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ON THE STATUS OF *NECTOCAECILIA FASCIATA* TAYLOR, WITH A DISCUSSION OF THE PHYLOGENY OF THE TYPHLONECTIDAE (AMPHIBIA: GYMNOPHIONA)

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ABSTRACT: *Nectocaecilia fasciata* Taylor is a junior synonym of *Chthonerpeton indistinctum* Reinhardt and Lütken. The range of *Nectocaecilia* is restricted to northern South America. A hypothesis of phylogenetic relationships among the four genera of the Typhlonectidae is proposed, and alternative hypotheses are evaluated. The recently established genus *Pseudotyphlonectes* and other higher taxonomic categories proposed by Lescure et al. (1986) for the Typhlonectidae are invalid. *Pseudotyphlonectes* is a junior synonym of *Typhlonectes* Peters. It is suggested that phylogenetic studies of the Gymnophiona should proceed independently of taxonomic considerations until a compelling hypothesis is accepted.

Key words: *Nectocaecilia*; *Chthonerpeton*; *Potomotyphlus*; *Typhlonectes*; *Pseudotyphlonectes*; Phylogeny; Taxonomy; Typhlonectidae; Gymnophiona

RECENTLY, within a single year, three separate taxonomic treatments and hypotheses of phylogeny of the Gymnophiona were published. These three works differed in scope, methodology, and results. Duellman and Trueb (1986) used cladistic techniques to analyze relationships among families and subfamilies. They relied heavily on characters that Nussbaum (1977, 1979) had reported, and their results are essentially in agreement with his, resulting in a single taxonomic change. Laurent (1986) and Lescure et al. (1986) both produced hypotheses of intra-generic relationships within the Gymnophiona. Laurent's methodology was not made clear, but that of Lescure et al. was claimed to be cladistic. The latter authors' phylogenetic hypothesis was coupled with a proposal for major taxonomic rearrangements within the Gymnophiona. The phylogenies and taxonomic treatments of these authors are markedly different from each other and from that of Duellman and Trueb (1986). Nussbaum and Wilkinson (in press) critically evaluated the three phylogenetic hypotheses and concluded that the proposed phylogenies of Laurent (1986) and Lescure et al. (1986) are not supported by the evidence and that too little is presently known about variation in caecilian characteristics to justify taxonomic rearrangements at or above the familial level.

The taxonomy of the Gymnophiona is also unstable at the generic and specific levels. Research is constantly revealing taxa that are invalid and errors in established taxonomic treatments (Nussbaum, 1985, 1986*a*, in press; Nussbaum and Gans, 1981; Savage and Wake, 1972; Wilkinson, 1988). At present, genera are poorly defined, and for many there can be little guarantee that they are natural. Whilst such problems persist, hypotheses of intra-generic relationships are flawed by their reliance on possibly artificial units. Thus, it is important to redefine natural units that may then serve as a basis for meaningful comparison.

In this paper, I point out one such problem in the genus *Nectocaecilia*. By restricting the concept of *Nectocaecilia*, I evaluate its position within the Typhlonectidae and present evidence for an alternative phylogenetic hypothesis for the typhlonectid genera. I argue that this hypothesis should be preferred over those proposed by Laurent (1986) and by Lescure et al. (1986). I cannot evaluate the work of Duellman and Trueb (1986) with the evidence presented here, because they did not address the interrelationships of the typhlonectid genera.

METHODS

Counts of vertebrae in the nuchal region were made from radiographs. Specimens in which the nuchal region was well defined and clearly delimited by the third nuchal groove (= first primary groove) were used. For some specimens, pins were used as radio-opaque markers and were positioned perpendicular to the body surface at the level of the third nuchal groove or were inserted into the body at this level. Counts made in these ways did not differ from counts made from radiographs of the same specimens without markers using the visible constriction corresponding to the third nuchal groove to delimit the nuchal region. These counts are frequently not whole numbers, presumably because the external muscular sheath, to which the dermis attaches, is itself not strongly attached to deeper vertebral structures (Gaymer, 1971; Naylor and Nussbaum, 1980), and relative movement between the vertebral column and external annular or nuchal grooves is possible. Most frequently, fractional numbers of nuchal vertebrae are encountered in preserved specimens that have the nuchal region bent or otherwise contorted.

Postcloacal vertebral counts were made from radiographs using pins inserted into the cloacal aperture perpendicular to the body surface. The numbers of postcloacal vertebrae may be subject to artifactual variation, increasing with dehydration as the soft body parts shrink around the vertebral column (Nussbaum, in press). The range of postcloacal vertebrae in *Chthonerpeton* is increased by such variation, but for the purposes of this paper, it was not necessary to discriminate between counts derived from well preserved or dehydrated specimens.

Measurements were made to the nearest 0.1 mm with dial calipers, except total lengths, measured to the nearest 1 mm by stretching specimens along a meter rule.

In order to evaluate the results and methodology of Lescure et al. (1986), their data for the Typhlonectidae were reanalyzed with a computerized parsimony algorithm (PAUP, version 2.4: Swofford, 1985). All characters that varied across the typhlonectid taxa considered by Lescure et al. were included in the reanalysis. These characters were recoded in binary form using the morphoclines of Lescure et al., except for their annulation character for which polarization of the character states was not possible. For this character, the states reported by Lescure et al. in the "remarques sur segments succesion antero-posterieure" section of their data matrix were assigned symbols and run unordered.

The topology of the cladogram of Lescure et al. (1986) was specified and PAUP was used to distribute the character states upon this cladogram so as to minimize homoplasy. The ALLTREES routine of PAUP was used to generate all possible cladogram topologies and to identify the ones that best fit the data. PAUP provided consistency indices for each of these trees and for the cladogram of Lescure et al. which facilitated comparison.

STATUS OF *NECTOCAECILIA FASCIATA*

Taylor (1968) established the genus *Nectocaecilia* to receive *Chthonerpeton petersii* Boulenger, a species then known only from the holotype and for which the only available locality was the Upper Amazon; *C. haydee* Roze, from Venezuela; and two new forms, *N. ladigesi,* from Rio Moju, Brazil, and *N. fasciata* from Buenos Aires, Argentina. These taxa were linked by the unique combination of characters: sub-triangular nares, tentacular apertures far forward behind the nares (as in *Typhlonectes* and *Potomotyphlus*), and the absence or vague trace of a fin in adults (well developed in *Typhlonectes* and *Potomotyphlus,* absent in *Chthonerpeton*). Taylor (1970) described a further species of *Nectocaecilia* (*N. cooperi*), from Rio Magdalena, Colombia, which Wilkinson (1988) showed was based on a single aberrant specimen of *Typhlonectes natans* (Fischer).

