

## ON THE LIFE HISTORY OF THE CAECILIAN GENUS *URAEOTYPHLUS* (AMPHIBIA: GYMNOPTIONA)

MARK WILKINSON

*Dept. of Geology, University of Bristol, Queens Road, Bristol BS8 1RJ, UK*

*(Accepted 28.5.91)*

### ABSTRACT

Previous workers have suggested that uraeotyphlid caecilians are probably oviparous with direct development. Contrary to these suggestions *Uraeotyphlus oxyurus* has a larval stage with typically larval morphological features including a lateral line system, 'spiracles', and labial folds. Two larvae and one metamorphic specimen of *U. oxyurus* are described and aspects of their morphologies compared to that of adult *Uraeotyphlus*, the larvae of other caecilians and to that of aquatic adults of the Typhlonectidae. Gut contents indicate that the larva of this species is not a highly abbreviated non-feeding life history stage.

### INTRODUCTION

The monogeneric caecilian family Uraeotyphlidae comprises four nominate species from the state of Kerala, South India that share many primitive morphological attributes with caecilians of the 'primitive' families Rhinatrematidae and Ichthyophiidae, but which are thought to be closer cladistically to the more derived 'higher' families Scolecomorphidae, Typhlonectidae and Caeciliidae (Nussbaum 1979; Duellman & Trueb, 1986). As far as is known, rhinatrematids and ichthyophiids are oviparous and have a free-living larval stage whereas the majority of species of the higher families are either oviparous with direct development or are viviparous (Nussbaum, 1977; Wake, 1977).

Several opinions have been expressed concerning the life history of *Uraeotyphlus*. Ramaswami (1941) described the cranial anatomy of *U. narayani* and noted that the smallest specimen examined by him (a 90 mm juvenile) was essentially adult in its morphology. He consequently included among a list of characters distinguishing *Uraeotyphlus* and *Ichthyophis* the "highly abbreviated embryonic and larval periods and the appearance of adult characters very early in larval life if not in the embryos of *Uraeotyphlus*" (Ramaswami, 1941 p. 198). Wake (1977) listed *U. oxyurus* among the oviparous caecilian taxa as evidenced by unreported clutch data, and presumably based on the observed correlation between oviparity, large ova mass and large clutch size in caecilians for which more direct information on life histories is available. Nussbaum (1979) cited Ramaswami's (1941) observations as strong support for the inference that *Uraeotyphlus* has direct development with no free-living larval stage. Additionally, he noted that dissections had revealed large yolky eggs, typical of oviparous caecilians, and no fetuses. Neither of the latter workers cited Parker & Dunn's (1964) inclusion of *U. oxyurus* in a list of caecilians with free living larvae.

Nussbaum (1979) included the absence of a larval stage as a derived state in a cladistic analysis of the phylogenetic position of *Uraeotyphlus* relative to twelve other caecilian genera. Contrary to the text, *Uraeotyphlus* was scored as having the primitive state of this character in his data matrix. Duellman & Trueb (1986) recapitulated the same contradiction by describing *Uraeotyphlus* as presumably having direct development, but then scoring the Uraeotyphlidae as having larvae for the purposes of cladistic analysis of familial relationships within the Gymnophiona. Lescure *et al.* (1986) scored *Uraeotyphlus* as having direct development for the purposes of developing a

generic level phylogenetic hypothesis for caecilians. There is thus considerable confusion in the literature concerning the life history of *Uraeotyphlus* which requires clarification.

In 1882, the British Museum (Natural History) [BMNH] purchased three specimens of *Uraeotyphlus oxyurus* from Col. Beddome that are listed as larval specimens in the Museum's register. One of these specimens was exchanged with G. K. Noble and the American Museum of Natural History [AMNH] in 1925. The two BMNH specimens were almost certainly seen by Parker, and presumably formed the basis for inclusion of this species in Parker & Dunn's (1964) list. I have recently examined all three of the specimens collected by Col. Beddome over a century ago.

