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A new species of *Palaeopython* (Serpentes) and other extinct squamates from the Eocene of Dielsdorf (Zurich, Switzerland)

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Abstract

The lizard and snake fauna from the late middle–late Eocene (MP 16–MP 20) of Dielsdorf, near Zurich, Switzerland, is described comprehensively in this paper. Detailed comparisons of the Dielsdorf material with other extinct taxa allow us to establish a new species of the large "booid" genus *Palaeopython*, i.e., *Palaeopython helveticus* sp. nov., characterized by a unique combination of vertebral features, most prominently a highly vaulted neural arch. Other squamates of the Dielsdorf assemblage comprise the large lizard *Palaeovaranus* sp. and as many as three other taxa of snakes, i.e., *Palaeopython* cf. *fischeri*, *Palaeopython* sp. (morphotype 3), and "Booidea" indet. We conducted micro-CT scanning in the *Palaeovaranus* dentary, which confirmed the presence of plicidentine in this lizard genus. Micro-CT scanning was also conducted in differently sized snake vertebrae from our sample, revealing that the respective anatomical differences were probably due to ontogenetic variation. This is the first time that micro-CT scanning is applied in *Palaeovaranus* and *Palaeopython*. The importance of this method for potentially clarifying the taxonomy and precise affinities of extinct snakes is addressed. We also provide digital 3D model reconstructions of the *Palaeovaranus* dentary and *Palaeopython* vertebrae (including that of the holotype of *Palaeopython helveticus* sp. nov.) for the first time. The palaeobiogeographic significance of the Dielsdorf lizards and snakes is discussed and the sympatric occurrences of the genera *Palaeovaranus* and *Palaeopython* throughout the Eocene of Europe are presented in detail.

Keywords Squamata · Eocene · Switzerland · *Palaeopython* · *Palaeovaranus* · New genus and species

1 Introduction

Fossils of Cenozoic squamates from Switzerland have been known since the middle of the 19th century, with important lizard and snake finds described from the late Eocene of Mormont-Saint-Loup, near Lausanne (Pictet et al. 1855–1857). The importance of these finds was highlighted by the fact that the Swiss remains were extensively discussed and variously served as a means of comparison with subsequent lizard and snake fossils from Western Europe (e.g., Filhol 1876, 1877a, b, c; de Rochebrune 1880; Zittel 1887–1890). Despite these early discoveries, Swiss extinct squamates subsequently received only minor attention, with few records described and figured ever since, all of which originate from a rather low number of Eocene and Miocene localities (Hoffstetter 1962; Hünermann 1978, 1981; Rosselet 1991; Bolliger 1992; Jost et al. 2015; Mennecart et al. 2016).

The fissure fillings of Dielsdorf, Zurich Canton, range from the middle Eocene (MP 13) up to the early Oligocene

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(MP 22) and have yielded a large array of vertebrates, mostly mammals (Rosselet 1991, 1993). Squamate fossils from Dielsdorf were first reported by Hünermann (1978), who described a lizard dentary, which he assigned to varanoids. In the publication of his Diploma Thesis, Rosselet (1991) described the whole vertebrate fauna from Dielsdorf, focusing mostly on mammal taxa and the overall biostratigraphy of the locality's fissure fillings. The same author provided brief descriptions and taxonomic assignments of squamates as well, but among the abundant material, he figured only one snake vertebra, which was only presented in a single (anterior) view (Rosselet 1991:Fig. 23). Here we describe in detail the extinct squamates from Dielsdorf, provide updated taxonomic allocations, and figure all specimens in multiple views for the first time. The large snake remains from Dielsdorf are herein referred to the new taxon *Palaeopython helveticus* sp. nov., characterized by a unique combination of vertebral anatomical traits, and the respective material is compared in detail with all large-sized extinct "booids" from Europe. The ontogenetic vertebral variability within snakes is discussed and CT scanning was conducted in different-sized specimens from Dielsdorf in order to detect and evaluate it in our fossil assemblage. The biogeographic importance of the Dielsdorf lizards and snakes and its relevance to the Paleogene European squamate faunas is discussed.

2 Materials and methods

All specimens described herein originate from the fissure fillings of Dielsdorf and are permanently curated at the collections of PIMUZ. Study, photography, and CT scanning of the fossil material from Dielsdorf was conducted in PIMUZ. For comparative purposes, fossil material of multiple Paleogene lizards and snakes, and particularly those pertaining to the genera *Palaeovaranus*, *Palaeopython*, and *Paleryx*, was studied in the collections of MNHN, GMH, NHMUK, and NHMW. Extant comparative material includes numerous skeletons of lizards and snakes from the collections of the HNHM, MDHC, MNCN, MNHN, NHMW, NMP, PRIF UK, SMF, and ZZSiD.

Three snake vertebrae (PIMUZ A/III 631, PIMUZ A/III 634, and PIMUZ A/III 636) of different sizes and the *Palaeovaranus* dentary (PIMUZ A/III 234) from Dielsdorf were scanned with a Nikon XTH 225 ST CT Scanner housed at the Anthropological Department of the University of Zurich. The micro-computed tomography scan of the vertebrae was taken with a voltage of 91 kV and a current of 345 µA, yielding a voxel size of 0.03758 mm, with no filter used. The dentary was scanned with a voltage of 162 kV, a current of 102 µA, yielding a voxel size of 0.01654 mm, again with no filter used. Reconstruction of the digital stack for virtual 3D reconstruction was achieved using VG Studio Max 2.2. The micro-CT scan data and the 3D surface files (.STLs) are available on MorphoMuseuM (Georgalis and Scheyer 2019).

Anatomical abbreviations: CL, centrum length of vertebra; LAG, lines of arrested growth; NAW, neural arch width; PR–PR, width across the two prezygapophyseal articular facets.

Institutional abbreviations: BSPG, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; GMH, Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, now referred to as the Geiseltalsammlung, housed as part of the Zentralmagazin Naturwissenschaftlicher Sammlungen, Halle, Germany; HNHM, Hungarian Natural History Museum, Budapest, Hungary; 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; NHMUK, Natural History Museum, London, United Kingdom; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; NMP, Národní Muzeum Praha, Prague, Czech Republic; PIMUZ, Paläontologisches Institut und Museum der Universität Zurich, Zurich, Switzerland; PRIF UK, Faculty of Natural Sciences, Comenius University, Bratislava, Slovakia; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; USTL, Université de Sciences et Tecniques du Languedoc, Montpellier, France; YPM, Yale Peabody Museum of Natural History; ZZSiD, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

3 Geological settings and palaeoecology of Dielsdorf

Dielsdorf is a fissure filling locality, situated around 13 km north west from the city of Zurich, in the Canton of Zurich, Switzerland. The fissure fillings of Dielsdorf span from the middle Eocene (MP 13) up to the early Oligocene (MP 22), with the majority of the remains, however, pertaining to middle (MP 16) and late Eocene (MP 18–MP 20) ages (Rosselet 1991, 1993). In particular, Fissure 1 spans from MP 14 to MP 20, Fissure 2 and Fissure A from MP 16 to MP 20, and Fissure B from MP 17 to MP 20. The geology of the locality was described in much detail by Rosselet (1991, 1993).

Dielsdorf has produced a large array of mammal fossils, pertaining to marsupials, erinaceomorphs, leptictids, perissodactyls, cetartiodactyls, primates, and rodents

(Rosselet 1991, 1993). Besides the squamates, the only other reptile group identified in Dielsdorf is crocodylians (Rosselet 1991). On the basis of its mammalian fauna, Dielsdorf has been suggested to represent a tropical to subtropical environment, with alternating landscapes of dense forests and savannas (Rosselet 1993).

Squamate finds described herein originate from Fissures A, B, and 2, therefore all pertain to a late middle to late Eocene age (MP 16 or MP 17 until MP 20). Few squamate specimens originate from unknown fissures within Dielsdorf, though it is much probable that they originate as well from the three fissures mentioned above; in any case they are also treated as to pertain to a late middle to late Eocene age.

4 Systematic Palaeontology

Squamata Oppel, 1811
Anguimorpha Fürbinger, 1900
Platynota Duméril and Bibron, 1835
Palaeovaranidae Georgalis, 2017
Palaeovaranus Zittel, 1887–1890
Type species: *Palaeovaranus cayluxi* Zittel, 1887–1890.
Palaeovaranus sp.
Figures 1, 2, 3, 4

Material: Fissure A: a left dentary (PIMUZ A/III 234; Figs. 1, 2, 3) and two caudal vertebrae (PIMUZ A/III 626 and PIMUZ A/III 627; Fig. 4).

Description:

Dentary: The dentary is 27 mm long and achieves a maximum height at its posterior end of 5 mm (Figs. 1, 2). The dentary bears six preserved teeth, four of which are rather complete, whereas two fragmentary tooth bases are also visible. In total, there are 13 preserved tooth positions on the dentary. No signs of replacement teeth are discernible outwardly or in the CT scan. Teeth are subpleurodont and their bases demonstrate weak infolding creating low ridges (Fig. 1d, e) formed by plicidentine. There is no sign of serration on the teeth. In virtual longitudinal and horizontal sections through the dentary, several fine structures of the teeth are visible, such as the enamel crowns, the central pulp cavities, and the infolding of the plicidentine in the roots (Fig. 3). The smaller preserved teeth are more or less straight, whereas the larger ones have their dorsal tips directed posteriorly. Meckel's groove is open almost throughout the dentary, is rather narrow at its anterior and middle portions, whereas it widens considerably in the posterior part (Figs. 1b, 2b). As revealed in the 3D model based on the CT scan data (Fig. 2b), this posterior part of the dentary around Meckel's groove shows shallow articular facets for the splenial dorsally and ventrally (extending posteriorly from the eleventh tooth position onward), indicating that this part of Meckel's groove would have been covered by the splenial bone medially. The splenial articular facets end dorsally at slightly posteriorly from the level of the fourth preserved tooth (counting from anteriorly), whereas ventrally end slightly more anteriorly. A facet for the articulation with the angular is also visible (Fig. 2b). The intramandibular septum extends to the posterior end of the preserved tooth row. In labial view (Fig. 1a, b), five elongated labial foramina are present across the length of the dentary, situated at irregular intervals. The foramina enter the dentary and combine into the central alveolar canal (housing the inferior alveolar nerve branch of the fifth or trigeminal nerve) that extends throughout the dentary. In dorsal view (Figs. 1c, 2c), the anteriormost edge of the dentary becomes rather laterally inclined. The ventral surface of the dentary is almost flat across most of its portion with a shallow longitudinal groove being present from about the sixth to the eleventh tooth position from anterior, but it becomes inclined dorsally at its anteriormost part (Fig. 2b, d). It can be the case that this shallow longitudinal groove was for the attachment of the muscle M. geniohyoideus, as it has been suggested for other lizards (Haas 1960).

Caudal vertebrae: Both vertebrae are not completely preserved, with PIMUZ A/III 626 missing most of the right transverse process, both haemapophyses (chevrons), and the dorsal-most edge of the neural spine, and PIMUZ A/III 627 missing both chevrons and parts of the left transverse process and right postzygapophysis (Fig. 4), but both preserve slightly damaged pedicles for articulation with the chevrons. PIMUZ A/III 626 is the larger one (CL = 14.4 mm, PR–PR = 7 mm; Fig. 4a–f), in comparison to PIMUZ A/III 627 (CL = 11.4 mm, PR–PR = 6.9 mm; Fig. 4g–l). In anterior view (Fig. 4a, g), the cotyle is rather deep, large, and elliptical and faces relatively anteroventrally. The prezygapophyses are significantly dorsally tilted. The transverse processes are large, though their distal terminations are not preserved. They are flattened dorsoventrally and extend laterally from the centrum, being almost horizontal at PIMUZ A/III 626 and slightly lateroventral in PIMUZ A/III 627. The diameter of the neural canal is rather small. The neural spine is rather high and becomes gradually thinner distally. In posterior view (Fig. 4b, h), the condyle is large and elliptical. The neural arch is arched and triangular. The postzygapophyses are relatively small-sized. The pedicles for articulation with the chevrons seem to have been relatively thick. In dorsal view (Fig. 4c, i), the neural spine is developed solely on the posterior half of the neural arch. The prezygapophyseal articular facets are broad, with an almost subcircular outline. The transverse processes are situated in the anterior half of the centrum and extend laterally, although, due to preservation, their full length cannot be evaluated. The postzygapophyses are

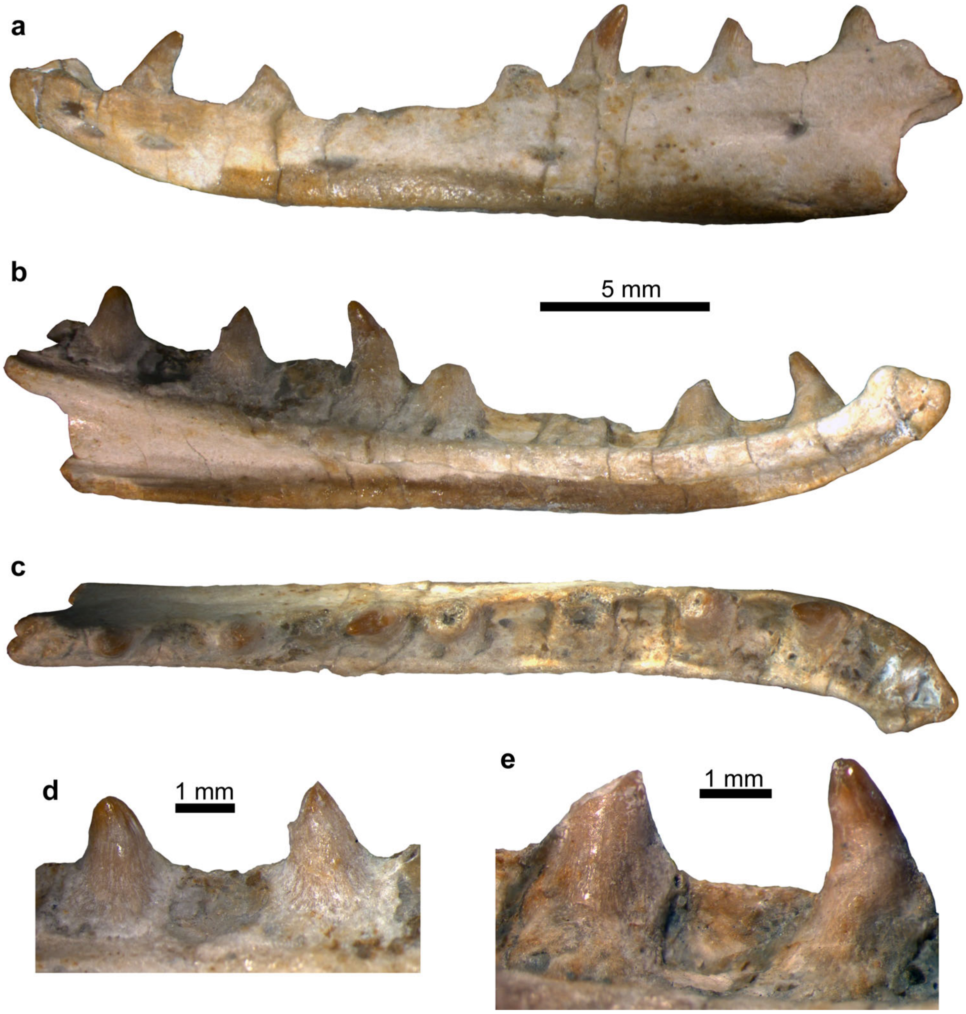

Fig. 1 Left dentary (PIMUZ A/III 234) of *Palaeovaranus* sp., in labial (**a**), medial (**b**), and dorsal (**c**) views; **d**, **e** close up of teeth of the same specimen

relatively small, not surpassing the level of condyle's posterior edge. In ventral view (Fig. 4d, j), the inner surface of the cotyle is largely visible. The pedicles for articulation with chevron bones are located rather close to the condyle [a condition considered to be derived for lizards (Gauthier et al. 2012)] and they face posteroventrally. There are no signs of autotomic septa in either of the two specimens. A longitudinal groove runs throughout the centrum, originating posteriorly between the two pedicles and reaching anteriorly the level of the cotyle. In lateral view (Fig. 4e, f, k, l), both vertebrae are rather elongate, especially PIMUZ A/III 626. The neural spine is posteriorly inclined, forming an angle of about 120^{o} with the neural arch. The neural spine of PIMUZ A/III 626 is wider, especially at its base, in comparison with that of PIMUZ A/III 627. The prezygapophyses extend anteriorly slightly beyond the level of the cotyle.

Remarks: The dentary PIMUZ A/III 234 can be attributed to Palaeovaranidae (and to the currently sole known genus *Palaeovaranus*) based on its overall shape, its recurved teeth, and the presence of plicidentine in its tooth bases (Georgalis 2017; see Kearney and Rieppel 2006 for definition of plicidentine). The two caudal vertebrae (PIMUZ A/III 626 and PIMUZ A/III 627) can be assigned to *Palaeovaranus* based on the absence of autotomic septa and the presence of pedicles for articulation with chevron bones being situated rather close to the condyle (Georgalis 2017).

Palaeovaranids were important components of the Paleogene lizard faunas from Europe, and were for several decades called under the invalid name necrosaurids (e.g., Hoffstetter 1943; Rage 1978, 1988; Augé 2005; Augé and Smith 2009; Rage and Augé 2015). However, Georgalis (2017) recently demonstrated that the name *Necrosaurus* Filhol 1876 was a nomen nudum and not available for nomenclatural purposes according to ICZN (1999), with the appropriate genus name being instead *Palaeovaranus* Zittel, 1887–1890. Furthermore, after a long held misconception over the authorship and the exact type material of the genotype of *Palaeovaranus*, Georgalis (2017) clarified these issues in detail, and placed this genus into his new family Palaeovaranidae. Two valid species of *Palaeovaranus* are currently known, i.e., the type species,

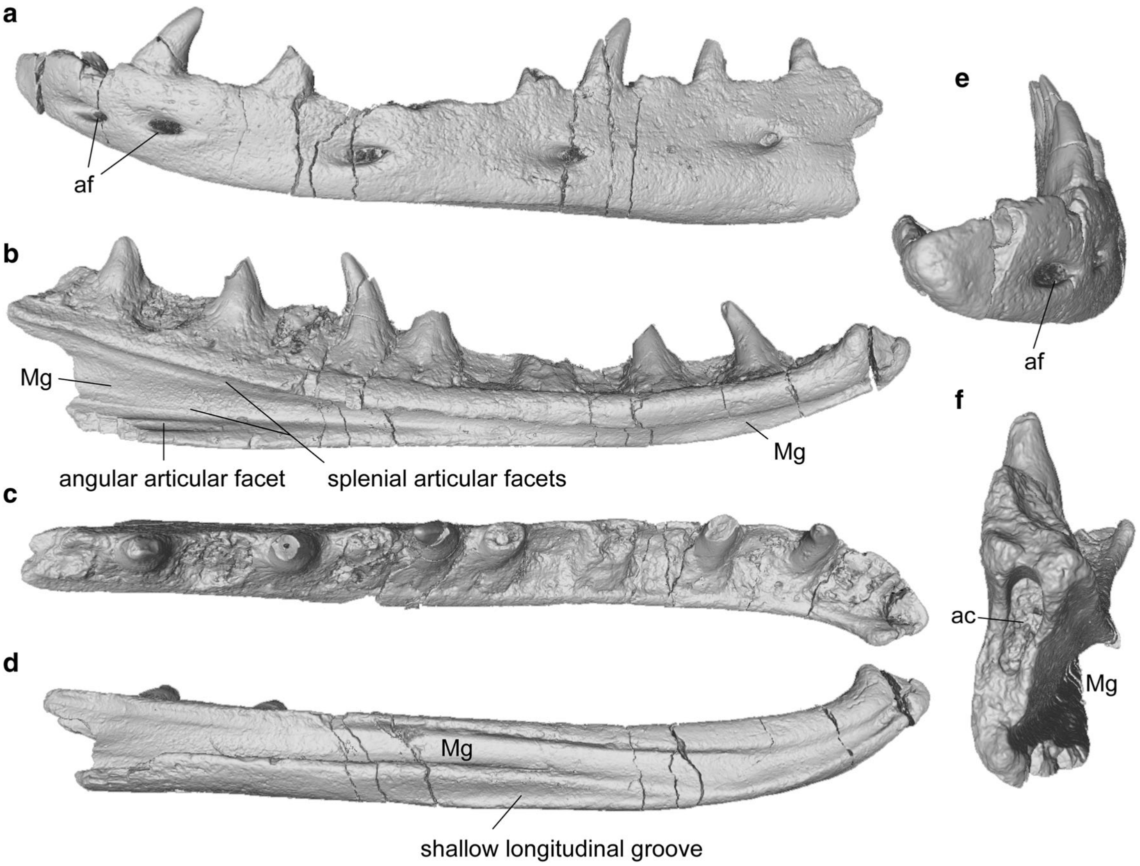

Fig. 2 3D model of the left dentary (PIMUZ A/III 234) of *Palaeovaranus* sp., in labial (**a**), medial (**b**), dorsal (**c**), ventral (**d**), anterior (**e**), and posterior (**f**) views. *ac* alveolar canal, *af* alveolar foramen, *Mg* Meckel's groove

Palaeovaranus cayluxi Zittel, 1887–1890, from the Eocene of France, and *Palaeovaranus giganteus* (Kuhn, 1940b) from the Eocene of Germany and France, however, several indeterminate records have additionally been described from the Eocene and Oligocene of Western and Central Europe (Georgalis 2017).

