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An assemblage of giant aquatic snakes (Serpentes, Palaeophiidae) from the Eocene of Togo

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Abstract

We here describe a monospecific assemblage of giant aquatic snakes from the middle Eocene of Kpogamé, Togo. The material, consisting of large isolated vertebrae, is referred to *Palaeophis africanus*, an enigmatic palaeophiid species, which was so far otherwise known only from a limited number of vertebrae from the middle Eocene of Nigeria and Angola. Material from the late Eocene of the eastern USA that had been referred to the same species, is here instead considered too fragmentary for species-level determination and *Palaeophis africanus* is thus so far restricted to Africa. With the aid of micro-CT scanning, we present 3D models of 17 vertebrae, pertaining to different portions of the vertebral column. We provide detailed comparisons of the new material with all named African species of the genus *Palaeophis*. A tentative diagnosis of *Palaeophis africanus* is provided. With more than 50 vertebrae, the new Togolese specimens represent the most abundant known material attributed to *Palaeophis africanus* and significantly enhance our knowledge of the vertebral anatomy and intracolumnar variation for this taxon. Furthermore, this adds to the, as yet, extremely scarce fossil record of squamates from central western Africa, a region where Paleogene herpetofaunas are only rather poorly known.

Keywords: *Palaeophis*, Serpentes, Eocene, Africa, Vertebral anatomy, Taxonomy

Introduction

Palaeophiids (Palaeophiidae) comprise an enigmatic lineage of snakes, which achieved a wide geographic distribution during the Paleogene, spanning across large portions of Europe, Asia, Africa, North and South America (Smith & Georgalis, in press). Among palaeophiids rank some of the largest known snakes of all time, with certain taxa reaching truly gigantic sizes (McCartney et al., 2018; Rage, 1983a, 1983b). Palaeophiids were all aquatic (or at least semi-aquatic) and inhabited a range of freshwater, estuarine, shallow marine coastal, and even open marine environments (Georgalis et al., 2020; Hoffstetter, 1958; Hutchison, 1985; Rage et al., 2003; Rage, 1983a, 1983b). Two palaeophiid genera are recognized with certainty, i.e., *Palaeophis* Owen, 1841, and *Pterosphenus* Lucas, 1898. A third genus, *Archaeophis* Massalongo, 1859, has been occasionally referred to this family, but this assignment should only be considered as tentative (Georgalis et al., 2020; Smith & Georgalis, in press). Both *Palaeophis* and *Pterosphenus* are known exclusively by vertebrae and ribs. The total absence of cranial elements significantly hinders a more precise understanding of their phylogenetic relationships (Georgalis et al., 2020; Smith & Georgalis, in press). As such, their affinities with other snake groups remain largely unknown and unsettled. They were originally and for a long time considered to bear affinities with boas and/or pythons (Rage, 1983a;

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Rochebrune, 1880), while other hypotheses placed them in their own distinct group, Cholophidia, together with a number of Cretaceous hind-limbed forms (Hoffstetter, 1939; Nopcsa, 1923a, 1923b), or even thought to be related to extant acrochordids (Wallach et al., 2014; Zvonok & Snetkov, 2012). Nevertheless, there is currently a relative consensus that palaeophiids are not related to the group encompassing boas and pythons (i.e., the Constrictores sensu Georgalis & Smith, 2020), but probably lie more basally within Alethinophidia (Georgalis et al., 2020; Head et al., 2005; McCartney & Seiffert, 2016; Rage & Werner, 1999; Smith & Georgalis, in press).

In Africa, palaeophiids have been known since the very beginning of the twentieth century (Andrews, 1901, 1906; Janensch, 1906). However, despite these early discoveries, only a few subsequent descriptions followed during the next decades, all of them originating from a small number of Paleogene localities of this continent (Andrews, 1924; Antunes, 1964; Arambourg, 1952; Folie et al., 2021; Hoffstetter, 1960, 1961; Houssaye et al., 2013, 2019; McCartney & Seiffert, 2016; McCartney et al., 2018; Rage, 1983b; Zouhri et al., 2018, 2021). Sudanese and Moroccan Cretaceous remains have been referred (or at least tentatively referred) to palaeophiids, extending the stratigraphic distribution of the group back to the Mesozoic (Rage & Werner, 1999; Rage & Wouters, 1979). Four different palaeophiid species have been established from African deposits: *Palaeophis maghrebianus* Arambourg, 1952, from the early Eocene of Morocco (Arambourg, 1952; Houssaye et al., 2013), *Palaeophis colossaeus* Rage, 1983b, from the early–middle Eocene of Mali (Houssaye et al., 2019; McCartney et al., 2018; O'Leary et al., 2019; Rage, 1983b), *Palaeophis africanus* Andrews, 1924, from the middle Eocene of Nigeria and Angola (Andrews, 1924; Folie et al., 2021), and *Pterosphenus schweinfurthi* (Andrews, 1901) from the middle–late Eocene of Egypt and Libya (Andrews, 1901, 1906; Hoffstetter, 1961; Janensch, 1906; McCartney & Seiffert, 2016).

We here describe several vertebrae from the middle Eocene (Lutetian) of Togo, an area which so far lacked Eocene snake fossil remains. The new Togolese specimens are referred to *Palaeophis africanus*. With the application of micro-CT scanning, 3D models of 17 vertebrae, pertaining to different portions of the vertebral column, are provided, as well as comparisons to all other African species of *Palaeophis* are performed. The new Togolese snake assemblage represents the most abundant material known so far for *Palaeophis africanus*, thus allowing a better knowledge of the anatomy and intraspecific variability of this taxon and of African palaeophiids as a whole.

Institutional abbreviations

HNHM: Hungarian Natural History Museum, Budapest, Hungary; MDHC: Massimo Delfino Herpetological Collection, Università di Torino, Italy; MGP-PD, Museo di Geologia e Paleontologia dell'Università di Padova, Padova, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; PIMUZ, Palaeontological Institute and Museum of the University of Zurich, Zurich, Switzerland; UM, Université de Montpellier, Montpellier, France; ZPW, University of Wrocław, Wrocław, Poland; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland.

Geological settings

The Togolese phosphate deposits extend from Aveta in the southwest to Dagbati in the northwest (Colonna-Cimera, 1961; Johnson, 1987; Slansky, 1962; Visse, 1957) (Fig. 1). They are now exploited by the *Société Nouvelle des Phosphates du Togo* (SNPT) in two quarries at Kpogamé (SW) and Dagbati (NE). Early palaeontological and sedimentological studies were carried out in the northeastern part of the Kpogamé quarry (Cappetta & Traverse, 1988; Johnson, 1987; Johnson et al., 2000). Stratigraphically, the phosphate complex overlies a lower Eocene palygorskite-rich claystone (Johnson, 1987), which constitutes the upper unit of the Tabligbo Group. The phosphate complex comprises three informal lithostratigraphic units, from the base to the top (Johnson, 1987; Slansky, 1962): the phosphatic marl (15–20 m thick), the phospharenite layer (2–8 m thick), and the phosphatic clay (0.5 to 10 m thick). The phospharenite layer is continuous laterally with calcareous phosphate in the southeast of the basin. In the 1980s, when the specimens described here were collected, the phospharenite layer included a condensed horizon in the transitional zone between the calcareous phosphate formation and phospharenite that was referred to the '*Bone Bed du Mur*' (BBM) by Cappetta and Traverse (1988) and Gingerich and Cappetta (2014). This horizon yielded numerous fragments of internal casts of gastropods, bivalves, and nautilid fragments (Johnson, 1987; Slansky, 1962), along with a rich vertebrate fauna, including chondrichthyans and bony fishes (Cappetta & Traverse, 1988), pseudo-toothed birds (Bourdon & Cappetta, 2012), early cetaceans, sirenians, and indeterminate terrestrial mammals (Gingerich & Cappetta, 2014; Kassegne et al., 2021). Another condensed horizon resting on the carbonatized and phosphatized bed, referred to as the '*Bone Bed*

