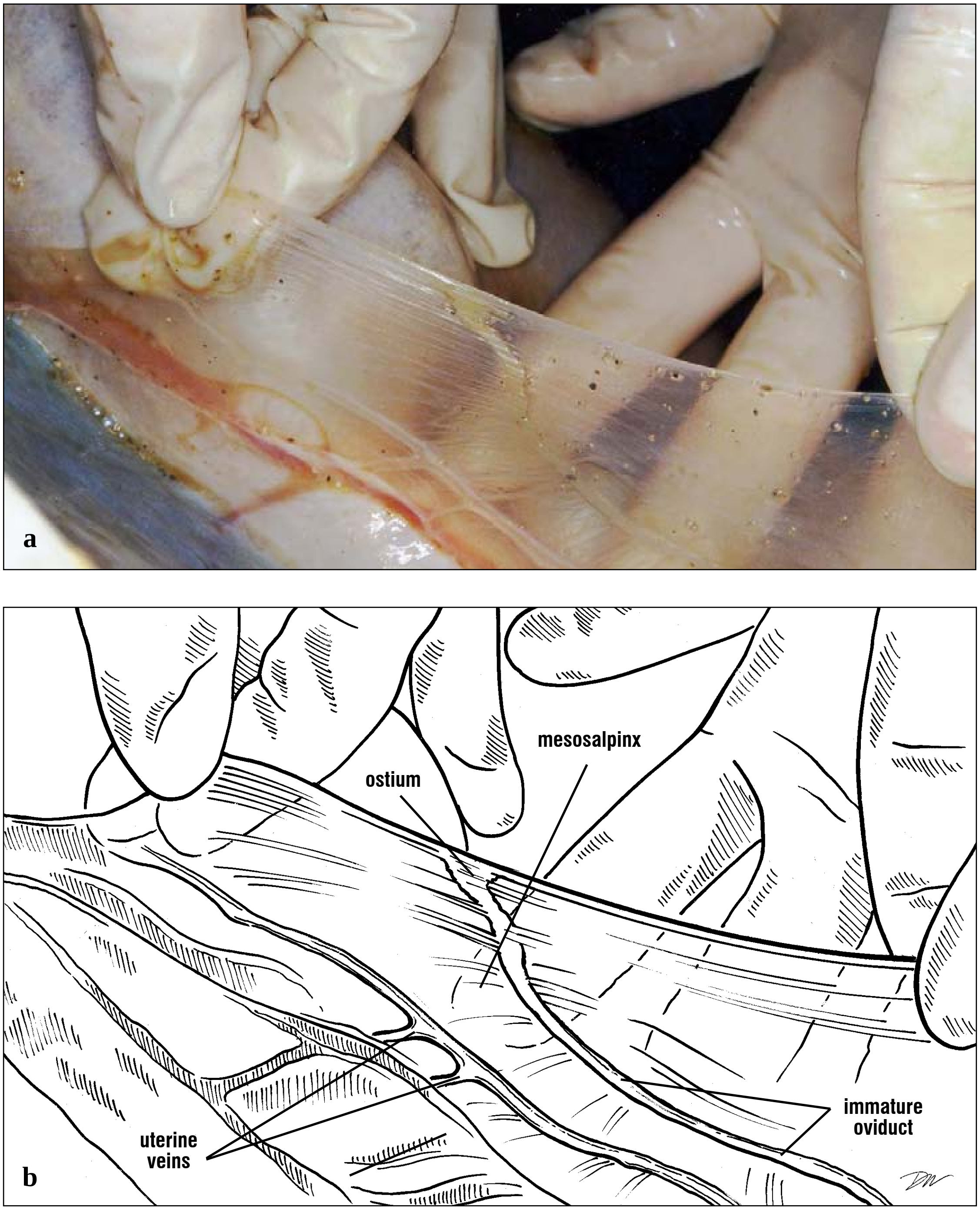
Figs. 226a and 226b. *Eggs, follicles, and corpora albicans in a reproductively active loggerhead. This oviduct holds shelled eggs. Above the oviduct are several sizes of maturing follicles and the scars (corpora albicans) remaining from the sites of ovulated follicles.*

The oviduct of immature turtles is a thin walled tube (Figs. 224-225). As females mature, the walls of the oviduct thicken and the lumen increases in diameter. It appears folded along its length when not active (Fig. 227). The oviduct can be described functionally (but not in gross structure) as having 5 regions: the ostium (or infundibulum), aglandular segment, magnum, shell gland, and vagina. The ostium remains thin-walled but increases in size (Figs. 228-229). The oviduct of mature females is muscular and mobile. It is assumed that the ostium migrates across the ovary surface collecting the ovulated follicles.

