

## Patterns of Peripheral Innervation of the Tongue and Hyobranchial Apparatus in Caecilians (Amphibia: Gymnophiona)

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**ABSTRACT** The innervation of the musculature of the tongue and the hyobranchial apparatus of caecilians has long been assumed to be simple and to exhibit little interspecific variation. A study of 14 genera representing all six families of caecilians demonstrates that general patterns of innervation by the trigeminal, facial, glossopharyngeal, and vagus nerves are similar across taxa but that the composition of the "hypoglossal" nerve is highly variable. Probably in all caecilians, spinal nerves 1 and 2 contribute to the hypoglossal. In addition, in certain taxa, an "occipital," the vagus, and/or spinal 3 appear to contribute fibers to the composition of the hypoglossal nerve. These patterns, the lengths of fusion of the contributing elements, and the branching patterns of the hypoglossal are assessed according to the currently accepted hypothesis of phylogenetic relationships of caecilians, and of amphibians. An hypothesis is proposed that limblessness and a simple tongue, with concomitant reduced complexity of innervation of muscles associated with limbs and the tongue, has released a constraint on pattern of innervation. As a consequence, a greater diversity and, in several taxa, greater complexity of neuroanatomical associations of nerve roots to form the hypoglossal are expressed.

The tongue of gymnophione amphibians (caecilians) is simple relative to that of other amphibians. Many salamanders and frogs have elaborate and diverse morphologies and mechanisms for tongue protrusion and retraction in prey capture. However, caecilians do not use their tongues in prey capture and exhibit limited morphological diversity of tongue structure (M.H. Wake and K. Schwenk, unpubl. observ.). Details of tongue and hyobranchial morphology per se have been described for only a few species (*Ichthyophis glutinosus*, *Hypogeophis rostratus*, and *Grandisonia alternans*; Teipel, '32; Marcus, '32). M.H. Wake and Schwenk are examining the comparative morphology and development of the tongue and hyobranchial apparatus in caecilians (unpubl. observ.). The caecilian tongue is a fleshy pad in the floor of the mouth. In many taxa, the anterior and lateral edges of the tongue adhere to the mucosa covering the inside of the lower jaw. The margin of the tongue is free in only a few taxa, and it is scarcely protrusible. In some caecilians, the tongue bears pronounced nar-

ial plugs that insert into the internal nares (Taylor, '68).

The tongue is composed primarily of fibers of the genioglossus muscle, which contains extensive vascular sinuses. The epithelium covering the tongue varies inter- and intraspecifically in its depth, arrangement of flaps and folds, and numbers and distribution of mucosal cells (M.H. Wake and K. Schwenk, unpubl. observ.). The hyobranchial apparatus characteristically lies well posterior to the pad of the tongue. Although the hyobranchium seems to have limited involvement in tongue function [except perhaps in larval rhinatrematids (M.H. Wake, '89; O'Reilly, '90)], it is involved in respiration. The hyobranchial skeleton has been illustrated in a number of studies of skull development and structure (summarized in M.H. Wake and Hanken, '82) and by Nussbaum ('79), in his consideration of the phylogenetic relationships of the rhinatrematids. Bemis et

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al. ('83) described the skeleton and musculature of the apparatus in their assessment of feeding mechanics in *Dermophis mexicanus*, and M.H. Wake ('89) examined the comparative morphology and development of the apparatus, especially in rhinatrematids.

Little is known about the innervation of the tongue of caecilians, in contrast to the situation for salamanders and frogs. Teipel ('32) reconstructed the innervation of the tongue of *Hypogeophis rostratus* from serial sections. Waldschmidt (1887) briefly considered the anatomy of the brain and the cranial nerves in *Hypogeophis rostratus*, *Ichthyophis glutinosus*, *Schistometopum thomensis*, and *Siphonops annulatus*, emphasizing the latter. Kuhlenbeck ('22) alluded to cranial nerve roots in his description of the morphology of the caecilian brain; his material included the species studied by Waldschmidt. Norris and Hughes ('18) compared the cranial and anterior spinal nerves of several species in a landmark paper. They concluded that there is little interspecific variation among caecilians. They also indicated that, in contrast to other amphibians, caecilians lack such features as the Jacobson's commissure; the ramus communicans between cranial nerves VII, IX, and X; the ramus pretrematicus of IX; and the ramus auricularis of XII. Norris and Hughes reported that caecilians have only two pairs of "branchial" nerves, owing to the "rudimentary condition of the branchial arches." They also implied that all caecilians have an occipital nerve, which they considered to be "a ventral division of a spinal nerve," and they infer that "there is no anastomosis between the occipital and the vagus in any caecilian."

D.B. Wake et al. ('83) and Roth et al. ('84) examined tongue innervation in several species of plethodontid salamanders as part of a study of the functional morphology and evolution of feeding mechanisms, particularly those involving a rapid, highly protrusible tongue. They reported differences in innervation that are correlated with tongue function; several of these are systematically significant. Their conclusions are relevant to this study and provide a basis for limited comparison.

Patterns of innervation are considered to be conservative in evolution. Furthermore, it is generally assumed that nerve-muscle relationships are established early in ontogeny and that they remain stable, although functions may change. Therefore, nerve-muscle

relationships are thought to remain stable during phylogeny, so that muscle homologies can be assessed in part by patterns of innervation (Northcutt, '79; D.B. Wake et al., '83).

The present study of innervation patterns in caecilians was undertaken to determine the following. First, is the morphologically simple tongue and hyobranchial apparatus associated with simple and uniform patterns of innervation across taxa? Second, are differences in innervation related to composition of the nerves? Third, is there functional or phylogenetic significance to patterns of lingual innervation? Based on the condition in most frogs and salamanders, I assume that (1) branches of the trigeminal nerve (V) innervate the adductor complex and the floor of the mouth; (2) branches of the facial nerve (VII) innervate the interhyoideus muscle, regardless of its components and functions, and the floor of the mouth; (3) the glossopharyngeal (IX) and the vagus (X) innervate the pharynx and the branchial muscles; and (4) the glossopharyngeal and hypoglossal innervate the muscles of the tongue and the hyoid apparatus, as in other amphibians. Working hypotheses include the following. First, because the skeletal morphology of the hyobranchium and its musculature are relatively simple and rather uniform in adult caecilians, the pattern of innervation will be uniform as well. Second, the hypoglossal nerve will be composed primarily of spinal nerve 1, although there may be some contribution from spinal nerve 2 (as there is in other amphibians; D.B. Wake et al., '83), the occipital nerve, and perhaps spinal nerve 3 (as indicated by Norris and Hughes, '18).

The composition of the hypoglossal nerve and the nature of the occipital nerve are particularly important problems because of conflicting reports of their presence and structure. Terminology is part of the problem. For consistency, I use the term "hypoglossal" for that combination of nerves that binds as a single trunk, extends anteriorly, then branches to innervate the muscles of the tongue and hyobranchial apparatus. I use the term "occipital," rather than "hypoglossal," to refer to the nerve that emerges from an occipital arch foramen and fuses with spinal 1 in some caecilians (see discussion below).

#### MATERIALS AND METHODS

Representatives of the six recognized families in the order Gymnophiona (Duellman

and Trueb, '86) were available for studies of patterns of innervation: *Epicrionops bicolor* and *E. petersi* (Rhinatreumatidae), *Ichthyophis kohtaoensis* and *I. sp.* (larva) (Ichthyophiidae), *Uraeotyphlus narayani* (Uraeotyphlidae), *Dermophis mexicanus*, *Gymnopsis multiplicata*, *Caecilia occidentalis*, *Oscacilia ochrocephala*, *Idiocranium russeli*, *Geotrypetes seraphini*, *Boulengerula boulengeri*, *Hypogeophis rostratus*, *Grandisonia alternans* (Caeciliidae), *Typhlonectes natans* and *Chthonerpeton indistinctum* (Typhlonectidae), and *Scolecormorphus uluguruensis* and *S. vittatus* (Scolecormorphidae). Specimens of each of these taxa were prepared by whole-body clearing and subsequent staining with Sudan Black B for myelinated peripheral nerves and alizarin red-S for bone (Fig. 1), according to the protocols of either Filipski and Wilson ('84) or Nishikawa ('87), as modified for caecilians (see below). Three adults of various sizes and a fetus of *D. mexicanus*, and two adults of *T. natans*, *G. seraphini*, and *S. uluguruensis*, as well as larval and adult *Ichthyophis*, were prepared to check the consistency of both staining and of nerve patterns, at different developmental stages within and among taxa.

