First fossil of *Varanus* Merrem, 1820 (Squamata: Varanidae) from the Miocene Siwaliks of Pakistan

**Andrea VILLA**
Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA/ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona (Spain) andrea.villa@icp.cat (corresponding author)

**Massimo DELFINO**
Dipartimento di Scienze della Terra, Università degli Studi di Torino, via T. Valperga Caluso 35, 10125 Torino (Italy)
and Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA/ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona (Spain) massimo.delfino@unito.it

Submitted on 23 May 2020 | accepted on 15 September 2020 | published on 14 February 2022

**ABSTRACT**
In the ‘50s of the XX century, a German expedition lead by Richard Dehm collected a large amount of fossil remains from northern Pakistan. Among these was an isolated trunk vertebra of a lizard, which is here referred to *Varanus* sp. The collecting site of this specimen is not precisely known, but it most likely comes from middle to early late Miocene Siwalik sediments of the Chinji Formation. This is the first published record of a fossil lizard from the Neogene of Pakistan and adds to the very patchy record of *Varanus* Merrem, 1820 in Asia. It further supports previous reconstructions of a warm climate for the middle to early late Miocene of the Siwaliks.

**RÉSUMÉ**
Premier fossile de *Varanus* Merrem, 1820 (Squamata: Varanidae) du Miocene des Siwaliks du Pakistan. Dans les années 50 du XXème siècle, une expédition allemande dirigée par Richard Dehm a recueilli une grande quantité de restes fossiles dans le nord du Pakistan. Parmi ceux-ci se trouvait une vertèbre isolée du tronc d’un lézard, qui est ici désigné comme *Varanus* sp. Le site de collecte de ce spécimen n’est pas connu précisément, mais il provient très probablement de sédiments des Siwaliks du Miocène moyen à supérieur (Formation de Chinji). Il s’agit de la première occurrence publiée d’un lézard fossile du Néogène du Pakistan. Il s’ajoute à l’enregistrement très disparate du genre *Varanus* Merrem, 1820 en Asie. Cette occurrence soutient également les reconstructions précédentes d’un climat chaud, du Miocène moyen au début du Miocène supérieur, dans les Siwaliks.
INTRODUCTION

In 1955-1956, a palaeontological joint expedition of the Institut für Paläontologie und historische Geologie of the Ludwig-Maximilians-Universität München (today Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie) and the Bayerische Staatssammlung für Paläontologie und Historische Geologie (today Staatliche Naturwissenschaftliche Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, SNSB-BSPG) lead by Prof. Richard Dehm explored northern Pakistan in search for fossils (Dehm et al. 1958). They returned to Munich with an extensive collection of remains, coming from Neogene sediments exposed near the villages of Chinji, Dhok Pathan, and Nagri (Siwalik Group) and now stored in the SNSB-BSPG. Studies on the fossil mammal remains recovered in this and previous expeditions in the area by the Munich team reported the presence of deinotheres (Dehm et al. 1963), equids (Hussain 1971), primates (Dehm 1983, 1984; Pickford 2010), rhinocerotids (Heissig 1972), and tragulids (Guzmán-Sandoval & Rössner 2021). Pickford (2010) further mentioned still unpublished occurrences of other groups, including anthracotheres, carnivorans, equids, gomphotheres, ruminants, and suids. The Pakistani collection in the SNSB-BSPG lacks any trace of amphibian remains (AV, pers. obs.), whereas reptiles are represented by crocodylians, turtles, and squamates. Of these, only snakes were studied by Hoffstetter (1964), who described vertebrae of an indeterminate Python and of a new large acrochordid, Acrochordus dehmi.

Fossils of crocodylians and turtles will be the subject of future dedicated works, but we here add to the squamate fauna by describing the only other fossil of this group of reptiles that we were able to find in the SNSB-BSPG collections: an isolated lizard vertebra. No precise locality was available for this fossil, but some information can be retrieved from the labels (Fig. 1). It was collected by members of Dehm's expedition on the first day of February 1956 (Fig. 1A), somewhere between Marianwala and Kas. Both these villages are located south of Chinji (Fig. 2), in an area where the Chinji Formation crops out. Numerous collecting sites are marked in the surroundings of these two villages in the original maps from the expedition (AV, pers. obs.), but neither on the maps nor on the original diaries any lizard vertebra is noted despite the original label clearly states that the fossil was recognised as such (Fig. 1A). The Chinji Formation is currently considered middle to early late Miocene in age (11.2-14.2 Ma; Barry et al. 2002; Patnaik 2016).

