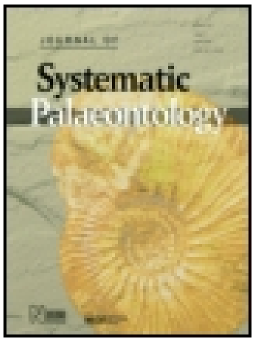

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A new species of *Varanus* (Anguimorpha: Varanidae) from the early Miocene of the Czech Republic, and its relationships and palaeoecology

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Skeletal remains of a new early Miocene (Ottnangian, MN 4 mammal zone) monitor lizard, *Varanus mokrensis* sp. nov., are described from two karst fissures in the Mokrá-Western Quarry (1/2001 Turtle Joint; 2/2003 Reptile Joint), Czech Republic, providing the first documented example of a European varanid for which osteological data permit a well-supported assignment to the genus *Varanus*. The new species is morphologically similar to the Recent Indo-Asiatic varanids of the *Varanus bengalensis* group. It differs from all other *Varanus* species on the basis of a single autapomorphy and a combination of 11 characters. As a distinguishing feature of *V. mokrensis*, the parietal and squamosal processes of the postorbitofrontal form a narrowly acute angle. The teeth show distinct, smooth cutting edges along the mesial and distal margins of the apical portion of their crowns. This feature is not observed in most extant Asiatic *Varanus* species and may represent a plesiomorphic condition. The results of parsimony phylogenetic analyses, with and without character reweighting, reveal poor resolution within *Varanus*. A Bayesian analysis shows *V. mokrensis* to be closely related to extant representatives of the Indo-Asiatic *Varanus* clade, with close affinities to the *V. bengalensis* species group. The topology of the Bayesian tree supports the hypothesis that Miocene monitors from Mokrá are representatives of a lineage that is ancestral to the well-defined clade of extant African varanids, including the early Miocene *V. rusingensis*. In addition, our results support a Eurasian origin for the varanid clade. The extant African *Varanus* species probably originated in the late Oligocene. The radiation of African varanids probably occurred during the late Oligocene to early Miocene time interval. The occurrence of *Varanus* in the early Miocene of Mokrá-Western Quarry corresponds to the warm phase of the Miocene Climatic Optimum. Remains of a diverse aquatic and heliophobe amphibian fauna at the 2/2003 Reptile Joint site indicate more humid conditions than those at the 1/2001 Turtle Joint site.

http://zoobank.org/urn:lsid:zoobank.org:pub:B1553295-8AC7-42F0-91C4-51C4C13F1C9D

Keywords: morphology; palaeoecology; phylogeny; skull; *Varanus*

Introduction

The anguimorph genus *Varanus* includes today's monitor lizards (Varanidae Hardwicke & Gray, 1827), a clade of mid-sized to large, mostly carnivorous (some frugivorous) squamates widely distributed in tropical and subtropical regions, and with a fossil record dating back to the Late Cretaceous. Altogether, 79 valid species are currently assigned to *Varanus* (W. Böhme 2003; Koch *et al.* 2010; Uetz *et al.* 2017). Most published checklists recognise three major species groups formally supported by mtDNA analyses (e.g. Ast 2001), namely an African group, an Indo-Asiatic group (divided into two distinct clades), and an Indo-Australian group. Unlike mtDNA analyses, all morphological studies place the family Varanidae (e.g. McDowell & Bogert 1954; Estes 1983; Carroll 1993) in the clade Varanoidea Münster, 1834 (= Platynota Baur, 1890 *sensu* Estes 1983; Carroll 1993) together with two other extant families, the Helodermatidae Gray, 1837 and the Lanthanotidae Steindachner, 1878. However, several studies have recognized only two extant family-rank clades within Varanoidea, namely Helodermatidae and Varanidae. The close relationship between *Varanus* and *Lanthanotus* has long been supported by morphological studies of extant taxa (Rieppel 1980a, b), and further corroborated by mtDNA analyses (Fuller *et al.* 1998; Ast 2001).

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This paper has three aims: (1) provide a detailed description of the cranial and postcranial material of a new species of *Varanus* from the early Miocene deposits of the Mokrá-Western Quarry locality in the Czech Republic; (2) analyse the interrelationships of *Varanus*; and (3) investigate the palaeoecology of the Mokrá-Western Quarry. The anatomical terminology is based on Fejérváry-Lángh (1923), Fejérváry (1935), Bahl (1937), Säve-Söderbergh (1946, 1947), Bellairs (1949), Oelrich (1956), Romer (1956), Shrivatsava (1963, 1964a, b), Hoffstetter & Gasc (1969), Bellairs & Kamal (1981) and Conrad (2004, 2006).

Brief review of the fossil record of varanoids and *Varanus*

The interrelationships of varanoids remain in a state of flux. Several key fossil taxa, including *Saniwa* Leidy, 1870, *Saniwides* Borsuk-Białynicka, 1984 and *Cherminotus* Borsuk-Białynicka, 1984 (Gilmore 1922, 1928; Borsuk-Białynicka 1984), have been largely neglected in phylogenetic analyses, including many of the earliest large-scale studies of squamate relationships (Pregill *et al.* 1986; Estes *et al.* 1988). Other extinct varanoid genera described in the last few decades, including *Estesia*, *Aiolosaurus* and *Ovoo* (Norell *et al.* 1992, 2007; Norell & Gao 1997; Gao & Norell 2000), require proper phylogenetic placement. Based on comparative osteological observations, Lee (1997) regarded the Late Cretaceous *Saniwides* from Mongolia (Borsuk-Białynicka 1984; Pregill *et al.* 1986; Estes *et al.* 1988) as the sister taxon to *Varanus* Merrem, 1820. However, *Saniwa* and *Cherminotus*, both assigned to Varanidae together with the Late Cretaceous *Telmasaurus* and extant *Varanus* (Gao & Norell 1998), are probably more closely related to *Varanus* than *Saniwides* is (Norell & Gao 1997; Gao & Norell 1998; Norell *et al.* 2007; Rieppel & Grande 2007). The Late Cretaceous (Campanian) *Ovoo gurvel* from Mongolia has been described as a stem-*Varanus* (Norell *et al.* 2007). Aside from its possible impact on the interrelationships of varanoids as a whole, our knowledge of Late Cretaceous varanoids has interesting palaeobiogeographical implications. Specifically, data from these taxa may support an Asiatic rather than an African origin for the radiation of European *Varanus* species.

The oldest fossils attributed to *Varanus* consist of vertebrae from the late Eocene of the Birket Qarun Formation in Egypt (Holmes *et al.* 2010). The earliest recorded European species in this genus, commonly referred to as *Iberovaranus catalaunicus* (Hoffstetter, 1969), comes from the MN 3/MN 4 mammal zone transition of Spain (type material from Can Mas, El Papiol, Barcelona), France and Germany (M. Böhme 2001). However, *Iberovaranus* has been recently synonymized with *Varanus* and the species *V. catalaunicus* is now regarded as a *nomen dubium* (Delfino *et al.* 2013b). Other more or less contemporary localities have yielded *Varanus* or *Varanus*-like remains, including Spain (*Varanus* sp. from San Roque 4A; aff. *Iberovaranus* sp. and *Iberovaranus* cf. *I. catalaunicus* from Agramon and Ateca 1; M. Böhme & Ilg 2003), France (*Varanus* sp. from Artenay and Béon 1; Rage & Bailon 2005), Germany (*Iberovaranus* and *Varanus* from Petersbuch 2 and 28; M. Böhme 2002; M. Böhme & Ilg 2003) and the Czech Republic (Mokrá-Western Quarry site; Ivanov *et al.* 2006).

Four valid extinct species of *Varanus* are reported from Europe and Africa. The first species is *V. rusingensis* Clos, 1995 from the early Miocene of Kenya, Rusinga Island, Kiakanga Hill, the oldest known representatives of which are from the Songhor site (~20 Ma; Clos 1995; Rage & Bailon 2005). The second species is *V. hofmanni* Roger, 1898 from the middle Miocene (MN 6 mammal zone) of Stätzling, Germany (Roger 1898, 1900; Fejérváry 1918; Hoffstetter 1969), also known from the early to late Miocene of France, Spain, Austria and Hungary (Hoffstetter 1969; Alférez Delgado & Brea López 1981; Tempfer 2005; Venczel 2006; Ivanov 2009). However, the type material of *V. hofmanni* is represented by one cervical vertebra, three trunk vertebrae and one caudal vertebra. This taxon is regarded by some authors as a *nomen dubium* (M. Böhme 2002; Delfino *et al.* 2011). The third species is *V.* (*Varaneades*) *amnhophilis* Conrad, Balcarcel & Mehling, 2012 from the late Miocene (Turolian) of Samos (Greece) (Conrad *et al.* 2012). The fourth species is *V. marathonensis* Weithofer, 1888 from the late Miocene and early Pliocene of Spain, Greece, Hungary and Turkey (Weithofer 1888; Bolkay 1913; Fejérváry 1918; Rage & Sen 1976; Sen & Rage 1979; Estes 1983; Delfino *et al.* 2013a; Pérez-Ramos *et al.* 2016). *Varanus* sp. from the middle Miocene of Gratkorn (Austria) is based on a well-preserved dentary, a fragmentary maxilla, and several vertebrae and ribs (M. Böhme & Vasilyan 2014).

Middle and late Miocene varanids from Kazakhstan (*V. pronini* Zerova & Chkhikvadze, 1986), Ukraine (*V. semjonovi* Zerova & Chkhikvadze 1986) and Moldova (*V. tyrasiensis* Zerova & Chkhikvadze, 1983; *V. lungui* Zerova & Chkhikvadze, 1986) are known exclusively from several isolated vertebrae (Lungu *et al.* 1983; Levshakova 1986; Zerova & Chkhikvadze 1984, 1986). Presumed autapomorphies of these species may in fact be attributed to incomplete preservation and/or intraspecific variation. Therefore, the status of these four taxa must await a thorough revision of available material.

An additional species, *V. darevskii* Levshakova, 1986, known from incompletely preserved skull material from the early Pliocene of Tadjikistan, has been attributed to the subgenus *Psammosaurus* Fitzinger, 1826 and is hypothesized to be closely related to the extant *V.* (*Psammosaurus*) *griseus* (Daudin, 1803). However, Levshakova's (1986) assignment was questioned by Molnar (2004).

The large *V. sivalensis* Falconer, 1868 from the Pliocene–early Pleistocene of the Siwalik Hills, India (Falconer 1868) was described on the basis of a fragmentary humerus and two trunk vertebrae. Although its humerus is distinct from that of the very similar extant *V. komodoensis* Ouwens, 1912, its trunk vertebrae fall within the range of morphological variation documented in Recent *V. salvator* (Laurenti, 1768), thus casting doubt on its affinities to *V. komodoensis* (Hocknull *et al.* 2009).

In summary, many nominal fossil varanid species are based on insuffcent material (mostly isolated vertebrae). The European *V. catalaunicus* is a *nomen dubium*, and *V. pronini*, *V. semjonovi*, *V. tyrasiensis* and *V. lungui* are also regarded by some authors as *nomina dubia* (Delfino *et al.* 2011) and need revision (Rage & Bailon 2005).

Material and methods

Abundant early Miocene (MN 4) vertebrate material, including varanids, has been reported from two karst fissures in Moravia (Czech Republic): 1/2001 Turtle Joint and 2/2003 Reptile Joint (Fig. 1). The new early Miocene *Varanus* species from Mokrá-Western Quarry described here represents one of the oldest known and most complete European records of this genus. Its discovery is particularly important in light of its cranial anatomical features, which are unique among early Miocene European varanids.

Four fossiliferous karst fissures were discovered in the course of fieldwork undertaken in the years 2002–2005 on karst floors at 410 m above sea level (asl), 395 m asl and 380 m asl. The two most fossiliferous fissures (altogether 7.5 m^3, about 13 tons) are both from the floor at 380 m asl, and are referred to as 1/2001 (from Turtle Joint) and 2/2003 (from Reptile Joint) hereafter. All material from these two fissures was washed in sieves of 2 mm, 1 mm and 0.5 mm mesh size. In order to separate fossil specimens from the non-calcareous sand-clayey sediments, we used H_2O_2 in aqueous solution with optimum concentration corresponding approximately to a 1 (H_2O_2 30%):100 (H_2O) ratio. After dissolving the clayey component, we used a regulated stream of running water for final washing. An environmental electron microscope LEO 1540 VP and Leica MZ 16 microscopic system equipped with a Leica DFC 480 digital camera (5 mpx) were used for examination and photography of the fossil material.

Material has been deposited in the collections of the Department of Geological Sciences, Masaryk University, Brno, under registration numbers SMM/009-09-11/372009, Pal. 1000–1238. The osteological specimens used for comparative studies are listed in the Supplemental material.

Body size estimation

We follow Conrad *et al.* (2012, table 1) in using snout-vent length (SVL) as a proxy for body size (tail length is variable even within individual species). The length of the posteriormost presacral vertebra (DVL) of fossil *Varanus* from Mokrá-Western Quarry was compared to vertebrae of *Varanus* species in the 'Indo-Asiatic A' clade (*sensu* Ast 2001), based on the assumption that the new taxon scaled similarly to members of that clade. In particular, the vertebra in question resembles closely those of taxa in the *V. bengalensis* group (Conrad *et al.* 2012). Body size estimations were based on a regression analysis performed in STATISTICA, v. 10.

Phylogenetic analysis methods

In order to assess the phylogenetic position of the new *Varanus* species, we assembled a data matrix of 449 osteological characters coded for 87 taxa. We included extant and extinct *Varanus* species, as well as several outgroup taxa selected according to the results of the most recent squamate phylogenies (Supplemental Appendices 1, 2 and 3; Conrad *et al.* 2012). We performed two maximum parsimony analyses and two Bayesian inference analyses. The two parsimony analyses, carried out in TNT v. 1.1 (Goloboff *et al.* 2008), differed in the use of equal vs implied weighting of characters (Goloboff 1993). In both cases, a reduced version of the data matrix was used, after applying safe taxonomic reduction (Wilkinson 1995) in the Claddis package of R (Lloyd 2015). The parsimony settings were as follows: heuristic searches; 50,000 random stepwise addition sequences; tree bisection-reconnection branch-swapping algorithm, keeping a single tree in memory at the end of each addition sequence; branch-swapping subsequently applied to all trees in memory, with the option of saving multiple trees (Quicke *et al.* 2001). The same settings were applied to the implied weighting analysis. This technique assigns an implied weight W to each character, measured as $W = K/(K + Max - Obs)$, where Max and Obs are, respectively, the maximum possible and the observed number of changes for a character. K is a constant of concavity, an integer that ultimately determines the most parsimonious tree as the tree which maximizes the W value across all characters. The Bayesian analyses (Supplemental Appendices 4 and 5) were carried out in MRBAYES v. 3.0b4 (Huelsenbeck & Ronquist 2001) with the following default settings: equal prior probability of all tree topologies; unconstrained branch lengths; equal state frequencies. Briefly, Bayesian analysis establishes the posterior probability of a tree given a data matrix, a model for character evolution, and a prior model of character-state frequency (e.g. Pollitt *et al.* 2005). The posterior probability of a tree is proportional to its likelihood times the prior probability of that tree (i.e. the probability without reference to the

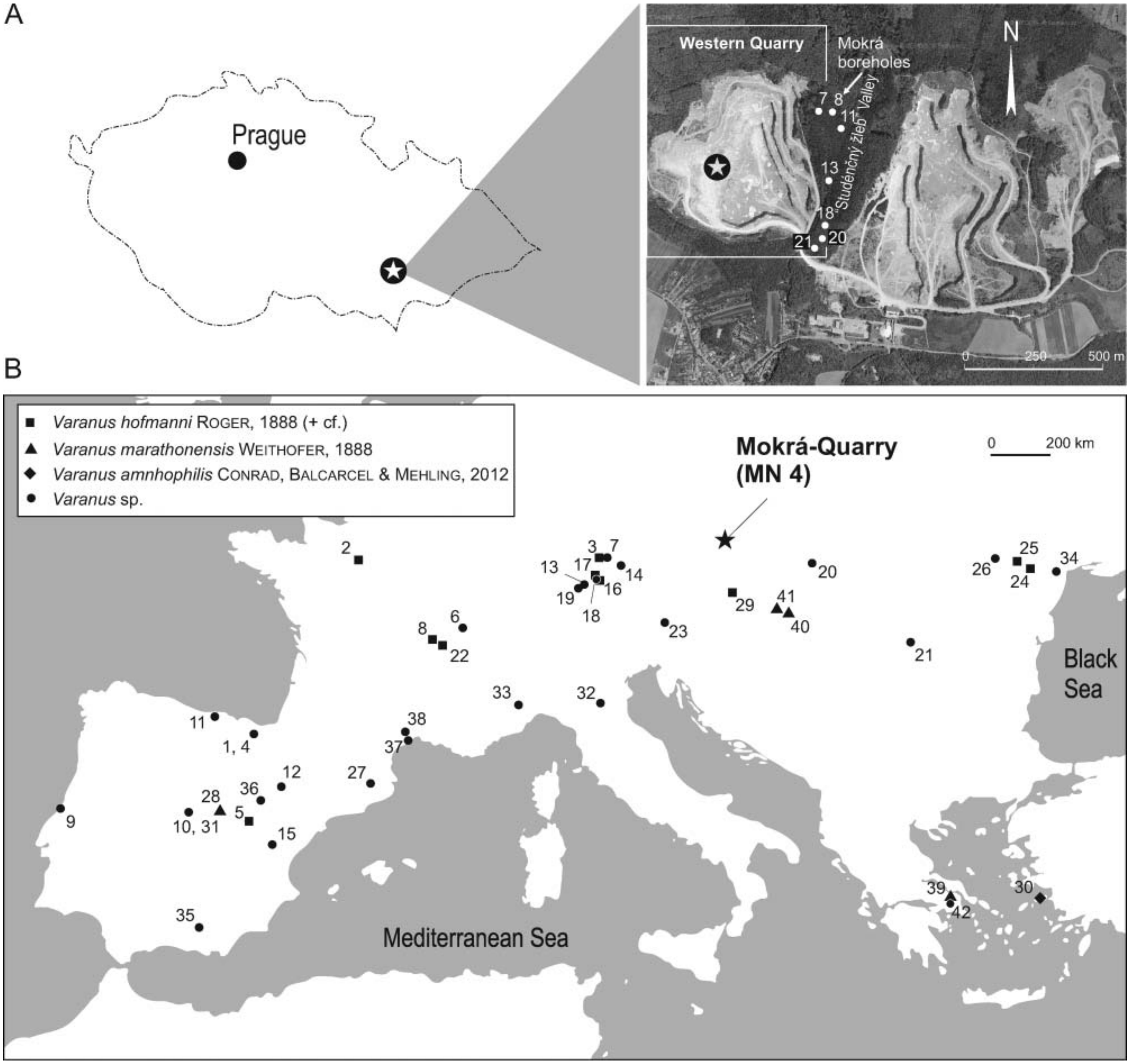

Figure 1. **A,** position of the locality Mokrá-Western Quarry (modified after http://www.mapy.cz). Position of the 1/2001 Turtle Joint and the 2/2003 Reptile Joint is indicated by a star. Numbered circles indicate positions of Mokrá boreholes. **B,** European localities with fossil monitor lizards: 1 – San Roque, MN 3; 2 – Artenay, MN 4a; 3 – Petersbuch 2, 8, 28, MN 4a; Petersbuch 5, 36, MN 4; Petersbuch 41, MN 5; Petersbuch 39, 68, MN6; Petersbuch 31, MN 7; Petersbuch 18, MN 8-9; 4 – San Marcos, MN 4; 5 – Córcoles, MN 4; 6 – Béon 1, MN 4; 7 – Erkertshofen, MN 4b; 8 – Vieux-Collonges, MN 4/5; 9 – Amor, MN 5; 10 – Las Umbrias 12, 18, 19, MN 5, Las Umbrias 11, MN 6; 11 – Vargas 11, MN 5; 12 – Villafeliche, MN 5; 13 – Ziemetshausen, MN 5; 14 – Gisseltshausen 1b, MN 5; 15 – Toril 3B, MN 6; 16 – Unterzell, MN 6; 17 – Stätzling, MN 6; 18 – Laimering, MN 6; 19 – Hohenraunau b. Krumbach, MN 6; 20 – Litke, MN 6; 21 – Subpiatră, MN 6; 22 – La Grive, MN 7+8; 23 – Gratkorn, MN 7+8; 24 – Varnitza, MN 9; 25 – Kalfa, MN 9; 26 – Bujor, MN 9b; 27 – Can Llobateres, MN 10; 28 – Cerro de los Batallones, MN 10; 29 – Kohfidisch, MN 10/11; 30 – Samos 1, MN 11; 31 – El Arquillo, MN 13; 32 – Cava Monticino, MN 13; 33 – Verduno, MN 13; 34 – Cherevichnoie, MN 13; 35 – Moreda a, MN 15; 36 – Layna, MN 15; 37 – Sète, MN 15; 38 – Balaruc 2, MN 15-MN 16; 39 – Pikermi, MN 16; 40 – Beremend, MN 16; 41 – Csarnóta, MN 16; 42 – Tourkobounia 5, Middle Pleistocene. **A,** modified from Ivanov *et al.* (2006); **B,** data according to Roger (1898, 1900), Hoffstetter (1969), Antunes & Rage (1974), Alférez Delgado & Brea López (1981), Antunes & Mein (1981), M. Böhme & Ilg (2003), Hír & Venczel (2005), Rage & Bailon (2005), Tempfer (2005), Ivanov *et al.* (2006), Venczel (2006), Ivanov (2009), Conrad *et al.* (2012), Delfino *et al.* (2013a, b), M. Böhme & Vasilyan (2014), Colombero *et al.* (2014), Venczel & Hír (2015), Pérez-Ramos *et al.* (2016) and Georgalis *et al.* (2017).

original matrix). The tree landscape is explored using Markov chain Monte Carlo (MCMC) algorithms to find trees that have maximal posterior probability. The distribution of the posterior probabilities is represented by a 50% majority-rule consensus in which the Bayesian support is given as a posterior probability on all internal branches. The support value on a branch is interpreted as the probability of retrieving the group subtended by that branch, given the data matrix, the model of character evolution, and the character-state frequency (e.g. Archibald *et al.* 2003). We carried out 1,000,000 MCMC iterations, sampling every 100th generation, and discarding the first 10,000 trees following the recommended burn-in. We considered all posterior probability values above 90% to be strong, and those below 50% to be weak (e.g. Tsuji *et al.* 2010). In the Bayesian topologies, a value of 1 indicates the probability of the partition indicated by the relevant branch. For ease of figure presentation, we indicate only partitions with a value of 1; all the others have a value of 0.5. Using the Markov k (Mk) model for morphological data, we specified two types of rate distribution for character changes across the tree, namely equal and gamma, permitting respectively equal probability of between-state changes and variable rates of change across characters (e.g. Tsuji *et al.* 2010; Wright & Hillis 2014). Stationarity was deemed to be satisfactory, with split frequency values only slightly higher than 0.05.

