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Systematics of the Thirteen-scaled Green Snake *Philothamnus carinatus* (Squamata: Colubridae), with the description of a cryptic new species from Central and East Africa

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ABSTRACT

Recent molecular phylogenies of African Green Snakes suggested the geographically widespread species *Philothamnus carinatus* includes at least two distinct lineages. We utilised an integrative taxonomic approach with morphological and genetic data to reconcile the taxonomic status of these cryptic lineages, including the recently described taxon *P. brunneus* from West Africa. We sequenced three mitochondrial (16S, cyt *b* and ND4) and two nuclear (c-mos and RAG1) genes from several Central African populations of *P. carinatus* and combined our data with other closely related species to infer a maximum likelihood phylogenetic tree with IQ-TREE. Our results are consistent with previous studies that showed *P. cf. carinatus* populations from Democratic Republic of the Congo (DRC) represent a cryptic lineage that is distinct from *P. carinatus sensu stricto* in Cameroon, Central African Republic, Equatorial Guinea (including Bioko Island), Gabon, eastern Nigeria, Republic of the Congo, and extreme western DRC. In our preferred tree, *P. brunneus* (limited to 16S molecular data) was recovered as a relatively long branch in a moderately supported clade with *P. carinatus sensu stricto*, whereas *P. cf. carinatus* populations from northern Angola, most of DRC, and East Africa (Burundi, Kenya, Rwanda, Tanzania and Uganda) were described as a new species. A possible hybrid population between south-eastern Cameroon and north-western DRC is consistent with an increasing body of evidence suggesting the Ubangi River might represent a hybrid zone area.

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INTRODUCTION

African Green and Bush Snakes (*Philothamnus*) are a common component of the vertebrate fauna of sub-Saharan Africa in habitats ranging from montane forests to savannahs (Hughes 1983). Diurnal, mostly arboreal, and fast-moving, *Philothamnus* rarely exceed 1 m in total length. Many Green Snake species frequent areas with water, where frog prey are abundant, but they will also eat fish, lizards, and nestling birds. *Philothamnus* are oviparous and some species have been documented to lay their eggs in communal nests (Pitman 1974; Spawls et al. 2018; Chippaux and Jackson 2019).

Like many other groups of snakes in Africa (e.g., *Boaedon*, Greenbaum et al. 2015), different species of *Philothamnus* have remarkably similar morphology, including many overlapping scale counts. In his taxonomic revision of the genus (including *Chlorophis*, eventually synonymised with *Philothamnus sensu* Broadley 1966), Loveridge (1958: 52) noted that, "unfortunately the more we know of variation in these reptiles, the more difficult it becomes to devise a clear, yet comprehensive, key". In his landmark study of the genus, based on over 5 000 examined specimens, Hughes (1985) documented over a century of taxonomic confusion by herpetologists, and he revised the genus to include 18 species and "possibly" two subspecies. In recent decades, one new species was described (*P. hughesi*, Trape and Roux-Estève 1990), two West African synonyms of *P. heterodermus* (*P. bellii* and *P. pobeguini*) were elevated to full species (Trape and Baldé 2014), and updated keys to *Philothamnus* were published (e.g., Meirte 1992; Chippaux 2006; Spawls et al. 2018; Chippaux and Jackson 2019; Trape 2023). However, morphology-based identification of museum specimens remains challenging and has been likened to "a can of worms" (Nielsen et al. 2021).

Recent molecular phylogenies of *Philothamnus* have provided some taxonomic resolution and identified new species. Utilising mitochondrial genes (16S rRNA and cyt *b*), Jesus et al. (2009) focused on Green Snakes (*Philothamnus* and its sister taxon *Hapsidophrys*) from the Gulf of Guinea Islands, and their results confirmed the species-level status of three taxa (*H. lineata, H. principis* and *H. smaragdina*) from these oceanic islands. Engelbrecht et al. (2019) utilised data from three mitochondrial (16S, cyt *b* and ND4) and two nuclear (c-mos and RAG1) genes to construct a well-supported phylogeny of 16 *Philothamnus* taxa. Their analysis identified cryptic lineages in two taxa (*P. carinatus* and *P. semivariegatus*), and *P. natalensis occidentalis* was elevated to species-level status. Most recently, Trape et al. (2021) utilised a phylogeny derived from a single mitochondrial gene (16S) to reconcile the taxonomy of the *Philothamnus heterodermus* group in West and Central Africa, and two new cryptic species were described — *Philothamnus mayombensis*, previously confused with *P. heterodermus*, was described from the rainforest of the Mayombe region in extreme western Democratic Republic of the Congo (DRC), and *P. brunneus*, previously considered a population of *P. carinatus*, was described mostly from forests of West Africa.

Herein, we focus on the Thirteen-scaled Green Snake (*Philothamnus carinatus*), originally described from Cameroon (Andersson 1901), so named because it usually has 13 dorsal scale rows at midbody. Until recently, the species was primarily known from forests and "well-wooded savanna" from Guinea to Kenya and south to northern Angola and southeastern DRC (Hughes 1985; Marques et al. 2018; Spawls et al. 2018; Chippaux and Jackson 2019). The phylogeny and species-delimitation analyses of Engelbrecht et al. (2019) suggested that populations from Gabon and Republic of the Congo

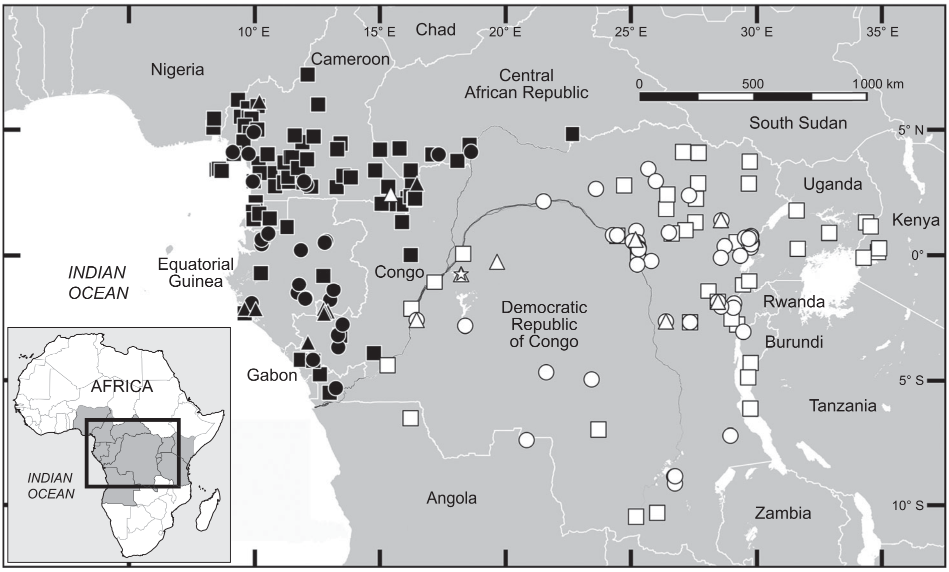

Figure 1. Distribution map of Central Africa showing localities of *Philothamnus carinatus sensu stricto* (black symbols) and *P.* cf. *carinatus* (white symbols). Circles represent examined natural history specimens, triangles are genetic samples, squares are literature records, and the type locality of the new species described herein is shown with a star. The Congo and Ubangi rivers are highlighted in black.

represented a distinct species from those in DRC, but topotypic samples from Cameroon were not available. Trape et al. (2021: figure 1) combined their newly sequenced 16S data with those from Engelbrecht et al. (2019) to produce an updated phylogeny. Their preferred tree recovered a moderately supported clade of *P. carinatus*, including two genetically divergent samples from Guinea, which were described as a new species, *P. brunneus*. This new species was diagnosed by 16S genetic divergence (4–8%), a “habituellement” (usually) uniform brown dorsum without darker crossbars, and a larger average number of ventrals in comparison to *P. carinatus sensu stricto*, but the latter comparison did not include a statistical test. Thus, the name *P. brunneus* formally replaced *P. carinatus* in West Africa, but the eastern extent of the former taxon’s distribution could not be identified with certainty (Trape et al. 2021).