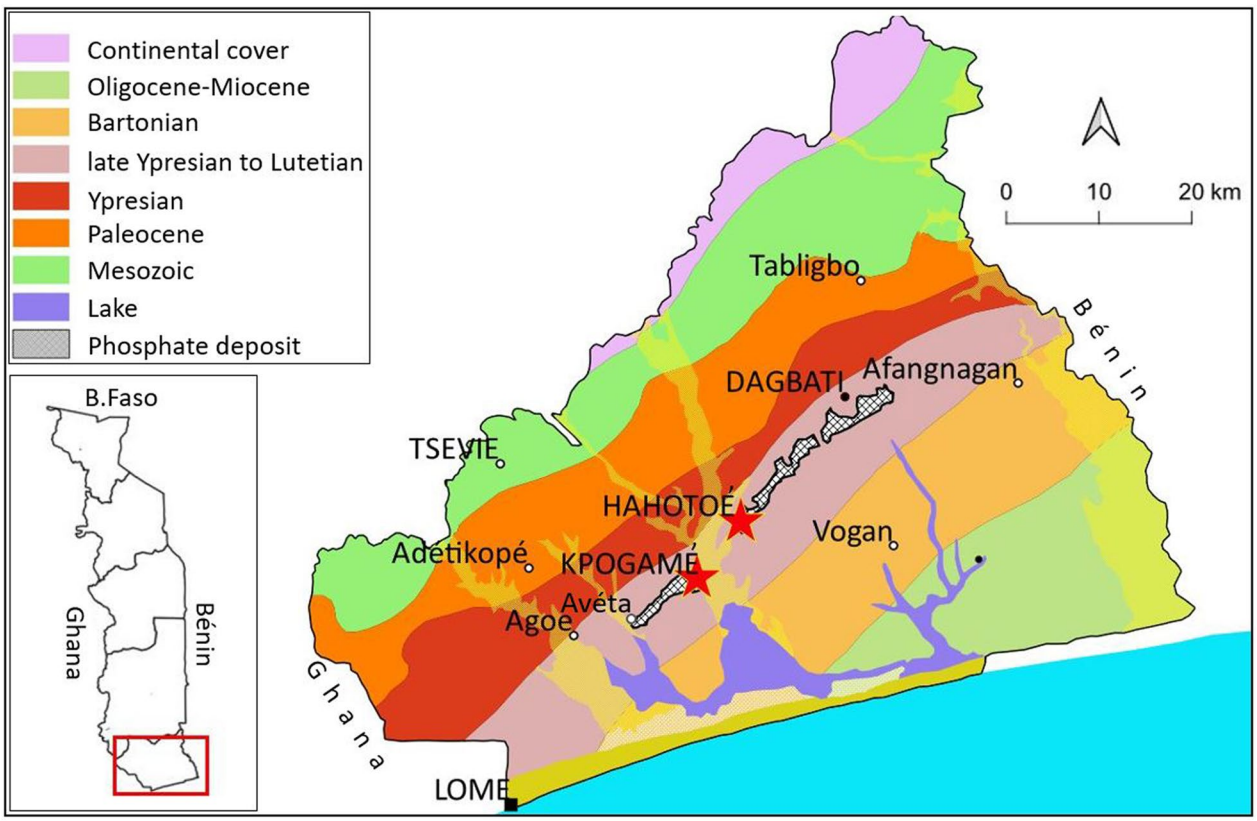


Fig. 1 Geological map of Togo indicating the fossil quarry of Kpogamé

reposant sur la couche carbonatée' (BBR), also yielded similar invertebrate and vertebrate faunas (Cappetta & Traverse, 1988; Gingerich & Cappetta, 2014). Based on planktonic foraminifera, Cappetta and Traverse (1988) proposed to assign the phospharenite to the planktonic foraminiferal zone P11 (middle Lutetian, ca. 47–44 Ma: Berggren & Pearson, 2005; 46–43 Ma. Johnson (1987) , Johnson et al. (2000), and Vandenberghe et al. (2012) used bioclasts and mineralogy to characterize the depositional environment of the phosphates of Kpogamé, and proposed a shallow marine environment of average salinity with moderate deposition energy. These phosphate deposits also include a substantial amount of continental minerals such as kaolinite and quartz, traces of plants marked by the presence of pollens (Johnson et al., 2000), as well as some remains of terrestrial mammals (Gingerich & Cappetta, 2014), which clearly indicate the close proximity of the coast.

Material and methods

Palaeophiid remains described here were surface-collected as isolated specimens from the BBM horizon in the 1980s by Michel Traverse, former mining engineer at Kpogamé-Hahotoé, during several field campaigns at the north-eastern part of the Kpogamé quarry. Additional specimens were collected by one of us (HC) during fieldwork in 1985. The snake material pertains to different individuals, of various ontogenetic stages. All the Togolese specimens described here are housed in the collections of the University of Montpellier, France (specimen numbers preceded by KPO).

3D reconstructions

The vertebrae were imaged using high-resolution microtomography (µCT) at the MRI platform of the *Institut des Sciences de l'Evolution de Montpellier* (ISEM). Image segmentation of the vertebral elements was performed on the µCT images with Avizo.Lite 2019.4 (Visualization Sciences Group) software. The 3D virtual restoration was performed with MorphoDig software (v. 1.5.3; Lebrun 2018) and the virtually restored 3D models are deposited in MorphoMuseuM (Georgalis et al., 2021).

Comparisons

For comparative purposes, fossil specimens of palaeophiids (including multiple type specimens) were studied in the collections of MGP-PD, MNHN, NHMUK, NHMW, PIMUZ, and ZPW. Skeletal material of extant snakes

was also studied at HNHM, MDHC, MNCN, MNHN, NHMW, ZPW, and ZZSiD.

Anatomical terminology

Terminology of the vertebral anatomy of palaeophiid snakes follows Rage (1983a), Rage et al. (2003), McCartney et al., (2018), and Georgalis et al. (2020).

Systematic palaeontology

Squamata Oppel, 1811

Serpentes Linnaeus, 1758

Palaeophiidae Lydekker, 1888

Genus *Palaeophis* Owen, 1841

Species *Palaeophis africanus* Andrews, 1924

Figures 2, 3, 4, 5, 6, 7, 8, 9

Material: 51 isolated trunk vertebrae (UM KPO 21–UM KPO 71).

Description: All vertebrae are large and robust (Figs. 2, 3, 4, 5, 6, 7, 8, 9). They vary in size, with centrum lengths ranging between 19 and 31.5 mm (see Appendix 1). The majority of the available vertebrae pertain to the anterior or anterior mid-trunk portion of the column (Figs. 2, 3, 4, 5, 6, 7), while few of them can be identified as mid-trunk vertebrae (Figs. 8, 9). There are no posterior trunk vertebrae in our sample. All vertebrae are relatively laterally compressed, with this compression being more prominent in anterior trunk vertebrae.

The neural spine commences almost immediately posterior to the level of the zygosphene, but its anterior edge is still separated from the anterior border of the zygosphene. The height of the neural spine cannot be assessed as it is broken in all specimens. The neural spine is getting thicker in dorsal view towards its posterior portion (i.e., triangular neural spine in cross section). Such thickness in the posterior portion of the neural spine is more pronounced in some specimens (e.g., UM KPO 27). Neural spine foramina are present, with their shape, size, and number not being consistent among the different vertebrae. The neural arch is vaulted. The posterior median notch of the neural arch is not preserved in most specimens—only in UM KPO 35 (and to a lesser degree in UM KPO 26 [Fig. 6c]) it is preserved, being rather deep. Most pterapophyses are damaged; when preserved, they are moderately prominent but they do not extend much dorsally [e.g., UM KPO 26 (Figs. 6a–b, 7b)].

The zygosphene is massive and thick in anterior view. It is usually almost triangular, but its thickness varies. Its dorsal level is usually slightly to moderately convex, with its median portion being elevated dorsally. In some specimens, this dorsal elevation is rather prominent, forming a distinct triangle (e.g., UM KPO 32 [Fig. 4m]). In most cases, the zygosphene is wider than the cotyle, but it can be narrower in some specimens (UM KPO 35). Interestingly, all specimens display a distinctly large and deep pit or fossa at the mid-level surface of the zygosphene in anterior view, which becomes rather deep in certain specimens (e.g., UM KPO 21 [Fig. 9e], UM KPO 23 [Fig. 5f], UM KPO 27 [Fig. 7i–j], UM KPO 31, UM KPO 32 [Fig. 4m], UM KPO 35). This feature is also present in the smallest specimens (e.g., UM KPO 34). In dorsal view, the zygosphene is concave, with two prominent lateral lobes and no median one (e.g., UM KPO 22 [Fig. 2c]; UM KPO 33 [Fig. 3c]). In some specimens, this concavity of the zygosphene in dorsal view is so prominent that it takes the shape of a high-angled V (e.g., UM KPO 22 [Fig. 2c]). Parazygosphenal foramina are absent.

When preserved, the zygantrum is wide and tall. Its walls are relatively thick (e.g., UM KPO 26 [Figs. 6b, 7b], UM KPO 28 [Fig. 7f]), although this thickness significantly decreases in small specimens (e.g., UM KPO 34 [Figs. 4p, 5a]). Intrazygantral foramina are present and can be prominent (e.g., UM KPO 28 [Fig. 5b]). One intrazygantral foramen is usually present right at the centre of the zygantrum, along with two prominent foramina on each zygantral facet (e.g., UM KPO 30 [Fig. 8b]). However, in some specimens this medial foramen is absent (UM KPO 37), while in some others, there is only a single medial foramen in the zygantrum, i.e., there are no foramina inside each zygantral facet (e.g., UM KPO 26 [Figs. 6b, 7b]).

The prezygapophyses extend anterolaterally in dorsal view and anterodorsally in lateral view, and dorsolaterally in anterior view. The prezygapophyseal articular facets are small. There are no prezygapophyseal accessory processes. A prezygapophyseal buttress runs longitudinally from the level of the prezygapophysis and ventrally up to the paradiapophysis, being rather pronounced in certain specimens (e.g., UM KPO 28) including some of the smallest specimens (e.g., UM KPO 34). Postzygapophyses are damaged in most specimens. When preserved, they are always small (e.g., UM KPO 30 [Fig. 8c–d], UM KPO 31). The postzygapophyseal articular facets are small and oval-shaped (e.g., UM KPO 30 [Fig. 8d], UM KPO 31). The interzygapophyseal constriction is rather shallow and becomes almost straight in anterior trunk vertebrae (e.g., UM KPO 22 [Fig. 2c]). The interzygapophyseal ridges are distinct. Most specimens possess a scar-like structure below the level of the interzygapophyseal ridge, which is probably for muscle attachment (e.g., UM KPO 25 [Fig. 4k], UM KPO 30 [Fig. 8e–f]).

