Development of the Tectum in Gymnophiones, With Comparison to Other Amphibians

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ABSTRACT  Tectal development in a number of caecilian (Gymnophiona: Amphibia) species was examined and compared with that in frogs and salamanders. The caecilian optic tectum develops along the same rostrocaudal and lateromedial gradients as those of frogs and salamanders. However, differences exist in the time course of development. Our data suggest that, as in salamanders, simplification of morphological complexity in caecilians is due to a retardation or loss of late developmental stages. Differences in the time course of development (heterochrony) among different caecilian species are correlated with phylogenetic history as well as with variation in life histories. The most pronounced differences in development occur between the directly developing Hypogeophis rostratus and all other species examined. In this species, the increase in the degree of morphological complexity is greatly accelerated. J. Morphol. 236:233–246, 1998. © 1998 Wiley-Liss, Inc.

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The visual system of amphibians is strongly correlated with phylogenetic history (Roth et al., '83, '90; Wake, '85; Schmidt and Wake, '91). Differences in the visual system are apparent among the three orders of amphibians (frogs [Anura], salamanders [Urodela], and caecilians [Gymnophiona]), as well as among species within each order. These differences concern the absolute and relative sizes of eyes (Wake, '85; Roth et al., '90), eye morphology (Wake, '85; Linke et al., '86), degree of frontal direction of the eyes (Roth, '87), patterns of visual projections (Fritzsch, '80; Fritzsch et al., '85; Himstedt and Manteuffel, '85; Rettig and Roth, '86), and tectal morphology (Roth et al., '90, '93). The morphologically most complex optic tectum among amphibians is found in frogs. They possess a multiply laminated tectum (Potter, '69) in which many cells can be found in the superficial neuropil. Such cells have migrated from their periventricular origin during the course of development, and are known as "migrated" cells. This condition is in contrast to salamanders and caecilians, which have a secondarily simplified tectal morphology (Schmidt and Wake, '91; Roth et al., '94) with a more or less homogeneous periventricular gray and a superficial neuropil that exhibits very few migrated cells. Despite variable reduction of the visual system among caecilians, the degree of morphological complexity (lamination and number of migrated cells) in the most developed caecilian tectum is greater than in that in most salamanders (Schmidt and Wake, '91, '97), suggesting that internal dynamics might be more important for tectal differentiation than external influences. Compared with salamanders, caecilians vary especially in the localization of migrated cells. Although salamanders possess very few migrated cells that are present equally in both the medial and lateral parts of the tectum, the majority of migrated cells in caecilians occurs in the lateral part of the tectum (Schmidt and Wake, '91, '97).

Many studies (e.g., Roth et al., '93; Schmidt and Roth, '93) have demonstrated that differences in brain morphology are related to heterochrony (i.e., dissociations or relative changes in patterns of development). For...
example, in salamanders, the simplification of the tectum mesencephali is thought to be due to paedomorphosis characterized by a loss or retardation of late ontogenetic processes, particularly the migration of cells into the superficial neuropil (Schmidt and Roth, '93). It is not known whether the low degree of morphological differentiation in the tectum of caecilians also is due to paedomorphosis, or if other factors, such as the reduction of the peripheral visual system, might contribute to the simplification.

Two major factors have been shown to be related to interspecific variation during brain development: (1) differences in genome size (Roth et al., '93), and (2) differences in life histories (Rettig and Roth, '86; Schmidt et al., '88; Wake and Roth, '89). Both were shown to play an important role during brain development in salamanders (Schmidt and Böger, '93; Roth et al., '93).

In salamanders, an increase in genome size is thought to be correlated with the occurrence of paedomorphosis, in that it leads to a general slowing down of development (Wake, '66; Cavalier-Smith, '78; Horner and MacGregor, '83; Sessions and Larson, '87; Roth et al., '89, '93). Frogs possess smaller genomes than salamanders (Olmo, '83). The genome sizes of caecilians lie between those of frogs and salamanders (Olmo, '83; Schmidt and Roth, '93). Presuming that there is a relationship between an increase in genome size and the degree of paedomorphosis, one would expect that paedomorphosis does not affect brain development as strongly in caecilians as it does in salamanders.

