tions, a fectorial membrane with spatially graded bulk, the position of the contact membrane at the posterior end of the chamber instead of along its medial margin, and possibly by the polarization of the hair cells. In anurans, such as Ascaphus truei (Fig. 14-15A), and presumably in salamanders and caecilians with a single patch of papilla amphibiorum, the frequency range of sensitivity is 100–600 Hz. Extension of this frequency range beyond 600 Hz seems to depend on the posterior elongation of the posterior patch of hair cells. This was shown to be the case in the elongate patch in Rana catesbeiana by E. Lewis et al. (1982), who determined the best excitatory frequencies for auditory stimuli of 29 afferent axons of the auditory nerve innervating the papilla amphibiorum. Forty axons with frequencies at or below 300 Hz terminated in the anterior region of the papilla; ten axons with frequencies of 400–550 Hz terminated in the central region; and five axons with frequencies of more than 550 Hz terminated in the posteriormost region.

**Equilibrium.**—The neuroepithelia and associated gelatinous cupulae of the crista ampulare and the maculae of the utriculus, saccus, and lagena are equilibrium receptors. According to the summary by E. Lewis and Leverenz (1982), in the semicircular ducts the viscosity and inertia of the endolymph apparently combine with the viscoelasticity of the cupulae to translate rotational motions about particular axes into stereociliary strain; at the same time, rotational motion about the orthogonal axes and linear motion along any axis are rejected. The calciferous masses of the otolithic maculae and the viscoelastic gelatinous membrane associated with each sensory patch apparently combine to translate linear motion into stereociliary strain. Directional selectivity in the maculae appears to be provided by the polarization patterns of the hair cells. Apparently the crista neglecta in caecilians also is a receptor for head motions (Wever and Gans, 1976).

**NERVOUS SYSTEM**

Although the nervous system of amphibians is somewhat more highly developed than that in fishes, amphibians retain the primitive pattern of nerve-cell bodies around the ventricles of the brain. In contrast to the everted forebrain of fishes, there is an invagination of the hemispheres in amphibians; this construction is like that of amniotes, which, unlike amphibians, have a definitive cerebral cortex. Amphibians have two meninges, a vascularized pia mater attached to the brain and spinal cord and a tough, outer dura mater adjacent to the bones.

Herein the classic regions of the nervous system are discussed in the following order—brain, cranial nerves, spinal cord and spinal nerves, and autonomic nervous system. Some developmental aspects of the nervous system are discussed in Chapter 7. Neurophysiology and ultrastructure are treated only in a general way; an extensive literature is available on these subjects (see Jørgensen, 1974; Llinás and Precht, 1976; and Okabe and Uech, 1976).

**Brain**

The morphology of the brain has been studied in Rana esculenta by Gaupp (1896); nearly all modern treatments of the gross morphology of the anuran brain are based on that work. Kuhlenbeck (1922) provided a detailed description of the brain of the caecilian Hypogeophis rostratus, and Kuhlenbeck et al. (1966) presented additional information on the forebrain of caecilians. The brain of
*Salamandra salamandra* was described by Francis (1934), and the most exhaustive study is that by Herrick (1948) on *Ambystoma tigrinum*. Noble (1931b) made general comparisons of the brains of the three living orders of amphibians.

**Forebrain.** The forebrain is differentiated into the telencephalon and diencephalon (Fig. 14-16). The telencephalon is composed of a pair of bilateral olfactory bulbs and cerebral hemispheres; it is shorter but farther invaginated in anurans than in salamanders and caecilians. The olfactory nerve (C.N. I) exits from the anteroverentral surface of the olfactory bulb in anurans and hynobid salamanders and from the anterolateral surface in other salamanders and caecilians; in the latter, the base of the nerve is comparatively massive. Each cerebral hemisphere is divided into a dorsal pallium and ventral subpallium; their distinction is marked by a sulcus on the inner surface of the ventricles and in anurans by a groove on the outer surface. In the subpallium, a medial septum is distinguished from lateral basal ganglia. Also, the pallium is differentiated into an internal hippocampus and external pyriform primordium.

Differentiation of an accessory olfactory lobe in the anterior part of the cerebral hemisphere occurs in caecilians and anurans; it is poorly developed in most salamanders and is absent in neotenic anurans. The degree of development of the accessory olfactory lobe is positively correlated with development of Jacobson’s organ, which is absent in neotenic salamanders. The amygdaloid

![Figure 14-16. Brain of *Salamandra salamandra*. A. Lateral (midsagittal section). B. Dorsal. C. Ventral. Cranial nerves are indicated by roman numerals. Abbreviations: gang = ganglion, r = ramus. Adapted from Francis (1934).](image-url)
nucleus (a prominence on the lower surface of the cerebral hemisphere) is correspondingly well developed in anurans and caecilians, as is the striatum (external tissue of the subpallium). The relative development of the latter also seems to be correlated with an increase in exteroceptive tracts.

The telencephalon is the receptor for sensory impulses derived from the olfactory epithelium of the nasal sacs and from Jacobson's organ. Although there is a concentration of olfactory fibers in the olfactory bulbs (and accessory olfactory lobes when present), all parts of the cerebral hemispheres receive impulses from the olfactory fibers. The septum and stratum are synaptic stations where olfactory fibers join with fibers from the thalamus and midbrain. A peripheral wandering of cells from the hippocampus and pyriform areas is most extensive in anurans. In amniotes, these cells lead to the development of cell laminae in the pallium separate from the periventricular cells; these laminae cells differentiate into correlation centers, whereas the periventricular cells remain pathways for relatively simple reflexes.

The unpaired posterior part of the forebrain, the diencephalon, consists of three major parts—epithalamus, thalamus, and hypothalamus. The epithalamus is composed of the habenular ganglia, a choroid plexus (a vascular invagination into the third ventricle), and the pineal organ. The habenular ganglia receive fibers from the telencephalon. A tract of olfactory fibers, the fasciculus retroflexus, extends posteroventrally from the habenular ganglia to the interpeduncular nucleus in the mesencephalic tectum; in salamanders, this nucleus projects posteriorly into the medullary tectum, but this projection has not been noted in anurans or caecilians.

The pineal organ (= epiphysis) is a small projection, best developed in anurans, attached to the dorsomedian surface of the epithalamus by a few fibers. These fibers contain the frontal and pineal tracts (parietal nerve), fibers of which enter the pretectal region in the posterior part of the epithalamus. The lateral and ventral walls of the diencephalon are constituted by the thalamus, which contains a web of connecting fibers with all contiguous parts of the brain, which make the thalamus an important center for sensory correlation. For example, even though the optic nerves enter the neurocranium and have a chiasma under the thalamus, these optic tracts pass posterodorsally to the optic lobes of the midbrain. However, on their way to the midbrain the optic tracts give off collateral fibers which synapse in the thalamus with fibers of other sensory systems.

Posterodorsally, the hypothalamus is a bilobate projection of the diencephalon. The hypothalamus is divided into preoptic and tuberoinfundibular regions. In addition to numerous connecting fibers with the ventral thalamus, the magnocellular preoptic nucleus is connected with the ventral lobe of the hypothalamus, and distinct areas of the parvocellular tuberoinfundibular nuclei are connected with the hypophysial portal vessels. The hypothalamus is an important center for control of the autonomous nervous system.

**Midbrain.** The midbrain, or mesencephalon, is made up of the dorsal tecta (optic lobes) and the basal tegmental or peduncular portion. The latter transmits motor impulses. The peduncular region receives fibers from practically all parts of the brain anterior to the midline; its primary function is to control mass movements of the body and limbs. Also, this is the site of origin of two eye muscles (C.Ns. III and IV).

The optic lobes and tissues composing the optic tectum are best developed in anurans and least developed in caecilians. In anurans, the tectum has white and gray strata. Fibers from the optic tract spread throughout the tectum. The function of the optic tectum is the visual control over movements of the body as a whole, and particularly the orientation of the body and conjugate movements of the eyeballs with reference to objects in the visual field.

Just below the optic lobes is the torus semicircularis. This subcortical cluster of cells is the principal receptor site for afferent auditory fibers from the bulbocerebellar tract in the cerebellum.

