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# Terminal Nerve and Olfactory Forebrain

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## INTRODUCTION

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Most vertebrates have two rostral nerves: the **olfactory nerve** and the **terminal nerve**. Some tetrapods have a third rostral nerve, the **vomeronasal nerve**, in addition to the olfactory and terminal nerves. The olfactory and vomeronasal nerves, along with the sense of taste, constitute the chemosensory system. The modality of the terminal nerve has not yet been established.

The rostral chemosensory nerves are composed of the axons of bipolar receptor cells that, along with secretory supporting cells, form the olfactory epithelium of the nasal cavities. Their axons terminate within the most rostral parts of the brain. The olfactory nerve terminates within the **olfactory bulb** in fishes. In tetrapods, the site of termination of the olfactory nerve is called the **main olfactory bulb** to distinguish it from the site of termination of the vomeronasal nerve, the **accessory olfactory bulb**. The collections of axons that originate in the olfactory bulb(s) and project to areas within the rest of the brain are referred to as tracts. Thus, in diapsid reptiles, for example, the olfactory nerve terminates in the main olfactory bulb, and the main olfactory bulb gives rise to the **olfactory tract**, which terminates in the **olfactory cortex** in the telencephalon.

In this chapter, we will first discuss the organization of the olfactory nerve system in Group I and Group II vertebrates. Then we will discuss the vomeronasal nerve system in tetrapods. The system that involves the terminal nerve differs somewhat in its organization and functional role from the other two rostral nerve systems and will be discussed last. The terminal nerve system will first be discussed in general terms for vertebrates, and then its special features in teleosts will be considered.

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## OLFACTORY SYSTEM

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The olfactory nerve arises from neurons in the olfactory epithelium that have dendritic endings specialized for the detection of chemical stimuli and that project into the olfactory bulb. The paired olfactory bulbs are formed by evagination during development, whether the telencephalic hemispheres are formed by evagination, as in most vertebrate groups, or by eversion, as in ray-finned fishes.

The olfactory input through the olfactory bulbs is a two-neuron relay system in which the **receptor cells** project to cells called **mitral cells** (for their resemblance to a bishop's mitre) (Fig. 29-1). The multiple ramifications of both the axon of the receptor cell (R) and the dendrite of the mitral cell (M) form a complex sphere, called a **glomerulus** (G), where they meet, like the joining of two hands with the fingers partially flexed and intermingled. **Granule cells** (Gr) are also present in the olfactory bulb, and along with centrifugal inputs from the forebrain, influence the processing of olfactory information in the bulb.

The olfactory bulbs relay olfactory information to the olfactory pallium via the olfactory tracts. The relative lengths of both the olfactory nerves and the olfactory tracts are variable. In many vertebrates, including some cartilaginous and bony fishes, the olfactory bulbs are sessile in position, that is, they are juxtaposed to the telencephalon. In these cases, the olfactory nerves may be of shorter or longer length, depending on the distance of the olfactory epithelium from the olfactory bulbs. In other cartilaginous and bony fishes, the olfactory bulb lies close to the olfactory epithelium, and the olfactory tract is an elongated structure running between the olfactory bulb and the telencephalon.

The olfactory pallium is usually thought of as a distinct cytoarchitectonic area in the telencephalon that has afferent

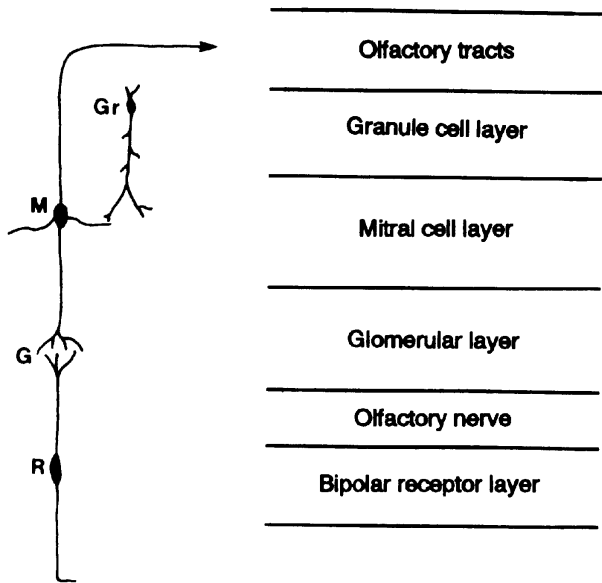


FIGURE 29-1. Olfactory bulb organization in vertebrates: schematic drawing of an olfactory bipolar receptor cell (R) with its axon terminating in a glomerulus (G) formed by the receptor axon terminals and the distal branches of the dendrite of a mitral cell (M), which in turn projects to the olfactory cortex (arrow). A granule cell (Gr) is also shown terminating on a dendrite of the mitral cell.

olfactory innervation, but such a working definition is acceptable only as a first approximation. Other criteria, such as topology, cytoarchitecture, efferent projections, and histochemical characteristics, are also important in defining and distinguishing pallial areas, but data on these aspects of the olfactory system in anamniotes are limited. Olfactory fibers terminate in more than one distinct pallial area in a number of anamniotes, and some of these areas appear to be part or all of the dorsal pallium on topological, cytoarchitectonic, and/or histochemical grounds. However, due to the relative dearth of information on the latter features and on efferent connections of these pallial areas, identifying them as homologues of specific pallial areas in amniote vertebrates is somewhat hazardous.

Among the telencephalic regions in amniotes that receive olfactory inputs relayed from the olfactory pallium is a subset of a group of nuclei, collectively called the **amygdala**. In amphibians and many amniotes, another part of the amygdala receives direct vomeronasal input from the accessory olfactory bulb. The latter system of projections will be discussed below in this chapter. The amygdala's other connections and its relation to the limbic system, of which it is considered a part, will be discussed in Chapter 30.

## Group I

In lampreys, the olfactory bulbs contain a **glomerular layer** that lies deep to the olfactory nerve fibers, a **layer of mitral cells**, and a **granular cell layer** that contains cells of varying morphology. Axons from cells in the granular cell layer contribute to the olfactory tracts along with the mitral cell axons. Olfactory bulb projections are dense within a large area in the telencephalon, which has been identified as the **lateral**

**pallium** (Fig. 29-2) partly because of this heavy olfactory input. A sparser olfactory projection is also present to the area identified as the dorsal pallium and possibly to the medial pallium as well.

In squalomorph sharks, the olfactory bulbs [Fig. 29-3] are covered by a layer of olfactory nerve fibers, deep to which are a **glomerular layer** and an **internal cellular layer**. The latter layer contains both mitral and granular cells. The layers of the olfactory peduncle can be traced into a **medial** as well as a **lateral pallial area**, which are thus interpreted as subdivisions of the lateral pallium in receipt of olfactory projections [Fig. 29-3(B)].

In nonteleost ray-finned fishes, the olfactory bulbs [Fig. 29-4] are covered by an outer layer of olfactory nerve fibers over the **glomerular layer**. Deep to the glomerular layer is an **external cellular layer** that contains both mitral cells and smaller, **periglomerular cells**. The axons of the periglomerular cells project peripherally to the receptor cells in the olfactory epithelium. A layer primarily of **secondary olfactory fibers** lies deep to the external cellular layer. This layer is primarily composed of the axons of mitral cells and divides into the medial and lateral olfactory tracts. The deepest layer of neurons is the **internal cellular layer** and contains granule cells.

Due to the development of the telencephalon by eversion instead of evagination, the most medial pallial field, sometimes designated **P1** [Fig. 29-4], is the part of the pallium in receipt of olfactory bulb projections via the lateral olfactory tract. The olfactory fibers terminate on the more distal parts of the dendrites of the pallial cells, which lie in a periventricular position. This pallial area is thought to be homologous to the lateral, olfactory pallium of vertebrates with evaginated telencephalic hemispheres.

In the coelacanth *Latimeria*, the olfactory bulb is covered by olfactory nerve fibers and contains a glomerular layer, a cellular zone that is presumed to contain mitral cells, and a more internal zone of granular cells. During the development of the telencephalon in *Latimeria*, the ventral, subpallial part evaginates. The dorsal, pallial part does not undergo an evagination, however, but is thickened and similar to the everted, pallial part of the telencephalon in ray-finned fishes. The olfactory tract lies in a central position within the pallial part of the telencephalon (Fig. 29-5).

