Zoomorphology (1985) 105:277–295

Zoomorphology

© Springer-Verlag 1985

The comparative morphology and evolution of the eyes of caecilians (Amphibia, Gymnophiona)

Marvalee H. Wake
Department of Zoology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

Summary. Caecilians (Amphibia, Gymnophiona) have been reported to have 'vestigial' eyes, to lack some or all of the extrinsic eye muscles and their nerves, and to utilize eye muscles and glands, or derivatives of them, to effect movement of the tentacle, a chemosensory structure unique among vertebrates. Morphological evidence indicates that the eye is a functional photoreceptor in virtually all species examined, with an intact retina and optic nerve. The pattern of retention of extrinsic muscles varies. The ontogeny of the eye of *Dermophis mexicanus* is typical of that of most vertebrates, though components of accommodation never develop. Several taxa are reported in the literature to lack various eye structures; the present study reveals them to be variously present. Evolutionary trends in caecilian eye morphology include the following: (1) the eye is overlain by thicker, often glandular skin, to overlain by bone as well as skin; (2) extrinsic muscles become attenuate, and some to all may be lost; (3) the retina has the typical vertebrate layered organization, to having a reduced cell number, to becoming net-like rather than stratal; (4) the optic nerve is present, becoming attenuate, perhaps represented only by glial cells; (5) the lens is round (aquatic forms, larval and adult) to spheroid; lens crystalline to cellular (retention of the embryonic condition) to amorphous to absent; (6) the vitreous body is reduced or lost; (7) the cornea adheres to the overlying dermis or periosteum; the lens is free to adherent to cornea to adherent to both cornea and retina. Scolecomorphids have the eye pulled out of the socket and embedded in the tentacle under the skin of the upper jaw. This pattern of trends in eye reduction is similar to that observed in other vertebrate lineages that are fossorial or troglobitic.

A. Introduction

Caecilians are structurally modified for a fossorial existence – they are elongate, limbless, and have flattened, heavily ossified skulls. Their eyes are small, and covered by skin or skin and bone. Most caecilians upon which field observations have been made are nocturnal foragers (Taylor 1968; Wake pers. obs.). Further, caecilians have a highly elaborated chemosensory system, utilizing both narial olfaction and the tentacle, a structure unique to caecilians among vertebrates, whose lumen is continuous with the Jacobson's organ. It has long been known that the tentacle coopts eye muscles, nerves, and glands during its development and subsequent function (Leydig 1868; Wiedersheim 1879; P. and F. Sarasin 1887–1890). The retractor bulbi, innervated by the abducens nerve, becomes the retractor of the tentacle; an internal rectus muscle, innervated by the oculomotor nerve, is often the retractor of the tentacle sheath; the levator bulbi, innervated by a branch of the ramus mandibularis of the trigeminal, becomes the compressor muscle of the glands surrounding the tentacle; and the Harderian gland, which lubricates the orbit in most terrestrial vertebrates, moistens the tentacular channel.

Because of the small size of the eye, its covering layers, the loss to the tentacle of structures associated with the eye in other vertebrates, and the fossorial or swimming and nocturnal habitus of the animals, many workers have considered the caecilian eye "rudimentary", "vestigial", and/or "degenerate" (Norris and Hughes 1918; Walls 1942) despite, or because of, their own investigations of caecilian cranial structure.

Work on various species suggests a mosaic pattern of loss of extrinsic eye muscles and their nerves, and their utilization by the tentacle, and of the functional properties of the eye. For example, Norris (1917) and Norris and Hughes (1918) considered the eyes of all caecilians rudimentary, but in those species with the eye covered by skin, they thought that the eye probably was affected by light. They stated that such forms have some or all of the eye muscles and nerves present, but mostly vestigial or modified for use by the tentacle. The other group that Norris recognized included the species in which the eye is covered by bone (maxillary and/or squamosal, rarely frontal) as well as by skin, and Norris and Hughes declared that "the optic nerve and all the eye-muscles and eye-muscle nerves, except the retractor bulbi and its nerve, the abducens, have completely disappeared". I infer that Norris considered such eyes non-functional as photoreceptors. However, the literature is in conflict about the presence or absence of certain eye structures both within and among species. Therefore, as part of a larger study of the developmental and functional morphology of the head of caecilians, I have undertaken an examination of the eye and tentacle of a number of species in several families. I here present information on the comparative morphology and development and function of the eye. I offer a new interpretation of the structure of the eye and its variation, and consider the morphological evidence that allows interpretation of function.

Table 1. Heads sectioned for study

Taxon	Total length (mm)	Developmental stage
Ichthyophiidae		
Ichthyophis sp.	111	Larva
Ichthyophis glutinosus	344	Adult
Ichthyophis orthoplicatus	380	Adult
Uraeotyphlus narayani	151	Adult
Caeciliidae		
Afrocaecilia taitana	246	Adult
Boulengerula boulengeri	171	Adult
Caecilia occidentalis	510, 489	Juvenile
Dermophis mexicanus	5–398	10 embryos, 14 fetuses, 6 juveniles, 7 adults
Geotrypetes grandisonae	101	Larva
Geotrypetes seraphini	15–335	1 embryo, 2 juveniles, 2 adults
Gymnopis multiplicata	200, 370	1 juvenile, 1 adult
Hypogeophis rostratus	5–224	6 embryos, 2 adults
Idiocranium russeli	94	Adult
Oscaecilia ochrocephala	432	Adult
Schistometopum thomense	224	Adult
Scolecomorphidae		
Scolecomorphus kirkii	275	Adult
Scolecomorphus ulunguruensis	271	Adult
Typhlonectidae		
Typhlonectes compressicaudus	15–350	1 embryo, 1 fetus, 1 juvenile, 2 adults

B. Materials and methods

Whole heads of adult specimens of eighteen species representing four families (see Table 1 for taxa and other data) were decalcified, embedded in low-viscosity nitrocellulose (LVN), sectioned frontally with a sliding microtome, mounted and stained with haematoxylin-eosin, saffranin red-O, picro-ponceau, Heidenhain's azan, or Mallory's trichrome (Humason 1978; Thomas 1983). The heads of larvae and fetuses of additional species representing three families (see Table 1) were prepared in LVN or epoxy or paraffin and stained with alcian blue or as above. An ontogenetic series of heads of *Dermophis mexicanus* (35 heads; 5–398 mm total length [TL]; see Table 1) was prepared by embedding either in paraffin or LVN, sectioning frontally, sagittally, or transversely, and staining as above in order to examine development of the eye and associated structures. Measurements were taken using an ocular micrometer. Therefore representatives of four of the five families of caecilians, the major life history modes and stages, and the world-wide distribution of the order were available for study.

C. Results

I. Comparative anatomy of the adult eye

The eye of adult *Dermophis mexicanus* (Dumeril and Bibron) of the family Caeciliidae displays the characteristics of the eyes of most caecilians. I describe it in some detail, then compare the eyes of other species to it. In a 267 mm TL specimen (a young adult), the orbit is in a socket that is bounded laterally by the margins of the maxilla and squamosal, and medially by the sphenethmoid complex. The orbit is covered by a thick layer of dermis and epidermis (Figs. 28, 29). In larger adults a monolayer of large mucous glands lies in the dermis, but glands are absent in the skin over the lens region of the eye in juveniles and young adults. The cornea and sclera of the orbit are adherent to the connective tissue of the covering dermis. The lens is large, spherical, and somewhat cellular, both internally and in its epithelium, and is adherent to the cornea. The diameter of the lens is 0.22 mm; of the orbit is 0.6 mm. The iris is effectively the diameter of the lens, and the lens protrudes through the iris. There are no sphincters or muscles of accommodation associated with iris or lens. The chorioid layer is heavily pigmented. The retina is well developed, covering virtually the entire inner surface of the eye. There are two layers in the outer nuclear layer, two in the inner nuclear layer, and 2–3 in the ganglionic (the numbers of rows of nuclei in the three layers are referred to subsequently as the 'retinal formula'). The retina apparently is composed entirely of rods, which do not appear to contain droplets, as Walls (1942) observed in *Ichthyophis*. A well developed optic nerve (0.9 mm dia where it leaves the orbit) extends from the medio-ventral quadrant of the eye to the optic chiasma. All six extrinsic eye muscles (rectus internus, r. inferior, r. superior, r. externus, obliquus superior, and o. inferior) are present and innervated by the appropriate cranial nerves (see discussion). The retractor and levator bulbi are not associated with the orbit, but with the tentacle. The orbit is surrounded by the extensive Harderian gland except laterally, where it is in contact with the dermis.

1. Family Ichthyophiidae. *Ichthyophis glutinosus* (Linnaeus).

Orbit bulges into outline of head, covered by thick, unpigmented, aglandular skin. Orbit 0.6 mm dia, very similar to the "two-thirds mm" reported by Walls (1942). Lens

Fig. 1. *Ichthyophis* sp. larva (111 mm TL). The lens is crystalline, and free of cornea and retina. The retina is very well developed, especially the outer nuclear layer. Abbreviations: *b* bone; *bv* blood vessel; *c* cornea; *ch* chorioid layer; *d* dermis; *e* epidermis; *em* extrinsic muscle; *emp* extrinsic muscle primordium; *gl* ganglionic layer; *hg* Harderian gland anlage; *il* inner layer; *inl* inner nuclear layer; *l* lens; *lr* lens rudiment; *m* melanocytes; *mrt* musculus retractor tentaculae; *on* optic nerve; *ont* optic nerve tract; *ov* optic vesicle; *pov* primary optic vesicle; *r* retina; *rf* retinal fibers; *ri* rectus inferior; *s* sclera; *sg* skin gland; *sga* skin gland anlage; *sk* skin. Scale bars = 0.1 mm, except where indicated otherwise. In virtually all specimens, preservation artifact is exhibited by retinal detachment from the chorioid layer, and often by the dissociation of lens, retina, cornea, and skin in situations in which these are adherent in life. See text for further description

Fig. 2. *Ichthyophis orthoplicatus* (330 mm TL). The skin overlying the eye is thin. The lens is large, half the diameter of the orbit, and is cellular centrally, lamellate peripherally. The cornea is adherent to lens and skin. See Fig. 1 for abbreviations and scale

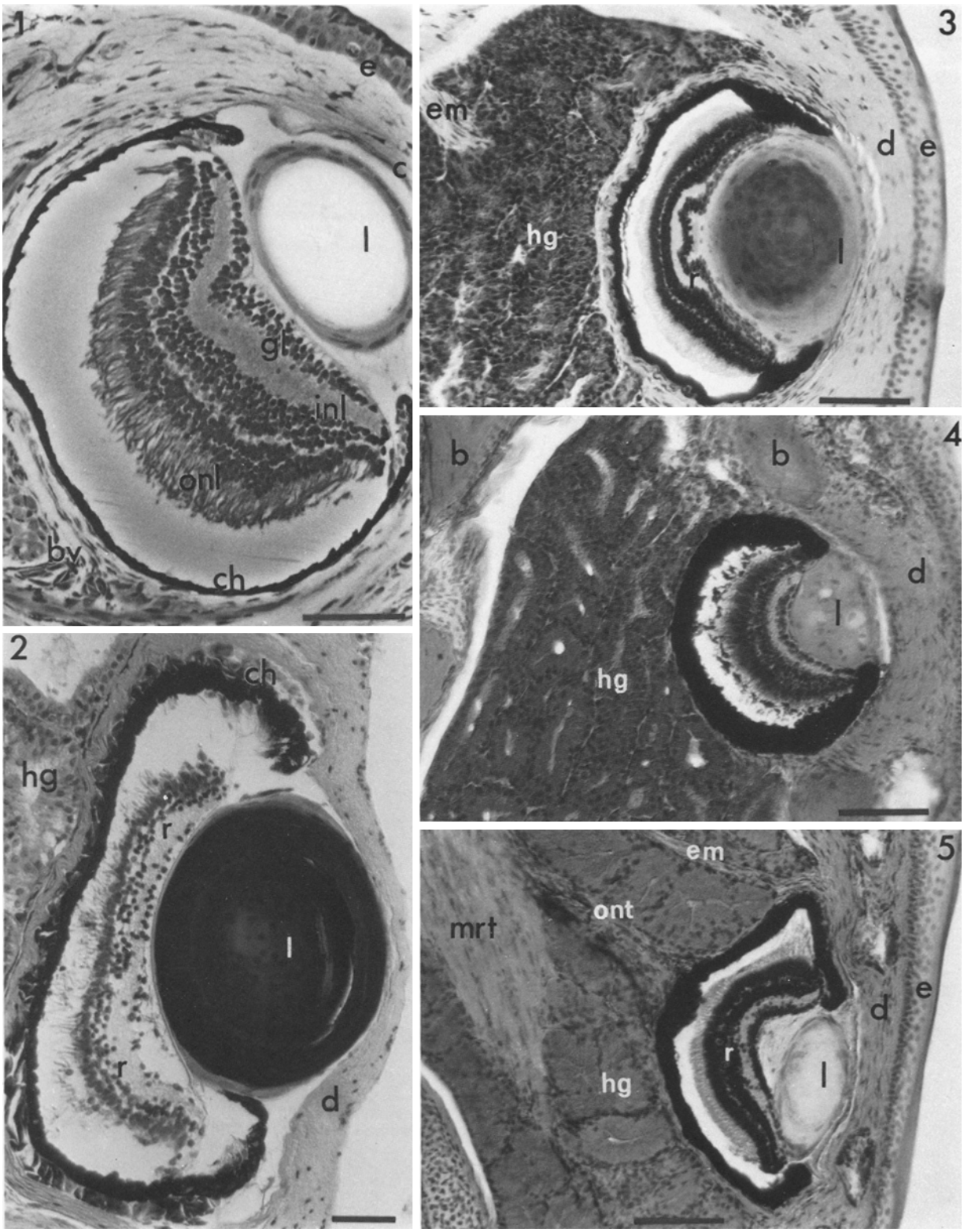


Fig. 3. *Uraeotyphlus narayani* (151 mm TL). The lens is large and cellular, adherent to cornea and retina. The retina folds, peripherally into two shallow folds, centrally into a single deep fold. See Fig. 1 for abbreviations and scale