Taylor (1968:269) distinguished *Nectocaecilia fasciata* from the other species of *Nectocaecilia* by its low number of primary annuli, and he reported that the holotype and only known specimen is in the Museo di Zoologia, University of Torino, IMZT 2817 (since recatalogued as IMZT An-786; see Elter, 1981). I recently examined the small collection of caecilians in Torino and found that IMZT An-786 is a specimen of *Chthonerpeton indistinctum* Reinhardt and Lütken (Figs. 1A, 2A). This specimen differs significantly from Taylor's type description of *N. fasciata*; only the number of primary annuli and tooth counts reported by Taylor are similar to my data for IMZT An-786 (Table 1).

It would seem that Taylor's type description was based on a different specimen, and if this was the case, *Nectocaecilia fasciata* would be a nomen dubium until either the unknown "holotype" or new specimens corresponding to Taylor's description are discovered. Taylor's data for the "holotype" of *N. fasciata* includes a 1.0 mm projection of the snout. This is anomalous because the Typhlonectidae is a family typified by strongly recessed mouths, and a typhlonectid as large as the holotype (390 mm total length) should have a snout projection greater than 3.0 mm. If Taylor actually examined a specimen that corresponds to his description of *N. fasciata,* then it is surprising that this specimen was referred by Taylor to the Typhlonectidae, and that the minimally recessed mouth, which would be its most distinctive feature, was neither commented upon nor used as a diagnostic character by Taylor.

In the Museo Civico di Storia Naturale, Genova, there is a specimen of *Typhlonectes natans* (MSNG 379/A) which was received as a gift from the University of Torino and which agrees fairly well with Taylor's description of *Nectocaecilia fasciata* excepting the projection of the snout and the tooth and annular counts (Table 1). This specimen is a male and the dorsal "fin" is basically restricted to a ridge, developing into a free fold only above the terminus.

The IMZT collections contain, in addition to the single specimen of *Chthonerpeton indistinctum,* two more specimens of *Typhlonectes natans* and five of *Siphonops annulatus* (Mikan). In the latter species, the projection of the snout is far less than in any typhlonectid and is comparable to that reported by Taylor for *Nectocaecilia fasciata.* I suspect that Taylor examined all of these specimens, including the *T. natans* now in Genova, and confused his data such that his description of *N. fasciata* was a composite of data recorded from *C. indistinctum* with its low number of annuli, *T. natans* with its large sub-triangular nares and closely positioned

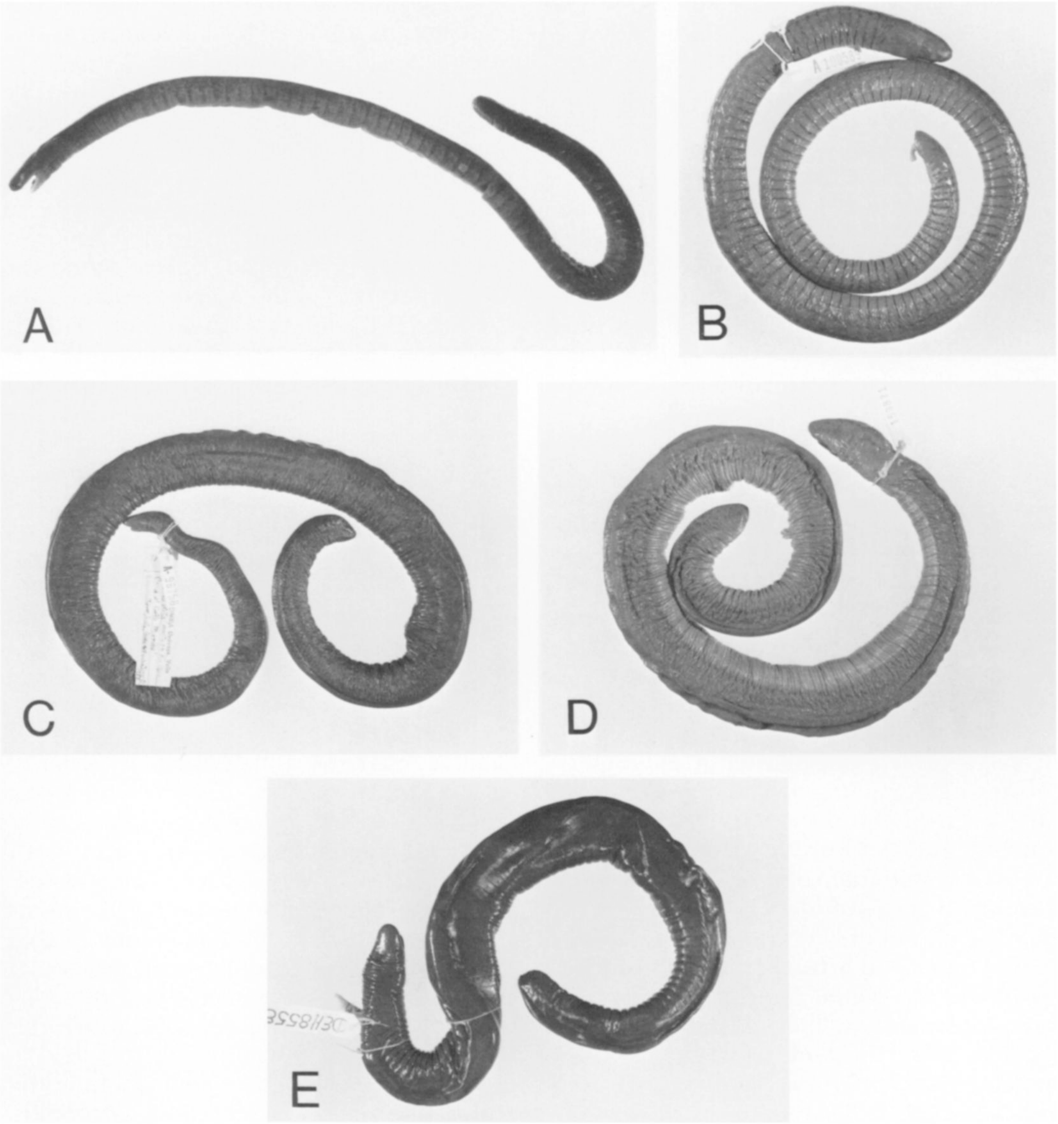

FIG. 1.—Whole body photographs of representative typhlonectids. (A) *Chthonerpeton indistinctum*, IMZT An-786, Total length (TL) = 175 mm. (B) *Nectocaecilia petersii*, AMNH A100589, TL = 505 mm. (C) *Potomotyphlus kaupii*, MCZ 96758, TL = 605 mm. (D) *Typhlonectes natans*, CAS 153871, TL = 570 mm. (E) *Typhlonectes compressicaudus*, CM 90091, TL = 464 mm. Note the development of middorsal free folds, modification of the terminal shield and lateral compression of the body in (C), (D), and (E) and their absence in (A) and (B).

tentacular apertures, and *S. annulatus* with its feebly projecting snout. These features distinguished Taylor's *N. fasciata* from all other caecilians.

