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Chapter 8

EVOLUTION AND DEVOLUTION: THE CASE OF BOLITOGLOSSINE SALAMANDERS

*Gerhard Roth and David B. Wake, Brain Research Institute,
University of Bremen (GR) Museum of Vertebrate Zoology,
University of California, Berkeley (DBW)*

INTRODUCTION

In the past, the evolution of the nervous system, including the brain, was envisioned as a near monotonic increase in size, both absolute and relative, as well as in morphological and functional complexity (Ariens-Kappers et al., 1936; Romer, 1970; Jerison, 1973; Kühlenbeck, 1977; Northcutt, 1981; Ebbesson, 1980, 1984; Sarnat and Netsky, 1981; Starck, 1982). This process of *encephalization* was assumed to start with a simple nerve plexus (as found in current cnidarians) from which emerged central nervous systems and, subsequently, by a number of significant increases in structural and functional complexity, brains (i.e., supraesophageal [cerebral] ganglia) as in platyhelminths, nemathelminths, nemertines, molluscs, annelids, and arthropods. Encephalization was thought to continue with the vertebrates, where a series of increases in structural and functional complexity characterize the evolutionary transitions from myxinoids and petromyzontids to mammals (Ariens-Kappers et al., 1936). Such an increase was viewed as favoring sensory, motor, and cognitive functions, which, in turn, contributed directly to evolutionary success (i.e., persistence, species proliferation, and number of individuals).

Such a conception of the evolution of nervous systems as a process of essentially continuous encephalization is no longer justified (see Wullimann, this volume, Chapter 1). During phylogeny, some taxa have evolved complex brains, but at the same time others have secondarily simplified brains, giving the impression of a kind of *devolution* (i.e., secondary simplification). Examples of the latter, as revealed by cladistic analysis (Roth and Wullimann, 1996), are the following: (1) Platyhelminths (about 16,000 species) are the first group of metazoans that possess bilaterally symmetrical central nervous systems. Among the freely living platyhelminths, the "turbellarians," taxa are found (e.g., the Acoela) that have completely lost a central nervous system. Moreover, the nervous systems of trematods and cestods (several thousand species) are all secondarily simplified. (2) Among molluscs, many of the 100,000 species of gastropods and all bivalves (Lamellibranchiata, 20,000 species) have

moderately to strongly simplified nervous systems. (3) Strong secondary simplification of the central nervous system is likewise found in some groups of annelids (e.g., in hirudineans [Oligochaeta] and in arthropods (e.g., in mites [Acari, Arachnida; more than 30,000 species]). (4) Tentaculates (about 5000 species) as well as hemichordates and urochordates have relatively simple central nervous systems compared with other invertebrates and either represent independent cases or one single case of secondary simplification in the last common ancestor of tentaculates and deuterostomes. In other words, among invertebrates, secondary simplification of nervous systems is at least as common as is an increase in structural and functional complexity.

Among vertebrates (Fig. 8.1A), secondary simplification of nervous systems seems a rare event. There are, however, at least three groups of vertebrates that have undergone profound simplification of the central nervous system, viz., salamanders, caecilians, and lepidosirenid lungfishes. There are cases of weaker secondary simplification of the central nervous system in other taxa as well (e.g. in frogs) and of simplification at least with respect to some traits of the nervous system (e.g., unlayered or three-layered [as opposed to six-layered] isocortex in cetaceans and insectivores) (Nieuwenhuys et al., 1998).

Secondary simplification of nervous systems seems counterintuitive under a strict adaptationist's view. Why should reduction in brain size, nerve cell number, and morphological complexity or even the loss of sensory systems be advantageous for survival? Of course, one can find adaptive scenarios even for simplification (e.g., getting rid of developmentally or metabolically "expensive" structures or functions that are no longer needed in certain environments). This is a reasonable explanation for cases in which simplification is part of a transition to sedentary or parasitic life, as is found in many invertebrates (e.g., trematods, cestodes, bivalves, hirudineans, tentaculates, hemichordates, and urochordates). Even here, however, an important question remains to be answered: Which came first, the simplification or the changes in life style? The case of the Echinodermata remains enigmatic: Why did they give up a bilateral central nervous system? Equally unexplained are the cases of secondary simplification found among vertebrates. The most dramatic one is the case of tongue-projecting salamanders, the Bolitoglossini.

THE BOLITOGLOSSINI

The Bolitoglossini, or tongue-projecting salamanders, represent, with about 180 species described, the largest group among the family Plethodontidae (about 275 species), which, in turn, comprises more than two thirds of all extant salamanders (order Caudata, approximately 400 species) (Fig. 8.1B,C). Thus, bolitoglossines constitute about 50% of living salamander species. They are almost exclusively found in North, Central, and South America (including Brazil and Bolivia) and are the only truly tropical salamanders. The largest number of species and the highest morphological and ecological diversity within the bolitoglossines are found in Central America. Several species of the genus *Hydromantes* represent the only bolitoglossines

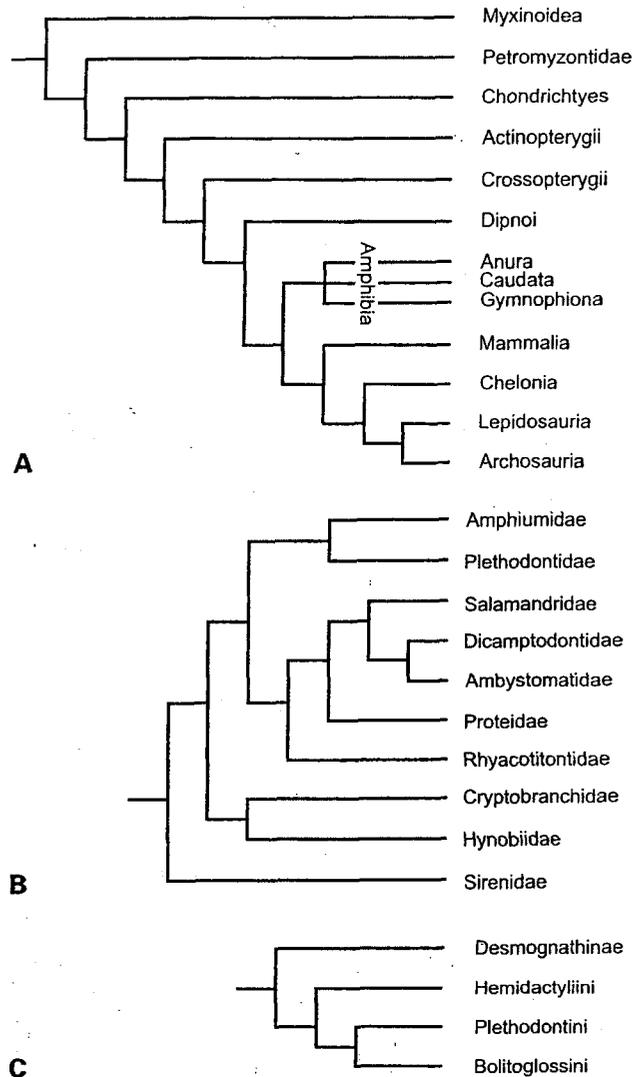


Figure 8.1. (A) Phylogenetic relationships of extant vertebrates. (From Roth et al., 1993.) (B) Phylogenetic relationships of extant taxonomic families of salamanders (Caudata). (After Larson and Dimmick, 1993.) (C) Phylogenetic relationships of plethodontids. (After Wake, 1966.)

living outside the New World; they are found in southern France, northern Italy, and Sardinia, although some North American species of *Hydromantes* occur in California. All nonbolitoglossine plethodontids are found exclusively in North America. The Plethodontidae are believed to have originated in eastern North America, in the Appalachian highlands, where they inhabited mountain brooks (Wilder et al., 1920; Dunn, 1926; Wake, 1966). Apparently as an adaptation to this habitat, they underwent

reduction and eventually complete loss of lungs—an event that occurred several times among salamanders other than plethodontids living in similar habitats (Beachy Bruce, 1992). Plethodontid salamanders compensate their lunglessness by exchange through a highly vascularized skin and mouth cavity.