In lungfishes, the olfactory bulbs contain a superficial olfactory nerve layer, a **glomerular layer**, an **external plexiform layer** of fibers, a **mitral cell layer**, an **internal plexiform layer**, and an **internal granular cell layer**. The transition zone between the olfactory bulb and the pallium is marked by a loss of the glomerular layer. Olfactory fibers project to areas identified, on topological, cytoarchitectonic, and histochemical grounds, as both the lateral and dorsal pallia.

In some tetrapods, both a main olfactory bulb (in receipt of olfactory nerve fibers) and an accessory olfactory bulb (in receipt of vomeronasal nerve fibers) are present. In amphibians the main olfactory bulb [Figs. 29-6 and 29-7] comprises a superficial layer of olfactory afferent fibers (rostral to the level shown in the figure), a **glomerular layer**, an **external plexiform layer**, a **mitral cell layer**, and an **internal granular cell layer**. As is also the case in lungfishes, the granular cell layer is relatively thick and densely packed with cells. In amphibians, mitral cell axons enter the lateral olfactory tract [Fig. 29-7] and

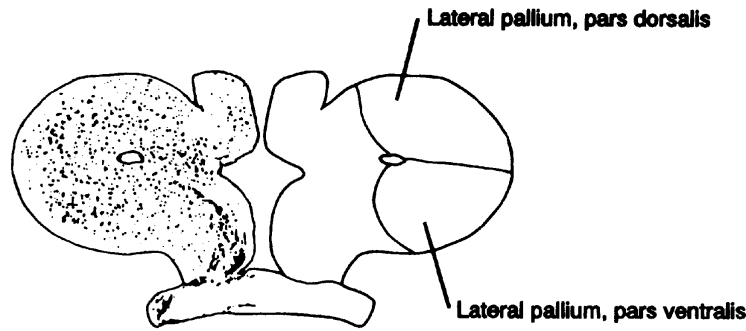


FIGURE 29-2. Transverse hemisection with mirror-image drawing through the telencephalon of a lamprey. Adapted from Northcutt (1981) with additional data from Northcutt and Puzdrowski (1988). Redrawn, with permission, from the *Annual Review of Neuroscience*, Volume 4, © 1981, by Annual Reviews Inc.

terminate in the **lateral pallium** and the ventral half of the dorsal pallium. In frogs, some fibers from the medial olfactory tract reach part of the rostral medial pallium, and in salamanders, some medial olfactory tract fibers terminate in rostral parts of both the medial and dorsal pallia.

A number of connections of the lateral pallium, in addition to its input from the olfactory bulb, have been studied in amphibians. The lateral pallium also receives afferent projections from the medial pallium and from the septum, amygdala, entopeduncular nucleus, preoptic area, anterior and central parts of the dorsal thalamus, and infundibular hypothalamus. Thus, the olfactory processing done by the lateral pallium is modulated by a number of forebrain inputs. The output of the lateral pallium in amphibians is predominantly within the telencephalon—to the olfactory bulb, medial pallium, dorsal pallium, diagonal band, septum, and striatum. While the lateral pallium also projects directly to the infundibular hypothalamus, the main route by which the lateral pallium influences the hypothalamus is through the medial pallium.

### Group II

In hagfishes, the olfactory nerves enter the olfactory bulb [Fig. 29-8] and terminate on the dendrites of mitral cells within the **glomerular layer**. A **periglomerular layer** and the **mitral cell layer** lie deep to the glomerular layer rostrally. In a more caudal part of the olfactory bulb, an **internal granular cell layer** is present. Both mitral and granule cells contribute axons to the olfactory tract.

The pallium of the telencephalon in hagfishes can be divided into five major divisions, three of which are shown in Figure 29-8, and the lateral olfactory tract projects massively to all five divisions. The lateral olfactory tract forms deep and superficial divisions that course within the deepest (**P5**) and the most superficial (**P1**) pallial divisions, respectively. The deep division of the lateral olfactory tract is unique to hagfishes. Whether the entire pallium in hagfishes is homologous to the lateral, piriform pallium of other vertebrates or is a field homologue of two or more of the pallial areas present in other vertebrates is an unresolved question. Studies of the efferent projections of the various divisions of the pallium and of other afferent projections may help to clarify telencephalic organization in these animals.

In Group II cartilaginous fishes, the olfactory bulb is superficially covered by a layer of olfactory receptor cell axons and contains **glomerular, mitral, and granular cell layers**. Fibers from the olfactory bulb divide into lateral and medial olfactory tracts in Group II sharks and terminate in the dorsal and lateral pallia. In skates (Fig. 29-9), only a single olfactory tract can be distinguished. This tract terminates in the lateral pallium and may also innervate a region on the medial border of the lateral pallium called **nucleus a**.

In teleosts, the olfactory nerve fibers form a superficial layer over the olfactory bulb. The olfactory bulb [Fig. 29-10] contains **glomerular, mitral, secondary olfactory fiber, and internal granular cell layers**. An example of a mitral cell in a carp is shown in Figure 29-11, although the morphology varies to some extent. A second type of neuron is present in the mitral cell layer in at least some teleosts and is called a **ruffed cell** in reference to the presence of many pedunculated protrusions on the initial portion of the axon. The axons of ruffed cells are believed to project into the telencephalon along with the mitral cell axons. The ruffed cells are unusual neurons, however, in that their dendrites surround the dendrites of the mitral cells

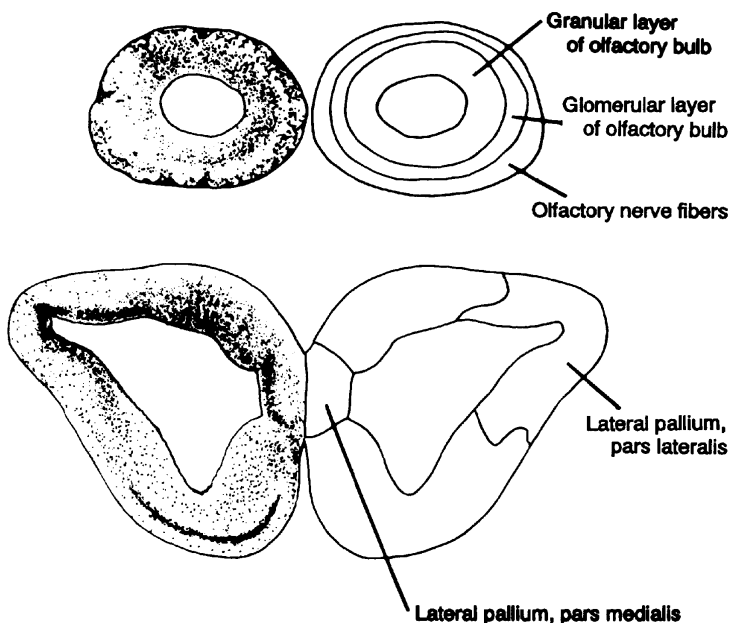


FIGURE 29-3. Transverse hemisections with mirror-image drawings through the olfactory bulb (top) and telencephalon of a squalomorph shark (*Squalus acanthias*). After Northcutt et al. (1988).

