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Tentacle Development in *Dermophis mexicanus* (Amphibia, Gymnophiona) With an Hypothesis of Tentacle Origin

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ABSTRACT The development of the tentacle, a chemosensory and perhaps tactile structure unique among vertebrates to gymnophione amphibians is described in *Dermophis mexicanus* and *Gymnopis multiplicata.* The tentacle is associated with the vomeronasal organ and its glands, and utilizes several structures usually associated with the eye, such as the Harderian gland, the retractor and levator muscles, and their nerves. Innervation of the tentacle itself is from the trigeminal nerve. We present an hypothesis that the tentacle originated from modified eye components.

The tentacle apparatus, unique among vertebrates to the caecilians, is similar in its Bauplan among all adult gymnophiones. Its major components include the tentacle aperture, sac, sheath, fold, and ducts, the vomeronasal organ and its gland, the retractor and compressor muscles, the Harderian gland, and the trigeminal and eye muscle nerves. Nevertheless, the sizes and shapes of these structures and their proportions differ among species. For example, the tentacle aperture varies in its position between the eye and the nostril and, thus, is a useful character for species determination.

MATERIALS AND METHODS

An ontogenetic series of embryos (5 to 30 mm total length [TL], fetuses (35–110 mm TL), juveniles (115–250 mm TL), and adults (> 250 mm TL) of *Dermophis mexicanus* provided the primary data base for this study. Specimens were collected near San Marcos, San Marcos Province, Guatemala, and are deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, California.

Whole embryos, heads of fetuses, juveniles, and adults were serially sectioned variously (transversely, sagittally, or frontally) at 7–10 μ, and consecutive sections in serial groups of three were stained with hematoxylin-eosin, picro-ponceau, and Mallory's azan. Developmental stages of *Gymnopis multiplicata* from a number of localities in Costa Rica were similarly prepared. The specimens are part of the CRE collection at the University of Miami, Miami, Florida. Sections were drawn with the aid of a camera lucida and reconstructions prepared.

RESULTS

Description of general adult structure

We describe the tentacle apparatus of an adult *Dermophis mexicanus* (Fig. 1A,B) in order to illustrate the complex relations of the structures concerned. The tentacle sac, often called the sheath of the tentacle, is the epithelial structure that encloses the tentacle apparatus and the eye. The tentacle aperture is the opening of the sac to the snout. The wall of the sac, or sheath proper, consists of dense connective tissue with an epithelial surface layer. At the orifice, this surface layer is continuous with the outer skin surface layer of the cheek. The sac extends from its aperture to the eye, and is embedded in spongy connective tissue that is rich in veins. The collecting ducts of the branched, tubular, exocrine Harderian gland terminate in the base of the cavity sheath. Within this cavity or sheath lies the more or less involuted tentacle fold.

Along its entire extent, the tentacle fold originates from the wall of the tentacle sheath and curves into the lumen of the sheath. It is the fold, which moves within the sheath and which in some species can be protruded from the tentacle aperture, that usually is referred to as the "tentacle." The tentacle of *Ichthyophis glutinosus* has been described in some detail (Wiedersheim 1879, 1880; Sarasin and Sarasin 1887-1890; Badenhorst, '78; Fox, '85). In this species, the specialized fold is involuted and, therefore, highly protrusible (Billo, '86); owing to its protrusibility, the whole tentacular complex

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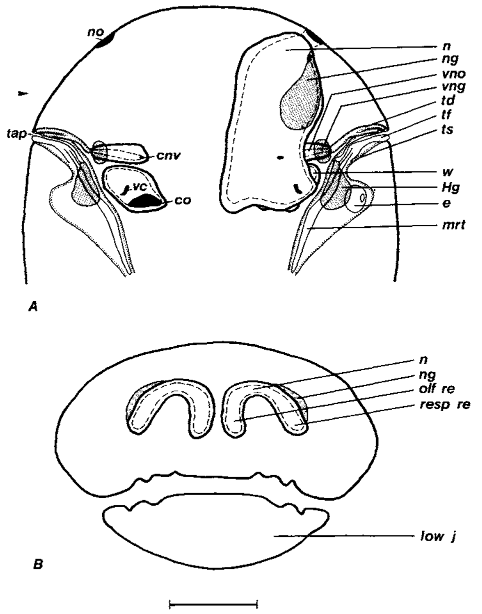

Fig. 1. *Dermophis mexicanus* adult. A. Dorsal view of the head illustrating eye, nasal, and tentacle elements. B. Cross-section at the level of arrowhead in A. Bar = 2 mm.

