CHAPTER 4
THE EVOLUTION OF BODY, BRAIN, BEHAVIOR, AND MIND IN QUADRUPED AMPHIBIANS AND REPTILES
Terrestrial Vertebrate Adaptations

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4.1. Somatic, Neural, Behavioral, and Mental Adaptations in Newts and Frogs: Our Amphibian Legacy

4.1.1. Amphibians: The Transition from Water to Land. Cartilaginous and bony fishes occupied all aquatic niches by the beginning of the Devonian, about 400 m.y.a. (Fig. 3-1). Thus, pressure was beginning to build up at some sites on some piscine species to leave the water and seek safety on land, and where lakes and seas dried out, other species were compelled to do so to survive. That transition from aquatic to terrestrial niches has been taken much earlier by invertebrates (arachnids, insects, gastropods), providing added incentive for some fishes to assume an amphibious life style to feed on land. Amphibians appeared during the late Devonian period of the Paleozoic era about 375-385 m.y.a. (Carroll, 1988; 2009; Ahlberg et al., 1996; Shimizu, 2001; Benton, 2004; Daeschler et al., 2006). It is believed that these transitional species, such as Ichthyostega (Fig. 4-1A), descended from lobe-finned fishes that had lungs for breathing and modified fins that enabled them to crawl on land (Schultze, 1977; Hinchcliffe and Johnson, 1980; Coates and Clack, 1990, 1991). The forelimbs of Ichthyostega appear to have been weight bearing, enabling them to haul themselves to dry land with their hindquarters dragging (Ahlberg et al., 2005). It was not until the Carboniferous (about 350 m.y.a.) that more advanced amphibians emerged, such as Labyrinthodonts, which could effectively walk on land (Panchen, 1975). The Labyrinthodonts were large animals, some several meters long, with heavy skulls, sharp teeth and strong vertebrae. It is likely that there were early amphibian species with different life styles, some spending most of their time in the water, others increasingly depending on terrestrial resources and returning to the water to shelter and breed. The Labyrinthodonts, as well as the Lepospondyls, became extinct during

![Ichthyostega](Ichthyostega_BW.jpg)  
![Bony Skeleton](Ahlberg et al. 2005.)

Fig. 4-1. Reconstruction of the appearance of Ichthyostega (A), and the structure of its bony skeleton (B). (A, from Ichthyostega_BW.jpg. B, from Ahlberg et al. 2005.)
the Permian and Jurassic era (270-135 m.y.a.) and were replaced by newts and salamanders (Fig. 4-2, urodela), and frogs and toads (Fig. 4-3, anurans) that survive to this day.

The abandonment by amphibians of the relatively stable aquatic milieu for the bounteous but unstable world of dry land, with its many opportunities as well as challenges, was a momentous event in vertebrate history, one that necessitated the evolution of several new organs. These included: (i) lungs for extracting oxygen from the air (perhaps derived from the air bladders of fish); (ii) forelimbs and hind limbs for locomotion on land (derived from the pectoral and pelvic fins of ancestral fish); (iii) a freely turning head attached to the trunk by the mobile neck; (iv) some accessories to existing sense organs, such as a moist and prehensile tongue for gustatory exploration, and external ears for hearing; and (v) a more complex brain.

Life on land is more difficult than life in water, and amphibians have never succeeded in completely adapting themselves to terrestrial living. To begin with, the conservation and replenishment of water, which is the ubiquitous internal milieu of all living beings, is a challenging task on dry land. Due to their lack of full adaptation, most amphibians inhabit an aqueous medium in at least some phases of their life cycle. Most of them return to water to breed because they have not evolved eggs with a fluid filled sac, the amnion, which protects
the developing embryo from desiccation. After hatching, many amphibians spend their early life in the water as tadpoles, with tails used for swimming and gills for breathing. They do not develop functional lungs until they have metamorphosed. Moreover, lacking a diaphragm, the amphibian lung is a less efficient air exchange apparatus than the lungs of higher vertebrates. Amphibians rely on a subcutaneous bed of blood vessels to absorb oxygen from the air and expel carbon dioxide. Having a porous skin, they are liable to dry out. Finally, since skin breathing requires a high ratio of surface area to volume, the large-bodied amphibians that have evolved could survive only in moist habitats.

Notwithstanding these handicaps, amphibians became dominant creatures of littoral and swampy environments for nearly 100 million years (Carroll, 2009). Then, they became extinct during the Jurassic, with only the furtive newts and salamanders, and the more specialized frogs and toads, surviving to this day in circumscribed environments. However, amphibians are of great interest from an evolutionary perspective because our lungs, and our four limbs with their articulated digits, are an amphibian legacy, and so are our mobile head and tongue, as well as some components of our spinal cord and brain.

4.1.2. Somatic, Behavioral, and Neural Adaptations in Amphibians. Most salamanders live in moist environments beneath leaves, rocks, or logs (terrestrial salamanders), others in trees (arboreal salamanders), still others (particularly newts), spend much time in water (Petranka, 1998). Some species are small, other may reach a foot or more in length. Salamanders begin their life as larvae with external gills and no limbs but large tails for swimming. As they metamorphose, most of them shed their gills, develop limbs, and use their lungs for air breathing. Salamanders are solitary predators, lying in ambush until a cricket, a spider, a worm, a slug, or the like, comes close, then with a rapid flick of the tongue the victim is captured. They may also scavenge on the remains of decaying animals. Most salamanders are nocturnal but some are active during the day, particularly on rainy days. Lacking scales, salamanders cannot survive in a dry milieu and being cold-blooded, they are active only when the weather is warm. In winter, they hibernate underneath the ground or bury themselves in mud. Beginning in the spring, they become sexually mature and travel to a breeding pond to mate. Following a courtship display, the male clasps the female (amplexus), and transfers a capsule of sperms (spermatophore) to the female. The female lays the fertilized eggs, numbering from several hundred to over a thousand, and attaches them to some plant and leaves them there to hatch.

Frogs and toads are more abundant and widespread than salamanders, and are also more specialized, having powerful hind legs for hopping and leaping (Mattion, 1987). Most species are limited to moist and warm areas; those that live in temperate zones are active during the warm seasons. During winter, they bury themselves underground and hibernate. Like salamanders, most frogs wait for a prey to appear and then, with rapid flick of their sticky tongue, catch them. Others may leap forward to catch a flying insect with their mouth open, or dive into the water to catch a tadpole or small fish. Although, they lack claws on their digits, some have spades that they use to dig or as a weapon when they engage in territorial fights. Others have special pads on their toes, which act like suction cups, enabling them to move with ease over steep and smooth surfaces (Fig. 4-3A). Prompted by warm and moist weather, frogs move to a breeding ground near water and the males advertise their readiness to mate by
Fig. 4-3. A. Frog using its toe pads to climb on a glass surface.
B. Mating male and female toad.  (Credit: Gary Nafis, califomiaherps.com.)
vocalizing, producing croaks by exhaling air amplified by balloon-like vocal sacs. Some frogs croak in unison, creating a chorus. When a female approaches a vocalizing male's territory, he jumps on her back, clasps her, and stays with her until she lays her eggs, which he then fertilizes (Fig. 4-3B). Typically, the female lays thousands of eggs encased in sacs or tubes, which she attaches to some vegetation in shallow water.

Evolutionary Origins of the Limbs, Hands, and Feet in Behavior. An important amphibian contribution to our somatic constitution was the evolution of the paired forelimbs and hindlimbs (Fig. 4-1). The amphibian limbs with their distinctive skeletal elements, including digits, are a conserved trait of all quadruped vertebrates, as well as biped humans. These appendages are also present in modified form in tetrapods with arboreal adaptations, such as birds and bats, and those with aquatic adaptations, such as dolphins and whales.

The pair of ancestral amphibian forelimbs, jointed to the anterior pectoral girdle, consist in all quadruped vertebrates of the same skeletal elements: one proximal bone (humerus), and two distal bones (radius and ulna; Fig 4-4C). The pair of hindlimbs, jointed to the posterior pelvic girdle, consist likewise of one proximal bone (femur), and two distal bones (tibia and fibula; Fig. 4-4A, B). The hand of amphibians and humans (Fig. 4-4C) consists of three sets of skeletal elements: the carpals (wrist bones) jointed proximally with the ulna and radius, and distally with the metacarpals (palm bones), and the phalanges (finger bones) jointed with the metacarpals. The corresponding elements of the foot consists of the tarsals, metatarsals, and toe bones (Fig. 4-4A, B, D). In extinct Labyrinthodonts as well as extant salamanders and frogs, the hands have four digits; the feet, five digits (Figs. 4-4A, B). The complex bony structure of the amphibian limbs has undergone drastic modifications in many vertebrate lines but have largely been conserved in quadruped reptiles, basal mammals and, significantly, in primates (Fig 4-4 C, D).

There are fundamental differences in some of the uses of the forelimbs and hindlimbs in different vertebrates. Considering only amphibians and mammals (including monkeys, apes and man), the following is worth noting. Amphibians use their limbs mainly for locomotion: newts and salamanders for crawling, climbing and burrowing; frogs and toads also to leap over long distances. While salamanders can lift their body off the ground and walk, more commonly they drag their body with their limbs positioned laterally (Fig. 4-2). There is some dimorphism between the structure and uses of the amphibian forelimbs and hindlimbs. During locomotion, the salamander forelimbs, aided by the digits, grab and pull the animal forward by a flexor action, the larger hindlimbs propel it forward by an extensor action (Gray et al., 1997). The long, radiating digits, acting largely in unison, provide an extensive surface area for contact with the substratum and serve principally as grabbing and anchoring instruments. Frogs’ limbs are more powerful and their dimorphism is more pronounced (Fig. 4-3). For instance, frogs may wipe their mouth with one of the forelimbs after ingesting a prey (Ewert, 1980), and use their hindlimb to remove an irritant from their body (Berkinblit, 1986). However, amphibians do not use their forelimbs for such precision tasks as catching a flying insect in midair or pick something off the ground. Rather, they use their tongue and mouth as manipulatory organs. In basal mammals, such as insectivores and rodents, and particularly prosimians, the hands and mobile fingers are increasingly employed as manipulatory organs, such as pick berries and
THE FOOT OF AMPHIBIANS

A. Labyrinthodont

B. Salamander

C. Human hand

D. Human foot

Fig. 4-4. The bony structure of the foot in an extinct Labyrinthodont (A) and modern salamander (B) (abbreviations: c1-c4 centralia; d1-d5 distal tarsals; f fibulare; i intermedium; pt pretarsal element; Roman numerals indicate digits; t tibiale). Bony structure of the dorsal right human hand (C) and plantar surface of the left foot (D). (A, B, modified from Romer, 1970. C, modified From Marzke, 1999. D. Modified, from Woodburne, 1973.)
fruits, tear objects apart, and groom themselves and others. Finally, in quadruped monkeys, knuckle-walking apes, and biped humans the grasping hands and dexterous fingers have evolved into precision instruments, enabling them to palpate and manipulate objects not only for practical purposes, such as feeding, but in order to examine and become familiar with their physical properties.

**THE AMPHIBIAN LIMBS AND DIGITS: A LESSON IN EVOLUTIONARY HISTORY.** The anatomy of our limbs and digits provides us with an important lesson regarding our evolutionary origins. The biblical story is that we are God’s special creation. God created man with a mission: to obey and live by His commandments, adulate and worship Him, and contemplate His wisdom. Intuitively, this creation myth makes excellent sense. How else could such a complex organism come into existence but by the design of a Creator? And why else can we think and reason, and have a moral sense? But what about the created beasts, what function do they serve? The answer was that God created them, each species separately, to serve a role in that Divine Design: some to provide us with nutrients and raw materials for clothing and shelter; others to pull plows or carry heavy loads; still others (vermin and pests) to irritate and harm us if, failing to obey God’s commands, we merit punishment.

This creation myth was challenged by the scientific discovery that life began on this planet billions of years ago, much before humanity has emerged. As our planet cooled and became habitable, life emerged in the form of teeming unicellular organisms. This was followed by the emergence of multicellular plants and animals. Some of these species endured while others became extinct and, filling vacated niches, the latter were replaced by new species, many with more advanced traits than their predecessors. The stage leading to human origins, anthropoid evolution, commenced only a few dozen million years ago, with the emergence of monkeys and apes, followed by primitive humans with small brains, and ending with the emergence of modern humans with large brains and an evolving culture. The creation myth was accordingly modified recently by admitting the transmutation of species, but postulating that that was the product of an “Intelligent Design.” God did not create man and animals in a few days but did so gradually, starting with simple forms and improving them gradually. The Scala Naturae of medieval thinkers, the Great Chain of Being, came to be seen as a reflection of orthogenetic evolution, the unerring linear progression from the simple to the complex, from the good to the better. The Creator had from the outset a plan of what humans should be like and, much as intelligent inventors of machines and engineers do, started out by creating simpler living forms and replaced them progressively with better ones.

So let us examine whether our possession of four limbs with digits supports the idea of orthogenetic evolution by design or, instead, that of random evolution steered by organic selection forces? It is a fact that having inherited the hindlimbs of amphibians we can walk and run, and having inherited our forelimbs with their long digits, we can fabricate and manipulate things. But were the four amphibian limbs design-based “pre-adaptations” for human use or a fortuitous legacy that required a lot of “tinkering” to make them suitable for human use? We have four extremities, rather than six limbs like arthropods have, because of our amphibian heritage. (Arthropods colonized terrestrial habitats by the late Silurian, preceding amphibians by more than 50 million years [Pisani et al., 2004]). Evolving four limbs, amphibians were
able to crawl or run on land, using their tongue or large mouth to capture prey. However, four limbs do not constitute an intelligent preadaptation for human biped locomotion. How much better off we would be had we inherited six limbs. Running on four extremities, we could be as swift as some of the big cats are, and have as well two arms anchored to a stable body to capture prey and manipulate objects. Being bipeds with a tetrapod heritage, we have to learn as infants to walk on our hindlimbs; we have to remain fully conscious to do so once we acquire that skill (we collapse when we faint and have to lie down when we sleep); and once we get old, we have to use a cane or a wheelchair to walk and maintain our precarious balance. Had Intelligent Design been behind human evolution, amphibians would have had six extremities or, alternatively, the tetrapod vertebrate design would have been abandoned in higher vertebrates and replaced with six extremities.

