

Edited by Marvalee H. Wake

Hyman's Comparative Vertebrate Anatomy

Third

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Comparative
Vertebrate
Anatomy

Third Edition

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ns and T. S. Parsons, 6:1-157. New York: Academic

62. The structure of the ovary-vertebrates. S. Zucker-
e ovary, pp. 121-42. New York: Academic Press.

0. The development of the vertebrate excretory system.
59-87.

62. The structure of the ovary-mammals. In S. Zucker-
vary, pp. 143-88. New York: Academic Press.

970. Placentation in the garter snake *Thamnophis sir-*
. 131:52-87.

rel, J.; and Petal, J. 1966. Considerations sur le plan
ization du rein des mammifères. *C. r. Ass. Anat.* 50:

reproduction. In *Physiology of the amphibia*, ed. B.
18. New York: Academic Press.

and Marshall, F. H. A. 1952. Cyclical change in the
gans of the lower vertebrates. In F. H. A. Marshall,
roduction, pp. 156-225. London: Longmans, Green.
The ovarian cycle of mammals. New York: Nafner

Muller, A. F., eds. 1969. *The kidney: Morphology, bio-*
iology. 2 vols. New York: Academic Press.

Mechem, J. S. 1974. Reproductive and courtship pat-
ology of the amphibia, ed. B. Lofts, 2:310-522. New
c Press.

76. Evolution of viviparity in mammals. In *Reproduc-*
ls, ed. C. R. Austin and R. V. Short, 6:32-70. New
ge University Press.

3. *From Fish to Philosopher*. Boston: Little, Brown.

Guttman, S. I., eds. 1977. *The reproductive biology of*
w York: Plenum Press.

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The Comparative Anatomy of the Nervous System and the Sense Organs

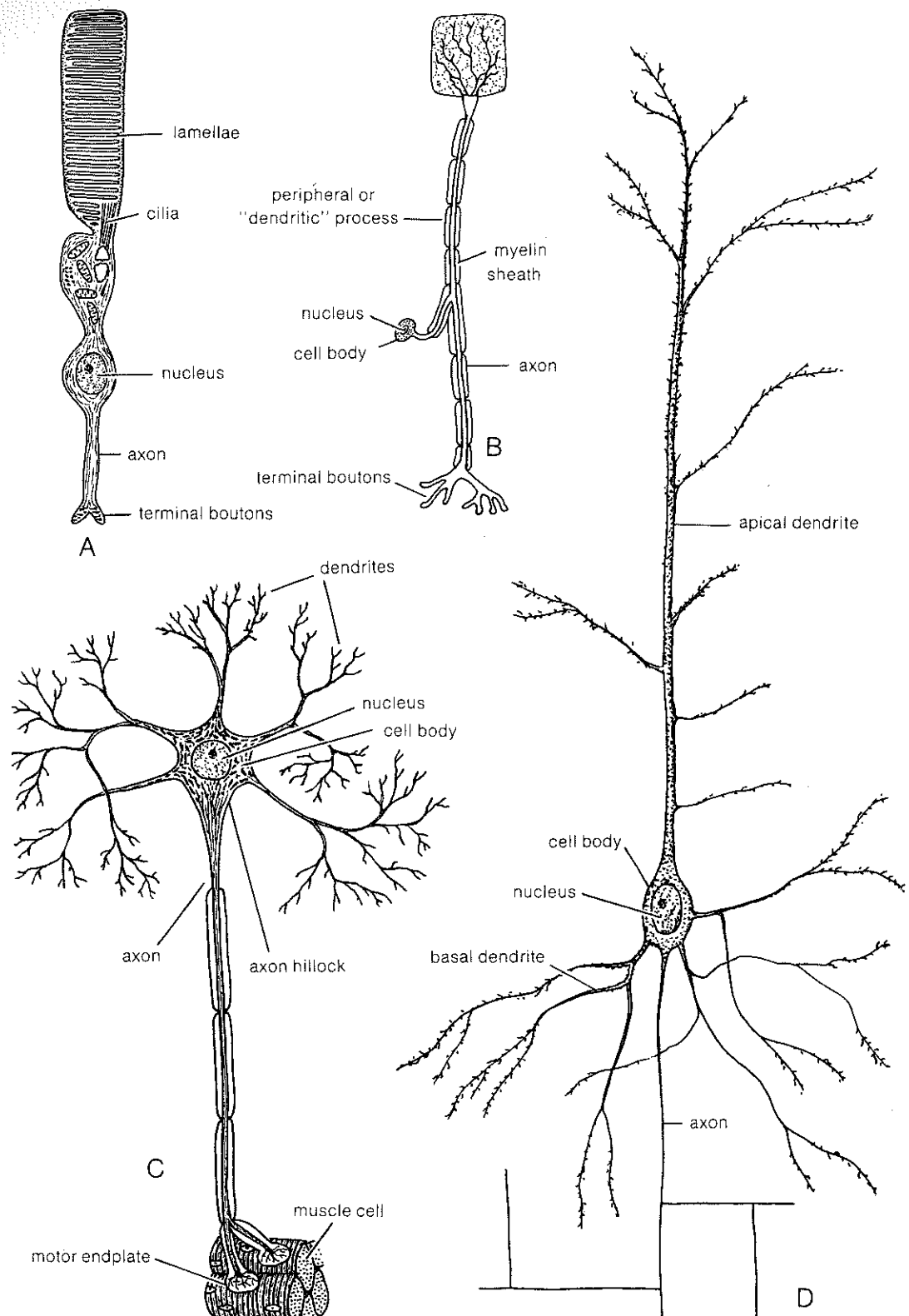
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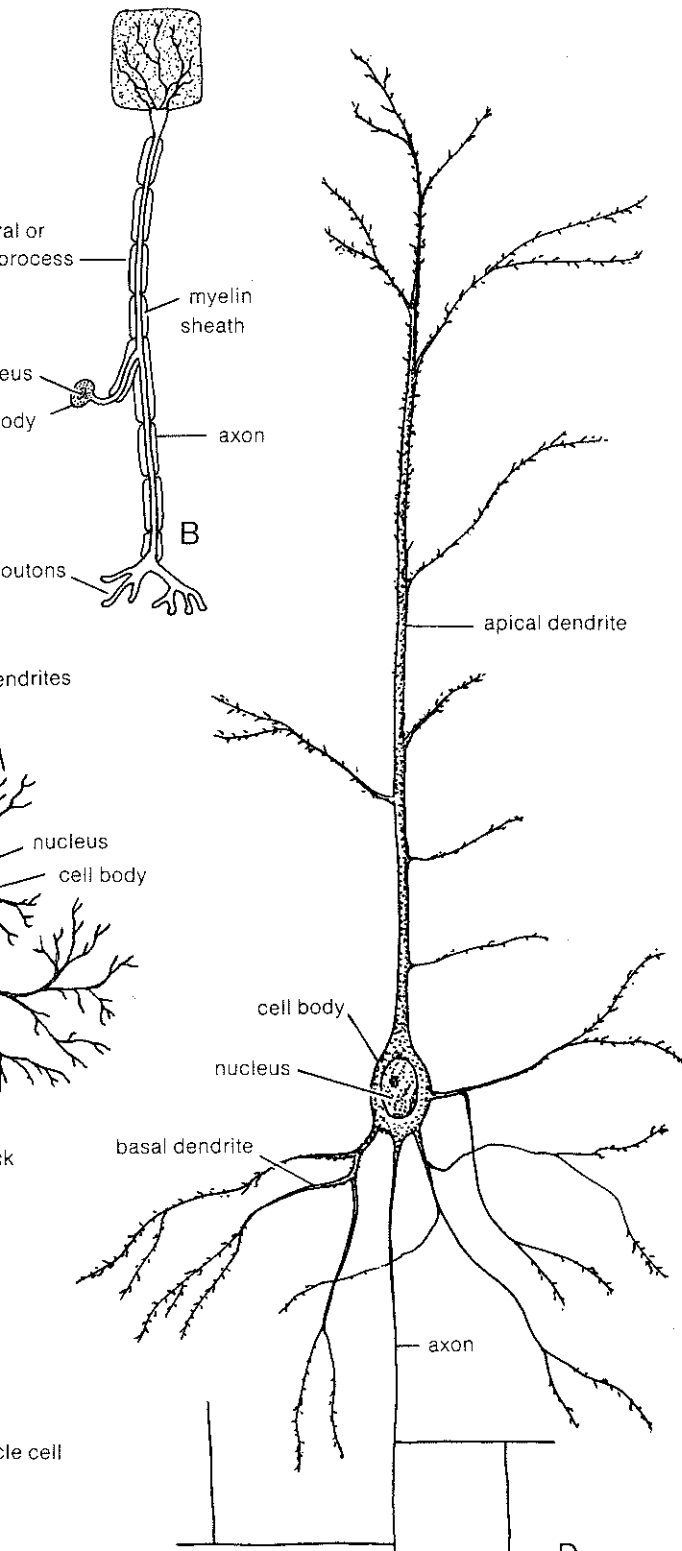
A. General Considerations