All Bolitoglossini are terrestrial. They lack aquatic larvae and have direct development (i.e., eggs are laid on land) from which tiny but adultlike salamanders hatch (Fig. 8.2.). During embryonic development, bolitoglossines do not form larval structures such as a larval hyobranchial apparatus, as do other directly developing plethodontids. The evolution of direct development and of terrestriality appears to be unrelated to lunglessness, because direct development and strict terrestriality have evolved independently many times among both lung-breathing and lungless amphibian taxa (Duellman and Trueb, 1986). The great success of plethodontid salamanders, which in some regions may exceed birds and small mammals in biomass, is certainly related to the evolution of direct development and terrestriality because these animals are thereby freed from a biphasic life cycle and from dependence on free surface water—features that constrain other amphibians. According to some estimates, terrestrial plethodontids, and bolitoglossines in particular, have invaded the m

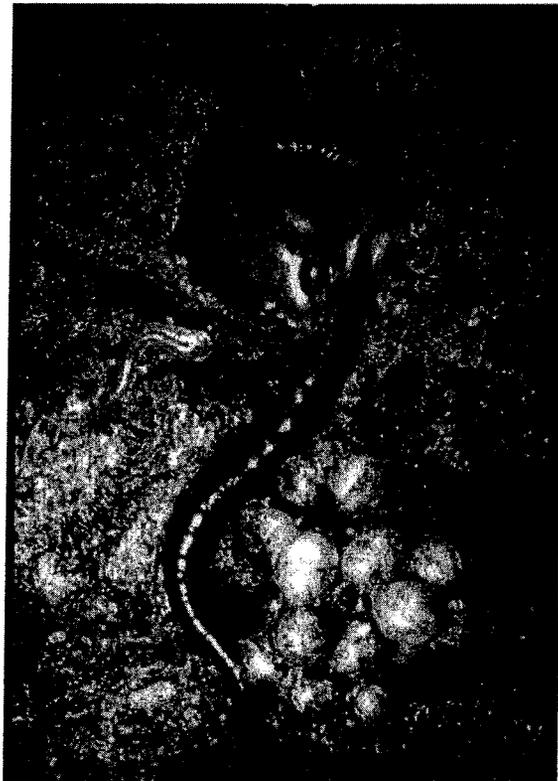


Figure 8.2. *Bolitoglossa* with eggs. (Courtesy of Dr. U. Dicke.)

diverse habitats from earthworm holes and limestone caves to bromeliads and moss mats in the trees of the tropical rain and cloud forests (Wake, 1987). Many tropical bolitoglossines are facultatively or strictly arboreal, and, not surprisingly, have diverse locomotor specializations, including acrobatic ability for life in three-dimensional environments.

Bolitoglossines are characterized by a unique feeding mechanism, i.e., a projectile tongue (Lombard and Wake, 1976, 1977, 1987; Roth, 1987). It consists of a greatly elongated hyobranchial apparatus with the tongue muscles at its anterior tip. During projection, it forms a slender projectile that is projected up to 80% of head plus body length (Deban et al., 1997) (Figs. 8.3 and 8.4). In salamanders with a biphasic life cycle, this apparatus develops from the skeleton of the hyoid and branchial arches. It consists of an unpaired median basibranchial (BB), which lies in the floor of the mouth. Two pairs of ceratobranchials (CB) articulate with the posterior end of the BB. The first and second CB on either side extend posteriorly, approaching each other, and together articulate with the epibranchial (EB). On each side of this apparatus a pair of cerytohyals lies in the floor of the mouth. In plethodontids, their anterior portion forms a flattened blade, which is attached to the lower jaw by the geniohyoideus muscle (see below), while their posterior end is cylindrical and hooked and attached to the upper jaw suspension by a ligament. The tongue pad, which contains the tongue muscles proper, is situated at the anterior end of the BB and is covered by numerous glands.



Figure 8.3. Tongue projection in *Hydromantes supramontis*. This salamander has the longest projectile tongue relative to body length. (From Deban et al., 1997.)

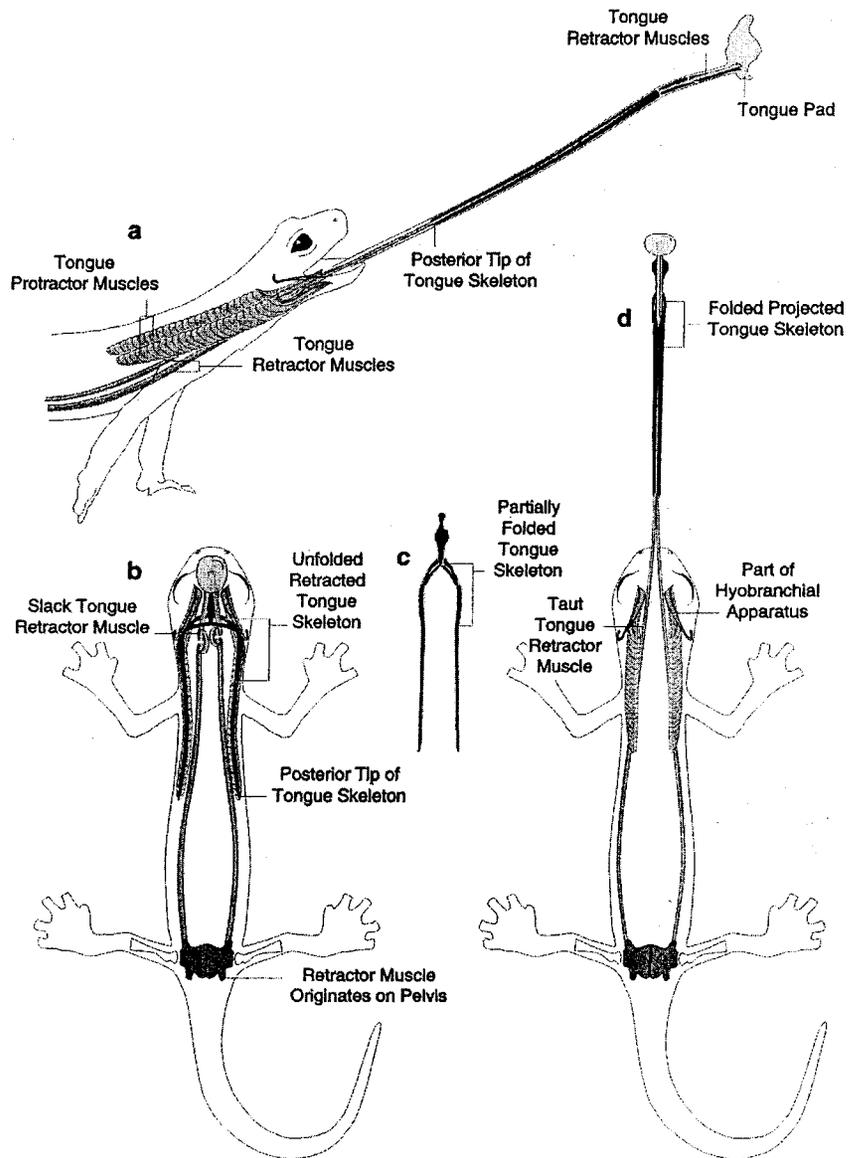


Figure 8.4. Tongue-projection system of *Hydromantes supramontis*. (a) Lateral view corresponding to Figure 8.3 showing the tongue skeleton (black) projected completely out of the mouth and bilaterally paired tongue protractor and retractor muscles. (b) Dorsal view with tongue skeleton in the unfolded retracted position, elongate posterior elements sheathed in protractor muscles, and slack, looped retractor muscles originating on the pelvis. (c) Tongue skeleton partially folded as in an early stage of projection. (d) Dorsal view showing the tongue skeleton projected entirely from the body, beyond the contracted protractor muscles, which are anchored anteriorly to the portion of the hyobranchial apparatus that remains in the mouth. The retractor muscles, now taut, run the full length of the extended tongue and body. (From Deban et al., 1997.)

The main muscles associated with this skeleton are (Fig. 8.4) (1) The subarcualis rectus I muscle, which encircles the caudal end of the EBs, forming a bulb, and extends rostrally along this element, forming a muscular sheath. It then attaches broadly to the ventral surface of the flattened anterior end of the ceratohyals. (2) The rectus cervicis profundus, which originates from the puboischium and runs along the body axis to the anterior part of the BB. (3) The geniohyoideus lateralis, which arises at the lateral edge of the ceratohyals and extends to the lower jaw. (4) The genioglossus, which—if present—extends from the ventral surface of the lower jaw on each side of the symphysis and inserts dorsally in the substance of the rostral tongue.

In all generalized salamanders (e.g., most salamandrids and ambystomatids), the hyobranchial apparatus exerts a dual function in metamorphosed animals (viz., respiration and feeding). It serves as a buccal pump for respiration in that it expands the buccal cavity. During prey capture, the tongue is pushed out of the mouth by a limited forward movement of the hyobranchial skeleton. In the Bolitoglossini, the tongue apparatus has undergone a dramatic evolution, including substantial elongation of epibranchials and loss of the genioglossus muscle, leading to free tongues in the sense that the entire hyobranchial apparatus plus retractor muscle (rectus cervicis profundus), and not only the tongue muscle proper, are projected out of the mouth (Lombard and Wake, 1976, 1977; Deban et al., 1997) (Figs. 8.3 and 8.4). The development of such a highly mobile tongue appears to be intimately connected to a reduction or loss of lungs (Wake, 1982; Roth and Wake, 1985a). This event freed the hyobranchial apparatus from the function of serving as a lung pump, giving it the chance to evolve in the direction of feeding alone. In *Bolitoglossa occidentalis*, the whole tongue reaction takes place in about 10 ms (Thexton et al., 1977); in the genus *Hydromantes*, having the longest tongue, it lasts 80 to 100 ms (Roth, 1976) (Figs. 8.3 and 8.4).

