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Source: Copeia, 107(1) : 22-35

Published By: The American Society of Ichthyologists and Herpetologists

URL: https://doi.org/10.1643/CH-18-098

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Copeia 107, No. 1, 2019, 22–35

A Cryptic New Species of *Polemon* (Squamata: Lamprophiidae, Aparallactinae) from the Miombo Woodlands of Central and East Africa

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African snake-eaters of the genus *Polemon* are cryptic, fossorial snakes that mainly inhabit the forests of central, eastern, and western Africa. Molecular results from a previous study demonstrated that *Polemon christyi* is not monophyletic—two distinct lineages were recovered from Uganda (the type locality) and southeastern Democratic Republic of the Congo (DRC). Genetic data indicated differences in sequence divergence and encoded amino acids between these lineages. Based on these molecular differences and diagnostic differences in morphology, we describe the lineage from southeastern DRC as a new species. Literature records indicate that it likely occurs in adjacent Tanzania and Zambia. It is the first species of *Polemon* to be described in over 70 years.

THE 13 species of currently recognized snakes of the genus *Polemon* are cryptic, fossorial inhabitants of forests and woodland/savanna mosaic habitats throughout central, eastern, and western Africa (Chippaux, 2006; Uetz et al., 2018). Snakes, particularly typhlopids, form their main diet, hence the common name 'Snake Eaters.' Most species of the genus rarely exceed 80 cm total length, but they can be voracious predators that consume snakes of equal size (Pitman, 1974; Kusamba et al., 2013; Spawls et al., 2018). Like many other lamprophiids, these fossorial and secretive snakes are poorly known, both in terms of natural history and taxonomy (i.e., low numbers of specimens available in museums), but most species have grooved rear fangs and are ophiophagous, nocturnal, and oviparous (Spawls et al., 2018). Many species also have prominent yellow or orange neck bands (Underwood and Kochva, 1993; Spawls and Branch, 1995; Spawls et al., 2018).

Based on hemipenial, dentition, and osteological characters, Bogert (1940) gave the first definitive arrangement of aparallactines, which included the genera *Amblyodipsas*, *Aparallactus*, *Brachyophis*, *Chilorhinophis*, *Elapotinus*, *Hypoptophis*, *Macrelaps*, *Micrelaps*, *Poecilopholis*, *Polemon*, and *Xenocalamus*. De Witte and Laurent (1943, 1947) revised aparallactines into three groups, with *Elapocalamus* (Boulenger, 1911), *Chilorhinophis* (Werner, 1907), *Polemon* (Jan, 1858), *Miodon* (Duméril, 1859), *Cynodontophis* (Werner, 1902), and *Melanocalamus* (de Witte, 1941) comprising their "Deuxième Groupe," which was characterized by the presence of a maxillary-ectopterygoid foramen. Currently, only two genera from the "Deuxième Group" are recognized, with all genera except *Chilorhinophis* placed in the synonymy of *Polemon* (Laurent, 1956a; Hughes and Barry, 1969; Resetar and Marx, 1981). In a recent, major phylogenetic analysis of aparallactines, these two fossorial genera were recovered as sister taxa with strong support (Portillo et al., 2018: fig. 2).

Relationships within the genus *Polemon* have historically been poorly understood and reliant solely on morphological data. Only recently have relationships within the genus been studied with molecular data (Fig. 1; e.g., Pyron et al., 2013; Figueroa et al., 2016; Portillo et al., 2018). Because many of the species share morphological characters that often overlap, taxonomic classification of species of *Polemon* has been challenging. Many of the 13 currently recognized species were historically considered to be geographic variants or synonyms of fewer species (Loveridge, 1942, 1944; de Witte and Laurent, 1947; Pitman, 1974; Spawls et al., 2018). For example, the poorly known species *P. christyi* was considered to be a race of either *P. collaris* or *P. gabonensis* at different times (Loveridge, 1942, 1944, 1957; Pitman, 1974). This is unsurprising, because the three taxa overlap considerably in morphological characters, including ventral and subcaudal scale counts (de Witte and Laurent, 1947; Pitman, 1974). However, de Witte and Laurent (1947) and Laurent (1956a) considered *P. christyi* to be a distinct species based on dorsal coloration, because it has a grayish black dorsum and lacks a neck band, whereas *P. collaris* and *P. gabonensis* both have a yellowish band on the neck. *Polemon christyi* is also partially sympatric with another superficially similar member of the genus, *P. graueri*, which can be grayish black dorsally, but with a more slender build and a larger number of ventral scales (de Witte and Laurent, 1947; Pitman, 1974). Currently, *P. christyi* is considered to occur throughout much of the Albertine Rift region (Spawls et al., 2018), including eastern Democratic Republic of Congo (DRC; absent from the western lowlands, *sensu* Broadley, 1998), South Sudan (Wallach et al., 2014), and western Kenya (Lötters et al., 2007), to northern Zambia (Broadley et al., 2003) and Tanzania (Loveridge, 1944; Caro et al., 2011; Spawls et al., 2018), with a single record from northern Malawi (Mercurio, 2007). Recent molecular results demonstrated that *P. christyi*

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Submitted: 25 July 2018. Accepted: 2 November 2018. Associate Editor: B. Stuart.
© 2019 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-18-098 Published online: 24 January 2019

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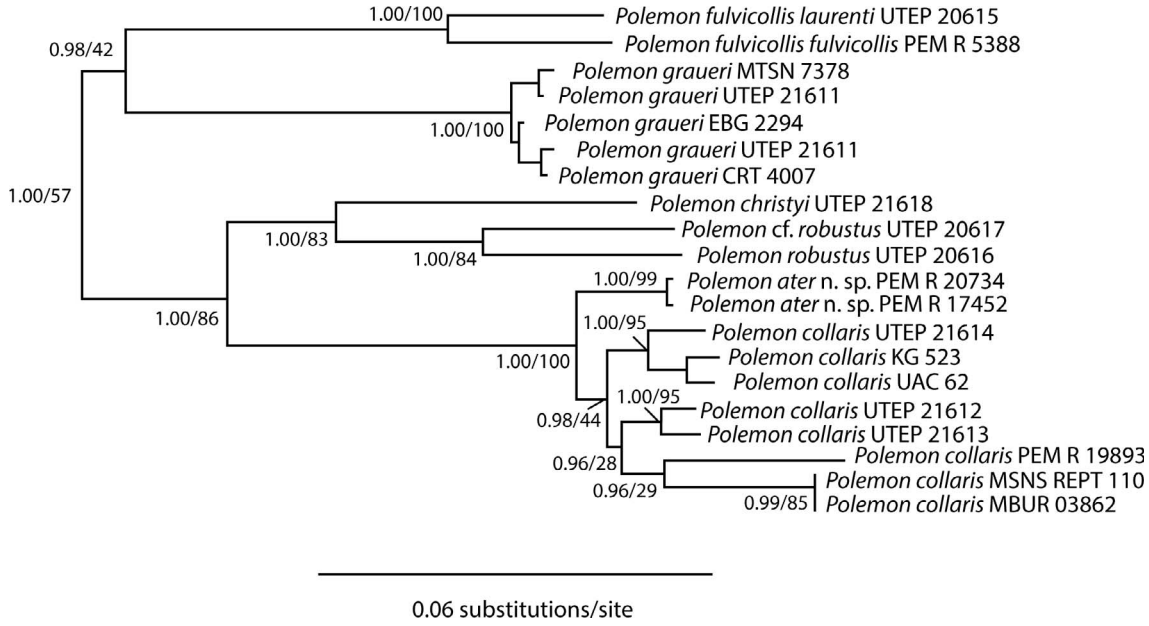


Fig. 1. Phylogenetic tree depicting relationships of African *Polemon*, based on Portillo et al. (2018). Branch support values are Bayesian inference posterior probabilities/maximum likelihood bootstrap support values. See Data Accessibility for tree file.

is not monophyletic—topotypic *P. christyi* is found in eastern Africa and is sister to central African *P. robustus*, whereas a second lineage occurs in southeastern DRC and is sister to the widespread species *P. collaris* (Figs. 1, 2; Portillo et al., 2018). Herein, we examine the taxonomic status of these lineages of *P. christyi* in more detail with morphological data and additional molecular analyses.

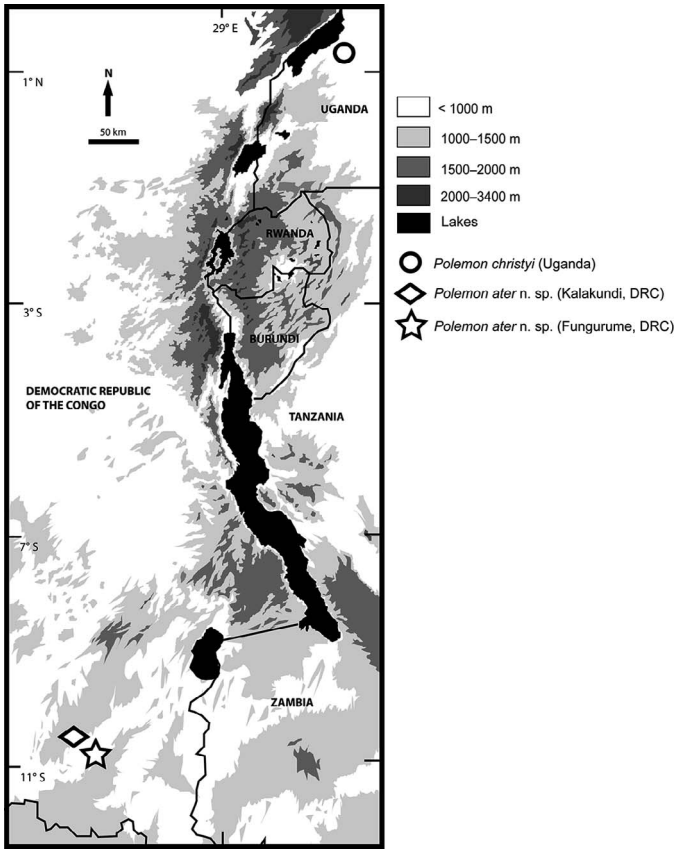


Fig. 2. Map of Central Africa showing sampling localities for *Polemon christyi* and *P. ater*. Star represents the type locality for the new species.

MATERIALS AND METHODS

Molecular analyses.—To understand molecular variation within the genus *Polemon*, we used data from three mitochondrial (16S, cyt *b*, and ND4) and two nuclear genes (c-mos and RAG1) that were sequenced and analyzed in a phylogenetic context in the study of Portillo et al. (2018). Levels of sequence divergence between haplotypes were inferred using uncorrected p-distances calculated from MEGA version 7.0 (Kumar et al., 2016). We also analyzed differences in amino acid translation of the protein-coding genes ND4 and cyt *b* for samples of *Polemon christyi* (UTEP 21618) and *P.* cf. *christyi* (PEM R20734 and PEM R17452). No nuclear data were available for *P. christyi*.

