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ON THE CLASSIFICATION AND PHYLOGENY OF CAECILIANS (AMPHIBIA: GYMNOPHIONA), A CRITICAL REVIEW

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ABSTRACT: The phylogeny of the Gymnophiona is poorly understood and until recently received little attention. Within the past three years, four separate classifications of caecilians were published. Two of these classifications, those of Wake (1985, 1986) and Duellman and Trueb (1986), are conservative and do not differ substantially from the classification of Taylor (1968, 1969*a*) as modified by Nussbaum (1977, 1979). However, the classifications of Laurent (1986) and Lescure et al. (1986) differ radically from the others and from each other. Laurent's classification is biased by a priori biogeographical considerations and is otherwise difficult to evaluate, because he did not clarify his methodology or justify his dendrogram by explaining his characters and their transformations. Lescure et al. claimed that their analysis of caecilian phylogeny and their classification are based on strict cladistic principles; however, like Laurent, they did not explain their procedures and used distributional data in deriving their phylogeny. There is no logical basis for using non-inherited characters such as geographic distribution to estimate phylogenies, and we disagree with this practice. Lescure et al. relied heavily on their scheme of annular development in determining their cladogram. We demonstrate that their interpretation of the ontogeny and phylogeny of caecilian annuli is wrong. We reject the cladogram of Lescure et al., because (1) many of the characters upon which it is based are poorly defined and incorrectly coded (83% of the transformations are either changes in annulation or geographic distribution) and (2) it is not supported by rigorous cladistic analyses of their own data. The classification of Lescure et al. is based on their seriously flawed cladogram and incorporates dubious classification procedures.

Present knowledge does not allow establishment of a robust, phylogenetic classification of caecilians. We present an interim classification of caecilians with diagnoses to the generic level, recognizing six families (Rhinatrematidae, Ichthyophiidae, Uraeotyphlidae, Scolecomorphidae, Caeciliaidae, Typhlonectidae) and 34 genera. The first four families are likely to survive cladistic analysis, but the Caeciliaidae is a paraphyletic subgroup of a monophyletic clade that includes the caeciliaid and typhlonectid genera. Various attempts to subdivide the Caeciliaidae are either clearly wrong or unconvincing and, in all cases, are based on inadequate data and procedures. We recognize no categories of Gymnophiona other than family, genus, and species.

Key words: Amphibia; Gymnophiona; Caecilians; Classification; Annulation

CAECILIANS comprise one of the three extant orders of amphibians. They are essentially ectothermic, anamniotic, tetrapod vertebrates with elongate and annulate body form. Living species are limbless and girdleless and have reduced eyes, a pair of sensory tentacles on the snout, an intromittent organ (phallodeum) in males, and a unique dual jaw-closing mechanism. Primitive species have numerous subdermal scales, a terminal mouth, and a short tail; whereas advanced species have few or no scales, a subterminal mouth, and no tail. They are primarily adapted for burrowing, with a few species secondarily adapted for life in aquatic or semiaquatic habitats, and they are restricted to tropical environments. Caecilians are the least studied and understood of the modern amphibians.

The diversity of caecilians was considered to be extremely low until the 1960's when Taylor began to publish his important systematic studies of the group. The appearance in 1968 of Taylor's monograph on the caecilians of the World was a pivotal event in caecilian biology. The monograph included a summary of the existing caecilian literature and descriptions of many new taxa. However, in spite of Taylor's monumental efforts, it is abundantly clear that the diversity of caecilians remains poorly known. There are far too few specimens available in museums to assess the validity of many species or to confidently decide whether some speci-

A female and newborn *Schistometopum thomense* from Ihla de São Tomé (0° 41′ N 6° 01′ E), Gulf of Guinea, photographed by Ronald A. Nussbaum.

mens represent undescribed species. Many species are represented by a single or a few specimens, some of which were collected more than 100 years ago and are without explicit locality data. Detailed studies of ontogenetic and sexual variation, and of variation within and between populations of caecilians, are wanting. Most of the existing literature on caecilians concerns preliminary taxonomy and descriptive morphology. There is almost no published information concerning the physiology, ecology, life history, and behavior of caecilians. In light of their tropical restriction and the accelerating destruction of tropical environments, it is particularly disturbing that the diversity and adaptations of caecilians are so poorly known.

The facts that caecilians are restricted to the tropics and are difficult to collect have contributed to their neglect, but the lack of a stable and logical systematic framework for caecilians has also impeded progress in caecilian biology. Until the diversity, phylogeny, and biogeographic relationships of caecilians are better understood, biologists in non-systematic disciplines are likely to continue to ignore them.

Considering the state of caecilian systematics, the several recent publications (Duellman and Trueb, 1986; Laurent, 1984, 1986; Lescure et al., 1986; Wake, 1985, 1986; Wake and Campbell, 1983) on this subject should be welcomed. However, there is little agreement among these proposals, and some of them are technically flawed, especially those proposing the most radical changes. In short, we believe that the phylogenetic reconstructions of caecilians proposed by Laurent (1984, 1986) and Lescure et al. (1986) are ill-founded. They are based on numerous factual errors, poorly defined characters, unwarranted assumptions, and unexplained procedures; contain internal contradictions; are biased by a priori biogeographic considerations; and ignore the basic tenets of cladistics. The problem is compounded by Lescure et al. (1986), who used their poorly supported phylogenetic tree and unconventional concept of cladistic classification as justification for formally naming many new higher taxa of caecilians. We believe the proposals of Laurent (1984, 1986) and Lescure et al. (1986) will seriously hinder progress in caecilian systematics and biology if left unchallenged.

It is our aim in this paper to review caecilian systematics. The literature prior to 1968 is largely ignored as it is sparse and mainly concerns descriptions of genera and species and issues relevant to nomenclatural priority. We include new data only where it is necessary to clarify issues. We propose an interim classification of caecilians that reflects the limited present understanding of caecilian phylogeny, and we provide diagnoses of the Gymnophiona to the generic level.

HISTORY OF CAECILIAN CLASSIFICATION

Prior to the appearance of Taylor's (1968) monograph, all caecilians were placed in a single family (Caeciliaidae), no suprafamilial names had ever been proposed other than the ordinal, no infrafamilial names other than genera and species existed, and only 117 nominate species and 21 genera were recognized. Taylor (1968) described two new families (Ichthyophiidae and Typhlonectidae), 13 new genera, and 40 new species and listed a total of 3 families, 34 genera, and 157 species of caecilians. No other taxonomic categories (except a very few subspecies) were used by Taylor. The following year, Taylor (1969*a*) named a new family (Scolecomorphidae) and divided the family Caeciliaidae into two subfamilies, the Caeciliinae [sic] and Dermophiinae. Taylor's classification as of 1969 is summarized in Table 1. Nussbaum (1977) demonstrated that the South American "ichthyophiids" differed substantially from the Asiatic members of the family and placed the South American forms in a new family, the Rhinatrematidae. Later, the Indian genus *Uraeotyphlus* was transferred from the Caeciliaidae to a new subfamily of the Ichthyophiidae (Nussbaum, 1979). Up to this time, no serious attempt had been made to establish categories of caecilians between the ordinal and familial levels. Peters' (1879) refer-

TABLE 1.—Classification of Gymnophiona according to Taylor (1968, 1969*a*).

Family Ichthyophiidae
Genera: *Caudacaecilia, Epicrionops, Ichthyophis, Rhinatrema*

Family Scolecomorphidae
Genera: *Scolecomorphus*

Family Caeciliidae [sic]
Subfamily Caeciliinae [sic]
Genera: *Caecilia, Oscaecilia*
Subfamily Dermophiinae
Genera: *Afrocaecilia, Boulengerula, Brasilotyphlus, Copeotyphlinus*, Cryptosophis*, Dermophis, Gegeneophis, Geotrypetes, Grandisonia, Gymnopis, Herpele, Hypogeophis, Idiocranium, Indotyphlus, Lutkenotyphlus, Microcaecilia, Mimosiphonops, Parvicaecilia, Praslinia, Pseudosiphonops, Schistometopum, Uraeotyphlus*

Family Typhlonectidae
Genera: *Chthonerpeton, Nectocaecilia, Potomotyphlus, Typhlonectes*

* Genera no longer recognized.

ence to the "Gymnocaeciliae" and the "Lepidocaeciliae" as subfamilial groupings has been ignored, because they are clearly artificial. Wake and Campbell (1983) and Wake (1985, 1986) transferred some caeciliaid genera from the subfamily Dermophiinae to the Caeciliainae, but named no new suprageneric taxa. Laurent (1984) elevated the Dermophiinae to family status and established a new subfamily, Herpelinae, as a division of the Dermophiidae. Laurent (1986) later elaborated this scheme, but named no new taxa. Lescure et al. (1986) proposed two new suborders, five additional families, and numerous intermediate taxa of caecilians (Appendix) based on a putatively cladistic analysis of old and new characters. Duellman and Trueb (1986) analyzed a limited number of characters cladistically resulting in the elevation of the ichthyophiid subfamily Uraeotyphlinae to family rank and no other significant changes.

Critique of Wake's and Campbell's Classification

Wake and Campbell (1983) described the genus *Minascaecilia* from Guatemala. As a result of their evaluation of the relationships of this new genus, they suggested changes in the composition of the caeciliaid subfamilies Caeciliainae and Dermophiinae, but did not modify Taylor's (1969*a*) diagnoses of these two subfamilies. They expanded the Caeciliainae, which formerly contained only the two genera *Caecilia* and *Oscaecilia,* to include *Minascaecilia* and two genera, *Microcaecilia* and *Parvicaecilia,* transferred from the Dermophiinae. They stated (p. 861) that all five of these genera have large recurved teeth and that "The characters expressed by Taylor (1969*b*) for *Caecilia* and *Oscaecilia* to erect the subfamily apply to all five genera."

Taylor (1969*a*) did not provide a formal diagnosis in the original description of the Caeciliainae. He stated only that the subfamilial characters were the generic characters of *Caecilia* and *Oscaecilia.* In addition, Taylor (1969*a*) mentioned hypertrophied teeth and large numbers of vertebrae in reference to caeciliaines in his key to families and subfamilies of Gymnophiona. In his paper on caecilian skulls, which appeared the same year, Taylor (1969*b*) reported that the frontals are usually completely separated by the mesethmoid in the Caeciliainae and in contact in the Dermophiinae, but mentioned exceptions to this in both subfamilies. He also stated that the vomers had enlarged anterior processes notching the nasopremaxillae in the Caeciliainae and that, in the Dermophiinae, the tentacular aperture is confined to the maxillopalatine. Thus, the diagnoses of the Caeciliainae and Dermophiinae were never clearly stated and contain considerable ambiguity.

The characters given by Taylor (1968,

TABLE 2.—Comparison of the diagnostic characters of the Caeciliinae, *Microcaecilia*, and *Parvicaecilia* from Taylor (1968, 1969*a,b*).*

	Caeciliinae (sensu Taylor)	*Microcaecilia*	*Parvicaecilia*
Eye visible	Yes or no[a]	Yes or no[a]	—
Bone over eye	Present or absent[a]	Present[a]	Present[a]
Orbit and tentacular groove	Not continuous[a]	—	Continuous[a]
Opening of tentacular groove	Border of maxillopalatine and nasopremaxilla[b]	—	—
Temporal fossa	Absent[a]	—	—
Frontals	Usually separated by mesethmoid[b]	—	—
Anterior process of vomer	Enlarged, notching nasopremaxillae[b]†	—	—
No. of vertebrae	High[c]	—	—
Tooth replacement	Usually group loss[a]	—	—
Tooth size	Hypertrophied[c]	—	—
Splenial teeth	Present[a]	Absent[a]	Absent[a]
Secondary annuli	Present or absent[a]	Present[a]	Present[a]
Dermal scales	Present or absent[a]	Present[a]	Present[a]
Subdermal scales	Present or absent[a]	—	—
Tentacular aperture	Below naris on underside of snout[a]	Close to eye[a]	Close to eye[a]
Terminal shield	Present or absent[a]	—	Absent or very small[a]

* From [a] Taylor (1968); [b] Taylor (1969*b*); [c] Taylor (1969*a,b*).

† The only known character that may be unique to and universal in the "Caeciliinae."

1969*a,b*) for the Caeciliainae, as well as for *Microcaecilia* and *Parvicaecilia*, are summarized in Table 2. Only one of the characters listed (enlarged anterior process of the vomer) may be unique and diagnostic of the Caeciliainae sensu Taylor, and this character may eventually be found in noncaeciliaine genera. Wake's and Campbell's (1983) view that all the characters of the Caeciliainae are equally true of *Microcaecilia*, *Minascaecilia*, and *Parvicaecilia* is not supported.

Nussbaum (1988) showed that *Minascaecilia* Wake and Campbell is a junior synonym of *Gymnopis* Peters, and that *Minascaecilia sartoria* Wake and Campbell is a junior synonym of *Gymnopis syntrema*. The fact that *Gymnopis* is, according to Wake (1985, 1986), a dermophiine points out the current confusion surrounding the phylogeny and classification of caecilians.

CRITIQUE OF DUELLMAN'S AND TRUEB'S CLASSIFICATION

Duellman and Trueb (1986) used cladistic methods to analyze the distribution of 22 characters across six familial and subfamilial taxonomic units of caecilians. The data and polarizations used were largely those of Nussbaum (1977, 1979). The results of their analysis are essentially consistent with those of Nussbaum (1979) and provide little new information. Duellman and Trueb (1986) correctly pointed out that some of the family groups of caecilians are based on relatively few derived characters. They also pointed out, as did Nussbaum (1979), that the family Ichthyophiidae (sensu Nussbaum, 1979) was paraphyletic. In order to eliminate the paraphyly, they raised the ichthyophiid subfamily Uraeotyphlinae to family rank.

The cladistic analysis of Duellman and Trueb (1986) suffers from their use of familial rank groups as taxonomic units. This procedure led them to make erroneous character state assignments. For example, the two derived character states isolating the Typhlonectidae, lateral compression of the body and possession of "anal claspers," are found only in a subset of typhlonectid genera (present in *Potomotyphlus* and *Typhlonectes*, absent in *Chthonerpeton* and *Nectocaecilia*). Otherwise, the classification of Duellman and Trueb (1986) is logically constructed and is confused only by the inclusion of Wake's and Campbell's (1983) modifications, which were based to a large extent on the mistaken belief that

Minascaecilia (= *Gymnopis*) is a caeciliaine.

CRITIQUE OF LAURENT'S CLASSIFICATION

Laurent (1984) suggested revision of caecilians based on a superficial and partly erroneous analysis of a single character, namely, the fate of the postfrontal (= ocular or orbital) bone. Laurent claimed that the postfrontal is free in the relatively primitive Ichthyophiidae, but fused either to the maxillopalatine anteriorly or to the squamosal posteriorly in other groups. Contrary to Laurent, the postfrontal of ichthyophiids (and uraeotyphlids) is often fused or partially fused to one or the other or both of the adjacent bones (Nussbaum, 1979). The fact that it can be free or fused in various ways among ichthyophiid species (and varies even within species) suggests that it is a labile character and, therefore, should be used with caution. Certainly it should not be used as the sole basis for defining major groups of caecilians.

Laurent (1984) claimed that, aside from the Ichthyophiidae, the postfrontal is fused to the squamosal in all other caecilians except for the genera *Caecilia* and *Oscaecilia*. Laurent offered no evidence to support this assertion. Apparently, be believes that the position of the eye, whether it is covered by bone or not, determines whether the postfrontal is fused anteriorly to the maxillopalatine or posteriorly to the squamosal. This assumption is unwarranted, especially in the case of the Scolecomorphidae. In scolecomorphids, there is no orbit; the vestigial eye rides on the tentacle so that its original position is indeterminable without recourse to embryological studies. Furthermore, there are several genera (e.g., *Gymnopis* and *Dermophis*) in which the eye, whether under bone or not, is positioned exactly between the maxillopalatine and squamosal so that a decision based on eye position is arbitrary. In the case of the scolecomorphids and almost all other genera of caecilians, there is no published information on the development of the skull bones that would support Laurent's assertions, nor does Laurent offer any suggestion that such data exist. In fact, the few available developmental data indicate that, among dermophiines, the postfrontal may either be fused to the squamosal (*Hypogeophis*, Marcus et al., 1935) or simply lost (*Dermophis*, Wake and Hanken, 1982).

Based on his unsubstantiated assertion concerning the fate of the postfrontal, Laurent restricted the Caeciliaidae to include *Caecilia* and *Oscaecilia* and elevated the subfamily Dermophiinae to family status. This action restricted the Caeciliaidae to the neotropics, but the Dermophiidae contained genera spread across Central and South America, Africa, the Seychelles Archipelago, and India. Laurent (1984) attempted to resolve the biogeographic relationships of the Dermophiidae by assuming that an Old World–New World vicariant event had divided the Dermophiidae into two clades. He enlisted a second character, presence or absence of splenial teeth, as evidence for the reality of the Old and New World clades. According to Laurent (1984), the family Dermophiidae can be subdivided into the neotropical Dermophiinae lacking splenial teeth (except *Gymnopis*) and the Old World Herpelinae having splenial teeth (except *Boulengerula*). The loss of splenial teeth is an uncomplicated transition that has a relatively high probability of occurring independently. Laurent seemed to acknowledge this by including *Boulengerula*, which has no splenial teeth, in his Herpelinae. On the other hand, Laurent's interpretation of the presence of splenial teeth in the neotropical genus *Gymnopis* is unclear. Does he believe *Gymnopis* has retained the ancestral condition contrary to all other dermophiines? Or, does he think that *Gymnopis* has re-evolved splenial teeth? Laurent (1984) failed to point out that presence or absence of splenial teeth varies within the Asian family Ichthyophiidae (present in *Ichthyophis*, absent in *Caudacaecilia*), a fact which casts further doubt on the value of this character in establishing monophyletic clades.