Roth et al. ('93) presented a phylogenetic analysis of the evolution of the brain in vertebrates, using 23 neuroanatomical characters, including those of the tectum. Their most parsimonious conclusion is that a complex brain is the ancestral condition, and secondary simplification occurred independently in hagfishes, lepidosirenid lungfishes, and salamanders and caecilians. Therefore, assuming that frogs possess the ancestral condition of adult tectal morphology and of tectal development, and given the information about the ontogenetic sequence of tectal development in frogs (Schmidt and Roth, '93), we have a means of evaluating whether differences in the degree of morphological complexity in caecilians are also due to changes in the time course of development, as has been shown in salamanders (Schmidt and Roth, '93) by comparing the tectal development in frogs with that of caecilians. Heterochronies associated with differences in life histories may be due to changes in the action of hormones (Gilbert, '91). For instance, experimental studies on skull development (Hanken and Summers, '88a,b; Hanken and Hall, '88) and on the development of the nervous system (Schmidt and Böger, '93) provide evidence that direct development is due to an increase in thyroxine levels. The consequence is an acceleration of developmental processes as well as a decoupling of ontogenetic processes leading to the development of a mosaic of characters similar to those found in many direct-developing salamanders.

In order to investigate the relationship among different life history strategies and changes in the time course of development, we compared the ontogenetic sequence of tectal development in a diversity of caecilian species that exhibit various life history modes.

**MATERIALS AND METHODS**

Species and stages examined

Tectal development was studied in five species of three of the six families of the Order Gymnophiona (Duellman and Trueb, '86; Nussbaum and Wilkinson, '89; Hedges et al., '93); we currently accept Typhlonectidae as a distinct family, as do most researchers on caecilian biology) that have different life history strategies. Families and species include Ichthyophidae: Ichthyophis kohtaoensis (Southeast Asia [Thailand]; oviparous); Caeciliidae: Dermophis mexicanus and Gymnopus multiplicata (both Central America [Mexico to Panama and Costa Rica, respectively]; both viviparous); Hypogeophis rostratus (Seychelle Islands; direct development); and Typhlonectes compressicaudus (South America [north-central]; oviparous). Caeciliidae: Derhyphisia mexicanus and Gymnopus multiplicata (both Central America [Mexico to Panama and Costa Rica, respectively]; both viviparous); Hypogeophis rostratus (Seychelle Islands; direct development); and Typhlonectes compressicaudus (South America [north-central]; oviparous). Most animals were collected, dispatched, and preserved immediately in the field.

Tectal development was studied in the heads of animals at different ontogenetic stages. Parameters for choosing stages were (1) presumed time past fertilization, and (2) size (total length [TL]): Ichthyophis kohtaoensis (newly hatched larva/66 mm); Dermophis mexicanus (1.5 months/20 mm, 2 months/37 mm, 2.5 months/40 mm, 3 months/49 mm, 5 months/79 mm); Gymnopus multiplicata (2 months/30 mm, 3 months/54 mm, 5 months/84 mm); Typhlo-
nectes compressicaudus (approximately 3 months/46 mm); Hypogeophis rostratus (age undeterminable/38 mm).

Methods
Specimens were fixed in 10% neutral buffered formalin for a minimum of 72 hr and preserved in 70% ethanol. Heads were removed, decalcified in 3% formic acid, embedded in paraffin, and transversely sectioned at 10 µm. Every third slide was stained with picroponceau (for connective tissue; nuclei of brain cells were particularly well stained) hematoxylin and eosin (H&E) (for contrast), or Mallory’s azan (for tissue distinctivity) according to standard procedures (Humason, ’79). Other series were stained with Palmgren’s silver specifically to display neuron morphology. In sections stained using these methods, regions of notable cell proliferation can be distinguished from those with no or low proliferation by dark staining of nuclei and the appearance of elongated neurons in addition to compact cells.

RESULTS
Tectal development in frogs and salamanders

The anuran tectum is a conspicuously multilayered structure that is divided into nine alternating cellular and fiber layers (Potter, ’69). Many migrated cells (≈30%) are found in the superficial fiber layer. By contrast, the salamander tectum is characterized by a thick periventricular cellular layer and an outer fiber layer that contains only few migrated cells (Roth et al., ’93).

