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Phylogenetics and Integrative Taxonomy of African Water Snakes (Squamata: Colubridae: Grayia)

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PHYLOGENETICS AND INTEGRATIVE TAXONOMY OF AFRICAN WATER SNAKES (SQUAMATA: COLUBRIDAE: *GRAYIA*)

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PHYLOGENETICS AND INTEGRATIVE TAXONOMY OF AFRICAN WATER SNAKES (SQUAMATA: COLUBRIDAE: *GRAYIA*)

by

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THESIS

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Abstract

Grayia is a genus of relatively large (1.5 – 2.5 m) aquatic Afrotropical snakes. Recent molecular phylogenies recovered *Grayia* in its own distinct subfamily (Grayiinae), which was strongly supported as the sister group to Colubrinae. Because tropical African snakes are generally understudied, the relationships within *Grayia* are poorly known. Due to high degrees of intra- and interspecies variation, identification is often difficult and previous studies involving *Grayia* included misidentified specimens in other genera. The goal of this study is to create a phylogenetic tree that can be used to understand the relationships and taxonomy of *Grayia* via an integrative taxonomic approach that combines molecular and morphological data. Two nuclear (BDNF, NT3) and four mitochondrial genes (COI, cyt *b*, 16S and ND4) were used to construct phylogenetic trees with Maximum likelihood and Bayesian inference methods; outgroups included the genera *Calamaria*, *Sibynophis*, and *Masticophis*. The phylogenetic trees recovered two clades*, Grayia caesar* + *G. tholloni* and *G. ornata* + *G. smithii*, which the time-calibrated BEAST analysis estimated to have diverged from each other in the mid-Oligocene. *Grayia ornata* was found to consist of two distinct subclades, one from west and one from east, of the Congo and Ubangi Rivers. This suggests that these large rivers may be more of a barrier than previously believed. Molecular and morphological evidence supports a new cryptic species of *Grayia* from the upper and middle Congo River and its tributaries. This new species is estimated to have diverged from its nearest sister species, *G. ornata*, in the mid- to late Miocene—which coincides with the divergence dates of sister taxa within other Central African snake genera (Boaedon [Family Lamprophiidae], Atheris [Family Viperidae], and Polemon [Family Lamprophiidae]).

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1. Introduction

The world is currently undergoing a biodiversity crisis. African biodiversity, in particular, is threatened by a number of global change drivers including but not limited to deforestation, overhunting, pollution, and climate change (Sodhi et al. 2007, Archer et al. 2021, Marcantonio et al. 2021). Out of the top ten countries considered to be the most vulnerable in a recent climate change impact study, eight were in Africa (Marcantonio et al. 2021). Sampling is often difficult in many areas of Africa—because of remoteness, civil unrest, and disease outbreaks—and therefore our knowledge of African biodiversity is severely limited (Tolley et al. 2016, Greenbaum 2017). There are likely many species that will be lost in the wild before they are even known to science (Costello et al. 2013, Lees and Pimm 2015). In particular, cryptic species—or species that are morphologically similar but genetically distinct—are in urgent need of conservation protection. The field of molecular systematics aids in furthering our understanding of these understudied species and allows us to build phylogenies to reconcile the complicated taxonomy of African herpetofauna. Furthermore, it allows us to identify cryptic species that might require targeted conservation efforts and funding. The genus of interest for this study (Squamata: Colubridae: *Grayia*) represents an understudied and poorly known group of snakes. While not much is known about this aquatic snake genus compared to terrestrial ones, most people traveling though the waterways of Africa have sighted these snakes at one point in time. For example, in 1815, Captain Tuckey—in his "*Narrative of an Expedition to Explore the River Zaire*…" mentions killing a large watersnake that made its way into his boat (Tuckey 2006). Furthermore, *Through the Dark Continent* by Henry M. Stanley, there are descriptions of "lead-colored water-snakes…about 7 feet in length and 2 inches in diameter" that are likely referring to a *Grayia* species.

Grayia is a genus of aquatic Afrotropical snakes that is currently composed of four species: *Grayia caesar* (Günther 1863, Long-tailed African Water Snake), *G. ornata* (Bocage 1866 a,b , Ornate African Water Snake), *G. tholloni* (Mocquard 1897, Thollon's African Water Snake), and *G. smithii* (Leach 1818, Smith's African Water Snake, previously known as *G. smythii*) (Gruschwitz et al. 1991, Chippaux and Jackson 2019, Boundy 2020). These species are diurnal and mainly aquatic, often found in a variety of different lakes, rivers, and streams. However, they are known to shelter in thick waterside vegetation and artificial waterside constructions (Spawls et al. 2018). The genus is not always tied to large water bodies; *Grayia tholloni*, for example, is often found in small streams (Spawls et al. 2018). The western portion of both the Congo and Ubangi rivers often act as a barrier to terrestrial and arboreal snakes (e.g., *Toxicodryas* [Greenbaum et al. 2021]). However, because *Grayia* are almost exclusively aquatic, rivers likely serve as dispersal routes rather than barriers. *Grayia ornata* is believed to venture onto land only for basking and egg laying, although some authors suggest that this species could be considered partially arboreal because it frequently hunts from branches overhanging water (Perret 1957, Chippaux 2001, Pauwels et al. 2002, Ernst et al. 2020).

Grayia have a diet of fish and amphibians, but there have been some observed dietary differences correlated with sex and species. Adult male *G. smithii* feed primarily on the aquatic pipid frog *Xenopus tropicalis*, and secondarily, on tadpoles of the more terrestrial genus *Ptychadena* (Luiselli 2006). Adult female *G. smithii* were found to feed primarily on *Ptychadena* species and consume significantly more terrestrial *Sclerophrys* toads. While *G. smithii* and *G.*

tholloni are known to feed on fish and toads, *Grayia ornata* is considered primarily piscivorous, with several records documenting consumption of various catfish (Chippaux 2001). One adult female, collected in Garamba National Park in Democratic Republic of the Congo (DRC), was found to contain a juvenile, headless *Clarias* sp. (Family Clariidae), and the stomach of a young male *G. ornata* collected from Monte Alen National Park in Equatorial Guinea contained a *Parauchenoglanis* sp. (Family Claroteidae) (Pauwels et al. 2000). More recently, during the specimen examinations conducted for this study, the posterior part of a *Clarias* catfish was found in a specimen from Garamba National Park in DRC. Frogs, shrimp, and small rodents were also removed from the stomachs of *G. ornata* during dissection (Pauwels et al. 2002).

Reproduction strategies are presumed to be the same throughout the genus, but studies have primarily focused on *G. smithii*. *Grayia smithii* females were found to lay clutches of 3–4 eggs in different locations at different times (Akani and Luiselli 2001). This strategy, used by some turtles to avoid nest predation, had not been previously recorded in free-ranging snakes and it is hypothesized that this behavior is linked to reducing egg mortality from predation (Akani and Luiselli 2001).

The distribution of this genus varies by species. *Grayia ornata* and *G. caesar* have central African ranges, whereas *G. smithii* and *G. tholloni* have extensive sub-Saharan Africa distributions. *Grayia ornata* is found from Cameroon to Angola. In Central Africa, *G. ornata* are frequently found in a variety of aquatic habitats and often captured by fishermen in gill nets (Chippaux and Jackson 2019). They are strongly associated with forest habitat but can also be found in swamp forest habitat in the Republic of the Congo (Chirio and Ineich 2006, Chippaux and Jackson 2019). *Grayia caesar* is found from the island of Bioko in Equatorial Guinea to

Nigeria, the Central African Republic (CAR) and DRC, although there is some debate regarding whether their range extends as far as Nigeria. Chippaux and Jackson (2019) are one of the few authors to extend *G. caesar's* distribution as far west as Nigeria. They typically inhabit small to medium–sized streams in forest habitat (Chirio and LeBreton 2007, Pauwels and Vande Weghe 2008). *Grayia smithii* can be found from Senegal to Tanzania in waterside vegetation or water, usually in savanna (Spawls et al. 2018). In Nigeria, *G. smithii* can be found in mangroves, but they are strongly associated with rainforest habitats (Butler and Reid 1986, Luiselli and Akani 2002, Luiselli and Akani 1999, Chippaux and Jackson 2019). In DRC, they have been found in lowland rainforest habitat—several specimens collected by Dr. Greenbaum in DRC (Epulu) were found in this habitat (Schmidt 1923). This species is found throughout semi-deciduous and dense evergreen forests in Cameroon as well as high–altitude savannas and "hautes terres de l'Ouest "(western highlands) (Chirio and LeBreton 2007). *Grayia smithii* has previously been found as far northeast as South Sudan (Loveridge 1955). Lastly, *G. tholloni* is found from Kenya to Angola and as far north as Chad (Roussel and Villiers 1965). They are known to inhabit lakes, rivers, and streams in woodland, moist savannas, and savanna–forest mosaics habitats (Chirio and LeBreton 2007, Spawls et al. 2018, Chippaux and Jackson 2019). They prefer medium to large waterways and have been recorded as far east as Kenya (Hughes 1983).

These non-venomous snakes are naturally long and stocky, between 1.5–2.5 m. The tail is usually long, over 40% of the body length in *G. tholloni*. The dorsal scales of this genus are smooth and lack apical pits. Loreal scales are usually present in all four species and there are never suboculars present (Spawls et al. 2018, Chippaux and Jackson 2019). The hemipenes of a *G. ornata* dissection has been described as unusually long, extending as far as the seventeenth subcaudal, forking at the twelfth one, with a sulcus dividing at the sixth one (Bogert 1940). This species possesses a unique accessory scale found among the upper labials. These scales are referred to as the extralabial scales (rarely as cunate scales), and there are typically 1–2 present, usually between the 5th and 6th supralabial. This scale has only been recorded in *Grayia ornata*, and can be used as a diagnostic character. *Grayia caesar* is one of the more morphologically unique species within *Grayia*. The long and thin body, elongate tail, and large eyes are not typical of aquatic snakes (Pauwels and Vande Weghe 2008). The maxilla of *G. caesar* has been noted as distinctly different from the other three species within *Grayia* and the number of teeth is usually greater than 35, which increase in size from the front of the mouth to the back (Chippaux 2001). Furthermore, *G. caesar*, aptly named the long-tailed watersnake, often has more subcaudal scales than ventral scales. This trait is not typical in snakes, and aside from *G. caesar*, has been documented in genera such as *Cercophis*, *Dendrophidion*, *Leptophis*, *Uromacer*, *Uromacerina*, *Xenoxybelis*, and some species from Madagascar such as *Liopholidophis grandidieri* (Mertens 1968, Cadle 1996, Zassi-Boulu et al. 2019). One study found that *G. caesar* displayed several sexually dimorphic characteristics: anal scale state, number of white bands on body, number of ventral scales, and number of subcaudal scales (Pauwels et al. 1998). *Grayia smithii* is the largest species within *Grayia*, with the longest recorded individual measuring 2,550 mm (Doucet 1963). This species has the smallest number of maxillary teeth (< 24) that have been described as “more sharply recurved in the anterior of the bone” (Bogert 1940). Stucki-Stirn (1979) described the dentition of *G. smithii* as long and recurved in order to better allow them to catch slippery prey. Lastly, *Grayia tholloni* is a midsize member of the genus, with the longest individual measuring 1,200 mm (Villiers 1975). This species is typically dark brown with white scales forming bands across its body. This patterning tends to fade with age and makes identification of older individuals more challenging.

Grayia are often mistaken for the Banded Water Cobra (*Naja annulata*), because they have a similar body size, shape, and color pattern. This is considered by some authors to be an example of mimicry, but others (Chippaux and Jackson 2019) believe it may be convergence to a similar ecological niche. There is often a high degree of intra- and interspecific morphological variation within *Grayia*. This has made identification difficult and previous studies involving *Grayia*—and several "*Grayia*" samples on GenBank—included misidentified specimens in other genera.

Grayia are often used by local people in a variety of ways, including as a form of "bushmeat" food, especially during the dry season. Specifically, *G. ornata* is considered an excellent source of protein and is often captured and eaten by women and children (Pauwels et al. 2002). *Grayia* also have a variety of medicinal uses. *Grayia ornata* comprises the basic component of a remedy for childbirth delivery complications, and its body is used as a bangle around the ankle of newborns to "suck out sickness" (Pauwels et al. 2002). They are also used in so-called "vaccinations," which are believed to enhance swimming ability and ensure high fishing success (Pauwels et al. 2002). Thus, this genus is an important part of the practical and cultural lives of many African people.

The species within *Grayia* have undergone a variety of name changes since the early 19th century. The first description of *Grayia ornata* (Bocage 1866 a,b) was under the name *Macrophis ornatus*, *G. caesar* (Günther 1863) was originally *Xenurophis caesar* (the sole member of the *Xenurophis* genus), and *G. smithii* (Leach 1818) was *Coluber smythii;* only, *G. tholloni* (Mocquard 1897) was originally described in the current genus. *Coluber smythii* (now *Grayia smithii*) was discovered in 1815 "in great plenty" near Embomma (now Boma, DRC) and was collected on Captain Tuckey's expedition exploring the Congo River. The species was later described by William Elford Leach (1818). The next mention of this genus was a synonym of *G. smithii* described in 1844 by Hallowell and was named *Coluber laevis* (Wallach et al. 2014). *Coluber laevis* would later be synonymized with *Coronella triangularis*—from "West Africa"—by Hallowell in 1854. Hallowell (1857) would then move *Coronella triangularis* to *Heteronotus triangularis* which would later be renamed *Glaniolestes triangularis* by Slack in 1862—but few authors acknowledged this new genus and *H. triangularis* would still be used for many years. The next year in 1858, the genus *Grayia* was first named in honor of the British herpetologist John Edward Gray with the type species *Grayia silurophaga* (now *G. smithii*) from "West Africa" (Günther 1858, Beolens et al. 2012). *Lejonotus schlegeli*, a rarely mentioned synonym of *G. smithii* from Ghana*,* was the next to be described by Jan in 1863 (Wallach et al. 2014). In the same year that Jan described *Lejonotus schlegeli,* Günther (1863) described *Xenurophis caesar* (the sole member of the *Xenurophis* genus) with the type specimen from "Fernando Po" (now the island of Bioko in Equatorial Guinea). Three years later in 1866, Bocage would write about a novel species of watersnake from "Duque de Bragança" (now Calandula, Angola) named *Macrophis ornatus* which he believed to be representative of a new genus*.* That same year, *H. triangularis* would be transferred to the genus *Grayia* as *Grayia triangularis* (Bocage 1866a, b). In 1877, Peters would describe a synonym *of G. ornata* called *Glaniolestes ornatus* (Marques et al. 2018). This species did not have a type locality mentioned and was placed in the *Glaniolestes* genus originally created by Slack (1862) which included *Glaniolestes triangularis*. Mocquard (1887) described *Grayia furcata*— now a synonym of *G. ornata* from "Congo par la Mission de Brazza" (i.e., Brazzaville, Republic of the Congo) (Boulenger 1901, Bocage 1895). In the same year, Bocage (1887) relegated *C. triangularis* and *H. triangularis* as synonyms of *G. smithii.* Three years later, Mocquard (1891) would once again describe a new species of *Grayia* from "San Benito" (Equatorial Guinea). He called the novel species *Grayia longicaudata,* which would later be recognized as a synonym of *G. caesar* (Wallach et al. 2014). In 1895, Bocage would recognize the similarities between *G. furcata*, *Glaniolestes ornatus* and *M. ornatus* and list all three as synonyms of *Grayia ornata*. Two years after this revision of *Grayia*, Mocquard (1897) would describe *Grayia tholloni* based on four syntypes from "Brazzaville, French Congo" (Republic of the Congo). Along with this species description, Mocquard was able to notice the similarities between *X. caesar*, *G. smithii* and *G. ornata* and he suggested uniting *Xenurophis* and *Grayia*. Later, Boulenger (1901) described *G. faciata* (now *G. tholloni*) based on a single specimen from "South-west of Lake Tanganyika, Lemaire Mission" (DRC) and described it as a transition from *Grayia* to *Xenurophis*. This transition species led him to agree with Mocquard that *Xenurophis* and *Grayia* should be united. Boulenger (1909) later listed four members within the genus *Grayia*: *G. tholloni*, *G. ornata*, *G. smithii,* and *G. caesar*. At the same time, he would remove *Grayia giardia* (identifying it as *Tropidonotus olivaceus* [now *Natriciteres olivacea]*) and *Grayia lubrica* (identifying it as *Tropidonotus laevissimus* [now *Lycodonomorphus laevissimus*]) from the genus and confirm Bocage's claims that *G. furcata* should be considered a synonym of *G. ornata*. Sternfeld (1910) would base his description of *Grayia striata* on a single juvenile specimen from "Kamerun, Bezirk Lome" (Cameroon, Lome district). *Grayia striata* was representative of the longitudinally striped phase of *G. ornata* and was later synonymized with the latter taxon (Schmidt 1923). Lastly, in 1923, Werner would describe *Grayia hydrina*, but because of the abnormally high scale counts (182 ventrals), this is likely not a member of *Grayia,* and is not a known synonym of any of the four species currently in the genus.

Grayia superficially resemble natricines, but molecular phylogenies have failed to consistently ally the former snake group with any other families (Cadle 1994, Vidal and Hedges 2002, Lawson et al. 2005, Vidal et al. 2007). More recent molecular phylogenies recovered *Grayia* in its own distinct subfamily (Grayiinae), which was strongly supported as the sister group to Colubrinae in two studies (Nagy et al. 2007, Pyron et al. 2013). Although the relationships between snake subfamilies is poorly resolved, Calamariinae and Colubrinae are often listed as sister groups to Grayiinae (Pyron et al. 2013, Figueroa et al. 2016). Unfortunately, because tropical African snakes are generally understudied, the relationships within *Grayia* are poorly known.

Only three *Grayia* species (*G. caesar*, *G. ornata,* and *G. smithii*) are currently evaluated for threat status and none are considered endangered, but this study is likely to identify cryptic species that are genetically distinct and in need of urgent conservation protection because of increasing pollution, dams, and hunting that threaten most of Africa’s freshwater vertebrates (Sodhi et al. 2007, Biginagwa et al. 2016, Cutler et al. 2020). The reality of the situation is that although the snakes within *Grayia* are not currently threatened with extinction, this is likely to change in the near future. Furthermore, with the prevalent human use of these snakes for “bushmeat” and various cultural practices, their populations are likely to decline more rapidly.

The goal of this study is to build a phylogenetic tree that can be used to understand the relationships and taxonomy of *Grayia* via an integrative taxonomic approach that combines molecular and morphological data. Though not jointly analyzed, the results generated from the phylogenetic analyses will be compared and reconciled with those of the morphological analysis in order to form robust taxonomic conclusions. The General Lineage Concept (de Queiroz 2007) will guide my recognition of species boundaries as separately evolving metapopulations. Molecular data will be combined with traditional morphological data (measurements and scale counts) and used for species recognition.

2. Materials and Methods

2.1 Molecular phylogenetics

2.1.1 Taxon sampling

Sixty total *Grayia* tissue samples, representing all four species, were obtained from various museum collections, universities, private collections (Table 2), and combined with published molecular data from GenBank (n = 2). Many of the specimens were collected by Dr. Eli Greenbaum and his Congolese colleagues from eastern DRC from 2007–2012. Field seasons 2007 through 2009 were during the dry season, whereas 2009/2010, 2010/2011 and 2011/2012 were during the wet season. Specimens collected by Chifundera Kusamba, Wandege M. Muninga, and Mwenebatu M. Aristote were collected from DRC in 2014 (dry season) and 2015 (wet season).

2.1.2 DNA extraction, PCR, and sequencing

DNA extractions were conducted with Qiagen DNeasy tissue kits (Qiagen Inc., Valencia, CA, USA). Four mitochondrial (16S, COI, cyt *b*, and ND4) and two nuclear genes (BDNF and NT3) were amplified using standard PCR techniques with the following primers (Table 1) for BDNF: BDNF-F and BDNF-R (Noonan and Chippindale 2006), NT3: NT3-F3 and NT3-R4 (Noonan and Chippindale 2006), COIF: fishCO1 and fishCO1R (Deichmann et al. 2017), cyt *b*: L14910 and H16061 (Burbrink et al. 2000), 16S: L2510mod/16Sar, and H3056/16Sbr (Zaher et al. 2009), and ND4: ND4 and HIS1276 (Arèvalo et al. 1994, Pook et al. 2009). Twenty-five µL PCR reactions were conducted with an initial denaturation step of 90°C for 2 minutes, followed by denaturation at 95°C for 35 seconds, annealing at 50°C for 35 seconds, and extension at 72°C for 95 seconds with 4 seconds added to the extension per cycle for 32 cycles. Amplification products were visualized on a 1.5% agarose gel stained with Invitrogen SYBR safe DNA gel stain (Thermo Fisher Scientific, Waltham, MA, USA). Successful PCRs were purified with Agencourt Ampure XP magnetic bead solution (Beckman Coulter Inc., Indianapolis, IN, USA) and sequenced with an ABI 3500 automated sequencer at the University of Texas at El Paso (UTEP) Genomic Analysis Core Facility.

2.1.3 Sequence alignment and phylogenetic analyses

The resulting sequences, supplemented with material from GenBank, were aligned using MUSCLE (Edgar 2004) within the program Mesquite v3.70 (Maddison and Maddison 2015). Hypervariable regions of the 16S gene were removed (22 bp), and further minor manual adjustments and editing were carried out in MacClade v4.08 (Maddison and Maddison 2005) or Mesquite. Based on a previous study of snake phylogeny, *Masticophis* (Colubrinae), *Calamaria* (Calamariinae), and *Sibynophis* (Sibynophiinae) were chosen as outgroups and the latter genus was used to root the tree (Pyron et al. 2014). The time-calibrated BEAST analysis included sequences obtained from GenBank from the genus *Achalinus* (Xenodermatidae) to calibrate the tree using the divergence between Colubroidea and its nearest sister taxon (Head et al. 2016).

The aligned sequences were then used to construct phylogenetic trees from concatenated data with Maximum Likelihood (ML) and Bayesian Inference (BI) methods. ML analyses were conducted in RAxML (Stamatakis 2014) via the CIPRES Science Gateway (https://www.phylo.org/) and BI using BEAST v2.5 (Bouckaert et al. 2019). Initial single-gene phylogenetic analyses were conducted in RAxML to ensure similar topologies and then concatenated datasets were used for subsequent analyses. Datasets for the analyses were partitioned by codon position in single-gene datasets, and in combined-gene datasets by gene and codon position.

For RAxML, a random starting tree was used and all parameters were estimated. The GTRGAMMA model was used for all partitions. The resulting support values for the clades inferred by ML analyses were assessed with the rapid bootstrap algorithm with 1000 replicates. For BEAST, models of evolution for each marker were selected using the program MEGA v6.0 (Tamura et al. 2013) to establish the best model of evolution. In cases where the model selected in MEGA v6.0 was not available in BEAST v2.5, the next-best model was selected, or the rate categories and other parameters were set to match the best model. A relaxed-clock model with a Yule tree model prior was used. The time calibration for divergence dating was set using two known fossil calibration dates: the Pan-Colubroidea node estimated between 50.5 and 72.1 million years ago, using a uniform prior, and the Colubridae + Elapoidea node estimated at a minimum age of 30.9 ± 0.1 million years ago, using a log normal prior (Head et al. 2016). Bayesian analyses were conducted with random starting trees and run for 20 million generations with Markov chains sampled every 1,000 generations. To confirm that the various runs converged, the program Tracer v1.7 (Rambaut et al. 2018) was used to ensure ESS values were above 100. Burn-in was set at 25%, and thus 5,000 of the initial trees were discarded. The trees produced were summarized using TreeAnnotator (Drummond and Rambaut 2007) and phylogenies were visualized with FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

In addition, a gene tree-species tree analysis was conducted in BEAST v2.5 using the *BEAST template (Bouckaert et al. 2019). The gene tree-species tree was created using the same concatenated, aligned, and partitioned dataset from the previous BEAST analysis. Taxon sets were created using the clades indicated by the ML and BI trees, and a relaxed-clock model was used along with a Yule model prior. The gene tree-species tree was set to run for 50 million generations with burn-in set to 25%. Trees were summarized and visualized using TreeAnnotator and Figtree v1.4.4, respectively.

Sequence divergence analyses were calculated with uncorrected p-distances in the program MEGA v6.0. Lastly, a species-delimitation analysis was conducted using the GYMC method through the splits R package (Ezard and Fujisawa 2009). The time-calibrated BI tree was used as the ultrametric guide tree for the analysis and a single-tree method was used. The analysis was run for 10,000 generations, sampled every 100 generations, and the first 1,000 trees were discarded as burn in.

2.2 Morphological analyses

The morphological portion of this project consisted of examination of hundreds of natural history specimens from multiple collections in the US, Africa, and Europe. Specimens used in the morphological analysis are listed in Supplemental Table 1, and all museum acronyms follow Sabaj (2020). Morphological data collected from the literature were obtained from the following sources: Boettger (1889), Loveridge (1936), Laurent (1956), Laurent (1960), Villiers (1966), Broadley (1991), Pauwels et al. (2002), and Portik et al. (2016). In total, data were obtained from 717 total specimens: 248 *Grayia ornata*, 273 *Grayia smithii*, 161 *Grayia* *tholloni*, and 35 *Grayia ceasar*. Project collaborator and Belgian herpetologist Olivier Pauwels collected morphological data from hundreds of *Grayia* specimens and is responsible for the majority of the morphological dataset. These data comprise both morphometric measurements and meristic counts that were recorded from preserved specimens with digital calipers and the aid of a stereomicroscope. Mensural characters included snout–vent length (SVL), from tip of snout to anterior edge of vent; tail length (TaL), from tip of tail to posterior edge of vent; total length (TL), from tip of snout to tip of tail; head width (HW), measured at widest point of the head near jaw rictus; eye width (EW), measured as the horizontal width; head length (HL), from tip of snout to posterior edge of parietal; naso–ocular distance (NOD), from the posterior edge of nostril to front of eye orbit; rostral height (RH), from the apical point of the lingual furrow to the intersection of the rostral and two internasials; rostral width (RW), distance between the right and left intersection points between the rostral, supralabial, and nasal; frontal length (FL), measured as the distance between the anterior point where the frontal meets the prefrontals and the posterior point where the frontal meets the parietals; frontal width (FW), from the left and right intersection points between the frontal, supraocular, and prefrontal; frontal–rostral distance (F–R Dist.), measured as the distance between the posterior-most point of the rostral to the intersection points of the frontal and two prefrontals; internasals contact (IC), measuring the median contact between internasal scales; prefrontals contact (PrC), measured as the median contact between prefrontal scales; parietals contact (PaC), as the median contact between prefrontal scales; distance between nostrils (INOSDIST), from the antero-superior points of the nostrils across the internasals; loreal width (LW), from the anteriormost point along the supralabials to the posterior most point along the supralabials; loreal height (LH), measured from the anteriormost point along the supralabials to the intersection between the loreal, postnasal, and prefrontal; lower anterior temporal length (LA–T), measured as the maximum distance between two points of the lower anterior temporal; lower anterior temporal–loreal distance (LA–TL), as the minimum distance between the lower anterior temporal and the loreal; anterior sublingual length (ASL), as the maximum distance between two points of the anterior sublingual; anterior sublingual width (ASW), measured as the distance between the infralabials and posterior contact points between the first infralabial and sublingual; and interocular distance (ID), from the lateral edges of the eyes. Meristic characters included ventral scale counts—made using both the standard method (i.e., first scale that is broader than long) (VENTS) and the method of Dowling (1951) (VENTD)—subcaudals (SCDL); postoculars (POSTOC); preoculars (PREOC); supralabials (SUPRA); infralabials (INFRA); prefrontals (PFRO); 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); number of infralabials in contact with the anterior chin shields (TCHIN); number of supralabials in contact with the orbit (TEYE); body bands as the number of dorsal bands between the head and cloaca; and tail bands as the number of bands on the dorsal part of the tail between the tail tip and cloaca (cream or yellow bands in *G. caesar* and *G. tholloni* and dark brown or black bands in *G. ornata* and *G. smithii*). In *G. ornata*, the extralabials—described as the accessory scale found in between supralabials—and extralabial contact, referring to which two supralabial scales the extralabial is found between, were also recorded. All measurements and scale counts were taken on the right side of the body unless noted otherwise.

2.3 Statistical analyses

Statistical comparisons of selected measurements and counts were conducted using two-tailed t-tests, principal component analysis (PCA), and analyses of covariance (ANCOVA). PCA analyses of mensural data were conducted in R v4.03 and used to identify patterns of variation in the data (R Foundation for Statistical Computing, Vienna, Austria). Each dataset was separated based on sex and the individual specimens were categorized into populations based on placement within the phylogenetic tree, unique morphological features, and locality.

Several populations were grouped based on their placement within the Congo River. Lower Congo specimens consisted of those located between the Kinsuka rapids (Kinshasa, DRC) and the mouth of the Congo River. Middle Congo specimens consisted of those located between Kinshasa and the Boyoma rapids (Kisangani, DRC), and upper Congo specimens consisted of those found upstream of the Boyoma Falls.

For *G. ornata*, specimens were separated into three distinct populations for the morphological analysis. Initially, the three populations consisted of the green clade indicated in the phylogenetic tree (Figs. 1–2) from the mid and upper Congo River, all the specimens outside of the Congo River Basin, and those that were found within the basin but were not genetically identified as a possible new species. The initial PCA conducted on these groups did not form distinct clusters in multivariate space and thus new groups were created. For the final analysis, *G. ornata* was separated into a population from the Ogooué River Basin, and surrounding areas in Equatorial Guinea and Cameroon (referred to as Ogooué *G. ornata* below, N = 7). These specimens were unique in that they all had 19 scale rows at midbody, which were not found in any specimens from the Congo Basin. The other two populations consisted of the green clade indicated in the phylogenetic tree and four morphological specimens (*G.* cf. *ornata*, N = 10), and all other specimens (*G. ornata*, N = 231).

Grayia smithii was initially divided into eight different populations based on geographic patterns in morphological variation. The Atlantic River Basin population, Chad River Basin population, lower Congo River population, eastern striped population, Semliki River/Lake Edward population, western population, Garamba National Park population, and middle–upper Congo population. The initial PCA indicated that these groups were not distinct and the groupings were reconsidered. The final analyses were conducted on four populations that had distinct morphological characters: *Grayia smithii* from the Congo, Chad, Atlantic and Nile River Basins (Central African *G. smithii*, N = 165), striped population found in eastern DRC and Uganda (Eastern Striped *G. smithii*, N = 11), Semliki River/ Lake Edward population (Semliki/Edward *G. smithii*, N = 5), and a western population found in Senegal, Guinea, Sierra Leone, Liberia, Côte d'Ivore, Ghana, Togo, Benin, and Nigeria (Western *G. smithii*, N = 81).

Grayia tholloni was initially divided into a population consisting of specimens from outside the Congo Basin, the Congo Basin, Lake Tanganyika, Nile River Basin, West Africa (Senegal, Gambia, Guinea, and Nigeria), Kenya, Ethiopia, and the Zambezi River Basin. These groups were primarily chosen based on locality—as previous studies on aquatic organisms have recorded high genetic diversity between river basins and high levels of endemism in the Great Lakes (Steenberge et al. 2020, Ortiz-Sepulveda et al. 2020). Other populations, such as West African *G. tholloni*, were chosen because of geographic patterns in morphological variation. The initial PCA conducted on these groups did not form distinct clusters in multivariate space and new groups were created. The final groups for the analysis were created based on locality and distinct morphological characters, and consisted of populations from Lake Tanganyika (Lake Tanganyika *G. tholloni*, N = 5), Nile River Basin (Nile *G. tholloni*, N = 16), West Africa (Western *G. tholloni* from Senegal, Gambia, Guinea, and Nigeria, N = 9), and *G. tholloni* from the Congo, Chad, and Atlantic River Basins (Central *G. tholloni* N = 131).

Grayia caesar was initially divided into seven populations based on locality: lower Congo River, middle Congo River, upper Congo River, Nile River Basin, Ogooué River Basin, Bioko, and specimens outside the Congo Basin. The initial PCA on the seven groups did not form distinct clusters and *G. caesar* was restructured into one population (N = 36).

For the mensural data t-tests, only adults were used with a SVL > 400 mm, whereas t-tests with meristic data included individuals of all sizes. Before the t-tests were conducted, each variable was tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965). If the data were not normal, they were either normalized through transformations or the non-parametric Wilcoxon test was used (Wilcoxon 1945), as indicated in the results. Analyses of covariance (ANCOVA) were conducted in Minitab (State College, PA: Minitab, Inc.) with snout–vent length as the covariate to eliminate the effect of size (Packard and Boardman 1999).

3. Results

3.1 Molecular

The molecular dataset included 3 *Grayia caesar*, 35 *G. ornata*, 16 *G. smithii*, and 6 *G. tholloni* (Table 2). Including outgroups, a total of 66 sequences (60 generated for the first time in this study) were used to build the ML and BI phylogenetic trees of *Grayia*. The dataset included the mitochondrial genes 16S (491 base pairs [bp]), cyt *b* (1112 bp), ND4 (689 bp), COI (680 bp), and the nuclear genes BDNF (660 bp), and NT3 (488 [bp]) for a total of 4159 bp. The maximum likelihood tree (Fig. 1) and Bayesian Inference time-calibrated tree (Fig. 2) recovered a monophyletic *Grayia* with two well-supported clades, including *Grayia ornata* + *G. smithii*, and *G. caesar* + *G. tholloni*. Both trees recovered two reciprocally monophyletic clades of *G. ornata*. One clade of *G. ornata* (*sensu stricto*) consisted of specimens from both within and outside the Congo Basin, and was strongly supported. The second clade (*Grayia* cf. *ornata*), found within the Congo Basin in the upper and middle Congo River and its tributaries, was well supported and markedly divergent from the other clade of *G. ornata*. The BI tree indicated that *Grayia* diverged from its nearest sister clade in the late Eocene (median age 38.6 Mya). The *Grayia ornata* + *G. smithii* clade and *G. caesar* + *G. tholloni* clade diverged in the mid-Oligocene (median age 31.3 Mya). Diversification between the four species is estimated to have occurred during the late Oligocene, with *G. smithii* and *G. ornata* diverging 24.9 Mya and *G. caesar* and *G. tholloni* diverging 23.4 Mya. Lastly, the two *G. ornata* clades (*sensu stricto* and *G.* cf. *ornata*) are estimated to have diverged during the mid-Miocene (median age 15.8 Mya).

The results of the gene tree-species tree (Fig. 3) were mostly consistent with those of the time-calibrated BI analysis, but the divergence dates indicated in the former occurred slightly later. The gene tree-species tree indicated that *Grayia* diverged from its nearest sister clade in the late Eocene (34.9 Mya). The *G. ornata* + *G. smithii* clade and the *G. tholloni* + *G. caesar* clade diverged during the mid-Oligocene (median age 27.3 Mya). The two *G. ornata* clades split from *G. smithii* during the early Miocene (median age 20.5 Mya), and the *Grayia tholloni* and *G. caesar* clades diverged from each other during the early Miocene (median age 20.9 Mya). Lastly, the tree indicated that *G.* cf. *ornata* diverged from *G. ornata* in the late Miocene (median age 8 Mya).

Multiple amino acid substitutions were observed between *G.* cf. *ornata* and *G. ornata*. For COI, the 61st codon position translated to isoleucine in *Grayia* cf. *ornata* and valine in *G. ornata*. For cyt *b*, five amino acid translation differences were found between *G. ornata* and *G.* cf. *ornata*: position 100 was isoleucine in *G.* cf. *ornata* and alanine in *G. ornata*; position 105 was threonine in *G.* cf. *ornata* and isoleucine in *G. ornata*; position 175 was isoleucine in *G.* cf. *ornata* and valine, alanine, threonine or serine in *G. ornata*; position 262 was valine in *G.* cf. *ornata* and threonine or isoleucine in *G. ornata*; and position 367 was valine or isoleucine in *G.* cf. *ornata* and alanine in *G. ornata*. The gene ND4 had three amino acid translation differences between *G.* cf. *ornata* and *G. ornata*: position 401 translated into serine in *G.* cf. *ornata* and isoleucine in *G. ornata*; position 574 was alanine in *G.* cf. *ornata* and threonine in *G. ornata*; and position 595 translated to isoleucine in *G.* cf. *ornata* and threonine or alanine in *G. ornata.*

Sequence divergence analyses between *G.* cf. *ornata* and *G. ornata* recovered high uncorrected p-distances in mitochondrial genes (cyt *b*: 10.54–25.00%, COI: 6.62–17.35%, ND4:

11.39–14.04%, 16s: 0.85–3.93%). The two nuclear genes used in this study had substantially lower sequence divergence (BDNF: 0.0–0.83%, NT3: 0.0–1.96%). Species delimitation analyses indicated that there were seven total species within *Grayia* (p-value = 2.72e -4, Fig. 1). *Grayia ornata* was split into four distinct species in total. *Grayia* cf. *ornata* was well supported as a species (.98) and the analysis also supported two other, distinct *G. ornata* species. The first of these latter putative species contained nine samples with localities outside the Congo basin (MBUR 3399, MNHN 1977.6517, TR 3685, TR4661, MCZ R188643, MTD 48961, TR 4627, and MBUR 2929) and the second contained four samples (EBG 2636, CRSN 85, CRSN 86, and CRSN 87) from northeastern DRC in the Ituri lowland rainforest. These two putative species only received moderate support (.90 and .70). The remainder of the *G. ornata* samples were grouped into one species with a low support value (.36). *Grayia smithii*, *G. tholloni* and *G. caesar* were both supported as single species.

3.2 Morphological

In total, 776 *Grayia* specimens (693 morphological, 60 genetic, and 23 genetic samples with morphological data) [Figs. 4–9, Tables 2–9, Supplemental Table 1]) were examined from across sub-Saharan Africa. Through the analysis of these specimens, various misidentifications were discovered within the dataset—one of which represents a new country record. One sample of *G. smithii* (ET_17), that was initially identified in the field as *G. tholloni*, expands the distribution of *G. smithii* to include Ethiopia (Largen and Spawls 2010).

The results of the analyses comparing *G.* cf. *ornata* (Males N = 7, Females N = 3) to *G. ornata sensu stricto* (Males N = 127, Females N = 98) resulted in four significantly different characters in females and twelve in males. For t-tests, female *G.* cf. *ornata* had a significantly lower number of subcaudals ($p < 0.0000$), body bands ($p = 0.0478$), and the number of infralabials touching the chin shields ($p = 0.0033$), and a significantly higher number of supralabials (Wilcoxon Test, $p = 0.012$) than *G. ornata*. T-tests on males revealed twelve significantly different characters. Male *G.* cf. *ornata* had significantly lower infralabials (Wilcoxon Test, $p = 0.0144$), body bands ($p < 0.0000$), head length ($p = 0.0448$), SVL ($p = 0.0208$), tail length ($p = 0.0326$), NOD ($p = 0.0066$), frontal length ($p = 0.0413$), frontal width ($p = 0.0212$), frontal–rostral distance ($p = 0.0396$), internasals contact ($p = 0.0123$), anterior sublingual width ($p = 0.0091$), anterior sublingual length ($p = 0.0196$), and subcaudals ($p = 0.0050$) than *G. ornata*. The ANCOVAs resulted in four significantly different characters in females: anterior sublingual length ($p = 0.0380$), frontal width ($p = 0.0350$), loreal length ($p = 0.0530$), and lower anterior temporal–loreal distance ($p = 0.0270$) were significantly lower in *G.* cf. *ornata*. The ANCOVAs for males resulted in two significantly different characters: internasals contact ($p = 0.0110$) was significantly lower, and rostral height ($p < 0.0000$) was significantly higher in *G.* cf. *ornata*.

The statistical analyses comparing the Ogooué *G. ornata* (Males $N = 4$, Females $N = 9$) to *G. ornata sensu stricto* (Males $N = 127$, Females $N = 98$) resulted in multiple significantly different characters. For females, there were a total of 25 significantly different characters. Ogooué *G. ornata* had significantly higher SVL ($p = 0.0083$), distance between the nostrils ($p < 0.0000$), VENTD ($p = 0.0001$), VENT ($p = 0.0006$), DSRN (Wilcoxon Test, $p < 0.0000$), DSRM (Wilcoxon Test, $p < 0.0000$), DSRV (Wilcoxon Test, $p = 0.0013$), and significantly lower ID ($p = 0.0010$), NOD ($p = 0.0516$), rostral width ($p = 0.0005$), frontal width ($p = 0.0147$), frontal–rostral distance ($p = 0.0105$), internasals contact ($p= 0.0129$), prefrontal contact ($p < 0.0000$), loreal length ($p = 0.0037$), lower anterior temporal length ($p < 0.0000$), lower anterior temporal–loreal distance ($p = 0.0499$), body bands ($p = 0.0171$), EW ($p = 0.0285$), HL ($p = 0.0480$), anterior sublingual length ($p = 0.0214$), anterior sublingual width ($p = 0.0264$), and extralabials ($p = 0.0219$). Male Ogooué *G. ornata*, had significantly higher rostral height ($p = 0.0328$), frontal length ($p = 0.0069$), loreal length ($p = 0.0157$), anterior sublingual width ($p = 0.0351$), VENTD ($p < .0000$), VENT ($p = 0.0053$), DSRN (Wilcoxon Test, $p = 0.0007$), and significantly lower anterior sublingual length ($p = 0.0273$), and infralabials (Wilcoxon Test, $p = 0.0500$). The ANCOVAs conducted between the Ogooué *G. ornata* and *G. ornata sensu stricto* recovered three statistically different characters in females and two in males. For female Ogooué *G. ornata*, EW ($p = 0.0360$), internasals contact ($p = 0.0260$), and loreal height ($p = 0.0050$) were significantly higher than *G. ornata*. For male Ogooué *G. ornata*, the anterior sublingual length ($p = 0.0050$) and HW ($p = 0.0120$) were significantly higher than *G. ornata sensu stricto*.

T-tests comparing *G. smithii* populations from Congo, Chad, and the Atlantic and Nile River Basins (Central African *G. smithii*, Males N = 77, Females N = 98) with Western (Nigeria and other localities in West Africa) *G. smithii* (Males N = 46, Females N = 35) resulted in nine statistically significant characters in males and ten statistically significant characters in females. For male Central African *G. smithii*, internasals contact ($p = 0.0098$), VENTD (Wilcoxon Test, $p < 0.0000$), VENT (Wilcoxon Test, $p = 0.0011$), subcaudals (Wilcoxon Test, $p = 0.0119$), DSRM (Wilcoxon Test, $p = 0.0199$), and DSRV (Wilcoxon Test, $p = 0.0032$) were significantly lower, and HW (Wilcoxon Test, $p = 0.0319$), number of infralabials touching chin shields (Wilcoxon Test, $p = 0.0450$), and body bands (Wilcoxon Test, $p = 0.0062$) were significantly higher than Western *G.*

smithii. For female Central African *G. smithii*, EW ($p = 0.0250$), HL ($p = 0.00446$), internasals contact ($p = 0.0017$), loreal length (Wilcoxon Test, $p = 0.0010$), anterior sublingual length ($p = 0.0146$), VENTD ($p < 0.0000$), VENT ($p = 0.0027$), and DSRV (Wilcoxon Test, $p = 0.0006$) were significantly lower, and body bands (Wilcoxon Test, $p = 0.0276$) and loreal height ($p = 0.0028$) were significantly higher than Western *G. smithii*. The ANCOVAs conducted on the Central African *G. smithii* and Western *G. smithii* resulted in nine differences in males and six differences in females. For male Central African *G. smithii*, anterior sublingual length ($p < 0.0000$), EW ($p = 0.0060$), frontal–rostral distance ($p < 0.0000$), internasals contact ($p < 0.0000$), and loreal length ($p < 0.0000$) were significantly lower, and rostral height ($p < 0.0000$), ID ($p = 0.0060$), HW ($p = 0.0080$), and distance between the nostrils ($p = 0.0060$) were significantly higher than Western *G. smithii*. For females Central African *G. smithii*, anterior sublingual length ($p < 0.0000$), internasals contact ($p < 0.0000$), and loreal length ($p = 0.0060$) were all significantly lower, and rostral height ($p < 0.0000$), ID ($p < 0.0000$), and distance between the nostrils ($p < 0.0000$) were all significantly higher than Western *G. smithii*.