Laurent (1984, 1986) did not address the complication for his scheme added by Wake and Campbell (1983) who transferred *Minascaecilia*, *Microcaecilia*, and *Parvicaecilia* from the Dermophiinae to the Caeciliainae prior to Laurent's proposal. Laurent did not explicitly reject this arrangement, but seemingly did so by restricting the Caeciliaidae to *Caecilia* and *Oscaecilia*.

Laurent (1986) included a dendrogram of relationships among caecilian genera. He provided no information on how the dendrogram was constructed, and he included only distributional information and the number of derived states present in each genus on the dendrogram. Laurent (1986) did not indicate what these derived characters were and how they were determined to be derived. Therefore, his phylogenetic hypothesis is completely unsupported.

The phylogenetic tree of Laurent (1986) is clearly based in part on biogeographical considerations. This is indicated both on his dendrogram and in the text of his two treatments (1984, 1986). Although it is clear that caecilian phylogeny and biogeography have been influenced by Gondwanan vicariance, there is no reason to assume, as did Laurent, that assemblages presently restricted to single Gondwanan fragments are monophyletic. Laurent's biogeographic bias is further demonstrated by his assumption (1986) that the neotropical Caeciliaidae and Typhlonectidae are independently derived from the more primitive neotropical Rhinatrematidae. The only evidence offered, post hoc, by Laurent for this hypothesis is the presence of splenial teeth in all three families. The presence of splenial teeth is an ancestral character state, which also occurs in many Old World groups, and, therefore, it cannot be used as evidence for relationships among the three neotropical families in question. In any case, Laurent does not explain how a single character state, derived or not, shared by three taxa can provide evidence for independent derivation of two of the taxa from the third.

CRITIQUE OF LESCURE, RENOUS, AND GASC

Lescure et al. (1986), hereafter referred to as LRG, proposed sweeping changes in caecilian classification, establishing 61 new suprageneric names for caecilians. The authors stated that the new names are demanded by strict adherence to cladistic principles, which they claim to have followed faithfully. We will first examine the character data matrix used by LRG to establish their cladistic hypothesis and then review their methodology.

Annulation

Preliminary comments.—Other than the major bifurcation in their cladogram, which is based on the presence or absence of the septomaxilla, the phylogeny and classification of LRG depend to a large extent on their analysis of annulation. In fact, 39 (72%) of 54 character state transformations indicated on their cladogram are changes in annulation. Therefore, it is important to understand their concept of the evolution of annulation patterns in caecilians. As with the other character transformation series used by these authors, they provided little explanation of terminology and did not justify character state polarities. They cited another of their papers (Renous et al., 1986) as the source for explanation.

Terminology.—The terminology proposed by LRG to describe evolutionary transformations in annulation is novel and highly confusing. Furthermore, the annulation states that they attributed to many caecilian taxa do not correspond to those previously accepted for those taxa (see below), and they did not explain the discrepancies.

Behind the occiput of caecilians lie two collars marked by three transverse grooves. These nuchal grooves may or may not completely encircle the nuchal region, depending on species and individual variation. In some species, the two collars are divided dorsally by transverse annular grooves. In addition, irregular transverse grooves may occur laterally and ventrally on the collars. The collars are partly underlaid with muscles that are not divided by myosepta, such as the modified jaw-closing muscles (Nussbaum, 1977, 1983 and references therein). The presence of undivided muscles in this region may explain the absence of a 1:1 relationship between collars and vertebrae. Usually three or four, rarely five or six, vertebrae lie below the two collars (Table 3). Immediately behind the second collar is the first primary annulus followed by many more primary annuli. Each primary is associated with one vertebra, at least along most of the trunk region. The 1:1 relationship between primaries and vertebrae often breaks down in the extreme posterior part of the body. Primary annuli may be divided by one secondary groove into two secondary annuli, and each secondary annulus may be divided by one tertiary groove into two tertiary annuli, so that there may be four tertiary annuli per primary annulus.

According to Renous et al. (1986), four types of annulation systems are recognizable among the Gymnophiona: (1) primary system, with one annulus per vertebra; (2) secondary system, with two annuli per vertebra; (3) tertiary system, with four annuli per vertebra; and (4) quaternary system, with six or eight annuli per vertebra. The last category is novel, as species with quaternaries have never before been reported.

The terminology of Renous et al. (1986) differs in that, where secondaries and tertiaries occur, they are considered to have replaced primaries, which explains their reference to forms having secondaries only or tertiaries only. In the conventional terminology, a multiannulate form having secondaries and tertiaries developed all along their bodies, would be considered to have primaries, secondaries, and tertiaries, which are externally indistinguishable. The conventional terminology is preferable to that of Renous et al. (1986) for the following reason. Those annular grooves that appear first in ontogeny (see below) delimit primary annuli. Primary annuli may subsequently be subdivided by secondary and tertiary grooves. Primary annuli are in no way fundamentally altered by their subsequent subdivision. Primary annuli that have been subdivided once by secondary grooves, or once by secondary grooves and again by two tertiary grooves, are still primary annuli. Primary annuli of forms that have only undivided primary annuli are homologous with primary annuli of species that have some or all of them divided by secondary, and even tertiary, grooves. Considerable confusion will result if these homologies are not recognized, and it is possible that such confusion led LRG into their unconventional terminology and incorrect view of annular ontogeny and phylogeny.

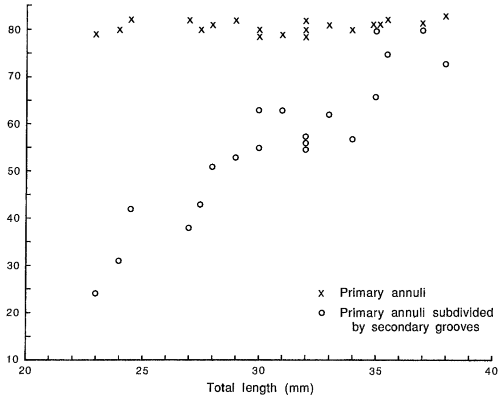

FIG. 1.—Ontogeny of subdivided primary annuli in embryos of *Grandisonia larvata*. Over the size range illustrated, the correlation between total length and number of secondary grooves is high ($r = 0.939$, $n = 20$). Secondary grooves are added in an orderly anterior progression beginning with the posteriormost primary annulus.

Annular development.—In the ontogeny of multiannulate caecilians—those with subdivided primary annuli—the primary grooves appear initially, and secondaries form in a wave that begins posteriorly and spreads anteriorly, followed by the appearance of the tertiaries in the same way. In a series of embryos of the caeciliaid *Grandisonia larvata*, the number of primary annuli divided by secondary grooves increases with body size, and the secondaries are added sequentially in an anterior direction beginning with the posteriormost primary annulus (Fig. 1). In these embryos, the secondary grooves first appear dorsolaterally as a series of aligned glands in a shallow groove or more rarely on a ridge. Older (more posterior) secondaries are more complete dorsally and ventrally, and most of the older secondaries eventually completely encircle the body. In adults, some of the anteriormost secondary grooves appear to be in an arrested state of development as they do not completely subdivide the primary annuli. The same

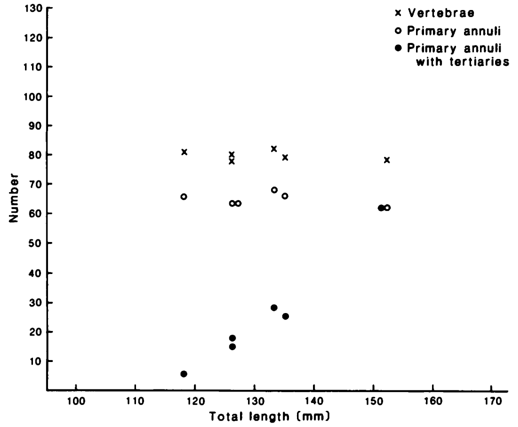

FIG. 2.—Ontogeny of tertiary grooves in free-living larvae of *Epicrionops petersi*. Over the size range illustrated, all of the primary annuli are already subdivided by secondary grooves. Tertiary grooves are added in the same manner as secondaries, by progressive posterior to anterior addition. The graph illustrates the relationship between total length and the number of vertebrae, primary annuli, primary annuli with secondary grooves, and primary annuli with both secondary and tertiary grooves.

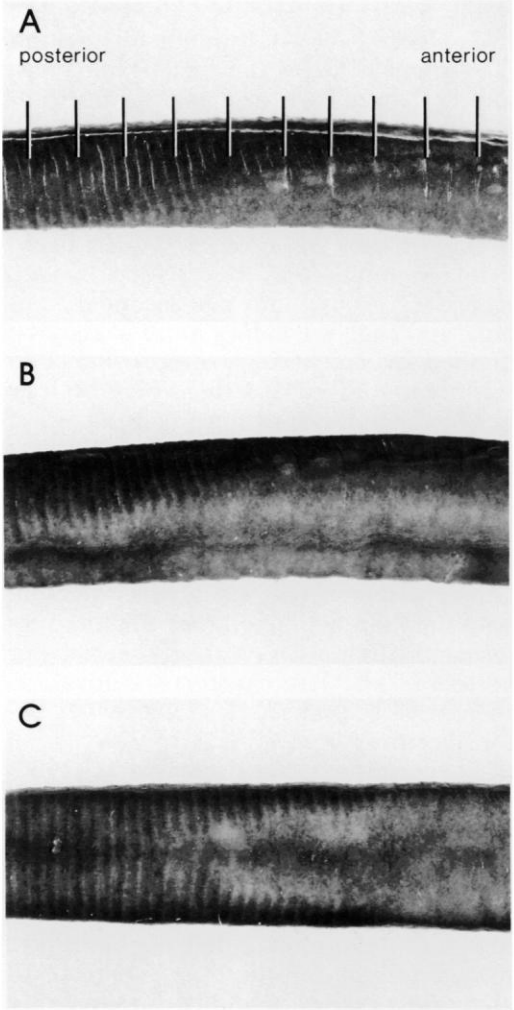

FIG. 3.—Lateral (A), ventrolateral (B), and ventral (C) views of a larval *Epicrionops petersi* (University of Michigan Museum of Zoology, UMMZ 165496, 152 mm snout–vent length). The vertical lines in A indicate primary annular grooves. Anteriorly, primary annuli are subdivided only by a single secondary annular groove. Posteriorly, the primary annuli are subdivided again by tertiary annular grooves so that each primary annulus includes one secondary groove and two tertiary grooves. The divisions begin dorsally and spread ventrally, as can be seen in B and C. Subdivision begins at the terminus and progresses anteriorly.

ontogenetic pattern occurs in the caeciliaid *Hypogeophis rostratus*, a species that has considerably fewer secondaries in the adult than *G. larvata*. In adult *H. rostratus*, secondaries rarely occur anterior of the posterior 10 to 15 primaries. Encapsulated embryos 38 mm total length or longer already have the adult condition. Embryos 34 mm total length or smaller have primaries only. A single 35 mm embryo was found, and only the last six of its primary annuli were subdivided by secondaries.

A series of larvae of the rhinatrematid *Epicrionops petersi* yielded additional information. All the primary annuli of these larvae are already subdivided by secondary grooves, but the number of primaries divided by tertiary grooves in this series increases with total length in an anterior direction (Fig. 2). The tertiaries form initially as dorsal grooves that spread ventrally to eventually encircle the body. The two sides of each tertiary groove meet midventrally, and the point of complete encirclement shifts anteriorly with age (Figs. 3, 4). In adults, all grooves completely encircle the body, and primary, secondary, and tertiary grooves cannot be distinguished externally.

In embryos of the oviparous caeciliaid *Afrocaecilia taitana*, no secondaries appear in any encapsulated stage or in the smallest hatchling (29 mm total length) among our sample, which has 130 primaries, close to the adult average. Therefore, in this species without secondaries in the adult stage, no transient secondaries occur in embryos as would be predicted by the scheme of LRG (see below). In species of the scolecomorphid genus *Scolecomorphus*, the same pattern occurs. These viviparous forms have primaries only in adults and no transient secondaries in embryos.

Thus, the ontogeny suggests an evolutionary transformation series: (1) the ancestral state of undivided primary annuli only; (2) the derived state of primary annuli divided in binary fashion by secondary grooves, developmentally beginning at the posterior end of the body; and (3) a further derived state in which the primary annuli subdivided by secondary grooves are further subdivided by the appearance of two tertiary grooves, one on each side of the secondary groove, developing in the same manner as the secondaries. The primary grooves that delimit the primary annuli of caecilians are presumably homologous to the costal grooves of salamanders. These primary grooves correspond to the myosepta of salamanders and most caecilians (Naylor and Nussbaum, 1980; Nussbaum and Naylor, 1982) and, therefore, provide a simple explanation for the 1:1 correspondence between primary annuli and vertebrae in the trunk region. This relationship breaks down under the collars, as noted above, and toward the body terminus where vertebrae are greatly reduced in size and almost always outnumber the primary annuli (Nussbaum, 1985). Given the primitive plan of segmentation in vertebrates, the observed ontogenetic pattern in caecilians, and the condition observed in salamanders (an outgroup), the evolutionary transformation scheme outlined above is the most parsimonious one.

LRG indicated that between the collars and the vent there is one primary annulus per vertebra. This is true, as was indicated earlier by Greeff (1884), Brauer (1899), Dunn (1942), Taylor (1968), and others, all of whom used it as a working principle. Renous et al. (1986) stated that more complex annular patterns arise by a process of binary division. Again, this is correct, as had been noted previously by Greeff (1884), Taylor (1968), and others. However, they further stated that each successive state of complication appears successively from the front, behind the collars, and proceeds posteriorly. This concept is incorrect, as was demonstrated above, and it is important to note that most of their phylogenetic reconstruction of caecilians is based on this fallacious principle. Renous et al. (1986) argued, as had previous authors, that skin metamerism is induced from dermal metamerism, but they presented no supporting data or references. This is a reasonable hypothesis which, if true, would explain the basic correspondence between annuli, musculature, and vertebrae. They then asserted that subse-

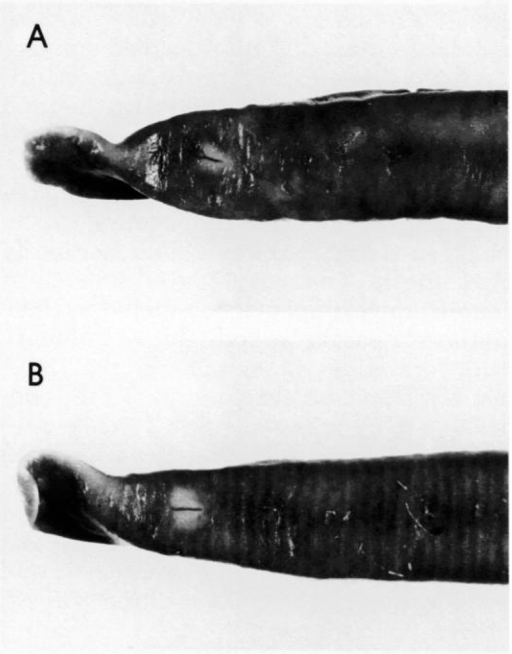

FIG. 4.—Ventral views of a young (A) larval *Epicrionops petersi* (UMMZ 165497, 118 mm SVL) and an older larva (B) of the same population (UMMZ 165496, 152 mm SVL). In A, the secondary and tertiary annular grooves have not yet extended to the ventral surface. In B, the primary, secondary, and tertiary annular grooves completely encircle the posterior body region and do so as far forward as the point shown in Fig. 3C of the same specimen.

quent subdivision respects the cephalocaudal gradient of primordia development and, thus, begins anteriorly and spreads posteriorly. The authors stated further that loss of secondary divisions, or simplification, occurs in the same manner as the process of complication, i.e., beginning behind the collars and propagating posteriorly towards the vent without necessarily reaching it. This unsupported scheme of annular development is considered by these authors to parallel exactly the evolutionary transformations in annulation that have occurred in caecilian lineages. To the contrary, all of the available evidence presented above indicates that the progression proposed by Renous et al. (1986) is incorrect.

We agree with Renous et al. (1986) that secondary grooves appear in ontogeny and phylogeny as a terminal addition (Greeff, 1884, apparently was the first to point this out; also see Brauer, 1899). However, it is clear that the reappearance of a primitive character state (undivided primary annuli), which constitutes an evolutionary reversal, after such a terminal addition is most simply explained by the process of terminal deletion. Thus, in the case of annuli, the first secondaries to be lost would be those that appeared last. Loss of the first secondaries to appear, without the loss of all secondaries (non-terminal deletion) seems less likely, because of the interactive nature of development, in which successive stages are often built upon or are dependent upon earlier stages (as in induction).