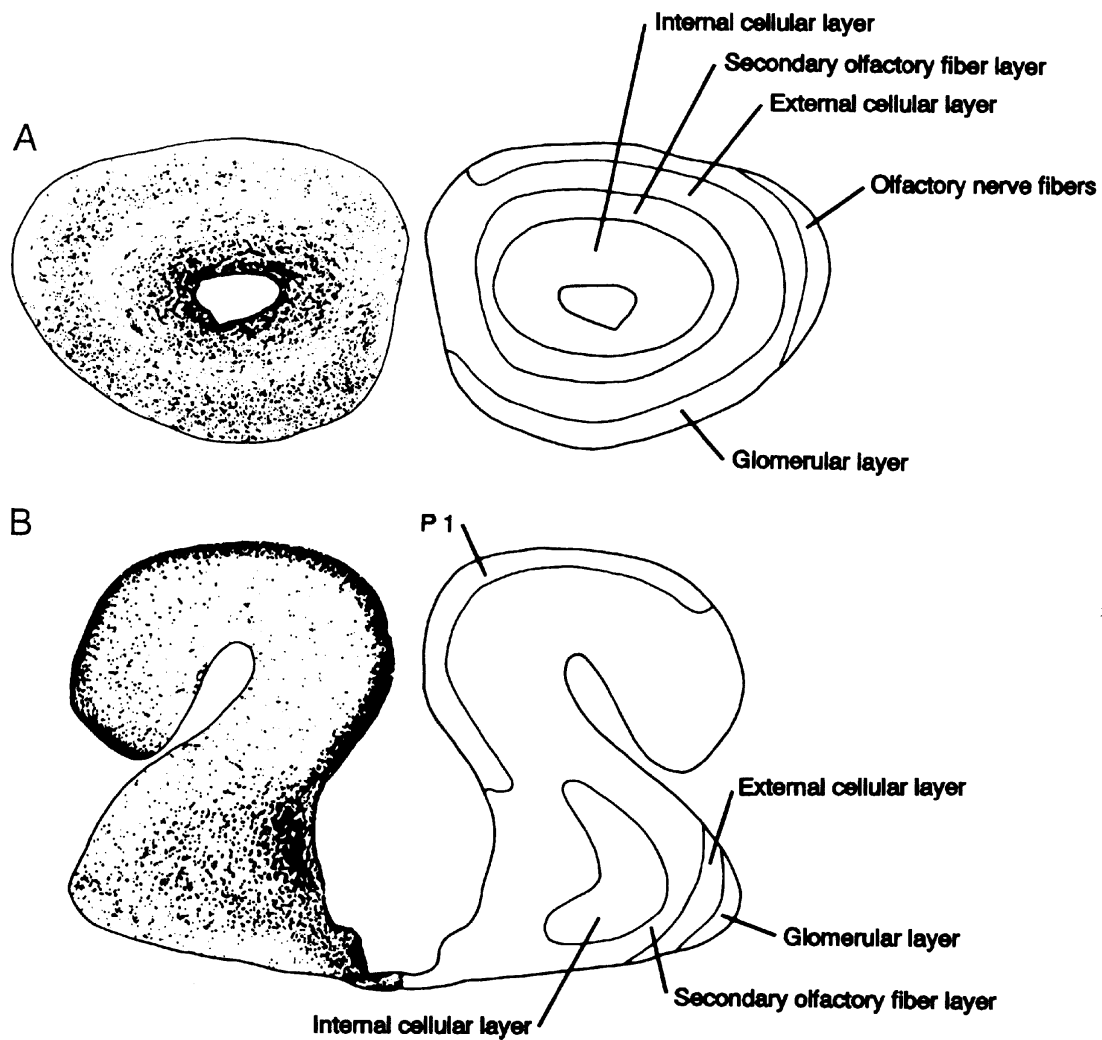


FIGURE 29-4. Transverse hemisections with mirror-image drawings through the olfactory bulb (top) and rostral telencephalon of a bichir (*Polyterus palmis*). After Northcutt and Davis (1983).

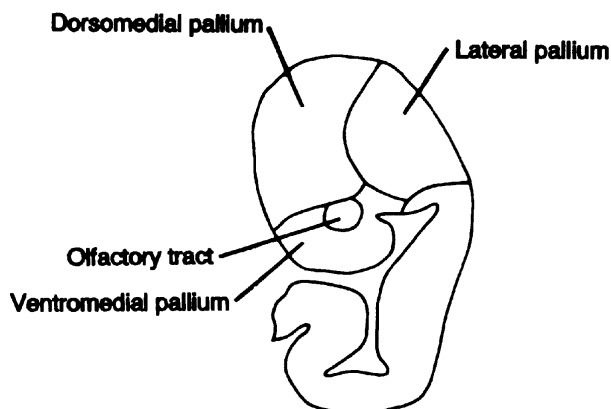


FIGURE 29-5. Drawing of a transverse hemisection through the right telencephalon of the coelacanth (*Latimeria chalumnae*). Adapted from Nieuwenhuys and Meek (1990b). Used with permission of Plenum Publishing Corp.

like glial processes, rather than receiving an array of synaptic inputs, while the ruffed portion of their axons have reciprocal synapses with granule cells. Their function in olfactory processing and their evolutionary origin remain to be determined. The granular cells of teleosts have smooth dendrites; they lack axons and appear to play a major role in the integration of olfactory information within the olfactory bulb.

The olfactory tract in teleosts comprises medial and lateral divisions. The olfactory fibers terminate predominantly within the **posterior zone of area dorsalis telencephali** [Fig. 29-10]. Recently, evidence of direct projections from the olfactory receptor cells to the posterior zone of area dorsalis and to the ventral and commissural nuclei of area ventralis (see Fig. 30-9) has also been found. Receptor cell axons that bypass the glomeruli of the mitral cells and continue to the telencephalon along with the axons of the mitral cells account for these projections.

The olfactory system has been studied in most detail in mammals. The neuronal organization of the mammalian olfactory bulb is shown semischematically in Figure 29-12. The chemosensory receptor cells terminate on mitral cell dendrites within the glomeruli in the **glomerular layer**. Centrifugal fibers, which arise in sites in the basal forebrain and project back to the olfactory bulb within the olfactory tract, synapse on

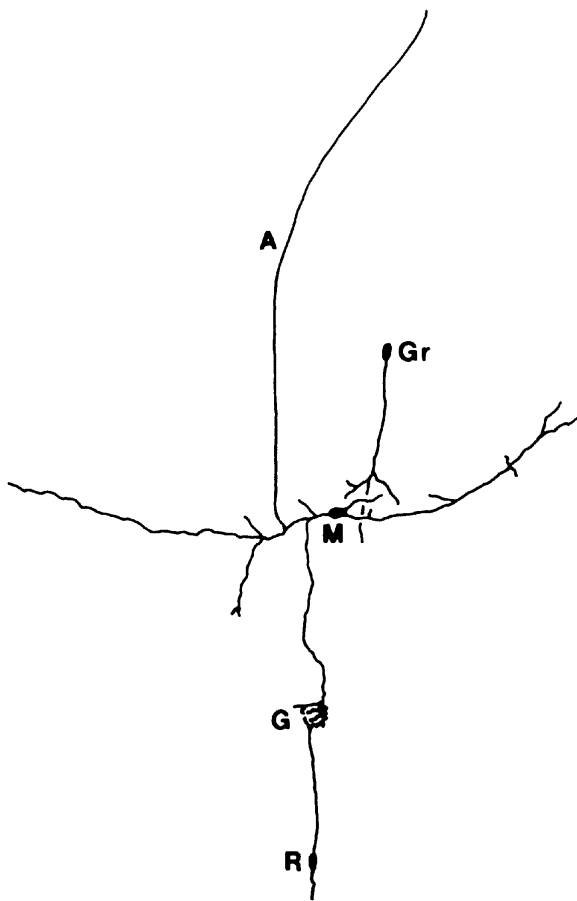


FIGURE 29-6. Drawing of a mitral cell (M) in the olfactory bulb of a frog (*Rana pipiens*) as seen in a Golgi preparation. An olfactory receptor cell (R) synapses on a glomerulus (G) on the distal end of a mitral cell dendrite. A granule cell (Gr) also synapses on the mitral cell. The axon (A) of the mitral cell projects to olfactory cortex. Adapted from Scalia et al. (1991).

the dendrites of granule cells, which, in turn, have reciprocal synapses with the mitral cell dendrites.

As in a variety of other vertebrates, the olfactory bulb in mammals gives rise to medial and lateral olfactory tracts. These tracts project to the **olfactory cortex**, which lies on the ventral surface of the telencephalon, and to neighboring areas including an **anterior olfactory nucleus** and the **olfactory tubercle** (see Fig. 29-19). These latter structures are sometimes considered to be parts of the olfactory cortex itself. The olfactory cortex comprises a **frontal olfactory cortex** lying next to the lateral olfactory tract and a more caudal, **temporal olfactory cortex**. The latter encompasses the **cortical part of the amygdala**, which receives vomeronasal projections.

The olfactory cortex in mammals projects to a variety of sites within the forebrain. It projects to some neighboring isocortical areas, to nucleus accumbens (ventral striatum), to limbic areas including the amygdaloid complex and the hippocampal formation, and to the lateral part of the hypothalamus. The olfactory cortex also has a substantial efferent projection to a nucleus in the dorsal thalamus called the **mediodorsal nucleus**.

