



# Tadpoles of three western African frog genera: *Astylosternus* Werner, 1898, *Nyctibates* Boulenger, 1904, and *Scotobleps* Boulenger, 1900 (Amphibia, Anura, Arthroleptidae)

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## Abstract

Herein, we describe the tadpoles of six *Astylosternus* species, *A. fallax*, *A. cf. fallax*, *A. laurenti*, *A. montanus*, *A. perreti*, *A. ranoides*, and *Scotobleps gabonicus*, and redescribe the tadpoles of *A. batesi*, *A. diadematus*, *A. laticephalus*, *A. occidentalis*, *A. rheophilus*, and *Nyctibates corrugatus*. All *Astylosternus* tadpoles are adapted to torrent currents and share a long, oval body, slightly flattened in lateral view, with very long muscular tails with narrow fins. The jaws are massive, serrated, and often show a tooth-like medial projection (fang) in the upper jaw. Body proportions of *Astylosternus* tadpoles are extremely similar. The best characters to distinguish species might be life coloration and potentially the shape of labial papillae. The tadpole of *Scotobleps gabonicus* is similar to *Astylosternus* and differs only slightly by a narrower body with a shorter and rounder head. The upper jaw of *Scotobleps* carries two or three lateral fangs instead of one medial one. The tadpole of *Nyctibates corrugatus* is easily distinguishable from the other two genera on the basis of their very long, eel-shaped body and tail and the bluish-black color.

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larval stages

Lower Guinea forest

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## Introduction

The anuran family Arthroleptidae comprises eight genera, all being endemic to sub-Saharan Africa (Frost 2018). The species-rich genera, *Arthroleptis* Smith, 1849 and *Leptopelis* Günther, 1859, are widespread and occur in forest and open habitats (Blackburn 2008; Schiøtz 1999). Whereas all *Arthroleptis* seem to reproduce by terrestrial, direct development (Guibé and Lamotte 1958a; Lamotte and Perret 1963; Wager 1986; Schweiger et al. 2017), *Leptopelis* deposit their clutches in soil, from where the hatched, long and slender, exotrophic tadpoles move into lentic or lotic waters (Rödel 2000; Channing 2008; Barej et al. 2015). The genus *Cardioglossa* Bou-

lenger, 1900 is restricted to western and central Africa and has stream-dwelling tadpoles with special morphological characteristics like an eel-shaped body and an elongated spiraculum (Hirschfeld et al. 2012). The genus *Leptodactylodon* Andersson, 1903, is restricted to the western part of central Africa. The tadpoles are likewise stream dwellers, but presumably live in the interstitial spaces between pebbles and have special funnel mouths (Mapouyat et al. 2014). The tadpoles of the Hairy Frog, *Trichobatrachus* Boulenger, 1900, live in torrent, mountainous streams from eastern Nigeria, south to northern Angola (Ernst et al. 2014). They are comparatively short and robust with a huge oral sucker and numerous rows of keratodonts (Mertens 1938; Channing et al. 2012).

Two of the three remaining genera, *Astylosternus* Werner, 1898 and *Nyctibates* Boulenger, 1904, have large, long and very muscular stream-dwelling tadpoles, as far as is known (Amiet 1971; Channing et al. 2012). The tadpole of *Scotobleps* Boulenger, 1900, a monotypic genus ranging from south-eastern Nigeria to Gabon and the Republic of the Congo (Portik et al. 2017) is unknown, as are the tadpoles of various *Astylosternus* species.

During the last 15 years we collected numerous tadpoles of morphologically similar, torrenticolous arthroleptid tadpoles, apparently belonging to 10 species of *Astylosternus*, *Nyctibates corrugatus*, and *Scotobleps gabonicus*. We present re-descriptions of tadpoles of six species (*A. batesi*, *A. diadematus*, *A. laticephalus*, *A. occidentalis*, *A. rheophilus*, and *N. corrugatus*) and new tadpole descriptions for six additional species, amongst them the first from the genus *Scotobleps*.

## Material and methods

### Collection, preservation, deposition and barcodes

Tadpoles were collected with dip nets and anesthetized in chlorobutanol solutions before being either preserved in formalin (5–10%) or ethanol (75%). All were finally stored in 75% ethanol. Prior to preservation tail tips of representative specimens were preserved separately in 96% ethanol for genetic investigations. All tadpole vouchers and tissue samples are deposited at the collection of the Museum für Naturkunde Berlin (ZMB; see descriptions). For comparisons we examined further adult frogs and corresponding sequences from the collections of Natural History Museum of Geneva (MHNG; Geneva, Switzerland) and the Zoological Research Museum A. Koenig (ZFMK; Bonn, Germany). Tadpoles were assigned to species by DNA-barcoding, using up to 558 bp of the mitochondrial 16S rRNA gene; for exact laboratory procedures see Mapouyat et al. (2014) and Barej et al. (2015). All sequences of tadpoles and adults have been produced for this study and deposited at GenBank (for accession numbers see tadpole descriptions). Comparisons between sequences were carried out using BioEdit 7.0.9.0 (Hall 1999).

### Character assessment

All measurements were taken by FG and MR. Measurements of randomly chosen vouchers were measured by both persons and the entire dataset only put together after these measures did not differ. Measures were taken with a digital caliper (accuracy  $\pm 0.1$  mm) and a measuring ocular on a Leica MZ95 dissecting microscope (accuracy  $\pm 0.02$  mm).

The following measurements were taken: TL (total length), BL (body length), TAL (tail length), BH (body height at the point of the spiracle insertion), BW (maximum body width), TMW (tail muscle width at tail base), TMH (maximum tail muscle height), VFH (maximum height of ventral fin), DFH (maximum height of dorsal fin), MTH (maximum tail height), ED (horizontal eye diameter), ND

(horizontal nostril diameter), IOD (interorbital distance), IND (inter-nasal distance), SN (nostril-snout distance), EN (eye-nostril distance), ES (eye-snout distance), MW (mouth width), SP (spiracle length) and SSD (snout-spiracle distance). Based on these measures the following proportions were calculated: BL/TL, BH/BL, BW/BL, BH/MTH, TMW/BW, TMH/MTH, VFH/DFH, IND/IOD, ED/BL. All measurements are provided in Appendix 1.

In the text, measurements or ratios are usually summarized (for  $N \geq 3$ ) and given as: mean  $\pm$  standard deviation and range (min–max). As we tried to predominately use genotyped specimens for the descriptions and the tail tips were missing in most of them (see above), the total length was either determined in comparison with alternative specimens of the same series and developmental stage or estimated based on the usual tail shape of the group. The mouthpart formulae are in accordance with Dubois (1995). In addition, the number, form and arrangement of the labial papillae were accessed and described. We further checked for a lateral line system. As all tadpoles proved to possess such organs in an identical arrangement, we excluded it from the species-specific tadpole descriptions and instead present a summary description at the end of the result section. The terminology of lateral lines follows Escher (1925). The staging of tadpoles was according to Gosner (1960). Whenever possible we tried to choose tadpoles of Gosner stages 25–30 for descriptions. Descriptions of life coloration are based on photos taken in the field.

### Illustrations

Photos of entire tadpoles were taken with a Canon EOS 50D digital camera and a 50 mm 1:2.5 lens. Mouthpart pictures were taken with a stacking camera (Leica DFC490) on a Leica Z16 APO A microscope. Single exposures were combined using the Automontage® software v. 5.03.0061 (Syncroscopy). All pictures were edited with Adobe Photoshop v. 18.1.0. Schematic sketches of the keratodont formulae are usually based on several individuals of the respective species.

### Analysis of morphological differences

To test, if and how the tadpoles of the different species can be distinguishable, we plotted indices of our various measures against each other and ran a Principle Component Analysis (PCA) using qti-Plot and Past 3.18 (Hammer et al. 2001). Before running the PCA, all measures were standardized against the respective body lengths.

## Results

### Tadpole descriptions

#### *Astylosternus batesi* (Boulenger, 1900)

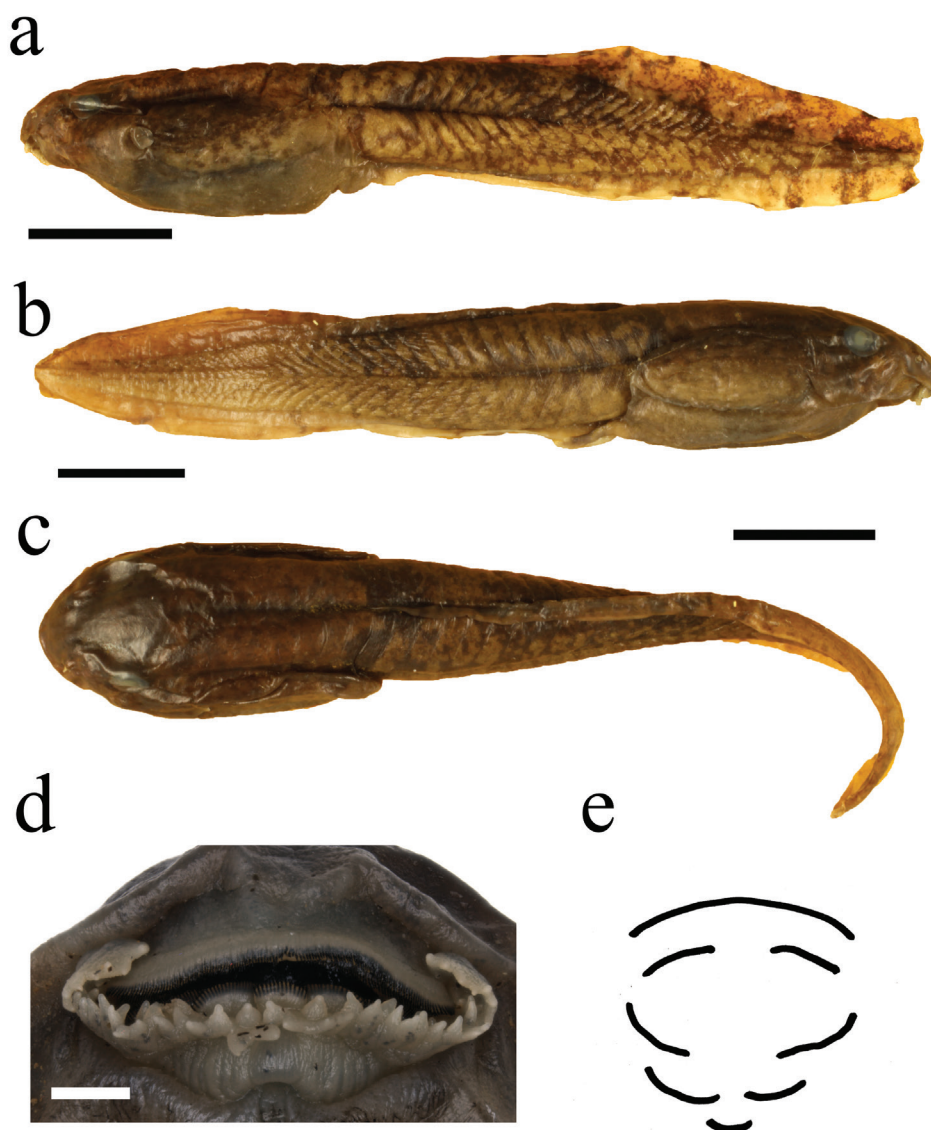
**Material examined.** ZMB 82863 (GenBank MK318840), Gosner stage 25, Cameroon, Mt Kala, 899

m, 3°50'27.66"N, 11°20'52.44"E, 9 November 2011, leg. M.F. Barej, H.C. Liedtke & N.L. Gonwouo; ZMB 82864 (GenBank MK318841), Gosner stage 25, Cameroon, Ebo Forest, Bekob, 893 m, 4°21'51.96"N, 10°25'10.26"E, 30 September 2011, leg. M. Dahmen; ZMB 82865 (GenBank MK318842), Gosner stage 25, Cameroon, Ebo Forest, Bekob, 852 m, 4°21'54.36"N, 10°25'17.22"E, 1 September 2011, leg. M. Dahmen; ZMB 82866 (GenBank MK318843), 2 tadpoles, Gosner stage 25, Cameroon, Ebo Forest, Bekob, 917 m, 4°21'27.42"N, 10°25'5.94"E, 9 January 2011, leg. M. Hirschfeld & F. Grözinger; ZMB 82784 (GenBank MK318844), Gosner stage 36, Cameroon, Ebo Forest, Bekob, 807 m, 4°21'54.3"N, 10°25'24.54"E, 10 January 2011, leg. M. Hirschfeld & F. Grözinger.

All tadpoles were caught in small to medium-sized streams. The description is mainly based on ZMB 82865 and ZMB 82784. Genotyped tadpoles have been

compared with an adult frog (MC11\_205; GenBank MK318905) from Mount Kala, near Kala village, Cameroon. The genotyped individuals were genetically almost identical, the maximum uncorrected p-differences in pairwise comparisons was 0.2% (1 bp).

**Description.** Long slender tadpole with long, muscular tail and narrow fins (Fig. 1); body oblong oval in dorsal and lateral view; back with a medial longitudinal-depression; snout rounded in dorsal view, more narrow-rounded in lateral view; body length approximately 0.3 (31.3–36.7%,  $N = 3$ ) of total length; body height  $46.3 \pm 5.6\%$  of body length; body width  $60.5 \pm 6.0\%$  of body length; eyes positioned dorsolaterally, eye diameter  $11.3 \pm 1.4\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $75.2 \pm 9.7\%$  of interorbital distance; tail fins narrow, dorsal and



**Figure 1.** *Astylosternus batesi* tadpoles; **a** ZMB 82865 (Gosner stage 25) and **b–d** ZMB 82784 (Gosner stage 36); **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.



ventral fin originating from tail base, ventral fin height narrow, reaching  $70.7 \pm 4.7\%$  of dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $91.7 \pm 11.5\%$  of maximum tail height; tail axis width  $41.3 \pm 11.4\%$  of body width; tail axis height  $59.8 \pm 13.9\%$  of maximum tail height; tail tip rounded; vent tube dextral; body with large lateral air sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula  $1:2/2+2:1$ ; anterior lip only lateral with papillae, large rostral gap; posterior lip with 2–3 rows of approximately 20 uniform papillae, papillae triangular and approximately as long as broad (Fig. 1d); black jaw sheaths massive and serrated; upper jaw with a big medial projection (fang); lower jaw U-shaped with a medial notch.

The largest tadpole, still Gosner stage 25 (ZMB 82865), measured 25 mm body length. The most developed specimen (ZMB 82784, Gosner stage 36) had similar body length of 24.7 mm. When reconstructing the tail tip of the largest specimens by the shape of tails in smaller specimens we estimate the maximum total length of *A. batesi* tadpoles to be 60–80 mm.

**Coloration in preservation.** Brown, slightly fading from snout to tail; dorsal surfaces with irregular dark speckles; ventral surfaces without or only few darker markings;

tail fins sometimes with dark blotches or speckles, partly transparent. Life color of very small specimens with much yolk, were much lighter than larger specimens (Fig. 2), showing distinct black blotches on body and tail axis, tail fins completely transparent.

**Variation.** According to Channing et al. (2012) the anterior lip has three rows of keratodonts,  $1:2+2/2+2:1$ . We cannot exclude that our specimens lost the very short third row, likewise it is possible that populations vary in this character. Channing et al. (2012) describe coloration to be partly yellowish or reddish on back and flanks, ventrally bluish to violet, dark spots on all surfaces, less-so on the venter. Angel (1930) described a tadpole as *Gampsosteonyx batesi*. As this tadpole originated from an area that is outside the present day range of *A. batesi*, the description might have been based on another *Astylosternus* species (Channing et al. 2012).

**Taxonomic remark.** Whereas all genotyped tadpoles were genetically almost identical amongst each other and an adult from Mount Kala, Cameroon, further genetic comparisons with specimens from across the range of the species revealed three distinct genetic lineages (results not shown). Our tadpoles originated from Cameroon. All genetic samples from Gabon and the Republic of Congo, fell into a different clade. As the type locality of *A. batesi* however, is



**Figure 2.** Young *Astylosternus batesi* tadpoles (ZMB 82863) in life, Gosner stage 25 at a total length of about 15 mm, still with large amounts of yolk.



“Benito River, Gaboon” (Boulenger 1900), the tadpoles on which our descriptions is based may thus actually belong to an undescribed species within the *A. batesi*-complex.

