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HOW DO ONTOGENY, MORPHOLOGY, AND PHYSIOLOGY OF SENSORY SYSTEMS CONSTRAIN AND DIRECT THE EVOLUTION OF AMPHIBIANS?

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Abstract.—The evolutionary success of extant amphibians is accompanied by secondary simplification of sense organs and of the nervous system. Strong morphological reduction is found in the lateral line system and in the auditory and visual systems. Canal neuromasts are absent; additional loss of epidermal neuromasts and ampullary organs generally corresponds to terrestrial life. Reduction of the auditory system of some anurans and of many salamanders and caecilians affects middle and inner ear structures as well as central auditory structures. The visual system of caecilians and salamanders is strongly reduced with respect to the number and morphology of retinal ganglion cells and the morphological differentiation of central visual areas, particularly the tectum opticum. The extremes of secondary simplification are found in the salamanders of the plethodontid tribe Bolitoglossini. At the same time, these salamanders are one of the most successful groups of amphibians, and they possess the most derived feeding system and a variety of specializations of the visual system. In amphibians, there is a close correspondence between the degree of secondary simplification on the one hand and genome size (DNA content) and cell size on the other. We hypothesize that this process is the major cause of the observed secondary simplification.

Amphibians (frogs [Anura], salamanders [Caudata], and caecilians [Gymnophiona]) are a diverse and successful group of vertebrates. There are about 3,500 species of frogs, 360 species of salamanders, and 170 species of caecilians (Frost 1985). On the basis of recent morphological and biochemical studies, living amphibians are thought to be a monophyletic group (the Lissamphibia) and to be the living sister taxon of the Amniota (De Queiroz and Cannatella 1987; Trueb and Cloutier 1987).

Among anurans, recent cladistic analysis distinguishes four groups: (1) the discoglossoids, a grade that includes primitive families such as Bombinatoridae (e.g., Ascaphus, Leiopelma, Bombina) and Discoglossidae (e.g., Alytes, Discoglossus), (2) Neobatrachia, including Ranidae, Bufonidae, and Leptodactylidae, (3) Pipoidea (e.g., Xenopus, Pipa), and (4) Pelobatoidea (e.g., Pelobates, Scaphiopus). There is some debate over which of the latter three groups are considered the most derived.

The six families of caecilians include the primitive families Rhinatrematidae, Ichthyophiidae, and Uraeotyphlidae and the derived families Scolecomorphidae, Caeciliidae, and Typhlonectidae (Nussbaum 1977).

Living salamanders are generally believed to be monophyletic (Hecht and Ed-

wards 1977; Duellman and Trueb 1986; Larson 1991). On the basis of many mor-
phological studies, the family Plethodontidae is believed to have the largest num-
ber of derived, or apomorphic, traits; that is, it is believed to be the "most
evolved" group. Among plethodontids, the tribe Bolitoglossini, including all trop-
ical salamanders, is believed to be the most derived group (D. B. Wake 1966;
Hecht and Edwards 1977; Duellman and Trueb 1986). The family Plethodontidae
comprises about two-thirds of all salamander species, and about two-thirds of
plethodontids are bolitoglossines (D. B. Wake 1966; Frost 1985).

Amphibians exhibit a high ecological diversity. They occupy habitats in water,
on land, in trees, underground, in caves, and so forth. In addition, they possess
an unusually high diversity of reproductive strategies and life histories: external
and internal fertilization, egg laying, aquatic larvae, terrestrial larvae, direct de-
velopment with or without metamorphosis, live birth, and many kinds of brooding
behavior and parental care (Duellman and Trueb 1986).

In contrast to this diversity, amphibians have long been considered primitive
tetrapods, and salamanders in particular have been viewed as being among the
most primitive vertebrates. However, decades ago, leading comparative morphol-
ogists and neuroanatomists such as Herrick (1948) and Romer (1970) had already
hypothesized that modern amphibians (Lissamphibia) have many derived charac-
ters and may have undergone secondary simplification with respect to their laby-
rinthodont ancestors. As we discuss below, this idea is supported by the study
of sensory systems and the brain. The reasons for such secondary simplification
are not fully understood; in this article, we present the hypothesis that it is a
consequence of an increase in genome size. If this hypothesis is correct, many
of the important characters of amphibian sensory and nervous systems must be
viewed as the result of developmental constraints rather than as adaptive features.

SENSORY SYSTEMS OF AMPHIBIANS

In the plesiomorphic state, amphibians possess all of the major sensory systems
found in other groups of anamniote vertebrates (i.e., olfactory, somatosensory,
auditory, vestibular, mechanoreceptive and electroreceptive lateral line, and vi-
sual systems). It is often thought that the evolutionary success of a group of
animals is related to an increase in the morphological complexity and physiologi-
cal efficiency of its sensory systems. Indeed, the history of vertebrates is filled
with examples of spectacular sense organs that are believed to be responsible for
the adaptive radiation of the groups that possess them (Ryan and Keddy-Hector
1992). Some examples include the infrared detection system of snakes, the echo-
location system of bats, and the magnetic sense of birds. Furthermore, the evolu-
tionary success of tetrapods and especially amniotes is often attributed to an
increase in the relative size and morphological complexity of the brain.

In the following sections, we discuss the apparent paradox of evolutionary
and functional morphology: the evolutionary success of extant amphibians is
accompanied by the remarkable process of secondary simplification of sensory
systems and of the nervous system. This simplification has occurred indepen-
dently many times, although the degree of reduction varies substantially among

different groups of amphibians and different sensory systems. The most dramatic example of this paradox is found in the bolitoglossine salamanders. It is this group that, on the one hand, shows a spectacular adaptive radiation and extreme specialization within the Neotropics but, on the other hand, shows extreme cases of secondary morphological reduction both inside and outside the nervous system. We therefore discuss the case of the Bolitoglossini in greater detail.