The palaeovaranid dentary from Dielsdorf shares an overall resemblance and several anatomical features with both *Palaeovaranus cayluxi* and *Palaeovaranus giganteus*, but there are also several differences from these two taxa in terms of the shape, size, and curvature of the teeth, the number and position of the labial foramina, the extent and broadness of Meckel's groove, and the lateral inclination of the symphyseal area in dorsal view. Nevertheless, the exact phylogenetic relationships among *Palaeovaranus* spp. are not yet fully resolved and there are still even major issues regarding their precise affinities with other lizard groups (Georgalis 2017). As such, we here refrain from referring the Swiss specimen to either one of the two above mentioned taxa or name it as a new species, and we instead rather prefer to refer it as *Palaeovaranus* sp. An interesting feature in the Dielsdorf dentary is the fact that Meckel's groove is open almost throughout the entire specimen, despite the fact that it significantly diminishes in width in its anterior and mid-portions. This is in contrast with other known dentaries of *Palaeovaranus*, in which Meckel's groove is almost entirely closed anteriorly or is at least extremely small [e.g., Geiseltal (middle Eocene): see figure in Haubold 1977; Phosphorites du Quercy (Eocene or Oligocene): see figures in Fejérváry 1935; Kuhn 1940b; Augé 2005; Hampshire, England (late Eocene): see figure in Klembara and Green 2010]. Furthermore, the anteriormost edge of the dentary becomes rather laterally inclined in dorsal view, a feature that is reminiscent of certain extinct and extant helodermatids (e.g., Figures in Bhullar and Smith 2008), including also the only named European taxon, *Eurheloderma gallicum* Hoffstetter, 1957 from the Eocene of the Phosphorites du Quercy, France (Hoffstetter 1957). The dentition, however, in helodermatids is different than the Dielsdorf form. Nevertheless, a lateral outward bulge of the parapet of the anteriormost portion of the dentary in dorsal view has been documented also for other palaeovaranids, although not to the same curvature degree (e.g., Klembara and Green 2010). Furthermore, the micro-CT scan of the dentary from Dielsdorf (Fig. 3) confirms the presence of plicidentine in

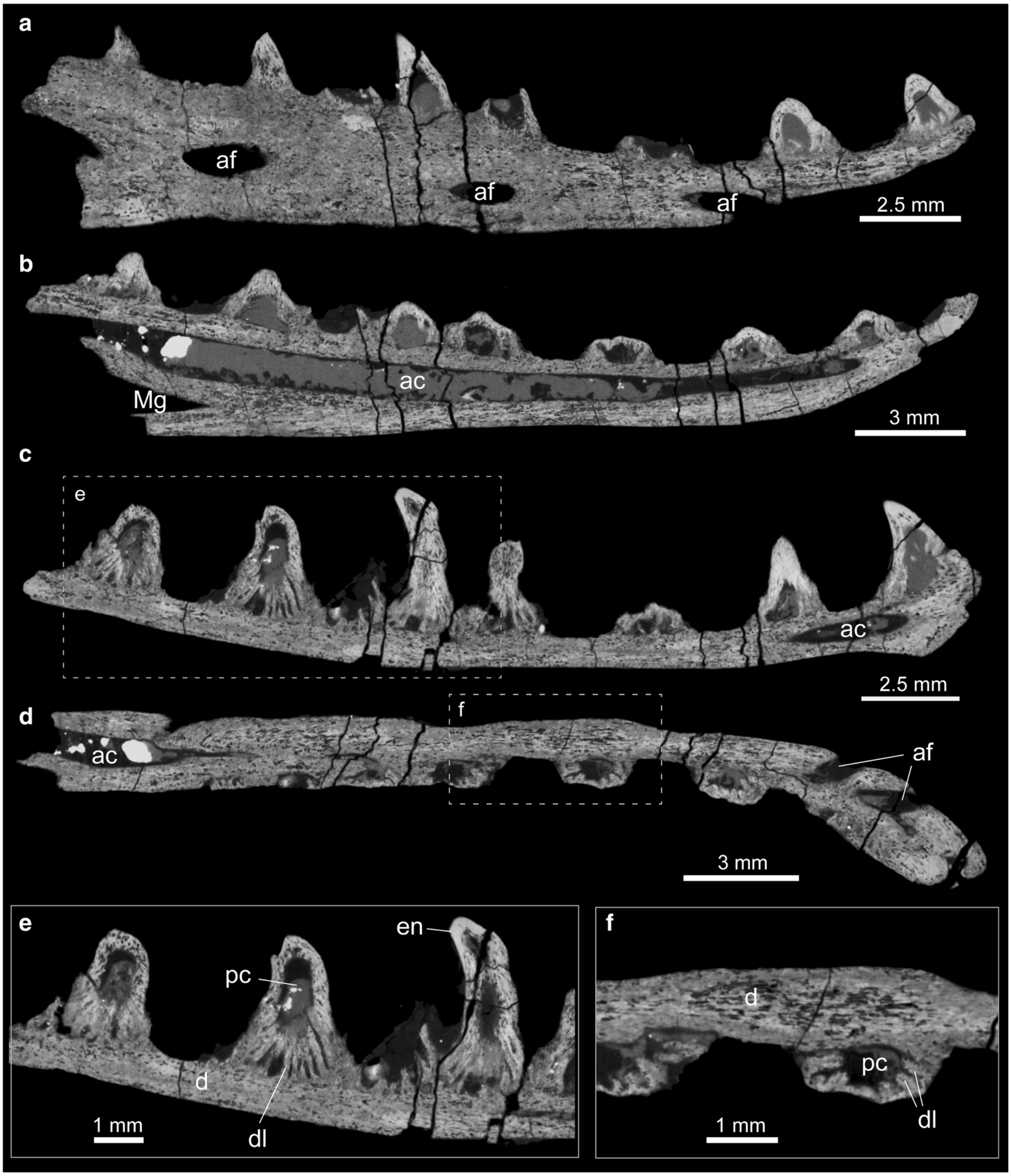

Fig. 3 Virtual sections of the CT scan data of the left dentary (PIMUZ A/III 234) of *Palaeovaranus* sp. **a**–**c** Longitudinal sections though the specimen focusing on different aspects of the dentary bone and the teeth; **d** horizontal section of the specimen showing the tooth roots in cross-section; **e** close-up of the tooth structure with plicidentine, pulp cavity and enamel crown; **f** close-up of the tooth base with dentine lamellae of the plicidentine extending into the pulp cavity. *I–VIII* tooth or remnants of tooth bases in the dentary, *ac* alveolar canal, *af* alveolar foramen, *d* dentary, *dl* dentine lamellae, *en* enamel, *Mg* Meckel's groove, *pc* pulp cavity

Palaeovaranus, a feature that has been variously suggested to be present in that genus (Augé and Smith 2009; Klembara and Green 2010; Georgalis 2017). Note that plicidentine is otherwise present in several vertebrate groups, including also varanids (Kearney and Rieppel 2006; Georgalis et al. 2017).

Despite the diagnostic features observed on palaeovaranid caudal vertebrae (Georgalis 2017), which on certain occasions can permit a direct identification, these elements have not been frequently described and figured in the literature. As such, the only studies, which have described and documented palaeovaranid caudal vertebrae have so far been those dealing with such specimens from

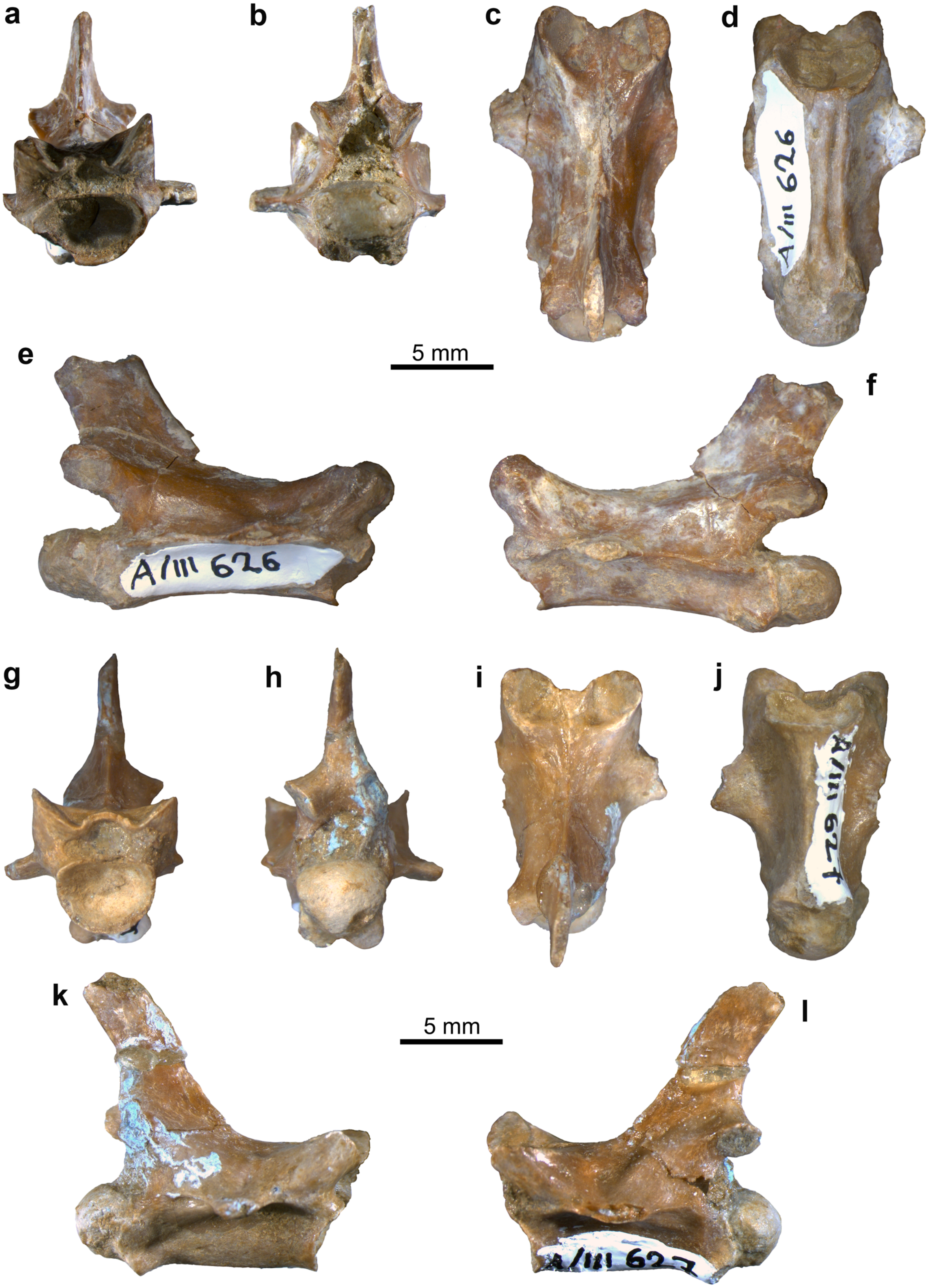

Fig. 4 Caudal vertebrae of *Palaeovaranus* sp.: **a**–**f** caudal vertebra (PIMUZ A/III 626) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), right lateral (**e**), and left lateral (**f**) views; **g**–**l** caudal vertebra (PIMUZ A/III 627) in anterior (**g**), posterior (**h**), dorsal (**i**), ventral (**j**), right lateral (**k**), and left lateral (**l**) views

the late Eocene (MP 18) of Sainte Néboule, Quercy, France (Rage 1978), the late Eocene (MP 18) of the Isle of Wight, England (Rage and Ford 1980), the indeterminate Eocene of an imprecisely known locality in the Phosphorites du Quercy [part of the syntype series of *Palaeovaranus filholi* De Stefano, 1903, and material formerly referred to *Iguana europaea* by De Stefano (1903)], and the early Oligocene of Valbro, also in Quercy (Rage and Augé 2015).

Considering that the Dielsdorf material was not found associated together, it is impossible to state with absolute certainty that both the cranial and the postcranial elements pertained to the same taxon. Following, however, a biogeographic rationale, it is much more parsimonious to treat the material as pertaining to a single species, taking into consideration that many (though not all) coeval European palaeovaranid-bearing localities yielded one species of *Palaeovaranus* (Augé 2005; Georgalis 2017). This assumption is further supported by the absolute size of all specimens, which denotes an origination from animals of similar size. Differences among the two caudal vertebrae are mostly confined to size, but also to the wideness of the neural spine in lateral view, the orientation and position of the transverse processes, the shape of the cotyle and condyle, and the degree of vaulting of the neural arch. Such differences could be probably attributed either to intracolumnar variation within the tail of the animal or even ontogenetic variation.

It is worth mentioning that the dentary PIMUZ A/III 234 was the first squamate fossil described from Dielsdorf (Hünermann 1978). In that paper, Hünermann (1978) described and figured that specimen and referred it to Varanoidea; curiously, however, Hünermann (1978) made preliminary comparisons of the Swiss material only with varanids, neglecting totally the palaeovaranids. Rosselet (1991) referred that dentary to as "*Necrosaurus* sp." and he tentatively referred to the same taxon the two caudal vertebrae described herein, though he provided no figure for that material.

Serpentes Linnaeus, 1758
Alethinophidia Nopcsa, 1923
Macrostomata Müller, 1831
"Booidea" Gray, 1825
Genus *Palaeopython* Rochebrune, 1880
Type species: *Python cadurcensis* Filhol, 1877a.
Palaeopython helveticus sp. nov.
Figures 5, 6, 7, 8, 9, 10, 11

Holotype: PIMUZ A/III 634, a (probably anterior mid-) trunk vertebra of an adult individual (Figs. 5, 6).

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

Referred material: Fissure A: a posterior trunk vertebra of a (probably) sub-adult individual (PIMUZ A/III 633; Fig. 7f–k), a mid-trunk vertebra of a young (subadult or juvenile) individual (PIMUZ A/III 637; Fig. 8g–l), and two posterior trunk vertebrae of rather young individual(s) (PIMUZ A/III 631 and PIMUZ A/III 632; Figs. 10, 11); Fissure 2: an anterior trunk vertebra of an adult individual (PIMUZ A/III 635; Fig. 7a–e); Fissure B: a mid-trunk vertebra of a young (subadult or juvenile) individual (PIMUZ A/III 636; Figs. 8a–f, 9).

Geographic and stratigraphic distribution: MP 16–MP 20, late Bartonian–late Priabonian, late middle–late Eocene, Dielsdorf, Fissures A, B, and 2, Zurich Canton, Switzerland.

Diagnosis: *Palaeopython helveticus* sp. nov. can be assigned to "booid" snakes on the basis of possessing strongly built vertebrae, the centrum triangular and wider than long in ventral view, the vertebrae higher than long in lateral view, prezygapophyseal accessory processes relatively reduced or absent, and paradiapophyses non-divided or only slightly divided into diapophyseal and parapophyseal portions. *Palaeopython helveticus* sp. nov. can be differentiated from all other "booid" snakes by the unique combination of the following characters: an extremely high and vaulted neural arch, a feature that is most prominent in anterior mid-trunk vertebrae, but still present in posterior trunk vertebrae; rather vaulted neural arch also in vertebrae of subadult and juvenile individuals (though not so vaulted as in adult ones); vertebral size large, with CL of adult specimens exceeding 10 mm; high neural spine in lateral view, especially in mid-trunk vertebrae; thick neural spine in dorsal view; a rather thick zygosphene in anterior view in vertebrae of adult individuals; the centrum much widened anteriorly; dorsal roof of the zygosphene relatively convex in anterior view, with its lateral edges not upturned dorsally; zygosphene wider than the cotyle in anterior view, at least in adult individuals; prezygapophyses extending rather laterally in dorsal view; a deep zygantrum; a massive and rather deep cotyle; deep paracotylar fossae with no paracotylar foramina; usual presence of two small neural spine foramina, at least in adult and subadult specimens; shallow interzygapophyseal constriction.

Etymology: The species epithet "*helveticus*" derives from Confoederatio Helvetica, the Latin official name for Switzerland, referring to the geographic origin of the new taxon.

Description of the holotype PIMUZ A/III 634: This is the largest (CL = 10.5 mm, PR–PR = 18 mm) and one of the best preserved snake vertebrae from Dielsdorf, missing only part of the left postzygapophysis and a small portion of the right postzygapophysis (Figs. 5, 6). In anterior view (Figs. 5a, 6a), the zygosphene is rather thick, has a trapezoidal shape, and its dorso-lateral edges extend laterally. Its dorsal roof is relatively convex. The width of the

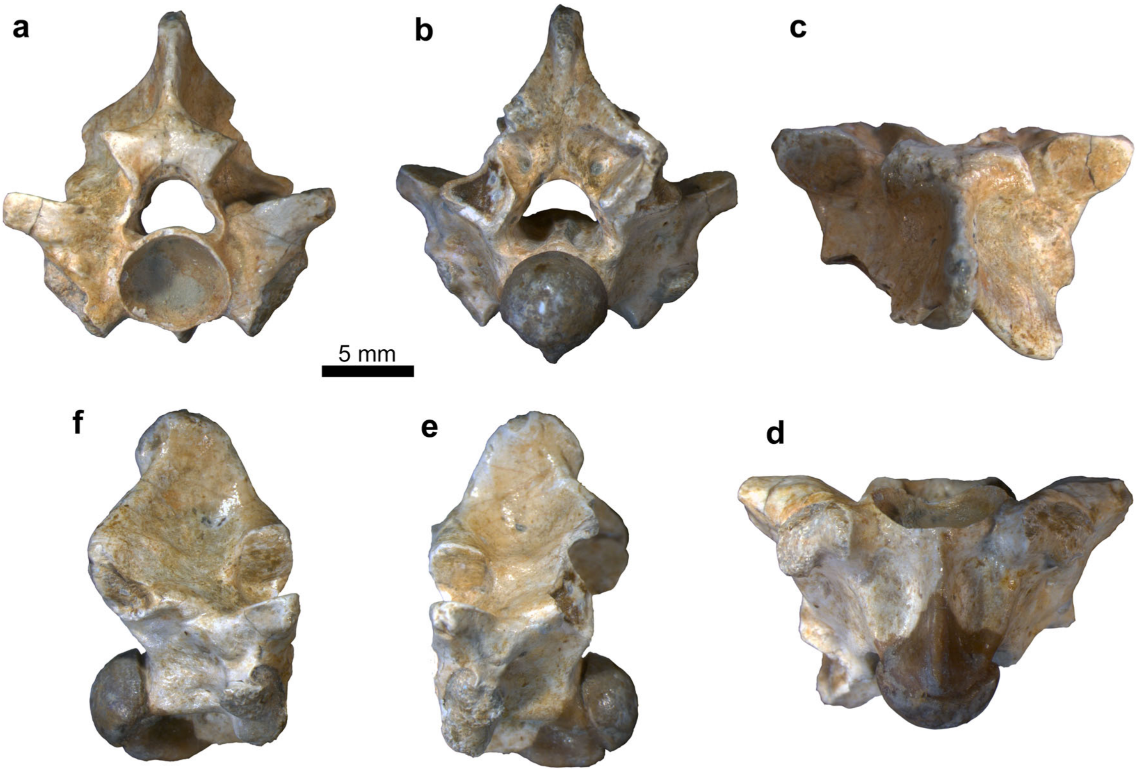

Fig. 5 Holotype trunk vertebra (PIMUZ A/III 634) of *Palaeopython helveticus* sp. nov., in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views

zygosphene (7.3 mm) is slightly larger than that of the cotyle. The surface of the zygosphene is not smooth, as there is a small median tubercle at around its mid-portion, near its ventral level. The neural spine is relatively massively built without dorsal thickening. The neural canal is almost triangular in shape and there is a distinct longitudinal ridge ("epapophysis" sensu Holman 2000) at the middle of its bottom level. The cotyle is large, rounded (with slightly depressed its ventral margin), and rather deep. No paracotylar foramina are present. The prezygapophyses are relatively thick and extend well above the level of the dorsal level of the cotyle, reaching almost the dorsal surface of the neural canal. The paradiapophyses extend below the ventral level of the cotyle. In posterior view (Figs. 5b, 6b), the neural arch is extremely vaulted. The zygantrum is deep and wide, being also wider than the condyle. A pair of deep foramina is present at depth in the zygantrum. The condyle is rounded, large, and robust. In dorsal view (Figs. 5c, 6c), the vertebra is wider than long. The neural spine covers most of the midline of the neural arch, commencing shortly after the zygosphenal lip. The zygosphene is almost straight, with only slight signs of the two lateral indistinct lobes. The prezygapophyses are anterolaterally inclined and extend much more laterally than anteriorly. The prezygapophyseal articular facets are large and oval. The interzygapophyseal constriction is shallow. In ventral view (Figs. 5d, 6d), the centrum is much wider than long, being much more widened anteriorly than posteriorly. The paradiapophyses are not divided into diapophyseal and parapophyseal portions. The haemal keel runs throughout the whole midline of the centrum, commencing immediately right from the ventral lip of the cotyle, and it is relatively sharp. Two small subcentral foramina are present, being situated at each side of the haemal keel, at around its mid-portion. In lateral view (Figs. 5e, f, 6e, f), the vertebra is higher than long. The neural spine is high, ascending gradually, and both its anterior and posterior margins are inclined posteriorly. Its dorsal surface is slightly eroded, but it was overhanging posteriorly. The base of the neural spine commences above the zygosphenal articular facets. There is one small foramen on each side of the neural spine. The zygosphenal articular facets are rather large and almost circular. The interzygapophyseal ridges are prominent. Two large lateral foramina are present, one at each lateral side of the vertebra, right below the interzygapophyseal ridge. The subcentral ridges are distinct, almost straight, commence almost immediately after the paradiapophyses, and terminate prior to the condylar neck. The paradiapophyses are massive and not strongly divided into diapophyseal and parapophyseal portions. The subcentral foramina are well visible also from this view. The haemal keel is rather high,

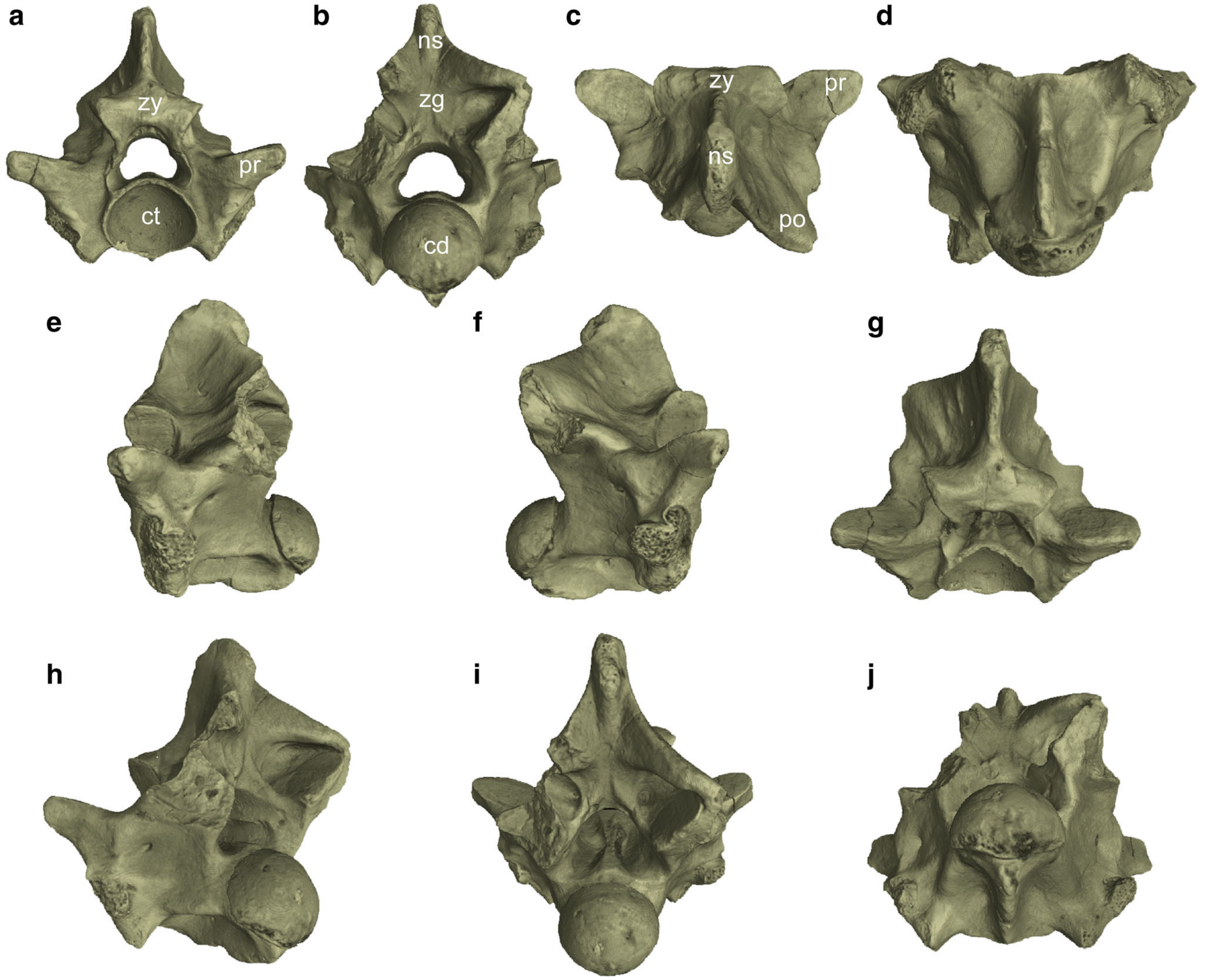

Fig. 6 3D models of the holotype trunk vertebra (PIMUZ A/III 634) of *Palaeopython helveticus* sp. nov., in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**), anterodorsal (**g**), posterolateral (**h**), posterodorsal (**i**), and posteroventral (**j**) views. *ct* cotyle, *cd* condyle, *ns* neural spine, *po* postzygapophysis, *pr* prezygapophysis, *zg* zygantrum, *zy* zygosphene

especially at its posterior part, where it projects ventrally, and resembles a short but massive hypapophysis (plate-like haemal keel sensu Auffenberg 1963); its posterior edge reaches the level of the condyle.