**Hindbrain.** The posterior part of the brain consists of the cerebellum and the medulla oblongata (rhombencephalon), which is continuous with the spinal cord. The cerebellum consists of paramedian dorsal protrusions and a more lateral pair of auricular lobes that are an anterior continuation of the acousticolateralis system of the medulla. The histological structure of the cerebellum of anurans is more complex than that of other amphibians. Anurans have a cerebellar nucleus and tracts to the peduncular region of the midbrain. Also, in anurans there is true lamination of cells and fibers, and the Purkinje cells (interlaminar flask-shaped cells) have a more definitive structure than in other amphibians.

In comparison with other vertebrates, the cerebellum is small, especially in terrestrial adult amphibians. It is the center for motor coordination, and the small size presumably is correlated with the comparatively simple locomotor activities of amphibians. The degree of development of the auricular lobes is correlated with the presence of a lateral-line system. Thus, larvae and neotenic salamanders have proportionately larger auricular lobes.

Situatated between the cerebellum and the medulla is the isthmus, a region which is distinct in early development, but which becomes incorporated into the anterior part of the medulla in adults. Afferent fibers coming from practically all parts of the brain terminate in the isthmus. Here, too, is the chief sensory nucleus of the trigeminal nerve (C.N. V). Efferent fibers from many centers converge in the isthmic tegmentum. The isthmic region is the chief regulator of the jaw musculature.

The medulla is the widened and flattened anterior part of the spinal cord, from which it differs by having a largely
membranous dorsal surface with a cluster of blood vessels, which forms as the choroid plexus a vascular diverticulum extending into the ventricle of the medulla. Like the spinal cord, the medulla is divided into a ventromedian motor region and a dorsolateral sensory region. The later is the acousticocerebral region, which merges with the auricular lobes of the cerebellum. Between the dorsal and ventral portions of the medulla is a region of synaptic junction of sensory and motor fibers. In the anterior part of this region in salamanders are the giant Mauthner cells which have axons that extend the length of the spinal cord to the caudal musculature; these fibers function in the regulation of swimming movements. Vestibular and (in larvae) lateral-line fibers have synapses with Mauthner cells.

In primitive tetrapods, more of the medulla was contained within the skull than in living amphibians, so that all 12 cranial nerves exited from the skull. In living amphibians, the hypoglossus nerve (C.N. XIII) is associated with the first spinal nerve. Of the 11 cranial nerves exiting from the skull, 7 (C.Nn. V–XII) enter the medulla and send afferent and efferent fibers to specific locations within the medulla. In the ventral motor portion of the medulla, the nuclei of the cranial nerve fibers are arranged in numerical order; this separation (particularly nuclei of C.Nn. VII, IX, and X) is more evident in anurans than in other amphibians. The sensory nuclei of C.Nn. V and VII are anastomosed in salamanders but not in anurans.

The medulla controls actions of swallowing, digestion, heartbeat, and respiration, as well as jaw action and some locomotor responses.

Fibers of the auditory nerve (C.N. VIII) enter the medulla as discrete branches through a dorsal root and a ventral root, where they become associated with a dorsal medullary nucleus of small cells and a ventral nucleus of large cells, respectively. Anurans are unique among anamniotes in having a pair of superior olivary nuclei, located on the ventral side of the medulla. Cells of the superior olivary nucleus receive input from the dorsal medullary nucleus and the contralateral superior olivary nucleus. Fibers from the dorsal medullary and superior olivary nuclei form the lateral bulbocerebral tract which extends anteriorly to the torus semicircularis of the midbrain. Anurans also have a large nuclear mass, the nucleus isthmi, in the tegmentum; it may have some auditory function. The function of the complex auditory receptor system in anurans is discussed in Chapter 4.

Finally, the medulla exits the cranium through the foramen magnum and becomes the spinal cord. Although there are nerve fibers from the medulla anteriorly into the midbrain and fibers from the forebrain posteriorly into the midbrain, there is no uninterrupted pathway from the forebrain to the spinal cord.

**Cranial Nerves**

The cranial nerves of amphibians have received only cursory attention for more than 50 years. In the most recent review of anurans, Nieuwenhuys and Odpal (1976:813) stated: “In this survey we have relied heavily on the exhaustive analysis of Gaupp (1896).” Gaupp’s work was on one species of anuran, *Rana esculenta*. Basic descriptive morphology of the cranial nerves of salamanders was done by Coghill (1902) on *Ambystoma tigrinum* and by H. Norris (1908, 1913) and by Francis (1934) on *Amphiuma means*, *Siren lacertina*, and *Salamandra salamandra*, respectively. The work of earlier authors is reviewed by H. Norris and Hughes (1918) in their description of the nerves in a few species of caecilians.

In the following synopsis, which is based entirely on the literature concerning a few species, the cranial nerves (C.N.) are described; unless specified otherwise, the description is applicable to all three living orders.

**C.N. I (Olfactory).** The first visceral sensory nerve leaves from the ventrolateral border of the olfactory lobe and passes through the fenestra olfactoria into the nasal capsule where it divides into the ramus profundus and the ramus dorsalis. Fibers of the ramus dorsalis enter the olfactory lobe proper and are connected via olfactory tracts with secondary olfactory centers in the cerebral hemisphere. The fibers of the ramus profundus extend posteriorly into the accessory olfactory bulbs. The ramus dorsalis innervates the olfactory epithelium of the nasal sac. The main branch of the ramus profundus innervates the vomeronasal epithelium of Jacobson’s organ, and the ramus medialis nasi pierces the roof of the nasal capsule to supply the skin of the dorsal snout. Various other branches of the ramus profundus seem to be homologous in the living orders, although different names have been used (Jurgens, 1971). The principal variations in these are: (1) the branches in Xenopus are similar to those of salamanders (Paterson, 1939), (2) Cryptobranchus is different from other salamanders in that the ramus lateralis nasi does not enter the nasal capsule secondarily, and (3) in caecilians the ramus lateralis nasi innervates the tentacular sheath, and the ramus medialis nasi is divided into two main branches.

**C.N. II (Opticus).** This somatic sensory element actually is part of the brain. It enters the floor of the diencephalon where it crosses with its contralateral counterpart to form the optic chiasma. After crossing, the nerve ascends the lateral wall of the diencephalon as an external bundle of fibers, the tractus opticus. Most of these fibers spread in the superficial layer of the roof of the midbrain, but smaller contingents terminate in the thalamus, hypothalamus, and tegmentum of the midbrain. The optic nerve exits the neurocranium via the large optic foramen (or fenestra), which is an hiatus between the sphenethmoid and prootic. The nerve is covered by a fibrous connective-tissue sheath and is continuous with the layer of nerve cells on the inner surface of the eye. In caecilians in which the eye is covered by skin (e.g., *Demorphis, Geotrypetes, Ichthyophis*), the optic nerve is
rudimentary; it passes from the optic foramen, along the retractor muscle of the tentacle, and through the orbital glands to the eye. In caecilians in which the eye is vestigial and covered by bone (e.g., *Caecilia, Oosomecaecilia*), the optic nerve is absent. The optic nerve is greatly reduced in diameter in subterranean salamanders; the nerve is continuous with the brain in *Proteus* and *Haideotriton* but usually not in *Typhiotriton* (Brandon, 1968).

**C.N. III (Oculomotorius).** The fibers of the third nerve emerge from the ventral surface of the mesencephalon and exit the neurocranium via the oculomotor foramen just posterior to the optic foramen. The bulk of the nerve consists of somatic efferent fibers that innervate four eye muscles. Within the orbit the nerve divides into two rami; the ramus superior innervates the m. rectus superior, and the ramus inferior innervates the m. obliquus inferior and the mm. rectus inferior and anterior. Close to the point of division of the somatic rami, a smaller bundle of fibers belonging to the visceral afferent category forms the ramus communicans to the ramus ophthalmicus profundus (C.N. V); after synaptic interruption in the ganglion ciliare, the fiber bundle innervates the intrinsic eye muscle, the smooth m. sphincter pupillae. In caecilians having the eye covered by skin, the efferent nerves are reduced (*Dermophis* or vestigial *Ichthyophis*), whereas they are absent in caecilians in which the eyes are covered by bone. There is no connection of the oculomotor with the trigeminal (C.N. V) in caecilians.