Morphological analyses.—Specimens examined for this study (Material Examined) were collected from multiple localities throughout sub-Saharan Africa, and are housed in the collections of the Port Elizabeth Museum, the University of Texas at El Paso Biodiversity Collections, and the Royal Belgian Institute of Natural Sciences. Additional aparallactine specimens, including relevant type specimens, were cited or examined from a diversity of collections and institutions as listed in the Material Examined.

Specimens were examined under a Zeiss Stemi 2000-C stereo microscope, and photographs were taken with a Canon Rebel T3i DSLR camera and Canon 6D full frame DSLR camera. Characters were chosen from previous taxonomic studies of advanced snakes (LaDuc and Johnson, 2003; Devitt et al., 2008; Moyer and Jackson, 2011; Anderson and Greenbaum, 2012; Greenbaum et al., 2015). Snout–vent length (SVL) was measured with a metric ruler and rounded to the nearest 1.0 mm. All other measurements were taken from the right side of the body with digital calipers under a dissecting microscope and rounded to the nearest 0.1 mm.

Morphological data consisted of 18 mensural and 14 meristic characters. Mensural data included: snout–vent length (SVL); tail length (TL); head width (HW)—measured at widest point of head; head length (HL)—measured at angle of jaw, from posterior edge of mandible to tip of snout; naso-

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ocular distance (NOD; taken at the anterior border of the eye to posterior border of nare); eye to snout length (ES; taken at the anterior border of the eye); interocular distance (ID); eye diameter (EW; anterior–posterior); internasal scale width (INAS); rostral scale height (RH); rostral scale width (RW); frontal scale length (FL); frontal scale width (FW); chin shield length (CSL); chin shield width (CSW); prefrontal scale length (PFL); prefrontal scale width (PFW); and mouth gape (MG). Meristic data included: number of ventral scales (VENT)—following the standard and Dowling methods (Dowling, 1951); subcaudals (SCDL); dorsal scale rows at the neck (DSRN; one head length posterior to jaw rictus); dorsal scale rows at midbody (DSRM); dorsal scale rows one head length anterior to the cloaca (DSRC); prefrontals (PFRO; size and number); internasals (INAS; size and number); number of supralabials (SUPRA); number of supralabials in contact with the eye (SUIE); number of infralabials (INFRA); number of supralabials in contact with chin shields (LLC); preoculars (PRE); postoculars (PO); and temporal arrangement (T).

Mean, standard deviation, and range of mensural and meristic characters were calculated for each group indicated by the phylogeny. To eliminate the effect of size, analyses of covariance (ANCOVA) were conducted with snout–vent length as the covariate (Packard and Boardman, 1999). Principal components analyses (PCA) of mensural data were conducted in Minitab 15 (Minitab Statistical Software, State College, PA) and used to identify patterns of variation in the data. All analyses used the covariance matrix. PCA analyses were conducted using log-transformed mensural data (measurements pertaining to the head). Residual data obtained from the ANCOVA analyses were used for PCA analyses.

RESULTS

Molecular analyses.—Cytochrome *b* distances ranging from 2.5% to 5.3% were observed between *Polemon* cf. *christyi* (hereafter referred to as *P. ater,* new species) and its sister taxon *P. collaris*, and a genetic divergence of 14.0% was recovered between *P. ater,* new species, and *P. christyi* (Supplementary Table 1; see Data Accessibility). Genetic distances of ND4 ranged from 2.4% to 3.6% between *P. ater,* new species, and *P. collaris*, and a genetic divergence of 14.1% was recovered between *P. ater,* new species, and *P. christyi* (Supplementary Table 1; see Data Accessibility). Divergences recovered from the 16S gene and nuclear DNA data sets were noticeably lower; uncorrected p-distances calculated from 16S, c-mos, and RAG1 ranged between 0% to 0.8% (*P. ater,* new species, and *P. collaris*) and 0.4% (*P. ater,* new species, and *P. christyi*; Supplementary Table 1; see Data Accessibility). Cytochrome *b* and ND4 divergences between *P. ater,* new species, and other species of *Polemon* are shown in Supplementary Table 1 (see Data Accessibility).

Twenty-five major differences in amino acid translation were noted in ND4 and cyt *b* data from lineages of *Polemon* from DRC and Uganda. For ND4, amino acid codon positions 43, 47, 116, 130, 134, 164, 169, 189, 211, 213, 217, and 223 translated to threonine, alanine, isoleucine, threonine, leucine, threonine, leucine, methionine, methionine, methionine, methionine, and proline for *P. ater,* new species, whereas the same positions translated to alanine, serine, threonine, alanine, isoleucine, valine, phenylalanine, threonine, leucine, threonine, alanine, and serine in *P. christyi*. For cyt *b*, amino acid codon positions 57, 58, 63, 69, 76, 108, 113, 149, 151, 153, 162, 171, 175, 180, and 185 translated to methionine, threonine, cysteine, isoleucine, threonine, threonine, isoleucine, threonine, leucine, valine, asparagine, alanine, isoleucine, threonine, and leucine for *P. ater,* new species, whereas the same positions translated to isoleucine, methionine, tyrosine, threonine, isoleucine, valine, threonine, alanine, isoleucine, isoleucine, aspartic acid, threonine, leucine, isoleucine, and serine in *P. christyi*.

Morphological analyses.—Morphometric data for examined specimens of *Polemon* (*P. christyi*, *P. ater,* new species, and *P. collaris*) are presented in Tables 1 and 2. The principal components analysis (PCA) with head morphometric data regressed against SVL is shown in Figure 3 and Table 1. The first two PC axes accounted for most of the variation in the data (87.5%; Fig. 3, Table 1). The first PC axis was an indicator of general head size relative to body size; specimens towards the right of the graph were considered to have larger heads relative to body length. The second PC axis loaded negatively for head length; negative values on this axis were correlated with shorter heads relative to body length (Fig. 3). The PC analysis showed a clear separation between *P. ater,* new species, and samples of *P. collaris*, but there was some overlap between *P. ater,* new species, and samples of *P. christyi* (Fig. 3).

We found a large amount of overlap in morphological characters (size and scalation) between several taxa of *Polemon* (*P. christyi* [$n = 5$], *P. ater,* new species, [$n = 2$], *P. collaris* [$n = 8$], and *P. gabonensis* [$n = 8$]; Table 2; Chippaux, 2006; Chirio and LeBreton, 2007; Pauwels and Vande weghe, 2008). This is common within the genus because species are morphologically conserved. The easiest way to distinguish these lineages of *Polemon* is by a combination of characters including shape of the postocular, shape of the nasal scales, dorsal coloration, ventral coloration, and presence/absence of an orange or yellow neck band.

Conclusion.—The two populations, *P. christyi* and *P. ater,* new species, are distinguished by subtle differences in morphology and substantial mitochondrial molecular differences. Moreover, *P. ater,* new species, is known only from grassland/miombo woodland, whereas *P. christyi* occurs mostly in forest, although it enters grassland and woodland in northeastern DRC (de Witte, 1966; Pitman, 1974). We consider these differences to indicate that these lineages are specifically distinct, and therefore describe the population from southeastern DRC as a new species.

Polemon ater, new species

Black Snake-eater
urn:lsid:zoobank.org:act:6256E503-4C74-4033-BABE-CEE8C42A067E
Figures 4, 5, 6; Table 2

Miodon gabonensis christyi, Loveridge (1944; part): 170, 178–180.
Miodon christyi, Laurent (1947; part): 10.
Miodon christyi, de Witte and Laurent (1947; part): 8, 60, 73–75, figs. 67–69.
Miodon christyi, de Witte (1953): 264–265, fig. 91.
Miodon christyi, Laurent (1955; part): 293.
Miodon christyi, Laurent (1956b): 252.
Miodon collaris christyi, Loveridge (1957; part): 283.
Miodon christyi, Broadley and Pitman (1960): 437, 447.
Miodon christyi, Bourgeois (1968: part): 179, 284.
Polemon christyi, Broadley (1971): 26, 76.

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Table 1. Principal components analysis (PCA) comparing *Polemon ater,* new species, with *P. christyi* and *P. collaris*, with natural log-transformed morphometric data regressed against SVL. Eigenvalues, percent variance, cumulative variance, and loadings are shown for the first three principal components. See Materials and Methods for abbreviations.

Variable	PC1	PC2	PC3
RESI 1 (SVL/HL)	0.738	−0.617	0.207
RESI 2 (SVL/HW)	0.41	0.244	−0.605
RESI 3 (SVL/NOD)	0.019	−0.028	−0.113
RESI 4 (SVL/ES)	0.083	0.104	−0.368
RESI 5 (SVL/ID)	0.129	0.007	−0.061
RESI 6 (SVL/EW)	0.033	0.024	−0.006
RESI 7 (SVL/INAS)	0.146	−0.084	−0.331
RESI 8 (SVL/RH)	0.06	0.061	−0.067
RESI 9 (SVL/RL)	0.089	0.123	−0.146
RESI 10 (SVL/FL)	0.093	0.144	−0.106
RESI 11 (SVL/FW)	0.008	0.033	−0.068
RESI 12 (SVL/CSL)	0.064	0.133	−0.078
RESI 13 (SVL/CSW)	0.036	0.006	−0.072
RESI 14 (SVL/PFL)	0.048	0.002	−0.094
RESI 15 (SVL/PFW)	0.019	0.047	−0.158
RESI 16 (SVL/MG)	0.462	0.693	0.493
Eigenvalue	6.9697	1.1179	0.5637
Proportion	0.754	0.121	0.061
Cumulative	0.754	0.875	0.936

Miodon christyi, Pitman (1974: part): 135, 165–168, 205, colour plate M, fig. 3, plate XII.
Polemon christyi, Welch (1982; part): 142.
Polemon christyi, Hughes (1983; part): 316, appendix A.
Polemon christyi, Chifundera (1990; part): table 1.
Polemon christyi, Broadley and Howell (1991; part): 29, 35, 62.
Polemon christyi, Broadley (1998; part): xxx.
Polemon christyi, Behangana and Goodman (2002; part): 64.
Polemon christyi, Spawls et al. (2002; part): 426.
Polemon christyi, Broadley et al. (2003): 95–96, fig. 17.
Polemon christyi, Broadley and Cotterill (2004; part): 47, 52.
Polemon christyi, Spawls et al. (2004; part): 426.
Polemon christyi, Chirio and Ineich (2006; part): 58.
Polemon christyi, Lötters et al. (2007; part): 98–99, plate 12.
Polemon christyi, Caro et al. (2011; part): 561.
Polemon christyi, Wallach et al. (2014; part): 561, table 1.
Polemon christyi, Tilbury and Branch (2014): 36–38, figs. 1 (two figures labeled fig. 1).
Polemon christyi, Spawls et al. (2018; part): 461, unnumbered figure.