According to LRG, loss of secondary annuli occurs initially at the place where they first develop (behind the collars by their scheme) rather than where they last develop, and, thus, loss is not explicable in terms of simple reversal by terminal deletion. In fact, in their hypothesis, reversal by terminal deletion is impossible, and, in the ontogenetic and phylogenetic changes envisioned by them, only the process of terminal addition can occur. Thus, if there was an ancestral ontogeny A → B, from which the ontogeny A → B → C was derived, then in the scheme of ontogeny and phylogeny of LRG, reappearance of B as the last stage in the ontogeny could not occur through simple loss of C (reversal through terminal deletion), but only through the de novo addition of B onto an ontogeny that included C (i.e., A → B → C → B). As demonstrated above, such changes are not observed in the ontogenies of extant caecilians, a fact that falsifies LRG's hypothesis; or requires an ad hoc argument, that complicated changes (non-terminal deletions) occurred in addition to the numerous terminal additions envisioned by LRG, to explain the observed ontogenies.

In summary, we have evidence that secondaries and tertiaries appear posteriorly and spread anteriorly during development and believe that loss of secondaries and tertiaries occurs in the opposite direction. On the other hand, LRG stated that secondary and tertiary annuli appear anteriorly and spread posteriorly and that loss occurs in the same direction, and they provided no evidence.

Evolution of annular patterns.—There are four general states of annulation in modern caecilians: (A) *Species with undivided primary annuli only.* (B) *Species with primary annuli and with some proportion but not all the primary annuli subdivided by secondary grooves.* In these species, the anteriormost secondary grooves do not completely encircle the body; hence the primary annuli are only partly subdivided. The secondary grooves increase in length posteriorly so that at some point along the body, each primary annulus may be completely subdivided by a secondary groove, and here the grooves delimiting primary annuli cannot be distinguished externally from secondary grooves. Where complete secondary grooves occur, the primary grooves still correspond to the internal myosepta and can be positively identified by dissection. In practice, primaries easily can be identified externally by counting every other groove (which is either a primary or a secondary groove, depending on the starting point) after the point at which primary and secondary grooves are no longer externally distinguishable. (C) *Species with secondary grooves subdividing every primary annulus.* In all cases, the anteriormost secondary grooves do not completely encircle their primary annuli and easily can be distinguished externally on the anterior part of the trunk. A few species, such as *Grandisonia larvata,* normally have state B, but a few individuals have state C, illustrating the gradual transition between B and C. (D) *Species with all primary annuli completely encircled with secondary and tertiary grooves.* This is the condition of the later ontogenetic stages and the adult animals. In the early ontogenetic stages, secondary and tertiary grooves may not completely encircle the body, as described above for *Epicrionops petersi.* The simplest evolutionary polarization of this series of states, given the ontogenetic pattern described above, is A → B → C → D.

Reduction in the number of secondary grooves, and even complete loss of secondaries, could easily occur in caecilians by arrested development (paedomorphosis or terminal deletion), and this almost certainly has occurred. The number of secondaries in species with state B varies considerably, and those individuals of a population with relatively few secondaries have fewer anterior secondaries, not fewer posterior secondaries. If an individual has a single secondary groove, it will be, with rare exception, on the posteriormost primary. Exceptionally, it may be on the next to last primary.

Two genera, *Caecilia* and *Microcaecilia,* contain species with and without secondaries. In both these genera, most species have secondaries. Those few species lacking secondaries almost certainly are derived from ancestors that had secondaries, based on the logic of outgroup comparisons. Some species of *Caecilia* (e.g., *C. abitaguae*) that normally have a few secondaries confined to the terminal region of the body include occasional individuals without any secondaries. In these species, the functional significance of secondaries cannot be very great as there are zero to few present. Because of this, it seems likely that these species were derived from ancestors with numerous secondaries, in which the secondaries served some function contributing to individual fitness. The outgroup criterion also suggests this.

Some genera, such as *Afrocaecilia* and *Boulengerula,* have only primaries. However, based on the condition of their assumed relatives, these caecilians have secondarily lost a more complicated annulation pattern, which included the presence of secondaries. The same interpretation applies to the four genera of the family Typhlonectidae (*Chthonerpeton, Nectocaecilia, Typhlonectes, Potomotyphlus*), which have only primary annuli and sometimes pseudosecondary grooves. Among living caecilians, retention of the primitive annulation pattern of undivided primaries only (state A) seems possible only for the African scolecomorphids.

Although loss of secondary grooves certainly has occurred, there is no evidence for the secondary loss of tertiary grooves. This is because there are no known examples of species with tertiaries in the adult, in which the tertiaries do not occur along the full length of the body. The transition C → D, therefore, may be unique and unreversed indicating monophyly of caecilians with tertiaries. This suggestion is further supported by the absence of concordance between primary grooves and underlying myosepta in the two families (Ichthyophiidae and Rhinatrematidae) with tertiaries (Nussbaum and Naylor, 1982). In the adults of these families, annulation of the skin has become uncoupled from body segmentation, even though skin annulation is developmentally related to body segmentation.

Because of the mode of development of secondary grooves, which suggests a simple mechanism for increasing or decreasing in number, and the known distribution of secondary grooves among closely related genera and species, it is clear that annulation states A and B and states B and C have shifted back and forth phylogenetically resulting in reversals and independent derivations. Therefore, annulation patterns must be used cautiously in phylogenetic reconstruction of caecilians.

Ontogeny of annular grooves.—Analysis of annulation patterns is further complicated by the manner in which the annular grooves develop. Annuli are conventionally described as complete if the annular grooves completely encircle the body and incomplete if they are interrupted dorsally or ventrally. In the ontogeny of multiannulate forms, the secondary and tertiary grooves appear first as incomplete grooves and then lengthen to completely encircle the body. The secondary groove that divides a primary annulus may first appear as two small, dorsolateral grooves which lengthen to join first dorsally and then ventrally, or, a single middorsal secondary groove may appear and grow laterally eventually conjoining midventrally. At any point in ontogeny, very short secondary grooves can be seen forming anteriorly, longer secondary grooves further posteriorly, and perhaps complete grooves even further posteriorly. In many species, development of secondary grooves stops in the adults, leaving incomplete grooves anteriorly grading into complete secondary grooves posteriorly. The ontogeny suggests that incomplete secondaries may have evolved before complete secondaries. It is also likely that incomplete primaries, both dorsally and ventrally, are ancestral to complete primaries as is suggested by the incomplete costal grooves of salamanders. However, in most cases, the presence of only incomplete primary grooves in some modern caecilians is likely to be secondarily derived, based on outgroup comparisons and the fact that the ontogenetic pattern is simple and seemingly easily reversed.

Postcloacal annulation.—The postcloacal segmentation pattern of caecilians is related to the phenomenon of annulation, and our interpretation differs from that of LRG and Renous et al. (1986). The latter authors erroneously reported that Nussbaum (1977) defined tails of Gymnophiona as postcloacal extensions of the body. In fact, Nussbaum (1977, 1979) identified true tails of caecilians by the presence of complete postcloacal annuli. Renous et al. (1986) defined tails by the presence of postcloacal vertebrae. The problem with the latter definition is that, because of the complete loss of the pelvic girdle in caecilians, a minor forward shift of the cloacal opening following the evolutionary loss of tail vertebrae results in the reappearance of a "tail" (pseudotail). Of course, postcloacal annuli might also reappear, but the evidence discussed below suggests that once lost, postcloacal annuli do not reappear attendant with a forward shift in the position of the cloaca.

Fundamental vertebrate metamerism and outgroup comparisons (e.g., salamander tails) suggest that, ancestrally, postcloacal external segmentation accompanied postcloacal vertebrae (tails). Loss of postcloacal vertebrae is a derived feature found in the majority of living species of caecilians, and this loss correlates with the loss of postcloacal external segmentation. In some caecilians, there is an unsegmented terminal shield (Taylor, 1968), which includes the cloacal opening. This shield, or "cone" of LRG, may or may not contain vertebrae posterior to the cloacal opening (Nussbaum, 1985).

The size, and even the presence or absence of a terminal shield, varies within and between genera of the family Caeciliaidae. *Siphonops* and allied genera have a well-defined terminal shield not supported by vertebrae. The genus *Caecilia* contains species with and without a terminal shield, and the genus *Parvicaecilia* has a small unsegmented terminal portion of the body that is questionably a terminal shield.

Some typhlonectids have a poorly defined terminal shield that lacks external annulation and may include a very small postcloacal vertebral column consisting of 0–6 tiny vertebrae. Outgroup (Caeciliaidae) comparison for the Typhlonectidae suggests that, within this lineage, absence of postcloacal vertebrae is ancestral and that there has been a reversal within this family (Wilkinson, 1989).

In scolecomorphids, there is an unsegmented terminal shield supported by vertebrae (Nussbaum, 1985).

In summary, it appears that the presence of postcloacal vertebrae in caecilians with postcloacal annuli (ichthyophiids, rhinatrematids, uraeotyphlids) is not a condition homologous to that observed in caecilians with postcloacal vertebrae in unsegmented terminal shields (some caeciliaids, scolecomorphids, some typhlonectids). We view the former as true tails (ancestral) and the latter as pseudotails (derived). In regard to the view of LRG, it is illuminating that none of the three primary categories or eight subcategories of types of body termini described by Renous et al. (1986) map together in a meaningful way on the LRG cladogram.

Anomalies.—LRG did not clearly report their annular character states. The states are listed twice in their data matrix, first in terms of which kinds of annuli are present in the various taxa and then in a section on the anterior to posterior succession of annular complication and simplification. The states are also reported in diagnoses and on dendrograms. Very often, the states for a given taxon do not correspond between sections. There are numerous inconsistencies of this kind; we will mention only two examples. In their character matrix, the genera *Epicrionops* and *Rhinatrema* are listed as having primary annuli, but primaries are not indicated for these genera in the dendrogram nor in the diagnoses. *Typhlonectes natans* is listed as having secondaries and tertiaries in the character matrix, but has only incomplete tertiaries in the diagnosis, and neither of these patterns corresponds with what is indicated on their dendrogram. Therefore, three different patterns are indicated for *T. natans*, a species for which they erected a new genus (*Pseudotyphlonectes*). In many cases, annulation patterns listed in the character matrix are not included in the diagnoses, nor are they necessarily mapped onto their trees. No explanation was given for this, and it is impossible to determine whether LRG used all of their data in constructing their trees. This same pattern of inconsistency occurs in their use of other characters.

Our observations of the annular patterns of various caecilian taxa differ from those of LRG in numerous ways. We will address only a few of these, the first of which involves an additional problem in terminology. LRG reported (in their character matrix) the presence of quaternary annular grooves in the genera *Caudacaecilia*, *Ichthyophis*, and *Epicrionops*. Production of quaternaries in caecilians would require further subdivision of each primary annulus. If this occurred, then, between each pair of primary grooves, there should be seven other grooves: one secondary, two tertiaries, and four quaternaries. Such a concentration of grooves dividing single primary annuli does not occur in the Gymnophiona. Taylor (1968) pointed out that in multiannulate forms, annular grooves frequently bifurcate so that annular counts made at different positions along the body may vary. These bifurcations are irregular in position and frequency, and, because of this, we view them as developmental anomalies. Possibly LRG considered these bifurcations to be quaternary grooves.

LRG claimed that the genera *Caudacaecilia*, *Ichthyophis*, and *Rhinatrema* have a system of secondaries posterior to a system of tertiaries. This is contrary to the traditional view that these forms have tertiary grooves along the entire body behind the collars and is virtually falsified by the ontogenetic pattern described above for the closely related *Epicrionops petersi*. We believe LRG were misled by the following circumstances. The postcloacal vertebrae of these forms become successively smaller, but the width of the postcloacal annuli remains the same. Thus, a postcloacal vertebra may be associated with fewer than the five annular grooves that would represent a primary subdivided by secondary and tertiary grooves. Apparently, the reduced number of grooves associated with postcloacal vertebrae are interpreted by LRG as secondaries only. This interpretation is erroneous, because for these annuli to be subdivided by secondary grooves only, there would have to be three annular grooves per vertebra, and this relationship does not occur. The relationship that does occur is irregular and clearly results from the gradual reduction in size of tail vertebrae; this reduction is not accompanied by a parallel reduction in the widths of the annuli (distance between primary grooves). LRG also indicated that primary annuli with secondaries only occur anterior to primary annuli with tertiaries in these three genera. This clearly is not the case, and we have no explanation for this anomalous report.

Several genera are also reported by LRG to have undivided primary annuli posterior to primary annuli with secondary grooves. Traditionally, all of the taxa so listed by LRG are viewed as having undivided primary annuli anteriorly, followed by primaries that are subdivided by secondaries. This anomalous report of LRG cannot be explained by their terminology in which primary annuli, once subdivided, are no longer called primary annuli, because they claimed that these taxa have only primary annuli posteriorly even though these are clearly subdivided. The only explanation that we can offer for LRG's interpretation is the possibility that they were again confused by the gradual reduction in size of vertebrae near the terminus. Because of this size reduction, the vestigial vertebrae will at some point approach the size equal to the distance between a primary groove and adjacent secondary groove, because the latter distance does not decrease as fast as vertebral length near the body terminus. At this point, a secondary annulus could be mistaken for a primary annulus if the developmental pattern of subdivided annuli is ignored or not understood.

The presence of secondary and tertiary grooves in typhlonectids, as reported by LRG is at odds with the observations of Taylor (1968, 1969*a*) and others including us, who view typhlonectids as having undivided primary annuli only. They reported tertiary annular systems in *Potomotyphlus* and *Typhlonectes natans* and, furthermore, claimed that the tertiary grooves are complete in the former and incomplete in the latter. In fact, only the anteriormost annular grooves of these two taxa are ever complete, and, according to LRG, these are not the tertiary grooves. We cannot explain LRG's apparently erroneous report of tertiary grooves in these two taxa.

All typhlonectids, according to LRG have secondary annuli. This we believe is not true, but it is a more difficult problem to resolve because of the occurrence of pseudosecondaries in some typhlonectids, which LRG may have mistaken for secondaries. Peters (1879) and Fuhrmann (1914) both reported secondaries in typhlonectids (*Typhlonectes natans* and *T. compressicaudus*), but others, Dunn (1942) and Taylor (1968, 1969*a*) for examples, considered them to be absent from this family. The primary annular grooves of typhlonectids correspond to the underlying myosepta (Nussbaum and Naylor, 1982), and hence each primary annulus contains a single vertebra. Pseudosecondary grooves divide the primary annuli in some species. These pseudosecondaries usually occur in a lateromedial position, which is the position of true, incomplete secondaries, and they are never complete. We do not consider them to be homologous with the true secondaries of other caecilians for the following reasons. First, the structure of true secondary grooves is the same as that of primary grooves, but the "secondary grooves" of typhlonectids differ fundamentally in structure from the primary grooves. The primary annular grooves of typhlonectids do not contain scales and superficially have the appearance of dark vertical lines. Closer examination reveals each dark line to be a composite of one or two darkish bands and a medial row of enlarged, white, granular glands. The dark coloration of the bands results from the absence of underlying smaller (mucous) glands which elsewhere obscure the dark cutaneous capillary beds beneath the epidermis. The pseudosecondary grooves have a row of medial enlarged glands as in the primaries, but the enlarged glands are smaller and are not bordered on each side by a dark band. In other words, the pseudosecondary groove is indicated only by a short vertical row of slightly enlarged glands. Second, the distribution of pseudosecondaries in typhlonectids does not parallel that of true secondaries of other families. In the latter, as explained above, secondaries are always present posteriorly if they are present at all and extend anteriorly to varying degrees. Pseudosecondaries may be randomly distributed or concentrated along the midbody and absent anteriorly and posteriorly, and they seldom occur in every primary even where they are concentrated. Third, pseudosecondary grooves are small and irregularly shaped, which is not the case with true secondaries. Fourth, pseudosecondaries are much more highly variable in number within species than true secondaries. And, last, pseudosecondaries are not present in all typhlonectid species and are absent from species of *Chthonerpeton*, the most primitive and most terrestrial genus (Nussbaum, 1986*a*; Nussbaum and Wilkinson, 1987). We interpret the absence of pseudosecondaries in *Chthonerpeton* and their presence in some of the more derived and more aquatic members of this family as evidence that they are an evolutionary novelty in these derived forms, and perhaps represent an aquatic adaptation.

LRG may consider pseudosecondaries to be true secondaries, but this cannot account for their claim that secondaries occur in *Chthonerpeton* because all of the species of this genus have neither secondaries nor pseudosecondaries. Alternatively, these authors may have considered wrinkles or creases in the skin to be secondaries. These wrinkles, which are commonly observed in typhlonectids and usually not in other taxa, are artifacts of preservation. That this is true can be determined by comparing the condition of living typhlonectids to the condition after preservation and by carefully examining the structure of the wrinkles of preserved specimens.

Numerous other problems exist in LRG's coding of annular character states. For examples, their state "IIIinc" indicates taxa with incomplete tertiary grooves (no such taxa exist), and none of their taxa is coded "Iinc," even though there are numerous forms with incomplete primary grooves. Their report of incomplete secondaries in scolecomorphids is clearly erroneous and cannot be explained by terminological differences. Because of this, we are uncertain whether their use of the term incomplete refers to annuli that do not completely circle the body or to some other phenomenon.

It is difficult to envision how LRG could use their interpretation of annular evolution to construct a phylogeny. They considered numerous changes in states to be possible and believed that many states could be arrived at by alternative hypothetical series of transformations. LRG did not explain how they resolved this problem. In tracing out annular character state changes along the different branches of their trees, it is evident that evolutionary steps were left out on some branches and occur in different directions in different clades with no clear pattern.