Both methods of bulk staining require modifications of timing of certain steps for caecilians, and both have positive and negative features. The Filipski–Wilson protocol, with time in stains and macerating and clearing solutions adjusted for size of specimen, produces both faster staining and faster clearing. However, because the glycerine solutions are highly basic, the nerve stain fades very rapidly. Preparations must be photographed immediately upon completion. The Nishikawa protocol, also with time in steps adjusted for size of specimens, produces a much more nearly permanently stained preparation. However, it is most effective for smaller specimens, because clearing of larger ones (> 200 mm total length) is difficult, owing to the length of time of the staining step and the density of connective tissues of larger animals. Furthermore, alizarin staining is not nearly as effective as it is under the Filipski–Wilson protocol, and this can be important if foramina and other structures must be identified.

Heads of an ontogenetic series of *Dermophis mexicanus* (5, 15, 20, 30, 40, 45, 60, 115, 167, and 370 mm total length) were serially sectioned and stained according to Palmgren's protocol (Humason, '79). Microscopic

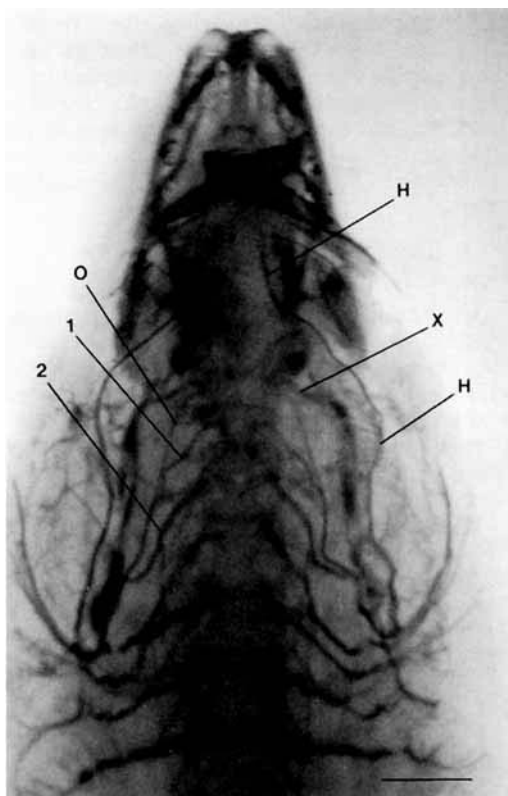


Fig. 1. Cleared and stained (Sudan black B for nerves, alizarin for bone) *Scolecormorphus uluguruensis* to illustrate nerves that contribute to the hypoglossal nerve, the course of the hypoglossal, and other posterior cranial and anterior spinal nerves. Scale bar = 1 mm.

#### Abbreviations for all figures

H	hypoglossal
O	occipital
V	trigeminal
VII	facial
IX	glossopharyngeal
X	vagus
1	spinal nerve 1
2	spinal nerve 2
3	spinal nerve 3
4	spinal nerve 4

examination and reconstruction of peripheral nerves were done to provide a detailed comparison with the pattern observed in bulk-stained whole animals.

#### RESULTS

The general pattern of innervation of the tongue and the hyobranchial musculature is described first; then species-specific deviations from the general pattern are described. Near-brain patterns (i.e., enclosed in the

skull) are not presented because evidence from sections indicates that there is little interspecific variation. Jaw-opening and closing muscles (except the interhyoideus posterior), ventral throat constrictors, and laryngeal and cutaneous components are not considered. Motor innervation is emphasized.

*General patterns of innervation*

Cranial nerve VII (facial)

The ramus jugularis innervates the interhyoideus and interhyoideus posterior muscles. I do not distinguish an "omo-humero-maxillaris (sphincter colli)," as did Norris and Hughes ('18), and I question their interpretation of its homologies. The ramus jugularis bifurcates, and a large branch enters the interhyoideus posterior (which has become a jaw adductor; see Bemis et al., '83; Nussbaum, '83), and its twigs fan out through the length of the muscle. I find no evidence of the nervus lingualis reported in *Hypogeophis* by Teipel ('32); Norris and Hughes ('18) did not mention it either.

Cranial nerve IX (glossopharyngeal)

The glossopharyngeal and vagus nerves emerge from the skull together; the glossopharyngeal and vagus trunk ganglia, when apparent, are in close contact, perhaps fused (as reported by Norris and Hughes, '18). The glossopharyngeal nerve has several branches, mostly mixed motor and sensory. Of the primary branches, the anterior-most innervates the dorsal wall of the pharynx (ramus pharyngeus IX of Norris and Hughes); the next (ramus lingualis IX) innervates the musculature of the ceratohyal, including subarcualis rectus I, and the tongue.

Cranial nerve X (vagus)

The vagus trunk has several branchial sensory branches; the ramus intestino-accessorius X branches to the more posterior branchial musculature. I concur with Norris and Hughes ('18) that a ramus communicans between the IX-X complex and cranial nerve VII is absent in caecilians, although it is conspicuous in other amphibians. Although Norris and Hughes do not so indicate, the vagus nerve contributes to, or at least anastomoses with, the spinal nerve 1 component of the hypoglossal in several taxa.

Occipital nerve

Norris and Hughes ('18) reported a distinct occipital nerve, rare in urodeles and

unknown in anurans, to be present in several caecilians. They stated that it is distinct from, but parallel to, the IX-X complex, from which it is separated by a blood vessel in some species. The occipital may or may not pass through the vagus ganglion. It innervates the rectus subvertebralis and dorsal trunk musculature, and in *Geotrypetes*, *Dermophis*, and *Caecilia*, but not in *Oscacilia* and *Ichthyophis*, contributes to the hypoglossal nerve. Norris and Hughes considered the occipital to be "a ventral division of a spinal nerve" that lies within the skull and exits the skull via a foramen. They clearly considered the occipital nerve to be distinct from the vagus, however.

I consider the "occipital" to be a separate but parallel nerve that emerges from the skull, usually through the foramen with the IX-X; it joins spinal nerve 1 a short distance from the foramen. The nerve is present in *Dermophis*, *Geotrypetes* (both confirming the observations of Norris and Hughes), *Gymnopsis*, *Typhlonectes*, and *Scolecormorphus*. I found no evidence of an occipital nerve in other genera [although the nerve was reported in *Oscacilia*, *Caecilia*, and *Ichthyophis* by Norris and Hughes ('18)]. It should be noted that Norris and Hughes considered the dorsal branch of the vagus nerve reported in *Siphonops* by Wiedersheim (1879) to be an occipital. Terminology of this nerve is a problem and is discussed below.

Spinal nerve 1

Spinal nerve 1 innervates the anterior part of the rectus abdominis musculature, cutaneous components, and contributes to the hypoglossal nerve in all caecilians (with the possible exception of *Gegeneophis*—see below). It enters the base of the tongue and extends through its length, giving off several branches to the genioglossus and, apparently, the geniohyoideus.

Spinal nerve 2

Spinal nerve 2 also contributes to the hypoglossal nerve in all caecilians. Spinal nerves 1 and 2 join and extend anteriorly as one trunk. In several taxa, the length of the union is short; the trunk splits into two components, each of which enters the body of the tongue separately and gives off numerous branches. The two trunks may fuse again anteriorly in the tongue. Spinal nerve 2 has a major trunk that extends posteriorly to innervate the vertebralis and cutaneous musculature of many segments.

### Spinal nerve 3

Spinal nerve 3 contributes to the hypoglossal nerve in *Ichthyophis*, as observed by Norris and Hughes in larvae but not in adults. Conversely, I find the spinal nerve 3 association in an adult of *Ichthyophis kohtaoensis*, but not in a larval *Ichthyophis* from the Philippines, and in *Uraeotyphlus*. The fusion is limited, only at the juncture of spinal nerves 1 and 2 in *Uraeotyphlus*, but starts well along the course of the hypoglossal and is extensive in *Ichthyophis*. Spinal nerve 3 also has a major extension far posteriorly that gives off numerous branches to the musculature of the body segments.

