



Early Miocene dispersal of the lizard *Varanus* into Europe: Reassessment of vertebral material from Spain

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***Iberoveranus* Hoffstetter, 1969 was erected as a monotypic genus of varanine varanid lizard on the basis of a single trunk vertebra from the Miocene of Spain. Thanks to the study of the holotype, as well as of a still undescribed cervical vertebra from the same locality, we show that the vertebral morphology of *Iberoveranus* is contained within the known variability of *Varanus*. Therefore, *Iberoveranus* Hoffstetter, 1969 is considered a subjective junior synonym of *Varanus* Merrem, 1820, and the species *Iberoveranus catalaunicus* Hoffstetter, 1969 should be considered a nomen dubium.**

Introduction

The phylogenetic and biogeographic relationships of fossil European Monitor lizards have recently been revised by Conrad et al. (2009, 2011), and Delfino et al. (2011) focused only on the fossils referred to *Varanus*. Conrad (2008) and Conrad et al. (2008) only minimally commented on *Iberoveranus* Hoffstetter, 1969, a monotypic genus that was erected on the basis of a single trunk vertebra from the Miocene of Can Mas, close to El Papiol, about 15 km from Barcelona (Catalonia, Spain). Hoffstetter (1969) considered *Iberoveranus* to be the most primitive member of the Varaninae, but owing to the poor quality of the material, Clos (1995) and Conrad et al. (2011) regarded *Iberoveranus* as too fragmentary to be included in phylogenetic analyses. Nonetheless, other authors identified the morphological characters of *Iberoveranus* from other localities, sometimes with doubts concerning the specific identification. For example, Antunes and Rage (1974) and Antunes and Mein (1981) referred to *Iberoveranus* a few isolated vertebrae from three early–middle Miocene localities of Portugal. Böhme and Ilg (2003) listed about 10 more localities from Spain and Germany with possible remains of *Iberoveranus*, with an age span from Burdigalian (MN3) to Langhian (MN6). Here we re-examine the holotype of *Iberoveranus* and another specimen from the same locality, in order to consider its validity.

Institutional abbreviations.—ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain; IPS, collections of the ICP (formerly Institut de Paleontologia de Sabadell); ZFMK, Zoologisches Forschungsmuseum Koenig, Bonn, Germany.

Other abbreviations.—CMA, Can Mas, El Papiol, Barcelona, Spain.

Geological and geographical setting

CMA is a loosely-defined paleontological site, which includes Miocene levels of reddish to brownish clays from several quarries that were situated close to the house of Can Mas, about 1 km NW from the town of El Papiol (Crusafont et al. 1955). This locality, which should not be confused with the homonymous, Vallesian locality of “Can Mas”, in the area of els Hostalets de Pierola (Crusafont and Truyols 1954)—corresponds to the early Miocene Lower Continental Complex of the Vallès-Penedès Basin; it is mainly composed of reddish terrigenous deposits of varied lithology, deposited in the context of alluvial fan systems (Agustí et al. 1985; Casanovas-Vilar et al. 2011b). An MN4 age (i.e., circa 17–16 Ma; Agustí et al. 2001) has been customarily given to CMA (Agustí et al. 1985; Fortelius 2011), which is consistent with the presence of *Gomphotherium angustidens* (cited by Crusafont et al. 1955), although this taxon does not exclude an earlier, MN3 age (Agustí et al. 2001; Casanovas-Vilar et al. 2011a). Further refinement is precluded by the lack of associated rodents. An attribution to MN4 would also be supported by the record of *Eotragus* reported by Fortelius (2011). However, an inspection of the available macromammalian fossils from CMA housed at the ICP yielded no remains of the bovid *Eotragus*. Interestingly a single mandibular fragment of the paleomerycid *Lagomeryx* (DMA, personal observations), was located, but does not discriminate between MN3 and MN4.

Systematic palaeontology

Order Squamata Opper, 1811

Superfamily Varanoidea Camp, 1923

Family Varanidae Gray, 1827

Genus *Varanus* Merrem, 1820

Type species: Varanus varius (White, 1790).

Varanus sp.

Figs. 1, 2.

1955 *Ophisaurus* sp.; Crusafont et al. 1955: 237–238.