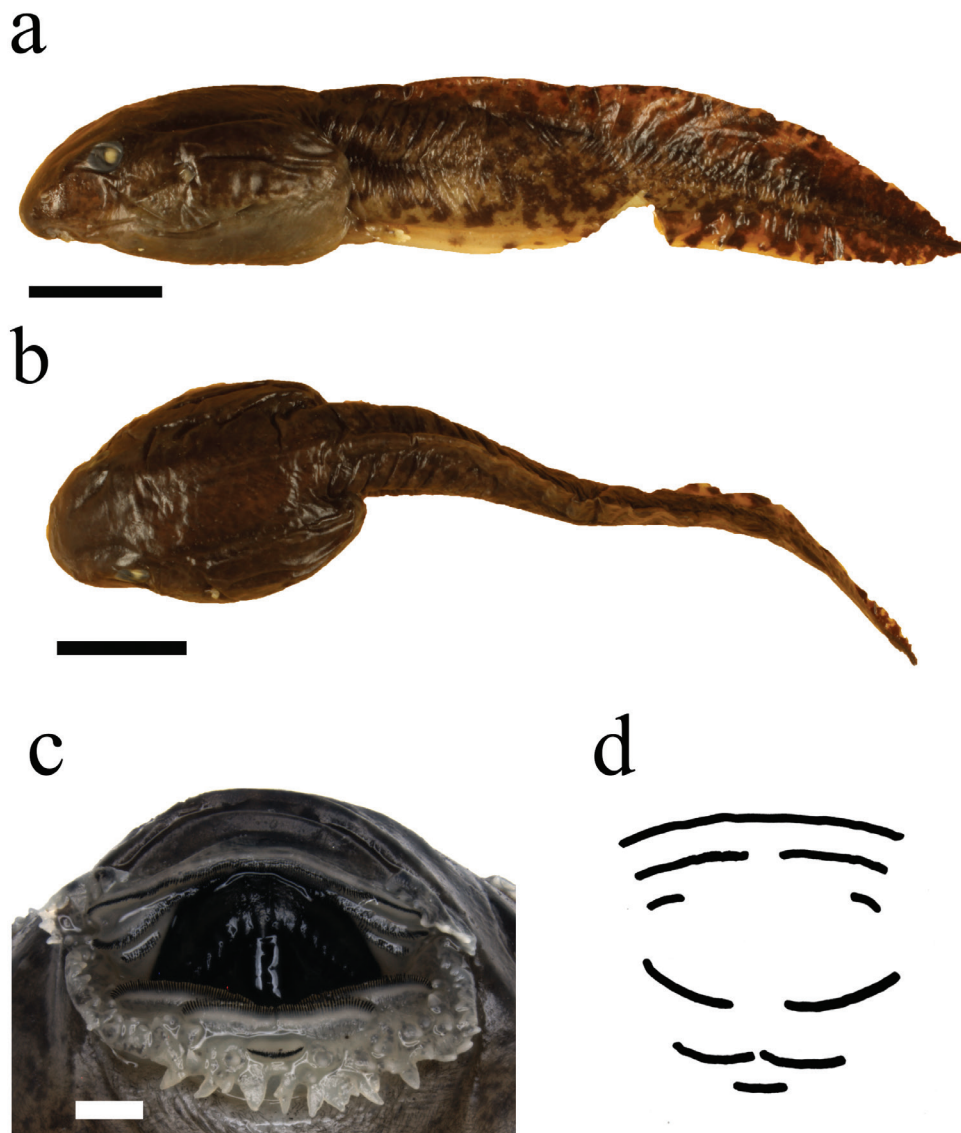
***Astylosternus diadematus* Werner, 1898**

**Material examined.** ZMB 82799 (GenBank MK318845), 1 tadpole, Gosner stage 25, Cameroon, Mt Manengouba, Nkikok, 1328 m, 5°5'34.5"N, 9°49'3.8"E, 8 September 2011, leg. M. Hirschfeld; ZMB 82870 (GenBank MK318846), 1 tadpole, Gosner stage 25, Cameroon, Mt Manengouba, M'Bourouko, 1459 m, 5°4'3.48"N, 9°51'56.22"E, 1 December 2010, leg. M. Hirschfeld; ZMB 88345, 1 tadpole, Gosner stage 25, Cameroon, near Korup National Park, Mokango, 621 m, 5°8'11.29"N, 9°4'37.43"E, 9 May 2014, leg. F. Mühlberger; ZMB 88346, 1 tadpole, Gosner stage 36, Cameroon, near

Korup National Park, Mokango, 502 m, 5°7'36.51"N, 9°4'9.49"E, 10 May 2014, leg. F. Mühlberger.

The two specimens from Mount Manengouba were caught in medium-sized streams in gallery forest; the Korup specimens were from small creeks in rainforest. The description is mainly based on ZMB 82799 and ZMB 88346. Genotyped tadpoles have been compared with two adults from Mount Nlonako, Cameroon (ZFMK 81585 and ZFMK 81702; GenBank MK318847, MK318848). The uncorrected pairwise p-difference between the tadpoles and between the tadpoles and the adults ranged from 0.2–0.7% (1–3 bp).

**Description.** Long robust tadpole with muscular tail (Fig. 3); body oval in dorsal and lateral view; snout rounded in dorsal view, slightly more pointed in lateral view; body length approximately 0.3 (32.8–32.9%,  $N = 2$ ) of total length; body height  $46.7 \pm 4.5\%$  of body length;



**Figure 3.** *Astylosternus diadematus* tadpole (ZMB 88346) at Gosner stage 36; **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

body width  $60.7 \pm 7.8\%$  of body length; eyes positioned dorsolaterally, eye diameter  $11.5 \pm 1.0\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $70.9 \pm 3.5\%$  of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base, ventral fin height  $67.7 \pm 3.2\%$  smaller than dorsal fin height; highest part of tail axis approximately in the middle of the tail; body height  $82.2\text{--}85.7\%$  ( $N = 2$ ) of maximum tail height; tail axis width  $47.4 \pm 4.8\%$  of body width; tail axis height  $69.8 \pm 5.4\%$  of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula  $1:2+2/2+2:1$ ; anterior lip only with lateral papillae and large rostral gap; posterior lip with two rows of around 20 papillae, central papillae long and narrow, papillae becoming smaller towards angles of the mouth (Fig. 3c); black jaw sheaths massive and serrated; upper jaw with a medial fang, lower jaw U-shaped with medial notch.

The largest tadpole (ZMB 88346, Gosner stage 36) had 72 mm total length (body length: 23 mm).

**Coloration in preservation.** Brown to dark brown, dorsal surfaces darker, venter lighter and more grayish; flanks densely beset with diffuse and small brown spots; intensity of patterning decreases from back to vent; tail fins slightly transparent, dorsal fin with dark patterning, ventral fin with fewer dark spots.

**Variation.** ZMB 88346 had a particularly high body ( $95.4\%$  of maximum tail height) and a keratodont formula of  $1:2+2/1+1:2$ . Channing et al. (2012) report the keratodont formulae  $3+3/2+2:1$  and  $3+3/1+1:2$ , as well as lighter coloration and less dark spots. The latter differences possibly are due to preservation differences.

### *Astylosternus fallax* Amiet, 1978

**Material examined.** ZMB 82868 (GenBank MK318849), 3 tadpoles, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 373 m,  $4^{\circ}20'54.66''\text{N}$ ,  $10^{\circ}14'24.3''\text{E}$ , 16 July 2011, leg. M. Dahmen & M. Hirschfeld; ZMB 82869 (GenBank MK318850), 1 tadpole, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 306 m,  $4^{\circ}20'35.64''\text{N}$ ,  $10^{\circ}14'0.54''\text{E}$ , 29 September 2010, leg. M. Hirschfeld & M.-O. Rödel.

All tadpoles were caught in forest streams. The description is mainly based on ZMB 82868. Genotyped tadpoles have been compared with an adult from Bekop, Ebo forest, Cameroon (ZMB 82787; GenBank MK318851). The two tadpoles and the adult were genetically identical.

**Description.** Long slender tadpole with long, muscular tail (Fig. 4); body oval in dorsal and lateral view; snout rounded in dorsal and lateral view; body length  $36.3 \pm 2.6\%$  of total length; body height  $40.3 \pm 3.3\%$  of body length; body width  $56.2 \pm 4.4\%$  of body length; eyes po-

sitioned dorsolaterally, eye diameter  $11.4 \pm 0.5\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $74.1 \pm 7.0\%$  of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height narrower,  $68.9 \pm 11.5\%$ , than dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $96.6 \pm 14.8\%$  of maximum tail height; tail axis width  $45.6\% \pm 10.0\%$  of body width; tail axis height  $69.3 \pm 4.7\%$  of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostro-ventral, narrower than interorbital distance; keratodont formula  $1:2+2/2+2:1$ ; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of app. 20 triangular papillae (Fig. 4c), papillae of inner row (or rows) shorter than in the marginal row; black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

The tadpoles (all Gosner stage 25) ranged from 45 mm to 74 mm total length.

**Coloration in preservation.** Basic color light brown, the dorsal surfaces darker; back and tail with irregular, big, dark brown spots or blotches; venter light with few or no dark speckling; tail fins beige, semitransparent with dark brown spots.

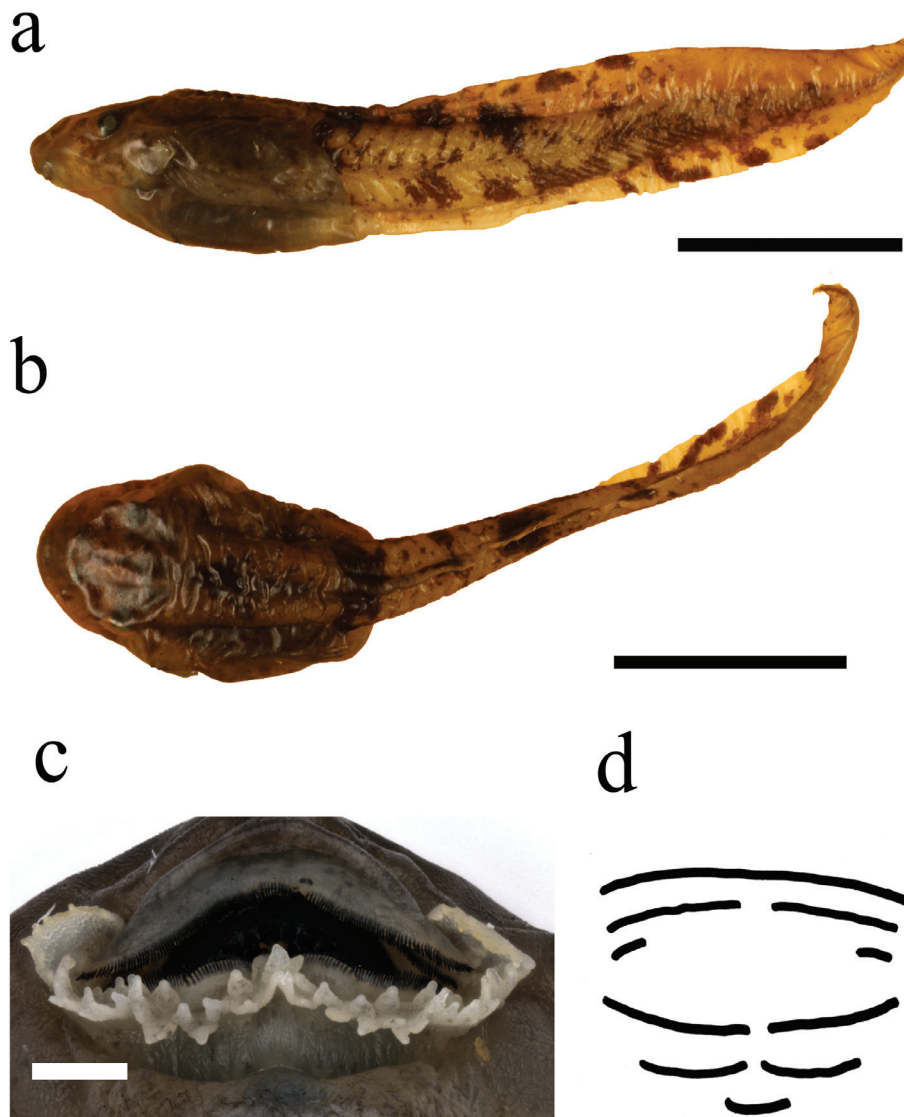
**Taxonomic remarks.** Morphologically and genetically tadpoles of this species were very similar to *A. laurenti* and a taxon (here termed *A. cf. fallax*) which genetically was intermediate between *A. fallax* and *A. laurenti* (for respective tadpole descriptions see below). The uncorrected pairwise p-difference between *A. fallax* and *A. laurenti* was 2.55%, between *A. fallax* and *A. cf. fallax* it was 1.85%, and between *A. laurenti* and *A. cf. fallax* the distance was 1.99%. Further morphological and genetically research is necessary to conform if these three lineages represent distinct species or merely are representatives of one, genetically variable species.

### *Astylosternus cf. fallax* Amiet, 1978

**Material examined.** ZMB 82867 (GenBank MK318852), Gosner stage 25, Cameroon, foot of Mt Nlonako, Ekomtolo, 477 m,  $4^{\circ}49'58.46''\text{N}$ ,  $9^{\circ}55'33.42''\text{E}$ , 24 November 2011, leg. M.F. Barej, H.C. Liedtke, N.L. Gonwouo & M. Hirschfeld.

The tadpole was caught in a forest stream. The genotyped tadpole has been compared with the two adults from Mount Nlonako, Cameroon (ZFMK 81164 and ZFMK 81608; GenBank MK318853, MK318854). The tadpole was genetically identical to these adults (compare Taxonomic remarks in the description of the *A. fallax* tadpole).

**Description.** Long slender tadpole with long, muscular tail (Fig. 5); body oval in dorsal view, bullet-shaped in



**Figure 4.** *Astylosternus fallax* (ZMB 82868 B; Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

lateral view; snout rounded in dorsal and lateral view; body length 31.7% of total length; body height 34.9% of body length; body width 48.4% of body length; eyes positioned dorsolaterally, eye diameter 10.7% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 86.7% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height narrower, 73.2% of dorsal fin height; highest part of tail approximately at two-thirds of the tail; body height 72.3% of maximum tail height; tail axis width 52.6% of body width; tail axis height 65.3% of maximum tail height; tail tip pointed; vent tube dextral; body with lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostroventral, narrower than interorbital distance; keratodont formula 1:2+2+2/2+2:1; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of ca 20 massive papillae, papillae of margin-

al row are distinctly longer than of inner rows (Fig. 5c); black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

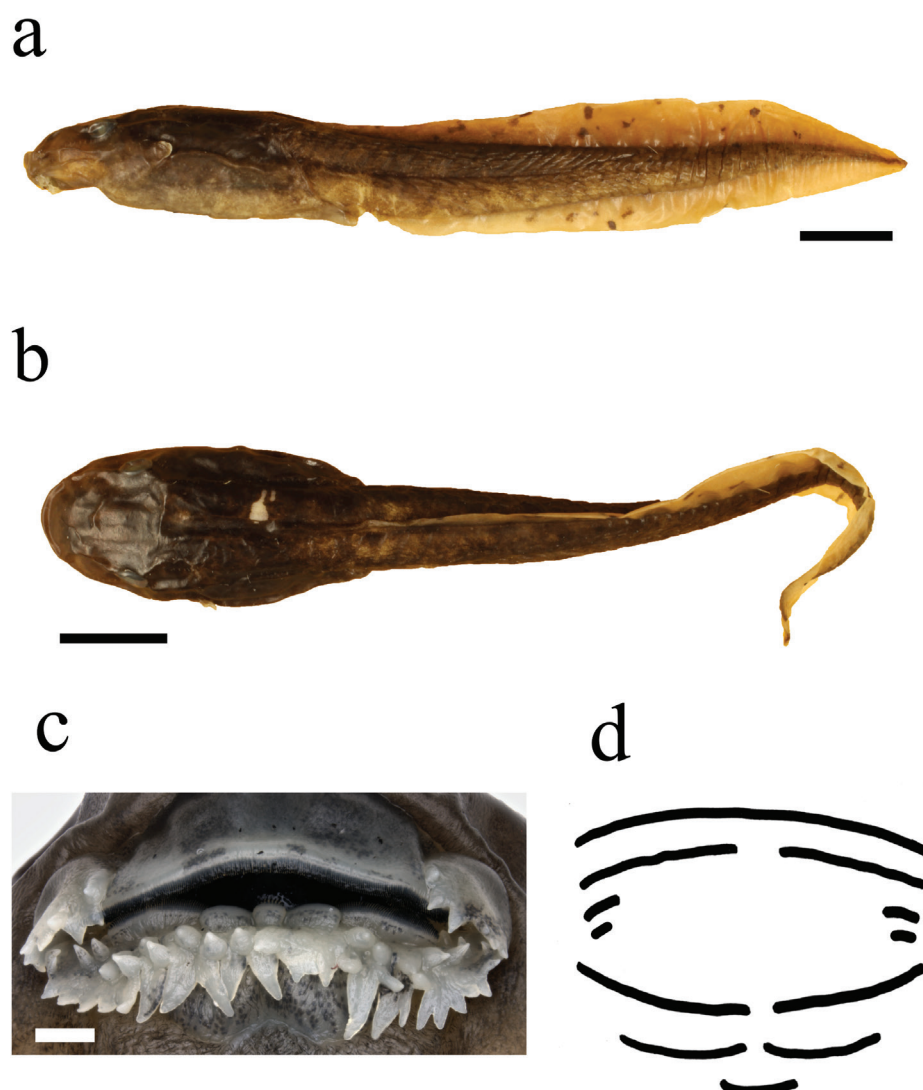
The tadpole (Gosner stage 25) measures 97.4 mm in total length.

