Villa, Andrea; Wings, Oliver; Rabi, Márton. «A new gecko (Squamata, Gekkota) from the Eocene of Geiseltal (Germany) implies long-term persistence of European Sphaerodactylidae». Papers in Palaeontology, Vol. 8, Issue 3 (May/June 2022), art. e1434. DOI 10.1002/spp2.1434

A NEW GECKO (SQUAMATA, GEKKOTA) FROM THE EOCENE OF GEISELTAL (GERMANY) IMPLIES LONG-TERM PERSISTENCE OF EUROPEAN SPHAERODACTYLIDAE

by ANDREA VILLA[1,]*, OLIVER WINGS[2], *and* MÁRTON RABI[2,3,]*

[1]Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifci ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain; e-mail: andrea.villa@icp.cat ORCiD: https://orcid.org/0000-0001-6544-5201

[2]Natural Sciences Collections, Martin Luther University Halle-Wittenberg, Domplatz 4, 06108 Halle (Saale), Germany; e-mail: oliver.wings@zns.uni-halle.de

[3]University of Tübingen, Institute for Geosciences, Hölderlinstraße 12, 72074 Tübingen, Germany; e-mail: marton.rabi@uni-tuebingen.de ORCiD: https://orcid.org/0000-0002-6482-6683

*corresponding authors

Abstract: Gekkota (geckos and pygopods) constitute a diverse and early diverging clade of squamates, but their highly fragmentary fossil record allows only limited insights into their evolutionary history. Even long-known classic Paleogene fossil Lagerstätten, such as the Eocene Messel and Geiseltal, remained uniformative for gecko evolution. Here we describe an articulated near-complete crown-gekkotan skull from the Eocene of Geiseltal. The skull represents one of the most complete and oldest fossil geckos from the Cenozoic and warrants naming the new taxon *Geiseleptes delfinoi* gen. et sp. nov. Parsimony analysis of an expanded morphological dataset comprehensively sampling fossil geckos recovers at least two lineages in the Paleogene of Europe: Gekkonidae and Sphaerodactylidae. Further clades may have been present but require further support. The new species, together with several other European extinct taxa, belongs to the extant clade Sphaerodactylidae. Published molecular phylogenies imply a European dispersal from Africa for the clade and *G. delfinoi* constrains the timing of this event to no later than the middle Eocene. Within Sphaerodactylidae, several Eocene, Oligocene, and Miocene species form the stem-lineage of the extant European-endemic *Euleptes europea* of which *G. delfinoi* is the oldest representative. We here define the new clade *Euleptinae* for this group. Euleptine geckos had an unusually long evolutionary history in Cenozoic Europe and represent one of the very few vertebrate clades with a persistent presence since the early Paleogene, indicating extreme adaptability. As the oldest known crown-sphaerodactylid, *Geiseleptes delfinoi* represents an important fossil calibration for divergence dating analyses of geckos.

Key words: Paleogene, Europe, phylogeny, Sphaerodactylidae, lizards, geckos

Geckos are an iconic group of squamate reptiles, mostly known for the ability of some of their representatives to climb using adhesive toepads (Autumn *et al.* 2002; Russel, 2002; Gamble *et al.* 2012; also present in skinks and anoles). Their group is rather diverse and widespread, living on all continents except Antarctica with more than 2000 extant species currently recognised (Vitt & Caldwell 2009; Uetz *et al.* 2021). These include mainly nocturnal and diurnal lizards with an arthropod based diet, even though species that forage on other food resources (such as fruits, nectar or other vertebrates; Daza *et al.* 2009; Vitt & Caldwell 2009) exist too. Extant geckos inhabit a variety of different habitats, such as forests, deserts and even environments shaped by human presence (Davis 1974; Howard & Parmerlee 2001; Newbery & Jones 2007; Bauer 2013).

The fossil record of geckos consists mostly of isolated skeletal elements and few articulated specimens. It goes back at least to the late Early Cretaceous (*Cretaceogekko burmae*; Arnold & Poinar 2008; Daza *et al.* 2014), with the majority of taxa coming from the Cenozoic of Europe. A number of Jurassic taxa have been proposed in the past as being related to or even included in Gekkota, the crown clade of geckos. These include *Ardeosaurus*, *Bavarisaurus*, *Eichstaettisaurus*, *Palaeolacerta*, and *Yabeinosaurus*. However, these conclusions were later reinterpreted. *Ardeosaurus* and *Yabeinosaurus* were recovered nested within scincoids (and likely closely related to Scincidae) in a recent phylogenetic analysis by Tałanda (2018). Conrad (2018), on the other hand, recovered both *Bavarisaurus* and *Eichstaettisaurus* as basal 'scincogekkonomorphs' and *Palaeolacerta* as an ardeosaurid. If the latter is true, *Palaeolacerta* should also be a scincoid following Tałanda's (2018) results. However, given that *Palaeolacerta* is not included in Tałanda's matrix, this still awaits confirmation. Furthermore, *Eichstaettisaurus* is a sister taxon to *Norellius* (which is a basal gekkonomorph; Conrad & Norell 2006; Conrad & Daza 2015) in Tałanda's analysis, thus indicating different relationships among the early gekkonomorphs. Therefore, *Eichstaettisaurus* might be the only known Jurassic stem-Gekkota, as it seems to be confirmed by recent combined evidence analyses (e.g., Pyron 2017, and related supplementary files; see also Simões & Pyron 2021). Nevertheless, the presence of more derived squamates (i.e., putative "scincomorphs" and anguimorphs; Rage 2013) in the Bathonian of Europe suggests that the gekkotan lineage must have separated at least in the Middle Jurassic. This is in line with age ranges retrieved for the split of the total-group gekkotan lineage from other crown squamates in recent works (Pyron 2017; Simões *et al.* 2020; Simões & Pyron 2021). Simões *et al.* (2018) estimated it even earlier, into the Late Triassic.

Four named taxa referred to either stem or crown gekkotans are known from the Cretaceous, besides a still unnamed and undescribed Early Cretaceous form from Siberia briefly mentioned by Skutchas (2006), unnamed specimens preserved in the mid-Cretaceous Burmese amber (Daza *et al.*

2016; Fontanarrosa *et al.* 2018), and a possible gekkotan frontal from the Maastrichtian of Northeastern Spain (Blanco *et al.* 2016). Eggshells with geckoid morphology are also reported from the latest Cretaceous of Romania (Csiki-Sava *et al.* 2016). The oldest material attributed to crown gekkotans include *Cretaceogekko burmae*, an amber-preserved specimen coming from the late Early Cretaceous of Myanmar (Arnold & Poinar 2008), even though the identity of this material as a member of Gekkota is still debatable (for limitations of amber specimens, see also Fontanarrosa *et al.* 2018). It was originally attributed to Gekkonidae, but Daza *et al.* (2014) treated it as a Gekkota incertae sedis. Three other amber-embedded specimens attributed to geckos were recently reported by Daza *et al.* (2016), also from the Cretaceous of Myanmar. Among these is a well-preserved hatchling, which was included in a phylogenetic analysis and recovered as sister to all other gekkotans (Daza *et al.* 2016). Both *Hoburogekko suchanovi* (Early Cretaceous) and *Gobekko cretacicus* (Late Cretaceous) come from the Gobi Desert in Mongolia. *Hoburogekko*, originally described as Gekkonidae s.l. by Alifanov (1989), was recovered as sister taxon to the carphodactylid *Phyllurus* by Daza *et al.* (2012) and later in a basal polytomy within Gekkota by Daza *et al.* (2013). This polytomy also included the younger *Gobekko* (which is therefore not a gekkonid s.l. as originally inferred by Borsuk-Białynicka, 1990). The same position was recovered for *Gobekko* by Conrad & Norell (2006), whereas it is a sister taxon to all gekkotans in the analysis performed by Conrad (2008). As already mentioned, the Early Cretaceous *Norellius nyctisaurops* from the Altai region (Mongolia) is a basal gekkonomorph (Conrad & Norell 2006; Conrad & Daza 2015; Tałanda 2018). Another Mongolian taxon, *Myrmecodaptria microphagosa* from the Late Cretaceous locality of Ukhaa Tolgod, was referred to Gekkota by Gao & Norell (2000). However, *Myrmecodaptria* is related to more derived squamates according to Conrad & Norell (2006) and Conrad (2008) and even to Scincoidea according to Gauthier *et al.* (2012) and Tałanda (2018).

Cenozoic gekkotans are mostly represented by indeterminate and isolated remains (for an overview, see e.g., Daza *et al.* 2014; Villa & Delfino 2019a). Paleogene records come almost exclusively from Europe (Daza *et al.* 2014). Five extinct species are currently known: *Yantarogekko balticus* from the early Eocene of the Amber Coast in the Samland Peninsula (Bauer *et al.* 2005); *Laonogekko lefevrei* from the early Eocene of France (Augé 2003); *Rhodanogekko vireti* from the middle Eocene of France (Hoffstetter 1946); *Cadurcogekko verus* from the late Eocene of France (Augé 2005; Bolet *et al.* 2015; note that Bolet et al., 2015: fig. 1, incorrectly figured a maxilla of *Cadurcogekko piveteaui* instead of the one they selected as the holotype of *C. verus*); and *Cadurcogekko piveteaui* from the late Eocene or early Oligocene of France (Hoffstetter 1946; Georgalis *et al.* 2021a). The phylogenetic position of these species is still a matter of debate (Daza *et al.* 2014). A peculiar specimen showing primitive features associated to gekkotan synapomorphies was recently briefly reported by Smith *et al.* (2018) from the Eocene Messel Pit in Germany. Outside Europe, Paleogene geckos are reported from the late Paleocene of Brazil (material currently lost; Estes 1970, 1983; Daza *et al.* 2014), the late Paleocene of Morocco (attributed to Gekkonidae; Augé & Rage 2006; Bailon *et al.* 2017), the latest early-early middle Eocene of Algeria (Rage *et al.* 2021), the late Eocene of California (material currently lost; Schatzinger 1975; Golz & Lillegraven 1977; Estes 1983; Daza *et al.* 2014), and the late Oligocene of Tanzania (Müller *et al.* 2018).

The first undisputed representatives of extant families date back to the Neogene. Again, the majority of the extinct species currently known from this period were found in Europe. These European taxa include: *Gerandogekko arambourgi* and *Gerandogekko gaillardi* from the early and late Miocene of France respectively (Hoffstetter 1946; Daza *et al.* 2014); *Euleptes gallica* from the early Miocene of France and Czech Republic (Müller 2001; Čerňanský & Bauer 2010); *Euleptes klembarai* from the middle Miocene of Slovakia (Čerňanský *et al.* 2018); and *Palaeogekko risgoviensis* from the middle Miocene of Germany (Schleich 1987). With the only exception of *P. risgoviensis* (the phylogenetic relationships of which are still unclear; Daza *et al.* 2014), all these species are referred to Sphaerodactylidae. According to Daza *et al.* (2014), evidence for specific separation between *G. arambourgi* and *G. gaillardi* is weak. They could be conspecific, even though this cannot be confidently stated based on the material currently available. *Euleptes* is further reported from the early Miocene of Germany (Müller & Mödden 2001) and, tentatively, the late Miocene of Italy (Colombero *et al.* 2017). A phylogeny of the diverse extinct European gekkotan species is so far lacking. Extinct sphaerodactylids are also known from the Miocene of the Dominican Republic, being represented by amber-embedded specimens all attributed to the extant genus *Sphaerodactylus* (*Sphaerodactylus ciguapa*, *Sphaerodactylus dommeli*, and *Sphaerodactylus* spp.; Böhme 1984; Kluge 1995; Grimaldi 1996; Grimaldi *et al.* 2000; Daza & Bauer 2012; Daza *et al.* 2014). Pygopodids are represented in the Neogene by a single early Miocene Australian fossil attributed to the extinct *Pygopus hortulanus* (Hutchinson 1997), whereas fossil diplodactylids are known from the lower Miocene of New Zealand (Diplodactylidae indet.; Lee *et al.* 2009; Daza *et al.* 2014) and the middle Pliocene of Australia (*Diplodactylus* cf. *steindachneri*; Hutchinson & Mackness 2002). Daza *et al.* (2014) also discussed the possible relationships of Paleogene European taxa with diplodactylids, but definitive evidence for that was lacking. Neogene fossils referred to the extant gekkonid genus *Alsophylax* are reported from the late Miocene of Russia (Vasilyan *et al.* 2017). The occurrences of *Gekko* sp. from the Oligocene and Miocene of Europe mentioned by Böhme & Ilg (2003) were never properly published and need to be confirmed (Villa & Delfino

2019a). Miocene indeterminate gekkonids are also known from few African countries, namely Kenya (Pickford & Andrews 1981), Morocco (Bailon *et al.* 2017), and Namibia (Rage 2008).

From Quaternary deposits, only fossils of extant taxa are known. Pleistocene and/or Holocene geckos are reported from Argentina, Australia, New Zealand, New Caledonia, the Fiji Islands, Aldabra Atoll in the Seychelles, Africa, the Middle East, and Europe. A number of these occurrences pertain to indeterminate forms, but remains identified at genus or even species level are also present. Remains referred to the phyllodactylid *Homonota* sp. were reported from the late Quaternary (Late Pleistocene or younger) of Argentina by Albino (2005, 2020) and Agnolin & Jofré (2011). Dentaries of *Pygopus* sp. were found in two Australian caves, in Holocene deposits (Mead *et al.* 2008). Daza *et al.* (2015) reported *Bavayia crassicollis*, *Bavayia* sp., *Gehyra georgpotthasti*, and *Nactus pelagicus* from Holocene sites on Tiga Island (also called Tokanod) in The Loyalty Islands. *Gehyra oceanica*, *Gehyra* aff. *vorax*, *Gekko* sp., and *Nactus pelagicus* were identified in various Late Pleistocene to Holocene sites in the Fiji (Worthy & Anderson 2009; Worthy & Clark 2009). Worthy & Holdaway (1996) and Holdaway & Worthy (1997) reported various taxa from different localities in New Zealand, including representatives of the genera *Gekko*, *Hoplodactylus*, and *Naultinus*. In the Quaternary of Europe, gekkotan fossils referred to three of the extant genera inhabiting Europe (namely, *Euleptes*, *Hemidactylus*, and *Tarentola*) are known from the Mediterranean region, in some cases even showing morphologies that appear closely related with the extant European species (Villa & Delfino 2019a).