Fig. 4. *Caecilia occidentalis* (510 mm TL). The orbit is small (0.24 mm dia). The lens is cellular and somewhat amorphous, adherent to cornea and retina. The chorioid is thick. The Harderian gland is unusually large, filling a large cavity behind the eye. See Fig. 1 for abbreviations and scale

Fig. 5. *Hypogeophis rostratus* (224 mm TL). The lens is adherent to cornea and to retina except in the quadrant behind which the optic nerve exits. The rectus superior and the tentacular retractor muscles are shown, as in the optic nerve tract. The latter lies on the tentacular retractor muscle for much of its course. The orbit is unnaturally flattened in this specimen. See Fig. 1 for abbreviations and scale

crystalline, with thick epidermis cellular laterally. Lens slightly spherical, 0.3 mm dia. Middle of lens free of cornea, though cornea is adherent peripherally. Chorioid layer very thick, deeply pigmented. Optic nerve unusually well developed (0.1 mm dia) in contrast to that of adults of other species. Retinal formula 2-2-2, similar to the 2-2-(2-3) reported for the species by Walls (1942). Full complement of extrinsic muscles present, as is a very well developed retractor tentaculi.

Ichthyophis orthoplicatus Taylor (Fig. 2). Eye in this species similar in viritually all respects to that described above for *I. glutinosus*. However, structure of lens in marked contrast; lens cellular internally, lamellate with few nuclei peripherally; lens attached to both cornea and retina in specimen examined.

Ichthyophis sp. (Fig. 1). Specimen examined is a large (111 mm TL) free-living larva, the only such specimen available for analysis. Orbit well formed, 0.45 mm dia; overlain by thick aglandular dermis and thin epidermis. Lens 0.15 mm dia, a crystalline sphere with a thin epidermis, cellular laterally but not medially. Lens not adherent to cornea nor retina; space between lens and cornea greater than that between lens and retina. Chorioid well pigmented; where it forms the iris, underlain by a circular layer of unpigmented cells attached to retina, but not to lens. Retina well deveoped, formula 2-3-(2-3). Optic nerve 0.02 mm dia. Six extrinsic eye muscles present, all insert on orbit. Tentacle has not begun to develop; no separate retractor anlage. Whether it develops later, as in *Dermophis*, or shifts position, as indicated by Engelhardt (1924) and Walls (1942) cannot be determined.

Uraeotyphlus narayani Seshachar (Fig. 3). Orbit 0.3 mm dia, covered by aglandular dermis and epidermis. Lens round, proportionally the largest observed at 0.2 mm dia; cellular centrally (least so at its greatest diameter), lamellar peripherally. Epidermal layer lamellar, thick, deepest laterally. Lens adheres completely to cornea, and to retina except centrally – there retina folds, initially (peripherally) in two shallow folds that deepen medially (centrally) to a single fold. Space between lens and retina coursed by hyaloid tissue strand. Retina complex, flattened peripherally, retinal formula 2-2-(1-2), stouter centrally, formula 1-(3-4)-2. Retinal shape remniscent of the folding effected by some other vertebrate species to afford accommodation in the absence of a lens control mechanism (see below). Optic nerve well developed, 0.06 mm dia. Eye lies in Harderian gland medially. Full complement of extrinsic musculature present, retractor tentaculi is well developed, corroborating Ramaswami's (1941) report.

2. Other Caeciliidae. *Caecilia occidentalis* Taylor (Fig. 4). The orbit small, 0.24 mm dia, in Harderian gland, overlain by thick connective tissue and skin. Skin aglandular over center of orbit. Lens cellular, not spherical but amorphous; 0.13 mm at greatest depth; fused to cornea and retina. Retina well developed, retinal formula (2-3)-2-(2-3) centrally and 2-2-2 peripherally. Optic nerve very attenuate (0.01 mm dia). Only rectus inferior identifiable of extrinsic muscles; present as few fibres only on the right orbit, absent from the left in my sections. Retractor tentaculi stout, passes ventro-medially to antero-laterally behind orbit.

Hypogeophis rostratus (Cuvier) (Fig. 5). Orbit lateromedially flattened in this specimen, 0.35×0.23 mm, similar to the 0.3 dia reported by Walls (1942). Lens cellular at center, lamellar peripherally; slightly spherical, 0.12 mm dia; outermost lens epithelial layer thick, cellular. Lens adherent to cornea and retina, except where optic nerve exits, there a small space is filled with amorphous material, traversed by the hyaloid strand. Lens fused with iris at its greatest diameter, protrudes half of its diameter beyond iris to cornea. Retina well developed, formula 2-3-2 centrally, 1-3-1 anteriorly; similar to Arnold's (1935) report of (2-3)-3-(2-3) centrally, (2-3-(1-2)-1 at the 'border'. Chorioid thick, well pigmented, as Arnold reported, but contradicting Walls (1942). Optic nerve slender, 0.04 mm dia. All six extrinsic muscles, and a stout retractor tentaculi, present.

Geotrypetes seraphini (Dumeril) (Fig. 9). Orbit 0.33 mm dia, overlain by skin. Epidermis thin, no glands in dermis overlying eye. Cornea adherent to dermis. Lens cellular centrally, lamellar peripherally; adherent to cornea and retina; epidermis thin; lens round. Lens diameter 0.15 mm. Iris fused to lens. Retinal formula 2-(2-3)-2 centrally, 1-2-1 peripherally. Chorioid layer deeply pigmented. Optic nerve slender, 0.02 mm dia. Four extrinsic eye muscles present, attenuate: rectus externus, r. internus, r. inferior, and an obliquus. Harderian gland primarily below eye and in tentacular channel.

Geotrypetes grandisonae Taylor (Fig. 10). Orbit in late larva well developed, 0.2×0.25 mm, overlain by thick, aglandular, very cellular dermis and multi-layered, cellular epidermis, characteristic of larval skin. Lens virtually round, 0.12×0.125 mm, vestigially cellular. Lens has very thin slightly cellular epidermis, adheres to cornea, cornea to dermis, lens adheres on medial circumference to retina. Lens also fused to pigmented chorioid layer. Retinal formula is 2-(3-4)-2. Optic nerve thin, 0.025 mm dia. Four extrinsic muscles present, and the retractor tentaculi with slip to orbit. Tentacle embryonic, but retractor tentaculi attached to it; lumen of tentacle perforate to external environment. Orbit in Harderian gland medially; gland not well developed, two or three complexly twining tubules.

Schistometopum thomense (Barboza du Bocage). Eye covered by skin, orbit 0.25 mm dia. Lens spheroid, 0.13 mm dia, has three regions of different density and staining characteristics: center an acellular stroma; surrounded by lamellate layer with few nuclei; peripheral layer of interwoven strands containing numerous elongate cells. Lens free of

Fig. 6. *Typhlonectes compressicaudus* (90 mm fetus). The skin over the eye is very thin. The lens is round, free of cornea and retina. The optic nerve is slender (0.04 mm dia). The Harderian gland anlagen are present. See Fig. 1 for abbreviations and scale

Fig. 7. *Typhlonectes compressicaudus* (321 mm TL adult). The lens is round and proportionally very large; it is adherent to cornea and peripherally to the retina. The skin over the eye is thick but aglandular. See Fig. 1 for abbreviations and scale

Fig. 8. *Dermophis mexicanus* (282 mm TL). This section through the ventral edge of the eye illustrates the chorioid layer and adjacent bone; the rectus inferior is stout. See Fig. 1 for abbreviations and scale

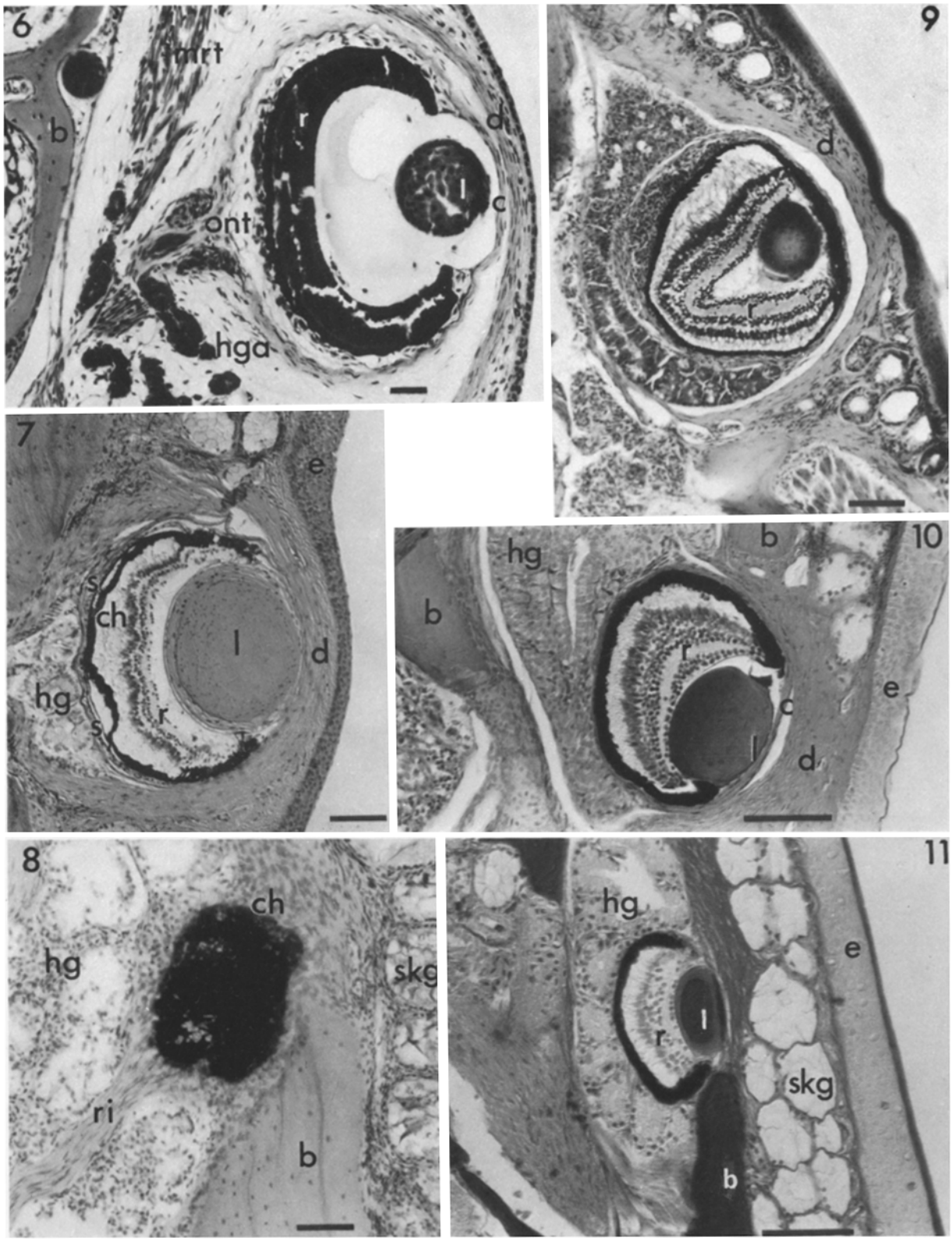


Fig. 9. *Geotrypetes seraphini* (245 mm TL). The lens is small, less than half the diameter of the orbit. The Harderian gland is small. The skin over the orbit is thin. See Fig. 1 for abbreviations and scale

Fig. 10. *Geotrypetes grandisonae* (101 mm TL larva). The skin over the orbit is thick but aglandular. The lens is nearly round and more than half the diameter of the orbit. See Fig. 1 for abbreviations and scale.

Fig. 11. *Idiocranium russeli* (94 mm TL). The skin over the orbit is thick and glandular. The lens adheres to cornea and retina. The orbit is small, even for a small species, and the Harderian gland is large. See Fig. 1 for abbreviations and scale

cornea, held to retina only by connective tissue strands to iris. Retina well developed, formula 2-3-2 centrally, 1-2.5-1.5 peripherally. Optic nerve very thin, 0.01 mm dia, but clearly extends from the ganglionic layer posteriorly. Chorioid heavily pigmented. Extrinsic muscles cannot be counted, since the eye was dissected from the specimen, but at least three are present.