The Role of Vision in Amphibian Behavior. As in humans, vision plays an important role in the behavior of amphibians, particularly frogs and toads (Ingle, 1976a). Most anurans have well-developed medially directed eyes with overlapping binocular visual fields (Fig. 4-3B). Their laminated retina has a complex organization, with two types of pigmented rods, red and green, and two types of cones, single and double (Fig. 4-5A). The photosensitive rods and cones are interconnected by way of a meshwork of vertically aligned bipolar cells and horizontally oriented amacrine cells, and there is a layer of ganglion cells whose axons form the optic nerve (Dowling, 1968; Fig. 4-5B). The processing of visual input begins at the retinal level where many ganglion cells have receptive fields that selectively respond to stimuli moving in one or another direction (Lettvin et al., 1959; Backstrom et al., 1978). There is some evidence for color vision in frogs that is independent of light intensity (Donner and Reuter, 1976).

Pattern Discrimination in Prey Catching. Salamanders snap with higher frequency at stripes that move like worms, in the direction of their long axis, than stripes that move perpendicular to their long axis (Himstedt et al., 1976). Most commonly, frogs and toads catch prey with a fast tongue flicking (Fig. 4-6). Leopard frogs use tongue flicking to capture short pieces of an earthworm, and a jaw action to capture longer pieces (Anderson and Nishikawa, 1996). The features of a frog’s tongue or jaw action differ when elicited by different types of prey, such as termites, crickets, earthworms or mice (Valdez and Nishikawa, 1997). Ewert (1980) distinguished six movements in the prey catching of toads: (i) orienting toward the prey, (ii) approaching it, (iii) visual fixation of the target, (iv) snapping, (v) swallowing, and (vi) wiping the mouth clean with the paws of the forelimbs. If the prey is swiftly removed during visual fixation, snapping, swallowing and wiping are still performed, indicating that these are stereotypically-sequenced ballistic movements rather than actions guided by sensory feedback. In general, small moving objects elicit snapping by frogs, whereas large looming objects trigger defensive reactions, such as freezing, ducking, shuffling backward or leaping forward (Ingle, 1976b). Importantly, it is the real size of an object rather than the size of its retinal image that determines whether a frog will snap at or avoid an object (Ewert, 1980). This indicates perceptual object constancy. It is assumed that object constancy is mediated by monocular cues of distance because it is displayed by frogs with a single eye (Ewert, 1980). However, it appears that the great accuracy with which frogs catch moving prey is aided by binocular vision. One-eyed frogs continue to snap at worms but their success at hitting them is deficient (Ingle, 1976b).
Fig. 4-5.  A. Red rod cell and single cone receptor cell in the frog retina.  B. Diagram of the synaptic organization of the frog retina.  (A, Modified, from Donner and Reuter, 1969.  B, Modified, from Dowling, 1968.)

PREY-CATCHING FROG

Fig. 4-6. Sequence in prey catching by a frog.  (From Tinbergen, 1951.)
Structure and Functions of the Amphibian Spinal Cord and Brainstem. The spinal cord of the frog resembles the human spinal cord (Nieuwenhuys, 1964; Altman and Bayer, 2001). The dorsal horn of the gray matter is composed of small neurons and is the target of dorsal root afferents. The ventral horn contains the large multipolar motor neurons that are the source of ventral root efferents. But there are some notable differences. In humans both the cervical enlargement, which innervates the forelimbs, and the lumbar enlargement, which innervates the hindlimbs, are prominent, in the frog only the lumbar enlargement is prominent (Fig. 4-7A). In the latter region, the motor neurons are arranged in several columns. Motor neurons forming the medial columns innervate the muscles of the trunk; those in the lateral columns innervate the muscles of the hindlimb, ankle, and toes in a topographic order (Cruce, 1974a). This topographic organization has been conserved in all higher vertebrates (Ryan et al., 1998). Another notable difference is that the spinal white matter is much smaller relative to the gray matter in the frog than in man (Fig. 4-7B). Since the bulk of the white matter is composed of ascending and descending fiber tracts, this indicates much sparser interconnection between the brain and spinal cord in frogs than in humans. This applies in particular to the absence of the spinothalamic and corticospinal tracts that control human volitional behavior. Components of the amphibian brainstem—the medulla, parts of the pons and the cerebellum, and the midbrain tectum and tegmentum—share similarities with the human brainstem.

Role of the Spinal Cord in Amphibian Locomotion. Notable among neural advances in amphibians relative to fishes is the evolution of spinal cord circuits that control quadruped locomotion. We have described earlier the role of spinal cord pattern generators in the coordination of swimming in lampreys (Section 2.5.4). The coordination of quadruped locomotion on solid ground is a far more difficult enterprise than swimming in buoyant water. Quadruped locomotion requires easing or lifting the body off the ground, rhythmic coordination of the stepping cycle, maintenance of postural balance when off the ground, and coordination of the limbs in such operations as grabbing, digging, and scratching. What spinal mechanisms mediate the stepping cycle? Sherrington (1906), who investigated this matter in decapitated cats, proposed that the rhythmic stepping cycle is produced by a chain of reflexes mediated by feedback from stretch receptors embedded in the extensor and flexor muscles of the limbs. However, evidence was already available by the time Sherrington offered this hypothesis that quadruped locomotion in amphibians is not a chain reflex. Hering (1897) found in frogs that cutting the afferents of a limb—which prevents sensory signals from stretch receptors reaching the spinal cord—does not affect their ability to swim or walk. More recent studies have established that deafferentation of all four limbs in newts, frogs and toads does not interfere with their ability to walk or jump in a normal fashion (Weiss, 1950). Hence, the coordination of routine locomotion must be mediated in amphibians, much as it is in fish, not by peripherally initiated reflexes but by central pattern generators. While the properties of these pattern generators remain to be elucidated, it has been demonstrated that spinal pattern generators are responsible for the wiping reaction demonstrated in decapitated frogs (Berkinblit et al., 1986). This automatism, which is triggered by local skin irritation, consists of the following sequence of movements: flexion of the hindlimb on the irritated side of the body; spreading of the digits; placing the limb behind the irritant; approaching the irritant with spread digits; and, finally, removing the irritant with a rapid extension of the whole limb (Fig. 4-8). This is a variant of the scratching response displayed by all higher vertebrates, including
Fig. 4-7. The frog/toad nervous system with emphasis on spinal cord structure. **A.** Parts of the nervous system showing divisions of the brain and spinal cord. **B.** Gray and white matter in the lumbar enlargement. **C.** Lateral lumbar motoneurons. **A,** modified figure 2-5 from Altman and Bayer (2000); **B, C,** modified Figure 2-8 from Altman and Bayer (2000).
mammals. In the frog, as in fish, the spinal mechanisms responsible for locomotion are under the control of efferents from the midbrain (Rubinson, 1968; Ten Donkelaar et al., 1981), in particular, the reticular formation (Joseph and Whitlock, 1968; Adli et al., 1999; Dityatev et al., 2001).

ROLE OF THE MEDULLA IN AMPHIBIAN BREATHING. While some newts and salamanders retain their gills for ventilation through adulthood, most adult amphibians use their lungs for breathing. The neural mechanisms of breathing have been studied in frogs. Using the technique of fictive breathing (recording rhythmic discharge patterns from nerve roots or from single neurons in decerebrate preparations maintained in vitro) a spontaneously bursting column of neurons was identified in the medulla of frogs (Perry et al., 1995). The frequency of these recorded bursts in decerebrate frogs is comparable to the breathing rhythm of the living animal and is pH sensitive, the rate decreasing by alkaline perfusion and increasing by acid perfusion (McLean et al., 1995). This rhythmic discharge is not the property of single neurons but that of an assembly of neurons (McLean and Remmers, 1997). A superordinate system that modulates the discharge of lower-level respiratory neurons in the bullfrog is located in the pontine nucleus isthmi (Kinkead et al., 1997). Inactivation of this site transforms the variable breathing seen under different conditions to a uniform rhythm. There are also midbrain sites that modulate the autonomous rhythm of the lower-level pattern generators (Milsom et al., 1999; Reid et al., 2000). These findings indicate that the brainstem circuits coordinating the basic breathing rhythm evolved in amphibians.

ROLE OF THE MIDBRAIN IN THE VISUAL GUIDANCE OF AMPHIBIAN BEHAVIOR. As in fish, so also in amphibians (Fig. 4-9), the main target of optic tract fibers is the highly laminated optic lobe. These fibers terminate contralaterally in a topographic, or retinotopic, order (Singman and Scalia, 1990) and synapse with dendrites of smaller neurons in the superficial layers, and with dendrites of larger neurons in the deeper layers of the optic lobe (Székely and Lázár, 1976; Montgomery and Fite, 1989; Fig. 4-7B). Some of the large neurons are the source of efferent fibers that project to the midbrain tegmentum and the medulla and, indirectly, to the spinal cord (Masino and Grobstein, 1989, 1990). Behavioral studies have revealed that the optic lobe plays a major role in the coordination of avoidance behavior and prey catching of frogs. Optic
lobe ablation abolishes their avoidance behavior (Ingle, 1976a) and prey catching (Comer and Grobstein, 1978), and severance of its connections with the medulla abolishes orienting toward a visual target (Masino and Grobstein, 1989). Snapping can be elicited in the toad by electric stimulation of circumscribed loci in the optic lobe (Ewert, 1980). However, the coordination of escape behavior involves other brain circuits, including the nucleus isthmi of the midbrain and the pretectal-thalamic region. The optic lobe has been preserved in all vertebrates and is known in mammals as the superior colliculus (optic tectum). Notably, however, the superior colliculus receives a decreasing proportion of optic fibers in the ascending order of primates, with most of them being re-routed to terminate in the thalamic dorsal lateral geniculate nucleus, the relay station to the visual cortex. In primates, the function of the superior colliculus is limited to the control of eye movements and gaze (Sparks 1999).

In salamanders (Finkenstädt, 1980) and toads (Ewert, 1980) with intact optic lobes, destruction of the pretectal-thalamic area abolishes the escape response and the animals henceforth respond to both small and large objects by snapping. A specific midbrain structure that has been implicated in this visual function is the nucleus isthmi—the same structure that, as we noted earlier, modifies the routine breathing pattern. The nucleus isthmi receives ipsilateral afferents from the optic lobe (McCart and Straznicky, 1988; Pollak et al., 1997) and projects back bilaterally to the optic lobes (Gruberg et al., 1989; Dann and Beazley, 1990; Kulik and Matesz, 1997). Visually guided prey-catching and threat avoidance is abolished in frogs after destruction of the nucleus isthmi (Caine and Gruberg, 1985), and partial nucleus isthmi lesions produce localized scotoma (blind fields) in the contralateral monocular field (Gruberg et al., 1991). The apparent blindness (visual neglect) produced by nucleus isthmi lesions, which does not itself receive direct optic input from the retina, suggests that this brainstem structure plays a role in the perceptual processing the visual information relayed by the optic tectum. A small

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**Fig. 4-9.** The laminated optic lobes in a frog. (From Ariëns-Kappers et al. 1936.)
region in the mammalian midbrain, called parabigeminal nucleus, may be the homologue of the nucleus isthmi.

Structure and Function of the Amphibian Forebrain. The amphibian forebrain (Fig. 4-10) is more advanced than that of fishes (Figs. 3-10, 3-12), as there is a clear separation between the telencephalon surrounding the lateral ventricles and the diencephalon surrounding the third ventricle (Fig. 4-11). As in higher vertebrates, the amphibians telencephalon is composed of a dorsal pallial region (cortex) and a ventral ganglionic region (striatum). However, the pallium and striatum are both rudimentary in amphibians, as illustrated in stained sections from a newt (Fig. 4-11A). The cell bodies of neurons are situated near the lining of the ventricle, much as they do in the embryonic brains of higher vertebrates, and only have a few dendritic branches. The latter radiate into the superficial fibrous layer (Figs. 4-11B, C). This differs from the neocortex of mammals in which the cell bodies form a distinct structure—the gray matter, or cortical plate—sandwiched between a superficial fibrous layer and the underlying white matter.

THE BULLFROG BRAIN

Fig. 4-10. The CNS of the bullfrog, in ventral (A), sagittal (B), and dorsal (C) views. (Modified, from Kicliter and Ebbeeson, 1976.)
the amphibian pallium. In the bullfrog brain, the pallium surrounds the lateral ventricle and has several components (Fig. 4-12). Some investigators consider the cell-sparse lateral pallium as the “general cortex.” However, it does not have the laminated organization of the mammalian cerebral cortex. Most of the neurons, as noted, are situated in a periventricular position adjacent to the persisting neuroepithelium. The medial pallium may be homologous with the subiculum and Ammon’s horn of the mammalian hippocampal formation. However, there is no indication for the presence of a dentate gyrus. Adjacent to the hippocampus is the well-developed septum. The ventral pallium (Fig. 4-12A) is the target of olfactory fibers; hence, it is identified as the rhinencephalon. It may be the primordium of the piriform cortex (Herrick, 1948).

The amphibian hippocampus has extensive connections with the septum (González and López, 2002; Endepols et al., 2005; Moreno and González, 2007), much like the mammalian hippocampus. The septum receives input from the olfactory bulb, amygdala, basal ganglia, anterior thalamus, and brainstem (Roden et al., 2005). Septal efferents target the aforementioned structures as well as the hypothalamus (Endepols et al., 2005). An examination

**Fig. 4-11.** a. Stained sections of the newt pallium at an anterior (1) and a posterior (2) level. Retrogradely labeled neurons (b) and olfactory tract fibers (c) in the lateral pallium. (Scale bars: a=200µm; b=50µm; c=100µm. Abbreviations: Acc, nucleus accumbens; Apl, anterolateral amygdala; Apm, anteromedial amygdala; Dp, dorsal pallium; lcp, lateral cellular prominence; Lp, lateral pallium; Mp, medial pallium; S, septum; Str, striatum; vcp, ventral cellular prominence; Figure 1 from Moreno and González, 2007.)
of the telencephalon in fiber-stained sections (Fig. 4-13) reveals that, with the exception of a small fornix (Fig. 4-12B), there are no large fiber tracts in the pallium. This differs from the mammalian cerebral cortex, which is the target of a large complement of thalamocortical fibers and is the source of the large corticospinal efferent system. Hence, the inference is justified that the different pallial areas of amphibian telencephalon are homologous with the mammalian limbic allocortex rather than the neocortex (Shimizu, 2001).

