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Original article

The oldest lamprophiid (Serpentes, Caenophidia) fossil from the late Oligocene Rukwa Rift Basin, Tanzania and the origins of African snake diversity ☆

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ABSTRACT

Extant snake faunas have their origins in the mid-Cenozoic, when colubroids replaced booid-grade snakes as the dominant species. The timing of this faunal changeover in North America and Europe based on fossils is thought to have occurred in the early Neogene, after a period of global cooling opened environments and made them suitable for more active predators. However, new fossils from the late Oligocene of Tanzania have revealed an early colubroid-dominated fauna in Africa suggesting a different pattern of faunal turnover there. Additionally, molecular divergence times suggest colubroid diversification began sometime in the Paleogene, although the exact timing and driving forces behind the diversification are not clear. Here we present the first fossil snake referred to the African clade Lamprophiinae, and the oldest fossil known of Lamprophiidae. As such, this specimen provides the only potential fossil calibration point for the African snake radiation represented by Lamprophiidae, and is the oldest snake referred to Elapoidea. A molecular clock analysis using this and other previously reported fossils as calibration points reveals colubroid diversification minimally occurred in the earliest Paleogene, although a Cretaceous origin cannot be excluded. The elapoid and colubrid lineages diverged during the period of global warming near the Paleocene-Eocene boundary, with both clades diversifying beginning in the early Eocene (proximate to the Early Eocene Climate Optimum) and continuing into the cooler Miocene. The majority of subclades diverge well before the appearance of colubroid dominance in the fossil record. These results suggest an earlier diversification of colubroids than generally previously thought, with hypothesized origins of these clades in Asia and Africa where the fossil record is relatively poorly known. Further work in these regions may provide new insights into the timing of, and environmental influences contributing to, the rise of colubroid snakes.

1. Introduction

Modern colubroid-dominated snake faunas appeared in North America and Europe after the migration of colubroid snakes from Asia in the late early Miocene (Szyndlar and Schleich, 1993; Ivanov, 2001; Rage, 2013), possibly coincident with a cooling global climate and the spread of open habitats favorable to widely foraging predators (Savitzky, 1980). Whether the timing of colubroid dominance was globally synchronous is unclear; a similar pattern may occur in Australia, although the Oligocene record is somewhat sparse (Scanlon et al., 2003). In South America, there is a gap in the fossil record spanning the middle Eocene to the Miocene (Albino and Brizuela, 2014). In Africa, fossils from the late Oligocene of Tanzania revealed one of the oldest colubroid dominated faunas worldwide, suggesting an earlier arrival of colubroid snakes there (McCartney et al., 2014). To date, the only other Paleogene snake fauna that features more colubroids than booid-grade snakes is from the Eocene Cambay Formation of Gujarat, India (Rage et al., 2008).

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Molecular evidence suggests that the colubroid radiation had been under way by the time these forms came to dominate the fossil record, with most estimates suggesting an early Paleogene origin in Asia (Kelly et al., 2009; Vidal et al., 2009; Pyron and Burbrink, 2012). The fossil record is congruent with this early origin, given the occasional occurrence of colubroid snakes in the early Paleogene (Rage, 1974; Holman, 1993; Augé et al., 1997; Parmley and Holman, 2003; Head et al., 2005; Rage et al., 2008, 1992; Smith, 2013), and possibly even the Late Cretaceous of Sudan (Rage and Werner, 1999). Molecular evidence also suggests a rapid radiation with most extant subfamilies appearing prior to the Neogene (Kelly et al., 2009; Vidal et al., 2009; Pyron and Burbrink, 2012). Unfortunately, the fact that the snake fossil record is largely composed of vertebrae means that many colubroid clades cannot be recognized in the fossil record; there has thus been no confirmation of the presence of these subclades, nor means of providing calibration points for refining molecular clock estimates. In particular, the large Afro-Eurasian clade Lamprophiidae, a group estimated to have originated in Africa during the Eocene (Kelly et al., 2009; Pyron and Burbrink, 2012), is unidentified in the fossil record outside of vertebrae referred to the psammophiine *Malpolon* from the Pliocene and Pleistocene of Europe and North Africa (Szyndlar, 1991, 1988; Holman, 1998; Bailon, 2000).

In this paper, we report a new snake fossil from the late Oligocene Nsungwe Formation of the Rukwa Rift Basin in southwestern Tanzania. Fossils from the Nsungwe Formation have already provided important information from gaps in the terrestrial African fossil record, including representative invertebrates (Feldmann et al., 2007; Roberts et al., 2016; Epa et al., 2018), fishes (Gottfried et al., 2007; Stevens et al., 2016; Claeson et al., 2020), frogs (Blackburn et al., 2015; Blackburn et al., 2019), mammals, including primates (Stevens et al., 2005, 2006a, 2006b, 2009a, 2009b, 2013), and lizards (Müller et al., 2018), in addition to colubroid and booid snakes (McCartney et al., 2014). The new snake is an African file snake (species formerly referred to *Gonionotophis*) belonging to Lamprophiinae, providing the only fossil evidence of the entire subfamily and a minimum age of divergence for Lamprophiidae. We use this novel calibration point to inform and revise divergence estimates for caenophidian snakes.