Nothing is known about any substantial variation in the somatosensory and vestibular systems among amphibians. Thus, we do not discuss these two systems. A more complete discussion of these topics (containing full anatomical data) with respect to secondary simplification in salamanders is in preparation.

Olfactory System

Amphibians possess a dual olfactory system: the olfactory system proper, contained in the olfactory bulb, and the accessory or vomeronasal system, situated in a bulb caudal to the main olfactory bulb. The primary olfactory system is thought to be involved in the detection of prey and enemy odor, whereas the accessory olfactory system apparently serves for intraspecific communication (territorial and mating behavior; Dawley 1984; Jaeger 1986; Houck and Reagan 1990). This dual system is relatively well developed in all amphibians, whether aquatic or terrestrial, with the remarkable exception of the neotenic cave-dwelling salamander *Proteus anguinus,* which is reported to possess no vomeronasal system (Seydel 1895). There are, however, shifts in the relative sizes of the primary and accessory olfactory systems. Some salamander species (plethodontine and bolitoglossine plethodontids) have a relatively large primary and a relatively small accessory olfactory system, whereas in other species (desmognathine and hemidactyliine plethodontids, salamandrids) the reverse situation is found (Schmidt et al. 1988).

Lateral Line System

In the plesiomorphic state of gnathostome vertebrates, the lateralis system consists of a mechanoreceptive system with both canal neuromasts and epidermal neuromasts and an electroreceptive system with ampullary organs (Northcutt 1984a; fig. 1). Although all amphibians lack canal neuromasts, this plesiomorphic state undergoes changes in different amphibian groups with respect to epidermal neuromasts and ampullary organs.

Among salamanders, three different groups can be distinguished with respect to the degree of development of the lateral line system (Wake et al. 1987; Fritzsch 1989): (1) species with aquatic larvae and aquatic to semiaquatic adults that possess epidermal neuromasts and ampullary organs throughout life (Cryptobranchidae, Hynobiidae, Proteidae, Amphiumidae, and some isolated representatives of other families) or have organs that disappear periodically, (2) species with aquatic larvae and a terrestrial stage that either retain epidermal neuromasts and ampullary organs throughout life or lose them at metamorphosis, and (3) live-bearing or directly developing terrestrial species that either transiently possess neuromasts and ampullary organs (*Salamandra atra*) or never possess them (the plethodontid tribes Plethodontini and Bolitoglossini). A distinct dorsal nucleus receiving
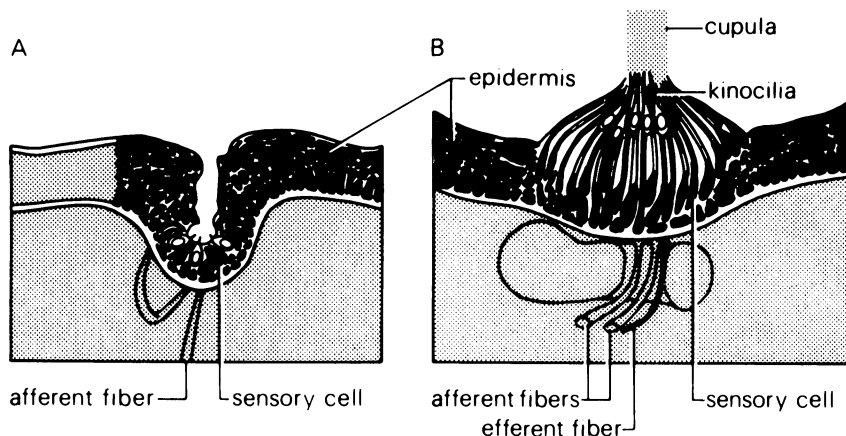
Fig. 1.—Structure of amphibian lateral line organs (salamander *Triturus alpestris*). *A,* Ampullary organ of the electroreceptive system; *B,* epidermal neuromast of the mechanoreceptive system. (From Duellman and Trueb 1986.)

lateral line afferents is present within the medulla oblongata in all species except the directly developing bolitoglossines, which lack both electroreceptive and mechanoreceptive organs (Fritzsch 1989).

In caecilian species with aquatic to semiaquatic larvae and terrestrial adults, epidermal neuromasts and ampullary organs are lost at metamorphosis (Hetherington and Wake 1979; Fritzsch and Wake 1988). Viviparous species with aquatic adults never develop neuromasts but retain ampullary organs throughout life. Strictly terrestrial viviparous species develop neither neuromasts nor ampullary organs. Species with direct development and terrestrial adults have both epidermal neuromasts and ampullary organs (M. H. Wake, personal communication). The dorsal nucleus situated within the medulla oblongata and receiving the lateral line afferents is smaller in fossorial species (Fritzsch 1989).

Anurans lack ampullary organs. In some species with aquatic larvae and adults, neuromasts persist throughout life (e.g., *Xenopus*) or disappear at metamorphosis. They survive in some species with aquatic larvae and terrestrial adults (e.g., *Bombina*) or disappear at metamorphosis (most species). Neuromasts are retained throughout life in species with direct development and aquatic adults (e.g., *Pipa*), are transiently present in some species with direct development and terrestrial adults, or are absent throughout development (e.g., *Eleutherodactylus*). In all frogs, a dorsal nucleus is absent (Fritzsch 1989).