Rana temporaria

The optic tectum of the frog Rana temporaria develops along rostrocaudal and lateromedial gradients. The lateral part of the rostral tectum differentiates first and the medial part of the caudal tectum differentiates last (Schmidt and Roth, ’93). At early stage 24 (Gosner, ’60), cell proliferation takes place over the entire width of the ependymal layer, more strongly laterally than medially (Fig. 1A). A superficial neuropil is absent. This mode of cellular proliferation is found over all the tectum (rostral, central and medial). From stage 25 (in the rostral tectum) and stage 31 (in the caudal tectum), cell proliferation occurs in both a medial and in a lateral zone, with an intermediate zone of low cell proliferation lying between these zones. At this time, cellular proliferation is somewhat more intense in the medial than in the lateral zone. The superficial neuropil begins to develop, and the first migrated cells appear. The lateral part of the tectum is always the first part in which a superficial neuropil and migrated cells are found, and the region where, compared with the medial zone, cell proliferation increases initially and then also decreases first. From stage 30 (in the rostral tectum) and stage 37 (in the caudal tectum), the zone of medial cell proliferation decreases. Lamination starts at stage 28 in the rostral tectum and at stage 37 in the caudal tectum.

Pleurodeles waltl

As in Rana temporaria, the tectum of the salamander Pleurodeles waltl develops along rostrocaudal and lateromedial gradients. The mode of cellular proliferation is similar to that of Rana temporaria. However, in general, cell proliferation in Pleurodeles is less extensive than in Rana temporaria. This becomes most obvious at midlarval and late ontogenetic stages. At early stages (33–37 [staging according to Gallien and Durocher, ’57], in the rostral tectum), cell proliferation occurs all over the entire width of the ependymal layer, with a slight concentration in the lateral part of the tectum (Fig. 1B). The superficial neuropil begins to develop at stage 34. The small numbers of migrated cells do not appear before stage 36. The tectum of Pleurodeles exhibits no distinct multiple lamination. Starting at stage 38, cell proliferation decreases, beginning in the rostral tectum. At this time there is a stronger cell proliferation in the medial than in the lateral zone of the tectum. Cell proliferation in the lateral zone is minimal and also decreases in the medial zone, starting in the rostral tectum at stage 42. At this stage, Pleurodeles is only 20% throughout its larval period.

Tectal development in caecilians

The caecilian tectum, like that of salamanders, appears rather simple and consists primarily of a periventricular cellular layer and a superficial fiber layer, that, however, contains relatively more migrated cells than salamanders. In caecilians, migrated cells occur primarily in the lateral part of the tectum rather than in the medial part. Among caecilians, there are differences in the complexity of the cellular layer, as well as in the number of migrated cells (Schmidt
and Wake, '97). In some species (e.g., Gymnopis multiplicata), the periventricular cellular layer is homogeneous, whereas in other species (e.g., Dermophis mexicanus, Ichthyophis kohtaoensis, Hypogeophis rostratus, and Typhlonectes compressicandus), it is traversed by fibers that in most cases do not constitute continuous layers. Among the caecilian taxa examined, Hypogeophis, Typhlonectes, and Ichthyophis possess a moderate degree of morphological complexity and a moderate number of migrated cells within the superficial neuropil. Gymnopis and Dermophis both possess many migrated cells. However, in contrast to Gymnopis, which has a homogeneous cellular layer, Dermophis has the most complex tectum among the genera examined.

Fig. 1. Sequence of tectal development in the frog Rana temporaria (A,C,E) and the salamander Pleurodeles waltl (B,D,F). Transverse sections of the central tectum. A,B: Early stages, shortly after hatching. C,D: Midlarval stages. E,F: Shortly before metamorphosis. Bar = 100 µm. In both species, cell proliferation (arrows) occurs all over the tectum during early stages (A,B) and is restricted to a lateral and medial zone at later stages (C,D). Cell proliferation in Pleurodeles is less than in Rana and stops earlier in relative to the time of metamorphosis.
In all the caecilian species examined, the ontogenetic sequence of cellular proliferation and cellular migration is basically the same as that described for frogs. However, there are changes in the time course of development and in the intensity of cell proliferation. As in Rana, cell proliferation takes place over all the ependymal layer early in development, with a concentration in the lateral part of the tectum (Figs. 2, 3, 6). At later developmental stages the rate of lateral cell proliferation decreases. In contrast to Rana, there is no increase in cell proliferation in the medial zone. Tectal development in caecilians also proceeds along rostrocaudal and lateromedial gradients. The lateral part of the rostral tectum is the first part in which a superficial neuropil and migrated cells are found; the medial part of the caudal tectum is the region in which these processes occur last.

