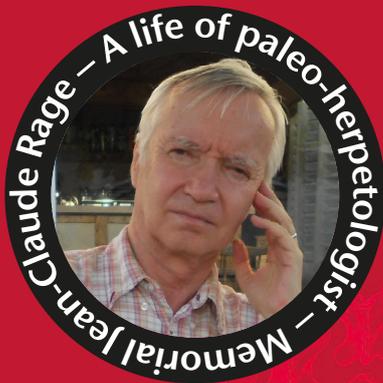


geodiversitas

2021 • 43 • 27



Jean-Claude Rage, a life dedicated to paleoherpetology

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Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas is a fast track journal published by the Museum Science Press, Paris

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

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Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 1280-9659/ ISSN (électronique / *electronic*): 1638-9395

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Submitted on 8 June 2020 | accepted on 16 September 2020 | published on 20 December 2021

[urn:lsid:zoobank.org:pub:0D7107CF-754A-4D7C-9478-2151D0936254](https://doi.org/10.5252/geodiversitas2021v43a27)

Steyer J.-S., Augé M. & Métais G. 2021. — Jean-Claude Rage, a life dedicated to paleoherpetology, in Steyer J.-S., Augé M. L. & Métais G. (eds), Memorial Jean-Claude Rage: A life of paleo-herpetologist. *Geodiversitas* 43 (27): 1401-1409. <https://doi.org/10.5252/geodiversitas2021v43a27>. <http://geodiversitas.com/43/27>

ABSTRACT

Jean-Claude Rage (1943-2018) was a renowned vertebrates paleontologist who dedicated his career to fossil amphibians and reptiles, which earned him the highest reputation. He was CNRS Emeritus Director of Research in Paris and worked in the laboratory of paleontology of the Muséum national d'Histoire naturelle (MNHN) together with the authors of this article (JSS and MA were also his Master and PhD students). Jean-Claude has established himself as an outstanding herpetologist and taxonomist with numerous publications (more than 250 articles, see below) throughout his career. The aim of this article is not to describe in details his very rich career (see Steyer & Buffetaut 2012 for details) but to show how important his research was, and is still, and to go deeper in his personality to show that his intellectual legacy should be considered as a model today.

KEY WORDS
Paleoherpetology,
obituary.

RÉSUMÉ

Jean-Claude Rage, une vie dédiée à la paléoherpétologie.

Jean-Claude Rage (1943-2018) était un paléontologue des vertébrés renommé, qui a consacré sa carrière aux amphibiens et reptiles fossiles, ce qui lui a valu sa grande réputation. Directeur de recherche émérite du CNRS à Paris, il a travaillé au laboratoire de paléontologie du Muséum national d'Histoire naturelle (MNHN) avec les auteurs de cet article (JSS et MA étaient également ses étudiants de Master et de Doctorat). Jean-Claude s'est imposé comme un herpétologue et un taxonomiste hors pair avec de nombreuses publications (plus de 250 articles, voir ci-dessous) tout au long de sa carrière. Le but de cet article n'est pas de décrire en détail sa très riche carrière (voir Steyer & Buffetaut 2012 pour plus de détails) mais de montrer à quel point ses recherches étaient et sont encore importantes, et d'approfondir sa personnalité pour montrer que son héritage intellectuel devrait être considéré comme un modèle aujourd'hui.

MOTS CLÉS
Paléoherpétologie,
nécrologie.

BIOGRAPHIC SKETCH

Jean-Claude was born at Lyon, France, on 1st March 1943 during the World War 2: he is the youngest of three children (his elder sister died before he was born). At that time, Lyon was freshly occupied by the Nazi occupant which settled repressive corporations such as the Gestapo and the Waffen-SS. Lyon was also a high place of the Resistance as early as 1940. At home, Jean-Claude learnt to read and to draw very early. He lost his father at the age of 10 and his family moved to Boën-sur-Lignon then Saint-Chamond, in the Département de la Loire. In these less urban environments, the young Jean-Claude discovered nature and became passionate about natural sciences, particularly geology and herpetology – although he was afraid of snakes: “Kid, I was awfully scared by snakes [...] I went to holidays in corners where they were many snakes, and numerous legends [...] I hesitated for a moment between zoology, by taking an interest in snakes, or geology, and I chose to link both by working on paleontology of snakes.” (Rage 2008).