The mediodorsal nucleus relays olfactory information to **prefrontal cortex**, and prefrontal cortex in humans (Fig. 29-13) has been implicated as the site of many higher, conscious

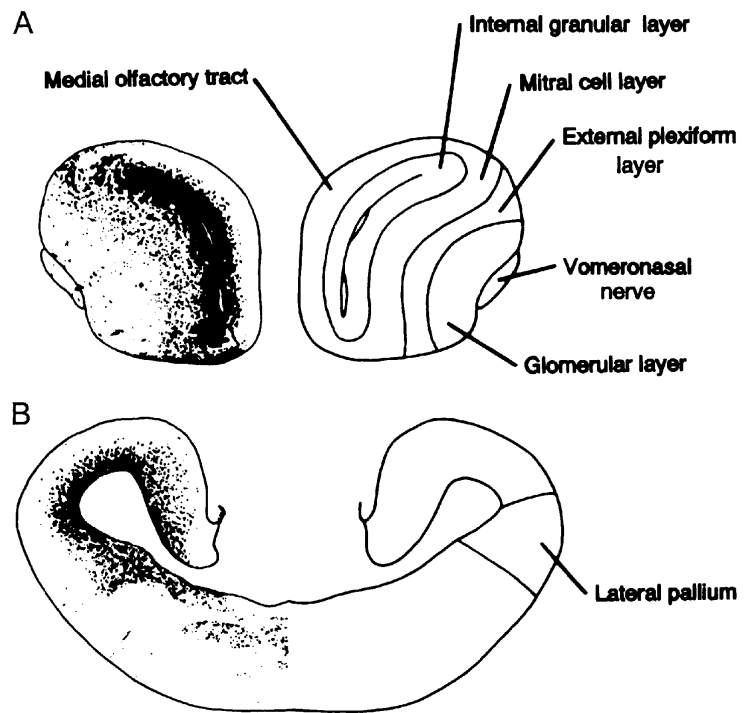


FIGURE 29-7. Transverse hemisections with mirror-image drawings through the olfactory bulb (top) and telencephalon of a tiger salamander (*Ambystoma tigrinum*). Adapted from Northcutt and Kicliter (1980). Used with permission of Plenum Publishing Corp.

cortical functions and as being dysfunctional in disorders such as schizophrenia. The cortical area of the projection of the mediodorsal nucleus is also richly innervated by dopaminergic fibers that arise in the brainstem. Among mammals, primates have an exceptionally large prefrontal cortical area. (Echidnas also have a very extensive prefrontal cortex but may have acquired this expansion independently.)

In diapsid reptiles (Fig. 29-14), the main olfactory bulb is covered by olfactory nerve fibers and contains a **glomerular layer** of glomeruli and periglomerular cells, an **external granular layer** of small cells, an **external plexiform layer** with a few displaced mitral cells, a **mitral cell layer**, an **internal plexiform layer**, and a densely packed **internal granular layer**. The olfactory tract projects to the **lateral, or piriform, cortex** in the lateral part of the telencephalic pallium, shown in a lizard in Figure 29-15. The olfactory bulbs of birds and turtles are organized in a like manner, as are their projections to lateral cortex. Efferent projections of the lateral cortex have been studied to some extent in nonsynapsid amniotes; lateral cortical efferents to nucleus dorsomedialis in the dorsal thalamus of birds recently have been described.

Studies of the distribution of dopaminergic fibers in the forebrain of birds have shown that a lateral and caudal part of the dorsal ventricular ridge, called the **posterodorsolateral neostriatum** (Fig. 29-16), is markedly rich in dopaminergic fiber innervation. While this site has been assigned to the dorsal ventricular ridge, its continuity with the dorsal cortical part of the telencephalon is important to note. A similarly located part of the dorsal ventricular ridge that is rich in dopamine has been found in lizards, although not in snakes or turtles. Behavioral studies in birds have shown that ablation of this part of the

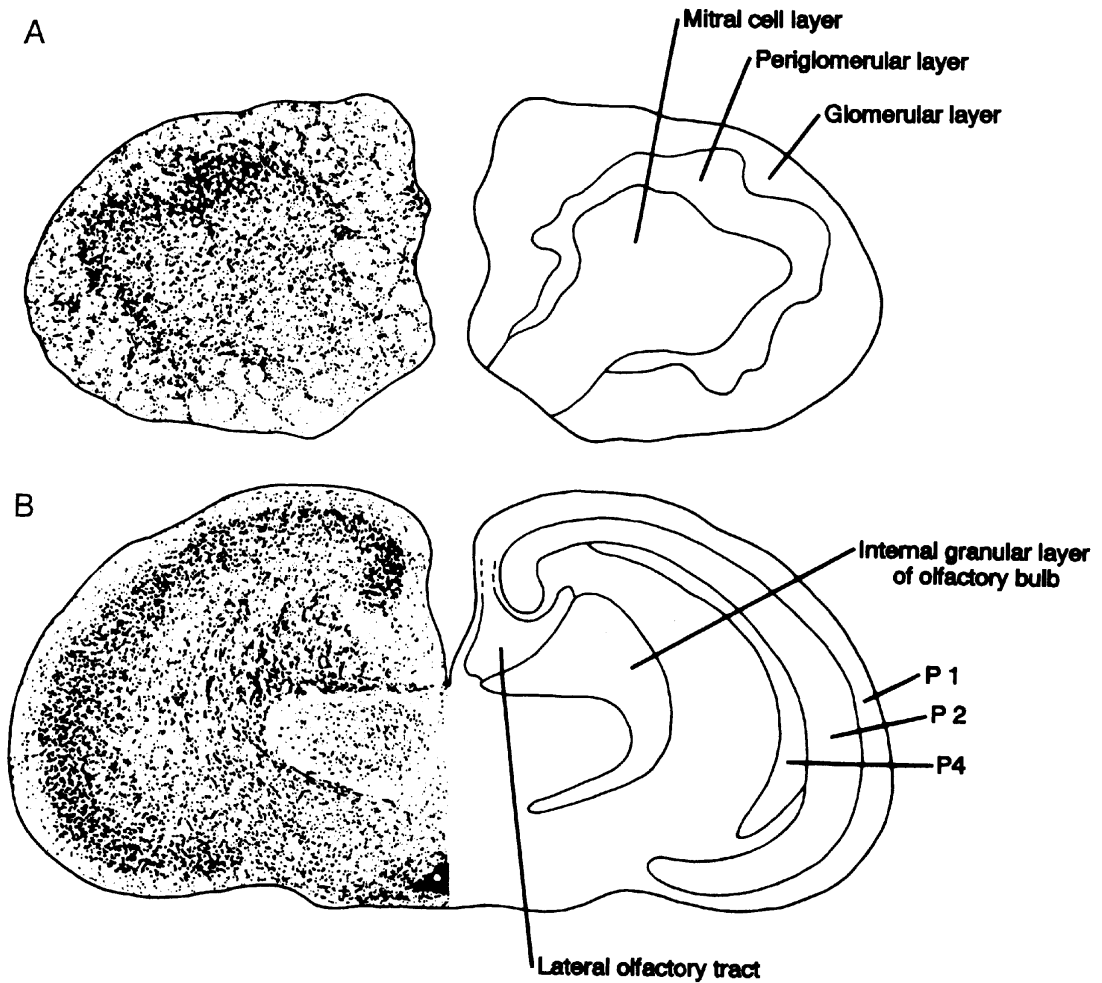


FIGURE 29-8. Transverse hemisections with mirror-image drawings through the olfactory bulb (A) and telencephalon of a hagfish (*Eptatretus stouti*). Adapted from Wicht and Northcutt (1992). Used with permission of S. Karger AG.