Institutional abbreviations

MNHN: Muséum national d'Histoire naturelle, Paris, France; **NHMUK**: Natural History Museum, London, UK; **NMA**: Naturmuseum Augsburg, Augsburg, Germany; **NMP**: National Museum, Prague, Czech Republic; **Pal.**: Department of Geological Sciences, Masaryk University, Brno; **SMF**: Senckenberg Museum, Frankfurt, Germany; **UF**, University of Florida, Gainesville, USA; **ZZSiD**: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

Systematic palaeontology

Order **Squamata** Oppel, 1811
Superfamily **Varanoidea** Münster, 1834
Family **Varanidae** Hardwicke & Gray, 1827
Genus ***Varanus*** Merrem, 1820
†***Varanus mokrensis*** sp. nov.
(Figs 2–7)

Diagnosis. Mid-sized *Varanus* with estimated snout-vent length up to about 38 cm; differs from all other species in the genus on the basis of a single autapomorphy – parietal and squamosal processes of postorbitofrontal forming a distinctly acute angle – and the following combination of features: (1) short septomaxilla with flat dorsal surface; (2) frontal and anterolateral postorbital processes of postorbitofrontal forming obtuse angle; (3) posterior margin of nasal lobe of frontal situated in middle of dorsal width of rostral process; (4) posterior margin of anteroposteriorly elongated frontal relatively narrow; (5) parietal with wide subrectangular fronto-postfrontal processes, anteriorly arched fronto-parietal suture, and parietal foramen situated significantly posterior to anterior margin of bone (more than one-third of parietal plate length); (6) distance between medially converging parietal crests of parietal shortest in posterior quarter of parietal plate length; (7) otoccipital with very distinct occipital crest at base of paroccipital process; (8) pointed conical teeth with distally recurved apices and prominent smooth mesial and distal cutting edges; (9) trunk vertebrae with moderately developed depression between pars tectiformis and medial margin of prezygapophyses and with posterolaterally directed postzygapophyses forming a right angle; (10) preacetabular process of ilium prominent and directed at right angle to pubic process; and (11) bifurcated iliac crest prominent.

Derivation of name. The species name *mokrensis* refers to the Mokrá-Western Quarry locality.

Holotype. 2/2003 Reptile Joint: parietal (Pal. 1097, Fig. 3H, I).

Paratypes. 1/2001 Turtle Joint: left maxilla (Pal. 1023, Fig. 2A, B; Pal. 1024, Fig. 2C–E), left septomaxilla (Pal. 1020, Fig. 2I, J). 2/2003 Reptile Joint: left postorbitofrontal (Pal. 1117, Fig. 3A, B), left frontal (Pal. 1090, Fig. 3E, F), parietal (Pal. 1098, Fig. 3G), left palatine (Pal. 1134, Fig. 4A, B), right pterygoid (Pal. 1131, Fig. 4D, E), right quadrate (Pal. 1152, Fig. 4F), right prootic (Pal. 1104, Fig. 4G, H), left otoccipital (Pal. 1109, Fig. 4J–M), basioccipital (Pal. 1014, Fig. 4N), basisphenoid (Pal. 1114, Fig. 5A–C), right dentary (Pal. 1140, Fig. 5E–G), left surangular (Pal. 1144, Fig. 5H, I), right articular (Pal. 1150, Fig. 5K, L), left ilium (Pal. 1154, Fig. 5M, N), cervical vertebra (Pal. 1159, Fig. 6C, D), middle trunk vertebra (Pal. 1183, Fig. 6I–M). 1/2001 Turtle Joint: sacral vertebra (Pal. 1066, Fig. 6Q).

Referred material. 1/2001 Turtle Joint: frontal (2 left + 3 right), Pal. 1000–1004; parietal, Pal. 1005–1007; left prootic, Pal. 1008; otoccipital (1 left + 3 right), Pal. 1009–1012; basisphenoid, Pal 1013; basioccipital, Pal. 1014–1015; postorbitofrontal (2 left + 2 right), Pal. 1016–1019; septomaxilla (2 left + 1 right), Pal. 1020–1022; maxilla (3 left + 2 right), Pal. 1023–1027; fragmentary toothed bones, Pal. 1028–1032; left pterygoid, Pal. 1033; right palatine, Pal. 1034; left dentary, Pal. 1035–1036; left surangular, Pal. 1037; left articular, Pal. 1038; right quadrate, Pal. 1039; cervical vertebrae, Pal. 1040–1043; trunk

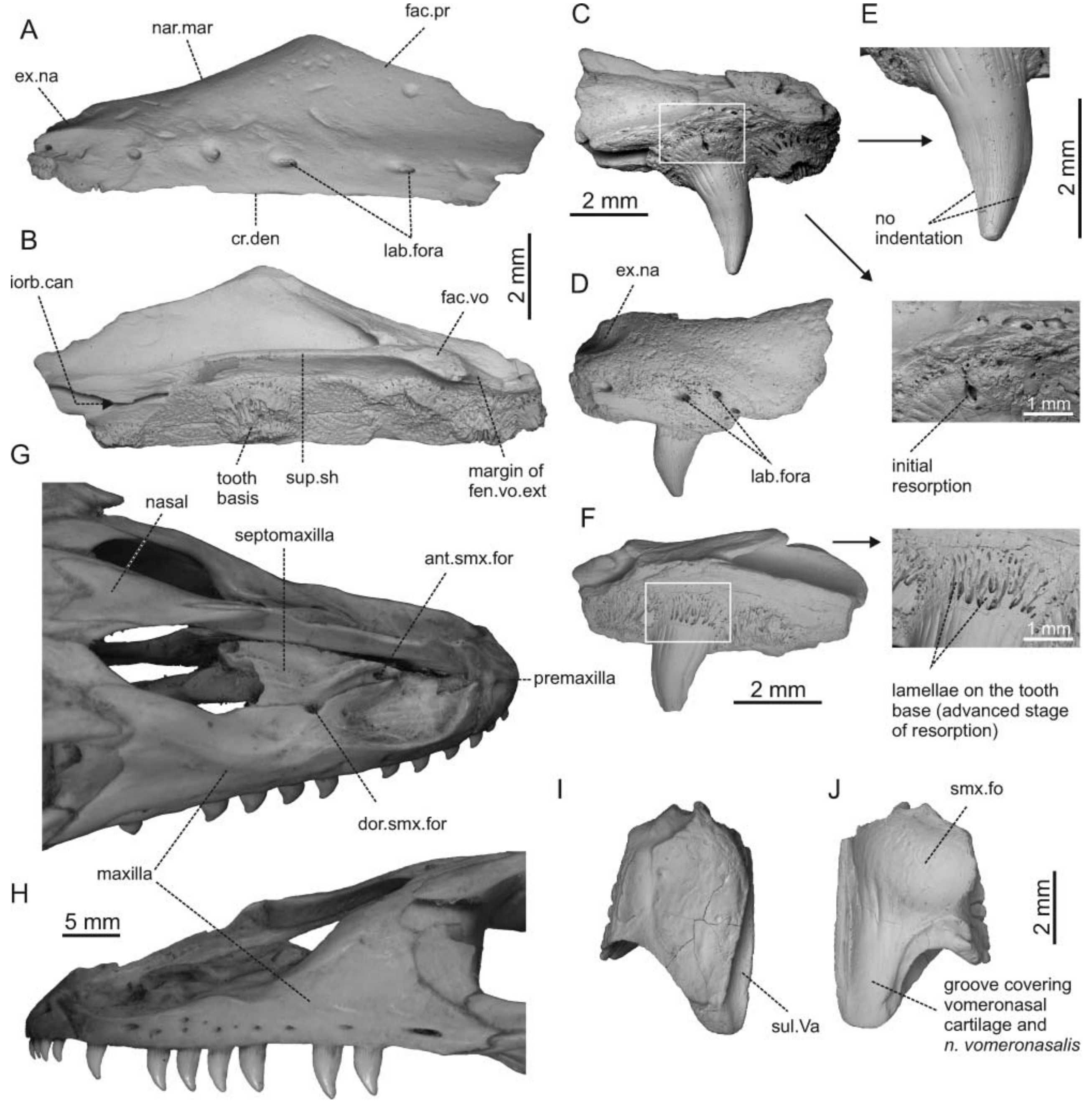

Figure 2. Miocene and extant species of *Varanus*. **A, B, C–E, I, J,** *Varanus mokrensis* sp. nov.; **A, B,** Pal. 1023 (1/2001 Turtle Joint), fragmentary left maxilla in lateral (**A**) and medial (**B**) views; **C**–**E,** Pal. 1024 (1/2001 Turtle Joint), fragmentary rostral part of the left maxilla with preserved tooth in medial (**C**) and lateral (**D**) views, and tooth detail (**E**) with clearly developed keel without any trace of indentation; **F,** Pal. 1026 (1/2001 Turtle Joint), fragmentary right maxilla in medial view, the tooth base shows an advanced stage of resorption; **I, J,** Pal. 1020 (1/2001 Turtle Joint), left septomaxilla in dorsal (**I**) and ventral (**J**) views. **G, H,** snout of extant *Varanus bengalensis*, SMF 63456, in laterodorsal (**G**) and lateral (**H**) views. Abbreviations: ant.smx.for, anterior septomaxillary foramen; cr.den, crista dentalis; dor.smx.for, dorsal septomaxillary foramen; ex.na, excavatio nasalis; fac.pr, facial process; fac.vo, facet for contact with vomer; fen.vo.ext, fenestra vomeronasalis exonaria; iorb.can, infraorbital canal; lab.fora, labial foramina; nar.mar, narial margin; smx.fo, septomaxillar fossa; sul.Va, sulcus for opthalmic + ethmoidal nerve and ethmoidal artery; sup.sh, supradental shelf.

vertebrae, Pal. 1044–1065; sacral vertebrae, Pal. 1066–1068; caudal vertebrae, Pal. 1069–1087.

2/2003 Reptile Joint: frontal (5 left + 4 right), Pal. 1088–1096; parietal, Pal. 1097–1103, prootic (2 left + 3 right), Pal. 1104–1108; otoccipital (2 left + 3 right), Pal. 1109–1113; basisphenoid, Pal. 1114–1116; postorbitofrontal (3 left + 2 right), Pal. 1117–1121; septomaxilla (2 left + 1 right), Pal. 1122–1124; maxilla (2 left + 4 left or right), Pal. 1125–1130; pterygoid (2 left + 1 right), Pal. 1131–1133; palatine (2 left + 1 right), Pal. 1134–1136; dentary (3 left + 4 right), Pal. 1137-1143; surangular (3 left + 2 right), Pal. 1144–1148; articular (left + right), Pal. 1149–1150; quadrate (2 left + 1 right), Pal 1151–1153; ilium (3 left + 2 right), Pal. 1154–1158; cervical vertebrae, Pal. 1159–1171; trunk vertebrae, Pal. 1172–1206; sacral vertebrae, Pal. 1207–1210; caudal vertebrae, Pal. 1211–1238.

Type locality and horizon. Mokrá-Western Quarry, Czech Republic: 1/2001 Turtle Joint and 2/2003 Reptile Joint. Both joints date back to the early Miocene, Eggenburgian or Ottnangian, Orleanian, MN 4 (Ivanov *et al.* 2006; Sabol *et al.* 2007).

Description

Skull

Maxilla. The subtriangular maxilla contacts the premaxilla anteriorly, the septomaxilla, vomer and premaxilla medially, and the prefrontal, lacrimal, jugal, ectopterygoid and maxillary process of the palatine posteriorly (Fig. 2A–F). Its anteromedial extension forms the ventral rim of the exonarial fenestra (excavatio nasalis *sensu* Mertens 1942). All preserved maxillae are fragmentary with broken anterior and posterior extremities.

The sharp supradental shelf is expanded medially in its anterior part where it meets the vomer forming the posterolateral emargination of the external vomeronasal pit. The orifice of the infraorbital canal (for the nervus alveolaris superior and maxillary artery; Bellairs 1949), situated immediately dorsal to the supradental shelf, is delimited anterodorsally by a short, distinct crest. Anteriorly, the supradental shelf continues medially into a distinct facet for the contact with the vomer, and also forms the posterior margin of the exonarial fossa. The most complete left maxilla shows six tooth positions. Seven labial foramina occur in the most completely preserved maxilla. Foramina are more closely spaced anteriorly at the level of the posterior termination of the exonarial fenestra. A distinct depression on the dorsal surface of the anterior part of the maxillary fragments indicates that the excavatio nasalis was relatively short anteroposteriorly.

Remarks. The prefrontal process is not preserved, but the facial process was presumably very tall in lateral view, as suggested by the inclination of the narial margin, and enlarged posteriorly near the contact with the prefrontal and lacrimal. In its general shape (Fig. 2G, H), the maxilla resembles that of *V. bengalensis* (Daudin, 1802), although in adults of the latter species the laterally depressed maxillary teeth do not have distinctly broad basal portions (Mertens 1942, pl. 25, figs 195, 196) and their crowns may be rounded in lateral view (Mertens 1942, pl. 25, fig. 196).

Septomaxilla. The approximately trapezoidal, paired septomaxilla is situated between the nasal process of the premaxilla and the maxillae. Laterally, it borders the flat anteromedial margin of the maxilla (Fig. 2I, J). Its anterior part forms a short, stout process.

A distinct, ventrally positioned septomaxillary fossa is present. In life, this fossa housed the cartilaginous capsule of the Jacobson's organ. The anteromedial margin of the fossa is broken. A triangular process with a distally narrowing longitudinal groove projects posteriorly from the fossa. This process extended dorsally over the paraseptal cartilage (Bellairs 1949; Jollie 1960). The sharp posterolateral process of the septomaxilla formed the roof of the free posterior termination of the chondrocranial lamina transversalis anterior. In dorsal view, a distinct sulcus is visible along the medial margin of the septomaxilla (sulcus pro ramus frontalis ophthalmici nerve [V] *sensu* Bahl 1937). In life, this sulcus probably accommodated the narrowing medial branch of the ethmoidal nerve (Shrivatsava 1963; Va, nervus ophthalmicus + nervus ethmoideus *sensu* Bellairs 1949) and the collateral ethmoidal artery. A short crest is visible anterolaterally proximal to the suture with the widened rostral portion of the maxilla. The crest originally bordered a distinct groove that presumably extended anteriorly almost to the level of the foramen septomaxillaris anterior (for its position in extant *V. bengalensis*, see Fig. 2G). The lacrimal duct (ld 2 – lower lacrimal duct *sensu* Shrivatsava 1963) was situated within the groove in life, and presumably ran ventrally and medially and opened below the Jacobson's organ (Bellairs 1949).

Postorbitofrontal. The paired postorbitofrontal is enlarged posteriorly and forms three processes (Fig. 3A, B) situated along the medial and anterolateral margins of the bone. It articulates with the parietal and frontal medially and with the squamosal posteriorly.

In dorsal view, the postorbitofrontal contacts the posterolateral process of the frontal anteromedially via a long, robust, proximally wide frontal process (processus frontalis). The gracile distal termination of the process is not preserved, but it is assumed to have been very elongate, based on the strongly enlarged triangular facet for the postorbitofrontal attachment observed in the frontal

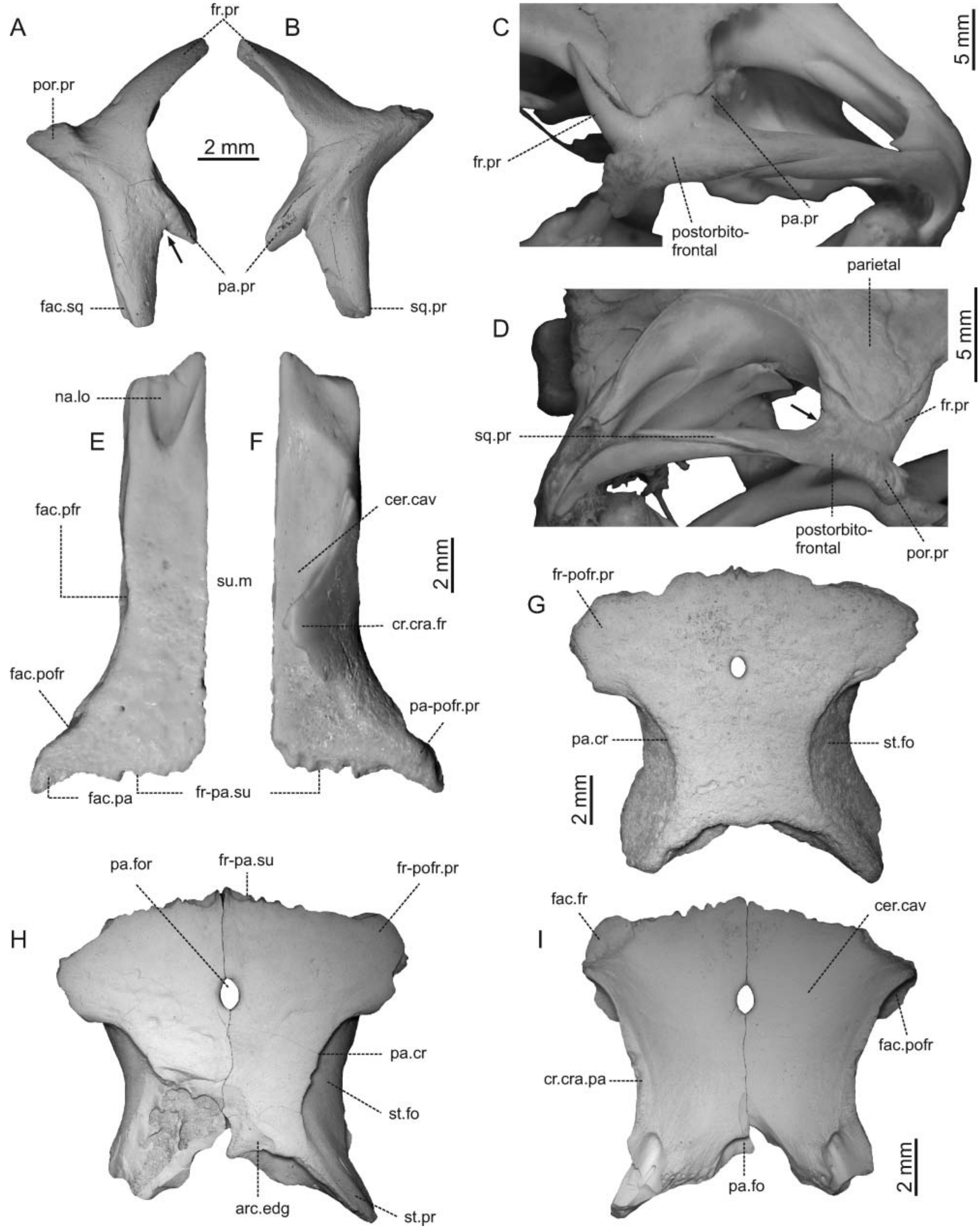

Figure 3. Postorbitofrontal of species of *Varanus*. **A, B, E, F, G–I** *Varanus mokrensis* sp. nov.; **A, B,** Pal. 1117 (2/2003 Reptile Joint), left postorbitofrontal in dorsal (**A**) and ventral (**B**) views; **E, F,** Pal. 1090 (2/2003 Reptile Joint), left frontal in dorsal (**E**) and ventral (**F**) views; **G,** Pal. 1098 (2/2003 Reptile Joint), **H, I,** Pal. 1097 (2/2003 Reptile Joint), parietal in dorsal (**G, H**) and ventral (**I**) views; **C,** left

bone. The postorbital and frontal processes are orientated slightly ventrally, and form an obtuse angle between them. The short posteromedially directed parietal process is attached to the anterolateral border of the parietal, and forms a conspicuously acute angle with the posteriorly directed squamosal process (Fig. 3A – see arrow). The robust squamosal process was probably short and, together with the squamosum, participated in the formation of the anterior supratemporal arch.

