The Anatomy of Representative Vertebrates: Behavioral Systems

LABORATORY

34

OVERVIEW

In this series of laboratories (33–36), we use four representative vertebrates to illustrate evolutionary or phylogenetic trends within the subphylum Vertebrata. To better understand these trends it is important to determine whether an anatomical feature that seems structurally and functionally similar in different animals can be traced to a common ancestral origin. Since the highest degree of similarity between structures is often observed during embryonic development, before adult specializations have obscured fundamental features, we can study the evolutionary origins of similar structures by comparing their embryological origins. Structures that show fundamental embryological or developmental similarities, suggesting a common evolutionary origin (or common genetic heritage), are said to be **homologous.**

In constructing phylogenies, it is helpful to determine the sequence in which homologous characteristics originated in the evolution of a particular group of organisms. When only two groups share a characteristic not present in other groups at the same level of classification, they are said to have "recently" diverged from a common ancestor. The shared characteristic is called a **derived** (or **advanced**) **character.** The characteristic that gave rise to the derived character evolved earlier in the lineage and is called an **ancestral** (or **primitive**) **character.*** In using these characters to compare groups, we must keep in mind that "ancestral" and "derived" are relative terms and must be thought of in relation to an organism's position on the phylogenetic tree (see Figure 27-II). For example, the tympanic membrane and middle ear of a frog are *derived* when compared with the open spiracle (first gill slit) of the dogfish shark, but *ancestral* when compared with the recessed tympanic membrane separating the outer and middle parts of the ear in the rat.

In this laboratory you will study anatomical homologies that help us to understand the evolution of **behavioral systems.** Organs and organ systems constituting the behavioral systems include the **sensors** (affectors) discussed in Exercise A, the **control systems** (the nervous and endocrine systems) described in Exercise B, and the **effectors,** systems that produce externally directed activities (behavior), outlined in Exercise C.

STUDENT PREPARATION

Prepare for this laboratory by completing Laboratory 33 and reading the text pages indicated by your instructor. Familiarizing yourself in advance with the information and procedures covered in this laboratory will give you a better understanding of the material and improve your efficiency.

**Since the terms "primitive" and "advanced" carry judgmental connotations that do not apply to their technical meanings, it is best to use the terms "ancestral" and "derived" when possible.*

If dissection tools are not provided, bring your dissecting kit to laboratory with you. Do not wear contact lenses to this laboratory.

You will *not* dissect all four representative vertebrates—the behavioral systems are complicated and some are covered in other laboratories. Instead, you will dissect one representative vertebrate selected to illustrate anatomical features of the behavioral systems. Two members of your group should work through Exercises A and B using the shark, while the two other members move on to Exercise C using the rat. Be sure to read the introductory material for each exercise and review all the material covered in the assigned exercises by sharing observations within your group.

✓ EXERCISE A Sensors (Affectors)

Sensors continuously monitor the environment and are ready to produce signals in response to changes in the surroundings. There are a variety of sensors: those that sample the external environment, those that are in contact with the internal environment, and those that receive information from chemicals, light, and mechanical sources, including vibrations and the position of the organism and its parts. In early vertebrates, special sensors—the olfactory epithelia, the eyes, and the ears—developed in close association with the central nervous system. In fishes and aquatic amphibians, the lateral-line system is integrated with the ear (acoustico-lateralis system) and provides information about surrounding currents, body movements, low-frequency sounds, and, in some, the electromagnetic fields around the organism. The sensors of the lateral-line system are functional only in a dense, aqueous medium. In animals that made the transition to land, this system is not functional and is lost. Terrestrial animals evolved a variety of sensors distributed over the body surface and among the internal organs to monitor the position of body organs, touch, pressure, temperature, and other features of the changing environment. (In Laboratory 39, you will explore many of these sensors in your own body.)

Many of the types of vertebrate sensors that monitor the external environment are listed in Table 34A-1. Study this table to note some of the phylogenetic trends as you proceed with your dissections.

✓ PART I The Lateral-Line System

The lateral-line system and inner ear form the **acoustico-lateralis system.*** Sensors of the acoustico-lateralis system, the **neuromasts** (Figure 34A-1a), are located over much of the body surface and are associated with the **lateral-line canal** (Figure 34A-1b) in all aquatic vertebrates. This canal is located between the dorsal and ventral muscles of the body and has several branches that extend into the head. The neuromasts of the lateral line are composed of organs containing "hair cells" with small sensory cilia that are stimulated by bending. These cilia are embedded in a covering cap which is deflected by contact or by currents produced by movements in the surrounding water. The neuromasts act as **mechanoreceptors,** providing information about mechanical forces acting on the surface of the body. The neuromasts also provide information about the position of various parts of the body, serving the function of **proprioceptors,** specialized sensors in tetrapods that signal the position of individual bones and muscles.

These same structures may also sense low-frequency vibrations or "sounds" in the water, acting as **phonoreceptors.** Specialized neuromasts found on the head (ampullary organs) also act as **electroreceptors,** recording the electrical patterns produced by the muscles of the fish and by surrounding objects.

Acoustico-lateralis" implies an association with hearing (acoustico-). Actually, the ancestral inner ear structure of aquatic vertebrates senses the position and change in position of the head and has only a limited ability to detect very low-frequency (sound) vibrations transmitted through the water. Hearing becomes important in some bony fishes but is best developed in terrestrial vertebrates in association with accessory structures of the middle (and outer) ear. It is, therefore, preferable to refer to this system as the octavo-lateralis system because of the involvement of the eighth cranial nerve (octavo-) in both static and acoustic sensory systems. Sensory input from the lateral-line sensors is carried by fibers in adjacent cranial nerves (seven, nine, and ten), so the compound name "octavo-lateralis" remains appropriate. We have elected, however, to retain the more familiar name, acoustico-lateralis, for this system.

Table 34A-1 Vertebrate Sensors

Receptors	Sense	Organ	Location	Phylogenetic Trends
Chemoreceptors	Smell (distant sources)	Olfactory epithelia	Nares	Sensory epithelia, associated with shallow, surface pits in ancestral fishes, extend inward to connect with the mouth.
	Taste (contact sources)	Taste buds	Body surface, mouth	Concentrated on the head and mouth in fishes; confined to the mouth cavity in terrestrial vertebrates and to the tongue in mammals.
Photoreceptors	Vision	Eyes	Head (lateral surface)	Protective lids develop in fishes; glands moisten and lubricate the surface in terrestrial vertebrates.
	Time	Median eyes (pineal, parapineal glands)	Head (dorsal surface)	Dorsal "eyes" develop in the earliest jawless fishes; lose sensory function in mammals.
Mechanoreceptors				
Phonoreceptors	Hearing	Neuromasts; organ of Corti (lagena)	Inner ear	Hearing becomes much more important in terrestrial forms; organ of Corti becomes elongated.
Statoreceptors	Position	Neuromasts	Inner ear	Several different bands of neuromasts are found in the representative vertebrates.
	Acceleration	Semicircular canals (and neuromasts)	Inner ear	All vertebrates have three canals (except lampreys and hagfishes).
	Distant-touch	Neuromasts	Lateral line	Present only in aquatic vertebrates.
Pressure and touch receptors	Contact stimuli	Dermal sensors	Skin	Develop in terrestrial animals; replace lateral-line sensors
Electroreceptors	Electromagnetic fields	Ampullary organs	Lateral line	Well developed in fishes with electric organs.
		Dermal sensors	Mandible	Found in one mammal, the platypus.
Thermoreceptors	Temperature	Free nerve endings	Skin, brain	Free nerve endings in terrestrial vertebrates.
Proprioceptors	Organ position	Tendon organs, muscle spindles, other encapsulated sensors	Muscles, joints	Appear in fishes; replace lateral-line sensors in terrestrial vertebrates.
Nociceptors	Pain	Free nerve endings	Most organs	Absent in nervous tissues; nature of pain obscure in fishes.

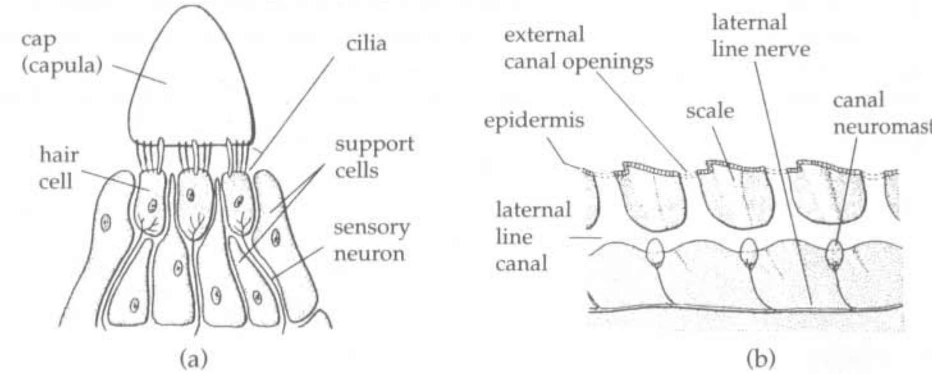

Figure 34A-1 *(a) A neuromast organ of the lateral-line system. (b) The lateral-line canal and neuromasts in a bony fish.*

Objectives

☐ Locate components of the lateral-line system and understand their sensory roles.