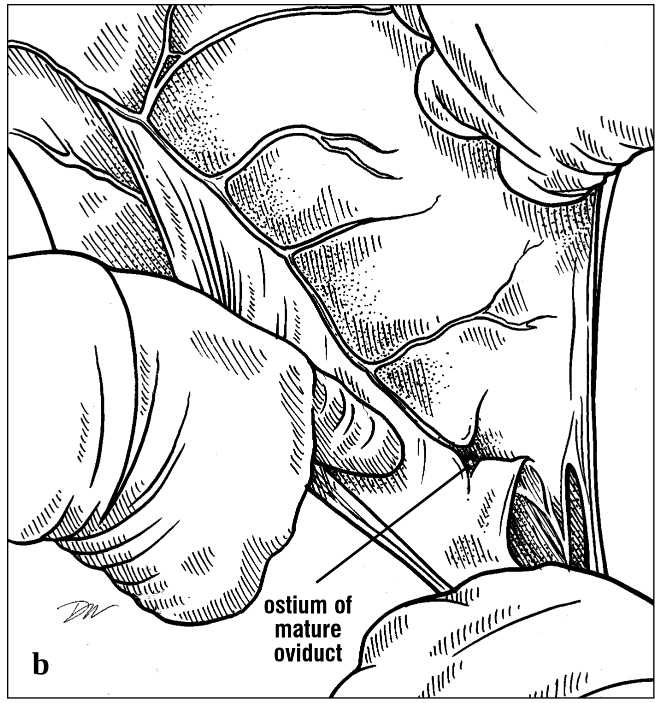




Figs. 227a and 227b. *Mature oviduct of a leatherback. The mature oviduct has a large lumen and the walls have undulatory folds. The mesosalpinx and mesotubarium enlarge to accommodate the mature structures. The distal ends would normally enter the cloaca. The proximal end is the site of the ostium.*



Figs. 228a and 228b. *The ostium of an immature oviduct. The ostium is flattened when not active; the funnel-shaped opening is small in young turtles.*



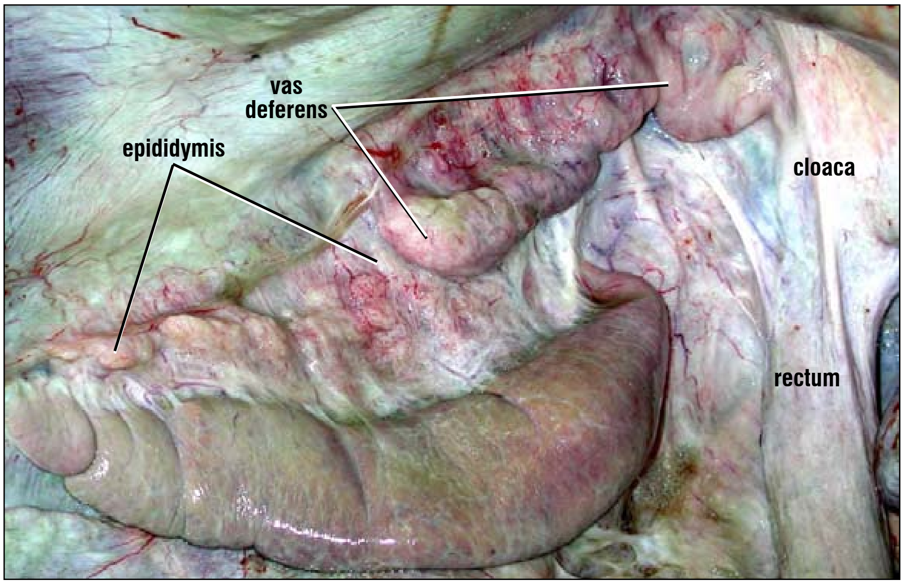
Figs. 229a and 229b. *The ostium of a mature oviduct. The ostium of this leatherback's oviduct is large, funnel-shaped and thin walled. The base of the ostium opens into the aglandular part of the proximal oviduct.*

In preparation for nesting, an entire clutch of follicles matures and ovulates together. Once in the ostium, each follicle travels past the aglandular segment and into the magnum (anterior glandular region) where it is coated with layers of albumen. After about 3 days, the follicles pass to the shell gland where the protein and carbohydrate shell membrane (chorion) and the aragonite shell matrix are secreted. The shell calcification takes about 6 to 7 days. Eggs pass to the vagina where they remain until deposition, several days later. During deposition, the posterior oviduct allows eggs to pass to the cloaca, then out the vent into the nest. The cloaca forms a tubular orifice in nesting turtles. The structures that form this "egg tube" are unknown.