Description of referred material: PIMUZ A/III 635 is probably an anterior trunk or at least anterior mid-trunk vertebra, judging from the presence of a hypapophysis, the smaller size (PR–PR = 15.2 mm), and the rather short prezygapophyses in anterior view. The vertebra apparently belongs to an adult individual. However, not a lot can be said about this specimen, as it is a much more incomplete vertebra than the holotype, missing all its dorsal surface (i.e., the whole neural arch, neural spine, zygosphene, zygantrum, and the right postzygapophysis), as also most of the condyle and part of the ventral portion of the hypapophysis (Fig. 7a–e). In anterior view (Fig. 7a), the prezygapophyses are rather short and dorsally inclined. The cotyle is large and almost circular in shape, with its ventral margin slightly depressed. No paracotylar foramina are present. The hypapophysis is clearly visible, projecting below the ventral level of the cotyle. In posterior view (Fig. 7b), the postzygapophyses (only the left one is preserved) are massive and their dorsolateral edges are inclined downwards. The condyle and the posterior portion of the hypapophysis are strongly eroded. In dorsal view (Fig. 7c), the postzygapophyseal articular facets are large and subtriangular. The prezygapophyses are facing more dorsally than in the holotype, but still they extend laterally. In ventral view (Fig. 7d), the hypapophysis is sharp. The paradiapophyses are massive and there is no clear distinction between the diapophyseal and parapophyseal portions. In lateral view (Fig. 7e), the hypapophysis projects

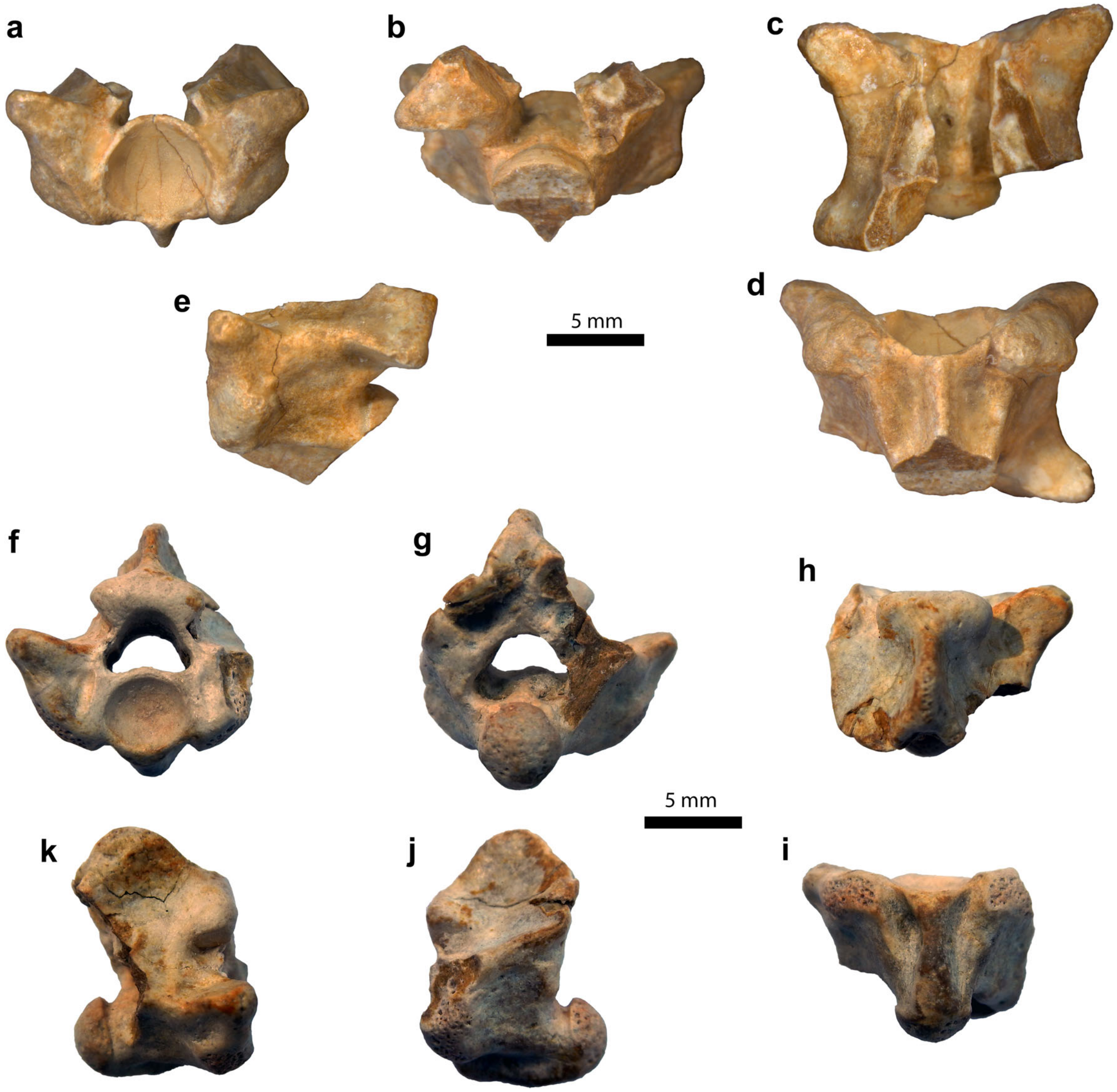

Fig. 7 Trunk vertebrae of *Palaeopython helveticus* sp. nov.: **a**–**e** trunk vertebra (PIMUZ A/III 635) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f**–**k** trunk vertebra (PIMUZ A/III 633) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), left lateral (**j**), and right lateral (**k**) views

gradually posteroventrally, though the extent of its ventral projection cannot be evaluated as this structure is broken.

PIMUZ A/III 633 is a relatively small vertebra (CL = 7.4 mm), missing most of the left prezygapophysis and most portions of both postzygapophyses (Fig. 7f–k). Its overall size and the downward inclination of the edges of the zygosphene denote that it does not pertain to an adult individual; rather, it is probably a sub-adult. In anterior view (Fig. 7f), the zygosphene is somewhat arched and its dorsolateral edges are facing downwards. As such, both the dorsal and ventral surfaces of the zygosphene are convex. The zygosphene is thinner than in the holotype. The prezygapophyses are much dorsally inclined. The neural canal is almost trapezoidal in shape and there is a distinct median ridge ventrally (“epapophysis” sensu Holman 2000). Deep and vertically elongated paracotylar fossae are present, with no paracotylar foramina. The cotyle is relatively small and almost circular in shape. In posterior view (Fig. 7g), most of the posterior portion of the neural arch is damaged but it seeems nevertheless that it has been vaulted. The condyle is small and almost circular in shape. In dorsal view (Fig. 7h), the zygosphenal lip is almost straight, with no lateral or median lobes present. The prezygapophyses extend laterally and only slightly dorsally. The prezygapophyseal articular facets are oval-shaped. The neural spine is thick. In ventral view (Fig. 7i), the centrum is widened anteriorly. The haemal keel is thick and runs throughout the midline of the centrum; it is almost uniform in shape and thickness, with only a slight constriction at its anterior portion. The paradiapophyses are

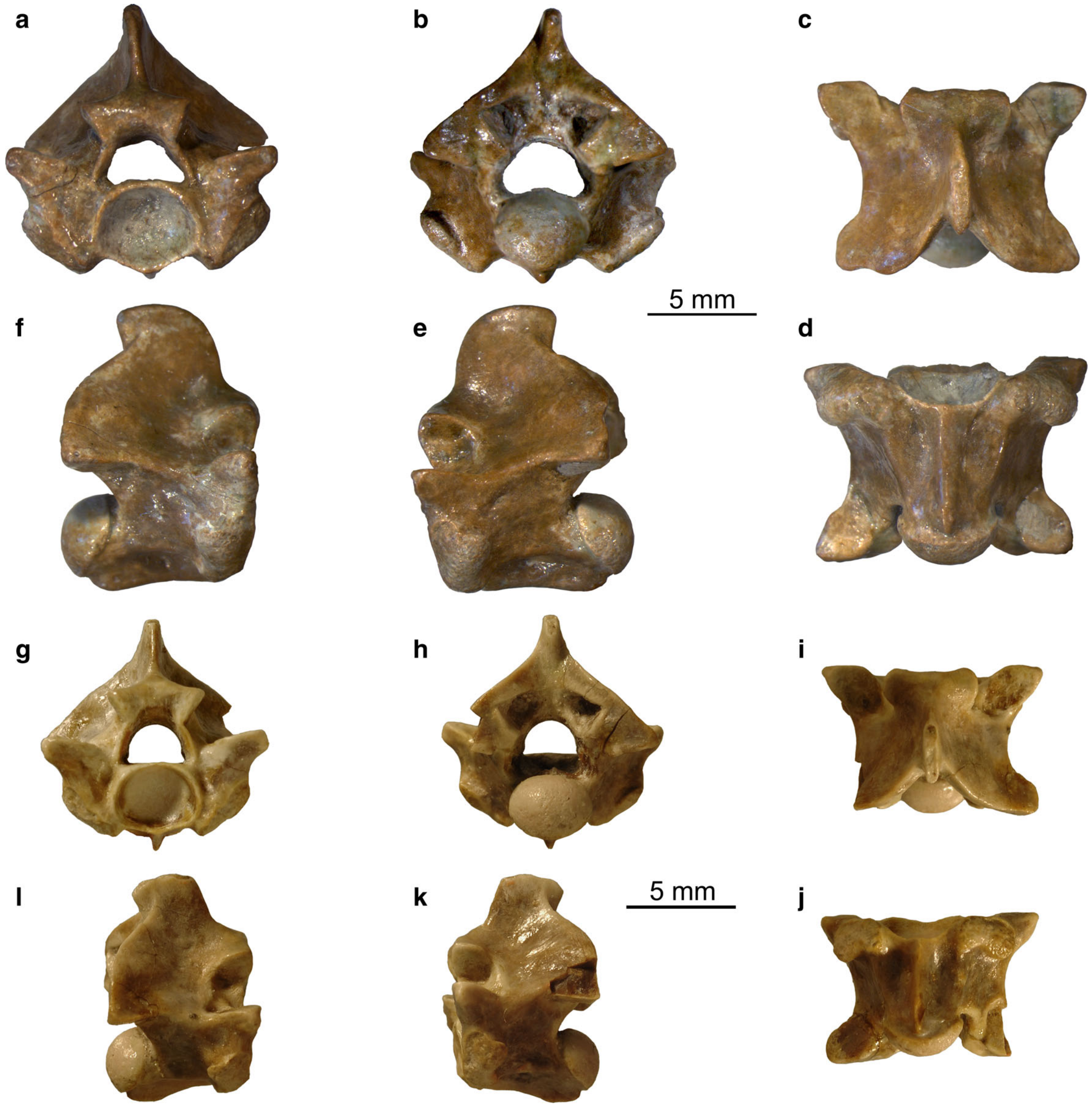

Fig. 8 Trunk vertebrae of young individuals of *Palaeopython helveticus* sp. nov.: **a**–**f** trunk vertebra (PIMUZ A/III 636) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views; **g**–**l** trunk vertebra (PIMUZ A/III 637) in anterior (**g**), posterior (**h**), dorsal (**i**), ventral (**j**), left lateral (**k**), and right lateral (**l**) views

rather eroded but seem to have been large in life. In lateral view (Fig. 7j–k), the vertebra is proportionally higher than long. The neural spine is moderate in height, covering most of the midline of the neural arch. It anteriorly commences almost immediately behind the zygosphene and gradually ascends in height. The haemal keel is prominent and projects ventrally across its length. There is a distinct condylar neck.

PIMUZ A/III 636 is a complete specimen, apparently the most complete vertebra among the Diesldorf material (Figs. 8a–f, 9). The vertebra is relatively moderate in size (CL = 8.3 mm, PR–PR = 11.8 mm); its rather sharp haemal keel and the overall shape and size denote an origination of that vertebra from the mid-trunk region (more precisely probably the anterior mid-trunk region), probably pertaining to a subadult individual. In anterior view (Figs. 8a, 9a), the zygosphene is moderately thick. Its dorsal roof is convex. The width of the zygosphene is smaller than that of the cotyle. The prezygapophyses are relatively small and are rather dorsally inclined, reaching almost the dorsal level of the neural canal. The cotyle is relatively elliptical in shape. Paracotylar fossae are present next to each side of the cotyle. In posterior view (Fig. 8b, 9b), the neural arch is distinctly vaulted. The zygantrum is deep. The condyle is elliptical in shape. In dorsal view (Figs. 8c, 9c), the zygosphenal lip is almost straight, with

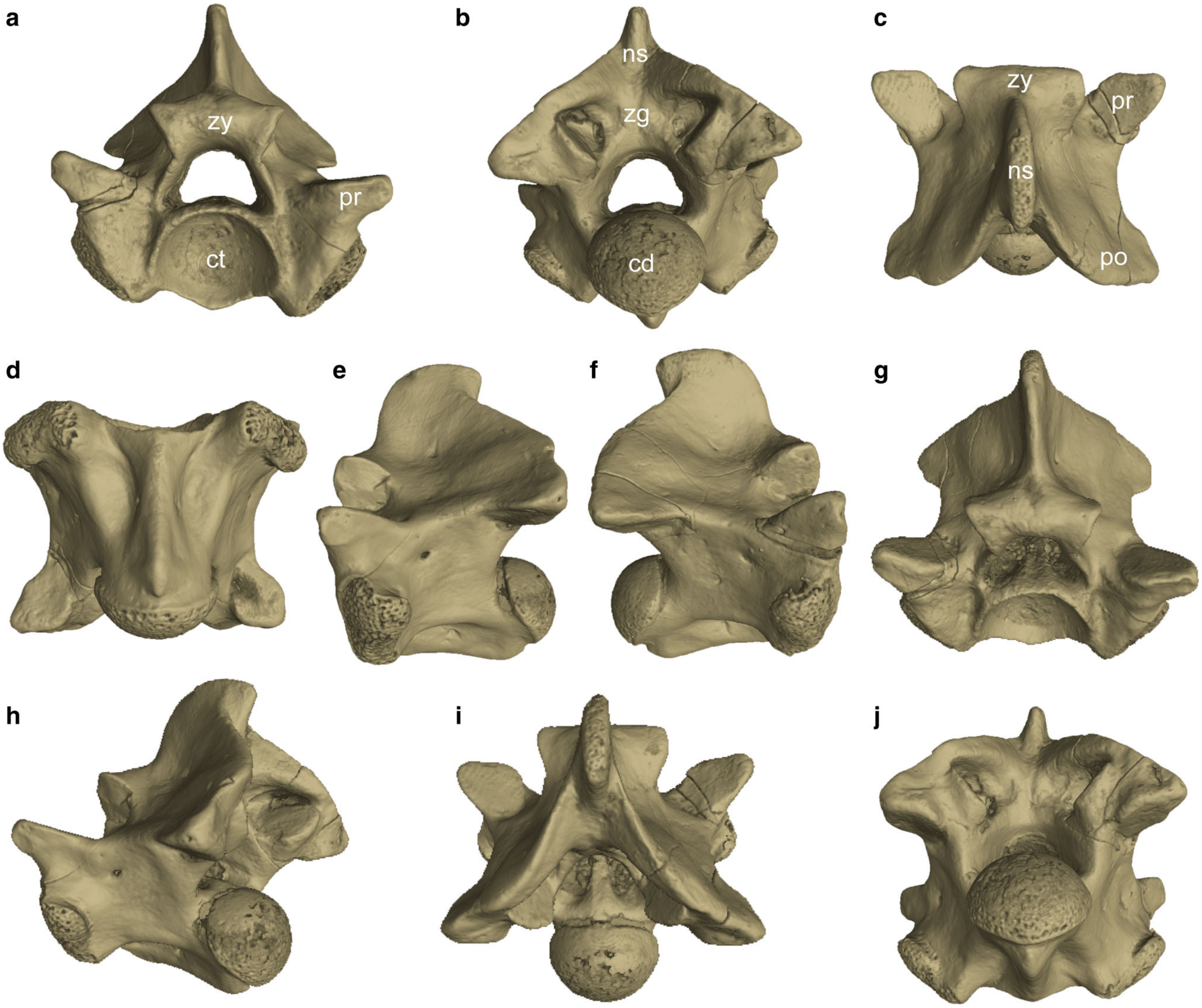

Fig. 9 3D models of a trunk vertebra (PIMUZ A/III 636) of a young individual of *Palaeopython helveticus* sp. nov., in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**), anterodorsal (**g**), posterolateral (**h**), posterodorsal (**i**), and posteroventral (**j**) views. *ct* cotyle, *cd* condyle, *ns* neural spine, *po* postzygapophysis, *pr* prezygapophysis, *zg* zygantrum, *zy* zygosphene

slight signs of lateral and median lobes. The prezygapophyses are rather laterally inclined. The prezygapophyseal articular facets are large and almost triangular in shape. The postzygapophyses extend laterally, almost to the same extent as the prezygapophyses. The paradiapophyses are visible below the prezygapophyseal articular facets. The posterior median notch of the neural arch is deep. In ventral view (Figs. 8d, 9d), the centrum is widened anteriorly (though not as much as the large vertebrae of adults). The haemal keel is rather sharp and thin; it commences anteriorly from the ventral lip of the cotyle and terminates at the condylar neck. Two subcentral foramina are present, one at each side of the haemal keel, situated at around its mid-length. The paradiapophyses are massive, with no clear division among the diapophyseal and parapophyseal parts. The postzygapophyseal articular facets are triangular to oval-shaped. In lateral view (Figs. 8e–f, 9e–f), the vertebra is higher than long. The neural spine is relatively short; its anterior margin is widely rounded and its posterior margin is posteriorly inclined. The neural spine commences at the level of the posterior border of the zygosphene and seems to become high rather abruptly (and not gradually as in adult specimens, including the holotype). Similarly to the holotype, there is a foramen on each lateral side of the neural spine. The postzygapophyses extend posteriorly up to the same level as the posterior level of the condyle. Two lateral foramina are present, one at each side of the vertebra, situated below the interzygapophyseal ridges. The subcentral ridges are

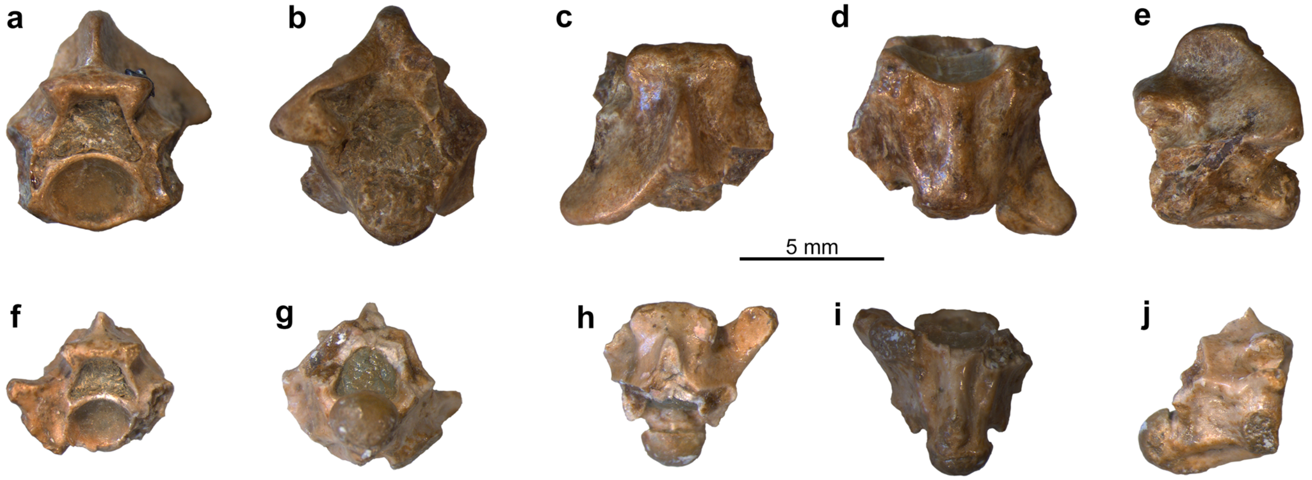

Fig. 10 Trunk vertebrae of even younger individuals of *Palaeopython helveticus* sp. nov: **a**–**e** trunk vertebra (PIMUZ A/III 632) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), and left lateral (**e**) views; **f**–**j** trunk vertebra (PIMUZ A/III 631) in anterior (**f**), posterior (**g**), dorsal (**h**), ventral (**i**), and right lateral (**j**) views

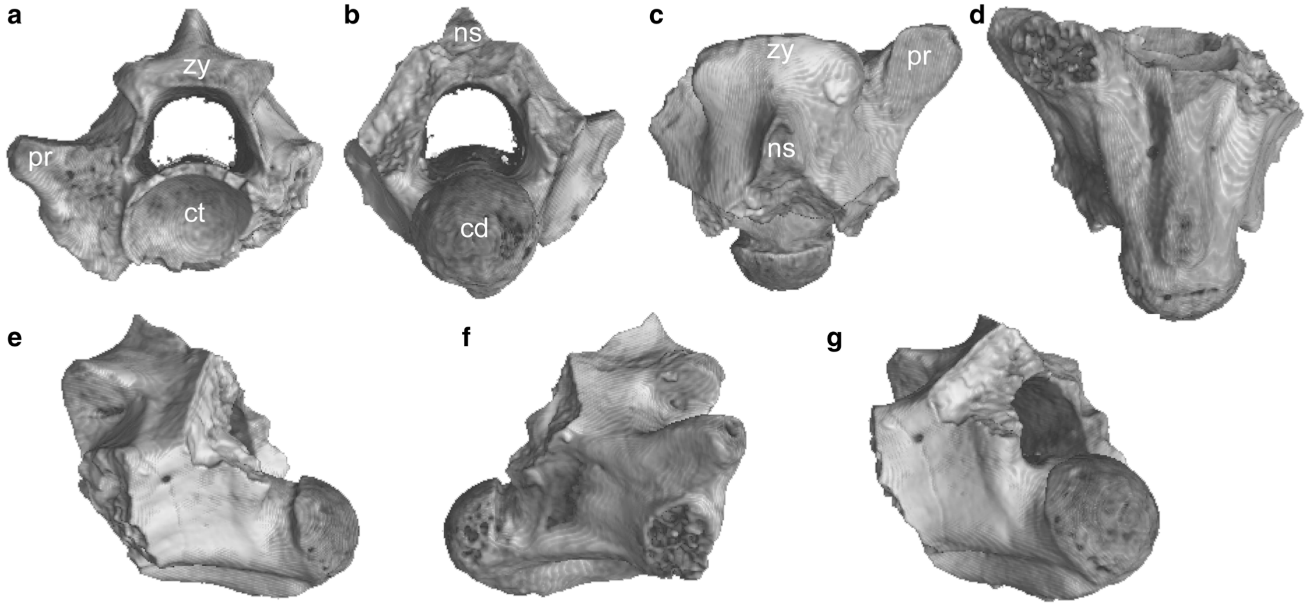

Fig. 11 3D models of a trunk vertebra (PIMUZ A/III 631) of a young individual of *Palaeopython helveticus* sp. nov., in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**), and posterolateral (**g**) views. *ct* cotyle, *cd* condyle, *ns* neural spine, *po* postzygapophysis, *pr* prezygapophysis, *zg* zygantrum, *zy* zygosphene

distinctly convex. The subcentral foramina are visible from this view as well. There is a slight condylar neck.

