Development and demography of larval *Epicrionops bicolor* (Amphibia: Gymnophiona: Rhinatrematidae)

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**ABSTRACT**

Information on even the most basic biological aspects is often missing for many species and even higher taxa of caecilians. As in other amphibians, development is plesiomorphically biphasic and aquatic larvae are present in Rhinatrematidae, Ichthyophiidae, and some Indotyphlidae. However, only very little information on larval morphology and ecology is available. Here I describe a series of *Epicrionops bicolor* larvae and metamorphs from Peru and provide details on the development of the annulation pattern, colouration, external gills, lateral line system, and other morphological characters and discuss the taxonomic value of lateral line characters. Specimens were collected at two different times of the year, allowing inferences of a few key demographic characteristics. Hatching probably occurs around August and September at a size of approximately 55 to 65 mm. Larval development takes about 1 year to complete and metamorphosis occurs at around 180–190 mm total length.

**Introduction**

With about 214 described species [1], Gymnophiona or caecilians comprise the smallest of the three amphibian orders. Although caecilians are widely distributed throughout the tropics and subtropics of the world [2], comparatively little is known for most species about even basic aspects of their biology. One aspect for which little information is generally available is breeding biology, although various recent studies have highlighted a surprising diversity of caecilian breeding strategies and development [3–7]. As far as is known, a biphasic life-history with an aquatic larva and a metamorphosis is plesiomorphic for Gymnophiona and is retained in the two basal-branching families Rhinatrematidae and Ichthyophiidae [7]. Aquatic larvae are furthermore found in some species of Indotyphlidae, but these are thought to be of a secondary nature; all other caecilian species are either direct developing or viviparous [7].

Most studies related to caecilian development and life history have focussed on various aspects of morphological development [e.g. 8–12], predominantly in terecanote caecilians. For rhinatrematid or ichthyophiid caecilians, few detailed studies are available that focus on aspects of larval biology [e.g. 13,14], and only some descriptions of larvae are available [15–17]. No keys exist that would aid in the identification of larval caecilians. This partly reflects the overall paucity of larger series in collections, which would be necessary to establish reliable, specific characters for identification. At the same time, larval caecilians seem to be relatively frequently collected (see, for instance, the large proportion of larval vouchers in [18]) that could be utilized in species identification. Being able to reliably identify larvae would benefit the study of caecilians and their conservation, especially given that a substantial proportion of caecilian species is only known from the holotype [19,20] or very few specimens overall that have often been collected decades ago [21,22]. The original descriptions are also occasionally imprecise [23], which further complicates a reliable identification of caecilian specimens.

Caecilians are generally cryptic, and adults are not commonly found in routine surveys. While caecilian larvae also tend to hide among plants and debris, larvae are often comparatively more easily collected [2]. Also, as in other cryptic amphibian species [24], the larval life span usually exceeds the duration of the annual breeding season and caecilian larvae have thus a great potential as indicators for the presence of a species in survey work. This potential, however, is currently not realized because of the large gaps in our knowledge of larval identities and basic taxonomic work is needed to fill these gaps. I here describe a series of larval *Epicrionops bicolor* and provide data on morphological changes during larval development as well as morphometric and meristic data. I particularly focus on the mechanosenory lateral line system, which seems to have the potential to differentiate species [25].

**Material and methods**

Available for study were 24 specimens from the collections of the National Museum of Natural History, Smithsonian Institution (USNM346162-76; USNM3462...
87-65). The collection consists of 22 larval specimens, one late metamorphic and one fully transformed individual. Based on the relevant meristic and morphometric characters [19], the specimens best fit the description of Epicrionops bicolor subcaudalis Taylor, 1968, though I follow current taxonomic treatments in not recognizing subspecies. The specimens were collected by Robert P. Reynolds and Antonio Salas at: Paucartambo, Cuzco, Peru, 68 km (by road) NE of Puente Union on Rio Tachila (=Bosque de las Nubes, KM 150 on Paucartambo-Atalaya road; 1700 m asl; 13°04'13"S; 71°34'00"W). Specimens were collected in two batches from two different sites about 0.5 km from each other. The first batch (USNM346162-76) was collected on 9 September 1991 from a small, water-filled ditch adjacent to the main road and lined by a steep, forested bank on one side. The ditch was filled with dead, decaying leaves and the specimens were found hiding inside the submerged leaf mats. The second batch (USNM346287-95) was collected on 23 June 1993 from a pool at the base of a small waterfall, where the specimens were collected from under rocks along the edge of the pool. The bottom of the pool was filled by layers of dead leaves. Judging from the state of preservation, the specimens were presumably fixed in formalin and are now stored in 70% Ethanol.

