THE TAXONOMIC STATUS OF THE CAECILIAN GENUS *URAEOTYPHLUS* PETERS

By Ronald A. Nussbaum

INTRODUCTION

The caecilian genus *Uraeotyphlus* contains four species (*malabaricus, menoni, narayani, oxyurus*) confined to southern peninsular India. Taylor (1968) assigned *Uraeotyphlus* to the family Caeciliidae, at the same time noting the possibility that the genus belonged to the family Ichthyophiidae. Taylor (1969a,b) later examined a skull of *U. oxyurus* (MCZ 9484) and concluded that *Uraeotyphlus* was a caeciliid assignable to the subfamily Dermophiinae. Taylor's (1969b) description of the skull of *U. oxyurus* differs, however, from earlier descriptions of *U. oxyurus* and *U. malabaricus* (Peters, 1881; Parker, 1927) and *U. narayani* (Ramaswami, 1941). These conflicting observations led me to reexamine Taylor's material (MCZ 9484) as well as two freshly prepared skulls of *U. narayani* (UMMZ 139811, 146887). In addition, I have examined other aspects of the morphology of *Uraeotyphlus* and have compared the genus to 12 other caecilian genera, representing all described families of caecilians and all major land masses where caecilians occur. The results show that Taylor's (1969b) description of the skull of *U. oxyurus* is erroneous and that *Uraeotyphlus* cannot be assigned to any family based on current family descriptions.

In this paper, I transfer *Uraeotyphlus* from the family Caeciliidae to the family Ichthyophiidae, describe a new subfamily to receive *Uraeotyphlus*, and redefine the family Ichthyophiidae.

FAMILY CHARACTERISTICS

The contrasting features of the Caeciliidae and Ichthyophiidae are listed in Table 1. Taylor (1969a) gave other characteristics for these two families, but only those compared in Table 1 are constant. In brief, ichthyophiids are tailed caecilians which have retained many of the bony elements of the primitive amphibian skull, and caeciliids are tailless caecilians with certain skull bones lost or fused to adjacent bones.

TABLE 1

COMPARISON OF CAECILIIDAE AND ICHTHYOPHIIDAE

Character	Caeciliidae	Ichthyophiidae
1. Septomaxillae	missing or fused to adjacent elements	present
2. Nasals and pre-maxillae	fused (= nasopremaxillae)	present as separate elements
3. Prefrontals	missing or fused to adjacent elements	present
4. Postfrontals	missing or fused to adjacent elements	present[1]
5. Tail	absent[2]	present

[1] Sometimes partially or completely fused to the squamosal or maxillopalatine (see text).
[2] Reported exceptions are *Uraeotyphlus, Copeotyphlinus,* and two species of *Grandisonia* (see text).

The exceptional caeciliids with tails are *Uraeotyphlus, Copeotyphlinus* and diminutive species of *Grandisonia*. The discrepancy associated with *Uraeotyphlus* disappears with transference to the Ichthyophiidae. *Copeotyphlinus* is a taxonomic curiosity described by Taylor (1968) in spite of the fact that not a single

specimen is known to exist. I will argue elsewhere (Nussbaum, in press) that the description of *Copeotyphlinus* is based on a caeciliid, probably *Caecilia* or *Oscaecilia*, with a false tail. Taylor (1968) stated that *Grandisonia brevis* and *G. diminutiva* have rudimentary tails. However, the "tails" of these two species are small, fleshy postanal protuberances which lack complete annuli. Therefore it is not likely that these forms have true tails as defined by the presence of postanal vertebrae.

CHARACTERISTICS OF URAEOTYPHLUS

SKULL MORPHOLOGY.—Ramaswami (1941) described the skull of *U. narayani* in detail and compared it to the skulls of other caecilian genera. He showed that this species has distinct septomaxillae, prefrontals, and postfrontals (= orbitals of some authors) and that the nasals and premaxillae are not fused to form paired nasopremaxillae. I have confirmed these observations on two specimens of *U. narayani* (Fig. 1).

The skulls of *U. malabaricus* and *U. oxyurus* were examined by Parker (1927) who stated that both have distinct pre- and post-frontals. Parker did not mention the condition of the septo-maxillae and the nasal-premaxilla articulation, but suggested that *Uraeotyphlus* may be closely related to *Ichthyophis*.

According to Peters (1881), the skull of *U. oxyurus* is similar in general morphology to the skull of *Ichthyophis*, having separate septomaxillae and distinct pre- and postfrontals. This report conflicts with Taylor (1969b), who stated (p. 620): "The pre-frontals and septomaxillae are not present and the premaxillae and nasals are fused, forming the large nasopremaxillae." Taylor's observations were based on a single dried skull of *U. oxyurus* (MCZ 9484) which I have examined. The skull was prepared by handpicking and is considerably damaged; only the right side is reasonably intact. The right septomaxilla is missing, but a notch is present in its normal position, which suggests this tiny element was lost during preparation. The right prefrontal is clearly present and there is no fusion between the nasal and premaxilla, contrary to Taylor.

