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SNAKES FROM THE CENOZOIC OF EUROPE
– TOWARDS A MACROEVOLUTIONARY AND PALAEOBIOGEOGRAPHIC SYNTHESIS

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Revision of the enigmatic snake *Plesiotortrix edwardsi* Rochebrune, 1884 from the Phosphorites du Quercy, France

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ABSTRACT
Plesiotortrix edwardsi Rochebrune, 1884 was one of the first snake taxa to be described from the Phosphorites du Quercy, France. The taxon was established in the second half of the 19th century, based on three articulated vertebrae that were found in an unknown locality in the area of Quercy. Originally, only a brief description was provided coupled with a lithograph that depicted the holotype specimen in anterior and dorsal views. Nevertheless, *Plesiotortrix* Rochebrune, 1884 has since frequently appeared in ophidian literature across the past 140 years and even emended diagnoses have been proposed, but still, its exact affinities have been obscure. I investigated the holotype and only known specimen and I am herein providing, for the first time, photographs and detailed comparisons with other snakes. Several inaccuracies are identified among the original lithograph and the actual specimen, which have inevitably affected past anatomical comparisons and taxonomic interpretations. *Plesiotortrix* is probably belongs Constrictores but a more precise, family level, determination is not possible. Moreover, the incompleteness of the holotype and only known specimen, coupled with a totally unknown intracolumnar variation of the taxon, lead me to consider *Plesiotortrix edwardsi* to be a nomen dubium.

KEY WORDS
Serpentes,
Constrictores,
taxonomy,
Quercy,
Paleogene.

RÉSUMÉ
Révision de l'énigmatique serpent Plesiotortrix edwardsi *Rochebrune, 1884 des Phosphorites du Quercy, France.*
Plesiotortrix edwardsi Rochebrune, 1884 a été l'un des premiers taxons de serpents décrits dans les Phosphorites du Quercy, France. Le taxon a été établi dans la seconde moitié du XIXe siècle, à partir de trois vertèbres articulées trouvées dans une localité inconnue du Quercy. À l'origine, seule une brève description était fournie, accompagnée d'une lithographie représentant le spécimen holotype en vues antérieure et dorsale. Néanmoins, *Plesiotortrix* Rochebrune, 1884 est depuis fréquemment apparu dans la littérature sur les ophidiens au cours des 140 dernières années et même des diagnoses modifiées ont été proposées, mais ses affinités exactes restent obscures. J'ai étudié l'holotype ainsi que le seul spécimen connu et je fournis ici, pour la première fois, des photographies et des comparaisons détaillées avec d'autres serpents. Plusieurs inexactitudes sont identifiées entre la lithographie originale et le spécimen réel, qui ont inévitablement affecté les comparaisons anatomiques et les interprétations taxonomiques passées. *Plesiotortrix* est probablement attribuable aux Constrictores, mais une détermination plus précise, au niveau familial, n'est pas possible. De plus, le caractère incomplet de l'holotype et du seul spécimen connu, couplé à une variation intracolumnaire totalement inconnue du taxon, m'amène à considérer *Plesiotortrix edwardsi* comme un nomen dubium.

MOTS CLÉS
Serpentes,
Constrictores,
taxonomie,
Quercy,
Paléogène.