### MATERIALS AND METHODS

Specimens were examined with the assistance of a binocular dissection microscope. All measurements were made to the nearest 0.1 mm with dial callipers except total lengths which were measured to the nearest 1 mm by stretching the specimens along a ruler. Short incisions were made in the posterior gut and urodeal part of the cloaca to allow examination of ingested material. Figures were prepared from camera lucida drawings.

### RESULTS

The smallest of the three specimens, BMNH 82.12.12.11 is unquestionably larval. It has a total length (TL) of 87 mm, and differs most obviously from metamorphosed specimens in the possession of labial folds that are associated with aquatic suction feeding (O'Reilly, 1988), external nares that are lateral and subtriangular rather than dorsal and subcircular, and a pair of small but well defined spiracles, one on each side (Fig. 1a).

The labial folds are developed along the lateral margins of both the lower and upper jaws. With the mouth closed or only slightly opened, the upper fold extends over, and lateral to, the lower fold. Close to the angle of the jaws, upper and lower folds interdigitate and are probably not normally separated in life. Rostrally the upper folds gradually diminish in size and eventually completely disappear, leaving a small anteromedial oral aperture that is unguarded by labial folds (Fig. 2a). The form of the labial folds would clearly concentrate the full suction effect of buccal expansion to the region of the anteromedial oral aperture during feeding.

The spiracle of larval caecilians is associated with the distal tips of the third and fourth ceratobranchials and is therefore not