1969 *Iberoveranus catalaunicus* sp. nov.; Hoffstetter 1969: 1052, fig. 1.

1983 *Iberoveranus catalaunicus* Hoffstetter, 1969; Estes 1983: 182.

1974 *Iberoveranus catalaunicus* Hoffstetter, 1969; Antunes and Rage 1974: 52.

2004 *Iberoveranus catalaunicus* Hoffstetter, 1969; Molnar 2004: 36–37, fig. 2.11.

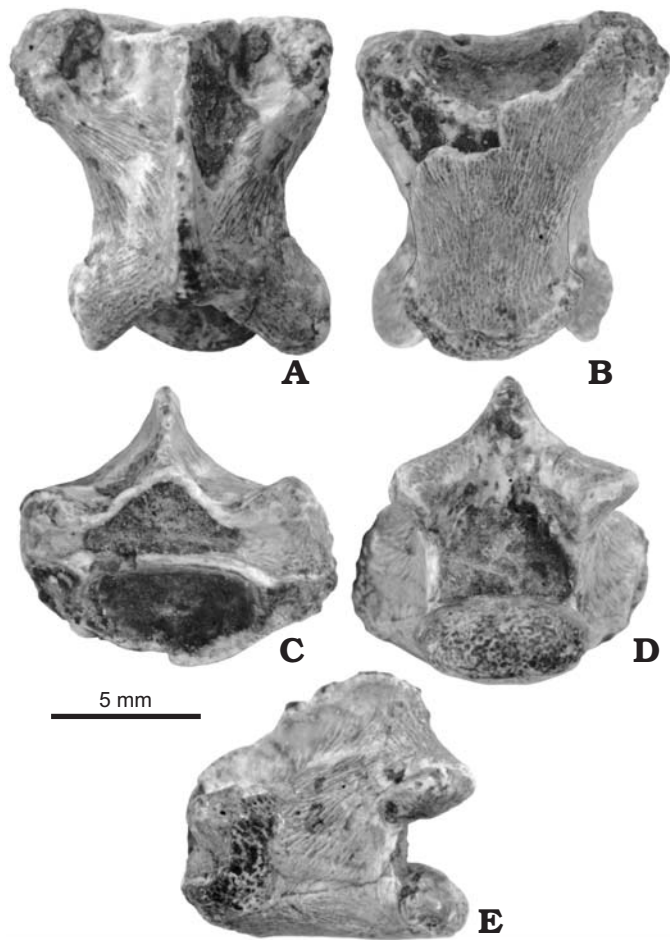


Fig. 1. Varanid lizard *Varanus* sp. from Can Mas, early Miocene, IPS 58437; holotype of *Iberoveranus catalaunicus* Hoffstetter, 1969, a taxon here considered as taxonomically non valid. Trunk vertebra in dorsal (A), ventral (B), anterior (C), posterior (D), and left lateral (E) views.

Material.—IPS 31701, cervical vertebra; IPS 58437, trunk vertebra, holotype of *Iberoveranus catalaunicus* Hoffstetter, 1969 from Can Mas, El Papiol, Barcelona, Spain, early Miocene.

Description.—IPS 58437, the type specimen of *Iberoveranus catalaunicus*, is an eroded, partial trunk vertebra (Fig. 1). Only the base of the neural spine is preserved, and the surface of the centrum is broken at its right anterolateral sector. Conversely the synapophyses, prezygapophyses, left postzygapophysis, and the condyle are significantly eroded. The centrum is procoelous and slightly convex ventrally in transverse section. No foramina are evident. In ventral view, the centrum is approximately triangular in shape, with a clear precondylar constriction (width at the constriction 4.9 mm; maximum width of the cotyle 5.8 mm; ratio 0.84), reduced by the erosion of the condyle. The cotyle and condyle are depressed. The cotyle faces anteroventrally so that the inner surface of the cotyle is largely visible in ventral view, whereas the condyle shows a symmetric orientation with the surface only minimally exposed. Therefore, there is a significant difference between the minimum, 8.4 mm, and the maximum, 10.6 mm, centrum lengths (measures taken ac-