INTRODUCTION

The Phosphorites du Quercy in southern France represents one of the most important regions for palaeophidiology, with abundant fossil remains of snakes having been described already since the second half of the 19th century (Gervais 1873; Filhol 1877; Rochebrune 1880, 1884; Zittel 1887-1890; Lydekker 1888a, b; de Stefano 1905). These fossil remains include mainly disarticulated vertebrae but also cranial elements and even mummified trunk portions of bodies are known (Filhol 1877; Rochebrune 1880; Georgalis *et al.* 2021c). Several genera and species have been established upon this material from Quercy, the majority of which named more than 100 years ago. During the past five decades, novel descriptions of abundant material from new excavations or from the old collections, coupled with the redescription of previously known taxa (e.g. Hoffstetter & Rage 1972; Rage 1974, 1978, 1984, 1988, 2013; Augé & Rage 1995; Szyndlar & Rage 2003; Rage & Augé 2015; Georgalis *et al.* 2021c; 2025) plus a more comprehensive knowledge of the cranial and vertebral morphology and intracolumnar variation of extant snakes (e.g. Smith 2013; Head 2021; Smith & Georgalis 2022; Szyndlar & Georgalis 2023), have significantly advanced our understanding of fossil snakes from Quercy. However, still certain "historical" taxa remain rather poorly known and their exact taxonomic status and phylogenetic affinities are largely unresolved. This has profound consequences and impact on our knowledge of the taxonomic diversity but also on nomenclature, as these 19th century established taxa, if indeed valid, have clearly nomenclatural priority over other subsequently named forms.

One prominent such case of enigmatic Quercy snakes is *Plesiotortrix edwardsi* Rochebrune, 1884. This taxon was originally established by Rochebrune (1884) upon three articulated trunk vertebrae from Quercy. Besides, like most other fossil remains from Quercy collected during the 19th and early 20th centuries, the holotype and only known specimen of *Pl. edwardsi* lacks any precise locality and age data (see Rage 2006; Georgalis 2017; Georgalis *et al.* 2021a, c, 2023; Pelissié *et al.* 2021); accordingly, its age has been only tentatively treated as lying within the late Eocene and Oligocene (e.g. Rage 1984; Wallach *et al.* 2014; Smith & Georgalis 2022). The name *Plesiotortrix* Rochebrune, 1884 has variously appeared in palaeontology textbooks and the taxon has been continuously mentioned in palaeoherpetological papers over more than a century (see Discussion below). Nevertheless, practically all that has been known about this enigmatic taxon is Rochebrune's (1884) brief (and admittedly, rather generalized) description, and the original lithographs of the specimen (presented only in dorsal and anterior views). I here provide a redescription of the holotype and only known specimen of *Pl. edwardsi*, coupled with photographs (for the first time) and detailed comparisons with other extinct and extant taxa, providing implications about its exact affinities and validity. Furthermore, the original lithographs of the taxon are shown to contain major inaccuracies regarding the actual morphology of the specimen, leading thus to several erroneous taxonomic treatments of *Plesiotortrix* over the past 150 years.

MATERIAL AND METHODS

The holotype of *Plesiotortrix edwardsi* described herein is permanently curated at the collections of the Muséum national d'Histoire naturelle, Paris (MNHN). For comparative purposes, abundant fossil and extant snake skeletons were studied at the collections of GMH, HNHM, ISEZ, MGPT-MDHC, MNCN, MNHN, NHMUK, NHMW, PIMUZ, SMF, and UM. Anatomical terminology of snake vertebrae follows Szyndlar & Georgalis (2023). Taxonomy of extant snakes follows Wallach *et al.* (2014), Boundy (2021), and Szyndlar & Georgalis (2023); taxonomy of extinct snakes follows Smith & Georgalis (2022).

INSTITUTIONAL ABBREVIATIONS

GMH	Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle;
HNHM	Hungarian Natural History Museum, Budapest;
ISEZ	Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków;
MGPT-MDHC	Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
PIMUZ	Palaeontological Institute and Museum of the University of Zurich;
SMF	Paleoherpetology collection, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main;
UM	Institut des Sciences de l'Évolution, Université de Montpellier.

SYSTEMATIC PALAEONTOLOGY

SERPENTES Linnaeus, 1758
ALETHINOPHIDIA Nopcsa, 1923
CONSTRICTORES Oppel, 1811a
(*sensu* Georgalis & Smith 2020)
Genus *Plesiotortrix* Rochebrune, 1884

Plesiotortrix edwardsi Rochebrune, 1884
(Fig. 1)

Plesiotortrix edwardsi Rochebrune, 1884: 156.