**Coloration in preservation.** Basic color light brown with darker and speckled dorsal surface; venter light and grayish with few or no dark speckling; tail fins beige, semitransparent with irregular tiny dark brown spots. In life the color was of a duller, darker brown (Fig. 6).

*Astylosternus laurenti* Amiet, 1978

**Material examined.** ZMB 88353 (GenBank MK318855), 1 tadpole, Gosner stage 25, Cameroon, Korup National





**Figure 5.** *Astylosternus cf. fallax* (ZMB 82867, Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; compare Fig. 6; black bars = 1 cm, white bar = 1 mm.

Park, Bera, 564 m, 5°21'59.57"N, 8°59'45.6"E, 22 May 2014, leg. F. Mühlberger.

The tadpole was caught in a forest stream. It was genotyped and compared with an adult from east of Ntale village, Banyang-Mbo, Cameroon (MCZ A-136785; GenBank MK318856); the uncorrected p-difference was 0.2% (1 bp) (compare Taxonomic remarks in the description of the *A. fallax* tadpole).

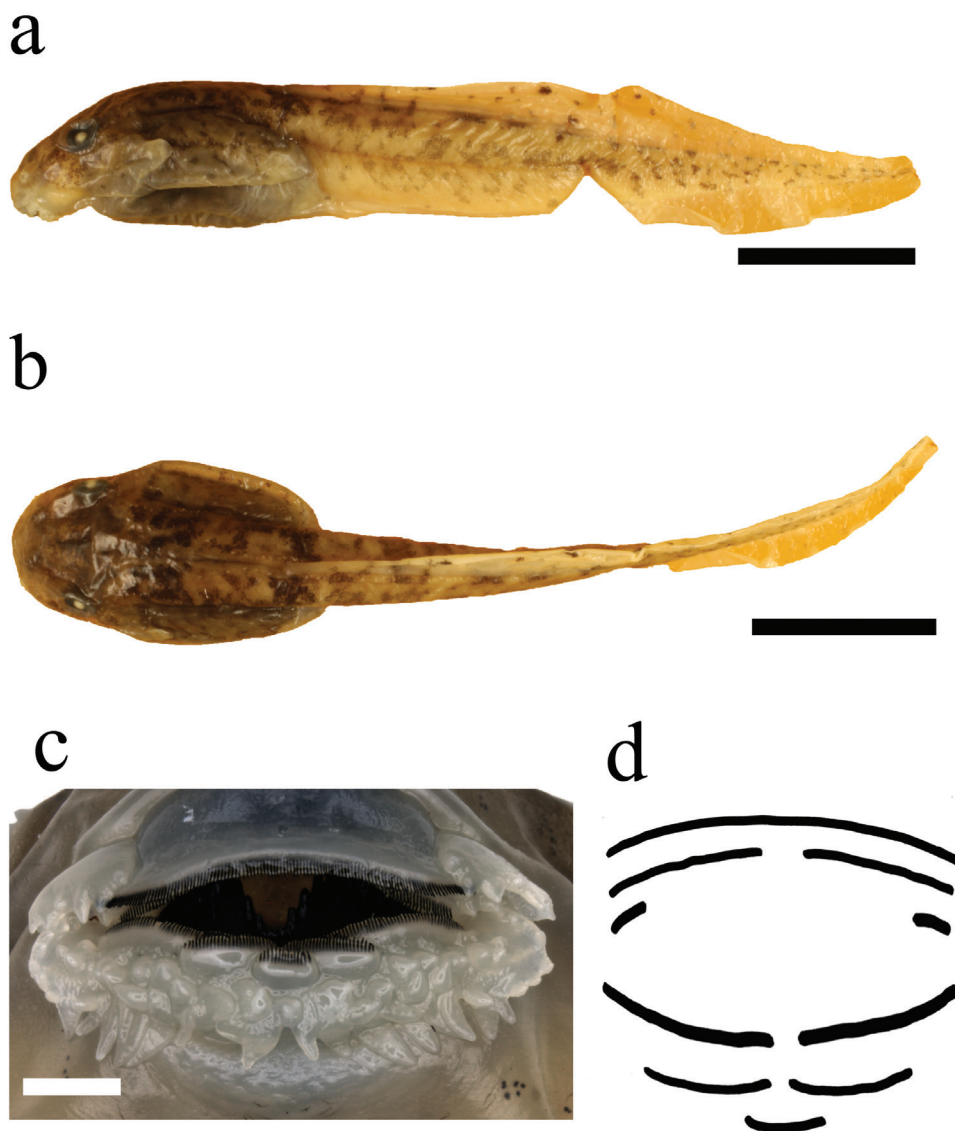
**Description.** Long slender tadpole with long, muscular tail (Fig. 7); body oval in dorsal view, bullet-shaped in lateral view; snout rounded in dorsal view, more narrowly rounded in lateral view; body length 34.2% of total length; body height 41.8% of body length; body width 54.8% of body length; eyes positioned dorsolaterally, eye diameter 13.0% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 77.1% of interorbital distance; tail fins nar-

row, dorsal and ventral fin originating from tail base; ventral fin height narrower, measuring 72.2% of dorsal fin height; highest part of tail slightly behind the middle of the tail; body height 77.1% of maximum tail height; tail axis width 47.4% of body width; tail axis height 61.5% of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth positioned rostroventral, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with lateral papillae and big rostral gap; posterior lip with 2 or 3 rows of ca 20 triangular papillae (Fig. 7c), papillae of inner row (or rows) shorter than in the marginal row; black jaw sheaths massive and serrated; upper jaw sheath with a small medial fang, lower jaw U-shaped with a broad medial notch.

The tadpole (Gosner stage 25) measures 51.7 mm in total length.



**Figure 6.** *Astylosternus cf. fallax* in life coloration (ZMB 82867, Gosner stage 25).



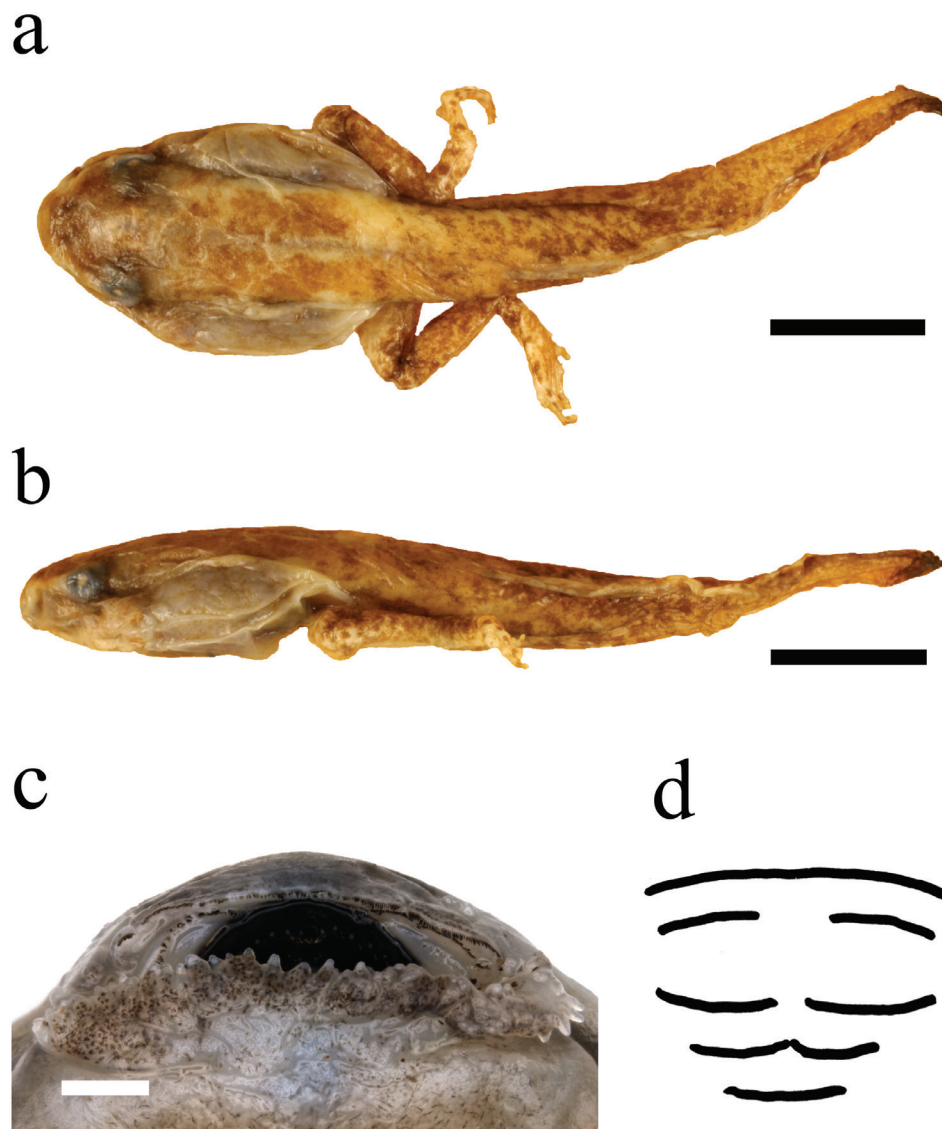
**Figure 7.** *Astylosternus laurenti* (ZMB 88353; Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

**Coloration in preservation.** Basic color light brown, the dorsal surfaces darker; back and tail axis with irregular, dark brown spotted patterns; ventral surfaces light with few or no dark speckling; tail fins beige, semitransparent with tiny dark brown spots on dorsal fin.

*Astylosternus laticephalus* Rödel, Hillers, Leaché, Kouamé, Ofori-Boateng, Diaz & Sandberger, 2012

**Material examined.** ZMB 75460 (Gosner stage 39, Ghana, Afao Hills, 531 m, 6°15'19.36"N, 2°17'37.14"W, 28 March 2007, leg. C.O. Boateng & A. Hillers). This tadpole was already assigned to *A. laticephalus* and described in Rödel et al. (2012) and in Channing et al. (2012). The tail tip is lost, so total length was taken from Rödel et al. (2012). This specimen has various preservation artifacts.

**Description.** Long tadpole with muscular tail; body oval in dorsal and lateral view (Fig. 8); snout broadly rounded in dorsal view, almost truncated in lateral view; body length 36.4% of total length; body height 29.5% of body length; body width 69.6% of body length; eyes positioned dorso-laterally, eye diameter 11.0% of body length; nostrils positioned dorsally, closer to snout tip than to eyes; inter-nos-tril distance 34.4% of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base, ventral fin narrower, 82.6% of dorsal fin height; body height around 130% of maximum tail height; tail axis width 35.4% of body width; tail axis height 65.1% of maximum tail height; vent tube dextral, body with huge lateral sacs, extending from halfway in between eye level and spiracle to end of body; short spiracle (almost impossible to see), sinistral; mouth ventral and close to snout, mouth smaller than interorbital distance; labial tooth formula 1:1+1/1+1:2, the



**Figure 8.** *Astylosternus laticephalus* (ZMB 75460, Gosner stage 39); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.



first pair rows in the lower lip are very close to each other (Rödel et al. 2012 interpreted this as being 1:1+1/3); anterior lip with lateral papillae and large rostral gap; posterior lip with 1 or 2 rows of small, uniformly rounded papillae (Fig. 8c), which are as long as they are wide; black, massive, serrated jaws; upper jaw broadly arched with a small medial fang, lower jaw broadly V-shaped.

The maximum size of *A. laticephalus* tadpoles is estimated to be around 60–70 mm. The total length of ZMB 75460 is 62.1 mm.

**Coloration in preservation.** General color light brown or beige, with irregular small brown spots covering body and tail; ventral surfaces of body more grayish, dark speckling almost absent; tail tip darker.

### *Astylosternus montanus* Amiet, 1978

**Material examined.** ZMB 82871 (GenBank MK318857), 2 tadpoles, Gosner stage 28 (A) and stage 25 (B), Cameroon, Mt Manengouba, 1290 m, 4°58'23.76"N, 9°52'31.8"E, 21 November 2010, leg. M. Hirschfeld; ZMB 82872, Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1365 m, 5°0'33"N, 9°46'30"E, 14 December 2010, leg. M. Hirschfeld; ZMB 82873, 2 tadpoles, Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.82"E, 16 December 2010, leg. M. Hirschfeld; ZMB 82874 (GenBank MK318860), 2 tadpoles, Gosner stage 35, Cameroon, Mt Manengouba, Ebonemin, 1417 m, 5°1'27.6"N, 9°45'53.2"E, 15 August 2011, leg. M. Hirschfeld; ZMB 82875 (GenBank MK318861), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.4"N, 9°45'46.7"E, 16 August 2011, leg. M. Hirschfeld; ZMB 82876 (GenBank MK318862), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.8"E, 7 October 2011, leg. M. Hirschfeld.

All tadpoles were caught in small to medium-sized streams. The description is mainly based on ZMB 82875. The genotyped tadpoles have been compared with an adult from Mount Rata, Rumpi Hills, Cameroon (MHNG 2715.35; GenBank MK318863). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0.20–0.71% (1–4 bp).

**Description.** Robust tadpole with long muscular tail (Fig. 9); body bullet-shaped in dorsal view, more oval in lateral view; back with a longitudinal medial depression; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length  $33.3 \pm 1.0\%$  of total length; body height  $43.8 \pm 4.5\%$  of body length; body width  $55.8 \pm 5.0\%$  of body length; eyes positioned dorsolaterally, eye diameter  $10.5 \pm 0.8\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $81.8 \pm 11.5\%$  of interorbital distance; tail fins narrow; ventral fin originating from tail base, dorsal fin slightly behind, ventral fin height  $70.7 \pm$

$6.8\%$  of dorsal fin height; highest part of tail at about middle of tail length; body height  $104.6 \pm 12.2\%$  of maximum tail height; tail axis width  $47.9 \pm 9.3\%$  of body width; tail axis height  $70.2 \pm 10.2\%$  of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, close to snout, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with large rostral gap, only few small papillae anterior to angles of mouth; posterior lip with two rows of around 30 triangular papillae, slightly longer than wide with rounded tips (Fig. 9c); black, massive, serrated jaw sheaths; upper jaw arched with a small medial projection (fang), lower jaw V-shaped.

The largest tadpole in Gosner stage 25 has a body length of 22.5 mm; the longest one (Gosner stage 28) had a total length of 73.2 mm.

**Coloration in preservation.** Basic color brownish, dorsal surfaces darker than ventral ones, turning into yellow, tail lighter brown; tail axis with few dark speckles; tail fins very light brown, semitransparent and with a longitudinal row of small spots on the margin of dorsal fin.

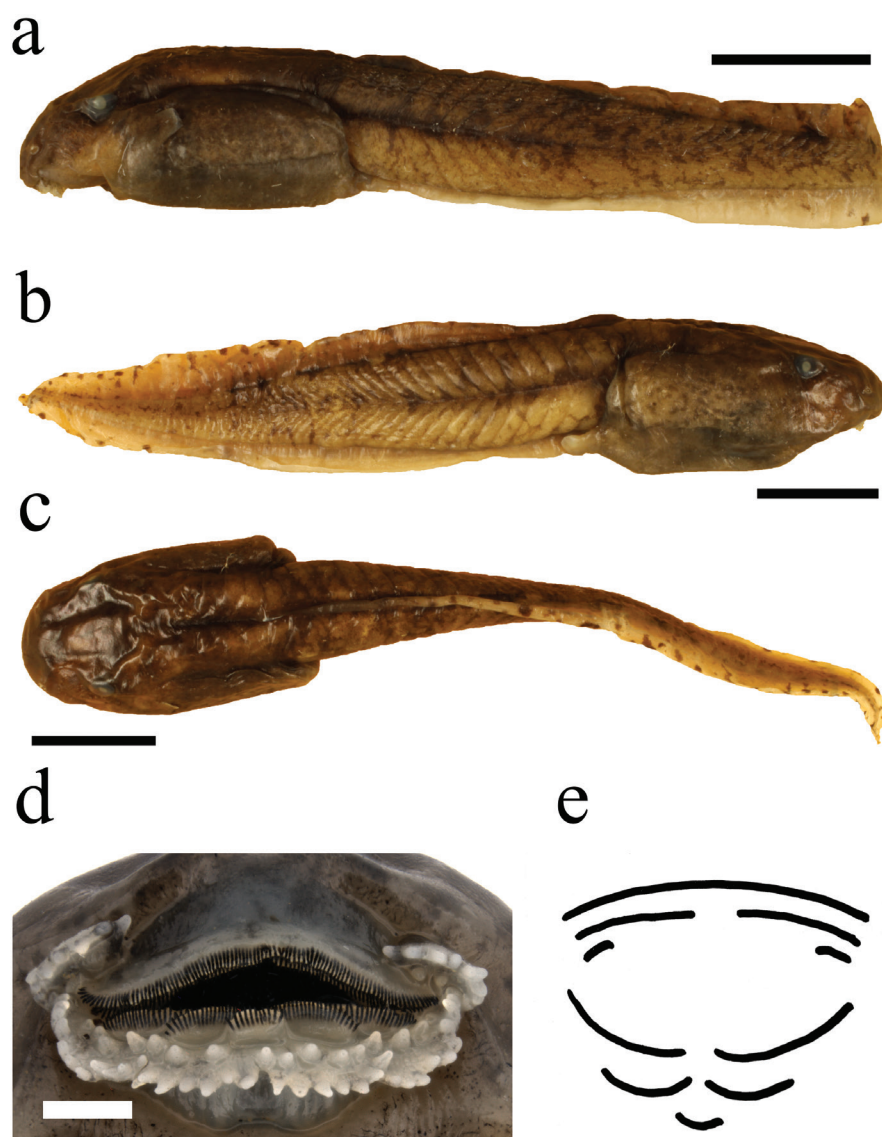
**Taxonomic remarks.** As in *A. batesi* and *A. fallax*, we have molecular evidence for cryptic diversity in *A. montanus*. Apart from the above listed material, we had access to further samples which represented an additional genetic lineage. The distances between the two clades reached an uncorrected pairwise distance of 2.5%.

