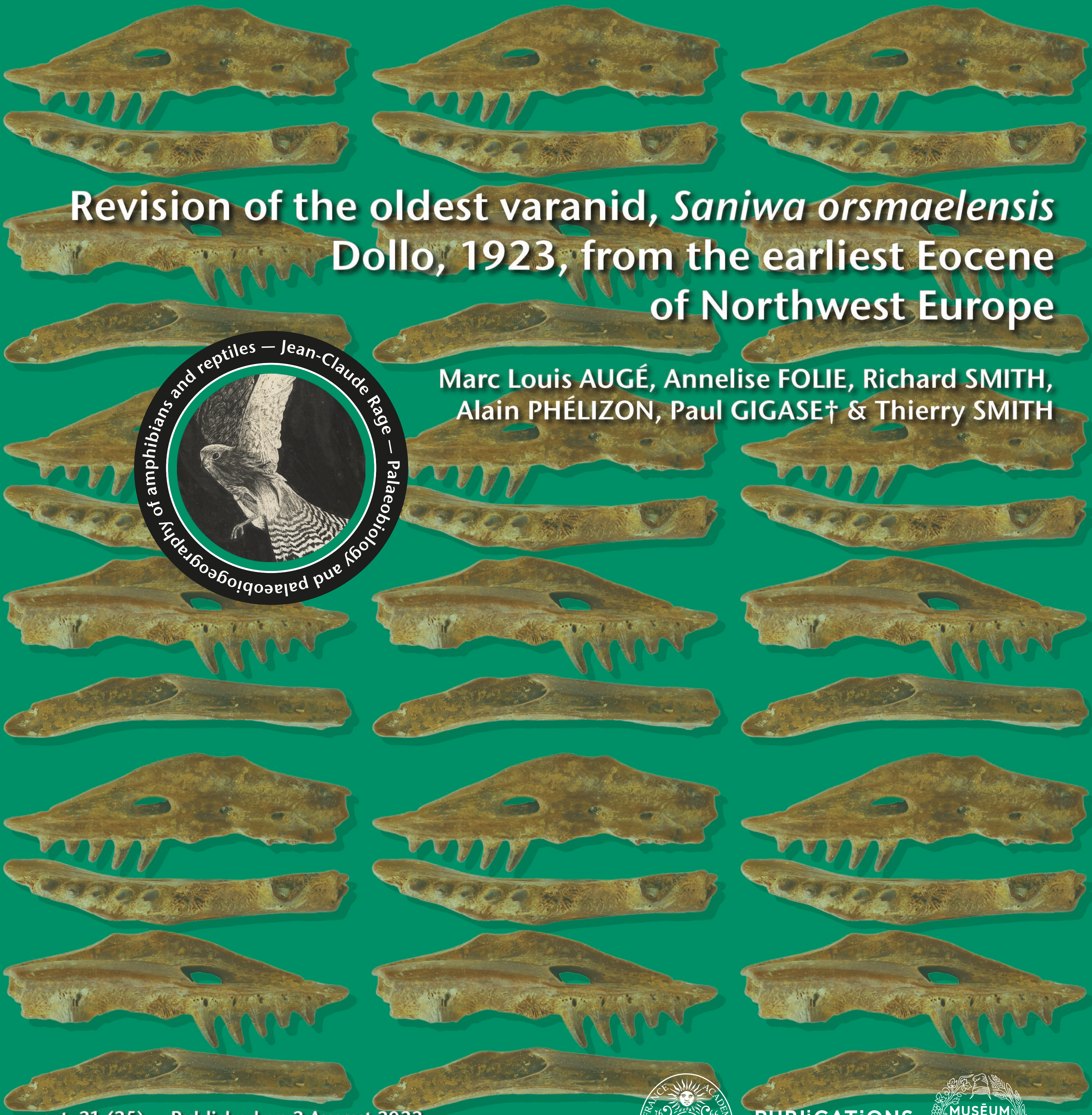
comptes rendus
palevol
2022 • 21 • 25



Revision of the oldest varanid, *Saniwa orsmaelensis* Dollo, 1923, from the earliest Eocene of Northwest Europe

Marc Louis AUGÉ, Annelise FOLIE, Richard SMITH,
Alain PHÉLIZON, Paul GIGASE† & Thierry SMITH

Jean-Claude Rage — Palaeobiology and palaeobiogeography of amphibians and reptiles

art. 21 (25) — Published on 2 August 2022
www.cr-palevol.fr

PUBLiCATiONS SCiENTiFiQUES

Directeurs de la publication / *Publication directors*:
Bruno David, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

Rédacteurs en chef / *Editors-in-chief*: Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

Assistante de rédaction / *Assistant editor*: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

Mise en page / *Page layout*: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

Révisions linguistiques des textes anglais / *English language revisions*: Kevin Padian (University of California at Berkeley)

Rédacteurs associés / *Associate editors*:

Micropaléontologie/*Micropalaeontology*
Maria Rose Petrizzo (Università di Milano, Milano)

Paléobotanique/*Palaeobotany*
Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/*Metazoa*
Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/*Palaeoichthyology*
Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*
Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*
Juliana Sterli (CONICET, Museo Paleontológico Egidio Feruglio, Trelew)

Lépidosauromorphes/*Lepidosauromorphs*
Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*
Eric Buffetaut (CNRS, École Normale Supérieure, Paris)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*
Lorenzo Rook (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*
Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*
K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*
Roberto Macchiarelli (Université de Poitiers, Poitiers)

Archéologie préhistorique/*Prehistoric archaeology*
Marcel Otte (Université de Liège, Liège)

Rédactrice invitée / *Guest editor* (**, took charge of the editorial process of the article*/a pris en charge le suivi éditorial de l'article):
Nathalie Bardet*

Référés / *Reviewers*: https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal

Couverture / *Cover*:
Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / Comptes Rendus Palevol *is indexed by:*
- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par / *Articles and nomenclatural novelties published in* Comptes Rendus Palevol *are registered on:*
- ZooBank® (http://zoobank.org)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol *is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Geodiversitas***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie***.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*
Comptes Rendus Mathématique, ***Comptes Rendus Physique***, ***Comptes Rendus Mécanique***, ***Comptes Rendus Chimie***, ***Comptes Rendus Géoscience***, ***Comptes Rendus Biologies***.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / https://sciencepress.mnhn.fr

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (https://creativecommons.org/licenses/by/4.0/)
ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

Revision of the oldest varanid, *Saniwa orsmaelensis* Dollo, 1923, from the earliest Eocene of northwest Europe

Marc Louis AUGÉ
Centre de Recherche en Paléontologie de Paris (CR2P), UMR 7207 CNRS-MNHN-SU,
Département Origines et Évolution, Muséum national d'Histoire naturelle,
CP38, 75 rue Cuvier, F-75005 Paris (France)
marc.louis.ed.auge@gmail.com

Annelise FOLIE
Institut royal des Sciences naturelles de Belgique, Service Scientifique du Patrimoine,
29 rue Vautier, B-1000 Bruxelles (Belgium)
annelise.folie@naturalsciences.be (corresponding author)

Richard SMITH
Institut royal des Sciences naturelles de Belgique, Direction opérationnelle Terre
et Histoire de la Vie, 29 rue Vautier, B-1000 Bruxelles (Belgium)
richardsmithpal@hotmail.com

Alain PHÉLIZON
Société d'Étude des Sciences Naturelles de Reims,
122 bis rue du Barbâtre, 51100 Reims (France)
alain.phelizon@orange.fr

Paul GIGASE†
Prins Albertlei 15, box 11, 2600 Berchem (Belgium)

Thierry SMITH
Institut royal des Sciences naturelles de Belgique, Direction opérationnelle Terre
et Histoire de la Vie, 29 rue Vautier, B-1000 Bruxelles (Belgium)
thierry.smith@naturalsciences.be

Submitted on 7 March 2019 | Accepted on 23 March 2021 | Published on 2 August 2022

urn:lsid:zoobank.org:pub:1BDC59E6-C9BC-4596-98A0-F6E63F862679

Augé M. L., Folie A., Smith R., Phélizon A., Gigase P. & Smith T. 2022. — Revision of the oldest varanid, *Saniwa orsmaelensis* Dollo, 1923,from the earliest Eocene of northwest Europe, *in* Folie A., Buffetaut E., Bardet N., Houssaye A., Gheerbrant E. & Laurin M. (eds), Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage. *Comptes Rendus Palevol* 21 (25): 511-529. https://doi.org/10.5852/cr-palevol2022v21a25

ABSTRACT

Saniwa is an extinct genus of varanid squamate from the Eocene of North America and Europe. Up to now, only one poorly known species, *Saniwa orsmaelensis* Dollo, 1923, has been reported from Europe. Diagnostic material was limited to vertebrae with only preliminary description and no figure provided, except of one dorsal vertebra that was designated as the lectotype. New specimens from the earliest Eocene of Dormaal, Belgium and Le Quesnoy, France, including recently recovered skull material, are described and illustrated here. These fossils representing the oldest varanid squamate allow further comparisons with the type species, *Saniwa ensidens* Leidy, 1870, from the early and middle Eocene of North America and to propose a new diagnosis for *S. orsmaelensis*. Its arrival in Europe is probably linked to rapid environmental changes around the Paleocene Eocene Thermal Maximum (PETM). The occurrence of *S. orsmaelensis* is restricted to the early Eocene of northwest Europe and paleogeographic considerations regarding the distribution of the genus *Saniwa* Leidy, 1870 suggest an Asian origin, but an African origin cannot be completely excluded.

KEY WORDS
Eocene,
Europe,
Dormaal,
Varanidae,
Saniwa.

RÉSUMÉ

Révision du plus ancien varanidé, Saniwa orsmaelensis *Dollo, 1923, de l'Éocène basal du Nord-Ouest de l'Europe.*

Saniwa est un genre éteint de squamate varanidé de l'Éocène européen et nord-américain. Jusqu'à maintenant, seule une espèce, *Saniwa orsmaelensis* Dollo, 1923 était rapportée en Europe. Le matériel diagnostique était limité à des vertèbres, décrites assez brièvement et non figurées, à l'exception d'une vertèbre dorsale, désignée comme lectotype. De nouveaux spécimens de l'Éocène basal de Dormaal, Belgique et Le Quesnoy, France, incluant des restes crâniens sont décrits et illustrés dans cet article. Ces fossiles qui représentent le plus ancien squamate varanidé permettent de nouvelles comparaisons avec l'espèce-type *Saniwa ensidens* Leidy, 1870, de l'Éocène moyen d'Amérique du Nord ainsi qu'une nouvelle diagnose de *S. orsmaelensis*. Son arrivée en Europe est probablement liée aux rapides changements environnementaux aux alentours du Maximum Thermique Paléocene Éocène (PETM). La présence de *S. orsmaelensis* est limitée à l'Éocène inférieur du nord-ouest de l'Europe et les considérations paléogéographiques liées à la distribution du genre *Saniwa* Leidy, 1870 suggèrent une origine asiatique, bien qu'une origine africaine ne puisse être complètement exclue.

MOTS CLÉS
Éocène,
Europe,
Dormaal,
Varanidae,
Saniwa.

INTRODUCTION

The genus *Saniwa* Leidy, 1870 is an Eocene varanid mainly known from the North American fossil record. The type species *Saniwa ensidens* Leidy, 1870 was originally described from the Bridger Formation of Sweetwater County, Wyoming. The type specimen of that species, USNM 2185, a disarticulated partial skeleton, came from the middle Eocene and was thoroughly reviewed by Gilmore (1922, 1928) and Estes (1983). Some years ago, Rieppel & Grande (2007) described a beautifully preserved complete articulated skeleton of *S. ensidens* from the late early Eocene of Green River Formation, Wyoming. Subsequently, Conrad *et al.* (2008) used these new data in a cladistic analysis of *S. ensidens* and of varanid relationships more generally. Finally, Smith *et al.* (2018) presented new data on the morphology of the pineal complex of this squamate based on two isolated parietal bones from the Bridger Formation. At present, *Saniwa* is widely regarded as the sister taxon to crown *Varanus* Merrem, 1820 (e.g. Pregill *et al.* 1986; Conrad *et al.* 2008, 2012), closing a long debate on the phylogenetic position of this genus; formerly Gilmore (1922, 1928), Camp (1923) and McDowell & Bogert (1954) placed the genus *Saniwa* in its own subfamily Saniwinae Camp, 1923. Following the recent work of Augé & Guével (2018) based on a matrix of 27 taxa and 21 vertebral characters, the assignment of *Saniwa* to Varanidae (*sensu* Estes *et al.* 1988) is supported by three synapomorphies: cotyle and condyle strongly expanded laterally; presence of more than eight cervical vertebrae; and on caudal vertebrae, chevrons are anterior to the posteroventral margin of the centrum. Moreover, *Saniwa*, *Varanus griseus* (Daudin, 1803), and *V. exanthematicus* (Bosc, 1792) form a clade supported by five synapomorphies (Augé & Guével 2018).

Over the years, numerous species have been named in the genus *Saniwa*, most based on vertebrae from North American localities (see Gilmore 1928; Hecht & Hoffstetter 1962; Estes 1983; Conrad 2008). Affinities of these vertebrae with the genus *Saniwa* are immediately indicated by their tapering centra with expanded condylar ends whose articular surface is invisible from ventral view and the presence of rudimentary zygosphene and zygantrum. According to Gilmore (1928) and Estes (1983), the differences from *S. ensidens* are mostly based on absolute size and minor variations in vertebral morphology. Moreover, the type specimens of *S. brooksi* Brattstrom, 1955, *S. crassa* (Marsh, 1872), *S. grandis* (Marsh, 1872), and *S. paucidens* (Marsh, 1872) are not sufficiently preserved for specific diagnosis. Rieppel & Grande (2007) considered these purported species as junior synonyms of *S. ensidens*. Finally, Smith (2006) described cranial material (dentary, parietal) from the late Eocene of North Dakota and named the new species *Saniwa edura* Smith, 2006 which may be the youngest definite record of varanid squamates in North America (Estes 1983; Sullivan & Holman 1996; Smith 2006).