Remarks. The angle between the frontal and parietal processes may increase with age (Mertens 1942, pl. 23, p. 167) (Fig. 3C, SMF 54157), as documented for *Varanus flavescens* (Hardwicke & Gray, 1827); ZZSiD 456 and *V. benagalensis* (Fig. 3D, NHMUK 1974.2479). Such an increase results from the increasing anteroposterior width of the processus fronto-postorbitofrontalis of the parietal.

Frontal. The paired frontal forms most of the dorsal part of the orbital margin. The frontal cranial crests (cristae cranii *sensu* Oelrich 1956; ventro-lateral processes *sensu* Scanlon 2005) are the most prominent structures on the ventral surface of the bone. They extend ventromedially and almost completely enclose the olfactory canal (Fig. 3E, F). The canal is subtriangular in cross section.

In dorsal view, the medial and lateral margins of the frontal are parallel. The bone carries a short anteromedial process and a large posterolateral process. The bone is widest at the level of the parietal suture. Its medial margin is straight and smooth. Its posterolateral margin forms a strong process directed slightly posteriorly. This process would be wedged between the postorbitofrontal and the parietal in life. The triangular parietal tab is well developed. The posterior margin of the distinct lobus nasalis (margo nasalis posterior), where the frontal meets the posterolateral process of the nasal, is situated at the level of the mid-width of the rostral process of the frontal. The medial descending process has a broad base. The lateral descending process is broken off close to its base. The flat dorsal surface of the frontal is smooth anterior to the orbital margin. The broad orbital portion of the bone shows traces of the dorsal sculpture in the form of polygonal fields separated by low weak ridges. In ventral view, the medioventrally directed ventrolateral process of the frontal cranial crest is distinctly developed. The frontoparietal suture is interdigitated. In lateral view, the triangular depression for the articulation with the prefrontal is conspicuously developed, and its posterior margin reaches slightly posterior to the mid-length of the bone. The articular facet for the postorbitofrontal is indistinct. In medial view, the anterior portion of the dorsal margin of the frontal narrows, and the medial descending process of the bone is slightly inclined ventrally. In anterior view, the anterior margin of the crista cranii frontalis is directed distinctly ventrally, and its posterior margin is arched in a medial direction.

Parietal. The unpaired parietal covers dorsally the posterior portion of the braincase (Fig. 3G–I). It articulates with the frontal anteriorly and the parietal posteriorly. The frontoparietal suture is interdigitating. A flexible movable joint occurs between the parietal and the prootic.

In dorsal view, the flat parietal table is covered by a weakly developed ornamentation consisting of irregular shallow grooves. The anterolateral processes are anteroposteriorly broadened and project slightly laterally. The distance between the medially converging parietal crests is shortest at the level of the posterior quarter of the parietal table length. Farther posteriorly, the parietal crest extends onto the dorsal surface of the incompletely preserved supratemporal processes. The basal portions of the posterolaterally diverging supratemporal processes form an almost right angle. The parietal crest contributes to the dorsal margin of a large and anteroposteriorly short supratemporal fossa, which extends from the postorbitofrontal articulation, through the parietal process, to the unpreserved posterior tip of the supratemporal process. The fossa is mediolaterally broadest immediately posterior to the level of the maximal constriction of the parietal crests. The anteromedial part of the fossa is covered by the slightly extending parietal crest. The parietal foramen lies at a level slightly anterior to the mid-length of the parietal table.

In ventral view, the facet for the articulation with the posterolateral process of the frontal is anterolaterally broad. The crista cranii parietalis is deepest halfway between the parietal foramen and the posterior border of the parietal table. Distinct marginal grooves are preserved on either side of the crista cranii in one specimen (Pal. 1097). The posterior section of the crista cranii is short and forms the anterolateral constriction of a deep depression visible at the base of the supratemporal process. The parietal fossa forms a wide and shallow depression on the posterior wall of the parietal table. In lateral view, the bases of the supratemporal processes are orientated ventrally. A ledge-like lateral margin of the parietal table

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postorbitofrontal of extant *Varanus flavescens*, SMF 54157, in laterodorsal view; **D,** right postorbitofrontal of extant *Varanus bengalensis*, NHMUK 1974.2479, in laterodorsal view. Abbreviations: arc.edg, arcuate edge; cer.cav, cerebral cavity; cr.cra.fr, crista cranii frontalis; cr.cra.pa, crista cranii parietalis; fac.fr, facet for contact with frontal; fac.pa, facet for contact with parietal; fac.pfr, facet for contact with prefrontal; fac.pofr, facet for contact with postorbitofrontal; fac.sq, facet for contact with squamosum; fr-pa.su, fronto-parietal suture; fr-pofr.pr, frontalo-postorbitofrontal process; fr.pr, frontal process; na.lo, nasal lobe; pa.cr, parietal crest; pa.fo, parietal fossa; pa.for, parietal foramen; pa-pofr.pr, parietal-postorbitofrontal process; pa.pr, parietal process; por.pr, postorbital process; sq.pr, squamosal process; st.fo, supratemporal fossa; st.pr, supratemporal process.

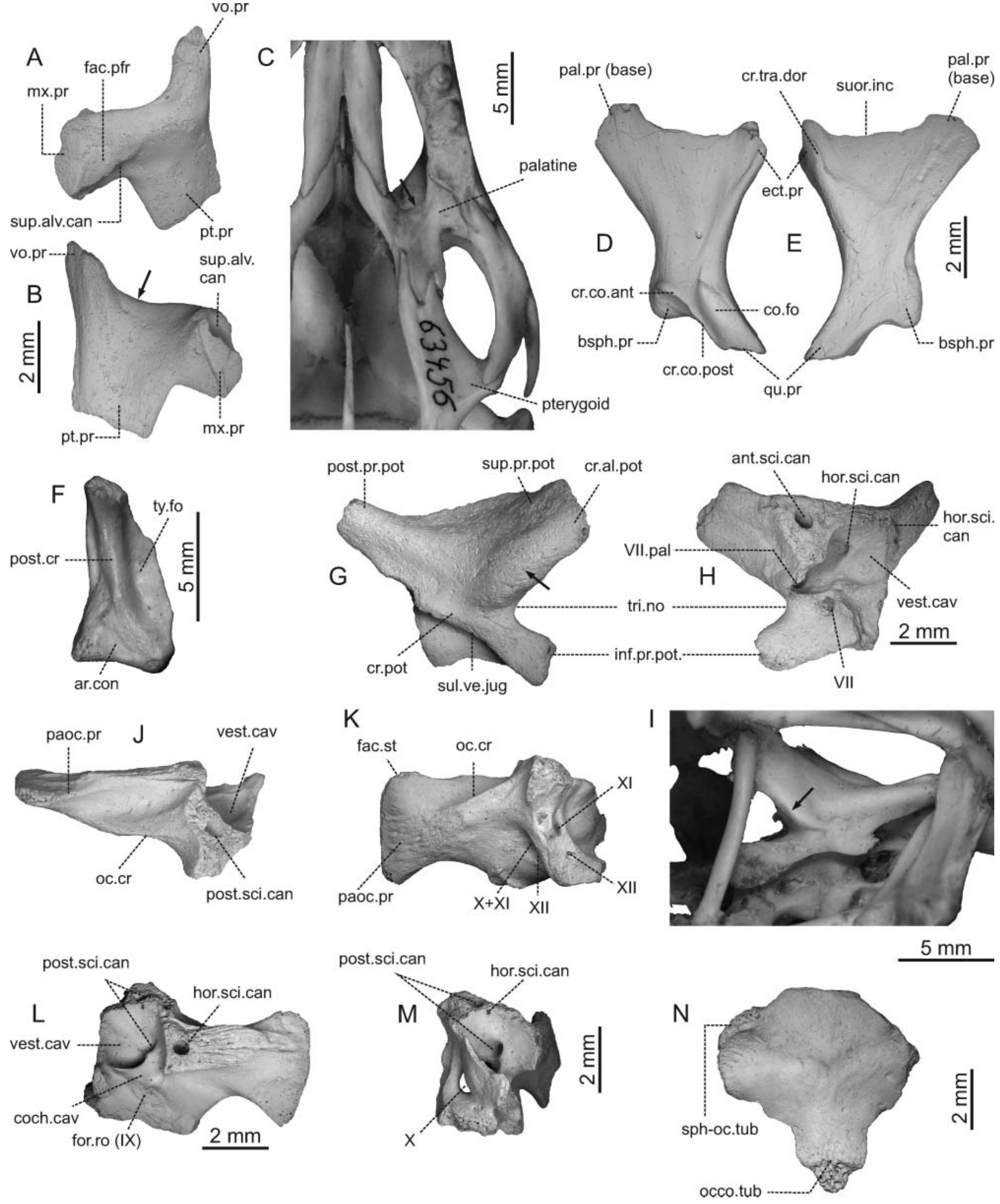

Figure 4. Miocene and extant species of *Varanus*. **A, B, D–H, J–N,** *Varanus mokrensis* sp. nov. **A, B,** Pal. 1134 (2/2003 Reptile Joint), left palatine in dorsal (**A**) and ventral (**B**) views; **D, E,** Pal. 1131 (2/2003 Reptile Joint), right pterygoid in dorsal (**D**) and ventral (**E**) views; **F,** Pal. 1152 (2/2003 Reptile Joint), right quadrate in caudal view; **G, H,** Pal. 1104 (2/2003 Reptile Joint), right prootic in lateral (**G**) and medial (**H**) views; **J–M,** Pal. 1109 (2/2003 Reptile Joint), left otoccipital in dorsal (**J**), caudal (**K**), cranial (**L**) and medial (**M**) views; **N,** Pal. 1014 (1/2001 Turtle Joint), basioccipital in ventral view. **C, I.** extant *Varanus bengalensis*, SMF 63456; **C**, left palatine in ventral view; **I,** left prootic in lateral view. Abbreviations: ant.sci.can, anterior semicircular canal; ar.con, articular condyle; bsph.pr,

covers the articulation of the parietal with the parietal process of the postorbitofrontal.

Remarks. The course of the parietal crests indicates a well-developed attachment for the musculus pseudotemporalis superficialis, such as is found in extant durophagous species of *Varanus*, including *V. niloticus* (Linnaeus, 1766), *V. exanthematicus* (Bosc, 1792) and *V. olivaceus* Hallowell, 1857 (Mertens 1942, pl. 23, figs 166, 168). In these species and in the extinct *V. rusingensis* from the early Miocene of Kenya (Clos 1995), the parietal crests approach one another closely in a posterior direction (Clos 1995). Such crests often occur in adult specimens and may form a distinct ridge in the midline of the posterior margin of the bone (e.g. *V. olivaceus*; Mertens 1942, pl. 24, fig. 172; SMF 72156). Specimens of *V. mokrensis* represent adults of average size (about 374.9 mm SVL). In this taxon, the converging parietal crests fail to come in contact with one another and the features of the dentition indicate that it had a weaker pseudotemporalis superficialis muscle than the above-mentioned species. We infer, therefore, that *V. mokrensis* was not a durophagous taxon.

Palatine. The irregularly shaped, toothless palatine bears three processes (Fig. 4A, B). The wide and posteriorly directed pterygoid process (broken off in all specimens) is connected to the pterygoid. The thin, anteromedially directed vomerine process connects to the vomer. The maxillary process is directed anteroposteriorly, but its anterior extremity is not preserved. The posterior end of this process contacts the jugal and ectopterygoid. The anterior border of the palatine forms the posterior margin of the internal nostril.

In anterior view, the infraorbital foramen (maxillo-palatine foramen *sensu* Mertens 1942 and Jollie 1960) forms the orifice of the superior alveolar canal running through the base of the maxillary process.

Remarks. The elliptical to almost circular infraorbital foramen of the palatine and the proximally slender processus vomerinus are also observed in extant *V. bengalensis* (MNHN 1884-4, 1886-649). The elongate maxillary process forms an obtuse angle with the vomerine process, and this suggests that the posterior nares were probably wide and short (as indicated also by the short septomaxilla) unlike in *V. bengalensis* (Fig. 4B, C – see arrows). The same development of posterior nares occurs in African monitors, which are considered to form the sister group to all other *Varanus* species.

Pterygoid. In ventral view, the triradiate pterygoid is slightly curved medially and shows no trace of dentition (Fig. 4D, E). Its anterior portion is flat, whereas its posterior portion forms a long and gracile quadrate process orientated posterolaterally. The anteromedial portion of the pterygoid projects into a flat and wide palatine process. The latter process articulates with the posterior border of the palatine. Anterolaterally, the pterygoid articulates with the ectopterygoid. The posterior terminations of all three processes are broken in all specimens.

In dorsal view, the crista columellaris anterior is wide and weakly developed. The crista columellaris posterior, forming the posteromedial border of the elongated fossa columellae, is sharp and decreases in height towards the posterior termination of the columellar fossa. The anterior margin of the columellar fossa reaches as far as the posterior termination of the markedly deep sulcus which widens and diminishes anteriorly. The basisphenoid process projects medially. The articular surface for the basipterygoid process of the basisphenoid is slightly rugose. In ventral view, the basal portion of the palatal process narrows posteriorly. The more gracile ectopterygoid process is broken near its base. The low but distinct crista transversa dorsalis courses close to the lateral margin of the ectopterygoid process. The suborbital incisure is shallow and gradually merges into the wide base of the pterygoid process.

Quadrate. Only the trochlear part of the quadrate is present (Fig. 4F). It has a wide articular condyle for the junction with the articular. A small triangular facet for the articulation with the pterygoid is present at the medial border of the articular condyle. The tympanic fossa is deep and wide, and bears a wide outer ridge for the attachment of the dorsal and anterior borders of the tympanic membrane. The lateromedially wide and strongly developed posterior crest extends as far as the tympanic part of the articular condyle.

Prootic. The prootic forms the anterior and anteroventral portion of the auditory capsule (Fig. 4G, H). The prootic articulates with the supratemporal process of the

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basisphenoid process; co.fo, columellar fossa; coch.cav, cochlear cavity; cr.al.pot, crista alaris prootica; cr.co.ant, crista columellaris anterior; cr.co.post, crista columellaris posterior; cr.pot, crista prootica; cr.tra.dor, crista transversa dorsalis; ect.pr, ectopterygoid process; fac.pr, facial process; fac.st, facet for contact with supratemporal; for.ro, foramen rotundum; hor.sci.can, horizontal semicircular canal; inf.pr.pot, inferior process of prootic; IX, foramen for glossopharyngeal nerve; mx.pr, maxillary process; occo.tub, occipitocondylar tubercle; oc.cr, occipital crest; pal.pr, palatal process; paoc.pr, paroccipital process; post.cr, posterior crest of quadratum; post.pr.pot, posterior process of prootic; post.sci.can, posterior semicircular canal; pt.pr, pterygoid process; qu.pr, quadrate process; sph-oc.tub, spheno-occipital tubercle; sul.ve.jug, sulcus venae jugularis; suor.inc, suborbital incisure; sup.alv.can, superior alveolar canal; sup.pr.pot, superior process of prootic; tri.no, trigeminal notch; ty.fo, tympanic fossa; vest.cav, vestibular cavity; VII, foramen for the facial nerve; VII.pal, foramen for palatine branch of the facial nerve; vo.pr, vomerine process; X, foramen for vagus nerve; XI, foramen for accessory nerve; XII, foramen for hypoglossal nerve.

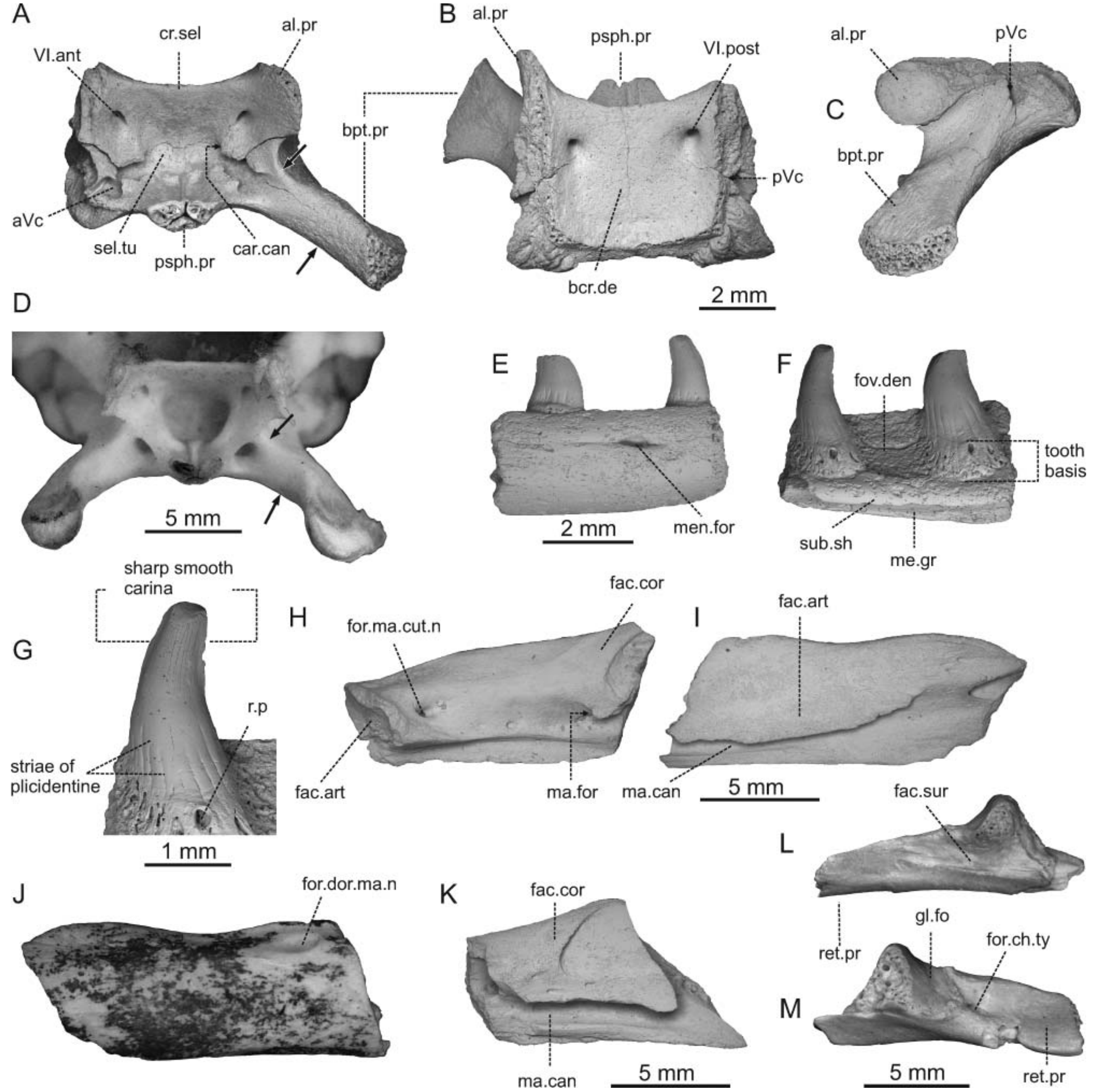

Figure 5. Miocene and extant species of *Varanus*. **A–C, E–M,** *Varanus mokrensis* sp. nov. **A–C,** Pal. 1114 (2/2003 Reptile Joint), basisphenoid in anterior (**A**), dorsal (**B**), and lateral (**C**) views; **E–G,** Pal. 1140 (2/2003 Reptile Joint), right dentary in lateral (**E**) and medial (**F**) views, a sharp mesial and distal carina is developed on the anteriorly situated tooth (**G**); **H–J,** Pal. 1144 (2/2003 Reptile Joint), almost complete left surangular in medial view broken on the two parts (**H, I**) and anterior part of surangular in lateral view (**J**); **K,** Pal. 1037 (1/2001 Turtle Joint), left surangular in medial view; **L, M,** Pal. 1150 (2/2003 Reptile Joint), right articular in medial (**L**) and dorsal (**M**) views. **D,** basisphenoid of extant *Varanus bengalensis* (MNHN 1886–649) in cranial view. Abbreviations: al.pr, alary process of basisphenoid; aVc, anterior orifice of the Vidian canal; bcr.de, basicranial depression; bpt.pr, basipterygoid process; car.can, carotid canal; cr.sel, crista sellaris; fac.art, facet for contact with articular; fac.cor, facet for contact with coronoid; fac.sur, facet for contact with surangular; for.ch.ty, foramen chorda tympani; for.dor.ma.n, foramen for re-entry of the dorsal branch of the mandibular nerve; for.ma.cut.n, foramen for mandibular cutaneous nerve; fov.den, fovea dentalis; gl.fo, glenoid fossa; ma.can, mandibular canal; ma.for, mandibular foramen; me.gr, Meckel's groove; men.for, mental foramen; psph.pr, parasphenoid process; pVc, posterior orifice of the Vidian canal; ret.pr, retroarticular process; r.p, resorption pit; sel.tu, sella turcica; sub.sh, subdental shelf; VI.ant, anterior orifice of the canal for abducens nerve; VI.post, posterior orifice of the canal for abducens nerve.