In this paper, we report on gekkotan fossil material coming from the Eocene site of Geiseltal in Germany, including an articulated, incomplete skull. This specimen represents the worldwide oldest sphaerodactylid and one of the most complete fossil gekkotan from Europe. It belongs to a new taxon, which is here included in the first phylogenetic analysis of all European gekkotan fossil species and warranting the definition of a new clade of European Sphaerodactylidae.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The former Geiseltal lignite (brown coal) deposits, 20 km SSW of Halle (Saale), Saxony-Anhalt, Germany (Fig. 1), were exploited in several opencast mines. The strata also yielded a diverse fossil flora and fauna often characterized by exceptional preservation (e.g., Krumbiegel *et al.* 1983; Voigt 1988). The Geiseltal fossillagerstätte consisted of three major coal seams intercalated by clastic deposits. Depending on the influx of carbonate-rich waters which allowed fossil preservation, dozens of vertebrate fossil localities with variable preservational conditions were distributed vertically and horizontally within Geiseltal (e.g., Haubold & Thomae 1990). Regional spore-pollen biostratigraphy suggested a Lutetian age (middle Eocene, Spore/Pollen Zone 14/15–15; Krutzsch

1966, 1970, 1976; Krutzsch *et al.* 1992) for the fossillagerstätte. Biochronology of mammal faunas at Geiseltal established the middle Eocene Mammal Paleogene levels (MP) 11–13 (= Geiseltalian); the whole fossillagerstätte is ranging from MP 11 to MP 14, spanning more than the Lutetian (Franzen & Haubold 1986, 1987; Haubold 1987, 1989; Schmidt-Kittler *et al.* 1987; Haubold & Thomae 1990). The gecko-yielding site Cecilie IV was located in the upper Middle Coal, which was assigned to MP 13 (Haubold & Thomae 1990). However, a recent study of perissodactyls indicates a lower diversity and an underestimation of taphonomy and collecting bias in local mammal biochronology (Ring *et al.* 2020). We thus refrain from assigning individual coal seams to MP levels at the moment. Faunal similarities with the Messel fossillagerstätte (e.g., cf. Smith *et al.* 2018 and Steinheimer & Hastings 2019) roughly indicate an age of the gecko remains from Geiseltal as around the late early or middle Eocene (Messel is spanning the Ypresian–Lutetian boundary which is at 47.8 Ma; Cohen *et al.* 2013; see Lenz *et al.*, 2015, for dating Messel). See Georgalis *et al.* (2021b) for further details on the age and duration of Geiseltal.

The Site Cecilie IV is also called “Trichter Nordost” (“Pit NorthEast” in the original descriptions; Weigelt 1934). It represents a circular sinkhole in the gypsum karst of Upper Buntsandstein strata underlying the bog (Krumbiegel *et al.* 1983). The water-filled sinkhole probably served as a watering point during the dry season (Krumbiegel *et al.* 1983). The often-steep banks of the sinkholes acted as trapping pits in which many vertebrates perished (Krumbiegel *et al.* 1983). Anaerobic conditions at the bottom of the pit combined with a rapid sedimentation rate enhanced preservation of the carcasses (Krumbiegel *et al.* 1983). Cecilie IV was one of the most productive vertebrate sites in Geiseltal, having produced among other fossils the remains of 14 mammal skeletons and skulls, five birds, 75 “lizards”, 10 crocodilians, 46 turtles, 16 snakes, and 18 frogs (Weigelt 1934).

MATERIAL AND METHODS

This paper is based on fossil material stored in the Geiseltal Collection, a part of the Natural Sciences Collections at the Martin Luther University Halle-Wittenberg in Halle (Saale). The holotype was collected and prepared by Lothar Nöth in the year 1933. GMH Ce IV-4123-1932 was excavated by Wiesemann in the year 1932 and subsequently prepared by Ehrhard Voigt. Both specimens are preserved on nitro cellulose lacquer/resin. Photographs of the holotype of the new species were taken with a Canon EOS 6D Mark II and a Canon EOS 80D. The holotype was microCT scanned using a Tomoscope HV 500-Werth at the Fraunhofer-Entwicklungszentrum Röntgentechnik EZRT of the Fraunhofer-Institut für Integrierte Schaltungen IIS in Deggendorf, Bavaria, Germany. Taxonomic names above the species level highlighted in italics are formally defined clade names (de Queiroz *et al.* 2020) including the new clade name, *Euleptinae*, defined below following the PhyloCode. Anatomical terminology follows Villa *et al.* (2018) and Villa & Delfino (2019b).

Phylogenetic analysis

As no previous studies performed a phylogeny of European fossil gekkotans, the Geiseltal gecko was included into the matrix of Conrad (2018). This dataset was originally designed for a global analysis of squamates, but we here limit the taxon sampling to gekkotans and gekkotan-related taxa. The outgroups used include *Pamelina* (as in Conrad's original analysis), *Sphenodon*, and *Dibamus*. For our analysis, we added the Geiseltal taxon, all published European fossil gekkotans (except the highly fragmentary *Gerandogekko arambourgi*, which was removed for our second analysis), and the four extant gecko species most broadly distributed in Europe (*Euleptes europaea*, *Hemidactylus turcicus*, *Mediodactylus kotschyi*, and *Tarentola mauritanica*). We furthermore added ten new characters (see Appendix S1) and reworded state 9 for C403 ("Dentition, number of teeth in each premaxilla") as "10 or more", to acknowledge the fact that extant European taxa can have 11 teeth. Of the new characters, one is parsimony uninformative (C845). We implemented a molecular scaffold for extant taxa using the phylogeny of Gamble *et al.* (2015) and allowed fossil taxa to float into this topology.

Conrad's (2018) matrix is an updated version of previous squamate datasets (e.g., Conrad, 2008, 2015; Conrad *et al.*, 2008, 2011, 2012), some of which already focused on gekkotans and relatives (Daza *et al.*, 2012, 2013). Although he did not mention it explicitly, Conrad (2018) inverted the states of C175 ("Mandible, posterior mylohyoid foramen") in his character definitions (his appendix II). As a matter of fact, state 0 was "present" and state 1 was "absent" in the matrix used by Conrad & Norell (2006; the original work from which this character is taken), Conrad (2008), and Daza *et al.* (2013), whereas they are reversed in Conrad (2018). The reversal of the states appears to be intentional and coded consistently: Conrad (2008) figured a mandible of *Heloderma* clearly showing a posterior mylohyoid foramen (figure 38E) and *Heloderma* is consequently scored as 0 in the matrix of Daza *et al.* (2013), whereas Conrad (2018) scored *H. horridus* as 1 (foramen present). In a similar way, *Sphenodon* (which lacks the foramen) is scored as 0 by Conrad (2018), whereas rhynchocephalians were scored as 1 by Daza *et al.* (2013). For most of the geckos, on the other hand, C175 was incorrectly scored as 1 in the first version of the matrix (Conrad 2008) and by inverting the states it was corrected by Conrad (2018; still scored as 1). C176 (related to the position of the same foramen) is scored as inapplicable for geckos in the old matrix (as correct if the foramen is not present), but it scored as either 0 or 1 in the later version. Taking all of this into account (and following a preliminary survey of the morphology in select species), we follow Conrad (2018) with the exception of *Gobekko* and *Hoburgekko*. Adding to this, Conrad (2018) wrote that he deactivated characters 236, 242 and 364 (he wrote 363 in his appendix II, but it is actually 364 as written in the text) as in previous analyses, but actually he completely removed the characters from the final matrix.

We used Daza *et al.*'s (2013) scorings for *Gobekko* and *Hoburogekko* for C1–361 (these updates were ignored by Conrad, 2018), and for the rest of the characters (not present in Daza *et al.*'s matrix), we kept Conrad's (2018) scorings. For the new characters, we based our scorings on Daza *et al.*'s (2012, 2013) descriptions of the two Mongolian taxa. Characters that were scored as "-" (inapplicable) by Daza *et al.* (2013) were scored as "?" by Conrad (2018), but are here rescored as "-". This applies only to taxa that were already present in Daza *et al.*'s matrix and only to the first 361 characters. We follow Conrad (2018) in treating multistate characters that form a morphocline ordered.

Extant European gekkotans were scored based on personal observations of material stored in the Massimo Delfino Herpetological Collection (MDHC) at the Department of Earth Sciences of the University of Torino (Italy), as well as on data available in the literature (Bauer *et al.*, 1997; Speybroeck *et al.*, 2016; Villa *et al.*, 2018). Fossil taxa were scored based on published data and personal observations (type material of *C. piveteaui* and *G. arambourgi* stored in the Muséum national d'Histoire naturelle in Paris). The matrix was constructed in MESQUITE v3.61 (Maddison & Maddison, 2017) and analyzed with TNT v1.5 (Goloboff *et al.*, 2008). The analysis was run with the Traditional search with two rounds (second round with starting trees from RAM) of tree bisection reconnection using 1000 replicates with 10 trees saved per replicate.

Institutional abbreviations. GMH, "Geiseltalmuseum Halle" = Geiseltal Collection, ZNS, Martin Luther University Halle-Wittenberg, Germany; MDHC, Massimo Delfino Herpetological Collection, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Italy.

SYSTEMATIC PALAEONTOLOGY

SQUAMATA Oppel, 1811

GEKKOTA Camp, 1923

SPHAERODACTYLIDAE Underwood, 1954

EULEPTINAE new clade name

Phylogenetic definition. The largest clade containing *Euleptes europaea* (Gené, 1839) but not *Teratoscincus scincus* (Schlegel, 1858).

Derivation of name. From *Euleptes*, only extant genus included within the clade.

Reference phylogeny. Gamble *et al.* (2015) [primary] and this study.

Composition. The following genera currently comprise *Euleptinae*: *Cadurcogekko* Hoffstetter, 1946, *Euleptes* Fitzinger, 1843, *Geiseleptes* gen. nov., and *Gerandogekko* Hoffstetter, 1946.

Diagnosis. The clade is unambiguously diagnosed by the following characters: presence of depressions/grooves on the dorsal surface of the frontal, along the posterolateral margins of the bone (C837: 0 → 1).

Remarks. As the phylogeny of the present study does not include the external specifier *Teratoscincus scincus* (extant sister-species of *Euleptes europaea*), we add an apomorphy based diagnosis in order to support the placement of fossil species to *Euleptinae*. An additional apomorphy recovered by our phylogenetic analysis include a lateral groove behind the last ventrolateral foramen of the maxillae (reversed in *Gerandogekko*, 840: 0 → 1).

Genus *GEISELEPTES* nov.

LSID. urn:lsid:zoobank.org:act:2DD0FEC3-A7D8-4C92-A496-9E1485301CA3

Type species. Geiseleptes delfinoi gen. et sp. nov.

Derivation of name. From Geisel, the river that gave name to the fossillagerstätte Geiseltal, and -leptes, in reference to *Euleptes*, the only extant European sphaerodactylid and close relative to the herein-described Geiseltal taxon.

Diagnosis. As for type species.

Geiseleptes delfinoi sp. nov.

Figs 2–5

Derivation of name. Specific name honours Massimo Delfino, leading European palaeo- and neoherpetologist, who greatly contributed to the study of both fossil and leaving amphibians and reptiles and inspired us (as well as many others) in pursuing the same path.

Holotype. GMH Ce IV-4057-1933, a partially articulated and fragmentary skull.

Locality and horizon. Geiseltal fossillagerstätte, Site Cecilie IV (=”Trichter Nord-Ost”), upper Middle Coal (oMK), late early or middle Eocene.

Diagnosis. The phylogenetic analysis recovered three unambiguous autapomorphies for the taxon: frontoparietal suture U-shaped and anteriorly arched in dorsal view (C70: 1 → 0); orbital process of the prefrontal terminating within the anterior 1/3 of the orbit (C383: 2 → 1); short grooves along posterolateral margins of frontal (C389: 1 → 0). For a differential diagnosis and comparison, see the Remarks section below.

Description

The holotype (Fig. 2), and only specimen currently referred to the new taxon, is represented by a heavily crushed skull. During preparation, it was separated into two parts, herein named a and b respectively, which are now hosted on the same support. Part a (Fig. 3) includes most of the cranium and part of the lower jaws, being visible in lateral view. Part b (Fig. 4) includes part of the two lower jaws and part of the left maxilla, exposed in ventral view. Other bones and fragments of bones are also represented in part b, but they cannot be confidently identified. The micro-CT scans revealed that the unexposed portion of the specimen is very poorly preserved and mainly consists of heavily crushed bone fragments. Because of this, the description is mainly based on what is visible directly on the exposed surface, even though some additional details were retrieved with the scans.

Cranium. The nasals (Fig. 3A,B) are preserved but rather fragmentary. The internasal suture is still recognisable. They are anteroposteriorly elongated and dorsally smooth. It seems that they taper slightly anteriorly, but this might have been enhanced by the crushing. The frontal (Figs. 3, 5A,B) is unpaired. It was originally hourglass-shaped, with a moderate constriction at midlength. The anterior end is completely crushed and cannot be described. The posterior end shows long and slender posterolateral processes. The posterior margin is distinctly concave. The dorsal surface appears smooth, but a very short and shallow groove is visible extending along the lateral margin of the distal portion of each posterolateral process (Fig. 5A,B). The ventral surface is partially visible only with the scans, but just the posterior end of the bone can be described, due to strong fragmentation of the rest of the bone. In the scan, it is possible to see the low posterior portion of the left crista cranii running along the lateral margin and the posterolateral process. Medially to the crista, the ventral surface of the posterior end of the frontal is smooth. A shallow, but rather wide articulation surface for the postorbitofrontal is visible on the right lateral side of the posterior end of the bone. The anterior end of this articulation surface is located far from the posterior end of the dorsal process of the prefrontal. The preserved length of the frontal can be measured as 5 mm, but the bone was probably slightly more than 6/7 mm (probably even about 8 mm) in origin. The parietals (Figs. 3, 5A,B) are paired and poorly preserved, but an original rectangular shape is recognisable based on what remains. The anterior margin is slightly concave. By the anterolateral corner, the anterolateral process is well developed and has a rounded end. There is no notch medially to it. The posterior end is not preserved. Judging from the preserved portion of the lateral margin of the left parietal, the lateral lamina seems poorly developed. The dorsal surface of the parietal table is smooth, except for few very shallow grooves, possibly representing a light sculpturing, that are present near the anterolateral corner of the left element (this area is broken off in the right parietal). The postparietal processes are missing. Only the alveolar portion and a small part of the facial process of the right maxilla (Fig. 3A,B) are preserved, whereas only the alveolar portion of the left maxilla (Fig. 4), including the posterior process, is exposed in ventral view. The lateral surface of the preserved portion of the facial process is smooth. At least six ventrolateral foramina are recognisable. The posteriormost one is located on the posterior process and is followed by a long and shallow groove (Fig. 5A,B). Dorsally to these foramina, two other small foramina are visible: one near the anterior end and one near the posterior end of the facial process. The last ventrolateral foramen and the related groove are visible on the left maxilla also. The ventral end of the anterior margin of the facial process displays a gentle curvature. The anterolateral process is well developed. The posterior process is long and rather slender, tapering posteriorly and ending with a pointed tip. The teeth of the right maxilla are only visible in the scans, because they are partially covered by matrix, but they can be easily observed also in the actual specimen in the left one. They are pleurodont, cylindrical, closely spaced and rather slender. They are small at the anterior end, slightly increase in size posteriorly, but then become smaller again towards the posterior end. The tooth row reaches the posterior end of the posterior process. At least 13 tooth positions can be counted in the right maxilla, but most of the tooth row is hidden. The left element, on the other hand, shows at least 27 tooth positions. Few teeth in the left maxilla are preserved enough to show the crowns: these are identical to those of the dentaries (see below). Some of them clearly display two parallel cutting edges, oriented mesiodistally. The right maxilla is roughly 9.5 mm long. The preserved portion of the left one is 9 mm long, but it should have been longer when intact, reaching the same size of its counterpart. The right prefrontal (Figs. 3A,B, 5A,B) is crescent-shaped in lateral view. The orbitonasal flange is large. The exposed dorsal surface and the posterior surface are smooth. The anterodorsal process is broken and neither the orbitonasal flange projection nor the distal end of the posteroventral process is visible. The pointed dorsal process is rather robust and long. It is as long as the orbitonasal flange is wide. The small right postorbitofrontal (Figs.