Dermophis mexicanus

20-mm TL. Cell proliferation occurs over the entire width of the ependymal layer in the rostral, central, and caudal tectum (Fig. 2A,C,E). A small amount of superficial neuropil that diminishes rostrocaudally is found in the lateral tectum. There are no migrated cells.

37-mm TL. Cell proliferation is concentrated in the lateral tectum. It is least in the rostral tectum and most extensive in the caudal tectum. Compared with the 20-mm individual, cell proliferation in the 37-mm TL animal is decreased medially in all parts of the tectum. In the rostral and in the central tectum, a few migrated cells occur in the ventralmost part of the lateral tectum. Substantial numbers of migrated cells are found in the adjacent thalamic and segmental areas. No migrated cells are found in the caudalmost part of the tectum. The superficial neuropil is present in the lateral tectum, but there is very little neuropil in the medial tectum. The amount of superficial neuropil diminishes rostrocaudally.

49-mm TL. The rostral tectum lacks distinctive zones of cellular proliferation (Fig. 2B). In the central tectum, cell proliferation is restricted to a lateral zone (Fig. 2D). There is no cell proliferation in the medial zone. The caudal tectum (Fig. 2F) exhibits an extensive cell proliferation that is concentrated in the lateral zone. Less cell proliferation occurs in the medial tectum. In the rostral and central tectum, few migrated cells are found in the lateral part. The caudal tectum does not have any migrated cells. The superficial neuropil is best developed in the rostral tectum and diminishes caudally. The caudalmost tectum has only a small amount of neuropil in both the lateral and the medial areas (Fig. 2F).

79-mm TL. The rostral and the central tectum lack zones of cellular proliferation. An extensive cell proliferation is found only in the caudal tectum where it is concentrated laterally. Migrated cells are found in the rostral as well as in the central and the caudal tectum, but they are mainly restricted to the lateral tectum. Very few migrated cells occur in the medial tectum. The superficial neuropil is most developed in the rostral and central portions of the tectum, but a lesser amount of neuropil is present in the caudal tectum, where it is better developed in the lateral than in the medial part.

Gymnopus multiplicata

20-mm TL. Cell proliferation occurs over the entire width of the ependymal layer in the rostral, central, and caudal tectum (Fig. 2A,C,E). A small amount of superficial neuropil that diminishes rostrocaudally is found in the lateral tectum. There are no migrated cells.

37-mm TL. Cell proliferation is concentrated in the lateral tectum. It is least in the rostral tectum and most extensive in the caudal tectum. Compared with the 37-mm specimen of Dermophis. There is little cell proliferation in the rostral tectum (Fig. 3A), but it occurs equally in the medial and the lateral zones. Extensive cell proliferation occurs laterally and to a lesser degree medially within the central tectum (Fig. 3C). Cell proliferation increases caudally, and is greater in the lateral than in the medial zone (Fig. 3E). Very few migrated cells are apparent in the rostral and central tectum, but none is found in the caudalmost tectum. The superficial neuropil is best developed in the lateral part of the rostral tectum and diminishes caudomedi ally.

54-mm TL. At this stage, there is little to no cellular proliferation in the rostral and central tectum (Fig. 3B,D). Extensive proliferation occurs in the lateral zone of the caudal tectum (Fig. 3F), and less proliferation occurs in the medial zone. Few migrated cells are found in the rostral tectum. More migrated cells are found in the rostral tectum. More migrated cells are found in the central tegmentum. There are still no migrated cells in the caudalmost tectum. The superficial neuropil is best developed in the lateral part of the rostral tectum and diminishes caudomedi ally.

84-mm TL. Cell proliferation is completed in the rostral, central, and caudal tectum. In all parts of the tectum (rostral, central and caudal), the superficial neuropil
is well developed, and a substantial number of migrated cells appear in the lateral part of the tectum. Very few migrated cells are apparent in the medial part of the tectum.