ording to Bailon and Rage 1994, biased by the erosion of the vertebra). Prezygapophyseal facets are clearly tilted dorsally but their shape cannot be evaluated because of abrasion. The space between the prezygapophyseal facets and the neural spine is not markedly recessed. The anterior edge of the neural arch is slightly eroded (and asymmetric in dorsal view), but it seems likely that it was markedly tectiform in anterior view and approximately straight or slightly concave in dorsal view. There is no hint of a “pseudozygosphenon” or of a structure similar to it (see Holmes et al. 2010). The posterior edge of the neural arch is rather high, with posterodorsal edges quite steep in posterior view. A “pseudozygantrum” is absent. The lateral erosion of the postzygapophyses (mostly of the left one) contributes to the narrowness of the posterior section of the neural arch. The best preserved postzygapophyseal facet is tilted at about 45° and oval-shaped. On the lateral and dorsal surfaces of the neural arch there are distinct “fibrous” striae, which are particularly evident possibly following moderate surface erosion (note that the apparent striae on the ventral surface of the centrum are not “fibrous” structures). Because the neural spine is broken at the base and the dorsal surface of the neural arch is eroded in the anterior sector, it cannot be confirmed that the neural spine was developed along the entire length of the neural arch as reported by Clos (1995). The thickness of the remnants of the neural spine suggests that it was likely developed only in the posterior half of the neural arch. The remnants of the synapophyses indicate that they were rather massive. The size of the neural canal, filled with matrix, cannot be evaluated.

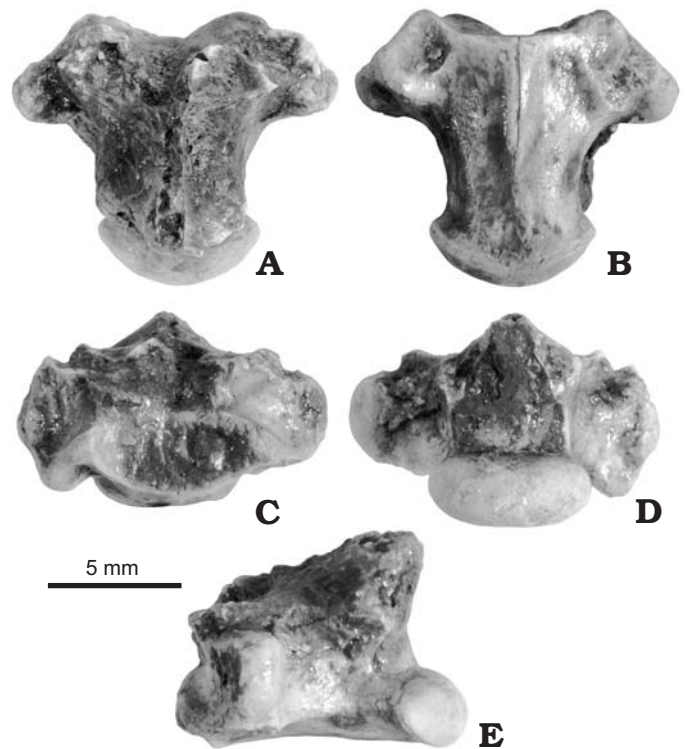


Fig. 2. Varanid lizard *Varanus* sp. from Can Mas, early Miocene, IPS 31701. Cervical vertebra dorsal (A), ventral (B), anterior (C), posterior (D), and left lateral (E) views.

IPS 31701 is a partially preserved posterior cervical vertebra from CMA previously catalogued as “cf. *Testudo* sp.?” (Fig. 2). The neural spine, the left parapophysis, and the pre- and postzygapophyses are broken off, but the ventral surface of the centrum is well preserved. The centrum, 9.5 mm long, is slightly convex transversely and not as triangular in shape as that of IPS 58437. A hint of a median keel is present in its anterior sector. The centrum has a distinct, obtuse precondylar constriction (width at the constriction 4.9 mm; maximum width of the cotyle 6.2 mm; ratio 0.78), which involves a significant portion of the lateral side of the centrum. The cotyle and condyle are markedly dorsoventrally depressed; although the dorsal rim of the cotyle, as preserved, did not overhang the preceding condyle, this is likely an artefact of erosion. The ventral edge of the condyle is close to the posterior edge of the centrum (so that only a little portion of the condyle is visible in ventral view). The synapophyses are massive, nearly vertical and strikingly laterally projected, so that the vertebra is 12.3 mm wide at their level. They are ventrally linked to the edge of the cotyle by a sub-horizontal ridge (“ventral parapophyseal lamina” in Houssaye et al. 2011). The diapophysis and parapophysis are well defined and slightly separated by a posterior concavity; the former is larger than the latter. Between the parapophyses and the rim of the cotyle there is shallow concavity posteromedially marked by a step.

