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Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe

Georgios L. Georgalis^{1*} , Márton Rabi^{2,3} and Krister T. Smith^{4,5} 

Abstract

Large constrictor snakes, referred to the genera *Palaeopython* and *Paleryx*, are an ecologically prominent part of the fauna of Europe during the Paleogene. Most species were named over a century ago and their taxonomy is largely based on isolated vertebrae. Furthermore, the majority of named taxa originate from imprecisely known localities within the Phosphorites du Quercy, in southern France, and thus their exact age is not known. We critically review and re-diagnose these genera based on personal examination of all existing type material, an array of new specimens, and a detailed literature review. We consider *Palaeopython* and *Paleryx* to be valid and propose vertebral characters to distinguish them. We recognize three valid species of *Palaeopython*, i.e. *Palaeopython cadurcensis* (type species) from the Phosphorites du Quercy, *Palaeopython ceciliensis* from Geiseltal, and *Palaeopython helveticus* from Dielsdorf (Switzerland), and one valid species of *Paleryx*, i.e. *Paleryx rhombifer* (type species) from Hordle Cliff (England). Four other species, which were previously treated as members of *Palaeopython* and *Paleryx*, i.e. "*Palaeopython*" *filholii* and "*Palaeopython*" *neglectus* from the Phosphorites du Quercy, "*Palaeopython*" *fischeri* from Messel, and "*Paleryx*" *spinifer* from Geiseltal, are also considered as valid but pertain to other genera. Among these four taxa, "*Palaeopython*" *fischeri* has been recently assigned to its own genus, *Eoconstrictor*. A new genus, *Phosphoroboa* gen. nov. is established to accommodate "*Palaeopython*" *filholii*. We designate a lectotype for *Palaeopython cadurcensis* and establish that the paralectotype maxilla and dentary are reasonably referred to this species. New material attributed to *Palaeopython cadurcensis* is described from the old collections of the Phosphorites du Quercy. *Paleryx cayluxi*, another species established from the old collections of the Phosphorites du Quercy, is synonymized here with *Palaeopython cadurcensis*. We further clarify important errors in the original description and figures of *Paleryx cayluxi*, identify the exact specimens that comprise the type series, and designate a lectotype. Much new material is described for *Palaeopython ceciliensis* from its type area in Geiseltal and intracolumnar variation is considered. We describe additional vertebral and cranial material of *Paleryx rhombifer* from its type area in Hordle Cliff. Based on this cranial material, we suggest non-booid affinities for *Paleryx rhombifer*. We designate a lectotype for *Paleryx depressus* and agree with its previous suggested synonymy with *Paleryx rhombifer*. We re-describe the lectotype and paralectotypes of "*Palaeopython*" *neglectus* and refer and describe new material of this species from the Phosphorites du Quercy, paying special attention to intracolumnar variation; we also defer a decision on its generic relations until more abundant and complete material can be studied. We describe

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*Correspondence: georgios.georgalis@pim.uzh.ch

¹ Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland

Full list of author information is available at the end of the article



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new vertebral material of the booid *Eoconstrictor* cf. *fischeri* from Geiseltal; similar material was previously known only from Messel and Dielsdorf. We determine that *Eoconstrictor fischeri* contains two distinct and unrelated species and describe intracolumnar variation in the nominotype. We clarify certain issues regarding the type series of *Paleryx spinifer*, designate a lectotype, and report previously unrecognized cranial material associated with the latter specimen; we transfer this species to *Eoconstrictor* based on cranial features and recombine it as *Eoconstrictor spinifer* comb. nov. We finally describe much new vertebral and cranial material of *Phosphoroboa filholii* comb. nov. from the Phosphorites du Quercy (both from the old collections but also from the late Eocene localities of Escamps A and C), paying special attention to intracolumnar variation. Based on this cranial material from Escamps, we identify *Phosphoroboa* gen. nov. as a booid. An analytical approach is undertaken in many isolated remains in order to quantify vertebral structures and assess intracolumnar variation, as well as associating isolated cranial elements to vertebral-based taxa. 3D models of the type material of the Geiseltal and Messel taxa are presented. The importance of vertebrae in the taxonomy of fossil Constrictores is addressed, although it is acknowledged that it is cranial material that can afford the most reliable phylogenetic conclusions. The diversity, distribution, biogeographic origins, and final demise and extinction of large Constrictores in the Paleogene of Europe are discussed.

Keywords: *Palaeopython*, *Paleryx*, New genus, Serpentes, Taxonomy, Biogeography, Paleogene, Anatomy

Introduction

Large constrictor snakes—belonging to the lineage Constrictores Opper, 1811a (sensu Georgalis & Smith, 2020), which encompasses boas and pythons—are a diverse and ecologically prominent part of terrestrial faunal assemblages in the European Paleogene. For instance, in the early–middle Eocene site of Messel, Germany, specimens referred to the species *Palaeopython* (currently *Eoconstrictor*) *fischeri* Schaal, 2004, which reached over 2 m in length, are among the most abundant squamate species and are known to have consumed higher-level carnivores such as small crocodylians (Greene, 1983), lizards (Smith & Scanferla, 2016) and carnivorous mammals (Gunnell et al. 2018). These large constrictors have been known since the middle of the nineteenth century (Owen, 1850) and partly due to their prominence (in respect of size and abundance) have been accorded a great deal of taxonomic attention. Yet, many species were established on the basis of isolated vertebrae, others on the basis of both vertebral and cranial material, and after 170 years of study their taxonomy is perhaps understandably muddled.

The aim of this paper is to disentangle the complex alpha taxonomy of the largest Constrictores from the Paleogene of Europe, which have variously been referred to the genera *Palaeopython* and *Paleryx* (Barnes, 1927; De Stefano, 1905; Filhol, 1877a, 1877b, 1877c; Georgalis & Scheyer, 2019a; Kuhn, 1939a; Lydekker, 1888a; Owen, 1850; Rage, 1974; Rochebrune, 1880, 1884; Schaal, 2004). More specifically, we critically review the type material and the taxonomic status of all nominal species in order to identify valid species and phenetically defensible genera. We view this work as a necessary first step towards clarifying the phylogenetic relationships of the species concerned, and it will facilitate continuing studies on more complete material from the

German Konservat-Lagerstätten of Messel and Geiseltal. Most taxa are named on the basis of isolated vertebrae, and characters of isolated vertebrae are poorly suited to establishing phylogenetic relationships (e.g., Smith, 2013; Smith & Georgalis, in press). We also describe and figure previously undescribed cranial and vertebral material from the key Paleogene localities of the Phosphorites du Quercy (France), Geiseltal (Germany), Messel (Germany), and Hordle Cliff (United Kingdom). We further apply novel analytical practices to quantify certain vertebral structures, which can be used for disentangling intracolumnal and intraspecific variation. An analytical approach is also undertaken to infer association of isolated cranial elements to species typified by vertebral material.

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; GMH, Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle, Germany; HLMD, Hessisches Landesmuseum Darmstadt, Darmstadt, Germany; MBS, Naturhistorisches Museum, Basel, Switzerland; MDHC, Massimo Delfino Herpetological Collection, University of Torino, Torino, Italy; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; MTM, Hungarian Natural History Museum, Budapest, Hungary; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMP, Národní Muzeum Praha, Prague, Czech Republic; PIMUZ, Palaeontological

Institute and Museum, University of Zurich, Zurich, Switzerland; SMF-ME, Messel vertebrate collection, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany; SMF-PH, Paleoherpétology collection, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main, Germany; SMNK-PAL, Palaeontology collection of Staatliches Museum für Naturkunde Karlsruhe, Germany; UM, Université de Montpellier, Montpellier, France; UW_r, University of Wrocław, Wrocław, Poland; YPM, Yale Peabody Museum; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

Material and methods

The fossil specimens described herein are permanently curated at the collections of GMH, HLMD, MNHN, NHMUK, NHMW, PIMUZ, SMF-ME, SMNK-PAL, UM, and YPM. The 3D model of SMF-ME 929 was generated using smartSCAN 3D (Breuckman GmbH) with post-processing in PolyWorks v12 (InnovMetric Software Inc.). Extant material of Constrictores was used for comparative purposes and in the analytical methods, housed at the collections of CM, MDHC, MNCN, MNHN, MTM, NHMW, NMP, SMF-PH, UW_r, and ZZSiD. Additionally, many comparisons were made with CT scans available at Digimorph (<http://Digimorph.org> 2002–2020).

Measurements and their anatomical abbreviations follow Auffenberg (1963). In particular, CL=centrum length, measured ventrally and including the condyle; CoH=cotyle height; CoW=cotyle width; NAH=neural arch height; NAW=neural arch width, measured at the maximum interzygapophyseal constriction; NSPL=neural spine length; PO-PO=distance between the outer edges of the postzygapophyses; PR-PR=distance between the edges of the prezygapophyses; ZGH=zygantrum height; ZW=zygosphene width (see Fig. 1). To facilitate intracolumnar and interspecific analysis of the degree of vaulting, we introduce a “vaulting ratio”, which is measured in posterior view. A line connecting the outer edges of the postzygapophyses (distance PO-PO of Auffenberg, 1963) serves as the baseline. The vaulting ratio is then the height of the roof of the zygantrum to the PO-PO line, measured on the midline, to the half-width of PO-PO (Fig. 1).

The taxonomic history sections, listing of type material and type localities, diagnoses, and the overall format in the “Systematic palaeontology” part follow recent taxonomic reviews of fossil turtle groups (e.g., Georgalis & Joyce, 2017; Georgalis et al., 2021b; Joyce, 2016). As such, the taxonomic histories of each species presented below include only the establishments of new species, new

combinations, incorrect spellings of generic names or species epithets, and lectotype designations and thus do not include every single mention of each taxon into the literature. Taxonomy of extant snakes follows Georgalis and Smith (2020) for Constrictores, and for its inclusive clades, Pyron et al. (2014) for Booidea, and Reynolds et al. (2014) and Wallach et al. (2014) for Pythonoidea.

Localities and age

The snake material described herein originates from the Eocene of the Phosphorites du Quercy (various, unknown localities plus the precisely dated Escamps A and C [late Eocene, MP 19]), the early–middle Eocene (MP 11) of Messel, the late early or middle Eocene of Geiseltal, and the late Eocene (MP 17) of Hordle Cliff, The United Kingdom (Fig. 2). For reasons of completeness, we also refigure the holotype of *Palaeopython helveticus* from the late middle–late Eocene (MP 16–20) of Dielsdorf, Switzerland.

Phosphorites du Quercy, France

It is now known that the various localities of the Phosphorites du Quercy span a significant stratigraphic range, from the early Eocene (MP 8+9) until the early Miocene (MN 3), although the majority of them range from late middle Eocene (MP 16) to late Oligocene (MP 28) (Georgalis, 2017; Georgalis et al., 2021a; Rage, 2006; Sigé & Hugueney, 2006). Also, these localities are distributed over a considerable geographic area, extending over the current Departments of Lot, Tarn-et-Garonne, Tarn, and Aveyron, pertaining to the administrative region of Occitanie, in southern France (Sigé & Hugueney, 2006). Specimens from the so-called “old collections” from the Phosphorites du Quercy, which were mostly collected during the second half of the nineteenth century, originate from many different localities, and most lack any precise locality data. This applies to all type material of all named species of *Palaeopython*. As such, specimens from MNHN that were described in the nineteenth and early twentieth centuries lack precise locality data and this fact, frustratingly, concerns also the type material of *Palaeopython cadurcensis*, “*Palaeopython neglectus*,” and *Phosphoroboa filholii* comb. nov.

Among this type material, only for the paralectotype “mummy” of “*Palaeopython neglectus*” (MNHN.F QU16324) can a more precise age be estimated, but still of course accurate locality data are lacking. The age for this specimen can be estimated to pertain around the late middle–late Eocene (late Bartonian–late Priabonian [MP 16–19 or 20, about 40–34 Ma]). This assumption is based on the recent suggestion that all of the few snake and amphibian “mummified” specimens from the Phosphorites du Quercy described and figured by Filhol (1877a,

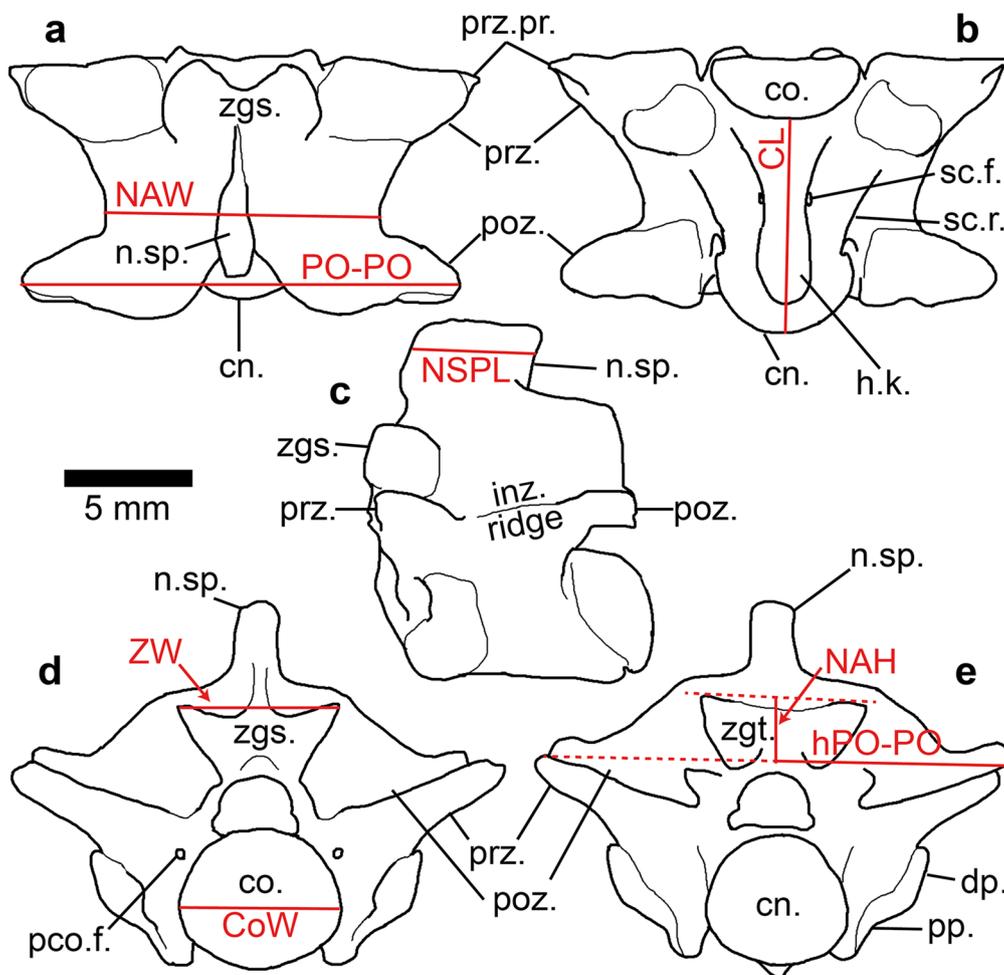
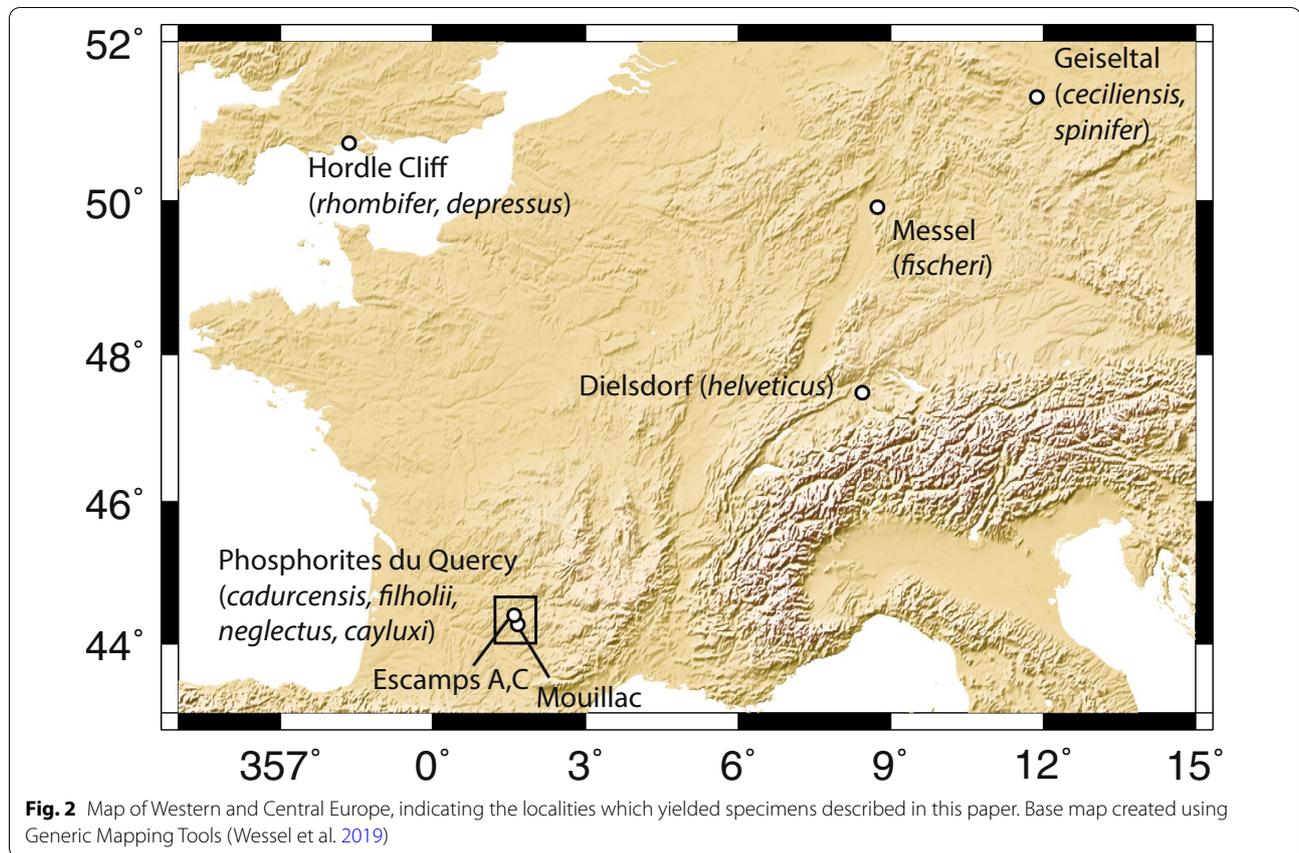


Fig. 1 Generalized figure of the vertebral anatomy of Constrictores, based on a trunk vertebra of *Boa constrictor* (specimen SMF-PH 40). Anatomical structures labelled in black and measurements labelled in red. CL, centrum length, measured ventrally and including the condyle; cn., condyle; co., cotyle; CoW, cotyle width; dp., diapophysis; h.k., haemal keel; hPO-PO, half-width of distance between the outer edges of the postzygapophyses; inz. ridge, interzygapophyseal ridge; NAH, neural arch height; NAW, neural arch width, measured at the maximum interzygapophyseal constriction; nsp., neural spine; NSPL, neural spine length; pco.f., paracotylar foramen; poz., postzygapophysis; PO-PO, distance between the outer edges of the postzygapophyses; pp., parapophysis; prz., prezygapophysis; prz. pr., prezygapophyseal accessory process; sc.f., subcentral foramen; sc.r., subcentral ridge; zgs., zygosphene; zgt., zygantrum; ZW, zygosphene width

1877b, 1877c) originate from a single locality, the age of which is constrained by the “mummy” of *Thaumastosaurus gezei* Rage & Roček, 2007, a frog that is also known in other well-dated localities from the area (see Laloy et al., 2013; Tissier et al., 2016). In addition, we remark that in the earliest brief description of such “mummified” amphibian and snake specimens, Filhol (1873a) mentioned that these originated from the “dépôts de phosphates de chaux de l’Aveyron”, and therefore the area could be potentially more geographically constrained within the Department of Aveyron. However, an alternative interpretation was recently made by Lemmiere et al. (2021), who suggested that all “mummified” specimens

could probably originate from a single, unknown, locality in the vicinity of Escamps, Department of Lot, and more particularly, potentially from one of the sites of Les Rosières (MP 17–19) or Les Tempories (MP 19). If this latter interpretation is correct, then the geographic provenance of the paralectotype “mummy” MNHN.F QU16324 is from the Department of Lot (and not Aveyron), but still its age is roughly identical (MP 17–19) with that of previous recent suggestions of Laloy et al. (2013) and Tissier et al. (2016).

This uncertainty about the exact provenance data (and therefore the age) also applies to the rich and abundant NHMW and YPM Quercy material. Many



NHMW specimens (NHMW 2019/0032/0001; NHMW 2019/0032/0005; NHMW 2019/0033/0001–NHMW 2019/0033/0041; NHMW 2019/0033/0049–NHMW 2019/0033/0084; NHMW 2019/0033/0130–NHMW 2019/0033/0153) are lacking labels, besides the basic information “Quercy”. Several NHMW specimens (NHMW 2019/0032/0003–NHMW 2019/0032/0004; NHMW 2019/0033/0085–NHMW 2019/0033/0129) are accompanied by an old label written in French “Trouvés dans diverses exploitations du Tarn-et-Garonne et du Lot” which suggests the mixed nature of the material. Three specimens (NHMW 2019/0020/0001–NHMW 2019/0020/0003) had only an old French label written “Trouvés dans le Département du Lot et du Tarn et Garonne”, whereas a few more specimens (NHMW 2019/0032/0002; NHMW 2019/0033/0042–NHMW 2019/0033/0048) had a relatively new label written in German “Schlangen Oligozän Quercy” [apparently this Oligocene corresponds to an older concept of that age, which is now instead considered as late Eocene (e.g., Bonis et al., 1973)]. The most precise locality information in the NHMW sample was given for specimen NHMW 2019/0066/0001, which was accompanied by a new label termed “Mouilliac bei Caylux”. However, this information

only denotes that it originated near the village of “Mouilliac” (currently called Mouillac), near Caylux, in the Department of Tarn-et-Garonne but is too general, as there are plenty of different localities in that vicinity (see map in Bonis et al., 1973: fig. 1). Overall, the NHMW *Palaeopython* and *Phosphorboa* gen. nov. material was accompanied by a vertebra of the Eocene “erycine” *Cadurceryx* and an array of lizard remains, pertaining to both Eocene and Oligocene taxa, hence further suggesting the mixed nature of the localities (see Georgalis et al., 2021a for these NHMW lizards).

Regarding the YPM material, the only available information denotes that it was collected near the village of Mouillac. However, like with the Mouillac material from NHMW, with only this information at hand, it is impossible to state whether they were all collected from a single or more than one of the several known localities in the area of Mouillac. Furthermore, besides snakes, the YPM Quercy material includes squamates that are both of Eocene and Oligocene age, such as *Saniwa* (Eocene) and *Pseudeumeces* (Oligocene).

The dentary NHMUK PV R 3489 also originates from an unknown locality near the village of Mouillac. The vertebral material from the collections of NHMUK bears

the basic information “Caylux, Tarn-et-Garonne”, which apparently hints towards some nearby locality(ies) near that town (modern spelling “Caylus”).

Lastly, a small number of vertebrae and skull elements of *Phosphoroboa filholii* comb. nov. from the collections of UM represent the only specimens from the Phosphorites du Quercy that bear precise locality data, originating from Escamps (A and C), a locality in the Department of Lot, that pertains to the late Eocene (MP 19) (Augé, 2005, 2012; Georgalis, 2017; Rage, 2006; Sigé & Huguene, 2006). Although located in different Departments, Escamps is relatively geographically near Mouillac, the area that yielded the YPM specimens and the dentary NHMUK PV R 3489. Escamps is a rather important locality, representing the namesake of the “landmark-level” (“niveau-repère” of Crochet et al., 1981) of Escamps, the final such level that precedes the “Grande Coupure” (Crochet et al., 1981; Rage, 1984a).

Messel, Germany

The Messel Pit (colloquially “Messel”) is located about 20 km south of Frankfurt am Main, Hesse, Germany. Messel has yielded a diverse vertebrate fauna, with many specimens characterized by exceptional, exquisite preservational attributes, including gut contents and the remains of scales, plumage and fur (Smith et al., 2018). There is also a rich arthropod fauna (Wedmann, 2018) and flora (Collinson et al., 2012; Lenz & Wilde, 2018). Messel represents an ancient maar lake formed by a phreatomagmatic eruption at 48.2 Ma (Lenz et al., 2015). All fossils derive from the Middle Messel Formation, which represents the stable phase of the lake’s history, in which a permanent stratification of the water column prevailed (Goth, 1990). The excavation sites in the pit span an interval of about 22–28 m (there is some uncertainty in the exact horizon of individual specimens) corresponding to c. 160–200 ka. Astronomically calibrated pollen profiles suggest that this profile spans the Ypresian–Lutetian boundary (Lenz et al., 2015).

Geiseltal, Germany

The former Geiseltal brown coalfield (today occupied by the Geiseltal lake), 30 km south of Halle (Saale), Sachsen-Anhalt, Germany, yielded a diverse fossil flora and fauna often characterized by exceptional preservation (e.g., Barnes, 1927; Krumbiegel et al., 1983). The fossiliferous part of the Geiseltal succession consisted of three major coal seams intercalated by silty and sandy clastic deposits with a maximal thickness of ca. 290 m. Vertebrate localities (“quarries”) of variable preservational conditions were distributed vertically and horizontally within the coal seams (e.g., Haubold & Thomae, 1990). Specimens of large Constrictores in Geiseltal, described herein, have

been recovered from the quarries IX, LII, I, VI, XXII, XLI, LIX, XXXIII, XXXV–XXXVIII, Cecilie I–IV, and Leonhardt I and III; among them, quarry Cecilie I is the type locality of the two named species from Geiseltal. The succession has long been considered Eocene in age (e.g., based on the tapiromorph *Lophiodon*; Schroeder, 1913) and lithostratigraphic correlation with nearby coalfields grading into heterotypic marine deposits (e.g., Quitzow, 1948). Regional spore–pollen biostratigraphy suggested an age spanning the entire Lutetian (middle Eocene, Spore/Pollen Zone 14/15–15; Krutzsch, 1966, 1970, 1976; Krutzsch et al. 1992). Jaeger (1971) also suggested Lutetian age for the Geiseltal fauna (middle Lutetian for the “Mittelkohle”—“middle coal” seam) based on similarities with the Bouxwiller mammals from Alsace in France, coming from lacustrine beds that can be correlated with the marine Lutetian (middle Eocene).

The works of Krutzsch apparently inspired the subsequent biochronology using mammal faunas, which established Geiseltal as the reference locality for the middle Eocene Mammal Paleogene levels (MP) 11–13 (=Geiseltalian). Geiseltal was considered to range from MP 11 to MP 14 and span the Lutetian (Franzen & Haubold, 1987; Haubold, 1987, 1989; Haubold & Thomae, 1990; Schmidt-Kittler et al., 1987). While apparent faunal similarities with Messel reasonably assume close age proximity, the temporal duration of the Geiseltal record is in fact less straightforward. A recent revision of propalaeothere and tapiromorph perissodactyls, taxa largely underpinning mammal biochronology at Geiseltal, however, found that earlier taxonomies are not reproducible and revealed a considerably lower diversity across the section than previously thought (Ring et al., 2020). Moreover, the mammal biochronology of Geiseltal, while based on first and last occurrence of index species, does not consider apparent taphonomic and collecting bias. Rigorous assignment of the various coal seams (Unter-, Mittel-, Oberkohle—lower, middle and upper coal) to MP levels is therefore impossible at the moment.

Until the regional palynostratigraphy of Krutzsch is better correlated with marine deposits, the inferred 5–11 Myr duration of the Geiseltal record (Franzen, 2005; Haubold & Thomae, 1990; Krutzsch, 2011) is doubtful. Considering the maximum present-day tropical carbon accumulation rate in peat with modelled mass loss during coalification (Large & Marshall, 2015), the deposition of fossiliferous lignite seams with the same minimal vertical thickness as in Geiseltal (70 m) has been estimated to require just over 1 Myr (Ring et al., 2020). The maximal thickness of the fossiliferous Geiseltal lignite seams totals 210 m and therefore requires ca. 3 Myrs at this depositional rate (67 cm/10 Kyr; Large & Marshall,

2015). The expected relatively low organic carbon content of the Geiseltal lignite seams (max. 60%, but usually significantly lower; Gusterhuber, 2007) and the inferred constant paratropical climate (Ring et al., 2020 and references therein) suggest that considering the maximal accumulation rate is reasonable (Large & Marshall, 2015). The total thickness of the clastic interbeds is 80 m, which may correspond to 800 Kyr calculating with the lower end of modern-day fluvial sedimentation rate (0.02 cm/year; Ferring, 1986) and the higher end of compaction rate (0.2 cm/year; Meckel et al., 2007). Consequently, based on sedimentation and compaction rates, the maximal temporal span of the bottom and top of the Geiseltal fossil record can be conservatively estimated to ca. 3.8 Myr. These being said, fossil remains from Geiseltal are dated around the late early or middle Eocene.

Hordle Cliff, England

The Hordle Cliff (also known in old literature under the name Hordwell) area in southern England is known since the first half of the nineteenth century and yielded a diverse array of vertebrate taxa, including several species of reptiles (Benton & Spencer, 1995; Holman & Harrison, 1998a, 1998b; Holman et al., 2006; Hooley, 1905; Klembara & Green, 2010; Lydekker, 1888a; Owen, 1850; Owen & Bell, 1849; Seeley, 1876). From there, Owen (1850) described the fossil constrictors *Paleryx rhombifer* and *Paleryx depressus*. All specimens described by Owen (1850) were collected from Hordle Cliff, with no precise stratigraphical data available; however, from Hastings (1852) it can be deduced that all Hordle Cliff snake remains were probably collected either from “Hastings Bed 1” (which now corresponds to the “Rodent Bed”) and from the upper part of “Hastings Bed 15” (which now corresponds to the “Mammal Bed”) (Milner et al., 1982). In any case, both “Rodent Bed” and “Mammal Bed” of Hordle Cliff are parts of the Totland Bay Member of the Headon Hill Formation and are currently considered as coeval (MP 17) (Klembara & Green, 2010), so we can be confident at least about the age of both *Paleryx rhombifer* and *Paleryx depressus* type material.

Taxonomic history and history of discoveries of the European large fossil Constrictores

In the middle of the nineteenth century, Richard Owen (1850) established a new genus of fossil snakes, *Paleryx*, comprising two species, *Paleryx rhombifer* and *Paleryx depressus*, on the basis of isolated vertebrae from the late Eocene of Hordle Cliff. This act marked the first ever description of a constrictor in the history of snake palaeontology, taking into consideration that the previously described giant aquatic snakes of the genus *Palaeophis* Owen, 1841, from the Eocene of the United Kingdom,

which were originally considered to have affinities with boas and pythons (e.g., Owen, 1841, 1850), are no longer considered to have close affinities with that lineage (e.g., Georgalis et al., 2020b; Rage et al., 2003). Only a few years later, Pictet et al. (1855–1857) described and figured vertebral material from the Eocene of mount Mormont, near Éclépens, Switzerland, which they assigned to two forms: one large-sized taxon, which they referred to *Python* Daudin, 1803a, and for which they estimated a total length of 3.25 to 3.5 m, and a smaller-sized one, which they suggested that it was referable to either *Python* or *Paleryx*. Gervais (1873, 1876) figured a trunk vertebra from the Phosphorites of Quercy, which he tentatively considered as comparable to *Palaeophis* (misspelled as “*Paléophis*”); however, this material was soon later re-identified as pertaining instead to constrictors by Filhol (1877a, 1877b, 1877c), and subsequently to *Palaeopython* (Rage, 2006). Filhol (1877a, 1877b, 1877c) established a new extinct species of *Python* (i.e. *Python cadurcensis*) on the basis of cranial and vertebral material from the Phosphorites of Quercy. A few years later, Rochebrune (1880) established his new genus *Palaeopython* in order to accommodate this Quercy form, regarding it as distinct enough from the extant species of *Python* and particularly *Python molurus* (Linnaeus, 1758) and *Python sebae* (Gmelin, 1789). In the same paper, Rochebrune (1880) also described a second species of this genus, *Palaeopython filholii*, on the basis of a single trunk vertebra, again from the Phosphorites du Quercy. Rochebrune (1884) later referred additional specimens to both *Palaeopython cadurcensis* and *Palaeopython filholii* and also established a third species of the genus, *Palaeopython neglectus*, again from the Phosphorites du Quercy. Zittel (1887–1890) described and figured an additional vertebra of *Palaeopython cadurcensis* from Quercy. The same author discussed the then-named species of both *Palaeopython* and *Paleryx* and provided emended diagnoses for both genera, but nevertheless he admitted the strong resemblance between them (Zittel 1887–1890). Lydekker (1888a) described several new specimens of both *Paleryx rhombifer* and *Paleryx depressus* and suggested that *Palaeopython* resembles *Paleryx* so greatly that the two genera should probably be considered synonyms, but he did not express this with certainty and furthermore left open the possibility that *Palaeopython cadurcensis* could be generically distinct as well. In another paper published in the same year, Lydekker (1888b) appeared even more confident about the synonymy of *Palaeopython* with *Paleryx*, whereas he also tentatively placed *Palaeopython filholii* into the synonymy of *Paleryx depressus*. This purported synonymy was subsequently followed by several authors who treated *Paleryx* as the valid genus name for the large Quercy constrictor (De Stefano, 1903, 1905;

Kuhn, 1939a, 1963; Nicholson & Lydekker, 1889; Romer, 1956; Swinton, 1926).

Other authors of the early and middle twentieth century defied this synonymy opinion and chose to treat *Palaeopython* and *Paleryx* as distinct (e.g., Arltdt, 1909; Auffenberg, 1963; Barnes, 1927; Gilmore, 1938; Hoffstetter, 1955; Huene, 1956; Nopcsa, 1928; Počta, 1905; Simpson, 1933; Williston, 1925; Woodward, 1932). Portis (1901) established his new species *Palaeopython sardus* on the basis of cranial material from the middle Miocene of Monte Albu, Sardinia, Italy, an occurrence that seemed to be the youngest record of *Palaeopython*, but this material has recently been demonstrated by Delfino et al. (2014) to not even to be a snake at all, but instead to represent a fish—accordingly, this taxon is omitted from consideration herein. De Stefano (1905), who accepted the synonymy of *Palaeopython* with *Paleryx*, described several new specimens from the Phosphorites du Quercy, which he referred to *Paleryx rhombifer*, *Paleryx filholii* (sic), *Paleryx neglectus*, but also established a fourth species of large constrictor, *Paleryx cayluxi*. Barnes (1927) described the first fossil constrictors from Germany by establishing two new species, *Palaeopython ceciliensis* and *Paleryx spinifer* from the middle Eocene of Geiseltal. Again from Geiseltal, Weigelt (1929) described and figured several large vertebrae, but he misidentified them for the large lizard *Palaeovaranus Zittel*, 1887–1890. When comparing his newly described giant Paleogene Argentinean taxon *Madtsoia bai* with European fossil large constrictors, Simpson (1933) pointed out important features of both *Palaeopython* and *Paleryx* that could differentiate them not only from his South American form, but also from each other. Gilmore (1938) also treated the two European genera as valid and proposed further characters that could differentiate *Palaeopython* from the North American *Boavus* Marsh, 1871. The most complete material of *Palaeopython* to that date was described by Kuhn (1939a), including partial skeletons with skulls from Geiseltal. The same author further properly referred Weigelt's (1929) vertebrae to snakes and particularly to *P. ceciliensis*, but he assigned both this taxon and *P. spinifer* to a single genus, *Paleryx* (Kuhn, 1939a). Since then, the beautiful snake skeletons from Geiseltal have received little attention, with only sporadic mentions with figures in the next decades (Krumbiegel et al., 1983). After a relatively long period without new descriptions or new remains, fieldwork occurring at various Eocene localities within the Phosphorites du Quercy during the past five decades resulted in the recovery of new material of large snakes. Much of this material remains undescribed, but important descriptions were published (Rage & Augé, 2010; Rage, 1974, 1978, 1988b). The most comprehensive of these works was that of Rage (1974) on Quercy

snakes, which allowed a better understanding of *Palaeopython*. In this work, Rage (1974) once again regarded *Palaeopython* and *Paleryx* as distinct, a view that has been widely accepted since then (e.g., Carroll, 1988; Georgalis & Scheyer, 2019a; Holman et al., 2006; Rage & Augé, 1993, 2010; Rage, 1984b, 1987, 2001; Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993; Wallach et al., 2014). The same author described additional vertebral and cranial material from Quercy, which he referred to *Palaeopython filholii* (Rage, 1974). Furthermore, for the first time since the end of the nineteenth century, Rage and Ford (1980) described additional material of *Paleryx rhombifer* from the late Eocene of the United Kingdom and also synonymized *Paleryx depressus* with the former species; subsequent mentions of *Paleryx rhombifer* from the Eocene of the United Kingdom were also made by Milner et al. (1982), Benton and Spencer (1995), and Holman et al. (2006) but were accompanied by no figures and therefore cannot be evaluated.

Moreover, the well-known and exceptionally preserved fossil locality of Messel, Germany, began to yield beautiful Eocene specimens similar to *Palaeopython*, initially briefly documented by Greene (1983), based on a cast, and by Habersetzer and Schaal (1990), the latter eventually becoming one of the paratypes of the recently described *Messelopython freyi* Zaher and Smith, 2020. More detailed studies revealed that the Messel form was specifically distinct from all other known taxa and afforded the establishment of a species of its own, *Palaeopython fischeri* (Schaal, 2004; see also Smith & Scanferla, 2016; Smith et al., 2018). Rosselet (1991) briefly described *Palaeopython* remains from the vertebral material from the middle to late Eocene of Dielsdorf, Switzerland. That material, along with other specimens from Dielsdorf, was subsequently extensively described and figured by Georgalis and Scheyer (2019a), who established another new species, *Palaeopython helveticus*. Finally, Scanferla and Smith (2020b) established the genus *Eoconstrictor* to accommodate the Messel species *Palaeopython fischeri* and, on the basis of a phylogenetic analysis, they suggested booid affinities for this taxon.

Systematic palaeontology

Owen (1850) highlighted the close resemblance of *Paleryx* with the extant genera *Eryx* Daudin, 1803b, and *Python*. Subsequent early workers highlighted the strong (or even congeneric) affinities of *Palaeopython* and *Paleryx* with *Python* (De Stefano, 1905; Filhol, 1877a, 1877b, 1877c; Lydekker, 1888b; Nicholson & Lydekker, 1889; Palacký, 1884; Rochebrune, 1880, 1884). Nevertheless, these extinct genera were until recently almost universally considered to be boids (Kuhn, 1939b, 1963; McDowell, 1987; Rage, 1974, 1984b, 1987; Szyndlar,

1994; Szyndlar & Böhme, 1993; Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993; Underwood, 1976), though in most of these taxonomic concepts of past decades, boids included both boas and pythons (see Georgalis & Smith, 2020). In its original establishment, Rochebrune (1880) placed *Palaeopython* into Pythonidae, for which group he followed the terminology of Duméril (1853) as Holodontiens—Pythonides. Palacký (1884), Zittel (1887–1980), Nicholson and Lydekker (1889), De Stefano (1905), and Počta (1905) also followed such placement into Pythonidae, considering it distinct from Boidae (their Boaeidae). Among recent authors, only Wallach et al. (2014) and Boundy (2021) treated *Palaeopython* and *Paleryx* as pythonids, though they did not provide any rationale for such a taxonomic arrangement. The taxonomic assignment of the two Paleogene genera to boids has been primarily made on the basis of cranial anatomy, and particularly the pterygoid, maxilla, and palatine morphology (Rage, 1974, 1984b; Szyndlar & Rage, 2003). So far, paracotylar foramina on the vertebrae of *Palaeopython* [a feature that is characteristic of certain booids (Georgalis, 2019; Georgalis et al., 2019b; Ivanov, 2000; Szyndlar & Rage, 2003)] had never been documented, with the exception of a record by Szyndlar and Rage (2003) who mentioned (but did not figure) a vertebra from Quercy (AMNH 242) that was clearly referable to *Palaeopython* and possessed a pair of paracotylar foramina. We here document the presence of paracotylar foramina in a few vertebrae of *Palaeopython cadurcensis* and *Palaeopython ceciliensis*, as well as in a few specimens of *Paleryx rhombifer* and *Phosphoroboa filholii* comb. nov., thus demonstrating that this feature, though rare, was still more widespread than previously thought. Furthermore, the extreme thickness observed in the zygosphenes of the vertebrae of some members of *Palaeopython* is in fact more reminiscent of pythonids rather than that of similarly sized boids. Rage (1974) considered the morphology of a pterygoid from the late Eocene of Escamps, which he referred to *Phosphoroboa filholii* comb. nov. (then placed in *Palaeopython*), to be more reminiscent of booids instead of pythonoids—we here redescribe and refigure this pterygoid and concur with its booid affinities. Moreover, Habersetzer and Schaal (1990), using X-radiographs, reported the presence of premaxillary teeth (a typical feature of pythonoids) in a specimen (SMF-ME 710) similar to *Palaeopython* from the early–middle Eocene of Messel—this observation on that material was subsequently questioned by Baszio (2004). Zaher and Smith (2020) later referred that specimen to the pythonoid *Messelopython freyi*, which in fact has premaxillary teeth; therefore, this specimen does not pertain to *Palaeopython*.

Georgalis and Scheyer (2019a) suggested that it is more secure to assign *Palaeopython* and *Paleryx* to “Booidea” sensu lato, which currently corresponds to Constrictores sensu Georgalis and Smith (2020), the clade comprising both boas and pythons. We also here treat both these two genera as Constrictores incertae sedis, thus not implying any closer relationship to either the lineages of Booidea or Pythonoidea. We note nevertheless, that based on the cranial morphology of *Paleryx rhombifer*, booid affinities are excluded for this taxon (see that entry below). Similarly, “*Palaeopython neglectus*” is also treated as Constrictores incertae sedis. On the other hand, the two species of *Eoconstrictor* (i.e. *Eoconstrictor fischeri* and *E. spinifer* comb. nov.) afford a more precise taxonomic placement, as this genus has recently been demonstrated to pertain to Booidea (sensu Pyron et al., 2014), having in particular close phylogenetic affinities with extant Neotropical boas (Scanferla & Smith, 2020b). We also suggest booid affinities for *Phosphoroboa filholii* comb. nov., based primarily on the cranial remains we describe from Escamps.

Detailed measurements of the type specimens of the species discussed below are presented in Table 1. See Appendix 4 for a hierarchical taxonomy of the valid taxa described in this paper.

Squamata Oppel, 1811b

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Constrictores Oppel, 1811a (sensu Georgalis and Smith, 2020)

Genus *Palaeopython* Rochebrune, 1880

Type species: *Python cadurcensis* Filhol, 1877a.

Referred species: *Palaeopython ceciliensis* Barnes, 1927, and *Palaeopython helveticus* Georgalis and Scheyer, 2019a.

Geographic and stratigraphic distribution: see Table 3.

Diagnosis: *Palaeopython* is assigned to Constrictores on the basis of its vertebrae being strongly built, the vertebrae taller than long, the centrum triangular and wider than long, prezygapophyseal accessory processes small, paradiapophyses undivided or only weakly divided into diapophyseal and parapophyseal portions, and lack of parazygantral foramina. *Palaeopython* can be differentiated from *Paleryx* and *Phosphoroboa* gen. nov. by the following features: larger size, with CL of mid-trunk vertebrae commonly >10 mm and up to 19 mm; very thick, strongly trapezoidal zygosphenes with flat anterior face in fully grown individuals; shallow, asymmetrical

Table 1 Detailed measurements of the type specimens of the species discussed in this paper

Species	Specimen	CL	NAW	CL/NAW	NSPL	NSPL/CL	PR-PR	CoH	CoW	ZW	ZW/CoW	NAH	hPO-PO	NAH/hPO-PO
		CL	NAW	CL/NAW	NSPL	NSPL/CL	PR-PR	CoH	CoW	ZW	ZW/CoW	NAH	hPO-PO	NAH/hPO-PO
<i>Palaeopython cadurcensis</i>	MNH.N.F. QUI16318 (lectotype)	c. 12.09	c. 18.48	0.65	c. 6.75	0.56	NA	NA	NA	NA	1.17	NA	NA	0.40
<i>Palaeopython ceciliensis</i>	GMH Ce I-2978-1926 (holotype)	NA	NA	NA	NA	NA	NA	6.14	6.89	8.54	1.24	NA	NA	NA
<i>Palaeopython helveticus</i>	PIMUZ A/III 634 (holotype)	10.5	14.75	0.71	5.30	0.50	18.0	5.39	6.12	7.3	1.19	NA	NA	NA
<i>Paleryx thombifer</i>	NHMUK PV OR 25259 (holotype)	8.36	9.33	0.90	4.00	0.48	14.39	4.73	5.30	5.51	1.04	2.79	7.36	0.38
<i>Paleryx depressus</i>	NHMUK PV OR 25261(1) (lectotype)	NA	NA	NA	NA	NA	NA	1.77	2.81	2.88	1.02	0.94	3.44	0.27
<i>Paleryx depressus</i>	NHMUK PV OR 25261(2) (paralectotype)	5.10	5.52	0.92	NA	NA	8.55	2.63	3.01	3.18	1.06	0.79	3.72	0.21
<i>Messelopython freyi</i>	SMNK-ME 461 (holotype)	c. 4.66	4.60	1.01	1.94	0.42	7.22	NA	2.80	3.01	1.08	1.34	3.02	0.44
<i>"Palaeopython" neglectus</i>	MNH.N.F. QUI16326 (lectotype)	6.08	6.98	0.87	3.41	0.56	10.82	3.56	3.68	4.99	1.36	c. 2.36	5.27	0.45
<i>Eoconstrictor fischeri</i>	SMF-ME 929 (holotype)	7.64	8.15	0.94	3.56	0.47	12.94	4.08	4.10	5.54	1.35	2.66	6.70	0.40
<i>Eoconstrictor spinifer</i> comb. nov.	GMH Ce I-2979-1926 (part of lectotype)	8.12	7.34	1.11	3.11	0.38	11.09	3.19	3.85	4.64	1.21	2.66	5.59	0.48
<i>Phosphoroboa filholii</i> comb. nov.	MNH.N.F. QUI16322 (holotype)	10.36	9.95	1.04	4.92	0.47	18.05	5.19	5.82	7.14	1.23	3.10	9.00	0.34

Note that the dimensions of the now lost lectotype of *Paleryx cayluxi* are not listed. All measurements in mm. For abbreviations, see "Material and methods"

interzygapophyseal constriction, extending no more medially than the mid-point of the prezygapophyseal articular facet; deeper paracotylar fossae; relatively sharp, slightly projecting ventral median keel present on centrum; small median tubercle on zygosphene usually present; and zygosphene broadly concave with anterolateral horns. *Palaeopython* can be differentiated from *Eoconstrictor* by the presence of a flared posterior process of the maxilla, a much thicker zygosphene, and relatively shorter mid-trunk vertebrae (CL/NAW ratio < 0.9). *Palaeopython* can further be differentiated from roughly co-occurring *Phosphorboa* gen. nov. by the presence of a flared posterior process of the maxilla, a longer neural spine on mid- and posterior trunk vertebrae (NSPL/CL > 0.5), and wider zygosphene (ZW/CoW > 1.2 on mid-trunk vertebrae). *Palaeopython* can further be differentiated from *Messelopython* by its larger size, shorter palatine process of the maxilla, a longer neural spine (NSPL/CL > 0.5 on mid-trunk vertebrae), and wider zygosphene (ZW/CoW > 1.2 on mid-trunk vertebrae).

Remarks: Rage (2001:Table 1b) provided important characters to distinguish several extinct and extant constrictors, including *Palaeopython* from *Paleryx*. Regarding the latter two genera, he particularly noted differences in the shape of the prezygapophyseal articular facets, the shape of the centrum, and the shape of the posterior median notch of the neural arch. We accept that the centrum shape often differs from that of *Paleryx* due in part to the convex subcentral ridges. However, we find that the posteromedian notch on the neural arch is variable even in the type series of *Palaeopython cadurcensis*. Also, we find that the prezygapophyseal articular facets grow much broader during ontogeny in vertebrae of the same position in extant *Boa constrictor* Linnaeus, 1758 (SMF-PH 45 vs. SMF-PH 40), suggesting that this reported difference may just be allometric; however, the main reason that this character does not obtain in our taxonomic scheme is because we have altered the composition of *Palaeopython* with respect to Rage's (1984b, 2001) conception.

Of the new features we have adduced, it is noteworthy that the shallow and asymmetrical interzygapophyseal constriction (reaching its deepest point posterior to mid-length) is seen in some extant constrictors. In *Boa constrictor*, it appears to be developed in a stable manner over a very large range of body size, as seen in specimens SMF-PH 46 and SMF-PH 40.

Like many other nineteenth century named genera, *Palaeopython* suffered from numerous misspellings throughout its long taxonomic history, with exaggerating name morphs such as "*Palaeophyton*" (e.g., Počta, 1905), which would literally translate as "old plant" in Greek!

Palaeopython cadurcensis (Filhol, 1877a)

(= *Paleryx cayluxi* De Stefano, 1905)

lectotype designation

Figures 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14 and 15

Taxonomic history: *Python cadurcensis* Filhol 1876b (nomen nudum); *Python cadurcensis* Filhol, 1877a (new species); *Palaeopython cadurcensis* Rochebrune, 1880 (new combination); *Paleryx rhombifer* = *Palaeopython cadurcensis* Lydekker, 1888b (junior synonym); *Paleopython cadurcensis* Palacký, 1898 (incorrect spelling of genus name and species epithet); *Palaeopython Cadurcensis* De Stefano, 1905 (emended spellings of genus name and species epithet); *Palaeophyton cadurcensis* Počta, 1905 (incorrect spelling of genus name).

Type material: MNHN.F QU16318 (formerly MNHN QU 318) (lectotype, herein designated), five articulated mid-trunk vertebrae (Filhol, 1877a, figs. 441–442; Filhol, 1877b, figs. 441–442; Filhol, 1877c, figs. 441–442; Georgalis & Scheyer, 2019a, fig. 15c; Figs. 3e, f, 4); MNHN.F QU16321 (formerly MNHN QU 321) (paralectotype), a complete left (not "right" as stated by Wallach et al., 2014) maxilla with teeth (Filhol, 1877a, figs. 435, 436; Filhol, 1877b, figs. 435, 436; Filhol, 1877c, figs. 435, 436; Rochebrune, 1884, pl. II.4; Rage, 1984b, fig. 12a; Figs. 3a, b, 5); MNHN.F QU16317 (formerly MNHN QU 317) (paralectotype), a right (not "left" as stated by Wallach et al., 2014) dentary with some preserved teeth (Filhol, 1877a, figs. 437, 438; Filhol, 1877b, figs. 437, 438; Filhol, 1877c, figs. 437, 438; Rochebrune, 1884, pl. II.3; Rage, 1984b, fig. 12b; Figs. 3c, d, 6); unknown collection (paralectotype), an isolated mid-trunk vertebra (Filhol, 1877a, figs. 439–440 and 443–444; Filhol, 1877b, figs. 439–440 and 443–444; Filhol, 1877c, figs. 439–440 and 443–444; Fig. 3g–j); unknown collection (paralectotypes), (unknown number of) vertebrae (Filhol, 1877a, not figured).

Type locality: Unknown precise locality, Phosphorites du Quercy, France; probably middle or late Eocene.

Previously referred material and range: Middle Eocene (MP 16), Lavergne, Quercy, France (referred material of Rage, 2013); middle Eocene (MP 16), Le Bretou, Quercy, Tarn-et-Garonne, France (referred material of Rage, 1988b); middle Eocene (MP 16), Robiac, Gard, Occitanie, France (material referred to *Paleryx cayluxi* by Rage, 1984b); middle or late Eocene, unknown precise locality(ies), type area, Phosphorites du Quercy, France (referred material of Rochebrune, 1880, Lydekker, 1888a, De Stefano, 1905, and Georgalis and Scheyer, 2019a; material referred to *Palaeopython filholii* [partim] by Rochebrune, 1884; material referred to *Paleryx rhombifer* by Lydekker, 1888a; material referred

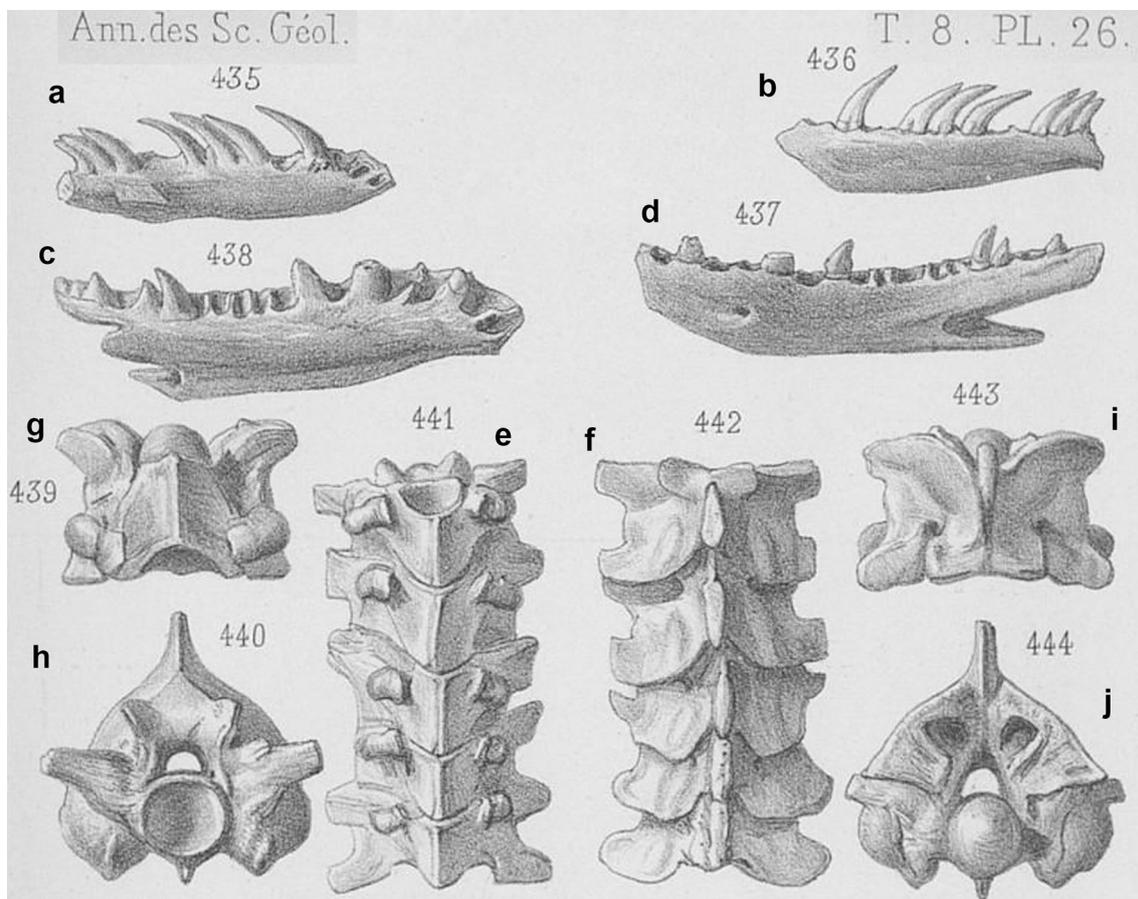


Fig. 3 Original lithograph of the type material of *Palaeopython cadurcensis* from imprecisely known localities in the Phosphorites du Quercy: **a**, **b** paralectotype left maxilla MNHN.F QU16321 in medial (**a**) and labial (**b**) views; **c**, **d** paralectotype right dentary MNHN.F QU16317 in medial (**c**) and labial (**d**) views; **e**, **f** lectotype (herein designated) five articulated trunk vertebrae MNHN.F QU16318 in ventral (**e**) and dorsal (**f**) views; **g–j** paralectotype (currently non-located) trunk vertebra in ventral (**g**), anterior (**h**), dorsal (**i**), and posterior (**j**) views. Note that the figures represent the reverse images of the respective specimens, as is the common practice in lithography. Modified from plate 26 of Filhol (1877a)—numbers 435–444 corresponds to the original figure numbering of that publication. The same exactly lithograph appeared in Filhol (1877b, 1877c)

to *Paleryx rhombifer* by De Stefano, 1905; lectotype of *Paleryx cayluxi* De Stefano, 1905).

Referred material discussed herein: Phosphorites du Quercy, imprecise localities (Figs. 7, 8, 9, 10, 11, 12, 13, 14 and 15): 26 trunk vertebrae (MNHN.F QU16319, MNHN.F QU16343–MNHN.F QU16357, NHMUK PV R 428 [two vertebrae], NHMW 2019/0032/0001–NHMW 2019/0032/0005, NHMW 2019/0033/0003, NHMW 2019/0033/0037, NHMW 2019/0033/0051) and a probable cloacal vertebra (NHMUK PV R 2799(1)). **Phosphorites du Quercy, imprecise localities near Mouillac:** two trunk vertebrae (NHMW 2019/0066/0001 and YPM-VPPU 29855).

Diagnosis: *Palaeopython cadurcensis* can be referred to the genus *Palaeopython* by the presence of the full list of characters given for that genus. *Palaeopython cadurcensis* differs from *Palaeopython helveticus* in being much

larger (up to 19 mm centrum length) and having a less vaulted neural arch and thicker zygosphene. *Palaeopython cadurcensis* differs from *Palaeopython ceciliensis* in its larger size, in having less vertically oriented zygosphenal articular facets, and in the presence of a weak zygosphenal tubercle. *Palaeopython cadurcensis* differs from both *Palaeopython ceciliensis* and *Palaeopython helveticus* in having more laterally extended, squared off prezygapophyses.

Description of the lectotype (MNHN.F QU16318): MNHN.F QU16318 is a string of five large articulated mid-trunk vertebrae (Fig. 4). The three anterior vertebrae have a centrum length (CL) of c. 12.1 mm. The anterior view is discernible only in the anterior-most vertebra (Fig. 4a), showing that the zygosphene is extremely thick. There is a small tubercle at mid-height on its anterior face. The lateral edges of the zygosphene project strongly

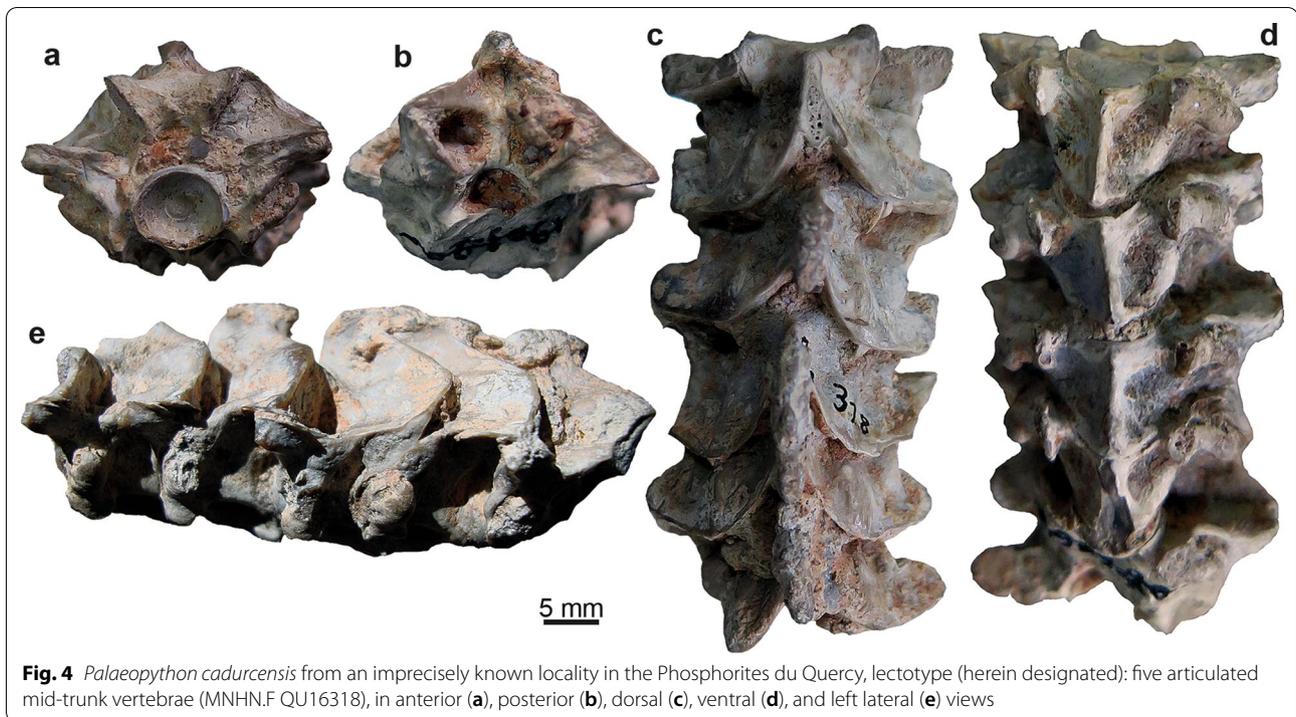


Fig. 4 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy, lectotype (herein designated): five articulated mid-trunk vertebrae (MNHN.F QU16318), in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

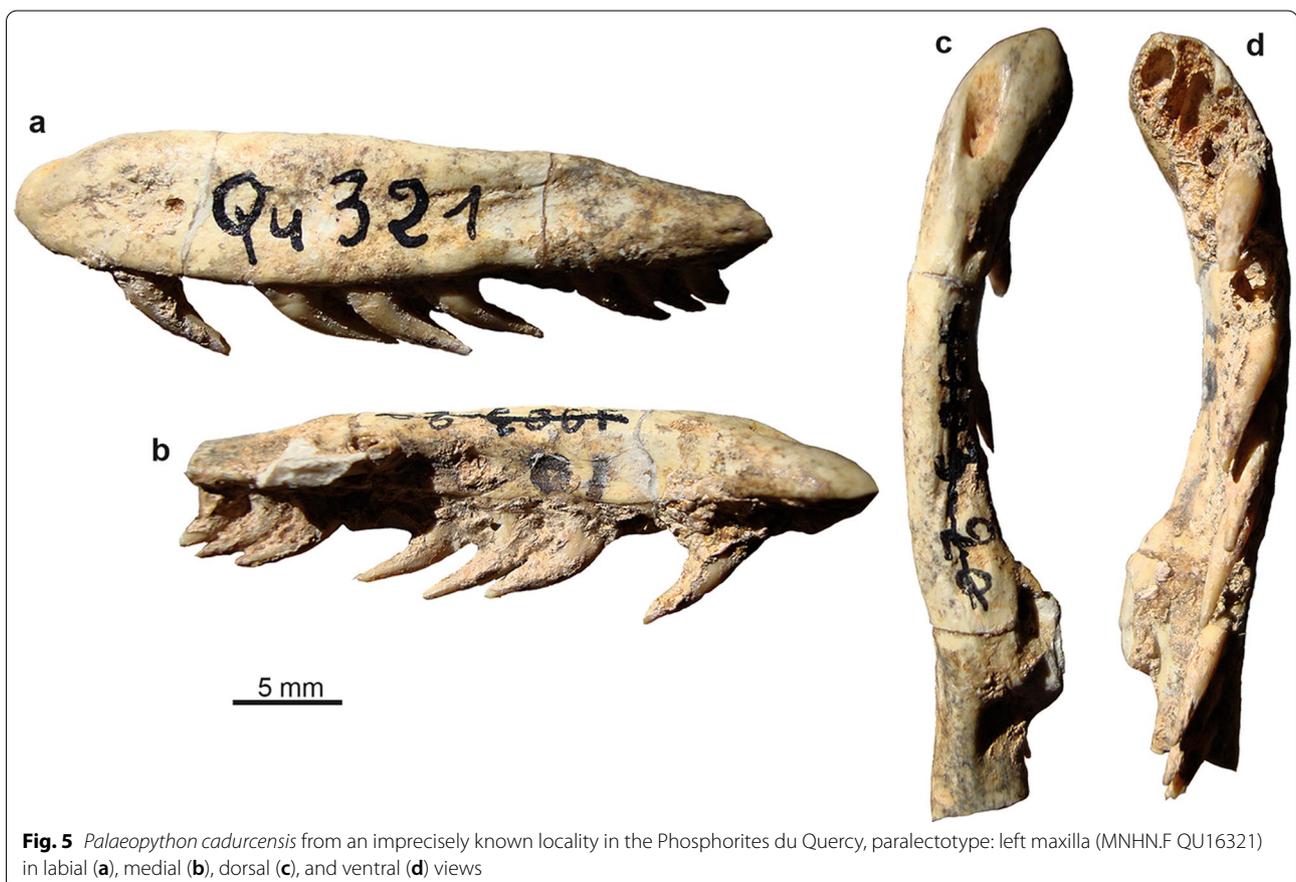


Fig. 5 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy, paralectotype: left maxilla (MNHN.F QU16321) in labial (a), medial (b), dorsal (c), and ventral (d) views



Fig. 6 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy, paralectotype: right dentary (MNHN.F QU16317) in labial (a), medial (b), dorsal (c), and ventral (d) views

dorsally and anteriorly, achieving a horn-shape. The zygosphene is much wider than the cotyle (12.9 mm and 11.0 mm, respectively; ratio ZW/CoW = 1.17). The cotyle is deep and almost circular. No paracotylar foramina are present. The prezygapophyses project laterally and slightly dorsally, so that the angle subtended by the zygosphenal and prezygapophyseal articular facets is 43–47°. The shape of the neural canal cannot be fully evaluated, due to adhering sediment, but it appears to be roughly triangular in cross-section. The posterior view can only be studied in the posterior-most vertebra (Fig. 4b). The vaulting ratio is 0.38, i.e. moderately vaulted. The zygantrum is deep and is marked dorsally by prominent, elongate zygantral mounds (sensu Hecht in McGrew, 1959) on the dorsal surface of the neural arch. The shape of the condyle cannot be evaluated, as that portion of the vertebra is damaged. In dorsal view (Fig. 4c), the vertebrae are wider than long. The neural spines are relatively thick and they develop almost immediately after the zygosphene. The neural spine overhangs the median notch of the neural arch posteriorly. The postzygapophyses are subrectangular and project strongly laterally. The prezygapophyses also project laterally and the prezygapophyseal articular facets are oval. The prezygapophyseal accessory processes are small and acute. The zygosphene is exposed only on the anterior-most vertebra. It is concave (sensu

Auffenberg, 1963). In ventral view (Fig. 4d), the centrum is subtriangular, being much widened anteriorly. The haemal keel is fairly sharp throughout its length; it extends along nearly the entire length of the centrum and grows slightly deeper posteriorly. The paradiapophyses are only weakly divided into dorsal diapophysis and ventral parapophysis; the former is weakly convex and the latter is weakly concave and projects below the centrum. In lateral view (Fig. 4e), the vertebrae are much taller than long. The neural spine is best preserved in the second vertebra. The neural spine is moderately high and posteriorly inclined.

Description of the paralectotype vertebra figured in Filhol (1877a, 1877b, 1877c): This is an isolated trunk vertebra (Fig. 3g–j). Taking into account that the specimen cannot be located, the description herein is based on the original lithographic illustration of Filhol (1877a, 1877b, 1877c). As such, certain features might be subjected to inaccuracies. Like the lectotype, it probably pertains to the mid-trunk region from the vertebral column, though possibly more anteriorly in the series. The specimen is similar to the lectotype, and therefore we focus on major differences and features not visible in the lectotype. The zygosphene is less concave than in the lectotype. A small tubercle on the zygosphene appears to be absent. The diapophysis appears to be more prominent

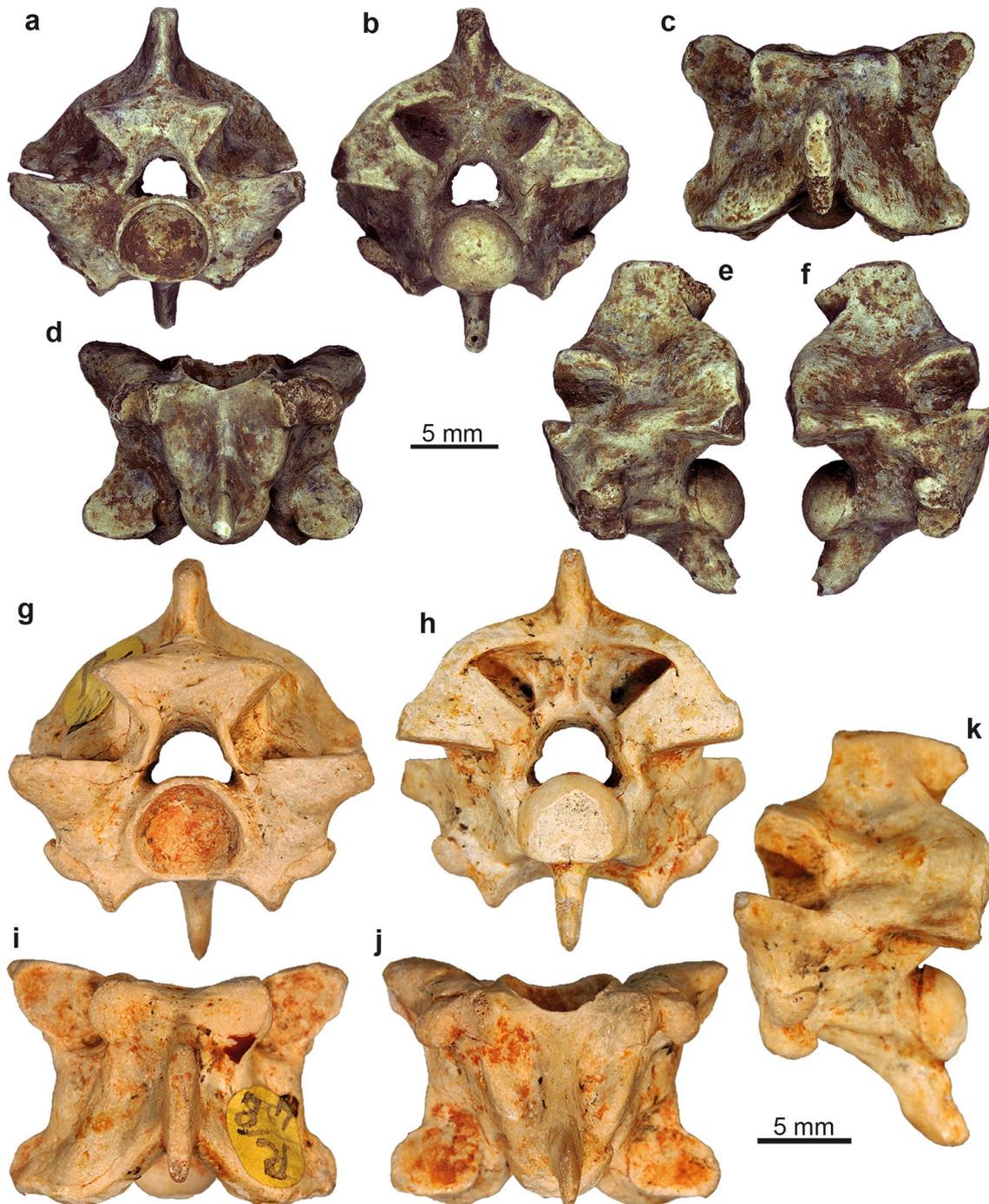


Fig. 7 *Palaeopython cadurcensis* from imprecisely known localities in the Phosphorites du Quercy: **a–f** anterior trunk vertebra (NHMW 2019/0032/0004) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views; **g–j** anterior trunk vertebra (NHMUK PV R 428(1)) in anterior (**g**), posterior (**h**), dorsal (**i**), ventral (**j**), and left lateral (**k**) views

than the lectotype, but its dorsal margin is less sharp. The angle subtended by the zygosphenal and prezygapophyseal articular facets is somewhat greater, which is consistent with the much greater vaulting of the neural

arch. The neural canal is small and triangular. The neural spine is taller. Zygantral mounds may be present, but they are much less discrete than in the lectotype. The condyle is nearly circular, just slightly taller than wide,

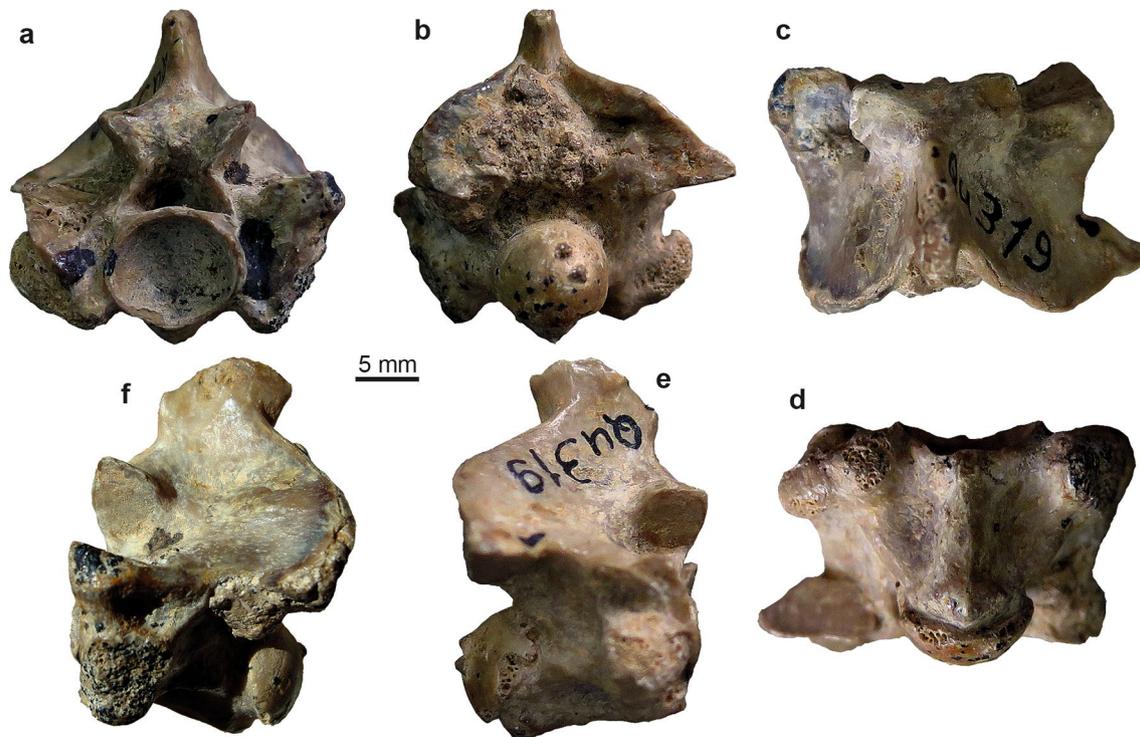


Fig. 8 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: mid-trunk vertebra (MNHN.F QU16319), formerly considered a syntype of the species, in anterior (a), posterior (b), dorsal (c), ventral (d), right lateral (e), and left lateral (f), views. This specimen was originally figured as a lithograph by Rochebrune (1884:pl. II.3^a–3^b)

and (like the cotyle) is significantly larger than the neural canal. The lateral view is not depicted in the lithographic illustration.