<u>Males</u>: The male reproductive tract consists of paired **testes**, **epididymi**, **deferent ducts** (vas deferens = ductus deferens), suspensory ligaments (**mesorchium** from the body wall to the testis), and a single **penis**. Müllerian ducts may persist as a pair of small, flat, thin-walled tubes in some males. When present, they are located along the lateral body wall (suspended by a mesotubarium) from the duct to the testis or peritoneum overlying the kidney. They will often extend toward the anterior third of the body, lateral to the lung.

The testis is fusiform shaped (Fig. 222). The cranial pole is located just posterior to the lung; it extends posteromedially toward the cloaca. Along its dorsal surface, it is attached by the mesorchium to the peritoneum overlying the kidney. The testis is light tan or yellow in some species and gray to pink in others. Sperm are produced in the testis and are conveyed via very small efferent ductules to the epididymis, which lies lateral or posterolateral to the testis. The vas deferens leads from the epididymis to the cloaca at the base of the penis, demarked by the **corpra cavernosum** (Fig. 222). The testis, epididymis, and vas deferens change in size and form with age and between breeding and nonbreeding seasons (Fig. 230). Testes in mature breeding males are often twice as long as their diameter and filled with white fluid (sperm and accessory gland fluid).

The genital papilla elongates into the penis during maturation. The penis is retracted except during mating, trauma, or death; it lies in the ventral floor of the cloaca. It is composed of a pair of **corpora cavernosa** and a "**urethral groove**" (= sulcus spermaticus; Fig. 231). During mating, the corpora cavernosa are supplied with blood via the hypogastric and internal iliac veins. When erect, the walls of the urethral groove meet dorsally to form a functional tube through which sperm and fluids pass. Some species have ornamented structures (e.g., spines or flaps that have a triradiate form) on or near the glans penis at the distal tip (Fig. 232).



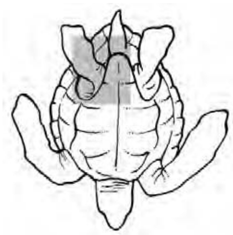


Fig. 230. *Mature loggerhead testis and accessory ducts (posteroventral view). The testes, epididymis, and vas deferens in a mature male during breeding season. The vas deferens lead to the base of the penis in the ventral floor of the cloaca.*

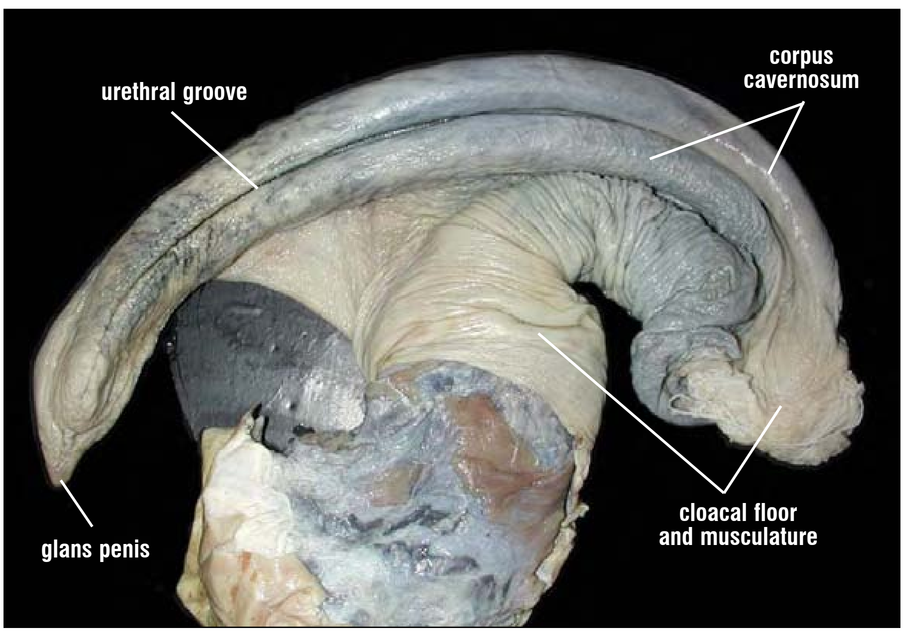
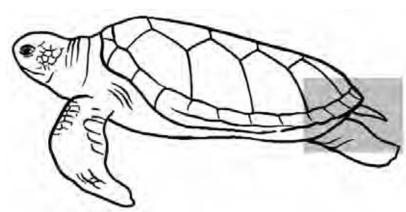