THE AMPHIBIAN BASAL GANGLIA. The two identified components of the amphibian basal ganglia are the paleostriatum, which may be homologous with the nucleus accumbens, and the amygdala (Marin et al., 1997a, b, c; 1998; Moreno and González, 2004; Roth et al., 2004; Laberge and Roth, 2005). Both receive a large olfactory input, and a smaller and indirect visual and auditory input from the midbrain (Northeutt and Ronan, 1992; Marin et al., 1997a, b; Roth and Westhoff, 1999). The amphibian paleostriatum, like the mammalian neostriatum, has a dopaminergic input from the brain stem (Wilczynski and Northcutt, 1983a; Dubé et al., 1990; González and Smeets, 1991) and contains substance P and enkephalin neurons (Reiner et al., 1998). However, it lacks a substantial reciprocal connection with the pallium (Reiner et al., 1998) as does the mammalian striatum. The major output of the amphibian paleostriatum is to the midbrain tectum and tegmentum by way of several pretectal nuclei (Finkenstädt et al., 1983; Wilczynski and Northcutt, 1983b; Marin et al., 1997b). Some of the efferents contain substance P and enkephalin (Merchanthaler et al., 1989; Schmidt et al., 1989; Taban and Cathieni, 1983). The tectum, tegmentum, and reticular formation, in turn, have large outputs to the premotor nuclei (pattern generators) of the spinal cord (Rubinson, 1968; ten Donkelaar et al, 1981; Masino and Grobstein, 1989, 1990). Unlike the dorsal pallium, the ventral telencephalon is traversed by large fiber tracts—the medial and lateral forebrain bundles—and its two halves are interconnected by the anterior commissure (Fig. 4-13). In mammals, these fiber bundles are components of the limbic system implicated in emotional behavior.

THE AMPHIBIAN DIENCEPHALON. The absence of the neocortex in amphibians is paralleled by the relatively small size of the thalamus. The mammalian neocortex receives a massive thalamic input but thalamic projection to the amphibian pallium is meager (Veenman et al., 1989). The amphibian thalamus receives a fiber projection from the spinal cord (Munoz et al., 1994), which suggests the presence of a spinothalamic tract that is implicated in nociceptive functions in mammals. The only thalamic region that is well developed in amphibians is the habenular nucleus (epithalamus); it may play a role in the activation of seasonal reproductive functions (Kemali et al., 1990). In contrast to the thalamus, the hypothalamus, including the preoptic area, is well developed in amphibians. (We discuss below its physiological and endocrine functions.)

In summary, the forebrain of amphibians shows some advances when compared with fishes. However, the amphibian pallium is composed only of two layers: a thin, cell-dense band in a periventricular position and a thicker fibrous region superficially. The principal neuron of the periventricular gray matter is a simple pyramidal cell furnished with a few dendrites projecting into the external white matter (Fig. 4-11). This is unlike the stratified neocortex of higher vertebrates. Hence, the amphibian forebrain is justly characterized as paleocephalic limbic system that, as we shall argue below, is associated with the affective regulation of behavior.
Fig. 4-12. Cell-stained sections of the forebrain of the bullfrog from rostral to caudal (A-C). (Modified, from Kicliter and Ebbeson, 1976.)
Fig. 4-13. Fiber-stained sections of the forebrain of the bullfrog from rostral to caudal (A-C). (Modified, from Ariëns-Kappers et al., 1936.)
4.1.3. Amphibian Affects, Perception, and Cognition. We have previously argued that affects play a role in the guidance of fish behavior (Section 3.2). We justified that by using such objective criteria as neuroendocrine reactions and emotional expressions when they are aroused or stressed, and the presence of brain structures and mechanisms that, in mammals and man, are associated with feelings and emotions. Using these criteria, there is ample evidence that pain, fear, anger, and sexual ardor play an important role in amphibian behavior. There is also some evidence that, tested under appropriate conditions, amphibians can learn from individual experience. However, the available evidence indicates that their perceptual and cognitive abilities are quite limited.

Endocrine and Neural Mechanisms and Emotional Expressions in Amphibians. Amphibians are carnivores that live by hunting but because of their small size they are also at great risk of themselves becoming the prey of larger animals. Accordingly, they are furtive animals, hiding through much of the day under leaves and rocks, and relying on their cryptic coloration for camouflage. When hunting, they use stealth: with a rapid flick of their tongue they stun their victim, often larger than themselves, and opening their large mouth fitted with sharp teeth (Fig. 4-14A) they quickly swallow it. When threatened or attacked they respond swiftly with species-specific defensive reactions (Kiester, 1977). Newts and salamanders spray a poisonous secretion on their attacker, and advertise their toxicity by displaying vivid body markings on their head and neck (Fig. 4-14B). Frogs and toads either freeze when threatened by a looming object, thereby making themselves difficult to detect, or leap into the nearby pond or river to escape. Alternatively, they respond to threat by an aggressive display, such as raising themselves off the ground, becoming inflated with air that makes them appear larger, or they spray a distasteful or venomous substance to deter the attacker.

ENDOCRINE AND NEURAL MECHANISMS OF PAIN IN AMPHIBIANS. The pain we experience is mediated by nociceptive afferents that convey to the CNS potential damage or actual injury to skin, muscle, and viscera. The nociceptive fibers are thin, unmyelinated axons that contain a peptide, substance P, as a neurotransmitter, and terminate superficially in the dorsal horn of the spinal cord (reviewed in Altman and Bayer, 2001). These substance P-containing cells and fibers are present in the frog not only in the spinal cord but also in several brain regions. These include: the periaqueductal gray, the reticular formation, the tectum, and nucleus isthmi in the brainstem (Stuesse et al., 2001); the preoptic area and hypothalamus of the diencephalon; and the septum, basal ganglia and nucleus accumbens in the telencephalon (Inagaki et al., 1981; Taban and Cathieni, 1983). Co-localized with substance P at these sites is enkephalin (Taverna et al., 1993; Stuesse et al., 2001), an endogenous opioid that ameliorates pain. Two enkephalin-containing pathways have been identified in the frog: one originating in the nucleus isthmi, and another that courses in the lateral forebrain bundle (Lázár et al., 1990). It has been reported that the stimulus threshold that elicits stress reactions in frogs is elevated after the administration of a moderate dose of morphine, and that this analgesic effect persists for over two hours (Pezalla, 1983). This morphine-induced analgesia is greatly reduced after the administration of naloxone, an opioid antagonist, much as it does in mammals. These two lines of evidence—the presence of neural mechanisms that mediate pain in humans and the ameliorating effect of analgesics—support the inference that amphibians feel pain when injured.
OFFENSIVE AND DEFENSIVE NEWT POSTURES

Fig. 4-14. A. The large mouth and sharp teeth of a hunting newt. B. Defensive display of a threatened newt. (A. Courtesy of Val Johnson. B. Courtesy of Gary Nafis. CaliforniaHerps.com.)
ENDOCRINE AND NEURAL MECHANISMS OF FEAR AND ANGER IN AMPHIBIANS. The defensive (fear) and offensive (rage) reactions of amphibians are associated with endocrine and visceral changes similar to those found in mammals. Captured frogs respond with an increase in serum corticosteroid levels, and that reaction is attenuated over time in association with an increase in the concentration of beta-endorphin, an endogenous opioid (Mosconi et al., 1994). Neurons containing corticotropin releasing factor (CRF) have been localized in the olfactory bulb, the pallium, the amygdala and the hypothalamic preoptic area (Bhargava and Rao, 1993). In the newt, intracranial administration of CRF increases hypothalamic dopamine and serotonin levels, paralleling that seen in mammals in response to physical and mental stress (Lowry et al., 2001). As in mammals, so also in frogs, administration of opioid antagonist increases plasma levels of corticosteroids whereas beta-endorphin decreases it (Zerani and Gobbetti, 1992). Neurons containing melanin-concentrating hormone (MCH), which plays a role in affective skin color changes, are present with highest concentration in the dorsal hypothalamus, and their axons are distributed to the olfactory bulb, the amygdala, the septum, some thalamic nuclei and the midbrain (Lázár et al., 2002). Finally, as in mammals, the hypothalamus and several brainstem structures are implicated in the fear and rage reactions of amphibians. In the frog, neurons containing noradrenaline, serotonin or dopamine are concentrated in the hypothalamus, the reticular formation, the locus coeruleus, and the raphe nuclei of the brain stem (Marín et al., 1996). The axons of these neurons target the basal ganglia, the nucleus accumbens and the amygdala (Gonzalez and Smeets, 1993) as well as the spinal cord (Tan and Miletic, 1990).

ENDOCRINE AND NEURAL MECHANISMS OF AMOROUSNESS AND PARENTAL AFFECTION IN AMPHIBIANS. Seasonal changes, such as rainfall or rise in temperature, are among the environmental factors that initiate gonadal maturation and consequent visceral and endocrine changes in amphibians. The latter, in turn, prompt a series of highly motivated sexual and reproductive behaviors, including migration to breeding sites, sexual advertising, courtship behavior, and mating. Fertilization is internal in most newts and salamanders, and external in frogs and toads. Newts and salamanders engage in elaborate courtship behavior (Burnie and Wilson, 2001). In many species, the males develop distinctive color markings and a prominent crest during the breeding season. The ornamented male dances around the female and, fanning its tail, spreads pheromones (chemical stimulants) that induce receptivity in the female (Houck and Reagan, 1990; Houck et al., 2006). The male finally embraces the female and transfers its sperms in capsules called spermatophores. The eggs laid, are guarded either by the female or the male. Removal of the gonads abolishes some or all of these sexual and parental activities but the administration of steroids—testosterone or related androgens in the male, and estradiol in the female—restores them. In frogs, seasonal reproductive maturation prompts the solitary male to proceed to a collective breeding site where it advertises its amorousness by loud croaking (Wells, 1977). A male frog may emit a different kind of call when a competing male rather than a female approaches its territory, and that warning call either makes the intruder retreat or the two males may start to fight (Gerhardt, 1989). The chorus of the aroused males attracts the gravid females in the neighborhood and, overcoming their normal aversion for physical contact, the male approaches and clasps the receptive female, and the two stay embraced for some time while the prodded female lays her eggs and the male ejects its sperms. In clawed frogs, the receptive female responds with her own call to the male’s vocalization, and the two engage in a duet before mating (Tobias et al., 1998).
Exposure to the mating chorus has been experimentally shown to raise the blood androgen levels of male frogs (Chu and Wilczynski, 2001). This increase in androgen concentration, which augments sexual ardor, is facilitated by the release of gonadotropin releasing hormones (GnRH). There are two types of GnRH in amphibians, one concentrated in neurons of the hypothalamic preoptic area, septum and the pituitary gland, the other in the midbrain (D’Aniello et al., 1995; Collin et al., 1995). Stimulation and lesion studies have implicated the preoptic area in the facilitation of courtship behavior of male frogs (early studies are reviewed by Aronson, 1970.) Preoptic lesions abolish the male’s sexual calling (Schmidt, 1989) whereas electrical stimulation of the preoptic area (Schmidt, 1968; Wada and Gorbman, 1977b; Schmidt and Kemnitz, 1989) or implantation of testosterone pellets into it (Wada and Gorbman, 1977a), augment vocalization. Another potent hormone that facilitates the action of androgen and estradiol in amphibians is arginine vasotocin (AVT). The injection of an agonist of this peptide increases calling frequency and courtship behavior in males and egg laying in females (Moore, 1992; Boyd, 1994a; Burmeister et al., 2001). Removal of the gonads abolish, and steroid implants restore these AVT-induced sexual drive, indicating that AVT works synergistically with steroid hormones (Moore, 1992).

It is noteworthy in this context that two hormones related to AVT—oxytocin and vasopressin—are involved in mammalian reproductive processes that are absent in amphibians. In mammals, oxytocin secreted by magnocellular hypothalamic neurons and passed to the pituitary gland induces uterine contractions during parturition, and vasopressin induces milk ejection by the mammary glands after delivery. Moreover, in addition to the magnocellular hypothalamic sites and the pituitary gland, there are oxytocin-containing parvocellular neurons and binding sites in select brain areas of mammals, particularly in the preoptic area, the bed nucleus of the stria terminalis, amygdala, and the nucleus accumbens. This parvocellular system has been implicated in mammals in the facilitation of maternal care and altruistic behavior, such as nest building, and retrieval, licking and grooming of the young (Insel and Shapiro, 1992; Keverne and Kendrick, 1992; Pedersen et al., 1992; Numan and Insel, 2003) as well as in fostering pair-bonding in social species (Insel and Shapiro, 1992b; Bielsky et al., 2005; Beery et al., 2008). In the frog, AVT-containing neurons and fibers have been localized in several regions: the hypothalamic preoptic area and the suprachiasmatic nucleus; the telencephalic amygdala, nucleus accumbens, and septum; and the auditory and vocalizing regions of the hindbrain (Boyd, 1994a, b; Gonzalez et al., 1995; Marler et al., 1999). There is some evidence that the concentration of AVT in some of these areas varies between males and females, and during different phases of the reproductive cycle. Amphibian AVT may play a role in the temporary bonding between a male and a female during mating, as well as parental behavior displayed by those that guard or carry about the fertilized eggs (such as the midwife toad).

**SUMMARY: THE AFFECTS OF AMPHIBIANS.** The reviewed evidence suggests that basic emotions play a pivotal role in amphibian behavior. These emotions include pain when injured; anger and fear when facing predators and competitors; amorousness when engaging in courtship and mating behavior; and rudiments of parental affection when protecting the fertilized eggs and caring for the young. Emotional mobilization may be involved when a newt or frog lying in ambush swiftly strikes any small moving or flying target, bites and swallows it. This reaction may be mediated by a feeling of hunger that is not unlike what we experience when
starved. When a frog freezes or flees upon sighting an approaching large object, it may be overcome by fright much as we do in a similar situation. When a frog defending its territory stands its ground, assumes a threatening posture and fights the intruder, it may be experiencing something akin to the emotion we call anger or rage. When a male frog changes its solitary life style during the breeding season and proceed to the breeding ground and begins to croak to attract a female, its behavior may be motivated by amorousness. Finally, something akin to what we know as parental affection may motivate the parental behavior displayed by those amphibians that guard their eggs and protect their young.