Holotype.—PEM R20734, subadult male, Democratic Republic of the Congo, Lualaba Province, Fungurume, 10.5338°S, 26.3375°E, 1189 m, C. Tilbury, 12 February 2014 (Tilbury and Branch, 2014).

Paratype.—PEM R17452, adult female, Democratic Republic of the Congo, Lualaba Province, Kalakundi, 10.6550°S, 25.9325°E, 1472 m, W. R. Branch, 25 January 2008.

Referred material.—Given the morphological similarities (scale counts and coloration) between southern populations previously referred to *P. christyi*, we provisionally assign records from southeastern DRC (de Witte and Laurent, 1943, 1947; de Witte, 1953; Laurent, 1956b), Zambia (Broadley, 1971; Broadley et al., 2003), and west-central Tanzania

Table 2. Morphometric data (in mm) and meristic scale counts for examined specimens of *Polemon christyi*, *P. collaris*, and *P. ater*, new species. For character abbreviations, see Materials and Methods. Data are shown as mean±standard deviation with range in parentheses. Asterisks next to species names indicates data included from type specimens.

Character	*Polemon ater, new species, female (*n* = 1) paratype	*Polemon ater, new species, male (*n* = 1) holotype	*Polemon christyi* females (*n* = 2)	*Polemon christyi* males (*n* = 3)	*Polemon collaris* females (*n* = 4)	*Polemon collaris* males (*n* = 4)
SVL	640	254	758.5±20.5 (744–773)	430.0±213.0 (231–654)	502.3±116.0 (364–642)	372.9±163.8 (230–608)
TL	27.9	17.0	38.1±3.46 (35.6–40.5)	30.2±16.6 (15.7–48.4)	24.3±1.5 (22.3–25.8)	28.2±10.0 (14.7–38.5)
HL	13.6	7.9	22.9±5.2 (19.2–26.6)	13.1±5.7 (8.8–19.5)	14.0±2.0 (11.5–16.4)	11.5±4.1 (9.1–17.6)
HW	10.2	4.5	14.4±1.9 (13.0–15.7)	8.8±4.8 (4.7–14.1)	8.3±0.8 (7.1–8.9)	7.3±2.4 (5.4–10.9)
VENT	–	211	229.5±0.7 (229–230)	205.7±5.9 (199–210)	239.3±9.5 (231–251)	206.8±18.0 (180–219)
SCDL	15	20	17.5±2.1 (16–19)	20	17.5±1.3 (16–19)	23.3±1.7 (21–25)
DSRM	15	15	15	15	15	15
SUPRA	7	7	7	7	7	7
INFRA	7	7	7	7	7	7
PREOC	1	1	1	1	1	1
POSTOC	2	2	2	2	2	2

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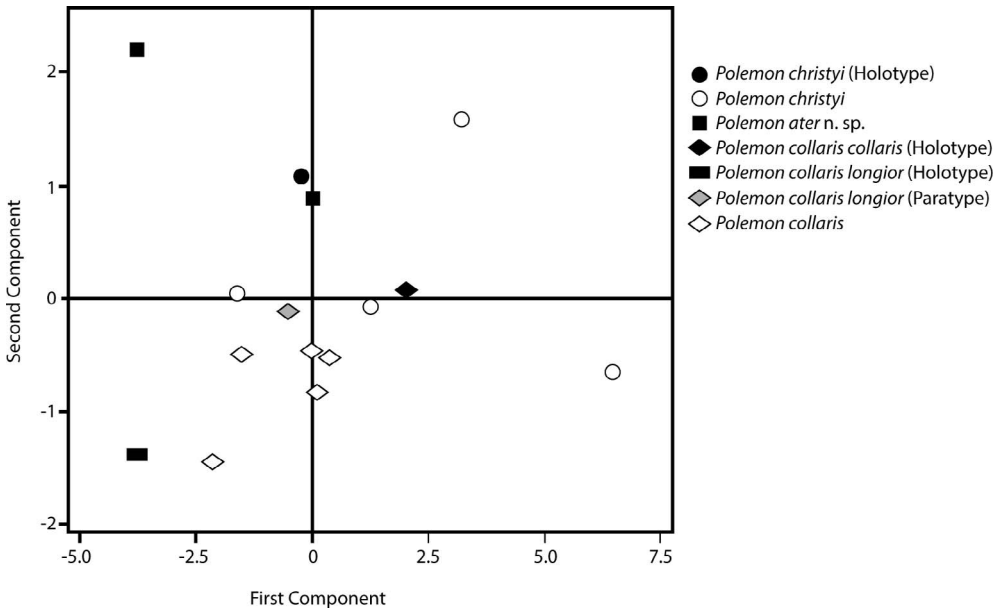


Fig. 3. Scatter plots of PC1 and PC2 scores for the analysis with morphometric data regressed against SVL for examined specimens of *Polemon*.

(Loveridge, 1944; Caro et al., 2011; Spawls et al., 2018) to *P. ater*.

Diagnosis.—*Polemon ater* is a medium to large aparallactine. The dorsum and venter are uniformly grayish black or black, with ventrals and subcaudals each edged posteriorly in silver white, lacking any lighter tones or shades anywhere on the dorsum and lacking a distinct collar; the preocular scale is irregular in shape (somewhat triangular with a rounded top); dorsally the head narrows towards the snout. Cytochrome *b* and ND4 pairwise sequence divergence rates between *P. ater* and its closest relative (*P. collaris*) ranged between 2.5% to 5.3%.

Comparisons.—(Figs. 4, 5, 6; Table 2) Based on examined material and published details (Boulenger, 1903; de Witte, 1941, 1953, 1962, 1966; de Witte and Laurent, 1943, 1947; Laurent, 1956a, 1956b, 1960; Pitman, 1974; Broadley and Howell, 1991; Meirte, 1992; Broadley et al., 2003; Chippaux, 2006; Trape and Mané, 2006; Chirio and LeBreton, 2007; Pauwels and Vande weghe, 2008), *P. ater* differs from *P. acanthias* by dorsal coloration (grayish black or black vs. whitish or pale reddish with five black stripes in *P. acanthias*), having a divided cloacal plate (entire in *P. acanthias*), and ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white in *P. acanthias*); from *P. barthii* by the number of postocular scales (two vs. one in *P. barthii*), the shape of the preocular scale (irregular vs. trapezoidal in *P. barthii*), dorsal coloration (grayish black or black vs. olive in *P. barthii*), having a divided cloacal plate (entire in *P. barthii*), and ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. yellowish white in *P. barthii*); from *P. bocourti* by the shape of the preocular scale (irregular vs. triangular in *P. bocourti*), and lacking a distinct collar (distinct creamy yellow collar in *P. bocourti*), having a divided cloacal plate (entire in *P. bocourti*), and having a narrower snout; from *P. fulvicollis* by the number of ventral scales (202–242 vs. 247–267 in *P. fulvicollis*), body shape (stout vs. slender and long in *P. fulvicollis*), ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white in *P. fulvicollis*), and lacking a distinct collar (yellowish or orange collar present in *P. fulvicollis*); from *P. gracilis* by the number of infralabials (seven vs. six in *P. gracilis*), the number of ventral scales (202–242 vs. 246–284 in *P. gracilis*), ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white or cream in *P. gracilis*), and absence of a collar (yellowish collar present in *P. gracilis*); from *P. graueri* by the number of ventral scales (202–242 vs. 222–262 in *P. graueri*), ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. cream or white in *P. graueri*), and shape of the preocular (irregular vs. triangular in *P. graueri*); from *P. griseiceps* by the number of ventral scales (202–242 vs. 177–200 in *P. griseiceps*) and ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. cream or white in *P. griseiceps*); from *P. neuwiedi* by dorsal coloration and pattern (grayish black or black vs. pale brown with three black stripes in *P. neuwiedi*) and ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white in *P. neuwiedi*); from *P. notatus* by dorsal coloration (grayish black or black vs. pale brown with two series of round black spots in *P. notatus*), number of ventral scales (202–242 vs. 181–200 in *P. notatus*), ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white in *P. notatus*), and number of postocular scales (two vs. one or two in *P. notatus*); from *P. robustus* by the shape of the preocular scale (irregular vs. rectangular and long vertically in *P. robustus*), lack of a distinct collar (yellowish orange collar present in *P. robustus*), shape of the snout laterally (narrow vs. wide in *P. robustus*), and number of ventral scales (202–242 vs. 163–189 in *P. robustus*); from *P. christyi*, to which it is morphologically most similar, by the shape of the postocular scales (upper postocular scale is noticeably larger than the lower postocular scale vs. equal-sized postocular scales in *P. christyi*) and shape of the nasal scales (square-like vs. irregular shaped in *P. christyi*); from *P. collaris* by lacking a distinct collar (tan or yellow collar present in *P. collaris*), the shape of the postocular scales (top postocular scale is noticeably larger than the bottom postocular scale vs. equal-sized postocular scales in *P. collaris*), shape of the nasal scales (square-like vs. irregular