In this study, we combine all previously published genetic data for *Philothamnus carinatus* with newly sequenced samples from Cameroon, Central African Republic (CAR), and multiple localities throughout DRC. Our integrated taxonomy utilises phylogenetic trees, sequence divergence estimates, and morphometric data to describe a cryptic new species of *Philothamnus* from northern Angola, most of DRC, and East Africa (Burundi, western Kenya, Rwanda, Tanzania and Uganda).

Materials and methods

DNA Extraction, PCR amplification and Sequencing

Using primers from several previous studies (Table 1), we generated new sequence data for five genes (16S ribosomal RNA [16S], cytochrome *b* [cyt *b*], nicotinamide adenine

Table 1. Polymerase chain reaction primers used in the molecular portion of this study, their sequences, and sources.

	Primers	Primer sequence	Source
16S	L2510mod/16Sar	CCGACTGTTTAMCAAAAACA	Zaher et al. (2009)
	H3056/16Sbr	CTCCGGTCTGAACTCAGATCACGTRGG	
cyt *b*	L14910	GACCTGTGATMTGAAAACCAYCGTTGT	Burbrink et al. (2000)
	H16061	CTTTGGTTTACAAGAACAATGCTTTA	
ND4	ND4	CACCTATGACTACCAAAAGCTCATGTAGAAGC	Arèvalo et al. (1994), Pook et al. (2009)
	HIS1276	TTCTATCACTTGGATTTGCACCA	
c-mos	S77	CATGGACTGGGATCAGTTATG	Slowinski and Lawson (2002)
	S78	CCTTGGGTGTGATTTTCTCACCT	
RAG1	G396 (R13)	TCTGAATGGAAATTCAAGCTGTT	Groth and Barrowclough (1999)
	G397 (R18)	GATGCTGCCTCGGTCGGCCACCTTT	

dehydrogenase subunit four [ND4], and nuclear markers oocyte maturation factor Mos [c-mos] and recombination-activating gene one [RAG1]) from eight samples of *Philothamnus carinatus* collected in Cameroon, CAR, and DRC. One of these samples (NMP-P6V 73345) from Bamo Forest, Mejung, Northwest Province, Cameroon (initially misidentified as *P. heterodermus*, O'Shea 2018: 211; Chippaux and Jackson 2019: 349) is *ca.* 250 km NNE of the type locality at Mapanja, Southwest Province, Cameroon, and we consider it to represent topotypic material. To improve data quality, new data (16S gene) from two samples of DRC *P. carinatus* and selected outgroup taxa included in Engelbrecht et al. (2019) were generated (Supplementary Table 1).

Genomic DNA was isolated from alcohol-preserved muscle tissue samples with the Qiagen DNeasy tissue kit (Qiagen Inc., Valencia, CA, USA). Polymerase chain reactions (PCRs) were carried out in 25 µL PCR reactions with an initial denaturation step of 95 °C for 2 minutes (min), followed by denaturation at 95 °C for 35 seconds (s), annealing at 50 °C for 35 s, and extension at 72 °C for 95 s with 4 s added to the extension per cycle for 34 cycles. Amplification products were visualised with a 1.5% agarose gel stained with SYBR Safe DNA gel stain (Invitrogen Corporation, Carlsbad, CA, USA). The PCR products were purified with AMPure magnetic bead solution (Beckman Coulter, Indianapolis, IN, USA) and sequenced with BigDye Terminator Cycle Sequencing Kits (Applied Biosystems, Foster City, CA, USA) on an ABI 3500 automated sequencer at the University of Texas at El Paso (UTEP) Genomic Analysis Core Facility.

Phylogenetic analyses and sequence divergence

We placed newly generated *Philothamnus carinatus sensu lato* DNA sequences ($n = 13$) into a phylogenetic framework with closely related species (*P. brunneus, P. hoplogaster, P. macrops, P. mayombensis* and *P. ruandae*), and outgroup taxa used by Engelbrecht et al. (2019), including *Dispholidus* sp., *Hapsidophrys lineata*, *H. smaragdina,* and *Thelotornis kirtlandii*. All analyses were conducted for a total of 38 individuals and five molecular markers (including GenBank data for $n = 25$). Sequences were aligned and trimmed, and alignments of protein-coding genes were confirmed for the absence of stop codons in MEGA v.10.2.6 (Kumar et al. 2018). The final concatenated alignment contained a total of 2975 bp: 16S, 410 bp ($n = 35$), cyt *b*, 606 bp ($n = 25$), ND4, 612 bp ($n = 27$), c-mos, 519 bp ($n = 31$), and RAG1, 828 bp ($n =$ 24). We executed two phylogenetic analyses with the concatenated dataset, including: a 378-bp fragment of the 16S gene with 32 ambiguously aligned nucleotides of the hypervariable region removed via Gblocks (Talavera and Castresana 2007), and the complete 410-bp fragment of the 16S gene, aligned manually with MEGA.

We inferred species trees by employing the concatenation approach in IQ-TREE v.2.2.0 (Minh et al. 2022) and topology support was obtained via the ultrafast bootstrap approximation (UFBoot2) with 1000 replicates (Hoang et al. 2018). This approximation outperforms similar approaches in that it is significantly faster, obtains less biased support values, and incorporates an ultrafast and automatic model selection for a provided partition scheme (Minh et al. 2013, 2020; Hoang et al. 2018). An edge-linked proportion partition model was applied to accommodate different evolutionary rates between loci while searching for the best-fit evolutionary models via ModelFinder within IQ-TREE (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Minh et al. 2020).

We implemented the single branch test in IQ-TREE for 1000 replicates. The latter uses nearest-neighbour-interchanges, computes the likelihood of alternative branching patterns, and ultimately compares the current topology with the best alternative by means of an approximate likelihood-ratio test (aLRT) with the Shimodaira-Hasegawa (SH)-like algorithm (Guindon et al. 2010). We considered species relationships to be strongly supported when node values were: UFBoot2 ≥ 95%, an unbiased support and not comparable to standard bootstrap ≥ 80 (Minh et al. 2013, 2020), and SH-aLRT ≥ 80% (Guindon et al. 2010; Minh et al. 2013, 2020). We also follow the verbiage of Chan et al. (2020), who described UFBoot2 values ≥ 89 as “relatively high” and values ≥ 83 as “moderate” support. Compared to bootstrapping, the SH-aLRT is a decisive statistical test; thus, support values are usually conservative (Guindon et al. 2010).

Net average 16S sequence divergence (*p*-distances) between currently recognised and putative *Philothamnus* species were calculated in MEGA. We used the bootstrap method with 1000 replicates with the pairwise-deletion option.

Morphological data

During opportunistic fieldwork in DRC from 2007–2015, three of us (EG, MMA, WMM) collected specimens that were photographed, sampled for genetic tissues, preserved in 10% buffered formalin, and transferred to 70% ethanol for long-term storage at the University of Texas at El Paso Biodiversity Collections (UTEP). We examined additional natural history specimens (Appendix 1) from collections listed by Sabaj (2020). Morphometric data from individual *Philothamnus carinatus* specimens of both sexes were also obtained from Perret and Mertens (1957), Knoepffler (1966), Villiers (1966), Pauwels et al. (2002a, b, 2016), Pauwels and David (2008), and Carlino and Pauwels (2015). Additional literature records were obtained from de Witte (1927, 1933, 1941, 1953), Loveridge (1936a, b, 1958), Bogert (1940), Laurent (1960), Skelton-Bourgeois (1961), Dunger (1973), Pitman (1974), Roux-Estève and de Witte (1975), Hughes (1985), Trape (1985), Hinkel (1993), Drewes and Vindum (1998), Akani and Luiselli (2002), Broadley (2002), Chippaux (2006), Pauwels et al. (2004, 2019a, 2020), Chirio and Ineich (2006), Chirio and LeBreton (2007), Jackson and Blackburn (2007), Wallach et al. (2014), Spawls et al. (2018), Chippaux and Jackson (2019), Ernst et al. (2020), Sánchez-Vialas et al. (2022), Badjedjea et al. (2023), and Pauwels and Colyn (2023). Coordinates for several localities listed by de Witte (1933) were found to be imprecise or in error and were updated using information from the Royal Museum for Central Africa (RMCA) collection manager (G. Cael, pers. comm.), Davis and Misonne (1964), and Google Maps (https://www.google.com/maps).