Discussion

After the remarkable but partial works by Mertens (1942, 1950, 1959), knowledge of the osteology of genus *Varanus* has been advanced thanks to the identification of a few hundred phylogenetically informative characters summarized and updated by Conrad et al. (2011). Although the fine morphology of the 73 species currently ascribed to *Varanus* (Uetz et al. 2011) is still imprecisely known and the intra- and interspecific variation of several characters largely underexplored, it is now clear that the degree of precondylar constriction can significantly vary among species. The constriction is always present in *Varanus*, yet can vary from weakly expressed (state 1 of character 233) to so well developed that it is less than 80% of the maximum condylar diameter and “a right or acute angle is formed between the condyle and the centrum just anterior to the posterolateral part of the condyle (state 2 of character 233)” (Conrad et al. 2011: 267).

According to Hoffstetter (1969), *Iberoveranus* differs from *Varanus* in having a more elongate neural arch, a narrower condyle, and a less pronounced precondylar constriction. These presumed differences are partly explained by the preservation of the type vertebra (condyle, pre- and postzygapophyses are somewhat eroded) and partly to interspecific variability within *Varanus*. In particular, the vertebrae of some extant species, such as *Varanus griseus* (Daudin, 1803) (Fig. 3A), match well with the trunk vertebra IPS 58437. The precondylar constriction of the latter is of 84%, corresponding to state 1 of character 233 (Conrad et al. 2011), but this result is considerably altered by the erosion of the condyle. In fact, the constriction of posterior cervical vertebra IPS 31701, which has a perfectly preserved condyle, is 78%, corresponding to state 2, indicating therefore that this could likely be

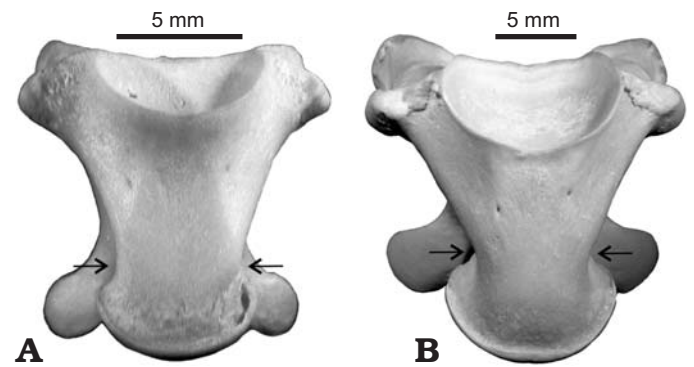


Fig. 3. Trunk vertebrae of extant varanid lizards in ventral view. **A.** *Varanus griseus* (Daudin, 1803), ZFMK 53533. **B.** *Varanus salvator* (Laurenti, 1768), ZFMK 90471. Note the different development of the precondylar constriction (indicated by the arrows) and the proportions of the centrum and the condyle.

the morphology and state of the vertebrae of the CMA monitor lizard. The average precondylar constriction of the trunk vertebrae of *V. griseus* ZFMK 14883 and ZFMK 53533 is about 76%, corresponding again to state 2, even if the general shape of the centrum is quite different from that of other congeneric species, such as *Varanus salvator* (Laurenti, 1768), with the same status (see Fig. 3B).

Finally, it is worth mentioning that, according to Molnar (2004), the vertebrae of *Iberoveranus catalaunicus* resemble those of helodermatids because of the slight development of the precondylar constriction. Although it is true that the condition of IPS 58437 could be considered intermediate between that shown by, for example, *V. salvator* and helodermatids, the absence of any constriction in the latter (Conrad et al. 2011; state 0 of character 233), among other characters, excludes referral of IPS 58437 to these taxa.