MATERIAL AND METHODS

The subject of this study is a single vertebra, numbered SNSB-BSPG 1956 II 2010. The vertebra was photographed with a Leica M205 microscope equipped with the Leica Application Suite V 4.10 at the Università degli Studi di Torino. Photographs of the labels were taken with a Samsung WB252F Digital Camera. The terminology used for the vertebral laminae follows that used by Tschopp (2016).

SYSTEMATICS

Order SQUAMATA Oppel, 1811
Family VARANIDAE Gray, 1827
Genus Varanus Merrem, 1820
Varanus sp.

DESCRIPTION

SNSB-BSPG 1956 II 2010 (Fig. 3) is a large and elongated trunk vertebra, with a procoelous centrum. It is moderately well preserved, but the anterior part and most of its left lateral surface are covered by a hard sandstone matrix that was not removed in order not to damage the fossil. In ventral
Fossil Varanus from the Miocene of Pakistan

GEODIVERSITAS • 2022 • 44 (7)

view (Fig. 3A), the centrum is subtriangular, with posteriorly converging and straight lateral margins. The ventral surface is flat, without keel. In spite of the matrix covering, the ventral margin of the anterior cotyle is clearly located posteriorly compared to the dorsal margin (Fig. 3A); thus, the anterior cotyle was facing anteroventrally. In posterior view (Fig. 3B), the centrum is dorsoventrally compressed. The posterior condyle is strongly eroded, but a distinct precondylar constriction is still recognisable in ventral view (Fig. 3A). The width of the centrum at the constriction is 5 mm, whereas the anterior cotyle can be estimated as about 8 mm wide. This would indicate a constriction/cotyle width ratio of 0.63. On the right lateral surface (Fig. 3C), the base of the synapophysis is visible, even though the rest of the latter is not preserved anymore. Nevertheless, it was dorsoventrally elongated. The vertebra has no postzygaprezygapophyseal lamina, but a very poorly distinct posterior centrosynapophyseal lamina is present (Fig. 3C). In dorsal view (Fig. 3D), a distinct interzygapophyseal constriction is visible. Being covered by sediment, the prezygapophyses are not clearly visible. The postzygapophyses are better exposed. Zygapophyses are subcircular to suboval and dorsally inclined of about 45°. Each prezygapophysis is separated by the pars tectiformis of the neural arch by a deep groove (Fig. 3D). The pars tectiformis does not bear a zygosphene, and no zygantrum is visible on the posterior edge of the neural arch. The posterior half of the latter is raised compared to the pars tectiformis (Fig. 3E, 3F). The neural spine is well developed, even though broken along its entire length. It starts at the anterior margin of the neural arch and is laminar for most of its length (originating the prespinal lamina sensu Tschopp 2016), but it thickens slightly by the posterior end of the neural arch where it is broken off (Fig. 3D). The dorsal surface of the neural arch displays a distinct striation (Fig. 3D), composed of fine and dense striae that run posterodorsally from the sides of the arch towards the neural spine. On each side of the same surface, a robust and dorsally-rounded lamina connects the posterior corner of each prezygapophysis with the base of the neural spine around midlength of the vertebra (Fig. 3C, D, F). We named this structure mediodi spinal lamina. It marks the anterior margin of the raised posterior half of the neural arch. Posteriorly, the spinopostzygapophyseal laminae are robust but not sharp (Fig. 3B). Due to the covering sediment, it is not possible to describe the centropostzygapophyseal laminae. Further, the broken neural spine hinders the description of a postspinal lamina, in case it was present (as is usually the case at least in Varanus exanthematicus; Tschopp 2016). The preserved minimum length of the vertebral centrum (measured at midline starting from the ventral margin of the cotyle) is 11 mm.