In addition to standard measures and counts [e.g. 26,27], some additional measurements were taken in accordance with larval morphology as follows (see Table 1): distance between snout tip and anterior margin of gill opening; distance between tip of lower jaw and anterior margin of gill opening; head width at level of gill opening. All measurements except total length were taken with a digital calliper to the nearest 0.1 mm under a dissection microscope. Total length (TL) was measured to the nearest 1 mm using a ruler. Number of vertebrae was counted from X-ray images. Sex was determined by direct inspection of the gonads through a small incision into the body wall. In selected specimens, the presence of scales was determined by opening the scale pockets dorsally at midbody and just anterior to the vent. Drawings of the lateral line system were prepared with the aid of a camera lucida and digital photographs were taken with a Zeiss Discovery V12 Stereomicroscope. Terminology of the lateral line system follows Hetherington and Wake [25] for the lateral line system of the head region and Wilkinson [28] for the lateral line system of the trunk. The correlation between body size and number of neuromasts and ampullary organs. The specimens collected in September were fixed with their mouth open, which facilitated the counting of teeth in this series. No attempt was made to count teeth of specimens of the June sample to avoid damaging the specimens. Standard morphometric and meristic data are presented in Tables 1 and 2.

Annulation pattern and scales
The smallest larvae showed only weak indications of primary annuli on the lateral sides of the body, although these were generally very indistinct and difficult to count, and the tail was free of any indication of annuli (Figure 1(c)). The first indication of a subdivision of the primary annuli was present in a larva of 130 mm TL. In this specimen faint, short secondary grooves were present on the lateral most side of the primary annuli in the posterior midbody region. By around 155 mm TL (Figure 1(d)), annuli had become distinct and an increase in body size generally corresponded with an increase in number of annuli (Tables 1 and 2). No distinction between secondary and tertiary annular folds was visible. The development of the tail annuli seems to lag somewhat behind those of the body. In all larvae, tail annuli, where present, were not very distinct, incomplete, and only laterally developed. Even in the largest larvae, the posterior quarter of the tail did bear no indication of annuli. In the metamorphic specimen, the tail was completely annulated, although the annuli of the posterior third of the tail remained dorsally and ventrally incomplete and only faintly indicated at the very tail end (Figure 1(e)), whereas the fully transformed specimen had complete tail annuli. The development of the tail annuli seemingly lags behind the body annuli and the annulation of the posterior half of the tail only seems to happen during metamorphic climax (Table 1). All larvae furthermore lack distinct nuchal collars and grooves (Figure 1(a)).

Scales were absent in a larva of 131 mm TL. The first small, scattered scales were found dorsally just posterior to the cloaca in a larva of 160 mm TL. In larvae of 180 mm TL, large scales were present dorsally just before the cloaca and formed a single row. The same condition was found in the metamorphic and fully transformed specimens.

Colouration
The smallest specimens already had a very faint lateral band that was less darkly pigmented than the rest of the body; the body was otherwise uniformly darkly pigmented. This band faded somewhat in the posterior third of the body but was still discernible. In specimens of about 100 mm TL, the lateral band was weakly yellow and relatively narrow in most specimens; the colour still faded somewhat along the posterior half of the body. In specimens of 150–160 mm TL and larger, the lateral stripe was strongly coloured and broader in most specimens. Specimens of this size also had a prominent patch of yellow colouration on the
Table 1. Morphometric and meristic data for *Epicrionops bicolor* larvae, metamorphs, and subadult collected in September 1991. Asterisk (*) denotes undifferentiated, indistinct, or otherwise difficult to count. All measurements are in mm.