#### *Species-specific variation*

Variation from the general innervation patterns described above occurs in most of the caecilian taxa examined. The following comments are organized by taxon within families, and in order of the description of nerves presented above.

#### *Epicrionops bicolor* larva 177 mm TL

The ramus jugularis of the facial nerve courses *over* the retroarticular process of the jaw. It bifurcates, and both branches curve slightly anteriorly to innervate the interhyoideus anteriorly and the pharyngeal wall. *Epicrionops* has a single interhyoideus posterior and concomitantly does not have a large posterior trunk of the ramus jugularis. The glossopharyngeal nerve breaks into several branches at the lateral border between ceratobranchials I and II. It sends a large branch to subarcualis rectus I and a second posteriorly to the other branchial musculature. A third branch curves anteriorly, ventral to the branchial skeleton, and enters the body of the tongue. The vagus nerve is most peculiar. It sends several branches to the branchiometric musculature, and a stout intestino-accessorius trunk curves posteriorly. At the level of the second vertebra, a branch running dorsal to the spinal nerves extends posteriorly as well. In addition, a third major branch of the vagus emerges at that point and recurves anteriorly, apparently re-entering the skull through the foramen for the facial nerve. This branch is not joined with other nerves and seems to lack branches (although staining may not be fully adequate to ascertain this). It does not appear to be the recurrent laryngeal, because it emerges far posterior to the larynx and extends only anteriorly. It may be a communicating ramus of

VII/IX/X, as is known in salamanders, but this is not clear because its origin is not observed. Spinal nerves 1 and 2 fuse at the lateral border of ceratobranchial IV to form the hypoglossal nerve. Just after the point of fusion, a branch extends to the rectus cervicis musculature. Also at that point, the hypoglossal directly underlies the intestino-accessorius trunk of the vagus and appears to be bound to it. I cannot demonstrate that the nerves actually join, however, and I doubt that this occurs because of the position and limited extent of the connection. The hypoglossal continues as a single trunk into the body of the tongue, where it ramifies.

#### *Epicrionops petersi* larva 124 mm TL (Fig. 2A)

The ramus jugularis of the facial nerve courses posteriorly before curving anteriorly and branching in the interhyoideus. The glossopharyngeal sweeps farther anteriorly before it branches. The vagus branches into three major trunks at the level of ceratobranchial IV. The hypoglossal nerve is formed by fusion of spinal nerves 1 and 2, and there is a small collateral from spinal 3 as well. The hypoglossal, just at the fusion of spinal nerves 1 and 2, is bound to the vagus for a short distance as well. The two trunks cannot be separated by teasing but appear distinct visually because of the discrete staining of their fibers.

#### *Ichthyophis* sp. larva 140 mm TL

The ramus jugularis bifurcates after it emerges from the skull and sends stout anteriorly directed branches to the interhyoideus and the pharyngeal wall. The nerve sends a smaller, posteriorly directed branch to the interhyoideus posterior, where it branches immediately to innervate the muscle. The glossopharyngeal is distinct from the vagus at its emergence from the skull. It bifurcates at the level of the lateral border of the ceratohyals and sends branches to the subarcualis rectus muscles; one branch curves more anteriorly to enter the body of the tongue, where it splits immediately, sending numerous twigs throughout the tongue. The vagus sends several branches to the ceratobranchial musculature; the ramus intestinalis-accessorius courses posteriorly. The vagus lies ventral to spinal nerves 1 and 2 and does not communicate with them. Spinal nerves 1 and 2 fuse shortly after their emergence from vertebral foramina, send branches laterally, and curve anteriorly as the hypoglossal ramus. The hy-

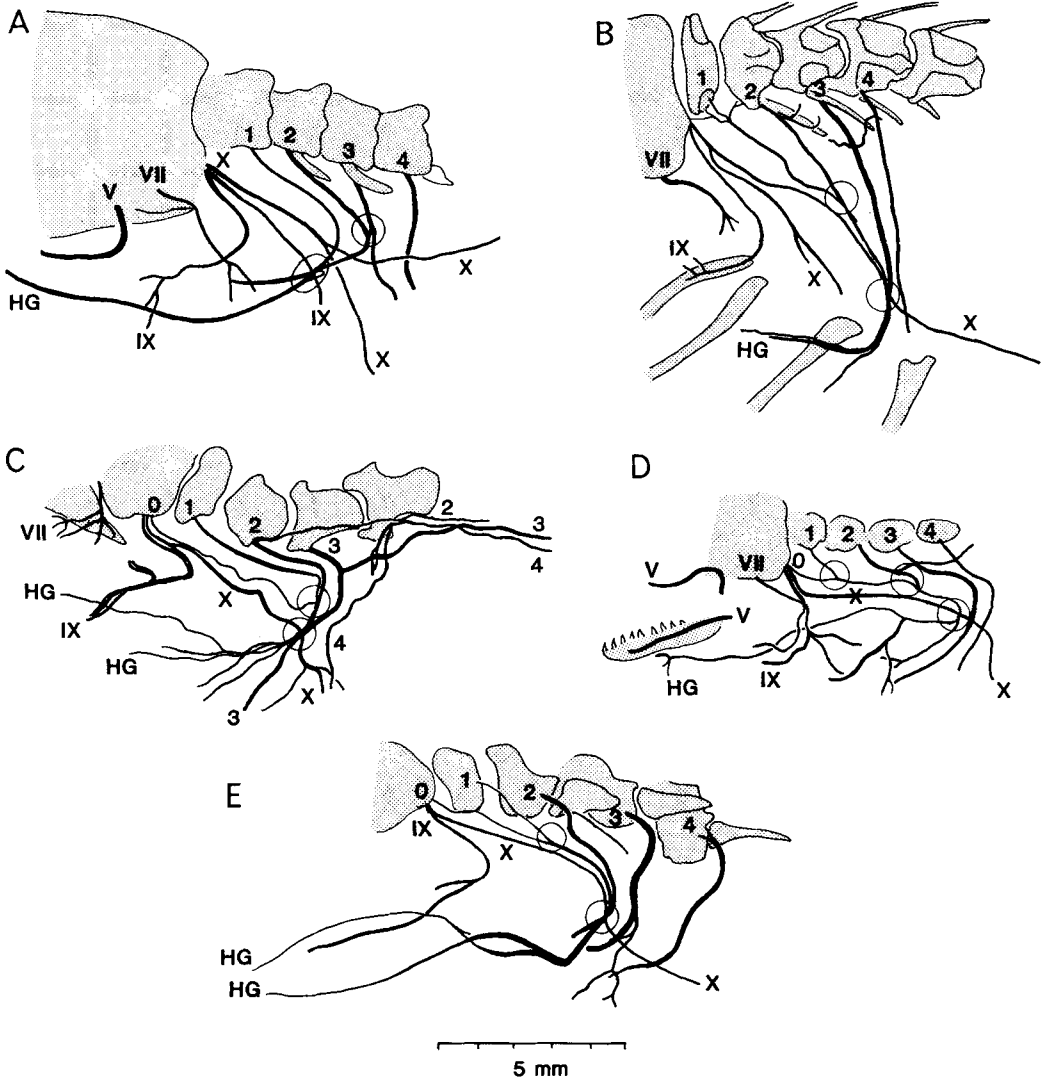


Fig. 2. Camera lucida drawings of posterior cranial and anterior spinal nerves of representatives of five families of caecilians. Points of fusion and ramification of the hypoglossal nerve are surrounded by circles. **A:** *Epicrionops petersi* (Rhinatreumatidae). Note that *Epicrionops* has a collateral branch of spinal 3 that joins the hypoglossal nerve distal to the fusion of spinal 1 and 2. **B:** *Ichthyophis kohtaoensis* (Ichthyophiidae). Spinals 1 and 2 fuse near the vertebral column, and more peripherally a branch of spinal 3 fuses with the hypoglossal trunk. **C:** *Uraeotyphlus narayani* (Uraeotyphlidae). The occipital is fused to spinal 1 and 2, a branch of 3 then fuses more distally, followed by a branch of X. Branches of spinal 2, 3, and 4 ramify to the hyobranchial musculature independently of

the hypoglossal trunk. **D:** *Scolecomorphus uluguruensis* (Scolecomorphidae). In *Scolecomorphus*, the hypoglossal is composed of a fusion of the occipital with spinal 1, which more peripherally fuses with spinal 2. Branches of 2 and 3 innervate hyobranchial musculature, as does the hypoglossal. **E:** *Typhlonectes natans* (Typhlonectidae). *Typhlonectes* has a hypoglossal composed of a proximal fusion of occipital and spinal 1, joined more distally by spinal 2. The hypoglossal trunk bifurcates in elongate branches to the hyobranchial musculature and the tongue. The ramification of cranial nerve VII in the interhyoid muscle and of IX in the branchial musculature are indicated in all figures.

glossal bifurcates at the level of ceratobranchial II, and the two nerves enter the tongue. Spinal nerve 3 has a stout trunk that courses posteriorly; the nerve gives off branches to many body segments and also has a branch that curves anteriorly. Spinal 3 is not associated with the hypoglossal, however, for when the latter is lifted with forceps, it is clear that the two nerve trunks are separate. Staining of the fine branches of the anterior ramus of spinal nerve 3 is inadequate to ascertain exactly which muscles are innervated.