Identification

The following combination of features clearly indicates that the Pakistani trunk vertebra found in the SNSB-BSPG collections pertains to Varanus (Hoffstetter 1943; Estes 1983; Smith et al. 2008; Holmes et al. 2010): anterior cotyle facing ventrally due to posteriorly-located ventral margin; presence of precondylar constriction; complete absence of a more-or-less developed zygosphene/zygantrum complex; and presence of dorsal striation. The newly-named structure, the mediodi spinal lamina, also supports the identification of the vertebra as a

Fig. 2. — Map of Pakistan (A) and of northern Punjab (B), showing the area where the villages of Marianwala and Kas are located (small square in B) south of Chinji.
to these, we now add scincids from the Chattian of Paali Nala (Pakistani fossils, with only the agamid snake record, lizards are extremely underrepresented among Elapidae indet. (Tortonian to Messinian). Compared to the “colubrines” Colubroidea morph. B (Tortonian to Messinian), as well as booids s.l. (Burdigalian to Messinian); the colubroids (Serravallian), and ?Boidae indet. (Serravallian); indeterminate acrochordid taxa (Neogene Siwaliks recorded the presence of various different Rage 1987). Paleogene snakes are then found in Lutetian (indeterminate of Vivas et al. 2003), but this character is not evaluable in SNSB-BSPG 1956 II 2010 because of its complete erosion. Nevertheless, if this vertebra represents an adult (or subadult) individual, the minimum length of the vertebral centrum suggests that it probably belonged to a small-bodied monitor species (see measurements in e.g., Conrad et al. 2012, and Vasilyan & Bukhsianidze 2020), with a snout-vent length possibly higher than 300 mm and not exceeding 500 mm. A confident estimate of the size is not advisable due to uncertainties regarding the real position of the vertebra in the column, as well as the unknown intracolumnar variation.

DISCUSSION

The squamate fossil record in Pakistan is so far dominated by snakes. Most occurrences come from Neogene (i.e., Siwalik) sediments, with only few others coming from the Paleogene. The oldest squamate fossils from Pakistan are two vertebrae of Gigantophis from the Danian (Rage et al. 2014). Younger Paleogene snakes are then found in Lutetian (indeterminate erycines, boines and unidentified snakes from Chorlakki; Rage 1987) and Chattian (indeterminate snakes from the Paali Nala; Böhme & Ilg 2003) sediments. Snakes found in the Neogene Siwaliks recorded the presence of various different taxa (Hoffstetter 1964; Böhme & Ilg 2003; Head 2005): the acrochordid A. dehni (Burdigalian to Tortonian); the booids Python sp. (Burdigalian to Messinian), cf. Erycinae indet. (Serravallian), and ?Ophidae indet. (Serravallian); indeterminate booids s.l. (Burdigalian to Messinian); the colubroids Gansophis potuwrensis (Messinian), Colubroidea morph. A (Serravallian), Colubroidea morph. B (Tortonian to Messinian), as well as indeterminate colubroid snakes (Burdigalian to Messinian); the “colubrines” Chorathophis padwrenensis (Tortonian), Stiaoophis downsi (Serravallian to Messinian), and indeterminate “colubrine” snakes (Langhian to Tortonian); indeterminate naticines (Tortonian); and the elapids Bunogus sp. (Tortonian) and ?Elapidae indet. (Tortonian to Messinian). Compared to the snake record, lizards are extremely underrepresented among Pakistani fossils, with only the agamid Tinosaurus sp. reported from the Lutetian of Chorlakki (Rage 1987) and indeterminate scincids from the Chattian of Paali Nala (Böhme & Ilg 2003). To these, we now add Varanus sp. from the middle to early late Miocene of the Chinji Formation. To our knowledge, this is the first published record of a non-snake squamate from the Neogene of Pakistan. Another occurrence of Pakistani Varanus is listed in the fosFARbase database (Böhme & Ilg 2003) from Winnewala. The only formation reported to crop out at Winnewala is the Dhok Pathan Formation (Hoffstetter 1964; Head 2005), which is dated between 10.1 and c. 3.5 Ma, late Miocene to early Pliocene, by Barry et al. (2002). Given that, fossils coming from this locality should be younger than the herein studied vertebra supposedly coming from the Chinji Formation. Unfortunately, we were unable to find Varanus remains from Winnewala in the SNSB-BSPG collection, where they should be stored, and consequently to confirm this occurrence and potentially make comparisons with SNSB-BSPG 1956 II 2010.