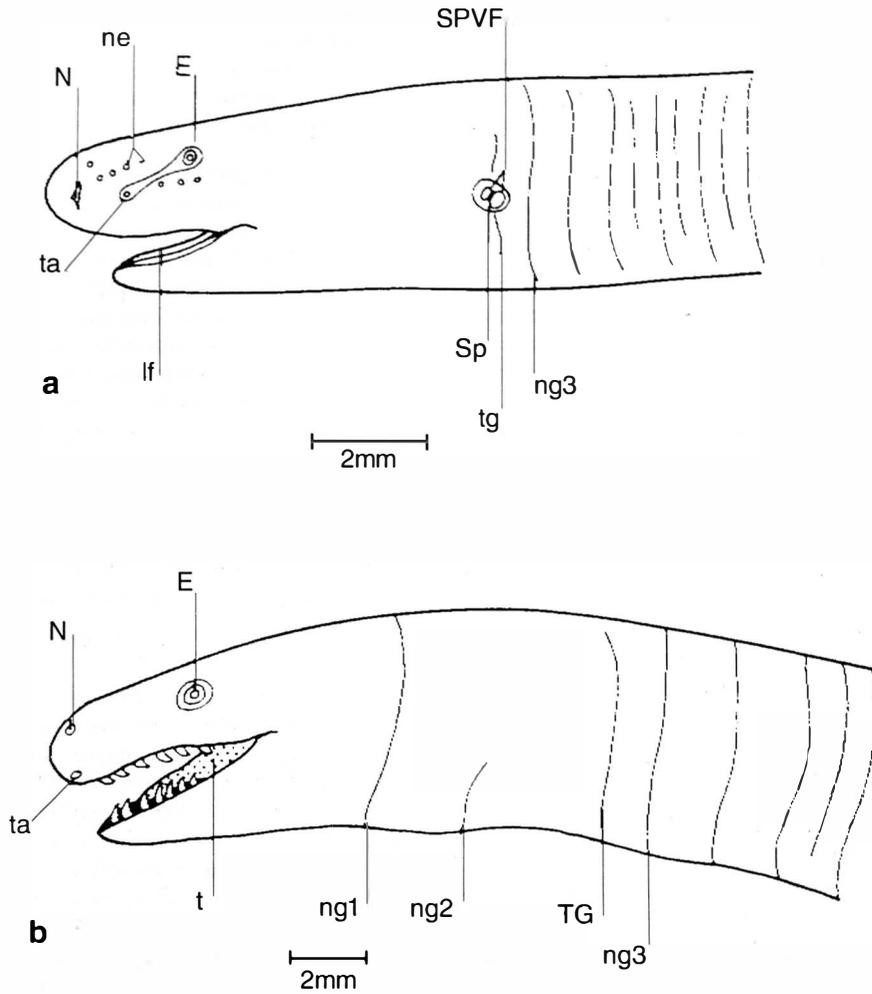


Fig. 1. Comparative lateral views of the head and anterior trunk of (a) larval (AMNH 23659) and (b) adult (BMNH 82.12.12.10) specimens of *Uraeotyphlus oxyurus*. Abbreviations: E, eye; lf, labial fold; N, naris; ne, neuromasts; ng1 - ng3, 1st - 3rd nuchal groove; Sp, spiracle; SPVF, spiracular 'valve' flaps; t, tongue; ta, tentacular aperture; tg and TG, transverse groove.

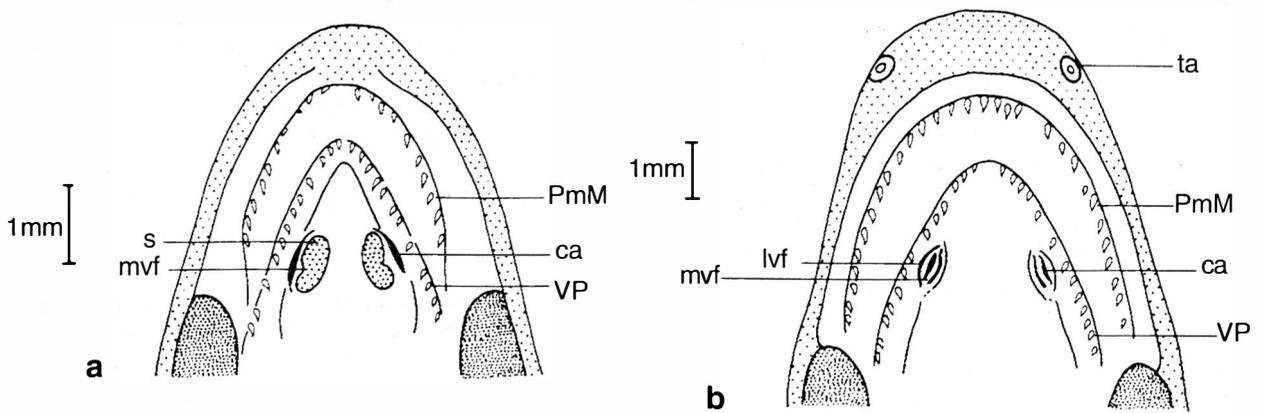


Fig. 2. Comparative palatal views of the buccal cavity of (a) larval (AMNH 23659) and (b) adult (BMNH 82.12.12.10) specimens of *Uraeotyphlus oxyurus*. Abbreviations: ca, choanal aperture; lvf, lateral choanal valve flap; mvf, medial choanal valve flap; PmM, premaxillary-maxillary tooth series; s, sac-like medial expansion of medial choanal valve flap; ta, tentacular aperture; VP, vomero-palatine tooth series.

homologous with the spiracle of elasmobranchs. Each spiracular aperture is guarded by a pair of well developed fleshy flaps that are continuous with the surrounding skin. These fleshy, valve-like flaps make the spiracular aperture narrow and elongate (Fig. 1a) and presumably aid in closure of the spiracle. There is no indication of gills, although the spiracular area extends as a depression a little anterior to the aperture and this anterior region was presumably equipped with the external gills, that may be assumed to characterise an earlier stage in the ontogeny of this species.

