

Rediscovery, natural history, and conservation status of *Idiocranium russeli* Parker, 1936 (Amphibia: Gymnophiona: Indotyphlidae)

David J. Gower^a*, Marcel T. Kouete^{b,c}, Thomas M. Doherty-Bone^a, Echalle S. Ndeme^d and Mark Wilkinson^a

^aDepartment of Life Sciences, The Natural History Museum, London, UK; ^bProject Cameroon Herpetology, Conservation Biology Foundation, Yaoundé, Cameroon; ^cZoological Society of London, London, UK; ^dConservation and Research for Endangered Species, Zoological Society of San Diego, Yaounde, Cameroon

(Received 15 March 2014; accepted 25 June 2014; first published online 19 August 2014)

The indotyphlid caecilian amphibian Idiocranium russeli Parker, 1936 is the only nominal species in its genus. Apart from two additional, largely overlooked locality records that we consider to be of an undescribed species, I. russeli is known with certainty from only a single collection of c.50 specimens from a single locality in 1933. We report new material from fieldwork in 2012 carried out in the vicinity of the type locality. Digging surveys at 34 sites for a total of >2000 person minutes found 50 I. russeli at 15 of these sites, extending the known range of the species by more than 40 km south and from an elevation of c.670 m to 104-820 m. The species probably occurs in nearby Nigeria and in some protected areas, is tolerant of some human disturbance, and is likely to move from Data Deficient to Least Concern on the IUCN Red List. Males have relatively longer and wider heads than females. Total length measured for preserved specimens is less than for freshly anaesthetized specimens, by up to 14.1%. Previously, preserved I. russeli were reported as having a maximum length of 114 mm, but the new sample includes specimens with total lengths of 145 mm in preservation and 167 mm when fresh. The sex of the smallest independent specimens (total length 62 mm in preservation) could be determined from examination of the gonads, hatchlings are c.30 mm, and I. russeli is confirmed as one of the smallest known caecilian species.

Keywords: abundance; caecilian; Cameroon; Mamfe; reproduction; size

Introduction

The caecilian amphibian *Idiocranium russeli* Parker, 1936 is the sole described species in a genus endemic to Cameroon. Parker (1936) described the genus and species on the basis of a series of 49 specimens collected from 'Makumunu' at 2200 feet (= 670 m) in south-western Cameroon during a 1932–1933 (not 1934–1935 *contra* Wake 1986) expedition by Ivan T. Sanderson. Sanderson (1935a, 1935b) made passing references to 'coecilian' discoveries in Asumbo (the hills north of Mamfe in which Makumunu lies) in brief reports of his expedition, and he subsequently (Sanderson 1937) published a non-specialist book about his extensive fieldwork in south-western Cameroon that includes an account of the discovery of *I. russeli*.

There are reports of *I. russeli* based on three specimens collected in April 1947 by A. Monard from two additional Cameroon localities, Ndikiniméki and Kon, far

^{*}Corresponding author. Email: d.gower@nhm.ac.uk

(c.220–230 km) to the south-east of the type locality (Perret and Mertens 1957; Perret 1966; see also LeBreton 1999). These reports and specimens were overlooked by Taylor (1968), who reported incorrectly (p. 626) also that the type locality was 'now in Nigeria', and by Wake (1986) and Lawson (1993), who stated that the species had been collected only once. However, Loader and Wilkinson (2004) suggested that the conspecificity of the specimens previously referred to *I. russeli* needed checking and, based on differences in external morphology and osteology (pers. obs.), we consider the populations at Ndikiniméki and Kon to represent a second, as yet undescribed, species of *Idiocranium*.

Idiocranium russeli is best known for reportedly being the world's smallest caecilian, or the smallest along with the Seychelles indotyphlid *Hypogeophis brevis* Boulenger, 1911 (e.g. Taylor 1968; Wake 1986; Lawson 1993; Duellman and Trueb 1994; Clarke 1996; Nussbaum 1998; Hofrichter 2000; Vitt and Caldwell 2013). Parker (1936) reported adults of *I. russeli* at a maximum size of 114 mm 'snout to vent' (as the vent is almost at the body terminus this, if it is actually what Parker measured, is likely only *c*.1 mm less than total length) and also reported mature females as small as 90 mm 'associated with developing eggs'. The smallest paratype reported by Parker (1936) was 51 mm and had (p. 162) 'no trace of larval or embryonic characters'. Wake (1986) reported a maximum total length (based on the same material available to Parker) as 114 mm (p. 1) or 113 mm (table 1), and the smallest 50 mm. Encyclopaedia Britannica (2014) gives the maximum length at 104 mm.

In their revised classification of caecilians, Wilkinson et al. (2011) tentatively included *Idiocranium* in the Indotyphlidae based primarily on overall similarity to other indotyphlids. The Indotyphlidae otherwise comprises the Ethiopian monotypic endemic *Sylvacaecilia* Wake, 1987 and 19 species from five genera endemic to either Seychelles or peninsular India. In a phylogenetic exploration of traditional morphology and neuroanatomical data, Wilkinson (1997) recovered *Idiocranium* as closely related to the indotyphlid *Hypogeophis* Peters, 1879. The phylogenetic analyses of Maddin et al. (2012), of morphological data including new evidence from braincase osteology, and San Mauro et al. (2014), of complete mitochondrial genome sequences, both support the referral of *Idiocranium* to Indotyphlidae.

Having been collected with certainty only once from a single locality nearly 80 years ago, *I. russeli* has been assessed as Data Deficient in the IUCN Red List global conservation assessments (IUCN 2013). The majority of caecilian species are currently classified as Data Deficient and it has been suggested that the best way to change this situation is through targeted fieldwork (e.g. Doherty-Bone et al. 2011; Kotharambath et al. 2012). This proposition has not been tested much thus far, though it could have important implications for determining whether and how to expend effort to determine the conservation requirements of rarely encountered and poorly known organisms. Here we report new collections of *I. russeli* based on targeted new fieldwork, and provide new data on its distribution and habitat associations, conservation status, reproductive biology, and size.

Materials and methods

The new fieldwork reported here was conducted in September 2010 and April and May 2012. Fieldwork was targeted (non-random), with the main aim to locate specimens of *I. russeli*. In 2010 we surveyed only four closely grouped sites near the

town of Mamfe. In 2012, we began searching in Makamune (a more common spelling for Makumunu that we encountered and use here, though we have also seen Mokomono and Mukumunu), that we understood to be the type locality of *I. russeli*, and then in and around other villages in the vicinity of Mamfe, Manyu Division, South West Region, Cameroon. Our focus was between Makamune and Mamfe because this was the route along which Sanderson worked in 1932–1933 (Sanderson 1935b, 1936) and because it remains one of the more accessible routes in the area. The 34 localities that we surveyed are summarized in Tables 1 and 2, and the main centres (of fieldwork and of human habitation) are indicated in Figure 1. Surveys were initiated by talking to local people, showing them live and preserved caecilians (collected elsewhere in Cameroon) and/or photographs of African caecilians, and describing the type of habitat that we expected them to occur in (moist, organically rich soil in shady places). At each village, local people directed us to likely habitats. We spent less than one hour at each locality regardless of whether I. russeli was found. At each locality we dug soil to a depth of typically c.30 cm using between one and five heavy-duty, steel-bladed digging hoes. We recorded the total person hours and minutes spent digging and/or the estimated total surface area of soil dug. A total of 2145 person minutes (35.75 person hours) of digging surveys were carried out. Soils were characterized using the hand method reported by Dubbin (2001), and soil temperatures were recorded at a depth of c.15-20 cm. Canopy cover was estimated by eye for ground areas of approximately 6×6 m, with estimated values agreed by two people where possible.

As far as possible, all *I. russeli* that we encountered were collected. Specimens were given a lethal dose of the anaesthetic MS222, fixed in 5–10% aqueous formaldehyde for approximately 48 hours, washed in water and stored in 70% ethanol or industrial methylated spirits. Specimens have been deposited in the Natural History Museum, London as BMNH 2008.688. Total length (TL, to nearest 1 mm) of specimens was recorded prior to fixation (under anaesthesia) and three months after fixation by carefully but firmly stretching specimens against a ruler.