Procedure

1. Find the light-colored, fine line along the side of the body of your shark. This line indicates the position of the lateral-line canal which lies beneath it. This canal, plus a complex of canals on the head, contains sensors of the lateral-line system, the neuromasts. (Individual neuromasts are also widely distributed over the body but cannot be seen without a microscope.)

   a. *The lateral-line system has been described as giving an animal a sense of "distant-touch." What does this mean?* ______________________________

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2. Push on the skin of the head. You should be able to find patches of pores from which a shiny, jellylike substance exudes under pressure. These are the openings of the **ampullary organs of Lorenzini,** specialized sensors of the lateral-line system that are sensitive to mechanical stimulation and weak electrical fields. They are used in the detection of prey.

   b. *Can you think of other uses for electroreceptors besides the detection of nearby objects?* __________

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✓ PART 2 The Inner Ear

The inner ear is a second component of the acoustico-lateralis system. In fishes, the inner ear is not specialized as an organ of hearing (phonoreception), but is primarily an organ associated with sensing changes in position of the organism (or its head)—a form of mechanoreception called **statoreception** (the ancestral function of the inner ear). Only in terrestrial vertebrates, which receive sound waves propagated in the air, does the inner ear develop specializations for hearing.

Recall that the ear of a mammal consists of three parts: the outer, middle, and inner ears. Embryologically, the outer and middle ears of mammals are derived from the first gill slit, the spiracle, of their ancestors. In sharks, the ancestral pattern persists: the spiracle still connects the pharynx with the exterior. Frogs and turtles have only a middle and an inner ear—the tympanic membrane bounding the middle ear is flush with the surface of the head. In mammals, the tympanic membrane is recessed from the surface, thus forming an outer ear, which channels sound waves to the tympanic membrane. Sound waves in the air are transduced by the tympanic membrane of terrestrial vertebrates into mechanical vibrations that are transmitted to the inner ear via a bone (or bones) of the middle ear.

The inner ear is a membranous sac, the **membranous labyrinth,** filled with a fluid called **endolymph.** The membranous labyrinth is embedded in the base of the skull surrounded by a **bony labyrinth**—the membranous labyrinth is like a cast within a mold.

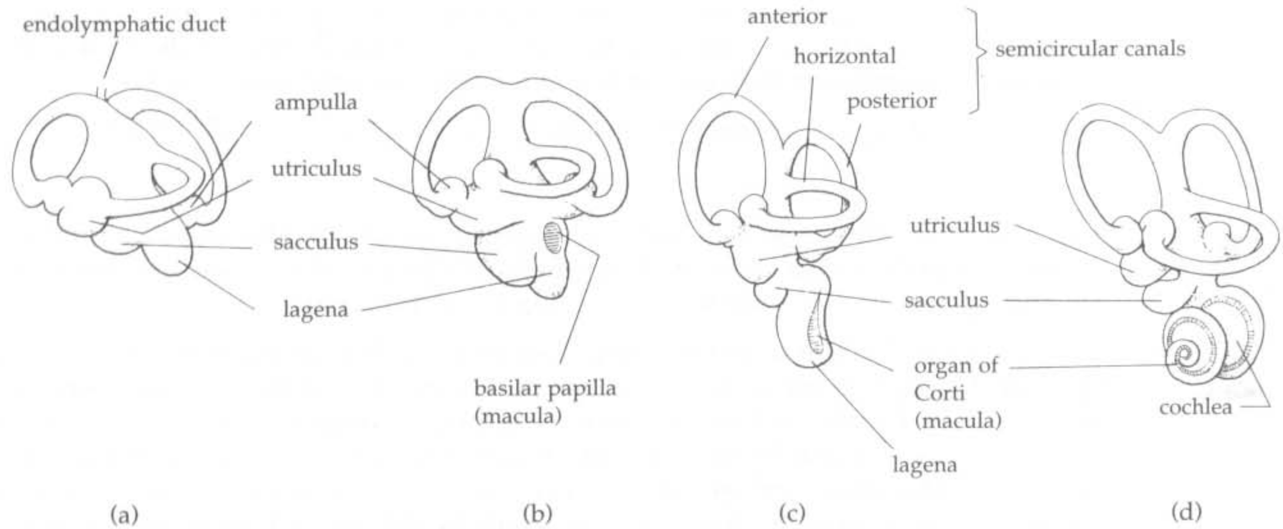

Figure 34A-2 *Membranous labyrinths of (a) shark, (b) turtle, (c) bird, and (d) mammal. The inner ears of all of these vertebrates have three semicircular canals as part of the utriculus. All also possess one or more clusters of sensory hair cells within the utriculus, within the sacculus proper, and within the lagena, a saclike extension of the sacculus. In birds and mammals, the macula within the lengthening lagena is called the organ of Corti and is associated with hearing. Note that the lagena becomes coiled in mammals, increasing the total length of the duct and, possibly, the auditory acuity of the ear.*

The membranous labyrinth is divided into two parts: the vestigial endolymphatic sac which, in sharks, remains connected to the surface of the body by a duct, and the **utriculus** and the **sacculus** (Figure 34A-2a). The most obvious parts of the utriculus are three **semicircular canals** or **ducts**, which lie at right angles to each other and at an angle of 45° to the body axis. Each canal has an expanded region, the **ampulla,** near its base, and projecting into each ampulla is a typical neuromast organ (**crista**) which can be deflected by movements of the endolymph within the canal. When the head moves, fluid flows within the labyrinth (*why?*) and differentially bends the hair cells within each of the semicircular canals, thus providing the organism with a perception of the direction of its movements.

The utriculus and sacculus also contain several neuromast organs in which the hair cells are arranged in small clusters (**cristae**) or broader bands (**maculae**). The caps of these neuromasts are impregnated with calcium salts, forming "ear stones" or **statoliths.** These statoreceptors respond to the force of gravity and provide the organism with a sense of "up" and "down." (Statoliths can also be affected by low-frequency vibrations and may serve as crude sound receptors, or **phonoreceptors.**)

In most fishes, there is a short ventral extension (**lagena**) of the utriculus; with the transition to land, this elongated to form the **cochlear duct** found in birds and mammals. Within the cochlear duct, hair cells form the **organ of Corti,** an elongate macula, (Figure 34A-2c, d), the principal sensory structure involved in hearing.

Objectives

☐ Dissect the inner ear of the shark and learn its role in determining position.

Procedure

1. Examine the dorsal surface of the head of your shark along the midline between the two spiracles (use a magnifying lens if necessary). Locate the small pair of **endolymphatic pores** along the midline. These pores open into the endolymphatic ducts of the inner ear and enable

sharks to take small grains of sand into the inner ear, where they are incorporated into statoliths. The statoliths are coupled to hair cells to signal the position of the head. (Note that the inner ear is separated from the exterior in the adults of other vertebrates.)

a. What material increases the mass of statoliths in vertebrates that cannot take up sand?

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2. Beginning *behind* the eye on the left side of the head, remove the skin and muscles from the top and side of the cartilaginous skull to behind the spiracle on that side. Remove tissues ventrally behind the eye to the level of the upper jaw (Figure 34A-3).
3. Refer to Figure 34A-3 (or to an embedded skull in which dye has been injected into the bony labyrinth) to help you anticipate the location of the structures of the inner ear. Using your one-piece scalpel (cartilage knife), *carefully* shave away cartilage from the skull. (*Do not* use a two-piece scalpel—it will fold back on your finger!) Use care so that you do not accidentally flip a piece of the fixed cartilage into your eye (wear glasses as a precaution—no contact lenses). As you approach the inner ear, you should be able to see the horizontal semicircular canal through the semitranslucent cartilage before breaking into the cavity of the bony labyrinth in which it lies. Be careful—remove little slivers at a time! Once you break through the cartilage into the bony labyrinth, continue to shave cartilage away from the membranous labyrinth, exposing the length of the first semicircular canal and the remaining structures of the inner ear. Use Figure 34A-3 to help you follow the position of the parts of the membranous labyrinth as you work.
4. Remove the membranous labyrinth from the skull, place it in a small finger bowl with water, and study it. (If prepared specimens are provided, observe them.) Identify the anterior and horizontal **semicircular canals** with their common duct, the anterior **utriculus** (Figure 34A-2a). Find the posterior semicircular duct. At the base of each semicircular canal, find an expanded segment, the **ampulla.** Find the ventral **sacculus** with its extension, the **lagena.**

b. What is the function of the three semicircular canals? ______________________

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c. What structure does the lagena form in birds and mammals? ______________________

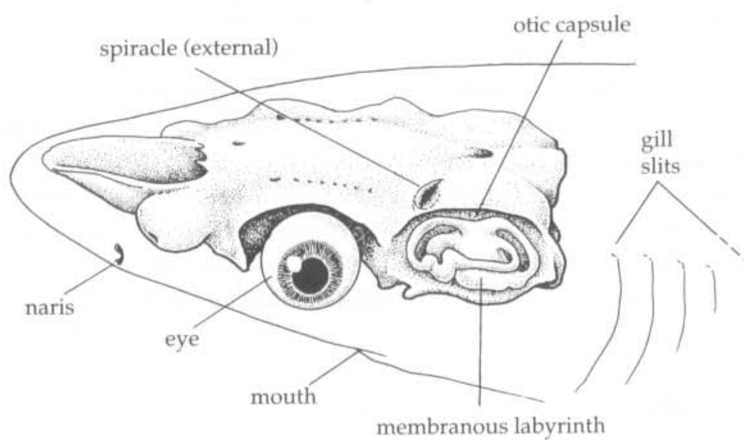

Figure 34A-3 *The head of the shark, showing the region to be skinned and cleared of muscles. The membranous labyrinth of the inner ear is shown in place within the chondrocranium.*

PART 3 Other Sensors of the Head

The nasal epithelia form a primitive sensory system in all vertebrates. The sensory elements (hair cells) are **chemoreceptors** stimulated by molecules carried in water or air from distant sources. In most sensors, specialized epithelial cells receive stimuli and transduce them into electrical events that are relayed to separate sensory neurons. These sensory neurons then carry the nerve impulses to the central nervous system. In the olfactory system, however, the hair cells themselves function as neurons that carry information directly to the brain. Unlike most nerve cells, olfactory neurons that are renewed throughout the life of the organism.

