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Copeia, Vol. 1996, No. 3. (Aug. 1, 1996), pp. 550-562.

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Copeia, 1996(3), pp. 550–562

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MARK WILKINSON AND RONALD A. NUSSBAUM

The taxonomic history of the monogeneric caecilian family Uraeotyphlidae and hypotheses concerning its phylogenetic position are briefly reviewed. Previous phylogenetic analyses identified Uraeotyphlidae as sister to a “higher” caecilian clade that includes the families Caeciliidae, Scolecomorphidae, and Typhlonectidae. However, two distinctive derived features of the cardiovascular system are characteristic of Uraeotyphlidae and Ichthyophiidae and provide support for the alternative hypothesis that they are sister taxa. Characters of significance for phylogenetic relationships of Uraeotyphlidae are reviewed. Parsimony analysis of a combined data set, including new characters and others drawn from the literature, supports the hypothesis that Uraeotyphlidae is sister to the Ichthyophiidae; the new characters are instrumental in producing this result. A compatibility analysis lends further support to this conclusion.

THE caecilian genus *Uraeotyphlus* comprises four species from the State of Kerala in southwestern peninsular India. As reviewed by Nussbaum (1979), Taylor (1968) introduced the first familial classification of caecilians and assigned *Uraeotyphlus* to the large and diverse Caeciliidae but was of the opinion (p. 696) that “There is a strong possibility that the genus *Uraeotyphlus* actually should be referred to the Family Ichthyophiidae.” However, Taylor’s (1969a, 1969b) subsequent descriptions of the skull of *Uraeotyphlus oxyurus* led him to conclude that his assignment of this taxon to Caeciliidae was correct. Contradictions between Taylor’s (1969a, 1969b) and earlier studies of the cranial anatomy of *Uraeotyphlus* (Peters, 1881; Parker,

1927; Ramaswami, 1941) prompted Nussbaum (1979) to use cladistic techniques to reassess the phylogenetic relationships and taxonomic position of *Uraeotyphlus*.

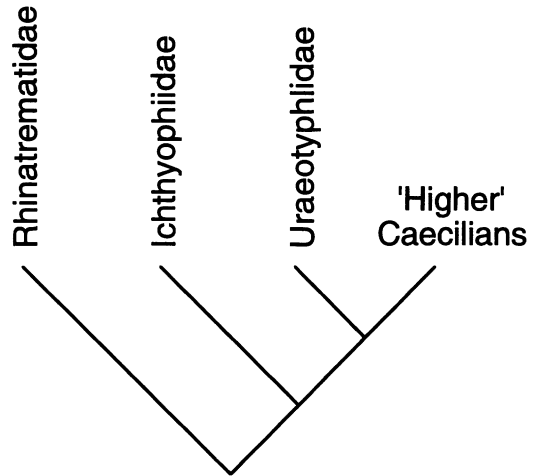
Nussbaum’s (1979) analysis yielded 43 characters drawn from the literature and from his studies of the skull, external anatomy, myology, and life history. These were scored for 13 genera of caecilians, including *Uraeotyphlus* and representatives of the five family-level taxa recognized at that time. The phylogenetic position of *Uraeotyphlus* was investigated through generation of a Prim Network (a minimum spanning tree) and by clique analysis (Estabrook et al., 1977). These methods agreed in their placement of *Uraeotyphlus* (Fig. 1a) as sister to a clade

that includes the families Caeciliidae, Typhlonectidae, and Scolecomorphidae (the "higher" caecilians for the purposes of this paper), with Ichthyophiidae as sister to the uraeotyphlid-higher caecilian clade (Fig. 1a). We refer to the hypothesis that *Uraeotyphlus* is more closely related to a higher caecilian clade than to other caecilians as hypothesis 1.

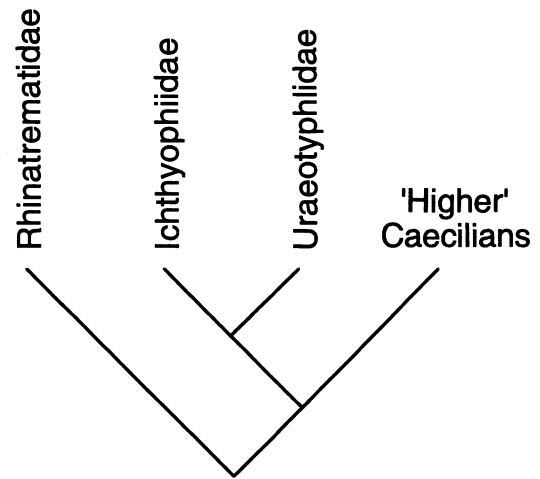
Nussbaum (1979) considered that continued inclusion of *Uraeotyphlus* in Caeciliidae would necessitate major redefinition of both this family and Ichthyophiidae. He acknowledged that a strict cladistic classification of *Uraeotyphlus* precluded its assignment to Ichthyophiidae because the latter would then be paraphyletic. However, on grounds that such an assignment would require the least taxonomic rediagnosis, he transferred *Uraeotyphlus* to Ichthyophiidae and divided the family into subfamilies Ichthyophiinae (= Ichthyophiidae sensu Taylor) and monogeneric Uraeotyphlinae.

In 1986, three reviews of caecilian phylogeny and classification were published. Laurent (1986) followed Nussbaum's (1979) classification of *Uraeotyphlus* but presented a tree where *Uraeotyphlus* was sister to Scolecomorphidae. Lescure et al. (1986) elevated Uraeotyphlinae to family rank, although their cladogram placed *Uraeotyphlus* as sister to the ichthyophiine ichthyophiids, *Ichthyophis* and *Caudacaecilia*, and was therefore cladistically consistent with Nussbaum's classification. Duellman and Trueb (1986) presented an analysis of higher level caecilian phylogenetic relationships using Wagner parsimony (Kluge and Farris, 1969) and a reduced set of characters mostly derived from Nussbaum (1979). Their results supported hypothesis 1; they also elevated Uraeotyphlinae to family rank to render Ichthyophiidae monophyletic.