In the Asian continent, Varanus fossils are known from the early Miocene of China and Kazakhstan (Böhme & Ilg 2003; Malakhov 2005; Vasilyan et al. 2017), the middle Miocene of Kazakhstan (Böhme & Ilg 2003), the middle to early late Miocene of Pakistan (this work), the late Miocene of Armenia, Georgia, India, Kazakhstan, and Russia (Chkhikhvadze 1985; Rage et al. 2001; Böhme & Ilg 2003; Vasilyan et al. 2017; Vasilyan & Bukhsianidze 2020; Čerňanský et al. 2020), the Pliocene of India and Turkey (Falconer 1868; Lydekker 1886, 1888; Hocknull et al. 2009; Sen et al. 2017), as well as the Quaternary of India, Indonesia, and Thailand (Falconer 1868; Lydekker 1886, 1888; Hooijer 1972; Patnaik et al. 2008; Hocknull et al. 2009; Suraprasit et al. 2016). Most of the Quaternary remains are referred to extant species, whereas all the Neogene ones are not identified at the species level. The only exception to this frame is Varanus stovlenisi, an extinct species described from the Pliocene to Early Pleistocene of India (Falconer 1868; Lydekker 1886, 1888; Hocknull et al. 2009). However, Hocknull et al. (2009) casted doubts on the real taxonomic identity of the three specimens assigned to this taxon, a humerus and two vertebrae: the authors stated that the humerus, which has Pliocene age, might indeed show sufficient differences to sustain its own taxonomic status, whereas the dorsal vertebrae, found in Early Pleistocene deposits, are comparable with Varanus salvator in their morphology and size. Considering all of this, our knowledge of the evolutionary history of Varanus in Asia is still rather patchy and clearly needs more in-depth studies based on the recovery of further material.

This bears significance not only for the history of this clade in this continent, but also for its European and African representatives. The biogeographical origin of the genus Varanus is still a debated issue (Villa et al. 2018), with both African (Fuller et al. 1998; Ast 2001; Holmes et al. 2010) and Eurasian (Amer & Kumazawa 2008; Conrad et al. 2012; Ivanov et al. 2018) origins proposed as possible alternatives. Nevertheless, the origin is to be found in the Paleogene, as indicated by the oldest Varanus remains coming from the Eocene of Egypt (Holmes et al. 2010). The absence of confidently diagnosable Varanus species prior to the early Miocene and, in Asia, even to pre-Quaternary times, however, hinders a better understanding of this problem. Detailed identification

Villa A. & Delfino M.
of the Asian fossil monitor lizards could have a direct role in unveiling the origin of the populations that inhabited Europe at least from the early Miocene (Delfino et al. 2013) to the Middle Pleistocene (Georgalis et al. 2017). A recent revision of European monitors by Villa et al. (2018) suggested the presence of at least two lineages in Europe, the second one (represented by Varanus marathomensis from the latest middle to the late Miocene) originating from an Asiatic ancestor. It would be, thus, interesting to comprehend if and which of the Asian Varanus, including the one from Pakistan here described, could be related to this dispersal wave.

This cannot be stated considering only morphological characters, given that known Asian remains of Varanus are represented in most cases by poorly-significant vertebral material. Nevertheless, Siwalik snakes could be potentially of help in drawing some hypotheses about relationships between European and Pakistani squamate faunas. Most Siwalik snake genera and species are not shared with Europe (Head 2005), thus suggesting ecological barriers and different biogeographic units. Based on stratigraphic distribution of snake fossils, Head (2005: 30) stated that “partition of European and South Asian biogeographic theaters occurred no later than middle Miocene”. However, it should be also noted that the pattern reported for snakes does not reflect the mammalian palaeobiogeographic dynamics (Patnaik 2016): as a matter of fact, mammal faunal exchanges were indeed present between the Indian subcontinent and both Africa and likely Europe in the considered time interval. Further data are therefore needed to shed light on the biogeographic relationships of Neogene lizards from Pakistan and the Indian subcontinent as a whole.