With regard to feeding strategy, many frogs and salamanders are hunters in that they actively search for prey. In contrast, Bolitoglossines are mostly ambush feeders, that is, they sit and wait (often under a cover or in a cavity) until prey comes by. The evolution of an ambush strategy probably was forced by the inability of bolitoglossines to move fast because of very low metabolic levels (see below). It may have been impossible in terrestrial environments to elude predators while hunting prey. An ambush strategy is safer and metabolically less costly, but it requires a fast and precise feeding mechanism, such as a free, projectile tongue, and very good depth perception abilities, which, in turn, require binocular, stereoscopic vision. Not surprisingly, bolitoglossine salamanders have more frontally located eyes than do other salamanders and most frogs, and therefore have a larger binocular visual field (Linke et al., 1986).

In the Bolitoglossini, we find a substantial number of retinal fibers to project to the ipsilateral optic tectum (Fig. 8.5.) in addition to the contralaterally projecting ones (Rettig and Roth, 1986). This is uncommon among other amphibians as well as among most other vertebrates except some mammals. In the bolitoglossines ipsilateral retinotectal projections may serve to enable direct comparison between information from the left and right eye in the context of stereopsis. Recent neurophysiological experiments suggest that bolitoglossines make use of the disparities between the contralateral and direct and indirect ipsilateral retinotectal projections to

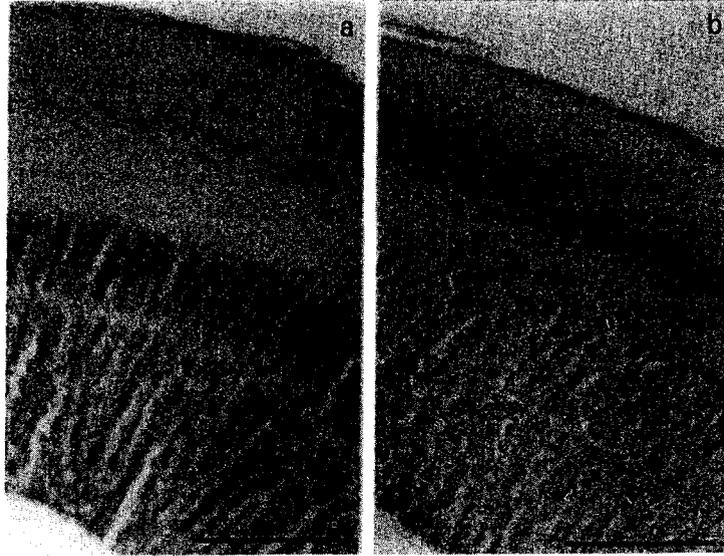


Figure 8.5. Cross section through the optic tectum of *Plethodon jordani* (a) and *Hydromantes italicus* (b) showing differences in ipsilateral retinotectal projections as revealed by retrograde biocytin labeling. Bars = 50 μ m. (Courtesy of Dr. W. Wiggers.)

locate prey objects and to calculate their movement trajectories (Wiggers and Roth, 1991; Wiggers et al., 1995). Excellent stereopsis may explain why these animals almost never miss their prey and feed on prey items such as collembolans that normally escape other amphibians (Roth, 1987).

In summary, tongue-projecting salamanders are able to engage in rapid, efficient ambush feeding. Logically, one might expect these animals to possess brains at least as complex as those of frogs exhibiting comparable standards of performance in speed and precision of visually guided feeding behavior (e.g., *Rana temporaria* or *Eleutherodactylus coqui*).

THE BRAIN OF SALAMANDERS AND FROGS

The brain of salamanders—like that of other amphibians—may be divided into five major parts: (1) telencephalon; (2) diencephalon including praetectum; (3) mesencephalon; (4) cerebellum; and (5) medulla oblongata (Fig. 8.6). There is no pons in the amphibian brain.

The telencephalon (a and b in Fig. 8.6B) is composed of olfactory bulbs, pallial structures (dorsal, lateral, and medial pallium; and amygdala pars lateralis) and subpallial structures (nuclei septi, amygdala pars medialis, and striatum, including nucleus accumbens). The medial pallium represents the dorsomedial wall of the hemisphere

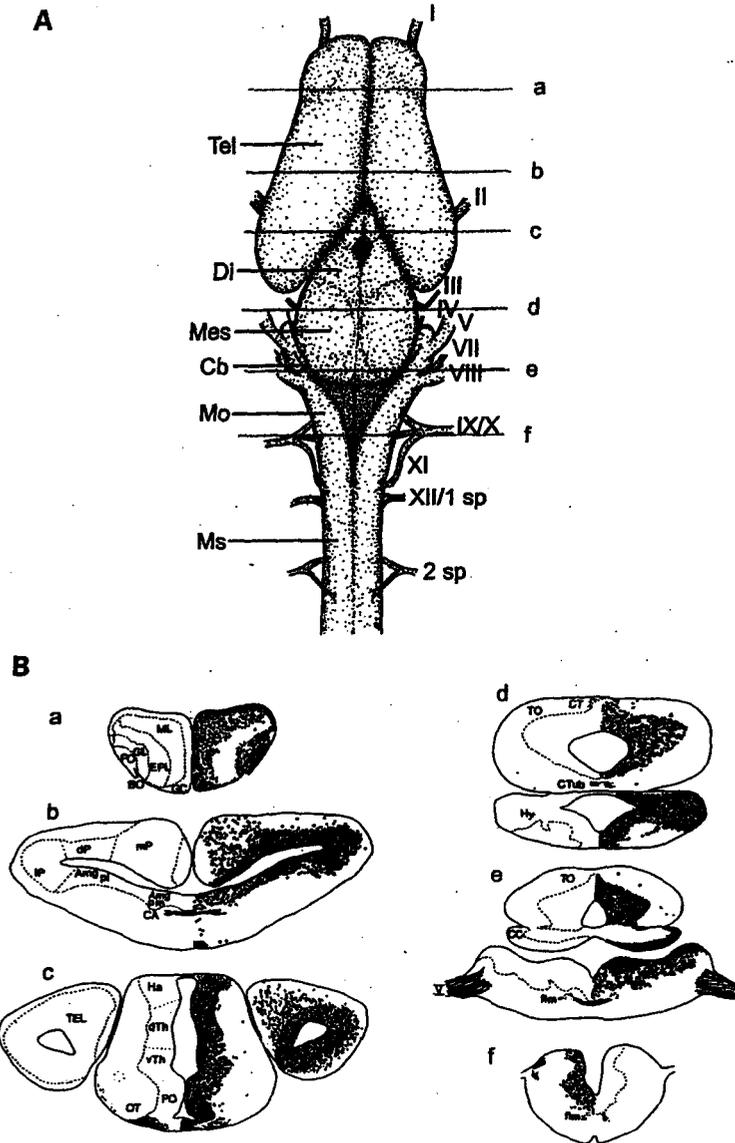


Figure 8.6. (A) Dorsal view of the brain of *Bolitoglossa subpalmata*. (B) Selected cross sections through the brain of *Bolitoglossa subpalmata* at sites indicated in A. (a) Telencephalon at the level of the olfactory bulbs. (BO) (b) Caudal telencephalon at the level of the anterior commissure. (CA) (c) Mid diencephalon (Di). (d) Mid mesencephalon (Mes). (e) Caudal mesencephalon/cerebellum/rostral medulla oblongata. (f) Mid medulla oblongata (Mo) at the entrance of the 9th nerve. Amg pl, amygdala pars lateralis; Amg pm, amygdala pars medialis; BO, bulbus olfactorius; Cb, cerebellum; CC, corpus cerebelli; CT, commissura tecti; CTub, commissura tuberculi posterioris; dP, dorsal pallium; dTh, dorsal thalamus; EPL, external plexiform layer; fIm, fasciculus longitudinalis medialis; GC, layer of granule cells; GL, glomerular layer; Ha, habenula; Hy, hypothalamus; lP, lateral pallium; ML, layer of mitral cells; mP, medial pallium; OT, optic tract; PO, nucleus praeopticus; TEL, telencephalon; TO, tectum opticum; vTh, ventral thalamus. (After Roth, 1987.)

and is considered to be homologous to the mammalian hippocampus, at least with regard to Ammon's horn and subiculum (Northcutt and Kaas, 1995; Roth and Westhoff, 1999). The dorsal pallium includes the pallial walls dorsal to the medial pallium and may be regarded as homologous to at least part of the mammalian isocortex (Butler and Hodos, 1996; Northcutt and Kaas, 1995). The lateral pallium is considered a homologue of the mammalian olfactory (piriform) cortex. The amygdala consists of two distinct nuclei, the pars lateralis of pallial origin, and the pars medialis of subpallial origin. The septal nuclear complex occupies the ventromedial wall of the cerebral hemispheres below the medial pallium. The striatum occupies the ventrolateral wall of the telencephalic hemisphere in a position immediately caudal to the accessory olfactory bulb.