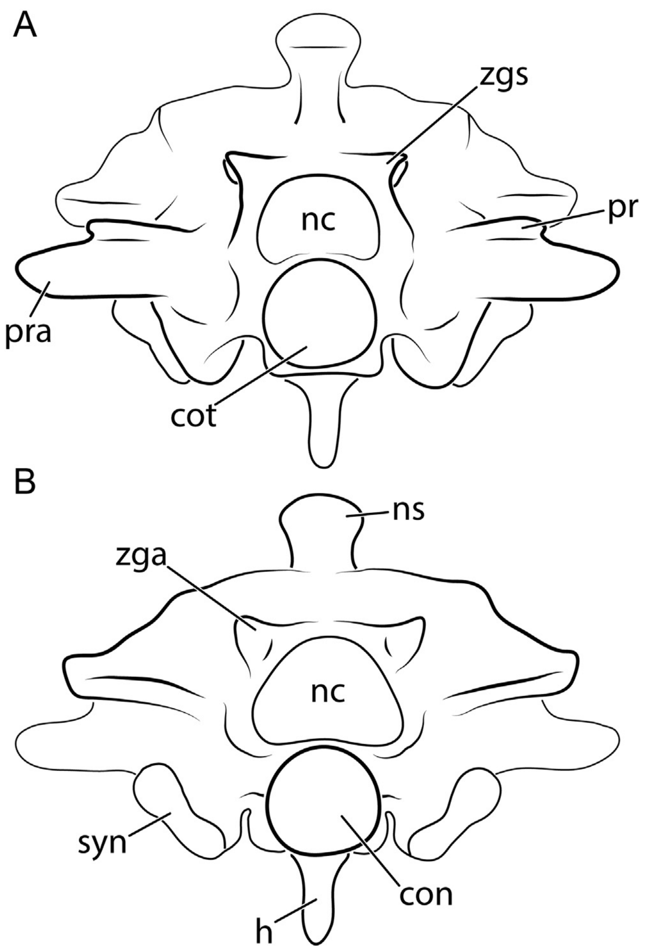

Fig. 1. Anatomical features of African file snake vertebrae, based in part upon RRBP 07143. **A**. Anterior view. **B**. Posterior view. Abbreviations: con, condyle; cot, cotyle; h, hypapophysis; nc, neural canal; ns, neural spine; pr, prezygapophysis; pra, prezygapophyseal accessory process; syn, synapophis; zga, zygantrum; zgs, zygosphene.

2. Material and methods

Mechanical preparation of the fossil was completed by K. Whitman at the Ohio University Fossil Preparation and Imaging Facility. The specimen was scanned using a Nikon XTH 225 ST micro-computed tomography scanner in the Shared Materials Instrumentation Facility at Duke University, Durham, NC. The specimen was scanned at a voxel dimension of 20.03 μm^3, at a voltage of 114 kV and amperage of 127 μa. Processing of the scans to construct and visualize the digital model was conducted in Avizo (FEI) 8.0 using volume and isosurface rendering. A 3D model of the specimen is included in the supplemental materials (Appendix A). Specimen measurements were taken using ImageJ v. 1.44o (Schneider et al., 2012). Snake vertebral morphology and terminology as used throughout this paper are provided in Fig. 1.

Sequence data and an initial topology were obtained from a 12-locus mixed nuclear/mitochondrial sequence analysis that included 4161 squamate taxa (Pyron et al., 2013). The matrix and tree were trimmed to only snakes (1262 taxa), with each locus assessed for representation within the snakes and particularly within Lamprophiidae. Four of the 12 genes in the supermatrix (16S rRNA, 12S rRNA, Cytochrome B, and ND4) were selected for a Bayesian divergence dating analysis using MCMCTREE (Yang and Rannala, 2006; Rannala and Yang, 2007). These four mitochondrial genes were included because they were present in both a majority of the snakes and in three or more of the included species of African file snakes. The matrix and tree were trimmed to 103 representative taxa (Appendices C, D) using the Newick utilities (Junier and Zdobnov, 2010). First, taxa were removed if they did not contain sequence data from any of the four selected genes. Next, taxa were selected based on the following criteria: (*i*) all included African file snakes except *Mehelya capensis* plus a member of each genus in Lamprophiinae, (*ii*) one or two members of each other subfamily in Lamprophiidae, and (*iii*) one or two members of each other family of snakes. *Meheyla capensis* was excluded from the analysis due to a misidentification of the material in GenBank, resulting in *Mehelya poensis* being identified as *M. capensis* (first noted in Kelly et al., 2011). Individual taxa were chosen using these criteria based on maximizing the total number of bases of aligned sequence. Branch lengths were removed from the tree and fossil calibration times were added, including the new lower bound of 25 Ma from the present study for the age of the *Hormonotus*-African file snake split. Other calibration points include those from Head (2015) for basal snakes, and those from Head et al. (2016) for Caenophidia.