For Sanderson's and our new preserved material, we used dial callipers to measure head length and width. The former was measured as the distance between the snout tip and first nuchal groove (laterally, behind the corner of the mouth) and the latter as the greatest transverse width of the head between the back of the mouth and the first nuchal groove.

Results

Distribution

Based on external morphology, chiefly colour and numbers and visibility of secondary annular grooves, and skull osteology (unpublished data), we do not consider the populations from Ndikiniméki and Kon to be *I. russeli* but instead an undescribed congeneric species that will be documented elsewhere. Thus, *I. russeli* is known only from the region approximately between the towns of Mamfe and Akwaya in South West Region, Cameroon.

We found *I. russeli* in 15 of the 34 localities we searched in the Mamfe–Akwaya region (Table 2; Figure 1). The species was found at elevations of 104–820 m, with the elevation of surveyed localities ranging from 89 to 820 m. Excluding clutches of eggs

| 2016 |
|---------|
| April |
| 08 |
| :04 |
| 02 |
|] at |
| lge. |
| bric |
| Caml |
| of (|
| rersity |
| Jniv |
| Ę |
| þ |
| led |
| oac |
| vnl |
| Do |
| _ |

| | Locality | Date | Start time | Habitat | Canopy % | Soil | Soil temp °C |
|----------------------|----------------------------------------------------------------|---------------------------------------------------------------------------------------------------|-------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------|-------------------------|----------------------|
| - 1 m 4 m | Nchanga 1 Nchanga 2 Nchanga 3 Nchanga 4 Makamune 1 | 22 September 2010 22 September 2010 22 September 2010 22 September 2010 16 April 2012 | 10:15 10:35 11:45 12:30 11:00 | Cacao agriculture and home gardens Cacao agriculture and home gardens Cacao agriculture and home gardens Cacao agriculture and home gardens Disturbed gallery forest between river and | 60-80 | SCL/CL | |
| 9 | Makamune 2 Makamune 3 | 16 April 2012 16 April 2012 | 12:30 13:00 | agriculture Small disturbed forest patch within agriculture Secondary forest with interspersed agriculture | 75 0-50 | CL SCL | 23.6 24.2 |
| 8 6 | Makamune 4 Makamune 5 | 17 April 2012 17 April 2012 | 08:15 09:00 | Secondary forest mixed with fallow agriculture Secondary forest mixed with fallow agriculture | 0-40 0-10 | SCL/L SCL | 23.7 23.2 |
| 11 10 | Makamune 6 Makamune 7 Tinta 1 | 17 April 2012 17 April 2012 19 April 2012 | 10:45 11:30 08:45 | Small secondary forest patch Secondary forest bordering cacao plantation Mixed secondary forest and agriculture | 40 30–80 30–40 | CL/L SCL/CL SICL | 23.5 23.5 23.2 |
| 13 15 15 | Tinta 2 Tinta 3 Tinta 4 | 19 April 2012 19 April 2012 19 April 2012 | 10:00 11:20 11:35 | Mixed secondary forest and agriculture Secondary forest mixed with fallow agriculture Open area very recently cleared by slash & burn | 30 $40-80$ 0 | SiCL SCL/SiCL/CL | 23.1 22.7 |
| 16 17 18 19 | Tinta 5 Tinta 6 Tinta 7 Atolo | 20 April 2012 20 April 2012 20 April 2012 20 April 2012 | 09.10 09.35 09.50 14:00 | Mixed secondary forest and agriculture Mixed secondary forest and agriculture Disturbed secondary forest Close to forest: grassy area among houses | 30 60 40 | SCL | |
| 20 | Kakpenyi 1 Kakpenyi 2 | 21 April 2012 21 April 2012 | 09:15 10:00 | Agricultural habitat recently cleared and burnt Small secondary forest next to housing and cacao | 0 75 | SCL LS/SL/ CL/SCL | 25.3 24.0 |
| 22 23 24 | Kakpenyi 3 Kakpenyi 4 Akwa | 21 April 2012 21 April 2012 26 April 2012 | 11:00 12:15 12:40 | Small secondary forest next to housing and cacao Disturbed secondary forest Secondary forest being cleared for cacao and other crops | 30 60–80 | SC SCL/CL | 24.3 |

Table 1. Locality features and fieldwork occurrence data. See Table 2 for locality coordinates and elevations.

| April 2016 |
|---------------|
| ∞ |
| 0 |
| 4 |
| $\frac{1}{2}$ |
| 0.0 |
| ÷ |
| 9 |
| e |
| <u>–</u> |
| ٠Ĕ |
| -g |
| Cam |
| F |
| versity c |
| . Е |
| 5 |
| <u> </u> |
| S |
| 1 |
| ĕ |
| g |
| ö |
| nl |
| B |
| 0 |
| |

Table 1. (Continued).

| 25 | Nyang | 28 April 2012 | 08:45 | Secondary forest being cleared for cacao and other | |
|-----|------------------|----------------------|----------|--------------------------------------------------------------------------|------|
| | | | | crops | |
| 26 | Mukonyong | 29 April 2012 | 09:30 | Secondary forest being cleared for cacao and other | 26.7 |
| | | | | crops | |
| 27 | Eshobi 1 | 30 April 2012 | 09:25 | Beside river in cultivated area | |
| 28 | Eshobi 2 | 30 April 2012 | 09:55 | Shaded cacao agriculture | |
| 29 | Eshobi 3 | 30 April 2012 | 10:55 | Beside stream in open area within village 0 | |
| 30 | Tali 1 | 2 May 2012 | 09:35 | Mixed cultivated area in village, by small lake | |
| 31 | Tali 2 | 2 May 2012 | 09:50 | Secondary palm-rich forest with some cacao | 24.8 |
| 32 | Bakebe | 3 May 2012 | 09:25 | Secondary forest | 25.3 |
| 33 | Mfainchang | 4 May 2012 | 00:60 | Mixed small-holding agriculture | |
| 34 | Banyang- Mbo | 7 May 2012 | 12:55 | Primary forest | |
| Not | e: CL, clay loam | ; L, loam; LS, loamy | sand; SC | sandy clay; SCL, sandy clay loam; SiCL, silty clay loam; SL, sandy loam. | |

| - |
|--------------------------------|
| \circ |
| $\overline{\mathbf{O}}$ |
| |
| |
| ·= |
| |
| 9 |
| ~ |
| ~ |
| ~~ |
| ∞ |
| \circ |
| - |
| 4 |
| Č |
| <u> </u> |
| 10 |
| 41 |
| \circ |
| |
| Ħ |
| <i>co</i> |
| |
| ്ന് |
| 5 |
| $\circ n$ |
| - |
| · Ħ |
| 4 |
| 0 |
| |
| H |
| = |
| <u>_</u> |
| () |
| |
| \sim |
| Ľ |
| of (|
| of (|
| / of (|
| ty of (|
| ity of (|
| sity of (|
| rsity of (|
| ersity of (|
| versity of (|
| iversity of (|
| iiversity of (|
| niversity of (|
| Jniversity of 6 |
| University of (|
| [University of 6 |
| / [University of 6 |
| y [University of 6 |
| by [University of 6 |
| by [University of 6 |
| d by [University of 6 |
| ed by [University of 6 |
| led by [University of 6 |
| ded by [University of 6 |
| aded by [University of 6 |
| oaded by [University of 6 |
| loaded by [University of 6 |
| nloaded by [University of 6 |
| nloaded by [University of 0 |
| wnloaded by [University of 6 |
| ownloaded by [University of 0 |
| ownloaded by [University of 0 |
| Downloaded by [University of 0 |

9

Table 2. Locality coordinates and elevation, fieldwork effort and numbers of independent (i.e. not attended by mother) Geotrypetes seraphini, Herpele squalostoma and Idiocranium russeli encountered.