### *Astylosternus occidentalis* Parker, 1931

**Material examined.** ZMB 77317, 2 tadpoles, Gosner stage 25, Guinea, Déré, 419 m, 7°36'20.0"N, 8°15'36.5"W, 7 August 2010, leg. M. Hirschfeld; ZMB 77440, Gosner stage 25, Guinea, Ziam, 664 m, 8°23'99.3"N, 9°17'13.7"W, leg. M. Hirschfeld; ZMB 77438, Gosner stage 26, Guinea, Fouta Djallon, Chûte Saala, 939 m, 11°17'26.2"N, 12°29'58.0"W, July 2010, leg. C. Brede & J. Doumbia; ZMB 77439, Gosner stage 25, Guinea, Fouta Djallon, Chûte Dintin, 760 m, 10°49'13.1"N, 12°11'30.7"W, 24 July 2010, leg. C. Brede & J. Doumbia; ZMB 75368 2 tadpoles, Gosner stage 41 (A) and 37 (B), Sierra Leone, Gola North, leg. J. van der Winden; ZMB 37564, Gosner stage 26, Guinea, Mt Nimba, leg. M. Lamotte.

The description is mainly based on the two tadpoles accessioned as ZMB 77317. These and ZMB 77440 have been already described by Rödel et al. (2012), who also provide genetic sequences for specimens across the entire range of the species.

**Description.** Long slender tadpole with strong, muscular tail (Fig. 10); body oval in dorsal and lateral view; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length  $31.1 \pm 2.8\%$  of total length;



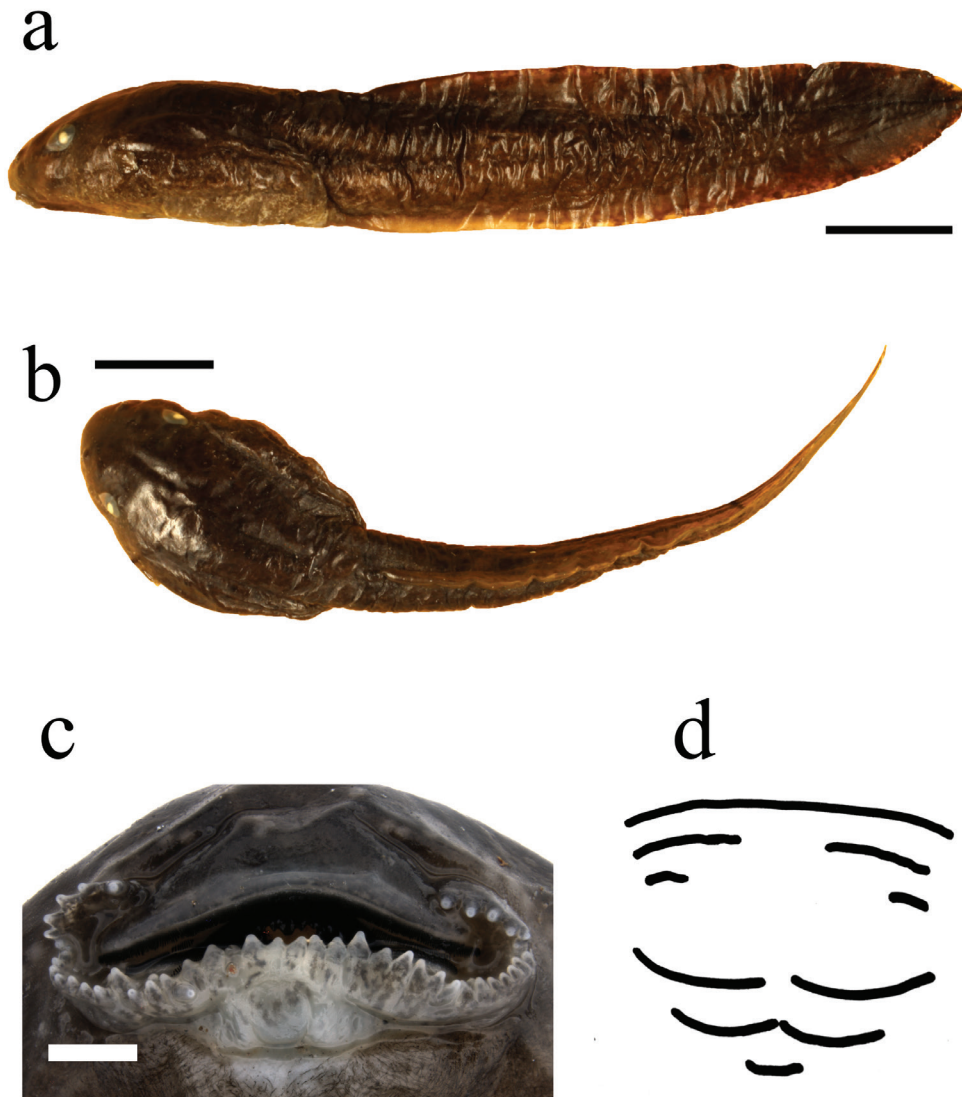
**Figure 9.** *Astylosternus montanus* tadpoles, **a, c, d** ZMB 82875 (Gosner stage 25), and **b** ZMB 82871 (Gosner stage 28); **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

body height  $40.2 \pm 2.2\%$  of body length; body width  $56.1 \pm 4.9\%$  of body length; eyes positioned dorsolaterally, eye diameter  $11.5 \pm 2.3\%$  of body length; nostrils positioned dorsally, closer to snout tip than to eyes; inter-nostril distance  $62.2 \pm 2.7\%$  of interorbital distance; tail fins narrow; ventral fin originating from tail base, dorsal fin insertion a bit posterior to tail base; ventral fin height  $71.6 \pm 13.7\%$  of dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $84.8 \pm 9.4\%$  of maximum tail height; tail axis width  $53.1 \pm 8.6\%$  of body width; tail axis height  $71.9 \pm 14.2\%$  of maximum tail height; tail tip broadly pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, very close to snout, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with a few lateral papillae and large rostral gap; posterior lip with 2–3

rows of about 30 short and triangular papillae (Fig. 10c); papillae of inner row smaller than those of marginal row; black, massive, serrated jaw sheaths; upper jaw broadly arched with a small medial projection (fang), lower jaw narrowly U-shaped.

The largest tadpole in Gosner stage 25 measured 95.9 mm total length. Gosner stage 41 tadpole measured 77.5 mm. Tadpoles with more than 10 cm total length have been caught (Guibé and Lamotte 1958b; MOR unpubl. data).

**Coloration in preservation.** Body more or less uniform dark brown; ventral lighter, slightly grayish; tail fin margins are missing dark pigmentation; last third of tail darker to almost black (Fig. 10). In life, ventral surfaces grayish; lateral and dorsal parts, as well as tail, with a small but very dense yellow and brown speckling (Fig. 11). This pattern progressively becomes denser and darker towards tail tip.



**Figure 10.** *Astylosternus occidentalis* tadpole, ZMB 77317A (Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

**Variation.** ZMB 75368 (Gosner stage 41) is very light brown in comparison to other specimens. According to Lamotte (1985), tooth row P2 is continuous and not divided, thus tooth row formula would be 1:2+2/1+1:2. According to Lamotte, the body is almost evenly pigmented, with lighter lateral sacs and lightly speckled tail. The tadpole of this species was first described by Lamotte and Zuber-Vogeli (1954) as *A. diadematus*. Parker (1936) mentioned *A. occidentalis* tadpoles from Liberia. More recent descriptions have been published by Channing et al. (2012) and Rödel et al. (2012).

#### *Astylosternus perreti* Amiet, 1978

**Material examined.** ZMB 82877 (GenBank MK318864), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1365 m, 5°0'33"N, 9°46'30"E, 14

December 2010, leg. M. Hirschfeld; ZMB 82879 (GenBank MK318865), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N, 9°46'5.82"E, 16 December 2010, leg. M. Hirschfeld; ZMB 82880 (GenBank MK318866), Gosner stage 25, Cameroon, Mt Manengouba, near Pastoral Nkongsamba, 1457 m, 4°59'13.26"N, 9°52'45.9"E, 18 January 2011, leg. M. Hirschfeld & F. Grözingen; ZMB 82881 (GenBank MK318867), 2 tadpoles, 1 genotyped, both Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.4"N, 9°45'46.7"E, 16 August 2011, leg. M. Hirschfeld; ZMB 82882 (GenBank MK318868), Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.45"N, 9°46'5.82"E, 7 October 2011, leg. M. Hirschfeld; ZMB 82883 (GenBank MK318869), 2 tadpoles, 1 genotyped, both Gosner stage 25, Cameroon, Mt Manengouba, Ebonemin, 1372 m, 5°0'46.5"N,





**Figure 11.** Life coloration of an *Astylosternus occidentalis* tadpole (ZMB 88550, Gosner stage 25), Foya forest, Liberia, 96.9 mm total length.

9°46'5.8"E, 7 October 2011, leg. M. Hirschfeld; ZMB 82884A, Gosner stage 28, ZMB 82884B (GenBank MK318870), Gosner stage 27, Cameroon, Mt Manengouba, Ebonemin, 1342 m, 5°0'46.5"N, 9°46'30.9"E, 8 October 2011, leg. M. Hirschfeld; ZMB 82816 (GenBank MK318871), Gosner stage 26, Cameroon, Mt Manengouba, Ebonemin, 1356 m, 5°1'33.42"N, 9°45'46.74"E, 13 December 2010, leg. M. Hirschfeld.

All tadpoles were caught in small to medium-sized streams and rivers in secondary and very degraded forests. The description is mainly based on ZMB 82881B and ZMB 82884B. Genotyped tadpoles have been compared with an adult from Mount Kupe, Cameroon (MHNG 2715.38; GenBank MK318872). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0–0.4% (0–2 bp).

**Description.** Long slender tadpole with strong and muscular tail (Fig. 12); longish oval in dorsal view, slightly flatter in lateral view; back with medial, longitudinal depression; snout broadly rounded in dorsal view, more narrowly rounded in lateral view; body length  $31.2 \pm 2.2\%$  of total length; body height  $43.4 \pm 4.5\%$  of body length; body width  $54.7 \pm 5.9\%$  of body length; eyes positioned dorsolaterally, eye diameter  $12.0 \pm 1.5\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $87.7 \pm 5.1\%$  of interorbital distance; tail fins narrow; dorsal and ventral fin originating from tail base; ventral fin height  $79.9 \pm 6.8\%$  of dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $98.8 \pm 11.2\%$  of maximum tail height; tail axis width  $48.5 \pm 10.3\%$  of body width; tail axis height  $72.3 \pm 7.3\%$  of maximum tail height; tail tip very narrow, filamentous; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with only a few lateral papillae and large rostral gap; posterior lip with 2 or 3 rows of ca 20–30 small, broadly triangular (shark tooth-shaped) papillae (Fig. 12c), medial papillae bigger than lateral ones; black, massive, serrated jaw sheaths; upper

jaw broadly arched with a small medial projection (fang), lower jaw narrow U- to V-shaped.

The largest tadpole in Gosner stage 25 measured 26.2 mm body length and had an approximate total length of 78 mm. The most advanced specimen at Gosner stage 28 had a total length of 108.1 mm.

**Coloration in preservation.** Body dark brown; tail very light brown to beige; lateral sacs and ventrum lighter brown or dark gray; a broad dark brown longitudinal band on tail axis reaching about middle to two-thirds of tail length, proximate end of tail with smaller dark speckles; fins light yellowish beige (Fig. 12). In life body and tail light brown with black blotches on back and broad black bands and spots on tail axis; lateral sacks light grayish brown; tail fins transparent greyish brown (Fig. 13).

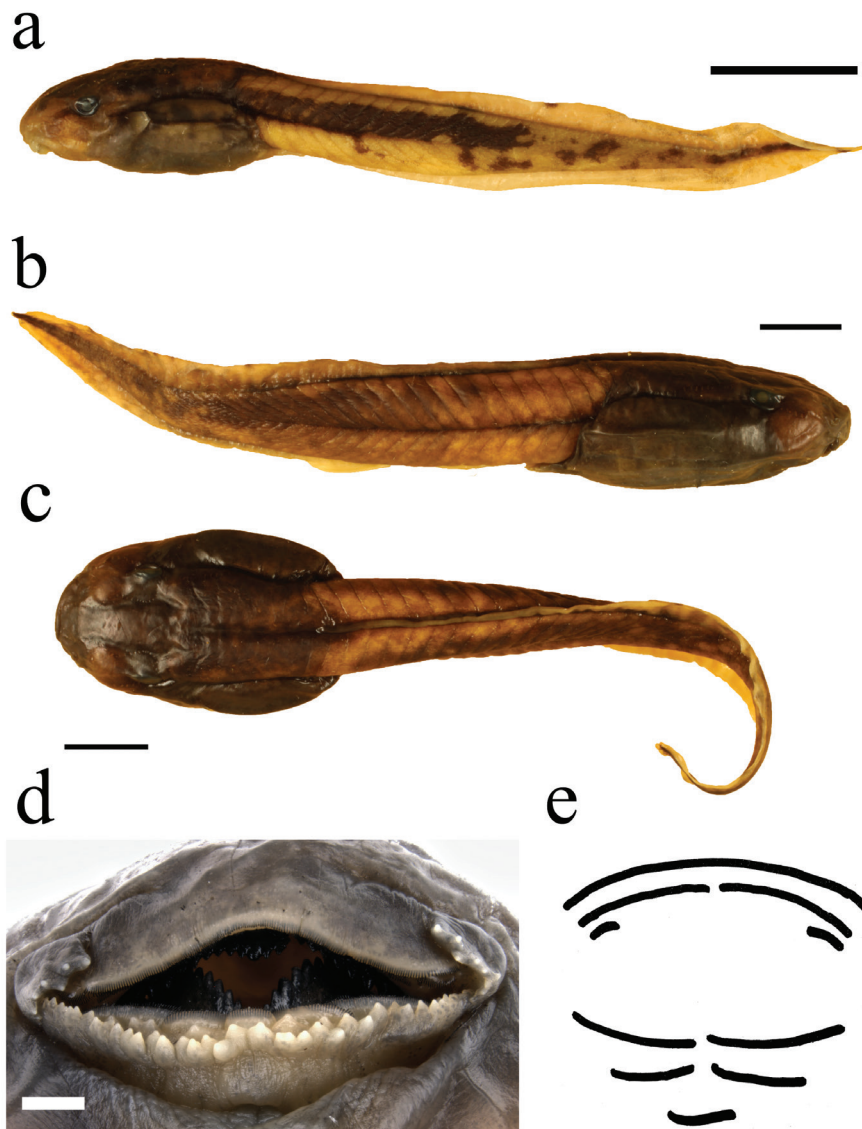
**Variation.** In larger specimens (Fig. 12b, c) the dark pattern on body and tail axis seems to fade, base color becomes darker. Size and arrangement of dark marks differ between specimens (Figs 12b, c, 13).

**Taxonomic remarks.** Whereas all genotyped tadpoles and the comparative adult were genetically almost identical, a single specimen (MHNG 2715.40 from Mofako Balue, Rumpi Hills) differed genetically by about 2%, indicating intraspecific genetic variability or cryptic diversity. The tadpoles used for the description are from the area of the type locality (Mouandong) of *A. perreti*.

### *Astylosternus ranoides* Amiet, 1978

**Material examined.** ZMB 82823 (GenBank MK318873), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2135 m, 5°0'35.4"N, 9°51'24.8"E, 7 August 2011, leg. M. Hirschfeld.

The tadpole was caught in a medium-sized river within a heavily degraded forest fragment. The tail tip had been taken as tissue sample; the continuation of the tail tip was thus reconstructed based on the generalized tail shape of the genus, and total length estimated (compare Fig. 14a).