T-tests comparing Central African *G. smithii* (Males $N = 77$, Females $N = 98$) with Semliki/Edward *G. smithii* (Males $N = 2$, Females $N = 3$) found no differences in males and 16 in females. Central African females had significantly lower SVL ($p < 0.0000$), HW ($p = 0.0306$), EW ($p = 0.0074$), HL ($p = 0.0042$), NOD ($p = 0.0002$), distance between nostrils ($p = 0.0308$), ID ($p = 0.0406$), frontal length ($p = 0.0030$), frontal width ($p = 0.0038$), frontal rostral distance ($p < 0.0000$), internasals contact ($p = 0.0002$), prefrontal contact ($p = 0.0212$), anterior sublingual length ($p = 0.0357$), anterior sublingual width ($p = 0.0201$), and significantly higher VENTD ($p = 0.0217$), and VENT ($p = 0.0190$) than Semliki/Edward *G. smithii*. The ANCOVAs conducted on the

Central African *G. smithii* and Semliki/Edward *G. smithii* resulted in three differences in males and two differences in females. For males, distance between the nostrils ($p = 0.0330$), rostral height ($p = 0.0350$), and rostral width ($p = 0.0380$) were all significantly lower in the Central African population. For females, HW ($p < 0.0000$) and parietals contact ($p = 0.0120$) were significantly lower in the Central African population.

T-tests comparing Central African *G. smithii* (Males N = 77, Females N = 98) with the eastern DRC and Uganda striped *G. smithii* (Eastern striped *G. smithii*, Males N = 5, Females N = 6) resulted in four differences in females and seven in males. In females, postoculars (Wilcoxon Test, $p < 0.0000$), VENTD (Wilcoxon Test, $p = 0.0300$), and Infralabials (Wilcoxon Test, $p = 0.0455$) were significantly lower, while infralabials touching chin shields (Wilcoxon Test, $p = 0.0010$) were significantly higher in the Central African population. In males, SVL ($p = 0.0179$), lower anterior temporal–loreal distance ($p = 0.0225$), anterior sublingual length ($p = 0.0318$), VENT (Wilcoxon Test, $p < 0.0000$), VENTD (Wilcoxon Test, $p < 0.0000$), and infralabials were significantly lower, and the number of infralabials touching chin shields (Wilcoxon Test, $p = 0.0143$) and body bands (Wilcoxon Test, $p = 0.0240$) were significantly higher in Central African population. The ANCOVAs conducted on the Central African *G. smithii* and Eastern striped *G. smithii* resulted in two differences in males and nine differences in females. For males, HW ($p = 0.0060$) and loreal length ($p < 0.0000$) were significantly lower in Central African population. For females, anterior sublingual width ($p = 0.0460$), frontal length ($p = 0.0170$), frontal rostral distance ($p = 0.0290$), HL ($p < 0.0000$), ID ($p < 0.0000$), distance between the nostrils ($p < 0.0000$), loreal length ($p < 0.0000$), NOD ($p = 0.0480$), and rostral height ($p < 0.0000$) were significantly lower in the Central African population.

T-tests comparing Semliki/Edward *G. smithii* (Males N = 2, Females N = 3) with Western *G. smithii* (Males N = 46, Females N = 35) recovered two differences between males and seven differences between females. For males, the infralabials touching the chin (Wilcoxon Test, $p = 0.0141$) and the number of body bands (Wilcoxon Test, $p = 0.0376$) were significantly higher in Semliki/Edward *G. smithii*. For females, SVL ($p = 0.0004$), HL ($p = 0.0238$), NOD ($p = 0.0029$), frontal length ($p = 0.0423$), frontal width ($p = 0.0261$), frontal–rostral distance ($p = 0.0214$), and prefrontal contact ($p = 0.0168$) were significantly higher in Semliki/Edward *G. smithii*. The ANCOVAs conducted on the Semliki/Edward *G. smithii* and Western *G. smithii* resulted in four differences in males and six difference in females. In males, anterior sublingual length ($p = 0.0390$), distance between nostrils ($p = 0.0090$), and rostral height ($p = 0.0100$) were significantly higher, and loreal length ($p = 0.0440$) was significantly lower in Semliki/Edward *G. smithii*. For females, anterior sublingual length ($p = 0.0100$), ID ($p < 0.0000$), distance between the nostrils ($p = 0.0010$), lower anterior temporal length ($p = 0.0370$), and rostral height ($p = 0.0480$) were significantly higher, and internasals contact ($p < 0.0000$) was significantly lower in Semliki/Edward *G. smithii.*

T-tests comparing Eastern striped *G. smithii* (Males N = 5, Females N = 6) and Western *G. smithii* (Males N = 46, Females N = 35) recovered seven differences in males and six differences in females. For males, distance between the nostrils ($p = 0.0207$), ID ($p = 0.0138$), and rostral height ($p = 0.0213$) were significantly higher, and loreal length ($p = 0.0385$), postoculars (Wilcoxon Test, $p < 0.0000$), infralabials (Wilcoxon Test, $p = 0.0292$), and infralabials touching the anterior chin shields (Wilcoxon Test, $p = 0.0011$) were significantly lower in

Eastern Striped *G. smithii*. The ANCOVAs conducted on the Eastern Striped *G. smithii* and Western *G. smithii* resulted in no differences in males or females.

T-tests comparing Semliki/Edward G*. smithii* and Eastern Striped *G. smithii* recovered no differences between the two groups. The ANCOVAs conducted on the Semliki/Edward *G. smithii* and Eastern Striped *G. smithii* resulted in one difference in males, and one difference in females. For males, frontal length (p = 0.0120) was significantly lower in Semliki/Edward *G. smithii,* and for females, distance between the nostrils (p = 0.0190) was significantly higher in Semliki/Edward *G. smithii.*

T-tests comparing *G. tholloni* from Congo, Chad, and Atlantic River Basins (Central African *G. tholloni*, Males N = 74, Females N = 57) with Western (Nigeria and other localities in West Africa) *G. tholloni* (Males N = 4, Females N = 5) recovered eight differences in males and five differences in females. For males, EW (p < 0.0000), NOD (p = 0.0023), frontal length (p = 0.0429), parietals contact (p = 0.0379), and loreal height (p = 0.0269) was significantly higher, and VENTD (Wilcoxon Test, p = 0.0032), VENT (Wilxocon Test, p = 0.0052), supralabials (Wilcoxon Test, p = 0.0027), and the supralabials in contact with the eye (Wilcoxon Test, p = 0.0451) were significantly lower in Central African *G. tholloni*. For females, distance between the nostrils (p = 0.0099), and the supralabials in contact with the eye (Wilcoxon Test, p = 0.0010) were significantly lower, and frontal width (p = 0.0479), anterior sublingual width (p = 0.0341), and postoculars (Wilcoxon Test, p = 0.0011) were significantly higher in Central African *G. tholloni*. The ANCOVAs conducted on the Central African *G. tholloni* and Western *G. tholloni* resulted in two differences in males and five differences in females. For males, frontal length (p = 0.0100) and head length (p = 0.0400) were significantly higher in *G. tholloni* from Congo, Chad, and Atlantic River Basins. For females, ID (p = 0.0340), distance between the nostrils (p = 0.0040), parietals contact (p = 0.0290), and rostral height (p = 0.0110) were significantly lower, and prefrontals contact (p = 0.0220) was significantly higher in Central African *G. tholloni*.

T-tests comparing Lake Tanganyika *G. tholloni* (Males N = 3, Females N = 2) to Nile *G. tholloni* (Males N = 9, Females N = 7) recovered one difference in males and no differences in females. In males, VENTD (p = 0.0042) was significantly higher in Lake Tanganyika *G. tholloni*. The ANCOVAs conducted on the Lake Tanganyika *G. tholloni* and Nile *G. tholloni* populations resulted in two differences in males and no differences in females. For males, HL (p = 0.0140), and NOD (p = 0.0020) were significantly higher in Lake Tanganyika *G. tholloni*.

T-tests comparing Lake Tanganyika *G. tholloni* (Males N = 3, Females N = 2) with Western *G. tholloni* (Males N = 4, Females N = 5) recovered no differences in males or females. The ANCOVAs conducted on the Lake Tanganyika *G. tholloni* and Nile *G. tholloni* resulted in one difference in males and two differences in females. For males, the lower anterior temporal–loreal distance (p = 0.013) was significantly higher in Lake Tanganyika *G. tholloni*. For females, NOD (p = 0.0260) was significantly lower, and parietals contact (p = 0.0390) was significantly higher in Lake Tanganyika *G. tholloni*.

T-tests comparing Nile *G. tholloni* (Males N = 9, Females N = 7) with Western *G. tholloni* (Males N = 4, Females N = 5) recovered two differences in males and one difference in females. In males, VENTD (p = 0.0243) and VENT (p = 0.0256) were significantly lower in Nile *G. tholloni*. For females, the supralabials in contact with the eye (p = 0.0121) were significantly lower in Nile *G. tholloni*. The ANCOVAs conducted on the Nile *G. tholloni* and Western *G. tholloni* identified four differences in males and one difference in females. In males, EW (p = 0.0340), frontal length (p = 0.0020), rostral height (p = 0.0230), and frontal width (p = 0.0350) were significantly higher in Nile *G. tholloni*. In females, distance between the nostrils (p = 0.0150) was significantly lower in Nile *G. tholloni*.

The *G. caesar* (Table 9) dataset consisted of 35 individuals. No geographic patterns of variation were observed in the dataset and no distinct populations were identified in the preliminary PCA; therefore, no population comparisons were conducted.

Three total PC analyses were conducted with natural log-transformed mensural and meristic data (Figs. 10–12, Tables 10–12). The PC analysis conducted on *G. ornata sensu stricto*, Ogooué *G. ornata* and *G.* cf. *ornata* (Fig. 10, Table 10) did not clearly distinguish the three populations. The first principal component axis was responsible for 91.7% of the total variation, the second for 1.6%, and the third for 1.3%. The variables that most heavily contributed to the PCA were SVL, ID, RW, and HL. The PC analysis conducted on Central African *G. smithii*, Eastern striped *smithii*, *G. smithii* from the Semliki River and Lake Edward, and Western (Nigeria and other localities in West Africa) *G. smithii* did not recover any morphological separation between groups (Fig. 11, Table 11). The first principal component was responsible for 94.6% of the variation observed between the populations, the second for 1.1%, and the third for 1.0%. Snout–vent length (SVL), anterior sublingual width, and rostral width were the variables that primarily contributed to the PC analysis. The third PC analysis conducted on Central African *G. tholloni*, *G. tholloni* from Lake Tanganyika, *G. tholloni* from the Nile River basin, and *G. tholloni* from West Africa, recovered no morphological separation between groups (Fig. 12, Table 12). The first axis was responsible for 91.0% of the variation, the second for 1.8% of the variation, and the third for 1.4% of the variation. The variables that most heavily contributed to the PC analysis were SVL, HW, and anterior sublingual width.

Although the phylogenetic trees and morphological analyses identified two species present in *G. ornata sensu lato*, the species delimitation analysis identified four species. Conflict in species boundaries based on different sources of information is explored in detail below (see Discussion). Despite this, the molecular and morphological results support *G*. cf. *ornata* as a new, cryptic species of *Grayia.*

Striking color pattern differences are evident between specimens in the *G.* cf. *ornata.* and *G. ornata sensu stricto* clades (Fig. 13). *G.* cf. *ornata* has a darker brown or even gray background dorsal color with fewer body bands in both males and females compared to *G. ornata sensu stricto*. The ventral side of *G.* cf. *ornata* is much darker and heavily speckled with black spots whereas *G. ornata sensu stricto* has a much lighter ventral side with little to no speckling except toward the tail (Fig. 10). The chin and neck of *G.* cf. *ornata* are black and often have cream-colored dots in the center of the chin shields, whereas the chin and neck of *G. ornata sensu stricto* are typically light cream, sometimes light gray, with occasional white spots on the chin shields. This chin and head coloration is common in younger *G. ornata sensu stricto* specimens; however, this coloration can be seen on adult specimens of *G.* cf. *ornata*. Lastly, the labial scales of *G.* cf. *ornata* are usually black with cream-colored spots on the center of each infralabial, whereas *G. ornata sensu stricto* have lighter cream-colored or brown labial scales—typically edged with brown or black.

3.3 Species Descriptions and Accounts

(Reptilia: Squamata: Colubridae)

***Grayia* _____ sp. nov.**
(Figs. 13–17, Tables 3–4)

This cryptic new species is from DRC and northeastern Angola, ranging from the middle to upper Congo River and its tributaries. It is likely sympatric with *G. ornata sensu stricto* in the middle Congo River. This new species is recognized by well-supported and divergent clades in the phylogenetic analysis (Figs. 1–3), amino-acid differences in protein coding genes, sequence divergence, coloration, and statistically significant morphological differences, including scale counts and measurements (see Results).

Diagnosis. A species of *Grayia* found in the middle and upper Congo River and its tributaries, within DRC and Angola. This species is defined by 9–10 supralabials in females (vs. 8 in *G. caesar*, 7–9 [rarely 10] in *G. ornata*, 7–8 in *G. smithii*, and 7–8 [rarely 9] in *G. tholloni*); 22–24 body bands (vs. 21–30 in *G. caesar*, 17–35 (rarely 12, 14 or 16) in *G. ornata*, 20–45 [rarely < 20] in *G. smithii*, and 27–62 [rarely 8] in *G. tholloni*); 899 mm maximum SVL (vs. 965 mm in *G. caesar*, 1,190 mm in *G. ornata*, 1,400 mm in *G. smithii*, and 900 mm in *G. tholloni*); maximum TaL 262 mm (vs. 692 mm in *G. caesar*, 366 mm in *G. ornata*, 545 mm in *G. smithii*, and 490 mm in *G. tholloni*); maximum TL 988 mm (vs. 1,322 mm in *G. caesar*, 1,520 mm in *G. ornata*, 2,550 mm in *G. smithii*, and 1,211 mm in *G. tholloni*); dorsum dark brown, gray, to nearly black with relatively few black body bands (vs. *G. caesar* blackish or dark gray with pale cream bands outlined in black; *G. ornata* varies from tan to brown or gray with numerous black body bands;

G. smithii dark brown with darker brown or black chevrons, and pale cream, yellow scalloped, or triangle pattern on the lower flanks; *G. tholloni* brown or gray with faint, thin cream bands running down the body); venter with numerous black spots (vs. ventral side of *G. caesar* and *G. tholloni* light cream; ventral side of *G. ornata* is primarily light cream with occasional dark brown or black speckling—especially toward the tail; ventral side of *G. smithii* is cream with occasional black spotting along the lateral edges of the ventral scales); dark brown head and chin usually with white or cream-colored speckling on the chin shields and circular cream-colored dots on the infralabial scales (vs. *G. caesar* gray head with two white or yellow black-edged bands on each side of the posterior section of the head and a pale cream or white chin; *G. ornata* dark brown or gray head, and a darker chin with cream or white speckling in juveniles but this fades into a solid light cream in adults with occasional white spotting and labial scales ranging from gray to cream or light brown that are edged with dark brown or black; *G. smithii* solid brown or dark brown head with a pale cream or yellow chin; *G. tholloni* gray or brown head with black striping on the labial scales and a cream chin).

Holotype. EBG 2739, adult male, DRC, South Kivu Province, Mungombe, (S03.04419, E028.25566), 1072 m, collected by Chifundera Kusamba, Wandege M. Muninga, and Mwenebatu M. Aristote on the 14 March 2011 (Fig. 14).

Paratypes. CFS34 g, adult female, DRC, South Kivu Province, Sake, (S03.26808, E028.12071, 655 m), collected by Mwenenatu M. Aristote with a net from a fish pond at the edge of lowland forest on 1 May 2018 (Fig. 15); RBINS 18816, adult male, DRC, Tshopo Province, Uma, (N0.908333, E26.505556); RBINS 18901 adult male, DRC, Tshopo Province, Yoko, (N00.17377N, E25.17201E); RBINS 18902 adult male, DRC, Tshopo Province, Yoko, (N00.17377N, E25.17201E) (Fig. 15).

Description of the holotype. Adult male, SVL 721 mm, TL 264 mm; head long (19.69 mm), triangular, head width 22.97 mm; eye width 4.6 mm, circular pupil; naso-ocular distance 5.51 mm; distance between the nostrils 5.34 mm; interorbital distance 9.97 mm; rostral height 3.39 mm; rostral width 6.67 mm; frontal length 7.87 mm; frontal width 4.66 mm; frontal–rostral distance 5.80 mm; internasals contact 2.99 mm; prefrontals contact 2.99 mm; parietals contact 6.45 mm; loreal rectangular and large with no tapering, height 1.92 mm, width 2.8 mm; lower anterior temporal length 6.63 mm; lower anterior temporal–loreal distance 7.78 mm; anterior sublingual is long, length 8.38 mm, width 3.64 mm; 1/1 preocular; 2/2 postoculars; supralabials 9/9, 4th/5th in contact with orbit; infralabials 10/10, 1st on each side in contact with menial, 1st–5th in contact with anterior chin shield; temporal scale formula 2+3, extralabials 1/1, between 5th–6th/6th–7th supralabials; body large and rounded, dorsal scale rows one head length posterior to jaw rictus 17, dorsal scale rows at midbody 17, dorsal scale rows one head length anterior to vent 16; scales smooth without apical pits; ventral scales (standard) 146, ventral scales (Dowling) 145; paired subcaudals 78; cloacal scale divided.

Coloration (in life) of the holotype. Dorsum dark brown with 23 darker brown bands across the body, which are solid until midbody, where they bifurcate on the flanks. Tail dark, almost black with no visible banding. Top and sides of the head are dark brown, with each scale bordered on all sides with black; solid black supralabials and infralabials with circular cream spots in the center of each scale. Ventral side is cream with a yellowish tint and heavily speckled with black spots that increase in density toward the tail and the head. Neck and chin are almost completely black with cream-colored spots on the chin shields and cream speckling on the neck. Ventral side is solid black, from the tail tip to three head lengths from the cloacal scale and forms a gradient anteriorly into a yellowish cream.

Coloration (in preservative) of the holotype. The dark brown dorsum has become dark greenish brown with grayish flanks. The ventral patterning, head coloration, and speckling has not changed.

Variation. Morphometric variation in *Grayia* **sp. nov.** can be seen in Tables 3–4. Snout–vent length ranged from 227–899 mm in the three female specimens and between 421–726 mm in the four male specimens. The largest specimen was the adult female paratype (CFS34 g, 899 mm SVL) from Sake, DRC. Body coloration was typically dark brown or gray with 22–24 black body bands. A juvenile specimen (PEM R19473, SVL 227 mm, Lunda-Norte, Angola) was very dark brown dorsally with an entirely black ventral side. This juvenile specimen, pictured in two publications (Branch 2018, Pietersen et al. 2021), was described as “not resembling” other *G. ornata* in a recent book review (Spawls 2022). An adult male (ELI 258, SVL 635 mm) from Kyolo, DRC had an aberrant color pattern that was uniform brownish tan with no bands (Fig. 17). This specimen had a heavily speckled ventral side with a series of black spots forming a line down the center of the ventral scales. The chin was black with no white spots on the chin shields or labial scales. ELI 258 also had a lower number of ventral scales: 137 (standard) and 135 (Dowling). The central line on the venter formed by a series of black dots was also observed in RBINS 18985.

Diet. The similar habitats and overlapping distributions suggest that the diet of *Grayia* **sp. nov.** is likely similar to that of *G. ornata*, but no stomach contents have been examined or documented.

Habitat. The holotype, EBG 2739, was collected near Mungombe village, which lies in a transitional forest zone between the lowland rainforest of the Congo Basin and the foothills of the western Itombwe Plateau. The paratype, CFS 34g, was collected in a stream near Sake, which is only ~25 km from the holotype and lies in the same transitional forest zone. ELI 258 was collected in the upper Congo River Basin near Lake Kabamba, which is the northernmost of the Upemba Depression lakes (Broadley and Cotterill 2004). The specimen was collected in the water at the eastern shore of the lake. *Grayia ornata* is typically found in a variety of aquatic habitats in Central Africa (Chippaux and Jackson 2019) and the habitat information gathered on *Grayia* **sp. nov.** suggests that the two species share many of the same habitat preferences.

Geographic Distribution. All specimens were found within DRC except for one specimen (PEM R19473) that was found at a ferry crossing in northeastern Angola. All samples were found within the Congo River Basin. Five out of the nine total genetic samples were found in the upper Congo River—upstream of the Boyoma Rapids. The other four genetic samples were collected in the middle Congo River and its tributaries. Out of the four *Grayia* **sp. nov.** identified by morphology alone, three were found just downstream of the Boyoma Rapids, and the fourth was found in Yoko, just upstream of the Boyoma Rapids.

Etymology.

Grayia caesar **(Günther 1863)**

(Fig. 18, Table 9)

Xenurophis caesar: Günther (1863); type locality: "Fernando Po" [= Bioko Island, Equatorial Guinea]
Grayia longicaudata: Mocquard (1891); type locality: "San Benito" [= Bioko Island, Equatorial Guinea]
Xenurophis caesar guentheri: Stucki-Stirn (1979); type locality: Nyasoso, Cameroon

Grayia caesar was originally described as *Xenurophis caesar*, the sole member of the *Xenurophis* genus, by Albert Günther in 1863. Günther described the single specimen (BMNH 1946.1.6.38) as having a slender, rounded body with an elongate tail and large eyes. The specimen was noted to have 15 scale rows, one large preocular, two narrow postoculars, 8 upper labials (the 4th and 5th in contact with the orbit), a temporal formula of 2 + 3, 145 ventrals, a SVL of 469.9 mm, tail length of 228.6 mm, and 28 narrow "grayish, blacked-edged cross streaks" on the body extending down the flanks to the belly. Six yellow "dots" were reported to from a ring on the crown of the specimen's head and two yellow, black-edged bands were present on each side of the posterior section of the head. This specimen was found in Fernando Po (= Bioko Island, Equatorial Guinea) and is now considered the type specimen of *G. caesar*. *Xenurophis caesar* would later be placed into the genus *Grayia* by Boulenger (1901).

In 1891, Mocquard described *Grayia longicaudata*, a synonym of *G. caesar*. Two male specimens from San Benito in Equatorial Guinea were used in the description, one of which was intact and measured 1.30 m in total length. The specimens were noted to have a cylindrical body that terminated in a long tail, which was more than half of the total body length. Mocquard remarked that *Grayia longicaudata* had one preocular, two postoculars, 8 supralabials (the 4th and 5th in contact with the orbit), and moderately large eyes.

In 1979, Stucki-Stirn described an irregularly colored *G. caesar* that he coined *Xenurophis caesar guentheri*. The specimen displayed a chocolate brown head with white markings on the dorsal surface. The lateral surface had white lines over a very large preocular, both postoculars, and the neck. The chin was white and the ventrals yellowish. The dorsum was brown with 23 "clear cut" bands and an irregular yellow spotted pattern visible on the dorsum toward the tail.

Diagnosis. A species within *Grayia* with a Central African distribution including Cameroon, Equatorial Guinea, Gabon, Republic of the Congo, Angola, DRC, CAR, and northern Zambia. The species is defined by the following characters: maximum SVL 965 mm (vs. 1,190 mm in *G. ornata*, 1,400 mm in *G. smithii*, 900 mm in *G. tholloni*, and 899 mm in *Grayia* **sp. nov.**); maximum TL 1,322 mm (vs. 1,520 mm in *G. ornata*, 2,550 mm in *G. smithii*, 1,211 mm in *G. tholloni*, and 988 mm in *Grayia* **sp. nov.**); maximum TaL 692 mm (vs. 366 mm in *G. ornata*, 545 mm in *G. smithii*, 490 mm in *G. tholloni*, and 262 mm in *Grayia* **sp. nov.**); DSRM 15 (vs. 17–19 [rarely 15] in *G. ornata*, 16–17 [rarely 15 or 18] in *G. smithii*, 15 in *G. tholloni*, and 17 in *Grayia* **sp. nov.**); 2 upper labial scales in contact with the eye (vs. 1–2 in *G. ornata*, 1–2 in *G. smithii*, 1 [rarely 2 or 4] in *G. tholloni*, and 1 in *Grayia* **sp. nov.**); 122–146 ventrals (Dowling), < 130 in males > 135 in females (vs. 135–163 in *G. ornata*, 142–167 in *G. smithii*, 131–150 in *G. tholloni*, and 135–152 in *Grayia* **sp. nov.**); 140–162 subcaudals, > 150 in males < 150 in females (vs. 65–90 in *G. ornata*, 75–110 in *G. smithii*, 100–134 in *G. tholloni*, and 69–79 in *Grayia* **sp. nov.**); 8 supralabials (vs. 8–9 [rarely 7] in *G. ornata*, 7–8 in *G. smithii*, 7–9 in *G. tholloni,* and 8–10 in *Grayia* **sp. nov.**); cloacal scale single in females, divided in males (vs. always divided in *G. ornata*, *G. smithii*, *G. tholloni,* and *Grayia* **sp. nov.**); > 35 maxillary teeth (vs. < 27 in *G. ornata*, < 24 in *G. smithii*, < 30 in *G. tholloni,* < 27 in *Grayia* **sp. nov.**); blackish or dark gray dorsum with pale cream bands outlined in black (vs. *G. ornata* brown, gray, or tan body color with dark brown or black body bands that bifurcate on the flanks; *G. smithii* dark brown dorsum with darker brown or black chevrons and pale cream, yellow scalloped, or triangle pattern on the lower flanks; *G. tholloni* brown or gray dorsum with faint, thin cream bands running down the body; *Grayia* **sp. nov.** dark brown or gray dorsum with a small number of black bands that bifurcate on the flanks); slender, delicate body with a proportionately long tail (vs. thick, stout bodies with moderately sized tails in *G. ornata*, *G. smithii*, *G. tholloni,* and *Grayia* **sp. nov.**).

Redescription of the Holotype. BMNH 1946.1.6.38 adult female, SVL 475 mm, tail incomplete, TL > 123 mm; head long, length 16.6 mm; head width 12.60 mm; eye width 5.76 mm, circular pupil; naso-ocular distance 4.65 mm; distance between the nostrils 3.40 mm; interorbital distance 7.00 mm; rostral height 2.15 mm; rostral width 4.48 mm; frontal length 6.75 mm; frontal width 4.48 mm; frontal–rostral distance 4.49 mm; internasals contact 1.90 mm; prefrontals contact 3.01 mm; parietals contact 5.40 mm; loreal height 1.52 mm, width 2.10 mm; lower anterior temporal length 5.10 mm; lower anterior temporal–loreal distance 6.80 mm; anterior sublingual length 6.63 mm; anterior sublingual width 2.47 mm; 1/1 preocular; 2/2 postocular; supralabials 8/8, 4th and 5th in contact with orbit; infralabials 10/10, 1st on each side in contact with menial, 1st–5th in contact with anterior chin shield; dorsal scale rows one head length posterior to jaw rictus 15, dorsal scale rows at midbody 15, dorsal scale rows one head length anterior to vent 15; scales smooth without apical pits; 28 body bands; ventral scales (standard) 142, ventral scales (Dowling) 141; > 39 paired subcaudals; cloacal scale divided.

Variation. Morphometric variation in *G. caesar* can be seen in Table 9. The number of maxillary teeth can range between 35 and 38 (Bogert 1940). They are typically small, closely set and increase in size from the anterior to posterior of the mouth (Bogert 1940, Chippaux 2001, 2006). The temporal formula for this species is usually 2 + 3. They have 8 upper labials (the 4th and 5th in contact with the eye) and 10 infralabials (5 in contact with the first anterior chin shield) (Chippaux and Jackson 2019). In the examined specimens the infralabials varied from 9 to 10 with the occasional rare specimen displaying 8 or 11. The maximum length (TL) for this species was previously recorded from an individual measuring 1,148 mm (Roux-Estève 1965). The maximum total length recorded from our examined specimens was from a male (MNHN 1885.765, Litoral Province, Equatorial Guinea) measuring 1,322 mm. The maximum SVL (965 mm) was recorded from a female (MNHN 1987.1421, Republic of Congo) with an incomplete tail. The number of subcaudal scales is often higher than the number of ventral scales in this species, although the tail of our examined specimens was rarely complete. The subcaudal scales ranged from 140–162 and only one examined specimen (RMCA 20261, North Kivu Province, DRC) had more ventrals (Dowling, 148) than subcaudals (142). One study found that *G. caesar* displayed several sexually dimorphic characteristics: anal scale state (single in males, divided in females), number of white bands on body (21–28 in males, 26–30 in females), number of ventral scales (< 130 in males and > 135 in females), and number of subcaudal scales (> 150 in males, < 150 in females) (Pauwels et al. 1998). These sexually dimorphic characteristics were consistent with the examined specimens. The ventral side of *G. caesar* can range from cream to yellow. One specimen that Stucki-Stirn (1979) coined *Xenurophis caesar guentheri* had odd coloration with a yellow spotted pattern on the dorsum near the tail.

Diet. This species has been recorded eating various fish and amphibians, but few documented records exist (Chirio and LeBreton 2007).

Hemipenes. The hemipenes of *G. caesar* have been described as simple with a bifurcated spermatic furrow (Chippaux 2006, Pauwels and Vande Weghe 2008).

Behavior. Juvenile specimens have been reported as “not aggressive” but *G. caesar* captured by fisherwomen in “Monts De Cristal” (Crystal Mountains National Park, Gabon) have been described as aggressive (Pauwels and Vande Weghe 2008).

Habitat. This species is primarily reported in small to medium streams in semi-deciduous and dense evergreen forests (Chirio and LeBreton 2007, Pauwels and Vande Weghe 2008, Zassi-Boulu et al. 2019). In the CAR, *G. caesar* is reported as a forest species (Trape 1985, Chirio and Ineich 2006). *Grayia caesar* has been described as “jamais très abondante” (never very abundant) throughout its habitat (Chirio and LeBreton 2007).

Grayia ornata (Bocage 1866 a,b)

(Figs. 19–21, Tables 3,4)

Macrophis ornatus: Bocage (1866 a,b); type locality: “Duque de Bragança” [= Calandula, Angola]
Glaniolestes ornatus: Peters (1877); type locality: none listed
Grayia furcata: Mocquard (1887); type locality: “Congo par la Mission de Brazza” [= Brazzaville, Republic of the Congo]
Grayia striata: Sternfeld (1910); type locality: “Kamerun,Bezirk Lome” [= Lome District, Cameroon]

Macrophis ornatus was described in 1866 by José Vicente Barbosa du Bocage. This new species was described by Bocage in two papers that were published in the November issue of the same journal (Bocage 1866a, Bocage 1866b, Marques et al. 2018). Three specimens—two adults and a juvenile—were collected from Duque de Bragança (= Calandula, Angola), and presumed not only to be a novel species, but representative of a new genus (Wallach et al. 2014). Bocage stated that this species was abundant in the localities where specimens were collected. *Macrophis ornatus* would later be synonymized with *G. ornata* by Bocage (1895).

Glaniolestes ornatus was an infrequently used synonym of *G. ornata* first described by Peters in 1877. No further information is listed regarding the type specimen for this species. The genus *Glaniolestes* was created in 1857 by Slack and originally included *G. triangularis*, a synonym of *G. smithii*.

Mocquard (1887) described *Grayia furcata* based on a single specimen (MNHN 1886.218) found in Brazzaville, Republic of the Congo. The specimen was a large female (SVL = 700 mm, TL = 295 mm) with 12 infralabials, 17 scale rows, 146 ventral scales (standard) and 88 subcaudals. The type specimen had a brownish-gray body coloration and pale gray labials with a black posterior edge. The ventral side was “blanc-sale” (dirty-white), fading to dark brownish-black toward the tail. Mocquard compared this specimen to *Grayia silurophaga* (now *G. smithii*) and noted that it was distinguished by the greater number of supralabials (9 in *Grayia furcata* compared to 7 in *Grayia silurophaga*) and color pattern variation. In 1895, Bocage suggested that *Grayia furcata* was synonymous with *Grayia ornata* and later Boulenger 1909 would come to the same conclusion.

In 1910, Sternfeld would base the description of *Grayia striata* on one juvenile specimen (ZMB 21864) from the "Lome District" of Cameroon. The specimen was 27 cm long with 152 (standard) ventral scales, 17 scale rows at midbody, 78 subcaudals, 8–10 supralabials and a temporal formula of 2 + 3. The coloration of this specimen was noted as a deep black—on both the dorsal and ventral sides. The specimen had three narrow white lines, one starting from each eye and running along the flanks, and the third running straight down the middle of the back. These stripes gradually faded posteriorly. The neck and throat were spotted and streaked with white and a broken white transverse band was on the neck. The description of *Grayia striata* provided by Sternfeld matches the description of the longitudinally striped color phase of *G. ornata* and Schmidt (1923) considered *G. striata* to be a synonym of *G. ornata*.

Diagnosis. *Grayia ornata* is a member of the genus *Grayia* with a Central African distribution including Cameroon, Equatorial Guinea, Gabon, Republic of the Congo, Angola, DRC, CAR, Burundi, and Northern Zambia. The species is defined by the following characters: maximum SVL 1,190 mm (vs. 965 mm in *G. caesar*, 1,400 mm in *G. smithii*, 900 mm in *G. tholloni*, and 899 mm in *Grayia* **sp. nov.**); DSRM 17–19 [rarely 15] (vs. 15 in *G. caesar*, 16–17 [rarely 15 or 18] in *G. smithii*, 15 in *G. tholloni*, and 17 in *Grayia* **sp. nov.**); 1–2 upper labial scales in contact with the eye (vs. 2 in *G. caesar*, 1–2 in *G. smithii*, 1 [rarely 2 or 4] in *G. tholloni*, and 1 in *Grayia* **sp.**

nov.); 65–90 subcaudals (vs. 140–162 subcaudals in *G. caesar*, 75–110 in *G. smithii*, 100–134 in *G. tholloni*, and 69–79 in *Grayia* **sp. nov.**); 8–9 [rarely 7] supralabials (vs. 8 in *G. caesar*, 7–8 in *G. smithii*, 7–9 in *G. tholloni*, and 8–10 in *Grayia* **sp. nov.**); brown, gray or tan body color with a large number of dark brown or black body bands that bifurcate on the flanks (vs. blackish brown body color with pale cream bands outlined in black in *G. caesar*; dark brown body color with darker brown or black chevrons and pale cream, yellow scalloped, or triangle pattern on the lower flanks in *G. smithii*; brown or gray body color with faint, thin cream bands running down the body in *G. tholloni;* and dark brown or gray body color with a small number of black bands that bifurcate on the flanks in *Grayia* **sp. nov.**); 0–3 extralabial scales present (vs. extralabial scales never present in *G. caesar*, *G. smithii* and *G. tholloni,* and 0–2 extralabial scales present in *Grayia* **sp. nov.**)

Variation: Morphometric variation in *G. ornata* can be seen in Tables 3–4. *Grayia ornata* is one of the larger species within the genus with the largest recorded individual (TL) measured at 1,520 mm (Knoepffler 1966). The longest total length (1,466 mm) from the examined specimens was recorded from a male (AMNH R12570) from the "Belgian Congo" (DRC). Snout–vent length of the largest individual used in this study was recorded from a female (RBINS 3747, Mpala, DRC) measured at 1,190 mm. The temporal formula for this species is typically 2 + 3. Numerous specimens examined in this study had either fused or divided temporal scales that resulted in abnormal temporal formulas. The temporal formulas observed included 1 + 2, 1 + 3, 2 + 2, 2 + 4, 2 + 3 + 4, and 3 + 3. The number of infralabials are usually between 10–12 (4–6 in contact with the first anterior chin shield) (Chippaux and Jackson 2019).

The number of infralabials observed in the examined specimens were typically between 10–12, but some individuals had as few as 7 or 9. *Grayia ornata* usually has between 8–9 (rarely 7) supralabials. The number of supralabials in contact with the eye varies from 1–2, and usually the 4th and 5th supralabials make this contact. The number of extralabials (also known as cunate scales) are typically between 1–2 and are usually located between the 5th and 6th supralabials. Rare individuals with 3 extralabials were observed and multiple individuals had no extralabials. This species typically has between 17 and 19 midbody dorsal scale rows (Chippaux and Jackson 2019), but some rare individuals had as few as 15. There are between 135–164 ventrals (standard), and 65–90 subcaudals present in the examined specimens. The cloacal scale and subcaudals of this species are divided (Chippaux and Jackson 2019). Only one *G. ornata* specimen (RBINS 16290) from Mbomo, Gabon was recorded with a single, undivided anal scale. The dentition of *G. ornata* has been described as uniform in size with ~27 sharply recurved maxillary teeth (Bogert, 1940).

Grayia ornata has two distinct color morphs within the species (Pauwels et al. 2002). The cross-barred color phase is by far the most common and is characterized by relatively wide body bands that bifurcate on the flanks of the body near the ventral scales. The other form is known as the longitudinally striped phase and has dark brown or black stripes that extend along the length of the body (Fig. 19). Based on specimens in museum collections and observations of wild specimens, this phase is rare. From the 248 total *G. ornata* specimens examined in this study, only twelve displayed the longitudinally striped color phase. *Grayia ornata* typically have a light-cream venter that becomes brown or gray toward the tail with dark brown or black speckling. The neck and chin are typically light cream or gray with occasional white spots on the chin shields, and the labial scales range from gray to cream or light brown. The head and labial scales are typically bordered on all sides with dark brown or black. One specimen (CRSN 85, Aweza-Libulu, DRC) had an aberrant color pattern resulting in the absence of body patterning (Fig. 19). This specimen was uniformly grayish-tan with a cream ventral side and no bands on the body or tail. *Grayia ornata* also has a unique color inversion between juveniles and adults (Pauwels and Vande Weghe 2008). The juveniles are typically dark brown or almost black, with light white or orange bands (Fig. 20) (Laurent 1950). As they age, their color shifts to a lighter brown or grey body color with dark brown or even black body bands. This color inversion is likely responsible for the white-striped *G. striata* described by Sternfeld (1910). The specimen he described was a juvenile of the longitudinally striped phase, that had white stripes instead of the black stripes seen in adults. Some individuals (MTD 48961, Serra do Pingano, Angola) have bright brown, almost yellowish-orange body coloration with black speckling on the head and between the black body bands (Fig.19). Others specimens (MTD 49656, Angola) are almost entirely dark brownish-black with patches of yellowish-orange on the chin and flanks (Fig 19).

Diet. *Grayia ornata* is primarily piscivorous and frequently consumes catfish (Chippaux 2001). Records of *G. ornata* from Garamba National Park (DRC) and Monte Alen National Park (Equatorial Guinea) documented prey items including two species of catfish (*Clarias* sp., Family Clariidae and *Parauchenoglanis* sp., Family Claroteidae) (Pauwels et al. 2000). Pauwels (2002) documented the stomach contents of specimens from Gabon that included frogs, shrimp, and small rodents. During the specimen examination conducted for this study, the posterior part of a *Clarias* catfish was found in a specimen (RBINS 11193) from Garamba National Park in DRC.

Broadley (1983) recorded a *G. ornata* from Zambia with a large frog in its stomach that he identified as *Rana angolensis* (likely *Amietia delalandii*) (Frost 2023).

Hemipenes. The hemipenes of *G. ornata* are bilobed and have a bifurcated spermatic furrow (Bogert 1940). Each lobe is slender and has numerous spinules with the distal end having 5 spines. There are typically two large basal spines and three smaller spine pairs that decrease in size distally (Bogert 1940, Pauwels and Vande Weghe 2008). Bogert (1940) remarked that an individual *G. ornata* from DRC had an “unusually long” hemipenis. The hemipenis extended to the 17th subcaudal and forked at the 12th, with a sulcus that divided at the sixth subcaudal.

Behavior. Various authors consider *G. ornata* to be partially arboreal, because they spend much of their time hunting from branches overhanging rivers—sometimes up to three meters above the water’s surface (Perret 1957, Chippaux 2001, Pauwels et al. 2002, Ernst et al. 2020). While some reports consider *G. ornata* to be a solitary species that hunts underwater, primarily at dusk and throughout the night (Pauwels et al. 2002, Pauwels and Vande Weghe 2008), one report suggests that *G. ornata* from Angola are not solitary and instead live in pairs (Laurent 1964). *Grayia ornata* is described as a shy species that is not typically aggressive (Chirio and LeBreton 2007). This passive behavior is reflected in the superstition that if one is bitten by *G. ornata*, it is a sign they have participated in deviant behavior (Pauwels et al. 2002). They rarely bite when handled (Chirio and LeBreton 2007, Carlino and Pauwels 2015).

Habitat. In Central Africa *G. ornata* are considered a forest species and are frequently found in a variety of aquatic habitats, leading to their capture in gill nets by fishermen (Chirio and Ineich 2006, Chippaux and Jackson 2019, Zassi-Boulu et al. 2019). *Grayia ornata* can also be found in swamp forest habitat in Republic of the Congo (Chippaux and Jackson 2019). In Cameroon, *G. ornata* has been found in small–medium sized streams in semi-deciduous and dense evergreen forests, as well as forest-savanna mosaics (Chirio and LeBreton 2007). In Gabon, *G. ornata* can be found in a wide variety of habitats, from dense forest streams to swamps, and even large rivers such as the Ogooué and Ivindo (Pauwels and Vande Weghe 2008). In Angola, they are exclusive to "closed-forest riparian systems" in rock pools and streams (Ernst et al. 2020).

***Grayia smithii* (Leach 1818)**

(Fig. 22, Tables 5–6)

Coluber smythii: Leach (1818); type locality: "Embomma" [= Boma, DRC]
Coluber laevis: Hallowell (1844b); type locality: "Africa"
Coronella triangularis: Hallowell (1854); type locality: "Western Africa"
Heteronotus triangularis: Hallowell (1857); type locality: "Liberia"
Glaniolestes triangularis: Slack (1862); type locality: "Western Africa" and "Liberia"
Grayia silurophaga: Günther (1858); type locality: "West Africa" and "Africa"
Lejonotus schlegeli: Jan (1863); type locality: "Ashantee and Patria?" [= Ghana: Ashanti: Unknown country]
Grayia triangularis: Bocage (1866); type locality: "Zaire River" [= Congo River]

Grayia smithii was described by William Elford Leach in 1818 as *Coluber smythii*. Leach remarked that this new species was found "in great plenty" near Embomma (now Boma, DRC) on the ground. He noted *C. smythii* was brownish-gray with a whiteish ventral side and triangular whitish spots—bordered by sooty black scales—on the anterior flanks. The back was faintly marked with "transverse narrow whitish bands" that were spotted with black. Two specimens are listed as the possible type specimens (BMNH 1946.1.1.67 [formerly BMNH

49.9.15.10] or BMNH 1946.1.5.16), and the British Museum of Natural History also lists both specimens as the type for *G. silurophaga* (now a synonym of *G. smythii*) (Marquez et al. 2018). This is believed to be a result of Günther including Leach's type specimens in his description of *G. silurophaga* (Marquez et al. 2018). The lectotype for *G. smithii* (BMNH 1946.1.1.67 [formerly BMNH 49.9.15.10]) was designated by Boulenger in 1894 (Wallach et al. 2014)). *Coluber smythii* was later transferred to *Grayia* by Günther (1895).

In 1844, Hallowell described *Coluber laevis* from "Africa." No information was listed for the original syntypes, but he described the species as having a moderately sized head with two postoculars and two preoculars. The tail was long and tapering, and the specimen had 150 ventral scales (standard) and 100 subcaudal scales. The color of the dorsum was bronze above with 8 or 10 yellowish bands on the upper part of the body and neck. Four or five more bands continued toward the midbody, but they were described as indistinct. Hallowell noted that the yellow bands were formed by the separation of an equal number of broad, dark purple bands that coalesced on the posterior part of the body and formed yellow triangles on the snake's flanks. The name *Coluber laevis* was already in use because Lacepède (1789) had previously described *Coluber laevis* (a synonym of *Coronella austriaca*). The *Coluber laevis* described by Hallowell (1844) would later be considered a synonym of *G. smithii* (Wallach et al. 2014).