Description of the paralectotype maxilla (MNHN.F QU16321): MNHN.F QU16321 is a large, incomplete left maxilla (Fig. 5). We consider the assignment of this specimen to the same species as the holotype to be justified on the basis of the size of the teeth, which is similar to the size of the paralectotype dentary teeth (see “Remarks” below). The premaxillary process is smooth and rounded. It is club-shaped, growing in width anteriorly before tapering again to a point. Like in other snakes, it lacks an articulation facet for the premaxilla. On its dorsal surface there opens a large anterior dorsal foramen [sensu Scanlon (2001), probably homologous with the “anterior superior alveolar foramen” of Smith and Gauthier (2013) in lizards], located above the anterior part of the 3rd tooth position. The foramen continues anteriorly as a deep, anterolaterally trending groove; it grows in width anteriorly as well, thus maintaining a nearly constant width ratio of 0.26–0.27 with respect to the premaxillary process. A relatively strong remnant of the lizard facial process (sensu Gauthier et al., 2012) rises at the level of the anterior dorsal foramen and diminishes gradually,

disappearing at roughly the level of the palatine process. On the medial side of its posterior half is a set of smooth grooves and, posteriorly, a depression that indicate where the prefrontal articulated. The grooves suggest a more intimate connection of the maxilla and prefrontal than in *Boa* Linnaeus, 1758. There is a single, relatively small labial foramen at the level of the boundary between the 4th and 5th tooth positions. Near the posterior end of the facial process, at approximately the level of the palatine process, is a small, horizontal groove of unknown significance; there might be a tiny foramen at its anterior end.

The palatine process has a relatively short base (covering tooth positions 8–10), more reminiscent of booids; its distal extremity is broken. On its dorsal surface near the anterior base is a medially opening foramen, homologous with the superior alveolar foramen of lizards (Maisano & Rieppel, 2007), which receives the maxillary artery and superior alveolar nerve. There is a deep fossa on the dorsal surface of the bone level with the posterior margin of the palatine process, which might house a second foramen, although this was not ascertained during our respective visits. Note that in the bolyeriid *Casarea dussumieri* (Schlegel, 1837), a fossa is present (where it receives the “suborbital ossification” of Maisano and

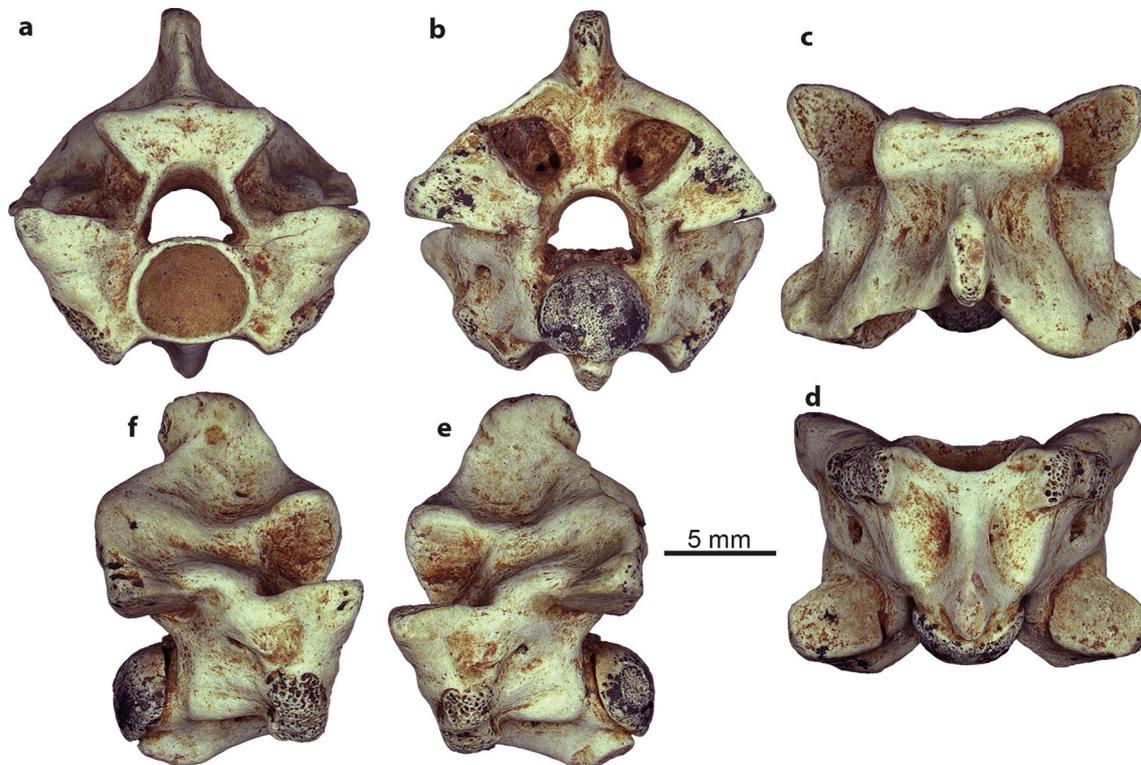


Fig. 9 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: anterior to anterior mid-trunk vertebra (NHMW 2019/0033/0051) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

Rieppel [2007]) but not a foramen, whereas in *Boa* there is a foramen in the same position that communicates with the superior alveolar canal. The posterior process (sensu Oelrich, 1956) of the maxilla is broken.

The specimen contains 13–14 tooth positions and 7 teeth. The teeth are conical. Their surfaces are generally smooth, except for a small, horizontal depression near the labial base of several middle teeth. It was not ascertained during our visits whether cutting edges (sensu Scanlon, 2001) are present. Our photographs, however, show a fine lingual cutting edge on at least the sixth tooth (Fig. 5); on the labial surfaces it is unclear. The anterior teeth are longest, and tooth length decreases posteriorly, gradually and continuously. While all teeth are recurved, the anterior teeth are less so than the posterior ones.

Description of the paralectotype dentary (MNHN.F QU16317): MNHN.F QU16317 is a large (47.0 mm long), nearly complete right dentary (Fig. 6). We consider assignment of this specimen to the same species as the lectotype to be justified by consideration of size (see "Remarks" below). The bone is tall, even at its anterior end, with a depth (measured in the middle of the jaw) to length (measured to the tip of the surangular process) ratio of about 0.22. This value is 37–275% higher than

in any other measured constrictor [0.16 in *Boa imperator* Daudin, 1803a, 0.14 in *Chilabothrus striatus* (Fischer, 1856), 0.11 in *Lichanura trivirgata* Cope, 1861a, 0.13 in *Calabaria reinhardtii* (Schlegel, 1851), 0.08 in *Loxocemus bicolor* Cope, 1861b, 0.12 in *Python bivittatus* Kuhl, 1820, 0.14 in *Aspidites melanocephalus* (Krefft, 1864), 0.15 in *Eryx colubrinus* (Linnaeus, 1758) (all from Digimorph), 0.15 in *Candoia carinata* (Schneider, 1801) (specimen MBS 7103)] and could be an autapomorphy. However, it is notably similar to the pathological left dentary of *Boa imperator* FMNH 31182 (Digimorph), and ratios presented by Hoffstetter (1959: Fig. 2) suggest that other constrictors like the Madagascan Sanziniidae Romer, 1956, and the Neotropical *Eunectes* Wagler, 1830, may be similar.

Tooth morphology is difficult to compare with the paralectotype maxilla, because the anterior teeth in the dentary are poorly preserved. The fourth tooth from the rear is short, but its degree of curvature is not incompatible with that of the maxillary teeth. The mesial-most tooth locus is offset, directed more medially than dorsally, and the parapet of the dentary is reduced. This feature is also found in at least some *Boa* spp. (CM 145311), *Ungaliophis continentalis* Müller, 1880 (data from

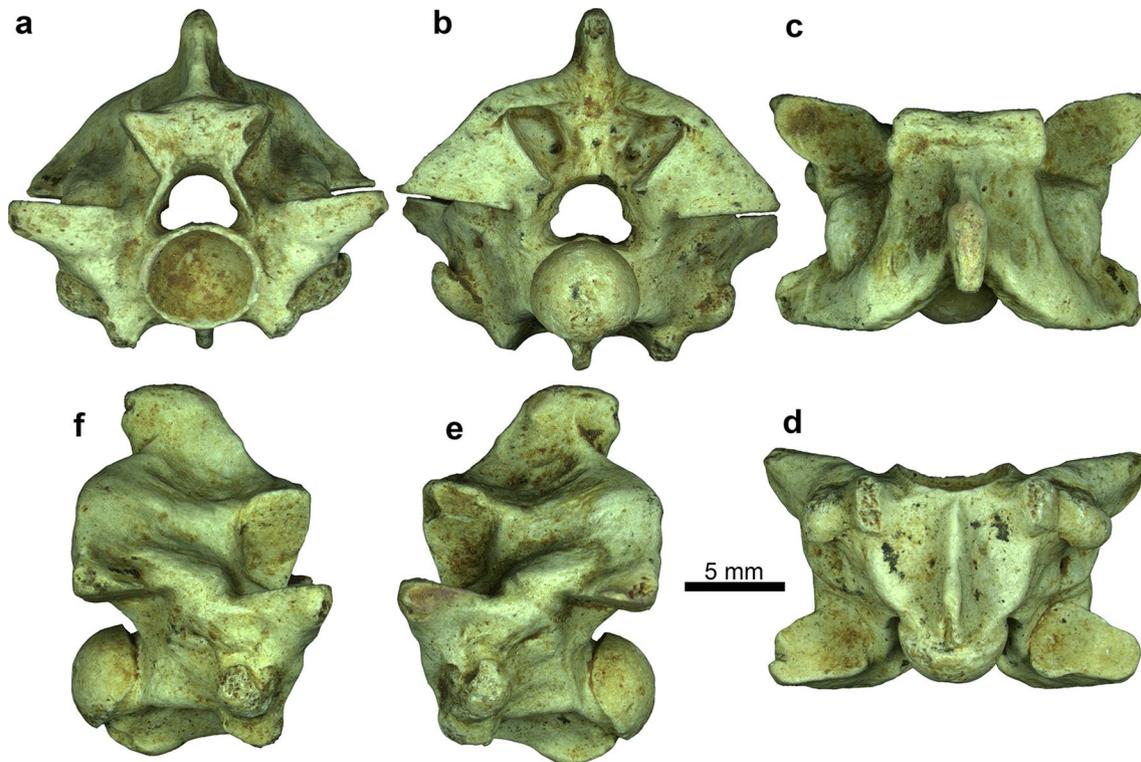


Fig. 10 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: anterior to anterior mid-trunk vertebra (NHMW 2019/0033/0037) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

Digimorph), but it is apparently variable; for instance, it is found only on the left side of *Boa imperator* (data from Digimorph). It was not found in other Digimorph scans of constrictors. In *Boa imperator*, this appears to be compensated by a more recurved tooth, so that the tooth itself is not directed medially.

The specimen preserves 18 tooth positions and six partial teeth, only one of which is close to complete. A single large mental foramen opens at the level of the fourth tooth position. The lateral surface of the bone is nearly vertical, curving medially only near the ventral margin. The ventral margin runs parallel to the dorsal margin in the posterior two-thirds of the bone, but beneath the fifth tooth there is an inflection point where the margin runs abruptly more dorsally. The bone is thickened along this ventral rim anteriorly. The surangular notch is deep, separating the dentigerous posterodorsal process from the posteroventral process and exposing the intramandibular septum laterally, as in *Boa* and *Python*. Unlike in most extant boids, the posterodorsal process is much more posteriorly extensive than the posteroventral process; in this respect it is more similar to certain pythonids [e.g., *Python bivittatus*, *Morelia riversleighensis* (Smith and

Plane, 1985) (see Scanlon, 2001:fig. 4)] and *Xenopeltis unicolor* Reinwardt in Boié, 1827.

The Meckelian groove is open throughout the length of the dentary. The suprameckelian lip is tall; anteriorly it is somewhat concave in transverse section, posteriorly somewhat convex. The posterior prong of suprameckelian lip seen in the paralectotype MNHN.F QU16317, termed the posteroventral prominence by Scanlon (2001), is also present in all suitably prepared (disarticulated) constrictors; in extant taxa it is braced medially by the splenial and coronoid and a facet is observed in this position in this fossil specimen.

Description of other vertebral material from Quercy—intracolumnar variation (Figs. 7, 8, 9, 10, 11, 12, 13, 14 and 15): Two specimens (NHMW 2019/0032/0004 and NHMUK PV R 428(1)) could be securely identified as anterior trunk vertebrae (Fig. 7). They are smaller than most mid- and posterior trunk vertebrae (CL around 9.0 mm). The neural arch is vaulted (vaulting ratio=0.50) but not in an exceeding degree for a vertebra in this position. The neural spine is slightly taller than in the lectotype, inclining posteriorly and broadening slightly distally. The zygosphenes are relatively thick in anterior view, though not as thick as

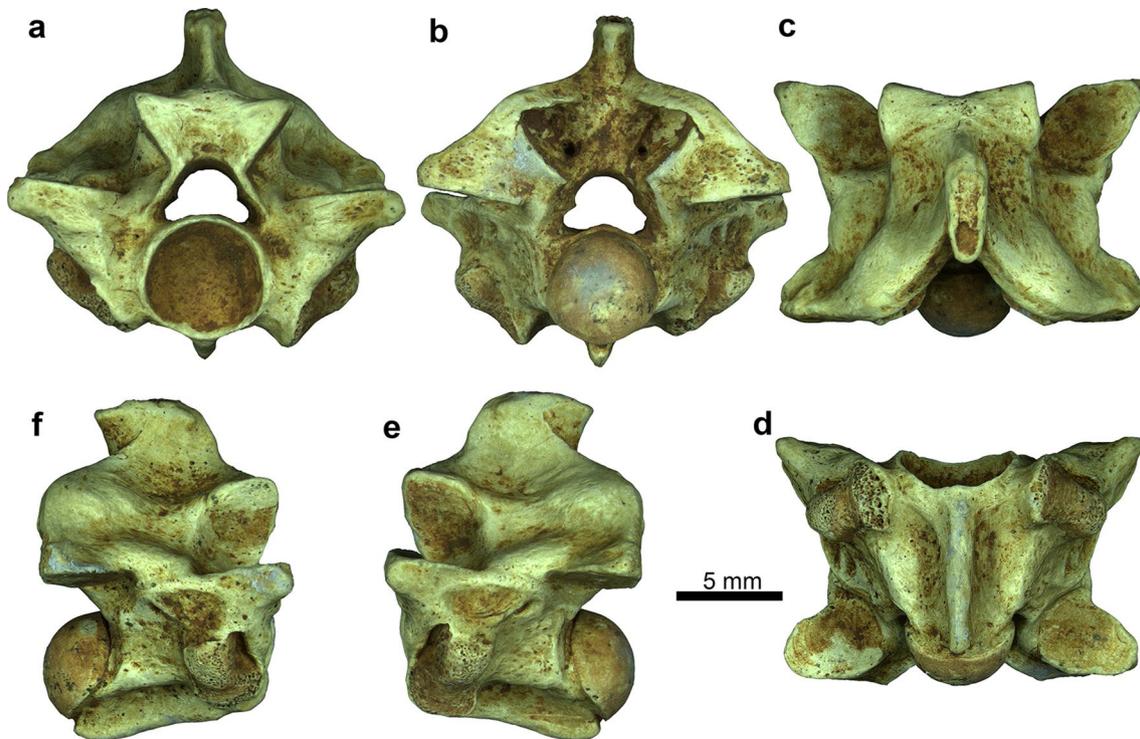


Fig. 11 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: mid-trunk vertebra (NHMW 2019/0033/0003) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

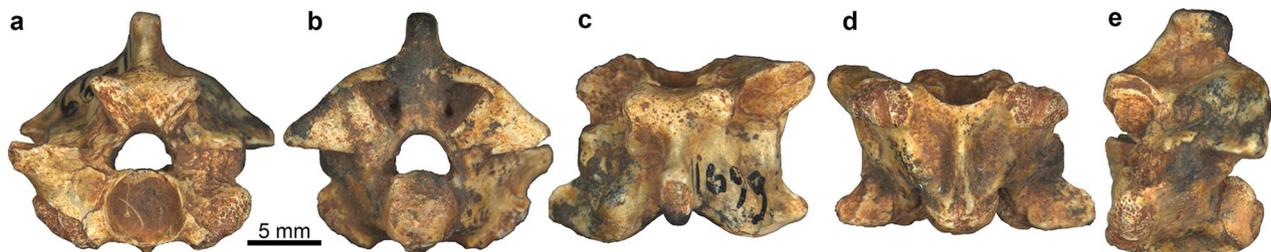


Fig. 12 *Palaeopython cadurcensis* from imprecisely known locality near Mouillac, Phosphorites du Quercy: mid-trunk vertebra (YPM-VPPU 29855) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

in the succeeding trunk vertebrae. Its width exceeds that of the cotyle on NHMW 2019/0032/0004 (as on the lectotype and all other vertebrae assigned to the species). The hypapophysis is relatively thick and long; in NHMW 2019/0032/0004 its terminus is broken but seems to not extend beyond the condyle (Fig. 7a–f), but in NHMUK PV R 428(1) it is fully preserved, is large and exceeds posteriorly the level of the condyle in lateral view (Fig. 7g–k). The centrum is widened anteriorly, though not to the same extent as in succeeding mid-trunk vertebrae. The diapophysis and parapophysis are more distinct than in the lectotype. Cotyles and condyles are nearly circular.

Mid-trunk vertebrae are all wider than long (Figs. 8, 9, 10, 11, 12, 13). Although sample size is small, they apparently show a relatively high vaulting ratio (0.39–0.49), the lectotype being at the low end of this range. The zygosphenes are extremely thick in all specimens. The largest referred specimen is MNHN.F QU16319, with centrum length near 19 mm (Fig. 8); the lateral asymmetry of the zygosphenes in this specimen is presumably due to deformation or pathology. A small tubercle around the mid-level of the zygosphenes is usually present (e.g., lectotype MNHN.F QU16318). The zygosphenes usually have more or less distinct and prominent lateral edges, resembling

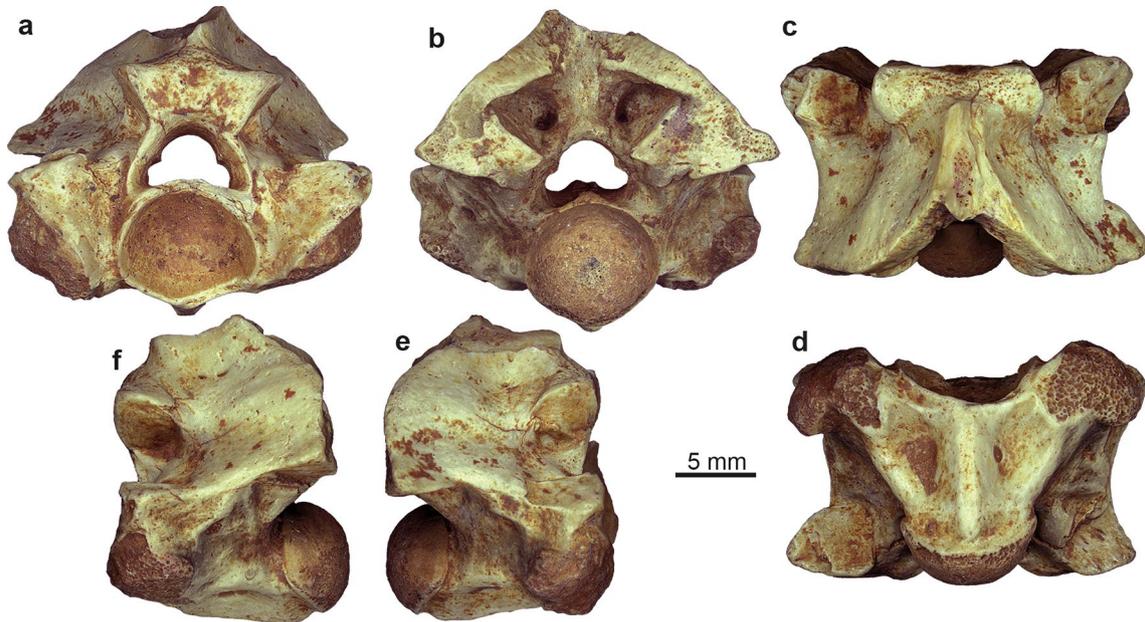


Fig. 13 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: mid- to posterior trunk vertebra (NHMW 2019/0032/0003) in anterior (a), posterior (b), dorsal (c), ventral (d), right lateral (e), and left lateral (f) views

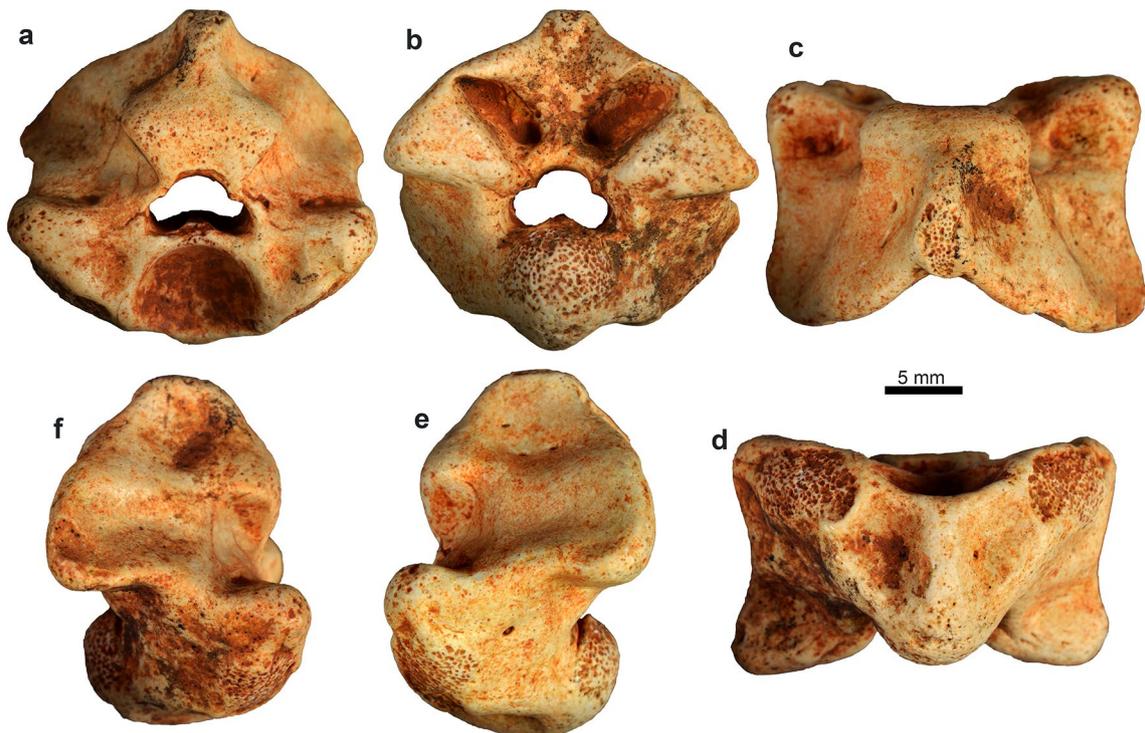


Fig. 14 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: posterior trunk vertebra (NHMW 2019/0032/0002) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views. Note that the vertebra is considerably eroded

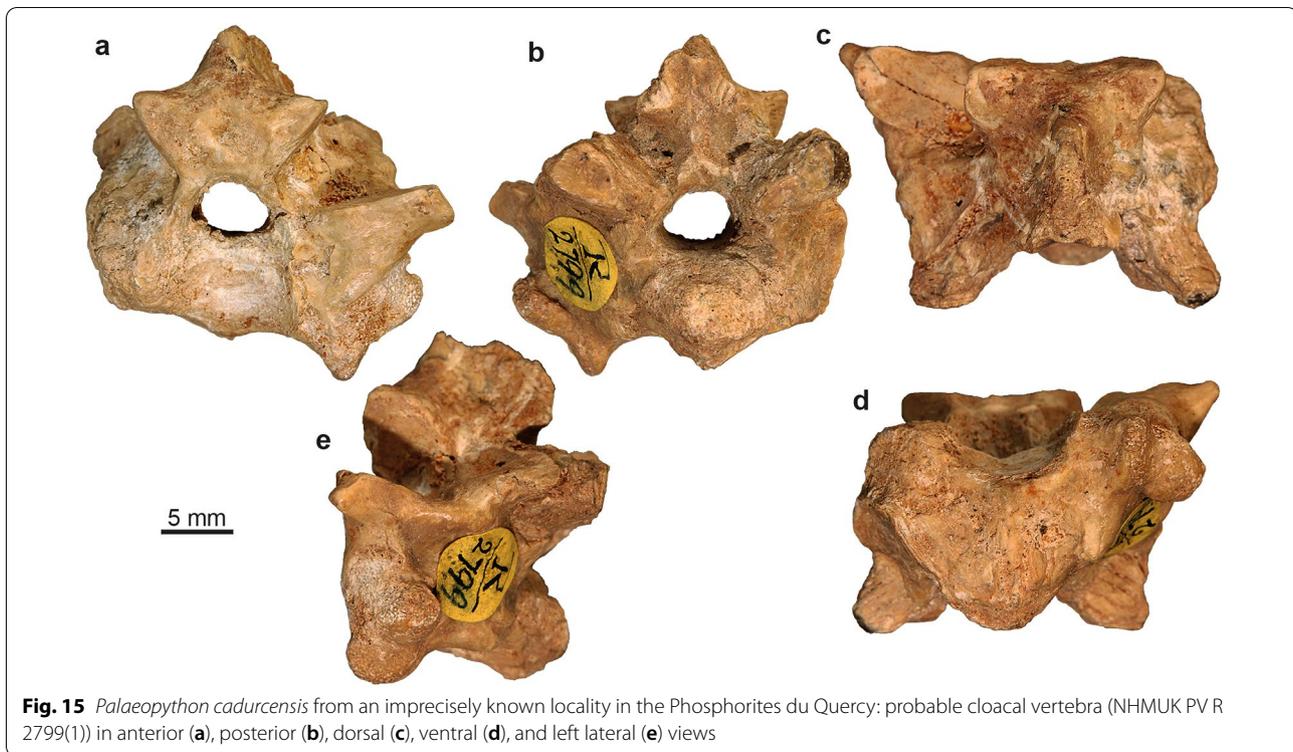


Fig. 15 *Palaeopython cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: probable cloacal vertebra (NHMUK PV R 2799(1)) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

horns. The cotyle can be rather large and deep. The neural spine can be quite tall and is slightly inclined posteriorly. In the neural canal, a distinct raised area (“subneural process” sensu Auffenberg, 1963; “epapophysis” sensu Holman, 2000) is usually prominent, especially in posterior view. The subcentral ridges are generally laterally convex. Subcentral foramina sometimes present and can be rather large (e.g., NHMW 2019/0032/0003). Paracotylar foramina are absent with the sole exception of NHMW 2019/0033/0003, where a large such foramen lies on the right side of the cotyle (Fig. 11a).

Posterior trunk vertebrae have a much wider haemal keel (e.g., MNHN.F QU16345; NHMW 2019/0032/0002). In one large, but eroded, posterior trunk vertebra (NHMW 2019/0032/0002), the centrum is much compressed anteroposteriorly (Fig. 14). Subcentral foramina are usually present. The zygosphene is still thick in vertebrae of this region. The neural arch is less vaulted than in mid-trunk vertebrae. Neural spine foramina (sensu Georgalis & Scheyer, 2019a) can be also present here, as seen on the left side of NHMW 2019/0032/0002.

The only known probable cloacal vertebra is NHMUK PV R 2799(1) (Fig. 15). Judging from the wide and the relatively dorsoventrally high haemal keel, it seems that it probably pertains to the anterior cloacal region (or possibly the posterior-most trunk). Most of the lymphapophyses (only the left is partially preserved) is broken in

this specimen. The zygosphene is here also rather thick (Fig. 15a). The interzygapophyseal constriction is shallow. Prezygapophyseal accessory processes are slightly more prominent than elsewhere in the column.

Caudal vertebrae are currently unknown for this species.

Remarks: Filhol (1877a) established *Python cadurcensis*, providing a description and figures of cranial and postcranial material from the Phosphorites du Quercy. Filhol (1877a, 1877b, 1877c) also tentatively referred the vertebral material that had been previously described and figured by Gervais (1873, 1876) to his new species. He already noted the strong resemblance of this material both to extant *Python* and to the fossil constrictors from the late Eocene of Switzerland that had been described by Pictet et al. (1855–1857) (Filhol, 1877a, 1877b, 1877c). A few years later, Rochebrune (1880) established his new genus *Palaeopython* in order to accommodate this Quercy form, regarding it as distinct enough from the extant species of *Python* and particularly *Python molurus* (Linnaeus, 1758) and *Python sebae* (Gmelin, 1789). The same author later referred to *Palaeopython cadurcensis* additional specimens (Rochebrune, 1884). Since then, only a limited number of specimens have been referred to *Palaeopython cadurcensis*, with brief descriptions and few figures (Rage, 1988b, 2013).

A clarification regarding the appropriate authorship and authorship date of *Palaeopython cadurcensis* is needed. There is a broad consensus that these are attributed to “Filhol, 1877” (e.g., Georgalis & Scheyer, 2019a; Kuhn, 1939b; Rage, 1974, 1978, 1984b; Schaal, 2004; Szyndlar & Schleich, 1993; Wallach et al., 2014). In fact, the name *Python cadurcensis* appeared earlier. Specifically, 1 year prior to his three 1877 (a, b, c) papers, Filhol (1876b:28) mentioned the presence of vertebrae resembling those of the extant genus *Python* (“vertèbres ... appartenant à des Pythons de grande taille”), originating from different localities within the Phosphorites du Quercy (“J’ai eu de Caylux et d’autres gisements de phosphorite”). Filhol (1876b) further stated that these Quercy vertebrae were different from the fossil “Python-like” vertebrae described by Pictet (1855–1857) from the Eocene of Switzerland, though he did not mention even a single feature that could differentiate the Swiss and French forms. Filhol (1876b:28) additionally referred a dentary “supporting” 17 teeth to the same species (“une demi-mâchoire inférieure supportant dix-sept dents qui provient de la même espèce”). In these sentences discussing this vertebral and dentary material, Filhol (1876b) applied no binomen to characterize these specimens, though in the next paragraph of the same page, he introduced the name *Python cadurcensis* for the first time (“Ainsi, à l’époque miocène inférieure, il existait dans le centre de la France une faune de Reptiles ayant ... et le *Python cadurcensis*, des affinités fort remarquables avec la faune africaine actuelle”) (Filhol, 1876b:28). He therefore made only a simple mention of the name *Python cadurcensis* in his biogeographic conclusions (Filhol, 1876b), without a direct referral of the material, although of course it is clear that with that name, he was almost certainly referring to the snake material he was discussing in the above paragraph.

There are three major problematic issues regarding this initial introduction of the name *Python cadurcensis* by Filhol (1876b) in the literature: (i) there was no description of the vertebrae from Quercy, whereas the author in fact based his taxonomic identification on this material; (ii) the fact that Filhol (1876b) provided the number of teeth (17) supported by the dentary could comply as a minimum description for publications prior to 1931 (ICZN, 1999:Article 12.1), even though this is a rather trivial statement, but he treated this specimen only as a “referred” one (“qui provient de la même espèce”) and did not base his taxonomic identification on this element; and (iii) there is no direct association of the name *Python cadurcensis* with any specific material, the name appearing only in the next paragraph concerning biogeography. For all these reasons, we consider that, according to ICZN (1999:Article 12.1) for species named prior

to 1931, Filhol (1876b) did not make the name available for nomenclatural purposes and *Python cadurcensis* Filhol 1876b should be considered a nomen nudum.

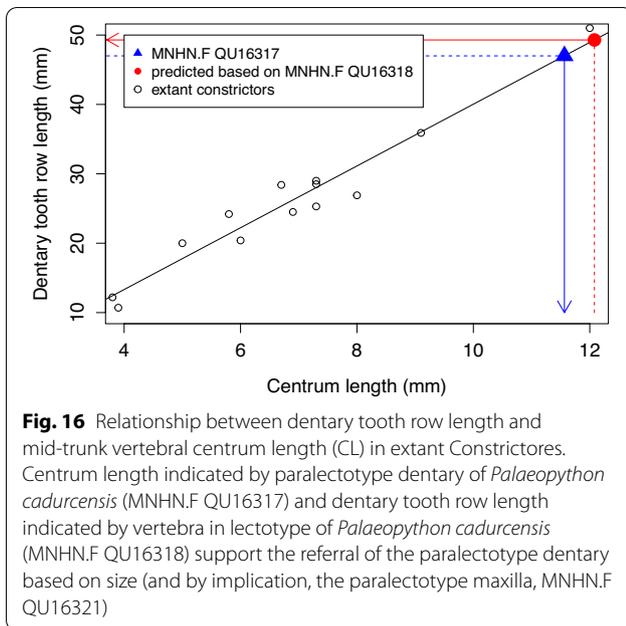
The name *Python cadurcensis* appeared in the following year in three practically indistinguishable publications by Filhol (1877a, 1877b, 1877c), where the author formally described and figured vertebral material, a maxilla, and a dentary. The last specimen is probably the same one mentioned in his short note of the previous year (Filhol, 1876b), taking into consideration the fact that it bears 17 tooth positions. It is not feasible to determine which of the three 1877 papers was published first and should thus have priority and be attributed the authority of the species. The paper of Filhol (1877b) is in fact the published thesis of that author incorporating practically the whole text of Filhol (1877a, 1877c) plus the previously published descriptions of some Quercy mammals (Filhol, 1876a). All subsequent authors dealing with the taxon *Palaeopython cadurcensis* have attributed authorship to Filhol, 1877a, i.e. his paper in the “Annales des Sciences géologiques” (Georgalis & Scheyer, 2019a; Georgalis et al., 2020c; Kuhn, 1939b; Lydekker, 1888a, 1888b; Rage, 1974, 1978, 1984b, 1988b; Rochebrune, 1880, 1884; Szyndlar & Rage, 2003; Szyndlar & Schleich, 1993; Wallach et al., 2014). Curiously, certain of these authors (Rage, 1974, 1984b, 1988b; Szyndlar & Rage, 2003; Wallach et al., 2014) also attributed authorship to Filhol (1877a), but in their reference list they cited the journal name as “Annales des Sciences géologiques” but the number of pages [1–561 (or 1–562 in Wallach et al. 2014)] is identical to the one of Filhol (1877b). In the absence of more precise data about the exact publication dates of the 1877 papers of Filhol (1877a, 1877c; only for the 1877b is a date of publication, 18 July 1877, provided), we follow the prevailing view of the ophidian literature and attribute authorship to Filhol, 1877a (see ICZN, 1999:Article 21.3, for dates of publication incompletely specified).

There is further ambiguity about the exact type series of this species. Filhol (1877a) stated that there were multiple vertebrae found (in different localities within Quercy), corresponding to different size ranges but with similar morphology (“Les vertèbres que j’ai réunies ont des tailles diverses et elles possèdent toutes les mêmes caractères”), providing measurements for the largest one. Filhol (1877a, 1877b, 1877c) did not designate any of the specimens as the holotype, so by definition all specimens he mentioned in this text (and not only the ones he described or figured) are the syntypes of *Python cadurcensis* (ICZN, 1999:Article 73.2 and Recommendation 73F). The identity and number of the cranial syntypes are clear, though how many and which vertebrae are the syntypes of this species cannot be evaluated with certainty. The figures of

Filhol (1877a) clearly show a maxilla (MNHN.F QU16321; Filhol, 1877a:figs. 435, 436), a dentary (MNHN.F QU16317; Filhol, 1877a:figs. 437, 438), a string with five articulated trunk vertebrae (MNHN.F QU16318; Filhol, 1877a:figs. 441, 442), plus one other single trunk vertebra depicted in ventral (Filhol, 1877a:fig. 439), anterior (Filhol, 1877a:fig. 440), dorsal (Filhol, 1877a:fig. 443), and posterior views (Filhol, 1877a:fig. 444). To make things even more complicated, there are erroneous numbers in the figure captions of the publication of Filhol (1877b), i.e. “Figs. 436, 437” for the maxilla, “Fig. 442, 443” for the dentary, and “Fig. 440 à 445” for the vertebrae, although in fact the actual figure numbers are identical with those of Filhol (1877a). In the figure caption, Filhol (1877a) simply stated “Fig. 439 à 444. Vertèbres de *Python cadurcensis*”, so it cannot be ascertained, just from the published figures, whether the “single” vertebra was indeed an isolated one or its various views corresponded to certain vertebrae from the figured articulated ones. Judging from the published figures of Filhol (1877a), we tend to regard this “single” isolated trunk vertebra as indeed a distinct, different specimen from the other syntype with the five articulated trunk vertebrae (MNHN.F QU16318). Our personal observation of the string of the five articulated trunk vertebrae (MNHN.F QU16318; herein designated as the lectotype) at MNHN reveals that the anterior view of its first vertebra and the posterior view of its last vertebra are much different from Figs. 440 and 444, respectively, of Filhol (1877a), thus supporting our view that Figs. 439, 440, 443, and 444 do not pertain to the former specimen; for instance, in MNHN.F QU16318 the zygosphene is much more concave. Additionally, we also tend to consider that the four views of the “isolated” trunk vertebra of Filhol (1877a) all depict a single specimen, as it can be suggested by the distinct postzygapophyseal tubercles that are present in the ventral and dorsal views (his figs. 439 and 443, respectively) and the similar degree of the vaulting of the neural arch, the thickness of the neural spine and the haemal keel, and the overall shape of the paradiapophyses, as observable in the anterior and posterior views (his figs. 440 and 444, respectively). Rage (1984b) considered that this latter single vertebra “syntype” specimen was the isolated mid-trunk vertebra MNHN.F QU16319 (formerly MNHN QU 319), which, however, is a different specimen that was originally figured by Rochebrune (1884:pl. 2.3^a–3^b) and was not figured by Filhol (1877a, 1877b, 1877c). On the museum label of MNHN.F QU16319, it is stated that this specimen is a syntype and figured in Rochebrune’s (1884) work. This specimen (MNHN.F QU16319) is apparently identical to that shown in Rochebrune’s (1884) figure 3^a and 3^b, albeit mirrored. Indeed, it is characterized by a

peculiar asymmetry, skewed to the right in anterior view, particularly the neural arch and the zygosphene, whereas the same features are visible on the left side of the figured specimen in Rochebrune’s (1884) lithograph; the fact that the figure of the publication represents a mirror image of the actual specimen was a common practice for lithographs in nineteenth century’s papers (see also Georgalis, 2017; Georgalis et al., 2020b). Wallach et al., (2014), however, erroneously stated that this vertebra is the same single vertebra that was figured by Filhol (1877a, 1877b, 1877c: figs. 439–440, 443–444), but that figure definitely corresponds to a different specimen. From the text of Rochebrune (1884), we find no indication that the vertebra he figured (MNHN.F QU16319) was part of the syntype series of *Python cadurcensis*; to the contrary it seems that it was a more recent find and not available at the time of the publication of Filhol (1877a, 1877b, 1877c), as Rochebrune (1884:150) stated that the fossil snake material described in that paper was found later than his 1880 work (“Récemment, M. le D^r Filhol a bien voulu nous confier l’étude des restes découverts par lui depuis notre publication. Les nouveaux documents, que nous devons à la gracieuse obligeance de notre savant confrère...”), and few pages later, in the description of his new *Palaeopython cadurcensis* material, he distinguished the new vertebrae from the ones previously published by Filhol (“Nos vertèbres, comme celles de M. le D^r Filhol, disions-nous...”) (Rochebrune, 1884:154). As such, contrary to the opinion of Rage (1984b), the vertebra MNHN.F QU16319 cannot be considered a syntype and should be excluded from the type series of *Palaeopython cadurcensis*; it is here simply considered as a referred specimen of this species (Fig. 8). Accordingly, the only vertebral material in the original syntype series which can confidently be identified are the five articulated trunk vertebrae (MNHN.F QU16318; Fig. 4). The whereabouts of the “single” mid-trunk vertebra figured by Filhol (1877a:figs. 439, 440, 443, and 444) are unknown, and this specimen could not be located in the collections of MNHN.

Finally, we consider the referral of the maxilla (MNHN.F QU16321) and dentary (MNHN.F QU16317) syntypes (now paralectotypes) to the same species as the lectotype string of five vertebrae (MNHN.F QU16318). To assess whether their assignment to the same species as the lectotype is justified, we measured the centrum length of a mid-trunk vertebra and dentary length in 1 extinct and 13 different extant taxa of Constrictores (see Appendix 3) and conducted major axis regression (Fig. 16). According to the model, an animal producing the lectotype with CL = 12.1 mm is expected to have a dentary 47.7 mm in length. This value is closely



comparable to the paralectotype dentary MNHN.F QU16317 (47.0 mm). Since no other known constrictor from Quercy is known to be so large, and potentially co-occurring *Phosphoroboa filholii* comb. nov. is considerably smaller and also has other dentigerous bones that can reasonably be assigned to it (see that respective entry below), we consider the assignment of MNHN.F QU16317 to be justified. Furthermore, in the paralectotype maxilla (MNHN.F QU16321) the teeth have similar dimensions to those of the dentary, so that the same justification can be made here. The three specimens are therefore reasonably considered to pertain to the same species, *Palaeopython cadurcensis*.

At the same time there is no reason to believe that the cranial and vertebral syntypes available to Filhol (1877a, 1877b, 1877c) come from the same individual, and it also cannot be fully excluded that these syntypes are a chimaera representing more than one species (though unlikely, as our model in the previous paragraph indeed favours conspecificity). Therefore, in order to maintain nomenclatural stability, it is necessary to designate one of these syntypes as the lectotype of *Palaeopython cadurcensis*. We designate the five articulated trunk vertebrae MNHN.F QU16318 as the lectotype of this species, taking into consideration that it possesses important diagnostic features and can be directly compared with other fossil Constrictores (see also in Discussion for our rationale on selecting vertebral material as the lectotype).

Accordingly, the maxilla MNHN.F QU16321, the dentary MNHN.F QU16317, and all other not currently located or identified vertebrae mentioned by Filhol (1877a) should be considered as paralectotypes of *Palaeopython cadurcensis*.

It further seems probable that these “Python-like” vertebrae and dentary that Filhol (1876b, 1877a, 1877b, 1877c) discussed were relatively newly found, as there is not a single mention of that material in his previous publications on Quercy fauna (Filhol, 1873a, 1873b). In contrast, the large lizard from Quercy (*Palaeovaranus cayluxi*) was mentioned in both 1873 and 1876 papers (Filhol, 1873b, 1876b; see Georgalis, 2017).

In addition to the above-mentioned material, there are other purported occurrences of this species that have never been described or figured and therefore are not treated here (see Table 3). We further consider that the four vertebrae from the late Eocene of Hordle Cliff, UK, referred to *Palaeopython cadurcensis* by Holman et al. (2006) should not be referred to this species. This material was only briefly described and never figured, but judging from the rather small dimensions of the English material provided by Holman et al. (2006), we think it more plausible that the material pertains to another taxon, potentially to *Paleryx*. Material from the late Eocene of mount Mormont, Vaud, Switzerland was originally referred to *Python* sp. by Pictet et al. (1855–1857) but subsequently referred to *Palaeopython cadurcensis* by Filhol (1877a, 1877b, 1877c); pending a redescription of the Mormont material, we treat that occurrence as *Palaeopython* sp.

It is further worth highlighting that *Palaeopython cadurcensis* is the largest snake recovered from the Phosphorites of Quercy (Rage, 1974) and furthermore the largest member of the genus *Palaeopython*. Among European snakes, the size of *Palaeopython cadurcensis* would only be surpassed by species of the aquatic genus *Palaeophis*. Notably, the trunk vertebra MNHN.F QU16319 (Fig. 8) represents one of the largest constrictor vertebrae known, surpassing true giants in other continents, such as *Chubutophis grandis* Albino, 1993 from the early Eocene of Argentina (Albino, 1993).

Palaeopython cf. *cadurcensis*

Figure 17

Material: A trunk vertebra (NHMW 2019/0032/0001) and a trunk vertebra (probably collections of BSPG, currently lost) figured by Zittel (1887–1890:fig. 559).

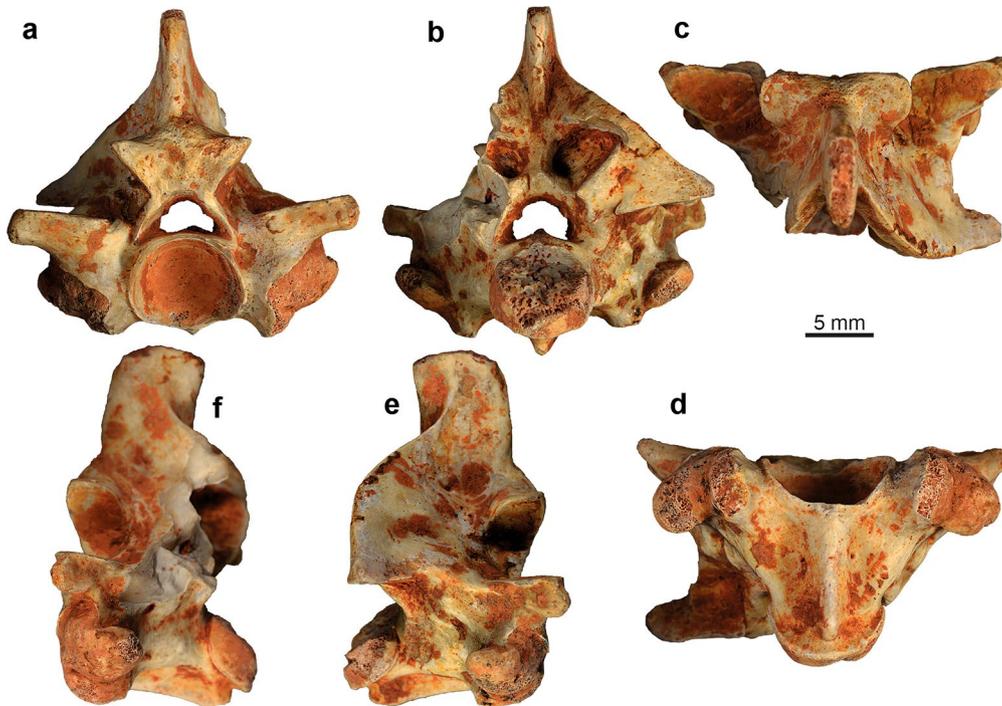


Fig. 17 *Palaeopython* cf. *cadurcensis* from an imprecisely known locality in the Phosphorites du Quercy: mid-trunk vertebra (NHMW 2019/0032/0001) in anterior (a), posterior (b), dorsal (c), ventral (d), right lateral (e), and left lateral (f) views

Locality: The NHMW specimen originates from an imprecise locality (probably middle or late Eocene), Phosphorites du Quercy, France; Zittel's (1887–1890) material originates from Escamps (late Eocene, MP 19), Phosphorites du Quercy, Lot, France.

Remarks: NHMW 2019/0032/0001 resembles *Palaeopython cadurcensis* in many respects, especially in the thickness of the zygosphenes and the overall shape and size (Fig. 17). Nevertheless, there are certain differences, such as the more vaulted neural arch (vaulting ratio 0.55) and the exceedingly high neural spine. The vertebra can be further differentiated from *Palaeopython helveticus* by its more massive zygosphenes and more massive paradiapophyses.

Two additional vertebrae, figured by Zittel (1887–1890:fig. 559) and De Stefano (1905:pl. IV.12; originally referred to *Paleryx rhombifer*), are characterized by high neural arches and bear a resemblance to NHMW 2019/0032/0001. We tentatively place the Zittel's specimen here as well.

Whether this taxon represents a distinct rather large form in the area of Quercy or simply some extreme variation of *Palaeopython cadurcensis* cannot be resolved for the moment.

Palaeopython ceciliensis Barnes, 1927

Figures 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30 and 31

Taxonomic history: *Palaeopython ceciliensis* Barnes, 1927 (new species); *Paleryx ceciliensis* Kuhn, 1939a (new combination).

Type material: GMH Ce I-2978-1926 (holotype), an incomplete mid-trunk vertebra, missing its posterior-most portion (posterior portion of ventral surface of centrum, condyle, both postzygapophyses, posterior part of neural arch, most parts of prezygapophyses, and most part of neural spine) (Barnes, 1927, pl. I.7; Georgalis & Scheyer, 2019a, fig. 15h; Figs. 18, 19, Additional file 1: Model 1).

Type locality: Quarry Cecilie I, Geiseltal, Saxony-Anhalt, Germany; late early or middle Eocene.

Referred material and range: Known exclusively from the late early or middle Eocene of its type area, Geiseltal, Saxony-Anhalt, Germany. Found in the following quarries [in stratigraphical order]: quarry LII; quarry XXII; quarry XLI; quarry XXXV; quarry XXXVI; quarry Cecilie IV; type locality, quarry Cecilie I; quarry Cecilie III; imprecisely known quarry(ies).

Referred material discussed herein (all from quarries of Geiseltal [in stratigraphic order]) (Figs. 20,

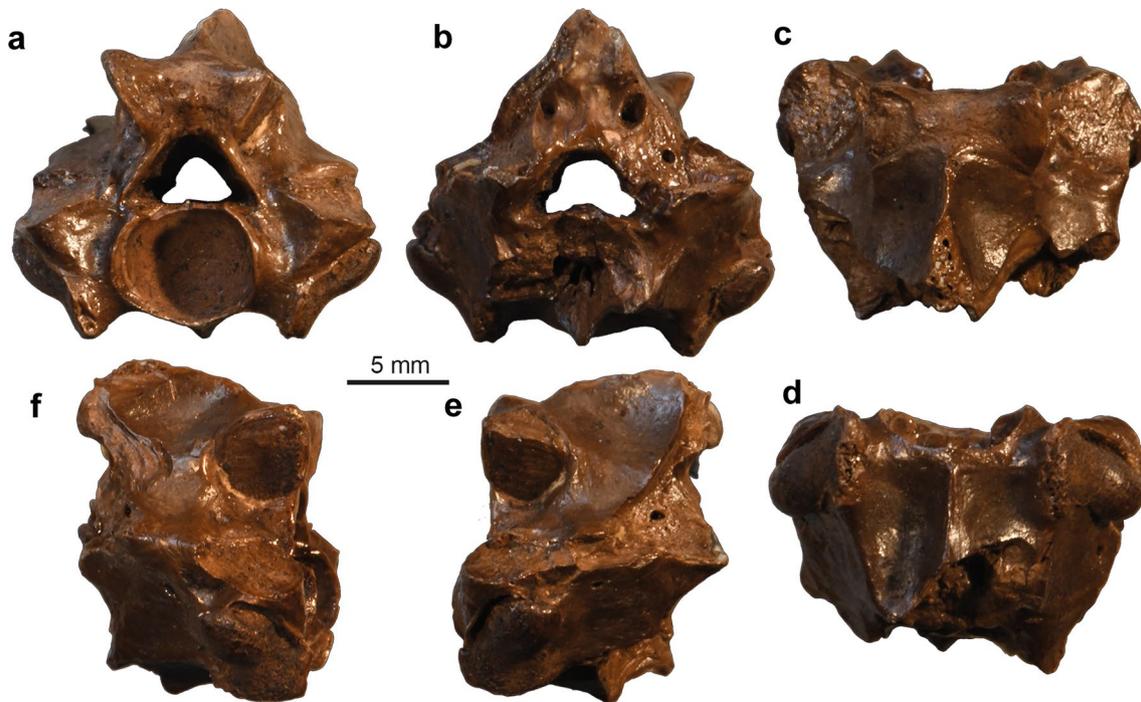


Fig. 18 *Palaeopython ceciliensis* from quarry Cecilie I, Geiselal, holotype: mid-trunk vertebra (GMH Ce I-2978-1926) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

21, 22, 23, 24, 25, 26, 27, 28, 29, 30 and 31): quarry LII (Fig. 20): a mid-trunk vertebra (GMH LII-37-1971); quarry XXII (Fig. 21): two trunk vertebrae (GMH XXII-39-1965) and a small-sized skeleton on matrix (GMH XXII-556-1965); quarry XLI (Fig. 22): three mid-trunk vertebrae (GMH XLI-60a-1966, GMH XLI-60b-1966, and GMH XLI-60c-1966), and one anterior trunk vertebra (GMH XLI-314b-1968); quarry XXXV (Fig. 23): two articulated anterior mid-trunk vertebrae (GMH XXXV-485c-1963), a mid-trunk vertebra (GMH XXXV-404-1963), a mid-trunk vertebra (GMH XXXV-386-1963 [tentative referral]), and two posterior trunk vertebrae (GMH XXXV-485a-1963 and GMH XXXV-485b-1963); quarry Cecilie XXXVI (Fig. 24): articulated trunk vertebrae and remains of ribs on matrix (GMH XXXVI-41-1962); quarry Cecilie IV (Figs. 25, 26): several articulated and disarticulated trunk vertebrae and ribs on a matrix (GMH Ce IV-5854-1933 [several], GMH Ce IV-5849-1933 [several], GMH Ce IV-5850-1933 [several], GMH Ce IV-5858-1933 [several], and GMH Ce IV-5858b-1933 [several]), and a fragmentary skeleton with several disarticulated vertebrae and ribs (GMH Ce IV-5857-1933); quarry Cecilie I (type locality) (Figs. 27, 28): an anterior/mid-trunk vertebra (GMH Ce I-Y-42-1926), 19 large mid-trunk vertebrae and three tiny vertebral fragments (GMH Ce I-5837-1926; originally described as *Palaeovaranus* by Weigelt,

1929:fig. 2; Fig. 27), a mid-trunk vertebra (GMH Ce I-5834a-1926), and several trunk vertebrae (GMH Ce I-5835d-1929 [tentative], GMH Ce I-5835e-1929, GMH Ce I-5835f-1929, GMH Ce I-5835g-1929); quarry Cecilie III (Fig. 29): an articulated 2.3 m skeleton with crushed skull and 243 vertebrae [GMH Ce III-5867-1933; figured in Kuhn (1939a:pl. I.3 and II.3), Weigelt (1934:pl. IX.1), and Krumbiegel et al. (1983:fig. 114); Fig. 29; probable referral]; unknown quarry(ies) (Figs. 30, 31): several large trunk vertebrae (GMH Y-38) and four strings of articulated trunk vertebrae (GMH Y-40-1964).

Diagnosis: *Palaeopython ceciliensis* can be referred to the genus *Palaeopython* by the presence of the full list of characters given for that genus. It can be differentiated from all other species of *Palaeopython* by the unique combination of the following characters: size moderate with CL around 10 mm (but rarely reaching up to 13 mm), neural arch of mid- and posterior trunk vertebrae less vaulted, neural spine of posterior mid- and posterior trunk vertebrae significantly lower than that of the mid-trunk ones, and median tubercle on the zygosphene in anterior view absent or only weakly developed. *Palaeopython ceciliensis* can be further differentiated from the co-occurring in Geiselal *Eoconstrictor* cf. *fischeri* by its much larger size, the much thicker zygosphene, the relatively much lower neural spine in the posterior trunk vertebrae, the absent or poorly developed median

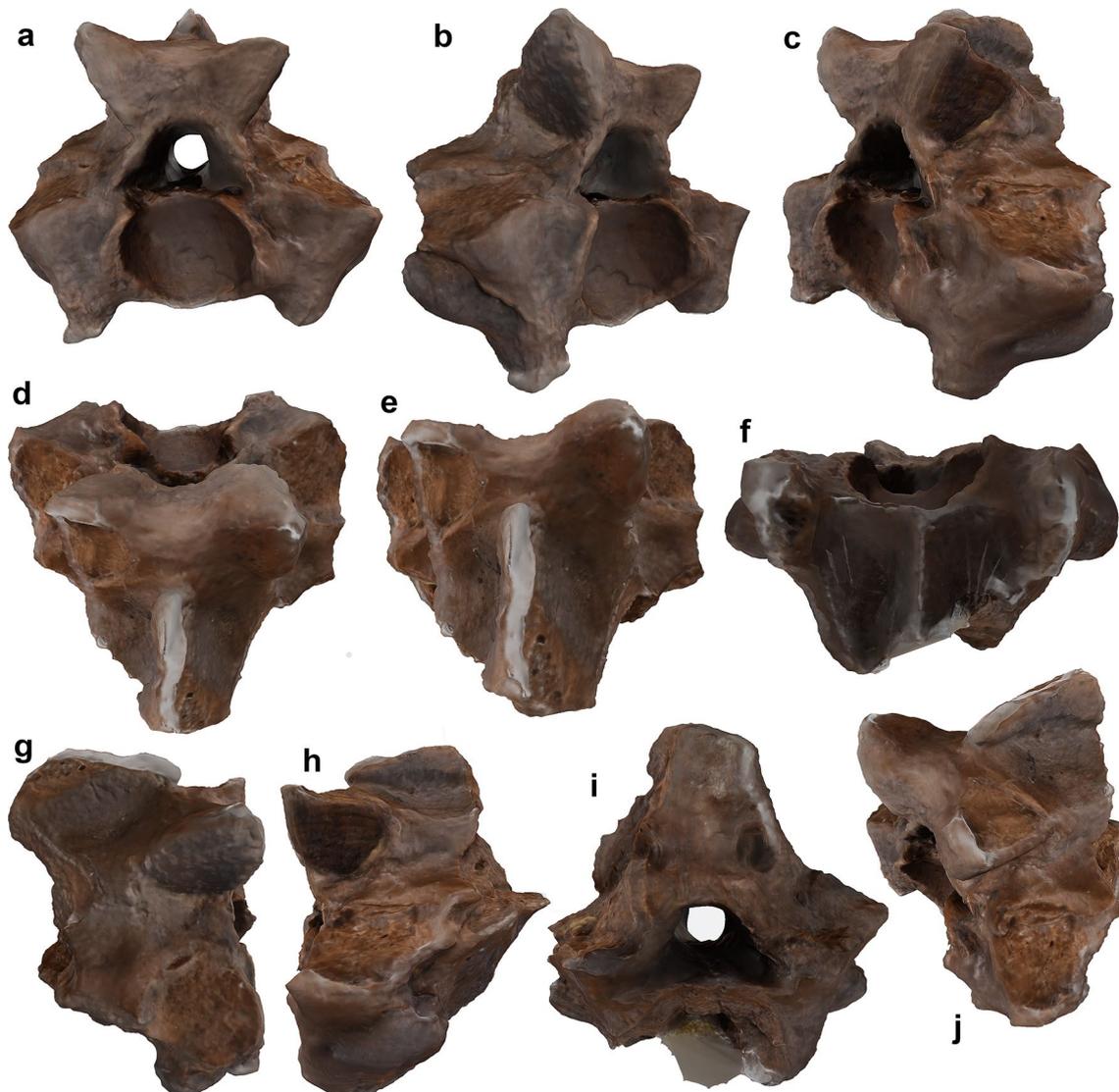
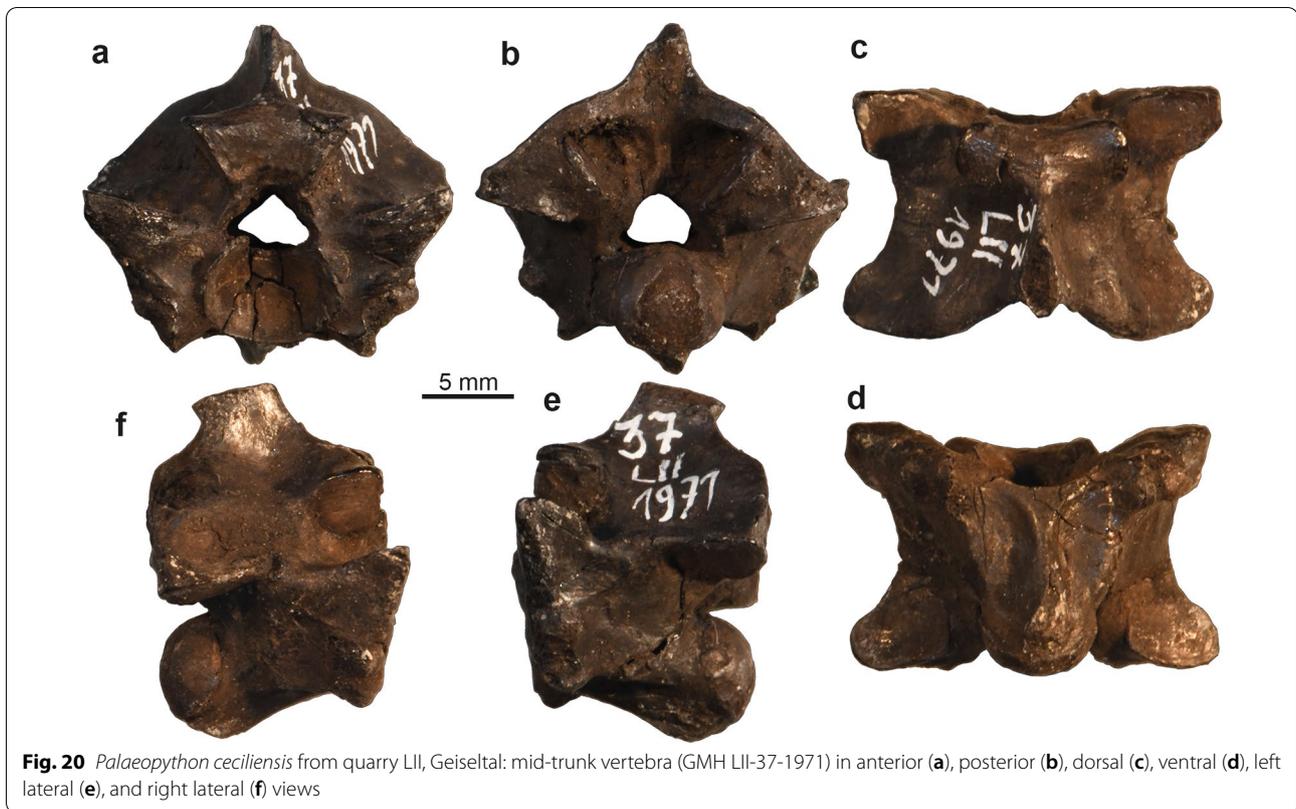


Fig. 19 *Palaeopython ceciliensis* from quarry Cecilie I, Geiseltal, holotype: 3D models of mid-trunk vertebra (GMH Ce I-2978-1926) in anterior (a), anterolateral (b, c), anterodorsal (d), dorsal (e), ventral (f), right lateral (g), left lateral (h), posterior (i), and dorsolateral (j) views. Images only at approximately the same scale

tubercle on the zygosphenes, and the more massive paradiapophyses.

Description of the holotype (GMH Ce I-2978-1926): This specimen is an incomplete mid-trunk vertebra, missing the posterior part of the centrum along with the condyle, posterior part of neural arch, most of neural spine and zygantrum, and both postzygapophyses (Figs. 18, 19, Additional file 1: Model 1). In anterior view (Figs. 18a, 19a), the zygosphenes are extremely thick and slightly wider than the cotyles. The lateral edges of the zygosphenes are slightly upturned, making the roof concave. A small tubercle is present on the anterior surface of the zygosphenes at around mid-height. The cotyle

is slightly depressed and quite deep. The neural canal is nearly triangular. No paracotylar foramina are present, but paracotylar fossae do exist and are relatively deep. The parapophyses project ventrally below the centrum, but not greatly so, consistent with the position of the vertebra in the column. Little can be said about the posterior view, including the shape of the condyle or the zygantrum (Figs. 18b, 19i). Nevertheless, a small median impression at the ventral margin of the zygantrum confirms that the succeeding vertebra also possessed a median tubercle on its zygosphenes. A pair of large endozygantral foramina (sensu Head, 2005) is present. In dorsal view (Figs. 18c, 19e), the vertebra is wider than long. The anterior margin



of the zygosphene is slightly concave and the lateral edges are prominent. The articular surfaces of the zygosphene are steep. The prezygapophyseal articular facets are missing but seem to have been large and broad. The anterior edge of the neural spine starts well behind the anterior margin of the zygosphene; it rises at first gradually as a thin, arching flange before the thick (broken) part of the neural spine proper develops in the posterior half of the vertebra. The neural arch width (NAW) is 15.5 mm. In

ventral view (Figs. 18d, 19f), the haemal keel grew relatively sharp by mid-length. Relatively sharp subcentral ridges give the centrum a triangular shape. A rather small subcentral foramen is present on the right side of the haemal keel (the left side is unknown). The paradiapophyses are massive and elliptical. In lateral view (Figs. 18e, f, 19g, h), the vertebra is taller than long. The zygosphenal articular facets are massive. Lateral foramina are present just posterior to the diapophysis and below the

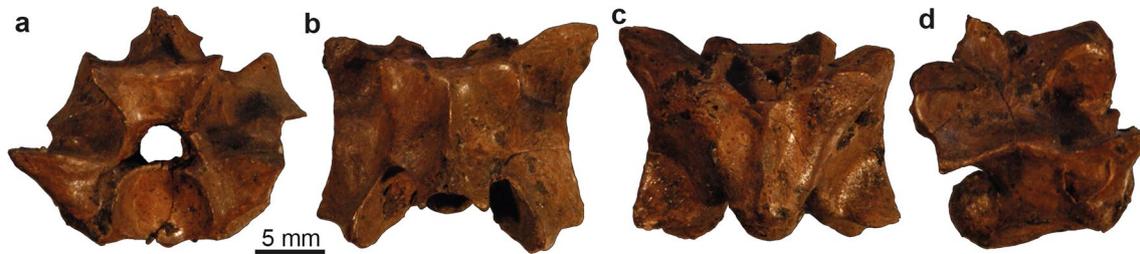


Fig. 22 *Palaeopython ceciliensis* from quarry XLI, Geiseltal: mid-trunk vertebra (GMH XLI-60a-1966) in anterior (a), dorsal (b), ventral (c), and right lateral (d) views

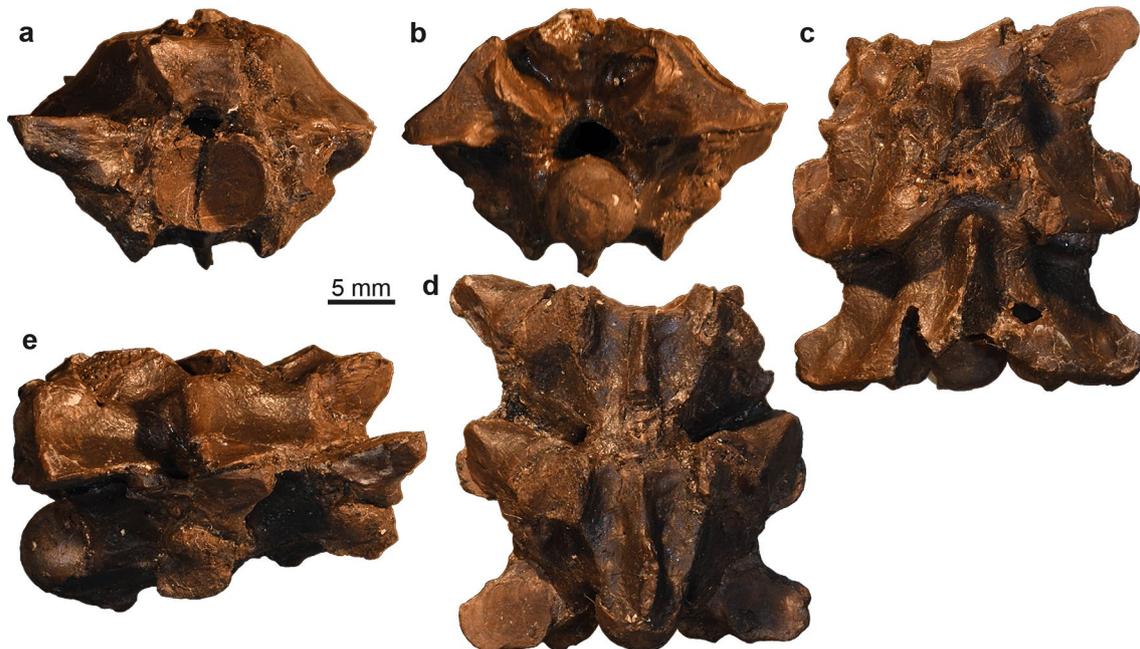


Fig. 23 *Palaeopython ceciliensis* from quarry XXXV, Geiseltal: two articulated anterior mid-trunk vertebrae (GMH XXXV-485c-1963) in anterior (a), posterior (b), dorsal (c), ventral (d), and right lateral (e) views

interzygapophyseal ridge. The diapophyses and parapophyses are distinct but are not divided.

Description of additional vertebrae—intracolumnar variation (Figs. 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30 and 31): Anterior trunk vertebrae are characterized by the presence of a hypapophysis instead of a haemal keel (Fig. 30). The shape of the hypapophysis in lateral view varies, depending (at least in part) on the position of the vertebra in the anterior trunk series, being either long and thin (e.g., GMH Y-38b) or (more usually) relatively anteroposteriorly long (e.g., GMH Y-38d; Fig. 30e). Succeeding anterior trunk or anterior mid-trunk vertebrae possess a rather vaulted neural arch and a tall neural spine (e.g., GMH Y-38).

Mid-trunk vertebrae can achieve a large size, with CL approaching or even surpassing 10 mm (e.g., GMH LII-37-1971; GMH XLI-314b-1968); the largest measurable specimen has CL = 13 mm. The zygosphene is rather thick in anterior view (e.g., GMH Ce I-5834a-1926; GMH Ce I-Y-42-1926; GMH LII-37--1971). The zygosphene is wider than the cotyle. There is usually no median tubercle on the zygosphene, although rarely this structure is weakly present (e.g., GMH Ce I-Y-42-1926). The zygosphene usually possesses two distinct lateral lobes, which can be rather prominent in certain large-sized specimens, resembling “bull’s horns” in anterior view (e.g., GMH LII-37-1971, GMH Ce I-5834a-1926, GMH Y-38a). They are sometimes upturned (e.g., GMH Ce I-5837b-1926), sometimes not (e.g., GMH LII-37-1971). The cotyle is



Fig. 24 *Palaeopython ceciliensis* from quarry XXXVI, Geiseltal: several articulated vertebrae on matrix (GMH XXXVI-41-1962)

usually large, deep, and slightly elliptical, though in certain specimens it is distinctly elliptical (e.g., GMH Ce I-5837f-1926). Prezygapophyseal articular facets are large and can be rather pointed in certain specimens (e.g., GMH Y-42-1926). Prezygapophyseal accessory processes are present, although usually they are small. The prezygapophyses are usually inclined. The distal edges of

the prezygapophyseal articular facets are rather pointed. The paradiapophyses are massive. The centrum is much widened anteriorly. The haemal keel is thick and sharp and extends along nearly the entire length of the centrum. Subcentral foramina usually occur, though in some specimens they are absent (e.g., GMH Ce I-Y-42-1926). The neural spine is thick. The neural spine in mid-trunk vertebrae is relatively tall; however, posterior mid- and posterior trunk vertebrae have instead a much lower neural spine (e.g., GMH LII-37-1971, GMH Y-38f, and GMH Y-38i; small articulated skeleton on matrix GMH XXII-556-1965).

Posterior trunk vertebrae have a wide haemal keel (Fig. 31). In certain cases, the haemal keel expands anteriorly and posteriorly (e.g., GMH LII-37-1971; Fig. 20d). The zygosphene is still thick and prominent also in this portion of the vertebral column, and some specimens possess the prominent lateral lobes in dorsal view (e.g., GMH XXXV-485b-1963). Paracotylar foramina are absent in all vertebrae throughout the column, except for a single large posterior mid- or posterior trunk and an anterior trunk vertebra (GMH Y-38c and GMH Y-38e, respectively), though in all other associated vertebrae of the same collection number [i.e. GMH Y-38 (many vertebrae)], this feature is always lacking.