In palaeoenvironmental terms, Varanus indicates a warm palaeoclimate (mean annual temperature ranging from 14.8°C to 28.1°C according to Böhme 2003) for the Chinji Formation. This partially agrees with the landscape reconstructions based on palaeobotanical studies (Srivastava et al. 2014; Patnaik 2016) suggesting dominance of evergreen to deciduous forests reflecting warm and humid conditions with high rainfall during the middle Miocene of the Siwaliks. The Siwalik sediments in Pakistan deposited in a fluvial environment (Barry et al. 2002; Head 2005). As far as the Chinji Formation is concerned, the riverine system originated fine-grained sandstone deposits that are still present as a covering on at least some of the fossil remains, such as the herein studied Varanus vertebra but also other fossils stored in the SNSB-BSPG (AV, pers. obs.). The most abundant squamate found in the whole Pakistani Siwalik sequence is A. dehmi (Hoffstetter 1964; Head 2005), which is considered a fully-aquatic animal. This is particularly evident in the Chinji and Nagri Formations, but subsequently, there is a rise in the occurrence of terrestrial and semi-aquatic taxa from around 10 Ma onwards (Dhok Pathan Formation; Head 2005). Based on rough correlations between monsoonal precipitation patterns, the transition towards a C4-dominated vegetation, and the
increasing diversity in Siwalik snakes, Head (2005) suggested a possible link between the latter and increasing seasonality in the area and diversification of the available habitats, which would have favoured the onset of a more diverse reptilian fauna. *Varanus* currently displays a wide variety of ecological adaptation and includes species strongly linked with water environments (e.g., *V. salvator*, which nowadays is widely spread in Southeast Asia; Pianka et al. 2004; Eidenmullen 2007). Acquiring information on the ecological preference of the species represented by SNSB-BSPG 1956 II 2010 is impossible, even though the finding of only one remain in the Pakistani Siwaliks may suggest a low relation with water for the represented monitor when considering the pattern showed by snakes. Further studies of squamate fossils from the area are strongly needed to enhance our knowledge of their distribution, evolution, and ecology in the Neogene of Pakistan.

Acknowledgements

The study of SNSB-BSPG 1956 II 2010 benefited significantly from the help of Gertrud Rössner (Munich), who assisted AV in defining the possible provenance and age of the specimen and shared information about Dehm’s expedition to Pakistan. We also thank Madelaine Böhme (Tübingen) for discussions about the Winnewala *Varanus* occurrence, the two reviewers, Davit Vasilyan (Porrentruy) and Martin Ivanov (Brno), for their valuable comments that improved an earlier version of the manuscript, as well as the editor Emmanuel Côtez (Paris). This work originated during a visit to the SNSB-BSPG collection in 2017 supported by an EAVP Research Grant provided to AV manuscript, as well as the editor Emmanuel Côtez (Paris). This study of SNSB-BSPG 1956 II 2010 benefited significantly from the help of Gertrud Rössner (Munich), who assisted AV in defining the possible provenance and age of the specimen and shared information about Dehm’s expedition to Pakistan. We also thank Madelaine Böhme (Tübingen) for discussions about the Winnewala *Varanus* occurrence, the two reviewers, Davit Vasilyan (Porrentruy) and Martin Ivanov (Brno), for their valuable comments that improved an earlier version of the manuscript, as well as the editor Emmanuel Côtez (Paris). This work originated during a visit to the SNSB-BSPG collection in 2017 supported by an EAVP Research Grant provided to AV by the European Association of Vertebrate Palaeontologists. Oliver Rauhut (Munich) is thanked for help while visiting the collection back then. During part of the development of this work, AV was funded by the Alexander von Humboldt Foundation through a Humboldt Research Fellowship. MD is supported by Fondi di Ateneo dell’Università di Torino (2018-2019), Generalitat de Catalunya (CERCA Program), and Spanish Agencia Estatal de Investigación (CGL2016-76431-P, AEI/FEDER, EU). The original maps used for Fig. 2 are freely available at d-maps (https://d-maps.com/).