Divergence times were estimated using the MCMCTREE program (Yang and Rannala, 2006; Rannala and Yang, 2007) of PAML (v. 4.1; Yang, 2007), implementing an independent rates clock (clock = 2) and substitution model HKY85 (model = 4; Hasegawa et al., 1985) (Appendix B). This model was chosen rather than

K2P (Kimura, 1980) because that model assumes equal frequency of the four nucleotides, which was not true for our data. The mean substitution rate prior for each gene (substitutions per 100 myr) was obtained by running baseml on the four genes using the median time of the most recent common ancestor for each calibration point. Various priors for birth/death, branch rate variation, and transition/transversion rate were tried to ensure convergence was to a global rather than a local maximum. The highest scoring model was run for 20,000 generations with a burn-in of 2000, and the process was replicated three times to ensure convergence of results (correlation between dates for separate runs: $R^2 = 0.9998$ in this analysis). The analysis was run using the trimmed phylogeny from Pyron et al. (2013), as well as a modified tree including an alternate arrangement of species within the African file snakes based on a recent analysis (Broadley et al., 2018). To ensure this result was not a methodological artifact, we also ran TreePL (Smith and O'Meara, 2012) using the Serpentes portion of the tree from Pyron et al. (2013), with the same fossil calibrations (tree and parameters file provided in Appendices E and F).

Institutional abbreviations: RRBP, Rukwa Rift Basin Project (identifier used by the Tanzanian Antiquities Unit), Dar es Salaam, Tanzania; USNM, National Museum of Natural History, Washington, DC, USA; YPM, Yale Peabody Museum, New Haven, CT, USA.

3. Geologic context

The fossil specimen described in this study was recovered from outcrop exposures of the Songwe Mb. of the Nsungwe Fm. at the southern end of the Rukwa Rift Basin, a segment of the Western Branch of the East African Rift System, in southwestern Tanzania (Fig. 2). The Nsungwe Fm. represents an upward fining rift-fill succession of alluvial fan (Utengule Mb.) to volcanic-rich fluvial and lacustrine (Songwe Mb.) strata (Roberts et al., 2004). The richly fossiliferous Songwe Mb. has produced one of the richest and most diverse Paleogene vertebrate and invertebrate faunas in Sub-Saharan Africa (e.g., Stevens et al., 2008, 2013).

The Nsungwe Fm. has been precisely dated as late Oligocene, with deposition transpiring between ~26 and 24 Ma, based on Ar/Ar and U-Pb dating of numerous intercalated bentonite horizons (devitrified ash beds) and magnetostratigraphy (Roberts et al., 2012; Stevens et al., 2013). The snake fossil reported in this study comes from a reversed polarity interval at a locality termed TZ-01S (South). The site correlates to the ~180–190 m level in the type section along Nsungwe River Section (Roberts et al., 2016), which sits at the base of Chron C7Ar, indicating an age range between 24.984 and 25.097 Ma.

The TZ-01S locality is characterized by a 3 m thick succession of interlaminated coarse-grained, poorly sorted, ripple-cross laminated, muddy sandstones; mottled red and green siltstones and mudstones with calcium carbonate nodules, slickensides and rootlets; and thin maroon bentonites. These deposits are interpreted to represent an abandoned fluvial channel belt within a volcanically active landscape. Most fossils from this unit, including the snake vertebra described herein, come from the poorly sorted, muddy sandstone facies.

4. Results

4.1. Systematic paleontology

Serpentes Linnaeus, 1758
Caenophidia Hoffstetter, 1939
Colubroidea Oppel, 1811
Lamprophiidae Fitzinger, 1843
Lamprophiinae Fitzinger, 1843
Gen. et sp. indet.

Referred specimen: RRBP 07143, posterior trunk vertebra.

Locality and horizon: Late Oligocene Nsungwe Formation, locality TZ-01 South, Rukwa Rift Basin, southwest Tanzania.

Measurements: see Table 1.

Description: Specimen RRBP 07143 (Fig. 3) is the only vertebra recovered to date from this taxon in the Nsungwe Fm. It is a posterior trunk vertebra, identified by the presence of deep subcentral