3A,B, 5A,B) is partially preserved and Y-shaped. The anterior process is long and tapers anteriorly. Its anterior end is missing. The posterior process is completely missing. Laterally, there is a well-developed lateral process, which is triangular and shorter than the anterior process. A small foramen is visible at the base of the posterior process (Fig. 5A,B). The ventral ends of both quadrates (Figs. 3, 5A,B) are preserved. Both have a wide mandibular condyle, the medial side of which is flat and ventrally less developed than the lateral side. There is no medial lamina. A poorly preserved, slender and rod-like bone preserved posteriorly to the posterior process of the maxilla and dorsally to the coronoid might be the right epipterygoid (Fig. 3). Part of the left epipterygoid is also preserved, being clearly visible only in the scan near the left quadrate (Figs. 3B). A long bone located ventrally to the mandibular end of the left quadrate might be part of the left pterygoid (Figs. 3A,B, 5A,B), including mainly the quadrate process. This latter process is distinctly curved in lateral direction, but its posterior end is not visible. A flat area on the medial surface near the anterior end of the exposed portion of the bone might represent the poorly marked basipterygoid fossa. The anterior portion of the bone is crushed. A small piece of bone located dorsally to the posterior process of the right maxilla is most likely the right ectopterygoid (Fig. 3). It has a rather flat aspect and seems to taper anteriorly. Only a small portion of the bone is visible, but the articulation surface with the pterygoid flange of the pterygoid is visible posteriorly. Part of the otooccipital region might be visible posteriorly, but the bones are difficult to interpret. A rather long and robust bone might be the right paroccipital process seen in dorsal view (Fig. 3A,B), but it seems rather robust. Anteriorly to it, there is also a void and curved structure that might be one of the semicircular canals.

Lower jaw. Both dentaries are preserved (Figs. 3, 4). On the medial side, the Meckelian fossa is closed in a tubular structure by the expansions of the ventral margin and the subdental shelf. The tubular structure is narrow and tapers anteriorly. The mandibular symphysis is preserved only in the left dentary, even though in poor condition. It was most probably narrow and slightly dorsally inclined. The lateral surface of the dentaries is smooth. The complete series of the mental foramina is not recognisable, given that only three of them are visible on the left dentary and none on the right one. The ventral margin of these slender bones is straight. The posterior portion of the dentaries is damaged and so the posterior processes are not clearly recognisable. At least 18 tooth positions are visible on the right dentary, whereas the left one displays at least 14 of them (four by the anterior end in part a and the rest in part b). Teeth are pleurodont, cylindrical, slender and closely spaced. The crown is rather pointed and does not bend significantly in posteromedial direction. It is also not striated lingually. The preserved part of the right dentary is 8.5 mm long. Estimating the length of the left one is difficult. The portion preserved on part a (i.e., the anterior end) is roughly 5.5 mm long, whereas that on part b is about 8 mm. However, it is not clear how much these two portions are superimposed. Nevertheless, it is possible to estimate the complete original length of the dentary at around 10 mm. The right coronoid is preserved in part a (Fig. 3). It is slender and concave in medial direction. The anteromedial process is not visible, but a short labial process is exposed. The coronoid process is dorsally broken, but it was connected to the posteromedial process by an osseous lamina. The posteromedial process is long and thin. Its distal tip is not clearly visible, but it seems rounded in ventral view. Part b preserves the left coronoid (Fig. 4), which is clearly visible only in the scans and has a morphology that is comparable with that of the right one. Most of the left compound bone and part of the right one are very poorly preserved in part b (Fig. 4). In part a (Fig. 3), the right compound bone is visible in lateral view, whereas part the left one is displaced dorsally and it is visible in ventral view. The angular was most likely fused to the compound bone, as evidenced by the lack of an evident articular surface for this bone in the left element. The lateral surface of the bone is smooth, with a large anterior surangular foramen located anteriorly near the dorsal margin. The posterior surangular foramen is visible only on the left element and only in the scans. It appears rather large and it seems somehow shifted towards the dorsal margin of the bone, even though the crushed state of the specimen renders its recognised position less confident. The right compound bone is broken just by the position of the articular condyle. The posterior end of the left one shows an expansion, which most likely also represents the condyle. A narrow posterior projection is probably the retroarticular process, the posterior end of which is broken.

Remarks

GMH Ce IV-4057-1933 can be clearly referred to gekkotans due to the presence of distinctive features, such as the unpaired and hourglass-shaped frontal, paired and elongated parietals, presence of a Y-shaped postorbitofrontal, completely closed Meckelian fossa on the dentary, and pleurodont and closely-spaced teeth with an unstriated crown (Sumida & Murphy 1987; Evans 2008; Villa *et al.* 2018).

However, it displays significant differences compared to all fossil species of geckos previously reported from the European continent, as well as to the four most common extant European gekkotans. This allows assignment to its own taxon. *Geiseleptes delfinoi* differs from *Cadurcogekko piveteaui* in having grooves instead of depressions in the posterior portion of the frontal, a posterior margin of the frontal that is concave instead of straight, and a smooth lateral surface of the maxilla (Hoffstetter 1946; Augé 2005, Daza *et al.* 2014). *Cadurcogekko piveteaui* probably had also more teeth than *Geiseleptes* (38 maxillary teeth according to Augé, 2005, but

Daza *et al.*, 2014, estimates between 40 and 44 teeth for the maxilla of the French species). *Geiseleptes delfinoi* differs from *C. verus* in having smooth maxillae and frontal (Augé 2005; Daza *et al.* 2014; Bolet *et al.* 2015). It differs from both *Gerandogekko arambourgi* and *G. gaillardi* because of the shorter grooves on the frontal and at least from *G. arambourgi* in the presence of the posterior groove on the maxilla (Hofstetter 1946; Daza *et al.* 2014). It also differs from *Laonogekko lefevrei* in the presence of a groove posteriorly to the last ventrolateral foramen in the maxilla (Augé 2003, 2005; Daza *et al.* 2014). Similar to *C. piveteaui*, *L. lefevrei* may also have more teeth than the Geiseltal species: Augé (2003, 2005) reported 38 maxillary teeth and 45 dentary teeth, but Daza *et al.* (2014) gave a slightly lower (up to 33 tooth positions in the most complete specimen) dentary teeth count. *Geiseleptes delfinoi* differs from *Palaeogekko risgoviensis* in having a posterior groove on the maxilla and in the distinctly larger size (Schleich 1987; Daza *et al.* 2014). It also differs from *Rhodanogekko vireti* in the frontal that is less constricted at midlength, dorsally smooth and provided with a concave posterior margin and posterior grooves (Hofstetter 1946; Estes 1983; Daza *et al.* 2014). Differences between *Geiseleptes delfinoi* and *Euleptes klembarai* include the significantly larger size (the length of the maxilla is almost double), the posterior groove and the anterolateral process on the maxilla that are better developed in the German taxon (Čerňanský *et al.* 2018). *Geiseleptes delfinoi* differs from *E. gallica* mainly because of its distinctly larger size (Müller 2001; Čerňanský & Bauer 2010; Daza *et al.* 2014); all the diagnostic features of *E. gallica* are located either on the premaxilla or on the facial process of the maxilla, which are respectively completely or partially unknown for *Geiseleptes delfinoi.* Due to its peculiar preservational nature (it is preserved in amber), it is difficult to compare *Yantarogekko balticus* to other fossil geckos. Nevertheless, *Geiseleptes delfinoi* is distinctly larger than this early Eocene species (Bauer *et al.* 2005).

As far as the extant European species are concerned, *Geiseleptes delfinoi* differs from *E. europaea* in (Villa *et al.* 2018): posterior margin of frontal concave; posterior grooves on the frontal less marked and shorter; well-marked articular surfaces with postorbitofrontal on the frontal; larger size (based on both the length of frontal and maxilla); dorsal surface of the parietals largely smooth, but with few grooves; anterolateral process of the maxilla more developed; posterior process of the maxilla pointed; dorsal process of the prefrontal robust; presence of a lateral process on the postorbitofrontal; presence of a foramen on the postorbitofrontal. It differs from *Hemidactylus turcicus* in (Villa *et al.* 2018): frontal and maxilla smooth; presence of posterior grooves on the frontal; posterior margin of frontal concave; anterolateral process of the parietal narrower; absence of a notch medially to the anterolateral process of the parietal; lateral lamina of the parietal poorly developed; groove present posteriorly to last ventrolateral foramen on the maxilla; larger size (based on maxilla); presence of a lateral process on the postorbitofrontal; presence of a foramen on the postorbitofrontal; and maybe also posterior surangular foramen shifted dorsally. It differs from *Mediodactylus kotschyi* in (Villa *et al.* 2018): presence of posterior grooves on the frontal; absence of a notch medially to the anterolateral process of the parietal; lateral lamina of the parietal poorly developed; dorsal surface of the parietals largely smooth, but with few grooves; anterolateral process of the maxilla more developed; anterior margin of the facial process not vertical; groove present posteriorly to last ventrolateral foramen on the maxilla; larger in size (based on maxilla); dorsal process of the prefrontal robust; presence of a lateral process on the postorbitofrontal; presence of a foramen on the postorbitofrontal; posterior surangular foramen shifted dorsally. It also differs from *Tarentola mauritanica* in (Villa *et al.* 2018): presence of posterior grooves on the frontal; posterior margin of the frontal concave; anterolateral process of the parietal well developed; lateral lamina of the parietal poorly developed; dorsal surface of the parietals largely smooth, but with few grooves; absence of a notch on the anterior margin of the facial process of the maxilla; presence of a groove posterior to the last ventrolateral foramen on the maxilla; presence of a foramen on the postorbitofrontal.

Geiseleptes delfinoi also displays some similarities with both the fossil and the extant European gekkotans. It shares a moderately constricted frontal with *Cadurcogekko, G. arambourgi,* and *L. lefevrei,* the presence of posterolateral grooves on the frontal with *E. europaea* and *Gerandogekko,* and the concave posterior margin of the frontal with *G. arambourgi* and *M. kotschyi*. According to Bauer *et al.* (2005), *Y. balticus* could have an expanded (i.e., not strongly constricted) frontal, which would be similar to *Geiseleptes*. The posterolateral grooves on the frontal are shallow in both *Geiseleptes delfinoi* and *Gerandogekko,* whereas they are more marked in *E. europaea*. The articular surface with the postorbitofrontal is visible on the frontal also in *C. piveteaui, G. arambourgi, H. turcicus, L. lefevrei,* and *T. mauritanica*. The dorsal surface of the frontal is smooth in *E. europaea*, *Gerandogekko*, *L. lefevrei* (Augè, 2003, mentions a dermal ornamentation, but Daza *et al.*, 2014, wrote that it is just the result of erosion of a rather smooth dorsal surface of the bone), *M. kotschyi*, *T. mauritanica*, and probably also *Y. balticus* (according to Bauer *et al.*, 2005, this species probably lacks ossified osteoderms on the frontal), whereas the maxilla is laterally smooth in *Euleptes, G. gaillardi, L. lefevrei, M. kotschyi, P. risgoviensis,* and *T. mauritanica*. The posterior groove on the maxilla is shared by *Geiseleptes delfinoi*, *Cadurcogekko,* and *Euleptes*. Other maxillary features that are shared by *Geiseleptes delfinoi* with other species are a similar degree of development of the anterolateral process (with *H. turcicus* and *T. mauritanica*) and the pointed posterior process (with *H. turcicus, M. kotschyi,* and *T. mauritanica*). The parietal of *Geiseleptes delfinoi* is similar to the one of *E. europaea* and *M. kotschyi* in having a well-developed anterolateral process, the one of *E. europaea* in having a poorly-developed lateral lamina and no notch medially to the anterolateral process, and the one of *H. turcicus* in the presence of grooves on the dorsal surface (even though they are fewer in the Geiseltal species). The prefrontal of *Geiseleptes delfinoi* recalls those of both *H. turcicus* and *T. mauritanica* in the robustness of its dorsal process. The postorbitofrontal of *Geiseleptes delfinoi* displays a lateral process as in *T. mauritanica*. In the end, the dorsally-shifted posterior surangular foramen (if confirmed) would be shared by *Geiseleptes delfinoi*, *E. europaea*, and *T. mauritanica*.

?Gekkota indet.

Material. GMH Ce IV-4123-1932, a slab with a number of disarticulated and very poorly preserved skeletal elements.

Description

This specimen is a mix of different small-sized bones, mainly postcranial elements. Most of them are slender limb bones, but there is also a left maxilla. The morphology of the maxilla recalls that of a gecko, but the bone is too poorly preserved and the teeth are not well visible. The morphology appears somehow similar to the right maxilla of GMH Ce IV-4057-1933. Two small femoral condyles are also visible on the slab.