| (Continued) | | | | | | | | |
|--------------------|------------|----------|--------|-----------|--------------------------|------------|-----|-------------------|
| G. seraphini (1*) | 0 | | 50 | 109 | 5.844 N, 9.3969333 E | Mukonyong | 26 | 29 April 2012 |
| H. squalostoma (1) | - | | 75 | 125 | 5.9530667 N, 9.4214333 E | Nyang | 25 | 28 April 2012 |
| Ι | 7 | | 35 | 104 | 6.0587167 N, 9.4783333 E | Akwa | 24 | 26 April 2012 |
| G. seraphini (2) | 1 | 10 | 100 | 366 | 6.2368889 N, 9.5261111 E | Kakpenyi 4 | 23 | 21 April 2012 |
| I | 0 | 5 | 40 | 450 | 6.2460556 N, 9.5241944 E | Kakpenyi 3 | 22 | 21 April 2012 |
| G. seraphini (4) | 1 | 12 | 110 | 436 | 6.2454167 N, 9.5245 E | Kakpenyi 2 | 21 | 21 April 2012 |
| G. seraphini (2) | 0 | 8.5 | 70 | 435 | 6.2448056 N, 9.5254444 E | Kakpenyi 1 | 20 | 21 April 2012 |
| G. seraphini (1) | 0 | | 50 | 301 | 6.2130333 N, 9.4886 E | Atolo | 19 | 20 April 2012 |
| Ι | | ŝ | 30 | 820 | 62655556 N, 9.5155556 E | Tinta 7 | 18 | 20 April 2012 |
| G. seraphini (2*) | 0 | 7 | 15 | 791 | 6.2663889 N, 9.5145 E | Tinta 6 | 17 | 20 April 2012 |
| Ι | 1 | 1.5 | 15 | 745 | 6.2685 N, 9.5143889 E | Tinta 5 | 16 | 20 April 2012 |
| Ι | 1 | ż | ż | 647 | 6.2825556 N, 9.51325 E | Tinta 4 | 15† | 19 April 2012 |
| G. seraphini (11*) | 11* | 10 | 130 | 721 | 6.2678889 N, 9.5095278 E | Tinta 3 | 14 | 19 April 2012 |
| G. seraphini (3*) | 0 | 12 | 135 | 676 | 6.2725556 N, 9.5124167 E | Tinta 2 | 13 | 19 April 2012 |
| Ι | *8 | 9 | 100 | 685 | 6.27325 N, 9.5125833 E | Tinta 1 | 12 | 19 April 2012 |
| G. seraphini (2) | 5 | 6 | 80 | 529 | 6.322 N, 9.5163056 E | Makamune 7 | 11 | 17 April 2012 |
| G. seraphini (3) | 1 | 18 | 120 | 521 | 6.32125 N, 9.5149444 E | Makamune 6 | 10 | 17 April 2012 |
| G. seraphini (2*) | 4 | 40 | 220 | 516 | 6.3204444 N, 9.5150278 E | Makamune 5 | 6 | 17 April 2012 |
| Ι | 2 | 8 | 90 | 522 | 6.3208611 N, 9.5149722 E | Makamune 4 | 8 | 17 April 2012 |
| I | 0 | | 50 | 488 | 6.3323611 N, 9.5192778 E | Makamune 3 | ٢ | 16 April 2012 |
| G. seraphini (1) | 7 | 5 | 60 | 508 | 6.3323611 N, 9.5169167 E | Makamune 2 | 9 | 16 April 2012 |
| G. seraphini (1) | 6 | 16 | 135 | 518 | 6.32375 N, 9.5171111 E | Makamune 1 | S | 16 April 2012 |
| I | 0 | | 35 | 164 | 5.68023 N, 9.2532 E | Nchanga 4 | 4 | 22 September 2010 |
| I | 0 | | 25 | 165 | 5.69079 N, 9.25482 E | Nchanga 3 | ю | 22 September 2010 |
| H. squalostoma (1) | 0 | | 50 | 159 | 5.69561 N, 9.26511 E | Nchanga 2 | ы | 22 September 2010 |
| I | 0 | | 25 | 162 | 5.69397 N, 9.26702 E | Nchanga 1 | - | 22 September 2010 |
| Other caecilians | I. russeli | (m^2) | mins | (m) | Coordinates | Locality | | Date |
| | | Area dug | Person | Elevation | | | | |

238 D.J. Gower et al.

| Table 2. (Continued | .(1) | | | | | | |
|--------------------------------------------|--------------------|---------------------------------------|----------------------------------------------------|--------------|------------------------------|----------|--------------------|
| 30 April 2012 | 27 | Eshobi 1 | 5.7833167 N, 9.3832333 E | 68 | 30 | 0 | I |
| 30 April 2012 | 28 | Eshobi 2 | 5.7806667 N, 9.38495 E | 111 | 20 | 0 | I |
| 30 April 2012 | 29 | Eshobi 3 | 5.7858167 N, 9.3617 E | 127 | 25 | 0 | I |
| 2 May 2012 | 30 | Tali 1 | 5.5779833 N, 9.6626333 E | 162 | 15 | 0 | I |
| 2 May 2012 | 31 | Tali 2 | 5.5773667 N, 9.6619333 E | 181 | 40 | 0 | H. squalostoma (1) |
| 3 May 2012 | 32 | Bakebe | 5.5703333 N, 9.5610833 E | 164 | 50 | 0 | G. seraphini (4) |
| | | | | | | | H. squalostoma (1) |
| 4 May 2012 | 33 | Mfainchang | 5.6182333 N, 9.5037 E | 220 | 60 | 0 | I |
| 7 May 2012 | 34 | Banyang- | 5.2535167 N, 9.5843 E | 338 | 09 | 0 | I |
| | | Mbo | | | | | |
| Notes: *At least one †The specimen from | clutch locality | of eggs and/or you 15 was provided | ng also found. by local people and the duration | of digging o | r size of area dug here is n | ot known | |

| | umour |
|-------------|---------|
| | not k |
| | is 1 |
| | here |
| | dug |
| | irea |
| | of å |
| | size |
| | or |
| | ligging |
| | of e |
| | ation |
| | dur |
| | the |
| | and |
| | ople |
| | l pe |
| Octa | loca |
| ann a | by |
| 2 | ded |
| 5 | ovi |
| | pr |
| μ Ω Ω | was |
| 5 | 15 |
| ומות | cality |
| 2 | n Ic |
| | fro |
| 1745 | len |
| | specin |
| 22.0 | he |
| ~ | |



Figure 1. Map of the vicinity of Mamfe, south-western Cameroon, indicating towns (squares), villages (circles) and position of focal points of localities where soil-digging surveys were conducted. See Tables 1 and 2 for details. Blue lines = major rivers; solid black line = Cameroon–Nigeria border; dotted lines = protected area boundaries. Protected areas abbreviated as follows: BMWS = Banyang Mbo Wildlife Sanctuary; CRNP = Cross River National Park; EFR = Ejagham Forest Reserve; KNP = Korup National Park; MFR = Mone Forest Reserve; N-A FR = Nta-Ali Forest Reserve; TNP = Takamanda National Park.

and/or young (and a single specimen provided by local people from a non-quantitative survey at locality 15), a total of 49 independent *I. russeli* were found at a mean rate of 1.37 per person hour of digging (2.26 per person hour for those sites where this species was found), compared to 39 *Geotrypetes seraphini* (Duméril, 1859) (1.09 and 1.77 per person hour, respectively) and four *Herpele squalostoma* (Stutchbury, 1836) (0.11 and



Figure 2. Distribution and abundance of *Idiocranium russeli* along a regional 'transect' showing variation with elevation and latitude found during fieldwork in 2010 and 2012. Smallest circles indicate no specimens found; size of other circles is proportionate to abundance from 1 to 8 animals (to the nearest 1) per 100 minutes of digging. For locality details and raw abundance data see Tables 1 and 2. Locality 15 is not included because it was not part of a quantitative survey.