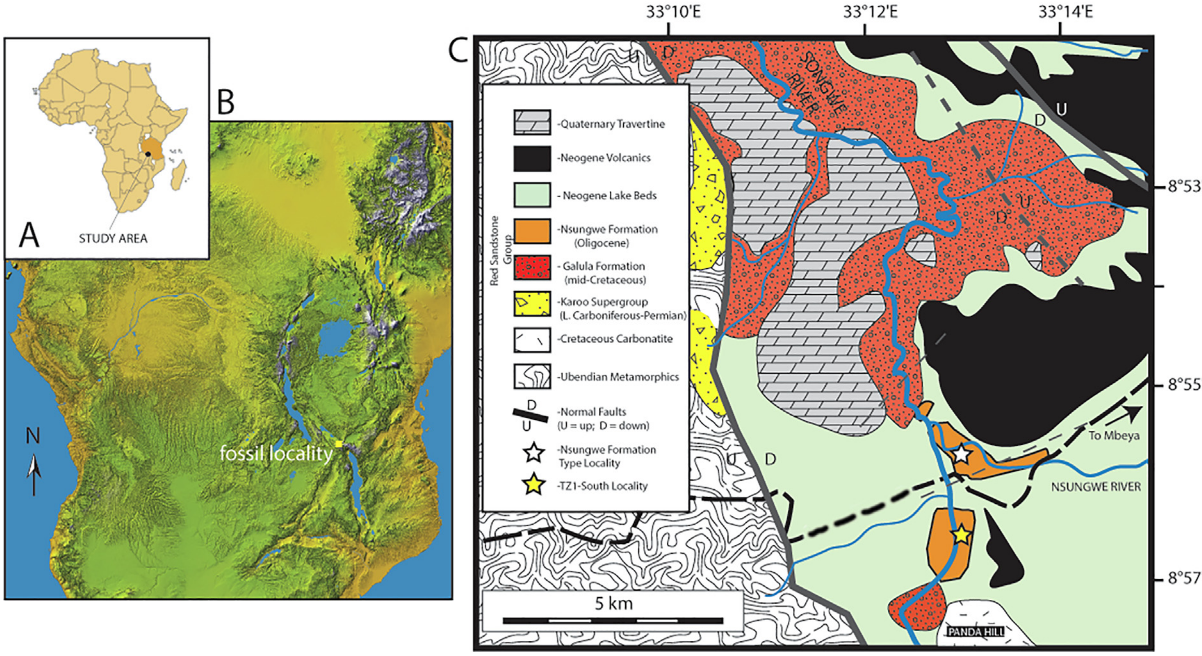

Fig. 2. Location and geologic setting of TZ-01 South in the Nsungwe Formation of the Rukwa Rift Basin in Southwest Tanzania. **A**. Map showing the location of the study area. **B**. Physical map of central Africa showing the locality in the East African Rift system. **C**. Geological map of the Rukwa Rift Basin region, with the type locality for the Nsungwe Formation and TZ-01 South indicated by stars.

Table 1
Measurements (in mm) of the unnamed African file snake posterior trunk vertebra (RRBP 07143).

Specimen	NAW	ZSW	CTW	CTH	PRW	POW	PrPo	NH
RRBP 07143	3.3	1.6	1.1	1.0	4.2	3.8	3.5	1.0

CTH, cotyle height; **CTW**, cotyle width; **NAW**, neural arch width measured immediately posterior to the prezygapophysis; **NH**, neural spine height; **POW**, width across the postzygapophyses; **PrPo**, distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis; **PRW**, width across the prezygapophyses; **ZSW**, zygosphene width.

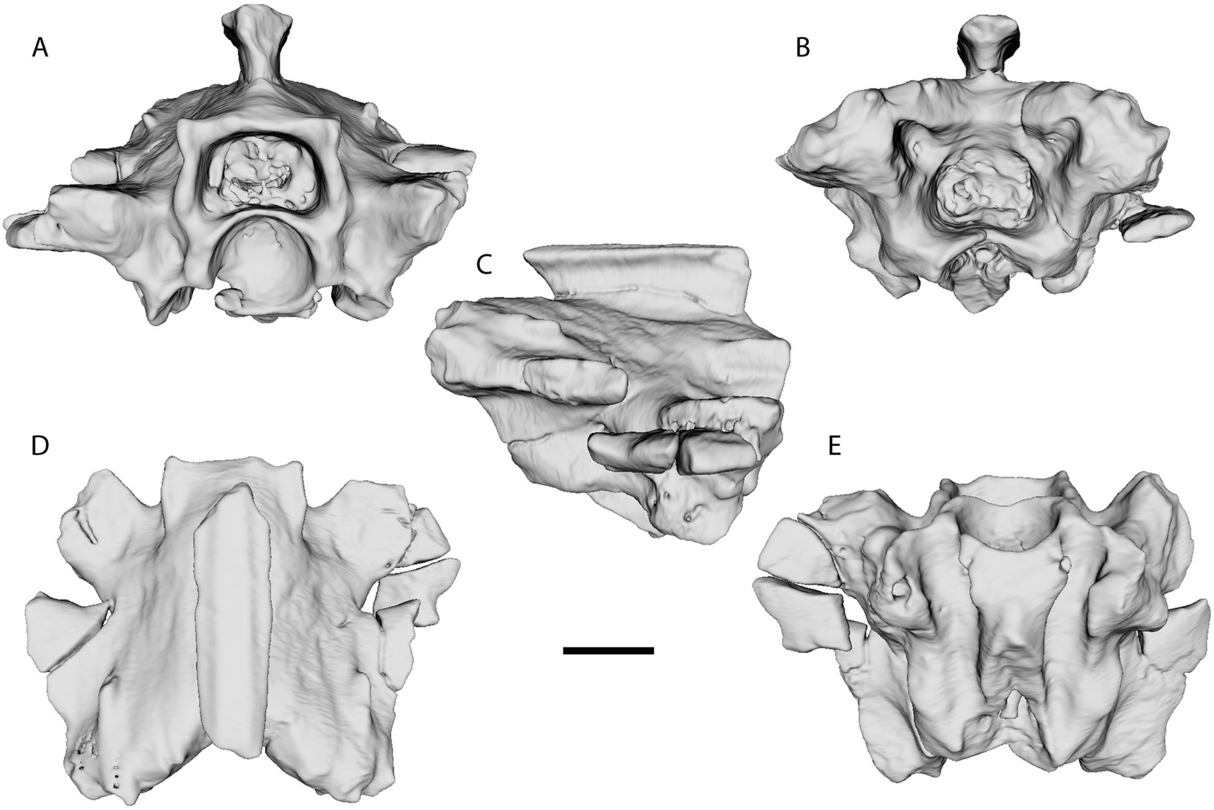

Fig. 3. Posterior trunk vertebra (RRBP 07143) of an African file snake from the late Oligocene of Tanzania in anterior (**A**), posterior (**B**), lateral (**C**), dorsal (**D**) and ventral (**E**) views. See Appendix A for a 3D model of this specimen. Scale bar: 1 mm.

fossae that house lymphatic tissue in extant snakes (LaDuke, 1991). The vertebra is anteroposteriorly short and mediolaterally wide with a centrum that is abraded posteriorly resulting in loss of the condyle. It preserves several vertebral processes not found in most snakes, but is missing the left prezygapophyseal accessory process.