GLOSSAL SKELETON.—The glossal skeleton of *Uraeotyphlus* is similar to that of the ichthyophiid genera *Ichthyophis* and *Cau-dacaecilia* and is unlike that of any known caeciliid. The cerato-hyals (CH) of *Uraeotyphlus* and ichthyophiids meet in the midline
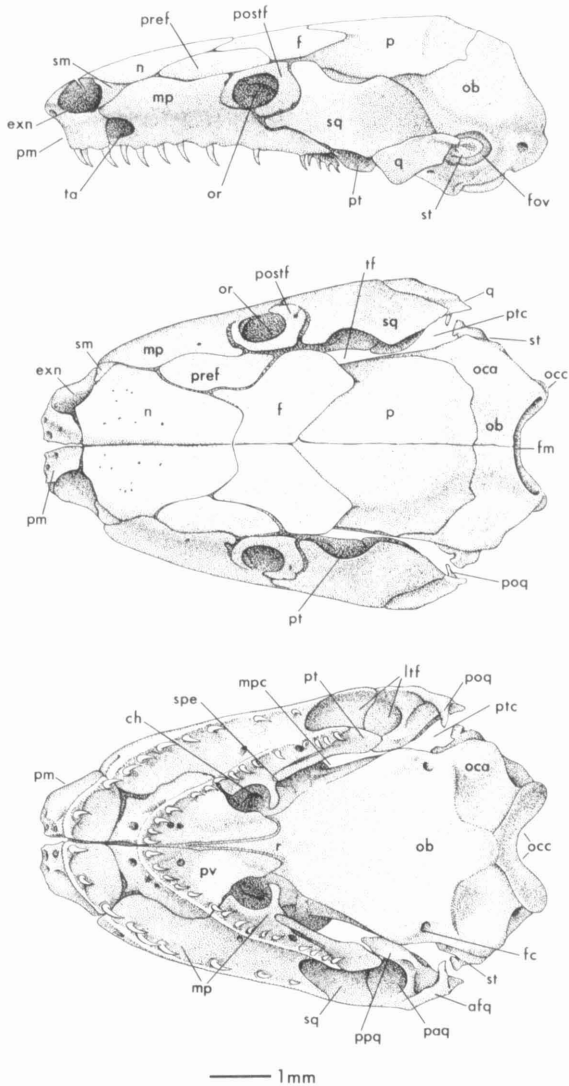
FIG. 1. Lateral, dorsal, and ventral views of the skull of *Uraeotyphlus narayani* (UMMZ-146887). *afq.* articular facet of quadrate; *ch.*, choana; *exn.*, external naris; *f.*, frontal; *fc.*, carotid foramen; *fm.*, foramen magnum; *fov.*, foramen ovale; *ltf.*, lower temporal fossa; *mp.*, maxillopalatine; *mpc.*, mediopalatinal cavity; *n.*, nasal; *ob.*, os basale; *oca.*, otic capsule; *occ.*, occipital condyle; *p.*, parietal; *paq.*, processus ascendens; *pm.*, premaxilla; *postf.*, postfrontal; *poq.*, processus oticus of quadrate; *ppq.*, processus pterygoideus of quadrate; *pref.*, prefrontal; *pt.*, pterygoid; *ptc.*, petro-occipital cavity; *pv.*, prevomer; *q.*, quadrate; *r.*, parasphenoidal rostrum of os basale; *sm.*, septomaxilla; *spe.*, sphenethmoid; *sq.*, squamosal; *st.*, stapes; *ta.*, tentacular aperture; *tf.*, temporal fossa.

to form a V-shaped structure which is joined to the first ceratobranchials (CB_1) via a distinct first basibranchial (BB_1) (Fig. 2). The posteriormost ventral arch of caecilians is thought to represent a fusion of ceratobranchials three and four ($CB_3 + CB_4$) (Nussbaum, 1977). In *Uraeotyphlus* and ichthyophiids the distal ends of $CB_3 + CB_4$ are slightly expanded and lie on either side of the arytenoid cartilages (Fig. 2).

By contrast, the ceratohyals of caeciliids are recurved, resulting in a M-shaped element (Fig. 2). BB_1 is short and indistinct in caeciliids, and the distal expansion of $CB_3 + CB_4$ greatly exceeds that which occurs in *Uraeotyphlus* and ichthyophiids. In caeciliids, the arytenoid cartilages have shifted anteriorly relative to the distal ends of $CB_3 + CB_4$.

The glossal skeletons of scolecomorphids and typhlonectids resemble those of caeciliids, whereas the rhinatrematid genera have distinctive glossal skeletons in which the posterior elements are reduced in size (*Epicrionops* and *Rhinatrema*) and number (*Rhinatrema*) (Nussbaum, 1977). Also, the arytenoid cartilages of rhinatrematids lie posterior to the glossal skeleton in contrast to all other caecilians.

In summary, glossal skeletons of caecilians fall into three groups: (1) *Uraeotyphlus*-ichthyophiid, (2) caeciliid-scolecomorphid-typhlonectid, and (3) rhinatrematid. These are preliminary groupings, and much further study is needed for validation. For the present, I wish only to emphasize the striking similarity between *Uraeotyphlus* and ichthyophiid caecilians.

ANNULAR FOLDS.—The primary (one/vertebra) and secondary annuli of ichthyophiids are complete (completely encircle the body) along the full length of the body, and the primaries cannot be distinguished from the secondaries by external examination. Ichthyophiids have 2-4 secondaries/primary, as revealed by X-ray examination. Caeciliids often have incomplete secondaries anteriorly, and some species lack secondaries entirely. In caeciliids, there is only one secondary annulus/primary annulus.

Uraeotyphlus has incomplete secondaries anteriorly and only one secondary/primary (Taylor, 1968; personal observation). *Uraeotyphlus* resembles caeciliids in these characteristics.