Morphological data from 147 examined specimens and 18 literature records (Figure 1) included 20 mensural and ten meristic characters, temporal formulae, and qualitative observations of colour pattern (based on colour photos in life when available). Snout–vent length (SVL) and tail length (TL) measurements were recorded to the nearest millimetre (mm) with a flexible ruler in the field prior to preservation (UTEP specimens collected by EG from DRC in 2009–2015) or in the laboratory after preservation (all other specimens). A subset of adult specimens (10 *P. carinatus* males, 13 *P. carinatus* females, 18 *P.* cf. *carinatus* males, 13 *P.* cf. *carinatus* females) examined by EG (to eliminate the effect of inter-observer bias) also included the following measurements: head length (HL; measured at angle of jaw, from posterior edge of mandible to tip of snout); head width (HW; measured at widest point of head); naso-ocular distance (NOD; taken at the anterior border of the orbit 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); internarial distance (IND); rostral scale height (RH; measured in a vertical line in the midpoint of the scale); 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); mouth gape (MG; measured from snout to posterior edge of last supralabial); loreal scale length (LL); and loreal scale width (LW).

To facilitate comparisons with historical and recent publications, ventral scale counts were made using the standard method (i.e., the first scale that is broader than long, VENTS) and the method of Dowling (1951) (VENTD), and other scale counts included subcaudals (SCDL), dorsal scale rows one head length posterior to jaw rictus (DSRN), dorsal scale rows at midbody (DSRM), dorsal scale rows one head length anterior to vent (DSRV), supralabials (SUPRA), infralabials (INFRA), preoculars (PREOC), and postoculars (POSTOC). Scale counts were taken on the right side of the body unless it was damaged. In the following descriptions of morphological data, a slash (/) represents characters from the right and left sides of the body. Analyses of mensural data were limited to adult specimens with a snout–vent length (SVL) of 300 mm and larger. Statistical comparisons were made with the student's *t*-test; each variable was checked for normality using the Shapiro-Wilk test in R v. 4.03 (R Core Team, 2021). If any variables violated normality, the data were either normalised through transformations or a Wilcoxon test was used in place of a *t*-test. To eliminate the effect of size, we conducted an analysis of covariance (ANCOVA) with snout–vent length as the covariate (Packard and Boardman 1999) on specimens examined by EG in the program Minitab (State College, PA, USA).

RESULTS

Phylogenetic analyses and sequence divergence

Results from ModelFinder, according to the BIC criterion, designated the best models per gene partition as follows: HKY + F + R2 (16S), TPM3u + F + G4 (cyt *b*), HKY + F + G4 (ND4), HKY + F (c-mos and RAG1). In our preferred tree (with hypervariable regions of 16S removed, Figure 2), *Philothamnus hoplogaster* and *P. macrops* were recovered as sister taxa in a weakly supported (70 UFBoot2/44 SH-aLRT) clade, which was strongly supported

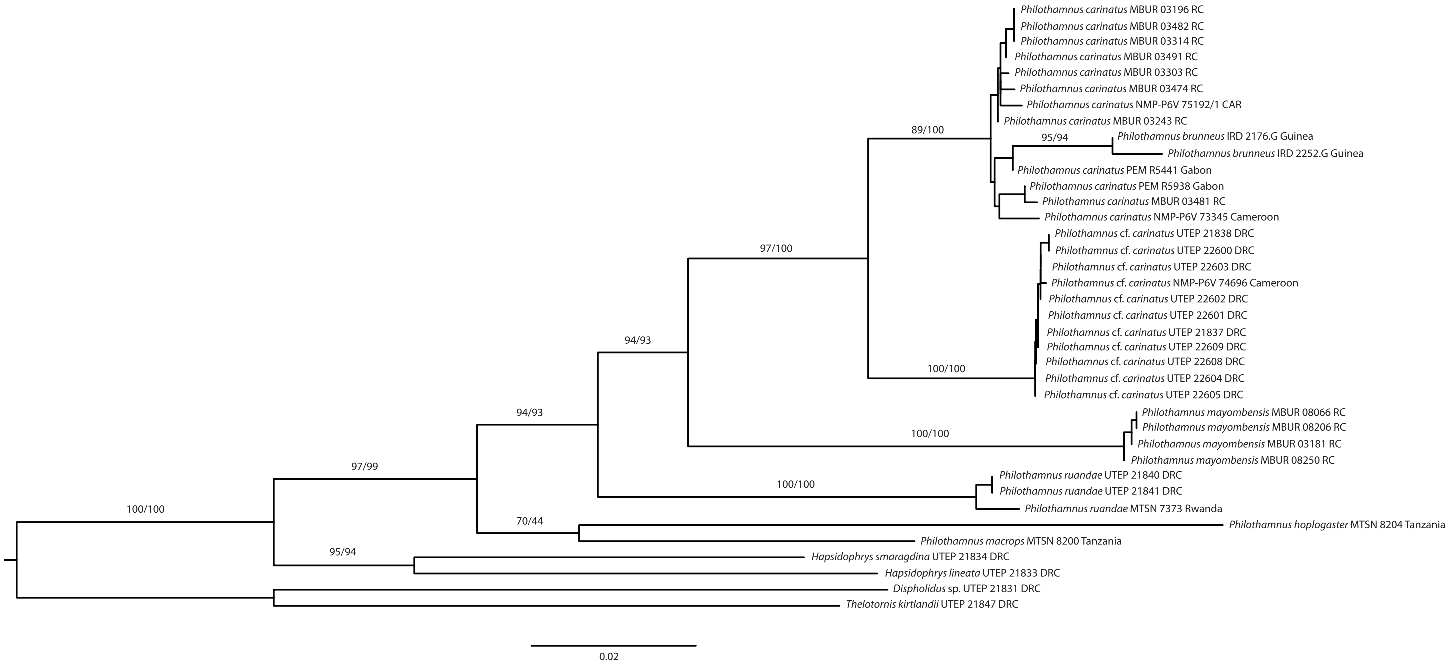

Figure 2. Maximum-likelihood IQ-TREE phylogeny from the concatenated dataset, including 16S (hypervariable regions removed), cyt *b*, ND4, c-mos, and RAG1. Branch support values are listed as ultrafast bootstrap support values/values from the likelihood-ratio test (aLRT) with the Shimodaira-Hasegawa (SH)-like algorithm.

as the sister group to all other analysed *Philothamnus*. This tree contained several well-supported clades, including *Philothamnus* + *Hapsidophrys*, *Hapsidophrys*, *Philothamnus*, *P. ruandae*, *P. mayombensis*, *P. brunneus*, and a strongly supported clade including *P. carinatus* (*sensu lato*) + *P. brunneus*. The latter clade included two subclades: (1) a clade with relatively high support (89 UFBoot2/100 SH-aLRT) including *P. carinatus sensu stricto* from Cameroon, CAR, Gabon, and Republic of the Congo + *P. brunneus* from Guinea; and (2) a strongly supported clade including *P.* cf. *carinatus* from DRC and a single sample (NMP-P6V 74696) from south-eastern Cameroon. Our analysis with the entire 16S gene (Supplementary Figure 1) was similar to our preferred tree, except a well-supported clade of *P. brunneus* was recovered as sister to *P.* cf. *carinatus* (DRC and one sample from south-eastern Cameroon [NMP-P6V 74696]) with only moderate support (83 UFBoot2/77 SH-aLRT).