The tentacular aperture is far anterior to the eye but posterior to the level of the naris. The eye and tentacular aperture are connected by a faint eye-tentacle stripe that indicates the position of the tentacle organ under the dermis. In adult *Uraeotyphlus* the tentacular aperture is further anterior, directly below, or below and slightly anterior to the dorsal naris, and the tentacle organ is covered by the maxillopalatine with no indication of an eye-tentacle stripe (Fig. 1b). Also unlike the adult condition there are no scales associated with the relatively poorly marked annuli and the skin is distinctly thinner and less glandular. Although a full adult complement of annuli are present in the larva, the nuchal collars are not clearly differentiated (Fig. 1). There are further differences between this larva and adults in characters of the buccal cavity (see below).

The larva also differs from those of ichthyophiids and rhinatrematids described by Taylor (1968, 1970) and Hetherington & Wake (1979) and from the larvae of the caeciliid *Sylvacaecilia grandisonae* described by Largen *et al.*, (1972). There appears to be no indication of a lateral line system and the tail bears no fin and lacks any substantial lateral compression.

A second specimen AMNH A23659 is slightly larger (TL 85 mm) than the former but is also distinctly larval. Despite its slightly larger size, this specimen appears less developed than the former in having the tentacular aperture distinctly closer to the eye and therefore further from the adult position. There are also a few poorly indicated neuromast organs on the head belonging to the infraorbital and supraorbital series (Fig. 1a). In other features this specimen is similar to the former.

The jaws of this specimen have been cut clearly revealing the larval features of the buccal cavity of this and the former specimen. Teeth of the premaxillary-maxillary series do not extend posterior to the choanae, whereas in adults they extend posterior to the choanae close to the posterior level of the vomeropalatine series (Fig. 2a). The choanae of adult *Uraeotyphlus* are guarded by a pair of fleshy valve flaps, one lateral and one medial, that lie deep within the choanae but are just visible in palatal view (Fig. 2b). In the larvae the lateral valve flap is present in the adult position, but the medial flap extends into the buccal aperture of the choana and effectively conceals the deeper lateral flap. On its medial side, the medial choanal valve flap is continuous with a large membranous sac filled with a loose fibrous connective tissue. The membranous sac occupies most of the lumen of the choana and displaces the medial valve flap laterally, thereby restricting the buccal aperture of the choana to a narrow slit. The medial valve flap also bears a small but distinctive fleshy medial process (Fig. 2a).

The tongue of larval *Uraeotyphlus* is formed by the anterior margin of the copula that projects into the buccal cavity with a mobile transverse free edge and little intrinsic muscular or

glandular tissue. It is thus a primary tongue (Edgeworth, 1935). The fleshy, muscular tongue of the adult (Fig 1b) must form during metamorphosis as the copula disappears, and thus represents a secondary tongue. It appears far less mobile than the larval tongue.

The largest specimen of the series BMNH 82.12.12.12 (TL 95 mm) appears mostly adult in its morphology. There is no remnant of labial folds, the nares have attained a dorsal adult position and the tentacular aperture is much closer to, but not quite yet at, the adult position. Similarly the choanal valves, teeth and tongue have the adult configuration. A tiny subcircular spiracular aperture surrounded by a weak 'gill scar' and lacking the well-developed fleshy flaps of the larvae is present. There are no scales in the annular folds although the skin is distinctly thicker and more glandular than in the larvae. This specimen appears to have nearly completed metamorphosis.

All three specimens have gut contents that include a mixture of organic (chitinous arthropodal) and mineral debris that indicates that they had been actively feeding. In addition, there is no indication of persistent yolk reserves in any of the specimens.

## DISCUSSION

It is clear that at least one species of *Uraeotyphlus* has a life history that includes a free-living and self-nourishing larval stage. In the absence of larval specimens of the other species it is not possible to infer their mode of life history with great certainty. It is possible that *U. narayani*, the species studied by Ramaswami (1941), does have direct development, but the small size at which an essentially adult morphology is encountered in this species cannot be considered as strong evidence for the occurrence of direct development because metamorphosis in *U. oxyurus* must occur at a comparably small size. It is more likely that the Uraeotyphlidae, like the 'primitive' families Rhinatrematidae and Ichthyophiidae, is characterised by a larval stage and therefore, until there is positive evidence to the contrary, this is how the family or genus would best be scored if included in any phylogenetic analysis incorporating life history information as character data.