1.12 per person hour, respectively). *Idiocranium russeli* occurred in sympatry with two other caecilian species: *G. seraphini* at nine of 15 sites; *H. squalostoma* at one of 15; no single site yielding all three species. Only one locality yielded both *G. seraphini* and *H. squalostoma* (Table 2). We found early life-history stages of *I. russeli* (eggs or hatchlings) attended by adults at three localities and of *G. seraphini* (newborns attended by adults) at five localities, these occurring in sympatry at one locality (locality 14).

Of the 19 localities where we did not find *I. russeli*, most (14) were below 400 m elevation, and most (13) were in the more southern part of the survey 'transect', south of 6° N. Only one *I. russeli* was found in any of the 14 localities surveyed south of 6° N. In comparison, 12 of the 20 localities further north yielded *I. russeli* specimens (Figure 2). It is our impression that *I. russeli*, at this time, was most readily found in very wet places, in a range of soil types and degree of canopy cover. Above 300 m, we failed to find *I. russeli* at only six of 19 sites surveyed and of these one (locality 7) had dry soil, one (locality 20) had recently been cleared by slash and burn, and one (locality 17) was searched for only 0.25 person hours. Photographs of habitat in the survey area are shown in Figure 3.

Size

We were able to determine sex of all the independent (i.e. excluding those attended by mothers) *I. russeli* that we collected from examination of gonads. We found males



Figure 3. Photographs showing some habitats in the survey area, April 2012. (A) View approximately south from disturbed habitat on the outskirts of Kakpenyi to less disturbed forest in the nearby hills; (B) view approximately north along the Makamune valley from the northern edge of Tinta, the locality 'Tinta 4' is the recently burned patch at the centre of the picture; (C) digging fieldwork at 'Tinta 3'; (D) digging fieldwork at 'Makamune 4'.

and females of fresh TL 76–167 and 66–140 mm, respectively (TL post-fixation 71–145 and 62–122 mm, respectively) (Table 3; Figure 4).

Among Sanderson's collection, Parker (1936) reported 'juvenile' *I. russeli* as small as 51 mm 'from snout to vent'. From the same material, Wake (1986) reported a specimen of TL 50 mm (measured here as 52 mm). The TLs of preserved animals from Sanderson's collection recorded by us are, on average, 5.1% (range from – 2.7 to 13.7%, standard deviation \pm 3.6; correlation coefficient 0.98; linear regression y = 6.718 + 0.978x) greater than those reported by Wake (1986) with only three of 29 comparative measures shorter in this study (Table 4). The TLs of specimens from our new collection (Table 3) in preservation range from 0.7% to 14.1% (mean 7.9% \pm 3.1) shorter than when measured fresh (correlation coefficient 0.98; linear regression y = 7.075 + 0.858x).

Sex ratio and sexual dimorphism

Overall there is no indication of a biased sex ratio in the new sample of *I. russeli* (28 females, 23 males). Males have significantly (p < 0.0001) proportionately larger heads than females based on ANCOVA (TL as the covariate) for both head length

Table 3. Data for 51 *Idiocranium russeli* collected from the Mamfe region of Cameroon in 2010. All specimens are accessioned under BMNH 2008.688 and are here identified individually by field tags (all of which have an 'MW' prefix).

| Field tag | Sex | TLf | TLp | Mass | HL | HW |
|-----------|-----|-----|-----|------|-----|-----|
| 8350 | F | 106 | 103 | 0.91 | 4.6 | 2.9 |
| 8360 | F | 104 | 100 | 0.75 | 4.4 | 3.0 |
| 8468 | F | 134 | 119 | 1.84 | 5.2 | 3.6 |
| 8472 | F | 122 | 115 | 1.04 | 4.8 | 3.2 |
| 8480 | F | 125 | 110 | 1.17 | 5.1 | 3.2 |
| 8483 | F | 140 | 122 | 1.46 | 5.5 | 3.5 |
| 8486 | F | 85 | 79 | 0.57 | 4.2 | 2.7 |
| 8495 | F | 125 | 114 | 1.06 | 4.8 | 3.1 |
| 8509 | F | 100 | 88 | 0.75 | 4.3 | 3.0 |
| 8511 | F | 120 | 110 | 1.35 | 5.3 | 3.5 |
| 8618 | F | 120 | 110 | 1.40 | 5.1 | 3.6 |
| 8625 | F | 130 | 118 | 1.48 | 4.8 | 3.4 |
| 8627 | F | 122 | 113 | 1.21 | 4.9 | 3.3 |
| 8629 | F | 134 | 120 | 1.38 | 5.2 | 3.7 |
| 8631 | F | 66 | 62 | 0.32 | 3.6 | 2.3 |
| 8649 | F | 118 | 115 | 0.94 | 4.7 | 3.3 |
| 8650 | F | 126 | 122 | 1.33 | 5.3 | 3.6 |
| 8661 | F | 125 | 120 | 1.04 | 4.8 | 3.3 |
| 8662 | F | 117 | 113 | 1.25 | 4.9 | 3.4 |
| 8663 | F | 74 | 69 | 0.35 | 3.8 | 2.4 |
| 8683 | F | 108 | 100 | 1.06 | 4.6 | 3.1 |
| 8686 | F | 109 | 100 | 0.75 | 4.5 | 3.1 |
| 8688 | F | 120 | 110 | 1.06 | 5.0 | 3.1 |
| 8690 | F | 105 | 97 | 0.73 | 4.6 | 3.0 |
| 8692 | F | 114 | 104 | 0.83 | 4.8 | 3.0 |
| 8693 | F | 98 | 90 | 0.72 | 4.2 | 2.9 |
| 8380 | F | | 95 | | 4.7 | 3.0 |
| 8550 | F | | 118 | | 4.8 | 3.3 |
| 8359 | Μ | 96 | 93 | 0.59 | 4.4 | 2.8 |
| 8364 | Μ | 118 | 105 | 1.06 | 5.2 | 3.6 |
| 8370 | Μ | 139 | 138 | 2.48 | 6.5 | 4.0 |
| 8466 | Μ | 149 | 128 | 2.56 | 6.0 | 4.1 |
| 8469 | Μ | 161 | 145 | 2.97 | 6.9 | 4.6 |
| 8482 | Μ | 131 | 118 | 1.35 | 5.3 | 3.6 |
| 8477 | Μ | 76 | 71 | 0.40 | 3.9 | 2.7 |
| 8488 | Μ | 111 | 100 | 0.94 | 5.0 | 3.3 |
| 8489 | М | 85 | 80 | 0.47 | 4.3 | 2.7 |
| 8490 | Μ | 110 | 100 | 1.10 | 5.3 | 3.5 |
| 8491 | Μ | 117 | 108 | 0.93 | 5.2 | 3.3 |
| 8513 | Μ | 167 | 145 | 2.54 | 6.7 | 4.5 |
| 8607 | Μ | 143 | 134 | 3.40 | 6.9 | 4.8 |
| 8630 | Μ | 115 | 107 | 1.07 | 4.9 | 3.5 |
| 8633 | М | 102 | 92 | 0.76 | 4.4 | 3.0 |
| 8647 | М | 102 | 94 | 0.82 | 4.5 | 3.2 |
| 8648 | Μ | 112 | 106 | 0.98 | 4.9 | 3.4 |

(Continued)

| Table | 3. (| (Continued) | |
|-------|------|-------------|--|
| | | | |

| Field tag | Sex | TLf | TLp | Mass | HL | HW |
|-----------|-----|-----|-----|------|-----|-----|
| 8679 | М | 130 | 120 | 1.35 | 5.7 | 3.6 |
| 8684 | М | 112 | 102 | 1.02 | 5.3 | 3.5 |
| 8687 | Μ | 120 | 104 | 1.09 | 5.3 | 3.6 |
| 8691 | М | 102 | 92 | 0.78 | 5.0 | 3.4 |
| 8212 | М | | 72 | | 3.8 | 2.5 |
| 8382 | Μ | | 104 | | 4.8 | 3.1 |

Notes: TLf = fresh total length; TLp = preserved total length; HL = distance between tip of snout and first collar groove, measured laterally (head length); HW = maximum head width between corner of mouth and first collar groove. Dimensions in mm, mass in g. Blank cells indicate data not recorded.