Hallowell described *Coronella triangularis*, without listing a type specimen, in 1854. The species had a "general resemblance to *Coronella laevis*" although Hallowell noted that the markings, number of scale rows, and length of tail were different. Hallowell remarked that this species may be considered a representative of *Coronella laevis* in Western Africa. In 1857, Hallowell concluded that *C. triangularis* was not a member of the *Coronella* genus and the species was transferred to the genus *Heteronotus*. *Heteronotus triangularis* had a long head with one preocular, 2 postoculars, and eight supralabials (with the 4th in contact with the eye). Hallowell noted *H. triangularis* had a thick, cylindrical body with 17 scale rows at midbody. The coloration of the head was "yellowish above mingled with olive" and the posterior supralabials were bordered inferiorly with black. The body color was "olive above" with 15 yellow, narrow transverse bands. The chin and throat were yellow with black spots. The flanks of the body had a series of 28 lateral, olive-colored triangular markings with yellow triangular interspaces. The SVL was reported as 1 ft. 4 inches (406.4 mm) and the tail was 8 inches (203.6 mm). In 1857, because *Heteronotus* was previously preoccupied by Hemiptera insects, the snake genus *Heteronotus* was changed to *Glaniolestes* (Slack 1862). *Coronella triangularis*, *Heteronotus triangularis,* and *Glaniolestes triangularis* would later be recognized as a synonym of *G. smithii* (Bocage 1887, Loveridge 1957).

In 1858, Günther described a "purplish brown" species of watersnake based on three adults from "West Africa" and "Africa," and a juvenile from "Africa." He named this new species *Grayia silurophaga* and noted that it had reddish-white crossbands that were bordered with black and widened toward the ventral side. *Grayia silurophaga* had a stout, cylindrical body with a long, tapering tail. The species had 7 supralabials (the 4th in contact with the eye), 17 scale rows at midbody, a temporal formula of 2 + 3, and a divided anal scale. The belly was uniformly yellowish with a black line "down the medial suture of the subcaudals." The teeth were "smooth, strong and of equal length." *Grayia silurophaga* became the type species for the genus *Grayia* and would later be listed as a synonym of *G. smithii* (Loveridge 1957).

Lejonotus schlegeli is a rarely used synonym of *G. smithii*, first described by Jan in 1863. This species is only mentioned once with no information about a type specimen other than its general locality in “Ashantee” and “Patria?” (Jan 1863). *Lejonotus schlegeli* was included as a synonym of *G. smithii* by Wallach et al. 2014.

In 1866, Bocage described *Grayia triangularis*, based on a single specimen from the Congo River. Little information exists on the original type specimen, but Günther (1888) would later describe a young *G. triangularis* as uniform black on the “whole of the lower parts.” Günther would also describe a *G. triangularis* from Gabon with aberrant coloration, including irregular whitish longitudinal lines on the side of the body, uniform brownish-gray body color and black “lower parts.” This taxon is now considered a synonym of *G. smithii* (Boulenger 1915, Marques et al. 2018)

Grayia smythii was corrected to *Grayia smithii* by a variety of authors (Laurent 1956, de Witte 1962, Meirte 1992, Pauwels and Meirte 1996, Trape and Roux-Estève 1995). While some consider this correction to be a misspelling (Wallach et al. 2014), others (Laurent 1956, Meirte 1992, Pauwels and Meirte 1996) argue that the species was likely named after Dr. Smith—who was present on the original expedition.

Diagnosis. *Grayia smithii,* as recognized herein, is found throughout sub-Saharan Africa including Senegal, Guinea, Sierra Leone, Liberia, Côte d’Ivore, Ghana, Togo, Benin, Nigeria, Cameroon, Chad, CAR, Republic of the Congo, DRC, Angola, northern Zambia, Uganda, Sudan, and Ethiopia. The species is defined by the following characters: maximum SVL 1,400 mm (vs. 965 mm in *G. caesar*, 1,190 mm in *G. ornata*, 900 mm in *G. tholloni*, and 899 mm in *Grayia* **sp.**

nov.); maximum TaL 545 mm in *G. smithii* (vs. 692 mm in *G. caesar*, 366 mm in *G. ornata*, 490 mm in *G. tholloni*, and 264 mm in *Grayia* **sp. nov.**); maximum TL 2,550 mm (vs. 1,322 mm in *G. caesar*, 1,520 mm in *G. ornata*, 1,211 mm in *G. tholloni*, and 988 mm in *Grayia* **sp. nov.**); 16–17 [rarely 15 or 18] (vs. 15 in *G. caesar*, 17–19 [rarely 15] in *G. ornata*, 15 in *G. tholloni*, and 17 in *Grayia* **sp. nov.**); 1–2 upper labial scales in contact with the eye (vs. 2 in *G. caesar*, 1–2 in *G. ornata*, 1 [rarely 2 or 4] in *G. tholloni*, and 1 in *Grayia* **sp. nov.**); 75–110 subcaudals (vs. 140–162 subcaudals in *G. caesar*, 65–90 in *G. ornata*, 100–134 in *G. tholloni*, and 69–79 in *Grayia* **sp. nov.**); 7–8 supralabials (vs. 8 in *G. caesar*, 8–9 [rarely 7] in *G. ornata*, 7–9 in *G. tholloni*, and 8–10 in *Grayia* **sp. nov.**); < 24 maxillary teeth (vs. > 24 in *G. caesar*, *G. ornata*, *G. tholloni*, and *Grayia* **sp. nov.**); and dark brown dorsum with darker brown or black chevrons and pale cream, yellow scalloped, or triangle pattern on the lower flanks (vs. *G. caesar* black or gray dorsum with pale cream bands outlined in black; *G. ornata* brown, gray or tan dorsum with dark brown or black body bands that bifurcate on the flanks; *G. tholloni* brown or gray dorsum with faint, thin cream bands running down the body; and *Grayia* **sp. nov.** dark brown or gray dorsum with a small number of black bands that bifurcate on the flanks).

Description of the Lectotype. BMNH 1946.1.1.67 (formerly BMNH 48.9.15.10) subadult male, SVL 345 mm, TL 155 mm; head length 13.45 mm; head width 8.75 mm; eye width 3.5 mm, circular pupil; naso–ocular distance 3.75 mm; distance between the nostrils 2.57 mm; interorbital distance 5.75 mm; rostral height 1.63 mm; rostral width 3.84 mm; frontal length 6.15 mm; frontal width 3.03 mm; frontal–rostral distance 3.13 mm; internasals contact 1.99 mm; prefrontals contact 1.76 mm; parietals contact 4.07 mm; loreal small, height 0.80 mm, width 1.58 mm; lower anterior temporal length 5.20 mm; lower anterior temporal—loreal distance 4.93 mm; anterior sublingual is midsize; length 5.20 mm; width 2.30 mm; 1/1 preocular; 2/2 postocular; supralabials 7/8, 4th in contact with orbit; infralabials 10/10, 1st on each side in contact with menial, 1st–5th in contact with anterior chin shield; temporal scale formula 2 + 3; dorsal scale rows one head length posterior to jaw rictus 17, dorsal scale rows at midbody 16, dorsal scale rows one head length anterior to vent 15; scales smooth without apical pits; 35 body bands; ventral scales (standard) 149, ventral scales (Dowling) 148; 96 paired subcaudals; cloacal scale divided; ventral striping extending dorsoventrally along the edges of the anterior ventral scales.

Variation: Morphometric variation in *G. smithiii* can be seen in Tables 5–6. *Grayia smithii* is the largest species within *Grayia*, with the longest recorded individual (TL) measuring 2,550 mm (Doucet 1963). The largest specimen examined through the course of this study was an adult female (BMNH 1959.1.7.7, Mjanji, Uganda) with a TL of 1,855 mm. This species is typically brown or tan with darker brown or black chevrons, but some specimens can have a distinctly greenish body color (Lanza and Vanni 1976, Stucki-Stirn 1979). The latter author also reported a melanistic individual that had an almost entirely dark brownish-black dorsum. The venter of *G. smithii* is pale cream or yellow, and certain individuals have a bright yellow chin and neck. This light ventral color extends onto the lower 1/3 of the snake's flanks in scalloped or triangle patterns. The color pattern in this species can vary heavily based on age and older individuals typically have more faded patterning (Fig. 22). Many *G. smithii* specimens have black or gray spots on the lateral edges of each ventral scale, and West African *G. smithii* (Fig. 20) have rows of distinct black or gray spots that form lines extending dorsoventrally along the edges of their anterior ventral scales (Greenbaum and Carr 2005). This striping is mostly restricted to West African specimens; however, some eastern DRC specimens have ventral striping. *Grayia smithii* typically have 7 supralabials (the 4th in contact with the eye) and 11 pale, black-edged lower labials (5 in contact with the anterior chin shields) (Villiers 1951a, Villiers 1951b, Chippaux and Jackson 2019). Several examined specimens had 8 supralabials and two (ZRC 2.3447, JCK 10609) had 6 supralabials. The examined specimens had 9–11 infralabials, but four specimens (AMNH R12179, AMNH R45903, RBINS 11204e, RMCA 7438) had only 8. The temporal formula is typically 2 + 3, but several examined specimens had aberrant temporal formulae because of fused or divided scales. Temporal formula variation included 1 + 3, 2 + 2, and 1 + 2 + 3. There are 16–17 dorsal scale rows at midbody, but one specimen (VW 2136, Kinsuka, DRC) had 18. The examined specimens had 142–167 ventral scales (Dowling) and 83–110 paired subcaudals. Two female specimens had abnormally low subcaudal counts of 72 (VW 79-1212, Kinsuka, DRC) and 75 (JCK 10609, Semliki, Uganda). According to Chippaux and Jackson (2019), females typically have more than 154 (standard) ventral scales, whereas males have less than 161; females have fewer than 100 subcaudals and males have more than 89. This held true for all characters except the number of ventrals in females. There were 10 female specimens that had < 154 ventral scales (standard), with some specimens having as few as 145.

Diet. *Grayia smithii* eats mainly fish and amphibians (Chippaux 2006), but there have been some observed dietary differences correlated with sex (Luiselli 2006). The latter study found that adult male *G. smithii* feed primarily on the aquatic pipid frog *Xenopus tropicalis*, and secondarily, on tadpoles of the more terrestrial genus *Ptychadena.* Adult female *G. smithii* were found to feed primarily on *Ptychadena* species and consume significantly more terrestrial *Sclerophrys* toads. In Cameroon, *G. smithii* consume fish (mainly mudfishes) and various frogs (Stucki-Stirn 1979). Cansdale (1948) noted that *G. smithii* "takes frogs freely" in captivity.

Hemipenes. A specimen examined by Bogert (1940) from Avakubi, DRC had an elongate, bifid hemipene that extended to the 12th subcaudal with a sulcus dividing at the 5th one. Each lobe of the hemipene was long and slender with "spinules near the crotch" that increase in size to form "needle-like" spines. The specimen had enlarged spines near the hemipene division and on opposite sides of the sulcus, there were two rows (7 pairs) of enlarged spines, which decreased distally in size. Bogert further noted that there were various small spines present near the hemipene bifurcation. He compared the hemipene of *G. smithii* to that of *G. ornata* and stated that they are remarkably similar. *Grayia smithii* was noted to have more numerous basal spines than *G. ornata*, along with a slightly longer hemipene and alternate arrangement of spinules on the two lobes.

Reproduction. *Grayia smithii* females were found to lay clutches of 3–4 eggs in different locations at different times (Akani and Luiselli 2001). This strategy, used by some turtles to avoid nest predation, had not been previously recorded in free-ranging snakes and it is hypothesized that this behavior is linked to reducing egg mortality from predation (Akani and Luiselli 2001). Stucki-Stirn (1979) noted that *G. smithii* in Cameroon spend most of their time in the water during mating. Multiple gravid specimens (MNHN 1921.443, RBINS 2709, RBINS 2710, MNHN 1996.6440) were examined, each with 12–17 eggs. There are records of *G. smithii* with 23 eggs in the oviducts, each nearing the size of a chicken egg (Angel et al. 1954). Loveridge (1937) recorded a female *G. smithii* with “numerous” developing eggs measuring 20 x 10 mm in size.

Behavior. *Grayia smithii* is considered diurnal and highly active (Stucki-Stirn 1979, Böhme 2000). This species spends the majority if its time in the water, and surfaces frequently to breathe (Stucki-Stirn 1979). Some authors note that this species is easily angered and quick to bite (Chirio and LeBreton 2007), while others (Zassi-Boulou et al. 2020) state that they are “generally not aggressive”.

Habitat. In Nigeria, *G. smithii* have been found in mangroves, but are more strongly associated with swamp (moist lowland) and rainforest habitats (Butler and Reid 1986, Luiselli and Akani 1999, 2002, Chippaux and Jackson 2019). There are records of this species occurring in the waterways of Nigerian savannas (Butler and Reid 1990). In Cameroon, *G. smithii* is commonly associated with dense evergreen and semi-deciduous forests, high-altitude savannas, and “hautes terres de l'Ouest” (western highlands) (Chirio and LeBreton 2007). They typically prefer medium to large streams, and are not found in stagnant water (Chirio and LeBreton 2007). Studies investigating snake habitats in the rainforests of Eket recovered evidence that that these snakes shift habitat types between seasons. In most recorded cases, *G. smithii* inhabiting ponds would move to freshwater rivers during the dry season. The specimens that did not shift habitat types were already found in rivers (Luiselli et al. 2005). During the dry season in Guinea, Greenbaum and Carr (2005) captured *G. smithii* in the Niger river.

Grayia tholloni **(Mocquard 1897)**

(Fig. 23, Tables 7–8)

Grayia tholloni: Mocquard (1897); type locality: "Brazzaville, French Congo" [= Republic of the Congo]
Grayia fasciata: Boulenger (1901); type locality: "South-west of Lake Tanganyika, Lemaire Mission" [= southeastern DRC]

Grayia tholloni was first described by François Mocquard in 1897. The type specimens for this species consisted of four specimens (MNHN 1890-40, MNHN 1890-152, MNHN 1896.66, and MNHN 1896.67) from French Congo (Republic of the Congo)—two from Brazzaville and two from the "Musée de Toulouse." The largest specimen was a male (MNHN 1896.66) measuring 810 mm in total length. Mocquard described *G. tholloni* as having a "museau assez élevé" (rather high muzzle) that was short and rounded. The temporal formula was 2 + 3 with 8 supralabials (the 4th in contact with the eye) and 9–10 infralabials (with the first five in contact with the anterior chin shield). The four syntypes were reported to have 15 scale rows, 130–136 ventrals (standard), divided anal scales, and 115–129 subcaudal scales. Their coloration was described as blackish-brown on the dorsum with 50–55 grayish-white transverse stripes that were two to three scale lengths apart from each other. These stripes gradually disappeared posteriorly. The labial scales were reported as "jaune sale" (dirty yellow) with a black stripe on the posterior edges of the supralabials and infralabials. Moquard remarked that this species is very similar to *Xenurophis caesar* because of the proportionately long tail and the number of scale rows. Mocquard (1897) suggested that this new species should be placed in the genus *Grayia* along with *X. caesar* (now *G. caesar*), *G. smithii* and *G. ornata*. Boulenger (1909) would later reaffirm this by placing *G. caesar*, *G. ornata*, *G. smithii*, and *G. tholloni* into the same genus.

Boulenger would describe *Grayia fasciata* in 1901 from a young specimen collected in DRC, south-west of Lake Tanganyika. This specimen was small (SVL 240 mm, TL 80 mm) and was noted to have a temporal formula of 2 + 3 with 8 upper labials (the 4th in contact with the eye), and 15 scale rows. The type specimen had 142 ventrals (standard), a divided anal scale, 100 subcaudals, and 30 maxillary teeth. Boulenger noted that the specimen was blackish above with the anterior of the body "barrée de blanchâtre" (barred with whitish). The ventral side was described as white with a small black spot at the lateral edges of each ventral plate. Boulenger considered this species as the "le passage" (transition) from *Grayia* to *Xenurophis*. *Grayia fasciata* was later synonymized with *G. tholloni* by Schmidt (1923).

Diagnosis. *Grayia tholloni* is found throughout sub-Saharan Africa including Senegal, Gambia, Guinea, Nigeria, Cameroon, Chad, CAR, Republic of the Congo, Angola, northern Zambia, Uganda, Kenya, Rwanda, Burundi, Tanzania, South Sudan, Sudan, Chad, and Ethiopia. The species is defined by the following characters: maximum SVL 900 mm (vs. 965 mm in *G. caesar*, 1,190 mm in *G. ornata*, 1,400 mm in *G. smithii*, and 899 mm in *G. sp nov.*); maximum TaL 490 mm (vs. 692 mm in *G. caesar*, 366 mm in *G. ornata*, 545 mm in *G. smithii*, and 262 mm in *Grayia* **sp. nov.**); maximum TL 1,211 mm (vs. 1,322 mm in *G. caesar*, 1,520 mm in *G. ornata*, 2,550 mm in *G. smithii*, and 988 mm in *Grayia* **sp. nov.**); 15 DSRM (vs. 15 in *G. caesar*, 17–19 [rarely 15] in *G. ornata*, 16–17 [rarely 15 or 18] in *G. smithii*, and 17 in *Grayia* **sp. nov.**); 1 [rarely 2 or 4] upper labial scales in contact with the eye (vs. 2 in *G. caesar*, 1–2 in *G. ornata*, in 1–2 *G. smithii*, and 17 in *Grayia* **sp. nov.**); 100–134 subcaudals (vs. 140–162 in *G. caesar*, 65–90 in *G. ornata*, 75–110 in *G. smithii*, and 69–79 in *Grayia* **sp. nov.**); 7–9 supralabials (vs. 8 in *G. caesar*, 8–9 [rarely 7] in *G. ornata*, 7–8 in *G. smithii*, and 8–10 in *G. sp nov.*); < 30 maxillary teeth (vs. > 35 in *G. caesar*, < 27 in *G. ornata*, *G. smithii*, and *Grayia* **sp. nov.**); and brown or gray dorsum with faint, thin cream bands running down the body (vs. *G. caesar* black or gray dorsum with pale cream bands outlined in black; *G. ornata* brown, gray or tan dorsum with dark brown or black body bands that bifurcate on the flanks; *G. smithii* dark brown dorsum with darker brown or black chevrons and pale cream, yellow scalloped, or triangle pattern on the lower flanks; and *Grayia* **sp. nov.**dark brown or gray dorsum with a small number of black bands that bifurcate on the flanks).

Description of the Lectotype. MNHN 1896.66 adult male, SVL 440 mm, TL 370 mm; left side of head damaged, somewhat short (15.97 mm), rounded (width = 10.75 mm); eye width 4.37 mm, circular pupil; naso–ocular distance 4.20 mm; distance between the nostrils 3.40 mm; interorbital distance 5.82 mm; rostral height 1.80 mm; rostral width 3.70 mm; frontal length 6.98 mm; frontal width 3.27 mm; frontal–rostral distance 4.12 mm; internasals contact 1.94 mm; prefrontals contact 2.39 mm; parietals contact 4.75 mm; loreal height 1.50 mm, loreal width 2.10 mm; lower anterior temporal length 6.11 mm; lower anterior temporal—loreal distance 4.98 mm; anterior sublingual length 5.49 mm; anterior sublingual width 2.37 mm; 1/1 preocular; 2/2 postocular; supralabials 8/8, 4th in contact with orbit; infralabials 9/10, 1st on each side in contact with menial, 1st–5th in contact with anterior chin shield on the left, 1st–4th in contact with the anterior chin shield on the right; temporal scale formula 2 + 3; body large and rounded, dorsal scale rows one head length posterior to jaw rictus 15, dorsal scale rows at midbody 15, dorsal scale rows one head length anterior to vent 15; scales smooth without apical pits; 59 body bands; ventral scales (standard) 134, ventral scales (Dowling) 133; heart above ventrals 27–31; 127 paired subcaudals; cloacal scale divided.

Variation. Morphometric variation in *G. tholloni* can be seen in Tables 11–12. The longest (TL) recorded *G. tholloni* was an individual measuring 1,200 mm (Villiers 1975). One of the longest specimens recorded in this study was a male (VW 79-1142, Kinsuka, DRC) with a SVL measuring 900 mm. However, the tail for this specimen was incomplete and total length could not be determined. One female specimen and one specimen of indeterminate sex (BMH 1979.164, MNHN 1996, respectively) had the longest total length at 1,211 mm. *Grayia tholloni* is typically dark brown with white scales forming bands across its body. The tail is usually dark brown and the ventral side is pale cream. They typically have distinct black striping on their upper and lower labial scales with a cream-colored chin (Fig. 23). *Grayia tholloni* have 7–8 upper labials (with the 4th in contact with the eye) that are cream-colored and outlined with dark brown or black (Chippaux and Jackson 2019). Some specimens had 9–10 supralabials. Typically, there are 9–10 infralabials (5 in contact with the anterior chin shield), but some specimens had 11. The temporal formula is 2 + 3, with frequent variation observed, including 2 + 2, 3 + 3, 2 + 4, and 2 + 3 + 4. There are typically 15 scale rows across the entire body length, but the dorsal scale rows at the neck can range from 15–17. The literature reports that the ventral scales for this species typically range from 130 to 150 (standard, < 141 in males and > 137 in females) (Chippaux and Jackson 2019). The specimens examined in this study had between 132 and 151 ventrals (standard) and there were several specimens that deviated from the typical ventral counts seen between the sexes. Two males (RMCA 437, AMNH 96104) from Lake Tanganyika, DRC and Nigeria had more than 141 ventral scales (142 and 146, respectively). The subcaudals and cloacal scale were always divided. The subcaudal scales ranged between 100–134. Literature records indicated there are at least 30 maxillary teeth present in this species (Mocquard 1897, Boulenger 1901)

Diet. This species primarily feeds on fish and amphibians (Chippaux 2006). The examined specimens had a variety of fish, amphibians, and even insects recovered from their stomachs. One specimen (VW 80-2040, Kinsuka, DRC) had two unknown species of fish and multiple nematodes found in the stomach. A second specimen (VW 80-2041, Kinsuka, DRC) had frog legs—likely from the *Ptychadena* genus—collected from the stomach, while a third (FMNH 214794, Kinsuka, DRC) had four frogs, one insect (Orthoptera), and one nematode present in the stomach.

Reproduction. Two gravid females (MNHN 1988.2342, RMCA 27556) from Republic of Congo and Kinshasa Province, Kinshasa, DRC were examined, each with nine eggs present.

Habitat. *Grayia tholloni* usually inhabit lakes, rivers, and streams in moist savanna and woodland (Spawls et al. 2018, Chippaux and Jackson 2019). In Cameroon*,* they are found in medium to large waterways within evergreen forests, highland (humid) savannas, savanna-forest mosaics, and the montane tropical forests of the western highlands (Chirio and LeBreton

2007). In the CAR, they are listed as a savanna species (Chirio and Ineich 2006) and in inland Kenya, they are restricted to “extreme western localities” associated with water (Hughes 1983). In Nigeria, this species is sympatric with *G. smithii*, but some authors noted that unlike *G. smithii*, *G. tholloni* is not found in Nigerian forests (Butler and Reid 1990).

4. Discussion

Prior to this study, the relationships within *Grayia* were largely unexplored and inferences were made based primarily on morphological similarity. For example, *G. ornata* and *G. smithii* are believed to be more closely related to each other, because of similarities in scale counts, than to *G. caesar* (Mocquard 1897, Boulenger 1901). The distinct *G. ornata* + *G. smithii* and *G. tholloni* + *G. caesar* clades recovered in the phylogenetic trees were able to lend support to some of these hypotheses regarding their relatedness. There is also sufficient molecular and morphological evidence to suggest a new cryptic species of *Grayia* in the same clade as *G. ornata* and *G. smithii*. Generally, there was high concordance between the analyses preformed. The ML and BI trees had well-supported, identical topologies and the gene tree-species tree analysis recovered similar divergence dates to the concatenated BEAST tree. The marginal differences in divergence times could be because the gene tree-species tree approach jointly analyzes population sizes, species tree topology, gene trees, and divergence times. This approach can account for processes such as incomplete lineage sorting, horizontal transfer, and gene duplication/extinction that cause gene tree discordance, potentially producing more reliable divergence time estimates (Heled and Drummond 2009). Gene tree-species tree methods are believed to perform better than concatenation since concatenated trees can have erroneously deep divergence times (Edwards et al. 2007). Concatenated trees do not account for coalescent stochasticity and assume that the gene copies diverged when the species did—which could be responsible for the deep divergent times seen in the concatenated BEAST tree. While the concatenated phylogenetic trees inferred that there were five total species in the genus *Grayia*, the species delimitation analysis indicated that there were seven. This “oversplitting” is a known problem with species delimitation analyses, and previous studies have shown that these analyses can favor models with a larger number of species (Chan et al. 2017, Jackson et al. 2017, Sukumaran and Knowles 2017, Chan and Grismer 2019). The number of delimited species can often be a direct reflection of the number of populations present. Furthermore, this problem is worsened when more loci are included (Rannala and Yang 2020). Looking at the agreement across data types, the analysis of the morphological data found multiple statistically significant characters that supported the molecular conclusions. However, there were some areas of disagreement. *Grayia tholloni* and *G. smithii* were indicated to be singular species in the molecular analysis, yet there were several significant morphological characters found between populations. There is high degree of intra- and interspecific variation in *Grayia*, and these significant characters could represent clines. Furthermore, molecular phylogenies do not always align with traditional taxonomies made using morphology alone. This can be caused by various factors including phenotypic convergence, mistakes with homology identification, or the complexities of inheritance of morphological traits (Voet et al. 2022). In a paper by Hahn and Nakhleh (2016), it was suggested that traits may evolve along gene trees rather than species trees and therefore traits may be discordant with species tree topology. Although there can be some degree of discordance between molecular and morphological data, simultaneous analysis—or analysis that utilizes multiple sources of information such as morphology and genes—is still believed to provide the most comprehensive view of evolutionary relationships (Lee and Palci 2015).

I identified a genetically and morphologically distinct taxon, *Grayia sp. nov*.. which is widespread and found on both sides of the eastern Congo River, primarily in the middle and upper Congo River (Figs. 5,6). The Congo River is subdivided into three distinct parts: the lower, middle, and upper. These sections are separated by various rapids and large waterfalls that have been known to serve as geographic barriers leading to speciation in various aquatic fauna (Schwarzer et al. 2011, Alter et al. 2015, Steenberge et al. 2020). In particular, the lower Congo River has a high degree of fish diversity, and aside from the Lake Tanganyika cichlid radiations, is estimated to contain nearly 30% of the total fish species found in the basin (Alter et al. 2017). There is some debate regarding where the of the separation point between the middle and Upper Congo River. The geomorphological delimitation between the Upper Congo River and the Middle Congo River lies at the Wagenya falls—which is the downstream portion of the Boyoma falls, located at Kisangani (Runge 2008). The ecoregions of the Upper Congo River, which are defined based on freshwater species and ecological processes, are comprise two distinct sections: the Upper Congo and Upper Congo Rapids ecoregions. The Upper Congo Rapids ecoregion extends downstream of Wagenya falls, and therefore downstream of the geomorphological start of the Upper Congo River (Abell et al. 2008). In this study, I defined the Upper Congo River as beginning at Boyoma falls, which aligns with the hydrological delineation between the Upper and Middle Congo River. There is a degree of overlap between the distributions of *G. ornata* and *Grayia* **sp. nov.** (Figs. 5,6). Generally, *Grayia* **sp. nov.** occurs in the upper and middle Congo River and its tributaries. One sample from Angola was found in a tributary from the lower portion of the middle Congo River. This implies that *Grayia* **sp. nov.**may be more widespread than currently recognized, possibly because the central Congolian lowland forests are poorly sampled (de Perre et al. 2019). Allopatric speciation—because of the number of large waterfalls found in the upper Congo River—could be the cause of the divergence between these two species. These large waterfalls in the southern Congo frequently isolate fish fauna from the rest of the Congo Basin (Kasongo Ilunga et al. 2020, Steenberge et al. 2020) and foster high levels of genetic divergence. However, because the distributions of *G. ornata* and *Grayia* **sp. nov.** overlap in the middle Congo River and its tributaries, these putative barriers may have been recently circumvented.

The phylogenetic trees recovered two well-supported subclades within *G. ornata.* The first subclade, consisting of nine samples, was found west of the Congo and Ubangi rivers, and had only one sample (MTD 48961, Uige Angola) from south of the Congo and Ubangi divide. The second subclade, consisting of 16 samples, contained a sample (ELI 1740) from Bandundu (DRC) that is genetically identical to a sample (CG 17_027) from Cuvette Etoumbi in the Republic of Congo. However, with these two exceptions, the subclades are divided by the fast flowing, lower portion of the Congo and Ubangi Rivers. The two samples (MTD 48961, CG 17_027) presumed to have crossed the lower Congo and Ubangi rivers may be recent migrants or an example of introgression. Although *Grayia* are exclusively aquatic, the division between these subclades suggests that the Congo and Ubangi rivers might be barriers as they are in other groups of snakes (e.g., Greenbaum et al. 2021)

Grayia ornata from the Ogooué River Basin (and surrounding area), noteworthy for having 19 dorsal scale rows at midbody (DSRM), were primarily found in the Ivindo River. Many of the specimens were from Makokou, which is geographically isolated because of its separation from the main course of the Ogooué by three large waterfalls. However, there are five specimens (PEM R263, BMNH 1966.374, AMNH R50550, AMNH R5272, MNHN 1995-9386) from Equatorial Guinea, Cameroon, and CAR that had 19 DSRM. Furthermore, there were three specimens

(MNHN 1967-375, MNHN 1967-380, and MNHN 1967-381) with 17 DSRM from the Ivindo River. The specimens from this population were found to have 25 statistically significant differences for females and nine for males (see Results). However, the ANCOVAs recovered only three statistically significant differences in females and two in males. Furthermore, the PCA (Fig. 11, Table 10) showed a high degree of overlap between this population and both *G. ornata* and *Grayia* **sp. nov.** Two genetic samples (MCZ R188643 and MNHN 1977.6517) from Gabon, with the latter directly collected from the Ivindo River, showed very little genetic distinction from the other populations of *G. ornata* in the phylogenetic trees (Figs. 1–2). These two Ogooué Basin specimens were recovered in a clade with other *G. ornata* from outside the Congo Basin, including a specimen (MTD 48961) from Angola that was found ~200 km from the type locality of *G. ornata*—likely making it near topotypic. The species delimitation analysis identified the Ogooué Basin *G. ornata* as a distinct species; however, this could be a result of the analysis identifying a population split as species divergence (Luo et al. 2018). Given the totality of this evidence, we consider all populations of *G. ornata* (red clade in Figs. 1–2) to be conspecific.

Grayia smithii populations had observable morphological differences. *Grayia smithii* from West Africa have very distinct striping on the ventral side near the head. This ventral pattern is not present in any *G. smithii* east of Nigeria, save for some specimens from eastern DRC and Uganda. T-tests highlighted significant differences between Western *G. smithii* (from Nigeria and other Western Countries) and all other *G. smithii* populations. The ANCOVAs recovered significant difference between Western *G. smithii* and all other populations except the eastern DRC and Uganda striped *G. smithii* (see Results). However, the ML tree (Fig. 1) recovered almost no genetic divergence between the West African *G. smithii* and other *G. smithii*. The BI tree (Fig.

2) did show a small, very recent possible split between the West African *G. smithii* and all other *G. smithii*, but the posterior support values were extremely low (0.22 and 0.13 respectively). The Semliki River/Lake Edward population was not differentiated from the Eastern Striped form in either the t-tests or ANCOVAs; however, both the Semliki/ Lake Edward and Eastern Congo form had some significant differences from the lower Congo form in females. Although some differences were observed, the sample size for the Semliki River/Lake Edward population and Eastern Striped population were relatively small (M = 2, F = 3 and M = 5, F = 6 respectively).

All five populations of *G. tholloni* overlapped heavily in the PCA (Fig. 13, Table 12). Unlike *G. smithii*, there were very few morphological characteristics differentiating the populations. The Western *G. tholloni* had the most significantly different characteristics found between all other populations (see Results). Western *G. tholloni* males had considerably more ventral scales than the other populations, however the females had very few or no differences between populations in the t-tests. The ANCOVAs did show considerably more significant differences between the Western *G. tholloni* and all other groups. Two specimens from Western Africa (8480 S and RBINS 20168) were included in the phylogenetic analyses and neither tree indicated that the West African *G. tholloni* is genetically distinct from other *G. tholloni* (Fig. 1–2). One specimen of *G. tholloni* (ELI 203) had a slight branch length difference in the ML tree (Fig. 1), and was separated from the rest of *G. tholloni* in the BI tree (Fig. 2) having diverged around 6–8 Mya. The branch lengths were not long enough to indicate a new species. This specimen is one of two samples collected from the upper Congo River in DRC though the divergent sample was found much further upriver near Lake Kabamba, whereas the other sample was found near Katako-Kombe in Sankuru Province, DRC.

The dated BI tree (Fig. 2) indicated that *Grayia* diverged from its nearest sister clade in the late Eocene (median age 38.6 Mya). This date near the Eocene-Oligocene boundary is consistent with the divergence between other African subfamilies such as Atractaspidinae, Aparallactinae, and Lamprophiidae (Portillo et al. 2018, McCartney et al. 2021). Furthermore, the rapid diversification between African elapoid families occurred during this time period (Kelly et al. 2009). The divergence date between *Grayia* and its nearest sister clade coincides with the mid-Eocene Climatic Optimum, which occurred around 40 Mya (O'Brien et al. 2020, Couvreur et al. 2021). This was followed by rapid cooling until the Eocene–Oligocene transition (Couvreur et al. 2021), when a mass extinction event called the Grande Coupure (33.9–33.4 Mya) significantly impacted aquatic organisms in both marine and freshwater environments, and led to rapid species diversification (Zaher et al. 2019). The divergence of the *G. smithii* + *G. ornata* clade from the *G. tholloni* + *G. caesar* clade happened around the mid to late Oligocene. The further divergence of *G. smithii* from *G. ornata* and *G. tholloni* from *G. caesar,* happened during the late Oligocene. As the Oligocene progressed (29–24 Mya), there were increasingly warmer global temperatures with seasonal precipitation (O'Brien et al. 2020, Couvreur et al. 2021). These changing climate conditions could have led to the diversification seen within *Grayia* at this time. The BI tree indicated that *Grayia* **sp. nov.** diverged from *G. ornata* around 16 Mya in the mid-Miocene. The mid-Miocene climate optimum (between 15–17 Mya), marks an age of major global climatic change. In fact, this period is considered one of the most crucial ages for tropical regions in Africa (Plana 2004, Couvreur et al. 2021). Palaeodrainage disruption, closure of seaways, formation of mountain rifts, and even pCO_2 variations that occurred during this time period heavily changed the climate of Africa (Couvreur et al. 2021). Furthermore, temperatures during this time rose drastically after the previous trend of Cenozoic cooling (Methner et al. 2020). These substantial changes in climate led to rapid speciation (Böhme 2003, Feakins and Demenocal 2010, Methner et al. 2020, Aduse-Poku et al. 2022) and could be responsible for the split seen between *G. ornata* and *Grayia* **sp. nov.**

The gene tree-species tree analysis (Fig. 3) recovered marginally different divergence dates than the time-calibrated BI tree. Instead of diverging in the mid-Miocene (16 Mya), *Grayia* **sp. nov.** was indicated to have split from *G. ornata* during the late Miocene (8 Mya). Though these divergence dates are 8 million years apart, the mid-Miocene climate optimum could have still played a critical role in the split seen between *G. ornata* and *Grayia* **sp. nov.** Furthermore, the late Miocene (5.4–7 Mya) experienced a global cooling, drying, and enhanced seasonality that could have further influenced the divergence between the two species (Herbert et al. 2016). This date in the late Miocene also coincides with the divergence dates of sister taxa within other Central African snake genera such as *Boaedon* (Family Lamprophiidae), *Atheris* (Family Viperidae), and *Polemon* (Family Lamprophiidae) (Menegon et al. 2014, Greenbaum et al. 2015, Portillo et al. 2019). The divergence dates of the *G. smithii* + *G. ornata* clade and the *G. tholloni* + *G. caesar* clade were relatively close in both analyses (31.1 Mya vs. 27.3 Mya). The divergence of the *G. ornata* + *Grayia* **sp. nov.** clade from *G. smithii* was indicated to have taken place in the early Miocene in the gene tree-species tree analysis compared to the late Oligocene in the BI tree. The same shift from a late Oligocene to mid-Miocene divergence was found between *G. tholloni* and *G. caesar*.

Future directions include population genetics studies that could help establish the exact biogeographic barriers responsible for the speciation seen within *Grayia,* and determine if introgression is occurring across the Congo and Ubangi Rivers. More genetic sampling across all five species, especially in reptile biodiversity hotspots such as the Upper Congo (Broadley and Cotterill 2004), would allow for further morphological comparisons and identify any additional cryptic species that may still be hidden within *Grayia*. Furthermore, increased sampling in the lower and middle Congo River and its tributaries would also clarify the distribution of *Grayia* **sp. nov.** This work will further improve our understanding of diversity in *Grayia* and highlight regions and populations in need of conservation action.

Key to the species within the Genus *Grayia*

1a Extralabial scale present……………………………………………………….…………5
1b Extralabial scale absent………………………………………………………………....2

2a Dorsal scale rows at midbody = 15…………………………………………………..3
2b Dorsal scale rows at midbody > 15…………………………………………………..4

3a 1 supralabial in contact with the eye; subcaudals < 140; anal scale divided…... *G. tholloni*
3b 2 supralabials in contact with the eye; subcaudals > 140; anal scale single or divided………………………………………………………………... *G. caesar*

4a 7–8 supralabials; > 85 subcaudals; pale cream, scalloped or triangle pattern on the lower flanks…………………………………………………………………… *G. smithii*
4b 8–9 supralabials; < 90 subcaudals; dark brown or black body bands that bifurcate on the flanks……………………………………………………………………....5

5a Ventral side heavily speckled with dark brown or black dots; head and neck dark brown, nearly black with cream spots on the chin and infralabials…. *Grayia* **sp. nov.**

5b Ventral side cream–colored with little to no black or dark brown speckling; chin and labial scales light cream……………………………………………….. *G. ornat*

5. Conclusion

The integrative taxonomic approach taken in this study uses both the conclusions gathered by the molecular data, and those gathered by the morphological data, in conjunction, to form robust conclusions about species relationships. From the ML and BI trees generated from this study, the species relationships within the genus *Grayia* are clear. Both trees had identical topology and strong support values for the monophyly of the genus, a *G. ornata* + *G. smithii* clade, and the *G. caesar* + *G. tholloni* clade. The divergence dates for these clades in the late Oligocene coincide with known climactic events occurring during the period that influenced speciation across the globe.

For *Grayia smithii*, the morphological results suggest that the West African populations may be significantly different from the rest of *G. smithii*. This is supported by several characters in both the t-tests and ANCOVAs that are statistically different, as well as differences in color pattern. However, these results are not supported by the phylogenies or the species delimitation analyses. The same was true for the other *G. smithii* populations used in the statistical analysis. Although there is a high degree of intraspecific variation within *G. smithii*, we cannot conclude that multiple species are present.

Grayia tholloni had very few morphological characters separating populations, but there was some evidence that Western populations from Senegal, Guinea, and Nigeria were significantly different from the other groups. The molecular results did not support distinct species within *G. tholloni* and samples from West Africa were closely related to those from Central Africa in both phylogenetic trees. Only one specimen (ELI 203), from the upper Congo

River, had a marginally different branch length within the phylogenetic trees. However, with the low sample size, additional material is needed to examine the status of this population in the future.

The three samples of *G. caesar* used in the morphological analyses—two from outside the Congo Basin and one from inside—were not genetically distinct in either the ML or BI tree. These results, combined with the lack of morphological differentiation, suggest that multiple species are not present within *G. caesar*.

The Ogooué River Basin *G. ornata*, with 19 scale rows at midbody, had numerous morphological characters that were significantly different from other *G. ornata*. Furthermore, there are no records of *G. ornata* present within the Congo Basin that have 19 scale rows at midbody. Previously published records of specimens with this scale count within the Congo Basin were re-examined during the course of this study by project collaborator Olivier Pauwels, and the scale counts were corrected. Although there is some morphological evidence that this population is distinct, the PCA for the Ogooué Basin *G. ornata*, other *G. ornata*, and *Grayia* **sp. nov.** did not show distinct clusters for these putative taxa. Furthermore, the phylogenetic trees do not indicate that the Ogooué Basin *G. ornata* are genetically distinct from other samples of *G. ornata*. The species delimitation analysis did indicate that the Ogooué Basin *G. ornata*—in a clade with other *G. ornata* from outside the Congo Basin—is a separate species. This could be a result of the species delimitation analysis over-splitting this clade and identifying a population split as species divergence. There is some evidence that this population is morphologically distinct, but the totality of the data do not support it as a distinct species.

For *G. ornata* and *Grayia* **sp. nov.**, the molecular results—including ML and BI phylogenetic trees, species delimitation analysis, sequence divergence analysis, and amino acid translations, suggest that *Grayia* **sp. nov.** represents a new, cryptic species of *Grayia*. These results are supported by the statistical analyses conducted on morphometric characters. While specimens from these taxa were not morphologically distinct in the PCA, there were various counts and measurements found through t-tests and ANCOVAs that were significantly different between the two species. Because *Grayia* **sp. nov.** is a cryptic species, it has many overlapping characters with *G. ornata*, and this is a pattern seen in many groups of African snakes (e.g., Greenbaum et al. 2015, Portillo et al. 2019, Greenbaum et al. 2021). This overlap makes correct identification difficult without genetic data.

In concluding that *Grayia* **sp. nov.** represents a new, cryptic species within *Grayia*, the conservation implications must be considered. *Grayia ornata* is currently classified as Least Concern by the IUCN Red List. This classification does not take into consideration the new cryptic species currently grouped into *G. ornata*. There is some amount of geographic separation between these two species, with *Grayia* **sp. nov.** occurring further upriver than most *G. ornata*. However, this cannot solely be used to differentiate the species, because there is overlap between their distributions in the middle portion of the Congo River and its tributaries. Further genetic sampling in the middle and upper portions of the Congo River would likely strengthen the conclusions made in this study and possibly identify the exact biogeographic barriers that are responsible for the speciation patterns seen here.

As we continue to see species declines, it is imperative to improve understanding of biodiversity in order to prevent its extinction. Cryptic species are particularly vulnerable to extinction because cryptic complexes with broad geographical ranges are often comprised of multiple species with more limited distributions (Bickford et al. 2007). This can also cause incorrect assessments of endemism and diversity in certain habitats—leading to lower conservation priorities. Thus, the ability to identify cryptic species complexes can aid in informing targeted conservation efforts (Bickford et al. 2007). Unfortunately, the majority of known cryptic species are overlooked in many research fields as they are typically undescribed (Fišer et al. 2018). While *Grayia* is a common, widespread genus, it is still threatened by the same global-change drivers that impact all African biodiversity. Furthermore, *G. ornata*—and likely *Grayia* **sp. nov.**—are frequently killed and eaten, or used in traditional medicine by local people. Without future conservation efforts, these conditions can leave even the most abundant species hurtling toward extinction.

