



Rare, but not unique: a new specimen of the enigmatic gecko *Rhodanogekko vireti* from the lower Oligocene of southern Germany

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Rhodanogekko vireti is one of the least known extinct geckos. It was described based on an isolated frontal from the middle Eocene of France, which until now includes the only material assigned to this species. In this contribution, we report an additional isolated frontal, coming from the lower Oligocene of southern Germany, which can be attributed to *R. vireti* based on a strong middle constriction and a dorsal rugose sculpturing. The new fossil extends the stratigraphic record of the species by about 10 Myr, and it is the first evidence for its presence outside France. The phylogenetic position of *Rhodanogekko* is still uncertain, but affinities with Sphaerodactylidae were suggested previously. If this is correct, the new frontal from Germany would fit into a stratigraphic gap without recorded confident sphaerodactylids in Europe, spanning the entire Oligocene. However, *Rhodanogekko* lacks the posterodorsal depressions or grooves apomorphic for frontals of Euleptinae, the subfamily including all European sphaerodactylids, extant and extinct. Additional fossils are needed to understand the relationships between *Rhodanogekko* and other gekkotans, and we here highlight the potential borne by the late Paleogene fossil record from southern Germany for new discoveries of these reptiles.

Introduction

Geckos are rare findings in the fossil record (Estes 1983; Daza et al. 2014; Villa and Delfino 2019; Villa et al. 2022). Despite this, several extinct species are known, mostly from Europe and in most cases represented only by isolated and fragmentary bones (Hoffstetter 1946; Schleich 1987; Müller 2001; Augé 2003, 2005; Bolet et al. 2015; Čerňanský et al. 2018, 2022, 2023; Georgalis et al. 2021; Villa 2023; but see Bauer et al. 2005, and Villa et al. 2022, for two notable exceptions). Well preserved specimens are also available as inclusions in amber (Böhme 1984; Bauer et al. 2005; Arnold and Poinar 2008; Daza and Bauer 2012; Daza et al. 2014, 2016). Among the least known extinct geckos is *Rhodanogekko vireti* Hoffstetter, 1946, whose holotype and only known specimen is an isolated frontal from the middle Eocene of Lissieu, in France. We here report an additional frontal (NMA 2025-2/2197), which can be assigned to *R. vireti* due to morphological congruence with the holotype. The specimen comes from the locality Weißenburg 23 (Fig. 1B), which was located in the quarry of the company “Schotter-und

Steinwerk Weißenburg” (Bavaria, district of Mittelfranken), and more precisely in the north-eastern former extraction area of the quarry. The locality was a karst fissure filling in the Jurassic limestone (Malm Delta), exposed in the years 2009 and 2010 over several meters directly below the ground surface to a depth of 3 m. The matrix of different coloured clays contained components such as iron ores, boulders from the White Jurassic limestones, and Cretaceous relics. The finds of isolated fossils yielded a small Oligocene (Rupelian, MP 21/22) fauna with *Palaeotherium medium* Cuvier, 1804, *Diplobune bavaria* Fraas, 1870, *Pseudosciurus suevicus* Hensel, 1856, and *Suevosciurus ehingensis* Dehm, 1937.

Institutional abbreviations.—NMA, Naturmuseum der Stadt Augsburg, Germany.

Material and methods

NMA 2025-2/2197 (Fig. 2) is housed in the Naturmuseum der Stadt Augsburg (NMA). Terminology used in the descriptions follows Villa et al. (2018). Measurements were taken with ImageJ v. 1.54 (Rasband 1997–2018).

Systematic palaeontology

Order Squamata Oppel, 1811

Infraorder Gekkota Camp, 1923

Genus *Rhodanogekko* Hoffstetter, 1946

Type species: *Rhodanogekko vireti* Hoffstetter, 1946 (Lissieu, France; middle Eocene).

Rhodanogekko vireti Hoffstetter, 1946

Fig. 2.

Material.—NMA 2025-2/2197, an isolated frontal; Weißenburg 23, Bavaria, Germany, early Oligocene.