Figure 4. Size of newly collected sample of *Idiocranium russeli*. (A) Preserved length frequency distribution; (B) fresh total length versus mass.

(Figure 5A) and head width (Figure 5B). The four (fresh TL) or five (preserved TL) largest animals were male, but 13 of the longest 21 (fresh TL) were female (Figure 4). Males and females are not significantly different in TL based on the t-test (p = 0.704) or u-test (p = 0.8571).

Colour

Parker (1936) reported *I. russeli* as 'blue-grey above, lighter beneath', though we assume he did not see live animals himself. The specimens we found were variable in colour in life, generally brown, some darker (towards blue-grey) and a few substantially paler (brownish pink) (Figure 6). All were paler ventrally than dorsally. Although not immediately obvious to the naked eye, the specimens have a middorsal stripe (clearly seen in photographs taken with flash, Figure 6) demarcated by dorso-lateral flanks that have a dense spotting of pale glands. The superficially aglandular dorsal stripe is not apparent on the posterior third where the annular grooves become dorsally complete. The annular grooves are not obvious to the naked eye anteriorly but are increasingly well marked posteriorly, appearing paler than the adjacent skin macroscopically (Figure 6), with each groove associated with a row of large whitish

Table 4. Data for 30 specimens of *Idiocranium russeli* collected by I.T. Sanderson from near Mamfe in 1933. This is the subset of Sanderson's specimens that were measured by both Wake (1986) and in this study (data from this study given in parentheses). Our observations of sex were the same as those reported by Wake (1986) unless otherwise indicated.

| Tag | Sex | TL | HL | HWja |
|------------------|-------|-----------|-----------|-----------|
| BMNH 1946.9.5.71 | F | 102 (104) | 5.3 (4.8) | 3.5 (3.3) |
| BMNH 1946.9.5.73 | F | 104 (108) | 5.2 (4.4) | 3.1 (3.3) |
| BMNH 1946.9.5.76 | М | 104 (106) | 5.2 (4.9) | 3.2 (3.3) |
| BMNH 1946.9.5.77 | F | 111 (115) | 5.2 (4.7) | 3.2 (3.2) |
| BMNH 1946.9.5.78 | F | 102 (105) | 5.0 (4.6) | 3.0 (3.0) |
| BMNH 1946.9.5.79 | F | 95 (101) | 5.1 (4.7) | 3.0 (2.9) |
| BMNH 1946.9.5.80 | F | 95 (108) | 5.0 (4.7) | 2.9 (3.1) |
| BMNH 1946.9.5.81 | M (F) | 77 (80) | 4.6 (4.2) | 2.5 (2.6) |
| BMNH 1946.9.5.82 | | 50 (52) | 3.9 (3.3) | 1.9 (2.0) |
| BMNH 1946.9.5.83 | М | 104 (110) | 5.2 (5.2) | 3.5 (3.7) |
| BMNH 1946.9.5.84 | F | 105 (113) | 5.3 (4.8) | 3.3 (3.1) |
| BMNH 1946.9.5.85 | (M) | 67 (71) | 3.8 (3.9) | 2.6 (2.5) |
| BMNH 1946.9.5.86 | F | 85 (95) | 4.9 (4.5) | 3.0 (3.0) |
| UCMZ 1 | F | 104 (108) | 4.8 (4.7) | 3.0 (3.2) |
| UCMZ 3 | (F?) | 61 (65) | 3.3 (3.5) | 2.1 (2.1) |
| UCMZ 5 | F (M) | 88 (95) | 4.3 (4.2) | 2.2 (2.8) |
| UCMZ 7 | F | 95 (100) | 4.7 (4.5) | 2.9 (3.0) |
| UCMZ 8 | F | 110 (107) | 6.6 (4.8) | 2.4 (3.0) |
| UCMZ 9 | Μ | 104 (110) | 5.0 (5.0) | 3.3 (3.3) |
| UCMZ 10 | M (F) | 107 (114) | 4.5 (4.7) | 2.8 (2.9) |
| UCMZ 11 | F | 110 (107) | 4.2 (4.3) | 2.7 (2.9) |
| UCMZ 12 | М | 103 (107) | 4.3 (4.6) | 3.4 (3.2) |
| UCMZ 13 | F | 96 (103) | 3.8 (4.3) | 2.9 (2.9) |
| UCMZ 14 | Μ | 98 (105) | 4.5 (4.9) | 3.0 (3.0) |
| UCMZ 16 | F | 109 (107) | 4.0 (4.6) | 3.1 (3.0) |
| UCMZ 17 | F | 98 (106) | 4.7 (4.7) | 2.9 (3.3) |
| UCMZ 20 | Μ | 74 (79) | 3.8 (4.1) | 2.5 (2.5) |
| UCMZ 21 | F | 112 (115) | 5.1 (4.7) | 3.3 (3.0) |
| UCMZ 26 | (M) | 73 (76) | 3.5 (3.8) | 2.2 (2.3) |
| UCMZ 27 | F | 89 (95) | 3.8 (4.3) | 2.8 (2.8) |

Notes: TL = total length; HL = head length; HWja = head width at level of jaw articulation.Wake (1986) did not state how she measured head length, but in this study it was measured as the distance between the tip of the snout and the first collar groove, measured laterally. Specimens are stored in the Natural History Museum, London (BMNH prefix) and the University of Cambridge Museum of Zoology (UCMZ). Dimensions in mm.

glands. Sanderson's specimens have a similar colour pattern to our newer material but are now generally paler, some being a pale tan.

Reproductive biology

Some adults of the type series of *I. russeli* were reported as being found coiled around clutches of eggs (Parker 1936; Sanderson 1937) but there are no eggs among the



Figure 5. Sexual size dimorphism in heads for newly collected sample of male (squares) and female (diamonds) *Idiocranium russeli*. (A) Fresh total length versus preserved head length; (B) fresh total length versus preserved head width.



Figure 6. Photograph showing appearance and colour variation of four *Idiocranium russeli* from Makamune, site 7 (locality 11, see Tables 1, 2) in life. Note the increasing demarcation of annular grooves posteriorly, colour variation among individuals, and presence of middorsal stripe. Total length of palest specimen shown here was 130 mm when freshly anaesthetized.

material of *I. russeli* in London, Cambridge or Harvard, and Wake (1986, p. 12) reported that these eggs 'are not deposited in any museum, according to my multiple inquiries'. To the best of our knowledge, the only eggs preserved from Sanderson's collection are in the Hubrecht collection, Museum für Naturkunde, Berlin, one of

which was illustrated by Richardson et al. (1998: fig. 1) as 'Idiocranium sp.' without further details.

As well as finding independent specimens of *I. russeli* of TL as short as 66 (fresh) or 62 (preserved) mm, we also found three adult females (fresh TL 96-104 mm) attending clutches of one, two and three eggs, and one adult female (fresh TL 125 mm) attending two eggs and three hatchlings (fixed TL 31–34 mm), one of the latter eggs hatched the same day into a hatchling of fixed TL 28 mm. Embryos in eggs were almost all well developed, with long feathery gills, little remaining yolk, clearly demarcated annular grooves, and erupted tentacles (similar to the specimen shown by Richardson et al. 1998, fig. 1f). The least well-developed embryos we found were approximately similar to Brauer's (1899; see Müller 2006) 'stage' 38, and the most developed embryos and hatchling that emerged upon collection were 'stage' 48 (H. Müller pers. comm). The encapsulated embryos bore no indications of larval features such as spiracles, tail fins, lateral line organs and labial folds (e.g. Wilkinson 1992; San Mauro et al. 2014), and these features are absent also in the smallest young (see also Parker 1936), such that *I. russeli* is further confirmed as having direct development. Although small young were found with attending adults by Sanderson and us, these young lack vernal (sensu San Mauro et al. 2014) teeth (Parker and Dunn 1964), they are not much smaller than the smallest independent specimens known, and there is no evidence that extended parental care in this species includes maternal dermatophagy (sensu Kupfer et al. 2006).