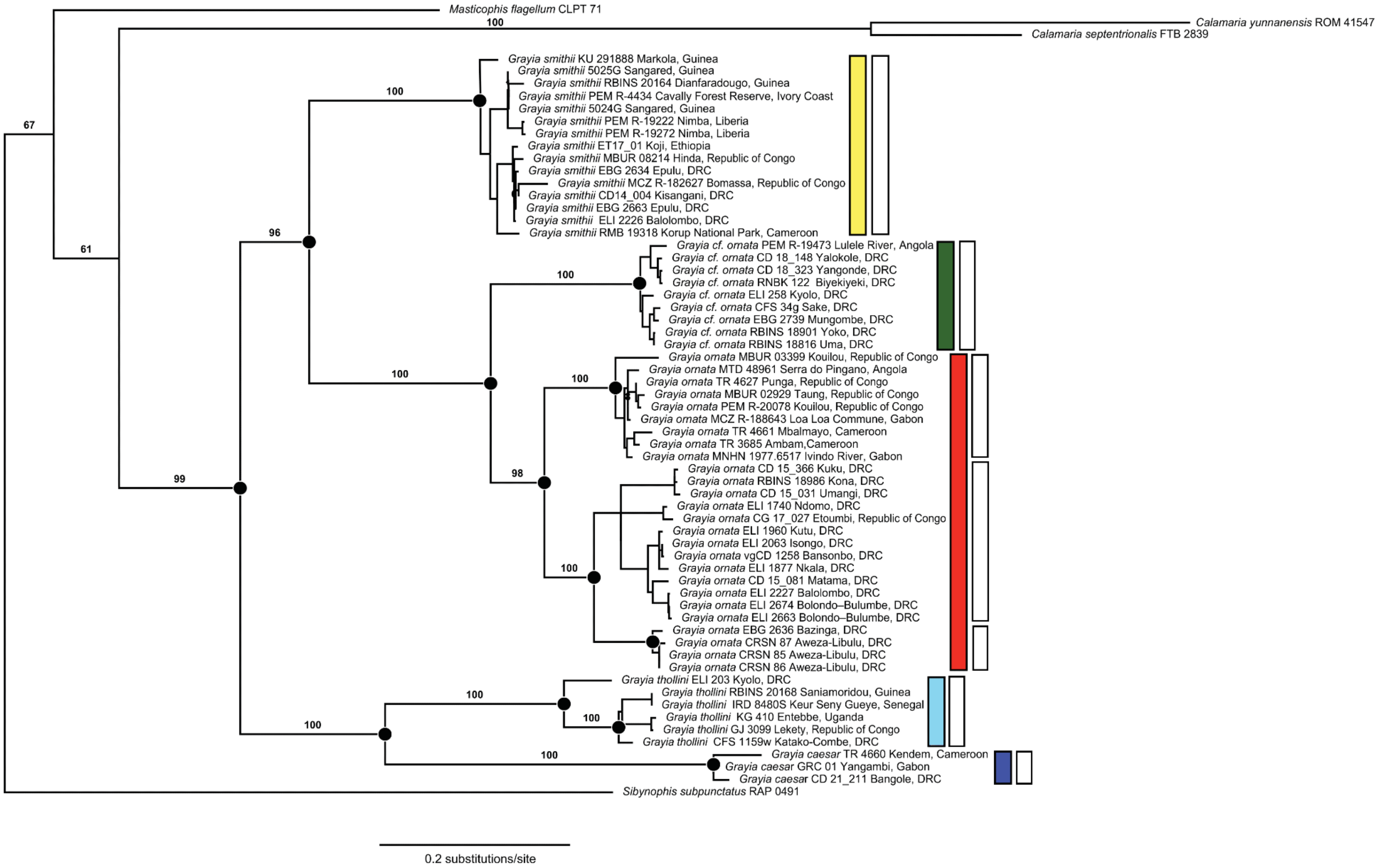

Figure 1: Combined maximum likelihood and Bayesian inference tree of *Grayia* based on four mitochondrial (16S, COI, cyt *b*, and ND4) and two nuclear (BDNF and NT3) genes. Branch support values are maximum likelihood bootstrap support values. Black circles indicate a node with posterior support values ≥ 0.95. Species delimitation analysis (GMYC) inferred species are indicated by vertical white side bars.

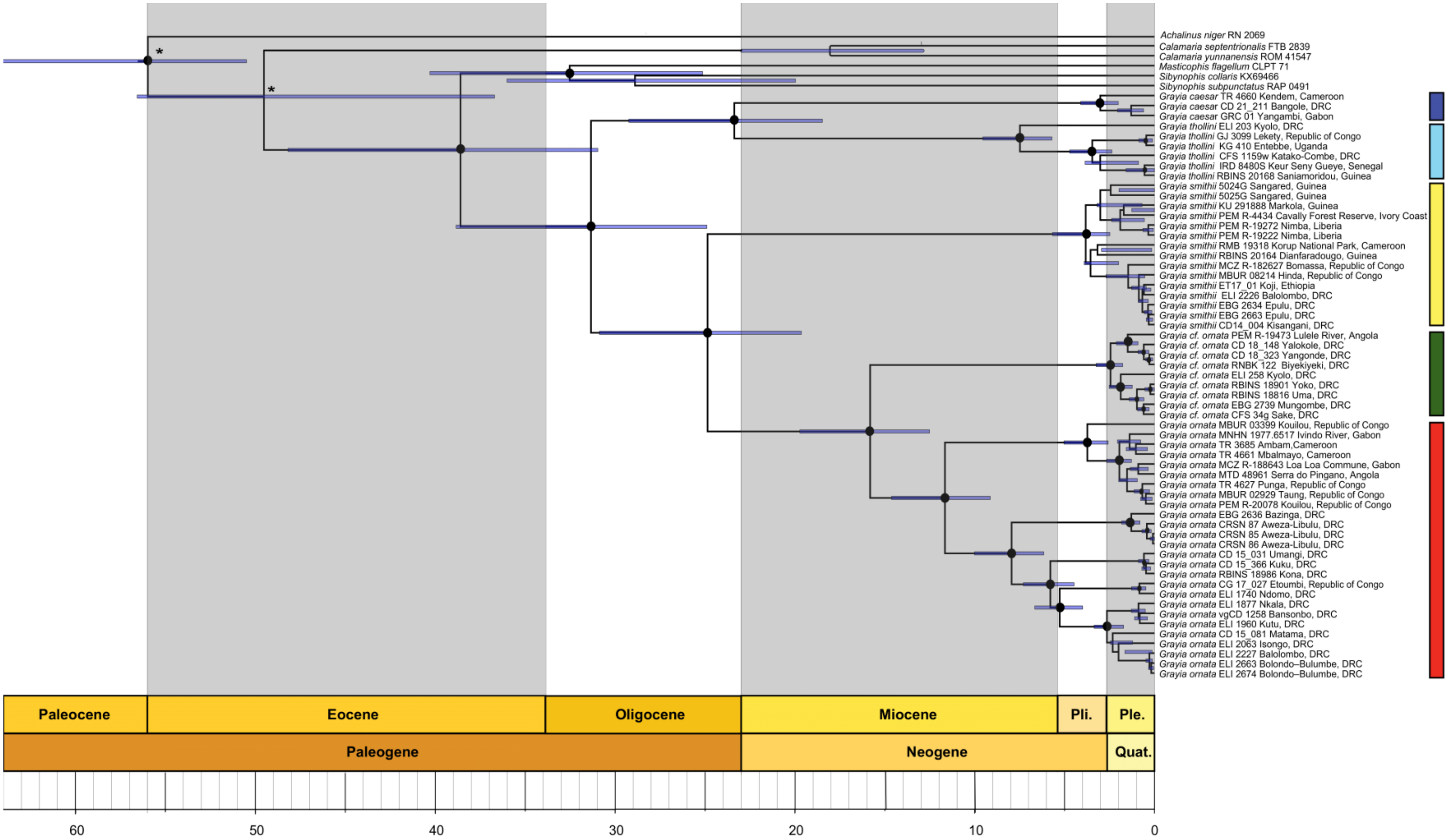

Figure 2: Bayesian Inference, time-calibrated tree of *Grayia* based on four mitochondrial (16S, COI, cyt *b*, and ND4) and two nuclear (BDNF and NT3) genes. Nodes with posterior support values ≥ 0.95 are denoted by a black circle and node bars indicate 95% confidence intervals. Fossil-calibration points are indicated by asterisks.

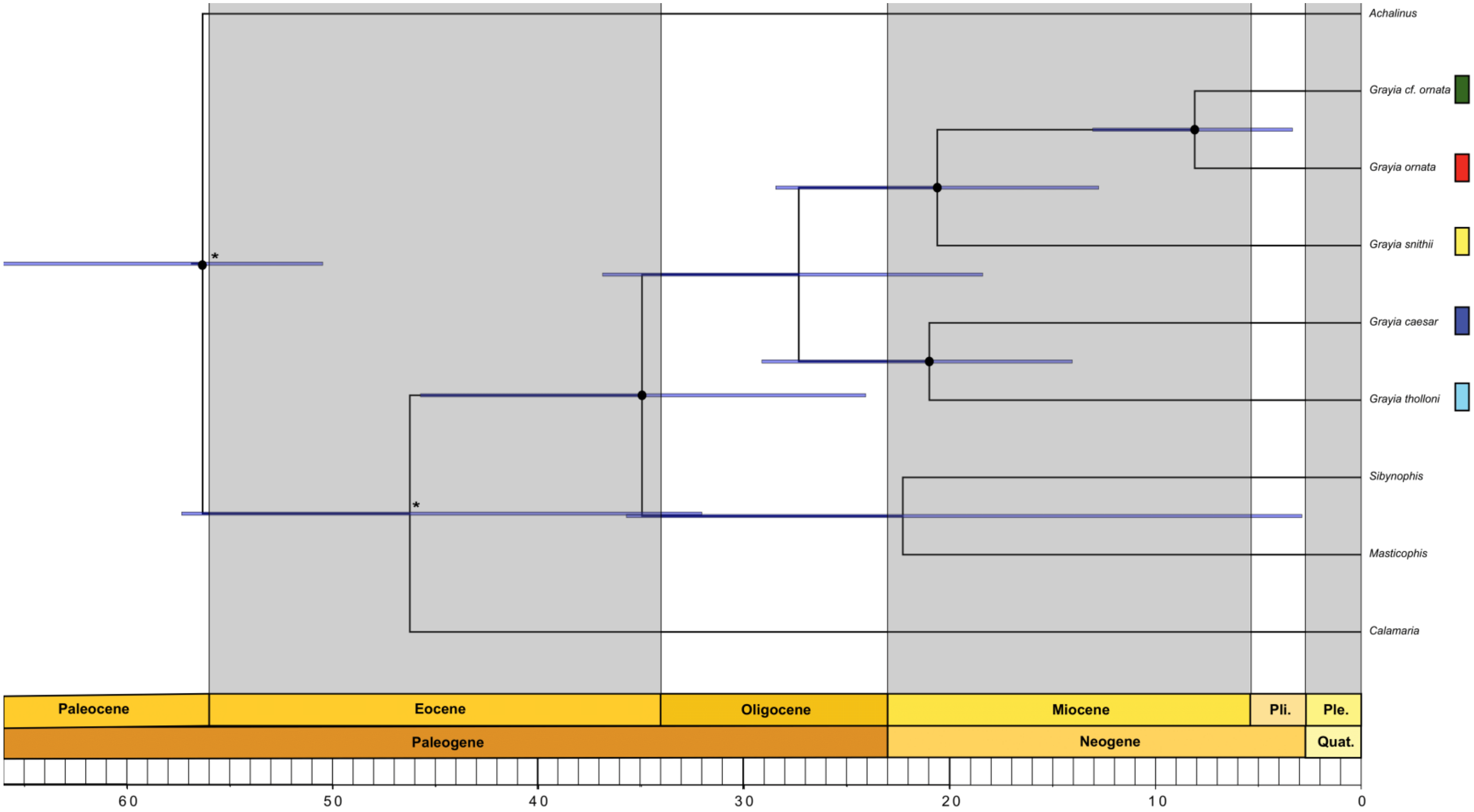

Figure 3: Bayesian Inference, time-calibrated gene tree-species analysis of *Grayia* based on four mitochondrial (16S, COI, cyt *b*, and ND4) and two nuclear (BDNF and NT3) genes. Nodes with posterior support values ≥ 0.95 are denoted by a black circle and node bars indicate 95% confidence intervals. Fossil-calibration points are indicated by asterisks.

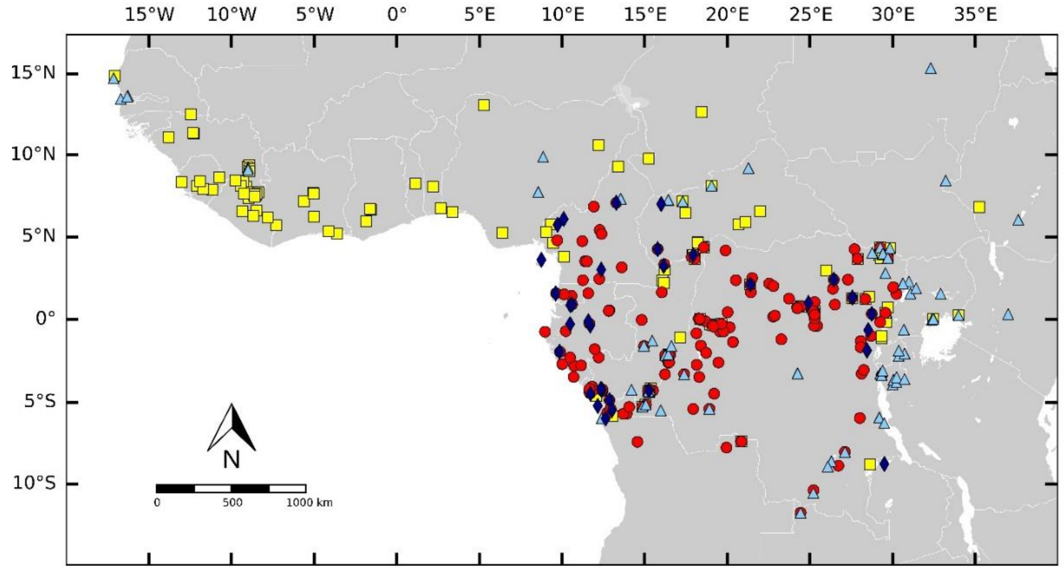

Figure 4: Map of Central and West Africa showing localities of all the samples (both molecular and morphological) used in this study. Bodies of water are white. Symbol colors match the color-coded clades in Figs. 1–3. Circles = *G. ornata*, diamonds = *G. caesar*, triangles = *G. tholloni*, and squares = *G. smithii*.

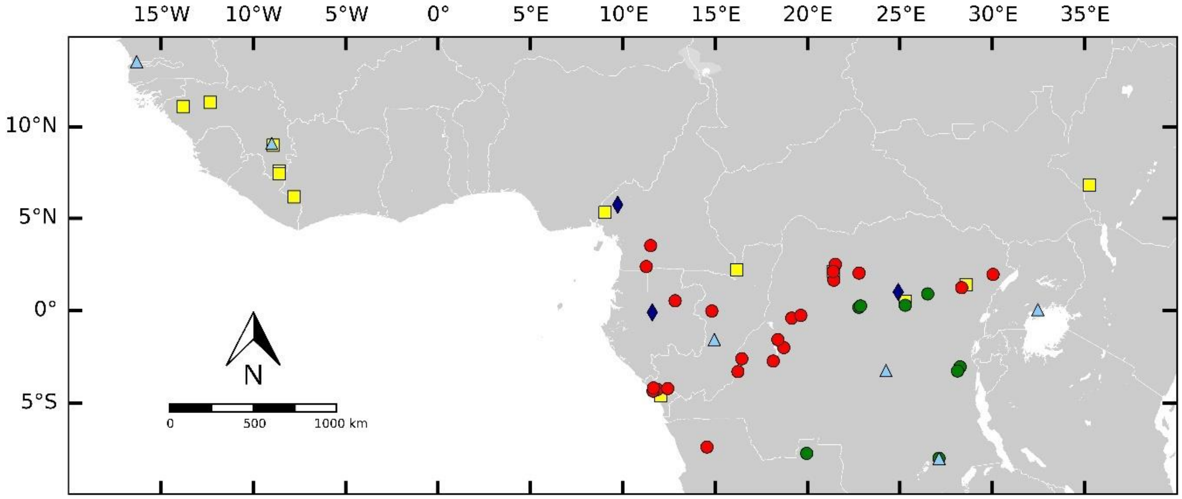

Figure 5: Map of Central and West Africa showing localities of genetic samples used in this study. Bodies of water are white. Symbol colors match the color-coded clades in Figs. 1–3. Circles = *G. ornata*, diamonds = *G. caesar*, triangles = *G. tholloni*, and squares = *G. smithii*.

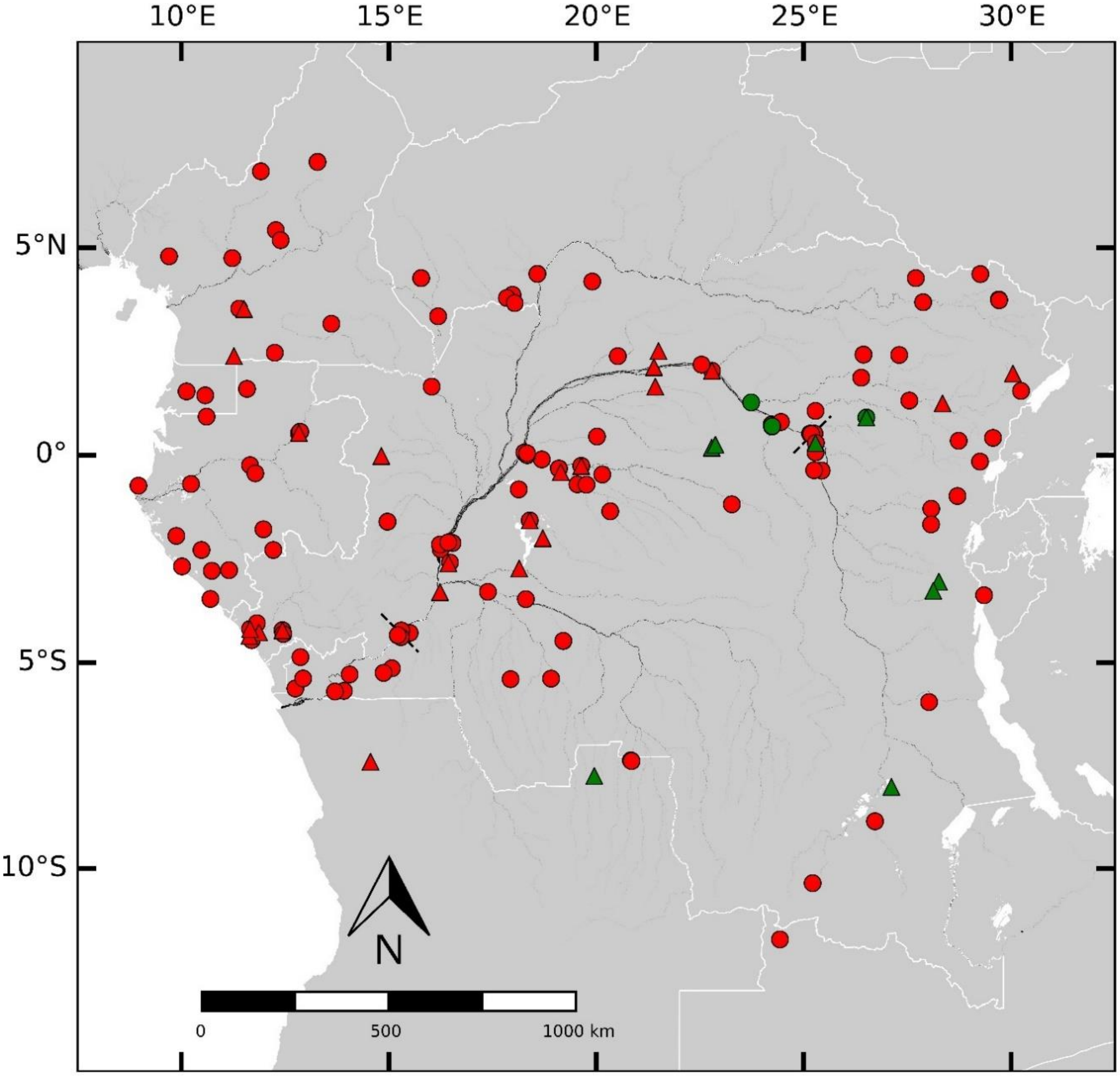

Figure 6: Map of Central Africa showing localities of the molecular and morphological *G. ornata* samples used in this study. The confluence of the western Congo and Ubangi Rivers are shown in black with the separation points between the lower, middle, and upper Congo indicated by dashed black lines. Bodies of water are white. Red circles = *G. ornata sensu stricto* morphological specimens; red triangles = *G. ornata sensu stricto* genetic samples; green circles = *G.* cf. *ornata* morphological specimens, green triangles = *G.* cf. *ornata* genetic samples.

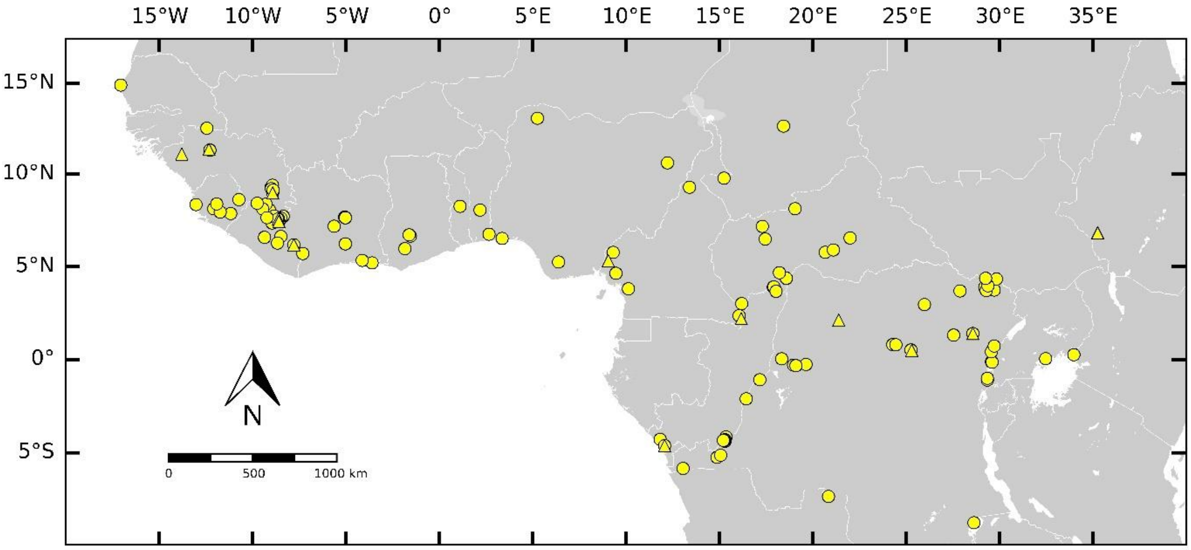

Figure 7: Map of Central and West Africa showing localities of the molecular (triangles) and morphological (circles) *G. smithii* samples used in this study. Bodies of water are white.

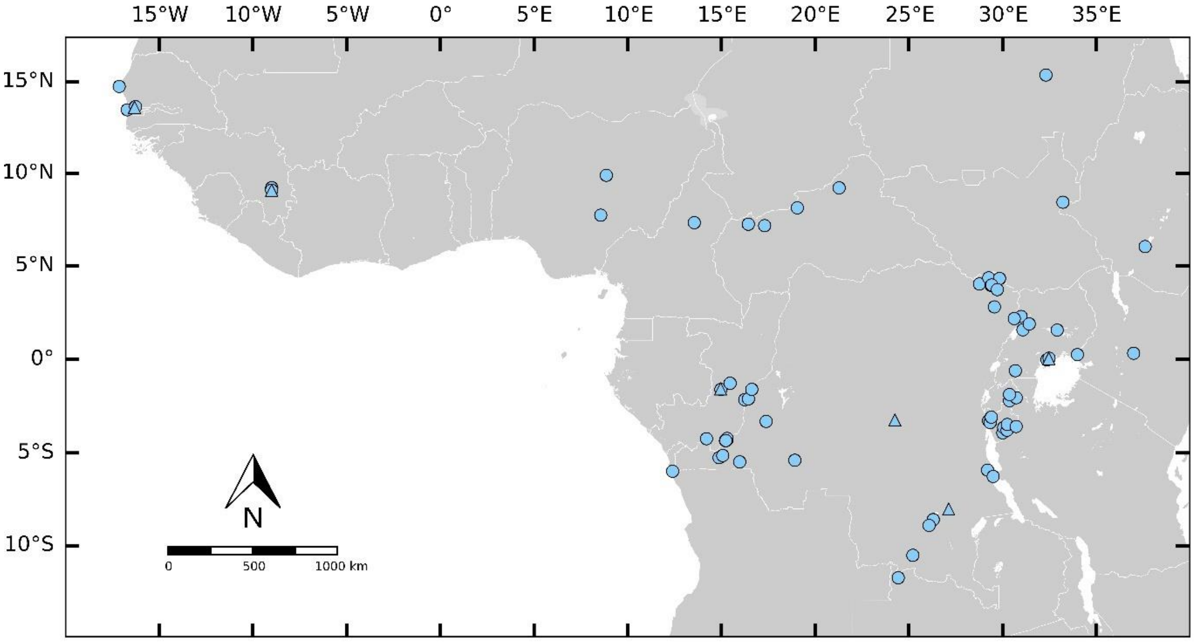

Figure 8: Map of Central and West Africa showing localities of the molecular (triangles) and morphological (circles) *G. thollonii* samples used in this study. Bodies of water are white.

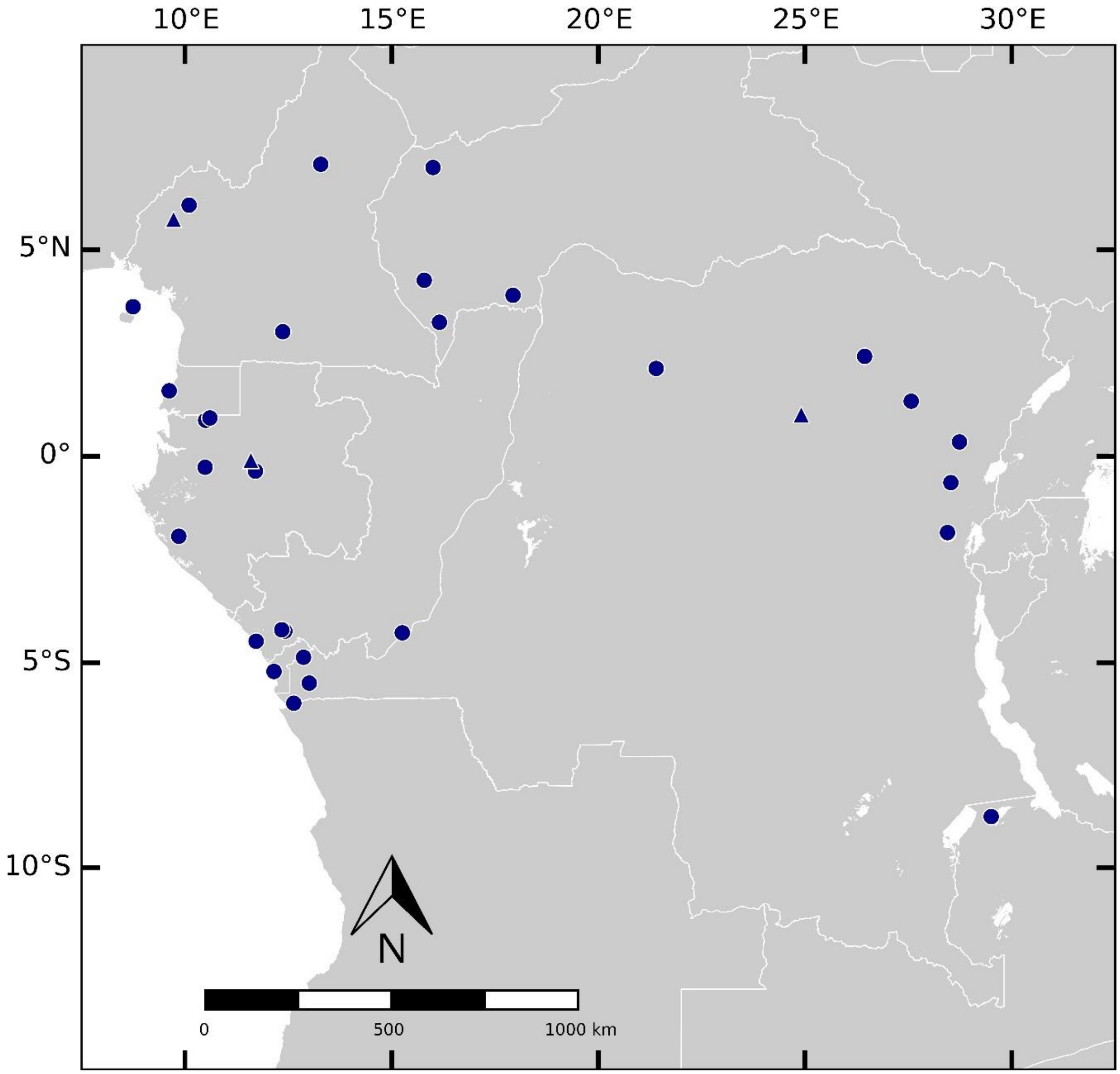

Figure 9: Map of Central and West Africa showing localities of the molecular (triangles) and morphological (circles) *G. caesar* samples used in this study. Bodies of water are white.

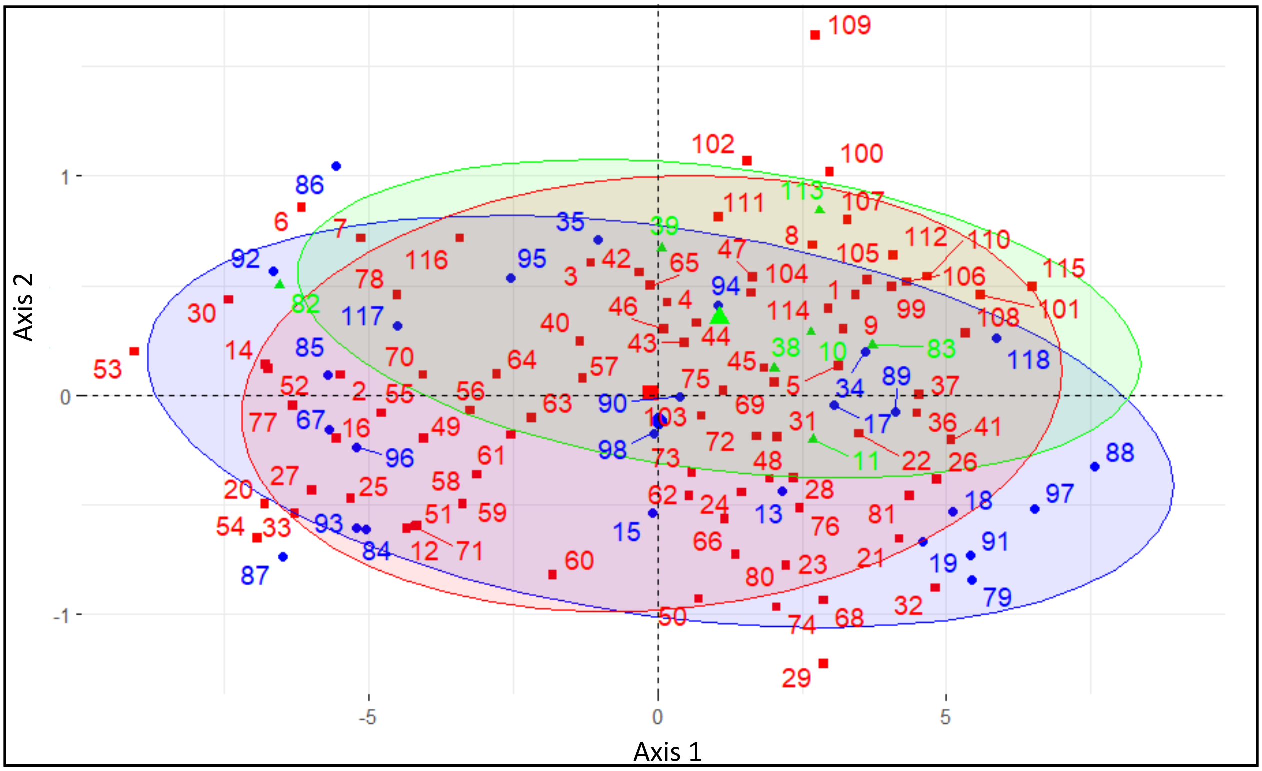

Figure 10: Principal Component Analysis of *Grayia ornata*. The colors and shapes denote the various populations. Blue circles = Ogooué River Basin *G. ornata* population, red triangles = *G.* cf. *ornata*, and green squares = *G. ornata.*

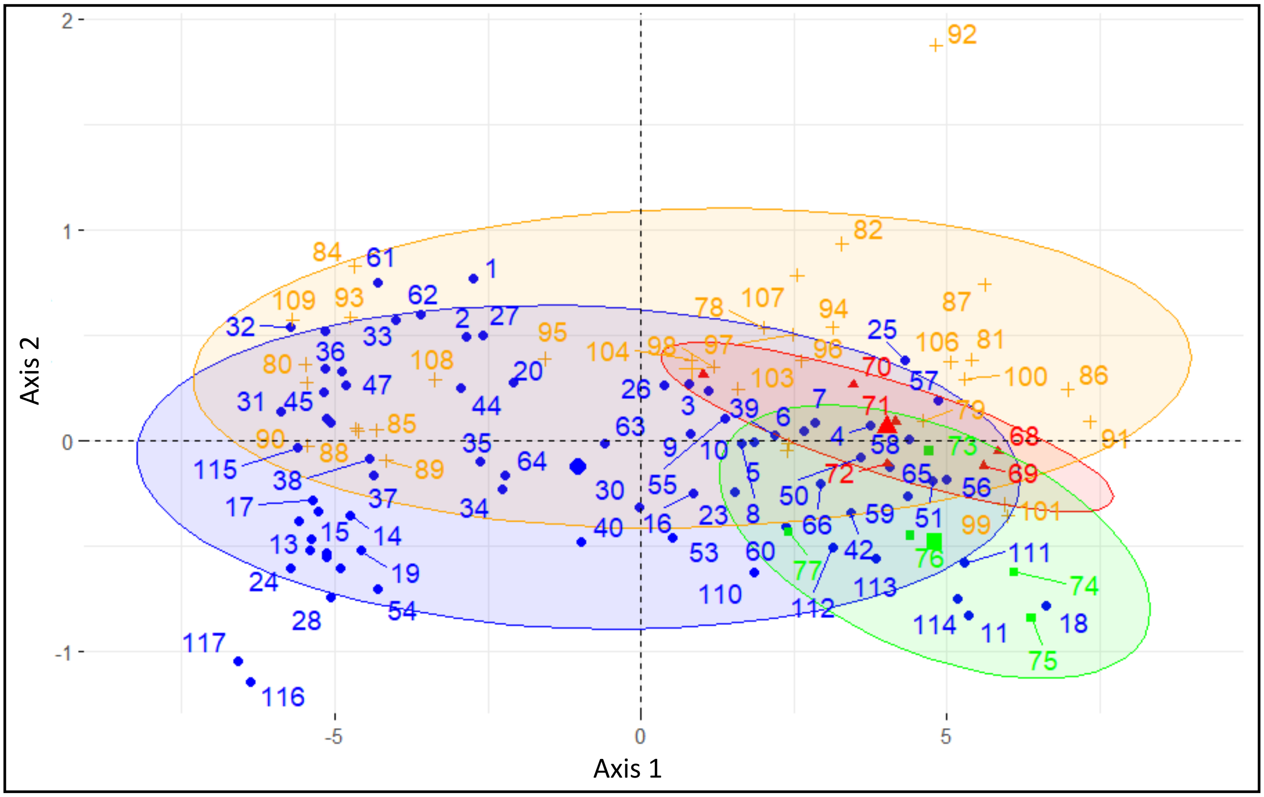

Figure 11: Principal Component Analysis of *Grayia smithii*. The colors and shapes denote the various populations. Blue circles = *Grayia smithii* from the Congo, Chad, Atlantic and Nile River Basins, red triangles = striped *G. smithii* from eastern DCR and Uganda, green squares = *G. smithii* from the Semliki River and Lake Edward, and orange crosses = Western *G. smithii* (specimens from Nigeria and other localities in West Africa).

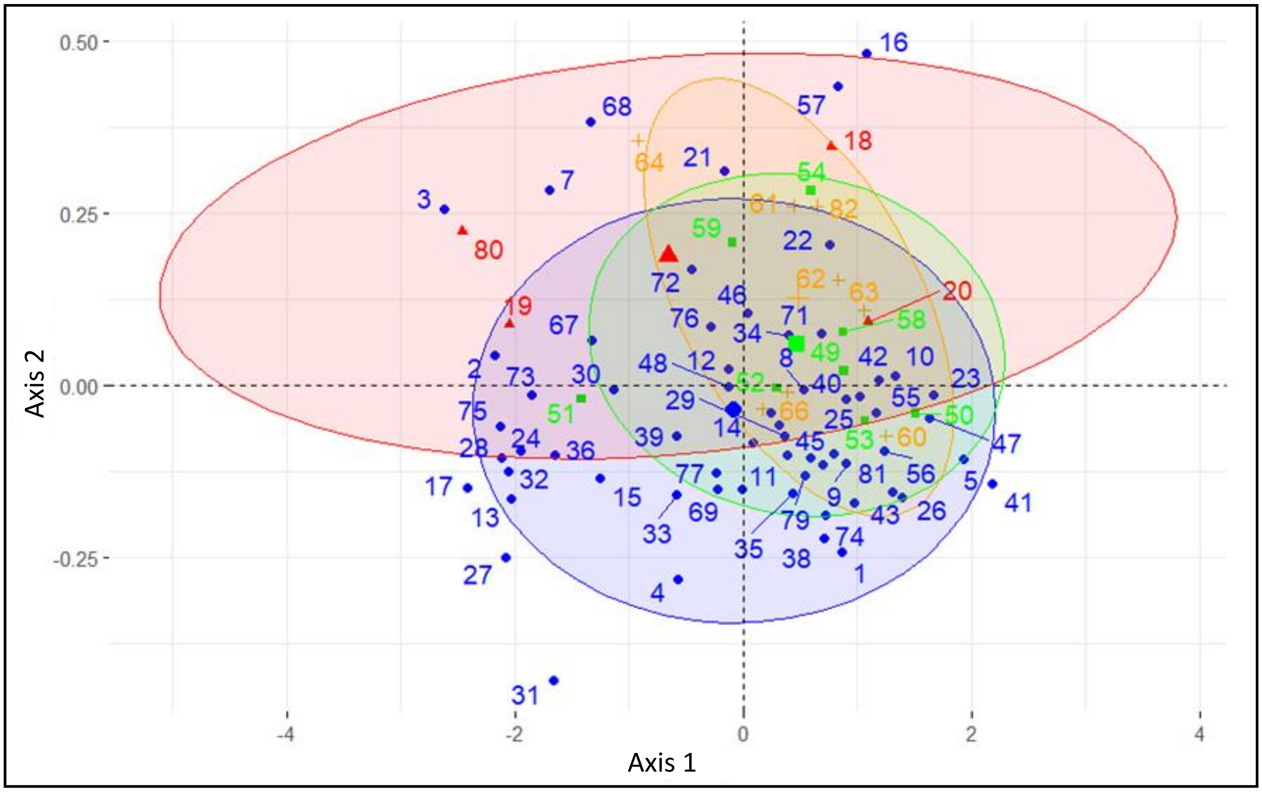

Figure 12: Principal Component Analysis of *Grayia tholloni*. The colors and shapes denote the various populations. Blue circles = *G. tholloni* from the Congo, Chad, and Atlantic River Basins, red triangles = *G. tholloni* from Lake Tanganyika, green squares = *G. tholloni* from the Nile River basin, orange crosses = *G. tholloni* from West Africa (specimens from Nigeria and other localities in West Africa).

Figure 13: Color pattern differences between *G.* cf. *ornata* and *G. ornata.* (A) Entire body in dorsal view of an adult male *G. ornata* (ELI 1740) from Ndomo, DRC, (B) entire body in dorsal view of an adult female of *G.* cf. *ornata* (CFS 34g) from Sake, DRC, (C) ventral side of adult male *G. ornata* (ELI 2227) from Balolombo Village, DRC, (D) ventral side of an adult male *G.* cf. *ornata* (EBG 2739) from Mungombe, DRC, (E) head in left lateral view of an adult male *G. ornata* (ELI 2227), and (F) head in right lateral view of an adult female G. cf. *ornata* (CFS 34g).

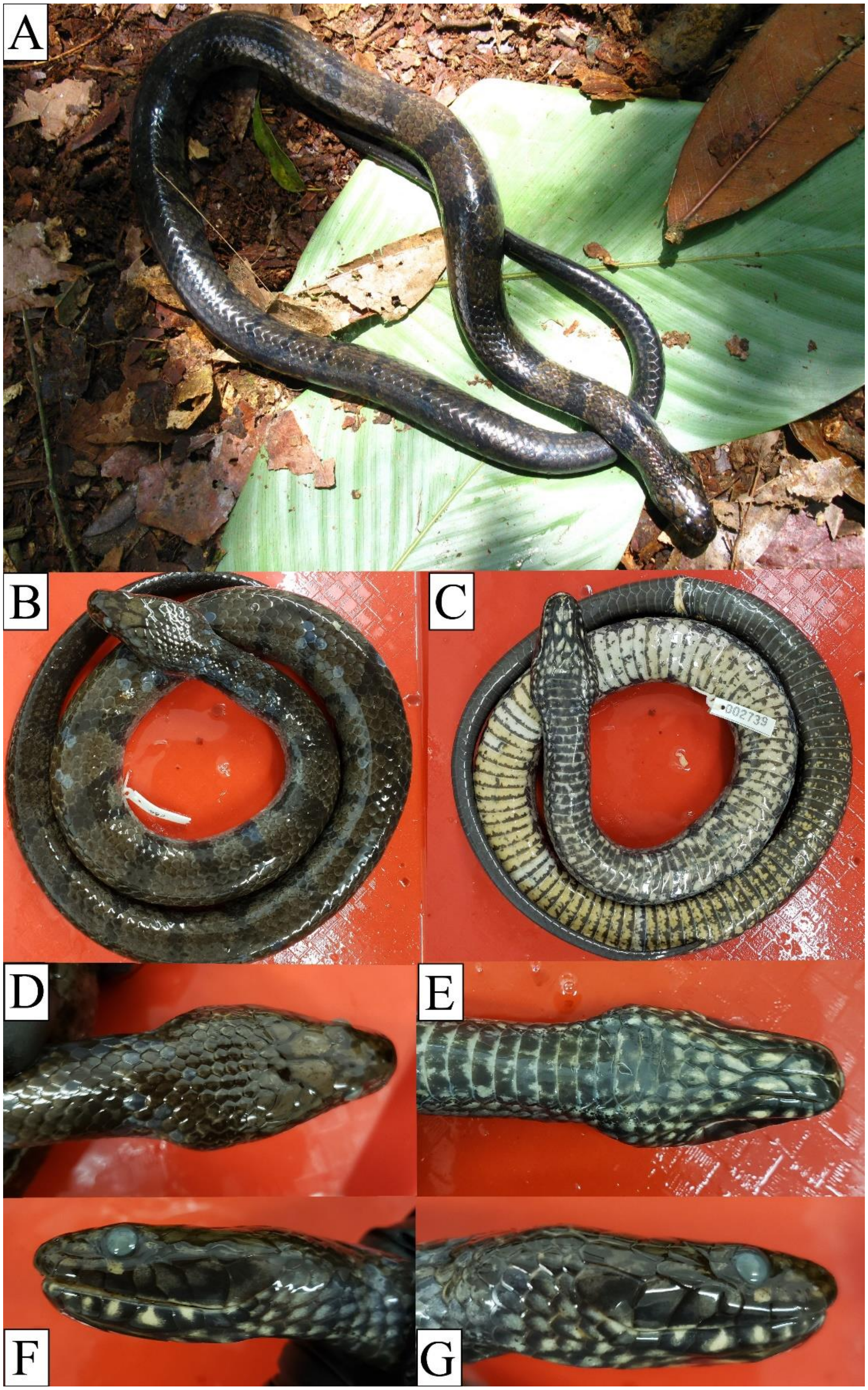

Figure 14: Holotype of *Grayia* **sp. nov.** (EBG 2739, Mungombe, DRC) (A) specimen in life, (B) entire body in dorsal view (C) entire body in ventral view, (D) head in dorsal view, (E) head in ventral view, (F) head in left lateral view, (G) and head in right lateral view.