The diencephalon (c in Fig. 8.6B) is divided into the epithalamus, dorsal thalamus, ventral thalamus, and hypothalamus. The epithalamus contains the epiphysis and the habenular nuclei, including the commissura habenularum. The dorsal thalamus is separated from the epithalamus by the sulcus dorsalis at the ventricular side. Similarly, the ventral thalamus is separated from the dorsal thalamus by the sulcus medialis and from the hypothalamus by the sulcus ventralis. The praetectum, or *synencephalon*, extends around the commissura posterior rostrally adjacent to the pars intercalaris thalami and descends ventrocaudally. Dorsally, it includes the nucleus praetectalis, ventrally and ventrocaudally, the nucleus Darkschewitsch.

The mesencephalon of amphibians (d and e in Fig. 8.6B) is divided into the tectum, a subtectal sensory zone, and the tegmentum. The tectum is treated later in greater detail in the section on the visual system. The auditory subtectal center corresponding to the anuran torus semicircularis is embedded completely in the periventricular gray matter and shows no, or very little, lamination. The tegmentum is a conglomerate of several nuclei adjacent to the rhombencephalic isthmus nucleus.

The cerebellum is small and simply organized (e in Fig. 8.6B). It consists of the corpus cerebelli, the auricula cerebelli (which are enlargements of the sensory zones of the medulla oblongata), and a nucleus cerebelli, situated ventral to the corpus cerebelli and homologized by Herrick (1948) to the deep cerebellar nuclei of mammals.

The medulla oblongata (e and f in Fig. 8.6B) is the area of termination or origin of cranial nerves IV (trochlear), V (trigeminal), VI (abducens), VII (facialis), VIII (stato-acusticus), IX (glossopharyngeus), X (vagus), and XII (hypoglossus). Its dorsal part, the alar plate of His, receives all sensory fibers from the head (except olfactory and optic fibers, which enter the forebrain), including general visceral parasympathetic sensory and gustatory fibers, as well as fibers from the trunk lateral-line system, if present. In the ventral basal plate of the medulla oblongata, the motor nuclei of nerves V to X, and partly the nucleus of nerve XII, are situated. The motor nuclei are surrounded by neurons of the reticular formation. This motor system is the coordination center of head and neck motor function, including mouth and tongue movements involved in feeding (Roth and Wake, 1985b).

In frogs as well as in most other vertebrates, many of the mentioned brain regions have a complex morphology exhibiting multiple lamination and the formation of distinct nuclei, which are often found in a migrated position. For example, the

mesencephalic tectum of frogs consists of nine alternating cellular and fiber layers between the ventricle and the brain surface (Székely and Lázár, 1976), and the thalamus contains a number of morphologically distinct nuclei, some of which possess a laminar organization (Neary and Northcutt, 1983). A similar degree of histological differentiation is found in the mesencephalic tegmentum and the auditory torus semicircularis of frogs (Potter, 1965; Feng, 1983) (Fig. 8.7a-d). In contrast, the

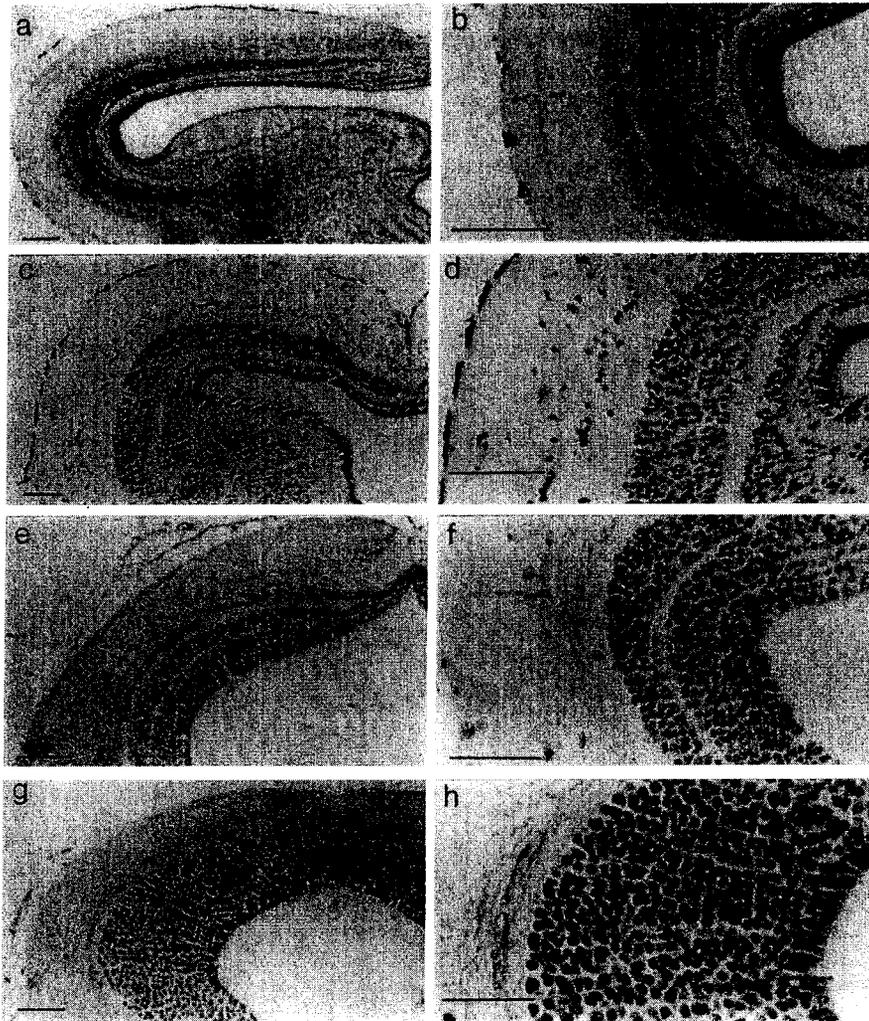


Figure 8.7. Cross sections through brains of frogs and salamanders at the level of the tectum and the dorsal tegmentum/torus semicircularis showing differences in cell size and morphological complexity. Photomicrographs are at both low (*left*) and higher (*right*) magnification (a,b). *Eleutherodactylus coqui* (cell diameter 5.8 μm); (Courtesy of Dr. Dicke, University of Bremen.) (c,d) *Bombina orientalis* (cell diameter 9.9 μm). (e,f) *Plethodon jordani* (cell diameter 11.8 μm). (g,h) *Hydromantes italicus* (cell diameter 12.5 μm). For further explanation, see text. Bars = 50 μm .

tectum, tegmentum, and thalamus of salamanders show an essentially bilayered structure, consisting of a periventricular layer of neurons (gray matter) and a superficial layer of afferent and efferent fibers and dendrites of neurons (white matter) (Fig. 8.7e-h). Only a few neurons are found in a migrated position within the white matter (Roth et al., 1990). An example is the nucleus praetectalis superficialis, which can be found in a migrated or partially migrated position. The minimum of morphological complexity among amphibians is found in the brains of bolitoglossines, which show no lamination of the tectum and no migrated nuclei at all; the spinal cord exhibits no lateral motor column present in all other limbed vertebrates (Roth and Wake, 1985b; Wake et al., 1988) (Fig. 8.8). In morphological terms, the brain of adult bolitoglossines strongly resembles that of early larvae of frogs.

This situation is just the opposite of what we would expect in the face of the specialization of bolitoglossines toward highly efficient feeding and arboreal life and the great evolutionary success of these animals in terms of speciation, ecological diversity, and biomass. Before drawing conclusions from these data, however, we examine the visual system, the most relevant sensory system involved in feeding behavior of these animals.

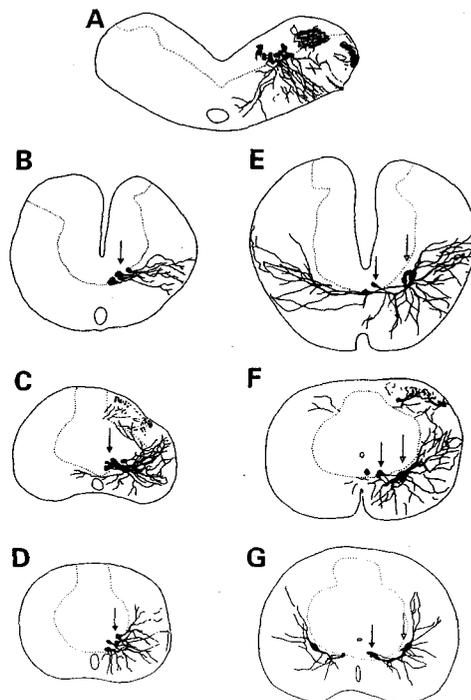


Figure 8.8. Reconstruction of transverse sections through motor nuclei related to feeding in plethodontid salamanders. A-D, *Batrachoseps attenuatus*, E-G, *Plethodon jordani*. (A) Motor nucleus of the facialis nerve. (B,E) Motor nucleus of the first spinal/hypoglossal nerve. (C,F) Motor nucleus of the second spinal nerve. (D,G) Motor nucleus of the accessory spinal nerve. While *Plethodon* possesses both a medial (arrow with solid arrowhead) and a lateral motor column (arrow with open arrowhead) in the spinal motor nuclei, *Batrachoseps* lacks a lateral motor column. (From Roth, 1987.)