The eyes are also part of a sensory system in all vertebrate groups. As **photoreceptors** they are stimulated by light. The relative shapes of elements within the eye and the way in which they accommodate to objects situated at different distances may vary in different vertebrates, but the basic structure of the eye is remarkably constant in all vertebrates.

✓ EXERCISE B Control Systems

Rapid responses to environmental stimuli are usually mediated by the **nervous system;** slower, longer-lasting responses may involve components of the **endocrine system.** Working together, these two systems allow the vertebrate to make adaptive adjustments to input from the environment (behavior) and to maintain a relatively constant internal environment (homeostasis).

✓ PART I The Nervous System

The nervous system is composed of two parts: the **central nervous system (CNS)** and the **peripheral nervous system (PNS).** The central nervous system includes the dorsal **spinal cord** and its anterior expansion, the **brain.** Within the CNS, sensory input and past experience are evaluated against the genetically determined range of potential responses, and behavioral and physiological actions are initiated. The PNS constitutes the "wiring" that brings information in (from the sensors) and takes command signals out (to the effectors).

CENTRAL NERVOUS SYSTEM

During embryonic development, the anterior portion of the neural tube enlarges and forms three primary divisions; two of these subdivide later to form a total of five regions in the adult brain. These regions are:

Prosencephalon (Forebrain)	**1.** Telencephalon **2.** Diencephalon
Mesencephalon (Midbrain)	**3.** Mesencephalon
Rhombencephalon (Hindbrain)	**4.** Metencephalon **5.** Myelencephalon

Functionally, however, the brain is organized into only two major areas, the **brainstem,** which is a continuation of the spinal cord, and three dorsal expansions (hemispheres or lobes) associated with the primary sensors of the head—the nose, eyes, and acoustico-lateralis system, including the ears (Figure 34B-1).

Much of the brainstem is made up of nerve-fiber tracts, including an ancestral coordinating system of neurons participating in motor and other control activities, called the **reticular system,** and groups of cell bodies (**nuclei**) that act as "relay stations."

Cranial nerves of the peripheral nervous system connect to the brainstem, which functions as a "visceral brain," playing a major role in many of the homeostatic adjustments of the body, including regulation of blood pressure, heart rate, sleep/wake cycles, reproductive cycles, the intake of food and water, and the secretory activity of the pituitary gland, which, in turn, regulates many other body functions.

In contrast, the dorsal expansions of the brain function as a "somatic brain," initiating and coordinating behavioral events and integrating them with functions of the brainstem.

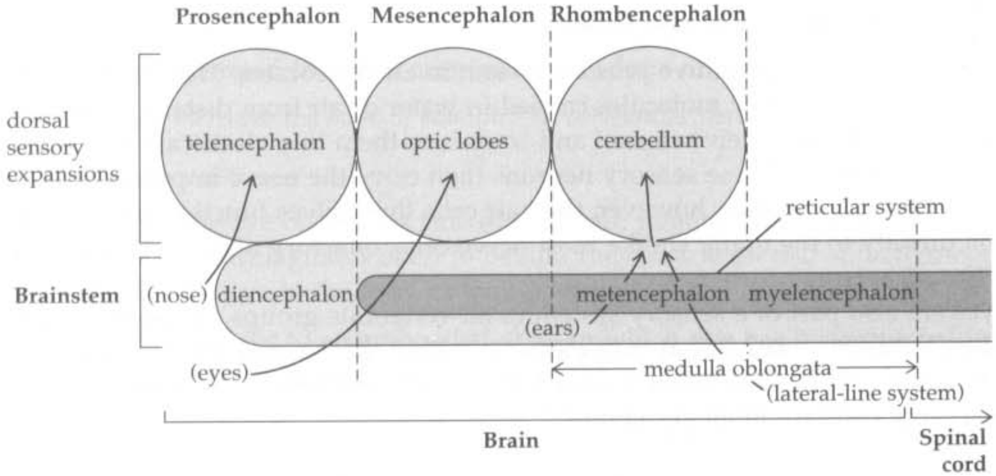

Figure 34B-1 *The brain of vertebrates is functionally divided into the brainstem (which includes an ancient control area, the reticular system), and three dorsal hemispheres or lobes. The most anterior of these dorsal lobes (the telencephalon) is associated with the sense of smell; the second (the optic lobes), with vision; and the third (the cerebellar hemispheres) with input from the inner ear and lateral-line system. The brainstem is continuous with the spinal cord.*

The first of the dorsal expansions of the brain includes the **telencephalon,** part of the forebrain, connected to the sensors of the nose through **olfactory lobes** in all vertebrates. In the earliest vertebrates, the highest proportion of sensory input was provided by nasal epithelia. Phylogenetically, there is a trend toward the enlargement of the telencephalon, leading to the formation of the prominent **cerebral hemispheres.** As the telencephalon became larger, certain motor activities came to be initiated within this region.

The second expansion, the **optic lobes** of the midbrain (**mesencephalon**), receives visual information from the eyes. As vision increased in importance to vertebrates, particularly terrestrial vertebrates (which live in surroundings where light is not attenuated by water nor vision obscured by sediment), this region increased in size and many more behavioral activities began to be initiated in this area of the brain. Information can pass from this area to the cerebral hemispheres of the forebrain, where conflicts between visual and olfactory input may be resolved. In the evolution of mammals, the increasingly important task of coordinating visual information was taken over by the cerebral hemispheres, and the optic lobes themselves decreased in size (Figure 34B-2).

The third expansion forms the **cerebellum,** a pair of hemispheres derived from the upper portion of the metencephalon. This area is associated with sensory input from the acoustico-lateralis system (ear and lateral line) in aquatic vertebrates and from the ear and various proprioceptors in terrestrial vertebrates. The cerebellum receives information about body position (from statoreceptors), changes in body position (from the semicircular canals of the inner ear), movements in the surrounding medium in fishes (from the lateral-line neuromasts), and the position of major muscles and bones in terrestrial vertebrates (from proprioceptors). The cerebellum does not initiate movements or behavior; instead, it integrates the command decisions made in the cerebral hemispheres and optic lobes with information about the position of the organism and its parts.

With the relative unimportance of hearing in fishes, no major expansion of brain tissue is associated with this function. With the origin of the organ of Corti in terrestrial vertebrates, however, important auditory information is projected to the dorsal midbrain.

This basic organization of the brain is found in all vertebrates. There are relative differences in the volume of the dorsal expansions based upon the relative importance of sensors (and muscular control). Follow these changes in Figure 34B-2. In the shark with its massive trunk muscles, the cerebral hemispheres are no larger than the olfactory lobes and the optic lobes are also relatively small, but the