Auditory System

Most anurans have well-developed and highly specialized peripheral and central auditory systems (fig. 2). However, several groups of anurans have undergone reduction or loss of the middle ear (*Bombina;* Stadtmüller 1931). Both salamanders and caecilians have a simplified periphery in that they lack an external ear (tympanum) and a middle ear cavity. The middle ear bones are reduced, particu-
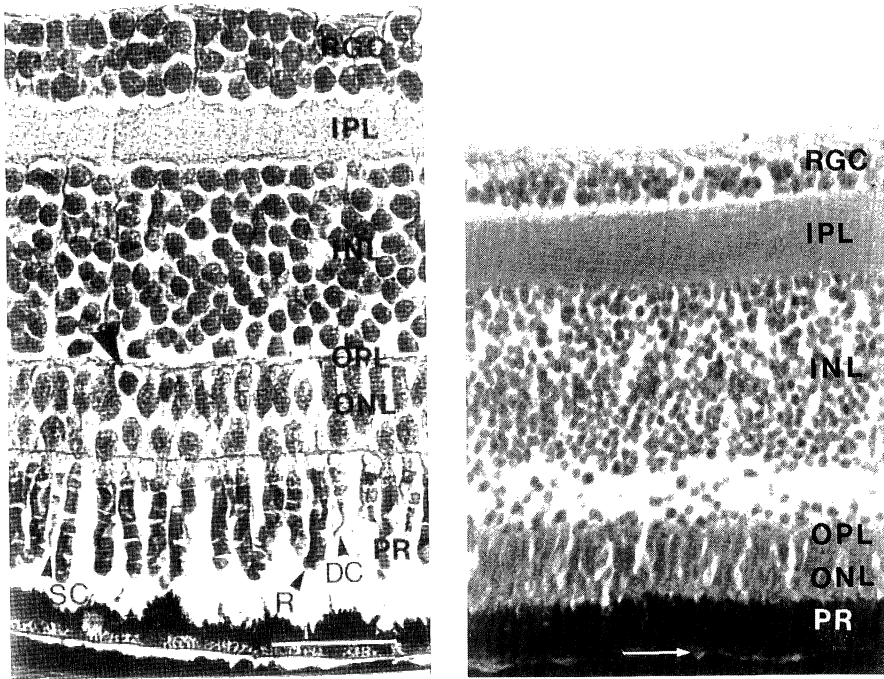
Fɪɢ. 3.—Comparison between the retinae of a salamander (*Plethodon cinereus; left*) and a frog (*Dendrobates tricolor; right*). Remarkably, *Dendrobates*, although having a much larger eye, has a thinner retina (211 μm) than *Plethodon* (264 μm). Note the more numerous, smaller cells in the frog as compared with the salamander. In *Dendrobates*, the photoreceptors are immersed in the dark pigment layer; the *white arrow* indicates the outer margin of the layer of photoreceptor outer segments. *R*, Rods; *SC*, single cones; *DC*, double cones and presumably one displaced bipolar cell (*large black arrowhead*); *INL*, inner nuclear layer; *ONL*, outer nuclear layer; *IPL*, inner plexiform layer; *OPL*, outer plexiform layer; *PR*, layer of photoreceptor outer segments; *RGC*, layer of retinal ganglion cells. Bars represent 50 μm.
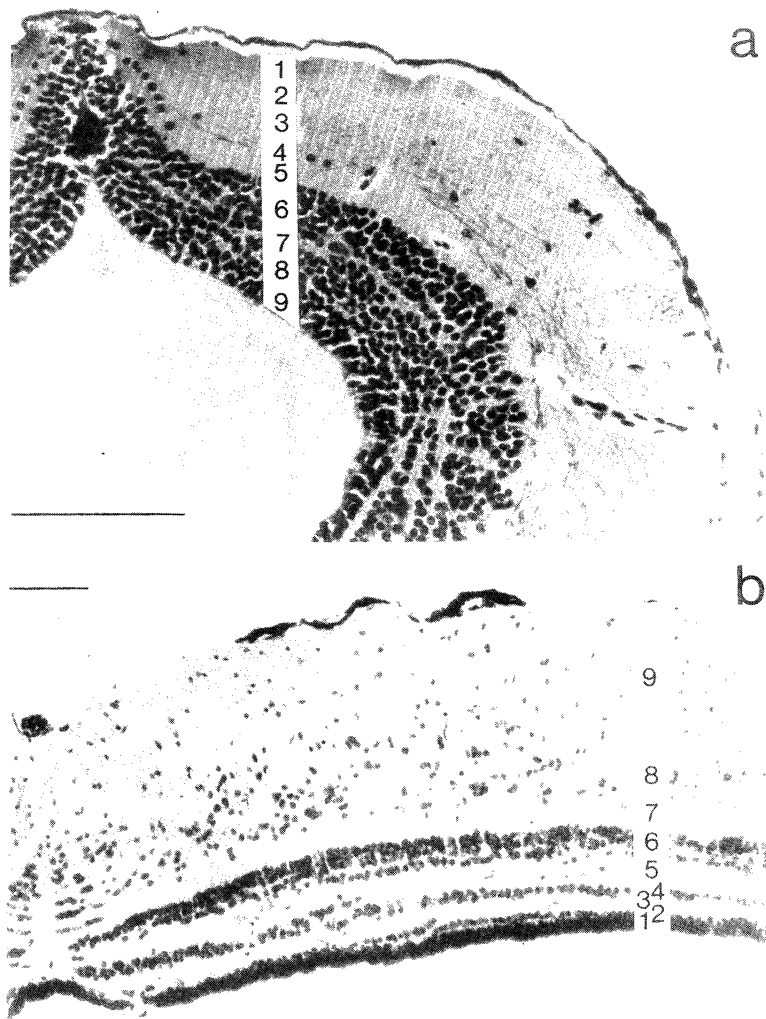
FIG. 4.—Comparison between the optic tecta of a salamander (*Pleurodeles waltl; a*) and a toad (*Bufo bufo; b*). Transverse sections through the midtectum are shown. Numbers indicate tectal cellular and fiber layers for urodeles (Roth 1987) and for anurans (Potter 1969). Note the differences in cell size and number and horizontal lamination of the tectum, particularly with respect to cells migrated into the superficial tectal layers (layers 1–5 in salamanders, 7–9 in frogs), between the salamander and the frog. Bars represent 100 μm. (From Roth et al. 1990a.)