*Ichthyophis kohtaoensis* adult (Fig. 2B)

The small ramus jugularis of the facial nerve bifurcates shortly after emergence from the skull to innervate the pharyngeal wall and the interhyoideus anteriorly, and the interhyoideus posteriorly. The glossopharyngeal forms several branches at the level of the ceratohyal, and a ramus enters the body of the tongue, where it sends several branches anteriorly. The vagus is distinct from the glossopharyngeal, sends branchial branches immediately on its emergence from the skull, and a stout ramus intestino-accessorius curves posteriorly, dorsal to the spinal nerves. Spinal nerve 1, curiously, appears to have two roots of origin emerging from the atlas vertebra; there is also a communicating ramus that emerges from the second vertebra and immediately joins spinal nerve 1. The ramus is not connected to spinal 2, and appears to have its own foramen in the vertebra. Spinal nerve 2 is a stout trunk that immediately sends branches to the vertebral musculature, but its main trunk fuses with that of spinal nerve 1 to form the hypoglossal ramus. Spinal nerve 3 has a similar distribution to that of spinal nerve 2, and it fuses with the hypoglossal ramus at the level of the border of ceratobranchials II and III. The hypoglossal ramus, now composed of spinal nerves 1, 2, and 3, sends a branch to the ceratobranchial musculature, and courses anteriorly to enter the tongue. It sends branches throughout the tongue, but does not have the distinct bifurcation observed in many other taxa.

*Uraeotyphlus narayani* (Fig. 2C)

The ramus jugularis branches extensively just after it emerges from the skull, fanning into the interhyoideus complex and the pharyngeal wall. The glossopharyngeal and vagus nerves emerge almost as a common trunk, separate at the midlevel of the atlas. The

glossopharyngeal curves anteriorly and sends a major branch to the branchial musculature before extending into the body of the tongue. It remains a trunk with small branches until approximately the middle of the tongue, where it ramifies extensively. The vagus nerve has the typical pattern, and extends dorsally over the anteriorly directed hypoglossal before it branches into its major trunks. However, at the point at which the glossopharyngeal and the vagus diverge in different directions, an additional slender nerve emerges that joins spinal nerve 1 just before the latter fuses with spinal nerves 2 and 3 to form the hypoglossal nerve. It is not clear whether this nerve is the occipital, which extends from the skull together with the glossopharyngeal and the vagus, or whether it is a ramus of the vagus alone. Spinal nerve 1 contributes most of its fibers to the hypoglossal; spinal nerve 2 contributes a large trunk to it but also has a large trunk that extends posteriorly over many segments to innervate the vertebral and body wall musculature. These two branches emerge separately from a single foramen in mid-vertebra. Spinal nerve 3 also emerges mid-vertebrally, and branches to produce one trunk that extends anteriorly to form part of the hypoglossal nerve, and another very long trunk that innervates the body musculature. Spinal nerve 4 has a similar pattern, with several branches emerging from the vertebral foramen. One branch extends anteriorly, one ventrally, and one over many body segments posteriorly; however, the anterior branch does not contribute to the hypoglossal.

*Hypogeophis rostratus* (Fig. 3A)

The ramus jugularis of the facial nerve has the typical pattern for caecilians, with extensive branching in the interhyoideus posterior. The hypoglossal is formed of a fusion of spinals 1 and 2, which immediately curves anteriorly and bifurcates posterior to the end of the retroarticular process of the lower jaw. Spinal nerve 2 is somewhat unusual in that it is a very large trunk; a small ramus joins spinal 1 well before the fusion of the major trunk of spinal 2 with spinal 1. Spinal 2 also sends a long, slender, branching trunk posteriorly shortly after it emerges from the vertebral foramen. Spinal 3 does not contribute to the hypoglossal but does send superficial branches anteriorly as well as its major trunk extending posteriorly.

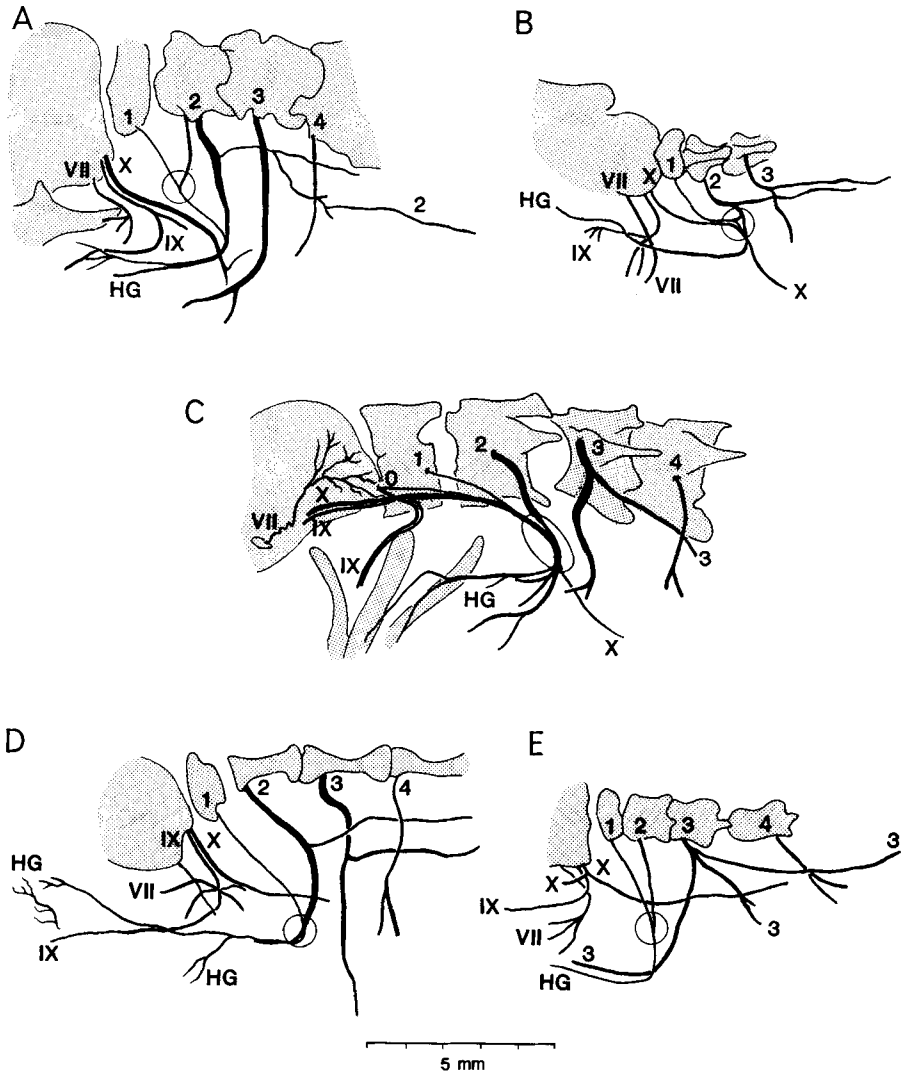


Fig. 3. Camera lucida drawings of posterior cranial and anterior spinal nerves of representatives of the family Caeciliidae. **A:** *Hypogeophis rostratus*. Note the proximal fusion of spinal 1 with a ramus of spinal 2, which fuses peripherally with the main trunk of spinal 2. **B:** *Boulengerula boulengeri*. *Boulengerula* has fusions of X and spinal 1 collaterals to spinal 2. **C:** *Dermophis mexicanus*.