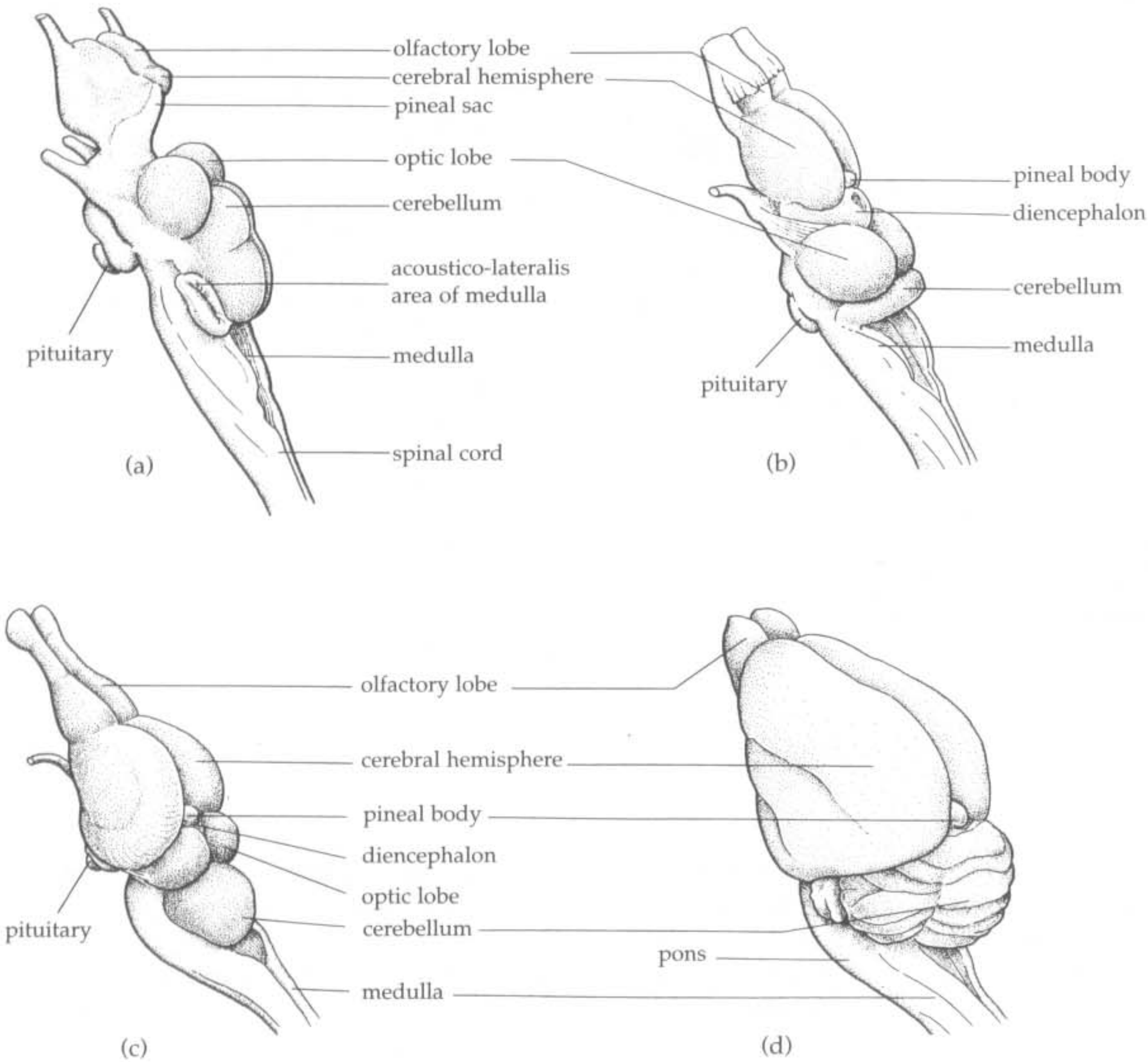

Figure 34B-2 *Brains of (a) shark, (b) frog, (c) turtle, and (d) rat. Note the progressive increase in the size of the cerebral hemispheres through the series and the reduction of the optic lobes to two of the corpora quadrigemina (located beneath the cerebral hemispheres, not visible here) in mammals.*

cerebellum is prominent. In the frog and turtle, the optic lobes are much larger than in the shark, reflecting the importance of vision in these terrestrial vertebrates. As the relative mass of the trunk muscles decreases, the cerebellum becomes somewhat reduced. Note that the most interesting trend is the increase in size of the cerebral hemispheres moving from the shark to the frog to the turtle and then to the rat. In mammals, the organization of the brain shows some innovations that go well beyond a basic increase in relative size of the cerebral hemispheres (Figure 34B-2).

Another part of the central nervous system, the spinal cord, begins at the back of the skull and extends into the tail. Like the brainstem, it includes two types of tissues: **white matter** (myelinated nerve cell fibers) and **gray matter** (nerve cell bodies). Within the spinal cord (and brainstem), the cell bodies are located centrally (Figure 34B-3) and are grouped functionally as sensory or motor and as somatic or visceral. **Sensory fibers** carry information from sensors to the central nervous system; **motor fibers** carry commands from the central nervous system to effectors. **Somatic fibers** innervate superficial parts of the body and generally mediate behavior at a conscious, voluntary level. **Visceral fibers** innervate deeper structures and mediate subconscious, involuntary responses.

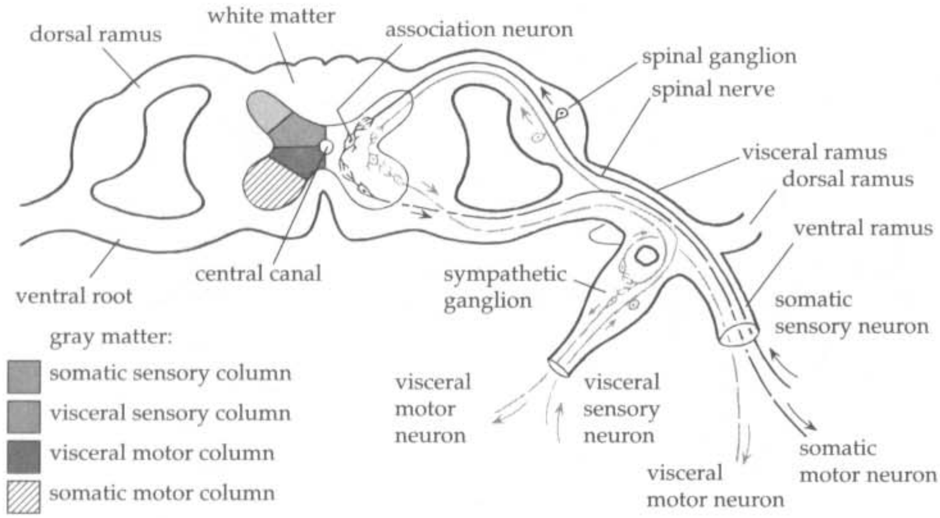

Figure 34B-3 *The mammalian spinal cord and spinal nerves. The organization of cell bodies in the gray matter of the spinal cord is suggested to the left. The pathway of somatic and visceral fibers and of sensory and motor fibers is shown on the right.*

Finally, remember that the central nervous system develops as a hollow tube. The central cavity or **neurocoel** includes the various ventricles of the brain and the neural canal in the spinal cord; it is filled with **cerebrospinal fluid** secreted by vessels of the connective tissue sheaths (**meninges**) surrounding the brain and by special vascular organs, the **choroid plexus** (*telae choroideae*), in the ventricles of the diencephalon and rhombencephalon.

PERIPHERAL NERVOUS SYSTEM

Directly associated with the central gray columns are fibers, comprising the **spinal nerves,** that join the spinal cord through two roots. These **dorsal** and **ventral roots** merge outside the spinal cord to form a complete spinal nerve. During the course of evolution, visceral motor fibers joined the somatic motor fibers in the ventral root and, in mammals, the dorsal root has finally become sensory and the ventral root motor.

As soon as the roots join to form the spinal nerve, they split into branches (**rami**). The dorsal ramus carries fibers to and from the dorsal musculature; the ventral ramus serves the ventral musculature. Visceral fibers travel to various internal organs. Visceral *motor* fibers form the **autonomic nervous system (ANS),** characterized by having two neurons in the motor "chain" or pathway; there is a synapse in the chain along its course, either in special visceral ganglia near the spinal cord or in the organ innervated. (Somatic and visceral sensory innervations have single-neuron pathways.) As we move through the vertebrate phyla, there is a trend toward the functional separation of this dual innervation such that the autonomic nervous system is divided into two opposing (antagonistic) systems: the sympathetic nervous system and the parasympathetic nervous system. Generally, physiological activities promoted by one system are retarded by the other.

In the cranial nerves associated with the brainstem, the roots remain unconnected. Dorsal root nerves contain all sensory and visceral motor fibers, and ventral root nerves contain only somatic motor nerve fibers. There are also three special somatic sensory nerves associated with the brain: the olfactory nerve (composed of fibers from the olfactory neurons), the optic tract (composed of neurons from the eye), and the stato-acoustic nerve (containing sensory neurons from the inner ear).

Objectives

- List the parts of the vertebrate brain and explain the association of each with sensory input and motor outflow.
- Describe the organization of spinal and cranial nerves in the shark.

Procedure

Central Nervous System

1. Carefully remove the skin and tissues that remain on the dorsal portion of the shark's head above, and lateral to, the entire cartilaginous skull, leaving the eyes in place in their orbits for now. Use Figure 34B-4 to guide you in your dissection. Once the dorsal and lateral aspects of the skull are exposed, shave away the cartilage of the skull using your one-piece scalpel. Begin in the area where the inner ear was removed and remove tissue medially and anteriorly. You will encounter the cerebellum, and, once it is exposed, you should be able to remove larger pieces of cartilage without damaging the brain. As you move laterally, you will encounter branches of several cranial nerves—they are white and relatively delicate. Try to preserve them.