The nervous system is anatomically and functionally the most complex system of the vertebrate body. Its organization is still not as fully understood as the other organ systems, although in the last decade, new and exciting experimental methods have become available that allow us to begin to understand its organization better. At present, the phylogeny of the vertebrate nervous system is known only in very vague outline. Tantalizing bits of information hint at its organization and history. This chapter will describe some of the variation that exists in vertebrate nervous systems and suggest the functional significance of that variation.

1. The Parts of the Nervous System

The structural unit of the nervous system is the *nerve cell*, or *neuron*, which consists of the cell body and one or more processes, or *neurites*, that may be very long. The most generalized neuron is the *neurosensory cell*, in which the usually elongated cell body is situated at the surface of the body and acts as a *sensory receptor* and also as a *conductor*. Its inner end continues as a nerve fiber, the *axon*, joining the central nervous system. Neurosensory cells are common in invertebrates, but among vertebrates they are limited chiefly to the olfactory epithelium and the retina of the eye (fig. 13.1). A more specialized neuron is the *unpolarized nerve cell*, usually with several neurites, along which impulses pass in either direction. This type of neuron is commonly found in invertebrate nervous systems. The most specialized neuron, the type found in vertebrates, is the *polarized nerve cell*, which receives impulses along one or more processes, the *afferent* processes, or *dendrites*, and sends them out along one process, the *efferent* process, or *axon*. Axons and dendrites differ histologically as well as functionally. Neurons are also classified by the number and arrangement of the neurites they possess. Neurons that possess a single dendrite and a single axon are called *bipolar* neurons. Bipolar neurons are usually neurosensory neurons. Neurons that possess a single neurite are called *pseudounipolar* neurons. These neurons develop from bipolar neuroblasts and secondarily fuse their two neurites. Pseudounipolar neurons make up the dorsal root ganglia of the spinal nerves and ganglia of the cranial nerves. Neurons that possess more than one dendrite are called *multipolar* neurons. Multipolar neurons consti-





with a considerable degree of dendritic overlapping from adjacent neurons. These neurons appear to process afferent signals of very heterogeneous origin, and such populations are referred to as regions of *neuropil*. More specialized neurons have fewer dendrites with greater morphological complexity and little or no overlap from adjacent neurons. These more specialized neurons appear to process afferent signals of a homogeneous origin. Such cellular populations are most frequently found in multiple laminae called cortices.

An aggregation of nerve cell bodies outside the central nervous system is called a *ganglion*. A similar group inside the central nervous system is termed a *nucleus*. A *nerve* is a bundle of axons outside of the central nervous system. A similar group of axons inside the central nervous system is termed a *tract*. The axons of neurons are encased in a proteolipid sheath that begins just distal to the body and continues almost to the termination of the axon. This sheath lies external to the cellular membrane of the axon. Axons surrounded by such sheaths are said to be *myelinated* and are frequently referred to as *white fibers*. In the past, many axons were thought to lack such a sheath. They were said to be *unmyelinated* and were frequently referred to as *gray fibers*, but electron microscopy has shown that most gray fibers possess a thin sheath. The myelin sheath was once believed to be a nonliving structure secreted by neuroglial cells found near axons. It is now known, however, that the myelin sheath is a series of living plasma membranes of the neuroglial cells that are wrapped around the axon. The myelin sheath is not continuous along the length of an axon but is broken at intervals. In axons outside the central nervous system, these regions of discontinuity along the axon are termed the *nodes of Ranvier*. Electron microscopy has recently demonstrated that similar nodes are found around axons inside the central nervous system. Neuroglial cells and their myelin sheaths have been related to a number of functions: they electrically insulate axons; they are involved in the exchange of metabolites with neurons; they transport material differentially between blood and neurons; and they may have a trophic role in the regeneration of axons.

The distal ends of axons are finely branched and, except for those in specialized contacts on muscle, glands, and blood vessels, normally have small knobs (*boutons terminaux*) near cell bodies, dendrites, or the proximal portions of axons. In vertebrates there is not cytoplasmic continuity between cells, and the space between the boutons of one neuron and the cellular membrane of a second neuron is called a *synapse*. When a nerve impulse is generated in the dendrites and cell body of a neuron, it spreads down the axon to the boutons. There a chemical is released that may cause the second neuron to generate an impulse. Impulses reaching a bouton do not always cause a second neuron to generate an impulse. The second neuron may react only to a specific rhythm of bouton transmissions, or frequently boutons may actually inhibit a second neuron

formed by the arches of the vertebrae. Brain and cord are composed of both nerve cell bodies, which form the *gray matter*, and nerve fibers, which form the *white matter*, so called because the thicker myelin sheaths lend a white color. The peripheral nervous system consists of the *cranial nerves*, arising from the brain, and the *spinal nerves*, arising from the spinal cord. Both kinds of nerves consist of the axons of nerve cell bodies found inside the brain or cord or in outside ganglia. The nerves, especially the spinal nerves, are markedly metameric in arrangement—typically there is a pair of nerves to each body segment—but this metamerism is probably imposed upon the nerves by the metamerism of the muscles and vertebrae. The autonomic nervous system controls and regulates in general the visceral activities of the body and the organs that subserve those functions, such as the heart and the digestive tract, the smooth musculature in several systems, secreting glands, blood vessels, and the respiratory and urogenital systems. It consists of a ganglionated cord lying to either side of the vertebral column along the dorsal coelomic wall, of ganglia in the head and among the viscera, and of connecting and distributing nerves.