Remarks

The bones in this specimen (at least the maxilla) might indeed pertain to a gecko, maybe even the same taxon as GMH Ce IV-4057-1933. However, the preservation is not good enough to clearly confirm that.

PHYLOGENETIC ANALYSIS

A first iteration of the analysis failed to recover the currently recognised topology of gekkotan phylogenetic relationships based on molecular data (as reported by Gamble *et al.*, 2015), and we therefore rerun the analysis with the same settings and six constraints to force the monophyly of: a) Diplodactylidae + (Pygopodidae + Carphodactylidae); b) Pygopodidae + Carphodactylidae; c) Eublepharidae + (Sphaerodactylidae + (Gekkonidae + Phyllodactylidae)); d) Sphaerodactylidae + (Gekkonidae + Phyllodactylidae), e) Sphaerodactylidae; and f) Gekkonidae. All fossil gekkotans were treated as wild-card taxa in this second iteration. The second run resulted in 568 trees with a minimum length of 783 steps. The strict consensus tree (Fig. 6A) recovered most of the ingroup taxa, including *Geiseleptes*, in a wide polytomy, though. *Gerandogekko arambourgi*, a poorly-known taxon only scored for a few characters, is a wild-card taxon and since it is operationally identical to the congeneric *G. gaillardi* (Daza *et al.*, 2014, even question whether they represent separate species), we removed it from the analysis. The analysis without *G. arambourgi* obtained 20 trees with a length of 782 steps. In the strict consensus tree (Fig. 6B), an early-branching clade including the Cretaceous *Norellius* and *Gobekko* is recognised that is sister to *Hoburogekko* and the crown clade Gekkota. *Geiseleptes* is always recovered within Sphaerodactylidae. Pruning *Euleptes gallica*, *Laonogekko lefevrei*, and *Palaeogekko risgoviensis* resulted in an almost completely-resolved strict consensus tree (Fig. 6C), in which a polytomy persisted within Sphaerodactylidae and including *Geiseleptes*, all remaining species of *Euleptes*, *G. gaillardi*, and *Cadurcogekko*. In the strict consensus, Sphaerodactylidae is supported by three synapomorphies (C137, 403, 429) and the less inclusive new clade *Euleptinae* by five (C242, 837, 840, 843, 846). Alternative positions of the pruned taxa are shown in Fig. 6C. For the time being, we are not able to further resolve the relationship within this European sphaerodactylid clade. Regarding other extinct European gekkotans, *Rhodanogekko* is nested within the Carphodactylidae in all analyses, whereas *Yantarogekko* is sister to *Phelsuma* inside Gekkonidae. Consistency and Retention indexes of the analysis without *G. arambourgi* are 0.579 and 0.397, respectively.

DISCUSSION

*Antiquity of European sphaerodactylid gekkotans (*Euleptinae*)*

With few exceptions, the gekkotan fossil record is largely represented by isolated remains, for which a confident phylogenetic framework is often difficult to assess. *Geiseleptes* thus presents itself as an important specimen to shed light on the relationships of fossil geckos, in particular when it comes to Paleogene representatives of the clade from Europe. This taxon shows unique features that ally it with a single species within the extant European inhabitants: the Mediterranean endemic sphaerodactylid *Euleptes europaea*. In both *G. delfinoi* and *E. europaea* a groove is present on the lateral surface of the posterior process of the maxilla (starting from the last ventrolateral foramen), as well as on each posterolateral process of the frontal dorsally. The combination of these features is unknown in any other living European gekkotans (Villa *et al.* 2018) and is absent in other extant members of Sphaerodactylidae too (Daza *et al.* 2008; J.D. Daza, pers. comm. 2020). Short posterolateral dorsal grooves on the frontal may be present in at least one Asiatic sphaerodactylid (*Pristurus carteri*; see Daza *et al.* 2014: fig. 4D), and some pygopodoids have a maxillary groove behind the last ventrolateral foramen (Daza *et al.* 2014: p. 445–446). These features are variably present also in fossil gekkotans from Europe. Fossil maxillae referred to extinct *Euleptes* display the posterior groove on the maxilla. This is unknown for the Czech *E. gallica* reported by Čerňanský &

Bauer (2010): the authors made no mention of this feature and did not figure the lateral surface of the maxillae. At the moment, there are no frontals referred to extinct *Euleptes* species, and thus the presence and development of grooves on the posterolateral processes cannot be evaluated. When it comes to extinct European genera, the grooves/depressions on the maxilla and the frontal are present in *Cadurcogekko piveteaui*, whereas in *Gerandogekko arambourgi* the maxillary groove is absent. *Gerandogekko* was referred to Sphaerodactylidae (Daza *et al.* 2014), a consideration that is supported by, among other things (i.e., wide frontals, amphicoelous vertebrae; Daza *et al.* 2014), the frontal groove morphology shared with *Euleptes*.

Our phylogenetic analysis recovers the presence of both the posterior maxillary grooves and depressions/grooves on the posterolateral process of the frontals as unambiguous synapomorphies of a European sphaerodactylid clade composed by *Geiseleptes*, *G. gaillardi*, two out of three *Euleptes* species, and *Cadurcogekko* spp. (Fig. 6C; see also Appendix S2). Other synapomorphies include a broad ascending nasal process of the premaxilla, a rounded dorsal end of the facial process of the maxilla, and cervical vertebrae devoid of hypapophyseal keel. We here define *Euleptinae* for this clade, including sphaerodactylids more closely related to *E. europaea* than to *Teratoscincus scincus*. The maxillary groove is unknown for *G. gaillardi* and absent in *G. arambourgi* (removed from the final analysis). Thus, depending on the position of these taxa, the ungrooved condition may be plesiomorphic for *Euleptinae* or, alternatively, a reversal occurred at least in *Gerandogekko arambourgi*. Since no other extant sphaerodactylids show the combination of maxillary/frontal grooves, *G. delfinoi* is confidently reconstructed as an early representative of the lineage leading to the extant *E. europaea* (i.e., a member of *Euleptinae*), irrespective of a limited sample size of extant sphaerodactylids in our phylogeny. The origin of euleptine sphaerodactylids can thus be traced back at least to the middle Eocene (Fig. 7). This is consistent with the molecular divergence estimate of Gamble *et al.* (2015), which dated the divergence between *E. europaea* and its closest extant relative into the mid-Cretaceous. Based on the temporal distribution of *Euleptinae* (Fig. 7), the clade is best interpreted as a permanent resident of Europe since the early Paleogene. Their survival through major climatic shifts (from greenhouse to icehouse conditions) and faunal turnovers (Eocene/Oligocene transition, Oligo-Miocene transition, and several others during the Neogene and Quaternary) implies extreme adaptability (or alternatively geographical shifts and recolonizations, which are however not supported by a literal interpretation of the current fossil record). Hardly any other vertebrate groups from the European early Paleogene appear to survive in the continent till today with all exceptions being reptiles and amphibians. Phylogenies and the currently known fossil record of lacertid (Čerňanský & Smith 2018), as well as anguid lizards (Rage 2012; Klembara *et al.* 2019), blanid amphisbaenians (Čerňanský et al. 2015), and discoglossine and perhaps pelobatid frogs (Rage 2012) are best interpreted as persistent presence of at least some members of these clades since the Eocene. In the case of lacertids, anguids, and blanids, the fossil record of these groups in Africa and Asia is incompletely sampled, however, and key Paleogene species are yet to be included into global phylogenies.

Euleptine gekkotans were more diverse and widespread in the past in Europe (Fig. 7, 8), with different taxa potentially coexisting (i.e., *Gerandogekko* and *Euleptes* during the early Miocene, and *Euleptes* and possibly *Palaeogekko* in the middle Miocene; Fig. 7). Eventually, *E. europaea* remained the only survivor of the European euleptine lineage, even though with a large gap encompassing the whole Pliocene and the Quaternary. Together with the overall scarcity of the fossil record, this currently prevents any attempt at reconstructing the reasons behind this. A single mention of a still-unpublished occurrence of a form closely related to *E. europaea* in Sardinia by Villa & Delfino (2019a) supports the establishment of this lineage in the Mediterranean already since the late Early Pleistocene (A.V., pers. obs.) and is consistent with a central Mediterranean insular center of origin proposed by Delaugerre *et al.* (2011).

European sphaerodactylid palaeobiogeography

Even considering the extra-European record of sphaerodactylids, *Geiseleptes* is the oldest definite occurrence of the clade worldwide (Fig. 7). This cannot be seen as an evidence of a European origin for the clade, though, given that both splits between Sphaerodactylidae and other closely-related gekkotan clades, as well as between Old-World and New-World sphaerodactylids were estimated to occur in the Cretaceous (Gamble *et al.* 2008). The extant genus *Sphaerodactylus* is known to have been present on the island of Hispaniola during the Miocene (Böhme 1984; Kluge 1995; Grimaldi 1996; Grimaldi *et al.* 2000; Daza & Bauer 2012; Daza *et al.* 2014), but nothing else is known about the past histories of African, Asian and American sphaerodactylids (Fig. 7, 8). According to Gamble *et al.* (2015), the closest living relative of *Euleptes* is the Asian *Teratoscincus*, but these two taxa are sister to the African *Saurodactylus fasciatus*. Based on Gamble *et al.*'s (2015) phylogeny and the distribution of extant taxa, the most parsimonious scenario is an African origin of European Sphaerodactylidae with a subsequent dispersal to Europe giving rise to the *Euleptes* lineage. *Geiseleptes delfinoi* implies that this dispersal took place no later than the middle Eocene. Nevertheless, the biogeographic history of the European sphaerodactylid clade may turn out to be more complex once the Asian fossil record is better sampled. An Old-World origin for *Geiseleptes* is at odds with American affinities suggested for other Geiseltal squamates (e.g., *Geiseltaliellus*, glyptosaurine anguids; Smith 2009; Sullivan 2019) and other squamate faunas from the European early Paleogene (Smith & Gauthier 2013; Rage 2013; Smith 2017; Scanferla & Smith 2020; Smith

& Scanferla 2021) and best explained by the comparably older age of the clade (*Euleptes* split from its closest living relative, *Teratoscincus,* in the Cretaceous; Gamble *et al.* 2015). It should be noted, however, that some evidence of the presence in Eocene Europe of African-related taxa are already known (e.g., putative cordylids/cordyliforms; Augé 2003, 2005; Bolet & Evans 2013).

Relationships of other European extinct gekkotans

Apart from sphaerodactylids, our phylogenetic analysis yielded interesting results regarding other extinct gekkotans. The Eocene amber-preserved *Yantarogekko balticus* was recovered as a gekkonid, in agreement with the study describing this taxon but lacking a phylogeny (Bauer *et al.* 2005). *Rhodanogekko vireti* is found nested within the Carphodactylidae, a clade that is endemic of Australia and has currently no fossil record. This is rather surprising from a palaeobiogeographical point of view, but should be taken with caution given that *Rhodanogekko* is known only from an isolated frontal. Daza *et al.* (2014) reported similarities shared by *Rhodanogekko* and the Afroasiatic sphaerodactylid *Pristurus*, hinting at either close phylogenetic relationships or convergence to explain them. Inclusion of at least this latter genus in future analyses would be needed in order to better clarify the systematics of *Rhodanogekko*. Our analysis was not focused on understanding the relationships of Cretaceous stem gekkotans, but it is interesting to note that we were able to recover a clade formed by *Norellius* and *Gobekko* and *Hoburogekko* as subsequent sister to all Gekkota.

CONCLUSION

The Eocene squamate assemblage of Geiseltal is characterized by a high diversity of taxa, including members of anguids, iguanids, eolacertids, palaeovaranids, boids, and a species possibly related to aniliids (Krumbiegel *et al.* 1983). To these, a new sphaerodactylid gekkotan is now added, represented by an incomplete skull. This new gecko taxon, *Geiseleptes delfinoi*, is part of the stem lineage of the only extant European sphaerodactylid, the Mediterranean-endemic *Euleptes europaea*. A phylogenetic analysis was not able to clearly disentangle the detailed relationships within European extinct and extant sphaerodactylids, but it resulted in the recovery of almost all European extinct gekkotan species as members (or possible members in the case of the unstable taxa) of this clade. The name *Euleptinae* is here proposed to accommodate all European sphaerodactylids, both extant and extinct. *Euleptinae* appears to have a permanent presence in the European fauna since the early Paleogene, in marked contrast with the Neogene origin of almost all other vertebrates of the continent, implying exceptional ecological flexibility. Among European fossil gekkotans, only *Yantarogekko* and *Rhodanogekko* are consistently placed outside Sphaerodactylidae. The first one is confirmed as a gekkonid, whereas the second one is nested within Carphodactylidae, even though possible affinities with some sphaerodactylids were reported for this genus as well in the past (Daza *et al.* 2014) and convergence with the Australian carphodactylids of the only frontal referred to it should be taken into account before completely accepting this result. Sphaerodactylids in modern Europe are only represented by *E. europaea* in a limited range in the Western Mediterranean, whereas phyllodactylids and gekkonids are more widely distributed and diverse (Speybroeck *et al.* 2016, 2020). In contrast to this pattern, Sphaerodactylidae appears to be the dominant clade of gekkotans in Europe during the Cenozoic. A literal reading of the fossil record implies that ancestors of extant gekkonids and phyllodactylids may have entered Europe in more recent times (i.e., late Neogene or Quaternary; Villa & Delfino 2019a).

In any case, *Geiseleptes delfinoi* is the oldest certain sphaerodactylid known to date, not only for Europe but worldwide, and it is therefore an important calibration point for future divergence dating analyses. It will also be important for the reconstruction of character distributions and phylogenetic relationships within this group of geckos, given its preservation. *Euleptes europaea* is nested within a clade of ancestrally-nocturnal gekkotans (Gamble *et al.* 2015), suggesting that *Geiseleptes* may also have been nocturnal. Unfortunately, this is not supported by morphological evidence at the moment. The tooth shape, on the other hand, recalls the condition typically observed in insectivorous geckos (Sumida & Murphy 1987; Villa *et al.* 2018). Thence, *Geiseleptes* likely had an arthropod-based diet, a thing that agrees well with the rich record of insects from Geiseltal (Krumbiegel *et al.* 1983; Steinheimer & Hastings 2019). Despite our extensive search, we found only a single specimen referable to *G. delfinoi* (plus another possible indeterminate gekkotan fossil, which may represent the same taxon) in the Geiseltal Collection. This is puzzling considering the large number of often well-preserved lizard remains from the Geiseltal deposits. It is plausible that this gecko lived further away from the swamps and water bodies of the lignite depositional area and is therefore poorly represented in the Geiseltal taphocoenosis.