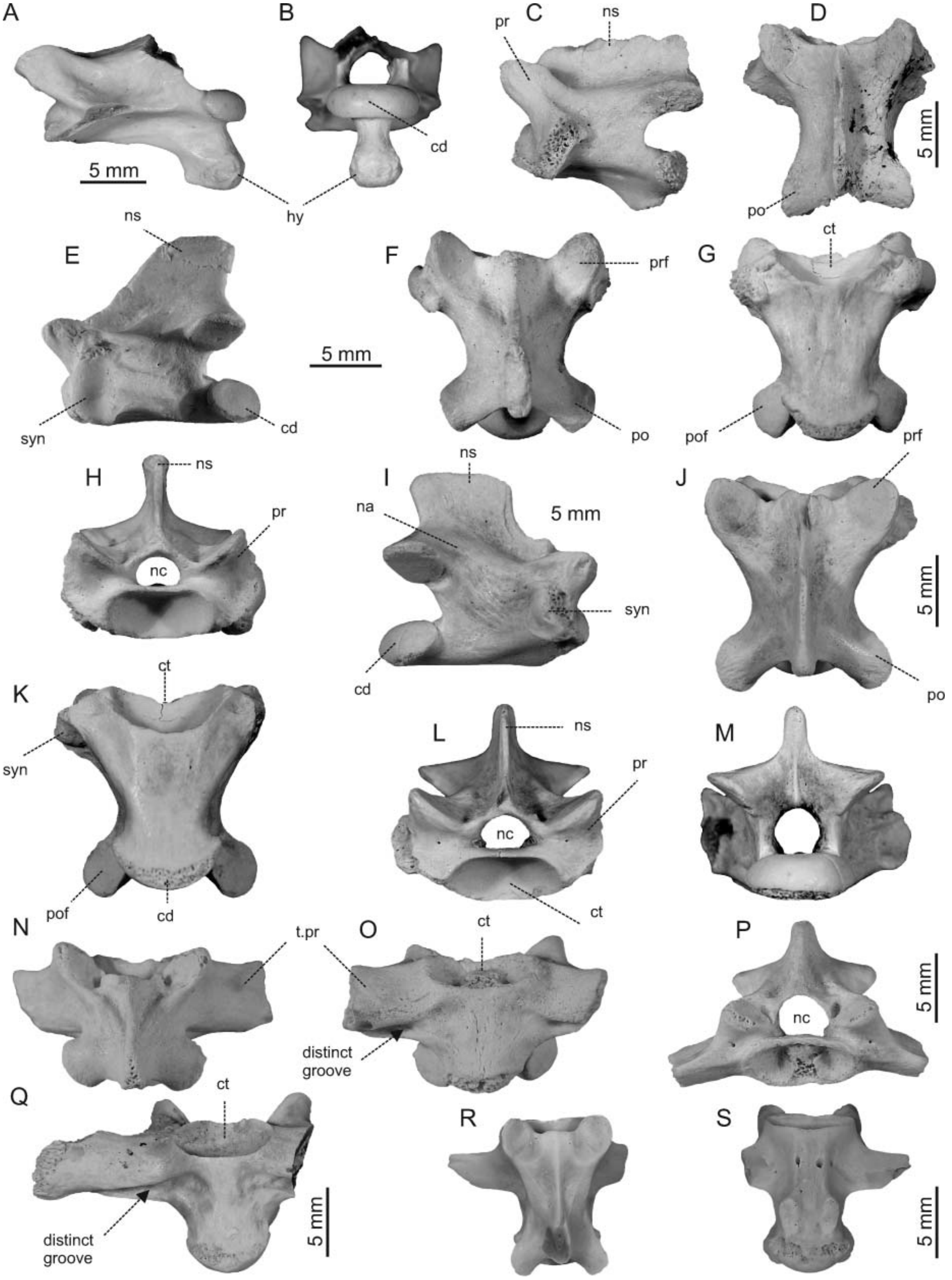

Figure 6. *Varanus mokrensis* sp. nov. **A, B,** Pal. 1040 (1/2001 Turtle Joint), cervical vertebra in lateral (**A**) and caudal (**B**) views; **C, D,** Pal. 1159 (2/2003 Reptile Joint), cervical vertebra in lateral (**C**) and dorsal (**D**) views; **E**–**H,** Pal. 1172 (2/2003 Reptile Joint), anterior trunk vertebra in lateral (**E**), dorsal (**F**), ventral (**G**) and cranial (**H**) views; **I**–**M,** Pal. 1183 (2/2003 Reptile Joint), middle trunk vertebra in lateral (**I**), dorsal (**J**), ventral (**K**), cranial (**L**) and caudal (**M**) views; **N**–**P,** Pal. 1207 (2/2003 Reptile Joint), sacral vertebra in dorsal (**N**), ventral (**O**) and cranial (**P**) views; **Q,** Pal. 1066 (1/2001 Turtle Joint), sacral vertebra in ventral view; **R, S,** Pal. 1215 (2/2003 Reptile Joint), anterior caudal vertebra in dorsal (**R**) and ventral (**S**) views. Abbreviations: cd, condyle; ct, cotyle; hy, hypapophysis; na, neural arch; nc, neural canal; ns, neural spine; po, postzygapophysis; pof, postzygapophyseal articular facet; pr, prezygapophysis; prf, prezygapophyseal articular facet; syn, synapophysis; t.pr, transverse process.

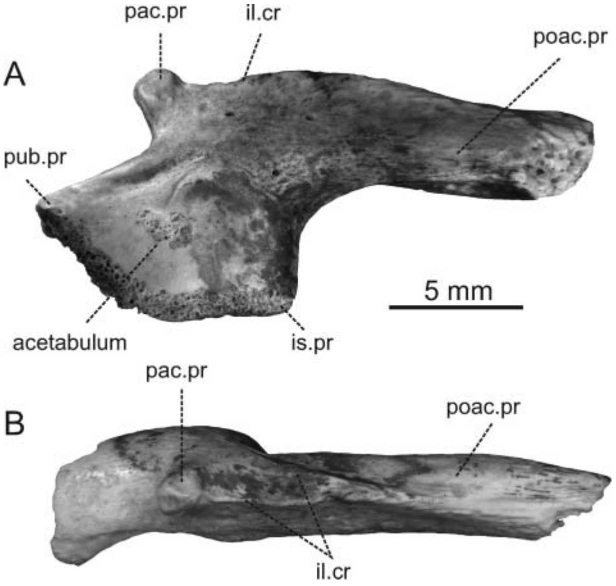

Figure 7. *Varanus mokrensis* sp. nov. **A, B,** Pal. 1154 (2/2003 Reptile Joint), left ilium in lateral (**A**) and dorsal (**B**) views. Abbreviations: il.cr, iliac crest; is.pr, ischial process; pac.pr, preacetabular process; poac.pr, postacetabular process; pub.pr, pubic process.

parietal and the epipterygoid anterodorsally, the supraoccipital posterodorsally, the exoccipital posteriorly, the basioccipital posteroventrally and the basisphenoid anteroventrally. It is irregularly triaxial (Bellairs & Kamal 1981; Rieppel & Zaher 2000), and shows an alary process (processus prooticus anterioris superioris *sensu* Bellairs & Kamal 1981), an anterior inferior process (processus prooticus anterioris inferioris – *sensu* Bellairs & Kamal 1981), and a posteriorly directed posterior process.

In lateral view, the anterior inferior process is dorsoventrally flattened. It is blunt and its anterior surface bears a shallow groove for the articulation with the alary process of the basisphenoid. A distinct rounded trigeminal notch occurs between the anterior inferior and the anterior superior processes. In extant *Varanus*, the shallow groove is adjacent to the posterior narrower part of a membrane perforated by the exit orifice for the trigeminal nerve. The anterior superior process forms a movable articulation with the underside of the lateral bevelled edge of the parietal and with the external dorsal extremity of the epipterygoid. The lateral crest (crista alaris prootici) is wide and blunt. The posterior process of the prootic contacts the external surface of the paroccipital process of the otoccipital. The inferior process of the prootic forms a crest (crista prootica; crista otosphenoidea – *sensu* Bahl 1937) situated dorsal to a deep groove for the jugular vein (sulcus pro vena capitalis lateralis – *sensu* Bellairs & Kamal 1981). A small foramen for the exit of the palatal branch of the facial nerve (VII. pal.) lies in the anterior section of the groove. A much larger foramen for the exit of the hyomandibular branch (VII. hm.) is situated just posterior to the former foramen. In medial view, the cavum vestibulare housing the membraneous labyrinth (utriculus + saculus) has a wide orifice. A somewhat smaller deep cochlear cavity, surrounded by strongly damaged cochlear ridge, occurs on its anteroventral portion.

A large orifice for the vertically orientated anterior semicircular canal is situated at the anterior margin of the vestibular cavity. The orifice for the horizontal semicircular canal occurs inside the vestibular cavity and close to the dorsal margin of the latter, and is situated posteroventral to the orifice of the anterior semicircular canal. The horizontal semicircular canal passes along the external wall of the prootic and continues to the opisthotic portion of the otoccipital, close to the base of the inner margin of the processus prooticus posterioris. One to two minute foramina are situated at the base of the alary process, immediately anteroventral to the foramen for the anterior semicircular canal. A large foramen for the facial nerve (VII) is situated close to the base of the anterior inferior process.

Remarks. The posterior orifice for the Vidian canal of the basisphenoid is situated close to the junction of this bone with the prootic. Such an orifice is also documented in the extinct *V. amnhophilis* and *V. priscus* (Owen, 1859) (Conrad *et al.* 2012, p. 5, fig. 2G, J; Head *et al.* 2009, p. 449). The prootic of *V. mokrensis* generally resembles that of *V. bengalensis* (MNHN 1886-649; MNHN 1884-4; SMF 63456), but differs from the latter (Fig. 4I – see arrow) in showing a more robust lateral edge of the alary process (crista alaris prootici, Fig. 4G – see arrow).

Otoccipital. The otoccipital forms the posterolateral wall of the cerebral cavity and participates in the formation of the posterior wall of the auditory capsule (Fig. 4J–M). A substantial portion of the laterally projecting paroccipital process is formed by the opisthotic (Bellairs & Kamal 1981). The exoccipital portion articulates with the basioccipital ventrolaterally. The opisthotic portion is situated almost at a right angle to the exoccipital, and articulates with the prootic anteriorly and laterally, and with the posterior portion of the supraoccipital dorsally (Bahl 1937; Mertens 1942).

The opisthotic forms a posterolaterally enlarged and ventrally directed process. The dorsally located rounded facet for the junction with the supratemporal occurs at the distal termination of the paroccipital process. The orifice of the horizontal semicircular canal is situated at the base of the paroccipital process. The inner exit of the semicircular canal is situated within the recessus utriculi, in close proximity to the medioventrally situated ampulla anterior, leading to the small orifice for the posterior semicircular canal. The orifice for the posterior semicircular canal is situated at the dorsal surface of the opisthotic portion. A depression on the base of the paroccipital process marks the posterior boundary of the fenestra vestibuli. There is a well-preserved composite foramen for the exit of the cranial nerves X+XI, the entry of the occipital branch of the inner carotid artery, and the exit of the jugular vein. The small foramen for the hypoglossal nerve (XII) is separated from the foramina for cranial nerves X+XI by a bony septum. Small foramina for the nerves XI (dorsally) and XII (ventrally) are situated close to the medial margin of the otoccipital. The crista tuberalis is dorsally arched. The dorsal surface of the paroccipital process bears a deep and laterally enlarged depression posteriorly limited by the distinct lateral occipital crest. The slit-like jugular foramen for the common exit of the jugular vein and cranial nerve X occurs at the posteroventral margin of the otoccipital.

Basioccipital. The basioccipital forms the floor of the posterior portion of the braincase (Fig. 4N). It articulates with the basisphenoid anteriorly and with the exoccipitals laterally.

In ventral view, the anteriorly widened margin of the basioccipital is either slightly convex medially (Pal. 1014) or straight (Pal. 1015). The basipterygoid processes are situated laterally; their anterolateral margins protrude ventrally into the falciform spheno-occipital tubercles (Pal. 1014). The lateral margin of the basioccipital is slightly concave between the basipterygoid process and the strongly damaged occipitocondylar tubercle forming the medial portion of the occipital condyle. The ventral surface of the basioccipital is more or less flat. Distinct depressions are present at the base of the basipterygoid processes of larger specimens (Pal. 1014). The medial crest is indistinct (Pal. 1014). In dorsal view, a shallow oval depression marks the point where the medulla oblongata terminates.

Remarks. It is impossible to distinguish *Varanus* from Mokrá-Western Quarry from extant representatives of *V. bengalensis* on the basis of preserved basioccipitals only. The basioccipital of *Varanus mokrensis* closely resembles that of *V. bengalensis* in the marked posterior displacement of the basipterygoid processes and in the nearly straight margin of the bone in plan view. Although Mertens (1942, p. 183) reported that the basioccipital morphology of *V. bengalensis* is very similar to that of *V. salvator*, the latter species exhibits much more laterally enlarged depressions at the base of its basipterygoid processes (MNHN 1886-284), and the cranial margin of the bone is clearly convex (MNHN 1886-284; ZZSiD 256).

Basisphenoid. The basisphenoid forms the floor of the anterior braincase (Fig. 5A–C). Its straight posterior margin articulates with the basioccipital and, dorsally, with the prootic. The cultriform process (processus parasphenoideus) is not preserved.

In dorsal view, the posteriorly flexed anterior margin of the basicranial depression (crista sellaris; dorsum sellae – *sensu* Rieppel & Zaher 2000) covers the sella turcica. A funnel-like hypophyseal fossa is present in the central portion of the sella turcica. The lateral margins of the basicranial depression protrude anterolaterally into the distinct wedge-like alary processes. A posterior orifice for the abducens nerve (VI) is situated in the anterolateral portion of the basicranial depression. Each basipterygoid process is directed anterolaterally. Its distal extremity widens anteromedially and posterolaterally. The anterior margin of the basicranial depression (crista sellaris) is orientated ventrally and the anterior orifice for the abducens nerve (VI) is situated close to the dorsolateral margin of the sella turcica. The orifice is narrow or even slit-like. The fossa hypophyseos is divided by the distinct vertical retractor crest into two halves; the foramina for the internal carotid artery occur in both halves. The cranial branch of the internal carotid enters these foramina, and passes into the sella turcica. The anterior orifices of the Vidian canals for the transmission of the palatine branch of the internal carotid artery and the palatine branch of the facial nerve (vidian nerve – *sensu* Oelrich 1956) are situated within the slit-like depressions laterally bordered by the short and sharp crests present at the base of the basipterygoid processes. In lateral view, the basipterygoid processes are anteroventrally directed and the posterior orifices of the Vidian canals (pVc – canalis Vidianus posterius) are situated ventral to the crista prootica, about halfway between the base of the basipterygoid process and the posterior border of the bone (Säve-Södenbergh 1947).

Remarks. The angle formed by the basipterygoid processes of the basisphenoid is about 120° in *V. mokrensis*, in contrast to about 90° in the extinct *V. darevskii* (Levshakova 1986, p. 103). The basipterygoid processes of *V. mokrensis* are characterized by a narrow base and enlarged distal extremities, the latter being distally narrower than those of extant African varanids – *V. niloticus* (Linnaeus, 1766), *V. exanthematicus* (Bosc, 1792), *V. albigularis* (Daudin, 1802), and *V. ornatus* Daudin, 1803 (see Mertens 1942; M. Ivanov, pers. obs.). The basisphenoid of *V. mokrensis* resembles most closely that of *V. bengalensis*; however, the posterior orifices of the Vidian canals are smaller in diameter and almost slit-like in *V. mokrensis*, and unlike the relatively large circular orifices observed in extant specimens of Bengal monitors (e.g. MNHN 1886-649). The anterior orifices of the Vidian canals are laterally bordered by distinct crests in *V. mokrensis*, whereas in *V. bengalensis* these crests are either absent or very slightly developed (Fig. 5C, D – see arrows). In cranial view, the ventral margins of the straight basipterygoid processes form an obtuse-angled triangle in *V. mokrensis*, whereas *V. bengalensis* has relatively shorter basipterygoid processes (Fig. 5C, D – see arrows).

Lower jaw. Dentary. Several highly fragmentary dentaries are preserved (Fig. 5E–G). Both the rostral and posterior portions of all fragments are broken. In medial view, the narrow sulcus Meckeli remains open throughout the entire length of the dentary. The best-preserved fragment (Pal. 1140) possesses three tooth positions with two damaged teeth (Fig. 5E, F).

Surangular. One of several preserved surangulars is almost complete; only its posterior margin is missing (Fig. 5H–J). It is a massive and laterally compressed bone (Fig. 5H–K), anteriorly sutured to the dentary, dorsally to the coronoid, ventrally and medially to the splenial and articular, and ventrolaterally to the angular.

In lateral view, a distinct orifice for the mandibular cutaneous nerve (posterior supra-angular foramen – *sensu* Oelrich 1956), being a part of the mandibular division of cranial nerve V, is situated in close proximity to the broken posterior tip of the bone. The canal passes through the posterior portion of the dentary, which is triangular in cross section, and leads into the bone. Another foramen for re-entry of the dorsal branch of the mandibular nerve is situated close to the base of the coronoid process. The slit-like foramen which is visible in anterolabial view is surrounded by the bony tissue of the surangular and situated in a shallow depression. In medial view, there is a distinct groove situated at the anterior termination of the fossa Meckeli. The groove was originally enclosed by the articular from both ventral and medial sides and also by the cuneate angular in its anterior portion. This wide mandibular canal, which is circular in cross section, served for the entry of the inferior main branch of the mandibular nerve (nervus alveolaris inferior) and mandibular artery. At the same time, it served for the re-entry of the mandibular vein (Bahl 1937). The deep groove situated at the anterodorsal portion of the surangular represents the re-entry of the canal for another branch of the mandibular nerve that passes through the entire length of the bone.

Remarks. The distinct foramen for re-entry of the dorsal branch of the mandibular nerve (Fig. 5J) is situated far from the anterior border of the bone. In African varanids, particularly in *V. niloticus* (e.g. MNHN 1964-50), this foramen is situated distinctly anteriorly. It is difficult to observe this foramen in numerous articulated specimens, e.g. *V. albigularis albigularis* (Daudin, 1802) (Mertens 1942, pl. 26, fig. 201) or *V. griseus* (e.g. MNHN 1895-366). The surangular of *V. mokrensis* closely resembles that of *V. salvator* (Laurenti, 1768) (MNHN 1888-198) particularly by the length/height ratio and the convex body of the bone; the surangular of *V. bengalensis* (MNHN 1886-649) and *V. flavescens* (UF 64743) is relatively flat in contrast to that of *V. mokrensis*. However, the foramen for the re-entry of the dorsal branch of the mandibular nerve is situated even more posteriorly in *Varanus* from Mokrá-Western Quarry, approximately halfway between the anterior border of the bone and the orifice of the distinct cutaneous nerve.

