Earliest occurrence of glyptosaurid lizards from Europe

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Glyptosauridae represents a bizarre group of lizards that are heavily armored, covered across their body with distinctive osteoderms. Glyptosaurids are iconic members of Eocene herpetofaunas from the Northern Hemisphere, including Europe, where they eventually became extinct in the latter continent at the "Grande Coupure" extinction event at the Eocene/Oligocene boundary. As their oldest European fossils have so far been documented in the earliest Eocene, it has been commonly accepted that glyptosaurids dispersed to that continent from North America (where they are already known from Late Cretaceous and Paleocene localities), somewhen after the Paleocene–Eocene Thermal Maximum (PETM) at around 56 Ma, following a similar dispersal pattern of several other terrestrial vertebrates. We here describe an isolated osteoderm from the upper Paleocene (MP 6) of Cernay in the Paris Basin, France, which can be identified with certainty as a glyptosaurid. A detailed overview of all glyptosaurid occurrences from Europe is also provided. Even if scarce and limited, the new material from Cernay provides definite evidence that glyptosaurids arrived in Europe earlier than previously thought, apparently being one of the so called "precursor" dispersers that managed to arrive in Europe before the PETM.

Key words: Squamata, Glyptosauridae, biogeography, Paleocene, Paris Basin.

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Introduction

Glyptosaurid lizards (Glyptosauridae) represent an important faunal component across Paleogene faunal assemblages of the northern hemisphere, known from many localities in Europe, North America, and Asia (Sullivan 1979, 2019; Estes 1983; Augé 2005; Čerňanský et al. 2023a). This group of heavily armored lizards is characterized by the presence of osteoderms, which also possess a unique histological structure, the osteodermine (Buffrénil et al. 2010, 2011). Although glyptosaurids puzzled early researchers, with different taxonomic affinities having been proposed during the late 19th and early 20th centuries (e.g., close to helodermatids; Boulenger 1891, 1918; Nopcsa 1908, 1928), there is now consensus that they are closely related to anguids; actually, for a long time in the past decades they were included as a subfamily of an expanded concept of Anguidae (e.g., Gilmore 1928; Hoffstetter 1962b; Meszoely 1970; Rage 1978, 1988; Sullivan 1979, 2019; Gauthier 1982; Estes 1983; Rage and Augé 2003; Augé 2005; Augé and Sullivan 2006; Klembara and Green 2010; Sullivan et al. 2012; Bolet 2017; Čerňanský and Augé 2019; Georgalis et al. 2021) and recently they were elevated to the family level, as Glyptosauridae, by Čerňanský et al. (2023a), an opinion that has since started to meet acceptance (Čerňanský et al. 2024, 2026; Lemierre and Georgalis 2025; Syromyatnikova 2025). They are divided into two major groups, i.e., Glyptosaurinae (sensu Čerňanský et al. 2023a; Glyptosaurini in alternative taxonomies) and (the probably paraphyletic) "Melanosaurinae" (sensu Čerňanský et al. 2023a; or "Melanosaurini" in alternative taxonomies).

Glyptosaurids in Europe have a relatively rich fossil record, spanning from the lowermost Eocene (MP 7) up to the uppermost Eocene (MP 19) (Augé 2005; Sullivan 2019;

Čerňanský et al. 2023a, 2024, 2026; see below). Their record is also rather rich in North America, where it is stratigraphically substantially longer, ranging from the Upper Cretaceous up to the "middle" Oligocene (Gilmore 1928; Meszoely 1970; Estes 1983; Scarpetta 2019; Sullivan 2019). In contrast, the Asian glyptosaurid record is considerably poorer, confined to only a few remains spanning from the middle Eocene up to the lower Oligocene (Sullivan and Dong 2018; Čerňanský and Augé 2019; Syromyatnikova 2025). Accordingly, their presence in the Paleocene of North America and their abrupt presence in Europe during the earliest Eocene has led to the common assumption that glyptosaurids dispersed from North America to Europe sometime slightly after the Paleocene–Eocene Thermal Maximum (PETM) at around 56 Ma (e.g., Sullivan 1979, 2019; Augé 2005; Čerňanský et al. 2023a, 2024).