2. The Development of the Nervous System

The central nervous system is formed by the enfolding of the ectoderm along the middorsal region of the embryo to form a tube (see chap. 4). That portion of the tube situated in the head becomes the brain, and that part posterior to the head becomes the spinal cord. The original single layer of enrolled ectoderm cells proliferates to form a thick zone of cells around the central cavity; most of these become nerve cells, but some give rise to supporting cells or neuroglia.

The location of this zone of nerve cell bodies, or gray matter, around the central cavity is believed to be the ancestral arrangement retained in a modified form throughout vertebrates in the spinal cord; but in the brain of all vertebrates there is considerable migration of the gray matter toward the periphery of the brain wall.

Neurites arise from the embryonic nerve cells and may remain in the central nervous system to form a peripheral zone of myelinated fibers, the white matter, or may grow out of it to form the nerves. The ganglia outside the brain and cord result from the migration of nerve cell bodies, mostly from the neural crests, a pair of longitudinal strands left outside the neural tube at the time of its closure.

In the development of the brain the original, simple tube becomes marked off by a transverse ventral fold into two regions, the primitive *forebrain* and *hindbrain* (fig. 13.2). This fold is situated just behind the future *infundibulum*, and it also marks approximately the anterior end of the notochord. The anterior part of the primitive forebrain, called the *telencephalon*, puts out paired lateral swellings, which become the *cerebral hemispheres*. The region behind this is the *diencephalon*, and it soon shows a dorsal evagination, the *pineal apparatus* (fig. 13.2C). The *diencephalon* becomes marked off by a constriction from the last part

the arches of the vertebrae. Brain and cord are composed of cell bodies, which form the *gray matter*, and nerve fibers, in the *white matter*, so called because the thicker myelin is a white color. The peripheral nervous system consists of the *nerve roots*, arising from the brain, and the *spinal nerves*, arising from the spinal cord. Both kinds of nerves consist of the axons of nerve cell bodies and inside the brain or cord or in outside ganglia. The nerves, like the spinal nerves, are markedly metameric in arrangement—there is a pair of nerves to each body segment—but this metamericism probably imposed upon the nerves by the metamerism of the vertebral column. The autonomic nervous system controls and regulates the visceral activities of the body and the organs that perform these functions, such as the heart and the digestive tract, the respiratory and urogenital systems. It consists of a ganglionated nervous system, with a pair of ganglia on either side of the vertebral column along the dorsal and ventral roots of ganglia in the head and among the viscera, and of connecting nerves.

The nervous system is formed by the enfolding of the ectoderm in the mid-dorsal region of the embryo to form a tube (see chap. 4). The part of the tube situated in the head becomes the brain, and that part extending to the head becomes the spinal cord. The original single layer of ectoderm cells proliferates to form a thick zone of folded cells; most of these become nerve cells, but some give rise to supporting cells or neuroglia.

The arrangement of this zone of nerve cell bodies, or gray matter, around the central cavity is believed to be the ancestral arrangement retained in form throughout vertebrates in the spinal cord; but in the higher vertebrates there is considerable migration of the gray matter to the periphery of the brain wall.

Nerve fibers arise from the embryonic nerve cells and may remain in the central nervous system to form a peripheral zone of myelinated fibers, the *nerve sheath*, or may grow out of it to form the nerves. The ganglia outside the brain and cord result from the migration of nerve cell bodies, which in the neural crests, a pair of longitudinal strands left outside the tube at the time of its closure.

In the development of the brain the original, simple tube becomes divided by a transverse ventral fold into two regions, the *forebrain* and *hindbrain* (fig. 13.2). This fold is situated just behind the *notochord*, and it also marks approximately the anterior end of the *notochord*. The anterior part of the primitive forebrain, called the *telencephalon*, puts out paired lateral swellings, which become the *cerebral hemispheres*. The region behind this is the *diencephalon*, and it has a dorsal evagination, the *pineal apparatus* (fig. 13.2C). The

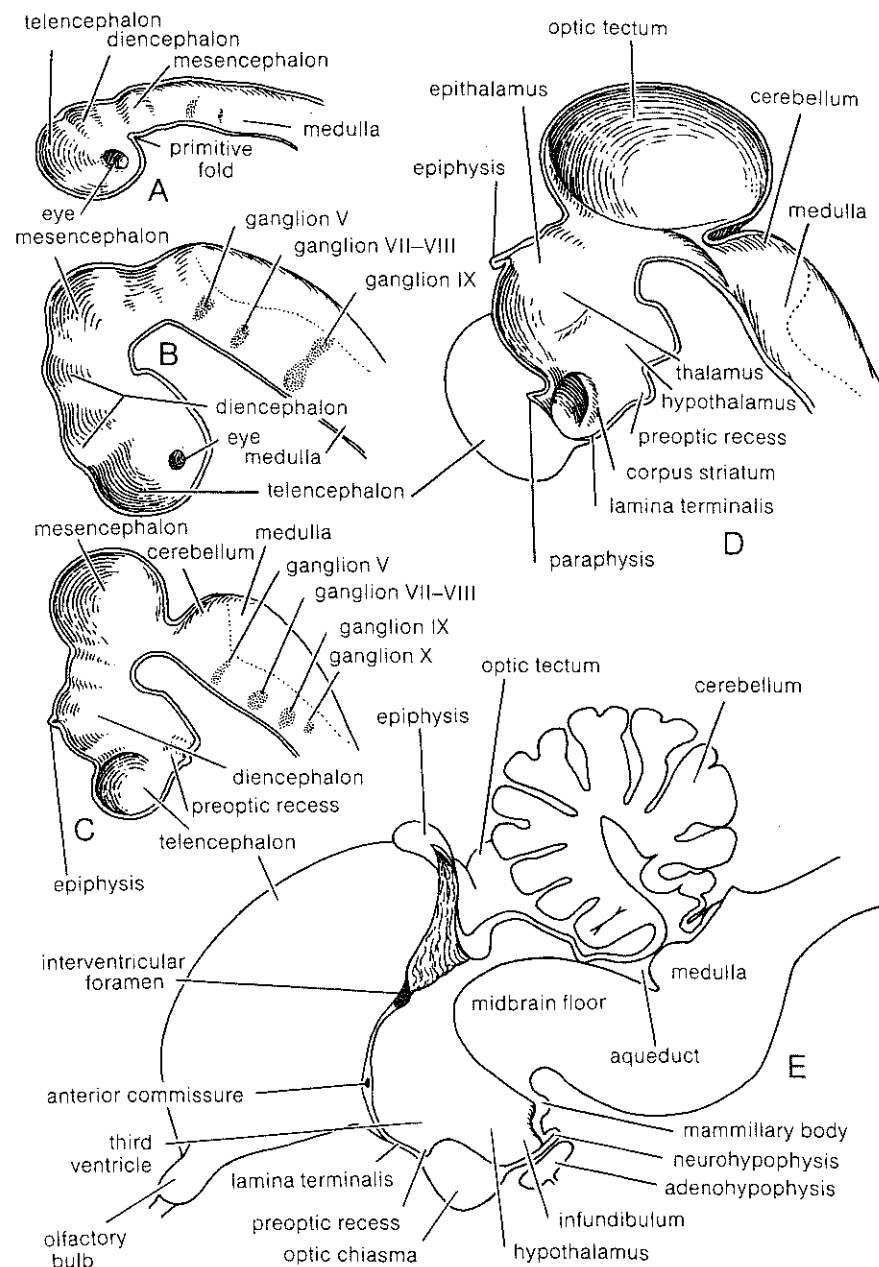


Fig. 13.2. Stages in the embryonic development of the chick brain as seen in sagittal view. *A*, primitive or ventral fold stage at which three major brain divisions can be recognized; *B*, main regions of brain have developed, as have the cranial nerve ganglia; *C*, epiphysis appears and cerebral hemispheres have expanded; *D*, paraphysis appears and optic tectum has expanded; *E*, olfactory