Description.—NMA 2025-2/2197 is a fairly complete unpaired frontal, missing the entire left posterolateral process, as well as the tip of the right posterolateral process, and with a damaged anterior end. The preserved length (i.e., measured as the longitudinal line from the most anterior preserved portion, located at the left anterolateral corner, to the frontoparietal suture) of the frontal is 9.8 mm, but the broken anterior end could have made up for 0.5 or 1 mm more. The frontal is nar-

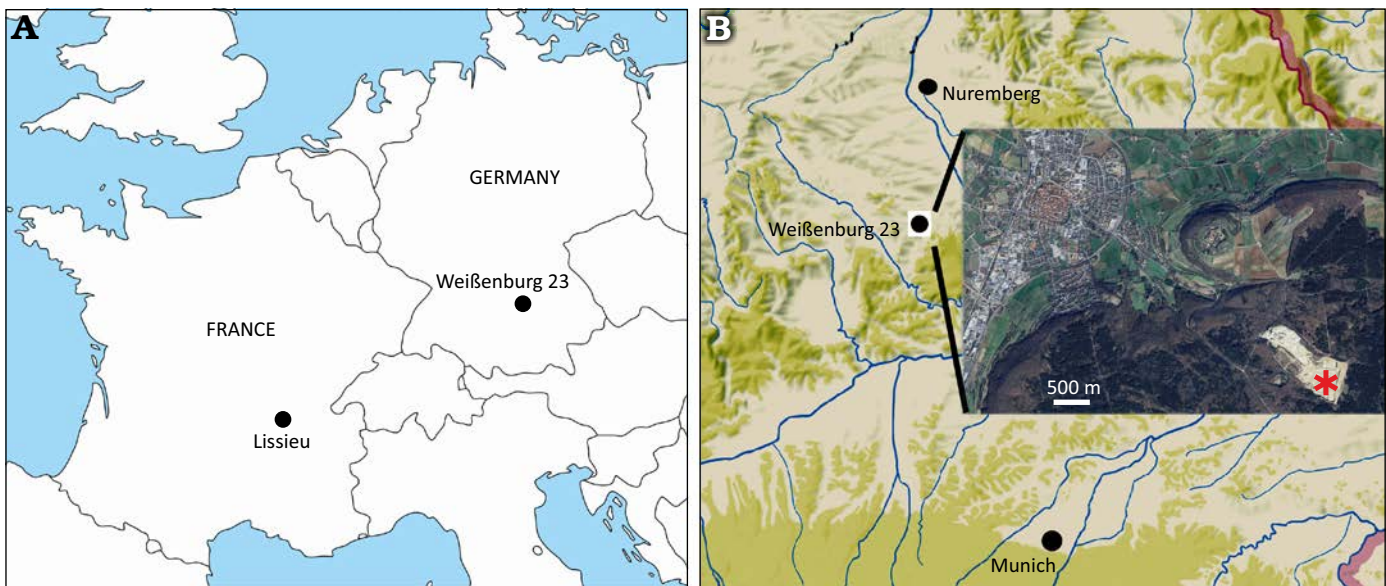


Fig. 1. Locations of the two known occurrences of *Rhodanogekko vireti* Hoffstetter, 1946. **A.** Map of France and Germany with the localities of Lissieu (type locality of the species) and Weißenburg 23. **B.** Map with the location of the village of Weißenburg in Bavaria, Germany, and the location of Weißenburg 23 (asterisk) in the “Schotter-und-Steinwerk Weißenburg” quarry. Map in A based on an original from d-maps (https://d-maps.com/carte.php?num_car=2232&lang=en).

row, with a strongly constricted middle portion that expands slightly at the anterior end and to a higher extent at the posterior end. The width at the narrowest point, at about midlength, is about 1.5 mm. The dorsal surface is almost completely covered by a low dermal sculpturing made up of closely packed rugosities (more scattered in the posterior portion). The size of the rugosities varies, but they are moderately large when considered in proportion with the bone. Only the posterolateral processes are smooth. Posterior to the middle constriction, the dorsal surface is slightly concave, while it is flat in the rest of the bone. There are no depressions or grooves along the lateral margins of the frontal, which are slightly raised instead. Due to the breakage, the morphology of the anterior end of the frontal (i.e. mainly the area articulating with the nasals, which is completely missing) cannot be evaluated. The posterior end displays a straight posterior margin and well-developed and wide posterolateral processes. The preserved part of frontoparietal suture is 5.1 mm wide, but this is only a part of the original width due to the missing portion of the posterolateral processes. Ventrally, the cristae cranii are well developed and partially fuse at midline. This fusion is complete only in the anterior portion of the frontal, and the cristae clearly separate at midlength, leaving posteriorly a wide opening in ventral view. A closed suture line is also visible in the posterior half of the fused portion of the cristae, a potential evidence of immaturity. Anteriorly, the anterior processes of the cristae cranii are very short. The exposed ventral surface of the frontal is flat both anteriorly and posteriorly, with no ridge at midline. By the distal end of the preserved posterolateral process, a low ridge on the lateral margins marks a slender and triangular articulation surface developed along the margin on the ventral surface. On each lateral surface of the frontal, there is a very long and slender articulation surface for the maxilla

and prefrontal, reaching about midlength of the bone. A clear articulation surface with the postorbitofrontal, on the other hand, is not visible.