THE VISUAL SYSTEM OF BOLITOGLOSSINES

The visual system consists of the retina and its diencephalic and mesencephalic neuropils, the mesencephalic tectum, the pretectum, and the dorsal and ventral thalamus of the diencephalon, as well as the nucleus of the basal optic root and the suprachiasmatic nucleus. Another nucleus closely related to the visual system is the nucleus isthmi.

Retina and Retinofugal System

Plethodontid as well as nonplethodontid salamanders have four different morphological types of retinal ganglion cells (RGC) (Linke and Roth, 1989). In anurans, the number of types of RGC is higher, from five to seven types in *Rana pipiens* (Frank and Hollyfield, 1987). There are also differences among anurans and urodeles in the number of RGC and consequently in the number of axons of the optic nerve. Frogs have up to 470,000 optic fibers and accordingly RGC (*Rana pipiens*; Maturana, et al., 1960). In salamanders, the number of optic nerve fibers/RGC ranges from a minimum of 26,000 in the plethodontid *Batrachoseps attenuatus* (Linke and Roth, 1990) to 75,000 in the salamandrid *Notophthalmus viridescens* (Ball and Dickson, 1983). Most fibers of the optic nerve cross in the chiasma opticum to the opposite side of the brain. A certain number of the fibers, however, turn back to the ipsilateral side of the brain (see below). In salamanders and frogs, three visual terminal fields can be distinguished within the rostral thalamus, viz., the corpus geniculatum thalamicum, the neuropil Bellonci pars lateralis, and the neuropil Bellonci pars medialis. In the pretectum, retinal afferents laterally form the pretectal neuropil and more medially the uncinata field. These thalamic and pretectal projection sites are present both contralaterally and ipsilaterally, although in all amphibians—with the exception of bolitoglossines—the ipsilateral sites are much weaker than the contralateral ones (Fite and Scalia, 1976; Fritzsche, 1980; Rettig and Roth, 1986).

In the tectum of frogs, four laminae of retinofugal fibers are formed (Székely and Lázár, 1976): lamina 1 and lamina 2 are situated in layer 9 immediately below the tectal surface and consist mostly of thin, unmyelinated fibers; lamina 3 contains myelinated fibers and is situated above tectal layer 8; lamina 4, consisting of a few, thick unmyelinated fibers, is located in layer 8 and beneath it. Singman and Scalia (1990), on the basis of retrograde horseradish peroxidase tracing experiments, estimated that in *Rana pipiens* 2.3% of the overall population of ganglion cells project to the ipsilateral tectum. In the superficial white matter of the tectum of bolitoglossines as well as of other salamanders, axons of ganglion cells constitute three layers/laminae (with several sublaminae) (Wiggers, 1998). These contain direct afferents from the contralateral as well as from the ipsilateral retina, the latter amounting to 30% of the former (Rettig and Roth, 1986) (Fig. 8.5). Recent recordings in our laboratory from retinotectal afferents in the plethodontid salamanders *Plethodon jordani* and *Hydromantes italicus* suggest that RGC terminating in layer 1 tend to have relatively small receptive fields with strong inhibitory surround and

respond best to changes in contrast and size of small objects. RGC in layer 2 tend to have wider receptive fields with weaker inhibitory surround and respond best to motion largely irrespective of stimulus size. Terminals in layer 3 on average again have wide receptive fields with very weak inhibitory surround. Most of these latter RGC exhibit very short latencies and are most sensitive to slow motion (Mandon and Roth, 1997). In frogs, four response types of RGC terminating in the tectum have been consistently described (Maturana et al., 1960; Grüsser and Grüsser-Cornehls, 1976), the first two of which largely correspond to layer-1 RGC of salamanders, the third to layer-2 RGC, and the fourth to layer-3 RGC of salamanders.

Thus, apart from the dramatic reduction in number of RGC and optic nerve fibers, differences in morphology and physiology between bolitoglossines and frogs are minor. Frogs may have one more morphological and physiological class of RGC judged from morphology and physiology compared with salamanders. This may be the reason for the existence of four instead of three laminas of optic nerve terminals inside the tectal white matter. The number of retinal terminal fields in the diencephalon and mesencephalon is the same in salamanders and frogs. The bolitoglossines, however, stand out among amphibians in having substantially more ipsilateral retinothalamic, retinopretectal, and retinotectal fibers than other amphibian taxa (Fig. 8.5).

Tectum

In addition to major differences in morphology of the tectum, there is a dramatic difference between anurans and urodeles in number of tectal neurons (Roth et al., 1994; 1998). Among salamanders, the lowest number of tectal neurons is found in *Batrachoseps attenuatus* (35,000) and the highest in *Salamandra salamandra* (150,000). The average number of tectal neurons in salamanders is 75,000. Among frogs, the lowest number of tectal neurons is found in *Arenophryne rotunda* (132,000) and the highest in *Eleutherodactylus coqui* (1,700,000). The average number of tectal neurons in the frogs is 720,000. Thus, frogs on average have about 10 times more tectal neurons than salamanders. Only the frog *Arenophryne rotunda* has fewer tectal neurons than any salamander. The low number of tectal neurons in salamanders compared with frogs goes along with a very low number of neurons found in migrated positions inside the white matter. In frogs, the percentage of such migrated tectal neurons ranges between 16.1 and 27.6. In salamanders, the percentage of migrated neurons ranges between 0.7 and 5, with the lowest values invariably found in the bolitoglossines (Roth et al., 1990).

Recently, comparative studies on the cytoarchitecture of the tectum were carried out in our laboratory in a number of frogs (*Discoglossus pictus*, *Eleutherodactylus coqui*) and salamanders (*Hydromantes italicus*, *Plethodon jordani*), using retrograde tracing and intracellular injection of biocytin (Dicke and Roth, 1996; Röckenhäuser and Roth, 1997; Dicke, 1999; Roth et al., 1999). In the two frog species, five types of descending projection neurons were identified (A in Figure 8.9). Type 1 neurons have a candelabra-like dendritic tree arborizing primarily in the most superficial retinorecipient lamina A or B of layer 9; the axons arborize bilaterally in the

