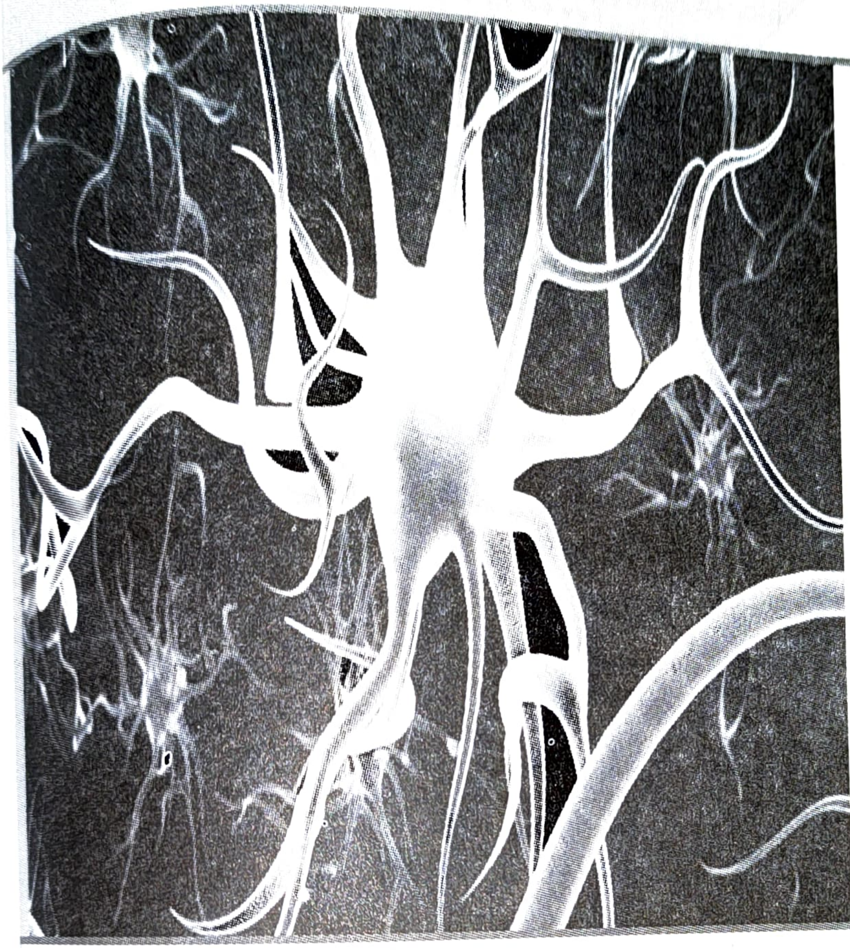
46 Chapter

Nervous System in Vertebrates



Contents of this Chapter

NERVOUS SYSTEM AND ITS FUNCTIONS

The nervous system is meant to perceive stumuli detected by the receptors and transmit them to the concerning parts of the body and finally respond to responses through effectors. The nervous system is highly specialised in vertebrates and plays at least three vital roles.

1. Response to stimuli. Responding to all sorts of stimuli, it acquaints the organism with them so that the organism may react and orient itself favourably in the surrounding environment.

2. Coordination. In association with endocrine system, the nervous system also serves to coordinate and integrate the activities of various parts of the body so that they act harmoniously as a unit. This makes possible the integrated control of the internal body environment (**homeostasis**). However, the nervous system brings about rapid coordination by means of nerves, whereas the endocrine system does so gradually and slowly by secreting hormones into blood.

3. Learning. In higher vertebrates at least, the nervous system serves as a centre for learning by accumulating memories from past experiences.

ANATOMY OF NERVOUS SYSTEM : THE NEURON

The nervous system is formed of nerve cells, **neurons**, which are surrounded by **neuroglia**, a tender network of connective tissue. Neurons are the distinct units of nervous tissue and are of ectodermal origin.

Structure of neuron. A neuron has a **cell body** or **cyton** from which arise two types of **fibres.**

(*i*) Cyton. A cyton has a nucleus and numerous basophilic **Nissl's granules**. These granules are made of ribonucleic acid. They produce new cytoplasm in neurons and are also concerned with protein synthesis in nerve cells. The cytoplasm of cyton has fine threads or **neurofibrils**, forming a network. Mass of nerve cell bodies found in the brain or spinal cord is called nucleus and a similar mass found outside the central nervous system is known as a **ganglion.**

(*ii*) Nerve fibres. A neuron has a number of processes or fibres projecting from the cell body. These fibres on the basis of movement of nervous impulse are of two types : (*a*) **Dendrites.** These are generally several short branching processes having Nissl's granule, and close to the cell body. They are **afferent** because the neuron receives impulses through them. (*b*) **Axon.** Axon or **axis cylinder** is a single process which is generally long and without Nissl granules. It has terminal branches, called **axon endings**, which have small swellings at their ends. Axons are **efferent** because impulses are sent out through them.

Dendrites lie in contact either with receptors or with the axon endings of another neuron, from either of which they receive stimuli. Neurofibrils found in the cytoplasm of cyton extend both into the dendrites and axons and their branches. They probably transmit impulses.