Acknowledgements.

This study was supported by the VolkswagenStiftung Research in Museums grant (Az. 90 978) awarded to M.R. We are grateful to Juan D. Daza (Sam Houston State University) for help with the original matrix and discussions on characters. Massimo Delfino, Loredana Macaluso, and Lukardis C. M. Wencker (all from the Università degli Studi di Torino) are thanked, respectively, for: access to comparative material of extant geckos; taking and sharing photographs of fossil taxa; and help with the phylogenetic analysis. Michael Stache and Frank Steinheimer (Martin Luther University, Halle-Wittenberg) are thanked for hosting M.R. and A.V. during their stay at the Geiseltal Museum.

This study benefited from useful discussions with Aaron M. Bauer (Villanova University), Arnau Bolet (Institut Català de Paleontologia Miquel Crusafont), and Krister Smith (Senckenberg Museum). We thank the editors Kenneth Angielczyk and Sally Thomas, as well as the two reviewers Juan D. Daza and Marc Augé (Muséum national d'Histoire naturelle), for their useful comments that significantly improved this paper. Original maps used for Fig. 8 are freely available online at d-maps (https://d-maps.com/carte.php?num_car=2232&lang=it and https://d-maps.com/carte.php?num_car=231325&lang=it) and from Wikimedia Commons. A.V. was supported by a Humboldt Research Fellowship from the Alexander von Humboldt Foundation during part of the development of this work; he is now funded by the Agencia Española de Investigación, with a Juan de la Cierva-Formación grant (FCI2019-039443-I / AEI / 10.13039/501100011033). This is publication number 359 of the Museum of Geology and Palaeontology of the Università degli Studi di Torino.

DATA ARCHIVING STATEMENT

Phylogenetic data for this study are available in MorphoBank (O'Leary & Kaufman 2012) (http://morphobank.org/permalink/? P4069); scan data in MorphoSource (https://doi.org/10.17602/M2/M409939 (image stack); https://doi.org/10.17602/M2/M407451(mesh)). This published work and the nomenclatural acts it contains have been registered with ZooBank: http://zoobank.org/References/D59964BB-2E5E-492F-BCAE-0D73BF8B5181.

SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

Appendix S1. New characters added in the phylogenetic analysis.

Appendix S2. List of apomorphies (character numbers follow TnT: i.e., starting from 0) for selected clades, calculated based on the pruned consensus tree (Fig. 6C, with *Gerandogekko arambourgi* inactivated, and without *Palaeogekko*, *Laonogekko*, and *Euleptes gallica*).

AUTHOR CONTRIBUTION

Conceptualization A Villa, M Rabi; **Data Curation** A Villa, O Wings, M Rabi; **Formal Analysis** A Villa, M Rabi; **Funding Acquisition** M Rabi; **Investigation** A Villa, M Rabi; **Methodology** A Villa, O Wings, M Rabi; **Project Administration** O Wings, M Rabi; **Resources** O Wings, M Rabi; **Supervision** O Wings, M Rabi; **Validation** A Villa, O Wings, M Rabi; **Visualization** A Villa, O

Wings, M Rabi; **Writing – Original Draft Preparation** A Villa, O Wings, M Rabi; **Writing – Review & Editing** A Villa, O Wings, M Rabi.

REFERENCES

AGNOLIN, F. and JOFRÉ, G. 2011. Nuevos registros de Squamata (Reptilia) para el Pleistoceno Superior del norte de la provincia de Buenos Aires, Argentina. *Papéis Avulsos de Zoologia*, **51**, 49–58. [In Spanish]

ALBINO, A. M. 2005. A late Quaternary lizard assemblage from the southern Pampean Region of Argentina. *Journal of Vertebrate Paleontology*, **25**, 185–191.

ALBINO, A. M. 2020. The Cenozoic lizard record of the Pampean Region. *Geodiversitas*, **42**, 175–183.

ALIFANOV, V. R. 1989. The oldest gecko (Lacertilia, Gekkonidae) from the Lower Cretaceous of Mongolia. *Paleontologicheskii Zhurnal*, **1989**, 124–126. [In Russian]

ARNOLD, E. N. and POINAR, G. 2008. A 100 million year old gecko with sophisticated adhesive toe pads, preserved in amber from Myanmar. *Zootaxa*, **1847**, 62–68.

AUGÉ, M. L. 2003. La faune de Lacertilia (Reptilia, Squamata) de l'Éocène inférieur de Prémontré (Bassin de Paris, France). *Geodiversitas*, **25**, 539–574.

— 2005. Évolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle*, **192**, 1–369.

— and RAGE, J.-C. 2006. Herpetofaunas from the upper Paleocene and lower Eocene of Morocco. *Annales de Paléontologie*, **92**, 235–253.

AUTUMN, K., SITTI, M., LIANG, Y. A., PEATTIE, A. M., HANSEN, W. R., SPONBERG, S., KENNY, T. W., FEARING, R., ISRAELACHVILI, J. N. and FULL, R.J. 2002. Evidence for van der Waals adhesion in gecko setae. *Proceedings of the National Academy of Sciences of the United States*, **99**, 12252–12256.

BAILON, S., HOSSINI, S. and RAGE, J.-C. 2017. Les amphibiens et lépidosauriens du Cénozoïque du Maroc. 453–484. *In* ZOUHRI, S. (ed). *Paléontologie des vertébrés du Maroc: état des connaissances.* Mémoires de la Société géologique de France, **180**, 624 pp.

BAUER, A. M. 2013. *Geckos: the animal answer guide.* The John Hopkins University Press, Baltimore, 192 pp.

— BÖHME. W. and WEITSCHAT, W. 2005. An early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion. *Journal of Zoology*, **265**, 327–332.

— GOOD, D. A. and BRANCH, W. R. 1997. The taxonomy of the southern african leaf-toed geckos (Squamata: Gekkonidae), with a review of old world “*Phyllodactylus*” and the description of five new genera. *Proceedings of the California Academy of Science*, **49**, 447–497.

BLANCO, A., BOLET, A., BLAIN, H.-A., FONDEVILLA, V. and MARMI, J. 2016. Late Cretaceous (Maastrichtian) amphibians and squamates from northeastern Iberia. *Cretaceous Research*, **57**, 624–638.

BÖHME, M. and ILG, A. 2003. fosFARbase [accessed 2019 April]. www.wahrestaerke.com/

BÖHME, W. 1984. Erstfund eines fossilien Kugelfingergeckos (Sauria: Gekkonidae: Sphaerodactylinae) aus Dominikanischem Bernstein (Oligozän von Hispaniola, Antillen). *Salamandra*, **20**, 212–220.

BOLET A., DAZA J. D., AUGÉ, M. and BAUER, A. M. (2015). New genus and species names for the Eocene lizard *Cadurcogekko rugosus* Augé, 2005. *Zootaxa*, **3985**, 265–274.

— EVANS, S. E. 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain). *Palaeontologia Electronica*, **16**, 8A.

BORSUK-BIAŁYNICKA, M. 1990. *Gobekko cretacicus* gen. et. sp. n., a new gekkonid lizard from the Cretaceous of the Gobi Desert. *Acta Palaeontologica Polonica*, **35**, 67–76.

CAMP, C. L. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History*, **48**: 289–481.

ČERŇANSKÝ, A., AUGÉ, M. L. and RAGE, J.-C. 2015. A complete mandible of a new amphisbaenian reptile (Squamata, Amphisbaenia) from the late middle Eocene (Bartonian, MP 16) of France. *Journal of Vertebrate Paleontology*, **35**, e902379.

ČERŇANSKÝ, A. and BAUER, A. M. 2010. *Euleptes gallica* Müller (Squamata: Gekkota: Sphaerodactylidae) from the Lower Miocene of North-West Bohemia, Czech Republic. *Folia Zoologica*, **59**, 323–328.

— DAZA J. D. and BAUER, A. M. 2018. Geckos from the middle Miocene of Devínska Nová Ves (Slovakia): new material and a review of the previous record. *Swiss Journal of Geosciences*, **111**, 183–190.

— SMITH, K. T. 2018. Eolacertidae: a new extinct clade of lizards from the Palaeogene; with comments on the origin of the dominant European reptile group – Lacertidae. *Historical Biology*, **30**, 994–1014.

COHEN, K. M., FINNEY, S. C., GIBBARD, P. L. and FAN, J.-X. 2013; updated. The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204.

COLOMBERO, S., ALBA, D. M., D'AMICO, C., DELFINO, M., ESU, D., GIUNTELLI, P., HARZHAUSER, M., MAZZA, P. P. A., MOSCA, M., NEUBAUER, T. A., PAVIA, G., PAVIA, M., VILLA, A. and CARNEVALE, G. 2017. Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleoecological and paleoclimatological implications. *Palaeontologia Electronica*, **20.1.10A**, 1–66.

CONRAD, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History*, **310**, 1–182.

— 2015. A new Eocene casquehead lizard (Reptilia, Corytophanidae) from North America. *PLoS ONE*, **10**, e0127900.

— 2018. A new lizard (Squamata) was the last meal of *Compsognathus* (Theropoda: Dinosauria) and is a holotype in a holotype. *Zoological Journal of the Linnean Society*, **183**, 584–634.

— AST, J. C., MONTANARI, S. and NORELL, M. A. 2011. A combined evidence phylogenetic analysis of Anguimorpha (Reptilia: Squamata). *Cladistics*, **27**, 230–277.

— BALCARCEL, A. and MEHLING, C. 2012. Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). *PLoS ONE*, **7**, e41767.

— and DAZA, J. D. 2015. Naming and rediagnosing the Cretaceous gekkonomorph (Reptilia, Squamata) from Öösh (Övörkhangai, Mongolia). *Journal of Vertebrate Paleontology*, **35**, e980891.

— and NORELL, M. A. 2006. High-resolution X-ray computed tomography of an Early Cretaceous gekkonomorph (Squamata) from Öösh (Övörkhangai; Mongolia). *Historical Biology*, **18**, 405–431.

— RIEPPEL, O. and GRANDE, L. 2008. Re-assessment of varanid evolution based on new data from *Saniwa ensidens* Leidy, 1870 (Squamata, Reptilia). *American Museum Novitates*, **3630**, 1–15.

CSIKI-SAVA, Z., VREMIR, M., VASILE, Ş., BRUSATTE, S. L., DYKE, G., NAISH, D., NORELL, M. A. and TOTOIANU, R. 2016. The East Side Story – The Transylvanian latest Cretaceous continental vertebrate record and its implications for understanding Cretaceouse–Paleogene boundary events. *Cretaceous Research*, **57**, 662–698.

CUVIER, G. 1817. *Le Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Déterville libraire, Imprimerie de A. Belin, Paris, 350 pp.

DAVIS, W. K. 1974. The Mediterranean gecko, *Hemidactylus turcicus* in Texas. *Journal of Herpetology,* **8**, 77–80.

DAZA, J. D., ABDALA, V., THOMAS, R. and BAUER, A. M. 2008. Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). *Journal of Morphology,* **269**, 1340–1364.

— ALIFANOV, V. R. and BAUER, A. M. 2012. A redescription and phylogenetic reinterpretation of the fossil lizard *Hoburogekko suchanovi* Alifanov, 1989 (Squamata, Gekkota), from the Early Cretaceous of Mongolia. *Journal of Vertebrate Paleontology,* **32**, 1303–1312.

— and BAUER, A. M. 2012. A new amber-embedded sphaerodactyl gecko from Hispaniola, with comments on the morphological synapomorphies of the Sphaerodactylidae. *Breviora,* **529**, 1–28.

DAZA, J. D., BAUER, A. M., SAND, C., LILLEY, I., WAKE, T. A. and VALENTIN, F. 2015. Reptile remains from Tiga (Tokanod), Loyalty Islands, New Caledonia. *Pacific Science*, **69**, 531–557

— — and SNIVELY, E. D. 2013. *Gobekko cretacicus* (Reptilia: Squamata) and its bearing on the interpretation of gekkotan affinities. *Zoological Journal of the Linnean Society*, **167**, 430–448.

— — — 2014. On the fossil record of the Gekkota. *The Anatomical Record*, **97**, 433–462.

— HERRERA, A., THOMAS, R. and CLAUDIO, H. J. 2009. Are you what you eat? A geometric morphometric analysis of gekkotan skull shape. *Biological Journal of the Linnean Society,* **97**, 677–707.

— STANLEY, E. L., WAGNER, P., BAUER, A. M. and GRIMALDI, D. A. 2016. Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. *Science Advances*, **2**, e1501080.

DE QUEIROZ, K., CANTINO, P. D. and GAUTHIER, J. A. 2020. *Phylonyms. A companion to the PhyloCode*. CRC Press, Boca Raton, 1352 pp.

DELAUGERRE, M., OUNI, R. and NOUIRA, S. 2011. Is the European Leaf-toed gecko *Euleptes europaea* also an African? Its occurrence on the Western Mediterranean landbrige islets and its extinction rate. *Herpetology Notes,* **4**, 127–137.

ESTES, R. 1970. Origin of the recent North American lower vertebrate fauna: an inquiry into the fossil record. *Forma et Functio*, **3**, 139–163.

— 1983. *Handbuch der Paläoherpetologie 10A. Sauria terrestria, Amphisbaenia*. Friedrich Pfeil, Munich, 249 pp.

EVANS, S. E. 2008. The skull of lizards and Tuatara. 1–347. *In* GANS, C., GAUNT, A. S. and ADLER, K. (eds). *Biology of the Reptilia. Volume 20. Morphology H. The Skull of Lepidosauria.* Society for the Study of Amphibians and Reptiles, Ithaca, New York, 758 pp.

FITZINGER, L. 1843. *Systema Reptilium (Amblyglossae).* Braumüller et Seidel, Vienna, 106 pp.

FONTANARROSA, G., DAZA, J. D. and ABDLA, V. (2018). Cretaceous fossil gecko hand reveals a strikingly modern scansorial morphology: qualitative and biometric analysis of an amber-preserved lizard hand. *Cretaceous Research*, **84**, 120–133.

FRANZEN, J. L. and HAUBOLD, H. 1986. The middle Eocene of European mammalian stratigraphy. Definition of the Geiseltalian. *Modern Geology*, **10**, 159–170.

— — 1987. The biostratigraphic and palaeoecologic significance of the Middle Eocene locality Geiseltal near Halle (German Democratic Republic). *Münchner Geowissenschaftliche Abhandlungen A*, **10**, 93–100.