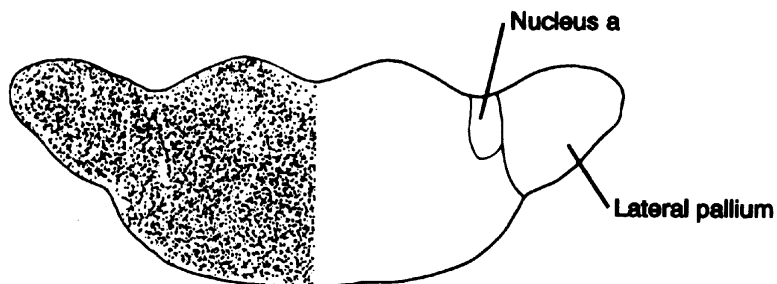


FIGURE 29-9. Transverse hemisection with mirror-image drawing through the telencephalon of a skate (*Raja eglanteria*). Adapted from Northcutt (1978).

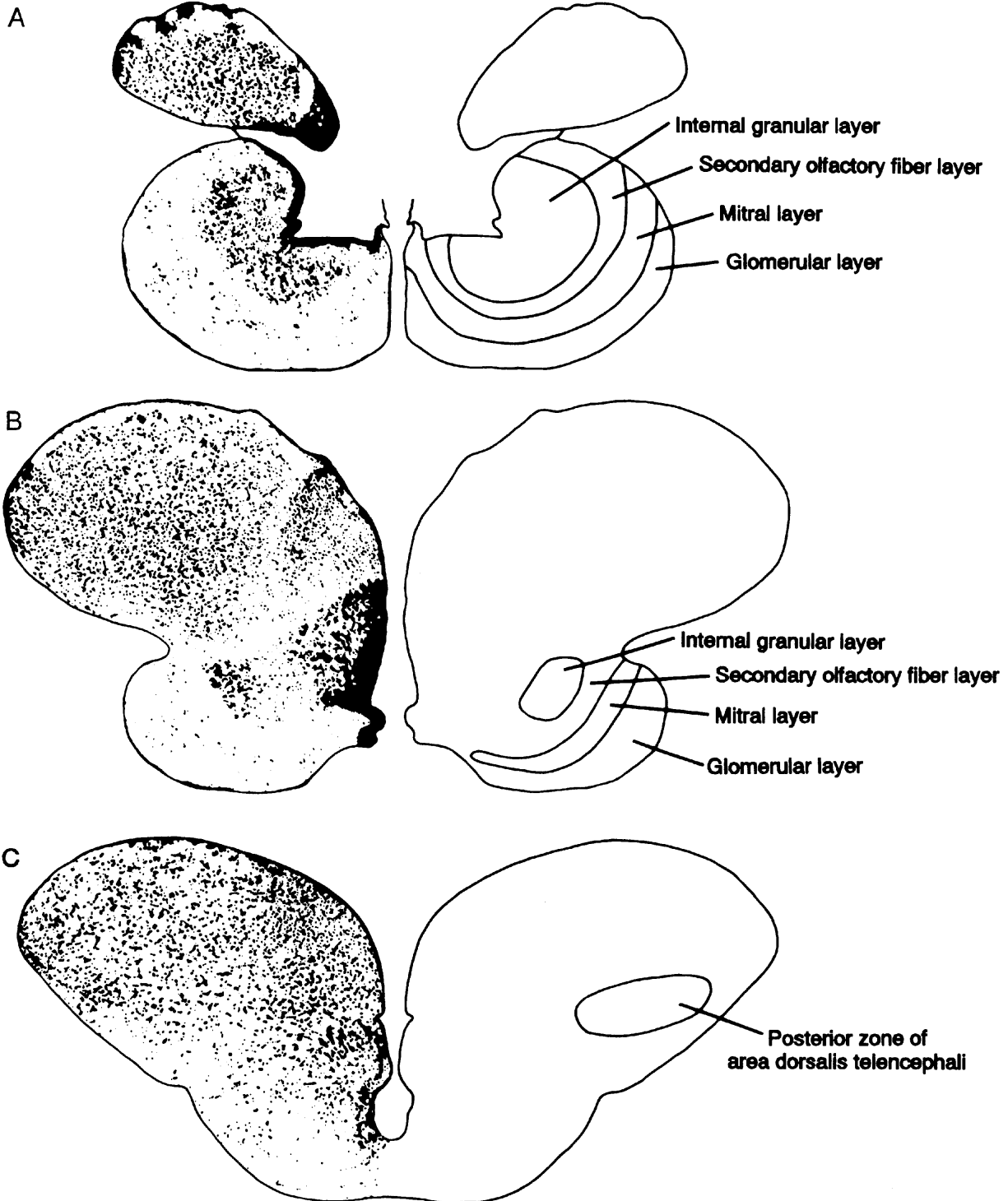


FIGURE 29-10. Transverse hemisections with mirror-image drawings through the olfactory bulb (A) and telencephalon in a teleost (*Salmo gairdneri*). Adapted from Northcutt and Davis (1983).

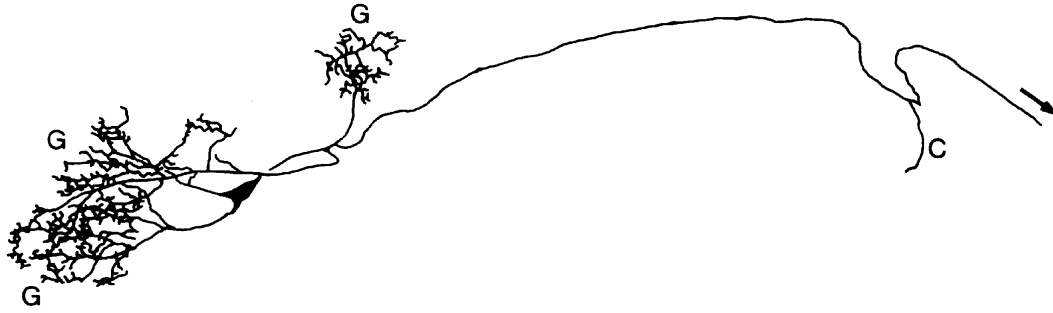


FIGURE 29-11. Drawing of a mitral cell as reconstructed from a Golgi preparation in the olfactory bulb of a carp. The distal part of the mitral cell dendrite ramifies to form several glomerular tufts (G). The axon gives off a collateral branch (C) before continuing into the telencephalon (arrow). Data from Satou (1990).

brain results in deficits in tasks requiring delayed alternation, which are similarly impaired by prefrontal cortical ablations in mammals.

The possible homology of the posterodorsolateral neostriatum in birds and of the corresponding part of the dorsal ventric-

ular ridge in other nonsynapsid amniotes with the prefrontal cortex in mammals would be strongly supported if an olfactory input projection system through the dorsal thalamus could be identified. Nucleus dorsomedialis receives an afferent projection from piriform cortex, but a possible pathway from this