Nerve fibre. An axon is covered with one or two sheaths and is then called a **nerve fibre**. A nerve fibre has a central thin cytoplasmic strand, the **axis cylinder**. It is continuous with the cell body or cyton. The nerve

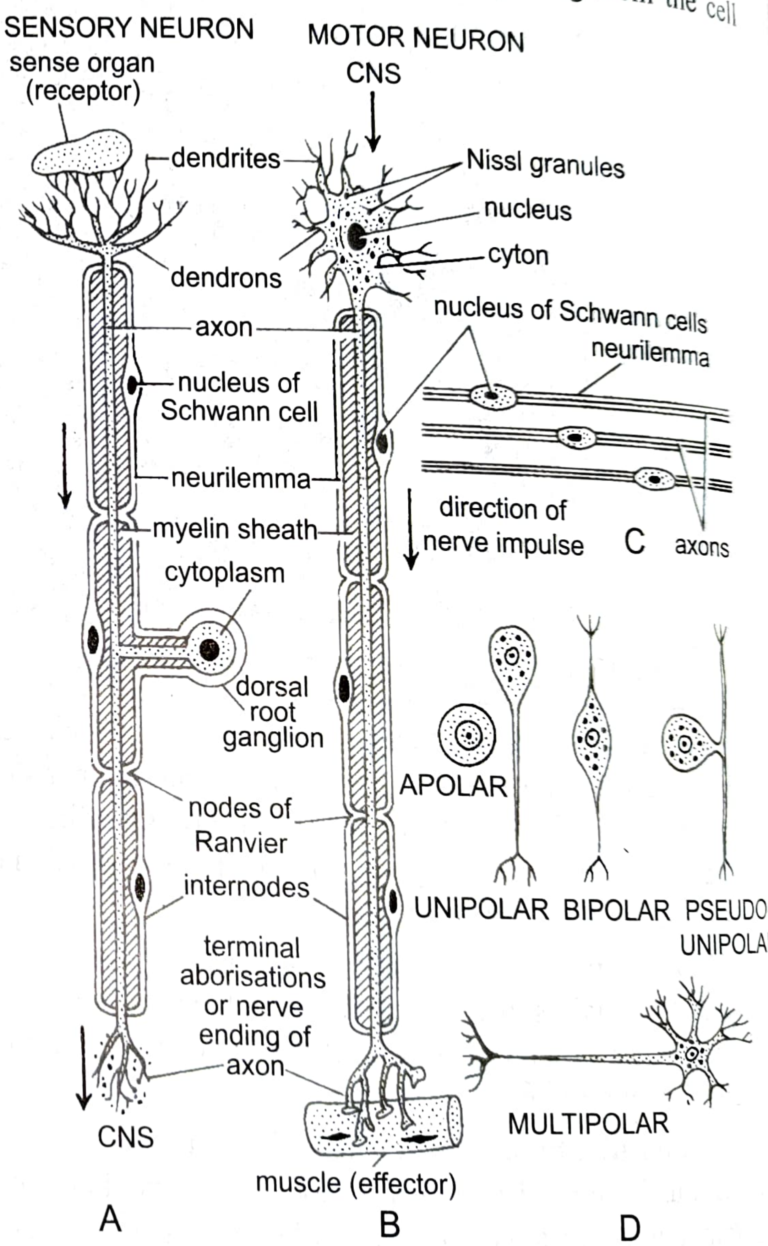


Fig. 46.1. Structure of neurons and nerve fibres. A–Senso neuron; B–Motor neuron; C–Non-medullate nerve fibres; D–Kinds of neurons.

the acetylch[illegible] destroyed by enzymes. The impulses travel in only one direction in neurons, from the dendrites to the cell body and then through the axon.

Development of the Central Nervous System

In a vertebrate embryo the mid-dorsal strip of ectoderm form a longitudinal thickening, known as a **medullary** or **neural plate**. The neural plate sinks downwards but its edges grow upwards to form **neural folds**. The neural folds grow towards each other and eventually fuse to form a hollow **neural tube** of several layers of cells above the notochord. The lateral ectoderm re-forms above the neural tube. The cells of the neural tube produce two kinds of cells, the **neuroblasts** and **spongioblasts**. The neuroblasts develop into neurons, while the spongioblasts form the neuroglia and ependymal cells lining the neural canal. The neural tube at first is open at both ends, having a **neuropore** in front communicating with the exterior, posteriorly the neural tube communicates with the archenteron cavity by a very short **neurenteric canal**, but both openings are soon closed. The anterior end of the neural tube enlarges forming the brain, while the remaining neural tube will give rise to the spinal cord. The cavity of the neural tube will become the ventricles of the brain and central canal of the spinal cord.

Development of brain. The anterior thickened, enlarged end of the neural tube known as **encephalon** is the embryonic brain. It undergoes differential growth and acquires two constrictions, which divide it into a series of three lobes, the **primary cerebral vesicles**. The primary cerebral vesicles are a **forebrain** or prosencephalon, a **midbrain** or mesencephalon, and a **hindbrain** or rhombencephalon. This embryonic brain is bent downwards between the forebrain and midbrain in the region of the mesencephalon and this curvature is known as **cranial flexure** or cephalic flexure. In later development the cranial flexure is lost in cyclostomes, fishes, amphibians and reptiles, but persists in birds and mammals.

1. Forebrain. The forebrain or **prosencephalon** is further sub-divided by a constriction into an anterior **telencephalon** and a posterior **diencephalon**. The anterior wall of the telencephalon is known as **lamina terminalis** which marks the original anterior boundary of the brain. The telencephalon grows beyond the lamina terminalis and forms paired **cerebral hemispheres**. The roof of the cerebral hemispheres becomes the **pallium** and its ventro-lateral thicker walls form the **corpora striata**. Each cerebral hemisphere has a cavity, the **lateral ventricle**. From the antero-ventral part of the telencephalon paired **olfactory lobes** (rhinencephalon)