**C.N. IV (Trochlearis).** This somatic efferent nerve originates ventromedially in the posterior part of the mesencephalon, passes dorsally in a deep groove (cerebellomesencephalic fisure), crosses with its contralateral counterpart in the anterior medullary velum, and exits the cranium via the optic foramen or a small, oblique foramen anterodorsal to the optic foramen. This nerve supplies a single eye muscle, the m. obliquus superior. Francis (1934) discussed variation in this nerve in sala-manders, noting that in *Salamandra* the nerve divides before or after leaving the cranium; the smaller branch innervates the m. obliquus superior, and the larger one anastomoses with the ramus ophthalmicus profundus (C.N. V). In at least some caecilians with the eye covered by skin (e.g., *Dermophis, Hypogeophis*), a thin trochlear nerve is present, but it has not been observed in others.

**C.N. V (Trigeminus).** The trigeminal originates from the lateral surface of the medulla and exits the cranium via the large prootic foramen, which contains the Gasserian ganglion, from which branches of the trigeminal nerve arise. The largest branch, the sensory ramus ophthalmicus profundus, contains somatic afferent fibers. This ramus actually arises from a second ganglion (ophthalmic ganglion) in caecilians; in all amphibians it bifurcates into six major branches that innervate the skin on the snout, top of the head, and facial region, as well as penetrate the eyeball (superior and inferior ciliary rami). A ventral branch anastomoses with the ramus palatinus (C.N. VII) and innervates the tissues of the mouth under the nasal organs; this anastomosis is absent in caecilians. Shortly after leaving the Gasserian ganglion, the ramus maxillo-mandibularis, which contains both visceral motor fibers and somatic sensory fibers, bifurcates. The ramus maxillaris has three major branches; two of these supply the skin of the eyelids and the temporal region of the head, whereas motor fibers innervate the eye muscle, m. levator bulbi (except in caecilians, all of which lack this muscle). The ramus mandibularis also contains somatic sensory and visceral motor fibers; it divides into three major branches. One of these supplies the m. levator mandibulae, and another innervates the skin over the angle of the jaw and the posterior mandible. The primary mandibular branch divides into a ramus mentalis, which innervates the dentary and skin along the anterior part of the mandible, and the ramus intermandibularis, which supplies sensory fibers to the skin between the rami of the jaws and motor fibers to the mm. intermandibularis and submentalis. In the caecilians, the m. compressor glandulae orbitais is innervated by the ramus mandibularis (Badenhorst, 1978), which is partially anastomosed with the ramus maxillaris. A branch of the latter innervates the tentacular sheath in caecilians.

**C.N. VI (Abduens).** This somatic motor nerve arises from the ventral surface of the medulla and exits the neurocranium via the optic foramen in anurans and caecilians and via a separate foramen abduens in salamanders. In the orbit the nerve bifurcates, each ramus innervating one of two eye muscles, the mm. rectus lateralis and retractor bulbi. In caecilians, the nerve innervates the retractor muscle of the tentacle, which is homologous with the m. retractor bulbi of other amphibians. In those caecilians having the eye covered by skin (e.g., *Ichthyophis*), the m. rectus lateralis is present and innervated by the abducens, whereas in those caecilians in which the eye muscles are degenerated, that branch of the abducens is absent.

**C.N. VII (Facialis).** The slender facial nerve originates on the ventrolateral surface of the medulla and exits the neurocranium through a foramen into the cavity formed by the tripodial attachment of the palatoquadrate (salamanders) or quadrate (anurans and caecilians). It is composed of branchiomotor and visceral efferent fibers. The facial nerve is closely associated with the auditory nerve (C.N. VIII) within the neurocranium. Outside the neurocranium the nerve passes anteriorly to the Gasserian ganglion. From that point the ramus palatinus extends anteriorly and innervates the roof of the mouth; it anastomoses with the ramus ophthalmicus profundus (C.N. V) in salamanders and anurans. Also, the Harderian glands in the orbit and the intermaxillary gland in the roof of the mouth are innervated by the ramus palatinus. The major part of the facial nerve consists of the truncus hyo-mandibularis, which exits between the otic and basal
C.N. VIII (Auditory). The auditory nerve is made up primarily of special somatic afferent fibers, but it also contains some efferent axons that exert an inhibitory influence on the spontaneous activity of the vestibular afferent fibers in anurans. Although these different fibers leave the lateral surface of the medulla, they maintain their integrity anteriorly to the torus semicircularis below the optic ventricle of the midbrain. In salamanders and caecilians, the auditory nerve is intimately associated with the facial nerve in the otic capsule. In salamanders, the two nerves have a common acoustic-facialis ganglion, but in caecilians the auditory nerve seems to have a separate but poorly developed ganglion. In anurans, the auditory nerve remains distinct from the facial. The auditory nerve trifurcates and enters the auditory capsule via three foramina in salamanders, but has only two rami (and foramina) in anurans and caecilians. The ramus anterior innervates the utriculus and ampullae of the anterior and lateral canals (also the sacculus in anurans). The ramus posterior innervates the ampullae of the posterior canal, the papilla lagena, and the papilla amphibiorum in all three orders; in caecilians, this branch also innervates the sacculus, and in anurans, the papilla basilaris. The sacculus is innervated by a ramus medianus in salamanders.

C.N. IX (Glossopharyngeus). This small nerve consisting of branchiomotor and visceral efferent and afferent fibers arises directly in front of the first root of the vagus (C.N. X) on the lateral wall of the medulla. Both nerves exit the neurocranium via the postotic foramen immediately posterior to the otic capsule, where they form a large glossopharyngeal-vagus ganglion. Except in caecilians, one branch of the glossopharyngeal passes anteriorly to communicate with the facial nerve (C.N. VII). Branchiomotor fibers of the ramus muscularis innervate the m. subarcualis rectus I. The dorsal buccal mucosa is innervated by visceral afferent fibers of the ramus pharyngeus, and the tongue by the same kind of fibers in the ramus lingualis, which also probably supplies special visceral afferent fibers to the taste buds of the tongue.

C.N. X (Vagus). The origins of the vagus, glossopharyngeal, and accessory nerves are difficult to distinguish in amphibians. Different authors recognize two to four roots of the vagus, but apparently only two exist; the others represent the roots of the glossopharyngeal and accessory nerves. The vagus and glossopharyngeal (C.N. IX) exit the neurocranium via the postotic foramen; once outside the cranium the two nerves form a common glossopharyngeal-vagus ganglion (also apparently incorporating the accessory nerve). The vagus consists of branchiomotor and visceral efferent fibers; the latter constitute the main peripheral path of the parasympathetic system. The branchiomotor fibers innervate three throat muscles—mm. transversus ventralis, cephalo-dorsal-sobrygues, and subarcualis rectus I. Sensory fibers supply the mucosa of the mouth and pharynx. A ramus auricularis provides afferent fibers to the tympanic region in anurans and salamanders. Various branches of the main part of the vagus, the laryngeus ventralis, innervate the smooth muscles and glands of the esophagus and stomach, as well as the muscles of the lungs and heart.

C.N. XI (Accessorius). This small motor nerve emerges from the lateral wall of the medulla with the roots of the vagus. It innervates a single pectoral suspensor muscular, the m. eculiarius.

C.N. XII (Hypoglossus). The primordia of this nerve are in the first and second spinal nerves, but this nerve contains fibers which represent the hypoglossal nerve in amniotes; therefore, it can be considered with the cranial nerves. It exits from the spinal cord either through a foramen in Presacral I (salamanders and caecilians) or through an intervertebral foramen between Presacrals I and II (anurans). This nerve innervates the muscles associated with the tongue—mm. geniohyoides, genioglossus, hyoglossus, and rectus cervicis.

Lateral-line Nerves. The lateral-line organs of larval amphibians and certain ones that are aquatic as adults (pump frogs and obligate neotenic salamanders) are innervated by branches of cranial nerves. Except for those groups mentioned, these nerves degenerate at metamorphosis. The ampullary organs and neuromasts of the snout are innervated by the ramus lateralis anterior of the facial nerve (C.N. VII), and the other parts of the lateral-line system of the head by the ramus lateralis posterior (and its many branches) of the vagus nerve (C.N. X). The fibers of these nerves enter the medulla at the same point as those of the auditory nerve (C.N. VIII).