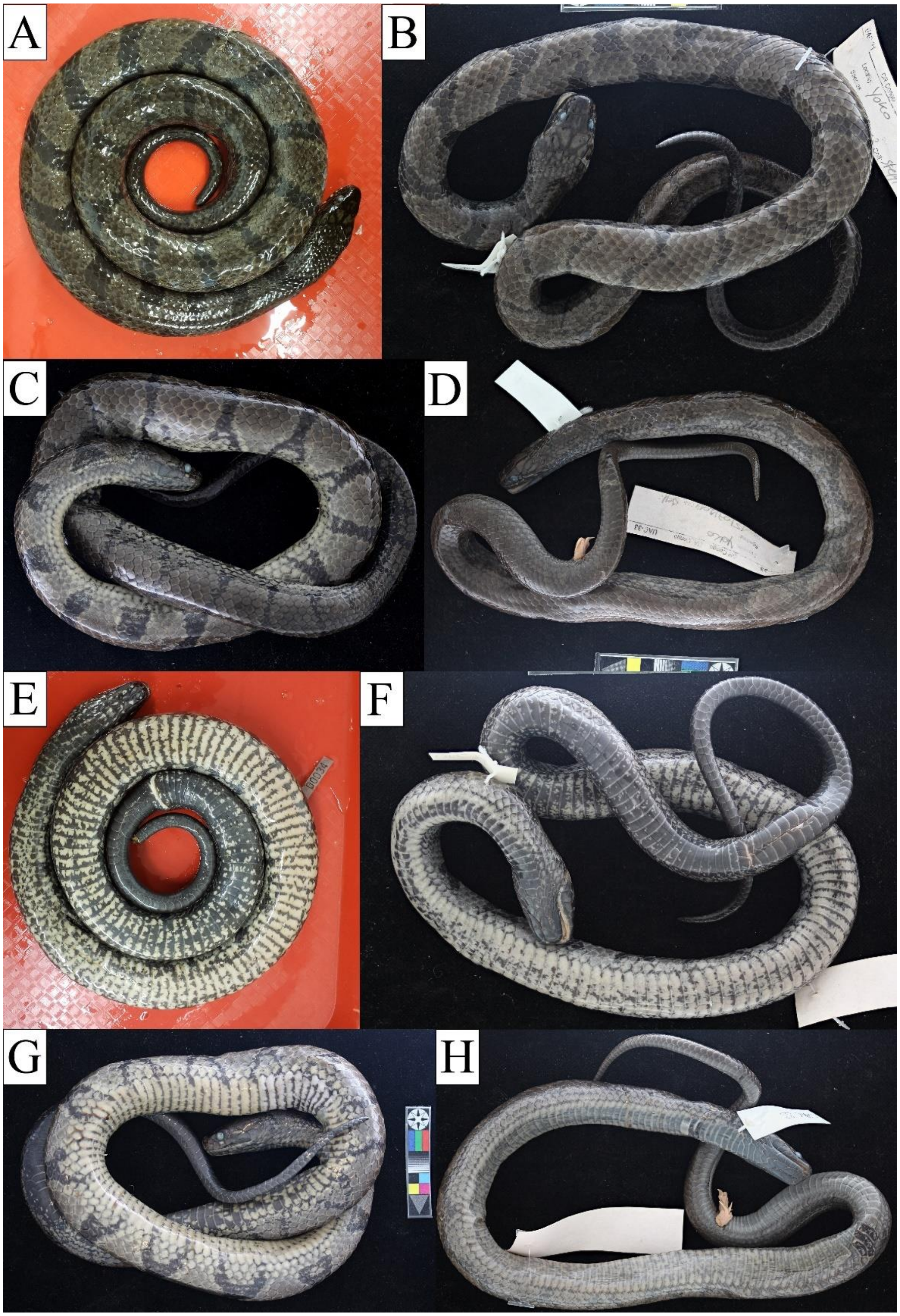

Figure 15. Paratypes of *Grayia* **sp. nov.** (A) entire body in dorsal view of CFS 34 g, from Sake DRC (B) entire body in dorsal view of RBINS 18901 from Yoko DRC, (C) entire body in dorsal view of RBINS 18816 from Uma DRC, (D) entire body in dorsal view of RBINS 18902 from Yoko DRC, (E) entire body in ventral view of CFS 34g, (F) entire body in ventral view of RBINS 18901, (G) entire body in ventral view of RBINS 18816, and (H) entire body in ventral view of RBINS 18902.

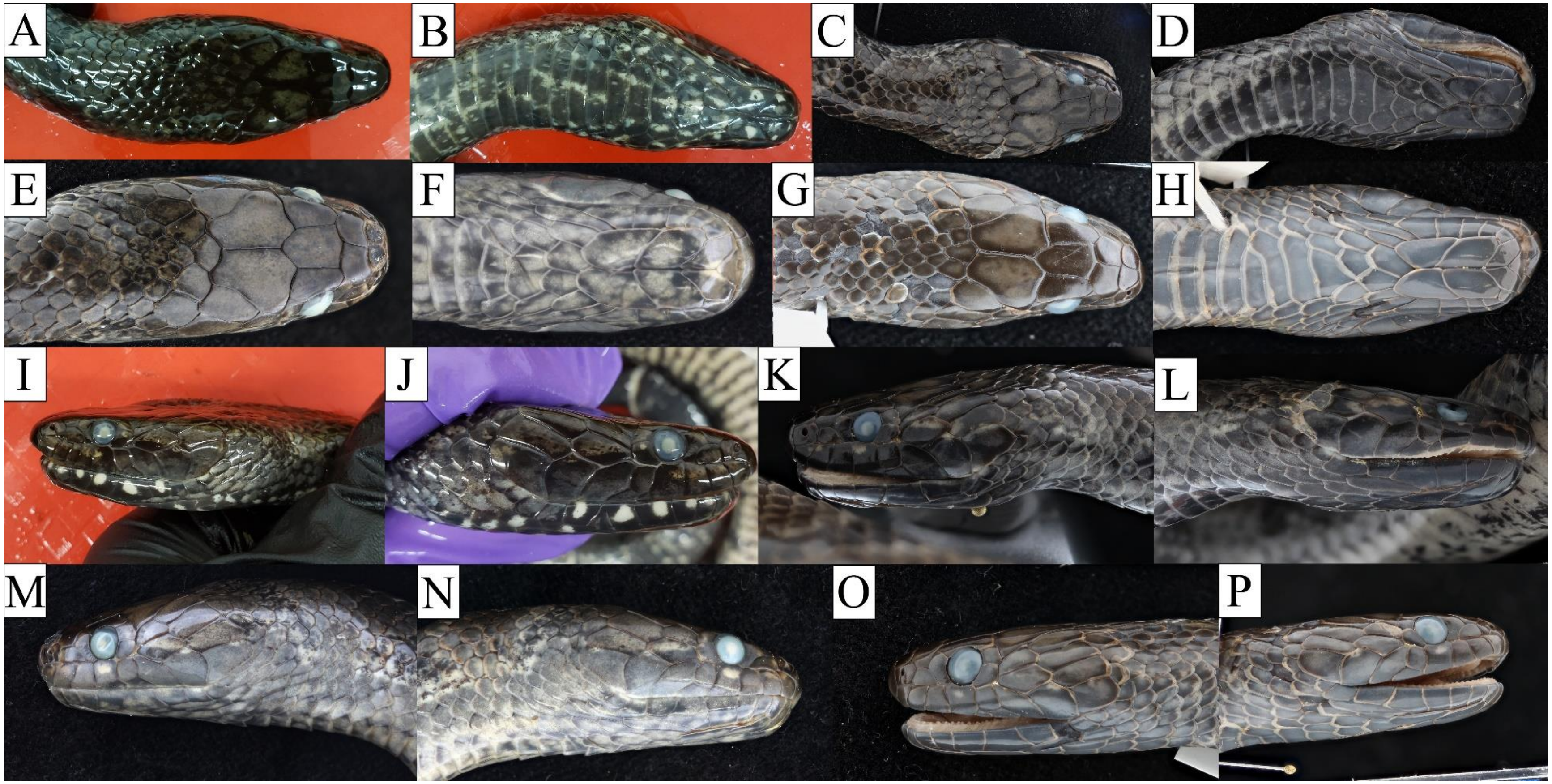

Figure 16: Paratypes of *Grayia* **sp. nov.** (A) Head in dorsal view of CFS 34 g, from Sake DRC, (B) head in ventral view of CFS 34g, (C) head in dorsal view of RBINS 18901 from Yoko DRC, (D) head in ventral view of RBINS 18901, (E) head in dorsal view of RBINS 18816 from Uma DRC, (F) head in ventral view of RBINS 18816, (G) head in dorsal view of RBINS 18902 from Yoko DRC, (H) head in ventral view of RBINS 18902, (I) head in left lateral view of CFS 34g, (J) head in right lateral view of CFS 34 g, (K) head in left lateral view of RBINS 18901, (L) head in right lateral view of RBINS 18901, (M) head in left lateral view of RBINS 18816, (N) head in right lateral view of RBINS 18816, (O) head in left lateral view of RBINS 18902, (P) and head in right lateral view of RBINS 18902.

Figure 17: Aberrant male *Grayia* **sp. nov.** (ELI 258, Kyolo DRC) lacking banding. (A) Entire body of specimen in dorsal view in life, (B) entire body of specimen in ventral view in life, (C) entire body of preserved specimen in dorsal view, (D) entire body of preserved specimen in ventral view, (E) head in dorsal view, (F) head in ventral view, (G) head in left lateral view, (H) and head in right lateral view.

Figure 18: Photos of adult *G. caesar* preserved specimens (AMNH R50520 from Metet Cameroon, and AMNH R12182 from Niapu DRC). (A) Entire body in dorsal view (AMNH R50520), (B) entire body in ventral view (AMNH R50520), (C) head in right lateral view (AMNH R50520), (D) and head in left lateral view (AMNH R12182).

Figure 19: Color variation within *G. ornata*. (A) MTD 49696 from Angola in life (Photo: R. Ernst), (B) MTD 48961 from Serra do Pingano, Angola in life (Photo: R. Ernst), (C) entire body in dorsal view of CRSN 85 from Aweza-Libulu DRC with no body bands, (D) entire body in ventral view of CRSN 85 with no body bands in life, (E) entire body in dorsal view of preserved specimen CRSN 85, (F) entire body in ventral view of preserved specimen CRSN 85, (G) entire body in dorsal view of the longitudinally striped color phase of *G. ornata* from Penka-Michel, Cameroon (Photo: M. LeBreton).

Figure 20: Juvenile *G. ornata* color pattern inversion. (A) Entire body in dorsal view of ELI 2064 from Isongo, DRC in life, (B) entire body in dorsal view of ELI 1877 from Nkala, DRC in life, (C) entire body in ventral view of ELI 2065 from Isongo, DRC in life, (D) entire body in ventral view of ELI 1877 in life.

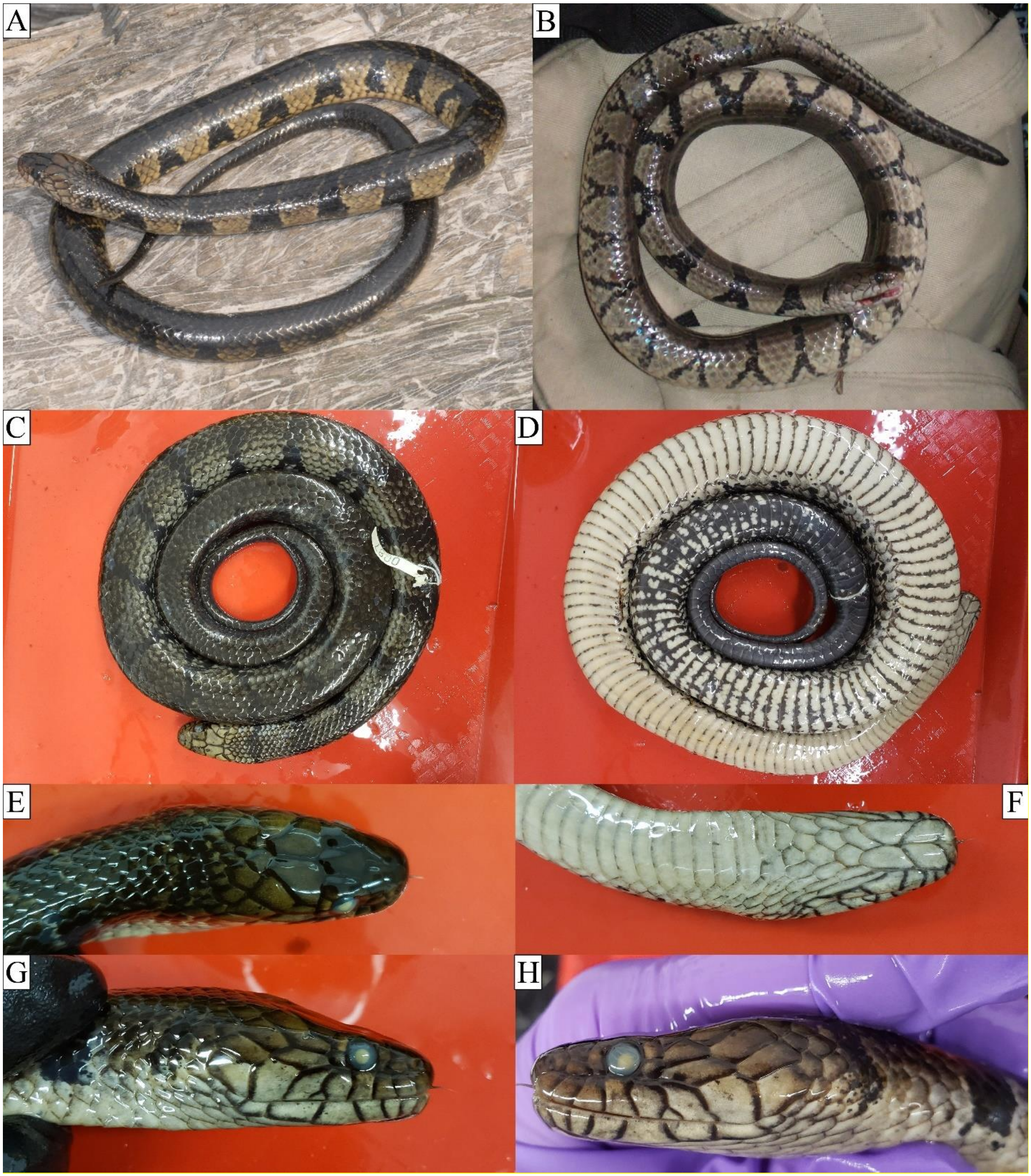

Figure 21: *Grayia ornata*. (A) ELI 2227 from Balolombo DRC in life, (B) ELI 1740 from Ndomo DRC in life, (C) entire body in dorsal view of CRSN 87 from Aweza-Libulu DRC, (D) entire body in ventral view of ELI 2352 from Bomputu DRC, (E) head in dorsal view of ELI 2352, (F) head in ventral view of ELI 2352, (G) left lateral view, and (H) right lateral view of head of ELI 2352.

Figure 22: Photos of preserved specimens of *G. smithii*. (A) Juvenile EBG 2634 from Epulu DRC in life, (B) Adult ELI 2226 from Balolombo DRC in life, (C) entire body in dorsal view of a West African adult (PEM R19279, Yekepa Liberia), (D) entire body in ventral view of a West African adult (PEM R19279), (E) entire body in dorsal view of an adult (AMNH R12157, Avakubi DRC), (F) entire body in dorsal view of a juvenile (EBG 2634), (G) entire body in ventral view of an adult (AMNH R12157), (H) entire body in ventral view of a juvenile (EBG 2634), (I) head of an adult (AMNH R12153, Avakubi DRC) in left lateral view, (J) head of a juvenile (EBG 2634) in left lateral view, (K) head of an adult (AMNH R12153) in right lateral view, (L) head of a juvenile (EBG 2634) in right lateral view.

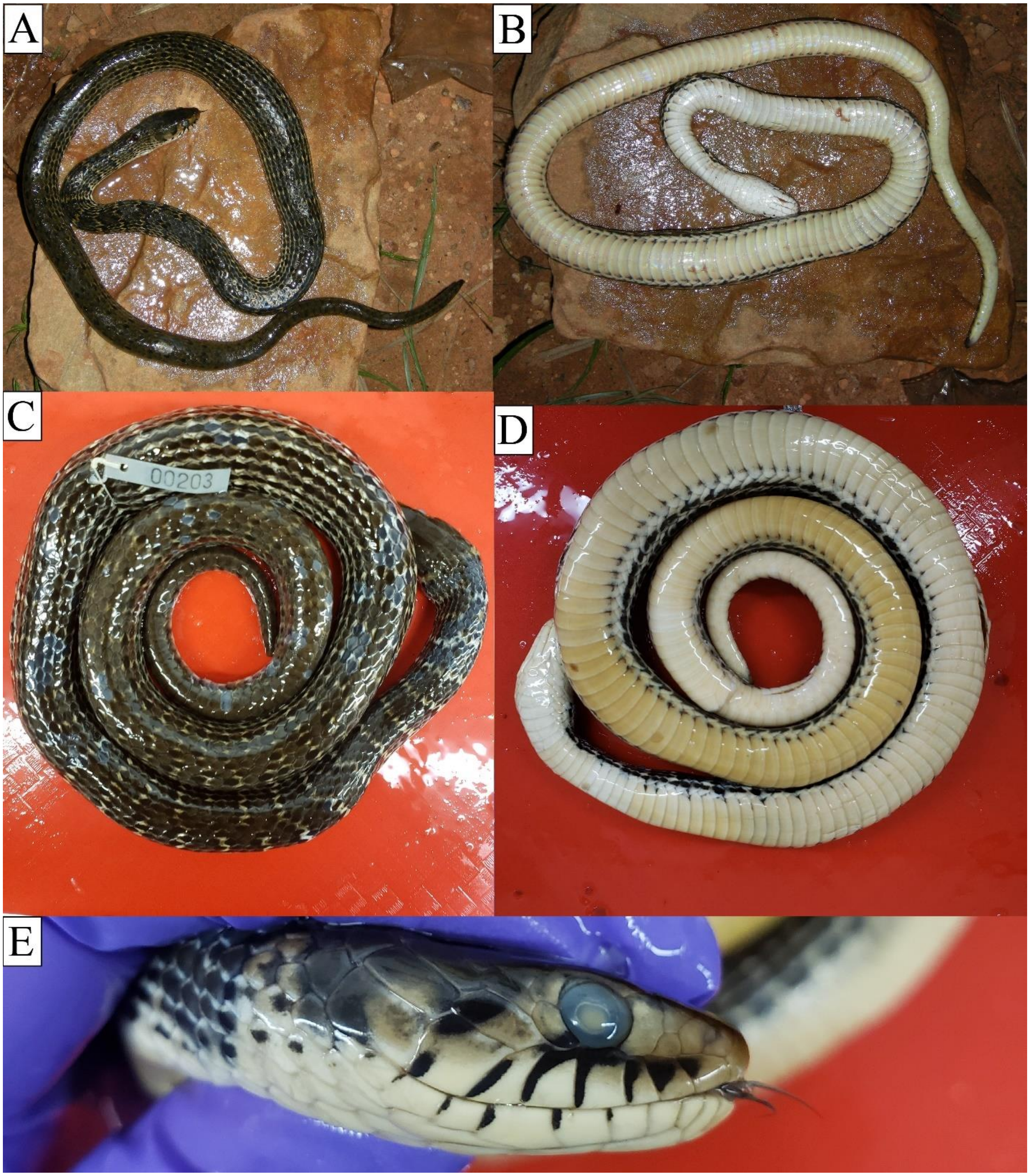

Figure 23: Photos of an adult *G. tholloni* specimen (ELI 203, Kyolo DRC). (A) entire body in dorsal view life, (B) entire body in ventral view in life, (C) entire body in dorsal view of preserved specimen, (D) entire body in ventral view of preserved specimen, (E) head in right lateral view.

Table 1: Genetic primers used in the molecular portion of this study, their sequences, and sources.

Primers		Primer Sequence	Source
BDNF	BDNF-F	GACCATCCTTTTCCTKACTATGGTTATTTCATACCT	Noonan and Chippindale (2006)
	BDNF-R	CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC	
NT3	NT3-F3	ATATTTCTGGCTTTTCTCTGTGGC	Noonan and Chippindale (2006)
	NT3-R4	GCGTTTCATAAAAATATTGTTTGACCGG	
CO1	fishCO1	TCAACYAATCAYAAAGATATYGGCAC	Deichmann et al. (2017)
	fishCO1R	ACTTCYGGGTGRCCRAARAATCA	
cyt *b*	L14910	GACCTGTGATMTGAAAACCAYCGTTGT	Burbrink et al. (2000)
	H16061	CTTTGGTTTACAAGAACAATGCTTTA	
16S	L2510mod/16Sar	CCGACTGTTTAMCAAAAACA	Zaher et al. (2009)
	H3056/16Sbr	CTCCGGTCTGAACTCAGATCACGTRGG	
ND4	ND4	CACCTATGACTACCAAAAGCTCATGTAGAAGC	Arèvalo et al. (1994), Pook et al. (2009)
	HIS1276	TTCTATCACTTGGATTTGCACCA	

Table 2: Voucher numbers, localities, and GenBank accession numbers for genetic samples. DRC = Democratic Republic of the Congo, CAR = Central African Republic.

Species	Field Number	Catalog Number	16S	ND4	cyt *b*	COI	BDNF	NT3	Locality
Achalinus niger	RN 2069	—	MT590304	—	MT590306	—	—	—	Taiwan: Hualien County: Xiulin Township (N24.182622, E121.392856)
Calamaria septentrionalis	FTB 2839	—	KR814637	KR814708	KR814699	—	—	—	China: Guangdon
Calamaria yunnanensis	—	ROM 41547	KX694625	—	KX694891	—	KX694702	KX695000	—
Masticophis flagellum	CLPT 71	—	MG673309	MG672612	MG672797	—	—	MG673154	USA: Florida State: Tallahassee (N30.38642, W84.33236)
Sibynophis subpunctatus	RAP 0491	—	KC347373	KC347516	KC347471	—	—	—	Sri Lanka: Hambantota District: Yala National Park
Sibynophis collaris	—	ROM 25618	KX694665	—	—	—	—	—	—
Grayia caesar	TR 4660	—	—	—	—	—	—	—	Cameroon: Southwest Region: Kendem
Grayia caesar	CD 21_211	—	—	—	—	—	—	—	DRC: Tshopo Province: Yangambi Bangole, camp, stream (N01.0085, E24.9076)
Grayia ceasar	GR C01	—	—	—	—	—	—	—	Gabon: Ogooué-Ivindo Province: Yangambi
Grayia ornata	CRSN 85	—	—	—	—	—	—	—	DRC: Ituri Province: Aweza-Libulu (N01.96356, E30.03868, 1176 m)
Grayia ornata	CRSN 86	—	—	—	—	—	—	—	DRC: Ituri Province: Aweza-Libulu (N01.96356, E30.03868, 1175 m)
Grayia ornata	CRSN 87	—	—	—	—	—	—	—	DRC: Ituri Province: Aweza-Libulu (N01.96356, E30.03868, 1175 m)
Grayia ornata	ELI 1877	—	—	—	—	—	—	—	DRC: Mai-Ndombe Province: Nkala Village, Mbali River (S02.603910, E16.437048, 450 m)
Grayia ornata	ELI 1740	—	—	—	—	—	—	—	DRC: Mai-Ndombe Province: Ndomo (S03.30093, E16.23034, 278 m)
Grayia ornata	EBG 2636	—	—	—	—	—	—	—	DRC: Ituri Province: Bazinga (N01.24554, E28.34337, 737 m)
Grayia ornata	ELI 2674	—	—	—	—	—	—	—	DRC: Équateur Province: Bolondo-Bulumbe Village, Momboyo River (S00.40747, E19.14425, 312 m)
Grayia ornata	CD 15_081	—	—	—	—	—	—	—	DRC: Mongala Province: Lopori River, Matama
Grayia ornata	CD 15_366	—	—	—	—	—	—	—	DRC: Mongala Province: Mongala N, Kuku
Grayia ornata	CG 17_027	—	—	—	—	—	—	—	Republic of the Congo: Cuvette-Ouest Department: Etoumbi, Tchérré 10km SW (S00.022694, E14.815028)
Grayia ornata	ELI 2227	—	—	—	—	—	—	—	DRC: Équateur Province: Balolombo Village, Busira River (S00.25939, E19.63575, 305 m)

Grayia ornata	ELI 1960	—	—	—	—	—	—	—	DRC: Mai-Ndombe Province: Village of Kutu, Fimi River (S02.7300, E18.14425, 312 m)
Grayia ornata	RE_ANS01	MTD 48961	—	—	—	—	—	—	Angola: Uíge Province: Serra do Pingano, creek near basin of waterfall (S07.682222, E14.934444)
Grayia ornata	TR 3685	—	—	—	—	—	—	—	Cameroon: South Region: Ambam
Grayia ornata	TR 4661	—	—	—	—	—	—	—	Cameroon: Centre Region: Mbalmayo
Grayia ornata	TR 4627	—	—	—	—	—	—	—	Republic of the Congo: Kouilou Province: Punga
Grayia ornata	MBUR 02929	—	—	—	—	—	—	—	Republic of the Congo: Kouilou Province: Taung: near Tar Road
Grayia ornata	MBUR 03399	IRSN	—	—	—	—	—	—	Republic of the Congo: Kouilou Province
Grayia ornata	ELI 2063	—	—	—	—	—	—	—	DRC: Mai-Ndombe Province: Isongo, Lake Mai-Ndombe: Forest (S01.5704, E18.3962)
Grayia ornata	—	MNHN 1977.6517	AY611866	—	AY612048	—	—	—	Gabon: Ogooué-Ivindo Province: Ogooué, cours d'eau Ivindo, 2 km en aval des rapides de Loa Loa
Grayia ornata	MBUR 3013	PEM R20078		—	—	—	—	—	Republic of the Congo: Kouilou District: Vemba River (S04.1856944, E11.6548333)
Grayia ornata	ELI 2663	—	—	—	—	—	—	—	DRC: Équateur Province: Isankele Village, 2 km E of Bolondo-Bulumbe, River
Grayia ornata	CD 15_031	—	—	—	—	—	—	—	DRC: Mongala Province: Umangi (N02.12, E21.39, 340 m)
Grayia ornata	vgCD 1258	—	—	—	—	—	—	—	DRC: Mai-Ndombe Province: Bansonbo
Grayia ornata	CRT 3792	RBINS 18986	—	—	—	—	—	—	DRC: Mongala Province: Kona
Grayia ornata	—	MCZ R188643	—	—	—	—	—	—	Gabon: Ogooué-Ivindo Province: Ivindo, Loa loa commune
Grayia **sp. nov.**	EBG 2739	—	—	—	—	—	—	—	DRC: South Kivu Province: Mungombe (S03.04419, E28.25566, 1072 m)
Grayia **sp. nov.**	ELI 258	—	—	—	—	—	—	—	DRC: Haut-Lomami Province: Kyolo (S08.01388, E027.11285, 560 m)
Grayia **sp. nov.**	—	RBINS 18816	—	—	—	—	—	—	DRC: Tshopo Province: Uma (N00.908333, E26.505556)
Grayia **sp. nov.**	CD 18_148	—	—	—	—	—	—	—	DRC: Tshuapa Province: Kokolopori, Yalokole, village (N00.25, E022.87, 500 m)
Grayia **sp. nov.**	CD 18_323	—	—	—	—	—	—	—	DRC: Tshuapa Province: Kokolopori, Yangonde, Luo (Mariga) River (N00.18, E22.78, 395 m)
Grayia **sp. nov.**	RNBK 122	—	—	—	—	—	—	—	DRC: Tshuapa Province: Kokolopori, Biyekiyeki, swamp
Grayia **sp. nov.**	CFS 34g	—	—	—	—	—	—	—	DRC: South Kivu Province: Sake, River

Grayia **sp. nov.**	UAC_21	RBINS 18901	—	—	—	—	—	—	DRC: Tshopo Province: Yoko (N00.292227314, E25.28375198)
Grayia **sp. nov.**	ANG 098	PEM R19473	—	—	—	—	—	—	Angola: Lunda Norte Province: Lulele River ferry crossing (S07.7473611, E19.9509444)
Grayia smithii	EBG 2634	—	—	—	—	—	—	—	DRC: Ituri Province: Epulu (N01.40140, E28.57000, 747 m)
Grayia smithii	EBG 2663	—	—	—	—	—	—	—	DRC: Ituri Province: Epulu (N01.39848, E28.57110, 737 m)
Grayia smithii	EBG 965	KU 291888	—	—	—	—	—	—	Guinea: Labé Region: Markola, ca. 4 km W of Labe (N11.3428, W12.3369, 980 m)
Grayia smithii	ELI 2226	—	—	—	—	—	—	—	DRC: Équateur Province: Balolombo Village, Busira River (S00.25939, E19.63575, 305 m)
Grayia smithii		MCZ R–182627	—	—	—	—	—	—	Republic of the Congo: Sangha Region: 15km S.W. of Bomassa
Grayia smithii	MBUR 08214	—	—	—	—	—	—	—	Republic of the Congo: Kouilou Region: 2.8 km E of Hinda (S04.6175833, E12.0625)
Grayia smithii	NR 239	PEM R19279	—	—	—	—	—	—	Liberia: Nimba County: Fish traps in streams from Mt Gangra, near Yekepa (N07.5784167, W08.6106389)
Grayia smithii	NR 28	PEM R19222	—	—	—	—	—	—	Liberia: Nimba County: Bata Village, on road to East Nimba Nature Reserve (N07.4405, W08.5929167)
Grayia smithii	—	RBINS 20164	—	—	—	—	—	—	Guinea: Kankan Region: Dianfaradougo (N08.985278, W08.925000)
Grayia smithii	ET 17_01	—	—	—	—	—	—	—	Ethiopia: SNNP Region: Koji (Magenteya) (N06.81008, E35.25386, 1266 m)
Grayia smithii	CD 14_004	—	—	—	—	—	—	—	DRC: Tshopo Province: Tshopo Kisangani, 17km on road to airport (N00.5, E025.3, 430 m)
Grayia smithii	RMB 19318	—	—	—	—	—	—	—	Cameroon: Ndian Division: Mundemba town, Korup National Park, Chimpanzee camp
Grayia smithii	5024 G	—	—	—	—	—	—	—	Guinea: Southwest Region: Sangared
Grayia smithii	5025 G	—	—	—	—	—	—	—	Guinea: Southwest Region: Sangared
Grayia smithii		PEM R4434	AY611878	—	AY612060	—	—	—	Côte d'Ivoire: Montagnes District: Cavally Classified Forest Reserve, tributary of River Dibo
Grayia smithii	KEA 367	—	—	—	—	—	—	—	—
Grayia tholloni	ELI 203	—	—	—	—	—	—	—	DRC: Haut-Lomami Province: Kyolo (S08.02005, E027.11645, 583 m)
Grayia tholloni	CFS 1159w	—	—	—	—	—	—	—	DRC: Sankuru Province: Katako-Kombe (S03.24329, E024.24856, 506 m)
Grayia tholloni	—	RBINS 20168	—	—	—	—	—	—	Guinea: Nzérékoré Region: Saniamoridou (N08.985278, W08.925000)

Grayia tholloni	KG 410	—	—	—	—	—	—	—	Uganda: Central Region: Entebbe
Grayia tholloni	—	IRD 8480 S	—	—	—	—	—	—	Senegal: Fatick Region: Keur Seny Gueye, Djikoya River
Grayia tholloni	GJ 3099	—	—	—	—	—	—	—	Republic of the Congo: Cuvette Region: Lekety village

Table 3: Meristic data from both sexes of *Grayia ornata* (Angola, Cameroon, CAR, DRC, Republic of the Congo, and Zambia), *G.* cf. *ornata* (upper and middle Congo River and its tributaries in DRC and Angola), and the Ogooué Basin *G. ornata* (Gabon, Cameroon, and Equatorial Guinea). See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	***Grayia ornata*** **female (N = 98)**	***Grayia ornata*** **male (N = 127)**	***Grayia*** **cf.** ***ornata*** **female (N = 3)**	**Grayia cf.** ***ornata*** **male (N = 7)**	**Ogooué** ***Grayia ornata*** **female (N = 9)**	**Ogooué** ***Grayia ornata*** **male (N = 4)**
VENT	151.59 ± 4.40 (141–164)	148.47 ± 4.71 (139–164)	152.67 ± 1.53 (151–154)	145.71 ± 4.15 (137–150)	157.56 ± 3.58 (151–163)	151.50 ± 1.29 (150–153)
VENTD	149.16 ± 4.81 (135–162)	146.13 ± 4.87 (136–163)	151 ± 1.73 (149–152)	144.29 ± 4.31 (135–148)	156.44 ± 3.73 (150–163)	150.50 ± 1 (150–152)
SCDL	74.31 ± 5.54 (65–89)	79.38 ± 4.37 (67–90)	69	75.57 ± 2.51 (72–79)	77 ± 2.94 (73–80)	84 ± 1.41 (83–85)
POSTOC	2.00 ± 0.14 (1–3)	2.02 ± 0.13 (2–3)	2	2	2	2
PREOC	1.00 ± 0.00 (1–1)	1	1	1	1	1
SUPRA	8.06 ± 0.92 (0–10)	8.06 ± 0.36 (7–10)	9 ± 1 (8–10)	8.14 ± 0.38 (8–9)	8	8
TEYE	1.04 ± 0.25 (0–2)	1.04 ± 0.20 (1–2)	1	1	1.11 ± 0.35 (1–2)	1
INFRA	8.06 ± 0.32 (7–9)	8.06 ± 0.33 (7–9)	10.67 ± 0.58 (10–11)	9.86 ± 0.38 (9–10)	10.33 ± 0.71 (9–11)	10 ± 0.82 (9–11)
TCHIN	1.04 ± 0.20 (1–2)	1.05 ± 0.21 (1–2)	4.67 ± 0.58 (4–5)	4.86 ± 0.38 (4–5)	5	5
DSRN	10.61 ± 0.71 (8–12)	11.42 ± 9.00 (9–111)	17	16.86 ± 0.38 (16–17)	19.11	19
DSRM	4.91 ± 0.32 (4–6)	4.90 ± 0.35 (4–6)	17	17	18.78	17.50 ± 1 (17–19)
DSRV	10.51 ± 0.74 (7–13)	10.44 ± 0.63 (9–12)	16.33 ± 1.15 (15–17)	15.86 ± 0.90 (15–17)	17 ± 0.71 (17–19)	16.50 ± 1 (15–17)
Extralabials	4.89 ± 0.40 (4–7)	4.98 ± 0.97 (4–15)	1.33 ± 0.58 (1–2)	1.43 ± 0.53 (1–2)	0.89 ± 0.35 (0–1)	1
Extralabials touching	5.66 ± 0.46 (4.6–6.7)	5.61 ± 0.44 (4.7–6.8)	5.6	4.6	5.60	5.60
Body Bands	24.91 ± 4.65 (12–35)	25.08 ± 4.09 (14–33)	23 ± 1 (22–24)	22 ± 0.89 (21–23)	19.83 ± 3.36 (16–25)	20.75 ± 2.5 (18–24)

Table 4: Mensural data from both sexes of *Grayia ornata* (Angola, Cameroon, CAR, DRC, Republic of the Congo, and Zambia), *G.* cf. *ornata* (upper and middle Congo River and its tributaries in DRC and Angola), and the Ogooué Basin *G. ornata* (Gabon, Cameroon, and Equatorial Guinea). All measurements were collected on adults (SVL > 400 mm). See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	***Grayia ornata*** **female (N = 52)**	***Grayia ornata*** **male (N = 83)**	***Grayia* cf. *ornata*** **female (N = 2)**	**Grayia cf. *ornata*** **male (N = 7)**	**Ogooué *Grayia ornata*** **female (N = 4)**	**Ogooué *Grayia ornata* male (N = 3)**
SVL	753.19 ± 190.21 (411–1190)	694.04 ± 140.69 (420–1115)	653 ± 347.90 (407–899)	560 ± 114.93 (421–726)	576.56 ± 399.76 (213.–1114)	765.33 ± 62.45 (699–823)
TaL	242.44 ± 64.33 (127–353)	258.47 ± 49.25 (147–355)	128	213 ± 43.36 (156–262)	152 ± 132.01 (84–350)	278
TL	964.69 ± 244.03 (539–1330)	945.80 ± 197.45 (567.00–1466.00)	535	770.33 ± 172.59 (577.33–988)	558.75 ± 447.01 (319–1229)	977
HW	22.98 ± 5.32 (14.61–36.23)	20.76 ± 4.42 (12.70–30.93)	18.21 ± 6.89 (13.33–23.08)	18.33 ± 4.00 (13.55.33–23.58)	17.73 ± 10.91 (8.02–35.25)	25.86 ± 5.52 (21.06–31.89)
EW	4.40 ± 0.71 (3.00–6.40)	4.27 ± 0.54 (2.69–5.57)	3.97 ± 1.05 (3.22–4.71)	3.86 ± 0.56 (3.23.86–4.60)	4.06 ± 1.24 (2.95–5.85)	4.68 ± 0.47 (4.20–5.14)
HL	21.15 ± 3.63 (13.87–28.87)	19.77 ± 2.73 (14.08–25.51)	17.72 ± 4.89 (14.26–21.18)	17.58 ± 2.27 (14.31.58–20.11)	17.10 ± 7.45 (11.49–28.47)	22.13 ± 1.30 (20.67–23.17)
NOD	6.52 ± 1.45 (3.75–9.38)	5.88 ± 1.01 (4.05–9.03)	4.96 ± 1.78 (3.70–6.22)	4.93 ± 0.65 (4.08.93–5.65)	5.06 ± 2.61 (3.05–8.72)	7.26 ± 1.05 (6.36–8.41)
INOSDIST	5.57 ± 1.05 (3.45–7.77)	5.29 ± 1.03 (3.25–7.35)	5.01 ± 1.61 (3.87–6.14)	4.84 ± 0.58 (4.10.84–5.59)	4.70 ± 2.46 (2.28–7.87)	5.33 ± 0.17 (5.22–5.53)
ID	10.53 ± 1.67 (7.03–13.61)	9.86 ± 1.65 (6.50–13.76)	8.94 ± 3.33 (6.58–11.29)	8.63 ± 1.34 (6.86.63–10.18)	8.28 ± 4.46 (4.20–14.12)	10.90 ± 0.87 (10.03–11.76)
RH	3.37 ± 0.68 (2.14–4.59)	3.20 ± 0.67 (1.70–5.45)	3.53	3.14 ± 0.54 (2.43.14–3.77)	2.72 ± 1.37 (1.47–4.64)	3.53 ± 0.20 (3.33–3.73)
RW	6.51 ± 1.40 (2.21–8.64)	6.14 ± 0.91 (4.10–7.97)	6.93	5.49 ± 0.82 (4.51.49–6.67)	5.34 ± 2.86 (2.04–8.94)	6.95 ± 0.75 (6.31–7.78)
FL	8.54 ± 1.43 (5.89–11.59)	7.94 ± 1.27 (3.28–10.64)	7.08 ± 1.67 (5.90–8.26)	7.17 ± 0.76 (5.99.17–7.88)	6.92 ± 2.64 (4.84–11.03)	9.17 ± 0.38 (8.74–9.45)
FW	5.47 ± 1.00 (3.47–7.57)	5.11 ± 0.85 (3.20–7.10)	4.28 ± 1.11 (3.49–5.06)	4.36 ± 0.64 (3.54.36–5.12)	4.40 ± 1.90 (2.80–7.02)	5.78 ± 0.42 (5.31–6.13)
F–R Dist.	6.45 ± 1.19 (4.27–8.96)	6.02 ± 1.09 (3.87–8.67)	5.21 ± 1.90 (3.86–6.55)	5.08 ± 0.90 (3.95.08–6.44)	5.14 ± 2.81 (2.94–8.91)	6.80 ± 0.73 (5.96–7.32)
IC	3.40 ± 0.79 (2.02–5.21)	3.10 ± 0.70 (1.73–4.91)	2.43 ± 1.04 (1.69–3.16)	2.27 ± 0.64 (1.86.27–3.38)	3.03 ± 1.47 (1.58–5.12)	3.61 ± 0.52 (3.18–4.18)
PrC	3.10 ± 0.61 (1.88–4.94)	2.81 ± 0.52 (1.70–4.10)	2.73 ± 0.93 (2.07–3.39)	2.56 ± 0.52 (1.91.56–3.16)	2.26 ± 1.42 (0.62–4.05)	3.09 ± 0.51 (2.56–3.58)
PaC	6.45 ± 1.17 (4.06–9.94)	6.10 ± 0.78 (4.33–7.80)	5.47 ± 0.89 (4.84–6.10)	5.25 ± 1.26 (2.86.25–6.56)	5.34 ± 2.07 (3.40–8.52)	6.46 ± 0.35 (6.09–6.78)
LH	1.94 ± 0.37 (1.10–2.78)	1.72 ± 0.78 (0.00–6.78)	1.67 ± 0.68 (1.19–2.15)	1.56 ± 0.29 (1.03.56–1.92)	1.20 ± 0.60 (0.62–2.02)	2.11 ± 0.21 (1.95–2.35)
LL	3.86 ± 0.70 (2.45–5.14)	3.35 ± 0.80 (0.00–4.86)	2.84 ± 1.20 (1.99–3.69)	2.63 ± 0.49 (2.09.63–3.61)	2.95 ± 1.40 (1.62–4.58)	4.00 ± 0.23 (3.80–4.25)
LA–T	8.20 ± 1.80 (2.68–11.20)	7.56 ± 1.24 (5.10–10.28)	6.13 ± 1.90 (4.79–7.47)	7.14 ± 3.26 (4.88.14–14.37)	6.70 ± 3.60 (3.45–10.90)	8.52 ± 0.91 (7.49–9.20)
LA–TL	8.11 ± 1.27 (5.45–10.14)	7.03 ± 1.04 (4.35–9.81)	6.18 ± 1.80 (4.90–7.45)	6.23 ± 1.14 (4.66.23–7.78)	7.16 ± 2.58 (4.65–11.23)	8.00 ± 0.92 (7.33–9.05)
ASL	9.33 ± 1.64 (6.10–12.89)	8.52 ± 1.42 (5.71–11.74)	7.12 ± 2.79 (5.14–9.09)	7.14 ± 1.07 (5.31.14–8.38)	7.71 ± 3.89 (3.94–13.23)	10.59 ± 0.78 (9.81–11.36)
ASW	4.59 ± 0.92 (2.89–6.35)	4.17 ± 0.84 (2.05–6.60)	3.55 ± 1.42 (2.54–4.55)	3.47 ± 0.50 (2.75.47–4.02)	3.65 ± 1.98 (1.85–6.65)	4.98 ± 0.36 (4.57–5.26)