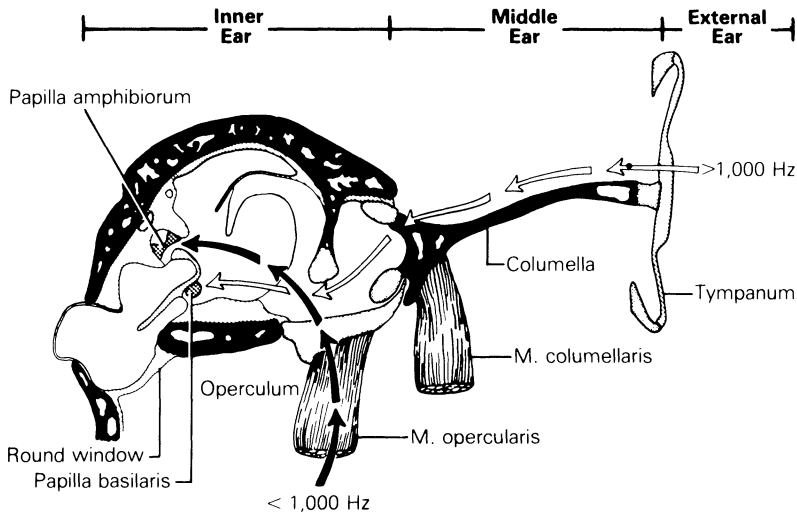Fig. 2.—Peripheral auditory system of amphibians. The diagram shows the ear of frogs, with indication of the two transmission pathways for low (musculus opercularis, papilla amphibiorum) and high (tympanum, columella, papilla basilaris) sound frequencies. Reductions of the ear in amphibians always affect the high-frequency pathway first. (From Duellman and Trueb 1986.)

larly in species of the salamander family Plethodontidae and in caecilians (Lombard 1977; Fritzsch and Wake 1988).

The plesiomorphic state of the auditory epithelia of amphibians is represented by the presence of two papillae: a papilla basilaris, specialized for sound frequencies between 1,000 and 5,000 Hz, and a papilla amphibiorum, unique to amphibians, specialized for low-frequency sounds between 20 and 1,000 Hz. Most frogs have a well-developed papilla basilaris and papilla amphibiorum. However, in frogs with a reduced middle ear, a reduction is found in the size of the papillae and in the number of hair cells (Walkowiak 1980; Will and Fritzsch 1988). Among salamanders, the papilla basilaris is reduced in a number of genera and is absent in some salamandrids and all members of the families Plethodontidae, Sirenidae, and Proteidae (Lombard 1977; Lewis and Lombard 1988). In caecilians, too, a number of species lack a papilla basilaris. The papilla amphibiorum of both salamanders and caecilians is simplified compared to that of anurans; it has only one instead of two patches of neuroepithelium (Lewis 1981, 1985). The intermediate nucleus of the medulla oblongata is considered to be the auditory nucleus of salamanders and caecilians, but it is missing in bolitoglossine salamanders. Frogs also lack an intermediate nucleus, but they possess a unique dorsolateral nucleus that serves as the main auditory center (Fritzsch 1988; Will and Fritzsch 1988).

Visual System

Whereas caecilians are characterized by a strong reduction of both the peripheral and the central visual system (M. H. Wake 1985), most frogs and salamanders

depend heavily on the visual system, especially in the context of feeding behavior (Roth 1987). Nevertheless, salamanders generally show strong morphological reduction of their visual system, and even the visual system of frogs must be considered reduced, at least to some degree, compared with that of other vertebrates.

Reduction of the visual system of amphibians concerns the number of receptor cells and neurons, the number of morphologically distinct types of neurons, the degree of morphological differentiation of nerve cells, the number of retinofugal visual projection areas, and the degree of morphological differentiation of visual areas.

Extensive quantitative data are available only on the visual systems of anurans and salamanders. Therefore, we restrict the following discussion mainly to anuran and urodele amphibians.

In amphibians, as well as in all other groups of vertebrates, the retina represents the first level of processing of visual information. The retinal ganglion cells send their axons, constituting the optic nerve and tract, to four different parts of the brain: the thalmus, the pretectum, the optic tectum, and the tegmentum of the midbrain. Here, the endings of the optic tract fibers form so-called retinofugal projection sites.

Retina.—Frogs and salamanders possess the same general organization of the retina (i.e., the same layered structure and the same types of neural elements): photoreceptors (rods, cones, double cones), four types of interneurons (horizontal, bipolar, amacrine, and interplexiform cells), and retinal ganglion cells (for an overview see Roth 1987; fig. 3 [see p. S109]). However, salamanders have fewer retinal cells than frogs. For example, in anurans, the number of retinal ganglion cells and, accordingly, of optic nerve fibers ranges from about 60,000 in *Xenopus* (Wilson 1971) to 470,000 in *Rana pipiens* (Maturana 1959). In salamanders, by contrast, retinal ganglion cells range between 25,000 in *Batrachoseps* (Linke and Roth 1989) and 75,000 in *Notophthalmus* (Ball and Dickson 1983). The reduced eye of the caecilian genus *Typhlonectes* has about 4,000 retinal ganglion cells (Fritzsch et al. 1985). The degree of myelination of optic nerve fibers ranges from 7% to 14% in anurans (Maturana 1959; Wilson 1971; Dunlop and Beazley 1984) and from 0% (*Batrachoseps*) to 7% (*Notophthalmus*) in salamanders. Bolitoglossine salamanders generally have the lowest degree of myelination of optic nerve fibers (0%–4%; Linke and Roth 1990).