Idiocranium russeli Parker (Fig. 11). Orbit proportionately small in this most diminutive of caecilian species at 0.21×0.13 mm. Eye covered by highly glandular dermis with a thick basal fibrous connective tissue layer and a well developed epidermis. Much of orbit covered ventrally by squamosal bone ledge. Lens crystalline with few cell nuclei present; lens epidermis thin with a few large nuclei. Lens fused to cornea, cornea to dermis, and medial aspect of lens to retina; lens somewhat flattened, 0.1×0.6 mm. Retinal formula 2-2-(2-1). Optic nerve minute, barely measurable at 0.005 mm dia. Four extrinsic muscles present, one represented by only two fibers. One is the retractor tentaculi, which has slip to orbit. See discussion of extrinsic musculature below.

Oscaecilia ochrocephala (Cope) (Fig. 13). Orbit small, 0.2 mm dia, embedded medially in Harderian gland and lying under 0.1–0.2 mm bone, 0.5 mm skin with two layers of dermal glands and a thick epidermis. Lens vestigial, an infolding of the lateral stroma containing a few nuclei larger than those of the retina. Retina loosely organized medially in a stromatous net with an ill-defined ganglionic layer; formula of 2-1 for the nuclear layers. Cells few and large. Optic nerve present, attenuate, 0.02 mm dia where it exits eye. Chorioid pigmented. Harderian gland unusual, highly vascularized, traversed by large capillaries, has mass of lateral muscle posteriorly. One postero-ventral extrinsic muscle present, another may be represented by a stout connective tissue strand which extends anteriorly through Harderian gland to bony rim of orbit.

Gymnopis multiplicata Peters (Fig. 12). Orbit overlain by bone and skin. Central part of eye lies at articulation of maxillary and squamosal bones. Lens amorphous, in contact with a connective tissue layer, presumably the reduced cornea, immediately underlying the periosteum. Lens 0.17 mm dia at greatest depth, appears to lack an epithelial layer. Cushion of cells surrounds portion of lens in contact with exterior connective tissue. Retina well differentiated, formula (1-2)-3-1. Chorioid layer well pigmented. Iris in contact with lens, lens with retina. Optic nerve is attenuate, 0.025 mm dia at the orbit, then a minute strand lying on the retractor tentaculi. The orbit is 0.33 mm dia. I cannot distinguish any extrinsic musculature.

Afrocaecilia taitana (Loveridge) (Fig. 14). Orbit covered by bone, overlain by glandular dermis and epidermis. Eye extremely reduced (0.12 mm dia), adherent to periosteum anteriorly, embedded in Harderian gland elsewhere. Lens absent. Retina amorphous but continuous structure lining sphere of orbit, anteriorly through posteriorly, as though optic cup did not invaginate during development. Slight central hollowing suggests two irregular layers. Optic nerve very tenuous (0.005 mm dia, lying very near m. retractor tentaculi). Eye lacks cellular chorioid layer, though evidence of melanin posteriorly on orbit; pigment dispersed irregularly, in contrast to that of eyes in other species examined. Extrinsic eye muscles absent, except for scant fibers of a ventrally inserting muscle near course of the optic nerve. Retractor tentaculi well developed; orbit lies on it. It is possible that fibers of other extrinsic muscles are incorporated into it, if they develop at all.

Boulengerula boulengeri Tornier (Fig. 17). Specimen not well fixed; eye appears to be the most reduced of those examined. Orbit lies under bone and skin; pulled to postero-ventral margin of the bony cavity by connective tissue strands, which deform orbit so that it is 0.13×0.06 mm. Lens, optic nerve, and chorioid pigment absent. Retina present, represented by rather few nuclei lying in stroma, arranged as a deformed bilayered net. Harderian gland very small, lies medially to orbit. Retractor tentaculi in the Harderian gland; small, as de Villiers (1938) indicated. Connective tissue strands may be a vestige of the rectus inferior muscle, which may be the last of the extrinsics to disappear. De Villiers (1938) indicates an "eye muscle" in his Figure 8, but does not otherwise refer to it.

3. Family Scolecomorphidae. *Scolecomorphus kirkii* Boulenger (Fig. 16). Eye, as in most species of the genus and therefore the family, out of socket under squamosal and embedded in tentacle; eye on posterior side of tentacle and covered by a deep glandular dermis and thick epidermis. Orbit 0.23 mm dia. Lens round, 0.15 mm dia, cellular, cells few and held in a loose stromatous net. Lens adherent to cornea, which lies under the dermis of upper jaw; lens also adherent to retina. Retinal formula 1.5-3-(1-2); retina 0.06 mm deep. Optic nerve present, attenuate, 0.05 mm dia where it leaves the orbit. Chorioid layer pigmented. Two attenuate extrinsic muscles attach to orbit, probably retractor inferior and superior oblique. Two kinds of glands associated with tentacle and eye, a posterior set that resembles the Harderian gland, and an anterior epithelial set. A layer of the latter form a glandular pocket between the cornea and the dermis.

Scolecomorphus uluguruensis Barbour & Loveridge (Fig. 15). Orbit, as in *S. kirkii*, pulled out of the socket under bone, lies embedded in tentacle under skin, which contains numerous glands. (This is contrary to de Villier's

Fig. 12. *Gymnopis multiplicata* (370 mm TL). The lens is amorphous and adheres to retina and cornea, and the cornea to the overlying bone. The retina is well organized. See Fig. 1 for abbreviations and scale

Fig. 13. *Oscaecilia ochrocephala* (432 mm TL). The lens is rudimentary and the retina a bilayer. Note the attenuate extrinsic muscle. The Harderian gland is large and exceptionally vascular. See Fig. 1 for abbreviations and scale

Fig. 14. *Afrocaecilia taitana* (246 mm TL). The lens is absent and the retina amorphous. The eye adheres to the overlying bone. The chorioid layer is not pigmented. See Fig. 1 for abbreviations and scale

Fig. 15. *Scolecomorphus uluguruensis* (271 mm TL). The eye is embedded in the tentacle and is drawn out of the socket, lying under the skin of the upper jaw. The eye is oriented so that the lens is medial, and the net-like retina and chorioid layer are lateral toward the skin. The eye is much reduced relative to that of *S. kirkii* (Fig. 28). See Fig. 1 for abbreviations and scale

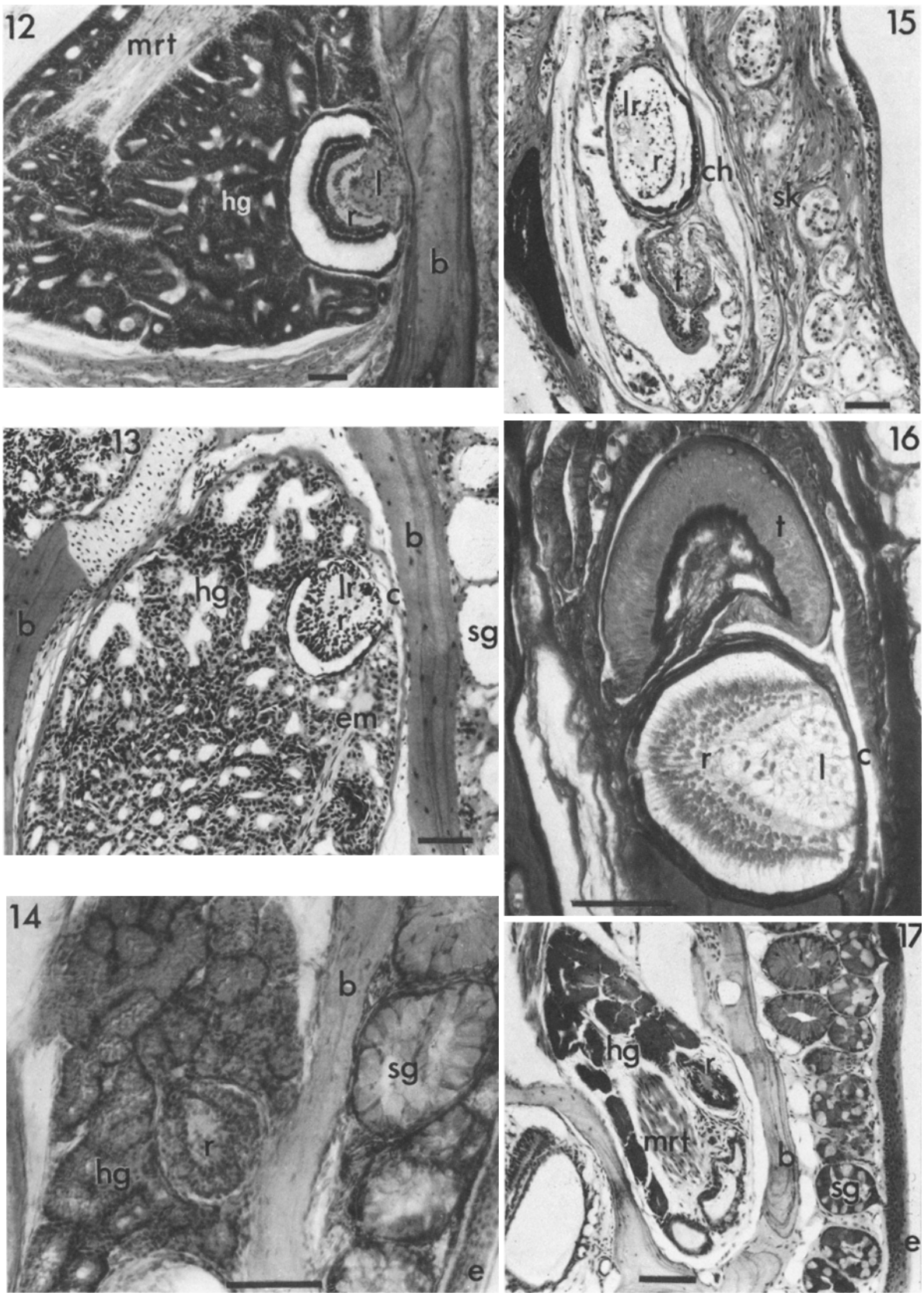


Fig. 16. *Scolecomorphus kirkii* (275 mm TL). The eye is embedded in the tentacle. The lens is cellular and adheres to the cornea. The retina has three nuclear layers and the eye has a densely pigmented chorioid layer. See Fig. 1 for abbreviations and scale

Fig. 17. *Boulengerula boulengeri* (171 mm TL). The eye is very reduced; an amorphous retina is present. Extrinsic muscles are absent, and evidence of an optic nerve is meager. See Fig. 1 for abbreviations and scale

(1938) report, in which he stated that the eye is hidden by the paraquadrate [=squamosal], but perhaps corroborates Ramaswami's (1941) statement that the eye is not covered by bone.) Both eyes oriented so that the pigmented chorioid layer is lateral, abutting the dermis, and the lens is medial. Ramaswami (1941) states that the eye is directed toward the lower jaw, and devoid of lens, extrinsic muscles, or optic nerve. Eye not small, 0.18×0.28 mm. Lens rudimentary, some 6–8 cells and 0.03 mm dia, recessed in orbit, held by stroma. Lens adheres to retina and to connective tissue of capsule of orbit. Outer nuclear layer of retina one layer deep; the other two nuclear layers are a few cells irregularly distributed in a stromatous net. Neither extrinsic muscles nor an optic nerve are discernable. Eye, twice diameter of tentacle, and the tentacle, held in pocket of connective tissue that has a glandular epithelial lining and which is entered by several capillaries. Obviously, considerable variation in eye morphology can exist among species in the same genus.

4. Family Typhlonectidae. *Typhlonectes compressicaudus* (Dumeril & Bibron) (Fig. 6). Orbit proportionately large; in young adults examined, 0.6 mm dia; bulges into outline of head, covered by thick layer of aglandular dermis and epidermis. Glands encroach in dermis over periphery of orbit, but are not present in skin overlying lens. Lens round 0.35 mm dia, slightly cellular. Epidermal layer thick medially, thin laterally, less cellular with different staining characteristics than center of lens. Lens adheres to cornea, peripherally to retina. Thin hyaloid strand present, connecting the two structures. Retina well developed, formula 2-3-2. Optic nerve attenuate, 0.06 mm dia. Orbit lies in Harderian gland. Five extrinsic eye muscles identifiable, rectus superior, obliquus superior, rectus externus, rectus inferior, and obliquus inferior. I do not observe a rectus medialis, but it is possible that its few fibers may be in the same plane as the very large retractor tentaculi.

A 90 mm fetus of the same species has an eye rather similar to that of the large adult (Fig. 7). Eye bulges under thin aglandular dermis and very thin epidermis. Orbit 0.56×0.43 mm, lens 0.21 mm dia. Lens very round, cellular, with a flat cellular epithelium. Lens free, with a large space between it and cornea, and it and retina. Retinal formula (1-2)-3-(2-3), the latter layer very cell dense. Optic nerve 0.04 mm dia. Chorioid layer deeply pigmented. Harderian gland developing, several capillaries present in socket. Five extrinsic eye muscles present, more attenuate but in the position of those of the adult.