out a dorsal enlargement, the *cerebellum* (fig. 13.2E), and the remainder and greater part of the hindbrain is the *myelencephalon* or *medulla oblongata*, characterized by its thin roof and the large nerve ganglia along its side walls (fig. 13.2C). The medulla oblongata is continuous with the spinal cord, from which it is not definitely delimited. These five main regions of the embryonic brain persist as such in the adult brain, developed by thickenings, folds, and outgrowths of their walls.

3. The Meninges The central nervous system does not fill the bony canal in which it lies but is separated from it and protected by fluid and by connective tissue membranes, the meninges. In cyclostomes and fishes there is usually but one membrane, the *primitive meninx*. Amphibians, reptiles, and birds have two, an outer *dura mater* and an inner *secondary meninx*. In mammals there are three meninges: a relatively tough outer *dura mater* and two delicate inner ones, the *arachnoid* and the *pia mater*, both differentiations of the secondary meninx. The *pia mater* is closely associated with the brain and cord, into which it may send connective tissue partitions, and is separated by a considerable *subarachnoid space* from the web-like *arachnoid*. Outside the *dura mater* there is also a fat-vascular cushioning layer. The spaces around the brain and cord and between the meninges are in communication with the central canal of the cord and the ventricles of the brain, and all are filled with the *cerebrospinal fluid*, differing little from blood plasma.

4. Gross Features of the Adult Central Nervous System The brain and spinal cord of vertebrates demonstrate the same kinds of morphological specialization as do other vertebrate body systems. That is to say, as vertebrates have adapted to different ways of life their brains reflect these specialized ways of life. The nuclei and tracts, which reflect much of this specialization, are described in the following section on the functional divisions of the nervous system.

All vertebrates possess the same number of brain divisions (fig. 13.3), but they vary in both absolute and relative volumes among species. These differences reflect both phylogenetic organization and physiological specialization for a particular ecological niche. Neurobiologists have often ranked living vertebrates and their brains in terms of their taxonomy and then spoken of their structure as though it had not changed in millions of years. The brain of a living frog may be a very poor substitute for the brain of an amphibian that lived 400 million years ago. We must always ask what structures in living vertebrate brains have been inherited from their ancient ancestors with little change, and what structures have been greatly modified in the course of their evolution. Does the brain of a living lamprey closely resemble the brain of an ancient ostracoderm, from which the lamprey sprang? How have nuclei and tracts changed from ancestral reptiles to modern reptiles, or to modern mammals? These questions and many more are only now beginning to be answered, and

caudal enlargement, the *cerebellum* (fig. 13.2E), and the remainder of the hindbrain is the *myelencephalon* or *medulla oblongata*, characterized by its thin roof and the large nerve ganglia along its walls (fig. 13.2C). The medulla oblongata is continuous with the spinal cord, from which it is not definitely delimited. These five main divisions of the embryonic brain persist as such in the adult brain, despite the various thickenings, folds, and outgrowths of their walls.

The central nervous system does not fill the bony canal in which it lies. It is separated from it and protected by fluid and by connective tissue membranes, the meninges. In cyclostomes and fishes there is usually only one membrane, the *primitive meninx*. Amphibians, reptiles, and birds have two, an outer *dura mater* and an inner *secondary meninx*. In mammals there are three meninges: a relatively tough outer *dura mater* and two delicate inner ones, the *arachnoid* and the *pia mater*, both differentiated from the secondary meninx. The *pia mater* is closely associated with the brain and cord, into which it may send connective tissue partitions, the arachnoid, separated by a considerable *subarachnoid space* from the web-like *arachnoid*. Outside the *dura mater* there is also a fat-vascular cushioning layer. The spaces around the brain and cord and between the meninges are in communication with the central canal of the cord and the ventricles of the brain, and all are filled with the *cerebrospinal fluid*, different from blood plasma.

The brain and spinal cord of vertebrates demonstrate the same kinds of evolutionary specialization as do other vertebrate body systems. That is, as vertebrates have adapted to different ways of life their brains have evolved these specialized ways of life. The nuclei and tracts, which reflect the results of this specialization, are described in the following section on the functional divisions of the nervous system.

All vertebrates possess the same number of brain divisions (fig. 13.3), but they vary in both absolute and relative volumes among species. These differences reflect both phylogenetic organization and physiological specialization for a particular ecological niche. Neurobiologists have often spoken of living vertebrates and their brains in terms of their taxonomy and evolution, as though it had not changed in millions of years. The brain of a living frog may be a very poor substitute for the brain of an amphibian that lived 400 million years ago. We must always remember that structures in living vertebrate brains have been inherited from ancient ancestors with little change, and what structures have been modified in the course of their evolution. Does the brain of a lamprey closely resemble the brain of an ancient ostracoderm, from which the lamprey sprang? How have nuclei and tracts changed from ancestral reptiles to modern reptiles, or to modern mammals? These questions and many more are only now beginning to be answered, and

the band-like cord (fig. 13.4B) lies on the notochord. In tetrapods the cord presents *cervical* and *lumbar enlargements*, associated with the limbs; these are usually absent in fishes and limbless tetrapods such as snakes. The cord extends the full length of the vertebral canal in generalized