The hypoglossal is composed of spinal 1 and 2 and the occipital. Spinal 3 has the multiple elongate branches characteristic of many caecilians. **D:** *Caecilia occidentalis*. The hypoglossal includes elements of spinal 1 and 2 and a ramus of X. **E:** *Oscaecilia ochrocephala*. The hypoglossal is composed of spinal 1 and 2.

#### *Grandisonia alternans*

The pattern of innervation and trunk composition in *Grandisonia* is very like that of *Hypogeophis*. It differs only in two regards; the small ramus from spinal 2 to spinal 1 is not present, and the fusion of spinal 1 and 2 is much closer to the vertebral column in *Grandisonia* than in *Hypogeophis*.

#### *Boulengerula boulengeri* (Fig. 3B)

The specimen representing *Boulengerula boulengeri* has an unusual hypoglossal configuration. The patterns of the facial and the glossopharyngeal are standard. Spinal 1 fuses with the vagus as the vagus passes posteriorly. The fused nerves send short communicating ramus to the trunk of spinal 2, just

after a long branch of 2 extends posteriorly. The fused X-1 nerve curves posteriorly and laterally, branching in the pharyngeal musculature and extending posteriorly. A major trunk of spinal 2 curves anteriorly as the hypoglossal. It may include fibers from spinal 1 and the vagus via the communicating ramus from that bundle. The hypoglossal of *Boulengerula* seems unique among the caecilians examined, in that it is composed largely of spinal nerve 2.

#### *Idiocranium russeli*

The ramus jugularis of the facial branches extensively into the interhyoideus posterior musculature just posterior to the end of the retroarticular process of the lower jaw. The glossopharyngeal branches immediately in several directions after it emerges from the foramen with the vagus. The vagus sends a small ramus communicans to spinal nerve 1. Spinals 1 and 2 fuse extensively some distance from their respective vertebral foramina. The fused bundle curves anteriorly from the inception of the fusion, sending off several posterior branches and then branching extensively at the anterior end of the tongue. Spinal 2 has a slender trunk that extends posteriorly, emerging about midway between the vertebral foramen and the fusion with spinal 1. Spinal 3 also has a long, posteriorly directed trunk; spinal 4 branches in multiple directions after it emerges and does not appear to have a long, concentrated posterior trunk.

#### *Geotrypetes seraphini*

Patterns of facial and glossopharyngeal nerves are standard. The vagus gives rise to an anterior branch immediately after its emergence from the foramen; the branch extends laterally before curving posteriorly. The vagus parallels the hypoglossal for a short distance but appears free of it. An occipital emerges from the vagus foramen and fuses with spinal 1, well before spinal 1 fuses with spinal 2. Spinal 1 has a branch that extends posteriorly shortly after its emergence from the vertebral foramen; the branch passes over the emerging spinal 2 but does not join it. However, at the point at which the occipital fuses with spinal 1, spinal 1 sends a ramus communicans to spinal 2, and spinal 2 sends one to spinal 3 at the same level. Spinals 1 and 2 fuse for a short distance and form the hypoglossal, but the hypoglossal trunk bifurcates almost immediately.

#### *Dermophis mexicanus* (Figs. 3C, 4C)

The innervation patterns of the facial and the glossopharyngeal are standard. Glossopharyngeal innervation of the larynx and the hyobranchial musculature are clear in this specimen. The vagus has an anteriorly directed branch just behind the lower jaw. An occipital emerges with the vagus and joins spinal 1 posteriorly. Spinals 1 and 2 fuse for a short distance to form the hypoglossal, but then the trunk bifurcates, ramifying and fusing in tissue under the hyoid apparatus, throughout the body of the tongue, and in the pharynx. Spinal 3 branches shortly after its emergence into an anterolaterally directed trunk and a posteriorly directed trunk. Both serve body wall musculature.

#### *Gymnopsis multiplicata*

The composition of the hypoglossal and distribution of the posterior cranial and other anterior spinal nerves are similar to that of *Dermophis*. *Gymnopsis* also possesses an occipital nerve; however, that nerve fuses with spinal 1 only on the right side of the specimen examined. The nerve is present on the left but is not fused.

#### *Caecilia occidentalis* (Fig. 3D)

This species appears to have the generalized pattern for caecilians, with the standard innervation patterns of facial, glossopharyngeal, and vagus, spinals 1 and 2 fusing some distance from their foramina to form the hypoglossal, and the hypoglossal having both posterior branches to the pharynx and extensive branching in the anterior part of the tongue. Spinals 2 and 3 also have long, slender, posteriorly directed trunks.

#### *Osaecilia ochrocephala* (Fig. 3E)

*Osaecilia ochrocephala*, too, has the generalized or simplified innervation pattern. The only unusual feature of this species is that, in addition to the lateral and posterior trunks of spinal 3, there is an anteriorly directed branch that curves into the tongue and courses in parallel with the hypoglossal but that is free of it. Peripheral staining was so weak that I could not determine what area the branch innervates.

#### *Typhlonectes natans* (Figs. 2E, 4A)

*Typhlonectes natans* is distinguished by having an occipital nerve that fuses with spinal 1 well before the latter fuses with spinal 2 to form the hypoglossal. The hypo-