If this interpretation is accepted, *Nectocaecilia fasciata* cannot be a nomen dubium. The named holotype of *N. fasciata* is IMZT An-786, and so I consider *Nectocaecilia fasciata* Taylor to be a junior synonym of *Chthonerpeton indistinctum* Reinhardt and Lütken. The other nominal species of *Nectocaecilia* are known only from South America no farther south than the Amazon drainage, and the anomaly of

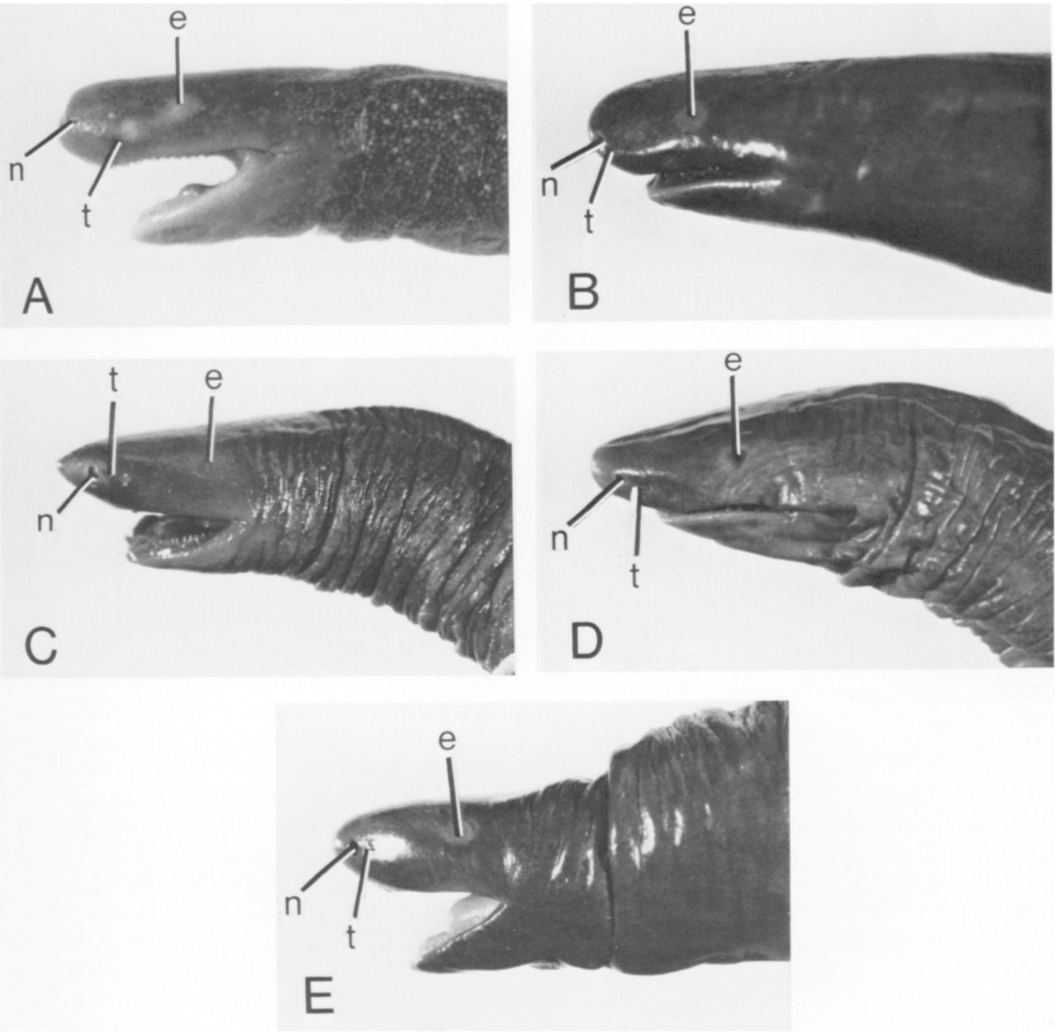

FIG. 2.—Left side of the head of representative typhlonectids showing relative positions of the eye (e), tentacular aperture (t), and naris (n). (A) ***Chthonerpeton indistinctum***, IMZT An-786, Head length (HL = distance from snout tip to first nuchal groove) = 8.6 mm. (B) ***Nectocaecilia petersii***, AMNH A100589, HL = 13.3 mm. (C) ***Potomotyphlus kaupii***, MCZ 96758, HL = 12.4 mm. (D) ***Typhlonectes natans***, CAS 153871, HL = 23.3 mm. (E) ***Typhlonectes compressicaudus***, CM 90090, HL = 17.5 mm. Note the strong projection of the snout beyond the recessed mouth that is typical of all typhlonectids, and the naris shape; ovate in (A), sub-triangular in (B), (C), (D), and (E).

a congener as far south as Argentina is now removed.

Of the remaining species of *Nectocaecilia*, the validity of *N. haydee* is uncertain and *N. ladigesi* is a *Typhlonectes* (Wilkinson, unpublished), but *N. petersii*, the type species, is a distinctive, undoubtedly valid species which has no middorsal ridge nor free fold and has sub-triangular narial apertures with the tentacular apertures close behind them. By restricting consideration of *Nectocaecilia* to *N. petersii* only, it becomes possible to evaluate the phylogenetic position of *Nectocaecilia* within the Typhlonectidae.