Spinal Cord and Spinal Nerves
Details of the morphology and ultrastructure of the spinal cord in anurans were provided by Ebbsen (1976) and Sotelo and Grotlo (1976), respectively. The gross morphology of the spinal nerves in anurans is based on Gauthier's (1896) work on Rana esculenta, whereas that of Salamandra salamandra was described by Francis (1934) and that of caecilians by H. Norris and Hughes (1918).

Spinal Cord. The basic structure of the anterior part of the spinal cord is similar in the three living groups of amphibians. The cord is contained in the neural canal of the vertebrae and completely covered by bone of the imbricate neural arches, except in some anurans, in which
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nonimbriate neural arches leave portions of the spinal cord exposed. The dorsal surface is formed by nuclei where somatic afferent fibers terminate; the lower part of the cord is formed by visceral efferent cells, below which are somatic efferent cells. Axons from the medulla extend for varying distances along the cord. For example, in anurans, fibers from C.N. IX and X extend to the second and third spinal segments, from C.N. VIII to the sixth segment, and from C.N. V to the seventh segment. In salamanders, fibers of Mauthner cells extend from the medulla throughout the length of the spinal cord.

The spinal cord is uniform in size anterior to the sacrum except for the slight brachial and lumbar enlargements in the regions of the brachial and sciatic plexuses in anurans and salamanders. Posteriorly, the spinal cord diminishes in size in salamanders. In anurans, the cord terminates as such at the level of the sixth spinal nerve; succeeding nerves extend independently in the neural canal, and a slight, median cord terminates in the coccyx.

Spinal Nerves. Each body segment is supplied with a pair of spinal nerves. In anurans, each nerve exits the spinal cord intervertebrally, except the tenth and eleventh (if present) which exit via foramina in the coccyx. Vertebral fusion in some anurans (e.g., pipids and bufonids) results in the nerves exiting via foramina in the fused vertebrae. In caelatans, the nerves exit via foramina in the anterior vertebrae (vertebrae 1–3 in Typhlonectes to 1–20 in Ichthyophis) (M. Wake, 1980). The first spinal nerve always exits through a foramen in the first vertebra of salamanders, but the exits of the nerves in other vertebrae are variable (Edwards, 1976). In some salamanders (e.g., ophidids), all other spinal nerves exit intervertebrally, whereas in plethodontids all nerves exit through foramina in the vertebrae, and members of some other families are intermediate—some nerves are intravertebral and others are intervertebral.

With the exception of the first spinal nerve (S.N. 1), which has no dorsal root in adults (dorsal root and ganglion atrophy at metamorphosis), all spinal nerves have a dorsal root with a large dorsal root ganglion and a ventral root which fuses with the dorsal root just peripheral to the ganglion. At this point the small dorsal branch of the spinal nerve passes dorsally to innervate the skin and muscles of the dorsal trunk (also, dorsal lymph sacs in anurans). The large ventral branch of each spinal nerve innervates ventral and lateral skin and muscles of the body and the limbs. A ramus communicans extends from each ventral branch to the sympathetic nerve cord.

The number of body segments, and therefore the number of vertebrae is highly variable in amphibians. Most anurans have only 10 pairs of spinal nerves, although more than 20 are present in particular, all but 1 or 2 postaxial nerves are present in the tail during the absorption of the tail at metamorphosis. A small nerve, the occipital nerve, anterior to S.N. 1 is uncommon in anurans and salamanders, but in caelatans it has dorsal and ventral branches, as well as an anastomosis with the hypoglossal (C.N. XII). In all three groups, S.N. 1 innervates neck musculature, and the hypoglossal fibers (C.N. XII) innervate the tongue muscles.

Spinal nerves in the thoracic region are interconnected to form the brachial plexus. In Salamandra, the plexus is formed primarily by S.N. 3 and 4 with some contributions from S.N. 2 and 5. In salamanders primarily innervates muscles of the pectoral girdle, but a branch connects with S.N. 3. Prior to this fusion, S.N. 3 gives off the ramus supracarneous which innervates pectoral muscles. S.N. 3 receives a branch from S.N. 4 and becomes the extensor nerve, which bifurcates into two branches that innervate the extensor muscles of the forelimb. S.N. 4 has branches to thoracic muscles and to the m. rectus abdominis. After receiving a branch from S.N. 3, S.N. 4 gives off a branch to the m. pectoralis. Subsequently there is a fine branch from S.N. 5, after which the main branch of S.N. 4 enters the ventral part of the forelimb as the brachial nerve to innervate the flexor muscles.

The arrangement of nerves forming the brachial plexus is different in anurans. In Rana, the plexus is formed by S.Ns. 2 and 3, which have a connecting ramus; both nerves have branches to muscles of the pectoral girdle. The brachial nerve supplying the flexor muscles of the forelimb is derived from S.N. 2, and the extensors of the forelimb are innervated by S.N. 3. Thus, in the course of shortening the trunk region, a rearrangement of spinal nerves has occurred, with S.N. 2 in anurans assuming the brachial nerve that is a branch of S.N. 4 in salamanders.

Numerous experiments have shown that during development peripheral nerves will develop in transplanted limb buds (see Saxen and Toivonen, 1962; for review). For example, Detweiler (1927) showed that in salamander larvae a primordium transplanted to a more posterior portion of the body became innervated by the segment of the spinal cord juxtaposed to the transplant.

The sciatic or cranial plexus of nerves that innervate the hindlimb is formed in the vicinity of the sacral vertebrae in salamanders. In Salamandra, which has 16 presacral vertebrae, the plexus is formed by S.Ns. 16 and 17 with a contribution from S.N. 15. The latter has an obturator branch to the m. puboischiofemoralis, an iliohypogastric branch to the muscles of the lateral and ventral body wall, and a branch which anastomoses with S.N. 16. After receiving this branch, S.N. 16 gives off a branch to S.N. 17 and becomes the femoral nerve which innervates the extensor muscles of the hindlimb. S.N. 17 exits from the sacral vertebra and after receiving the branch from S.N. 16 becomes the sciatic nerve which innervates the flexor muscles of the hindlimb. Small ram of S.N. 14 and 18 also make contributions to the sciatic plexus.

Three spinal nerves form the sciatic plexus in anurans. In Rana, these are S.N. 7 which exits between Presacrals VII and VIII, S.N. 8 which exits between Presacral VIII
and the sacrum, and S.N. 9 which exits between the sacrum and the coccyx. S.N. 7 gives off an iliohypogastric branch to muscles of the lateral and ventral body wall; thus, it seems to be homologous with S.N. 15 in Salamandra. S.Nn. 7–9 extend posterior under the m. iliohypogastricus to the base of the hindlimb, where they form the sciatic plexus. S.Nn. 7 and 8 fuse, and this bundle anastomoses with S.N. 9, which receives a branch from S.N. 10. Just after the fusion of S.Nn. 7 and 8, the crusurals nerve branches off and enters the hindlimb to innervate the extensor muscles. The main branch from the plexus is the sciatic nerve, which with its many branches innervates the flexor muscles of the hindlimb. Brachial and sciatic plexuses are absent in caecilians.

The ventral branches of the spinal nerves between the brachial and sciatic plexuses are rather uniform; each gives off branches to the lateral and ventral musculature and to the skin. The same general pattern exists throughout the length of the body in caecilians and in the tail of salamanders. In anurans, S.N. 10 fuses with a branch of S.N. 9 to form an ischiococcygeal plexus, from which nerves pass to the bladder, cloaca, oviducts, and posterior lymphatic hearts. In primitive anurans, S.N. 11 anastomoses with the ischiococcygeal plexus.

Autonomic Nervous System
The autonomic nervous system is essentially the same in the three living orders of amphibians. Detailed descriptions of the system are given by Gaupp (1896) for Rana esculenta and by Francis (1934) for Salamandra salamandra. A brief description of the system in caecilians is provided by H. Norris and Hughes (1918).

The autonomic part of the peripheral nervous system innervates smooth muscles and glands; it has its own set of ganglia separate from the central nervous system but connected with it by communicating rami. Unlike the peripheral nerves of the central nervous system, motor neurons do not extend from the central nervous system to the innervated organs. Instead, the neurons terminate in peripheral ganglia where they synapse with the dendrites of cell bodies of the peripheral nerves that continue to the organs.