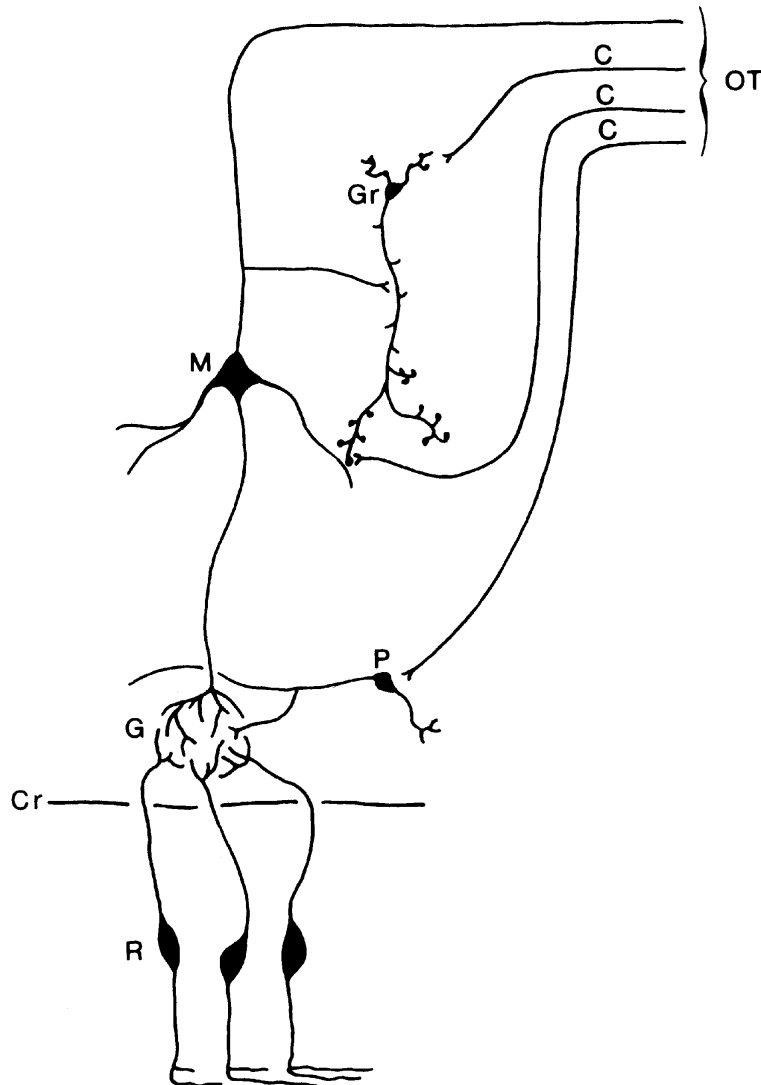


FIGURE 29-12. Schematic drawing of the organization of the olfactory bulb in mammals. Abbreviations: C: centrifugal fibers; Cr, cribriform plate; G, glomerulus; Gr, granule cell; M, mitral cell; OT, olfactory tract; P, periglomerular cell; R, receptor cell. Adapted from Heimer (1995, p. 271). Used with permission of Springer-Verlag.

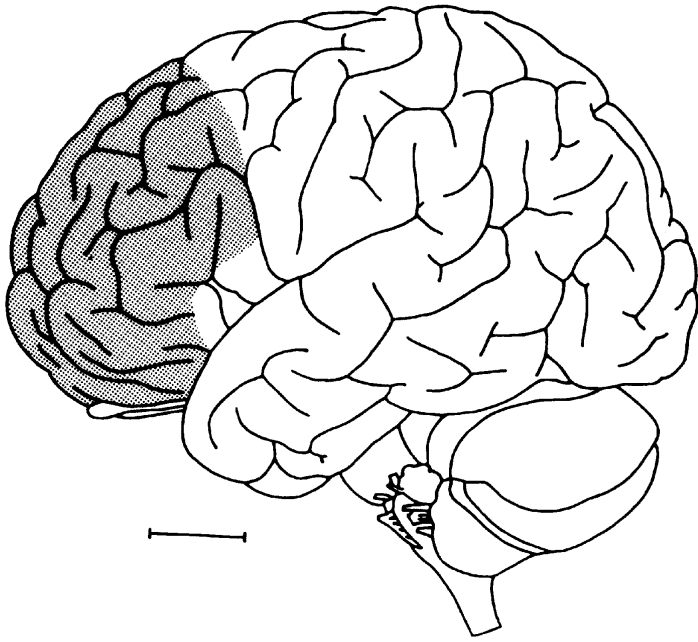


FIGURE 29-13. Drawing of the brain of a primate (*Homo sapiens*). Prefrontal cortex is indicated by shading. Adapted from Nieuwenhuys et al. (1978). Used with permission of Springer-Verlag.

nucleus to the dopamine-rich area of the neostriatum has not yet been described. Alternatively, the dopamine-rich part of the dorsal pallium may be plesiomorphic for amniotes, but the dorsal thalamic olfactory relay to this part of the pallium may have evolved only in mammals.

The role of a strong olfactory input to the prefrontal cortex in mammals is still somewhat enigmatic, as some mammals, such as primates, are generally considered to have reduced their use of the olfactory system in favor of other senses, particularly vision. Olfactory input may be more important than previously realized in both limbic and neocortical functions—including emotion, memory, learning, awareness of self, social interactiveness, and the set of distinctive behavioral characteristics unique to the individual.

### VOMERONASAL SYSTEM

A vomeronasal nerve is present in amphibians and, among amniotes, in mammals and most squamate reptiles (lizards and snakes). It is absent in the thecodonts (crocodiles and birds) and in turtles. Whether it is present in the rhynchocephalian *Sphenodon* is unclear. Until recently, this nerve was believed to be absent in some mammals, including some of the primates, but recent evidence suggests that it is probably present in all

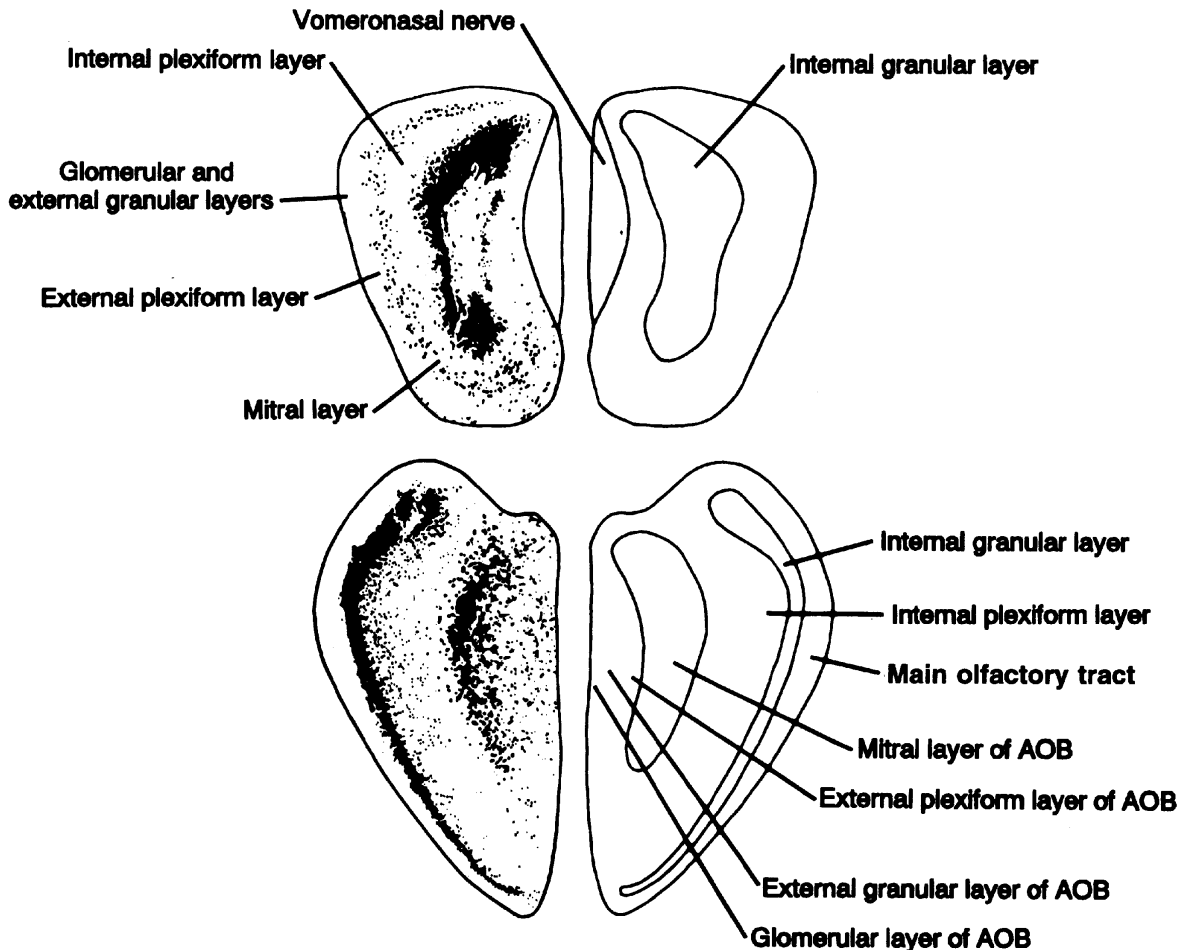


FIGURE 29-14. Transverse sections with mirror-image drawings through the main olfactory bulb (top) and the main and accessory olfactory bulbs in a snake (*Elaphe obsoleta rosalleni*). Adapted from Halpern (1980). AOB = accessory olfactory bulb. Used with permission of Plenum Publishing Corp.

