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Introduction to: Snakes from the Cenozoic of Europe – towards a macroevolutionary and palaeobiogeographic synthesis

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Snakes have long been important components of most European ecosystems. This is not readily obvious to herpetologists given that the modest extant taxonomic richness represents simply a glimpse of their astonishing abundance in Europe during much of the Cenozoic. Indeed, the fossil record documents a high taxonomic diversity of snakes, which included a plethora of distinct shapes, sizes, feeding and reproductive adaptations, ecological strategies, and locomotion (Rage 1984; Ivanov 2022; Smith & Georgalis 2022). Interestingly (as of February 2025), as many as 162 extinct species have been established from the Cenozoic of Europe; these 162 species have been assigned to 92 different genera, among which 56 genera are extinct and established upon European fossil material, 10 genera are extinct and have originally established upon fossil material from other continents, and 26 represent extant genera (GLG, unpublished data). This high diversity included both early representatives of extant clades that now inhabit the continent, such as erycids, colubrids, natricids, and viperids (Szyndlar 1984, 1991a, b; Ivanov 2022), giant forms of extant clades of the continent (Georgalis *et al.* 2016), as well as taxa that are now absent from Europe, such as pythonids and elapids (Rage 1984; Szyndlar 1991a, b; Szyndlar & Rage 2003; Zaher & Smith 2020; Ivanov 2022), but also a parade of unique, bizarre, and now extinct clades, such as palaeophiids, russellophiids, and anomalophiids (Rage 1983, 1984; Georgalis *et al.* 2020; Smith & Georgalis 2022; Fig. 1).

Fossil snake remains from the European Cenozoic consist primarily of isolated vertebrae (Rage 1984; Szyndlar 1984, 1991a, b; Venczel 2000; Szyndlar & Rage 2003; Ivanov 2022; Smith & Georgalis 2022; Fig. 1). Articulated vertebrae and cranial remains are less common (e.g. Owen 1850; Szunyoghy 1932; Hoffstetter 1939; Szyndlar 1984; Ivanov 1999; Venczel 2000; Szyndlar & Rage 2003; Georgalis *et al.* 2021; Georgalis & Scheyer 2022; Čerňanský 2024; Fig. 1), while complete skeletons are exceptionally rare and typically limited to a few Fossillagerstätte localities (Meyer 1845; Massalongo 1859; Janensch 1906; Kuhn 1939; Szyndlar 1992; Szyndlar & Böhme 1996; Baszio 2004; Smith & Scanferla 2016, 2021, 2022; Scanferla & Smith 2020; Zaher & Smith 2020; Georgalis *et al.* 2021; Seghetti *et al.* 2022; Palci *et al.*

FIG. 1. — Selected type specimens of European Cenozoic snakes: **A**, paratype skeleton (HLMD-Be 165) of *Messelopython freyi* Zaher & Smith, 2020, from the early to middle Eocene of Messel, Germany; **B**, holotype skeleton (SMF-ME 1828 A-B) of *Messelophis variatus* Baszio, 2004, from the early to middle Eocene of Messel, Germany; **C**, syntype trunk vertebra (NHMUK PV OR 33209) of *Palaeophis typhaeus* Owen, 1850, in right lateral view, from the early Eocene of Bracklesham, England; **D**, holotype trunk vertebra (ISEZ FR/RKI-10000) of *Natrix longivertebrata* Szyndlar, 1984, in right lateral view, from the

2024; Fig. 1). Remarkably, even mummified portions of snake bodies have been recovered in exceptional cases (Filhol 1877; Rochebrune 1884; Georgalis *et al.* 2021; Fig. 1)! Notably, the beautifully preserved skeletons from the Fossillagerstätte localities of Messel and Geiseltal in Germany have provided and continue to provide critical insight into the cranial anatomy and intracolumnar variation of multiple extinct snake taxa (Kuhn 1939; Baszio 2004; Scanferla & Smith 2020; Zaher & Smith 2020; Smith & Scanferla 2021, 2022; Georgalis *et al.* 2021; Palci *et al.* 2024; Fig. 1). Additionally, these fossils offer valuable information on palaeoecology and trophic interactions (e.g. Smith & Scanferla 2016).