POSITION OF TENTACULAR APERTURE.—The opening for the tentacle lies midway between the eye and the naris or is closer to the eye in ichthyophiids. In *Uraeotyphlus,* the tentacular aperture is far forward, just below and slightly anterior or slightly posterior of the naris. In this respect, *Uraeotyphlus* resembles
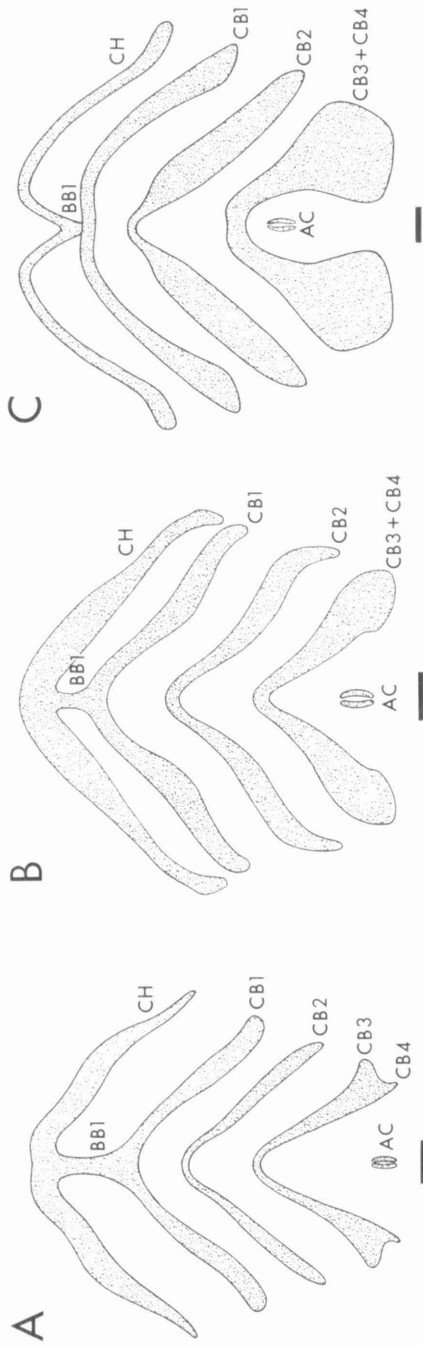
FIG. 2. Glossal skeletons of caecilians. A. *Caudacaecilia weberi* (Ichthyophiidae). B. *Uraeotyphlus narayani* (Ichthyophiidae). C. *Gymnopis multiplicatus* (Caeciliidae). CH = ceratohyal, BB1 = first basibranchial, CB1 = first ceratobranchial, CB2 = second ceratobranchial, CB3 = third ceratobranchial, CB4 = fourth ceratobranchial, AC = arytenoid cartilages. Line = 1 mm.

some caeciliids. But the tentacular aperture of a few caeciliid genera is very close to the eye (*e.g., Gymnopis, Microcaecilia, Praslinia*); therefore the forward position of the tentacular aperture in *Uraetophylus* cannot be viewed as a caeciliid characteristic.

KARYOLOGY.—Caecilian karyology recently has been reviewed by Morescalchi (1973), Wake and Case (1975), and Seto and Nussbaum (1976). Few caecilians have been karyotyped; even so, a pattern, in many ways parallel to that observed in frogs and salamanders, is beginning to emerge. Primitive groups of all three orders have high numbers of chromosomes and many microchromosomes, and advanced groups have fewer chromosomes and fewer or no microchromosomes.

Table 2 is a list of caecilians karyotyped to date and ranked by chromosome number. *Uraeotyphlus* is seen to be intermediate between the primitive ichthyophiids and the advanced caeciliids in karyotype characteristics. The only caeciliid with more chromosomes than *Uraeotyphlus* is *Geotrypetes seraphini*, and this species has fewer microchromosomes than *Uraeotyphlus*.

LIFE HISTORY.—According to Taylor (1968, 1969a), the presence of an aquatic larval stage is diagnostic of the family Ichthyophiidae. Unfortunately, this diagnostic feature is only hypothetical because the life history of the majority of ichthyophiids is completely unknown. Among rhinatrematids, a few *Epicrionops* are known to be oviparous and at least one species has aquatic larvae. The life history of *Rhinatrema* is unknown. Caeciliids either have larval stages (*Geotrypetes grandisonae*), or abbreviated larval stages (*Hypogeophis rostratus*), or direct terrestrial development (some *Grandisonia*), or they are live bearing (*Dermophis mexicanus, Geotrypetes seraphini*). As far as is known, typhlonectids and scolecomorphids are viviparous. The life history of *Uraeotyphlus* is unknown, but Ramaswami (1941) reported that very small specimens of *U. narayani* (90 mm total length) have all of the morphological features of fully metamorphosed adults. This fact strongly suggests that *Uraeotyphlus* has direct terrestrial development with no larval stage, or perhaps a very abbreviated larval stage. *Uraeotyphlus* is not likely to be viviparous because dissections so far have revealed only large yolky eggs or spent ovaries with no developing embryos in the oviducts (personal observation), and because fully-yolked ovarian eggs in

Uraeotyphlus are larger than the ovulated eggs of viviparous caecilians (Marvalee Wake, personal communication).