PHYLOGENY OF THE TYPHLONECTIDAE

The family Typhlonectidae consists of four genera. *Nectocaecilia* seems intermediate in its most apparent characteris-

TABLE 1.—Morphometric and meristic data reported for *Nectocaecilia fasciata* by Taylor (1968:269–271) and original data for IMZT An-786 (*Chthonerpeton indistinctum*) and for MSNG 379/A (*Typhlonectes natans*) believed to have been confused in Taylor's description of *N. fasciata*. All measurements in mm.

	N. fasciata (data from Taylor)	*C. indistinctum* (IMZT An-786)	*T. natans* (MSNG 379/A)
Total length	390	175	385
Number of annuli	76	74	89
Width	22	6.5	16*
Length divided by width	17.7	26.9	24.1
Head width	14	5	12
Head length to 1st nuchal groove	17	8.6	16.3
Head length to 2nd nuchal groove	23	11.6	21.3
Head length to 3rd nuchal groove	28.2	13.6	28.2
Projection of snout beyond mouth	1.0	1.8	3.2
Tentacular aperture to naris	0.7	0.12	0.7
Premaxillary-maxillary teeth	28	27	—
Vomeropalatine teeth	27	24	—
Dentary teeth	24	26	—
Splenial teeth	6	6	—

* Width measurement affected by maceration of body musculature.

tics between *Chthonerpeton* on the one hand, and *Potomotyphlus* and *Typhlonectes* on the other. The lack of a middorsal ridge or free fold in *Chthonerpeton* and *Nectocaecilia* (Fig. 1A,B) is probably primitive. The presence of well developed free folds in females of *Typhlonectes* (ridges or free folds in males) and in both sexes of *Potomotyphlus* (Fig. 1C–E) is probably a shared derived feature (found in the adults of no other caecilian genus). This is evidence that *Potomotyphlus* and *Typhlonectes* are sister taxa. *Nectocaecilia* shares with *Potomotyphlus* and *Typhlonectes* (Fig. 2B–E) tentacular apertures that are close behind the nares and subtriangular narial apertures. In *Chthonerpeton* (Fig. 2A), the tentacular apertures are more nearly equidistant between the eyes and nares, and the narial apertures are more ovate and elongate.

All of the evidence that I discuss indicates monophyly of two groups: the first including the three genera *Nectocaecilia*, *Potomotyphlus*, and *Typhlonectes*, with *Chthonerpeton* the sister taxon of this assemblage, and the second composed of *Potomotyphlus* and *Typhlonectes*.

MONOPHYLY OF *NECTOCAECILIA*, *POTOMOTYPHLUS*, AND *TYPHLONECTES*

Neither of the positions of the tentacular aperture found in the Typhlonectidae corresponds exactly to the positions found in any other caecilian genus, and thus both positions might be derived relative to other Gymnophiona. The intermediate position in *Chthonerpeton* is more closely approached in other forms. Amongst neotropical genera, a position of the tentacular aperture intermediate between the eye and naris is typical (exceptions to this are *Rhinatrema*, *Epicrionops*, *Caecilia*, and *Oscaecilia*), but it is usually closer to the lip (e.g., *Dermophis*) or closer to the eye and more distant from the lip (e.g., *Siphonops*) than in *Chthonerpeton*. Thus the evidence suggests that the position of the tentacular aperture in *Chthonerpeton* may be primitive for the Typhlonectidae. If both states are independently derived from a different state in the last common ancestor of these genera, then this would indicate monophyly of the genus *Chthonerpeton*, and of a group composed of the three genera *Nectocaecilia*, *Potomotyphlus*, and *Typhlonectes*. If the condition in *Chthonerpeton* is primitive relative to the condition of the other typhlonectid genera, this would still constitute evidence of monophyly of the *Nectocaecilia*-*Potomotyphlus*-*Typhlonectes* group, but not of monophyly of *Chthonerpeton*. The possibility that the intermediate position of the tentacular aperture is derived from the more anterior position, which would constitute evidence only for monophyly of *Chthonerpeton*, seems unlikely. Thus, I interpret the position of the tentacular aperture in *Nectocaecilia*, *Potomotyphlus*, and *Typhlonectes* as a shared derived character indicating monophyly of this group. Nussbaum (1977, 1979) used an argument from ontogeny to polarize these character states. Duellman and Trueb (1986) simplified Nussbaum's (1979) treatment of this character. Both of these interpretations are consistent with that proposed here.

The same interpretation can be applied to the shape of the narial apertures. Both conditions found in the Typhlonectidae might be independently derived from some different form, or any one state could be primitive relative to the other. Among other caecilians, narial aperture shape is typically subcircular, but in some species of *Caecilia* and *Siphonops*, they may be slightly ovate and elongated, approaching the condition in *Chthonerpeton*, which may thus be primitive for the Typhlonectidae. That ovate narial apertures might be derived from sub-triangular ones seems unlikely, and I conclude that sub-triangular narial apertures are a shared derived trait indicating monophyly of the *Nectocaecilia-Potomotyphlus-Typhlonectes* group.

In caecilians, the right lung is typically small and the left is smaller still, often little more than a small diverticulum. Within the Typhlonectidae, the lungs demonstrate different degrees of elongation. *Chthonerpeton* clearly has the most primitive pattern with a very short left lung and a right lung that stretches posteriorly to about the level of the posterior end of the liver. *Nectocaecilia, Potomotyphlus,* and *Typhlonectes* share the derived features of a right lung that extends caudally much further than the liver, and a left lung that is also well developed. Both of these features are good evidence for the monophyly of this group of three genera.

In non-typhlonectid caecilians, it is not always easy to determine the presence of choanal valves, because they may be concealed deep within the small choanae, hence knowledge of their occurrence is very limited. I have observed them within the neotropical genera *Caecilia* and *Dermophis* where they are small and deep, and Taylor (1968) reported them in *Grandisonia* from the Seychelles archipelago. Choanal valves may well be widespread in the Gymnophiona but not visible in superficial examination. In the Typhlonectidae, the choanal apertures are larger and the valves are larger and more superficial, and these are probably derived features indicating monophyly of this family. Within the family, *Chthonerpeton* has the smallest choanal apertures and the smallest and deepest choanal valves. Larger choanae and larger valves are present in the other three genera, forming a graded series of increasing size. I interpret this as two parallel evolutionary transformation series in which *Chthonerpeton* has the most primitive states (the smallest choanae and smallest valves), *Potomotyphlus* and *Typhlonectes* share the most derived states (extremely enlarged choanae and valves), and *Nectocaecilia* has intermediate states (moderately enlarged choanae and valves). Shared possession of the derived states of these two characters (moderately or extremely enlarged choanal apertures and choanal valves) is evidence of monophyly of the *Nectocaecilia-Potomotyphlus-Typhlonectes* group. These three genera also share superficial placement of their choanal valves, and this is also a shared derived feature indicating their monophyly. In Nussbaum's (1979) cladistic analysis, enlarged choanae were considered derived. His treatment, however, included only a single typhlonectid genus. I have extended this treatment by subdividing this character to reflect the different character states present in the Typhlonectidae.