The European Cenozoic fossil record of snakes dates back to the Paleocene and encompasses a wide geographic distribution. As such, it provides valuable insights into major climatic events, dispersals, faunal turnovers, and extinctions that shaped the European Cenozoic faunas, ultimately leading to the emergence of extant taxa. Such prominent events that affected European snake faunas include the high temperatures observed during the Paleocene-Eocene Thermal Maximum (PETM) and the Early Eocene Climatic Optimum (EECO), the cooling that triggered the "Grande Coupure" at the Eocene-Oligocene boundary, or the distinct palaeogeographic settings that arose during the formation of the "*Gomphotherium* Landbridge" during the Early Miocene, and the Messinian Salinity Crisis during the Miocene-Pliocene boundary (Szyndlar & Rage 2003; Rage 2013; Zaher *et al.* 2019; Georgalis *et al.* 2021; Ivanov 2022; Georgalis & Szyndlar 2022; Smith & Georgalis 2022). However, significant gaps remain from both a stratigraphic and a geographic point of view. Indeed, stratigraphically speaking, some geological epochs, such as the Paleocene and the Oligocene, are underrepresented, compared to other epochs, in the European snake fossil record (Smith & Georgalis 2022). Most notably from a geographic point of view, the Eastern portions of the continent remain notably less sampled for fossil snakes than Western and Central Europe (e.g. Ivanov 2022; Smith & Georgalis 2022).

European snake fossils have been known for over two centuries, with the earliest discoveries dating back to the early 19th century (Karg 1805). Throughout that century, notable fossil snake discoveries continued to capture the interest of European palaeontologists, including remarkable or enigmatic forms, such as the giant aquatic genus *Palaeophis* Owen, 1841, from England, the giant viper *Laophis* Owen, 1857, and *Python euboicus* Römer, 1870 – representing the first record of the extant genus *Python* Daudin, 1803, in Europe – both from Greece, as well as the constrictor *Palaeopython* Rochebrune, 1880, from France (Owen 1841, 1850, 1857; Meyer 1845; Römer 1870; Filhol 1877; Rochebrune 1880, 1884). The 20th century witnessed continued advancements in fossil snake discoveries in Europe, driven particularly by the comprehensive and meticulous work of Robert Hoffstetter, Jean-Claude Rage, and Zbigniew Szyndlar, who significantly enhanced our understanding of taxonomic diversity, cranial and vertebral diagnostic features, and intracolumnar variation in snakes (e.g. Hoffstetter 1939; Hoffstetter & Rage 1972; Rage 1974, 1983, 1984; Szyndlar 1984, 1991a, 1991b). In recent decades, our understanding of the taxonomic diversity and anatomy of Cenozoic fossil snakes from Europe has accelerated significantly, aided by the use of recent technologies such as micro-computed tomography (μCT) scanning (Bell *et al.* 2021) and by an improved knowledge of the skeletal anatomy of extant taxa (Zaher *et al.* 2019; Szyndlar & Georgalis 2023). Despite these advances, significant gaps remain, as many taxa have yet to be adequately described and the phylogenetic relationships of several groups are still poorly understood, hindering a full understanding of snake evolution in the European Cenozoic.

With this new volume in *Comptes Rendus Palevol*, we aim to address significant gaps in our knowledge of the snake fossil record during the European Cenozoic. The forthcoming contributions in this volume will encompass a range of topics, including:

- descriptions of new taxa and revisions of poorly documented taxa;
- identifications of novel anatomical features in the skull and vertebrae of fossil snakes;
- studies of articulated skeletons from Fossillagerstätte localities, enhanced by the application of micro-computed tomography (μCT) scanning;
- documentation of new fossil snake occurrences from underexplored regions of Europe;
- revised taxonomic frameworks for enigmatic and previously ambiguous extinct snake groups;
- studies of palaeobiogeography, dispersal events, extinction and survivorship dynamics of snakes across the Cenozoic of Europe, using sophisticated analytical methods.

We anticipate that this volume will provide fresh perspectives on the evolution of Cenozoic snakes in Europe, while also serving as a trigger for future research and new discoveries about these fascinating and charismatic reptiles!