Abbreviations

cnv, Connection of nasal sac to vomeronasal organ
co, Choanal opening to mouth cavity
dls, Dorsolateral sac
dltu, Dorsolateral tube
e, Eye
Hg, Harderian gland
Hga, Anlage of Harderian gland
low j, Lower jaw
mrt, Musculus retractor cloacae
n, Nasal sac
ng, Nasal gland
no, Nostril
nt, Nasal tube
olf re, Olfactory region
resp re, Respiratory region
ta, Tentacle anlage
tap, Tentacle aperture
td, Tentacle ducts
tf, Tentacle fold
ts, Tentacle sac
vng, Vomeronasal gland
vnoa, Anlage of vomeronasal organ
w, Choanenschleimbeutel

has become known simply as the "tentacle" (Müller, 1831). *Dermophis mexicanus* has a much simpler fold that lacks a free end and is not involuted; therefore, the tip of the tentacle fold appears only sporadically as a small bulge in the tentacle aperture during activity.

The tentacle aperature is the only portion of the complex that always is apparent externally. In an adult *D. mexicanus*, it is situated anterolaterally from the eye about one-third of the distance from eye to nostril (Taylor, '68).

The tentacle ducts connect the orifice of the tentacle sac with the cavity of the vomeronasal organ (Sarasin and Sarasin, 1887-1890; Badenhorst, '78). The walls of these ducts consist of a double-layered mantle of connective tissue; the inner has longitudinal, the outer circular fibers. The lumen of the vomeronasal organ is lined with stratified cuboidal epithelium. The ducts coalesce to form a single duct that enters the lateral vomeronasal organ. In some species (e.g., *I. glutinosus*) multiple ducts enter as separate ducts into the vomeronasal organ.

The vomeronasal organ lies oblique and ventral to the nasal sac, and is rich in olfactory epithelium. The ventral epithelium is thicker than the dorsal, is turned toward the ventral side of the nasal sac, and has an extensive olfactory epithelium. The dorsal, thinner portion has a continuous microvillar margin. The vomeronasal fila olfactiva, as well as the axons of the ventral olfactory cells of the nasal or olfactory sac or cavity, unite in the ventral branch of the olfactory tract (= tractus olfactorius ventralis; Waldschmidt, 1887), which runs to the olfactory bulb. The vomeronasal axons proceed to the accessory olfactory bulb (A. Schmidt, personal communication). Dorsally, the most lateral vomeronasal lumen receives the outlets of the tubular vomeronasal gland. The fused tentacle ducts enter laterally into the vomeronasal organ. Medially, the vomeronasal organ is continuous with the nasal cavity. The horseshoe-shaped nose cavity of *D. mexicanus* has a lateral respiratory and a medial olfactory portion (Fig. 1B). The vomeronasal connection to the nasal sac lies ventromedially in the lateral respiratory part of the sac. The lumina of both nasal and vomeronasal organs are joined.

The tubular Harderian gland is much larger in all caecilians than in other amphibians and has outlets into the base of the tentacle sac. It is an enlarged gland that fills the socket of the orbit and extends to the tentacular sheath area. The gland surrounds the eye except in the corneal area (Wake, '85). In older and larger individuals, the gland is proportionally larger.

The extrinsic eye muscles of caecilians are specialized and may be reduced from the standard vertebrate Bauplan of four rectus and two oblique muscles (Wake, '85). Typically, amphibians have retractor and levator bulbi muscles. In caecilians, the former is homologous to the m. retractor tentaculi which is innervated by the abducens (Norris and Hughes, '18). The m. levator bulbi is modified to compress the Harderian gland and is innervated by the maxillary trigeminus (Norris '17; Norris and Hughes, '18). According to Walls ('42) and Norris ('17), the m. rectus internus, or a slip from it, retracts the sheath of the tentacle. We discuss only the specialized eye muscles involved in the tentacle apparatus. A few fibers of the retractor (tentaculi) muscle, which in other amphibians usually inserts on the orbit, insert on the proximal part of the tentacle fold in caecilians. The circumference of this elongate muscle decreases from its origin on the neurocranium to its insertion on the tentacle fold. The m. retractor tentaculi passes behind the orbit and pierces the Harderian gland. The clasp-shaped compressor (tentaculi) muscle encloses the Harderian gland. This muscle seems to lack an origin; a small slip extends posteriorly and joins the anterior adductor muscles of the jaw. The muscle inserts dorsally and ventrally on collagenous connective tissue of the sac. The m. rectus internus passes through the m. retractor tentaculi (Ramaswami, '41; Wake, '85). It was not possible to determine whether the small slip inserting on the sheath (Walls, '67) is a portion of the m. rectus internus or the m. retractor tentaculi. All other extrinsic eye muscles are developed in *D. mexicanus*, but are reduced (Ramaswami, '41; Wake, '85).