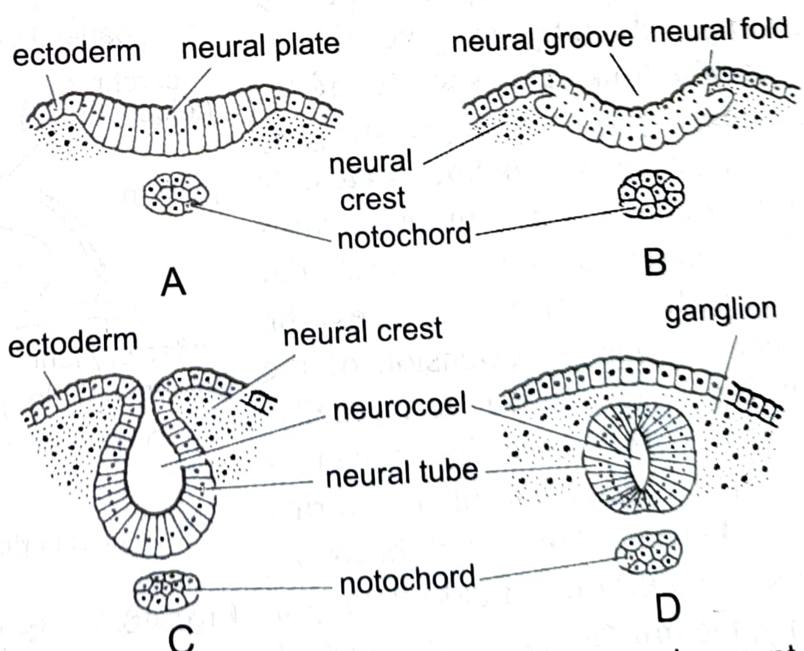


Fig. 46.4. Stages in the embryonic development of central nervous system in T.S.

grow out towards the nose. Each olfactory lobe has a cavity, the **rhinocoel,** which communicates with the lateral ventricle of its side. The **diencephalon** or thalamencephalon has an upper **epithalamus**, a middle **thalamus,** and a lower **hypothalamus**. Dorsally the diencephalon gives out a median unpaired **paraphysis**, which is well developed in fishes but is much reduced in reptiles and birds and is absent in mammals. Behind the paraphysis the diencephalon gives out two more unpaired evaginations, an anterior **parietal body** and a posterior **pineal body** or **epiphysis**. The parietal body forms an eye in lampreys, some fishes, and many reptiles, in others it is lost in the adult. The pineal body forms a simplified eye in lampreys but in all other vertebrates it becomes glandular and is believed to be an endocrine gland, but there is no real evidence for this, most probably the pineal body is a vestigial organ of no functional significance. Between the thalami of diencephalon is a **third ventricle** which communicates with each lateral ventricle by an aperture called a **foramen of Monro**. The thalami give rise to optic vesicles which form parts of the eyes. The roof of the diencephalon is a thin ependymal layer which fuses with the vascular piamater to form a **tela choroidea**. Vascular folds of the tela choroidea project into the third ventricle forming an **anterior choroid plexus**. The lower part of the diencephalon known as hypothalamus forms a ventral **infundibulum**. An ectodermal evagination of the roof of the stomodaeum forms a **Rathke's pouch** or **hypophysis**, which fuses with the infundibulum to form a **pituitary body** or **hypophysis cerebri**, which loses its nervous character and becomes an important endocrine gland. Except in a few lower forms the Rathke's pouch loses its connection with the stomodaeum. The fibres of the optic nerves cross in front of the infundibulum to form an **optic chiasma**.

2. Midbrain. The midbrain or **mesencephalon** has a thick roof. Its dorso-lateral walls form two **optic lobes** (four in mammals). The optic lobes are hollow, each having an **optocoel** except in mammals where they have no cavity and are solid. The ventral wall of mesencephalon forms thick **crura cerebri**, which are tracts of nerve fibres joining the diencephalon with the hindbrain. Passing through the mesencephalon from the third to the fourth ventricle is a narrow **iter** or **aqueduct of Sylvius**, which in non-mammals is also connected to the optocoels.

3. Hindbrain. The hindbrain or **rhombencephalon** forms a **metencephalon** from its anterior dorsal part. The metencephalon enlarges dorsally to give rise to a **cerebellum**. The surface of the cerebellum has a layer of gray matter, called **cerebellar cortex**. In birds and mammals there is thick white matter below the cerebellar cortex. In lower vertebrates the cerebellum has an extension of the fourth ventricle known as cerebellar ventricle or **metacoel**. The remaining part of the rhombencephalon forms a **myelencephalon**, which becomes a thick **medulla oblongata** having a cavity, the **fourth ventricle**. The roof of the medulla has a **posterior choroid plexus** formed in the same way as the