Without justification, Lescure et al. (1986) considered four vertebrae in the nuchal region primitive and three or five derived. They reported that all of the typhlonectid taxa that they considered have three nuchal vertebrae; however, I find (based on larger samples) that the number of nuchal vertebrae is variable within the Typhlonectidae (summarized in Table 2). *Chthonerpeton* has three nuchal vertebrae, whereas *Nectocaecilia, Potomotyphlus,* and *Typhlonectes* all have four or more. Also contrary to Lescure et al. (1986), the dominant condition found in possible neotropical outgroups for the Typhlonectidae (*Dermophis, Gymnopis, Siphonops, Caecilia, Epicrionops*) is three nuchal vertebrae (Wilkinson, unpublished).

Lescure et al. (1986) reported the presence of "tails", which they equated with postcloacal vertebrae, in *Typhlonectes* and their absence in *Potomotyphlus* and

TABLE 2.—Summary of numbers of nuchal and postcloacal vertebrae in genera and species of the Typhlonectidae.

	Numbers of vertebrae					
	Nuchal			Postcloacal		
	Range	$\bar{x}$	*n*	Range	$\bar{x}$	*n*
Chthonerpeton	2.8–3.8	3.24	40	0–3	1.71	33
Nectocaecilia	4.0–4.5	4.09	10	3.5–5	4.07	7
Potomotyphlus	4.0–5.0	4.06	15	4–5	4.2	14
Typhlonectes natans	4.0	4.0	35	3.5–6	4.31	38
T. compressicaudus	4.0–4.5	4.03	15	4–7	5.5	8

Chthonerpeton. There are good reasons to prefer Nussbaum's (1979) equating of "true tails" with postcloacal external segmentation supported by postcloacal vertebrae, because these "true tails" are probably not homologous with postcloacal vertebrae that occur in the absence of postcloacal external segmentation. My investigations show that within the Typhlonectidae only *Chthonerpeton* may lack postcloacal vertebrae (Table 2). This condition is also typical of neotropical caeciliids (an outgroup) indicating that it is primitive for the Typhlonectidae. I interpret four nuchal vertebrae and several (>3) postcloacal vertebrae, in the absence of postcloacal external segmentation, as derived character states which are shared by, and are evidence of monophyly of, the *Nectocaecilia-Potomotyphlus-Typhlonectes* group.

The gills of fetal typhlonectid caecilians attach to the nuchal region in generically specific patterns that are readily interpretable phylogenetically (R. A. Nussbaum, personal communication). In *Chthonerpeton,* each gill attaches laterally, and the bases are widely separated dorsally. This pattern of attachment is typical of non-typhlonectid caecilians and is probably primitive for the Typhlonectidae. Fetal *Nectocaecilia* have gills that attach dorsolaterally and, as a consequence, the bases of the two gills are only slightly separated middorsally. In the fetuses of both *Typhlonectes compressicaudus* (Dumeril and Bibron) and *T. natans,* there is dorsal attachment of both gills, which are fused at their bases with no middorsal separation. The condition in *Chthonerpeton* is considered the most primitive, that of *Typhlonectes* the most derived, and that of *Nectocaecilia* intermediate between these two.

MONOPHYLY OF *POTOMOTYPHLUS* AND *TYPHLONECTES*

In addition to sharing middorsal ridges or free folds, these two genera are sister taxa, as indicated by the size of their choanal apertures and choanal valves, modification of the body terminus, features of the cloacal disc, lateral compression of the body, and fully aquatic habits.

It is commonly stated that the typhlonectids are aquatic; however, only *Typhlonectes* and *Potomotyphlus* are truly aquatic. Both *Chthonerpeton* and *Nectocaecilia* are more accurately described as semiaquatic (Nussbaum, 1986*b*; Tanner, 1971). Correlated with the aquatic habits of *Typhlonectes* and *Potomotyphlus* is lateral compression of at least the posterior part of the body. In contrast, *Chthonerpeton, Nectocaecilia,* and the adults of all other caecilians have roughly cylindrical or often slightly dorsoventrally compressed bodies. Nussbaum (1979) considered lateral compression to be a derived feature reflecting the aquatic specialization of the genus *Typhlonectes.* Duellman and Trueb (1986) followed Nussbaum but erroneously considered lateral body compression to be a characteristic of the Typhlonectidae as a whole. I interpret both the lateral compression and fully aquatic habits of *Typhlonectes* and *Potomotyphlus* as shared derived characters.

Another common assertion is that the body terminus surrounding the cloacal aperture forms a sucking or even prehensile organ used by the males for attachment to females during copulation (e.g., Taylor, 1968). The only reports of copulation in typhlonectids (Barrio, 1969; Murphy et al., 1977) lend no support to this speculation, and there are good reasons, based on the morphology of this region, to discount this notion (Wilkinson, unpublished). In many caecilians, the cloacal aperture lies within a bluntly rounded, externally unsegmented, terminal portion of the body termed an unsegmented terminal shield. The cloacal disc (the typically unpigmented region about the cloacal aperture that bears architecture continuous with the internal architecture of the cloacal walls) lies within the shield. In non-typhlonectid caecilians, the disc is small and not or only scarcely recessed. Within the Typhlonectidae, this condition is most closely approached in *Chthonerpeton* and *Nectocaecilia.* In contrast to this, the cloacal discs of *Potomotyphlus* and *Typhlonectes* are much enlarged, the disc is recessed to varying degrees, and there is variable development of adjacent, flap-like folds of skin. These folds, which may be well developed in either sex, and enlarged cloacal discs gave rise to the notion of "suckers" or "claspers" in males. Additionally, there is strong sexual dimorphism in the shape of the terminal shield of *Potomotyphlus* and *Typhlonectes,* the females having terminal shields that are pointed rather than bluntly rounded. This sexual dimorphism does not exist in *Chthonerpeton* and *Nectocaecilia.* I interpret the enlarged size of the cloacal disc, the flap-like modifications of the body terminus about the disc, and the strong sexual dimorphism in the shape of the terminal shield as three shared derived features indicating monophyly of *Potomotyphlus* and *Typhlonectes.* Nussbaum (1979) considered "anal claspers" to be a derived feature of *Typhlonectes,* and following this author, Duellman and Trueb (1986) erroneously considered this modification to be typical of the Typhlonectidae as a whole.