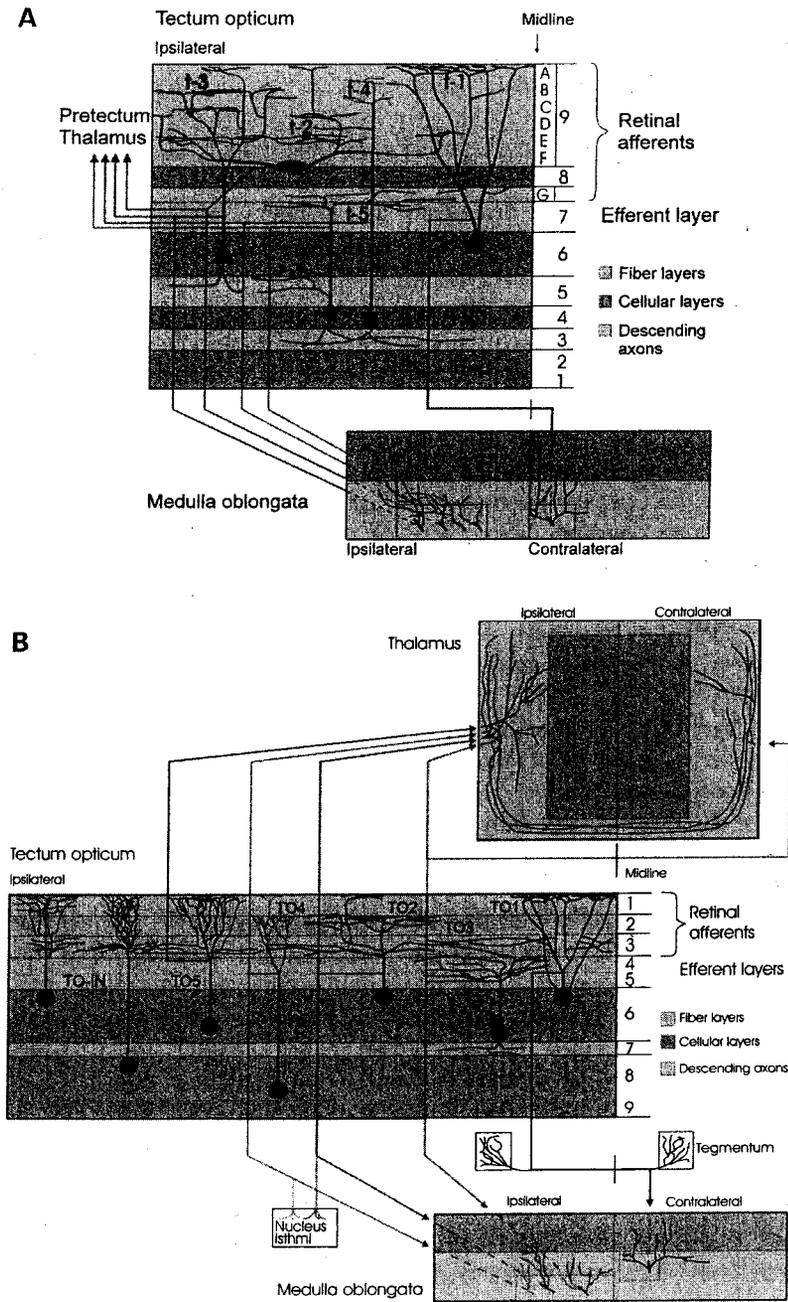


Figure 8.9. Morphological types of tectal neurons and axonal projection pattern in frogs and salamanders, as revealed by tract tracing and intracellular biocytin labeling. A: Frogs (*Discoglossus pictus*, *Eleutherodactylus coqui*). From Dicke and Roth, 1996. B: Salamanders (*Plethodon jordani*, *Hydromantes italicus*). From Roth et al., 1999. For further explanation see text.

tegmentum and descend *contralaterally*, constituting the *crossed* tecto-bulbo-spinal tract. No ascending axonal projections exist. Type 2 neurons have horizontally oriented spindle-shaped somata and a wide dendritic tree that forms up to four laminae in layer 9, the uppermost lamina overlapping with laminae A/B of retinal afferents. Type 3 neurons have pear-shaped or pyramidal somata; their dendritic tree arborizes in the deeper two laminae inside layers 9 and 8. Both types of neurons have axons ascending to the ipsilateral praectum and thalamus, while the descending axon remains ipsilateral, constituting the *uncrossed* tecto-bulbo-spinal tract. Type 4 neurons have long and slender primary dendrites arborizing in the upper two retino-recipient laminae. They appear to have the same axonal projection pattern as types 2 and 3 neurons. Type 5 neurons have a primary dendrite that divides at the border between the periventricular gray and the white matter in a T-shaped fashion into several horizontally extending secondary and tertiary dendrites, which are mostly confined to layer 7. These neurons again have (mostly bilaterally) ascending and (exclusively ipsilaterally) descending projections. There are a number of types of tectal interneurons, (i.e., cells with no axons or axons that do not leave the tectum), that together seem to constitute about 95% of tectal cells. These five types of projection neurons are largely consistent with the types described by Székely and Lázár (1976) in *Rana esculenta* on the basis of Golgi staining and Lázár et al. (1983) and Antal et al. (1986) by retrograde labeling using cobaltic lysine as a tracer.

In the salamanders *Plethodon* and *Hydromantes*, again five types of projection neurons, called TO1 to TO5, exist (B in Fig. 8.9): TO1 neurons arborize primarily in the uppermost layer (layer 1) of retinal afferents and less intensely in layer 3. They have no ascending axons; their descending axon arborizes bilaterally in the tegmentum and constitutes the *crossed* tecto-bulbo-spinal tract. TO2 neurons arborize primarily in the intermediate and deep layers of retinal afferents (layers 2 and 3). Their ascending axon projects to the praectum and thalamus, while their descending axon constitutes the *lateral uncrossed* tecto-bulbo-spinal tract. TO3 neurons arborize predominantly in the deep retino-recipient layer (layer 3) and in the efferent fiber layers (layers 4 and 5). They project to the praectum and thalamus; with their descending axons they contribute to the *uncrossed* tecto-bulbo-spinal tract. TO4 neurons arborize predominantly in layers 2 and 3 and have ascending projections to the praectum and thalamus; their ipsilaterally descending axon occupies a position lateral to the axons of TO2 neurons. TO5 neurons arborize in layers 1 and 2 or in all three layers of retinal afferents and have ascending projections; they either have no descending axons or these axons reach only the level of the nucleus isthmi. There are various subtypes of TO interneurons with respect to differences in dendritic arborization and stratification pattern, which constitute about 95% of tectal neurons.

In summary, despite the dramatic differences in overall morphology of the tectum, the cytoarchitecture and projection pattern of tectal neurons is essentially the same in frogs and salamanders. The same is true with respect to the response properties of tectal neurons. Recordings from the tectum of the toad *Bufo bufo* (Roth and Jordan, 1982) and the salamander *Hydromantes italicus* (Roth, 1982) under the same experimental conditions yielded no indication that the responses of anuran tectal cells to visual stimuli are more complex than those of salamanders.

THE FATE OF OTHER SENSORY SYSTEMS

There is no sign of reduction in the primary *olfactory* system of bolitoglossines compared with other amphibian taxa, whereas the accessory olfactory system appears to be simpler morphologically compared with salamanders with a biphasic life history, but the same "simple" appearance is found in frogs (Schmidt et al., 1988). The *somatosensory*, including the *proprioceptive*, system of plethodontid salamanders is similar to that of other salamanders and frogs as regards primary afferents, but shows remarkable differences with respect to the secondary pathways ascending to the mesencephalon and diencephalon (Dicke and Mühlenbrock-Lenter, 1998). There are more ascending tracts in *Plethodon* and bolitoglossines (*Hydromantes*, *Bolitoglossa*), and these tracts show substantial ipsilateral projections, whereas in the salamandrid *Pleurodeles*, ranid frogs, and *Xenopus*, projections are almost exclusively contralateral. Nothing precise is known about the *vestibular* system of salamanders.

In bolitoglossines, an *electroreceptive* and *mechanoreceptive lateral-line system* is absent, apparently because of their strict terrestriality, whereas all other salamanders possess both systems either permanently or during their aquatic stages. The *auditory system* of salamanders in general and of the Bolitoglossini in particular appears to be much simpler than in frogs. Most frogs have a well-developed auditory periphery with a tympanum and a single middle-ear bone (columella) that has a special extracolumellar extension to the tympanum. The tympanum is absent in some species of several families, and some of these species exhibit a reduction of the middle ear (e.g., *Bombina*; Stadtmüller, 1931; Smirnov, 1989). All salamanders lack an external ear (tympanum) and a middle ear cavity. One or two small middle-ear bones (operculum, columella/stapes) are fused to each other or to the otic capsule or are entirely lost (Hetherington, 1988). Most frogs have a well-developed inner ear with a papilla basilaris, the presumed homologue of the basilar lamina of amniotes, which is involved in the perception of high frequencies, and a papilla amphibiorum, a structure unique to the inner ear of amphibians and involved in the perception of low frequencies. The papilla basilaris is reduced in a number of salamander genera and is completely absent in all members of the family Plethodontidae (Lombard, 1977; Lewis and Lombard, 1988). The papilla amphibiorum is also reduced in size in plethodontids (Lombard, 1977).

In the medulla oblongata of nonbolitoglossine salamanders, the dorsal nucleus of the lateral-line sensory area receives information from the electroreceptive lateral-line system, and an intermediate nucleus receives afferents from mechanoreceptive neuromasts in its rostral portion and from the inner ear in its caudal portion, and the ventral nucleus has only vestibular functions. A dorsal and intermediate nucleus are absent in the bolitoglossines. Nonbolitoglossine salamanders have a migrated superior olive and a torus semicircularis that shows some degree of lamination; both structures are important auditory centers. In bolitoglossines, the superior olive is unmigrated and the torus semicircularis un laminated, and both are morphologically indistinct.

In frogs, no dorsal nucleus and no rostral intermediate nucleus exist, whereas the caudal intermediate nucleus is present (Fritzsche et al., 1984; Will, 1988). In addition, there is a dorsolateral nucleus unique to anurans that receives afferents only from the papilla amphibiorum and serves as the main auditory center. The superior olive is found in a migrated position. The torus semicircularis consists of five subnuclei showing extensive cell migration and lamination. An exception is *Bombina orientalis*, in which the torus is unmigrated (Walkowiak, W., University of Köln personal communication, 1996).

In summary, in bolitoglossines some sensory systems such as the visual, somatosensory, and olfactory systems, apparently are in a structural and functional state comparable or even superior to those of other salamanders and to frogs, while other sensory systems, such as the auditory system, show strong reduction or are completely lost, such as the electro- and mechanosensory system.