Typhlonectes compressicaudus

46-mm TL. Compared with other taxa, tectal cell proliferation in Typhlonectes is much reduced. Hardly any proliferative zones can be distinguished except in the caudal tectum (Fig. 4E), where cell proliferation occurs over the entire width of the ependymal layer (Fig. 4C). No difference in proliferative activity is found between the lateral and medial tectum as described in Gymnopus and Dermophis. There are very few migrated cells in the lateral part of the rostral tectum (Fig. 4A). Compared with Dermophis and Gymnopus at similar sizes, the relative size of the neuropil is very small. Also in Typhlonectes, the neuropil is more developed in the rostral than in the caudal tectum.

Fig. 2. Sequence of tectal development in Dermophis mexicanus (viviparous). A,C,E: 20-mm animal. B,D,F: 49-mm animal. Transverse sections of the rostral (A,B), central (C,D), and caudal (E,F) tectum. In the 20-mm animal, cell proliferation (arrows) occurs all over the ependymal layer in the rostral (A), central (B), and caudal (C) tectum. In the 49-mm animal, this early pattern of cell proliferation only occurs in the caudal tectum. In the central tectum, cell proliferation is restricted to a lateral zone. Proliferation already stopped in the rostral tectum. Bar = 100 µm.
Hypogeophis rostratus

38-mm TL. At this stage, tectal development is nearly complete. Neither rostral (Fig. 4B), central (Fig. 4D), nor caudal (Fig. 4F) tectum. In the 30-mm animal, cell proliferation (arrows) occurs in all parts of the tectum, but only the caudal tectum shows the early pattern of cell proliferation (cell proliferation all over the ependymal layer; arrows). In the central (C) tectum, proliferation is restricted to a lateral zone. In the rostral tectum (A), cell proliferation is highly reduced. In the 54-mm animal, cell proliferation only occurs in the caudal tectum (arrows). Bar = 100 µm.

Ichthyophis kohtaoensis

66-mm TL. At this stage, tectal development is well advanced. No distinctive zones are found in the rostral, central, and caudal tectum (Fig. 5). A few migrated cells occur in the rostral, central and caudal tectum. These
are concentrated in the lateral tectum. More migrated cells are found in the thalamus and tegmentum.

DISCUSSION

Our examination shows that the caecilian tectum develops along the same rostrocaudal and lateromedial gradients (Straznicky and Gaze, '72; Schmidt and Roth, '93) as those of frogs and salamanders (Fig. 6). However, there are differences in the time course of development regarding cellular proliferation and the degree of cellular migration. Differences in the time course of tectal development exist not only between frogs and salamanders, but also among caecilian species. Our results suggest that interspecific differences in tectal development are related to differences in life histories among caecilian taxa.
Is the simplification of the tectum in caecilians due to heterochrony?

It is well known that heterochrony plays an important role in creating phylogenetic change (Wake, '66; Gould, '77; Alberch, '80, '82). Comparative studies of frogs and salamanders provide evidence that the simplified brain morphology in salamanders represents the retention of early ontogenetic features into the adult stage, thus, the adult morphology is paedomorphic. Our results suggest that the simplification of tectal morphology in caecilians is also due to paedomorphosis. However, tectal development in caecilians is not as strongly affected by paedomorphosis as is tectal development in salamanders.

In caecilians, cellular proliferation occurs all over the tectum at early ontogenetic stages but concentrates in the caudal tectum at late stages. In frogs, the homogeneous layer of extensive cell proliferation splits off during development, so that at later stages cell proliferation occurs in distinct medial and lateral proliferative zones (Figs. 1, 6). These two zones differ in degree of cellular proliferation. The lateral zone exhibits most extensive cell proliferation at early ontogenetic stages but, in this zone, cell proliferation also decreases earlier than in the medial zone. In the medial zone, the peak of proliferative activity is found at later developmental stages and the decrease in cell proliferation occurs later than in the lateral zone. This sequence of tectal development is concordant with that described in other vertebrates, such as trout (Richter, '81; Mansour-Robaey and Pinganaud, '90). In salamanders, simplification of tectal morphology is due to a decrease in cell proliferation both in the lateral zone and in the medial zone (Schmidt and Roth, '93). Cell proliferation in salamanders is suppressed during late as well as during early developmental stages (Fig. 6). Caecilians differ from frogs but are similar to salamanders in that, in general, the medial zone shows very low proliferative activity that never increases (Fig. 6), but it decreases early in development. Consequently, the late-occurring mode of cell proliferation is delayed in caecilians. By contrast, the pattern of early cellular proliferation is similar to that of frogs but differs from that of salamanders. In caecilians, extensive cell proliferation within the lateral zone occurs early and persists until mid-developmental stages (Fig. 6). This is in contrast to salamanders, in which cell proliferation in the lateral zone is greatly reduced. Differences in patterns of cellular proliferation between salamanders and caecilians are concordant with differences in the distribution of migrated cells at the adult stage. In the adult salamander tectum, there are very few migrated cells in the medial and in the lateral tectum. In contrast to
salamanders, migrated cells in the caecilian tectum, although few in number, are concentrated mainly in the lateral tectum (Schmidt and Wake, '91).