Nussbaum and Wilkinson (1989) critically reviewed caecilian systematics and showed the phylogenetic hypotheses of Laurent (1986) and Lescure et al. (1986) to be unsupported. The position of *Uraeotyphlus* in the hypothesis of Lescure et al. (1986) was based on misinterpretation of development and evolution of caecilian annulation patterns. In addition, reanalysis of their data by using parsimony failed to produce tree topologies consistent with their hypothesized placement of *Uraeotyphlus*, producing instead hypothesis 1, as in Nussbaum's (1979) and Duellman and Trueb's (1986) analyses. Nussbaum and Wilkinson (1989) accepted Duellman and Trueb's (1986) proposal that Uraeotyphlinae be elevated to family rank but rejected subfamilial and suprafamilial groups proposed by other workers.



(a) Hypothesis 1



(b) Hypothesis 2

Fig. 1. Alternative hypotheses of the phylogenetic position of Uraeotyphlidae.

More recently, Hillis (1991) used a data set based on Duellman and Trueb (1986) to reanalyze caecilian familial interrelationships. He modified Duellman and Trueb's data to account for the corrections of Nussbaum and Wilkinson (1989) but did not describe these modifications or present the modified data set. He found that the phylogenetic position of Uraeotyphlidae was the least stable part of the phylogeny: a single most-parsimonious tree required 28 steps and supported hypothesis 1, but trees in which the

TABLE 1. DATA MATRIX SUMMARIZING TAXONOMIC DISTRIBUTION AND POLARITY OF CHARACTER DATA USED IN NUMERICAL PHYLOGENETIC ANALYSES. Missing data or uncertain polarity is represented by ?. Character numbers are those of Nussbaum (1979), as modified in the Appendix. Multistate characters are represented by binary factors that are distinguished by alphabetic suffixes.

Taxa	Characters									
	123344 ab	56789	11111 00123 ab	11111 55667 abab	11222 89000 abc	22222 23457	22233 89912 ab	33344 56902	44444 34567	44 89
Ancestral state	00000	00000	00000	00000	00000	00000	00000	00000	000??	00
<i>Epicrionops</i>	01000	01101	00000	00000	00100	00000	00000	00000	00000	00
<i>Rhinatrema</i>	01000	01101	00000	00000	00100	00000	00010	000??	?00??	00
<i>Ichthyophis</i>	01100	00010	10111	10100	11010	11111	01000	00000	01111	11
<i>Caudacaecilia</i>	01100	00010	10111	10100	11010	11111	01001	00000	01111	11
<i>Uraeotyphlus</i>	00110	00010	10111	10101	11010	11111	01100	00000	01111	10
<i>Scolecophorus</i>										
<i>phus</i>	10110	00110	11101	?110?	110??	11111	11101	00011	10000	00
<i>Typhlonectes</i>	10111	11110	11011	11111	11011	11111	01010	10001	10000	10
<i>Schistometo-</i>										
<i>pum</i>	10111	11110	10001	11111	11011	11111	01010	01001	10000	00
<i>Siphonops</i>	10111	11110	10111	11111	11011	11111	01111	01100	10000	00
<i>Osaecilia</i>	10111	11110	10011	11111	11011	11111	11110	1101?	?0000	00
<i>Hypogeophis</i>	10111	11110	10101	11111	11011	11111	01010	00000	10000	00
<i>Dermophis</i>	10111	11110	10011	11111	11011	11111	01111	01101	10000	00
<i>Gegeneophis</i>	10111	11110	10101	11111	11011	11111	11010	10000	10000	00
<i>Boulengerula</i>	10111	11110	10001	11110	11011	11111	11010	00000	10000	00
<i>Praslinia</i>	10001	11110	10011	11111	11011	11111	00010	00000	00000	00

positions of Ichthyophiidae and Uraeotyphliidae were reversed, or in which these two families were sister taxa, required only two additional steps. Similarly, bootstrap proportions were lower (77%) for the node linking the Uraeotyphliidae to the higher caecilians than for any other nodes (98–99%).

In this paper, we reconsider the phylogenetic position of Uraeotyphliidae in the light of two newly documented, distinctive, and derived cardiovascular character states that are shared by Uraeotyphliidae and Ichthyophiidae. These features are incompatible with hypothesis 1 and provide evidence for the alternative view, hypothesis 2, that Ichthyophiidae and Uraeotyphliidae are sister taxa (Fig. 1b).

MATERIALS AND METHODS

Information on caecilian morphology was obtained by dissection of alcohol-preserved specimens and from dry and/or cleared-and-stained skeletal preparations. Observations were made with a binocular dissection microscope. Anatomical figures were prepared from camera lucida drawings. The character data used in the numerical phylogenetic analyses (Table 1) are based on that of Nussbaum (1979), expanded

through the addition of new taxa and new characters and with modifications to the coding of some characters. Data and details of coding are presented in the Appendix. To simplify cross-referencing, numbers used to refer to characters are those in Nussbaum's (1979) data matrix, with minor modifications. New characters are assigned numbers 44–49; binary factors of multistate characters are distinguished by a letter suffix. Representatives of genera included in Nussbaum's (1979) data matrix were examined and scored for cardiovascular characters. Two additional caeciliid taxa, *Boulengerula taitanus* and *Praslinia cooperi*, were examined and scored for all characters. These additional taxa have novel combinations of character states that provide evidence of homoplasy in some of the characters previously used to support hypothesis 1.

Polarity was specified by inclusion of a hypothetical ancestor coded with assumed primitive character states, based on outgroup and/or ontogenetic criteria, and coded as equivocal (?) when there was no clear evidence of polarity. Nonpolar analyses excluded the hypothetical ancestral taxon and produced unrooted trees. Although unrooted trees do not provide hypotheses of monophyly, they may be consistent or inconsistent with such hypotheses. All mul-

tistate characters were treated as ordered and represented by their binary factors (using additive binary coding) so that phylogenetic utility of distinct character state transformations could be assessed separately (Kluge, 1976).

Parsimony analyses used the branch-and-bound method implemented in PAUP 3.1.1 (Swofford, 1993). Topological constraints were used to assess differences in tree lengths required by alternative hypotheses. Probabilistic compatibility analyses used PICA95 (Wilkinson, 1995). Further details of numerical phylogenetic analyses are given below.