Articular. The articular is an elongated bone whose massive retroarticular process extends far behind the quadrate/articular joint (Fig. 5L, M). Only the posterior portion of the bone is preserved; it has a distinct transversely concave glenoid fossa. The retroarticular process is long and stout and its distal extremity widens posteriorly. A well-developed retroarticular fossa is situated posterior to the articular facet. An aperture for the entrance of the chorda tympani branch of cranial nerve VII occurs within the fossa.

Dentition (Figs 2C–F, 5E–G)**.** The teeth are conical and laterally flattened. They have mesiodistally broadened bases with distinctly developed longitudinal striations (as a result of furrowed plicidentine). The tooth bases of the fully developed teeth are either massive with small resorption pits or are formed by a system of laminae indicating an advanced stage of resorption preceding the tooth replacement (Rieppel 1978). Distinct and sharp cutting edges are present at the mesial and distal margins of the tooth crown; the surface of the cutting edge is smooth.

Remarks. The most immediately recognizable trait of the *Varanus mokrensis* dentition is the distinctly developed smooth cutting edge along the mesial and distal margins of the apical part of the tooth crown. Most of the extant Asiatic varanids have developed trenchant and posteriorly directed teeth with serrated cutting edges. Varanids with a molariform dentition show adaptations to durophagy (e.g. extant *V. niloticus*, *V. exanthematicus*, *V. olivaceus* and extinct *V. rusingensis*; Mertens 1942; Rieppel & Labhardt 1979; Clos 1995) and may have developed a short cutting edge without indentation, but this character was observed only in subadult specimens (Ivanov 2009). In members of the closest outgroup to *Varanus* (i.e. platynotan representatives of *Lanthanotus*, Helodermatidae and Anguidae) the cutting edge is either absent or developed (but lacks indentation). Therefore, it is possible to presuppose that the presence of the smooth edge in adult specimens of *Varanus* represents plesiomorphic condition.

Postcranial skeleton

Cervical vertebrae. Most of the preserved cervical vertebrae are fragmentary, usually with broken neural spines and hypapophyses (Fig. 6A–D). The height of the neural spine depends on the position within the cervical region of the vertebral column. In lateral view, the posterior cervical vertebrae with distally broken neural spines were characterized by neural spines probably as anteroposteriorly long as dorsoventrally high, or somewhat lower in the cranio-caudal direction. Anterior cervical vertebrae possess distinctly anteroposteriorly enlarged and conspicuously low neural spines. Anteriorly, the neural spine reaches the anterior margin of the neural arch. Posteriorly, the neural spine extends as far as the posterior termination of the neural arch. The bases of the transverse processes are directed laterally. The anterior margin of the hypapophysis extends as a low ridge as far as the vicinity of the cotylar rim. The hypapophysis distinctly rises at about centrum midlength. In dorsal view, the oval prezygapophyseal articular facets extend laterally to form the wide prezygapophyseal area. The interzygapophyseal constriction occurs at about vertebral mid-length. In ventral view, the anterior margin of the vertebral centrum base is widened laterally and gradually passes into the transverse process. The posterior margin of the centrum is narrow anterior to the laterally wide condylar base. In anterior view, the neural arch is moderately vaulted. Its anterior margin is triangular to slightly round in cross section and is situated between the markedly dorsally tilted prezygapophyses. The cotyle is prominently depressed dorsoventrally. The distal termination of the hypapophysis is pear shaped and is distinctly developed particularly in the posterior cervical vertebrae.

Remarks. Fragmentary cervical vertebrae of *Varanus mokrensis* have developed hypapophyses with laterally widened distal terminations. This is typical for all representatives of the genus *Varanus*. Several fragmentary vertebrae from the cervical region indicate that the neural spine of *Varanus mokrensis* was low and antero-posteriorly distinctly enlarged in contrast to all observed extant representatives of Indo-Asiatic group (Ast 2001). In this respect, cervical vertebrae of *V. mokrensis* resemble extant *V. griseus* recently inhabiting Africa and southwestern Asia.

Trunk vertebrae. Numerous well-preserved trunk vertebrae enable studies of the intracolumnar variability, particularly as regards the shape of the neural spine (Fig. 6E–M). In lateral view, the neural spine of the middle trunk vertebrae is about two to three times anteroposteriorly longer than tall. Its anterior margin is posterodorsally inclined; this inclination is more distinct in the posterior trunk vertebrae. Therefore, the distal termination of the neural spine is relatively short in the posterior trunk vertebrae. The synapophyses are massively built and markedly large in several vertebrae. The lateral foramina, which occur close behind the posterodorsal margin of synapophyses, are very small and indistinct. In dorsal view, the interzygapopyseal constriction occurs about at two-thirds of the vertebra length close before the posterolaterally directed and laterally relatively narrow postzygapophyses (compared to prezygapophyses). The prezygapophyses are strongly laterally widened, and the prezygapophyseal articular facets are of anterolaterally enlarged oval shape. The dorsal margin of the neural spine is posteriorly slightly laterally thickened. In ventral view, the vertebral centrum is elongated and wide anteriorly whereas the basal portion of the markedly laterally widened condyle is strongly constricted. Synapophyses are directed laterally. In cranial view, the prezygapophyses are conspicuously tilted dorsally, the synapophyses are short and directed laterally. The neural arch is moderately vaulted and its roof-like posterior margin rises dorsally to the base of the neural spine. The neural canal is irregularly circular to subtriangular in cross section. The cotyle is depressed dorsoventrally. Small paracotylar foramina are developed in depressions at both sides between the cotyle and upraising base of the prezygapophyses in many vertebrae. In some cases, the foramina are not paired and they are often absent.

Sacral vertebrae. All sacral vertebrae are fragmentary (Fig. 6N–Q). In ventral view, they differ from the vertebrae of the trunk region by the distinctly shorter centrum length/neural arch width ratio. The dorsoventrally depressed transverse processes are not distally narrowed. Typical is the presence of a groove at the posterior margin of the transverse processes. This groove is strongly widened medially. In posterior view, the condyle is distinctly laterally widened with a wide and shallow medial groove extending dorsoventrally.

Caudal vertebrae. Several preserved caudal vertebrae are fragmentary and with a broken neural spine (Fig. 6R, S). Rarely preserved isolated neural spines are posterodorsally strongly elongated. In dorsal view, the prezygapophyseal articular facets are oval and the dorsoventrally flattened transverse processes are directed laterally.

Ilium. One almost complete left ilium is characterized by the distinct bifurcated iliac crest situated dorsal to the acetabulum (Fig. 7A, B). In lateral view, the postacetabular process is massively built with a dorsoventrally wide base. The preacetabular process is prominent with a blunt termination; it is directed at a right angle to the pubic process of the ilium. The posterior margin of the ischial process is perpendicular to the direction of the posteriorly projected postacetabular process.

Comparisons and discussion

Five extinct species of the genus *Varanus* – *V. hofmanni*, *V. amnhophilis*, *V. marathonensis*, *V. darevskii* and *V. sivalensis* (eastern European taxa with poor description or illustration are excluded) – are known from Eurasia, and two of these have been recorded from adjacent territories in eastern Europe and Asia: *Varanus darevskii* from

Tadjikistan (Levshakova 1986) and *V. sivalensis* from India (Falconer 1868; Hocknull *et al.* 2009). Of these two species, only *Varanus darevskii* is known from cranial material (albeit incompletely preserved; Levshakova 1986). The two south-east European species, *V. amnhophilis* and *V. marathonensis*, are generally acknowledged to represent valid species; the latter one, however, needs revision. The new species of *Varanus* from Mokrá-Western Quarry differs from all known extinct (including *V. darevskii*, *V. hofmanni*, *V. amnhophilis*, *V. marathonensis*, *V. sivalensis*, *V. hooijeri* (Indonesia; Brongersma 1958), *V. rusingensis* (Kenya) and *V.* (= *Megalania*) *priscus* (Australia; Owen 1859, 1880; Molnar 1990, 2004)) and extant species in one autapomorphic character, which is the distinctly sharp angle between the parietal and squamosal processes of the postorbitofrontal (Fig. 3A, D – see arrows). However, as regards extinct species of *Varanus*, the postorbitofrontal is preserved only in *V. darevskii*.

Furthermore, *Varanus mokrensis* differs from all known species of *Varanus* by the following combination of characters:

1. The septomaxilla is short with a flat dorsal surface.

Remarks. In *Varanus mokrensis*, the septomaxilla is shorter and anteroposteriorly enlarged and the dorsal ridge is absent compared with that in *V. darevskii*; in all remaining seven extinct species, the septomaxilla is not preserved. If compared to extant species, the septomaxilla of *Varanus mokrensis* resembles only that in *V. bengalensis* by a particularly posteriorly enlarged medial process (Fig. 2G). The process is about twice as long as the lateral process. However, *V. mokrensis* differs from *V. bengalensis* by the flat dorsal surface of the septomaxilla, whereas in *V. bengalensis* this dorsal surface is concave with a very distinct crest emarginating the lacrimal duct and extending as far as the posterior border of the bone. Either the medial process of the remaining representatives of the genus *Varanus* is distinctly shorter, or the lateral process is only slightly developed (Mertens 1942). Although the rostral process of the septomaxilla is damaged in *V. mokrensis*, it may be estimated that it was shorter compared with that in extant specimens of *V. bengalensis* (e.g. MNHN 1884-4; SMF 60428; see also Bahl 1937; Mertens 1942; Bellairs 1949). The short septomaxilla indicates that the snout portion of the skull of *V. mokrensis* was probably relatively short, similar to that of *V. olivaceus* (UF 57536; SMF 72156), *V. flavescens* (UF 64743; SMF 11546) and especially extant Australian varanids of the subgenus *Odatria* (W. Böhme 2003; Mertens 1942, pp. 156–158).

2. The frontal and anterolaterally directed postorbital processes of the postorbitofrontal form an obtuse angle.

Remarks. The postorbitofrontal is not preserved in other extinct species. In extant species, an obtuse angle between the frontal and anterolaterally directed postorbital process of the postorbitofrontal occurs in *Varanus olivaceus* (SMF 72156), *V. salvadorii* (SMF 58064), and Australian *V. mertensi* (SMF 53275) and *V. giganteus* (SMF 53263). The postorbitofrontal of *V. mokrensis* differs from those in the above-mentioned species by the distinctly sharper angle between the parietal and squamosal processes of the postorbitofrontal.

3. The posterior margin of the nasal lobe of the frontal is situated mid-way along the rostral process width.

Remarks. In extinct *V. darevskii* the nasal lobe is situated at the medial margin of the bone. Moreover, the frontal narrows in the middle of the orbit length (Levshakova 1986), unlike in *V. mokrensis*. The nasal lobe of the massively built frontal of extinct *V. priscus* is also situated in the middle of the rostral process width. However, the frontal of *V. priscus* is short and laterally wide with the prominent sagittal crest along the median suture between the frontals (Molnar 1990), contrary to *V. mokrensis*. In all six remaining extinct species, the frontal is not preserved. In extant species, the nasal lobe situated mid-way along the rostral process width occurs in adult specimens of *Varanus salvator* (e.g. NHMUK 64.9.2.77), *V. jobiensis* (SMF 75817) and *V. olivaceus* (Ahl, 1932) (SMF 72156). However, *V. mokrensis* differs from *V. salvator* by the distinctly narrower posterior half of the bone. In *V. jobiensis*, the facet for contact with the prefrontal is situated far from the facet for contact with the postorbitofrontal, and the lateral descending process is massively built, compared with *V. mokrensis*. In *V. olivaceus*, the frontal is relatively wide and short, in contrast to *V. mokrensis*.

4. The posterior margin of the anteroposteriorly enlarged frontal is narrow.

Remarks. The same condition occurs in extinct *V. darevskii* which differs from *V. mokrensis* by the medial position of the nasal lobe and frontal constriction in the middle of the orbit. In *V. priscus*, the posterior margin of the relatively short and massively built frontal is distinctly laterally wide, contrary to the slender frontal of *V. mokrensis*. The narrow posterior margin of the anteroposteriorly enlarged frontal occurs in extant *Varanus indicus* (Daudin, 1802); SMF 11635, *V. doreanus* (Meyer, 1874); SMF 33290, and Australian *V. gilleni* (Lucas & Frost, 1895) (SMF 11627) and *V. gouldii gouldii* (Gray, 1838); SMF 59018. In the frontal of *V. indicus*, the axis of the relatively short nasal lobe is directed posterolaterally, in contrast to the posteriorly directed nasal lobe in *V. mokrensis*. *Varanus mokrensis* differs from *V. doreanus* by the more distinctly developed nasal lobes, whereas nasal lobes in *V. doreanus* are markedly short. The body of the frontal is clearly narrower in *V. gilleni* and *V. gouldii gouldii* if compared to *V. mokrensis*. The frontal of *Varanus mokrensis* is particularly similar to that of *V. bengalensis* (Mertens 1942, pl. 22, pp. 160, 161; SMF 60428; MNHN 1886-649), although the body of the bone is more slender in *V. mokrensis*. In *V. mokrensis*, the posterior margin of the nasal lobe is situated mid-way along the rostral process width. In adult specimens of *V. bengalensis*, the nasal lobe occurs close to the lateral margin of the rostral process (MNHN 1886-649). The posterior margin of the frontal of *V. mokrensis* is relatively narrow, if compared with that of *V. bengalensis* (MNHN 1886-649; Mertens 1942, pl. 22, pp. 160, 161).

5. Parietal with wide, roughly rectangular fronto-postfrontal processes, and anteriorly arched fronto-parietal suture, and with the parietal foramen situated posteriorly far from the anterior margin of bone (more than one-third of the parietal plate length).

Remarks. Regarding extinct species, the parietal is known in *V. darevskii*, *V. rusingensis*, *V. hooijeri* and *V. priscus*. *Varanus darevskii* lacks wide fronto-postfrontal processes. *Varanus rusingensis* (and possibly *V. hooijeri*) has developed wide fronto-postfrontal processes; however, both species differ from *V. mokrensis* by the much more developed constriction of converging parietal crests. *Varanus priscus* differs from *V. mokrensis* by its much larger dimensions, more slender fronto-postfrontal processes, the presence of a straight frontoparietal suture, and the parietal foramen situated close to the anterior margin of the bone (Molnar 1990). Regarding extant species, the wide, roughly rectangular fronto-postorbitofrontal process of the parietal occurs only in *Varanus bengalensis* (e.g. SMF 63456), *V. flavescens* (e.g. SMF 11546) and *V. rudicollis* (Gray, 1845); e.g. SMF 59216. All of the above-mentioned species possess a straight frontoparietal suture, whereas in *V. mokrensis* this suture is arched anteriorly. *Varanus mokrensis* further differs from *V. bengalensis* by the greater distance between medially converging parietal crests. The shortest distance between the medially converging parietal crests is situated very close to the posterior border of the parietal plate in *V. flavescens*, contrary to *V. mokrensis* in which this constriction is shifted to the posterior quarter of the parietal plate length. Moreover, the parietal foramen is situated more anteriorly in *V. flavescens* if compared to *V. mokrensis*.

6. Distance between the medially converging parietal crests of the parietal is the shortest in the posterior fourth of the parietal plate.

Remarks. The distance between the supratemporal fossae (measured at the level of the narrowest portion of the parietal), in the posterior quarter of the parietal plate, is distinctly shorter in *Varanus mokrensis* in contrast to extinct *V. darevskii* (Levshakova 1986, p. 104, fig. 2), but not as short as in extinct *V. rusingensis* (Clos 1995, p. 256, fig. 1A), *V. hooijeri* (Brongersma 1958, pl. IV/1) and *V. priscus* (Molnar 1990, p. 440, fig. 2C, D). The same distance between the medially converging parietal crests as observed in *V. mokrensis* occurs in extant *V. griseus* (Mertens 1942, pl. 22, p. 162; NMP 22180; NMP 22948; NMP 22181; MNHN 1895-366) and *V. rudicollis* (SMF 59216; SMF 67586). *Varanus mokrensis* differs substantially from *V. griseus* by the presence of a wide, roughly rectangular fronto-postorbitofrontal process, which is narrow in *V. griseus*, and by the narrower and anteriorly arched margin of the frontoparietal suture. The frontoparietal suture is straight in *V. rudicollis*.

7. Otoccipital with very distinct occipital crest at base of the paroccipital process.

Remarks. Regarding extinct species, the otoccipital is known only in *V. amnhophilis* and *V. priscus*. In *V. mokrensis*, the paroccipital process of the otoccipital is relatively long and massively built, with a distinctly ventrally enlarged distal termination which is similar to that of extinct *V. amnhophilis* (Conrad *et al.* 2012, p. 5, fig. 2G–I). In *V. priscus*, the otoccipital is rather fragmentary with a broken distal termination (Head *et al.* 2009, p. 448, fig. 1). Both extinct species lack the distinct depression on the dorsal surface of the paroccipital process which is conversely present in *V. mokrensis*. The massively built and distally enlarged paroccipital process of the otoccipital occurs in extant Asiatic varanids of the *V. bengalensis* group, in particular *V. bengalensis* (e.g. MNHN 1886-649; MNHN 1884-4) and *V. flavescens* (e.g. UF 64743), as well as *V. salvator* (Laurenti, 1768); NHMUK 1961.1761, *V. olivaceus* (e.g. UF 53917) and *V. salvadorii* (Peters & Doria, 1878); SMF 67670. However, the depression at the dorsal surface of the paroccipital process is never as distinct as in *Varanus mokrensis*. Moreover, the elongate and prominent posterior occipital crest in *V. mokrensis* is directed distinctly lateroventrally and is straight along most of its length. These features are not present in extant representatives of the genus *Varanus*.

8. Pointed conical teeth with distally recurved apices and prominent smooth mesial and distal cutting edges.

Remarks. The distinct and smooth mesial and distal cutting edges in pointed teeth do not occur in extinct *V. rusingensis*, *V. hooijeri* and *V. priscus* (Clos 1995; Brongersma 1958; Anderson 1930; Hecht 1975) or in *Varanus* sp. from Gratkorn (M. Böhme & Vasilyan 2014). In the remaining extinct species the teeth are unknown. As regards extant species, the smooth cutting edges occur in several species of subgenera *Odatria* Gray, 1838, *Empagusia* Gray, 1838 and *Varanus*: *V.* (*Odatria*) *timorensis*

(Gray, 1831), *V.* (*O.*) *tristis* (Schlegel, 1839), *V.* (*O.*) *eremius* Lucas & Frost, 1895, *V.* (*O.*) *caudolineatus* Boulenger, 1885, *V.* (*Empagusia*) *nebulosus* (Gray, 1831), *V.* (*E.*) *rudicollis* and *V.* (*V.*) *giganteus* (Gray, 1845). *Varanus mokrensis* differs from the above-mentioned *Varanus* (*Odatria*) species by the anteroposteriorly wider base of the subrectangular frontal-postorbitofrontal process of the parietal and a distinctly higher ratio of the maximum parietal roof width to the narrowest portion of the parietal roof. *Varanus mokrensis* differs from *Varanus* (*Empagusia*) species in its distinctly shorter septomaxilla; moreover, the parietal roof of *V.* (*E.*) *rudicollis* is laterally wide and anteroposteriorly short relative to that of *V. mokrensis*. The new taxon differs from *V.* (*V.*) *giganteus* in the shortest distance between the medially converging parietal crests in the posterior quarter of the parietal plate, whereas in *V. (V.) giganteus* the same constriction is situated much more anteriorly (SMF 53263).

9. Trunk vertebrae with moderately developed depression between pars tectiformis and medial margin of prezygapophyses and posterolaterally directed postzygapophyses which form a right angle.

Remarks. The trunk vertebrae have distinctly smaller dimensions compared with those of extinct *Varanus amnhophilis*, *V. marathonensis*, *V. sivalensis* and *V. priscus*. The precondylar constriction (81% of the condylar width, n = 9) is less distinct compared with *V. amnhophilis* (75% in the first and 77% in the second preserved dorsal vertebra; Conrad *et al.* 2012), *V. hofmanni* (78%, type specimen NMA 86-471) and *V. rusingensis* (78%, n = 7; Clos 1995). Moreover, *V. mokrensis* exhibits postzygapophyses that are narrow compared with the prezygapophyses, in contrast to the conditions in *V. sivalensis* and *V. marathonensis* (Hocknull *et al.* 2009; Fejérváry 1918; Rage & Sen 1976). *Varanus mokrensis* differs from extinct *V. hofmanni* and *Varanus* sp. from Gratkorn (M. Böhme & Vasilyan 2014) by the less markedly developed depression between the pars tectiformis and the medial margin of the prezygapophyses, as well as by the posterolaterally directed postzygapophyses which delimit a right angle. Regarding extant species, the trunk vertebrae of *V. mokrensis* closely resemble those of *V. griseus* (NMP 22180, 22181 NMP) in the width of pre- and postzygapophyses and angle, which together form left and right postzygapophysis. However, the posterior part of the neural arch of the extant *V. griseus* rises less conspicuously than that of *V. mokrensis*.