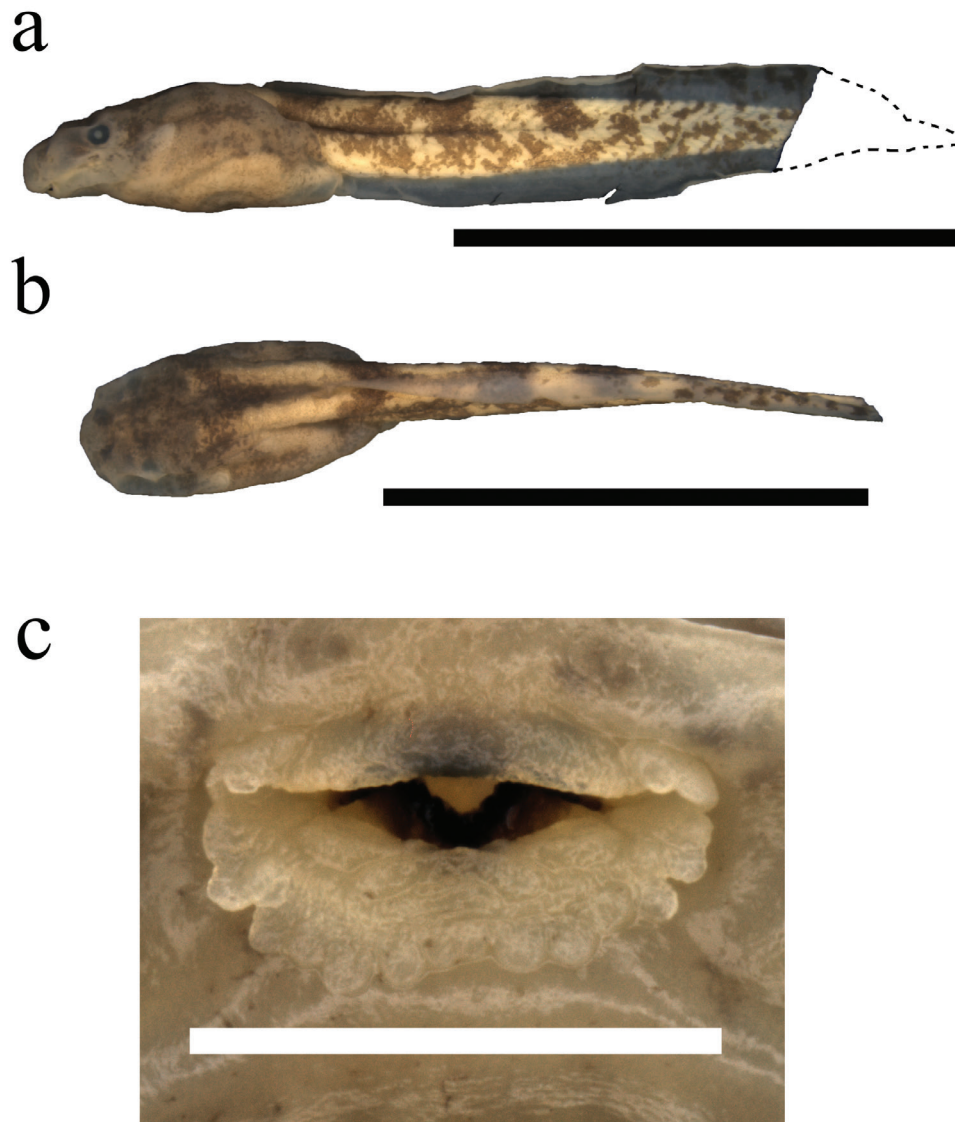


**Figure 12.** *Astylosternus perreti* tadpoles, **a** ZMB 82881 (Gosner stage 25), and **b–d** ZMB 82884A (Gosner stage 28); **a–b** lateral view; **c** dorsal view; **d** oral disc; **e** sketch of keratodont arrangement; black bars = 1 cm, white bar = 1 mm.



**Figure 13.** Life coloration of an *Astylosternus perreti* tadpole from Mount Manengouba, Cameroon (ZMB 82816, Gosner stage 25–27).





**Figure 14.** *Astylosternus ranoides* tadpole, ZMB 82823 (Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; the black color of the fins on the figure is due to the black background, the fins are light grey and transparent with little dark patterning; black bars = 1 cm, white bar = 1 mm.

The tadpole's sequence has been compared with an adult from Kodmin, Cameroon (ZFMK 67364; GenBank MK318874). The two sequences were identical.

**Description.** Long slender tadpole with narrow, muscular tail (Fig. 14); body longish oval in dorsal view, more flattened in lateral view; snout broadly rounded in dorsal view, almost truncate in lateral view; body length 34.1% of total length; body height 45.2% of body length; body width 58.1% of body length; eyes positioned dorsolaterally, eye diameter 9.6% of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance 83.3% of interorbital distance; tail fins narrow; dorsal and ventral fin originating at tail base; ventral fin height 81.8% of dorsal fin height; highest part of tail approximately in the last third of the tail; body height 82.4% of maximum tail height; tail axis width

33.3% of body width; tail axis height 61.8% of maximum tail height; exact form of tail tip unknown; vent tube dextral; body with lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout tip, narrower than interorbital distance; no keratodonts; anterior lip with large rostral gap, only two papillae on each side, close to angles of jaw; posterior lip with about 15 short roundish papillae (Fig. 14c); massive black, serrated jaws, both more or less U-shaped.

Total length of this tadpole was estimated to be about 18 mm (Fig. 14a). The absence of keratodonts implies that the tadpole is in a very early stage of development.

**Coloration in preservation.** Body light brown to beige, slightly speckled; tail axis yellowish with large dark brown blotches; tail fins with dark patterning, but predominately transparent (in Fig. 14a the background was black).



***Astylosternus rheophilus* Amiet, 1978**

**Material examined.** ZMB 82885 (GenBank MK318875), Gosner stage 25, ZMB 82886 (GenBank MK318876), Gosner stage 39 and ZMB 82886A, Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2114 m, 5°0'51.78"N, 9°49'24.24"E, 8 November 2010, leg. M. Hirschfeld; ZMB 82887 (GenBank MK318877) and ZMB 82887A, Gosner stage 36, Cameroon, Mt Manengouba, Pola, 1719 m, 5°3'27.96"N, 9°49'39"E, 2 December 2010, leg. M. Hirschfeld; ZMB 82888 (GenBank MK318878), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2088 m, 5°2'7.6"N, 9°50'46.8"E, 3 August 2011, leg. M. Hirschfeld; ZMB 82889 (GenBank MK318879) and ZMB 82889A, Gosner stage 26, Cameroon, Mt Manengouba, near Abdou, 5°2'13"N, 9°51'24.5"E, 4 August 2011, leg. M. Hirschfeld; ZMB 82890 (GenBank MK318880), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2100 m, 5°1'4.6"N, 9°51'54.9"E, 5 August 2011, leg. M. Hirschfeld; ZMB 82891 (GenBank MK318881), Gosner stage 25, Cameroon, Mt Manengouba, near Caldera, 1889 m, 5°2'26.2"N, 9°48'30"E, 6 August 2011, leg. M. Hirschfeld; ZMB 82892 (GenBank MK318882), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1788 m, 5°3'26.6"N, 9°50'10.2"E, 2 September 2011, leg. M. Hirschfeld; ZMB 82893 (GenBank MK318883), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1719 m, 5°3'27.9"N, 9°49'39"E, 6 September 2011, leg. M. Hirschfeld; ZMB 82894 (GenBank MK318884), Gosner stage 25, Cameroon, Mt Manengouba, Nkikok, 1328 m, 5°5'34.5"N, 9°49'3.8"E, 8 September 2011, leg. M. Hirschfeld; ZMB 82895 (GenBank MK318885) and ZMB 82895A, Gosner stage 25, Cameroon, Mt Manengouba, M'Bouroukou, 1518 m, 5°3'48.2"N, 9°52'0.1"E, 22 September 2011, leg. M. Hirschfeld; ZMB 82896 (GenBank MK318886), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2042 m, 5°2'26.3"N, 9°51'18.9"E, 23 September 2011, leg. M. Hirschfeld; ZMB 82897 (GenBank MK318887) and ZMB 82897A, Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 1992 m, 5°2'13"N, 9°51'24.5"E, 24 September 2011, leg. M. Hirschfeld; ZMB 82898 (GenBank MK318888), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2088 m, 5°2'7.6"N, 9°50'46.8"E, 25 September 2011, leg. M. Hirschfeld; ZMB 82899 (GenBank MK318889), Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2135 m, 5°0'35.4"N, 9°51'24.8"E, 28 September 2011, leg. M. Hirschfeld; ZMB 82900 (GenBank MK318890), Gosner stage 25, Cameroon, Mt Manengouba, Nkack, 1466 m, 5°2'17.4"N, 9°46'27.3"E, 13 October 2011, leg. M. Hirschfeld; ZMB 82901 (GenBank MK318891), Gosner stage 27, ZMB 82901A, Gosner stage 26, ZMB 82901B, Gosner stage 25, Cameroon, Mt Manengouba, near Caldera, 1889 m, 5°2'26.2"N, 9°48'30"E, 17 October 2011, leg. M. Hirschfeld; ZMB 82902 (GenBank MK318892), Gosner stage 25, Cameroon, Mt Manengouba, Pola, 1788 m, 5°3'26.6"N, 9°50'10.2"E, 20 Oc-

tober 2011, leg. M. Hirschfeld; ZMB 82828 (GenBank MK318893), Gosner stage 25, Cameroon, Mt Manengouba, near Abdou, 2012 m, 5°2'24"N, 9°51'39.3"E, 26 September 2011, leg. M. Hirschfeld; ZMB 79241, Gosner stage 25, Cameroon, Mt Manengouba, near summit, 2042 m, 5°2'26.3"N, 9°51'18.9"E, 4 August 2011, leg. M. Hirschfeld.

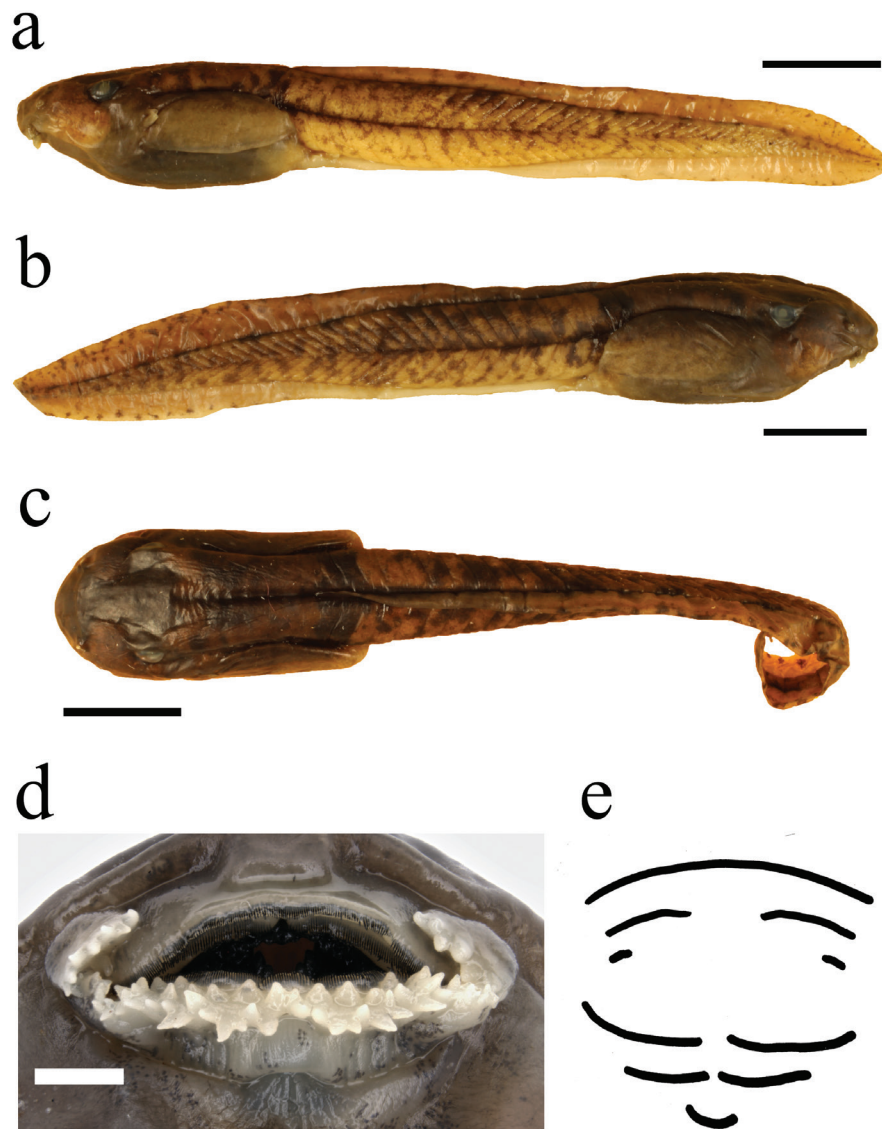
All tadpoles were collected from streams in gallery forest and very degraded forest fragments. The description is mainly based on ZMB 82892 and ZMB 82901. The genotyped tadpoles have been compared with an adult from the Tchabal Mbabo, Cameroon (ZFMK 75632; GenBank MK318894). The uncorrected pairwise p-difference between tadpoles and between tadpoles and the adult ranged from 0–0.2% (0–1 bp).

**Description.** Long robust tadpole with almost parallel flanks and long, muscular tail (Fig. 15); body bullet-shaped in dorsal view, oval but slightly flattened in lateral view; back with a longitudinal medial depression; snout rounded in dorsal view, more narrowly rounded in lateral view; body length  $32.8 \pm 1.7\%$  of total length; body height  $42.2 \pm 4.5\%$  of body length; body width  $55.3 \pm 5.5\%$  of body length; eyes positioned dorsolaterally, eye diameter  $10.8 \pm 1.0\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $82.8 \pm 5.5\%$  of interorbital distance; tail fins narrow, dorsal and ventral fin originating from tail base; ventral fin height  $79.9 \pm 6.8\%$  of dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $98.4 \pm 9.6\%$  of maximum tail height; tail axis width  $46.5 \pm 6.9\%$  of body width; tail axis height  $71.2 \pm 9.9\%$  of maximum tail height; tail tip narrow and pointed; vent tube dextral; body with large lateral sacs, extending from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout, in almost terminal position, narrower than interorbital distance; keratodont formula 1:2+2/2+2:1; anterior lip with large rostral gap, short, round papillae restricted to corner of mouth; posterior lip with 2 or 3 rows of about 20–30 uniform, slender, triangular papillae; massive, black and serrated jaws, upper jaw arched with a big medial fang, lower jaw narrowly V-shaped, without visible notch.

The largest specimen at Gosner stage 25, as well as the largest specimen at Gosner stage 36, were the two largest tadpoles in our samples, both reaching about 80 mm total length.

**Coloration in preservation.** Body light to dark brown, lateral sacs and ventral surfaces lighter, more grayish; fine brown speckling on tail axis, fading from dorsal to ventral parts; fins largely beige transparent, with tiny brown dots along the margin of the last third of dorsal and ventral fin.

**Variation.** Except the large size range of tadpoles all in Gosner stage 25, tadpoles were very uniform in color-



**Figure 15.** *Astylosternus rheophilus* tadpoles; **a** ZMB 82901A, Gosner stage 26 and **b–d** ZMB 82892, Gosner stage 25; **a–b** lateral, and **c** dorsal view; **d** oral disc; **e** sketch of keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

ation, body and mouth part proportions and characteristics. The tadpole of *A. rheophilus* was already described by Channing et al. (2012). These authors give an additional keratodont formula as 1:2+2/1:1+1:1.