| Life stage/Sex | USNM 346162 | -63 | -64 | -65 | -67 | -68 | -69 | -70 | -71 | -72 | -73 | -74 | -75 | -66 | -76 |
|----------------|-------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Total length   | 175         | 167 | 155 | 165 | 161 | 151 | 189 | 108 | 112 | 104 | 84  | 65  | 58  | 184 | 205 |
| Number of vertebrae | 78          | 81  | 79  | 80  | 81  | 81  | 81  | 82  | 79  | 81  | 78  | *   | *   | 79  | 79  |
| Number of annuli | 289         | 284 | 260 | 284 | 267 | *   | 291 | *   | *   | *   | *   | *   | *   | *   | 298 |
| Annuli interrupted by doecal disc | 8           | 6   | 6*  | 7*  | *   | *   | 7   | *   | *   | *   | *   | *   | *   | 6   | 8   |
| Tail annuli    | 12*         | 18  | *   | 14* | 15* | *   | 17  | *   | *   | *   | *   | *   | *   | *   | 26  |
| Snout tip to gill slit | 13.5        | 13.1| 12.2| 12.6| 11.5| 15.0| 8.7 | 9.4 | 7.8 | 7.6 | 6.8 | 6.1 | -   | -   | -   |
| Snout tip to first nuchal groove | -            | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 11.0| 11.4|
| Snout tip to angle of jaws | 5.4         | 5.0 | 5.0 | 4.1 | 4.1 | 4.0 | 5.0 | 3.0 | 3.5 | 2.8 | 2.9 | 2.5 | 2.4 | 5.8 | 7.2 |
| Length of first nuchal groove | -           | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 4.0 | 2.3 | 4.0 |
| Head width at first nuchal groove | -          | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 7.8 | 8.1 |
| Head width at angle of jaws | 7.6         | 8.0 | 7.2 | 7.5 | 7.2 | 6.6 | 7.5 | 4.8 | 4.9 | 4.4 | 4.0 | 3.2 | 2.9 | 7.3 | 7.1 |
| Internarial distance | 2.9         | 2.9 | 2.6 | 2.7 | 2.9 | 2.4 | 3.0 | 2.1 | 2.2 | 1.8 | 1.7 | 1.4 | 1.4 | 2.2 | 2.3 |
| Interocular distance | -           | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 5.5 | 5.2 |
| Intertentacular distance | 4.6         | 4.7 | 4.2 | 4.2 | 4.3 | 4.3 | 5.3 | 3.5 | 3.5 | 2.9 | 2.6 | 2.3 | 2.1 | 5.0 | 5.0 |
| Distance naris-tentacle | -           | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 3.0 | 3.4 | -   | -   |
| Distance naris-eye | 3.3         | 3.2 | 3.0 | 3.0 | 3.1 | 2.7 | 3.3 | 2.1 | 2.3 | 2.1 | 1.6 | 1.4 | 1.2 | 3.6 | 3.7 |
| Distance tentacle-margin upper lip | -          | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 1.3 | 1.2 | 1.3 |
| Distance naris-first nuchal groove | -         | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 10.2| 10.4| 10.2| 10.4|
| Distance tentacle-tip of snout | -          | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 3.5 | 4.2 | -   | -   |
| Distance tentacle-angle of jaws | -          | -   | -   | -   | -   | -   | -   | -   | -   | -   | -   | 1.9 | 3.1 | -   | -   |
| Distance eye-angle of jaws | 1.0         | 1.1 | 0.8 | 1.0 | 1.0 | 0.5 | 0.8 | 0.5 | 0.6 | 0.4 | 0.4 | 0.4 | 0.4 | 1.6 | 2.5 |
| Distance snout tip – anterior margin of mouth | 0.9       | 0.8 | 0.9 | 0.7 | 0.7 | 0.4 | 1.2 | 0.8 | 0.8 | 0.7 | 0.8 | 0.5 | 0.6 | 0.6 | 0.6 |
| Width at mid-body | 9.7         | 8.1 | 9.0 | 8.4 | 8.4 | 7.7 | 9.5 | 5.3 | 5.6 | 4.8 | 4.8 | 4.1 | 2.4 | 9.1 | 8.1 |
| Width at level of vent | 5.4         | 4.4 | 4.5 | 4.6 | 4.4 | 4.6 | 5.5 | 3.0 | 2.9 | 2.8 | 2.6 | 2.1 | 1.7 | 6.3 | 5.7 |
| Distance vent-body terminus | 11.1       | 12.7| 11.4| 11.3| 11.2| 11.8| 13.8| 8.8 | 9.2 | 9.5 | 7.9 | 6.2 | 5.7 | 12.7| 12.0|
| Premaxillary-maxillary teeth | -           | 21  | 24  | 20  | 19  | 19  | 19  | 18  | 18  | 16  | 20  | 15  | 18  | 16  | 32  |
| Vomeropalatine teeth | -           | 20  | 27  | 24  | 24  | 27  | 28  | 30  | 20  | 25  | 26  | 23  | 19  | 26  | 29  |
| Dentary teeth | -           | 22  | 24  | 22  | 24  | 27  | 26  | 29  | 21  | 20  | 19  | 20  | 20  | 29  | 29  |
| Inner mandibular teeth | *           | 16  | 13  | 17  | 10  | 13  | 14  | 13  | 10  | 12  | 9   | 8   | 9   | 12  | 18+ |
Table 2. Morphometric and meristic data for *Epicrionops bicolor* larvae collected in June 1993. Asterisk (*) denotes undifferentiated, indistinct, or otherwise difficult to count. All measurements are in mm.