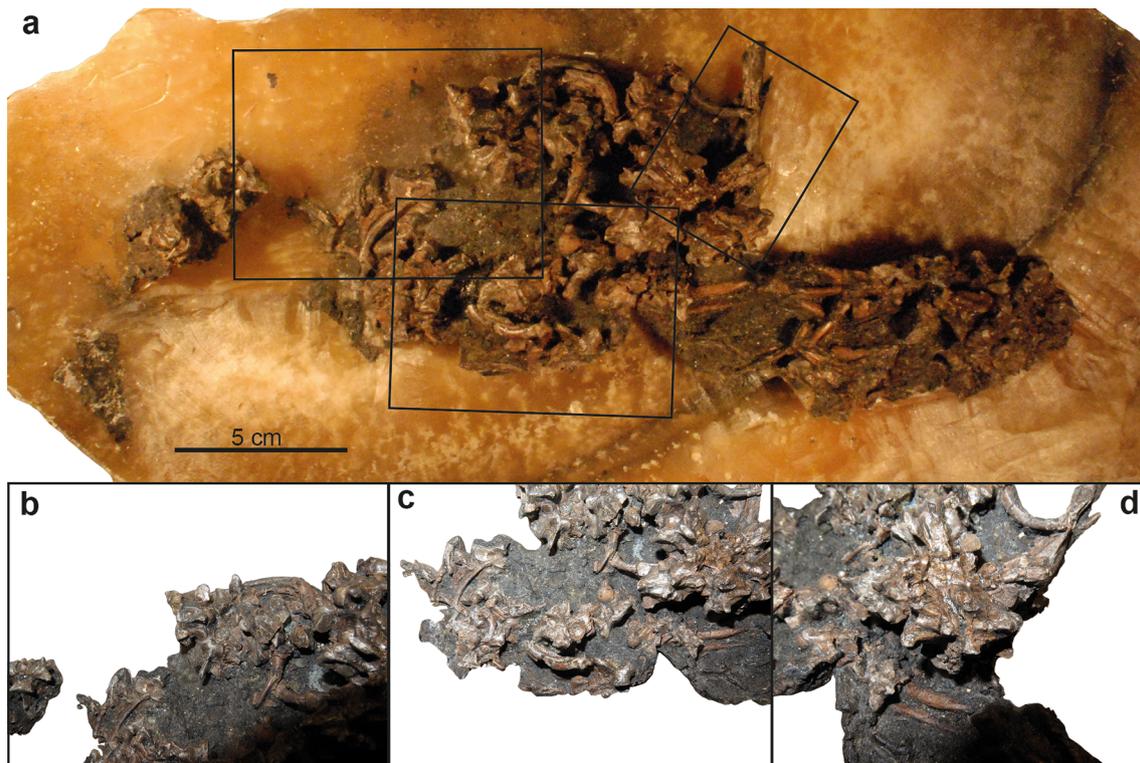


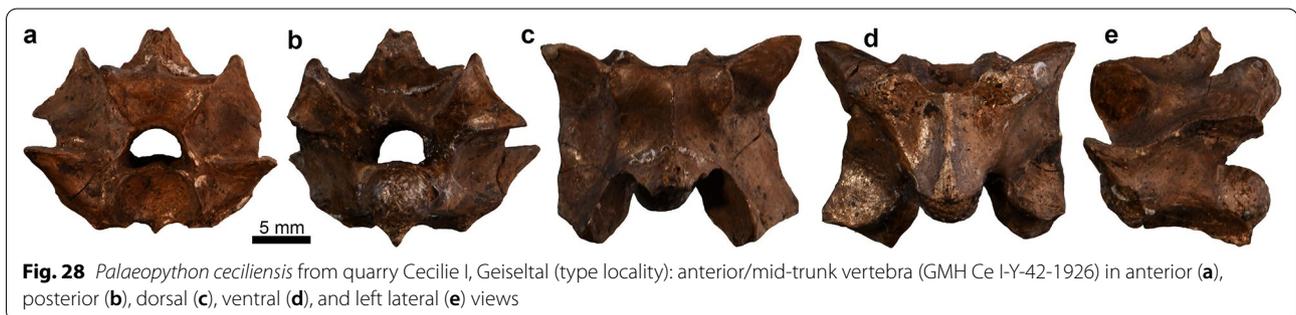
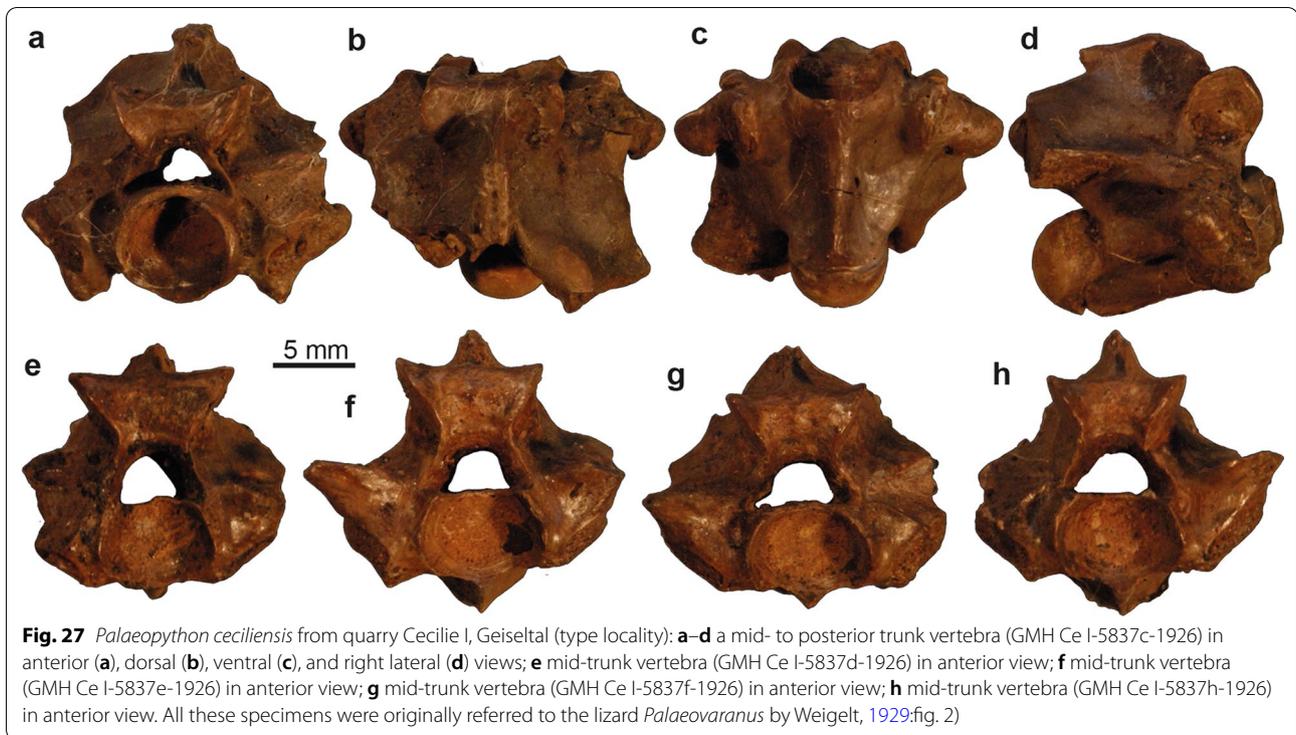
Fig. 25 *Palaeopython ceciliensis* from quarry Cecilie IV, Geiseltal: **a** several articulated and disarticulated trunk vertebrae and ribs on a matrix (GMH Ce IV-5854-1933); **b-d** close ups of the same specimen



Remarks: Barnes (1927) established *Palaeopython ceciliensis* on the basis of an incomplete vertebra from the quarry Cecilie I, in Geiseltal. A couple of years later, additional large snake vertebrae were described from Geiseltal but were originally assigned to the large lizard taxon *Palaeovaranus* by Weigelt (1929); that material was subsequently referred to *Palaeopython ceciliensis* (Kuhn, 1939a; see also Georgalis, 2017). Kuhn (1939a) redescribed this species, reassigned it to *Paleryx*, and also referred to it, among others, a relatively complete, large (2.3 m long) skeleton (GMH Ce III-5867-1933) (Fig. 29). Rage (1984b) disputed the generic attribution of this Geiseltal taxon to *Paleryx* and followed the original

concept of Barnes (1927) in considering it as a member of *Palaeopython*. Nevertheless, the same author considered that not a lot more can be said about this species, and he was further sceptical of Kuhn's (1939a) referral of GMH Ce III-5867-1933 to the same taxon, a view subsequently shared by Szyndlar and Böhme (1993).

Palaeopython ceciliensis is the largest snake species in the Geiseltal assemblage. Besides the many disarticulated vertebrae, several articulated and disarticulated skeletons are also known, some of which comprising also skull remains (Figs. 21, 24, 25, 29). Certain specimens achieved truly large size, such as the 2.3 m skeleton GMH Ce III-5867-1933 (Fig. 29) and even larger sizes were probably



achieved, as judged by the large size of certain vertebrae, up to 13 mm in CL.

In some vertebrae of *Palaeopython ceciliensis*, growth rings on the prezygapophyses (e.g., GMH Ce I-5835a-1929, GMH Ce I-5835f-1929) and/or postzygapophyses (e.g., GMH XLI-314b-1968) can be observed. Sometimes this is correlated with evidence of erosion of the bone surface, such as exposure of the zygantrum through the dorsal surface of the neural arch (e.g., GMH Ce I-Y-42-1926). A similar exposure of the zygantrum has been described also in the North American Oligocene species, *Coprophis dakotaensis* Parris and Holman, 1978, a taxon aptly named for having been recovered from a coprolite, thus suggesting that it arises via etching in gastric fluids (Parris & Holman, 1978). Accordingly, one can hypothesize that crocodylians, the largest reptilian

predators in Geiseltal and which are known to possess highly acidic gastric fluids (Fisher, 1981), consumed larger snakes, as extant alligators are known to do in the southeastern United States (e.g., Wolfe et al., 1987). This would be ironic considering that it is large constrictors that consumed smaller crocodylians in Messel (Greene, 1983), and it remains a hypothesis to be tested. Regardless, growth rings can be used to determine the ontogenetic stage of an individual (e.g., Petermann & Gauthier, 2018; Venczel et al., 2015).

The vertebral anatomy of *Palaeopython ceciliensis* shows resemblance to the other two *Palaeopython* spp. and we agree with the original taxonomic opinion of Barnes (1927) in placing it in that genus. We further anticipate that the available skull material of this taxon that can be studied with the application of



Fig. 29 *Palaeopython ceciliensis* from quarry Cecilie III, Geiseltal: articulated, 2.3 m, skeleton with crushed skull and 243 vertebrae (GMH Ce III-5867-1933). This specimen was originally figured by Kuhn (1939a:pls. I.3 and II.3), Weigelt (1934:pl. IX.1), and Krumbiegel et al. (1983:fig. 114). Referral to the species is probable, though not definite

microcomputed tomography, will shed important light on its cranial anatomy and exact phylogenetic relationships.

***Palaeopython helveticus* Georgalis and Scheyer, 2019a**

Figure 32

Taxonomic history: *Palaeopython helveticus* Georgalis and Scheyer, 2019a (new species).

Type material: PIMUZ A/III 634 (holotype), an anterior mid-trunk vertebra of an adult individual (Rosselet, 1991, fig. 23; Georgalis & Scheyer, 2019a, figs. 5, 6, 15a, 17i–l, supplementary Fig. 1c; Georgalis & Scheyer, 2019b, unnumbered subfig. on top right in fig. 1; Fig. 32).

Type locality: Fissure A, Dielsdorf, Zurich Canton, Switzerland; MP 16–20, late Bartonian–late Priabonian, late middle–late Eocene.

Referred material and range: MP 16–20, late Bartonian–late Priabonian, late middle–late Eocene, Dielsdorf, Fissures A, B, and 2, Zurich Canton, Switzerland (referred material of Georgalis & Scheyer, 2019a).

Diagnosis: See Georgalis and Scheyer (2019a).

Remarks: This taxon was recently described in detail by Georgalis and Scheyer (2019a) on the basis of isolated vertebrae from the late middle–late Eocene of Dielsdorf, Switzerland. These authors also presented 3D surface

models and applied micro-CT scanning to vertebrae of *Palaeopython helveticus*, allowing also an in depth analysis of the ontogenetic variation (Georgalis & Scheyer, 2019a, 2019b). For detailed descriptions of this taxon, we refer the reader to Georgalis and Scheyer (2019a).

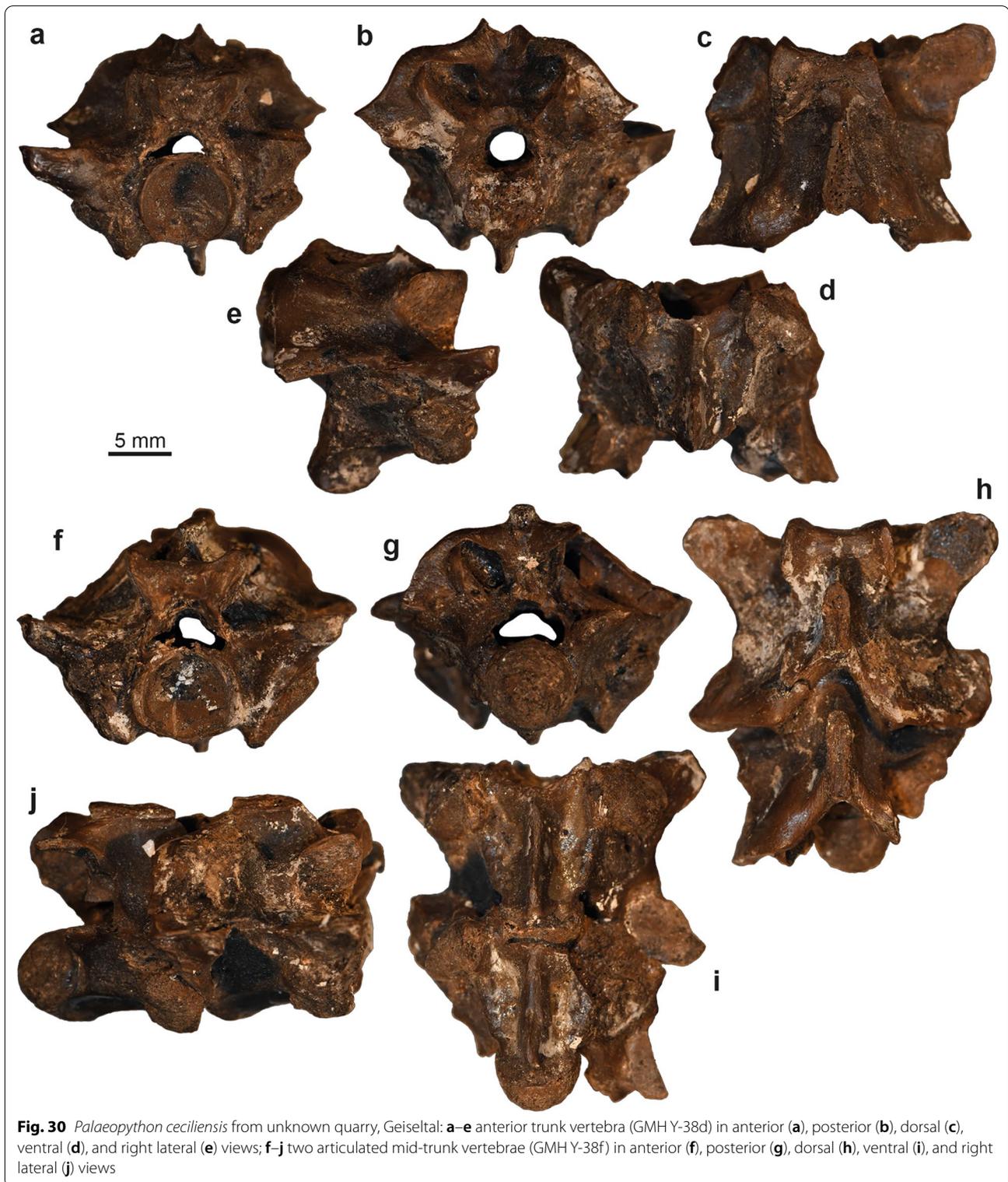
Genus *Paleryx* Owen, 1850

Type species. *Paleryx rhombifer* Owen, 1850.

Other valid species included: None.

Geographic and stratigraphic distribution: see Table 3.

Diagnosis: *Paleryx* is assigned to Constrictores on the basis of possessing strongly built vertebrae, the centrum wider than long, the vertebrae taller than long in lateral view, prezygapophyseal accessory processes small, paradiapophyses undivided or only weakly divided, and parazygantral foramina absent. Similar to Pythonoidea in having a palatine foramen and a maxillary process of the palatine located anterior to the pterygoid articulation. Size moderate, with CL maximally around 10 mm; ratio of neural spine length to centrum length < 0.5. *Paleryx* can be differentiated from all other known European Paleogene Constrictores by the following unique



combination of features: ratio of zygosphenes width to cotyle width < 1.1 in mid- and posterior trunk vertebrae, generally lower neural spine (especially on posterior

trunk vertebrae), and posterior trunk vertebrae with depressed neural arch (vaulting ratio < 0.25). *Paleryx* can be further differentiated from *Palaeopython* by its smaller

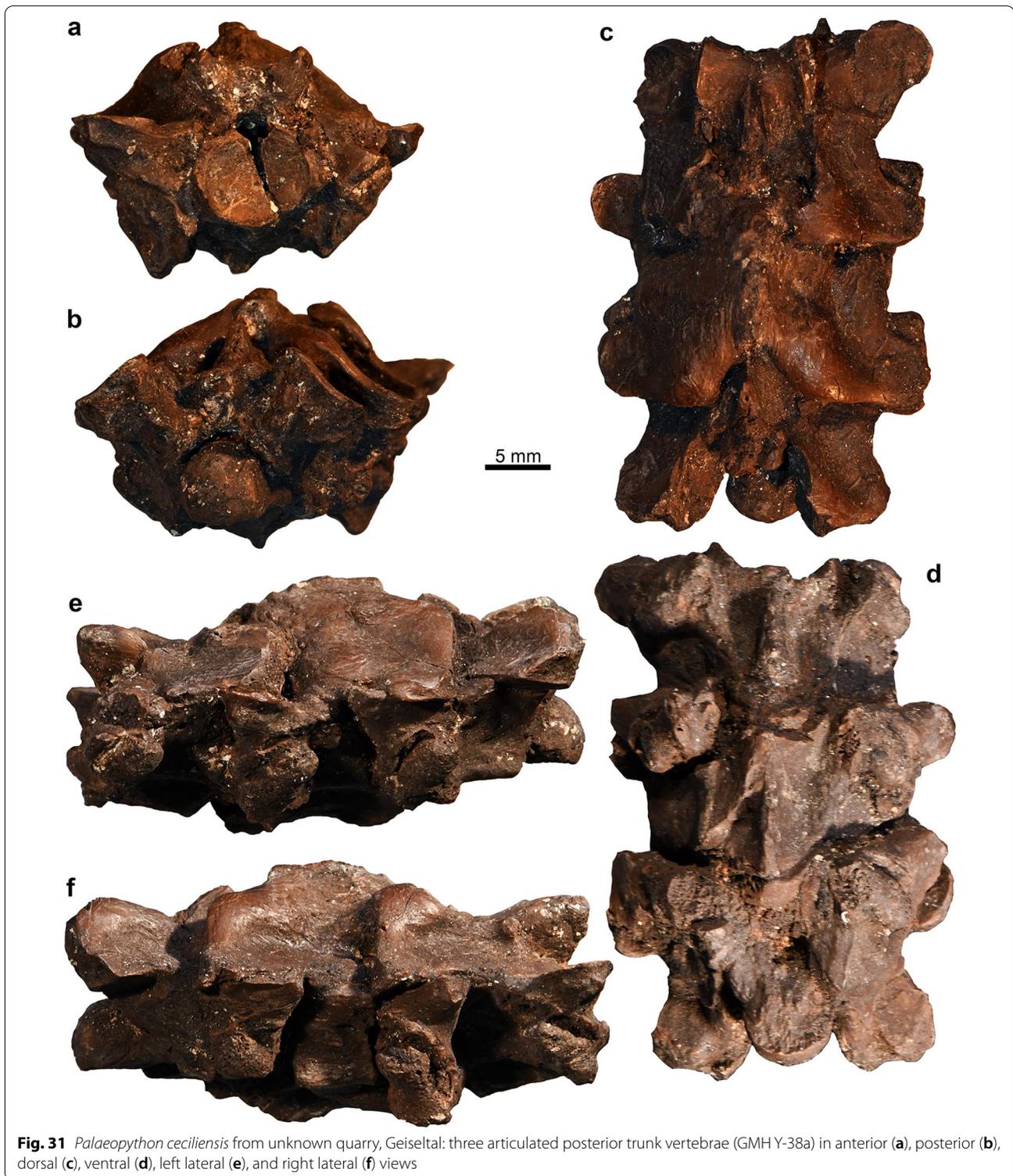


Fig. 31 *Palaeopython ceciliensis* from unknown quarry, Geiseltal: three articulated posterior trunk vertebrae (GMHY-38a) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

size, much thinner zygosphene without prominent anterolateral horns, deeper interzygapophyseal constriction, and shallower paracotylar fossae.

Remarks: Owen (1850) established the genus *Paleryx* from the late Eocene of the United Kingdom and noticed vertebral similarities with the extant genera *Eryx* and *Python*, as well as the extinct *Palaeophis*. The supposed

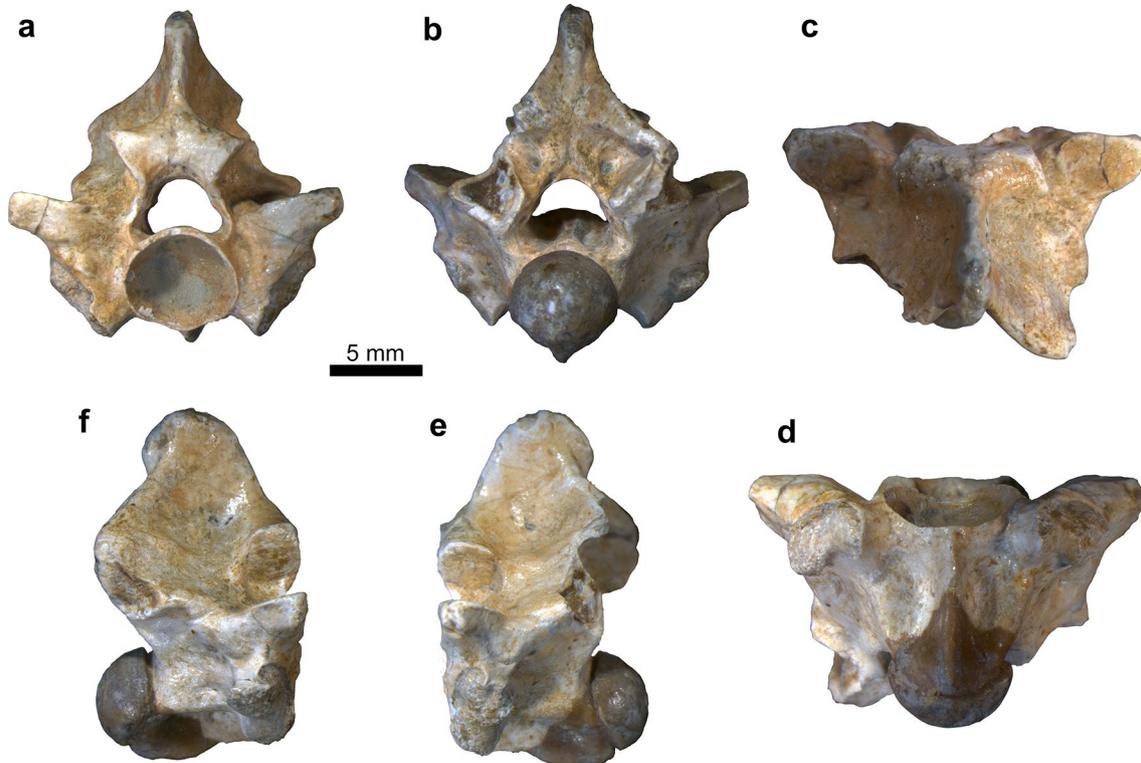


Fig. 32 *Palaeopython helveticus* from Dielsdorf: holotype trunk vertebra (PIMUZ A/III 634) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views. Figure reproduced from Georgalis and Scheyer (2019a:fig. 5); copyright by the Swiss Geological Society

close resemblance to *Eryx* was subsequently followed by other workers (e.g., Seeley, 1885), and Carus (1868) formally placed it into Erycidae. For a long time during the late nineteenth and the twentieth century, *Paleryx* was considered as the senior synonym of *Palaeopython* (see “Taxonomic history and history of discoveries of the European large fossil constrictors”). Swinton (1926) reported that his newly erected taxon *Daunophis langi* from the Pliocene of Myanmar was rather similar to *Paleryx*, an opinion that could not be confirmed by Szyndlar and Rage (2003). Swinton (1926) also erroneously stated that *Paleryx* persisted until the early Miocene. Simpson (1933) noted some resemblance of *Paleryx* with his newly described giant Paleogene Patagonian form *Madtsoia bai*, especially as far as it concerns the ratio of the width of the zygosphenes to the cotyles and also the general proportions of the neural arch and the neural spine. Nevertheless, Simpson (1933) admitted the distinctiveness of *Paleryx* from *Madtsoia*. Interestingly, Romer (1956) not only considered *Paleryx* as the senior synonym of *Palaeopython*, but he tentatively synonymized with the former genus also *Palaelaphis* Rochebrune, 1884 (for which he erroneously provided an authorship date of 1886 instead of 1884); however, he

provided no justification for such taxonomic assignment. In any case, both species of *Palaelaphis* (i.e. *Palaelaphis antiquus* Rochebrune, 1884 and *Palaelaphis robustus* Rochebrune, 1884) originate from unknown localities within the Phosphorites du Quercy and are currently considered as nomina dubia, with their material representing indeterminate Constrictores (Rage, 1984b; Szyndlar & Rage, 2003).

We here recognize *Paleryx* as a non-booid snake, comprising a single valid species, *Paleryx rhombifer* (with *Paleryx depressus* being its junior synonym). *Paleryx* is known with certainty only from the late Eocene of England.

Similarly to the case of many other taxa named in the nineteenth century, the genus name *Paleryx* suffered from important misspellings, such as *Palaeryx* by Massalongo (1859), *Palaeeryx* by Palacký (1884), and *Paleoeryx* again by Palacký (1898).

Paleryx rhombifer Owen, 1850

(= *Paleryx depressus* Owen, 1850)

Figures 33, 34, 35, 36, 37 and 38

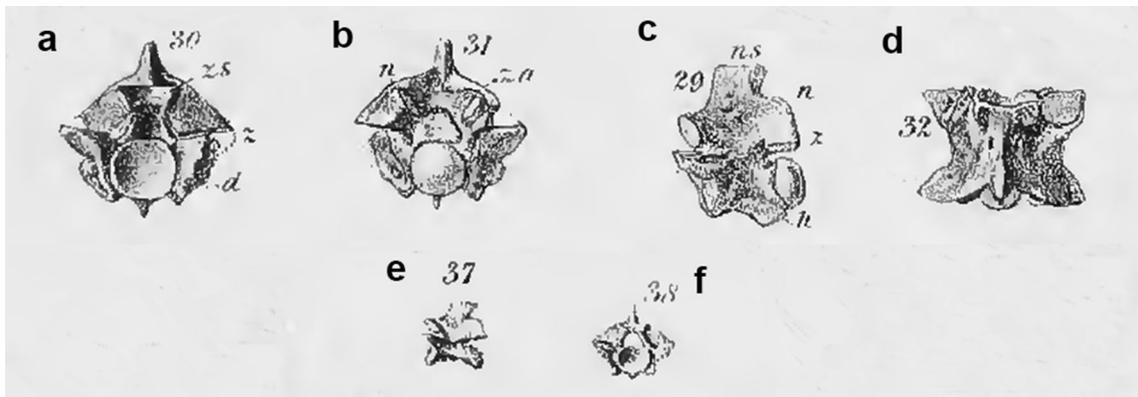


Fig. 33 Original lithograph of the type material of *Paleryx rhombifer* (holotype, NHMUK PV OR 25259 (a–d) and *Paleryx depressus* (lectotype [herein designated], NHMUK PV OR 25261(1) (e, f). Image modified from plate XIII of Owen (1850)

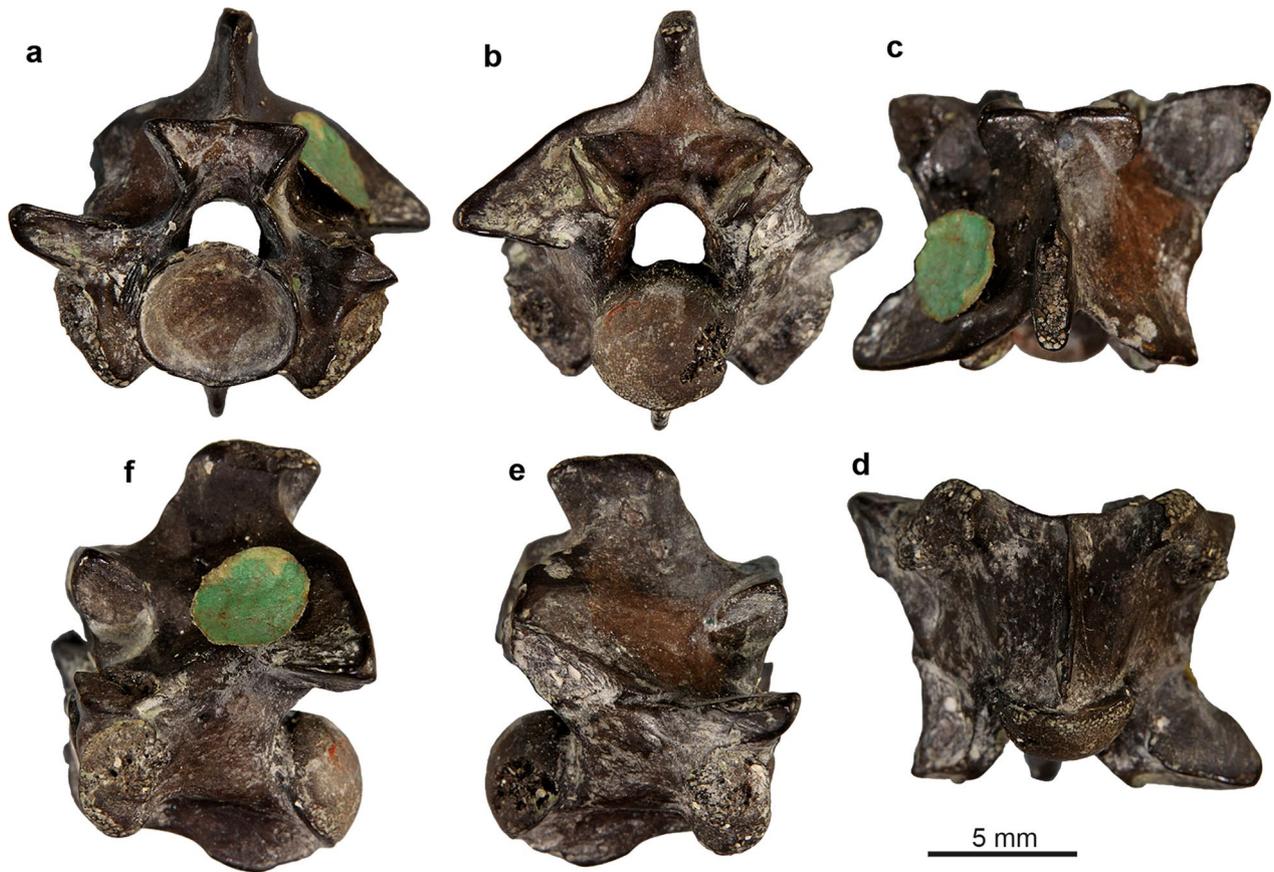


Fig. 34 *Paleryx rhombifer* from Hordle Cliff: holotype anterior mid-trunk vertebra (NHMUK PV OR 25259) in anterior (a), posterior (b), dorsal (c), ventral (d), right lateral (e), and left lateral (f) views



Fig. 35 *Paleryx rhombifer* from Hordle Cliff (type material of *Paleryx depressus*): **a–c** lectotype (herein designated) mid-trunk vertebra (NHMUK PV OR 25261(1)) of *Paleryx depressus* in anterior (**a**), posterior (**b**), and left lateral (**c**) views; **d–g** paralectotype posterior trunk vertebra (NHMUK PV OR 25261(2)) of *Paleryx depressus* in anterior (**d**), posterior (**e**), dorsal (**f**), ventral (**g**), and left lateral (**h**) views; (**i, j**) paralectotype mid-trunk vertebra (NHMUK PV OR 25261(3)) of *Paleryx depressus* in dorsal (**i**) and ventral (**j**) views

Taxonomic history: *Paleryx rhombifer* Owen, 1850 (new species); *Paleryx rhombifer* = *Palaeopython cadurcensis* Lydekker, 1888b (senior synonym); *Paleoeryx rhombifer* Palacký, 1898 (incorrect spelling of genus name); *Paleryx rhombifer* = *Paleryx depressus* Rage and Ford, 1980 (senior synonym).

Type material: NHMUK PV OR 25259 (holotype), an anterior mid-trunk vertebra (probably not anterior trunk vertebra as stated by Rage, 1984b) (Owen, 1850, pl. XIII.29–32; Owen, 1849–1884, pl. 2.29–32; Pictet, 1853–1857, pl. XXX.4–6; Lydekker, 1888a, fig. 55; Benton and Spencer, 1995, fig. 9.7.e; Georgalis & Scheyer, 2019a,

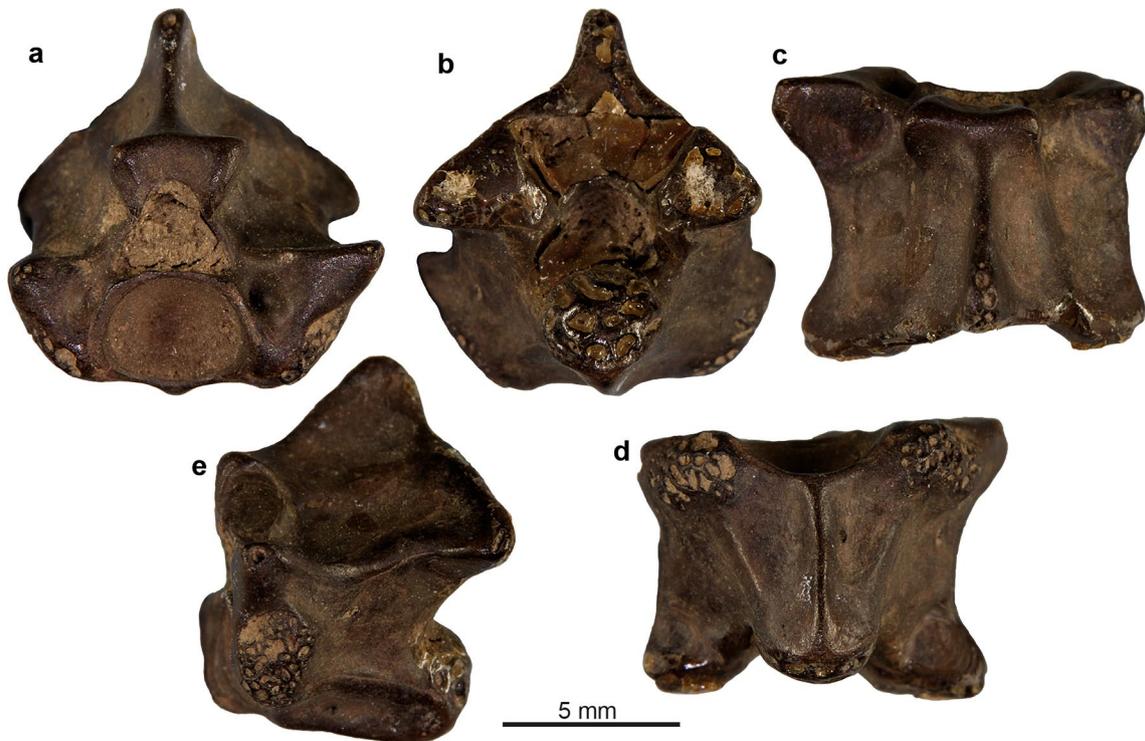


Fig. 36 *Paleryx rhombifer* from Hordle Cliff: mid-trunk vertebra (NHMUK PV OR 32840(1)) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views. Specimen originally referred to the lizard *Placosaurus margariticeps* by Lydekker (1888a)

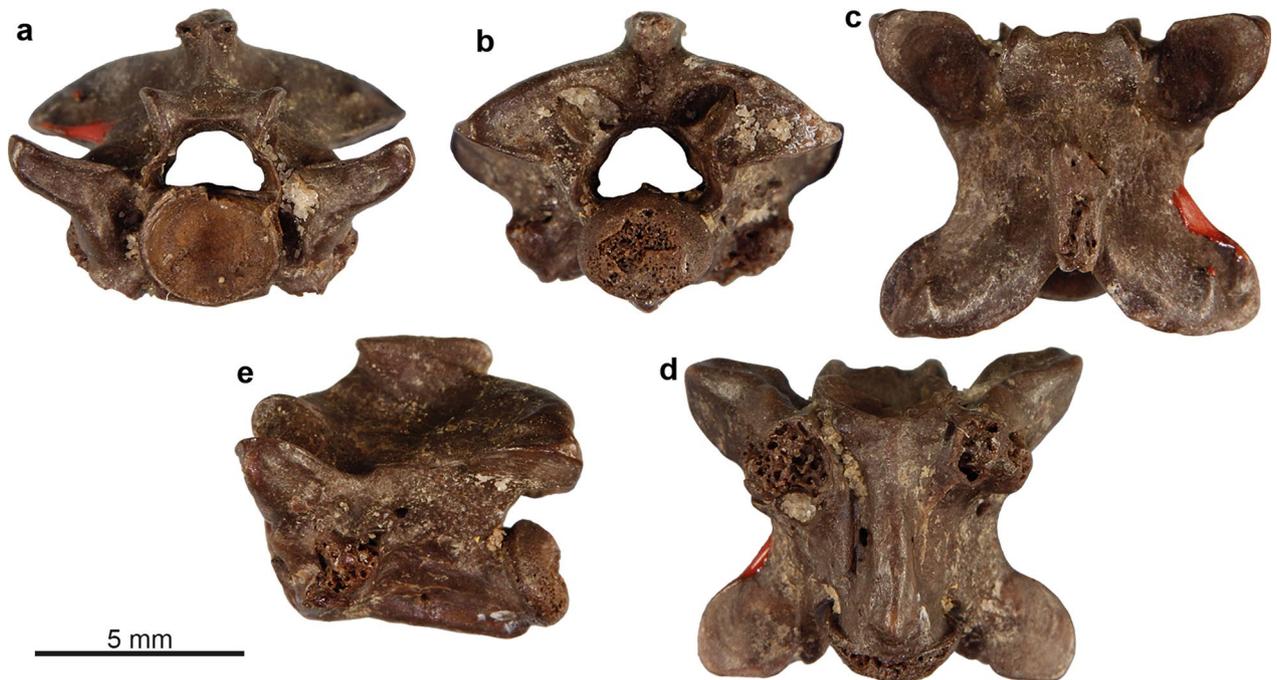


Fig. 37 *Paleryx rhombifer* from Hordle Cliff: posterior trunk vertebra (NHMUK PV OR 32838(1)) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views



Fig. 38 *Paleryx rhombifer* from Hordle Cliff: left palatine (NHMUK PV R 10907) in labial (a), medial (b), ventral (c), anterior (d), and posterior (e) views. Black lines indicate the entrance and exit of the palatine foramen

fig. 15k; Figs. 33a–d, 34). Cast exists at the collections of MNHN.

Type locality: Hordle (=Hordwell) Cliff, Hampshire, United Kingdom; Headon Hill Formation, Totland Bay Member, Mammal Bed or Rodent Bed, MP 17, late Eocene.

Referred material and range: Late Eocene (MP 18), Headon Hill, Isle of Wight, United Kingdom (referred material of Rage & Ford, 1980); late Eocene (MP 18/19), Fishbourne, Isle of Wight, United Kingdom (referred material of Rage & Ford, 1980); late Eocene (MP 19), type area, Hordle Cliff, Hampshire, United Kingdom (type material of *Paleryx depressus* Owen, 1850; referred material of Lydekker, 1888a; material referred to *Paleryx depressus* by Lydekker, 1888a; material referred to *Placosaurus margariticeps* by Lydekker, 1888a).

Referred material discussed herein (all from Hordle Cliff) (Figs. 35, 36, 37 and 38): A mid-trunk vertebra [NHMUK PV OR 25261(1) (lectotype of *Paleryx depressus*, herein designated)], two posterior trunk vertebrae [NHMUK PV OR 25261(2) and NHMUK PV OR 25261(3) (paralectotypes of *Paleryx depressus*)], many trunk vertebrae [NHMUK PV OR 32838], several trunk vertebrae [NHMUK PV OR 32840 (originally described as *Placosaurus margariticeps* by Lydekker, 1888a)], and a left palatine (NHMUK PV R 10907).

Diagnosis: As for the genus *Paleryx* (see above).

Description of the holotype (NHMUK PV OR 25259): NHMUK PV OR 25259 is an anterior mid-trunk vertebra missing most of the left prezygapophysis and part of the right postzygapophysis (Fig. 34). In anterior view (Fig. 34a), the zygosphenes are rather thick, with its dorsal level being significantly wider than its ventral one. The zygosphenal roof is straight. The neural spine is only moderately high. The neural canal is small and semicircular. The prezygapophyses are relatively thick, probably reflecting the occurrence of a small, now eroded prezygapophyseal accessory process; the prezygapophyseal articular facets are only slightly dorsally inclined. The cotyle is nearly circular. No paracotylar foramina are present but paracotylar fossae exist. The paradiapophyses are partly eroded, but it is obvious that they were not divided into diapophyseal and parapophyseal parts. The parapophyseal portions of the paradiapophyses project ventrally below the cotyle. In posterior view (Fig. 34b), the neural arch is moderately vaulted and possesses a distinct angulation at the dorsolateral corner of the zygantrum. The zygantrum is deep. The condyle is almost circular. In dorsal view (Fig. 34c), the zygosphenes are almost straight and the two lateral lobes are poorly developed. The neural spine is relatively thick and its base commences posterior to the level of the zygosphenal facets.

The prezygapophyseal articular facets are oval and have an oblique long axis. The interzygapophyseal constriction is symmetrically rounded and extends medially past the mid-point of the prezygapophyseal articular facet. In ventral view (Fig. 34d), the centrum is triangular. The haemal keel is sharp, extending along nearly the entire length of the centrum, commencing at the ventral lip of the cotyle and ending at the base of the condyle. The postzygapophyseal articular facets are subtriangular. Two small subcentral foramina are present, at around mid-length on the centrum, situated on each side of the haemal keel. In lateral view (Fig. 34e, f), the neural spine is posteriorly inclined, with parallel anterior and posterior margins and its posterodorsal edge slightly overhanging the posteromedian notch of the neural arch. A pair of tiny neural spine foramina is present. Two small lateral foramina are present, one at each side of the centrum, situated below the interzygapophyseal ridges. The subcentral ridges are almost straight. The haemal keel is tall, especially at its posterior portion, where it resembles a hypapophysis.

Description of additional vertebrae—intracolumnar variation (Figs. 35, 36 and 37): In the transition from the anterior trunk vertebrae to the mid-trunk ones, the hypapophysis is substituted by a haemal keel, which gradually diminishes in dorsoventral height more posteriorly in the vertebral column. In mid-trunk vertebrae, the haemal keel takes the shape of a thin longitudinal ridge that crosses the whole midline of the centrum (e.g., Fig. 36d). The zygosphenes are thick but can be thin in small vertebrae. There are deep paracotylar fossae next to the cotyle but usually without paracotylar foramina; a notable exception is NHMUK PV OR 32840(1), where a large paracotylar foramen is present on the left side (Fig. 36a). The neural arch is vaulted. The neural spine is thick and moderately high dorsoventrally. The interzygapophyseal constriction is moderately expressed, but in NHMUK PV OR 32840(1) it is rather shallow (like in *Palaeopython*).

In posterior trunk vertebrae, the neural arch becomes rather depressed and the haemal keel is very wide (e.g., Fig. 35g). One other notable feature of these vertebrae is that the zygosphenes are much thinner in comparison with the preceding ones. The neural spine is also thick but becomes significantly dorsoventrally lower; in NHMUK PV OR 32838(1) it overhangs both anteriorly and posteriorly (Fig. 37e). The interzygapophyseal constriction is more prominent.

Cloacal and caudal vertebrae are so far unknown for this species.

Description of cranial material: A single cranial element, the left palatine NHMUK PV R 10907, has been recovered from Hordle Cliff (Fig. 38). Its size is broadly consistent with the overall vertebral dimensions of

Paleryx rhombifer, the sole large constrictor recognized from Hordle as well as the whole British Eocene, and accordingly, we tentatively assign it to the same species. The element has seven tooth positions, and the 5th and 7th teeth are complete. Tooth size, to judge by the tooth bases, appears to decrease from front to back. It is unlike that of any known booid in having a maxillary process located well anterior of the pterygoid articulation, namely at a level between the 5th and 6th teeth (Fig. 38c). The process is finger-like, tapering as it curves anteriorly. The broad maxillary facet is located on its anteroventral surface. A palatine foramen is present, as in Pythonoidea but not Booidea, which is noteworthy for extending a considerable distance along the lateral surface of the bone anterior to the maxillary articulation in a channel that is overhung dorsally and partly dorsolaterally (Fig. 38a, d, e).

The choanal process appears to have a broad base, but its original extent is uncertain; dorsal to it are elaborations of unknown significance. The pterygoid facet is short but deep, approximately one tooth base in length; at depth it is acutely angled in cross-section, implying a dorsally sharp palatine process of the pterygoid. Anteriorly on the lateral side of the bone is a horizontal ridge of unknown significance. The bone tapers anteriorly in height. Its medial surface is gently concave.

Remarks: *Paleryx rhombifer* and *Paleryx depressus* are the first fossil Constrictores described worldwide (Owen, 1850). The original material of *Paleryx rhombifer* and *Paleryx depressus* described by Owen (1850) was initially part of the collection of the Marchioness of Hastings, but they landed in the collections of the British Museum in 1855. Lydekker (1888a) referred to both *Paleryx rhombifer* and *Paleryx depressus* numerous vertebrae from England and Quercy, as he considered that the *Palaeopython* material from the latter French region in fact belonged to the British genus. However, he did not figure any of the referred specimens from the United Kingdom; one of them (NHMUK PV OR 32838(unknown sub-number)) was figured for the first time almost one century later (Rage, 1984b:fig. 13a). Notably, Lydekker (1888a) tentatively also referred to *Paleryx rhombifer* and *Paleryx depressus* trunk vertebrae from the early Miocene (MN 1/2) of Saint-Gérard-le-Puy, France, thus expanding significantly the distribution of *Paleryx* into the Neogene. However, it seems more probable that this material pertains to the “erycine” *Bransateryx* Hoffstetter and Rage, 1972, which is found in the same locality (Hoffstetter & Rage, 1972; Rage, 1974). Rage and Ford (1980) and later Rage (1984b) considered that the differences among *Paleryx rhombifer* and *P. depressus* (vertebrae more depressed, haemal keel thicker and less produced,

zygosphenes thinner, neural spine lower and more posteriorly inclined) could simply be attributed to intracolumnar variation, as indeed the types pertained to different regions within the vertebral column. This taxonomic opinion has been generally followed ever since, in the few subsequent mentions of these English constrictors (e.g., Benton and Spencer, 1995; Wallach et al., 2014).

Lydekker (1888a) also referred several vertebrae from the late Eocene of England to *Placosaurus margariticeps* (Gervais, 1876), a glyptosaurine lizard from Quercy, originally tentatively described as a species of the genus *Varanus* Merrem, 1820. However, our direct observation of the material confirms that these vertebrae (NHMUK PV OR 32840) can in fact be referred to *Paleryx rhombifer* based on their possession of the diagnostic characters given above.

The material from the Phosphorites du Quercy referred by Lydekker (1888a) and De Stefano (1905) to *Paleryx rhombifer* is considered to belong to *Palaeopython cadurcensis*.

The palatine from Hordle Cliff described above is the first cranial element attributed to *Paleryx rhombifer*. The maxillary process is reminiscent in shape and in its position anterior to the palatine articulation to that of a previously published palatine (UM PRR 2001) from the late Eocene (MP 17) of Perrière in Quercy, which was referred to "*Palaeopython* sp." by Rage (1984b), but the latter specimen appears to lack a palatine foramen (see Rage, 1984b:fig. 12C). As mentioned above, the presence of a palatine foramen would allow rejection of booid affinities for *Paleryx rhombifer* and make pythonoid ones plausible, especially given the recognition of the stem pythonid *Messelopython freyi* in the Eocene of Europe (Zaher & Smith, 2020). However, as this feature also does exist in other snakes outside Constrictores (e.g., Lee & Scanlon, 2002), we refrain from formally referring *Paleryx rhombifer* to Pythonoidea, pending the recovery of more cranial material from the type locality.

See also *Paleryx depressus* below for further details about the synonymy of that species with *Paleryx rhombifer*, and the description of its type specimens.

Genus Incertae Sedis

"*Palaeopython*" *neglectus* Rochebrune, 1884

Figures 39, 40, 41 and 42, 44, 45

Taxonomic history: *Palaeopython neglectus* Rochebrune, 1884 (new species); *Paleryx neglectus* De Stefano, 1905 (new combination); *Palaeopython neglectus* Rage, 1984b (lectotype designation); [*Palaeopython neglectus*] Rage and Augé, 1993 (nomen dubium).

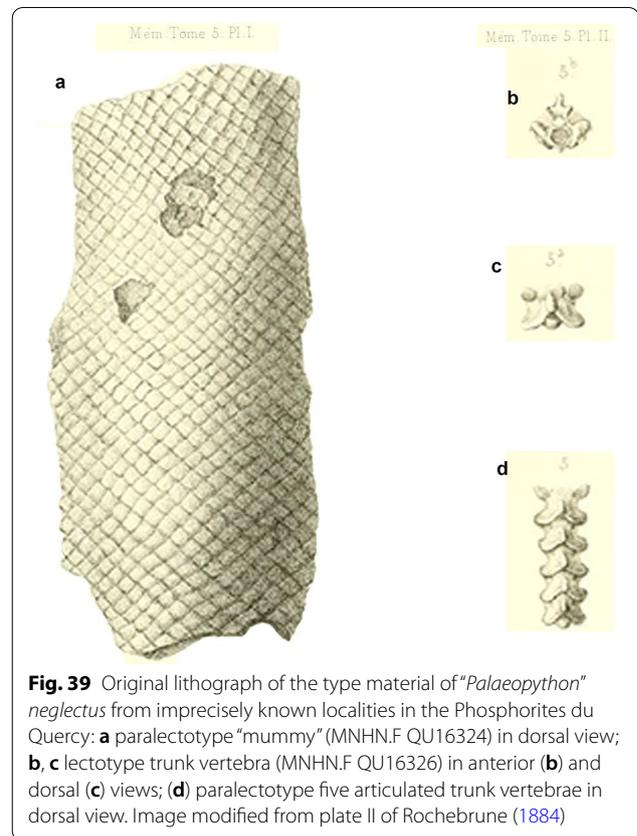


Fig. 39 Original lithograph of the type material of "*Palaeopython neglectus*" from imprecisely known localities in the Phosphorites du Quercy: **a** paralectotype "mummy" (MNHN.F QU16324) in dorsal view; **b, c** lectotype trunk vertebra (MNHN.F QU16326) in anterior (**b**) and dorsal (**c**) views; **(d)** paralectotype five articulated trunk vertebrae in dorsal view. Image modified from plate II of Rochebrune (1884)

Type material: MNHN.F QU16326 (lectotype), a trunk vertebra (Rochebrune, 1884, pl. II.5^a, II.5^b; Figs. 39b, c, 40); MNHN.F QU16325 (paralectotype), five articulated trunk vertebrae (Rochebrune, 1884, pl. II.5; Figs. 39d, 41); MNHN.F QU16324 (paralectotype), a "mummy" (Rochebrune, 1884, pl. I.1, I.1^a; Figs. 39a, 42).

Type locality: Unknown exact locality, Phosphorites du Quercy, France; probably late middle or late Eocene.

Previously referred material and range: Probably late Eocene, type area, Quercy, France (referred material of De Stefano, 1905).

Referred material discussed herein (all from the Phosphorites du Quercy, imprecise localities near Mouillac) (Figs. 44, 45): 12 isolated trunk vertebrae (one anterior, nine mid- and two posterior trunk vertebrae; YPM-VPPU 29856–YPM-VPPU 29859 and YPM-VPPU 30360–YPM-VPPU 30367) and two articulated mid-trunk vertebrae (YPM-VPPU 30368).

Diagnosis: "*Palaeopython neglectus*" is assigned to Constrictores on the basis of possessing strongly built vertebrae, the centrum wider than long, the vertebrae taller than long in lateral view, prezygapophyseal accessory processes small, paradiapophyses undivided or only weakly divided, and parazygantral foramina absent. "*Palaeopython neglectus*" differs from *Palaeopython* spp.

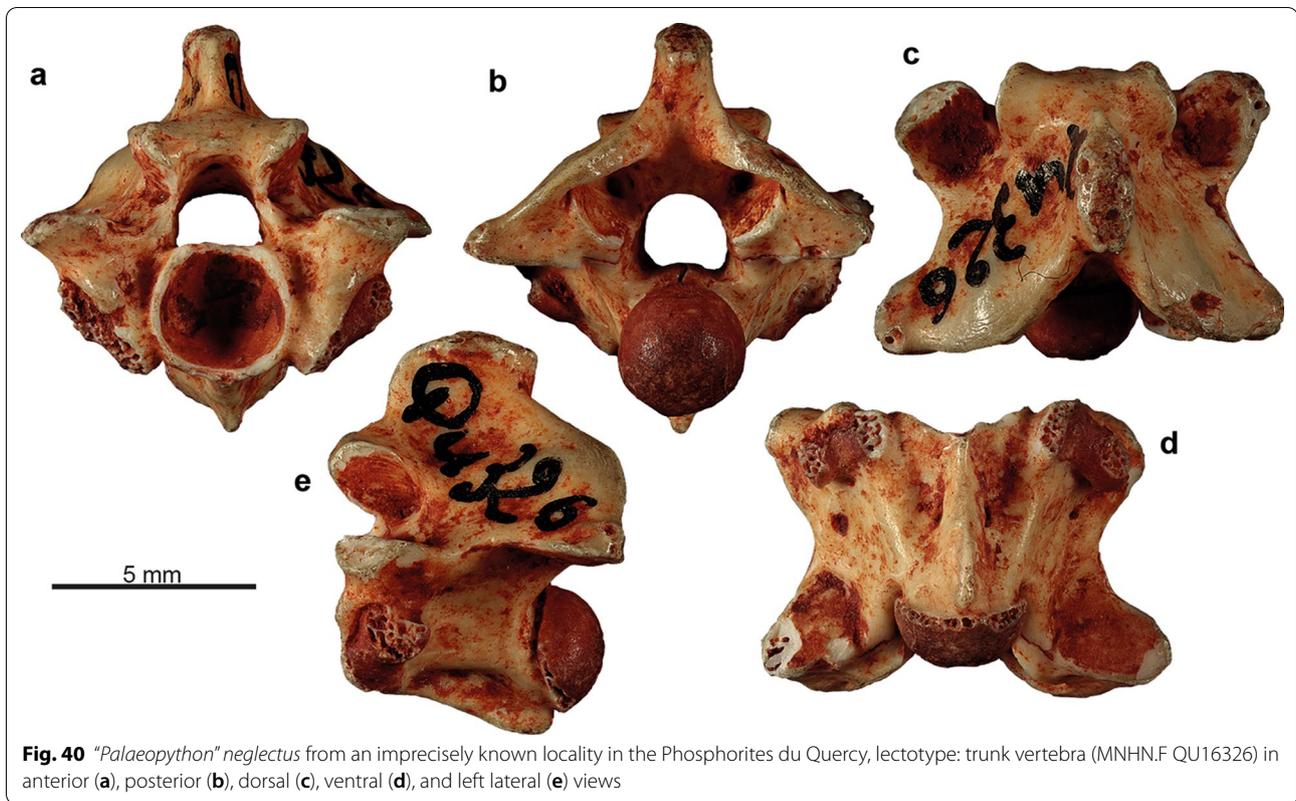


Fig. 40 "*Palaeopython*" *neglectus* from an imprecisely known locality in the Phosphorites du Quercy, lectotype: trunk vertebra (MNHN.F. QU16326) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

in being smaller, in having a deeper, symmetrical interzygapophyseal constriction, and in having a neural spine that extends well onto the roof of the zygosphenes. "*Palaeopython*" *neglectus* differs from *Paleryx* and *Phosphoroboa* gen. nov. in having a longer neural spine and a wider zygosphenes on mid- and posterior trunk vertebrae.

Description of the lectotype (MNHN.F. QU16326): The lectotype is an almost complete trunk vertebra, with the edges of its prezygapophyses being eroded (Fig. 40). The zygosphenes is broad, with moderately well-developed lateral lobes. A small median tubercle is found just above the neural canal (Fig. 40a). The distal ends of the prezygapophyses are eroded, but the articular surfaces appear to be nearly horizontal and elevated slightly above the top of the centrum. The neural spine is anteroposteriorly long, beginning as a short, thin, nearly vertical lamina at the level of the middle of the zygosphenal articular facet. It is slightly posteriorly inclined, with parallel anterior and posterior margins, and its dorsal edge appears rounded. Since that edge is capped by finished bone, it is unlikely that the rounding is purely artificial. The cap also suggests that the individual was ontogenetically advanced.

The neural arch has low, elongate zygantral mounds on its posterior half. The laminae of the posterior margin of the neural arch are broadly rounded and do not

extend beyond the postzygapophyses. Between them is a deep posteromedian notch that exposes the neural canal in front of the condyle. In posterior view, the neural arch is vaulted (Fig. 40b). Its dorsal edge appears curiously downturned along the posterior margin. A field of tiny foramina is present lateral to the zygantrum on either side. At depth the zygantrum is pierced by a pair of foramina.

The interzygapophyseal constriction is rounded and appears to have been moderately deep (Fig. 40c), although the erosion of the prezygapophyses makes explicit comparison to other taxa difficult. A pair of lateral foramina is present well below the interzygapophyseal ridges. The centrum is triangular and the subcentral ridges straight (Fig. 40d). The centrum does not widen as much anteriorly as in *Palaeopython*. There is a sharp haemal keel that grows in prominence posteriorly and reaches its maximum extent just in front of the condyle, leaving virtually no space between haemal keel and condyle; it is straight in lateral profile and extends below the condyle (Fig. 40e). The lymphatic grooves are deep and extend anteriorly between the cotyle and parapophyses. A pair of subcentral foramina is present.

The deep cotyle is nearly circular, slightly taller than wide, and has a flattened dorsal edge. The neural canal

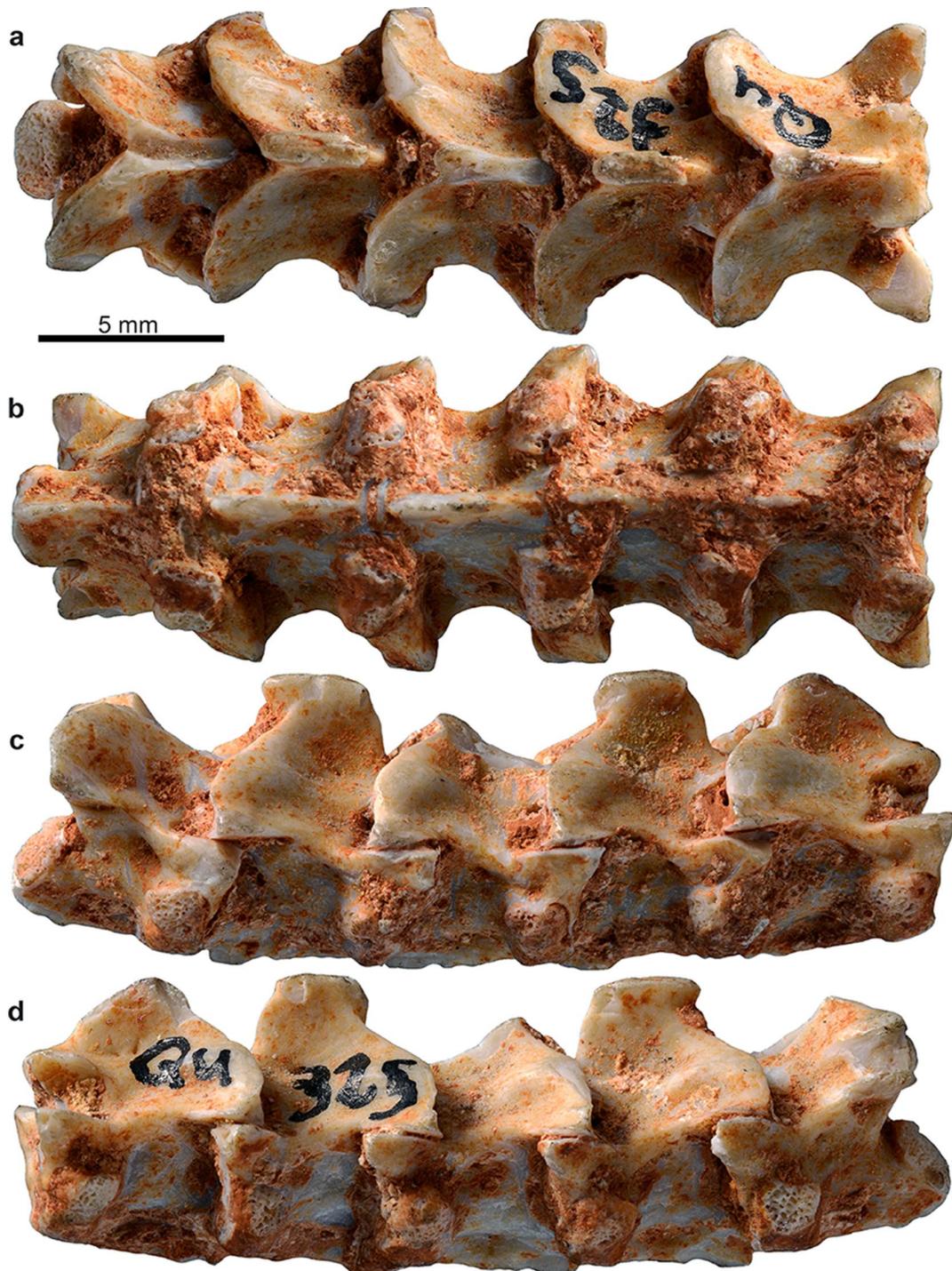


Fig. 41 *Palaeopython neglectus* from an imprecisely known locality in the Phosphorites du Quercy, paralectotype: five articulated trunk vertebrae (MNHN.F QU16325) in dorsal (a), ventral (b), right lateral (c), and left lateral (d) views

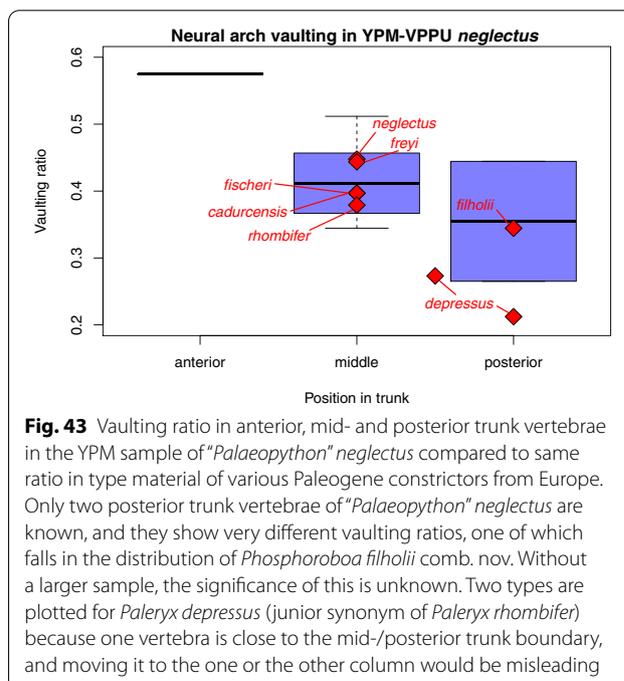
has the shape of a rounded arch. The paradiapophyses are undivided. The condyle is thick and round.

Judging from the shape and sharpness of the haemal keel, the vaulting of the neural arch, and the height of the neural spine, we consider that the lectotype vertebra



originates from around the mid-trunk region of the column.

Description of the paralectotype articulated trunk vertebrae (MNHN.F QU16325): The paralectotype MNHN.F QU16325 comprises five relatively complete articulated trunk vertebrae (Fig. 41). The zygosphenes is discernible only in the first vertebra. In dorsal view, it possesses two prominent lateral lobes along with a (less prominent) median one (Fig. 41a). The neural spine in dorsal view is anteroposteriorly long, with its anterior edge reaching as a short, thin, nearly vertical lamina almost at the level of zygosphenes. The neural spine in lateral view is moderately high and slightly posteriorly inclined (Fig. 41c, d). This element is complete in the second and fourth vertebrae, where it is visible that its dorsal level is almost straight. The posteromedian notch of the neural arch is rather deep (Fig. 41a). The prezygapophyses are not much dorsally inclined in anterior and lateral views, while they extend anterolaterally in dorsal view. The prezygapophyseal articular facets are broad and oval. Prezygapophyseal accessory processes are present, being better preserved in the first vertebra. The interzygapophyseal constriction is rounded and deep (Fig. 41a). The paradiapophyses are massive and are only weakly divided. The ventral surface is relatively eroded and still covered with much sediment in all vertebrae (Fig. 41b). The



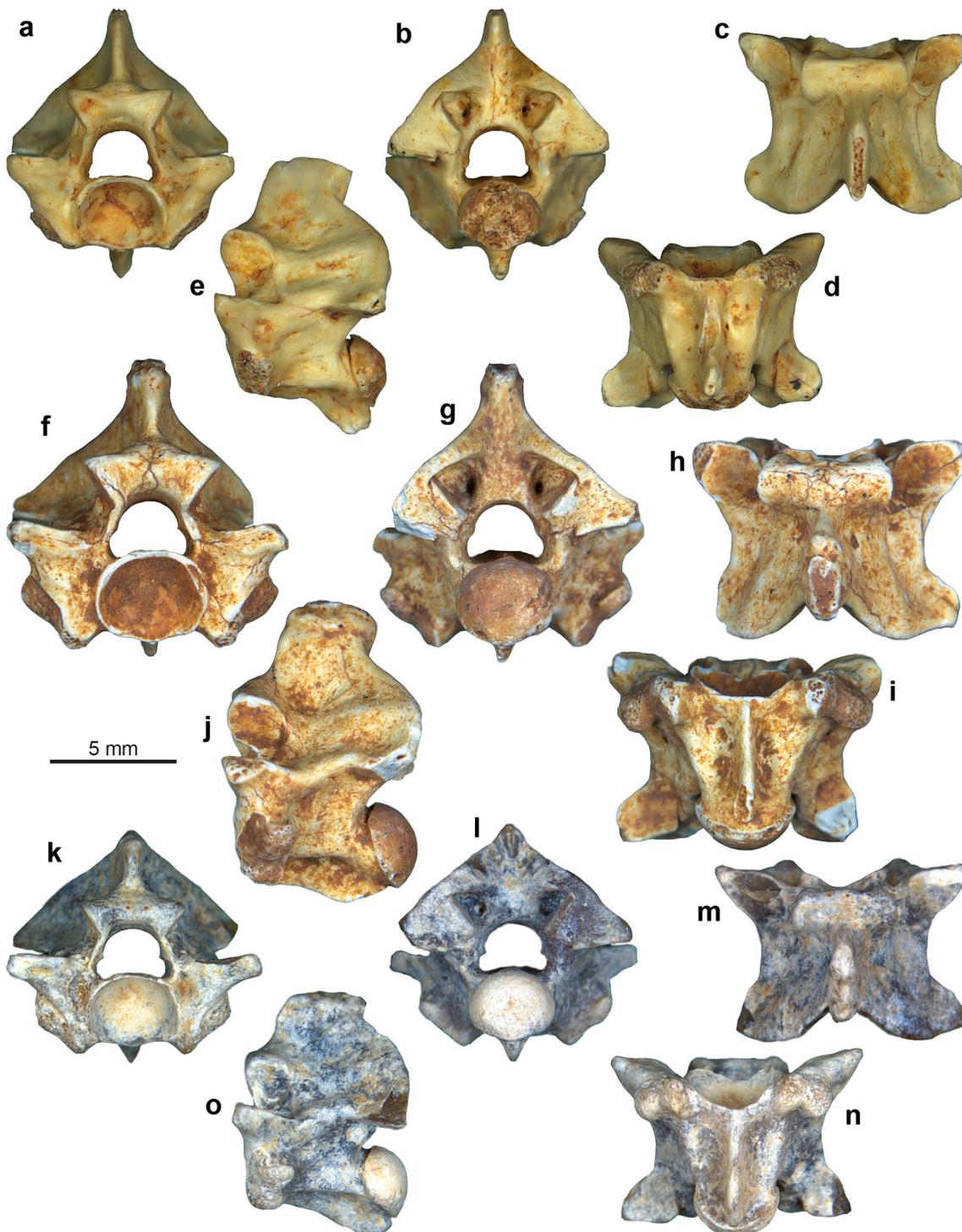


Fig. 44 *Palaeopython neglectus* from imprecisely known locality(ies) near Mouillac, Phosphorites du Quercy: **a–e** anterior trunk vertebra (YPM-VPPU 29859) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** anterior trunk vertebra (YPM-VPPU 29857), more posterior than the previous one, in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k–o** anterior trunk vertebra (YPM-VPPU 30366), more posterior than the previous one, in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views

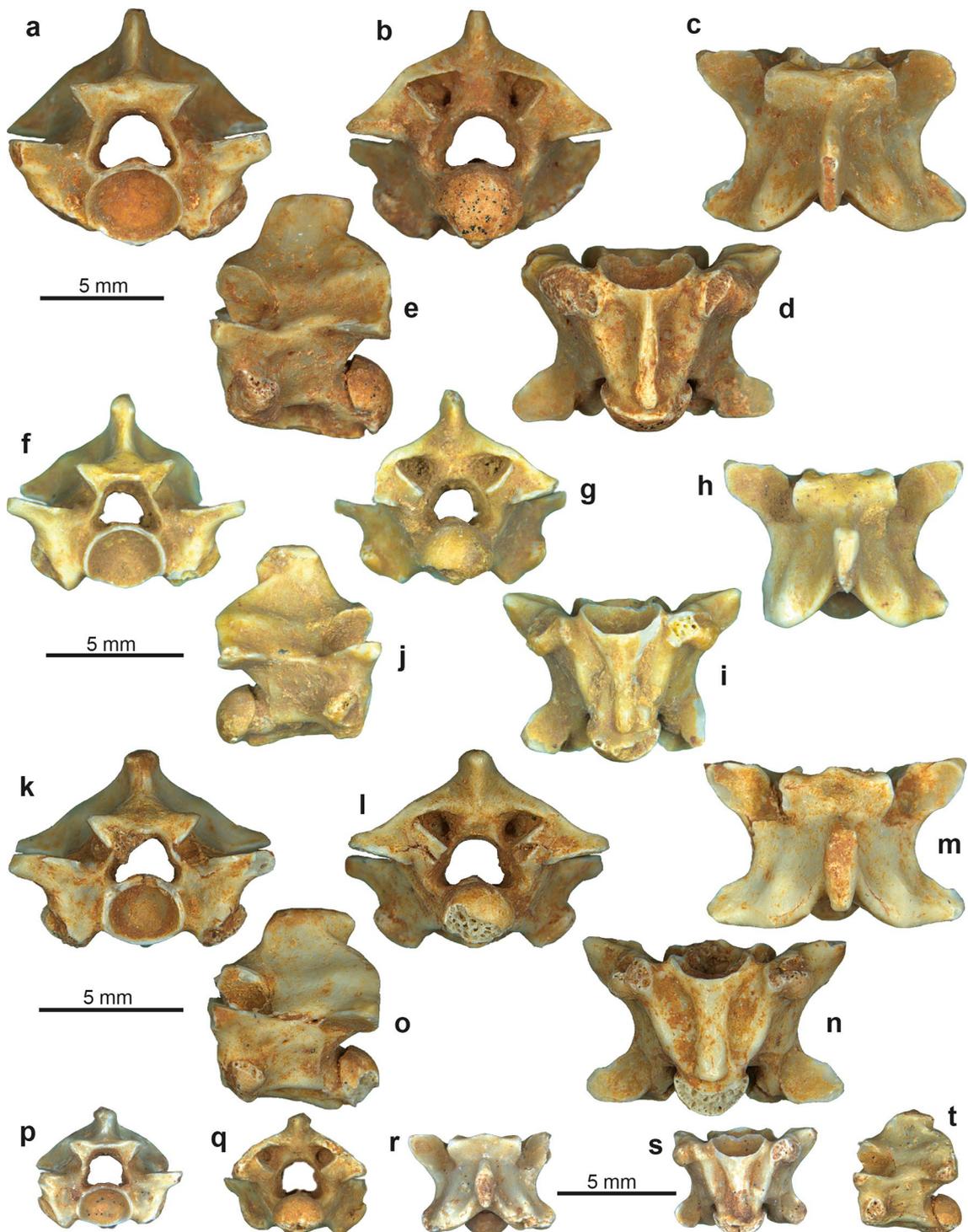
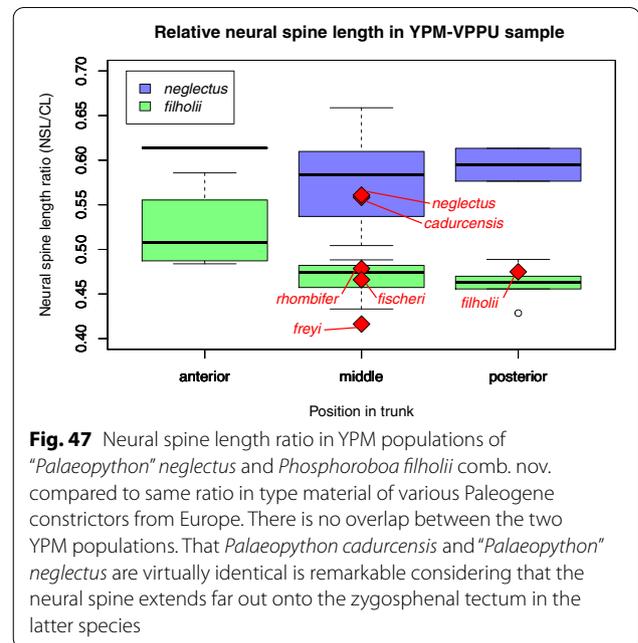
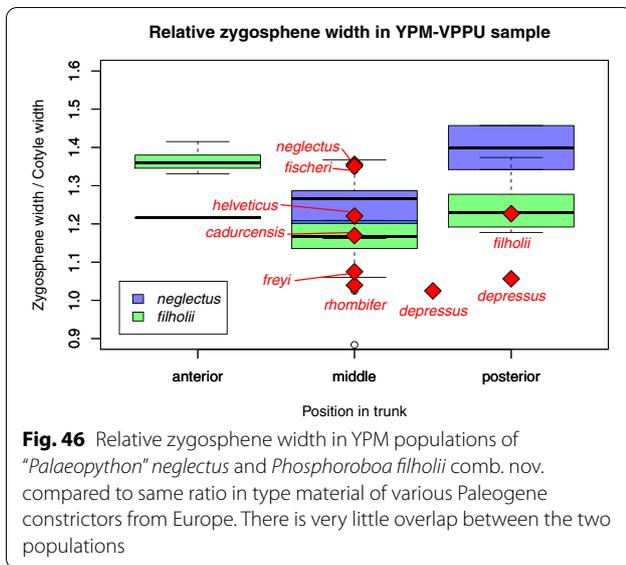


Fig. 45 *Palaeopython* *neglectus* from imprecisely known locality(ies) near Mouillac, Phosphorites du Quercy: **a–e** mid-trunk vertebra (YPM-VPPU 30363) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** mid-trunk vertebra (YPM-VPPU 30362) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and right lateral (**j**) views; **k–o** posterior trunk vertebra (YPM-VPPU 29858) in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views; **p–t** posterior trunk vertebra (YPM-VPPU 30367) in anterior (**p**), posterior (**q**), dorsal (**r**), ventral (**s**), and left lateral (**t**) views



haemal keel is sharp and seems to extend over most of the midline of the centrum. The sharpness of the haemal keel and the vaulting of the neural arch denote that these vertebrae originate from around the mid-trunk region.