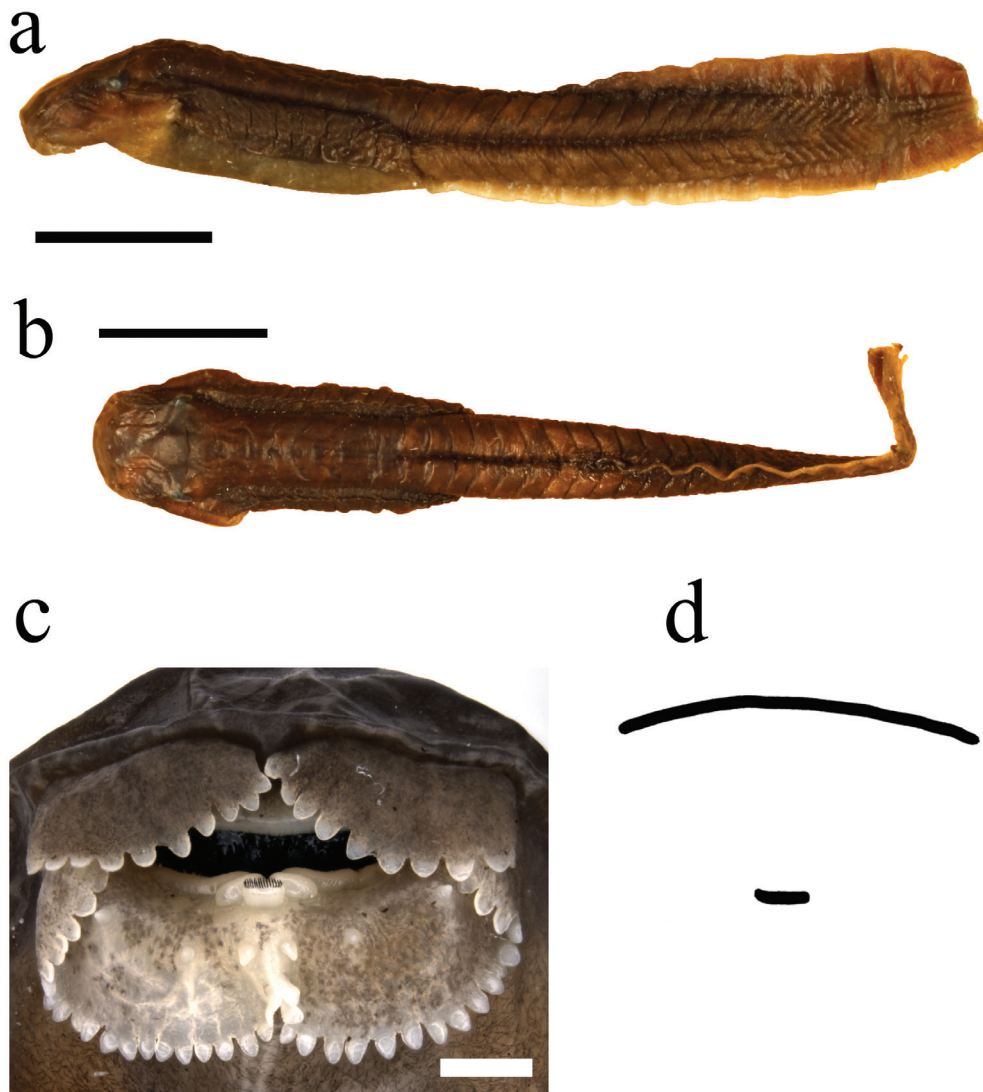
#### *Nyctibates corrugatus* Boulenger, 1904

**Material examined.** ZMB 82109, Gosner stage 25, Cameroon, Mt Kala, near Kala village, 848 m, 3°50'31.86"N, 11°21'4.32"E, 9 November 2015, leg. M.F. Barej, H.C. Liedtke & L.N. Gonwouo; ZMB 82112, Gosner stage 25, Cameroon, Ebo Forest, Njuma, 311 m, 4°21'55.68"N, 10°25'18.48"E, 6 October 2011, leg. M. Dahmen; ZMB 82115, Gosner stage 26, Cameroon, Ebo Forest, Njuma, 255 m, 4°20'51.06"N, 10°13'35.04"E, 27 September 2010, leg. M. Hirschfeld & M.-O. Rödel; ZMB 82116,

Gosner stage 25, Cameroon, Ebo Forest, Bekop, 825 m, 4°21'55.68"N, 10°25'18.48"E, 10 January 2011, leg. M. Hirschfeld & F. Grözinger; ZMB 88351 (GenBank MK318904), Gosner stage 25, Cameroon, Korup National Park, Esukutan, 422 m, 5°22'24.81"N, 8°59'51.35"E, 20 May 2014, leg. F. Mühlberger).

All tadpoles were collected from small to medium-sized forest streams. The description is mainly based on ZMB 82112 and ZMB 82115. The latter specimen was the bases of the description by Channing et al. (2012). The *N. corrugatus* tadpole was first described by Amiet (1971). The genotyped tadpole has been compared with an adult from the vicinity of Ediensoa, Cameroon (GenBank DQ283361). The two sequences were identical.

**Description.** Very long and robust, but still slender tadpole with strong, muscular tail (Fig. 16); body oblong



**Figure 16.** *Nyctibates corrugatus* tadpole (ZMB 82112, Gosner stage 25); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; the downward bent head (**a**) is a preservation artifact; black bars = 1 cm, white bar = 1 mm.

oval to almost rectangular in dorsal view (Fig. 16b shows some artificial shrinking), flattened and elongated in lateral view, belly region fatter than head; snout rounded in dorsal view, more narrowly rounded in lateral view; body length  $38.0 \pm 1.3\%$  of total length; body height  $29.0 \pm 3.5\%$  of body length; body width  $39.5 \pm 0.7\%$  of body length; eyes positioned dorsolaterally, eye diameter  $6.4 \pm 0.9\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $83.4 \pm 4.9\%$  of interorbital distance; tail fins narrow, ventral fin originating from tail base, dorsal fin originates at about first third of the tail; ventral fin height  $76.5 \pm 3.3\%$ , than dorsal fin height; highest part of tail in the last third; body height  $81.8 \pm 8.3\%$  of maximum tail height; tail axis width  $53.4 \pm 2.9\%$  of body width; tail axis height  $62.3 \pm 6.8\%$  of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral air sacs, extending

from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and narrower than interorbital distance; labial tooth formula 1/1; anterior labium consists of two semicircular lobes, the edges carrying a row of short round marginal papillae, the gap between the two lobes very small; posterior labium a wide, flat lobe, carrying one row of about 20–30 uniform, short round marginal papillae, a few further, widely spaced small, wart-like papillae are arranged in one transversal row across the labium; heavily serrated, black jaws; upper jaw broadly arched with a medial fang, lower jaw broadly V-shaped without a notch.

The largest specimen (Gosner stage 25) measured 81 mm total length.

**Coloration in preservation.** Body and tail including fins plain brown in preservation; ventrum brighter and more





**Figure 17.** *Nyctibates corrugatus* tadpole in life coloration (ZMB 82115, Gosner stage 26), from Ebo forest, southern Cameroon.

grayish; ventral fin brighter and more transparent than dorsal fin (Fig. 16). In life the tadpoles are dark brown to almost black with a blue tinge along the lower parts of flanks, belly and tail axis (Fig. 17). ZMB 82109 shows large areas of little or absent pigmentation, what might be a preservation artifact.

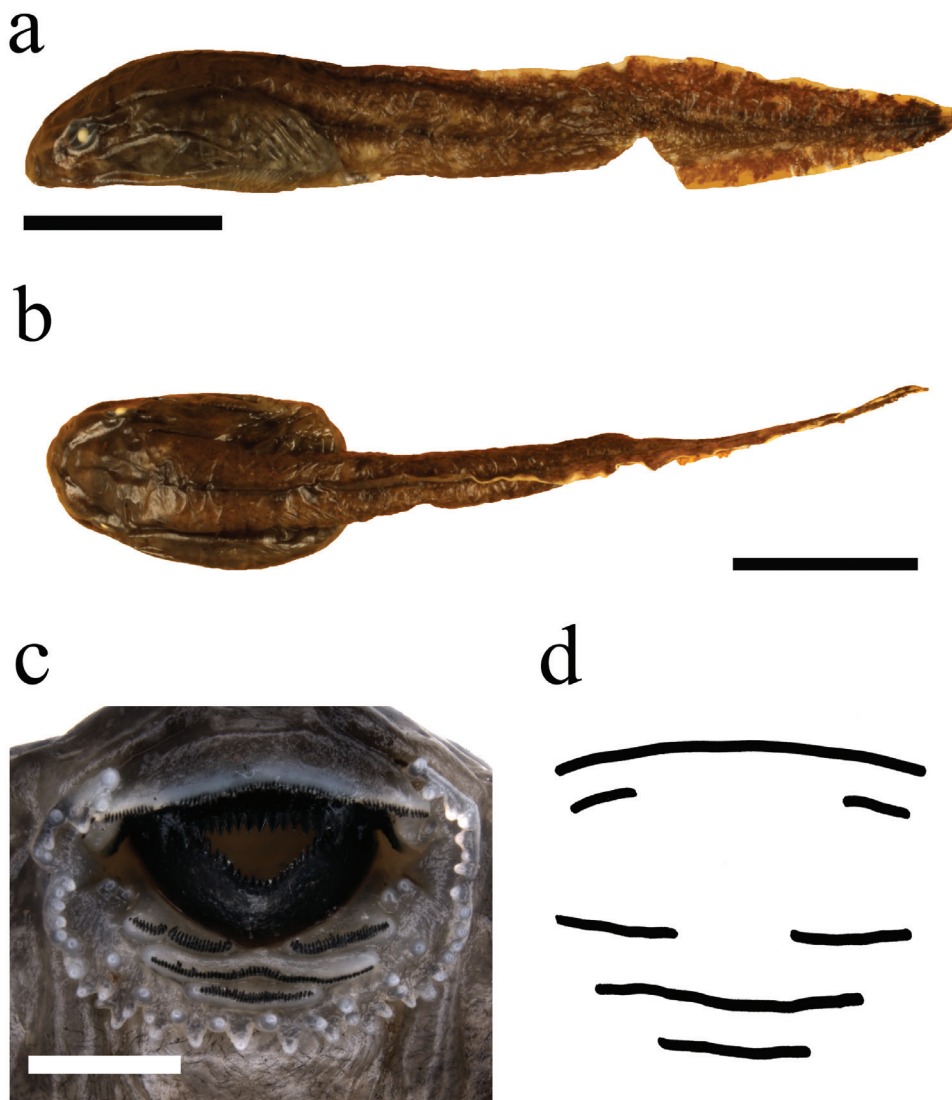
### *Scotobleps gabonicus* Boulenger, 1900

**Material examined.** ZMB 82118 and ZMB 82118A, both tadpoles Gosner stage 25, Cameroon, Ebo Forest, Ndogbanguengue, 113 m, 4°24'36.54"N, 10°10'10.19"E, 22 September 2012, leg. M. Dahmen; ZMB 88347 (GenBank MK318895), Gosner stage 41, Cameroon, near Korup National Park, Mokango, 5°8'2.26"N, 9°5'17.02"E, 8 May 2014, leg. F. Mühlberger; ZMB 88348 (GenBank MK318896), Gosner stage 25, Cameroon, near Korup National Park, Mokango, 758 m, 5°8'40.46"N, 9°5'6.70"E, 9 May 2014, leg. F. Mühlberger; ZMB 88349 (GenBank MK318897), Gosner stage 39, Cameroon, near Korup National Park, Mokango, 533 m, 5°7'50.1"N, 9°3'46.4"E, 10 May 2014, leg. F. Mühlberger; ZMB 88350 (GenBank MK318898), Gosner stage 25, Cameroon, Korup National Park, Esukatán, 189 m, 5°23'8.54"N, 9°0'36.72"E, 19 May 2014, leg. F. Mühlberger; ZMB 88354 (GenBank MK318899), Gosner stage 25, Cameroon, Korup National Park, Bera, 298

m, 5°21'5.47"N, 8°59'12.27"E, 23 May 2014, leg. F. Mühlberger; ZMB 88355 (GenBank MK318900), Gosner stage 35, ZMB 88356 (GenBank MK318901), Gosner stage 38, Cameroon, near Korup National Park, Ikundukundu, 147 m, 5°2'25.1"N, 8°55'3"E, 1 June 2014, leg. F. Mühlberger; ZMB 88357 (GenBank MK318902), Gosner stage 25, Cameroon, Korup National Park, Ikenge, 292 m, 5°16'30.86"N, 9°6'47.28"E, 13 May 2014, leg. F. Mühlberger.

All tadpoles were caught in small to medium-sized streams and rivers in low- to middle-altitude forests. The description is mainly based on ZMB 88355. The genotyped tadpoles have been compared with an adult from Big Massaka, Cameroon (MHNG 2716.24; GenBank MK318903). The uncorrected pairwise p difference between tadpoles and between tadpoles and the adult ranged from 0–0.4% (0–2 bp).

**Description.** Long slender tadpole with slim, muscular tail (Fig. 18); body egg-shaped in dorsal view, slightly flattened in lateral view; snout rounded in dorsal view, more narrow-rounded and sloping in lateral view; body length  $32.6 \pm 1.0\%$  of total length; body height  $40.0 \pm 5.9\%$  of body length; body width  $56.1 \pm 3.4\%$  of body length; eyes positioned dorsolaterally, eye diameter  $11.7 \pm 1.2\%$  of body length; nostrils positioned dorsolaterally, closer to snout tip than to eyes; inter-nostril distance  $59.5 \pm 10.2\%$  of interorbital distance; tail fins narrow, dorsal and ven-



**Figure 18.** *Scotolepis gabonensis* tadpole (ZMB 88355, Gosner stage 35); **a** lateral, and **b** dorsal view; **c** oral disc; **d** keratodont arrangement; black bars = 1 cm, white bar = 1 mm.

tral fin originating from tail base, ventral fin height  $64.5 \pm 5.9\%$ , of dorsal fin height; highest part of tail approximately in the middle of the tail; body height  $87.9 \pm 11.2\%$  of maximum tail height; tail axis width  $41.5 \pm 7.2\%$  of body width; tail axis height  $68.5 \pm 10.1\%$  of maximum tail height; tail tip pointed; vent tube dextral; body with large lateral sacs, reaching from spiracle to end of body; short spiracle, sinistral; mouth ventral, near snout and smaller than interorbital distance; labial tooth formula 1:2/2:2; anterior lip carries no marginal papillae, posterior lip carries 2 or 3 rows of around 20–30 variable papillae, small lobe on each corner of the mouth (Fig. 18c), large rostral gap, papillae short and triangular (with rounded tip), marginal papillae bigger than those of inner row; jaws massive, black and fully keratinized; both jaws sharply serrated, upper jaw almost rectangular with 2 or 3 enlarged fangs on each side, lower jaw V-shaped without a notch.

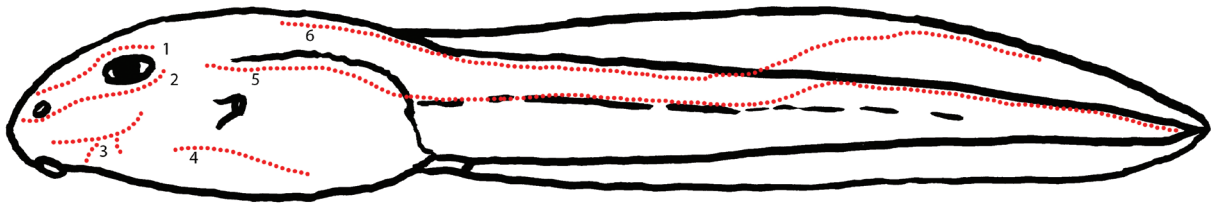
The largest tadpole (ZMB 88347, Gosner stage 41) measured 62.2 mm. The tadpoles of Gosner stages 38 and 39 all measured about 60 mm total length.

**Coloration in preservation.** Body brown, lateral sacs slightly more grayish; tail uniform dark brown at tail base, slightly fading to a fine but dense pattern of lighter brown speckles towards tail tip; fins yellowish brown with a dark reddish brown pattern.

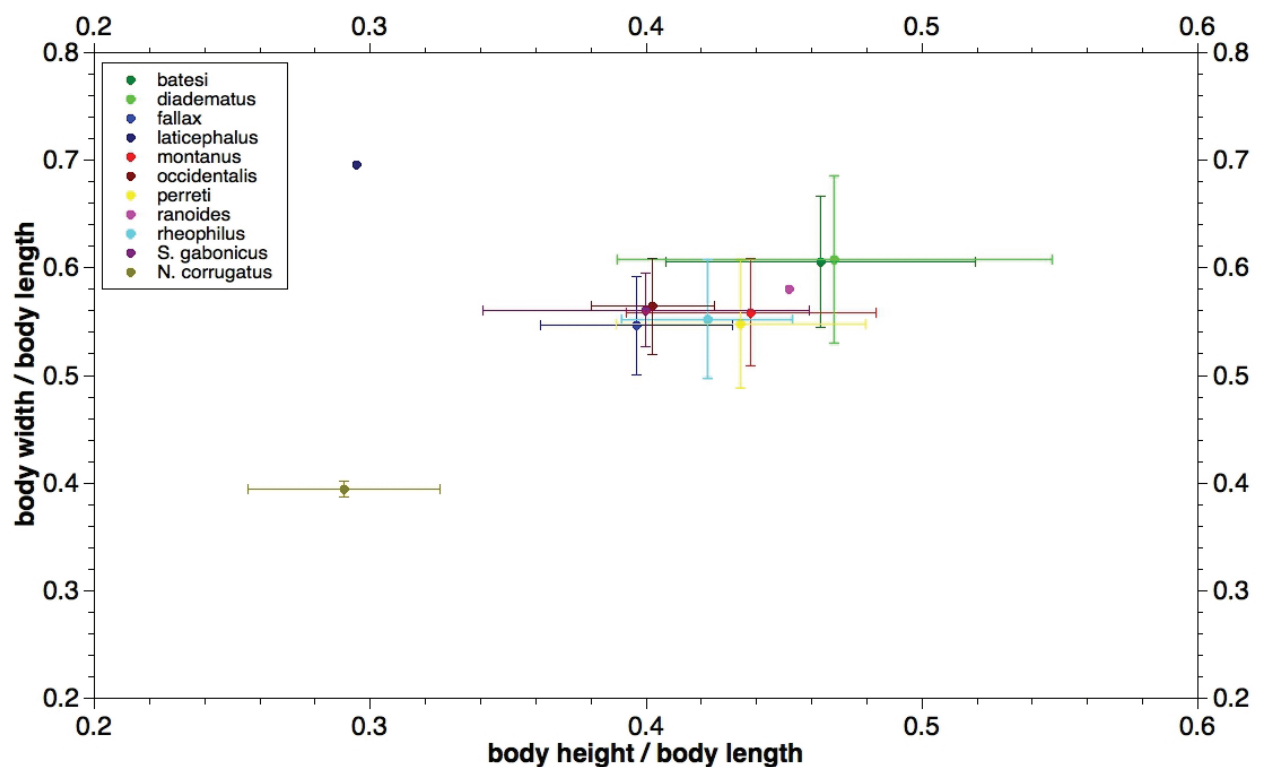
#### **Lateral line-system of the *Astylosternus*, *Nyctibates*, and *Scotolepis* tadpoles**

All investigated tadpoles exhibited a similar and complex lateral line-system (LLS), which is usually well developed (Fig. 19). We did not observe any species-specific differences. Some variation occurred on LLSs of the face (number 3 in Fig. 19). However, this varied intra- and





**Figure 19.** General arrangement of lateral line-system in tadpoles of the genera *Astylosternus*, *Nyctibates* and *Scotobleps*; 1 = supraorbital line, 2 = infraorbital line, 3 = area comprising an angular, an oral, a gular and a jugular line, 4 = lower lateral body line, 5 = middle lateral body line, 6 = upper lateral body line, terminology after Escher (1925).