Stratigraphic and geographic range.—*Rhodanogekko vireti* is only known from its type locality (Lissieu, middle Eocene of France) and the new occurrence reported herein from the lower Oligocene of Germany (Fig. 1A).

Discussion

Among gekkotans, the combination of a strong frontal constriction and dorsal rugose sculpturing is unique to *R. vireti*, which was most likely a large gecko with large eyes (Daza et al. 2014). The constricted frontal, together with the fused cristae cranii, further implies a narrowed olfactory tract for this extinct gecko. The new fossil from Weißenburg 23 shares the above-mentioned frontal features with the holotype of the species, but it is much smaller (the holotype is more than 13 mm in anteroposterior length, based on the photos provided by Daza et al. 2014: fig. 4). This size difference might be accounted for by a potential younger ontogenetic stage of NMA 2025-2/2197, which can be inferred from the incomplete obliteration of the midline suture between the cristae cranii. Attribution of NMA 2025-2/2197 to *R. vireti* widely extends the stratigraphic record of this species, for about 10 Myr from the middle Eocene well into the Oligocene. It further highlights its presence in southern Germany, at least for its youngest occurrence. The precise phylogenetic relationships of *Rhodanogekko* are currently unknown: recent phylogenetic analyses including fossil gekkotans from Europe (Villa et al. 2022; Villa 2023) consistently recovered it nested within the Australian endemic Carphodactylidae Kluge, 1967, but this is likely due to convergence in frontal morphology and poor