After schooling in Saint-Etienne, Jean-Claude returned to Lyon, at the university, with the aim to become a paleontologist. In 1968, he defended his Master’s thesis entitled “*Contribution à l’étude des anoures quaternaires*” and he was offered a position as associate researcher at the CNRS. Then he moved to Paris for preparing a PhD on snake evolution (“Paléontologie, phylogénie et paléobiogéographie des serpents”) and this was also where he met his future wife Agnès Lauriat, today Emeritus Professor in paleomalacology at the Muséum national d’Histoire naturelle, Paris (MNHN). In 1976, Jean-Claude defended his PhD and obtained a permanent research position at the CNRS. He spent his career at the University of Paris 6, then at the MNHN from 1997.

AN IMPRESSIVE CONTRIBUTION

Jean-Claude started to work on fossil amphibians and quickly enlarged his anatomical skills to various other groups of herps in space and time: for example, his monography on fossil snakes (Rage 1984) is still a reference in the domain, as are most of his articles (e.g., Rage 2013). His contribution is very impressive: Jean-Claude published more than 250 articles, three books, 29 book chapters. His very high level of precision, his generosity and vast knowledge of amphibians and reptiles have made Jean-Claude one of the most reputed expert of Mesozoic and Cenozoic, and his expertise was often demanded in many international collaborative programs. His seminal work on often original fossil material has led him to propose 24 new genera and 48 species of amphibians and reptiles (Table 1). He was so reputed and appreciated that one genus and seven species have been dedicated to him (Table 2). Jean-Claude was also a gifted scientific artist and his drawings helped him to interpret and portray the complexity of herps anatomy (for example the complex and diagnostic morphology of

snake vertebrae), as attested by the beautiful illustrations in most of his articles. He had always at least one anatomical drawing in progress to illustrate an article (Fig. 1). He taught us that “drawing, it is already describing” and that this (learnable) activity is indeed the best way to enter deeply into the anatomy and morphology of specimens.

PRECURSOR IN VARIOUS FIELDS

In addition to the skills mentioned above, Jean-Claude made valuable contributions to many other fields including paleobiogeography (see below). Precursor in various fields in France, he was one of the first paleontologists to study micro-remains of herps, using and developing the screen-washing techniques commonly used by paleomammalogists with whom he spent a lot of time early in his career excavating fossils from the famous fissure fillings of Quercy. In an academic context that generally favored large and media-friendly groups such as dinosaurs, crocodiles or giant mammals, Jean-Claude showed with intelligence that this minute paleobiodiversity is at least as important as the large fauna in terms of paleoenvironments and life evolution.

Very open-minded, Jean-Claude was also one of the first paleontologists in France to use computer-assisted cladistics for testing the phylogenetic relationships (e.g., Rage 1982). Yet he always used this methodology with parsimony, i.e. considering cladistics as a tool, not as a religion. For him, fossils are the sole bearers of characters and do not change, unlike cladogram(s) which may evolve.

Jean-Claude was also one of the first paleontologists using non-marine amphibian and reptile taxa to test the connections between tectonic plates. He showed the great potential and relevance of the continental herpetological faunas in term of paleobiogeography (e.g., Gheerbrant & Rage 2006). For example, he studied crucial and inedit herpetofaunas from various Gondwanan localities, such as those from the late Cretaceous of India, that led to different paleotectonic scenarios such as the timing of collision of the Indian Subcontinent with Asia (Sahni *et al.* 1982; Prasad & Rage 1995). This approach is remarkable because at this time, tectonics was still a young scientific field, which often ignored the paleontological data in the paleogeographical reconstructions. This shows again that Jean-Claude had a large range of scientific interests and expertise, he was always available and ready to help: the door of his office was always open for anyone having a question, and the drawers of his collections open for cooperation.