| Life stage/Sex | USNM 346287 | USNM 346289 | USNM 346290 | USNM 346291 | USNM 346292 | USNM 346293 | USNM 346294 | USNM 346295 | USNM 346296 |
|---------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| Total length  | 160-180     | 180-181     | 151-165     | 163-171     | 131-148     | 148-153     |
| Total No. annuli | *           | 302         | 277*        | *           | 283*        | *           |
| Annulli interrupted by cloacal disc | *           | 6           | 6*          | 5           | *           | *           |
| Tail annuli   | *           | 17*         | 16*         | 13*         | *           | *           |
| Distance snout tip-gill slit | 12.3        | 14.2        | 13.0        | 12.7        | 12.4        | 12.6        |
| Snout tip to angle of jaws | 5.2         | 5.8*        | 5.3*        | 5.0*        | 4.3*        | 4.3*        |
| Tip of lower jaw to gill slit | 11.9        | 13.4        | 12.6        | 11.8        | 11.4        | 11.9        |
| Distance eye-angle of jaws | 1.1         | 1.3         | 1.5         | 1.3         | 1.0         | 1.2         |
| Width at level of vent | 12.9        | 13.7        | 14.0        | 12.3        | 12.8        | 13.2        |
| Width at mid-body | 7.5         | 7.9         | 8.0         | 7.1         | 7.6         | 7.6         |
| Width at level of vent | 4.0         | 5.3         | 4.6         | 3.4         | 3.8         | 4.1         |
| Distance snout tip – anterior margin of mouth | 0.7          | 0.5         | 0.6         | 0.6         | 0.7         | 0.6         |
| Premaxillary-maxillary teeth | *           | *           | *           | *           | *           | *           |
| Vomeropalatine teeth | *           | *           | *           | *           | *           | *           |
| Dentary teeth | *           | *           | *           | *           | *           | *           |
| Inner mandibular teeth | *           | *           | *           | *           | *           | *           |
| Number of vertebrae | 80          | 81          | 82          | 83          | 81          | 84          |

Table 3. Meristic data on neuromasts are given in Table 3. In general, neuromasts were far more distinctive than ampullary organs in all specimens. Especially along the trunk, ampullary organs were macroscopically often virtually indistinguishable from the various skin glands associated with the annuli. Individual rows showed both weak positive or negative correlations between neuromast number and total length, but none of these were statistically significant (Table 3). The lateral line system of a younger and an older larva is illustrated in Figure 2.

### Lateral line system

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### Nasal series

Neuromasts of the nasal line stretched from the underside of the snout ("upper lip") onto the anterior dorsal side of the head, medial of the naris. The row was more or less straight, but curved laterally at its dorsal-most end, with the degree of curvature very variable among the examined specimens. The separation of the nasal line from the supraorbital and infraorbital lines was not very distinct in some of the specimens, and in some of these, the supraorbital line appeared as a posterior continuation of the nasal line. On the ventral side of the snout, the infraorbital line extended along the upper margin of the mouth ("upper lip") and the nasal line originated in close proximity, also giving the impression of a continuity of both rows in some specimens.

### Supraorbital series

The supraorbital line formed an S-shaped curve that originated anteromedially on the dorsal side of the

posterolateral sides of the head, just anteroventral to the gill slit (Figure 1(a,b)). This patch was very faint and ill-defined in the smallest larvae but did become increasingly more prominent during larval development. All larvae furthermore showed some light colouration around the edges of the mouth ("lips") and the corner of the mouth (Figure 1(a)), along the inside of the lower jaw (in ventral view), as well as a diffuse patch on the throat. In older larvae, these areas of light colouration became increasingly more yellow. Some older larvae also had a lighter-coloured edge of the tailfin and a subtle yellow wash along the sides of the tail (Figure 1(d)). In all larvae, the cloaca was within an oval, whitish area of skin.