Here we describe glyptosaurid material from the upper Paleocene (MP 6) of Cernay in the Paris Basin, France. The material is limited to a single osteoderm; however, it clearly demonstrates, for the first time, the presence of glyptosaurids in Europe prior to the PETM. Biogeographic implications of the new find from Cernay are discussed, coupled with a thorough overview of the European glyptosaurid fossil record.

Institutional abbreviations.—NMB, Natural History Museum of Basel, Switzerland.

Other abbreviations.—MP, Mammal Paleogene Zone; PETM, Paleocene–Eocene Thermal Maximum.

Geological setting

The fossil material described herein is permanently curated in the collections of the Natural History Museum of Basel (NMB). The material was likely excavated by Burkart Engesser in 1986 (see below for details).

Approximately 150 km east-northeast of Paris lies an area that has yielded numerous early Paleogene vertebrate fossil localities, historically central to mammalian studies (e.g., Lemoine 1880, 1889; Depéret 1906; Russell 1964; Biochrom'97 1997; Duprat 1997). These localities bracket the PETM, a major global warming event dated to 56.0 Ma (Tabuce et al. 2025), and have been essential for understanding early Cenozoic mammalian evolution in Europe (Stehlin 1909). Recent preliminary reassessments of the herpetofauna have further highlighted the importance of these assemblages for reconstructing dispersal patterns and evolutionary dynamics under global environmental change (Georgalis and Mennecart 2025; Macaluso et al. 2025).

These fossil sites were deposited within a complex transition zone between terrestrial and shallow marine deltaic systems, influenced by repeated transgression-regression episodes and marked by strong lateral and local sedimentological variability (Estes et al. 1967; Louis 1996; Duprat 1997). Situated on the "Mont de Berru", approximately 5 km

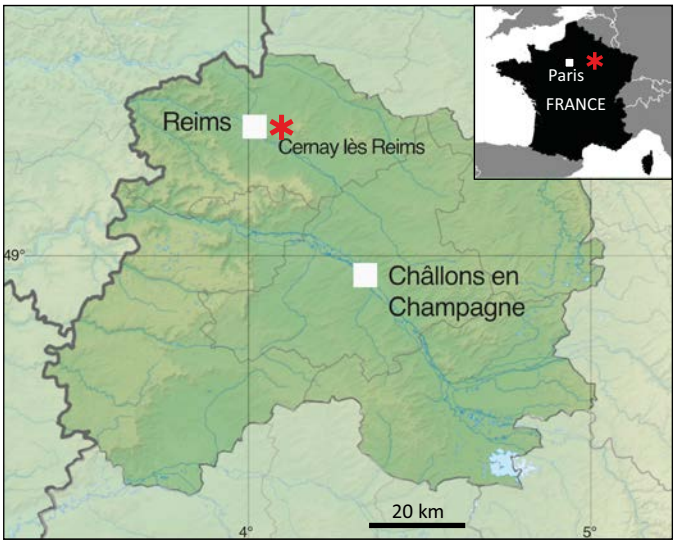

Fig. 1. Map of the Department of Marne, showing the position of the locality of Cernay (asterisk); in the inset, map of France, showing the position of the locality.

east of Reims, localities have been excavated at Cernay-lès-Reims (Lemoine quarry) and Berru (Mouras quarry) (Estes et al. 1967) (Fig. 1). The Cernay Conglomerate Formation, in particular, has yielded some of the oldest Cenozoic terrestrial vertebrate assemblages in Europe, including emblematic Paleocene mammals such as *Plesiadapis tricuspidens*, *Arctocyon primaevus*, and *Dissacus europaeus* (Biochrom'97 1997). Sediments range from sands and limestones to marls, lignites, and gravels, and contain marine, freshwater, and terrestrial fossils (Louis 1996). Fossil discoveries on the Mont de Berru date back to Aumonier and Eck in 1869 (Aumonier and Eck 1873), but the most extensive investigations of the Cernay locality were conducted by Lemoine throughout the late 19th century (e.g., Lemoine 1879, 1880, 1891). Lemoine's collections are largely housed at the Muséum national d'Histoire naturelle (MNHN), in Paris (Gaudry 1898; Boyer et al. 2012), though several specimens were donated to other institutions, including the NMB (notably in 1892 and 1898). Additional Cernay specimens entered the Basel collections throughout the early 20th century, before World War II and the death of Stehlin in 1941 (e.g., 1906, 1908, 1912, 1913, 1920, 1925, 1928, 1934, 1938, 1939, 1940). A later collecting campaign, most likely organized by Burkart Engesser, took place in 1986 (24 July and 24 September), and the material described herein likely originates from this expedition.