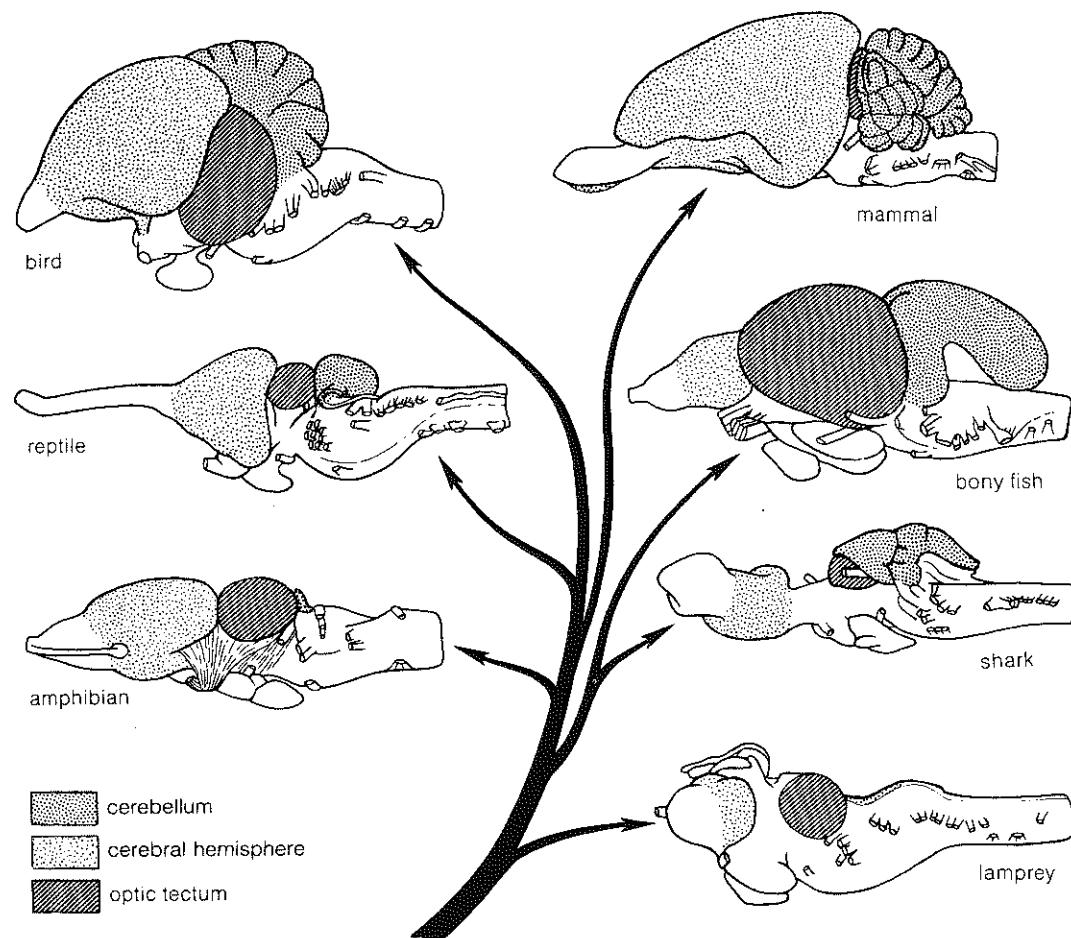


Fig. 13.3. Relative development of major brain divisions in a series of vertebrates. Brains are not drawn to scale. Modified after Northcutt 1977 (McGraw-Hill encyclopedia of science and technology. New York: McGraw-Hill).

fishes, reptiles, and birds; but in mammals and many teleosts it is much shorter than the vertebral column, tapering to a fine strand, the *terminal filament*. The cavity of the spinal cord is reduced to a very small *central canal* in the adult, and this is lined by a one-layered columnar epithelium, termed the *ependyma*. The gray matter of the cord, composed chiefly of nerve cell bodies and nonmyelinated axons, occupies its central region

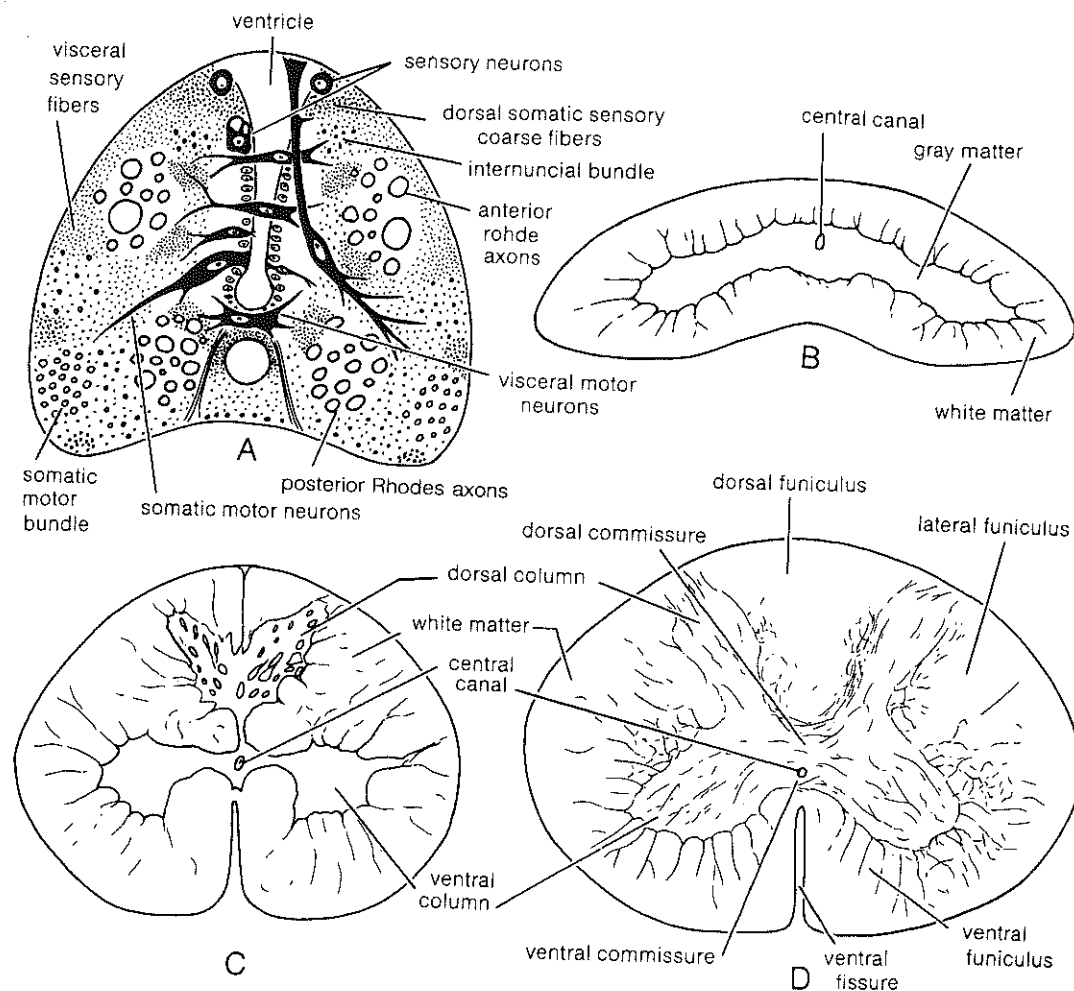
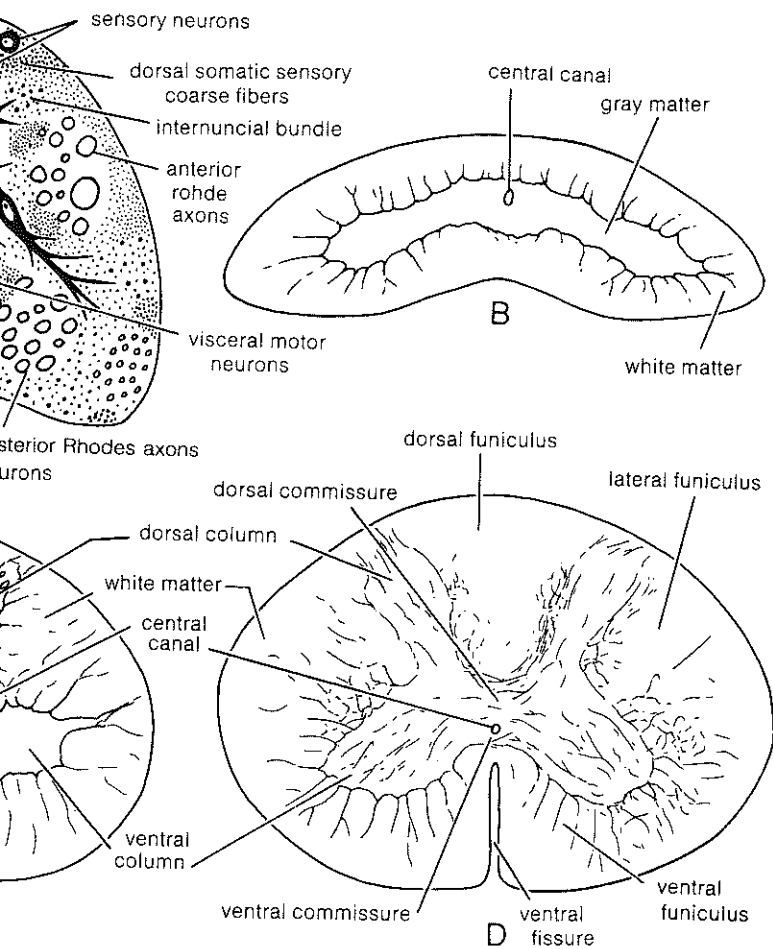