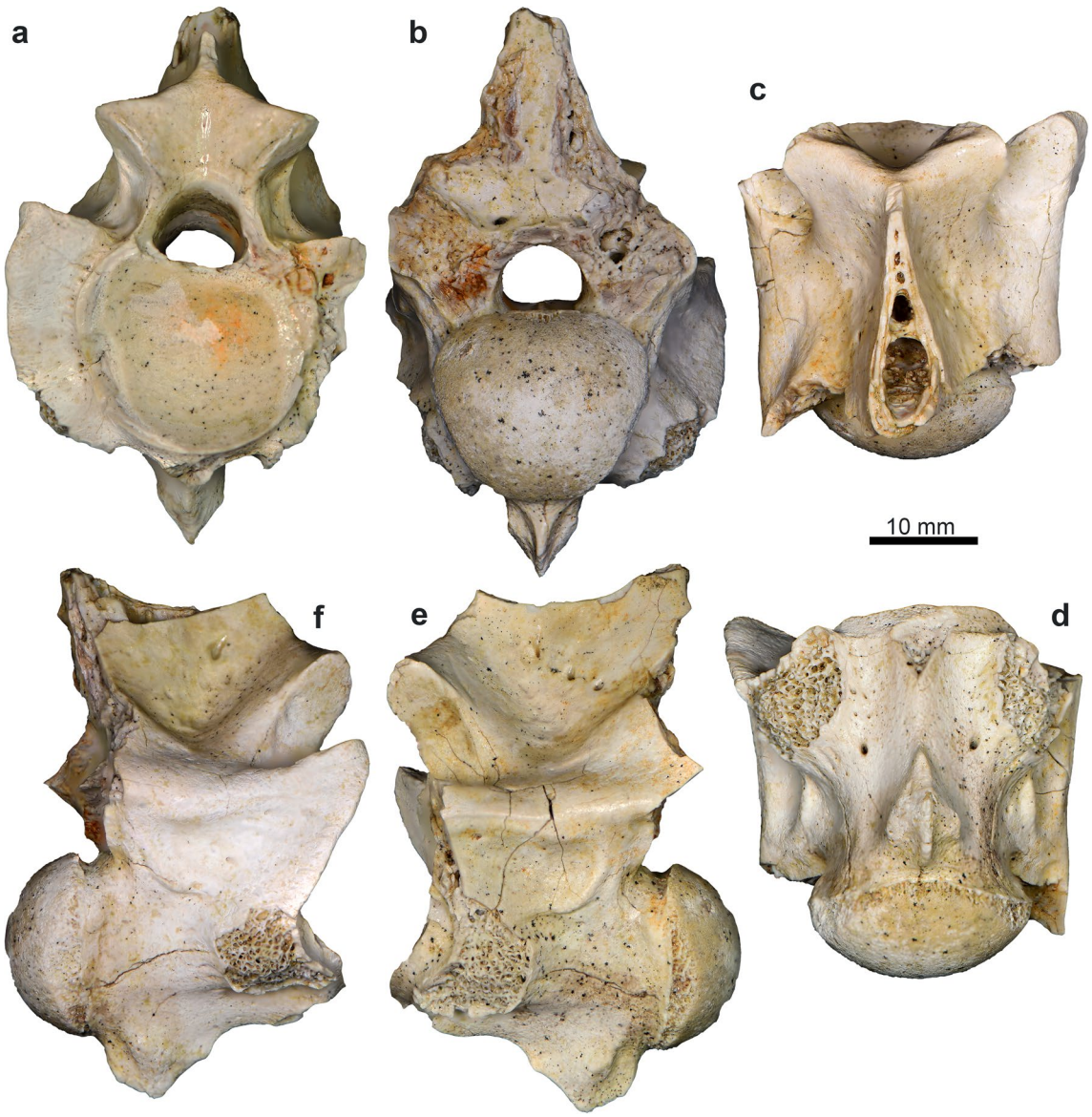


Fig. 2 Anterior trunk vertebra UM KPO 22 in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views. Note that the anterior hypapophysis is broken in these photographs, a damage that occurred after the micro-CT scanning of this specimen, where that structure was complete (see Fig. 4a–d)

The neural canal is usually relatively small, much smaller than the cotyle and condyle, possessing an overall semicircular shape. A distinct ridge is present in some specimens, running throughout a portion of the mid-level of its ventral surface (UM KPO 26 [Figs. 6b, 7a–b], UM KPO 27). Lateral foramina are prominent in some specimens, and multiple of them can be present on each lateral side of the vertebra (e.g., UM KPO 26 [Fig. 7d]; UM KPO 27 [Fig. 7k]).

Cotyle and condyle are situated at an almost horizontal axis. The cotyle displays distinct thick lips and is large, deep, and circular to elliptical in shape. Paracotylar fossae are deep. Paracotylar foramina are present. One paracotylar foramen is visible next to the cotyle in most specimens—it is not possible to tell if these foramina are consistently present on both sides of the cotyle, as the respective areas are usually not fully complete on both sides in most specimens. In some specimens, the paracotylar foramina can be doubled on one side (e.g., UM KPO 21 [Fig. 9e]), or even doubled on both sides of the cotyle (e.g., UM KPO 27 [Fig. 7i–j]). The condyle is large,

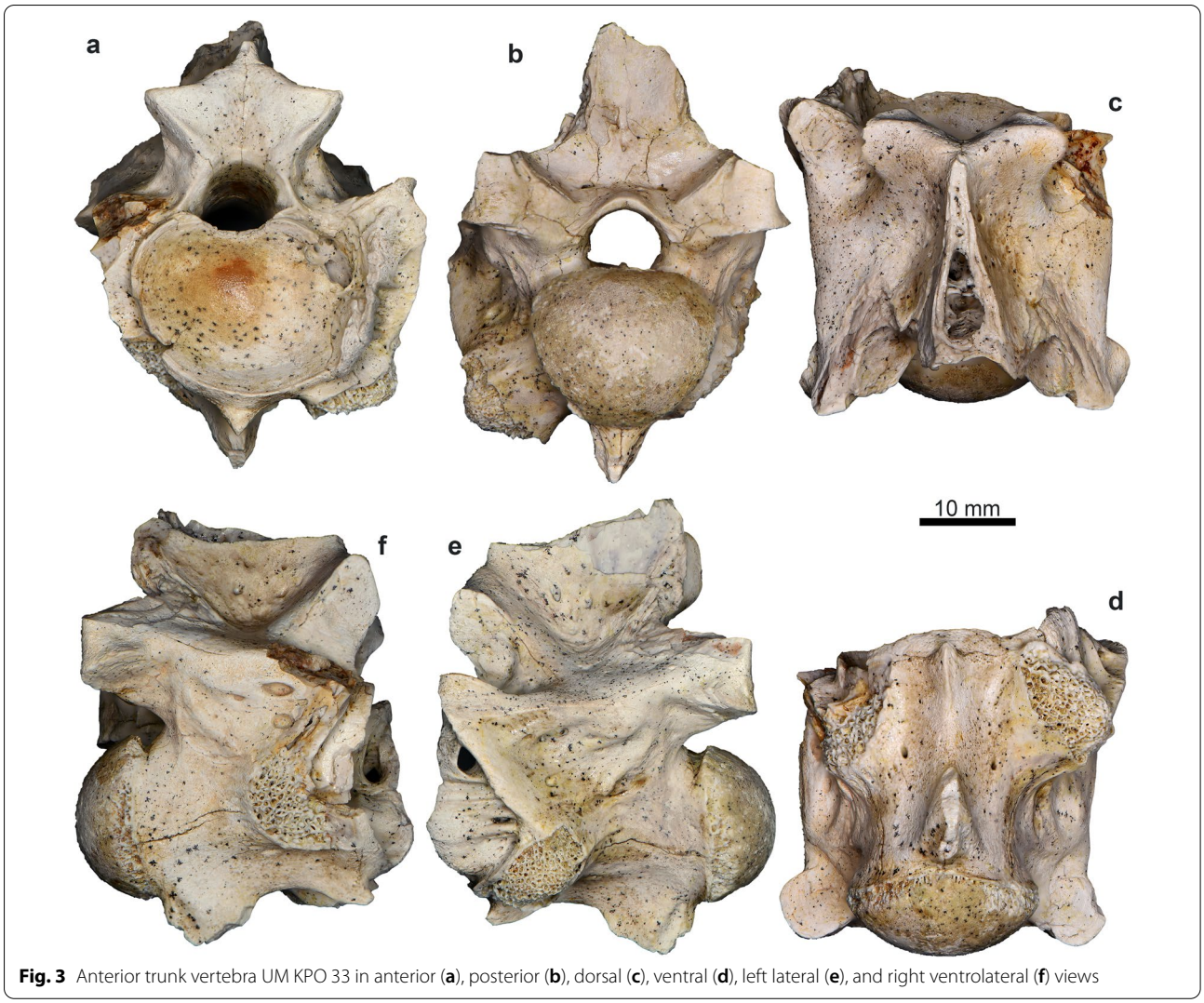


Fig. 3 Anterior trunk vertebra UM KPO 33 in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right ventrolateral (**f**) views

sometimes massive (e.g., UM KPO 22 [Fig. 2b]; UM KPO 25 [Fig. 4j]; UM KPO 27).