II. Development of the eye in Dermophis mexicanus

The embryology of the eye of caecilians is in accord with the general vertebrate pattern until metamorphosis and the appearance of the tentacle. Even so, there are variations on the theme consistent with the absence or reduction of many features normally present in the adult eye. I therefore describe the development of the eye and its associated muscles and glands in *Dermophis mexicanus* from specimens 5 mm total length through adults of nearly 400 mm TL.

5 mm TL (Fig. 18). Primary optic vesicle well formed, connected to prosencephalon by the constricted optic stalk. Vesicle in contact with epidermal ectoderm, thickened in the contact region.

8 mm TL. Optic stalk constricted, but optic vesicle has not begun to invaginate. Lens placode component thickened.

10 mm TL (Fig. 19). Optic vesicle fully invaginated, forming secondary optic vesicle. Lens vesicle also fully invaginated, hollow, has no ductal connection to epidermal ectoderm, but is overlain by an epidermal monolayer. A second 10 mm specimen has thin outer (pre-chorioid) and thick inner (pre-retinal) layers more distinctly forming the secondary optic vesicle.

22 mm TL (Fig. 20). Melanocytes present in chorioid monolayer. Inner layer greatly thickened, several cell layers deep, but not organized. Lens hollow cellular structure filling corneal gap of optic cup.

35 mm TL (Figs. 21, 22). Chorioid layer well established, retina differentiating, having a thick outer layer and a thin inner layer. A thin hyaloid vessel to lens extends from the central artery, and retinal fibers appear to be invading the thin optic stalk.

44 mm TL (Fig. 23). Chorioid a densely pigmented monolayer; retina dense, with an elongate outer nuclear layer apparent but no other differentiation. Cornea and sclera established. Lens well vascularized (large cells present in center, peripherally reduced epithelial cellular layer). Optic nerve and multiple vessels procede medially in course of chorioid fissure of optic stalk as the fissure closes. Mesenchymatous masses that appear to be primordia for three extrinsic muscles are present outside the orbit. Cells not striated, lack origins and insertions.

58 mm TL (Fig. 24). Eye very similar to that of the above-described specimen. Retina in two amorphous layers. Hyaloid artery regressed but represented by connective tissue strand. Ventro-posterior and antero-dorsal muscles in contact with orbit, but not with their origins. Mesenchymatous anlage of the tentacle aggregated. Third muscle present in the 44 mm specimen differentiating in situ, not in contact with any other structures.

68 mm TL (Fig. 25). Little change from the condition reported above, except tentacle differentiated into "core" and "wall" components (see below). Anlage of fourth extrinsic muscle aggregated, but not differentiated.

72 mm TL. Retina three distinct nuclear layers, nuclei of outer nuclear layer larger than those of other layers. Lens composed of large cells. Optic nerve well developed, relatively stout. Orbit well vascularized following closure of chorioid fissure. Two extrinsic muscles have established origins on medial wall (sphenethmoid) of socket, probably rectus inferior and obliquus superior. Tentacle continues to differentiate, but is not associated with musculature. Harderian gland anlagen have appeared posterior to orbit.

80 mm TL. Lens protrudes through iris; presumptive

Fig. 18. The embryo is 5 mm total length (*TL*). The primary optic vesicle is connected to the prosencephalon by the optic stalk. Thickening peripherally and invagination have begun. Bar = 0.02 mm. See Fig. 1 for abbreviations

Fig. 19. 10 mm TL. The secondary optic vesicle and the lens vesicle are fully formed; the lens is free of epidermal ectoderm. See Fig. 1 for abbreviations and scale

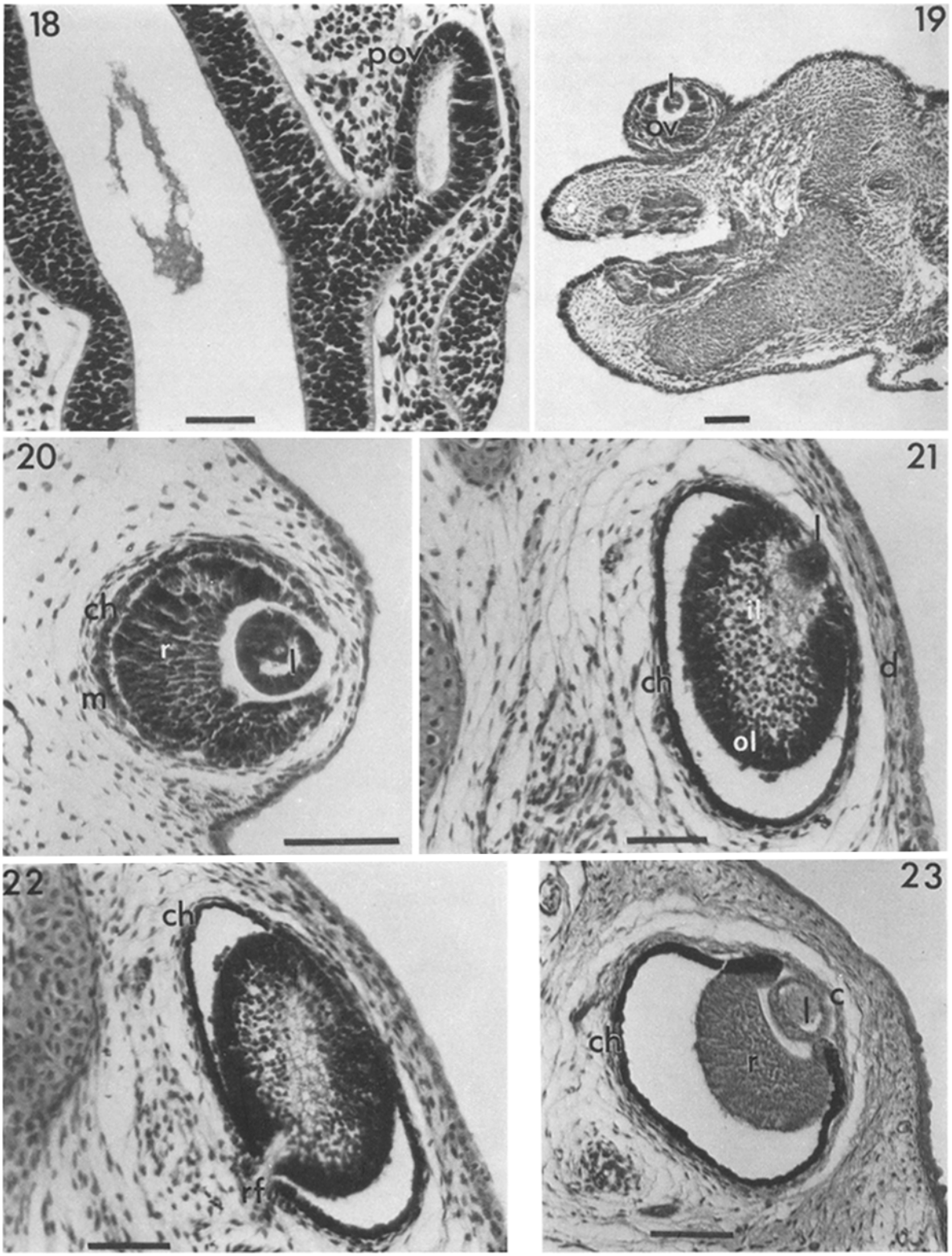


Fig. 20. 22 mm TL. The retina is thickened; the lens hollow. Melanocytes are present in the chorioid. Bar = 0.05 mm. See Fig. 1 for abbreviations

Fig. 21. 35 mm TL. The retina has differentiated to a thick outer and a thin inner layer of cells. See Fig. 1 for abbreviations and scale

Fig. 22. 35 mm TL. Retinal fibers invade the path of the degenerating optic stalk. See Fig. 1 for abbreviations and scale

Fig. 23. 44 mm TL. The lens is solid and cellular. The retina is dense. The cornea and sclera are differentiated. Extrinsic muscle primordia are forming. See Fig. 1 for abbreviations and scale

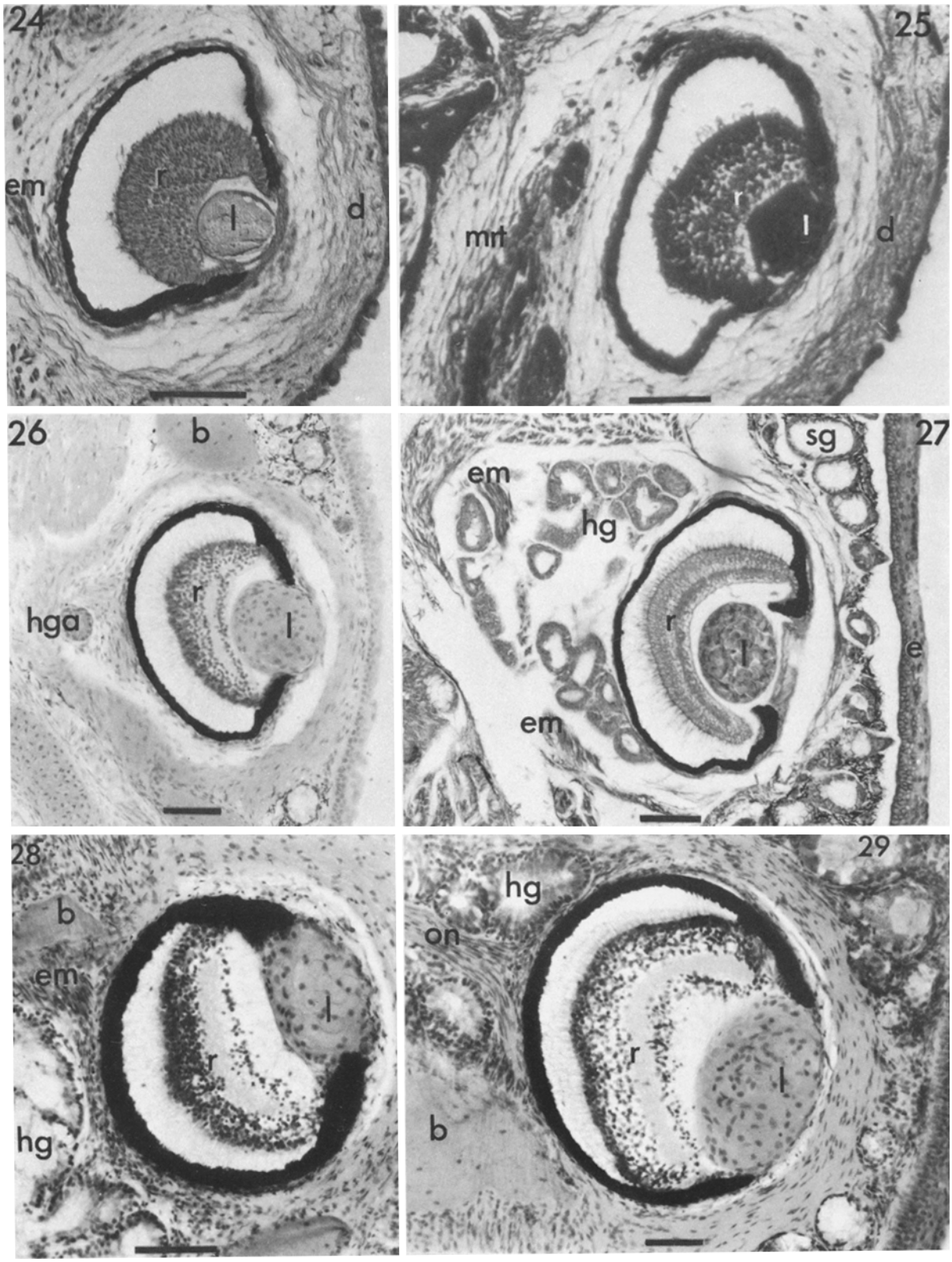


Fig. 24. 58 mm TL. The eye is little changed from the 44 mm stage. The extrinsic muscles are differentiating, and two are in contact with the orbit. See Fig. 1 for abbreviations and scale

Fig. 25. 68 mm TL. The retina is distinctly bilayered. The retractor muscle of the tentacle is developing *in situ*. It never contacts the orbit. See text for discussion. See Fig. 1 for abbreviations and scale

Fig. 26. 105 mm TL. In this large fetus, the retina has three nuclear layers. The lens protrudes through the iris. Harderian gland anlagen are aggregated, as are skin gland anlagen. See Fig. 1 for abbreviations and scale

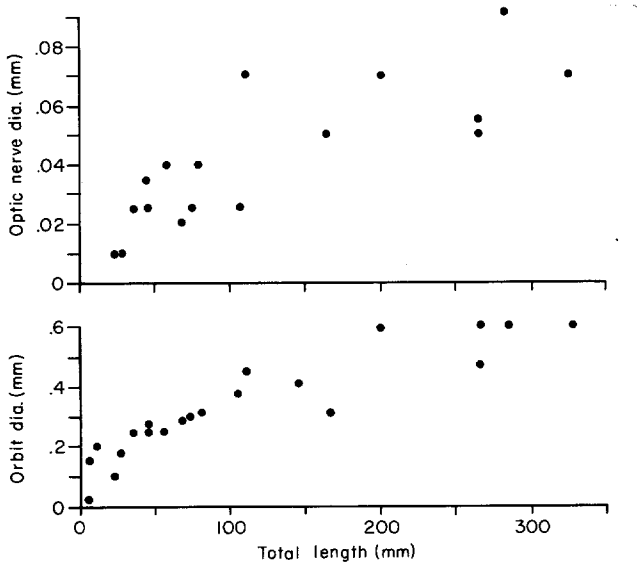


Fig. 30. Growth of orbit and optic nerve in an ontogenetic series of *Dermophis mexicanus*

cornea thin and in complete contact with lens and orbit. Retinal layers better differentiated. A sixth muscle anlage aggregated posterior to orbit. More Harderian gland anlagen have appeared; hollow monolayered spherical structures.