The autonomic nervous system consists of two parts—sympathetic and parasympathetic. Neurons of the sympathetic system leave the central nervous system via spinal nerves. A pair of sympathetic trunks ventrolateral to the vertebral column receive neurons from the central nervous system via communicating rami to sympathetic ganglia along this trunk; numerous communicating fibers exist between the two trunks. Synapses of the preganglionic and peripheral neurons occur in these ganglia. Small nerves leave the sympathetic trunk and follow major arteries to the visceral organs. These nerves tend to form intricate plexuses, such as the solar plexus formed by branches from Sympathetic Ganglia III–V and supplying the stomach and adjacent parts of the alimentary canal.

Neurons of the parasympathetic system leave the central nervous system via cranial nerves. Rami extend from the gasserian ganglion of C.N. V and the glossopharyngeal vagus ganglion of C.Nn. IX and X to the first sympathetic ganglion. A separate branch of C.N. X, the laryngeal ventrals (= pneumogastric), innervates smooth muscles in the lungs, heart, and stomach.

Sympathetic and parasympathetic fibers are carried in the same nerves, as are sensory fibers from the viscera to the central nervous system. The impulses of the sympathetic and parasympathetic fibers are antagonistic in their effects. For example, sympathetic impulses act to halt peristalsis in the gut, to tighten the sphincters in the gut, and to increase the rate of heartbeat; parasympathetic impulses have the opposite effect.

Interrelationships of Components
The complexities of the nervous system are becoming better understood through electrophysiological, developmental, and behavioral studies (see Llinás and Precht, 1976, for review). The reception of external stimuli has been discussed in the previous sections: Integument; Sense Organs. Reception of stimuli from the cranial or spinal nerves to correlation centers in the brain, which respond via motor pathways to the peripheral system. Both sensory and motor pathways of the brain arise from, and terminate on, a limited set of neurons in the spinal cord. These spinal neurons form the basic reflex arcs and are the only elements other than cranial nerves that transmit sensory information to the brain. Furthermore, the efferent pathways of the brain can affect organs of the body only via these spinal elements.

The pathways in the brain are numerous and complex; they are discussed in detail by Nieuwenhuys and Opdam (1976), Scalia (1976a, 1976b), and Sotelo (1976).

Circulatory and Respiratory Systems
The transportation of oxygen and metabolic products through the body is dependent on an effective system of ion binding, a pumping mechanism, and an efficient vascular system. These are the blood, heart, and the blood and lymph vessels, respectively. In contrast to other vertebrates, amphibians have diverse modes of respiration—pulmonary, branchial, or buccopharyngeal. Each of these modes involves different vascular systems to provide effective transport of oxygen from and carbon dioxide to the respiratory surfaces. Consequently, the circulatory and respiratory systems are discussed together.

Blood
The blood of amphibians is composed of plasma containing erythrocytes, leucocytes, and thrombocytes. Except for the erythrocytes, the other constituents are capable of passing out of the blood vessels into the lymphatic system. A thorough account of the structural and physiological properties of the blood in amphibians by Foxon
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(1964) is summarized here. In adults, hematopoiesis takes place mainly in the spleen, but in anurans erythrocytes also are formed in the marrow of the long bones at metamorphosis and upon emergence from hibernation. Granular leucocytes are formed in the liver in some adult salamanders and in the kidneys in proteins. Considerable differences exist in sites of hematopoiesis, as do physiological properties of the blood, between larvae and adults (see Chapter 7).

The red blood cells, erythrocytes, typically are nucleated and elliptical. There is a great range in size, and amphibians have the largest known erythrocytes. The greatest length is 40–70 μm in obligate neotenic salamanders; the largest are in *Amphiuma* (erythrocytes are larger in larvae than in metamorphosed amphibians). In anurans the length is 17.7–26.5 μm. Endoerythrocytes (erythroplasts) are rare in anurans, but as many as 5% of the erythrocytes are nucleated in plethodontid salamanders, and erythroplasts make up 95% of the total in *Batrachoseps attenuatus* (Emmel, 1924).

Counts of erythrocytes are roughly proportional to the size of the cells. In *Amphiuma means* the erythrocytes are 70 μm in length, and there are about 30,000/mm³, whereas comparable figures for some other species are: *Proteus anguinus* 58 μm, 36,000/mm³; *Necturus maculosus* 54 μm, 51,000/mm³; *Rana catesbeiana* 25.5 μm, 460,000/mm³; and *Hyla versicolor* 20.7 μm, 900,000/mm³ (Szwarc and G. Czopek, 1966).

Distinct biochemical differences exist between hemoglobins in larvae and those in adults (see Chapter 7: Other Biochemical Changes). Hemoglobins in metamorphosed amphibians have a lower affinity for oxygen than larval hemoglobins, but they release oxygen more readily at the oxygen tensions that prevail in the tissues of terrestrial adults.

The white cells are made up of agranular leucocytes (lymphocytes and monocytes) and granular leucocytes (basophils, neutrophils, and eosinophils). Normally all of these cells are nucleated, but enucleated cells occur in salamanders. The ratio of leucocytes to erythrocytes is 1:20–70. The size of leucocytes is relatively constant at a length of 30–32 μm. Foxon (1964) noted that comparative counts of the number of granular and agranular leucocytes is known for only a few species; he listed *Bombina variegata* as having 25% granular and 75% agranular leucocytes, and *Salamandra atra* as having 65% granular and 35% agranular leucocytes.

Thrombocytes or spindle cells typically are nucleated, but enucleated cells (thromboplastids) have been reported in some species of salamanders. These cells presumably function like the platelets in mammals.

**Heart and Aortic Arches**

The structure and function of the heart have been discussed in detail by J. Simons (1959), Foxon (1964), and Kumar (1975). Usually the heart of amphibians has been described as being composed of three chambers—two atria and one ventricle. However, a septum dividing the ventricle into right and left chambers is known in some salamanders (*Siren* and *Necturus*) (J. Putnam and J. Dunn,

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*Figure 14.17. Ventral view of the heart of an anuran, *Rana catesbeiana*, partly sectioned in the frontal plane to show internal structure. The circulatory pathway of oxygenated blood is indicated by solid arrows and that of deoxygenated blood by broken arrows. Adapted from W. Walker (1967).*
Integumentary, Sensory, and Visceral Systems

1978), and some caecilians (e.g., Ichthyophis and Hypogphys) have extensive trabeculae in the ventricle (Rameswami, 1944; Lawson, 1966).

Although the hearts of the three living orders of amphibians are similar in gross morphology (Fig. 14-17), there are differences in relative proportions and in the internal structure. In most salamanders and anurans the left atrium is much smaller than the right, but in some anurans (e.g., Xenopus) the two atria are about equal in size. In caecilians, the right atrium is much smaller than the left. Anurans have a complete interatrial septum, and the septum is fenestrated in caecilians and all salamanders except Siren. In plethodontid salamanders the atrial division consists of a membranous septum and a sinoatrial valve (J. Putnam and D. L. Kelly, 1978). The sinus venosus is divided into right and left portions by indentations of the wall of the sinus or by a pair of transverse valves in caecilians, and by constrictons of the inner wall in anurans; there is no division of the sinus venosus in salamanders. A sinoventricular fold is present in salamanders but not in caecilians or anurans.

A conus arteriosus receives blood from the left atrium and becomes the median truncus arteriosus. Within the conus is the spiral valve which is absent in at least some plethodontid salamanders (Nel, 1970). The aortic arches divide from the truncus arteriosus. The truncus is short in salamanders, exceedingly short in anurans, and greatly elongate in caecilians. The aortic arches of adults are derived from the visceral arches (V.A.) of larvae; the first two visceral arches are lost. Only some salamanders have a full complement of aortic arches as adults. The carotid arch (V.A. III) delivers blood to the head. The systemic arch (V.A. IV) delivers blood to the body, including parts of the head but excluding the pharynx and lungs (and to a varying extent the skin). The third arch (V.A. V) is separate proximally but becomes confluent with the systemic arch in Salamandra and with the pulmonary arch in Necturus; it is small and not connected to other arches in Cryptobranchus and Amblystoma, and it is absent in adult plethodontids (J. Putnam and Sebastian, 1977). The pulmonary arch (V.A. VI) supplies the lungs and the walls of the pharynx; cutaneous branches also supply skin, but this branch is reduced or absent in plethodontid salamanders. Only three arches persist in anurans; the third arch is absent.