Discussion

Distribution and conservation status

The type locality of *I. russeli* is remote in terms of communications and transport (during our visit the 'road' between Mamfe and Ote was unpaved and the trail between Ote and Makamune was not accessible by car and was travelled instead on foot), but it was reasonably clearly documented by Sanderson (1935a, 1935b, 1936, 1937) and we were able to find it and *I. russeli* readily on our first visit to the area. Indeed, we found our first specimen within 15 minutes of commencing digging at our first site. Wake (1986, p. 1) mentioned 'the absence of opportunities to recollect' *I. russeli* since Sanderson's work, but we assume that previous failure to recollect this species is attributable to the absence of dedicated efforts to do so rather than a lack of opportunity *per se*.

Parker (1936) reported the type locality of *I. russeli* as 'Makumunu' without further details. Sanderson's (1935a, 1935b, 1936, 1937) reports do not include caecilian locality data, other than stating that his *I. russeli* specimens came from an area of transition between forest and grassland near one of Sanderson's camps in the Assumbo hills (Sanderson 1937). In his report of fieldwork in Asumbo, Sanderson (1935b) did not mention Makumunu; the only village he mentioned in the Asumbo hills is instead Tinta. Tinta and Makamune lie only approximately 7 km apart, at similar elevations (approximately 700 and 600 m, respectively) in the same valley (of the Makamune river). According to the Hubrecht collection catalogue and to Sanderson's specimen collection list archived in the Herpetology Section of the Natural History Museum, London, Sanderson's material was from Tinta. Thus, in all probability, the type locality of *I. russeli* is Tinta and not Makumune.

Our surveys suggest that *I. russeli* is somewhat patchily distributed but locally abundant within its known range (as is *G. seraphini* in the same region). Our sampling was not randomized or stratified sufficiently to determine habitat tolerances with confidence, but along the Mamfe–Akwaya 'transect' it seems that *I. russeli* might be restricted to the northern end, in the Asumbo Hills, and is more likely to be found (at least at the time of year that we sampled) in cooler, moister, generally shaded soils. Lawson (1993) reported *G. seraphini* and *H. squalostoma* in Korup National Park (1260 km²) but did not find *I. russeli* there, though he suggested that it might be expected in at least the northern sections of the park that approach Mamfe. However, Korup is further south than the southernmost localities that we surveyed (Figure 1) and at which we failed to find *I. russeli*.

Despite some recent effort (e.g., Kouete et al. 2012, 2013), as far as we are aware, dedicated digging surveys for caecilians in Cameroon have been very sparse and patchy. We expect *I. russeli* to occur more widely than we report here, at least within south-western Cameroon and probably into adjacent parts of Nigeria (including Cross River National Park). The furthest north (Makamune) and south (Nyang) localities for *I. russeli* are approximately 43 km apart. The species is locally common and clearly tolerates at least low to moderate habitat disturbance. We expect it to occur also in the protected areas of Takamanda National Park ($c.670 \text{ km}^2$) and Mone River Forest Reserve ($c.540 \text{ km}^2$) close to the west and south-east, respectively, of the new localities we report, and its distribution covers multiple (threat-defined) 'locations' sensu IUCN (IUCN Standards and Petitions Subcommittee 2011). Although we do not know its tolerance to more intensive agriculture, such as the currently expanding plantations of cacao in the region, we see no immediate cause for concern for the survival of the species. A more formal analysis, particularly if the presence of I. russeli can be confirmed in protected areas, will likely see the species transferred from Data Deficient to Least Concern. The leading potential threat outside of protected areas is likely habitat change caused by slash and burn clearing for agriculture, and possibly the application of agrochemicals, though further work is required to assess this.

Phenology and reproduction

Sanderson's Cameroon expedition took place August 1932 to August 1933 (Sanderson 1935a). We cannot find precise dates for his *I. russeli* collection in any publication, but Sanderson's collection list archived in the Herpetology Section of the Natural History Museum, London states that the eggs were found at Tinta on 27 April 1933. This is consistent with Sanderson's (1936, p. 199, 205) report of collecting frogs in Tinta and Makamune only in April and May. Sanderson (1936) reports a long wet season in the Mamfe region, from the end of March to the end of October (peak June–September). Digging surveys have yet to take place in the region outside of April, but the two collections made thus far are consistent with eggs being laid at the beginning of the rainy season. Sanderson discovered adults attending eggs of *I. russeli* and young of *G. seraphini*, respectively (Parker 1936) and we found the same (as well as adults attending hatchlings of *I. russeli*), with broods of the two species occurring sympatrically at one locality. Sanderson's collection list states that the young *G. seraphini* were found also at Tinta on 27 April 1933. As far as we are

aware, these are the only reports of sympatric, approximately synchronous breeding in multiple caecilian species, though it is likely to occur with other species elsewhere.

Sanderson (1937) reported *I. russeli* egg clutches on small underground mounds of soil being guarded by adults that spat liquid when disturbed, a behaviour unreported in any other caecilian, whether or not guarding eggs. In our experience, the exact configuration of nest chambers is difficult to observe during typical digging surveys for caecilians, but we observed nothing to indicate that *I. russeli* differs from many other oviparous caecilians in its basic nest construction – a small hollow in the topsoil (the distinctiveness of the walls of the chamber varying, perhaps with soil composition and moistness). No *I. russeli* spat at us when collected, and none of us has seen such behaviour in capturing or handling more than 1000 caecilians of different species of all 10 currently recognized families, although some specimens have discharged liquid from their vent, a defensive behaviour well known in some other amphibians. We do not consider the behaviour reported by Sanderson (1937) to be typical for *I. russeli*, and we suggest that Sanderson possibly mistook forceful discharge from the vent for spitting. Wake (1986, p. 12) considered spitting by *I. russeli* to be a 'functional near-impossibility'.

The largest clutch we found was of five (two eggs, three hatchlings). Wake's (1977, p. 81) attribution of Sanderson (1937) reporting a clutch size of six is presumably based on his (p. 221) narration '... it revealed half a dozen crystal-clear and perfectly spherical eggs ...'. Clutch size in Sanderson's collection is not apparent from the Hubrecht collection catalogue or in Sanderson's collection list archived in the Herpetology Section of the Natural History Museum, London.

Sexual dimorphism

Despite being one of the smallest caecilian species known, *I. russeli* is sexually dimorphic in head size, with males having relatively larger heads. This is the most widespread form of external sexual dimorphism known to occur (and to have been tested for) in caecilians (e.g. Nussbaum and Pfrender 1998), and has been reported also in two other indotyphilds (Nussbaum and Pfrender 1998; Presswell 2002): *Hypogeophis rostratus* (Cuvier, 1829) and *Gegeneophis ramaswamii* Taylor, 1964 respectively. In agreement with expectations from fecundity selection, female caecilians attain larger body sizes than males in all dimorphic caecilian species studied thus far (Kupfer 2007, 2009). In our sample, the largest *I. russeli* were males, but this is not statistically significant, such that larger samples will be required to test further whether *I. russeli* is exceptional among caecilians in this respect.

Size

Even when alive or freshly anaesthetized, individual caecilians do not have a fixed length, and differences in measured TL arise through the method used (including the degree of stretching), state of preservation, as well as stochasticity (unpublished data). Wilkinson et al. (2013: Table 1) reported that total length in seven specimens of the siphonopid *Microcaecilia dermatophaga* Wilkinson et al., 2013 was 9.4–14.8% (mean 12.1) shorter in fixed than live specimens, but beyond this we are unaware of published comparative data. We assume the difference noted between our and Wake's measures of TL of Sanderson's sample of *I. russeli* is explained mostly by differences in the degree of stretching that is applied to specimens being measured and

not to shrinkage occurring since the 1980s. We suspect that, in general, we stretch specimens during measurement of TL more than some other workers. The data presented here indicate that caution is required before conducting quantitative analyses that combine data generated by multiple observers and/or fresh and preserved material, especially for smaller specimens. We doubt that the relatively larger differences in head length and width in some of Sanderson's specimens as reported here and by Wake (1986) are due to differences in how these measurements are taken, and we cannot wholly explain the differences in sex determination in some of these specimens. It might be that some specimen tags and specimens have been accidentally mixed since the previous studies.