In previous works, the sheath of the tentacle fold frequently was not distinguished from the tentacle sac. Herein the tentacle sac is defined as the connective tissue sac rich in collagen fibers that encloses most of the structures of the tentacle apparatus. Structures included are the sheath, fold, Harderian gland, retractor muscle, compressor muscle, all extrinsic eye muscles, the eye and the nerve ends that innervate the foregoing structures. The sheath is only the anterior portion of the tentacle sac with the invaginated tentacle fold.

Stages of development of the tentacle of Dermophis mexicanus

Embryos

5 mm. The primary optic vesicle is well formed and connected to the prosencephalon by a constricted optic stalk. The vesicle is in contact with the epidermal ectoderm, which is thickened in the contact region. The nasal placode is present rostrally in ventral position.

8 mm. The optic stalk is deeply constricted and the lens placode is thickened. The nasal placode begins to invaginate.

10 mm. The optic vesicle is fully invaginated, forming the secondary optic vesicle. The lens vesicle also is fully invaginated. Invagination of the nasal placode has resulted in a tube that extends from the external naris to the internal naris. The wall of this tube is undifferentiated. The outgrowing fila olfactiva connect the tube with the most anterior part of the prosencephalon, but are not yet separated into the dorsal and ventral olfactory branches of adults.

14–15 mm. The eye is losing its superficial position, i.e., the ectoderm is overgrowing it from the periphery. The wall of the developing olfactory epithelium is thickening. The tentacle anlage seems to be present ventrorostrally to the eye in the form of a minute ectodermal elevation.

22–23 mm (Fig. 2). The anlage of the vomeronasal organ is present as a thickening of the ventral hind part of the nasal sec. The previously elevated tentacle anlage maintains the same position relative to the eye, but now is surrounded by an ectodermal rim and resembles a depressed plug (Fig. 2B).

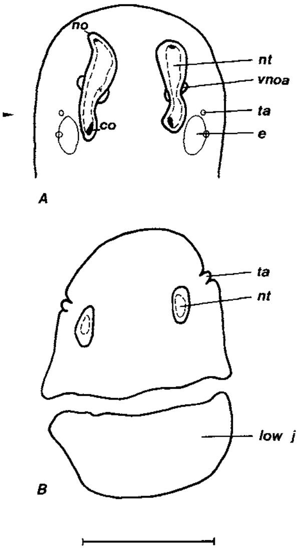

Fig. 2. 22-23-mm *D. mexicanus* embryo. A. Dorsal view of the head illustrating eye, nasal, and tentacle elements. B. Cross-section at the level of arrow in A. Bar = 1 mm.

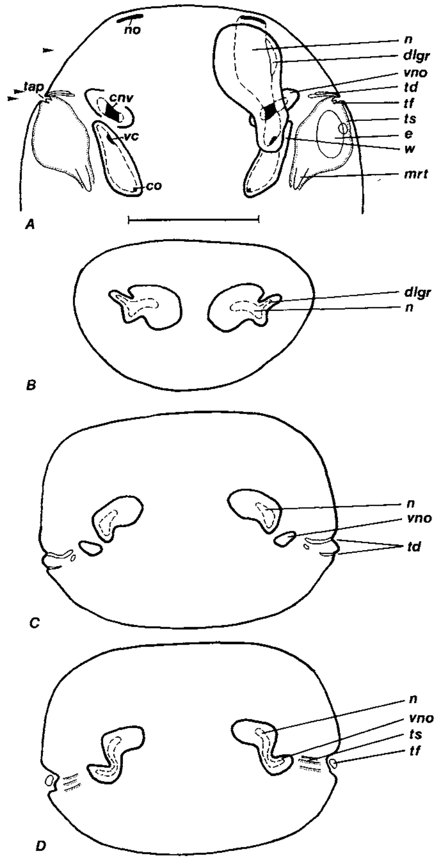

Fig. 3. 34–35-mm *D. mexicanus* fetus. A. Dorsal view of the head illustrating eye, nasal, and tentacle elements. B. Cross-section at the level of upper arrowhead in A. C. Cross-section at the level of medial arrowhead in A. D. Cross-section at the level of lower arrowhead in A. Bar = 1 mm.