TAXONOMIC HISTORY. — *Plesiotortrix edwardsi* Rochebrune, 1884 (new genus and species); [*Plesiotortrix edwardsi*] Rage & Augé 1993 (nomen dubium). Note that the "Taxonomic history" section here deals only with novel nomenclatural acts, new taxonomic combinations, or novel taxonomic renderings of the taxon, similarly to the style proposed in other recent reptilian papers (e.g. Joyce 2016, 2017; Georgalis & Joyce 2017; Georgalis *et al.* 2021c).

HOLOTYPE AND ONLY KNOWN SPECIMEN. — MNHN.F.QU16332 (formerly MNHN QU 332), three articulated trunk vertebrae (Rochebrune 1884; pl. II.6, II.6a; this paper: Figs 1; 2).

LOCALITY AND AGE. — Similar to most other fossil specimens collected during the 19th century, there are no precise locality data for the holotype of *Plesiotortrix edwardsi*, apart from the general information that it originates from the Phosphorites du Quercy. However, this is still vague, taking into consideration that the Phosphorites du Quercy include at least 170 fissure filling localities, distributed over a broad geographic area, encompassing large parts of the current departments of Lot, Tarn-et-Garonne, Tarn, and Aveyron, all in the administrative region of Occitanie (Rage 2006; (Sigé & Hugueney 2006; Georgalis *et al.* 2021a, c, 2023; Pelissié *et al.* 2021). They also stratigraphically span over a considerable time period, from the early Eocene (MP 8+9) until the Early Miocene (MN 3); however, most of the respective fossiliferous localities range between the late middle Eocene (MP 16) and the late Oligocene (MP 28) (Rage 2006; Sigé & Hugueney 2006; Georgalis *et al.* 2021a, c; Pelissié *et al.* 2021), though still important finds have also been recovered from the older (early Eocene) and younger (Early Miocene) sites (e.g. Čerňanský 2023; Čerňanský *et al.* 2023a, b).

DESCRIPTION

The holotype and only known specimen of *Plesiotortrix edwardsi* consists of three articulated trunk vertebrae. The three vertebrae are relatively well preserved, but still have parts of their prezygapophyses and neural spines damaged and their paradiapophyses are eroded (Fig. 1). The vertebrae are moderately small, with an average centrum length (CL) for each vertebra of approximately 3.3 mm and a neural arch width (NAW) of 3.9 (ratio CL / NAW approximately 0.8). In anterior view (Fig. 1A), the zygosphene is straight and relatively thin. The neural canal is trapezoidal in shape. The prezygapophyses are only slightly inclined, but they clearly reach above the level of the floor of the neural canal. The cotyle is large and circular. Deep fossae are present on each lateral side of the cotyle; no paracotylar foramina are present. In posterior view (Fig. 1B), the neural arch is moderately depressed, with a vaulting ratio (*sensu* Georgalis *et al.* 2021c) equal to 0.38. The parapophyseal portion of the paradiapophysis (fully preserved only in the right paradiapophysis of the third vertebra) extends ventrally below the level of the cotyle and condyle. The condyle is large and slightly elliptical. In dorsal view (Fig. 1D), the zygosphene possesses two incipient lateral lobes and a wide median lobe. The neural spine commences slightly posteriorly from the level of the zygosphene; its base becomes wider and distinctly saddle-shaped towards the posterior half of the neural arch. The prezygapophyseal articular facets are massive and broad. The interzygapophyseal constriction is deep. In ventral view (Fig. 1C), the centrum is wider than long. A distinct haemal keel runs almost throughout the midline of the ventral surface of the centrum. It is relatively thin and has the same width across its whole length; it commences anteriorly at around the ventral lip of the cotyle and terminates posteriorly right prior to the condylar lip. Prezygapophyseal accessory processes are present, with their tip only slightly projecting beyond the prezygapophyseal articular facets. The subcentral grooves are deep. Subcentral foramina are visible, situated next to the haemal keel. The paradiapophyses are eroded in the three vertebrae with the exception of the right paradiapophyses of the last vertebra, which is almost complete. There seems to be no clear differentiation into diapophyses and parapophyses; in the almost completely preserved right paradiapophysis of the third vertebra, it seems that the parapophyseal portion is slightly larger than the diapophyseal one. The postzygapophyseal articular facets are large and their posterior edge is somehow acute. In lateral view (Fig. 1E, F), the neural spine is damaged and practically only its base is preserved. A small condylar neck is present. The subcentral ridges are slightly convex. The haemal keel slightly projects ventrally, with its dorsoventral height being higher towards its posteriormost section.