Is *Idiocranium russeli* the smallest known caecilian? If size is taken to equate to total length, then the question could refer to minimum TL at sexual maturity or maximum TL, and the answer might depend on whether fresh or preserved TL is measured and/or how TL is measured. For maximum preserved TL, reported values are 145 mm for I. russeli (this study) and 112 for the main known contender Hypogeophis brevis (Taylor 1968) a species known from a much smaller sample. Few comparative data have been published but we suspect that, based on body shape, at the same total length H. brevis are heavier than I. russeli (Taylor 1968 reports length divided by width as 21–28 and 14.6 for the two species, respectively). Caecilian parental care and especially copulation are rarely observed, and determining sexual maturity in caecilians otherwise, from gross examination of gonads, is not trivial unless volky ova (or foetuses, in viviparous species) are found in oviducts. Parker (1936) reported spermatozoa in the testis of a male I. russeli of TL 107 mm and females as small as 90 mm 'associated with developing eggs', and we have been able to determine the sex of specimens of *I. russeli* as small as 62 mm preserved TL. Comparative data are limited but, among other indotyphilds, Measey et al. (2003) were unable to determine the sex of Gegeneophis ramaswamii under TL of 100 mm (maximum reported TL for this species 375 mm: Presswell 2002), and Largen et al. larvae of Sylvacaecilia grandisonae (Taylor, 1970) (maximum (1972) reported reported TL of species 260 mm) as large as 117 mm.

The hatchlings of *I. russeli* that we found (*c*.30 mm) are substantially smaller than late-stage embryos of the indotyphilds *Gegeneophis ramaswamii* (up to at least 61 mm: Müller et al. 2005) and *Hypogeophis rostratus* (up to at least 56 mm: Müller 2006). Hatchlings of 'about 28 mm' (Kupfer et al. 2006) and as small as 30 mm (Kupfer et al. 2008) have been reported for the skin-feeding herpelid *Boulengerula taitanus* Loveridge, 1935. We are unaware of hatchling or newborn caecilians substantially shorter than 30 mm.

Wake and Donnelly (2010) considered the siphonopid *Microcaecilia iwokramae* (Wake and Donnelly, 2010) to be the smallest New World caecilian but this was based on the single known specimen, a mature female of 112 mm TL, and two of us (DJG, MW, pers. obs.) have measured fresh individuals of this species up to 198 mm TL. Clearly, *I. russeli* is among the very smallest of known caecilians in terms of either its maximum size or size at reproductive maturity (and probably also at hatching).

Acknowledgements

This work was funded primarily by the US Fish & Wildlife's Wildlife Without Borders – Amphibians in Decline scheme, Zoological Society of London's EDGE Fellowship scheme, Conservation International's Lost Amphibians scheme, and The Royal Geographical Society, all of which we gratefully acknowledge. Additional funding that contributed to the work presented here was granted by the Zoological Society of London (Erasmus Darwin Barlow Grant), the Royal Zoological Society of Scotland, the Natural History Museum, London and the Institute of Zoology, London.

We are greatly indebted to many Cameroonian people of Mamfe Division who helped us with logistics and generously provided field assistance and hospitality. We thank the people of the villages of Ote, Kakpenyi, Tinta, Makamune, Atolo, Bashou, Nyang, Akwa, Bakebe, Tali and Nta-Ali. We particularly acknowledge the assistance of Apa Eric Ongbanya and Anya Aaron Sassa (Makamune), Tata Eric Tunda (headteacher, Tinta), Augustin and Gabriel (Kakpenyi), Wilfred and Rafael (Tinta), Joseph (Atolo), John (Bashou), Essa Leonel (Akwa), Ashu Thomas Takwa (Nyang), Emmanuel Abunga (Mukonyong), Ojong Phillipe Tabot (Eshobi), Regent (Tali), Peter (Bakebe), Joseph (Mfainchang), Njouki George and Asho Smith (Nta-Ali).

We also thank Gespo for looking after us in the field, Helen Meredith, Jeff Dawson and Cath Lawson for work on MTK's EDGE fellowship, Simon Loader for his fieldwork with us in Cameroon in 2008, and Ngane Benjamin Kome and Nono Gonwouo for support throughout. Peter Giere provided information on Sanderson's material in the Hubrecht Collection, Berlin, and Hendrik Müller staged the embryos and measured some hatchlings.

References

- Boulenger GA. 1911. List of the batrachians and reptiles obtained by Prof. Stanley Gardiner on his second expedition to the Seychelles and Aldabra. Trans Linn Soc Lond, 2nd Ser Zool. 14:375–378. doi:10.1111/j.1096-3642.1911.tb00534.x
- Brauer A. 1899. Beiträge zur Kenntnis der Entwicklungsgeschichte unde der Anatomie der Gymnophionen. Zool Jb Anat. 12:477–508.
- Clarke BT. 1996. Small size in amphibians its ecological and evolutionary implications. Zool Soc Lond Symp. 69:201–224.
- Cuvier GLCFD. 1829. Le Règne Animal Distribué d'Après son Organisation, pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée. Nouvelle Edition, Revue et Augmentée par P.A. Latreille. Volume 2. Paris: Deterville.
- Doherty-Bone TM, Ndifon RK, San Mauro D, Wilkinson M, LeGrand GN, Gower DJ. 2011. Systematics and ecology of the caecilian *Crotaphatrema lamottei* (Nussbaum) (Amphibia: Gymnophiona: Scolecomorphidae). J Nat Hist. 45:827–841. doi:10.1080/ 00222933.2010.535921

Dubbin W. 2001. Soils. London: The Natural History Museum; 110 p.

- Duellman WE, Trueb L. 1994. Biology of amphibians. 2nd ed. Baltimore (MD): The Johns Hopkins University Press; 670 p.
- Duméril AHA. 1859. Reptiles et poisons de l'Afrique Occidentale. Étude précédée de considerations generales sur leur distribution géographique. Arch Mus Natl Hist Nat Paris. 10:138–268.
- Encyclopaedia Britannica [Internet]. 2014. [cited 2014 May 26]. Available from: http://www.britannica.com
- Hofrichter R. 2000. Amphibian systematics. In: Hofrichter R, editor. The encyclopedia of amphibians. Toronto: Key Porter Books Ltd; 263 p; p. 36–63.
- IUCN. 2013. IUCN Red List of threatened species [Internet]. Version 2013.2; [cited 2014 Feb 5]. Available from: http://www.iucnredlist.org
- IUCN Standards and Petitions Subcommittee. 2011. Guidelines of using the IUCN Red List categories and criteria [Internet]. Version 9.0; [cited 2013 Aug 19]. Available from: http://www.iucnredlist.org/documents/RedListGuidelines.pdf