Four purported members of the genus *Saniwa* have been recognized outside North America. *Saniwa orsmaelensis* Dollo, 1923 was originally described by Dollo (1923), based on dorsal vertebrae from the earliest Eocene of Dormaal, Belgium (MP7; Fig. 1). Stritzke (1983) described and named the species *Saniwa feisti* Stritzke, 1983 from a nearly complete skeleton preserved in the Messel shales (Germany, middle Eocene, MP11) but recurrent doubts have been expressed about the referral of this fossil (e.g. Augé 2005; Conrad *et al.* 2008). Recently, Smith *et al.* (2018) proposed the new combination *Necrosaurus feisti* (Stritzke, 1983), although Georgalis (2017) considered that this species could eventually pertain to the genus *Palaeovaranus* Zittel, 1887-1890. Ameghino (1899) named *Saniwa australis* Ameghino, 1899 on the basis of specimens from the Lower Miocene of Argentina (Santa Cruz beds), but the South American taxon turned out to be a *nomen dubium* because the fossils have never been figured or revised and are now considered lost (Báez & de Gasparini 1977; Estes 1983). In Asia, vertebrae from the Eocene of Kyrgyzstan have been referred to as ?*Saniwa* (Averianov & Danilov 1997); however, according to Conrad (2008), they lack varanid characters and are of little diagnostic value.

Estes (1983) gave a summary of the taxonomic status of *S. orsmaelensis*. He regarded this species as not different from *S. ensidens* and possibly representing a brief Eocene dispersal of *S. ensidens* in Europe, while the two continents were connected. Studies have long been hampered by the lack of diagnostic material (it consisted mainly of vertebrae) and because no adequate figures have been given nor a type chosen (Godinot *et al.* 1978). Hecht & Hoffstetter (1962) described and compared some specimens of *S. orsmaelensis* with *S. ensidens* but no figure was provided. Hoffstetter (1968: fig. 2) figured the specimen IRSNB R 298 from the original material of Dollo and Estes (1983) designated it as a lectotype. Afterwards Augé (1990a, b) revised some specimens of the type locality and from other early Eocene localities (Condé-en-Brie, Mutigny, MP8+9, France) and Augé (2005) proposed a diagnosis for *S. orsmaelensis*, exclusively based on vertebral morphology.

Here we describe and figure vertebrae, an incomplete maxilla, and a femur mentioned by Dollo (1923), a dentary and a humerus mentioned by Hecht & Hoffstetter (1962), and new vertebrae from Dormaal, Belgium, the type locality of *S. orsmaelensis*. We also report vertebrae, a dentary, and a parietal recently recovered from the locality of Le Quesnoy, Paris Basin, France (early Eocene, MP7; Nel *et al.* 1999; Fig. 1) that we also refer to *S. orsmaelensis*.

ABBREVIATIONS

Institutions

CB	Condé-en-Brie collection;
FMNH PR	Field Museum of Natural History (Chicago, IL);
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels;
MNHN	Muséum national d'Histoire naturelle, Paris;
MRAC	Musée royal de l'Afrique Centrale, Tervuren;
MU	Mutigny collection;
PTRM	Pioneer Trails Regional Museum (Bowman, ND);
QNY	Le Quesnoy collection;
R	fossil Reptilia collection;
USNM	United States National Museum (now National Museum of Natural History; Smithsonian Institution; Washington, DC);
YPM VP	Yale Peabody Museum of Natural History, New Haven, CT, Vertebrate Paleontology collections.

Other abbreviations

MP	reference-level of the mammalian biochronological scale for the European Paleogene. BiochromM'97;
PETM	Paleocene Eocene Thermal Maximum.

Fig. 1. — Map showing early Eocene (MP7) localities that have yielded squamate fossils in western Europe. The **stars** indicate localities that have yielded *Saniwa* Leidy, 1870 remains. The presence of *Saniwa* is restricted to the Northern Province as opposed to the Meridional Province (see Marandat *et al.* 2012).

SYSTEMATIC PALEONTOLOGY

Order SQUAMATA Oppel, 1811
Suborder ANGUIMORPHA Fürbringer, 1900
Superfamily Varanoidea Gray, 1827
Family Varanidae Gray, 1827

Genus *Saniwa* Leidy, 1870

Type species. — *Saniwa ensidens* Leidy, 1870 by original designation.

Saniwa orsmaelensis Dollo, 1923

Lectotype. — IRSNB R 298, dorsal vertebra (Hoffstetter 1968: fig. 2; Estes 1983: fig. 48D; Molnar 2004: fig. 2.11).

Type locality. — Dormaal, Flemish Brabant, Belgium, earliest Eocene, MP7.

Referred material. — Dormaal (MP7). IRSNB: 2 incomplete left maxillae, IRSNB R 393, Vert-8818-01; 2 incomplete left dentaries, IRSNB R 394; 3 fragmentary jaws, Vert-20681-03, Vert-20681-04, Vert-20681-05; 7 dorsal vertebrae, IRSNB R 116, IRSNB R 395, Vert-8737-04, Vert-8793-05, Vert-8818-03, Vert-16786-13, Vert-20681-02; 15 caudal vertebrae, IRSNB R 115, IRSNB R 396, IRSNB R 397, Vert-8685-01, Vert-8685-02, Vert-8818-04, Vert-8818-05, Vert-16786-14, Vert-16786-15, Vert-16786-16, Vert-20681-06; Vert-20237-05, Vert-20237-07, Vert-20237-08, Vert-20237-09; 19 dorsal vertebrae and 17 caudal vertebrae (unnumbered from collection P. Gigase); three anterior dorsal vertebrae, 23 dorsal vertebrae and 35 caudal vertebrae (unnumbered from collection R. Smith); one incomplete right humerus, IRSNB R 398; one femur, IRSNB R 69; one incomplete ilium?, Vert-16786-11.

Erquelinnes-Jeumont (MP7), IRSNB: four dorsal vertebrae Vert-6433-01, Vert-6433-02, Vert-6433-03, Vert-6433-04.
Le Quesnoy (MP7): 15 dorsal vertebrae, MNHN.F.QNY1.1152a-i, MNHN.F.QNY2.1155a-e, MNHN.F.QNY2.1158; 14 caudal vertebrae, MNHN.F.QNY1.1153a-f, MNHN.F.QNY2.1154, MNHN.F.QNY2.1156a-g) and tentatively 1 parietal, MNHN.F.QNY2.1157.

EMENDED DIAGNOSIS. — Differs from the genus *Varanus* in having a pseudozygosphene-pseudozygantrum complex on dorsal vertebrae and postzygapophyses aligned with the neural arch; differs from *Varanus* and *Saniwa ensidens* in having the supradental table of the maxilla that bears four teeth behind the last labial foramen; differs from *Saniwa ensidens* and *S. edura* by lateral margins of the parietal table not upturned; differs further from *S. ensidens* in having a parietal table narrower, parietal foramen surrounded by an ovoid-circular raised ridge, presence of a single pineal foramen (the parietal foramen); differs from *Saniwa edura* in having a rather smooth parietal table, and many closely spaced basal infoldings present on tooth bases.

DESCRIPTION

Skull and mandible

Maxilla (Fig. 2). Specimen IRSNB R 393 (lot 8737 in Hecht & Hoffstetter 1962) is an incomplete right maxilla briefly described by Dollo (1923). The anterior part and nearly all the facial process are lacking. However, the posterior part of the bone is complete and indicates that it was slender. Hecht & Hoffstetter (1962: 10) have already carefully described this fossil but they did not provide figure. Although partially preserved, this maxilla shows relevant morphologic characters. In labial view, the external surface of the maxilla is unsculptured. Three labial foramina are aligned on the ventral edge of the maxilla, the last foramen (at the level of the fifth tooth position from the rear) is by far the largest. These foramina are located in a shallow, mesiodistally directed concavity. The ventral edge of the maxilla is slightly eroded anteriorly (mostly at the level of the seventh tooth position from the rear). Medially, the supradental table (*sensu* Rage & Augé 2010) forms an obtuse ventral angle with the lateral wall, and no sulcus dentalis (dental gutter) is present. Eight tooth positions are preserved, the five most posterior teeth are almost complete and are posteriorly decreasing in size. The sub-pleurodont teeth are mediolaterally compressed, pointed, posteriorly recurved and their bases are enlarged. Mesio-distal keels very likely developed but are now eroded. All teeth have basoapical striae that betrayed the presence of plicidentine.

The dorsal surface of the supradental table bears a large maxillary foramen at the level of the fifth tooth from the rear. Posteriorly there is a shallow, wide concavity without any furrow for the contact with the jugal. The posterior extremity of the maxilla is posterolaterally directed, rounded with a slight step behind the last tooth.

Dentary (Fig. 3). Specimen IRSNB R 394 from Dormaal consists of the anterior part of an incomplete left dentary which is broken just behind the ninth tooth position. All the teeth are broken off and only two tooth bases (seventh and ninth) are visible. As preserved, this dentary is lightly built, elongated and shallow as in most extant *Varanus* species. The labial surface of the dentary is slightly convex and bears six irregularly spaced labial foramina, the first at the level of the boundary between the first and second tooth. Anteriorly, the dentary curves somewhat medially.

In lingual view, the Meckelian groove is open; its anterior part is a shallow sulcus that faces only ventrally, curving to the mandibular symphysis. Behind the fourth tooth position it becomes posteriorly wider and opens ventrolingually. The mandibular septum is not observable because the posterior part of the dentary is broken. The medial rim of the subdental table (surface inclined in cross section and extending as far as the dental crest *sensu* Rage & Augé 2010) is crescentic, this concavity is widely present among anguimorph squamates (Estes 1964). Medial to the tooth bases, no subdental shelf or sulcus dentalis are present and a subrounded surface forms the upper margin of the Meckelian groove.

On the poorly preserved tooth base of the seventh tooth, many closely spaced basal infoldings are present and these longitudinal striations are interpreted as an indication of the presence of plicidentine (Odermatt 1940; Bullet 1942; Caldwell 2003). This base is expanded and shows that the tooth attachment in this specimen is of the “subpleurodont type” or “fully pleurodont” as defined by Zaher & Rieppel (1999).

Comparisons. All characters of the dentary and maxilla (overall morphology, subpleurodont implantation of the teeth, basal infoldings, plicidentine), caniniform morphology of the teeth) support platynotan, more precisely varanid relationships. Hecht & Hoffstetter (1962) expressed doubts about the referral to *Saniwa* and they did not exclude a possible referral to *Palaeovaranus* (previously *Necrosaurus sensu* Georgalis, 2017), e.g. by the presence of four teeth behind the maxilla foramen. However, at present the teeth of *Palaeovaranus* from Dormaal are known (from two undescribed dentaries) and their morphology differ significantly from that of *Saniwa*.

Hecht & Hoffstetter (1962) pointed out the varanid features present in the maxilla IRSNB R 393: teeth sub-pleurodont, caniniform with development of plicidentine on their bases; enlargement of the last labial foramen such as in *Varanus salvator* (Dollo, 1923). However, Hecht & Hoffstetter (1962) also noted a character that distinguishes this maxilla from those of extant varanids (genus *Varanus*): the supradental table hosts four teeth behind the last labial foramen while in the genus *Varanus* only one or two teeth are present behind this foramen. In other words, the posterior part of this maxilla extended well below the orbit, in contrast with the maxilla of extant varanids that is excluded from the orbit. This plesiomorphic feature also appears in *S. ensidens* in which five teeth are present after the last labial foramen (Dollo 1923), and Gilmore (1922, 1928), Estes (1983: 184), Rieppel & Grande (2007) confirmed the presence of a long posterior (zygomatic) process of the maxilla in *S. ensidens*, which underlies the orbit with the last two or three teeth in a suborbital position, a plesiomorphic condition that is universally absent in *Varanus*, according to Rieppel & Grande (2007).

Fig. 2. — **A**-**D**, *Saniwa orsmaelensis* Dollo, 1923, Dormaal, Belgium. Left maxilla, IRSNB R 393, in labial (**A**), ventral (**B**), lingual (**C**), and dorsal (**D**) views. Abbreviations: **llf**, last lateral foramen; **mf**, maxillary foramen; **pl**, plicidentine; **st**, supradental table. Scale bar: 5 mm.

Parietal (Fig. 4). Specimen MNHN.F.QNY2.1157 from Le Quesnoy, France, is a well-preserved, unpaired bone, rectangular and comparatively elongated antero-posteriorly (Fig. 4). The extremities of the two anterolateral processes and, posteriorly, the two supratemporal processes are broken off.

The dorsal surface of the parietal table bears some traces of weathering; otherwise it is fairly smooth except for weak striations developed near the parietal foramen. No osteodermal encrustations are present and the lateral margins of the parietal table are not upturned. The large parietal foramen opens anteriorly on the parietal table, it is not located on the fronto-parietal suture (Gilmore 1928; Estes 1983). The parietal foramen is surrounded by a raised ovoid to circular ridge. Anteriorly, the frontoparietal suture was not interdigitated except for some slight interdigitations near the midline of the frontal; inconspicuous anterolateral facets for the articulation with the frontal are present.