Uncorrected p-distances for the 16S gene between *P. brunneus* and *P. carinatus sensu stricto* (Cameroon, CAR, Gabon, and Republic of the Congo) were moderate (average = 2.69 ± 0.78 standard deviation; range 2.0–3.9%), and similar distances were found between *P. brunneus* and *P.* cf. *carinatus* (one sample from Cameroon [NMP-P6V 74696] and all individuals from DRC; average = 2.70 ± 0.82 standard deviation; range 2.2–3.2%). Distances between *P. carinatus sensu stricto* and *P.* cf. *carinatus* were slightly less (average = 2.28 ± 0.72 standard deviation; range 2.0–3.2%). Five major differences in amino acid translation were noted in cyt *b* data from our *P. carinatus sensu stricto* populations and *P.* cf. *carinatus* populations including: position 255 (threonine in *P. carinatus* vs. isoleucine in *P.* cf. *carinatus*), position 453 (alanine in *P. carinatus* vs. threonine in *P.* cf. *carinatus*), position 495 (threonine in *P. carinatus* vs. alanine in *P.* cf. *carinatus*), position 579 (phenylalanine in *P. carinatus* vs. leucine in *P.* cf. *carinatus*), and position 594 (leucine in *P. carinatus* vs. methionine in *P.* cf. *carinatus*). Position 597 of the ND4 gene translated to isoleucine in *P. carinatus*, whereas it translated to leucine in *P.* cf. *carinatus*.

Morphological analyses

Based on well-supported clades in our preferred phylogenetic tree (Figure 2), statistical comparisons were made between *Philothamnus carinatus sensu stricto* (Cameroon, CAR, Gabon, and Republic of the Congo) with *P.* cf. *carinatus* (Angola and DRC east of the Congo/Ubangi River). Results of our morphological analyses are shown in Table 2. *Philothamnus carinatus* had significantly longer TL than *P.* cf. *carinatus* in both males ($P = 0.047$) and females ($P = 0.034$); *P. carinatus* also had significantly more subcaudals than *P.* cf. *carinatus* in males ($P = 0.028$) and females ($P = 0.012$). Our ANCOVA analyses detected significant differences between *P. carinatus* and *P.* cf. *carinatus* for RH in males ($P = 0.010$), RW in males ($P = 0.019$), and MG in females ($P = 0.035$).

Based on the significant differences and molecular results discussed above (Figure 2), and species delimitation analyses by Engelbrecht et al. (2019), we consider populations from the Cabinda Enclave of Angola, Cameroon (with the exception of genetic sample NMP-P6V 74696), CAR, Equatorial Guinea (including Bioko Island), Gabon, Republic of the Congo, and extreme western DRC north of the Congo River as *P. carinatus sensu stricto*. Populations from Angola (excluding the Cabinda Enclave), Burundi, DRC east and south of the Congo/Ubangi Rivers, Kenya, Rwanda, Tanzania, and Uganda are recognised as a new species below.

Table 2. Morphometric data (in mm for adults > 300 mm SVL) and meristic scale counts (adults and juveniles) for both sexes of *Philothamnus carinatus sensu stricto* from Cameroon, Central African Republic, Gabon, Republic of the Congo, and extreme western Democratic Republic of the Congo, and *P.* cf. *carinatus* from Angola, Burundi, and Democratic Republic of the Congo. Sample sizes for all measurements except SVL and TL are shown in boldface. Data are shown as mean ± standard deviation with range in parentheses.

Character	*Philothamnus carinatus* Males (*n* = 24 [**10**])	*Philothamnus* cf. *carinatus* Males (*n* = 66 [**18**])	*Philothamnus carinatus* Females (*n* = 24 [**13**])	*Philothamnus* cf. *carinatus* Females (*n* = 51 [**13**])
SVL	446.4 ± 79.1 (384–700)	439.0 ± 57.6 (312–548)	479.7 ± 70.1 (365–592)	444.8 ± 59.1 (316–570)
TL	172.6 ± 15.1 (151–210)	162.0 ± 22.3 (114–208)	165.5 ± 22.1 (137–205)	149.5 ± 20.1 (113–190)
TL/SVL	0.4 ± 0.03 (0.3–0.5)	0.4 ± 0.02 (0.3–0.5)	0.4 ± 0.02 (0.3–0.4)	0.3 ± 0.02 (0.3–0.4)
HL	14.2 ± 0.50 (13.7–15.1)	14.4 ± 0.83 (12.9–16.1)	15.4 ± 1.42 (13.3–17.2)	14.2 ± 1.20 (11.9–16.2)
HW	8.4 ± 0.70 (7.3–9.8)	8.8 ± 0.91 (7.3–10.8)	9.4 ± 1.55 (7.6–12.2)	8.5 ± 1.01 (7.1–10.2)
NOD	3.3 ± 0.21 (3.0–3.6)	3.2 ± 0.20 (2.8–3.5)	3.6 ± 0.38 (3.0–4.3)	3.2 ± 0.35 (2.6–3.8)
ES	5.3 ± 0.38 (4.5–5.8)	5.2 ± 0.41 (4.4–5.9)	5.6 ± 0.61 (4.7–6.4)	5.0 ± 0.63 (3.6–6.0)
ID	8.5 ± 0.76 (7.0–9.2)	8.6 ± 0.55 (7.8–9.8)	9.1 ± 1.10 (7.1–10.6)	8.5 ± 0.73 (7.5–9.6)
EW	4.3 ± 0.35 (3.9–5.1)	4.4 ± 0.24 (4.0–4.9)	4.5 ± 0.36 (3.9–5.1)	4.2 ± 0.38 (3.7–4.9)
IND	3.7 ± 0.33 (3.3–4.3)	3.7 ± 0.25 (3.2–4.1)	4.0 ± 0.52 (2.9–4.7)	3.6 ± 0.38 (3.1–4.2)
RH	1.9 ± 0.16 (1.6–2.2)	2.1 ± 0.32 (1.7–2.9)	2.2 ± 0.38 (1.8–3.0)	2.1 ± 0.27 (1.7–2.5)
RW	3.4 ± 0.26 (2.9–3.8)	3.5 ± 0.24 (3.2–4.0)	3.7 ± 0.40 (3.1–4.2)	3.4 ± 0.37 (2.8–4.0)
FL	4.7 ± 0.20 (4.5–5.2)	4.7 ± 0.32 (4.3–5.4)	4.9 ± 0.43 (4.4–5.7)	4.7 ± 0.38 (4.1–5.2)
FW	3.9 ± 0.21 (3.6–4.2)	3.8 ± 0.34 (3.1–4.4)	3.9 ± 0.31 (3.4–4.2)	3.6 ± 0.25 (3.0–4.0)
CSL	4.7 ± 0.39 (4.2–5.4)	4.7 ± 0.45 (3.8–5.9)	4.9 ± 0.65 (4.1–5.9)	4.7 ± 0.58 (3.5–5.5)
CSW	2.03 ± 0.15 (1.9–2.3)	2.02 ± 0.15 (1.7–2.3)	2.08 ± 0.24 (1.7–2.5)	1.95 ± 0.25 (1.5–2.3)
PFL	2.4 ± 0.24 (2.1–2.8)	2.3 ± 0.14 (2.1–2.6)	2.5 ± 0.28 (2.0–2.9)	2.3 ± 0.25 (1.9–2.7)
PFW	2.5 ± 0.24 (2.3–3.0)	2.6 ± 0.16 (2.3–2.9)	2.8 ± 0.46 (2.2–3.5)	2.4 ± 0.24 (2.1–2.8)
MG	15.5 ± 0.80 (14.2–16.9)	15.4 ± 1.04 (13.6–17.3)	16.2 ± 1.57 (14.0–18.6)	15.5 ± 1.35 (12.9–17.1)
LL	2.1 ± 0.17 (1.8–2.3)	2.1 ± 0.21 (1.8–2.6)	2.2 ± 0.24 (1.8–2.6)	2.2 ± 0.24 (1.8–2.7)
LW	1.2 ± 0.27 (1.0–1.9)	1.2 ± 0.12 (0.9–1.4)	1.2 ± 0.17 (0.9–1.5)	1.2 ± 0.14 (0.9–1.4)
VENTS	150.3 ± 3.7 (144–155)	149.6 ± 3.6 (142–154)	157.6 ± 4.2 (150–162)	156.3 ± 5.5 (148–167)
VENTD	147.7 ± 4.0 (140–154)	148.1 ± 3.5 (139–155)	156.3 ± 3.6 (149–163)	155.8 ± 4.6 (146–166)
SCDL	87.2 ± 4.3 (79–96)	85.0 ± 3.4 (78–93)	82.0 ± 4.8 (73–92)	78.8 ± 3.7 (71–87)
DSRN	13	13	13	13
DSRM	13	12.9 ± 0.4 (11–13)	13	13
DSRV	10.9 ± 0.5 (9–11)	11	11.1 ± 0.4 (11–13)	11
SUPRA	9	9.0 ± 0.2 (8–10)	9.1 ± 0.3 (9–10)	9.0 ± 0.3 (8–10)
INFRA	9.7 ± 0.7 (8–11)	9.7 ± 0.6 (8–12)	9.8 ± 0.6 (8–11)	9.7 ± 0.6 (7–11)
PREOC	1	1	1.1 ± 0.2 (1–2)	1.0 ± 0.1 (1–2)
POSTOC	2.2 ± 0.4 (2–4)	2.1 ± 0.3 (2–4)	2	2.0 ± 0.3 (1–3)

Squamata: Serpentes: Colubridae: Colubrinae

Philothamnus chifunderai sp. nov. Chifundera's Green Snake (Figures 3–4, Table 2).