105 mm TL (Fig. 26). Lens still cellular in center; protrudes through iris. Small, discrete space between lens and retina. Retina at center has 3 rows of nuclei in inner nuclear layer, 2 in ganglionic layer, and an irregular 1 in outer layer. Peripherally 2 in inner layer and ganglionic also poorly differentiated. Six extrinsic eye muscles in contact with the orbit and the medial wall of the socket; recognizable by position, origin, and insertion. Tentacular retractor differentiated, parallels course of tentacle, originates on socket wall, has indication of some fibers inserting on tentacle, but is not yet striated. Other intrinsic muscles striated, presumably capable of function. More gland anlagen present.

110 mm TL. Structure much the same as 105 mm specimen. Retinal layers more discrete. Chorioid thick, well pigmented monolayer. Retractor tentaculi not yet striated. Optic nerve still increasing in diameter (see Fig. 30), as is orbit.

147 mm TL. Orbit spherical; lens adherent to cornea only at center. Iris contacts lens medially at its diameter; lens protrudes through iris the length of its radius. Lens 0.19 mm dia, cellular. Retina effectively two layers, outer layer with elongate nuclei in outermost layer. Optic nerve better developed. Extrinsic muscles show scant striation. Harderian gland nearly fills socket.

164 mm TL (Fig. 27). Orbit lateromedially compressed and elongated. Lens has cellular center and protrudes through iris. Lateral aspect of orbit, including lens, overlain by cornea and bound to it by fibrous connective tissue. Cornea a discrete layer, but adherent to lower layer of dermis. Skin overlying cornea thin, lacks mucous or "poison" glands only over orbit. Extrinsic eye muscles well developed and of approximately equivalent diameters, except for retractors of tentacle and its sheath. These muscles stout flattened structures. Harderian gland well developed behind orbit. No muscles of accommodation, ciliary body, etc., present, a characteristic of all caecilians.

199 mm TL. Lens cellular, completely free of contact with cornea, so that there are fluid-filled chambers in front of and behind lens. Retina is still two layers, effectively in contrast to the 105 mm specimen. Harderian gland extends into the tentacular channel. Extrinsic muscles and retractor tentaculi striated. Given that there is relatively little fusion of the orbit to overlying tissues, it is possible that the extrinsic muscles may be functional, and rotate the orbit in these juvenile caecilians.

264–267 mm TL (Figs. 28, 29). Structure is little changed from the 164 mm specimen. Lens protrudes through iris; attached to cornea and iris. Retina has three nuclear layers with a very well developed inner plexiform layer. Extrinsic muscles more attenuate than formerly, especially the obliques. Harderian gland extends into tentacular channel. In the 267 mm specimen, lens adheres strongly to cornea, and is deformed into cavity of orbit by the hyaloid strand.

282 mm TL (Fig. 8). Eye has adult form. Lens diameter of iris but free of cornea. Retina well differentiated, formula 2-2-(2-3). Space between lens and retina, and in this well fixed eye, a connective tissue strand runs between lens and retina, perhaps vestige of hyaloid artery. Muscles as described above. Socket notably more extensive, bone surrounding optic nerve, whereas much space previously, and laterally maxilla circumscribes orbit. Optic nerve leaves orbit posteroventrally, passing through optic foramen in sphenethmoid bone.

325–327 mm TL. Structure as described above, with extrinsic muscles somewhat more attenuate and tentacular retractor stout. Harderian gland massive, with tentacular retractor coursing through it. Lens cellular, held to iris at its edge by connective tissue. Gap between lens and cornea, with no evidence of fibers between the two, but orbit is shrunken so cannot determine whether this is artifact or the lens really is not adherent.

D. Discussion

I. General pattern of development

The embryology of the eye of caecilians is similar to that of vertebrates in general (see Nelsen, 1956 and most em-

Fig. 27. 164 mm TL. The juvenile eye has a well formed retina. The lens is free of the retina, but attached by fibers to the cornea. The epidermis is thickened, and dermal skin glands are interrupted only over the orbit. See Fig. 1 for abbreviations and scale

Fig. 28. 264 mm TL. In the mature eye, the lens is held to the cornea by connective tissue fibers. Extrinsic muscles and Harderian glands are well developed. See Fig. 1 for abbreviations and scale

Fig. 29. 267 mm TL. The optic nerve (sheath shown) is relatively stout (0.05 mm dia), the orbit 0.6 mm dia. The skin over the eye is thick in adults. See Fig. 1 for abbreviations and scale

bryology texts), especially in terms of early development. Yet there are significant differences in later development, especially in the lack of initiation of components of accomodation, the establishment of the extrinsic musculature, and the fusion of cornea to dermis or periosteum. In addition, there are differences in developmental timing and pattern between species with free-living larvae and live bearers.

The development of the eye of *Hypogeophis rostratus* and *Grandisonia alternans* (Stejneger) was described by Arnold (1935). However, he did not consider the extrinsic musculature, glands, etc. Arnold also concentrated on premetamorphic development, so comparisons of later stages, especially involving the influence of the tentacle, cannot be made. Conversely, Engelhardt's (1924) description of the eye and tentacle of *Ichthyophis glutinosus* dealt largely with the musculature and its innervation rather than the development of the entire system. The series of *H. rostratus* and *G. alternans* described by Arnold (1935) is very complete for early embryology but the ontogenetic series of *D. mexicanus* is more complete for the entire sequence and provides finer discrimination of timing. Engelhardt (1924) had three specimens 170–240 mm TL for his study of eye and tentacle muscles and eye structure generally in *Ichthyophis glutinosus*, so he relied on the descriptions by Sarasin and Sarasin (1887–1890) of the embryology of the eye and its musculature. I consider the development of the extrinsic musculature below, in conjunction with the analysis of interspecific patterns of musculature.

Dermophis ontogeny described herein is much like that of *Hypogeophis* and *Grandisonia* (Arnold 1935) and *Ichthyophis* (Sarasin and Sarasin 1887–1890), especially in premetamorphic stages. These species provide comparison among a fairly large (adult body size) species with free-living larvae, a medium and a small direct-developer (eggs laid on land; metamorphosed young hatch), and a live-bearer (metamorphosed young born after oviductal retention, apparently always with maternal nutrition after the yolk is exhausted). Some of the differences between *Ichthyophis* and the other genera may be correlated with utilization of vision during the larval period. The skin overlying the orbit is thin, and the epidermis is larval in character, only a few cells deep and lacking a keratinized layer.

II. The larval eye

In larval *Ichthyophis* (Sarasin and Sarasin 1887–1890; pers. obs.) the cornea is free of the dermis, and there is a space between cornea and lens greater than that between lens and retina (Fig. 1). The lens is well developed, only its lateral epidermis cellular (but see Peter 1898). The lens is virtually round, suggesting reasonably good visual acuity in virtually all planes of intersection of light with the retina (see discussion of lens morphology below). The retina is well developed with several nuclei in each layer; rods are large. The optic nerve is not large, though the ganglionic layer of the retina has 2–3 rows of nuclei, suggesting multiple fibers. All of the extrinsic muscles are well developed, including the retractor and levator bulbi, and associated with the orbit, as Walls (1942) reported. Since the tentacle appears at metamorphosis, larvae lack that structure. The skin overlying the orbit is thin, and the epidermis is larval in character, only a few cells deep and lacking a keratinized layer. The relatively well developed lens, retina, orbit, and musculature suggest the probability of effective photoreception in these larvae. Further, the orbit is freer of attachment to the dermis than in other caecilians, so it is possible that the levator and retractor bulbi may be able to move the orbit as in a number of other amphibians. However, it should be noted that larval *Ichthyophis* have a mode of sensory perception in addition to vision, hearing, and nontentacular, nasal olfaction. They have a lateral line neuromast system and ampullary electroreceptors (Hetherington and Wake 1979) and the latter may well supplement any photoreception possible. The neuromasts disappear at metamorphosis.

The eye of late-larval *Geotrypetes grandisonae* (Fig. 10) also has a nearly round lens, suggesting visual acuity. However, dermis, cornea, lens, and retina are all adherent in sequence, and the pigmented chorioid adheres to the lens. I find only four extrinsic muscles. The tentacle is poorly formed, though its lumen is perforate to the surface, and the retractor tentaculi is stoutly attached to the tentacle, not the eye.

Direct-developing and fetal eyes. Development of eyes in species that do not have free-living larvae circumvents certain aspects seen in *Ichthyophis*. Lenses characteristically are spherical, but not round. Lenses may develop much more slowly, retaining their embryonic cellular state even throughout life, in contrast to that of the post-hatching larva which is already more advanced. However, the morphology of the lens of *I. orthoplicatus* suggests that lens development may vary within the genus, so a fast developmental rate may not distinguish species with free-living larvae. Development of the extrinsic musculature may be delayed, as seen in *D. mexicanus*. In particular, the retractor tentaculi develops near metamorphosis and is never associated with the orbit (see below). I suspect that in species that lack certain extrinsic muscles, those muscles never develop, rather than developing and subsequently regressing. Optic nerve development is variable. It appears to increase in size during development and after metamorphosis in both *Ichthyophis* and *Dermophis* (Fig. 30), but Arnold (1935) reported regression in diameter at approximately metamorphosis in *Hypogeophis* and *Grandisonia*. He also reported a reduction in thickness of the retina with ontogeny. I do not see this in *Dermophis*, and am concerned that Arnold did not indicate where he measured this thickness in all eyes, nor did he indicate whether a reduction in number of retinal cells is involved. This is a crucial point in evaluating retinal change. It is my impression that the developing retina may appear thick though not cell dense, but with further organization of the layers of the retina, it may look thinner, despite packing more cells. It appears that in *Dermophis* the retina may be effectively bilayered without a discrete ganglionic layer until maturity, or two years after birth.

III. Comparative morphology of adult eyes

a) The lens. The lens in caecilians is spherical, a condition correlated with reduced light (caves, fossorial situations) that maximizes acuity by transmission of light nearly equally to virtually the entire retinal receptor arc. The round lens of free-living larvae and aquatic adults may maximize this condition (see above); however, lenses of most adult caecilians are spherical, which should maximize visual acuity in low-photic environments (Walls 1942; Rodieck 1973). The variation observed among species of caecilians

Table 2. Lens morphology in caecilians (state 1 = lens absent; 2 = rudimentary; 3 = amorphous, cellular; 4 = cellular; 5 = crystalline outer layer, cellular inner; 6 = cellular outer layer, crystalline inner; 7 = crystalline bilayer; r = round; s = spherical; + = state present)

Species	State						
	1	2	3	4	5	6	7
Ichthyophiidae							
Ichthyophis sp. larva						+s	
Ichthyophis glutinosus					+s		
Ichthyophis orthoplicatus					+s		
Uraeotyphlus narayani					+r		
Caeciliidae							
Afrocaecilia taitana	+						
Boulengerula boulengeri	+						
Caecilia occidentalis			+				
Dermophis mexicanus				+s			
Geotrypetes grandisonae (larva)					+r		
Geotrypetes seraphini				+s			
Gymnopis multiplicata			+				
Hypogeophis rostratus					+s		
Idiocranium russeli						+s	
Oscaecilia ochrocephala		+					
Schistometopum thomense						+s	
Scolecomorphidae							
Scolecomorphus kirkii				+r			
Scolecomorphus uluguruensis		+					
Typhlonectidae							
Typhlonectes compressicaudus				+r			

is correlated with pattern of development of the lens and its epidermis. Table 2 shows the variation in shape and histology among species analyzed.