In addition, salamanders possess fewer morphologically distinct types of retinal ganglion cells than frogs. In salamanders, there are four types of ganglion cells, which differ in size and shape of the soma and the dendritic tree and in the pattern of dendritic arborization within the inner plexiform layer. This arborization pattern determines the neurophysiological response properties of the cells (Linke and Roth 1989). In anurans, five to seven different morphological types of retinal ganglion cells have been described (Kalinina 1976; Frank and Hollyfield 1987), although the pattern of lamination within the inner plexiform layer is the same. In addition, retinal ganglion cells in salamanders give the appearance of a somewhat immature morphology compared with those of frogs (Linke and Roth 1989).

Retinofugal projections.—The system of terminal sites of optic nerve fibers within the frog brain includes two thalamic (neuropil Bellonci, geniculate thalamic neuropil) and two pretectal (uncinate field, "posterior thalamic," or pretectal neuropil) termination sites as well as a projection to the mesencephalic tectum ("tectum opticum") and to the tegmentum (basal optic neuropil) (Fite and Scalia 1976). Salamanders have the same general pattern but possess two neuropils Bellonci, a medial and a lateral one (Fritzsch 1980). Plethodontids, among salamanders, and bolitoglossines, among plethodontids, have the highest degree of morphological differentiation of retinofugal projection sites (Rettig and Roth 1986). In caecilians, retinofugal projection sites include a thalamic and a pretectal area, in addition to the projections to the tectum and the tegmentum (Clairambault et al. 1980; Fritzsch et al. 1985).

In all three orders of amphibians, the thalamic and pretectal visual neuropils receive input mainly from the contralateral eye, but a substantial number of afferent fibers comes from the ipsilateral eye. In contrast, the optic tectum of anurans receives mostly contralateral retinal afferents, and ipsilateral projections are very sparse (Fite and Scalia 1976). Salamanders, however, have a substantial amount of ipsilateral afferent fibers to the tectum, particularly from the temporal retinal quadrant to the rostral tectum, which corresponds to the frontal visual field. The most extensive ipsilateral retinofugal projections to the tectum are found in bolitoglossine salamanders (Rettig and Roth 1986). In caecilians, ipsilateral fibers are restricted to a small medial band (medial optic tract; Clairambault et al. 1980; Fritzsch et al. 1985; Himstedt and Manteuffel 1985).

Morphology and cytoarchitecture of the tectum.—In amphibians, the tectum is the main center for the convergence and processing of visual information. With respect to the overall morphology of the tectum, there is a striking difference between frogs on the one hand and salamanders (and caecilians) on the other (figs. 4 [see p. S110], 5). In frogs, the tectum exhibits a distinct multiple lamination consisting of nine alternating fiber and cellular layers (according to the nomenclature of Potter 1969). In comparison with teleosts (Vanegas et al. 1984), reptiles (Northcutt 1984b), and birds (Hunt and Brecha 1984), frogs have a lower degree of tectal lamination.

The following morphological types of tectal neurons have been described in ranid and bufonid anurans (Szekely and Lazar 1976; Lazar et al. 1983): large pear-shaped cells, small pear-shaped cells, pyramidal cells, and large ganglionic cells. In the tecta of other vertebrates, we often find a much larger number of morphological cell types, for example, up to 14 types in teleosts (Meek and Schellart 1978).

The tectum of salamanders as well as that of caecilians has an even simpler morphological organization, which consists of a periventricular zone of cell bodies and a superficial zone containing dendrites of neurons and afferent and efferent fibers. In salamanders, we find three morphological types of tectal neurons: small pear-shaped cells (type 3 cells), large pear-shaped cells (type 2 cells), and cells located in the upper part of the periventricular gray matter (type 1 cells; Roth et al. 1990a).

Despite the differences in gross morphology of the tectum, the morphology and
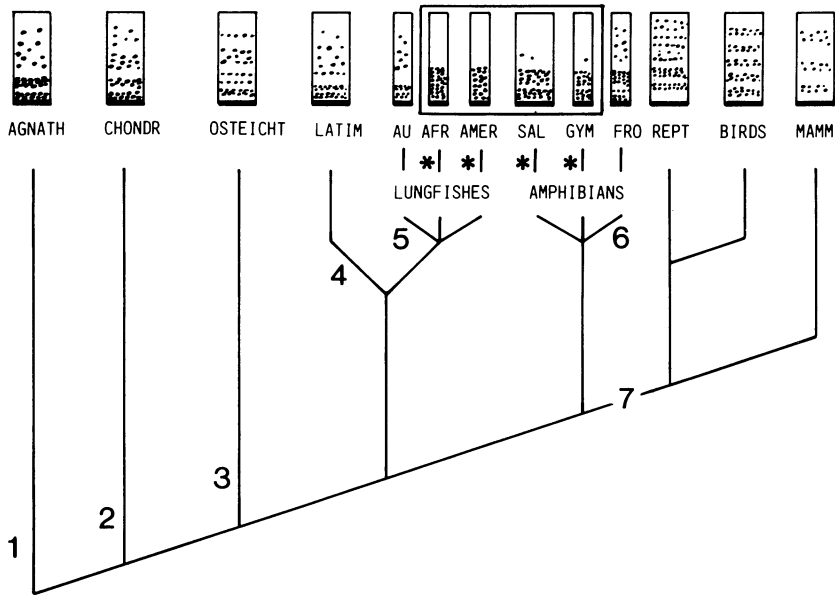
Fig. 5.—Phylogenetic diagram showing the pattern of cytoarchitecture of the optic tectum in representative groups of vertebrates (agnathans, chondrichthyans, osteichthyans [except sarcopterygians], Latimeria, Australian, African, and South American lungfishes, salamanders, gymnophiones, frogs, reptiles, birds, and mammals). The diagram demonstrates that a multilaminated tectum is found in all groups of vertebrates except lepidosirenid lungfishes (African and South American species), salamanders, and gymnophiones. The bilaminated tectum of these groups (indicated by asterisks) is assumed to be the result of secondary simplification in the context of paedomorphosis. If a bilaminated tectum represented the primitive (plesiomorphic) condition of vertebrates, a multilaminated tectum must have evolved independently at least seven times, as indicated by the numbers.

the projection pattern of the tectal cells of frogs and salamanders closely resemble each other (Roth et al. 1990a). Type 1 cells of salamanders correspond to the large ganglionic cells of anurans. The crossed and uncrossed tectobulbospinal tracts essential for visual guidance of behavior originate from these two types of cells. Type 2 cells of salamanders resemble large pear-shaped and pyramidal cells of frogs. They are involved in both descending and ascending pathways. Type 3 cells of urodeles and small pear-shaped cells of anurans are comparable and give rise to the tectothalamic and tectoisthmic tracts, or else they are local neurons ("interneurons").