A single large hypapophysis is present in all mid-trunk vertebrae. Instead, in all anterior trunk vertebrae (which form the majority of the available specimens) there are two hypapophyses (e.g., UM KPO 22 [Figs. 2, 4a–d]). The anterior hypapophysis is more prominent in more anterior vertebrae, while it is incipient across the transition between anterior and mid-trunk vertebrae (e.g., UM KPO 26 [Fig. 6]). The shape and full size of the anterior hypapophysis can rarely be evaluated, as it is partially or almost completely damaged in most cases. When preserved, it faces anteroventrally, either more ventrally than anteriorly (e.g., UM KPO 22 [Fig. 4a, c–d]) or either more anteriorly than ventrally (e.g., UM KPO 26 [Figs. 6, 7c–d], UM KPO 33 [Fig. 3, 4e–f, h), being nevertheless always smaller than the posterior hypapophysis. The shape and size of the posterior hypapophysis are variable. When preserved, the posterior hypapophysis can be much ventrally projecting (e.g., UM KPO 23 [Fig. 5j–k], UM KPO 28 [Figs. 5d–e, 7h], UM KPO 31, UM KPO 36); this element can be considerably thick ventrally (e.g., UM KPO 35 [Fig. 7l–m). In specimens showing a robust posterior hypapophysis, a distinct ridge runs throughout its midline, which is clearly visible in ventral, anterior, and posterior views (e.g., UM KPO 31, UM KPO 37 [Fig. 4q]). In some anterior trunk vertebrae, the two hypapophyses are connected by a ridge (e.g., UM KPO 22 [Fig. 4b]); however, this ridge diminishes in height in the transition between anterior mid- and mid-trunk vertebrae, but is still relatively thick and rounded (e.g., UM KPO 24 [Fig. 9l], UM KPO 35 [Fig. 7l]). Subcentral foramina are prominent. Paradiapophyses are damaged or at least highly eroded in almost all specimens. In fact, the left paradiapophysis is only preserved in UM KPO 34 and faces ventrally (Fig. 5a)—it seems that it does not reach

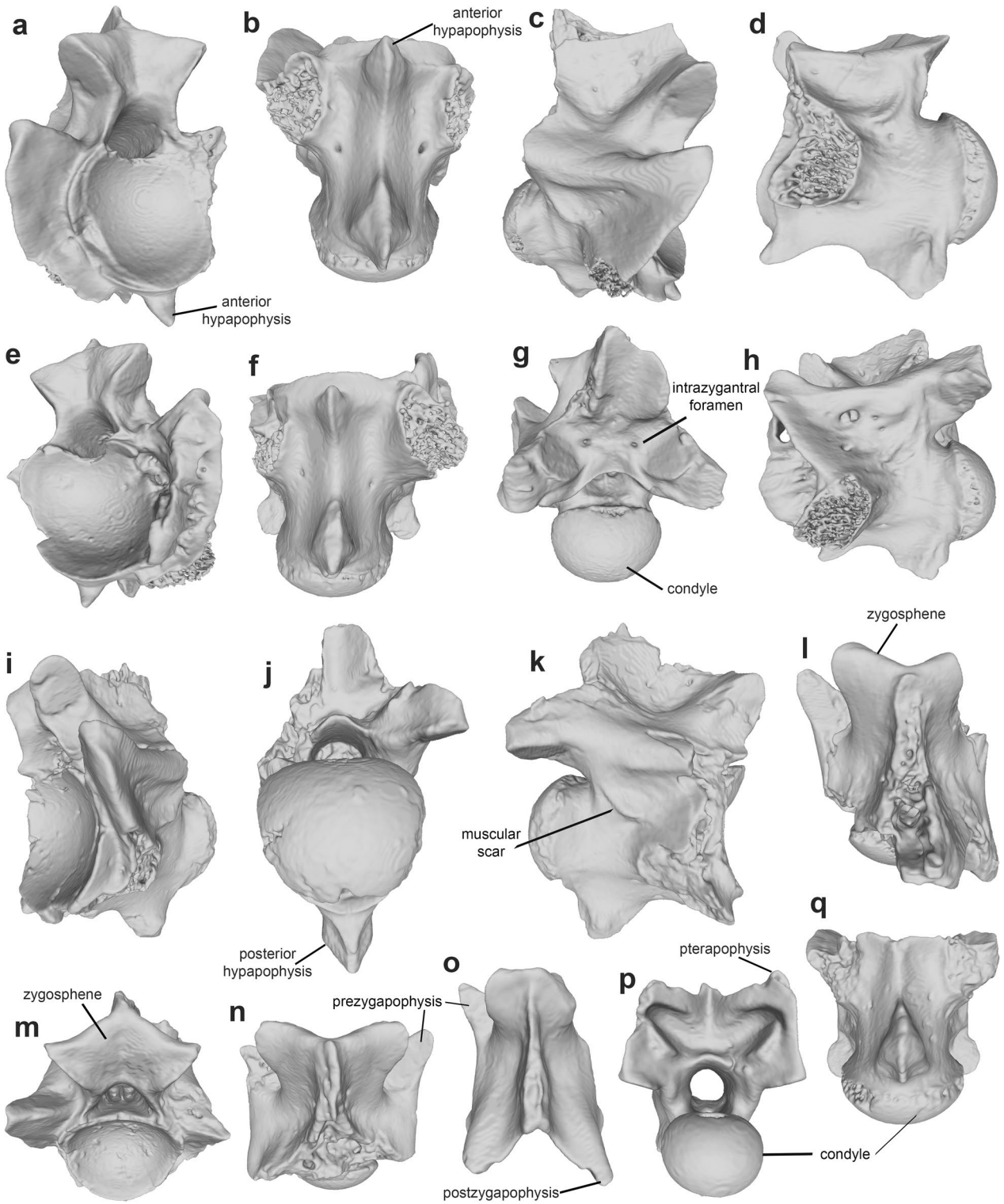


Fig. 4 3D models of anterior and anterior mid-trunk vertebrae: **a–d** UM KPO 22 in right anterolateral (**a**), ventral (**b**), right lateral (**c**), and left ventrolateral (**d**) views; **e–h** UM KPO 33 in left anterolateral (**e**), ventral (**f**), posterodorsal (**g**), and left lateral (**h**) views; (**i–l**) UM KPO 25 in left anterolateral (**i**), posterior (**j**), right lateral (**k**), and dorsal (**l**) views; **m–n** UM KPO 32 in anterodorsal (**m**) and dorsal (**n**) views; (**o–p**) UM KPO 34 in dorsal (**o**) and posterior (**p**) views; (**q**) UM KPO 37 in ventral view. Specimens not to the same scale

the same ventral extent as the posterior hypapophysis, but the full extent of that hypapophysis cannot be estimated with full certainty.

Remarks: The vertebrae described here can be assigned to Palaeophiidae on the basis of their robustness, tallness, and lateral compression, the presence of pterapophyses, the horizontality of the cotyle–condyle axis, the rather large cotyle and condyle, the presence of a second, small hypapophysis in its anterior trunk vertebrae (i.e., anterior hypapophysis, right ventrally to the cotyle), the presence of compressed prezygapophyseal buttresses that form a ridge extending from the dorsal border of the paradiapophyses up to the prezygapophyseal articular facets, the dorsoventrally thick zygosphene, and the presence of large intrazygantral foramina (characters from Georgalis et al., 2020; Houssaye et al., 2013; McCartney et al., 2018; Rage et al., 2003; Rage, 1983a). The material can be further referred to the genus *Palaeophis* on the basis of its relatively small pterapophyses and the neural spine rising posteriorly from the level of the zygosphenal roof (characters from Houssaye et al., 2013; Parmley & Case, 1988; Parmley & DeVore, 2005; Rage, 1983a; Rage et al., 2003). Indeed, referral to *Pterosphenus* can be discarded, as the vertebrae from Togo are much broader and possess more laterally directed prezygapophyses and postzygapophyses, prezygapophyses extending more dorsally than the ventral level of the neural canal, and a not so distinctly convex zygosphene (Janensch, 1906; McCartney & Seiffert, 2016; Rage et al., 2003). See "Discussion" below for a justification of the referral of the Togo specimens to *Palaeophis africanus* and comparison with all other African *Palaeophis* spp.