The lack of a fin and lateral compression of the tail in the larvae of *U. oxyurus* is puzzling because these features are found in the larvae of ichthyophiids and rhinatrematids. It is probable that both larval specimens have begun metamorphosis because they are close to the size of the third, and clearly metamorphic, specimen, have no or only faint indications of a lateral line system, and the tentacle has begun to migrate forward to the adult position from the orbit. It is therefore possible that a fin and laterally compressed tail may be present at an earlier, premetamorphic stage of ontogeny. Younger specimens are, however, unknown.

The external nares of most caecilians are dorsolateral. Dorsal nares are a distinctive and probably derived feature of adult *Uraeotyphlus* that are also found in the Scolecomorphidae and several genera of the Caeciliidae (*Caecilia*, *Geotrypetes*, *Hypogeophis*, *Idiocranium*, and *Oscacecilia*). All these forms with dorsal nares also have anteriorly placed tentacular apertures. The transition from lateral to dorsal nares in *Uraeotyphlus* appears to be associated with the forward ontogenetic migration of tentacle to the anterior adult position. Dorsal migration of the external nares may represent a common epigenetic response in all these forms to the forward migration of the tentacle and

consequent 'crowding' of the rostrum of the snout. This possible epigenetic interaction and lack of independence should be borne in mind if tentacle and naris positions are to be used as characters for phylogeny estimation.

Adult caecilians typically have subcircular external nares, with the exception of the aquatic or semi-aquatic typhlonectid genera *Nectocaecilia*, *Potomotyphlus* and *Typhlonectes*. These are the only adult caecilians that have subtriangular nares (Taylor, 1968; Wilkinson, 1989) similar to those seen in larval *Uraeotyphlus*. The aquatic larvae of ichthyophiids and rhinatrematids also have subtriangular external nares that transform into the more typical adult subcircular shape at metamorphosis (pers. obs.) and the same transition is seen in the larvae and adults of the caeciliid *Sylvacaecilia grandisonae* (Largen *et al.*, 1972). Thus there seems to be a correlation between subtriangular external nares and an aquatic habitus, although the significance of this correlation is not clear. The ontogenetic transformation from subtriangular to subcircular naris shape in 'primitive' caecilians, together with the probability that the subtriangular adult condition is derived within the Typhlonectidae (Wilkinson, 1989) suggests that the derived typhlonectid condition may be pedomorphic. It also provides an example of incongruence between the outgroup and ontogenetic criteria for assessing character state polarities.

The unusual arrangement of the choanal valves of *Uraeotyphlus* which results in a greatly restricted choanal aperture parallels the condition seen in adults of the aquatic typhlonectid *Potomotyphlus*. In this form the valve flaps are also relatively superficial and are partially fused (Nussbaum & Wilkinson, 1989). *Potomotyphlus* is a relatively small headed form that presumably takes prey of restricted size (Wilkinson, 1991). *Uraeotyphlus* larvae are presumably mainly suction feeders and may therefore also be restricted to prey of small size. One speculative explanation of the choanal similarity of *Potomotyphlus* and *Uraeotyphlus* larvae is that the reduction in size of the functional choanal aperture in both forms, whilst accomplished in different ways, may be a common response to the increased problem of prey becoming lodged in the choanae attendant upon the utilization of relatively small prey items. Alternatively, the occlusion of the larval choanal aperture in *Uraeotyphlus* may enhance the efficiency of suction feeding by preventing the flow of water into the buccal cavity through the choanal apertures during rapid buccal expansion.

#### ACKNOWLEDGEMENTS

I thank Darrell Frost (AMNH), Nick Arnold and Barry Clarke (BMNH) and their institutions for the loan of *Uraeotyphlus* and Ron Nussbaum for helpful discussion. This work was supported by SERC grant GR/F 87912.

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