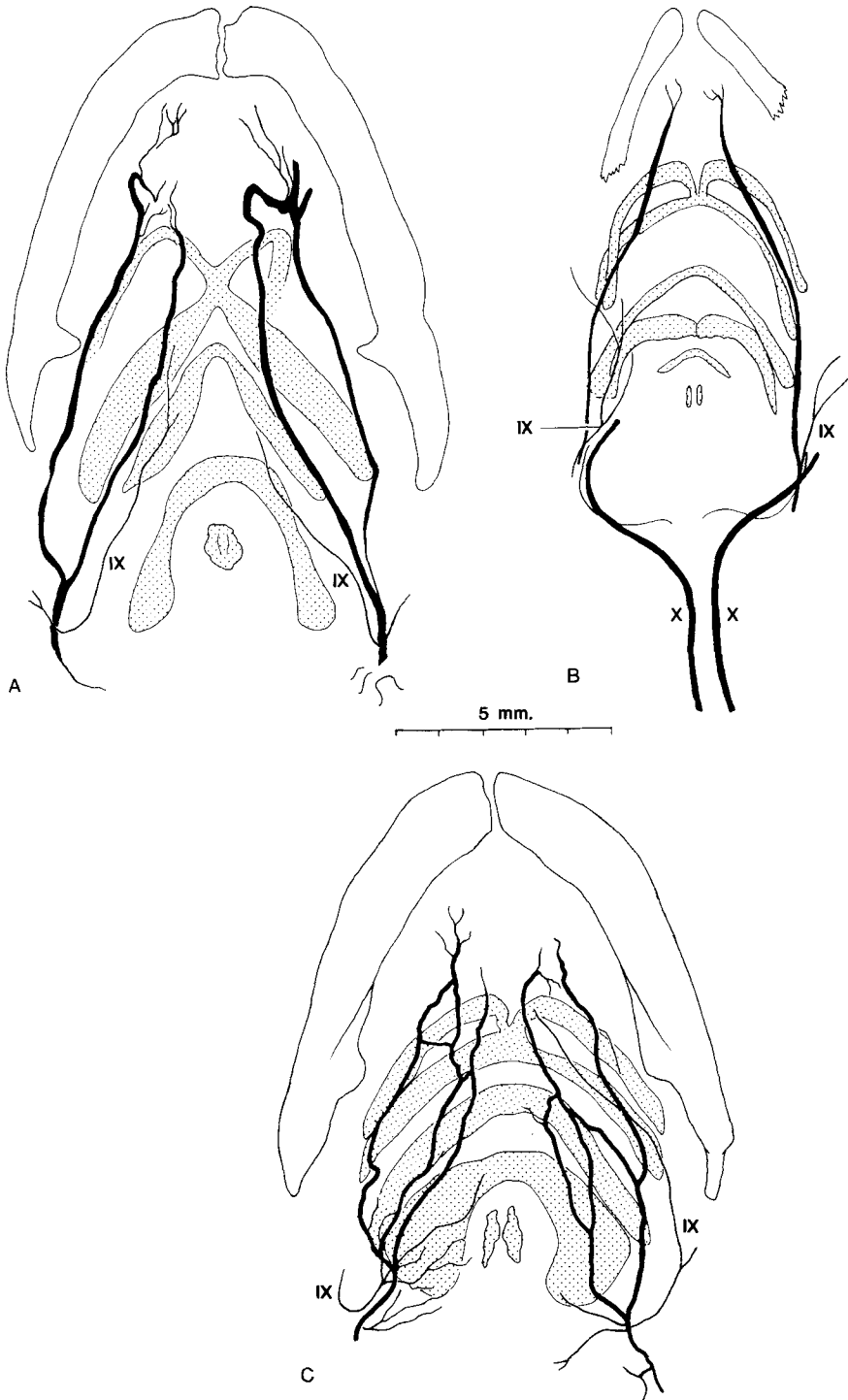


Fig. 4. Camera lucida drawings of branching patterns of the hypoglossal in the hyobranchial musculature and the tongue of representative caecilians. **A:** *Typhlonectes natans* (Typhlonectidae). The hypoglossal branches behind the jaw articulation and then fuses and ramifies in the tip of the tongue. The slender glossopharyngeal lies medial to the hypoglossal and sends branches to the hyobranchial musculature and the tongue. **B:** *Scolecomorphus uluguruensis* (Scolecomorphidae). The hypoglossal

is elongate and ramifies most strongly in the tongue tip. The glossopharyngeal branches extensively to the hyobranchial musculature. **C:** *Dermophis mexicanus* (Caeciliidae). The hypoglossal branches and fuses serially, with small ramifications to the hyobranchial musculature and the tongue tip. The glossopharyngeal also branches extensively to innervate the hyobranchial musculature and the tongue.

glossal bifurcates after a short distance of fusion, having paired trunks on each side that send small branches to the hypobranchial musculature, and then branch extensively at the tip of the tongue. Spinal 2 divides just beyond its foramen to send a slender trunk posteriorly. Spinal 3 branches laterally, and does not appear to have the elongate posterior trunk that characterizes several species.

#### *Chthonerpeton indistinctum*

The innervation pattern of *Chthonerpeton* is similar to that of *Typhlonectes*, except that it lacks an occipital nerve. Also, the hypoglossal does not bifurcate, but branches extensively throughout the hypobranchial musculature and the tongue.

#### *Scolecormorphus uluguruensis* (Figs. 1, 2D, 4B)

The patterns of the facial and the glossopharyngeal are standard. A stout occipital joins spinal 1 well before it fuses with spinal 2, to form the hypoglossal. The hypoglossal remains a single trunk, sending small branches along its course until it branches extensively in the tip of the tongue. The vagus passes dorsal to the point at which spinal 1 and 2 fuse, and bifurcates at that point into a stout anterior, multiply-branching ramus and a long, posteriorly directed trunk. Spinal 3 has a shorter, posteriorly directed trunk than that observed in many species.

#### *Scolecormorphus vittatus*

The innervation pattern in this species closely resembles that of its sister-taxon, *S. uluguruensis* (above). Observable differences are that, in *S. vittatus*, spinal 3 has an anteriorly directed branch that passes dorsal to the hypoglossal and apparently innervates the skin covering the hyobranchial apparatus, and spinal 2 has a stout posteriorly directed trunk, which serves axial musculature, that is absent in *S. uluguruensis*.

#### DISCUSSION

There is considerably more variation in the innervation patterns of the posterior cranial and the anterior spinal nerves among families and genera of caecilians than has been suggested by previous investigators. The composition and distribution of the hypoglossal nerve, the nature of the occipital nerve, and the innervation patterns of the ramus jugularis of the facial nerve, of the glossopharyn-

geal, and of the first, second, and third spinal nerves vary significantly among genera but appear to be fairly consistent among species within a genus. There is little difference in the *general* patterns of innervation by the vagus, facial, and glossopharyngeal nerves among the caecilians examined. The comparative anatomy of these nerves awaits detailed study.

The nerve-staining technique poses some problems, because its effectiveness varies with size of animals, the methods of fixation and preservation, and the time elapsed since fixation. However, the preparations are quite consistent among animals of different sizes preserved at the same time and in the same way. Artifact of technique is such that, when sampling animals of differing quality of preservation, smaller nerves may take up less (to no) stain in poorly preserved animals relative to well-preserved animals. Hence, staining indicates nerves that are surely present. This problem can only be resolved by staining larger samples of recently carefully fixed and preserved animals of taxa for which staining is questionable. A sample of specimens of different sizes and sexes from one population of *Dermophis mexicanus* was prepared to assess variation in nerve staining; variation was found to be minimal.

#### The occipital nerve

The occipital nerve has received considerable attention for more than a century. Its presence or absence and its origin have been reported for many vertebrate taxa, but it still is not clear exactly what it is. Many workers during the nineteenth century described an occipital nerve (particularly in fishes and in some amphibians), and most considered it to be composed of ventral motor components of the nerves of post-otic segments. Marcus ('10) discussed its affinities in a careful but little-known discussion of the segmentation of the head. He considered the occipital nerve of caecilians to be "occipital z" of a series of occipital ventral roots of post-otic segments. He mentioned that nerve z is not easy to find ("*nicht so leicht zu finden*"; p. 382) in some taxa and that it is apparent only at certain stages of development in some animals. Fox ('54, '57, '62, '65) extensively examined the posterior cranial and anterior spinal nerves in urodeles, anurans, and lungfish. He generally used the term "hypoglossal" to refer to nerves representing metotic segments that emerge through foramina anterior to the occipital arch. "Occipito-spinal" nerves are

those of more posterior occipital arches that are incorporated into the skull (cf. *Neoceratodus*, Fox, '62, pp. 242-243). By this convention, the first spinal nerve is that associated with the first neural arch, independent of the skull. However, Fox did not use the convention consistently. He refers to "a small hypoglossal (spino-occipital) foramen," (Fox, '57, p. 365). Fox, like Marcus, was particularly concerned with establishing serial homology of the nerves, skull and vertebral elements, and pronephric units.

Northcutt ('79) pointed out that the numbers of head segments involved in formation of the skull vary among vertebrates, and there is no general agreement on the ancestral number. He noted that in the region between the medulla and the spinal cord, the anterior spinal nerves undergo modification and reduce their sensory roots to become primarily somatic motor. When these elements are located outside the skull, as in cyclostomes, they are called *spino-occipitals*. When they are within the skull, "they are termed *occipital* nerves, since they exit through the occipital region of the skull." The amniote spinal accessory and hypoglossal nerves are also "within the skull" and are products of the pattern of modification as well. Northcutt stated that "Even in mammals, the spinal accessory and hypoglossal nerves contain somatic sensory cells scattered along their roots and therefore these nerves cannot be considered to be pure somatic motor nerves. In all vertebrates these nerves, whether we call them occipital nerve or cranial nerves, innervate anterior trunk epimeric musculature and cranial hypobranchial musculature." Thus, an occipital nerve is defined as a nerve that emerges from the occipital region of the skull, apparently distinct from the vagus.

Considerable dogma about the occipital nerve has crept into textbooks. For example, Hildebrand ('88) stated that the occipital nerve of the shark is the homologue of the hypoglossal, and he illustrated it as arising from two ventral roots that fuse to become the hypobranchial nerve, which he stated is a mixed sensory and motor nerve. Yet, two pages later in his general discussion of cranial nerves, he characterized the hypoglossal as an exclusively somatic motor nerve that innervates the muscles of the throat and tongue. He stated that it is "a cranial nerve in amniotes and some labyrinthodonts and a cervical nerve (called the hypobranchial

nerve) in cyclostomes and fishes. It is derived from several postotic somites (the same for which the vagus was the dorsal nerve) and joins the central nervous system by a linear series of twigs." By omission, he emphasized the difficulty in characterizing the nerve in amphibians.