A MODEL OF BENEVOLENCE

The professionalism and generosity of Jean-Claude led to many durable and trustful collaborations with various colleagues in the world, whatever their age (students, young researchers,

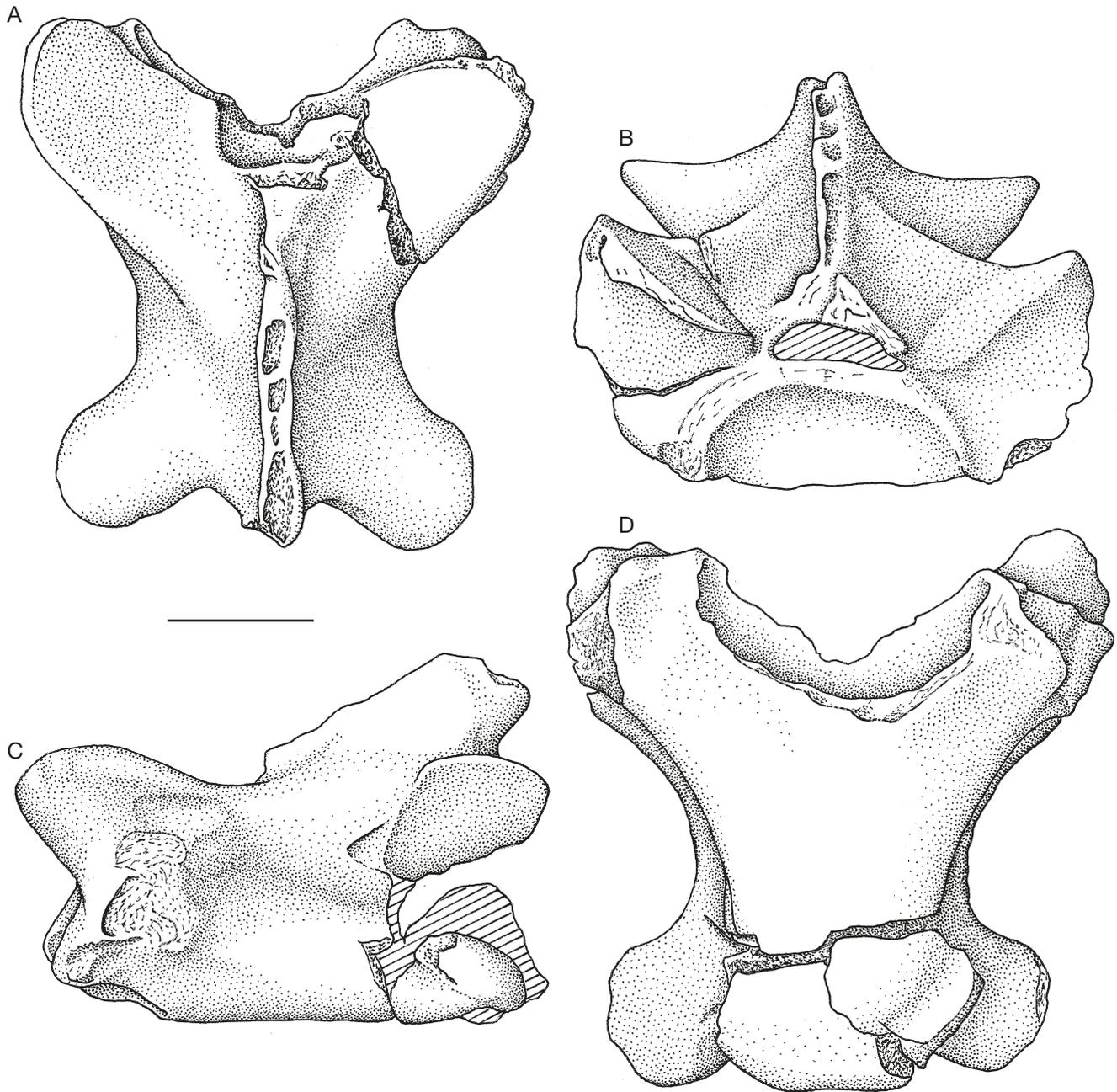


FIG. 1. — Anatomical drawings made by Jean-Claude Rage and showing the very high anatomical precision and dotted technique he used in his illustrations (vertebra of a *Varanus* Merrem, 1820 from the Neogene of Afghanistan in dorsal (A), anterior (B), lateral (C) and ventral (D) views, reproduced from Lapparent *et al.* 2020a: 419, fig. 5. Scale bar: 5 mm).