The neural spine is dorsoventrally restricted and thick with a transverse dorsal expansion. The dorsal border is straight, and projects posteriorly beyond the base of the spine producing an overhang. The anterior edge is broken, but what is preserved suggests a vertical ventral portion, with an anterior projection, although the extent of the overhang is not clear. On the posterior third of the arch there is a low ridge parallel to the main vertebral axis. The ridge is closer to the postzygapophysis than to the neural spine. Along the edge of the neural arch posterior to the ridge, but separated from it by a low gap is a small, posteriorly directed prong. Medial to this process there is a small protuberance that projects posteromedially into the vertebral notch. The zygosphene is crenate, with a weakly convex dorsal edge and facets that project dorsally. The zygantrum is dorsoventrally short with a horizontal roof; the fossae are shallow and widely set with a large intrazygantral foramen in the center of each. The neural canal projects dorsally between the zygantral facets. The neural arch lamina overlying the zygantrum is thick and convex. The neural canal is slightly wider than the cotyle, and is wider than tall.

The zygapophyses project laterally. The prezygapophyseal facets are incomplete bilaterally, preventing complete assessment of their shape. Partial preservation of the right facet suggests that it is oval in shape. The postzygapophyseal facet lies on a greatly expanded, aliform process and is not clearly defined. It is damaged, so its shape is uncertain. The facets lie very near the horizontal plane. Ventral to the right prezygapophysis, the prezygapophyseal accessory process is broadly expanded into a flange that extends horizontally. Its total length cannot be determined due to breakage, but it is at least as long anteroposteriorly as the preserved prezygapophyseal facet. The postzygapophysis is expanded into a broad, horizontal aliform process that projects laterally. The base of this process extends anteriorly as far as the prezygapophysis; the cranial edge is anteriorly curved so that it overlaps the prezygapophyseal accessory process anteriorly. The lateral extent of the postzygapophyseal process is not known due to damage.

The centrum is abraded posterior to the midpoint such that no features are preserved posteriorly. The cotyle is circular. The paracotylar fossa is dorsoventrally elongate, and lies midway between the cotyle and synapophysis. It contains two foramina that are situated on a dorsoventral line in the middle of the fossa. The synapophyses are poorly preserved, but the diapophysis and parapophysis are only weakly separated. There is a thick subcentral ridge that extends posteriorly from the synapophysis; it is weakly convergent with its counterpart. The subcentral lymphatic fossa is deep, and contains a small subcentral foramen close to the hemal keel at the midpoint between the cotyle and condyle. The hemal keel is very wide and expands slightly under the cotyle with a ventrolateral cotylar process. Anteriorly, the subcentral fossae open anteriorly, producing deep notches between the parapophyses and ventrolateral lip of the cotyle.

Remarks: Specimen RRBP 07143 exhibits several synapomorphies consistent with African file snakes, including the unusual shapes of the prezygapophyseal accessory and postzygapophyseal processes, and the presence of an additional ridge on the neural arch. These features occur in species assigned to *Gonionotophis*, *Mehelya*, and *Limaformosa* (Bogert, 1964; JAM pers. obs. in *Gonionotophis brussauxi* [YPM HERR 008632, Morphosource media number M29574-56661] and *Limaformosa crossi* [USNM 320700]). They are not reported in other lamprophiid species and do not occur in *Hormonotus modestus*, a species that lies within the sister clade to African file snakes (Bogert, 1964).

Expanded or extra processes occur rarely in trunk vertebrae of snakes generally. The elapid *Bungarus* has a similarly expanded prezygapophyseal accessory process and all but two species also have a flange-like postzygapophysis (Slowinski, 1994: fig. 2); however, the prezygapophyseal accessory process is not as strongly expanded, except in *Bungarus flaviceps*, a species which lacks a postzygapophyseal flange (Slowinski, 1994). Additionally, there is no ridge on the neural arch lamina, and the neural spine is substantially taller than it is in African file snakes (Hoffstetter, 1939). *Xenodermus javanicus* bears a process on the postzygapophysis, but it is distinct from the postzygapophyseal facet rather than forming a single, alar structure, and the vertebra lacks an expanded prezygapophyseal accessory process (Bogert, 1964). The postzygapophysis of *Xenopholis* is similarly flange-like, but the flange is less distinctly separated from the prezygapophysis, the prezygapophyseal accessory process is not elaborated, and the neural spine is substantially thicker than that of African file snakes, being nearly as wide as the zygosphene (Boulenger, 1896).

4.2. Divergence estimation

The divergence times estimated by the molecular clock analysis conducted herein are broadly congruent with previously reported dates for major clades, but with earlier divergence estimates for colubroid subclades than most previous analyses (Table 2). The resulting time-calibrated phylogeny is presented in Fig. 4. Crown-group snake (Serpentes) divergence is estimated to have occurred during the Early Cretaceous at 110 Ma, and Caenophidia in the Late Cretaceous at 71 Ma. Major colubroid clades likely diverged in the early Cenozoic, with diversification of most clades underway by the end of the Paleogene. Elapoidea follows this pattern, with Lamprophiidae and Elapidae likely diverging in the early Eocene (~50 Ma) and their constituent subfamilies throughout the Eocene and Oligocene. The divergence of African file snakes from their sister taxon *Hormonotus* is recovered at ~31 Ma (Oligocene) with crown diversification beginning in the Miocene, either at 21 Ma using the Pyron and colleagues (2013) arrangement of African file snakes (Fig. 4), or at 23 Ma in the model produced using the relationships found in Broadley and colleagues (2018), available in Appendix H.