Late Pliocene (MN 16), of Rębielice Królewskie IA, Poland; **E**, holotype trunk vertebra (MNHN.F.VCO29) of *Python europaeus* Szyndlar & Rage, 2003, in dorsal view, from the Early-Middle Miocene (MN 4/5) of Vieux-Collonges, France; **F**, syntype trunk vertebra (MNHN.F.LGA53) of "*Typhlops*" *grivensis* Hoffstetter, 1946, in dorsal view, from the Middle Miocene (MN 7/8) of La Grive, France; **G**, holotype trunk vertebra (MNHN.F.CB1603) of *Russellophis tenuis* Rage, 1975, in ventral view, from the early Eocene (MP 8/9) of Condé-en-Brie, France; **H**, right maxilla (GMH Ce I-5826-1926) part of the lectotype of *Eoconstrictor spinifer* (Barnes, 1927), in labial view, from the late early to early middle Eocene of Geiseltal, Germany; **I**, holotype trunk vertebra (PIMUZ A/III 634) of *Palaeopython helveticus* Georgalis & Scheyer, 2019, in anterior view, from the late middle to late Eocene of Dielsdorf, Switzerland; **J**, paralectotype mummified trunk portion (MNHN.F.QU16329) of *Rageophis lafonti* (Filhol, 1877) from the Eocene of the Phosphorites du Quercy, France (this specimen serves also as a paralectotype of *Tachyophis nitidus* Rochebrune, 1884); **K**, holotype posterior caudal vertebra (MNHN.F.COD1) of *Bransateryx vireti* Hoffstetter & Rage, 1972, in anterior view, from the late Oligocene (MP 30) of Coderet, France; **L**, paralectotype left dentary (MNHN.F.QU16336) of *Palaelaphis antiquus* Rochebrune, 1884, in medial view, from the Eocene or Oligocene of the Phosphorites du Quercy, France. Collections: A, Hessisches Landesmuseum Darmstadt; B, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, C, Natural History Museum, London, D, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow; E-G, J-L, Muséum national d'Histoire naturelle, Paris; H, Geiseltalmuseum of Martin-Luther Universität Halle-Wittenberg, Halle; I, Palaeontological Institute of the University of Zurich. Scale bars: A, 50 mm; B, 40 mm; C, J, 10 mm; D, F, 1 mm; E, 3 mm; G, K, 2 mm; H, I, L, 5 mm. Photo credits: A, HZ; B, Anika Vogel; C-L, GLG.

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REFERENCES

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.

Baszio S. 2004. — *Messelophis variatus* n. gen. n. sp. from the Eocene of Messel: a tropidopheine snake with affinities to Erycinae (Boidae). *Courier Forschungsinstitut Senckenberg* 252: 47-66.

Bell C. J., Daza J. D., Stanley E. L. & Laver R. J. 2021. — Unveiling the elusive: X-rays bring scolecophidian snakes out of the dark. *The Anatomical Record* 304 (10): 2110-2117. https://doi.org/10.1002/ar.24729

Čerňanský A. 2024. — The first lacertid and partly articulated snake from the Middle Miocene of the Devínska Kobyla Hill in Slovakia, from the type locality of the earliest known seal. *Comptes Rendus Palevol* 23 (24): 385-399. https://doi.org/10.5852/cr-palevol2024v23a24

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 5. F. Dufart, Paris, 365 p., pls 59-70. https://doi.org/10.5962/bhl.title.70894

Filhol H. 1877. — Recherches sur les Phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. Part. II. *Annales des Sciences géologiques* 8: 1-340.

Georgalis G. L. & Scheyer T. M. 2019. — A new species of *Palaeopython* (Serpentes) and other extinct squamates from the Eocene of Dielsdorf (Zurich, Switzerland). *Swiss Journal of Geosciences* 112: 383-417. https://doi.org/10.1007/s00015-019-00341-6

Georgalis G. L. & Scheyer T. M. 2022. — Crushed but not lost: a colubriform snake (Serpentes) from the Miocene Swiss Molasse, identified through the use of micro-CT scanning technology. *Swiss Journal of Geosciences* 115 (15), 9 p. https://doi.org/10.1186/s00015-022-00417-w

Georgalis G. L. & Szyndlar Z. 2022. — First occurrence of *Psammophis* (Serpentes) from Europe witnesses another Messinian herpetofaunal dispersal from Africa – biogeographic implications and a discussion of the vertebral morphology of psammophiid snakes. *The Anatomical Record* 305 (11): 3263-3282. https://doi.org/10.1002/ar.24892

Georgalis G. L., Szyndlar Z., Kear B. P. & Delfino M. 2016. — New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. *Swiss Journal of Geosciences* 109: 103-116. https://doi.org/10.1007/s00015-016-0210-y

Georgalis G. L., Del Favero L. & Delfino M. 2020. — Italy's largest snake: redescription of *Palaeophis oweni* from the Eocene of Monte Duello, near Verona. *Acta Palaeontologica Polonica* 65 (3): 523-533. https://doi.org/10.4202/app.00711.2019

Georgalis G. L., Rabi M. & Smith K. T. 2021. — Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology* 140 (18), 140 p. https://doi.org/10.1186/s13358-021-00224-0

Hoffstetter R. 1939. — Contribution à l'étude des Elapidæ actuels et fossiles et de l'ostéologie des Ophidiens. *Archives du Muséum d'Histoire Naturelle de Lyon* 15: 1-78.