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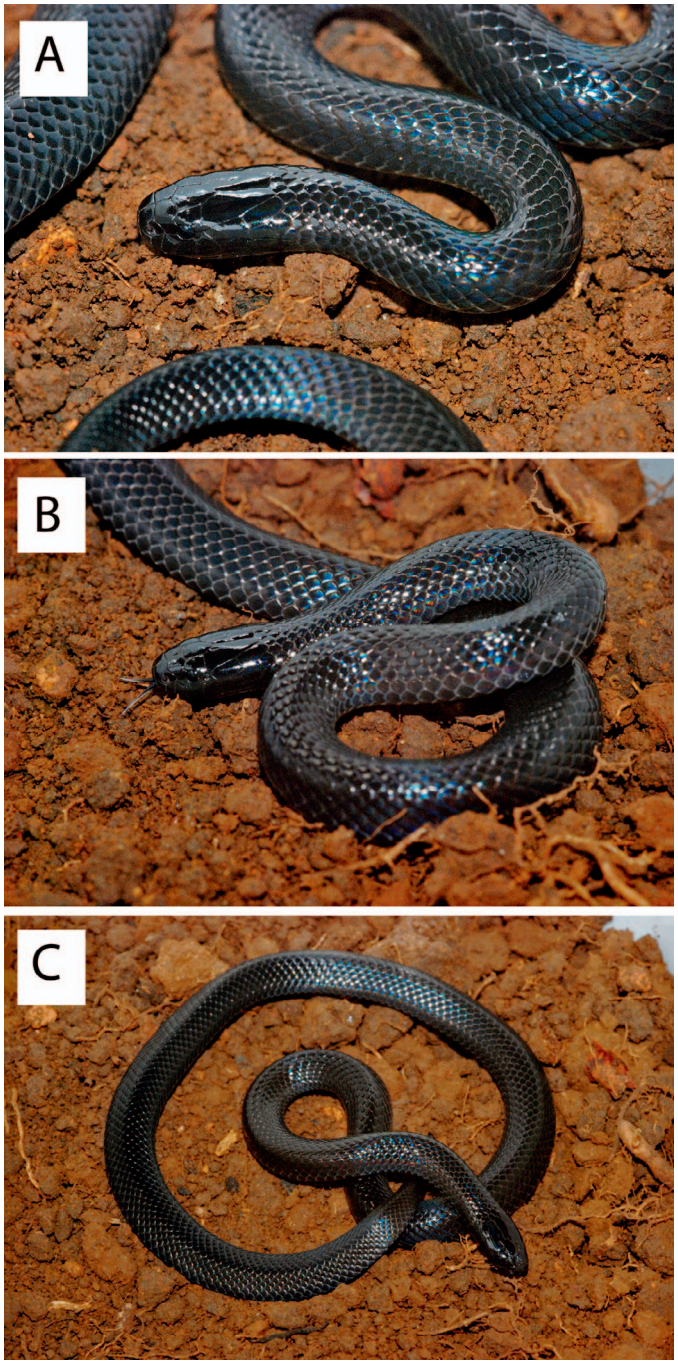


Fig. 4. Photographs of the holotype of *Polemon ater,* PEM R20734 (254 mm SVL), subadult male from Fungurume, Lualaba Province, Democratic Republic of the Congo, in life (photos: CRT). (A) Closeup of head; (B) anterior body and tongue; (C) entire body.

shaped in *P. collaris*), ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. white or cream in *P. collaris*), and a narrower head; and also from *P. gabonensis* by the shape of its preocular scale (irregular vs. elongated and triangular in *P. gabonensis*), shape of the postocular scales (top postocular scale is noticeably larger than the bottom postocular scale vs. equal-sized postocular scales in *P. gabonensis*), shape of the nasal scales (square-like vs. irregular shaped in *P. gabonensis*), a less robust snout, lack of a distinct collar (yellowish light gray collar present in *P. gabonensis*), and ventral coloration (grayish black or black with silver-white edging on ventral and subcaudal scales vs. creamy yellow lower labials and venter in *P. gabonensis*).

Description of the holotype.—(Figs. 4, 5, 6; Table 2) Subadult male 254 mm SVL; interocular distance 3.1 mm, pupil round, eye diameter 0.9 mm; no loreal; body cylindrical; tail short (17.0 mm, 6.69% of SVL); body stout; head slightly distinct from neck; dorsally, head slightly wider than neck and progressively narrower towards tip of snout; laterally, head narrow, widest point at back of head and narrower at nostrils; nostrils visible from above; scales smooth and glossy. Supralabials 7 (left)/7 (right), 3^{rd}–4^{th}/3^{rd}–4^{th} contacting orbit; infralabials 7/7, 1^{st} on each side in contact behind mental, 1^{st}–4^{th}/1^{st}–4^{th} contacting anterior chin shields; 1/1 preocular; 2/2 postoculars; temporals 1+1/1+1; two internasals; nasal divided; frontal is longer (2.5 mm) than wide (1.6 mm); dorsal scales 15 one head length posterior to jaw rictus, 15 at midbody, and 15 one head length anterior to cloaca; ventrals 211 (Dowling count: 208); cloacal plate divided; all paired subcaudals 20. Maxillary dentition—two small anterior teeth, followed by a very large, deeply grooved fang positioned anterior to eye, followed posteriorly by 12 smaller teeth on each side. These data are nearly identical to those reported by Tilbury and Branch (2014).

Coloration of the holotype in life.—(Fig. 4) Dorsum and venter uniform glossy grayish black, with ventrals and subcaudals each edged posteriorly in silver white (Tilbury and Branch, 2014). The anterior forked portion of the tongue is silver white, which transitions to grayish black posteriorly.

Coloration of the holotype in preservative.—Dorsum and venter uniform grayish black; slightly lighter in color than found in life.

Variation.—Mensural and meristic variation between the two examined specimens of *Polemon ater* are shown in Table 2. The paratype (PEM R17452) was a badly damaged adult female. There were no differences between the two specimens in terms of coloration in preservative, as both were uniform grayish black dorsally and ventrally. The female is larger (640 mm SVL), has fewer subcaudals (15), and has a proportionately shorter tail (4.35% of SVL). The largest known specimen (806 mm SVL) is from Solwezi, Zambia (Broadley et al., 2003). Ventrals were not counted for the paratype because it was badly damaged. Literature records of specimens from southeastern DRC and Zambia report ventral ranges of 202–242 and subcaudal ranges of 15–24 (de Witte, 1953; Laurent, 1956b; Broadley and Pitman, 1960; Broadley et al., 2003). Broadley and Pitman (1960) and Broadley et al. (2003) noted that specimens from Zambia may have one or two postoculars, and temporal formulas were either 1+1 or 0+1+1. De Witte (1953) reported that a specimen from Upemba National Park in southeastern DRC contained one postocular on the left side, and two postoculars on the right side. Specimens from southeastern DRC and Zambia are reported to be uniformly grayish black, bluish black, or black, both dorsally and ventrally (de Witte, 1953; Broadley et al., 2003), but Broadley et al. (2003: 95) noted ventral coloration "may have varying degrees of white on the neck or belly." Laurent (1956b) noted that a young male specimen from Dilolo (Lualaba Province, DRC) still had a distinct grayish collar in preservative, suggesting that juvenile or subadult *P. ater* might have a distinct collar. Morphometric and meristic

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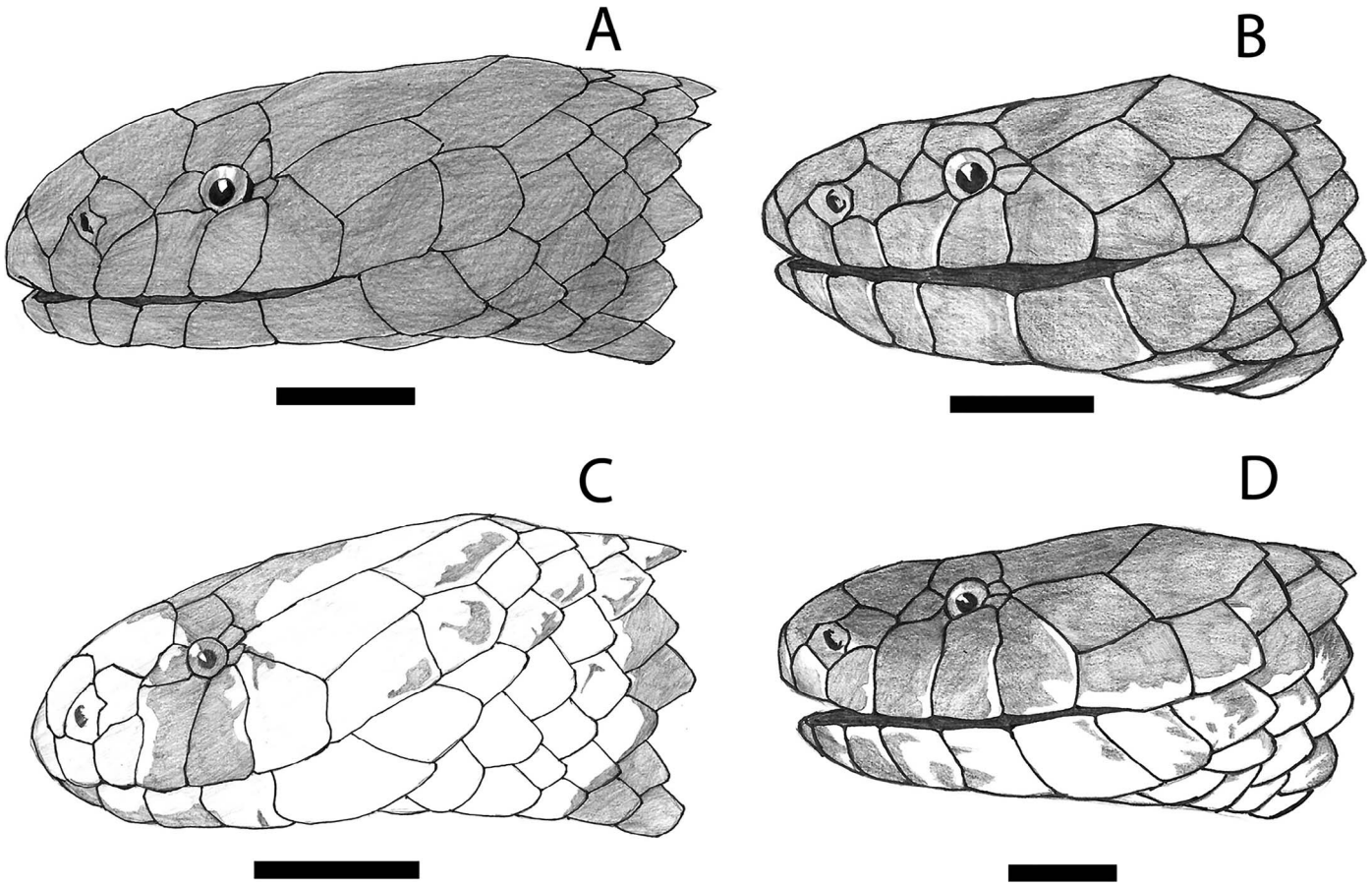


Fig. 5. Line drawings of lateral views of the (A) holotype of *Polemon ater* (PEM R20734), (B) holotype of *P. christyi* (BMNH 1946.1.8.88), (C) holotype of *P. collaris* (ZMB 10045), and (D) paratype of *P. gabonensis* (BMNH 1946.1.3.4). Scale bars represent 2 mm.

data for examined specimens of *Polemon christyi, P. collaris,* and *P. ater* are shown in Table 2.