### External gills

All larval specimens possessed small, external gills, but there was considerable variation in the shape and arrangement of these. In general, the gill slit and external gills were contained within a sunken-in oval to diamond shaped area (Figure 1(a)). In most specimens, two external gills were present. These were positioned anterior to the gill slit and usually consisted of a short stem with a few (1–5, median 2) gill filaments, which did not project much beyond the rim of the depressed gill area (Figure 1(k,l)). There was considerable variation in the number of gill filaments present, both between specimens and between right and left gills of the same specimen and individual filaments were frequently fused. In most specimens, the gills had a short stem from which the filaments branched, but in some, the filaments seemed to originate directly from the skin and gave the impression of a bush- or glove-like structure. In addition, accessory, individual filaments were present in some specimens that originated either from the floor of the gill area or the bordering rim.
snout, somewhat behind the naris. It bent outwards and then inwards again in front of the eye, then medi-ally around the eye and terminated just behind the eye. The supraorbital line was not clearly separated from the nasal (see above) and infraorbital line in some of the specimens, where the supra- and infraor-bital lines seemed to fuse behind the eyes.

**Infraorbital series**
The infraorbital line is made up of more or less evenly spaced neuromasts and originated from a medial posi-tion on the underside of the snout (“upper lip”). From the tip of the snout, it ran along the anterior margin of the mouth to about the level of the nostril, from where the line started arching upwards and away from the mouth and along the lateral side of the snout towards the eye, where it passed below the eye and then arched upwards again behind the eye. It terminated somewhat behind the eye, with the distance from the eye being variable among the examined specimens.

**Postorbital series**
Neuromasts of the postorbital series formed a short, down-ward sloping line posterior to the mouth, about halfway between the eye and the gill opening. It consisted of only a few (max. 5) neuromasts. Between one to three additional neuromasts were present in the area between the postor-bital and oral lines in all specimens. These seemed to be

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Figure 1. Aspects of larval development in *Epicrionops bicolor*. (a) lateral view of the head and gill region in a large larva (180 mm TL); (b) lateral view of the head and gill region in a metamorphic specimen (184 mm TL); (c) tail end of a small larva (58 mm TL), arrow heads indicate primary annuli; (d) tail end of a large larva (155 mm TL); (e) tail end of a metamorphic specimen, arrow in C, D, and E indicates the position of the cloaca; (f) orbital region of a large larva (155 mm TL) showing no indication of tentacle development; (g) first external indication of developing tentacle (arrow) in a large larva (175 mm TL); (h) differentiated tentacle (arrow) in a metamorphic specimen (184 mm TL); external gills and gill slit in a larva of 108 mm TL in ventral view (i, right side, cranial towards the right), close-up view of left gill (k, cranial towards the left), and close-up of right gill (l, cranial towards the right); close-up of nearly closed gill slit in a metamorphic specimen (184 mm TL); I – 1st gill, II – 2nd gill, gs – gill slit, TL – total length. Not to scale.
| Specimen (USNM) | Total length in mm | Number of neuromasts |
|----------------|------------------|----------------------|
|                | Specimen (USNM) | Nasal series | Supra-orbital series | Infra-orbital series | Post-orbital series | Supra-spiracular series | Oral series | Accessory oral series | Mandibular series | Gular series | Ventro-lateral trunk series | Dorso-lateral trunk series |
| 346175         | 346175           | 58             | 0.68               | 8/7               | 15/17*             | 1*                  | 10/8           | 1*                  | 10/7          | 1*                  | 3*                  |
| 346172         | 346172           | 65             | 0.8/7              | 6/6               | 8/7               | 17/18*              | 1*              | 21/20*             | 1*              | 1/2                 | 10/10*              |
| 346173         | 346173           | 84             | 0.8/9              | 8/9               | 9/9               | 19/19               | 1*              | 21/20*             | 1*              | 1/2                 | 3*                  |
| 346170         | 346170           | 104            | 0.8/7              | 7/7               | 12/13*             | 3/4                 | 17/18*         | 1*                  | 19/20*         | 1/2                 | 20/17*              |
| 346287         | 346287           | 160            | 0.8/8              | 7/7               | 16/20              | 21/20*              | 1*              | 21/20*             | 1*              | 1/2                 | 20/17*              |
| 346169         | 346169           | 189            | 6/7                | 7/7               | 18/18              | 15/17               | 1*              | 19/20*             | 1*              | 1/2                 | 10/10*              |
| 346164         | 346164           | 167            | 5/6                | 4/4               | 15/18              | 12/17*              | 1*              | 19/20*             | 1/2              | 1/2                 | 9/5*                |
| 346163         | 346163           | 163            | 5/6                | 4/4               | 15/18              | 12/17               | 1*              | 19/20              | 1/2              | 1/2                 | 9/5*                |
| 346162         | 346162           | 155            | 4/4                | 3/3               | 13/13*             | 12/17               | 1*              | 19/20*             | 1/2              | 1/2                 | 9/5*                |
| 346161         | 346161           | 131            | 4/4                | 3/3               | 13/13*             | 12/17               | 1*              | 19/20*             | 1/2              | 1/2                 | 9/5*                |
| 346160         | 346160           | 122            | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346159         | 346159           | 112            | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346158         | 346158           | 94             | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346157         | 346157           | 84             | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346156         | 346156           | 78             | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346155         | 346155           | 67             | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |
| 346154         | 346154           | 59             | 3/3                | 2/2               | 10/8*              | 9/11*               | 1*              | 17/18*             | 1/2              | 1/2                 | 9/5*                |