5. Discussion

The snake fauna from the late Oligocene Nsungwe Fm. of the Rukwa Rift is surprisingly modern in makeup, predominantly composed of colubroid snakes. Specimens recovered thus far can largely be assigned to clades that currently inhabit the region, including two elapids and a form that strongly resembles the extant pseudoxyrhophiine *Duberria* (see McCartney et al., 2014). The new vertebra reported herein adds to that list a member of the lamprophiine African file snakes.

The presence of a colubroid-dominated snake assemblage during the late Oligocene representing a number of modern clades suggests that African snake faunas may have a distinct evolutionary trajectory through the Cenozoic when compared with those known from Europe and North America. This may partly result from the relative isolation of Africa from other landmasses during the Paleogene. Once the ancestors of the African clades arrived on the continent, they could evolve in isolation from the predominantly booid-dominated faunas that persisted through the Oligocene elsewhere.

5.1. Paleobiology

Extant African file snakes are small, nocturnal, secretive species that specialize on ectothermic prey, including amphibians, lizards, and other snakes (Loveridge, 1939; Broadley, 1959; Shine et al., 1996; Luiselli et al., 1998). Some species even have hinged teeth for the purpose of eating relatively hard-bodied, cylindrical prey like other snakes and certain lizards (Savitzky, 1981). There are ample small ectotherms known from the Nsungwe Fm., including frogs, snakes and lizards (McCartney et al., 2014; Blackburn et al., 2015; Müller et al., 2018; Blackburn et al., 2019); assuming a similar dietary preference to extant species, any of these could conceivably have been part of the diet of the Oligocene file snake.

Table 2
Comparison of node-based divergence times of major snake clades from this study and other recent analyses.

Clade	This Paper	TreePL	Zaher et al. (2019)	Burbrink and Pyron (2008)	Kelly et al. (2009)	Zheng and Wiens (2016)	Vidal et al. (2009)
Serpentes	109.7	113	93.9	144.2	113.7	128.1	159.9
Alethinophidia	94.6	93.9	64.7	134.4	68.5	92.7	105.8
Caenophidia	71.1	67.5	55.7	58.7	63	80.6	90.7
Colubroidea	65.9	61.2	52.6	48.7	51.7	75.2	82.2
Viperidae	23.6	23.8	30.7	32.9	-	42.8	-
Elapoidea	50.4	53.6	32.3	35.7	43	47.9	41.5
Lamprophiidae	47.8	52.1	31.7	32.8	-	46.8	-
Lamprophiinae	42.1	42.2	25.1	-	26.4	35.3	-
Psammophiinae	32.3	33.1	20.4	-	22.2	29.9	-
Pseudoxyrhophiinae	33.2	42.2	24.9	-	28.7	35.6	-
Elapidae	45.1	47.3	30.5	25.6	31.2	46.5	-
Colubridae	49.7	56.4	33.2	38.2	-	48.7	39.8
Dipsadinae	40.8	51.9	31.5	-	-	41.5	-
Natricinae	33.4	42.9	26	-	-	36.9	-