10. Preacetabular process of the ilium prominent and directed at a right angle to the pubic process.

Remarks. Regarding extinct taxa, the ilium is known only in *V. rusingensis* (Clos 1995, p. 256, fig. 1E) and *V. priscus* (Hecht 1975, pp. 243–244). *Varanus rusingensis* differs from *V. mokrensis* by the less massively built and much more anteriorly inclined preacetabular process. In *V. priscus* this process is very long, knob-like and oriented horizontally, unlike in *V. mokrensis*. The prominent preacetabular process of the ilium, which is directed anterodorsally rather than anteriorly and forms a right angle to the long pubic process, is known in extant Asiatic *V. bengalensis* (MNHN 1886-649) and Australian *V. varius* (White, 1790); MNHN 1851-853. *Varanus bengalensis* differs from *V. mokrensis* in the absence of a distinct and very long bifurcated iliac crest. In *V. varius* the acetabular part of the ilium is much smaller than that of *V. mokrensis.*

11. Bifurcated iliac crest prominent.

Remarks. In *V. rusingensis* and *V. priscus*, the bifurcated iliac crest is absent. Moreover, the excavation situated on the inner surface below the iliac crest is prominent in *V. rusingensis*, whereas in *V. mokrensis* this excavation is shallow. Regarding extant representatives, the distinctly developed bifurcated iliac crest is absent in *Varanus bengalensis* (MNHN 1886-649). In *V. varius*, the acetabular part of the ilium is much smaller compared with *V. mokrensis*.

Results

Body size estimation

The average SVL/DVL for the extant Indo-Asiatic A clade of *Varanus* (Conrad *et al.* 2012, table 1) is 36.22 (standard deviation [SD] of 2.562; y intercept [yi] = 42.21; x intercept [xi] = −64.96; $R^2 = 0.994$). If *V. mokrensis* is scaled similarly to other 'Indo-Asiatic A'-clade (Ast 2001) *Varanus*, we estimate (Fig. 8) its length as 374.9 mm (± 19.94 mm with a 95% confidence interval) based on the length of the posterior dorsal vertebra (DVL). Based on the data concerning extant representatives of *Varanus* (Pianka *et al.* 2004; Conrad *et al.* 2012, table 2), *V. mokrensis* was a medium-sized monitor.

Phylogenetic analysis

Complete lists of characters and character states are reported in Supplemental Appendices 1, 2 and 3. We analysed 449 morphological characters coded for 87 taxa. The coding comes from Conrad *et al.* (2012). Safe taxonomic reduction identified six 'unstable' taxa, including five species of *Varanus* present in the analysis of Conrad *et al.* (2012), namely: B. Qarun, *V. bivittatus*, *V.* cf. *marathonensis* (topotypic fragmentary skull where a possible association with the holotypic vertebra needs a revision – Rage & Sen 1976; Estes 1983; Conrad *et al.* 2012),

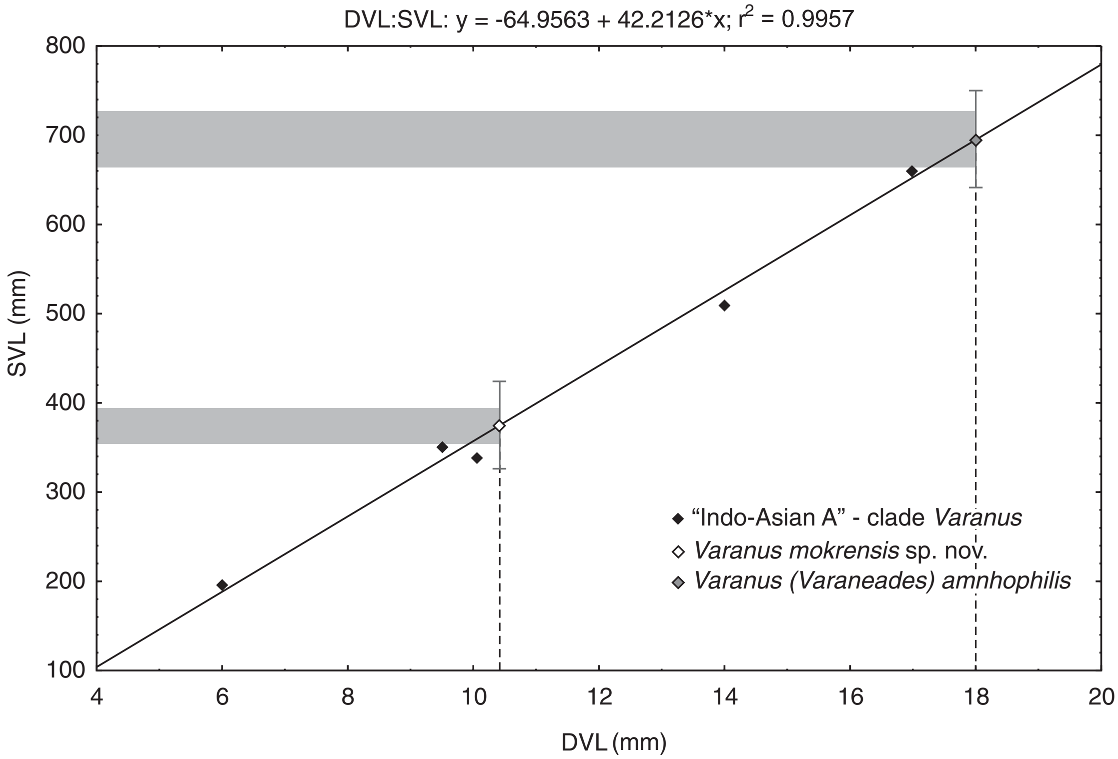

Figure 8. Body size estimation (snout-vent length, SVL) of *Varanus mokrensis* sp. nov. and *Varanus amnhophilis* (AMNH FR 30630) based on comparison of posterior dorsal vertebra length (DVL). The solid black trend line was calculated using extant species (see Conrad *et al.* 2012, table 1) from the 'Indo-Asiatic A' clade of *Varanus* (SVL/DVL, y intercept [yi] = 42.21, x intercept [xi] = -64.96, R^2 = 0.996). Grey bars indicate predictive size range within 95% confidence interval; the vertical bars indicate predictive size range within 95% prediction interval.

V. keithhornei (Wells & Wellington, 1985), *V. marathonensis* (holotypic trunk vertebra – Rage & Sen 1976; Estes 1983) and *V. panoptes horni* (Böhme, 1988). These taxa were excluded from the maximum parsimony analyses. Maximum parsimony analyses were terminated when a maximum of 50,000 trees were obtained. The unweighted analysis yielded hardly any resolution. The reweighted strict consensus of 3136 trees shows very poor resolution within the *Varanus* clade (Fig. 9), with the only exception being a relatively well-supported Indo-Australian *Odatria* clade. Although the topology of the majority consensus tree derived from the reweighted analysis also showed poor resolution (Fig. 10), it showed that most extant African species, together with the extinct *V. rusingensis* from the early Miocene (MN 3 Zone) of Kenya (Clos 1995), belong to a well-supported (but rather unresolved) clade. This clade forms the sister group to the extant *V. rosenbergi* (Mertens, 1957). *Varanus mokrensis* is a member of a lineage that is ancestral to most African species, including *V. exanthematicus*, *V. ornatus*, *V. niloticus* and *V. albigularis*. As regards the results of the Bayesian analyses (Figs 11, 12), the analysis that employed gamma rates (Fig. 12) showed generally better resolution, with a relatively well-supported Indo-Australian clade as well as an Indo-Asiatic A clade (see Ast 2001), including a well-supported *Soterosaurus* clade.

Bayesian analyses run with equal and gamma rates show *V. mokrensis* to be a member of the extant representatives of the Indo-Asiatic A clade of *Varanus* with close affinities to the *V. bengalensis* species group (*Empagusia* clade; see W. Böhme 2003 and Koch *et al.* 2013). The topology of the Bayesian tree using both rate types supports the hypothesis that Miocene monitors from Mokrá are representatives of a lineage ancestral to the extant African varanids plus the early Miocene *V. rusingensis* (Figs 11, 12). There are six well-documented trans-Tethyan mammal dispersal phases between Eurasia and Africa throughout the Palaeogene, with the last important dispersal phase (from Laurasia to Africa) at the Priabonian/Rupelian boundary (Gheerbrant 1987, 1990, 2001; Gheerbrant & Rage 2006). It is possible that the first representatives of varanids might have dispersed into Africa from Eurasia as early as the late Eocene, i.e. long before the initial rifting and formation of the Eritrean Red Sea in the late Oligocene (27.5–23.8 Ma; Bosworth *et al.* 2005). This assumption is supported by the fact that most outgroup members of the genus *Varanus* come from Eurasia. The oldest known varanids with possible affinity to

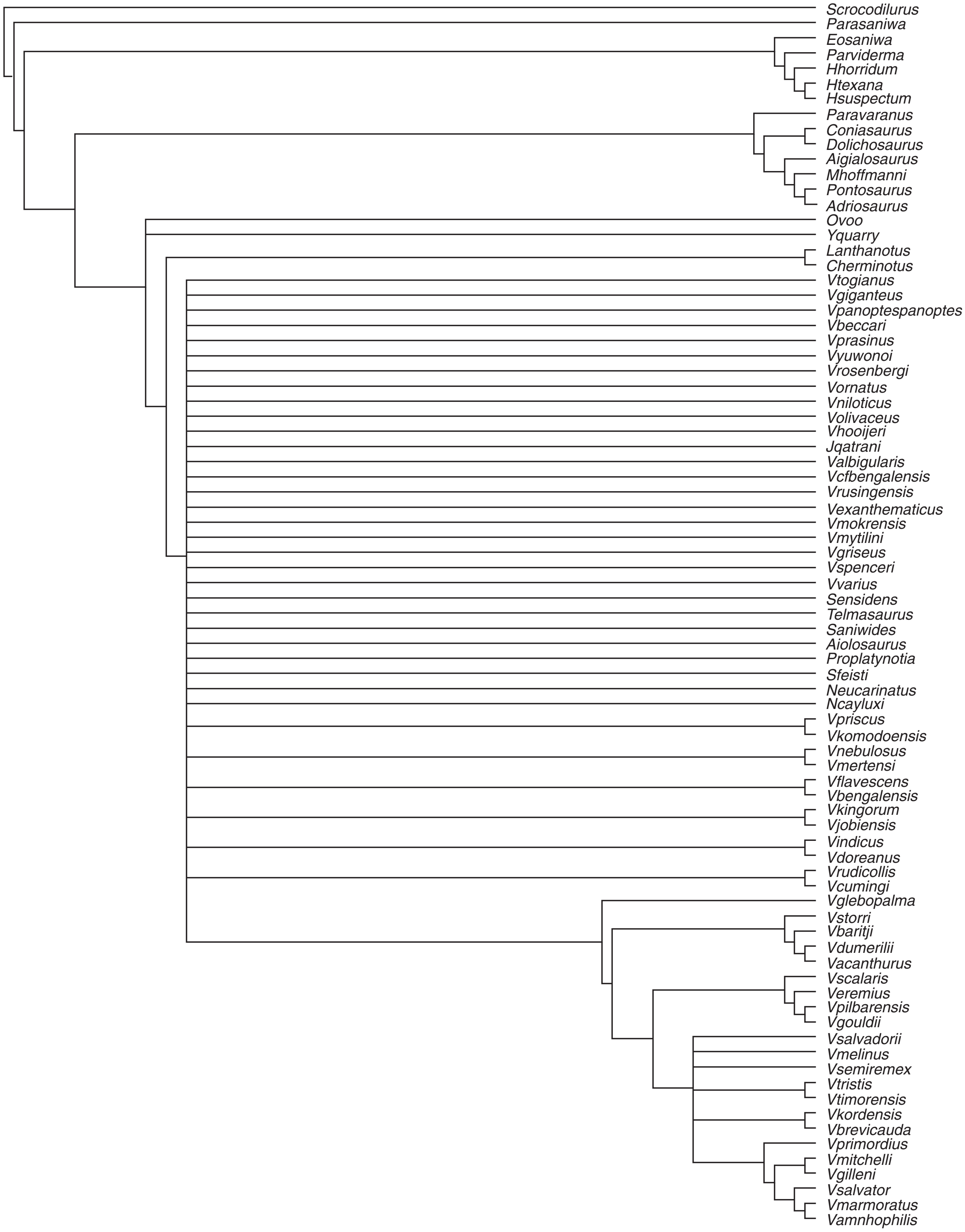

Figure 9. Reweighted strict consensus tree.

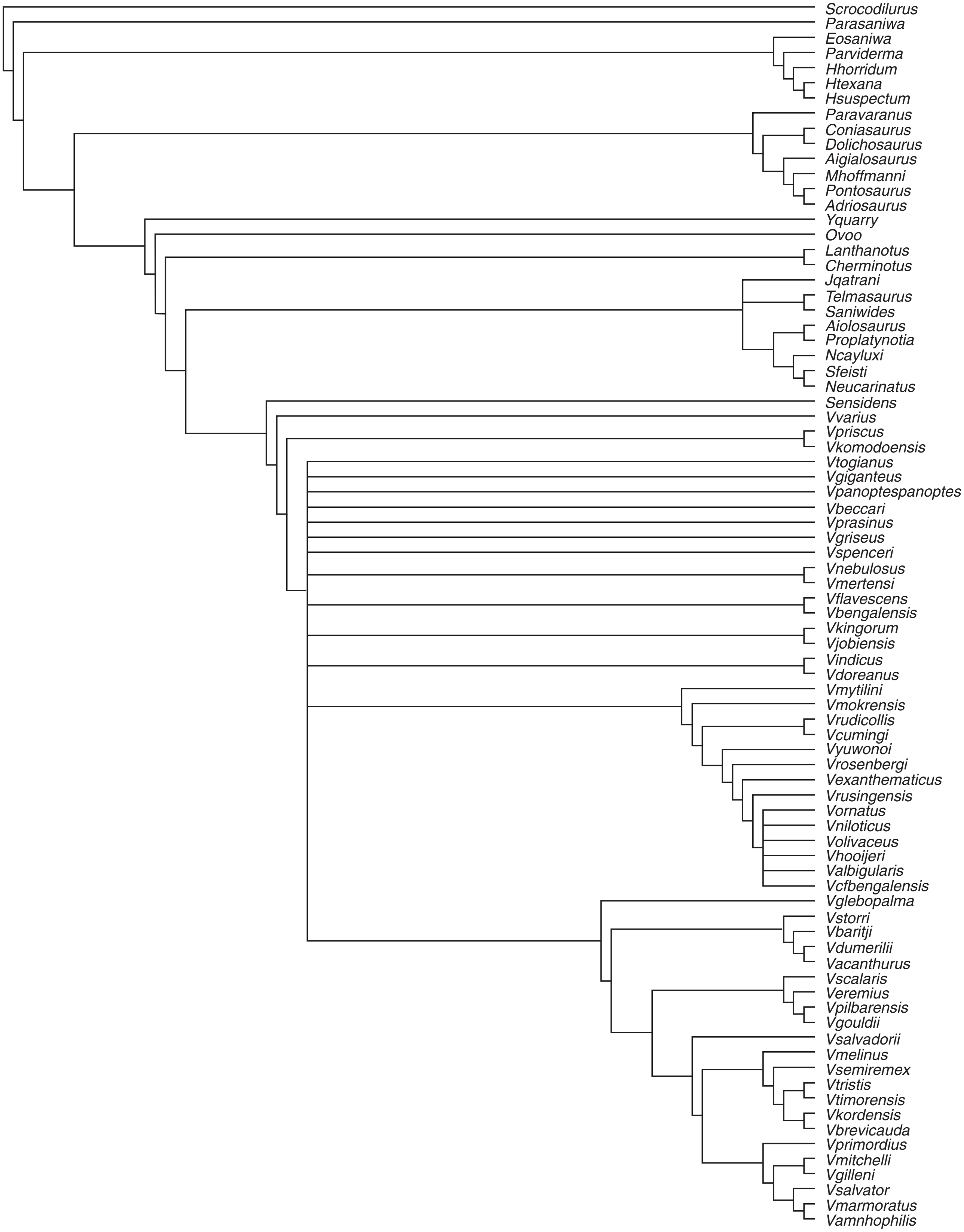

Figure 10. Reweighted majority consensus tree.

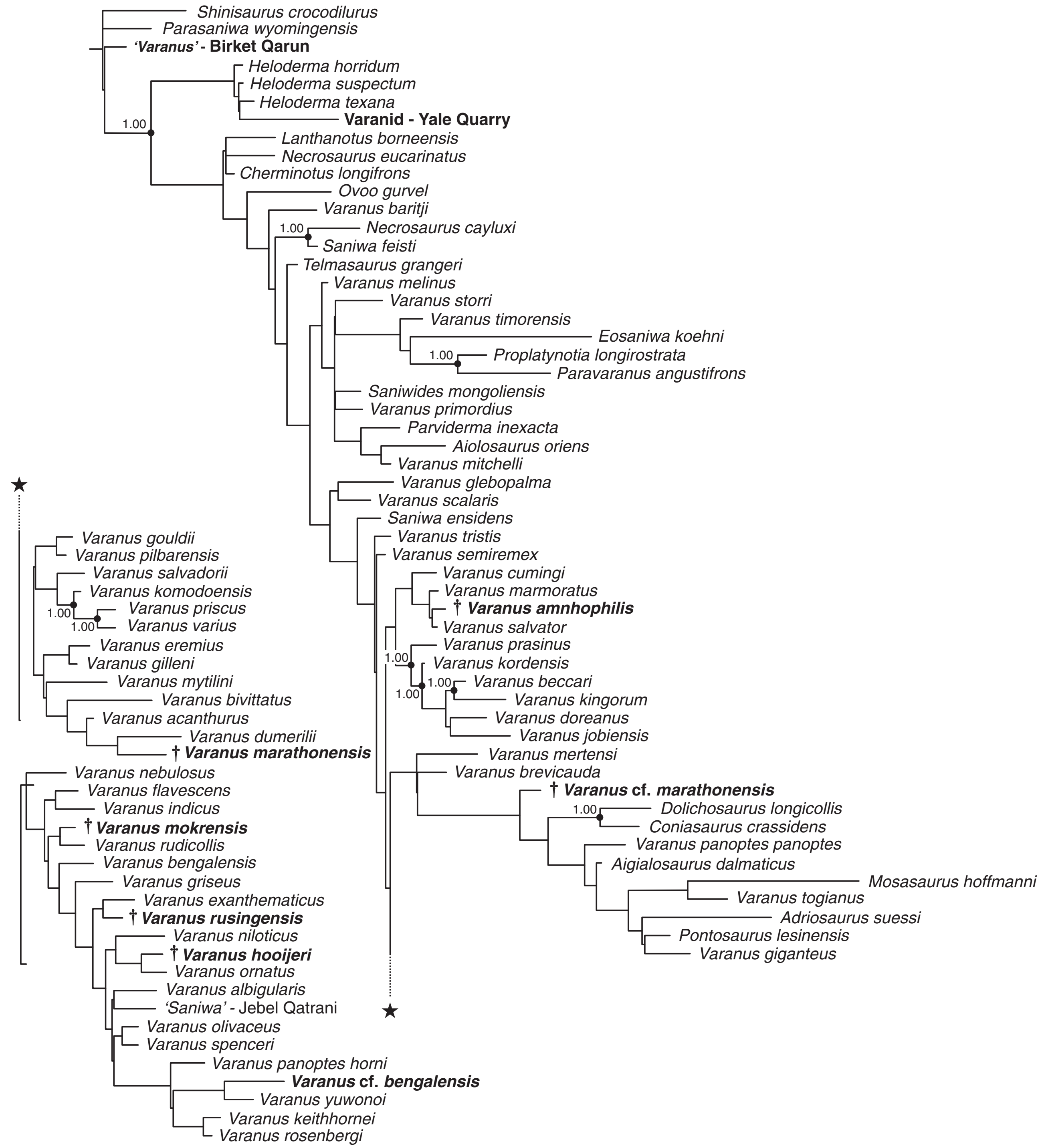

Figure 11. The majority rule of consensus topology used in the Bayesian analysis (without constraints). Bold – fossil varanids; † – extinct *Varanus* species; black dots – posterior probability (PP) 100%, remaining nodes 50%.