The vertebra PIMUZ A/III 637 is also a rather complete specimen, missing only part of the left postzygapophysis (Fig. 8g–l). It is almost identical to PIMUZ A/III 636 described above, although it is smaller in size (CL = 6.6 mm, PR–PR = 11.8 mm). Its relatively sharp haemal keel, the deep subcentral grooves, and the overall shape and size denote an origination of that vertebra from the mid-trunk or posterior middle trunk region, probably pertaining to a subadult individual. In anterior view (Fig. 8g), the zygosphene is convex. The prezygapophyses are dorsally inclined. The cotyle is relatively elliptical. Deep paracotylar fossae are present next to the cotyle. In posterior view (Fig. 8h), the neural arch is much vaulted. The zygantrum is deep. The condyle is large and elliptical. In dorsal view (Fig. 8i), the zygosphene is slightly concave with two small lateral lobes present. The prezygapophyses extend laterally. The prezygapophyseal articular facets are relatively large and subtriangular. Minute prezygapophyseal accessory processes are present. The postzygapophyses extend laterally, almost reaching the same level as the prezygapophyses. The posterior median notch of the neural arch is deep. In ventral view (Fig. 8j), the centrum is widened anteriorly [though again not as much as in adult specimens (including the holotype)]. The haemal keel is rather sharp; it runs most of the midline of the centrum. The paradiapophyses are large, with no clear distinction among the diapophyseal and parapophyseal portions. The postzygapophyseal articular facets are large and almost triangular to oval in shape. In lateral view (Fig. 8k–l), the vertebra is higher than long. The neural spine is relatively short. It is posteriorly inclined and there is a distinct infolding at its dorso-posterior part. It commences anteriorly behind the level of the zygosphene. The zygosphenal facets are deep. The subcentral ridges are straight to only slightly convex. The haemal keel projects ventrally and this projection is more prominent across its posterior half.

PIMUZ A/III 632 is a small vertebra (CL = 5 mm), missing both prezygapophyses and most of the right postzygapophysis, while the paradiapophyses are much eroded (Fig. 10a–e). Judging from the rather small size, the overall shape, the large diameter of the neural canal, the thickness of the zygosphene, and the thickness of the haemal keel, it seems to pertain to a rather young individual and to originate from around the posterior trunk region. In anterior view (Fig. 10a), the zygosphene is thin, with its dorsal roof almost straight. The neural canal is trapezoidal in shape. The cotyle is large, distinctly elliptical in shape, and wider than the zygosphene. In posterior view (Fig. 10b), the neural arch is much vaulted. In dorsal view (Fig. 10c), the zygosphene is almost straight. The neural spine is moderately thick. The posterior median notch of the neural arch is deep. In ventral view (Fig. 10d), the centrum is anteriorly widened. The haemal keel is thick and seems to run most of the midline of the centrum; it is in uniform in shape and thickness throughout its length, with the exception of only a rather slight constriction at around its mid-height. The postzygapophyseal articular facets are enlarged and oval-shaped. In lateral view (Fig. 10e), the vertebra is higher than long. The neural spine is rather short. The dorsal level of the neural spine is almost straight and its posterior edge is slightly posteriorly inclined. The subcentral ridges are strongly convex. The haemal keel projects ventrally from the centrum and its ventral level is almost straight.

PIMUZ A/III 631 is a rather small vertebra (CL = 4.2 mm, estimated PR–PR around 6 mm), missing the left prezygapophysis, both postzygapophyses, most of the neural spine and the posterior portion of the neural arch, while the paradiapophyses are strongly eroded (Figs. 10f–j, 11). Judging from the rather small size, the overall shape, the thickness of the zygosphene, and the thickness of the haemal keel, it seems to pertain to a rather young individual and to originate from around the posterior trunk region. In anterior view (Figs. 10f, 11a), the zygosphene is thin, with its dorsal margin being slightly convex. The neural canal is almost trapezoidal in shape. The prezygapophyses are dorsally inclined, though to a much lesser degree than in vertebrae of adult specimens. The cotyle is relatively large and elliptical. Deep paracotylar fossae are present next to each side of the cotyle. In posterior view (Figs. 10g, 11b), the neural arch is rather vaulted. The condyle is relatively large and slightly elliptical in outline. In dorsal view (Figs. 10h, 11c), the zygosphene is eroded, though it seems to have been relatively convex. The prezygapophyses are elongated and are anterolaterally inclined. The prezygapophyseal articular facets are elongated and oval in shape. The neural spine is moderately thick. In ventral view (Figs. 10i, 11d), the centrum is widened anteriorly, though not to the same extent as in vertebrae of adult individuals. The haemal keel is moderately thick, covering most of the midline of the centrum, but terminating posteriorly before the condylar neck. Two subcentral foramina are present, being relatively large and situated at each side of the haemal keel. In lateral view (Figs. 10j, 11e, f), the vertebra seems to have been relatively higher than long. The zygosphenal facets are large. Lateral foramina are present below the interzygapophyseal ridges. A slight, small condylar neck is present. The subcentral ridges are almost straight to slightly convex.

Intracolumnar and ontogenetic vertebral variability: Fully adult individuals of *Palaeopython helveticus* sp. nov. seem to be represented solely by the holotype PIMUZ A/III 634 and the referred specimen PIMUZ A/III 635, whereas PIMUZ A/III 633 seems to represent an earlier ontogenetic stage, probably a sub-adult. PIMUZ A/III 636 and PIMUZ A/III 637 seem to represent younger sub-adults or even juvenile individuals, while PIMUZ A/III 632 and PIMUZ A/III 631 seem to pertain to even younger individuals. Trunk vertebrae of adult individuals of *Palaeopython helveticus* sp. nov. are characterized by large size, a rather vaulted neural arch, a thick zygosphene, massive paradiapophyses, a much widened anteriorly centrum, dorsally inclined prezygapophyses in anterior view, and a large, deep, and more rounded cotyle. Differences among the two adult vertebrae appear mainly in the degree of convexity of the subcentral ridges in lateral view and the size of the prezygapophyseal articular facets in dorsal view, though these could be attributed to intraspecific or intracolumnar variation. Posterior trunk vertebrae are relatively smaller (though they are currently unknown for fully adult specimens), possess a still vaulted neural arch, but the haemal keel is relatively thick in ventral view, instead of sharp as in mid-trunk vertebrae. The most characteristic feature of the posterior trunk vertebra PIMUZ A/III 633 is its strange zygosphene that is curved downwards and is relatively thinner. Such shape of the zygosphene could be indicative of an earlier ontogenetic stage (see Sect. 5 below) and we therefore prefer to treat it as belonging to a sub-adult. Nevertheless, similarly to the other vertebrae referred to this species, the zygosphene of PIMUZ A/III 633 is still relatively thick, the neural arch is rather vaulted in posterior view, the prezygapophyses are much inclined dorsally, the cotyle is large and rounded, and the neural spine is thick. Apart from the thickness of the haemal keel, other differences among mid-trunk and posterior trunk vertebrae appear in the extent and the orientation of the prezygapophyseal articular facets in dorsal view; these can be attributed to intracolumnar, intraspecific, or ontogenetic variation. No cloacal or caudal vertebrae are so far known for this species. In comparison with adults and the sub-adult PIMUZ A/III 633, vertebrae of much younger individuals are characterized by smaller size, less massively built overall structure, thinner zygosphene in anterior view, less high (but still vaulted) neural arch in posterior view, shorter neural spine in lateral view, less massive prezygapophyseal articular facets, and centrum less widened anteriorly. One further interesting feature of the intermediate-sized specimens of sub-adults or juveniles (PIMUZ A/III 636 and PIMUZ A/III 637) is that the width of the zygosphene is smaller or almost equal to that of the cotyle. Also, these specimens possess lateral lobes on their zygosphene in dorsal view. Additionally, the neural spine is shorter than that of the adult specimens (feature nevertheless subjected also to intracolumnar variation) but still possesses a characteristic infolding in their posterodorsal edge, whereas it augments in height relatively abruptly and not gradually. Other important differences between these two specimens and the adult ones are a more convex zygosphene in anterior view, thinner prezygapophyseal articular facets in dorsal view, a less wide zygantrum, and a more elliptical condyle. Nevertheless, the vaulted neural arch, the much dorsally inclined prezygapophyses in anterior view, the thick neural spine in dorsal view, and the massive paradiapophyses are features that resemble the above described vertebrae of adult individuals, suggesting that these were subjected to little or no degree of transformation during ontogeny. Finally, the smallest-size available vertebrae of *Palaeopython helveticus* sp. nov. (PIMUZ A/III 631 and PIMUZ A/III 632) are apparently pertaining to rather young individuals. They are characterized by an overall small size (CL between 4 and 5 mm), a much thinner zygosphene in anterior view, and a relatively more depressed and elliptical cotyle. There is a gradual decrease in the anterior widening of the centrum in ventral view from PIMUZ A/III 632 to PIMUZ A/III 631, which can be attributed to some kind of ontogenetic or intracolumnar variation. An interesting feature is the rather short neural spine in lateral view of PIMUZ A/III 632 (this structure is not preserved in PIMUZ A/III 631), although there is a general trend that ophidian vertebrae have short neural spines in their posterior trunk vertebrae; this could indicate that the neural spine is subjected to an important degree of transformation during ontogeny, from rather short ones in young individuals to tall ones in fully adults. Nevertheless, both these small vertebrae have a rather vaulted neural arch in posterior view. Thus, while it is obvious that *Palaeopython helveticus* exhibited significant ontogenetic and intracolumnar variation in its vertebrae, the most important diagnostic feature (the rather high neural arch in posterior view) appears to be almost constant throughout its ontogeny and throughout the vertebral column. Besides, such assignment of these intermediate- and smaller-sized specimens is also supported by CT scanning data (see Discussion below).

Remarks: *Palaeopython helveticus* sp. nov. is distinguished from all other extinct “booids” from Europe by a combination of several features, most prominently its extremely vaulted neural arch in posterior view. The fact that the neural arch appears to be rather vaulted also in smaller vertebrae pertaining to young individuals reveals that this feature characterized the taxon throughout its ontogeny. Furthermore, it is known that anterior trunk (i.e., cervical) vertebrae of “booids” are generally characterized by a relative vaultness of their neural arch in posterior view [e.g., see figures in Szyndlar and Rage 2003]; however, taking into consideration that all available specimens of *Palaeopython helveticus* sp. nov. originate from different portions of the trunk, the extreme vaultness of the neural arch cannot be correlated with an origination of the vertebrae from the anterior trunk region.

Palaeopython helveticus sp. nov. can be confidently assigned to the widespread Eocene European genus *Palaeopython* on the basis of several vertebral features and further seems to resemble mostly the probably coeval and geographically proximate *Palaeopython cadurcensis* (Filhol, 1877a) from the late Eocene of the Phosphorites du Quercy, France, and to a lesser degree the older taxon *Palaeopython ceciliensis* Barnes, 1927, from the middle Eocene of Geiseltal, Germany (see Sect. 5 below for an extensive comparison of the new Swiss form with other extinct and extant taxa).

The holotype PIMUZ A/III 634 can be identified as a trunk vertebra, judging from the absolute large size, the presence of haemal keel, and the absence of haemapophyses, lymphapophyses, and pleurapophyses. The fact that the haemal keel in lateral view is deep (i.e., projecting ventrally in its posterior portion) and resembles a hypapophysis hints at an origination of the vertebra from the anterior portion of the mid-trunk; in that respect, the specimen resembles an anterior/mid-trunk vertebra (specimen BSPG 1976 XXII 5857) of *Bavarioboa hermi* Szyndlar and Schleich, 1993, from the Miocene of Germany

(Fig. 19H of Szyndlar and Rage 2003). However, in the latter specimen, that structure is more prominent and can be more confidently identified as a hypapophysis ("vestigial hypapophysis" in Szyndlar and Rage 2003:47), thus denoting an origination from an even more anterior region of the trunk, in comparison with the holotype of *Palaeopython helveticus* sp. nov. The first anterior trunk (i.e., cervical) vertebrae in "booids" usually possess elongated and thin hypapophyses in lateral view (e.g., Gilmore 1938; Szyndlar and Rage 2003), which are much different from the condition seen in the holotype PIMUZ A/III 634. Nevertheless, mid-trunk vertebrae of the large-sized *Palaeopython cadurcensis* have also sometimes a prominent haemal keel in lateral view [e.g., the large mid-trunk vertebra MNHN QU 16319 (Fig. 15d)], whereas haemal keels rather similar to that of the holotype of the Swiss form are also present in anterior mid-trunk vertebrae of the German taxon *Palaeopython ceciliensis* (e.g., specimen GMH XXXV-485-1963c; pers. observ. at GMH). On the other hand, certain extant and extinct "booids" are known to possess hypapophyses or hypapophysis-like structures in their posteriormost trunk vertebrae, although usually these structures are thicker in ventral view and generally these vertebrae are relatively smaller and have more depressed neural arches than the preceding ones (e.g., see figures in Szyndlar and Rage 2003; specimen MDHC 116 of *Python regius*). Nevertheless, the holotype of the North American large Eocene "booid" *Boavus occidentalis* Marsh, 1871 (YPM 511) was identified as a posterior trunk vertebra (Gilmore 1938:Fig. 2), has a haemal keel that projects ventrally in its posterior portion in lateral view, like an obtuse projection, but also has a rather vaulted neural arch and a relatively large size (CL 9.45 mm). In all these respects, this specimen resembles PIMUZ A/III 634. These being said, we herein consider that the holotype of *Palaeopython helveticus* sp. nov. (PIMUZ A/III 634) probably originates from the anterior mid-trunk region (but not the anterior trunk [cervical]) of the column, but we cannot exclude the possibility that it pertains to the posteriormost one.

The holotype specimen of *Palaeopython helveticus* sp. nov., PIMUZ A/III 634, and also the referred vertebra PIMUZ A/III 635, were initially referred by Rosselet (1991) to the French taxon *Palaeopython filholii* (misspelling constantly that species epithet as "*filholi*"). However, *Palaeopython filholii* is characterized by a relatively depressed neural arch (de Rochebrune 1880, 1884; Rage 1984; see Sect. 5 below). In addition, Rosselet (1991) referred the probably not fully adult PIMUZ A/III 633 to ?*Palaeopython* sp. whereas he generically and specifically distinguished the intermediate-sized PIMUZ A/III 636 and PIMUZ A/III 637, which he referred to *Paleryx* ?*rhombifer*. The much smaller specimens PIMUZ A/III 631 and PIMUZ A/III 632 were simply referred by Rosselet (1991) to indeterminate "boines".

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Palaeopython fischeri Schaal, 2004
Palaeopython cf. *fischeri*
Figure 12

Material: Fissure A: a posterior trunk vertebra (PIMUZ A/III 630; Fig. 12a–f); probably Fissure 2: an anterior trunk or anterior mid-trunk vertebra (PIMUZ A/III 628; Fig. 12g–k); imprecisely known Fissure: a posterior trunk vertebra (PIMUZ A/III 4558; Fig. 12l–p).

Description: The best preserved specimen (PIMUZ A/III 630) is small in size (CL = 5.5 mm, PR–PR around 7.5 mm). It is still incomplete, missing the distant edges of both prezygapophyses and part of the right postzygapophysis (Fig. 12a–f). In anterior view (Fig. 12a), the zygosphene is relatively thin, with its dorsal roof almost flat. A prominent median tubercle is visible. The prezygapophyses are only slightly inclined dorsally. The neural canal is trapezoidal in shape. The cotyle is almost rounded, with the ventral side of the cotylar rim slightly depressed. Deep paracotylar fossae surround the cotyle from both right and left sides. The paradiapophyses project ventrally but only slightly below the ventral rim of the cotyle. In posterior view (Fig. 12b), the neural arch is vaulted. The zygantrum is deep. The neural spine is relatively thick and short in height. The condyle is rather eroded, but appears to have been small and relatively rounded. The haemal keel is thick and projects below the surface of the condyle. In dorsal view (Fig. 12c), the median tubercle of the zygosphene is prominent and also two distinct lateral lobes are clearly visible. The prezygapophyseal articular facets are incompletely preserved, however, it seems that they were originally small. The neural spine begins to develop in the posterior portion of the zygosphene. In ventral view (Fig. 12d), the centrum is slightly widened anteriorly. The haemal keel is prominent and thick, almost uniform in shape, and runs throughout the whole midline of the centrum, from the ventral level of the cotyle to the ventral level of the condyle. The paradiapophyses are eroded but seem to have been large in size. In lateral view (Fig. 12e–f), the neural spine is rather short and almost vertical in height. Its base encompasses about two-thirds the length of

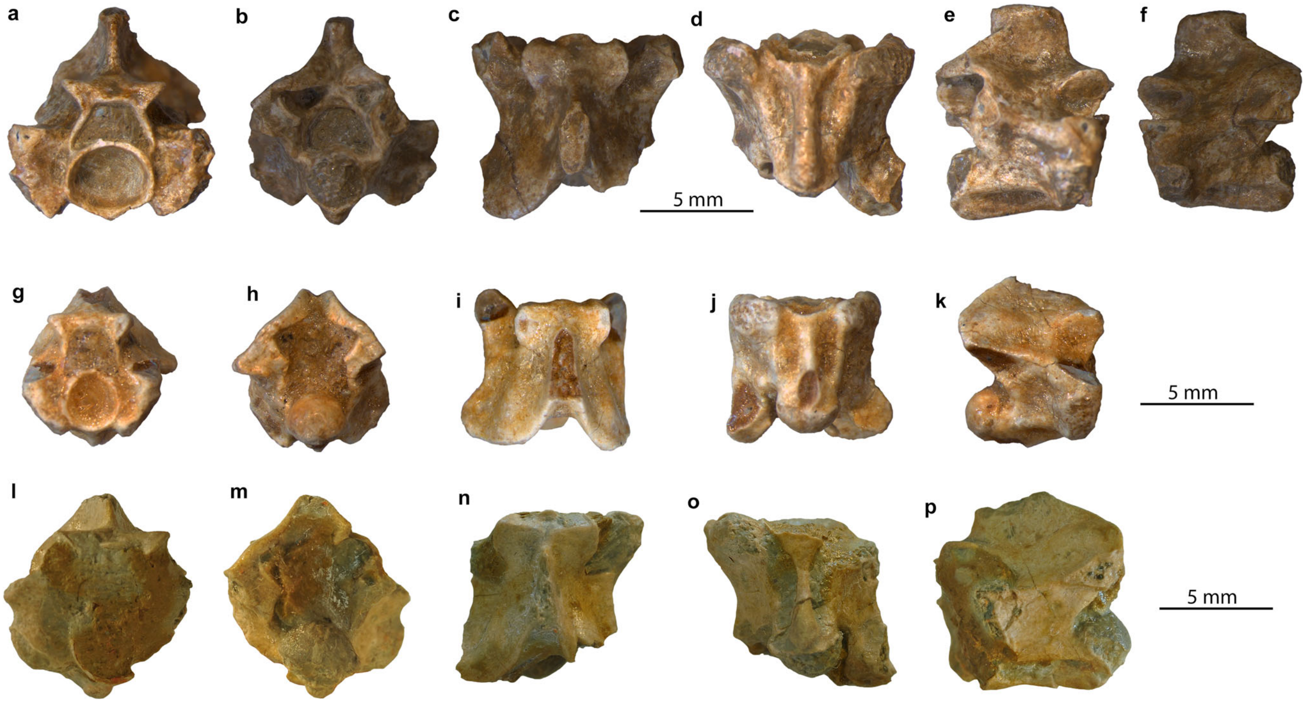

Fig. 12 Trunk vertebrae of *Palaeopython* cf. *fischeri*: **a**–**f** posterior trunk vertebra (PIMUZ A/III 630) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), right lateral (**e**), and left lateral (**f**) views; **g**–**k** anterior trunk or anterior mid-trunk vertebra (PIMUZ A/III 628) in anterior (**g**), posterior (**h**), dorsal (**i**), ventral (**j**), and right lateral (**k**) views; **l**–**p** posterior trunk vertebra (PIMUZ A/III 4558) in anterior (**l**), posterior (**m**), dorsal (**n**), ventral (**o**), and left lateral (**p**) views

the neural arch and its dorsal edge is almost straight. The subcentral ridges are slightly convex. The haemal keel is prominent, projecting slightly more ventrally at its posterior portion. Small lateral foramina are present.

The smaller vertebra (PIMUZ A/III 628) that is tentatively referred to the same taxon is less complete, missing most of the neural spine, most of the prezygapophyses, and part of the hypapophysis (Fig. 12g–k). The vertebra is small with a CL of 4.7 mm and estimated PR–PR of less than 8 mm. In anterior view (Fig. 12g), the zygosphene is relatively thin, with its dorsal roof almost straight. A median tubercle is present on the zygosphene. The neural canal is trapezoidal in shape. The cotyle is small and somehow dorsoventrally elongated. The paradiapophyses project only slightly ventrally from the level of the cotyle. In posterior view (Fig. 12h), the neural arch is rather vaulted, and there is a distinct angle in the midlevel of each of the postzygapophyses. The condyle is rounded. In dorsal view (Fig. 12i), two lateral lobes are developed on the zygosphene. The prezygapophyses are directed more anteriorly than laterally. The prezygapophyseal articular facets are small. The neural spine is mostly broken but its preserved base indicates that it was probably thick. In ventral view (Fig. 12j), the centrum is rectangular, maintaining a nearly constant width, with only a slight widening in its anterior part. The subcentral ridges are prominent. The paradiapophyses are eroded but they seem to have been originally large. In lateral view (Fig. 12k), the zygosphenal facets are deep. The subcentral ridges are convex. The hypapophysis is broken off close to its base.

PIMUZ A/III 4558 is the largest specimen (CL = 6.4) but is fragmentary, missing most of the left prezygapophysis, most of the right postzygapophysis, part of the neural spine and the neural arch, whereas the cotyle, the condyle, and the paradiapophyses are rather damaged (Fig. 12l–p). In anterior view (Fig. 12l), the zygosphene is thin and almost straight. The prezygapophyses are only slightly inclined dorsally. In posterior view (Fig. 12m), the neural arch is vaulted. In dorsal view (Fig. 12n), the median tubercle of the zygosphene is prominent and clearly visible. In ventral view (Fig. 12o), the haemal keel is wide (though not so wide as in PIMUZ A/III 630), extends across most of the midline of the centrum, and possesses a distinct constriction at around its anterior to mid-level. In lateral view (Fig. 12p), the haemal keel projects well ventrally from the centrum.

Remarks: These three specimens are characterized by a rather high neural arch and a relatively thin zygosphene, similarly to the equal-sized individuals of *Palaeopython helveticus* sp. nov. described above. Nevertheless, these three specimens possess features that deviate from the general morphotype of the above established species.