Table 5: Meristic data for both sexes of West African *Grayia smithii* (from Nigeria and other localities in West Africa), eastern DRC and Uganda striped *G. smithii*, *G. smithii* from Congo, Chad, the Atlantic and Nile River Basins, and *G. smithii* from Lake Edward and the Semliki River. See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	**Western *Grayia smithii* female (N = 35)**	**Western *Grayia smithii* Male (N = 46)**	***Eastern Striped Grayia smithii* Female (N = 6)**	**Eastern Striped *Grayia smithii* Male (N = 5)**	**Lake Edward/Semliki River *Grayia smithii* female (N = 3)**	**Lake Edward/Semliki River *Grayia smithii* male (N = 2)**	**Congo, Chad, Atlantic and Nile Grayia *smithii* female (N = 98)**	**Congo, Chad, Atlantic and Nile Grayia *smithii* male (N =77)**
VENT	161.76 ± 3.61 (154–168)	152.62 ± 2.90 (147–166)	164.50 ± 0.84 (163–165)	152.60 ± 2.19 (149–155)	165 ± 1.73 (164–167)	153.50 ± 0.71 (153–154)	159.40 ± 2.88 (152–164)	150.66 ± 3.14 (146–160)
VENTD	160.09 ± 3.52 (153–167)	151.07 ± 2.86 (146–164)	161.67 ± 0.52 (161–162)	150.20 ± 1.92 (147–152)	162.67 ± 2.08 (161–165)	151 ± 1.41 (150–152)	155.86 ± 3.26 (145–162)	147.81 ± 3 (142–157)
SCDL	91.50 ± 3.62 (85–99)	100.11 ± 3.89 (88–110)	92.50 ± 3.54 (90–95)	98	94 ± 0 (94–94)	98.50 ± 2.12 (97–100)	90.05 ± 9.51 (72–98)	97.36 ± 7.39 (87–107)
POSTOC	2	2	2	1.60 ± 0.55 (1–2)	2	2	1.98 ± 0.14 (1–2)	1.99 ± 0.12 (1–2)
PREOC	1	1	1	1	1	1	1	1.01 ± 0.12 (1–2)
SUPRA	7	7	7	7	7	7	7.03 ± 0.49 (3–8)	7.05 ± 0.28 (6–8)
TEYE	1.03 ± 126.17 (1–2)	1	1	1	1	1	1	1.01 ± 0.12 (1–2)
INFRA	10.21 ± 126.64 (9–11)	10.20 ± 0.55 (9–11)	10.17 ± 0.41 (10–11)	9.40 ± 0.89 (8–10)	10.67 ± 0.58 (10–11)	9.50 ± 0.71 (9–10)	10.15 ± 0.78 (6–11)	10.08 ± 0.74 (9–12)
TCHIN	4.94 ± 126.24 (4–5)	4.98 ± 0.15 (4–5)	4.83 ± 0.41 (4–5)	4.60 ± 0.55 (4–5)	4.67 ± 0.58 (4–5)	5	4.88 ± 0.35 (4–6)	5.50 ± 5.85 (4–55)
DSRN	17	17.04 ± 0.30 (17–19)	17	17	17	17	17.10 ± 0.42 (16–19)	17.05 ± 0.46 (15–19)
DSRM	17	16.98 ± 0.15 (16–17)	17	17	17	17	16.93 ± 0.39 (1–18)	16.76 ± 0.62 (15–17)
DSRV	15.31 ± 0.72 (15–17)	15.13 ± 0.40 (15–17)	15	15	15	15	15.02 ± 0.20 (150–1)	14.96 ± 0.26 (13–15)
Body Bands	32.39 ± 126.53 (0–38)	28.15 ± 9.80 (0–43)	41.67 ± 3.51 (38–45)	0	36	35.50 ± 0.71 (35–36)	33.45 ± 9.85 (–42)	30.25 ± 10.34 (0–41)

Table 6: Mensural data for both sexes of West African *Grayia smithii* (from Nigeria and other localities in West Africa), eastern DRC and Uganda striped *G. smithii* (Eastern DRC), *G. smithii* from Congo, Chad, Atlantic and Nile River Basins, and *G. smithii* from Lake Edward and the Semliki River. All measurements were collected on adults (SVL > 400 mm). See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	**Western *Grayia smithii* female (N = 22)**	**Western *Grayia smithii* Male (N = 30)**	**Eastern Stiped *Grayia smithii* Female (N= 6)**	**Eastern Striped *Grayia smithii* Male (N = 4)**	**Lake Edward/Semliki River *Grayia smithii* female (N = 3)**	**Lake Edward/Semliki River *Grayia smithii* male (N = 2)**	**Congo, Chad, Atlantic and Nile Grayia *smithii* female (N = 45)**	**Congo, Chad, Atlantic and Nile Grayia *smithii* male (N =37)**
SVL	949.13 ± 263.36 (467–1400)	715.80 ± 140.22 (455–1013)	1115 ± 218.79 (690–1310)	859 ± 160.25 (619–970)	1202.67 ± 46.49 (1150–1238)	824.50 ± 112.43 (745–904)	526.76 ± 322.51 (200–1289)	489.97 ± 278.35 (192–1157)
TaL	326.18 ± 81.84 (165–505)	356.96 ± 73.41 (205–470)	415.50 ± 183.14 (286–545)	296 ± (296–296)	493	399 ± 60.81 (356–442)	198.71 ± 122.06 (74–488)	241.61 ± 144.08 (91–506)
TL	1190.55 ± 326.30 (632–1835)	1067.52 ± 199.80 (660–1456)	1415.50 ± 621.55 (976–1855)	915 ± (915–915)	1731	1223.50 ± 173.24 (1101–1346)	683.94 ± 423.50 (239–1777)	798.68 ± 419.48 (283–1614)
HW	25.64 ± 7.39 (12.72–38.03)	20.64 ± 3.93 (11.01–26.51)	30.36 ± 9.16 (15.49–41.36)	22.52 ± 5.56 (15.53–28.30)	28.94 ± 2.38 (26.35–31.03)	23.43 ± 0.81 (22.85–24)	16.53 ± 8.94 (7.40–38.60)	16.20 ± 8.66 (7.10–33.48)
EW	5.37 ± 0.72 (3.85–7)	4.82 ± 0.49 (3.70–5.65)	5.44 ± 0.56 (4.48–5.89)	5.09 ± 0.04 (4.55–5.41)	5.74 ± 0.30 (5.53–6.08)	5.11 ± 0.43 (4.80–5.41)	3.91 ± 1.12 (2.50–6.75)	3.82 ± 1.06 (2.50–6.14)
HL	25.41 ± 4.90 (16.07–34.52)	22.34 ± 3.08 (16.01–27.69)	26.39 ± 3.97 (19.66–29.75)	24.13 ± 2.85 (20.03–26.56)	29.53 ± 1.77 (27.51–30.79)	24.58 ± 2.78 (22.61–26.54)	18.04 ± 6.43 (10.96–34.50)	16.73 ± 5.65 (11.20–27.73)
NOD	7.01 ± 1.40 (4.30–9.55)	5.86 ± 1.01 (3.80–7.88)	7.55 ± 1.34 (5.15–8.80)	6.44 ± 0.82 (5.25–7.05)	8.41 ± 0.40 (7.95–8.66)	6.41 ± 0.86 (5.80–7.02)	4.87 ± 1.92 (2.51–9.95)	4.43 ± 1.72 (2.45–7.80)
INOSDIST	5.65 ± 1.33 (3.47–7.89)	4.78 ± 1.09 (2.60–7.19)	5.84 ± 1.22 (4.19–7.07)	5.49 ± 0.36 (5.07–5.79)	8.02 ± 0.89 (7–8.62)	6.63 ± 1.07 (5.87–7.38)	4.43 ± 1.86 (2.25–8.96)	3.92 ± 1.59 (2.08–8.15)
ID	10.75 ± 2.13 (6.48–14.17)	9.37 ± 1.44 (6.30–11.94)	12.20 ± 2.00 (8.75–14.79)	11.26 ± 0.91 (9.96–11.98)	14.61 ± 1.99 (12.33–16)	11.26 ± 1.52 (10.18–12.33)	8.18 ± 3.23 (4.24–16.07)	7.49 ± 2.82 (4.30–14.14)
RH	3.44 ± 0.88 (1.97–4.91)	2.89 ± 0.55 (1.65–3.90)	3.73 ± 0.74 (2.63–4.40)	3.32 ± 0.23 (3.03–3.54)	4.61 ± 0.77 (3.74–5.19)	3.86 ± 0.77 (3.31–4.40)	2.67 ± 1.21 (1.23–5.71)	2.34 ± 0.93 (1.35–4.49)
RW	6.99 ± 1.60 (4.00–9.70)	5.96 ± 0.95 (3.86–7.41)	8.20 ± 1.39 (5.86–9.58)	6.90 ± 0.87 (5.78–7.74)	8.55 ± 0.98 (7.43–9.23)	7.21 ± 1.06 (6.46–7.96)	4.95 ± 2.05 (2.55–10.18)	4.46 ± 1.75 (2.60–8.64)
FL	10.42 ± 1.81 (7.21–13.59)	9.47 ± 1.22 (7.00–12.01)	11.18 ± 1.75 (8.02–12.92)	9.84 ± 0.84 (8.61–10.41)	11.60 ± 0.52 (11.25–12.20)	10.62 ± 0.69 (10.13–11.11)	7.64 ± 2.53 (4.77–14.23)	7.09 ± 2.19 (4.67–11.60)
FW	6.00 ± 1.04 (4.18–8.16)	5.20 ± 0.78 (3.28–6.71)	6.66 ± 1.18 (4.52–7.77)	5.77 ± 0.69 (4.83–6.33)	7.05 ± 0.46 (6.55–7.47)	5.39 ± 0.89 (4.76–6.02)	4.26 ± 1.61 (2.40–8.33)	3.84 ± 1.29 (2.11–6.37)
F–R Dist.	7.02 ± 1.58 (4.00–9.75)	5.94 ± 1.00 (4.04–7.77)	6.97 ± 1.28 (5.13–8.01)	6.51 ± 0.87 (5.20–6.94)	7.99 ± 0.33 (7.62–8.27)	6.56 ± 0.93 (5.90–7.22)	4.65 ± 1.86 (2.45–8.76)	4.14 ± 1.69 (2.20–8.01)
IC	4.13 ± 1.10 (2.15–6.66)	3.58 ± 0.83 (2.29–5.86)	3.86 ± 0.62 (3.01–4.41)	3.52 ± 0.51 (2.86–4.08)	4.07 ± 0.18 (3.87–4.21)	3.47 ± 0.72 (2.96–3.98)	2.37 ± 1.00 (1.20–4.57)	2.16 ± 0.91 (1.00–4.44)
PrC	2.81 ± 0.52 (1.79–3.85)	2.35 ± 0.42 (1.73–3.75)	3.06 ± 0.43 (2.20–3.40)	2.84 ± 0.38 (2.34–3.27)	3.43 ± 0.25 (3.15–3.63)	2.60 ± 0.58 (2.19–3.01)	2.12 ± 0.80 (0.94–4.70)	1.87 ± 0.83 (0.90–4.14)
PaC	7.90 ± 2.15 (2.14–12.72)	7.48 ± 1.13 (4.86–9.61)	9.12 ± 1.52 (6.52–11.18)	8.29 ± 1.10 (6.88–9.34)	10.55 ± 1.74 (9.22–12.52)	8.07 ± 0.81 (7.50–8.64)	6 ± 2.02 (3.76–12.05)	5.81 ± 1.85 (3.83–10.03)
LH	2.01 ± 0.60 (0.97–3.58)	1.63 ± 0.28 (1.07–2.17)	1.98 ± 0.41 (1.50–2.22)	–	1.85 ± 0 (1.85–1.85)	1.74 ± 0.23 (1.57–1.90)	1.29 ± 0.53 (0.60–3.06)	1.15 ± 0.44 (0.62–2.14)
LL	3.48 ± 1.36 (2.16–8.96)	2.69 ± 0.41 (2.05–3.51)	2.52 ± 0.67 (1.86–3.54)	1.97 ± 0.44 (1.57–2.55)	3.09 ± 0.55 (2.70–3.48)	2.59 ± 0.37 (2.33–2.85)	2.03 ± 0.87 (0.80–4.45)	1.80 ± 0.72 (0.60–3.60)
LA–T	12.51 ± 2.91 (7.46–18.43)	10.03 ± 1.70 (6.35–13.09)	14.07 ± 2.47 (9.72–16.02)	11.15 ± 1.86 (8.61–12.87)	13.94 ± 3.42 (10–16)	11.71 ± 0.71 (11.21–12.21)	8.30 ± 3.84 (4.53–19.90)	7.37 ± 3.38 (3.60–15.53)
LA–TL	8.21 ± 1.42 (5.30–11.17)	6.98 ± 0.85 (5.40–8.50)	9.12 ± 1.15 (7.52–10.37)	7.63 ± 0.83 (6.41–8.28)	9.39 ± 0.90 (8.55–10.34)	7.35 ± 0.62 (6.91–7.79)	6.11 ± 1.88 (3.72–10.80)	5.57 ± 1.74 (2.80–9.82)

ASL	10.43 ± 2.38 (6.03–14.53)	8.97 ± 1.61 (5.75–11.68)	10.95 ± 1.82 (7.52–12.32)	9.03 ± 1.51 (6.79–10.02)	11.43 ± 1.22 (10.32–12.73)	9.13 ± 0.77 (8.58–9.67)	6.59 ± 2.77 (3.52–13.45)	6.10 ± 2.40 (3.63–10.99)
ASW	4.83 ± 1.25 (2.65–7.35)	3.95 ± 0.75 (2.50–5.38)	5.23 ± 1.15 (3.50–6.77)	4.63 ± 1.03 (3.21–5.48)	5.56 ± 0.49 (5–5.92)	4.56 ± 0.67 (4.08–5.03)	3.12 ± 1.48 (1.50–6.58)	2.81 ± 1.32 (1.35–5.46)

Table 7: Meristic data for both sexes of West African *Grayia tholloni* (from Nigeria and other localities in West Africa), *G. tholloni* from the Nile River Basin, *G. tholloni* from the Congo, Chad and Atlantic River basins, and *G. tholloni* from Lake Tanganyika. See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	**Western *Grayia tholloni* female (N = 5)**	**Western *Grayia tholloni* Male (N = 4)**	**Nile River Basin *Grayia tholloni* Female (N = 7)**	**Nile River Basin *Grayia tholloni* Male (N = 9)**	***Congo, Chad and Atlantic Grayia tholloni* female (N = 57)**	***Congo, Chad and Atlantic Grayia tholloni* male (N = 74)**	**Lake Tanganyika *Grayia tholloni* female (N = 2)**	**Lake Tanganyika *Grayia tholloni* male (N = 3)**
VENT	145 ± 2.74 (141–148)	140.75 ± 3.59 (138–146)	147 ± 3.65 (143–151)	133.71 ± 1.25 (132–136)	144.33 ± 2.43 (140–151)	135.62 ± 2.28 (132–141)	142 ± 2.83 (140–144)	141.50 ± 0.71 (141–142)
VENTD	143.20 ± 2.39 (140–146)	139.25 ± 3.20 (137–144)	144 ± 158.55 (283–150)	133.44 ± 3.28 (131–141)	141.50 ± 3.19 (131–149)	134.14 ± 3.26 (127–150)	140.50 ± 2.12 (139–142)	138 ± 1 (137–139)
SCDL	113.25 ± 4.72 (109–120)	118.50 ± 6.36 (114–123)	119 ± 0 (119–119)	125.50 ± 3.79 (120–128)	119.15 ± 5.48 (104–130)	120.97 ± 7.47 (100–134)	122	–
POSTOC	1.80 ± 0.45 (1–2)	2	2 ± 158.55 (283–2)	2)	2	2.01 ± 0.12 (2–3)	2.50 ± 0.71 (2–3)	2
PREOC	1.00 ± 0.00 (1–1)	1	1	1	1	1.01 ± 0.12 (1–2)	1	1
SUPRA	7.80 ± 0.45 (7–8)	8.25 ± 0.50 (8–9)	7.83 ± 0.41 (7–8)	8	8.07 ± 0.26 (8–9)	7.99 ± 0.12 (7–8)	8	8
TEYE	1.60 ± 0.55 (1–2)	1.50 ± 0.58 (1–2)	1	1.29 ± 0.49 (1–2)	1.18 ± 0.51 (1–4)	1.18 ± 0.56 (1–4)	1	2 ± 1.73 (1–4)
INFRA	10	10	9.67 ± 0.52 (9–10)	9.43 ± 0.98 (8–10)	10 ± 0.46 (9–12)	9.78 ± 0.48 (8–11)	10	9.33 ± 1.15 (8–10)
TCHIN	5	5	5.17 ± 0.41 (5–6)	5 ± 0 (5–5)	4.91 ± 0.39 (4–6)	4.89 ± 0.32 (4–5)	5	4.67 ± 0.58 (4–5)
DSRN	15	15	15.40 ± 0.89 (15–17)	15.33 ± 0.71 (15–17)	15.18 ± 0.51 (15.–17)	15.05 ± 0.28 (15–17)	15	15.67 ± 1.15 (15–17)
DSRM	15	15	15	15 ± 0 (15–15)	15	15	15	15
DSRV	15	15	15	14.56 ± 0.88 (13–15)	15	14.97 ± 0.23 (13–15)	15	15
Body Bands	0	0	53	55	52.22 ± 5.43 (44–62)	50.55 ± 10.20 (27–59)	0	–

Table 8: Mensural data from both sexes of West African *Grayia tholloni* (from Nigeria and other localities in West Africa) *G. tholloni* from the Nile River Basin, *G. tholloni* from the Congo, Chad and Atlantic River basins, and *G. tholloni* from Lake Tanganyika All measurements were collected on adults (SVL > 400 mm). See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	**Western *Grayia tholloni* female (N = 5)**	**Western *Grayia tholloni* Male (N = 3)**	**Nile River Basin *Grayia tholloni* Female (N = 4)**	**Nile River Basin *Grayia tholloni* Male (N = 4)**	***Congo, Chad and Atlantic Grayia tholloni* female (N = 44)**	***Congo, Chad and Atlantic Grayia tholloni* male (N = 37)**	**Lake Tanganyika *Grayia tholloni* female (N = 1)**	**Lake Tanganyika *Grayia tholloni* male (N = 1)**
SVL	545.40 ± 70.43 (445–620)	456 ± 49.43 (425–513)	598.50 ± 83.51 (536–715)	517 ± 99.09 (417–654)	577.91 ± 97.56 (414–787)	488.11 ± 89.40 (400–900)	590	436
TaL	335.75 ± 61.47 (264–412)	310 ± 0 (310–310)	361.50 ± 181.73 (233–490)	128 ± 0 (128–128)	381.59 ± 86.69 (139–488)	323.91 ± 84 (74.67–402)	420	109
TL	867.50 ± 134.72 (709.–1032)	0	1020.50 ± 260.92 (836–1205)	782 ± 0 (782–782.)	941.33 ± 186.86 (475–1211)	806.05 ± 110.15 (492.67–958)	1010	545
HW	13.59 ± 1.13 (12.48–15.20)	12.23 ± 1.34 (11.23–13.76)	13.46 ± 1.34 (12.42–14.97)	12.99 ± 1.62 (11.63–14.78)	15.49 ± 3.14 (11.09–23)	12.94 ± 2.43 (9.95–21)	15.75	13.27
EW	4.78 ± 0.51 (4.27–5.35)	4.08 ± 0.03 (4.05–4.10)	4.63 ± 0.58 (4.21–5.29)	4.62 ± 0.29 (4.40–4.95)	4.58 ± 0.75 (3–5.73)	4.45 ± 0.28 (3.96–5)	4.65	4.58
HL	16.80 ± 0.83 (15.46–17.60)	14.75 ± 0.66 (14.30–15.51)	16.87 ± 1.42 (15.35–18.17)	16.56 ± 1.80 (14.51–17.85)	17.36 ± 1.71 (14.98–21.45)	15.81 ± 0.90 (14.38–17.45)	17.20	17.34
NOD	4.65 ± 0.41 (4.12–5.09)	4.12 ± 0.02 (4.10–4.14)	4.72 ± 0.64 (4.03–5.30)	4.29 ± 0.29 (3.95–4.47)	4.91 ± 0.49 (4.25–5.85)	4.47 ± 0.42 (3.60–5.25)	4.60	4.44
INOSDIST	3.73 ± 0.17 (3.52–3.94)	3.36 ± 0.45 (3–3.86)	3.48 ± 0.30 (3.15–3.72)	2.88 ± 0.39 (2.64–3.33)	3.35 ± 0.44 (2.85–4.20)	3.17 ± 0.43 (2.49–4.13)	3.32	3.79
ID	7.09 ± 0.64 (6.29–7.80)	6.06 ± 0.77 (5.46–6.93)	6.69 ± 0.40 (6.43–7.15)	6.34 ± 0.28 (6.12–6.66)	6.92 ± 0.74 (5.56–8.22)	6.15 ± 0.50 (5.20–7.16)	6.57	7.84
RH	2.60 ± 0.18 (2.47–2.86)	2.12 ± 0.23 (1.87–2.30)	2.33 ± 0.38 (1.90–2.60)	2.48 ± 0.20 (2.26–2.65)	2.51 ± 0.25 (1.96–2.92)	2.20 ± 0.22 (1.75–2.54)	2.55	2.47
RW	4.57 ± 0.31 (4.22–4.96)	3.96 ± 0.19 (3.76–4.13)	4.88 ± 0.30 (4.56–5.14)	4.36 ± 0.28 (4.04–4.56)	4.77 ± 0.62 (3.79–6.09)	4.19 ± 0.40 (3.31–4.91)	4.76	4.64
FL	7.44 ± 0.47 (7.05–8.21)	6.52 ± 0.30 (6.34–6.87)	7.52 ± 0.77 (6.76–8.29)	7.66 ± 0.58 (7.00–8.11)	7.92 ± 0.82 (6.66–9.32)	7.13 ± 0.48 (6.43–7.96)	8.06	7.27
FW	3.67 ± 0.41 (3.11–4.20)	3.67 ± 0.29 (3.39–3.97)	4.09 ± 0.18 (3.93–4.28)	4.12 ± 0.26 (3.94–4.41)	4.21 ± 0.42 (3.60–5.04)	3.80 ± 0.30 (3.27–4.44)	4.34	3.57
F–R Dist.	4.28 ± 0.37 (3.79–4.75)	4.11 ± 0.45 (3.80–4.63)	4.35 ± 0.19 (4.13–4.50)	4.32 ± 0.47 (3.81–4.72)	4.66 ± 0.62 (3.67–5.95)	4.09 ± 0.48 (3.37–5.05)	4.51	4.90
IC	1.96 ± 0.13 (1.80–2.12)	1.63 ± 0.20 (1.44–1.84)	1.92 ± 0.34 (1.58–2.25)	1.80 ± 0.24 (1.57–2.04)	1.91 ± 0.31 (1.40–2.67)	1.72 ± 0.21 (1.23–2.11)	2.12	2.25
PrC	2.36 ± 0.46 (1.65–2.74)	2.50 ± 0.21 (2.26–2.63)	2.53 ± 0.41 (2.19–2.98)	2.75 ± 0.31 (2.41–3.01)	2.79 ± 0.29 (2.24–3.19)	2.52 ± 0.32 (1.87–3)	2.65	2.32
PaC	5.32 ± 0.36 (4.82–5.60)	4.62 ± 0.23 (4.40–4.85)	5.06 ± 0.26 (4.76–5.26)	4.74 ± 0.55 (4.39–5.38)	5.14 ± 0.63 (3.88–6.69)	4.97 ± 0.46 (4.07–5.58)	4.46	5.25
LH	1.42 ± 0.21 (1.21–1.75)	1.24 ± 0.01 (1.23–1.25)	1.40 ± 0.25 (1.16–1.65)	1.27 ± 0.10 (1.20–1.38)	1.59 ± 0.31 (0.85–2.19)	1.40 ± 0.24 (0.91–1.80)	1.45	1.06
LL	2.38 ± 0.43 (1.81–3.00)	2.04 ± 0.13 (1.91–2.17)	2.17 ± 0.32 (1.92–2.53)	2.46 ± 0.44 (2.06–2.93)	2.55 ± 0.45 (1.79–3.38)	2.32 ± 0.27 (1.90–2.78)	2.10	2.14
LA–T	6.53 ± 0.52 (5.70–7.05)	5.58 ± 0.32 (5.25–5.89)	6.95 ± 1.01 (6.07–8.05)	6.42 ± 0.54 (6–7.03)	6.82 ± 1.12 (5.48–9.46)	5.88 ± 0.51 (4.76–6.55)	7.28	6.41
LA–TL	5.62 ± 0.57 (4.82–6.38)	4.78 ± 0.37 (4.45–5.18)	5.82 ± 0.20 (5.71–6.05)	5.19 ± 1.08 (3.94–5.83)	5.96 ± 0.92 (4.89–8.15)	5.00 ± 0.50 (4.20–6.40)	5.40	5.21
ASL	5.95 ± 0.72 (5.03–6.82)	5.47 ± 0.36 (5.05–5.71)	6.59 ± 0.97 (5.76–7.65)	5.91 ± 0.83 (4.99–6.61)	6.65 ± 1.07 (5.05–9.36)	5.94 ± 0.54 (4.75–7)	6.85	5.69
ASW	2.55 ± 0.22 (2.41–2.93)	2.29 ± 0.19 (2.13–2.50)	2.80 ± 0.64 (2.10–3.35)	2.62 ± 0.34 (2.34–3)	2.90 ± 0.43 (2.03–3.85)	2.32 ± 0.25 (1.64–2.70)	2.62	2.24

Table 9: Meristic and mensural data from both sexes of *Grayia caesar.* Mensural data were collected on adults (SVL > 400 mm), and meristic counts were collected on all specimens. See Materials and Methods for character abbreviations. Data are shown as the mean ± standard deviation with range in parentheses.

Character	***Grayia caesar* female (N = 18)**	***Grayia caesar* males (N = 17)**
SVL	560.06 ± 269.99 (193–965)	524.35 ± 158.97 (197–705)
TaL	204.20 ± 127.37 (144–432)	441.50 ± 196.57 (181–692)
TL	346.25 ± 6.99 (338–355)	849.63 ± 356.33 (378–1322)
HW	13.50 ± 4.50 (7.51–21.02)	13.66 ± 3.13 (8–19)
EW	5.83 ± 1.19 (4.09–7.49)	5.80 ± 0.89 (4.21–6.87)
HL	18.15 ± 4.81 (11.94–25.16)	20.26 ± 6.66 (12.20–35)
NOD	5.15 ± 1.72 (2.90–8.28)	4.82 ± 1.72 (0.42–7.00)
INOSDIST	3.73 ± 1.05 (2.17–5.60)	4.22 ± 1.00 (2.64–5.48)
ID	7.91 ± 2.27 (4.73–11.30)	7.98 ± 1.41 (5.08–9.51)
RH	2.20 ± 0.76 (1.20–3.50)	2.17 ± 0.45 (1.30–2.65)
RW	5.03 ± 1.49 (3.13–7.20)	4.84 ± 0.71 (3.28–5.75)
FL	7.78 ± 2.14 (4.89–10.85)	7.53 ± 1.32 (5.18–9.14)
FW	5.06 ± 1.48 (3.13–7.20)	4.84 ± 0.71 (3.28–5.75)
F–R Dist.	5.07 ± 1.64 (2.93–7.82)	5.01 ± 1.26 (3.02–7.05)
IC	2.34 ± 0.79 (1.00–3.46)	2.18 ± 0.51 (1.27–2.85)
PrC	3.03 ± 1.47 (1.28–7.71)	2.86 ± 0.70 (1.54–3.70)
PaC	5.50 ± 1.06 (3.95–7.13)	5.97 ± 0.93 (4.34–7.32)
LH	1.78 ± 0.57 (1.03–2.73)	1.72 ± 0.45 (0.92–2.28)
LL	2.43 ± 0.80 (1.15–3.70)	2.48 ± 0.50 (1.55–3.10)
LA–T	5.99 ± 2.09 (3.22–9.66)	6.24 ± 1.34 (3.65–7.60)
LA–TL	6.91 ± 1.63 (4.65–9.23)	6.53 ± 1.09 (4.64–7.75)
ASL	7.10 ± 2.34 (4.12–10.91)	6.97 ± 1.44 (4.44–8.72)
ASW	2.65 ± 1.00 (1.35–4.23)	2.67 ± 0.68 (1.38–3.50)
VENT	142.59 ± 2.79 (139–148)	126.62 ± 1.33 (125–129)
VENTD	140.28 ± 2.49 (136–146)	124.76 ± 1.60 (122–127)
SCDL	144 ± 2.92 (140–147)	158.63 ± 4.10 (151–162)
POSTOC	2	2
PREOC	1	1
SUPRA	8	8
INFRA	9.67 ± 0.59 (8–10)	9.71 ± 0.47 (9–10)
TCHIN	4.94 ± 0.24 (4–5)	5 ± 0 (5–5)
DSRN	15.11 ± 0.47 (15–17)	15
DSRM	15	15
DSRV	15	15

Table 10: Principal component analysis, with log-transformed mensural data, comparing *G. ornata*, Ogooué *G. ornata*, and *G. cf ornata.* Loadings, eigenvalues, percent variance and cumulative variance are shown for the first three principal components. See Materials and Methods for variable abbreviations.

Variable	PC1	PC2	PC3
SVL (mm)	0.241124	0.162361	0.117873
HW	0.237385	0.190613	0.107205
EW	0.233186	-0.20265	-0.11455
HL	0.244734	0.014691	-0.03746
NOD	0.237532	-0.29395	-0.02497
INTERNOSDIS	0.231265	0.490586	-0.02777
ID	0.242193	0.246933	-0.01579
RH	0.234074	0.445604	0.093745
RW	0.241168	0.119942	0.068971
FL	0.230801	-0.18126	-0.14796
FW	0.236745	-0.19291	-0.1562
F–R Dist.	0.241043	0.041052	-0.14999
IC	0.229473	-0.00763	-0.6021
PrC	0.224301	-0.31492	0.593803
PaC	0.227149	-0.01177	0.371066
LA–T	0.229312	-0.28185	-0.13388
ASL	0.239831	-0.2061	0.002891
ASW	0.240074	-0.04447	0.073255
Eigenvalue	16.497	0.287	0.227
Proportion	0.917	0.016	0.013
Cumulative	0.917	0.932	0.945

Table 11: Principal component analysis, with log-transformed mensural data, comparing *G. smithii* from the Congo, Chad, Atlantic and Nile River Basins, striped *G. smithii* from eastern DCRC and Uganda, *G. smithii* from the Semliki River and Lake Edward, and Western *G. smithii* (from Nigeria and other localities in West Africa). Loadings, eigenvalues, percent variance and cumulative variance are shown for the first three principal components. See Materials and Methods for variable abbreviations.

Variable	PC1	PC2	PC3
SVL (mm)	0.234	0.032	0.010
HW	0.231	-0.105	-0.124
EW	0.229	0.155	0.068
HL	0.229	0.189	-0.035
NOD	0.233	0.146	-0.052
INTERNOSDIS	0.226	-0.458	-0.318
ID	0.231	-0.279	-0.226
RH	0.227	-0.432	-0.196
RW	0.234	-0.077	-0.064
FL	0.233	0.042	-0.069
FW	0.231	0.084	0.029
F–R Dist.	0.233	0.163	-0.020
IC	0.224	0.327	0.012
PrC	0.223	0.268	0.155
PaC	0.213	-0.424	0.854
LA–T	0.229	0.048	-0.075
LA–TL	0.231	0.120	0.104
ASL	0.233	0.117	0.056
ASW	0.234	0.050	-0.047
Eigenvalue	17.971	0.215	0.195
Proportion	0.946	0.011	0.010
Cumulative	0.946	0.957	0.967

Table 12: Principal component analysis, with log-transformed mensural data, comparing *G. tholloni* from the Congo, Chad and Atlantic River basins, *G. tholloni* from Lake Tanganyika, *G. tholloni* from the Nile River basin, and *G. tholloni* from West Africa (from Nigeria and other localities in West Africa). Loadings, eigenvalues, percent variance and cumulative variance are shown for the first three principal components. See Materials and Methods for variable abbreviations.

Variable	PC1	PC2	PC3
SVL (mm)	0.353	0.174	0.102
HW	0.282	0.215	0.111
EW	0.153	0.009	0.029
HL	0.187	-0.001	-0.046
NOD	0.215	-0.030	-0.005
INTERNOSDIS	0.203	0.211	-0.667
ID	0.200	0.260	-0.048
RH	0.230	0.196	0.100
RW	0.221	0.060	-0.021
FL	0.165	-0.020	0.079
FW	0.175	0.019	0.147
F–R Dist.	0.222	0.103	0.041
IC	0.210	-0.004	-0.054
PrC	0.216	-0.125	0.145
PaC	0.157	-0.027	-0.256
LH	0.222	-0.762	-0.380
LL	0.197	-0.361	0.483
LA–T	0.238	-0.023	0.115
LA–TL	0.177	0.128	-0.074
ASL	0.219	-0.069	0.018
ASW	0.248	-0.091	0.032
Eigenvalue	1.485	0.030	0.022
Proportion	0.910	0.018	0.014
Cumulative	0.910	0.929	0.942

Supplemental Table 1: *Grayia* specimens used in the morphological analysis. Collection acronyms follow Sabaj (2020). VW acronym indicates a specimen from Van Wallach's personal collection. Specimens without detailed locality information were marked with a * next to their locality and were placed in the center of the country or region in figs. 4–9. DRC = Democratic Republic of the Congo, CAR = Central African Republic.

Species	Field Number	Catalog Number	Locality	Source
Grayia ceasar		RMCA 20261	DRC: North Kivu Province: between Irangi and Hombo, 900m. terr. from Kelehe or from Walikale	(Laurent 1960)
Grayia caesar		AMNH R50520	Cameroon: Adamawa Region: Metet	
Grayia caesar		AMNH R12182	DRC: Bas-Uele Cameroon: Adamawa: Niapu	
Grayia ceasar	No. 1042		Republic of the Congo: Kouilou Region: Dimonika	(Villiers 1966)
Grayia ceasar	IRS 2372		DRC: North Kivu Province	VW
Grayia ceasar	IRS 2437		DRC: North Kivu Province: Irangi	VW
Grayia ceasar	IRS 2625		DRC: North Kivu Province	VW
Grayia ceasar	IRS 2626		DRC: North Kivu Province	VW
Grayia ceasar	No. 50520		Cameroon: Adamawa Region: Metet	(Boettger 1889)
Grayia ceasar		BMNH 1908.5.25.18	Gabon: Moyen-Ogooué Province: Abanga River	
Grayia ceasar		BMNH 1918.11.12.26	CAR: Ouham-Pendè Prefecture: (N07, E016)	
Grayia ceasar		BMNH 1919.8.16.88	DRC: Ituri Province: Avakubi	
Grayia ceasar		MNHN 1885.765	Equatorial Guinea: Litoral Province: "San Benito, Gabon"	
Grayia ceasar		MNHN 1885.766	Equatorial Guinea: Litoral Province: San Benito, Gabon"	
Grayia ceasar		MNHN 1964.472	CAR: Lobaye Prefecture: Boukoko	
Grayia ceasar		MNHN 1966.727	Republic of the Congo: Kouilou Region: Dimonika	
Grayia ceasar		MNHN 8800	CAR: Lobaye Prefecture: Oubanghi	
Grayia ceasar		RBINS 10881	DRC: Kongo Central Province: Mayumbe, Ganda-Sundi	
Grayia ceasar		RBINS 16256	Gabon: Woleu-Ntem Province: Nzogbour, Dpt du Haut-Komo (N00.926667, E10.604722, 580 m)	
Grayia ceasar		RBINS 16257	Gabon: Woleu-Ntem Province: Nkassi, Dpt du Haut-Komo (N00.866944, E02.175, 535 m)	
Grayia ceasar		RMCA 305	DRC: Mongala Province: Ubangi, Umanghi	
Grayia ceasar		RMCA 1663	DRC: Kongo Central Province: Malela	
Grayia ceasar		BMNH 94.8.4.13	Republic of the Congo: Kouilou Region: Mouth of the Loango	
Grayia ceasar		BMNH 1911.5.30.11	Cameroon: South District: Bitye	
Grayia ceasar		BMNH 1912.4.1.10	Angola: Cabinda Province: Nkutu," Portuguese Congo" (Loango River)	
Grayia ceasar		BMNH 1912.6.27.24	Cameroon: South District: Bitye	
Grayia ceasar		BMNH 1946.1.6.38	Equatorial Guinea: Fernando Po*	
Grayia ceasar		BMNH 1958.1.4.95	Cameroon: Northwest District: Bafut	
Grayia ceasar		MNHN 1980.1092	Gabon*	

Grayia ceasar		MNHN 1987.1421	Republic of the Congo*
Grayia ceasar		MNHN 1987.1423	Republic of the Congo*
Grayia ceasar		MNHN 1996.6640	CAR: Sangha-Mabaèrè Prefecture: Belemboke
Grayia ceasar		MNHN 1996.6641	CAR: Sangha-Mabaèrè Prefecture: Belemboke
Grayia ceasar		RMCA 1928	DRC: Kongo Central Province: Temvo
Grayia ceasar		RMCA 18199	DRC: North Kivu Province: Manguretshipa, Territoire de Lubero (1000 m)
Grayia ceasar		RMCA 19027	DRC: North Kivu Province: Hombo, Région de Walikale
Grayia ceasar		RMCA 20261	DRC: North Kivu Province: Territoire Kalehe-Walikale, entre Irangi et Hombo, (900 m)
Grayia ceasar		RMCA 27922	DRC: Kongo Central Province: Ganda Sundi, Mayumbe
Grayia ceasar		MNHN 1994.8076	CAR: Mabaèrè-Kadèi Prefecture: Berberati
Grayia **sp. nov.**	ANG 098	PEM R19473	Angola: Lunda-Norte Province: Ferry Crossing, Lulele River
Grayia **sp. nov.**		RBINS 18816	DRC: Tshopo Province: Uma (N00.908333, E26.505556)
Grayia **sp. nov.**		RBINS 18901	DRC: Tshopo Province: Yoko (N00.293611, E25.288917)
Grayia **sp. nov.**	CFS34g		DRC: South Kivu Province: Sake, Primary Forest
Grayia **sp. nov.**	EBG 2739		DRC South Kivu Province: Mungombe
Grayia **sp. nov.**	ELI 258		DRC: Haut-Lomami Province: Kyolo
Grayia **sp. nov.**		RBINS 18988	DRC: Tshopo Province: Lieki (N00.691944, E24.235000)
Grayia **sp. nov.**		RBINS 19476	DRC: Tshopo Province: Uma (N00.908333, E26.505556)
Grayia **sp. nov.**		RBINS 18985	DRC: Tshopo Province: Bomane (N01.27, E23.731944)
Grayia **sp. nov.**		RBINS 18902	DRC: Tshopo Province: Yoko (N00.293806, E25.288917)
Grayia ornata		BMNH 89.7.6.4	Gabon: Ogooue-Maritime Province: Sette Cama, (Cette Cama)
Grayia ornata		BMNH 1908.5.25.16	Gabon: Ogooué-Maritime Province: Eliva-Evolo, Ogewa
Grayia ornata		BMNH 1912.4.1.9	DRC: Kwilu Province: Mayili
Grayia ornata		MNHN 1884-19	Gabon: Nyanga Province: Mayumba (sur la côte S.E.)
Grayia ornata		MNHN 1967-379	Gabon: Woleu-N'Tem Province: Oyem
Grayia ornata		MNHN 1967-380	Gabon: Ogooué-Ivindo Province: Makokou, grand marigot, route fang
Grayia ornata		MNHN 1967-381	Gabon: Ogooué-Ivindo Province: Makokou
Grayia ornata		MNHN 1971-381	Republic of the Congo*
Grayia ornata		MNHN 1986-1549	Rupublic of the Congo: Rivière Lubé, sous-affluent du fleuve Zaïre, situé près de l'embouchure du Congo au sud du Gabon*
Grayia ornata		MNHN 1987-1428	Republic of the Congo: Plateaux Department: Leketi

Grayia ornata	MNHN 1987-1431	Republic of the Congo: Plateaux Department: Leketi
Grayia ornata	MNHN 1987-1432	Republic of the Congo*
Grayia ornata	MNHN 1987-1433	Republic of the Congo*
Grayia ornata	MNHN 1994-3379	CAR: Lobaye Prefecture: Bagandou
Grayia ornata	MNHN 1994-3384	CAR: Mambéré-Kadéï Prefecture: Berberati
Grayia ornata	MNHN 1994-3385	CAR: Lobaye Prefecture: SCAD, pont
Grayia ornata	MNHN 1995-9386	Equatorial Guinea: Centro Sur Province: Parc National de Monte Alen
Grayia ornata	RBINS 483 B	DRC: Kongo Central Province: Lufu
Grayia ornata	RBINS 3758	DRC: Tshopo Province: Yangambi
Grayia ornata	RBINS 4871	DRC: Tshopo Province: Yangambi (fleuve)
Grayia ornata	RBINS 8985	DRC: Haut-Katanga Province: Kaswabilenga, rég. cours inférieur de la Lupiala, affl. rive droite Lufira (700 m)
Grayia ornata	RBINS 8986	DRC: Haut-Katanga Province: Kaswabilenga, rég. cours inférieur de la Lupiala, affl. rive droite Lufira (700 m)
Grayia ornata	RBINS 16277	Gabon: Woleu-Ntem Province: Dpt du Haut-Komo, Nzogbour (N00.926667, E10.604722, 580 m)
Grayia ornata	RBINS 16290	Gabon: Ngounie Province: Dept du Louetsi-Bibaka, Mbomo (S02.283333, E12.216667, 636 m)
Grayia ornata	RBINS 16325	Gabon: Nyanga Province: Moukalaba River, along the road Tchibanga-Digoudou, near the ferry (S02.783333, E10.733333, 36 m)
Grayia ornata	RBINS 16352	Gabon: Nyanga Province: Moukalaba River, along the road Tchibanga-Ndende near Ndenguilila (S02.766667, E11.150000, 280 m)
Grayia ornata	RBINS 18928	DRC: Tshopo Province: Yoko (N00.293806, E25.288917)
Grayia ornata	RBINS 18986	DRC: Mongala Province: Kona (N02.033056, E22.786944)
Grayia ornata	RBINS 18987	DRC: Tshopo Province: Lieki (N00.691944, E24.235000)
Grayia ornata	RBINS 19152	DRC: Tshopo Province: Bagwase
Grayia ornata	RBINS 19682	DRC: Tshopo Province: Kisangani (N00.518611, E25.260278)
Grayia ornata	RBINS 19683	DRC: Tshopo Province: Amadjabe (N00.06667, E25.28333)
Grayia ornata	RBINS 19801	DRC: Tshopo Province: Amadjabe (N00.06667, E25.28333)
Grayia ornata	RMCA 1358	DRC: Kongo Central Province: Congo da Lemba
Grayia ornata	RMCA 1880 B	DRC: Bas Congo*
Grayia ornata	RMCA 2078	DRC: Équateur Province: Eala
Grayia ornata	RMCA 6800	DRC: Mai-Ndombe Province: Kunungu
Grayia ornata	RMCA 6849	DRC: Mai-Ndombe Province: Kunungu
Grayia ornata	RMCA 7503	DRC: Mongala Province: Bumba
Grayia ornata	RMCA 9473	DRC: Équateur Province: Eala
Grayia ornata	RMCA 9608	DRC: Tshopo Province: Stanleyville