Hoffstetter R. 1946. — Les Typhlopidae fossiles. *Bulletin du Muséum National d'Histoire Naturelle, Paris (Série 2)* 18 (3): 309-315.

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

Ivanov M. 1999. — The first European pit viper from the Miocene of Ukraine. *Acta Palaeontologica Polonica* 44: 327-334.

Ivanov M. 2022. — Miocene Snakes of Eurasia: a review of the evolution of snake communities, *in* Gower D. & Zaher H. (eds), *The Origin and Early Evolution of Snakes*. Cambridge University Press, Cambridge: 85-110. https://doi.org/10.1017/9781108938891.007

Janensch W. 1906. — Über *Archaeophis proavus* Mass., eine Schlange aus dem Eocän des Monte Bolca. *Beiträge zur Paläontologie und Geologie Östreich-Ungarns und des Orients* 19: 1-33.

Karg J. M. 1805. — Ueber den Steinbruch zu Oeningen bey Stein am Rheine und dessen Petrefacte. *Denkschriften der Vaterländischen Gesellschaft der Aerzte und Naturforscher Schwabens* 1: 1-74.

Kuhn O. 1939. — Die Schlangen (Boidae) aus dem Mitteleozän des Geiseltales. *Nova Acta Leopoldina, Neue Folge* 7 (47): 119-133.

Massalongo A. 1859. — *Specimen photographicum animalium quorumdam plantarumque fossilium agri Veronensis*. Vicentinius et Franchinius Excudebant, Verona, 101 p.

Meyer H. Von. 1845. — *Zur Fauna der Vorwelt. Fossile Saeugethiere, Voegel und Reptilien aus dem Molasse-Mergel von Oeningen*. Verlag der S. Schmerber'schen Buchhandlung, Frankfurt am Main, vi + 52 p.

Owen R. 1841. — Description of some ophidiolites (*Palæophis toliapicus*) from the London Clay of Sheppey, indicating an extinct species of serpent. *Transactions of the Geological Society Second Series* 6: 209-210. https://doi.org/10.1144/transgslb.6.1.209

Owen R. 1850. — Part III. Ophidia (*Palæophis*, &c.), *in* Owen R. (ed.), *Monograph on the fossil Reptilia of the London Clay and of the Bracklesham and other Tertiary beds*. Palæontographical Society of London, London: 51-63. https://doi.org/10.5962/bhl.title.107492

Owen R. 1857. — On the fossil vertebræ of a Serpent (*Laophis crotaloïdes*, Ow.) discovered by Capt. Spratt, R.N., in a Tertiary Formation at Salonica. *Quarterly Journal of the Geological Society of London* 13: 196-199. https://doi.org/10.1144/GSL.JGS.1857.013.01-02.28

Palci A., Onary S., Lee M. S. Y., Smith K. T., Wings O., Rabi M. & Georgalis G. L. 2024. — A new booid snake from the Eocene (Lutetian) Konservat-Lagerstätte of Geiseltal, Germany, and a new phylogenetic analysis of Booidea. *Zoological Journal of the Linnean Society* 202 (2): zlad179. https://doi.org/10.1093/zoolinnean/zlad179

Rage J.-C. 1974. — Les Serpents des Phosphorites du Quercy. *Palaeovertebrata* 6: 274-303.

Rage J.-C. 1975. — Un Caenophidien primitif (Reptilia, Serpentes) dans l'Eocène inférieur. *Compte rendu sommaire des seances de la Societe Geologique de France* 1975 (2): 46-47.

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

Rage J.-C. 1984. — Serpentes, *in* Wellnhofer P. (ed.), *Encyclopedia of Paleoherpetology*. Part 11. Gustav Fischer, Stuttgart, New York, 80 p.