REFERENCES

Amer S. A. M. & Kumazawa Y. 2008. — Timing of a mtDNA gene rearrangement and intercontinental dispersal of varanid lizards. *Genes & Genetic Systems* 83: 273-280. https://doi.org/10.1266/ ggs.83.275

Ast J. C. 2001. — Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). *Cladistics* 17: 211-226. https://doi.org/10.1006/clad.2001.0169

Barr J. C., Morgan M. E., Flynn L. J., Pilbeam D., Behrensmeyer A. K., Raza S. M., Khan I. A., Badgley C., Hicks J. & Kelley J. 2002. — Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology* 28: 1-71. https://doi.org/10.2307/367

Böhme M. 2003. — The Miocene Climatic Optimum: evidence from ecotothermal vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195: 389-401. https://doi.org/10.1016/S0031-0182(03)00367-5

Bohme M. & Ilg A. 2003. — fosFARbase, http://www.wahre-staerke.com/ (accessed April 2020).

Camatti M., Villa A., Wenczer L. C. M., Bauer A. M., Stanley E. L. & Delfino M. 2019. — Descriptive osteology and patterns of limb loss of the European limbless skink *Oplioionurus punctatissimus* (Squamata, Scincidae). *Journal of Morphology* 285: 313-345. https://doi.org/10.1111/jpm.13017

Černánský A., Yaryhin O., Cicekova J., Wernburg L., Haš M. & Klemba J. 2019. — Vertrebal comparative anatomy and morphological differences in anguine lizards with a special reference to *Pseudopus apodus*. *The Anatomical Record* 302: 232-257. https://doi.org/10.1002/ar.23944

Černánský A., Syromyatnikova E. V. & Jablonski D. 2020. — The first record of amphibian and anguimorph lizards (Reptilia, Squamata) from the upper Miocene Solnechnodolsk locality in Russia. *Historical Biology* 32 (7):869-879. https://doi.org/10.1080/02724634.2018.1539973

Chkhikvadze V. M. 1985. — Preliminary results of studies on tertiary amphibians and squamate reptiles of the Zaian Basin, in DAREVSKY I. (ed.), Problems in Herpetology. Proceedings of the 6th All-Union Herpetological Conference, Tashkent, 18-20 September 1985, Leningrad, Nauka: 234-235.

Conrad J. L., Ast J. C. A., Montanari S. & Norelli M. A. 2011. — A combined evidence phylogenetic analysis of Anguimorph (Reptilia: Squamata). *Cladistics* 27: 230-277. https://doi.org/10.1111/j.1096- 0031.2010.00330.x

Conrad J. L., Balcarcel A. M. & Mehlung C. M. 2012. — Earliest example of a giant monitor lizard (*Varanus, Varanidae, Squamata*). *PLoS ONE* 7: e41767. https://doi.org/10.1371/ journal.pone.0041767

Dehm R. 1983. — Miocene hominoid primate dental remains from the Siwaliks of Pakistan, in Ciochon R. L. & Corrucci R. S. (eds), New Interpretations of Ape and Human Ancestry. Springer, Boston: 527-537. https://doi.org/10.1007/978-1-4684-8854-8_20

Dehm R. 1984. — Molar size enlargement in Siwalik hominoid primates and its significance. *Coueur Forschungsinstitut Senckenberg* 69: 49-52.

Dehm R., Oettingen-Spielberg T. zu & Vidal H. 1958. — Palaeontologische und geologische Untersuchungen im Tertiär von Pakistan. I. Die Münchner Forschungsreise nach Pakistan 1955-1956. *Abhandlungen der Mathematisch-Naturwissenschaftliche Klasse der Bayerischen Akademie der Wissenschaften* 90: 5-13.

Dehm R., Oettingen-Spielberg T. zu & Vidal H. 1963. — Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. III. Deinotherium von Pakistan. *Abhandlungen der Mathematisch-Naturwissenschaftliche Klasse der Bayerischen Akademie der Wissenschaften* 114: 1-34.

Delfino M., Raje J.-C., Bolet A. & Alba D. M., 2013. — Early Miocene dispersal of the lizard *Varanus* into Europe: reassessment of vertebral material from Spain. *Acta Palaeontologica Polonica* 58: 731-735.

Eidenmüller B. 2007. — *Monitor Lizards. Natural History, Captive Care & Breeding*. Edition Chimaira, Frankfurt am Main, 176 p.