Description of the paralectotype "mummy" (MNHN.F QU16324): The paralectotype "mummified" specimen MNHN.F QU16324 comprises a section of the trunk 16 cm in length (Fig. 42). It is rounded on one side in cross-section and flattened on the other. It is covered in what appear to be phosphatized scales: rhomboidal and without keels. Curiously, a row of transversely elongated ventral scales (gastrosteges), as expected in an alethinophidian snake (Lee & Scanlon, 2002), does not appear to be present. No vertebrae or ribs are discernible externally.

Description of newly referred material—intracolumnar variation (Figs. 44, 45): In general, intracolumnar variation is typical for Constrictores. The neural arch is much more vaulted in anterior trunk vertebrae (Fig. 43), and a hypapophysis is present (Fig. 44). The hypapophysis is replaced on mid-trunk vertebrae by a haemal keel, which is sharply defined by deep subcentral grooves on posterior trunk vertebrae. On anterior trunk vertebrae, the centrum is nearly parallel-sided in ventral view. On mid- and especially posterior trunk vertebrae (Fig. 45), in contrast, the centrum becomes triangular, although it does not achieve the very broad proportions seen in *Palaeopython cadurcensis*. Sample size for the posterior trunk is low ($n=2$), and whereas vaulting in one of the specimens is just like in the mid-trunk, vaulting in the other is much lower (Fig. 43), like in *Phosphoroboa filholii* comb. nov. Without a larger sample size it is difficult to interpret that result.

The width of the zygosphene is poorly constrained on anterior trunk vertebrae ($n=1$) but the ratio of zygosphene to cotyle width, in contrast to *Phosphoroboa filholii* comb. nov., is notably lower than on mid- and especially posterior trunk vertebrae in *"Palaeopython" neglectus* (Fig. 46). On mid- and posterior trunk vertebrae, the relative zygosphene width is greater in *"Palaeopython" neglectus* than in *Paleryx rhombifer* and *Phosphoroboa filholii* comb. nov. (Fig. 46). The difference in zygosphene width between *"Palaeopython" neglectus* and *Phosphoroboa filholii* comb. nov. in the YPM-VPVU sample is statistically significant. Most important is the length of the neural spine. The ratio of neural spine length to CL is everywhere >0.51 , in contrast to *Phosphoroboa filholii* comb. nov. (Fig. 47). While a high ratio is technically also true of *Palaeopython cadurcensis*, it is only in *"Palaeopython" neglectus* that the anterior end of the neural spine clearly lies over the zygosphene. This is true throughout the trunk column.

Remarks: Rochebrune (1884) established *Palaeopython neglectus* upon an isolated vertebra, five articulated vertebrae, and one "mummy" from (an) imprecise locality(ies) in the Phosphorites du Quercy. Rochebrune (1884) emphasized that this species shared several characteristics with both pythonids (his Pythonides) and booids (his Boæides), however, he chose to assign it still to the genus *Palaeopython*, with which he identified several features in common. He further noted that the "mummified" trunk portion (the paralectotype MNHN.F QU16324) resembled the skin of extant *Python* spp. De Stefano (1905) described and figured additional material from Quercy,

which he referred to the same species. He moved the species to *Paleryx*, the genus that he considered as the valid name for both English and French large-sized constrictors (De Stefano, 1905), an attribution that was subsequently followed by Kuhn (1939b). Rage (1974, 1984b) totally dismissed the “mummified” specimen and considered that the taxon was based solely on the one isolated (MNHN.F QU16326) and the five articulated vertebrae (MNHN.F QU16325). The same author also regarded that the articulated trunk vertebrae do not pertain to the same species as the isolated trunk vertebra (Rage, 1974, 1984b), while he formally designated the latter specimen as the lectotype of the species (Rage, 1984b). As for its affinities, Rage (1984b) only questionably referred “*P. neglectus* to *Palaeopython*.”

As with the case of the type and referred material of *Phosphoroboa filholii* comb. nov. discussed below, there is an apparent confusion arising from the plates and plate captions of Rochebrune (1884). In the explanation of the respective figures (plate II, figs. 5, 5^a and 5^b; Fig. 39b–d), it gives the impression that Rochebrune (1884) only had one vertebral specimen available [the “mummy” was depicted in a different plate (pl. I.1, I.1^a; Fig. 39a)]. According to his caption, his “figure 5” depicts a string of five articulated vertebrae (Fig. 39d), whereas his “figures 5^a and 5^b” represent “les mêmes grossies” (“the same [plural, i.e. vertebrae] enlarged”) in anterior and dorsal views respectively (Fig. 39b, c). As such, it is not fully clear from the original plate of Rochebrune (1884) which and how many vertebral specimens are the syntypes of this species and it becomes even more perplexing with the statement “les mêmes” by Rochebrune (1884), implying a single specimen. However, in that case that there is depicted only a single vertebral specimen, if fig. 5^a, and 5^b of Rochebrune (1884) truly represented the same specimen with his fig. 5, then they must have been an abstraction of the latter, where the anterior-most vertebra in the string would be the primary object to which the condyle of the posterior-most vertebra was added. Nevertheless, Rage (1974) recognized that the isolated vertebra in the plate of Rochebrune (1884) was not the same specimen as the five articulated vertebrae. He also later designated the isolated vertebra as the lectotype as he felt that the (paralectotype) articulated trunk vertebrae do not pertain to the same species as the lectotype (Rage, 1984b). Indeed, in support of Rage’s opinion, the collections of MNHN host two different vertebral specimens that bear labeling that associate them to “*Palaeopython neglectus* and Rochebrune’s (1884) plate, one isolated trunk vertebra (MNHN.F QU16326) and five articulated trunk vertebrae (MNHN.F QU16325). These two specimens bear much resemblance with the ones figured in the plate of Rochebrune (1884) and any difference may be accounted to

inaccuracy of the original lithograph. That being said, the original type series of “*Palaeopython neglectus* consists of an isolated vertebra (lectotype), a string of five articulated vertebrae (paralectotype), but also a “mummy” (paralectotype).

As mentioned before, Rage (1984b) suggested that the paralectotype articulated trunk vertebrae (MNHN.F QU16325) do not pertain to the same species as the lectotype. However, we here tend to disagree with this opinion. The paralectotype vertebral string bears the important diagnostic features observed on the lectotype, most prominently the neural spine extending onto the roof of the zygosphenon, the deep interzygapophyseal constriction, and the deep posterior median notch of the neural arch (Fig. 41). Similarities in the height and shape of the neural spine and the shape of the zygosphenon also favour conspecificity. Accordingly, we consider that Rochebrune (1884) was correct and the paralectotype MNHN.F QU16325 is aptly referred to “*Palaeopython neglectus*.”

As for the “mummified” paralectotype specimen MNHN.F QU16324 (Fig. 42), vertebrae cannot be examined externally, and its reference to the same species as the lectotype is unsupportable until micro-CT studies can compare the vertebrae that presumably are contained within. It is currently impossible to assess whether the paralectotype MNHN.F QU16324 does or does not pertain to “*Palaeopython neglectus*.” See “Localities and age” above for a discussion about the probable age of this specimen, considered to pertain to around the late middle–late Eocene (late Bartonian–late Priabonian [MP 16–19 or 20, about 40–34 Ma]).

A comment about De Stefano’s (1905) referred specimens is needed here; his specimens are currently lost and only his figures remain. De Stefano (1905) supposedly figured two different pairs of articulated vertebrae which he assigned to this species. He stated in his figure captions (p. 47) that his plate V, figs. 3 and 4, illustrate two different specimens (both being two articulated vertebrae) of this species (De Stefano, 1905). However, as we show below, the specimen in De Stefano (1905:pl. V.3) is in fact the ventral view of the holotype of *Paleryx cayluxi* that he figured in figs. 1, 2 of the same plate (see “Remarks” in the entry of *Paleryx cayluxi* below). As such, the only specimen of “*Palaeopython neglectus*” figured by De Stefano is that in his fig. 4 of his plate V. Because of the long neural spine, we view attribution to this species as plausible.

While there are some noteworthy features in the lectotype, it is the YPM material that proves that these features (especially the long neural spine) are characteristic. It fits *Palaeopython* in some respects (e.g., the ratio of NSPL to CL), but not in others (e.g., it has no thick zygosphenon), and it is clearly distinct from *Paleryx* and

Phosphoroboa gen. nov. (see also Appendix 2). That being said, the generic attribution of this species is uncertain: available names of medium-sized Constrictores from the Phosphorites du Quercy do exist, such as *Palaeolaphis* Rochebrune, 1884, *Tachyophis* Rochebrune, 1884, *Plesiotortrix* Rochebrune, 1884, and *Rageophis* Wallach, 1986, all of which are currently considered nomina dubia or at least they are not adequately known (Szyndlar & Rage, 2003; Wallach et al., 2014). In any case, the vertebral morphology of the type species of these medium-sized genera, seems to deviate from that of “*Palaeopython*” *neglectus*, while the lectotype *Rageophis lafonti* (MNHN.F QU16342; a “mummified” trunk portion with several articulated vertebrae and ribs) does not allow direct observation of its vertebrae in dorsal view, thus it cannot be deduced whether the neural spine extends onto the roof of the zygosphene. However, we notice that there is some resemblance in the vertebral morphology with the recently described pythonoid *Messelopython freyi* from Messel (Zaher & Smith, 2020). In particular, the two species show a similar level of vaulting of mid-trunk vertebrae and a similar shape of the interzygapophyseal constriction. Furthermore, although the tip of the neural spine is short in *M. freyi*, its expanded base extends out onto the zygosphenal tectum, potentially an intermediate condition on the way to the highly elongated neural spine seen in “*P.*” *neglectus*. We provisionally leave the species “*P.*” *neglectus* in “*Palaeopython*” but signify with quotation marks that this attribution probably is in error. Only new anatomical data, preferably from skull elements, will be able to clarify the true phylogenetic affinities of this species.

Booidea Gray, 1825 (sensu Pyron et al., 2014)

Genus *Eoconstrictor* Scanferla and Smith, 2020b

Type species: *Palaeopython fischeri* Schaal, 2004.

Other species included: *Paleryx spinifer* Barnes, 1927.

Geographic and stratigraphic distribution: see Table 3.

Diagnosis: *Eoconstrictor* is assigned to Constrictores on the basis of possessing strongly built vertebrae, the centrum wider than long, the vertebrae taller than long in lateral view, prezygapophyseal accessory processes small, paradiapophyses undivided or only weakly divided, parazygantral foramina absent, maxillary process of premaxilla tapering to a point distally, and dentary mental foramen displaced caudally. *Eoconstrictor* can be differentiated from other snakes by the following combination of derived features (where known): edentulous premaxilla with bifid vomerine processes; mid-sagittal keel along

the basioccipital contributing to V-shaped cross-section; 11 pterygoid teeth; the vertebral column with up to 369 vertebrae, of which up to 72 are postcloacal vertebrae. *Eoconstrictor* can be differentiated from *Palaeopython* in lacking the flared posterior process of the maxilla and having a less thick zygosphene with prominent lamellar tubercle. *Eoconstrictor* can be differentiated from *Paleryx* in lacking a palatine foramen, in having a generally taller neural spine (especially on posterior trunk vertebrae), and lacking a depressed neural arch on posterior trunk vertebrae. *Eoconstrictor* differs from the booid *Phosphoroboa* gen. nov. in having a lower pterygoid tooth count (11) and in having a U-shaped frontoparietal suture.

Remarks: Scanferla and Smith (2020b) erected the new genus *Eoconstrictor* to encompass *Palaeopython fischeri*, which they determined that was not closely related to *Palaeopython*. Their phylogenetic analyses found *E. fischeri* to be on the stem of Neotropical boas, i.e. Boidae sensu Pyron et al. (2014), i.e. exclusive of Sanziniidae Romer, 1956, and *Candoia* Gray, 1842. Below, we recognize the Geiseltal *Paleryx spinifer* as a second species of *Eoconstrictor*, expanding the stratigraphic and geographic distribution of the genus.

Eoconstrictor fischeri (Schaal, 2004)

Figures 48, 49, 50, 51, 52 and 53

Taxonomic history: *Palaeopython fischeri* Schaal, 2004 (new species); *Eoconstrictor fischeri* Scanferla and Smith, 2020b (new combination).

Type material: SMF-ME 929 (holotype), two strings of three and four articulated trunk vertebrae, respectively (not a single trunk vertebra as stated by Wallach et al., 2014), from a single individual (Schaal, 2004, fig. 1; Smith & Scanferla, 2016, fig. 2f; Figs. 48, 49 and 50, Additional file 2: Model 2); SMF-ME 1002 (paratype), a complete skeleton with skull (Schaal, 2004, figs. 2–3).

Type locality: Messel Pit, Hesse, Germany; Middle Messel Formation, MP 11, early–middle Eocene. Both holotype and paratype derive from layers 1–3 m above marker bed Alpha and are therefore middle Eocene (Lutetian) in age following either of the two alternative astronomical calibrations of Lenz et al. (2015).

Previously referred material and range: Early–middle Eocene (MP 11; see Lenz et al., 2015), Middle Messel Formation, type locality only, Messel, Hesse, Germany (referred material of Smith & Scanferla, 2016; this paper; referred material of Schaal, 2004, in part).

The oldest known Messel specimens originate from around marker bed Alpha (either Ypresian or Lutetian boundary, depending on which of the two alternative astronomical calibrations of Lenz et al. (2015) is accepted.

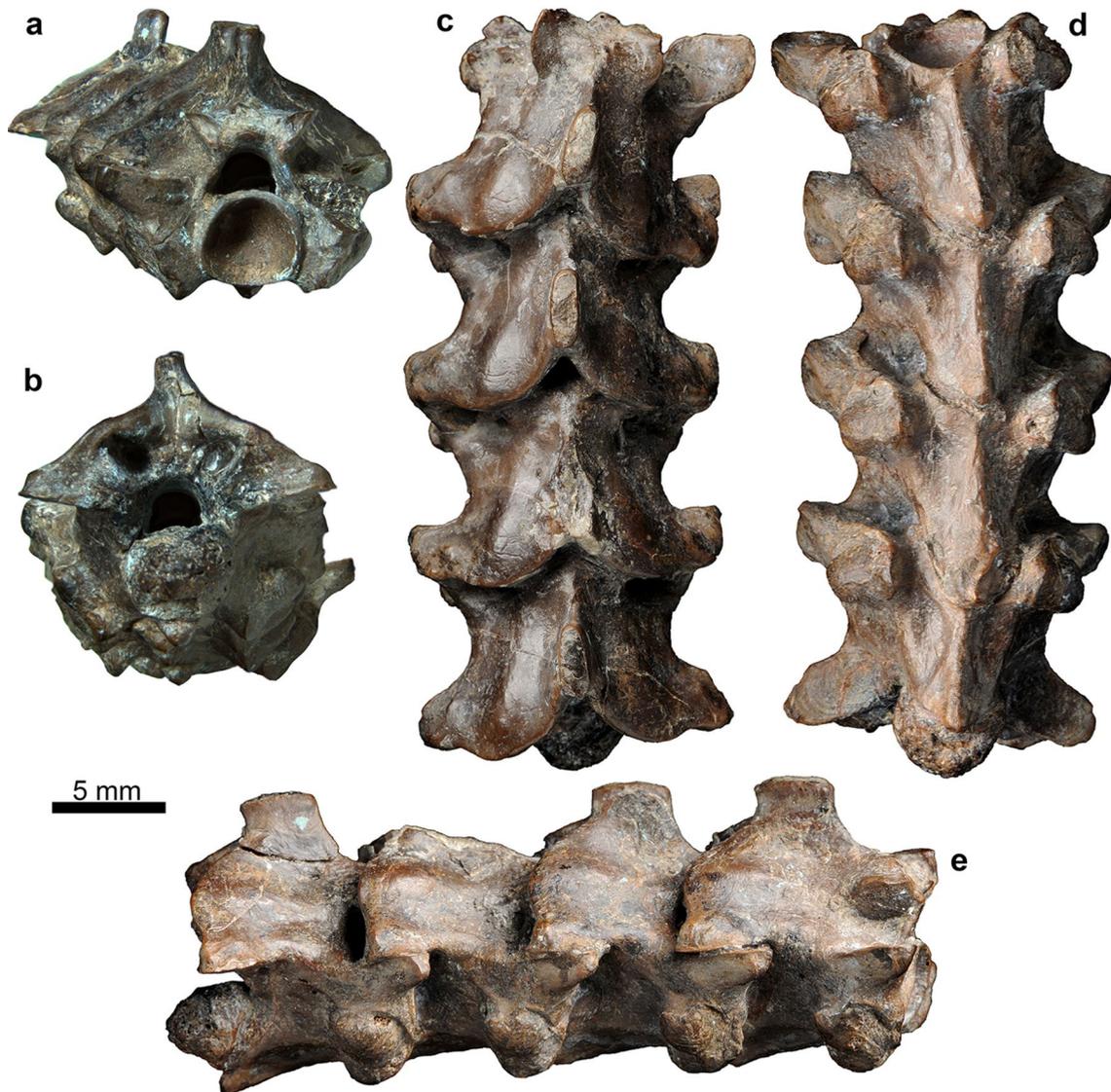


Fig. 48 *Eoconstrictor fischeri* from Messel, holotype (part) (SMF-ME 929): string of four articulated vertebrae in anterior (a), posterior (b), dorsal (c), ventral (d), and right lateral (e) views. This string was originally closely connected with the other part of the holotype, string of Fig. 50, of which it was placed more anteriorly

Referred material discussed herein (all from Messel) (Figs. 51, 52 and 53): SMF-ME 1545 (partial skeleton with skull fragments), SMF-ME 1607 (partial skeleton), SMF-ME 2504 (nearly complete skeleton with disarticulated skull), SMF-ME 11332 (complete skeleton of juvenile with skull), SMF-ME 11398 (complete skeleton). The specimens derive from layers ranging from 5 to 2 m below marker bed M (SMF-ME 1545) to 3 m below marker bed Alpha. Marker beds Alpha and M are separated by about 24 m in the profile. Note that there are several more mid-sized Constrictores known from Messel, but their comparison with the type material of *Eoconstrictor fischeri*

is complicated by the high state of articulation. Further study may identify some of these as individuals of *Eoconstrictor fischeri*.

Diagnosis: *Eoconstrictor fischeri* can be differentiated from *Eoconstrictor spinifer* comb. nov., in having four labial foramina in the maxilla, 15–18 maxillary teeth, palatine with 5 teeth and a long maxillary process, dentary with 18–19 teeth, relatively thin zygosphenes with strong, lamellar median tubercle on all trunk vertebrae, and a narrow and almost triangular cotyle on mid-trunk vertebrae.

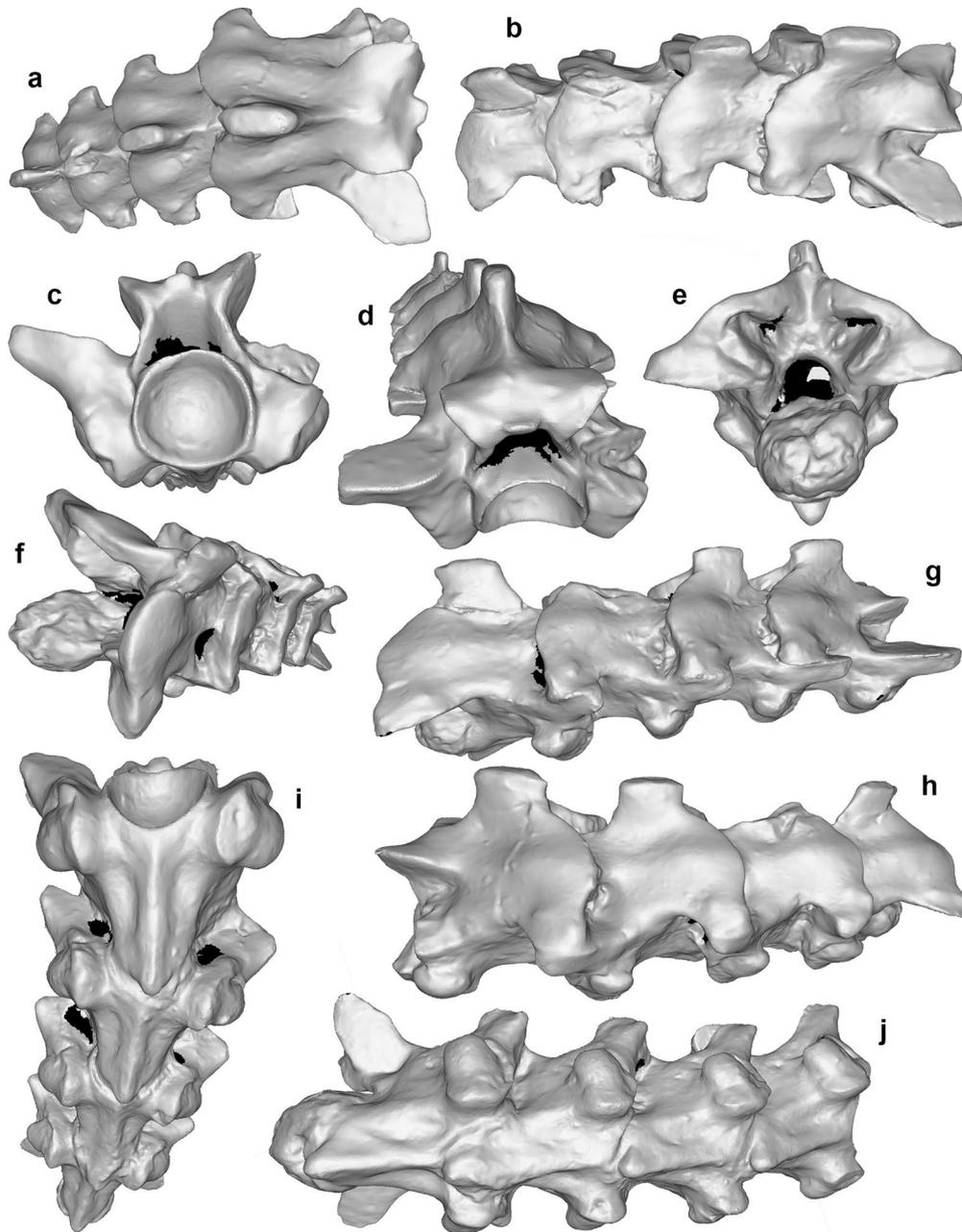
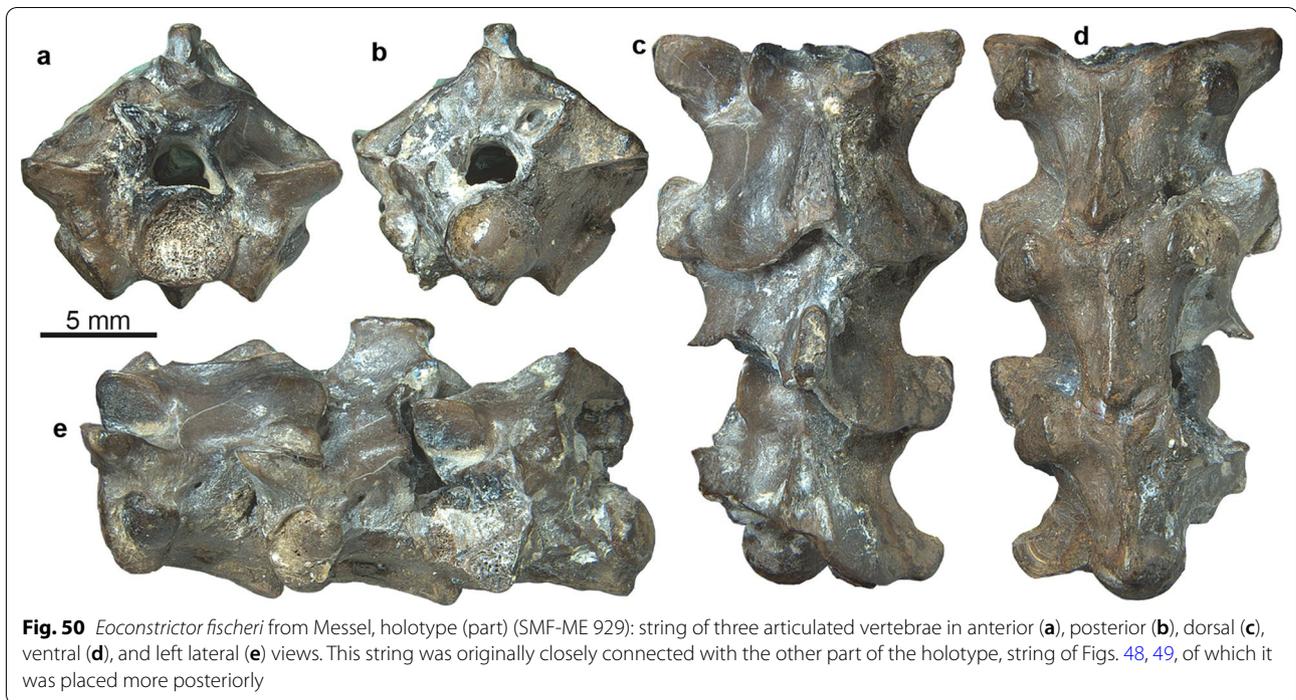


Fig. 49 *Eoconstrictor fischeri* from Messel, holotype (part) (SMF-ME 929): 3D models of the string of four articulated trunk vertebrae in dorsal (a), dorsolateral (b), anterior (c), anterodorsal (d), posterior (e), posterodorsal (f), right lateral (g), left lateral (h), ventral (i), and ventrolateral (j) views. Images not to the same scale

Description of the holotype (SMF-ME 929): The holotype SMF-ME 929 consists of two strings consisting of three and four mid-trunk vertebrae, respectively (Figs. 48, 49 and 50). These were previously closely connected, the string with four in front of the string with three. The vertebrae are massively built. The zygosphenes have large, upturned lateral lobes, which make the zygosphenal roof

concave, and a distinctive median tubercle at mid-height. The tubercle, unlike in examined members of *Palaeopython*, *Paleryx*, and *Phosphoroboa* gen. nov., is lamellar: dorsoventrally compressed and mediolaterally wide. The large prezygapophyses have oval articular facets, with the long axis somewhat oblique. Growth rings are present on the left prezygapophyseal articular facet of the string of



three (Fig. 50c). Prezygapophyseal accessory processes are very weak and scarcely visible below the prezygapophysis in dorsal view.

The neural spine begins to rise steeply behind the posterior margin of the zygosphenal articular facets. It is relatively short, with a flat top and parallel anterior and posterior margins. On one vertebra, it has a slightly overhanging posterior margin. The neural spine is mediolaterally thick, but its dorsal edge is not clearly expanded. The dorsal edge appears well-ossified, suggesting an ontogenetically advanced individual. The neural arch rises posteriorly. Several vertebrae evince weak tubercles in the position of epizygapophyseal spines, but they are low and rounded. Zygantral mounds are low and rounded to elliptical. The posterior border of the neural arch is nearly straight in posterior view, showing only a slight angulation. However, it is drawn out into a pair of broad, rounded flanges that project slightly beyond the posterior end of the postzygapophyses. Between these flanges is a moderately deep median notch that just barely reaches the anterior margin of the condyle. A pair of foramina opens at depth in the zygantrum.

The interzygapophyseal constriction is smoothly rounded and deep, extending well past the mid-point of the prezygapophyseal articular facet (Figs. 48c, 49a, 50c). Lateral foramina are located well below the interzygapophyseal ridge. The haemal keel is sharp-edged with a thick base and extends from just beyond the cotyle almost to the condyle. The subcentral ridges are straight

to slightly concave. The centrum is an elongate triangle in ventral view.

The cotyle is deep and narrower than the zygosphene. The two exposed cotyles are nearly triangular (Figs. 48a, 49c, 50a). Paracotylar fossae are present (Schaal, 2004) but very shallow. Paracotylar foramina are absent (Schaal, 2004). The paradiapophyses are almost undivided and project a little below the cotyle. The one well-preserved condyle is circular.

Description of additional vertebrae—intracolumnar variation (Figs. 51, 52 and 53): In SMF-ME 2504, the vertebral column is stretched out and in places disarticulated, yielding (in contrast to most Messel specimens) a better understanding of intracolumnar variation (Fig. 53). The median tubercle on the zygosphene is apparently developed throughout trunk series, although it can only be evaluated at intervals.

Distinct hypapophyses, marking the anterior trunk vertebrae, are present on at least the first 70 trunk vertebrae. Here the neural arch is highly vaulted. The anterior three trunk vertebrae have slender, rodlike, highly posteriorly inclined neural spines, but thereafter they are laterally compressed. On anterior trunk vertebrae, the anterior and posterior margins of the neural spine are parallel, but on mid- and posterior trunk vertebrae the anterior margin becomes relatively more oblique due to the development of a thin, convex anterior flange to the neural spine proper. The flange begins more anteriorly, above the posterior end of the zygosphene. The neural spine is of



Fig. 51 *Eoconstrictor fischeri* from Messel: complete, 201 cm long, skeleton with skull (SMF-ME 1607). Specimen was originally figured by Keller and Schaal (1988:fig. 194) and Schaal (2004:fig. 5)

similar height and is particularly long on the anterior-most four or five trunk vertebrae; it is relatively shorter thereafter, but this is compensated by the tall neural arch. Neural spine height rises thereafter and apparently reaches its greatest height in the posterior portion of the anterior trunk series. It declines thereafter, but is of similar height in mid- and posterior trunk vertebrae. The projection of the neural spine over posteromedian notch is similar throughout trunk series.

On many mid-trunk vertebrae the posterodorsal margin of the neural arch is concave on either side, rather than straight, in posterior view, forming a continuous curve that extends from the lateral edge of the postzygapophysis onto the neural spine. Subcentral foramina are present on all vertebrae in which the ventral surface is exposed. Zygantral mounds are poorly developed throughout the trunk series; weak, sometimes elongated, sometimes rounded bumps are present on some vertebrae, although in some cases they can be magnified by

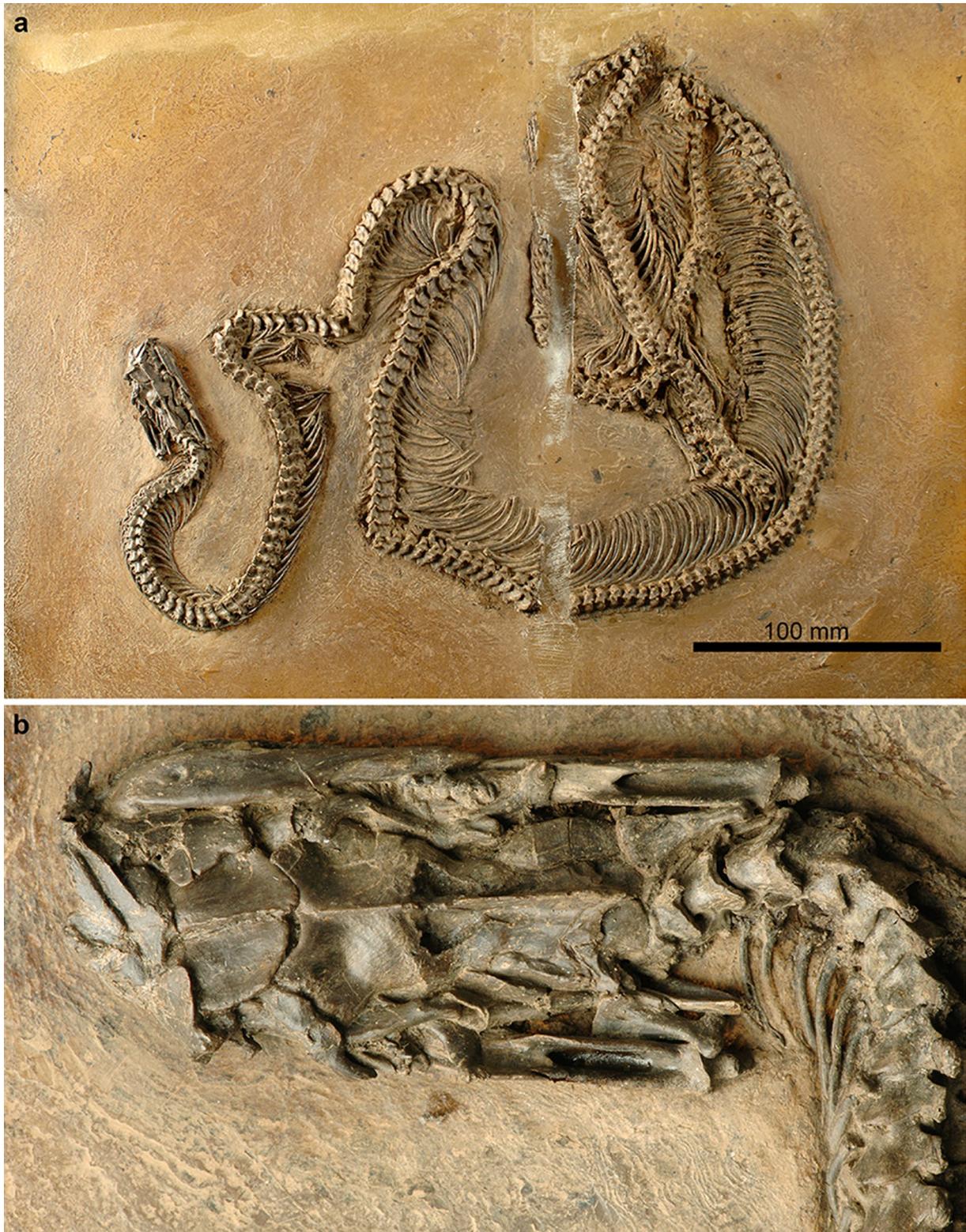


Fig. 52 *Eoconstrictor fisheri* from Messel: **a** complete skeleton with skull (SMF-ME 11398); **b** close up of the skull and the anterior trunk region of the same specimen



Fig. 53 *Eoconstrictor fischeri* from Messel: **a** articulated skeleton with skull (SMF-ME 2504); **b** close up of skull remains of the same specimen. Specimen originally figured by Schaal (2004:figs. 6, 7)

or attributed to taphonomic artefacts. Very common, and throughout the vertebral column, are neural spine foramina.

On the posterior trunk vertebrae there is a blunt haemal keel instead of a sharp ridge; it is bounded by lymphatic grooves that grow in prominence posteriorly. The anterior end of the keel has an abrupt terminus, so that it

projects very slightly below the centrum. On the posterior region of the posterior trunk vertebrae the anterior margin of the haemal keel grows into a weak but distinct and later moderate hypapophysis. The subcentral ridges also grow in prominence and grow acute posteriorly.

The prezygapophyseal accessory processes are weak throughout the trunk series, and slightly anteroposteriorly compressed, but in the caudal series they are more prominent and rounded in cross-section, taper to a sharp tip, and become more anteriorly directed. Haemapophyses are present. Distally in the tail the zygosphenes disappear, and the neural spine becomes long, covering almost the entirety of the neural arch.

Remarks: This species was originally established at Messel, and more than a dozen specimens have been recognized, including several rather complete and articulated skeletons with skulls (Scanferla & Smith, 2020b; Schaal, 2004; Smith & Scanferla, 2016; Smith et al., 2018). We are faced with two difficulties in the taxonomic analysis of this species. First is the original selection of a short, isolated string of vertebrae as the holotype, because parts of a whole can present no more diagnostic features than the whole, and normally present many fewer. Second, significant cranial and minor vertebral differences shown by at least two of the specimens in the original description, HLMD-Me 15426 and SMNK-PAL 2347, indicate that these represent a large constrictor not closely related to the SMF-ME specimens with skulls.

The prominent, distinctive zygosphenal tubercle of SMF-ME 929 is also seen in SMF-ME 2504 and SMF-ME 11398, and skull form in SMF-ME 1002, SMF-ME 2504, SMF-ME 11332, and SMF-ME 11398 is quite similar. Thus, despite the limited holotype, we believe that *Eoconstrictor fischeri* is valid and other, more complete specimens in the SMF-ME collection were correctly referred to it. Scanferla and Smith (2020b) revised the taxonomy and elucidated the phylogenetic relations of this species. The relations of the second species, specimens of which were originally included in *E. fischeri*, will be the subject of a later contribution.

The knowledge of the palaeoecology of *Eoconstrictor fischeri* was enhanced by Smith and Scanferla (2016), who described an exceptionally preserved juvenile specimen (SMF-ME 11332) from Messel with an individual of the lizard *Geiseltaliellus maarius* Smith, 2009, in its stomach. Other large fossils from that locality also revealed trophic habits of these snakes (Greene, 1983; Gunnell et al., 2018; Mayr & Schaal, 2016; Smith et al., 2018). However, the attribution of isolated regurgitates to *E. fischeri* must now be re-assessed following the recognition of more than one large constrictor in the locality.

Eoconstrictor cf. fischeri

Figures 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66 and 67

Referred material and range: Geiseltal, late early or middle Eocene (in stratigraphic order): quarry IX; quarry I; quarry VI (including VIa); quarry XXII; quarry XLI; quarry XXXIII; quarry XXXV; quarry XXXVI; quarry XXXVII; quarry XXXVIII; quarry Cecilie IV; quarry Leonhardt III; quarry Cecilie I (this paper). **Dielsdorf, late middle–late Eocene (MP 16–20):** Fissure A, Fissure 2 and imprecisely known fissure (referred material of Georgalis & Scheyer, 2019a).

Referred material discussed herein (all from Geiseltal [in stratigraphic order]) (Figs. 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66 and 67): **quarry IX (Fig. 54):** two trunk vertebrae (GMH IX-260b1-1953 and GMH IX-260b2-1953), nine trunk vertebrae and three fragments of ribs probably pertaining to a single individual (GMH IX-696-1952); **quarry I (Fig. 55):** 37 trunk vertebrae (GMH I-10111-1949); **quarry VI (Fig. 56):** three trunk vertebrae (GMH VI-370b-1950, GMH VIa-529a-1952, and GMH VIa-529b-1952); **quarry XXII (Fig. 57):** two trunk vertebrae (GMH XXII-761-1966), 16 trunk vertebrae and a pterygoid fragment (GMH XXII-Y-43), 12 trunk vertebrae along with four vertebral and two rib fragments (GMH XXII-Y-44-1965), and a string of several articulated trunk vertebrae (GMH XXII-604b-1965); **quarry XLI (Fig. 58):** many trunk vertebrae (GMH XLI-139-1966, GMH XLI-148-1966, GMH XLI-165a-1966, GMH XLI-165b-1966, GMH XLI-165c-1966, GMH XLI-165d-1966, GMH XLI-165e-1966, GMH XLI-155-1966 [six trunk vertebrae vertebrae], GMH XLI-104-1966, GMH XLI-153-1966, GMH XLI-213-1967, GMH XLI-117-1966 [eight trunk vertebrae], GMH XLI-302-1968 [three vertebrae], GMH XLI-158-1966 [two vertebrae], GMH XLI-162-1966 [two articulated and three isolated large trunk vertebrae], GMH XLI-159-1966 [five large vertebrae], GMH XLI-314c-1968 [a trunk vertebra plus a fragment of the articulated succeeding one], GMH XLI-325-1968 [many trunk vertebrae]), a string of six articulated trunk vertebrae and remains of ribs (GMH XLI-157-1966), a string of three small articulated trunk vertebrae and ribs (GMH XLI-50-1966), two trunk vertebrae and ribs (GMH XLI-160-1966); **quarry XXXIII:** a trunk vertebra along with three vertebral and two rib fragments (GMH XXXIII-16-1962) and two strings of articulated mid-trunk vertebrae (GMH XXXVIII-61-1964); **quarry XXXV (Fig. 59):** several trunk vertebrae (XXXV-274-1963, GMH XXXV-380-1963, GMH XXXV-131a-1963, GMH XXXV-131b-1963, GMH XXXV-577-1963, GMH XXXV-552-1963 [six vertebrae], GMH XXXV-235-1963 [two trunk vertebrae],

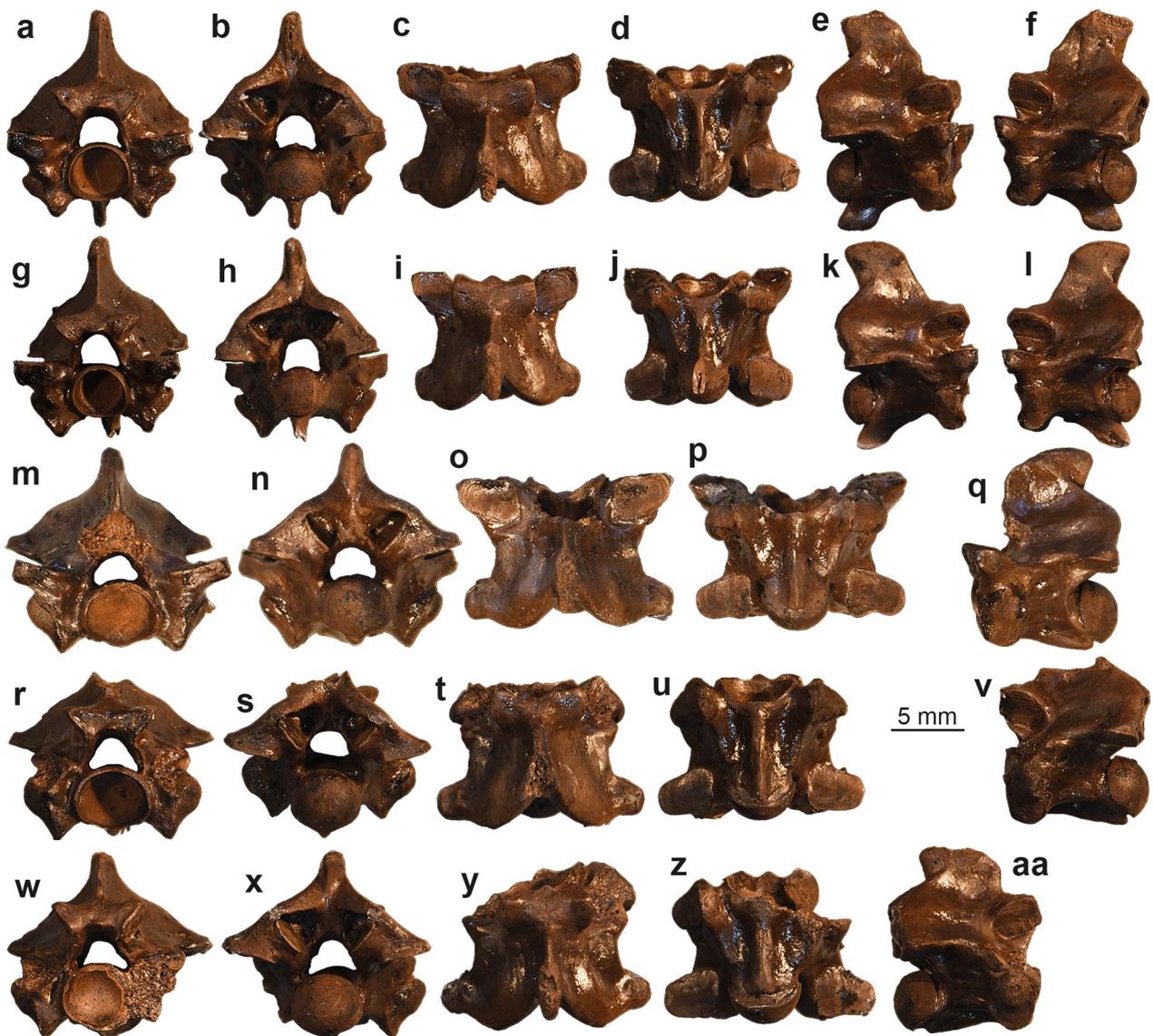
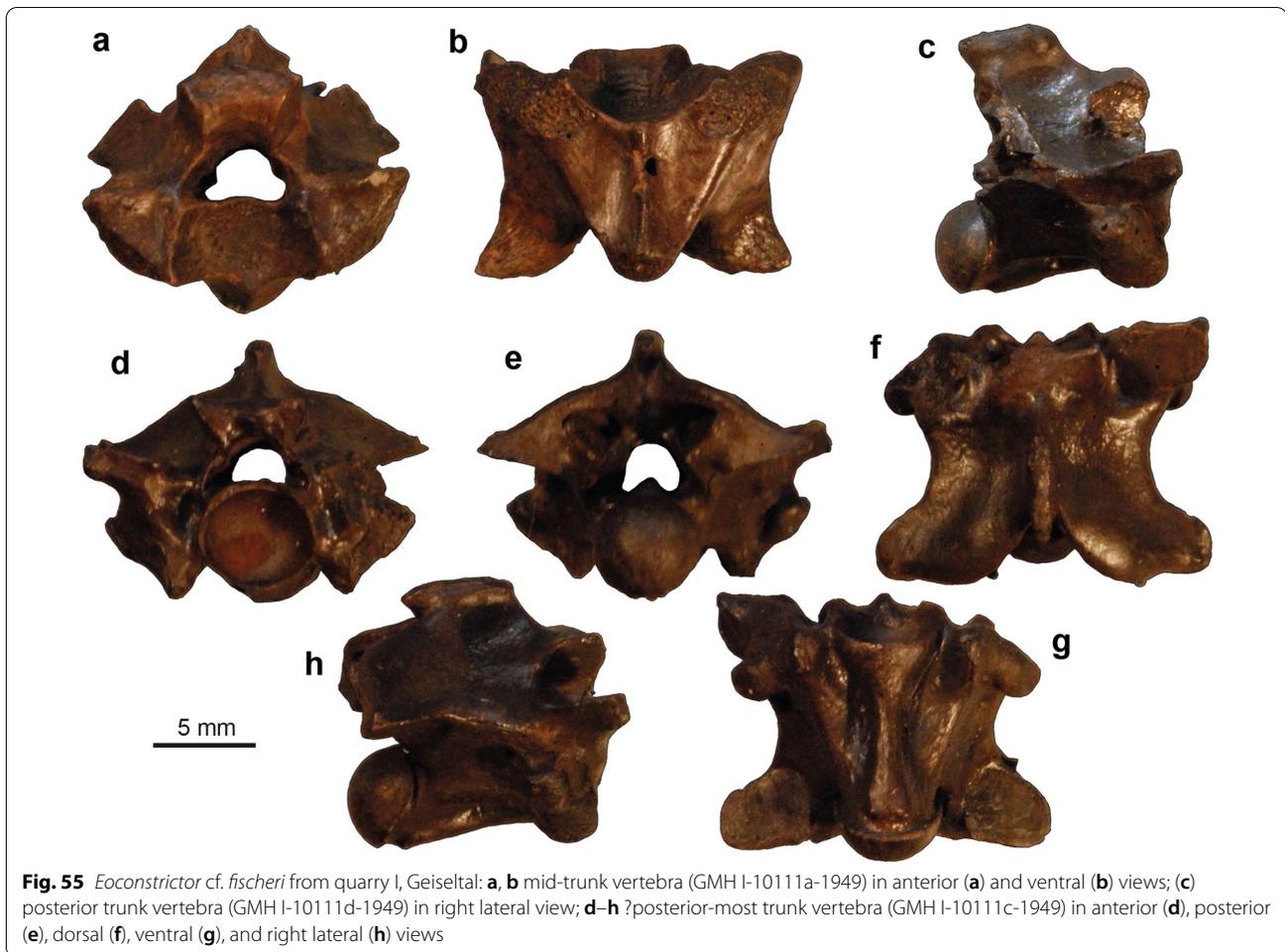


Fig. 54 *Eoconstrictor* cf. *fischeri* from quarry IX, Geiseltal: **a–f** anterior trunk vertebra (GMH IX-696b-1952) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), right lateral (**e**), and left lateral (**f**) views; **g–l** anterior trunk vertebra (GMH IX-696c-1952) in anterior (**g**), posterior (**h**), dorsal (**i**), ventral (**j**), right lateral (**k**), and left lateral (**l**) views; **m–q** anterior mid-trunk vertebra (GMH IX-696f-1952) in anterior (**m**), posterior (**n**), dorsal (**o**), ventral (**p**), and left lateral (**q**) views; **r–v** posterior mid- or posterior trunk vertebra (GMH IX-696d-1952) in anterior (**r**), posterior (**s**), dorsal (**t**), ventral (**u**), and left lateral (**v**) views; **w–aa** posterior trunk vertebra (GMH IX-696a-1952) in anterior (**w**), posterior (**x**), dorsal (**y**), ventral (**z**), and right lateral (**aa**) views

GMH XXXV-435b-1963 [two vertebrae], GMH XXXV-401-1963 three articulated mid-trunk vertebrae (GMH XXXV-310-1963), and a trunk vertebra (GMH XXXV-403-1963); **quarry XXXVI** (Figs. 60, 61): a string of several articulated trunk vertebrae and ribs (GMH XXXVI-530-1963), two trunk vertebrae (GMH XXXVI-376b-1963 and GMH XXXVI-476-1963 [two fragments of vertebrae]), and a partial skeleton with many articulated vertebrae and ribs [GMH XXXVI-87-1962; originally figured by Krumbiegel et al. (1983:fig. 115); Fig. 61];

quarry XXXVII (Fig. 62): several trunk vertebrae (GMH XXXVII-179a-1970, GMH XXXVII-179b-1970, GMH XXXVII-179c-1970, GMH XXXVII-179d-1970, and GMH XXXVII-94-1964 [two pairs of two articulated trunk vertebrae and four isolated trunk vertebrae]); **quarry XXXVIII** (Figs. 63, 64): a large, partial, relatively three dimensional skeleton including series of articulated vertebrae and ribs (GMH XXXVIII-24-1964) and several articulated and disarticulated vertebrae and fragments of a skull on a matrix (GMH XXXVIII-7-1964); **quarry**



Cecilie IV (Fig. 65c–h): a trunk vertebra (GMH Ce IV-2912b-1933; originally referred to *Paleryx spinifer* and figured by Kuhn, 1939a:pl. III.2a–d; Fig. 65c–h), several fragmentary disarticulated trunk vertebrae (GMH Ce IV-2912-1933), a trunk vertebra with two disarticulated ribs (GMH Ce IV-4649-1934), a trunk vertebra and a rib (GMH Ce IV-5856-1933), and several disarticulated trunk vertebrae and ribs on a matrix (GMH Ce IV-5855-1933); **quarry Leonhardt III (Fig. 65a–b):** an anterior trunk vertebra (GMH Leo III-2933-1934); **quarry Cecilie I (Figs. 66, 67):** a small matrix with several articulated and disarticulated trunk vertebrae and remains of ribs (GMH Ce I-5852-1931), several trunk vertebrae (GMH Ce I-5836-1929), many small trunk vertebrae (GMH Ce I-1930-1931), ten anterior and mid-trunk vertebrae (GMH Ce I-5831-1926-29), eight trunk vertebrae along with vertebral fragments and ribs (GMH Ce I-5832-1929), six trunk vertebrae (GMH Ce I-5834b-1926, GMH Ce I-5834c-1926, GMH Ce I-5834d-1926, GMH Ce I-5834e-1926, GMH Ce I-5834f-1926, and GMH CI-5834g-1926), and several trunk vertebrae (GMH

Ce I-5835a-1929, GMH Ce I-5835c-1929, GMH Ce I-5835h-1929 (originally figured by Kuhn, 1939a:pl. III.5; Fig. 67f–j), GMH Ce I-5835i-1929, and GMH Ce I-5835j-1929); **unknown quarry:** an anterior trunk vertebra, five mid-trunk vertebrae, and four vertebral fragments (GMH Y-46).

Description: Anterior trunk vertebrae have a taller neural arch and neural spine (e.g., GMH IX-696b-1952). These vertebrae bear a hypapophysis (Figs. 54a–l, 65a, b). The hypapophysis is relatively broad and short. It varies in shape and size, even within vertebrae of the same individual, depending on the relative position of the vertebra in the column (e.g., GMH IX-696b-1952 and GMH IX-696c-1952), but never surpasses the posterior border of the condyle. A prominent median tubercle on the zygosphenes also occurs in the anterior trunk vertebrae. However, rarely this median tubercle is missing, and the zygosphenes in anterior view has a strange, downwardly directed curved shape. Also, certain anterior trunk vertebrae have a relatively thick zygosphenes (GMH Leo III-2933-1934; Fig. 65a, b). The prezygapophyses are not so

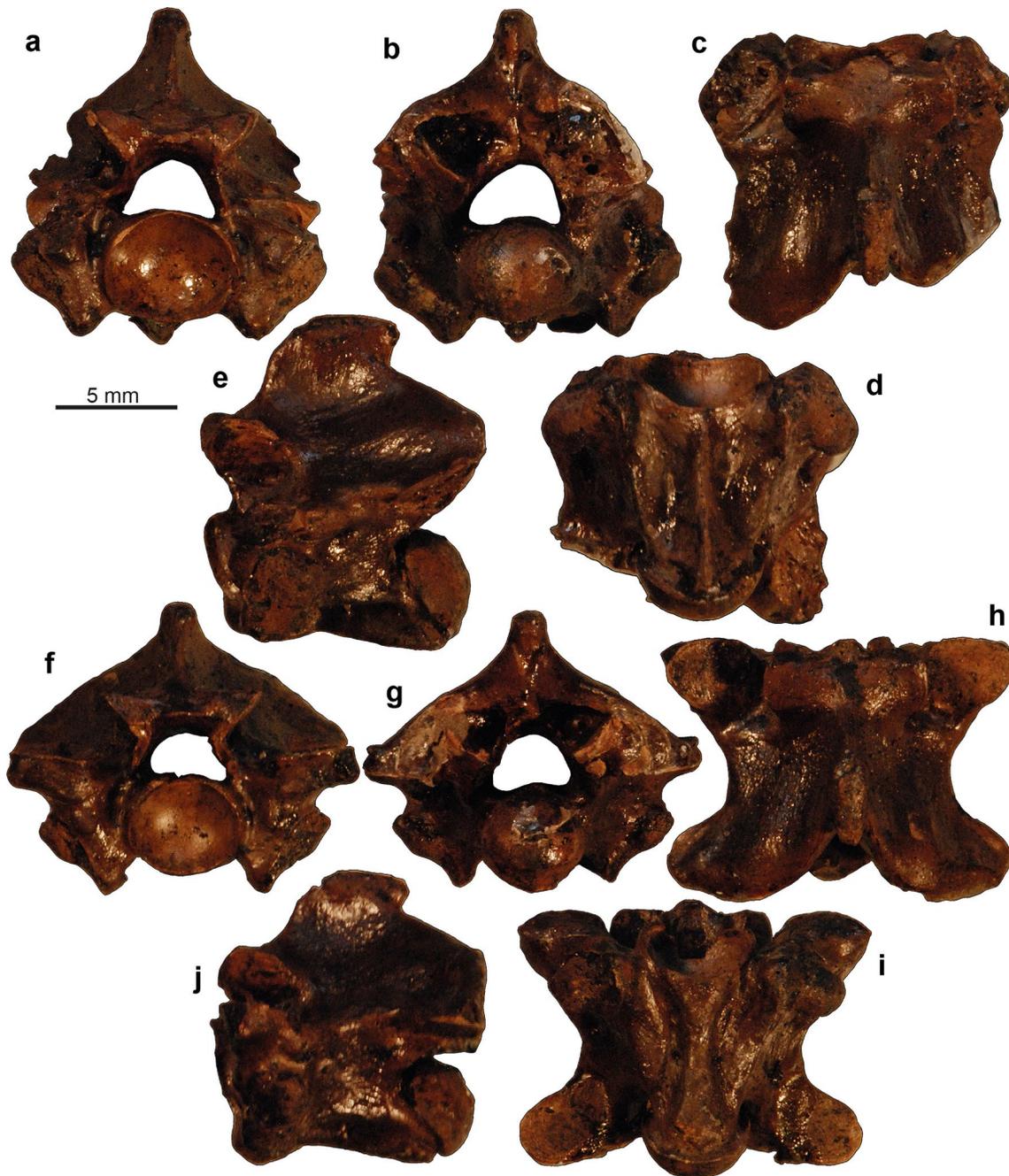


Fig. 56 *Eoconstrictor cf. fischeri* from quarry VI, Geiseltal: **a–e** mid-trunk vertebra (GMH VIa-529a-1952) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–h** posterior trunk vertebra (GMH VIa-529b-1952) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views

inclined as in *Palaeopython ceciliensis* and can be almost horizontal in anterior view and level with the dorsal margin of the cotyle (e.g., GMH XXXV-310-1963). Prezygapophyseal accessory processes can be present, though small.

Mid-trunk vertebrae have a sharp haemal keel (e.g., GMH Ce I-5835c-1929). Their average CL is between 8 and 10 mm (see Appendix 1). Smaller specimens have a CL of around 6 mm (e.g., GMH XLI-302-1968), while certain specimens can achieve a relatively large vertebral size [e.g., GMH XXII-Y-43a and GMH XXII-Y-43b

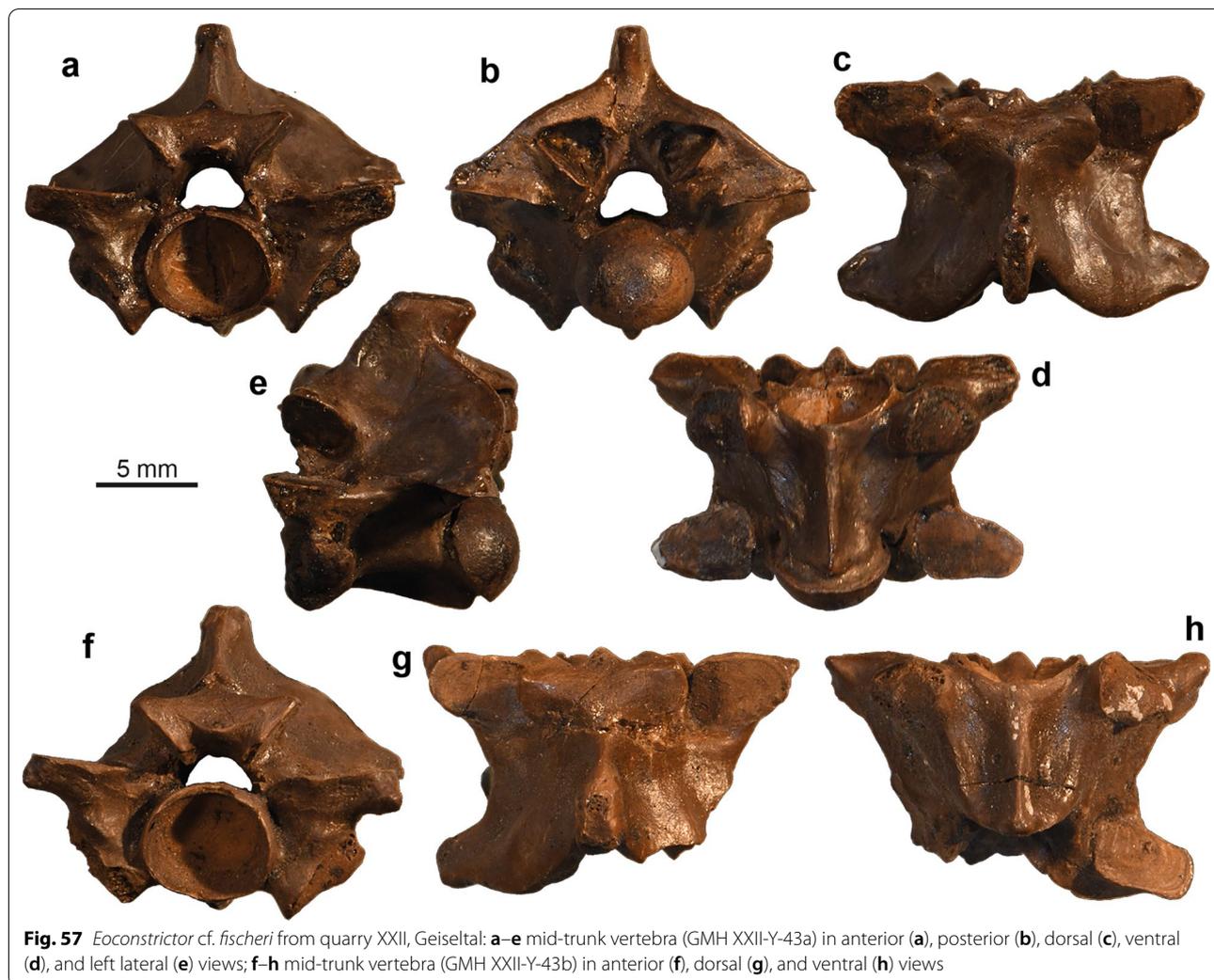


Fig. 57 *Eoconstrictor* cf. *fischeri* from quarry XXII, Geiseltal: **a–e** mid-trunk vertebra (GMH XXII-Y-43a) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–h** mid-trunk vertebra (GMH XXII-Y-43b) in anterior (**f**), dorsal (**g**), and ventral (**h**) views

(Fig. 57)] and, rarely, surpass a CL of 12 mm (e.g., GMH XLI-148-1966; Fig. 58h, i). The centrum is not so widened anteriorly (but see GMH XXXV-310-1963 for an exception). In certain cases, the median tubercle on the zygosphenes is extremely prominent [e.g., GMH XXII-Y-43a (Fig. 57a); GMH XXXVI-87-1962 (Fig. 61c)]. Rarely, however, the median tubercle is either extremely small or even totally absent (e.g., GMH XXXV-577-1963, GMH Ce IV-4649-1934 [but this identification is tentative]). In rare cases observed in certain large specimens, the zygosphenes are dorsally concave and two prominent lateral lobes are visible in dorsal view (e.g., GMH XXXV-310-1963). The paradiapophyses are large and undivided. The zygantrum is deep. The neural spine is usually short, posteriorly inclined [e.g., GMH XXII-Y-43a (Fig. 57e), GMH XXXV-380-1963, GMH XXXV-131b-1963 (Fig. 59j); GMH XXXVII-179a-1970 (Fig. 62e); GMH XLI-162-1966; GMH Ce IV-2912-1933 (Fig. 65g, h)]. Subcentral foramina are situated usually on both sides of the

haemal keel, and in certain cases they are rather prominent (e.g., GMH Ce I-5835i-1929). In certain specimens, the prezygapophyseal accessory processes are distinct, though still small [e.g., GMH XLI-155a-1966 (Fig. 58c, d); GMH XLI-314c-1968 (Fig. 58f, g)].

In posterior mid- and posterior trunk vertebrae, the neural arch becomes depressed [e.g., GMH IX-696d-1952 (Fig. 54c); GMH VIa-529b-1952 (Fig. 56g)]. The neural spine is slightly shorter than on the preceding vertebrae. As such, they are comparatively taller than the neural spines of the posterior trunk vertebrae of the co-occurring *Palaeopython ceciliensis*. In a single specimen (GMH XXXVI-376b-1963), the dorsal surface of the neural spine slightly overhangs both anteriorly and posteriorly, in contrast to the situation observed in all other trunk vertebrae, where this structure is overhanging only posteriorly. The haemal keel in these vertebrae is wider. It is not uniform in shape throughout its length but is markedly constricted at its middle part, resembling thus

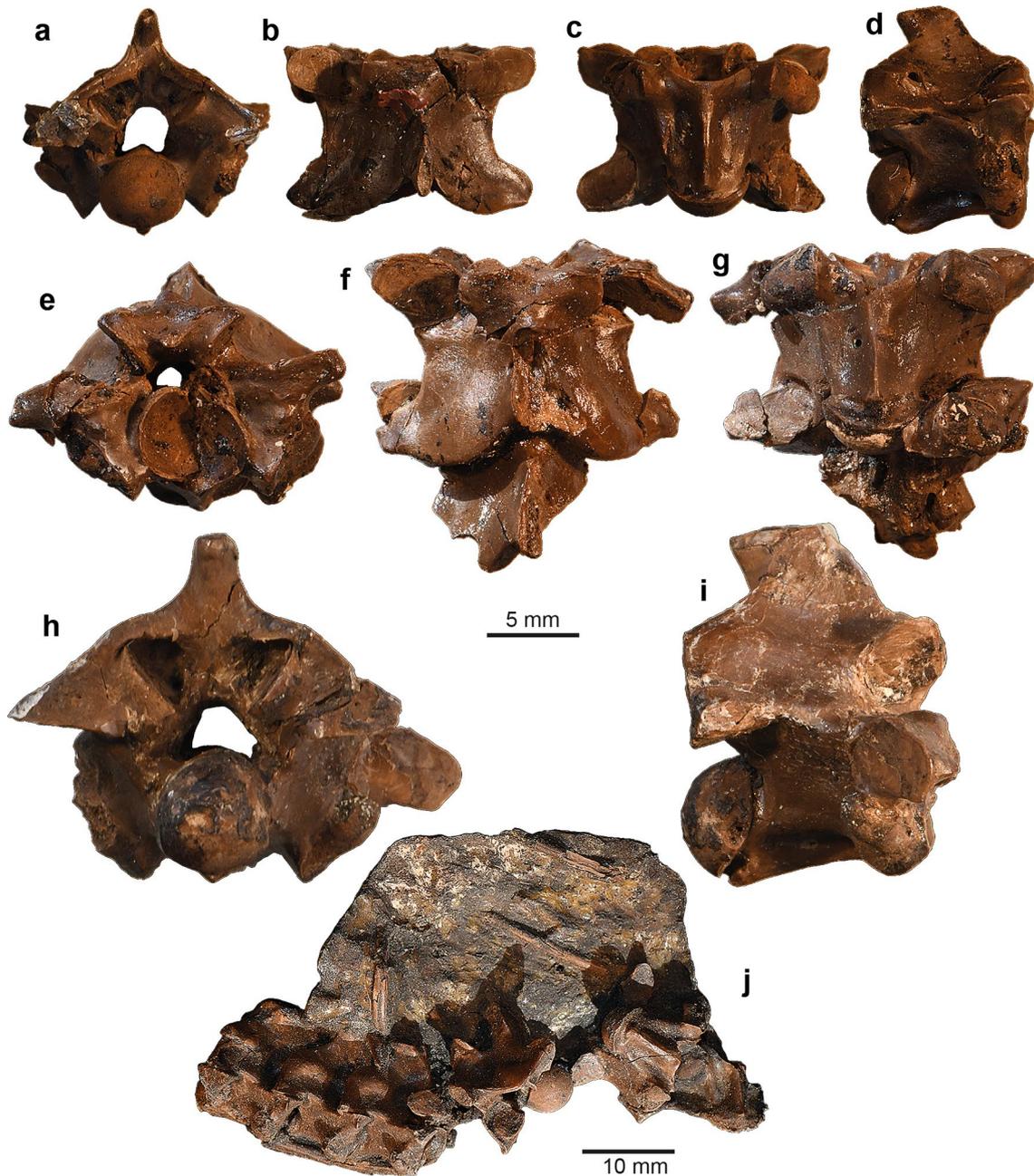


Fig. 58 *Eoconstrictor cf. fischeri* from quarry XLI, Geiseltal: **a–d** mid-trunk vertebra (GMH XLI-155a-1966) in posterior (**a**), dorsal (**b**), ventral (**c**), and right lateral (**d**) views; **e–g** mid-trunk vertebra with fragment of articulated succeeding vertebra (GMH XLI-314c-1968) in anterior (**e**), dorsal (**f**), and ventral (**g**) views; **h, i** posterior trunk vertebra (GMH XLI-148–1966) in posterior (**h**) and right lateral (**i**) views; **j** string of articulated vertebrae and some ribs (GMH XLI-157-1966)

an hourglass [e.g., GMH IX-260b1-1953, GMH XXXVI-376b-1963, and GMH VIa-529b-1952 (Fig. 56i)]. In certain cases, the prezygapophyses can be relatively long.

Remarks: Outside the type locality of Messel, a form compared to *Eoconstrictor fischeri* was recently described from the Eocene of Dielsdorf, Switzerland, by Georgalis

and Scheyer (2019a). We here agree with this taxonomic referral of that Swiss material as *Eoconstrictor cf. fischeri*—these specimens were described and figured in much detail by Georgalis and Scheyer (2019a), and there is no need to repeat it here. We now further recognize that a similar form was also present in Geiseltal, which



Fig. 59 *Eoconstrictor cf. fischeri* from quarry XXXV, Geiseltal: **a–e** mid-trunk vertebra (GMH XXXV-131a-1963) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** mid-trunk vertebra (GMH XXXV-131b-1963) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k, l** three articulated mid-trunk vertebrae (GMH XXXV-310-1963) in dorsal (**k**) and ventral (**l**) views

we also refer as *Eoconstrictor cf. fischeri*. This taxon is represented in Geiseltal by numerous isolated vertebrae, originating from multiple different quarries, as well as several articulated and disarticulated skeletons (Figs. 60,

61, 63, 64, 66). The Geiseltal form shares with *Eoconstrictor fischeri* from Messel a relatively thin zygosphene with strong, lamellar median tubercle, and a narrow and almost triangular cotyle. In Geiseltal, these specimens

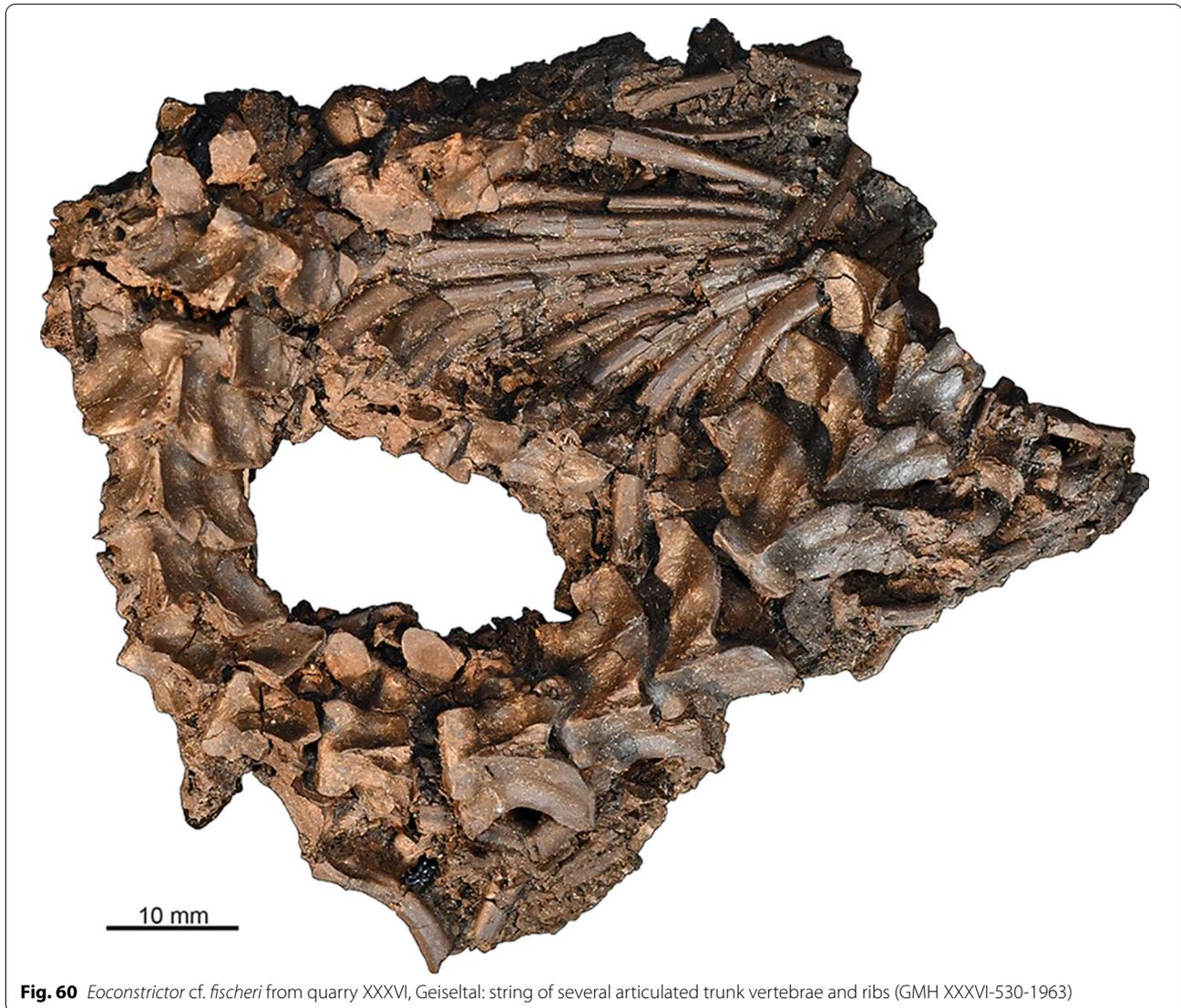


Fig. 60 *Eoconstrictor* cf. *fischeri* from quarry XXXVI, Geiseltal: string of several articulated trunk vertebrae and ribs (GMH XXXVI-530-1963)

can be differentiated from the co-occurring *Palaeopython ceciliensis* by their much smaller vertebral size, much thinner zygosphenes, the relatively higher neural spine in the posterior trunk vertebrae, the presence of a prominent median tubercle on the zygosphenes, and the less massive paradiapophyses. Given the great similarity of the cranial lectotype material of *Eoconstrictor spinifer* comb. nov. to cranial specimens of *E. fischeri* from Messel, we suspect that most trunk vertebrae of the former might also be similar to those of the latter. The fundamental problem here is that *Eoconstrictor spinifer* comb. nov. is essentially a taxon based on a cranium, which is difficult to compare to these vertebrae—the only available vertebrae of *E. spinifer* comb. nov. are anterior-most trunk ones, which nevertheless indeed show certain differences (i.e. no median tubercle on the zygosphenes and no prezygapophyseal accessory processes) from the

available respective ones of *E. cf. fischeri*. Associated specimens may provide new insight.