Perception and Learning in Amphibians. Amphibians manifest pattern perception when they respond discriminatively to objects differing in shape and size, and memory when they learn to discriminate different visual patterns in an experimental setting.

PERCEPTION OF PATTERN, DEPTH AND DISTANCE IN AMPHIBIANS. As we noted earlier, frogs display the ability to perceive the size of objects when they snap at a moving small object and flee from a large one (Ingle, 1976a; Ewert, 1980). They can also be trained to discriminate between such moving visual patterns as a circle, a triangle or a star (Pache, 1932). Perceiving the real size of an object irrespective of its retinal image indicates size constancy, an ability that, in turn, presumes depth perception and distance estimation. That ability was demonstrated in hopping toads that had to jump accurately across a chasm or a fence to reach a target (Lock and Collett, 1980). Frogs can also accurately judge the size of openings that they may or may not fit through when they try to escape from a container (Ingle, 1973; Saltzman et al., 2004). Experiments suggest that distance estimation by toads depends on feedback information about the curvature of the lens (accommodation) used when focusing of a target (Douglas et al., 1988).

LEARNING AND MEMORY IN AMPHIBIANS. It has been known for some time that frogs and toads quickly learn to abstain from snapping at substances that they initially find attractive but are inedible (Schaeffer, 1911; Buytendijk, 1918b). Schaeffer’s study showed that after 4-7 trials, toads stopped snapping at disagreeable hairy caterpillars, and that this learned aversion persisted for at least 10 days. When the presentation of an earthworm was coupled with an electric shock, frogs learned to refrain from snapping at the prey in as few as 2 trials. Indeed, some frogs learned to avoid stinging red ants or bees in a single trial (Buytendijk, 1918a, Cott, 1936). With regard to habituation, a recent study showed that frogs learn to recognize the mating call of nearby neighbors by displaying reduced aggressivity (Bee and Gerhardt, 2001). Discrimination of two vibratory stimuli, one associated with reward and the other with punishment, has also been demonstrated in frogs (Elepfandt, 1985). That discrimination was retained for at least one month. Frogs also showed evidence of improvement of learning following a series of reversal tasks. The first reversal was mastered within 4 days, the second within 2 days, and the third within a single day. Because frogs and toads are stalkers rather than active hunters, their spatial learning has been difficult to investigate. Yerkes (1903) tested the spatial learning ability of tree frogs in a two-choice maze in which the arm that led to a water tank was cued by a colored card. After a few trials, the time spent in the blind alley was greatly reduced, and after 100 trials, the frogs proceeded directly to the target with few or no errors. Buytendijk (1918a, b) reported that toads learn to take the shortest route around a glass partition for a food
reward, and resume the direct route as soon as the obstacle is removed. That habit was retained for at least 30 days. Brattstrom (1990) found that by slightly dehydrating toads and making them run a simple T-maze for water as a reward, the animals mastered a position habit (right turn) in 3-4 days and most of them readily learned to reverse that habit (turn left). However, it took the toads many more trials to master a complicated maze (Fig. 4-15).

**BRAIN MECHANISMS OF PERCEPTION IN AMPHIBIANS.** As we noted earlier, the amphibian telencephalon is more advanced than that of fishes but it is still best characterized as a limbic system, one associated with affective processes rather than cognitive functions. The little information currently available indicates that the mesencephalon and diencephalon play a far more important role in visual pattern discrimination in amphibians than does the telencephalon. For instance, it has been reported that nucleus isthmi lesions in frogs (with intact optic lobes) abolish visual prey orienting behavior (Caine and Gruberg, 1985; Gruberg et al., 1991), and that salamanders with thalamic-pretectal lesions snap at targets irrespective of their shape or size (Finkenstädt, 1980). This maladaptive behavior is not seen following ablation of the telencephalon. It has also been reported that basal ganglia lesions,

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**Fig. 4-15.** A. Rapid mastery of a simple T maze habit by toads, and its reversal. B. Design of a complex maze. C. Slower mastery of a complex maze, with different criteria. (From Brattstrom, 1990.)
but not pallial lesions, interfere with visually mediated prey orienting behavior in frogs (Patton and Grobstein, 1998). The striatum may exercise this perceptual function through its direct and indirect connections with the optic tectum (Marín et al., 1997c).

**Brain mechanisms of learning in amphibians.** There is some evidence that the telencephalon is involved in memory-based processes in amphibians, since forebrain lesions produce either learning deficits or amnesia for what has been mastered prior to the operation. According to an old report, a simple maze task that frogs mastered in 20 trials was abolished following forebrain ablation (Burnett, 1912). A recent study indicates that lateral telencephalic lesions in newts leads to the extinction of a learned response (Wenz and Himstedt, 1990). However, it is possible that most of the deficits produced by telencephalic lesions are due to changed affectivity rather than to cognitive deficits. Early studies (reviewed by Aronson, 1970) noted that following forebrain removal, frogs and salamanders become inactive for hours or even days, and display little behavioral spontaneity. Aronson interpreted this behavioral alteration to reflect reduced affectivity.

**4.1.4. Our Amphibian Legacy.** Most important of our amphibian visceral and somatic legacy are the lungs that enable us to obtain oxygen from the air and our limbs that empower us to move about on the ground. Most important of our amphibian neural legacies are the brainstem mechanisms that regulate breathing and the spinal pattern generators that coordinate quadruped locomotion. There are indications of some advance in amphibian in the differentiation of the telencephalon when compared with fishes, and some advances in the affective control of behavior, particularly in the regulation of reproductive processes. The latter is supported by the fact that amphibians need to produce fewer offspring to maintain their population than do most fishes. The number of eggs that gravid fishes lay ranges from millions to a several dozens, among amphibians that ranges from several thousands to a few dozen. Some amphibians leave the fertilized eggs floating in the water, or attach them in strings to plants, but provide them with no more protections. Predators consume them before hatching, and the same fate befalls the majority of the emerging tadpoles. Other amphibians, particularly those that lay their eggs out of the water in wet holes or under logs, produce fewer eggs. While the American bullfrog lays up to 20,000 eggs that are abandoned after spawning, toads lay fewer eggs. The midwife toad lays 20-60 eggs that the male carries wrapped around his body, whereas the Surinam toad lays even fewer eggs that the male places on the female’s back. The skin of the female swells thereafter and forms pockets around the eggs where the young mature and do not leave until after metamorphosis. Evidently, some amphibians invest effort and energy in protecting their offspring but parental care is not the norm among most of them, as is the case in mammals. In contrast to some affective advances, there is little evidence for advances in extant amphibians in perceptual, mnemonic and cognitive abilities relative to fishes. The incomplete terrestrial adaptations and limited neural and mental advances of amphibians may have been the factors why they failed to become the dominant occupants of terrestrial habitats as did their successors, the reptiles.
4.2. Somatic, Neural, and Behavioral Advances in Lizards: Our Reptilian Legacy

4.2.1. The Evolution of Reptiles. Reptiles emerged about 320-270 m.y.a. during the late Carboniferous and early Permian periods of the Paleozoic era (Romer, 1966; Carroll, 1988; 2009; Sumida and Martin, 1997; Benton, 2004). This took place over a period of 25-50 million years after the earliest amphibians began to occupy terrestrial niches (Section 4.1.1). An early reptile was Hylonomus, a small animal resembling a lizard (Fig. 4-16A). It had sharp teeth, suggesting an insectivorous life style. Diadectes of the mid-Permian was a much sturdier and larger reptile, but still had short, splayed legs (Fig. 4-16B). By the late Permian, reptiles diversified greatly and some, such as the large Lycaenops (Fig. 4-16C), acquired large canine teeth and longer, vertically aligned legs. The Mesozoic, between 225-270 m.y.a., marked the Age of Reptiles. This was the period when reptiles ranging in size from small to gigantic, became the dominant inhabitants of the lands, with some of them, like the Crocodilia, returning to the waters, and the Pterosaurs evolving flying skills. The dinosaurs, some of them the largest land animals that have ever lived on this planet, became dominant during the Jurassic but perished about 65 m.y.a. Thereafter, only four reptilian orders survived: lizards and snakes (Squamata), turtles and tortoises (Chelonia), crocodiles and alligators (Crocodilia), and the near extinct tuatara (Sphenodon).

4.2.2. Visceral, Somatic, and Neural Advances in Reptiles. Relative to amphibians, reptiles are distinguished by several advanced traits. These include: (a) improved respiratory and circulatory systems; (b) a sturdy skeletal frame with powerful jaws and limbs; (c) a tough skin with scales that protects them from desiccation; (d) amniotic eggs that allows reptilian embryos to develop inside an aqueous sac, freeing parents from the need to return to the water to lay their eggs; and (e) some advances in the organization of the CNS, in particular the enlargement and elaboration of the forebrain.

Visceral and Somatic Advances. A great reptilian advance has been the evolution of the amniotic egg. The amphibian embryo, which is encased in an anamniotic egg, requires an aqueous medium for its early development. The reptilian amniotic egg is furnished with several membranes: the allantois, the chorion, and the amnion (Fig. 4-18). The compartments created by these membranes not only protect the embryo against desiccation and temperature fluctuations but also allow gas exchange through the embedded capillary system. For further protection, the reptilian eggs have a leathery or calcified shell. These eggs, of course, have to be fertilized before they are laid. Hence, in reptiles internal fertilization is a requisite of reproduction. Typically, the female buries the fertilized eggs in a protected terrestrial site where they hatch by themselves, as turtles do, or builds a nest and protect the eggs, as alligators and crocodiles do.

The lung of most amphibians is a simple sac-like structure in which gas exchange is limited to the outer surface. Amphibians get much of the oxygen they need by diffusion through their moist, porous skin that is richly supplied with capillaries. That, of course, means that they rapidly become dehydrated in a dry environment. The improved lung of most reptiles has a bronchus with many branches for more efficient gas exchange (Grigg, 1992). The lung
ANCIENT REPTILES - SKELETONS

A. Hylonomus

B. Diadectes

C. Lycaenops

Fig. 4-16. The skeletons of extinct reptiles. Hylonomus, a small lizard-like reptile (A); the much larger and sturdier Diadectes (B), and the mammal-like carnivore, Lycaneops (C). (Modified, from Romer, 1966; Benton, 2004.)
ANCIENT REPTILES
RECONSTRUCTIONS

A. Hylonomus

B. Diadectes

C. Lycaenops

Fig. 4-17. Reconstructions of Hylonomus (A), Diadectes (B,) and Lycaenops (C). (A, from Hylonomous_BW.jpg, B, from Diadectes_BW.jpg, C, from lyca4.jpg.)
THE ANAMNIOTIC AND AMNIOTIC EGG

Fig. 4-18. Comparison of the anamniotic egg of amphibians (A) and the amniotic egg of reptiles (B). (A, modified from Strickberger [1996]; B, modified from kentsimmons.uwinnipeg.ca/16cm05/1116/chordate.htm)

CIRCULATORY SCHEME IN CROCODILES

Fig. 4-19. A schematic diagram of the circulatory scheme and four-chambered heart of the crocodile. (Modified, from Grigg, 1992.)
is either ventilated by axial muscles or, in the case of crocodilians, by the muscular diaphragm. This advance has allowed reptiles to acquire a tough, virtually impermeable skin with a horny epidermis and with scales for added protection in a dry environment. Some reptiles have three-chambered hearts (with a single ventricle), much like amphibians, but others, like crocodiles, have a more efficient four chambered heart with completely separated pulmonary and systemic circulation (Fig. 4-19).

With reference to somatic changes, most extant reptiles crawl with their limbs extended laterally and unload their weight by resting on the ground between steps (Gans et al., 1997). However, when aroused, they can lift their body off the ground, eliminating the drag exerted by the ventrum of the body, and can run fast for a short period. Running, of course, requires improved neural control of postural balance.

Neural Advances: An Overview. In the following analysis of neural advances in reptiles, we review studies carried out in extant lizards (including the near extinct tuatara), turtles, and crocodiles. We do not deal with snakes since these limbless reptiles have evolved adaptations that took them farthest from our putative reptilian ancestors. A notable advance in the evolution of the CNS in reptiles relative to fishes and amphibians has been the expansion of the telencephalon. We illustrate that by Polyak’s (1957) drawings of the size of the forebrain in the northern pike (Fig. 4-20A), the leopard frog (Fig. 4-20B), and the painted turtle (Fig. 4-20C). Using eye size to match their brains, the optic lobes are roughly of the same, as viewed from the top, in all three species but there is a progressive increase in the size of their telencephalon. A comparison of the fresh turtle brain in sagittal view (Fig. 4-21) with the same view of the goldfish brain (Figs. 3-12A-C) illustrates the same point.

Spinal Cord, Cerebellum, and Midbrain. We begin our analysis of neural advances in reptiles with a brief description of the structure and functions of the spinal cord, followed by a more detailed analysis of the hindbrain and the forebrain.

The Spinal Cord and Locomotion. In reptiles, as in amphibians, the spinal cord is the principal mechanism of limb coordination. When the spinal cord is severed from the brain to eliminate higher-level influences, tactile stimulation of the turtle skin still triggers rhythmic swimming movements and scratching (Robertson et al., 1985; Mortin et al., 1985; Berkowitz and Stein, 1994). Correspondingly, electrical stimulation of different spinal cord sites in turtles triggers either coordinated fictive swimming or scratching (Juranek and Currie, 2000).