Fig. 13.4. Transverse section of the spinal cord showing the location and extent of neuronal cell bodies (gray matter) and more peripheral axonal pathways (white matter). A, *Branchiostoma*; B, larval lamprey; C, shark; D, mammal.

passing above and below it as the *dorsal* and *ventral commissures*, respectively. In anamniotes the gray matter varies in section from a rounded or quadrangular shape to a shape somewhat like an inverted T and Y (fig. 13.4C); in cyclostomes it forms a broad band (fig. 13.4B). The white matter, constituted of ascending and descending bundles or tracts of myelinated axons, forms a thick peripheral zone of the cord and is divided by the gray columns into *dorsal*, *lateral*, and *ventral funiculi* (fig. 13.4D). Columns and funiculi are, of course, less evident and defined in anamniotes, and they also differ in shape and proportions at different levels of the cord. The funiculi may be subdivided into



13.4. Transverse section of the spinal cord showing the location and distribution of neuronal cell bodies (gray matter) and more peripheral axonal pathways (white matter). A, *Branchiostoma*; B, larval lamprey; C, shark; D, teleost fish.

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ity of the skull, and the shape of this cavity conforms to the contours of the brain. The brain rests ventrally on the chain of cartilage bones ossified in the floor of the chondrocranium. Although the brain is bent at the mesencephalon in the embryos of all vertebrates, it straightens out in line with the longitudinal body axis in the later development of anamniotes. A permanent flexure is limited to amniotes and is especially notable in the brains of primates. The arrangement of the gray and white matter of the cord persists into the caudal part of the brain, but anteriorly the gray and white matter intermingle irregularly; in the cerebral hemispheres and cerebellum the gray matter forms a peripheral stratum over more central white matter. The white matter of the brain consists of ascending and descending tracts connecting various parts of the brain and cord; the gray matter consists mostly of "nuclei" (also called centers), that is, aggregates of cell bodies whose axons form the tracts of the white matter or issue in the cranial nerves.

The fifth, most posterior part of the brain, the myelencephalon or *medulla oblongata*, is continuous with the spinal cord through the foramen magnum and cannot be definitely delimited from the cord, although the boundary is usually placed just anterior to the level of the first spinal nerve. The rear part of the medulla is similar to the spinal cord, having a thick wall around the very small central canal. This canal soon widens out, however, into a large rhomboidal or triangular cavity, termed the *fourth ventricle*; its roof is greatly thinned out and consists only of the ependymal epithelium. To the outside of this, however, there adheres the richly vascularized pia mater, the two together forming the *tela choroidea*. In certain regions this is invaginated into the cavity of the fourth ventricle as vascularized tufts, known as *choroid plexi*. The walls of the medulla consist chiefly of the nuclei of origin and of termination of the fifth through the twelfth cranial nerves and their connections. These nuclei are arranged in generalized vertebrates according to their functions into four longitudinal columns (see below, under functional components), and this arrangement persists more or less throughout vertebrates.

The fourth division of the brain, or metencephalon, forms dorsally the *cerebellum*. This is of slight development in cyclostomes and amphibians, consisting of a ledge in front of the tela choroidea of the medulla, but is large in fishes of active habits, such as selachians and teleosts. It is of rather small size in most reptiles but increases in size and complexity in birds and mammals. Typically it consists of a median portion, the *body* or *corpus*, and a pair of lateral lobes, which are called *auricular lobes* after their shape in selachians, and which contain extensions of the fourth ventricle, the *auricular recesses*. In amniotes the auricular lobes are usually called the *floccular lobes*. The body of the cerebellum is generally marked by transverse fissures, which increase in number in birds and mammals, where the corpus seems more or less

and appear to be concerned with muscles of the distal parts of the paired appendages. The cerebellum has a surface layer of gray matter known as the *cerebellar cortex*, and in birds and mammals this is underlain by a particularly thick stratum of white matter, so that sections of the cerebellum of these groups show the familiar "arbor vitae," lobulations of white matter covered by gray. It is characteristic of the teleost cerebellum that there is a thick invaginated lobe, termed the *valvula*. The cerebellum usually contains a cavity, the *cerebellar ventricle*.

The floor of the metencephalon shows little differentiation from the medulla in anamniotes, but, with increasing importance of the cerebellar hemispheres, its tracts and nuclei increase in volume and functional significance. Hence in mammals this floor, termed the *pons*, has a conspicuous fibrous structure, visible on the ventral surface in front of the medulla.

The functions of the cerebellum, insofar as they are known, are the coordination of muscular movements, the maintenance of muscular tone, and the equilibration of the body in space. Consequently, it has connections with many levels of the central nervous system, but particularly with sensory impulses from muscles and joints (*proprioceptive impulses*) and with the equilibratory mechanism of the inner ear.

The *mesencephalon* or *midbrain*, the third division of the brain, is also best developed dorsally, where its thick roof, known as the *optic tectum*, usually has two curved eminences (the *optic lobe*). In mammals there are four such externally apparent eminences, the *corpora quadrigemina*; the anterior pair are called the *superior colliculi*, the posterior pair the *inferior colliculi*. The inferior colliculi are present in fish but are not evident externally. Their exposure on the surface in mammals results from differences in embryonic development. The midbrain floor consists chiefly of tracts to and from other parts of the brain. The quantitative increase in tracts from the cerebral hemispheres of mammals results in a pair of conspicuous bundles, the *cerebral peduncles*, visible externally on the ventral surface of the midbrain. The midbrain is solid in mammals except for a narrow canal, the cerebral aqueduct (formerly the aqueduct of Sylvius), which passes through it from the fourth ventricle. In nonmammalian vertebrates the optic lobes are usually hollow, containing cavities, termed the *optic ventricles*, which open into the aqueduct.

The *diencephalon*, the second division of the brain, is chiefly a relay center for the cerebral hemispheres, and consequently its size and importance parallel those of the latter. It has a central cavity, the *third ventricle*, into which the aqueduct opens, and which in mammals is much compressed laterally. The roof of the third ventricle is thinned to an ependyma and forms a tela choroidea, which has choroid plexi projecting into the interior or, in certain anamniotes (petromyzonts, some ganoid fishes, selachians, some reptiles), choroid lamellae.