***Eoconstrictor spinifer* (Barnes, 1927) comb. nov.**

lectotype designation

Figures 68, 69, 70, 71, 72, 73 and 74

Taxonomic history: *Paleryx spinifer* Barnes, 1927 (new species).

Type material: GMH Ce I-2979-1926 (lectotype [part]), a “block” including the left atlantal neural arch, three almost complete anterior trunk vertebrae, remains of ribs, fragments of other vertebrae, as well as basioccipital, and right prootic (Barnes, 1927, pl. I.1; Figs. 68a, b, 69, Additional file 3: Model 3); GMH Ce I-5823-1926 (lectotype [part]), an incomplete parietal (Barnes, 1927,



pl. I.5b; Figs. 68c, d, 70, Additional file 4: Model 4); GMH Ce I-5824-1926 (lectotype [part]), a right pterygoid (Barnes, 1927, pl. I.4; Figs. 68e, f, 71, Additional file 5: Model 5); GMH Ce I-5826-1926 (lectotype [part]),

a right maxilla (Barnes, 1927, pl. I.2, I.3; Figs. 68g–j, 72, Additional file 6: Model 6); GMH Ce I-5822-1926 (paralectotype), two isolated anterior trunk vertebrae (the second one has also together the anterior-most portion of a

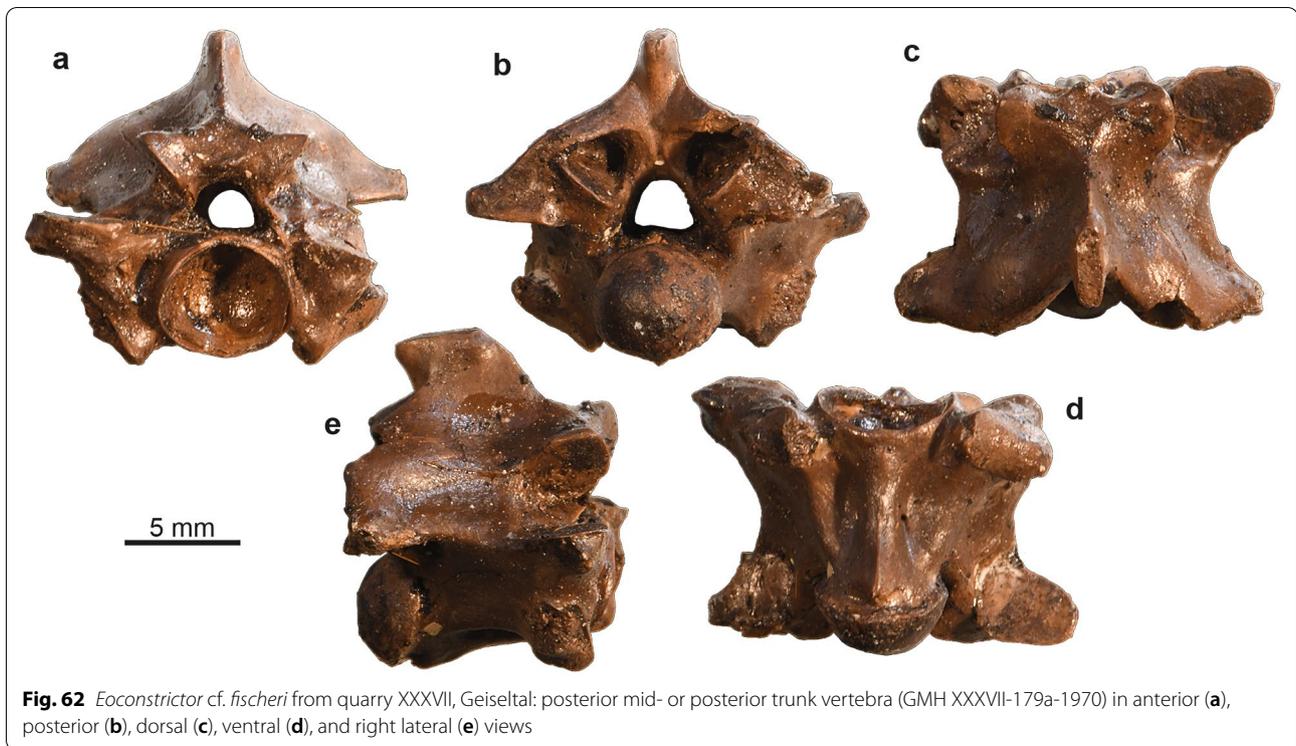


Fig. 62 *Eoconstrictor* cf. *fischeri* from quarry XXXVII, Geiseltal: posterior mid- or posterior trunk vertebra (GMH XXXVII-179a-1970) in anterior (a), posterior (b), dorsal (c), ventral (d), and right lateral (e) views

succeeding vertebra stuck in its posterior part) (Barnes, 1927, pl. I.5, I.5a, I.6, I.6a; Figs. 73, 74, Additional file 7: Model 7).

Barnes (1927:7) apparently overlooked the cranial elements in GMH Ce I-2979-1926 but noted that the skull fragments—among which he counted not only the potential parietal, but also the pterygoid (GMH Ce I-5824-1926), the maxilla (GMH Ce I-5826-1926), and a palatine fragment that we have not been able to identify—were associated with the same block (“dabei befindlich”). This suggests that most of these “syntypes”, almost all of which derive from the skull or anterior-most vertebral column, pertain to a single individual and were subsequently catalogued as different specimens. Furthermore, based on the numbering one might think that the isolated anterior trunk vertebrae (GMH Ce I-5822-1926) were also isolated from the block; Barnes (1927:9) himself noted that they were found in the same, several-centimetre-thick sediment layer, and given their state of preservation he speculated that they pertained to the same individual. We suggest, therefore, that the syntype series comprises two specimens: (1) the associated specimen (catalogued as GMH Ce I-2979-1926, GMH Ce I-5823-1926, GMH Ce I-5824-1926, and GMH Ce I-5826-1926), and (2) the two isolated anterior trunk vertebrae (GMH Ce I-5822-1926), which possibly derive from the same individual. Among these two, and for the sake of nomenclatural and

taxonomic stability, we designate the first syntype as the lectotype of *Eoconstrictor spinifer* comb. nov.

Type locality: Quarry Cecilie I, Geiseltal “Obere Mittelkohle”, Saxony-Anhalt, Germany; late early or middle Eocene.

Referred material and range: None—taxon so far exclusively known by its type material.

Diagnosis: *Eoconstrictor spinifer* comb. nov. differs from *Eoconstrictor fischeri* in having fewer labial foramina on the maxilla, and in the absence of a median tubercle on the zygosphenes and prezygapophyseal accessory processes on the anterior-most trunk vertebrae.

Description of the lectotype: The lectotype comprises specimens GMH Ce I-2979-1926, GMH Ce I-5823-1926, GMH Ce I-5824-1926, and GMH Ce I-5829-1926 (Figs. 68, 69, 70, 71 and 72, Additional file 3: Model 3, Additional file 4: Model 4, Additional file 5: Model 5, Additional file 6: Model 6).

GMH Ce I-2979-1926 is a block with the left atlantal neural arch, three almost complete anterior trunk vertebrae, remains of ribs, and fragments of other vertebrae as well as cranial elements (Figs. 68a, b, 69, Additional file 3: Model 3). The dorsal portion of the atlas, the tectum (sensu Jandzík and Bartík, 2004), is a medially curving flange whose dorsal margin is rounded in lateral view. Two processes are present laterally, a posterodorsal process at the base of the tectum and a more robust

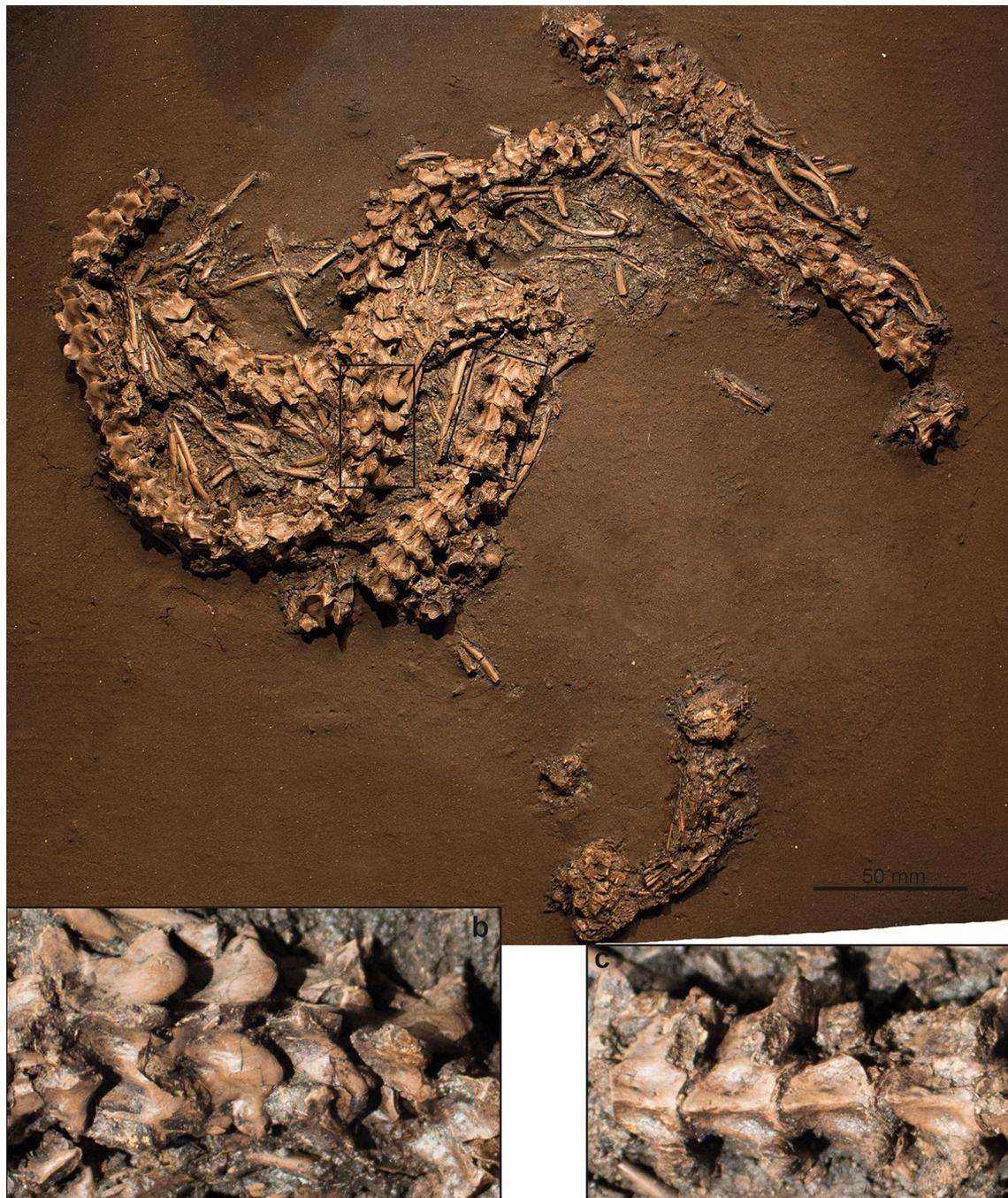


Fig. 63 *Eoconstrictor* cf. *fischeri* from quarry XXXVIII, Geiseltal: **a** large, partial skeleton including series of articulated vertebrae and ribs (GMH XXXVIII-24-1964); **b, c** close up of several articulated vertebrae of the same specimen

transverse process. The pedicel for articulation with the oto-occipital and the odontoid process of the axis is present. In one of the vertebral fragments, the hypapophysis is perfectly preserved. The zygosphenes are slightly wider than cotyle. The hypapophysis is sharp. Cotyles are more circular than elliptical. The postzygapophyses are wide;

the zygantrum is triangular. The zygosphenes are thin. In two, the neural spines are broken, and even in the third, where it is preserved, it is hidden by other remains.

The ventral surface of the incomplete basioccipital is divided into an anterior part and a projecting posterior part, the condyle, which set off by a strong neck. The

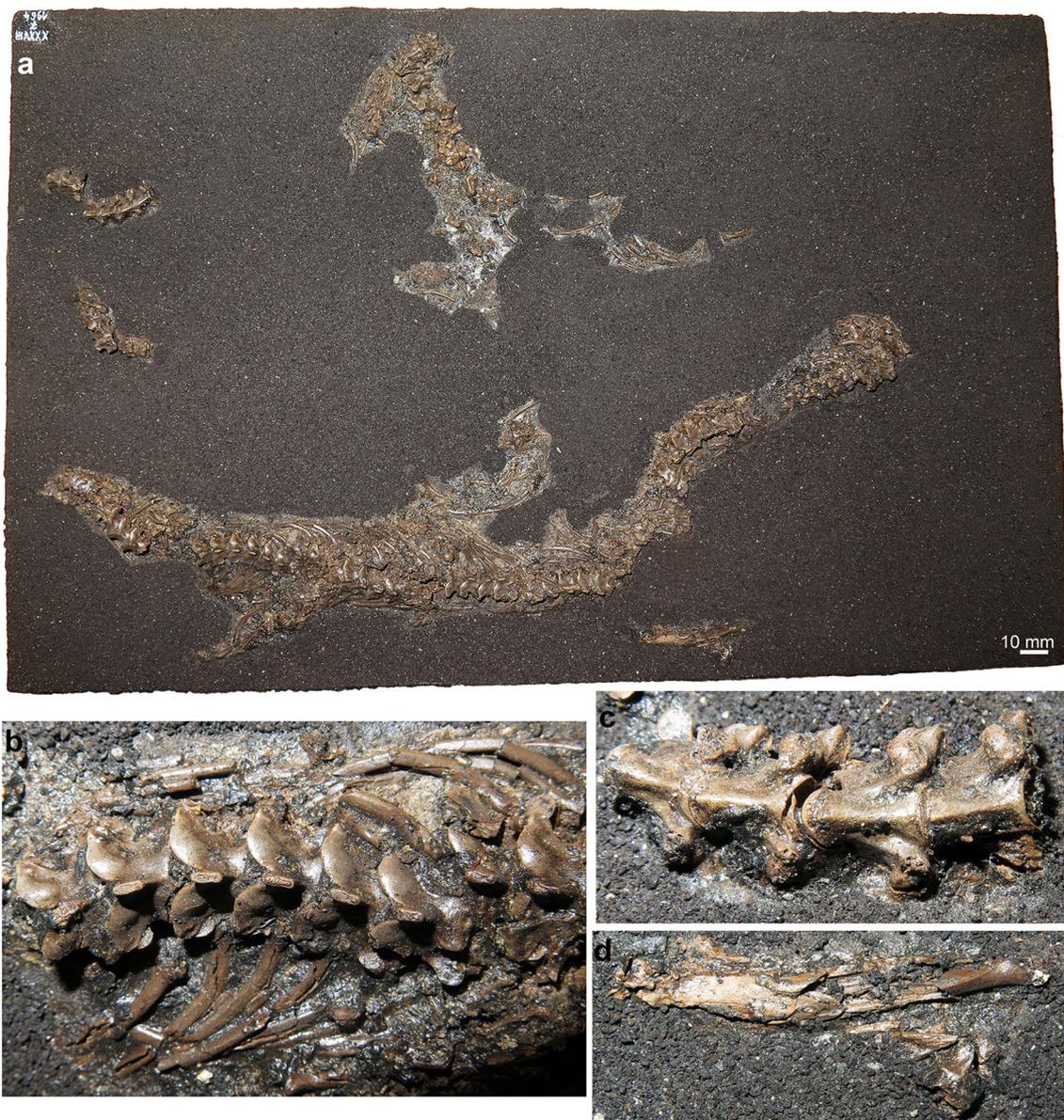


Fig. 64 *Eoconstrictor* cf. *fischeri* from quarry XXXVIII, Geiseltal: **a** several articulated and disarticulated vertebrae and fragments of a skull on a matrix (GMH XXXVIII-7-1964); **b–d** close ups of the same specimen: **b** articulated vertebrae in dorsal view and remains of ribs; **c** articulated vertebrae in ventral view; **d** fragments of skull. Close up photographs not to the same scale

anterior part bears a median crest on which the inclined surfaces for muscle attachment (probably *m. protractor quadrati*; see Cundall, 1986) converge. The anterior margin appears to be a concave V-shape, which the basisphenoid would have overlapped. In dorsal view the concave brain cavity is pentagonal, with a transverse posterior margin and a pointed anterior one.

We identified a partial right prootic in the block. The foramen for the mandibular branch of the trigeminal nerve (V3) has a sharp, acute anterior margin, as in *Boa*

and *Ungaliophis* Müller, 1880, and also *Eoconstrictor fischeri* (Scanferla & Smith, 2020b). It is bounded ventrally by a strong buttress, which in *Ungaliophis* is ventrally scored, forming a groove that continues into the posterior opening of the Vidian canal; the buttress is absent in *Eryx* and apparently present in *Boa* and *Candoia*, where, however, it does not have the same close relation to the Vidian canal. The expanse of bone anterior to the V3 opening suggests that an ophidiosphenoid (sensu Gauthier et al., 2012, “pleurosphenoid” of Rieppel,

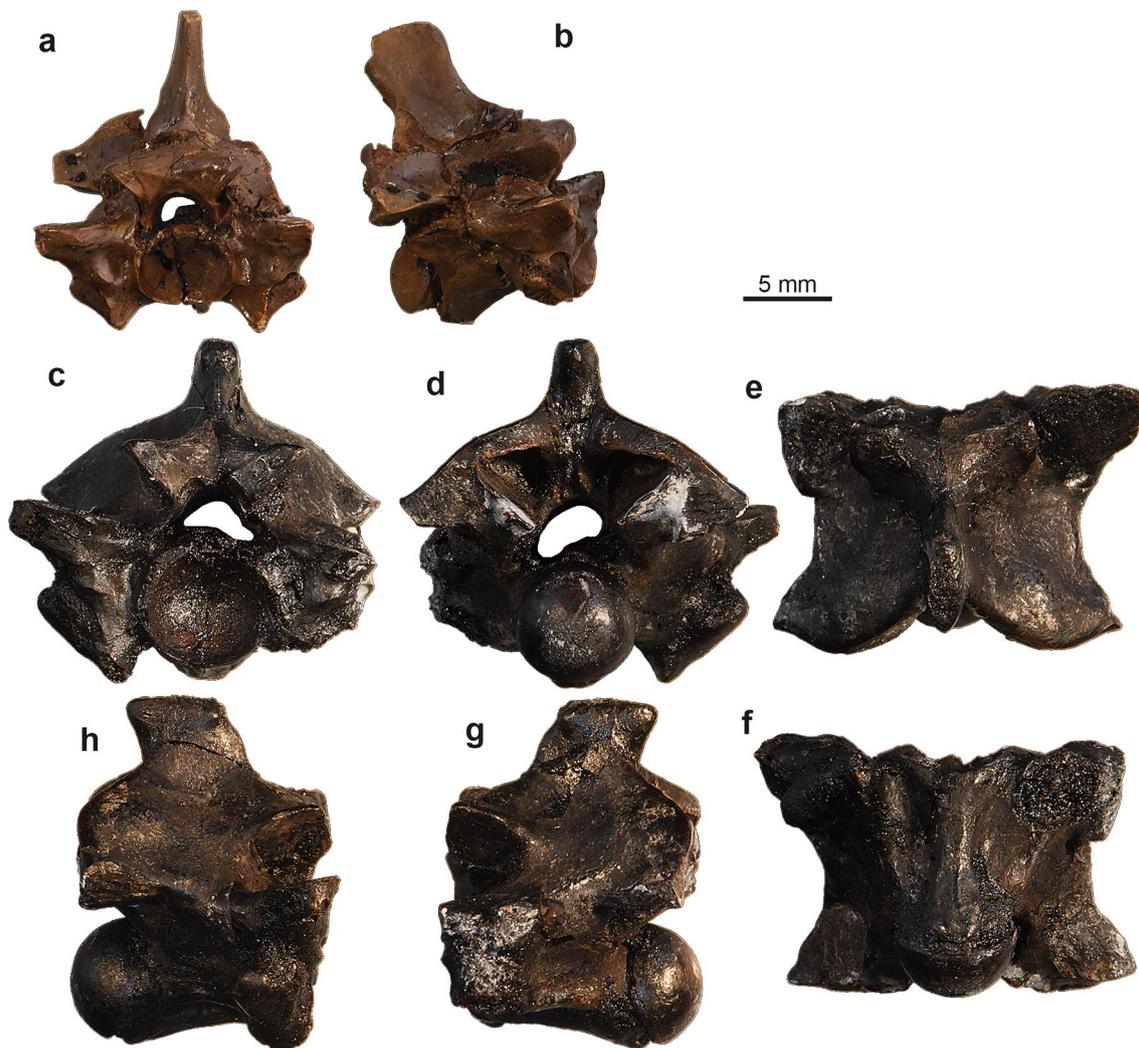


Fig. 65 *Eoconstrictor* cf. *fischeri* from quarries Leonhardt III and Cecilie IV, Geiseltal: **a, b** anterior trunk vertebra (GMH Leo III-2933-1934) in anterior (**a**) and right lateral (**b**) views; **c-h** posterior mid- or anterior posterior trunk vertebra (GMH Ce IV-2912b-1933) in anterior (**c**), posterior (**d**), dorsal (**e**), ventral (**f**), left lateral (**g**), and right lateral (**h**) views [this specimen was originally referred to as *Paleryx spinifer* and figured by Kuhn (1939a:pl. III.2a-d)]

1976) is present. The opening for the maxillary branch of the trigeminal nerve (V2) may be preserved anteriorly, although it cannot be determined whether it was fully enclosed by the prootic or open anteriorly. A relatively large foramen, perhaps comparable to those identified by Maisano and Rieppel (2007) in *Casarea dussumieri*, appears to be present in the ophidiosphenoid. Dorsally is part of the facet for the supratemporal. In medial view the internal opening of the trigemino-facialis chamber can be made out.

The element identified as a parietal by Barnes (1927), GMH Ce I-5823-1926, is very narrow (Figs. 68c, d, 70, Additional file 4: Model 4); possibly it represents the posterior, narrowed extension of a bone similar to that in

Boidae. In this interpretation, the dorsal surface is keeled and three-pronged, with an elongate, tapering median process that overlapped the oto-occipitals on the midline and a pair of thinner, less extensive lateral processes (less so than in *Eoconstrictor fischeri*; Scanferla and Smith, 2020b), somewhat asymmetrically developed, that overlapped the dorsolateral surfaces of the oto-occipitals. The left descending flange is partially preserved where it articulated with the prootic.

GMH Ce I-5824-1926 comprises most of the right pterygoid, including its articulation facets for the palatine, ectopterygoid, and parabasisphenoid but lacking the distal end of the quadrate ramus (Figs. 68e, f, 71, Additional file 5: Model 5). The palatine process is tall with

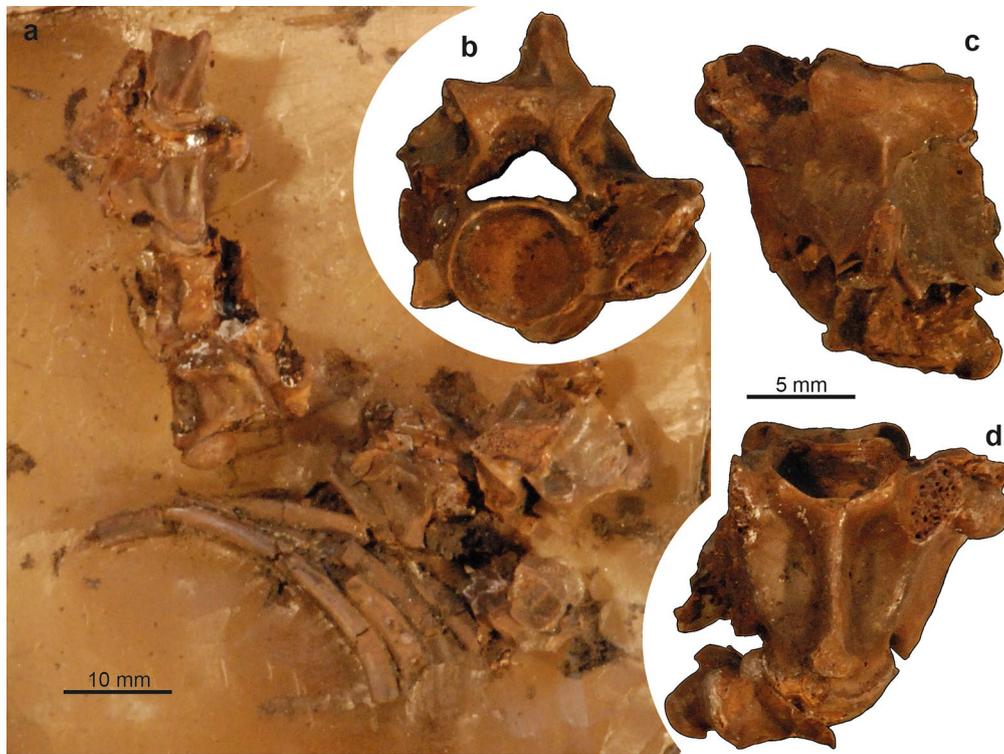


Fig. 66 *Eoconstrictor cf. fischeri* from quarry Cecilie I, Geiseltal: **a** small matrix with several articulated trunk vertebrae and remains of ribs (GMH Ce I-5852-1931); **b–d** close up of a posterior trunk vertebra from the same specimen in anterior (**b**), dorsal (**c**), and ventral (**d**) views

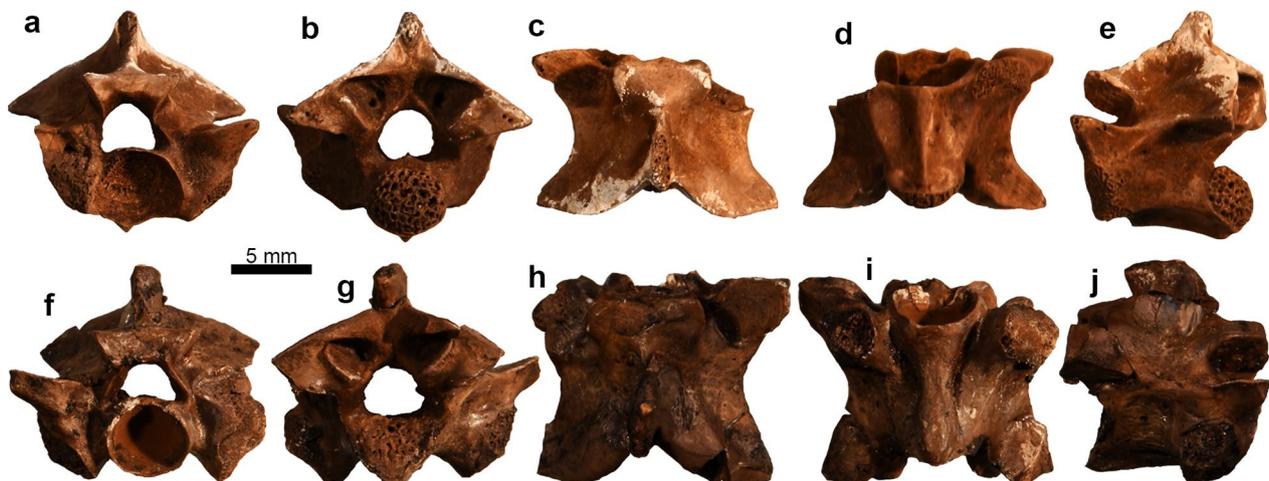
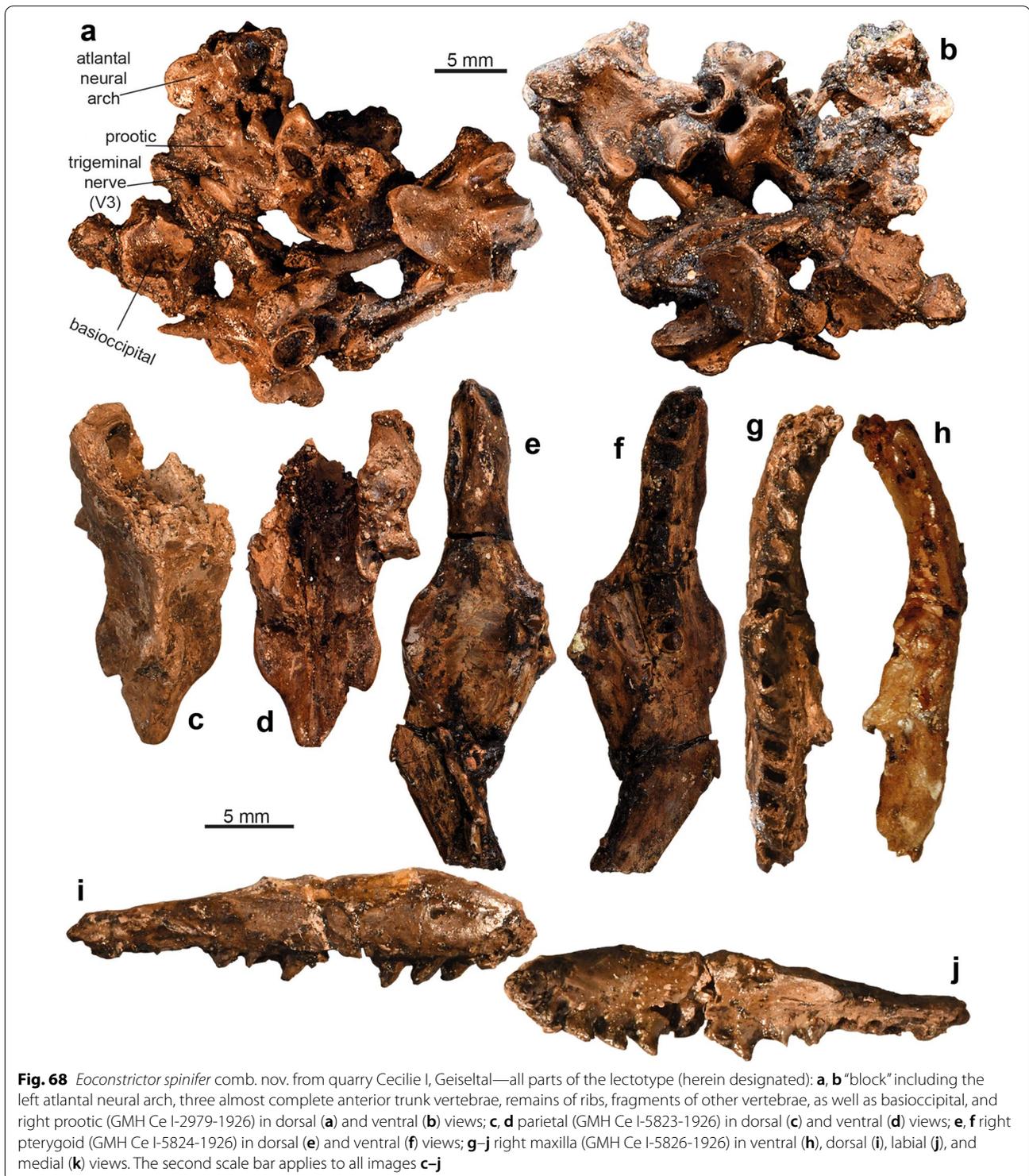


Fig. 67 *Eoconstrictor cf. fischeri* from quarry Cecilie I, Geiseltal: **a–e** mid-trunk vertebra (GMH Ce I-5835c-1929) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left posterolateral (**e**) views; **f–j** posterior trunk vertebra (GMH Ce I-5835h-1929) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and right lateral (**j**) views [this specimen was originally figured by Kuhn (1939a:pl. III.5)]

a dorsal keel and terminates bluntly, lacking a strong anterior edentulous prong, unlike in *Loxocemus*. Its dorsomedial surface bears a deeply incised elongate facet for the posterior prong of the palatine that extends over

four tooth spaces. The ventromedial margin of that facet is drawn out into a ridge, but a distinct process (as seen in some boids; see below under *Phosphoroboa filholii* comb. nov.) is absent, similar to *Eoconstrictor fischeri*.



The palatine process bears a single, inwardly curving row of approximately 11 teeth, as in *E. fischeri*, which grow somewhat smaller posteriorly. The last tooth is at the level of the posterior end of the ectopterygoid

facet, as in ungaliophiines, *Boa* and *Candoia* but unlike in *Eryx*. The ectopterygoid facet is a robust, laterally directed, comma-shaped depression, taller at the posterior end and rising and tapering anterodorsally. At the



Fig. 69 *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal—part of the lectotype (herein designated): 3D models of the “block” including the left atlantal neural arch, three almost complete anterior trunk vertebrae, remains of ribs, fragments of other vertebrae, as well as basioccipital, and right prootic (GMH Ce I-2979-1926) in various views. Images not to the same scale

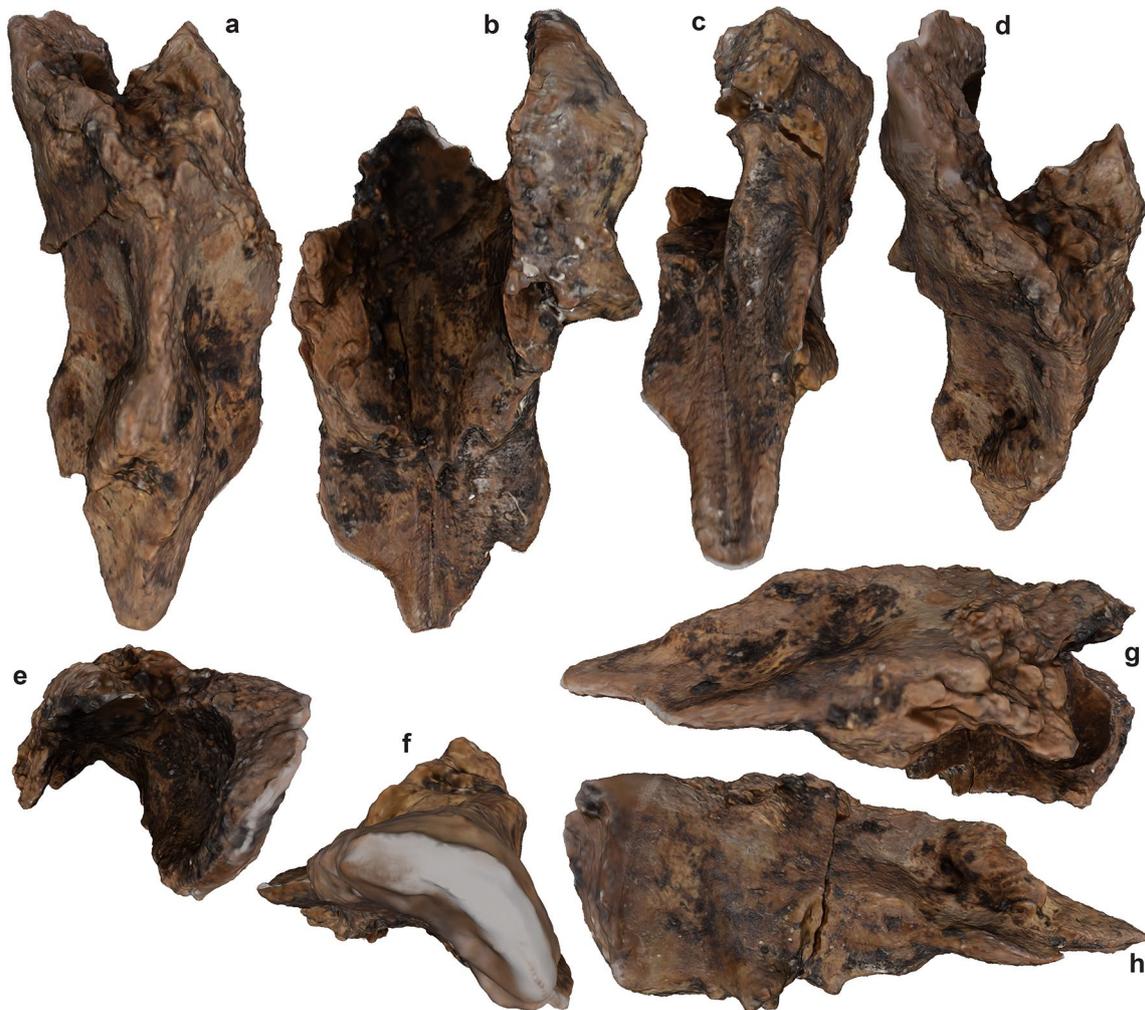


Fig. 70 *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal—part of the lectotype (herein designated): 3D models of the parietal (GMH Ce I-5823-1926) in dorsal (a), ventral (b), posteroventral (c), anterodorsolateral (d), anterior (e), posterior (f), right lateral (g), and left lateral (h) views. Images not to the same scale

basipterygoid articulation the pterygoid bears a rounded, medially expanded flange. This flange rotates onto the dorsal surface of quadrate ramus, forming a dorsal keel that bounded a deep, elongate dorsally or dorsomedially directed fossa, as in many Boidae and Pythonidae.

GMH Ce I-5826-1926 is a nearly complete right maxilla, but its anterior and posterior ends are broken (Figs. 68g, h, 72, Additional file 6: Model 6). On the dorsal surface of the premaxillary process is an elongate well, at the base of which one large and several small foramina open, similar to the paralectotype maxilla of *Palaeopython cadurcensis* MNHN.F QU16321. At a slightly posterior level to this well on the lateral side of the bone is a single, large labial foramen, unlike in *Eoconstrictor fischeri*, where there are four (Scanferla & Smith, 2020b). A

weak remnant of the lizard facial process is present, as in constrictors generally, but it decays more rapidly than in MNHN.F QU16321, so that the posterior process of the maxilla is more slender. The palatine process is asymmetrical, growing gradually in width posteriorly, reaching an apex, and then decaying abruptly, similar to *Boa*. Foramina associated with the palatine process are unclear. The lateral margin is straight, as in *E. fischeri* (see Scanferla & Smith, 2020b).

The bone preserves 14–15 tooth positions and four complete and several partial teeth located in the anterior and middle portion. The teeth are recurved and conical, and everywhere short and thick, even in the anterior part of the bone. Tooth morphology in the maxilla is homogeneous in some other Constrictores, such as *Loxocemus*



bicolor and Ungaliophiinae (Digimorph), but contrasts sharply with that seen in other constrictors, especially *Corallus* Daudin, 1803a.

Description of paralectotype GMH Ce I-5822-1926: This specimen comprises two isolated anterior trunk vertebrae (Figs. 73, 74, Additional file 7: Model 7). The first

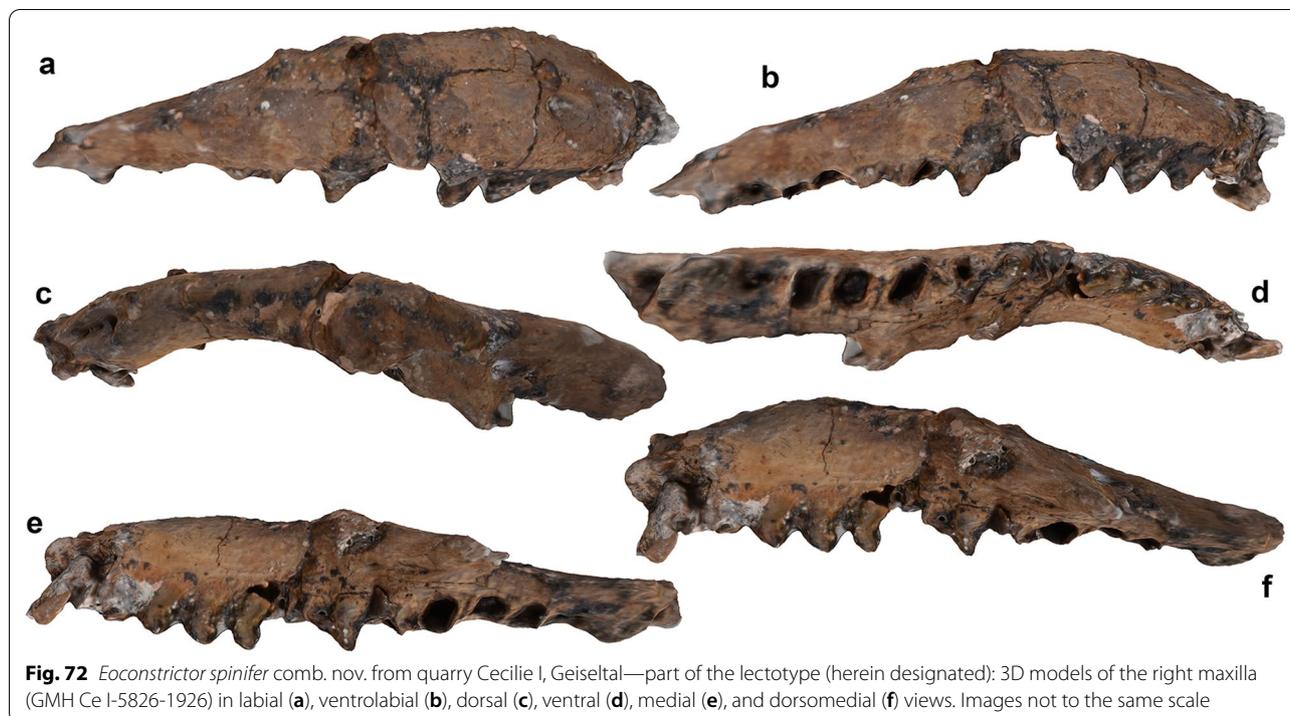


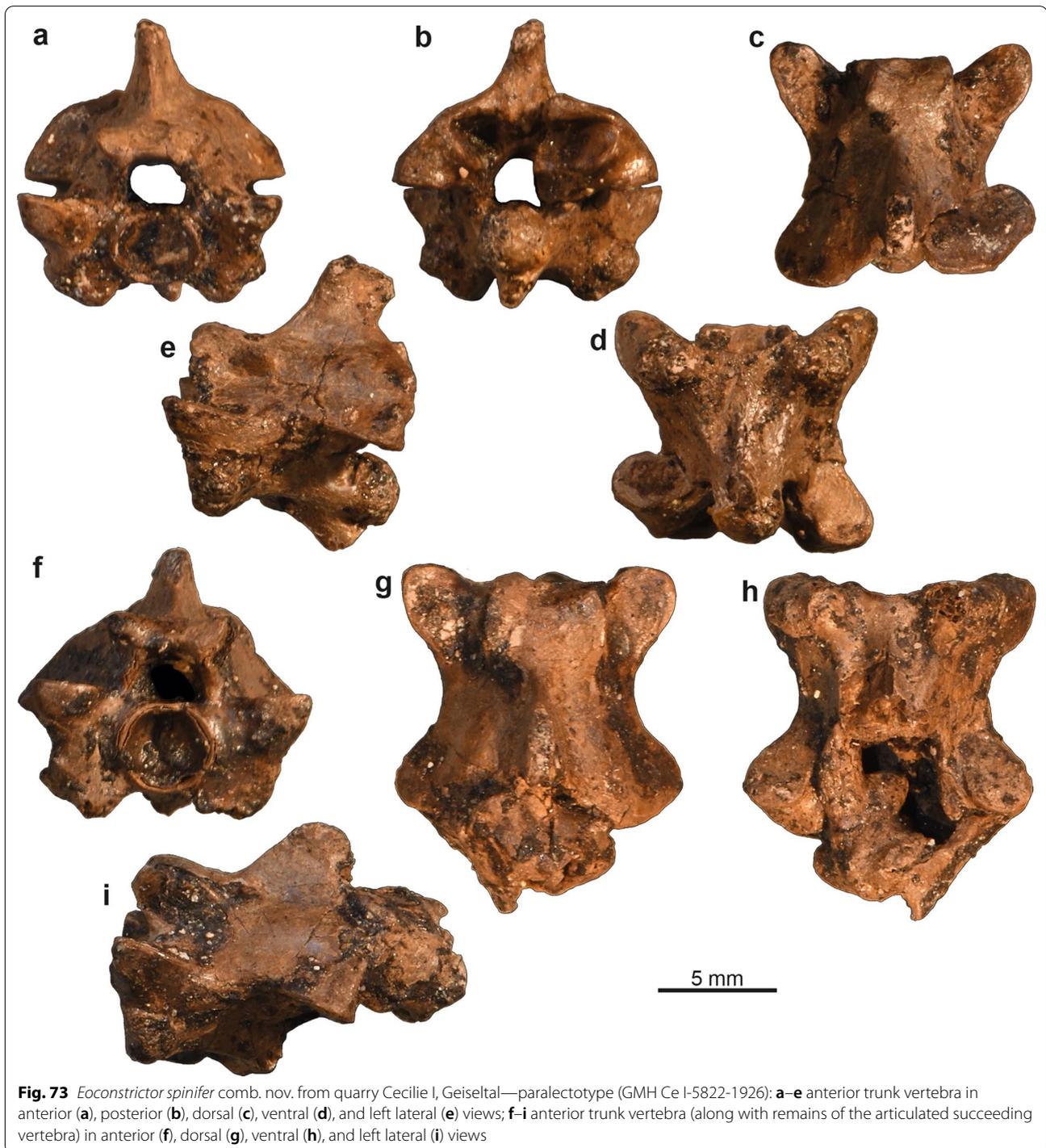
Fig. 72 *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal—part of the lectotype (herein designated): 3D models of the right maxilla (GMH Ce I-5826-1926) in labial (a), ventrolabial (b), dorsal (c), ventral (d), medial (e), and dorsomedial (f) views. Images not to the same scale

is almost complete, missing only the dorsal-most part of the neural spine, the left lateral edge of the zygosphene, the dorsal surface of the cotyle, and the ventral-most portion of the hypapophysis (Figs. 73a–e, 74). In anterior view (Figs. 73a, 74a), the zygosphene wider than the cotyle (4.8 vs. 3.6 mm, respectively). The neural canal is slightly irregular, probably artifactual. The cotyle is slightly depressed. The prezygapophyseal articular facets are slightly inclined. No paracotylar foramina are present, but paracotylar fossae exist. In posterior view (Figs. 73b, 74d), the neural arch is vaulted, rendering the dorsal surface of the zygantrum almost triangular. The condyle is rounded. In dorsal view (Fig. 73c), the thin anterior edge of the neural spine extends just barely onto the roof of the zygosphene. The prezygapophyses are directed anterolaterally and their distal end extends slightly beyond the anterior level of the zygosphene. The prezygapophyseal articular facets are oval. No prezygapophyseal accessory processes are present. The neural spine is relatively thick. In ventral view (Figs. 73d, 74i), the hypapophysis is thick, and its base extends over most of the centrum, but its tip is broken. The centrum is much widened anteriorly. Subcentral ridges are present. A deep subcentral foramen is present on the right side from the hypapophysis at around the middle of the centrum. The paradiapophyses are relatively robust and undivided. It is worth noting that the right postzygapophysis is smaller than the left one and is oriented differently; it is unclear whether this

can be attributed to preservational factors or represents a pathology. In lateral view (Figs. 73e, 74m), the neural spine is relatively tall and posteriorly inclined. A small lateral foramen can be observed on the left side.

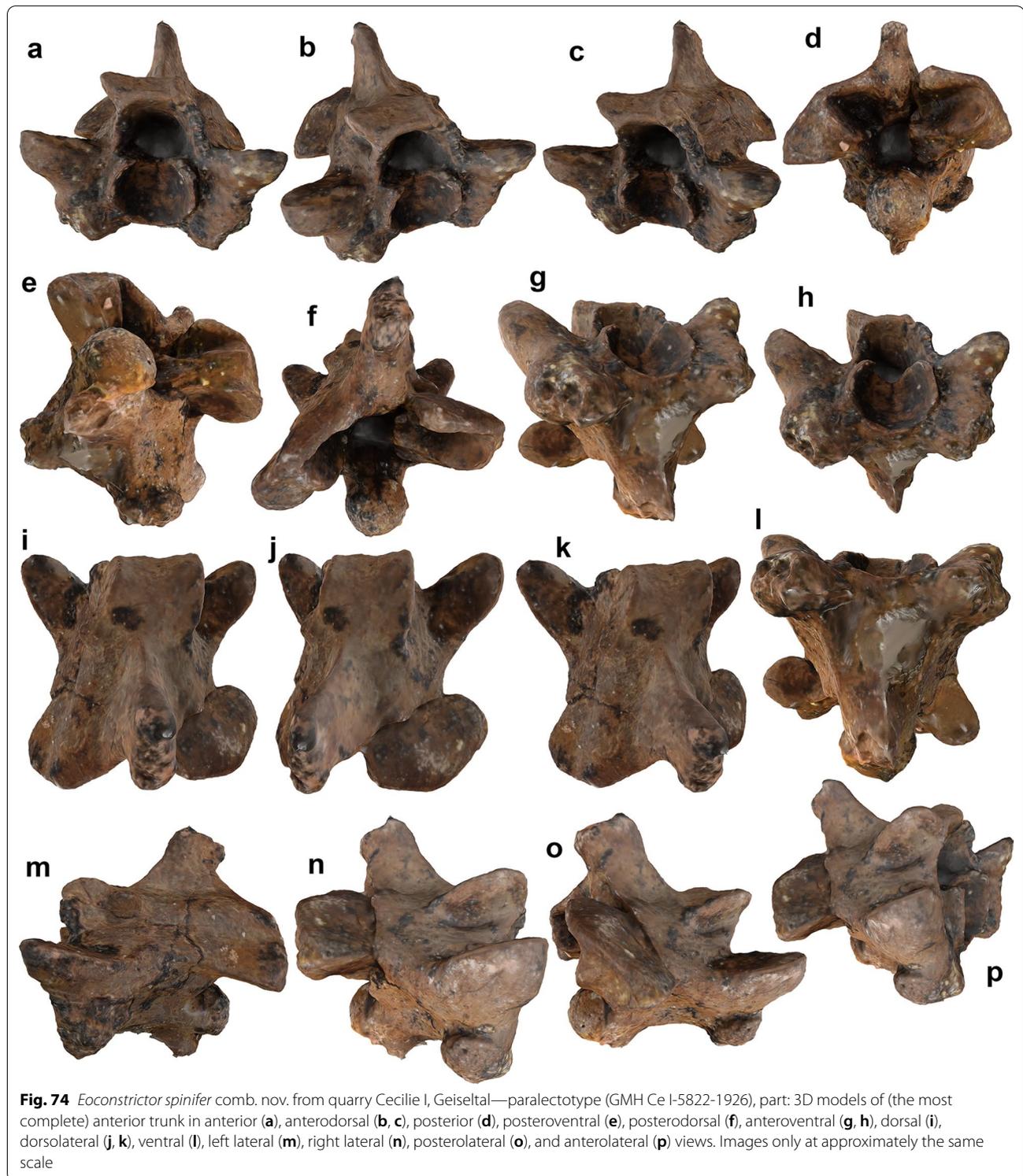
The second vertebra is most probably also an anterior trunk one, missing the posterior part of its ventral surface along with its condyle, whereas remains of the anterior-most portion of a succeeding vertebra are stuck in its zygantrum and around the postzygapophyses (Fig. 73f–i). The centrum is rather narrow. A hypapophysis seem to have been originally present but only its relatively steep base is now preserved. The zygosphene is wider than the cotyle. The paradiapophyses are robust and weakly divided. The dorsal-most edge of the neural spine is eroded. The neural spine appears to be strongly inclined posteriorly. The zygosphene is not especially thick, but it is still thicker than in the anterior trunk vertebra.

Remarks: The species was originally established upon both vertebral and cranial material as a second, distinct snake species from Geiseltal (Barnes, 1927). Simpson (1933) regarded this taxon as one of the best-preserved fossil constrictors described up to that time worldwide. Kuhn (1939a) referred to this taxon four additional specimens from the quarries Cecilie I and Cecilie IV of Geiseltal, including a rather complete, though crushed, skeleton with skull. Rage (1984b) only questionably followed the generic attribution of this taxon, as he demonstrated that it in fact shares features with both *Paleryx*



and *Palaeopython*. Indeed, even many of the isolated vertebrae (e.g., GMH Ce IV-2912-1933) that Kuhn (1939a) described and figured as *Paleryx spinifer* in fact pertain to *Eoconstrictor* cf. *fischeri* (see above). We here reject Kuhn's referral of additional specimens to this species, and *Eoconstrictor spinifer* is so far confined exclusively to its lectotype and paralectotype specimen.

It was suggested by Kuhn (1939a) that certain cranial features of *Eoconstrictor spinifer* comb. nov. resemble pythonids, especially the toothed premaxilla of a specimen (GMH Ce IV-5864-1933) referred by that author to the same species (see Szyndlar, 1994), whereas other characters were considered more reminiscent of booids (Szyndlar & Böhme, 1993). However, we were unable to



identify any premaxillary teeth in GMH Ce IV-5864-1933 and furthermore, we cannot refer this specimen to *Eoconstrictor spinifer* comb. nov. and we rather treat it as *Constrictores* indet. (see that entry and the respective figure of that specimen below). In any case, we have to highlight

that there is a strong cranial resemblance among the lectotype of *Eoconstrictor spinifer* comb. nov. and *E. fisheri*. Such similarities among the two species are mostly evident in the anatomy of the basioccipital, maxilla, and

pterygoid. Still, there are sufficient differences that lead us to conclude that they are distinct species.

Genus *Phosphoroboa* nov.

Type species: *Palaeopython filholii* Rochebrune, 1880.

Etymology: The genus name *Phosphoroboa* originates from the Greek “Φώσφορος” (“Phosphoros”), referring to its presence in the Phosphorites du Quercy, and the extant genus *Boa*. Gender is masculine.

Diagnosis: *Phosphoroboa* gen. nov. is assigned to Constrictores on the basis of possessing strongly built vertebrae, the centrum wider than long, the vertebrae taller than long in lateral view, prezygapophyseal accessory processes small, paradiapophyses un-divided or only weakly divided, and the lack of parazygantral foramina. *Phosphoroboa* gen. nov. can be assigned to Booidea based on the projection anteromedial to the palatine articulation on the pterygoid and the deep lateral facet for the ectopterygoid articulation on the pterygoid. Size moderate, with CL maximally around 10 mm; ratio of neural spine length to centrum length < 0.5 ; and ratio of zygosphene width to cotyle width low, < 1.2 on mid-trunk vertebrae. *Phosphoroboa* gen. nov. differs from the booid *Eoconstrictor* in having a higher pterygoid tooth count (14) and a V-shaped frontoparietal suture. *Phosphoroboa* gen. nov. can be differentiated from *Paleryx* by possessing wider zygosphene in anterior view and neural arch less depressed on posterior trunk vertebrae. *Phosphoroboa* gen. nov. can be further differentiated from *Palaeopython* by its smaller size, more depressed neural arch, thinner and narrower zygosphene, shorter neural spine on mid- and posterior trunk vertebrae, centrum less widened anteriorly, and postzygapophyseal articular facets less expanded laterally, and the absence of a flared posterior process of the maxilla. Further comparisons with other European Constrictores are presented in “Remarks” section.

Other species included: None.

Geographic and stratigraphic distribution: see Table 3.

Remarks: The cranial and vertebral material from the locality of Escamps, as well as those from the old collections of the Phosphorites du Quercy enable a more comprehensive understanding of the anatomy and relationships of “*Palaeopython*” *filholii*. Especially the cranial remains from Escamps enable a more precise placement within Constrictores, by referring the species to Booidea (see Description of these elements below). Considering its distinction from *Palaeopython* and *Paleryx*, in search for a possible available candidate genus name for “*Palaeopython*” *filholii*, we compared this species with all named genera of Booidea from Europe, as well as all

named genera of Constrictores from the Phosphorites du Quercy. As there are adequate differences with all these taxa (see details in the next paragraph), we consider it justified to establish a new genus, *Phosphoroboa* gen. nov., in order to accommodate “*Palaeopython*” *filholii*.

In particular, *Phosphoroboa* gen. nov. can be differentiated from *Eoconstrictor* by the morphology of the pterygoid and parietal (see Diagnoses of *Eoconstrictor* and *Phosphoroboa* gen. nov.). *Phosphoroboa* gen. nov. can be differentiated from *Bavarioboa* Szyndlar and Schleich, 1993, referred species of which are known also from the Oligocene of the Phosphorites du Quercy, in the neural spine length, the shape of the haemal keel in the posterior-most trunk, and its pterygoid morphology, with its pterygoid crest more extended medially and its ectopterygoid process being less prominent laterally and located more posteriorly. *Phosphoroboa* gen. nov. can be readily distinguished from the charinaid *Rageryx* Smith and Scanferla, 2021, from Messel by its larger size and the absence of complex accessory processes on caudal vertebrae. *Phosphoroboa* gen. nov. can be distinguished from the other two charinaid genera from Messel, i.e. *Messelophis* Baszio, 2004, and *Rieppelophis* Scanferla et al., 2016, by its larger size and different shape of neural spine. Other named genera of Constrictores from the Phosphorites du Quercy include *Palaelaphis*, *Tachyophis*, *Plesiotortrix*, *Rageophis*, *Cadurceryx* Hoffstetter and Rage, 1972, *Szyndlaria* Augé and Rage, 2010, *Platyspondylia* Rage, 1974, *Cadurcobia* Rage, 1978, and, of course, *Palaeopython*. A number of differences enable the distinguishment of *Phosphoroboa* gen. nov. from the larger *Palaeopython* (see details in Diagnosis of *Phosphoroboa* gen. nov. above). *Phosphoroboa* gen. nov. can be readily distinguished from the “erycine” *Cadurceryx* by the absence of complex accessory processes on caudal vertebrae. *Phosphoroboa* gen. nov. can be distinguished from *Platyspondylia* by its much larger size, higher neural spine, and thicker zygosphene. *Phosphoroboa* gen. nov. can be distinguished from *Szyndlaria* by its much larger size and rather different shape of neural spine and haemal keel. *Phosphoroboa* gen. nov. can be distinguished from *Cadurcobia* by its larger size, its much more depressed neural arch, and shorter and differently shaped neural spine. *Phosphoroboa* gen. nov. seems to be much different from *Plesiotortrix* in possessing a much longer centrum and neural spine that is not confined to the posterior part of the neural arch. Comparison of *Phosphoroboa* gen. nov. with *Rageophis* is difficult, as the lectotype of the type species *Rageophis lafonti* is a “mummified” trunk portion with several articulated vertebrae and ribs; nevertheless, the ventral view of the vertebrae of *R. lafonti* is directly discernible and it seems that they possess more elongated centra, more robust diapophyses, and more laterally directed prezygapophyses,

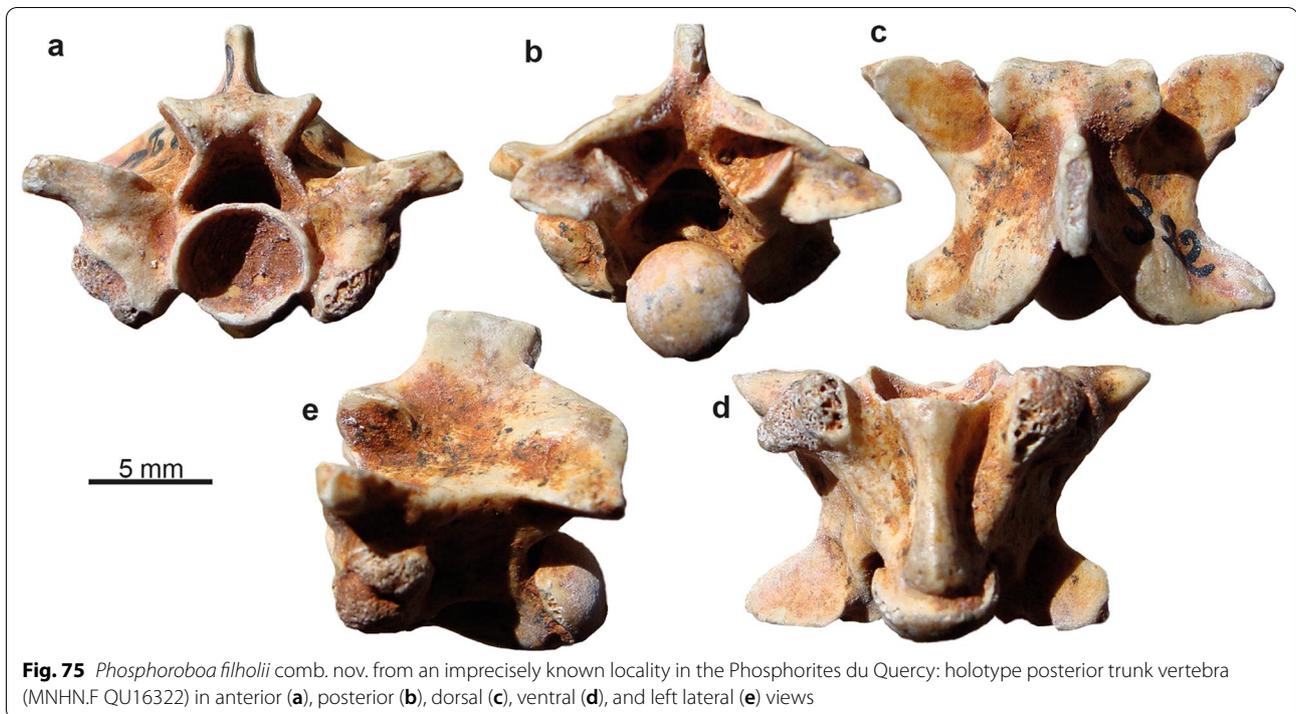


Fig. 75 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: holotype posterior trunk vertebra (MNHN.F QU16322) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

in comparison with *Phosphoroboa* gen. nov. *Phosphoroboa* gen. nov. can be differentiated from the type species of *Palaelaphis*, i.e. *Palaelaphis antiquus* (currently considered to be a nomen dubium; Rage, 1984b; Szyndlar & Rage, 2003) by its more depressed neural arch, thicker zygosphene, and different shape of neural spine. Finally, *Tachyophis nitidus* Rochebrune, 1884, another species that is currently considered to be a nomen dubium (Rage, 1984b; Szyndlar & Rage, 2003), bears some resemblance with *Phosphoroboa filholii* comb. nov. in terms of the relatively depressed neural arch. However, the lectotype of *T. nitidus*, four articulated vertebrae (MNHN.F QU16331), which is also the only specimen that can be securely associated with this species, has a rather small size (CL around 2.5 mm) and the specimen probably pertains to a young individual, as it has been already suggested by Rage (1974, 1984b). As such, considering its early ontogenetic stage, *Tachyophis* is properly considered a nomen dubium. We further note that the paralectotype pterygoid (MNHN.F QU16330) of *Tachyophis nitidus* bears resemblance with the pterygoid (UM ECC 2501) of *Phosphoroboa filholii* comb. nov. from Escamps, but in any case, this former specimen cannot be referred with certainty to *T. nitidus* and being simply a paralectotype, it has no actual nomenclatural power. Another taxon of Constrictores from Quercy is *Pylmophis gracilis* Rochebrune, 1884, currently considered a nomen dubium (Rage, 1984b; Szyndlar & Rage, 2003); note, however, that *Pylmophis* Rochebrune, 1880, cannot be an available name, as the Quercy taxon

Pylmophis gracilis is a referred species and the genus is typified by a Miocene natricid, i.e. *Coluber sansaniensis* Lartet, 1851 (currently placed into *Natrix* Laurenti, 1768; Rage, 1981). Finally, as *Phosphoroboa* gen. nov. is a member of Booidea, affinities with the non-booid constrictors *Paleryx* and *Messelopython* are readily discarded; as such, resemblance in the vertebral anatomy between *Phosphoroboa* gen. nov. and *Paleryx* should only be considered as superficial, not alluding to actual phylogenetic relationships (see also “Remarks” in the entry of *Phosphoroboa filholii* comb. nov., below).

Nomenclatural acts: This published work and the nomenclatural act it contains have been registered in ZooBank, the official registry of zoological nomenclature for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘<http://zoobank.org/>’. The LSID for this publication is: urn:lsid:zoobank.org:pub:44C5A053-CDE4-477E-AEEE-63F3860FA4C0. The LSID for this new genus name *Phosphoroboa* gen. nov. is: urn:lsid:zoobank.org:act:880E62D3-8435-4818-A157-8068924B36F4

***Phosphoroboa filholii* (Rochebrune, 1880) comb. nov.**

Figures 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85 and 86, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102 and 103

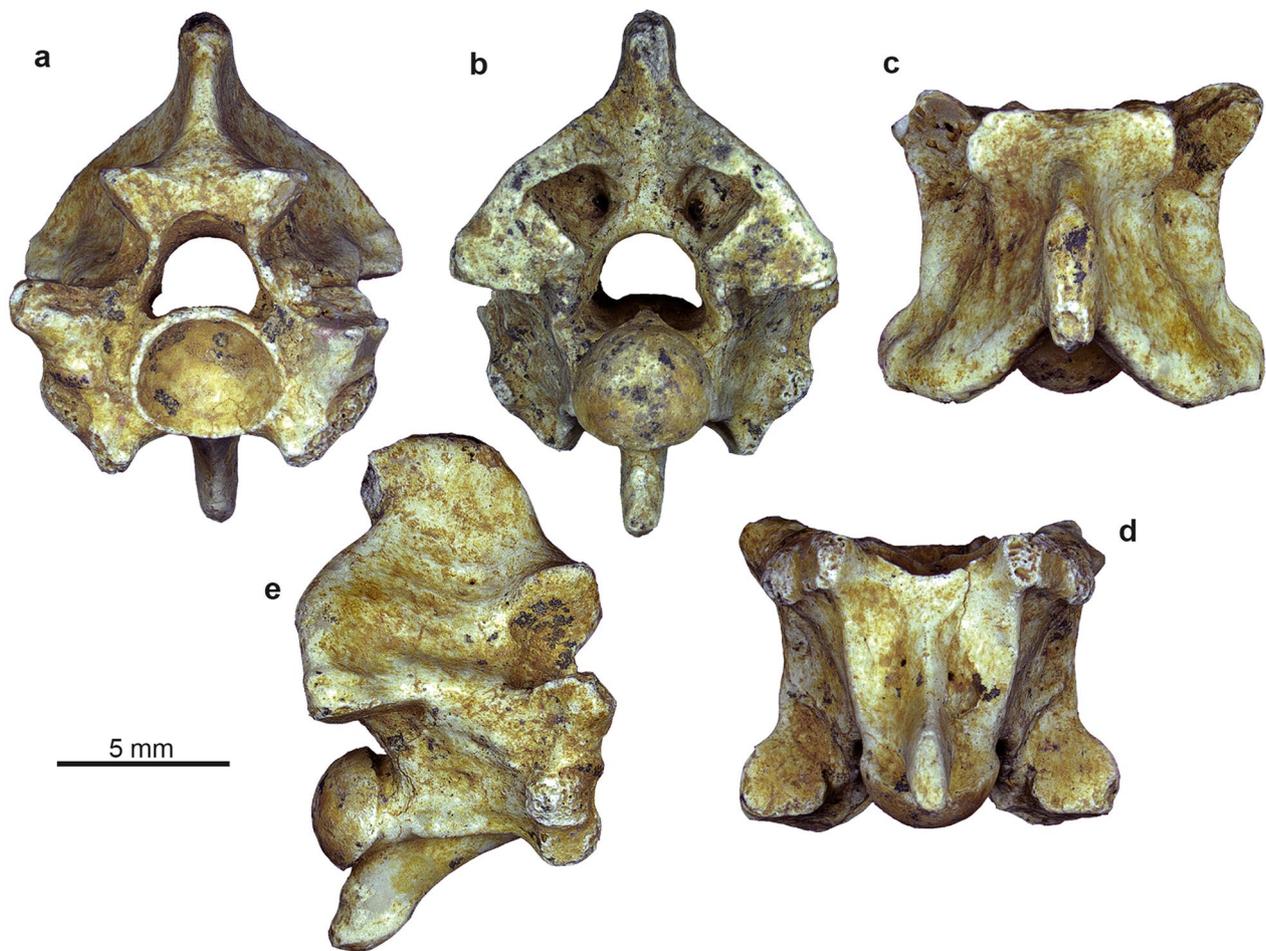


Fig. 76 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: anterior trunk vertebra (NHMW 2019/0033/0018) in anterior (a), posterior (b), dorsal (c), ventral (d), and right lateral (e) views

Taxonomic history: *Palaeopython filholii* Rochebrune, 1880 (new species); *Palaeopython filholi* Rochebrune, 1884 (variant spelling of species epithet); *Paleryx filholi* Lydekker, 1888a (new combination and variant spelling of species epithet); *Paleryx depressus* = *Palaeopython filholi* Lydekker, 1888b (junior synonym and variant spelling of species epithet); *Paleopython filholi* Palacký, 1898 (incorrect spelling of genus name and variant spelling of species epithet).

Type material: MNHN.F QU16322 (formerly MNHN QU 322) (holotype), a posterior trunk vertebra (Rochebrune, 1880, pl. XII. 5^a, 5^b, and 5^c; Rochebrune, 1884, pl. II.4^b, II.4^c; Rage, 1974, fig. 3A; Krumbiegel et al., 1983, fig. 116A; Rage, 1984b, fig. 13b; Georgalis & Scheyer, 2019a, fig. 15i; Fig. 75).

Type locality: Unknown exact locality, Phosphorites du Quercy, France; probably middle or late Eocene.

Previously referred material and range: Middle or late Eocene, type area, Quercy, France (referred material

of Rochebrune, 1884, Lydekker, 1888a, De Stefano, 1905, and Georgalis & Scheyer, 2019a; material referred to *Paleryx depressus* by Lydekker, 1888a); late Eocene (MP 19), Escamps A and C, Quercy, Lot, France (Rage, 1974).

Referred material discussed herein: Phosphorites du Quercy, Escamps A locality, Lot, France (MP 19, late Eocene): a parietal (UM ECA 2543) and a left dentary (UM ECA 2544); **Phosphorites du Quercy, Escamps C locality, Lot, France (MP 19, late Eocene):** six trunk vertebrae (UM ECC 2572–UM ECC 2577), two cloacal vertebrae (UM ECC 3095 and UM ECC 3096), two caudal vertebrae (UM ECC 3097 and UM ECC 3098), and a left pterygoid (UM ECC 2501); **Phosphorites du Quercy, imprecisely known localities:** three articulated trunk vertebrae (MNHN.F QU16323), two articulated trunk vertebrae (NHMW 2019/0033/0007), 150 trunk vertebrae (NHMW 2019/0033/0001, NHMW 2019/0033/0002, NHMW 2019/0033/0004–NHMW 2019/0033/0006, NHMW 2019/0033/0008–NHMW 2019/0033/0036,

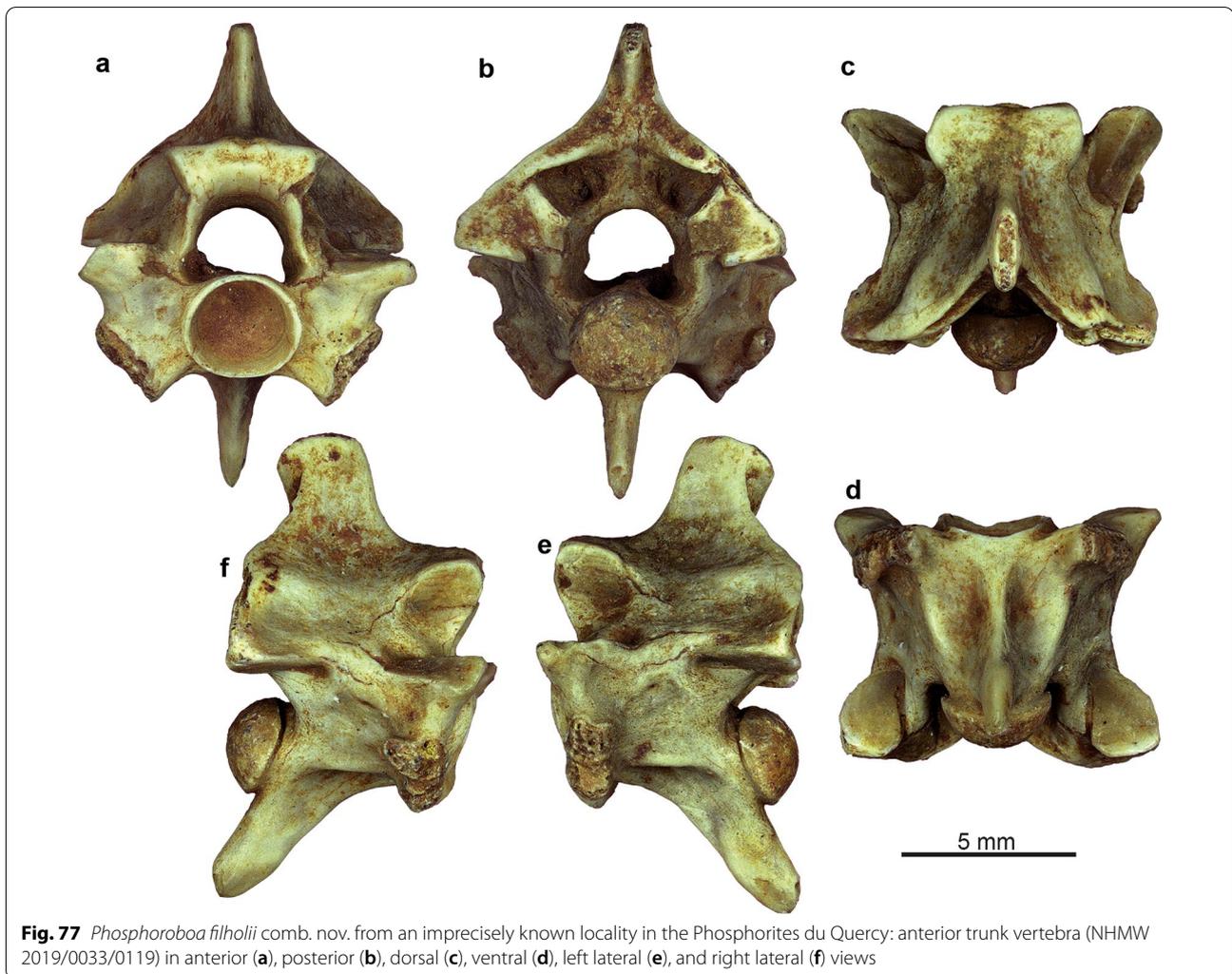


Fig. 77 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: anterior trunk vertebra (NHMW 2019/0033/0119) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

NHMW 2019/0033/0038–NHMW 2019/0033/0050, NHMW 2019/0033/0052–NHMW 2019/0033/0154), a left maxilla (NHMW 2019/0020/0001), a right dentary (NHMW 2019/0020/0002), and a left pterygoid fragment (NHMW 2019/0020/0004); *Phosphorites du Quercy, imprecise localities near Mouillac*: 27 trunk vertebrae (5 anterior, 17 middle and 5 posterior trunk; YPM-VPPU 30369–YPM-VPPU 30395) and two dentaries (NHMUK PV R 3489 and YPM-VPPU 30397).