CAUSES AND CONSEQUENCES OF SIMPLIFICATION IN THE CONTEXT OF PAEDOMORPHOSIS

A simple morphology characterized by the partial to complete absence of certain traits may represent a primitive (plesiomorphic) state, or it may be simplified or lost. One way in which a trait can be lost phylogenetically is secondary simplification, as, for example, may happen when an ontogenetic trajectory is truncated or when the rate of development is slowed to the point that sexual maturation occurs before morphology has attained the degree of development characteristic of ancestral and closely related forms. To determine if absence is primary or if it is a secondary loss, a phylogenetic analysis is required. For salamanders this necessitates knowledge of the ontogeny and adult morphology of relevant outgroups (viz., caecilians, anurans, amniotes, lungfishes, coelacanths, bony fishes, cartilaginous fishes, and lampreys) (cf. Fig. 8.1A). For a given character and depending on phylogenetic topology, if more than half of the outgroups for which the character state is known are more complex than salamanders, then the hypothesis that the character is secondarily simplified in salamanders is more parsimonious than the hypothesis that it is plesiomorphically simple in salamanders. In such a cladistic analysis based on 23 neural characters, Roth et al. (1993) demonstrated that salamanders are indeed secondarily simplified. Furthermore, among salamanders (Fig. 8.1B), species of the plethodontid tribe Bolitoglossini have the lowest degree of lamination and cell migration in the brain and exhibit the highest degree of secondary simplification. A parallel case of secondary simplification of the central nervous system are the American and African lungfishes (*Lepidosiren* and *Protopterus*, Dipnoi, family Lepidosirenidae). Whereas the Australian lungfish *Neoceratodus*, the coelacanth *Latimeria*, and actinopterygian fishes have more complex brains, including a multilaminated tectum mesencephali, the brain and particularly the tectum of lepidosirenids are as simple as those of salamanders (Northcutt, 1987).

Roth et al. (1993) argued that secondary simplification arises from *paedomorphosis*, a form of heterochronic evolution in which traits that characterize juveniles of

ancestral taxa appear in the adult stage of descendant taxa. Pedomorphosis commonly involves different degrees of retardation, reduction, or absence of traits in adult organisms as compared with phylogenetic outgroups (Gould, 1977; McKinney and McNamara, 1991). Thus, a mosaic of fully developed (adult) traits, weakly expressed traits, and missing characters appears in adult stages of pedomorphic animals.

What are the reasons for simplicity of the salamander and particularly the bolitoglossine brain? How can the apparent paradox be solved that those salamanders showing the most sophisticated visual behavior among amphibians (i.e., the Bolitoglossini) have the simplest brain morphology among vertebrates?

The hypothesis presented here is that the observed differences in the morphology of the central nervous system between salamanders and lepidosirenid lungfishes (and to a lesser degree caecilians and a number of frogs) on the one hand and other vertebrate taxa on the other are largely a consequence of *differences in genome and cell size*. Genome size refers to the amount of DNA, here given for haploid genome (note that some authors, e.g., Olmo [1991], report *diploid* genome sizes). Differences in genome size among vertebrates are not due to polyploidy (which occurs in some populations of amphibians, but is absent in bolitoglossines), but to an increase in noncoding, mostly middle-repetitive DNA sequences (Horner and MacGregor, 1983; Olmo, 1991).

Genome size varies enormously among organisms. Among vertebrates, the smallest genome is found in teleost fishes, with less than 1 pg DNA per haploid nucleus, while lungfishes (Dipnoi) have genome sizes up to 142 pg, the largest genomes found in any animal (Olmo, 1983). Among salamanders, the smallest genome (13.7 pg) is found in the plethodontid *Desmognathus wrighti* (Hally et al., 1986; Sessions, 1984; Sessions and Larson, 1987) and the largest (83 pg) in the neotenic (perennibranchiate) *Necturus maculosus* (Olmo, 1983). The plethodontid salamander *Hydromantes italicus* (77 pg) appears to have the largest genome of any terrestrial animal, although several tropical bolitoglossine plethodontids (e.g., *Bolitoglossa subpalmata*, 64 pg) approach this value (Sessions and Larson, 1987). Species of the Bolitoglossini, on average, have larger genome sizes than other plethodontids and than other salamander families, except for the neotenic/perennibranchiate species (Olmo, 1983; Sessions and Larson, 1987).

Caecilians (Gymnophiona) also have relatively large genomes, but the largest known caecilian genome (13.2 pg per haploid nucleus; M. Wake, University of California, Berkeley, personal communication, 1998) is less than the smallest found in salamanders (13.7 pg). The smallest genome size among anurans (about 1 pg) is found in *Limnodynastes ornatus*, and the largest is found in *Arenophryne rotunda* (19 pg; Roberts, in litteris.). Although frogs generally have the smallest genome sizes among amphibians, *Bombina orientalis* has a relatively large genome (10 pg; Olmo, 1983) and shows clear signs of secondary simplification in neural as well as non-neural characters (see above). Caecilians have genome sizes intermediate between those of salamanders and anurans and have many secondarily reduced neural and non-neural characters (Schmidt and Wake, 1997). From the few characters studied in detail, the degree of simplification of caecilians appears to lie between that of anurans and salamanders.

A phylogenetic analysis reveals that an increase in genome size has occurred independently in lungfishes and amphibians as well as within the three amphibian orders Anura, Caudata, and Gymnophiona (Olmo, 1991). Furthermore, even among

plethodontid salamanders (Fig. 8.1C), genome size appears to have increased several times independently (Sessions and Larson, 1987), especially in the tribes Plethodontini and Bolitoglossini. In all cases studied, the increase in genome size has the same important morphological consequences, including (1) increase in cell size; (2) decrease in cell metabolic rate; (3) decrease in cell division rate; and (4) decrease in cell differentiation rate (Van't Hof and Sparrow, 1963; Goin et al., 1968; Olmo, 1983; Sessions and Larson, 1987). These consequences lead to animals that have (1) large cells, (2) low metabolic rates, (3) few cells, (4) slow growth and slow differentiation processes, and (5) morphologies that appear to be simple, but rather are the result of *secondary simplification*.

Although the correlation between genome size and cell size is robust, that between genome size and metabolic rate in salamanders has been questioned by Licht and Lowcock (1991) on the grounds that previous studies were carried out *in vitro*. They used data from Gatten et al. (1991) for active animals, based on measurements of standard metabolic rates ($\mu\text{l O}_2/\text{g/hr}$) at 5°, 15°, 20° and 25°C to show a marginally significant correlation ($p < 0.02$) with genome size at 15°C and a significant correlation ($p < 0.001$) at 25°C, but not at the two other temperatures. They argue that a temperature of 25°C is unusually high for most urodeles and close to a lethal limit for amphibian development. Tropical bolitoglossines are, however, regularly active at such temperatures (e.g., *Bolitoglossa occidentalis*, *B. rufescens*), and Mexican ambystomatid salamanders have been recorded at temperatures in excess of 25°C on a number of occasions (Feder et al., 1982). Unfortunately, Licht and Lowcock included only three species of tropical salamanders in their study, and their data on metabolic rates of these species were incomplete.

The correlation between genome and cell size arises from the fact that large amounts of DNA lead to large nuclei and consequently to large cell volumes. Recently, Roth et al. (1994) studied the effect of genome and cell size in the brains of 22 species of salamanders and 19 species of frogs. There was a significant correlation between genome size and tectal cell diameter. In frogs, morphological complexity of the tectum was negatively correlated with cell size, while brain size was correlated with neither cell size nor morphological complexity. This means that frogs with smaller cells have more complex tecta (as well as other brain centers) independent of brain size. In salamanders, the degree of morphological complexity of the tectum was again negatively correlated with cell size, but in addition brain size was correlated with body size and with cell size (i.e., salamanders with larger brains tend to have larger cells and those with smaller brains have smaller cells).

Among anurans, the least complex morphologies of the tectum as well as of other parts of the brain were found in the species *Arenophryne rotunda* and *Bombina orientalis*—two species that have the largest and second largest genomes and cells among frogs studied thus far and are considered to be highly paedomorphic based on non-neural as well as neural characters (Smirnov, 1989; Roberts, *in litteris*); (Fig. 8.7c,d). Conversely, frogs with small genomes and cell sizes such as *Limnodynastes ornatus* and *Eleutherodactylus coqui* have very complex tecta (Fig. 8.7a,b). Among salamanders, small-sized species with relatively large cells but small brains such as *Batrachoseps attenuatus* and *Thorius narisovalis* have the least complex brains, but

larger sized bolitoglossines with very large genomes and cells such as *Hydromantes italicus* exhibited similarly "simple" brain morphologies. On the other hand, larger sized salamanders with relatively small genome and cell sizes like *Ambystoma mexicanum* have the most complex brains among urodeles, and those with intermediate genome and cell sizes like *Plethodon jordani* exhibit intermediate degrees of morphological complexity (Fig. 8.7e,f).