TABLE 2

CAECILIAN CHROMOSOMES

Species	Family	Diploid Number	Number of Micro-Chromosomes	Authority
*Ichthyophis beddomei**	Ichthyophiidae	42	≅ 15 pairs	Seshachar (1937)
Ichthyophis glutinosus	Ichthyophiidae	42	11 pairs	Nussbaum, unpublished
Ichthyophis kohtaoensis	Ichthyophiidae	42	11 pairs	Nussbaum, unpublished
Ichthyophis orthoplicatus	Ichthyophiidae	42	11 pairs	Seto and Nussbaum (1976)
Geotrypetes seraphini	Caeciliidae	38	4 pairs	Stingo (1974)
Uraeotyphlus narayani	Ichthyophiidae	36	≅ 10 pairs	Seshachar (1939)
Uraeotyphlus menoni	Ichthyophiidae	36	≅ 7 pairs	Elayidom *et al.* (1963)
Gegenophis carnosus	Caeciliidae	30	≅ 10 pairs	Seshachar (1944)
Dermophis mexicanus	Caeciliidae	26	5 pairs	Wake and Case (1975)
Gymnopis multiplicata	Caeciliidae	24 or 26	4 or 5 pairs	Wake and Case (1975)
Grandisonia alternans	Caeciliidae	26	1 pair	Nussbaum, unpublished
Hypogeophis rostratus	Caeciliidae	26	1 pair	Nussbaum, unpublished
Caecilia occidentalis	Caeciliidae	24	0	Barrio *et al.* (1970)
Siphonops paulensis	Caeciliidae	24	0	Barrio *et al.* (1972)
Chthonerpeton indistinctum	Typhlonectidae	20	0	Barrio *et al.* (1971)

*Reported as *Ichthyophis glutinosus*; see Seto and Nussbaum (1976).

COMPARISON OF *URAEOTYPHLUS* TO OTHER GENERA

MATERIALS AND METHODS.—In addition to *Uraeotyphlus,* the following specimens were examined. Caeciliidae: *Dermophis mexicanus* (UMMZ S-2420), *Gegenophis carnosus* (UMMZ

138824), *Hypogeophis rostratus* (UMMZ 146993-7), *Oscaecilia ochrocephala* (UMMZ 75997, 76706, 97415, 98360), *Schistometopum gregorii* (UMMZ 147009-18), *Schistometopum thomense* (UMMZ 118065), *Siphonops annulatus* (UMMZ S-1014). Ichthyophiidae: *Caudacaecilia weberi* (CAS 21766, 28979), *Ichthyophis glutinosus* (UMMZ 135191). Rhinatrematidae: *Epicrionops petersi* (USNM 160360), *Rhinatrema bivittatum* (BMNH 1976.102, MNHN 585, 1899.101, RMNH 17667). Scolecomorphidae: *Scolecomorphus vittatus* (UMMZ 65044). Typhlonectidae: *Typhlonectes* sp. (UMMZ S-2899). BMNH = British Museum of Natural History, London; CAS = California Academy of Science, San Francisco; MNHM = Musée National d'Histoire Naturelle, Paris; RMNH = Rijksmuseum van Natuurlijke Histoire, Leiden; UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

I relied on the literature for anatomical details for some genera: *Dermophis* (de Jager, 1939a), *Gegenophis* (Ramaswami, 1943), *Hypogeophis* (Gewolf, 1923; Lawson, 1963, 1965; Marcus *et al.,* 1935), *Ichthyophis* (Visser, 1963; Wiedersheim, 1879), *Oscaecilia* (de Jager, 1939b), *Schistometopum* (Els, 1963), *Scolecomorphus* (Brand, 1956; de Villiers, 1938), and *Siphonops* (Wiedersheim, 1879). Taylor (1968, 1969b) provided useful anatomical data for all genera.

Forty-three characters were analyzed and scored for the 13 genera. The characters, their states, and distributions across taxa are given in Appendices I and II. Arguments for the ancestral and derived states of characters 1 to 27 are given by Nussbaum (1977). Arguments for the directedness of characters 28 to 43 are presented in Appendix III.

I used a Prim Network algorithm (Edwards and Cavalli-Sforza, 1963; Farris, 1970) to estimate evolutionary relationships among the 13 genera. The method provides a minimum-length, nondirected graph which depicts branching sequences and internodal lengths based on the number of character state changes between taxa. An hypothetical ancestor, with all the characters in the primitive state, was included in the analysis. The resultant Prim Network may be viewed as a crude evolutionary tree (Farris, 1970; Fitch, 1977).

The Prim Network method does not test for compatibility among characters; therefore, convergences and reversals are included in the calculations which produce the tree. As an independent test of the results of the Prim Network, I examined

the intergeneric relationships based only on those characters among the 43 which proved to be compatible. The method used is described by Estabrook *et al.* (1977).

RESULTS. —The Prim Network results are summarized in Figure 3. As expected, *Uraeotyphlus* is separated by fewer steps from *Ichthyophis* and *Caudacaecilia* than it is from the complex of caeciliid genera with which it is currently classified. The intermediacy of *Uraeotyphlus* between the ichthyophiid and caeciliid genera does not necessarily imply that *Uraeotyphlus* is directly ancestral to caeciliids, but does imply that *Uraeotyphlus* shares a more recent common ancestor with caeciliids than with ichthyophiids.

Compatibility analysis resulted in two largest cliques of 31 characters each. The next largest clique size was 29 (3 cliques). The trees produced by these larger cliques are very similar, the differences occurring only in the branching sequences of the upper branches (the positions of the caeciliid and typhlonectid genera are affected). The tree resulting from one of the largest cliques of 31 characters is presented in Figure 4. The other largest clique of 31 characters produces a tree that differs from Figure 4 only in that (1) the hypothetical ancestor of *Scolecomorphus* is also ancestral to *Schistometopum* (which becomes equivalent to *Hypogeophis* and *Dermophis*), (2) *Schistometopum* is ancestral to *Siphonops*, (3) *Schistometopum* is ancestral to *Oscaecilia* (which becomes equivalent to *Gegenophis*), and (4) *Oscaecilia* is ancestral to *Typhlonectes*.

Currently, there seems to be no basis for choosing among the trees produced by equally large cliques in compatibility analysis. However, in this case the problem is not serious because I am not presently concerned with the relationships among the caeciliid genera.