The lateral margins of the parietal table are concave and form descending lateral walls that certainly received the pseudotemporalis superficialis muscle, as is also the case in *Varanus*. Posteriorly, the supratemporal processes are broken

Fig. 3. — **A**-**C**, *Saniwa orsmaelensis* Dollo, 1923, Dormaal, Belgium. Left dentary fragment, IRSNB R 394, in lingual (**A**), labial (**B**), and dorsal (**C**) views. Abbreviation: **pl**, plicidentine. Scale bar: 5 mm.

but their bases diverge posterolaterally. Thus, the posterior border of the parietal is broadly concave.

On the ventral side, two weak crests separate the basis of the supratemporal processes from the main part of the parietal. The deep parietal fossa is located between those crests, well behind the parietal foramen. The ventral surface is rather smooth except for a strange circular depression in the parietal fossa. Because this depression does not open on the dorsal side of the parietal and is located well behind the parietal foramen, on a midpoint between the parietal foramen and the posterior border of the parietal, it could likely not represent a pineal foramen (*sensu* Smith *et al.* 2018), whereas the pineal foramen of *S. ensidens* is located just behind the parietal foramen (Smith *et al.* 2018: fig. 2B, C). This depression is considered here to represent the parietal fossa. A similar structure is observed on a parietal of *Pseudopus apodus* (Pallas, 1775) (Klembara *et al.* 2017a: fig. 17D12; b: fig. 6B) and *Ophisaurus manchenioi* Blain & Bailon, 2019 (Blain & Bailon 2019: fig. 3B).

Comparisons. This parietal closely resembles those of *Varanus* and *S. ensidens*: temporal muscles originate from the dorsolateral surface of the parietal rather than from the ventral surface, leaving a wide amuscular parietal table; deep posterior parietal fossa; ventral ridges moderately developed; osteoderms reduced or absent; anterior position of the parietal foramen; general morphology of the bone (McDowell & Bogert 1954; Pregill *et al.* 1986). According to Evans (2008), the parietal foramen of *Varanus* is small, but Mertens (1942) noted significant ontogenetic variation of the relative size of the parietal foramen among the *Varanus* species . Also, the frontoparietal suture is likely simpler in *Saniwa* and more complex in *Varanus* (Conrad *et al.* 2008). Recently, Smith *et al.* (2018) described the pineal complex of the parietal of the *S. ensidens* specimens from the Bridger Formation in the Bridger Basin, Wyoming, with the presence of a widely open parietal foramen and a smaller pineal foramen. This complex is unfortunately not observable on specimen FMNH PR2378 of *S. ensidens* from Green River (Rieppel & Grande 2007) or on specimen PTRM 5380 of *S. edura* (Smith, 2006). However, similarities can be noted between the parietal MNHN.F.QNY2.1157 of *S. orsmaelensis* (Fig. 4) and that of the type specimen USNM 2185 of *S. ensidens* (Gilmore 1922: pl. 9, fig. 11). Indeed, anteriorly, the shape and location of the pineal foramen, the width of the parietal between the crests and the posterior border of the bone (concave anteriorly and forming a large notch) are very similar. The pineal foramen is described as being on the fronto-parietal suture. However, because the parietal of *S. ensidens* is not complete anteriorly, we cannot be sure of this, and specimen FMNH PR2378 described by Rieppel & Grande (2007) confirms that the pineal foramen is well enclosed in the parietal. The two bones differ by the extension of the parietal processes, which are more laterally expended on *S. ensidens* than on *S. orsmaelensis*.

Vertebrae

Dorsal vertebrae (Fig. 5). Vertebrae are procoelous with roughly triangular, tapering centra, condyles and cotyles oval, laterally expanded and with a flange. The articular surface of the condylar ball is directed dorsally, and the condylar surface is scarcely apparent in ventral view. This situation appears reversed for the cotyle.

In dorsal view, the neural arch is slanting anteriorly with the presence of anterior pars tectiformis. A weak midline keel runs along the neural arch, but it does not reach the anterior margin of the vertebra. Its posterior end is flared and markedly taller than the anterior end, forming the neural spine when preserved. Hence the neural spine is, at best, moderately antero-posteriorly elongated.

The prezygapopyseal facets form an angle of about 40 degrees with the horizontal plane. The anterior aspect of the neural arch presents a pair of rudimentary inclined elevations. Clearly, they do not possess articular facets and they cannot be considered real zygosphenes. As Albino & Brizuela (2014) recognized, there is no zygosphenal articulation in Anguidae and more generally in extant Anguimorpha. This structure is not homologous to the zygosphene and it is called pseudozygosphene, according to Hoffstetter & Gasc (1969) (for additional comments on zygosphenes see Albino & Brizuela 2014). Pseudozygantrum is only variably present at the rear of the vertebra.

In lateral view, the synapophyseal facets are approximately vertical and they extend the entire height of the centrum.

In ventral view, a precondylar constriction is visible at the rear of the centrum. This constriction is less developed than on the dorsal vertebrae of *S. ensidens* (see Gilmore 1928). The ventral aspect of the centrum is smooth (without ridges) and slightly convex transversely. Pregill *et al.* (1986) noted that a marked precondylar constriction of the vertebrae is an autapomorphic feature of the *Varanus* lineage because this constriction is very weak or absent in *Lanthanotus* Steindachner, 1877 and *Heloderma* Wiegmann, 1829 and absent in Palaeovaranidae (Rage, 1978).

FIG. 4. — **A**-**C**, *Saniwa orsmaelensis* Dollo, 1923, Le Quesnoy, France. Parietal, MNHN.F.QNY2.1157, in posterior (**A**), dorsal (**B**), and ventral (**C**) views. Abbreviations: **pfr**, parietal foramen; **pfs**, parietal fossa. Scale bar: 5 mm.

Caudal vertebrae (Fig. 6). The centrum is rather elongated and narrow, there is no trace of autotomic septum and the cotyle and condyle are, as on the dorsal vertebrae, oval (dorsoventrally flattened). In lateral view, the vertebrae only preserve the dorsoventrally flattened bases of the transverse processes (one per side) that are attached to the anterior fourth of the centrum. In dorsal view, the prezygapophyseal facets are oval and project beyond the lateral margins of the neural arch. Between them, there is no evidence of a pseudozygosphene. No striae are present on the neural arch. The neural spine of a caudal vertebra from Dormaal (specimen IRSNB R 397, Fig. 6H) is preserved. It is moderately high and rather antero-posteriorly extended but it does not reach the anterior margin of the vertebra. Its anterior margin is somewhat concave and its posterior margin slants posterodorsally. In ventral view, a pair of short articular protuberances located on the posterior third of the ventral surface of the centrum indicates the point of articulation of the chevron bones. A ridge runs anteriorly from the base of each protuberances and a median concavity occupies the space between the two ridges. As in *S. ensidens*, the precondylar constriction is less developed than on dorsal vertebrae.

Comparisons. These vertebrae present anguimorph characters such as a smooth ventral surface of the centrum, synapophyses nearly vertical and hemicylindrical, and two keels on the ventral face of the centrum of the caudal vertebrae (Augé & Guevel 2018). Moreover, the general morphology of the vertebrae resembles those of extant varanids by the following characters: presence of a single pair of postero-laterally oriented transverse processes placed in the anterior part of the centrum and absence of an autotomic plane, orientation of the cotyle and condyle are of characteristic varanid form (e.g. posterior retraction of the ventral rim of the cotyle) and the well developed chevron facets just anterior to the posterior margin of the centrum on caudal vertebrae (Etheridge 1967; Augé & Guevel 2018). This last character would be a synapomorphy of the Varanidae (Augé & Guevel 2018). Additional similarities to varanid taxa are the anteriorly depressed neural arch (pars tectiformis), presence of a distinct precondylar constriction, and absence of a median ventral ridge on the dorsal vertebrae. These two last features also occur in the agamid genus *Uromastyx* Merrem, 1820 (Hoffstetter & Gasc 1969; Rage & Augé 2015). However, the caudal vertebrae of *Uromastyx* (present in the European Paleogene, Oligocene epoch) as in most agamids are characterized by circular cotyle

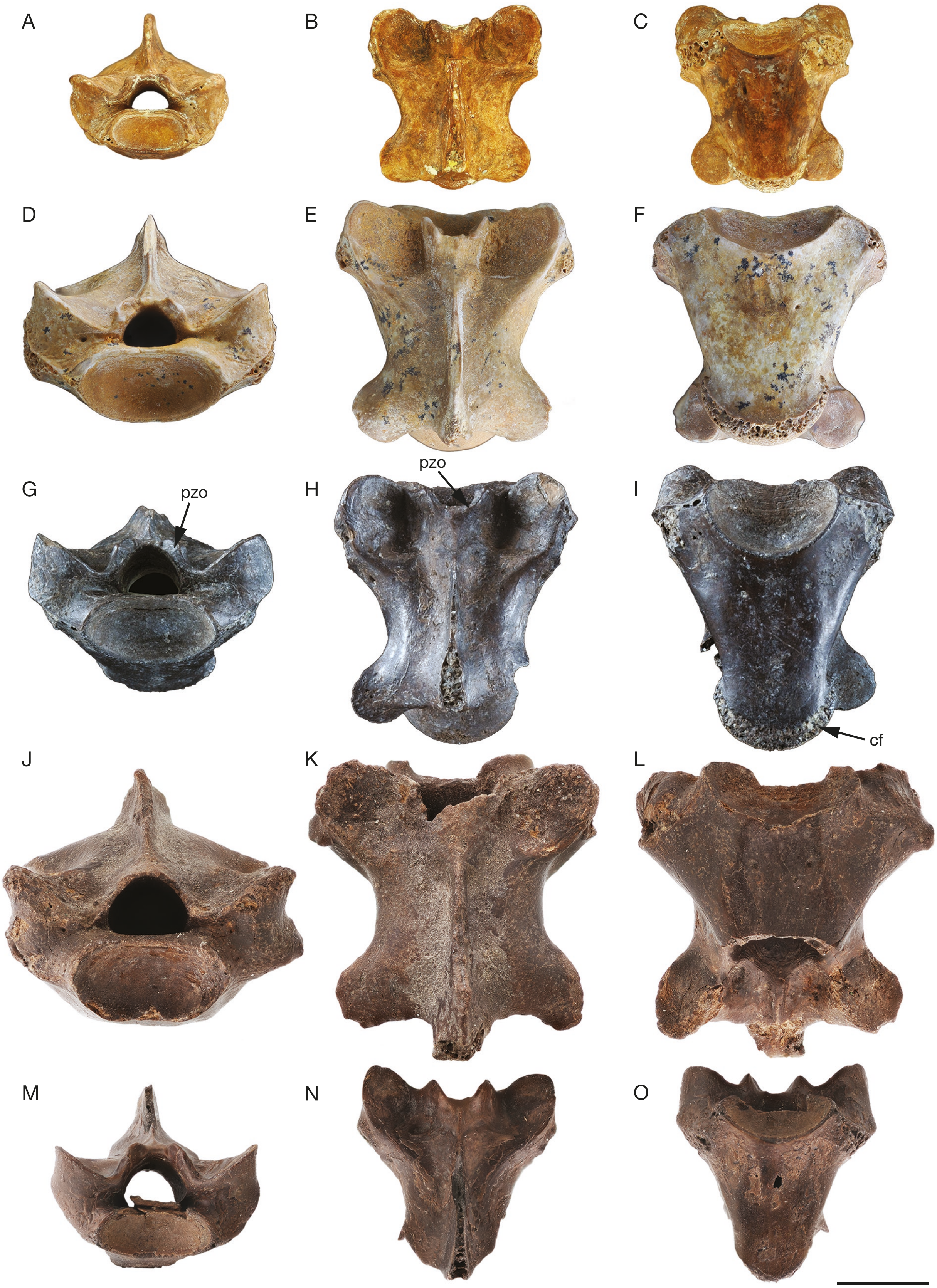


FIG. 5. — *Saniwa orsmaelensis* Dollo, 1923. Dorsal vertebrae: **A**-**C**, Dormaal, Belgium, IRSNB R 298, in anterior (**A**), dorsal (**B**) and ventral (**C**) views; **D**-**F**, Dormaal, Belgium, IRSNB R 395, in anterior (**D**), dorsal (**E**) and ventral views (**F**); **G**-**I**, Le Quesnoy, France, MNHN.F.QNY2.1158, in anterior (**G**), dorsal (**H**) and ventral views (**I**); **J**-**L**, Le Quesnoy, France, MNHN.F.QNY2.1155a, in anterior (**J**), dorsal (**K**) and ventral views (**L**); **M**-**O**, Le Quesnoy, France, MNHN.F.QNY2.1155b, in anterior (**M**), dorsal (**N**), ventral views (**O**). Abbreviations: **cf**, condyle flange; **pzo**, pseudozygosphene. Scale bar: 5 mm.