It is presently unknown how increased genome size leads to retardation of brain development. There may be general effects of increased DNA replication times and, accordingly, longer cell cycle times or the effect of low metabolic rate on brain development, or more specific effects such as retarded expression of developmental genes or disturbance of epigenetic tissue interactions. Studies in our laboratory point to differences in the spatial and temporal pattern of upregulation and downregulation of cell surface and cell adhesion molecules between frogs and amniotes on the one hand and salamanders on the other (T. Becker et al., 1993; C.B. Becker et al., 1993). Not all developmental processes in the amphibian brain are retarded to the same degree. Rather, it seems that developmental processes that occur early in development are less affected than are those occurring late, which are either strongly retarded or are lacking entirely. This effect is combined with the degree of genome size increase (i.e., retardation or lack of late processes is more pronounced in species with larger genomes). The dorsal telencephalon is a late-differentiating brain structure and seems to be most affected by retardation. In all three orders of amphibians, it is very simply organized and is usually considered the morphologically least complex among gnathostome vertebrates except lepidosirenid lungfishes (Northcutt, 1987), although anurans have a somewhat more complex telencephalon than salamanders. Another late-developing brain structure is the cerebellum. Compared with most other vertebrates, it is small in anurans, even smaller in salamanders with relatively small genome sizes, and smallest in salamanders with large genomes. In contrast, the tectum and diencephalon develop relatively early, and accordingly both structures are less simplified in frogs than in salamanders (and lepidosirenid lungfishes), with caecilians ranging in between. Finally, the same holds for the medulla oblongata and spinal cord, which generally develop very early. One of the latest events occurring here is the formation of a lateral motor column due to the migration of secondary motor neurons from medial to lateral (Nishikawa et al., 1991). Accordingly, all frogs and those salamanders with small genome sizes have a well-developed lateral motor column, whereas species with large genome sizes (i.e., the Bolitoglossini) have functional "lateral" motor column neurons that fail to migrate.

Increases in genome and consequently cell size have happened many times in the animal kingdom (as well as among plants) and invariably led to increased developmental times and paedomorphic morphologies. There is no universal agreement on the origin and significance of increased genome size in vertebrates. According to the selfish DNA hypothesis (Ohno, 1972; Doolittle and Sapienza, 1980; Orgel and Crick, 1980), genome size tends to increase until this tendency is halted by countervailing selection. This would mean that an increase in genome size is a purely genomic event with no advantage or even with strong disadvantage for the organism, which has to compensate for any disadvantages in order to survive.

Attempts have been made by Szarski (1983) to view an increase in genome size in salamanders as an adaptation for survival in harsh environments ("frugal" strategy): Large genomes lead to large cells, which lead to low metabolic rates requiring less oxygen supply and less investment into nutrition. It is true that salamanders in general have very low oxygen demands (a factor that makes their cells very suitable for in vitro studies) and that they can survive for months without food intake. The latter allows them to retreat for extended periods of time into microhabitats where food is scarce (such as caves), and low demands of oxygen supply could be favorable for the lungless plethodontids, which exhibit the lowest metabolic rates among vertebrates. At the same time, such a "submergent" behavior (*sensu* Maiorana, 1976) minimizes exposure to predators, particularly given the fact that in the tropics predation intensity is extraordinarily high.

Another argument put forward by Szarski (1983) is that it must be more economical to build an organism from a smaller number of larger cells instead of using a large number of smaller cells. While the former arguments might be valid, the latter certainly is not, because salamanders with few and large cells develop very slowly and reach sexual maturity much later on average than other amphibians (up to 7 years in *Hydromantes italicus*). If there is a selective advantage of an increase in genome and cell size in the sense of a "frugal" strategy in salamanders in general and in bolitoglossines in particular, it is outbalanced by negative consequences such as retardation of development and simplification of the nervous system.

WHAT DO BOLITOGLOSSINES TELL US ABOUT EVOLUTION IN GENERAL AND BRAIN EVOLUTION IN PARTICULAR?

The case of bolitoglossines illustrates how a genomic, possibly nonadaptive event may deeply influence (via reproductive style and lifestyle) all levels of the life of an organism, including geographic distribution of the taxon to which it belongs. At the same time, we learn how organisms, during their "struggle for survival," developed compensatory mechanisms in order to circumvent the constraints resulting from an increase in genome size.

In the Bolitoglossini, we indeed find a unique combination of constraints resulting from an increase in genome size and its inevitable consequences for the organism as well as "tricks" that helped these animals to escape from the evolutionary trap. The first of such events was the evolution of lunglessness, which freed the hyobranchial apparatus from the constraint of serving as a lung pump, making a further evolution of the feeding function possible. The second step was the evolution of direct development and its opportunities, as explained above. Furthermore, direct development circumvents the formation of a complex larval hyobranchial apparatus. Both evolutionary steps—causally unrelated to each other—favored the formation of a specialized feeding apparatus (i.e. a free, projectile tongue). This was an important event because, due to their low metabolic rates, bolitoglossines are incapable of sustained fast locomotion in order to escape predators. Therefore, they had to become ambush

feeders. In this context, increased frontality of the eyes and an increase in direct ipsilateral retinotectal projections apparently formed the basis of excellent depth perception abilities required for the use of a projectile tongue during ambush feeding. Ambush feeding and direct development facilitated arboreal life or terrestrial life in caves (it is hard to be an active hunter while climbing on trees or on the walls of caves).

What are possible compensatory processes in bolitoglossines for the observed simplicity of brain morphology and the strongly reduced number of neurons? As to simple morphology, it is to date not completely clear what functional significance the opposite situation (*viz.*, a high degree of lamination and the formation of migrated nuclei or columnar structures) has. Separation of input and output and parallel processing of information may be facilitated by lamination, formation of nuclei, and columns, but there are numerous examples where complex information processing may happen in un laminated nerve tissue as well (e.g., un laminated dorsoventricular ridge in birds vs. laminated isocortex in mammals; Nieuwenhuys et al., 1998). In the amphibian tectum, the degree of lamination is strictly correlated with the number of afferent fibers and tectal neurons (see above), and it may be that tecta with a low number of afferent fibers and tectal neurons simply do not “need” a strict separation of input, output, and information processing modules. Thus, the most striking morphological difference between bolitoglossine salamanders and most other vertebrates may be a consequence of the reduction in cell proliferation rate.

Nevertheless, the fact remains that bolitoglossines have very few neurons in their brains and sensory systems—probably the fewest compared with other vertebrates with functioning sensory systems. The entire brain of most salamanders contains less than 1 million neurons (*i.e.*, less than the brain of a honey bee). Frogs may have 5 to 10 times more neurons in their brains. Mathematical modeling and computer simulation of neuronal functions demonstrate that very smart sensory, motor, and even simple cognitive functions can be achieved by networks composed of relatively few neurons. A principle that in this context is particularly relevant in bolitoglossines is *population coding*. This principle means that certain kinds of information are not processed separately by specialized (“dedicated”) neurons, but involve the joint activity of neurons with partially overlapping response properties. One great advantage of neuronal networks based on population coding is the robustness of their functions against reduction in the number of participating neurons. In plethodontid salamanders, such population coding is assumed to be present in the recognition and localization of objects (Eurich et al., 1995; Roth et al., 1998), and it has been shown by computer simulation that these functions are not dramatically reduced even when the number of neurons involved is reduced by 50% (Eurich et al., 1995). Thus, effective object recognition and localization may be accomplished by a relatively low number of neurons.

Population coding does not, however, always have the same power as networks containing many “dedicated” neurons with more specialized functions. This seems to be particularly true, when, for example, high spatial visual resolution or vision at distance is needed. Recent studies comparing *Bombina* and *Hydromantes* indeed demonstrate that the frog is better in both functions than the salamander (Göckel and Roth, 1998). A remarkable feature of the bolitoglossine visual system in this context

is that it is restricted to frontal vision. Whereas many amphibians have 360° vision (some frogs even have a caudal binocular field) and eagerly respond to prey objects situated in the caudal visual field, this is not observed in bolitoglossines. Such a restriction to frontal vision was permitted only by changes in feeding strategy from hunting to ambush feeding. Inside the brain of bolitoglossines, two-thirds of tectal neurons have frontally oriented receptive fields and constitute a relatively large binocular field. This dedication of tectal neurons to frontal vision enhances the otherwise poor spatial resolution power (e.g., in the context of stereoscopic vision). The presence of an increased number of direct ipsilateral retinotectal terminals may further increase the resolution power. At the same time, the distance at which bolitoglossine salamanders reliably respond to prey items with orienting behavior is reduced from more than 1 m in most frogs to about 30 cm. In combination with the fact that visual neurons respond to angular rather than absolute size, this reduction in response distance increases visual acuity by a factor of 3 to 4.

Finally, networks being composed of large numbers of neurons seems to be required for complex and fast learning and memory formation going on in the juvenile and adult brain (i.e., beyond early imprinting processes). Students of amphibian behavior constantly noticed that the learning abilities of juvenile and adult amphibians are limited to a few domains (e.g., the distinction between palatable and noxious food items or finding their way back to their territory). Cross-modal information transfer seems to be particularly poor (e.g., from olfactory to visual). It may, thus, well be that reduction in sensory and behavioral plasticity is the price that animals with a reduced number of neurons in their brains and sense organs must pay for escaping the evolutionary trap constituted by an increase in genome size.

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