Elongation of the body and reduction of the left lung have resulted in some modifications of the aortic arches of caecilians. Only two arches persist: the third is absent, and the carotid and systemic are fused. Usually two systemic-carotid arches and two pulmonary arteries arise from the long truncus arteriosus. After the divergence of the carotid arteries, the systemic arteries extend posteriorly to merge into the median dorsal aorta in most caecilians (Fig. 14-18). In others (e.g., Dermophis) the two systemic arteries unite anterior to the heart to form the dorsal aorta. Asymmetrical reduction of the arches is known in some genera. For example, only the right systemic arch persists in Harpela and Chthonerpeton and only the left in Hypogphys. In some caecilians, such as Ichthyophis, the right pulmonary artery is larger than the left. In Geogeneophis the left pulmonary artery is absent; the small left lung is supplied by a branch from the right pulmonary artery.

The tissues of the heart obtain nutrients and oxygen from the blood passing through the organ. In addition, caecilians have a network of coronary veins covering the ventricle; blood in these veins is derived from the cavity of the ventricle and passes into the sinus venosus. Foxon (1964) suggested that these veins supply the muscular wall of the ventricle and that this system of coronary veins suggests that this system of coronary veins argues for a mixing of oxygenated and deoxygenated blood in the ventricle.

Major modifications of the aortic arches take place during metamorphosis with the change from branchial to pulmonary or cutaneous respiration; these changes are more dramatic in the lungless plethodontid salamanders and far less noticeable in the perennibranchiate neotenic salamanders (Fig. 14-19). In larvae, the carotid arch supplies the internal gills; it and the systemic and third arches also supply the external gills. In cryptobranchid and protoid salamanders a carotid duct exists between the affer-
ent branches of the carotid and systemic arches. The pulmonary arch does not enter a gill, but it may be connected to the third arch by a duct (ductus Botalli). This duct is variably present in salamanders; it is present in cryptobranchids, present or reduced in salamandrids and ambystomatids, and absent in proteids and plethodontids (McMullen, 1938). During metamorphosis, anastomoses form between the efferent and afferent branches of each branchial arch; as the gills are resorbed, the anastomoses take over the entire blood flow.

In amphibians blood leaves the single ventricle by routes which may lead to the head, body, skin, or lungs (except in the lungless plethodontid salamanders). Blood returning from the head, body, and skin enters the left atrium via the sinus venosus, and from the lungs enters the left atrium via the pulmonary vein (Fig. 14-17). The skin is an important respiratory surface in many amphibians, but blood that has been oxygenated there is mixed with blood from the body in the right atrium. Thus, as emphasized by Foxon (1964), the circulatory arrangement in amphibians may be expected to show marked specialization correlated with their peculiar respiratory methods.

The detailed description of cardiac respiration of Rana temporaria provided by J. Simons (1959) shows that little mixing takes place as blood passes from the atria to the ventricle. The destination of any particular blood corpuscle on leaving the ventricle is determined largely by its position in the ventricle. Thus, blood from the left side of the ventricle passes up one side of the spiral valve in the conus arteriosus into the carotid arteries and the right systemic arch; simultaneously, blood from the right side of the ventricle passes mainly up the other side of the spiral valve and into the left systemic arch. During the early part of ventricular systole, a stream of blood flows over the spiral valve from the cavum aorticum into the cavum pulmocutaneum and on into the left systemic arch; thus, some oxygenated blood goes into that arch. The slight differences in pressure among the aortic arches are insufficient to regulate the flow of blood from the ventricle.

The foregoing account of the flow of blood in the heart and aortic arches may be typical of terrestrial anurans, but a different pattern is evident in the aquatic Xenopus, which relies more on pulmonary than on cutaneous respiration (De Graaf, 1957). In Xenopus blood returning from the lungs passes to all parts of the ventricle. Upon ventricular contraction, the blood is distributed to carotid, systemic, and pulmocutaneous arches. Despite this apparent mixing in the ventricle, most blood returning to the right atrium passes into the pulmocutaneous artery, which has a much lower diastolic pressure than the carotid and systemic arteries.

Studies on cardiac circulation in salamanders have provided conflicting interpretations. Segregation of oxygenated and deoxygenated blood takes place in Amphiura tridactylus, but no differential distribution occurs in Salamandra salamandra or Triturus cristatus (Foxon, 1964). Differential distribution may be especially important in aquatic salamanders (e.g., Amphiura and Siren) living in poorly oxygenated water, and presence of a ventricular septum in Siren (also a complete interatrial septum) and in Necturus indicates that differential distribution may be complete in those salamanders. The presence of a sinoatrial valve that controls blood flow between the atria seems to be associated with the loss of the pulmonary vein in plethodontid salamanders.

No experimental data are available on cardiac circulation in caecilians, but on the basis of morphology it seems most likely that mixing of oxygenated and deoxygenated blood takes place in the ventricle. However, the extensive ventricular trabeculae may function in partial segregation of the blood as it is pumped out of the ventricle.
Vascular System

The arrangement of arteries and veins has been described for Rana esculenta by Gaupp (1896), Xenopus laevis by Millard (1941), and Salamandra salamandra by Francis (1934); some general patterns in caecilians were given by Wiedersheim (1879). Obviously, only gross differences and similarities in the vascular systems of the three orders can be addressed here; furthermore, with the exception of the components of the aortic arches, little is known about the variation in the pattern of vessels within groups. For example, Millard (1941) pointed out differences in the vessels in the pelvic region between X. laevis and R. esculenta, and Szercli (1948) noted numerous interspecific differences in the vessels of the facial and pelvic regions among anurans. The presence of adequate descriptions of only a few species is complicated further by a multiplicity of names and inadequate knowledge of homologies. Consequently, the following commentary is very general and is intended only to serve as an introduction to the major aspects of the vascular system.

Arteries. As noted in the preceding discussion of the heart and aortic arches, profound differences exist in the number and arrangement of the aortic arches. The arteries are discussed in relation to the aortic arches from which they are derived (Fig. 14-20).

Carotid system.—The left and right common carotids originate from their corresponding systemic-carotid axes in caecilians, or from the persisting arch in those taxa in which one of the arches has been lost. The common carotids originate from their corresponding arches in salamanders and primitive anurans (leioptelmatis, discoglossids, and pipids); both carotid arteries originate in association with the left systemic arch in other anurans. Immediately before the divergence of the internal and external carotid arteries there is an enlargement of the common carotid in anurans and salamanders. This enlargement, the so-called carotid gland, contains a membranous labyrinth and apparently functions to divert blood into the external carotid artery which diverges at an obtuse angle from the common carotid. No carotid gland exists in caecilians, in all of which the two carotid arteries diverge in an anterior direction.

The external carotid artery delivers blood to the muscles of the tongue and the floor of the mouth via four major branches: (1) muscular artery to the mm. rectus cervix and interhyoideus posterior, (2) thyroid artery to the thyroid gland, (3) sublingual artery to the tip of the snout where branches go to the tongue and the m. geniohyoideus, and (4) lingual artery to the tongue.

The internal carotid artery supplies the upper jaw and cranium, which it enters by way of the carotid canal and the basicranial fenestra. The major branches are: (1) cerebral artery with many branches supplying the choroid plexuses of the brain, (2) lateral preotral (= stapedial) artery to the ear with branches to the eye-lids (temporal artery) and to the roof of the mouth (mandibular artery), and (3) ophthalmic artery. The latter exits the cranium via the oculomotor foramen; branches supply the eye, the eye muscles, and the eyelids. An anterior branch of the ophthalmic anastomoses with a branch of the occipital (= palatonasal) artery and enters the nasal capsule.