The morphoclines in the size of the choanae and the size of the choanal valves provide evidence of monophyly of these two genera. Extreme enlargement of the choanae and of the choanal valves are the most derived states, and both are shared by *Potomotyphlus* and *Typhlonectes.*

If the gills of fetal *Potomotyphlus* (presently unknown) are fused at their bases rather than separate, this would constitute additional evidence for monophyly of *Potomotyphlus* and *Typhlonectes.* If, however, the gills of fetal *Potomotyphlus* prove to be like those of *Chthonerpeton,* this would be evidence contradicting my interpretation of monophyly of these two genera. In either case, both *T. compressicaudus* and *T. natans* share the derived condition of fused gill bases, and this is compelling evidence that these two species share a more recent common ancestor than either does with *Nectocaecilia* or with *Chthonerpeton.*

ALTERNATIVE HYPOTHESES OF THE PHYLOGENY OF THE TYPHLONECTIDAE

A hypothesis of phylogeny for the four typhlonectid genera, based on the evidence considered above, is represented by the cladogram in Fig. 3A. Alternative phylogenies to this have recently been proposed. In his dendrogram, Laurent (1986) divided the four genera into two subgroups, *Chthonerpeton* with *Nectocaecilia* and *Potomotyphlus* with *Typhlonectes* (Fig. 3B). Unfortunately, Laurent (1986) did not provide any evidence in support of his phylogeny of the Gymnophiona. This lack of evidence renders his hypothesis immune to critical evaluation, and it remains no more than unsupported speculation. In terms of the evidence presented here, if Laurent's hypothesis of the phylogeny of the Typhlonectidae were correct, it would indicate either the independent derivation of sub-triangular nares, tentacular apertures close to the nares, relatively elongate left and right lungs, enlarged choanae, enlarged and superficial choanal valves, increase in the numbers of nuchal and postcloacal vertebrae, and dorsally attaching fetal gills in *Nectocaecilia* and in the *Potomotyphlus-Typhlonectes* clade, or the presence of all these features in the ancestral typhlonectid and their subsequent multiple reversal in *Chthonerpeton.*

Lescure et al. (1986) presented a new classification of the Gymnophiona based

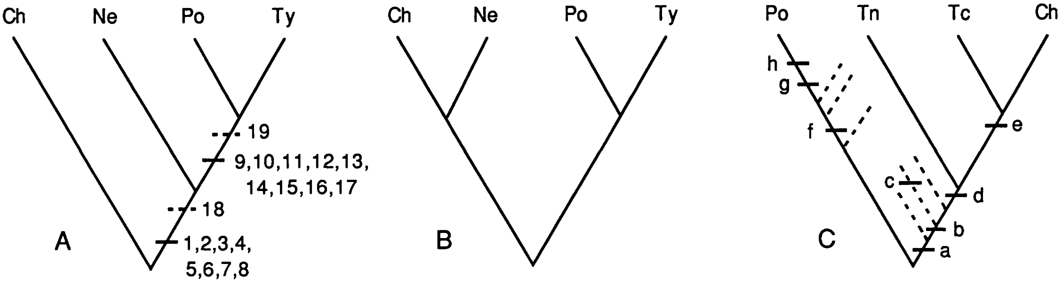

FIG. 3.—Alternative hypotheses of phylogenetic relationships among typhlonectid caecilians: (A) based on evidence discussed in this paper; (B) after Laurent (1986); (C) modified from Lescure et al. (1986). Character state transformations in cladogram C (a–h) are those of Lescure et al., and dotted lines on this cladogram indicate hypothetical taxa. 1 = sub-triangular narial apertures; 2 = tentacular apertures close behind nares; 3 = left lung well developed; 4 = right lung well developed; 5 = intermediate enlarged choanal apertures; 6 = intermediate enlarged choanal valves; 7 = superficial choanal valves; 8 = more than three nuchal vertebrae; 9 = several postcloacal vertebrae; 10 = extreme enlargement of choanal aperture; 11 = extreme enlargement of choanal valves; 12 = a middorsal ridge or free fold; 13 = lateral compression; 14 = fully aquatic; 15 = much enlarged cloacal discs; 16 = skin flaps bordering cloacal disc; 17 = pointed body terminus in females; 18 = dorsal attachment of fetal gills; 19 = fusion of fetal gill bases. Dashed lines indicate character states unknown in *Potomotyphlus*. a = II; b = III+II; c = III; d = II+III+II; e = I+IIinc; f = III+II+I; g = II+III+II+I; h = I+II+III+II+I. Ch = *Chthonerpeton*; Ne = *Nectocaecilia*; Po = *Potomotyphlus*; Ty = *Typhlonectes*; Tn = *Typhlonectes natans*; Tc = *Typhlonectes compressicaudus*.

on the distribution of 16 character state transformation series and biogeographic data across 30 taxa representing 27 genera. Sixty-one new suprageneric names (rather a large number considering the number of taxa) were established in the new classification. These authors established formal names for not only every monophyletic group, but also for every possible rank within a clade, even when no divergence (branching) is evident. Thus, the genus *Potomotyphlus*, which they hypothesized to be the sister taxon to the rest of the typhlonectid groups (excluding *Nectocaecilia*, which was not included in the analysis, see Fig. 3C), was placed in a monogeneric epifamily of equal rank to the group comprising the other typhlonectids, and a family, subfamily, infrafamily, and tribe were also named.

Potomotyphlus was established by Taylor (1968:256). The alternative spelling *Potamotyphlus* appeared in the errata of some editions of this work. This latter spelling was used by Lescure et al. (1986) for this genus and for all higher taxonomic rank names they proposed that utilized this generic name as a root. These authors presumably considered the original spelling *Potomotyphlus* to be an incorrect spelling; however, as this spelling appears several times in the original work, it can hardly have been a lapsus calami or printer's error. Art. 32(c)(ii) of the Code clearly states that "incorrect transliteration or latinization . . . are not to be considered inadvertent errors". Therefore *Potomotyphlus* is the correct spelling.