retired colleagues), their field (geologists, paleontologists, zoologists, embryologists etc.) and their status (institutional or amateur). Jean-Claude has always considered students as colleagues not as school-boys(girls), and without any paternalism – he was all but a mandarin and taught us that “a good plant does not need a tutor”.

Jean-Claude was also a truly objective scientist, not involved in any politics nor group of influencers (hidden or not): deaf only with one ear, he used to stay voluntarily far away from the gossips and the lobbies, which could tarnish the image of a person or a laboratory.

His personal life was very rich and his family important for him; he was a devoted husband, father and grandfather (Fig. 2). Besides his skills for the drawing, he was also a great photographer and a Science-fiction reader as evidenced by the impressive number of books in his personal library. He also liked sports and walking trails (Fig. 3) with his wife Agnès during holidays, “the best way to visit and discover a region in France”, he used to say.

His culture went far beyond paleontology: one of us, MA, remembers Jean-Claude during a congress excursion at Poitiers, giving the assistance a true lecture of medieval



FIG. 2. — Jean-Claude Rage with his wife and one of their grandchildren. Photo: Estelle de Moissy.

History by describing precisely architectural characters of the outstanding heritage of that city. Precursor in many fields, generous and kind person, Jean-Claude is therefore a model of deontology. He passed away several years ago, but for those who knew him, his memory remains intact. We are proud to dedicate these two volumes of *Geodiversitas* untitled “Jean-Claude Rage, a life dedicated to paleoherpe-

tology” to him. These volumes presented here include significant contributions that all fit the wide scientific interests of Jean-Claude, all along his career. These papers cover a long time span from Triassic to Recent, and deal with many parts of the world. Moreover, these contributions are diverse in their scopes and approaches including tomography, and they thus offer important progresses in various domains.



FIG. 3. — Jean-Claude Rage taking a break during a walking trail near Châteauneuf-les-Bains, Auvergne in 2015. Photo: Agnès Lauriat-Rage.

Čerňanský & Augé (2019) report new lizard's material from the Oligo-Miocene of the valley of lakes, Mongolia, suggesting that the Stehlin's Grande Coupure is not as well marked in East Asia as it is in Europe. Bochaton *et al.* (2019) provide a review of sub-recent dipsadid snake fossils from the Guadeloupe Islands and question the putative consumption of snake meat by past Amerindian populations. Dong *et al.* (2019) report an articulated skeleton of a new stem squamatan lizard from the late Jurassic of China. Lapparent *et al.* (2020a) (including Jean-Claude) provide an interesting review of Neogene amphibians and reptiles from Afghanistan, an area where the vertebrate fossil record is almost unknown for the entire Cenozoic. This fossil material was collected in the 1970s during MNHN field campaigns headed by Emile Heintz in the Kabul Area (Heintz *et al.* 1978). It provides important insight about the origin and set up of extant herpetofauna of Afghanistan. Klembara & Čerňanský (2020) revise the cranial anatomy of the anguine lizard *Ophisaurus acuminatus* from the late Miocene of Germany by using

high-resolution X-ray and microcomputed tomography that reveal intriguing new anatomical features. The paper of Zouhri *et al.* (2021) (including Jean-Claude) provides important information about the vertebrate assemblage (including interesting snakes) from the Bartonian Aridal Formation of Gueran (southwestern Morocco) which is otherwise known for yielding one of the world's richest Bartonian archaic whale assemblage. Augé *et al.* (2021) and Ivanov *et al.* (2020) examine the effect of hyperthermal events, the Paeocene-Eocene Thermal Maximum (PETM, *c.* 56 Ma) and the early Miocene hyperthermal event (*c.* 17-18 Ma) respectively, on the herpetofaunas of Europe. Smith & Scanferla (2021) describe a new boid snake based on a nearly complete skeleton from the Eocene Messel Lagerstätte. Their phylogenetic analysis places this taxon at the base of a North American clade, thus further supporting the close affinities of Euro-American squamate fauna during the early Eocene. The paper of Albino (2020) deals with the Neogene fossil record of lizards from the Pampean region of northern Argentina