**Figure 20.** Comparison of two morphological characters (body width and body height) against body length in the tadpole species investigated; *Astylosternus* spp. and *Scotobleps gabonicus* had very similar body shapes; *Nyctibates corrugatus* tadpoles (olive) are much more elongated; the single tadpole of *A. laticephalus* (dark blue dot) had a very flattened body, being proportionally the widest.

interspecifically, and it was not always obvious if the differences were real or due to our difficulty in observing the respective lines. Particularly well visible were the supra- and infraorbital lines, as well as lower, middle and upper lateral body lines (Fig. 19).

#### Morphological comparison of the *Astylosternus*, *Nyctibates*, and *Scotobleps* tadpoles

Morphological variability between the investigated tadpoles was relatively minor. We compared various indices (ratios) of body measurements against each other and performed PCAs (e.g. Fig. 20) to determine species-specific differences in morphological characters (most re-

sults not shown). PCA axes 1–4 accounted for 73% of the cumulative, overall morphological variability of the examined tadpoles. However, there were no significant differences between the species, and it was apparent that only tadpoles of *Nyctibates corrugatus* differed distinctly from all the other species, when comparing body shape (length-corrected width vs height), by having an exceptionally elongated and muscular body. The only other tadpole occupying a unique morphospace was *Astylosternus laticephalus* (Fig. 8). However, measurements were based on only one tadpole in a very advanced stage of development. *Scotobleps gabonicus* seems to have a shorter and rounder head than the other species.



## Discussion

The genus *Astylosternus* Werner, 1898 currently comprises 12 species (Amiet 1989; Rödel et al. 2012), which occur in West and western Central Africa, with a small distribution gap in Togo and Benin, the Dahomey-Gap. Most species are found in Cameroon, with many species restricted to small altitudinal zones of mountainous regions in the west of the country. There, they inhabit a variety of forests and varying stream types (Mertens 1938; Amiet 1989; Oates et al. 2004; Plath et al. 2004; Herrmann et al. 2005). In contrast, the widespread *A. batesi* (Boulenger, 1900) and *A. occidentalis* Parker, 1931 prefer humid lowland forests, where their tadpoles are often found in small, shallow, slow flowing creeks (Amiet 1989; Rödel et al. 2012). *Nyctibates corrugatus* predominantly occurs in western Cameroon, but its distribution ranges from the Nigerian Oban Hills in the north to the mainland of Equatorial Guinea in the south (Frétey and Blanc 2000). The preferred tadpole habitats are very fast flowing streams with stony bottoms. Similarly, *Scotobleps gabonicus* is known from southern Nigeria, through Cameroon, south to western Democratic Republic of the Congo (Portik et al. 2017). Tadpoles were all observed in small to medium-sized streams and rivers in low- to middle-altitude forests. Thus, the tadpoles of the species examined here, live in different habitats, ranging from lowland to mountainous forest streams (Fig. 21), and one might expect some adaptive morphological differences as a result.

Herein, we describe for the first time the tadpoles of five *Astylosternus* species, *A. fallax*, *A. laurenti*, *A. montanus*, *A. perreti*, *A. ranoides*, and *Scotobleps gabonicus*. The tadpoles of five additional *Astylosternus* species, *A. batesi*, *A. diadematus*, *A. laticephalus*, *A. occidentalis*, *A. rheophilus*, and *N. corrugatus* were redescribed, partly based on more specimens (see Channing et al. 2012 and literature cited therein for original descriptions). Based on our investigations, we confirm previous results (e.g. Angel 1930; Lamotte and Zuber-Vogeli 1954; Lamotte 1985; Channing et al. 2012; Rödel et al. 2012) characterizing all *Astylosternus* tadpoles as adapted to torrent currents. They share a long, oval body, slightly flattened in lateral view, with very long muscular tails. The tail fins are narrow, the ventral fin usually is 20–30% narrower than the dorsal fin, and with the tip being mostly pointed. A longitudinal medial depression on the back and large lateral sacs are likewise visible in all specimens. They have massive, serrated jaws, often with a tooth-like medial projection (fang) in the upper jaw. The mouth is always located ventrally but very close to the snout tip. The keratodont formula was 1:2+2/2+2:1 or 1:2+2/1+1:2, and all species have short marginal papillae, which, however, vary in form and length between species. The anterior lip usually has a rostral gap. Our new data mainly agree with previous descriptions, but slight deviations to the literature were noticed in keratodont formulae and coloration (see species accounts). However, both characters

usually vary to some extent with developmental stage and are known to be plastic in some species of amphibians (Martin and Pfennig 2011). For instance, Barej et al. (2015) observed an increasing number of keratodonts during ontogenesis. On the other hand, keratodonts may have worn-off over time or get lost during metamorphosis (e.g. see *A. batesi* account). Especially the tiny, last anterior keratodont row (A3 or A4) was sometimes missing. Tadpoles may become darker or distinct patterns fade and blur with development. For instance in *A. perreti* tadpoles pigmentation became denser with advanced developmental stages. Generally coloration in our descriptions may be less distinctive than in life due to preservation. Many tadpoles vouchers, placed directly in ethanol, show slightly wrinkled skin, in contrast to the smooth, bulging bodies of live individuals.

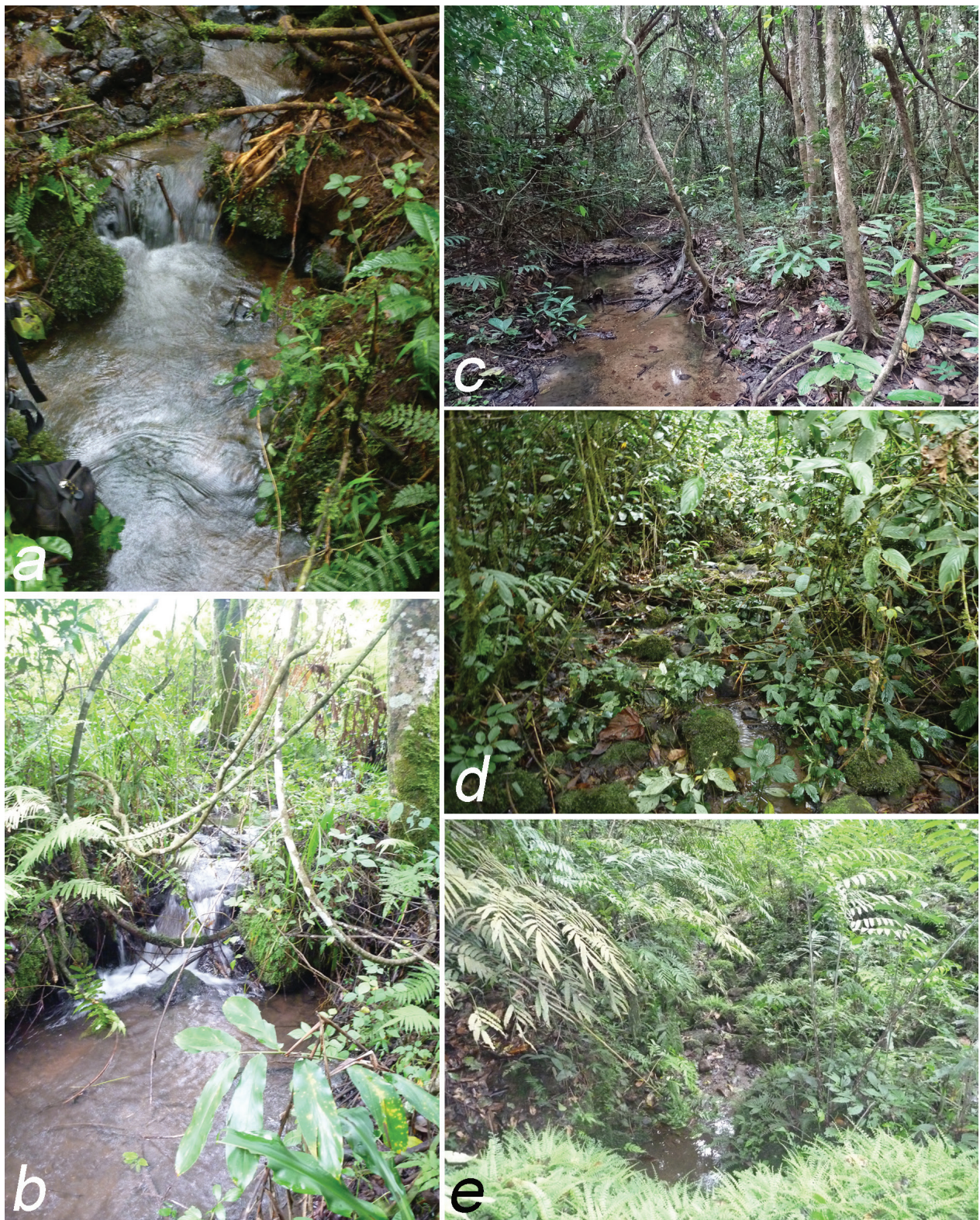
Body proportions of *Astylosternus* were extremely similar. Better characters to distinguish species could be coloration in life (not always available to us) and potentially the shape of labial papillae. For instance, *A. montanus* and *A. rheophilus* had very uniform, triangular papillae. In *A. perreti*, the triangular papillae became larger towards the center of the rows, while papillae of *A. diadematus* had a longish shape. All *Astylosternus* tadpoles (preserved) were more or less brownish. Some species were finely speckled on a lighter base, like *A. diadematus*. Others, like *A. perreti*, had distinct, large, brown marks on the tail or the speckling was dense to almost appearing uniformly brown, as in *A. occidentalis*.

The tadpole of *Scotobleps gabonicus* was similar to *Astylosternus* and only slightly differed in body shape, which was narrower with a shorter and rounder head (e.g. the eyes were closer to the snout). With a total length of around 60 mm, *Scotobleps* tadpoles also seemed to be smaller than those of *Astylosternus* species. The upper jaws of both genera were serrated, but in contrast to *Astylosternus*, *Scotobleps* upper jaw sheaths carried two to three lateral fangs instead of one medial one.

Tadpoles of *Nyctibates corrugatus*, described previously by Amiet (1971), were also similar to *Astylosternus* but nevertheless easily distinguishable on the basis of their shape and color. Their body is even more elongated, the tail longer, the dorsal fin originates at about one-third of the tail, and the tail tip is broadly rounded; thus, the body form is “eel-shaped” (Channing et al. 2012), and it was in fact not always easy to instantly tell these tadpoles apart from small fish when searching their habitats. They also have different mouth parts, and in particular lips, with conspicuous large, flat lobes. Lastly, the plain bluish-black color distinguishes them from any *Astylosternus* species. Nonetheless, all three genera were very similar morphologically, most likely as a result of convergent adaptation to similar stream environments (Lamotte and Lescure 1988, 1989a, b).

In contrast to the morphological similarity of the herein examined tadpoles, the three genera are markedly different to tadpoles of other arthroleptids. According to Altig and John-





**Figure 21.** Habitats of *Astylosternus* tadpoles; **a** *A. rheophilus* habitat at Mount Manengouba (5°02'7.56"N, 9°50'46.8"E, 2088 m), Littoral Province, Cameroun; **b** *A. diadematus* habitat at Mount Manengouba (5°04'3.48"N, 9°51'56.22"E, 1459 m), Littoral Province, Cameroun; **c** *A. occidentalis* habitat at Foya Proposed Protected Area; western Liberia (08°02'37.9"N, 010°24'35.1"W; photo: J. Glos); **d** *A. perreti* habitat at Mount Manengouba near Ebonemin (5°00'46.5"N, 9°46'5.82"E, 1372 m), South-West Province, Cameroun; **e** *A. ranoides* habitat at Mount Manengouba (5°00'51.78"N, 9°49'12.12"E, 2114 m), Littoral Province, Cameroun.



ston (1989) arthroleptid genera, except *Leptopelis* (some species with lentic tadpoles) and *Arthroleptis* (endotrophic larvae; Guibé and Lamotte 1958a), have exotrophic, lotic tadpoles with a general shape adapted to fast flowing currents. All have very muscular tails with reduced tail fins and delayed appearance of limbs to withstand the strong currents and reduce flow resistance (many large specimens, but in Gosner stage 25–30; see Appendix 1; compare with Lamotte and Zuber-Vogeli 1954; Doumbia et al. 2018). Despite these similarities, the genera show obvious differences, especially in the mouthparts. Tadpoles of *Leptodactylodon* are very slender and have a funnel mouth with reduced keratodonts (Mapouyat et al. 2014). The huge sucker mouth of *Trichobatrachus*, with narrow jaws but numerous rows of keratodonts, reflects their life history of rasping food from stones in strong currents (Mertens 1938). *Cardioglossa* lack keratodonts and seem to live in less strong currents, but are often well-hidden in sand and detritus, possibly indicated by their long spiracles which may reach the open water although the tadpole is entirely covered with sand (Hirschfeld et al. 2012).

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## Appendix 1

Measurements (in mm) of the arthroleptid tadpoles described in this study; given are museum accession numbers, Gosner stage (Gosner 1960), and individual measures. For abbreviations of measurements, see Material and methods.