Recently, several workers examined the brainstem of amphibians using horseradish peroxidase (HRP), fluorescent staining, and other marking techniques, in order to determine composition of nerves, extent and placement of nuclei, and so forth. The work of Roth et al. ('84, '88, '90), Roth and D.B. Wake ('85), and D.B. Wake et al. ('88) has focused on plethodontid and other salamanders. Using HRP techniques, they have demonstrated that certain plethodontid salamanders have a true spinal accessory nerve that innervates the neck musculature and that the ramus hypoglossus is composed only of the ventral, motor, first spinal nerve, which is therefore the homologue of the hypoglossal nerve of amniotes. The spinal accessory nerve extends forward, goes through the IX/X ganglion, enters the brain as the caudal-most root of the IX/X root complex, and then runs posteriorly in the brain and the cervical spinal cord to the motor nucleus of the second spinal nerve (without contact with the nuclei of the vagus or first spinal nerves), where its cells intermingle. Based on innervation of a branchial muscle, spinal motor nucleus, and point of entry to the brain, it is a true spinal accessory nerve. It is not an "occipital" nerve.

The brainstem of frogs has been similarly studied. Adult frogs lack a first spinal nerve; the hypoglossal is constituted of the second spinal. Matesz and Szekely ('77) and Stuesse et al. ('83) examined the nuclei and branching patterns of the hypoglossal in *Rana*, and Oka et al. ('87) and Takei et al. ('87) in *Bufo*. D.B. Wake et al. ('88) suggested that the evidence reported by these workers indicates that the dorsomedial hypoglossal nucleus of anurans is homologous to the hypoglossal nucleus of the rat. Oka et al. ('87) found a spinal accessory nerve and its nucleus in *Bufo*. D.B. Wake et al. ('88) considered the nerve and its nucleus homologous to that in salamanders. Roth et al. ('90) compared the brainstem organization, innervation patterns, and mechanics of the nerves and muscles involved in feeding in salamanders and frogs, summarizing considerable information.

I cannot comment on homology of the nerves in caecilians with those of other groups

based on my data. I wish to adopt a terminology that avoids the confusion of "hypoglossal" used both for an occipital arch nerve and for the aggregated body of nerves that innervate the tongue and some of the hyobranchial musculature. Therefore, I restrict my use of "hypoglossal" to the peripheral nerve that is the result of fusion of nerves and innervates the hypobranchial muscles of the tongue and hyoid, and use "occipital" for the nerve that precedes spinal 1 and emerges variously from the posterior part of the skull. In the absence of definitive work on the anterior spinal nerves of caecilians (although HRP and DiI experiments are under way), I consider an occipital nerve to be present if it emerges from the occipital region of the skull (usually through the same foramen as IX/X) and is clearly separate from the vagus at that point. I speculate that rami from the vagus to spinal nerve 1 (observed in *Caecilia occidentalis*, *Idiocranium*, and *Boulengerula*) and the curious multiple origin of spinal 1 in *I. kohtaoensis* might have been construed by other workers as variations of an occipital nerve. Because the occipital nerve, when present in caecilians, contributes only to the hypoglossal, rather than neck and cucullaris innervation, it should not be construed as a spinal accessory.

#### *Composition of the hypoglossal nerve*

The hypoglossal nerve in most salamanders is composed of components of the ventral roots of spinal nerves 1 and 2; there is a peripheral anastomosis of these two nerves, and the ramus hypoglossus, presumably carrying fibers of both, curves anteriorly into the tongue. However, the first spinal nerve constitutes the ramus hypoglossus in some plethodontid salamanders (Norris and Hughes, '18; Roth and D.B. Wake, '85; Roth et al., '84, '88; D.B. Wake et al., '88), *Amphiuma* (Norris, '08), and perhaps *Siren* (Norris and Hughes, '18), and is homologous to that of amniotes. The hypoglossal ramus of anurans is composed solely of fibers of the second spinal nerve (Nieuwenhuys and Opdam, '76). Norris and Hughes ('18) summarized work to that time on hypoglossal composition in gymnophiones. They reported that the hypoglossal is composed of the first spinal nerve only in *Oscacilia* (their *Herpele*), *Ichthyophis* [negating the work of Wiedersheim (1879) and Marcus ('10)]. The hypoglossal is a fusion of occipital and first spinal in *Geotrypetes*, *Dermophis*, and *Caecilia*; hypoglossal is a fusion of first and second spinals

in *Siphonops* (Fischer, 1843) and *Hypogeophis* (Marcus, '10). Ramaswami ('43) reported that the hypoglossal of *Gegeneophis carnosus* is formed by the union of spinals 2 and 3; he noted that spinal 1 "runs down without uniting with these." Leutenegger ('72) reported that the hypoglossal in *Nectocaecilia* is composed of two ventral roots and the first true spinal nerve 1, therefore "aus drei ventralen Wurzeln." She considered this situation comparable to "the amniote three spino-occipital nerves" and posited that there is a connection between gymnophiones and reptiles. My data confirm and extend some of these observations, contradict others, and supplement the information for these and other taxa.

In none of the caecilians that I examined (including those studied by Norris and Hughes) was there a hypoglossal composed only of spinal nerve 1. Hypoglossals in all taxa appeared to be products of, minimally, fusion of first and second spinals, and contributions from vagus, "occipital," and spinal nerve 3 were variously included. Norris and Hughes ('18) also observed fusion of first and second spinal nerves in *Oscacilia* and in *Siren*, but they concluded that "as motor and sensory branches are given off from the combination before the hypoglossus proper is reached it is probably that only first spinal fibers remain in it." It seems equally probable that these branches may be combinations and that the ramus hypoglossus remains a combination of fibers from the two anterior spinal nerves. This question can be resolved by selective staining with the first and second spinal roots with HRP and by determining whether anterograde staining of the hypoglossal occurs from only one or from both of these components, and also by staining the hypoglossal distal to the anastomosis to see whether the roots of both spinal 1 and spinal 2 are labeled retrogradely. This work is under way.

In the absence of definitive information that the postfusion hypoglossal does not carry fibers from one of its constituent nerves, I assume that the ramus hypoglossus includes fibers from all the nerves that fuse to form the tract from which the hypoglossus emerges. Therefore, my data support the observation in Norris and Hughes ('18; apparently reflecting Marcus, '10) that ventral branches of the first, second, and third spinal nerves unite to form what they call a hypobranchial nerve that gives off several

branches, including as a major trunk the hypoglossus, at least in some species.

If Ramaswami's ('43) report of the hypoglossal composition in *Gegeneophis carnosus* is correct, this is the only caecilian taxon examined (by anyone) in which the hypoglossal does not include a contribution from spinal nerve 1.

#### *Phylogenesis and the hypoglossal nerve*

Some structural features of the hypoglossal nerve may be of use to systematists. These features apparently are consistent within a species, and usually among species within a genus. Features include (1) the presence or absence of the occipital nerve, (2) the composition of the hypoglossal, (3) the distance from the vertebrae to the fusion of spinals 1 and 2 (greater than or less than 4.0 mm), (4) the length of that fusion (greater than or less than 3.3 mm), and (5) the ramification/distribution pattern of the branches of the hypoglossal (bifurcates or not after fusion, many or few branches to hyobranchial musculature, multiple branches in tongue musculature, or branching mostly at tongue tip). These characteristics are polarized and the data matrix presented and analyzed in M.H. Wake (submitted).

Several species in the genus *Ichthyophis* have a hypoglossal composed of contributions from spinal nerves 1, 2, and 3. They all lack an occipital nerve, according to my data, although Norris and Hughes ('18) report that it is present in *I. beddomi*. *Uraeotyphlus* also has its hypoglossal formed of three spinal nerves; it shares other, non-neuroanatomical, characteristics with ichthyophiids. *Epicrionops*, of the primitive family Rhinatrematidae (Nussbaum, '77), has a collateral from spinal 3 to spinal 2 (Fig. 2A) before the latter fuses with spinal 1 to form the hypoglossal. This is not the same pattern of fusion observed in *Ichthyophis* and *Uraeotyphlus*, but it may be a means by which spinal 3 also contributes to the hypoglossal nerve. *Epicrionops* lacks an occipital nerve. Both species examined have a long distance from the vertebrae to the fusion of spinals 1 and 2 and a long fusion before the hypoglossal ramifies.