Grayia ornata	RMCA 11479	DRC: Mai-Ndombe Province: Kunungu
Grayia ornata	RMCA 12060	DRC: Mai-Ndombe Province: Kunungu
Grayia ornata	RMCA 14862	DRC: Mai-Ndombe Province: Keseki, près de Kwamouth
Grayia ornata	RMCA 14868	DRC: Mai-Ndombe Province: Keseki, près de Kwamouth
Grayia ornata	RMCA 14901	DRC: Mai-Ndombe Province: Keseki, près de Kwamouth
Grayia ornata	RMCA 15760	DRC: Mai-Ndombe Province: Bolobo
Grayia ornata	RMCA 16101	DRC: Nord-Ubangi Province: Bosobolo, Ubangi
Grayia ornata	RMCA 20215	DRC: Mai-Ndombe Province: Bolobo
Grayia ornata	RMCA 21067	DRC: Mai-Ndombe Province: Bolobo
Grayia ornata	RMCA 21222	DRC: Mai-Ndombe Province: Kasai, Makaw, River
Grayia ornata	RMCA 28401	Angola: Lunda Norte Province: Environs de Dundo, Riv. Camundembele, affl. Luachimo
Grayia ornata	RMCA 73-18-R-49	Cameroon: South Region: Akom, 6 km N. van Oveng (N02.466667, E12.250000)
Grayia ornata	RMCA 83-24-R-47	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 83-24-R-48	DRC: Équateur Province: Bolondo
Grayia ornata	RMCA 83-24-R-50	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-86	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-87	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-88	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-89	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-90	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 88-33-R-78	DRC: Tshuapa Province: Wafanya (S01.350000, E20.333333)
Grayia ornata	RMCA 88-33-R-83	DRC: Tshuapa Province: Wafanya (S01.350000, E20.333333)
Grayia ornata	RMCA 88-33-R-84	DRC: Tshuapa Province: Wafanya (S01.350000, E20.333333)
Grayia ornata	RMCA 90-60-R-2	Republic of the Congo: Kouilou Region: Rivière Loudji à Mbena, filets maillants de nuit, ca. (S04.050000, E11.816667)
Grayia ornata	RMCA 91-70-R-5	Republic of the Congo: Kouilou Region: Rivière Loukoula, affl. Loukenene, sous-affl. Loeme, à 1 km en aval de Pounga
Grayia ornata	RMCA 91-70-R-6	Republic of the Congo: Kouilou Region: Rivière Loukoula, affl. Loukenene, sous-affl. Loeme, à 1 km en aval de Pounga
Grayia ornata	BMNH 1912.4.1.8	DRC: Kwilu Province: Mayili
Grayia ornata	BMNH 1966.374	Equatorial Guinea: Centro Sur Province: Evinayong region, Central Rio Muni (700 m)
Grayia ornata	MNHN 1886.218	Republic of the Congo: Brazzaville
Grayia ornata	MNHN 1896-527	Gabon: Moyen-Ogooué Province: Lambaréné, Vallée de l'Ogoué
Grayia ornata	MNHN 1967-375	Gabon: Ogooué-Ivindo Province: Makokou, Liboumba

Grayia ornata	MNHN 1967-376	Gabon: Ogooué-Ivindo Province: Loa Loa, bord de l'Ivindo
Grayia ornata	MNHN 1967-377	Gabon: Ogooué-Ivindo Province: Makokou, bord de l'Ivindo
Grayia ornata	MNHN 1967-378	Gabon: Ogooué-Ivindo Province: Makokou
Grayia ornata	MNHN 1967-382	Gabon: Ogooué-Ivindo Province: Makokou, bord de l'Ivindo
Grayia ornata	MNHN 1973-9	Cameroon*
Grayia ornata	MNHN 1987-1425	Republic of the Congo: Sangha Department: Ouesso
Grayia ornata	MNHN 1987-1426	Republic of the Congo: Kouilou Department: Dimonika
Grayia ornata	MNHN 1987-1427	Republic of the Congo: Kouilou Department: Dimonika
Grayia ornata	MNHN 1987-1429	Republic of the Congo: Cuvette Department: Leketi
Grayia ornata	MNHN 1987-1434	Republic of the Congo: Brazzaville
Grayia ornata	MNHN 1994.3382	CAR: Sangha-Mbaèrè Prefecture: Belemboke
Grayia ornata	MNHN 1994.8078	CAR: Ombella-M'poko Prefecture: Bangui
Grayia ornata	MNHN 1994.8080	CAR: Lobaye Prefecture: Route de M'Baiki
Grayia ornata	RBINS 2715	DRC: Kongo Central Province: Kisantu
Grayia ornata	RBINS 3744a	DRC: Tshopo Province: Lieki-Isangi
Grayia ornata	RBINS 3744b	DRC: Tshopo Province: Lieki-Isangi
Grayia ornata	RBINS 3747	DRC: Lualaba Province: Mpala, Rég. Kanzenze
Grayia ornata	RBINS 3757	DRC: Kinshasa Province: Bas-Congo: Kalina, au bord du fleuve Congo
Grayia ornata	RBINS 5431	DRC: North Kivu Province: Forêt rive droite Semliki, secteur Liboma, Parc Nat. Albert
Grayia ornata	RBINS 9111	DRC: South Kivu Province: Itebero, Territoire de Walikale
Grayia ornata	RBINS 10080	DRC: Équateur Province: Londo, dans marais, Lac Tumba
Grayia ornata	RBINS 10081	Burundi: Bujumbura Mairie Province: Usumbura, Ruanda
Grayia ornata	RBINS 10882	DRC: Kongo Central Province: Ganda-Sundi, Mayumbe
Grayia ornata	RBINS 11193	DRC: Haut-Uele Province: Rég. Bagbele, ex Parc Nat. Garamba
Grayia ornata	RBINS 11194	DRC: Haut-Uele Province: savane boisée, ex Parc Nat. Garamba
Grayia ornata	RBINS 16242	Gabon: Ngounié Province: Rivière Matombo à Itsiba, Département de Boumi-Louetsi (S01.781944, E11.978056, 670 m)
Grayia ornata	RBINS 16324	Gabon: Nyanga Province: Moukalaba River, along the road Tchibanga-Digoudou, near the ferry (S02.783333, E10.733333, 36 m)
Grayia ornata	RBINS 18927	DRC: Tshopo Province: Yoko (N00.293806, E25.288917)
Grayia ornata	RBINS 18989	DRC: Tshopo Province: Lieki (N00.691944, E24.235000)
Grayia ornata	RBINS 19025	DRC: Tshopo Province: Ubundu (S00.368889, E25.431694)
Grayia ornata	RBINS 19648	DRC: Tshopo Province: Amadjabe (N00.066670, E25.283330)

Grayia ornata	RBINS 19649	DRC: Tshopo Province: Amadjabe (N00.06667, E25.28333)
Grayia ornata	RMCA 1094	DRC: Kongo Central Province: Forêt du Mayumbe
Grayia ornata	RMCA 3466	DRC: Haut-Uele Province: Dika
Grayia ornata	RMCA 3626	DRC: Haut-Uele Province: Faradje
Grayia ornata	RMCA 4758	DRC: Tshopo Province: Panga (Aruwimi)
Grayia ornata	RMCA 7705	DRC: Kwilu Province: Gingungi, Kwango
Grayia ornata	RMCA 9427	DRC: Mongala Province: Binga
Grayia ornata	RMCA 10119	DRC: Équateur Province: Bamania
Grayia ornata	RMCA 11343	DRC: Mai-Ndombe Province: Kunungu
Grayia ornata	RMCA 15296	DRC: Équateur Province: Coquilhatville
Grayia ornata	RMCA 15671	DRC: Tshopo Province: "Environs de Stanleyville"
Grayia ornata	RMCA 15672	DRC: Tshopo Province: "Environs de Stanleyville"
Grayia ornata	RMCA 16366	DRC: Kongo Central Province: Lukula
Grayia ornata	RMCA 16928	DRC: Équateur Province: Bokuma
Grayia ornata	RMCA 19533	DRC: Équateur Province: Bamanya
Grayia ornata	RMCA 20569	DRC: Mai-Ndombe Province: Bolobo
Grayia ornata	RMCA 21034	DRC: Tshuapa Province: Ikela
Grayia ornata	RMCA 21035	DRC: Tshuapa Province: Ikela
Grayia ornata	RMCA 21985	DRC: Kinshasa Province: Stanley Pool
Grayia ornata	RMCA 28403	Angola: Lunda Norte Province: Dundo, Riv. Mussungue
Grayia ornata	RMCA 83-24-R-49	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 84-25-R-84	DRC: Équateur Province: Boloka sur Momboyo
Grayia ornata	RMCA 85-21-R-17	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 87-43-R-26	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 87-43-R-80	DRC: Équateur Province: Boteka
Grayia ornata	RMCA 88-33-R-80	DRC: Tshuapa Province: Wafanya, (S01.350000, E20.333333)
Grayia ornata	RMCA 88-33-R-81	DRC: Équateur Province: Imbonga
Grayia ornata	RMCA 88-33-R-82	DRC: Tshuapa Province: Wafanya, (S01.350000, E20.333333)
Grayia ornata	RMCA 89-20-R-80	DRC: Tshuapa Province: Wafanya, (S01.350000, E20.333333)
Grayia ornata	MNHN 1987-1430	Republic of the Congo: Plateaux Department: Leketi (S01.600000, E14.966667)
Grayia ornata	MNHN 1994-3380	CAR: Ombella-M’poko Prefecture: Bangui
Grayia ornata	MNHN 1994-3383	CAR: Mambéré-Kadéï Prefecture: Berberati

Grayia ornata		MNHN 1994.8079	CAR: Mambéré-Kadéï Prefecture: Berberati
Grayia ornata		MZULB 2571	DRC: Zoo de Leopoldville (not mapped)
Grayia ornata		AMNH R12161	DRC: Haut-Uele Province: Niangara
Grayia ornata		AMNH R12163	DRC: Haut-Uele Province: Faradje
Grayia ornata		AMNH R12164	DRC: Tshopo Province: Avakubi
Grayia ornata		AMNH R12165	DRC: Haut-Uele Province: Niangara
Grayia ornata		AMNH R12166	DRC: Haut-Uele Province: Niangara
Grayia ornata		AMNH R12167	DRC: Haut-Uele Province: Faradje
Grayia ornata		AMNH R12168	DRC: Haut-Uele Province: Faradje
Grayia ornata		AMNH R12169	DRC: Haut-Uele Province: Faradje
Grayia ornata		AMNH R12170	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12171	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12172	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12173	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12174	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12175	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12176	DRC: Bas-Uele Province: Niapu
Grayia ornata		AMNH R12177	DRC: Tshopo Province: Avakubi
Grayia ornata		AMNH R12178	DRC: "Belgian Congo" (not mapped)
Grayia ornata		AMNH R12570	DRC: "Belgian Congo" (not mapped)
Grayia ornata		AMNH R12571	DRC: Haut-Uele Province: Faradje
Grayia ornata		AMNH R50550	Cameroon: Adamawa Region: Metet
Grayia ornata	0832 P	PEM R26316	Gabon*
Grayia ornata		PEM R03473	DRC: Kinshasa Province: Kinsuka
Grayia ornata		PEM R05255	Gabon: Ogooué-Maritime Province: 11 km 305Â°NW of Doussala, Res. De Faune de la Moukalaba-Dougoua
Grayia ornata		PEM R05854	Gabon: Ogooué-Maritime Province: Ndogo Lagoon, last passage before Gamba
Grayia ornata	MBUR 03013	PEM R20078	Republic of the Congo: Kouilou Department: Vemba River
Grayia ornata		PEM R24964	Gabon: Ogooué-Maritime Province: Ndogo Lagoon, last passage before Gamba
Grayia ornata		PEM R24958	Gabon: Ogooué-Maritime Province: DOR at turning to Ossengue at swamp
Grayia ornata		BMNH 1912.4.1.7	DRC: Kwilu Province: Mayili
Grayia ornata		BMNH 1958.1.4.89	Cameroon*
Grayia ornata		BMNH 84.3.25.5	Gabon*

Grayia ornata		MNHN 1894-176	Gabon or Republic of the Congo: voisinage de la côte, Congo français (not mapped)	
Grayia ornata		MNHN 1987-1424	Republic of the Congo: Kouilou Department: Dimonika	
Grayia ornata		RMCA 11924	DRC: Ituri Province: Bunia	
Grayia ornata		RMCA 18192	DRC: North Kivu Province: Manguretshipa, Territoire de Lubero (1000 m)	
Grayia ornata		RMCA 3278	DRC: Haut-Uele Province: Medje	
Grayia ornata		RMCA 91-70-R-3	Republic of the Congo: Kouilou Department: Rivière Loukoula à la porte du Mayombe	
Grayia ornata		RMCA 91-70-R-4	Republic of the Congo: Kouilou Department: Rivière Loukoula, affl. Loukenene, sous-affl. Loeme, à 1 km en aval de Pounga	
Grayia ornata		RMCA 93-072-R-0001	Cameroon: Adamawa Region: Mayo Banyo Barki, bras mort du Mayo Banyo	
Grayia ornata		ZMB 21864	Cameroon: East Region: Lome Bezirk	
Grayia ornata	CRSN 85		DRC: Ituri Province: Aweza-Libulu (N01.96356, E30.03868, 1176m)	
Grayia ornata	ELI 2065		DRC: Mai-Ndombe Province: Isongo, Lake Mai-Ndombe, Forest (S01.5704, E18.3962, 309 m)	
Grayia ornata	ELI 2064		DRC: Mai-Ndombe Province: Isongo, Lake Mai-Ndombe, Forest (S01.5704, E18.3962, 309 m)	
Grayia ornata	ELI 1934		DRC: Mai-Ndombe Province: Nkala Village, Forest (S02.58578, E16.47376, 459 m)	
Grayia ornata	ELI 1877		DRC: Mai-Ndombe Province: Nkala Village, Mbali River (S02.603910, E16.437048, 450 m)	
Grayia ornata	ELI 1905		DRC: Mai-Ndombe Province: Nkala Village, Forest (S02.59057, E19.46370, 474 m)	
Grayia ornata	ELI 2227		DRC: Équateur Province: Balolombo Village, Busira River (S00.25939, E19.63575, 305 m)	
Grayia ornata	ELI 1740		DRC: Mai-Ndombe Province: Ndomo (S03.30093, E16.23034, 278 m)	
Grayia ornata	EBG 2636		DRC: Ituri Province: Bazinga (N01.24554, E28.34337, 737 m)	
Grayia ornata	ELI 1960		DRC: Mai-Ndombe Province: Village of Kutu, Fimi River (S02.7300, E18.14425, 312 m)	
Grayia ornata	ELI 2674		DRC: Équateur Province: Bolondo-Bulumbe Village, Momboyo River (S00.40747, E19.14425, 312 m)	
Grayia ornata	ELI 2066		DRC: Mai-Ndombe Province: Isongo, Lake Mai-Ndombe, Forest	
Grayia ornata	ELI 2352		DRC: Équateur Province: Bomputu Village, Salonga River (S00.46734, E20.14179, 310 m)	
Grayia ornata	ELI 2343		DRC: Équateur Province: Balolombo Village, Busira River, Forest (S00.25939, E19.63575, 305 m)	
Grayia ornata	ELI 2663		DRC: Équateur Province: Isankele Village, River, 2 km E of Bolondo-Bulumbe	
Grayia ornata	CRSN 86		DRC: Ituri Province: Aweza-Libulu, (N01.96356, E030.03868, 1175 m)	
Grayia ornata	CRSN 87		DRC: Ituri Province: Aweza-Libulu, (N01.96356, E030.03868, 1175 m)	
Grayia ornata	ELI 2063		DRC: Mai-Ndombe Province: Isongo, Lake Mai-Ndombe, Forest (S01.570400, E18.396200)	
Grayia ornata		BMNH 1979.160	DRC: Kinshasa Province: Kinshasa	
Grayia ornata		SDSNH 63884	DRC: Kinshasa Province: Kinshasa	
Grayia ornata	79-968		DRC: Kwilu Province: Kimbengi	VW
Grayia ornata		BMNH 1979.161	DRC: Kwilu Province: Kafumba	
Grayia ornata	79-1019		DRC: Kinshasa Province: Kinshasa	VW

Grayia ornata	79-1061		DRC: Kinshasa Province: Ngaliema	VW
Grayia ornata	79-1203		DRC: Kwilu Province: Kafumba	VW
Grayia ornata		FMNH 214743	DRC: Kongo Central Province: mbanza ngnngu	
Grayia ornata		PEM 3399	DRC: Kinshasa Province: Mimosa	
Grayia ornata		FMNH 2147744/ ZRC 23435	DRC: Kinshasa Province: Mimosa	
Grayia ornata		ZRC 23434	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	79-1460		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	79-1480		DRC: Kongo Central Province: mbanza ngnngu	VW
Grayia ornata		UF 53619	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214747	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214745	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214742	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214749	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 21752	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214753	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	79-1597		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	79-1598		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		NMV D55565	DRC: Kwilu Province: Kafumba	VW
Grayia ornata	79-16662		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	80-1693		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		LSUMZ 40728	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214748	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		UF 63440	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	80-1833		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	80-1834		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	1842		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		UF 63441	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	80-1885		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		UMMZ 182975	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		ZRC 23433	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214750	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		TAU 12619	DRC: Kinshasa Province: Kinsuka	

Grayia ornata		FMNH 21751	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	80-2020		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	80-2021		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		TAU 12622	DRC: Kinshasa Province: Kinsuka	
Grayia ornata		FMNH 214746	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	2204		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		UF 63442	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	2316		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		LSUMZ 40773	DRC: Kinshasa Province: Kinsuka	
Grayia ornata	2851		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	2852		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		RMCA. 18192	DRC: North Kivu Province: Manguretshipa,Terr. from Lubero (1000 m)	(Laurent 1956)
Grayia ornata		RMCA. 18193	DRC: Tanganyika Province: Nyunzu (700 m)	(Laurent 1956)
Grayia ornata		RMCA 21475	DRC: North Kivu Province: Mutakato, Terr de Walikale (600 m)	(Laurent 1956)
Grayia ornata		NMZL 1517	Zambia: Northwestern Province: Mwinilunga District	(Boettger 1889)
Grayia ornata	12978		DRC: Kabengere (not mapped)	(Loveridge 1936)
Grayia ornata		DFC P733	Gabon: Nkassi (not mapped)	(Pauwels et al. 2002)
Grayia ornata		SMF 52607	Cameroon: Centre Region: Bafia	(Pauwels et al. 2002)
Grayia ornata		CAS 256859	Cameroon: Southwest Region: foothills of mount kupe	(Portik et al. 2016)
Grayia ornata	79-1106		DRC: Kwilu Province: Kafumba	VW
Grayia ornata		MZUSP 8128	DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata	2319		DRC: Kinshasa Province: Kinsuka	VW
Grayia ornata		AMNH R5272	Cameroon: Ja River*	
Grayia smithii		BMNH 1904.2.23.6	Guinea: Labé Province: Labé	
Grayia smithii		BMNH 1912.9.18.6	Ghana: Central Region: Gold Coast, West of Dunkwa	
Grayia smithii		BMNH 1936.7.3.29	Uganda: Eastern Region: Mjanji, Victoria Nyanza, near Kenya border	
Grayia smithii		BMNH 1946.1.1.67 (formerly BMNH 48.9.15.10)	DRC: Kongo Central Province: Boma	
Grayia smithii		BMNH 1955.1.1.58	Sierra Leone: Eastern Province: Kenema	
Grayia smithii		BMNH 1959.1.7.11	Uganda: Eastern Region: Mjanji, Victoria Nyanza	
Grayia smithii		BMNH 1959.1.7.12	Uganda: Eastern Region: Mjanji, Victoria Nyanza	

Grayia smithii	BMNH 1960.1.4.78	Sierra Leone: Southern Province: Bo
Grayia smithii	BMNH 1963.1043	Sierra Leone: Southern Province: Bo
Grayia smithii	BMNH 68.5.27.5	Sierra Leone*
Grayia smithii	BMNH 1971.1319	Nigeria: Borno State: Waka near Biu, savanna, N. (N10.616667, E12.216667)
Grayia smithii	MNHN 1896-242	Liberia*
Grayia smithii	MNHN 1896-243	Liberia*
Grayia smithii	MNHN 1896-244	Liberia*
Grayia smithii	MNHN 1907-223	Côte d'Ivoire*
Grayia smithii	MNHN 1916-134	Benin: Dahomey*
Grayia smithii	MNHN 1921-15	CAR: Ouham Prefecture: Rivière de la Gribingui, N.
Grayia smithii	MNHN 1921-444	Guinea: Nzérékoré Region: N'Zérékoré, S.-E.
Grayia smithii	MNHN 1921-445	Guinea: Nzérékoré Region: N'Zérékoré, S.-E.
Grayia smithii	MNHN 1921-446	Guinea: Nzérékoré Region: Diéké
Grayia smithii	MNHN 1932-38	Liberia*
Grayia smithii	MNHN 1960-140	Guinea: Nzérékoré Region: Sérédou
Grayia smithii	MNHN 1962.13	Cameroon: North Region: Fleuve Bénoué
Grayia smithii	MNHN 1962.127	Senegal: Thiés Region: Lac Tanma
Grayia smithii	MNHN 1962.345	Guinea: Nzérékoré Region: Ziéla, Mont Nimba, S, E
Grayia smithii	MNHN 1964.471	CAR: Lobaye Prefecture: Boukoko
Grayia smithii	MNHN 1986.1616	Liberia: Nimba County: Mont Nimba
Grayia smithii	MNHN 1986.1688	Liberia: Nimba County: Cassava Farm, Mont Nimba
Grayia smithii	MNHN 1986.1806	Liberia: Nimba County: Grassfield, Nimba Research Station
Grayia smithii	MNHN 1986.1846	Liberia: Nimba County
Grayia smithii	MNHN 1988.164	Guinea: Nzérékoré Region: Sérédou
Grayia smithii	MNHN 1988-186	Côte d'Ivoire: Montagnes District: Parc Naturel Cavally
Grayia smithii	MNHN 1990.4745	Côte d'Ivoire: Vallée du Bandama District: Bouaké
Grayia smithii	MNHN 1990-5074	Guinea: Nzérékoré Region: Nion, Nimba (550 m)
Grayia smithii	MNHN 1991-339	CAR: Ouaka Prefecture: Bambari
Grayia smithii	MNHN 1991-372	CAR: Bangui Prefecture: (en ville)
Grayia smithii	MNHN 1994-3160	Côte d'Ivoire: Lagunes District: Lamto
Grayia smithii	MNHN 1994-3386	CAR: Bangui Prefecture

Grayia smithii	MNHN 1994-3389	CAR: Ombella-M'Poko Prefecture: Boali
Grayia smithii	MNHN 1994-7293	Côte d'Ivoire: Vallée Du Bandama District: Station de pisciculture, Bouaké
Grayia smithii	MNHN 1994.8084	CAR: Ouham-Pendé Prefecture: Kouki
Grayia smithii	MNHN 1995.3402	CAR: Lobaye Prefecture: SCAD, pont
Grayia smithii	MNHN 1996.6448	CAR: Ouaka Prefecture: Seko
Grayia smithii	RBINS 3944	DRC: Tshopo Province: Yangambi
Grayia smithii	RBINS 11200b	DRC: Haut-Uele Province: Utukuru/8, tête de source, Parc Nat. Garamba
Grayia smithii	RBINS 11202a	DRC: Haut-Uele Province: rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11203	DRC: Haut-Uele Province: rivière à cours boisé en partie, Parc Nat. Garamba,
Grayia smithii	RBINS 11204a	DRC: Haut-Uele Province: Nambirima, rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11204c	DRC: Haut-Uele Province: Nambirima, rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 13054	DRC: North Kivu Province: Rivière Rutshuru, affluent du Lac Edouard, Secteur Sud, ex Parc Nat. Virunga (1275 m)
Grayia smithii	RBINS 13055	DRC: North Kivu Province: Ngamba, passage bac de la Semliki, route Beni-Kasindi, Parc Nat. Virunga (900 m)
Grayia smithii	RBINS 16942	Côte d'Ivoire*
Grayia smithii	RBINS 17136	Senegal: Kèdougou Region: Bandi (N12.516667, W12.450000)
Grayia smithii	RBINS 19643	DRC: Tshopo Province: Kisanganii (N00.518611, E25.260278)
Grayia smithii	RBINS 19691	DRC: Tshopo Province: Kisanganii (N00.518611, E25.260278)
Grayia smithii	RBINS 20162	Guinea: Kankan Region: Kounian (N09.395000, W08.932500, 588 m)
Grayia smithii	RBINS 20164	Guinea: Kankan Region: Dianfaradougo (N08.985278, W08.925000, 750 m)
Grayia smithii	RBINS 20169	Guinea: Kankan Region: Kounian (N09.395000, W08.932500, 588 m)
Grayia smithii	RBINS 20170	Guinea: Kankan Region: Bankoro-Fassirou (N09.216389, W08.994722, 524 m)
Grayia smithii	RMCA 7438	DRC: Haut-Katanga Province: Lukonzobwa
Grayia smithii	RMCA 8768	DRC: Mai-Ndombe Province: Kunungu
Grayia smithii	RMCA 27535	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27538	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27540	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27543	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27544	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 28044	Côte d'Ivoire: Vallée du Bandama District: Kokondékro (Bouaké), Station de pisciculture
Grayia smithii	RMCA 28045	Côte d'Ivoire: Vallée du Bandama District: Kokondékro (Bouaké), Station de pisciculture
Grayia smithii	RMCA 28046	Côte d'Ivoire: Vallée du Bandama District: Kokondékro (Bouaké), Station de pisciculture
Grayia smithii	RMCA 28062	Côte d'Ivoire: Vallée du Bandama District: Kokondékro (Bouaké), Station de pisciculture

Grayia smithii	RMCA 28111	Cameroon: Littoral Province: Edea
Grayia smithii	RMCA 28399	Angola: Lunda Norte Province: Dundo, Barrage de la Luachimo
Grayia smithii	RMCA 29429	Côte d'Ivoire: Woroba District: Toyebli, River Cess
Grayia smithii	RMCA 30709	DRC: Haut-Uele Province: Parc National de la Garamba
Grayia smithii	RMCA 30714	DRC: Haut-Uele Province: Parc National de la Garamba
Grayia smithii	RMCA 80-36-R-12	Liberia: Grand Gedeh County: L.T.C.
Grayia smithii	RMCA 84-25-R-96	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 84-25-R-97	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 84-25-R-100	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 84-25-R-102	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 84-25-R-108	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 85-52-R-19	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 87-43-R-28	DRC: Équateur Province: Boteka
Grayia smithii	RMCA 92-059-R-2	Guinea: Boké Region: Kamouri, River Batapon, affl. Rio Nunez
Grayia smithii	BMNH 1902.11.10.8	Nigeria: Bayelsa State: Agberi, S.
Grayia smithii	BMNH 1906.5.30.2	Uganda: Central Region: Entebbe
Grayia smithii	BMNH 1909.2.23.7	Guinea: Labé Region: Labé
Grayia smithii	BMNH 1930.11.19.67	Sierra Leone: Eastern Province: Kankordu
Grayia smithii	BMNH 1936.7.3.30	Uganda: Eastern Region: Mjanji, Victoria Nyanza, near Kenya border
Grayia smithii	BMNH 1949.1.3.15	Nigeria: Lagos State: Yaba
Grayia smithii	BMNH 1950.1.2.6	Cameroon: Southwest Region: Kumba
Grayia smithii	BMNH 1952.1.9.23	Ghana: Ashanti Region: Gold Coast, Dechem Stream, Kumasi
Grayia smithii	BMNH 1952.1.9.24	Ghana: Ashanti Region: Gold Coast, Dechem Stream, Kumasi
Grayia smithii	BMNH 1953.1.2.45	Sierra Leone: Western Area: Newton, Colony
Grayia smithii	BMNH 1959.1.7.7	Uganda: Eastern Region: Mjanji, Victoria Nyanza
Grayia smithii	BMNH 1959.1.7.8	Uganda: Eastern Region: Mjanji, Victoria Nyanza
Grayia smithii	BMNH 1959.1.7.9	Uganda: Eastern Region: Mjanji, Victoria Nyanza
Grayia smithii	BMNH 1959.1.7.10	Uganda: Eastern Region: Mjanji, Victoria Nyanza
Grayia smithii	BMNH 1960.1.3.63	Sierra Leone: Southern Province: Njala
Grayia smithii	BMNH 1960.1.5.31	Ghana: Ashanti Region: Kumasi
Grayia smithii	BMNH 1969.2263	Nigeria: Sokoto State: Sokoto
Grayia smithii	BMNH 1971.374	Cameroon: Southwest Region: Mamfe

Grayia smithii	MNHN 1885.612	Côte d'Ivoire: Comoé District: Assinie
Grayia smithii	MNHN 1916.202	Benin: Plateau Department: dans un marigot, environs de Sakété, cercle de Porto-Novo (50 km au nord)
Grayia smithii	MNHN 1921.441	Guinea: Kankan Region: Kerouane, 200 km N de Nzérékoré
Grayia smithii	MNHN 1921.442	Guinea: Kankan Region: N'Zébéla, 50 km NW de Nzérékoré
Grayia smithii	MNHN 1921.443	Guinea: Nzérékoré Region: Nzérékoré
Grayia smithii	MNHN 1957-79	Côte d'Ivoire: Abidjan Autonomous District: Adiopodoumé, près d'Abidjan, station I.D.E.R.T.
Grayia smithii	MNHN 1963.881	CAR: Lobaye Prefecture: La Maboké
Grayia smithii	MNHN 1965.346	Guinea: Nzérékoré Region: Sérédou, 70 km au N. de Nzérékoré, Mont Nimba (à plus de 1000 m)
Grayia smithii	MNHN 1965.397	Chad: Mayo-Kebbi Region
Grayia smithii	MNHN 1978-1832	Chad*
Grayia smithii	MNHN 1986-1615	Liberia: Nimba County: Mt Nimba, Nimba Research Laboratory, Airfield Savanna
Grayia smithii	MNHN 1986-1626	Liberia*
Grayia smithii	MNHN 1986-1676	Liberia*
Grayia smithii	MNHN 1986-1830	Liberia: Nimba County: Airfield Savanna Natriciteres
Grayia smithii	MNHN 1987.1420	Republic of the Congo: Brazzaville Region: Kintele
Grayia smithii	MNHN 1988.149	Guinea: Nzérékoré Region: Sérédou
Grayia smithii	MNHN 1988-180	Côte d'Ivoire: Lagunes District: dans filet de pêche, Lamto, Bandema
Grayia smithii	MNHN 1988-181	Côte d'Ivoire: Lagunes District: dans filet de pêche, Lamto, Bandema
Grayia smithii	MNHN 1988-194	Côte d'Ivoire: Lagunes District: dans filet de pêche, Lamto, Bandema
Grayia smithii	MNHN 1991-321	CAR: Bangui Prefecture: Lycée Boganda
Grayia smithii	MNHN 1994.3388	CAR: Ombella-M'Poko Prefecture: Boali
Grayia smithii	MNHN 1994.3390	CAR: Ombella-M'Poko Prefecture: Boali
Grayia smithii	MNHN 1994.3391	CAR: Ombella-M'Poko Prefecture: Boali
Grayia smithii	MNHN 1994.8081	CAR: Bangui Prefecture: fleuve
Grayia smithii	MNHN 1994.8083	CAR: Ouham Prefecture: Bossangoa
Grayia smithii	MNHN 1996.6440	CAR: Haute-Kotto Prefecture: Bria
Grayia smithii	RBINS 2709	DRC: North Kivu Province: Rivière Molindi, entre Kirumba et Lac Kibuga, Parc Nat. Albert, Congo Belge (1000 m)
Grayia smithii	RBINS 2710	DRC: Tshuapa Province: Eala
Grayia smithii	RBINS 2713	DRC: Kongo Central Province: Kisantu
Grayia smithii	RBINS 2714	DRC: Kongo Central Province: Kisantu
Grayia smithii	RBINS 3745a	DRC: Bas-Uele Province: Zobia
Grayia smithii	RBINS 3745b	DRC: Bas-Uele Province: Zobia

Grayia smithii	RBINS 3756	DRC: Bas-Uele Province: Zobia
Grayia smithii	RBINS 5433	DRC: Haut-Uele Province: Gangala-na-Bodio, Parc Nat. de la Garamba
Grayia smithii	RBINS 5435	DRC: Haut-Uele Province: Gangala-na-Bodio, Parc Nat. de la Garamba
Grayia smithii	RBINS 5437	DRC: Haut-Uele Province: Gangala-na-Bodio, Parc Nat. de la Garamba
Grayia smithii	RBINS 10079	DRC: North Kivu Province: plage dans une pente concave en face de l'embouchure de la Museya, rive O. bac, P.N.A.
Grayia smithii	RBINS 11200a	DRC: Haut-Uele Province: Utukuru, tête de source, Parc Nat. Garamba
Grayia smithii	RBINS 11201	DRC: Haut-Uele Province: dans l'eau de la Garamba, Parc Nat. Garamba
Grayia smithii	RBINS 11202b	DRC: Haut-Uele Province: rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11202c	DRC: Haut-Uele Province: rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11204b	DRC: Haut-Uele Province: Nambirima, rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11204d	DRC: Haut-Uele Province: Nambirima, rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11204e	DRC: Haut-Uele Province: Nambirima, rivière à cours dénudé, Parc Nat. Garamba
Grayia smithii	RBINS 11205	DRC: Haut-Uele Province: marécages, Parc Nat. Garamba
Grayia smithii	RBINS 11206	DRC: Haut-Uele Province: ruisselets, Parc Nat. Garamba
Grayia smithii	RBINS 11207	DRC: Haut-Uele Province: Rég. Bagbele, Parc Nat. Garamba
Grayia smithii	RBINS 13053	DRC: North Kivu Province: Ishango-Semliki, déversoir du Lac Edouard, Parc Nat. Virunga (915 m)
Grayia smithii	RBINS 13056	DRC: North Kivu Province: Makayoba, affluent de la Djuma, Parc Nat. Virunga (750 m)
Grayia smithii	RBINS 18794	DRC: Tshopo Province: Yaikela (N00.806111, E24.283889)
Grayia smithii	RBINS 18984	DRC: Tshopo Province: Yaikela (N00.806111, E24.283889)
Grayia smithii	RBINS 19527	DRC: Kinshasa Province: “Bas-Congo”
Grayia smithii	RBINS 19681	DRC: Tshopo Province: Kisangani, rive droite (N00.518611, E25.260278)
Grayia smithii	RBINS 19791	DRC: Tshopo Province: Kisangani, rive droite (N00.518611, E25.260278)
Grayia smithii	RBINS 20160	Guinea: Kankan Region: Kounian (N09.395000, W08.932500, 588 m)
Grayia smithii	RBINS 20161	Guinea: Kankan Region: Kounian (N09.395000, W08.932500, 588 m)
Grayia smithii	RBINS 20163	Guinea: Nzérékoré Region: Gpaole (N07.639444, W09.229167, 411 m)
Grayia smithii	RBINS 20171	Guinea: Kankan Region: Damaro (N09.130556, W08.901944, 720 m)
Grayia smithii	RMCA 2410	DRC: Kinshasa Province: Kinshasa
Grayia smithii	RMCA 10248	DRC: Équateur Province: Eala
Grayia smithii	RMCA 27533	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27534	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27536	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia smithii	RMCA 27537	DRC: Kinshasa Province: Rapides de Kinsuka

Grayia smithii		RMCA 27539	DRC: Kinshasa Province: Rapides de Kinsuka	
Grayia smithii		RMCA 27542	DRC: Kinshasa Province: Rapides de Kinsuka	
Grayia smithii		RMCA 28037	Côte d'Ivoire: Vallée Bandama District: Kokondékro (Bouaké), Station de pisciculture	
Grayia smithii		RMCA 28042	Côte d'Ivoire: Vallée Bandama District: Kokondékro (Bouaké), Station de pisciculture	
Grayia smithii		RMCA 28043	Côte d'Ivoire: Vallée Bandama District: Kokondékro (Bouaké), Station de pisciculture	
Grayia smithii		RMCA 28400	Angola: Lunda Norte Province: Dundo, Barrage de la Luachimo	
Grayia smithii		RMCA 28542	Cameroon: Southwest Region: Kumba	
Grayia smithii		RMCA 28752	Côte d'Ivoire: Montagnes District: Toyebli, Rivière Nipoué	
Grayia smithii		RMCA 29690	Togo*	
Grayia smithii		RMCA 30074	DRC: Haut-Uele Province: Parc National de la Garamba	
Grayia smithii		RMCA 84-25-R-95	DRC: Équateur Province: Boteka	
Grayia smithii		RMCA 84-25-R-98	DRC: Équateur Province: Boteka	
Grayia smithii		RMCA 84-25-R-99	DRC: Équateur Province: Boteka	
Grayia smithii		RMCA 84-25-R-101	DRC: Équateur Province: Bolingo sur Tshuapa	
Grayia smithii		RMCA 84-25-R-103	DRC: Équateur Province: Boteka	
Grayia smithii		RMCA 84-25-R-104	DRC: Équateur Province: Boteka	
Grayia smithii		RMCA 84-25-R-105	DRC: Équateur Province: Boteka	
Grayia smithii		MNHN 1995.3401	CAR: Lobaye Prefecture: SCAD	
Grayia smithii	EBG 2663		DRC: Ituri Province: Epulu (N01.39848, E28.57110, 737 m)	
Grayia smithii	EBG 2664		DRC: Orientale Province: vicinity of Epulu (N01.39848, E28.57110, 737 m)	
Grayia smithii	ELI 2226		DRC: Équateur Province: Balolombo Village, Busira River (S00.25939, E19.63575, 305 m)	
Grayia smithii	JCK 10609/ELI 4140		Uganda: Semliki NP (not mapped_	
Grayia smithii	78-885		DRC: Kinshasa Province: Kinshasa	VW
Grayia smithii		BMNH 1979.162	DRC: Kinshasa Province: Mimosa	
Grayia smithii		LSUMZ 48408	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	79-1184		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1185		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1212		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1215		DRC: Kinshasa Province: Kinshasa	VW
Grayia smithii		PEM 3381	DRC: Kongo Central Province: bas-zaire mbanza-ngungu	
Grayia smithii	79-1398		DRC: Kinshasa Province: Mimosa	VW
Grayia smithii		UF 63443	DRC: Kinshasa Province: Mimosa	

Grayia smithii	79-1461		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214765	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		FMNH 214766	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		TAU 12624	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	79-1592		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214768	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	79-1594		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214770	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	79-1596		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1617		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1618		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	79-1661		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1674		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214767	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		NMV D55557	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	80-1841		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1843		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1862		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1872		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1883		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1884		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		PEM 3473	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		TAU 12626	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		FMNH 214764	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	80-1913		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1924		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1933		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-1964		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		UMMZ 172977	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		FMNH 214762	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	80-2023		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		UF 63446	DRC: Kinshasa Province: Kinsuka	

Grayia smithii		FMNH 214760	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		ZRC 2.3447	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	80-2027		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214761	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	80-2029		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-2030		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	80-2031		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		FMNH 214763	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	2136		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2137		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		ZRC 2.3448	DRC: Kinshasa Province: Kinsuka	
Grayia smithii	2139		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2153		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2154		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2155		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2240		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2310		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii	2313		DRC: Kinshasa Province: Kinsuka	VW
Grayia smithii		UF 63448	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		LSUMZ 40780	DRC: Kinshasa Province: Kinsuka	
Grayia smithii		PEM R03381	DRC: Kongo Central Province: Bbanza-Ngungu*	
Grayia smithii		PEM R03399	DRC: Kinshasa Province: Kinsuka, 12km west southwest Kinshasa	
Grayia smithii		PEM R03409	DRC: Kinshasa Province: Kinsuka, 12km west southwest Kinshasa	
Grayia smithii		PEM R03472	DRC: Kinshasa Province: Kinsuka*	
Grayia smithii		PEM R04434	Cote d'Ivoire: Montagnes District: Cavally Classified Forest Reserve, tributary of River Dibo	
Grayia smithii	NR 028	PEM R19222	Liberia: Nimba County: Bata Village, on road to East Nimba Nature Reserve	
Grayia smithii	NR 239	PEM R19279	Liberia: Nimba County: Fish traps in streams from Mt Gangra, near Yekepa	
Grayia smithii		PEM R20045	Liberia: Nimba Country: Lake near Yekepa	
Grayia smithii		PEM R20450	CAR: Sangha-mbaéré Prefecture: Prefecture de la Sangha-Mbaere, Reserve Speciale de Foret Dense de Dzanga-Sangha, 12.7 km NW of Bayanga, at camp 2	
Grayia smithii		PEM R20463	CAR: Sangha-mbaéré Prefecture: Prefecture de la Sangha-Mbaere, Park National de Dzanga-Ndoki, 38.6 km S of Lidjombo, at camp 3	
Grayia smithii		PEM R22724	Republic of the Congo: Kouilou*	

Grayia smithii	MBUR 08214	PEM R22725	Republic of the Congo: Kouilou Department: 2.8 km E of Hinda
Grayia smithii		AMNH R12153	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12154	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12155	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12156	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12157	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12158	DRC: Tshopo Province: Avakubi
Grayia smithii		AMNH R12159	DRC: Huat-uele Province: Faradje
Grayia smithii		AMNH R12179	DRC: Huat-uele Province: Niangara
Grayia smithii		AMNH R140428	Liberia: Lofa County: Via River (Liberia-Guinea border), 11 km N, 3 km E Ziggida
Grayia smithii		AMNH R142416	Liberia: Lofa County: Voinjama
Grayia smithii		AMNH R45903	DRC: Équateur Province: Lukolela, Congo R
Grayia smithii		AMNH R80224	DRC (Not mapped)
Grayia smithii		AMNH R80225	DRC (Not mapped)
Grayia smithii		AMNH R80226	DRC (Not mapped)
Grayia smithii	EBG 2634		DRC: Ituri Province: Epulu (N01.40140, E28.57000, 747 m)
Grayia tholloni		BMNH 1901.6.24.42	Uganda: Central Region: Entebbe, 3800 f.
Grayia tholloni		BMNH 1908.4.7.3	Sudan: Khartoum State: Egyptian Soudan, Barboi
Grayia tholloni		BMNH 1928.11.24.4	Uganda: Western Region: Tonia, Lake Albert
Grayia tholloni		BMNH 1928.11.24.5	Uganda: Northern Region: Muntu, Lake Kioga
Grayia tholloni		BMNH 1936.7.3.31	Uganda: Eastern Region: Mjanji, Victoria Nyanza
Grayia tholloni		BMNH 1951.1.3.50	Uganda: Western Region: Omubugoigo, Lake Albert
Grayia tholloni		BMNH 1955.1.4.70	Gambia: West Coast Region: Kotu Stream, 15-20 mls. S. of Bathurst
Grayia tholloni		BMNH 1959.1.6.11	Uganda: Western Region: Kokoba, Kaswali, Ankole, S.W.
Grayia tholloni		BMNH 1960.1.3.15	Kenya: Tura: Longhor*
Grayia tholloni		MNHN 1890-40	Republic of the Congo*
Grayia tholloni		MNHN 1890-152	Republic of the Congo: Plateaux Region: Brazzaville
Grayia tholloni		MNHN 1896.66	Republic of the Congo: Plateaux Region: Poste de Dieli, au confluent de l'Alima et du Congo
Grayia tholloni		MNHN 1896.67	Republic of the Congo: Plateaux Region: Poste de Dieli, au confluent de l'Alima et du Congo
Grayia tholloni		MNHN 1921-16	CAR: Ouham Prefecture: Gribingui, Nord
Grayia tholloni		MNHN 1972.141	Cameroon: Adamawa Region: Ngaoundéré