GAMBLE, T., BAUER, A. M., GREENBAUM, E. and JACKMAN, T. R. 2008. Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography*, **35**, 88–104.

— GREENBAUM, E., JACKMAN, T. R. and BAUER, A. M. 2015. Into the light: diurnality has evolved multiple times in geckos. *Biological Journal of the Linnean Society*, **115**, 896–910.

— — — RUSSELL, A. P. and BAUER, A. M. 2012. Repeated origin and loss of adhesive toepads in geckos. *PLoS ONE*, **7**, e39429.

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

GAUTHIER, J., KEARNEY, M., MAISANO, J. A., RIEPPEL, O. and BEHLKE, A. 2012. Assembling the squamate tree of life: Perspectives from the phenotype and the fossil record. *Bulletin of the Peabody Museum of Natural History*, **53**, 3–308.

GEORGALIS, G. L., ČERŇANSKÝ, A. and KLEMBARA, J. 2021a. Osteological atlas of new lizards from the Phosphorites du Quercy (France), based on historical, forgotten, fossil material. *Geodiversitas*, **43**, 219–293.

— RABI, M. and SMITH, K. T. 2021b. Taxonomic revision of the snakes of the genera *Palaeopython* and *Paleryx* (Serpentes, Constrictores) from the Paleogene of Europe. *Swiss Journal of Palaeontology*, **140**, 18.

GOLOBOFF, P. A., FARRIS, J. S. and NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786

GOLZ, D. J. and LILLEGRAVEN, J. 1977. Summary of the know occurences of terrestrial vertebrates from Eocene strata of southern California. *Contributions to Geology*, **15**, 43–65.

GRIMALDI, D. 1996. *Amber: Window to the past.* Harry N. Abrams, Publishers and American Museum of Natural History, New York, 216 pp.

— NGUYEN, T. and KETCHAM, R. 2000. Ultra-High-Resolution XRay Computed Tomography (UHR CT) and the study of fossils in amber. 77–91. *In* GRIMALDI, D. (ed). *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey.* Backhuys Publishers, Leiden, 498 pp.

HAUBOLD, H. 1987. Geiseltalium: ein neues Landsäugetier-Zeitalter im Paläogen. *Hallesches Jahrbuch für Geowissenschaften*, **12**, 120–121.

— 1989. Die Referenzfauna des Geiseltalium, MP levels 11 bis 13 (Mitteleozän, Lutetium). *Palaeovertebrata*, **19**, 81–93.

— THOMAE, M. 1990. Stratigraphische Revision der Wirbeltierfundstellen des Geiseltaleozäns. *Hallesches Jahrbuch für Geowissenschaften*, **15**, 3–20.

HOFFSTETTER, R. 1946. Sur les Gekkonidae fossiles. *Bulletin du Muséum National d'Histoire Naturelle*, **18**, 195–203.

HOLDAWAY, R. N. and WORTHY, T. H. 1997. A reappraisal of the late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand. *New Zealand Journal of Zoology*, **24**, 69–121.

HOWARD, J. G. and PARMERLEE, J. S. Jr. 2001. Natural history of the edificarian geckos *Hemidactylus mabouia*, *Thecadactylus rapicauda*, and *Sphaerodactylus sputator* on Anguilla. *Caribbean Journal of Science*, **37**, 285–288.

HUTCHINSON, M. N. 1997. The first fossil pygopod (Squamata, Gekkota), and a review of mandibular variation in living species. *Memoirs of the Queensland Museum*, **41**, 355–366.

— and MACKNESS, B. S. 2002. Fossil lizards from the Pliocene Chinchilla Local Fauna, Queensland, with a description of a new species. *Records of the South Australian Museum,* **35**, 169–184.

KLEMBARA, J., HAIN, M. and ČERŇANSKÝ, A. 2019. The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm – Westtangente in Germany. *Historical Biology,* **31**, 1016–1027.

KLUGE, A. G. 1995. Cladistic relationships of sphaerodactyl lizards. *American Museum Novitates*, **3139**, 1–23.

KRUMBIEGEL, G., RÜFFLE, L. and HAUBOLD, H. 1983. *Das eozäne Geiseltal*. A. Ziemsen Verlag, Wittenberg Lutherstadt, 227 pp.

KRUTZSCH, W. 1966. Die sporenstratigraphische Gliederung des Tertiärim nördlichen Mitteleuropa (Paläozän-Mitteloligozän), methodische Grundlagen und gegenwärtiger Stand der Untersuchungen. *Abhandlungen des Zentralen Geologischen Instituts*, **8**, 112–149.

— 1970. Die stratigraphisch verwertbaren Sporen-und Pollenformen des mitteleuropäischen Alttertiärs. *Jahrbuch für Geologie*, **3**, 309–379.

— 1976. Die Mikroflora der Braunkohle des Geiseltales, IV. Die stratigraphische Stellung des Geiseltalprofils im Eozän und die sporenstratigraphische Untergliederung des mittleren Eozäns. *Abhandlungen des Zentralen Geologischen Instituts,* **26**, 47–92.

— BLUMENSTENGEL, H., KIESEL, Y. and RÜFFLE, L. 1992. Paläobotanische Klimagliederung des Alttertiärs (Mitteleozän bis Oberoligozän) in Mitteldeutschland und das Problem der Verknüpfung mariner und kontinentaler Gliederungen (klassische Biostratigraphien – paläobotanisch-ökologische Klimastratigraphie – Evolutionsstratigraphie der Vertebraten). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **186**, 137–253.

LEE, M. S. Y., HUTCHINSON, M. N., WORTHY, T. H., ARCHER, M., TENNYSON, A. J. D., WORTHY, J. P. and SCOFIELD, R. P. 2009. Miocene skinks and geckos reveal long-term conservatism of New Zealand’s lizard fauna. *Biology Letters*, **5**, 833–837.

LENZ, O. K., WILDE, V., MERTZ, D. F. and RIEGEL, W. 2015. New palynology-based astronomical and revised ^{40}Ar/^{39}Ar ages for the Eocene maar lake of Messel (Germany). *International Journal of Earth Sciences*, **104**, 873–889.

MADDISON, W. P. and MADDISON, D. R. 2017. Mesquite: a modular system for evolutionary analysis. Available at http://mesquiteproject.org

MEAD, J. I., HOLLENSHEAD, M., SWIFT, S. L., BELL, C. J. and BAYNES, A. 2008. *Pygopus* (Squamata: Pygopodidae) from mid-Holocene cave deposits, Western and South Australia. *Records of the Western Australian Museum*, **25**, 87–93.

MÜLLER, J. 2001. A new fossil species of *Euleptes* from the early Miocene of Montaigu, France (Reptilia, Gekkonidae). *Amphibia-Reptilia*, **22**, 341–348.

— MÖDDEN, C. 2001. A fossil leaf-toed gecko from the Oppenheim-Nierstein Quarry (Lower Miocene, Germany). *Journal of Herpetology*, **35**, 529–532.

— ROBERTS, E., NAYLOR, E. and STEVENS, N. 2018. A fossil gekkotan (Squamata) from the late Oligocene Nsungwe Formation, Rukwa Rift Basin, Tanzania. *Journal of Herpetology*, **52**, 223–227.

NEWBERY, B. and JONES, D. N. 2007. Presence of Asian House Gecko *Hemidactylus frenatus* across an urban gradient in Brisbane: influence of habitat and potential for impact on native gecko species. 59–65. *In* LUNNEY, D., EBY, P., HUTCHINGS, P. and BURGIN, S. (eds). *Pest or guest: the zoology of overabundance.* Royal Zoological Society of New South Wales, Mosman, 270 pp.

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

PICKFORD, M. and ANDREWS, P. 1981. The Tinderet Miocene sequence in Kenya. *Journal of Human Evolution*, **10**, 11–33.

PYRON, R. A. 2017. Novel approaches for phylogenetic inference from morphological data and total-evidence dating in squamate reptiles (lizards, snakes, and amphisbaenians). *Systematic Biology*, **66**, 38–56.

RAGE, J.-C. 2008. Squamate reptiles from the lower Miocene of the Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia*, **20**, 93–103.

— 2012. Amphibians and squamates in the Eocene of Europe: what do they tell us? *Palaeobiodiversity and Palaeoenvironments*, **92**, 445–457.

— 2013. Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments,* **93**, 517–534.

RAGE, J.-C., ADACI, M., BENSALAH, M., MAHBOUBI, M., MARIVAUX, L., MEBROUK, F. and TABUCE, R. 2021. Latest Early-early Middle Eocene deposits of Algeria (Glib Zegdou, HGL50), yield the richest and most diverse fauna of amphibians and squamate reptiles from the Palaeogene of Africa. *Palaeovertebrata,* **44**, 1-32.

RING, S. J., BOCHERENS, H., WINGS, O. and RABI, M. 2020. Divergent mammalian body size in a stable Eocene greenhouse climate. *Scientific Reports,* **10**, 3987.

RUSSELL, A. P. 2002. Integrative functional morphology of the gekkotan adhesive system (Reptilia: Gekkota). *Integrative and Comparative Biology,* **42**, 1154–1163.

SCANFERLA, A. and SMITH, K. T. 2020. Exquisitely preserved fossil snakes of Messel: insight into the evolution, biogeography, habitat preferences and sensory ecology of early boas. *Diversity,* **12**, 100.

SCHATZINGER, R. 1975. Later Eocene (Uintan) lizards from the greater San Diego area, California. Unpublished MSc thesis, San Diego State University, San Diego, 212 pp.

SCHLEICH, H. H. 1987. Neue Reptilienfunde aus dem Tertiär Deutschlands. 7. Erstnachweis von Geckos aus dem Mittelmiozän Süddeutschlands: *Palaeogekko risgoviensis* nov. gen., nov. spec. (Reptilia, Sauria, Gekkonidae). *Mitteilungen der Bayerischen Staatssammlung für Palaeontologie und Historische Geologie,* **27**, 67–93.

SCHMIDT-KITTLER, N., BRUNET, M., GODINOT, M., FRANZEN, J. L., HOOKER, J. J., and LEGENDRE, S. 1987. European reference levels and correlation tables. Münchner Geowissenschaftliche Abhandlungen A, 10, 13–31.

SKUTSCHAS, P. P. 2006. Mesozoic amphibians from Siberia, Russia. 123–126. *In* BARRETT, P. M. and EVANS, S. E. (eds). *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings.* The Natural History Museum, London, 188 pp.

SIMÕES, T. R., CALDWELL, M. W., TAŁANDA, M., BERNARDI, M., PALCI, A., VERNYGORA, O., BERNARDINI, F., MANCINI, L and NYDAM, R.L. 2018. The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* **557**, 707–709.

SIMÕES, T. R. and PYRON, R. A. 2021. The squamate tree of life. *Bulletin of the Museum of Comparative Zoology*, **163**, 47–95.

SIMÕES, T. R., VERNYGORA, O. V., CALDWELL, M. W. and Pierce, S. E. 2020. Megaevolutionary dynamics and the timing of evolutionary innovation in reptiles. *Nature Communications*, **11**, 3322.

SMITH, K. T. 2009. Eocene Lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia: Squamata). *Bulletin of the Peabody Museum of Natural History*, **50**, 219–306.

— 2017. First crocodile-tailed lizard (Squamata: *Pan-Shinisaurus*) from the Paleogene of Europe. *Journal of Vertebrate Paleontology*, **37**, e1313743.

— ČERŇANSKÝ, A., SCANFERLA, A. and SCHAAL, S. F. K. 2018. Lizards and snakes – Warmth-loving sunbathers. 123–147. *In* SMITH, K. T., SCHAAL, S. F. K. and HABERSETZER, J. (eds). *Messel. An ancient greenhouse ecosystem.* Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, 355 pp.

— 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**, 135–230.

— SCANFERLA, A. 2021. A nearly complete skeleton of the oldest definitive erycine boid (Messel, Germany). *Geodiversitas*, **43**, 1–24.

SPEYBROECK, J., BEUKEMA, W., BOK, B. and VAN DER VOORT, J. 2016. *Field guide to the amphibians and reptiles of Britain and Europe.* Bloomsbury Publishing, London, 432 pp.

— BEUKEMA, W., DUFRESNES, C., FRITZ, U., JABLONSKI, D., LYMBERAKIS, P., MARTÍNEZ-SOLANO, I., RAZZETTI, E., VAMBERGER, M., VENCES, M., VÖRÖS, J. and CROCHET P.-A. 2020. Species list of the European herpetofauna – 2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. *Amphibia-Reptilia*, **41**, 139–189.

STEINHEIMER, F. D. and HASTINGS, A. K. 2019. HALLE: The Geiseltal Collection of Martin Luther University, Halle-Wittenberg. 271–280. In BECK, L. A. and JOGER, U. (eds.). *Paleontological Collections of Germany, Austria and Switzerland.* Springer Nature, Cham, 573 pp.

SULLIVAN, R.M. 2019. The taxonomy, chronostratigraphy and paleobiogeography of glyptosaurine lizards (Glyptosaurinae, Anguidae). *Comptes Rendus Palevol*, **18**, 747–763.

SUMIDA, S. S. and MURPHY, R. W. 1987. Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). *Canadian Journal of Zoology*, **65**, 2886–2892.

TAŁANDA, M. 2018. An exceptionally preserved Jurassic skink suggests lizard diversification preceded fragmentation of Pangaea. *Palaeontology*, **61**, 659–677.

UETZ, P., FREED, P., AGUILAR, R. and HOŠEK, J. (eds.), The Reptile Database, http://www.reptile-database.org, accessed November 2021.

UNDERWOOD, G. 1954. On the classification and evolution of geckos. *Proceedings of the Zoological Society of London*, **124**, 469–492.

VASILYAN, D., ZAZHIGIN, V. S. and BÖHME, M. 2017. Neogene amphibians and reptiles (Caudata, Anura, Gekkota, Lacertilia, and Testudines) from the south of Western Siberia, Russia, and Northeastern Kazakhstan. *PeerJ*, **5**, e3025.

VILLA, A., DAZA, J. D., BAUER, A. M. and DELFINO, M. 2018. Comparative cranial osteology of European gekkotans (Reptilia, Squamata). *Zoological Journal of the Linnean Society*, **184**, 857–895.

— and DELFINO, M. 2019a. Fossil lizards and worm lizards (Reptilia, Squamata) from the Neogene and Quaternary of Europe: an overview. *Swiss Journal of Palaeontology*, **138**, 177–211.

— — 2019b. A comparative atlas of the skull osteology of European lizards (Reptilia: Squamata). *Zoological Journal of the Linnean Society*, **187**, 829–928.