Other Characters Used By LRG

Preliminary comments.—LRG did not justify their character polarizations and did not clearly identify which character states were selected from the literature and which were from their observations. They cited Renous et al. (1986) for discussion and justification of their character state transformations. But, in this latter paper, only characters of annulation, squamation, and the body terminus were discussed, and polarizations were not given for all of these. Because only shared derived character states can be used to delimit sister groups, the criteria and reasoning for identifying the derived states of a suite of characters are essential aspects of cladistic investigation and should be open to review if phylogenetic inferences and changes in taxonomy based upon them are to have credibility.

LRG excluded some characters from their analysis on the basis that they were unknown for some taxa and others because they are functionally related to the niche of the taxa. Examples of the latter include characters related to aquatic habits (fins) and some related to burrowing (consolidation of the skull). There is no good reason to exclude characters from systematic studies because they are believed to be functional. First, such characters can be true homologies and, thus, evidence of monophyly delimiting cladistic groups. Second, our knowledge of the functions of the majority of characters is minimal and does not allow us to consistently differentiate functional from non-functional characters. In any case, LRG were inconsistent in that they included in their analysis characters that are unknown for many taxa and characters related to consolidation of the skull (loss or fusion of cranial elements).

Scalation.—The dermal scales of caecilians are arranged in rows within the annular grooves, and, therefore, patterns of scalation are related to patterns of annulation. LRG used two characters involving the distribution and abundance of scales along the body and no scale morphology in estimating caecilian phylogeny. The two multistate characters used were (1) number of scale rows per annular groove and (2) proportion of the body covered by scales. The authors coded the characters as follows: more scale rows per groove ancestral to fewer; and a higher proportion of the body covered ancestral to a lower proportion covered. They offered no explanation for their polarizations and selection of boundaries between character states, which are continuous variables, and they did not cite Taylor's (1972) monograph on caecilian scales.

Their treatment of scale row characters has many problems, which can be understood only in light of scale development. The ontogeny of scale rows closely parallels the ontogeny of annular grooves. As grooves develop in an anteriorly moving wave, so do the rows of scales contained in the grooves. At first, only a single row of small scales is present, followed by an increase in the number of rows until the final adult condition is attained. At the adult end point, the most recently formed anterior secondary grooves may have only a single row of small scales; whereas, the older more posterior grooves may contain many rows of larger scales. Therefore, the number of scale rows per annular groove and the proportion of the body covered by scale rows is correlated with the pattern of annulation and to some extent evolve in the same direction. It is clear, given the correlation between ontogeny of scale rows and annular grooves, that both the scale characters used by LRG have a high probability of reversals and convergencies for the same reasons outlined above in the section on annulation. LRG may have made coding mistakes and erroneous conclusions by not accounting for this.

LRG used the following transformation series for number of scale rows per annulus: more than 4 → 2 to 4 → 1 → 0. Because of the way this character was coded, genera exist that span at least two of these states, as is demonstrated by our unpublished data and that of Taylor (1972). Of a sample of 21 taxa scored by LRG, 11 (52%) are variable enough to span two of their states. Considering the four genera with tertiary annular grooves, *Caudacaecilia*, *Epicrionops*, *Ichthyophis*, and *Rhinatrema*, only the latter genus is confined to the state assigned to it by LRG. A few examples from among the taxa with secondary annular grooves further illustrate this problem. *Geotrypetes* and *Hypogeophis* fall in their category of 2–4 scale rows per groove, but the former genus has as many as nine and the latter genus as many as five rows per groove (Taylor, 1972), which places both of these genera in the more primitive category as well as in the one assigned to them by LRG. Similarly, the genera *Uraeotyphlus*, *Grandisonia*, *Gegeneophis*, *Dermophis*, and *Microcaecilia* cannot be placed unambiguously in their scheme; and *Caecilia gracilis* has two or more scale rows per annulus (Taylor, 1972; personal observations) rather than the one assigned to it by LRG.

The second scalation character used by LRG, proportion of body covered by scales, was also divided arbitrarily into states: total coverage → more than 90% covered → less than 90% covered → no scales. There are three difficulties with this coding scheme. First, as in the previous character, taxa overlap these categories, e.g., in *Caecilia* and *Ichthyophis*. The former contains species in all four categories (coded only in the >90% category by LRG); whereas the latter includes species in their first two categories (coded only in the first category by LRG). Second, most of the taxa (21 of 32, 66%) used by LRG are scored in the last two categories. Genera and species within these two categories are obviously heterogeneous groups assembled by arbitrary character state coding. For example, *Caudacaecilia* (Ichthyophiidae) and *Oscaecilia ochrocephala* (Caeciliidae) are placed together in the second category; whereas *Ichthyophis*, the obvious sister genus of *Caudacaecilia*, is placed in the first category, and *Caecilia*, the obvious sister genus of *Oscaecilia*, is placed in the third category. These and other peculiar associations of taxa and states of this character indicate an erroneous coding scheme. Third, the last state of this character is redundant with the last state of the other scalation character (scale rows). Their joint use results in weighting of a single character state (lack of dermal scales) that likely has evolved independently several times.

Length/width ratio.—The L/W ratio, defined as total length divided by body width, has been used by most caecilian taxonomists (e.g., Dunn, 1942; Taylor, 1968) as a tool to identify caecilians. This is a continuous variable which LRG divided, arbitrarily, into three states. The assumptions behind the polarization of this character are not given by LRG. Apparently, LRG believed that the primitive condition is stout-bodied and the attenuate condition derived. Although this polarity is defensible, their treatment of the character is not for the following reasons. First, there are problems with the measurements. Both width and length are affected by the state of preservation, including the amount of dehydration and contortion of the vertebral column. Length depends on the amount of stretching of the specimen, which varies between workers, and width depends on where along the body the measurement is taken. More importantly, the L/W ratio varies considerably with development in all species and varies sexually and seasonally in some species. There is no evidence that LRG accounted for any of these problems. Ontogenetic, sexual, and seasonal variation alone result in single species having more than one of the character states defined by LRG. Sawaya (1937), for example, reported variation in the L/W ratio of *Siphonops annulatus* that exceeds the entire range of character states described by LRG, and Taylor (1968) reported similarly great variation for species of *Chthonerpeton* and *Typhlonectes*. Our data indicate that ontogenetic variation in L/W ratios of several other species render LRG's state limits for this character meaningless. Apparently, LRG arrived at their state limits from very small sample sizes. Furthermore, this character has a high probability of reversal and convergence, and the distribution of body shape within and between genera shows that one or both have occurred.

Number of vertebrae.—The three character states of vertebral number used by LRG also are defined arbitrarily. Again, there are cases, both of single species that overlap two of their character states, and of genera (e.g., *Chthonerpeton* and *Siphonops*) with species that fall into different categories. Because LRG used the genus as their operational taxonomic unit, these multistate occurrences confuse their cladistic analysis. LRG scored low numbers of vertebrae as ancestral to high numbers. Again, this is defensible, but, because of the simplicity of this character, there is a high probability of reversal and convergence. The occurrence in several genera of species with different states is strong evidence that reversals and/or convergencies have actually happened. LRG claim that the number of vertebrae varies independently of attenuation and, thus, can be used as evidence of relationship independent of L/W ratios. This is at least partly wrong. Attenuation and high vertebral number are highly correlated in both *Caecilia* and *Chthonerpeton* and probably in other genera.

Number of nuchal vertebrae.—According to LRG, four vertebrae are ancestral to both three and five vertebrae under the collars in caecilians, but they do not explain this ordering. This character is potentially useful in that it involves the complex association of vertebrae, muscles and nuchal grooves and, therefore, might be coded in a meaningful way. However, as coded by LRG, one cannot be certain whether the simple differences in number of vertebrae under the collars result from real changes in the number of vertebrae or in elongation or shortening of the collars relative to the nuchal vertebrae. Because changes in this character may occur in sev-

TABLE 3.—Number of nuchal vertebrae and presence (+) or absence (−) of postcloacal vertebrae in caecilian genera according to Lescure et al. (1986) [LRG] compared to our observations (N&W).

	Nuchal vertebrae		Postcloacal vertebrae	
Genus	LRG	N&W*	LRG	N&W
Afrocaecilia	3	3.0–4.0 (29)†	+	± (8)
Boulengerula	3	3.0 (1)	+	− (1)
Caecilia gracilis	3	3.0–4.0 (5)	+	± (5)
Chthonerpeton	3	3.0–4.0 (40)	−	± (33)
Dermophis	4	3.0–3.5 (41)	+	± (4)
Epicrionops	4	3.0 (11)	+	+ (>20)
Gegeneophis	3	3.0–4.0 (14)	−	± (8)
Geotrypetes	3	3.0 (3)		
Grandisonia	3	3.0–6.0 (27)	+	± (11)
Gymnopis	4	3.0–3.5 (10)	+	± (7)
Herpele	4	3.0–3.5 (5)	+	+ (1)
Hypogeophis	3	3.0–4.0 (8)	−	− (1)
Ichthyophis	4	4.0 (10)	+	+ (>100)
Indotyphlus	4	3.0 (7)	+	− (1)
Lutkenotyphlus	3	3.0 (6)	+	− (1)
Microcaecilia	3	3.0 (6)	−	± (4)
Oscaecilia bassleri	3	3.0 (1)	+	− (1)
Oscaecilia ochrocephala	4	3.0–4.0 (9)	+	+ (5)
Potomotyphlus	3	4.0–5.0 (15)	−	+ (14)
Schistometopum	4	3.0–4.0 (12)	+	± (8)
Scolecomorphus	5	4.0–5.0 (6)	+	+ (>50)
Siphonops	3	3.0–3.5 (18)	−	± (5)
Typhlonectes compressicaudus	3	4.0–4.5 (15)	+	+ (8)
Typhlonectes natans	3	4.0 (35)	+	+ (38)
Uraeotyphlus	4	3.0–4.0 (15)	+	+ (>50)

* Estimated to the nearest half vertebra.

† Numbers in parentheses are sample sizes. Lescure et al. (LRG) did not give sample sizes.

eral ways, similar states may not reflect homology. Even if we accept the coding of LRG, there are significant differences between their data and our observations (we differ in 19 of 25 taxa compared, Table 3), and we found variation within some genera and even species (e.g., *Grandisonia* spp. have 3–6 nuchal vertebrae) that spans the range of their character states. Furthermore, the number of vertebrae under the collars may vary as a result of movement of the grooves defining the collars; this movement occurs because of dehydration and/or muscular contraction. Also, the number of vertebrae under the collars frequently is not a simple whole number as recorded by LRG. The authors did not mention these problems and apparently did not account for them.

Presence or absence of a tail.—As discussed above, we disagree with LRG in their view of the evolution of caecilian tails. The presence of postcloacal vertebrae may indicate either a true tail or a secondarily derived pseudotail, a possibility not entertained by LRG. Some of LRG's "tailed" caecilians are, by our analysis, falsely tailed. In addition, our data concerning the presence or absence of postcloacal vertebrae differ significantly from theirs (Table 3). Of 24 possible comparisons between their data and ours, we differ in 15. As examples, LRG claimed that *Afrocaecilia*, *Dermophis*, *Grandisonia*, *Gymnopis*, *Schistometopum*, and some species of *Caecilia* and *Oscaecilia* have tails. Our data clearly show that some individuals of these taxa do, and some do not, have "tails," depending on species and individual variation and the state of preservation. In regard to preservation, dehydrated specimens of *Gymnopis multiplicata* and *Gymnopis syntrema* may have a "tail," whereas well preserved specimens may not (Nussbaum, 1988). LRG reported other erroneous data, such as the absence of postcloacal vertebrae in the typhlonectid genus *Potomotyphlus*, and such data were used to diagnose new taxa (e.g., Potamotyphlidae).

Segmentation of the body terminus.—Loss of segmentation in the body terminus is derived from the presence of segmentation in the body terminus, according to LRG. Apparently, here these authors are referring to skin annulation and not segmentation of the muscles, but this is unclear. In either case, this polarization is sensible, but stands in contrast to their arguments elsewhere that changes in annulation occurred from anterior to posterior.

Loss of septomaxillae.—Loss, or fusion of the septomaxilla to adjacent bones, was considered to be derived by Nussbaum (1979) and LRG. Little weight should be given to this character because of the likelihood of independent loss. However, LRG used this as the only character defining the major bifurcation in their "cladogram," leaving one of their two major "clades" defined by a single ancestral character state.

Fate of the postfrontal bone.—Following Laurent (1984, 1986), LRG viewed the fusion of the postfrontal bone to either the maxillopalatine or squamosal bone as derived. As we indicated above, there are no developmental data to substantiate LRG's assertions regarding the fate of the postfrontal bone in the various taxa scored. To our objections given above, we add here that fusion of the postfrontal to the squamosal as reported by LRG for *Dermophis* contradicts the ontogenetic data of Wake and Hanken (1982). The latter authors showed that the postfrontal is lost through reduction rather than fusion to any bone. The morphocline presented by LRG is problematical. Their first transformation, postfrontal distinct → fused, suggests that "fusion" is itself an intermediate derived state, which is ancestral to either fusion to the maxillopalatine in some taxa or to the squamosal in others. This is clearly illogical. The possibility of loss of the postfrontal by reduction, as in *Dermophis*, is not part of their transformation series, even though they refer to "loss" of this bone in their text.

Postchoanal process of the maxillopalatine.—The states of this character are not clearly defined by LRG, nor is the polarization justified. Loss of the postchoanal process or its strong development are considered to be derived. Loss, according to LRG, occurs only in *Scolecomorphus*, and, if this were true, as a uniquely derived character state, it would be uninformative. However, Nussbaum (1985) showed that both the scolecomorphid genera have well developed postchoanal processes.

Fate of the pterygoid bone.—LRG logically scored loss of the pterygoid bone as derived. However, the fate of the pterygoid bone (loss or fusion to adjacent elements) cannot be known with certainty until developmental studies are completed. LRG did not indicate the existence of unpublished data of the kind necessary to properly score this character; therefore, we have little confidence in their scoring of this character.

Fate of the stapes.—Nussbaum (1979) considered the loss of the stapes to be derived in caecilians, and LRG apparently agreed. However, this is a derived character state unique to scolecomorphids, and as such it is uninformative beyond supporting scolecomorphid monophyly.

Perforation of the stapes.—Nussbaum (1979) showed that rhinatrematids and ichthyophiids have stapes that are perforated for the passage of the "stapedial" artery. This is clearly an ancestral state compared to the derived state of imperforate stapes (Nussbaum, 1977, 1979). LRG seem to agree with this interpretation. However, their treatment of this character is confusing. In their diagnosis of the family Geotrypetidae, they state that the stapes is perforate or imperforate, but both of the genera listed for this family are listed as having an imperforate stapes.

Loss of splenial teeth.—The loss of splenial teeth is undoubtedly derived as suggested by LRG. But, it is also clear that this uncomplicated loss state has evolved several times in the Gymnophiona. There are morphoclines between species within such genera as *Caecilia* and *Gymnopis*, illustrating the gradual transition from many to as few as one splenial tooth per side, and occasional specimens of species characterized by one per side have no splenial teeth on one or both sides. Complete loss of splenial teeth has occurred independently within the Ichthyophiidae and Caeciliaidae, and almost certainly within different clades of the Caeciliaidae. Prior to 1968, the genus *Ichthyophis* consisted of striped and unstriped species, each group of which also contained species with and without splenial teeth. Taylor (1968) described a new genus, *Caudacaecilia,* to receive the striped and unstriped species of *Ichthyophis* that lacked splenial teeth. This created a still unresolved incompatibility concerning the distribution of the states of the two characters stripedness and presence/absence of splenial teeth. Homoplasy must exist for at least one of these two characters within the ichthyophiid genera. There is no a priori reason to assume one of these characters is more conservative than the other. These observations suggest that the loss of splenial teeth should be used cautiously in reconstructing caecilian phylogeny.

Mode of reproduction.—LRG used three states for this character; polarized as follows: oviparity → ovoviviparity → viviparity. We agree with this characterization, but viviparity may have evolved independently a number of times. It is unclear how LRG used this character in their analysis, as it is coded as questionable or unknown for 21 of their 35 operational taxonomic units.

Larval development.—LRG identified and polarized three states of this character as follows: free larvae → direct development → larvae in oviducts. The first two states of this transitional series are logical, but we disagree with inclusion of the third state here. Presumably, "larvae in oviducts" refers to a form of viviparity and, therefore, is subsumed in the previous character. Furthermore, the term "larva" should be restricted to a free-living trophic stage of development. In any case, 15 of the 35 taxa studied by LRG are either not coded or are coded ambiguously for this character, and the larval development of some of the taxa that are coded, such as *Siphonops* and *Herpele,* has never been reported. Here, as well as for the other characters, LRG should have cited their sources.

Geographic distribution.—LRG included the geographic distribution of the 35 taxa as a character for reconstructing the phylogeny of caecilians. We disagree emphatically with this procedure. Our primary objection is that there is no logical basis for including non-inherited "characters" in phylogenetic analysis. Although there is often a high correlation between geographic distribution and relatedness, over-reliance on commonness of distribution can lead to mistakes in estimating phylogeny. Furthermore, if distributional data are used in constructing phylogenies, then the phylogeny cannot serve as an independent test of biogeographic hypotheses. In our view, LRG (and Laurent as well) have used methods that invalidate their conclusions regarding caecilian biogeography.