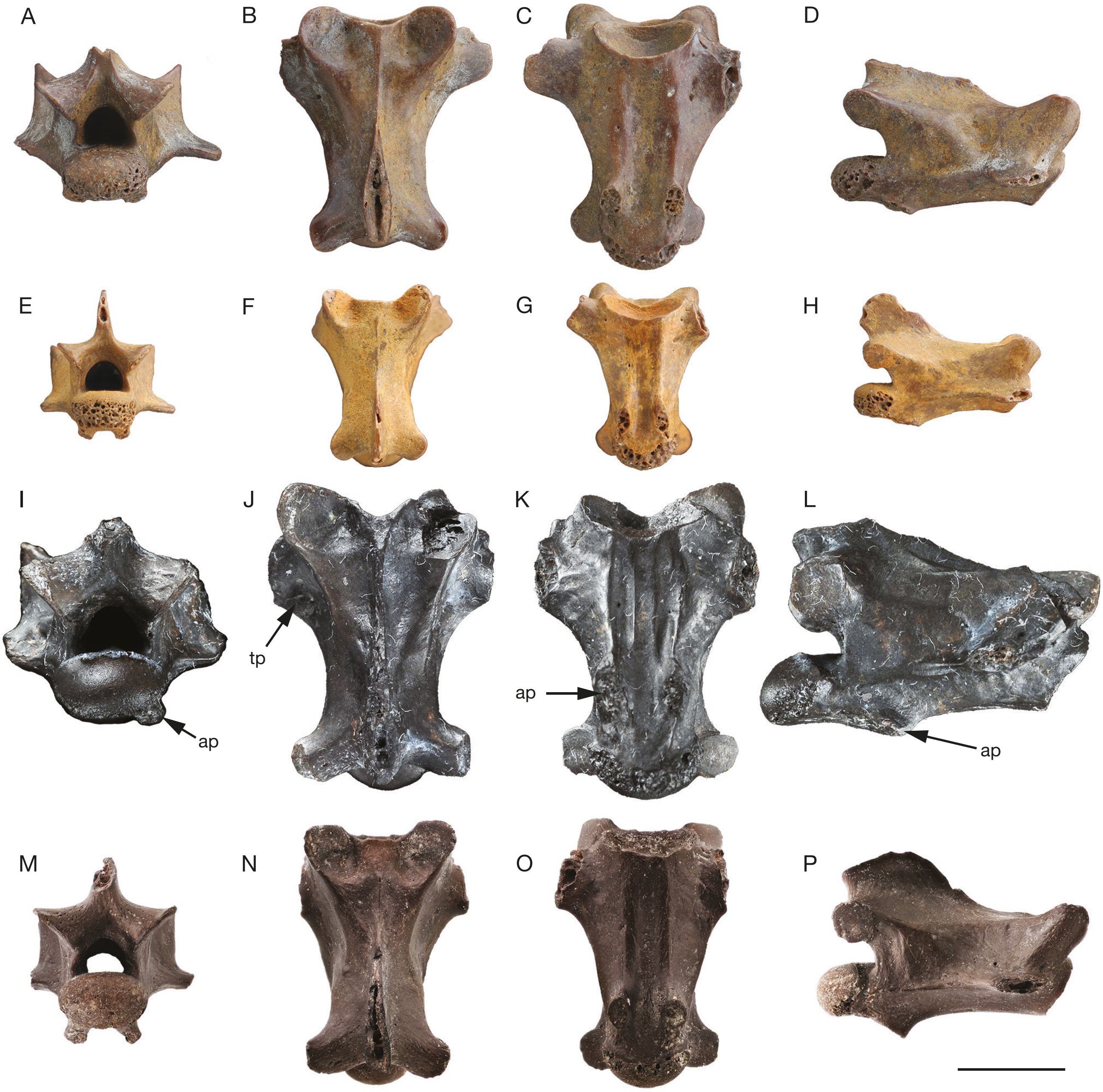


Fig. 6. — *Saniwa orsmaelensis* Dollo, 1923. Caudal vertebrae: **A**-**D**, Dormaal, Belgium, IRSNB R 396, in posterior (**A**), dorsal (**B**), ventral (**C**), and right lateral views (**D**); **E**-**H**, Dormaal, Belgium, IRSNB R 397, in posterior (**E**), dorsal (**F**), ventral (**G**), and right lateral views (**H**); **I**-**L**, Le Quesnoy, France, MNHN.F.QNY2.1154, in posterior (**I**), dorsal (**J**), ventral (**K**) and right lateral views (**L**); **M**-**P**, Le Quesnoy, France, MNHN.F.QNY2.1156, in posterior (**M**), dorsal (**N**), ventral (**O**) and right lateral views (**P**). Abbreviations: **ap**, articulation process with the chevron bones; **tp**, transverse process. Scale bar: 5 mm.

and condyle, devoid of articular surface for the chevron bones, and lateral transverse processes are attached to the mid-length of the centrum. The main characters that distinguish *Saniwa* from *Varanus* are the presence of a pseudozygosphene-pseudozygantrum complex on the dorsal vertebrae (e.g. Dollo 1923; Rieppel & Grande 2007) and the anterior border of the vertebrae (including the prezygapophyses) which forms a line instead of a central notch on *Varanus* vertebrae (Gilmore 1928). Moreover, the precondylar constriction is less marked than in *Varanus*. Several authors also indicate that the neural spine on the dorsal and caudal vertebrae of *Saniwa,* which is anteroposteriorly well developed and lower than in *Varanus,* is a diagnostic character of *Saniwa* (Dollo 1923; Estes 1983; Rieppel & Grande 2007). However, other authors also indicate that the shape, size and extension of the neural spine are changing both along the vertebral column and with ontogeny (Gilmore 1928; Rieppel & Grande 2007). This character has therefore to be considered with caution.

Limbs

Humerus (Fig. 7). Specimen IRSNB R 398 is the distal end of a right humerus; the ulnar and radial condyles are lacking (Fig. 7). The entepicondyle is incomplete but it seems well developed and it is set off from the posterior margin of the

Fig. 7. — **A**, **B**, *Saniwa orsmaelensis* Dollo, 1923, Dormaal, Belgium. Right distal humerus, IRSNB R 398, in ventral (**A**), and dorsal views (**B**). Abbreviations: **ent**, entepicondyle; **ectc**, ectepicondylar crest; **ectf**, ectepicondylar foramen; **sf**, small foramen. Scale bar: 5 mm.

diaphysis of the humerus. The entepicondylar foramen is absent as in *S. ensidens*. The ectepicondyle is broken but it is prolonged distally by a short ascending crest (ectepicondylar crest) which is pierced by an ectepicondylar foramen. In ventral view, a large triangular depression is present just proximal to the condyles and a small foramen opens on the proximal rim of the depression.

Comparisons. This bone is tentatively referred to *S. orsmaelensis* based on size and varanid features. The presence of an ectepicondylar crest is consistent with referral of the humerus to varanids and more specifically to *Saniwa* (Lécuru 1969). In addition, the large triangular depression above the condyles, pierced by a small foramen that opens on the proximal rim of the depression, is characteristic of varanid squamates (Smith 2009). According to Lécuru (1968) and Smith (2009) this foramen is observed in nearly all limbed squamates, but it is quite reduced or even absent in *Varanus*. Moreover, the absence of an olecranon scar on the dorsal side is also considered a varanid feature (Hecht & Hoffstetter 1962). A potentially conflicting character is the moderately laterally projected entepicondyle. Rieppel & Grande (2007) and Gilmore (1922, 1928) noted that the entepicondyle is more distinctly developed in *S. ensidens* than in *Varanus* but it is worth noting that the entepicondyle of the specimen from Dormaal is incomplete.

Two other large anguimorphans, *Palaeovaranus* and *Placosaurus* Gervais, 1848, are also present at Dormaal (Sullivan *et al.* 2012), and the morphology of their limbs is as yet virtually unknown. Hence the referral of this humerus to *Saniwa* cannot be accepted without reservations. As a last point, it could be worth noting that Hoffstetter left a manuscript note with the specimen indicating that he refers this humerus to *S. orsmaelensis*.

Femur (Fig. 8). The right femur IRSNB R 69 is 28 mm long and is nearly complete (Fig. 8). It lacks only the proximal main condyle (articulating with the acetabulum of the pelvis) and the distolateral condyle. It is long, slender and sigmoidal. Proximally, the greater trochanter is present and well developed. A scar is likely present along the shaft just below this latter trochanter. A shallow groove is present dorsally between the trochanter and the base of the proximal main condyle. The ventral side is smooth. Distally, a small rounded medial condyle is preserved. The lateral condyle is broken and preserves only its base, which suggests that it was oval. Dorsally, a deep groove between the two condyles extends perpendicularly to the shaft up to the diaphysis. Ventrally, the extremity of the lateral condyle extends and forms the base of a rounded crest. The epiphysis is therefore triangular in distal view.

Comparisons. The femur was first mentioned by Dollo (1923), who indicated that it presents varanid characters and can be attributed to *S. orsmaelensis*. However, Hecht & Hoffstetter (1962) indicated that its systematic attribution should be uncertain because it presents affinities with palaeovaranids. They also indicated that this bone could be a juvenile without epiphyses. None of the authors figured the specimens.

The femur from Dormaal, is very similar to that of *Varanus niloticus* (comparison to specimen MRAC 92-048-R-0038 from Togo). The specimen from Dormaal is about half the size of the recent one but presents the same sigmoid curve and the same structures. The lateral distal condyle is more distally extended. Some additional crests are developed on the recent specimen in lateral view at the level of the epiphyses. However, this could be due to erosion of the specimen. Given these similarities, we consider the femur IRSNB R 69 part of the material attributed to *S. orsmaelensis.*

Attribution of the material to *Saniwa orsmaelensis*

The bones described hereall come from the locality of Dormaal and are grouped together based on their individual morphology, their comparable size and proportion. Consequently, they are all attributed to a single taxon presenting clear anguimorph characters. Hecht & Hoffstetter (1962) indicated that three large anguimorphs are present in Dormaal: *Placosaurus* (Anguidae; Sullivan *et al.* 2012), *Palaeovaranus* (previously *Necrosaurus*, *Palaeovaranidae*), and *Saniwa* (Varanidae). Each of the bones described here presents varanid characteristics: subpleurodont and caniniform teeth presenting plicidentine, a large last (posterior) foramen on the maxilla, a single pair of transverse processes placed in the anterior part of the vertebral centrum, absence of an autotomic plane, cotyle visible ventrally, anteriorly depressed neural arch (pars tectiformis), presence of a distinct precondylar constriction, absence of a median ventral ridge on dorsal vertebra, well developed chevron facets anterior to the posterior margin of the centrum on caudal vertebrae, presence of a small ventral foramen above the humeral condyle, absence of an olecranon scar on the dorsal face of the humerus (Dollo 1923; Hecht & Hoffstetter 1962; Etheridge 1967; Smith 2009).

Referral of the specimens described here to the genus *Saniwa* is based on their general similarity to the type species *S. ensidens*: presence of four to five teeth behind the last labial foramen, pseudozygosphene-pseudozygantrum complex on the dorsal vertebrae, thin anterior end of the dentaries (Gilmore 1922; Dollo 1923; Hecht & Hoffstetter 1962). The similarities have already been mentioned several times in the literature (e.g. Hecht & Hoffstetter 1962; Rieppel & Grande 2007) and some authors (e.g. Estes 1983) even indicated that the two species could be synonymous with the Dormaal specimens representing just a brief incursion of *S. ensidens* in Europe. However, some differences have to be noted: the last (posterior) foramen of the maxilla is larger than on *S. ensidens* (Rieppel & Grande 2007: fig. 4 contra Fig. 2), presence of four teeth after the large last foramen of the maxilla instead of five teeth on *S. ensidens* (Dollo 1923). These differences are weak, especially because the variability is unknown and therefore it would not be parsimonious to consider the Dormaal taxon a new genus. This is why we refer them here to the species *Saniwa orsmaelensis*.

Dorsal and caudal vertebrae found at Le Quesnoy present the same morphology as the specimens from Dormaal (including the presence of a pseudozygosphene-pseudozygantrum complex, see Figs 5; 6). Additionally, the parietal also presents varanid characters such as the presence of two lateral crests instead of a single sagittal crest (*Palaeovaranus cayluxi* Zittel, 1887 [Augé 2005: fig. 188a]) or a narrow extension of the table ("*Necrosaurus eucarinatus*" Kuhn, 1940 [Augé 2005: figs 194, 195]) posteriorly (Rage 1978; Rage & Augé 2010). Because no other varanid taxa have been found at Le Quesnoy, we also attribute this parietal and the vertebrae to *S. orsmaelensis*.

In addition to these arguments, it has to be noted that Dormaal and Le Quesnoy are located in the same geographic area corresponding to the southern North Sea Basin (Northwestern Europe, Fig. 1) and sedimentary conditions are nearly similar: the Dormaal Sands are a series of fluviatile beds, typical of the lower part of the Tienen Formation which is very similar to the channel deposits of the Sparnacian facies of the Paris Basin (Smith & Smith 1996; Steurbaut *et al.* 1999). According to the paleobotanical association, the Dormaal paleoriver system was bordered by warm-temperate to humid subtropical forests (Fairon-Demaret & Smith 2002). The Le Quesnoy locality exposes a succession of fluvio-lacustrine deposits, typical of the Sparnacian facies. They are also indicative of a paleoriver system bordered by wet, subtropical forests with similar fauna and flora (Nel *et al.* 1999, 2004; Jacques & De Franceschi 2005).

Actually, if we compare the "lizards" (non-ophidian squamates) assemblages from Dormaal and Le Quesnoy, the species-poor locality (Le Quesnoy) is a subset of the assemblage of Dormaal (all "lizard" species and genera present at Le Quesnoy are shared with the assemblage of Dormaal). This pattern points to the similarity between the "lizard" assemblages from Dormaal and Le Quesnoy. Thus, their differences in diversity and abundance mainly reflect differences in quantity and exploitation of the fossiliferous substratum.