Diagnosis: As for the genus *Phosphoroboa* gen. nov.

Description of the holotype (MNHN.F QU16322): MNHN.F QU16322 is a nearly complete posterior trunk vertebra, with only its paradiapophyses being partially eroded (Fig. 75). In anterior view (Fig. 75a), the zygosphene is only moderately thick, having a trapezoidal shape, with its dorsolateral edges extending well laterally. Its dorsal surface is almost flat, with only a small convexity appearing posteriorly on the midline. There is a small tubercle at mid-height. The zygosphene is slightly wider

than the cotyle. The neural canal is triangular. The cotyle is deep and nearly circular. No paracotylar foramina are present. The prezygapophyses are only slightly inclined. In posterior view (Fig. 75b), the neural arch has a vaulting ratio of 0.34 and its posterior margin is straight, not angulated. The zygantrum is large and deep. The condyle is large and circular. In dorsal view (Fig. 75c), the vertebra is wider than long. The neural spine is moderately thick, and its anterior base commences well behind the zygosphene. The zygosphene has two slight lateral lobes and a median one. The prezygapophyses are laterally extensive, with the prezygapophyseal articular facets being oval, with the long axis oriented obliquely. Prezygapophyseal accessory processes are small and pointed. The interzygapophyseal constriction is prominent; it is smoothly and nearly symmetrically rounded and extends medially well beyond the mid-point of the prezygapophyseal articular facet. The posterior median notch of neural arch is deep. In ventral view (Fig. 75d), the centrum is triangular and

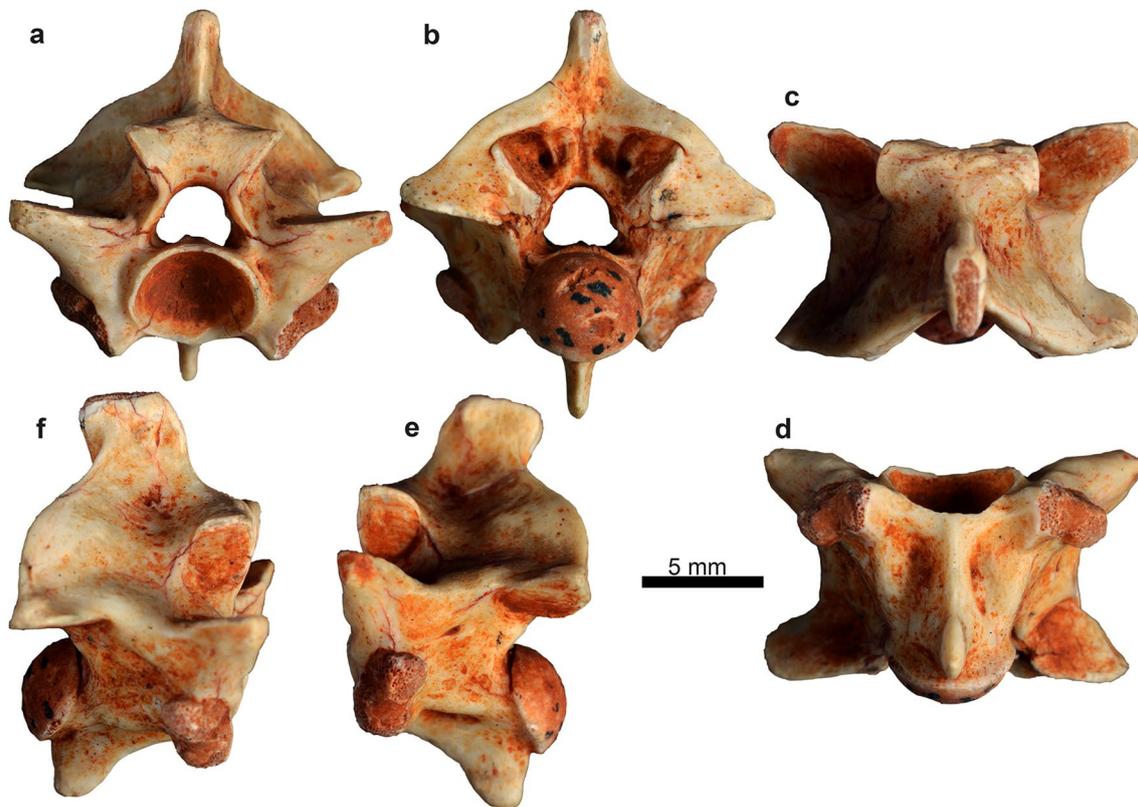


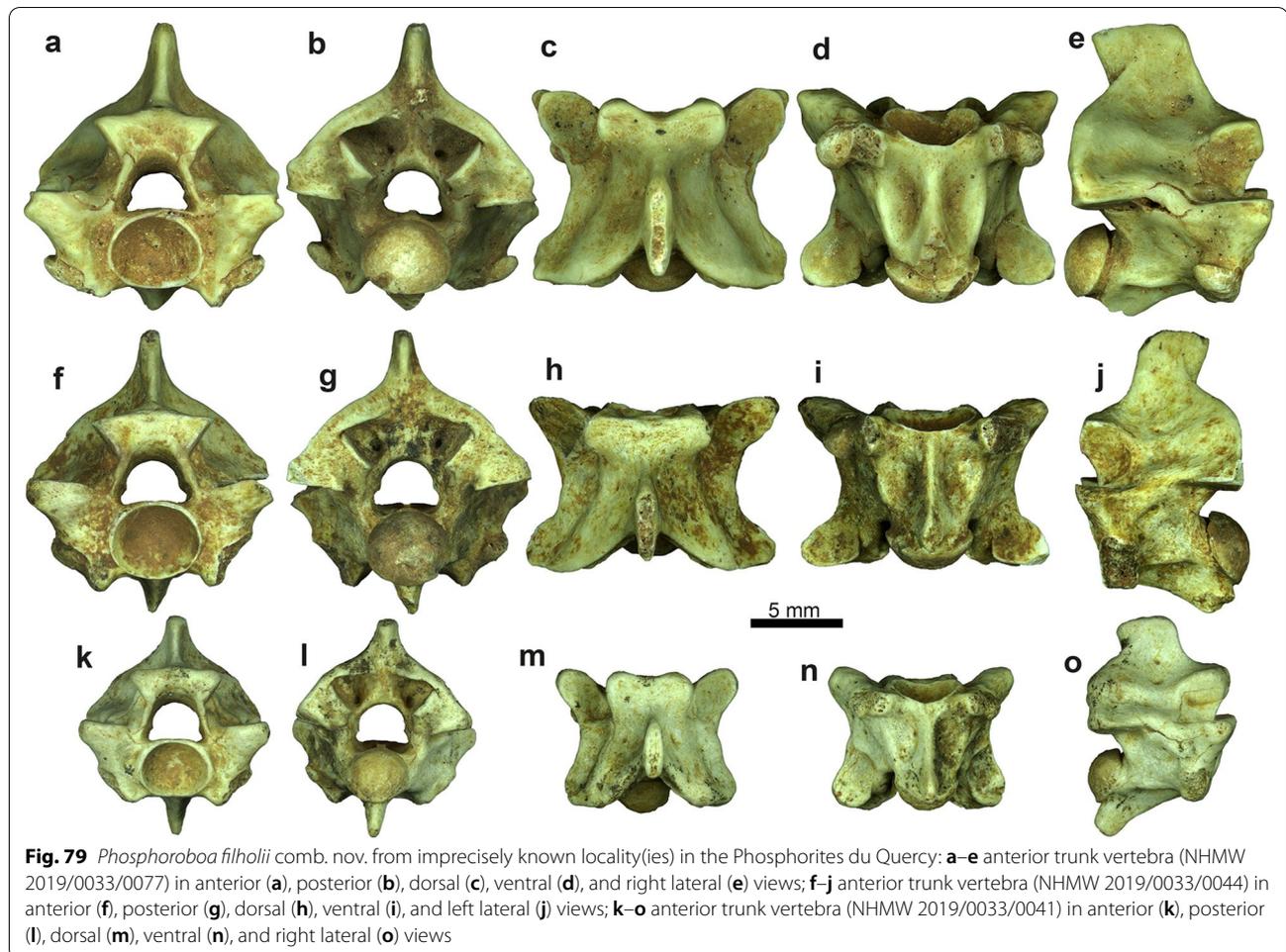
Fig. 78 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: anterior trunk vertebra (NHMW 2019/0033/0001) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e), and right lateral (f) views

its margins, the subcentral ridges, are straight or slightly concave. The haemal keel is thick and rounded and narrows at mid-length. The haemal keel commences at the ventral lip of the cotyle but terminates well before the condyle. The paradiapophyses are eroded, but it can be seen that the diapophyses and parapophyses were poorly divided. The postzygapophyseal articular facets are large and triangular. In lateral view (Fig. 75e), the vertebra is taller than long. The neural spine has parallel anterior and posterior margins and is posteriorly inclined, slightly overhanging the posteromedian notch of the neural arch. The subcentral ridges are convex. The haemal keel is prominent and its posterior edge reaches the level of the distinct condylar neck.

Note that the centrum length (CL) given here (10.36 mm) differs from the one (8.8 mm) provided by Rage (1974), which is in fact closer to the means in samples described below. We cannot account for difference. It is possible that his measurement did not include the condyle, or covered only the haemal keel, or used some less precise procedure.

Description of additional vertebrae from Quercy—*intracolumnar variation* (Figs. 76, 77, 78, 79, 80, 81,

82, 83, 84, 85 and 86, 91, 92, 93, 94 and 95): Vertebrae from practically all regions of the skeleton are available, so that individual and intracolumnar variation is adequately known. Anterior-most trunk vertebrae (e.g., UM ECC 2572; Fig. 82a–c) are smaller, they have a small, relatively thick hypapophysis, and they possess a less thick zygosphene and a larger neural canal. They have much more vaulted neural arch than succeeding vertebrae. The prezygapophyses and postzygapophyses are also smaller. The neural spine is tall, directed posteriorly [e.g., NHMW 2019/0033/0075; NHMW 2019/0033/0044 (Fig. 79)]. However, certain specimens possess a short neural spine (e.g., NHMW 2019/0033/0018; Fig. 76). Neural spine foramina can be present (e.g., NHMW 2019/0033/0018, NHMW 2019/0033/0044). Succeeding anterior trunk vertebrae are characterized by larger size and shorter neural spines. The neural spine can be relatively thick in few large specimens (e.g., NHMW 2019/0033/0019), reminiscent of the situation in *Palaeopython cadurcensis*. In one anterior trunk vertebra (UM ECC 2574), the zygosphene has a peculiar, curved, shape in anterior view. The neural arch is arched and can be quite vaulted (e.g., NHMW 2019/0033/0018; Fig. 76b). The shape of the



hypapophysis varies. The interzygapophyseal constriction can be shallow (e.g., NHMW 2019/0033/0018; Fig. 76c). The subcentral ridges are usually almost straight in lateral view [e.g., NHMW 2019/0033/0018 (Fig. 76e); NHMW 2019/0033/0019; NHMW 2019/0033/0042]. The subcentral grooves are rather prominent in certain specimens (e.g., NHMW 2019/0033/0019). In posterior-most anterior trunk vertebrae, the neural spine becomes broader in lateral view, and the hypapophyses are rather large.

Mid-trunk vertebrae are moderately large, with CL ranging between 4 and 10 mm, but most specimens toward the middle of this range (see Appendix 1). Mean CL in the NHMW sample was 6.9 mm (Fig. 87); in the YPM sample, 6.16 mm (Fig. 88). In mid-trunk vertebrae, the zygosphene often has three slightly or clearly distinct lobes in dorsal view (UM ECC 2576; NHMW 2019/0033/0055), although there are specimens where these lobes are indistinct (e.g., NHMW 2019/0033/0004) or even that the zygosphene is straight (e.g., NHMW 2019/0033/0037). The zygosphene can be moderately

thick, though in many specimens it is thinner (e.g., NHMW 2019/0033/0049; NHMW 2019/0033/0055). On mid-, as on all other trunk vertebrae, the zygosphene is as wide as or wider than the cotyle. The zygosphene often possesses the characteristic median tubercle, although it may be very slightly developed (e.g., NHMW 2019/0033/0054) and is sometimes totally absent (e.g., NHMW 2019/0033/0056). The neural spine is relatively short in lateral view, it is inclined posteriorly, and most usually it overhangs posteriorly (e.g., NHMW 2019/0033/0004). The neural spine commences well behind the zygosphene, a feature that seems to be consistent throughout the trunk column in individuals of different size. Lateral foramina are present and usually prominent. A prominent ridge in the postzygapophyses is clearly visible in lateral view, a feature that can be observed throughout vertebrae of the trunk column. The neural arch is less vaulted than in the anterior trunk vertebrae, the vaulting ratio being varying between about 0.34 and 0.44 independently of centrum length (Figs. 89, 90), and usually the posterior margin of the

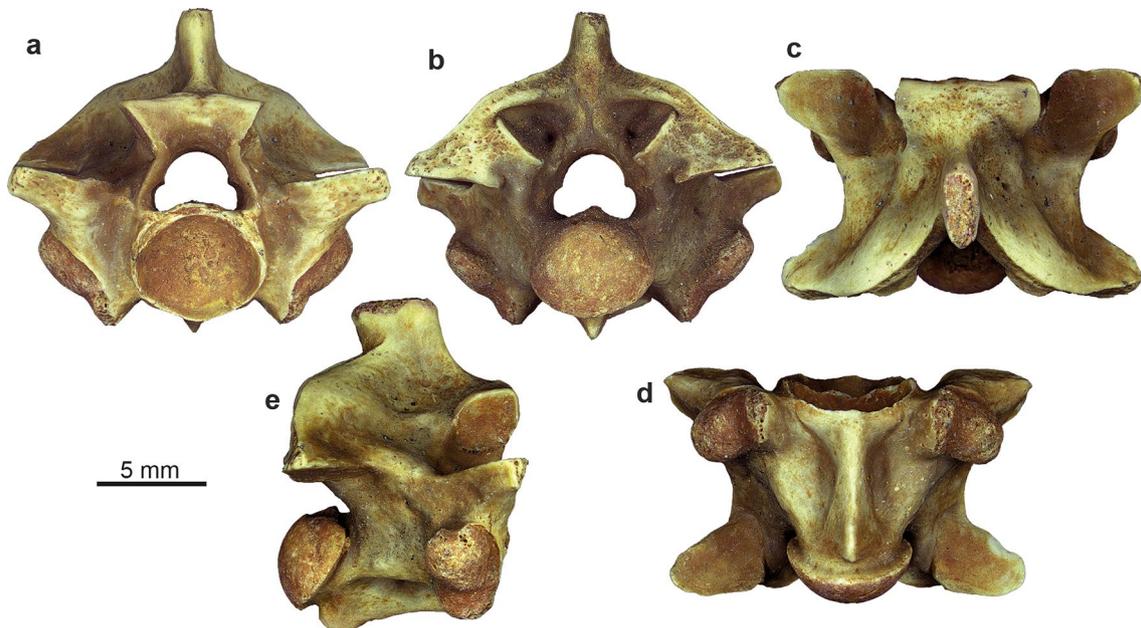


Fig. 80 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: anterior mid-trunk vertebra (NHMW 2019/0033/0050) in anterior (a), posterior (b), dorsal (c), ventral (d), and right lateral (e) views

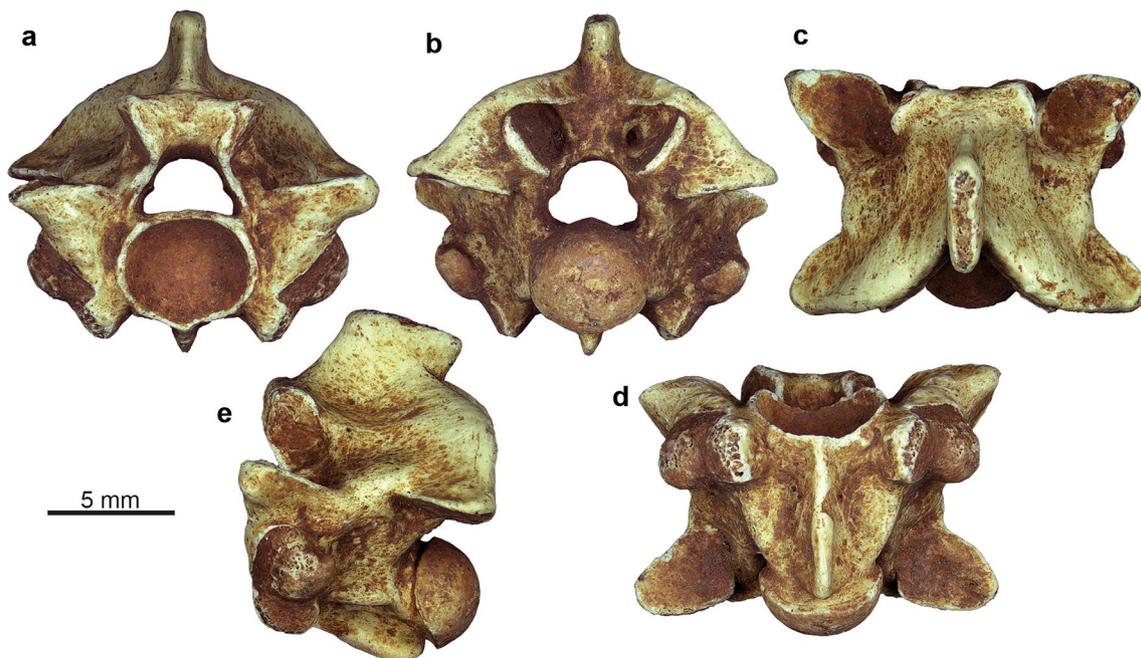


Fig. 81 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: anterior mid-trunk vertebra (NHMW 2019/0033/0054) in anterior (a), posterior (b), dorsal (c), ventral (d), and left lateral (e) views

neural arch is angulated above the lateral edges of the zygantrum. Nevertheless, certain small-sized specimens have much more vaulted and almost triangular-shaped neural arch (e.g., NHMW 2019/0033/0010). In the neural canal, a distinct raised area (“subneural process”

sensu Auffenberg, 1963; “epapophysis” sensu Holman, 2000) is usually prominent mid-ventrally (e.g., NHMW 2019/0033/0004), though this feature is not as thick as in specimens of *Palaeopython cadurcensis*. In one specimen (NHMW 2019/0033/0122), the neural canal has a

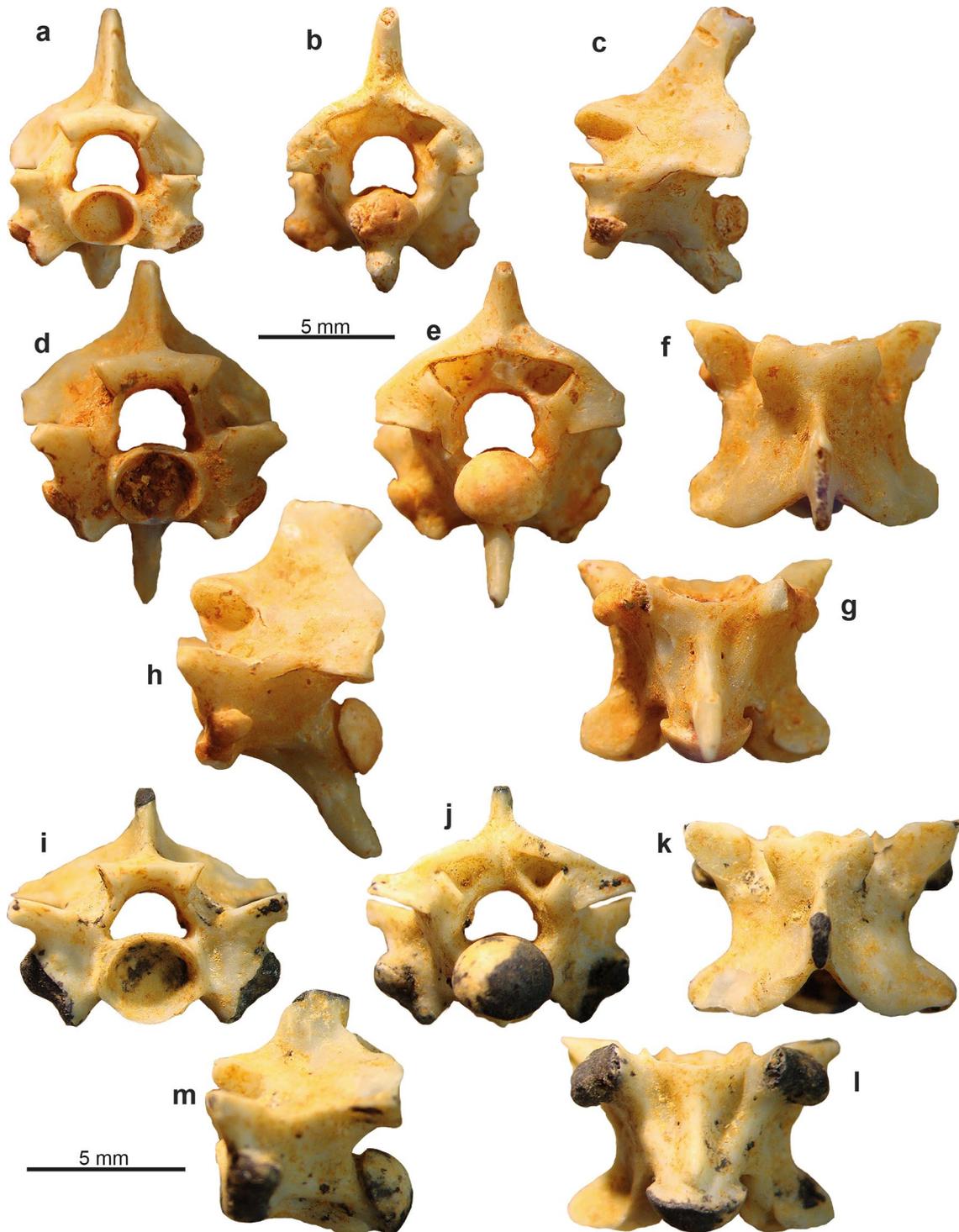


Fig. 82 *Phosphoroboa filholii* comb. nov. from the late Eocene of Escamps C, Phosphorites du Quercy: **a–c** anterior-most trunk vertebra (UM ECC 2572) in anterior (**a**), posterior (**b**), and left lateral (**c**) views; **d–h** anterior trunk vertebra (UM ECC 2575), more posterior than the previous one, in anterior (**d**), posterior (**e**), dorsal (**f**), ventral (**g**), and left lateral (**h**) views; **i–m** mid- to posterior trunk vertebra (UM ECC 2577) in anterior (**i**), posterior (**j**), dorsal (**k**), ventral (**l**), and left lateral (**m**) views

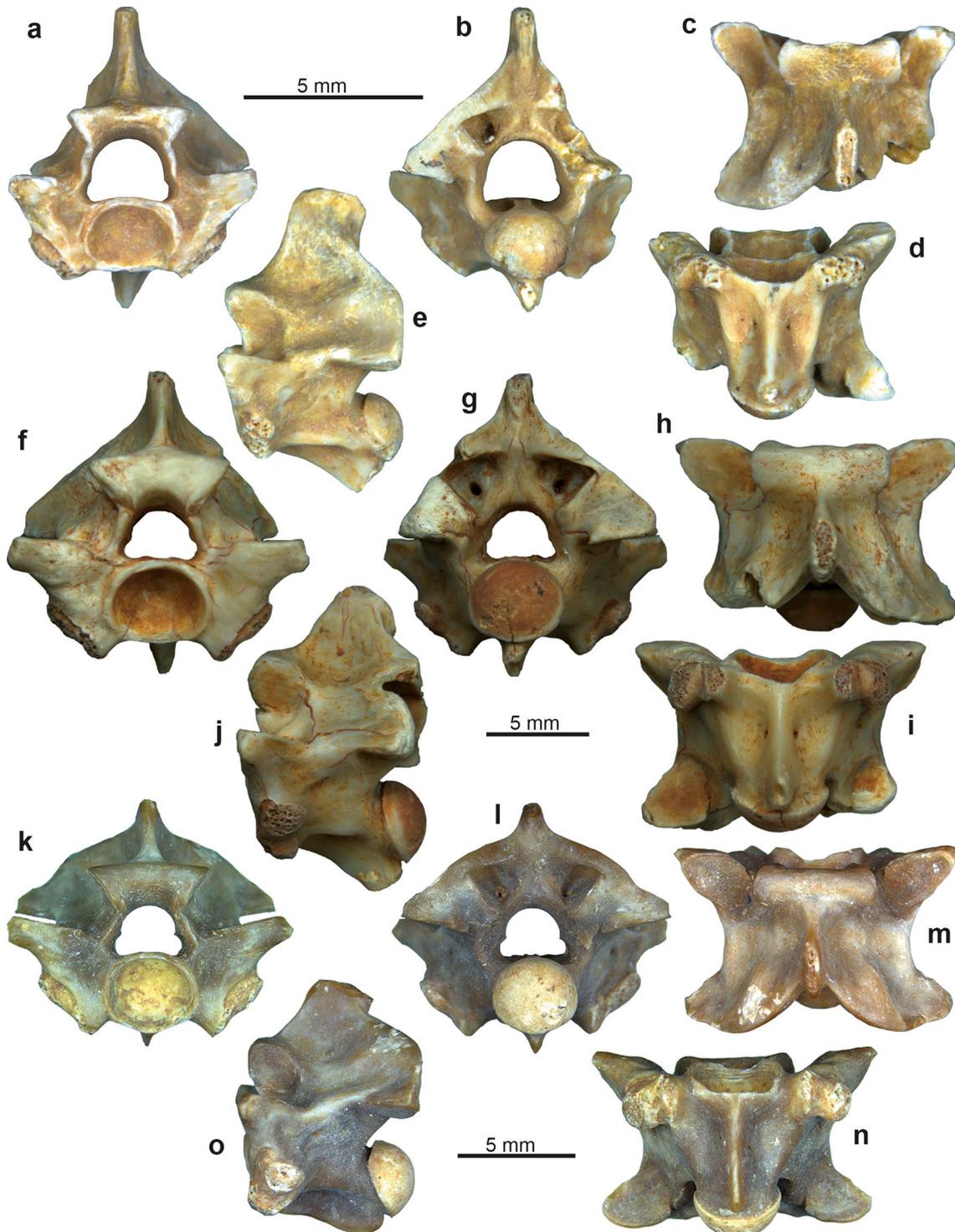


Fig. 83 *Phosphoroboa filholii* comb. nov. from imprecisely known locality(ies) near Mouillac, Phosphorites du Quercy: **a–e** anterior trunk vertebra (YPM-VPPU 30369) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** anterior trunk vertebra (YPM-VPPU 30371) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k–o** mid-trunk vertebra (YPM-VPPU 30380) in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views

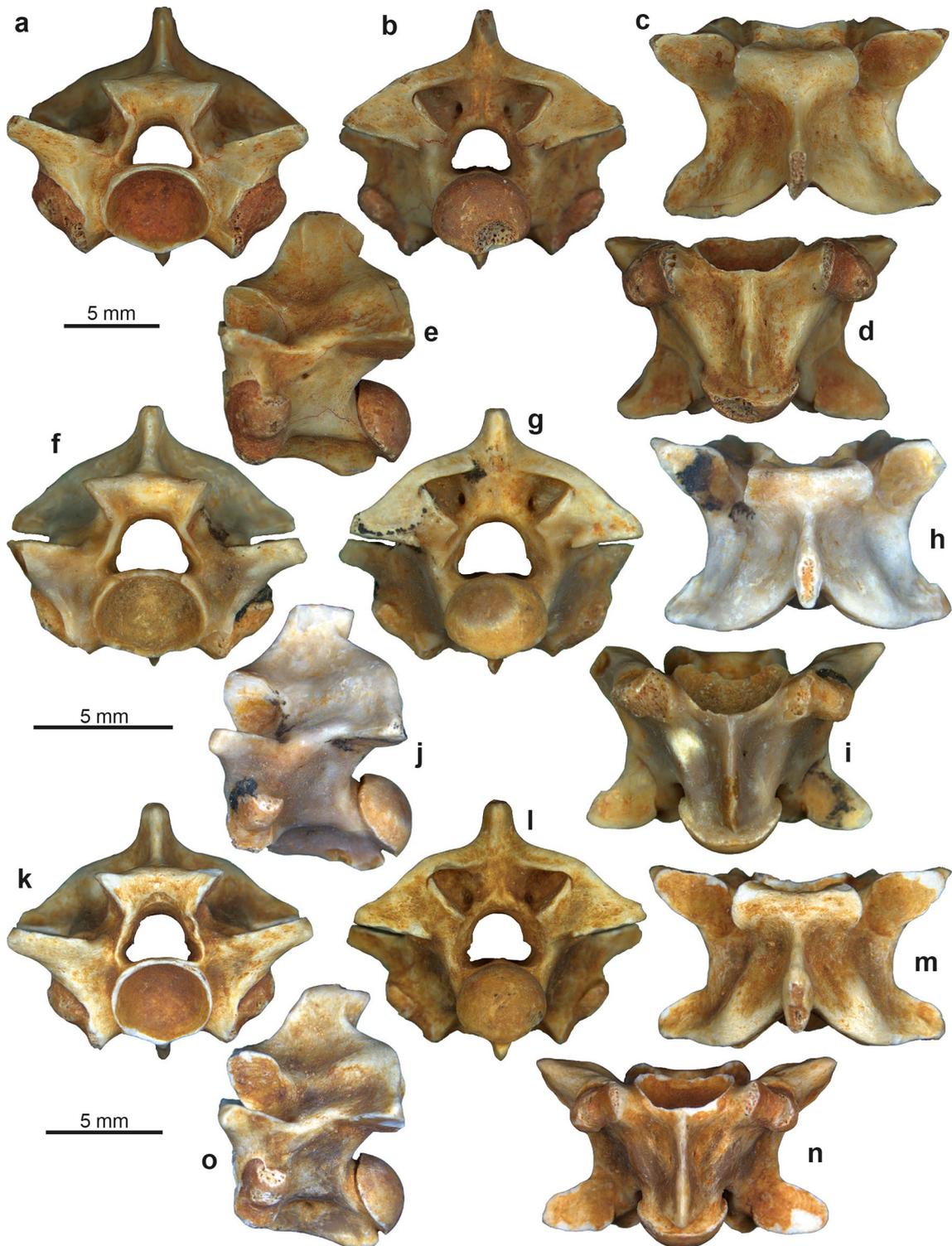


Fig. 84 *Phosphoroboa filholii* comb. nov. from imprecisely known locality(ies) near Mouillac, Phosphorites du Quercy: **a–e** mid-trunk vertebra (YPM-VPPU 30374) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** mid-trunk vertebra (YPM-VPPU 30381) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k–o** mid-trunk vertebra (YPM-VPPU 30383) in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views

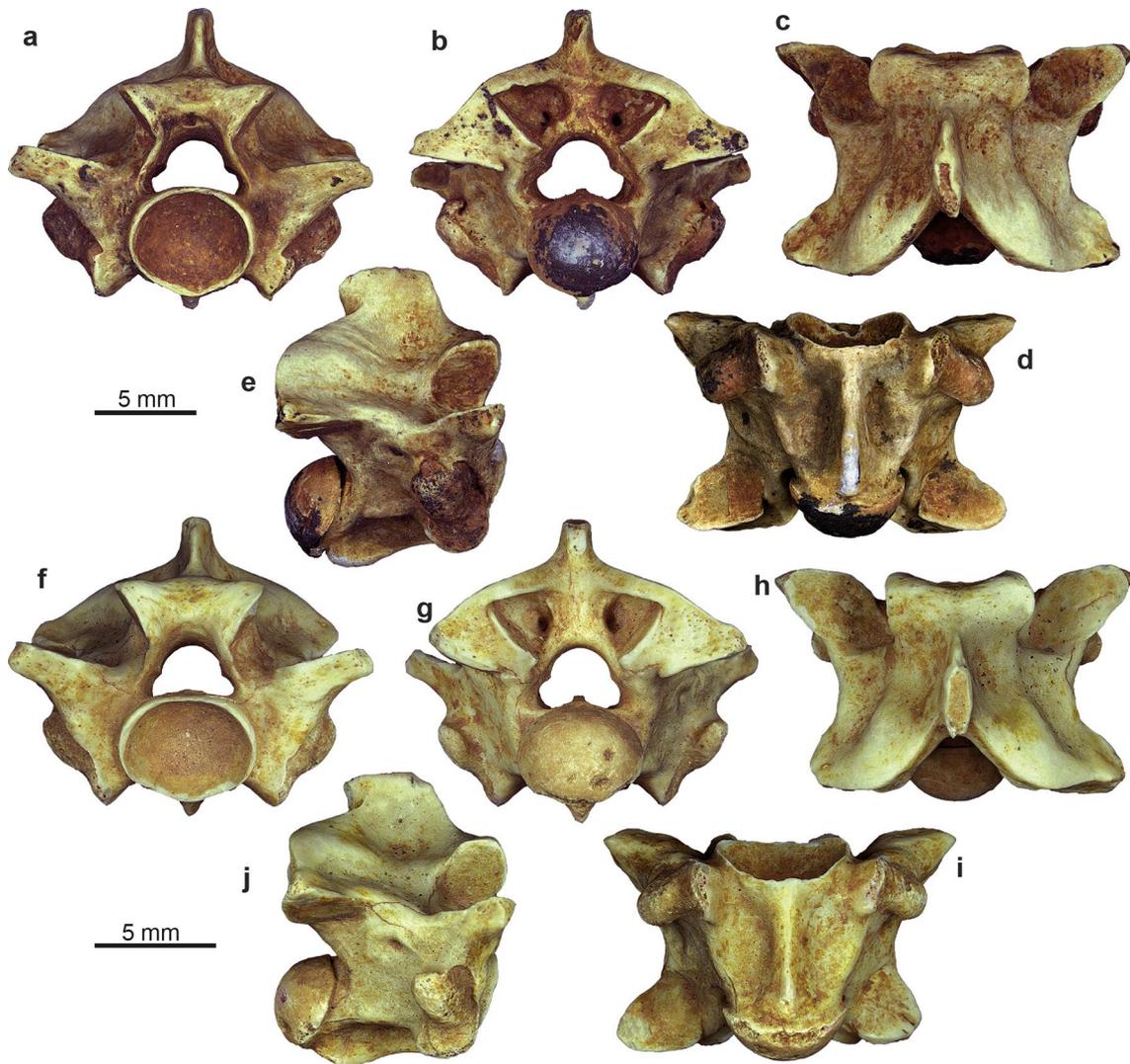
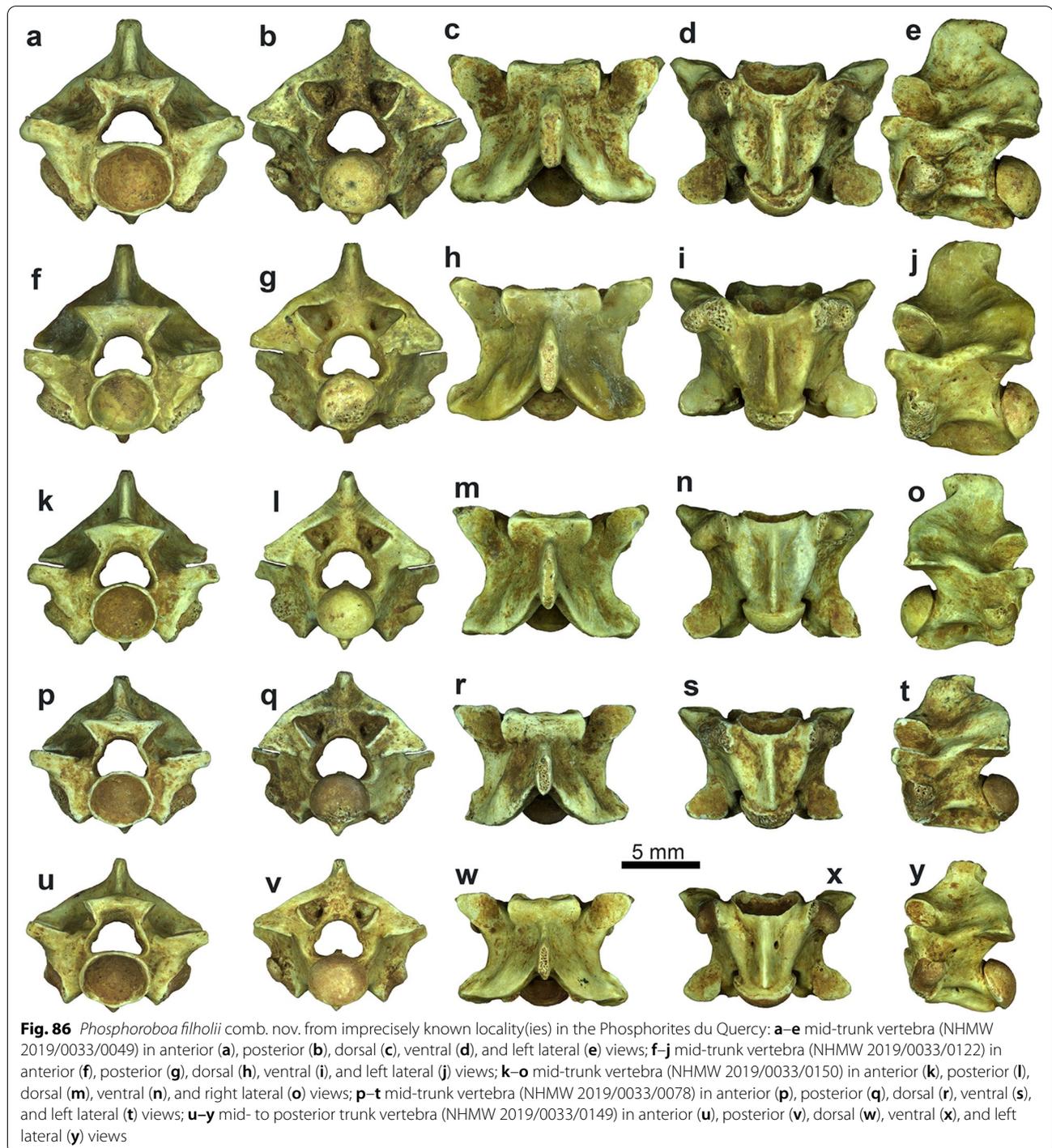


Fig. 85 *Phosphoroboa filholii* comb. nov. from imprecisely known locality(ies) in the Phosphorites du Quercy: **a–e** mid-trunk vertebra (NHMW 2019/0033/0056) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and right lateral (**e**) views; **f–j** mid-trunk vertebra (NHMW 2019/0033/0004) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and right lateral (**j**) views. The former specimen has been figured in Georgalis and Scheyer (2019a:fig. 15j)

distinct “trefoil” shape (Fig. 86f, g), but other specimens are similar. The prezygapophyses are dorsally inclined in anterior view (though usually not the same large extent as in *Palaeopython cadurcensis*). The prezygapophyseal articular facets are large and, almost always, oval in shape. Prezygapophyseal accessory processes are usually small or can be invisible, but rarely are fairly large (e.g., NHMW 2019/0033/0120; NHMW 2019/0033/0126). The posterior median notch of the neural arch is prominent. The cotyle is large and deep. Paracotylar foramina are almost always absent, with few exceptions (i.e. NHMW 2019/0033/0047). The zygantrum is always deep and two deep zygantral foramina are usually visible. In certain cases, a number of small foramina can be present next to

the zygantrum. The haemal keel is usually sharp on mid-trunk vertebrae and projects slightly below the condyle, even small specimens (e.g., NHMW 2019/0033/0048). Subcentral foramina are present and are occasionally large (e.g., NHMW 2019/0033/0149). A precondylar constriction is present. The condyle is massive and usually circular, and in one case it is vertically elliptical (NHMW 2019/0033/0047), a rather strange condition for snakes. Longitudinal ridges are found on some specimens on the posterior half of the neural arch (e.g., NHMW 2019/0033/0122; NHMW 2019/0033/0124), and zygantral mounds are commonly present. Additionally, in another specimen (NHMW 2019/0033/0151) there is an exceptionally large dorsal thickening of the neural spine



in dorsal view, a feature not uncommon in Constrictores (e.g., the extinct *Cheilophis huerfanoensis* Gilmore, 1938, *Albaneryx depereti* Hoffstetter and Rage, 1972, *Pterygoboa* Holman, 1976, *Cadurceryx filholi* Hoffstetter and Rage, 1972, and the extant *Epicrates cenchria* (Linnaeus, 1758); see figures in Hoffstetter & Rage, 1972; Rage, 1984b; Szyndlar & Rage, 2003).

In posterior mid- and posterior trunk vertebrae, the haemal keel becomes wider and thicker in ventral view and the neural arch becomes gradually even more depressed (e.g., the holotype MNHN.F QU16322; UM ECC 2577; NHMW 2019/0033/0002) (Figs. 75, 82i–m, 91, 92 and 93). Certain posterior trunk vertebrae achieve a peculiarly rather vaulted neural arch (e.g.,

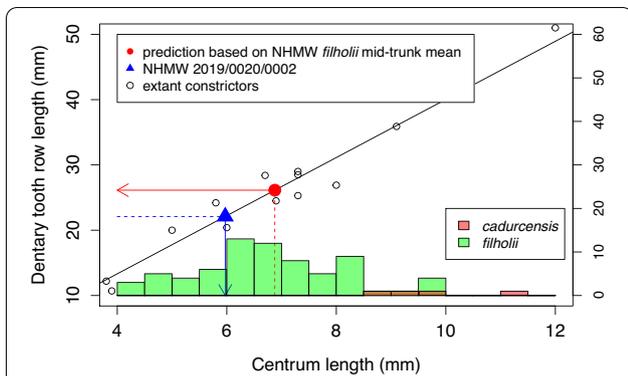


Fig. 87 Distribution of centrum length (CL) in NHMW sample of *Palaeopython cadurcensis* and *Phosphoroboa filholii* comb. nov. (frequency counts on right axis). Superimposed is the relationship between dentary tooth row length and mid-trunk vertebral centrum length (CL) in extant Constrictores (dentary size on left axis). Centrum length indicated by the dentary NHMW 2019/0020/0002 from the same sample and dentary tooth row length indicated by the population mean of *Phosphoroboa filholii* comb. nov. mid-trunk vertebrae support the referral of the dentary to *Phosphoroboa filholii* comb. nov.

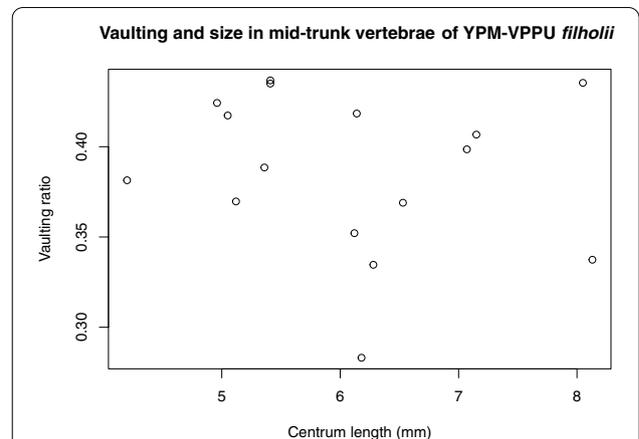


Fig. 89 Relationship between vaulting ratio and centrum length in mid-trunk vertebrae in the YPM collection of *Phosphoroboa filholii* comb. nov. suggests that these are uncorrelated over a broad ontogenetic range

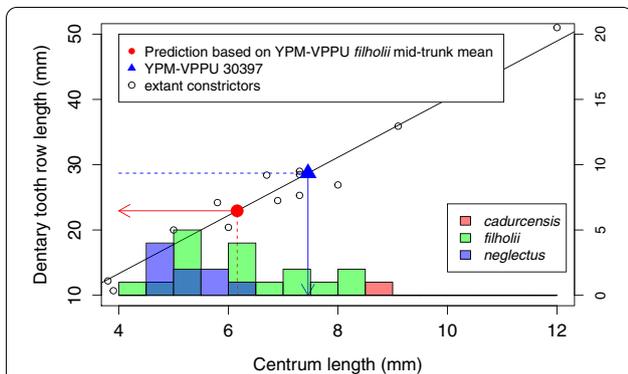


Fig. 88 Distribution of centrum length (CL) in YPM sample of *Palaeopython cadurcensis*, *Phosphoroboa filholii* comb. nov., and "*Palaeopython*" *neglectus* (frequency counts on right axis). Superimposed is the relationship between dentary tooth row length and mid-trunk vertebral centrum length (CL) in extant Constrictores (dentary size on left axis). Centrum length indicated by the dentary YPM-VPPU 30397 from the same collection and dentary tooth row length indicated by the population mean of *Phosphoroboa filholii* comb. nov. mid-trunk vertebrae support the referral of the dentary to *Phosphoroboa filholii* comb. nov.

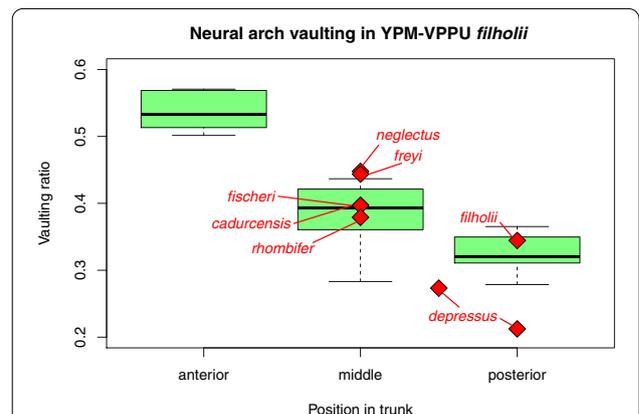


Fig. 90 Vaulting ratio in anterior, mid- and posterior trunk vertebrae in the YPM sample of *Phosphoroboa filholii* comb. nov. compared to same ratio in type material of various Paleogene constrictors from Europe. Two types are plotted for *Paleryx depressus* (junior synonym of *Paleryx rhombifer*) because one vertebra is close to the mid-/posterior trunk boundary, and moving it to the one or the other column would be misleading

NHMW 2019/0033/0083, NHMW 2019/0033/0084). Some posterior trunk vertebrae reach considerable size, with CL surpassing 10 mm (e.g., the holotype MNHN.F QU16322; NHMW 2019/0033/0035). The subcentral grooves (paralymphatic fossae) are more prominent than on mid-trunk vertebrae. The thick subcentral ridges can be straight or slightly convex and usually show the constriction at mid-length. The neural spine becomes also

gradually shorter but retains the posterior inclination. The zygantral mounds are usually found here as well, but there are specimens that lack them (e.g., NHMW 2019/0033/0036). The prezygapophyses are slightly inclined. Prezygapophyseal accessory processes are present in several specimens, especially in large ones (e.g., NHMW 2019/0033/0036). The interzygapophyseal constriction is generally smoothly rounded and moderately deep, extending medially beyond the mid-point of the prezygapophyses, although in some cases it is more shallow and/or squared off (e.g., NHMW 2019/0033/0129). The cotyle is always deep and varies in shape from almost

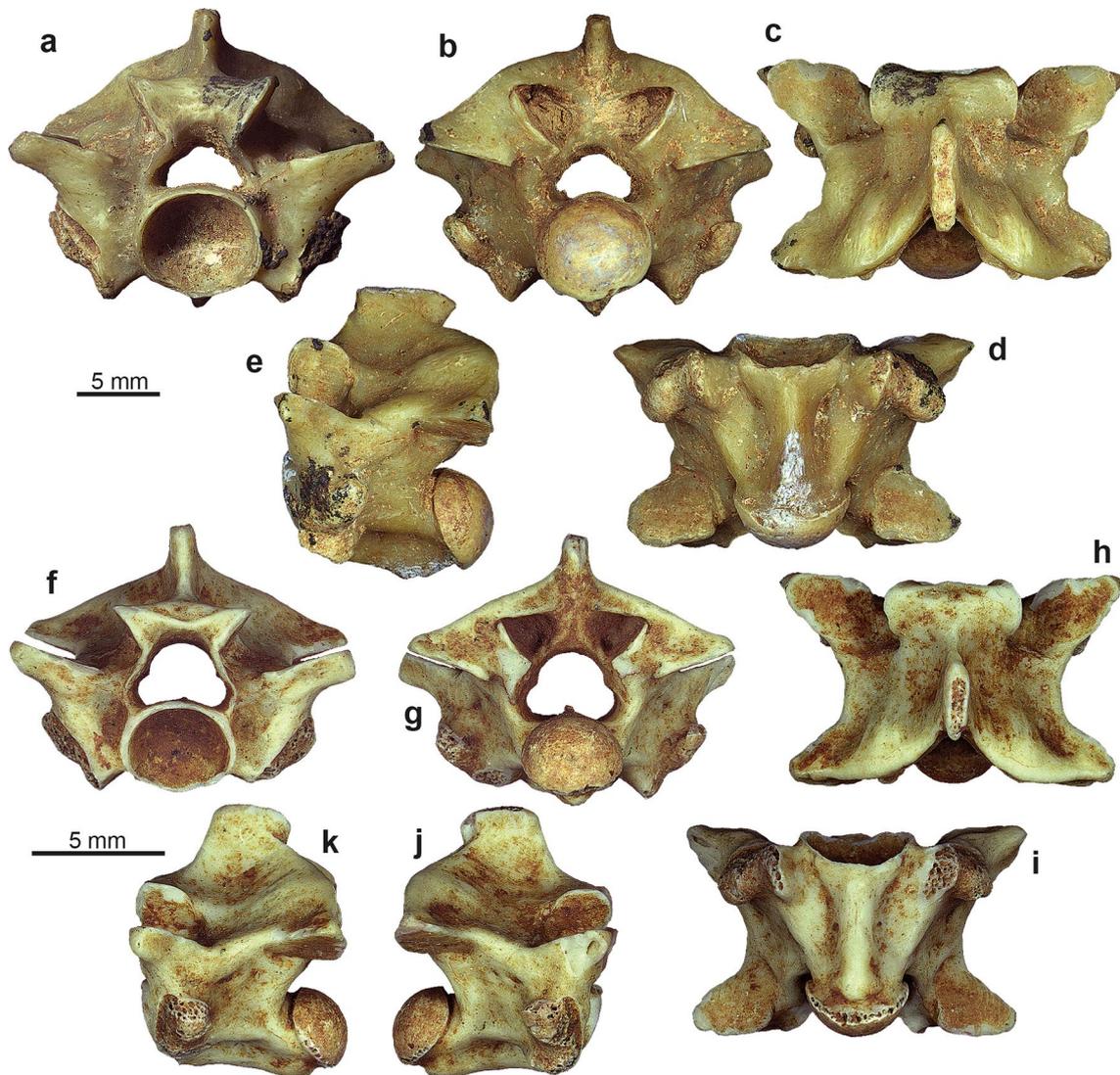


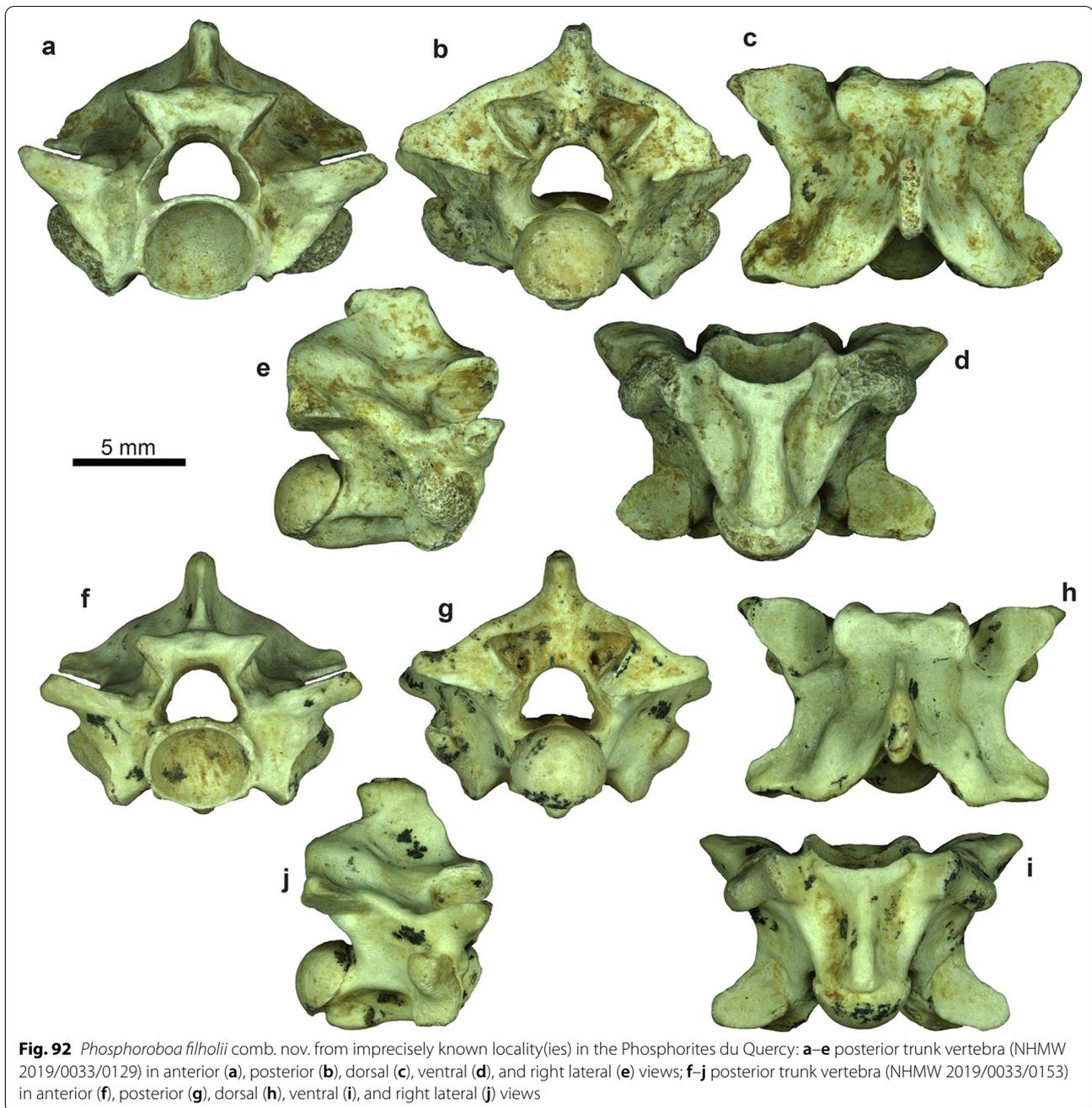
Fig. 91 *Phosphoroboa filholii* comb. nov. from imprecisely known locality(ies) in the Phosphorites du Quercy: **a–e** posterior trunk vertebra (NHMW 2019/0033/0002) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–k** posterior trunk vertebra (NHMW 2019/0033/0127) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), right lateral (**j**) and left lateral (**k**) views

totally circular to slightly elliptical. The paradiapophyses are massive, sometimes extending slightly more laterally than in the holotype (e.g., NHMW 2019/0033/0035). Paracotylar foramina are present in only two specimens [NHMW 2019/0033/0073; YPM-VPPU 30393 (Fig. 93a)], a feature that apparently is rather rare here as in the preceding regions.

In the posterior-most trunk vertebrae, as exemplified by YPM-VPPU 30395, a hypapophysis is present instead of a haemal keel (Fig. 93k–o), a feature known in other booids as well, including species of *Bavarioboa* (see figs. in Szyndlar and Rage, 2003). The hypapophysis there is relatively prominent and is ventrally exposed across a large portion of the centrum. Other notable features of

the posterior-most trunk vertebra YPM-VPPU 30395 are the vaulted neural arch (in comparison with the depressed ones in the preceding posterior trunk vertebrae), as well as the thick neural spine (Fig. 93k–m). Such increase in neural arch vaulting at the posterior-most part of the vertebral column, continuing into the cloacal vertebrae, seems to be relatively widely distributed among Constrictores, both extant and extinct (e.g., *Bavarioboa* spp., *Calamagras weigeli* Holman, 1972, and *Ogmophis compactus* Lambe, 1908) (see Smith, 2013; Szyndlar & Rage, 2003).

Growth rings in the postzygapophyseal articular facets are observed in few well-preserved specimens [e.g., NHMW 2019/0033/0043; NHMW 2019/0033/0122



(Fig. 86h); NHMW 2019/0033/0124; NHMW 2019/0033/0127 (Fig. 91h)].

Cloacal and caudal vertebrae are available for this species (Figs. 94, 95). Anterior cloacal vertebrae (i.e. UM ECC 3095) have a short hypapophysis instead of haemal keel (Fig. 95a–e), a feature that is present also in other fossil and extant constrictors [e.g., *Bavarioboa* spp. (Szyndlar & Rage, 2003) and *Ungaliophiinae* (Smith, 2013)]. The prezygapophyseal articular surfaces are nearly horizontal. The zygosphenal roof is flat and much

wider than the cotyle. The neural spine is shorter than on posterior trunk vertebrae. In posterior view, the neural arch rises more steeply from its lateral edge, but it then shows an inflection toward the medial so that, apart from the neural spine, it is nearly horizontal around the midline. The dorsal branch of the lymphapophysis extends laterally and slightly ventrally at first, turning then downward.

Proximal caudal vertebrae are similar to the cloacal vertebrae in many respects (i.e. UM ECC 3097; Fig. 96a–e).

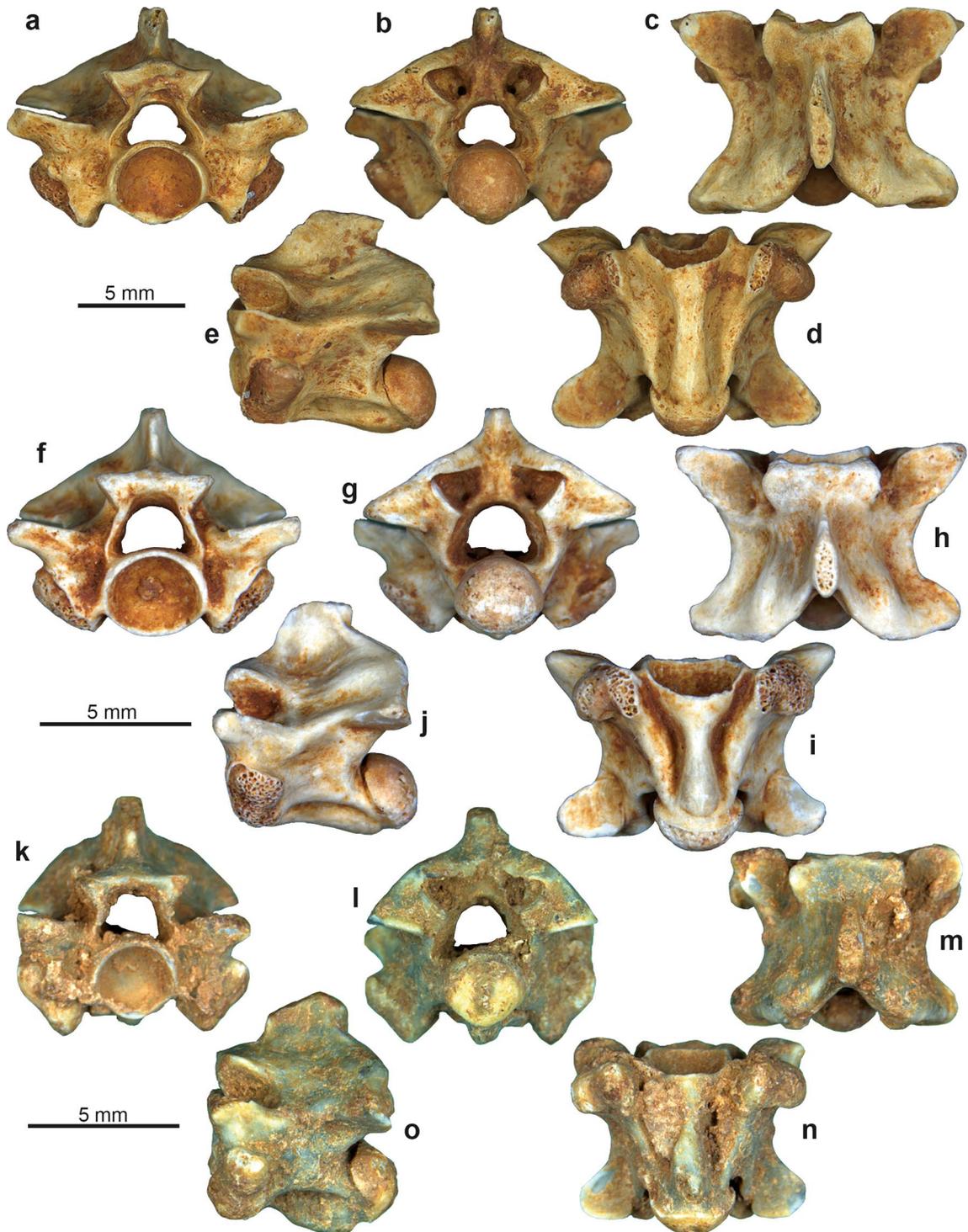
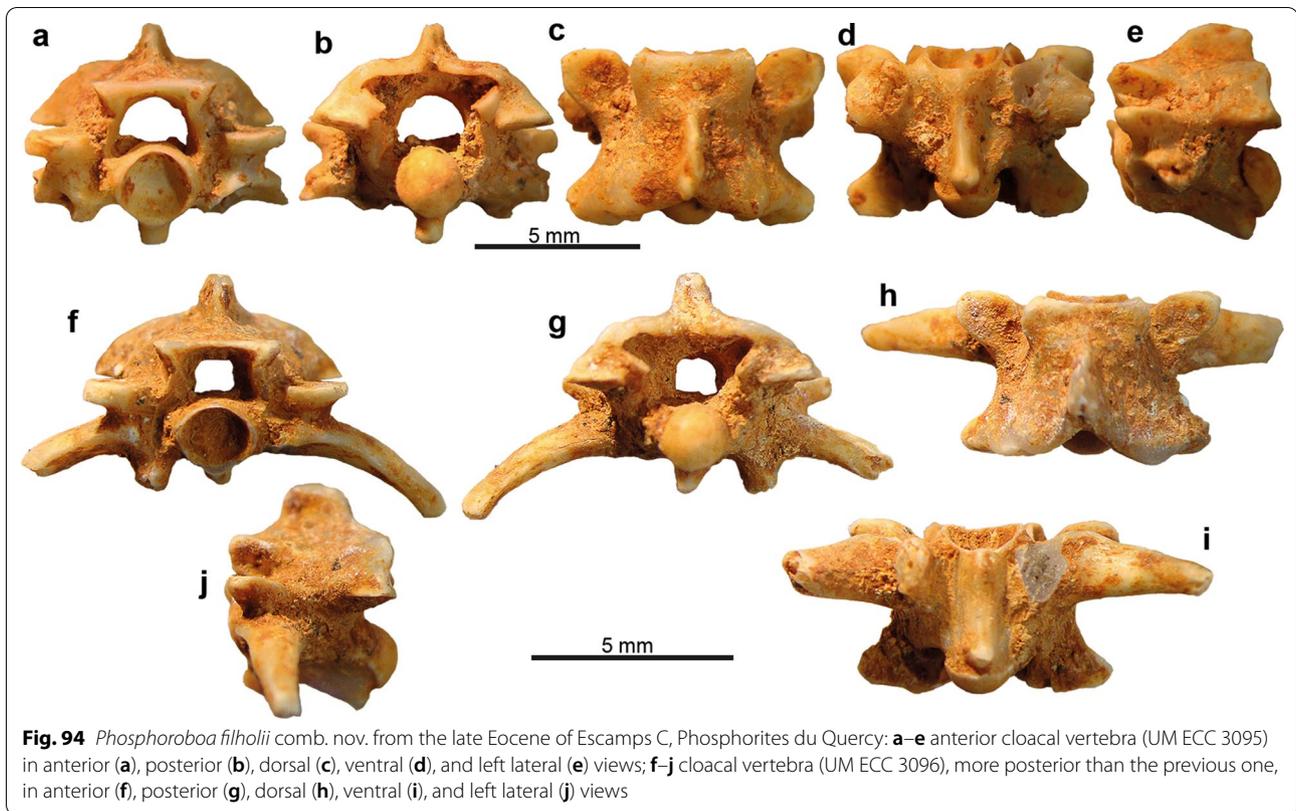


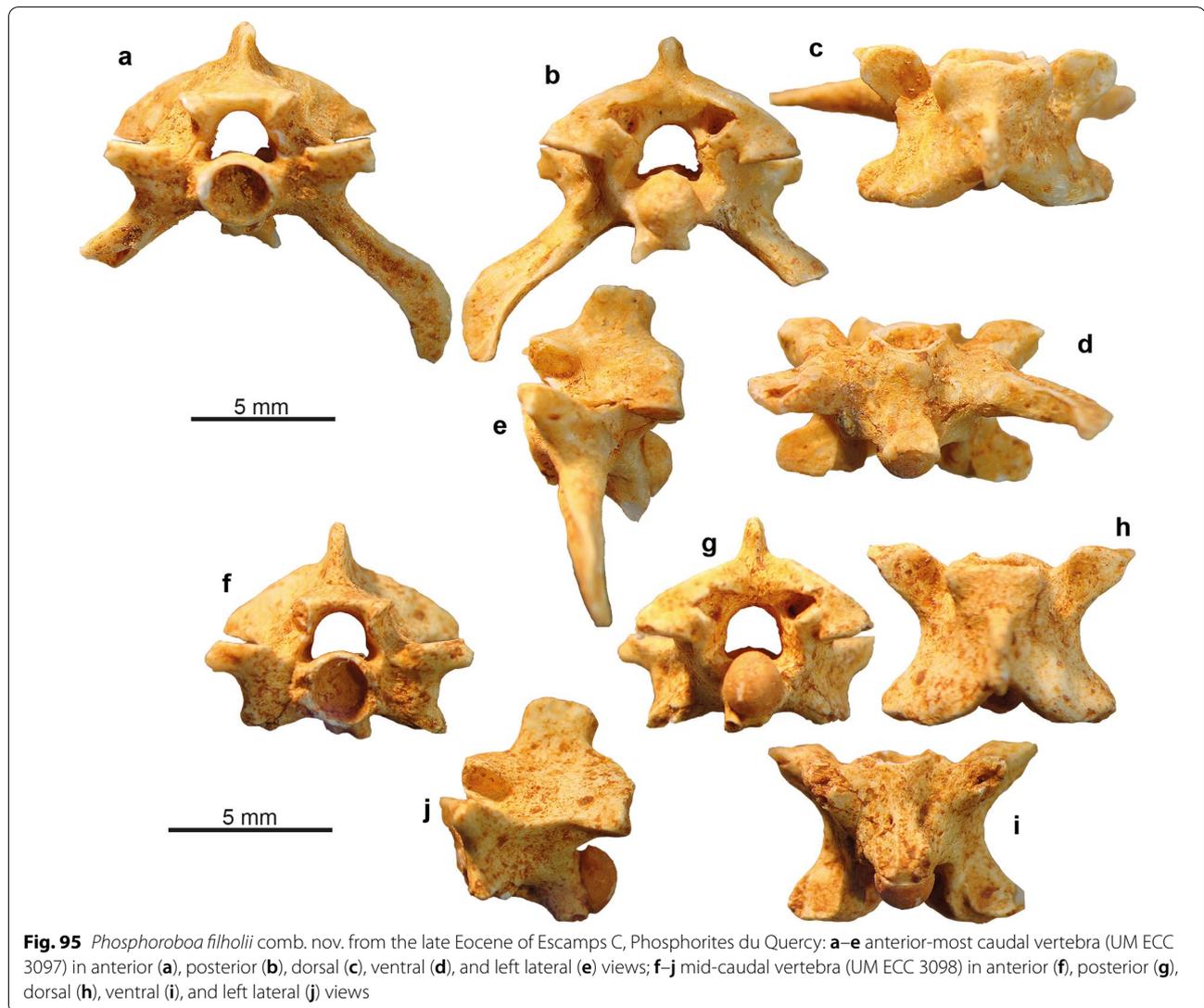
Fig. 93 *Phosphoroboa filholii* comb. nov. from imprecisely known locality(ies) in the Phosphorites du Quercy: **a–e** posterior trunk vertebra (YPM-VPPU 30393) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f–j** posterior trunk vertebra (YPM-VPPU 30394) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and left lateral (**j**) views; **k–o** posterior-most trunk vertebra (YPM-VPPU 30395) in anterior (**k**), posterior (**l**), dorsal (**m**), ventral (**n**), and left lateral (**o**) views



However, the neural arch is depressed and more like the holotype (without the steep sides and inflection point). The cotyle and condyle are more nearly rounded. The pleurapophysis extends straight ventrolaterally, curving sharply ventrally near its distal end. In lateral view, the pleurapophysis tapers continuously, but in anterior and posterior views it is seen to expand in width at the point where it turns ventrally; the anterior face shows an elongate groove that follows the curvature of the process, whereas the posterior face is flat. The hypapophysis is missing, replaced by anteroposteriorly short, paired hemapophyses present at the posterior-most end of the centrum. Anteriorly on the ventral surface of the centrum, just behind the edge of the cotyle is a peculiar median tubercle with a steeper anterior than posterior margin, reminiscent of the posterior end of a haemal keel on trunk vertebrae. These vertebrae are anteroposteriorly very short.

Middle caudal vertebrae are slightly longer, similar in proportion to mid-trunk vertebrae (i.e. UM ECC 3098; Fig. 96f–j). The neural spine is slightly taller, and the cotyle and condyle have the shape of compressed (dorsoventrally elongate) ovals. Just behind the cotyle, the centrum evinces slight, paired depressions, leading to the development of a structure like a haemal keel. Otherwise, they are similar to more proximal caudals.