Judging from the absolute shape, the vaulting of the neural arch, the depth of the subcentral grooves, and the width of the haemal keel, I assume that these three vertebrae originate from the mid- or anterior posterior trunk region of the column. This slightly contradicts Rochebrune's (1884) original description, who treated them as "vertèbres de la région pelvienne".

Fig. 1. — **A**-**F**, Holotype articulated trunk vertebrae (MNHN.F.QU16332) of *Plesiotortrix edwardsi* Rochebrune, 1884 in anterior (**A**), posterior (**B**), ventral (**C**), dorsal (**D**), right lateral (**E**), and left lateral (**F**) views. Scale bar: 5 mm.

DISCUSSION

Plesiotortrix edwardsi is one of the relatively commonly mentioned, though as yet rather enigmatic, snake taxa established from the Phosphorites du Quercy. Indeed, ever since its original description by Rochebrune (1884), *Plesiotortrix* has frequently appeared in several herpetological and palaeontological works and textbooks (e.g. Boettger 1884; Palacký 1898; de Stefano 1905; Nopcsa 1928; Hoffstetter 1939, 1955; Kuhn 1939; Papp *et al.* 1953; Romer 1956; Rage 1974, 1984, 2001, 2006; Carroll 1988; Rage & Augé 1993; Szyndlar & Schleich 1993; Szyndlar & Rage 2003; Wallach *et al.* 2014; Boundy 2021; Georgalis *et al.* 2021a, c; Smith & Georgalis 2022). However, practically most of these literature occurrences merely represent simple mentions of the taxon and only a few actually dealt with proposing revised taxonomic opinions; still, even these latter "revised opinions" were based exclusively on Rochebrune's (1884) brief description and figures.

Rochebrune (1884) originally described his new genus and species as a member of Aniliidae Stejneger, 1907 (his Tortricidae), hence the genus name *Plesiotortrix*, i.e., from the Greek word "πλησίον", meaning "near" and the genus name *Tortrix* Oppel, 1811b (currently being a synonym of *Anilius* Oken, 1816, as it is preoccupied by the insect *Tortrix* Linnaeus, 1758). In that contribution, Rochebrune (1884) provided solely a rather brief description and only two images of the specimen, which was depicted in figures 6 and 6a of his plate II, in dorsal and anterior views respectively (Fig. 2).