The Cernay fauna is the European reference level for MP 6 (Biochrom'97 1997), owing to its exceptionally rich mammalian assemblage (29 species recorded in 1967; 33 in 1997; Estes et al. 1967; Biochrom'97 1997). The fauna is late Paleocene in age (Thanetian). Numerical dating remains imprecise and varies among authors. The Thanetian spans between 59.24 and 56.0 Ma (Cohen et al. 2025). Earlier proposed ages of 52.9±1.9 Ma (Pomerol et al. 1977) and 55.7–55 Ma (Duprat 1997) for the Cernay fauna are now considered inconsistent with current chronostratigraphic frameworks.

More recent estimates place the Cernay fauna around 58.0 Ma (Escarguel et al. 1997) or between 57–56 Ma (Hooker and Collinson 2012). Among herpetofauna, from the Cernay/Mont-de-Berru area there have been described relatively few (but important) fossil remains of urodelans, anurans, choristoderans, crocodylians, turtles, and lizards (Gervais 1877; Estes et al. 1967; Vergnaud-Grazzini and Hoffstetter 1972; Rage 2003; Pérez-García 2012, 2020; Folie et al. 2013; Martin et al. 2014; Macaluso et al. 2025).

Systematic palaeontology

Squamata Oppel, 1811

Anguimorpha Fürbringer, 1900

Anguioidea Gray, 1825

Glyptosauridae Marsh, 1872 (sensu Čerňanský et al. 2023a)

Glyptosauridae indet.

Fig. 2.

Material.—One isolated osteoderm (NMB Cy.1144); Cernay, upper Paleocene (MP 6).

Description.—The osteoderm NMB Cy.1144 is incomplete, missing part of its posterior portion (Fig. 2). The osteoderm is rectangular; in dorsal view, its surface is covered by distinct tubercles, with the exception of its anteriormost one third of this surface, which is totally smooth (Fig. 2A$_1$). This smooth surface is more elevated than the remaining sculptured portion of the osteoderm, from which it is separated by a transverse groove. In the sculptured area, the prominent tubercles are of irregular size, though they are mostly