Systemic system.—The systemic arches extend anteriorly and then posteromedially to unite in the dorsal aorta; this unification is anterior to the heart in salamanders and usually just posterior to the heart in anurans. Several arteries diverge before the arches meet to form the dorsal aorta. The cutaneous artery supplies the thymus and parotid region. In salamanders the pharyngeal artery supplies the jaw muscles and the hyoid muscles; the mandibular branch supplies the lower jaw. In most anurans these structures are supplied by the auricular branch of the cutaneous magna artery which originates from the pulmonary arch. The occipital-vertebral artery in anurans divides into an occipital artery that extends anteriorly into the head and the vertebral artery that bifurcates and extends posteriorly on either side of the vertebral column. The occipital is the same as the palatonasal in salamanders, in which it and the vertebral artery have separate origins from the systemic arch. The occipital has several branches: (1) pharyngeal to walls of the pharynx, (2) pterygoid to the roof of the mouth, (3) maxillopalatine to the roof of the mouth and posterior region of the maxilla, and (4) anterior and posterior palatines to the palate. A final branch of the occipital artery is the orbitonasal, which passes below the eye muscles in salamanders and dorsal to those muscles in anurans. The orbitonasal has three nasal branches to the nasal capsule, two maxillary branches to the upper jaw, and an anterior orbital branch which anastomoses with a branch of the ophthalmic branch of the internal carotid artery. Posteriorly, the vertebral arteries have numerous small branches to the dorsal trunk musculature and to the skin on the dorsum.

The arteries supplying the organs in the coelom normally all emerge from the dorsal aorta. The large coeliacomesenteric artery originates just posterior to the confluence of the systemic arches; however, it emerges from the left systemic arch in most anurans but from the dorsal aorta in leioptelmatis, discoglossids, and pipids. This artery has many branches that have been given diverse names and seem to be variable in their arrangement; the terminology of Francis (1934) is followed here. The three major branches are: (1) gastro-epi- to the spleen and dorsal wall of the stomach, (2) duodeno- hepatic with many branches to the liver, duodenum, ventral wall of stomach, and gall bladder, and (3) duodeno- pancreatic to the pancreas and duodenum. Four to eight (in Salamandra) anterior mesenteric arteries originate from the dorsal aorta and supply the distal part of the small intestine, and three posterior mesenteric arteries deliver blood to the large intestine.
The arteries supplying the urogenital system consist of numerous small vessels to the gonads, oviducts, and kidneys. Each kidney is supplied by numerous, short renal arteries from the dorsal aorta to its dorsal surface; whereas its ventral surface is supplied by the superficial renal artery which emerges from the posterior oviducal artery just posterior to the kidney. Three oviducal arteries deliver blood to the anterior, middle, and posterior parts of the oviduct. The mesal and posterior oviducal arteries originate from the dorsal aorta, whereas the anterior one emerges from the dorsal aorta, subclavian artery, or vertebral artery. The oviducal arteries are smaller in males in which they supply the Müllerian ducts. Four or five ovarian (or spermatic) arteries diverge from each side of the dorsal aorta and carry blood to the gonads and fat bodies.

A large subclavian artery branches off from each systemic arch in anurans or from either side of the dorsal aorta just posterior to the heart in salamanders. Numerous small branches deliver blood to the muscles of the shoulder region, and a major branch, the brachial artery, supplies the forelimb. The epigastric artery branches off at the point of origin of the brachial artery in salamanders; it supplies the ventral pectoral region and the ventral body wall. In anurans this artery is part of the pulmonary system. In both groups it continues posteriorly to connect with the femoral artery.

The arrangement of arteries in the pelvic region and hindlimb differs from the pattern in salamanders. The dorsal aorta bifurcates to form a pair of common iliac arteries in anurans, whereas a trifurcation includes a caudal artery in salamanders. After giving off the femoral artery, which has an anastomosis with the epigastric artery, the common iliac continues on as the ischiadic artery. This is the major vessel entering the hindlimb; posterior and ventral thigh muscles are supplied by a major branch, the cutaneous femoral artery.

Pulmocutaneous system.—In caecilians and salamanders (except plethodontids) the pulmonary arches curve posterolaterally from the truncus arteriosus to enter the lungs. Along this short route, dorsal and ventral esophageal arteries emerge and pass anteriorly to deliver blood to the floor of the mouth, pharynx, and esophagus before the major vessel, the pulmonary artery, turns to enter the lungs. In lungless plethodontid salamanders in which the pulmonary arch is present, the pulmonary artery supplies the skin of the neck and dorsum and in some species it anastomoses with the epigastric artery. The pulmonary arch in anurans is much more important in delivering blood to the skin. The main vessel, the pul-
monary artery, delivers blood to the heart, but the large cutaneus magnus artery originates from the pulmocutaneous arch and supplies the skin of the dorsal and lateral body wall; a branch of the cutaneus magnus, the auricular artery, supplies the jaw muscles, hyoid muscles, and tissues of the lower jaw.

Veins. The venous system is more variable, especially peripherally, than the arterial system. A major difference exists among the living orders with respect to the receptacle of the systemic veins, the sinus venosus, from which blood passes into the right atrium via the sinoatrial opening on the dorsal side of the atrium. The sinus venosus is transversely elliptical in caecilians; the left portion is separated from the slightly smaller right portion by an internal indentation of the walls or by transversely situated valves. The sinus in salamanders is approximately triangular and is situated to the left of the midline; it is the same shape but medial in position in anurans.

Systemic veins.—The veins that enter the sinus venosus from all regions of the body are grouped into this category. The sinus venosus receives three major veins, the postcaval which enters the posterior part of the sinus, and the paired precaval veins (ducts of Cuvier) which enter the lateral corners of the sinus. The left precaval is exceedingly short because the juncture of the veins on the left side is adjacent to the sinus venosus; on the other hand, the right precaval extends across the dorsal surface of the heart to the dextral corner of the sinistrally offset sinus venosus.

Three major veins, the internal and external jugulars and the subclavian, enter the precaval vein (Fig. 14-21). A postcardinal vein is present in larvae and in adults of caecilians, salamanders, and leptoleptodactylnid and discoglossid frogs. The internal jugular receives many veins draining the palate, brain, and the orbital, nasal, and auditory regions; the vertebral vein collects blood from the muscles of the neck and drains into the internal jugular. The external jugular vein with its major confluent (facial, lingual, and thyroid veins) collects blood from the muscles of the head and tongue and the thyroid gland. The subclavian vein collects blood from the forelimb via the brachial veins, from the muscles and skin of the trunk via the anterior epigastric and lateral veins; the anterior part of the latter also is known as the cutaneus magnus vein. The postcardinal veins (when present) originate as a single vessel from the posterior part of the postcaval vein; shortly after the origin a bifurcation results in the two postcardinals that pass anteriorly on either side of the dorsal aorta to enter the precaval veins. The postcardinals
provide an alternate route for blood from the region of
the kidneys to the sinus venosus.

The postcaval originates near the posterior end of the
kidneys by the fusion of a large renal vein from each
kidney. The postcaval receives various vessels from the
kidneys and gonads and passes through the liver to the
sinus venosus. In anurans, right and left branches of the
hepatic vein from corresponding lobes of the liver coa-
lesce before entering the postcaval vein.

**Hepatic-portal system.**—A major vessel, the ventral
abdominal vein, is formed by the coalescence of veins in
the pelvic region. The pelvic veins fuse to form the ventral
abdominal in anurans, but in salamanders the coales-
cence also includes the median cloacal and posterior ves-
ticle veins from the cloaca and bladder, respectively. The
ventral abdominal vein passes forward along the ventral
midline and thence through the liver to the postcaval. In
the region of the liver it receives vesicles from the gall
bladder and the portal vein with branches from the stom-
ach and intestines.

**Renal-portal system.**—The veins of the hindlimb
combine (also with the caudal vein in salamanders) to
form the paired Jacobson’s veins which pass anteriorly
on the dorsolateral surface of the kidney, from which they
receive many small vesicles. Jacobson’s vein also re-
ceives blood from the ovotudal vein and then passes an-
teriorly to enter the postcaval vein.

There are distinct differences in the veins of the pelvic
region and hindlimb among anurans and between anur-
s and salamanders. For example, in *Salamandra* and
*Xenopus* the major vessel from the hindlimb is the isch-
ial vein, whereas the femoral vein is the major vessel
in *Rana*. Also, there are differences in the anastomoses
of the femoral and Jacobson’s veins.