Discussion

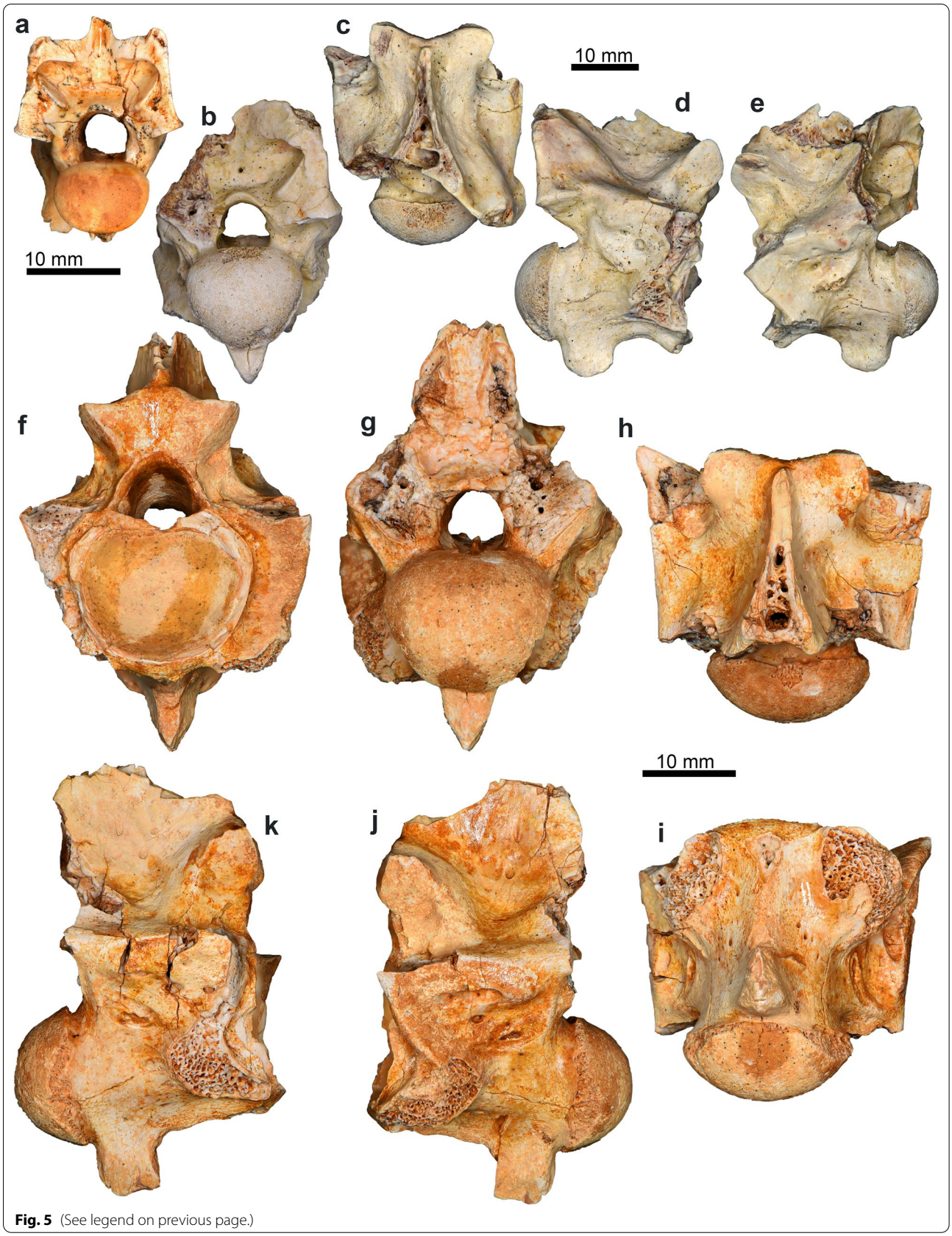
Considering their highly distinctive features, referral of isolated vertebrae to Palaeophiidae and *Palaeophis* is relatively straightforward. However, species-level identification of *Palaeophis* specimens is more problematic, as intraspecific and intracolumnar variations among palaeophiids are still largely unknown, while some anatomical features appear to be more widespread and/or variable than previously conceived. Attempts to decipher intracolumnar variation and diagnostic anatomical traits throughout parts of the palaeophiid vertebral column (e.g., Houssaye et al., 2013; Janensch, 1906; McCartney et al., 2018; Rage, 1983a) or ontogenetic variation (e.g., Parmley & Reed, 2003) have indeed proven useful, but species delimitations often remain vague. Such difficulties can be partially attributed to the fact that the original type material of *Palaeophis toliapicus* Owen, 1841, the type species of the genus, from the early Eocene of England, has never been adequately redescribed (GLG, in progress). In order to attempt a more precise determination of the Togolese material, we directly examined the holotypes of all three named African *Palaeophis* species, and a number of additional referred or undescribed specimens from Africa.

As was mentioned above, four different species of palaeophiids have been described from the Eocene of Africa. In addition, the continent has also yielded the most ancient remains of the group (i.e., Cretaceous), which, however, could not be assigned at the species level (Rage & Werner, 1999; Rage & Wouters, 1979). Among the named species, three pertain to *Palaeophis* (i.e., *Palaeophis africanus*, *Palaeophis maghrebianus*, and *Palaeophis colossaeus*), and one in *Pterosphenus* (i.e., *Pterosphenus schweinfurthi*), with the latter being the most adapted to the aquatic realm and characterized by an even more extreme vertebral morphology. *Pterosphenus schweinfurthi* has been described from the late Eocene of the Fayum, Egypt (Andrews, 1901, 1906; Janensch, 1906; McCartney & Seiffert, 2016) and the middle Eocene of the Idam Unit, Libya (Hoffstetter, 1961), while similar or even conspecific forms have been documented from the middle Eocene of Angola and the middle and late Eocene of Morocco (*Pterosphenus* cf. *schweinfurthi* of Antunes, 1964 and Zouhri et al., 2018, 2021). This species was originally placed in its own genus *Moeriophis* Andrews, 1901, but it was soon subsequently referred to the North American-typified genus *Pterosphenus* by the same author (Andrews, 1906).

Palaeophis maghrebianus has been described from the early Eocene of the Phosphates of Morocco (Arambourg, 1952; Houssaye et al., 2013) (Fig. 10k–o). *Palaeophis colossaeus* is known from the early–middle Eocene of the Tamaguélelt Formation, Mali (Houssaye et al., 2019; McCartney et al., 2018; O'Leary et al., 2019; Rage, 1983b) and represents the largest known palaeophiid snake (Fig. 10f–j). *Palaeophis africanus* was originally described from the middle Eocene of Abeokuta region, Nigeria (Andrews, 1924) (Fig. 10a–e), and was recently reported from the middle Eocene of the Congo Basin, Angola (Folie et al., 2021). Furthermore, two fragmentary vertebrae from the late Eocene of Georgia, USA have

(See figure on next page.)

Fig. 5 **a** Anterior trunk vertebra UM KPO 34 in posterior view (**a**); **b–e** anterior or anterior mid-trunk vertebra UM KPO 28 in posterior (**b**), dorsal (**c**), right lateral (**d**), and left lateral (**e**) views; **f–k** anterior or anterior mid-trunk vertebra UM KPO 23 in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), left lateral (**j**), and right lateral (**k**) views



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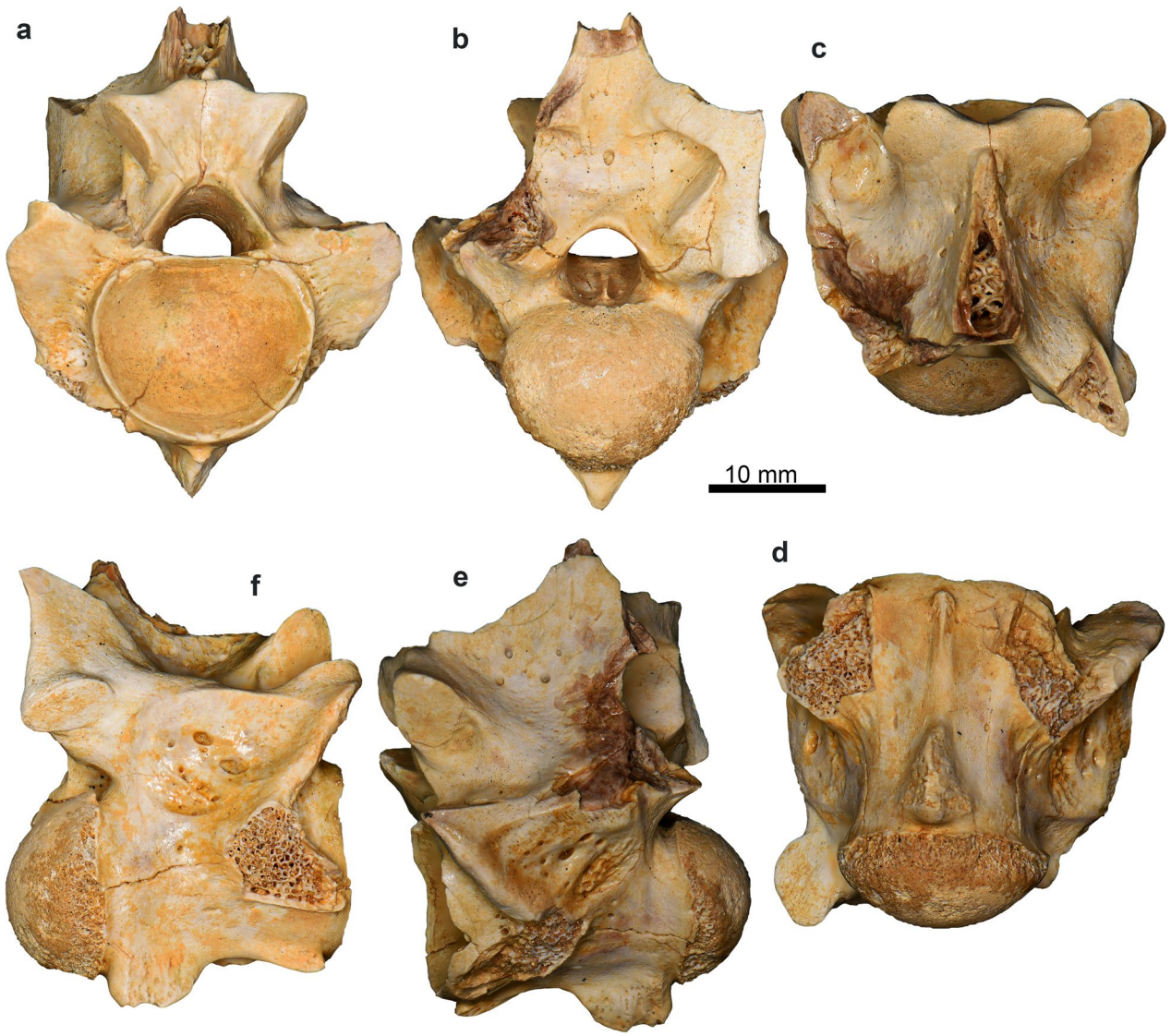

Fig. 6 Anterior to anterior mid-trunk vertebra UM KPO 26 in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right ventrolateral (**f**) views

been referred to as *Pa. africanus* (Parmley & DeVore, 2005), extending significantly both its geographic and stratigraphic distributions. However, this occurrence is based on a single published drawing that cannot afford any definite species-level referral. Consequently, it is more reasonable to consider this North American record as *Palaeophis* cf. *africanus*, and restrict *Pa. africanus* to Africa.