Rage J.-C. 2013. — Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments* 93: 517-534. https://doi.org/10.1007/s12549-013-0124-x

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

Rochebrune A. T. de 1884. — Faune ophiologique des Phosphorites du Quercy. *Mémoires de la Société des Sciences naturelles de Saône-et-Loire* 5: 149-164.

Römer F. 1870. — Über *Python Euboïcus*, eine fossile Riesenschlange aus tertiärem Kalkschiefer von Kumi auf der Insel Euboea. *Zeitschrift der Deutschen Geologischen Gesellschaft* 22: 582-590.

Scanferla A. & Smith K. T. 2020. — Additional anatomical information on the Eocene minute boas *Messelophis variatus* and *Rieppelophis ermannorum* (Messel Formation, Germany). *Vertebrate Zoology* 70 (4): 615-620. https://doi.org/10.26049/VZ70-4-2020-06

Seghetti S. M., Georgalis G. L., Tschopp E. & Delfino M. 2022. — A historical overview of the reptile fauna from the Eocene Bolca Fossil-Lagerstätte (Italy). *Bollettino della Società Paleontologica Italiana* 61: 119-143. https://doi.org/10.4435/BSPI.2022.14

Smith K. T. & Georgalis G. L. 2022. — The diversity and distribution of Palaeogene snakes: a review, with comments on vertebral sufficiency, *in* Gower D. & Zaher H. (eds), *The Origin and Early Evolution of Snakes*. Cambridge University Press, Cambridge: 55-84. https://doi.org/10.1017/9781108938891.006

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. https://doi.org/10.1007/s12549-016-0244-1

Smith K. T. & Scanferla A. 2021. — A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany). *Geodiversitas* 43 (1): 1-24. https://doi.org/10.5252/geodiversitas2021v43a1

Smith K. T. & Scanferla A. 2022. — More than one large constrictor lurked around paleolake Messel. *Palaeontographica, Abteilung A: Palaeozoology – Stratigraphy* 323 (1-3): 75-103. https://doi.org/10.1127/pala/2021/0119

Szunyoghy J. von 1932. — Beiträge zur vergleichenden Formenlehre des Colubridenschädels, nebst einer kraniologischen Synopsis der fossilen Schlangen ungarns mit nomenklatorischen, systematischen und phyletischen Bemerkungen. *Acta Zoologica (Stockholm)* 13 (1-2): 1-56. https://doi.org/10.1111/j.1463-6395.1932.tb00484.x

Szyndlar Z. 1984. — Fossil snakes from Poland. *Acta Zoologica Cracoviensia* 28: 1-156.

Szyndlar Z. 1991a. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios Geológicos* 47: 103-126.

Szyndlar Z. 1991b. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geológicos* 47: 237-266.

Szyndlar Z. 1992. — '*Coluber*' *kargii* von Meyer, 1845 (Serpentes: Viperidae), from the Miocene of Öhningen (Germany). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1992 (11): 692-700. https://doi.org/10.1127/njgpm/1992/1992/692

Szyndlar Z. & Böhme W. 1996. — Redescription of *Tropidonotus atavus* von Meyer, 1855 from the upper Oligocene of Rott (Germany) and its allocation to *Rottophis* gen. nov. (Serpentes, Boidae). *Palaeontographica A* 240 (4-6): 145-161. https://doi.org/10.1127/pala/240/1996/145

Szyndlar Z. & Georgalis G. L. 2023. — An illustrated atlas of the vertebral morphology of extant non-caenophidian snakes, with special emphasis on the cloacal and caudal portions of the column. *Vertebrate Zoology* 73: 717-886. https://doi.org/10.3897/vz.73.e101372

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

Venczel M. 2000. — *Quaternary snakes from Bihor (Romania)*. Publishing House of the Tarii Crisurilor Museum, Oradea, 142 p.

Zaher H. & Smith K. T. 2020. — Pythons in the Eocene of Europe reveal a much older divergence of the group in sympatry with boas. *Biology Letters* 16 (12): 20200735. https://doi.org/10.1098/rsbl.2020.0735

Zaher H., Murphy R. W., Arredondo J. C., Graboski R., Machado-Filho P. R., Mahlow K., Montingelli G. G., Quadros A. B., Orlov N. L., Wilkinson M., Zhang Y.-P. & Grazziotin F. G. 2019. — Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE* 14: e0216148. https://doi.org/10.1371/journal.pone.0216148

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