A similar taxonomic referral of *Plesiotortrix* into aniliids was also followed by Boettger (1884) and de Stefano (1905), with the latter author redescribing the taxon and providing an emended diagnosis. Interestingly, de Stefano (1905: 51, 52) mentioned that he had available in his material from Quercy, several vertebrae ("... alcunne vertebre pelvianne, contenute nella collezione Rossignol"), which could be assigned to *Plesiotortrix edwardsi*, however, a few lines later, he considered it likely that these vertebrae pertained to more than one species but he nevertheless admitted that he had no time to study and compare these specimens ("Probabilmente le vertebre da me osservate appartengono a più di una specie. La mancanza di tempo non mi ha permesso di fare in proposito un'accurata comparazione"). This absence of a detailed study of this material by de Stefano (1905) is also aptly reflected by the fact that he figured no vertebra assigned to *Plesiotortrix edwardsi* in his plates. Nopcsa (1928) placed *Plesiotortrix* within colubrids. Kuhn (1939) inexplicably placed it into elapids, along with other extinct snake taxa, i.e., *Pylmophis* Rochebrune, 1880, and *Tachyophis* Rochebrune, 1884, and the extant genera *Coelopeltis* Wagler, 1830 (synonym of *Malpolon* Fitzinger, 1826), and *Zamenis* Wagler, 1830! *Plesiotortrix* was subsequently considered as either a snake of uncertain affinities (Romer 1956), either a boid (Hoffstetter 1939; Szyndlar & Schleich 1993), either more generally a booid by Rage (1974), and either a probable boine by Rage (1984) (but note anyway that the concepts of Booidea Gray, 1825, Boidae Gray, 1825, and Boinae Gray, 1825 have been much altered over the past decades; see Szyndlar & Georgalis 2023). Hoffstetter (1955: 652) went even further to tentatively propose resemblance and potential affinities with the extant Western African constrictor *Calabaria* Gray, 1858. Rage (1974) tentatively proposed that the lectotype anterior trunk vertebra (MNHN.F.QU16339) of *Palaelaphis antiquus* Rochebrune, 1884, could pertain to *Plesiotortrix edwardsi*. Interestingly, both these species were established in the same publication (Rochebrune 1884), which implies, that in case of conspecificity one would be a senior synonym of the other. Following a direct study of both specimens, I consider it difficult to state whether the two are conspecific. Rage & Augé (1993) regarded *Plesiotortrix* to be a nomen dubium. More recently, *Plesiotortrix* was treated as valid by Wallach *et al.* (2014) and Boundy (2021), who continued to treat it as a member of Boidae and Booidea incertae sedis respectively. The most recent treatise of *Plesiotortrix* was made by Smith & Georgalis (2022), who treated it as valid and assigned it to Constrictores incertae sedis.

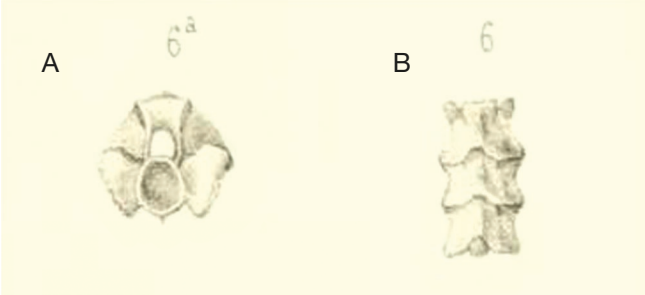

FIG. 2. — **A**, **B**, Original lithograph of the holotype articulated trunk vertebrae (MNHN.F.QU16332) of *Plesiotortrix edwardsi* Rochebrune, 1884 in anterior (**A**) and dorsal (**B**) views. Modified from Rochebrune (1884: pl. II). Note the inaccuracies of both images, compared with the actual specimen, as shown in the photographs in Figure 1 above.

Judging from my new investigation of the holotype of *Plesiotortrix edwardsi*, it is evident that the original lithographs presented in Rochebrune (1884) are rather erroneous, and the vertebrae in anterior and dorsal views appear in fact rather different than what they really are. The differences among the actual specimen and the lithographs are more apparent in regards to the thickness of the zygosphene (much thicker and more dorsally convex in the lithograph compared to reality), the interzygapophyseal constriction (it appears much narrow in the lithograph compared to reality), and the shape and size of the prezygapophyses (Figs 1; 2). This inconsistency between the original lithographs and the actual specimens represents unfortunately a common phenomenon observed in 19th century publications and it has been widely documented in recent revisions of other extinct snakes (e.g. Georgalis *et al.* 2016, 2021c) but also other extinct reptiles (e.g. Anquetin & Joyce 2014; Georgalis 2017; Georgalis & Joyce 2017).