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The *mesencephalon* or *midbrain*, the third division of the brain, is also best developed dorsally, where its thick roof, known as the *optic tectum*, usually has two curved eminences (the *optic lobe*). In mammals there are four such externally apparent eminences, the *corpora quadrigemina*; the anterior pair are called the *superior colliculi*, the posterior pair the *inferior colliculi*. The inferior colliculi are present in fish but are not evident externally. Their exposure on the surface in mammals results from differences in embryonic development. The midbrain floor consists chiefly of tracts to and from other parts of the brain. The quantitative increase in tracts from the cerebral hemispheres of mammals results in a pair of conspicuous bundles, the *cerebral peduncles*, visible externally on the ventral surface of the midbrain. The midbrain is solid in mammals except for a narrow canal, the cerebral aqueduct (formerly the aqueduct of Sylvius), which passes through it from the fourth ventricle. In nonmammalian vertebrates the optic lobes are usually hollow, containing cavities, termed the *optic ventricles*, which open into the aqueduct.

The *diencephalon*, the second division of the brain, is chiefly a relay center for the cerebral hemispheres, and consequently its size and importance parallel those of the latter. It has a central cavity, the *third ventricle*, into which the aqueduct opens, and which in mammals is much compressed laterally. The roof of the third ventricle is thinned to an indurated layer and forms a tela choroidea, which has choroid plexi projecting into the interior or, in certain anamniotes (petromyzonts, some bony fishes, selachians, some reptiles), *choroidal sacs*, often very large.

lon by a transverse enfolding, the *transverse velum*. The diencephalon is divisible throughout vertebrates into a dorsal *epithalamus*, a middle thick *thalamus*, and a ventral *hypothalamus* (fig. 13.2E). The epithalamus consists chiefly of the *epiphyseal apparatus* and a pair of small masses, termed the *habenulae*. The epiphyseal apparatus apparently consisted primitively of two outgrowths of a sensory nature, and in lampreys, some ganoids, and many reptiles there are still two outgrowths—an anterior *parapineal* or *parietal body* and a posterior *pineal body* or *epiphysis*. In petromyzonts each develops a simplified eye. In *Sphenodon* and a number of other reptiles the anterior or parietal outgrowth forms a well-differentiated eye (usually called pineal eye, but more correctly termed parietal eye), and the posterior outgrowth is the pineal body proper. In other vertebrates only the pineal outgrowth appears in the embryo, and this develops into the pineal body, with no trace of eye formation. Except in lampreys, the pineal body contains glandular cells similar to the endocrine glands, and the pineal secretions are known to affect gonads and pigment cells. The parietal eye of reptiles occupies the parietal foramen of the skull, which is noticeable in the skull of primitive extinct tetrapods and their crossopterygian ancestors. These facts suggest that vertebrates originally had three eyes, but this question must be left undecided.

The thalamus comprises the lateral walls of the diencephalon; it is composed of many relay and integration centers for tracts passing to and from the cerebral hemispheres. In reptiles and mammals the dorsal parts of the thalami are frequently fused across the third ventricle by a connection of gray matter termed the *intermediate mass*.

The hypothalamus or ventral part of the diencephalon has the following main parts: *optic chiasma* (crossing of the optic nerves at their entrance into the brain), *tuber cinereum*, *infundibulum*, *hypophysis*, and *mammillary* region. The hypothalamus reaches its greatest development in fishes, where it is believed to be an important correlation center for olfactory, gustatory, and other sensory impulses. The tuber cinereum is an area of gray matter behind the optic chiasma. It continues ventrally as the infundibulum, a stalk in which the cavity is an extension of the third ventricle and from which the hypophysis or pituitary body extends. The hypophysis is composed partly of the oral epithelium of Rathke's pouch (*adenohypophysis*) and partly of nervous tissue from the infundibulum (*neurohypophysis*). The hypophysis is a very important endocrine gland that secretes a number of hormones. In fishes and amphibians the infundibulum is expanded posteriorly into a pair of swellings, the inferior lobes, and below them extends a soft-walled, very vascular structure, the *saccus vasculosus* or *vascular sac*, which is close to the pituitary. The mammillary region is the most posterior part of the hypothalamus and usually has a single or paired swelling, the mammillary bodies.

them by way of a more or less elongated stalk, the *olfactory stalk* or *peduncle*. The olfactory bulbs are generally hollow but are secondarily solid in many teleosts and mammals. Their size is correlated with the development of the sense of smell, and hence they are very small in birds and relatively small in primates.

The cerebral hemispheres constitute the major part of the telencephalon. They form large lateral bulges to either side of the original median anterior brain wall, the lamina terminalis, which is thus left at the bottom of the cleft between the hemispheres (fig. 13.2E). Not infrequently, however, the olfactory bulbs or cerebral hemispheres or both may be secondarily fused together dorsally. The lamina terminalis extends forward and upward from the *preoptic recess*, a depression in front of the optic chiasma, to the *neuroporic recess*, the point of last closure of the neural folds of the embryo. Just below the neuroporic recess, the lamina terminalis contains two bundles, the *anterior* and the *pallial commissures*, which connect regions of the two hemispheres. Above the neuroporic recess the original telencephalic roof, extending backward to the velum transversum, is thinned to form a tela choroidea, from which choroid plexi project into the cavities of the cerebral hemispheres. Immediately in front of the velum transversum the telencephalic roof has a dorsal branched or folded evagination, the *paraphysis* (fig. 13.2E). This is evident in the embryos of all classes of vertebrates but does not persist in the adults of most tetrapods; its function is not known.

In most vertebrates the cerebral hemispheres are smooth, rounded, or elongated lobes not noticeably larger than the rest of the brain (fig. 13.3), but in amniotes they increase greatly in size.

Each cerebral hemisphere contains a cavity, known as the *lateral ventricle*, and these communicate with each other and with the third ventricle by a passage (or pair of passages) termed the *interventricular foramen* (formerly the *foramen of Monro*). In reptiles and birds these ventricles are somewhat reduced, but in mammals they are well developed though very irregular because of the bulgings of the hemisphere wall.

The cerebral hemispheres of vertebrates are formed embryonically in one of two ways (fig. 13.5). In cyclostomes, elasmobranchs, sarcopterygians, and tetrapods the cerebral hemispheres are said to be *inverted*. The unpaired prosencephalon embryonically forms a pair of cerebral hemispheres by evaginating the lateral walls of the early neural tube, and the cavity within each evagination is termed the lateral ventricle. In teleosts and other actinopterygians, the cerebral hemispheres are said to be *everted*. In these animals, the roof of the early neural tube proliferates and the thickened lateral walls bend outward on themselves so that the entire prosencephalon has opened out. These animals cannot be said to possess lateral ventricles in the strict sense. It appears that this divergence in telencephalic embryology arose with the ancient placodermi.