Summary comments on characters.—Few of the characters used by LRG are robust, most have a high probability of convergence, and few allow the possibility for higher resolution studies that could test the putative homologies. Some of their character states are arbitrary divisions of continua, which are overlapped by intraspecific and intrageneric variation not accounted for by the authors. This latter problem results largely from the small sample sizes of their data set, which is a general problem of their analysis as it could affect the coding of some of their noncontinuous characters as well. Some of their characters are poorly defined, many of the taxa are miscoded, some of the state transitions are illogical, and most of the transitions are not supported by reference to methods of determining the polarities. They also follow the unacceptable practice of using distributional data to construct their cladograms. The authors disregarded their own advice to utilize only characters that can be coded for all taxa, and they ignored their caveat that embryological studies are needed to determine the fate of cranial elements. Too few characters were used to justify their cladogram of 35 taxa.

Methodology of Lescure et al.

Cladogram construction.—LRG provided no information on the construction of their cladogram. We suspect the clado-

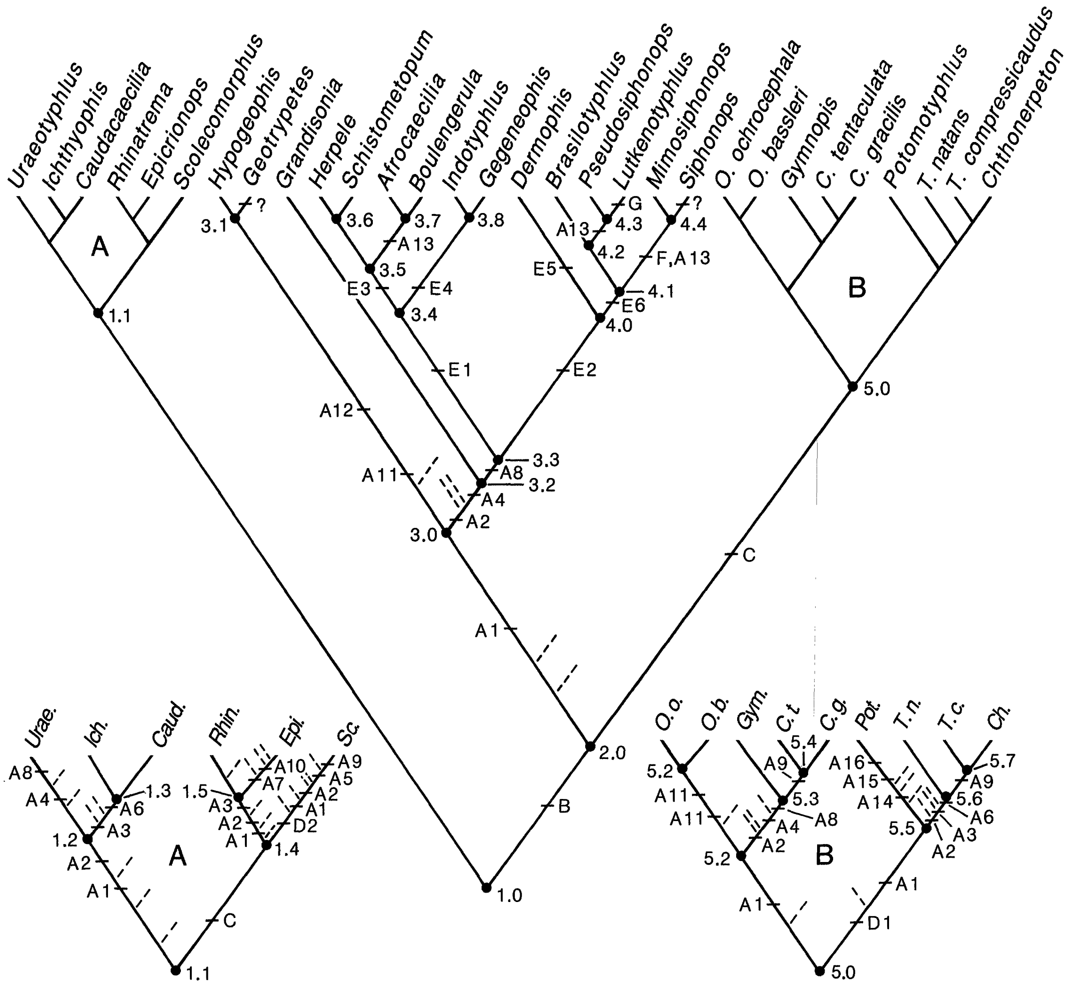

FIG. 5.—The cladogram of Lescure et al. (1986) redrawn with nodes 1.1 and 5.0 enlarged with more detail at the bottom. Character transformations are coded as follows. A = annulation, A1 = II+I, A2 = II, A3 = III+II, A4 = IIinc+II, A5 = I+II, A6 = II+III+II, A7 = III, A8 = I+IIinc+II, A9 = I+IIinc, A10 = IV+III, A11 = IIinc+II+I, A12 = IIinc+I, A13 = I, A14 = III+II+I, A15 = II+III+II+I, A16 = I+II+III+II+I; B = septomaxilla absent; C = postfrontal fused with maxilla; D = postchoanal process, D1 = fused to basal plate, D2 = absent; E = geographic distribution, E1 = Africa/Asia, E2 = America, E3 = Africa, E4 = India, E5 = Central America, E6 = South America; F = tail absent; G = more than 120 vertebrae; ? = unexplained character.

gram was hand drawn, because standard parsimony and compatibility algorithms applied to their data matrix will not produce their cladogram (see below). Furthermore, they may not have used all the data in their matrix, as only seven of the 17 matrix characters are mapped on their cladogram. Using the seven characters on their tree, there are 54 state transformations, 39 of which are changes in annulation. Of the remaining 15, six are geographic, two are not explained, and seven are various. If these were the only data used to produce their tree of 30 terminal taxa, then the tree cannot be robust. Their cladogram includes some character state transformations that we did not include in the above tabulation, because they are shown on branches that fade out, i.e., do not lead to terminal taxa. We will not consider these hypothetical divergences further, as there is no evidence that the indicated cladistic events ever occurred.

Specific problems.—In the preceding

sections, we noted problems with LRG's selection, definition, and analysis of characters. Here, we discuss a few examples of another set of problems with their study, namely the lack of internal consistency of their cladogram.

Their ancestral annulation state is I, primaries only. According to the scheme in their text, only a single transition from this ancestral state is possible: I → II+I (A1), which indicates the appearance of secondaries anteriorly. On their cladogram, this transition occurs independently in all lineages (six times). Therefore, this state transformation could be collapsed to below node 1.0 of their cladogram (see our Fig. 5). Similarly, the two branches diverging from node 1.4 both show the annulation transition II+I (A1) → II (A2), loss of primaries. Thus, the transition is common for the branch leading from node 1.1 to node 1.4, but it also occurs in the other branch leading from node 1.1, so it can be further collapsed to a transition between nodes 1.0 and 1.1. LRG considered these to be independent evolutionary events, even though the value of a character in phylogenetic inference is based on the premise that it is a reliable indicator of relationship, i.e., that its states are homologous across taxa and not independently derived.

The last state indicated on the line leading to *Epicrionops* is IV+III (quaternaries followed by tertiaries, A10). This is far from the state II+III+IVinc+III (secondaries followed by tertiaries followed by incomplete quaternaries, etc.) given for *Epicrionops* in their character matrix. It is not clear whether this is an inconsistency between the tree and the matrix or whether the authors have failed to indicate all of the many steps between the two states on their tree. In our view, this particular problem is academic, because neither of these states apply to *Epicrionops*.

The only characters that link the clade consisting of *Caudacaecilia, Ichthyophis,* and *Uraeotyphlus* at node 1.2 are the annular states II+I (A1) and II (A2), the first of which should be collapsed to below node (1.0) of their cladogram and the second to below node 1.1 (see above), leaving node 1.2 unsupported. The three genera thus left unsupported are separated from their sister-group, consisting of *Epicrionops, Rhinatrema,* and *Scolecomorphus,* by the fusion of the postfrontal with the maxillopalatine in the latter three genera. Apparently, more weight is given to this character than to the numerous and profound characters (including the presence of primaries only) that separate *Scolecomorphus* from the other two, in spite of the fact that fusion of the postfrontal and maxillopalatine occurs in nine other genera, according to their data matrix, which are mapped onto different parts of their cladogram.

The following is an example of another kind of problem with their cladogram. The last state indicated on the line between nodes 3.0 and 3.1 leading to *Geotrypetes* and *Hypogeophis* is IIinc+I (A12), an annulation state that applies only to *Hypogeophis* according to information provided elsewhere in their paper. *Geotrypetes* is reported elsewhere to have the annulation state IIinc+II+I (A11), which is the state that precedes IIinc+I (A12) in their transformation scheme. Thus, it is implied that *Geotrypetes* sustained a reversal in annulation. However, this implication is unnecessary and could be removed by simply placing the transition to IIinc+I (A12) on the line to *Hypogeophis* after node 3.1. Another anomaly is associated with this clade. A character state indicated by the letter "Y" is shown on the line leading to *Geotrypetes* after node 3.1. This transition is not explained, nor does a character "Y" appear in their character matrix and figure legend.

The last morphological character state on the line between nodes 3.2 and 3.8 leading to *Gegeneophis* and *Indotyphlus* is the annulation state I+IIinc+II (A8). This agrees with the state reported elsewhere for *Indotyphlus* but not for *Gegeneophis,* which is I+IIinc+II+I. Given our understanding of the authors' concept of the evolution of annulation, many steps separate the annulation states of *Gegeneophis* and *Indotyphlus.* Furthermore, the position on the cladogram of the last morphological character state (I+IIinc+II, A8) that unites these two genera is such that it also unites

10 additional genera scattered across Asia, Africa, and the Neotropics. Mostly geographic character states are used to sort out these 12 genera. In addition, three nongeographic characters transitions are used, and several bifurcations, for example, the one that separates *Herpele* and *Schistometopum,* have no indicated transformations. Additionally, no characters are given in support of node 3.6 linking the two latter genera. An unexplained transformation, "[3]," separates *Siphonops* and *Mimosiphonops.* In the case of *Gegeneophis* and *Indotyphlus,* it is clear that the only thing on the cladogram they have in common is their co-occurrence on the Indian Subcontinent.

The South American genera *Brasilotyphlus, Lutkenotyphlus, Mimosiphonops, Pseudosiphonops,* and *Siphonops* are linked together at node 4.1 on their cladogram based on the single character of occurrence on the same land mass. All except *Brasilotyphlus* have primary annuli only, the latter having secondaries as well as primaries. This suggests that *Brasilotyphlus* is the outlier, but *Brasilotyphlus* is placed closer to *Lutkenotyphlus* and *Pseudosiphonops* to the exclusion of *Mimosiphonops* and *Siphonops* based on the loss of a tail in the latter two genera (retention of an ancestral state in the former three genera). The result is an illogical branching sequence above node 4.1. Node 4.2 is completely unsupported and should be eliminated. Node 4.3 should be placed between nodes 4.1 and 4.4, leaving the line from node 4.1 to *Brasilotyphlus* unbranched. Node 4.3 is then supported by the annular state of primaries only, and node 4.4 by tail loss. Furthermore, the final non-geographic character state indicated (between nodes 3.2 and 3.3) on the line to *Brasilotyphlus* is the annular state I+IIinc+II (A8), which differs from its state reported elsewhere (I+IIinc+II+I). If the latter state is the correct state for *Brasilotyphlus* according to their scheme, then its state is the same as that of *Gegeneophis,* which is placed elsewhere (in the India clade, node 3.8).

Dermophis is split from the group of five Neotropical genera defined by node 4.1 because it occurs in Central America and the others in South America. Another Central American genus, *Gymnopis,* is not included in this geographical analysis and is placed on a clade (node 5.0) some distance from *Dermophis.* Node 5.0 is supported by a single character, the fusion of the postfrontal to the maxilla. There is good cytotaxonomic (Wake and Case, 1975), biochemical (Case and Wake, 1977) and morphological (Taylor, 1968, 1969*b*, 1972) evidence not discussed by LRG that *Dermophis* and *Gymnopis* are sister-taxa and should not be separated as LRG have done. Furthermore, LRG are not entirely correct in assigning the geographical state "Central America" to *Dermophis.* This genus, although it is mainly Central American, extends into northern South America (Taylor, 1968).

The only character that unites the *Oscaecilia* clade with the *Caecilia–Gymnopis* clade at node 5.2 of their cladogram is annular state II+I (A1), which, as explained above, can be collapsed to below their primary node, leaving this clade entirely unsupported. Two groups of the genus *Caecilia* are linked at node 5.4 by the annular state change I+IIinc+II (A8) → I+IIinc (A9). This transition is improperly placed on their cladogram because one of the groups, *Caecilia* I (= *C. tentaculata*), has the more primitive state I+IIinc+II (A8). Therefore, the transition should be placed after node 5.4 on the line leading to *Caecilia* II (= *C. gracilis*). If this is done, there is nothing left to support their *Caecilia* clade as separate from the *Gymnopis* clade (nodes 5.3 and 5.4 collapse).

The annular character state I+IIinc (A9), which is the only state linking *Chthonerpeton* and *Typhlonectes compressicaudus* at node 5.7 on their cladogram, is very distant from the last previously mapped state of this character, II+III+II (A6). This last state and another, III+II (A3), are included on their cladogram prior to node 5.6, which links *Chthonerpeton* and *Typhlonectes compressicaudus* with *T. natans* despite the fact that it is more parsimonious to place these two annulation character states after node 5.6 on the line to *T. natans.* When this is done, the transition at node 5.7 from state II (A2) to I+IIinc (A9) through reappearance of primaries is relatively simple. The fact that the annulation changes mapped by LRG onto this part of their cladogram are not the most parsimonious ones, in terms of their own scheme of annular evolution, is obfuscated by their failure to account for the change from II+III+II (A6) to I+IIinc (A9), which would require both reappearance of primaries and loss of tertiaries and posteriormost secondaries. In fact, such a series of transformations is difficult to conceive given LRG's scheme of annular evolution, because, according to their hypothesis, changes always occur anteriorly.

Reanalysis of the data of Lescure et al.—We analyzed the data of LRG (their Table 1) using a parsimony algorithm (PAUP, version 2.4; Swofford, 1985). We followed their polarization of characters, but used additive binary coding for most characters, and we excluded uniquely derived characters from the analysis, because they contain no cladistic information. Where character states were scored with question marks by LRG, we specified them as missing data. Of necessity, two characters, annulation and geographic distribution, were run unordered. The annulation character states used were those included in the "Remarques sur segments succession antério-postérieure" column of the LRG data matrix. Our matrix, thus extracted from LRG, contains 25 polarized binary characters and two unordered multistate characters. Taxa with two states reported for any given character were assigned the most primitive of the reported states. We used the consistency index (CI) to compare the results of each analysis. The CI is the minimum number of steps of character evolution hypothesized to account for all character states, divided by the actual number of steps needed to produce a given cladogram. CI comparisons are valid only between trees based on the same data matrix.

We analyzed the published cladogram of LRG by instructing PAUP to distribute character states on their cladogram so as to minimize homoplasy. Because we did not know whether LRG used all the data listed in their data matrix to generate their tree, or only those characters that they actually mapped onto their tree, we performed both analyses. The CI using all 27 characters is 0.273, and, using only the seven characters mapped onto their tree, the CI is 0.444.

We then used the PAUP algorithm to generate most parsimonious trees using their data and the branch swapping and mulpars options. These options (1) construct an initial Wagner Tree and swap branches to search for more parsimonious cladograms and (2) search for alternative cladograms that are equally as parsimonious as the most parsimonious cladogram found. This procedure does not guarantee that the most parsimonious tree will be found.

Using all 27 characters, PAUP generated a single most parsimonious tree with a CI of 0.380 (Fig. 6). There is very little similarity between this tree and the published tree of LRG (Fig. 5). Repeating the analysis using only the seven characters mapped onto their tree resulted in 300 equally parsimonious trees each with a CI of 0.552. There may have been more than 300 equally parsimonious trees in the data structure, but PAUP has a limit of 300. A strict consensus tree constructed from the 300 trees found by PAUP (Fig. 7) also does not resemble the LRG cladogram and has little resolution.

Further analyses were made using PAUP to generate trees using only the component genera of each of the major "clades" of LRG. We compared the CI's of these trees with those of the published topologies of LRG. In most of these analyses, we were able to use the "alltrees" or "bandb" options of PAUP, which guarantee finding the most parsimonious trees. In all but one case, PAUP generated different topologies, always with higher CI's than those of the trees published by LRG. With the single exception, the tree of LRG was one of five equally parsimonious trees. The results are summarized in Table 4.