Synonyms: *Chlorophis carinatus* (Boulenger 1915 [part], 1919a, b [part]; Schmidt 1923 [part]; de Witte 1933, 1941; Loveridge 1936a, b[part], 1942; Bogert 1940 [part])

Philothamnus heterodermus carinatus (Loveridge 1951 [part], 1958 [part]; de Witte 1953, 1962; Capocaccia 1961 [part]; Pitman 1974 [part])

Chlorophis heterodermus carinatus (Thys van den Audenaerde 1965, 1966)

Philothamnus carinatus (Hughes 1985 [part]; Broadley and Cotterill 2004; Wallach et al. 2014 [part]; Marques et al. 2018; Spawls et al. 2018 [part]; Chippaux and Jackson 2019 [part])

Holotype: UTEP 22601 (field no. ELI 2209), an adult male from Npenda village, east of Lake Tumba, Équateur Province, DRC (−00.7465, 18.2243, 311 m asl). Collected by Batwa forest people and brought to Eli Greenbaum, Chifundera Kusamba, Wandege M. Muninga, and Mwenebatu M. Aristote on 8 July 2013.

Paratopotypes: UTEP 22602 (field no. ELI 2210), an adult male; UTEP 22603 (ELI 2211), an adult female; both collected with the holotype.

Paratypes: RBINS 2729 (formerly under RBINS 10068), an adult male, and RBINS 2730 (formerly under RBINS 10254), an adult female, from Bolongo (Lisala), Mongala Province, DRC (02.1500, 21.5000). Collected by Schoonbroodt between 1 November and 8 December 1950. RMCA 16546, an adult female, from Bokoro, Mai-Ndombe Province, DRC (−02.8327, 18.3829). Collected by E. Jans in 1952.

Diagnosis: *Philothamnus chifunderai* can be distinguished from most congeners by the presence of 13 scale rows at midbody, an undivided anal scale, and a greenish, tan, or greyish dorsum in life with dark brown or black crossbars (rarely lacking crossbars). *Philothamnus chifunderai* differs from *P. carinatus* by having a significantly smaller TL and significantly fewer SCDL in both sexes, moderate 16S mitochondrial sequence divergence (2.0–3.2%), and six amino acid differences in the studied cyt *b* and ND4 fragments. *Philothamnus chifunderai* differs from *P. brunneus* by having a greenish, tan, or greyish dorsum in life with dark brown or black crossbars (vs. brownish dorsum always without crossbars in *P. brunneus*), moderate mitochondrial sequence divergence in the 16S gene (2.2–3.2%), and allopatric distribution in Central and East Africa (vs. West Africa in *P. brunneus*).

Description of holotype: Adult male, with a slender body (460 mm SVL), and long tail (167 mm TL), 36.3% of SVL; head long (14.4 mm HL) and narrow (9.22 mm HW), distinct from the neck, 3.1% of SVL; interocular distance 9.0 mm, pupil large and round, eye width 4.5 mm; loreal rectangular, twice as long (2.6 mm) as high (1.3 mm). Supralabials 9/9, 4th–6th/4th–6th contacting orbit; infralabials 9/10, 1st on each side in contact behind mental, 1st–5th/1st–5th contacting anterior chin shields; 1 preocular; 2 postoculars; temporals 2 + 2 + 2/2 + 2 + 2; two internasals; nasal divided; two prefrontals; frontal longer (5.0 mm) than wide (4.1 mm); dorsal scales 13 one head-length posterior to jaw rictus, 13 at midbody, 11 one head length anterior to vent, smooth without apical pits; VENTS 153, VENTD 152; anal plate entire; paired subcaudals 84.

Colouration of holotype in life: Dorsum of head, neck, body and tail glossy olive-grey with a series of dark brown crossbars, extending onto lateral margins of ventrals and entire ventral surface of tail. Mid-ventral and throat colouration creamy yellow. Iris orangish brown (Figure 3).

Figure 3. Photos of *Philothamnus chifunderai* sp. nov. a) adult male holotype (UTEP 22601) from Democratic Republic of the Congo (DRC), Équateur Province: Npenda village, in dorsal and b) ventral view, c) adult female (UTEP 21838) from DRC, Ituri Province, near Epulu, d) juvenile (UTEP 22608) from DRC, Tanganyika Province, road ca. 50 km W of Moba, e) adult female (UTEP 22604) from DRC, Mai-Ndombe Province, Nkala, f) adult female (UTEP 22603) from DRC, Équateur Province: Npenda village.

Variation: Mensural and meristic variation of the new species is shown in Table 2. Thys van den Audenaerde (1965) noted specimens from Kinshasa sometimes had 11 scale rows at midbody, and erroneously described the anal plate as divided (rarely entire). Colouration of our specimens ranged from a uniform olive green or brown to dark grey. Some individuals were patternless or had thin black bands along the length of the body. These bands were sometimes thicker in the anterior region of the dorsum, and more irregular or transitioning to speckles around midbody. Tails of banded specimens were often speckled or patternless, even in otherwise uniformly banded individuals. Interscalar skin was white or light blue. The head was either white or pale yellow along the middle supralabials and the pre- and postoculars, but otherwise matched the dorsal body colouration. Ventral colouration transitioned gradually from white or yellow at

Figure 4. Photos of the preserved holotype of *Philothamnus chifunderai* sp. nov. (UTEP 22601) in a) dorsal and b) ventral views, c) dorsal view of head, d) ventral view of head, e) left lateral view of head, f) right lateral view of head.

the head to pale olive green or grey around midbody, which then continued unchanged to the tail tip. Loveridge (1936b: 244) described the colouration of an individual from Sipi, Uganda as “dark olive with 104 deep-black, irregular crossbands between head and anus, represented on the tail by black flecks. The centre of the eye is black surrounded by a light area, then by a fine orange line, then by an olivaceous area flecked with black; outer-most ring, black”. Loveridge (1942: 270) described the dorsum of an adult male from Idjwi Island, Lake Kivu, DRC as dark olive, with “the vertebral series of scales edged baso-laterally with very pale blue, the outer scales on the outer baso-lateral side only also pale blue” with a white chin, yellowish throat, and pale green venter. Loveridge (1958: 61) described the dorsum of the species as “green or olive; young with more or less distinct dark crossbars that tend to disappear with age; vertebral scales baso-laterally edged with pale blue". The venter was described as yellowish green to pale green, with a white chin and yellowish throat. Pitman (1974) noted the dorsal colour ranges from green, dark green and olive to dark olive. Spawls et al. (2018: 487) noted this species often has a "bronze or yellow sheen", and the colour ranges from green, blue-green, olive-green, to blue (sometimes black), with blue or turquoise edges to scales between "darker" crossbars.

Hemipenis: Bogert (1940: 51) described the hemipenis based on specimens from west-central and north-eastern DRC as follows: not bifurcate, sulcus undivided, extending to sixth subcaudal. Well-developed basal spines, "merging distally into reticulate calyces", becoming flattened papillae.

Etymology: The specific epithet is a patronym for Dr Zacharie Kusamba Chifundera (who publishes under the name Chifundera Kusamba) of the Centre de Recherche en Sciences Naturelles, Lwiro and National Pedagogical University, Kinshasa, DRC. Known to his friends and colleagues as Chif, Chifundera, or Zacharie, we are inspired by Chifundera's lifelong passion for snakes and other herpetofauna of his native Democratic Republic of the Congo. The senior author owes his entire career in the country to the ongoing collaboration he established with Chifundera in 2007, and it is an honour to name a new species of snake for him.