With regard to the 17 characters employed by Lescure et al. (1986), the four typhlonectid taxa that they considered vary in only five (summarized in Table 3). Of these, one is presence of a "tail", which was scored incorrectly for *Potomotyphlus* and probably polarized incorrectly for the Typhlonectidae. A second character (fate of the postfrontal) has the derived state restricted to *Potomotyphlus* and is thus uninformative. These authors considered <100 vertebrae to be primitive and >100 derived. They made no attempt to justify this interpretation. They scored *Typhlonectes natans* with the derived condition and *Chthonerpeton* with the primitive condition. In fact, the range of vertebrae in *Typhlonectes natans* spans their arbitrarily defined character state cutoffs (Wilkinson, unpublished), and *Chthonerpeton* contains species that fall on either side of this character state division (Nussbaum, 1986*b*; Nussbaum and Wilkinson, 1987; Taylor, 1968). Similarly problematic is

TABLE 3.—Summary of character state distributions over the four typhlonectid taxa reported by Lescure et al. (1986). (1) Ratio of length to width: 0 = <30, 1 = between 30 and 40. (2) Number of vertebrae: 0 = <100, 1 = >100. (3) Fate of the postfrontal: 0 = fused, 1 = fused to the maxilla. (4) "Tail": 0 = present, 1 = absent. (5) Annulation. Character states represented by a 0 are primitive, those represented by a 1 are derived. Annulation character states are not polarized and are those reported by Lescure et al. (1986) in the "remarques" section of their data matrix.

	1	2	3	4	5
Chthonerpeton	0	0	0	1	I+IIinc
Potomotyphlus	1	1	1	1	I+II+III+II+I
Typhlonectes natans	1	1	0	0	IIinc+IIIinc+IIinc
T. compressicaudus	0	0	0	0	I+IIinc+(I)

their character based on the ratio of the body length to width for which the character state divisions are arbitrary, no justification of polarization is made, and the reported character states do not take into account ontogenetic, seasonal, and sexual intraspecific variation or intrageneric variation, the last of which is high in *Chthonerpeton* (Nussbaum, 1986*b*; Taylor, 1968).

The final differences involve annulation. Whereas some of the other characters employed by Lescure et al. (1986) were adequately defined, in the case of trunk annulation, both the character states themselves and their polarities were not made clear. In fact, the reported character states are completely at odds with presently accepted concepts and observations. Lescure et al. (1986) referred to another of their papers, Renous et al. (1986), for a discussion and justification of the morphoclines that they employed. However, Renous et al. (1986) did not, as they claimed, provide these justifications for the majority of their morphoclines. In their discussion of the evolution of annulation, they asserted that secondary and tertiary annuli form anteriorly first, respecting a cephalo-caudal ontogenetic gradient. Data from ontogenetic series of a number of caecilian species indicate that this assertion is erroneous and that Lescure et al. almost certainly have an erroneous notion of the evolution of caecilian annulation (Nussbaum and Wilkinson, in press).

I have reanalyzed the data from Lescure et al. (1986) for the Typhlonectidae. The results of this reanalysis (summarized in Fig. 4) show that their published cladogram is not the one that best fits their own data. These authors preferred the cladogram that necessitates independent derivation of two of their derived character states in *Potomotyphlus* and in *Typhlonectes natans* (or their reversal in *Chthonerpeton* and *T. compressicaudus*) over the more parsimonious cladograms (Fig. 4A,B,C) which do not require these extra steps. In doing this, Lescure et al. seem to have ignored some of their own "evidence" and relied solely on their interpretation of annular evolution to determine the genealogy of the typhlonectid taxa. Indeed, the only instances of character evolution mapped onto the typhlonectid portion of their cladogram concern annulation. Lescure et al. preferred to rely on annulation rather than use any of their other characters despite their own caveats that the annulation states of typhlonectids are difficult to determine and that those they reported are not certain. Over-reliance on the annulation character is also apparent in their treatment of the majority of non-typhlonectid taxa.

Based on the paraphyly of *Typhlonectes* indicated in their hypothesis, Lescure et al. (1986) established a new genus, *Pseudotyphlonectes*, to receive *T. natans*. The supposed paraphyletic status of *Typhlonectes* rests solely on the position of *Chthonerpeton* relative to the two species of *Typhlonectes* that were considered. That this position is erroneous is indicated by all the evidence that I have discussed.

In terms of the evidence that I have presented, the hypothesis of Lescure et al. (1986), if correct, would necessitate the loss in *Chthonerpeton* of sub-triangular nares, tentacular apertures close to the nares, relatively elongate lungs, enlarged choanae,