The main difference between the two taxa is that frogs have many more tectal neurons within and above the main efferent layer (i.e., layers 8 and 9 of Potter 1969) than do salamanders. In the tectum of *Rana esculenta*, for example, roughly 30% of the neurons are found above the periventricular cellular layers (Szekely and Lazar 1976). In contrast, 4.9% of the tectal cells in *Salamandra* and 3.3% in *Pleurodeles* are located superficially. In the bolitoglossine plethodontids, this percentage ranges from 0.7% (*Thorius narisovalis*) to 1.6% (*Hydromantes italicus;* Roth et al. 1990a).

DISCUSSION

The Degree of Simplification

The data reported here clearly show the existence of regressive events within most of the sensory systems present in amphibians. Whereas nothing specific is known about the fate of the somatosensory and the vestibular systems, the accessory olfactory system of terrestrial plethodontid salamanders shows at least some reduction. Strong morphological reduction is found in the lateral line, the auditory, and the visual systems. Within the lateral line system, amphibians do not form canal neuromasts, which are present in all other groups of anamniote vertebrates except the strongly simplified, paedomorphic lepidosirenid lungfishes (*Protopterus, Lepidosiren;* Northcutt 1987). Additional loss of epidermal neuromasts and ampullary organs generally corresponds with terrestrial life, during both phylogeny (direct development or viviparity) and ontogeny (postmetamorphic terrestrial life). Striking exceptions are some caecilian species with direct development and terrestrial adults that possess both epidermal neuromasts and ampullary organs.

The auditory system of some anuran species and of many salamander and caecilian species undergoes strong reduction that mostly affects middle and inner ear structures. Central structures are affected only in those areas, such as the superior olive or the torus semicircularis, that are smaller in size and have a lower degree of morphological differentiation (e.g., with respect to lamination and cell migration).

The visual system is reduced with respect to the number of neurons and the degree of morphological differentiation of both central areas and single cells. In contrast, all visual nuclei and central processing areas are present in those frogs and salamanders that have a functional visual system.

The amphibian order with the lowest degree of simplification of neural structures is the Anura. Among amphibians, the anuran sensory system and the anuran brain in general are closest in morphological differentiation to those of other tetrapods. However, the anuran visual system, despite its high efficiency, has a simpler structure than that of teleosts, reptiles, and birds. The anuran forebrain, like that of urodeles and caecilians, is highly simplified compared to that of all other gnathostome vertebrates, including chondrichthyans, osteichthyans, reptiles, birds, and mammals (Northcutt 1981). Only lepidosirenid lungfishes, which are also considered to be secondarily simplified (Northcutt 1987), have a similarly "simple" forebrain. The auditory system of most anurans is highly derived (e.g., the apomorphic dorsolateral auditory nucleus), particularly in the context of reproductive and territorial behavior, but, even in the anuran auditory system, simplification of the middle and inner ear has occurred in a number of species. In these species (e.g., *Bombina* and *Arenophryne;* G. Roth, D. B. Wake, and J. Blanke, unpublished data), signs of additional simplification can be found throughout the brain: for example, a smaller size and a lower degree of lamination of the tectum and the torus semicircularis and reduced differentiation of diencephalic nuclei (W. Walkowiak and G. Roth, unpublished observations).

In the two other amphibian orders, salamanders and caecilians, the degree of simplification is generally much greater than in anurans. This is evident throughout the whole brain with respect to the number of cells; the formation of anatomically distinct migrated nuclei in the diencephalon, pretectum, and mesencephalic tegmentum; the formation and number of laminae, for example, in the tectum and the torus semicircularis; the presence or absence of a lateral motor column in the spinal cord; the number of morphologically distinct types of neurons; and the degree of morphological differentiation of these neurons.

The extremes of secondary simplification are found in the salamanders of the plethodontid tribe Bolitoglossini (about 180 species), which comprises all tropical salamanders plus the Californian genus *Batrachoseps* and the Californian-European genus *Hydromantes*. These directly developing salamanders have invaded the most diverse habitats, living underground or in limestone caves, in crevices, under logs, in moss, on trees, or even (secondarily) in water (D. B. Wake 1966; Wake and Lynch 1976). All of them possess a highly derived feeding apparatus, namely, a projectile tongue (Lombard and Wake 1976, 1977, 1987; Roth 1976, 1987). Their visual system is highly specialized in that they possess relatively frontal eyes, have well-developed ipsilateral projections to the thalamic and pretectal visual areas and especially to the optic tectum (see above), and show an unusually large nucleus isthmi (Wiggers and Roth 1991). These features are assumed to be related to their precise depth perception, which allows them to catch fugitive prey.

At the same time, the Bolitoglossini show the highest degree of secondary simplification. More general features of secondary simplification include loss of lungs (characteristic of all plethodontid salamanders), loss of an aquatic larval stage (characteristic of all members of the plethodontid tribes Plethodontini and Bolitoglossini), and loss of most larval traits within the egg (i.e., several pairs of epibranchials) (Roth and Wake 1985a). The bolitoglossine nervous system possesses the lowest number of neurons per unit of volume and also the lowest degree of lamination, cell migration, and differentiation, including processes such as myelination of the optic nerve (Linke et al. 1985; Roth et al. 1988, 1990a; Linke and Roth 1989, 1990). Bolitoglossines are unique among limbed vertebrates in that they lack a lateral motor column within the spinal cord (Roth and Wake 1985b; Wake et al. 1988). These observations challenge the common assumption that there is a close relation between the structural complexity of the nervous system and the complexity of behavior.