Distribution: The species is known from the area south and east of the western Congo/Ubangi rivers in Angola, Burundi, DRC, Kenya, Rwanda, Tanzania, and Uganda (Spawls et al. 2018). A single individual (NMP-P6V 74696), possibly a hybrid, was detected from south-eastern Cameroon in genetic analyses (Figure 1).

Habitat: Most specimens were collected from localities in or near lowland rainforest, but one individual (UTEP 22608) was found crossing a road in savannah/woodland mosaic in south-eastern DRC. Schmidt (1923) noted an individual who fell from the thatch of a structure in a village onto a collector's table. Spawls et al. (2018: 487) included "forest islands" and "well-wooded savanna" in the habitat.

Natural history: Pitman (1974) noted the diet is mostly frogs, parasites include mites, and *Thelotornis kirtlandii* is known to eat this species. Spawls et al. (2018: 488) noted the species is "presumably diurnal", common in forest clearings, lays eggs, and inflates the body when threatened. Malonza and Bwong (2023) remarked that, in Kenya, the species is arboreal and it feeds on frogs and lizards.

Conservation: Given the large distribution of *P. chifunderai* in and near forests of the Congo Basin, including anthropogenically disturbed habitats, the species does not seem to be a strict forest specialist. Its large distribution and tolerance of deforested environments do not suggest it should be assessed as a threatened species at this time.

Squamata: Serpentes: Colubridae: Colubrinae

Philothamnus carinatus (Andersson, 1901) Thirteen-scaled Green Snake (Figures 5–7, Table 2). Synonyms: *Chlorophis carinatus* (Andersson 1901; Sternfeld 1908, 1909, 1917; Müller 1910; Boulenger 1915 [part], 1919a, b [part]; Schmidt 1923 [part], Bogert 1940 [part]; Mertens 1941)

Philothamnus nigrofasciatus (Buchholz and Peters in Peters 1875) *nomen rejiciendum*
Chlorophis heterodermus (Mocquard 1897; Boulenger 1906)
Chlorophis heterodermus carinatus (Perret and Mertens 1957; Mertens 1964)

Figure 5. Photos of *Philothamnus carinatus*. a) adult from Republic of the Congo, Lékoumou Department, Kissiki, b) juvenile from Republic of the Congo, Likouala Department, Nouabale-Ndoki National Park, c) adult from south-western Gabon, d) adult from south-western Gabon, e) adult from south-western Gabon, f) melanistic adult (ZFMK 94680) from Gabon, Ogooué-Ivindo Province, Ivindo National Park, near Ipassa research station.

Philothamnus heterodermus carinatus (Loveridge 1951 [part], 1958 [part]; Capocaccia 1961 [part]; Knoepffler 1966; Pitman 1974 [part])

Philothamnus heterodermus (Dunger 1973; Stucki-Stirn 1979)

Philothamnus carinatus was originally described by Andersson (1901) as *Chlorophis carinatus*, based on five specimens — four from "Mapanja, Cameroon" [04.116667, 9.116667, 765 m asl; coordinates from NRM, collected by Knutson and Valdau in 1885, and one from "Cameroon", collected by Knöppel in 1886 (Figure 6). Decades earlier, Buchholz and Peters (in Peters 1875) had named *Philothamnus nigrofasciatus* based on a single adult female (Figure 7) with a divided anal scale from "Cameruns" (= Douala, Cameroon; Frétey et al. 2014), and it was considered to be a synonym of *Philothamnus semivariegatus nitidus* by Loveridge (1958). Hughes (1977) examined the type of *P. nigrofasciatus*, noticed it had an entire anal scale, and realised it was consistent with *P. carinatus*. Douala (type locality of *P. nigrofasciatus*) is only about 60 km E of Mapanja (type locality of *P. carinatus*). Because the latter name had been used extensively whereas the former had not, Hughes (1977) proposed that *Chlorophis carinatus* should be granted nomenclatural

Figure 6. Photos of adult male lectotype (NRM 1973) of *Chlorophis carinatus* Andersson, 1901 in a) dorsal and b) ventral views, c) dorsal view of head, d) ventral view of head, e) left lateral view of head, f) right lateral view of head.

precedence over *Philothamnus nigrofasciatus*. This request was subsequently approved (International Commission on Zoological Nomenclature 1982). Wallach et al. (2014) included "*Herpetaethiops bellii* A.C.L.G. Günther, 1866 (*nomen oblitum*)" as a synonym of *P. carinatus*, but this action was reversed by Boundy (2020) as "in error" because the name had been a synonym of *P. heterodermus*. Now Günther's taxon is treated as a valid species, *Philothamnus bellii* (Günther, 1866), from Guinea, Sierra Leone and Liberia, West Africa (Trape and Baldé 2014; Boundy 2020; Trape et al. 2021).

Given the ambiguous locality of "Cameroon" for the syntype of *P. carinatus* (NRM 1972) collected by Knöppel in 1886, we take this opportunity to select a lectotype from the four syntypes collected by Knutson and Valdau in 1885 at Mapanja. We designate NRM 1973 (Figure 6), a subadult male (432 mm SVL), as the lectotype.

Figure 7. Photos of adult female holotype (ZMB 8320) of *Philothamnus nigrofasciatus* Buchholz and Peters, 1875 in a) dorsal and b) ventral views, c) dorsal view of head, d) ventral view of head, e) left lateral view of head, f) right lateral view of head.

Diagnosis: *Philothamnus carinatus* can be distinguished from most congeners by the presence of 13 scale rows at midbody, an undivided anal scale, and a greenish, bluish, brownish, or greyish dorsum in life, usually with dark brown or black crossbars, at least in the anterior part of the body. *Philothamnus carinatus* differs from *P. chifunderai* by having a significantly larger TL and significantly more SCDL in both sexes, moderate 16S mitochondrial sequence divergence (2.0–3.2%), and six amino acid differences in the cyt *b* and ND4 genes. *Philothamnus carinatus* differs from *P. brunneus* by having a greenish, bluish, brownish, or greyish dorsum in life, usually with dark brown or black crossbars, at least in the anterior part of the body (vs. brownish dorsum always without crossbars in *P. brunneus*), a smaller average number of ventrals (according to Trape et al. 2021), and moderate mitochondrial sequence divergence in the 16S gene (2.2–3.2%).

Variation: Morphological variation of *P. carinatus* is shown in Table 2. In the original description, Andersson (1901) observed that the dorsum was olive or green with "dark cross bars which disappear more or less with age". Sternfeld (1909) described Cameroonian snakes as olive green with black transverse bands. Müller (1910) described a juvenile from Cameroon as olive-brown with dark transverse bands, which were particularly prominent on the first half of the body. He also noted that an adult from Cameroon was dull bronze green with no markings. Sternfeld (1917) described an individual from Cameroon as dark olive green with black transverse spots and transverse bands, especially on the anterior portion of the body. Stucki-Stirn (1979: 295) described the colouration of individuals from Cameroon as "greenish-brown or blueish green with darker transverse bands", but some individuals lacked the bands altogether. He described the ventrals as "lighter green with yellowish shades". Chirio and LeBreton (2007) described the colouration of Cameroonian snakes as highly variable, with an olive green, bluish or grey dorsum, with or without dark transverse bands, and a light green or yellow venter. Jackson and Blackburn (2007) noted adult specimens from Republic of the Congo are green, but juveniles are brown (Figure 5b). Pauwels and Vande weghe (2008) described specimens from Gabon as grey, generally with dark transverse bands, at least in the anterior portion of the body. Trape (2023) noted that *P. carinatus sensu lato* has "un petit trait clair" (a small light line) on anterior dorsal scales. Our photos of specimens from Gabon include individuals that are tan (Figure 5c) or brown with yellowish flecks (Figure 5e), and one melanistic individual had canary-yellow supralabials (Figure 5f).