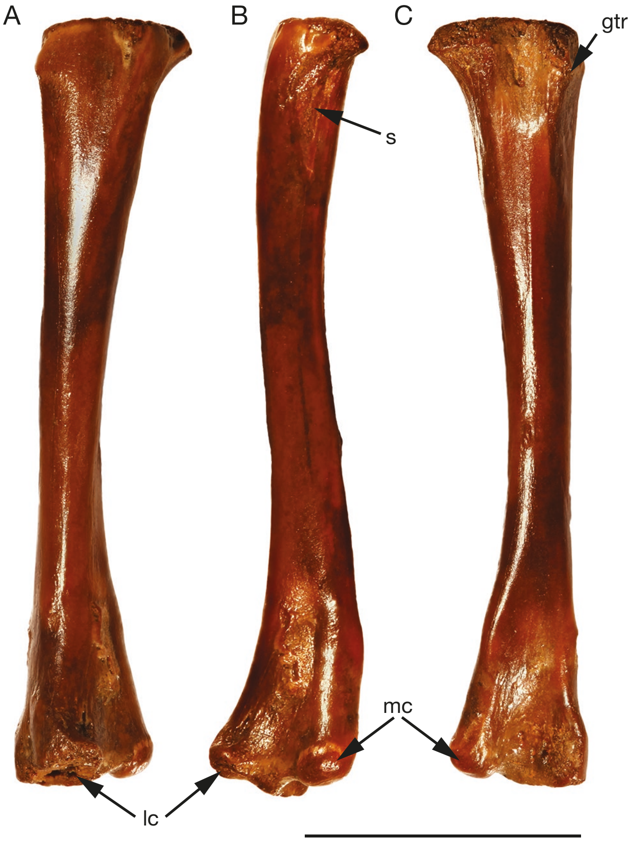


Fig. 8. — **A**-**F**, *Saniwa orsmaelensis* Dollo, 1923, Dormaal, Belgium. Right femur, IRSNB R 69, in dorsal (**A**), lateral (**B**), ventral (**C**), medial (**D**), proximal (**E**) and distal (**F**) views. Abbreviations: **gtr**, greater trochanter; **lc**, lateral condyle; **mc**, medial condyle; **s**, scar. Scale bar: 10 mm.

As Hecht & Hoffstetter (1962) recognized, the cranial elements of *Saniwa* are difficult to separate from those of a purported Varanoidea, the genus *Palaeovaranus* which is present at Dormaal. In contrast, the vertebrae attributed to *Palaeovaranus* or *Saniwa* are readily distinguishable: the centrum of the dorsal vertebrae of *Palaeovaranus* bears no precondylar constriction; in *Palaeovaranus*, articulations with the chevron bones of the caudal vertebrae are in contact with the condyle on the ventral side of the centrum and the transverse processes are inserted more posteriorly in the centrum than those of *Saniwa* (Rage 1978: fig. 5; Rage & Augé 2015: fig. 3).

Comparisons to skull elements of *Palaeovaranus* from the Eocene of the Phosphorites du Quercy (two species are currently described, *P. cayluxi* and *P. eucarinatus* [Estes 1983; Augé 2005]) allow further distinctions between *Saniwa* and *Palaeovaranus*.

Despite a similar overall morphology of the dentary of *S. orsmaelensis* and that of *Palaeovaranus* (e.g. *P. cayluxi*, Augé 2005: figs 185, 186), numerous closely spaced basal infoldings are present on the tooth base of *Saniwa* whereas there are few, widely spaced striations in *Palaeovaranus*. The parietal of *Palaeovaranus* presents prominent dermal incrustations on the parietal table, which are often represented by oval, keeled osteoderms characteristic of the genus. In contrast, the parietal of *Saniwa* is devoid of dermal incrustation.

Fig. 9. — **A**, **B**, *Saniwa orsmaelensis* Dollo, 1923, Avenay, France. Left dentary fragment, MNHN, unnumbered, in lingual (**A**), and labial views (**B**). Abbreviation: **pl**, plicidentine. Scale bar: 5 mm.

A large parietal fossa is present in *Palaeovaranus*, whereas it is less developed in *Saniwa*. The ventral crests on the ventral surface of the parietal are absent or extremely reduced in *Palaeovaranus*. Thus, although the skull elements of *Saniwa* superficially resemble those of *Palaeovaranus*, the two taxa are always distinguishable by several features. Beside this, on the caudal vertebrae, the transverse processes are close to the condyle, which is not the case for the *Palaeovaranus* vertebrae (Hecht & Hoffstetter 1962), and the condyle and cotyle are oval in *Saniwa* and more rounded in *Palaeovaranus* (Estes 1983).

Although the vertebrae do not bring new information to help the characterisation of *S. orsmaelensis*, it is not the case with the parietal, which brings additional data. Indeed, the parietal of *S. orsmaelensis* differs from that of *S. ensidens* by the oval shape of the parietal foramen (instead of a round foramen [Rieppel & Grande 2007]), by less laterally extended lateral processes (instead of well laterally extended processes [Smith et al. 2018]), by the parietal fossa which is more ventrally placed (instead of being posteriorly placed [Smith *et al.* 2018; Fig. 4]) and maybe the absence of a pineal foramen (presence of the foramen in specimens YPM VP 1074 and 613 from the Bridger Formation of Grizzly Buttes in Uinta County [Smith *et al.* 2018]). It resembles *S. edura* by the shape and size of the parietal foramen (Smith *et al.* 2018) but differs from this species by having a less ornamented surface. These differences are again too weak to identify a new genus and reinforce the validity of the species *S. orsmaelensis.*

Other material attributed to *Saniwa* sp. in the European early Eocene

Pourcy, early Eocene (MP7), Paris Basin, France: one dorsal vertebra, coll. Gigase.

Condé-en-Brie, early Eocene (MP8+9), Paris Basin, France: two caudal vertebrae MNHN.F.CB16459 and MNHN.F.CB16458 (Augé 1990b: fig. 12).

Avenay, early Eocene (MP8+9), fragmentary left dentary, collection A. Phelizon, MNHN, unnumbered (Fig. 9).

Mutigny, early Eocene (MP8+9), Paris Basin, France, two caudal vertebrae, MNHN.F.MU17498 (Fig. 10), two sacral vertebrae, MNHN.F.MU7909 (Augé 1990a: fig. 2).

Fossy (Paris Basin, France, MP8+9 or MP10): 1 caudal vertebra, collection M. Dion, unnumbered.

The morphology of these specimens (Figs 9; 10) does not differ from those of the dentary (Fig. 3) and vertebrae (Figs 5; 6) attributed to *S. orsmaelensis* and described above. However, examination of the dentary from Avenay (Fig. 9) reveals an interesting feature (tied to the presence of plicidentine). This bone is a medial portion of a large dentary preserving six tooth positions including two tooth bases. Implantation of the teeth are of the subpleurodonte type, as defined above. Their bases bear numerous tightly spaced infoldings. Each tooth has a large nutrient foramen located near the medial mid-point of the base. Their shaft is broken at approximately mid-height of the tooth, so the internal cavity of the tooth is exposed, and it appears that plicidentine is present in the form of dentine lamellae that subdivide the tooth cavity (Bullet 1942; Rieppel 1979; Maxwell *et al.* 2011). This kind of structure, visible in Varanidae, Helodermatidae Gray, 1837, Lanthanotidae Steindachner, 1877 but also in crossopterygians, amphibians, ichthyosaurs (Preuschoft *et al.* 1991), and Synapsida (Laass & Schillinger 2020), has likely a functional role to strengthen the tooth attachment to the jaws. A study based on snakes indicates that it could also increase the flexibility of the tooth base and absorb forces during bites (Scanlon & Lee 2002).

DISCUSSION

Features of *Saniwa orsmaelensis*

Saniwa orsmaelensis has often been regarded as a junior synonym of the type species *S. ensidens* (see introduction). Augé (1990a, 2005) listed vertebral characters that allow us to distinguish between the two species. These diagnostic features are revised here: *S. orsmaelensis* presents a large maxillary foramen (as in *Varanus salvator*) whereas it is nearly absent in *S. ensidens* (Dollo 1923); four teeth were likely present after the foramen whereas five are present on *S. ensidens* (Dollo 1923); teeth are closely spaced on *S. orsmaelensis* whereas teeth are separated on *S. ensidens* (Dollo 1923); precondylar constriction of the dorsal vertebrae are less developed in *S. orsmaelenis*; transverse processes on the caudal vertebrae of *S. orsmaelensis* are slightly anteriorly projected (see Fig. 6) whereas they attach nearly at a right angle to the side of the centrum in *S. ensidens* (Gilmore 1928: fig. 49; Rieppel & Grande 2007: fig. 8). In contrast, striae are often present on the neural arch of *Varanus* and *S. ensidens* (Rieppel & Grande 2007; Smith *et al.* 2008). The newly described parietal and mandibular specimens from Dormaal and Le Quesnoy allow further comparisons with *S. ensidens* and exhibit new diagnostic characters, in particular on the parietal. The parietal foramen of *S. orsmaelensis* is surrounded by an ovoid raised ridge whereas its margin is smooth (without ridge) in *S. ensidens*. The lateral margins of the parietal table are not upturned in contrast to the lateral margins of *S. ensidens* and *S. edura* (Smith 2006, 2009; Smith &

Gauthier 2013). The proportions of the parietals from the latter two species are different from that of *S. orsmaelensis*. Indeed, the parietal of *S. ensidens* is wider than that of *S. orsmaelensis*: the ratio length/width of the parietal table in *S. orsmaelensis* and *S. ensidens* (after Rieppel & Grande 2007: fig. 4) are respectively 1.75 and 1.20. Although Mertens (1942) noted ontogenetic variation of the relative width of the parietal table in *Varanus*, the difference observed here seems too large to be attributed to ontogenetic processes.

Saniwa orsmaelensis was probably close in size to *S. ensidens*. Curiously, Dollo indicated that *S. orsmaelensis* was probably one-third the size of *S. ensidens* (Dollo 1923: 79). This is exaggerated because the dentary of *S. ensidens* is only slightly larger than that of *S. orsmaelensis*: Gilmore (1928) noted that in the holotype of *S. ensidens*, three dentary teeth take up a total of 11.0 mm, whereas in the dentary of *S. orsmaelensis*, three middle dentary teeth take up 9.0 mm (specimens from Dormaal and Avenay). The ten most posterior dorsal vertebrae of the specimen FMNH PR 2378 of *S. ensidens* with a snout-vent length of 420 mm (Rieppel & Grande 2007) are 108.9 mm in length (average length of one vertebra is 10.9 mm). The length of 12 dorsal vertebrae of the holotype (USNM 2185) of *S. ensidens* is 126 mm (Gilmore 1928: 71) indicating that the average length of one vertebra is 10.5 mm, whereas the average length of dorsal vertebrae of *S. orsmaelensis* from Dormaal and Le Quesnoy is 9.1 mm (greatest length of the centrum on the sagittal line of the ventral side, articular surface of the condyle excepted).

Several other species have been described in the genus *Saniwa* but Rieppel & Grande (2007) considered these species junior synonyms of *S. ensidens*. At the moment, only *S. edura* from the late Eocene of North Dakota (Smith 2006) has not been synonymized. This species resembles *S. orsmaelensis* by the oval shape and size of the parietal foramen. However, it differs from *S. orsmaelensis* by the dorsal surface of its parietal, which is very rugose; the lateral margins of the parietal table are upturned; the frontoparietal suture is weakly convex anteriorly; the presence of coarse and discontinuously expressed infoldings along the tooth base; the ventral border of the dentary is more dorso-ventrally curved.

PALEOBIOGEOGRAPHIC CONSIDERATIONS

The genus *Saniwa* is currently considered a sister-group of *Varanus* to the exclusion of all other anguimorphs (e.g. Pregill *et al.* 1986; Conrad *et al.* 2008).

In Europe, the genus *Saniwa* first occurs in the earliest Eocene (MP7) and persists until the late early Eocene (MP8+9 or MP10). *Saniwa* has no close relatives in the European Paleogene and this absence argues for its appearance in Europe by immigration (to be fair, few European localities from the late Paleocene are known, namely Cernay-lès-Reims-Berru, Montchenot, and Rivecourt-Petit Pâtis (Russell 1964; Jehle *et al.* 2012; Smith *et al.* 2014). Hence, *S. orsmaelensis* is the only evidence of the brief incursion of varanid squamates in Europe during the Paleogene. It is worth noting that the genus *Palaeovaranus* has often been referred to platynotan squamates and it is present in the European Paleocene, Eocene and Oligocene, in particular in the localities of Cernay (MP6, Hoffstetter 1943), Dormaal and Le Quesnoy (Augé 2005) and perhaps at Rivecourt-Petit Pâtis (Smith *et al.* 2014). However, the phylogenetic affinities of *Palaeovaranus* cannot be addressed here.

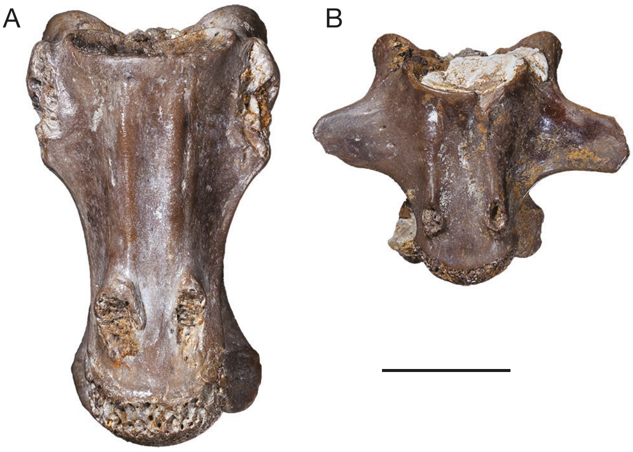


FIG. 10. — *Saniwa orsmaelensis* Dollo, 1923, Mutigny, France. Caudal vertebrae in ventral views: **A**, MNHN.F.MU17498a; **B**, MNHN.F.MU17498b. Scale bar: 5 mm.