As can be seen by comparison of Figures 3 and 4, Prim Network and compatibility analyses produce very similar results concerning the predicted evolutionary position of *Uraeotyphlus*. The genus is intermediate between the ichthyophiid and caeciliid genera, but is most similar to the ichthyophiid genera. The greater similarity of ichthyophiids and *Uraeotyphlus* results from a high proportion of ancestral character states held in common.
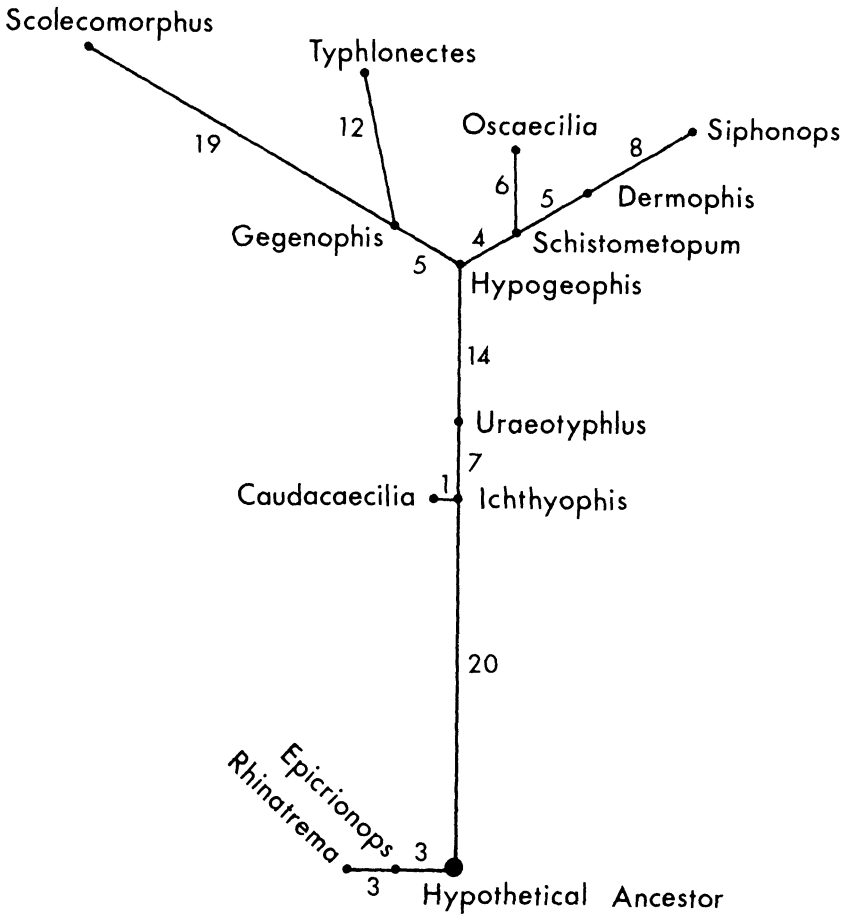
FIG. 3. Prim Network of 13 genera of caecilians based on 43 characters as explained in text.

DISCUSSION

TAXONOMIC STATUS OF URAEOTYPHLUS.—Ichthyophiid charac-teristics of *Uraeothpylus* include the presence of tail, the number and arrangement of the skull bones, and the form of the glossal skeleton. The only distinctly caeciliid characteristics of *Uraeotyphlus* are the incomplete secondaries, presence of only one secondary annulus/primary annulus, and the greatly recessed lower jaw. The common occurrence of these derived states in

FIG. 4. Tree resulting from a clique of 31 compatible characters (Nos. 1-7, 9, 13-27, 30, 33-34, 36-38, 41, 43). The number of character state changes separating OTUs and HTUs are given. Dashed lines indicate the taxa are not different from their ancestors.

Uraeotyphlus and caeciliids results either from convergence or from true phylogeny in which *Uraeotyphlus* and caeciliids share a more recent co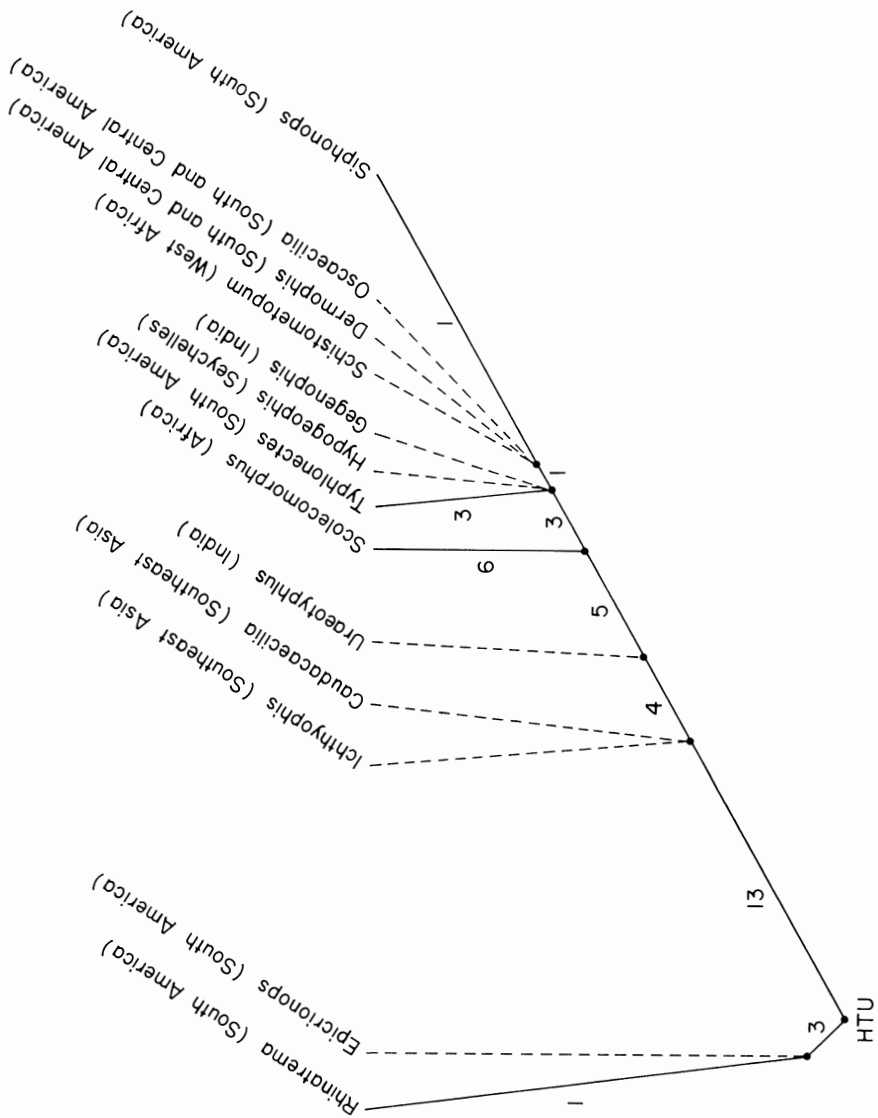mmon ancestor than do *Uraeotyphlus* and ichthyophiids. I have not been able to identify shared derived character states for *Uraeotyphlus* and ichthyophiids. Therefore, I have no basis for rejecting the trees shown in Figures 3 and 4 and will assume that *Uraeotyphlus* is truly intermediate between ichthyophiids and caeciliids.