We also analyzed the data of LRG with a compatibility algorithm (CLINCH, see

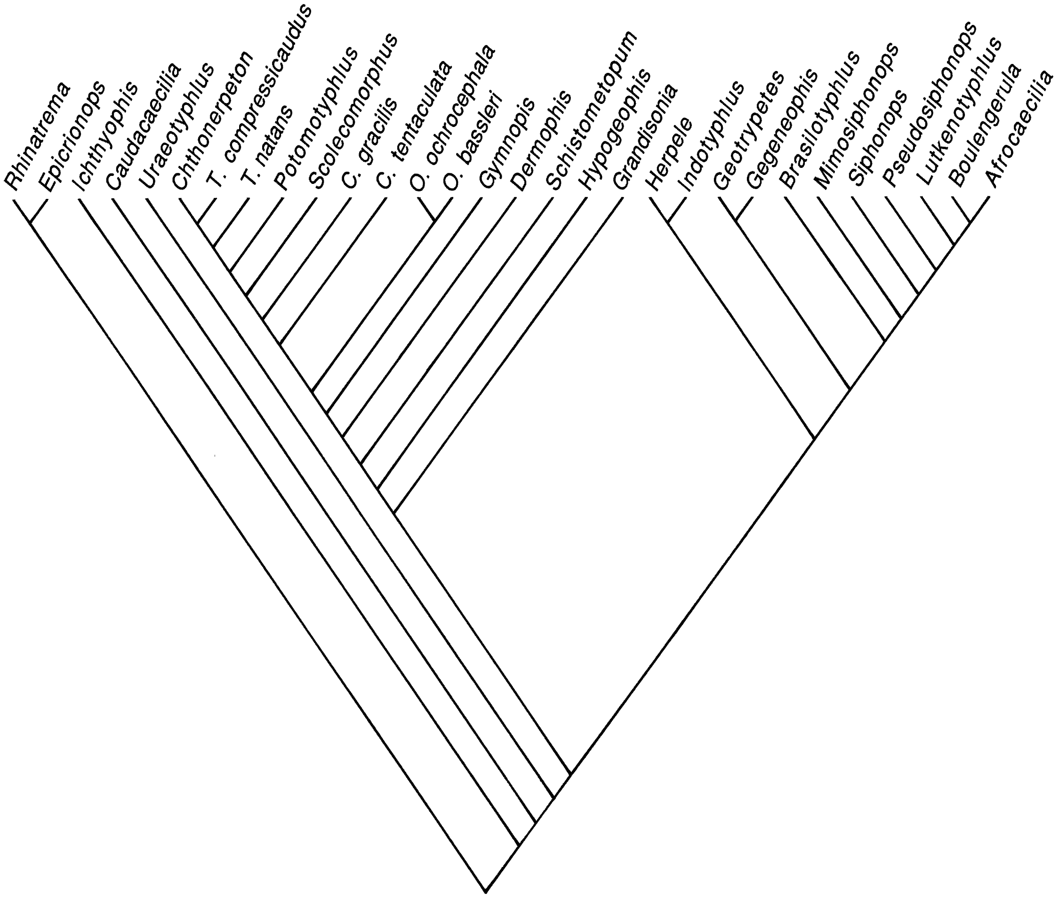

FIG. 6.—Single most parsimonious tree of 27 characters from the data matrix of Lescure et al. (1986) using the PAUP algorithm. CI = 0.380. There is very little similarity between this tree and the tree of Lescure et al. (cf. our Fig. 5).

Estabrook et al., 1977). We could not include the unordered multistate annulation and geographical characters in this analysis, and taxa with missing data were excluded. This left us with 25 binary characters and 23 taxa. CLINCH found a single largest clique of seven compatible characters, which were used to construct the cladogram (Fig. 8). The cladogram has little resolution, and relationships differ significantly from those of the LRG cladogram (Fig. 5).

Our analyses demonstrate that the LRG cladogram is not the best one in terms of their data. This conclusion holds regardless of whether all their characters are used or only the subset of seven characters mapped onto their tree. In addition, we emphasize that these analyses ignore the numerous coding problems associated with their data set, which we addressed in the preceding section. The small size of the largest clique and low consistency indices of the trees generated by PAUP indicate a high level of homoplasy in the characters used by LRG. Thus, we do not accept the single PAUP cladogram based on all the characters of LRG or the CLINCH cladogram as reasonable alternatives to the LRG cladogram. These trees are substantially different from each other, from the LRG cladogram, and from an earlier tree (Nussbaum, 1979), which was based on a compatibility clique containing 31 characters.

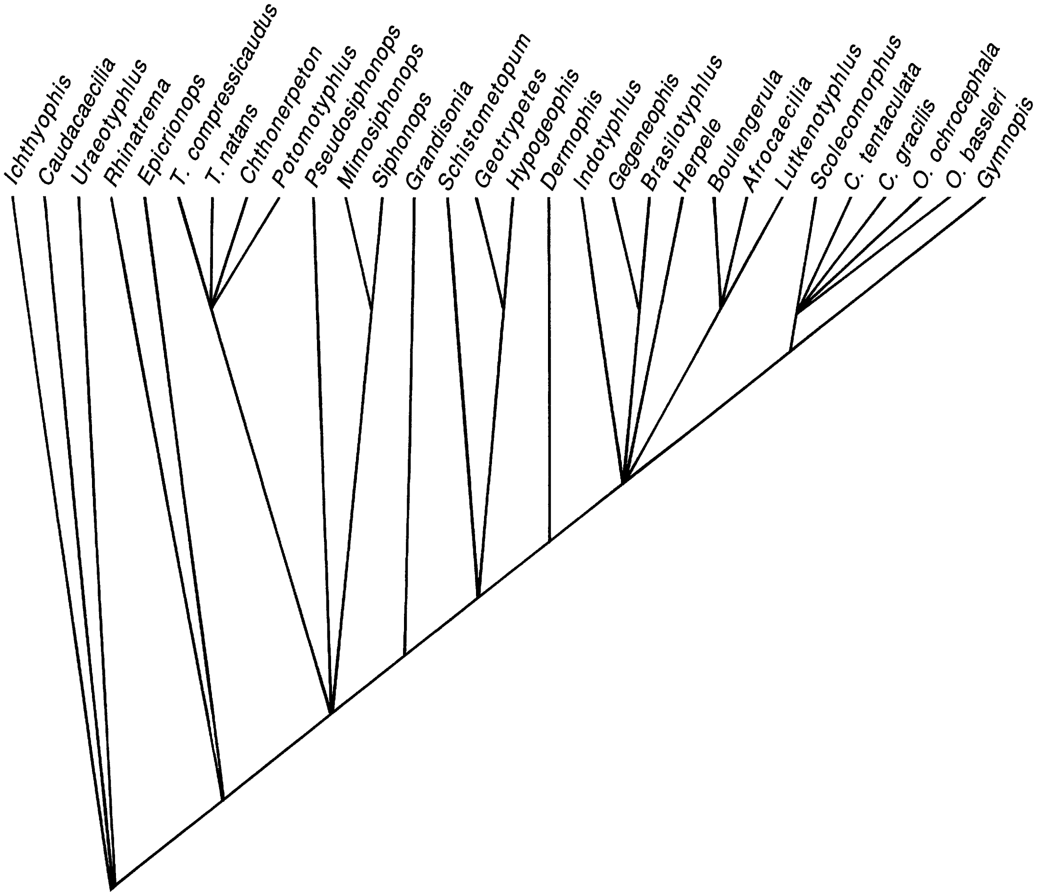

FIG. 7.—Consensus tree generated with the PAUP algorithm using the seven characters that Lescure et al. (1986) mapped onto their tree. PAUP identified 300 equally parsimonious trees using the seven characters, each with a CI of 0.552. This tree differs substantially from their tree (cf. our Fig. 5).

We conclude that the cladogram of LRG is not the one that best fits their data and, therefore, their classification, which is based on their cladogram, is likely to be flawed.

Taxonomic treatment.—LRG proposed 61 new names for a total of 67 suprageneric categories for caecilian classification. Because there are only 154 nominal species of caecilians, their classification yields 2.52 species per suprageneric category. The authors claimed that adherence to cladistic principles dictates the establishment of the new names. However, even if their cladistic analysis were valid, it would not justify the production of such a surfeit of names. Most cladists do not strictly embrace all the Hennigian tenets, and few have gone so far as to name a taxon for every branch point in a cladogram. LRG have gone even further, naming many taxa based on imagined bifurcations that include unknown (extinct?) lineages. Elsewhere, LRG do not adhere strictly to Hennigian principles. They violate the most important Hennigian/cladistic principle that monophyletic clades must be based on shared derived characters and not on shared ancestral characters. For example, their suborder Rhinatrematoidea (and other subordinal taxa on this "clade") is based on the presence of the septomaxilla, an ancestral character state. LRG placed all other caecilians in a second suborder (Caecilioidea) based on the loss of the septomaxilla. Presence or

TABLE 4.—Consistency indices (CI) for branches of the cladogram of Lescure et al. (1986) [LRG] using their characters and topologies compared to CI's of the same sets of taxa and characters generated by PAUP.

Generic group	Consistency indices LRG	Consistency indices PAUP	Number of equally parsimonious trees
1. *Scolecomorphus, Rhinatrema, Epicrionops, Ichthyophis, Caudacaecilia, Uraeotyphlus**	0.758	0.781	2
2. *Typhlonectes compressicaudus, T. natans, Chthonerpeton, Potomotyphlus**	0.700	0.875	3
3. *Caecilia tentaculata, C. gracilis, Gymnopis, Oscaecilia ochrocephala, O. bassleri**	0.846	0.846	5
4. 2 + 3†	0.667	0.737	2
5. *Schistometopum, Herpele, Afrocaecilia, Boulengerula, Indotyphlus, Gegeneophis**	0.771	0.900	1
6. *Siphonops, Mimosiphonops, Pseudosiphonops, Dermophis, Brasilotyphlus, Lutkenotyphlus**	0.694	0.806	1
7. 5 + 6†	0.439	0.644	2
8. 7 + *Grandisonia, Hypogeophis, Geotrypetes*‡	0.386	0.571	11

* Alltrees routine used to find the most parsimonious trees.
† Bandb routine used to find the most parsimonious trees.
‡ Branch swapping routine used; it does not necessarily find the most parsimonious tree.

absence of this small bone is an inadequate basis for establishing the major dichotomy in caecilian evolution.

On several monotypic branches of their cladogram, LRG used hypothetical state changes in annulation to diagnose successively lower ranked taxa. This treatment results in large numbers of redundant taxonomic categories (see Appendix). For example, the genus *Potomotyphlus* is the sole member of a tribe, infrafamily, subfamily, family, and epifamily.

In order to justify diagnosing of ranks within a monotypic clade, it would be necessary to have knowledge of the phyletic sequence of the appearance of novelties in non-branching taxa. Where only a single character state transformation series is involved, the temporal sequence of character changes is indicated by the polarization of the character states. Where two or more transformation series are involved, the sequence of appearance of these novelties in a lineage showing no divergence (cladogenesis) cannot be determined. Yet such knowledge is implied by some of the diagnoses employed by LRG. Many of their diagnoses are also not justifiable, because the diagnoses rest on character state transitions (e.g., the transition from annulation state I to II+I) that were not parsimoniously mapped on their cladogram.

LRG apparently believed that for each node on their cladogram, they must establish a formal name and rank, and that the number of ranks within sister lineages must be equal, even when there has been much divergence (many nodes) in one lineage but no divergence in the sister lineage. We do not believe this procedure is justified. Rather, we believe that only sister lineages can be considered to have equal rank. For example, given the cladogram in Fig. 9, the single lineage terminating in A is of equivalent rank to its sister lineage including B, C, D, E, F, and G; pairs of equivalent rank taxa could also be named at nodes 2, 3, 4, and 5. The only way a subsection of lineage A could be claimed to be of equal rank to any of the pairs of taxa in the sister lineage, or that the taxa uniting B and C could be claimed to be of equal rank to the taxa delimited by nodes 3, 4, and 5, would be if they were the same ages. Only with molecular techniques might one hope to elucidate the relative ages of the clade delimited at node 2 with those at nodes 3, 4, or 5, and any subdivision of the lineage terminating at A would simply result in the naming of arbitrary chronotaxa rather than real biological units.

CAECILIAN CLASSIFICATION

Changes in nomenclature should be proposed only when the supporting evidence is strong enough to assure stability. Clearly,

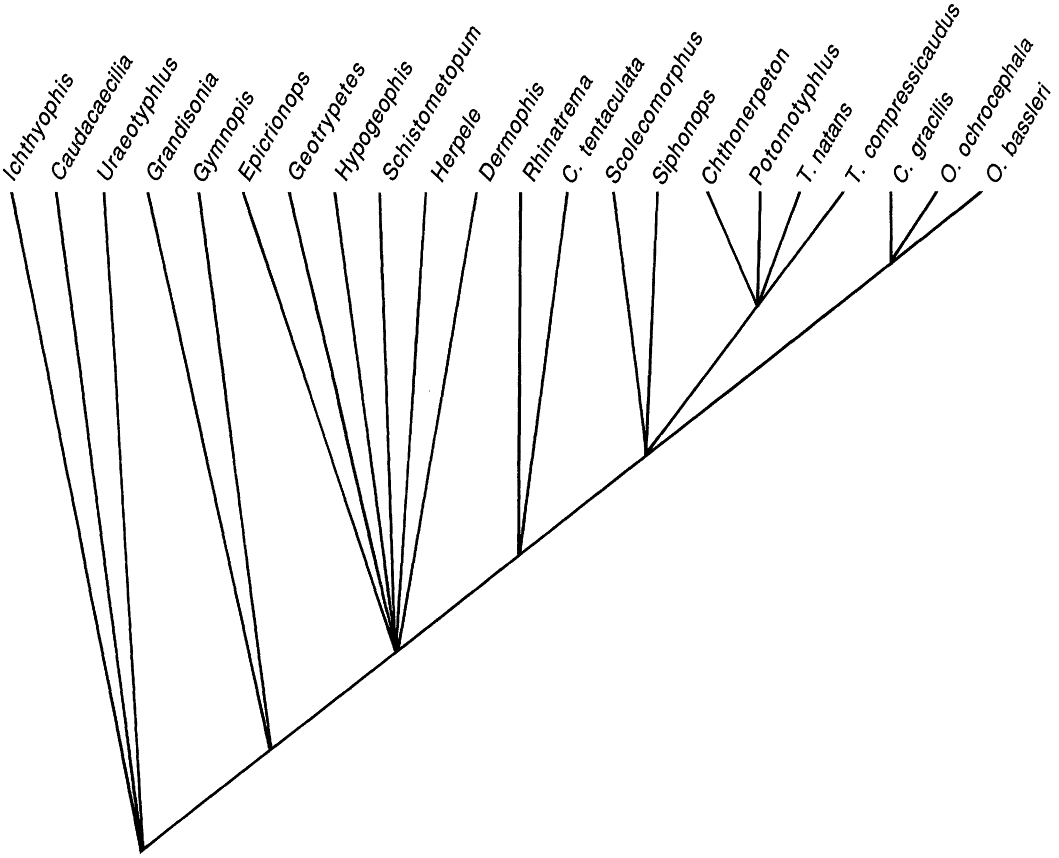

FIG. 8.—Tree resulting from compatibility analysis (CLINCH algorithm) of 25 binary characters and 23 OTU's from Lescure et al. (1986). The tree was generated from the single largest clique, which consisted of seven compatible characters. There is little resolution, and the tree is considerably different from the tree of Lescure et al. (cf. our Fig. 5).

the evidence presented by Laurent (1984, 1986) and LRG do not support their proposed classifications. In fact, most attempts to classify caecilians are based on inadequate data and procedures. Prior to 1968, only a single caecilian family, Caeciliaidae, was recognized, and this family existed almost by default, as systematists largely had ignored caecilians. The first serious attempts to classify caecilians (Taylor, 1968, 1969*a*) apparently were based on phenetics. Although Taylor did not use formal phenetic methods, he clearly grouped taxa by overall similarity. Taylor's two families Ichthyophiidae (modified by Nussbaum, 1977, 1979) and Scolecomorphidae are likely to survive rigorous cladistic analysis simply because they are very distinctive groups. However, Taylor's attempt to group the residual caeciliaid genera using similarity criteria was far less successful and has led to confusion. Taylor (1968) placed one group of four genera with presumed aquatic adaptations in a new family, Typhlonectidae. Even though it is now known that two of these genera are not entirely aquatic, typhlonectids are probably monophyletic (Wilkinson, 1989). But, the phylogenetic relationships of the typhlonectids to the remaining "caeciliaids" are largely unknown, and it is likely that the Caeciliaidae is paraphyletic with regard to the Typhlonectidae. Taylor's (1969*a*) subdivision of the remaining "caeciliaid" genera into two subfamilies, Caeciliainae and Dermophiinae, was strictly arbitrary. He recognized that *Caecilia* and *Oscaecilia* were closely related and placed them in a subfamily of their own leaving the remaining genera in the Dermophiinae. There was no cladistic basis for isolating these two genera, and Taylor could just as well have placed other groups of closely related genera (e.g., *Afrocaecilia* and *Boulengerula* or *Grandisonia* and *Hypogeophis*) in subfamilies.

Taylor's arbitrary treatment of the Caeciliaidae established an unfortunate paradigm that continues to confuse the systematics of the Gymnophiona. The modifications of caecilian classification proposed by Wake and Campbell (1983), Laurent (1984, 1986), and Duellman and Trueb (1986) are all based to some extent on the assumption that the Typhlonectidae, Caeciliainae, and Dermophiinae are meaningful units. An iconoclastic approach is more likely to produce a realistic caecilian phylogeny.

We present below a conservative classification of caecilians that is supported by present knowledge of the group. We suggest that the numerous names of suborders, infraorders, hyperfamilies, superfamilies, epifamilies, subfamilies, infrafamilies, tribes, subtribes, and infratribes (see Appendix) applied by LRG to caecilians not be used. There are three reasons for this suggestion. First, and most important, these taxa are founded largely on erroneous data and incorrect cladistic procedure. Second, we disagree with the practice of applying more than a single rank name to nondivergent lineages. Third, we reject a formal system of ranking taxa such as that used by LRG, which implies equivalence between taxa when no such equivalence necessarily exists.