Physiological and Behavioral Consequences of Simplification

In contrast to the large amount of comparative morphological data on sensory systems, comparative neurophysiological and behavioral data are sparse. Therefore, the central question of the consequences of secondary simplification in the different groups of amphibians is difficult to answer.

Comparative neurophysiological data exist about the visual system of frogs and salamanders in the context of object (e.g., prey) recognition. There have been studies of the response properties of tectal cells in a number of anuran and urodele species that used similar experimental methods. These studies yielded the surpris-

ing result that, despite the large differences in the morphology of the anuran and the urodele tectum, tectal cells of anurans and urodeles have very similar response properties. There are greater similarities between frog and salamander species that have the same prey preferences and feeding strategies than among frogs as a group or among salamanders as a group (Roth 1986, 1987).

Anurans have five to 10 times more visual neurons than plethodontids (especially bolitoglossines) of the same size. Yet the depth-perception abilities of the latter are often better, and sometimes much better, than those of the former (e.g., *Discoglossus, Ascaphus,* and to a lesser degree *Bufo bufo;* K. Nishikawa and G. Roth, unpublished observations). Apparently, bolitoglossines make use of multiple retinotopic tectal maps constituted by contralateral and (direct as well as indirect) ipsilateral retinal afferents, contralateral and ipsilateral isthmotectal projections, and tectotectal projections (Wiggers and Roth 1991). Furthermore, in bolitoglossine salamanders, most of the visual tectal map is used for a representation of the frontal 60° of the visual field (i.e., 30° to the right and to the left; Wiggers and Roth 1991), which makes the tectum something like a functional fovea that serves stereopsis at the expense of peripheral vision. These morphological and physiological features can be understood as compensation for the dramatic decrease in the number of visual neurons in bolitoglossine salamanders.

There are, however, differences between frogs and salamanders in the performance of certain tasks. For example, frogs can recognize small objects at greater distances and will, when highly motivated, respond to small prey that are 1.5 or even 2 m away. Salamanders, in contrast, rarely respond to prey objects at distances greater than 50 cm. Frogs' increased vision apparently results from the much larger number of photoreceptors and other visual cells per unit area of retinal surface that, accordingly, provide a much higher spatial visual resolution. Higher visual resolution is accompanied by a much higher activity level of behavior in frogs than in salamanders.

In frogs, the auditory system and sound communication play a central role in reproductive behavior. For anuran sound projection, the presence of a highly specialized larynx, lungs, and a hyoid apparatus is necessary. For sound perception, frogs have developed a new central auditory nucleus, the dorsolateral nucleus, in addition to peripheral adaptations. The degree of morphological complexity of peripheral and central auditory structures is paralleled by the complexity of the structure of the calls. Species with amplitude and/or frequency modulation of the call have a high number of hair cells and a high degree of lamination of the torus semicircularis (e.g., *Afrixalus;* W. Walkowiak, personal communication). *Bombina,* a species that exhibits simplification of the middle ear, the sensory epithelia, and the auditory centers, has very simple calls with no apparent time structure. In addition, the high-frequency domain (mediated by the basilar papilla) is reduced compared to most other frogs (Walkowiak 1980).

Some terrestrial salamanders that possess a larynx and lungs are capable of sound production (e.g., "squeaking"), mostly in the context of antipredator behavior. There is no evidence that salamanders use sounds for intraspecific communication. It has recently been shown that *Salamandra salamandra* has a functional auditory system and that neurons within the dorsal tegmental region, which

is homologous to the torus semicircularis of frogs, are sensitive to airborne sound (Manteuffel and Naujoks-Manteuffel 1990).

Thus functional auditory and sound production systems are a plesiomorphic trait for salamanders. It remains unclear why salamanders did not evolve an elaborate acoustic communication system like that of frogs. One reason could be that the hyobranchial apparatus has a very different fate in anurans and urodeles. In all urodeles, it is necessary for tongue feeding. In anurans, in which it is highly modified during metamorphosis, it plays a major role in calling but is not involved in feeding (Roth et al. 1990b).

Many salamanders, including all plethodontids, have lost their lungs and larynx and thus are incapable of producing sounds with these structures (although some plethodontid salamanders can "squeak" by pressing air out of their mouths or stomachs). In addition, as mentioned above, their peripheral auditory system is simplified (i.e., middle ear and inner ear structures [basilar papilla]). We view these reductions as a consequence of the overall simplification of sense organs and the nervous system. If this assumption is correct, then this secondary simplification in lungless salamanders has prevented the evolution of a sound communication system for reproduction or territorial defense. Pheromone communication, rather than sound production, plays a major role in reproductive and territorial behavior of salamanders, especially plethodontids (Dawley 1984; Jaeger 1986; Houck and Reagan 1990).

Phylogenetic and Ontogenetic Correlates of Simplification

The morphological simplification of the salamander nervous system is correlated with an increase in genome size, that is, quantity of nuclear DNA. The absolute highest genome sizes among animals are found in lepidosirenid lungfishes, which have genome sizes of 111 (*Lepidosiren paradoxa*) and 143 (*Protopterus aethiopicus*) picograms of DNA per haploid nucleus (Olmo 1983). These two groups are highly simplified, or "paedomorphic" (Bemis 1984; Northcutt 1987). Amphibians differ from all other animals because they have the second-largest genome size. Most vertebrates have genome sizes of 1–3 pg of DNA per haploid nucleus (fishes, 1 pg; birds, 1.5; reptiles, 2.5; mammals, 3; Olmo 1983). Frogs have from 0.9 pg (*Limnodynastes ornatus;* Olmo 1983) to 19 pg (*Arenophryne rotunda;* J. D. Roberts, personal communication). The largest caecilian genome size found so far is 13.2 pg (M. H. Wake, personal communication). The smallest genome size among salamanders (13.7 pg) is found in the plethodontid *Desmognathus wrighti* (Hally et al. 1986) and the largest in the neotenic *Necturus maculosus* (83 pg; Olmo 1983). However, many terrestrial plethodontid salamanders come rather close to this maximum number (e.g., *Hydromantes italicus,* 77 pg; Sessions and Larson 1987).