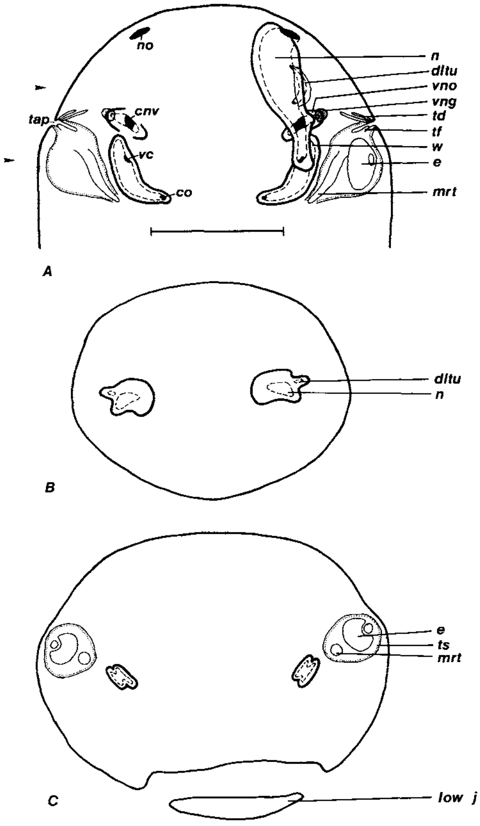

Fig. 4. 44-mm *D. mexicanus* fetus. A. Dorsal view of head illustrating eye, nasal, and tentacle elements. B. Cross-section at the level of upper arrowhead in A. C. Cross-section at the level of lower arrowhead in A. Bar = 1 mm.

25 mm. The tentacle ducts are forming. They begin to aggregate at the rostral rim of the tentacle anlage, and lack a lumen. The wall and lumen of the vomeronasal organ originates from the wall and lumen of the nasal sac, respectively. The demarcation of the tentacle sac is defined by aggregating cells.

Fetal stages

34-35 mm (Fig. 3).. The wall, not yet differentiated, and the lumen of the vomeronasal organ are connected dorsally to the ventral part of the nasal canal. A dorsolateral groove (Fig. 3B) is forming in the dorsal part of the nasal canal. The tentacle anlage has differentiated by evagination into a tiny fold within a small sheath. The tentacle aperture has the same ventrorostral position relative to the eye as had the previous tentacle anlage. The valve that separates the nasal sac and "Choanenschleimbeutel" (Sarasin and Sarasin, 1887-1890) in adults begins to develop as a fold from the lateral hind part of the nasal canal. The m. retractor tentaculi begins to differentiate in the most posterior part of the tentacle sac.

44 mm (Fig. 4). The fold that separates the nasal cavity and "Choanenschleimbeutel" has differentiated into a functional valve; i.e., it can close the choanal passage. The tentacle aperature still lies ventrorostral to the eye, which now is covered by skin. Both the tentacle fold and sheath are larger. The tentacle

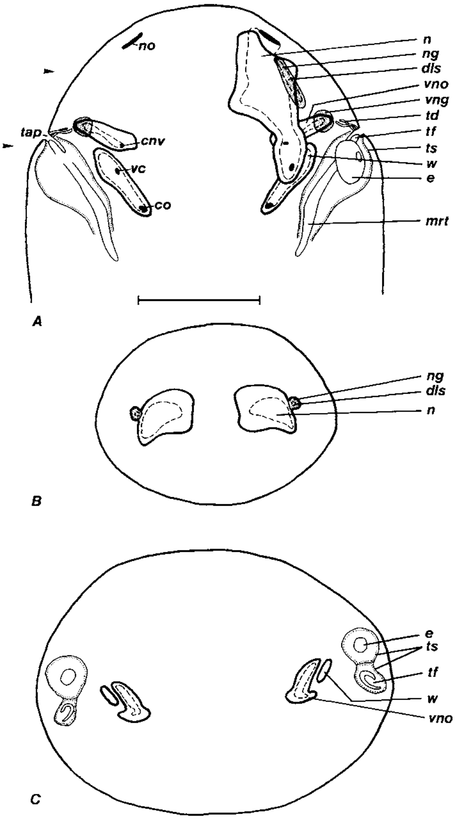

Fig. 5. 58-mm *D. mexicanus* fetus. A. Dorsal view of head illustrating eye, nasal, and tentacle elements. B. Cross-section at the level of upper arrowhead in A. C. Cross-section at the level of lower arrowhead in A. Bar = 1 mm.