A further character supporting the inclusion of the holotype of *Iberoveranus*, IPS 58437, in *Varanus* is the presence of striations of the neural arch, which are considered, along with the precondylar constriction, an apomorphy of *Varanus* (Smith et al. 2008). Such striations are not present in all *Varanus* species but “have arisen on the *Varanus* stem and are retained as plesiomorphy in many crown *Varanus*, especially the African forms” (Smith et al. 2008: 911).

Conclusions

The morphology of the type vertebra of *Iberoveranus catalaunicus* Hoffstetter, 1969, IPS 58437, as well as that of the only other varanoid vertebra from the same locality, IPS 31701, is clearly contained within the variability of extant *Varanus*. The nominal taxon *Iberoveranus* Hoffstetter, 1969 must therefore be considered a subjective junior synonym of *Varanus* Merrem, 1820. The taxonomic validity of the nominal taxon *Iberoveranus catalaunicus* Hoffstetter, 1969, the type and only species of this genus, is not supported by the characters already mentioned for the genus. Given that it is available in terms of nomenclature, but from a taxonomic viewpoint it cannot be either validated or

synonymized with other *Varanus* species on the basis of currently available material, it is here deemed a nomen dubium (see Mones 1989, for a review of this concept). The species binomen *Varanus catalaunicus* (Hoffstetter, 1969) comb. nov. could potentially be used in the future if a new comparative diagnosis becomes possible on the basis of new skeletal elements providing significant morphological information (e.g., skull elements; see Conrad et al. 2009; Delfino et al. 2011).

If the referral to MN3 of the CMA vertebrate assemblage is confirmed, the *Varanus* remains here described represent one of the earliest evidences of the dispersal of this genus into Europe, which is otherwise known with confidence from the MN4b of Béon 1 (Rage and Bailon 2005) and possibly from a few MN3 Spanish localities such as San Roque 4A (*Varanus* sp.) and Agramon and Ateca 1 (aff. *Iberoveranus* sp. and *Iberoveranus* cf. *I. catalaunicus*; Böhme and Ilg 2003).