Fig. 231. *Adult loggerhead penis (dorsal view). The marine turtle penis is part of the ventral floor of the cloaca. The two corpora cavernosa function in penile erection and elongation. The urethral groove, between the two cavernous bodies conveys sperm during mating. The penis is completely housed within the cloaca when not erect.*

Fig. 232. *Tail and penis of a Kemp's ridley. The long tail and distally positioned vent are distinctive of adult male turtles. This animal has a semi-erect penis with a subterminal horn on the ventral lobe of the glans penis. Not all species have ornaments on the penis. Generally, maturing males have a more distally positioned vent than a female of the same body size. However, not all males start maturation at the same size, so the combination of tail length and cloacal position should be used with caution when identifying the sex of the turtle.*



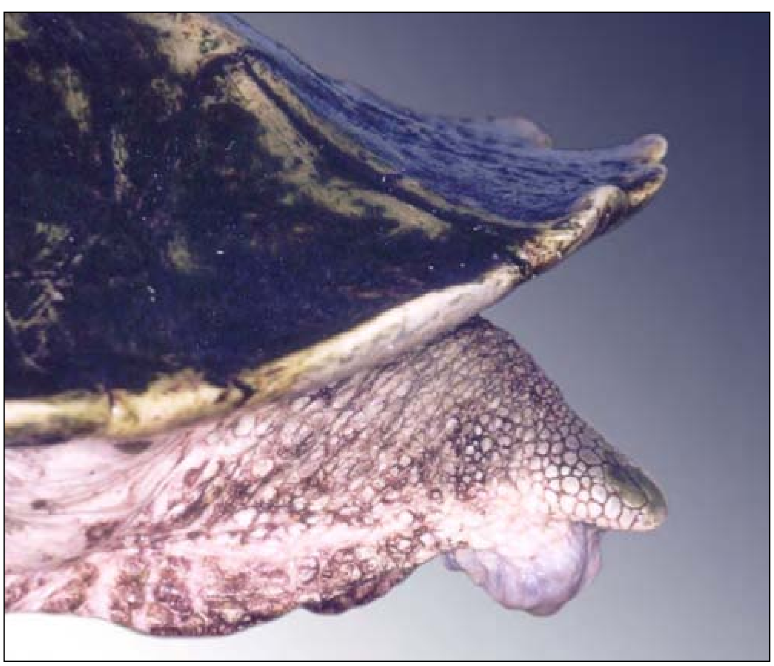


Fig. 233. *Tail of an adult female Kemp's ridley. The short tail and cloaca located proximally are characteristic of females and immature males. This female protruded the cloacal opening as is seen in nesting turtles.*

Sexual dimorphism. Adult females differ little in external morphology from large, immature males. Typically, females have a short tail and the cloacal opening (**vent**) is located roughly half way between the tip of the tail and the plastron's anal scute (Fig. 232). Within the cloaca, the genital papilla remains small as the clitoris on the floor of the cloaca. (Fig. 219).

In the Western North Atlantic, female loggerheads mature at an average SCL of 92 cm (range: 75-104 cm). Green turtle females mature and nest at an average SCL of 97 cm (range: 83-113 cm) and leatherback females are about 155 cm CCL (very few nesting females have been measured on U.S. beaches). The minimum size of a nesting female leatherback in the USVI was 133 cm CCL.

Adult males are characterized by a long tail with the cloacal opening near the tip, and strongly curved claws on the second digit. During breeding season, a decornification of the plastron occurs along and to each side of the midline (Fig. 233). The plastron becomes increasingly vascular and edematous. Male leatherbacks, have slightly concave plastrons. There is no evidence of decornification or increased plastral vascularization during leatherback breeding season.

Fig. 234. *Sexually mature male ridley. Male sexually dimorphic characteristics include an elongated tail, long curved claws, and, during breeding season, the midventral plastron becomes soft.*

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