This increase in genome size, resulting from the amplification of noncoding regions, has profound and well-known effects on organisms. An immediate consequence is an increase in cell size and a decrease in cell metabolic rate; furthermore, cell proliferation and cell differentiation rates are negatively correlated with an increase in genome size (Cavalier-Smith 1978, 1982, 1985; Horner and MacGregor 1983; Olmo 1983; Sessions and Larson 1987). From the neuroanatomical data presented above, it is evident that the brains of salamanders with large

genome sizes have fewer and larger cells, which are more densely packed and located near the periventricular gray matter, and they show a simpler morphology than brains of salamanders with small genome sizes (Roth et al. 1988, 1990*a;* Wake and Roth 1989). Preliminary studies on additional species of anurans that differ in genome size support this generalization (G. Roth, D. B. Wake, and J. Blanke, unpublished observations).

The current view of increasing genome size is fundamentally nonadaptive. "Selfish," highly repetitive DNA sequences propagate themselves within the nucleus until a genome size is reached at which any further increase is prevented by countervailing selection (Szarski 1976, 1983; Orgel and Crick 1980). Under this hypothesis, it would appear that, for unknown reasons, amphibians and lepidosirenid lungfishes have experienced less selection against increasing genome size than all other lineages of metazoans (Olmo 1983).

Regardless of the reasons why genome size has increased in amphibians, it is clear that it has had major effects on their morphology, ecology, and life history. Among terrestrial salamanders, the Bolitoglossini have both the largest genome size and the highest age at maturity (Vial 1968; Duellman and Trueb 1986). Ecologically, another effect of increasing genome size is low metabolic rate (Feder 1983). Together, low metabolic rate and delayed reproductive maturity combine to produce what ecologists would interpret as a "K-selected" life-history pattern, in which a few eggs are produced over a long life span. This type of life history is especially characteristic of the plethodontid salamanders (Houck 1982). Although the name "K-selection" implies evolution under a regime of intense intra- or interspecific competition, such a life-history pattern would also be expected to result from increasing genome size alone.

Morphological evolution is also affected by increasing genome size (Sessions and Larson 1987). The available data predict that, as genome size increases, the size of cells will increase, the number of cells will decrease, and the degree of cellular differentiation and cell migration will decrease. These processes combine to produce a morphology that appears embryonic compared to that of the nearest outgroup; that is, the morphology is paedomorphic (Wake and Roth 1989).

CONCLUSIONS

How must secondary simplification in amphibians be interpreted? Can it be viewed as adaptive (i.e., improving the survival of the respective groups)? Or must we view it as a constraint that is tolerated by natural selection and somehow compensated by other, perhaps adaptive, processes?

In the lateral line system, the observed reductions can be viewed as accompanying the evolution of terrestrial life and direct development, which has occurred independently many times within all three amphibian orders. It is possible that terrestrial life and direct development evolved first and that this led to the disappearance of the lateral line system. Terrestrial amphibians do not need a lateral line system; therefore, the system is sensitive to stochastic decay.

In the auditory system, a simple adaptive explanation for secondary simplification is difficult. It is hard to see why it is adaptive for frogs like *Bombina* to reduce the middle and inner ear and central auditory areas, such as the torus,

while most other frogs possess a specialized auditory system that is usually viewed as highly adaptive. Even more difficult to understand in adaptive terms is the case of the bolitoglossine salamanders, which have undergone the most radical reduction of the auditory system. There is no known fact that could explain why the loss of the basilar papilla, the reduction of the amphibian papilla, and the loss of the auditory nucleus are adaptive. Rather, it seems that the vibration sensitivity system, which appears to be highly evolved in the Bolitoglossini, uses the opercularis-vestibular pathway to compensate for the reduction of the auditory system.

The visual system of salamanders, especially of bolitoglossines, is the clearest example of simplification caused by internal constraints. Because bolitoglossines depend heavily on vision, there is no reason why reduction of the number of visual neurons (by 50%–90%) and simplification of tectal morphology should be advantageous for the visual guidance of behavior. Simplification in brain morphology and sensory systems is most likely an outcome of increased genome size.

We also observe changes in the visual system of bolitoglossine salamanders that improve visual acuity and stereopsis despite the strong reduction in the number of visual cells. These include increased eye frontality, the expanded representation of the temporal retina (corresponding to the frontal visual field) in the tectum, and the strong increase in direct ipsilateral retinofugal projections and in isthmotectal projections (Rettig and Roth 1986; W. Wiggers and G. Roth, unpublished observations). Furthermore, paedomorphic simplification, through suppression of ossification and loss of larval structures, has made possible the unique feeding apparatus of bolitoglossines (Roth and Wake 1985a).

In conclusion, we believe that increased genome size has led to highly constrained developmental patterns and to organism-wide reduction in structural complexity in amphibians. The simplified brains and sensory systems of amphibians, in particular, lead to a paradox. Why should these evolutionarily successful vertebrates have reduced the complexity of their brains and sense organs, when the trend has been toward increased complexity in other lineages? The solution to the paradox comes from the fact that paedomorphosis, the phenomenon of simplification itself, makes possible the development of compensatory processes through which functional integrity may be conserved or even improved. We thus observe that in this case both constraints and opportunities arise from the same genomic and developmental roots.

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