In North America, the first indisputable records of *Saniwa* are from the earliest Eocene Wa-0 biozone of Wyoming (Wasatchian, North American Land Mammal Age, Smith 2009) although there is a report of a *Saniwa*-like species from the mid-Paleocene of Wyoming (Sullivan 1982). *Saniwa edura* (Smith 2006) from the late Eocene of the North Dakota constitutes the latest definite record of Varanidae in North America (Sullivan & Holman 1996), whilst some poorly known fossils (vertebrae) from the Oligocene of Wyoming and Nebraska have been tentatively referred to *Saniwa* (Gilmore 1928; Estes 1983). Thus, there is no evidence of crown varanids in the Paleocene of North America and it seems that North American Varanidae from the earliest Eocene entered this continent from elsewhere (Smith 2009).

Although the timing of the faunal transition cannot be given very precisely, the first appearances of the genus *Saniwa* in the fossil record of Europe and North America are almost contemporaneous. One locality that has yielded *Saniwa* (Dormaal in Europe) falls in the Carbon Isotope Excursion whose base (onset) marks the Paleocene-Eocene boundary and the beginning of the Paleocene-Eocene Thermal Maximum (PETM), at the beginning of the Eocene epoch (56 Ma; Smith *et al.* 2006). Large biotic interchanges (the movement of species between geographically distinct biotas following the reduction or elimination of the barrier between them, Simpson 1947; Vermeij 2005) and diversification have been linked to rapid environmental change during the PETM.

If *Saniwa* has no clear relatives in the late Paleocene of Europe and North America, a question arises: where did this genus come from? At least 70 extant varanid species (genus *Varanus*) are present in Africa, Asia and Australia, so it is most probable that *Saniwa* expanded from Asia or Africa to Europe and North America. Early Eocene dispersal events between these continents have already been proposed mostly for mammal faunas (e.g. Teilhard de Chardin 1922; Dollo 1923; Gingerich 1989; Beard & Dawson 1999; Hooker & Dashzeveg 2003; Smith *et al.* 2006; Solé & Smith 2013) and incidentally for "lizard" faunas (Godinot & Lapparent de Broin 2003; Augé *et al.* 2012).

An African origin of *Varanus* has been suggested by Holmes *et al.* (2010), who attributed Egyptian late Eocene and early Oligocene vertebrae to *Varanus*. In addition, Smith *et al.* (2008) referred a vertebra from the early Oligocene of Egypt to a stem varanid and possibly to *Saniwa*. Several faunal dispersals between Africa and Laurasia have been proposed in the early Paleogene (Gheerbrant & Rage 2006) and particularly a Thanetian/Ypresian episode involving hyaenodontans and typical African mammal taxa. In addition, the first trans-Tethyan routes occupied a western area: namely, the Alboran and Apulian routes (Gheerbrant & Rage 2006: fig. 3). However, an African origin of the European *Saniwa* has several shortcomings: no varanid squamates are known in the early Paleogene of Africa, but admittedly this fossil record is very limited. A phylogenetic analysis (Conrad *et al.* 2012) that includes the Paleogene Egyptian fossils attributed to *Varanus* suggests that there is no evidence supporting their attribution to the *Saniwa*-*Varanus* clade. Moreover, several early Eocene localities (MP7) are known in Southern Europe (Southern France, Portugal, Spain; Antunes & Russell 1981; Marandat 1991; Marandat *et al.* 2012; Bolet 2017 [Fig. 1]) but at present none has yielded varanid remains. However, an indeterminate "Necrosauridae" is present in the early Eocene of Masia de L'Hereuet, Catalonia, MP8+9 (Bolet 2017).

Dispersal records of the genus *Varanus* into Europe come from several early Miocene (MN3-MN4) localities, mostly from Spain and Southern France (Hoffstetter 1968; Rage & Bailon 2005; Delfino *et al.* 2013). The last occurrence of *Varanus* in Europe dates from the middle Pleistocene of Greece (Georgalis *et al.* 2017). Dispersal of *Varanus* together with some other thermophilic taxa (Chamaeleonidae, Scolecophidia, Cordylidae) from Africa to Europe at the beginning of the Miocene was suggested by Čerňanský (2012). However, an African origin of European early Miocene varanids cannot be demonstrated unequivocally (Vidal *et al.* 2012; Rage 2013; Čerňanský *et al.* 2015).

Several molecular phylogenetic analyses (Fuller *et al.* 1998; Vidal *et al.* 2012) support an Asian origin for the family Varanidae. Moreover, earlier studies, based primarily on two factors, namely the present distribution of varanids and paleontological data, suggested that varanids arose in Laurasia (Fejérváry 1918; Hoffstetter 1968; Cogger & Heatwole 1981; Branch 1982). Varanoidea (synonym of Platynota) probably originated in the Cretaceous (but see Evans 1994, 2003 for an earlier origin) with records in Asia (e.g. Borsuk-Bialynicka 1984; Nessov 1988; Norell & Gao 1997), in Europe (e.g. Houssaye *et al.* 2013, see reviews in Rage 2013 and Csiki-Sava *et al.* 2015) and in North America (e.g. Estes 1964; Gao & Fox 1996; Nydam 2000; see review in Nydam 2013), that are exclusively on Laurasian continents.

The genera *Varanus* and *Saniwa* were reported from the Eocene of Asia (Mongolia and Kyrgyzstan, Reshetov *et al.* 1978; Alifanov 1993; Danilov 1997; Averianov & Danilov 1997) but as Rage & Bailon (2005) recognized, these reports are questionable. More recent reports of varanid (or varanoid) squamates from Asia come from the early Paleogene of Mongolia (Böhme 2007; Van Itterbeeck *et al.* 2007). Curiously, perhaps the best argument for the dispersal of stem varanids from Asia comes from the early Eocene of the Canadian Arctic (Ellesmere Island). Estes & Hutchison (1980) described dorsal vertebrae that are certainly varanid in their general shape: "they are distinctly varanid and might be referable to any of the described varanid genera". From a paleobiogeographical perspective, the High Arctic was a major corridor for terrestrial organisms dispersing between Asia and both Europe and North America, mostly during the PETM (Scotese 2004; Eberle & Greenwood 2012).

A rich and diverse assemblage of "lizards" appeared in Europe at the Paleocene/Eocene transition with a large increase in diversity occurring at both species and family level. The presence of *Saniwa* in Europe is relatively brief (early Eocene, MP7 to MP8+9 or MP10: "*Saniwa feisti*" from the middle Eocene of Messel is certainly a member of the genus *Palaeovaranus*, see introduction). In addition, several newcomers in Europe (blanid amphisbaenians, Agamidae) disappear from the continent (at least provisionally) at the same time (early-middle Eocene transition). Abiotic factors (mostly climatic) and biotic interactions structure the distribution and presence of species. Taphonomic and environmental bias may also explain absences in the fossil record. However, in that case, there are rather strong arguments against such bias: disappearance of the "lizard" taxa is not sudden but there is a steady decrease in their abundance during the early Eocene. At least, eight fossiliferous localities are known in the European middle Eocene, with very different environmental and taphonomic conditions and at no time has any yielded *Saniwa* remains. The loss of *Saniwa* in Europe seems contemporaneous with the end of the early Eocene Climatic Optimum, so the disappearance of presumed thermophilic "lizards" (varanids and agamids) may be tied to cooler conditions. On the other hand, potential competitors are also present in the early Eocene of Europe (*Palaeovaranus*, Glyptosaurinae, ?Helodermatidae). Here, it is worth noting that these squamate taxa are still present in the middle Eocene. However, only negative abundance correlations between *Saniwa* and these taxa could be regarded as the result of competitive exclusion.

Another hypothesis may be put forward: as a result of widespread migrations during the PETM, the early Eocene "lizard" community in Europe is one of the richest squamate assemblages known in the Paleogene (at least at the familial or subfamilial level). Several past and present biotic interchanges show that colonization pressure from outside tends to increase the regional species pool (Ricklefs 2005; Sax *et al.* 2005). However, what is the fate of those species following their establishment in the recipient biota? Some biogeographical theories (e.g. McArthur & Wilson 1967) predict the existence of a "species capacity or carrying capacity": species richness in a given area could be bounded at some equilibrium point. Hence, elevated colonization rates may lead to increased rates of species turnover and ultimately to the loss of some species (native or immigrant species, Sax *et al.* 2005). Thus, the diverse squamate community of the early Eocene may carry an extinction debt (Tilman *et al.* 1996), that finally leads to the loss of some taxa, e.g. *Saniwa*, Agamidae, blanid amphisbaenians. This notion of extinction debt may also pertain to mammals: most mammals dispersed into Europe around the PETM, a migration also termed the Mammalian Dispersal Event (Beard & Dawson 1999; Solé & Smith 2013). Afterwards (MP8+9), an important faunal turnover affected the European mammal fauna, with the rapid disappearance of several groups, particularly among carnivorous fauna (Arfianinae, Sinopinae, Oxyaenodonta; Solé *et al.* 2013, 2014).

The relative importance of these factors (biotic and abiotic) on the evolution of past and even recent biotic communities are difficult to separate. Rejmánek (1996) and Prins & Gordon (2014) affirm that the outcomes of invasion events are not predictable. Clearly their analysis during the early Eocene requires a thorough knowledge of the "lizard" record from that period, which is far beyond the goals of our taxonomic revision.

CONCLUSIONS

Although here we are considering specimens from three different MP7 localities (Dormaal, Erquelinnes and Le Quesnoy) of two different countries (Belgium and France), each of them presents characters converging with the identification of a varanid squamate at the earliest Eocene in the southern North Sea Basin. Moreover, there is no evidence of the presence of more than one varanid taxon in Dormaal or Le Quesnoy, and the link between these two localities are the dorsal and caudal vertebrae presenting the same morphology including the "famous" pseudozygosphene-pseudozygantrum typical of the genus *Saniwa*. After analysing the characters of the specimens, we reach the conclusion that the variability of some characters within varanid species is great and it would not be parsimonious to refer the material studied here to a different genus than *Saniwa*. This is why we support the validity of the species *S. orsmaelensis*.

The arrival of *S. orsmaelensis* in Europe is certainly linked to rapid environmental changes around the PETM. Large faunal exchanges during that period, especially between Europe and North America, are well documented for mammals and "lizards". Paleontological data suggest that the genus *Saniwa* migrated from Asia, perhaps with a stopover in North America, but at present an African origin cannot be completely excluded.

Note

The recent papers of Smith & Habersetzer (2021) on the middle Eocene palaeovaranid *Paranecrosaurus feisti* from Messel, Germany and Dong *et al.* (2022) on the early Eocene stem-varanid *Archaeovaranus lii* from Dajian, Hubei, China were not available to us before the acceptance of the present paper. This is especially important as we consider *Saniwa orsmaelensis* as probably closely related to *A. lii* based on morphological resemblances at the level of the maxillary, parietal and vertebrae.

Acknowledgements

We are grateful to P. Loubry and L. Cazes from the MNHN and J. Venderickx and J. Lalanne from the IRSNB for the photographs. We thank Robert Sullivan and Salvador Bailon for their constructive remarks, and Kevin Padian for improving the English. This research was supported by the Federal Science Policy Office of Belgium (BELSPO project BR/121/A3/PalEurAfrica).

REFERENCES

Albino A. M. & Brizuela S. 2014. — First record of squamate reptiles from the Oligocene of South America. *Alcheringa: an Australasian Journal of Palaeontology* 38 (3): 412-421. https://doi.org/10.1080/03115518.2014.886029

Alifanov V. 1993. — Some Peculiarties of the Cretaceous and Palaeogene Lizard Faunas of the Mongolian People's Republic. *Kaupia. Darmstädter Beiträge zur Naturgeschichte* 3: 9-13.

Ameghino F. 1899. — Sinopsis Geológico-paleontológica. Supplemento. Adiciones y Correcciónes. *Obras Completas* 12: 706.

Antunes M. T. & Russell L. D. E. 1981. — Le gisement de Silveirinha (Bas Mondego, Portugal) : la plus ancienne faune de Vertébrés connue en Europe. *Comptes rendus des séances de l'Académie des sciences. Série 2, Mécanique-physique, Chimie, Sciences de l'univers, Sciences de la Terre* 293: 1099-1102. https://gallica.bnf.fr/ark:/12148/bpt6k56531626/f573.item

Augé M. L. 1990a. — La faune de lézards et d'amphisbènes (Reptilia, Squamata) du gisement de Dormaal (Belgique, Eocène inférieur). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 60: 161-173.

Augé M. L. 1990b. — La faune de Lézards et d'amphisbènes de l'Eocène inférieur de Condé-en-Brie (France). *Bulletin du Muséum national d'Histoire naturelle,* 4e série, Section C, *Sciences de la terre, paléontologie, géologie, minéralogie* 12 (1): 111-141. https://www.biodiversitylibrary.org/page/55750433

Augé M. L. 2005. — *Évolution des lézards du Paléogène en Europe.* Muséum national d'Histoire naturelle (Mémoires du Muséum national d'Histoire naturelle; 192), Paris, 369 p.

Augé M. L. & Guével B. 2018. — New varanid remains from the Miocene (MN4–MN5) of France: inferring fossil lizard phylogeny from subsets of large morphological data sets. *Journal of Vertebrate Paleontology* 38 (1): e1410483. https://doi.org/10.1080/02724634.2017.1410483

Augé M. L., Folie A. & Smith R. 2012. — The early Eocene lizard fauna of Le Quesnoy (Paris Basin, France) and its paleobiogeographic implications, *in* Devleeschouwer X., Heyvaert V., Louwye S., Piessens K. & Smith T. (eds), *Abstracts, 4th International Geologica Belgica Meeting 2012.* Moving Plates and Melting Icecaps, Brussels: 105.