VITT, L. J. and CALDWELL, J. P. 2009. *Herpetology. An introductory biology of amphibians and reptiles - third edition.* Academic Press, Burlington, 697 pp.

VOIGT, E. 1988. Preservation of soft tissues in the Eocene lignite of the Geiseltal near Halle (Saale). *Courier Forschungsinstitut Senckenberg*, **107**, 325–343.

WEIGELT, J. 1934. Die Geiseltalgrabungen des Jahres 1933 und die Biostratonomie der Fundschichten. *Nova Acta Leopoldina NF*, **1**, 552–660.

WORTHY, T. H. and ANDERSON, A. 2009. Results of palaeofaunal research. 41–62. *In* CLARK, G. and ANDERSON, A. (eds). *The early prehistory of Fiji*. Terra Australis, **31**, 437 pp.

— and CLARK, G. 2009. Bird, mammal and reptile remains. 231–258. *In* CLARK, G. and ANDERSON, A. (eds). *The early prehistory of Fiji*. Terra Australis, **31**, 437 pp.

— and HOLDAWAY, R. N. 1996. Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, **26**, 275–361.

FIGURE CAPTIONS

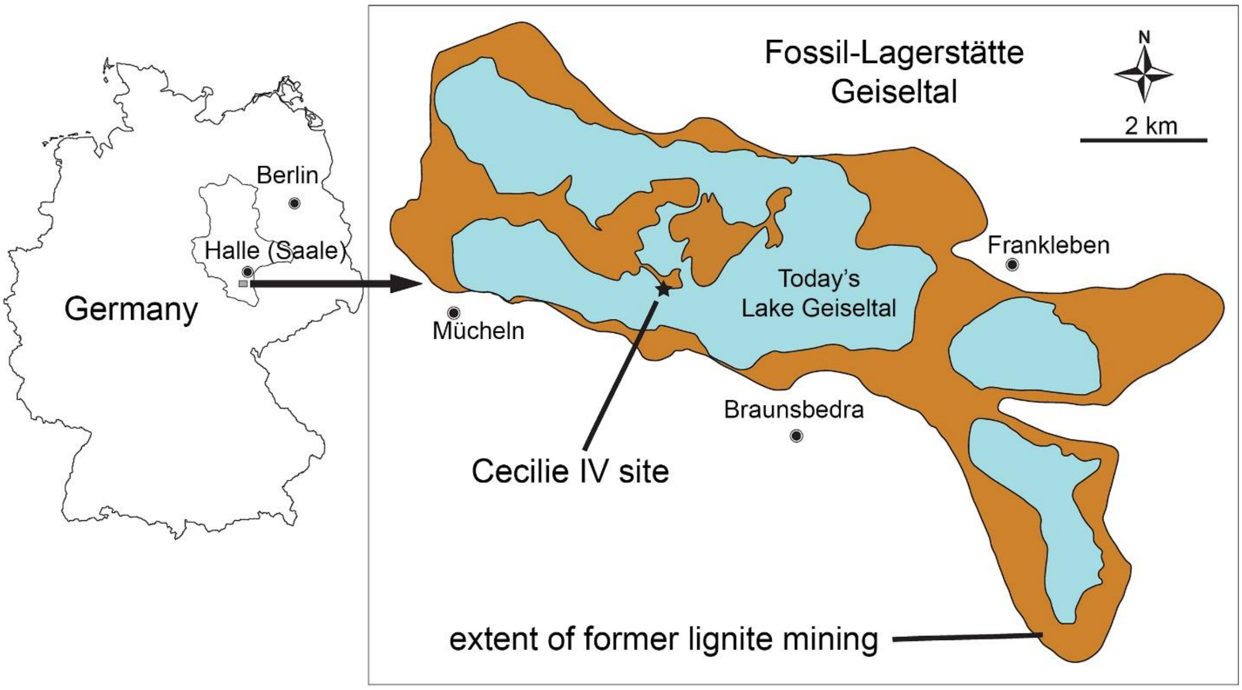

FIG. 1. Map of the Geiseltal fossillagerstätte, with its location in Germany and the position of Site Cecilie IV.

FIG. 2. Partially articulated skull of *Geiseleptes delfinoi* Villa *et al.* gen. et sp. nov. from the early late to middle Eocene of Geiseltal, Germany (GMH Ce IV-4057-1933) The skull was apparently

split during collection or preparation and both parts were subsequently mounted on the same lacquer film. Scale bar = 5 mm.

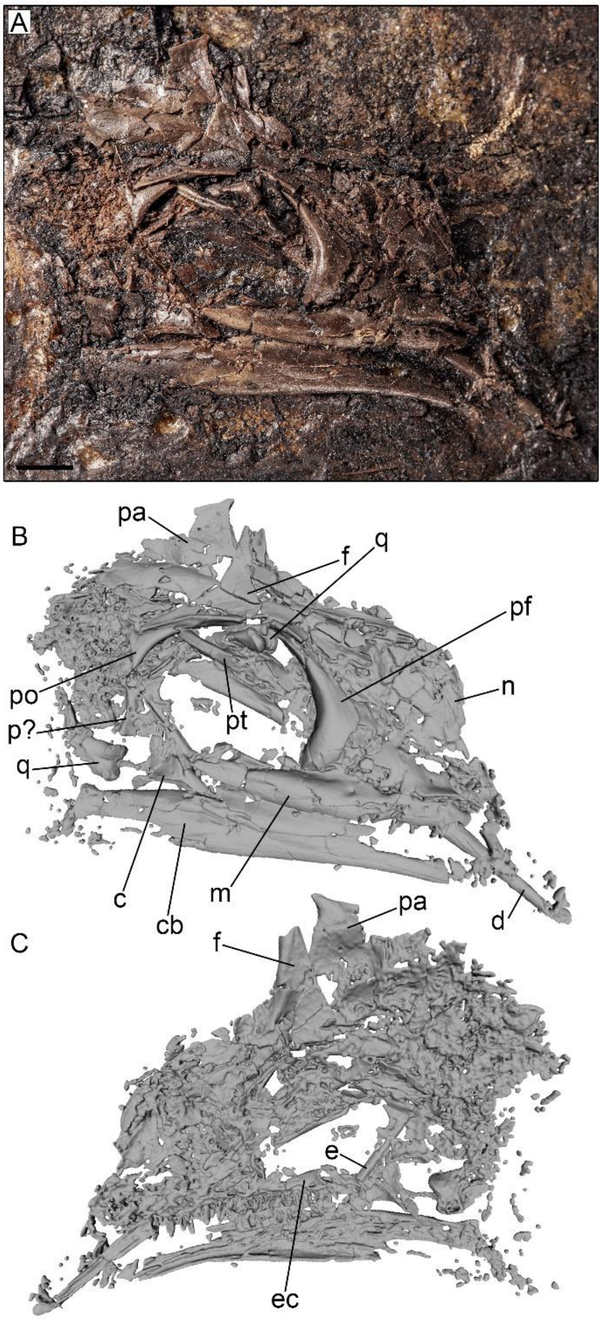

FIG. 3. *Geiseleptes delfinoi* Villa *et al.* gen. et sp. nov. from the early late to middle Eocene of Geiseltal, Germany (GMH Ce IV-4057-1933). Photo (A) and CT-scan images (B, C). C shows the unexposed surface. Abbreviations: c, coronoid; cb, compound bone; d, dentary; e, epipterygoid; ec, ectopterygoid; f, frontal; m, maxilla; n, nasal; pa, parietal; pf, prefrontal; po, postorbitofrontal; pt, pterygoid; p?, paroccipital process?; q, quadrate. Scale bar = 2 mm.

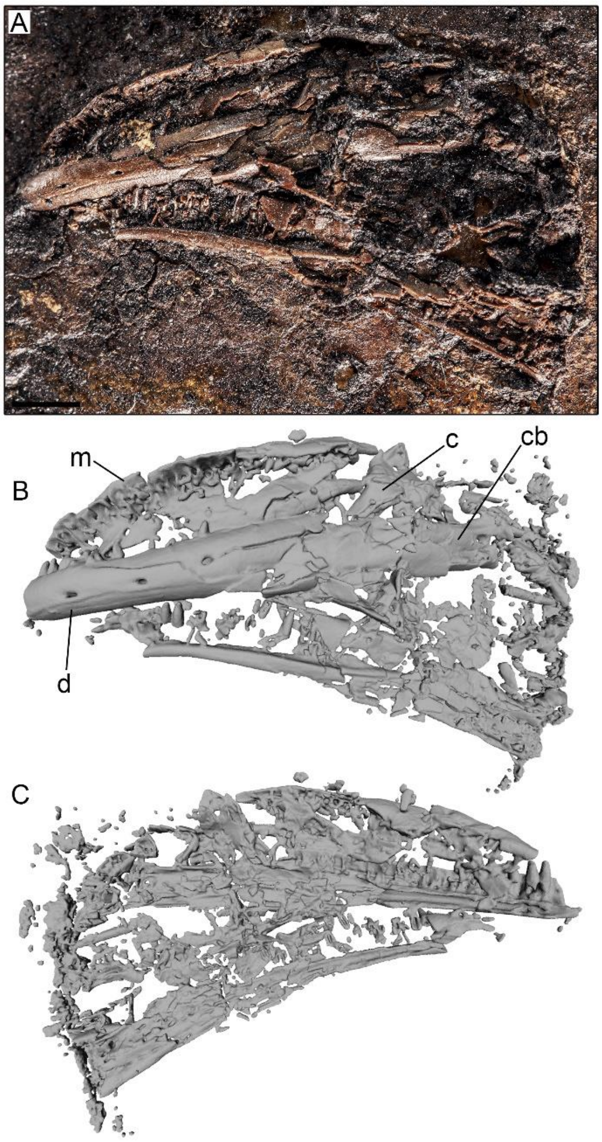

FIG. 4. *Geiseleptes delfinoi* Villa *et al.* gen. et sp. nov. from the early late to middle Eocene of Geiseltal, Germany (GMH Ce IV-4057-1933). Photo (A) and CT-scan images (B, C). C shows unexposed surface. Abbreviations: c, coronoid; cb, compound bone; d, dentary; m, maxilla. Scale bar = 2 mm.

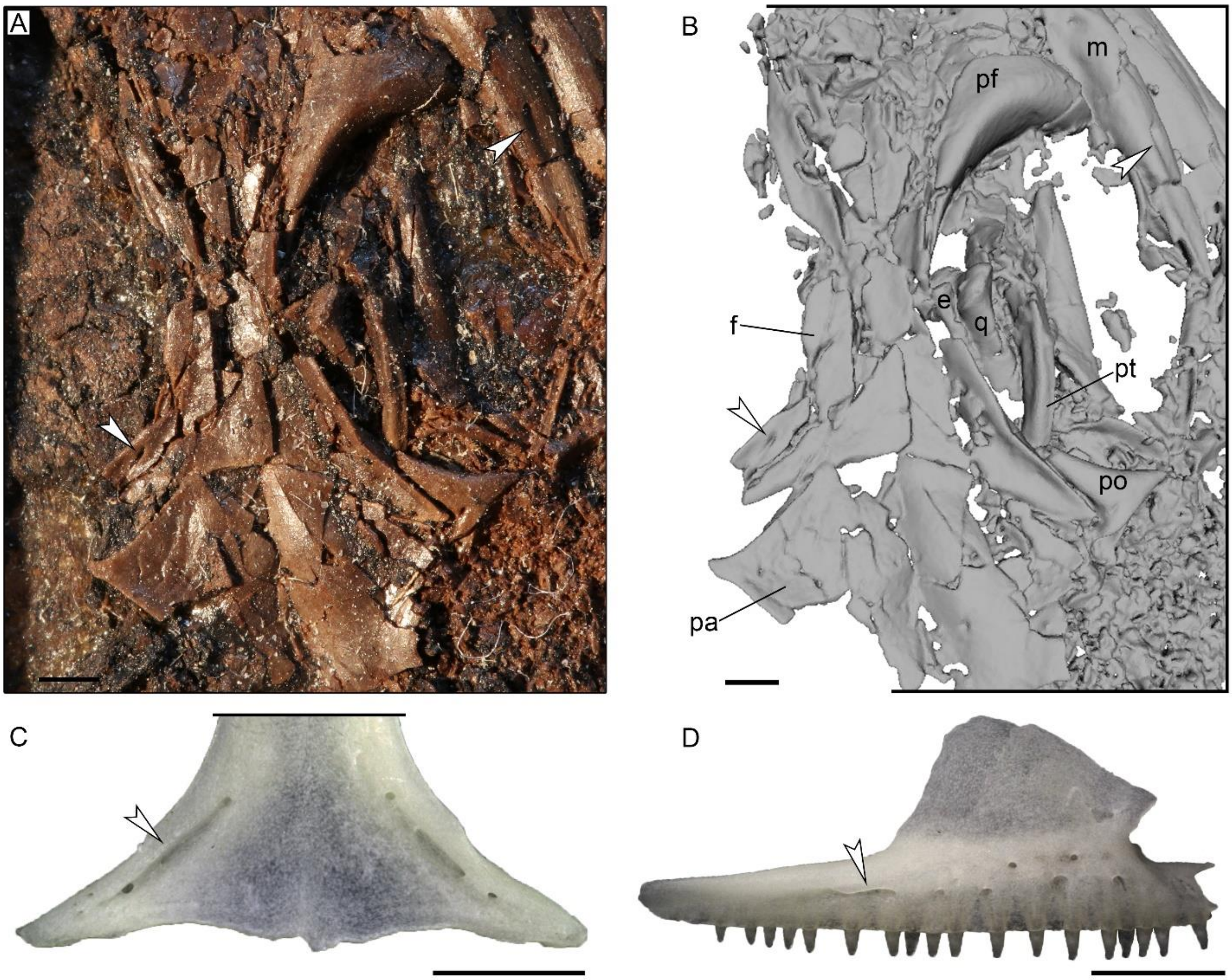

FIG. 5. Taxonomically-significant grooves on the skull of *Geiseleptes delfinoi* Villa *et al.* gen. et sp. nov. A, detail of GMH Ce IV-4057-1933. B, CT-scan image of the same area. C, posterior end of a frontal of *Euleptes europaea* (MDHC 389), in dorsal view for comparison. D, right maxilla of *Euleptes europaea* (MDHC 389), in lateral view for comparison. Arrows mark grooves on the posterolateral process of the frontal and on the posterior process of the maxilla. Abbreviations: e, epipterygoid; f, frontal; m, maxilla; pa, parietal; pf, prefrontal; po, postorbitofrontal; pt, pterygoid; q, quadrate. Scale bars = 1 mm.