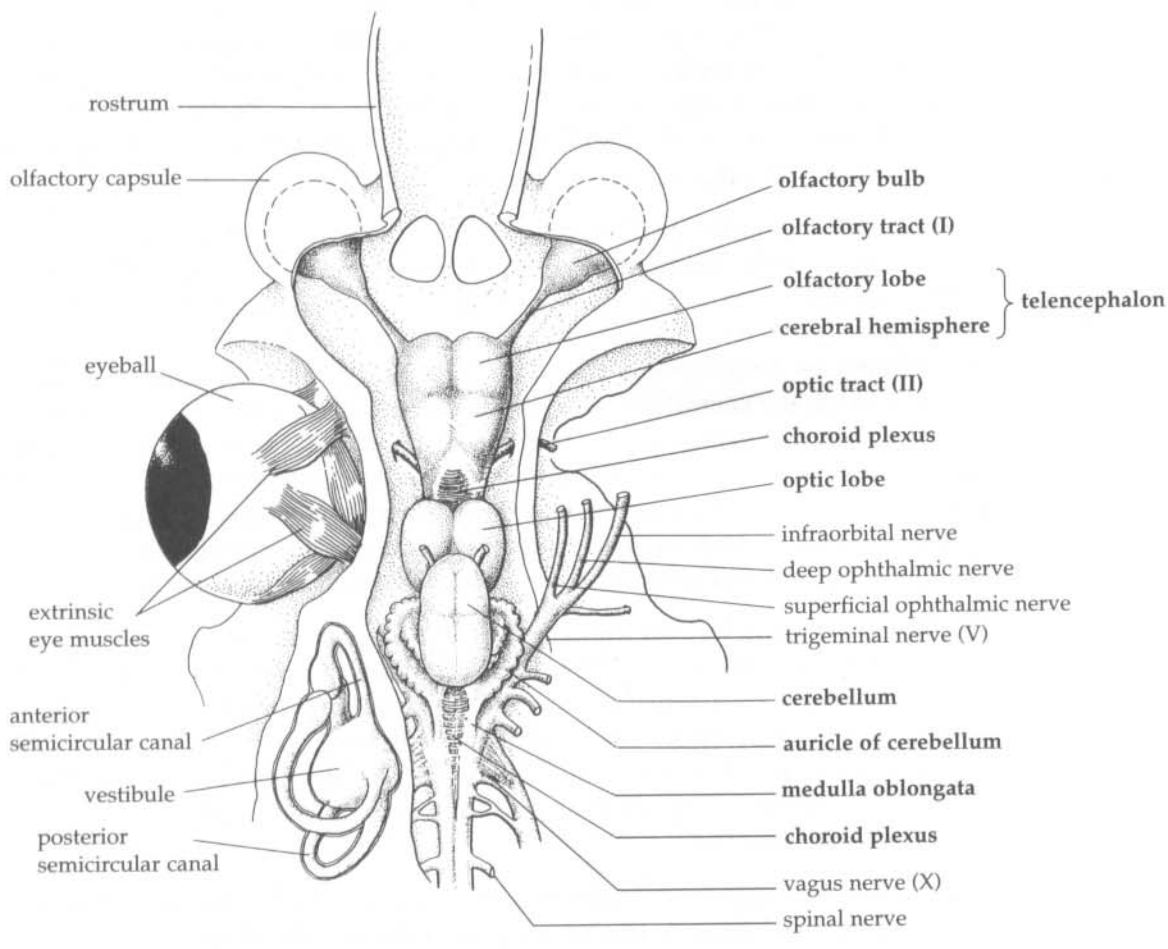

Figure 34B-4 *A frontal section through the head of the shark showing major sense organs, the brain, and several branches of cranial nerves.*

2. Note that the brain is covered by a tough outer membrane, the **dura mater** (or **dura**) and a thin, vascular **pia mater** (or **pia**). These membranes are connective tissue **meninges** that encase the brain. Use a dissecting needle to tear the dura apart. Vessels in the pia cover the brain (these vessels appear dark because hemoglobin in the blood loses its natural color on contact with formalin).

3. Beginning at the anterior end of the brain, locate the **olfactory lobes** and the **cerebral hemispheres** (the two parts of the telencephalon). The forebrain is mainly concerned with input from the olfactory sensors located in the external nares. The olfactory tract connects the sensors and olfactory bulb to the telencephalon.

   a. What are the functions of the cerebral hemispheres in sharks? ______________________

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   b. What added functions are assumed by the cerebral hemispheres in mammals?

   ____

   c. How do the cerebral hemispheres of sharks and mammals differ in relative size?

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   The second part of the forebrain, the diencephalon, is relatively undeveloped dorsally and is inconspicuous. It gives rise to the pineal body which extends through the roof of the skull. (In submammalian vertebrates, the pineal body or a similar structure is photoreceptive and may form an eyelike structure, the "third" or median eye. In humans, the pineal body is reduced to a small neuroendocrine organ—an endocrine organ of neural origin—that is embedded between the cerebral hemispheres. It produces melatonin, involved in the control of pigment cells and rhythms of activity, including sleep. The lateral walls of the diencephalon constitute the **thalamus,** a region of interconnections between fibers connecting the forebrain with other areas of the brain.

4. Find the dark area between the telencephalon and the optic lobes. This is the **choroid plexus,** a folded, vascularized membrane that produces the cerebrospinal fluid filling the cavity (neurocoel) of the central nervous system. It is also part of the diencephalon. If the brain is later removed, or if you have access to a model, study the ventral surface of the diencephalon. Find the optic nerves that enter this part of the forebrain through the **optic chiasma.** Behind the chiasma, locate the ventral extension of the diencephalon. This extends downward from the hypothalamus (the ventral part of the diencephalon) to form the **posterior pituitary gland,** which is wrapped by the **anterior pituitary gland.** Secretions of the anterior pituitary control the secretions produced by a number of other endocrine organs (gonads, thyroid, adrenal cortex) and a variety of processes (growth, reproduction, etc.). When you remove the brain from the skull, the pituitary gland will probably be torn off and remain in the skull. See whether you can find it.

5. Find the **optic lobes** located dorsally behind the cerebral hemispheres on each side of the brain and forming the roof of the midbrain. Ventrally, optic fibers pass from the eye through the optic nerve (which is really a tract of the brain) and into the diencephalon through the optic chiasma. There, fibers cross and pass to the opposite side of the brain (fibers from the left eye cross to the right side and vice versa). The nerve fibers then pass through the lateral walls of the diencephalon (the thalamus) and project to the optic lobes, where visual information is processed.

6. Find the **cerebellum** (the dorsal part of the metencephalon) located behind the optic lobes. Note that the cerebellum is the largest part of the shark's brain.

   d. How does the size of the cerebellum relate to the structures and functions of the shark's body?

   ____

7. Locate the second choroid plexus posterior to the cerebellum. It is formed from the roof of the myelencephalon. The myelencephalon and ventral part of the metencephalon form the **medulla oblongata.** This structure is continuous with the spinal cord and gives rise to several cranial nerves. Anteriorly, it connects with the midbrain and the diencephalon. Dissect away enough cartilage to follow the medulla to the back of the skull.

8. The spinal cord continues caudally from the brain. Remove the rear of the skull and trace the medulla oblongata to the spinal cord where it emerges from the brain case.

Peripheral Nervous System

9. Dissect away tissues lateral to the vertebral column in front of the first dorsal fin and locate several of the typical spinal nerves (see Figure 34B-4). Locate dorsal roots (with their spinal ganglia) and ventral roots.

   e. *What types of fibers travel through the dorsal root of the spinal nerve in the shark?*

   ____

   The ventral root? ______________________________________

10. The size of the different cranial nerves varies greatly, and branches of several may travel together for a part of their length. Several of these branches can be located without removing the brain from the brain case. Using Figure 34B-4, identify as many of the branches of the cranial nerves as you can. You should be able to find the large, **superficial ophthalmic nerve** (a branch of the fifth cranial nerve, the trigeminal), which passes through the orbit of the eye to the rostrum; the **optic "nerve"** (the second cranial nerve, actually a brain tract), which passes from the eye to the ventral diencephalon; the **vagus nerve** (cranial nerve ten), which innervates the last four pharyngeal arches and continues posteriorly to supply visceral (including autonomic) fibers to the heart and anterior abdominal organs.

11. If time permits, you may continue to cut away cartilage of the brain case ventrally and remove the brain intact. (As you do this, you will need to remove one eye—note the straplike extrinsic muscles that connect the eye with the skull. You might open the eye to see the lens and the sensory retina inside). As you cut ventrally, try to preserve the roots of the cranial nerves as they join the brain. Identify as many of the cranial nerves as you can. Try to find the vagus nerve as it emerges at several levels along the ventrolateral surface of the posterior medulla oblongata. Review the divisions of the brain ventrally. Can you find the pituitary gland?

✓ PART 2 The Endocrine System

All cells in our bodies affect adjacent cells through their metabolic activities and the release of waste materials. In the evolution of chemical controls, some of these products have come to assume a controlling role—first of neighboring cells and later of cells that are at a distance, with the product transported through the circulatory system. Those tissues or glands that have specialized in this direction form a functional group of ductless organs that make up the **endocrine system;** their secretions are known as **hormones.**

Chemical control mechanisms are ancient in vertebrates. Both lancelets and tunicates concentrate iodine in the endostyle at the base of their pharyngeal basket (Laboratory 27), which may be involved in the production of a hormone similar to that produced by the thyroid. The similar location of these glands and similar metabolic activities of their products suggest that the thyroid gland of vertebrates and the endostyle of protochordates may be homologous. This homology indicates a very early ancestry of endocrine control in the phylum.

Vertebrates have several different types of glands belonging to several different organ systems that produce hormones. In fact, since all cells influence adjacent cells, cells derived from any type of tissue may develop a controlling function. Thus, endocrine glands have developed within several systems including the nervous system, the digestive system, and the reproductive system.

We will make no attempt to systematically locate all of the endocrine organs, since many are associated with systems yet to be dissected. However, as you encounter them in later laboratories, keep in mind that it is the control systems, both nervous and endocrine, that enable the active animal to adjust rapidly to many environmental changes and to survive and reproduce.

✓ EXERCISE C Effectors: Muscles and Bones

In fishes, paired limbs supply little of the power used in swimming—rather, they fine-tune the fish's position in space. In terrestrial vertebrates, however, the appendages assume a supporting role. They carry the weight of the organism and must, in turn, be securely anchored to the trunk. In tetrapods, the bones supporting the hindlimbs (pelvic girdle) are attached to the vertebral column to provide this support. In contrast, the bones supporting the forelimbs (pectoral girdle) are never directly fused to the spinal column. Muscles and connective tissue link the pectoral girdle to the rib cage. In some vertebrates, the collar bone (clavicle) connects the girdle to the breastbone (sternum), which is, in turn, tied to the vertebral column by the ribs. In many terrestrial vertebrates, the pelvic girdle and hindlimbs play the larger role in locomotion on land, while the forelimbs may be modified for other purposes, including other types of locomotion (flight in birds and bats, for example).

a. How are the structures of the hindlimbs related to their function? ____________________

____

____

____

In the shark, trunk muscles flex the vertebral column, propelling the fish forward as the caudal fin pushes against the water. In terrestrial animals, muscles of the trunk remain important—the body bends from side to side and the appendages provide points of contact with the substrate, but little independent propelling force. As the limbs become more specialized and take over a major role in locomotion, muscles of the trunk are reduced and the muscles of the appendages become increasingly adapted for finer movements associated with individual skeletal elements. This principle of muscle and skeleton working together to provide externally directed movements is important throughout the vertebrate group.