The relationships among the 23 "caeciliaid" genera are not understood, and most are not adequately diagnosed. Therefore, we do not recognize subdivisions of the Caeciliaidae. The family Typhlonectidae is retained, but this taxon may be lost or modified when a reasonable phylogeny of the Gymnophiona is proposed. We acknowledge that family rank as used here does not indicate equivalence of the families recognized. We use this rank simply as one of convenience for providing stability given the lack of convincing alternative systems and lack of certainty concerning the phylogenetic relationships of caecilian taxa. For the present, we reject Dubois' (1984) suggestion that Ichthyophiidae Taylor, 1968, be replaced by "Epicriidae" Fitzinger, 1843. The latter name was not referred to in the caecilian literature after its first use until 1984, it is based on an objective junior synonym of *Ichthyophis*, and Fitzinger provided no diagnosis for his "Fam. Epicria." The family name Ichthyophiidae is based on a valid generic name and has been used frequently in the recent literature. We are appealing to the International Commission on Zoological Nomenclature to use its plenary powers to suppress Epicriidae in favor of Ichthyophiidae, and, until a decision is made, the Code requires the retention of the commonly used name, Ichthyophiidae.

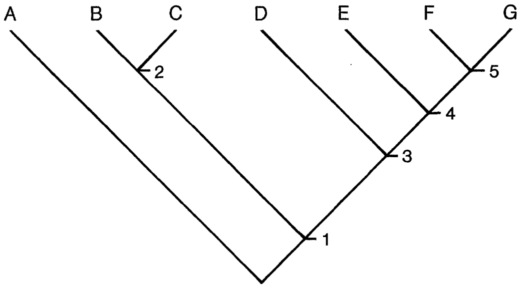

FIG. 9.—Hypothetical cladogram illustrating the problems with assigning equivalent ranks to divergent lineages that are not sister-taxa and with application of multiple ranks within non-branching lineages. See text for discussion.

The diagnoses provided below, especially for the caeciliaid genera, are not intended to distinguish the taxa cladistically. Cladistic diagnoses are not presently possible for most caecilian taxa, and there is no guarantee that all the taxa are valid. We have attempted to make the diagnoses of genera comparable within each family. The caeciliaid diagnoses are mostly composed of a core of standard taxonomic characters, the unique combination of which permits the identification of the genera. The core set consists of characters known for most genera, but some of the characters are unknown for some genera, and we indicate where this is the case. Where other distinctive characters are known, they are listed along with the core set. The species listed for each genus are the nominal species currently recognized.

Order GYMNOPHIONA Rafinesque, 1814

Diagnosis.—Lissamphibia without limbs and girdles; with paired sensory tentacles on the snout; with a dual jaw-closing mechanism consisting of the ancestral component (m. adductor mandibulae pulling up on ramus of lower jaw) and a unique, novel component (m. interhyoideus posterior pulling back and down on retroarticular process of lower jaw); and with an eversible phallodeum in males formed by a portion of the cloacal wall.

Content.—6 families, 34 genera, 154 species.

Distribution.—Pantropical, except for Madagascar and southeast of Wallace's Line. Caecilians have not yet been reported from central, equatorial Africa.

I. Family Rhinatrematidae Nussbaum, 1977

Diagnosis.—Gymnophiona with true tails consisting of a postcloacal segment with vertebrae, myomeres, and complete skin annuli; primary annuli divided by secondary and tertiary grooves; all annular grooves orthoplicate; numerous scales in all annular grooves and in some of the dorsal grooves of the collars; strongly zygokrotaphic skulls with the m. levatores mandibulae passing through the temporal fossae to meet at the midline of the skull along the interparietal suture; maxillopalatine in contact with the quadrate; squamosal widely separated from the frontal, notched posteriorly, the notch opposing a dorsolateral process of the os basale; premaxillae and nasals present as separate bones; mouth terminal; retroarticular process of lower jaw short and not curved dorsally; stapes pierced by stapedial artery; tentacle immediately anterior to or on the anterior edge of eye window; eyes visible externally, in a socket in the maxillopalatine; hyobranchium of adults with only two or three ceratobranchial elements decreasing in size posteriorly, with the larynx situated posterior to the hyobranchium (not enclosed between the two arms of the posteriormost ceratobranchials); hyobranchial elements of larvae mineralized, hyobranchium of metamorphosed individuals cartilaginous.

Content.—2 genera, 9 species.

Distribution.—Northern South America.

1. *Epicrionops* Boulenger, 1883*a*

Type species.—*Epicrionops bicolor* Boulenger, 1883*a*, by monotypy.

Diagnosis.—Rhinatrematids with three ceratobranchial arches in adults; a longitudinal cloacal opening; relatively long tail consisting of more than 11 postcloacal annuli; more than one row of scales per annular groove.

Content.—8 species: *bicolor, columbianus, lativittatus, marmoratus, niger, parkeri, peruvianus, petersi.*

Distribution.—Colombia, Ecuador, Peru, and Venezuela.

2. *Rhinatrema* Duméril and Bibron, 1841

Type species.—*Caecilia bivittata* Guérin-Méneville, 1829, by monotypy.

Diagnosis.—Rhinatrematids with two ceratobranchial arches in adults; transverse cloacal opening; relatively short tail consisting of 11 or fewer postcloacal annuli; a single row of scales per annular groove.

Content.—1 species: *bivittatum.*

Distribution.—Brazil, French Guiana, Guyana, and Surinam.

II. Family Ichthyophiidae Taylor, 1968

Diagnosis.—Gymnophiona with true tails; skull stegokrotaphic; m. levatores mandibulae confined beneath the skull roof, not meeting middorsally; distinct septomaxillae, premaxillae, nasals, and prefrontals; postfrontals distinct or partially or entirely fused to maxillopalatine or squamosal; frontal and squamosal in contact; no dorsolateral process on os basale; no posterior notch in squamosal; quadrate and maxillopalatine broadly separated; stapes pierced by stapedial artery; mouth nearly terminal; retroarticular process of lower jaw curved dorsally; tentacular opening between the eye and nostril, usually closer to the eye and below the eye–nostril line; ceratohyal arch U-shaped; four ceratobranchial arches in adults, arches 3 and 4 fused; larynx positioned between the distal ends of fused arches 3 and 4; all primary annuli subdivided by secondary and tertiary grooves; annular grooves angulate ventrally over most of the body, orthoplicate posteriorly only; numerous scales present in all but perhaps a few anterior annular grooves.

Content.—2 genera, 36 species.

Distribution.—India and Southeast Asia.

Comments.—The two ichthyophiid genera are separated by the presence or absence of splenial teeth. The high probability of independent loss of splenial teeth and the fact that this character is incompatible with other characters of the two genera indicate that one or both of the genera may be polyphyletic.

1. *Caudacaecilia* Taylor, 1968

Type species.—Ichthyophis nigroflavus Taylor, 1960*a*, by original designation.

Diagnosis.—Ichthyophiids without splenial teeth.

Content.—5 species: *asplenia, larutensis, nigroflava, paucidentula, weberi.*

Distribution.—Borneo, Malaya, Philippines, Sri Lanka (based on unpublished records), Sumatra.

2. *Ichthyophis* Fitzinger, 1826

Type species.—Caecilia glutinosa Linnaeus, 1758, by monotypy.

Diagnosis.—Ichthyophiids with splenial teeth.

Content.—31 species: *acuminatus, atricollaris, bannanicus, beddomei, bernisi, biangularis, billitonensis, bombayensis, dulitensis, elongatus, glandulosus, glutinosus, humphreyi, hypocyaneus, javanicus, kohtaoensis, laosensis, malabaricus, mindanaoensis, monochrous, orthoplicatus, paucisulcus, peninsularis, pseudangularis, sikkimensis, singaporensis, subterrestris, sumatranus, supachaii, tricolor, youngorum.*

Distribution.—Southeast Asia, India, Sri Lanka, southern Philippines, western Indo-Australian Archipelago.

Comments.—Taylor (1968:47–48) contradicted himself within a few lines by listing both *Caecilia glutinosa* Linnaeus and *Coecilia hypocyanea* van Hasselt as the generotype of *Ichthyophis.* According to Wake (1985:632), *Coecilia hypocyanea* F. Boie is the generotype of *Ichthyophis.* In fact, Fitzinger (1826:36) listed only a single valid species, *Caecilia glutinosa* Linnaeus, when he erected *Ichthyophis.* Therefore, *C. glutinosa* Linnaeus is the type species of *Ichthyophis* by monotypy.

III. Family Uraeotyphlidae Nussbaum, 1979

Diagnosis.—Gymnophiona with true tails; weakly stegokrotaphic skulls; m. levatores mandibulae confined beneath the skull roof, but may be visible through a small opening between the squamosal and parietal; number and arrangement of skull and lower jaw bones and configuration of the hyobranchium as in the Ichthyophiidae; stapes imperforate; mouth recessed or subterminal; tentacular opening far forward, below nostril; most primary annuli divided by secondary grooves, a few anterior primary annuli may not be subdivided, no tertiary grooves; annular grooves do not completely encircle the body; scales present.

Content.—1 genus, 4 species.

Distribution.—Southern peninsular India.

1. *Uraeotyphlus* Peters, 1879

Type species.—Coecilia oxyura Duméril and Bibron, 1841, by subsequent designation of Noble (1924).

Diagnosis.—As for the family.

Content.—4 species: *malabaricus, menoni, narayani, oxyurus.*

Distribution.—Southern peninsular India.

IV. Family Scolecomorphidae Taylor, 1969*a*

Diagnosis.—Gymnophiona that lack

stapes and foramina ovales; septomaxillae and prefrontals present; no internal process on the pseudoangular bone; no m. levator quadrati; a distinctive hyobranchium in which the flattened distal ends of the fourth branchial arch are connected by a transverse bar above the larynx; all primary annuli undivided.

Content.—2 genera, 5 species.

Distribution.—East and equatorial West Africa.

Comments.—Nussbaum (1985) reported a few vestigial scales in a few posterior annular grooves of one specimen of *Crotaphatrema lamottei.* Scales are otherwise unknown in the family.

1. *Crotaphatrema* Nussbaum, 1985

Type species.—*Herpele bornmuelleri* Werner, 1899, by original designation.

Diagnosis.—Scolecomorphids without temporal fossae; without diastemata between the vomerine and palatine series of teeth; and with the maxillary series of teeth extending further posteriorly than the palatine series.

Content.—2 species: *bornmuelleri, lamottei.*

Distribution.—Cameroon.

Comments.—The few known mature females of this genus contain large, yolky ovarian eggs, suggesting that members of this genus are oviparous (Nussbaum, 1985).

2. *Scolecomorphus* Boulenger, 1883*b*

Type species.—*Scolecomorphus kirkii* Boulenger, 1883*b*, by monotypy.

Diagnosis.—Scolecomorphids with temporal fossae; with diastemata between the vomerine and palatine series of teeth; and with all or most of the palatine teeth posterior to the maxillary teeth.

Content.—3 species: *kirkii, uluguruensis, vittatus.*

Distribution.—Kenya (?), Malawi, and Tanzania.

Comments.—Ovulated eggs of members of this genus are very small, and embryogenesis occurs in the oviducts. The mass of the embryo is much larger than the freshly ovulated egg indicating transfer of nutrients between the female and her oviductal embryos.

V. Family Caeciliaidae
Rafinesque, 1814

Diagnosis.—Gymnophiona with nasal and premaxilla fused; septomaxilla, prefrontal, and postfrontal lost or fused to adjacent bones; small "ectopterygoid" present or not; maxillopalatine widely separated from quadrate; temporal fossae usually absent, if present, m. levatores mandibulae do not pass dorsally through the fossae; M-shaped ceratohyal; larynx between distal ends of fused ceratobranchials 3 and 4; no tail, but a pseudotail may be present; some, none, or all primary annuli subdivided by secondary grooves; no tertiary grooves; scales present or absent; external gills of embryos in three rami (one ramus may be reduced or vestigial), not fused into long sac-like placentae.

Content.—23 genera and 88 species.

Distribution.—Tropical Central and South America, equatorial East and West Africa, islands of the Gulf of Guinea, Seychelles Archipelago, and India.

Comments.—Moore et al. (1984) pointed out that the family-group name Caeciliidae Gray, 1825 (Amphibia, Gymnophiona) is a senior homonym of Caeciliidae Kolbe, 1880 (Insecta, Psocoptera), and recommended that the International Commission on Zoological Nomenclature use its plenary powers to remove the homonymy by a spelling emendation of the insect name. Different proposals to remove the homonymy were subsequently published (summarized by Dubois, 1986). The International Commission on Zoological Nomenclature ruled (BZN, 1987, Opinion 1462, p. 263) that the homonymy be removed by changing the amphibian name from Caeciliidae Gray, 1825, to Caeciliaidae Rafinesque[-Schmaltz], 1814. We disagree with this ruling for several reasons. First, Rafinesque did not list any genus of caecilian under his family name "Cecilinia" and gave only an Italian vernacular name "Ceciliani." Therefore, it cannot be inferred, as was done by Dubois (1986), that Rafinesque's usage was based on an emendation of *Caecilia* (see article 33(b)(i) of the Code). The family name Ceciliidae Rafinesque must be considered to be based on an incorrect subsequent spelling, and, as such, it is not an available name (article 33(c) of the Code). Second, because neither description of, nor generic content of, nor other indications of the Cecilinia were specified by Rafinesque, this family-group name is a nomen nudum (article 12 of the Code) and is, thus, not available. The Commission did not address these issues in its Opinion. Regardless of these problems, we are required for the present to use the name recommended by the Commission.

1. *Afrocaecilia* Taylor, 1968

Type species.—*Boulengerula taitanus* Loveridge, 1935, by original designation.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid covered by frontals; splenial teeth present; no secondary grooves; no scales; tentacular opening nearer to eye than to external naris; an unsegmented terminal shield; no narial plugs; no diastema between the vomerine and palatine series of teeth, or sometimes a weak diastema is present; a vertical keel on the end of the terminal shield.

Content.—3 species: *changamwensis, taitana, uluguruensis.*

Distribution.—Kenya and Tanzania.

Comments.—*Afrocaecilia* is the obvious sister genus of *Boulengerula.* In addition to overall similarity, the two genera share the derived character of a vertical keel on the terminal shield. They are also similarly distributed geographically.

2. *Boulengerula* Tornier, 1897

Type species.—*Boulengerula boulengeri* Tornier, 1897, by monotypy.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid exposed between frontals; no splenial teeth; no secondary grooves; no scales; tentacular opening nearer to eye than to external naris; an unsegmented terminal shield; no narial plugs; a strong diastema between the vomerine and palatine teeth; a vertical keel on the end of the terminal shield.

Content.—1 species: *boulengeri.*

Distribution.—Tanzania.

Comments.—See comments under *Afrocaecilia.*

3. *Brasilotyphylus* Taylor, 1968

Type species.—*Gymnopis braziliensis* Dunn, 1945, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid covered by frontals; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no terminal shield; a very short series of premaxillary-maxillary teeth, not extending posterior of the choanae; a strong diastema between the vomerine and palatine teeth; a vertical keel on the body terminus.

Content.—1 species: *braziliensis.*

Distribution.—Brazil.

Comments.—Taylor (1968, 1971) pointed out a few similarities among *Brasilotyphlus, Afrocaecilia,* and *Boulengerula,* the most striking of which is the presence of a vertical keel on the body terminus of all three genera. Taylor (1971:183) believed, however, that "there is no apparent reason to suppose that *Brasilotyphlus* is related closely to either of the mentioned African genera." We disagree and think there is a distinct possibility that these three genera are monophyletic and may represent a trans-Atlantic link within the family.

4. *Caecilia* Linnaeus, 1758

Type species.—*Caecilia tentaculata* Linnaeus, 1758, by subsequent designation of Dunn (1942).

Diagnosis.—Caeciliaids with eye in a socket, not covered with bone; no temporal fossae; mesethmoid exposed between frontals; splenial teeth present; secondary grooves present or absent; scales present or absent; subdermal scales present or absent; tentacular opening directly below external naris, closer to naris than to eye; unsegmented terminal shield present or not; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel; teeth relatively few and large, usually replaced alternately in groups; vomeropalatine tooth row displaced posteriorly, not parallel to premaxillary-maxillary tooth row, diverging from the latter anteriorly forming an angle where the two rows meet rather than a semicircle.

Content.—32 species: *abitaguae, albiventris, antioquiaensis, armata, attenuata, bokermanni, caribea, corpulenta, crassisquama, degenerata, disossea, dunni, flavopunctata, gracilis, guntheri, inca, leucocephala, marcusi, mertensi, nigricans, occidentalis, orientalis, pachynema, perdita, pressula, subdermalis, subnigricans, subterminalis, tentaculata, tenuissima, thompsoni, volcani.*

Distribution.—Eastern Panama and northern South America.

Comments.—*Caecilia* is the largest and most complex genus of caecilians. Some species are almost certainly more closely related to species of the genus *Oscaecilia* than they are to other species of *Caecilia.* For example, some specimens of *C. gracilis* have the eye under bone as in *Oscaecilia*, and other specimens have the eye in a socket as in *Caecilia.*

5. *Dermophis* Peters, 1879

Type species.—*Siphonops mexicanus* Duméril and Bibron, 1841, by subsequent designation of Noble (1924).

Diagnosis.—Caeciliaids with eye in socket, not covered with bone; no temporal fossae; mesethmoid covered or exposed; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—3 species: *mexicanus, oaxacae, parviceps.*

Distribution.—Southern Mexico south to northwestern Colombia.

Comments.—Savage and Wake (1972) synonymized seven species of *Dermophis* with other species of *Dermophis.* Our unpublished data indicate that some of the synonymized species, e.g., *D. gracilior,* are valid.