The Cerebellum and Postural Coordination. Quadruped locomotion requires postural coordination to prevent toppling when the swinging limbs lose contact with the ground, and movement adjustments when obstacles are encountered or the direction of locomotion is changed. It is known from studies in higher vertebrates and man that cerebellar damage produces a variety of postural and motor disorders, including staggering, falling, tremor, and overshotting or undershooting when reaching for a target. Cerebellar coordination depends on proprioceptive information about the momentary position of the moving limbs, vestibular input about the inertial effects of acceleration and deceleration, tactile input about the changing properties of the substrate, and visual input about obstacles along the path traveled and the need
A. Northern Pike

B. Leopard Frog

C. Painted Turtle

Fig. 4-20. Comparison of the optic lobe and forebrain in the northern pike (A), the leopard frog (B), and the painted turtle (C). All three species are visual hunters with comparable eyes. (Modified, from Polyak, 1957.)
for changing mode or direction of locomotion to reach a target. The cerebellum, the principal brain mechanism responsible for the coordination of vertebrate posture and locomotion, is well developed in reptiles and is served by several auxiliary structures, including the inferior olive of the medulla downstream, and the red nucleus of the midbrain upstream (Künzle, 1985; Sarrafizadeh and Houk, 1994; Sarrafizadeh et al., 1996; Herrick and Keifer, 1997). The red nucleus, which modulates spinal cord motor functions by way of the rubrospinal tract in turtles, is a target of descending influences from the hypothalamus, the subthalamus and the pretectum (Herrick and Keifer, 1997; Martinez-Marcos et al., 1999).

But there are notable differences between the cerebellum of reptiles and mammals. There is no ascending pathway in reptiles from the cerebellum to the relay nuclei of the thalamus, as there is in mammals, and there is no descending pathway from the telencephalon to the cerebellum by way of the pontine gray nucleus (Künzle, 1985; Lustig et al., 1998; Keifer and Lustig, 2000). Reflecting this difference, the reptilian cerebellum consists mainly of the vermis (paleocerebellum); the lateral cerebellar hemispheres of mammals (the neocerebellum) is absent. As we have described elsewhere (Altman and Bayer, 1997), two “transcerebellar loops” are involved in the coordination of movement and posture in mammals. Information flows in the “lower transcerebellar loop” from the cerebellum to the mesencephalic red nucleus,
from the red nucleus to the medullary precerebellar nuclei, and thence back to the cerebellum. In the “upper transcerebellar loop” information flows from the cerebellum to the thalamus, from there to the cerebral cortex, and then back to the cerebellum by way of the pontine gray nucleus. We hypothesized that the lower loop is involved in the “reactive” (compensatory) control of posture and movement, whereas the upper loop is responsible for the “proactive” (anticipatory) control of posture and movement. The presence of the lower transcerebellar loop in reptiles suggests that this circuit is our reptilian legacy whereas the upper loop is a mammalian acquisition.

**MIDBRAIN VISUAL AND AUDITORY MECHANISMS.** In reptiles, the bulk of optic nerve fibers terminate in the highly laminated and large optic lobe (Fig. 4-22), much as they do in fishes and amphibians, and most of them cross in the optic chiasma (Guiloff and Kolb, 1992; Casini et al., 1993; Bennis et al., 1994b). But some optic nerve fibers also terminate in the pretectum (Fan et al., 1995), and in the thalamus and the hypothalamus (Hergueta et al., 1992; Bennis et al., 1994; Janik et al., 1994). There are also reciprocal connections between the optic lobe and some of the pretectal, thalamic and hypothalamic nuclei (Martinez-Marcos et al., 1998; Kenigfest et al., 2000). In turtles, optic lobe and pretectal neurons have large visual receptive fields and they preferentially respond to stimuli moving in a particular direction (Fan et al., 1995).

The cochlea of the inner ear is better developed in reptiles than in amphibians, although it is not coiled as in mammals (Retzius, 1881, 1884). In lizards, auditory nerve fibers project to the cochlear nucleus and other components of the medullary auditory system (Foster and Hall, 1978; Szpir et al., 1990, 1995). Higher-order auditory afferents ascend to the torus semicircularis (Fig. 4-22) of the midbrain, known in mammals as the inferior colliculus. Because the reptilian skin has a hard epidermis, the sensors responding to tactile, thermal, gustatory and related stimuli are concentrated in the head region, particularly the mobile tongue. Little is known about these somatosensory receptors. Ascending projections were traced in lizards from the sensory trigeminal nuclei to the pretectal nuclei and the thalamus (Desfilis et al., 1998). In turtles, the first-order somatosensory fibers of the dorsal column nuclei project to the pons, midbrain, hypothalamus, thalamus, and telencephalon (Siemen and Kunzle, 1994).

*The Reptilian Diencephalon.* The dorsal component of the diencephalon, the thalamus, is larger and more differentiated in reptiles than in lower vertebrates but much smaller than in mammals. And while it has some features common with the mammalian thalamus, there are some fundamental differences. In contrast, the reptilian hypothalamus is well developed and closely resembles the mammalian hypothalamus in its structure and functions.

**DIFFERENCES BETWEEN THE THALAMUS OF MAMMALS AND REPTILES.** The mammalian thalamus is a massive and complex structure with many distinctive cell aggregates, known as nuclei (Carpenter, 1976; Brodal, 1981; Jones, 1985). Several of these thalamic nuclei are relay stations that interconnect subcortical structures with the cerebral cortex. The medial geniculate nucleus relays information from the brainstem auditory nuclei and the midbrain inferior colliculus to the auditory projection areas of the temporal neocortex. The dorsal lateral geniculate nucleus relays input from the eyes to the occipital visual projection area.
The ventral posterolateral nucleus receives tactile input from the limbs, trunk and head, and relays that to the somatosensory cortex of the postcentral gyrus. The ventral anterior nucleus receives its major input from the striatum and its output is to the premotor cortex. The major input to the ventral lateral nucleus is from the deep cerebellar nuclei and its output is to the precentral motor cortex. Hence, these nuclei (which form the ventrolateral complex) relay somatosensory input and feedback (cerebellar, striatal) information to the sensory and motor areas of the neocortex.

We consider these posterior and lateral nuclei relaying information to the neocortex as components of the neothalamus. However, the mammalian thalamus also has medial, anterior and dorsal components that have other connections. The medial thalamic complex abutting
ALLIGATOR DIENCEPHALON

A

THALAMUS

Thalamic third ventricle
Habenula
Anteromedial n.
Lateral geniculate n.
Anteroventral n.
Optic tract
Forebrain bundle

Subthalamus

HYPOTHALAMUS

Hypothalamic third ventricle
Periventricular n.

B

THALAMUS

Thalamic third ventricle
Habenula
Dorsolateral n.
Lateral geniculate n.
Midline thalamic nuclei
Optic tract
Forebrain bundle

Zona incerta

HYPOTHALAMUS

Hypothalamic third ventricle
Periventricular n.

C

THALAMUS

Nucleus rotundus
Lateral geniculate n.
Optic tract
Reuniens n.?
Forebrain bundle

THALAMUS

Dorsomedial n.

HYPOTHALAMUS

Hypothalamic third ventricle
Ventromedial n.
Periventricular n.
the third ventricle is composed of several structures, from the habenular nuclei dorsally to the reuniens nucleus ventrally, that have sparse or no connections with the neocortex. For instance, the fibers of the reuniens nucleus target the hippocampus. The anterior thalamic nuclei receive afferents from the mammillary body and project principally to the cingulate gyrus. The latter, in turn, has extensive direct or indirect connections with such limbic structures as the septum, the hippocampus, and the amygdala, and such brainstem structures as the tegmentum and the periaqueductal gray. The major component of the dorsal complex is the dorsomedial nucleus, which has connections with the amygdala, septum, piriform cortex and orbitofrontal cortex, and perhaps also with the hypothalamus and the midbrain reticular formation. All these structures may be considered components of the more ancient limbic system. We shall argue that most components of the reptilian thalamus belong to the latter category and hence we designate them as components of the paleothalamus (Fig. 4-23).

Several thalamic nuclei have been identified in the diencephalon of reptiles but their homology with the mammalian thalamic nuclei is uncertain (Ariëns Kappers et al., 1936; Butler and Northcutt, 1973; Heredia et al., 2002). In contrast to the thalamic relay nuclei of mammals, which target the cerebral neocortex, the connections of the reptilian sensory nuclei are mainly with the ganglionic dorsal ventricular ridge and, to a lesser extent, the pallium (Lanuza et al., 1998; Guirado and Dávila, 2002). For instance, ascending projections were demonstrated in crocodiles from the somatosensory midbrain areas to several medial thalamic nuclei (Pritz and Stritzel, 1990) and from there to the dorsal ventricular ridge (Pritz and Stritzel, 1994). This is unlike the pattern of somatosensory projection from the dorsal column nuclei of the medulla to the posterolateral thalamic nucleus and thence to the postcentral gyrus of the neocortex. In general, the posterior and lateral neothalamic nuclei are poorly represented in reptiles and some of them may be altogether absent. Consider the lateral geniculate nucleus. In mammals, the dorsal lateral geniculate nucleus (dLGN) is a large structure, dedicated to relaying retinal input to the visual cortex. Among primates there is an increase in the proportion of optic tract fibers that terminate in the dLGN from prosimians to apes, relative to the proportion terminating in the superior colliculus (optic lobe), and there is a progressive increase from lower to higher mammals, in the lamination of the dLGN, from one invisible in rodents to distinct six layers in primates. There is a small structure designated as the LGN in reptiles (Papez, 1935; Butler and Northcutt, 1973; Cruce, 1974b; Kenigfest et al., 2000, 2004; Fig. 4-23A-B). However, it is only targeted by 16 per cent of the optic nerve fibers (Kenigfest et al., 1998). Most of the afferents of the LGN originate in the tectum (Reiner, 1994) and in some pretectal nuclei (Kenigfest et al., 1998, 2000, 2004). And while there is a small LGN projection to the pallium (Hall and Ebner, 1970; Hall et al., 1977; Mulligan and Ulinski, 1990; Kenigfest et al., 1995), the major outflow of the reptilian LGN is to the dorsal ventricular ridge of the basal ganglia (Manger et al., 2002). (There is also a small optic projection to the hypothalamus the suprachiasmatic nucleus, a structure that regulates the circadian rhythm [Janik et al., 1990; Bertolucci et al., 2000].) The reptilian LGN may be the homologue of the mammalian ventral lateral geniculate nucleus (vLGN).

Fig. 4-23. The alligator diencephalon, from rostral (A) to caudal (C). (Modified, from Ariëns-Kappers et al., 1936.)
Another difference is the absence of certain reptilian thalamic nuclei in the mammalian thalamus. Examples are the nucleus rotundus dorsally and the nucleus reuniens medially (Fig. 4-23). The large nucleus rotundus appears to be an integrative system with input from visual structures—the optic tectum and the pretectum, and the supraoptic and suprachiasmatic nuclei of the hypothalamus—and its principal output is to the dorsal ventricular ridge (Pritz, 1997; Lohman and van Voerden-Verkley, 1978; Rainey and Ulinski, 1982; Davila et al., 2002) and the amygdala (Guirado et al., 2000; Suarez et al., 2002). Structurally, the nucleus rotundus resembles the centromedian nucleus of the embryonic human thalamus (Bayer and Altman, 2005). The reptilian reuniens nucleus (which appears to be a different structure than the one with the same name in mammals) appears to be targeted by fibers of the toris semicircularis, the homologue of the auditory inferior colliculus in mammals (Belekhova et al., 1985). And whereas the mammalian reuniens nucleus is connected with the hippocampus, it projects in reptiles to the dorsal ventricular ridge (Foster and Hall, 1978; Belekhova et al., 1985; Pritz and Stritzel, 1992, 1994). This projection pattern is again in sharp contrast to what is seen in mammals where the thalamic medial geniculate nucleus projects to the auditory cortex.

THE CONCEPT OF PALEOTHALAMUS AND NEOPTHALAMUS. Butler (1995) hypothesized that the mammalian thalamus has two components, what she called the collothalamus and the lemnothalamus. The collothalamus receives visual, auditory and somatosensory input indirectly from the superior and inferior colliculi, and its principal output is to subcortical structures rather than the cortex. In contrast, the lemnothalamus—represented by the dLGN, the medial geniculate nuclei, and the ventrolateral group of thalamic nuclei—projects to the neocortex. The LGN and nucleus rotundus of reptiles may be components of the collothalamus but they may be lacking a lemnothalamus. If so, the multi-chain collothalamic system would constitute the ancient paleothalamus, whereas the more lemnothalamus—the “express pathway” to the neocortex (Altman and Bayer, 2001)—would constitute the more recent the neothalamus. If this interpretation is correct, the thalamus has undergone a major reorganization during vertebrate evolution during the transition from ancestral reptiles to mammals.

An Overview of the Reptilian Telencephalon. An important advance in the organization of the reptilian CNS has been the expansion and cellular differentiation of the telencephalon. We have illustrated earlier that growth by comparing the size of the telencephalon relative to the eye and the optic lobe in a fish (the northern pike, Fig. 4-20A), an amphibian (the leopard frog, Fig. 2-20B), and a reptile (the painted turtle, Fig. 4-20C). The reptilian telencephalon, much as the amphibian telencephalon, has a pallial (cortical) and a ganglionic (nuclear) component. As a primitive trait, the neurons of the amphibian pallium are situated in a periventricular position, with some of them scattered in a single fibrous layer. We have illustrated that in the newt (Fig. 4-11) and the frog (Fig. 4-12). A notable reptilian advance is that the pallial neurons form a distinct cellular layer (“gray matter”), sandwiched between an outer and an inner fibrous layer (“white matter”). This is illustrated in the alligator (Fig. 4-24, left column) and the near-extinct tuatara (Fig. 4-24, right column).

THE TWO TYPES OF REPTILIAN TELENCEPHALON. The forebrain of extant reptiles is of two types: one distinguished by a large and highly differentiated ganglionic component, the other with a larger and more highly differentiated pallial component. The former, the ganglioform
telencephalon, is illustrated in histological sections of the alligator brain (Fig. 4-24A). The latter, the pallioform telencephalon, is illustrated in matched sections of the tuatara brain (Fig. 4-24B). The pallium of the alligator (the hippocampus excepted) is thin and is composed of two layers: an outer fibrous layer and an inner cellular layer. This pallium abuts the massive basal ganglia, forming a circumferential shell around it. In contrast to the pallium, the basal ganglia are highly differentiated, being composed of several distinguishable nuclei that flank the comma-shaped lateral ventricle medially. The tuatara telencephalon is different. The pallium is composed of three layers: an outer and an inner fibrous layer, and a more densely packed cellular layer sandwiched between the two. And unlike the smooth pallium of the alligator, the tuatara pallium is convoluted and long, abutting a correspondingly folded and long lateral ventricle. The basal ganglia, in contrast, are small and undifferentiated. These are important differences. From an evolutionary perspective, the ganglioform telencephalon of the alligator may resemble an ancient line that has been the progenitor of the forebrain of birds, whereas the pallioform telencephalon of the tuatara has been the progenitor of the mammalian forebrain. From a functional perspective, as we argue below, the ganglioform telencephalon may be more of a hard-wired (pre-programmed) neural coordinating system, whereas the pallioform telencephalon more of a soft-wired (programmable) system.