PART I Muscles

Muscles are organs composed of tissues specialized for contraction (see Laboratory 32). Usually acting with elements of the skeleton, they form the most obvious effector system in vertebrates. Other effectors include electric organs (modified muscle and nerve tissues), pigment cells, and glands.

Muscles are classified as **somatic,** the voluntary skeletal muscles, and **visceral,** mainly the involuntary muscles of visceral organ systems. Somatic muscles are divided into two major groups: **axial** muscles, those associated with the skull and vertebral column, and **appendicular** muscles, those associated with the paired appendages. Fibers of somatic muscles are striated; those of visceral muscles are usually smooth.

In this exercise, you will learn to dissect and identify some somatic skeletal muscles of the shark and the rat.

Skeletal muscles generally have an origin, a belly, and an insertion (Figure 34C-1a). The **origin** is on a bone (or connective tissue sheath of an organ) and is the relatively "fixed," proximal end of the muscle. The **belly** of the muscle, containing the majority of the muscle fibers, is interlaced with connective tissue that continues as a **tendon,** attaching the muscle to its proximal origin and distal **insertion** (Figure 34C-1c). Skeletal muscles usually occur as antagonistic pairs: typically, contraction in one member of the pair flexes a limb; contraction in the other member extends the limb (Figure 34C-1a, b).

Muscles should be named for their origin and insertion, but many are named for their position or carry older names given to human muscles before consistent naming conventions arose. Homologies of muscles in widely separated groups of vertebrates are difficult to establish and may not be reflected in their names.

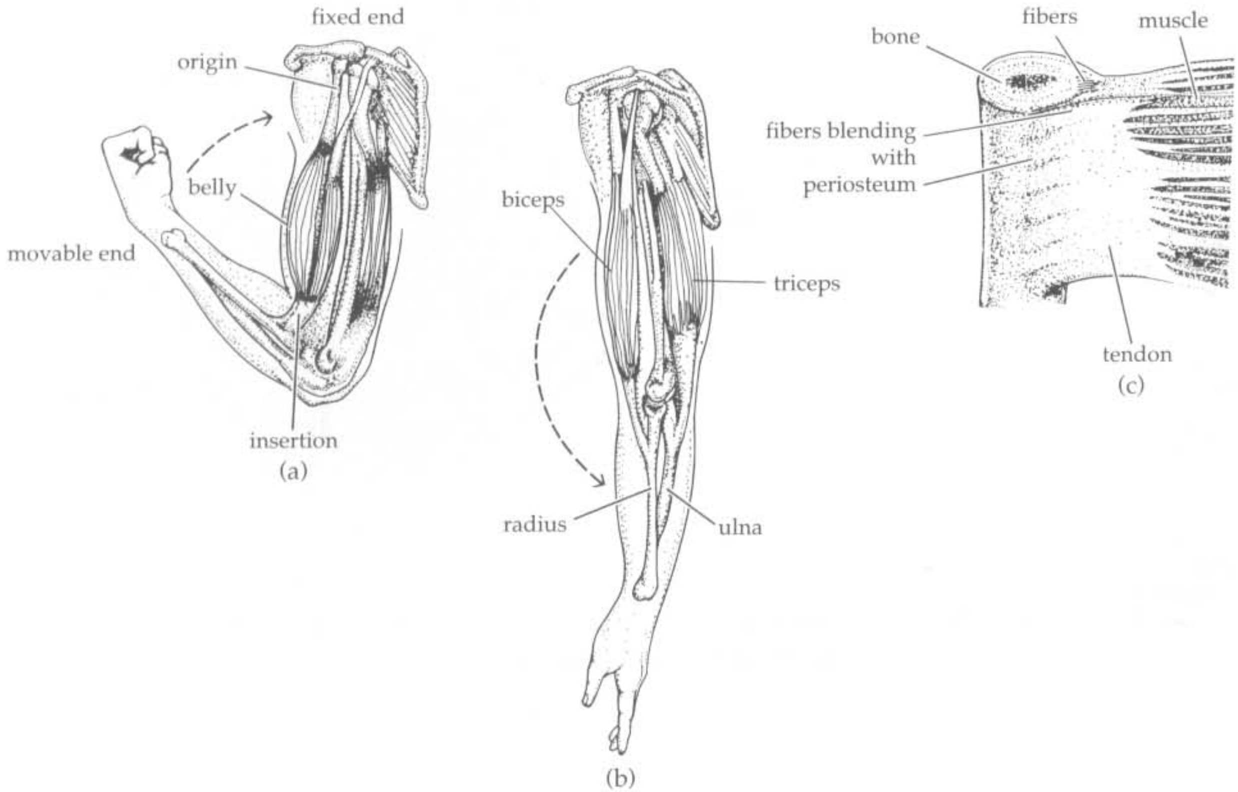


Figure 34C-1 *Structure of muscles. Skeletal muscles normally occur in antagonistic pairs: (a) the biceps flexes the human forearm and (b) its antagonist, the triceps, extends it. (c) A tendon attaches a muscle to bone.*

Objectives

- ☐ Study the general arrangement of the muscles of the trunk in the shark.
- ☐ Dissect the layers of muscles forming the body wall of the rat.
- ☐ Dissect some of the muscles of the forelimbs or hindlimbs of the rat.
- ☐ Examine the action of muscles working with bones to produce movements.

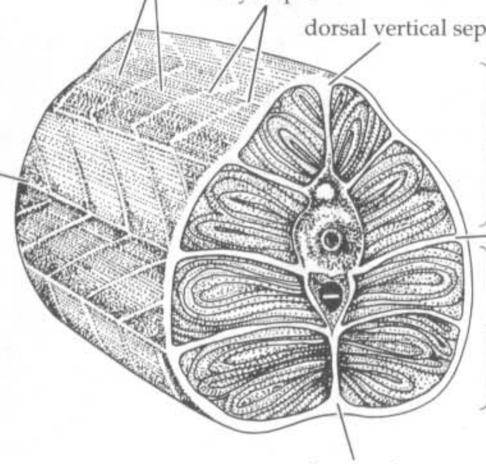
Procedure

The dissection should be done by two members of your group while the other two are dissecting the ear and brain of the shark (Exercises A and B). Be sure to share your results.

Trunk Muscles of the Shark

1. Study a demonstration specimen in which the skin has been removed from a segment of the shark's tail. Find the **horizontal septum,** a connective tissue sheet lying below the lateral-line canal. This separates the upper **epaxial muscles** from the lower **hypaxial muscles.** Short longitudinally arranged muscle fibers form **myomeres** separated by connective tissue septa, which serve as the origin and insertion points of the muscles (Figure 34C-2). In fishes, epaxial muscles serve the upper surfaces of the appendages and the hypaxial series provides muscles for the lower surfaces.

Figure 34C-2 *Trunk muscles of the shark.*



a. *How do you think shark muscles work to cause movement? Use the space below to make one or more drawings of the patterns of muscle contraction.*

Skinning the Rat

2. Place your rat in a dissecting pan. Obtain a piece of string. Tie it to one forelimb, loop it under the pan, and tie it to the other forelimb. Be sure that the string is tight enough to spread the forelimbs. Repeat this process with the hindlimbs.
3. If your specimen has had its circulatory system injected with colored latex, there will be a cut in the ventral neck region. If no incision is present, pinch a fold of skin in the midline of the neck, lifting it from the underlying tissues, and start a cut with your scissors. Separate the skin from the underlying tissues with a probe and insert your scissors under the skin. Cut along the midline toward the tail, lifting the skin with the scissors to avoid damaging underlying structures. Divert the incision to avoid the penis of the male, cutting on each side to form a **Y** around it.
4. Extend the cut from the midline to the paw of each limb. Starting at the midline, peel the skin away from the underlying tissues using your fingers or a probe. Loosen the skin around the limbs and work around the body toward the back. Cut through the skin around the wrist and ankle and free the skin from the lateral surface of the leg (you will need to untie the animal to do this). Cut through the skin around the neck, behind the ears, and peel the skin back toward the hind part of the body. Extend the caudal end of your mid-ventral incision dorsally around the base of the tail and remove the skin. Place it to one side—use it to wrap the rat's carcass for storage at the end of the laboratory.

Muscles of the Trunk

5. Place your skinned rat on its side in your dissecting tray. The neck forms the **cervical region** of the body. The **thoracic region** of the trunk includes that part of the trunk containing the rib cage and the pectoral girdle supporting the forelimbs. The **lumbar region** is between the rib cage and the pelvic girdle. The **pelvic region,** containing the pelvic girdle which supports the hindlimbs, is the most caudal region of the trunk. It is followed by the **caudal region** or tail.

6. A tough sheet of connective tissue covers the lumbar region of the back. Lateral to this, the **external oblique** muscle fibers of the trunk form a broad layer extending diagonally and caudally from the ribs to insert along a mid-ventral sheath of connective tissue. The **internal oblique** lies beneath and at right angles to the fibers of the external oblique. The internal oblique also inserts on the mid-ventral sheet of connective tissue. Using a dissecting needle, tease apart the fibers of the external oblique and the deeper fibers of the internal oblique.

7. Tease apart the fibers of the internal oblique to find the fibers of the **transversus abdominus,** a third layer of trunk muscles. If you separate these fibers, you will find the lining of the abdominal cavity, the peritoneum.