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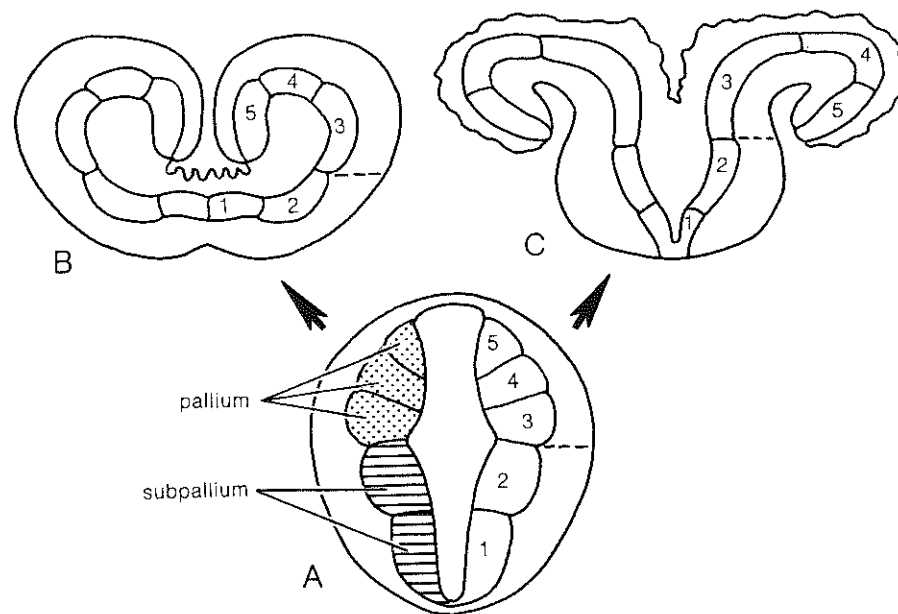


Fig. 13.5. Embryonic development of the telencephalon in vertebrates as seen in transverse section. *A*, early stage in development prior to formation of cerebral hemispheres. Neuroblasts are located next to central cavity (prosencephalon). *B*, in all vertebrates except ray-finned fishes cerebral hemispheres form by thickening and outpocketing of the lateral walls (evagination and inversion). *C*, in ray-finned fishes, the hemispheres form by eversion of the roof (pallium) resulting in a different topological organization. 1, septum; 2, striatum; 3, lateral pallium; 4, dorsal pallium; 5, medial pallium.

half, the *roof* or *pallium*, and a ventral half, the *floor* or *subpallial* region (fig. 13.5). In all tetrapods, the roof or pallium has three primary longitudinal zones (figs. 13.5, 13.6). The most medial zone (*PI* or *hippocampus*) is part of the limbic system and receives sensory information from many brain regions. It and the medial half of the dorsal zone (*PIIa* or *dorsomedial pallium*) are concerned with somatic and visceral integration. The lateral half of the dorsal zone (*PIIb* or *dorsolateral pallium*) is concerned with processing visual information. This pallial zone along with part of the lateral zone (*PIII* or *dorsal ventricular ridge*) forms a laminated cellular gray area called the *isocortex* (*neocortex*) in mammals. This zone is concerned with auditory, visual, and somatic sensory and motor processes in amniotic vertebrates. The other part of the lateral zone (*PIII* or *pyriform pallium*) is concerned with olfactory information.

The floor or subpallium is also divisible into three longitudinal zones (fig. 13.6). The most medial zone (*BIII* or *septum*) is also part of the limbic system. The ventral

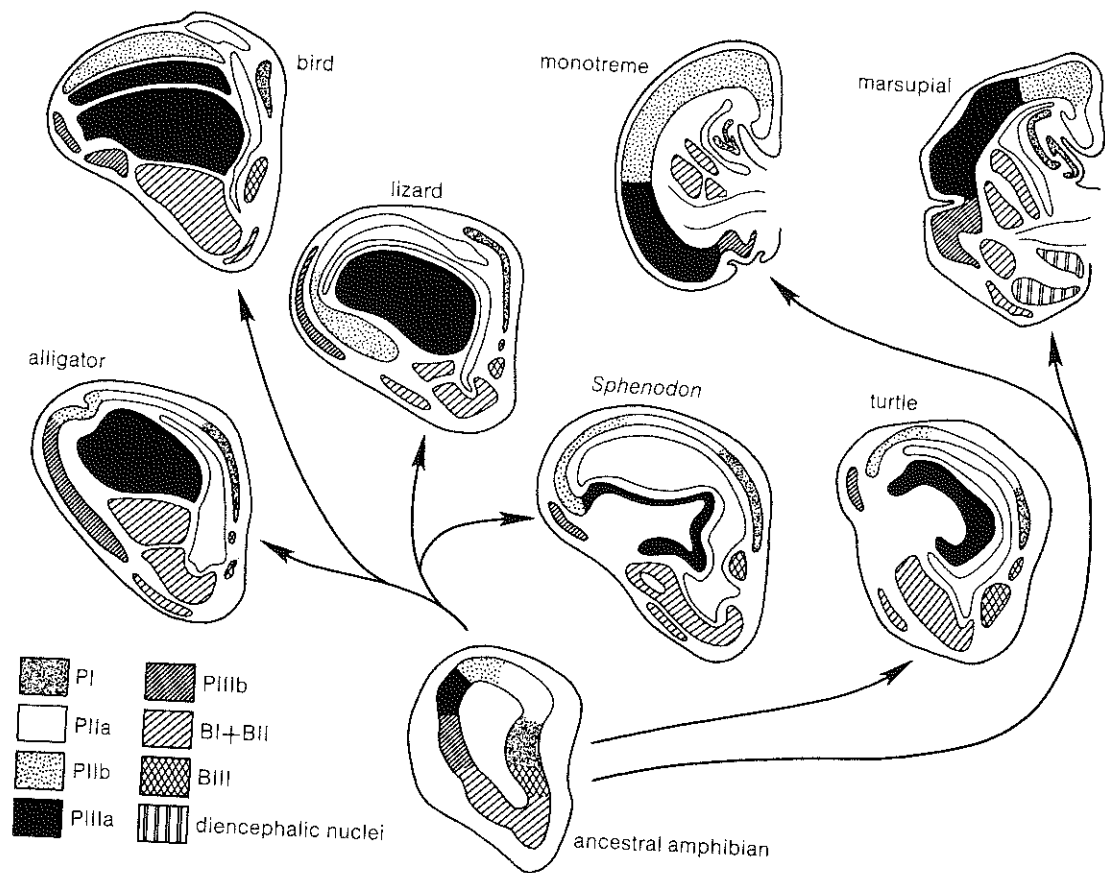


Fig. 13.6. Evolution of the cerebral hemisphere in land vertebrates as seen in transverse section of a single hemisphere. PI, hippocampus; PIIa, dorso-medial (cingulate) cortex; PIIb, dorsolateral cortex (isocortex); PIIIa, a second part of isocortex (dorsal ventricular ridge); PIIIb, lateral (pyriform) cortex; BI and II, corpus striatum; BIII, septal nuclei. Modified after Northcutt 1977 (*McGraw-Hill encyclopedia of science and technology*. New York: McGraw-Hill).

ancestral reptiles the lateral zone proliferated onto the surface to form part of the isocortex. In both cases the proliferation seems to have occurred in response to the increased functional significance of the processes being mediated by this lateral zone. While it is known that this region is involved in visual and auditory processes as well as motor control, the exact significance of the vast increase in volume is still not understood. It may, however, hold the key to an understanding of the evolution of the tetrapod telencephalon.

In eutherian mammals, a broad horizontal band of myelinated axons, the *corpus callosum*, connects the isocortical hemispheres.