DIFFERENCES BETWEEN CORTICAL AND GANGLIONIC ORGANIZATION. There are important structural and functional differences between the cortical (pallial) and the ganglionic organization of telencephalic neurons. The cortex is a superficial, stratified tissue composed of a cellular sheet, the gray matter, sandwiched between two fibrous layers, the white matter. The cellular sheet contains neuronal cell bodies and their dendrites, and incoming, locally terminating, and outgoing axons. The fibrous layers contain short- and long-distance afferent, efferent and commissural axons that interconnect a particular cortical area with other brain regions. The simplest cortex, the archicortex, contains a single cellular layer. A more complex type of cortex, known as allocortex or paleocortex, has two, three or four horizontal cellular layers composed of different types of neurons. The most complex cortex, the neocortex (isocortex), contains six cellular layers with different types of neurons, and in some areas some of the layers contain several sublayers. Embedded in these horizontal strata are vertical cell columns, and aggregates of such columns. These are targets of partially segregated input from different sources and are the source of output to different cortical and subcortical targets. It is generally assumed that increased cellular stratification and the multiplication of cell columns within a cortical region allow augmented interconnections with other brain regions.

Telencephalic ganglia and nuclei have a different neuronal organization. Nuclei are either surrounded by a fibrous capsule that separates them from other nuclei or are tightly packed with less obvious boundaries. They typically have a more homogeneous cellular composition than cortices do and their neuronal interconnections may be more circumscribed. Both from an evolutionary and a developmental perspective, there are fewer constraints on the expansion and reorganization of superficial cortical structures than for tightly packed nuclear structures. Being located superficially, cortices can expand and fold to accommodate more neurons and more incoming fibers for the modification or reorganization of existing circuits; nuclear structures are more constrained. Cortical organization has advantages over nuclear organization with respect to functions where there is a premium on modifiability and
VARIABILITY IN THE REPTILIAN TELENCEPHALON

A. ALLIGATOR

1. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Olfactory tubercle

2. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Septum
   - Nucleus accumbens
   - Amygdala

3. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Septum
   - Nucleus accumbens
   - Amygdala

B. TUATARA

1. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Olfactory tubercle

2. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Septum
   - Nucleus accumbens
   - Amygdala

3. Dorsal pallium
   - Hippocampus
   - Basal ganglia
   - Olfactory cortex
   - Septum
   - Nucleus accumbens
   - Amygdala
flexibility. Ganglionic organization is better suited for functions that can be solved by automatic computations performed by hardwired circuits. Predominant ganglionic organization of the telencephalon was the evolutionary route taken by birds confronted with the difficult but law-governed hydrodynamic challenges of flight control. Predominant cortical organization of the telencephalon was the path followed by mammals that opted for optimal exploitation of variable environmental resources on the basis of individual and group experience.

**Organization of the Reptilian Pallium.** Edinger (1911) divided the reptilian pallium into three regions: lateral, dorsal, and medial. According to current evidence, the lateral pallium has reciprocal olfactory connections, and a massive output to the hypothalamus (Hoogland and Vermeulen-Vanderzee, 1995; Striedter, 1997). Hence, it is considered a component of the rhinencephalon, perhaps the primordium of the piriform cortex. The dorsal pallium is often described as the “general cortex” (Crosby, 1917). Its homologue in mammals is uncertain. The cell-dense medial region has been considered the rudiment of the hippocampus (Ariëns Kappers et al. 1936; Hoogland et al., 1998). Current studies have confirmed that there are genomic affinities between the pallium of lower vertebrates and the cortex of mammals. For instance, both in the embryonic mouse (Walther and Gruss, 1991; Stoykova and Gruss, 1994) and the embryonic turtle (Striedter, 1997; Smith Fernandez et al., 1998; Moreno et al., 2010) Pax-6 and Emx-1 is expressed in the germinal region of the pallium, contrasting with Dlx-1 expression in the basal ganglia.

However, there are substantial differences between the reptilian pallium and the mammalian neocortex. First, unlike the gray matter of the mammalian neocortex, which has six cellular layers—variably composed of smaller granule cells, larger pyramidal cells, and a variety of other cell types—the reptilian pallium consists of a single cellular layer beneath a fibrous layer, or sandwiched between a superficial and a deep fibrous layer (Crosby, 1917; Connors and Kriegstein, 1986; Dávila et al., 1986). The cellular layer is densely packed with spiny pyramidal neurons (Fig. 4-25A) and the superficial and deep layers contain scattered smaller stellate neurons (Fig. 4-25B). Second, unlike the pyramidal cells of the mammalian neocortex, which have a thick and stout main dendrite that traverse several layers and have branches and twigs distributed in different layers, the pyramidal cells of reptiles have only a few dendrites. Two types of reptilian pyramidal cells have been described, those with apical dendrites spread in the superficial fibrous layer with an axon at the opposite pole, and cells that also have basal dendrites distributed in the deep fibrous layer. With few dendrites, the reptilian pyramidal cells receive sparse input from outside sources, hence their computing power must be limited. Third, unlike the mammalian neocortex that receives its principal afferent supply from the thalamus, ascending from the white matter underneath the cortex, the afferents of the reptilian pallium come mostly from other sources, course superficially, and then dip downward to reach the pyramidal cell dendrites (Super and Uylings, 2001). Fourth, whereas the mammalian thalamic fibers and their cortical terminals contain fast-acting glutamate neurotransmitters (Rustioni et al., 1988; Tsumoto, 1990; Kharazia and Weinberg, 1994), the afferents of the reptilian pallium

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**Fig. 4-24.** Cellular organization of the ganglioform telencephalon of the alligator (A) and the pallioform telencephalon of the tuatara (B). (A. Modified from Crosby, 1917. B. Modified, from Durward, 1930.)
contain principally slower-acting serotonergic, peptidergic, and GABAergic transmitters (de la Iglesia et al., 1994; Martinez-Guijarro et al., 1994). Fifth, although the reptilian dorsal pallium is the target of sensory fibers, there are no dedicated visual, auditory and tactile areas as in the mammalian neocortex. Instead, the sensory input is multimodal and without a topographic organization (Moore and Tschirgi, 1962). Sixth, the principal efferent outflow from the reptilian dorsal pallium is to the septum, amygdala, dorsal ventricular ridge, hypothalamus, and tegmentum (Lohman and van Woerden-Verkley, 1978; Hoogland and Vermeulen-Vandersee, 1989; Bruce and Neary, 1995a). There is no outflow to the spinal cord (Follett, 1989), as in the case of the mammalian neocortex. Indeed, stimulation of the dorsal reptilian pallium does not produce overt movements (Diebschlag, 1938). These observations suggest that the reptilian pallium has a modulatory rather than a topographically organized information-processing function.

THE REPTILIAN HIPPOCAMPUS. Notwithstanding the presumed homology between the medial pallium and the mammalian hippocampal formation, the putative reptilian hippocampus does not resemble its mammalian counterpart. The mammalian hippocampus consists of two large interlocking structures: Ammon’s horn (CA) marked by a layer of large pyramidal cells, and the dentate gyrus (DG) marked by a layer of densely packed, smaller granule cells. While this interlocking feature is fully developed in even the most primitive mammals (to be described in Chapter 5), that is not evident in any of the extant reptiles. Nonetheless, there is some support for the proposed homology. First, there is in reptiles a cell-dense medial band (Fig. 4-26A), composed of small cells (Fig. 4-26B). This may be the primordial dentate gyrus. Adjacent to this band is a cell sparse lateral region composed of less densely packed larger cells. This may be
homologous with the mammalian Ammon’s horn. Second, the fibrous layer of the latter region is rich in reptiles in zinc containing fibers (Lopez-Garcia and Martínez-Guijarro, 1988; Olucha et al, 1988; Smeets et al., 1989; Bernabeu et al., 1994; de la Iglesia and Lopez-Garcia, 1997; Fig. 4-26C). Zinc staining has been associated in mammalian hippocampus with axons of granule cells, the mossy fibers that synapse with Ammon’s horn pyramidal cells. But there are problems with this putative homology. As it has been discovered by Cajal (1911), the dentate granule cells in mammals have apical dendrites that arborize in the outer fibrous layer of the dentate gyrus, whereas the pyramidal cells have both apical and basal dendrites that arborize in both the inner and outer fibrous layers of Ammon’s horn. While there are reports available of these two types of neurons at these pallial sites (Luis de la Iglesia and Lopez-Garcia, 1997), their exact localization does not conform to the expected pattern. The organization of the putative hippocampus of reptiles warrants further investigation.

THE REPTILIAN HIPPOCAMPUS

Fig. 4-26. A. Forebrain of a lizard (Lacerta agilis). B. Pallium of a lizard (Varanus salvator) at a higher magnification. C. Zinc-staining of the outer and inner fiber layers of the pallium in a lizard (Podarcis hispanica). (A and B, modified from Ariëns-Kappers et al., 1936. C, modified from Bernabeu et al., 1994.)
THE REPTILIANS SEPTUM. The septum is well developed in reptiles and has several components (Figs. 4-24, 4-27A, 4-28A). Different septal nuclei have been distinguished on the basis of their connections with different regions of the hypothalamus (preoptic area, lateral hypothalamus, tuberal nucleus, mammillary body), the habenular nucleus, the midbrain tegmentum, and the pallium (Font et al., 1997, 1998) as well as the particular distribution of different histochemical markers (Moreno et al., 2010). Neurons in all septal nuclei are rich in GABA, and they also contain serotonin, substance P, and enkephalin as synaptic transmitters or modulators. As in mammals, the connections and neurochemical composition of the lizard septum suggest involvement in the regulation of visceral and endocrine functions and emotional mobilization.

THE REPTILIANS AMYGDALA. The reptilian amygdala has close connections with the olfactory system and also has a nonolfactory component (Martínez-García et al., 1991, 1993, 2002; Lohman and Smeets, 1993). Axons from the main olfactory bulb and the vomeronasal bulb, segregated in the olfactory tract, target not only different rhinencephalic structures but also different components of the amygdala, distinguished as the olfactory and the vomeronasal amygdala. The specific functions of these two olfactory systems are not currently understood since both appear to be involved in the regulation of feeding as well as reproductive behavior (Eisthen, 1997). The principal connections of the nonolfactory amygdala are with the basal ganglia (Lanuza et al., 1998; 2002). There are also different efferent outputs from different components of the reptilian amygdala. The principal efferent target of the medial amygdala is the ventromedial hypothalamic nucleus; of the lateral amygdala, the lateral hypothalamic area; and of the ventral amygdala, the posterior hypothalamus and the tegmentum (Lanuza et al., 1997, 2002). As in mammals, the amygdala has pallial and ganglionic components, suggesting that it is a component of the limbic system (Moreno and González, 2007). As we describe below, the amygdala of reptiles is implicated in emotional regulation, in particular fear and anger, much as it is in mammals.

The Reptilian Basal Ganglia. The basal ganglia are a major component of the reptilian telencephalon (Figs. 4-27, 4-28). We begin with a brief review of the organization of the mammalian basal ganglia and follow that by a consideration of the similarities as well as notable differences between the basal ganglia of reptiles and mammals.

THE MAMMALIAN BASAL GANGLIA. Traditionally, the mammalian basal ganglia are divided into (i) the striatum, composed of the caudate nucleus and the putamen, and (ii) the pallidum, composed of the external and internal segments of the globus pallidus (Carpenter, 1976; Brodal, 1981; Gerfen, 1992; Parent and Hazrati, 1995a, 1995b; Reiner et al., 1998). The striatum receives afferents from three main sources: the cortex, the thalamus, and the substantia nigra. The corticostriate afferents are collaterals of pyramidal tract axons that originate in different cortical areas and terminate topographically in the striatum. The thalamostriate afferents originate principally in the midline and intralaminar nuclei of the thalamus. The nigrostriatal afferents originate in the substantia nigra, the ventral tegmental area, and several other nuclei of the brainstem that contain DOPA as a neurotransmitter. The principal output of the striatum, by way of GABAergic spiny neurons, is to the pallidum (the striatopallidal projection) and the substantia nigra (the striatonigral projection). The pallidal axons target lower-level brainstem
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structures, including the substantia nigra, the subthalamus and some ventral tegmental nuclei. According to a recent conceptualization, the mammalian caudate nucleus, putamen and globus pallidus constitute the dorsal basal ganglia, and the olfactory tubercle and the nucleus accumbens the ventral basal ganglia (Alexander et al., 1986; Heimer et al., 1995; Robbins and Everitt, 2002; Groenewegen, 2007). Related to this classification is the idea that the glutamatergic and cholinergic circuitry of the caudate nucleus, putamen and dorsal putamen constitute the neostriatum, a complex sensori-motor feedback loop that modulates prefrontal cortical regions implicated in decision-making and the coordination and execution of skilled activities. In contrast, the nucleus accumbens, which targets limbic structures by way of the ventral pallidum, and is rich in GABA, dopamine and opioid transmitters and receptors, is a principal component of the paleostriatum, modulating behavior by such emotional processes as reward seeking and the avoidance of effort and punishment (hedonism). We use these new ideas to account for the similarities and differences in the organization of the reptilian and mammalian basal ganglia.

THE REPTILIAN BASAL GANGLIA. The reptilian basal ganglia share many structural and biochemical features with the mammalian basal ganglia. First, as in mammals, the most abundant cells of the reptilian dorsal striatum are small cells (Fig. 4-27C), characterized as spiny neurons (Reiner et al., 1998). Second, the reptilian dorsal striatum and, in particular, the nucleus accumbens (ventral striatum) are rich in nerve processes that contain calbindin-, dopamine- and substance-P positive neurons (Brauth et al., 1983; Brauth, 1984; Reiner, 1987; Reiner et al., 1998; Smeets et al., 2000; Stoof et al., 1987; Medina et al., 1993; Smeets, 1994; Henselmans and Wouterlood, 1994; Bennis et al., 1994a; Guirado et al., 1999a, 1999b; Smeets and González, 2000; Moreno et al, 2010) (Figs. 4-27, 4-28). Third, as in mammals, so also in reptiles the dopaminergic fibers originate in the substantia nigra and the ventral tegmental area (Parent, 1973) and interact with D1 and D2 receptors of striatal neurons (Richfield et al, 1987; Clark et al., 2000). Finally, as in mammals, the nucleus accumbens has connections not only with the medial and dorsal pallium but also with the preoptic area, the lateral hypothalamus, and the midbrain tegmentum (Smeets and Medina, 1995). These features suggest the involvement of the nucleus accumbens in visceral and emotional regulation.