**Correlation**

| Correlation | Neuroneumasts/TL | P Value |
|-------------|------------------|---------|
| 0.418       | 0.309            | 0.033   |
| 0.307       | 0.031            | 0.381   |
| 0.381       | 0.284            | 0.032   |

**Note:** Right/left, *indistinct and difficult to count or damaged.
more closely associated with the oral line in some specimens but were more closely positioned to the postorbital line in others. These additional neuromasts are here treated as accessory postorbital neuromasts.

**Supraspiracular series**

Neuromasts of the supraspiracular series formed a short line consisting of one to eight neuromasts just above the gill slit. In the largest larval specimen, supraspiracular neuromasts were absent.

**Oral series**

The oral lateral line was the most extensive of the lateral lines of the head region. It originated on the anterior lower jaw and extended close to the mouth along the lateral side of the lower jaw beyond the angle of the mouth and terminated somewhat anterior of the gill slit. Neuromasts were fairly evenly spaced, but their arrangement became slightly more scattered and irregular posterior to the postorbital line. The neuromasts formed a single line, but some individual (up to four), irregularly placed neuromasts were present that also seemed to be part of the oral lateral line. These irregular neuromasts were found only in the anterior part of the oral line, and their position was variable in that some were closer to the neuromasts of the main oral line while others were more isolated from it. These additional neuromasts are listed as accessory oral lateral line in Table 3.

**Mandibular series**

Neuromasts of the mandibular lateral line were more variably arranged and consisted of an anterior, mental part and a posterior part that were separated by a substantial gap. Especially in the mental region, neuromasts seemed more scattered in some specimens and did not form a well-defined line.

**Gular series**

Neuromasts of the gular series were rather indistinct and often difficult to count. Up to four neuromasts were present on each side of the posterolateral gular region. In some specimens, no gular series neuromasts were found, which may be a preservation artefact, although at least one well-preserved specimen showed no indication of gular neuromasts.

**Dorsolateral trunk series**

A few neuromasts were present in the anterior dorsal trunk area of some specimens. These seemed to form a distinct, postspiracular lateral line in the smaller specimens, but were mostly absent or at least not detectable in older specimens.

**Ventrolateral trunk series**

A number of neuromasts forming a distinct line along the ventrolateral side of the body were present in all larval specimens. Neuromasts in this series were not
evenly distributed along the lateral side of the trunk but appeared to be somewhat more numerous and densely spaced on the anterior trunk, behind the spiracle, as well as in the area just anterior of the cloaca. In the intermittent part, the neuromast seemed more loosely scattered. The neuromasts were distributed along the lateral side of the body and mostly within the lateral stripe. Moving from anterior to posterior, the trunk lateral line seemed to be very gradually sloping down from a lateral into a more ventrolateral position. The number of neuromasts in this series varied widely between the examined larvae, and part of this variation might be the result of detection difficulties. However, there seemed to be a trend towards a reduction of neuromasts in this series in larvae exceeding 150 mm TL, although this was not statistically significant (Table 3).

**Ampullary organs**

Ampullary organs were concentrated on the head, especially in the snout region, but were otherwise distributed throughout the body. In the smallest specimens, there was a distinct row of what seem to be ampullary organs along the ventrolateral side of the body. In general, ampullary organs were less conspicuous than neuromasts, and especially in the older specimens, ampullary organs were difficult to locate. This was particularly the case in the snout region, where the ampullary organs were increasingly obscured by the developing yellow adult colouration, especially along the lower jaw.