Habitat.—Specimens of *P. ater* were collected from localities in or near *Brachystegia* (i.e., miombo) woodlands of Lualaba Province, DRC (Fig. 7). The paratype was found dead in a pit in Kalakundi Copper Mine, where it had been killed by mine workers. Specimens from Upemba National Park in southeastern DRC were found in grassland-miombo woodland habitat near tributaries. Specimens from Zambia were found in miombo woodland and in some cases, there was gallery forest in the vicinity, although none of the specimens were found in gallery forests (Broadley et al., 2003). Specimens for this study were found in elevations ranging from 1189–1472 m. In Upemba National Park, de Witte (1953) found a male specimen as high as 1810 m.

Natural history.—Very little is known about the ecology and natural history of this species. Upon discovery at about 20:00 hrs, the behavior of the holotype was described as "atractaspoid," but it did not produce the neck flexure posturing that is typical for *Atractaspis* snakes that are in a defensive mode. However, "it did thrash and jerk, freeze with body dorsoventrally flattened, and occasionally display a small degree of neck flexion" (Tilbury and Branch, 2014: 36). The holotype was kept in captivity for some time after capture, during which it burrowed into soil of its container, but it preferred to shelter under pieces of bark at the surface of the soil. The animal refused offerings of food including earthworms, grasshoppers, newly-metamorphosed toadlets, and geckos (*Hemidactylus mabouia* and *Lygodactylus gutturalis*), but eventually it ate one *L. gutturalis* gecko (Tilbury and Branch, 2014).

Based on the natural history of other species of *Polemon*, *P. ater* is likely nocturnal and fossorial, although Hinkel and Fischer (1988) noted that *P. christyi* in Rwanda can be diurnal or nocturnal. The new species is known to consume snakes that are relatively large. The paratype (PEM R17452) was found with a very large (480 mm SVL) *Afrotyphlops schmidti* (PEM R17440) in its gut. The *Afrotyphlops schmidti* was about halfway consumed, but the thickness of this prey item (14.8 mm) exceeded the thickness of the specimen of *P. ater* (9.8 mm). Broadley et al. (2003) reported a 806 mm *P. ater* (as *P. christyi*) that consumed a 600 mm *Crotaphopeltis hotamboeia* and a 430 mm *P. ater* that consumed a 305 mm *C. hotamboeia*. Broadley et al. (2003) reported that Zambian specimens were usually seen at night after heavy rainfall. Spawls et al. (2018) noted this species may be found in leaf litter or below the surface, and it emerges from underground during the rainy season. Additionally, Spawls et al. (2018) stated that the species is known to consume *Afrotyphlops*, *Leptotyphlops*, and *C. hotamboeia*. *Polemon ater* is thought to lay eggs, but no clutch details are known (Hinkel and Fischer, 1988; Spawls et al., 2018).

Distribution.—The new species most likely occurs in southeastern DRC, Zambia, west-central Tanzania, and possibly as far north as Burundi (Broadley and Howell, 1991; Caro et al., 2011; Spawls et al., 2002, 2004, 2018; Tilbury and Branch, 2014). Specimens noted from Rwanda and Malawi (some of

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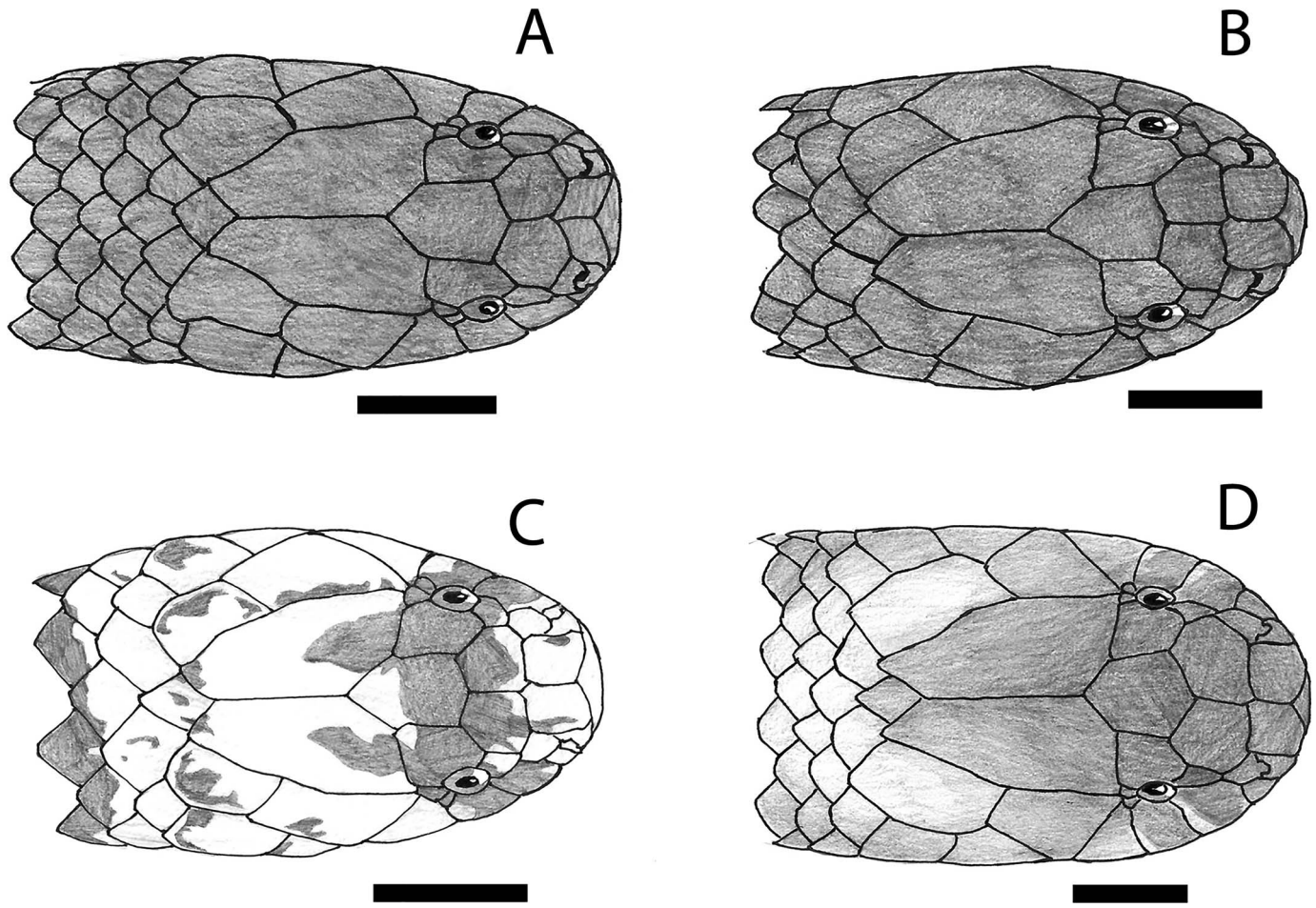


Fig. 6. Line drawings of dorsal views of the (A) holotype of *Polemon ater* (PEM R20734), (B) holotype of *P. christyi* (BMNH 1946.1.8.88), (C) holotype of *P. collaris* (ZMB 10045), and (D) paratype of *P. gabonensis* (BMNH 1946.1.3.4). Scale bars represent 2 mm.

which were found in elevations above 1995 m; de Witte, 1941; Laurent, 1956a; Hinkel and Fischer, 1988; Mercurio, 2007) may be attributable to *P. christyi*, *P. ater*, or an unknown species. Specimens noted from northeastern DRC, Uganda, South Sudan, and western Kenya are attributable to *P. christyi* (Tilbury and Branch, 2014; Wallach et al., 2014; Spawls et al., 2018), but some populations (e.g., Virunga National Park, DRC) require additional study to confirm their identification.

Etymology.—Derived from the Latin *atrum* in reference to the grayish black or black dorsal and ventral coloration that is present in all known specimens of *P. ater*.

DISCUSSION

Polemon ater is one of only a few lamprophiid species to be described from Central Africa in recent years (e.g., Greenbaum et al., 2015; Trape and Mediannikov, 2016) and the first species described from the genus in over 70 years. *Micrelaps tchernovi* was described in 2006, but in recent phylogenetic analyses, the genus was recovered outside the subfamily Aparallactinae (Figueroa et al., 2016; Portillo et al., 2018). As is the case with most species of aparallactines, morphological conservatism is common within *Polemon*. Meristic characters for several species (e.g., *P. collaris*, *P. christyi*, and *P. ater*) display considerable overlap, making specimens difficult to distinguish (Table 2). These species are most easily distinguished by coloration (presence of an orange or yellow collar, presence of dorsal stripes), head shape, and head scalation shape (Figs. 4–6).

Morphologically, the most similar species to the newly described *P. ater* is *P. christyi*, but the latter species is not sister to the former one, and was recovered in a well-supported clade with *P. robustus* (Fig. 1; Portillo et al., 2018). The latter study lacked genetic samples of *P. gabonensis*, but morphologically, *P. gabonensis* is readily distinguished by its large, broad snout (Figs. 5, 6; de Witte and Laurent, 1947). Moreover, *P. gabonensis* also has a distinct, creamy yellow venter that easily distinguishes it from *P. ater*, and the former species is only known from lowland rainforest, a habitat that is distinct from the miombo woodland/savanna habitat of *P. ater* (Broadley and Howell, 1991; Broadley et al., 2003; Chippaux, 2006; Chirio and LeBreton, 2007; Pauwels and Vande weghe, 2008; Portillo et al., 2018; Spawls et al., 2018).

Polemon ater is genetically most similar to *P. collaris*, and the sister relationship between the two species was strongly supported in maximum likelihood (RAxML) and Bayesian inference (MrBayes and BEAST) analyses (Fig. 1; Portillo et al., 2018). Morphologically, the two species can usually be distinguished by the grayish black or black dorsal and ventral coloration of *P. ater*. This contrasts with the vibrant yellow or cream collar (that may fade with age) and contrasting, creamy white venter that seems ubiquitous in many adult specimens of *P. collaris* (de Witte and Laurent, 1947; FP, pers. obs.). *Polemon collaris* was described from "Macange" (=Malanje, Malanje Prov., N Angola, 09°33′S, 16°20′E) and

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Fig. 7. Photograph of miombo woodland habitat of the paratype of *Polemon ater* in Kalakundi, Lualaba Province, Democratic Republic of the Congo (photo: WRB).

characterized (in part, and as its name implies) by a pale collar. An anomalous Angolan sample (PEM R19893), with a very faded grayish collar, grayish black dorsum, and grayish black, white-edged ventrals, showed substantial genetic differentiation (i.e., long branch length) from *P. ater* and other samples of *P. collaris* from DRC (Fig. 1). Its relationship to other Angolan populations possessing a pale collar (e.g., from Malanje, Cazengo ,and Pungo-Andongo) awaits further study (de Witte and Laurent, 1947; FP, pers. obs.). A surprising result from the phylogenetic analyses of Portillo et al. (2018) was the placement of *P. christyi*, which was recovered as sister to *P. robustus*. *Polemon christyi*, *P. collaris*, *P. gabonensis,* and *P. ater* all have similar ranges of ventral scale counts, yet *P. christyi* was found to be more closely related to *P. robustus* (Portillo et al., 2018), which is stockier in build and has substantially fewer ventral scales relative to most congeners (de Witte and Laurent, 1947).