Notably, however, there are many differences in the organization the reptilian and mammalian basal ganglia. First, the reptilian basal ganglia are not traversed by corticofugal (internal capsule) fibers and lack the patch and matrix organization of the mammalian striatum. Second, in contrast to mammals, the principal projection of the basal ganglia of reptiles is a descending one to various pretectal nuclei, the deep layers of the midbrain tectum, and the central gray and reticular formation of the brainstem (Voneida and Sligar, 1979; Brauth et al., 1983; Medina and Smeets, 1991). Third, the dorsal component of the reptilian basal ganglia—the dorsal ventricular ridge (DVR)—is both structurally and functionally very different from the neostriatum of mammals.

THE REPTILIAN DORSAL VENTRICULAR RIDGE. There is accumulating evidence that the DVR of reptiles is the target of higher-order visual auditory and somatosensory projections (Hall, et al., 1977; Foster and Hall, 1978; Belekhova, 1979; Balaban and Ulinski, 1981a, b; Bruce and Butler, 1984; Belekhova et al., 1985; Pritz and Stitzel, 1992, 1994; Smeets and González, 2000; Moreno et al, 2010) (Figs. 4-27, 4-28). As in mammals, the dopaminergic fibers originate in the substantia nigra and the ventral tegmental area and interact with D1 and D2 receptors of striatal neurons (Richfield et al, 1987; Clark et al., 2000). Finally, as in mammals, the nucleus accumbens has connections not only with the medial and dorsal pallium but also with the preoptic area, the lateral hypothalamus, and the midbrain tegmentum (Smeets and Medina, 1995). These features suggest the involvement of the nucleus accumbens in visceral and emotional regulation.
Fig. 4-27. A. Nissl-stained coronal section of the cellular organization of the lizard telencephalon. (Figure 1E from Guirado et al. 1999a. Abbreviations: Acc—nucleus accumbens; DVR—dorsal ventricular ridge; GP—globus pallidus; M, D, L—medial, dorsal, and lateral pallial areas; Nsl—lateral septal nucleus; Str—striatum; VP—ventral pallidum.) B. Matched section with calbindin-positive staining. (Figure 3A from Guirado et al. 1999b. Abbreviations: ADVR—anterior dorsal ventricular ridge; CTX—pallial areas; S—septum; ST—striatum.) C. Cellular organization of the basal ganglia at higher magnification in a section stained with hematoxylin and eosin. (Figure 1 from Guirado et al. 1999b. Abbreviations: 1-3 indicate layers in the ADVR—anterior dorsal ventricular ridge; CTX—pallial areas; S—septum; ST—striatum.)
Fig. 4-28. A. Calbindin-positive regions of the lizard telencephalon in a sagittal section. B. Dopamine-positive regions of the lizard basal ganglia in coronal section. C. Substance P-positive regions of the lizard basal ganglia. (After Guirado et al., 1999a. Abbreviations: Acc—nucleus accumbens; Bst—bed nucleus of the stria terminalis; DVR—dorsal ventricular ridge; Nsa—anterior septal nucleus; PO—preoptic area; TO—olfactory tubercle.)
Three components have been distinguished in the reptilian DVR: the medial, posterolateral, and anterolateral. The medial DVR receives auditory input from the “reuniens” nucleus; the posterolateral DVR receives somatosensory input from the medial and posteroventral nuclei; and the anterolateral DVR receives visual input from the nucleus rotundus. The DVR also receives non-sensory input from the substantia nigra, the midbrain reticular formation, the tegmentum, and the raphe nuclei of the pons (ten Donkelaar and De Boer-van Huizen, 1988). The principal output from DVR is to olfactory and limbic structures, including the lateral pallium, the amygdala, the nucleus accumbens, and the hypothalamus (Voneida and Sligar, 1979).

It has been argued by some investigators that because the DVR is a target of visual, auditory and somatosensory afferents, it is homologous with the neocortex of mammals (Smeets and González, 1994; Aboitiz, 1995; Striedter, 1997; Butler and Molnár, 2002; Lanuza et al., 2002). For several reasons, however, the DVR and the neocortex are better considered divergent rather than kindred higher-order telencephalic sensory processing systems. First, as noted earlier, the organization of the two is quite different. The mammalian neocortex is a stratified pallial system, the DVR is a subpallial ganglionic system (Figs. 4-27A, C). Second, whereas the mammalian neocortical sensory projection areas receive the bulk of their afferents from a dedicated, neothalamic relay system (the ventral posterior, dorsal lateral geniculate, and medial geniculate nuclei) the principal afferent supply of the DVR is from the tectum, the pretectum and an older, medial system of thalamic nuclei (the nucleus rotundus and the reuniens nucleus). Third, whereas the bulk of the afferents of the neocortex ascend from the ventrum of the gray matter, the afferents of the reptilian DVR descend from the dorsum of the gray matter (Heller and Ulinski, 1987). Fourth, in contrast to the mammalian neocortex which receives a relatively small and diffuse monoaminergic innervation, the reptilian DVR receives considerable dopamine, noradrenaline and serotonin innervation, with substantial differences in the concentration of these monoaminergic fibers in different DVR regions (Andreu et al., 1994). Fifth, there is a profound difference between the efferent systems of the neocortex and the DVR. The mammalian corticofugal system (the “pyramidal” corticospinal tract) is a massive, monosynaptic outflow to the motor neurons of the spinal cord that controls voluntary behavior. In contrast, the outflow from the DVR is a multisynaptic, “extrapyramidal” system that targets mostly limbic structures (amygdala, hypothalamus, tegmentum). These considerations, and the argument we make below—i.e., that the mammalian neocortex is a choice- and deliberation-based (“voluntary”) processing mechanism of behavior, whereas the DVR of reptiles and birds is a feeling- and emotion-based (“involuntary”) processing mechanism of behavior—warrant our inference that the two are fundamentally different telencephalic information-processing mechanisms.

4.2.3. Expressions of Feelings and Emotions in Reptiles. In an attempt to deal with the putative role of affects in reptilian behavior, we follow here the same indirect approach that we have used earlier to infer affects in fishes and amphibians. Specifically, we review the experimental evidence for endocrine changes and the display of emotional expressions in situations where reptiles are stressed, injured or threatened, and when they are sexually primed.
Endocrine and Brain Mechanisms of Fear and Anger in Reptiles. Both under natural conditions and in the laboratory, as lizards come into contact with one another they first engage in a display of aggressive posturing or actual fighting, followed by the establishment of a hierarchic dominance relationship (Greenberg and Crews, 1990; Phillips et al., 1993; Duffield and Bull, 2002; Greenberg, 2003). This agonistic behavior begins as the contestants begin to circle one another, and display such emotional expressions as a change of skin color, extension of a bright dewlap (Fig. 4-29), darkening of the skin behind the eyes (Fig. 4-30), expansion of their throat and spine crests, and such bodily movements as vigorous head-nods and pushups. For instance, when green anole lizards emerge from their dormancy in the spring, the males proceed to establish a territory of their own and defend that from intrusion by other males of the species. After a period of agonistic displays between two males, the skin color of one of the contestants changes from conspicuous green to a dull brown and its darkened eyespot fades. This signals its defeat and, if it cannot flee (as in a confined laboratory setting), the vanquished lizard submits itself to the victor by lowering its chin, shrinking its extended throat, retreating to a lower perch site, and abstaining from courting females (Summers and Greenberg, 1994). Significantly, these emotional reactions are associated with endocrine changes. In the subordinate, and presumably, anxious dull-colored lizard the blood concentration of corticosterone is elevated and testosterone concentration is lowered (Greenberg and Crews, 1990). There are also changes in the concentration of brain catecholamines (Summers et al., 1998; Korzan et al., 2001, 2006). If the dominant male is removed, it may take several days before the vanquished male starts courting females again, although that occurs more promptly if its testosterone level is artificially raised (Greenberg, 2003). The components of these emotional expressions—skin and eye color changes, dewlap extension, erection of spine crest, head bobbing, pushups, and the associated physiological and the concomitant endocrine changes—emerge during infancy and have the features of stereotypical reactions (Lovern and Jenssen, 2003).

Enocricne Mechanisms. As noted, eyespot darkening (Fig. 4-30) is one of the species-specific emotional expressions of agonism in green anolis lizards. In an experimental study, the eyespots of anolis lizards were painted either green, black or some other color, and the animals were made to face their own reflection in a mirror. The results showed that the “intruder” was attacked with the highest frequency when the reflected eyespots were black and with the lowest frequency when the reflected eyespots were green (Korzan et al., 2000a). Apparently, dark eyespots communicate that the “intruder” is hostile and that enrages the resident. Green eyespots (no color change) communicate lack of hostility and the “visitor” is more likely to be tolerated. There is evidence that neuroendocrine processes regulate these reactions. When free-living male lizards are captured and restrained, or when they are subjected to aggressive encounters with conspecifics, there is a large increase in brain levels and turnover of monoamines (Summers and Greenberg, 1994; Matt et al., 1997; Yang and Wilczynski, 2002; Watt et al., 2007). Monoamine changes have also been observed in staged fights among female lizards (Woodley et al., 2000) . There is initially an increase in telencephalic serotonin turnover in the assertive lizard and a decrease in the submissive one; after a while, the serotonin turnover subsides in the brain of the dominant lizard but endures for a long time in the submissive one (Summers and Greenberg, 1995; Summers et al., 1998; Baxter et al., 2001; Summers, 2001). Presumably, the rage of the winner dissipates but the fear and stress of the loser persists. Male lizards that do not possess a territory show higher brain serotonin turnover than those that do
LIZARD EMOTIONAL DISPLAY

Fig. 4-29. Resting (A) and emotionally aroused (B) Cuban brown anole lizard. (After FloridaGardener.com.)

LIZARD EYESPOT AND SKIN

Fig. 4-30. Eyespot (dark skin behind eye) and skin of the Floridian green anole lizard. (Modified after FloridaGarden.com.)
(Matter et al., 1998). This may be a reflection of their anxiety. After the administration of a serotonin reuptake inhibitor, dominant male anole lizards lose their status and show reduced aggression and eyespot color change when encountering conspecifics (Larson and Summers, 2001). Other hormones that modulate hostility in male lizards are corticosterone, which tends to inhibit aggression (Tokarz, 1987; DeNardo and Licht, 1993), and testosterone, which tends to augment it (Moore and Marler, 1987). In female lizards, territorial aggression is augmented both by testosterone and estradiol administration (Woodley and Moore, 1999).

**BRAIN MECHANISMS.** Early studies have suggested that ablation of the telencephalon in reptiles results in reduced emotionality, the operated animals becoming sluggish, abstaining from eating, and displaying little aggression (Goldby, 1937; Diebschlag, 1938). According to more recent investigations, the lizard brain regions undergoing hormonal changes in association with emotional arousal are the nucleus accumbens, basal ganglia, amygdala, and hippocampus (Greenberg et al., 1984; Korzan et al., 2000b, 2001, 2006; Larson and Summers, 2001; Watt et al., 2007). Stimulation and lesion studies have further contributed to the identification of the brain mechanisms of fear and anger in reptiles. Stimulation of the nucleus accumbens and basal ganglia in unrestrained lizards, triggers hostility (Tarr, 1982), and lesions of the basal ganglia and lateral forebrain bundle reduce hostility (Greenberg et al., 1979). Tonic immobility, a defensive fear reaction in lizards, is reduced following striato-amygadaloid lesions (Davies et al., 2002). Likewise, amygdala lesions were found to reduce aggression in caimans (Keating et al., 1937). In a study that used glucose metabolism as a marker of regional brain activation in lizards, hostility was associated with an increase in dorsolateral basal ganglia metabolism and a decrease in ventromedial basal ganglia metabolism; submissiveness was associated with the opposite regional metabolic pattern (Baxter et al., 2001a). These limbic telencephalic sites may be acting upon the midbrain tegmentum and reticular formation, because low-intensity electric stimulation of the latter sites triggers defensive behavior in lizards (Sugerman and Demski, 1978). Finally, as in mammals, so also in reptiles the limbic telencephalon receives extensive serotoninergic inputs from the reticular formation and raphe nuclei of the brainstem (Smeets and Steinbusch, 1988; Bennis et al., 1990; Ayala-Guerrero et al., 1991). In summary, while much more research is needed to accurately specify the brain regions that mediate anger and fear in reptiles, the current evidence point to the same limbic structures that have been implicated in these agonistic affects in mammals, including humans.

**Endocrine and Brain Mechanisms of Sexual and Parental Affects.** Many reptilian species are seasonal breeders and use various overt signals to communicate their sexual readiness to conspecifics. These signals, interpreted as species-specific emotional expressions, facilitate gonadal maturation in potential mating partners and the synchronization of their sexual transactions. The latter begins with courtship and is followed by copulation, and terminates (in some species) with some parental care that aids offspring survival. For instance, the presence of sexually primed whiptail lizard males induces ovarian maturation in the females, and the presence of reproductively mature females facilitates testicular recrudescence in males (Lindzey and Crews, 1988). Visual signals play a pivotal role in some reptiles in this synchronization, whereas in other species chemical signaling through pheromone release is the crucial signaling channel (Wade and Crews, 1998).
ENDOCRINE MECHANISMS OF REPTILIAN AMOROUSNESS. During the breeding season, circulatory levels of testosterone are elevated in male lizards, and estrogen levels reach their peak before and during ovulation in females (Moore and Crews, 1986). High concentration of these sex hormones instigates mating that is typically preceded by intense courtship behavior. Castrated males do not engage in courtship behavior but the peripheral administration of testosterone restores both courtship and copulation (Moore and Lindzey, 1992). Testosterone also facilitates receptivity in ovariectomized females (Winkler and Wade, 1998). The male green anole lizard courts the female by extending its conspicuous dewlap, accompanied by head bobbing (Cooper and Greenberg, 1992). While dewlap extension triggers fights between competing males during the breeding season, an aggressive response increased by high levels of testosterone (Tokarz et al., 2002), the female may respond positively to this emotional expression by approaching the suitor. Females do not display dewlap extension during courtship, although they may do so in agonistic encounters. Instead, the receptive female releases a pheromone during courtship and that induces the courting male to engage in rapid tongue-flicking. According to one study (Cooper and Perez-Mellado, 2002), there is an increase in the relative rate of tongue flicking in male lizards when presented with a swab dipped into organic material taken (a) from conspecific females versus males; (b) from conspecific nongravid females versus gravid females, and (c) from conspecific females versus strange females.