African monitors are known from isolated vertebrae from the late Eocene Birket Qarun Formation (Holmes *et al.* 2010) and the early Oligocene Jebel Qatrani Formation, both in the Fayum Province, Egypt (*Varanus* stem-clade, probably closely related to *Saniwa*; Smith *et al.* 2008). Although findings of the late Eocene varanids coincide with nuclear DNA estimates of the origination of *Varanus* (40.1 Ma; Portik & Papenfuss 2012), the phylogenetic position of these taxa is uncertain (Figs 11, 12; Conrad *et al.* 2012). It is plausible that the radiation of Eurasian varanids into Africa continued throughout the Oligocene, and multiple colonization events of Africa (probably via the Arabian Peninsula) cannot be excluded. The position of the early Miocene (~17–18 Ma; Sabol *et. al.* 2007)

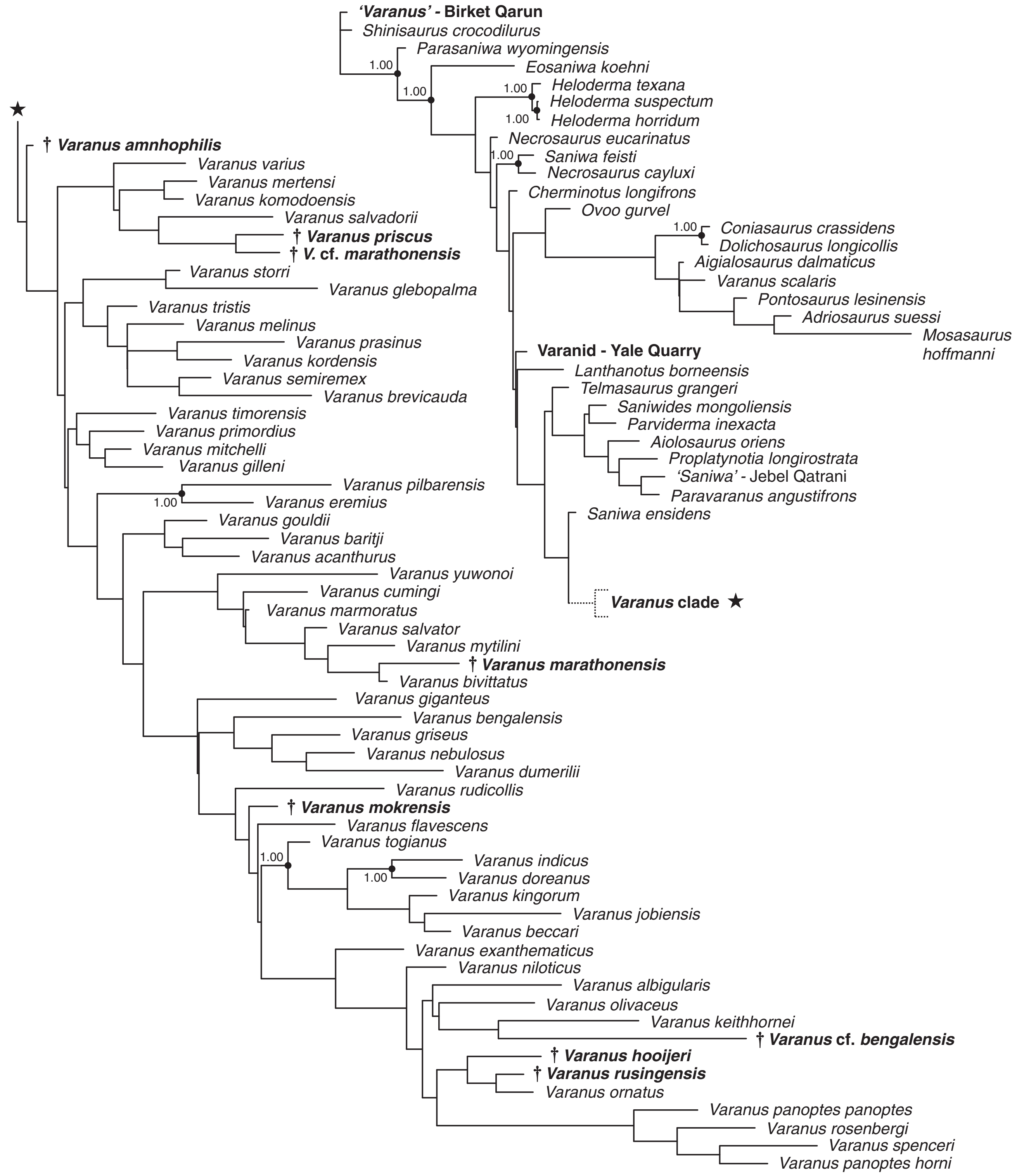

Figure 12. The majority rule of consensus topology used in the Bayesian analysis (with character-state change probability). Bold – fossil varanids; † – extinct *Varanus* species; black dots – posterior probability (PP) 100%, remaining nodes 50%.

V. mokrensis in the Bayesian analysis (particularly with the gamma rate), as well as the phylogenetic position and approximate age of the extinct African *V. rusingensis* (∼20 Ma; Clos 1995; Fig. 11), partly supports the hypothesis that the extant African species may have originated in the late Oligocene. The radiation of the African varanids may have continued throughout the Miocene, dotted by partial reverse routes into the Arabian

Peninsula, as suggested by the position of *V. yemenensis* (Böhme, Joger & Schätti, 1989; Portik & Papenfuss 2012). However, the Bayesian analysis with gamma rates, where the extinct *V. rusingensis* occurs in a terminal position (Fig. 12), reveals that the diversification of the African varanid clade may have been completed as early as the early Miocene. In addition, the dispersal of North African varanids into Iberia is unlikely, given that the accurately dated North African-Iberian dispersal of mammals (6.2 Ma) via ephemeral land bridges in the Strait of Gibraltar occurred long before the onset of the Messinian Salinity Crisis (5.59 Ma) resulting from the latest Miocene glaciation at 6.26 Ma (Gibert *et al.* 2013). The only known late middle Miocene varanid, an as yet unpublished *Varanus* from the Vallès-Penedès Basin in Catalonia (Spain) possibly referable to *Varanus marathonensis* (Delfino *et al.* 2011), is most probably of Eurasiatic origin, as is *V. amnhophilis* reported from the late Miocene (7.6–6.9 Ma) of Samos, Greece (Fig. 10; Conrad *et al.* 2012).

Discussion

Palaeoclimate

The amphibian and reptile assemblage from the 1/2001 Turtle Joint and 2/2003 Reptile Joint is rather diverse (Ivanov *et al.* 2006; Ivanov 2008, 2009). Based on M. Böhme *et al.* (2006), different ecophysiological groups occur in the early Miocene of Mokrá-Western Quarry (Supplemental Table 1).

The herpetofauna of the Mokrá-Western Quarry corresponds to the warm humid phase of the MCO (Miocene Climatic Optimum *sensu* M. Böhme 2003) during the early Miocene when mean annual temperatures (MAT) in Central Europe reached about 20°C. In the North Alpine Foreland Basin (NAFB), the occurrence of cordylid lizards indicates MAT > 17.4°C (M. Böhme 2003). Similarly, the presence of boid snakes with *Bavarioboa* cf. *hermi* Szyndlar & Schleich, 1993 in the southern part of the Moravian Karst (1/2001 Turtle Joint; 2/2003 Reptile Joint) also indicates a rather high MAT. The large boid snake from Mokrá-Western Quarry (Boidae gen. et sp. indet., large form), probably belonging to Pythonidae, is important because Central European representatives of Pythonidae Fitzinger, 1826 are known so far only from Griesbeckerzell, Germany (late MN 5 and base of MN 6). Pythons represent the most thermophilic members of the Squamata in the Miocene of Europe, and document MAT > 18.6°C (Ivanov & Böhme 2011).

Regarding humidity, there is a difference in the mean annual precipitation (MAP) between the two karst fissures. While the assemblage composition in the 1/2001 Turtle Joint indicates MAP = 461 ± 253 mm (Supplemental Table 1), the assemblage in the 2/2003 Reptile Joint indicates MAP = 864 ± 254 mm. The amphibian and reptile assemblage of the 1/2001 Turtle Joint, where heliophobic taxa are absent altogether, developed in a relatively drier phase of the MCO when MAP values were comparable with today's long-term average value for this area (MAP = 490.1 mm – www.chmi.cz).

Palaeoenvironment

Remains of fully aquatic amphibians in the Karst fissures suggest the possible presence of nearby lacustrine environments. The absence of ostracods and the scarcity of gastropods indicate oligotrophic to weakly mesotrophic conditions (Ivanov *et al.* 2006). The diverse amphibian fauna (Supplemental Table 1; Ivanov *et al.* 2006; Ivanov 2008) includes *Mioproteus* sp., *Triturus* aff. *roehrsi* Herre, 1955, *Triturus* cf. *marmoratus* (Latreille, 1800), *Triturus* sp., *Chioglossa meini* Estes & Hoffstetter, 1976, *Mertensiella mera* Hodrová, 1984, *Mertensiella* sp., and *Rana* sp. (synklepton *R. esculenta* Linnaeus, 1758). Among amniotes are turtles of the families Testudinidae Batsch, 1788 and Geoemydidae Theobald, 1868 (*Testudo* sp., *Ptychogaster* sp.; À. H. Luján, pers. comm.), and squamate reptiles (*Natrix* sp.). This assemblage indicates the presence of damp and marshy habitats with stagnant or slow-flowing waters in both localities of the Mokrá-Western Quarry. However, species adapted to more humid terrestrial environments are also recorded, such as *Chelotriton* sp. whose adults probably inhabited damp habitats with dense vegetation (Estes 1981). This is inferred from the known habitat preferences of the closely related extant *Tylototriton* Anderson, 1871 which usually inhabits humid, high mountain areas with dense vegetation, although adults of this species are known to cover distances of several tens of metres away from water reservoirs (Kuzmin *et al.* 1994). Although the development of amphibians is partly associated with aquatic habitats, the extinct pelobatid frog *Pelobates sanchizi* Venczel, 2004 was probably adapted to the dry sandy soil and well-drained substrates within inundation areas (Venczel 2004; M. Böhme & Vasilyan 2014). *Bufo* sp. is also adapted to drier conditions. Squamates belong to semiaquatic/heliophilic forms (*Natrix* sp.) and to heliophilic, fossorial or terrestrial forms, such as cf. *Blanus* sp., *Varanus* sp., *Pseudopus* sp., *Lacerta* sp., type I, *Lacerta* sp., *Bavarioboa* cf. *hermi*, and '*Coluber'* sp., type I, and *Vipera* sp. ('Oriental vipers' and 'European vipers'). Although the fillings of both karst fissures are approximately coeval (Ivanov *et al.* 2006), the scarcity or absence of certain aquatic or heliophobic forms of amphibians at the site 1/2001 Turtle Joint (rare occurrence of the genus *Triturus* Rafinesque, 1815; the absence of the genera *Chioglossa* Bocage, 1864 and *Mertensiella* Wolterstorff, 1925) indicates drier conditions (Ivanov 2008). This assumption is confirmed by the relatively higher proportion of 'Oriental vipers' in the faunal assemblage from this fissure.

The conclusions of our study are fully consistent with results of analyses of medium- and small-sized mammals (Ivanov *et al.* 2006; Sabol *et al.* 2007), the occurrence of which indicates a warm climate with a diverse mosaic of vegetation cover, possibly indicating open steppe and open forest environments with a system of rivers and swamps (Sabol *et al.* 2007).

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Supplemental data

Supplemental material for this article can be accessed at: https://doi.org/10.1080/14772019.2017.1355338

References

Ahl, E. 1932. Eine neue Eidechse und zwei neue Frösche vonder Insel Jobi. *Mitteilungen aus dem Zoologischen Museum in Berlin*, **17**, 892–899.

Alférez Delgado, F. & **Brea López, P.** 1981. Estudio preliminar de los restos de peces, anfibos y reptiles del yacimento de Corcoles (Guadalajara). *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica*, **79**, 5–20.

Anderson, C. 1930. *Meiolania platyceps* Owen and *Varanus* (*Megalania*) *priscus* (Owen). *Records of the Australian Museum*, **17**, 309–316.

Anderson, J. 1871. Description of a new genus of newts from western Yunan. *Proceedings of the Zoological Society of London*, **1871**, 423–425.

Antunes, M. T. & **Mein, P.** 1981. Vertébrés du miocène moyen de Amor (Leiria) – importance stratigraphique. *Ciências da Terra*, **6**, 169–188.

Antunes, M. T. & **Rage, J.-C.** 1974. Notes sur la géologie et la paléontologie du Miocène de Lisbonne. XIV: quelques Squamata (Reptilia). *Boletim da Sociedade Geológica de Portugal*, **19**, 47–60.

Archibald, J. K., **Mort, M. E.** & **Crawford, D. J.** 2003. Bayesian inference of phylogeny: a non-technical primer. *Taxon*, **52**, 187−191.

Ast, J. 2001. Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). *Cladistics*, **17**, 211–226.

Bahl, K. N. 1937. Skull of *Varanus monitor* (Linn.). *Records of the Indian Museum*, **39**, 133−174.

Batsch, A. J. C. G. 1788. *Versucheiner Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit den nöthigsten Abbildungen versehen. Erster Theil. Allgemeine Geschichte der Natur; besondre der Säugthiere, Vögel, Amphibien und Fische*. Akademische Buchhandlung, Jena.

Baur, G. 1890. On the characters and systematic position of the large sea lizards, Mosasauridae. *Science*, **16**, 1–262.

Bellairs, A. d'A. 1949. Observations of the snout of *Varanus*, and a comparison with that of other lizards and snakes. *Journal of Anatomy*, **83**, 116–146.

Bellairs, A. d'A. & **Kamal, A. M.** 1981. The chondrocranium and the development of the skull in recent reptiles. Pp. 1–263 in C. Gans & T. S. Parsons (eds) *Biology of the Reptilia 11*. Academic Press, London.

Bocage, J. V. B. du. 1864. Note sur la Découverte d'un Zoophyte de la familie Hyalochaetides sur la côte du Portugal. *Proceedings of the Zoological Society of London*, **1864**, 265–269.

Böhme, M. 2001. The oldest representative of a brown frog (Ranidae) from the early Miocene of Germany. *Acta Palaeontologica Polonica*, **46**, 119–124.

Böhme, M. 2002. *Palaeoclimate and aquatic ecosystems in the Neogene of Europe – new research approaches based on ectothermic vertebrates*. Unpublished habilitation thesis, Department of Geo- and Environmental Science, Ludwig-Maximillians University, Munich. [In German.]

Böhme, M. 2003. The Miocene Climatic Optimum: evidence from the ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 389–401.

Böhme, M. & **Ilg, A.** 2003. *FosFARbase*. Updated at: www.wahre-staerke.com/, accessed 25 August 2016.

Böhme, M. & **Vasilyan, D.** 2014. Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). *Palaeobiodiversity and Palaeoenvironments*, **94**, 21–40.

Böhme, M., **Ilg, A**, **Ossig, A.** & **Küchenhoff, H.** 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. *Geology*, **34**, 425–428.

Böhme, W. 1988. Der Arguswaran (*Varanus panoptes* Storr, 1980) auf Neuguinea: *Varanus panoptes horni* spp. n. *Salamandra*, **24**(2/3), 87–101.

Böhme, W. 2003. Checklist of the living monitor lizards of the world (family Varanidae). *Zoologische Verhandlungen*, **341** (25), 4–43.

Böhme, W., **Joger, U.** & **Schätti, B.** 1989. A new monitor lizard (Reptilia: Varanidae) from Yemen, with notes on ecology, phylogeny, and zoology. *Fauna of Saudi Arabia*, **10**, 433–448.

Bolkay, St. J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. *Mitteilungen aus dem Jahrbuch der königlichen ungarischen Geologischen Reichsanstalt*, **21**, 217–230.

Borsuk-Białynicka, M. 1984: Anguiomorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologica Polonica*, **46**, 5–105.

Bosc, L. 1792. *Lacerta exanthematica*. *Actes de la Société d'Histoire naturelle de la Paris*, **1**, 25.

Bosworth, W., **Huchon, P.** & **McClay, K.** 2005. The Red Sea and Gulf of Aden Basins. *Journal of African Earth Sciences*, **43**, 334–378.

Boulenger, G. A. 1885. *Catalogue of the lizards in the British Museum (Natural History)*. Vol. 2, 2nd edition, Printed by order of the Trustees, London, xiii + 497 pp.

Brongersma, L. D. 1958. On an extinct species of the genus *Varanus* (Reptilia, Sauria) from the island of Flores. *Zoologische Mededelingen*, **36**(7), 113–125.

Carroll, R. L. 1993. *Paläontologie und Evolution der Wirbeltiere*. Georg Thieme Verlag, Stuttgart, 684 pp.

Clos, L. M. 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *Journal of Vertebrate Paleontology*, **15**, 254–267.

Colombero, S., **Angelone, C.**, **Bonelli, E.**, **Carnevale, G.**, **Cavallo, O.**, **Delfino, M.**, **Giuntelli, P.**, **Mazza, P.**, **Pavia, G.**, **Pavia, M.** & **Repetto, G.** 2014. The Messinian vertebrate assemblages of Verduno (NW Italy): another brick for a latest Miocene bridge across the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie*, *Monatschefte*, **272**, 287–234.

Conrad, J. L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* AHL (Squamata, Anguiomorpha). *Zoological Journal of the Linnean Society*, **141**, 399–434.

Conrad, J. L. 2006. Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguiomorpha). *Journal of Morphology*, **267**, 759–775.

Conrad, J. L, **Balcarcel, A. M.** & **Mehling, C. M.** 2012. Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). *Plos One*, **7**(8), e41767.

Daudin, F. M. 1802. *Histoire naturelle, générale et particuliCre des Reptiles, ouvrage faisant suite, a l'histoire naturelle, générale et particulière composée par Leclerc de Buffon, et rediée par C. S. Sonnini*, vol. 3., F. Dufart, Paris, 426 pp.

Daudin, F. M. 1803. *Histoire Naturelle Generale et Particuliere des Reptiles*. Vol. 6. F. Dufart, Paris, 108 pp.

Delfino, M., **Abella J.**, **Sánchez, I.** & **Alba, D. M.** 2013a. A nearly complete *Varanus* skeleton from the late Miocene of Cerro de los Batallones (Madrid Basin). P. 33 in *Abstracts of 6th Annual Meeting of the European Association of Vertebrate Palaeontologists*. Villers-sur-Mer, France, 10–15 June 2013.

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

Delfino, M., **Alba, D. M.**, **Carmona, R.**, **Luján, À. H.** & **Robles, J. M.** 2011. European monitor lizards (Anguimorpha, Varanidae, *Varanus*): new materials and new perspectives. Abstracts of the 71st Annual Meeting Society of Vertebrate Paleontology, Paris Las Vegas, Las Vegas, Nevada, USA, November 2–5, 2011. *Journal of Vertebrate Paleontology*, **31**(Suppl. 2), 97–98.

Estes, R. 1981. Gymnophiona, Caudata. Part 2. Pp. 1–113 in P. Wellnhofer (ed.) *Handbuch der Paläoherpetologie 2 (Encyclopedia of paleoherpetology 2)*. Gustav Fischer Verlag, Stuttgart.

Estes, R. 1983. Sauria Terrestria. Part 10A. Pp. 1–249 in P. Wellnhofer (ed.) *Handbuch der Paläoherpetologie 10A (Encyclopedia of paleoherpetology 10A)*. Gustav Fischer Verlag, Stuttgart.

Estes, R., **de Queiroz, K.** & **Gauthier, J.** 1988. Phylogenetic relationships within Squamata. Pp. 119–281 in R. Estes & G. Pregill (eds) *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford.

Estes, R. & **Hoffstetter, R.** 1976. Les Urodèles du Miocène de La Grive-Saint-Alban (Isère, France). *Bulletin du Muséum national d'histoire naturelle*, sér. 3, **398**, 297–343.

Falconer, H. 1868. On fossil species of *Emys* from the Sewalik Hills, referable to the existing *Emys tecta* (Bell). Pp. 382–388 in C. Murchison (ed.) *Paleontological memoirs and notes of the late Hugh Falconer, AM, MD. Volume 1: Fauna Antiqua Sivalensis*. Robert Hardwicke Publishers, London.

Fejérváry, G. J. de. 1918. Contributions to a monography on fossil Varanidae and on Megalanidae. *Annales Musei Nationalis Hungarici*, **15**, 341–467.

Fejérváry, G. J. de. 1935. Further contributions to a monograph of the Megalanidae and fossil Varanidae – with notes on Recent Varanians. *Annales Musei Nationalis Hungarici*, **29**, 1–130.

Fejérváry-Lángh, A. M. 1923. Beiträge zu einer monographie der fossilen Ophisaurier. *Palaeontologia Hungarica*, **1**(7), 123–220.

Fitzinger, L. 1826. *Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologischen Museums zu Wien*. J. G. Heubner, Wien, 66 pp.