ducts have grown toward the lateral part of the vomeronasal organ. Three extrinsic eye muscles are differentiating from mesenchymatic tissue behind the eye. These have neither an origin nor an insertion, and their cells are not striated. The dorsolateral nasal groove of the 34–35-mm specimen has become constricted to form a dorsolateral tube that is open anteriorly and posteriorly (Fig. 4B). The m. retractor tentaculi originates from the wall of the neurocranium, but the adult insertion in the proximal tentacle fold is not yet established. The muscle is not yet striated. Dorsally, the vomeronasal organ maintains contact with the ventral part of the nasal canal, and the lumina of both are continuous.

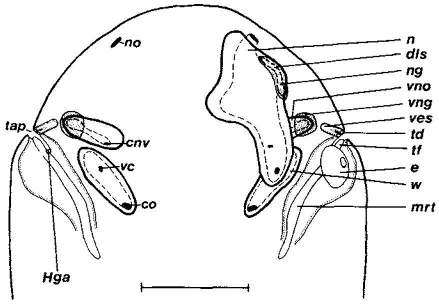

Fig. 6. 68-mm *D. mexicanus* fetus. Dorsal view of head illustrating eye, nasal, and tentacle elements. Bar = 1 mm.

58 mm (Fig. 5). The tentacle ducts continue to grow toward the vomeronasal organ. A small tubular gland, the vomeronasal gland, has differentiated and opens into the lateral lumen of the vomeronasal organ. Although the m. retractor tentaculi is larger in size and approaches the adult insertion position, it still is unstriated. The dorsolateral nasal tube has developed into a sac and lost its posterior opening. The tubular nasal gland begins to differentiate along this sac (Fig. 5B). Two eye muscles insert on the orbit but as yet have no origins and are unstriated.

68 mm (Fig. 6). The tentacle ducts have acquired lumina. At their proximal ends the ducts are united to a single short duct, forming a small vesicle. This proximal vesicle is separated from the vomeronasal organ by a septum of connective tissue in a maxillary foramen. The retractor muscle has established the adult insertion and is striated except in the insertion region. The anlagen of the fourth and fifth extrinsic eye muscles have aggregated. At the base of the sheath, the anlagen of the Harderian gland are present. They are spherical structures with a simple epithelium (Wake '85).

72 mm. The condition is similar to that of the 68 mm specimen. The anlagen of the Harderian gland increase in size and number and also appear posterior to the orbit around the m. retractor tentaculi.

80 mm (Fig. 7). The proximally fused tentacle ducts still are separated from the vomeronasal organ by the aforementioned septum in the maxillary foramen. A sixth eye muscle is forming. The retractor and compressor muscles have attained their adult but are not completely striated. The single anterior opening of the sac, lying dorsolaterally on the nasal sac, has shortened and has become the single outlet of the tubular nasal gland. The condition of a second 80-mm specimen examined is similar to that of the 105-mm specimen. (See discussion below of total length as a criterion of developmental stage.)

105 mm. All six eye muscles are present, striated and in contact with the orbit and the wall of the socket; they can be distinguished by position, origin and insertion (Wake, '85). The m. retractor tentaculi is striated except for some fibers supplying the tentacle fold. The large Harderian gland has outlets into the proximal cavity of the tentacle sac. The united tentacle ducts penetrate the connective tissue septum in the maxillary foramen by means of a small duct; thus the lumina of both fused ducts and vomeronasal organ now are connected. Because of this connection, the vomeronasal organ has an external chemosensory input independent of the nose and at the same time is a "functional" component of the tentacle apparatus.

110 mm. Its condition is similar to that of the 105-mm specimen except for the connection of the ducts with the vomeronasal organ; the united ducts have not yet penetrated the septum in the maxillary foramen. Although the fetus is longer, some or all structures are less well developed than in shorter, presumably younger fetuses.

Juveniles (post-birth) and adults

Once the ducts are connected to the vomeronasal organ, the whole tentacle apparatus seems to be functional. This state is achieved approximately at birth.

Juveniles (115–250 mm). After birth, no new structures are added to the tentacle apparatus. The tentacle aperature moves rostrally in the direction of the nostril and upper lip, and as a consequence, the inner structures within the tentacle sac, as well as the tentacle ducts, change in size, shape, and proportions.