6. *Gegeneophis* Peters, 1879

Type species.—*Epicrium carnosum* Beddome, 1870, by monotypy.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening midway between eye and external naris; no unsegmented terminal shield; small, bead-like narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—3 species: *carnosus, fulleri, ramaswamii.*

Distribution.—India.

7. *Geotrypetes* Peters, 1880

Type species.—*Caecilia seraphini* Duméril, 1859, by monotypy.

Diagnosis.—Caeciliaids with eye in socket, not covered with bone; temporal fossae present; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present on tongue; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—3 species: *angeli, pseudoangeli, seraphini.*

Distribution.—Equatorial West Africa.

Comments.—Wake (1987) recently subdivided *Geotrypetes*; see comments under *Sylvacaecilia.* Wake (1987) also indicated that *G. seraphini* may not have narial plugs. We have observed them in numerous specimens of *G. seraphini* and in other species of the genus, although they are often small and may be difficult to observe because of poor preservation.

8. *Grandisonia* Taylor, 1968

Type species.—*Hypogeophis alternans* Stejneger, 1893, by original designation.

Diagnosis.—Caeciliaids with eye in socket, not covered with bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present on more than one-half of the primary annuli, may be missing on some anterior primaries; scales present; tentacular opening variable in position, may be closer to external naris than to eye, nearly midway between eye and external naris, or slightly closer to eye; no unsegmented terminal shield; narial plugs present on tongue; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—5 species: *alternans, brevis, diminutiva, larvata, sechellensis.*

Distribution.—Seychelles Archipelago.

Comments.—There is good evidence based on karyology that the three Seychellean genera, *Grandisonia, Hypogeophis,* and *Praslinia,* are monophyletic (Nussbaum and Ducey, 1988). One of the six named species of *Grandisonia* (*G. diminutiva* Taylor) is invalid (Nussbaum, unpublished).

9. *Gymnopis* Peters, 1874

Type species.—*Gymnopis multiplicata* Peters, 1874, by monotypy.

Diagnosis.—Caeciliaids with eye covered by bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—2 species: *multiplicata, syntrema.*

Distribution.—Guatemala south to Panama.

Comments.—*Gymnopis,* the probable sister genus of *Dermophis,* has had a confused taxonomic history. Both *Copeotyphlinus* Taylor and *Minascaecilia* Wake and Campbell are considered by Nussbaum (1988) to be junior synonyms of *Gymnopis.*

10. *Herpele* Peters, 1879

Type species.—*Caecilia squalostoma* Stutchbury, 1834, by monotypy.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid slightly visible or not dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—2 species: *multiplicata, squalostoma.*

Distribution.—Equatorial West Africa, including the Gulf of Guinea island, Bioko (Fernando Po).

11. *Hypogeophis* Peters, 1879

Type species.—*Coecilia rostrata* Cuvier, 1829, by subsequent designation of Parker (1958).

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid not exposed dorsally; secondary grooves present, confined to posterior third or less of body; scales present; tentacular opening far forward, closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *rostratus.*

Distribution.—Seychelles Archipelago.

Comments.—See comments under *Grandisonia.*

12. *Idiocranium* Parker, 1936

Type species.—*Idiocranium russelli* Parker, 1936, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid widely exposed dorsally; frontals reduced, not in contact with maxillaries; nasal in contact with squamosal; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to external naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *russelli.*

Distribution.—Cameroon.

13. *Indotyphlus* Taylor, 1960*b*

Type species.—*Indotyphlus battersbyi* Taylor, 1960*b*, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; small narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *battersbyi.*

Distribution.—India, western Ghats.

14. *Lutkenotyphlus* Taylor, 1968

Type species.—Siphonops brasiliensis Lütken, 1852, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; dorsal exposure of mesethmoid unknown; no splenial teeth; no secondary grooves; no scales; tentacular opening closer to eye than to external naris; an unsegmented terminal shield; no narial plugs; premaxillary-maxillary series of teeth short, not extending posterior to the choanae; no diastema between the vomerine and palatine teeth; a diastema between the anterior ends of the two series of vomerine teeth in adults; no terminal keel.

Content.—1 species: *brasiliensis.*

Distribution.—Brazil, Paraguay.

Comments.—The status of this genus was reviewed by Nussbaum (1986*b*).

15. *Microcaecilia* Taylor, 1968

Type species.—Dermophis albiceps Boulenger, 1882, by original designation.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid not exposed dorsally; no splenial teeth; secondary grooves usually present, absent in one species; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vormerine and palatine teeth; no terminal keel.

Content.—5 species: *albiceps, rabei, supernumeraria, taylori, unicolor.*

Distribution.—Ecuador, French Guiana, Guyana, Surinam, Venezuela.

Comments.—Nussbaum and Hoogmoed (1979) redefined this genus.

16. *Mimosiphonops* Taylor, 1968

Type species.—Mimosiphonops vermiculatus Taylor, 1968, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; presence or absence of temporal fossae and dorsal exposure of mesethmoid unknown, probably as in *Siphonops*; splenial teeth present; no secondary grooves; no scales; tentacular opening nearly equidistant between eye and external naris; an unsegmented terminal shield; no narial plugs; a diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *vermiculatus.*

Distribution.—southern Brazil.

17. *Oscaecilia* Taylor, 1968

Type species.—Caecilia ochrocephala Cope, 1866, by original designation.

Diagnosis.—Caeciliaids with eye under bone; no temporal fossae; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; subdermal scales present or absent; tentacular opening directly below external naris, closer to naris than to eye; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel; teeth relatively few and large, replaced alternately in groups; vomeropalatine tooth row displaced posteriorly, not parallel to premaxillary-maxillary tooth row, diverging from the latter anteriorly forming an angle where the two rows meet rather than a semicircle.

Content.—8 species: *bassleri, elongata, equatorialis, hypereumeces, koepckeorum, ochrocephala, polyzona, zweifeli.*

Distribution.—Eastern Panama, northern South America.

Comments.—Differs from *Caecilia* only in that the eye is under bone, but see comments under *Caecilia.*

18. *Parvicaecilia* Taylor, 1968

Type species.—Gymnopis nicefori Barbour, 1924, by original designation.

Diagnosis.—Caeciliaids with eye in socket, not under bone; presence or absence of a temporal fossae and dorsal exposure of mesethmoid unknown; no splenial teeth; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; premaxillary-maxillary series of teeth short, not extending posterior to the choanae; no diastema between the vomerine and palatine teeth; no terminal keel.

Content.—2 species: *nicefori, pricei.*

Distribution.—Colombia.

19. *Praslinia* Boulenger, 1909

Type species.—*Praslinia cooperi* Boulenger, 1909, by monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; teeth small, uniform in size, more than 50 per row, except for splenials; mouth terminal; secondary grooves present; scales present; tentacular opening adjacent to anterior edge of eye; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *cooperi.*

Distribution.—Seychelles Archipelago.

Comments.—See comments under *Grandisonia.*

20. *Pseudosiphonops* Taylor, 1968

Type species.—*Pseudosiphonops ptychodermis* Taylor, 1968, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; presence or absence of temporal fossae and dorsal exposure of mesethmoid unknown, probably as in *Siphonops*; no splenial teeth; no secondary grooves; no scales; tentacular opening closer to external naris than to eye; an unsegmented terminal shield; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *ptychodermis.*

Distribution.—Brazil.

21. *Schistometopum* Parker, 1941

Type species.—*Dermophis gregorii* Boulenger, 1894, by original designation.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—5 species: *brevirostre, ephele, garzonheydti, gregorii, thomense.*

Distribution.—Kenya, Tanzania, Gulf of Guinea islands.

22. *Siphonops* Wagler, 1828

Type species.—*Caecilia annulata* Mikan, 1820, by monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid exposed dorsally; no splenial teeth; no secondary grooves; no scales; tentacular opening closer to eye than to external naris; an unsegmented terminal shield; no narial plugs; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—5 species: *annulatus, hardyi, insulanus, leucoderus, paulensis.*

Distribution.—Argentina, Bolivia, Brazil, Colombia, Ecuador, Guyana, Paraguay, Peru, and probably Uruguay.

23. *Sylvacaecilia* Wake, 1987

Type species.—*Geotrypetes grandisonae* Taylor, 1970, by original designation and monotypy.

Diagnosis.—Caeciliaids with eye in socket, not under bone; no temporal fossae; mesethmoid not exposed dorsally; splenial teeth present; secondary grooves present; scales present; tentacular opening closer to eye than to external naris; no unsegmented terminal shield; narial plugs present; no diastema between vomerine and palatine teeth; no terminal keel.

Content.—1 species: *grandisonae.*

Distribution.—Ethiopia.

Comments.—Taylor (1970) described the first known caecilian from Ethiopia as *Geotrypetes grandisonae* and suggested that this new form may not be a *Geotrypetes.* Wake (1987), following Taylor's lead, placed *G. grandisonae* in the new, monotypic genus *Sylvacaecilia* and suggested that *Sylvacaecilia* may be the sister taxon to a group comprising *Geotrypetes* and *Schistometopum.*

VI. Family Typhlonectidae
Taylor, 1968

Diagnosis.—Gymnophiona with the same number and arrangement of skull bones as caeciliaids, but "ectopterygoid" never present; mesethmoid always covered by frontals; temporal fossae present; eye never under bone; splenial teeth present; teeth monocuspid; tentacle small; choanae large with well developed valves; narial plugs present; relatively large cloacal disk; viviparous; embryonic gills fused into a large, sac-like structure on each side; undivided primary annuli only, or some primary annuli with pseudosecondary grooves.

Content.—4 genera and 12 species.

Distribution.—South America.

Comments.—The genus *Pseudotyphlonectes* of Lescure et al. (1986) is a junior synonym of *Typhlonectes* (Wilkinson, 1989). Wake (1975) reported a few vestigial scales in a few specimens of *Typhlonectes compressicaudus.* Otherwise, scales are unknown among typhlonectids.

1. *Chthonerpeton* Peters, 1879

Type species.—*Siphonops indistinctus* Reinhardt and Lütken, 1861, by monotypy.

Diagnosis.—Typhlonectids with the tentacular aperture intermediate in position between eye and external naris; tentacular groove open in adults, not covered with bone; fetal gills attaching laterally to the nuchal region, the two gill bases well separated dorsally; no lateral compression of the body; no middorsal ridge or free fold (fin); left lung rudimentary; external naris ovate; choanal valve aperture along entire length of valve; cloacal disk subcircular; semiaquatic habit.

Content.—6 species: *braestrupi, exile, indistinctum, onorei, perissodus, viviparum.*

Distribution.—Northern Argentina, Brazil, Ecuador, Uruguay.

Comments.—We consider three species, *C. corrugatum, C. erugatum, C. hellmichi,* to be junior synonyms of *C. indistinctum* (Nussbaum and Wilkinson, 1987).

2. *Nectocaecilia* Taylor, 1968

Type species.—*Chthonerpeton petersii* Boulenger, 1882, by original designation.

Diagnosis.—Typhlonectids with the tentacular aperture close behind external naris; tentacular groove partially roofed by bone in adults; fetal gills attaching dorsolaterally, the two gill bases slightly separated middorsally; no lateral compression of the body; no dorsal free fold or ridge; left lung well developed; subcircular cloacal disk; external naris subtriangular; choanal valve aperture along entire length of the valve; semiaquatic habit.

Content.—2 species: *haydee, petersii.*

Distribution.—Venezuela.

Comments.—Of the five previously recognized species, *N. cooperi,* is a junior synonym of *Typhlonectes natans, N. fasciata* is a *Chthonerpeton, N. ladegesi* is a *Typhlonectes,* and the validity of *N. haydee* is doubtful (Wilkinson, 1989). The above diagnosis of *Nectocaecilia* is based on the discovery that *Nectocaecilia petersii,* the generotype, is probably the only valid species of the genus.

3. *Potomotyphlus* Taylor, 1968

Type species.—*Caecilia kaupii* Berthold, 1859, by original designation.

Diagnosis.—Typhlonectids with the tentacular aperture close behind external naris; tentacular groove partially roofed with bone in adults; fetal gills unknown, predicted to be as in *Typhlonectes*; body laterally compressed; middorsal free fold or ridge present; left lung well developed, dilated, much wider than right lung; head small relative to body; cloacal disk subcircular posteriorly with a narrower anterior portion; external naris subtriangular; choana extremely large; choanal valve with aperture restricted to a small funnel-like flap; aquatic habit.

Content.—1 species: *kaupii.*

Distribution.—Amazonian Brazil, Ecuador, French Guiana, Peru, Venezuela.

Comments.—The family Potamotyphlidae, created by Lescure et al. (1986) for *Potomotyphlus,* is not recognized here. *Potomotyphlus melanochrus* is a junior synonym of *P. kaupii.*

4. *Typhlonectes* Peters, 1879

Type species.—*Caecilia compressicauda* Duméril and Bibron, 1841, by subsequent designation of Dunn (1942).

Diagnosis.—Typhlonectids with the

tentacular aperture close behind external naris; tentacular groove partially roofed by bone in adults; fetal gills attaching dorsally, the two gill bases fused dorsally with no separation; body laterally compressed, at least posteriorly, in adults; a middorsal ridge or free fold present; left lung well developed; cloacal disk subcircular; external naris subtriangular; choanal valve aperture along full length of valve, a single specimen known with no choanal valve opening; aquatic habit.

Content.—3 species: *compressicaudus, eiselti, natans.*

Distribution.—Colombia, Peru, Venezuela, French Guiana, Guyana, Amazonian Brazil. Nussbaum and Hoogmoed (1979) summarized evidence that *T. compressicaudus* occurs in Surinam. The latter species should be expected in Ecuador as well.

Comments.—Only three of the six nominal species, *T. compressicaudus, T. eiselti,* and *T. natans* are of certain validity (Wilkinson, 1989), and one of them (*T. eiselti*) probably represents an undescribed typhlonectid genus.

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APPENDIX

Classification of Lescure et al., 1986

- Order Gymnophiona
  - Suborder Rhinatrematoidea
    - Infraorder Rhinatrematidei
      - Hyperfamily Rhinatrematoides
        - Superfamily Rhinatrematoidea*
          - Epifamily Rhinatrematoidae*
            - Family Rhinatrematidae*
              - Genus *Epicrionops*
              - Genus *Rhinatrema*
      - Hyperfamily Scolecomorphoides
        - Superfamily Scolecomorphoidea*
          - Epifamily Scolecomorphoidae*
            - Family Scolecomorphidae*
              - Genus *Scolecomorphus*
                - Group *kirkii*
                - Group *lamottei*
    - Infraorder Epicriidei
      - Hyperfamily Epicrioides*
        - Superfamily Epicriodea*
          - Epifamily Epicriodae*
            - Family Epicriidae
              - Subfamily Epicriinae*
                - Infrafamily Epicriilae*
                  - Genus *Caudacaecilia*
                  - Genus *Ichthyophis*
            - Family Uraeotyphlidae
              - Subfamily Uraeotyphlinae*
                - Infrafamily Uraeotyphlilae*
                  - Genus *Uraeotyphlus*
  - Suborder Caecilioidea
    - Infraorder Caeciliidei
      - Hyperfamily Caecilioides
        - Superfamily Caeciliodea*
          - Epifamily Caeciliodae
            - Family Caeciliidae*
              - Subfamily Caeciliinae*
                - Infrafamily Caeciliilae
                  - Genus *Caecilia*
                    - Group *tentaculata*
                    - Group *gracilis*
                - Infrafamily Gymnopilae
                  - Genus *Gymnopis*
          - Epifamily Oscaecilioidae
            - Family Oscaeciliidae*
              - Genus *Oscaecilia*
                - Group *ochrocephala*
                - Group *bassleri*
      - Hyperfamily Typhlonectoides
        - Superfamily Typhlonectoidea*
          - Epifamily Typhlonectoidae
            - Family Typhlonectidae*
              - Subfamily Typhlonectinae*
                - Infrafamily Typhlonectilae*
                  - Supertribe Typhlonectoidi*
                    - Tribe Typhlonectini
                      - Genus *Chthonerpeton*
                      - Genus *Typhlonectes*

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* Indicates a redundant category.

Tribe Pseudotyphlonectini
Genus *Pseudotyphlonectes*
Epifamily Potamotyphloidae
Family Potamotyphlidae*
Subfamily Potamotyphlinae*
Infrafamily Potamotyphlilae*
Tribe Potamotyphlini*
Genus *Potamotyphlus*
Infraorder Siphonopidei
Hyperfamily Siphonopoides*
Superfamily Siphonopoidea*
Epifamily Siphonopoidae
Family Siphonopidae*
Subfamily Siphonopinae*
Infrafamily Siphonopilae
Supertribe Siphonopoidi
Tribe Siphonopini
Subtribe Siphonopiti
Genus *Mimosiphonops*
Genus *Siphonops*
Subtribe Pseudosiphonopiti
Infratribe Pseudosiphonopili
Genus *Lutkenotyphlus*
Genus *Pseudosiphonops*
Infratribe Brasilotyplili
Genus *Brasilotyphlus*
Tribe Dermophiini
Genus *Dermophis*
Supertribe Herpeloidi
Tribe Herpelini
Subtribe Herpeliti
Genus *Herpele*
Genus *Schistometopum*
Subtribe Afrocaeciliiti
Genus *Afrocaecilia*
Genus *Boulengerula*
Tribe Indotyphlini
Genus *Gegeneophis*
Genus *Indotyphlus*
Infrafamily Grandisoniilae
Genus *Grandisonia*
Epifamily Geotrypetoidae
Family Geotrypetidae*
Genus *Geotrypetes*
Genus *Hypogeophis*

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