Description of new cranial material from Quercy (Figs. 96, 97, 98, 99, 100, 101, 102 and 103): In the NHMW sample there are three marginal jaw elements, of which two can be referred to *Phosphoroboa filholii* comb. nov.: a left maxilla with several preserved teeth (NHMW 2019/0020/0001) (Fig. 96) and a right dentary with few preserved remains of teeth (NHMW 2019/0020/0002) (Fig. 99). Furthermore, another cranial element is in the NHMUK sample: a dentary with several preserved teeth (NHMUK PV R 3489) from an imprecise locality near Mouillac, Phosphorites du Quercy (Fig. 100) is assigned to the same taxon, based on its similarity to the NHMW dentary. Based on the same data-set used above in *Palaeopython cadurcensis* for studying the size relationship between CL of mid-trunk vertebrae and dentary tooth row length, we calculate that for an average-sized individual in the NHMW sample (CL = 6.9 mm) the expected dentary size is 25.6 mm, only 16% larger than NHMW 2019/0020/0002 (Fig. 87). NHMW 2019/0020/0001 is 10% larger (based on the average length of three tooth loci in the middle of the jaw). Only vertebrae of *Phosphoroboa filholii* comb. nov. have been identified in the NHMW sample that are even close to those sizes (Fig. 87). And *Phosphoroboa filholii* comb. nov. is by far the most abundant species of that sample (Fig. 87). For all these reasons we consider it probable that these marginal



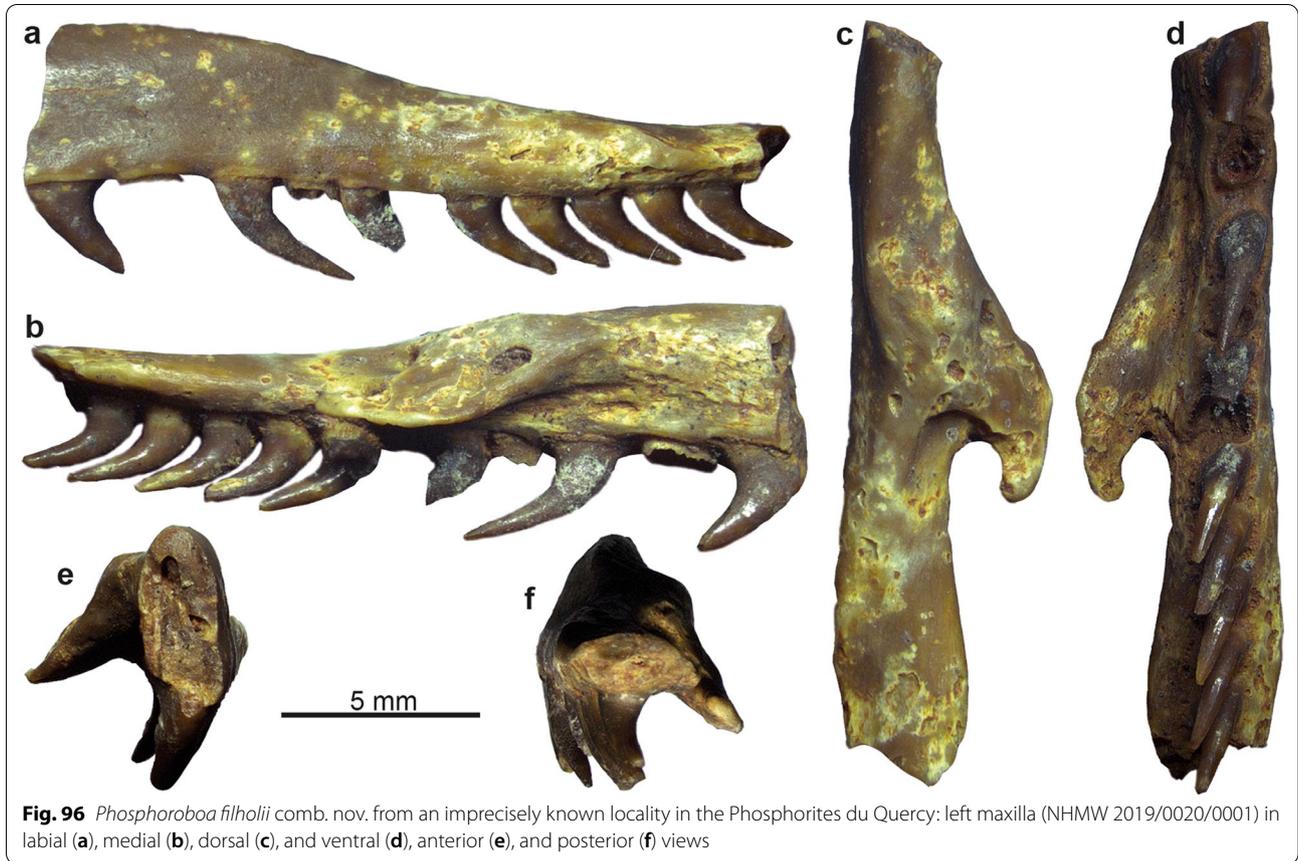
jaw bones pertain to that species. Another dentary from Quercy, YPM-VPPU 30397 (Fig. 98), can be referred here as well on the basis of similar size and abundance considerations (Fig. 88). Furthermore, three skull elements [a dentary (UM ECA 2544; Fig. 97), a pterygoid (UM ECC 2501; Fig. 101), and a parietal (UM ECA 2543; Fig. 103)] from Escamps are referred to this taxon. A fragmentary pterygoid (NHMW 2019/0020/0004) is also present in the NHMW collection (Fig. 102).

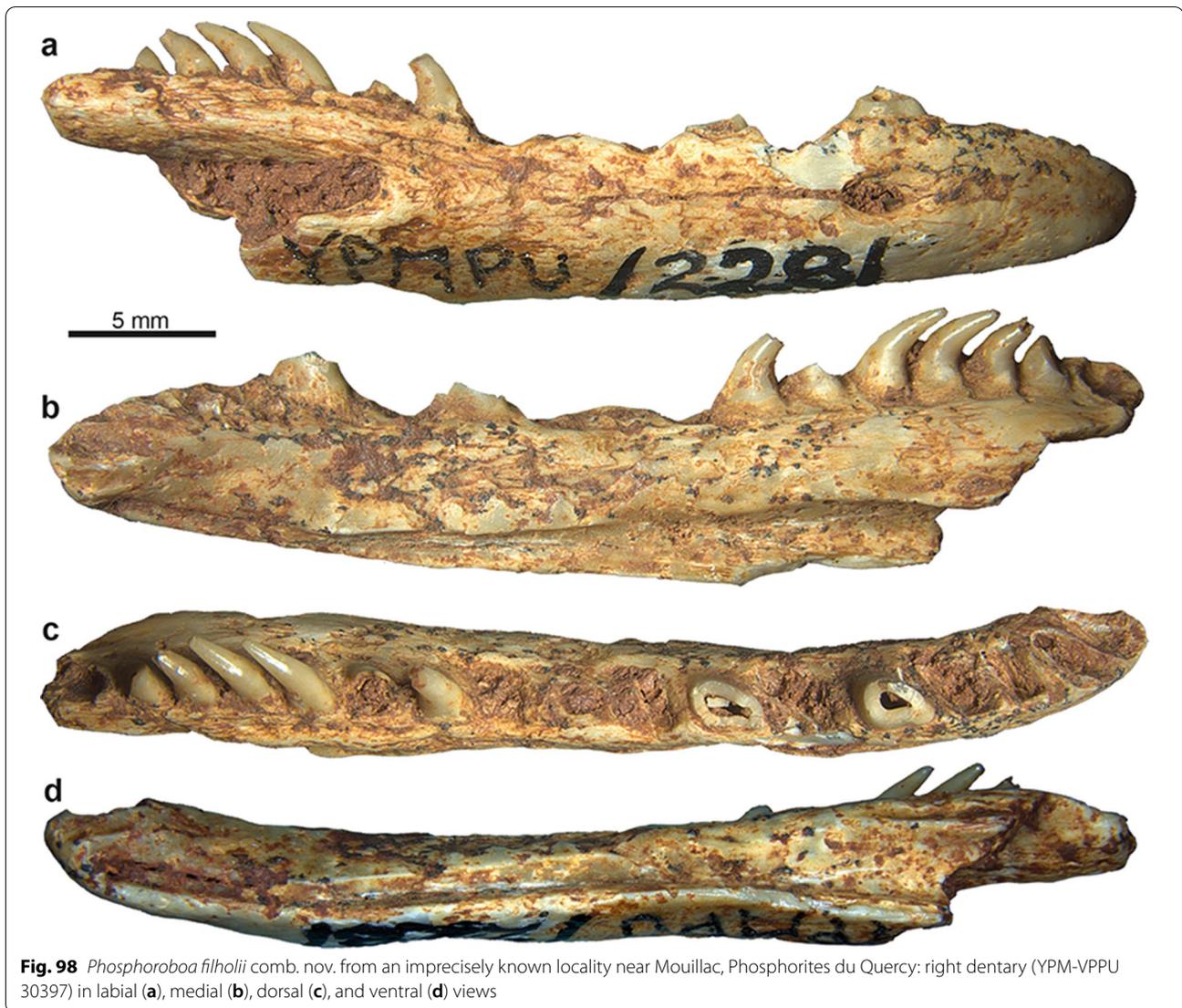
While we refer all these specimens to *Phosphoroboa filholii* comb. nov. for reasons given also below, we note that there are slight, but consistent, morphological differences in the samples. In particular, as described below, the Escamps and YPM-VPPU dentaries (Figs. 97, 98) share certain features (morphotype 1), and the NHMW and NHMUK dentaries (Figs. 99, 100) share others (morphotype 2). Similarly, the pterygoid from Escamps

(Fig. 101) is slightly different from the NHMW pterygoid (Fig. 102).

The only maxilla, NHMW 2019/0020/0001, retains 12 tooth positions (Fig. 96). The teeth are strongly distally reclined, even more so than in the dentary YPM-VPPU 30397. Tooth size decreases gradually but consistently from front to back. There is a strongly posteriorly inclined, parallel-sided palatine process with a hook-shaped distal tip, as in booids. On the anterodorsal surface of the base of the process is a large foramen, and probably a second foramen is present above the tooth row posterior to the level of the palatine process. In contrast to *Palaeopython cadurcensis* and *Messelopython freyi*, the lateral margin of the bone is straight.

The dentaries are similar in being relatively deep with a single, large mental foramen located beneath the 5th tooth from the front (Figs. 97, 98, 99 and 100).





The foramen is oval in lateral aspect except in NHMW 2019/0020/0002, where it is circular (Fig. 99a). The shape of the subdental shelf is almost identical, as far as they are preserved. In YPM-VPPU 30397 there are 17 preserved tooth positions, and possibly one or two are missing from the posterior end (Fig. 98). In NHMW 2019/0020/0002 the bone is ventrally bowed (Fig. 99), unlike in any other specimen. There are also 17 preserved tooth positions in this specimen; probably one or more teeth are missing in this specimen as well. In UM ECA 2544 there are 18 preserved tooth positions (Fig. 97). Given that the ventral margin of that dentary is incomplete, it appears that the posteroventral and posterodorsal processes were more similar in length than in *Palaeopython cadurcensis*.

There are two consistent differences between dentary morphotypes 1 (UM ECA 2544 and YPM-VPPU 30397) and 2 (NHMW 2019/0020/0002 and NHMUK PV R

3489). First, the surangular notch is much deeper in morphotype 1, more similar to other constrictors. In particular, in UM ECA 2544 and YPM-VPPU 30397 (Figs. 97, 98) the notch extends as far as the 12th tooth and well anterior of the splenial facet on the posteroventral prominence (sensu Scanlon 2001). In contrast, in NHMW 2019/0020/0002 (Fig. 99) the surangular notch terminates beneath the 17th tooth and at the anterior end of the posteroventral prominence; in NHMUK PV R 3489 (Fig. 100), the surangular notch must terminate at a level at or posterior to that in NHMW 2019/0020/0002. This reduced surangular notch appears to be a derived condition. Second, in morphotype 2 (NHMW 2019/0020/0002 and NHMUK PV R 3489) the posterior end of the dentary shows a lateral bulge that is absent in morphotype 1 (UM ECA 2544 and YPM-VPPU 30397).



Fig. 99 *Phosphoroboa filholii* comb. nov. from imprecisely known localities in the Phosphorites du Quercy: right dentary (NHMW 2019/0020/0002) in labial (a), medial (b), dorsal (c), and ventral (d) views

The most complete pterygoid is UM ECC 2501, which lacks much of the quadrate ramus (Fig. 101). The anterior end is wedge-shaped, with a small medial projection just beyond the tooth row. The palatine articulated on the medial and lateral side of this end. On the ventromedial side of the pterygoid, just below the palatine articulation, is a medial process. Such a process has been noted for booids (Rage, 1974); in particular, we find it to be present in *Boa* spp., *Chilabothrus angulifer* (Bibron, 1840 in Ramón de la Sagra, 1838–1843) (SMF-PE 61), and *Sanzinia madagascariensis* (Duméril & Bibron, 1844) [SMF-PH 56], but not in *Corallus caninus* (Linnaeus, 1758) (SMF-PH 74), *Epicrates cenchria* (SMF-PH 26), *Eunectes notaeus* Cope, 1862 (SMF-PH 60), *Chilabothrus striatus* (Digimorph), or *Candoia* spp. (Digimorph). Such a process is not known in Pythonoidea or in *Eoconstrictor* (see above). The ectopterygoid articulation is a lateral concavity, taller posteriorly than anteriorly. It is not set in a prominence, unlike in *Eoconstrictor* (see above). As in *Eoconstrictor* and many booids and pythonids, there is a medial flange at the basiptyergoid articulation that appears to rotate into a dorsal keel, although this is incompletely preserved.

NHMW 2019/0020/0004 is the anterior tip of a left pterygoid (Fig. 102). Only the anterior-most end of the

pterygoid, the palatine articulation, is preserved in this specimen. It is more robust than UM ECC 2501, and it does not have a distinct anteromedial process, only a low prominence in the same position. It contains eight tooth spaces with five partial teeth. These are relatively small and do not appear to change in size from anterior to posterior. The palatine facet is extensive on the dorsal surface, running as far as the level of the 7th tooth. It is elaborated by a small wedge-shaped facet on the medial side at the anterior end. There is strong, longitudinal dorsal keel extending from the anterior end to the level of the 3rd tooth, which would have inserted in a deep cleft at the posterior end of the palatine.

The parietal UM ECA 2543, which we refer to *Phosphoroboa filholii* comb. nov. on the basis of size and abundance (see below), is the sole known such snake element in the Phosphorites du Quercy (Fig. 103). The specimen is nearly complete. In dorsal view, it is nearly T-shaped, with strong postorbital processes (Fig. 103a). The frontoparietal suture is relatively narrow, only one-third the width of the bone, and V-shaped, with a much sharper midline notch than in *Eoconstrictor*. The swellings for the cerebral hemispheres are present, but not very prominent. The dorsomedian keel extends along the entire preserved length of the bone, up to the frontoparietal suture.

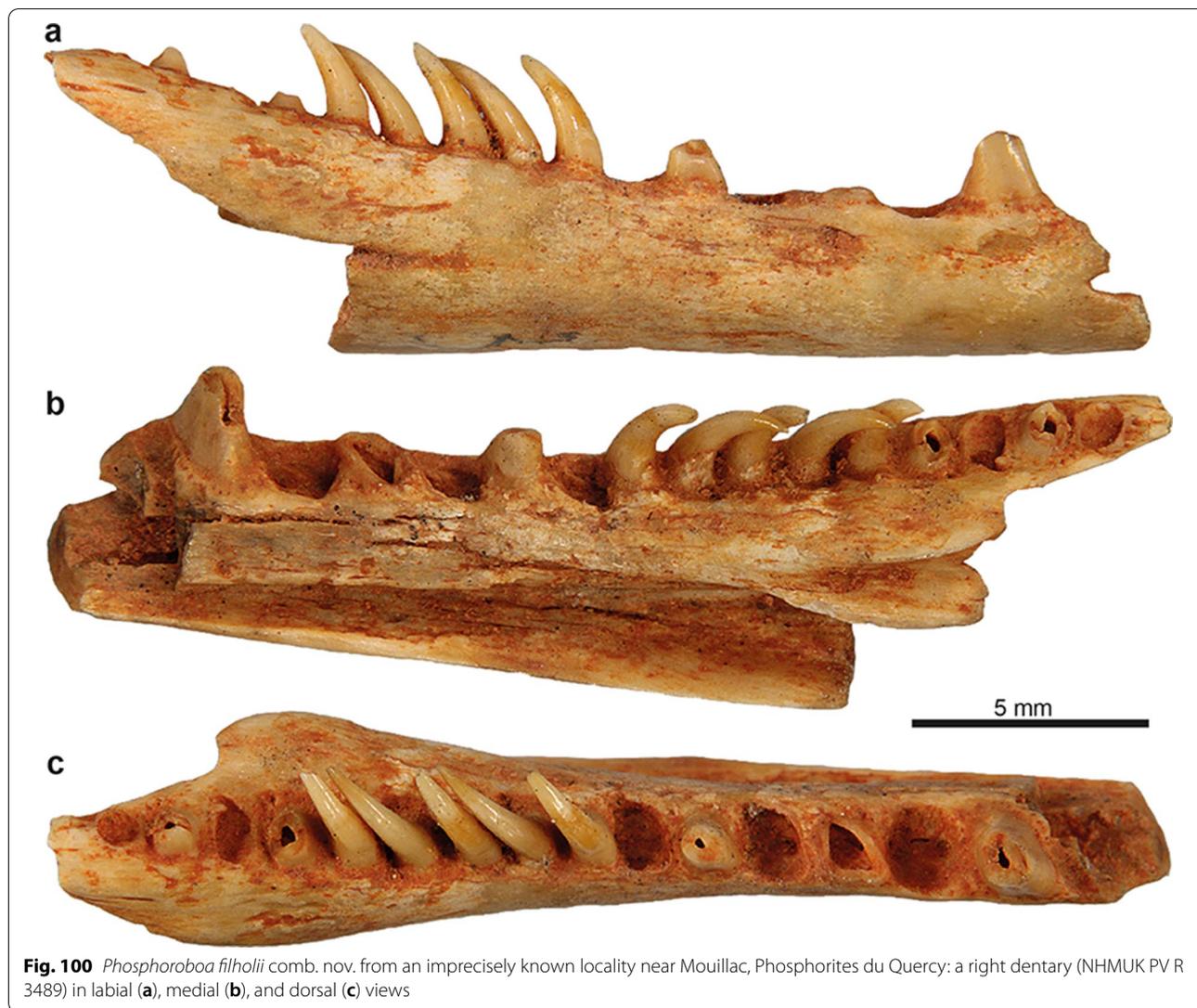


Fig. 100 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality near Mouillac, Phosphorites du Quercy: a right dentary (NHMUK PV R 3489) in labial (a), medial (b), and dorsal (c) views

Posterolateral processes appear to be much weaker than in *Eoconstrictor*, assuming they are reasonably complete. UM ECA 2543 preserves in ventral view the articulations with the chondrocranium (Fig. 103b). The descending flanges that embraced the parabasisphenoid rostrum approach one another closely anteriorly and diverge somewhat posteriorly. Two bilateral pairs of projections are present here, one medially at the trabeculae, and one laterally that bounded the optic foramen. The latter structure deeply notches the parietal.

Justification on the referral of the cranial material from Escamps: The late Eocene (MP 19) fossil sites of Escamps in the Phosphorites du Quercy have yielded a diverse squamate assemblage, consisting of several taxa of lizards and snakes, as presented in the faunal lists of Bonis et al. (1973) and Crochet et al. (1981). However, despite the number of snake taxa presented in those two

preliminary faunal lists, descriptions and figures of snake remains from Escamps have so far only been provided by Zittel (1887–1890) and Rage (1974).

Indeed, Zittel (1887–1890) figured a vertebra that he assigned to *Palaeopython cadurcensis*, a specimen which we here refer to *Palaeopython* cf. *cadurcensis* (see that entry above). Under the framework of their new, stratigraphically well-constrained collections in the Phosphorites du Quercy, Bonis et al. (1973) correlated Escamps with other nearby localities and identified three fossiliferous sites, namely Escamps A, B, C. Accordingly, specimens collected previously to that time from the area of Escamps, such as Zittel's (1887–1890) vertebra, cannot be precisely attributed to any of the three known sites of Escamps and it can even be the case that it originated from some nearby, slightly contemporary, site (see also "Remarks" below). Bonis et al. (1973) mentioned in their



Fig. 101 *Phosphoroboa filholii* comb. nov. from the late Eocene of Escamps C, Phosphorites du Quercy: left pterygoid (UM ECC 2501) in ventral (a), medial (b), and ventrolabial (c) views. A drawing of this specimen was originally figured by Rage (1974:fig. 3C)

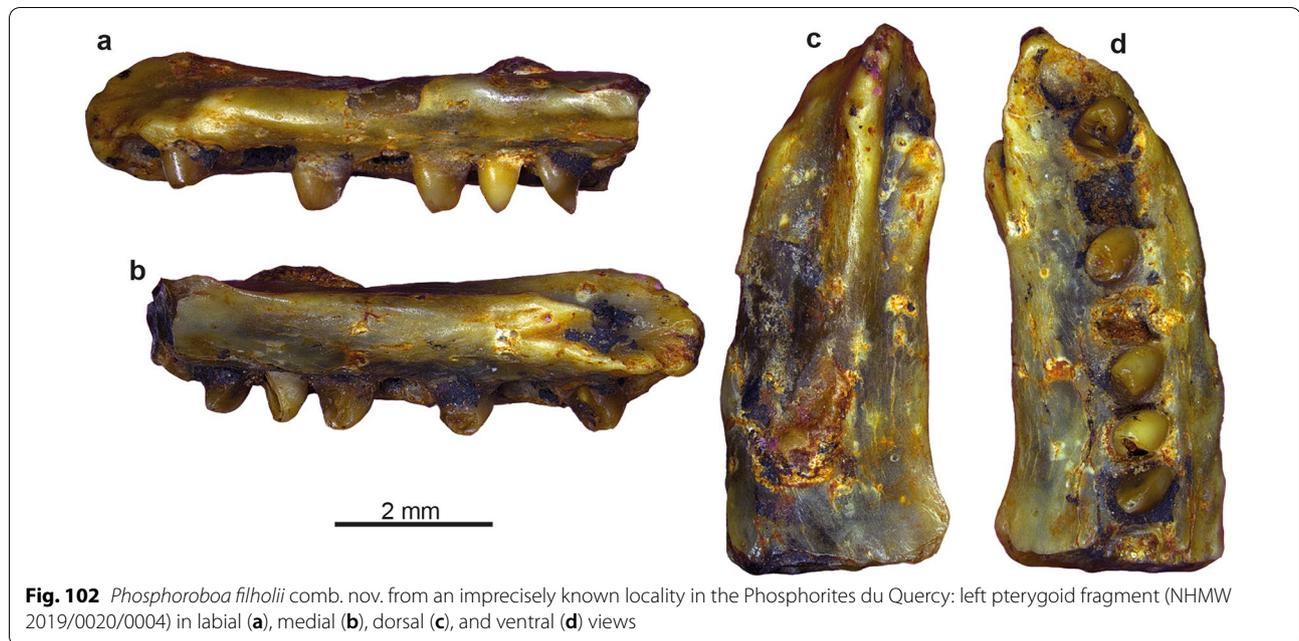


Fig. 102 *Phosphoroboa filholii* comb. nov. from an imprecisely known locality in the Phosphorites du Quercy: left pterygoid fragment (NHMW 2019/0020/0004) in labial (a), medial (b), dorsal (c), and ventral (d) views

list four different snake taxa from Escamps, for which they used the informal denominations “Boidae A”, “B”, “C”, and “D”, without any kind of description or figure. The following year, Rage (1974) described vertebral and cranial material from Escamps A and C, which he referred to *Palaeopython filholii*. He additionally mentioned that ribs and a fragment of a large dentary from Escamps (none of them figured) matched in size to *Palaeopython cadurcensis* and could pertain to that species. Crochet et al. (1981) provided an updated faunal list of snakes from Escamps, recognizing the following ten taxa: *Coniophis* sp., *Eoanilius europae*, *Palaeopython filholii* (sic), *Dunnophis cadurcensis*, *Cadurcobia insolita*, “Boidae C”, “D”, “K”, “L”, and “M”. Again, none of these was accompanied by any kind of description or figure.

In an attempt to properly refer the available cranial elements from Escamps described herein, it is essential to realize how many and which snake taxa were present in the locality. Of course, this is ultimately a difficult task, considering the total absence of descriptions or figures, and the nature and number of specimens of each taxon, particularly for forms that were not assigned to the genus level, such as all these enigmatic “Boidae C”, “D”, etc. (on these lettered taxa, see Smith and Georgalis, in press). It is first apparent that the Escamps faunal list of Crochet et al. (1981) is the updated version of the even more preliminary one of Bonis et al. (1973), following the intervening studies of Jean-Claude Rage, who participated as coauthor in both these 1973 and 1981 papers and who also in the meantime published significant results of his studies on Quercy snakes (Rage, 1974, 1978). As a result, several of the “lettered Boidae” of Bonis et al. (1973) were

more precisely assigned in Crochet et al. (1981) and the total number of distinct taxa was also reconsidered.

Of these 10 taxa from Escamps listed in Crochet et al. (1981), *Phosphoroboa filholii* comb. nov. is by far the most well documented and the only one described and figured by Rage (1974) from that locality. The same species was relatively abundant, as Rage (1974:284) explicitly stated “Escamps a fourni de nombreux éléments (vertèbres, côtes, un ptérygoïde gauche) appartenant à *P. filholii* (sic)”. The referral of the pterygoid UM ECC 2501 to *Phosphoroboa filholii* comb. nov. by Rage (1974) was made by means of size comparison, as he stated that all other “boids” (i.e. Constrictores in the modern sense) from Escamps were significantly smaller (“sa taille ne laisse aucun doute sur son appartenance spécifique, les autres Boidae du même gisement étant beaucoup plus petits que *P. filholii* (sic)”; Rage, 1974:285–286). Indeed, *Coniophis* sp., *Eoanilius europae*, *Dunnophis cadurcensis*, and *Cadurcobia insolita* are all tiny snakes, with centrum lengths not surpassing 3 mm. Boidae M was later subsequently described by Rage (1988b) as *Platyspondylia sudrei*, and it is indeed considerably smaller than *Phosphoroboa filholii* comb. nov. Our preliminary investigation of material of Boidae D, K, and L, confirms that they too are tiny snakes. For the remaining Boidae C, there is no information, as it has never been formally described, but we accept the view of Rage (1974) that this should also be smaller than *Phosphoroboa filholii* comb. nov. Finally, as noted above, the largest snake in Escamps should be a similar form to *Palaeopython cadurcensis* [though not mentioned in Crochet et al. (1981)], judging from the mention of Rage (1974) and perhaps the vertebra figured by Zittel (1887–1890).

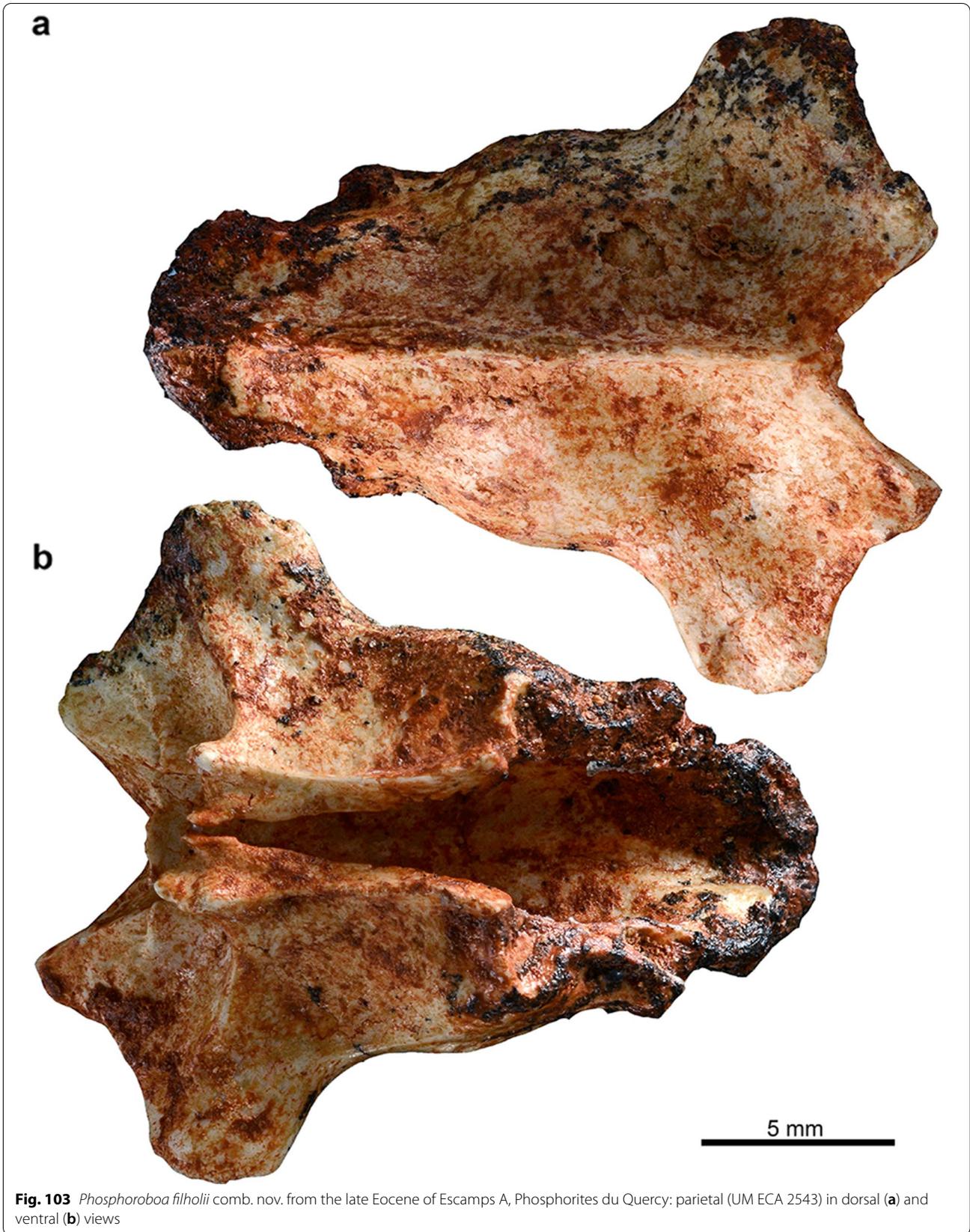


Fig. 103 *Phosphoroboa filholii* comb. nov. from the late Eocene of Escamps A, Phosphorites du Quercy: parietal (UM ECA 2543) in dorsal (**a**) and ventral (**b**) views

Therefore, on the basis of size and relative abundance, the parietal UM ECA 2543 and the dentary UM ECA 2544 from Escamps A, and the pterygoid UM ECC 2501 from Escamps C, can all be referred to *Phosphoroboa filholii* comb. nov. The identification of these three cranial elements enables a better understanding of the relationships of this taxon within Constrictores, suggesting affinities with Booidea. In addition, they can further provide direct means of comparisons with other isolated skull elements found in imprecisely known localities in the Phosphorites du Quercy.

The populations of Escamps and YPM-PU (if the latter are indeed a single population) share the same dentary morphology (dentary morphotype 1). As both populations also preserve posterior trunk vertebrae which are nearly identical to the holotype of *Phosphoroboa filholii* comb. nov., they are best viewed as representing the same species. Note also that all YPM-PU specimens originate from the area around Mouillac, which is not geographically far from Escamps. The NHMW and perhaps NHMUK samples are slightly different in dentary (i.e. dentary morphotype 2) and pterygoid morphology, and it is not yet clear what these differences mean. The greater robustness of the NHMW dentary and pterygoid specimens could represent sexual dimorphism, but the difference in the depth of the surangular notch of the dentary raises the prospect that they could represent different taxa.

Remarks: Originally established as *Palaeopython filholii* by Rochebrune (1880) upon a single trunk vertebra (MNHN.F QU16322) from the Phosphorites du Quercy, the same author later referred to this species three articulated vertebrae (MNHN.F QU16323), as well as the syntype (now paralectotype) maxilla (MNHN.F QU16321) of *Python cadurcensis* that was previously described by Filhol (1877a, 1877b, 1877c) (Rochebrune, 1884). Following his suggested synonymy of *Palaeopython* with *Paleryx*, Lydekker (1888a) placed *Palaeopython cadurcensis* into the latter genus, thereby also moving *Palaeopython filholii* to *Paleryx*. In the very same year, the same author went further and considered *Palaeopython filholii* as a probable junior synonym of the British *Paleryx depressus* (Lydekker, 1888b). Rage (1974) concluded that the referred specimens of Rochebrune (1884), i.e. the three articulated vertebrae MNHN.F QU16323 and the maxilla MNHN.F QU16321, cannot be assigned to the same species as the holotype vertebra of *Palaeopython filholii* but instead were more reminiscent of *Palaeopython cadurcensis*. He further described additional vertebrae and the pterygoid UM ECC 2501 from Escamps, which he referred to *Palaeopython filholii* (Rage, 1974).

A confusion arises when one deals with the plates and plate labels of Rochebrune's (1880, 1884) papers. Rochebrune (1880), in his plate XII, depicted a vertebra

(holotype, MNHN.F QU16322) in lateral, anterior, and dorsal views in figs. 5^a, 5^b, and 5^c, respectively. Rochebrune (1884), in his plate II, figured in addition to a maxilla (currently MNHN.F QU16321 [paralectotype of *Palaeopython cadurcensis*]; his fig. 4) and three articulated trunk vertebrae (currently MNHN.F QU16323; his fig. 4^a) also a single vertebra in dorsal and anterior views, respectively, labelled as “Les mêmes vertèbres grossies” (his fig. 4^b and 4^c). Rage (1974) suggested that figs. 4^b and 4^c from Rochebrune (1884) cannot be the same specimen as the three articulated vertebrae of fig. 4^a and instead suggested that this specimen was in fact the holotype MNHN.F QU16322 that was figured in Rochebrune (1880), despite important differences between the two lithographic illustrations, in which case the more accurate would be the one shown in Rochebrune (1884). We agree with Rage's (1974) opinion, although we must highlight that our first-hand observation of the holotype vertebra MNHN.F QU16322, reveals that it is still different from both images of Rochebrune (1880, 1884). Nevertheless, such inaccuracies in the lithographs of nineteenth century publications were not infrequent and they have been noted for other fossil snake taxa as well (see Georgalis et al., 2016 for a discussion).

In light of the abundant new material described herein, we identified several important features of this species. The available vertebrae of *Phosphoroboa filholii* comb. nov. show a general resemblance with *Paleryx rhombifer*, especially in terms of size, the ratio of zygosphene width to cotyle width in mid-trunk vertebrae (<1.2 in both taxa), the ratio of neural spine length to centrum length (<0.5 in both taxa), the relatively depressed neural arch of posterior trunk vertebrae (vaulting ratio <0.35 in both taxa), and the generally lower neural spine (especially on posterior trunk vertebrae). Nevertheless, there are still important vertebral differences among *Phosphoroboa filholii* comb. nov. and *Paleryx rhombifer*, namely in the width of the zygosphene, the depression of the neural arch on posterior trunk vertebrae and the angulation at the posterior margin of the neural arch (especially on posterior trunk vertebrae).

In any case, it is the new cranial material assigned to *Phosphoroboa filholii* comb. nov. which provides a valuable insight on the affinities of this species. So far, the only cranial element referred to *Phosphoroboa filholii* comb. nov. was the pterygoid (UM ECC 2501) from the Escamps C, described and figured by Rage (1974)—the paralectotype maxilla (MNHN.F QU16321) of *Palaeopython cadurcensis* that was referred by Rochebrune (1884) to *Phosphoroboa filholii* comb. nov. does not pertain to this species (Rage, 1974) and is aptly indeed referred to *Palaeopython cadurcensis* (see “Remarks” in the entry of *Palaeopython cadurcensis* above). Our redescription of the pterygoid UM ECC 2501 from Escamps C confirms

the suggestion of Rage (1974) about affinities of *Phosphoroboa filholii* comb. nov. with Booidea (see description of that specimen above). The other cranial elements from Escamps are also in concordance with booid affinities of this species. As such, despite the superficial vertebral similarity, any congeneric relationships of *Phosphoroboa filholii* comb. nov. with *Paleryx rhombifer* can be readily discarded, as the latter is a non-booid constrictor.

As is the case with other species established from the Phosphorites du Quercy during the nineteenth century, the exact type locality of *Phosphoroboa filholii* comb. nov. is not known with certainty. Nevertheless, as discussed also above, the holotype posterior trunk vertebra MNHN.F QU16322 shows a remarkable resemblance with posterior trunk vertebrae referred to the same species from the late Eocene (MP 19) of Escamps. Furthermore, certain lizard and snake fossils from the Phosphorites du Quercy, described during the late nineteenth century, are associated with the locality of Escamps (Zittel, 1887–1890), though it cannot be certain whether these were indeed recovered in the actual fossil locality of Escamps or some other nearby locality (see Georgalis, 2017). These being said, it could be the case that the holotype vertebra described by Rochebrune (1880) originated indeed from Escamps, or some nearby coeval (or at least relatively contemporary) late Eocene locality.

In any case, *Phosphoroboa filholii* comb. nov. is known with certainty only from the area of the Phosphorites du Quercy (see Table 3). Vertebral material from the late Eocene of mount Mormont, Switzerland, that was originally referred to *Paleryx* or *Python* sp. by Pictet et al. (1855–1857) but later referred to *Palaeopython filholii* by Rochebrune (1880), should be better currently treated as *Constrictores* indet., pending a comprehensive redescription of that Swiss material.

This taxon has suffered from a frequent variant spelling of its species epithet as “*filholi*” (Crochet et al., 1981; De Stefano, 1905; Kuhn, 1939b; Lydekker, 1888a, 1888b; Rage, 1974, 1978, 1984b; Rosselet, 1991; Zittel, 1887–1890), even by the same author that established it (Rochebrune, 1884). Nevertheless, it is rather straightforward from the original publication of Rochebrune (1880) that the correct spelling of the species epithet is “*filholii*” and as such, “*filholi*” has to be considered as a variant spelling (ICZN 1999:Article 58.14). And to make things even more complicated, other fossil squamates from the Phosphorites du Quercy that were named after Henri Filhol have in fact their species epithet as indeed spelled as “*filholi*” and not “*filholii*”, i.e. the “erycine” *Cadurceryx filholi*, the lacertid *Lacerta filholi* Augé, 1988, and the palaeowaranid *Palaeowaranus filholi* De Stefano, 1903. We consider that Article 33.3.1 of ICZN (1999) that mandates that “when an incorrect subsequent spelling is in prevailing usage and

is attributed to the publication of the original spelling, the subsequent spelling and attribution are to be preserved and the spelling is deemed to be a correct original spelling” does not need to be applied here, as the appearances of the taxon name in the literature are few, even if the variant spelling is proportionately common.

Constrictores indet. (large morphotype[s])

Figures 104, 105, 106, 107, 108, 109 and 110

Referred material discussed herein: Phosphorites du Quercy (imprecisely known locality) (Fig. 104): a right dentary (NHMW 2019/0020/0003) (Fig. 104). **Phosphorites du Quercy (imprecisely known locality near Mouillac) (Fig. 105):** a left palatine (YPM-VPPU 12,281) (Fig. 105). **Geiseltal (Figs. 106, 107, 108, 109 and 110):** a dentary fragment without teeth (GMH XXII-628-1965), several trunk vertebrae on matrix (GMH XXII-574-1965) and several articulated trunk vertebrae (GMH XXII-568-1965) from quarry XXII; a fragmentary right dentary with teeth (GMH XLI-310-1968), a dentary fragment (GMH XLI-90-1966), two fragmentary trunk vertebrae (GMH XLI-105-1966 and GMH XLI-182-1966), three articulated vertebrae (GMH XLI-59-1966), and one isolated rib (GMH XLI-314a-1968; Fig. 110) from quarry XLI; a partial skeleton with several trunk vertebrae and ribs, and a dentary (GMH XXXV-640-1970; Fig. 109a) and an isolated complete rib (GMH XXXV-256-1963) from quarry XXXV; an incomplete skeleton with many articulated vertebrae and ribs (GMH XXXVI-86-1962) from quarry XXXVI; a skeleton with several articulated vertebrae and ribs and an almost three dimensional skull (GMH LIX-3-1992) from quarry LIX; a skeleton with many articulated vertebrae and ribs and an almost three dimensional, damaged skull (GMH XXXVII-67-1964) from quarry XXXVII; several small trunk vertebrae (GMH XXXVIII-8-1964) from quarry XXXVIII; a skeleton with skull on a matrix [GMH Ce IV-5864–1933; originally figured by Kuhn (1939a:pls. II.2 and III.1); Fig. 106], several disarticulated trunk vertebrae on a matrix (GMH Ce IV-2967-1932), a portion of skeleton with fragmentary articulated vertebrae and remains of ribs (GMH Ce IV-2960-1933), a trunk vertebra on a matrix (GMH Ce IV-2925-1932), a string with three articulated trunk vertebrae plus many vertebral fragments (GMH Ce IV-2929-1933), fragmentary disarticulated vertebrae and ribs on a matrix (GMH Ce IV-5860-1933), fragmentary vertebrae and remains of ribs on a matrix (GMH Ce IV-5865-1933), and remains of articulated trunk vertebrae (GMH Ce IV-2971-1933) from quarry Cecilie IV; two strings of articulated trunk vertebrae and fragments of ribs (GMH Leo I-5866-1932; Fig. 109b) from quarry Leonhardt I; a fragmentary left maxilla with no preserved teeth [GMH

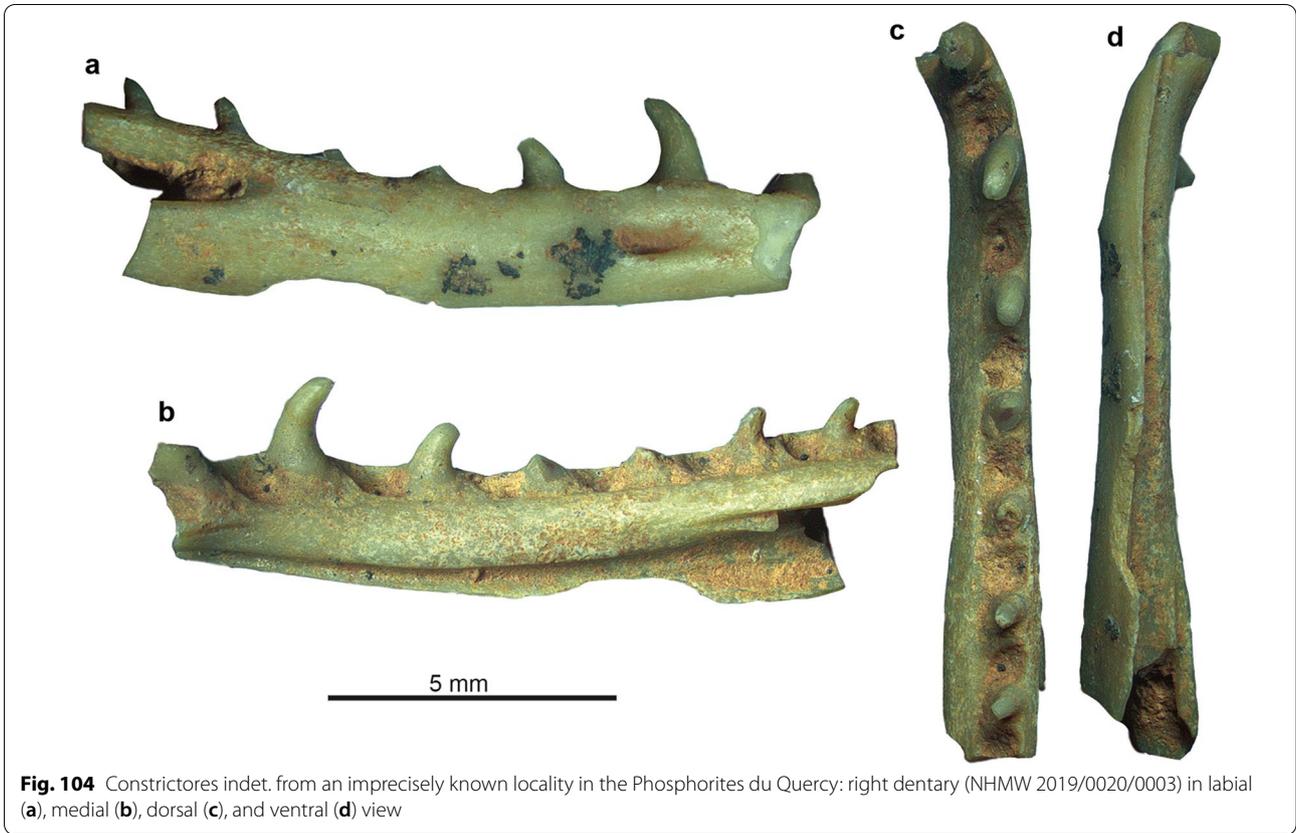


Fig. 104 *Constrictores* indet. from an imprecisely known locality in the Phosphorites du Quercy: right dentary (NHMW 2019/0020/0003) in labial (a), medial (b), dorsal (c), and ventral (d) view

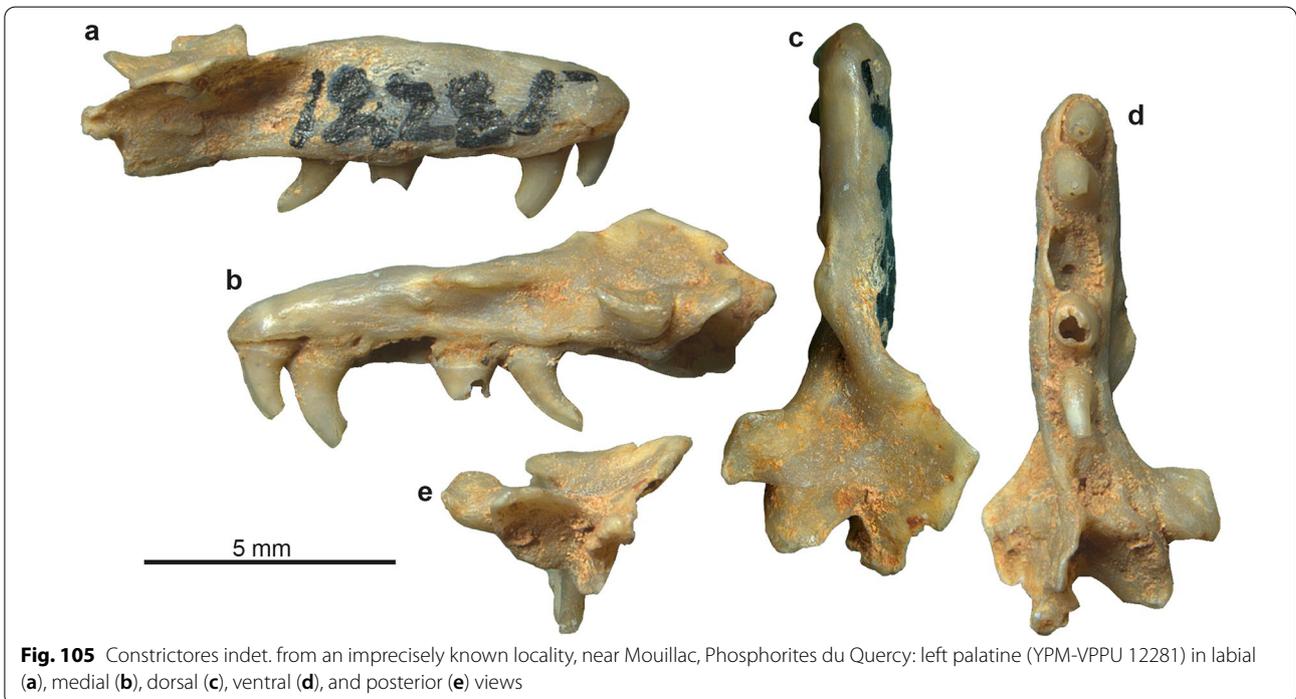


Fig. 105 *Constrictores* indet. from an imprecisely known locality, near Mouillac, Phosphorites du Quercy: left palatine (YPM-VPPU 12281) in labial (a), medial (b), dorsal (c), ventral (d), and posterior (e) views

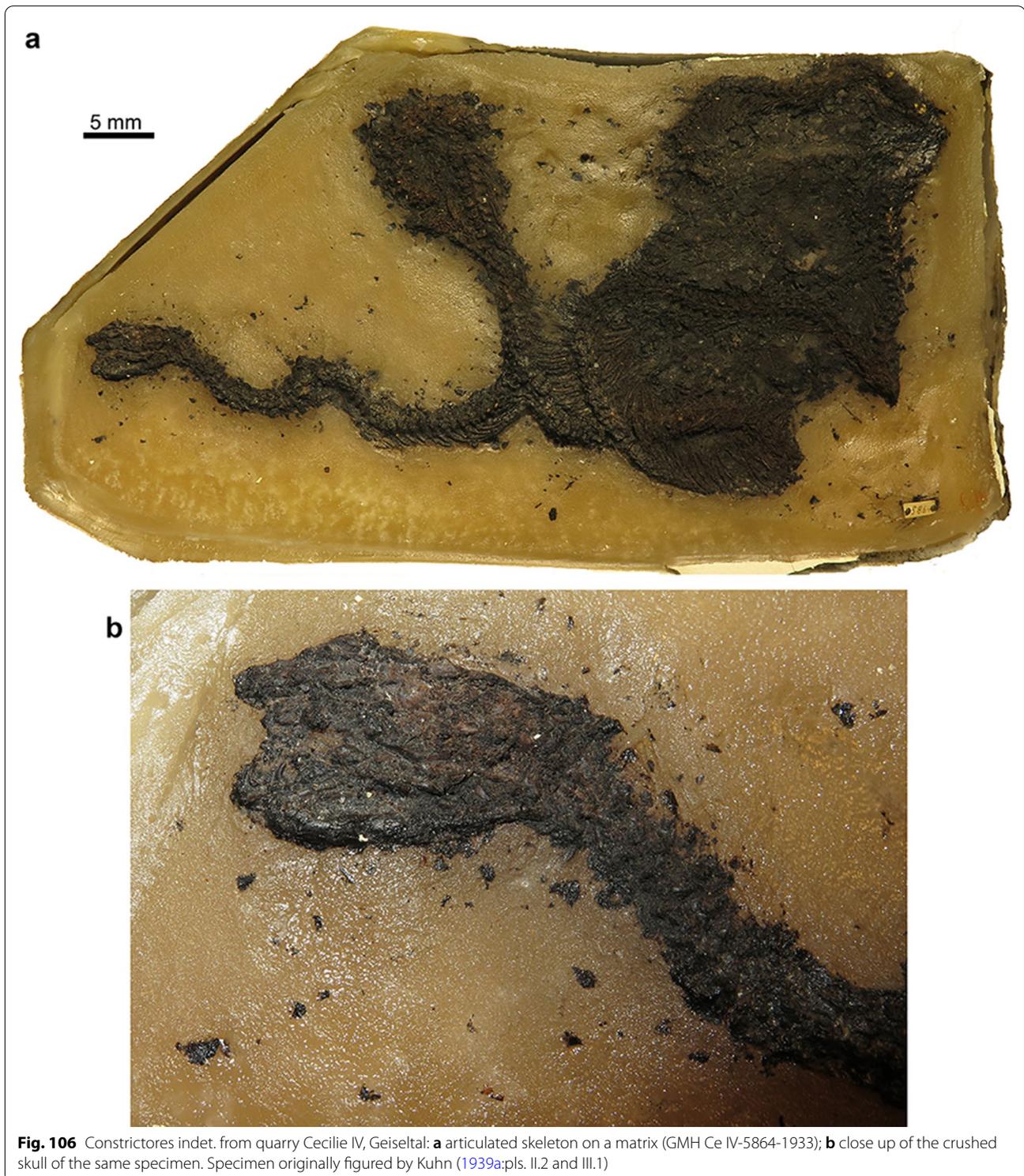


Fig. 106 Constrictores indet. from quarry Cecilie IV, Geiseltal: **a** articulated skeleton on a matrix (GMH Ce IV-5864-1933); **b** close up of the crushed skull of the same specimen. Specimen originally figured by Kuhn (1939a:pls. II.2 and III.1)

Ce I-2957; originally figured by Kuhn (1939a:pl. I.5)], a left maxilla broken into two pieces (GMH Ce I-5829-1926; originally figured by Kuhn (1939a:pl. I.4), a dentary fragment with broken teeth (GMH Ce I-5828-1926) and several trunk vertebrae (GMH Ce I-2930-1931[20

vertebrae], GMH Ce I-2931-1931) from quarry Cecilie I; a matrix with several articulated trunk vertebrae [GMH Ce II-5859-1930; originally referred to as *Paleryx spinifer* and figured by Kuhn (1939a:pl. II.1); Fig. 107] from quarry Cecilie II; anterior skeleton of a probably young



Fig. 107 Constrictores indet. from quarry Cecilie II, Geiseltal: several articulated trunk vertebrae on a matrix (GMH Ce II-5859-1930). Specimen originally figured by Kuhn (1939a:pl. II.1)

individual (“baby”), including crushed skull and several anterior trunk vertebrae and remains of ribs [GMH Ce III-2928-1932; originally figured by Kuhn (1939a:pl. I.1); Fig. 108], a fragmentary skeleton portion with several articulated vertebrae and ribs (GMH Ce III-5848-1932), and several disarticulated fragmentary trunk vertebrae and remains of ribs on a matrix (GMH Ce III-5843-1932) from quarry Cecilie III [originally figured by Kuhn (1939a)]; a trunk vertebra and four vertebral fragments (GMH Y-45), several fragmentary trunk vertebrae and remains of ribs (GMH Y-41), and a rather crushed skeleton with several articulated and disarticulated vertebrae and remains of ribs on a matrix (GMH Y-47) from unknown quarry.

Description and comparisons of the cranial material (Figs. 104, 105): NHMW 2019/0020/0003 is a

fragmentary right dentary (Fig. 104) that differs from the four other dentaries above assigned to *Phosphoroboa filholii* comb. nov. in several respects. It is smaller by about 22% than the other dentary in the NHMW collection, based on tooth socket dimensions in the middle of the jaw (which may account for its more delicate appearance); it has an elongate mental foramen much closer to the surangular notch; the orientation of the teeth is more lingual than distal; and it has an unusual groove beneath the posterior portion of the subdental shelf. Given these substantial differences, we cannot assign it to *Phosphoroboa filholii* comb. nov. On the other hand, there is no other taxon of appropriate size recognized in the NHMW sample.

YPM-VPPU 12281 is a left palatine with six tooth positions (Fig. 105). It cannot clearly be associated with



Fig. 108 *Constrictores* indet. from quarry Cecilie III, Geiseltal: anterior skeleton of a young individual ("baby"), including crushed skull and several anterior trunk vertebrae and remains of ribs (GMH Ce III-2928-1932) from quarry Cecilie III. Specimen originally figured by Kuhn (1939a:pl. I.1)

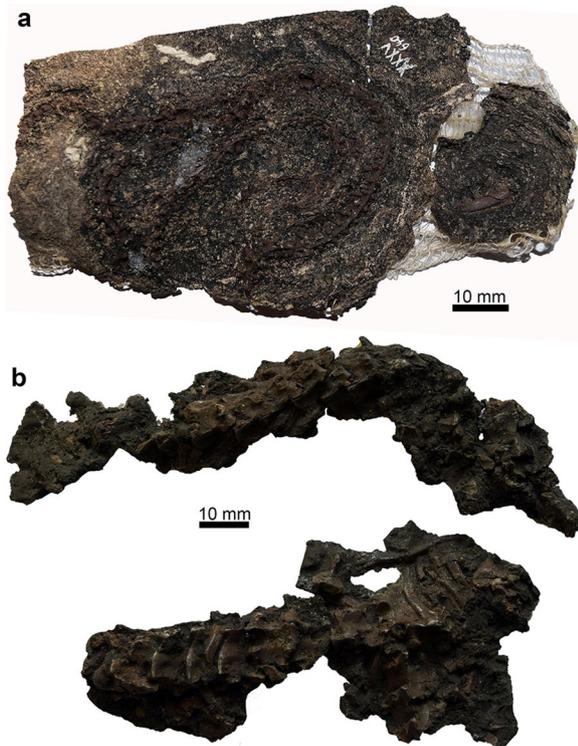


Fig. 109 *Constrictores* indet. from Geiseltal: **a** partial skeleton with several trunk vertebrae and ribs, and a dentary (GMH XXXV-640-1970) from quarry XXXV; **b** two strings of articulated trunk vertebrae and fragments of ribs (GMH Leo I-5866-1932) from quarry Leonhardt I



Fig. 110 *Constrictores* indet. from quarry XLI, Geiseltal: isolated rib (GMH XLI-314a-1968) in posterior (**a**) and anterior (**b**) views

Phosphoroboa filholii comb. nov. or "*Palaeopython*" *neglectus* from the same YPM-VPPU sample based on size or relative abundance. It is more typically booid in form, with a rectangular maxillary process located at the posterior end of the bone, just in front of the deep pterygoid facet; in this respect the bone is unlike the palatine associated with *Paleryx rhombifer* above. The two are similar, however, in possessing a medially projecting horizontal ridge on the lateral face. A relatively broad choanal process is present medially. If "*Palaeopython*" *neglectus* should turn out to be a pythonoid, then an attribution of this palatine to *Ph. filholii* comb. nov. becomes likely.

As for the Geiseltal cranial remains mentioned here (Figs. 106, 107, 108, 109, 110), they are either too fragmentary or their direct observation is hindered by matrix, so these cannot be confidently referred to any of the Geiseltal known species. Among them, specimen GMH Ce IV-5864-1933 is an articulated skeleton with a crushed

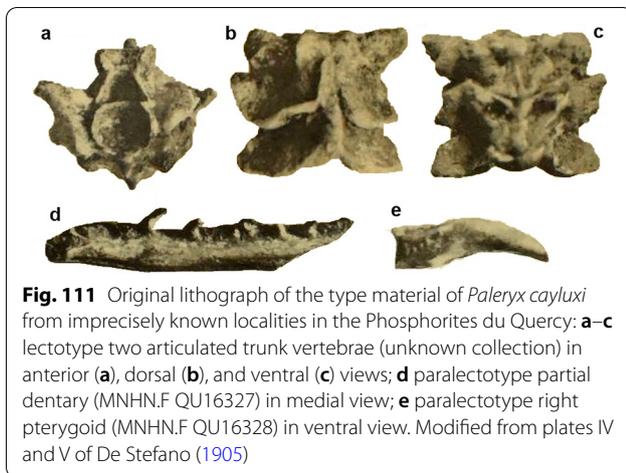


Fig. 111 Original lithograph of the type material of *Paleryx cayluxi* from imprecisely known localities in the Phosphorites du Quercy: **a–c** lectotype two articulated trunk vertebrae (unknown collection) in anterior (**a**), dorsal (**b**), and ventral (**c**) views; **d** paralectotype partial dentary (MNHN.F QU16327) in medial view; **e** paralectotype right pterygoid (MNHN.F QU16328) in ventral view. Modified from plates IV and V of De Stefano (1905)

skull (Fig. 106), which was originally described by Kuhn (1939a), who mentioned that its premaxilla is apparently toothed (“anscheinend bezahnt”)—premaxillary teeth are present in pythonoids and absent in booids (Szyndlar & Rage, 2003), but we could not observe such feature in this Geiseltal specimen and therefore, Kuhn’s (1939a) claim cannot be confirmed. Of particular interest is specimen GMH Ce III-2928-1932 (Fig. 108)—it possesses a well-developed, arched surangular ala. That would be unusual for known constrictors in the Eocene of Europe. The

pythonoid *Messelopython* has a strong prearticular ala, but not surangular (Zaher & Smith, 2020). And in known Paleogene European Booidea (*Eoconstrictor*, *Messelophis*, *Rieppelophis*, *Rageryx*) there is no expanded ala on either surangular or prearticular. The parabasisphenoid is reminiscent of *Rageryx*. The tips of the neural spines and the condyles look poorly ossified, which would indicate a juvenile stage.

Species currently not considered valid

Paleryx cayluxi De Stefano, 1905

(junior synonym of *Palaeopython cadurcensis* Filhol, 1877a)

lectotype designation

Figures 111, 112

Taxonomic history: *Paleryx cayluxi* De Stefano, 1905 (new species).

Type material: Unknown collection (lectotype, herein designated), two articulated trunk vertebrae (De Stefano, 1905, pl. V.1, V.2, and V.3; Fig. 111a–c), lost (Rage, 1984b, 2006); MNHN.F QU16328 (formerly MNHN QU 328) (paralectotype), a partial right pterygoid (De Stefano,

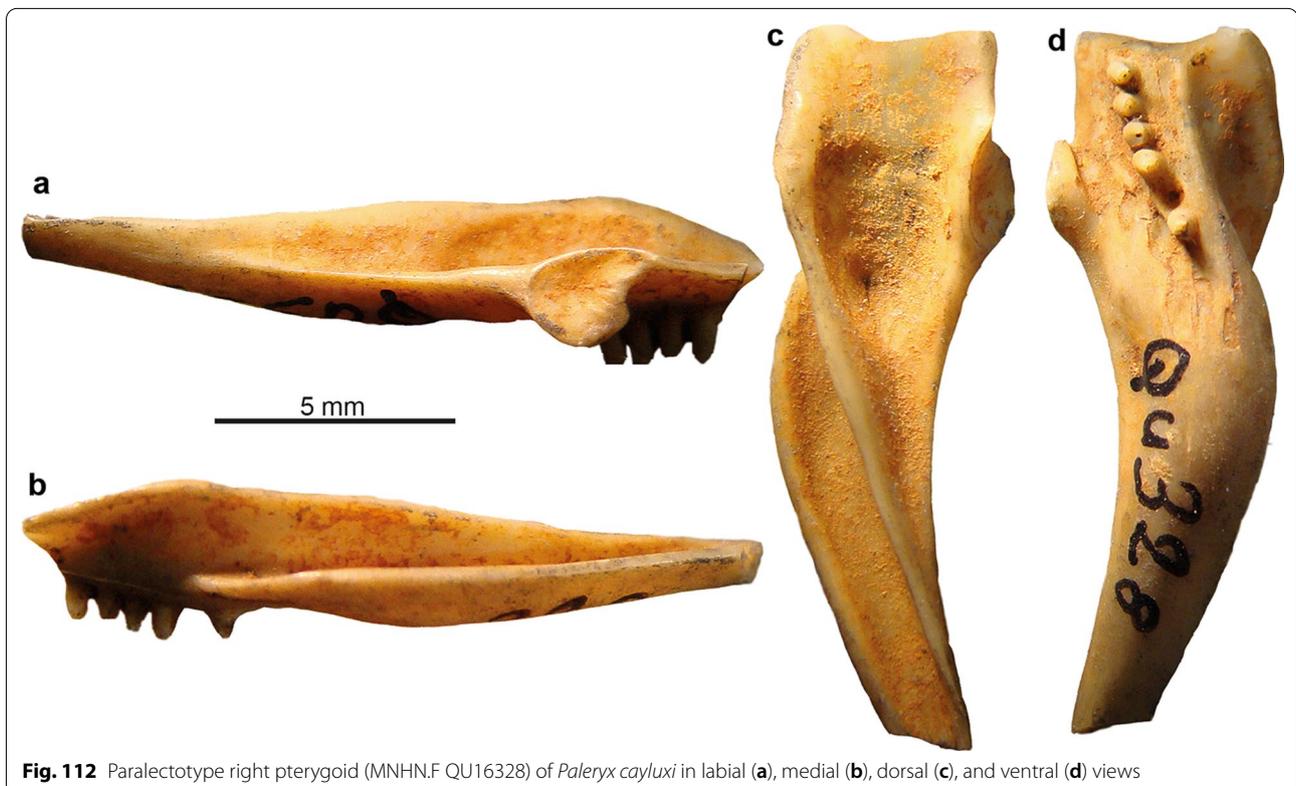


Fig. 112 Paralectotype right pterygoid (MNHN.F QU16328) of *Paleryx cayluxi* in labial (**a**), medial (**b**), dorsal (**c**), and ventral (**d**) views

1905, pl. IV.9; Figs. 111e, 112); MNHN.F QU16327 (formerly MNHN QU 327) (paralectotype), a partial dentary (De Stefano, 1905, pl. IV.10; Fig. 111d).

Type locality: Unknown exact locality, Phosphorites du Quercy, France; probably middle or late Eocene.

Description of the lectotype articulated trunk vertebrae: The specimen is currently lost and as such, all that can be said sources from the original lithograph of De Stefano (1905) (Fig. 111a–c). It consisted of two articulated trunk vertebrae of which the first missed most of the left prezygapophysis. The left postzygapophysis of the first vertebra is curiously arched. The zygosphene is relatively thick. The cotyle is deep and circular. The prezygapophyses are inclined. The interzygapophyseal constriction is shallow. The haemal keel is relatively wide. The paradiapophyses are robust. The neural spine is thick.

Description of the paralectotype cranial material: The right pterygoid, MNHN.F QU16328, is lacking part of the palatine process (Fig. 112). Six tooth positions and five partial teeth are present; the teeth are small, recurved and approximately equal in size. The tooth row extends slightly past the ectopterygoid articulation, which is a well-defined facet sitting on a projecting pedestal. At the basiptyergoid articulation the pterygoid bears a rounded, medially expanded flange. This flange rotates onto the dorsal surface of quadrate ramus, forming a dorsal keel.

Based on De Stefano's (1905: pl. IV: 10; Fig. 111d) illustration, the dentary MNHN.F QU16327 appears to contain about the same number of teeth (eighteen) as MNHN.F QU16317 (paralectotype of *Palaeopython cadurcensis*) and shows a similar shape of the jaw parapet. However, it does not appear to be as deep, a feature we emphasized in its description above. This might reflect breakage to the specimen.

Remarks: De Stefano (1905) established *Paleryx cayluxi* on the basis of cranial and vertebral material from imprecisely known (probably) Eocene locality(-ies) within the Phosphorites du Quercy.

A clarification about the type material is needed for this species as well. Rage (1984b) considered as syntype vertebral material only the (now lost) two articulated vertebrae (that were figured in De Stefano, 1905, pl. V.2 in dorsal view) and not the single vertebra (figured in De Stefano, 1905, pl. V.1 in anterior view). Apparently, Rage (1984b) considered that these two figures represented the same specimen, though this was not stated in De Stefano's (1905) captions. This opinion was subsequently adopted by Wallach et al. (2014). Judging from the original plates, we agree with Rage's (1984b) opinion, noting characters that support such assignments, i.e. the broken left prezygapophysis, the expansion of the right prezygapophysis, and the curiously arched anterior left postzygapophysis; moreover, fig. 1 of plate V of De Stefano (1905)

reveals that there is most probably also a succeeding vertebra behind the one seen in the image (doubled haemal keel).

Finally, we highlight an important error in De Stefano's (1905) figure captions and text with regard to his fig. 3 of plate V, which is titled as "*Paleryx neglectus* De Rochebrune sp.—Due vertebrae pelviane viste dal basso". However, fig. 3 of De Stefano (1905) represents, contrary to its caption, clearly the same specimen as the one in his figs. 1 and 2, as it can be judged by the outline of the postzygapophyses, the broken left prezygapophysis of the first vertebra, and the overall general shape of both vertebrae. Consequently, there is only a single vertebral element in the syntype series of *Paleryx cayluxi*, i.e. the two articulated vertebrae figured by De Stefano (1905) in anterior (his pl. V.1; Fig. 111a), dorsal (his pl. V.2; Fig. 111b), and ventral (his pl. V.3; Fig. 111c) views. The specimen shown in lateral (his pl. V.4) view, in contrast, is a different specimen (the caption refers to it as "altre" with respect to the caption of his pl. V.3) and probably the only illustration of the specimen he referred to *Paleryx neglectus* (herein "*Palaeopython*" *neglectus*). The lengths of the vertebrae, the separation of the neural spines from one another, and the distance of the posterior neural spine from the posterior end of the zygapophysis are inconsistent with the specimen in his plate V.1–3, and these features could additionally have led De Stefano (1905) to assign these two vertebrae to "*Palaeopython*" *neglectus* in the first place (see entry of this taxon above).

Rage (1984b) also suggested that this species may even represent a chimaera, as it could not be ascertained whether all cranial and postcranial syntypes belong indeed to the same species. However, he refrained from selecting one of the two syntype skull elements as the lectotype, considering that most fossil constrictors were based upon vertebrae. He further tentatively referred another vertebra (UM RBN 5301) from the middle Eocene (MP 16) of Robiac, Occitanie, France, to the same taxon, though he did not provide any figure of that material (Rage, 1984b). The same author apparently intended to render the latter vertebra as the neotype of this species, however, he refrained from doing so due to the crushed nature of this specimen (Rage, 1984b). In any case, he felt that, even though the syntype vertebrae were lost, there is no need to render this species a nomen dubium, as its vertebrae bear clear diagnostic traits (Rage, 1984b). As such, we are of the opinion that a lectotype should be designated and this should be the two articulated vertebrae. The designation of a specimen that is currently lost as the lectotype does not contradict ICZN (1999:Article 74.4), considering that this material has been illustrated. See Discussion for our rationale on designating one of the syntypes as the lectotype of this species.

De Stefano (1905) originally distinguished *Paleryx cayluxi* from all known fossil constrictors known at that time from Europe, among which, he noted the strongest resemblance with *Phosphoroboa filholii* comb. nov. Rage (1974, 1984b) considered that the original generic assignment of this taxon to *Paleryx* was erroneous; instead, he suggested that its vertebral morphology was reminiscent of the North American *Paraepicrates* Hecht in McGrew, 1959 (Rage, 1984b). However, he did not undertake any formal generic recombination. Few years later, Rage and Augé (1993) even stated that this species belongs to a new genus, but still they did not create a new generic name. Later still, Rage (2001) demonstrated a combination of vertebral characters (namely the conspicuous shortness of the vertebrae, marked depth of the interzygapophyseal constriction, and the transverse dimension of the zygapophyses) that was otherwise shared only with *Paraepicrates brevispondylus* Hecht in McGrew, 1959, the extant *Lichanura trivirgata*, and his newly established *Hechtophis austrinus* Rage, 2001, from the Paleogene of Brazil. Dowling (2002) envisaged *Paraepicrates* as the product of the Paleogene “Euramerican connection”, but he nevertheless regarded this genus as belonging to “erycines”. Note that Smith (2013) found no evidence for “erycines” in North America prior to the Miocene, but Smith and Scanferla (2021) described a stem member of North American “erycines” (= Charinainae), *Rageryx schmidi*, from Messel. Rage (2001) pointed out that, despite the seeming distinctiveness of the Quercy form, not a lot can be said on the basis of the original figures of De Stefano (1905). Note that Kluge (1988) regarded the genus *Paraepicrates* to be a junior synonym of the extant *Lichanura* Cope, 1861a, an opinion that is not followed herein.

We disagree with the proposed similarities of *Paleryx cayluxi* to *Paraepicrates* (Rage, 2001): (1) The vertebrae of *Paraepicrates brevispondylus* are not conspicuously short. We estimate a CL/NAW ratio of 0.86, similar to many constrictors, whereas in the lectotype of *Paleryx cayluxi* the ratio is 0.59, similar to the ratio in the lectotype of *Palaeopython cadurcensis* (0.65); (2) The interzygapophyseal constriction extends well beyond the mid-point of the prezygapophyseal articular facet in *Paraepicrates brevispondylus*, whereas in *Paleryx cayluxi* it is shallower; (3) The transverse expansion of the zygapophyses is comparable to that seen in the lectotype of *Palaeopython cadurcensis*.

Overall we find that the features of the lectotype of *Paleryx cayluxi* closely correspond to the diagnosis of *Palaeopython* given above. Furthermore, the flattening of the interzygapophyseal constriction, the lateral expansion and squaring off of the prezygapophysis, and the CL/NAW ratio < 0.70 (like *Palaeopython cadurcensis* but unlike all other measurable types discussed herein)

support an identity with *Palaeopython cadurcensis*. Only the comparatively narrow zygosphene is questionable, but since the right lobe of the prezygapophysis is very small and appears to be damaged in the lectotype, we do not accord this feature any taxonomic weight. Accordingly, we synonymize *Paleryx cayluxi* with *Palaeopython cadurcensis*. The taxonomic identity of the paralectotype pterygoid and dentary originally attributed (without justification) to the same species is uncertain. Among these, the paralectotype pterygoid MNHN.F QU16328 (Fig. 112) seems to be of booid affinities.

Paleryx depressus Owen, 1850

(junior synonym of *Paleryx rhombifer* Owen, 1850)

lectotype designation

Figures 33e–f, 35

Taxonomic history: *Paleryx depressus* Owen, 1850 (new species); *Paleryx depressus* = *Palaeopython filholi* Lydekker, 1888b (senior synonym); *Paleoeryx depressus* Palacký, 1898 (incorrect spelling of genus name); *Paleryx depressus* Kuhn, 1939b (erroneous designation as a type species of *Paleryx*); *Paleryx rhombifer* = *Paleryx depressus* Rage and Ford, 1980 (junior synonym).

Type material: NHMUK PV OR 25261(1) (lectotype, herein designated), a mid-trunk vertebra (Owen, 1850, pl. XIII.37–38; Owen, 1849–1884, pl. 2.37–38; Figs. 33e, f, 35a–c); NHMUK PV OR 25261(2) (paralectotype), a posterior trunk vertebra (Owen, 1850, not figured; Fig. 35d–h); NHMUK PV OR 25261(3) (paralectotype), a mid-trunk vertebra (Owen, 1850, not figured; Fig. 35i, j).

Type locality: Hordle (= Hordwell) Cliff, Hampshire, United Kingdom; Headon Hill Formation, Totland Bay Member, Mammal Bed or Rodent Bed, MP 17, late Eocene.

Description of the lectotype and paralectotype vertebrae (Fig. 35): The lectotype NHMUK PV OR 25261(1) is a well-preserved posterior mid-trunk vertebra (Fig. 35a–c). We focus here on particular points of similarity to NHMUK PV OR 25259, the holotype of *Paleryx rhombifer*, as well as on differences. The zygosphene is much thinner, but in shape it is otherwise similar: flat-topped with a straight anterior margin and no distinct lobes. The haemal keel is broader and subcentral grooves distinct, characters that suggest a more posterior position in the trunk; the haemal keel scarcely projects below the centrum. The neural spine is nearly identical to that in NHMUK PV OR 25259, but it is shorter and slightly more posteriorly inclined. The angulation of the posterior margin of the neural arch is slightly more pronounced than in NHMUK PV OR 25259, and the neural arch as a whole is more depressed. The neural canal is relatively large, as

seen in juvenile individuals. The cotyle is oval, in contrast to the circular cotyle of NHMUK PV OR 25259; a similar contrast is seen between juvenile and adult individuals of *Boa constrictor*.

The paralectotypes are not well preserved. The larger of the two, NHMUK PV OR 25261(2), which is the largest of the syntypes, evinces rounding of all projecting structures (zygapophyses, zygosphene, neural spine) (Fig. 35d–h). It is a posterior trunk vertebra, as indicated by the broad, round hemal keel and deep paralympathic grooves. The paradiapophyses do not extend below the cotyle. It is larger than the lectotype, and the cotyle is more rounded. The neural arch is less depressed than in the lectotype, but more so than the holotype of *Paleryx rhombifer* NHMUK PV OR 25259. However, the angulation of the posterior margin of the neural arch is not apparent. The haemal keel grows gradually in depth posteriorly, projecting below the centrum and reaching a maximum just in front of the condyle. The left portion of the zygantrium has been opened, consistent with considerable mass loss to the bone. The smallest of the syntypes, NHMUK PV OR 25261(3), now a paralectotype, is a mid-trunk vertebra (Fig. 35i–j). It lacks most of its right postzygapophysis. Judging from the sharpness of the haemal keel, we can assume that it originates from around the mid-trunk region.