Polemon christyi has been recorded from Uganda, western Kenya, Virunga National Park (eastern DRC), Upemba National Park (southeastern DRC), Garamba National Park (northeastern DRC), Lualaba Province (DRC), Central African Republic (record considered doubtful *sensu* Chirio and Ineich, 2006), Rwanda, Burundi, west-central Tanzania, Zambia, South Sudan, and northeastern Malawi (Boulenger, 1903, 1911, 1915; de Witte, 1941, 1953, 1955, 1975; de Witte and Laurent, 1943, 1947; Loveridge, 1944; Laurent, 1955, 1956a, 1956b, 1960; Broadley, 1971; Pitman, 1974; Spawls, 1978; Hinkel and Fischer, 1988; Joger, 1990; Broadley and Howell, 1991; Meirte, 1992; Vonesh, 2001; Behangana and Goodman, 2002; Broadley et al., 2003; Chippaux, 2006; Mercurio, 2007; Caro et al., 2011; Wallach et al., 2014; Spawls et al., 2018). These records encompass a large geographic area with multiple habitats in different elevations, and in some cases, it is not clear whether the specimens are referable to *P. ater*, *P. christyi*, or an unknown species.

Schmidt (1923) described *Miodon unicolor* (later placed in the synonymy of *P. christyi* by de Witte and Laurent, 1947) based on a single male specimen from lowland rainforest in Poko (Ituri rainforest), northeastern DRC. This specimen has 202 ventral scales and a uniformly dark bluish gray dorsum, with ventral scales edged with white. Based on these features and its locality, the specimen is likely attributable to *P. christyi* rather than *P. ater*. The shape of the nasal and postocular scales (based on the original description) of *Miodon unicolor* also closely matches that of *P. christyi* (Schmidt, 1923). De Witte (1941) described *Melanocalamus leopoldi* based on a female specimen from montane forest in Rwankeri, Rwanda (2200 m) with 245 ventral scales and fused preocular and prefrontal scales. This specimen contains more ventral scales than the two female specimens of *P. christyi* examined herein (but within range of Ugandan specimens, *sensu* Pitman, 1974), and also fused preocular and prefrontal scales, a trait that is not exhibited by either *P. ater* or Ugandan *P. christyi*. Laurent (1956a) placed *M. leopoldi* in the synonymy of *P. christyi*, but this action was seemingly rejected by de Witte (1962), and based on the absence of a preocular (because of fusion with the prefrontal), Meirte (1992) continued to recognize the former taxon as a valid species, and he retained

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Melanocalamus as a subgenus of *Polemon*. Wagner et al. (2014) also recognized *Polemon leopoldi* as a distinct species. Although Laurent's (1956a) action has been accepted by most authorities (e.g., Wallach et al., 2014; Spawls et al., 2018; Uetz et al., 2018), further examination of Rwandan populations is needed to determine with certainty whether *M. leopoldi* is conspecific with topotypic *P. christyi*.

Loveridge (1944) noted a specimen of *Miodon gabonensis christyi* (=*Polemon christyi*) from 4600 feet (1402 m) at Ilolo, located in present-day Ruaha National Park, Tanzania. No distinctive morphological features were noted by Loveridge (1944) for this specimen (MCZ R30401), and because the park contains both miombo woodland and evergreen forest (Mtui et al., 2016), further study is needed to determine the taxonomic status of this population. Several illustrations of the head of a specimen of *P. christyi* (RGMC 9809) from Usumbura (=Bujumbura), Burundi were shown by de Witte and Laurent (1947: figs. 67–69), and Laurent (1960) provided additional records from Uvira and nearby Makobola (DRC)—these records are intriguing because they are in a floodplain near the shore of Lake Tanganyika (EG, pers. obs.), although it is possible that some gallery forest was intact at the time of collection. *Polemon christyi* has also been recorded from Garamba National Park in northeastern DRC, but the specific locality and habitat where the specimen was found were not noted by de Witte (1966). Although the park is dominated by grasslands and woodlands, it contains some gallery forest (Hillman Smith et al., 2014). Six specimens of *P. christyi* reported by de Witte (1955, 1975) from Virunga National Park included Mutsora (savanna habitat, 1200 m) and Indray ("spiny" savanna and euphorbia habitat, 900 m), which are relatively xeric habitats in the park. Mercurio (2007) recorded a specimen of *P. christyi* from montane forest (1995 m) in the Wilindi Forest Reserve, northeastern Malawi. This specimen has six supralabial scales, unlike *P. christyi* and *P. ater*, which both have seven supralabials (Boulenger, 1903; de Witte, 1941, 1953; de Witte and Laurent, 1943, 1947; Laurent, 1956a, 1960; Pitman, 1974; Meirte, 1992; Broadley et al., 2003; Chippaux, 2006; Mercurio, 2007), but otherwise it has similar morphology. Further genetic and morphological examination of the Malawi population is needed to determine whether it represents *P. christyi*, *P. ater*, or an unknown species. The montane forest records of *P. christyi* from Rwanda (de Witte, 1941) and Malawi (Mercurio, 2007) were both found at higher elevations (2200 m and 1995 m, respectively) than the known elevational range of *P. ater* (1189–1810 m) or *P. christyi* (600–1760 m; de Witte, 1941, 1953; Pitman, 1974; Broadley et al., 2003; Mercurio, 2007; Spawls et al., 2018). We thus restrict the known range of *P. christyi* to forests, and possibly grasslands, woodlands, and savannas, of northeastern DRC, Uganda, South Sudan, and western Kenya. Additional work is needed on the species complex, but because specimens are rare and fieldwork in DRC is problematic for many reasons (Greenbaum, 2017), it will likely be many years before all of these populations can be examined with molecular data.

The BEAST results from Portillo et al. (2018) suggested that *P. ater* and *P. christyi* last shared a common ancestor during the early to mid-Miocene (around 16 mya), which coincided with a climactic optimum (Couvreur et al., 2008; Feakins and Demenocal, 2010). These results also indicated that *P. ater* diverged from its sister taxon, *P. collaris*, during the late Miocene (ca. 6 mya), when increasingly cool and arid conditions throughout central and eastern Africa likely fragmented populations of many squamates, eventually leading to their speciation (Greenbaum et al., 2018). Other Central African snake groups with similar dates of divergence between sister taxa include the lamprophiid genus *Boaedon* and viperid genus *Atheris* (Menegon et al., 2014; Greenbaum et al., 2015).

Interestingly, the species of *Polemon* that are morphologically similar to *P. ater* (*P. christyi, P. collaris*, and *P. gabonensis*) are mainly inhabitants of rainforests. Specifically, *Polemon christyi* is known from rainforests and associated forest relicts in Uganda, but it might occur in grasslands and woodlands in Garamba National Park, DRC (de Witte, 1966; Pitman, 1974). *Polemon ater* inhabits southeastern Lualaba, Haut-Katanga, and Haut-Lomami provinces of DRC, and Zambia, which are dominated by grasslands and miombo woodlands (de Witte, 1953; Broadley et al., 2003). Within Lualaba, Haut-Katanga, and Haut-Lomami provinces, plant species richness was highest within the miombo ecoregion (Broadley and Cotterill, 2004), and several unique species of reptiles are known from the region (e.g., Greenbaum et al., 2012; Medina et al., 2016). *Polemon ater* might have adapted to the miombo woodlands and savannas when arid climates in Africa increased after 9.6 mya (Feakins and DeMenocal, 2010).

Many non-forest habitats in southeastern DRC that are potential habitats of *P. ater* and other aparallactines (FP, unpubl. data) are exposed to degradation because of poor farming management, uncontrolled fires, mining, and other environmental degradation linked to human population growth. Because of these factors, these habitats are constantly at risk, especially unprotected regions in southeastern DRC miombo woodlands and savannas (Sodhi et al., 2007; Herrmann and Branch, 2013). Additionally, southeastern DRC is known to harbor high species diversity of plants, amphibians, reptiles, and birds (Broadley and Cotterill, 2004; Greenbaum et al., 2012; Larson et al., 2016; Medina et al., 2016). Given the results herein and from Portillo et al. (2018), it is likely that *P. ater* is endemic to the grasslands, miombo woodlands, and possibly forests of southeastern DRC, Zambia, and west-central Tanzania. Possible populations in Rwanda, Burundi, and Malawi require further study. Given the proximity of the Dilolo locality (Laurent, 1956b) to the border of DRC, *P. ater* is likely to be found in neighboring Angola.

MATERIAL EXAMINED

* Indicates type specimens. Institutional abbreviations follow Sabaj (2016), with the Royal Museum for Central Africa, Tervuren listed as RMCA R and the Royal Belgian Institute of Natural Sciences listed as RBINS.

Polemon acanthias: ZMB 51389, West Africa.

Polemon bocourti: MNHN-RA 1896.0553–54*, Vallee de l'Ogoone, Congo.

Polemon christyi: BMNH 1946.1.8.88*, Uganda; CAS 111863, Mabira Forest, Uganda; CAS 147905, Kakamega Forest, Kenya; CAS 204334, road between Kibale National Park and Fort Portal, near Kibale National Park turnoff, Uganda; UTEP 21618, road to Budongo Central Forest Reserve, Western Region, Uganda, 01.65357°N, 31.32806°E, 1084 m.

Polemon collaris: PEM R19893, Lunda Norte, Angola, 9.39922°S, 20.41323°E; UAC 62 (RBINS 18544), Yoko, DRC, 1.9300°N, 25.2525°E; UTEP 21612, Byonga, South Kivu,

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DRC, 03.33694°S, 28.12419°E, 710 m; UTEP 21613, Fizi, South Kivu, DRC, 04.27470°S, 28.92930°E, 1268 m; UTEP 21614, Salonga River, Watsi Kengo, Tshuapa, DRC, 00.91006°S, 20.62076°E, 332 m; ZMB 10045*, Kwango River, Angola; ZMB 20308, Cameroon.

Polemon collaris longior: RMCA R 1629*, Medje, DRC; RMCA R 15843*, Lutunguru, DRC.

Polemon fulvicollis: MNHN-RA 1886.0211*, Congo Brazzaville, Franceville.