We consider that all Togolese vertebrae pertain to a single taxon. Differences among the vertebrae with regard to the overall size, the shape and thickness of the zygosphene, the shape and orientation of anterior and posterior hypapophyses, the size of the cotyle and condyle, the lateral extension of the prezygapophyses, the shape and size of the neural canal, the number and size of the intrazygantral foramina, and the vertebral lateral compression can be attributed to intracolumnar variation. Indeed, some of these features are known for snakes to be subjected to a high degree of intracolumnar or intraspecific variation or to ontogenetic variability in snakes (e.g., the thickness of the zygosphene; see Georgalis & Scheyer, 2019).

It appears that the new Togolese material bears more resemblances with *Palaeophis africanus*. The most significant features shared among the Togolese material with that of the type and previously referred specimens

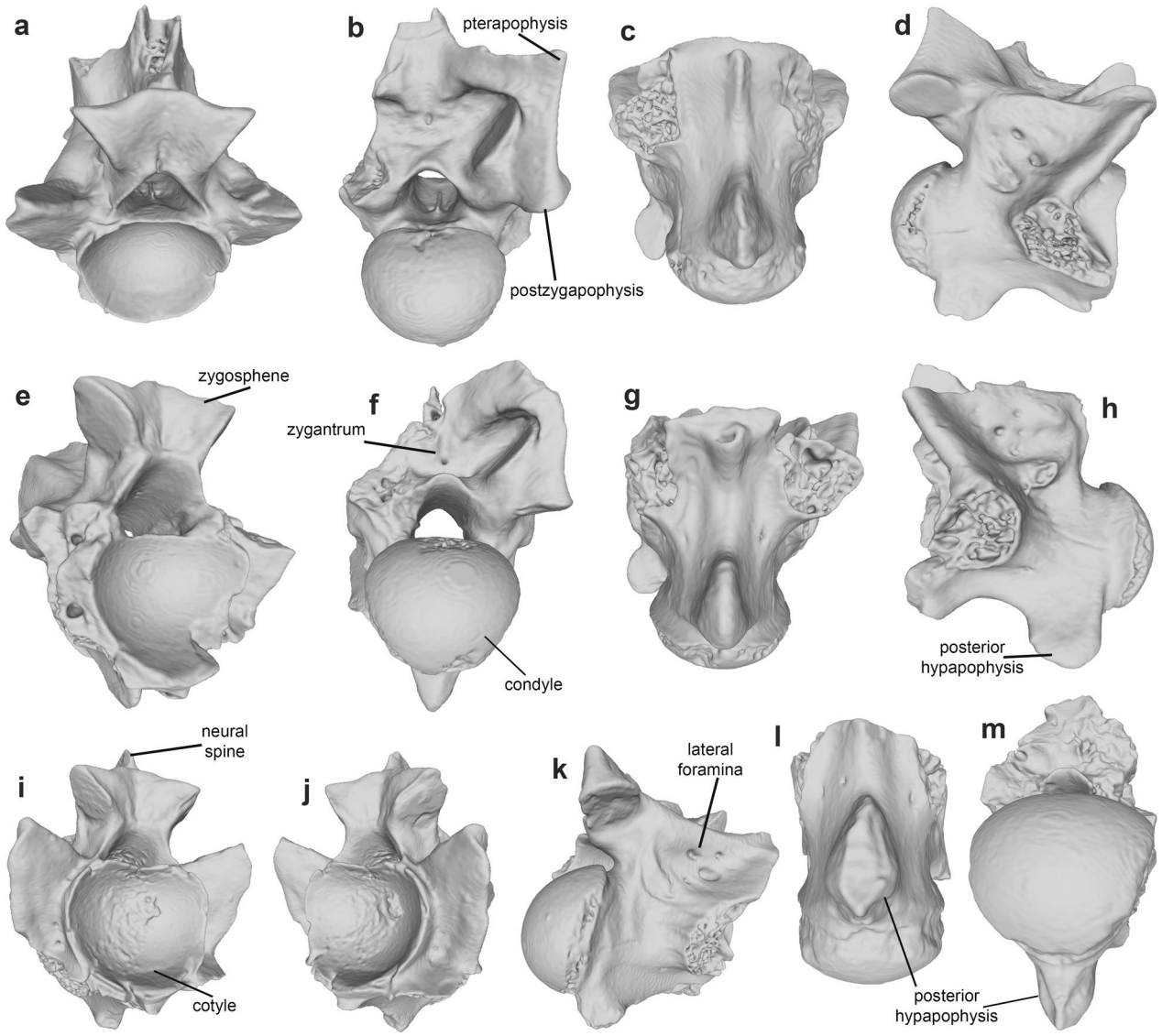

Fig. 7 3D models of anterior or anterior mid-trunk vertebrae: **a–d** UM KPO 26 in anterodorsal (**a**), posterior (**b**), ventral (**c**), and right lateral (**d**) views; **e–h** UM KPO 28 in right anterolateral (**e**), posterior (**f**), ventral (**g**), and left lateral (**h**) views; **i–k** UM KPO 27 in right anterolateral (**i**) left anterolateral (**j**), and right ventrolateral (**k**) views; **l–m** UM KPO 35 in ventral (**l**) and posterior (**m**) views. Specimens not to the same scale

(Fig. 10a–e) of *Pa. africanus* can be observed in the overall shape, robustness and lateral compression of the vertebrae, the thickness of the zygosphene, the prominence of the interzygapophyseal ridges, the shape of the neural spine and the prezygapophyses, the height of the pterapophyses, the presence of a muscular scar below the level of the interzygapophyseal ridge, and the absence of parazygosphenal foramina.

Furthermore, we can exclude conspecific affinities of the Togolese material from *Palaeophis maghrebianus* and *Palaeophis colossaeus*, on the basis of important differences in the vertebral anatomy (Fig. 10f–o). More particularly, the specimens described here can be differentiated from *Pa. maghrebianus* by their more distinct interzygapophyseal ridges, neural spine commencing more proximately to the level of the zygosphene, and larger ratio of zygosphene width to cotyle width (Fig. 10k–o). The differences are even more apparent with *Pa. colossaeus*, from which the Togolese specimens can be differentiated by their vertebrae being smaller, less robust and less massive, and more laterally compressed, by lacking parazygosphenal foramina, and possessing more prominent interzygapophyseal ridges, and less

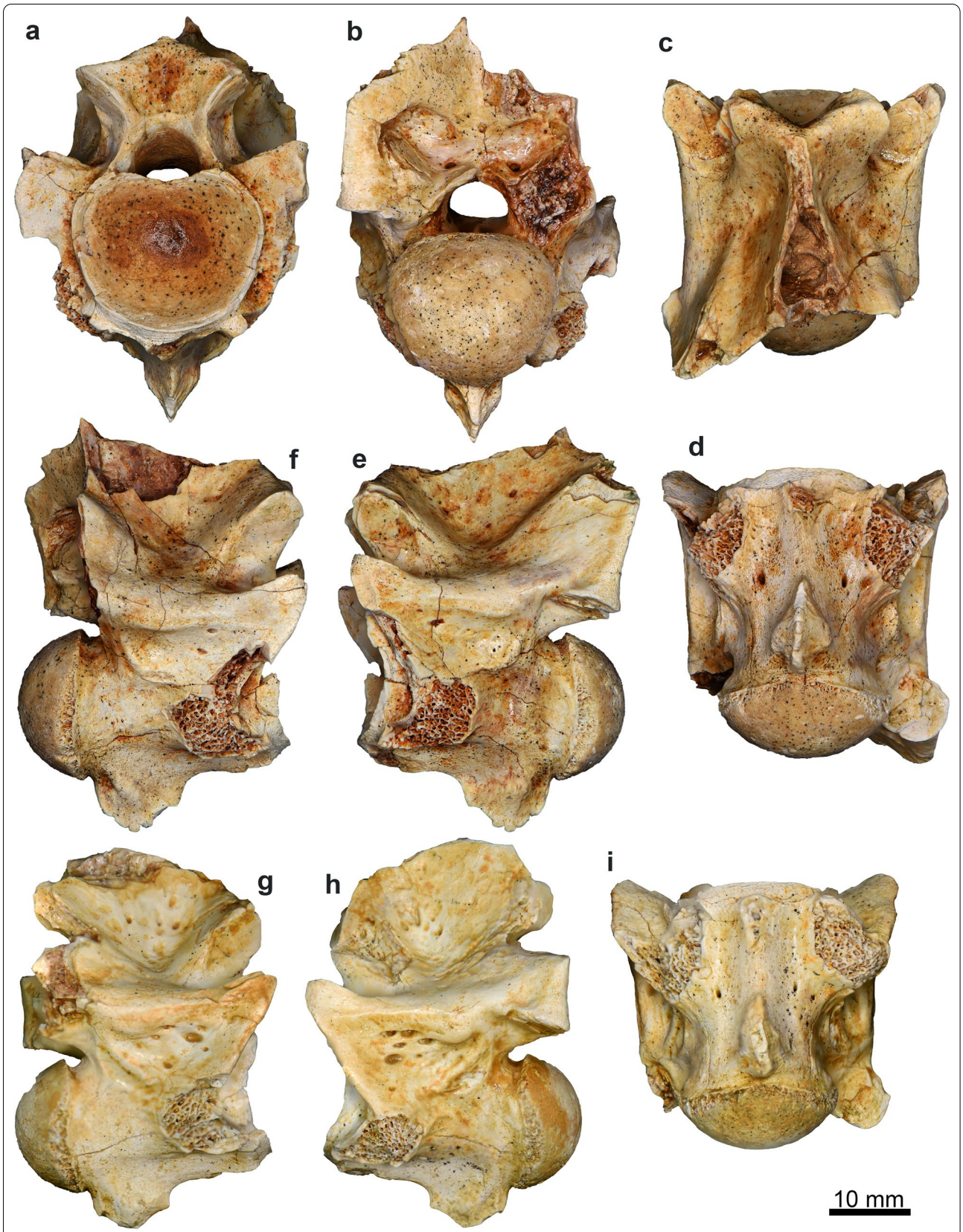

Fig. 8 **a–f** Mid-trunk vertebra UM KPO 30 in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views; **g–i** mid-trunk vertebra UM KPO 21 in right lateral (**g**), left lateral (**h**), and ventral (**i**) views