There is considerable variation among taxa in the state of the lens. Variation is not consistent with taxonomic groupings, nor with out-group comparisons of state of development, ecology, or 'evolutionary derivation'. The lens epidermis varies among adults of taxa of caecilians in thickness and in cellularity (proportion of nucleated cells present) vs. lamellar structure, and in the morphology of the central sphere of the lens. Given that cellular structure is embryonic and its retention paedomorphic, a lamellate or crystalline lens is developmentally advanced, both in terms of developmental rate and by out-group comparisons of lens condition in other amphibian and in non-amphibian taxa. The data suggest (Table 2) that the ichthyophiids have the best developed lens, and that typhlonectids, caeciliids (with much variation), and particularly scolecomorphids (with some variation) have slower developing and more embryonic (possibly less derived) lenses. Further, the data indicate that the more primitive caecilians (ichthyophiids, by out-group comparison of other characters) have the most highly developed lenses (and perhaps greater visual acuity, especially among larvae, as noted above). The aquatic typhlonectids have a well developed lens, possibly useful in the turbid waters in which they live. The caeciliids show a mosaic of lens development. Lenses range from well developed to amorphous to rudimentary to absent. Among caeciliids, larvae and diminutive paedomorphs (*Geotrypetes grandisonae* and *Idiocranium*) have the furthest developed lenses. Several species have intermediate development of the lens (crystalline structure presumed derived, by out-group comparison; cellular structure primitive and embryonic). A poorly organized, irregularly non-spherical lens characterizes *Caecilia occidentalis*, which has the orbit covered by skin and by bone. That of *Oscaecilia ochrocephala* and *Scoleomorphus uluguruensis* is rudimentary, represented only by a few cells. The diminutive *Afrocaecilia taitana* and *Boulengerula boulengeri*, whose eyes are covered by skin and bone, lacks a lens entirely. I infer that reduced transmission of light through the skin and/or skin and bone covering is correlated with the trend in lens morphology from 1) the 'adult vertebrate' state to 2) retention of the embryonic cellular morphology to 3) development of an amorphous lens to 4) complete suppression or delay of lens development.

b) The retina. Caecilian retinas characteristically have the eight-layered morphology typical of most vertebrates. The nuclear layers are easily identified and are usually well organized in three strata, the outer nuclear, the inner nuclear, and the ganglionic. Numbers of rows of nuclei in these layers and numbers of nuclei per row vary among taxa (see Table 3). Absolute counts of nuclei were not attempted due to thickness of sections and imperfect fixation. However, a comparison of the outer nuclear layer of, for example, *Uraeotyphlus* (Fig. 3) with that of *Dermophis* (Figs. 28, 29) indicates that *Uraeotyphlus* has greater numbers of more densely packed nuclei.

Retinas of all species examined appear to contain only rods, with no cones evident at all, as suggested by Walls (1942). There is little morphological variation in cells of the outer nuclear layer. However, more precise histology coupled with physiological measurements are under way to confirm this suggestion. There does appear to be variation among taxa in shape of the rods. Forms with fewer cells in the layer have 'bulky' rods with round nuclei and proportionately short outer segments (e.g., *Hypogeophis, Dermophis, Gymnopis, Caecilia, Idiocranium, Afrocaecilia, Typhlonectes*); those with many cells have rods with elongate nuclei and longer outer segments (e.g., *Ichthyophis, Uraeotyphlus, Geotrypetes*). Shape of the rods in the latter genera may be correlated with 'packing' the greater number of cells, or with increased visual perception, or with both aspects.

In the only recent study of caecilian photoreceptors, Storch and Welsch (1973) examined the ultrastructure of the chorioid layer and the receptor cells of *Ichthyophis kohtaoensis* Taylor. They found reduced numbers of organelles in receptor cells, and chorioid cells with a smooth basal plasma membrane and few apical cellular processes affording only a loose contact with the receptor cell outer segments. They interpreted these data as indicating "markedly decreased functional activity."

Preliminary electroretinograms of *Dermophis mexicanus* indicate retinal response similar to that of *Necturus*. Normal attenuation of response to multiple sequential stimuli also occurs (Wake and Hare, unpublished).

The major trends seen in retinal structure in caecilians are 1) apparent reduction in numbers of cells in more derived taxa (see above), and 2) breakdown of retinal organization in eyes that are extremely reduced in other ways as well. Only *Afrocaecilia taitana* and the closely related *Boulengerula boulengeri*, and to a lesser degree, *Scolecomorphus uluguruensis*, of all species examined, have the retina

Table 3. Retinal formulae in caecilians, compared with other vertebrates (Retinal formulae are numbers of nuclear layers in the outer nuclear, inner nuclear, and ganglionic layers of the retina at the center of the orbit)

	O	I	G	Net	Ref[a]
Family Ichthyophiidae					
Ichthyophis sp. (larva)	2	3	2–3		
Ichthyophis glutinosus	2	2	2		
	2	2	2.5		W
Uraeotyphlus narayani	2	3–4	2		
Family Caeciliidae					
Afrocaecilia taitana				x	
Boulengerula boulengeri				x	
Caecilia occidentalis	2–3	2	2–3		
Dermophis mexicanus	2	2	2–3		
Geotrypetes grandisonae (larva)	2	3–4	2		
Geotrypetes seraphini	2	2–3	2		
Gymnopis multiplicata	1–2	3	1		
Hypogeophis rostratus	2	3	2–3		
Idiocranium russeli	2	2	1–2		
Oscaecilia ochrocephala	2	1	0		
Schistometopum thomense	2	3	2		
Family Scolecomorphidae					
Scolecomorphus kirkii	1–2	3	1–2		
Scolecomorphus ulunguruensis	2			x	
Family Typhlonectidae					
Typhlonectes compressicaudus (fetus)	1–2	3	2–3		
Typhlonectes compressicaudus (adult)	1	2	2		
Osteichthyes					
Acipenser fulvescens	2	0.5	0.125		W
Amia	3		1		W
Protopterus	2	4	1		W
Ameiurus nebulosus	2	1	few		W
"Teleosts"	3	4	1		P
"Teleosts"	5	4	0.5		P
Amphibia					
Xenopus laevis	1	1.5	1		W
Rana temporaria	2	3	1		D
Rana pipiens	2	5	1		P
Triturus	1	6	2		D
Reptilia					
"Chelonians"	2	5	1		P
Sphenodon	8	16	4		P
Boa	3	3	1		P
Osyrhina spallanzani	1	5	1		P
Dennisonia superba	3	3	1		P
"Crocodiles"	2	1	4.5		P
Aves					
Hen	2.5	2.5	18		P
Marsh hawk	4	3	20		P
Robin	3	3	15		P
Albatross	6	5	26		P
Mammalia					
"Nocturnal placentals"	17	1	5		P
Loris	13	1	5		P
Rat	10	1	5		P
Chinchilla	9	1	3		P
Opossum	11	1	3		P

[a] References: D = Duke-Elder, 1958; P = Prince, 1956; W = Walls, 1942. See literature cited for full reference

as an amorphous but continuous layer that lines the entire orbit. The eye in these species is very reduced, covered by bone or pulled out from under bone, and lacks a lens, extrinsic muscles, and a cellular chorioid layer. An extremely attenuate optic nerve may be present. This morphology suggests that degeneration of retinal structure is one of the last events in the reduction of visual capacity in caecilians.

c) The optic nerve. An optic nerve is present in nearly all caecilians examined, even those with extreme of eye reduction (e.g., *Caecilia, Afrocaecilia*). It was not discernable in *Boulengerula boulengeri* or *Scolecomorphus uluguruensis*, but the specimens are not well preserved. The nerve may be very attenuate, and associated with a disorganized retina as in *Afrocaecilia*, but it need not be lost. The optic nerve is reported absent in *Dermophis* (de Jager 1939a), but Ramaswami (1941) and I both have found it (it is present in all eyes in some forty heads that I have sectioned of *D. mexicanus* even with routine staining); it is reported absent in *Boulengerula boulengeri* and *Scolecomorphus uluguruensis* (de Villiers 1938), *Oscaecilia* (*Coecilia* of de Jager 1939a, and *Herpele* of Norris and Hughes 1918) *ochrocephala*, and *Caecilia gracilis* Shaw (Norris and Hughes 1918). Ramaswami (1943) reported a poorly developed optic nerve in *Gegeneophis carnosus* (Beddome). Ramaswami (1941) summarized the literature on eye nerves (and muscles), and indicated some of the contradictions in these reports. I find them suspicious as well. My experience indicates that utilization of old, field-preserved specimens can lead to serious staining problems, for neural structures are among the first to degenerate. Though I have not had material representing some of the species examined by other workers, I have found structures that they reported missing in some of the species that we have both examined. I definitely find an optic nerve in *Oscaecilia ochrocephala* and await better material of *Boulengerula boulengeri* and *Scolecomorphus uluguruensis* before declaring the nerve absent. Further, I have examined species closely related phylogenetically to those in question, and species with virtually the same ocular morphology, and I have found that the eyes have optic nerves, though attenuate and buried in muscle. I suspect that as long as a retina in any form is present, an optic nerve is as well. The retina typically degenerates completely if the optic nerve is severed or absent (R. Eakin, pers. comm.). Thus far, all caecilians that I have examined, including those closely related to or the same as those in which retinas and nerves were reported absent, have had both retinas and indications of optic nerves. Among very attenuate nerves, I have not been able to ascertain whether their structure is glial, and thus non-functional (as reported for 'degenerate' eyes in other orders and classes of vertebrates), but the optic nerves of most taxa are morphologically capable of conduction.

d) Tissues covering the eye. Norris (1917) considered caecilian eyes of two types: eyes covered by dermis and epidermis were thought to retain muscles and nerves, and to be potentially functional; those covered by bone as well as skin were considered to have lost their muscles and nerves and to be vestigial and non-functional. This dichotomy does not hold, at least so explicity. Eyes covered by skin only in some species are quite reduced; conversely, in species with eyes covered by bone, some muscles and nerves, at least the optic nerves, are retained. Species with eyes cov-

ered by bone do show a greater amount of reduction. There are also ontogenetic and ecologic components to the amount of tissue covering the eye. Increase in dermal and epidermal depth with the development of skin glands and keratin in the outer epidermal layers appears at metamorphosis. In free-living larvae of *Ichthyophis*, dermis and epidermis are thin, and the epidermis is not keratinized. In *Geotrypetes grandisonae* (Fig. 10) there is thick dermal connective tissue, and the epidermis has a thin keratinized layer. Adults of the aquatic *Typhlonectes* (Fig. 6) have skin covering the eye similar to that of *G. grandisonae*. Reduced covering is correlated with both earlier stages of development and with the aquatic habitus. Adult *Caecilia, Geotrypetes, Hypogeophis, Uraeotyphlus*, and *Ichthyophis*, and juvenile *Dermophis* (see Figs.) examined, as well as *Siphonops* (Kohl 1892), all have the eye covered by dermis with considerable connective tissue and an epidermis of several cell layers, the outermost keratinized. Adult *Dermophis* and *Idiocranium* (Fig. 11) have eyes covered by glandular dermis and thick epidermis. *Afrocaecilia* (Fig. 14) and *Gymnopis* (Fig. 12) have eyes covered by bone and a very glandular skin. In *Gymnopis* there are no melanocytes in the dermis just over the eye, but pigment is continuous in *Afrocaecilia*. In scolecomorphids the eyes develop under bone, but are pulled out of the socket as the tentacle develops. The eyes are concomitantly modified (see discussion). As noted above, both of the latter genera have reduced extrinsic musculature and lenses, but both have attenuate optic nerves. See discussion of evolutionary trends below.

e) Harderian gland. The Harderian gland is much enlarged in all caecilians relative to other amphibians. It develops shortly before metamorphosis in both larvae and in nonlarval species. Caecilians lack a lacrimal gland. The Harderian gland functions to lubricate the channel of the tentacle, rather than the orbit (which cannot move). Prince (1956) notes that the Harderian gland is presumably an innovation for orbit lubrication in terrestrial vertebrates, but that there are numerous modifications of Harderian gland function. Tentacle lubrication is unique to caecilians, but in various reptiles, for example, Harderian gland secretion lubricates (1) the orbit, (2) the nasal orifice, (3) Jacobson's organ via the lacrimal duct, and (4) contributes to the saliva. In caecilians the Harderian gland usually fills the socket, and may extend into the tentacular area. The gland usually surrounds the orbit except for the corneal aspect. Exceptions to this are *Geotrypetes seraphini* (Fig. 9) in which the eye lies largely above the gland, and larval *Ichthyophis* (and *Dermophis* embryos and fetuses) in which the gland has not yet developed. The gland is well developed in the aquatic *Typhlonectes* (Fig. 7). The gland is small in *Boulengerula* (Fig. 17) and *Afrocaecilia* (Fig. 14). Its morphology is most unusual in *Oscaecilia ochrocephala* (Fig. 13), for it is highly vascular, and posteriorly has a large bulb of laterally arrayed muscle fibers, not seen in other taxa.

f) The extrinsic eye musculature. The musculature of caecilian eyes either typifies or is reduced from the standard vertebrate plan of four rectus and two oblique muscles, and as is typical of amphibians, levator and retractor bulbi muscles. In caecilians the retractor bulbi becomes the retractor tentaculi and is innervated by the abducens nerve. There is considerable agreement that the retractor bulbi is derived from a slip of the rectus externus (Edgeworth 1935). Probably the levator bulbi becomes the compressor of the Harderian gland, and the rectus internus, or a slip from it, retracts the sheath of the tentacle (Walls 1942). There has been considerable debate in the literature about the presence or absence of various muscles in various taxa, their innervation, and the homology of the retractors. Ramaswami (1941) reviewed this problem and resolved several of the issues. Later workers suggested other problems, summarized below.