RESULTS

Review of character evidence.—A number of characters, some used previously and some new, are potentially significant for inference of phylogenetic relationships of Uraeotyphlidae. Many of these characters are mutually incompatible, indicating that some must be homoplastic and potentially misleading. Here we provide an a priori assessment of the available character data. Because we included both polar and nonpolar characters, there is considerable scope for confusion over the precise relationship between characters and hypotheses.

To avoid confusion, we used the following terminology to apply specifically to relationships between binary characters or binary factors of multistate characters and hypotheses of interest. A character provides direct support for hypothesis 1 or 2 if similarity can be explained by a unique transformation to a hypothesized derived state in a branch uniting Uraeotyphlidae and higher caecilians (hypothesis 1) or a branch uniting Uraeotyphlidae and Ichthyophiidae (hypothesis 2). Direct support applies to polar characters and rooted trees. A character provides indirect support for hypothesis 1 or 2 if similarity can be explained by a unique transformation between character states in a branch that partitions taxa into the following: (1) Uraeotyphlidae and higher caecilians and (2) all other caecilians (hypothesis 1), or (1) Uraeotyphlidae and Ichthyophiidae and (2) all other caecilians (hypothesis 2). Indirect support pertains to nonpolar treatments of characters and unrooted trees. A character provides qualified support for hypothesis 1 or 2 if, given a hypothesis of limited homoplasy, similarity can be explained by assuming a single additional transformation in the branch uniting (rooted) or partitioning (unrooted) the sets of taxa as described above. A character contradicts hypotheses 1 or 2 if it supports an alternative hypothesis that implies hypotheses 1 and/or 2 to be untrue. A

character is consistent with hypothesis 1 or 2 if it neither supports nor contradicts the hypothesis.

Absence of tertiary annuli (character 2).—Nussbaum (1979) considered the presence of tertiary annuli to be a primitive condition. The lack of tertiary annuli in *Uraeotyphlus* and the higher caecilians thus provided direct support for hypothesis 1. More recently, Nussbaum and Wilkinson (1989) noted that the reverse polarity is more consistent with the condition of outgroup taxa and with annular ontogeny. If tertiary annuli are derived, the character supports a relationship between Ichthyophiidae and Rhinatrematidae and contradicts hypothesis 2. It also is incompatible with many other characters that indicate Rhinatrematidae to be sister to all other caecilians (Nussbaum, 1977; Wilkinson, 1992a, 1996) but is consistent with hypothesis 1.

Caecilian annulation patterns display tremendous variety, and it is clear that transformations in number of secondary annuli must have occurred many times independently (Nussbaum and Wilkinson, 1989). In contrast, there is no similar indication from patterns of variation within Gymnophiona that transformation to or from tertiary annuli has occurred more than once. Nussbaum and Naylor (1982) reported that trunk myomeres of adult rhinatrematid and ichthyophiid caecilians show no positional correspondence to external annular segmentation of the skin. This might be considered a distinct character but is probably tied to presence of tertiary annuli and is not considered a separate character in our analyses.

Duellman and Trueb (1986) employed a different treatment of variation in caecilian annulation patterns for their analysis of interfamilial relationships. They distinguished three character states in a linear ordered character: primary and secondary orthoplicate annuli throughout the length of the body (0) to primary and secondary annuli throughout the length of the body and anterior annuli angulate (1) to secondary annuli absent anteriorly or entirely (2). They coded Rhinatrematidae with state 0, Ichthyophiidae and Uraeotyphlidae with state 1, and higher caecilians with state 2. This treatment makes no use of the distinction between tertiary and secondary annuli, and as conceived and coded, the character is consistent with both hypotheses 1 and 2. However, there are problems with this treatment. First, most uraeotyphlids do not have secondary annuli throughout the length of the body, and none has angulate rather than orthoplicate anterior annuli. Second, we see no basis for considering

state 1 (angulate anterior annuli) to be an intermediate between states 0 and 2 (both orthoplicate anterior annuli). The character coding seems to confound variation in extent of secondary annuli with variation in annular shape. These might be better treated as distinct characters. It is more parsimonious to assume that the orthoplicate condition is homologous wherever it occurs in caecilians and that the angulate condition is independently derived in ichthyophiids.

Derived characters providing direct support for the hypothesis that *Ichthyophis* and *Caudacaecilia* are sister taxa have not been described previously, although this hypothesis has been advocated on the basis of close similarity (Wilkinson, 1991). Although angulate annuli have no significance for discriminating between hypotheses 1 and 2, we have included this character (character 49) in our analysis.

Scales in anterior annuli.—Duellman and Trueb (1986) considered absence of scales from anterior annuli to be derived, providing direct support for hypothesis 1. Ignoring uncertainty over polarity of this character, the observation that some ichthyophiids lack scales in their anteriormost annuli indicates that evolution of caecilian scale distribution patterns is probably more complex than indicated by their character coding and that there are no simple correspondences between variation in this feature and hypotheses 1 and 2. We have not used variation in the extent of caecilian scales in our analyses.

Subterminal mouth (character 3b).—*Uraeotyphlus* shares the derived condition of a strongly subterminal mouth with scolecomorphids, typhlonectids, and some caeciliids. All six caeciliid genera included in Nussbaum's (1979) analysis shared this derived condition. In the context of that analysis, this character provided direct support for hypothesis 1. However, there is variation in the degree to which the snout projects anteriorly beyond the lower jaws within the higher caecilians that was not represented in Nussbaum's (1979) data set. Within Seychellean caeciliids, a well-supported clade within the higher caecilians (Nussbaum and Ducey, 1988; Hass et al., 1993; Hedges et al., 1993), variation in this feature includes both extremes of the range of character states found among other caecilians. This indicates that evolution of this character has been homoplastic within Gymnophiona. Inclusion of the Seychellean caeciliid *Praslinia*, which has a terminal mouth, in our analysis precludes any direct support for hypothesis 1. In

our analyses, this character contradicts both hypotheses 1 and 2. At most, it can offer only qualified support for hypothesis 1.