These features include the presence of a prominent median tubercle on the zygosphene, visible in both anterior and dorsal views, the narrowness of the centrum in ventral view, with slight or no widening in ventral view (especially in the anterior trunk or anterior mid-trunk vertebra PIMUZ A/III 628 but also in the two posterior trunk ones), the distinct lateral lobes of the zygosphene in dorsal view, prezygapophyses not so dorsally inclined in anterior view and oriented more anteriorly and not laterally in dorsal view, and the short and almost vertical neural spine in lateral view. In certain respects, these specimens most resemble the holotype of *Palaeopython fischeri* (SMF-ME 929) from the early–middle Eocene (MP 11) of Messel, especially in the presence of the prominent median tubercle, the short and almost vertical neural spine, and the lateral lobes of the zygosphene (see figures in Schaal 2004). Nevertheless, *Palaeopython fischeri* is characterized by more depressed neural arch, its centrum relatively more widened anteriorly, and its prezygapophyses being directed more laterally than anteriorly in dorsal view (see figures in Schaal 2004). These three important differences, along with a stratigraphic and geographic rationale, preclude us from formally referring these two Dielsdorf specimens to the much older German species *Palaeopython fischeri*. We thus prefer to tentatively refer them as *Palaeopython* cf. *fischeri*. Apart from *Palaeopython fischeri*, such median tubercle on the zygosphene is also commonly present in *Palaeopython filholii* from the (probably late) Eocene of the Phosphorites du Quercy, France (Rage 1974, 1984), but the latter species has much more depressed neural arch than the three Swiss specimens. In any case, whatever their precise affinities with the Messel or the Quercy taxa may have been, it seems that PIMUZ A/III 630, PIMUZ A/III 628, and PIMUZ A/III 4558 represent a different species than *Palaeopython helveticus* sp. nov.

PIMUZ A/III 630 and PIMUZ A/III 4558 can be identified as posterior trunk vertebrae based on the thickness of the haemal keel, the deep subcentral grooves, and the overall shape of the vertebrae, with the former specimen probably originating from a more posterior region than the latter one. As for PIMUZ A/III 629, judging from the probable presence of a hypapophysis and the relative narrowness of the vertebral centrum, with the subcentral ridges almost parallel in ventral view, we consider that it originates from the anterior trunk or anterior mid-trunk region of the vertebral column.

Two of these specimens (PIMUZ A/III 628 and PIMUZ A/III 630) were initially mentioned and briefly described, but not figured by Rosselet (1991), with PIMUZ A/III 628 referred to indeterminate “boids”, whereas for PIMUZ A/III 630, a more precise determination was given, as indeterminate “boines”.

Palaeopython sp. (morphotype 3)

Figure 13

Material: Fissure 2: an anterior trunk or anterior mid-trunk vertebra of an adult individual (PIMUZ A/III 638; Fig. 13).

Description: The vertebra is incomplete, missing most of its left prezygapophysis, most parts of both postzygapophyses, the neural spine, the posterior part of the haemal keel (or hypapophysis), and the left paradiapophysis (Fig. 13). The vertebra is massive and relatively large, with CL = 9 mm and an estimated PR–PR approximately 13 mm. In anterior view (Fig. 13a), the zygosphene is extremely thick; it is wide (zygosphene width equals to 6.5 mm) and almost trapezoidal in shape. The dorsal roof of the zygosphene is almost straight. No median tubercle is present on the zygosphene. The prezygapophyses are dorsally inclined. Deep paracotylar fossae are present, with no paracotylar foramina. The cotyle is large. The paradiapophyses extend below the ventral level of the cotyle. In posterior view (Fig. 13b), the neural arch is rather vaulted. The condyle is almost circular in shape and the haemal keel (or hypapophysis) projects beneath it. In dorsal view (Fig. 13c), the zygosphenal lip is concave, with two distinct lateral lobes being present. The prezygapophyseal articular facets (only the right is preserved) are small and oval. The anterior base of the neural spine commences beyond the level of the zygosphene. In ventral view (Fig. 13d), the centrum is moderately widened anteriorly. The haemal keel (or hypapophysis) is thin; its posterior half is damaged but it seems that in life it was originally running throughout the whole midline of the centrum. The paradiapophyses are massive and there is no clear division between diapophyseal and parapophyseal portions. No prezygapophyseal accessory processes are present. In lateral view (Fig. 13e–f), the vertebra is much higher than long, even if the neural spine is not preserved. The zygosphenal facets are massive. The subcentral ridges are almost straight. The haemal keel (or hypapophysis) seems to have projected ventrally. The extent of this ventral projection of the haemal keel (or hypapophysis) cannot be verified but it seems that it was large, i.e., for this reason it cannot be concluded with certainty whether this structure represents a haemal keel or hypapophysis.

Remarks: PIMUZ A/III 638 can be identified as a trunk vertebra, due to the presence of a haemal keel (or hypapophysis), the absence of haemapophyses, pleurapophyses, and lymphapophyses, the overall shape, and the large absolute size. The seemingly ventral projection of the haemal keel (or hypapophysis) could denote the origination of the vertebra from either the anterior, anterior mid-trunk region; an alternative origination from the posteriormost trunk region seems to be rejected on the basis of the not deep subcentral grooves. Furthermore, the relatively slight anterior widening of the centrum, the shortness of the

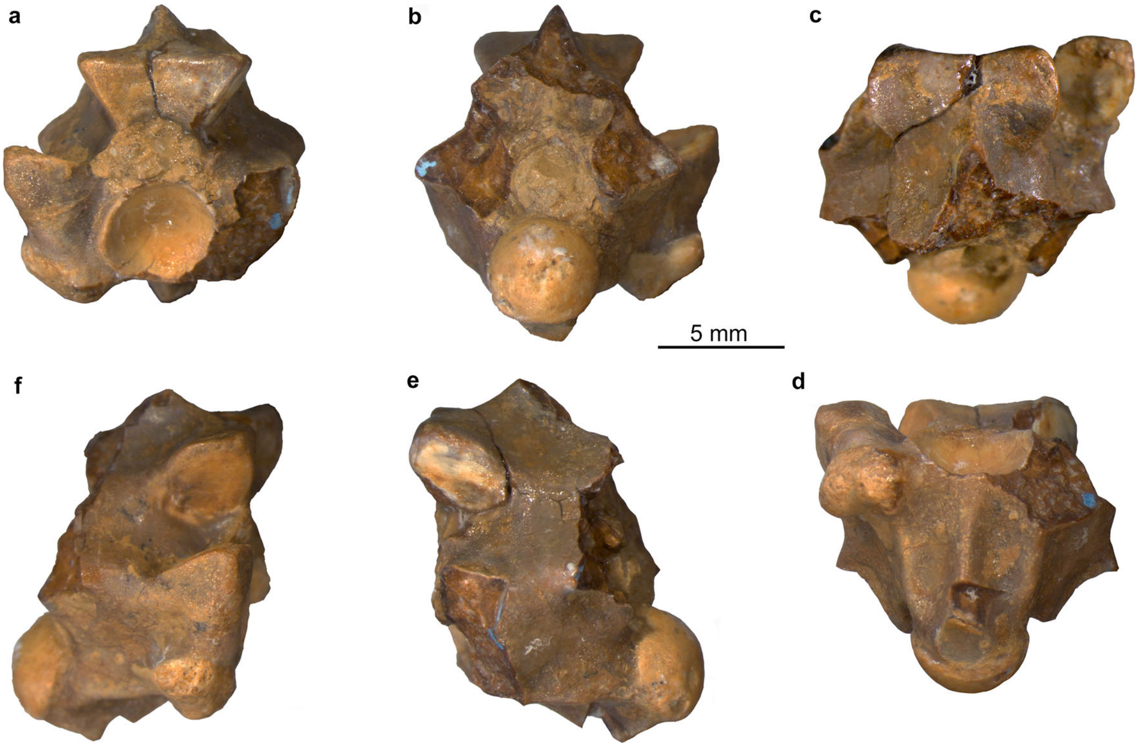

Fig. 13 Trunk vertebra (PIMUZ A/III 638) of *Palaeopython* sp. (morphotype 3), in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views

prezygapophyses in anterior view, and the absence of prezygapophyseal accessory processes are all indicative of an origination from the anterior trunk or anterior mid-trunk region of the vertebral column. Its large size, the thickness of the zygosphene, the overall shape of the prezygapophyses, and the diameter of the neural canal suggest that it pertained to an adult individual.

This specimen shares several features with the holotype and referred (adult) specimens of *Palaeopython helveticus* sp. nov. described above, such as the overall large size, the much vaulted neural arch, the dorsally inclined prezygapophyses, the anterior widening of the centrum, the massive paradiapophyses, the sharp haemal keel, and the large cotyle. However, important differences exist between PIMUZ A/III 638 and *Palaeopython helveticus* sp. nov., with the former specimen possessing an extremely thick and robust zygosphene in anterior view, an almost straight dorsal roof of the zygosphene in anterior view, a concave zygosphenal lip in dorsal view with two distinct lateral lobes, a significantly anteroposteriorly shorter centrum, less dorsally inclined prezygapophyses in anterior view, prezygapophyses directed more anteriorly than laterally in dorsal view (and not distinctly laterally as in the latter species), significantly less elongated prezygapophyseal articular facets, and anterior widening of the centrum in ventral view to a much lesser degree. PIMUZ A/III 638 appears also different from the other two species of *Palaeopython* that possess rather thick zygosphenes, i.e., *Palaeopython cadurcensis* and *Palaeopython ceciliensis*, in having significantly narrower centrum anteriorly in ventral view. All these differences seem to be rather important from a taxonomic point of view, however, considering our current inadequate knowledge of the intracolumnar, intraspecific, or ontogenetic variability within European extinct "booids", we refer PIMUZ A/III 638 as a third, indeterminate, morphotype of *Palaeopython*, tentatively distinguishing it from both other large "booids" from Dielsdorf, i.e., *Palaeopython helveticus* sp. nov. and *Palaeopython* cf. *fischeri*.

Rather interestingly, PIMUZ A/III 638 was tentatively referred by Rosselet (1991) to palaeophiids. Such identification of the latter specimen as a palaeophiid would mark the first occurrence of these Paleogene giant aquatic snakes in Switzerland. Trunk vertebrae of palaeophiids are indeed characterized by a thick zygosphene and a vaulted neural arch, however, they differ significantly from the Dielsdorf material in, among others, being much laterally compressed and possessing peculiar structures developed above the postzygapophyses, i.e., pterapophyses (Rage 1983, 1984; Rage et al. 2003). Accordingly, the presence of Palaeophiidae in Dielsdorf is not supported on the basis of the current material.

"Booidea" indet.

Figure 14

Material: Fissure B: a trunk vertebra (PIMUZ A/III 629; Fig. 14a–f); imprecisely known Fissure: a trunk vertebra

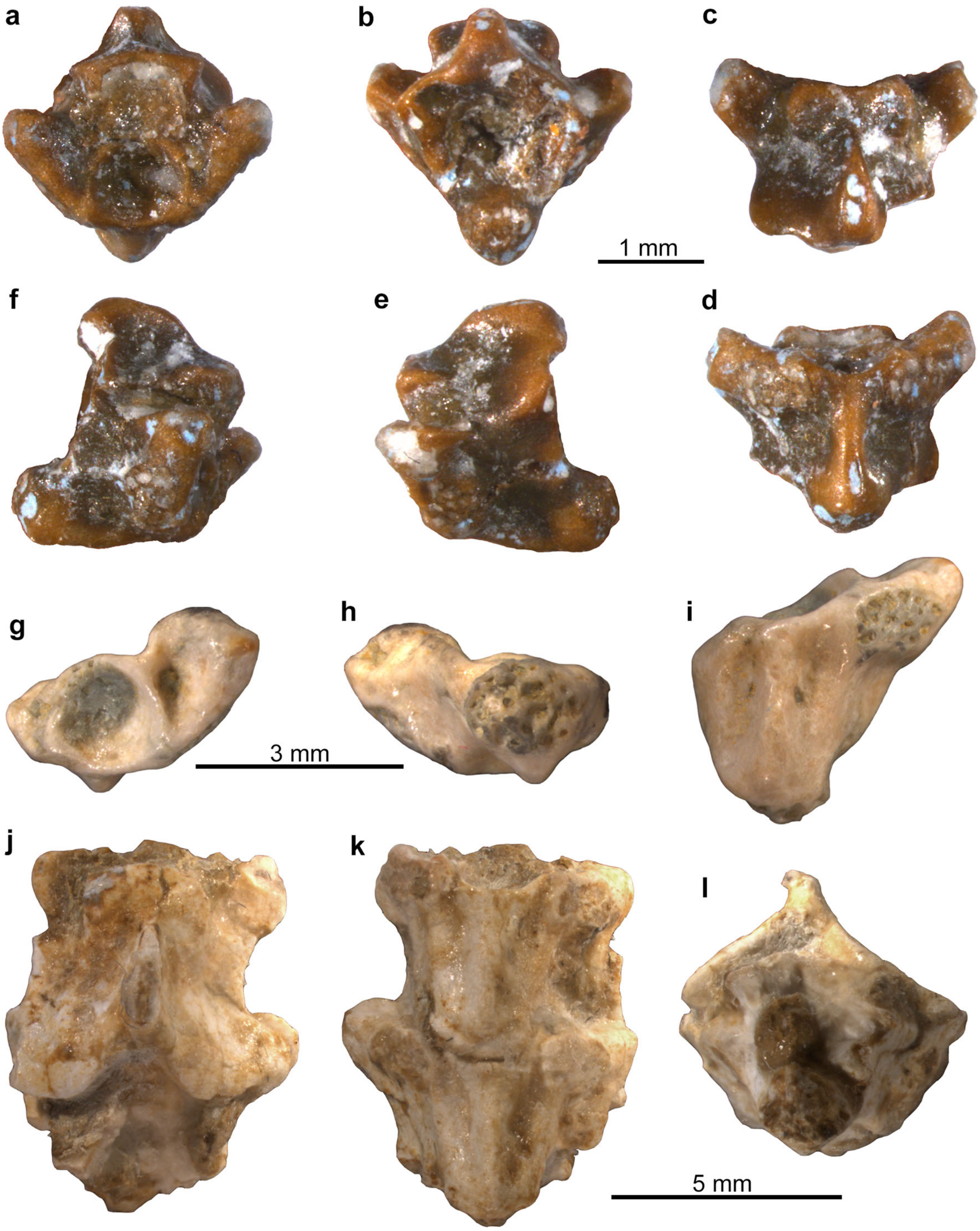

Fig. 14 Trunk vertebrae of "Booidea" indet.: **a**–**f** trunk vertebra (PIMUZ A/III 629) in anterior (**a**), posterior (**b**), dorsal (**c**), ventral (**d**), left lateral (**e**), and right lateral (**f**) views; **g**–**i** trunk vertebra (PIMUZ A/III 4561) in anterior (**g**), posterior (**h**), and ventral (**i**) views; **j**–**l** two articulated posterior trunk vertebrae (PIMUZ A/III 4560) in dorsal (**j**), ventral (**k**), and posterior (**l**) views

(PIMUZ A/III 4561; Fig. 14g–j) and two articulated posterior trunk vertebrae (PIMUZ A/III 4560; Fig. 14k–m).

Description and remarks: PIMUZ A/III 629 is the smallest snake specimen from Dielsdorf, with a CL of only 1.3 mm and PR–PR of 2.5 mm. Nevertheless, it is rather incomplete, missing most its right postzygapophysis, most of the neural spine, whereas its paradiapophyses are rather eroded (Fig. 14). In anterior view (Fig. 14a), the zygosphene is rather thin, with its dorsal roof being rather convex. The prezygapophyses are strongly inclined. The cotyle is small and circular in shape. Deep paracotylar fossae are present next to each lateral side of the cotyle. In posterior view (Fig. 14b), the neural arch is vaulted. The condyle is small and circular in shape. In dorsal view (Fig. 14c), the neural spine is relatively thick, with its base commencing anteriorly well behind the level of the zygosphene. The prezygapophyses extend laterally, with large prezygapophyseal articular facets. The zygosphenal lip is concave. In ventral view (Fig. 14d), the vertebra is wider than long. The haemal keel is relatively thick and crosses the whole mid-line of the centrum. The subcentral grooves are deep. The paradiapophyses are not divided into diapophyseal and parapophyseal portions. In lateral view (Fig. 14e–f), the neural spine is much inclined posteriorly. The haemal keel is prominent.

The fact that the vertebra is higher than long in lateral view, its centrum is relatively triangular and wider than long in ventral view, and the paradiapophyses are non-divided are all indicative of an assignment of PIMUZ A/III 629 to "booid" snakes. The relatively vaulted neural arch could even prompt for an attribution to a young individual of *Palaeopython helveticus* sp. nov. On the other hand, its strong posterior inclination of the neural spine in lateral view, the rather thin zygosphene in anterior view, and the concave zygosphene in dorsal view are important differences with the above mentioned species. Among named "booid" taxa, PIMUZ A/III 629 resembles mostly the diminutive English species *Hordleophis balconae* Holman, 1996, from the late Eocene of Hordle Cliff, especially in the rather small overall size, the posteriorly inclined neural spine in lateral view, the neural spine commencing well behind the zygosphene level in dorsal view, the vaulted neural arch in posterior view, the thin zygosphene in anterior view, the wide haemal keel, and the small and almost circular cotyle and condyle (see figures in Holman 1996). Nevertheless, *H. balconae* has never been described outside its type locality, and even there the species is not well documented. Pending a redescription and revision of *H. balconae*, in addition to the incomplete nature of PIMUZ A/III 629, we herein refrain from formally referring this Swiss specimen to *Hordleophis*, and prefer to treat it as an indeterminate "booid".

As for the other two specimens (PIMUZ A/III 4561 and PIMUZ A/III 4560), they are too fragmentary to allow any further taxonomic conclusion and therefore, it is not clear whether they pertain to any of the above described *Palaeopython* spp. PIMUZ A/III 4561 misses the whole dorsal part of the vertebra, its right prezygapophysis and both postzygapophyses (Fig. 14g–i). The two articulated vertebrae PIMUZ A/III 4560 are also incomplete, being rather eroded and missing both postzygapophyses of the second vertebra (Fig. 14k–m). Judging from the thickness of the haemal keel of the latter specimen, it apparently originates from the posterior trunk region of the vertebral column.

5 Discussion

5.1 Affinities of *Palaeopython helveticus* sp. nov

Palaeopython helveticus sp. nov. can be referred to the widespread Paleogene Western and Central European genus *Palaeopython* on the basis of its overall large vertebral size, the zygosphene trapezoidal in anterior view, the paradiapophyses extending ventrally beyond the ventral level of the cotyle, the rather deep posterior notch of the neural arch, the rather massive paradiapophyses, the rather sharp and relatively prominent haemal keel in mid-trunk vertebrae, and the shallow interzygapophyseal constriction. Among *Palaeopython* spp., *Palaeopython helveticus* sp. nov. resembles mostly the two largest species of the genus, *Palaeopython cadurcensis* from the late Eocene of the Phosphorites du Quercy, France, and *Palaeopython ceciliensis* from the middle Eocene of Geiseltal, Germany, especially in the presence of a thick zygosphene in anterior view, the vaulted neural arch in posterior view, the high neural spine in the anterior and mid-trunk vertebrae in lateral view, the thick neural spine in dorsal and anterior views, the centrum being much more widened anteriorly, the long and inclined dorsally prezygapophyses, the deep paracotylar fossae, the rather deep and massive cotyle, the deep and wide zygantrum, and the massive paradiapophyses. However, the vaultness of the neural arch achieves the largest degree in *Palaeopython helveticus* sp. nov., being much larger than all known specimens of *Palaeopython cadurcensis* (known from both mid- and posterior trunk vertebrae), and *Palaeopython ceciliensis* (known from both anterior, mid-, and posterior trunk vertebrae), and, in fact, any other *Palaeopython* specimen (Fig. 15a–i). Moreover, *Palaeopython cadurcensis* is much larger than *Palaeopython helveticus* sp. nov., with the former taxon reaching almost a CL of about 19 mm in the largest specimens (e.g., specimen MNHN QU 16319; Fig. 15d), whereas *Palaeopython helveticus* sp. nov., is characterized by a relatively smaller vertebral size (CL around 11 mm), but nevertheless, the fact that the holotype PIMUZ A/III 634 is probably an anterior mid-trunk (or at least a posteriormost trunk) and not a middle mid-trunk vertebra, implies that a higher CL could be achieved for the Swiss form. Furthermore, besides these important differences in the vaultness of the neural arch and the absolute vertebral size, *Palaeopython cadurcensis* can be differentiated from *Palaeopython helveticus* sp. nov. by the zygosphene being significantly much thicker in anterior view, the zygosphene with prominent lateral lobes that extend anteriorly in dorsal view and dorsally in anterior view, the (frequent) presence of a "bump" or tubercle on the anterior surface of the zygosphene, the larger and deeper