Polemon fulvicollis laurenti: RMCA R 4771*, Tongo, DRC; RMCA R 15430, Stanleyville (i.e., Kisangani), DRC; RMCA R 18246, Katche, Kivu, DRC; RMCA R 21569, Kivu, DRC; UTEP 21615, Bombole village, Bas-Uele, DRC, 02.27805°N, 25.14679°E, 467 m.

Polemon gabonensis: BMNH 1946.1.3.4, 5*, Cameroon Mountains, Cameroon; RMCA R 16087, Ibembo, DRC; RMCA R 16545, Bokoro, DRC; RMCA R 21030, Ikela, DRC; ZMB 21142, Cameroon.

Polemon gabonensis brachyurus: RMCA R 20326*, Idjwi Sud, DRC.

Polemon gabonensis schmidti: RMCA R 8008*, Stanleyville (i.e., Kisangani), DRC; RMCA R 10545*, Karawa, Ubangi, DRC.

Polemon graueri: CRT 4007 (RBINS 18543), Bomane, DRC, 1.270°N, 23.732°E; UTEP 21611, Rwenzori Mountains National Park, near Nyakalengisa entrance, Uganda, 00.36247°N, 29.99863°E, 2075 m; UTEP 21650, Idjwi Island, Bugarula, South Kivu, DRC, 02.05815°S, 029.05791°E, 1541 m; ZMB 20721*, Entebbe, Uganda.

Polemon griseiceps: BMNH 1946.1.21.90*, Bitye, South Cameroon.

Polemon notatus: ZMB 10271*, West Africa.

Polemon robustus: RMCA R 6803, 6851, 8761, 11839*, Kunungu, DRC; UTEP 21616, Lake Mai-Ndombe, Isongo, Mai-Ndombe, DRC, 01.34222°S, 18.23774°E, 309 m; UTEP 21617, Salonga River, Itala Village, Equateur, DRC, 00.62615°S, 20.20896°E, 322 m.

DATA ACCESSIBILITY

Supplemental material is available at https://www.copeiajournal.org/ch-18-098.

ACKNOWLEDGMENTS

Fieldwork by the last author in DRC was funded by the Percy Sladen Memorial Fund, an IUCN/SSC Amphibian Specialist Group Seed Grant, K. Reed, M.D., research funds from the Department of Biology at Villanova University, a National Geographic Research and Exploration Grant (no. 8556-08), UTEP, and the US National Science Foundation (DEB-1145459); E. Greenbaum, C. Kusamba, W. M. Muninga, and M. M. Aristote thank their field companions M. Zigabe, A. M. Marcel, M. Luhumyo, J. and F. Akuku, F. I. Alonda, and the late A. M'Mema. The Centre de Recherche en Sciences Naturelles and Institut Congolais pour la Conservation de la Nature provided project support and permits. Fieldwork by Z. T. Nagy in DRC was supported by the Belgian National Focal Point to the Global Taxonomy Initiative. D. F. Hughes, E. Greenbaum, and M. Behangana thank the Uganda Wildlife Authority of Kampala for necessary permits to work in Uganda. W. R. Branch thanks the National Research Foundation of South Africa (NRF) for funding, and Thomas Branch for collecting important specimens in northeastern Angola during mine exploration in the region. We thank W. Conradie of Port Elizabeth Museum for facilitating loans of specimens and providing measurement data for a prey item of the paratype of *P. ater*. F. Portillo and E. Greenbaum thank Danny Meirte of the Royal Museum for Central Africa for facilitating access to specimens and correcting crucial details of this paper. It is with great sadness that we note that our friend and colleague Prof. William Roy Branch did not live to see the publication of this manuscript. His passing is a huge loss to the many colleagues who treasured his friendship, advice, and counsel. We salute him as a true giant of African herpetology.

LITERATURE CITED

Anderson, C. G., and E. Greenbaum. 2012. Phylogeography of northern populations of the black-tailed rattlesnake (*Crotalus molossus* Baird and Girard, 1853), with the revalidation of *C. ornatus* Hallowell, 1854. Herpetological Monographs 26:19–57.

Behangana, M., and J. D. Goodman. 2002. Key to genera of snakes of Uganda (with a checklist of vernacular names). The Uganda Journal 48:33–70.

Bogert, C. M. 1940. Herpetological results of the Vernay Angola Expedition: With notes on African reptiles in other collections. Snakes, including an arrangement of African Colubridae. Bulletin of the American Museum of Natural History 77:1–107.

Boulenger, G. A. 1903. Descriptions of new snakes in the collection of the British Museum. The Annals and Magazine of Natural History 12:350–354.

Boulenger, G. A. 1911. On a third collection of reptiles and batrachians made by Dr. E. Bayon in Uganda. Annali del Museo Civico di Storia Naturale di Genova 5:1–9.

Boulenger, G. A. 1915. A list of the snakes of East Africa, north of the Zambesi and south of the Soudan and Somaliland and Nyassaland. Proceedings of the Zoological Society of London 85:611–640.

Bourgeois, M. 1968. Contribution à la morphologie comparée du crâne des ophidiens de l'Afrique Centrale. Publications de l'Université Officielle du Congo à Lubumbashi 18:1–293 + table.

Broadley, D. G. 1971. The reptiles and amphibians of Zambia. The Puku 6:1–143.

Broadley, D. G. 1998. Karl Patterson Schmidt and the reptiles volumes based on the collections of the American Museum Natural History Congo Expedition of 1909–1915. Introduction to Reptilia, p. ix–xxxiii. *In*: Contributions to the Herpetology of the Belgian Congo. K. P. Schmidt and G. K. Noble (eds.). Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Broadley, D. G., and F. P. D. Cotterill. 2004. The reptiles of southeast Katanga, an overlooked 'hot spot.' African Journal of Herpetology 53:35–61.

Broadley, D. G., D. T. Craig, and J. Wigge. 2003. Snakes of Zambia. Chimaira, Frankfurt am Main, Germany.

Downloaded From: https://bioone.org/journals/Copeia on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Broadley, D. G., and K. H. Howell. 1991. A check list of the reptiles of Tanzania, with synoptic keys. Syntarsus 1:1–70.

Broadley, D. G., and C. R. S. Pitman. 1960. On a collection of snakes taken in northern Rhodesia by Monsieur H. J. Bredo. Occasional Papers of the National Museums of Southern Rhodesia (Natural Sciences) 3:437–451.

Caro, T., O. S. Evans, E. Fitzherbert, T. A. Gardner, K. Howell, R. Drewes, and H. B. Shaffer. 2011. Reptiles of Katavi National Park, western Tanzania, are from different biomes. African Journal of Ecology 49:377–382.

Chifundera, K. 1990. Snakes of Zaire and their bites. African Study Monographs 10:137–157.

Chippaux, J. P. 2006. Les Serpents d'Afrique Occidentale et Centrale. IRD Éditions, Paris.

Chirio, L., and I. Ineich. 2006. Biogeography of the reptiles of the Central African Republic. African Journal of Herpetology 55:23–59.

Chirio, L., and M. LeBreton. 2007. Atlas des Reptiles du Cameroun. IRD Éditions, Paris.

Couvreur, T. L., L. W. Chatrou, M. S. Sosef, and J. E. Richardson. 2008. Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. BMC Biology 6:54.

de Witte, G. F. 1941. Batraciens et reptiles. Exploration du Parc National Albert, Mission G. F. DeWitte (1933–1935). Fascicle 33. Institut des Parcs Nationaux du Congo Belge, Brussels, Belgium.

de Witte, G. F. 1953. Exploration du Parc National de l'Upemba, 6, Reptiles. Exploration du Parc National de l'Upemba. Mission G.F. de Witte en collaboration avec W. Adam, A. Janssens, L. van Meel et R. Verheyen (1946–1949)—Reptiles. Institut des Parcs Nationaux du Congo Belge 6:1–322 + pl. I–XLI.

de Witte, G. F. 1955. La population de reptiles de la région de Mutsora (Kivu Nord). Bulletin des Séances: Académie Royale des Sciences Coloniales: Nouvelle Série 1:203–225.

de Witte, G. F. 1962. Genera des serpents du Congo et du Ruanda-Urundi. Musée Royal de l'Afrique Centrale: Annales serie in 8: Sciences zoologiques 104:1–203.

de Witte, G. F. 1966. Exploration du Parc National de la Garamba. Mission H. de Saeger en collaboration avec P. Baert, G. Demoulin, I. Denisoff, J. Martin, M. Micha, A. Noirfalise, P. Schoemaker, G. Troupin et J. Verschuren (1949–1952)—Reptiles. Bruxelles, Ouvrage publié avec l'appui du Ministère Belge de l'Éducation Nationale et de la Culture. Institut des Parcs Nationaux du Congo fascicule 48:5–108.

de Witte, G. F. 1975. Boidae, Colubridae, Elapidae et Viperidae, p. 62–108. *In*: Exploration du Parc National des Virunga. H. de Saeger, R. Roux-Ésteve, and G. F. de Witte (eds.). Fondation pour Favoriser Recherches Scientifiques en Afrique, Deuxième Série, Bruxelles.

de Witte, G. F., and R. F. Laurent. 1943. Contribution à la systématique des Boiginae du Congo Belge (Rept.). Revue de Zoologie et de Botanique Africaines 37:157–189.

de Witte, G. F., and R. F. Laurent. 1947. Révision d'un groupe de Colubridae Africains: Genres *Calamelaps*, *Miodon*, *Aparallactus*, et formes affines. Mémoires du Musée Royal d'Histoire Naturelle de Belgique (sér. 2) 29:1–134.

Devitt, T. J., T. J. LaDuc, and J. A. McGuire. 2008. The *Trimorphodon biscutatus* (Squamata: Colubridae) species complex revisited: a multivariate statistical analysis of geographic variation. Copeia 2008:370–387.

Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1:97–99.

Feakins, S. J., and P. B. Demenocal. 2010. Global and African regional climate during the Cenozoic, p. 45–56. *In*: Cenozoic Mammals of Africa. L. Werdelin and W. J. Sanders (eds.). University of California Press, Oakland, California.

Figueroa, A., A. D. McKelvy, L. L. Grismer, C. D. Bell, and S. P. Lailvaux. 2016. A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. PLoS ONE 11:e0161070.

Greenbaum, E. 2017. Emerald Labyrinth: A Scientist's Adventures in the Jungles of the Congo. ForeEdge, Lebanon, New Hampshire.