**Tentacle**

The differentiation of the tentacle was externally first apparent in specimens of between 150 and 165 mm length as a small pit immediately anteroventrally to the eye (Figure 1 (fg)). In the largest larval specimen, the tentacle formed a small bud that was demarcated anteriorly by a crescent-shaped crease of about a third of a circle segment. In the metamorphic (Figure 1(h)) and fully metamorphosed specimen, the bud-shaped tentacle was of a similar size as in the largest larva, but the tentacular crease formed about a half circle and had a more horizontal orientation. In all larval specimens that showed tentacular development, the tentacle or tentacle anlage was not very distinct and did not project beyond the level of the skin surface. The tentacle anlage did also not change position in larvae of different sizes and the metamorphosed specimens but appeared and remained in a position just anterior of the eye, as is characteristic for Rhinatrematidae.

**Demography**

The two collections of specimens contained different size classes (Figure 3). The collection made earlier in the year, in June 1993, contained specimens ranging from 131 mm to 181 mm TL (159.11 ± 15.74 mm, mean ± SD). The distribution is unimodal, which indicates a single age class (Figure 3). The collection of specimens from September 1991 contained larval specimens ranging from 58 mm to 189 mm. However, in contrast to the June collection, these specimens fell into two different size classes. Specimens of the first size class ranged from 58 mm to 112 mm TL (88.50 ± 23.13 mm, mean ± SD), while specimens from the second size class ranged from 151 mm to 189 mm TL (168.38 ± 13.43 mm, mean ± SD). The bimodal distribution of specimens in this collection indicates the presence of two age classes. In addition to the larvae, the September collection also contained one late metamorphic specimen of 184 mm TL, with nearly completely closed gill slits and greatly reduced tail fins, and a fully transformed specimen of 205 mm TL.

**Discussion**

**Larval morphology and development**

Caecilians are generally character-poor, and species are often difficult to reliably identify using morphological characters only. This is particularly the case in taxa that comprise numerous, superficially similar species. Larvae are even more difficult to identify, given that several of the standard morphometric landmarks (e.g. position of the tentacle) used for identifying adults will not develop until, or after, metamorphosis. In fact, no keys currently exist that would aid in larval identification and even just an assessment of morphological characters that could potentially be useful for identification purposes is currently lacking. One set of characters that would seem most promising to be taxonomically useful is the lateral line system and the arrangement and number of neuromasts has been used in the taxonomic determination of various groups of teleost fishes [29,30]. The lateral line system of larval Epicrionops and Ichthyophis was described by Taylor [16], and by Sarasin and Sarasin [31] and Hetherington and Wake [25] in detail in Ichthyophis. The observations made here generally agree with these reports, but some differences are apparent. In Epicrionops, neuromasts of the mandibular lateral line do not form a continuous sigmoid line on the anterior chin as in Ichthyophis [25,31], but are more scattered and separated into an anterior and posterior part of the row. In at least some Ichthyophis, the anterior neuromasts of the oral line are present in triple (most anterior) and double rows [25]. These very regular accessory neuromasts are absent in the examined larvae of E. bicolor, where only a few individual (up to four), irregularly placed neuromasts are present that seem to be part of the oral lateral line. In agreement with Wilkinson [28] and contrary to Taylor [16], I also only found two trunk rows of neuromasts in E. bicolor and agree with Wilkinson’s [28] assessment that the single trunk row seen in Ichthyophis likely corresponds to the dorsolateral series in Epicrionops.
In E. bicolor larvae examined here, the number of neuromasts within individual rows shows only modest variation, and only neuromast numbers within the mandibular, gular, and especially the ventrolateral trunk rows seem to be more variable (Table 3). There seems to be no significant change in neuromast numbers during larval development and young larvae do not seem to differ much from older larvae, which indicates that the neuromasts of most rows within the lateral line system remain unchanged right up to metamorphosis. A similar observation was made in Sylvaececlia grandisonae [32]. Taylor [16] stated that the variation in neuromast numbers he observed in E. petersi larvae is probably indicative of a loss of neuromast in older specimens. However, the data provided in his table [16, p.866] do not back up his assessment but instead show no age-related variation in neuromast numbers. Dünker et al. [33] stated that the lateral line organs degenerate during larval development in I. kohtaoensis, but Hetherington and Wake [25] found no significant differences in neuromast counts between the smallest and largest larvae of I. mindanoensis and two additional, unidentified species of Ichthyophis. Taylor [15] illustrated larvae of I. mindanoensis, I. supachai, and I. youngorum, and these differ clearly in the arrangement of the various rows of the lateral line system as well as in the number of neuromasts within individual rows. Hetherington and Wake [25] noted that Epicrionops differs from Ichthyophis in having substantially fewer neuromasts in most series and further reported consistent differences in neuromast numbers in various rows between three different species of Ichthyophis. The use of lateral line characteristics such as neuromast number and row arrangements appears promising in caecilian larval taxonomy and further studies should explore its utility in more detail in a broader range of species.