Given the information presented in this paper, *Uraeotyphlus* may be classified in three different ways. Firstly, *Uraeotyphlus* could be retained in the family Caeciliidae. This action would necessitate major redefinition of both the Caeciliidae and Ichthyophiidae and would obscure caecilian relationships at the family level. Secondly, a new family could be erected to accommodate *Uraeotyphlus*. If I have accurately determined the phylogenetic position of *Uraeotyphlus*, then by strict cladist philosophy, *Uraeotyphlus* could not be included in either the Caeciliidae or Ichthyophiidae, and a new family would have to be constructed for it. However, while I applaud cladistic methodology, I reject the cladist's philosophy of classification for many of the reasons given by Mayr (1974). Thirdly, *Uraeotyphlus* could be transferred to the Ichthyophiidae, a decision which would require minor redefinition of Ichthyophiidae. I prefer the third alternative, with recognition of two subfamilies of Ichthyophiidae: Ichthyophiinae Taylor to receive *Caudacaecilia* and *Ichthyophis* and a new subfamily for *Uraeotyphlus*.

DEFINITION OF ICHTHYOPHIIDAE.—Taylor (1968, 1969a) listed several anatomical and life history characteristics for the family Ichthyophiidae. Taylor's list of characters constitutes a description and not a diagnosis. Because the family has never been properly diagnosed, and because of taxonomic changes proposed here and in the recent literature (Nussbaum, 1977), I offer the following diagnoses.

ICHTHYOPHIIDAE TAYLOR

DIAGNOSIS.—Gymnophiona with distinct septomaxillae, premaxillae, nasals, and prefrontals; postfrontals (= orbitals) distinct in most species, may be partially or entirely fused to squamosal or maxillopalatine; frontal and squamosal in contact; no dorsolateral processes on *os basale*; quadrate and maxillopalatine broadly separated by squamosal; squamosal not notched posteriorly; stapes

distinct, loosely articulated to the quadrate; orbitosphenoids not exposed in ventral view; pterygoid distinct; sides of parasphenoid portion of *os basale* converge anteriorly; prevomers in contact posteriorly; prevomeropalatine teeth in continuous series; *processus retroarticularis* curved dorsally; ceratohyal arch V-shaped; ceratobranchial 4 fused to CB_3 in adults; CB_2 and CB_3 nearly as large as ceratohyal; first basibranchial distinct; larynx situated between distal ends of CB_3 + CB_4 and supported by *musculus dilator laryngeus* and *musculus dorsolaryngeus*; *musculus interhyoideus* inserts in connective tissue on side of neck; *musculus interhyoideus posterior* in two bundles; *musculi levatores mandibularum anteriores* largely confined under squamosals, do not meet in midline above parietals; *musculus depressor mandibulae* longitudinally oriented; *musculi subarcuales* II and III present; eye well developed, in socket, scales present, numerous; tail present; phallodeum aspinous.

ICHTHYOPHIINAE TAYLOR

DIAGNOSIS.—Ichthyophiids with stapes perforate for passage of stapedial artery; pterygoid not in contact with parasphenoid portion of *os basale*; no temporal fossa; 2-4 secondary annuli per primary annulus; primary and secondary annuli complete, orthoplicate posteriorly, angulate anteriorly on ventral surface; tentacular aperture midway between eye and naris or closer to eye, but never in contact with eye.

CONTENT.—Two genera, *Ichthyophis* Fitzinger, with 26 species and *Caudacaecilia* Taylor with 5 species; confined to the Oriental Region, including India, SE Asia, Philippines, and the western Malay Archipeligo.

URAEOTYPHLINAE SUBFAM. NOV.

DIAGNOSIS.—Ichthyophiids with imperforate stapes; pterygoid weakly in contact with parasphenoid portion of *os basale*; small temporal fossa; one secondary annulus per primary annulus; primary and secondary annuli do not completely encircle the body anteriorly, secondary annuli may be entirely absent anteriorly; tentacular aperture far forward, directly below naris or below and slightly anterior or posterior of naris.