Superficial Muscles of the Pectoral and Pelvic Girdles

8. Use your probe to separate the dorsal muscles of the shoulder and hip regions into separate structures. Refer to Figure 34C-3 to locate the muscles listed in Table 34C-1. If possible, find the origin and insertion of each muscle and determine the action performed by the muscle. For reference, several additional muscles are labeled in the figure. If time permits, locate as many of these muscles as possible.

   Note the added complexity of muscles found in the appendages of the rat in comparison with the simple repeated arrangement of muscles in the trunk of the shark.

   b. Where would you look for a muscle that antagonizes the acromiotrapezius?

   ___

Table 34C-1 Superficial Appendicular Muscles of the Rat

Muscle	Pectoral Girdle (dorsal) Origin (O) and Insertion (I)	Function
Acromiotrapezius	**O:** cervical and anterior thoracic vertebrae **I:** scapula (dorsal part of pectoral girdle)	Draws scapular medially
Clavotrapezius (anterior to and below acromiotrapezius)	**O:** skull **I:** clavicle (collar bone)	Pulls clavicle and scapula anteriorly
Spinotrapezius (posterior to acromiotrapezius)	**O:** posterior thoracic and anterior lumbar vertebrae **I:** scapula	Pulls scapula posteriorly
	Pelvic Girdle and Leg (dorsal)	
Gluteus superficialis	**O:** dorsal border of ilium (pectoral girdle) **I:** femur (thighbone)	Moves thigh away from the body
Biceps femoris (posterior to gluteus superficialis)	**O:** sacral and caudal vertebrae shank of leg **I:** distal femur and proximal tibia (shank bone)	Moves thigh away from the body, flexes
Semitendinosus (posterior to biceps femoris)	**O:** sacral and caudal vertebrae **I:** tibia	Flexes shank
Gastrocnemius (and Achilles tendon) (medial edge of leg)	**O:** femur **I:** bones of the foot	Extends the foot

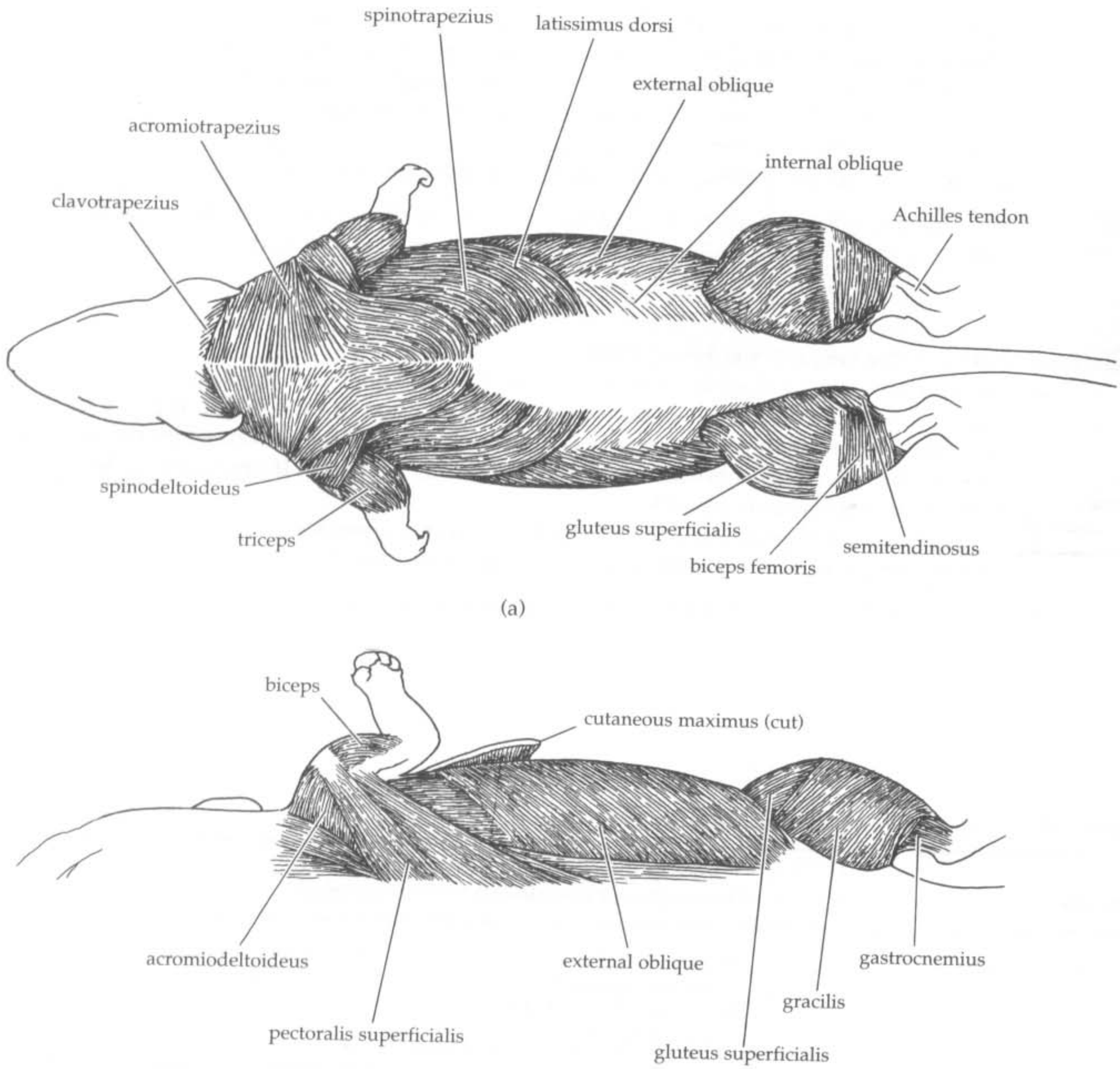


Figure 34C-3 *Muscles of the rat. (a) Dorsal view showing several superficial muscles of the trunk and appendages. The acromiotrapezius has been removed on the right side to show underlying muscles. (b) Ventral view of the pectoral and the pelvic musculature of the rat.*

c. *In dissecting muscles, did you find blood vessels (they are tough structures and are probably injected with colored latex)? Did you find nerves (tough, tendon-like white structures)?* ______________

d. *Where are blood vessels and nerves located with respect to the muscles you dissected?*

____

e. *Describe your technique for separating muscles. How do you know where to tear with the probe? How can you tell when you are within a muscle rather than between muscles?* ______________

____

f. How do the trunk muscles of the rat differ from those of the shark? ______________________

g. How do you think these differences relate to the structures and functions of the animals?

____

✓ PART 2 Bones

The skeleton of vertebrates protects some of the internal organs, supports the body, and provides the mechanical levers moved by muscles for procuring food, providing power for locomotion, and producing behavioral responses. It is an internal skeleton, or **endoskeleton.**

The vertebrate skeleton is composed of the following parts:

Axial skeleton	Skull Vertebral column
Appendicular skeleton	Pectoral girdle and forelimbs Pelvic girdle and hindlimbs
Visceral (pharyngeal) skeleton	In ancestral animals, the bony structure that supports the pharyngeal arches and to which gills are attached; parts of the pharyngeal skeleton later evolved into jaws, the base of the tongue, and the bones of the inner ear

Bones of the skeleton are derived from three sources: (1) bone preformed in cartilage, which gives rise to the basic endoskeleton; (2) dermal bone associated with the skin, which becomes incorporated into the skull and pectoral girdle in more advanced vertebrates; and (3) bones, also preformed in cartilage, associated with the visceral (pharyngeal) skeleton. The skull is the most complex element of the skeleton, containing bones from all three sources.

In this exercise, you will study the basic elements of the cartilaginous skeleton of the shark. (You can consult Laboratory 27, pages 27-12–27-14, for more detail about the appendicular skeletons of the frog and the turtle. Pages 27-14–27-18 cover the mammalian skeleton.) The skeleton of the shark shows clearly the basic arrangement of the skeletal system of vertebrates.

Objectives

- ☐ Examine the axial skeleton of the shark.
- ☐ Study the relationship of the visceral skeleton to the chondrocranium of the shark.
- ☐ Identify the major elements of the appendicular skeleton.

Procedure

Axial Skeleton—Skull

In the shark, the skull is made up of the **chondrocranium,** formed from cartilaginous elements of the axial skeleton, and the cartilaginous **visceral skeleton,** which forms the jaws and pharyngeal arches.

1. If a separate chondrocranium is available as a wet preparation or embedded in plastic, use it to study features of this part of the skull. Compare the structures that you can locate with those shown in Figure 34C-4. The location of the sense organs (olfactory capsules, orbits of the eye, and optic capsules) and brain should be familiar to you from the dissection in Exercise B. Note the anterior **rostrum,** a cartilaginous support for the snout. The caudal occipital region of the skull surrounds the **foramen magnum,** a large opening where the spinal cord exits the cranium.