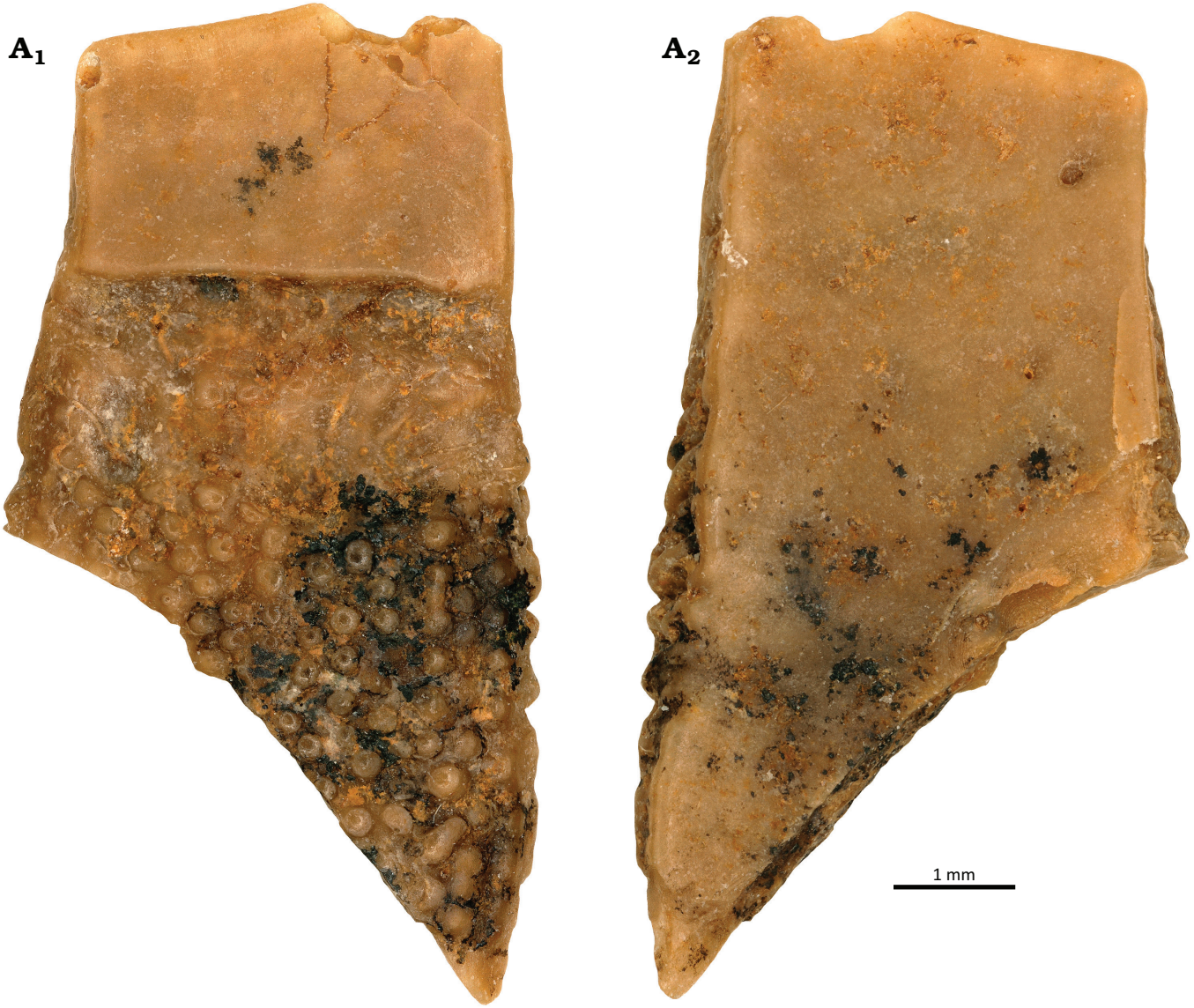

Fig. 2. Isolated osteoderm (NMB Cy.1144) of Glyptosauridae indet. from the upper Paleocene of Cernay, Paris Basin, France in dorsal (A$_1$) and ventral (A$_2$) views.

rounded and closely spaced to each other. There is no keel in the midline of the osteoderm. In ventral view, the osteoderm is smooth, being irregularly pierced only by a few small foramina (Fig. 2A$_2$).

Remarks.—The osteoderm NMB Cy.1144 can be referred to Glyptosauridae based on the ornamentation of its dorsal surface, covered by distinct tubercles (Hoffstetter 1962b; Sullivan 1979, 2019; Čerňanský et al. 2023a). Based on its rectangular overall shape, the shape and size of the tubercles, and the presence of a smooth area on approximately the anterior one third of its dorsal surface, the specimen represents a body osteoderm, rather than a cephalic one (e.g., Rage 1978; Estes 1983; Čerňanský et al. 2023a, 2024). Based on this single body osteoderm, it is not possible to assign the material to either Glyptosaurinae or either "Melanosaurinae" and therefore we solely treat it as Glyptosauridae indet.