Discrete postfrontals (character 7).—Ichthyophiids and uraeotyphlids are the only caecilians with discrete postfrontals. Nussbaum (1979) considered this to be a primitive character state. The distribution of the hypothesized, derived character state links rhinatrematids with higher caecilians and thus contradicts hypothesis 1. This character also contradicts the well-supported hypothesis that Rhinatrematidae is sister to all other caecilians, suggesting either that the hypothesized polarity is incorrect or that the character is homoplastic. If polarity were reversed, the character would provide direct support for hypothesis 2; if treated as nonpolar, it also provides indirect support for hypothesis 2.

Discrete postfrontals are present in the recently described Jurassic caecilian *Eocaecilia* (Jenkins and Walsh, 1993), providing additional support for Nussbaum's hypothesis of polarity. However, the form of the postfrontal of *Eocaecilia* is rather dissimilar to that of living caecilians. In ichthyophiids and uraeotyphlids, postfrontals are circumorbital bones that form complete or incomplete narrow bony rings around the orbits. In contrast, postfrontals of *Eocaecilia* are more expansive elements that make a more substantial contribution to the skull roof and are entirely postorbital. These differences leave room for doubt concerning homology of the postfrontal in *Eocaecilia* and in ichthyophiids-uraeotyphlids and consequently on its polarity.

Imperforate stapes (character 17).—Imperforate stapes is a derived condition that *Uraeotyphlus* shares with typhlonectids and most caeciliids, including all caeciliids included in Nussbaum's (1979) analysis in which the character provided direct support for hypothesis 1. However, the caeciliid *Boulengerula taitanus* also has a perforate stapes. Inclusion of this caeciliid in our analysis prevented this character from providing direct support for hypothesis 1. Thus, in our treatment, this character contradicts both hypotheses 1 and 2, and like the projection of the snout (character 3b), it can at most provide only qualified support for hypothesis 1.

Position of tentacular apertures (character 29b).—In *Uraeotyphlus*, the tentacular apertures are directly below the external nares (subnarial). This is a derived condition that is shared with some, but not all, caeciliids and with scolecomorphids. It contradicts both hypotheses 1 and 2.

Position of the tentacular aperture displays considerable intergeneric variation, so much so that Nussbaum (1979) described five distinct character states. Within Seychellean caeciliids, there is almost equally great variation in position of the tentacular aperture (three of the five character states), indicating that this character has undergone homoplastic evolution within Gymnophiona, possibly including independent origin of the subnarial position in the Seychellean species *Hypogeophis rostratus*.

There is little additional evidence to support a close phylogenetic relationship between those caecilians having subnarial tentacular apertures. All these caecilians have external nares that are relatively dorsal, but this adult position of the nares is probably not independent of the position of the tentacular apertures. In larval *Uraeotyphlus oxyurus*, nares migrate from an initial lateral position to the dorsal adult position as the tentacle and its aperture migrate anteriorly. This suggests that the more dorsal position of the nares may be an epigenetic response to the anterior migration of the tentacle (Wilkinson, 1992b) and therefore should not be treated as an independent character.

We included a modified coding of this character in our analysis. However, great variability in the position of the tentacular aperture, evidence of homoplasy, and lack of independent supporting evidence suggests that variation in this character should be interpreted cautiously and potentially given low weight in cases of conflict.

Division of the atria (character 44).—Caecilians have right and left atrial cavities that are usually separated internally by an interatrial septum. Among caecilians, ichthyophiids (*Ichthyophis* and *Caudacaecilia*) and *Uraeotyphlus* are unique in having the distal atria also separated externally (Fig. 2). External division of the atria in *Uraeotyphlus menoni* Annandale is apparent in Chatterjee (1936; Fig. 3) though not remarked upon in text. Similarly, presence of this feature in *Ichthyophis glutinosus*, and its absence in the caeciliid *Siphonops paulensis* and the typhlonectid *Chthonerpeton indistinctum*, is evident in Acolat (1939; Figs. 3, 8, 10), but there is no mention of this difference in text.

External, as opposed to internal, division of the atria is not a condition that is found in candidate outgroups to Gymnophiona, i.e., salamanders, frogs, and lungfishes, (Putnam, 1970), or in the plesiotypic rhinatrematids (Wilkinson, 1996), and therefore appears to be derived within caecilians. The distribution of this dis-

tinutive derived character state thus provides direct support for hypothesis 2.

Anterior extension of the pericardium (character 45).—In caecilians, the anterior limit of the pericardium is usually close to the atrial apex. In contrast, the pericardium of ichthyophiids and *Uraeotyphlus* is extended anteriorly such that there is a large preatrial pericardial space (Fig. 2). The more typical caecilian condition is comparable to outgroups and is thus considered primitive. The distribution of the derived state mirrors that of the external division of the atria, and in the absence of any clear functional linkage between them, it is interpreted as providing additional direct support for hypothesis 2.

Flexures in the musculus rectus lateralis (character 46).—Nussbaum and Naylor (1982) identified presence of two posterior internal flexures in the *m. r. lateralis* as a distinctive feature of *Uraeotyphlus*, *Ichthyophis*, and *Caudacaecilia*. All other caecilians that have been examined have a single posterior internal flexure in this muscle. The polarity and phylogenetic significance of this character is unclear. However, as a nonpolar character, it provides indirect support for hypothesis 2 and contradicts hypothesis 1.

Flexures in the musculus subvertebralis (character 47).—Nussbaum and Naylor (1982) also described presence of a single flexure in the *m. subvertebralis* as a unique feature of ichthyophiids and uraeotyphlids. The polarity of this character is also unclear from outgroup comparisons, such that it has the same potential phylogenetic significance as the previous trunk muscle character.

Tracheal lung (character 48).—Ichthyophiids, uraeotyphlids, and typhlonectids are the only caecilians where the trachea is expanded into an additional surface for respiratory gas exchange. Presence of a tracheal lung in *Typhlonectes* was reported by Fuhrmann (1914), and Wake (1974) mentioned that some caecilians, e.g., *Ichthyophis glutinosus*, have an accessory tracheal respiratory organ. Ramaswami (1944) noted this structure in *Ichthyophis* and *Uraeotyphlus* but described it as an anterior extension of the left lung. Outgroup comparison clearly suggests that this feature is derived, and as such, it contradicts hypothesis 1 but is consistent with hypothesis 2.