Nussbaum and Wilkinson [34] reported that the annular system in Epicrionops continues to differentiate during larval development, which is corroborated here. The annuli are initially present as primary annuli only and very indistinctly developed in the smallest larvae (Figure 1(c)). The full annulation pattern with tertiary annuli is only established in larvae of about 160 mm TL, with the exception of the tail, the last third of which remains free of annuli until metamorphosis. The tail fins, and perhaps part of the tail, are reduced at metamorphosis, as indicated by an increase in total length/tail length ratio (Tables 1 and 2).

One remarkable aspect of larval morphology and development in E. bicolor is the presence of external gills until metamorphosis, which was first mentioned by Wake [9]. In general, most caecilian embryos have three pairs of

![Figure 3. Size distribution of larval and metamorphosed specimens of Epicrionops bicolor collected in June 1993 (top) and September 1991 (bottom). Open bars represent larvae, grey metamorphs, and black fully transformed specimens. Number of specimens are on the y-axis, size classes (in mm) on the x-axis.](image-url)
external gills with numerous gill filaments (fimbriae) that branch off a central stem, which are usually resorbed or shed shortly before hatching/birth or within days thereafter [e.g., 33, 35]. Similarly developed gills are present in embryos of *E. peruvianus* [36] and presumably in all species of rhinatrematids. However, these are not completely resorbed but only greatly reduced in size and short external gills are present throughout larval life in at least *E. bicolor* (and perhaps *E. petersi* [9]), which is a substantial difference between larvae of *Epicrodonops* and those of other caecilians.

**Demography**

While the collection of specimens is not comprehensive in that it is not a year-round sample and also only includes one fully transformed specimen, it nonetheless allows for inferences of some key events in the development of *E. bicolor*. All specimens collected in June 1993 belong to a single age class, whereas specimens collected in September 1991 contain specimens of two age classes (Figure 3). The small specimens of the September sample likely represent newly and recently hatched larvae. Wake [9] reported a larva of 66 mm as being the smallest available specimen in a sample of 45 larvae of *E. bicolor* and Reiss [37] described the palatal morphology of an advanced embryo of 58 mm length of *E. petersi*, a species of roughly similar adult size as *E. bicolor*, indicating that hatching in *E. bicolor* probably occurs at around 55 to 65 mm TL. Compared to hatching sizes reported for *Ichthyophis* larvae (75 to 80 mm in *I. glutinosus* [35]; 65 to 76 mm in *I. kohtaoensis* [33]; 68 to 81 mm in *I. cf. kohtaoensis* [13]), hatching in *E. bicolor* seems to occur at a slightly smaller size, perhaps reflecting the overall smaller adult size [19, 38]. The largest larval specimen is 189 mm TL and the only available late metamorphic specimen is 184 mm, which suggests that larvae probably metamorphose at around 180 to 190 mm TL.

The presence of two different age classes in the September sample, including newly hatched larvae and their absence from the June sample, indicates that hatching likely commences in August and September, with breeding taking place in the preceding months. Egg deposition and embryonic development therefore seem to take place during the drier season of the year [39], with hatching coinciding with the start of the rainy season. In the Central American viviparous dermophid *Dermophis mexicanus*, newborns are similarly found at the beginning of the rainy season [40] and Moodie [41] reported that birth in *Typhlonectes compressicauda* coincides with the end of the dry season. In contrast, in *Ichthyophis* egg laying and embryonic development generally seems to coincide with the rainy season [14, 31, 35], while hatching seems to coincide with the end of the rainy season, and metamorphosis with the end of the dry season, although the latter events are somewhat more loosely correlated with local climate conditions [13, 35].

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**Author contributions**

HM conceived and designed the study, collected the data and wrote the manuscript.

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