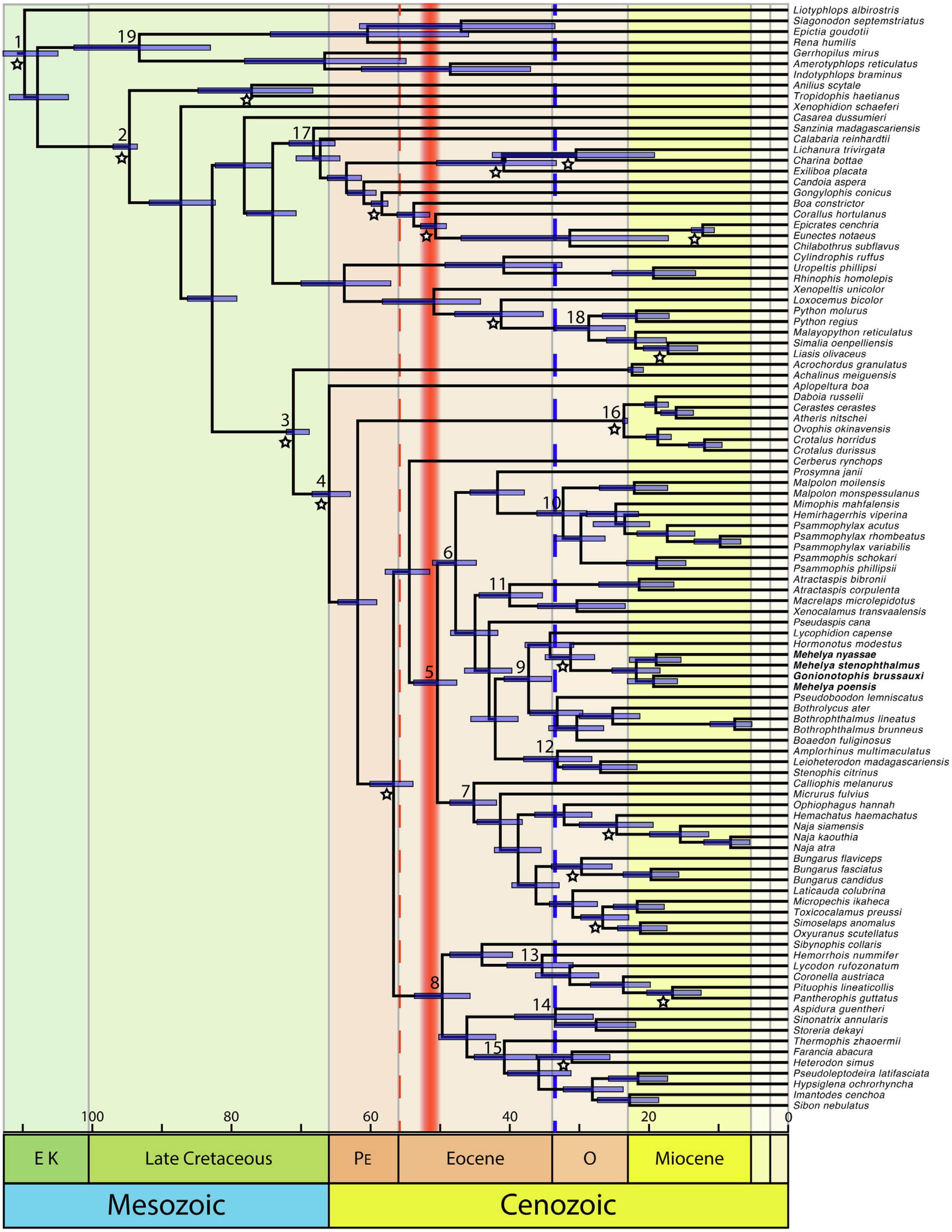

Fig. 4. Fossil-calibrated timetree of Serpentes based on four genes produced using mcmctree in PAML. The node bars represent the 95% confidence interval for node age. Those nodes that are calibrated by fossils are indicated by a star. The African file snakes are bolded. The dashed line in the Eocene represents the Paleocene-Eocene Thermal Maximum, the box indicates the early Eocene climatic optimum, and the dashed line in the Oligocene denotes the "Grande Coupure". Clades are indicated by numbers: 1, Serpentes; 2, Typhlopoidea; 3, Alethinophidia; 4, Boidae; 5, Pythonidae; 6, Caenophidia; 7, Colubroidea; 8, Viperidae; 9, Elapoidea; 10, Lamprophiidae; 11, Psammophiinae; 12, Atracastaspididae; 13, Lamprophiidae; 14, Pseudoxyrhophiinae; 15, Elapidae; 16, Colubridae; 17, Colubrinae; 18, Natricinae; 19, Dipsadinae.

Extant species are even known to take highly venomous snakes (Shine et al., 1996), a dietary selection that could be ancient given the presence of elapid snakes in the Rukwa Rift Basin fauna (McCartney et al., 2014). Prey were presumably subdued by constriction, as in extant species (Broadley et al., 2018).

African file snakes are diverse in habitat preference, occurring in forests, savanna, and even semi-desert conditions (Howell et al., 2018). Paleoenvironmental reconstructions of the Oligocene Rukwa Rift Basin deposits suggest seasonally arid wetlands with perennially available water (Roberts et al., 2010). Although extant species are not known to prefer wetlands, a semiarid environment fits well within the range of conditions tolerated by extant African file snakes.

5.2. Divergence times

The evolution and subsequent diversification of caenophidian snakes is a key event in the evolution of snakes, one that has resulted in the largest and most successful radiation of snakes alive today. Given their importance in modern faunas, the origins of this clade are understandably of great interest to paleontologists. The analysis herein, using a pruned phylogeny and sequence data from Pyron and colleagues (2013), provides the first investigation of the timing of the divergence of Caenophidia including a fossil calibration point within Lamprophiidae. Both the mcmctree and TreePL analyses agree broadly on dates, with the exception of pseudoxyrhophiine and colubrid divergences, which are found to be older in TreePL (Table 2). The results of this study are also congruent with previous divergence estimates in suggesting that several deep divergences within snakes occurred in the Cretaceous (Table 2); our analysis finds the appearance of caenophidians and possibly crown Colubroidea during that time as well. This suggests the survival of Caenophidians across the K-Pg extinction event, which is congruent with the probable occurrence of that clade in the Cretaceous of Sudan (Rage and Werner, 1999). Crown colubroids may have done the same, although the confidence interval for that clade suggests the possibility that they appeared early in the Paleogene. Divergences within the colubroid subclades do not generally occur until later, matching the fossil record of early Paleogene localities in which colubroid snakes were not particularly common species within snake faunas. These early divergences are similar to ages found in some previous studies (Vidal et al, 2009; Zheng and Wiens, 2016), but are distinctly older than other studies that find colubroids to be a Cenozoic radiation (Burbrink and Pyron, 2008; Kelly et al., 2009; Zaher et al., 2019). Although caenophidians are reported as early as the Late Cretaceous (Rage and Werner, 1999), a more recent origin for crown colubroids would be congruent with what is known of their fossil record, with the earliest definitive species reported from the early Eocene of India (Rage et al., 2003; Smith et al., 2016). It is important to note that Asia has been hypothesized as a center of origin for crown colubroids (Rage et al., 1992; Vidal et al., 2007), with the relatively poor Asian fossil record possibly accounting for the lengthy ghost lineages. Thus, focused field efforts in Asia may produce earlier colubroids than are currently known.