Absence of a larval stage (character 43).—Ramaswami (1941), Wake (1977), Nussbaum (1979),

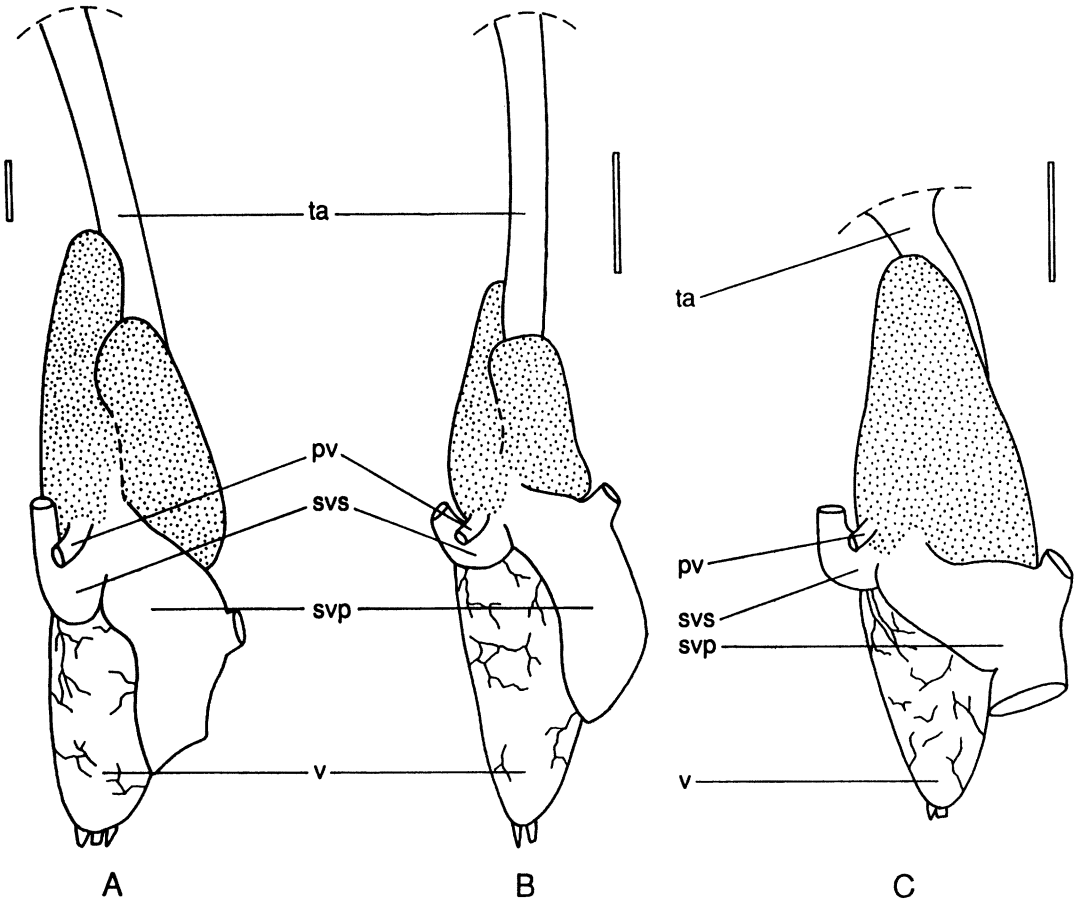


Fig. 2. Dorsal views of hearts of (A) *Ichthyophis bannanicus*, (B) *Uraeotyphlus narayani*, and (C) a caeciliid, *Geotrypetes seraphini*. External division of right and left atria (stippled area) and anterior extension of the pericardium are shown in A and B; the more typical undivided condition of the atria and more proximal limit of the pericardium is shown in C. Dashed line indicates position of the anterior limit of the pericardium. pv = pulmonary vein; svp = sinus venosus principale; svs = sinus venosus sinistra; ta = truncus arteriosus; v = ventricle. Bar = 2.0 mm.

and Duellman and Trueb (1986) all suggested that *Uraeotyphlus* probably had direct development rather than a discrete larval stage, but this was based on indirect inferences from ovarian egg size. Nussbaum (1979) interpreted the probable absence of a larva as providing direct support for hypothesis 1. Wilkinson (1992b) described the larval stage of *U. oxyurus* and argued that, although we do not know the condition in all uraeotyphlids, the condition in *U. oxyurus* should be taken as the generic condition for phylogenetic inference unless more compelling evidence that it is not is forthcoming. With this reassessment of uraeotyphlid life history, this character is equally consistent with hypotheses 1 and 2. In addition, some higher caecilians also have a larval stage, indicating that the direct support provided by this character for hypoth-

esis 1 in Nussbaum's (1979) analysis was a result of restricted sampling of higher caecilians.

Cartilaginous larval glossal skeleton.—Wake (1989) reported that the larval glossal skeleton of the rhinatrematid *Epicrionops* is unique among caecilians in being mineralized. Caeciliids that have well-developed (i.e., free-living, independently feeding) larval stages also have a mineralized larval glossal skeleton (Nussbaum and Wilkinson, unpubl.). Thus, among caecilian larvae, only ichthyophiids and uraeotyphlids appear to have only cartilaginous larval glossal skeletons. This may represent an additional derived feature that supports hypothesis 2. However, a clear interpretation is hampered because the only known uraeotyphlid larvae are nearly metamorphic (i.e.,

TABLE 2. CHARACTERS OF GREATEST SIGNIFICANCE FOR INTERPRETATION OF THE PHYLOGENETIC POSITION OF URAEOTYPHLIDAE, THEIR RELATIONSHIPS TO HYPOTHESES 1 AND 2, AND THEIR NONPOLAR LE QUESNE PROBABILITIES. C = character number, I = indirect support, D = direct support, X = contradicts, — = consistent.