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References

- Agustí, J., Cabrera, L., and Moyà-Solà, S. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallés-Penedés. *Paleontologia i Evolució* 18: 57–81.
- Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., and Parés, J.M. 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews* 52: 247–260.
- Antunes, M.T. and Mein, P. 1981. Vértébrés du miocène moyen de Amor (Leiria) importance stratigraphique. *Ciências da Terra* 6: 169–188.
- Antunes, M.T. and 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.
- Bailon, S. and Rage, J.-C. 1994. Squamates Néogènes et Pléistocènes du Rift occidental, Ouganda. In: B. Senut and M. Pickford (eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire*. Vol. 2: Palaeobiology. *CIFEG Occasional Publications* 1994/29: 129–135.
- Böhme, M. and Ilg, A. 2003. fosFARbase. Available at www.wahre-staerke.com/. Accessed October 10, 2011.
- Camp, C.L. 1923. Classification of the lizards. *American Museum of Natural History Bulletin* 48: 289–481.
- Casanovas-Vilar, I., Alba, D.M., Garcés, M., Robles, J.M., and Moyà-Solà, S. 2011a. Updated chronology for the Miocene hominoid radiation in Western Eurasia. *Proceedings of the National Academy of Sciences USA* 108: 5554–5559.
- Casanovas-Vilar, I., DeMiguel, D., Galindo, J., Robles, J.M., Garcés, M., and Cabrera, L. 2011b. The continental Burdigalian (early Miocene) of the Vallés-Penedés Basin (Catalonia, Spain). In: A. Pérez-García, F. Gascó, J.M. Gasulla, and F. Escaso (eds.), *Viajando a mundos pre-territos*, 93–100. Ayuntamiento de Morella, Morella.
- Clos, L.M. 1995. A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *Journal of Vertebrate Paleontology* 15: 254–267.
- Conrad, J.L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310: 1–182.
- Conrad, J.L., Ast, J.C., Montanari, S., and Norell, M.A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). *Cladistics* 27: 230–277.
- Conrad, J.L., Balcarcel, A., and Mehling, C. 2009. Miocene Asian invasion of Europe by *Varanus* (Varanidae). *Journal of Vertebrate Paleontology* 29 (3 supplement): 81A.
- Conrad, J.L., Rieppel, O., and Grande, L. 2008. Re-assessment of varanid evolution based on new data from *Saniwa ensidens* Leidy, 1870 (Squamata, Reptilia). *American Museum Novitates* 3630: 1–15.
- Crusafont, M. and Truyols, J. 1954. *Catálogo paleomastológico del Mioceno del Vallés-Penedés y de Calatayud-Teruel. Segundo Cursillo Internacional de Paleontología*. 25 pp. Museu de la Ciutat de Sabadell, Sabadell.
- Crusafont, M., de Villalta, J.F., and Truyols, J. 1955. El Burdigaliense continental de la cuenca del Vallés-Penedés. *Memorias y Comunicaciones del Instituto Geológico* 12: 1–247.
- Daudin, F.M. 1803. *Histoire Naturelle, Générale et Particulière des Reptiles, Vol. 8*. 447 pp. F. Dufart, Paris.
- Delfino, M., Alba, D.M., Carmona, R., Luján, À.H., and Robles, J.M. 2011. European monitor lizards (Anguimorpha, Varanidae, *Varanus*): new materials and new perspectives. *Journal of Vertebrate Paleontology* 31 (Supplement 2): 97–98.
- Estes, R. 1983. *Sauria terrestria, Amphisbaenia. Handbuch der Paläoherpetologie, part 10A*. 249 pp. Gustav Fischer Verlag, Stuttgart.
- Fortelius, M. (coordinator) 2011. Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki. Available at <http://www.helsinki.fi/science/now/>. Accessed January 26, 2012.
- Gray, J. 1827. A synopsis of the genera of saurian reptiles, in which some new genera are indicated and others reviewed by actual examination. *Annals of Philosophy* 2: 54–58.
- Hoffstetter, R. 1969. Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bulletin du Muséum National d'Histoire Naturelle* 40 (for 1968): 1051–1064.
- Holmes, R.B., Murray, A.M., Attia, Y.S., Simons, E.L., and 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. *Palaentology* 53: 1099–1110.
- Houssaye, A., Bardet, N., Rage, J.-C., Pereda Suberbiola, X., Bouya, B., Amaghzaz, M., and Amalik, M. 2011. A review of *Pachyvaranus crassispondylus* Arambourg, 1952, a pachyostotic marine squamate from the latest Cretaceous phosphates of Morocco and Syria. *Geological Magazine* 148: 237–249.
- Laurenti, J.N. 1768. *Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium australianorum, quod auctoritate et consensu*. 217 pp. Joan. Thomae, Vienna.
- Merrem, B. 1820. *Versuch eines Systems der Amphibien/Tentamen systematis amphibiorum*. 191 pp. J.C. Krieger, Marburg.
- Mertens, R. 1942. Die Familie der Warane (Varanidae). Zweiter Teil: der Schädel. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 465: 117–234.
- Mertens, R. 1950. Der Schädel von *Varanus salvadorii*. *Zoologischer Anzeiger* 145 (Supplement): 561–566.
- Mertens, R. 1959. Der Schädel des indischen Gelbwarans, *Varanus flavescens*. *Senckenbergiana Biologica* 40: 113–115.
- Molnar, R.E. 2004. The long and honourable history of monitors and their kin; In: E.R. Pianka and R.A. King (eds.), *Varanoid Lizards of the World*, 10–67. Indiana University Press, Bloomington.

- Mones, A. 1989. Nomen dubium vs. nomen vanum. *Journal of Vertebrate Paleontology* 9: 232–234.
- Oppel, M. 1811. *Die Ordnungen, Familien, und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. 108 pp. J. Lindauer, Munchen.
- Rage, J.-C., and 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.
- Smith, K.T., Bhullar, B.A.S., and Holroyd, P.A. 2008. Earliest African record of the *Varanus* stem-clade (Squamata: Varanidae) from the Early Oligocene of Egypt. *Journal of Vertebrate Paleontology* 28: 909–913.
- Uetz, P., Hallermann, J., and Hosek, J. 2011. *The Reptile Database*. Available at <http://www.reptile-database.org>. Accessed October 10, 2011.
- 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*. 229 pp. Debrett, London.

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