The responses of snake lineages to well-documented climatological events during the course of the Paleogene are only partly known. Two such significant warming events include the Paleocene-Eocene Thermal Maximum and the Early Eocene Climate Optimum (Kennett and Stott, 1991; Zachos et al., 2001), with one cooling event at the beginning of the Oligocene that resulted in the extinctions of the “Grande Coupure” in Europe and North America (Stehlin, 1909; Zachos et al., 2001). To a point, ectothermic lineages like snakes tend to thrive during periods of global warming. Indeed, at least three lineages of snakes reached their greatest known sizes during warming events in the early Paleogene (Head et al., 2009; McCartney et al., 2018). Also occurring during or near this time of global warming are (*i*) the divergence of crown-group non-viperid colubroid snakes, and (*ii*) the diversification of both Elapoidea and Colubridae, two clades representing the majority of extant caenophidian diversity (Pyron et al., 2013).

The effect of climatic cooling episodes (e.g., the “Grande Coupure”) upon snakes is best documented in Europe, where booid-grade snakes experienced extinctions that left a relatively small snake fauna to persist through the remainder of the Oligocene (Rage, 2013; Rage and Szyndlar, 2005; Cleary et al., 2018). It is not until the Miocene that colubroid snakes become dominant in Europe and North America (Tihen, 1964; Rage, 1987). Yet the results of our divergence analysis suggest that, with the exception of viperids, elapoid and colubrid subclade diversifications were underway even before the “Grande Coupure”, and certainly before their dominance elsewhere on the planet during the Miocene, although much of the within-clade diversification likely occurred after the climate cooled. The results of the TreePL analysis (Table 2; Appendix G) suggest a still earlier diversification for Colubridae, beginning during the Early Eocene Climate Optimum, with subclade crown diversification occurring well before the Oligocene. This stands in contrast to the results of some previous studies (Table 2), in which diversifications are hypothesized to have occurred either completely during or immediately following the global cooling event. A later diversification is more congruent with the fossil record from Europe and North America (detailed in Zaher et al., 2019), whereas the earlier diversification implied by our resultssuggests a hidden diversity of colubroid snakes may yet be discovered in late Eocene and Oligocene sites.

Colubroid diversity may be difficult to discern from the typical vertebral material that makes up most of the snake fossil record, because some clades are challenging to confidently identify by vertebral morphology alone. However, the search for identifiable early colubroids can perhaps be illuminated by their diversification patterns. The lamprophiid radiation appears to be African in origin (Kelly et al., 2009); if the clade appeared in the middle Eocene as our results suggest, the ancestors of these snakes must have reached that isolated continent by dispersal sometime before then. This strengthens the possibility that Elapoidea originated on continental Africa. To date, only a handful of Eocene snakes have been described from Africa, and among those described are indeterminate colubroid snakes from Egypt (McCartney and Seiffert, 2016) and Namibia (Rage et al., 2013). Although nothing precludes these early African colubroids from assignment to stem or early crown Elapoidea, the lack of diagnostic vertebral characters complicates the assignment of fossil snakes to that clade. Investigation of elapoid vertebral morphology, along with continued paleontological exploration throughout Africa may reveal the evolutionary origins of this clade. Likewise, the proposed Asian origin of several colubroid clades (possibly including Elapoidea and some of its subclades) suggests another under sampled region that may prove fertile ground for discovering elapoid origins through intensified field exploration. Indeed, Eocene of India has produced the earliest known definitive colubroid fossils (Rage et al., 2003; Smith et al., 2016), at a time when the subcontinent may have been close enough to receive migrants from the Asian mainland (Smith et al., 2016).

6. Conclusions

Unique in the Oligocene, the Rukwa Rift Basin snake fauna is remarkably modern in aspect. Adding to the Nsungwe Fm. fauna is the African file snake described herein, representing the oldest fossil that confidently referred to the extant African snake clade Lamprophiidae (and indeed the only known lamprophiine fossil).

The Nsungwe find also provides the only potential calibration for molecular clock analysis for Lamprophiidae. Using this calibration point results in slightly earlier divergence times than in some recent analyses (but see Zheng and Wiens, 2016) for both Elapoidea and Lamprophiidae, both clades thought to have evolved in Africa (Kelly et al., 2009). The timing of their origin and diversification suggests that colubroid dispersal from Asia into Africa predated significant expansion onto other landmasses. The results of this analysis highlight the importance of further paleoherpetological reconaissance in Africa and Asia, in order to more precisely identify the timing and pattern of colubroid evolution and dispersal around the globe.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices A-G. Supplementary information

Supplementary information (including a 3D model of the fossil [Appendix A], input files for mcmctree [Appendix B, mcmctree control file; Appendix C, phylogenetic tree; Appendix D, gene sequences] and TreePL [Appendix E, original tree; Appendix F, calibration points; Appendix G, results], and the timetree produced by use of the Broadley et al. (2018) topology [Appendix H]) associated with this article can be found online, at: https://doi.org/10.1016/j.geobios.2020.07.005.

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