In summary, our data suggest that simplification of morphological complexity in the optic tectum of caecilians is due to retardation or loss of late developmental stages. However, in contrast to salamanders, which show retardation of tectal development at early as well as at late stages, only late stages are retarded in caecilians. Thus, caecilians are not as strongly affected by paedomorphosis as are salamanders.

**Relationship between heterochronic development of the tectum and differences in life histories**

Heterochrony affecting the tectum occurs in all the three amphibian orders and among
species of caecilians. While the general rostrocaudal and lateromedial sequence of tectal development is the same, the time course differs among caecilians. Our data suggest that differences in tectal development are at least partially correlated with differences in life histories. However, the fact that variation in tectum developmental patterns also occurs among caecilian species that possess the same life history suggests that heterochronies are correlated with phylogenetic histories as well.

In order to compare patterns of heterochrony, criteria for the evaluation of the stage of tectal development must be established. Our criteria include the following: (1) the degree of cellular migration, (2) the size of the superficial neuropil, and (3) the morphological complexity of the periventricular cellular layer. During development, these parameters differ among the rostral, central, and caudal tectum. The rostral tectum differentiates earliest and the caudal tectum differentiates last. Therefore a comparison of the above-mentioned criteria among the rostral, central, and caudal tectum makes it possible to evaluate whether development is completed or whether it has just begun. A well-differentiated caudal tectum indicates that development is already completed. In contrast, an undifferentiated rostral tectum represents an early developmental stage.

Marked differences in tectal development occur between the direct-developing caecilian Hypogeophis and all other taxa examined. Our results show that in a 38-mm prehatching (15% of average adult length) Hypogeophis embryo, tectal development is far advanced. Cell migration has occurred all over the tectum with a concentration in the lateral part of tectum. In particular, the late-developing caudal tectum possesses many migrated cells. Also, a superficial neuropil has already developed in this region. Tectal morphology in a 38-mm Hypogeophis embryo resembles that found in a newly hatched larva of Ichthyophis at a length of 66 mm (25% of total average adult length). Thus, these species exhibit a dissociation of development of body size and tectal development. In the viviparous caecilians Gymnopis multiplicata and Dermophis mexicanus, a developmental stage of tectal development similar to the 38-mm Hypogeophis is not achieved until the animal reaches lengths of about 84 mm and 79 mm, respectively. The dissociation between body growth and tectal development in Hypogeophis suggests an ontogenetic repatterning that may be related to direct development. This finding is concordant with the situation in salamanders where characteristics in the morphology of the feeding apparatus and the visual system in members of the tribe Bolitoglossini (Family Plethodontidae) are attributed to an ontogenetic repatterning related to direct development (Wake and Roth, '89). Studies on Pleurodeles waltl, a salamandrid with an aquatic larval stage, demonstrate that an ontogenetic repatterning similar to that of direct-developing bolitoglossine salamanders can be induced by increasing thyroxine during early developmental stages (Schmidt and Böger, '93). Changes due to thyroxine include an acceleration of the rostro-caudal sequence of tectal development. The relationship among differences in life history, differences in the action of hormones, and neuronal development needs investigation in caecilians. Caecilians provide an unusual paradigm for examination of the association of hormones and life history strategies. Oviparous caecilians with free-living larvae typically have long larval periods (e.g., Ichthyophis glutinosus [Breckenridge and Jaysinghe, '79; Breckenridge et al., '87], but perhaps not Sylva caecilia grandisonae [Largen et al., '72]), they thus have a lengthy period of development dependent on endogenous hormones. Direct-developing animals presumably have a different interaction of maternal and embryonic hormones, as suggested by studies in frogs (Jennings and Hanke, '94) and salamanders (Schmidt and Böger, '93). The protracted gestation period in viviparous caecilians, with its dissociation of many developmental, especially "metamorphic" events, is probably the result of a complex interaction of fetal and maternal hormones (Wake, '89, '94). Among the taxa examined, Typhlonectes, a viviparous genus, is characterized by the slowest development that especially affects the development of the neuropil and cell migration (based on a 46-mm fetus, 10% of total average adult length, with fetal size representing sample size, not fetal maximum). We find few migrated cells, and there is little neuropil in all parts of the brain. However, relative to the development of the neuropil, the rostrocaudal retraction of proliferation zones is advanced and corresponds to that found in Dermophis (fetus 49 mm, 15% of average adult total length) and Gymnopis (54 mm, 15% of average adult total length). There are also differences concerning the distinction of proliferation zones. In Typhlonectes, no distinctive zones of cellular prolif-
eration can be distinguished except in the caudal tectum. Differences among viviparous species might be due to phylogenetic relationships. Closely related genera, such as Gymnopus and Dermophis, have the greatest similarities concerning the time course of tectal development. There are very few differences in the relationship between growth rate (in terms of body size) and tectal development in these genera.