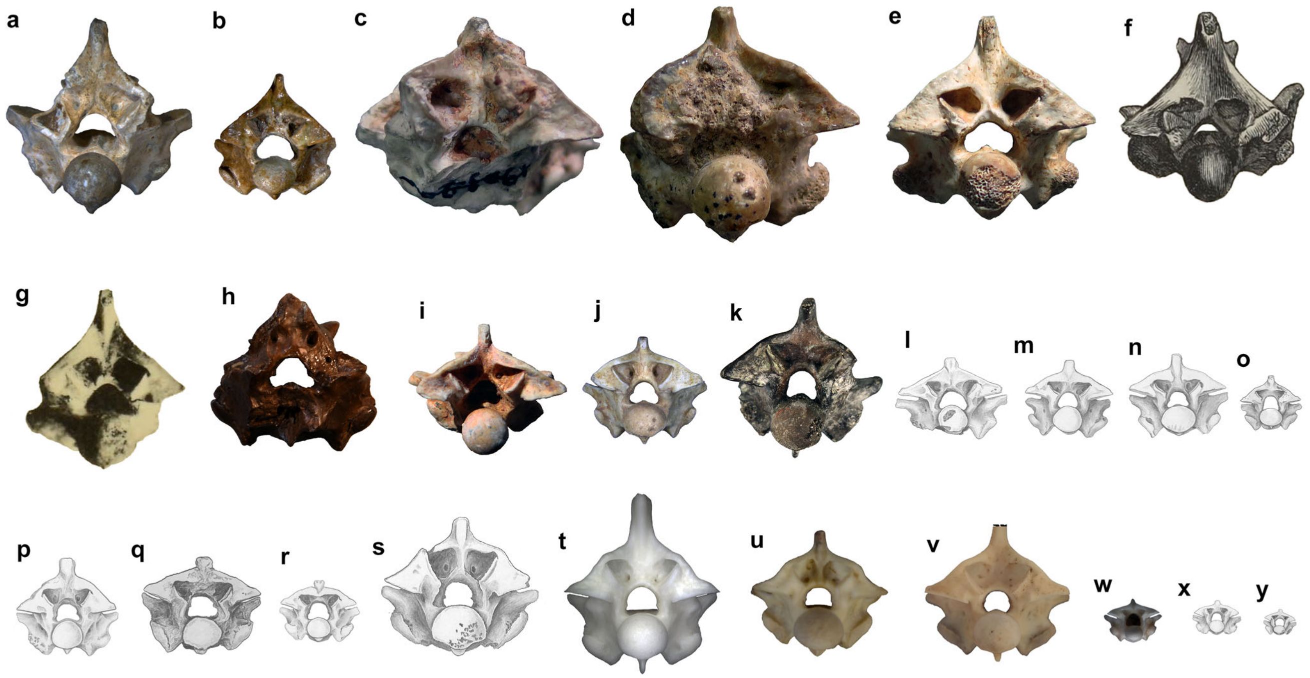

Fig. 15 The high vaultness of the neural arch of *Palaeopython helveticus* sp. nov. in comparison with other "booid" snakes: **a** holotype trunk vertebra (PIMUZ A/III 634) of *Palaeopython helveticus* sp. nov.; **b** trunk vertebra (PIMUZ A/III 636) of a younger individual of *Palaeopython helveticus* sp. nov.; **c** syntype mid-trunk vertebrae (MNHN QU 16318) of *Palaeopython cadurcensis* from the late Eocene of the Phosphorites du Quercy, France; **d** mid-trunk vertebra (MNHN QU 16319) of *Palaeopython cadurcensis* from the late Eocene of the Phosphorites du Quercy, France; **e** posterior trunk vertebra (MNHN QU 16345) of *Palaeopython cadurcensis* from the late Eocene of the Phosphorites du Quercy, France; **f** trunk vertebra (probably collections of BSPG, currently lost) of *Palaeopython cadurcensis* figured by Zittel (1887–1890:Fig. 559) from the late Eocene of the Phosphorites du Quercy, France; **g** trunk vertebra (?collections of MNHN, currently lost) of *Palaeopython cadurcensis* figured by De Stefano (1905:pl. IV.12; originally referred to *Paleryx rhombifer*) from the late Eocene of the Phosphorites du Quercy, France; **h** holotype mid-trunk vertebra (GMH CeI-2978-1926) of *Palaeopython ceciliensis* from the middle Eocene of Geiseltal Quarry Cecilie I, Germany; **i** holotype posterior trunk vertebra (MNHN QU 16322) of *Palaeopython filholii* from the ?late Eocene of Phosphorites du Quercy, France; **j** mid-trunk vertebra (NHMW 2019/0033/0056) of *Palaeopython filholii* from the ?late Eocene of Phosphorites du Quercy, France; **k** holotype trunk vertebra (NHMUK 25259) of *Paleryx rhombifer* from the late Eocene of Hordle Cliff, England; **l** holotype posterior trunk vertebra (USTL ESP 601) of *Bavarioboa bachensis* Szyndlar and Rage 2003, from the late Oligocene of Espeyrasse, France; **m** holotype mid-trunk vertebra (USTL MPF 1102) of *Bavarioboa vaylatsae* Szyndlar and Rage 2003, from the late Oligocene of Mas-de-Pauffié, France; **n** holotype mid-trunk vertebra (USTL PDS 3102) of *Bavarioboa crocheti* Szyndlar and Rage 2003, from the late Oligocene of Pech-Desse, France; **o** holotype mid-trunk vertebra (SMNS 58196-1) of *Bavarioboa minuta* Szyndlar and Rage 2003, from the late Oligocene of Herrlingen 8, Germany; **p** holotype mid-trunk vertebra (SMNS 59441-3) of *Bavarioboa herrlingensis* Szyndlar and Rage 2003, from the late Oligocene of Herrlingen 11, Germany; **q** holotype mid-trunk vertebra (BSPG 1976 XXII 5859) of *Bavarioboa hermi* from the early Miocene of Petersbuch 2, Germany; **r** holotype mid-trunk vertebra (SMNS 59091-3) of *Bavarioboa ultima* Szyndlar and Rage 2003, from the middle Miocene of Rothenstein 13, Germany; **s** holotype mid-trunk vertebra (MNHN VCO 29) of *Python europaeus* from the early/middle Miocene of Vieux Collonges, France; **t** mid-trunk vertebra (MDHC 116) of an extant *Python regius*; **u** mid-trunk vertebra (NHMW 35675) of *Python bivittatus* Kuhl 1820; **v** mid-trunk vertebra (HNHM 2004.77.1) of an extant *Boa constrictor* (the dorsal part of the neural spine is not shown); **w** mid-trunk vertebra (NHMW 21520) of an extant *Eryx jaculus* (Linnaeus 1758); **x** trunk vertebra (USTL PDS 3119) of *Platyspondylia lepta* Rage 1974, from the late Oligocene of Pech-du-Fraysse, France; **y** holotype mid-trunk vertebra (SMNS 87146-2) of *Platyspondylia germanica* Szyndlar and Rage 2003, from the late Oligocene of Herrlingen 11, Germany. All specimens figured in posterior view. Images courtesy of PIMUZ (**a**, **b**), MNHN (**c**, **d**, **e**, **i**), GMH (**h**), NHMW (**j**, **u**, **w**), NHMUK (**k**), MDHC (**t**), and HNHM (**v**). Images **l**–**s** and x–y are reproduced with permission of Zbigniew Szyndlar, modified from Szyndlar and Rage (2003). All images are only at approximate scale

zygosphenal articular facets, and the (rare) presence of paracotylar foramina. The large-sized *Palaeopython* material from the also Swiss and slightly coeval locality of Mormont-Saint-Loup, near Lausanne, originally described by Pictet et al. (1855–1857) and subsequently referred to *Palaeopython cadurcensis* by Filhol (1877a, b, c) and a few subsequent workers (de Rochebrune 1880; Hoffstetter 1962) seems to be distinguished from *Palaeopython helveticus* sp. nov. by possessing a more depressed neural arch in posterior view, wider zygantrum in posterior view, less dorsally inclined prezygapophyses in anterior view, and shorter neural spine in lateral view (see Pictet et al. 1855–1857:Fig. 8 of pl. VIII). It is more difficult to reassess the taxonomic allocation of the two smaller vertebrae figured from Mormont-Saint-Loup (Pictet et al. 1855–1857:Figs. 9, 10 of pl. VIII) as these specimens have a thinner zygosphene and resemble in certain respects the younger individuals of *Palaeopython helveticus* sp. nov. (e.g., PIMUZ A/III 636) but also certain specimens of *Palaeopython filholii* from the Phosphorites du Quercy. Whatever the case, these small specimens from Mormont-Saint-Loup have much less dorsally inclined prezygapophyses, more prominent zygosphene, and shorter neural spine than the small-sized specimens (or young individuals) of *Palaeopython helveticus* sp. nov. As such, it seems that its allocation of the Mormont-Saint-Loup large-sized material to the Quercy species *Palaeopython cadurcensis* appears more suitable for the moment, pending of course a complete redescription of the whole snake material from that locality. It has to be also noted though, there have been described two specimens that have been supposedly referred to *Palaeopython cadurcensis* (both from unknown localities of the Phosphorites du Quercy) that possess relatively much vaulted neural arch and high neural spine: these are a (probably posterior) trunk vertebra figured by Zittel (1887–1890:Fig. 559; this paper, Fig. 15f) and a (probably anterior mid-trunk) vertebra figured by De Stefano (1905:Figs. 11–11 of plate IV; this paper, Fig. 15g). These two specimens are currently lost but nevertheless, judging from the published figures, they still differ from *Palaeopython helveticus* sp. nov. by possessing less dorsally oriented prezygapophyses and different shapes of zygosphene and zygantrum. The German taxon *Palaeopython ceciliensis* is so far known from the works of Barnes (1927) and Kuhn (1939), though it still as yet remains poorly and inadequately known (Rage 1984), however, recent investigation of the whole described and undescribed material at GMH by one of us (GLG) revealed some resemblance with *Palaeopython helveticus* sp. nov. in terms of certain vertebral structures and the absolute vertebral size, but also important differences between the two forms exist as well: the former taxon possessing a shorter neural spine, which becomes extremely short in the posterior trunk vertebrae, usually distinct lateral lobes on the zygosphene visible in both anterior and dorsal views, a thicker zygosphene, and a relatively less vaulted neural arch. More rarely, anterior trunk or even mid-trunk vertebrae of *Palaeopython ceciliensis* can achieve a rather vaulted neural arch, as it is testified by such specimens in the collections of GMH [e.g., GMH Y-38j; the holotype of the species GMH CeI-2978-1926 (Fig. 15h)], however, apart from the non-common of this feature, it seems that it is absent for the posterior trunk region of the column in *Palaeopython ceciliensis*. As far as it concerns the other known *Palaeopython* species, they appear to be much different than the new Swiss taxon: *Palaeopython filholii* Rochebrune, 1880, from the late Eocene of Phosphorites du Quercy, France, and *Palaeopython fischeri* from the early–middle Eocene (MP 11) of Messel, Germany, are characterized by a much thinner zygosphene in anterior view, the frequent presence of a distinct, prominent tubercle in the middle of the zygosphene in anterior view, a significantly less vaulted and usually relatively depressed neural arch in posterior view, a thinner neural spine in dorsal and anterior views, centrum less widened anteriorly, relatively smaller and less inclined dorsally prezygapophyses, less deep paracotylar fossae, a relatively smaller cotyle, less deep and less wide zygantrum, and usually a prominent angle present at the middle of each postzygapophysis in posterior view (Rage 1974, 1984; Schaal 2004; GLG, pers. observ. at MNHN). Furthermore, it is characteristic that *Palaeopython filholii* is in fact primarily diagnosed by its rather flattened and depressed neural arch (Rage 1974, 1984), a feature, the state of which is exactly the opposite as the one observed in the new Swiss species (Fig. 15i–j). Even the small-sized vertebrae of *Palaeopython helveticus* sp. nov. pertaining to younger individuals(e.g., PIMUZ A/III 636 and PIMUZ A/III 631) that have a relatively thin zygosphene, are rather different from *Palaeopython filholii* and *Palaeopython fischeri*, most prominently by their still much vaulted neural arch and the absence of a prominent median tubercle in the zygosphene. “*Palaeopython*” *neglectus* de Rochebrune, 1884, is a so far poorly known species from an Eocene unknown locality within the Phosphorites du Quercy, France; nevertheless, judging from the published figure of the lectotype MNHN QU 16326 (de Rochebrune 1884:pl. 2.5a, 5b), it seems that “*Palaeopython*” *neglectus* could be distinguished from *Palaeopython helveticus* sp. nov. by its shorter neural arch and neural spine and more massive prezygapophyseal articular facets. A further, purported species of the genus, *Palaeopython sardus* Portis, 1901, from the early Miocene of Sardinia, Italy, was subsequently demonstrated by Delfino et al. (2014) to be not even a snake but rather representing in fact a fish; it is therefore not taken into further consideration here.

Besides *Palaeopython*, among other extinct “booid” taxa, *Palaeopython helveticus* sp. nov. bears certain resemblance with *Paleryx* Owen, 1850, a genus which has in the past variously been also suggested to be a senior synonym of *Palaeopython* (e.g., Lydekker 1888; De Stefano 1903, 1905; Kuhn 1939, 1963; Romer 1956), and the North American *Boavus* Marsh, 1871. *Palaeopython helveticus* sp. nov. can be differentiated from the type species of *Paleryx*, i.e., *Paleryx rhombifer* Owen, 1850, from the late Eocene of England, by its relatively larger size [CL of the holotype of *P. rhombifer* (NHMUK R25259) less than 8 mm], the much more vaulted neural arch (Fig. 15k), the higher neural spine, the cotyle being less wide than the zygosphene, the centrum being much more widened anteriorly, the different shape of prezygapophyseal articular facets, and the absence of paracotylar foramina (Owen

1850; Rage 1984; GLG, pers. observ. at NHMUK). Note that the "intermediate" in size specimens of *Palaeopython helveticus* sp. nov. (i.e., PIMUZ A/III 636 and PIMUZ A/III 637) were initially specifically distinguished from the large-sized ones and provisionally referred to *Paleryx rhombifer* by Rosselet (1991); however, this identification was apparently based solely on the fact that the zygosphene was wider than the cotyle in anterior view, a feature that has been variously used to distinguish *Palaeopython* spp. from *Paleryx* (e.g., Rage and Ford 1980; Rage 1984), but nevertheless we have to highlight that this character can be variable within "booids". *Paleryx depressus* Owen, 1850, also from the late Eocene of England, is generally regarded as a junior synonym of *Paleryx rhombifer* (e.g., Rage and Ford 1980; Rage 1984; Wallach et al. 2014); nevertheless, *Paleryx depressus* is significantly much different from *Palaeopython helveticus* sp. nov. in respect of its rather depressed neural arch, its much thinner zygosphene, its centrum less widened anteriorly, and its lower neural spine (GLG, pers. observ. at NHMUK). Another purported species of the same genus, "*Paleryx*" *cayluxi* De Stefano, 1905, from the Eocene or Oligocene of the Phosphorites du Quercy, France, is based on both cranial and vertebral material, which, however, could eventually not even pertain to the same taxon (Rage 1984). The only known vertebral material (the syntype two articulated trunk vertebrae) of "*Paleryx*" *cayluxi* is currently lost (Rage 1984; Wallach et al. 2014), however, judging from the original figures of De Stefano (1905:pl. 5), it seems that it was much different than *Palaeopython helveticus* sp. nov. in possessing a neural arch moderately to strongly depressed, a thinner zygosphene, and not so massive paradiapophyses. Finally, *Palaeopython helveticus* sp. nov. is much different from "*Paleryx*" *spinifer* Barnes, 1927, from the middle Eocene of Geiseltal, Germany, principally by its relatively larger vertebral size (CL of the latter taxon less than 8 mm), much thicker zygosphene, much more vaulted neural arch, higher neural spine in lateral view, neural spine commencing near the level of zygosphene in dorsal view (and not well beyond the zygosphene), and centrum much more widened anteriorly (Barnes 1927; GLG, pers. observ. at GMH). As far as it regards species of *Boavus*, this North American Eocene genus bears strong resemblance with *Palaeopython* (e.g., figures in Gilmore 1938; Brattstrom 1955; Rage 1984; Holman 2000). Especially, vertebrae of its genotype, *Boavus occidentalis*, are characterized by a vaulted neural arch and thick zygosphene [e.g., the holotype YPM 511 (see Gilmore 1938:Fig. 2)], which are reminiscent of the respective features of *Palaeopython helveticus* sp. nov. We acknowledge that the genus *Boavus* is in need of revision and this would eventually provide important insights into its precise taxonomic content, the validity or not of its inclusive species, and even its distinctiveness or not from the genus *Palaeopython*. Such undertake of *Boavus* is of course beyond the scope of this paper. Whatever the case, *Boavus* spp. seem to be distinct than the new species from Switzerland, in having relatively less dorsally inclined prezygapophyses and rather large and rounded cotyle, whereas such distinctiveness is further also supported by a geographic rationale. Nevertheless, the overall similarity and potential close affinities among *Palaeopython helveticus* sp. nov. (and other species of *Palaeopython*) with *Boavus* spp. should not appear at strange; rather than that, it is now generally accepted that several reptile groups share closely related or even congeneric forms during the Eocene of North America and Europe, with such affinities implying dispersal(s) from the former landmass to the latter one (probably via Greenland) during around the so called Paleocene–Eocene Thermal Maximum (e.g., Hoffstetter and Rage 1972; Augé 2005; Smith 2009; Georgalis and Joyce 2017). Among extant "booids", the pythonid *Python* Daudin, 1803, is much characterized by large size, a rather thick zygosphene, a vaulted neural arch, and high neural spine [e.g., trunk vertebrae of *Python regius* (Shaw, 1802); Rage 1984:Fig. 3a, b; MDHC 116 (this paper, Fig. 15t)], but still *Python* differs from *Palaeopython helveticus* sp. nov. in the different shape of zygosphene in anterior and dorsal views, the inclination of the prezygapophyses in anterior view, and the position, the shape, and the size of the paradiapophyses. Similarly, the extinct species *Python europaeus* Szyndlar and Rage, 2003, from the Miocene of Europe and *Python maurus* Rage, 1976, from the Miocene of Morocco have more depressed neural arch in comparison with *Palaeopython helveticus* sp. nov. (see figures in Rage 1976 and Szyndlar and Rage 2003; this paper, Fig. 15s). Finally, the Oligo-Miocene genus *Bavarioboa* Szyndlar and Schleich, 1993, which achieved a high diversity (seven species) and wide distribution in Western and Central Europe (Szyndlar and Schleich 1993; Szyndlar and Rage 2003), but also known from Anatolia (Szyndlar and Hoşgör 2012) is much different from *Palaeopython helveticus* sp. nov. in terms of its significantly smaller size, less vaulted neural arch in posterior view, much thinner zygosphene in anterior view, less widened centrum anteriorly, shorter neural spine in lateral view, less massive paradiapophyses, and the usual presence of distinct lateral lobes on the zygosphene in dorsal view (e.g., see figures in Szyndlar and Rage 2003; this paper, Fig. 15l–r).

As is the case with most extinct "booid" taxa, the proper allocation of *Palaeopython helveticus* sp. nov. to the family level cannot be resolved with certainty. *Palaeopython* was originally treated as a pythonid and not a boid (e.g., de Rochebrune 1880, 1884; Palacký 1884; Zittel 1887–1890). The distinction of pythons and boas was already identified by 19th century workers (e.g., Müller 1831; Duméril and

Bibron 1844; Troschel 1861). However, the general taxonomic trend of early to middle 20th century's taxonomic schemes lumped both pythonids and boids into a single family, Boidae, and accordingly, *Palaeopython* was subsequently treated as a boid, and interestingly the genus is currently even treated as a member of Boinae and not Pythoninae (e.g., Kuhn 1963; Rage 1978, 1984, 1988; Szyndlar and Rage 2003). In recent literature, only Wallach et al. (2014) placed *Palaeopython* into Pythonidae. Nevertheless, recent taxonomies treat boids and pythonids as distinct families (e.g., Slowinski and Lawson 2002; Vidal and Hedges 2009; Pyron et al. 2013; Reynolds et al. 2014; Hsiang et al. 2015; Figueroa et al. 2016; Harrington and Reeder 2017), though different topologies have variously arisen. The osteological distinction of pythonids from boids is mostly based on cranial features, whereas the vertebral morphology among the two lineages shares an overall strong resemblance, especially as it concerns the massively built vertebrae, the low ratio of CL/NAW, the usually high neural spines, the relatively thick zygosphene, and the overall shape (Frazetta 1975; Ivanov 2000; Szyndlar and Rage 2003). Main differences among pythonids and boids in terms of vertebral morphology include the presence (in several boids) or absence (in pythonids) of paracotylar foramina (Szyndlar and Schleich 1993; Szyndlar and Rage 2003) and a higher number of vertebrae in pythonids (e.g., Schaal 2004), however, the former character is known to be subjected to considerable degree of variation (Rage 2001). These being said, and considering that the most abundant remains of *Palaeopython* spp. are vertebrae, and particularly for the case of *Palaeopython helveticus* sp. nov., these constitute the sole known elements, we here refrain from referring *Palaeopython helveticus* into either Pythonidae or Boidae, pending a comprehensive description and phylogenetic analysis of fully articulated skeletons with skulls (e.g., complete specimens of *Palaeopython* from the localities of Messel and Geiseltal). Taking also into consideration the fact that pythonids and boids are probably more distantly related and could even pertain to distinct superfamilies, we here use the informal term "booid" in quotation marks to denote the group uniting all pythonids and boids.

5.2 Ontogenetic vertebral variability of snakes: a case study on *Palaeopython helveticus* sp. nov

Isolated vertebrae are the most common and abundant finds of snakes in the fossil record and as such, the taxonomy of extinct genera and species has been principally based on the study of these elements (Owen 1850; de Rochebrune 1880; Gilmore 1938; Auffenberg 1963; Rage 1984; Szyndlar 1984; Holman 2000). Nevertheless, their precise taxonomic identification is severely hampered by the fact that these elements are known to be subjected to a large degree of intracolumnar and intraspecific variability (Auffenberg 1963; Rage 1984; Szyndlar 1984; Szyndlar and Rage 2003), or, more rarely, even sexual variation (Bogert 1964) observed within a single taxon. Moreover, there appears to exist also significant ontogenetic variation within the vertebrae of a single species (Gans 1952; Gans and Oshima 1952; Auffenberg 1963; Szyndlar 1984; LaDuke 1991; Parmley and Reed 2003; Szyndlar and Rage 2003; Bochaton and Bailon 2018). In general, vertebrae of hatchlings are much shorter, they have a relatively large to enormous neural canal, a wide zygosphene, small prezygapophyses and postzygapophyses that are not extended laterally, and a wide, shallow posterior notch in the neural arch (LaDuke 1991). To the contrary, in vertebrae of old aged snakes (i.e., individuals reaching near their maximum size), the vertebral body is strongly broadened, the neural canal is extremely narrow, the neural arch is distinctly upswept above the zygantrum and extended posteriorly behind the level of the condyle, the subcentral and interzygapohyseal ridges are prominent, and the zygosphene possesses strongly developed lateral lobes and a vestigial median lobe (Szyndlar 1984; Szyndlar and Rage 2003). Vertebrae of juveniles differ from those of adults in several aspects, such as possessing a lower CL/NAW ratio, a comparatively broader neural arch, a much broader cotyle, a thinner zygosphene, prezygapophyses less developed but most principally, less extended laterally, a centrum less widened anteriorly, neural arch gently curved and not bulging above the zygantrum, and a larger neural canal (Szyndlar 1984; Rage 2001). It has been observed that the centrum length increases more rapidly than does its width throughout ontogeny (Szyndlar 1984; Szyndlar and Rage 2003). Even within differently aged adult individuals of the same species, variation is still known to occur: at least in most "booids", trunk vertebrae of smaller-sized (younger) adult individuals possess a rather shorter centrum, weaker interzygapophyseal constriction, a more anterior orientation of the prezygapophyses, a more posterior orientation of the postzygapophyses, shorter neural spine, cotyle and condyle clearly wider than high, and longer and thinner prezygapophyseal processes, in comparison with the ones of larger-sized (older) adult individuals (Bochaton and Bailon 2018). In addition, the shape of the prezygapophyseal and postzygapophyseal articular facets is usually more ovoid in smaller specimens and becomes more rectangular in larger ones (Bochaton and Bailon 2018). It has also been noted that the haemal keel may vary throughout ontogeny, being usually ridge-shaped in younger specimens, but becoming more flattened in older individuals (a feature observed at least for some dipsadids; Auffenberg 1958). At least for "booids", the vertebral centrum has been described as more anteroposteriorly tilted downward in lateral view in younger individuals (Albino 1993). As far as it concerns age determination, certain vertebral structures can offer insights: Petermann and Gauthier (2018) recently demonstrated a correlation pattern between ontogeny growth and lines inside the zygantrum, whereas the count of growth rings on the prezygapophyses and postzygapophyses has also been applied to indicate ontogenetic stage of fossil individuals (Venczel et al. 2015).

Differently-shaped zygosphenes are present in the Dielsdorf collection and in particular among vertebrae that we here consider as conspecific with *Palaeopython helveticus* sp. nov. The shape and the thickness of the zygosphene in anterior view changes drastically throughout ontogeny (Albino 1993); despite the fact that this feature is often used in ophidian palaeontology for systematic purposes, no detailed quantitative analysis of its transformation throughout ontogeny has so far been undertaken. It seems that zygosphenes that are much dorsally arched in anterior view could be indicative of an earlier ontogenetic stage. It is characteristic the case of the extant *Boa constrictor* Linnaeus, 1758, where in exactly the same vertebral position (i.e., 139th vertebra of the column), the adult specimen (SMF-PH 40) possesses a much thicker and differently shaped zygosphene than the younger individual (SMF-PH 45), with the latter having a distinctly arched zygosphene (Fig. 16). A similarly arched zygosphene is also present in the specimen PIMUZ A/III 633 of our fossil assemblage, although relatively thicker; we accordingly consider this specimen as pertaining to an earlier (though not much earlier) ontogenetic individual than the holotype PIMUZ A/III 634. Such arched zygosphenes are also present to specimens of other *Palaeopython* spp., such as an anterior trunk vertebra of *Palaeopython filholii* (MNHN ECC 2574) from the Phosphorites du Quercy and specimens of *Palaeopython* from Geiseltal (e.g., GMH XLI-314a-1968, GMH XLI-314d-1968, GMH XLI-314e-1968, and GMH XLI-314f-1968).