- Kotharambath R, Wilkinson M, Oommen OV, George S, Nussbaum RA, Gower DJ. 2012. On the systematics, distribution and conservation status of *Ichthyophis longicephalus* Pillai, 1986 (Amphibia: Gymnophiona: Ichthyophiidae). J Nat Hist. 46:2935–2959. doi:10.1080/00222933.2012.717972
- Kouete MT, Ndeme ES, Gower DJ. 2013. Further observations of reproduction and confirmation of oviparity in *Herpele squalostoma* (Stutchbury, 1836) (Amphibia: Gymnophiona: Herpelidae). Herpetol Notes. 6:583–586.
- Kouete MT, Wilkinson M, Gower DJ. 2012. First reproductive observations for *Herpele* Peters, 1880 (Amphibia: Gymnophiona: Herpelidae): evidence of extended parental care and maternal dermatophagy in *H. squalostoma* (Stutchbury, 1836). ISRN Zool. 269690. doi:10.5402/2012/269690
- Kupfer A. 2007. Sexual size dimorphism in amphibians: an overview. In: Fairbairn DJ, Blanckenhorn WU, Székely T, editors. Sex, size and gender roles. Oxford: Oxford University Press; p. 50–59.
- Kupfer A. 2009. Sexual size dimorphism in caecilian amphibians: analysis, review and directions for future research. Zoology. 112:362–369. doi:10.1016/j.zool.2008.12.001
- Kupfer A, Müller H, Antoniazzi MM, Jared C, Greven H, Nussbaum RA, Wilkinson M. 2006. Parental investment by skin feeding in a caecilian amphibian. Nature. 440:926–929. doi:10.1038/nature04403
- Kupfer A, Wilkinson M, Gower DJ, Müller H, Jehle R. 2008. Care and parentage in a skinfeeding caecilian amphibian. J Exp Zool. 309A:460–467. doi:10.1002/jez.475
- Largen MJ, Morris PA, Yalden DW. 1972. Observations on the caecilian Geotrypetes grandisonae Taylor (Amphibia Gymnophiona) from Ethiopia. Monit Zool Ital (N. Ser). 4:185– 205.
- Lawson DP. 1993. The reptiles and amphibians of the Korup National Park Project, Cameroon. Herpetol Nat Hist. 1:27–90.
- LeBreton M. 1999. A working checklist of the herpetofauna of Cameroon. Amsterdam: IUCN.
- Loader S, Wilkinson M. 2004. *Idiocranium russeli*. In: IUCN 2013. IUCN Red List of threatened species [Internet]. Version 2013.2. [cited 2014 Jan 9]. Available from: http:// www.iucnredlist.org
- Loveridge A. 1935. Scientific results of an expedition to rain forest regions in eastern Africa. I. New reptiles and amphibians from East Africa. Bull Mus Comp Zool. 79:3–19.
- Maddin HC, Russell AP, Anderson JS. 2012. Phylogenetic implications of the morphology of the braincase of caecilian amphibians (Gymnophiona). Zool J Linn Soc. 166:160–201.
- Measey GJ, Gower DJ, Oommen OV, Wilkinson M. 2003. Quantitative surveying of endogeic limbless vertebrates – a case study of *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae) in southern India. Appl Soil Ecol. 23:43–53. doi:10.1016/S0929-1393(02) 00175-0
- Müller H. 2006. Ontogeny of the skull, lower jaw, and hyobranchial skeleton of *Hypogeophis* rostratus (Amphibia: Gymnophiona: Caeciliidae) revisited. J Morphol. 267:968–986. doi:10.1002/jmor.10454
- Müller H, Oommen OV, Bartsch P. 2005. Skeletal development of the direct-developing caecilian Gegeneophis ramaswamii (Amphibia: Gymnophiona: Caeciliidae). Zoomorphology. 124:171–188. doi:10.1007/s00435-005-0005-6
- Nussbaum RA. 1998. Caecilians. In: Cogger HG, Zweifel RG, editors. Encyclopedia of reptiles and amphibians. 2nd ed. San Diego (CA): Academic Press; 238 p; p. 52–59.
- Nussbaum RA, Pfrender ME. 1998. Revision of the African caecilian genus Schistometopum Parker (Amphibia: Gymnophiona: Caeciliidae). Misc Publ Mus Zool, Univ Mich. 187:1–32.
- Parker HW. 1936. The amphibians of the Mamfe Division, Cameroons.-I. Zoogeography and systematics. Proc Zool Soc Lond. 106:135–163. doi:10.1111/j.1096-3642.1936.tb02284.x
- Parker HW, Dunn ER. 1964. Dentitional metamorphosis in the Amphibia. Copeia. 1964:75– 86. doi:10.2307/1440834

Perret J-L. 1966. Les amphibians du Cameroun. Zool Jb Syst Bd. 8:289-464.

- Perret J-L, Mertens R. 1957. Revision du materiel herpetologique du Cameroun, etudie par A. Monard Rev Suisse Zool. 64:73–78.
- Peters WCH. 1879. Über die Eintheilung der Caecilien und insbesondere über die Gattungen *Rhinatrema* and *Gymnopis*. Monats. König. Preuss. Akad. Wissen. Berlin. 1879:924–945.
- Presswell B. 2002. Morphological and molecular systematic studies of Asian caecilians (Amphibia: Gymnophiona) [Unpublished PhD thesis]. Glasgow: University of Glasgow.
- Richardson MK, Allen SP, Wright GM, Raynaud A, Hanken J. 1998. Somite number and vertebrate evolution. Development. 125:151–160.
- San Mauro D, Gower DJ, Müller H, Loader SP, Zardoya R, Nussbaum RA, Wilkinson M. 2014. Life-history evolution and mitogenomic phylogeny of caecilian amphibians. Mol Phyl Evol. 73:177–189. doi:10.1016/j.ympev.2014.01.009
- Sanderson IT. 1935a. The Percy Sladen zoological expedition to the British Cameroons, 1932– 33. Proc Linn Soc Lond. 147:25–29.
- Sanderson IT. 1935b. An expedition to the British Cameroons. Geog J. 85:113-141. doi:10.2307/1785988
- Sanderson IT. 1936. The amphibians of the Mamfe Division, Cameroons.-II. Ecology of the frogs. Proc Zool Soc Lond. 106:165–208. doi:10.1111/j.1096-3642.1936.tb02285.x
- Sanderson IT. 1937. Animal treasure. New York (NY): The Viking Press; 325 p.
- Stutchbury S. 1836. Description of a new species of the genus Chameleon. Trans Linn Soc Lond. 17:361–362. doi:10.1111/j.1095-8339.1834.tb00027.x
- Taylor EH. 1964. A new species of caecilian from India (Amphibia: Gymnophiona). Senckenb Biol. 45:227–231.
- Taylor EH. 1968. The caecilians of the World. Lawrence: University of Kansas Press.
- Taylor EH. 1970. A new caecilian from Ethiopia. Univ Kansas Sci Bull. 48:849-854.
- Vitt LJ, Caldwell JP. 2013. Herpetology. An introductory biology of amphibians and reptiles. Burlington (MA): Academic Press.
- Wake MH. 1977. The reproductive biology of caecilians: an evolutionary perspective. In: Taylor DH, Guttman SI, editors. Reproductive biology of amphibians. New York (NY): Plenum Press; p. 73–101.
- Wake MH. 1986. The morphology of *Idiocranium russeli* (Amphibia: Gymnophiona), with comments on miniaturization through heterochrony. J Morphol. 189:1–16. doi:10.1002/ jmor.1051890102
- Wake MH. 1987. A new genus of African caecilian (Amphibia: Gymnophiona). J Herpetol. 21:6–15. doi:10.2307/1564371
- Wake MH, Donnelly MA. 2010. A new lungless caecilian (Amphibia: Gymnophiona) from Guyana. Proc Roy Soc B. 277:915–922.
- Wilkinson M. 1992. On the life history of the caecilian genus Uraeotyphlus (Amphibia: Gymnophiona). Herpetol J. 2:121–124.
- Wilkinson M. 1997. Characters, congruence and quality: a study of neuroanatomical and traditional data in caecilian phylogeny. Biol Rev. 72:423–470. doi:10.1017/ S0006323197005069
- Wilkinson M, San Mauro D, Sherratt E, Gower DJ. 2011. A nine-family classification of caecilians (Amphibia: Gymnophiona). Zootaxa. 2874:41–64.
- Wilkinson M, Sherratt E, Starace F, Gower DJ. 2013. A new species of skin-feeding caecilian and the first report of reproductive mode in *Microcaecilia* (Amphibia: Gymnophiona: Siphonopidae). PLoS ONE. 8:e57756. doi:10.1371/journal.pone.0057756