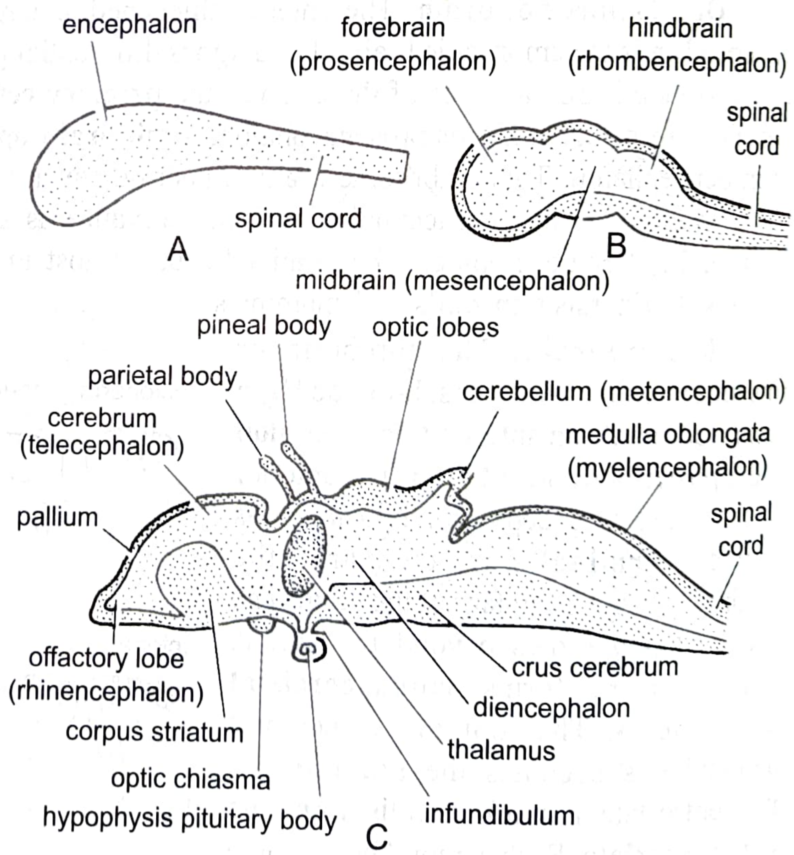


Fig. 46.5. Stages in development of brain. A–Anterior end of neural tube in lateral view; B–M.L.S. of embryonic brain to show three primary cerebral vesicles; C–Differentiation of brain from three vesicles.

anterior choroid plexus. In lower vertebrates the floor of the metencephalon and myelencephalon does not differ, but in higher forms the floor of the metencephalon thicknes due to many tracts of nerve fibres, and in mammals it forms a conspicuous **pons Varolii.**

Commissures. The two similar halves of the brain are connected by transverse tracts of nerve fibres, called **commissures**. In most vertebrates there are only anterior and posterior commissures, the **anterior commissure** originates in the lamina terminalis and lies in front of the third ventricle, it joins the two corpora striata. The **posterior commissure** lies in the roof of the diencephalon at its junction with the midbrain. In mammals there are several other commissures. The commissures make bilateral integration possible.

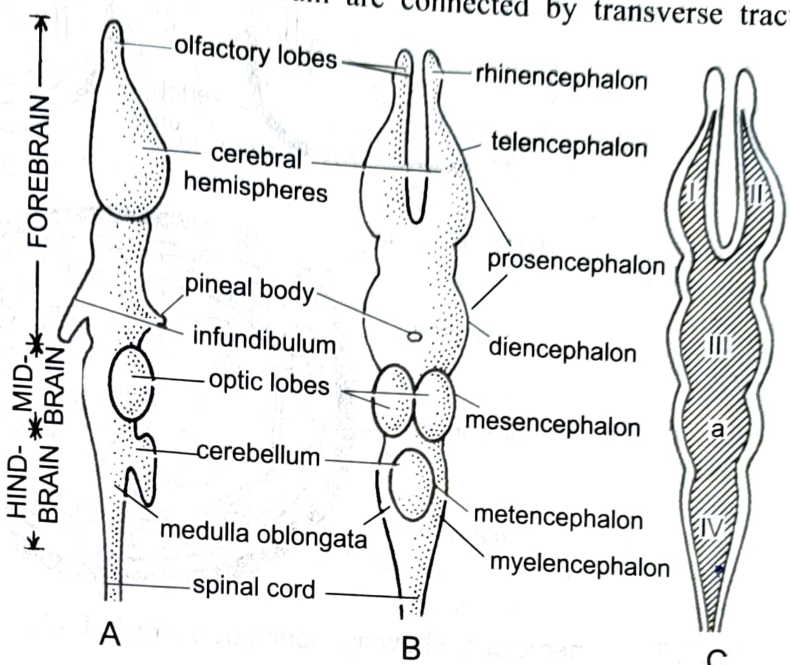


Fig. 46.6. Pattern of generalised vertebrate brain. A–Lateral view; B–Dorsal surface; C–H.L.S. showing ventricles.

Spinal cord. Nerve cord or spinal cord is formed from the neural tube behind the brain. The nerve cord is a cylindrical tube somewhat flattened dorso-ventrally. Its anterior end is wide where it is continuous with medulla, the posterior end generally tapers to a fine thread, the **filum terminale**. In fishes it extends to the posterior end of the tail. It extends the full length of the vertebral column in amphibians, reptiles and birds, but in mammals it is short and does not extend into the tail. In cyclostomes, fishes and limbless amphibians the nerve cord has a uniform diameter, but in tetrapoda it has two enlargements called **cervical** (**brachial**) and **lumbar** enlargements. They are formed due to a larger number of nerve cell bodies whose fibres form nerves going to limbs.

Histology. The nerve cord has a thin **central canal** lined with ciliated ependymal cells. On its mid-ventral side the nerve cord acquires a deep **ventral fissure**, mid-dorsally is a slight dorsal **sulcus** from which a **dorsal septum** extends into the interior. The dorsal septum and ventral fissure divide the nerve cord incompletely into two halves connected across the middle by commissures. There is an outer **white matter** with neurogila and nerve fibres, and an inner **gray matter** having nerve cell bodies, non-medullated fibres, and neuroglia. In **fishes** and **amphibians** the gray matter is rounded or quadrangular in section, but in **amniotes** it is H-shaped forming dorsal and ventral horns or columns. The gray matter divides the white matter into dorsal, lateral, and ventral **funiculi**.

Meninges. The brain and nerve cords are surrounded by protective connective tissue membranes called meninges. Their complexity increases with the advance in the scale of evolution.

In **cyclostomes** and **fishes** there is generally a single meninx, the **meninx primitiva** around the brain and spinal cord, it has a network of blood vessels. Between the skull or vertebral column and the meninx primitiva is a **perimeningeal space** filled with fat and connective tissue fibres.

In **amphibians, reptiles** and **birds** the meninx primitiva splits to form two meninges : an outer tough fibrous **duramater** and a thin vascular **piamater** covering the brain and nerve cord, between these two meninges is a **subdural space** having a small amount of fluid. Between the enclosing skeleton and the duramater is an **epidural space** having connective tissue, fat, and blood vessels.