Character	C	Hypothesis		Le Quesne probability
		1	2	
Tertiary annuli	2	I	X	0.086*
Mouth position	3a	X	—	0.174*
Mouth position	3b	X	X	0.102*
Prefrontals	6	X	—	0.095*
Postfrontals	7	X	I	0.011
Prevomer approximation	11	X	—	0.089*
Prevomer length	12	X	—	0.105*
Stapes	17	X	X	0.148*
Tentacle position	29a	X	—	0.182*
Tentacle position	29b	X	X	0.173*
Vent shape	31	X	—	0.525*
Splenials	32	X	X	0.512*
Atria	44	X	D	0.011
Pericardial space	45	X	D	0.011
Rectus laterales flexures	46	X	I	0.014
Subvertebralis flexures	47	X	I	0.014
Tracheal lung	48	X	—	0.165*

* Not significantly different from random ($P < 0.05$).

it is not known whether mineralization occurs in more premetamorphic larvae) and because the lack of a larval stage in many caecilians prevents meaningful comparison. Uncertainties associated with this character render its use in phylogenetic analyses premature, and it was not included in our analysis.

Other characters.—Several other characters included in Nussbaum's (1979) data offer neither direct nor indirect support for hypothesis 1 or 2 but contradict one or both of these hypotheses. Derived states of these characters are as follows: mouth slightly or more subterminal (character 3a), absence of prefrontals (character 6), prevomers in contact posteriorly (character 11), prevomers extended posteriorly (character 12), tentacle not adjacent to eye (character 29a), transverse or circular vent (character 31), and absence of splenial teeth (character 32). All of these characters contradict hypothesis 1, whereas all but one (splenial teeth) are consistent with hypothesis 2. Some of these features have patchy taxonomic distributions across Gymnophiona or unite a single rhinatrematid or ichthyophiid genus with some higher caecilians. It is plausible that evolution of all of these features has been homoplastic in Gymnophiona. These characters were retained in our analyses but in the case of conflict might be considered to be of low weight.

Summary.—Among characters previously employed for inferring caecilian phylogeny and that have some significance for phylogenetic placement of Uraeotyphlidae, there is little clear support for hypothesis 1. Four character states, absence of larval stage, absence of tertiary annuli, projection of snout, and imperforate stapes provided direct support for hypothesis 1 in Nussbaum's (1979) analysis. However, uraeotyphlids have a larval stage; there is uncertainty concerning polarity of tertiary annuli; and variation among higher caecilians, which was not represented in Nussbaum's analysis, indicate no direct correspondence between the latter two characters and hypothesis 1. In contrast, the two new cardiovascular characters provide direct support for hypothesis 2. Presence of postfrontals and the two trunk muscle characters provide indirect support for hypothesis 2 and are inconsistent with hypothesis 1. Various relations that pertain between characters and hypotheses 1 and 2 are summarized in Table 2.

Numerical phylogenetic analyses.—Our a priori assessments of characters suggest that hypothesis 2 is somewhat better supported than hypothesis 1. For numerical phylogenetic analyses, Nussbaum's (1979) data were modified through addition of the five cardiovascular, trunk myological, and respiratory characters; by addition of two new caeciliid taxa that display important

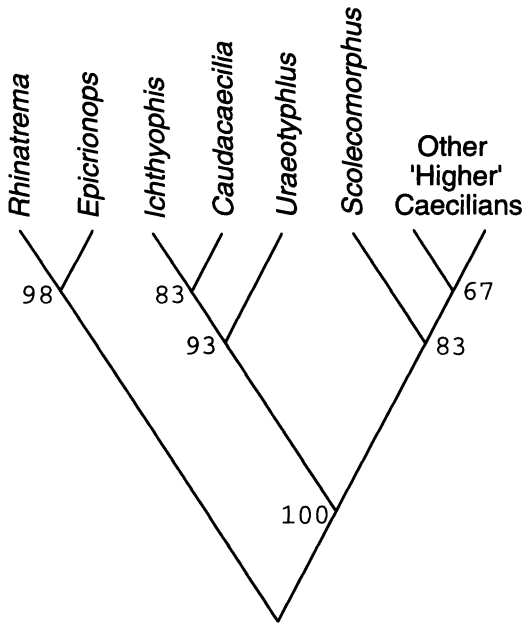


Fig. 3. Majority-rule, component consensus tree summarizing polar bootstrap analysis. Numbers indicate bootstrap proportions of corresponding nodes. A hypothetical ancestor (not shown) was used to root the tree.

combinations of character states; and by some reworking of the original characters. The data set and details of reworking of characters are described in the Appendix.

A polar parsimony analysis (all characters weighted equally) yielded a single most-parsimonious tree (MPT) with a length (L) of 75, a consistency index (C) of 0.627, and retention index (R) of 0.804, that supports hypothesis 2. An additional five (6.7%) steps were required by shortest trees supporting hypothesis 1. Nonpolar analysis, excluding the hypothetical ancestor, produced a qualitatively equivalent, most-parsimonious unrooted tree (L = 74, C = 0.635, R = 0.765). The shortest unrooted tree supporting hypothesis 1 also requires an additional five steps. A polar bootstrap analysis of the complete data set was also used to explore the strength of support for hypothesis 2. The uraeotyphlid-ichthyophiid clade appeared in 93 of 100 bootstrap replicates, a proportion exceeding that of other major clades (Fig. 3).

Parallel analyses were performed with either *Praslinia* and *Boulengerula* and/or characters 44–48 (the new characters offering direct, indirect, or qualified support to hypothesis 2) excluded. Corresponding polar and nonpolar analyses produced qualitatively identical results. Exclu-

sion of *Praslinia* and *Boulengerula* increased the number of MPTs to 10 but did not affect placement of Uraeotyphlidae. Exclusion of characters 44–48 increased the number of MPTs to nine, eight of which supported hypothesis 1 with the other supporting hypothesis 2. Exclusion of *Praslinia* and *Boulengerula* and characters 44–48 increased the number of MPTs to 11, all of which supported hypothesis 1. Shortest trees supporting hypothesis 2 in the absence of *Praslinia* and *Boulengerula* and characters 44–48 required only a single extra step.