and southernmost Brazil. Georgalis *et al.* (2021) used micro-CT scanning to reassess cranial and postcranial elements of lizards from the Phosphorites du Quercy, collected during the 19th century and which were ‘forgotten’ in various collections. Interestingly, Venczel *et al.* (2021) report new material of a hyloid frog from the Santonian of Hungary, which clearly suggests that anuran from the late Cretaceous of Europe had Gondwanan affinities. Three papers deal with Cenozoic turtles from Eurasia. Miocene freshwater and terrestrial turtles are discussed by Pérez-García *et al.* (2021) and Luján *et al.* (2021) based on fossil material from Spain and Czechia, respectively. In the same vein, Lapparent *et al.* (2021) report a new bothremydid turtle from the early Paleocene of Pakistan which brings interesting paleobiogeographic clues. In another contribution, Lapparent *et al.* (2020b) report a new pleurodiran Pelomedusoides turtle from the late Maastrichtian of the Iullemeden basin (Niger), and the biostratigraphy of sub-contemporaneous vertebrate assemblages of Western Africa is reviewed in details. The paper of Steyer *et al.* (2021) deals with Triassic temnospondyls from the Karoo rift basins of Tanzania and Zambia and shows that the group underwent a rapid recovery after the Permian-Triassic mass extinction in Africa. Syromyatnikova *et al.* (2021) report the occurrence of a cobra from the late Miocene of the Northern Caucasus which attests that some elapid snakes survived in the Black Sea area while the genus *Naja* was thought to be extinct in Central and Eastern Europe since the middle Miocene. Finally, Gardner *et al.* (2021) concentrate on albanerpetontids (salamander-like lissamphibians) from the late Miocene of Italy and review the European Cenozoic record of the family.

We hope that the readers will enjoy these volumes that reflect the diversity of Jean-Claude scientific interests. We thank the colleagues around the world who kindly replied positively to our call and contributed by both submitting their works and reviewing the works of colleagues. We are also glad that other volumes dedicated to Jean-Claude have been edited because these tributes are complementary, i.e. not concurrent: they show the great aura of the man.

Acknowledgements

We thank Agnès Lauriat-Rage (MNHN) and Estelle de Moissy (born Rage) who kindly provided photos of Jean-Claude, Emmanuel Côté and Didier Merle (both MNHN) for their bibliographic help and edition. We thank Dino Frey (Staatliches Museum für Naturkunde Karlsruhe) and the other members of the board of the European Association of Vertebrate Paleontology for their encouragement.

The complete issue is available in open access at the address: <https://sciencepress.mnhn.fr/en/articles/geodiversitas?fascicule=19039>. The cover of the PDF file of this publication contain some links toward the articles of the thematic issue.

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Submitted on 8 June 2020;
accepted on 16 September 2020;
published on 20 December 2021.

GENERA

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Oumtkoutia Rage & Dutheil, 2008
Eupodophis Rage & Escuillie, 2002
Podophis Rage & Escuillie, 2000
Procerophis Rage, Folie, Rana, Singh, Rose & Smith, 2008
Thaumastophis Rage, Folie, Rana, Singh, Rose & Smith, 2008
Vectophis Rage & Ford, 1980
Noterpeton Rage, Marshall & Gayet, 1993
Carentonosaurus Rage & Néraudeau, 2004
Indophis Rage & Prasad, 1992
Krebsophis Rage & Werner, 1999
Nubianophis Rage & Werner, 1999
Cadurcoba Rage, 1978
Eoanilius Rage, 1975
Hechtophis Rage, 2001
Herensugea Rage, 1996
Hoffstetterella Rage, 1998
Itaboraiophis Rage, 2008
Nigerophis Rage, 1975
Paraungaliophis Rage, 2008
Paulacoutophis Rage, 2008
Platyspondylia Rage, 1975
Russellophis Rage, 1975
Woutersophis Rage, 1980