Fuller, S., **Baverstock, P.** & **King, D.** 1998. Biogeographic origins of goannas (Varanidae): a molecular perspective. *Molecular Phylogenetics and Evolution*, **9**, 294–307.

Gao, K. & **Norell, M. A.** 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguiomorphan lizards. *American Museum Novitates*, **3230**, 1–51.

Gao, K. & **Norell, M. A.** 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History*, **249**, 1–118.

Georgalis, G., **Villa, A.** & **Delfino, M.** 2017. The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. *Journal of Vertebrate Paleontology*, doi: 10.1080/02724634.2017.1301946

Gheerbrant, E. 1987. Les Vertébrés continentaux de l'Adrar Mgorn (Maroc, Paléocène); une dispersion de mammifères transtéthysienne aux environs de la limite Mesozoïque/Cénozoïque? *Geodinamica Acta*, **1**, 233–245.

Gheerbrant, E. 1990. On the early biogeographical history of the African placentals. *Historical Biology*, **4**, 107–116.

Gheerbrant, E. 2001. *Histoire paléobiogéographique des mammifères paléogènes du domaine arabo-africain*. HDR thesis, University of Paris VI.

Gheerbrant, E. & **Rage, J.-C.** 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241**, 224–246.

Gibert, L., **Scott, G. R.**, **Montoya, P.**, **Ruiz-Sánchez, F. J.**, **Morales, J.**, **Luque, L.**, **Abella, J.** & **Leria, M.** 2013. Evidence for an African-Iberian mammal dispersal during the pre-evaporitic Messinian. *Geology*, **41**, 691–694.

Gilmore, C. W. 1922. A new description of *Saniwa ensidens* Leidy, an extinct varanid lizard from Wyoming. *Proceedings of the United States National Museum*, **60**, 1–28.

Gilmore, C. W. 1928. Fossil lizards of North America. *Memoirs of the National Academy of Sciences*, **22**, 1–201.

Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics*, **9**, 83–91.

Goloboff, P. A., **Farris, J. S.** & **Nixon, K. C.** 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 1–13.

Gray, J. E. 1831. A Synopsis of the species of the class Reptilia. Pp. 1–29 in E. Griffith (ed.), *The Animal Kingdom*, Vol. 9, Whittaker, Treacher & Comp., London.

Gray, J. E. 1837. General arrangement of the Reptilia. *Proceedings of the Zoological Society of London*, **1837**(5), 131–132.

Gray, J. E. 1838. Catalogue of the slender-tongued saurians, with description of many new genera and species. *Annals of Natural History*, **1**, 274–283, 388–394.

Gray, J. E. 1845. *Catalogue of the specimens of lizards in the collection of the British Museum*. Trustees of the British Museum/Edward Newman, London, xxvii + 289 pp.

Hallowell, E. 1857. Notes on the reptiles in the collection of the museum of the Academy of Natural Sciences. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**(4), 146–153.

Hardwicke, F. R. & **Gray, J. E.** 1827. A synopsis of the species of saurian reptiles, collected in India by Major-General Hardwicke. *Zoological Journal, London*, **3**, 214–229.

Head, J. J., **Barrett Fls, P. M.** & **Rayfield, E. J.** 2009. Neurocranial osteology and systematic relationships of *Varanus (Megalania) prisca* Owen, 1859 (Squamata: Varanidae). *Zoological Journal of the Linnean Society*, **155**, 445–457.

Hecht, M. K. 1975. The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. *Proceedings of the Royal Society of Victoria*, **87**, 239–250.

Hír, J. & **Venczel, M.** 2005. New middle Miocene vertebrate localities from Subpiatră (Bihor District, Romania). *Acta Palaeontologica Romaniae*, **5**, 211–221.

Hocknull, S. A., **Piper, P. J.**, **van den Bergh, G. D.**, **Due, R. A.**, **Morwood, M. J.** & **Kurniawan, I.** 2009. Dragon's paradise lost: palaeobiogeography, evolution and extinction of the largest-ever terrestrial lizards (Varanidae). *PLoS ONE*, **4**(9), e7241.

Hodrová, M. 1984. Salamandridae of the Upper Pliocene Ivanovce locality (Czechoslovakia). *Acta Universitatis Carolinae, Geologica*, **4**, 331–352.

Hoffstetter, R. 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considerations sur l'histoire de la familie. *Bulletin du Muséum National d'Histoire Naturelle*, **40**, 1051–1064.

Hoffstetter, R. & **Gasc, J.-P.** 1969. Vertebrae and ribs of modern reptiles. Pp. 200–310 in C. Gans, A. d'A. Bellairs & T. S. Parsons (eds) *Biology of the Reptilia. Volume 1, Morphology A*. Academic Press, New York.

Holmes, R. B., **Murray, A. M.**, **Attia, Y. S.**, **Simons, E. L.** & **Chatrath, 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.

Huelsenbeck, J. P. & **Ronquist, F.** 2001. MRBAYES. Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Ivanov, M. 2008. Early Miocene amphibians (Caudata, Salientia) from the Mokrá-Western Quarry (Czech Republic) with comments on the evolution of Early Miocene amphibian assemblages in Central Europe. *Geobios*, **41**, 465–492.

Ivanov, M. 2009. *Evolution of Neogene and Quaternary squamate assemblages (Diapsida: Squamata) in Central Europe*. Unpublished Associate Professor thesis, Masaryk University, 319 pp. [In Czech.]

Ivanov, M. & **Böhme, M.** 2011. Snakes from Griesbeckerzell (Langhian, Early Badenian), North Alpine Foreland Basin (Germany), with comments on the evolution of snake fauna in Central Europe during the Miocene Climatic Optimum. *Geodiversitas*, **33**, 411–449.

Ivanov, M., **Musil, R.** & **Brzobohatý, R.** 2006. Terrestrial and marine faunas from the Miocene deposits of the Mokrá Plateau (Drahany Upland, Czech Republic) – impact on palaeogeography. *Beiträge zur Paläontologie*, **30**, 223–239.

Jollie, M. J. 1960. The head skeleton of the lizard. *Acta Zoologica, Stockholm*, **41**, 1–64.

Koch, A., **Aulyia, M.** & **Ziegler, T.** 2010. Updated checklist of the living monitor lizards of the world (Squamata: Varanidae). *Bonn Zoological Bulletin*, **57**(2), 127–136.

Koch, A., **Ziegler, T.**, **Böhme, W.**, **Arida, E.** & **Auliya, M.** 2013. Pressing Problems: Distribution, threats, and conservation status of the monitor lizards (Varanidae: *Varanus* spp.) of Southeast Asia and the Indo-Australian Archipelago. *Herpetological Conservation and Biology*, **8**(Monograph 3), 1–62.

Kuzmin, S. L., **Dasgupta, R.** & **Smirina, É. M.** 1994. Ecology of the Himalayan newt (*Tylototriton verrucosus*) in Darjeeling Himalayas, India. *Russian Journal of Herpetology*, **1**(1), 69–76.

Latreille, P. A. 1800. *Histoire naturelle des salamandres de France: précédée d'un tableau méthodique des autres reptiles*. Villier, Paris, 61 pp.

Laurenti, J. N. 1768. *Austriaci Viennensis specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa Venena et antidota reptilium Austriacorum quod authoritate et consensu*. J. Thomae, Caes. Reg. Aulae Typogographi, Wien, 217 pp.

Lee, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society of London, Series B*, **352**, 53–91.

Leidy, J. 1870. Descriptions of *Emys jeansesi*, *E. haydeni*, *Baëna arenosa*, and *Saniwa ensidens*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1870**, 123–124.

Levshakova, I. J. 1986. A new *Varanus* from lower Pliocene of Tajikistan. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, **157**, 101–116. [In Russian.]

Linnaeus, C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I*. Editio decima, reformata, Laurentii Salvii, Holmiæ, 824 pp.

Linnaeus, C. 1766. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 12th edition, Salvius, Holmiæ, Sweden, 122 pp.

Lloyd, G. T. 2015. *Claddis: measuring morphological diversity and evolutionary tempo*. R package version 0.1. Updated at: https://github.com/graemetlloyd/Claddis, accessed 12 October 2015.

Lucas, A. H. S. & **Frost, C.** 1895. Preliminary notice of certain new species of Lizards from central Australia. *Proceedings of the Royal Society of Victoria*, **7**, 264–269.

Lungu, A. N., **Zerova, G. A.** & **Chkhikvadze, V. M.** 1983. Primary evidence on the Miocene *Varanus* of the North Black Sea littoral. *Sovshcheniia Akademii Nauk Gruzinskoi SSR*, **110**, 417–420. [In Russian.]

McDowell, S. B. Jr. & **Bogert, C. M.** 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bulletin of the American Museum of Natural History*, **105**, 1–142.

Merrem, B. 1820. *Versuch eines Systems der Amphibien/Tentamen systematis amphibiorum*. J. C. Krieger, Marburg, 191 pp.

Mertens, R. 1942. Die Familie der Warane (Varanidae). Zweiter Teil: Der Schädel. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **465**, 117–234.

Mertens, R. 1957. Ein neuer melanitischer Waran aus dem südlichen Australien (*V. gouldii rosenbergi*, subsp. nov.). *Zoologischer Anzeiger*, **159**, 17–20.

Meyer, A. B. 1874. Eine Mittheilung von Hrn. Dr. Adolf Meyer über die von ihm auf Neu-Guinea un den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin*, **1874**, 128–140.

Molnar, R. E. 1990. New cranial elements of a giant varanid from Queensland. *Memoirs of the Queensland Museum*, **29**, 437–444.

Molnar, R. E. 2004. The long and honourable history of monitors and their kin. Pp. 10–67 in E. R. Pianka, D. R. King & R. A. King (eds) *Varanoid lizards of the world*. Indiana University Press, Bloomington.

Münster, G. L. F. W. 1834. *Petrefacta Germaniae tam ea: quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenanae servantur quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata (Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angränzenden Länder, Theil 2 (1834-1840)*. Lithographischen Anstalt, Arnz & Comp., Düsseldorf.

Norell, M. A. & **Gao, K.** 1997. Braincase and phylogenetic relationships of *Estesia mongoliensis* from the Late Cretaceous of the Gobi Desert and the recognition of a new clade of lizards. *American Museum Novitates*, **3211**, 1–25.

Norell, M. A., **Gao, K.** & **Conrad, J.** 2007. A new platynotan lizard (Diapsida: Squamata) from the Late Cretaceous Gobi Desert (Ömnögov), Mongolia. *American Museum Novitates*, **3605**, 1–22.

Norell, M. A., **McKenna, M. C.** & **Novacek, M. J.** 1992. *Estesia mongoliensis*, a new fossil varanoid from the Late Cretaceous Barun Goyot Formation of Mongolia. *American Museum Novitates*, **3045**, 1–24.

Oelrich, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications of the University of Michigan Museum of Zoology*, **94**, 1–122.

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

Ouwens, P. A. 1912. On a large *Varanus* species from the island of Komodo. *Bulletin of the Botanical Gardens Buitenzorg*, **2**, 1–3.

Owen, F. R. S. 1859. Description of some remains of a gigantic land-lizard (*Megalania prisca*, Owen) from Australia. *Philosophical Transactions of the Royal Society of London*, **149**, 43–48, 2 pls.

Owen, F. R. S. 1880. Description of some remains of the gigantic land-lizard (*Megalania prisca*, Owen), from Australia. Part 2. *Philosophical Transactions of the Royal Society of London*, **171**, 1037–1050, 5 pls.

Pérez-Ramos A., **Abella J.**, **Luján, À. H.**, **Alba, D. M.**, **Delfino, M.** & **Morales, J.** 2016. Three-dimensional reconstruction of the skull of *Varanus marathonensis* from the Late Miocene of Batallones-3 (Madrid, Spain). P. 113 in E. Manzanares et al. (eds) *1st International Meeting of Early-stage Researchers in Palaeontology/1XIV Encuentro de Jóvenes Investigadores en Paleontología, new perspectives on the evolution of phanerozoic biotas and ecosystems*. 13–16 April 2016, Alpuente, Valencia, Spain, 204 pp.

Peters, W. C. H. & **Doria, G.** 1878. Catalogo del retilli e del batraci raccolti da O. Beccari, L. M. D'Alberts e A. A. Bruijn nella sotto-regione Austro-Malese. *Annali del Museo Civico de Storia Naturale di Genova*, **1**(13), 323–450.

Pianka, E. R, **King, D. R.** & **King, R. A.** eds. 2004. *Varanoid lizards of the world*. Indiana University Press, Bloomington, 608 pp.

Pollitt, J. R., **Fortey, R. A.** & **Wills, M. A.** 2005. Systematics of the trilobite families Lichidae Hawle & Corda, 1847 and Lichakephalidae Tripp, 1957: the application of Bayesian inference to morphological data. *Journal of Systematic Palaeontology*, **3**, 225–241.

Portik, D. M. & **Papenfuss, T. J.** 2012. Monitors cross the Red Sea: the biogeographic history of *Varanus yemenensis*. *Molecular Phylogenetics and Evolution*, **62**, 561–565.

Pregill, G. K., **Gauthier, J. A.** & **Greene, H. W.** 1986. The evolution of helodermatid squamates, with description of a new taxon and an overview of Varanoidea. *Transactions of San Diego Society of Natural History*, **21**, 167–202.

Quicke, D. L. J., **Taylor, J.** & **Purvis, A.** 2001. Changing the landscape: a new strategy for estimating large phylogenies. *Systematic Biology*, **50**, 60–66.

Rafinesque, C. S. 1815. *Analyse de la nature ou Tableau de l'univers et des corps organisés*. Jean Barravecchia, Palermo, 242 pp.

Rage, J.-C. & **Bailon, S.** 2005. Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas*, **27**, 413–441.

Rage, J.-C. & **Sen, S.** 1976. Les amphibiens et les reptiles du Pliocéne supérieur de Çalta (Turquie). *Géologie méditerranéenne*, **3**(2), 127–134.

Rieppel, O. 1978. The phylogeny of cranial kinesis in lower vertebrates, with special reference to the Lacertilia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **156**, 353–370.

Rieppel, O. 1980a. The phylogeny of anguinomorph lizards. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft*, **94**, 1–86.

Rieppel, O. 1980b. The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). *Amphibia-Reptilia*, **1**, 95–112.

Rieppel, O. & **Grande, L.** 2007. The anatomy of the fossil varanid lizard *Saniwa ensidens* Leidy, 1870, based on a newly discovered complete skeleton. *Journal of Paleontology*, **81**, 643–665.

Rieppel, O. & **Labhardt, L.** 1979. Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). *Herpetologica*, **35** (2), 158–163.

Rieppel, O. & **Zaher, H.** 2000. The braincase of mosasaurs and *Varanus*, and the relationships of snakes. *Zoological Journal of the Linnean Society*, **129**, 489–514.

Roger, O. 1898. Wirbelthierreste aus dem Dinotheriensande, II. Theil. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg (a.V.) in Augsburg*, **33**, 385–396.

Roger, O. 1900. Wirbelthierreste aus dem Dinotheriensande, III. Theil. *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg (a.V.) in Augsburg*, **34**, 53–70.

Romer, A. S. 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago, 772 pp.

Sabol, M., **Fejfar, O.**, **Horáček, I.** & **Čermák, S.** 2007. The Early Miocene micromammalian assemblage from Mokrá – 1/2001 Turtle Joint site (Morava, Czech Republic) – preliminary results. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykiane Brunensis, Geology*, **36**, 57–64.

Säve-Söderbergh, G. 1946. On the fossa hypophyseos and the attachment of the retractor bulbi group in *Sphenodon*, *Varanus* and *Lacerta*. *Arkiv för zoology*, **38**A, 1–24.

Säve-Söderbergh, G. 1947. Notes on the brain-case in *Sphenodon* and certain Lacertilia. *Zoologiska Bidrag från Uppsala*, **25**, 489–516.

Scanlon, J. D. 2005. Cranial morphology of the Plio–Pleistocene giant madtsoiid snake *Wonambi naracoortensis*. *Acta Palaeontologica Polonica*, **50**, 139–180.

Schlegel, H. 1839. *Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen und mit einem erläuternden Texte begleitet*. Arnz & Comp., Düsseldorf, xiv + 141 pp.

Sen, S. & **Rage, J.-C.** 1979. Pliocene vertebrate fauna of Çalta. *Bulletin of the Geological Society of Turkey*, **22**, 155–160. [In Turkish.]

Shrivatsava, R. K. 1963. The structure and the development of the chondrocranium of *Varanus*. Part I. The development of the ethmoidal region. *Folia anatomica Japonica*, **39**, 53–83.

Shrivatsava, R. K. 1964a. The structure and the development of the chondrocranium of *Varanus*. Part II. The development of the orbito-temporal region. *Journal of Morphology*, **115**, 97–108.

Shrivatsava, R. K. 1964b. The structure and the development of the chondrocranium of *Varanus*. Part III. The otic and occipital regions, basal plate, viscerocranium and certain features of the osteocranium of a juvenile. *Morphologisches Jahrbuch*, **106**, 147–187.

Smith, K. T., **Bhullar, B.-A.S.** & **Holroyd, P. A.** 2008. Earliest African record of *Varanus* stem-clade from Oligocene Egypt. *Journal of Vertebrate Paleontology*, **28**, 909–913.

Steindachner, F. 1878. Über zwei Eidechsen-Arten aus Süd-Amerika und Borneo. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, **38**, 93–96.

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*, Ser. B., **192**, 1–47.

Tempfer, P. M. 2005. The Herpetofauna (Amphibia: Caudata, Anura; Reptilia: Scleroglossa) of the Upper Miocene locality Kohfidisch (Burgerland, Austria). *Beiträge zur Paläontologie*, **29**, 145–253.

Theobald, W. 1868. Catalogue of reptiles in the Museum of the Asiatic Society of Bengal. *Journal of the Asiatic Society of Bengal*, **37**, i–vi + 7–88, i–iii.

Tsuji, L. A., **Müller, J.** & **Reisz, R. R.** 2010. *Microleter mckinzieorum* gen. et sp. nov. from the Lower Permian of Oklahoma: the basalmost parareptile from Laurasia. *Journal of Systematic Palaeontology*, **8**, 245–255.

Uetz, P., **Freed, P.** & **Hošek, J.** eds. 2017. *The reptile database*. Updated at: http://www.reptile-database.org, accessed 26 March 2017.

Venczel, M. 2004. Middle Miocene anurans from the Carpathian Basin. *Palaeontographica Abteilung A*, **271**, 151–174.

Venczel, M. 2006. Lizards from the Late Miocene of Polgárdi (W-Hungary). *Nymphaea, Folia naturae Bihariae*, **33**, 25–38.

Venczel, M. & **Hír, J.** 2015. Lissamphibians and squamate reptiles from the early middle Miocene of Litke, Northern Hungary. *Geobios*, **48**, 491–504.

Weithofer, A. 1888. Beiträge zur Kenntnis der Fauna von Pikermi bei Athen. *Beiträge zur Paläontologie und Geologie Oesterreich-Ungarns und des Orients*, **6**(3), 225–292.

Wells, R. W. & **Wellington, C. R.** 1985. A classification of the Amphibia and Reptilia of Australia. Australian *Journal of Herpetology, Supplementary Series*, **1**, 1–61.

White, J. 1790. *Journal of a voyage to new South Wales, with sixty-five plates of non descript animals, birds, lizards, serpents, curious cones of trees and other natural productions*. Debrett, London, 229 pp.

Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology*, **44**, 501–514.

Wolterstorff, W. 1925. Katalog der Amphibien-Sammlung im Museum für Natur- und Heimatkunde zu Magdeburg: Erster Teil, Apoda, Caudata. *Abhandlungen und Berichte aus dem Museum für Natur- und Heimatkunde*, **4**, 231–310.

Wright, A. M & **Hillis, D. M.** 2014. Bayesian analysis using a simple likelihood model outperforms parsimony for estimation of phylogeny from discrete morphological data. *PLoS ONE*, **9**, e109210.

Zerova, G. A. & **Chkhikvadze, V. M.** 1983. Primary evidence on the Miocene *Varanus* of the north Black Sea littoral. *Soobshcheniya Akademii Nauk Gruzinskoi SSR*, **110**(2), 417–420. [In Russian.]

Zerova, G. A. & **Chkhikvadze, V. M.** 1984. Review of Cenozoic lizards and snakes of the USSR. *Izvestia Akademii Nauk, Georgian Academy of Science*, **10**(5), 319–326. [In Russian with English abstract.]

Zerova, G. A. & **Chkhikvadze, V. M.** 1986. Neogene varanids of the USSR. Pp. 689–694 in Z. Roček (ed.) *Studies in herpetology*. Charles University, Prague.