We used a compatibility-based, randomization test to evaluate further the characters of significance for the phylogenetic position of Uraeotyphlidae. Randomization tests were introduced by Archie (1989) and Faith and Cranston (1991) in the context of parsimony analysis as a means of testing the null hypothesis that a data set is phylogenetically uninformative. Our test is of the null hypothesis that an individual character is phylogenetically uninformative. The test statistic, the Le Quesne probability, is the probability of the character having as few or fewer incompatibilities than actually are observed if assignment of its character states to taxa is random (Wilkinson, 1992c). The Le Quesne probability is estimated by repeated, random permutation of the assignment of character states to taxa or determined by an exhaustive enumeration of all possible permutations (Wilkinson, 1995). The exhaustive approach was used to determine nonpolar Le Quesne probabilities for all characters in the caecilian data and including all taxa. There is a striking correspondence between the Le Quesne probabilities of characters of significance for the phylogenetic position of the Uraeotyphlidae and our a priori assessments of character utility (Table 2). In this test, only characters that support hypothesis 2 appear to differ significantly from random.

DISCUSSION

Our a priori assessments of characters and numerical phylogenetic analyses suggest that Uraeotyphlidae is more closely related to Ichthyophiidae than to the higher caecilians, hypothesis 2. This hypothesis is supported by parsimony analysis of the full data, by relatively high bootstrap proportions, and by failure to reject the null hypotheses that supporting characters are phylogenetically uninformative. Using the complete data, hypothesis 1 requires an additional five steps. Multiple parsimony analyses excluding selected taxa and/or characters

demonstrate that the new characters are primarily, but not solely, responsible for these results. Hypothesis 2 is most parsimonious when the caeciliids *Praslinia* and *Boulengerula* are excluded and is among the multiple MPTs when the new characters are removed. Only with removal of both new characters and taxa, and a return to the more limited evidence presented by Nussbaum (1979), do the analyses provide unambiguous support for hypothesis 1. However, in that case, hypothesis 2 requires only a single extra step. *Praslinia* and *Boulengerula* are important to the analysis because of novel character combinations that imply that characters directly supporting hypothesis 1 in Nussbaum's (1979) analysis do not have a precise correspondence with this hypothesis and can provide only qualified support.

Although we consider that hypothesis 2 is the best estimate of the phylogenetic relationships of *Uraeotyphlus*, there remains some scepticism that this hypothesis corresponds to reality. Hypothesis 1 is overturned by the addition of a few new characters, and it may be that a few new characters that are incongruent with hypothesis 2 would suffice to overturn it. Our analyses also demonstrate the sensitivity of phylogenetic inferences to taxonomic sampling. The desirability of additional data and the potential for molecular data to help resolve basal relationships within Gymnophiona are clear.

Our view is that classificatory changes motivated by phylogenetic hypotheses should be proposed only when phylogenetic hypotheses are well supported. For this reason, we do not propose any modification to caecilian classification in accordance with hypothesis 2. Continued recognition of Uraeotyphlidae will mirror neither hypothesis 1 nor hypothesis 2 but has the virtue of being consistent with both.

ACKNOWLEDGMENTS

We thank the following curators and institutions for the loan of, or access to, specimens in their care: E. N. Arnold and B. T. Clarke, The Natural History Museum; a.k.a. British Museum (Natural History); D. Frost, American Museum of Natural History; J. Rosado, Museum of Comparative Zoology, Harvard University; and G. Smith, University of Michigan, Museum of Zoology. We thank P. Baldero for help in preparing figures. This work was supported in part by grants from SERC (GR/F 87912), NERC (GST/02/832), and NSF (DEB 881-7453). The PICA software is available from MW upon receipt of a disk (PC compatible).

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APPENDIX

Character data used for the numerical phylogenetic analyses are based primarily on Nussbaum (1979) subject to modifications of coding and the introduction of six additional binary characters and two additional terminal taxa. Because some of the genera used as terminal taxa in Nussbaum's analyses show inter- or intraspecific variation, we selected one or more species that are invariant for these characters to include in the analyses. *Bouleengerula* refers to *B. taitanus*, *Osaecilia* to *O. ochrocephala*, *Schistometopum* to *S. thomense*, and *Siphonops* to *S. annulatus*. Use of the generic name is simply an abbreviation.

Character data are given in Table 1. Character numbers 1–43 are those of Nussbaum (1979), with additional characters numbered 44–48. Multistate characters are represented by binary factors and labeled with an additional alphabetic identifier. Nussbaum's (1979) data matrix included a number of typographical errors that are corrected here. Of Nussbaum's 43 original characters, 20 (1, 3, 4, 5, 8, 11, 12, 13, 16, 18, 19, 22, 23, 24, 25, 27, 28, 32, 35) are unmodified except for additive binary coding of multistate characters. Other deviations from Nussbaum's (1979) character matrix or treatment of characters are described below. Estimates of character polarity are mostly those of Nussbaum (1979) and are indicated by scoring of the hypothetical ancestor, with 0 usually denoting the primitive condition. Seven characters (14, 30, 33, 34, 37, 38, 41) were excluded because their derived states are restricted to a

single terminal taxon and are phylogenetically uninformative.

Character 2: Polarity is reversed.

Character 6: *Rhinatrema*, *Epicrionops*, and *Scolecormorphus* are rescored.

Character 7: *Rhinatrema* and *Epicrionops* are rescored.

Character 9: *Epicrionops* is rescored.

Character 10a and b: Nussbaum's characters 10 and 26 concerned variation in size of the upper temporal fossa and in the origin of the musculus adductor mandibulae externus major (= *m. levatores mandibularum* anterior), respectively. These characters are not entirely independent, because it is not possible for the adductor muscle to extend through the fossa when the skull is stegokrotaphic and the fossa is closed. The characters have been combined here and represented as binary factors of a linear multistate character: upper temporal fossa large with musculus adductor mandibulae externus major extending through fossa and meeting at dorsal midline of skull (00) to fossa closed or nearly closed (10) to fossa large but adductor muscle not extending dorsally through the fossa (11). Nussbaum also distinguished between nearly closed and closed fossae as separate character states, but this distinction needs to be reevaluated and is not maintained here. Our ordering of the character assumes that the temporal fossa has been secondarily derived in species where adductor musculature does not extend through the fossa. This assumption explains this configuration of adductor musculature as the result of ancestral confinement within the adductor chamber by closed fossa.