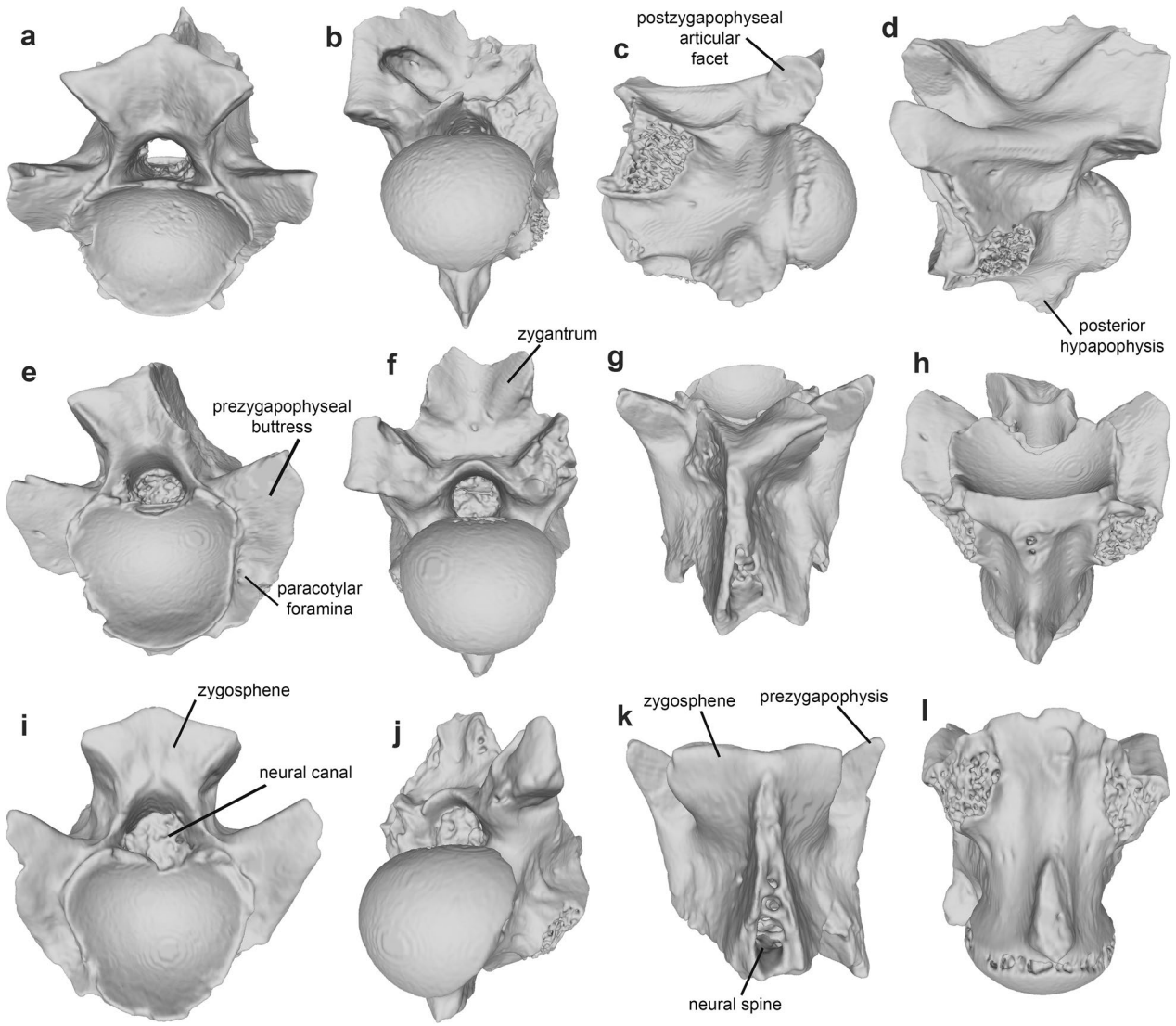

Fig. 9 3D models of anterior mid- or mid-trunk vertebrae: **a–d** UM KPO 30 in anterodorsal (**a**), posterior (**b**), left ventrolateral (**c**), and left lateral (**d**) views; **e–h** UM KPO 21 in anterior (**e**), posterior (**f**), dorsal (**g**), and anteroventral (**h**) views; **i–l** UM KPO 24 in anterior (**i**), right posterolateral (**j**), dorsal (**k**), and ventral (**l**) views. Specimens not to the same scale

massive, less thick, and more convex zygosphene in anterior view (Fig. 10f–j).

Accordingly, we refer the Togo material to *Palaeophis africanus*. Nevertheless, we have to highlight certain differences with the so far few other known vertebrae of this taxon. The most important difference between the specimens described here and previously published material of *Palaeophis africanus* lies in the morphology of the zygosphene. In anterior view, the zygosphene of all Togolese vertebrae bears a characteristic deep and large fossa. Such fossa seems to be absent in the Angolan specimens described by Folie et al. (2021). However, a very slight fossa (but of considerably less depth and width), seems to be present in the holotype of the species (NHMUK PV R 4964) (Fig. 10a–e), as well as in another referred (but not figured) specimen (NHMUK PV R 4965(1)) of Andrews (1924); the latter is figured here for the first time (Fig. 11). The potential diagnostic utility of this deep fossa remains difficult to assess in the current state of knowledge and we prefer to attribute these different morphologies to intraspecific variation. Another unusual feature of the Togolese *Palaeophis* is that the dorsal level of the zygosphene of many specimens is not straight but can instead be relatively convex, in anterior view. This feature has not been reported from other *Pa. africanus* specimens and is generally rather rare in all *Palaeophis* species. Such a

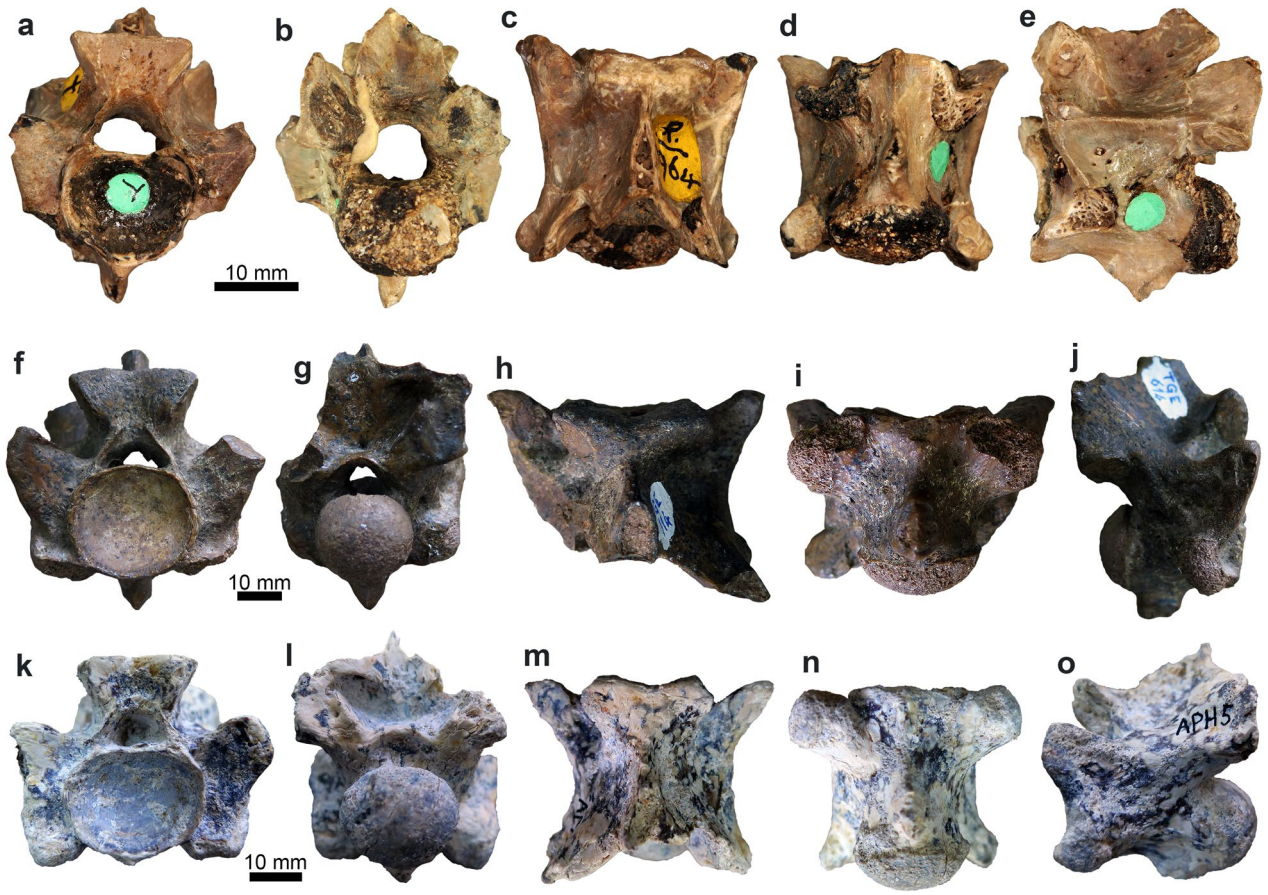

Fig. 10 Type specimens of all named African species of *Palaeophis*: **a–e** holotype trunk vertebra (NHMUK PV R 4964) of *Palaeophis africanus* from the middle Eocene of Oshosun Formation, Nigeria, in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** holotype trunk vertebra (MNHN.F. TGE615) of *Palaeophis colossaeus* from the early–middle Eocene of the Tamaguélelt Formation, Mali, in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and right lateral (**j**) views; **k–o** holotype trunk vertebra (MNHN.F. APH5) of *Palaeophis maghrebianus* from the early Eocene of the phosphates of Djemaïa, Oulad Abdoun, Morocco, in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views. From the collections of the Natural History Museum, London and the Muséum national d'Histoire naturelle, Paris