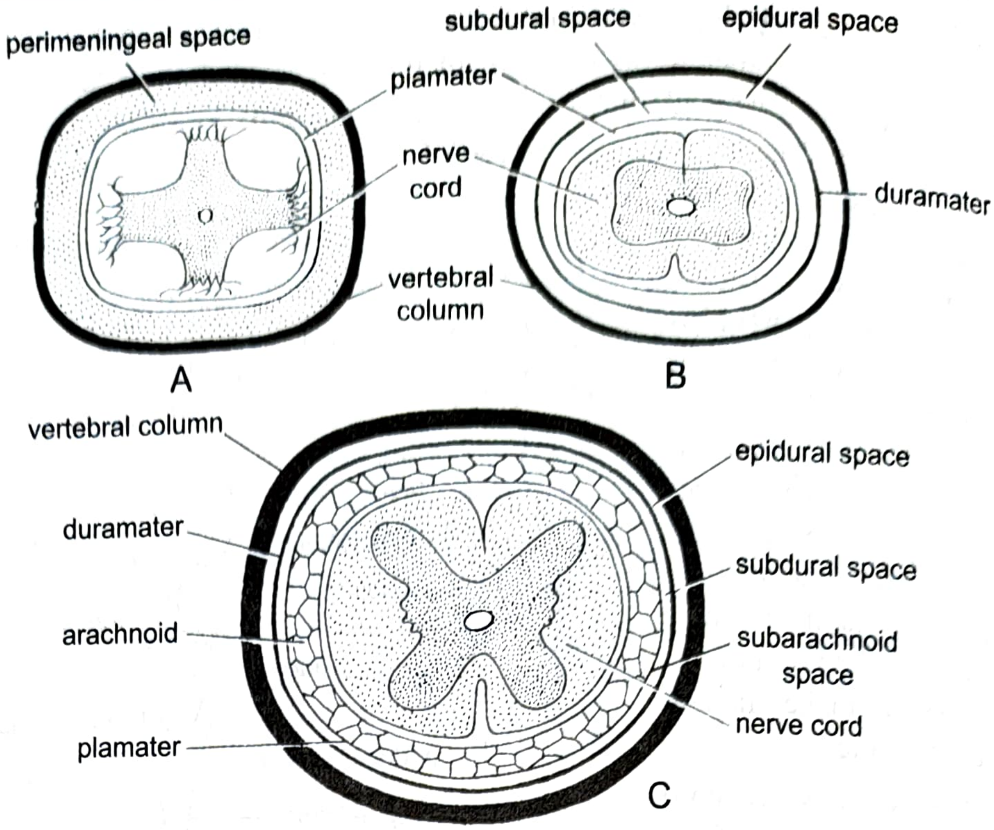


Fig. 46.7. T.S. of nerve cord showing meninges. A–Fish; B–Amphibian, reptile, and bird, C–Mammal.

In **mammals** there are three meninges, an outer duramater, a middle non-vascular **arachnoid membrane**, and an inner highly vascular **piamater**. Between the enclosing skeleton and the duramater is an epidural space in the region of the vertebral column only, but in the brain region the duramater fuses with the lining of the skull (endorachis) so that there is no epidural space. Between the duramater and the arachnoid is a subdural space, between the arachnoid and piamater is a **subarachnoid space** having a network of fine fibres, filled with **cerebrospinal fluid**. The piamater and the arachnoid being joined by fibres are together known as **leptomeninges**. The arachnoid forms **arachnoid villi** which return the cerebrospinal fluid to the venous blood. The cerebrospinal fluid is formed by the choroid plexuses, which fills the ventricles, central canal, subdural space, and subarachnoid space.

In the roof of the medulla are three apertures, a median **formen of Magendie**, and two lateral **foramina of Luschka**, through these foramina the cerebrospinal fluid passes into the spaces between the meninges so that the surface of the central nervous system is bathed by the fluid.

Neural crest. After the formation of the neural tube, masses of ectoderm cells appear on each side between the neural tube and ectoderm, these cells are **neural crests** which extend on each side along the whole length of the neural tube. The neural crests form segmental **dorsal root ganglia** of spinal nerves and ganglia of the autonomic sympathetic nerves. They also form parts of the ganglia of sensory cranial nerves. Some neural crest cells form those mesenchyme cells which give rise to **visceral arches**. While other neural crest cells form the **piamater** and **arachnoid** membrane of the central nervous system. Still other neural crest cells form **chromatophores** in lower vertebrates. **Chromaffin cells** of the medulla of adrenal glands arise from neural crest cells.

COMPARATIVE ACCOUNT OF BRAIN IN VERTEBRATES

1. Cyclostomata. The cerebral hemispheres are barely indicated. Two olfactory lobes are prominent. Cavities of cerebral hemispheres (lateral ventricles) are rudimentary. From the dorsal wall of diencephalon two median eye-like structures may arise. The anterior one is the parietal body and the posterior one is the pineal body. These two are vestigial in *Eptatretus* and absent in *Myxine*. The vental part of diencephalon gives rise to the infundibulum of the hypophysis as well as the posterior lobe. The optic lobes are not well differentiated.

Cerebellum is poorly developed due to sluggish and slow moving habit. Medulla oblongata is very well developed in all vertebrates since it serves as a centre for many vital body activities (respiration, heart action, metabolism, etc.). It also serves as a relay centre and in fishes is a centre for lateral line system and inner ear.