Character 15a and b: Nussbaum (1979) coded variation with respect to pterygoids as four states in a single, linear, ordered multistate character. In his data matrix, taxa scored as state C, "small and tends to fuse to adjacent bones," lack a distinct pterygoid. They have instead an elongate processus pterygoideus of the quadrate that presumably incorporated the pterygoid through evolutionary fusion. A small bone, referred to both as an ectopterygoid or a pterygoid, is present at the anterior margin of the processus pterygoideus of the quadrate in some taxa, and variability of this element was the basis for Nussbaum's character description. This element appears to form late in ontogeny through a splitting of the processus pterygoideus, and is therefore neither a pterygoid nor an ectopterygoid, and may be termed a pseudoectopterygoid (Wilkinson and Nussbaum, 1992). Only a single taxon, *Scolecormorphus*, was coded by Nussbaum (1979) as having the terminal derived condition of his multistate character (state D), "none or fused

to adjacent bones." Because the pterygoid appears to be absent in taxa other than *Scolecormorphus*, the character states have been redefined: pterygoids large distinct elements (00) to small distinct elements (10) to absent (11). Scolecormorphids are atypical in having neither a pterygoid nor a well-formed processus pterygoideus, and it is not possible to distinguish whether this unique condition arose subsequent to loss of the pterygoid, through replacement by a processus pterygoideus, or independently of any development of the latter process. Therefore, *Scolecormorphus* is scored as equivocal (using missing data) with respect to this character. The peculiar derived condition of scolecormorphids is an uninformative, singlet-derived character state (autapomorphy) in this data set and was not included.

Character 17: Nussbaum (1979) coded stapedial variation as a three-state linear, ordered, multistate character. His terminal derived condition (state C) "stapes absent" is a feature restricted to scolecormorphids and, as an uninformative autapomorphy, was not included here. Further, it is not possible to determine whether loss of the stapes was subsequent to, or independent of, loss of perforation. Thus, *Scolecormorphus* is coded as equivocal with respect to presence or absence of perforation in the stapes. Character 20a, b, and c: Posterior elements of the glossal skeleton, ceratobranchials (cb) 3 and 4, appear to have been reduced and/or lost in rhinatrematids and fused and enlarged in other caecilians (Nussbaum, 1977). Nussbaum (1979) described this variation as two characters (20 and 21). The first described reduction using a three-state character. The terminal character state "ceratobranchials 3 and 4 missing" (state C) is unique to *Rhinatrema* and was excluded because it is uninformative in the context of this analysis. The second character described the fusion and expansion of the posterior ceratobranchials but also included reduction as an independently derived state so that this feature was weighted doubly (because it is included in both characters). Scolecormorphids have a peculiar derived condition where posterior ceratobranchials of each side extend medially and fuse posterior to the larynx. Nussbaum included this as a further character state derived from the greatly expanded condition. Because this state is restricted to *Scolecormorphus*, it is therefore uninformative and was excluded. It is unclear whether this condition arose from fused and expanded ceratobranchials 3 and 4, as suggested by Nussbaum, or from fused but unexpanded ceratobranchials. Consequently, *Scolecormorphus* is coded as equivocal with respect to

these two character states. The revised coding is as follows: posterior glossal skeleton reduced in size, cb 4 absent (100) from not reduced in size cb 3 and 4 distinct (000) to cb 3 and 4 fused not much expanded (010) to cb 3 and 4 much expanded (011). The second of these states (000) is not known in any caecilian but corresponds to the assumed primitive condition and is used in coding the hypothetical ancestor.

Character 29a and b: Nussbaum (1979) described variation in position of the tentacular aperture with six character states (A–F) connected by a branching, character-state tree. However, only four of these character states were represented in the taxa included in the analysis (no taxa were scored as state B or as state E). Distinctions between states B and C, and between states D and E, may be useful in a broader analysis, but we have not maintained them here. In the context of this analysis, Nussbaum's state F is an uninformative, derived state of *Typhlonectes* and was not included. We treated the variation with a three-state character: tentacular aperture adjacent to eye (00) to more or less midway between the eye and naris (10) to below naris (11). We consider the condition of *Typhlonectes* to have been derived independently from the intermediate position found in the more generalized typhlonectid genus *Chthonerpeton* (Wilkinson, 1989).

Character 31: Nussbaum (1979) recognized transverse, circular, and longitudinal vents as discrete states with the circular condition intermediate between longitudinal and transverse. The distinction between circular and transverse vents is less clear cut than that between either and the longitudinal condition. We coded variation as vent longitudinal (0), transverse or circular (1).

Character 36: Mesethmoid covered dorsally (0), exposed between frontals (1). Nussbaum (1979)

described a third state (state C), "exposed between nasopremaxillae" that is restricted to *Idiocranium*, a genus not included in his or this study. This condition is not considered further. Character 39: Choanae not completely encircled by maxillopalatine (0), completely encircled (1). Nussbaum (1979) recognized "absence of the postchoanal process of the maxillopalatine" as a third, and independently derived character state. This was based on Brand's (1956) inaccurate reconstruction of the scolecomorphid skull from serial sections, and it is now known that scolecomorphids have a postchoanal process Nussbaum (1985). *Siphonops*, *Scolecomorphus*, and *Dermophis* are rescored.

Character 40: Some or all premaxillary-maxillary teeth relatively small (0), all enlarged (1). A third condition (state C), "a few lateral maxillary teeth enlarged," was described by Nussbaum (1979) as an independently derived character state. This is restricted to *Rhinatrema*, is uninformative, and was excluded. The relationship of this condition to the other states is uncertain, and *Rhinatrema* is scored as equivocal with respect to them.

Characters 42 and 43: Nussbaum's (1979) coding of two life-history characters for *Rhinatrema* and *Oscacaecilia* were based on quite indirect inferences. They are rescored as equivocal.

Character 44: Atria not divided externally (0), divided externally (1).

Character 45: Anterior pericardial space short and small (0), long and extensive (1).

Character 46: Posterior internal flexures in *m. rectus laterales* less than two (0), two (1).

Character 47: Internal flexures on *m. subvertebralis* none (0), one (1).

Character 48: Tracheal lung absent (0), present (1).

Character 49: Anterior annuli orthoplicate (0), angulate (1).