2. Examine the visceral skeleton in a complete skull or in a mounted skeleton. It is composed of seven pharyngeal arches (Figure 34C-5). The first or **mandibular arch** forms the upper and lower jaws (note that the upper jaw is not attached to the chondrocranium). The second arch is the **hyoid arch.** The first gill slit, the **spiracle,** lies between the hyoid arch and the upper

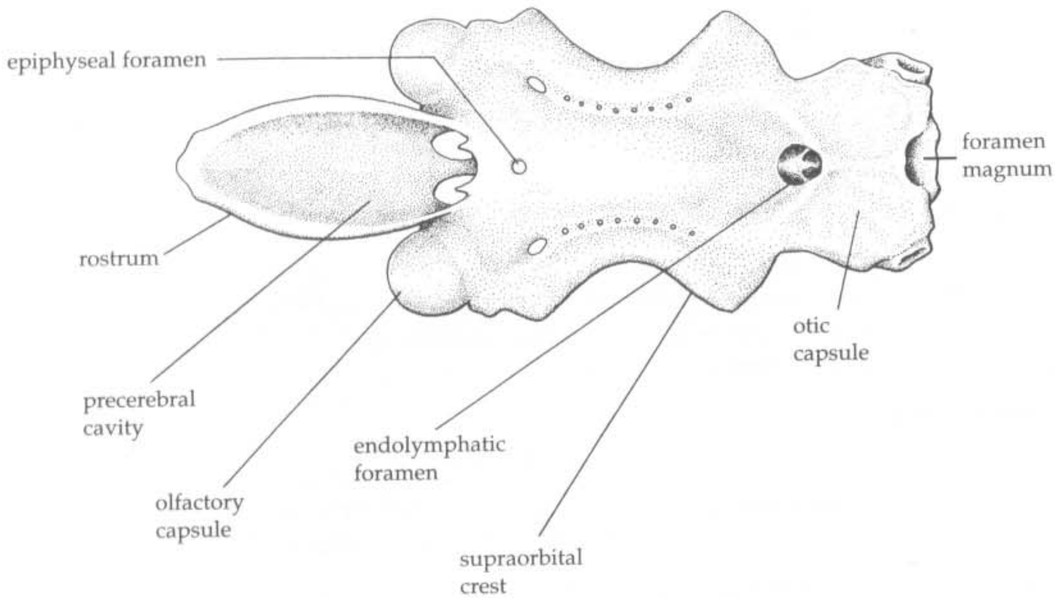


Figure 34C-4 *Dorsal view of the chondrocranium of the shark. Note that the photoreceptive pineal gland is located beneath the epiphyseal foramen.*

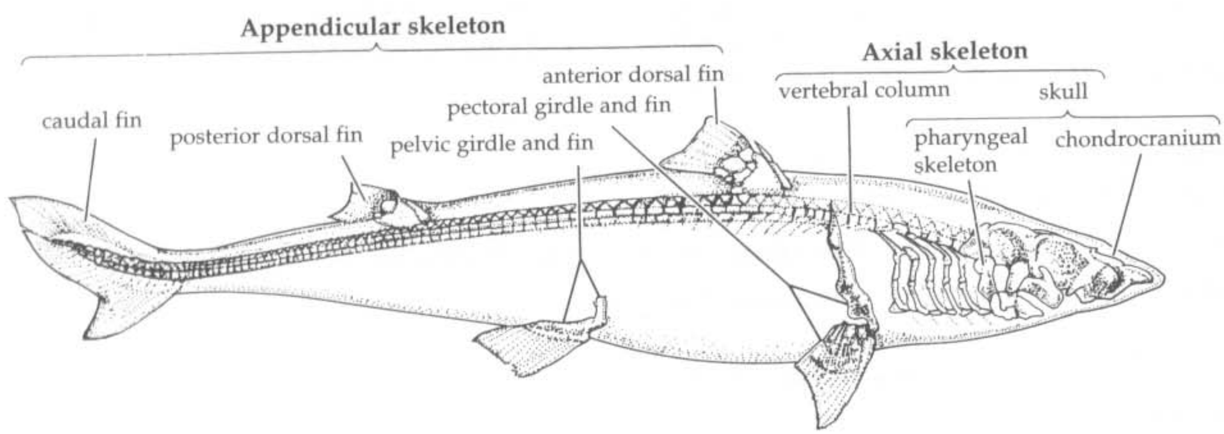


Figure 34C-5 *Skeleton of the shark.*

jaw. The last five arches form the skeletal elements that separate the remaining gill slits. With the transition to land, many elements forming the visceral skeleton have been reduced or lost, but some persist in the jaws, bones of the hyoid apparatus that supports the tongue, and bones of the middle ear.

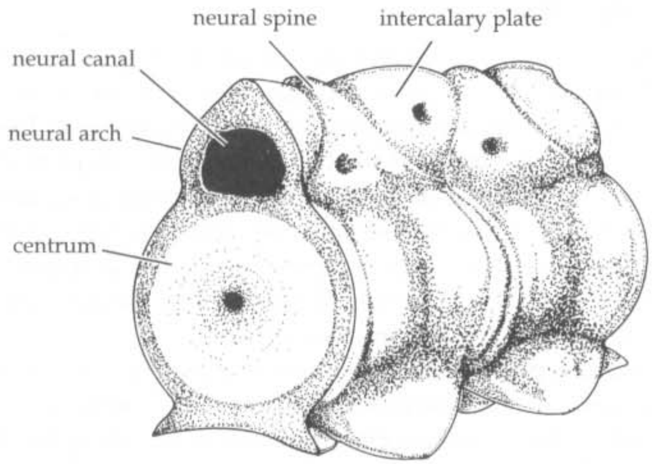
a. *Why do you suppose the spiracle has not developed into a complete gill slit and has been displaced dorsally in the shark?* ______________________________

____

Axial Skeleton—Spinal Cord

3. Study the remainder of the axial skeleton in the wet preparation (Figure 34C-5). The vertebral column is composed of cartilaginous vertebrae. Vertebrae of the trunk are composed of two parts, the solid, ventral **centrum** and the dorsal **neural arch** and **intercalary plate** which surround the spinal cord (Figure 34C-6). The face of each centrum is biconcave and is filled with gelatinous remnants of the embryonic notochord, which is continuous along the length of the spinal column, coursing through small openings in the centra. Vertebrae in the more anterior part of the trunk bear short rib cartilages attached to each centrum. Caudal vertebrae of the tail each have a **hemal arch** below the centrum enclosing the caudal artery and vein. In most vertebrates, remnants of the notochord exist only as the disks that separate the adjoining bones of the vertebral column. The persistence of the notochord in sharks probably represents an ancestral characteristic (which also characterizes the embryonic development of vertebrates).

Figure 34C-6 *Trunk vertebrae of the shark.*



4. On demonstration is a sagittal (dorsal to ventral) section through the midline of the vertebral column. Note the **centra,** the spaces filled with persistent notochord, and the neural canal filled with the spinal cord.

5. In the dissection on demonstration, locate the skeletal elements of the **dorsal fins** above the vertebral column. Compare their structure with that of the **caudal fin.** These structures are also part of the axial skeleton.

   b. *Which of the fins is most important in propelling the organism through the water?* __________

   c. *Can you suggest how the myomeric muscles work to move this fin? (It might help to make a drawing in the space below.)* __________

Appendicular Skeleton

6. The appendicular skeleton consists of the pectoral girdle and forelimbs and pelvic girdle and hindlimbs. Locate the pectoral girdle behind the last of the pharyngeal arches. It consists of a **U**-shaped bar and several cartilages that support the fibrous elements of the fin. Dermal elements are missing in the pectoral girdle of the shark.
7. Find the pelvic girdle. In the live shark it is embedded in the ventral body wall anterior to the cloacal opening. Like the pectoral girdle, it is made up of several endochondral elements that support fibrous elements in the fins.

Cartilages of the appendages associated with the pectoral and pelvic girdles of sharks bear no clear relation to the skeleton supporting the limbs of tetrapods. However, in the lobe-finned bony fishes, which gave rise to amphibians, bones of the appendages are arranged as they are in our limbs. (See Laboratory 27, pages 27-12–27-14.)

✓ PART 3 Other Effectors

Electric organs are present in several groups of cartilaginous and bony fishes. These organs are composed of highly modified muscle tissue, and their somatic motor fibers are arranged in series (like the cells of a battery) to produce a weak electric field surrounding the fish. Deviations in the electric field can be sensed by lateral-line sensors and may aid the fish in the detection of nearby objects. Electric discharges may also be detected by other fishes in the water and, like bird song or human speech, may be used in communication. In the electric eel, the electric catfish, and the electric ray, these electric organs have become highly developed to produce much larger currents and higher voltages. In the electric ray, currents may reach 50 amperes at 50 volts, yielding a power of 2,500 watts! Electric discharges of this magnitude paralyze surrounding fishes on which the animal can feed.

Chromatophores, pigment cells found in the integument, are also considered effectors in some vertebrates—remember that effectors are organs that produce externally directed responses. In some fishes, amphibians, and reptiles, chromatophores respond directly to light, contracting in bright light to concentrate their pigment and lighten the animal, and vice versa in dim light. In many of these organisms, they also respond to a hormone (melanophore-stimulating hormone or MSH) from the pituitary gland and to another hormone, melatonin (melanophore-concentrating hormone or MCH), from the pineal gland. In certain species such as flounders that can rapidly camouflage themselves to match changing background patterns, the chromatophores are innervated and the nervous system responds quickly to input from the eyes.

Integumentary glands can respond to local, hormonal, and nervous stimulation in various situations. In some fishes, mucous glands have become specialized as bioluminescent organs (**photophores**), producing light in the dark waters of the deep ocean to help in finding prey and mates. In some glands, light is produced when the gland is activated by motor nerves. Others contain cultures of luminescent bacteria which provide a constant source of light (emissions may be controlled by lidlike shutters).

Laboratory Review Questions and Problems

1. Complete the following table for the three major sense organs of the vertebrate head.

Sense Organ	Stimulus	Cranial Nerve	Brain Projection

2. How does the structure of the membranous labyrinth in our inner ear differ from that of the shark?

3. You place your hand on a hot burner on the stove. Describe what happens. (Outline sensory events, control events, and the effectors involved in your response.)

4. Explain how muscles and bones normally work together as effectors.

5. List the effectors found in vertebrates.