Greenbaum, E., S. A. Dowell Beer, P. Wagner, C. G. Anderson, C. O. Villanueva, P. Malonza, C. Kusamba, W. M. Muninga, M. M. Aristote, and W. R. Branch. 2018. Phylogeography of Jackson's Forest Lizard *Adolfus jacksoni* (Sauria: Lacertidae) reveals cryptic diversity in the highlands of East Africa. Herpetological Monographs 32:51–68.

Greenbaum, E., F. Portillo, K. Jackson, and C. Kusamba. 2015. A phylogeny of Central African *Boaedon* (Serpentes: Lamprophiidae), with the description of a new cryptic species from the Albertine Rift. African Journal of Herpetology 64:18–38.

Greenbaum, E., E. L. Stanley, C. Kusamba, W. M. Moninga, S. R. Goldberg, and C. R. Bursey. 2012. A new species of *Cordylus* (Squamata: Cordylidae) from the Marungu Plateau of south-eastern Democratic Republic of the Congo. African Journal of Herpetology 61:14–39.

Herrmann, H. W., and W. R. Branch. 2013. Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. Journal of Arid Environments 93:94–115.

Hillman Smith, K., J. Kalpers, L. Arranz, and N. Ortega (Eds.). 2014. Garamba: Conservation in Peace & War. Privately published by the authors, Johannesburg, South Africa.

Hinkel, H., and E. Fischer. 1988. Reptiles et Amphibiens du Rwanda: Et Leurs Environnement. Naturwissenschaftliche Forschungsgruppe Zentral- & Ost- Afrika, Johannes Gutenburg Universität, Mainz, Germany.

Hughes, B. 1983. African snake faunas. Bonner zoologische Beiträge 34:311–356.

Hughes, B., and D. H. Barry. 1969. The snakes of Ghana: a checklist and key. Bulletin de l'Institut français d'Afrique noire A 31:1004–1041.

Joger, U. 1990. The herpetofauna of the Central African Republic, with description of a new species of *Rhinotyphlops* (Serpentes, Typhlopidae), p. 85–102. *In*: Vertebrates in the Tropics: Proceedings of the International Symposium on Vertebrate Biogeography and Systematics in the Tropics, Bonn, June 5–8, 1989. R. Hutterer (ed.). Museum Alexander Koenig, Bonn, Germany.

Kumar S., G. Stecher, and K. Tamura. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33:1870–1874.

Kusamba, C., A. Resetar, V. Wallach, and Z. T. Nagy. 2013. Mouthful of snake: an African snake-eater's (*Polemon gracilis graueri*) large typhlopid prey. Herpetology Notes 6: 235–237.

LaDuc, T. J., and J. D. Johnson. 2003. A taxonomic revision of *Trimorphodon biscutatus vilkinsonii* (Serpentes: Colubridae). Herpetologica 59:365–375.

Downloaded From: https://bioone.org/journals/Copeia on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Larson, T., D. Castro, M. Behangana, and E. Greenbaum. 2016. Evolutionary history of the river frog genus *Amietia* (Anura: Pyxicephalidae) reveals extensive diversification in Central African highlands. Molecular Phylogenetics and Evolution 99:168–181.

Laurent, R. F. 1947. Notes sur quelques reptiles appurtenant a la collection du Musée Royal d'Histoire Naturelle de Belgique. Bulletin du Musée royal d'Histoire naturelle de Belgique 23:1–12.

Laurent, R. F. 1955. Aperçu de la biogéographie des batraciens et des reptiles de la region des Grands Lacs. Bulletin de la Société zoologique de France 79:290–310.

Laurent, R. F. 1956a. Contribution à l'Herpétologie de la Région des Grands Lacs de l'Afrique Centrale. I. Généralités. II. Chéloniens. III. Ophidiens. Annales du Musée Royal du Congo Belge, Tervuren (Belgique), Série in 8, 48:1–390.

Laurent, R. F. 1956b. Notes herpétologiques africaines. Revue de Zoologie et de Botanique Africaines 53:229–256.

Laurent, R. F. 1960. Notes complémentaires sur les chéloniens et les ophidiens du Congo oriental. Annales du Musée Royal du Congo Belge (Sciences Zoologiques) 84:1–86.

Lötters, S., P. Wagner, B. A. Bwong, S. Schick, P. K. Malonza, V. Muchai, D. V. Wasonga, and M. Veith. 2007. A Fieldguide to the Amphibians and Reptiles of the Kakamega Forest. National Museums of Kenya and University of Mainz, Nairobi and Mainz.

Loveridge, A. 1942. Scientific results of a fourth expedition to forested areas in East & Central Africa. Bulletin of the Museum of Comparative Zoölogy (Harvard) 91:237–373 + pl. 1–6.

Loveridge, A. 1944. Further revisions of African snake genera. Bulletin of the Museum of Comparative Zoology (Harvard) 95:121–247.

Loveridge, A. 1957. Check List of the Reptiles and Amphibians of East Africa (Uganda: Kenya: Tanganyika: Zanzibar). Bulletin of the Museum of Comparative Zoology (Harvard) 117:153–362 + xxxvi.

Medina, M. F., A. M. Bauer, W. R. Branch, A. Schmitz, W. Conradie, Z. T. Nagy, T. J. Hibbits, R. Ernst, D. M. Portik, S. V. Nielson, T. J. Colston, C. Kusamba, M. Behangana, M.-O. Rödel, and E. Greenbaum. 2016. Molecular phylogeny of *Panaspis* and *Afroablepharus* skinks (Squamata: Scincidae) in the savannas of sub-Saharan Africa. Molecular Phylogenetics and Evolution 100:409–423.

Meirte, D. 1992. Clés de determination des serpents d'Afrique. Museum Royal d'Afrique Centrale, Tervuren Belgique, Annales Musée Royal de l'Afrique Centrale (Sciences Zoologiques) 267:1–152.

Menegon, M., S. P. Loader, S. J. Marsden, W. R. Branch, T. R. B. Davenport, and S. Ursenbacher. 2014. The genus *Atheris* (Serpentes: Viperidae) in East Africa: phylogeny and the role of rifting and climate in shaping the current pattern of species diversity. Molecular Phylogenetics and Evolution 79:12–22.

Mercurio, V. 2007. *Polemon christyi* and *Elapsoidea boulengeri*: two new snake distribution records for Malawi. Salamandra 43:253–255.

Moyer, K., and K. Jackson. 2011. Phylogenetic relationships among the Stiletto Snakes (genus *Atractaspis*) based on external morphology. African Journal of Herpetology 60: 30–46.

Mtui, D., N. Owen-Smith, and C. Lepczyk. 2016. Assessment of wildlife populations trends in three protected areas in Tanzania from 1991 to 2012. African Journal of Ecology 55:305–315.

Packard, G. C., and T. J. Boardman. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? Comparative Biochemistry and Physiology, Part A 122:37–44.

Pauwels, O. S. G., and J. P. Vande weghe. 2008. Les Reptiles du Gabon. Smithsonian Institution, Washington, D.C.

Pitman, C. R. S. 1974. A Guide to the Snakes of Uganda. Wheldon and Wesley, Codicote, UK.

Portillo, F., W. R. Branch, W. Conradie, M.-O. Rödel, J. Penner, M. Barej, C. Kusamba, W. M. Muninga, M. M. Aristote, A. M. Bauer, J. F. Trape, Z. T. Nagy, P. Carlino, O. S. G. Pauwels… E. Greenbaum. 2018. Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophiidae). Molecular Phylogenetics and Evolution 127:288–303.

Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Resetar, A. R., and H. Marx. 1981. A redescription and generic reallocation of the African colubrid snake *Elapocalamus gracilis* Boulenger with a discussion of the union of the brille and postocular shield. Journal of Herpetology 15: 83–89.

Sabaj, M. H. (Ed.). 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). Electronically accessible at http://www.asih.org/, American Society of Ichthyologists and Herpetologists, Washington, D.C.

Schmidt, K. P. 1923. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909–1915. Part II. Snakes, with field notes by Herbert Lang and James P. Chapin. Bulletin of the American Museum of Natural History 49:1–146.

Sodhi, N. S., B. W. Brook, and C. J. A. Bradshaw. 2007. Tropical Conservation Biology. Blackwell Publishing, Malden, Massachusetts.

Spawls, S. 1978. A check list of the snakes of Kenya. Journal of East Africa Natural History Society and National Museum 31:1–18.

Spawls, S., and B. Branch. 1995. The Dangerous Snakes of Africa: Natural History: Species Directory: Venoms and Snakebite. Ralph Curtis Publishing, Sanibel Island, Florida.

Spawls, S., K. Howell, R. Drewes, and J. Ashe. 2002. A Field Guide to the Reptiles of East Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi. Academic Press, London.

Spawls, S., K. Howell, R. Drewes, and J. Ashe. 2004. A Field Guide to the Reptiles of East Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi. A & C Black, London.

Spawls, S., K. Howell, H. Hinkel, and M. Menegon. 2018. A Field Guide to East African Reptiles. Bloomsbury Publishing, London.

Tilbury, C., and B. Branch. 2014. *Polemon christyi* (Boulenger, 1903): Christy's Snake-Eater. African Herp News 61: 36–38.

Trape, J. F., and Y. Mané. 2006. Guide des Serpents d'Afrique Occidentale: Savane et Désert. IRD Éditions, Paris.

Trape, J. F., and O. Mediannikov. 2016. Cinq serpents nouveaux du genre *Boaedon* Duméril, Bibron & Duméril, 1854 (Serpentes: Lamprophiidae) en Afrique centrale.

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Bulletin de la Société Herpétologique de France 159:61–111.

Uetz, P., P. Freed, and J. Hošek (Eds.). 2018. The Reptile Database. http://www.reptile-database.org (accessed 25 July 2018).

Underwood, G., and E. Kochva. 1993. On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). Zoological Journal of the Linnean Society 107:3–64.

Vonesh, J. R. 2001. Natural history and biogeography of the amphibians and reptiles of Kibale National Park, Uganda. Contemporary Herpetology 4:1–14.

Wagner, P., I. Safari, and J. Chenga. 2014. *Polemon leopoldi*. The IUCN Red List of Threatened Species 2014: e.T13264660A13264666. http://dx.doi.org/10.2305/IUCN.UK.2014-3.RLTS.T13264660A13264666.en (Downloaded 27 September 2018).

Wallach, V., K. L. Williams, and J. Boundy. 2014. Snakes of the World: A Catalogue of Living and Extinct Species. Taylor and Francis, CRC Press, London.

Welch, K. R. G. 1982. Herpetology of Africa: A Checklist and Bibliography of the Orders Amphisbaenia, Sauria and Serpentes. Robert F. Krieger Publishing Company, Malabar, Florida.

Downloaded From: https://bioone.org/journals/Copeia on 28 Mar 2024
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