Ichthyophis glutinosus and other species of that genus examined have been found to have all of the extrinsic muscles present (Sarasin and Sarasin 1887–1890; Burkhardt 1891; Waldschmidt 1887; Engelhardt 1924; Norris and Hughes 1918; Walls 1942; Ramaswami 1941; this work). Norris and Hughes reported that the retractor bulbi is attached to the orbit during the larval period, but switches to the tentacle when that organ develops at metamorphosis, which Walls considered "seduction" of the retractor bulbi by the tentacle. I cannot identify a retractor bulbi in the late larva of *Ichthyophis* sp. in my sample. Visser (1963) reported that the optic nerve was vestigial and the trochlear absent. He did not comment on the musculature. Ramaswami (1948) also reported the trochlear absent in an embryo of *Ichthyophis*. There is no indication in either of these reports that the superior oblique, typically innervated by the trochlear, is missing, so staining may have been a problem. *Dermophis* has been controversial. Norris (1917) stated that only the rectus (r.) internus is absent in *D. mexicanus;* Norris and Hughes (1918) found all of the extrinsic muscles and their nerves present and considered the retractor tentaculi a modified r. internus. The muscles wee said to originate on the fascia over other muscles and tentacle rather than from the wall of the braincase. De Jager (1939a) reported all extrinsic muscles in *D. mexicanus* and *D.* (now *Schistometopum*) *gregorii* (Boulenger) degenerated. Ramaswami (1941) determined that all of the extrinsic muscles are present in *D. mexicanus* and that the retractor bulbi identified by Norris and Hughes is actually the r. internus, and that muscle passes through the retractor tentaculi. Therefore, there is not a separate retractor bulbi, and the retractor tentaculi is of the usual derivation from the r. bulbi. My developmental and adult material confirms Ramaswami's conclusions that all of the eye muscles are developed and have the expected relationships in *D. mexicanus*. De Jager (1938) also reported that the abducens nerve is absent in *D. mexicanus* though a large retractor tentaculi is present. Els (1963), examining *Schistometopum thomensis*, a west African congener of the east African *S. gregorii*, reported both trochlear and abducens nerves absent with no allusion to the muscles.

The meticulous work of Marcus (1910) described the development of all of the extrinsic muscles and their nerves, including an attenuate trochlear, in *Hypogeophis*. My material confirms this. In *Siphonops* Waldschmidt (1887) and Leydig (1868) refer to four extrinsic muscles, and the former mentioned that the trochlear and abducens nerves are absent. Kohl (1892), in a beautiful and rarely cited work, reported that all of the muscles and their nerves are present. Norris and Hughes (1918) found in *Geotrypetes (petersi) seraphini* six extrinsic muscles "all nearly vestigial" attached to the orbit, and two retractor tentaculi, one innervated by the abducens, the other extending to the tentacular sheath and innervated by the oculomotor. Again, I concur with Ramaswami (1941) that Norris and Hughes erred in

denying the existence of a rectus internus, which in turn affected their analysis of other muscles. Norris and Hughes reported all of the muscles and nerves absent in *Caecilia gracilis*. Ramaswami (1941) found that all of the extrinsic muscles are present in *Uraeotyphlus narayani*, and carefully described their courses. My material confirms his designations.

The remainder of species examined by others have their eyes covered by maxilla or squamosal or both bones, and the investigators generally conclude that the eye is vestigial and its extrinsic musculature and nerves and the optic nerve are absent, the eye represented only by a pigmented mass. A retractor tentaculi is always present, usually reported to be innervated by the abducens. This is the case for *Oscaecilia ochrocephala* (*Herpele* of Norris and Hughes, 1918, and *Coecilia* of de Jager 1939b), *Gegeneophis carnosus* (Ramaswami 1943), *Scolecomorphus uluguruensis* (de Villiers 1936, 1938; Brand 1956) (Ramaswami [1941] states that part of the eye is *not* under bone), and *Boulengerula boulengeri* (de Villiers, 1938, who also stated that there is no abducens for the retractor tentaculi and the tentacular apparatus is degenerated).

New material confirms the presence of all of the extrinsic and tentacular muslces in *Dermophis mexicanus, Ichthyophis glutinosus* and *I. orthoplicatus, Hypogeophis rostratus,* and *Uraeotyphlus narayani*. In addition, that condition obtains in *Typhlonectes compressicaudus, Geotrypetes seraphini, G. grandisonae,* and *Idiocranium russeli*. In the three latter species, the superior oblique is attenuate (especially in *Idiocranium,* in which it is some three fibers) and the slips of r. externus are difficult to distinguish from those of retractor tentaculi, which dominates the fiber course. I find three extrinsic muscles attached to the orbit of *Caecilia occidentalis*, an attenuate species closely related to *C. gracilis*, in which Norris and Hughes (1918) found neither extrinsic muscles nor optic nerve. The muscles present in *C. occidentalis* are the recti superior, inferior, and medialis (all presumably of oculomotor innervation). I examined four species with eyes covered by bone: *Afrocaecilia taitana*, closely related to the *Boulengerula boulengeri* examined by de Villiers (1938), *Boulengerula boulengeri, Oscaecilia ochrocephala*, and *Gymnopis multiplicata*, closely related to *Dermophis mexicanus*. These species have reduced eyes; *Afrocaecilia, Boulengerula*, and *Gymnopis* lack all of the extrinsic musculature, have attenuate, at best, optic nerves, and have retractor tentaculi, though that of *Boulengerula* is small. Two extrinsic muscles clearly are present in *Oscaecilia ochrocephala*, though all were reported absent by previous workers. The *Scolecomorphus* with their eyes embedded in the tentacle and pulled from under bone are an unusual situation. I agree with de Villiers (1938) in not finding extrins muscles in *Scolecomorphus uluguruensis*, but find two attenuate muscles in *S. kirkii* despite the "dislocation" of the orbit.

g) Development and homology of the retractor tentaculi. It seems apparent, based on the literature and on my ontogenetic series of *D. mexicanus*, that the retractor tentaculi is derived from r. externus and is homologous with the retractor bulbi. The abducens innervation is evidence for this homology. I cannot corroborate the "seduction" of r. bulbi from orbit to tentacle in *Ichthyophis*, for I do not have adequate larval material. However, I note that in *D. mexicanus*, all of the extrinsic muscles develop rather late, near the time of intraoviductal metamorphosis, and the r. externus and r. tentaculi develop in situ from mesenchymal aggregation. A few slips, representing r. externus, extend to the orbit. The majority of fibers form the r. tentaculi, which never is in association with the orbit but extends to the tentacle which is developing at the same time. There is never a r. bulbi associated with the orbit.

h) Origins and innervations of eye muscles. The literature is fraught with comments about the difficulty of tracing muscles from the orbit to their origins, locating and tracing the nerves that innervate them, and whether certain nerves are present at all. This is not surprising. The eyes are small, never even 1 mm dia; the muscles are very small, often 3–5 fibers. The nerves to these muscles are presumably even more attenuate. Almost invariably older workers used a single general staining method on serial sections of heads, appropriate to single specimens. I have compared general stains of several sorts, and find them inadequate to locate particular structures. When, for example, I compare a head stained with only one stain, be it hematoxylin and eosin, saffranin O, methylene blue, or Mallory's azan, with one stained serially with several specific stains (H and E, Mallory's azan, and picro-ponceau preferred), I am able to find structures not visible in singly stained heads. Even with good connective tissue stains (azan, picro-ponceau), I sometimes have difficulty ascertaining the origins of attenuate muscles, though they are usually traceable. Other authors often report particular nerves absent, though the muscles they ought to innervate are present. I can rarely identify nerves with surety in my triply stained material (except for the optic nerve, which is recognizable structurally and positionally). Other workers, and I for this study, did not use nerve-specific stains on their rare material. I have silver stained an ontogenetic series of heads of *D. mexicanus*, and the nerves are readily distinguishable. The details of that work are not the pervue of this paper and will be reported separately.

Most of the extrinsic eye muscles in the species I have examined are traceable to origins on the periosteum of bones of the eye socket in the general positions indicated by Edgeworth (1935) for most amphibians. Like other investigators, I cannot trace some attenuate muscles from the orbit to their origins, and lose them on the retractor tentaculi or within the Harderian gland. I do not infer that these structures are the origins of the extrinsic muscles, for I cannot identify the morphological attachments that indicate association. I suggest that such muscles are attenuate at their origins, and difficult to trace. The muscles are striated, so their morphology indicates capability of contraction.

i) Function of extrinsic musculature. It had long been thought that the extrinsic musculature of *all* amphibians was non-functional, and that only r. and l. bulbi effected movement of the orbit (Walls 1942; Prince 1956; Duke-Elder 1958). This was determined by optomotor tests, other physiological tests, and behavioral observations. However, recently Dieringer and Precht (1982) and Dieringer et al. (1982) have demonstrated horizontal movements in eyes of frogs of 3–6° that they believe controlled by extrinsic muscles, and Manteuffel et al. (1977) report involuntary movement of the eyes of salamanders (*Salamandra?*), and Rettig et al. (1981) report eye movement in larval *Triturus*

as the oculomotor neurons develop. However, though the muscles may indeed be functional, it is clear that the movements they induce are minimal. One therefore cannot assume that caecilian extrinsic muscle function then is markedly different from that of other amphibians. Muscle fibrils differentiate as spheres in *D. mexicanus*, and later, at the time they attach to the orbit, they become striated. This is evidence of coordinated activity (R. Strohman, pers. comm.). At that stage of development, the cornea is not yet fused to the dermis, and the Harderian gland does not surround the orbit, so movement is not impossible. Intraoviductal use of vision and concomitant eye positioning is not likely, though it is possible in free-living larvae. The extrinsic muscles of caecilians are attenuate relative to those of other amphibians (except certain salamanders; see below). I suggest that in all amphibians, including caecilians, the extrinsic musculature is utilized for low-level, perhaps almost isometric, position maintenance. In caecilians the relative attenuation of these structures is correlated with other morphological structures that provide maintenance of position, so that development of the muscles is not enhanced. Development may arrest at the juvenile stage. This heterochronic pattern would account for the development of all of the muscles, in a presumably juvenile state in some species, relative attenuation of later-developing muscles in some of those species, and finally the delay of development so long that some, and finally all, of the muscles never appear. Corroboration of this hypothesis is offered by the fact that in species which lack extrinsic muscles, the lens is embryonic or never develops, and development of the retina is retarded as noted above.

E. Conclusions

1. Evolutionary trends in caecilian eye morphology

I infer that (1) an orbit overlain by skin, but not by bone, (2) the presence of 4 recti, 2 oblique, and retractor and levator bulbi (modified for tentacular function), with their typical innervation, (3) presence of a relatively well developed optic nerve, (4) and a retina of multiple, well organized layers, (5) and a crystalline spherical lens, which is free of attachment to cornea and retina, (6) and a vitreous body, (7) the cornea fused to the underlying layer of the dermis, and (8) lack of components of accommodation constitute the primitive state in caecilians. This condition is observed in taxa considered primitive based on the other features of morphology and of reproductive biology. Modification of eye morphology includes the following transitional series relative to the primitive state: (1) eye overlain by thicker, often glandular, sometimes pigmented skin, to overlain by bone as well as skin; (2) attenuation of to reduction in number of extrinsic muscles, the superior oblique and its innervation by the trochlear (cranial nerve IV) lost first, the retractor bulbi component of the rectus externus innervated by the abducens (cranial nerve VI) always present as the retractor tentaculi; (3) retina present but losing stratal organization; (4) optic nerve present, becoming attenuate, perhaps reduced to glial cells; (5) lens round (larval and adult aquatic forms) to spheroid, lens cellular peripherally, medially, or completely to lens amorphous to lens absent; (6) reduction to loss of the vitreous body; primitive states 7 and 8 are retained in all caecilians. Clearly the trend is toward reduction of the eye in the derived state. Muscles and nerves become attenuate, and finally muscles and some nerves do not develop at all. Absence of muscles is a mosaic of loss, but loss of the superior oblique, and reduction of or loss of association of rectus externus with the orbit as its retractor bulbi component subsumes retraction of the tentacle are typical. An optic nerve is virtually always present, even though the retina is poorly developed. Retinal cell number, numbers of nuclear layers, and finally retinal organization, diminish. The lens retains an embryonic state (cellular) longer and longer, finally not developing at all. Attachment of the lens to adjacent structures, and of the orbit to its exterior, increases. Extremes in these features are correlated with increased covering of the eye by dermal and epidermal components and especially by bone, though reduction is seen in eyes of species relatively lightly covered as well. Increased covering is not correlated with any known conditions of the environment of the species.