Averianov A. O. & Danilov I. G. 1997. — A varanid lizard (Squamata: Varanidae) from the Early Eocene of Kirghizia. *Russian Journal of Herpetology* 4: 143-147. https://doi.org/10.30906/1026-2296-1997-4-2-143-147

Báez A. & de Gasparini Z. 1977. — Origenes y evolución de los anfibios y reptiles del Cenozoico de America del Sur. *Acta Geologica Lilloana* 14: 149-232.

Beard K. C. & Dawson M. R. 1999. — Intercontinental dispersal of Holarctic land mammals near the Paleocene-Eocene boundary: paleogeographic, paleoclimatic and biostratigraphic implications. *Bulletin de la Société géologique de France* 170 (5): 697-706.

Biochrom'97 1997. — Synthèses et tableaux de corrélations / Syntheses and correlation tables, *in* Aguilar J.-P., Legendre S. & Michaux J. (eds), *Actes du Congrès BiochroM'97*. Vol. 21. Mémoires et Travaux de l'Institut de Montpellier, École Pratique des Hautes Études, Sciences de la Vie et de la Terre, Montpellier: 769-805.

Blain H.-A. & Bailon S. 2019. — Extirpation of *Ophisaurus* (Anguimorpha, Anguidae) in Western Europe in the context of the disappearance of subtropical ecosystems at the Early-Middle Pleistocene transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 520: 96-113. https://doi.org/10.1016/j.palaeo.2019.01.023

Böhme M. 2007. — 3. Herpetofauna (Anura, Squamata) and palaeoclimatic implications: preliminary results, *in* Daxner-Höck G. (ed.), Oligocene-Miocene vertebrates from the Valley of Lakes (Central Mongolia): morphology, phylogenetic and stratigraphic implications. *Annalen des Naturhistorischen Museums in Wien* 108A: 43-52.

Bolet A. 2017. — First early Eocene lizards from Spain and a study of the compositional changes between late Mesozoic and early Cenozoic Iberian lizard assemblages. *Palaeontologia Electronica* 20.2.20A: 1-22. https://doi.org/10.26879/695

Borsuk-Bialynicka M. 1984. — Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica* 46: 5-105.

Branch W. R. 1982. — Hemipeneal morphology of platynotan lizards. *Journal of Herpetology* 16 (1): 16-38. https://doi.org/10.2307/1563902

Bullet P. 1942. — Beiträge zur Kenntnis des Gebisses von *Varanus salvator* Laur. Vierteljahresschrift Naturforsch. *Gesellschaft Zürich* 87: 139-192.

Caldwell M. W. 2003. — Holotype snout elements of *Saniwa ensidens* reassigned to cf. *Restes* sp. indet. (Xenosauridae). *Journal of Paleontology* 77 (2): 393-396. https://www.jstor.org/stable/4094746

Camp C. L. 1923. — Classification of the lizards. *Bulletin of the American Museum of Natural History* 48: 289-481. http://hdl.handle.net/2246/898

Cernansky A. 2012. — The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa. *Geodiversitas* 34 (4): 837-848. https://doi.org/10.5252/g2012n4a6

Cernansky A., Rage J. C. & Klembara J. 2015. — The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe. *Journal of Anatomy* 13 (2): 97-128. https://doi.org/10.1080/14772019.2014.897266

Cogger H. G. & Heatwole H. 1981. — The Australian reptiles: Origins, biogeography, distribution patterns and island evolution, *in* Keast A. (eds), *Ecological Biogeography of Australia*. Junk, The Hague: 1331-1373.

Conrad J. L. 2008. — Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of American Museum of Natural History* 310: 1-182. https://doi.org/10.1206/310.1

Conrad J. L., Rieppel O. & Grande L. 2008. — Re-assessment of varanid evolution based on new data from *Saniwa ensidens* Leidy, 1870 (Squamata, Reptilia). *American Museum Novitates* 3630, 15 p. https://doi.org/10.1206/596.1

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

Csiki-Sava Z., Buffetaut E., Osi A., Pereda Suberbiola X. & Brusatte S. L. 2015. — Island life in the Cretaceous – faunal composition, biogeography, evolution, and extinction of landliving vertebrates on the Late Cretaceous European archipelago. *Zookey* 469: 1-161. https://doi.org/10.3897/zookeys.469.8439

Danilov I. 1997. — Reptiles from the early Eocene of the Andarak 2 locality (Southern Fergana, Kyrgyzstan), *in* Rocek Z. & Hart S. (eds), *Abstracts of the third world congress of Herpetology*. Congress of Herpetology, Prague: 49.

Delfino M., Rage J. C., Bolet A. & Alba D. M. 2013. — Early Miocene dispersal of the lizard Varanus into Europe: Reassessment of vertebral material from Spain. *Acta Palaeontologica Polonica* 58 (4): 731-735.

Dollo L. 1923. — *Saniwa orsmaelensis*, Varanide nouveau du Landénien supérieur d'Orsmael (Brabant). *Bulletin de la Société belge de géologie, de paléontologie et d'hydrologie* 33: 76-82.

Dong L., Wang Y-Q., Zhao Q., Vasilyan D., Wang Y. & Evans S. E. 2022. — A new stem-varanid lizard (Reptilia, Squamata) from the early Eocene of China. *Philosophical Transactions of the Royal Society B* 377: 1847. https://doi.org/10.1098/rstb.2021.0041

Eberle J. J. & Greenwood D. R. 2012. — Life at the top of the greenhouse Eocene world – A review of the Eocene flora and vertebrate fauna from Canada's High Arctic. *Geologial Society of American Bulletin* 124 (1-2): 3-23. https://doi.org/10.1130/B30571.1

Estes R. 1964. — *Fossil vertebrates from the Late Cretaceous Lance Formation Eastern Wyoming*. University of California Publications in Geological Sciences, Berkley and Los Angeles, 180 p.

Estes R. 1983. — *Encyclopedia of Paleoherpetology*. Gustav Fischer Verlag/Stuttgart/New York, New York, 249 p.

Estes R. & Hutchison J. 1980. — Eocene lower vertebrates from Ellesmere Island, canadian arctic archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 30: 325-347. https://doi.org/10.1016/0031-0182(80)90064-4

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

Etheridge R. 1967. — Lizard caudal vertebrae. *Copeia* 4: 699-721. https://doi.org/10.2307/1441880

Evans S. E. 1994. — A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology* 37 (1): 33-49.

Evans S. E. 2003. — At the feet of the dinosaurs: the early history and radiation of lizards. *Biological Reviews* 78 (4): 513-551. https://doi.org/10.1017/S1464793103006134

Evans S. E. 2008. — The skull of Lizards and Tuatara, *in* Gans C, Gaunt A. S. & Adler K. (eds), *Biology of the Reptilia*. Vol. 20. *Morphology H, The Skull of Lepidosauria*. Society for the study of Amphibians and Reptiles, Ithaca: 1-347.

Fairon-Demaret M. & Smith T. 2002. — Fruits and seeds from the Tienen Formation at Dormaal, Palaeocene-Eocene transition in eastern Belgium. *Review of Palaeobotany and Palynology* 122 (1-2): 47-62. https://doi.org/10.1016/S0034-6667(02)00103-3

Fejérváry G. J. de 1918. — Contributions to a monography on fossil Varanidae and on Megalanidae. *Annales Historico-Naturales Musei Natural Hungarici* 16: 341-467.

Fuller S., Baverstock P. & King D. 1998. — Biogeographic origins of Goannas (Varanidae): a molecular perspective. *Molecular Phylogenetics and Evolution* 9 (2): 294-307. https://doi.org/10.1006/mpev.1997.0476

Fürbringer M. 1900. — Zur vergleichenden anatomie des Brustschulterapparates und der Schultermuskeln. *Jenaische Zeitschrift* 34: 215-718.

Gao K. & Fox R. C. 1996. — Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 33: 1-108. https://www.biodiversitylibrary.org/page/53808837

Georgalis G. L. 2017. — *Necrosaurus* or *Palaeovaranus*? Appropriate nomenclature and taxonomic content of an enigmatic fossil lizard clade (Squamata). *Annales de Paléontologie* 103 (4): 293-303. https://doi.org/10.1016/j.annpal.2017.10.001

Georgalis G. L., Villa A. & Delfino M. 2017. — The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. *Journal of Vertebrate Paleontology* 16 (2): e1301946. https://doi.org/10.1080/02724634.2017.1301946

Gheerbrant E. & Rage J.-C. 2006. — Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* 241 (2): 224-246. https://doi.org/10.1016/j.palaeo.2006.03.016

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 (2418): 1-28. https://doi.org/10.5479/si.00963801.60-2418.1

Gilmore C. W. 1928. — Fossil lizards of North America. *Memoirs National Academy of Science* 22: 1-201.

Gingerich P. D. 1989. — New Earliest Wasatchian mammalian fauna from the Eocene of Northwestern Wyoming : composition and diversity in a rarely sampled high- floodplain assemblage. *University of Michigan, Papers on Paleontology* 28, 97 p.

Godinot M. & Lapparent de Broin F. D. 2003. — Arguments for a mammalian and reptilian dispersal from Asia to Europe during the Paleocene-Eocene boundary interval, *in* Reumer J. W. F. & Wessels W. (eds), *Distribution and migration of tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn*. Vol. 10. Deinsea, Rotterdam: 255-275.

Godinot M., Lapparent de Broin F. D. F., Buffetaut E., Rage J.-C. & Russell D. E. 1978. — Dormaal : une des plus anciennes faunes éocènes d'Europe. *Comptes Rendus de l'Académie des Sciences, Paris, Série D* 287: 1273-1276.

Gray J. E. 1827. — A description of new species of saurian reptiles with a revision of the species of chamaeleons. *The Philosophical Magazine* 2 (9): 207-214. https://doi.org/10.1080/14786442708675648

Hecht M. & Hoffstetter R. 1962. — Note préliminaire sur les Amphibiens et les Squamates du Landénien supérieur et du Tongrien de Belgique. *Bulletin Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 38: 1-30.

Hoffstetter R. 1943. — Varanidae et Necrosauridae fossiles. *Bulletin du Muséum national d'Histoire naturelle* 15: 134-141.

Hoffstetter R. 1968. — Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l'histoire de la famille. *Bulletin du Muséum national d'Histoire Naturelle* 2e série, t. 40: 1051-1064. https://www.biodiversitylibrary.org/page/55343150

Hoffstetter R. & Gasc J.-P. 1969. — Chapter 5: Vertebrae and ribs of modern reptiles, *in* Gans C., Bellairs A. D. A. & Parson T. (eds), *Biology of the reptilians*. Vol. 1 (Morphology A). Academic Press, London: 201-213.

Holmes R. B., Murray A. M., Yousry S., 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. *Paleontology* 53 (5): 1099-1110. https://doi.org/10.1111/j.1475-4983.2010.00994.x

Hooker J. J. & Dashzeveg D. 2003. — Evidence for direct mammalian faunal interchange between Europe and Asia near the Paleocene-Eocene boundary, *in* Wing S. L., Gingerich P. D., Schmitz B. & Thomas E. (eds), *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. Vol. 369. Geological Society of America Special Paper, Boulder, Colorado: 479-500.

Houssaye A., Rage J.-C., Fernandez-Baldor F. T., Huerta P., Bardet N. & Pereda Suberbiola X. 2013. — A new varanoid squamate from the Early Cretaceous (Barremian-Aptian) of Burgos, Spain. *Cretaceous Research* 41: 127-135. https://doi.org/10.1016/j.cretres.2012.11.005

Jacques F. M. & De Franceschi D. 2005. — Endocarps of Menispermaceae from Le Quesnoy outcrop (Sparnacian facies, Lower Eocene, Paris Basin). *Review of Palaeobotany and Palynology* 135 (1-2): 61-70. https://doi.org/10.1016/j.revpalbo.2005.02.005

Jehle M., Godinot M., Delsate D., Phélizon A. & Pellouin J.-L. 2012. — A new late Paleocene micromammal fauna from Montchenot (Paris Basin). Preliminary results. *Palaeobiodiversity and Palaeoenvironments* 92: 487-496. https://doi.org/10.1007/s12549-012-0100-x

Klembara J., Dobiašová K., Hain M. & Yaryhin O. 2017a. — Skull Anatomy and Ontogeny of Legless Lizard Pseudopus apodus (Pallas, 1775) : Heterochronic Influences on Form. *The Anatomical Record* 300 (3): 460-502. https://doi.org/10.1002/ar.23532

Klembara J., Hain M. & Cernansky A. 2017b. — The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm – Westtangente in Germany. *Historical Biology* 31 (8), 12 p. https://doi.org/10.1080/08912963.2017.1416469

Laass M. & Schillinger B. 2020. — The first Record of Plicidentine in Varanopseidae (Synapsida, Pelycosauria). *Materials Research Society Proceedings* 15: 244-249.

Lécuru S. 1968. — *Myologie et innervation du membre antérieur des lacertiliens*. Muséum national d'Histoire naturelle (Mémoires du Muséum National d'Histoire Naturelle, Sér. A – Zoologie (1950-1992); 48 (3)), Paris: 127-215.

Lécuru S. 1969. — Étude morphologique de l'humérus des Lacertiliens. *Annales des Sciences Naturelles, Zoologie* 12e série 11: 515-558.

Leidy J. 1870. — Description of *Emys jeansei*, *E. haydeni*, *Baëna arenosa* and *Saniwa ensidens*. *Proceedings of the Academy of Natural Sciences, Philadelphia* 1870: 122.