SPECIES

Szyndlaria aureomontensis Rage & Augé, 2010
Pterosphenus biswasi Rage, Bajpai, Thewissen & Tiwari, 2003
Pterosphenus kutchensis Rage, Bajpai, Thewissen & Tiwari, 2003
Oumtkoutia anae Rage & Dutheil, 2008
Podophis descouensi (Rage & Escuillié, 2000)
Procerophis sahnii Rage, Folie, Rana, Singh, Rose & Smith, 2008
Russellophis crassus Rage, Folie, Rana, Singh, Rose & Smith, 2008
Thaumastophis missiaeni Rage, Folie, Rana, Singh, Rose & Smith, 2008

Vectophis wardi Rage & Ford, 1980
Micrurus gallicus Rage & Holman, 1984
Neonatrix crassa Rage & Holman, 1984
Neonatrix europaea Rage & Holman, 1984
Paleoheterodon arcuatus Rage & Holman, 1984
Texasophis meini Rage & Holman, 1984
Noterpeton bolivianum Rage *et al.*, 1993
Carentonosaurus mineaui Rage & Néraudeau, 2004
Indophis sahnii Rage & Prasad, 1992
Thaumastosaurus gezei Rage & Rocek, 2007
Coniophis dabiebus Rage & Werner, 1999
Krebsophis thobanus Rage & Werner, 1999
Nubianophis afaahus Rage & Werner, 1999
Cadurcoba insolita Rage, 1978
Calamagras gallicus Rage, 1977
Coluber cadurci Rage, 1974
Corallus priscus Rage, 2001
Dunnophis cadurcensis Rage, 1974
Dunnophis matronensis Rage, 1973
Eoanilius europae Rage, 1974
Hechtophis austrinus Hechtophis austrinus
Herensugea caristiorum Rage, 1996
Hoffstetterella brasiliensis Rage, 1988
Itaboraiophis depressus Rage, 2008
Madtsoia camposi Rage, 1998
Naja antiqua Rage, 1976
Natrix mlynarskii Rage, 1988
Nigerophis mirus Rage, 1975
Palaeophis colossaeus Rage, 1983
Paraungaliophis pricei Rage, 2008
Paulacoutophis perplexus Rage, 2008
Platyspondylia lepta Rage, 1974
Platyspondylia sudrei Rage, 1988
Python maurus Rage, 1976
Russellophis tenuis Rage, 1975
Testudo phosphoritarum (Rage, 1988)
Vipera maghrebiana Rage, 1976
Waincophis cameratus Rage, 2001
Waincophis pressulus Rage, 2001
Woutersophis novus Rage, 1980

APPENDIX 2. — Taxa dedicated to Jean-Claude Rage. Taxa in bold have been described in this special issue, dedicated to Jean-Claude Rage.

GENERA

Ragesaurus Bailon & Augé, 2012;
Ragechelus Lapparent de Broin, Chirio & Bour, 2020.

SPECIES

Eomadtsoia ragei Gómez, Garberoglio & Rougier, 2019 ([link to Fossilworks](#));
Lainodon ragei Gheerbrant & Astibia, 2012 ([link to Fossilworks](#));
Lapparentophis ragei Vullo, 2019 ([link to Fossilworks](#));
Latonia ragei Hossini, 1993;
Placosaurus ragei Sullivan, Augé, Wille & Smith, 2012 ([link to Fossilworks](#));
Purbicella ragei Evans, Jones & Matsumoto, 2012 ([link to Fossilworks](#));
Ventivorus ragei Mourer-Chauviré, 1988 ([link to Fossilworks](#));
Ragechelus sahelica Lapparent de Broin, Chirio & Bour, 2020;
Ragesaurus medasensis Bailon & Augé, 2012;
Sindhochelys ragei Lapparent de Broin, Métais, Bartolini, Brohi, Lashari, Marivaux, Merle, Warar & Solangi, 2021.