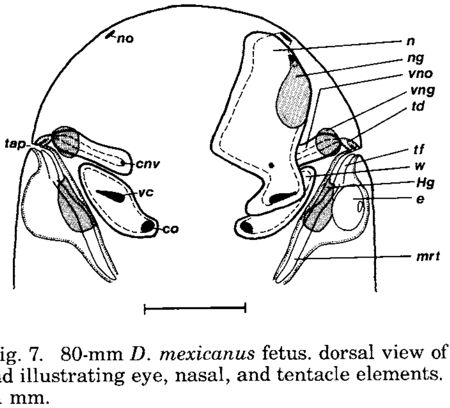

Fig. 7. 80-mm *D. mexicanus* fetus. dorsal view of the head illustrating eye, nasal, and tentacle elements. Bar = 1 mm.

Adults (250-398 mm). In young adults (TL 265 mm), the structures are established in their final position. The only structures that increase proportionally in size are the Harderian, vomeronasal, and nasal glands.

The developmental sequence of *D. mexicanus* is summarized in Table 1. This table also includes some eye and nasal structures, not only as ontogenetic components but as integrated elements of the functional tentacle apparatus (Billo, '86). The most striking features of the developmental sequence are:

1. The tentacle anlage aggregates as the dermis and epidermis differentiate.
2. Before the eye is incorporated in the tentacle sac, the sheath and fold of the tentacle have differentiated.
3. The fold, sheath, and aperture of the tentacle differentiate from the tentacle anlage just anterior to the eye. Only then does the tentacle aperature move rostrally. Concomitantly, the fold, sheath, and other associated structures shift forward (Figs. 1,7). In newborn and early juveniles, the adult tentacle position is not yet achieved.
4. Both tentacle ducts begin to aggregate just anterior to the tentacle orifice. They grow in the direction of the vomeronasal organ and unite proximally. The united ducts join the vomeronasal organ at a late fetal stage shortly before birth.
5. The Harderian gland begins to aggregate at the base of the sheath. Subsequently, it enlarges to the posterior pole of the orbit and fills the socket. It completes differentiation just after the union of the united tentacle ducts with the vomeronasal organ. The Harderian gland, as well as the nasal and vomeronasal glands, keeps growing relative to other structures, even in adults.
6. In chronological order, the development of the mm retractor and compressor tentaculi concur with the development of the extrinsic eye muscles. All these muscles aggregate and differentiate in situ from mesenchymal tissue. In *D. mexicanus* the retractor tentaculi never is in association with the orbit (Wake, '85), contrary to the observation of Norris and Hughes ('18) and Walls ('42) in larval *Ichthyophis*.
7. Apparently, the tentacle apparatus becomes functional shortly before birth by the connection of the tentacle ducts with the

vomeronasal organ (see statement 4), the differentiation of the Harderian gland, and the complete striation of the retractor and compressor muscles.

Tentacle development in Gymnopis multiplicata

Six stages of *Gymnopis multiplicata* were examined in order to compare tentacle development in a closely related species.

Embryos

10 mm. The primary optic vesicle is formed and connected to the prosencephalon by a constricted optic stalk. The lens placode is thickened. The nasal placode has aggregated.

12 mm. The nasal placode is invaginating.

15 mm. By invagination, the nasal sac now has an internal and external naris. The optic vesicle is fully invaginated to form the secondary optic vesicle. The lens vesicle has invaginated.

30 mm. The valve separating the nasal sac and choanal tube has differentiated. The anlage of the tentacle is present just ventrorostral to the eye in the same position as in *Dermophis mexicanus* and *Ichthyophis glutinosus* (Sarasin and Sarasin, 1897–1890; Badenhorst, '78). The vomeronasal organ is evaginating from the ventral nasal sac. The anlagen of the retractor tentaculi and compressor tentaculi are aggregating.

Fetuses

54 mm. The tentacle anlage has differentiated into the sac, sheath, and fold. The tentacle ducts are fused proximally to form a vesicle; this vesicle penetrates the ligaments in the maxillary foramen. The mm retractor and compressor tentaculi are partially striated. The vomeronasal organ has differentiated but lacks the lateral connection to the tentacle ducts.

84 mm. The fused tentacle ducts join the vomeronasal organ. The Harderian, nasal, and vomeronasal glands have differentiated. The tentacle aperture has moved forward to the adult position.