convexity has been previously documented only at certain anterior trunk vertebrae of *Palaeophis maghrebianus* from the early Eocene of Morocco and *Palaeophis oweni* Zigno, 1881, from the middle Eocene of Italy (see Houssaye et al., 2013; Georgalis et al., 2020), and to a lesser degree in *Palaeophis typhaeus* Owen, 1850, from the middle Eocene of England (Owen, 1850). In fact, the distinctly convex zygosphene is a diagnostic feature of *Pterosphenus*. However, this convexity is extreme in the latter genus (Janensch, 1906; McCartney & Seiffert, 2016; Rage et al., 2003) and thus differs from the condition observed in the Togolese material. Finally, the shape of the zygosphene in dorsal view is relatively different in comparison with the holotype of *Pa. africanus*, where this element is not so concave. Nevertheless, a more pronounced concavity is observable in one of the referred vertebrae (NHMUK PV R 4965(1)) of Andrews (1924) from Nigeria (Fig. 11c), as well as in the Angolan specimens described by Folie et al. (2021), though admittedly none of them reach the concavity observed in certain Togo vertebrae.

Taking into consideration the holotype and previously described specimens of *Palaeophis africanus* together with the abundant new material from Togo, we attempt to provide a (tentative) diagnosis for this species. *Palaeophis africanus* can be differentiated from other palaeophiid snakes by the combination of the following features: (i) vertebrae not very massive and slightly laterally compressed; (ii) massive and thick zygosphene; (iii) prominent interzygapophyseal ridges; (iv) neural spine commencing almost immediately after the zygosphene; (v) relatively short pterapophyses; (vi) well-developed prezygapophyses; (vii) presence of a muscular scar below the level of the interzygapophyseal ridge; (viii) presence of two hypapophyses in anterior and anterior mid-trunk vertebrae, and (ix) absence of parazygosphenal foramina. Note that the features in the zygosphenal morphology

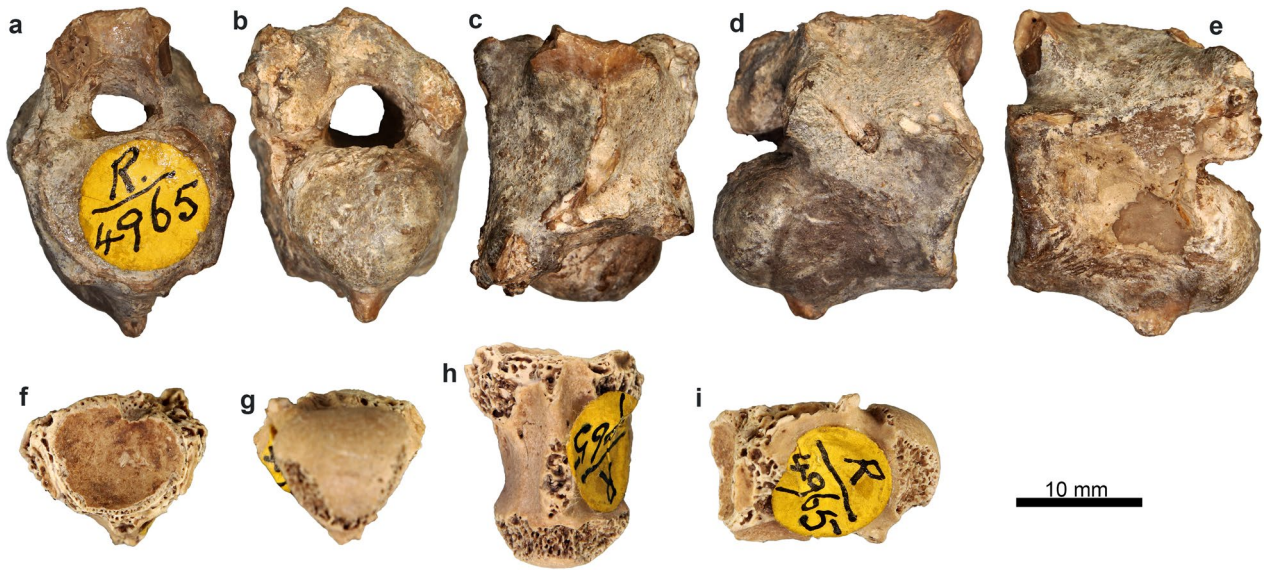

Fig. 11 Referred specimens of *Palaeophis africanus* from the middle Eocene of Oshosun Formation, Nigeria. **a–e** Trunk vertebra NHMUK PV R 4965(1) in anterior (**a**), posterior (**b**), dorsal (**c**), right lateral (**d**), and left lateral (**e**) views; **f–i** trunk vertebra NHMUK PV R 4965(2) in anterior (**f**), posterior (**g**), ventral (**h**), and left lateral (**i**) views. Both these specimens were originally mentioned by Andrews (1924) but had never been figured so far. From the collections of the Natural History Museum, London

of the Togo specimens discussed in the paragraph above may eventually have a diagnostic utility as well, however, this cannot yet be determined. For detailed differentiation of *Pa. africanus* from the other two African species of the genus, *Pa. colossaeus* and *Pa. maghrebianus*, see above.

The new Togo specimens, comprising more than 50 vertebrae, represent so far the most abundant known material attributable to *Palaeophis africanus*. Accordingly, it provides novel insights on the anatomy, diagnostic features and morphological variability of this so far enigmatic palaeophiid snake. Furthermore, the new finds shed new light on the Paleogene squamate fauna of Togo, which is extremely poorly known. In fact, the only so far published squamate specimen from the Paleogene of Togo was a snake specimen described and figured by Stromer (1910: fig. 13), originating from the Paleocene of Tabligbo. This specimen was originally tentatively referred by Stromer (1910) to the North American constrictor *Aphelophis* Cope, 1873 (misspelled as *Aphelopsis*), a genus currently considered to be a junior synonym of *Calamagras* Cope, 1873 (Wallach et al., 2014). However, Stromer's specimen from Tabligbo, currently probably lost, was recently reinterpreted by Smith and Georgalis (in press) as not being a member of Constrictores but instead pertaining to the aquatic nigerophiid genus *Amananulam* McCartney et al., 2018. It is thus evident that at least two different snake lineages were present in the Paleogene of Togo and we highly anticipate that future fieldwork will enhance our understanding of the diversity and evolution of Paleogene herpetofaunas of this unexplored area.

Appendix 1: Centrum lengths (CL) of all vertebrae from Kpogamé

Specimen	Centrum length (in mm)
UM KPO 21	30
UM KPO 22	31
UM KPO 23	26
UM KPO 24	24
UM KPO 25	28.5
UM KPO 26	25.5
UM KPO 27	28.5
UM KPO 28	27
UM KPO 29	Damaged—not available
UM KPO 30	31
UM KPO 31	30
UM KPO 32	29.5
UM KPO 33	30
UM KPO 34	Damaged—not available
UM KPO 35	27.5
UM KPO 36	27.5

Specimen	Centrum length (in mm)
UM KPO 37	23
UM KPO 38	Damaged—not available
UM KPO 39	31.5
UM KPO 40	Damaged—not available
UM KPO 41	Damaged—not available
UM KPO 42	Damaged—not available
UM KPO 43	24
UM KPO 44	26
UM KPO 45	26
UM KPO 46	Damaged—not available
UM KPO 47	Damaged—not available
UM KPO 48	21
UM KPO 49	28.5
UM KPO 50	Damaged—not available
UM KPO 51	30
UM KPO 52	29.5
UM KPO 53	20.5
UM KPO 54	19
UM KPO 55	Damaged—not available
UM KPO 56	Damaged—not available
UM KPO 57	Damaged—not available
UM KPO 58	Damaged—not available
UM KPO 59	Damaged—not available
UM KPO 60	29
UM KPO 61	28
UM KPO 62	Damaged—not available
UM KPO 63	Damaged—not available
UM KPO 64	24
UM KPO 65	Damaged—not available
UM KPO 66	Damaged—not available
UM KPO 67	19.5
UM KPO 68	Damaged—not available
UM KPO 69	Damaged—not available
UM KPO 70	Damaged—not available
UM KPO 71	Damaged—not available

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Authors' contributions

LH, GG, and GLG conceived the study; GLG analyzed the data and prepared the figures; LH CT-scanned the specimens and performed the 3D models; GLG, GG, and LH wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All fossil specimens described herein are permanently curated in the collections of the University of Montpellier. All other illustrated specimens are permanently curated at the collections of MNHN and NHMUK. The virtually restored 3D models of 17 vertebrae are deposited in MorphoMuseuM (Georgalis et al., 2021).

Declarations

Competing interests

The authors declare that they have no competing interests.

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