Species	Individual	Gosner	TL	BL	TAL	BH	BW	MTH	TMH	DFH	VFH	TMW	IOD	IND	SP	SSD	ES	SN	EN	ED	ND	MW
<i>A. batesi</i>	ZMB 82865	25	–	25.0	–	10.7	14.2	12.5	9.2	4	2.8	6.56	7.6	5.4	1.1	8.8	5.4	2.2	3.6	2.3	0.7	5
	ZMB 82864	25	–	6.8	–	2.6	3.5	3.4	2.21	1.4	1	1.7	2	1.4	0.2	3.6	1.4	0.6	0.8	0.8	0.25	1.2
	ZMB 82863	25	–	5.3	–	2.7	3.3	–	1.7	–	–	1	1.1	1	–	–	0.5	0.3	0.2	0.5	0.1	0.4
	ZMB 82866	25	–	8.04	–	3.74	4.66	3.8	1.93	1.4	1.1	1.78	2.3	2	0.2	3.7	1.9	0.7	1.2	1	0.25	1.6
	ZMB 82866 A	25	20.7	7.6	13.1	3.3	4.6	3.9	1.8	1.5	1	1.6	2.7	2	0.4	3.8	2.5	0.6	1.5	0.9	0.2	1.3
<i>A. diadematus</i>	ZMB 82866 B	25	25.2	7.9	17.3	4.3	5.6	4.1	1.9	1.7	1.1	2	3.4	2.3	0.5	4.3	2.7	0.9	1.6	1	0.2	1.5
	ZMB 82784	36	–	24.6	–	12	13.92	11.85	9.12	4	3	9	9.2	6.1	1.5	11	7.9	3	5	3	0.8	5.1
	ZMB 82799	25	–	18.71	–	7.5	9.9	8.75	5.67	3.1	2.1	4.38	6.1	4.6	0.7	9.4	4.7	1.8	3.2	2	0.7	3.5
	ZMB 82870	25	–	17.74	–	7.08	9.8	8.61	6.5	2.5	1.8	4.59	5.4	3.9	0.8	7.6	4.2	1.7	2.8	1.9	0.5	3.4
	ZMB 88234	25	52.8	17.3	35.5	9.3	11.6	–	7	2.8	1.8	6.3	6	4.1	1.1	7.8	4.7	1.6	3.2	2.1	0.5	–
<i>A. fallax</i>	ZMB 88346	36	72.1	23.7	48.4	12.7	16.1	13.3	9.2	4.8	3.2	7.1	9.6	6.5	1.4	10.5	6.5	2	4.8	3	0.7	5.1
	ZMB 82868	25	–	14.35	–	5.89	8.92	–	4.29	–	–	2.92	4.35	3.36	0.5	7	3.2	0.9	2.3	1.6	0.6	3
	ZMB 82868 A	25	58.7	21	37.7	8.7	11.9	9	6.6	3.3	2.2	6.5	8.4	6.5	1.4	10.7	7.5	2.8	4.6	2.5	0.6	7.1
	ZMB 82868 B	25	45.2	17.7	27.5	6.3	9.4	7.7	5.5	2.9	1.7	4.9	6.6	4.2	1.2	8.3	5.6	2	3.5	2.1	0.5	3.3
	ZMB 82869	25	74.75	25.44	49.37	10.96	13.42	9.84	6.34	4.3	3.5	5.74	7.8	6.1	1.3	12.3	5.9	1.9	4.1	2.8	1.2	5.5
<i>A. cf. fallax</i>	ZMB 82867	25	97.38	30.86	67.01	10.77	14.93	14.9	9.73	5.45	3.99	7.86	9	7.8	1.1	15	7.5	2.4	5.2	–	–	–
	ZMB 88353	25	51.7	17.7	34	7.4	9.7	9.6	5.9	3.6	2.6	4.6	7	5.4	1.6	8.1	4.8	1.2	3.7	–	–	–
	ZMB 75460	39	62.2	22.7	39.5	6.7	15.8	8.6	5.6	2.3	1.9	5.6	9.3	3.2	–	–	5.5	2.1	3.5	2.5	0.5	4.9
	ZMB 82875	25	–	22.48	–	10.18	12.57	10.71	7.77	3.7	2.6	6.53	7.2	6.6	1.2	11	5.6	1.9	3.2	2.4	0.7	4.7
	ZMB 82874	25	–	20.19	–	7.92	11.95	8.41	6.38	2.8	2.3	5.4	5.4	5.2	1	9	5	1.8	3.4	2.1	0.6	4.1
<i>A. montanus</i>	ZMB 82874 A	25	60.4	20.1	40.3	7.6	10	7.4	5	2.4	1.9	5	7	6.5	1.1	9.9	6	1.6	4.3	2.1	0.5	3.6
	ZMB 82871	25	–	14.65	–	6.8	9.36	6.19	5.56	2	1.5	4.62	4.3	3.7	–	6.7	3.7	1.1	2.4	1.5	0.4	3.3
	ZMB 82871 A	28	73.2	23.8	49.4	12.2	12.7	12.8	8.7	4	2.5	8.4	9.1	6.7	1.2	12.2	8.5	2	5.4	2.1	0.9	5
	ZMB 82871 B	25	52.5	18.3	34.2	7.7	9.2	8.3	5.6	3	1.9	4.9	6.1	4.5	1	9	5.2	2	3.2	1.8	0.6	3.4
	ZMB 82872	25	–	11.03	–	4.98	6.9	3.96	2.97	1.6	1.1	2.37	3.4	3	0.4	5.3	2.7	0.9	1.8	1.3	0.4	2.2
<i>A. occidentalis</i>	ZMB 82873	25	–	8.79	–	3.81	4.91	3.67	2.35	1.5	1	1.8	2.7	2.2	0.3	4.3	2.1	0.8	1.4	1	0.3	1.6
	ZMB 82873 A	25	34.7	11.4	23.3	5.6	6.5	4.6	2.4	1.9	1.3	2.6	4.5	3.4	0.8	5.2	3.2	0.7	2.6	1.2	0.4	2.1
	ZMB 82876	25	–	21.9	–	8.4	11.1	–	5.8	–	–	5.8	9	5.3	1.2	10	2.3	2.1	5	2.4	0.4	4.1
	ZMB 77317	25	75.9	25.4	50.5	10.6	15.4	13.3	9	4.1	3.5	7.5	9.6	5.9	1.6	10.8	6.3	1.9	4.5	3	0.6	5.9
	ZMB 37564	26	80.5	24.3	56.2	9.5	13.8	10	10	3	1.2	9	8.9	5.6	1.7	8.9	6.2	2	4.5	2.5	0.8	5
<i>A. perreti</i>	ZMB 75368	37	80.5	28.4	52.1	10.6	17	15.1	8	5	3.8	7	9.6	6	1.8	12	6.5	1.7	5.5	3.2	0.7	5.3
	ZMB 75368 A	41	77.5	24	53.5	10.6	13.3	13.3	11.5	7	3.9	2.7	6	5.4	1.8	11.9	6.6	2	4.3	4	0.6	4.7
	ZMB 77440	25	73.6	20.7	52.9	8.6	10.1	9	7	3	2.1	6.3	7.9	5.2	1.4	10.8	7	2.2	4.4	2.3	0.6	4.5
	ZMB 77438	26	–	28.5	–	10.8	14.8	14.4	9.3	5.1	3.9	8.6	10.2	6.4	1.4	13	8.4	2.5	5	3.5	0.8	5.4
	ZMB 77439	25	95.9	27.4	68.5	10.9	15.3	12.4	9.5	4	3.1	8.6	10.2	6.5	1.6	11	6.5	2	5	2.5	0.8	5.3
<i>A. perreti</i>	ZMB 82882	25	–	20.01	–	8.82	11.96	9.2	6.09	2.7	2.4	5.4	6.4	5.7	0.5	10.8	5.3	1.6	3.8	2.2	0.9	4.4
	ZMB 82881	25	–	24.91	–	11.09	13.36	11.09	9.87	3.5	3	8.11	7.9	6.6	0.4	13.2	6.4	1.5	5	2.9	0.5	5.6
	ZMB 82881	25	–	24.27	–	10.1	13.38	10.46	7.67	3.5	3	5.9	7.6	6.9	0.8	13.5	7	2.3	4.7	2.9	1.2	5.6
	ZMB 82881 A	25	58.6	16.9	41.7	8	9.1	7.3	5.3	2.4	2	5.1	6	5.3	1.3	8.2	5.1	1.3	4.2	1.9	0.6	3.9
	ZMB 82880	25	–	26.24	–	10.96	13.09	12.44	8.08	3.5	2.9	6.91	8.2	7.4	0.5	20	7.9	2.2	5.7	2.9	1.2	5.8
<i>A. perreti</i>	ZMB 82877	25	–	8.22	–	4.02	5.55	3.5	2.56	1	0.7	1.83	3	2.5	0.5	4.9	2	0.6	1.4	1.2	0.4	1.9
	ZMB 82883	25	–	5.31	–	1.94	2.49	2.39	1.78	1.1	0.9	1.36	2.2	2.1	0.3	3.5	1.4	0.6	0.8	0.7	0.2	1
	ZMB 82883 A	25	18.6	5.9	12.7	3	3.1	3	1.8	1.1	0.9	1.2	1.9	1.8	0.4	2.9	1.5	0.5	1.1	0.7	0.2	1
	ZMB 82879	25	–	7.59	–	3.33	4.31	2.84	2.11	1.4	1	1.44	3.3	2.7	0.5	4.9	2.4	0.8	1.6	1.1	0.3	1.9

Species	Individual	Gosner	TL	BL	TAL	BH	BW	MTH	TMH	DFH	VFH	TMW	IOD	IND	SP	SSD	ES	SN	EN	ED	ND	MW
<i>A. perreti</i> <i>A. ranoides</i>	ZMB 82884	27	–	30	–	11	14.3	12.1	9	3.8	3	8.8	10.3	9	(?) 1.5	13.8	9.9	2.4	7.9	3.2	1	5.9
	ZMB 82884 A	28	108.1	35.8	72.3	14.9	20.9	16.2	11.8	4.5	3.1	11.3	13	10.4	3	16.8	11.9	3	9.1	3.6	1	7.8
	ZMB 82823	25	18.2	6.2	–	2.8	3.6	3.4	2.1	1.1	0.9	1.2	1.8	1.5	0.2	2.8	1	0.35	0.7	0.6	0.1	0.9
	ZMB 82896	25	–	19.47	–	9.09	11.98	8.67	6.15	2.9	2.2	4.95	6.1	5.4	0.9	10.1	5.6	1.6	4	2.3	0.7	4.9
	ZMB 82899	25	–	13.73	–	5.5	7.3	5.96	4.5	1.9	1.4	3.34	4.4	3.8	0.5	7.1	1.7	1.3	2.6	1.6	0.5	3
	ZMB 82895	25	–	18.36	–	6.97	11.67	8.42	5.25	2.8	1.9	4.33	5.5	4.8	0.5	9	4.5	1.3	3.3	2.2	0.6	4.4
	ZMB 82895 A	25	79.8	26.5	53.3	12.5	12.3	11.5	9.2	3.8	2.9	7.1	9.4	6.2	1.6	11.5	7.5	2	5.6	2.5	0.6	5.5
	ZMB 82892	25	–	22.86	–	9.68	13.49	10.81	7.32	3.6	2.5	6.37	7.4	6.5	0.5	10.4	6.6	2.2	4.6	2.4	0.8	5.3
	ZMB 82891	25	–	19.51	–	8.38	11.25	8.79	5.89	2.7	2	5.13	6.1	5.3	0.5	9.5	4.9	1.6	3.5	2.1	0.7	4
	ZMB 82898	25	–	13.68	–	5.48	7.23	5.85	3.93	1.8	1.3	2.92	4.2	3.8	0.4	7.1	3.9	1.3	2.5	1.7	0.5	3.1
<i>A. rheophilus</i>	ZMB 82828	25	–	17.24	–	7.37	10.63	7.37	5.1	2.6	1.9	4.3	5.1	4.3	0.4	7.3	4.9	1.7	3.2	1.9	0.6	4
	ZMB 79241	25	–	19.3	–	8.08	11.62	8.16	5.98	3.1	2.2	5.2	6.4	5.2	0.5	10	5.7	1.8	3.9	2.3	0.7	5.5
	ZMB 82894	25	–	19.61	–	7.95	11	8.96	6.4	3	2.2	5.3	6.5	5	0.4	9.7	4.4	1.5	3.1	2.2	0.7	4.2
	ZMB 82897	25	–	18.75	–	7.94	10.14	8	6.14	2.5	2.2	4.44	5.6	4.9	0.6	9.2	5.3	1.9	3.4	2.1	0.7	4.4
	ZMB 82897 A	25	61.5	19.1	42.4	7.6	9.4	8	5.2	2.6	1.8	4.3	6.5	5.4	0.9	9	6.5	1.8	4.5	2	0.6	4
	ZMB 82900	25	–	26.18	–	10.81	13.57	11.1	8.43	4.2	3.1	7.75	8.3	7.1	1	13.8	8.2	2.8	5.4	3	1	5.9
	ZMB 82902	25	–	14.42	–	6.27	8.78	6.26	4.39	2.2	1.5	3.65	4.7	3.9	0.4	7.2	3.9	1.3	2.8	1.7	0.6	3.3
	ZMB 82890	25	–	12.01	–	5.69	7.29	5.65	4.01	1.7	1.3	3.3	4	3.5	0.5	6.3	3.1	1	2.2	1.3	0.4	3.3
	ZMB 82893	25	–	13.65	–	6.55	8.72	5.98	4.28	1.8	1.2	3	4.7	3.5	0.5	6.8	3.7	1.1	2.6	1.2	0.5	2.8
	ZMB 82888	25	–	12.84	–	5.65	7.33	4.26	4.66	1.7	1.4	2.79	3.9	3.4	0.4	6.4	3.4	1.1	2.4	1.5	0.5	3.2
<i>N. corrugatus</i>	ZMB 82885	25	–	23.28	–	9.57	12.03	9.78	6.46	3.3	2.6	5.43	7	6.2	0.7	10.7	6.3	1.9	4.4	2.1	0.8	4.9
	ZMB 82886	39	74.2	24	50.2	9.9	12.1	11.4	5.5	4.5	2.7	5.1	8.5	7	2	11.4	8	1.9	6	2.9	0.6	6
	ZMB 82886 A	25	38.8	13.5	25.3	6	8.5	6.5	4	2.1	1.3	3.8	5.5	4.1	0.5	6	4.4	1.1	3.6	1.3	0.4	3.2
	ZMB 82887	36	77	27.5	49.5	10.5	12	10.5	7	3.6	2.7	6.2	9.5	7.5	1.6	13.2	8.7	2.3	6.1	2.6	0.6	5.1
	ZMB 82887 A	36	79.2	25.6	53.6	9.9	12.5	10.6	7	3.2	2.3	6.8	9.4	7.5	2	12.4	8.5	2.1	6	2.5	0.7	5.1
	ZMB 82889	26	–	23.4	–	10.2	12.7	11.1	7.6	3.4	2.5	7.4	8.5	7	1.6	12	8	2.4	5.6	2.5	0.6	5.9
	ZMB 82889 A	26	76.4	23.6	52.8	11.1	12.3	11.5	8.5	4	2.6	7.8	9.5	7.9	1.5	11.5	8.5	2	6.5	2.5	0.5	6.1
	ZMB 82901	27	–	24.1	–	9.4	12.1	8.6	6.5	3.4	2.1	5.6	8.2	6.5	1.1	11	7.4	2.1	5.1	2.4	0.6	4.5
	ZMB 82901 A	26	74.2	23.2	51	9.5	12.3	9	6.5	2.9	2.6	5.9	8.1	6.9	1.1	11	7.9	2.1	5.3	2.5	0.7	5.1
	ZMB 82901 B	25	52.9	17.6	35.3	6.5	9.6	7	5.5	2	1.6	4.4	6.4	4.9	1	8.1	6	1.6	4.3	2	0.5	3.3
<i>S. gabonicus</i>	ZMB 82109	25	81.2	31.6	49.6	8	12.6	10.6	6.8	3	2.3	7.1	8.1	6.4	1.1	10.5	7.8	2.5	5.4	2	0.6	6.5
	ZMB 82112	25	–	22.9	–	6.6	9	8.5	5	3	2.4	5	5.6	5	0.9	9	6.5	2	4.5	1.6	0.5	5.3
	ZMB 82115	26	69.1	25.6	43.5	8.6	10.1	9.1	5.2	2.5	1.8	5.2	7	6	1	10.5	8.5	2.5	5.2	1.9	0.5	6.4
	ZMB 82116	25	–	27.2	–	7.1	10.4	9.5	5.5	3.5	2.7	5.2	6.9	5.9	1.4	11	8.5	3.2	5.3	1.6	0.5	6.6
	ZMB 88351	25	–	21.4	–	6.7	8.6	7.9	5.8	–	–	4.8	5.8	4.5	1.1	8	6	2	3.9	1.1	0.4	4.4
	ZMB 82118	25	–	6.3	–	1.9	3.5	–	1.2	–	–	1.2	2.3	1.5	0.5	3.5	1.9	0.5	1.2	0.8	0.1	1.1
	ZMB 82118 A	25	20.4	6.7	13.7	2	3.7	3.1	1.4	1	0.6	1.3	2.5	1.8	0.6	3.5	2.2	0.6	1.2	0.6	0.1	1.2
	ZMB 82830	25	–	10.4	–	4.6	5.4	–	3.2	–	–	2.9	3.5	2.4	–	–	2.4	1.3	2	1.2	0.1	2.1
	ZMB 88347	41	62.2	19	43.2	8.3	10.9	8.5	5.9	3.3	2.2	4.1	7.2	2.5	0.9	9	4.3	0.5	2.7	2.4	0.2	3.6
	ZMB 88348	25	37.5	11.8	25.7	4.5	6.6	5.1	3.8	1.9	1.4	3	4.5	2.6	1.1	6.5	3.3	1.1	2.1	1.4	0.2	2
	ZMB 88349	39	57.7	18.7	39	9.2	12.2	9	7	3.3	2.3	4.1	7.5	4.2	1.6	9.8	5.2	1.6	3.5	2	0.2	3.8
<i>S. gabonicus</i>	ZMB 88350	25	–	12.9	–	5.3	6.8	–	4	–	–	3.5	5	3.2	0.8	7	4.2	1.6	2.6	1.5	0.2	2.4
	ZMB 88354	25	47.5	15.5	32	5.9	8.6	6.8	4.5	2.7	1.6	3.2	5.8	3.9	0.9	7.6	4	1.2	2.7	1.7	0.2	3
	ZMB 88355	25	48.3	16.1	32.2	6.2	8.9	7.5	5.2	2.9	1.7	3.4	6.4	3.5	0.9	8	4.1	1.2	2.8	1.9	0.2	2.9
	ZMB 88356	38	55.3	18.7	36.6	8.1	10.3	9	6.8	3.2	1.9	5	7	3.8	1.6	9	5.1	1.6	3.6	2.3	0.2	3.5
	ZMB 88357	25	36.6	11.9	24.7	5.2	6.8	5.7	4	1.9	1.3	2.8	4.5	2.7	1	6.7	3.5	1.2	2.4	1.6	0.1	2.4



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