In the 84-mm specimen, all of the tentacle structures and functional connections (e.g., fused tentacle ducts connected with vomeronasal organ) are differentiated. Proportions, size, and shape change with progressing age, relative to the adult state. The less complete tentacle developmental sequence of *G. multiplicata* agrees with developmental data for *D. mexicanus.*

DISCUSSION

As noted in the introductory comments, two hypotheses were advanced by Sarasin and Sarasin (1887-1890) to account for the origin of the tentacle apparatus: either 1) the tentacle sheath evolved from an epidermal sensory groove into which the Harderian gland emptied mucus, or 2) the sheath represents an enlarged, common duct of the Harderian gland, and the tentacle fold is a secondary formation. Badenhorst ('78), in his study of development of *Ichthyophis glutinosus*, supports the second theory without providing supporting evidence. Although Fox ('85) mentioned both theories, he espoused neither.

Based on the following arguments, we believe both theories must be rejected. First, the tentacle ducts of caecilians are homologous to the lacrimal ducts of other vertebrates (Sarasin and Sarasin, 1887-1890). Thus, the anterior position of the tentacle aperture in caecilians must represent a derived state that evolved by means of an anterior migration of the orifice of each lacrimal duct along the sensory groove from the primitive, posterior position of the orifice. The sensory groove must have closed or invaginated into a sheath; its base probably effected contact with the m. retractor bulbi (which represented the m. retractor tentaculi), the rectus internus, and the Harderian gland.

It is unlikely that the tentacle sheath represents an enlarged, common duct of the Harderian gland, because every outlet of an excretory gland is bordered by a stratified cuboidal epithelium (Freeman and Bracegirdle, '75). None of the caecilians examined has a cuboidal epithelium in this area. On the contrary, the epithelium of the tentacle sheath and fold in *Ichthyophis* (Fox, '85), as well as in other species (personal observation), is characterized by five to seven layers of epithelial cells, including a cornified surface layer.

The question of the derivation of the tentacle in caecilians has been the starting point of many investigations. This descriptive work demonstrates the developmental sequence of tentacle structures of *Dermophis mexicanus* and, less completely, of *Gymnopis multiplicata.* From these ontogenetic data alone, we are not able to construct an hypothesis of the homology of the apomorphic structures concerned. Alberch ('85) discussed in detail the fundamental problems that may occur with the interpretation of developmental sequences. To carry out more reasonable sys-

TABLE 1. Developmental sequence of eye, nasal, and tentacle elements in Dermophis mexicanus

Total length (mm)	Eye	Nasal sac	Vomeronasal organ	Choanal valve	Choanenschleimbeutel	"Tentacle"
Pre-hatching embryos						
5	Primary optic vesicle	Placode				
8	Lens placode thickened	Placode invaginating				
Post-hatching embryos						
10	Secondary optic vesicle/lens vesicle invaginated	Nasal tube with internal and external nares				
14–15	Mesectoderm overgrowing eye from periphery	Undifferentiated wall thickening				Anlage (ectodermal elevation)
22–23			Anlage (a thickening in ventral nasal tube)			Anlage (plug-like and depressed)
25			Anlage evaginating			
Fetal stages						
34–35	Eyeball incorporated in tentacle sac			Anlage		Tentacle, aperture, sheath, and fold differentiated
44	Eye covered by skin			Differentiated	Built as a consequence of the choanal valve	
58		Differentiated epithelium	Differentiated epithelium			
68						Tentacle aperture moving rostrally
72						
80						
105						
110						
Juveniles (post-birth)						
115–250						
Adults						
250						Adult

(continued)

TABLE 1. Continued

Tentacle ducts	Tentacle sac	Nasal gland	Vomeronasal gland	Harderian gland	Retractor tentaculi	Compressor tentaculi	Extrinsic eye muscles	Total length (mm)
								5
								8
								10
								14–15
								22–23
Both ducts aggregating anterior to tentacle anlage	Aggregating							25
	Differentiated				Anlage	Anlage		34–35
Growing in direction of vomero nasal organ			Anlage				Anlage of three	44
	Anlage	Differentiated			A few muscle cells			58
With lumen and proximally united forming a vesicle			Anlage at the sheath's basis	Some muscle cells striated	Striated	Anlage of a fourth and fifth		98
		Differentiated		Anlage enlarged to posterior pole of orbit				72
						Completely striated	Anlage of a sixth	80
The united duct is connected to the vomeronasal organ					Differentiated		All six-differentiated and striated	105
				Differentiated				110
	Keeps growing in relation to other elements	Keeps growing in relation to other elements	Keeps growing in relation to other elements					115–250
								250