BRAIN MECHANISMS OF REPTILIAN REPRODUCTIVE AFFECTS. The hypothalamus and the related preoptic area, both of which are rich in sex-hormone receptors, play a major role in the regulation of sexual behavior, and different hypothalamic areas have been implicated in that regulation in males and females (sexual dimorphism). In whiptail lizards, the anterior hypothalamus and preoptic area is larger in the male than in the female, whereas the ventromedial hypothalamus is larger in the female than in the male (Crews et al., 1990). In castrated males, androgen implants in the anterior hypothalamus/preoptic area restore masculine sexual behavior (Rozendaal and Crews, 1989). In contrast, it is in the ventromedial hypothalamus that estrogen implants restore receptivity in ovariectomized females (Wade and Crews, 1991), and that is coupled with an increase in the concentration of estrogen receptors (Godwin and Crews, 1995). In line with these findings, anterior hypothalamus/preoptic area lesions impair courtship and copulatory behavior in males (Kingston and Crews, 1994) whereas ventromedial hypothalamic lesions impair receptivity in females (Kendrick et al., 1995). In male geckos, the concentration of androgen receptors is particularly high not only in the anterior hypothalamus/preoptic area but also in the septum and the amygdala (Moga et al., 2000; Rhen and Crews, 2001). In addition to androgen and estrogen, arginine vasotocin (AVT), facilitates reproductive behavior in reptiles, much as it does in fish (Section 3.2.3) and amphibians (Section 4.1.3). In sea turtles, the blood concentration of AVT increases as the animals begin to nest and lay their eggs on the beach, and decreases as soon as they return to the sea (Figler et al., 1989). Both in male and female anoles lizards, AVT-containing neurons are concentrated in the preoptic area, the hypothalamus and the medial septum, while AVT-containing nerve fibers are widely distributed throughout the brain (Propper et al., 1992). In the chameleon, vasopressin- and oxytocin-containing neurons are present in the supraoptic and paraventricular nuclei of the hypothalamus (Bennis et al., 1995). These neuroendocrine agents, we postulate, change the emotional disposition (mood) of animals such that instead of engaging in self-serving behavioral routines, such as feeding, they exert great effort in the self-negating behavior of propagating the species.
4.2.4. Perception, Memory, and Cognition in Reptiles. The olfactory, gustatory and visual sensory systems are well developed in reptiles. Omnivorous lizards select among opaque cups the one which hides a piece of fruit by responding to its airborne odor by a high rate of tongue flicking and cup biting (Cooper and Perez-Mellado, 2001). They discriminate different nutrients offered to them on a cotton swab, licking at a high rate the swab baited with sucrose and biting the swab dipped in fat or protein (Cooper et al., 2002). Insectivorous lizards respond with high frequency of tongue flicking to chemical extracts from prey but not those from plants (Cooper et al., 2000). Instead of using their tongue, the large carnivorous alligators and crocodiles lunge rapidly at the prey they detect, biting it, and tearing it apart by vigorous head shaking (Busbey, 1989). Turtles repeatedly snap at a bag containing fish or meat, and do the same if the bait is placed in a sealed transparent beaker (Honigmann, 1921). Lizards recognize suitable nutrients not only by smell but also by vision (Elias et al., 2000; Herrel et al., 2000) and they have well-developed color discrimination (Wagner, 1933; Benes, 1969).

Reptilian Memory and Learning. The migratory and homing behavior of marine turtles indicate that they rely on long-term memory for navigation. Emerging from sandy beaches, hatchlings rush to the sea and soon thereafter begin their migration to distant feeding areas along the continental shelf, or dispersing in the open ocean where visual landmarks do not exist, and then return to their natal beach to lay and bury their eggs (Meylan, 1995; Lohmann et al., 1997; Troëng et al., 2005). Using satellite telemetry, foraging female hawksbill turtles were found to return to natal nesting grounds after a journey of up two thousand kilometers away from it (Van Dam et al., 2008). It has been assumed that, much like homing salmon (Section 3.3.2), sea turtles are able to recognize their natal beach by imprinting on its distinctive chemical property. In a choice situation, turtles prefer water containing the chemical to which they were exposed as embryos or juveniles (Grassman, 1993). However, since sea turtles migrate for years over long distances in search of food, they must also use other than chemical cues than chemical ones that cannot disperse that far from the mouth of rivers. There is some evidence that turtles form an imprinted map of some feature of the Earth’s magnetic field (its inclination angle and/or intensity) along their traversed route (Avens and Lohmann, 2003; Lohmann et al., 2008).

Experimental Studies of Learning. The learning ability of reptiles has been studied experimentally in a variety of species (Burghardt, 1977; Suboski, 1992). Lizards readily master appetitive learning (Davidson and Richardson, 1970; Shafir and Roughgarden, 1994) and aversive learning tasks (Yori, 1978; Marcellini and Jenssen, 1991). They can also solve spatial tasks in a maze and show some capacity for reversal learning (Peterson, 1980; Day et al., 2003). In a pioneering study of spatial learning in turtles, Yerkes (1901) found that the animals gradually learned to reduce the time needed to escape from a box through a maze with several blind alleys, and after 10-20 trials proceeded directly to a favored rest area. According to Tinklepaugh (1932), turtles can master a maze with five blind alleys in as few as four trials. Turtles can also master a simple instrumental learning task and remember that for several months (Davis and Burghardt, 2007).

A recent study (López et al., 2000b) examined the features of maze learning in turtles with two procedures. In the place procedure, the turtles had to use extramaze cues in a room to find the reward. In the cue procedure they had to use a single intramaze visual cue to achieve
the same end. The results showed that when started from novel arms, the turtles trained by the two methods mastered the maze by relying on different cues: the animals trained with the cue procedure learned to recognize the signpost, those trained with the place learning relied on extramaze cues. Importantly, however, removal of some of the extramaze cues in the latter instance did not appreciably affect performance, suggesting that the turtles learned to rely on several extramaze cues to orient themselves. Finally, a tortoise has been tested in an eight-arm radial maze to study its foraging strategy (Wilkinson et al., 2007). It displayed a tendency not to return to baited arms which it has visited earlier, implying the use of working memory.

**Brain Mechanisms of Learning.** There are several reports regarding the brain mechanisms that mediate learning by reptiles (Peterson, 1980; Powers, 1990). Turtles with large lesions of the dorsal pallium learn simple visual discrimination tasks as readily as do normal animals (Hertzler and Hayes, 1967; Morlock, 1972; Bass et al., 1973; Reiner and Powers, 1983; Grisham and Powers, 1990), and so do lizards (Peterson, 1980). However, both lizards (Peterson, 1980) and turtles (Reiner and Powers, 1983) with dorsal lesions are impaired in reversal learning. In another set of studies, turtles were trained to solve a maze problem in which they could rely either on an intramaze visual cue or extramaze spatial cues to reach a goal (López et al., 2000b; Rodriguez et al., 2002). Turtles with medial pallium lesions showed no deficit in using a visual cue but they failed to navigate directly to the goal if they had to rely on extramaze cues. This was interpreted to indicate that lesions of the medial cortex in turtles, like lesions of the hippocampus in mammals, selectively impair map-like memory representations of the layout of the environment. That interpretation is partially supported by a recent study in which sham-operated and medial pallium-lesioned turtles were tested on the acquisition and reversal of a learning task with two procedures, either relying on extramaze visual cues or on an intramaze spatial cue (López et al., 2003). The lesioned turtles showed no deficit in the acquisition phase of either task but were handicapped in the reversal of the spatial task but not the visual task (Fig. 4-31).

4.2.5. **Our Reptilian Legacy.** Ancestral reptiles, presumably Therapsids of the late Triassic, have made major contributions to our visceral and somatic evolution. Paramount among them are the powerful lungs we have for breathing oxygen-rich air, the four-chambered heart for efficient distribution of the oxygenated blood to body and brain, and the production of amniotic eggs that can develop outside a fluid environment. These somatic and visceral advances were coupled with some advances in the differentiation of the reptilian brain. The telencephalon of reptiles is larger and more differentiated than that of amphibians and fishes. However, there is little evidence either for a growth spurt or transformation of the reptilian brain: the allometric encephalization index of both extinct (Jerison, 1973) and extant reptiles (Jerison, 2001) is in the range of amphibians and fishes. That is, reptiles are relatively small-brained vertebrates, in contrast to the large-brained birds and the still larger-brained mammals. With regard to their putative mental life, reptiles display only modest advances relative to fishes and amphibians. Reptilian behavior is largely governed by inborn affects with little, if any, contribution made by cognitive processes. When alligators or crocodiles move to-and-fro from water to land to maintain optimal body temperature, or lizards alternately bask in the sun or seek shade, they display affective likes and dislikes that serve them well since, being ectothermic (cold-blooded), they lack visceral mechanisms for temperature control. They display what looks
Fig. 4-31. The acquisition and reversal of a spatial place learning (A) and a visual cue learning (B) task in sham-operated and medial pallium-lesioned turtles (red, MC-les). (From López et al., 2003.)
like passions, when they ferociously attack a prey or savagely maul an intruder that enters their territory. But while they can act swiftly and effectively when emotionally aroused, they are constitutionally incapable of sustained exertion, which is so typical of so many endothermic (warm-blooded) vertebrates, whether fluttering birds or hustling-bustling mammals. When not engaged in the gratification of their basic needs, reptiles tend to be passive, lying prostrate on a floating log, a warm rock, a sunny wall, or immersed in a mudflat or cool puddle.

This intermittent rather than sustained behavioral style is partly due to the circumstance that the muscles of ectothermic reptiles are principally energized by anaerobic metabolism (the breakdown of glycogen and glucose into lactic acid) rather than by oxidative metabolism. As lactic acid accumulates in their circulatory system, reptiles quickly fatigue and require time to recuperate. But perhaps another reason is that reptiles rely little on individually acquired experience and cognitive abilities to guide their behavior, as mammals do, a life pattern that requires continuous transaction with the physical and social environment. Reptiles can see, hear and smell well; can remember the location of suitable resting, hiding, and feeding sites; and, as territorial animals, can discriminate among peers who are dangerous and those they can subdue and send fleeing. However, reptiles do not display curiosity about anything that does not directly relate to their vital needs. Consequently, their acquaintance with the objective features of the external world has to be very limited. This contrasts with the behavior and mental life of even the most primitive of mammals, like insectivores and rodents, which spend a considerable amount of their waking hours exploring every nook and cranny of their habitat, sniffing, licking, chewing on, palpating and tearing apart any novel object they encounter, and chasing, playing with, and grooming one another.

The different path of neural and mental evolution followed by birds and mammals may have had several causes. The fact that the reptilian forelimbs became transformed in birds into flying instruments, whereas in mammals, particularly in primates, the forelimbs became partially transformed into organs of object palpation and manipulation, must have been one of the causes. To take off and fly with ease, birds have to assess the direction and strength of air currents and thermal columns, they have to dive and make fast turns in midair to maneuver, avoid collisions when flying in formation, and land softly. Birds need a relatively large brain to accomplish all this but it is advantageous to keep not only the body but also the brain relatively light. Because preprogrammed ("hard-wired") neural circuits require far fewer neurons and interconnections than programmable ("soft-wired") circuits, there was selective pressure to coordinate as many of these behavioral routines as possible automatically. Indeed, built-in automatisms may be what some components of the complex avian basal ganglia are dedicated to. Mammals, as we describe in the next chapter, embarked on a different evolutionary path. Beginning with insectivores and rodents, and culminating in subhuman primates and humans, the forelimbs became transformed into dexterous instruments for object manipulation. There being less constraint on how heavy a brain can become on terra firma, it became advantageous to evolve a programmable neural system, one that provides optimal memory capacity, enhanced cognitive powers, and greater behavioral flexibility. We will argue, that our propensity to investigate and learn about the multifaceted properties of the objective world is the primary function of the evolving mammalian neocortex, which may have emerged in rudimentary form in a line of ancestral reptiles.
Chapter 4: Body, Brain, and Mind in Amphibians and Reptiles

It is likely that the small-brained alligators and crocodiles (or the extinct dinosaurs) are not representative of the reptiles that gave rise to mammals. We have described extant reptiles with two different types of forebrains. In one of them, like the alligator, the ganglionic component of the forebrain is better developed than the pallium. In the other, as in the near-extinct tuatara, it is the pallium that is more differentiated. We speculated that some ancient reptiles with a ganglionic telencephalon were ancestral to birds, others with a pallial telencephalon were ancestral to mammals. Importantly, in neither of the surviving reptilian lines does the pallium have the distinctive features of the mammalian neocortex. The pallium of reptiles is composed of a single cellular layer; the mammalian neocortex typically has six cellular layers. Nor does the reptilian pallium have a direct-line afferent system (the thalamocortical system) and an express-lane efferent system (the corticospinal tract). Not surprisingly, there is little evidence in reptiles relative to fishes and amphibians of considerable advances in perceptual and cognitive powers, features that characterize mammals, particularly primates. However, reptiles have left an enduring legacy with regard to our mental constitution, some of which may be looked upon as a burden rather than a gift. Although we have evolved into social beings, much of our behavior is suffused by the same egotistic dispositions that govern the life of reptiles. Our impulsiveness, covetousness, indifference to the plight of others and proneness to violence, are deeply embedded in the substratum of our CNS, the paleocephalic and neuroendocrine emotional mechanisms that are part of our reptilian heritage.