Among members of the family Typhlonectidae, both *Typhlonectes* (Fig. 2E) and *Chthonerpeton* have the hypoglossal composed of spinals 1 and 2, and *Typhlonectes* has an occipital contribution in addition. These genera differ in most other characteristics of the hypoglossal as well. Leutenegger's ('72) report of the hypoglossal composition in *Necto-*

*caecilia* to be of two roots of the presumed occipital that lie with the roots of IX/X and spinal nerve 1 is a unique condition. She does not indicate whether the fusion of these elements is peripheral; I infer that the occipital component exits the skull with IX/X and subsequently fuses with spinal 1, although this is not stated. Leutenegger does not present information about the innervation pattern of the nerve, and she does not illustrate this component.

The two species of *Scolecophorus* (family Scolecophoridae) investigated possess a hypoglossal formed of spinals 1 and 2 and an occipital (Figs. 1, 2D, 4B). They have long fusions of spinals 1 and 2 and innervation patterns similar to those of the hyobranchial and tongue musculature. A branch of spinal 3 curves anteriorly and gives off branches to the neck musculature before coursing posteriorly, in both species.

All members of the family Caeciliidae investigated in this study possess a hypoglossal composed of spinals 1 and 2; in some taxa, the hypoglossal receives contributions from an occipital and, in some spinal 1, receives a ramus from the vagus nerve before fusion with spinal 2. The West African genera *Geotrypetes* and *Idiocranium* have a hypoglossal, composed of spinals 1 and 2. *Geotrypetes* has an occipital contribution, as also noted by Norris and Hughes ('18). *Idiocranium* lacks an occipital but has a collateral to spinal 1 from the vagus before spinal 1 fuses with spinal 2. *Boulengerula*, as noted above, is an exception to the general pattern, for the hypoglossal appears to be composed predominantly of spinal 2, with a slender collateral from a short fusion of the vagus and spinal 1. Therefore, the latter contribute to some degree as well. *Boulengerula* lacks an occipital. *Hypogeophis* of the Seychelles has a hypoglossal formed of spinals 1 and 2 and lacks an occipital in adults, although Marcus ('10) observed one in a larva. The pattern of *Grandisonia*, also from the Seychelles, is similar to that of *Hypogeophis*. There is considerable variation in the fusion lengths and innervation patterns among these taxa. Ramaswami ('43) reported a major exception to the pattern in *Gegeneophis*; the hypoglossal is formed of spinals 2 and 3, and spinal 1 does not fuse with the complex. I do not have the material to confirm this.

Among New World caeciliids, *Dermophis* has a hypoglossal composed of spinals 1 and 2 and an occipital, as also reported by Norris

and Hughes ('18). The hypoglossal of *Gymnopsis* is formed much like that of *Dermophis*, save for the nonfusion of the occipital on one side in the one specimen examined (mentioned above). I suspect that this is an unusual individual variant, but must examine a series in order to determine any pattern. In both *Caecilia* and *Oscacaecilia*, the hypoglossal is formed of spinals 1 and 2. I do not observe an occipital, reported to be present in both by Norris and Hughes. This variance is possibly the result of a staining artifact, although I believe this interpretation is not likely. I do observe a small collateral from the vagus to spinal 1 before it fuses with spinal 2 in *Caecilia occidentalis*, but this is not the occipital figured by Norris and Hughes. *Siphonops* was observed by Wiedersheim (1879) and by Fuhrbringer (1897) to have an occipital. There is considerable variation of fusion lengths and of innervation patterns among these genera.

#### *Interpretation of hypoglossal structure*

The critical question is why there is so much variation in the composition of the caecilian hypoglossal nerve. I speculate that two characteristics of caecilians influence the structure of the nerve. First, caecilians are limbless, so limb and girdle musculature is absent (including that from the hyobranchial apparatus to the sternum), and the brachial plexus is absent. Therefore, the first spinal nerves are restricted in their innervation to axial and body wall musculature and to the remaining hyobranchial components. Second, the tongue of caecilians is simple relative to that of most amphibians, being a pad in the floor of the mouth. Its margins are not free in many species, and are free only for millimeters in others. Caecilians have a strong-bite feeding mechanism that apparently makes little use of the tongue, although the tongue may be involved in some positioning of the prey item in the mouth and certainly is involved in propelling the prey posteriorly and in swallowing it (Bemis et al., '83). I suggest that, given a loss of musculature that is normally innervated by anterior spinal nerves and a tongue of limited functional capacity, normal developmental (generative) rules might be relaxed, and variation in innervation is introduced. As a consequence, axonal outgrowth can result in multiple innervation of target muscles, or even new target muscles. Homology of muscles based on the criterion of innervation would then be questionable. The question might be asked why

variation in innervation does not obtain in other limbless organisms, such as snakes and some lizards, since innervation patterns owing to limb loss have some similarities. One reason might be that the second condition of this hypothesis—that the tongue is limited in function—is not met. Therefore, innervation of the tongues of most reptiles likely remains highly specific with little variation. Furthermore, the historical or phylogenetic constraint of the amniote hypoglossal structure would also be involved in maintaining this pattern.

The hypothesis of relaxed control of axonal outgrowth and pattern of innervation can be tested in several ways. First, other groups that meet both conditions of the hypothesis can be examined (e.g., certain salamanders with reduced limbs, eels). Second, variation within genera and species of caecilians must be explored using larger samples with both the bulk-staining techniques and with reconstruction from serial, nerve-stained sections (important in order to understand variation, not just to test this hypothesis). Third, the development of the musculature and its innervation must be carefully assessed in caecilians. Fourth, experimental removal of salamander limb buds before muscles and their innervation are established could assess whether new patterns of spinal nerve innervation result.

The "evolutionary scenario" that limb loss and tongue reduction result in increased variation in sources of innervation of the tongue is highly speculative but potentially testable. The development of such scenarios allows appropriate techniques to be brought to bear on questions of development, structure, function, phylogeny, and evolution.

#### ACKNOWLEDGMENTS

Over the years, many colleagues have assisted my work by collecting specimens or by gifts or loans of material. I thank Douglas L. Rossman and David C. Cannatella, Louisiana State University Museum of Zoology, for the loan of *Epicrionops bicolor* and *E. petersi*; Robert Drewes and Jacques Gauthier, California Academy of Science, for the loan of *Scolecormorphus uluguruensis*; Robert Inger and Hymen Marx, Field Museum of Natural History, for the loan of *Ichthyophis* sp.; Jose P. Rosado, Museum of Comparative Zoology, Harvard University, for the loan of *Scolecormorphus uluguruensis* and *S. vittatus*; Kenneth Joysey, Cambridge University, for the

loan of *Idiocranium russeli*; W. Ronald Heyer, United States Museum of Natural History, for the loan of *Grandisonia alternans*; Maureen Farrell, for collecting *Uraeotyphlus narayani*; Bernd Fritsch, University of Bielefeld, for collecting *Boulengerula boulengeri* and for use of it and of *Ichthyophis kohtaoensis*; Werner Himstedt, Technisches Hochschule Darmstadt, for hatchling *I. kohtaoensis*; Donald Lawson, University of Salford, for *Hypogeophis rostratus*; A. Stanley Rand, Smithsonian Tropical Research Institute, for *Osaecilia ochrocephala*; Rafael de Sa, University of Texas, for *Chthonerpeton indistinctum*; and Theodore J. Papenfuss, Robert L. Seib, David B. Wake, and Thomas A. Wake, University of California, Berkeley, for *Dermophis mexicanus*. Specimens not mentioned as loans from other institutions are deposited in the collections of the Museum of Vertebrate Zoology, University of California, Berkeley.

I appreciate the work of Kath Thomas, Kristen Nygren, and Enrique Lessa in preparing sectioned material and in making Palmgren's stain work on caecilians. David Wake and Andrea Schmidt provided constructive criticism of an early draft of the manuscript, and the comments of three anonymous reviewers aided this version significantly. The research was supported by National Science Foundation grants BSR 83-05771 and 87-06135, and initial writing was done while in Paris as a Visiting Professor at the University of Paris VII and recipient of a John Simon Guggenheim Foundation Fellowship.

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