2. Elasmobranchii. The brain is large and different from that of cyclostomes and bony fishes. In fishes, telencephalon is primarily olfactory in function and olfactory lobes are large in elasmobranchs. Each olfactory lobe has a rhinocoel cavity. The cerebral hemispheres (cerebrum) are better developed. Cerebrum in fishes, however, consists of a basal ganglionic mass known as **corpus striatum** and a thin, dorsal, epithelial layer called the **pallium** composed essentially of non-nervous tissue and the centre of brain activity is back in the mesencephalon. The **diencephalon** is narrow with a thin roof having an anterior choroid plexus below which is the third ventricle. Its lateral walls form thick thalami which serves primarily as a relay centre for olfactory and visual impulses and is associated with several sensory and glandular structures. Dorsally the diencephalon has a long-tubular **pineal body** and the floor of the diencephalon give rise to the stalk or infundibulum of the hypophysis as well as the posterior lobe. A thin-walled vascular sensory organ, **succus vasculosus** is attached to hypophysis. It is connected with the cerebellum by fibre tracts. The midbrain in fishes is the centre of nervous coordination. Dorsally it develops two prominences known as the optic lobes concerned with visual reception. Cerebellum is a centre of muscular coordination, it is larger than that of cyclostomes and dipnoans. Medulla is well developed and at its antero-lateral margins are present ruffle-like **restiform bodies,** which assist the cerebellum in the maintenance of equilibrium.

TABLE 46.1. **SUBDIVISIOS, PARTS AND ASSOCIATED STRUCTURES OF A VERTEBRATE BRAIN.**

Divisions	Subdivisions	Parts	Cavity	Associated Structure
	1. Telencephalon	Rhinencephalon	I Ventricle (*Rhinocoel*)	Olfactory bulbs Olfactory tracts Olfactory lobes Palaeocortex on pallium
		Cerebral hemispheres	II or Lateral Ventricles (*Paracoels*) ↓ Foramen of Monro ↓	Corpora striata or basal ganglia Corpus callosum Neocortex on pallium Paraphysis
I. Prosencephalon (Forebrain)	**2. Diencephalon**	Epithalamus (roof)	III Ventricle (*Diacoel*)	Habenulae Pineal apparatus Parapineal or parietal
		Thalamus (sides)		
		Hypothalamus (floor)		Hypothalmic nuclei Optic chiasma Median eminence Infundibular stalk Pituitary Saccus vasculosus Mamillary bodies Anterior choroid plexus
Mesencephalon (Midbrain)	—	Crura cerebri (floor)	*Iter* or *cerebral aqueduct*	Optic lobes } Tectum Auditory lobes } Cerebral peduncles
I. Rhombence-phalon (Hindbrain)	**1. Metencephalon** **2. Myelecephalon**	Cerebellum Medulla oblongata	IV Ventricle (*Metacoel*)	Trapezoid body Pons Restiform bodies Pyramids

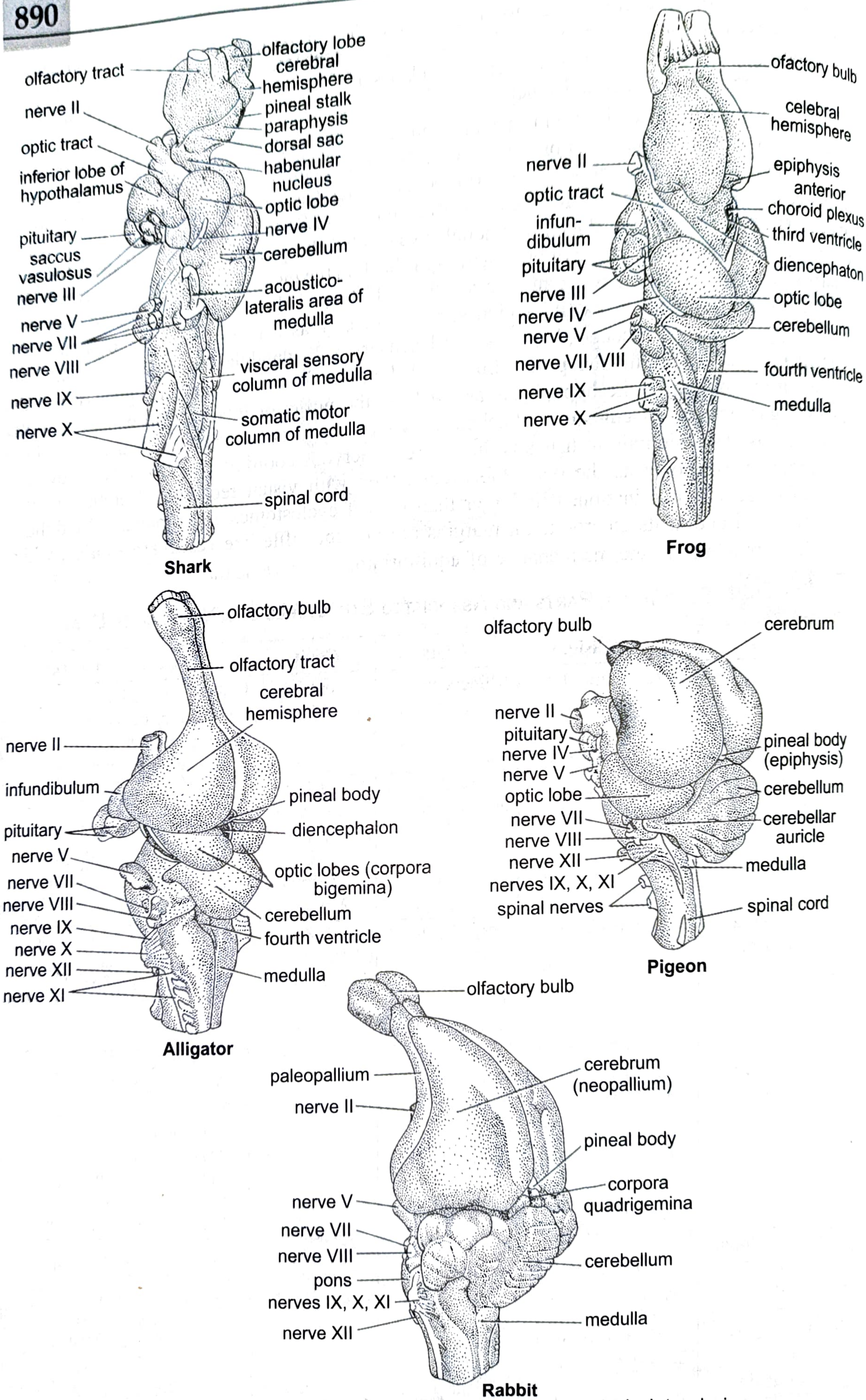


Fig. 46.8. Comparative anatomy of the vertebrate brain in lateral view.