It is thus apparent that vertebrae of a single species can become drastically transformed in the morphology, shape, and size of multiple structures during the ontogenetic transition hatchling–juvenile–sub-adult–adult. Unfortunately, isolated fossil vertebrae certainly offer not enough luxury to confirm and adequately evaluate such ontogenetic variability. As such, it can be often the case that ontogenetically variable features of fossil snake vertebrae have been instead given taxonomic value. With regard to the genus *Palaeopython*, no study on the ontogenetic vertebral variability had so far been conducted, even from localities that have yielded many specimens (e.g., de Rochebrune 1880, 1884; Rage 1974; Schaal 2004). In order to test whether several important anatomical differences that are observed across our snake vertebral assemblage have taxonomic value or are simply ontogenetically variable, we conducted CT scanning of three different specimens: the largest vertebra (PIMUZ A/III 634 (holotype of *Palaeopython helveticus* sp. nov.)], one of intermediate size (PIMUZ A/III 636), and one of the smallest vertebrae (PIMUZ A/III 631). Transverse, parasagittal, and horizontal sections in the three vertebrae revealed interesting features and consistent trends (Fig. 17). The length of the centra increases from Fig. 17d (CL = 4.2 mm) to Fig. 17 h (CL = 8.3 mm) to Fig. 17 l (CL = 10.5 mm). An also interesting feature is that the position of the subcentral foramina in the ventral surface of the centrum does not change. There is a trend towards increased thickness of cortical bone from Fig. 17b to Fig. 17f to Fig. 17j and Fig. 17d to Fig. 17h to Fig. 17l. Larger vascular spaces in the centrum (forming circle around the neural canal) become more elongate and more elaborate in shape from Fig. 17b to Fig. 17f to Fig. 17j. The large vascular cavities

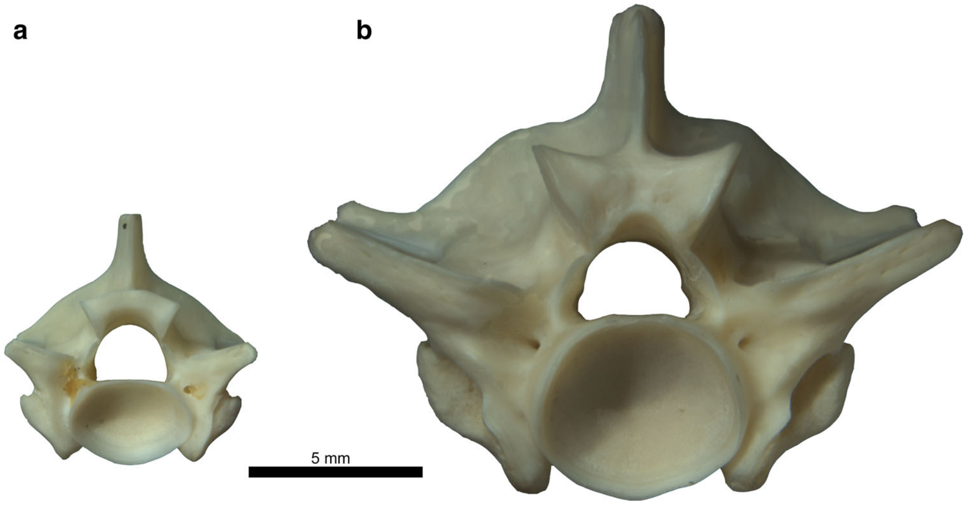

Fig. 16 Modification of the zygosphene shape throughout ontogeny of “booid” snakes: **a** the 139th vertebra of a young specimen of a *Boa constrictor* (SMF-PH 45); **b** the 139th vertebra of an adult specimen of *Boa constrictor* (SMF-PH 40). Both specimens in anterior view. Photographs by Krister Smith, courtesy of the Senckenberg Research Institute, Palaeoherpetology collection

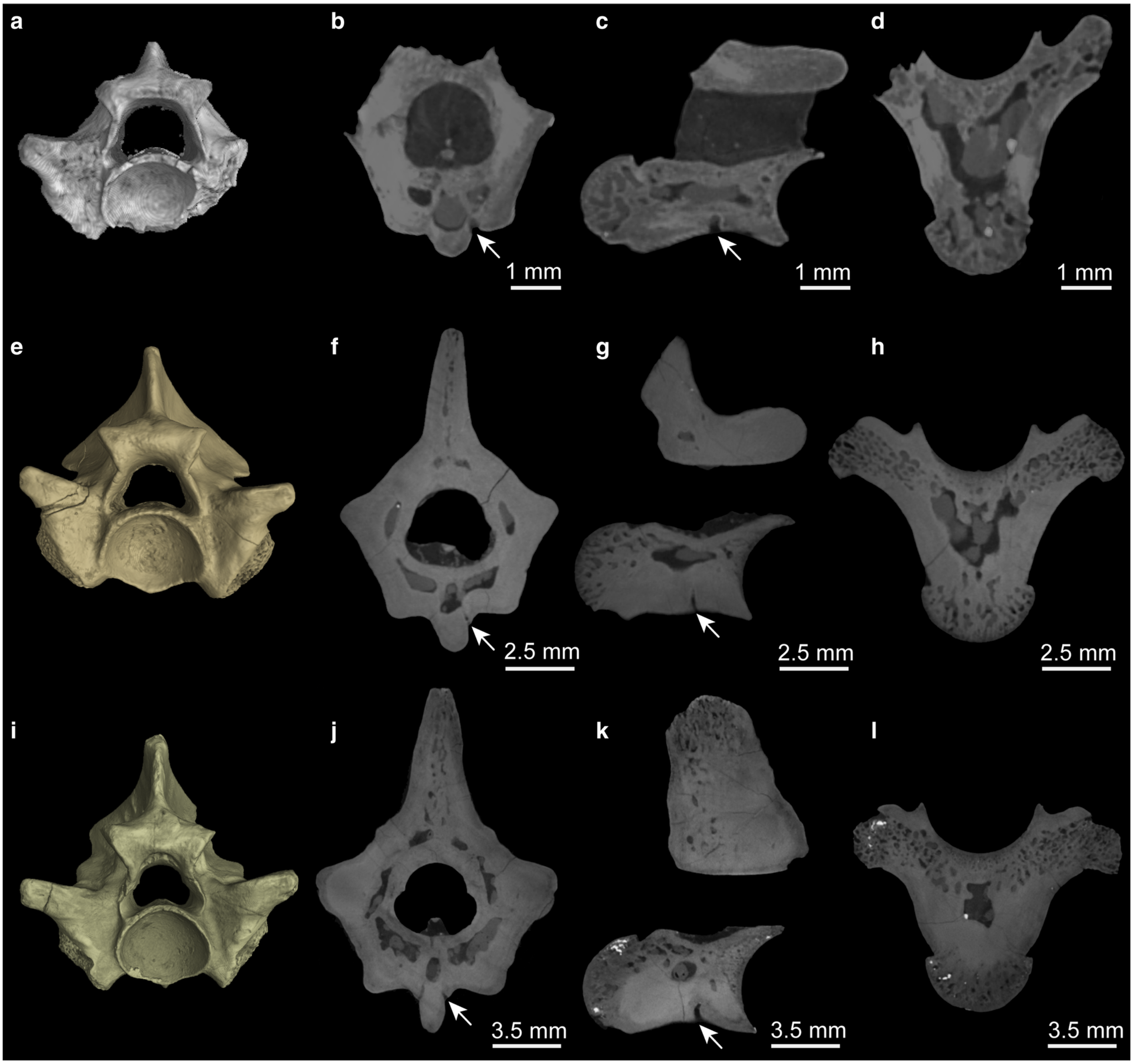

Fig. 17 Virtual comparison of vertebrae of *Palaeopython helveticus* sp. nov.: PIMUZ A/III 631 (**a**–**d**), PIMUZ A/III 636 (**e**–**h**), and the holotype PIMUZ A/III 634 (**i**–**l**). **a**, **e**, **i** virtual isosurface models showing the vertebrae in anterior view; not to scale. **b**, **f**, **j** transverse sections of vertebrae; white arrows indicate subcentral foramen next to haemal keel. **c**, **g**, **k** parasagittal sections with white arrows pointing at the same subcentral foramen next to the haemal keel. **d**, **h**, **l** horizontal sections at mid-height of centra

in the centrum appear to become proportionally restricted in anteroposterior extent from Fig. 17c to Fig. 17g to Fig. 17k. Other growth marks (e.g., LAGs, annuli and growth zones) in the bone tissue are not visible in these virtual sections and it is only in the largest specimen (i.e., the holotype PIMUZ A/III 634) that some faint growth marks in the thick ventral cortex part were visible. We consider that all these features can be attributed to ontogenetic variation instead of representing different species.

In order to get some further support for this claim, we also graphically inserted the outlines of the two smaller vertebral centra in sagittal plane (i.e., PIMUZ A/III 631 and PIMUZ A/III 636) over the image of the largest specimen (i.e., the holotype PIMUZ A/III 634), all in absolute scale (Supplementary Fig. 1). Interestingly, the two smaller outlines fit well in shape with the largest vertebra and seem to represent earlier growth stages of the latter specimen. According to all these CT scanning data, we herein refer the two smaller-sized vertebrae (the much smaller PIMUZ A/III 631 and the intermediate-sized PIMUZ A/III 636) to *Palaeopython helveticus* sp. nov. (the holotype PIMUZ A/III 634), and treat them as earlier ontogenetic stages of the same species. Note that the three vertebrae originate from two different fissure fillings within Dielsdorf [PIMUZ A/III 631 and PIMUZ A/III 634 from Fissure A (MP 16–MP 20); PIMUZ A/III 636 from Fissure B (MP 17–MP 20)] which could imply also that they are allotemporal [sensu Smith and Gauthier (2013); i.e., not absolutely contemporary], so some other kind of intraspecific variation/evolutionary change could also be the case, though ontogeny should be most likely considered the principal factor. This referral enhances our understanding of the vertebral anatomy of early ontogenetic stages of *Palaeopython helveticus* sp. nov. (see also the entry "Intracolumnar and ontogenetic vertebral variability" in the Systematic Palaeontology above) and provides evidence that the most distinctive feature of this species, i.e., the vaulting of the neural arch, changes only slightly during ontogeny. To the contrary, features that have been variously considered as taxonomically important and distinctive for extinct snakes, such as the thickness of the zygosphene, the ratio of the width of the cotyle versus the width of the zygosphene (e.g., Rage 1984; Holman 2000), can be attributed instead to ontogenetic variation. Interestingly, especially the latter character (the ratio of the width of the cotyle versus the width of the zygosphene) which seems to be variable in *Palaeopython helveticus* sp. nov. (< 1 in large-sized vertebrae and ≥ 1 in intermediate-sized vertebrae) does not seem to be ontogenetically variable in certain extant "booid" taxa, such as the large pythonid *Malayopython reticulatus* (Schneider, 1801) (e.g., juvenile specimen ZZSiD 436), but still quantitative analyses on this feature are currently lacking for extant forms. In any case, the herein presented results on the Dielsdorf snake assemblage further highlight the role of CT scanning in the study of extinct snakes and call for caution in taxonomic conclusions when dealing with localities that have yielded a small number of isolated vertebrae.

5.3 Palaeobiogeography: sympatry of *Palaeopython* and *Palaeovaranus*

The Dielsdorf squamate assemblage is so far not particularly diverse; nevertheless, the lizard and snake remains demonstrate the presence of typical representative genera of the European herpetofauna prior to the "Grande Coupure" extinction event that took place across the latest Eocene–earliest Oligocene boundary (Rage 2013; Georgalis 2017). More precisely, the identification of the large-sized lizard and snake genera *Palaeovaranus* and *Palaeopython* in the Dielsdorf assemblage provides a biogeographic connection with the Phosphorites du Quercy, from Eocene localities of which these two genera were originally established in the 19th century (Rochebrune 1880; Zittel 1887–1890). Indeed, the strong resemblance among the large snakes from the Eocene of Switzerland [material described from Mormont (Pictet et al. 1855–1857)] and those from the Phosphorites du Quercy was already pointed out by Filhol (1877a, b, c), followed subsequently by de Rochebrune (1880). With the present identification of *Palaeovaranus* in Dielsdorf, such herpetofaunal resemblance is also testified by that lizard lineage. Such broad geographic distribution of the genera *Palaeopython* and *Palaeovaranus* may have been facilitated by land interconnections between the Eocene large islands of the European Archipelago; taking into consideration that current palaeogeographic reconstructions of the late Eocene Europe place the localities yielding these two genera as parts of the same large island (e.g., Popov et al. 2004), the relatively high degree of species diversity, at least within *Palaeopython*, could be attributed to some kind of environmental or ecological obstacles that enabled "isolation" of certain endemic or at least narrowly distributed species (e.g., *Palaeopython helveticus* sp. nov.), although a so far unknown true geographic isolation cannot be ruled out with certainty. Regarding localities that yielded more than one species of *Palaeopython* and/or *Palaeovaranus* [Dielsdorf quarries could represent such a case, if *Palaeopython* cf. *fischeri* and *Palaeopython* sp. (morphotype 3) truly represent distinct forms than *Palaeopython helveticus* sp. nov.], then perhaps certain ecological or environmental factors favored such increasing intrageneric diversity of closely related, sympatric forms, probably via some kind of niche partitioning. The coexistence sympatrically of more than one distinct species of *Palaeopython* in Dielsdorf should not appear at strange, as certain localities are known to have yielded more than one species of that genus co-occurring together [e.g., Escamps, Quercy, France (Zittel 1887–1890; Rage 1974); several Geiseltal quarries (GLG, pers. observ.)]. The relatively high diversity of *Palaeopython* spp. in Western and Central Europe is reminiscent of the even higher species diversity of the Oligo-Miocene "booid" genus *Bavarioboa* (Szyndlar and Rage 2003) but also of the large diversity of extant pythonids across Africa, Asia, and Oceania (Wallach et al. 2014). Whether palaeovaranids also achieved a similarly high degree of diversity remains currently unknown, due to the fact that the skeletal anatomy of the two valid species (i.e., *Palaeovaranus cayluxi* and *Palaeovaranus giganteus*) is not adequately known and the potential intraspecific variability cannot be fully assessed (Georgalis 2017). Therefore, the various indeterminate occurrences of the genus *Palaeovaranus* in the Eocene of Europe (Georgalis 2017) could eventually pertain to distinct species, with this also potentially applying to the Dielsdorf material. Indeed, if we may consider modern monitor lizards (Varanidae) as a potential ecological analogue, it is well the case that certain areas in Australia, Asia, and Africa are currently inhabited by several co-existing extant species of the genus *Varanus* Merrem, 1820 (e.g., Pianka et al. 2004), with even as much as ten species co-occurring sympatrically in some regions (e.g., Kimberley region in Western Australia; D'Amore et al. 2018). As such, we may regard the idea of the relative abundance of different species of these large snakes and lizards as reasonable, especially when considering the much warmer climate of the Eocene in comparison with subsequent Neogene and Quaternary faunas.

It is further interesting to observe that fossils of the genera *Palaeovaranus* and *Palaeopython* have been frequently recovered from the same localities. Such shared occurrences among the two genera are known from the early–middle Eocene (MP 11) of Messel, Germany (Habersetzer and Schaal 1990; Schaal 2004; Smith and Scanferla 2016; Smith et al. 2018), the middle Eocene (MP 12–MP 14) of Geiseltal, Germany (Barnes 1927; Weigelt 1929; Kuhn 1939, 1940b; Haubold 1977), the middle Eocene (MP 14) of Lissieu, France (Augé 2005; Rage and Augé 2010), the middle Eocene (MP 16) of Lavergne, France (Augé 2005; Rage 2013), the middle Eocene (MP 16) of Le Bretou, France (Rage 1988), the late Eocene (MP 17) of Perrière, France (Rage 1984; Augé 2005), the late Eocene (MP 17) of the Mammal Bed in Hordle Cliff, England (Holman et al. 2006; Klembara and Green 2010), the late Eocene (MP 18) of Sainte Néboule, France (Rage 1978; Augé 2005), and the late Eocene (MP 19) of Escamps, France (Zittel 1887–1890; Fejérváry 1935; Rage 1974; Augé 2005), and perhaps also the (?several) imprecisely known localities from the "old collections" of the Phosphorites du Quercy (Filhol 1876, 1877a, b, c; de Rochebrune 1880, 1884; Lydekker 1888; De Stefano 1903, 1905; Stromer 1912; Kuhn 1940b; Augé 2005). However, preliminary descriptions and mentions in the literature may even imply that the two lizard and snake genera may have coexisted together even from much earlier: i.e., the Paleocene of Walbeck, Germany, from where, Kuhn (1940a) described material which he referred to the varanid genus *Saniwa* Leidy, 1870, but which is currently considered as a probable palaeovaranid (Augé 2005; Georgalis 2017), whereas the same author also described from that locality, a relatively large (23 mm long) maxillary fragment of a probable pythonid (Kuhn 1940a). This latter specimen could eventually pertain to *Palaeopython* or at least some closely related form, though without any accompanying figure and only the minor original description of Kuhn (1940a), its precise affinities cannot be determined with certainty. Early Eocene potential records of sympatric *Palaeovaranus* and *Palaeopython* also exist from the coeval (MP 7) localities of Dormaal, Belgium, and Le Quesnoy, France: from the former locality (Dormaal), *Palaeovaranus* sp. has been described and figured (Augé 1990, 2005), but there is also a mention of snake material tentatively referred to *Paleryx* by Hecht and Hoffstetter (1962); however, that snake material was only mentioned without any accompanying figure (collection numbers are provided though) and considering that *Palaeopython* was at that time considered as synonym of *Paleryx* (e.g., Kuhn 1963), we cannot exclude that the Dormaal material is referrable to *Palaeopython*. The latter locality (Le Quesnoy) yielded also an indeterminate palaeovaranid and a probable *Palaeopython* ("Groupe *Paleryx-Palaeopython*"; Nel et al. 1999), but again these records were accompanied by no description, figure, or at least collection numbers, and cannot therefore be evaluated with certainty. This is also the case of the middle Eocene (MP 16) of Grisolles, France (Russell et al. 1982; Augé 2005), the late Eocene (MP 17) of Aubrelong 2, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 17) of La Bouffie, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 17) of Lebratière (= Lebratières), France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 17) of Malpérié, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 17) of Rosières 5, Quercy, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 18) of Gousnat, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 18) of Coânac, France (Crochet et al. 1981; Augé 2005), the late Eocene (MP 18–MP 19) of Sindou, France (Crochet et al. 1981; Augé 2005), and the late Eocene (MP 19) of Rosières 2, France (Crochet et al. 1981; Augé 2005; only *Palaeovaranus* has been formally described) from where both *Palaeovaranus* and *Palaeopython* have been mentioned but not described or figured. Finally, there are also palaeovaranid-yielding localities, which have also yielded indeterminate "booids" which could eventually pertain to *Palaeopython*, but these latter remains have not been adequately described or figured [i.e., the early Eocene (MP 8/9) of La Borie, France (Laurent et al. 2010) and the middle Eocene (MP 13) of Saint-Maximin, France (Duffaud and Rage 1997)]. Besides, the snake remains from several localities within the Phosphorites du Quercy, which have yielded *Palaeovaranus* remains (Augé 2005; Georgalis 2017), are as yet incompletely studied. Taking all these into account, it is clear that *Palaeovaranus* spp. and *Palaeopython* spp. co-existed sympatrically in several areas across Western and Central Europe and for a long time period, spanning perhaps throughout the whole Eocene (Fig. 18). It seems that certain environmental and/or ecological factors favored the sympatric co-existence of these two large-sized reptile genera. In any case, whereas *Palaeovaranus* continues to be found in several early Oligocene localities, mainly from France (Georgalis 2017), this is not the case with *Palaeopython*, as the latter genus has not a single reliable record after the latest Eocene, apparently becoming extinct during the "Grande Coupure".

Fig. 18 Life reconstruction of *Palaeopython helveticus* sp. nov. and other faunal elements of the Dielsdorf palaeoenvironment during the late middle–late Eocene. In the foreground, an adult *Palaeopython helveticus* sp. nov. is approaching two microchoerine primates of the genus *Necrolemur*. On the tree trunk, a *Palaeovaranus* is resting. Two alligatorine crocodylians are seen inside the water, while an indeterminate chiropteran is flying above. The two large mammals on the far side of the bank are the perissodactyl *Palaeotherium magnum*, while the smaller one on their left represents the perissodactyl *Lophiotherium*

6 Conclusions

The Dielsdorf squamate assemblage is dominated by a new species of "booid" snake, *Palaeopython helveticus* sp. nov., which is characterized by a unique combination of vertebral features. Other squamate remains include a large lizard (*Palaeovaranus* sp.) and three other snake taxa (*Palaeopython* cf. *fischeri*, *Palaeopython* sp. [morphotype 3], and "Booidea" indet.). The smallest-sized snake specimen (indeterminate "booid") bears resemblance with the diminutive "booid" *Hordleophis balconae* from the late Eocene of the United Kingdom. Extensive comparisons with related extinct and extant forms demonstrate the distinctiveness of the new taxon *Palaeopython helveticus* sp. nov. Furthermore, CT scans of three vertebrae suggested that all anatomical differences among these specimens are probably due to ontogenetic variation. This is the first approach to disentangle the ontogenetic variability in the genus *Palaeopython*, whereas it highlights the role of CT scanning for deciphering such taxonomically complex issues. We further urge that caution should be taken when dealing with limited number of snake vertebrae in a single locality. Micro-CT scanning in the dentary of *Palaeovaranus* confirmed the presence of plicidentine in this lizard lineage. *Palaeovaranus* and *Palaeopython* have co-occurred sympatrically throughout most of the Eocene (and perhaps even earlier) in several different European localities.

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References

Albino, A. M. (1993). Snakes from the Paleocene and Eocene of Patagonia (Argentina): Paleoecology and coevolution with mammals. *Historical Biology, 7,* 51–69.

Auffenberg, W. (1958). A new genus of colubrid snake from the upper Miocene of North America. *American Museum Novitates, 1874,* 1–16.

Auffenberg, W. (1963). The fossil snakes of Florida. *Tulane Studies in Zoology, 10,* 131–216.

Augé, M. (1990). La faune de lézards et d'Amphisbènes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocène inférieur). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, 60,* 161–173.

Augé, M. (2005). Evolution des lézards du Paléogène en Europe. *Mémoires du Muséum National d'Histoire Naturelle, Paris, 192,* 1–369.

Augé, M., & Smith, R. (2009). An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene-Oligocene transition. *Zoological Journal of the Linnean Society, 155,* 148–170.

Barnes, B. (1927). Eine eozäne Wirbeltier-Fauna aus der Braunkohle des Geiseltals. *Jahrbuch des Halleschen Verbandes für die Erforschung der mitteldeutschen Bodenschätze, Neue Folge, 6,* 5–24.