Grayia tholloni	MNHN 1972.142	Cameroon: Adamawa Region: Ngaoundéré
Grayia tholloni	MNHN 1988.2340	Republic of the Congo*
Grayia tholloni	MNHN 1988.2342	Republic of the Congo*
Grayia tholloni	MNHN 1988.2343	Republic of the Congo*
Grayia tholloni	MNHN 1988.2344	Republic of the Congo*
Grayia tholloni	MNHN 1988.2345	Republic of the Congo*
Grayia tholloni	MNHN 1988.2346	Republic of the Congo*
Grayia tholloni	MNHN 1988.2347	Republic of the Congo*
Grayia tholloni	MNHN 1988.2349	Republic of the Congo*
Grayia tholloni	MNHN 1988.2350	Republic of the Congo*
Grayia tholloni	MNHN 1988.2352	Republic of the Congo*
Grayia tholloni	MNHN 1994.8077	CAR: Ouham-pendé Prefecture: Paoua
Grayia tholloni	MNHN 1994.8085	CAR: Ouham Prefecture: Kouki
Grayia tholloni	MNHN 1995.4172	Senegal: Fatick Region: Keur Bakar Mané, banks of Djikoye stream, Sine Saloum (N13.633333, W16.266667)
Grayia tholloni	RBINS 2711	DRC: Kongo Central Province: Kisantu, Bas-Congo
Grayia tholloni	RBINS 3741	DRC: Lulalaba Province: Mpala, Rég. Kanzenze
Grayia tholloni	RBINS 3742	DRC: Lualaba Province: Mpala, Rég. Kanzenze
Grayia tholloni	RBINS 11195	DRC: Haut-Uele Province: expansions marécageuses, Parc Nat. Garamba
Grayia tholloni	RBINS 11197	DRC: Haut-Uele Province: rivière à cours dénudé, Parc Nat. Garamba
Grayia tholloni	RBINS 11198	DRC: Haut-Uele Province: tête de source, Parc Nat. Garamba
Grayia tholloni	RBINS 20167	Guinea: Kankan Region: Bankoro-Fassirou (N09.216389, W08.994722, 524 m)
Grayia tholloni	RMCA 437	DRC: sud-ouest du Lac Tanganyika (not mapped)
Grayia tholloni	RMCA 4871	DRC: Haut-Lomami Province: Nyonga
Grayia tholloni	RMCA 5055	DRC: Haut-Lomami Province: Nyonga
Grayia tholloni	RMCA 11788	DRC: Mai-Ndombe Province: Village Ndva (Kunungu)
Grayia tholloni	RMCA 11811	DRC: Mai-Ndombe Province: Village Ndva (Kunungu)
Grayia tholloni	RMCA 11816	DRC: Mai-Ndombe Province: Village Ndva (Kunungu)
Grayia tholloni	RMCA 15127	DRC: Kongo Central Province: Inkisi
Grayia tholloni	RMCA 15753	DRC: Mai-Ndombe Province: Bolobo
Grayia tholloni	RMCA 16170	DRC: Ituri Province: Gabu
Grayia tholloni	RMCA 27555	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia tholloni	RMCA 27556	DRC: Kinshasa Province: Rapides de Kinsuka

Grayia tholloni		RMCA 27557	DRC: Kinshasa Province: Rapides de Kinsuka
Grayia tholloni		BMNH 1905.10.16.2	South Sudan: Upper Nile State: Polkom, Baro R., Sobat
Grayia tholloni		BMNH 1911.7.8.13	Uganda: Central Region: Bussu
Grayia tholloni		BMNH 1937.12.4.47	Nigeria: Benue State: Makurdi,
Grayia tholloni		BMNH 1959.1.4.57	Tanzania: Kigoma Region: Kibondo, Tanganyika
Grayia tholloni		BMNH 1969.291	Ethiopia: SNNPR State: Grassy clearing, Arba Minch, S.W. Lake Abaya
Grayia tholloni		BMNH 1979.164	DRC: Kinshasa Province: Kinsuka, 14 km W of Kinshasa
Grayia tholloni		MNHN 1964-145	Senegal: Dakar Region: Sebikotane
Grayia tholloni		MNHN 1966.728	Republic of the Congo: Pool Department: Marche
Grayia tholloni		MNHN 1987-1422	Republic of the Congo: Plateaux Department: Leketi
Grayia tholloni		MNHN 1987-1705	Republic of the Congo: Brazzaville Department: Brazzaville
Grayia tholloni		MNHN 1988-2341	Republic of the Congo*
Grayia tholloni		MNHN 1988-2348	Republic of the Congo*
Grayia tholloni		MNHN 1988-2351	Republic of the Congo*
Grayia tholloni		MNHN 1988-2353	Republic of the Congo*
Grayia tholloni	885C	MNHN 1996	CAR: Bamingui-Bangoran Prefecture: La Gounda
Grayia tholloni		RBINS 2712	DRC: Kongo Central Province: Kisantu
Grayia tholloni		RBINS 3740	DRC: Kongo Central Province: Kisantu
Grayia tholloni		RBINS 5434	DRC: Haut-Uele Province: Riv. Nakaka, Gangala-na-Bodio, P.N.G.
Grayia tholloni		RBINS 11196	DRC: Haut-Uele Province: tête de source, Parc Nat. Garamba
Grayia tholloni		RBINS 11199	DRC: Haut-Uele Province: tête de source, Parc Nat. Garamba
Grayia tholloni		RBINS 20165	Guinea: Kankan Region: Bankoro-Fassirou
Grayia tholloni		RBINS 20166	Guinea: Kankan Region: Bankoro-Fassirou
Grayia tholloni		RBINS 20168	Guinea: Kankan Region: Saniamoridou (N09.093056, W09.021389, 558 m)
Grayia tholloni		RMCA 2137	DRC: Kongo Central Province: Banane
Grayia tholloni		RMCA 5209	DRC: Haut-Lomami Province: Nionga
Grayia tholloni		RMCA 11812	DRC: Mai-Ndombe Province: Village Ndva, Kunungu
Grayia tholloni		RMCA 11813	DRC: Mai-Ndombe Province: Village Ndva, Kunungu
Grayia tholloni		RMCA 11814	DRC: Mai-Ndombe Province: Village Ndva, Kunungu
Grayia tholloni		RMCA 11815	DRC: Mai-Ndombe Province: Village Ndva, Kunungu
Grayia tholloni		RMCA 11817	DRC: Mai-Ndombe Province: Kunungu
Grayia tholloni		RMCA 15074	DRC: Kinshasa Province: Kalina

Grayia tholloni		RMCA 18197	Burundi: Rutana Province: Kiharo, Mosso, Territoire Rutana (1350 m)	
Grayia tholloni		RMCA 27554	DRC: Kinshasa Province: Rapides de Kinsuka	
Grayia tholloni		RMCA 78-13-R-2	Burundi: Bujumbura Mairie Province: Bujumbura	
Grayia tholloni		RMCA 87-11-R-29	Rwanda: Eastern Province: Rukoma, Sake	
Grayia tholloni		RMCA 91-89-R-1	Burundi: Bujumbura Rural Province: Plaine de Gatumba	
Grayia tholloni		MNHN 1994.3378	CAR: Ouham-Pendé Prefecture: Paoua	
Grayia tholloni		RBINS 20156	Guinea: Kankan Region: Founounkouroudou (N09.085000, W09.003056, 545 m)	
Grayia tholloni		RBINS 20157	Guinea: Kankan Region: Founounkouroudou (N09.085000, W09.003056, 545 m)	
Grayia tholloni		RBINS 20158	Guinea: Kankan Region: Founounkouroudou (N09.085000, W09.003056, 545 m)	
Grayia tholloni	CFS 1159w		DRC: Sankuru Province: Katako-Kombe (S03.243290, E24.248560, 506 m)	
Grayia tholloni	78-917		DRC: Kwilu Province: Kafumba	VW
Grayia tholloni	79-1098		DRC: Kwilu Province: Kafumba	VW
Grayia tholloni	79-1142		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1216		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		PEM 3364	DRC: Kwilu Province: Kikosi N Vanga	
Grayia tholloni	79-1343		DRC: Kongo Central Province: Bas-Zaire, Mbanza, Ngungu	VW
Grayia tholloni		PEM 3374	DRC: Kongo Central Province: Bas-Zaire, Mbanza, Ngungu	
Grayia tholloni		FMNH 214795	DRC: Kongo Central Province: Bas-Zaire, Mbanza, Ngungu	
Grayia tholloni		FMNH 214805	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		UF 63453	DRC: Kinshasa Province: Mimosa	UF
Grayia tholloni		FMNH 214801	DRC: Kinshasa Province: Mimosa	
Grayia tholloni	79-1400		DRC: Kinshasa Province: Mimosa	VW
Grayia tholloni		PEM 3410	DRC: Kinshasa Province: Mimosa	
Grayia tholloni		FMNH 214793	DRC: Kinshasa Province: Mimosa	
Grayia tholloni	79-1425		DRC: Kinshasa Province: Mimosa	VW
Grayia tholloni	79-1426		DRC: Kinshasa Province: Mimosa	VW
Grayia tholloni	79-1450		DRC: Kinshasa Province: Mimosa	VW
Grayia tholloni	79-1458		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1462		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1463		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1494		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		LSUMZ 40783	DRC: Kinshasa Province: Kinsuka	

Grayia tholloni	79-1510		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1511		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1512		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		FMNH 214794	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	79-1540		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	79-1541		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		FMNH 214797	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-1694		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	80-1733		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		TAU 12630	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-1911		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		FMNH 214799	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		NMV 55556	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		FMNH 214802	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2033		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		NMUSP 8132	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2035		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		ZRC 2.3450	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		MZUSP 8133	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2038		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		ZRC 2.3449	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2040		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	80-2041		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	80-2042		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		UMMZ 172979	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2044		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	80-2045		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		UMMZ 172980	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	80-2047		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		ZRC 2.3451	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	2133		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		FMNH 214798	DRC: Kinshasa Province: Kinsuka	

Grayia tholloni		FMNH 214796	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	2152		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni	2165		DRC: Kinshasa Province: Kinsuka	VW
Grayia tholloni		UF 63451	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		MZUSP 8135	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni		UF 63450	DRC: Kinshasa Province: Kinsuka	
Grayia tholloni	2304		DRC: Kinshasa Province: Kinsuka, Brickin	VW
Grayia tholloni		RMCA 18194	Rwanda: Eastern Province: Lake Nasho, Terr. De Kibungu (1250 m)	(Laurent 1956)
Grayia tholloni		RMCA 18195	Rwanda: Eastern Province: Rwankuba lake Mohasi, Terr. Of Kibungu (1450 m)	(Laurent 1956)
Grayia tholloni		RMCA 18196	Burundi: Ruyigi Province: Ruyigi (1600 m)	(Laurent 1956)
Grayia tholloni		RMCA 18197	Burundi: Rutana Province: Kiharo (1250 m)	(Laurent 1956)
Grayia tholloni		RMCA 18198	Burundi: Gitega Province: Nyaruhongo	(Laurent 1956)
Grayia tholloni		RMCA 437	Tanzania: Lake Tanganyika (not mapped)	(Laurent 1956)
Grayia tholloni		RMCA 10264	DRC: Ituri Province: Mahagi	(Laurent 1956)
Grayia tholloni		RMCA 3579	DRC: Haut-Uele Province: Arebi, Terr of Watsa	(Laurent 1956)
Grayia tholloni		RMCA 4352	DRC: Tanganyika Province: Kalemie (Albertville)	(Laurent 1956)
Grayia tholloni		RMCA 20411	Burundi: Bubanza Province: Bubanza (1150 m)	(Laurent 1960)
Grayia tholloni		NMZB 10660	Zambia: Northwestern Province: Mqinlunga District Northwestern NWZ	(Broadley 1991)
Grayia tholloni	12877		DRC: Haut-Lomami Province: Katobwe	(Loveridge 1936)
Grayia tholloni	No. 942		Republic of the Congo: Brazzaville Department: Marche	(Villiers 1966)
Grayia tholloni	ELI 203		DRC: Haut-Lomami Province: Kyolo (S08.02005, E27.11645, 583 m)	
Grayia tholloni		PEM R03364	DRC: Kongo Central Province: Kikosi, Bandundu region, 35km north northwest of Kikwit	
Grayia tholloni		PEM R03374	DRC: Kongo Central Province: Bbanza-Ngungu*	
Grayia tholloni		PEM R03410	DRC: Kinshasa Province: Kinsuka, Kinshasa Region, 12km west southwest Kinshasa	
Grayia tholloni	CMRK 380	PEM R27494	Burundi: Bujumbura Mairie Province: Bujumbura, near Club Circle Nautique, close to the shores of Lake Tanganyika	
Grayia tholloni		AMNH R12180	DRC: Haut-Uele Province: Faradje,	
Grayia tholloni		AMNH R12181	DRC: Haut-Uele Province: Garamba*	
Grayia tholloni		AMNH R96104	Nigeria: Plateau State: Jos	
Grayia tholloni		BMNH 1979.164	DRC: Kinshasa Province: Ngaliema, Mimosa on river	

References

Abell, R., M.L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, et. al. 2008. Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioScience 58:403–414.

Aduse-Poku, K., E. van Bergen, S. Sáfián, S.C. Collins, R.S. Etienne, L. Herrera-Alsina, P.M. Brakefield, et al. 2022. Miocene climate and habitat change drove diversification in *Bicyclus*, Africa's largest radiation of Satyrine butterflies. Systematic Biology 71:570–588.

Akani, G.C., and L. Luiselli. 2001. Ecological studies on a population of the water snake *Grayia smythii* in a rainforest swamp of the Niger Delta, Nigeria. Contributions to Zoology 70:139–146.

Alter, S.E., B. Brown, and M.L.J. Stiassny. 2015. Molecular phylogenetics reveals convergent evolution in lower Congo River spiny eels. BMC Evolutionary Biology 15:224.

Alter, S.E., J. Munshi-South, and M.J.L. Stiassny. 2017. Genomewide SNP data reveal cryptic phylogeographic structure and microallopatric divergence in a rapids-adapted clade of cichlids from the Congo River. Molecular Ecology, 26:1401-1419.

Angel, F., J. Guibé, J. Lamotte, and R. Roy. 1954. La réserve naturelle intégrale du Mont Nimba. XXXII. Serpents. Mémoires de l'Institut Français d'Afrique Noire 40:381–402.

Archer, E., L.E. Dziba, K.J. Mulongoy, M.A. Maoela, M. Walters, R. Biggs, M.C.C. Salem, et al. 2021. Biodiversity and ecosystem services on the African continent–What is changing, and what are our options? Environmental Development 37:100558.

Arèvalo, E., S.K. Davis, and J.W. Sites Jr. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in Central Mexico. Systematic Biology 43:387–418.

Beolens, B., M. Watkins, and M. Grayson. 2012. *The Eponym Dictionary of Reptiles*. Johns Hopkins University Press, Baltimore, Maryland.

Bickford, D., D.J. Lohman, N.S. Sodhi, P.K.L. Ng, R. Meier, K. Winker, K.K. Ingram, and I. Das. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology & Evolution 22:148–155.

Biginagwa, F.J., B.S. Mayoma, Y. Shashoua, K. Syberg, and F.R. Khan. 2016. First evidence of microplastics in the African Great Lakes: Recovery from Lake Victoria Nile perch and Nile tilapia. Journal of Great Lakes Research 42:146–149.

Bocage, J.V.B. 1866a. Lista dos reptis das possessões portuguezas d'Africa occidental que existem no Museu de Lisboa. Jornal de Sciencias Mathematicas, Physicas e Naturaes 1:37–56.

Bocage, J.V.B. 1866b. Reptiles nouveaux ou peu connus recueillis dans les possessions portugaises de l'Afrique occidentale, que se trouvent au Muséum de Lisbonne. Jornal de Sciencias Mathematicas, Physicas e Naturaes, Lisboa 1:57–78.

Bocage, J.V.B. 1887. Melanges erpetologiques. I. Reptiles et Batraciens du Congo. II. Reptiles de Dahomey. III. Reptiles de l'Ile du Prince. IV. Reptiles et Batraciens de Quissange (Benguella) envoyés par M. J. d'Anchieta. Jornal de Sciencias Mathematicas, Physicas e Naturaes, Lisboa 11:177–211.

Bocage, J.V.B. 1895. *Herpétologie d'Angola et du Congo*. Ministério da Marinha e das Colónias, Lisbonne, XX + 203 pp., pls. I–XIX.

Boettger, O. 1889. Herpetologische Miscellen. [I Epirus, II Corfu, III Kamerun, IV Gross-Namaland, V Transvaal, VI. Pondoland, VII Madagascar, VIII Madras, IX Java, X Nias, XI Nordwest-Peru]. Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main 1889:267–316.

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

Böhme, W. 2000. Diversity of a snake community in a Guinean rain forest (Reptilia, Serpentes). In: Rheinwald, G. (Ed), *Isolated Vertebrate Communities in the Tropics*. Proceedings of the 4th International Symposium, Bonner Zoologische Monographien.

Böhme, M. 2003. The Miocene Climatic Optimum: Evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 195:389–401.

Bouckaert, R., T.G. Vaughan, J. Barido-Sottani, S. Duchêne, M. Fourment, A. Gavryushkina, J. Heled, et al. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. PLoS Computational Biology 15:e1006650.

Boulenger, G.A. 1901. Materiaux pour la faune du Congo: Batraciens et reptiles nouveaux. Annales du Musee du Congo (Zoologie), Bruxelles 2:7–14.

Boulenger, G.A. 1909. On the ophidian genus *Grayia*. Proceedings of the Zoological Society of London 79:944–952.

Boulenger, G.A. 1915. A list of the Snakes of the Belgian and Portuguese Congo, Northern Rhodesia and Angola. Proceedings of the Zoological Society of London 85:193–223.

Boundy, J. 2020. *Snakes of the World*: *A Supplement* (1st ed.). CRC Press, Boca Raton, Florida.

Branch, W.R. 2018. Snakes of Angola: An annotated checklist. Amphibian and Reptile Conservation 12:41-82.

Broadley, D.G. 1983. Records of two species of *Grayia* (Serpentes: Colubridae) from Zambia. Black Lechew (new series) 5:21–25.

Broadley, D.G. 1991. The herpetofauna of northern Mwinilunga District, northwestern Zambia. Arnoldia Zimbabwe 9:519–538.

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.

Butler, J.A., and J.C. Reid. 1986. Habitat preferences of snakes in the southern Cross River State, Nigeria. In: Roček, Z. (Ed.), *Studies in Herpetology*. Charles University, Prague.

Butler, J.A., and J.C. Reid. 1990. Records of snakes from Nigeria. Nigerian Field 55:19–40.

Burbrink, F., R. Lawson, and J. Slowinski. 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. Evolution 54:2107–2118.

Cadle, J.E. 1994. The colubrid radiation in Africa (Serpentes: Colubridae): Phylogenetic relationships and evolutionary patterns based on immunological data. Zoological Journal of the Linnean Society 110:103–140.

Cadle, J.E. 1996. Snakes of the genus *Liopholidophis* (Colubridae) from eastern Madagascar: New species, revisionary notes, and an estimate of phylogeny. Bulletin of the Museum of Comparative Zoology at Harvard College 154:369–464.

Cansdale, G.S. 1948. Field notes on some Gold Coast snakes. Nigerian Field 13:43–50.

Carlino, P., and O. Pauwels. 2015. An updated reptile list of Ivindo National Park, the herpetofaunal hotspot of Gabon. Bulletin of the Chicago Herpetological Society 50:25–39.

Chan, K.O., A.M. Alexander, L.L. Grismer, Y.-C. Su, J. L. Grismer, E. S. H. Quah, and R. M. Brown. 2017. Species delimitation with gene flow: A methodological comparison and population genomics approach to elucidate cryptic species boundaries in Malaysian Torrent Frogs. Molecular Ecology 26:5435–5450.

Chan, K.O., and L.L. Grismer. 2019. To split or not to split? Multilocus phylogeny and molecular species delimitation of southeast Asian toads (family: Bufonidae). BMC Evolutionary Biology 19:95.

Chippaux, J.P. 2001. *Les Serpents d'Afrique Occidentale et Centrale*. *2nd Edition*. IRD Éditions, Paris.

Chippaux, J.P. 2006. *Les serpents d'Afrique occidentale et centrale*. *3rd Edition*. IRD Éditions, Paris.

Chippaux, J.P., and K. Jackson. 2019. *Snakes of Central and Western Africa*. Johns Hopkins University Press, Baltimore, Maryland.

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*. Publications Scientifiques du MNHN, IRD Éditions, Paris.

Costello, M.J., R.M. May, and N.E. Stork. 2013. Can we name Earth's species before they go extinct? Science (Washington) 339:413–416.

Couvreur, T.L.P., G. Dauby, A. Blach-Overgaard, V. Deblauwe, S. Dessein, V. Droissart, O. J. Hardy, et al. 2021. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. Biological Reviews 96:16–51.

Cutler, J.S., J.A. Olivos, B. Sidlauskas, and I. Arismendi. 2020. Habitat loss due to dam development may affect the distribution of marine-associated fishes in Gabon, Africa. Ecosphere 11:e03024.

Deichmann, J.L., D.G. Mulcahy, H. Vanthomme, E. Tobi, A. H. Wynn, B. M. Zimkus, and R. W. McDiarmid. 2017. How many species and under what names? Using DNA barcoding and GenBank data for west Central African amphibian conservation. PLoS ONE 12:e0187283.

de Perre, F., H. Leirs, and E. Verheyen. 2019. Paleoclimate, ecoregion size, and degree of isolation explain regional biodiversity differences among terrestrial vertebrates within the Congo Basin. Belgian Journal of Zoology 149:23–42.

de Queiroz, K. 2007. Species concepts and species delimitation. Systematic Biology 56:879–886.

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

Doucet, J. 1963. Les serpents de la République de Côte d'Ivoire. Généralités et serpents non vemmeux. Acta Tropica 20:201–259.

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

Drummond A.J., M.A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution 29:1969–1973.

Drummond, A.J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7:214.

Edgar, R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32:1792–1797.

Edwards, S.v., L. Liu, and D.K. Pearl. 2007. High-resolution species trees without concatenation. Proceedings of the National Academy of Sciences of the United States of America 104:5936–5941.

Ernst, R., T. Lautenschläger, M.F. Branquima, and M. Hölting. 2020. At the edge of extinction: A first herpetological assessment of the proposed Serra do Pingano Rainforest National Park in Uíge Province, northern Angola. Zoosystematics and Evolution 96:237–262.

Ezard T., and T. Fujisawa. 2009. SPLITS: SPecies' LImits by Threshold Statistics. R package version 1.0–18/r45, https://CRAN.R-project.org/package=SPlit.

Feakins, S., and P. Demenocal. 2010. Global and African Regional Climate Change during the Neogene. In: Werdelin, L., and W.J Sanders, (Ed.), *Cenozoic Mammals of Africa*. University of California Press, Oakland, California.

Fišer, C., C.T. Robinson, and F. Malard. 2018. Cryptic species as a window into the paradigm shift of the species concept. Molecular Ecology 27:613–635.

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 11:1–31.

Frost, Darrel R. 2023. Amphibian Species of the World: An Online Reference. Version 6.1 (24 January 2023). Electronic Database accessible at https://amphibiansoftheworld.amnh.org/index.php. American Museum of Natural History, New York, USA.

Greenbaum, E., and J.L. Carr. 2005. The herpetofauna of Upper Niger National Park, Guinea, West Africa. Scientific Papers, Natural History Museum, The University of Kansas 37:1–21.

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

Greenbaum, E., K.E. Allen, E.R. Vaughan, O.S.G. Pauwels, V. Wallach, C. Kusamba, W.M. Muninga, et al. 2021. Night stalkers from above: A monograph of *Toxicodryas* tree snakes (Squamata: Colubridae) with descriptions of two new cryptic species from Central Africa. Zootaxa 4965:001–044

Gruschwitz, M., S. Lenz, and W. Bohme. 1991. Zur Kenntnis der Herpetofauna von Gambia (Westafrika) Teil 2: Schlangen (Reptilia, Serpentes) herpetofaunistische Bewertung. Herpetofauna 13:27–34.

Günther, A. 1858. *Catalogue of Colubrine Snakes in the Collection of the British Museum*. Trustees of the British Museum, London.

Günther, A. 1863. Third account of new species of snakes in the collection of the British Museum. Annals and Magazine of Natural History, London (Series 3) 12:348–365.

Günther, A. 1888. Contribution to the knowledge of snakes of tropical Africa. Annals and Magazine of Natural History, London (Series 6) 1:322–335.

Günther, A. 1895. Notice of reptiles and batrachians collected in the eastern half of tropical Africa. Annals and Magazine of Natural History, London (Series 6) 15:523–529

Hahn, M. W., and L. Nakhleh. 2016. Irrational exuberance for resolved species trees. Evolution 70:7–17.

Hallowell, E. 1844. Description of new species of reptiles from Africa. Academy of Natural Sciences of Philadelphia 2:118–120

Hallowell, E. 1854. Remarks on the geographical distribution of reptiles, with descriptions of several species supposed to be new, and corrections of former papers. Proceedings of the Academy of Natural Sciences of Philadelphia (1854–1844) 7:98–105.

Hallowell, E. 1857. Notice of a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences of Philadelphia, by Dr. Henry A. Ford. Proceedings of the Academy of Natural Sciences of Philadelphia (1857–1858) 9:48–72.

Head, J., K. Mahlow, and J. Müller. 2016. Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidea, Colubridae. Palaeontologia Electronica 19:1–21.

Heled, J., and A.J. Drummond. 2009. Bayesian Inference of Species Trees from Multilocus Data. Molecular Biology and Evolution 27:570–580.

Herbert, T., K. Lawrence, A. Tzanova, L. Peterson, R. Caballero-Gill, and C. Kelly. 2016. Late Miocene global cooling and the rise of modern ecosystems. Nature Geoscience 9:843–847

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

Jackson, N.D., B.C. Carstens, A.E. Morales, and B.C. O'Meara. 2017. Species delimitation with gene flow. Systematic Biology 66:799–812.

Jan, G. 1863. *Elenco Sistematico Degli Ofidi Descritti e Disegnati per L'Iconografia Generale*. A. Lombardi, Milano.

Kasongo Ilunga, M., E. Abwe, E. Decru, A. Chocha Manda, and E. Vreven. 2020. Description of a new small-sized *Synodontis* species (Siluriformes: Mochokidae) that is important for local subsistence fisheries in the middle Lufira (upper Congo River, DR Congo). Journal of Fish Biology 96:1142–1159.

Kelly, C.M.R., N.P. Barker, M.H. Villet, and D.G. Broadley. 2009. Phylogeny, biogeography and classification of the snake superfamily Elapoidea: A rapid radiation in the late Eocene. Cladistics 25:38–63.

Knoepffler, L.P. 1966. Faune du Gabon (amphibiens et reptiles). 1. Ophidiens de l'Ogooué-Ivindo et du Woleu N'tem. Biologia Gabonica 2:3–23.

Lacepède, B.G.E. 1789. *Histoire Naturelle des Quadrupèdes Ovipares et de Serpens*. *Volume 2*. lmprimerie du Roi, Hôtel de Thou, Paris.

Lanza, B., and S. Vanni. 1976. On a small collection of Reptiles from north Zaire: (pubblicazioni del centro di studio per la faunistica ed ecologia tropicali del c.n.r.: Cxiil). Monitore Zoologico Italiano Supplemento 8:129–160.

Largen, M.J., and S. Spawls. 2010. *The Amphibians and Reptiles of Ethiopia and Eritrea*. Edition Chimaira, Frankfurt-am-Main.

Laurent, R.F. 1950. Reptiles et batraciens de la region de Dundo (Angola du Nord-Est). Publicações culturais da Companhia de Diamantes de Angola 10:7–17

Laurent, R.F. 1956. 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, Série in–8°, 48:1–390, pls. I–XXXI.

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

Laurent, R.F. 1964. Reptiles et Amphibiens de l'Angola (Troisième contribution). Publicações Culturais de Companhia de Diamantes de Angola 67:1–165.

Lawson, R., J.B. Slowinski, B.I. Crother, and F.T. Burbrink. 2005. Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 37:581–601.

Leach, W.E. 1818. Appendix. No. IV. A general notice of the animals taken by Mr. John Cranch, during the expedition to explore the source of the river Zaire. In: Tuckey, J.K. (Ed.), *Narrative of an Expedition to explore the River Zaire, usually called The Congo, in South Africa, in 1816, under the Direction of Captain*

*J. K. Tuckey, R. N., to which is added the Journal of Professor Smith, some General Observations on the Country and its Inhabitants, and an Appendix, containing the Natural History of that Part of the Kingdom of Congo through which the Zaire flows.*John Murray, London.

Lee, M.S.Y., and A. Palci. 2015. Morphological Phylogenetics in the Genomic Age. Current Biology 25:R922–R929.

Lees, A.C., and S.L. Pimm. 2015. Species, extinct before we know them? Current Biology 25:R177–R180.

Loveridge, A. 1936. African reptiles and amphibians in Field Museum of Natural History. Field Museum of Natural History Publication, Zoological Series 22:1–111.

Loveridge, A. 1937. Zoological results of the George Vanderbilt African expedition of 1934. Part VII—Reptiles and amphibians. Proceedings of the Academy of Natural Sciences of Philadelphia 89:265–296.

Loveridge, A. 1955. On snakes collected in the Anglo-Egyptian Sudan by J.S. Owen, Esq. Sudan Notes and Records, Khartoum 36:37–56.

Loveridge, A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). Bulletin of the Museum of Comparative Zoology of Harvard University 117:153–362.

Luiselli, L., and G.C. Akani. 1999. Habitats of snakes in the rainforests of Eket (Akwa-Ibom State, south-eastern Nigeria) (Squamata: Serpentes). Herpetozoa 11:99–107.

Luiselli, L., and G.C. Akani. 2002. An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria. African Journal of Ecology 40:220–227.

Luiselli, L. 2006. Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource. Journal of Tropical Ecology 22:91–100.

Luiselli, L., G.C. Akani, F.M. Angelici, L. Ude, and S. M. Wariboko. 2005. Seasonal variation in habitat use in sympatric Afrotropical semi-aquatic snakes, *Grayia smythii* and *Afronatrix anoscopus* (Colubridae). Amphibia-Reptilia 26:372–376

Luo, A., C. Ling, S.Y.W. Ho, and C.D. Zhu. 2018. Comparison of methods for molecular species delimitation across a range of speciation scenarios. Systematic Biology 67:830–846.

Maddison, W.P., and D.R. Maddison. 2005. MacClade: An analysis of phylogeny and character evolution. Version 4.08. Available at: http://macclade.org/index.html.

Maddison, W.P., and D.R. Maddison. 2015. Mesquite: A modular system for evolutionary analysis. Version 3.70. Available at: https://www.mesquiteproject.org/.

Marcantonio, R., D. Javeline, S. Field, and A. Fuentes. 2021. Global distribution and coincidence of pollution, climate impacts, and health risk in the Anthropocene. PLoS ONE 16:e0254060.

Marques, M., L. Ceríaco, D. Blackburn, and A. Bauer. 2018. Diversity and distribution of the amphibian and terrestrial reptiles of Angola atlas of historical and bibliographic records (1840–2017). Proceedings of the California Academy of Sciences 64:1–501.

McCartney, J.A., S.N. Bouchard, J.A. Reinhardt, E.M. Roberts, P.M. O'Connor, C. Mtelela, and N.J. Stevens 2021. The oldest lamprophiid (Serpentes, Caenophidia) fossil from the late Oligocene Rukwa Rift Basin, Tanzania and the origins of African snake diversity. Geobios 66–67: 67–75.

Meirte, D. 1992. Clés de détermination des serpents d'Afrique. Muséum Royal d'Afrique Centrale, Tervuren Belgique Annual Series Octavo Science Zoologique 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.

Mertens, R. 1968. Zur Kenntnis der Herpetofauna von Kamerun und Fernando Poo. Bonner zoologische Beiträge 19:69–84.

Methner, K., M. Campani, J. Fiebig, N. Löffler, O. Kempf, and A. Mulch. 2020. Middle Miocene long-term continental temperature change in and out of pace with marine climate records. Scientific Reports 10:7989.

Minitab 17 Statistical Software. 2010. State College, PA: Minitab, Inc. (www.minitab.com)

Mocquard, M.F. 1887. Sur les ophidiens rapports da Congo par la Mission de Brazza. Bulletin de la Société Philomathique de Paris 7:62–93

Mocquard, M.F. 1897. Sur une collection de Reptiles recueillis par M. Haug, à Lambaréné. Bulletin de la Société Philomathique de Paris 9:5–20

Mocquard, M.F. 1891. Séance du 22 Novembre 1980. Bulletin de la Société Philomathique de Paris (1890–1891) (8)3: 8–9.

Nagy, Z.T., N. Vidal, M. Vences, W.R. Branch, O.S.G. Pauwels, M. Wink, and U. Joger. 2007. Molecular systematics of African Colubroidea (Squamata: Serpentes). In: Hube, B., Sinclair, B., and K.H Lampe, (Eds.), *African Biodiversity*. Springer Nature, London.

Noonan, B.P., and P.T. Chippindale. 2006. Dispersal and vicariance: The complex evolutionary history of boid snakes. Molecular Phylogenetics and Evolution 40:347–358.

O'Brien, C.L., M. Huber, E. Thomas, M. Pagani, J.R. Super, L.E. Elder, and P.M. Hull. 2020. The enigma of Oligocene climate and global surface temperature evolution. Proceedings of the National Academy of Sciences (USA) 117:25302–25309.

Ortiz-Sepulveda, C., B. Stelbrink, X. Vekemans, C. Albrecht, F. Riedel, J. Todd, and B. van Bocxlaer. 2020. Diversification dynamics of freshwater bivalves (Unionidae: Parreysiinae: *Coelaturini*) indicate historic hydrographic connections throughout the East African Rift System. Molecular Phylogenetics and Evolution 148:106816.

Packard, G.C., and T. 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: Molecular & Integrative Physiology 122:37–44.

Pauwels, O.S.G., D. Meirte, and F. Chérot. 1998. *Grayia caesar* (African Banded Water Snake). Sexual dimorphism. Herpetological Review 29:170.

Pauwels, O.S.G., and D. Meirte. 1996. Contribution to the knowledge of the Gambian herpetofauna. British Herpetological Society Bulletin 56:27-34

Pauwels, O.S.G., A. Toham, and C. Chimsunchart. 2002. Recherches sur l'herpétofaune des Monts de Cristal, Gabon. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie, 72:59–66.

Pauwels, O.S.G., A. Toham, and G. Lenglet. 2000. *Grayia ornata* (Bocage, 1866), Ornate Water Snake. Diet. African Herp News 31:9–10.

Pauwels, O.S.G., A. Toham, and V. Mamonekene. 2002. Ethnozoology of the Dibomina (Serpentes: Colubridae: *Grayia ornata*) in the Massif Du Chaillu, Gabon. Hamadryad 27:136–141.

Pauwels, O.S.G., and J. Vande Weghe. 2008. *Reptiles du Gabon*. Smithsonian Institution, Washington, DC, pp. 272.

Perret, J.L., and R. Mertens. 1957. Étude d'une collection herpétologique faite au Cameroun de 1952 à 1955. Bulletin de l'Institut Français d'Afrique Noire 19:593

Peters, W.C.H. 1877. Übersicht der Amphibien aus Chinchoxo (Westafrika), welche von der Africanischen Gesellschaft dem Berliner zoologischen Museum übergeben sind. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1877:611–620.

Pietersen D., L. Verburgt, and J. Davies. 2021. *Snakes and Other Reptiles of Zambia and Malawi*. Struik Nature, Cape Town, South Africa.

Plana, V. 2004. Plana V. Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 359:1585–1594.

Pook, C.E., U. Joger, N. Stümpel, and W. Wüster. 2009. When continents collide: Phylogeny, historical biogeography and systematics of the medically important viper genus *Echis* (Squamata: Serpentes: Viperidae). Molecular Phylogenetics and Evolution 53:792–807.

Portik, D.M., G.F.M Jongsma, M.T. Kouete, L.A. Scheinberg, B. Freiermuth, W.P. Tapondjou, and D.C. Blackburn. 2016. A survey of amphibians and reptiles in the foothills of Mount Kupe, Cameroon. Amphibian and Reptile Conservation 10:37–67.

Portillo, F., W.R. Branch, W. Conradie, M.-O. Rödel, J. Penner, M. Barej, C. Kusamba, et al. 2018. Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophiidae). Molecular Phylogenetics and Evolution 127:288–303.

Portillo, F., W.R. Branch, C.R. Tilbury, Z.T. Nagy, D.F. Hughes, C. Kusamba, W.M. Muninga, et al. 2019. A cryptic new species of *Polemon* (Squamata: Lamprophiidae, Aparallactinae) from the miombo woodlands of Central and East Africa. Copeia 107:22–35.

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.

Pyron, R.A., C.R. Hendry, V.M. Chou, E.M. Lemmon, A.R. Lemmon, and F.T. Burbrink. 2014. Effectiveness of phylogenomic data and coalescent species-tree methods for resolving difficult nodes in the phylogeny of advanced snakes (Serpentes: Caenophidia). Molecular Phylogenetics and Evolution 81:221–231.

Rambaut A., A.J. Drummond, D. Xie, G. Baele, and M.A. Suchard. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67:901–904.

Rannala B., Yang Z. 2020. Species Delimitation. In: Scornavacca C., Delsuc F., and N. Galtier (Eds.), *Phylogenetics in the Genomic Era*. No commercial publisher, authors open access book.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R–project.org/.

Roussel, M.-R., and A. Villiers. 1965. Serpentes du Mayo-Kebbi (Tchad). Bulletin de l'institut Français d'Afrique Noire A, Dakar 27:1522-1533.

Roux-Estève, R. 1965. Les serpents de la région de la Maboké-Boukoko. Cahiers de la Maboke 3:51–92.

Runge, J. 2008. The Congo River, Central Africa. In: Gupta, A. (Ed*.), Large Rivers: Geomorphology and Management*. John Wiley & Sons, New Jersey.

Sabaj, M.H. 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669.

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

Shapiro, S.S., and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

Slack, J.H. (Ed.). 1862. *Handbook to the Museum of the Academy of Natural Sciences of Philadelphia*. Academy of Natural Sciences, Philadelphia.

Sodhi, N., B. Brook, and C. Bradshaw. 2007. *Tropical Conservation Biology*. Wiley-Blackwell, Oxford, United Kingdom.

Spawls, S., K. Howell, H. Hinkel, and M. Menegon. 2018. *Field Guide to East African Reptiles*. Bloomsbury, London, New Delhi, New York, and Sydney.

Spawls, S. 2022. Book Review. *Snakes and Other Reptiles of Zambia and Malawi,* by D. Pietersen, L. Verburgt, and J. Davies. Herpetological Review 53:719-721.

Schwarzer, J., B. Misof, S.N. Ifuta, and U.K. Schliewen. 2011. Time and origin of cichlid colonization of the lower Congo rapids. PLoS one 6:e22380.

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.

Stanley, H.M. 1988. *Through the Dark Continent*. In Two Volumes. Dover Publications, Mineola, New York. (Original work published 1878).

Steenberge, M., M. Vanhove, A. Manda, M. Larmuseau, B. Swart, F. Khang'mate, A. Arndt, et al. 2020. Unravelling the evolution of Africa's drainage basins through a widespread freshwater fish, the African sharptooth catfish *Clarias gariepinus*. Journal of Biogeography 47:1739-1754.

Sternfeld, R. 1910. Neue Schlangen aus Kamerun, Abessynien und Deutsch-Ostafrika. Mitteilungen aus dem Zoologischen Museum in Berlin 5:67–70

Stucki-Stirn, M.C. 1979. *A Comparative Study of the Herpetological Fauna of the former West Comeroon [sic]/Africa: With a Classification and Synopsis of 95 Different Snakes and Description of Some New Sub-species. Snake Report 721*. Herpeto-Verlag, Teuffenthal, Switzerland.

Sukumaran, J., and L.L. Knowles. 2017. Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Sciences of the United States of America 114:1607–1612.

Tamura K., Stecher G., Peterson D., Filipski A., and S. Kumar. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30:2725-9.

Tolley, K., G. Alexander, W. Branch, P. Bowles, and B. Maritz. 2016. Conservation status and threats for African reptiles. Biological Conservation 204:63–71.

Tuckey, J.K. 2006. *Narrative of an Expedition to Explore the River Zaire, Usually Called the Congo, in South Africa.* Rediscovery Books, East Sussex, United Kingdom.

Trape, J.-F. 1985. Les serpents de la région de Dimonika (Mayombe, République Populaire du Congo). Revue de Zoologie Africaine, Tervuren 99:135–140.

Trape, J.-F., and R. Roux-Estève 1995. Les serpents du Congo: Liste commentée et clé de détermination. Journal of African Zoology 109:31–50.

Vidal, N., and S.B. Hedges. 2002. Higher-level relationships of caenophidian snakes inferred from four nuclear and mitochondrial genes. Comptes Rendus Biologies 325:987–995.

Vidal, N., A.S. Delmas, and S.B. Hedges. 2007. The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes. In: Henderson, R. W., and R. Powell (Eds.), *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, Utah.

Villiers, A. 1951a. Mission A. Villiers au Togo et au Dahorney (1950). II–Ophidiens. Etudes Dahomeennes 5:17–43.

Villiers, A. 1951b. La collection de serpents de I'I.F.A.N. Bullietin de l'institute Français d'Afrique Noire 13:813–837.

Villiers, A. 1966. Contribution a la faune du Congo (Brazzaville), Mission A. Villiers et a. Descarpentries. XLII. Reptiles, Ophidiens. Bulletin de l'institut fonamental d'Afrique Noire. Serie A, Sciences naturelles. 28:1720–1760.

Villiers, A. 1975 *Les Serpents de I'Ouest Africain*. Institut Français d'Afrique Noire, Darkar, Senegal.

Voet, I., C. Denys, M. Colyn, A. Lalis, A. Konečný, A. Delapré, V. Nicolas, and R. Cornette. 2022. Incongruences between morphology and molecular phylogeny provide an insight into the diversification of the *Crocidura poensis* species complex. Scientific Reports 12:10531.

Wallach, V., K. Williams, and J. Boundy. 2014. *Snakes of the World: A Catalogue of Living and Extinct Species*. CRC Press, Boca Raton, Florida.

Werner, F. 1923. Neue Schlangen des Naturhistorischen Museums in Wien. Annalen Des Naturhistorischen Museums in Wien 36:160–166.

Wilcoxon, F. 1945. Individual comparisons by ranking methods. Biometrics Bulletin 1:80–83.

Zaher, H., F.G. Grazziotin, J.E. Cadle, R.W. Murphy, J.C. de Moura-Leite, and S.L. Bonatto. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American xenodontines: A revised classification and descriptions of new taxa. Papeis Avulsos de Zoologia 49:115–153.

Zaher, H., R.W. Murphy, J.C. Arredondo, R. Graboski, P.R. Machado-Filho, K. Mahlow, G.G. Montingelli, et al. 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). PLoS one 14:e0216148.

Zassi-Boulou, A.-G., J. Tchimbakala, M. Lise, and K. Jackson. 2020. A survey of snakes in the Patte d'Oie Forest Reserve (Brazzaville, Republic of Congo): An urban snake community in Central Africa. Herpetological Conservation and Biology 15:139–149.

Zassi-Boulou, A.-G., B. Zimkus, J. Goma-Tchimbakala, S. Boudzoumou, A. Mboungou-Louiki, and K. Jackson. 2019. Herpetological survey of the proposed Bambama-Zanaga mine site, Department of Lékoumou, Republic of Congo. Herpetological Conservation and Biology 14:470–480.

Curriculum Vita

I received my B.S. in Ecology and Evolutionary Biology with a minor in Art in the fall of 2019 from Stephen F. Austin State University with a GPA 3.96 overall, graduating Summa cum laude with honors. I will graduate in spring 2023 from the University of Texas El Paso (UTEP) with a M.S. in Biological sciences, and an overall GPA of 4.0.

Throughout my M.S. degree, I have presented my thesis research at two academic conferences. First, I presented a poster titled "Phylogenetics and Integrative Taxonomy of African Water Snakes (Squamata: Colubridae: *Grayia*)" at the 2021 Joint Meeting of Ichthyologists and Herpetologists in Phoenix; AZ. I also completed an oral presentation with the same title at the 2022 Herpetological Association of Africa (HAA) virtual mini symposium.

During my two and a half years at UTEP, I received three grants: the UTEP Dodson Research Grant for a total of $3,000 (Fall 2021), the Herpetologists League, E.E. Williams Research Grant for $500 (Summer 2022), and the Society for the Study of Amphibians and Reptiles Roger Conant Grant for $500 (Fall 2022). I also participated in an NSF funded Aspire Fellowship that focused on mentoring and professional development in preparation for teaching at two-year collages.

My work experience includes four years of teaching as a supplemental instructor at Stephen F. Austin State University where I received master tutor accreditation from the College Reading and Learning Association. I have also taught multiple courses during my time at UTEP including Human Anatomy and Physiology (BIOL 2111), Genetics (BIOL 3320), Microorganisms and Disease (BIOL 2330), and Organismal Biology (BIOL 1108).