Several of the above trends are heterochronic, possibly neotenic, probably progenetic. Development of muscles, nerves, lens and retina show delay, until they finally do not develop at all. This is not a complete and simple explanation of the pattern of caecilian eye structure, for the inception of the unique chemo-sensory tentacle, which coopts certain eye structures (r. and l. bulbi, r. internus [part], Harderian gland, etc.) and the correlation of development of certain structures with the habitats of the animals compounds the issue. There is no answer beyond mere speculation to the question of why caecilians alone among vertebrates should develop a tentacle with its Jacobson's organ-olfactory associations. Further, both larval and adult aquatic forms have round lenses, and all of the structures associated with the eye are relatively well developed. These species live in turbid waters, and visual acuity implementing other sensory modes has not been investigated. However, developmental delay is not involved in the very real reduction of certain eye structures in adults. Several authors have assumed that muscles and nerves develop "normally" then degenerate in adults. There is little evidence to support this, save for the general information in Sarasin and Sarasin (1887–1890), and, of great significance, Arnold's (1935) careful data showing that the diameter of the optic nerve and the thickness of the retina, but not lens or orbit size, reduce after hatching in both *Hypogeophis rostratus* and *Grandisonia alterans*, compared with pre-metamorphic size in these direct-developing species. Conversely, my data on eye development in *Dermophis mexicanus* (Fig. 30) indicate that the eye and its associated structures continue to grow through adulthood, but the rate of growth diminishes after birth. It would not be surprising for different patterns to obtain in different species.

2. Comparison with other vertebrates

There is a large literature on the eyes of animals living in low-light to dark habitats, such as caves and burrows. Some superb summary papers exist, as well as a number of reports on individual species. One very useful work (Kohl 1892) presented original information on the comparative morphology of eyes of species of cave fish, cave salamanders, a burrowing caecilian, and burrowing lizards, snakes, and mammals. This beautifully illustrated compendium is rarely cited by investigators of reduced eyes. Eigenmann

(1909) presented careful description and explicit comparison of the condition of the eye in cave and burrowing species, as well as a number of other aspects of the biology of cave-inhabiting taxa. His concluding essay on "The causes of individual and phyletic degeneration" is a landmark that should be read by all modern evolutionary biologists. He considered the phenomenon of degeneration in a framework evaluating the views of Lamarck, Darwin, and Weissman, among others, and found "the Lamarckian factor" appealing. His consideration of selection (in a pregenetic context) is well worth contemplating. Hanke (1912) presented much information on "rudimentary" eyes of amphibians and reptiles. Walls' (1942) treatise on eyes of all vertebrates is invaluable, and Prince (1956) and Duke-Elder (1958) have useful information on eye morphology. Dubost (1968) summarized a wealth of information on subterranean mammals, and Underwood's (1970) review of the structure of the reptilian eye is very useful, though it has scant information on the extrinsic musculature and nerves. Valuable papers on particular species with reduced eyes include those of Alt (1910), Brandon (1968), Hawes (1946), Schlampp (1892), Stone (1964), and Gundy (1977).

Though there is some variation on the theme, a striking similarity in ontogenetic and phylogenetic trends in the structure of the eye of taxa living in light-deprived environments exists across all vertebrate groups. When eye reduction in species of cave or fossorial animals in discrete phylogenetic lineages is compared, and assessment is made of degree of morphological change, often correlated with developmental and environmental information, similar trends are noted in several lineages. Kohl's (1892) and Eigenmann's (1909) work and that of others demonstrates that among fish, silurids, amblyopsids, and brotulids exhibit similar trends; these trends are repeated in plethodontid cave salamanders of several genera (see also Brandon, 1968), in amphisbaenean and typhlopid burrowing reptiles and in gophers and moles among mammals (see also Dubost 1968). The present work indicates that these trends obtain in caecilians. In all of these lineages, the trends summarized above are seen – the lens remains in the cellular, embroynic state, may become amorphous and then lost. Covering over the eye increases – eyelids fuse, skin thickens, bone may overlie the eye. The cornea fuses to overlying layers. Concomitantly, the vitreous body reduces, and the lens, if present, may fuse to cornea and/or retina. The retina and optic nerve are almost invariably the last structures to be reduced or lost. Several investigators (such as Stone 1964) have reported adequate retinas, but that the optic nerve is absent or does not reach the brain, so that the eye is functionless. It is a well known pathological phenomenon that the retina degenerates if the optic nerve is severed, and many people who work on eyes believe that an intact retina would not exist in the absence of an optic nerve (R.M. Eakin, pers. comm.). Since nerve stains were rarely used in these studies, I suggest that an intact retina indicates some central nervous system association and the possibility of function. Caecilians do not have eyes reduced to the extent seen in some cave fishes, and in mole-rats. The morphology of the caecilian eye, and to some extent the behavior of the animal, suggest that the eye may be functional in at least light vs. dark perception in all species examined. Certain developmental patterns and environmental constraints, resulting in common trends in morphology, appear to obtain in virtually all vertebrates with reduced eyes.

Acknowledgements. I thank T. Papenfuss and P. Williams for collecting *Geotrypetes*, T. Papenfuss, R. Seib, J. Cadle, D. Wake, and T. Wake for collecting *Dermophis*, A. Pazos for collecting *Caecilia*, R. Nussbaum for *Afrocaecilia*, A.S. Rand for *Oscaecilia*, M. Farrell for *Uraeotyphlus*, W. Breckenridge for *Ichthyophis glutinosus*, C. Gans for *Ichthyophis orthoplicatus*, R. Lawson for *Hypogeophis*, B. Fritzsch for *Boulengerula* and *Scolecomorphus uluguruensis*, A.G.C. Grandison for loan of and permission to process *Idiocranium russeli* and *Geotrypetes grandisonae*, R. Inger for that permission for a larval *Ichthyophis*, P. Alberch for *Scolecomorphus kirkii*, and J. Savage for allowing me to so process *Gymnopis*. R.E. Lombard, T.E. Hetherington, C. Hillery, A. Brown, G. Wurst, J. Hanken, W. Bemis and especially K. Thomas diligently prepared the sections. W. Hare facilitated the execution of the electroretinograms. This work is supported by the National Science Foundation.

References

Alt A (1910) On the histology of the eye of *Typhlotriton spelaeus*, from Marble Cave, Mo. Trans Acad Sci St. Louis 19:83–96

Arnold W (1935) Das Auge von *Hypogeophis*. Beitrag zur Kenntnis der Gymnophionen XXVII. Morphol Jahrb 76:589–625

Brand DJ (1956) On the cranial morphology of *Scolecomorphus uluguruensis* (Barbour & Loweridge). Ann Univ Stellenbosch 32A:1–25

Brandon RA (1968) Structure of the eye of *Haideotriton wallacei*, a North American troglobitic salamander. J Morph 124:345–352

Burckhardt R (1891) Untersuchungen am Hirn und Geruchsorgan von *Triton* und *Ichthyophis*. Zeit Wiss Zool 52:369–370

de Jager E (1938) A comparison of the cranial nerves and bloodvessels of *Dermophis mexicanus* and *Dermophis gregorii*. Anat Anz 86:321–347

de Jager E (1939a) Contributions to the cranial anatomy of the Gymnophiona. Further points regarding the cranial anatomy of the genus *Dermophis*. Anat Anz 88:193–223

de Jager E (1939b) The cranial anatomy of *Coecilia ochrocephala* Cope (further contributions to the cranial morphology of the Gymnophiona). Anat Anz 88:433–469

de Villiers CGS (1936) Some aspects of the amphibian suspensorium, with special reference to the palatoquadrate and quadratomaxillary. Anat Anz 81:225

de Villiers CGS (1938) A comparison of some cranial features of the East African Gymnophiones *Boulengerula boulengeri* Tornier and *Scolecomorphus uluguruensis* Boulenger. Anat Anz 86:1–26

Dieringer N, Precht W (1982) Compensatory head and eye movements in the frog and their contribution to stabilization of gaze. Exp Brain Res 47:394–406

Dieringer N, Precht W, Blight AR (1982) Resetting fast phases of head and eye and their linkage in the frog. Exp Brain Res 47:407–416

Dubost G (1968) Les mammiferes souterrains. Rev Ecol Biol Sol 5:99–133, 136–197

Duke-Elder S (1958) Systems of Ophthalmology. Vol 1. The Eye in Evolution. C.V. Mosby Co., St Louis

Edgeworth FH (1935) The Cranial Muscles of Vertebrates. Cambridge University Press, Cambridge

Els AJ (1963) Contributions to the cranial morphology of *Schistometopum thomensis* (Bocage). Ann Univ Stellenbosch 38A:39–64

Engelhardt F (1924) Tentakelapparat und Auge von *Ichthyophis*. Jena Z Naturwiss 60:241–305

Eigenmann CH (1909) Cave vertebrates of America. A study in degenerative evolution. Carnegie Inst Washington 104:1–241

Gundy GC (1977) Photoreceptor degeneration in the eyes of an amphisbaenian in response to constant light or constant darkness. J Exp Zool 201(2):169–176

Hanke V (1912) Die rudimentären Sehorgane einiger Amphibien und Reptilien. Arch f vergleich Ophthalmologie 6:323–342

Hawes RS (1946) On the eyes and reactions to light of *Proteus anguinus*. Q Rev Micros Sci 86:1–53

Hetherington TE, Wake MH (1979) The lateral line system in larval *Ichthyophis* (Amphibia: Gymnophiona). Zoomorph 93:209–225

Humason G (1978) Animal Tissue Techniques. W.H. Freeman, San Francisco

Kohl C (1892) Rudimentäre Wirbelthieraugen. T. Fischer's Verlag, Cassell

Kuhlenbeck H (1922) Zur Morphologie des Gymnophionengehirns. Jena Z Naturwiss 58:453–484

Leydig F (1868) Über die Schleichenlurche. Zeit Wiss Zool 18:283–286, 291–297

Manteuffel G, Plasa L, Sommer TJ, Wess O (1977) Involuntary eye movements in salamanders. Naturwiss 64:533

Marcus H (1910) Zur Entwicklungsgeschichte des Kopfes, II Teil. Beiträge zur Kenntnis der Gymnophionen IV. Festschr f R. Hertwig. 2:373–462

Nelsen OE (1956) Comparative Embryology of the Vertebrates. The Blakiston Co, New York

Norris HW (1917) The eyeball and associated structures in the blindworms. Iowa Acad Sci Proc 24:299–300

Norris HW, Hughes SP (1918) The cranial and anterior spinal nerves of the caecilian amphibians. J Morphol 31:490–557

Peter K (1898) Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. Morphol Jahrb 25:553–623

Prince JH (1956) Comparative Anatomy of the Eye. Charles C. Thomas Publ, Springfield Ill

Ramaswami LS (1941) Some aspects of the cranial morphology of *Uraeotyphlus narayani* Seshachar (Apoda). Rec Indian Mus Calcutta 43:143–207

Ramaswami LS (1943) An account of the head morphology of *Gegenophis carnosus* (Beddome), Apoda. J Mysore Univ 3:205–220

Ramaswami LS (1948) The chondrocranium of *Gegenophis* (Apoda Amphibia). Proc Zool Soc London 118:752–760

Rettig G, Fritzsch B, Himstedt W (1981) Development of retinofugal neuropil areas in the brain of the alpine newt, *Triturus alpestris*. Anat Embryol 162:163–171

Rodieck RW (1973) The Vertebrate Retina Principles of Structure and Function. W.H. Freeman Co., San Francisco

Sarasin P, Sarasin F (1887–1890) Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon. Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle, *Ichthyophis glutinosus*. C.W. Kreidel's Verlag, Wiesbaden

Schlampp KW (1892) Das Auge des Grottenolmes (*Proteus anguineus*). Zeit Wiss Zool 53:537–557

Stone LS (1964) The structure and visual function of the eye of larval and adult cave salamanders *Typhlotriton spelaeus*. J Exp Zool 156:201–218

Storch V, Welsch U (1973) Zur Ultrastruktur von Pigmentepithel und Photoreceptoren der Seitenaugen von *Ichthyophis kohtaoensis* (Gymnophiona, Amphibia). Zool Jb Anat 90:160–173

Taylor EH (1968) The Caecilians of the World. A Taxonomic Review. University of Kansas Press, Larence, KA. 848 pp

Thomas K (1983) A nitrocellulose embedding technique for vertebrate morphologists. Herp Rev 14:80–81

Underwood G (1970) The Eye. In: Gans C and TS Parsons (eds) Biology of the Reptilia, Vol 2. Academic Press, New York, pp 1–97

Visser MHC (1963) The cranial morphology of *Ichthyophis glutinosus* (Linne) and *Ichthyophis monochrous* (Bleeker). Ann Univ Stellenbosch 38A:67–102

Waldschmidt J (1887) Zur Anatomie des Nervensystems der Gymnophionen. Jena Z Naturwiss 20:468–470

Walls G (1942) The Vertebrate Eye and its Adaptive Radiation. Cranbrook Institute of Science, Bull 19, Bloomfield Hills, MI

Wiedersheim R (1879) Die Anatomie der Gymnophiona. Gustav Fischer Verlag, Jena

Received May 10, 1984