**Pulmonary system.**—The pulmonary veins arise from
the mesial surfaces of the lungs, fuse near the midline,
and enter the left atrium. A few small vesicles are received
from the esophagus.

**Lymphatic System**

A third series of vessels, the lymphatics, extends through-
out the body of amphibians; these vessels collect blood
(exclusive of erythrocytes) that seeps through the walls
of the capillaries and return it to the veins. The intestinal
lymphatics also collect fats, which are not absorbed by
the capillaries entering the veins.

The lymphatic system of *Salamandra* was described
by Francis (1934), who noted the fine subcutaneous net-
work of vesicles, especially laterally on the body and the
lymphatic sinuses in the head and at the bases of the
limbs. The subcutaneous lymphatics in salamanders empty
into the postcaval veins or various cutaneous vessels.
The visceral lymphatics parallel the digestive tract and
empty into the subclavian veins. Lymph is pumped through
the system by a series of contractile vesicles, the lymph
hearts. In *Salamandra* there are 15 pairs of lateral hearts—
4 postsacraally and 11 presacraally. Associated with the
lymph hearts are valves that restrict a unidirectional flow
of lymph in the vessels. Lymph is received in the hearts
from the cutaneous network and from branches from the
subvertebral vessels that collect lymph from the body
cavity. A central lymph heart associated with the truncus
arteriosus receives lymph from the head and neck and
delivers it to the lingual vein.

Caecilians differ from salamanders by having more than
200 lymph hearts situated intersegmentally under the skin
(H. Marcus, 1908); these hearts pump lymph into inter-
segmental veins.

Anurans have few lymph hearts; an anterior pair is
located beneath the scapulae, and one to five posterior
pairs are situated along the coccyx. Anurans differ from
other amphibians by having extensive subcutaneous lymph
spaces. These are separated by fine septa and are most
extensive in aquatic anurans. The spaces store water ab-
sorbed from the environment. Carter (1979) proposed
that excess water is excreted by the posterior lymph hearts
pumping water from the lymph spaces into the renal por-
tal vein and thence to the kidney.

**Respiratory System**

Amphibians have diverse modes of respiration. Larvae
have gills that are the primary respiratory structures, but
cutaneous respiration also takes place (see Chapter 6).
Most postmetamorphic amphibians have lungs; these and
the buccopharyngeal surfaces are the internal respiratory
structures; however, considerable gas exchange takes place
cutaneously in terrestrial amphibians (see Chapter 8).
Herein the structures associated with buccopharyngeal
and pulmonary respiration are discussed.

**Nares.** The nostrils (external nares) and the nasal duct
are intimately associated with the olfactory system (see
earlier section: Sensory Receptor Systems). The nasal
duct opens into the buccal cavity via the choana (internal
nares). The nares are closed by means of smooth muscles
in salamanders and caecilians; in anurans the nares are
closed by an upward swelling of the m. submentalis (Gans
and Pyles, 1983).

**Buccopharyngeal Cavity.** The mouth and pharynx
are lined with mucoid and ciliated epithelium that is highly
vascularized. In the floor of the pharynx is a longitudinal
slitlike aperture, the glottis, which leads to the larynx. The
glottis is bounded by the arytenoid cartilages, and the
glottis is opened and closed by the mm. dilatator laryngis
and constrictor laryngis, respectively.

**Larynx.** The larynx is a narrowly triangular chamber,
an elongated posterior tube, the trachea, is present in
salamanders, caecilians, and pipid frogs. The larynx is
supported by a series of semicircular cartilages, the so-
called lateral cartilages. The anterior pair is modified as
the arytenoid cartilages, which support the glottis and are
an integral part of the sound-production system in ani-
Lungs. Basically the lungs are paired organs. Although they are variable in size (small in Ascaphus) and especially large in some aquatic taxa (e.g., pipids and Telmatobius), paired lungs are invariably present in anurans. In pipids the lungs are reinforced by cartilage. Most salamanders (including the obligate neotenes) have well-developed, paired lungs, but in some taxa that inhabit mountain streams (e.g., Salamandrina and Rhyacochiton) the lungs are greatly reduced in size. Lungs are absent in all plethodontid salamanders. The lungs of caecilians are extremely elongate; the right and left lungs are approximately equal in length in some caecilians (e.g., Typhlonectes and Ichthyophis monochrous). In most caecilians the left lung is reduced, in some to about 10% of the length of the right lung, and the left lung is absent in Uraeotyphlus narayani (Baer, 1937).

Structurally, the lungs of terrestrial salamanders are conical sacs, more or less pointed posteriorly. The pulmonary membrane is folded to form internal septa, and each lung has two longitudinal compartments, one containing the pulmonary artery and the other the pulmonary vein. The septa are highly vascularized and covered with a thin epithelium except along their inner edges where ciliated and mucous cells cover the surfaces of smooth muscle. In obligate neotenic salamanders and some aquatic salamandrids (e.g., Notophthalmus and Triturus) the lungs have few septa and are comparatively poorly vascularized. In caecilians the elongate lung is infiltrated by cartilage; the inner surface is divided by a network of blood vessels, connective tissue, and smooth muscle which form alveoli. The lungs of terrestrial anurans are short but similar in structure except that they lack cartilage (except pipids) and the septa form more and smaller chambers.

In aquatic amphibians (especially obligate neotenic salamanders, some adult newts, pipid frogs, and possibly typhlonectid caecilians) the lungs seem to function more as hydrostatic organs than as respiratory organs. Some of these aquatic salamanders (e.g., Cryptobranchus, Ambystoma, and Triturus) breathe air through the nares, but Siren and Necturus take air in through the mouth (Atz, 1952), as pipid frogs do commonly.

Breathing. Observations and experiments on salamanders and anurans by Willem (1924), on a caecilian (Siphonops annulatus) by Mendes (1945), and sophisticated experiments by De Jongh and Gans (1969) on Rana catesbeiana have demonstrated that all amphibians studied breathe by means of a force-pump mechanism. Action of the throat musculature elevates and depresses the floor of the buccal cavity; this is analogous to the piston of the pump. When the nostrils are open and the buccal floor is depressed, air is drawn into the buccal cavity; closure of the nostrils and elevation of the buccal floor concomitant with the opening of the glottis forces air into the lungs. The cycle is reversed by the depression of the buccal floor while the glottis is open and the nares are closed; air is drawn out of the lungs into the buccal cavity. Subsequent closure of the glottis and opening of the nares combined with elevation of the buccal floor forces air out of the mouth. This mechanism is modified during vocalization in anurans (see Chapter 4).

Pulmonary respiration and buccopharyngeal respiration are complemented by cutaneous respiration in most terrestrial amphibians, and by cutaneous and branchial respiration in many aquatic amphibians. The differential rates of gas exchange are dependent on the degree of capillarity of the different respiratory surfaces as well as temperature and moisture of the skin. These functional aspects of respiration are discussed in Chapter 8.

UROGENITAL SYSTEM
The excretory and reproductive systems are closely associated in amphibians, as they are in all vertebrates, although these structures originate from different embryonic tissues (see Chapter 7). The urogenital system of salamanders was described in detail by Francis (1934), who based his work on Salamandra salamandra. Bhaduri (1953) and Bhaduri and Basu (1957) provided comparative descriptions of the system in anurans. The comparative morphology of the system in caecilians was described in detail by M. Wake (1968, 1970a, 1970b, 1972), and early development was treated by Fox (1963).

In this section the morphology of adults is described (Fig. 14-22). The ontogeny of the urogenital structures is covered in Chapter 7. The production of sperm and ova is discussed in relation to sexual cycles in Chapter 2, and kidney function is discussed in relation to water and ion balance in Chapter 8.

Kidneys. The kidneys in adult amphibians are paired structures lying on either side of the dorsal aorta. They develop from larval nephrostomes. In caecilians, anterior and posterior nephrostomes persist in the formation of the kidney; thus, caecilians have an opisthonephric kidney, in which some evidence of segmentation is retained in adults. The anterior part of the larval kidney (pronephros) is lost in adult anurans and salamanders; only the middle and posterior nephrostomes persist in adults, which therefore have a mesonephric kidney (Fig. 7-3).

The gross morphology of the kidneys differs in the