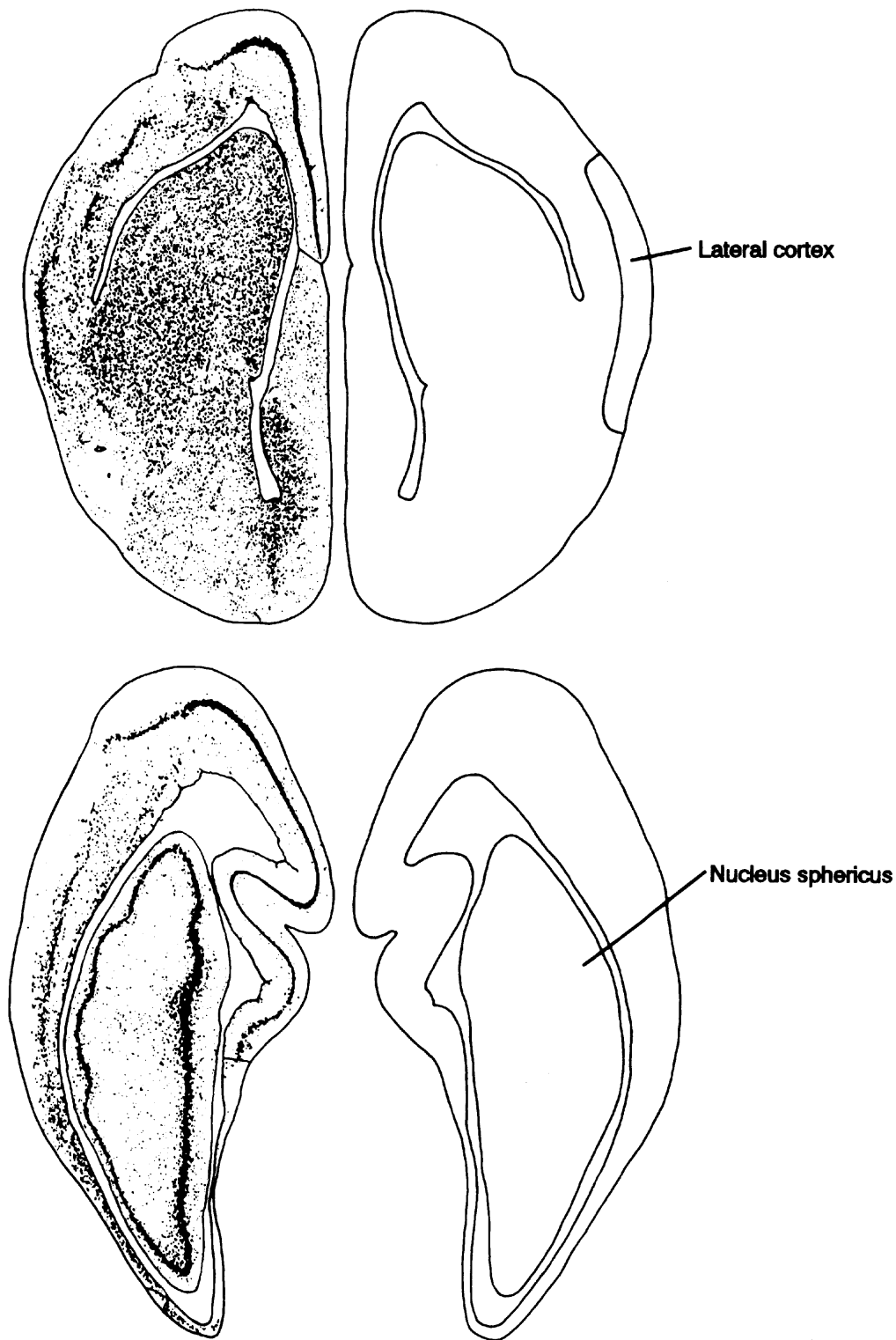


FIGURE 29-15. Transverse sections with mirror-image drawings through the telencephalon of a lizard (*Tupinambis nigropunctatus*). The upper section is more rostral. Adapted from Ebbesson and Voneida (1969). Used with permission of S. Karger AG.

mammals. The nerve has bipolar cells with dendrites ending in the olfactory epithelium, either in a restricted part of the olfactory epithelial area, as in urodele amphibians, or in a blind pouch next to the epithelial surface and called the **vomerona-**sal (or **Jacobson's**) **organ**, as in other amphibians and amni-

otes. The vomeronasal nerve projects to the accessory olfactory bulb.

In amphibians, the accessory olfactory bulb is present as a thickened part of the caudal wall of the main olfactory bulb. Neurons in the accessory olfactory bulb project to the ventrolat-

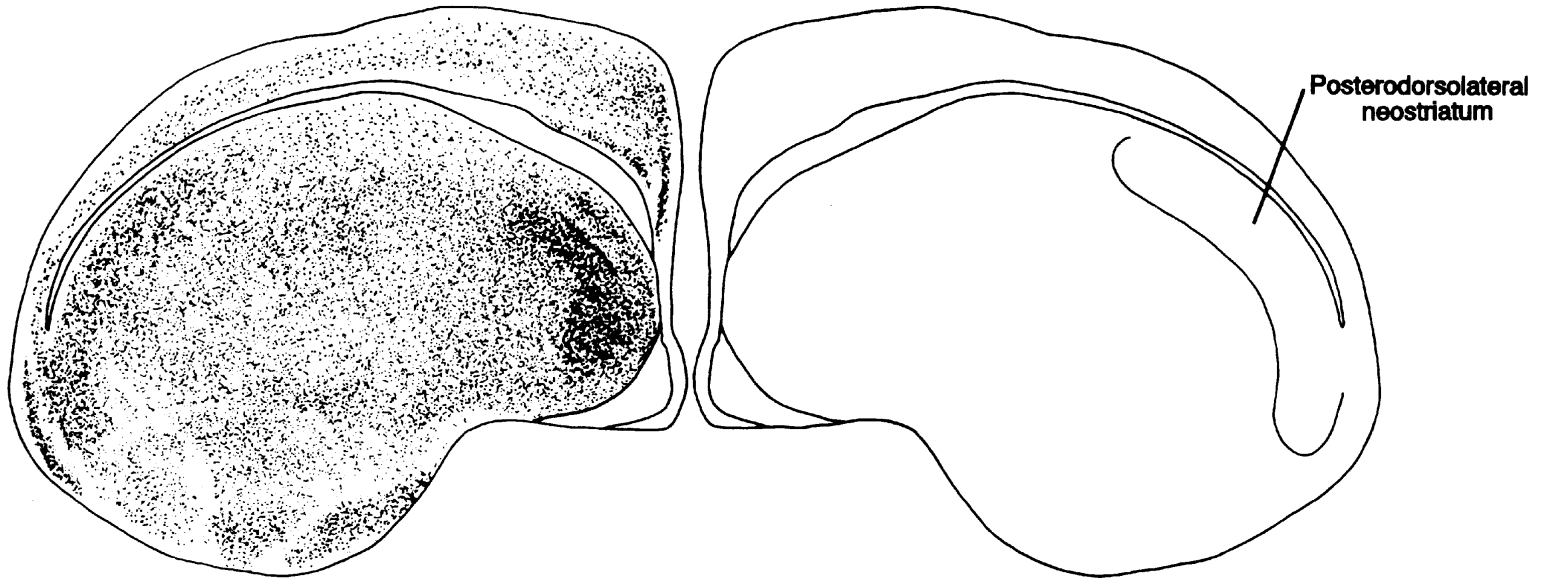


FIGURE 29-16. Transverse hemisection with mirror-image drawing through the telencephalon of a bird (*Columba livia*). Adapted from Karten and Hodos (1967) with additional data from Waldmann and Güntürkün (1993) and Divac and Mogensen (1985). Used with permission of The Johns Hopkins University Press.

eral tip of the lateral pallium, an area that is called the lateral prominence and may in fact be a part of the amygdala rather than of the lateral pallium. The accessory olfactory bulb projects most heavily to a more ventral part of the forebrain, called the **pars lateralis of the amygdala** (Fig. 29-17).

In amniotes, a number of subdivisions of the amygdala are present. In mammals, the amygdala (see Chapter 30) is frequently divided into **corticomedial** and **basolateral** divisions. Within the corticomedial division, the anterior cortical nucleus receives projections from the main olfactory bulb, while the posterior cortical and medial nuclei receive projections from the accessory olfactory bulb. Nuclei in the basolateral amygdala receive indirect olfactory input relayed through part of the olfactory cortex.