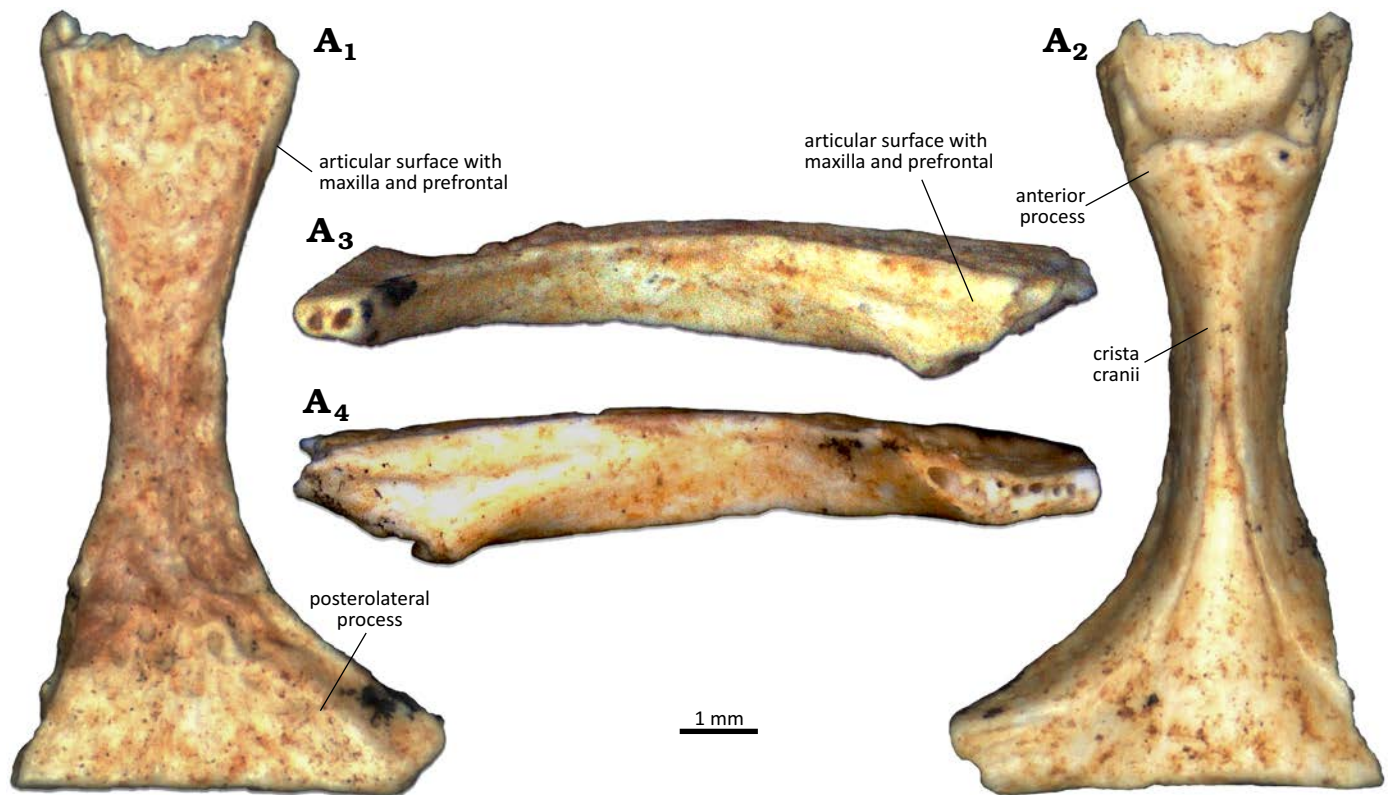


Fig. 2. Frontal (NMA 2025-2/197) of the gekkotan squamate *Rhodanogekko vireti* Hoffstetter, 1946 from the lower Oligocene of Weißenburg 23, Bavaria, Germany, in dorsal (A₁), ventral (A₂), right (A₃), and left (A₄) lateral views.

knowledge of *Rhodanogekko*. Rugose sculpturing in geckos evolved several times in pygopodoids, but at least once also in gekkonoids (Glynne et al. 2020: fig. 5). Daza et al. (2014) reported similarities between the frontals of *Rhodanogekko* and the sphaerodactylid *Pristurus* Rüppell, 1835, mainly based on the constriction. However, *Rhodanogekko* clearly differs from *Pristurus*, because in the latter the frontal is unsculpted (Daza et al. 2014: fig. 4C) and the cristae cranii are not fused ventrally (thus, lacking the tubular frontal of other gekkotans; Daza et al. 2014: fig. 4D). Affinity of *Rhodanogekko* with Sphaerodactylidae Underwood, 1954, would be much less problematic from a biogeographical point of view: as a matter of fact, sphaerodactylids are the dominant gekkotan family in Europe in the Paleogene and Neogene, based on our current knowledge of the fossil records of these squamates (Villa et al. 2022), and their remains were found both in Western and Central Europe. New fossils with *Rhodanogekko*-like frontals and additional bones associated are needed to solve this phylogenetic conundrum. Nevertheless, if *Rhodanogekko* is indeed a sphaerodactylid, the frontal from Weißenburg 23 would fit into the Oligocene gap spanning from the youngest Eocene species to the oldest Miocene ones, providing much needed information on the evolutionary history of this family just prior to the appearance in the Early Miocene of the first representatives of its only extant survivor in Europe (*Euleptes* Fitzinger, 1843, only living in western Mediterranean countries nowadays; Delaunay et al. 2011). Additional occurrences of indeterminate gekkotan fossils with potential

sphaerodactylid affinities reported by Čerňanský et al. (2016) from the upper Oligocene of Herrlingen 9 and 11, also in southern Germany, are further significant in this respect. On the other hand, *Rhodanogekko* clearly lacks dorsal depressions or grooves along the lateral margins in the posterior half of the frontal, the presence of which is the apomorphy of the subfamily encompassing all unambiguous sphaerodactylid genera from Europe, i.e., Euleptinae Villa et al., 2022. If part of the same family, *Rhodanogekko* might represent either a totally unrelated, non-euleptine taxon coexisting in Europe with the oldest known euleptines, a close relative who did not developed the apomorphic frontal feature yet, or even an euleptine who reversed to an undepressed/ungrooved frontal morphology.

Conclusions

Based on the new isolated frontal, we were able to identify the second fossil known of one of the most enigmatic extinct gekkotan species, *R. vireti*. The strongly constricted frontal morphology and the dermal sculpturing on the dorsal surface of the bone confidently allows an attribution to this species. This new occurrence stands out as evidence that *Rhodanogekko* survived in Europe for a long time (at least from the middle Eocene to the early Oligocene) and that its past distribution was more widespread and not limited to France, where the type locality is situated. Despite its unique morphology, *Rhodanogekko* is a significant taxon to understand the evolu-

tion of the European gekkotans, given that it could be related to sphaerodactylids but clearly not part of Euleptinae, the subfamily to which most of the extinct geckos from Europe belong. Its morphological affinities with *Pristurus* could suggest the presence in the Paleogene of Europe of similar geckos, with large eyes, narrow frontals, and perhaps short snouts. Given that we only know *Rhodanogekko* based on two isolated frontals, new fossils are needed, including additional skeletal elements which could be associated with *Rhodanogekko*-like frontals. Southern Germany proves promising for new discoveries on these reptiles, and further explorations of the late Paleogene fossil record from the area, looking for remains of geckos, are highly anticipated.

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