Marandat B. 1991. — Mammifères de l'Ilerdien moyen (Eocène inférieur) des Corbières et du Minervois (Bas-Languedoc, France) Systématique, biostratigraphie, corrélations. *Palaeovertebrata* 20: 55-144.

Marandat B., Adnet S., Marivaux L., Martinez A., Vianey-Liaud M. & Tabuce R. 2012. — A new mammalian fauna from the earliest Eocene (Ilerdian) of the Corbières (Southern France): palaeobiogeographical implications. *Swiss Journal of Geosciences* 105: 417-434. https://doi.org/10.1007/s00015-012-0113-5

Maxwell E. E., Caldwell M. W., Lamoureux D. O. & Budney L. A. 2011. — Histology of tooth attachment tissues and plicidentine in *Varanus* (Reptilia: Squamata), and a discussion of the evolution of amniote tooth attachment. *Journal of Morphology* 272 (10): 1170-1181. https://doi.org/10.1002/jmor.10972

McArthur R. H. & Wilson E. O. 1967. — *The theory of islands biogeography*. Princeton University Press, Princeton, 224p.

McDowell S. B. & 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): 1-142. http://hdl.handle.net/2246/1146

Mertens R. 1942. — Die Familie der Warane (Varanidae). Zweiter Teil: Der Schädel. Abhand. *Senckenberg. Naturforsch. Gesellsch.* 465: 117-234.

Molnar R. E. 2004. — The long and honorable history of Monitors and their kin, *in* Pianka E. R. & King D. R. (eds), *Varanoid lizards of the world.* Indiana University Press, Bloomington: 10-67.

Nel A., de Plöeg G., Dejax J., Dutheil D., De Franceschi D., Gheerbrant E., Godinot M., Hervet S., Menier J.-J., Augé M., Bignot G., Cavagnetto C., Duffaud S., Gaudant J., Hua S., Jossang A., de Lapparent de Broin F., Pozzi J.-P., Paicheler J.-C., Beuchet F. & Rage J.-C. 1999. — Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Eocène basal, MP7): Le Quesnoy (Oise, France). *Comptes rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes* 329 (1): 65-72.

Nel A., de Ploëg G., Millet J., Menier J.-J. & Waller. A. 2004. — The French ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. *Geologica Acta* 2 (1): 3-8. https://doi.org/10.1344/105.000001628

Nessov L. A. 1988. — Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta zoologica cracoviensis* 31: 475-486.

Norell M. & 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. http://hdl.handle.net/2246/3612

Nydam R. L. 2000. — A new taxon of Helodermatid-like lizard from the Albian-Cenomanian of Utah. *Journal of Vertebrate Paleontology* 20 (2): 285-294. https://doi.org/db8vf8

Nydam R. L. 2013. — Squamates from the Jurassic and Cretaceous of North America. *Palaeobiodiversity and Palaeoenvironments* 93: 535-565. https://doi.org/10.1007/s12549-013-0129-5

Odermatt C. 1940. — Beiträge zur Kenntnis des Gebisses von *Heloderma*. *Vierteljahresschrift der Naturforschenden Gesellschaft in Zürich* 85: 98-141.

Oppel M. 1811. — *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. J. Lindauer, München, 86 p. https://doi.org/10.5962/bhl.title.4911

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 the San Diego Society of Natural History* 21: 167-202. https://www.biodiversitylibrary.org/page/4287323

Preuschoft H., Reif W.-E., Loitsch C. & Tepe E. 1991. — The function of labyrinthodont teeth: big teeth in small jaws, *in* Schmidt-Kittler N. & Vogel K. (eds), *Constructional Morphology and Evolution.* Springer-Verlag, Berlin-Heidelberg: 151-171. https://doi.org/10.1007/978-3-642-76156-0_12

Prins H. H. & Gordon I. J. 2014. — A critique of ecological theory and a salute to natural history, *in* Prins H. H. & Gordon I. J (eds), *Invasion biology and ecological theory*. Cambridge University Press, Cambridge: 497-516.

Rage J.-C. 1978. — La poche à phosphate de Sainte-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. 5. Squamates. *Palaeovertebrata* 8: 201-215.

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

Rage J.-C. & Bailon S. 2005. — Amphibians and squamates reptiles from the late early Miocene (MN4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas* 27 (3): 413-441.

Rage J.-C. & Augé M. 2010. — Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. *Geobios* 43 (2): 253-268. https://doi.org/10.1016/j.geobios.2009.08.002

Rage J.-C. & Augé M. 2015. — Valbro: A new site of vertebrates from the early Oligocene (MP 22) of France (Quercy). III - Amphibians and squamates. *Annales de Paléontologie* 101 (1): 29-41. https://doi.org/10.1016/j.annpal.2014.10.002

Rejmanek M. 1996. — Species richness and resistance to invasions, *in* Orians G. H., Dirzo R. & Cushman J. H. (eds), *Biodiversity and ecosystem processes in tropical forests*. Springer Verlag, Berlin: 153-172. https://doi.org/10.1007/978-3-642-79755-2_8

Reshetov V. Y., Shevyreva N. S., Trofimov B. A. & Chkhikvadze V. M. 1978. — The vertebrates of the Andarak locality (middle Eocene). *Bjulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Geologicheskii* 53: 151-152 (in Russian).

Ricklefs R. E. 2005. — Chapter 7. Taxon cycles, insights from invasive species, *in* Sax D., Stachowicz J. & Gaines S. (eds), *Species Invasions.* Sinauer Associates, Sunderland: 165-199.

Rieppel O. 1979. — A functional interpretation of the varanid dentition (Reptilia, Lacertilia, Varanidae). *Gegenbaurs morphology Jahrbuch, Leipzig* 125 (6): 797-817.

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 (4): 643-665. https://doi.org/czrx82

Russell D. E. 1964. — *Les mammifères paléocènes d'Europe*. Muséum national d'Histoire naturelle (Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre; 8), Paris: 324 p.

Sax D. F., Brown J. H., White E. P. & Gaines S. D. 2005. — Chapter 17. The Dynamics of Species Invasions, *in* Sax D., Stachowicz J. & Gaines S. (eds), *Species Invasions*. Sinauer Associates, Sunderland: 447-465.

Scanlon J. D. & Lee M. S. Y. 2002. — Varanoid Dentition in Primitive Snakes (Madtsoiidae). *Journal of Herpetology* 36 (1): 100-106. https://doi.org/fkvksh

Scotese C. R. 2004. — Cenozoic and Mesozoic paleogeography: changing terrestrial biogeographic pathways, *in* Lomolino M. V. & Heaney L. R. (eds), *Frontiers of biogeography*. Sinauer, Sunderland: 9-26.

Simpson G. G. 1947. — Holartic mammalian faunas and continental relationships during the Cenozoic. *Geological Society of America Bulletin* 58 (7): 613-687. https://doi.org/d7smwr

Smith K. T. 2006. — A diverse new assemblage of Late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. *Palaeontographica electronica* 9 (5A): 44.

Smith K. T. 2009. — A new lizard assemblage from the Earliest Eocene (zone Wa0) of the Bighorn Basin, Wyoming, USA: biogeography during the warmest interval of the Cenozoic. *Journal of Systematic Palaeontology* 7 (3): 299-358. https://doi.org/10.1017/S1477201909002752

Smith K. T. & Gauthier J. A. 2013. — Early Eocene lizards of the Wasatch Formation near Bitter Creek, Wyoming: diversity and paleoenvironment during an interval of global warming. *Bulletin of the Peabody Museum of Natural History* 54 (2): 135-230. https://doi.org/10.3374/014.054.0205

Smith K. T., Čerňanský A., Scanferla A. & Schaal S. F. K. 2018b. — Lizards and snakes: warmthloving sunbathers, *in* Smith K. T., Schaal S. F. K. & Habersetzer J. (eds), *Messel: An Ancient Greenhouse Ecosystem*. Schweizerbart, Frankfurt am Main: 122-147.

Smith K. T., Bhullar B.-A. S. & 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 (3): 909-913. https://doi.org/dhs5g4

Smith K. T., Bullar B. A. & Habersetzer J. 2018a. — The Only Known Jawed Vertebrate with Four Eyes and the Bauplan of the Pineal Complex. *Current Biology* 28 (7): 1101-1107. https://doi.org/10.1016/j.cub.2018.02.021

Smith K. T. & Habersetzer J. 2021. — The anatomy, phylogenetic relationships, and autecology of the carnivorous lizard "Saniwa" feisti Stritzke, 1983 from the Eocene of Messel, Germany, *in* Folie A., Buffetaut E., Bardet N., Houssaye A., Gheerbrant E. & Laurin M. (eds), Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage. *Comptes Rendus Palevol* 20 (23): 441-506. https://doi.org/10.5852/cr-palevol2021v20a23

Smith T. & Smith R. 1996. — Synthèse des données actuelles sur les vertébrés de la transition Paléocène-Eocène de Dormaal (Belgique). *Bulletin de la Société belge de Géologie* 104 (1-2): 119-131.

Smith T., Rose K. D. & Gingerich P. D. 2006. — Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate Teilhardina during the Paleocene-Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences of the United States of America* 103 (30): 11223-11227. https://doi.org/10.1073/pnas.0511296103

Smith T., Quesnel F., de Plöeg G., De Franceschi D., Métais G., de Bast E., Solé F., Folie A., Boura A., Claude J., Dupuis C., Gagnaison C., Iakovleva A., Martin J., Maubert F., Prieur J., Roche E., Storme J.-Y., Thomas R., Tong H., Yans J. & Buffetaut E. 2014. — First Clarkforkian Equivalent Land Mammal Age in the Latest Paleocene Basal Sparnacian Facies of Europe: Fauna, Flora, Paleoenvironment and (Bio)stratigraphy. *PLoS ONE* 9: e86229. https://doi.org/10.1371/journal.pone.0086229

Solé F. & Smith T. 2013. — Dispersals of placental carnivorous mammals (Carnivoramorpha, Oxyaenodonta & Hyaenodontida) near the Paleocene-Eocene boundary: a climatic and almost worldwide story. *Geologica Belgica* 16: 254-261.

Solé F., Falconnet J. & Laurent Y. 2014. — New proviverrines (Hyaenodontida) from the early Eocene of Europe; phylogeny and ecological evolution of the Proviverrinae. *Zoological Journal of the Linnean Society* 171 (4): 878-917. https://doi.org/10.1111/zoj.12155

Solé F., Gheerbrant E. & Godinot M. 2013. — The Sinopaninae and Arfianinae (Hyaenodontida, Mammalia) from the Early Eocene of Europe and Asia; evidence for dispersals in Laurasia around the P/E boundary and for an unnoticed faunal turnover in Europe. *Geobios* 46 (4): 313-327. https://doi.org/10.1016/j.geobios.2013.02.003

Steurbaut E., De Coninck J., Roche E. & Smith T. 1999. — The Dormaal Sands and the Palaeocene/Eocene boundary in Belgium. *Bulletin de la Société géologique de France* 170: 217-227.

Stritzke R. 1983. — *Saniwa feisti* n. sp., ein Varanidae (Lacertilia, Reptilia) aus dem Mittel-Eozän von Messel bei Darmstadt. *Senckenbergiana lethaea* 64: 497-508.

Sullivan R. M. 1982. — Fossil lizards from Swain Quarry "Fort Union Formation" middle Paleocene (Torrejonian), Carbon County, Wyoming. *Journal of Paleontology* 56 (4): 996-1010.

Sullivan R. M. & Holman J. A. 1996. — Squamata, *in* Prothero D. & Emry R. (eds), *The terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge: 354-372.

Sullivan R. M., Augé M., Wille E. & Smith R. 2012. — A new glyptosaurine lizard from the earliest Eocene of Dormaal, Belgium. *Bulletin de la Société géologique de France* 183 (6): 629-635. https://doi.org/10.2113/gssgfbull.183.6.627

Teilhard De Chardin P. 1922. — Les Mammifères de l'Éocène inférieur français et leurs gisements. *Annales de Paléontologie* 11: 1-108.

Tilman D., May R. M., Lehman C. L. & Nowak M. A. 1996. — Habitat destruction and the extinction debt. *Nature* 371: 65-66. https://doi.org/10.1038/371065a0

Van Itterbeeck J., Missiaen P., Folie A., Markevich V. S., van Damme D., Dian-Yong G. & Smith T. 2007. — Woodland in a fluvio-lacustrine environment on the dry Mongolian Plateau during the late Paleocene: Evidence from the mammal bearing Subeng section (Inner Mongolia, P.R. China). *Palaeogeography, Palaeoclimatology, Palaeoecology* 243 (1-2): 55-78. https://doi.org/10.1016/j.palaeo.2006.07.005

Vermeij G. J. 2005. — Invasion as expectation, *in* Sax D. F., Stachowicz J. J. & Gaines S. D. (eds), *Species Invasions, insights into ecology, evolution and biogeography*. Sinauer Associates, Sunderland: 315-339.

Vidal N., Marin J., Sassi J., Battistuzzi F. U., Donnellan S., Fitch A. J., Fry B. G., Vonk F. J., Rodriguez de la Vega R. C., Couloux A. & Hedges B. S. 2012. — Molecular evidence for an Asian origin of monitor lizards followed by Tertiary dispersals to Africa and Australasia. *Biological Letters* 8 (5): 853-855. https://doi.org/10.1098/rsbl.2012.0460

Zaher H. & Rieppel O. 1999. — Tooth implantation and replacement in Squamates, with special reference to Mosasaur lizards and snakes. *American Museum Novitates* 3271: 1-19. http://hdl.handle.net/2246/3047

Submitted on 7 March 2019;
accepted on 23 March 2021;
published on 2 August 2022.