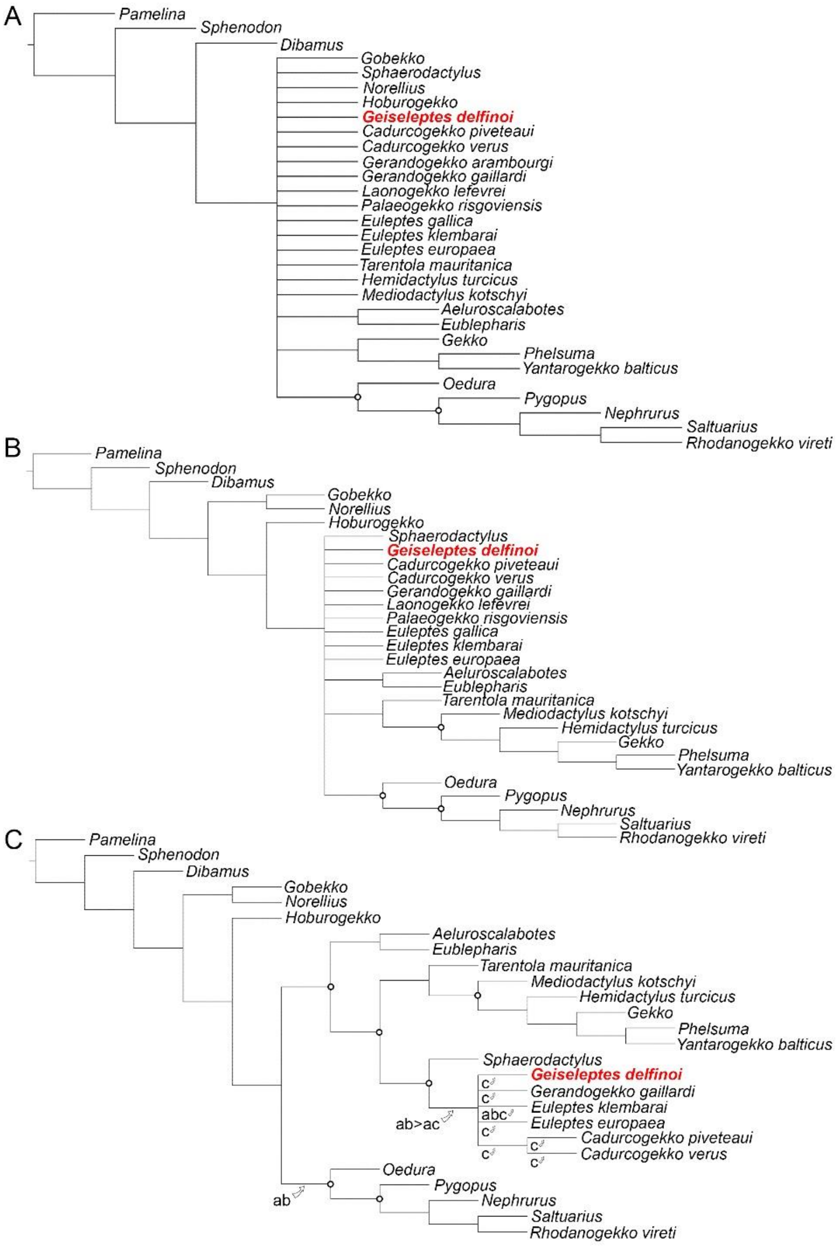

FIG. 6. Strict consensus trees resulting from the parsimony analysis using a molecular backbone constraint. A, Strict consensus tree of the analysis with the complete matrix. B, strict consensus tree of the analysis without *Gerandogekko arambourgi*, a poorly known taxon that is operationally identical to *G. gaillardi* and may even represent the same species. C, pruned strict consensus tree after excluding *Euleptes gallica*, *Laonogekko lefevrei*, and *Palaeogekko risgoviensis*. Arrows mark the possible positions of the pruned taxa in the pruned tree. White circles mark the constraints implemented in the analysis (not all constraints are mapped in A and B, because some clades are collapsed in a polytomy due to unstable wild-card taxa). Abbreviations: a, *L. lefevrei*; b, *P. risgoviensis*; c, *E. gallica*.

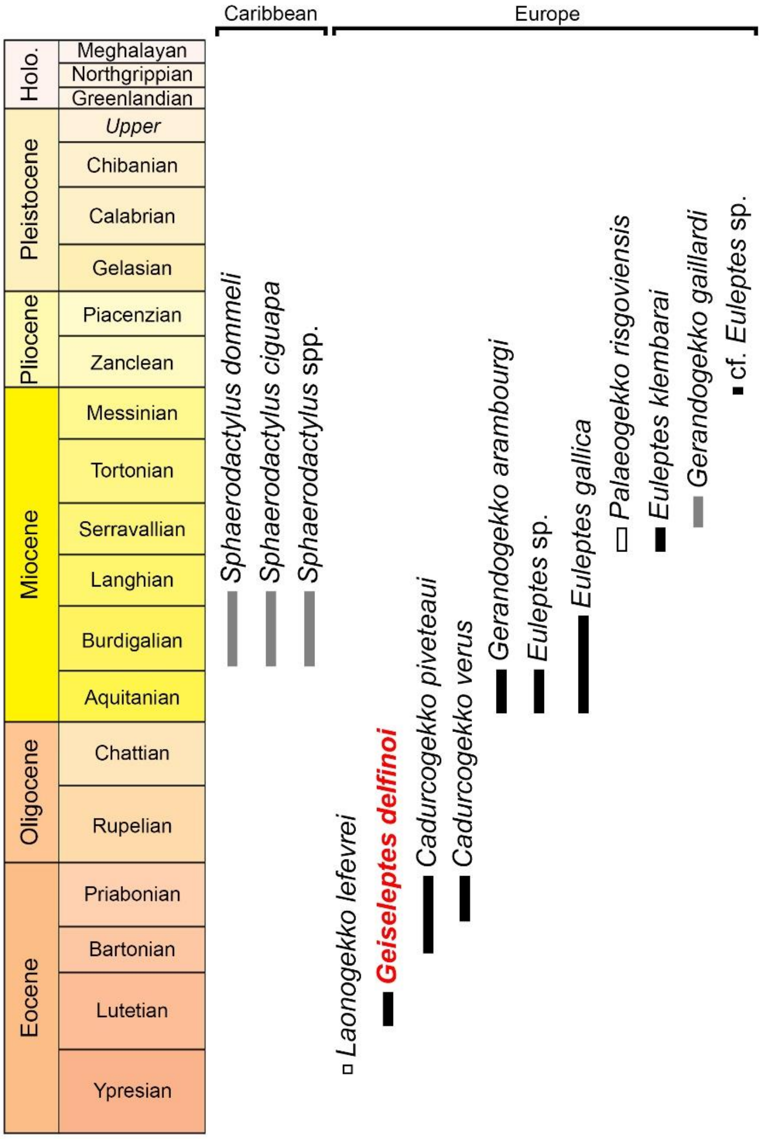

FIG. 7. Stratigraphic distribution of fossil Sphaerodactylidae. Age ranges in white represent unstable taxa that are recovered within sphaerodactylids in some of our trees, whereas age ranges in grey represent uncertain dates. Data were taken from: Schleich 1987; Müller & Mödden 2001; Augé 2003, 2005; Čerňanský & Bauer 2010; Daza & Bauer 2012; Daza et al. 2014; Bolet et al. 2015; Colombero et al. 2017; Čerňanský et al. 2018. Abbreviations: Holo., Holocene.

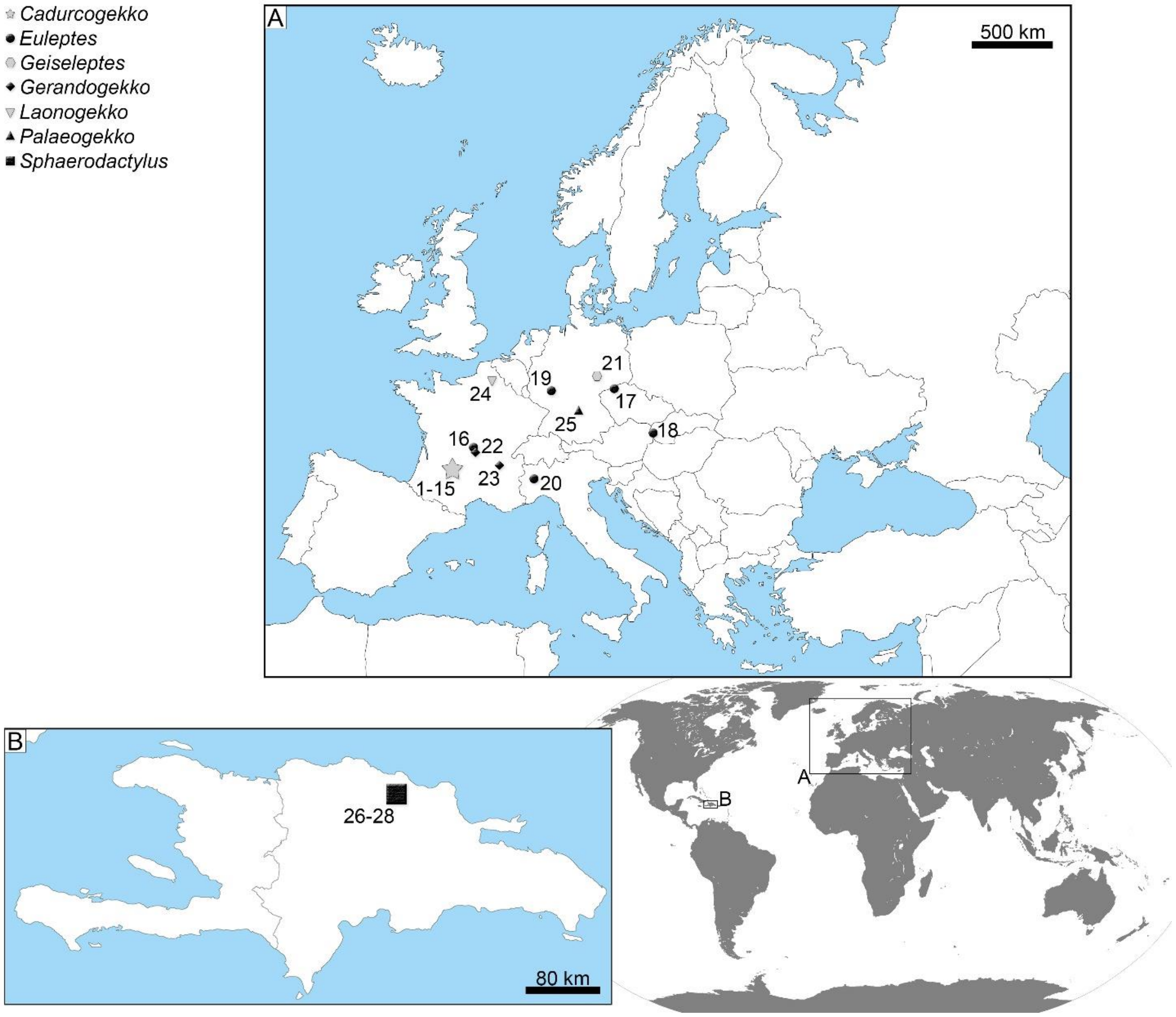

FIG. 8. Geographic distribution of fossil Sphaerodactylidae, in Europe (A) and the island of Hispaniola in the Caribbean (B). The map includes potential sphaerodactylids according to our phylogenetic analysis. Symbols represent different genera: *Cadurcogekko* (star); *Euleptes* (circle); *Geiseleptes* (hexagon); *Gerandogekko* (rhombus); *Laonogekko* (inverted triangle); *Palaeogekko* (triangle); *Sphaerodactylus* (quadrate). Grey symbols stand for Paleogene (Eocene) occurrences, whereas black symbols for Neogene (Miocene) ones. Larger symbols indicate multiple localities. Data sources are the same as in Fig. 7. Occurrences: 1. *Cadurcogekko piveteaui*, Le Bretou (MP 16, France); 2. *Cadurcogekko piveteaui*, Lavergne (MP 16, France); 3. *Cadurcogekko piveteaui*, Les Pradigues (MP 17, France); 4. *Cadurcogekko piveteaui*, La Bouffie (MP 17, France); 5. *Cadurcogekko piveteaui*, Malpérié (MP 17, France); 6. *Cadurcogekko piveteaui*, Perrière (MP 17, France); 7. *Cadurcogekko piveteaui*, Aubrelong 2 (MP 17, France); 8. *Cadurcogekko piveteaui*, Gousnat (MP 18, France); 9. *Cadurcogekko piveteaui*, St. Néboule (MP 18, France); 10. *Cadurcogekko piveteaui*, Sindou D (MP 18-19, France); 11. *Cadurcogekko piveteaui*, Coânac (MP 19, France); 12. *Cadurcogekko piveteaui*, Rosière 2 (MP 16, France); 13. *Cadurcogekko piveteaui*,

Escamps (MP 19, France); 14. *Cadurcogekko verus*, Les Pradigues (MP 17, France); 15. *Cadurcogekko verus*, Sindou D (MP 18-19, France); 16. *Euleptes gallica*, Montaigu-le-Blin (MN 2, France); 17. *Euleptes gallica*, Merkur North (MN 3, Czech Republic); 18. *Euleptes klembarai*, Zapfe‘s fissure fillings, Devínska Nová Ves (MN 6, Slovakia); 19. *Euleptes* sp., Oppenheim/Nierstein quarry (MN 2, Germany); 20. cf. *Euleptes* sp., Moncucco Torinese (MN 13, Italy); 21. *Geiseleptes delfinoi*, Geiseltal (middle Eocene, Germany); 22. *Gerandogekko arambourgi*, Saint-Gérand-le-Puy (MN 2, France); 23. *Gerandogekko gaillardi*, La Grive-Saint-Alban (MN 7-8, France); 24. *Laonogekko lefevrei*, Prémontré (MP 10, France); 25. *Palaeogekko risgoviensis*, Steinberg (MN 6, Germany); 26. *Sphaerodactylus ciguapa*, La Toca mine, Cordillera Septentrional (late early to early middle Miocene, Dominican Republic); 27. *Sphaerodactylus dommeli*, La Toca mine, Cordillera Septentrional (early to middle Miocene, Dominican Republic); 28. *Sphaerodactylus* spp., Cordillera Septentrional (early to middle Miocene, Dominican Republic).