3. Osteichthyes (Bony fish). The brain is more specialised than in elasmobranchs. Olfactory lobes are large, having no olfactory peduncles and are closely applied in front of the cerebral hemispheres. Each contains a rhinocoel continuous with the lateral ventricle. The cerebral hemispheres are better developed. The roof or pallium of the cerebral hemispheres is thin and non-nervous, consequently it is not equivalent to the pallium of other animals. The corpus striatum is very thick. The lateral ventricle is undivided. Dienceecephalon is small hidden dorsally by the midbrain. Only the pineal body with stalk is present. Parapineal body is not found in modern bony fishes. Melatonin has been identified in the pineal gland of certain fishes. It has an inhibitory effect on gonadial activity. In immature Pacific salmon (genus *Oncorhynchus*) melatonin content is 6 times more than that of adults. On the ventral side the diencephalon has an infundibulum to which the pituitary gland is attached below. Optic lobes are very large. Cerebellum is larger than that of elasmobranchs. **Restiform bodies** are also present in some bony fishes. **Vagal lobes** are the bulgings from the antero-lateral sides of medulla, and are found in bottom feeders which have taste buds on their body surface.

4. Amphibia. The nervous system of amphibians is still basically like that of fishes. The pallium of cerebral hemispheres is invaded for the first time in vertebrates by nerve cells due to which the cerebral hemispheres become enlarged in accordance with more complex activities of locomotion, hibernation, breeding, etc. The olfactory lobes are fused together in the median plane. The corpora striata form a thick floor of the cerebrum. The **diencephlaon** is short but optic fibres end in it. The pineal body is found in all amphibians, but only anurans possess a parietal body or a pineal end organ. The optic lobes are large and are the centre of brain activity like fishes. The members of this class are notably slow and sluggish in their movement, so the cerebellum is very small, like a simple narrow transverse band. Medulla is also small. Except in caecilians, flexures are lacking in amphibian brain.

5. Reptilia. The brain shows many features which are characteristic of the mammalian brain. In all anamniotes the midbrain is the centre of brain activity, but in reptiles for the first time there is a shift in the nerve centre to the cerebrum. This is correlated with a marked increase in the size of the cerebral hemisphere as a result of invasion of the pallium by many nerve cells so as to form the **neopallium**. Two long olfactory lobes are larger than that of amphibians due to greater thickness and enlargement of corpora striata. **Parietal eye** is found in *Sphenodon* and some modern lizards, but absent or vestigial in some other reptiles. Behind the optic lobes are present a pair of **auditory lobes** which are not hollow. The third ventricle is reduced and form a narrow **cerebral aqueduct**. Cerebellum is relatively larger than that of amphibians. However, it does not attain the size of sharks, and not near the size of birds or mammals. This is corelated with relatively limited locomotive powers of most reptiles.

6. Aves. The brain of birds shows a considerable advance over that of reptiles. In shape it is short, broad, and rounded. The olfactory lobes are extremely small and degenerate due to poor sense of smell. The **cerebral hemispheres** are very large and covers the diencephalon and optic lobes. Its size is due to enlargement of the corpus striatum rather than the cerebral cortex. The cerebral cortex is smooth. The size of corpora striata makes the lateral ventricles small. The **diencephalon** is covered dorsally by the cerebral hemispheres and cerebellum. It has a small dorsal pineal body, an anterior choroid plexus and a narrow third ventricle. The **thalami** are highly developed and are connected by fibres to the corpora striata and spinal cord.

The **midbrain** is highly developed with exceptionally large rounded optic lobes. This seems to be correlated with the remarkable powers of sight that birds possess.