TABLE 2. Homologies proposed for tentacle elements

Caecilians (e.g., *Dermophis mexicanus, Gymnopis multiplicata*)	Other terrestrial amphibians (e.g., *Triturus alpestris, Rana temporaria*)
M. retractor tentaculi	= M. retractor bulbi[1]
M. compressor tentaculi	= M. levator bulbi[3] = M. compressor of Harderian gland (Edgeworth, '35)
Harderian gland	= Harderian gland[1,2]
Tentacle ducts	= Lacrymal ducts = ductus nasolacrimalis[1]
Tentacle sac	= Conjunctiva of the eye
Tentacle sheath	= Conjunctival sac
Tentacle aperture	= Interpalpebral space
Tentacle fold	= Lower lid

[1] Terminology of Sarasin and Sarasin (1887–1890).
[2] Leydig (1860).
[3] Norris and Hughes ('18).

tematic analyses, the integration of ontogenetic data with ingroup and outgroup comparisons is necessary. With ontogenetic studies, the early embryological relative position of elements (anlagen) and their subsequent development are revealed. The relative position of an anlage is useful as a criterion of homology (in contrast to homoplasy) in the sense of Jardine ('69), but this single criterion is insufficient to prove homology; the existence of possible deletions, insertions, or reversals (Alberch, '85) must also be considered.

We infer that the hypothetical ancestor of all caecilians had functional eyes. This pertains to the case of either monophyletic ("Lissamphibian") or polyphyletic origin of the extant amphibians. Investigators (Leydig, 1860; Sarasin and Sarasin, 1887–1890; Norris, '17; Norris and Hughes, '18; Engelhardt, '24; Laubmann, '27; Marcus, '30; Edgeworth, '35; de Villiers, '38; Walls, '42; Badenhorst, '78; Wake, '85) have studied the modification of the lacrimal apparatus and other structures associated with the eye for function in the tentacle apparatus in both primitive and derived taxa (ascertained by other sets of characters). The homologies of the Harderian gland, tentacle ducts (Δ lacrimal ducts = ductus nasolacrimalis), vomeronasal organ, m. retractor tentaculi (Δ m. retractor bulbi), m. compressor tentaculi (= the m. compressor glandulae orbitalis of Edgeworth, '35, Δ m. levator bulbi) generally are accepted. This permits the assumption of a hypothetical ancestor with the functional eyes of a generalized terrestrial vertebrate. As did a number of taxa that became fossorial, caecilians modified most structures associated with the eye and thus lost many aspects of sight. The development of the chemosensory tentacle, utilizing ocular components, is unique to members of the Order Gymnophiona among vertebrates.

The epidermis over the caecilian eye differentiates at the same time the tentacle anlage aggregates in the inner (ventro-medial) corner of the eye (see figures in Wake, '85). Ontogenetic series of *Triturus alpestris* (Urodela) and *Rana temporaria* (Anura) (Billo, personal observation) show that the anlage of their lower lids is in the same position relative to the eye as the tentacle anlage in both *D. mexicanus* and *G. multiplicata.* Based on these ontogenetic, outgroup comparisons, we propose that the tentacle fold of caecilians and the lower lid of other amphibians are homologous structures. Accordingly, the conjunctival sac is homologous with the tentacle sheath and the conjunctiva as a whole with the tentacle sac, both consisting of dense connective tissue. These homologies are further suggested by the outlets of the Harderian gland—in caecilians into the tentacle sheath and in other terrestrial amphibians into the conjunctival sac in the area of the lower lid. Accepting these homologies and bearing in mind statements 1 to 7 in our summary of development of the tentacle of *D. mexicanus* (above), the tentacle aperture corresponds to the interpalpebral space (Table 2).

It appears that the interpalpebral space in caecilians is reduced in a medial direction. The result is a small aperture (tentacle aperture) on the medial (nasal) angle of the eyeball and the retraction of the lower lid into the reduced conjunctival sac (tentacle sheath). In some species, the tentacle extended forward, bringing the tentacle aperture near the mouth or the tip of the head. As a consequence, the conjunctival sac, as the tentacle sheath, detached from the conjunctiva surrounding the eye. In all caecilians examined, the eye is involved with the connective tissue of the tentacle sac. In some species, the eye lies under skin, in some under skin and bone (Norris and Hughes, '18; Taylor, '68; Wake, '85) or is drawn out onto the tentacle (Taylor, '68; Wake, '85). Thus is effected the complex eye-tentacle relationships seen among adult caecilians.

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