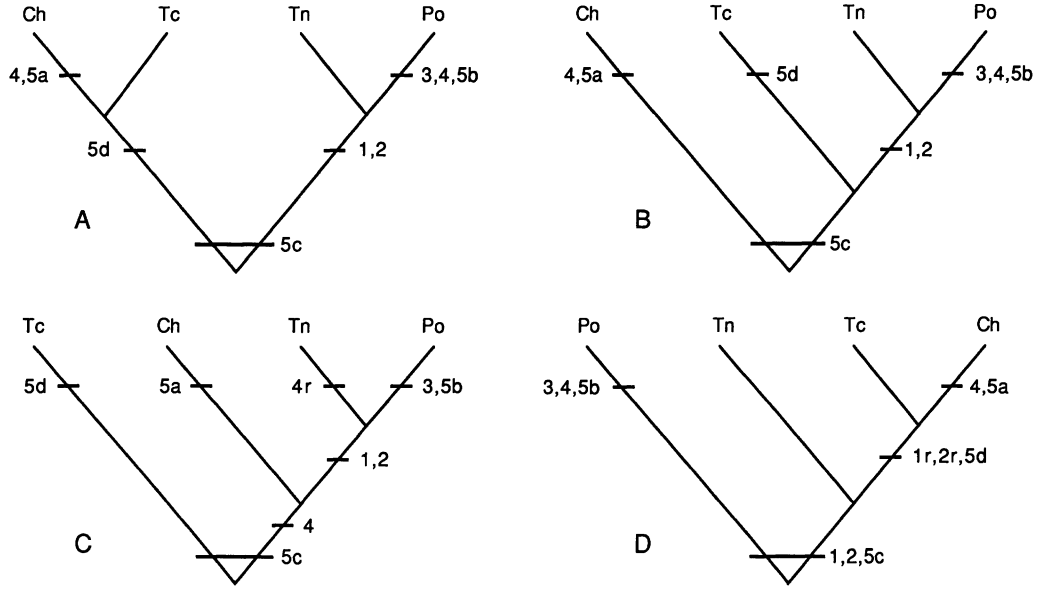

FIG. 4.—Reanalysis of the data of Lescure et al. (1986), showing the distribution of the character states summarized in Table 3. Cladograms A, B, and C are three equally most parsimonious interpretations of the data (all with a consistency index of 0.875). Cladogram D is the topology published by Lescure et al. (1986) with character state changes plotted so as to minimize the number of character state changes (consistency index of 0.7). Annulation states: a = I+IIinc; b =I+II+III+II+I; c = IIinc+IIIinc+IIinc; d = I+IIinc+(I). Ch = *Chthonerpeton*; Po = *Potomotyphlus*; Tn = *Typhlonectes natans*; Tc = *Typhlonectes compressicaudus*. For each cladogram, where homoplasy is indicated, alternative equally parsimonious interpretations of character evolution (convergence or reversal), which do not affect tree topology, are possible. Only one interpretation is shown. Non-annulation character state changes are from primitive to derived except where indicated. r = reversal.

enlarged and superficial choanal valves, lateral compression, middorsal ridges or free folds, more than three nuchal and several postcloacal vertebrae, modified terminal shields, enlarged cloacal discs, dorsally attaching gills with fused bases, and a fully aquatic lifestyle.

The numerous taxa erected by Lescure et al. (1986) within their "Potamotyphloidae" were each provided with a diagnosis. Which characters were employed for which diagnosis might at first seem arbitrary as the whole epifamily is monogeneric. In fact, successively lower taxonomic ranks were diagnosed through the exclusion of taxa not known to exist, but which are hypothesized as intermediate stages in the evolution of the trunk annulation. Considerable doubt must now be cast on the validity of Lescure et al.'s interpretation of the trunk annulation character, because in addition to the anomalous character states reported, the phylogenetic hypothesis that it was used to support is contradicted by all the evidence discussed here.

If my interpretation of typhlonectid phylogeny is correct, then not only is the genus *Pseudotyphlonectes* invalid, but so are all the new higher taxonomic categories that Lescure et al. (1986) applied to the Typhlonectidae (sensu Taylor, 1968), including the new family Potamotyphlidae. I consider that *Pseudotyphlonectes* Lescure, Renous, and Gasc is a junior synonym of *Typhlonectes* Peters. Furthermore, because the character of the annulation of the trunk as used by Lescure et al. has resulted in an unsatisfactory hypothesis of relationships within the Typhlonectidae, I have no confidence in its similar application elsewhere and consider the entire classification of the Gymnophiona proposed by Lescure et al. to be unsoundly based.

Taylor (1968:40) commented that "Until greater study is focussed on the cranium and other parts of the skeleton and also on the viscera, it would seem rather futile to try and trace evolutionary relationships in detail". Though much ground has been gained in our knowledge of caecilian phylogeny, we have not come so far down the road from 1968 that Taylor's cautionary words are without significance. While I do not want to discourage attempts to reconstruct the phylogeny of the Gymnophiona, it is recommended that such attempts be decoupled from taxonomic treatment until a greater understanding is achieved. The alternative to this is a period of great taxonomic instability and a plethora of names and ranks many of which will prove to be of no utility whatsoever.

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APPENDIX I

Material Examined

Typhlonectidae.—Chthonerpeton braestrupi: ZMUC R0234 (holotype). *C. corrugatum:* ZMH A00235 (holotype); ANSP 13948 (paratype). *C. erugatum:* ZMUC R0238 (holotype). *C. helmichi:* ZSZM 1/1964 (holotype). *C. indistinctum:* ZMUC R0235 (lectotype); AMNH A25506, A23508; CM 65022–25, 65037; CAS 85521; FML 032284; KU 197262–64; BMNH 83.1.19.2, 89.8.24.4, 1926.5.29.7; IMZT An 786; MNHN 4299; NMW 9148; USNM 65538, 95863, 257179; ZIN 1795.1, 1793, 1382, 1759; ZMB 6807, 34527–28; ZMH A00256. *C. onorei:* MNHG 2251.06 (holotype), 2251.07 (paratype). *C. viviparum:* BMNH 1947.2.13.84 (holotype); MCZ 24593; ZIN 1762.1; ZFMK 27687. *Nectocaecilia petersii:* BMNH 61.9.2.6 (holotype); AMNH 100590–91, 100890; MBUCV 960–61. *N. ladigesi:* ZSM 245 (holotype). *Potomotyphlus kaupii:* ZFMK 27684 (holotype); ZMH A00259–63, A01017–18; CAS 10848; CM 2906, 2908; ANSP 4926–27; MCZ A96785; BMNH 98.10.17.7; FMNH 206189; KU 128088; USNM 101105, 166415, 305344. *P. melanochrous:* NMW 9147 (holotype). *Typhlonectes anguillaformis:* AMNH 56252 (holotype). *T. compressicaudus:* MNHN 4269 (lectotype); CM 90090–91; CAS 125421–23; UMMZ 82854; LYON 81.1.1–4, 81.1.7–15, 81.1.17–32; MRHN 8681–83, 8743; BMNH 1982.103–104, 1916.4.12.1–2; ZFMK 42781; USNM 201693, 201695; MCZ A85381. *T. eiselti:* NMW 9146 (holotype). *T. natans:* ZMB 9522 (cotype); LACM 67414–517; UMMZ 172649–50; CAS 153871; IMZT An-781; MSNG 379/A.

Outgroups.—Caecilia gracilis: UMMZ 4710, 4711, 52507, 76676. *C. nigricans:* UMMZ 121035, 124109. *C. pachynema:* UMMZ 82902–03. *C. tentaculata:* UMMZ 89459, 177895. *Dermophis mexicanus:* UMMZ 152768–75. *Epicrionops marmoratus:* BMNH 1956.1.15.87 (holotype). *E. petersi petersi:* UMMZ 163243 (paratopotype). *Gymnopis multiplicata:* UMMZ 142682, 13170–72. *Lutkenotyphlus braziliensis:* UMMZ 182015. *Microcaecilia albiceps:* UMMZ 83051. *M. unicolor:* UMMZ 173394. *Oscaecilia ochrocephala:* UMMZ 167596–99. *Siphonops annulatus:* IMZT An-782–784; UMMZ 89460, 177895. *S. paulensis:* UMMZ 109665, 137582–83, 187585.