In any case, all these inaccuracies of the original lithograph inevitably led to false anatomical interpretations and the above mentioned drastically different taxonomic opinions. My firsthand observation of the holotype (MNHN.F.QU16332) of *Plesiotortrix edwardsi* clarifies certain aspects of various vertebral structures, allowing a more accurate taxonomic interpretation. Nevertheless, a major obstacle in further determining the affinities of *Plesiotortrix* is imposed by the fact that the neural

spines in all three articulated vertebrae of the holotype are much incomplete. It appears that the neural spine was running much (but not all) of the anteroposterior length of the neural arch and that its base was much more widened posteriorly, giving a saddle-shaped appearance, however, without any clue about its actual dorsoventral height, it is rather risky to assume its original shape and size.

Affinities of *Plesiotortrix* with the extinct madtsoiids and palaeophiids, which were present in the Eocene, can be readily discarded as these two groups are characterized by drastically different vertebral morphologies: madtsoiids possess more massive vertebrae, distinct parazygosphenal foramina, paracotylar foramina, prezygapophyses much dorsally inclined in anterior view, a small and depressed neural canal, and no prezygapophyseal accessory processes (Hoffstetter 1961; Rage 1984; Scanlon 2005; Vasile *et al.* 2013); palaeophiids possess distinctly laterally compressed vertebrae with pterapophyses, prominent prezygapophyseal buttresses, paradiapophyses situated much ventrally, and no prezygapophyseal accessory processes (Rage 1984; Georgalis *et al.* 2021b; Georgalis 2023). Similarly, affinities with other extinct Eocene forms from Europe and northern Africa, such as archaeophiids, nigerophiids, russellophiids, thaumastophiids, can be readily discarded due to their extremely different vertebral morphology (Rage 1978, 1984; Zaher *et al.* 2021; Smith & Georgalis 2022).

Affinities of *Plesiotortrix* with scolecophidians can be readily discarded, as the latter are characterized by an elongate centrum, absence of neural spine, prominent prezygapophyseal accessory processes, a depressed neural arch, a flattened ventral surface of the centrum with no haemal keel in mid- and posterior trunk vertebrae, absent or very shallow posterior median notch of the neural arch, and a much smaller size (see Szyndlar & Georgalis 2023). *Plesiotortrix* is reminiscent to aniliids, as it was originally envisaged by Rochebrune (1884), both sharing the presence of haemal keel in trunk vertebrae, the deep interzygapophyseal constriction, and the absence of paracotylar foramina (see Head 2021; Szyndlar & Georgalis 2023); however, differences exist in that in aniliids the neural spine crosses less part of the anteroposterior length of the neural arch, the posterior median notch of the neural arch is much shallower (or even absent), the prezygapophyses are more dorsally inclined in anterior view, and the cotyles are more depressed (see Szyndlar & Georgalis 2023). *Plesiotortrix* seems not to be related to tropidophiids, as in the latter group, trunk vertebrae bear a distinct broad hypapophysis in lateral view (instead of the relatively very short dorsoventrally haemal keep present in *Plesiotortrix*) (see Szyndlar & Georgalis 2023). *Plesiotortrix* cannot be assigned to cylindrophiids, because the latter, which are currently distributed in southern Asia and with no definite fossil record available, have more elongated centrum, more depressed neural arch, more depressed cotyles, absent or vestigial posterior median notch of the neural arch, and a relatively flat ventral surface of the centrum with almost no haemal keels (see Szyndlar & Georgalis 2023). *Plesiotortrix* cannot be referred to uropeltids, because the latter, which are currently endemic in India and Sri Lanka and with no definite fossil record available, have a relatively more elongate centrum, more depressed cotyle, more strongly dorsally inclined prezygapophyses, absent or very shallow posterior median notch of the neural arch, more depressed neural arch, neural spine confined solely to the posterior half of the neural arch, and (in some species) peculiar parasagittal posterior projections on the neural arch (see Szyndlar & Georgalis 2023). *Plesiotortrix* cannot be referred to caenophidians, as vertebrae of the latter are strikingly different, mainly characterized (usually) by a much more elongate centrum (with a few exceptions, e.g. acrochordids) and more pronounced prezygapophyseal accessory processes (see Zaher *et al.* 2019).