Distribution: The species is known from the area west of the Congo/Ubangi rivers in Cameroon, Central African Republic, Equatorial Guinea (including Bioko Island), Gabon, Republic of the Congo, and Nigeria (Dunger 1973; Chirio and Ineich 2006; Chirio and LeBreton 2007; Pauwels and Vande weghe 2008; Trape et al. 2021; Sánchez-Vialas et al. 2022). Based on the presence of dark brown or black crossbars and 13 scale rows at midbody, it is likely that some of the specimens of *P. heterodermus* (13–15 [usually 15] scale rows at midbody, usually patternless, Chippaux and Jackson 2019) mentioned by Dunger (1973) are *P. carinatus*. At least some of the Nigerian records of the former species by Blackwell (1967) and Butler and Reid (1986, 1990) might refer to *P. carinatus* as well, but no morphological details of the specimens were provided. As suggested by Trape et al. (2021), published records between Ghana and Nigeria (e.g., Togo, Segniagbeto et al. 2011) require additional scrutiny to determine whether they are attributable to *P. carinatus* or *P. brunneus*. However, Trape (2023) included Ghana and Togo in the distribution of the latter species, and his distribution map for *P. carinatus* illustrated a locality from south-western Nigeria that is consistent with Chippaux and Jackson (2019: figure 13.65). We tentatively assign a literature record from south-eastern Central African Republic (Figure 1) to *P. carinatus* because of its position on the right bank of the Mbomou River, the more northerly of the two main tributaries that form the Ubangi River downstream.

Habitat: Perret (1961) listed the species from southern forest in Cameroon. In Cameroon, Chirio and LeBreton (2007) noted the species is semi-arboreal in dense forests and gallery forests, but it is frequently encountered on the ground. Jackson and Blackburn (2007) encountered juveniles in the leaf litter of forests in Republic of the Congo. In Gabon, Pauwels and Vande weghe (2008) noted the species frequents grassy clearings at the edge of forest, and watercourses in gardens and plantations near forest. Because of its diurnal habits in open areas, it is one of the most frequently encountered species of snake in the country. Pauwels and David (2008) reported the encounter of an individual crossing a road in secondary forest during the day. Pauwels et al. (2019) photographed an individual at the entrance to Pahon Cave in Gabon. VG found the topotypic individual from Bamo near a river in forest (near the maximum altitudinal limit of Cameroonian lowland forests at almost 900 m asl) surrounded by agricultural submontane savannah in a hilly landscape during the day.

Natural history: Sternfeld (1917) noted an individual from Cameroon with several small frogs in its stomach. Stucki-Stirn (1979) remarked that the species eats amphibians and lizards in Cameroon. Akani and Luiselli (2002) noted that *Philothamnus carinatus* lays its eggs in the dry season in Nigeria, and they provided additional observations about reproductive biology and growth. In Gabon, Pauwels et al. (2002a) and Pauwels and Vande weghe (2008) noted the species feeds on frogs. A female captured in November contained two eggs. The latter authors observed a case of predation by the Congo serpent eagle *Dryotriorchis spectabilis* (Accipitridae) at Mouila, Gabon. Pauwels et al. (2016) dissected a female from Ivindo National Park in Gabon and found four eggs (length 18–20 mm, width approximately 6 mm).

Conservation: Given the large distribution of *P. carinatus* in and near forests of eastern West Africa and western Central Africa, including anthropogenically disturbed habitats, the species does not seem to be a strict forest specialist. Its large distribution and tolerance of deforested environments do not suggest it should be assessed as a threatened species at this time.

DISCUSSION

The identification of cryptic lineages within a geographically widespread species of colubrid snake (*Philothamnus carinatus*) in sub-Saharan Africa is consistent with several recent studies of colubriform snakes that utilised datasets ranging from fragments of the 16S gene (e.g., Hallermann et al. 2020) and multi-gene Sanger datasets (e.g., Engelbrecht et al. 2020) to thousands of loci generated from the ddRAD method (Allen et al. 2021). Because the only genetic data currently available for *Philothamnus brunneus* is a fragment of the 16S gene, our preferred phylogenetic tree (with hypervariable regions removed to avoid an ambiguous alignment, Figure 2), recovered this taxon in a clade with relatively high support (89 UFBoot2/100 SH-aLRT) with *P. carinatus sensu stricto*. However, given the limitations of the available data, we cannot eliminate the less-likely possibility that *P. brunneus* is sister to *P. chifunderai* (83 UFBoot2/77 SH-aLRT, Supplementary Figure 1); additional genes should be sequenced from the former taxon to confirm its taxonomic validity from *P. carinatus* and resolve its phylogenetic relationships in future studies.

Compared to our findings, Trape et al. (2021) used a different method to align the 16S data in their study (CLUSTAL W in the program BioEdit v 7.2.5) and they reported substantially higher sequence divergence values between *P. brunneus* and populations of *P. carinatus*. The Maximum Likelihood tree in the latter study was constructed with the program Topali 2.5, and the currently recognised taxa *P. brunneus*, *P. carinatus*, and *P. chifunderai* were effectively recovered as a polytomy in a weakly supported clade. These conflicting results highlight the limitations of systematics studies that are based only on relatively short fragments of the 16S gene, and they support the contention that such studies, at least in some cases with hypervariable regions, might be erratic and should be interpreted with caution (Chan et al. 2022).

The description of *Philothamnus chifunderai* resolves the unnamed, cryptic lineage of *P. carinatus* first identified from the phylogenetic tree and species delimitation analyses of Engelbrecht et al. (2019), which included the same suite of genes (16S, cyt *b*, ND4, c-mos, and RAG1) as our study. The 16S sequence divergence differences we noted between the parapatric species *P. chifunderai* and *P. carinatus* were moderate and comparable to Engelbrecht et al. (2019). The differences in amino acid translation of the mitochondrial protein-coding genes between these taxa, considered together with our statistically significant morphological differences, strongly support their recognition as distinct species. The 16S sequence divergence between these taxa was comparable to the differences we recovered between *P. chifunderai* and *P. brunneus*, which are also distinguished by their dorsal colouration. Although the eastern extent of the distribution of the latter taxon requires additional sampling to resolve, it does not seem to occur in most areas of Nigeria (J-F Trape, pers. comm.; Dunger 1973; Trape 2023), and we hypothesise that the Niger Delta is the easternmost possible biogeographic barrier that separates it from *P. carinatus* (see similar example of *Toxicodryas* in Greenbaum et al. 2021). The allopatric species *P. brunneus* and *P. chifunderai* are thus separated by a distance of at least 1 000 km.

The western Congo and Ubangi rivers have been proposed as biogeographic barriers to Central African populations of snakes, mammals, and plants, but there are few recent herpetological collections near the eastern side of the Ubangi to test the strength of the barrier (Greenbaum et al. 2021 and citations therein). The recovery of a sample (NMP-P6V 74696) from Mambele, south-eastern Cameroon within the strongly supported clade of DRC *P. chifunderai* is intriguing. Because we have encountered *Philothamnus* in riverside vegetation and other habitats near large bodies of water (EG, OSGP and VG, pers. obs.), it is reasonable to assume that some species are good swimmers that could cross large rivers, especially at times of the year when water levels are lower, and in areas where islets could serve as stepping stones. We hypothesise that the Ubangi River serves as a filter more than a barrier, and the Mambele sample is likely a hybrid or result of past introgression, but more data and sampling are needed to test this hypothesis.

Results from unpublished studies suggest the Ubangi River could represent a hybrid zone region for vertebrate taxa that cross the river relatively rarely. A population genetics study (ddRAD data) of the forest viperid *Bitis nasicornis* identified a hybrid individual (linking monophyletic clades on opposite sides of the Congo/Ubangi Rivers) between the Ubangi and Sangha Rivers in northern Republic of the Congo (ERV and EG, unpubl. data). A similar study (ddRAD data) of the forest-endemic frog *Phrynobatrachus auritus* recovered a hybrid population in north-western DRC, suggesting gene flow across the Ubangi River from south-eastern Cameroon (VG, unpubl. data). Future collecting efforts should focus on north-western DRC to obtain additional genetic samples that will facilitate more fine-scale studies of gene flow across the Ubangi River.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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APPENDIX 1

Additional material examined for morphological analyses. Collection acronyms follow Sabaj (2020). Localities of male and female specimens with detailed morphological data from the literature (included in morphological analyses) are also shown below with their citations. Specimens lacking detailed locality information are not mapped and are shown with an asterisk.