How do changes in the time course of tectal development in caecilians affect adult morphology?

A comparison of differences in the time course of tectal development with the degree of adult morphological complexity shows that different taxa may have similar adult tectal morphologies but may vary in the time course of development (e.g., Ichthyophis, Typhlonectes, and Hypogeophis). Adults of these species possess a moderate number of migrated cells and a moderate degree of morphological complexity within the periventricular gray (Schmidt and Wake, '97). Despite these similarities, the time course of development varies. In Hypogeophis, tectal development occurs quickly during early developmental stages, whereas tectal development proceeds slowly in Typhlonectes. The most parsimonious prediction is that an animal characterized by rapid development should have the greatest degree of morphological complexity as an adult, and an animal that develops slowly would have a lesser degree of morphological complexity as an adult. However, similarities in the degree of morphological complexity between Typhlonectes and Hypogeophis suggest a more complex scenario. The degree of morphological complexity not only depends on the rate of development, but also on the end-point of development or the onset of a slowdown in development. If the latter occurs early, the effects of a previous acceleration might be compensated. This may be the case in Hypogeophis, and it may be related to direct development. Similar changes in developmental rates were demonstrated in the salamander Pleurodeles wa! after hormonal treatments (Schmidt and Böger, '93). These studies show that an increase in thyroxine during early developmental stages leads to an acceleration of development. However, due to a shortening of the larval stage, these animals retain early ontogenetic characters. In salamanders, these effects, which are induced by thyroxine, are considered to be related to direct development (Schmidt and Böger, '93). The fact that the degree of morphological complexity of the tectum in Typhlonectes is similar to that in Hypogeophis indicates that despite a slower rate of development, a similar degree of morphological complexity can be achieved. Further investigation is needed to show whether this is due to an extension of developmental time.

A comparison of Hypogeophis with Gymnopus and Dermophis shows that, despite an early delay in development in Gymnopus and Dermophis, there are more migrated cells in adults of these two genera, which may be due to their extensive cell proliferation. The superficial neuropil increases concomitantly. Even though these processes occur relatively later during ontogeny, in comparison to Hypogeophis, they overcompensate for the early delay in development in Gymnopus and Dermophis.

However, in contrast to Gymnopus and Dermophis, cell proliferation in the tectum of the 46-mm Typhlonectes, another viviparous species in a different family, is limited and the superficial neuropil is relatively small. Typhlonectes possesses a moderate number of migrated cells during adulthood. Such differences illustrate the correlation with phylogenetic history, which may be distinctly different with regard to developmental patterns in taxa with the same reproductive modes.

In summary, our data show that phylogenetic history correlates with similarities in the time course of tectal development and thus leads to a similar morphological complexity in the adult brain. However, similarities in morphological complexity do not necessarily predict a similar time course of development. Alternatively, a similar degree of morphological complexity can be achieved as a result of variation in the onset and course of developmental processes (cell proliferation, development of the neuropil). The critical period is presumably the end of development (larval, direct-developing embryonic, or fetal) or the time when a general slowdown occurs. Our data suggest that heterochrony in caecilians is related to variation in life history strategies. Further investigation is needed to clarify the significance of variation in life histories and differences in the hormonal control involved in the regulation of development in amphibians.
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LITERATURE CITED