CONTENT.—One genus, *Uraeotyphlus* Peters, with 4 species; Oriental, confined to Peninsular India.

In addition to the distinguishing features listed above, species of the two subfamilies are likely to have very different life histories. Some ichthyophiines are known to have aquatic larvae, and the adults are usually found near streams or other wet areas. Uraeotyphlines are likely to have direct terrestrial development, and the adults are likely to be found in a broader range of terrestrial habitats and not so restricted to wet sites. Uraeotyphlines are probably better burrowers than ichthyophiines, as indicated by the anterior position of their tentacles, the greater recession of their lower jaw, and their more cylindrical bodies.

SUMMARY

Aspects of the morphology of the caecilian genus *Uraeotyphlus* are described, and the genus is compared to 12 other caecilian genera representing all described families of caecilians. Estimation of the phylogenetic position of *Uraeotyphlus* by both Prim Network and compatibility analysis suggests that *Uraeotyphlus* is currently misclassified. Accordingly, *Uraeotyphlus* is transferred from the Caeciliidae to the Ichthyophiidae. Two subfamilies of Ichthyophiidae are recognized: Ichthyophiinae to receive *Caudacaecilia* and *Ichthyophis*, and Uraeotyphlinae for *Uraeotyphlus*.

ACKNOWLEDGMENTS

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APPENDIX I

CHARACTERS AND THEIR STATES

Character No. 1. *tail;* present (state A), absent (state B); A is ancestral ($\rightarrow$) to B: 2. *number of secondary annuli/primary annulus;* > 1 (A), $= 1$ (B); A $\rightarrow$ B: 3. *mouth position;* terminal (A), slightly subterminal (B), subterminal (C); A $\rightarrow$ B $\rightarrow$ C: 4. *pre-maxillae-nasals;* separate (A), fused (B); A $\rightarrow$ B: 5. *septomaxillae;* present (A), absent or

fused to adjacent bones (B); A → B: 6. *prefrontals*; present (A), absent or fused to adjacent bones (B); A → B: 7. *postfrontals*; present (A), absent or fused to adjacent bones (B); A → B: 8. *squamosal-frontal*; no contact (A), contact (B); A → B: 9. *squamosal notch-os basale process*; absent (A), present (B); A → B: *temporal fossa*; large (A), nearly closed (B), closed (C); A → B → C: 11. *prevomer approximation*; widely separated posteriorly (A), in contact posteriorly (B); A → B: 12. *prevomer length*; extended posteriorly at least to mid-choana (A), extend posteriorly beyond mid-choana (B); A → B: 13. *parasphenoid*; parallel-sided (A), sides converge anteriorly (B); A → B: 14. *orbito-sphenoid*; vertically oriented (A), obliquely oriented (B); A → B: 15. *pterygoid*; large and free (A), small and free (B), small and tends to fuse to adjacent bones (C), none or fused to adjacent bones (D); A → B → C → D: 16. *basipterygoid process*; none (A), weakly developed (B), large (C); A → B → C: 17. *stapes*; present, perforate (A), present, imperforate (B), absent (C); A → B → C: 18. *quadrate-maxillopalatine*; contact (A), no contact (B); A → B: 19. *processus retroarticularis*; short and straight (A), usually longer, curved dorsally (B); A → B: 20. *glossal elements*; not reduced in size posteriorly (A), reduced in size posteriorly, ceratobranchial 4 missing (B), reduced in size posteriorly, certobranchials 3 and 4 missing (C); A → B → C: 21. *ceratobranchials 3 and 4*; separate, normal size (A), slightly expanded distally, fused (B), greatly expanded distally, fused (C), enclose larynx, fused (D), reduced in size (E); A → B → C → D, A → E: 22. *anterior fibers of musculus interhyoideus*; insert on ceratohyal (A), do not insert on ceratohyal (B), A → B: 23. *posterior fibers of musculus interhyoideus*; insert on processus retroarticularis (A), do not insert on processus retroarticularis (B); A → B: 24. *musculus interhyoideus posterior*; a single bundle (A), two bundles (B); A → B: 25. *orientation of musculus interhyoideus posterior*; oblique (A), longitudinal (B); A → B: 26. *musculi levatores mandibularum anteriores*; large, meet in midline above the interparietal suture (A), small, do not meet in midline (B); A → B: 27. *musculus depressor mandibulae*; vertically oriented (A), longitudinally oriented (B); A → B: 28. *eyes*; present, in socket (A), covered by bone (B); A → B: 29. *tentacle opening*; adjacent to eye (A), midway between eye and naris (B), midway between eye and naris and near lip (C), near and below nostril (D), anterior of and below nostril (E), near and directly behind nostril (F); A → B → C → D → E, D → F: 30. *phallodeum*; aspinous (A), with spines (B); A → B: 31. *vent shape*; longitudinal (A), circular (B), transverse (C); A → B → C: 32. *splenial teeth*; present (A), absent (B); A → B: 33. *Choanal openings*; small (A), large (B); A → B: 34. *anal clasper*; absent (A), present (B); A → B: 35. *narial plugs*; absent (A), present (B); A → B: 36. *mesethmoid*; covered by dermal bones (A), exposed between frontals (B), exposed between nasopremaxillae (C); A → B, A → C: 37. *frontals*, not or only narrowly separated by anterior processes of parietals (A), separated posteriorly by interposed anterior processes of parietals (B); A → B: 38. *prevomeropalatine teeth*; no diastema (A), diastema present (B); A → B: 39. *postchoanal flange of maxillopalatine*; present, does not completely encircle choana (A), not present (B), completely encircles choana (C); A → B, A → C: 40. *premaxillary-maxillary teeth*; many, uniform size (A), few, all enlarged (B), few, lateral maxillary teeth enlarged, recurved (C); A → B, A → C: 41. *posterior body*; rounded in cross-section (A), laterally compressed or keeled (B); A → B: 42. *reproductive mode*; oviparous (A), Ovoviviparous (B); A → B: 43. *development*; larval stage (A), direct (B); A → B.