In lizards and snakes, in which both olfactory and vomeronasal systems are present, the amygdala has three divisions, two of which receive direct olfactory input. The **olfactory amygdala** receives input from the main olfactory bulb, and the **vomeronal amygdala**, which is most often called **nucleus sphericus** (Fig. 29-15), receives input from the accessory olfac-

tory bulb (Fig. 29-14). In all amniotes and amphibians studied to date, the areas of termination of fibers from the main and accessory olfactory bulbs are separate. The pars lateralis of the amygdala in frogs, the posterior cortical and medial amygdaloid nuclei of mammals, and the nucleus sphericus in lizards and snakes appear to be homologous as pallial, vomeronasal-receptive cell groups.

The vomeronasal system plays an important role in mediating unconditioned and reinforcing properties of natural chemicals, such as those used for prey trailing by snakes. In mammals, the pheromonal cues detected by the vomeronasal system are essential for some components of normal copulatory behavior and affect the regulation of the onset of puberty, female cyclicity, the release of some hormones, the maintenance of pregnancy, maternal behavior, and other related functions.

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## TERMINAL NERVE

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The function of the terminal nerve is uncertain, although it is currently suspected of having a neuromodulatory role, regulating neuronal excitability in the various sites to which it projects, including areas within the more ventral and medial parts of the forebrain. The nerve has been found to project to the retina and to the optic tectum in teleost fishes. It was described in cartilaginous fishes by Fritsch in 1878 and by Locy in 1905 and is now known to be widely distributed among vertebrates. The dendrites of terminal nerve neurons are distributed on the nasal septum and are in close proximity to the blood vessels in that area. The cell bodies of these neurons are most frequently located within a nearby ganglion, but their position is variable, particularly within bony fishes.

The cell bodies of the terminal nerve contain **luteinizing hormone-releasing hormone (LHRH)**, which is sometimes alternatively called **gonadotropin-releasing hormone (GnRH)**. In mammals, most terminal nerve cell bodies lie in

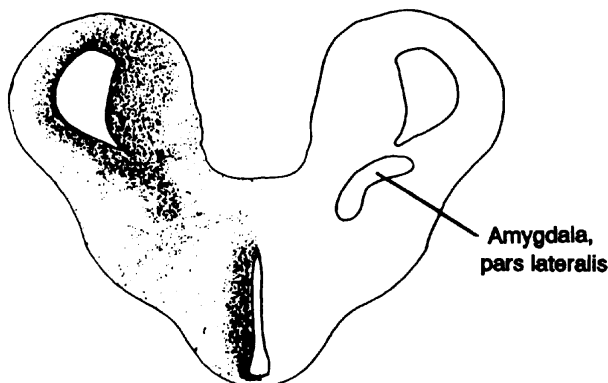


FIGURE 29-17. Transverse hemisection with mirror-image drawing through the telencephalon of a frog (*Rana catesbeiana*). Adapted from Wilczynski and Northcutt (1983).

the ganglion of the nerve, but some additional LHRH-containing cells lie along the course of the nerve as it enters the brain. The LHRH-containing fibers of the terminal nerve project to the preoptic area, the medial part of the hypothalamus, the main and accessory olfactory bulbs, olfactory cortex, parts of isocortex, and the midbrain. A possible role for the terminal nerve in pheromonal responses for reproductive behavior, including the promotion of ejaculation by copulating males, has been suggested; however, the contribution of the terminal nerve in this and other behaviors, versus the contribution of the medial part of the olfactory system, remains to be clarified.

In lampreys, neurons that resemble the terminal nerve cell bodies of other vertebrates lie along the olfactory nerve as it enters the olfactory bulb, and the axons have been traced to the ventral thalamus, the ventral part of the hypothalamus, and the mesencephalic tegmentum. Unlike other vertebrates, however, terminal nerve fibers in lampreys do not appear to contain LHRH. In cartilaginous fishes, terminal nerve cell bodies are positive for LHRH and lie within as many as three ganglia as well as along the distal part of the nerve itself. The nerve appears to project mainly to the preoptic area and the septum; fibers also terminate directly on cerebral blood vessels. In sturgeons, a number of GnRH positive cell bodies, presumably at least some of which are terminal nerve cell bodies, are distributed within the ventral part of the forebrain.

In lungfishes, the terminal nerve has two components: an anterior root (or **terminal nerve proper**) and a posterior root (also called the **nervus praepopticus**). Terminal/preoptic nerve fibers have been traced to the septum and to the preoptic nucleus, but the terminal sites of more caudally passing fibers that enter the lateral forebrain bundle have yet to be identified. Terminal nerve projections to septal, preoptic, and hypothalamic sites have been found in amphibians, where, as in other vertebrates, LHRH appears to play a role in reproductive behaviors via the hypothalamic-pituitary system. The central projections of the terminal nerve need further study in non-synapsid amniotes, but are probably to septal and preoptic-hypothalamic sites. The involvement of LHRH in various aspects of reproductive behavior has been established.

In teleost fishes, the terminal nerve cell bodies contain LHRH and project to medial, ventral sites in the forebrain. In teleosts in which the olfactory bulb is sessile, the majority of cell bodies of the terminal nerve do not lie in a ganglion but migrate into the medial and ventral parts of the forebrain. That intracerebral, LHRH-positive cells can originate from the medial olfactory placode and migrate into the forebrain has recently been confirmed with experimental embryological findings in mice. In teleosts, the migrated terminal nerve neurons project to visual structures, particularly the retina. Diencephalic neurons that project to the retina also have recently been found in sturgeons, but whether these neurons are LHRH (GnRH) positive and thus terminal nerve neurons remains to be confirmed.

In teleosts, the migrated neurons of the terminal nerve form a broken rostrocaudal column through the ventral parts of the telencephalon and diencephalon. They have been referred to collectively as the **nucleus olfactoretinalis** and have been found to receive an ascending projection from a set of neurons in the area of the isthmus located rostral to the locus coeruleus. Axons from the cell bodies of the terminal nerve project to the retina via the optic nerve. In the retina, many of the fibers synapse on dopamine-containing **interplexiform cells**. The effect of the terminal nerve innervation of the retina on visual functions remains to be elucidated.

The terminal nerve in fishes is believed to play a role in reproductive behaviors due to the LHRH content of its neurons. The olfactory system may, however, play a more prominent role in reproduction. Exposure to sex pheromones has been found to increase the activity of olfactory nerve neurons in the medial part of the olfactory bulb but not of terminal nerve neurons. Tactile stimulation, on the other hand, was found to result in a decrease of terminal nerve neuron activity, and the contribution of the terminal nerve to reproductive behavior may thus be related to the physical contact that occurs during spawning behavior.

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## EVOLUTIONARY PERSPECTIVE

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The olfactory nerve component of the rostral chemosensory system is present in all groups of vertebrates and is plesiomorphic for vertebrates. Olfactory projections to the pallium are restricted, mostly to the lateral pallium, in jawed vertebrates but are more extensive in lampreys and are to the entire pallium in hagfishes. From this distribution, extensive olfactory innervation of the pallium appears to be the plesiomorphic condition for vertebrates. Likewise, restricted pallial olfactory projections are the plesiomorphic condition for jawed vertebrates.

The presence of a terminal nerve in jawless vertebrates is questionable, but a terminal nerve is at least plesiomorphic for jawed vertebrates. In ray-finned fishes with sessile olfactory bulbs, the majority of cell bodies of the terminal nerve are in a migrated position within the brain. The projection of terminal nerve neurons to visual structures such as the retina is apomorphic in some or all ray-finned fishes. While both olfactory and terminal nerve systems are present in most vertebrates, variation does occur. In toothed whales, for example, both the olfactory and vomeronasal systems have been lost, but the terminal nerve system has been markedly expanded.

The vomeronasal system is present in some tetrapods but not in nontetrapod vertebrates and is apomorphic for tetrapods. It has been secondarily lost in thecodonts (crocodiles and birds) and turtles and may also have been reduced or lost in *Sphenodon*. Although previously believed to be absent in some mammals, particularly primates, recent evidence suggests that a vomeronasal system may have been retained in all mammals.

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## FOR FURTHER READING

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