It seems that *Plesiotortrix* should be most probably referred to Constrictores, both sharing together the low ratio of centrum length/neural arch width (< 1.1) (Georgalis & Smith 2020; Szyndlar & Georgalis 2023). Nevertheless, a more precise determination within Constrictores seems a difficult task: *Plesiotortrix* is reminiscent of boids, stem representatives of which were anyway present in the Eocene of Europe (Scanferla & Smith 2020; Georgalis *et al.* 2021c; Smith & Georgalis 2022; Palci *et al.* 2024), bearing an overall similar vertebral morphology (see figures in Szyndlar & Georgalis 2023). A similar vertebral morphology is also present in pythonids (Szyndlar & Georgalis 2023), stem representatives of which were also present in the Eocene of Europe (Zaher & Smith 2020; Smith & Georgalis 2022; Smith & Scanferla 2022). Erycids and charinaids possess similar trunk vertebrae to *Plesiotortrix*, in terms of the relatively small size and centrum length to neural arch width ratio, but their most distinctive anatomical structures for taxonomic identifications, lie within their caudal vertebrae (Szyndlar & Georgalis 2023). Ungaliophiids are currently present only in the Americas and they have an Eocene fossil record over both North America and Europe (Smith & Georgalis 2022), however, their vertebrae are drastically different from *Plesiotortrix*, primarily in being more elongated and much lightly built (Szyndlar & Georgalis 2023). Xenopeltids, currently present only southeastern Asia, have a vertebral morphology deviating much from other Constrictores, primarily characterized by lightly built vertebrae with centrum longer than wide (Szyndlar & Georgalis 2023). Loxocemids, currently present exclusively in Central America, are absent from the European fossil record, though they have been identified in the Eocene of North America (Smith 2013); nevertheless, this group is characterized by a distinctive morphology of the subcentral ridges and grooves (Smith 2013; Szyndlar & Georgalis 2023), which is not observed in *Plesiotortrix*. The remaining groups of Constrictores, i.e., bolyeriids (endemic to the Mascarenes Islands), sanziniids (endemic to Madagascar), and candoiids (endemic to some Pacific Ocean islands) can be excluded as potential affinities of *Plesiotortrix*, judging not only from their much different vertebral morphology (see Szyndlar & Georgalis 2023), but also taking into consideration a biogeographic rationale.

These being said, after these extensive comparisons, I consider that *Plesiotortrix* taxonomically (most probably) lies within Constrictores, but a more precise referral to the

family level is impossible. As for the distinctiveness of the Quercy taxon, unfortunately, the incompleteness of certain anatomical structures of the holotype does not allow much information that could differentiate it from other snakes. Supposedly diagnostic features of *Plesiotortrix* that have in the past appeared in the literature (e.g. neural arch rather vaulted; neural canal rather high; centrum length longer than neural arch; interzygapophyseal constriction shallow; paracotylar foramina absent; prezygapophyses in anterior view clearly above the floor of the neural canal; paradiapophyses not projecting beyond the ventral border of cotyle; posterior median notch of neural arch obtuse; see e.g. de Stefano 1905; Rage 1984, 2001) are in fact either based on the inaccurate original Rochebrune's (1884) lithograph (e.g. the supposedly vaulted neural arch or the supposedly thick zygosphene or the supposedly very narrow interzygapophyseal constriction) or are either widespread anatomical features that are present across distantly related snake taxa. Accordingly, the genus *Plesiotortrix* and the species *Plesiotortrix edwardsi* have to be considered as nomina dubia.

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