APPENDIX II
DISTRIBUTION OF CHARACTER STATES ACROSS TAXA

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Epicrionops	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	E	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Rhinatrema	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	C	E	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	C	A	A	A	
Ichthyophis	A	A	B	A	A	A	A	B	A	B	B	B	B	A	B	B	A	B	B	A	B	B	B	B	B	B	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	
Caudacaecilia	A	A	B	A	A	A	A	B	A	B	B	B	B	A	B	B	A	B	B	A	B	B	B	B	B	B	A	C	A	A	B	A	A	A	A	A	A	A	A	A	A	
Uraeotyphlus	A	B	C	A	A	A	A	B	A	B	B	B	B	A	B	B	B	B	B	A	B	B	B	B	B	B	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	
Scolecomorphus	B	B	C	A	A	B	B	A	A	B	B	A	B	B	D	B	C	B	B	A	D	B	B	B	B	B	B	D	B	A	B	A	A	A	A	B	B	B	A	B	B	
Typhlonectes	B	B	C	B	B	B	B	B	A	A	A	B	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	A	F	A	B	A	B	B	B	A	A	A	A	B	B	B	
Schistometopum	B	B	C	B	B	B	B	B	A	C	A	A	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	A	C	A	C	A	A	A	A	B	A	A	A	A	A	B	B
Siphonops	B	B	C	B	B	B	B	B	A	C	B	B	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	A	C	A	B	B	A	A	A	B	B	A	B	A	A	A	B
Oscaecilia	B	B	C	B	B	B	B	B	A	C	A	B	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	B	D	A	B	A	A	A	B	B	A	A	A	B	A	B	B
Hypogeophis	B	B	C	B	B	B	B	B	A	C	B	A	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	A	D	A	C	A	A	A	A	A	A	A	A	A	A	A	B
Dermophis	B	B	C	B	B	B	B	B	A	C	A	B	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	A	C	A	B	B	A	A	A	B	A	A	B	A	A	B	B
Gegenophis	B	B	C	B	B	B	B	B	A	C	B	A	B	A	C	C	B	B	B	A	C	B	B	B	B	B	B	D	A	B	A	A	A	B	A	A	A	A	A	A	A	A	B

APPENDIX III
DISCUSSION OF CHARACTER STATES

I have previously discussed the evolution of characters 1 to 27 (Nussbaum, 1977). Here, I wish to present a brief summary of my arguments for the direction of evolution of characters 28 to 43.

Character 28: An eye in a bony socket is the usual vertebrate condition and should be considered ancestral to vestigial eye, covered with bone. 29: The tentacle of caecilians is derived from the nasolacrimal duct, and the opening is observed to migrate anteriorly from the eye during ontogeny. If the ontogenetic sequence reflects the evolutionary history of the tentacle, then the evolutionary sequence listed in Appendix I is the most logical. 30: Most caecilians lack spines on the phallodeum. Since this condition is widespread across families, I consider it to be ancestral to the spined condition. 31: A longitudinal vent is characteristic of most tailed amphibians (salamanders and some caecilians). Therefore, this state is likely to be ancestral to a circular vent. The latter state is the logical transition to a transverse vent. 32: The widespread, toothed state of the splenial ridge among caecilians and the infrequent absence of splenial teeth among a few seemingly unrelated genera indicates that absence of splenial teeth is derived. 33: Enlarged choanal openings are correlated with the specialized aquatic habits of typhlonectids, and this state is therefore considered to be derived. 34: Anal "claspers" are unknown among the Amphibia, except for their occurrence in typhlonectid caecilians. By parsimony, the presence of "claspers" is argued to be the derived state. 35: The tongue of vertebrates is normally smooth, and therefore the presence of narial plugs on the tongues of some caecilians is considered to be derived. 36: The mesethmoid is normally covered by dermal bones in primitive amphibians. Dorsal exposure of the mesethmoid is therefore a derived state. 37: The frontal bones are closely approximated for their full length in most Amphibia, and posterior separation by interposed parietal processes is likely to be a derived condition. 38: Prevomeropalatine teeth in a continuous series is observed in larvae salamanders, most caecilians, and in many fossil amphibians. The continuous state is therefore considered ancestral to the interrupted state. 39: In most labyrinthodonts, a portion of the palatine bone forms the posteriolateral border of the choana. For this reason, I view the presence of a postchoanal flange on the palatine portion of the maxillopalatine in caecilians as ancestral to both loss of the flange and complete encirclement of the choana. 40: Premaxillary and maxillary teeth are relatively uniform in size among primitive salamanders and frogs. Enlargement of these teeth is therefore considered to be a derived feature of a few caecilian genera. 41: The posterior portion of the body of typhlonectids is laterally compressed (keeled). Because this condition is associated with other aquatic specializations in this group, it is likely to be a derived state. 42: Oviparity is the usual reproductive mode in fishes, frogs, and salamanders. By the outgroup criterion, this mode is considered to be ancestral to ovoviviparity in caecilians. 43: The presence of a larval stage in most frogs, primitive salamanders, and at least some labyrinthodonts argues that this stage is ancestral to direct development in caecilians.