Estes R. 1983. — *Handbuch der Paläonterpetologie* 104, Sauria terræstris. Amphibiaen. Friedrich Pfeil, München, 249 p.

Falconer H. P. 1868. — *Palaeontological Memoirs and Notes of the Late Hugh Falconer, A.M., M.D.* Robert Hardwick Publishers, Picadilly, 465 p. https://www.biodiversitylibrary.org/page/33569193

Fuller S., Baeverstock P. & King D. 1998. — Biogeographic origins of goannas (*Varanidae*): a molecular perspective. *Molecular Phylogenetics and Evolution* 9: 294-307. https://doi.org/10.1006/mpev.1997.0476

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. https://doi.org/10.1080/02724634.2017.1301946
Gray J. E. 1827. — A synopsis of the genera of saurian reptiles, in which some new genera are indicated and others reviewed by actual examination. Philosophical Magazine 2: 54-58. https://doi.org/10.1080/14786442708675620

Guzmán-Sandoval J. A. & Rossnier G. E. 2021. — Miocene chevrotains (Mammalia, Artiodactyla, Tragulidae) from Pakistan. Historical Biology 33 (5). https://doi.org/10.1080/08912963.2019.1661405

Head J. J. 2005. — Snakes of the Siwalik Group (Mammalia of Pakistan): systematics and relationship to environmental change. Palaeontology Electonica 8: 18A.

Heissig K. 1972. — Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. V. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-schichten. Abhandlungen der Mathematisch-Naturwissenschaftliche Klasse der Bayerischen Akademie der Wissenschaften 152: 1-112.

Hocknull S. A., Piper P. J., Van den Bergh G. D., Awe Dee R., Morwood M. J. & Kurniawan I. 2009. — Dragon's paradise lost: paleobiogeography, evolution and extinction of the largest ever terrestrial lizards (Varanidae). PLoS ONE 4: e7241. https://doi.org/10.1371/journal.pone.0007241

Hoffstetter R. 1943. — Varanidae et Nectrosauridae fossiles. Bulletin du Muséum national d'Histoire naturelle, série 2, 15: 134-141.

https://www.biodiversitylibrary.org/page/52906476

Hoffstetter R. 1964. — Les serpents du Néogène du Pakistan (couches des Siwaliks). Bulletin de la Société géologique de France S7-VI: 467-474. https://doi.org/10.2113/gssgbull.S7-VI.4.467

Holmes R. B., Murray A. M., Atta Y. S., Simons E. L. & Chattrath P. 2010. — Oldest known Varanus (Squamata: Varanidae) from the upper Eocene and lower Oligocene of Egypt: support for an African origin of the genus. Palaeontology 53: 1099-1110. https://doi.org/10.1111/j.1475-4983.2010.00994.x

Hoooker D. A. 1972. — Varanus (Reptilia, Sauria) from the Pleistocene of Timor. Zoologische Mededelingen 47: 445-448.

Hussain S. T. 1971. — Révision de Hipparion (Equidae, mammalia) from the Siwalik Hills of Pakistan and India. Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen 147: 1-68.

Ivanov M., Ruta M., Klembara J. & Bohme M. 2018. — A new species of Varanus (Anguimorpha: Varanidae) from the early Miocene of the Czech Republic, and its relationships and palaeoecology. Journal of Systematic Palaeontology 16: 767-797. https://doi.org/10.1080/14754983.2017.1355338

Lydekker R. 1886. — Fauna of the Karnul caves. Palaeontologia Indica, ser. 10, 4 (2): 23-58 + pls. https://www.biodiversitylibrary.org/page/54012533

Lydekker R. 1888. — Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part 1. Containing the orders Ornithosaurus, Crocodilia, Dinosauria, Squamata, Rynchocephalia, and Proterosaurus. British Museum, London, 309 p. https://doi.org/10.5962/bhl.title.61848

Malakhov D. V. 2005. — The early Miocene herpetofauna of Ayakoz (Eastern Kazakhstan). Biota 6: 29-35.

Merrem B. 1820. — Versuch eines Systems der Amphibien 1 (Tentamen Systematis Amphibiorum). J. C. Krieger, Marburg, 191 p.

Oppel M. 1811. — Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, Munich, 86 p.