Philothamnus carinatus: **CAMEROON:** NRM 1972*. Littoral Region: Mt. Nlonako: USNM 570849. "Kameruns" (= Douala): ZMB 8320. South Region: Olounou: RMCA 73-16-R-172–73. Sangmelima (Perret and Mertens 1957). Kribi: CM S4135. Southwest Region: Mapanja: NRM 1973–76. **CENTRAL AFRICAN REPUBLIC:** Lobaye Prefecture: Ngotto: MNHN 1997.3401. Ibengue: MNHN 1997.3402. Ombella-M'Poko Prefecture: Zimba: MNHN 1994.029, 1997.3403–05. **DEMOCRATIC REPUBLIC OF THE CONGO:** Kongo Central Province: Vaku: RMCA 12331. **GABON:** Estuaire Province: Makaban (00.567, 10.3167, 480 m asl) (Pauwels et al. 2002b). Kinguélé (00.45, 10.267, 80 m asl) (Pauwels et al. 2002b). Haut-Ogooué Province: Lékoko Department, Parc de la Lékédi: RBINS 18503. Mounana: MNHN 1980.1084. Ngounié Province: Boumi-Louétsi Department, Moudouma

(−01.735, 12.0533, 660 m asl): RBINS 16252. Diyanga: RBINS 16308, 16350–51. Itsiba: RBINS 16349 (Pauwels et al. 2002a). Ogooué-Ivindo Province: Koumameyong: RBINS 16362. Makokou (Knoepffler 1966). Ivindo National Park, Ipassa (00.51226, 12.8035) (Carlino and Pauwels 2015; Pauwels et al. 2016). Ogooué-Lolo Province: Mount Iboundji: RBINS 16272. Ogooué-Maritime Province: Rabi oilfield (Shell Gabon), gate to Ossengue Camp (−01.93, 09.87): USNM 561535. Woleu-Ntem Province: Song (00.633, 10.267, 360 m asl) (Pauwels et al. 2002b; Carlino and Pauwels 2015). Mbé Akélayong (00.87, 10.53, 530 m asl) (Pauwels et al. 2002b). **REPUBLIC OF THE CONGO:** Kouilou Department: Dimonika (Villiers 1966). Lékoumou Department: Sibiti: MNHN 1966.695 (Villiers 1966). Mbila (Villiers 1966). Kissiki (ca. −02.783, 13.516): USNM 584260. Sangha Department: MNHN 1932.74.*

Philothamnus chifunderai sp. nov.: **ANGOLA:** Lunda Norte Province: Dundo (−07.3789, 20.8240): RMCA 28378–79. **BURUNDI:** Bubanza Province: Musigati (−03.0658, 29.4596): RBINS 14.502, RMCA 79-15-R-36. **DEMOCRATIC REPUBLIC OF THE CONGO:** Bas-Uele Province: Bambesa: RMCA 4255, 4258–60, 4262A, 4263–64. Zobia (02.9555, 25.9820): RBINS 4256A–F. Ibembo: CM 69209–10. Ibembo (02.6496, 23.6150): RBINS 4266, 19821–23. Madié [= Medje] (02.3873, 27.3014): RMCA 1647 (2 specimens). Haut-Katanga Province: Parc National de l’Upemba, Kaswabilenga, cours inf. Lupiala, affl. dr. Lufira (−08.850, 26.7167, 700 m asl): RBINS 8504. Parc National de l’Upemba, Munoi, bifurcation riv. Lupiala, affl. dr. Lufira (−08.8333, 26.7333, 890 m asl): RBINS 8505–07. Parc National de l’Upemba, Lukawe, affl. dr. Lufira (−09.1290, 26.7460, 700 m asl): RBINS 8501, 8501A–B, 8502. Parc National de l’Upemba, Kande, aff. g. Lupiala et s.-affl. dr. Lufira (−08.8333, 26.7500, 700 m asl): RBINS 8503. Ituri Province: near Epulu (01.39693, 28.58587, 753 m asl): UTEP 21838. Kasai Province: Bulape: USNM 167125, 167131–37, 167138, 252703–06. Mai-Ndombe Province: Nkala (−02.60278, 16.45472, 474 m asl): UTEP 22604. Maniema Province: on road from Kindu to Lubile (−02.65728, 26.38861, 565 m asl): UTEP 22605. North Kivu Province: Parc National Albert [= Virunga National Park], Mutsora (00.3167, 29.7500, 1000 m asl): RBINS 6438, 6442, 13076. Parc National Albert, Tungula (0.5, 29.8): RBINS 5588. Parc National Albert, Secteur Munsenene, Riv. Djelele (−00.0072, 29.3348, 1100 m asl): RBINS 6430. Parc National Albert, Secteur Oycha, Manzumbu (00.7005, 29.5269, 1100 m asl): RBINS 6434, 6436. Parc National Albert, Riv. Kebikeba, Sect. Oycha (ca. 00.7005, 29.5269, 1100 m asl): RBINS 6439. Parc National Albert, Secteur Munsenene, marais près riv. Djelele, affl. Djelube (−00.0072, 29.3348, 1100 m asl): RBINS 6440. Parc National Albert, Secteur Liboma, marais près ruisseau Lungula, affl. Semliki (00.5342, 29.6518, 900 m asl): RBINS 6441. Parc National Albert, Mont Mitero, contrefort Ruwenzori, Secteur Haute Djelube, rive Lusilibe (ca. 00.4500, 29.7667, 1700m asl): RBINS 6431, 6433. Parc National Albert, Sect. Oycha, Tandibo, 4 km d’Oycha (00.7005, 29.5269, 1100 m asl): RBINS 6435, 6437. Parc National des Virunga, Village Tungudu (00.7690, 29.7637, 840 m asl): RBINS 12904, 19642. Parc National des Virunga, Abyalose, affl. de la riv. Djuma (00.7000, 29.7000, 800 m asl): RBINS 12905. Parc National des Virunga, Djuma, affl. de la Semliki (ca. 00.7167, 29.7500, 800 m asl): RBINS 13078. Parc National des Virunga, Mamudioma, affl. de la Djuma, nouvelle route de Watalinga (ca. 00.6667, 29.6667, 1000 m asl): RBINS 13079. Kihumba-Idjwi (−01.9442, 29.0958): RBINS 12849. Baie de la Maganga, Île Idjwi (1470 m asl): RMCA 18406. Manguretshipa (00.36667, 28.71667, 1000 m asl): RMCA 18404. Sankuru Province: Lusambo (−04.9654, 23.4414): RMCA 16377. South Kivu Province: Bunyakiri (−02.0756, 28.5732, 1000–1200 m asl): RBINS 8272, 8575, RMCA 18405. Région Tshabondo (ca. −0.09, 28.57): RBINS 9122. Irangi (−01.8833, 28.4500): RBINS 12847–48, 19773, UTEP 21837. Tshobondo [= Shabunda] (−02.6909, 27.3420, 1150–1200 m asl): RBINS 8576–77. Mushafi (1300 m asl): RBINS 9121.* Tshopo Province: Batisama (00.63245, 25.18335, 422 m asl): UTEP 22609. Bengamisa (00.9711, 25.2108): RBINS 19750. Kisangani, rive droite (00.5186, 25.2603): RBINS 19766, 19795. Ile Kongolo près de Kisangani (00.5607, 25.0731): RBINS 19680. Amadjabe (−00.0667, 25.2833): RBINS 19749, 19767, 19646. Yoko area (00.297667, 25.312556): RBINS 19306. Yoko area (00.293806, 25.288917): RBINS 19250, 19295, 19297–98, 19301, 19337. Yoko area (0.299722, 25.290444): RBINS 19246. Yoko area (0.325111, 25.257194): RBINS 19303. Yoko area (0.25325, 25.303086): RBINS 19340. Yaikela (0.806111, 24.283889): RBINS 18856. Bamakende (−00.216125, 25.803306): RBINS 19277. Uma area (00.908333, 26.505556): RBINS 19284, 19489. Bagwase (−00.3611, 25.2488): RBINS 18859–61, 19153. Route Yangambi, distr. Stanleyville (ca. 00.7991, 24.4502): RBINS 10250.