Bhullar, B.-A. S., & Smith, K. T. (2008). Helodermatid lizard for the Miocene of Florida, the evolution of the dentary in Helodermatidae, and comments on dentary morphology in Varanoidea. *Journal of Herpetology, 42,* 286–302.

Bochaton, C., & Bailon, S. (2018). A new fossil species of *Boa* Linnaeus, 1758 (Squamata, Boidae), from the Pleistocene of Marie-Galante Island (French West Indies). *Journal of Vertebrate Paleontology, 38,* e1462829.

Bogert, C. M. (1964). Snakes of the genera *Diaphorolepis* and *Synophis* and the colubrid subfamily Xenoderminae (Reptilia, Colubridae). *Senckenbergiana Biologica, 45,* 509–531.

Bolliger, T. (1992). Kleinsäuger aus der miozänmolasse der Ostschweiz. *Documenta Naturae, 75,* 1–297.

Brattstrom, B. H. (1955). New snakes and lizards from the Eocene of California. *Journal of Paleontology, 29,* 145–149.

Crochet, J.-Y., Hartenberger, J.-L., Rage, J.-C., Rémy, J. A., Sigé, B., Sudre, J., et al. (1981). Les nouvelles faunes de vertébrés antérieures à la "Grande Coupure" découvertes dans les phosphorites du Quercy. *Bulletin du Muséum National d'Histoire Naturelle, Series 4, 3,* 245–266.

D'Amore, D. C., Clulow, S., Doody, J. S., Rhind, D., & McHenry, C. R. (2018). Claw morphometrics in monitor lizards: Variable substrate and habitat use correlate to shape diversity within a predator guild. *Ecology and Evolution, 8,* 6766–6778.

Daudin, F. M. (1803). *Histoire naturelle, génerale et particulière des reptiles; Ouvrage faisant suite aux Oeuvres de Leclerc de Buffon, et partie du cours complet d'histoire naturelle rédigé par C.S. Sonnini, membre de plusieurs sociétés savantes Tome cinquième* (p. 365). Paris: F. Dufart.

de Rochebrune, A. T. (1880). Revision des ophidiens fossiles du Museum d'Histoire Naturelle. *Nouvelles Archives du Muséum d'Histoire Naturelle, 2ème Série, 3*, 271–296.

de Rochebrune, A. T. (1884). Faune ophiologique des Phosphorites du Quercy. *Mémoires de la Société des Sciences Naturelles de Saône-et-Loire, 5,* 149–164.

De Stefano, G. (1903). I sauri del Quercy appartenenti alla collezione Rossignol. *Atti della Societa Italiana di Scienze Naturali e del Museo Civili di Storia Naturale, Milan, 42,* 382–418.

De Stefano, G. (1905). Appunti sui Batraci e sui Rettili del Quercy appartenenti alla collezione Rossignol. Parte Terza. Coccodrilli–Serpenti–Tartarughe. *Bolletino della Società Geologica Italiana, 24,* 17–67.

Delfino, M., Zoboli, D., Carnevale, G., & Pillola, G. L. (2014). The rediscovered holotype of *Palaeopython sardus* Portis, 1901 from the Miocene of Sardinia belongs to a fish, not to a snake. *Bollettino della Società Paleontologica Italiana, 53,* 89–92.

Duffaud, S., & Rage, J.-C. (1997). Les remplissages karstiques polyphasés (Éocène, Oligocène, Pliocène) de Saint-Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l'Éocène moyen (MP 13). 2.– Systématique: Amphibiens et Reptiles. In J. P. Aguilar, S. Legendre & J. Michaux (Eds.), Actes du Congrès BiochroM'97. *Mémoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Études, 21*, 729–735.

Duméril, A. M. C., & Bibron, G. (1835). *Erpétologie générale ou histoire naturelle complète des reptiles. Tome second. Contenant l'histoire de toutes les espèces de l'ordre des tortues ou chéloniens, et les généralités de celui des lézards ou sauriens* (p. 680). Paris: Librairie Encyclopédique de Roret.

Duméril, A. M. C., & Bibron, G. (1844). *Erpétologie générale ou histoire naturelle complète des reptiles. Tome sixième, comprenant l'histoire générale des ophidiens, la description des genres et des espèces de serpents non venimeux, savoir, la totalité des vermiformes ou des scolecophides, et partie des circuriformes ou azémiophides; en tout vingt–cinq genres et soixante–cinq espèces* (p. 609). Paris: Librairie Encyclopédique de Roret.

Fejérváry de, G. J. (1935). Further contributions to a monograph of the Megalanidae and Fossil Varanidae, with notes on recent varanians. *Annales historico-Naturales Musei nationalis Hungarici, Pars Zoologica, 29,* 1–130.

Figueroa, A., McKelvy, A. D., Grismer, L. L., Bell, C. D., & Lailvaux, S. P. (2016). A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS One, 11,* e0161070.

Filhol, H. (1876). Sur les reptiles fossiles des phosphorites du Quercy. *Bulletin de la Société Philomathique de Paris, Série 6, 11,* 27–28.

Filhol, H. (1877a). Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Pt. II. *Annales des Sciences Géologiques, 8,* 1–340.

Filhol, H. (1877b). Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Pt. II. *Bibliothèque de l'Ecole des Hautes Études, Section des Sciences Naturelles, 16,* 1–338.

Filhol, H. (1877c). *Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères* (p. 561). Paris: G. Masson.

Frazzetta, T. H. (1975). Pattern and instability in the evolving premaxilla of boine snakes. *American Zoologist, 15,* 469–481.

Fürbringer, M. (1900). Zur vergleichenden anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift, 34,* 215–718.

Gans, C. (1952). The functional morphology of the egg-eating adaptations in the snake genus *Dasypeltis*. *Zoologica: Scientific Contributions of the New York Zoological Society, 37,* 209–244.

Gans, C., & Oshima, M. (1952). Adaptations for egg eating in the snake *Elaphe climacophora* (Boie). *American Museum Novitates, 1571,* 1–16.

Gauthier, J. A., Kearney, M., Maisano, J. A., Rieppel, O., & Behike, A. D. B. (2012). Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History, 53,* 3–308.

Georgalis, G. L. (2017). *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). *Annales de Paléontologie, 103,* 293–303.

Georgalis, G. L., & Joyce, W. G. (2017). A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. *Bulletin of the Peabody Museum of Natural History, 58,* 115–208.

Georgalis, G. L., & Scheyer T. M. (2019). 3D data related to the publication: A new species of *Palaeopython* (Serpentes) and other extinct squamates from the Eocene of Dielsdorf (Zurich, Switzerland). *MorphoMuseuM*, *5*, e93. doi: https://doi.org/10.18563/journal.m3.93

Georgalis, G. L., Villa, A., & Delfino, M. (2017). The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. *Journal of Vertebrate Paleontology, 37,* e1301946.

Gilmore, C. W. (1938). Fossil snakes of North America. *Geological Society of North America, Special Papers, 9,* 1–96.

Gray, J. E. (1825). A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. *Annals of Philosophy, Series 2, 10,* 193–217.

Haas, G. (1960). On the trigeminus muscles of the lizards *Xenosaurus grandis* and *Shinisaurus crocodilurus*. *American Museum Novitates, 2017,* 1–54.

Habersetzer, J., & Schaal, S. (1990). Röntgenmethoden zur Untersuchung fossiler unt rezenter Wirbeltiere. *Natur und Museum, 120,* 254–266.

Harrington, S. M., & Reeder, T. W. (2017). Phylogenetic inference and divergence dating of snakes using molecules, morphology and fossils: new insights into convergent evolution of feeding morphology and limb reduction. *Biological Journal of the Linnean Society, 121,* 379–394.

Haubold, H. (1977). Zur Kenntnis der Sauria (Lacertilia) aus dem Eozän des Geiseltals. In H. W. Matthes, & B. Thaler (Eds.), Eozäne Wirbeltiere des Geiseltales (Wissenschaftliche Beiträge 1977/2). *Martin-Luther-Universität Halle-Wittenberg, Wissenschaftliche Beiträge, 1977*, 107–112.

Hecht, M., & Hoffstetter, R. (1962). Note préliminaire sur les amphibiens et les squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, 38,* 1–30.

Hoffstetter, R. (1943). Varanidae et Necrosauridae fossiles. *Bulletin du Muséum National d'Histoire Naturelle, Série 2, 15,* 134–141.

Hoffstetter, R. (1957). Un Saurien hélodermatidé (*Eurheloderma gallicum* nov. gen. et sp.) dans la faune fossile des phosphorites du Quercy. *Bulletin de la Société Géologique de France Série, 6*(7), 775–786.

Hoffstetter, R. (1962). Additions à la faune reptilienne de l'Éocène supérieur de Mormont-Saint-Loup (Suisse). *Bulletin de la Société Géologique de France, 4,* 109–117.

Hoffstetter, R., & Rage, J.-C. (1972). Les Erycinae fossiles de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. *Annales de Paléontologie, 58,* 81–124.

Holman, J. A. (1996). A new genus of diminutive boid snake from the upper Eocene of Hordle Cliff, Hampshire, England. *Tertiary Research, 17,* 11–13.

Holman, J. A. (2000). *Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology* (p. 357). Bloomington and Indianapolis: Indiana University Press.

Holman, J. A., Harrison, D. L., & Ward, D. J. (2006). Late Eocene snakes from the Headon Hill Formation, southern England. *Cainozoic Research, 5,* 51–62.

Hsiang, A. Y., Field, D. J., Webster, T. H., Behlke, A. D. B., Davis, M. B., Racicot, R. A., et al. (2015). The origin of snakes: revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. *BMC Evolutionary Biology, 15,* 87.

Hünermann, K. A. (1978). Ein varanoider Lacertilier (Reptilia, Squamata) aus einer alttertiären Spaltenfüllung von Dielsdorf (Kt. Zürich). *Eclogae Geologicae Helvetiae, 71,* 769–774.

Hünermann, K. A. (1981). Die Glimmersandgrube am Rodenberg bei Schlattingen (Kt. Thurgau) als paläontologisches Studienobjekt in der Oberen Süsswassermolasse. *Mitteilungen der Thurgauischen Naturforschenden Gesellschaft, 44,* 7–32.

[ICZN] International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature. 4th edition* (306 p.). London: International Trust for Zoological Nomenclature.

Ivanov, M. (2000). Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône; France), with comments on the colonisation of western Europe by colubroids. *Geodiversitas, 22,* 559–588.

Jost, J., Kälin, D., Börner, S., Vasilyan, D., Lawver, D., & Reichenbacher, B. (2015). Vertebrate microfossils from the Upper Freshwater Molasse in the Swiss Molasse Basin: Implications for the evolution of the North Alpine Foreland Basin during the Miocene Climate Optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology, 426,* 22–33.

Kearney, M., & Rieppel, O. (2006). An investigation into the occurrence of plicidentine in the teeth of squamate reptiles. *Copeia, 2006,* 337–350.

Klembara, J., & Green, B. (2010). Anguimorph lizards (Squamata, Anguimorpha) from the Middle and Upper Eocene of the Hampshire Basin of Southern England. *Journal of Systematic Palaeontology, 8,* 97–129.

Kuhl, H. (1820). *Beiträge zur Zoologie und vergleichenden Anatomie* (152 pp.). Frankfurt: Hermannsche Buchhandlung.

Kuhn, O. (1939). Die Schlangen (Boidae) aus dem Mitteleozän des Geiseltales. *Nova Acta Leopoldina, Neue Folge, 7,* 119–133.

Kuhn, O. (1940a). Crocodilier- und Squamatenreste aus dem oberen Paleocän von Walbeck. *Zentralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B, 1940,* 21–25.

Kuhn, O. (1940b). Die Placosauriden und Anguiden aus dem Mittleren Eozän des Geiseltales. *Nova Acta Academia Leopoldina, Carolinska, 53,* 461–486.

Kuhn, O. (1963). Serpentes (Supplementum I). In F. Westphal (Ed.), *Fossilium Catalogus, I: Animalia, pars 103* (45 pp.). Gravenhage: Uitgeverij Dr. W. Junk.

LaDuke, T. C. (1991). The fossil snakes of Pit 91, Rancho la Brea, California. *Contributions in Science, Natural History Museum of Los Angeles County, 424,* 1–28.

Laurent, Y., Adnet, S., Bourdon, E., Corbalan, D., Danilo, L., Duffaud, S., et al. (2010). La Borie (Saint-Papoul, Aude): un gisement exceptionnel dans l'Éocène basal du Sud de la France. *Bulletin de la Société D'histoire Naturelle de Toulouse, 146,* 89–103.

Leidy, J. (1870). Descriptions of *Emys jeanesi*, *E. haydeni*, *Baena arenosa*, and *Saniwa ensidens*. *Proceedings of the Academy of Natural Science, Philadelphia, 1870*, 123–124

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (824 p.). Stockholm: Laurentii Salvii.

Lydekker, R. (1888). *Catalogue of Fossil Reptiles and Amphibians in the British Museum (Natural History) Part I Containing the Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria* (309 p.). London: British Museum (Natural History).

Marsh, O. C. (1871). Description of some new Fossil Serpents, from the Tertiary deposits of Wyoming. *The American Journal of Science and Arts, Series 3, 1,* 322–327.

Mennecart, B., Yerly, B., Mojon, P.-O., Angelone, C., Maridet, O., Böhme, M., et al. (2016). A new Late Agenian (MN2a, Early Miocene) fossil assemblage from Wallenried (Molasse Basin, Canton Fribourg, Switzerland). *Paläontologische Zeitschrift, 90,* 101–123.

Merrem, B. (1820). *Versuch eines Systems der Amphibien I (Tentamen Systematis Amphibiorum)* (p. 191). Marburg: J. C. Kriegeri.

Müller, J. (1831). Beiträge zur Anatomie und Naturgeschichte der Amphibien. *Zeitschrift für Physiologie, 4,* 190–275.

Nel, A., de Plöeg, G., Dejax, J., Dutheil, D., de Franceschi, D., Gheerbrant, E., et al. (1999). Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus de l'Académie des Sciences. Série II Fascicule A (Sciences de la Terre et des planètes), 329,* 65–72.

Nopcsa, F. (1923). *Eidolosaurus* und *Pachyophis.* Zwei neue Neocom-Reptilien. *Palaeontographica, 65,* 99–154.

Oppel, M. (1811). *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben* (p. 87). Munich: Joseph Lindauer, Munich.

Owen, R. (1850). Part III. Ophidia (Palaeophis & c.). In R. Owen (Ed.), *Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds* (pp. 51–63). London: Palaeontographical Society of London.

Palacký, J. (1884). Die Verbreitung der fossilen Schlangen in Europa. *Sitzungsberichte der Königlich Böhmischen Gesellschaft der Wissenschaften in Prag, 1884,* 165–166.

Parmley, D., & Reed, H. W. (2003). Size and age class estimates of North American Eocene palaeopheid snakes. *Georgia Journal of Science, 61,* 220–232.

Petermann, H., & Gauthier, J. A. (2018). Fingerprinting snakes: paleontological and paleoecological implications of zygantral growth rings in Serpentes. *PeerJ, 6,* e4819.

Pianka, R. E., King, D., & King, R. A. (2004). *Varanoid Lizards of the World* (p. 587). Bloomington: Indiana University Press.

Pictet, F. J., Gaudin, C. T., & de La Harpe, P. (1855–1857). Mémoire sur les Animaux vertébrés trouvés dans le terrain Sidérolithique du Canton de Vaud et appartenant à la faune Eocène. *Matériaux pour la Paléontologie Suisse, 1,* 1–120.

Popov, S. V., Rögl, F., Rozanov, A. Y., Steininger, F. F., Shcherba, I. G., & Kovac, M. (2004). Lithologic-Paleogeographic maps of Paratethys. *Courier Forschungsinstitut Senckenberg, 250,* 1–46.

Portis, A. (1901). Il *Palaeopython sardus* Port. Nuovo pitonide del miocene medio della Sardegna. *Bollettino della Società Geologica Italiana, 20,* 247–253.

Pyron, R. A., Burbrink, F. T., & Wiens, J. J. (2013). A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology, 13,* 93.

Rage, J.-C. (1974). Les Serpents des Phosphorites du Quercy. *Palaeovertebrata, 6,* 274–303.

Rage, J.-C. (1976). Les squamates du Miocène de Béni Mellal, Maroc. *Géologie Méditerranéene, 2,* 57–70.

Rage, J.-C. (1978). 5. Squamates. In: B. Geze, J.-C. Rage, F. Vergnaud-Grazzini, F. de Broin, E. Buffetaut, C. Mourier-Chauvire, J.-Y. Crochet, B. Sigé, J. Sudre, A. Remy, L. Langebadre, L. de Bonis, J. L. Hartenberger, & M. Vianey-Liaud (Eds.), La poche à Phosphate de Ste-Néboule (Lot) et sa faune de vertébrés du Ludien supérior. *Palaeovertebrata, 8,* 201–215.

Rage, J.-C. (1983). Les serpents aquatiques de l'Éocène européen. Définition des espèces et aspects stratigraphiques. *Bulletin du Muséum National d'Histoire Naturelle, Section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie, 4*(5), 213–241.

Rage, J.-C. (1984). Serpentes. In P. Wellnhofer (Ed.), *Encyclopedia of paleoherpetology, part 11* (p. 80). Stuttgart: G. Fischer.

Rage, J.-C. (1988). Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. I Amphibiens et Reptiles. *Palaeontographica Abteilung A, 205,* 3–27.

Rage, J.-C. (2001). Fossil snakes from the Paleocene of São José de Itaboraí, Brazil. Part II. Boidae. *Palaeovertebrata, 30,* 111–150.

Rage, J.-C. (2013). Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments, 93,* 517–534.

Rage, J.-C., & Augé, M. (2010). Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios, 43,* 253–268.

Rage, J.-C., & Augé, M. (2015). Valbro: A new site of vertebrates from the early Oligocene (MP 22) of France (Quercy). III—Amphibians and squamates. *Annales de Paleontologie, 101,* 29–41.

Rage, J.-C., Bajpai, S., Thewissen, J. G. M., & Tiwari, B. N. (2003). Early Eocene snakes from Kutch, Western India, with a review of the Palaeophiidae. *Geodiversitas, 25,* 695–716.

Rage, J.-C., & Ford, R. L. E. (1980). Amphibians and squamates from the Upper Eocene of the Isle of Wight. *Tertiary Research, 3,* 47–60.

Reynolds, R. G., Niemiller, M. L., & Revell, L. J. (2014). Toward a Tree-of-Life for the boas and pythons: Multilocus species-level phylogeny with unprecedented taxon sampling. *Molecular Phylogenetics and Evolution, 71,* 201–213.

Romer, A. S. (1956). *Osteology of the reptiles* (p. 772). Chicago: University Chicago Press.

Rosselet, C. (1991). Fie fauna der Spaltenfullungen von Dielsdorf (Eozan, Kanton Zurich). *Documenta Naturae, 64,* 1–177.

Rosselet, C. (1993). The Fauna from the Fissure Fillings of Dielsdorf (Eocene, Canton Zurich, Switzerland). A Short Review. *Kaupia, Darmstadter Beitrage zur Naturgeschichte, 3,* 151–155.

Russell, D. E., Bonde, N., Boné, E., de Broin, F., Brunet, M., Buffetaut, E., et al. (1982). Tetrapods of the Northwest European Tertiary Basin. International Geological Correlation Programme Project l24: the Northwest European Tertiary Basin. *Geologisches Jahrbuch, A, 60,* 5–74.

Schaal, S. (2004). *Palaeopython fischeri* n. sp. (Serpentes: Boidae), eine Riesenschlange aus dem Eozän (MP 11) von Messel. *Courier Forschungsinstitut Senckenberg, 252,* 35–45.

Schneider, J. G. (1801). *Historiae amphibiorum naturalis et literariae. Fasciculus secundus, continens Crocodilos, Scincos, Chamaesauras, Boas, Pseudoboas, Elapes, Angues, Amphisbaenas et Caecilias* (p. 364). Jenae: Friederici Frommann.

Shaw, G. (1802). *General zoology, or systematic natural history. Vol. III. Part II. Amphibia* (pp. 313–615). London: G. Kearsley.

Slowinski, J. B., & Lawson, R. (2002). Snake phylogeny: evidence from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution, 23,* 194–202.

Smith, K. T. (2009). Eocene Lizards of the Clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the Early Radiation of Iguanidae (Reptilia: Squamata). *Bulletin of the Peabody Museum of Natural History, 50,* 219–306.

Smith, K. T., Čerňanský, A., Scanferla, A., & Schaal, S. F. K. (2018). Lizards and Snakes–Warmth-loving Sunbathers. In K. T. Smith, S. F. K. Schaal, & J. Habersetzer (Eds.), *Messel: an ancient greenhouse ecosystem* (pp. 123–147). Stuttgart: Schweizerbart.

Smith, K. T., & Gauthier, J. A. (2013). Early Eocene lizards of the Wasatch Formation near Bitter Creek, Wyoming: diversity and paleoenvironment during an interval of global warming. *Bulletin of the Peabody Museum of Natural History, 54,* 135–230.

Smith, K. T., & Scanferla, A. (2016). Fossil snake preserving three trophic levels and evidence for an ontogenetic dietary shift. *Palaeobiodiversity and Palaeoenvironments, 96,* 589–599.

Stromer, E. F. (1912). *Lehrbuch der paläozoologie. II. Teil: wirbeltiere* (p. 325). Leipzig and Berlin: B. G. Teubner.

Szyndlar, Z. (1984). Fossil snakes from Poland. *Acta Zoologica Cracoviensia, 28,* 1–156.

Szyndlar, Z., & Hoşgör, I. (2012). Boine snake *Bavarioboa* from the Oligocene/Miocene of eastern Turkey with comments on connections between European and Asiatic snake faunas. *Acta Palaeontologica Polonica, 57,* 667–671.

Szyndlar, Z., & Rage, J.-C. (2003). *Non-erycine Booidea from the Oligocene and Miocene of Europe* (p. 111). Kraków: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.

Szyndlar, Z., & Schleich, H. H. (1993). Description of Miocene snakes from Petersbuch 2 with comments on the lower and middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beiträge zur Naturkunde B, 192,* 1–47.

Troschel, F. H. (1861). Über den Unterkiefer der Schlangen und über die fossile Schlange von Rott. *Archiv für Naturgeschichte, 27,* 326–360.

Venczel, M., Vasile, Ş., & Csici-Sava, Z. (2015). A Late Cretaceous madtsoiid snake from Romania associated with a megaloolithid egg nest—Paleoecological inferences. *Cretaceous Research, 55,* 152–163.

Vidal, N., & Hedges, B. S. (2009). The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *Comptes Rendus Biologies, 332,* 129–139.

Wallach, V., Williams, K. L., & Boundy, J. (2014). *Snakes of the world: a catalogue of living and extinct species* (p. 1237). Boca Raton, London and New York: CRC Press.

Weigelt, J. (1929). *Loricotherium Waltheri* ist doch kein Gürteltier, sondern eine Gürtlelechse: *Placosaurus Waltheri* n. sp. *Jahrbuch des Halleschen Verbandes für die Erforschung der Mitteldeutschen Bodenschätze, 8,* 187–191.

Zittel, K. A. (1887–1890). *Handbuch der Paläontologie. Palaeozoologie. III. Pisces, Amphibia, Reptilia, Aves* (900 p.). Munchen and Leipsig: Druck und Verlag von R. Oldenbourg.