Patnaik R. 2016. — Neogene-Quaternary mammalian paleobiogeography of the Indian subcontinent: an appraisal. Comptes Rendus Palevol 15: 889-902. https://doi.org/10.1016/j.jrcp.2015.11.004

Patnaik R., Badam G. L. & Murty M. L. K. 2008. — Additional vertebrate remains from one of the Late Pleistocene-Holocene Kurnool Caves (Muchchatla Chintamanu Gavi) of South India. Quaternary International 192: 43-51. https://doi.org/10.1016/j.quaint.2007.06.018

Pianka E. R., King D. R. & Allen King R. 2004. — Varanoid Lizards of the World. Indiana University Press, Bloomington, 588 p.

Pickford M. 2010. — Additions to the Dehm collection of Siwalik hominoids, Pakistan: descriptions and interpretations. Zitteliana A50: 111-125.

Rage J.-C. 1987. — Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Squamata. Contributions from the Museum of Paleontology of the University of Michigan 27: 187-193. https://hdl.handle.net/2027.42/48528

Rage J. C., Gupta S. S. & Prasad G. V. R. 2001. — Amphibians and squamates from the Neogene Siwalik beds of Jammu and Kashmir, India. Paläontologische Zeitschrift 75: 197-205. https://doi.org/10.1007/BF02988013

Rage J.-C., Metáis G., Bartolini A., Brohi I. A., Lashari R. A., Marivaux L., Merle D. & Solangi S. H. 2014. — First report of the giant snake Gigantophis (Madtsoiidae) from the Paleocene of Pakistan: paleobiogeographical implications. Geobios 47: 147-153. https://doi.org/10.1016/j.geobios.2014.03.004

Sen S., Delfino M. & Kazani C. 2017. — Çeştepe, a new early Pliocene vertebrate locality in Central Anatolia and its stratigraphic context. Annales de Paléontologie 103: 149-163. https://doi.org/10.1016/j.annpal.2017.01.004

Smith K. T., Bhullar B.-A. S. & Holroyd P. A. 2008. — Earliest African record of the Varanus stem clade (Squamata: Vara

nidae) from the early Oligocene of Egypt. Journal of Vertebrate Paleontology 28: 909-913. https://doi.org/10.1080/02724634.2008.1073548

Srivastava G., Mehrotra R. C., Shukla A. & Tiwari R. P. 2014. — Miocene vegetation and climate in extra peninsular India: megafossil evidences. Special Publication of the Palaeontological Society of India 5: 283-290.

Suraprasit K., Jaeger J. J., Chaimane Y., Chavasseau O., Yamee C., Tian P. & Panja S. 2016. — The Middle Pleistocene vertebrate fauna from Khok Sung (Nakhon Ratchasima, Thailand): biochronological and paleobiogeographical implications. ZooKeys 613: 1-157. https://doi.org/10.3897/zookeys.613.8309

Tschope E. 2016. — Nomenclature of vertebral laminae in lizards, with comments on ontogenetic and serial variation in Lacertini (Squamata, Lacertidae). PLoS ONE 11: e0149445. https://doi.org/10.1371/journal.pone.0149445

Vasilian D. & Bukhsianidze M. 2020. — The fossil record of the genus Varanus from the Southern Caucasus (Armenia, Georgia). PeerJ 8: e8322. https://doi.org/10.7717/peerj.8322

Vasilian D., Zazhigin V. S. & Bohme M. 2017. — Neogene amphibians and reptiles (Caudata, Anura, Gekkota, Lacertilia, and Testudines) from the south of Western Siberia, Russia, and Northeastern Kazakhstan. PeerJ 5: e3025. https://doi.org/10.7717/peerj.3025

Villa A., Abella J., Alba D. M., Almécija S., Bolet A., Koufos G. D., Knoll F., Luján A. H., Morales J., Robles J. M., Sánchez I. M. & Delﬁno M. 2018. — Revision of Varanus marathoonensis (Squamata, Varanidae) based on historical and new material: morphology, systematics, and paleobiogeography of the European monitor lizards. PLoS ONE 13: e0207719. https://doi.org/10.1371/journal.pone.0207719

Submitted on 23 May 2020; accepted on 15 September 2020; published on 14 February 2022.