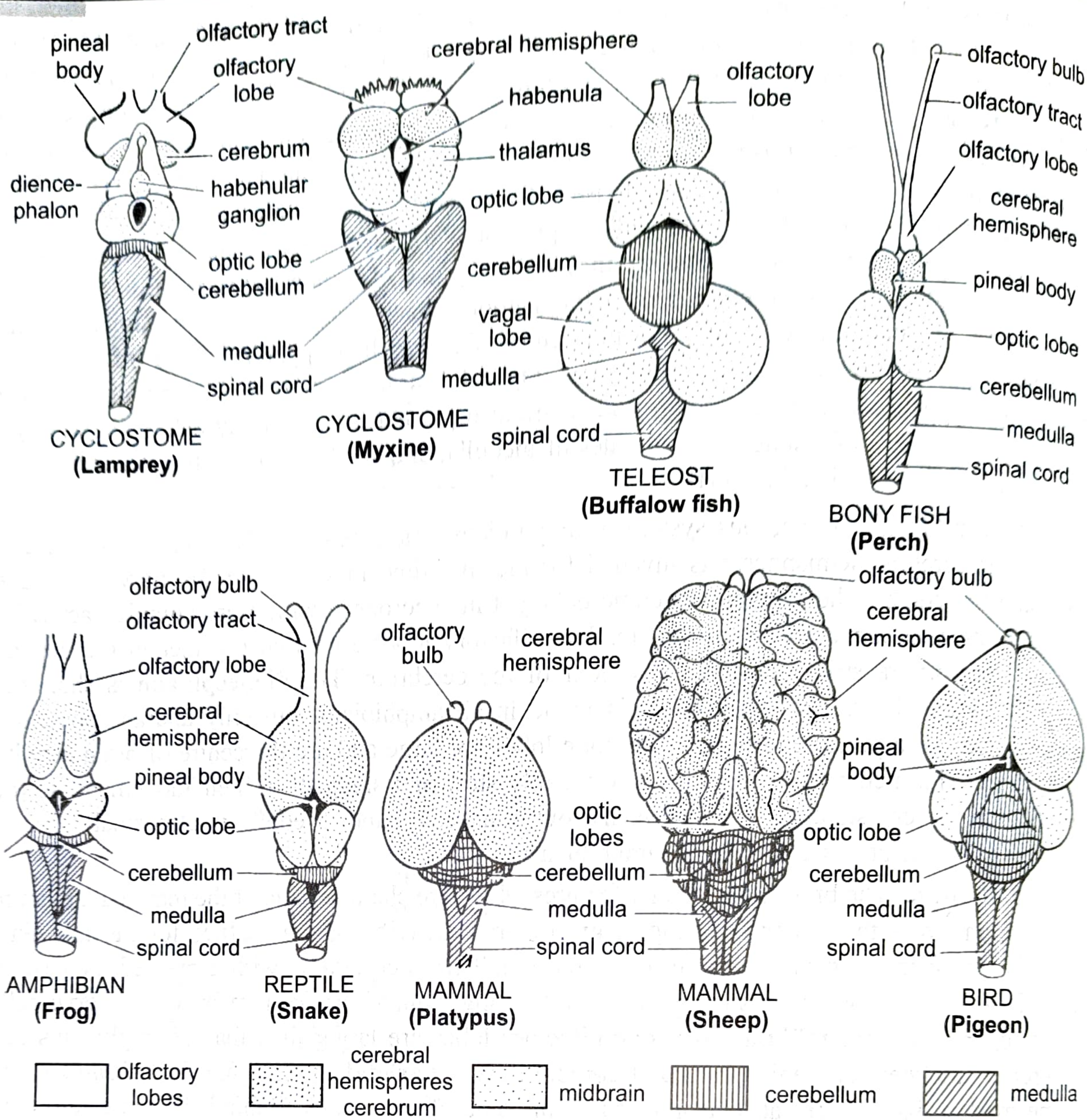


Fig. 46.9. Comparative anatomy of brains of representative vertebrates in dorsal view.

The **cerebellum** is larger than in reptiles and is deeply fissured, although it is not as large as in mammals. Ventral to cerebellum, the avian brain shows the beginning of the development of a pons. In the cerebellum masses of nerve cell bodies form nuclei so that it has outer layers of gray matter and an inner mass of white matter, forming a branching pattern called **arbor vitae**. A small projection of the fourth ventricle extends into the cerebellum. It controls equilibrium and movements in all places during flight. The medulla oblongata has a posterior dorsal choroid plexus and a fourth ventricle, which does not extend into the cerebellum.

7. Mammalia. The brain reaches its highest development in mammals with better integration and mastery over the environment. The cerebral hemispheres reaching the status of a dominant integrating part of the brain and acting as coordinating centres of the brain. The cerebral hemispheres in Prototheria are smaller and smooth like that of reptiles. In Metatheria, they are larger and smooth. In most eutherians, the cerebral hemispheres are immense, projecting forwards above the olfactory lobes and backwards above the diencephalon and midbrain and divided into lobes. They have convolutions on the surface so that there are ridges or **gyri** and depressions or **sulci**. The outer layer or cortex of the cerebrum is composed of gray matter. The right and left cerebral hemispheres are connected with one another by a broad white commissure, called the **corpus callosum**. The olfactory lobes are small compared with those of lower vertebrates.

The diencephalon consists of a dorsal **epithalamus,** a lateral **thalamus**, and a ventral **hypothalamus**. A pineal gland is present on the roof of the diencephalon, but it shows no eye-like structure. Thalamus is an important relay centre. Hypothalamus is very important in mammals and consists of four parts. These are the **infundibulum** forming the stalk and posterior lobe of the pituitary, the **optic chiasma**, where right and left optic nerves cross enroute to the brain; and the **mammillary bodies**, which integrate olfactory impulses. The hypothalamus controls a great many mammalian functions including blood pressure, sleep, water content, fat and carbohydrate metabolism, body temperature and possibly rhythmic activities such as moulting, migration and pituitary secretion.

The **midbrain** in mammals is of less importance than in lower vertebrates, in which it is really the brain centre. It is divided into four prominences, called the **corpora quadrigemina**. The two superior lobes are concerned with sight, whereas the two inferior lobes are probably concerned with hearing. The III ventricle or **iter** of midbrain is laterally compressed vertical passage called the **cerebral aqueduct**.

The **cerebellum**, which is the centre of control of body movement, is most highly developed in mammals. Its surface is convoluted and it is divided into a number of lobes : central lobe or **vermis,** two lateral lobes, and two outer floccular lobes. Beneath the cerebellum is a typical mammalian structure the **pons**. This relay centre is a conspicuous feature of the ventral metencephalon. **Pons Varolii** have crossing or decusating fibres connecting opposite sides of the cerebellar cortex. These are the transverse nerve fibres.

Besides pons, there is a short tract of transverse fibres, called **corpus trapezoideum** relaying impulses for sound.

The **medulla oblongata** lies ventrally and is much thickened. It has a dorsal posterior choroid plexus below which is the fourth ventricle joined in front to the iter and behind to the central canal. The medulla has centres for regulation of digestion, respiration and circulation.

PERIPHERAL NERVOUS SYSTEM

... from the central