Remarks: Owen (1850) established his new species *Paleryx depressus* on the basis of three trunk vertebrae from Hordle Cliff and only tentatively referred it to the genus *Paleryx*. He provided a very brief description and figure of only one vertebra in only two views (Owen, 1850). Lydekker (1888a:255) treated these three vertebrae as “type specimens” and later Rage (1984b) as syntypes. We also regard these three specimens as syntypes, and for reasons explained below, we designate one of them as the lectotype.

Rage and Ford (1980) and Rage (1984b) regarded that two of the “syntype” vertebrae belonged to juvenile individual(s), whereas the third was too fragmentary to draw any further conclusions. Because of the difference in ontogenetic stage, the syntypes cannot come from the same individual. Even if we still consider as most likely that all three syntypes still represent the same species, in order to promote stability of nomenclature, we herein designate the best-preserved of the syntypes as the lectotype (NHMUK PV OR 25261(1)), making the other two syntypes (the smallest [NHMUK PV OR 25261(3)] and largest [NHMUK PV OR 25261(2)]) paralectotypes. Notably, the herein designated lectotype NHMUK PV OR 25261(1) is not only the most complete specimen in the type series, but also the only one that was originally figured by Owen (1850). The holotype of *Paleryx rhombifer* and the lectotype of *P. depressus* are highly

similar (shape of the zygosphene, neural spine, posterior neural arch). Almost all of the differences that appear between them can be ascribed to ontogenetic (thickness of zygosphene, shape of cotyle) and positional (subcentral grooves, depressed neural arch) differences (Fig. 90). The relative width of the zygosphene is similar in all and lower than in *Phosphoroboa filholii* comb. nov. (Fig. 46). Only the degree of projection of the haemal keel does not comport with this statement; it could be indicative of intracolumnar or individual variation. Furthermore, the two specimens originate from the same beds. For these reasons, we are convinced that these specimens represent the same species-lineage, and we consequently regard *Paleryx depressus* to be a junior synonym of *Paleryx rhombifer*.

Note that Kuhn (1939b) erroneously considered that *Paleryx depressus* is the type species of the genus *Paleryx*, although it is clear that Owen (1850) had rendered *Paleryx rhombifer* as the type species, a fact that was also confirmed as such by other authors (e.g., De Stefano, 1905).

Discussion

The importance of vertebrae for fossil constrictor taxonomy

It is generally admitted that the cranial anatomy of Constrictores possesses important diagnostic characters and can provide significant clues about the phylogenetic relationships of these snakes, as it has already been demonstrated for both extant (e.g., Frazzetta, 1959, 1966; Kluge, 1991, 1993; Rieppel, 1977) and extinct (e.g., Scanferla & Smith, 2020b; Scanferla et al., 2016; Smith & Georgalis, in press) forms. However, the vast majority of fossil snake remains consists of vertebrae, so it is inevitable that their taxonomy largely relies on vertebral features (e.g., Auffenberg, 1963; Georgalis & Scheyer, 2019a; Georgalis et al., 2019a; Gilmore, 1938; Hoffstetter & Rage, 1972; Holman, 2000; Rage, 1984b; Simpson, 1933; Szyndlar, 1984; Szyndlar & Rage, 2003; Szyndlar & Schleich, 1994; Szyndlar et al., 2008). Indeed, important, distinctive vertebral features have been identified and considered as diagnostic, while it has been recognized that vertebral morphology is strongly influenced by phylogeny (Johnson, 1955). It is characteristic that among the currently accepted 44 named valid species of fossil Constrictores from Europe, 36 species are typified exclusively by vertebral material (i.e. their holotypes or lectotypes or all syntypes are vertebrae), whereas only three species have been established upon type series comprising both cranial and vertebral elements as syntypes, and other five species (i.e. *Messelophis variatus*, *Messelopython freyi*, *Python euboicus*, *Rageryx schmidi*, and *Rottophis atavus*) are typified by partial or complete articulated skeletons

Table 2 List of all named European fossil Constrictores in chronological order

Species	Distribution	Type material	References	Remarks
Valid species				
<i>Dunnophis matronensis</i> Rage, 1973	early Eocene (MP 7), Portugal; early and middle Eocene (MP 10, and MP 14), France	V	Rage (1973), Augé et al. (1997), Rage and Augé (2003, 2010)	
<i>Calamagrus gallicus</i> Rage, 1977	early Eocene (MP 8/9 and MP 10), France	V	Rage (1977), Augé et al. (1997), Schaal and Baszio (2004)	
<i>Messelophis variatus</i> Baszio, 2004	early–middle Eocene (MP 11), Germany	S	Baszio, 2004; Scanferla et al. (2016), Scanferla and Smith (2020a)	
<i>Rieppelophis ermannorum</i> (Schaal and Baszio, 2004)	early–middle Eocene, Germany	V	Schaal and Baszio (2004), Scanferla et al. (2016), Scanferla and Smith (2020a)	
<i>Ragenyx schmidti</i> Smith and Scanferla, 2021	early–middle Eocene (MP 11), Germany	S	Smith and Scanferla (2021)	
<i>Eoconstrictor fischeri</i> (Schaal, 2004)	early–middle Eocene (MP 11), Germany	V	Schaal (2004), Smith and Scanferla (2016), Smith et al. (2018); this paper	
<i>Messelopython freyi</i> Zaher and Smith, 2020	early–middle Eocene (MP 11), Germany	S	Habersetzer and Schaal (1990) Szyndlar and Böhme (1993), Zaher and Smith (2020)	<i>Palaeopython</i> sp. of Habersetzer and Schaal, 1990; "pythonine-like Boidae" of Szyndlar and Böhme (1993)
<i>Palaeopython ceciliensis</i> Barnes, 1927	late early or middle Eocene, Germany	V	Barnes (1927), Weigelt (1929), Kuhn (1939a), this paper	
<i>Eoconstrictor spinifer</i> (Barnes, 1927) comb. nov.	late early or middle Eocene, Germany	V, C	Barnes (1927)	
<i>Szyndlaria aureomontensis</i> Rage and Augé, 2010	middle Eocene (MP 14), France	V	Rage and Augé (2010)	
<i>Platyspondylia sudrei</i> Rage, 1988b	middle Eocene (MP 16), France	V	Rage (1988b)	
<i>Codurcyx filholi</i> Hoffstetter and Rage, 1972	middle and late Eocene (MP 16, MP 19, and imprecise locality), France	V	Hoffstetter and Rage (1972), Rage (1984b, 2013)	
<i>Dunnophis cadurcensis</i> Rage, 1974	middle and late Eocene (MP 16 and MP 17), France	V	Rage (1974, 1988b)	
<i>Palaeopython cadurcensis</i> (Filhol, 1877a)	late middle–late Eocene (MP 16, MP 17, MP 19, and imprecise localities), France	V, C (designation of vertebral material as lectotype made in this paper)	Filhol (1877a, 1877b, 1877c) Rochebrune (1880, 1884) Lydekker (1888a); Zittel (1887–1890); De Stefano (1905), Rage (1988b, 2013), Holman et al. (2006), Georgalis and Scheyer (2019a); this paper	Material from Switzerland described by Pictet et al. (1855–1857) is herein treated as <i>Palaeopython</i> sp.
<i>Palaeopython helveticus</i> Georgalis and Scheyer, 2019a	late middle–late Eocene (MP 16–20), Switzerland	V	Georgalis and Scheyer (2019a)	
<i>Hordaleophis balconae</i> Holman, 1996	late Eocene (MP 17), United Kingdom	V	Holman (1996)	
<i>Paraplatyspondylia batesi</i> Holman and Harrison, 1998b	late Eocene (MP 17), United Kingdom	V	Holman and Harrison (1998b)	

Table 2 (continued)

Species	Distribution	Type material	References	Remarks
<i>Totlandophis thomasa</i> Holman and Harrison, 1998a	late Eocene (MP 17), United Kingdom	V	Holman and Harrison (1998a)	
<i>Codurcenyx pearchi</i> Holman et al., 2006	late Eocene (MP 17), United Kingdom	V	Holman et al. (2006)	
<i>Palerix rhombifer</i> Owen, 1850	late Eocene (MP 17, MP 18, and MP 19), United Kingdom	V	Owen (1850), Lydekker (1888a), Rage and Ford (1980); this paper	
<i>Cadurcoba insolita</i> Rage, 1978	late Eocene (MP 18), France	V	Rage (1978)	
<i>Phosphoroboa filholii</i> (Rochebrune, 1880) comb. nov.	late Eocene (MP 19 and imprecise locality[ies]), France	V	Rochebrune (1880, 1884), Lydekker (1888a), De Stefano (1905), Rage (1974); this paper	Material from Switzerland described by Pictet et al. (1855–1857) is herein treated as <i>Constrictores</i> indet
<i>Rageophis lafonti</i> (Filhol, 1877a)	middle–late Eocene (MP 16–20) (imprecise locality), France	V	Filhol (1877a)	Age based on assumptions of Laloy et al. (2013 and Tissier et al. (2016; see also "Localities and age"
"Palaeopython" neglectus Rochebrune, 1884	middle or late Eocene (imprecise locality[ies]), France	V	Rochebrune (1884), De Stefano (1905); this paper	
<i>Plesiotritrix edwardsi</i> Rochebrune, 1884	Eocene or Oligocene (imprecise locality), France	V	Rochebrune (1884)	
<i>Falsenyx neervelpensis</i> Szyndlar et al., 2008	early Oligocene (MP 21), Belgium	V	Szyndlar et al. (2008)	
<i>Branstateryx vireti</i> Hoffstetter and Rage, 1972	early and late Oligocene (MP 22, MP 25, MP 28, MP 29, and MP 30), France and Germany	V	Hoffstetter and Rage (1972), Szyndlar (1987, 1994), Augé and Rage (1995), Szyndlar and Rage (2003), Rage and Szyndlar (2005)	
<i>Bavarioboa bachensis</i> Szyndlar and Rage, 2003	late Oligocene (MP 26), France	V	Szyndlar and Rage (2003)	
<i>Bavarioboa vaylatsae</i> Szyndlar and Rage, 2003	late Oligocene (MP 26), France	V	Szyndlar and Rage (2003)	
<i>Bavarioboa crocheti</i> Szyndlar and Rage, 2003	late Oligocene (MP 28), France	V	Szyndlar and Rage (2003)	
<i>Platyspondylia leptota</i> Rage, 1974	late Oligocene (MP 28 and MP 30), France	V	Rage (1974), Szyndlar and Rage (2003)	
<i>Bavarioboa herrlingensis</i> Szyndlar and Rage, 2003	late Oligocene (MP 28), Germany	V	Szyndlar and Rage (2003)	
<i>Rottophis atavus</i> (Meyer, 1855)	late Oligocene (MP 27 and MP 30), Germany	S	Meyer (1855), Szyndlar (1994)	
<i>Bavarioboa minuta</i> Szyndlar and Rage, 2003	late Oligocene (MP 28), Germany	V	Szyndlar and Rage (2003)	
<i>Platyspondylia germanica</i> Szyndlar and Rage, 2003	late Oligocene (MP 28), Germany	V	Szyndlar and Rage (2003)	

Table 2 (continued)

Species	Distribution	Type material	References	Remarks
<i>Bransateryx vireti</i> Hoffstetter and Rage, 1972	late Oligocene (MP 29–30), France; early Miocene (MN 1), Germany	V	Hoffstetter and Rage (1972), Szyndlar (1987), Szyndlar and Böhme (1993), Rage and Szyndlar (2005)	
<i>Python euboicus</i> Römer, 1870	early Miocene, Greece	S	Römer (1870)	
<i>Bavarioboa hermi</i> Szyndlar and Schleich, 1993	early Miocene (MN 4), Germany; early Miocene (MN 4), Czech Republic	V	Szyndlar (1987, 1991), Szyndlar and Schleich (1993), Szyndlar and Rage (2003)	
<i>Falsenyx petersbuchi</i> Szyndlar and Rage, 2003	early Miocene (MN 4), Germany; early Miocene (MN 4), Czech Republic	V	Szyndlar (1987, 1991), Szyndlar and Schleich (1993), Szyndlar and Rage (2003)	(Referred specimens of <i>Bransateryx septentrionalis</i> of Szyndlar, 1987 and Szyndlar, 1991; <i>Bransateryx septentrionalis</i> of Szyndlar and Schleich, 1993)
<i>Python europaeus</i> Szyndlar and Rage, 2003	early and middle Miocene (MN 4, MN 4/5, MN 5), France	V	Ivanov (2000), Szyndlar and Rage (2003), Rage and Bailon (2005), Rage (2013)	
<i>Bavarioboa ultima</i> Szyndlar and Rage, 2003	middle Miocene (MN 5), Germany	V	Szyndlar and Rage (2003)	
<i>Albanerxys depereti</i> Hoffstetter and Rage, 1972	middle Miocene (MN 6–MN 7/8), France	V	Hoffstetter and Rage (1972), Augé and Rage (2000)	
<i>Albanerxys volynticus</i> Zerova, 1989	late Miocene (MN 9), Ukraine	V	Zerova (1989), Szyndlar (1991)	
<i>Eryx primitivus</i> Szyndlar and Schleich, 1994	early Pliocene (MN 15), Spain	V	Szyndlar and Schleich (1994)	
Invalid species				
<i>Paleryx cayluxi</i> De Stefano, 1905	middle Eocene (MP 16) and middle or late Eocene (imprecise locality), France	V, C (designation of vertebral material as lectotype made in this paper)	De Stefano (1905), Rage (1984b)	Junior synonym of <i>Palaeopython caduacensis</i> (this paper)
<i>Paleryx depressus</i> Owen, 1850	late Eocene (MP 17), United Kingdom	V	Owen (1850)	Junior synonym of <i>Paleryx rhombifer</i> (Rage and Ford, 1980; this paper)
<i>Palaelaphis antiquus</i> Rochebrune, 1884	Eocene or Oligocene or early Miocene, France	V	Rochebrune (1884)	Nomen dubium (Rage, 1984b)
<i>Palaelaphis robustus</i> Rochebrune, 1884	Eocene or Oligocene or early Miocene, France	C	Rochebrune (1884)	Nomen dubium (Rage, 1984b)
<i>Elaphis boulei</i> De Stefano, 1905	Eocene or Oligocene or early Miocene, France	C, V	De Stefano (1905)	Nomen dubium (Rage, 1984b)
<i>Pylimnophis gracilis</i> Rochebrune, 1884	Eocene or Oligocene or early Miocene, France	V	Rochebrune (1884)	Nomen dubium (Rage, 1984b)
<i>Tachyophis nitidus</i> Rochebrune, 1884	Eocene or Oligocene or early Miocene, France	V	Rochebrune (1884)	Nomen dubium (Rage, 1984b)
<i>Bransateryx septentrionalis</i> Szyndlar, 1987	late Oligocene (MP 30), France	V	Szyndlar (1987)	Junior synonym of <i>Bransateryx vireti</i> (Szyndlar and Rage, 2003)

Table 2 (continued)

Species	Distribution	Type material	References	Remarks
<i>Batrophis gaudryi</i>	Miocene (MN 5), France	V	Rochebrune (1880)	Nomen dubium; could even pertain to Viperidae (Szyndlar and Rage, 2003)

Species that are now generally considered as nomina dubia are placed together in the bottom. Names in bold correspond to the species that are the focus of this paper. For the sake of convenience, taxa that were originally described as "tropicals" are also included here, even though it is unclear if they truly pertain to Constrictores

V, vertebral material; C, cranial material; S, skeleton with both cranial and articulated vertebral material

Table 3 List of all occurrences of the taxa discussed in this paper

Locality	Age	Taxa	References	Remarks
Dormaal, Belgium	MP 7, early Eocene	<i>Constrictores</i> indet	Hecht and Hoffstetter (1962)	Tentatively referred to <i>Paleryx</i> by Hecht and Hoffstetter (1962); not figured
Le Quesnoy, Oise, Hauts-de-France, Paris Basin, France	MP 7, early Eocene	<i>Constrictores</i> indet	Nel et al. (1999)	Originally identified as "Groupe <i>Paleryx-Palaeopython</i> "; not figured
Messel, Hesse, Germany	MP 11, early–middle Eocene	<i>Eoconstrictor fischeri</i> (TL), <i>Constrictores</i> indet. (large form)	Greene (1983), Schaal (2004), Smith and Scanferla (2016), Smith et al. (2018); this paper	
Geiseltal quarry IX, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Geiseltal quarry LII, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i>	This paper	
Geiseltal quarry I, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Geiseltal quarry VI, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Geiseltal quarry XXII, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry XLI, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry LIX, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry XXXIII, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Geiseltal quarry XXXV, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry XXXVI, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	Krumbiegel et al. (1983); this paper	
Geiseltal quarry XXXVII, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry XXXVIII, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	This paper	
Geiseltal quarry Cecilie IV, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Constrictores</i> indet. (large form)	Kuhn (1959a); this paper	
Geiseltal quarry Leonhardt I, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Constrictores</i> indet. (large form)	This paper	

Table 3 (continued)

Locality	Age	Taxa	References	Remarks
Geiseltal quarry Leonhardt III, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Geiseltal quarry Cecilie I, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> (TL), <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Eoconstrictor spinifer</i> comb. nov. (TL), <i>Constrictores</i> indet. (large form)	Barnes (1927), Weigelt (1929), Kuhn (1939a); this paper	
Geiseltal quarry Cecilie II, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Constrictores</i> indet. (large form)	Kuhn (1939a); this paper	
Geiseltal quarry Cecilie III, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Constrictores</i> indet. (large form)	Kuhn (1939a); this paper	
Geiseltal quarry unknown, Sachsen-Anhalt, Germany	late early or middle Eocene	<i>Palaeopython ceciliensis</i> , <i>Eoconstrictor</i> cf. <i>fischeri</i>	This paper	
Laprade, Quercy, Occitanie, France	MP 14, middle Eocene	<i>Constrictores</i> indet. (large form)	Rage and Augé (2010)	Not figured
Lissieu, Auvergne-Rhône-Alpes, France	MP 14, middle Eocene	<i>Constrictores</i> indet. (large form), <i>Constrictores</i> indet. (smaller form)	Rage and Augé (2010)	Material originally referred by Rage and Augé (2010) to <i>Palaeopython</i> sp. and another form similar to <i>Paleryx rhombifer</i> ; not figured
Grisolles, Paris Basin, Hauts-de-France, France	MP 16, middle Eocene	<i>Constrictores</i> indet. (large form)	Russell et al. (1982)	Not figured
Lavergne, Quercy, Occitanie, France	MP 16, middle Eocene	<i>Palaeopython cadurcensis</i>	Rage (2013)	
Le Bretou, Quercy, Occitanie, France	MP 16, middle Eocene	<i>Palaeopython cadurcensis</i> , <i>Palaeopython</i> aff. <i>cadurcensis</i>	Rage (1988b)	
Robiac, Occitanie, France	MP 16, middle Eocene	<i>Palaeopython cadurcensis</i>	Rage (1984b)	Referred to <i>Paleryx cayluxi</i> by Rage (1984b); never figured
Dielsdorf, Zurich, Switzerland	MP 16–20, late middle–late Eocene	<i>Palaeopython helveticus</i> (TL), <i>Eoconstrictor</i> cf. <i>fischeri</i> , <i>Palaeopython</i> sp. ("morphotype 3")	Rosselet (1991), Georgalis and Scheyer (2019a)	Referred to <i>Palaeopython</i> cf. <i>filholi</i> (sic), <i>Palaeopython</i> sp., <i>Paleryx</i> ? <i>rhombifer</i> , <i>Boidae</i> indet., <i>Boinae</i> indet., and <i>Palaeopneidae</i> (sic) indet. by Rosselet (1991)
Aubrelong 2, Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Bouffie (= La Bouffie), Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not described or figured
Lebratière (= Lebratières), Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not described or figured
Les Clapiès, Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not described or figured
Malpérié, Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not described or figured
Pernière, Quercy, Occitanie, France	MP 17, late Eocene	<i>Constrictores</i> indet. (large form)	Rage (1984b)	<i>Palaeopython</i> sp. of Rage (1984b)

Table 3 (continued)

Locality	Age	Taxa	References	Remarks
Hordle (= Hordwell) Cliff, Hampshire, UK	MP 17, late Eocene	<i>Paleryx rhombifer</i> (TL)	Owen (1850), Lydekker (1888a), Holman et al. (2006); this paper	Including type material of <i>Paleryx depressus</i> Owen, 1850; <i>Paleryx rhombifer</i> and <i>Paleryx depressus</i> of Lydekker (1888a); including <i>Placosaurus margariticeps</i> of Lydekker (1888a); non-figured material referred to <i>Palaeopython cadurcensis</i> by Holman et al. (2006) probably pertains to ? <i>Paleryx</i>
Rosières 5, Quercy, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Salême, Occitanie, France	MP 17, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Gousnat, Occitanie, France	MP 18, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Headon Hill, Isle of Wight, UK	MP 18, late Eocene	<i>Paleryx rhombifer</i>	Rage and Ford (1980)	
Sainte Néboule (Ste.-Néboule), Quercy, Occitanie, France	MP 18, late Eocene	<i>Palaeopython cadurcensis</i>	Rage (1978)	Not figured
Fishbourne, Isle of Wight, UK	MP 18/19, late Eocene	<i>Paleryx rhombifer</i>	Rage and Ford (1980)	Not figured
Coânac, Quercy, Occitanie, France	MP 18, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Sindou, Quercy, Occitanie, France	MP 18–19, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Escamps, Quercy, Occitanie, France	MP 19, late Eocene	<i>Palaeopython</i> cf. <i>cadurcensis</i> , <i>Phosphoroboa filholii</i> comb. nov.	Zittel (1887–1890), Rage (1974); this paper	
Mount Mormont (= Mormont = Maureremont), near Eclépens, Vaud, Switzerland	MP 19, late Eocene	<i>Palaeopython</i> sp., <i>Constrictores</i> indet.	Pictet et al. (1855–1857)	Referred to <i>Python</i> sp. and <i>Paleryx</i> or <i>Python</i> sp. by Pictet et al. (1855–1857); referred to <i>Python cadurcensis</i> by Filhol (1877a, 1877b, 1877c); referred to <i>Palaeopython filholii</i> by Roche-brune (1880)
Tabarly, Quercy, Occitanie, France	MP 19, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Rosières 1 (= Rosière 1 = Rosières A), Quercy, Occitanie, France	MP 19, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Rosières 2 (= Rosière 2 = Rosières B), Quercy, Occitanie, France	MP 19, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Rosières 4 (= Rosière 4 = Rosières IV), Quercy, Occitanie, France	MP 19, late Eocene	<i>Palaeopython cadurcensis</i>	Crochet et al. (1981)	Not figured or described
Quercy imprecise localities, Occitanie, France	Probably middle to late Eocene	<i>Palaeopython cadurcensis</i> (TL), <i>Palaeopython</i> cf. <i>cadurcensis</i> , ? <i>Palaeopython</i> sp., <i>Phosphoroboa filholii</i> comb. nov. (TL), “ <i>Palaeopython</i> ” <i>neglectus</i> (TL), <i>Constrictores</i> indet. (large form)	Filhol (1877a, 1877b, 1877c), Rochebrune (1880, 1884), Lydekker (1888a, 1888b), De Stefano (1905), Stromer (1912), Hoffstetter (1959), Georgalis and Scheyer (2019a); this paper	<i>Paleryx cayluxi</i> De Stefano, 1905 synonymized with <i>Palaeopython cadurcensis</i> (this paper); material referred to <i>Paleryx rhombifer</i> by Stromer (1912) and to <i>Palaeopython cadurcensis</i> by Hoffstetter (1959), is herein treated as ? <i>Palaeopython</i> sp.

Table 3 (continued)

Locality	Age	Taxa	References	Remarks
Bembridge, Isle of Wight, UK	MP 20/21, late Eocene/early Oligocene	Constrictores indet	Benton and Spencer (1995)	? <i>Palerix</i> sp. of Benton and Spencer (1995); not figured or described

Note that several localities yielded specimens that have so far never been figured and as such, these records should be taken into consideration only with caution
TL, type locality of species

with both skull and vertebral remains (Table 2). The same is true for the taxa of fossil Constrictores from Europe that are currently considered as nomina dubia or junior synonyms: seven are typified exclusively by vertebrae, whereas only one (i.e. *Elaphis boulei*) is typified by both cranial and vertebral syntypes, and only one (i.e. *Palaelaphis robustus*) is typified by a single cranial element (Table 2). Note that taxa from Europe that have been supposedly referred to “anilioids” (e.g., species of *Eoanilius* Rage, 1974) are not taken into consideration here, as their exact affinities within alethinophidians are not fully clear (Smith and Georgalis, in press). On the other hand, taxa that have been referred to “tropidophiids” (e.g., *Falseryx* spp., *Platyspondylia* spp., *Rottophis atavus*) are taken into consideration here, although it is not clear whether they are true constrictors or amerophidians (see Smith and Georgalis, in press). Also, *Scaptophis miocenicus* Rochebrune, 1880, is not taken into account here, as it is now generally accepted that it pertains to an extant snake, simply embedded with the sediment (Rage, 1981, 1984b); “*Ogmophis*” *europaeus* Szyndlar in Młynarski et al., 1982, from the middle Miocene (MN 7) of Poland is also discarded from consideration, as the type vertebral material has been re-identified as a colubroid (Szyndlar, 1991). This general trend of establishing fossil Constrictores (and generally for all snakes) species upon vertebral material (and not skull elements) is also the case for non-European taxa, such as North (Auffenberg, 1963; Gilmore, 1938; Holman, 2000) and South America (Albino, 1993; Rage, 2001, 2008), as well as for the solely two currently named species from Africa (McCartney et al., 2014; Rage, 1976).

Consequently, when selecting a lectotype from amongst type material consisting of several syntypes, the choice of a vertebra for that specimen helps maintaining taxonomic stability (see Rage, 1984b: lectotype designations of “*Palaeopython*” *neglectus*, *Palaelaphis antiquus*, *Pylmophis gracilis*, and *Tachyophis nitidus*), even if a cranial element was present among the syntypes of the species (e.g., *Palaelaphis antiquus*, *Pylmophis gracilis*, and *Tachyophis nitidus*).

It is furthermore interesting to note that several species of the constrictor genus *Bavarioboa*, were typified by vertebral material, although cranial elements from the type localities were already known upon their original description (e.g., *Bavarioboa crocheta* and *Bavarioboa minuta*; Szyndlar & Rage, 2003). The same applies to the pythonid *Python europaeus* and the “tropidophiids” *Platyspondylia germanica* and *Platyspondylia lepta* (Szyndlar & Rage, 2003). This is also the case for the “erycines” *Albaneryx depereti* and *Bransateryx vireti*, for which posterior caudal vertebrae were selected as the holotypes, whereas cranial elements (a right quadrate and a left dentary for the

former and a right maxilla, a left pterygoid, a left palatine, a right quadrate, and a left dentary for the latter) were simply considered paratypes of these species (Hoffstetter & Rage, 1972). The holotype (and only known specimen) maxilla of *Palaelaphis robustus* is not considered diagnostic and the taxon is generally regarded to represent a nomen dubium (e.g., Rage & Augé, 1993; Rage, 1984b; Szyndlar & Rage, 2003).

Taking into consideration all the above, it is evident that the type series (i.e. syntypes) of the Quercy taxa *Palaeopython cadurcensis* and *Paleryx cayluxi* hindered their exact affinities, as it cannot be fully ascertained that these isolated syntypes of each taxon all pertain to the same species (although for the case of the former taxon, conspecificity of the syntypes is most likely the case). Most importantly, however, the type material of *Palaeopython cadurcensis* and *Paleryx cayluxi* originates from (an) imprecisely known locality(-ies) within the Quercy area. For the different specimens (i.e. syntypes) of *Palaeopython cadurcensis*, Filhol (1877a:270) explicitly stated that they were collected in various localities within the Phosphorites du Quercy (“J’ai recueilli dans divers gisements des phosphorites des vertèbres et des portions de maxillaire supérieur et inférieur”). Therefore, it is possible that the two above-mentioned species are “chimaeras”, with their type series in fact pertaining to different (even if closely related) species. Especially in the case of *Palaeopython cadurcensis*, this is rather taxonomically hazardous, as this is the type species of *Palaeopython*, and it could directly jeopardize the validity of the genus. As such, our designation of the most complete vertebral (and not cranial) material as lectotypes for *Palaeopython cadurcensis* and *Paleryx cayluxi* is justified and necessary.

Spatiotemporal distribution, biogeographic origin, and extinction of *Palaeopython*, *Paleryx*, *Eoconstrictor*, and *Phosphoroboa* gen. nov.

Spatiotemporal distribution

The earliest Cenozoic occurrence of Constrictores from Europe was documented by Kuhn (1940) who described a maxillary fragment that he considered a probable pythoid from the Paleocene of Walbeck, near Magdeburg, Saxony-Anhalt, Germany. However, this record was unfortunately not accompanied by any figure or adequate description and as such it cannot be determined whether it pertains to any of the known genera of large Constrictores or even if it is indeed a constrictor, although its relatively large dimensions (length = 23 mm; Kuhn, 1940) may support such referral. A further European Paleocene (MP 6b) record of Constrictores exists from the locality of Rivecourt-Petit Pâtis, in the Paris Basin, France (Smith et al., 2014). Judging from the sole published figure of this specimen, i.e. a trunk vertebra figured only in anterior

view (Smith et al., 2014:fig. 7B), we would highlight resemblance of this material with *Palaeopython*, on the basis of its relatively large size, the thick and wide zygosphenes, and the overall shape; however, any more precise comparison cannot be conducted on the basis of that single published figure and we feel that it is better to refer this specimen as an indeterminate large constrictor.

Snake vertebrae from the coeval early Eocene (MP 7) localities of Dormaal, Belgium (Hecht and Hoffstetter, 1962), and Le Quesnoy, in the Paris Basin, France (Nel et al., 1997) have been referred to *Paleryx*, however, both these occurrences were only briefly discussed, without any accompanying figure that could enable evaluation of these identifications. The uncertainty about the exact affinities of the Dormaal and Le Quesnoy material is further hampered by the fact that *Paleryx* was for several decades considered as the senior synonym of *Palaeopython*; therefore, a formal description of this material is necessitated in order to assess with certainty whether they pertain to *Paleryx*, *Palaeopython*, *Messelopython*, *Eoconstrictor*, *Phosphoroboa* gen. nov. or some other constrictor genus. Interestingly also, the early and middle Eocene of France has yielded potential pythonoid remains, originating from the localities of Prémontré (MP 10; Augé et al., 1997) and Saint-Maximin (MP 13; Duffaud & Rage, 1997), however, both of these were only briefly described and not figured.

Otherwise, the earliest well-dated confirmed occurrence of large-sized Constrictores is the abundant and often exceptionally preserved material from the early–middle Eocene (MP 11) of Messel, Germany, which has been attributed to the booid *Eoconstrictor fischeri* (Scanferla & Smith, 2020b; Schaal, 2004; Smith & Scanferla, 2016; Smith et al., 2018). As stated above, a second, so far unnamed large constrictor was present in Messel, that was initially referred to *E. fischeri*. Messel has also yielded well-preserved skeletons of smaller species of Constrictores, i.e. *Messelophis variatus*, *Rieppelophis ermannorum*, and *Rageryx schmidi*, as well as the pythonoid *Messelopython freyi* (Baszio, 2004; Scanferla & Smith, 2020a, 2020b; Scanferla et al., 2016; Schaal & Baszio, 2004; Smith & Scanferla, 2021; Zaher & Smith, 2020). It can be stated without any doubt that the two German *Konservat-Lagerstätten* of Messel and Geiseltal have provided the most complete material of European large constrictors.

The different quarries of Geiseltal (late early or early middle Eocene) have yielded numerous remains of large constrictors and as such, offer a unique opportunity to study the evolution of these large snakes. Fossils of large Constrictores have been recovered from most quarries of Geiseltal, including the oldest (IX) and one of the youngest (Cecilie III). Previously, the youngest and oldest

quarries were considered to be separated by several million years (e.g., Franzen, 2005), but this needs revision and differences in taxonomic content may not reflect biological distribution (see “Localities and age”). The only quarries of Geiseltal that have not yielded fossils of Constrictores are XI, XIV, XV, XVIII, XLIII, IL, L, LVIII, XXVI, VII, XXXIV, Leonhardt V, Leonhardt VII, Leonhardt IX, Leonhardt X, and Cecilie V. However, several of these quarries have yielded fragmentary snake specimens that could eventually pertain to large constrictors, others have yielded only a few vertebrate remains, and plenty of large constrictor specimens have no precise provenance data and thus could potentially originate from any of the above-mentioned quarries. From Geiseltal, we recognize three taxa of Constrictores. The largest, *Palaeopython ceciliensis*, is known from several quarries. *Eoconstrictor* cf. *fischeri* is by far the most abundant constrictor from Geiseltal, known from practically all quarries that yielded large snakes (see Table 3). In several Geiseltal quarries, *E. cf. fischeri* is the only large constrictor found—it further co-occurs with the larger *Palaeopython ceciliensis* in all quarries that have yielded large Constrictores, with the exception of the quarries LII and Cecilie III (where only *Palaeopython ceciliensis* is present). Co-occurrence of these snake species in several Geiseltal quarries explains why isolated vertebrae catalogued under a single collection number at GMH appear to be chimaeras comprising both *Palaeopython ceciliensis* and *Eoconstrictor* cf. *fischeri*. These specimens include GMH XLI-314-1968, GMH Ce I-5835-1929, GMH Ce I-5834-1926, and GMH Y-38q. We consider that probably this perplexing situation can be attributed to the recovery of these snake finds in close proximity and/or initial erroneous identifications by the collectors; we have here distinguished these specimens and clarified this issue by splitting these specimen numbers. The third species, *Eoconstrictor spinifer* comb. nov., is so far known exclusively from quarry Cecilie I.

Outside of Messel and Geiseltal, only a few middle Eocene occurrences of *Palaeopython* and other large Constrictores exist, but this is certainly hampered by the fact that the old collections from Quercy cannot afford precise locality and age data (see below). As such, there are only five middle Eocene French localities yielding large Constrictores but three of these records were not accompanied by any kind of figure (Table 3). Two of these middle Eocene French occurrences (localities of Lissieu and Laprade), were considered by Rage and Augé (2010) to represent a species supposedly distinct from *Palaeopython ceciliensis* and *Eoconstrictor fischeri*. If this suggestion is correct, this would mark the presence of another species of large constrictor during the middle Eocene. However, as these vertebrae were not figured, this claim cannot be evaluated. In addition, as was mentioned above, another

middle Eocene French locality (Saint-Maximin [MP 13]) yielded also a potential pythonoid, which also has only been described and not figured (Duffaud & Rage, 1997)—in any case, this would imply for an even higher diversity of large Constrictores in the middle Eocene of France.

The various localities within the Phosphorites du Quercy are stratigraphically complex in and of themselves, an issue that magnifies problems associated with the type series of early described snake species, since these specimens (described over a century ago) possess no precise locality data (see “Localities and age”). The localities of the Phosphorites du Quercy span from the early Eocene (MP 8+9) until the early Miocene (MN 3), though the majority of the respective fossiliferous localities ranges between the late middle Eocene (MP 16) and the late Oligocene (MP 28) (Georgalis, 2017; Georgalis et al., 2021; Rage, 2006; Sigé & Huguene, 2006). As such, the exact age(s) of the large constrictor specimens recovered from the region during the nineteenth and early twentieth centuries, including the type material of *Palaeopython cadurcensis*, *Phosphoroboa filholii* comb. nov., “*Palaeopython*” *neglectus*, and *Paleryx cayluxi*, cannot be determined. Only for the paralectotype “mummy” of “*Palaeopython*” *neglectus*, there is indirect evidence suggesting a late middle–late Eocene age (see “Localities and age”). Nevertheless, there are known referred specimens of both *Palaeopython cadurcensis* and *Phosphoroboa filholii* comb. nov. in the new, stratigraphically constrained, collections from Quercy, i.e. the former taxon from both middle and late Eocene sites, and the latter only from the late Eocene of Escamps (Table 3). We accordingly consider the age of the type material pertaining within these respective age ranges of the referred specimens.

During the late Eocene, *Palaeopython* is known from several published occurrences, mainly from France, but also from Switzerland (Table 3). In the late middle–late Eocene (MP 16–20) of Dielsdorf, Switzerland, as many as three different species of large constrictors occur (*Palaeopython helveticus*, *Eoconstrictor* cf. *fischeri*, plus another large form, which was tentatively termed as *Palaeopython* sp. [morphotype 3]; see Georgalis & Scheyer, 2019a). This sympatry between the larger and smaller species within a single Eocene locality is reminiscent of the situation in Messel and Geiseltal described above.

Paleryx and its sole recognized valid species, *Paleryx rhombifer*, is currently confined to the late Eocene of England, with all purported occurrences from France (e.g., De Stefano, 1905; Lydekker, 1888a) pertaining instead to *Palaeopython cadurcensis* or to *Phosphoroboa filholii* comb. nov. Conversely, *Palaeopython* is shown here not to have existed in England, with the single purported occurrence (Holman et al., 2006) probably pertaining to *Paleryx*. For a general depiction of the distribution of the species discussed herein, see Fig. 113.

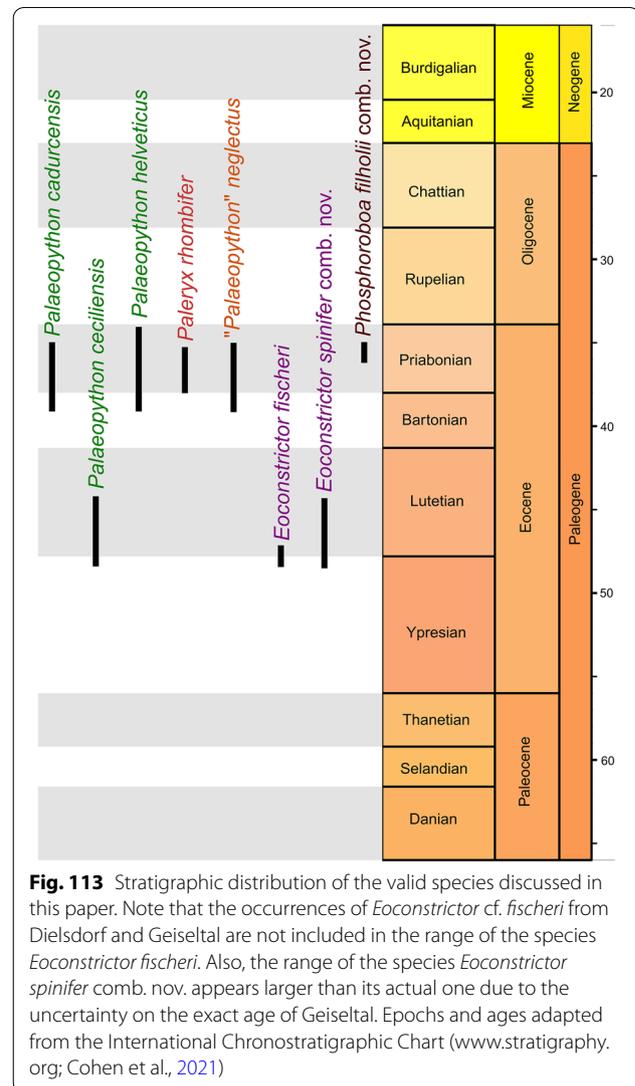


Fig. 113 Stratigraphic distribution of the valid species discussed in this paper. Note that the occurrences of *Eoconstrictor* cf. *fischeri* from Dielsdorf and Geiseltal are not included in the range of the species *Eoconstrictor fischeri*. Also, the range of the species *Eoconstrictor spinifer* comb. nov. appears larger than its actual one due to the uncertainty on the exact age of Geiseltal. Epochs and ages adapted from the International Chronostratigraphic Chart (www.stratigraphy.org; Cohen et al., 2021)

Palaeobiogeography

Eoconstrictor has been recently suggested to represent the stem-lineage of modern Neotropical Boidae (Scanferla & Smith, 2020b). Such affinities implied origins of this lineage from South America and subsequent arrival to Europe either via dispersal through Africa or dispersal through North America (Scanferla & Smith, 2020b). Both scenarios remain plausible as terrestrial vertebrate dispersals among Africa and Europe and North America and Europe were not uncommon during the Paleogene.

Recently, McCartney and Seiffert (2016) described an unnamed constrictor (“Booid A”) from the late Eocene of Fayum, Egypt, which they regarded to have important vertebral resemblance to European constrictors (especially *Palaeopython cadurcensis* and *Eoconstrictor fischeri*) and the North American *Boavus*, but still they nevertheless

differentiated it from all three genera. McCartney and Seiffert (2016) highlighted in the Egyptian form the prominent median tubercle on the zygosphene (shared with *E. fischeri*) and the dorsoventrally tall zygosphene and moderately vaulted neural arch (shared with *P. cadurcensis*). In the same form, McCartney and Seiffert (2016) referred also a maxilla, which, however, considered as distinct from that of *Palaeopython cadurcensis* by being less strongly curved and in having a longer palatine process that is posteriorly inflected. Judging from the published figures of McCartney and Seiffert (2016), we can observe that the vertebral morphology of the Fayum taxon deviates from that of *Palaeopython* spp., especially by its deeper interzygapophyseal constriction and the less thick zygosphene. The Fayum taxon is reminiscent of *Eoconstrictor* spp. in the presence and shape of the median tubercle on the zygosphene. It further shares with “*Palaeopython*” *neglectus* the deep interzygapophyseal constriction but still, the latter form differs by its neural spine reaching the level of the zygosphene. These being said, we definitely need more material in order to attest whether this Egyptian taxon bears affinities with European constrictors or instead represents some endemic African lineage.

In any case, potential trans-Tethyan dispersals between Europe and Africa during the early Paleogene should not appear as strange as they have been generally suggested for a number of different terrestrial fossil vertebrates (e.g., Angst et al., 2013; Borths & Stevens, 2019; Buffetaut & Angst, 2014; Erdal et al., 2016; Gheerbrant, 1990; Gheerbrant & Rage, 2006; Laloy et al., 2013; Rage, 1988a; Solé et al., 2015), whereas it has also been suggested for extant squamate lineages on the basis of molecular data (e.g., Lacertidae: Hipsley et al., 2009).

The exact origins of *Palaeopython* and *Paleryx* cannot be determined with certainty. *Palaeopython* shares an overall vertebral resemblance to species of the Eocene North American genus *Boavus*, and particularly the type and most well-known species *Boavus occidentalis* Marsh, 1871 (see figures in Gilmore, 1938, Rage, 1984b, and Holman, 2000). *Boavus affinis* Brattstrom, 1955, also has paracotylar foramina (see Brattstrom, 1955:Fig. 1A). Indeed, a similar biogeographic pattern, with dispersals of North American taxa to Europe (probably via Greenland) during the Paleocene–Eocene Thermal Maximum has been variously suggested for multiple terrestrial vertebrate lineages (Georgalis & Joyce, 2017; Godinot et al., 2003; Hooker, 2018), including multiple different lizard and snake groups (Augé, 2005, 2012; Baszio, 2004; Estes & Hutchison, 1980; Hoffstetter & Rage, 1972; Rage, 1973, 1977, 2013; Smith, 2009; Smith & Scanferla, 2021; Smith et al. 2018; Sullivan, 1979). On the other hand, we have to highlight that the Asian fossil record of Constrictores is extremely poor: only three species have been named,

i.e. the “erycine” *Calamagras turkestanicus* Danilov and Averianov, 1999, from the early Eocene of Kyrgyzstan, the “erycine” *Crythiosaurus mongoliensis* Gilmore, 1943, from the early Oligocene of Mongolia (originally identified as an amphisbaenian by Gilmore (1943); re-identified as snake by McDowell (1979), and the pythonid *Daunophis langi* Swinton, 1926, from the Pliocene of Myanmar.

Szyndlar and Rage (2003) speculated on an American origin for *Palaeopython* (in which genus they were back then also including *Phosphoroboa filholii* comb. nov.), as they considered it clearly distinct than the younger (late Oligocene–middle Miocene) and much smaller *Bavarioboa*, though at the same time they admitted that the two genera shared several anatomical cranial and postcranial features.

Alternatively, *Palaeopython* was even envisaged by Rage (2006, 2012) to have a South American origin, evoking an older suggestion of that author for dispersals of squamates from South America to Europe (e.g., Rage, 1988a, 1999), whereas the same author also described and figured a vertebra from the Paleogene of Brazil, for which he suggested a strong vertebral resemblance with *Palaeopython cadurcensis* (“Boinae A” of Rage, 2001:fig. 14). In favour of such a scenario, there is a recently growing evidence of a number of Neotropical (i.e. South American) lineages that have a fossil record in the Paleogene of Europe, including reptiles (e.g., Augé & Brizuela, 2020; Scanferla & Smith, 2020b), as well as non-volant birds (Angst et al., 2013). In fact, faunal and floral exchanges between the Paleogene South American and African landmasses have been recently inferred for multiple different clades of non-marine animals and plants (e.g., Antoine et al., 2012; Aranciaga Rolando et al., 2019; Bond et al., 2015; Chimento & Agnolin, 2020; Croft, 2016; Katinas et al., 2013). The identification of *Eoconstrictor* as booid suggests that at least one of the large European constrictors had South American origin (Scanferla & Smith, 2020b), though of course, an African origin with subsequent dispersals to Europe and South America could also be the case (as it has been suggested for several South American mammal clades; see Croft, 2016). As for *Phosphoroboa* gen. nov., we have no clear evidence on where exactly it lies within Booidea and therefore we cannot imply anything further about its origin. Admittedly, we need more complete specimens of large Constrictores from the European Paleogene in order to clarify their origins.

Extinction

The youngest verified occurrences of *Palaeopython* and *Paleryx* are known from the late Eocene of France (MP 19) and England (MP 18/19), respectively (Table 3). The booids *Eoconstrictor* and *Phosphoroboa* gen. nov. have their youngest verified occurrences in the late middle–late Eocene (MP 16–20) of Switzerland and the late Eocene (MP 19) of France, respectively (Table 3). No

such large Constrictores are known during the Oligocene, and it is only during the early Miocene that another lineage of large constrictors (*Python*) dispersed to Europe (Georgalis et al., 2020a, 2020c; Szyndlar & Rage, 2003). The largest constrictor from the Oligocene of Europe is *Bavarioboa*. This Oligo-Miocene snake genus is widespread in Western and Central Europe (Szyndlar & Rage, 2003), but also known from Anatolia (Syromyatnikova et al., 2019; Szyndlar & Hoşgör, 2012). *Bavarioboa* has been suggested to be of Asian origin, with the genus having dispersed to Europe from Asia twice, i.e. around the Oligocene and subsequently becoming extinct at the end of this epoch and then re-entering the continent again during the late early Miocene (Syromyatnikova et al., 2019; Szyndlar & Hoşgör, 2012; Szyndlar & Rage, 2003).

Bavarioboa was suggested to share several cranial and vertebral similarities, but also differences, with *Palaeopython* by Szyndlar and Rage (2003), who were nevertheless including in the latter genus also *Phosphoroboa filholii* comb. nov. The most characteristic shared feature among *Bavarioboa* and *Palaeopython* according to Szyndlar and Rage (2003) was the type of pterygoid–palatine articulation, but this comparison was based on the pterygoid from Escamps that is assigned to *Phosphoroboa filholii* comb. nov.

However, in light of the new anatomical information obtained from our re-description of the paralectotype maxilla and dentary of *Palaeopython cadurcensis* and the referred pterygoid of *Phosphoroboa filholii* comb. nov. from Escamps, as well as the newly described cranial material of *Paleryx rhombifer* from Hordle Cliff and *Phosphoroboa filholii* comb. nov. from the Phosphorites du Quercy, we find evidence for important differences in the cranial anatomy between both *Palaeopython*, *Paleryx*, and *Phosphoroboa* gen. nov. from that of the younger *Bavarioboa* (see Szyndlar & Rage, 2003 for figures of the cranial material of the latter genus). As such, the identification of a palatine foramen in *Paleryx rhombifer* readily discards booid affinities and, as a consequence, also affinities with *Bavarioboa*, taking into consideration that the latter genus pertains to Booidea (see also Smith and Georgalis, in press). Additionally, the shape of the posterodorsal process of the dentary of *Palaeopython cadurcensis* is much different than booids and approaches most the respective morphology of pythonoids (see description of the paralectotype dentary of this species above), while the available dentaries of *Bavarioboa* (*Bavarioboa crocheti*; Szyndlar & Rage, 2003:figs. 10, 13; *B. herrlingensis*; Szyndlar & Rage, 2003:fig. 16) have typical booid structure. As for the also booid taxon, *Phosphoroboa* gen. nov., its pterygoid morphology is derived with respect to *Bavarioboa* (see Remarks of the entry of that genus above). Important

vertebral differences between *Phosphoroboa filholii* comb. nov. and *Bavarioboa* spp. are present, notably in the length of the neural arch and the shape of the haemal keel in the posterior-most trunk. The lamellar, median tubercle on the zygosphene characteristic of *Eoconstrictor* is also a derived feature lacking in *Bavarioboa*. Previously suggested differences in vertebral features distinguishing *Bavarioboa* from the large Eocene constrictors have also been proposed, such as the thickness of the zygosphene and the vaulting of the neural arch (Szyndlar & Rage, 2003)—we further note that these features are not consistent among the several different *Bavarioboa* spp. and anyway, we also confirm that they still cannot approach the respective conditions observed in the Eocene taxa. These cranial and vertebral characters, while meagre, suggest that *Bavarioboa* represents an independent lineage from the Eocene taxa and that *Palaeopython*, *Paleryx*, *Eoconstrictor*, and *Phosphoroboa* gen. nov. did not survive the “Grande Coupure” at the Eocene–Oligocene boundary.

Appendix 1

Selected centrum lengths of vertebrae of *Palaeopython*, *Paleryx*, *Eoconstrictor*, and *Phosphoroboa* gen. nov. specimens treated in this paper. All measurements in mm.

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Palaeopython cadurcensis</i>	MNHN.F QU16318 (lectotype)	Mid-trunk	c. 12.1
<i>Palaeopython cadurcensis</i>	NHMW 2019/0032/0004	Anterior trunk	9.0
<i>Palaeopython cadurcensis</i>	NHMW 2019/0033/0051	Anterior to anterior mid-trunk	8.7
<i>Palaeopython cadurcensis</i>	MNHN.F QU16319	Mid-trunk	19.0
<i>Palaeopython cadurcensis</i>	NHMW 2019/0032/0005	Mid-trunk	10.0
<i>Palaeopython cadurcensis</i>	NHMW 2019/0033/0003	Mid-trunk	9.1
<i>Palaeopython cadurcensis</i>	NHMW 2019/0033/0037	Mid-trunk	9.0
<i>Palaeopython cadurcensis</i>	NHMW 2019/0033/0051	Mid-trunk	8.7
<i>Palaeopython cadurcensis</i>	NHMW 2019/0032/0003	Mid- to posterior trunk	10.8
<i>Palaeopython cadurcensis</i>	NHMW 2019/0032/0002	Posterior trunk	10.0
<i>Palaeopython cadurcensis</i>	YPM-VPPU 29855	Mid-trunk	8.8
<i>Palaeopython cf. cadurcensis</i>	NHMW 2019/0032/0001	Mid-trunk	11.4

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Palaeopython ceciliensis</i>	GMH Ce I-2978-1926 (holotype)	Mid-trunk	Non available	<i>Eoconstrictor cf. fischeri</i>	GMH XLI-302-1968	Mid-trunk	6.0
<i>Palaeopython ceciliensis</i>	GMH Ce I-Y-42-1926	Anterior or anterior mid-trunk	10.0	<i>Eoconstrictor cf. fischeri</i>	GMH XLI-213-1967	Mid-trunk	6.0
<i>Palaeopython ceciliensis</i>	GMH XXII-39-1965	Mid-trunk	8.0	<i>Eoconstrictor cf. fischeri</i>	GMH VIa-529a-1952	Mid-trunk	9.0
<i>Palaeopython ceciliensis</i>	GMH XXXV-386-1963	Mid-trunk	10.0	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-380-1963	Mid-trunk	10.0
<i>Palaeopython ceciliensis</i>	GMH XXXV-404-1963	Mid-trunk	7.0	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-274-1963	Mid-trunk	10.0
<i>Palaeopython ceciliensis</i>	GMH LII-37-1971	Mid-trunk	10.0	<i>Eoconstrictor cf. fischeri</i>	GMH Leo III-2933-1934	Anterior trunk	9.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 634 (holotype)	(Anterior) mid-trunk	10.5	<i>Eoconstrictor cf. fischeri</i>	GMH XLI-148-1966	Posterior trunk	12.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 636	Mid-trunk (young)	8.3	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-403-1963	Mid-trunk	9.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 637	Mid-trunk (young)	6.6	<i>Eoconstrictor cf. fischeri</i>	GMH Ce IV-2912b-1933	Posterior middle or anterior posterior trunk	12.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 633	Posterior trunk	7.4	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-131a-1963	Mid-trunk	11.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 632	Posterior trunk (young)	5.0	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-131b-1963	Posterior trunk	10.0
<i>Palaeopython helveticus</i>	PIMUZ A/III 631	Posterior trunk (young)	4.2	<i>Eoconstrictor cf. fischeri</i>	GMH XLI-139-1966	Posterior middle or anterior posterior trunk	8.0
<i>Paleryx rhombifer</i>	NHMK PV OR 25259 (holotype)	Anterior mid-trunk	8.36	<i>Eoconstrictor cf. fischeri</i>	GMH XXXV-577-1963	Posterior trunk	9.0
" <i>Palaeopython neglectus</i> "	MNHN.F QU16326 (lectotype)	Mid-trunk	6.1	<i>Eoconstrictor cf. fischeri</i>	GMH Ce IV-4649a-1934	Anterior trunk	8.0
" <i>Palaeopython neglectus</i> "	YPM-VPPU 29859	Anterior trunk	5.3	<i>Eoconstrictor spinifer</i> comb. nov	GMH Ce I-2979-1926 (part of lectotype)	Anterior trunk	8.1
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30360	Mid-trunk	5.4	<i>Phosphoroboa filholii</i> comb. nov	MNHN.F QU16322 (holotype)	Posterior trunk	10.36
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30361	Mid-trunk	4.6	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0001	Anterior trunk	9.1
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30362	Mid-trunk	4.7	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0002	Mid to posterior	10.1
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30363	Mid-trunk	5.9	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0004	Mid-trunk	9.2
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30364	Mid-trunk	4.8	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0005	Mid-trunk	9.8
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30365	Mid-trunk	4.7	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0006	Mid-trunk	4.9
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30366	Mid-trunk	5.1	<i>Phosphoroboa filholii</i> comb. nov	NHMK 2019/0033/0007 (two articulated vertebrae)	Posterior trunk	6.2 & 6.5
" <i>Palaeopython neglectus</i> "	YPM-VPPU 29856	Mid-trunk	5.7				
" <i>Palaeopython neglectus</i> "	YPM-VPPU 29857	Mid-trunk	6.1				
" <i>Palaeopython neglectus</i> "	YPM-VPPU 30367	Posterior trunk	3.4				
" <i>Palaeopython neglectus</i> "	YPM-VPPU 29858	Posterior trunk	4.8				
<i>Eoconstrictor fischeri</i>	SMF-ME 929 (the string of three vertebrae) (holotype)	Mid-trunk	7.6				

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0008	Mid-trunk	6.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0009	Mid-trunk	5.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0009	Mid-trunk	5.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0010	Mid-trunk	7.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0010	Mid-trunk	7.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0011	Mid-trunk	4.1
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0011	Mid-trunk	4.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0012	Posterior trunk	6.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0012	Posterior trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0013	Mid-trunk	7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0013	Mid-trunk	7	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0014	Posterior trunk	6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0014	Posterior trunk	6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0015	Mid-trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0015	Mid-trunk	6.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0016	Mid-trunk	6.1
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0016	Mid-trunk	6.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0017	Anterior trunk	7.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0017	Anterior trunk	7.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0018	Anterior trunk	7.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0018	Anterior trunk	7.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0019	Anterior trunk	8.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0019	Anterior trunk	8.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0020	Mid-trunk	8.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0020	Mid-trunk	8.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0022	Mid-trunk	7.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0001	Anterior trunk	9.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0023	Posterior middle or anterior posterior trunk	9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0002	Mid to posterior	10.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0024	Posterior trunk (probably anterior posterior)	6.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0004	Mid-trunk	9.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0025	Posterior trunk (probably anterior posterior)	7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0005	Mid-trunk	9.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0026	Mid-trunk	8.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0006	Mid-trunk	4.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0027	Mid-trunk	7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0007	Posterior trunk	6.2 & 6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0028	Anterior trunk	6.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0008	Mid-trunk	6.3				

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0029	Mid-trunk	6.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0050	Mid- to posterior trunk	9.1
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0030	Mid-trunk	6.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0052	Posterior trunk	8.7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0031	Posterior middle or anterior posterior trunk	5.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0053	Mid-trunk	7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0033	Posterior trunk	8.7	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0054	Mid-trunk	8.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0034	Posterior trunk (anterior posterior)	8.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0055	Mid- to posterior trunk	7.7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0035	Posterior trunk	10.7	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0056	Mid-trunk	7.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0036	Posterior trunk or posterior middle	9.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0057	Mid- to posterior trunk	7.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0038	Mid-trunk	9.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0058	Posterior trunk	5.6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0039	Mid-trunk	7.7	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0059	Mid-trunk	4.6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0040	Anterior trunk	5.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0061	Mid-trunk	8.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0041	Anterior trunk	6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0062	Mid-trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0042	Anterior trunk	9.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0063	Anterior middle	6.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0043	Anterior trunk	9.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0064	Anterior middle	7.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0044	Anterior trunk	7.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0065	Mid- to posterior trunk	7.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0045	Posterior trunk	9.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0066	Posterior trunk	6.0
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0046	Posterior trunk	7.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0067	Mid-trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0047	Mid-trunk	9.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0068	Mid-trunk	6.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0048	Mid-trunk	5.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0070	Mid-trunk	6.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0049	Mid-trunk	7.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0071	Posterior trunk	5.3

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0073	Posterior trunk	4.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0095	Mid-trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0074	Mid-trunk	4.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0096	Mid- to posterior trunk	4.7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0075	Anterior trunk	6.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0097	Mid- to posterior trunk	4.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0076	Anterior trunk	9.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0098	Mid-trunk	5.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0077	Anterior trunk	8.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0099	Mid-trunk	7.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0078	Mid-trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0100	Mid- to posterior trunk	8.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0079	Mid-trunk	5.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0101	Mid-trunk	7.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0080	Mid- to posterior trunk	7.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0102	Mid- to posterior trunk	7.6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0081	Posterior trunk	5.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0103	Mid-trunk	8.1
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0082	Posterior trunk	5.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0104	Mid- to posterior trunk	8.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0083	Posterior trunk	7.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0105	Anterior trunk	7.7
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0084	Posterior trunk	5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0106	Posterior trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0085	Mid-trunk	8.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0107	Posterior trunk	6.6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0086	Mid- to posterior trunk	8.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0108	Mid-trunk	7.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0089	Mid-trunk	7.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0109	Mid-trunk	6.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0090	Mid-trunk	6.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0110	Anterior trunk	7.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0091	Mid-trunk	7.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0111	Mid-trunk	6.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0092	Mid-trunk	5.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0112	Mid-trunk	6.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0093	Mid-trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0113	Posterior trunk	6.0
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0094	Mid-trunk	5.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0114	Posterior trunk	7.8

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0115	Anterior trunk	4.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0135	Mid-trunk	5.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0116	Anterior trunk	7.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0136	Mid-trunk	8.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0117	Anterior trunk	6.7	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0137	Posterior trunk	9.00
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0118	Anterior trunk	6.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0138	Posterior trunk	6.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0119	Anterior trunk	6.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0139	Posterior trunk	5.6
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0120	Mid-trunk	7.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0140	Posterior trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0121	Mid-trunk	8.3	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0141	Posterior trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0122	Mid-trunk	7.4	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0142	Anterior trunk	5.5
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0123	Mid-trunk	6.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0143	Mid-trunk	6.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0124	Mid-trunk	10.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0144	Mid-trunk	5.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0125	Mid-trunk	7.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0145	Mid-trunk	8.3
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0126	Mid-trunk	4.8	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0146	Mid-trunk	5.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0127	Posterior trunk	6.6	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0147	Mid-trunk	7.2
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0128	Posterior trunk	7.1	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0148	Anterior middle	6.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0129	Posterior trunk	8.2	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0149	Mid- to posterior trunk	6.0
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0130	Mid-trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0150	Mid-trunk	7.0
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0131	Mid-trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0151	Mid-trunk	4.4
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0132	Mid-trunk	7.0	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0152	Posterior trunk	6.8
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0133	Mid-trunk	8.5	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0153	Posterior trunk	6.9
<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0134	Mid-trunk	4.9	<i>Phosphoroboa filholii</i> comb. nov.	NHMW 2019/0033/0154	Anterior to anterior mid-trunk	9.0

Taxon	Specimen	Position in the vertebral column	Centrum length (CL)	Taxon	Specimen	Position in the vertebral column	Centrum length (CL)
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30369	Anterior trunk	3.8	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30384	Mid-trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30370	Anterior trunk	7.6	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30385	Mid-trunk	5.1
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30371	Anterior trunk	7.4	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30386	Mid-trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30372	Anterior trunk	6.8	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30387	Mid-trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30373	Anterior trunk	7.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30388	Mid-trunk	6.3
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30374	Mid-trunk	8.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30389	Mid-trunk	6.2
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30375	Mid-trunk	8.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30390	Mid-trunk	4.2
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30376	Mid-trunk	7.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30391	Posterior trunk	7.3
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30377	Mid-trunk	7.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30392	Posterior trunk	6.3
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30378	Mid-trunk	7.6	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30393	Posterior trunk	8.2
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30379	Mid-trunk	6.5	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30394	Posterior trunk	5.2
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30380	Mid-trunk	6.1	<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30395	Posterior trunk	5.4
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30381	Mid-trunk	5.1				
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30382	Mid-trunk	5.0				
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30383	Mid-trunk	6.1				

Appendix 2

Selected vertebral dimensions of the YPM sample. All measurements in mm. See “[Material and methods](#)” for explanation of the abbreviations. *NA*= not available.

Species	Specimen	Position in the vertebral column	CL	NAW	NSPL	PR-PR	CoH	CoW	ZW	NAH	hPO-PO	Notes
<i>Palaeopython cadurcensis</i>	YPM-VPPU 29855	Mid-trunk	8.81	13.61	4.32	18.1	5.26	5.63	7.67	4.00	9.38	
<i>Palaeopython neglectus</i>	YPM-VPPU 29859	Anterior trunk	5.33	6.49	3.27	8.99	2.79	3.52	4.28	2.54	4.42	
<i>Palaeopython neglectus</i>	YPM-VPPU 30360	Mid-trunk	5.44	7.01	2.83	9.32	NA	3.08	5.13	2.18	4.26	
<i>Palaeopython neglectus</i>	YPM-VPPU 30361	Mid-trunk	4.55	5.87	2.76	8.66	2.45	3.08	3.70	1.54	4.20	
<i>Palaeopython neglectus</i>	YPM-VPPU 30362	Mid-trunk	4.68	5.15	2.36	8.59	2.26	2.86	3.68	1.36	3.90	
<i>Palaeopython neglectus</i>	YPM-VPPU 30363	Mid-trunk	5.87	7.07	3.20	10.56	3.21	3.84	5.25	2.52	5.36	
<i>Palaeopython neglectus</i>	YPM-VPPU 30364	Mid-trunk	4.73	5.38	2.54	8.80	2.50	3.12	3.99	1.59	4.19	
<i>Palaeopython neglectus</i>	YPM-VPPU 30365	Mid-trunk	4.69	6.05	2.86	8.48	2.75	3.24	3.84	1.92	4.35	
<i>Palaeopython neglectus</i>	YPM-VPPU 30366	Mid-trunk	5.07	6.54	3.34	9.86	2.86	3.64	4.23	1.99	4.84	
<i>Palaeopython neglectus</i>	YPM-VPPU 29856	Mid-trunk	5.68	7.47	3.68	11.72	3.76	3.98	5.04	1.84	5.34	Condyle worn
<i>Palaeopython neglectus</i>	YPM-VPPU 29857	Mid-trunk	6.12	7.59	3.57	11.48	3.56	4.30	5.40	2.54	5.56	
<i>Palaeopython neglectus</i>	YPM-VPPU 30367	Posterior trunk	3.40	4.20	1.96	6.50	1.68	2.28	3.06	1.28	2.88	
<i>Palaeopython neglectus</i>	YPM-VPPU 29858	Posterior trunk	4.81	5.67	2.95	9.08	2.18	2.69	3.92	1.18	4.45	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30369	Anterior trunk	3.81	5.08	2.00	7.21	NA	2.63	3.50	1.75	3.41	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30370	Anterior trunk	7.58	7.88	4.44	10.54	2.96	3.48	4.73	3.06	5.38	Position uncertain
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30371	Anterior trunk	7.36	9.68	3.61	14.19	3.89	4.84	6.85	4.08	7.15	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30372	Anterior trunk	6.82	8.97	3.30	NA	3.56	4.57	6.15	3.34	6.66	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30373	Anterior trunk	7.07	7.99	NA	10.93	3.15	4.00	5.52	2.88	5.41	Position uncertain
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30374	Mid-trunk	8.13	9.81	3.91	16.09	4.50	5.60	6.53	2.49	7.38	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30375	Mid-trunk	8.05	10.44	3.81	15.98	4.73	5.46	6.60	3.30	7.58	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30376	Mid-trunk	7.07	9.70	NA	13.82	3.67	4.51	6.11	2.75	6.90	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30377	Mid-trunk	7.15	8.37	NA	12.61	3.94	4.46	5.33	2.31	5.68	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30378	Mid-trunk	7.56	10.38	NA	15.62	4.24	5.33	5.65	NA	7.23	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30379	Mid-trunk	6.53	8.68	3.10	12.64	3.75	4.78	5.24	2.14	5.80	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30380	Mid-trunk	6.14	7.88	2.66	11.72	3.30	3.86	5.18	2.46	5.88	
<i>Phosphoroboa filholii</i> comb. nov.	YPM-VPPU 30381	Mid-trunk	5.05	7.21	2.30	10.79	3.05	4.02	4.69	2.22	5.32	

Species	Specimen	Position in the vertebral column	CL	NAW	NSPL	PR-PR	CoH	CoW	ZW	NAH	hPO-PO	Notes
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30382	Mid-trunk	4.96	6.47	NA	9.83	2.83	3.74	4.50	1.96	4.62	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30383	Mid-trunk	6.12	7.92	2.81	12.69	3.56	4.18	5.60	2.25	6.39	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30384	Mid-trunk	5.41	6.78	NA	10.25	3.14	3.80	4.43	2.14	4.92	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30385	Mid-trunk	5.12	7.01	2.50	10.19	3.18	4.13	3.65	2.00	5.41	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30386	Mid-trunk	5.36	7.01	2.59	11.15	3.09	3.85	4.52	2.16	5.56	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30387	Mid-trunk	5.41	6.78	NA	NA	3.12	4.05	4.15	2.14	4.90	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30388	Mid-trunk	6.28	7.05	NA	10.90	3.18	3.82	4.45	1.74	5.20	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30389	Mid-trunk	6.18	7.36	NA	11.24	3.25	4.27	4.85	1.56	5.51	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30390	Mid-trunk	4.20	5.20	NA	8.18	2.29	3.20	3.87	1.56	4.09	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30391	Posterior trunk	7.33	8.42	3.34	12.97	3.96	4.54	5.80	2.21	6.05	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30392	Posterior trunk	6.30	8.02	2.92	12.53	3.65	4.69	5.59	1.93	6.21	Condyle and postzygapophyses broken
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30393	Posterior trunk	8.15	8.07	3.83	13.32	3.68	4.28	5.26	1.83	6.57	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30394	Posterior trunk	5.18	6.03	2.22	9.45	2.69	3.32	3.91	1.47	4.60	
<i>Phosphoroboa filholii</i> comb. nov	YPM-VPPU 30395	Posterior trunk	5.36	5.36	2.62	NA	3.60	4.52	6.21	1.36	3.89	More arched neural arch

Appendix 3

Centrum lengths of mid-trunk vertebrae and lengths of dentary tooth rows of certain extant species of Constrictores and an articulated skeleton of *Eoconstrictor fischeri*. These values were applied in the least-squares regression model of Fig. 16.

Family	Species	Specimen	Vertebral CL (mm) – middle of column	Dentary tooth row L (mm)
Pythonidae	<i>Morelia spilota</i>	SMF-PH 4	7.3	25.3
Pythonidae	<i>Morelia viridis</i>	SMF-PH 12	5.8	24.2
Pythonidae	<i>Python curtus</i>	MDHC 106	5.0	20.0
Pythonidae	<i>Python regius</i>	MDHC 456	7.3	29.0
Pythonidae	<i>Python sebae</i>	MDHC 121	12.0	51.0
Pythonidae	<i>Simalia boeleni</i>	SMF-PH 110	9.1	35.9
Boidae	<i>Boa constrictor</i>	SMF-PH 220	7.3	28.5
Boidae	<i>Chilabothrus angulifer</i>	SMF-PH 61	6.9	24.5
Boidae	<i>Epicrates cenchria</i>	SMF-PH 25	6.0	20.4
Boidae	<i>Eunectes notaeus</i>	SMF-PH 60	6.7	28.4
Erycidae	<i>Eryx colubrinus</i>	MDHC 172	2.5	8.0
Erycidae	<i>Eryx johnii</i>	SMF-PH 20	3.9	10.7
Charinidae	<i>Lichanura trivirgata</i>	SMF-PH 21	3.8	12.2
Booidea	<i>Eoconstrictor fischeri</i>	SMF-ME 2504	8.0	26.9

Appendix 4

Hierarchical taxonomy of the valid taxa described in this paper.

Constrictores Oppel, 1811a (sensu Georgalis and Smith, 2020)

Palaeopython Rochebrune, 1880

Palaeopython cadurcensis (Filhol, 1877a)

Palaeopython ceciliensis Barnes, 1927

Palaeopython helveticus Georgalis and Scheyer, 2019a

Paleryx Owen, 1850

Paleryx rhombifer Owen, 1850

“*Palaeopython*” *neglectus* Rochebrune, 1884

Booidea Gray, 1825 (sensu Pyron et al. 2014)

Eoconstrictor Scanferla and Smith, 2020b

Eoconstrictor fischeri (Schaal, 2004)

Eoconstrictor spinifer (Barnes, 1927) comb. nov.

Phosphoroboa gen. nov.

Phosphoroboa filholii (Rochebrune, 1880) comb. nov.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-021-00224-0>.

Additional file 1: Model 1 3D model of the holotype of *Palaeopython ceciliensis* from quarry Cecilie I, Geiseltal: mid-trunk vertebra (GMH Ce I-2978-1926).

Additional file 2: Model 2 3D model of part of the holotype of *Eoconstrictor fischeri* from Messel: the string of four articulated trunk vertebrae (SMF-ME 929).

Additional file 3: Model 3 3D model of the part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal: the “block” including the left atlantal neural arch, three almost complete anterior trunk vertebrae, remains of ribs, fragments of other vertebrae, as well as basioccipital, and right prootic (GMH Ce I-2979-1926).

Additional file 4: Model 4 3D model of the part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal: the parietal (GMH Ce I-5823-1926).

Additional file 5: Model 5 3D model of the part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal: the right pterygoid (GMH Ce I-5824-1926).

Additional file 6: Model 6 3D model of the part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal: the right maxilla (GMH Ce I-5826-1926).

Additional file 7: Model 7 3D model of the part of the paralectotype of *Eoconstrictor spinifer* comb. nov. from quarry Cecilie I, Geiseltal: (the most complete) anterior trunk vertebra (GMH Ce I-5822-1926).

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Authors' contributions

GLG analysed the data, wrote the text, photographed the specimens, and prepared figures. MR contributed to project design, data collection, data analysis, and manuscript writing. KS analysed the data, wrote the text, photographed the specimens, and prepared figures. 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 at the collections of GMH, HLMD, MNHN, NHMUK, NHMW, PIMUZ, SMF-ME, SMNK-PAL, UM, and YPM. 3D models of the type material of *Palaeopython ceciliensis*, *Eoconstrictor fischeri*, and *Eoconstrictor spinifer* comb. nov. are also deposited at the Morphosource repository (<https://www.morphosource.org/>): holotype of *Palaeopython ceciliensis*, mid-trunk vertebra GMH Ce I-2978-1926 (<https://doi.org/10.17602/M2/M368754>); part of the holotype of *Eoconstrictor fischeri*, the string of four articulated trunk vertebrae SMF-ME 929 (<https://doi.org/10.17602/M2/M368383>); part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov., the “block” including the left atlantal neural arch, three almost complete anterior trunk vertebrae, remains of ribs, fragments of other vertebrae, as well as basioccipital, and right prootic GMH Ce I-2979-1926 (<https://doi.org/10.17602/M2/M368760>); part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov., the parietal GMH Ce I-5823-1926 (<https://doi.org/10.17602/M2/M368767>); part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov., the right pterygoid GMH Ce I-5824-1926 (<https://doi.org/10.17602/M2/M368772>); part of the lectotype (herein designated) of *Eoconstrictor spinifer* comb. nov., the right maxilla GMH Ce I-5826-1926 (<https://doi.org/10.17602/M2/M368777>); part of the paralectotype of *Eoconstrictor spinifer* comb. nov., (the most complete) anterior trunk vertebra GMH Ce I-5822-1926 (<https://doi.org/10.17602/M2/M368782>).

Declarations

Competing interests

The authors declare that they have no competing interests.

Author details

¹Palaeontological Institute and Museum, University of Zurich, Karl Schmid-Strasse 4, 8006 Zurich, Switzerland. ²Department of Geosciences,

University of Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany. ³Natural Sciences Collections (ZNS), Martin-Luther University Halle-Wittenberg, Domplatz 4, 06108 Halle (Saale), Germany. ⁴Department of Messel Research and Mammalogy, Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325 Frankfurt am Main, Germany. ⁵Faculty of Biosciences, Goethe University, Max-von-Laue-Straße 13, 60438 Frankfurt am Main, Germany.

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