Discussion

Glyptosauridae represents an abundant group of heavily armored lizards, with an extensive Holarctic geographic distribution. Their record in Europe is rich (Depéret 1917; Hoffstetter 1962a; Sullivan 1979, 2019; Estes 1983; Augé 1990a, b, 2005; Augé and Sullivan 2006; Sullivan and Augé 2006; Klembara and Green 2010; Sullivan et al. 2012; Bolet 2017; Georgalis et al. 2021; Čerňanský et al. 2023a, 2024, 2026; Lemierre and Georgalis 2025; see full details in Table 1), also including beautifully preserved articulated skeletons from the Fossillagerstätte localities of Messel and Geiseltal (Kuhn 1940; Meszoely et al. 1978; Keller and Schaal 1988; Keller 2009; Smith et al. 2018). Notably though, their record is confined exclusively to the western and central portions of the continent, with no glyptosaurid occurrences known from Eastern Europe (Fig. 3), a pattern also reflecting the scarcity and rareness of Eocene squamate-yielding terrestrial localities in the eastern margins of the continent (see also Smith and Georgalis 2022). Their remains have been known in Europe since the 19th century (Gervais 1848–1852, 1876; Pictet et al. 1855–1857; Filhol 1876, 1882, 1894; Zittel 1887–1890; Lydekker 1888a; see full details in Table 1). This existing European fossil record attests to a moderate diversity in the continent, with at least nine valid species, spanning across the entire Eocene (Sullivan 2019; Čerňanský et al. 2023a; Lemierre and Georgalis 2025; see full details in Table 1): *Paraplacosauriops quercyi* (Filhol, 1882), *Paraxestops stehlini* Hoffstetter, 1962a, *Placosauriops weigelti* Kuhn, 1940, *Cadurcopanoplos vaylatsensis* Lemierre & Georgalis, 2025, *Gaultia ragei* (Sullivan et al., 2012), *Placosaurus estesi* Sullivan & Augé, 2006, *Placosaurus rugosus* Gervais, 1848–1852, *Placosaurus*? *europaeus* (Filhol, 1876), and *Sullivanosaurus gallicus* (Čerňanský et al., 2023a). In addition, a few other taxa have been also named from Europe but they are currently regarded as either nomina dubia or junior synonyms of the above-mentioned species (see full details in Table 1). The youngest occurrence of glyptosaurids in Europe is at the latest Eocene and they are totally absent from Oligocene localities of the continent, suggesting that they were extirpated from the continent during the "Grande Coupure" at the Eocene/Oligocene boundary (unlike the case of North America and Asia, where the group survived into the early Oligocene). Interestingly, a similar such pattern of broad extinctions in Europe and survival in Northern America and Asia is also observed in other vertebrate groups like ungulate mammals at the Eocene/Oligocene transition (Blanco et al. 2025) making this scenario more global among different tetrapod lineages.

Glyptosauridae in North America were also rather abundant and diverse and they achieved there an even greater temporal distribution, spanning from the Late Cretaceous up to the "middle" Oligocene (Marsh 1871, 1872; Gilmore 1928; Meszoely 1970; Sullivan 1979, 2019; Gauthier 1982; Estes 1983; Smith 2009, 2011a, b; Smith and Gauthier 2013; Scarpetta 2019). To the contrary, their Asian fossil record is considerably poor, confined to only a few remains spanning from the middle Eocene up to the early Oligocene (Gilmore 1943; Sullivan and Dong 2018; Čerňanský and Augé 2019; Syromyatnikova 2025).

Taking into consideration these distribution data, it has been widely accepted that glyptosaurids have been genuinely absent in the Paleocene of Europe and that they only managed to disperse to the continent from North America, immediately after the PETM. Indeed, glyptosaurids are notoriously absent from the (admittedly very) few Paleocene squamate-yielding localities from Europe (e.g., Čerňanský and Vasilyan 2024); a large anguimorph described and figured by Smith et al. (2014) from the uppermost Paleocene of Rivecourt, France, does not pertain to glyptosaurids but to some other anguimorph group (the figured osteoderm of Smith et al. 2014 does not bear the typical tuberculated ornamentation of glyptosaurids [that specimen is regarded here as Anguimorpha indet.], while the figured vertebra and the fragmentary dentary can likely only be identified as Anguimorpha indet.).

The description herein of a glyptosaurid from Cernay challenges the above scenario and demonstrates that this lizard group managed to disperse to Europe already slightly before the PETM. It is worth noting here that Lemoine (1878–1879: 403), who was the pioneer researcher in the locality of Cernay in the late 19th century, had already mentioned that among his (never described) material from that locality, there were remains reminiscent of the genus *Placosaurus* ("quelques plaques rappelleraient le genre *Placosaurus*"). This sentence, however, has fallen into oblivion and no subsequent researcher commented on this early mention, while Lemoine's Cernay lizard material is of unknown whereabouts (even though his Cernay mammal collection is deposited at the Museum National d'Histoire Naturelle, Paris; Gaudry 1898; Boyer et al. 2012).

But when and how did glyptosaurids arrived in Europe? A large number of terrestrial vertebrates (also including an array of reptile taxa) is now known to have dispersed

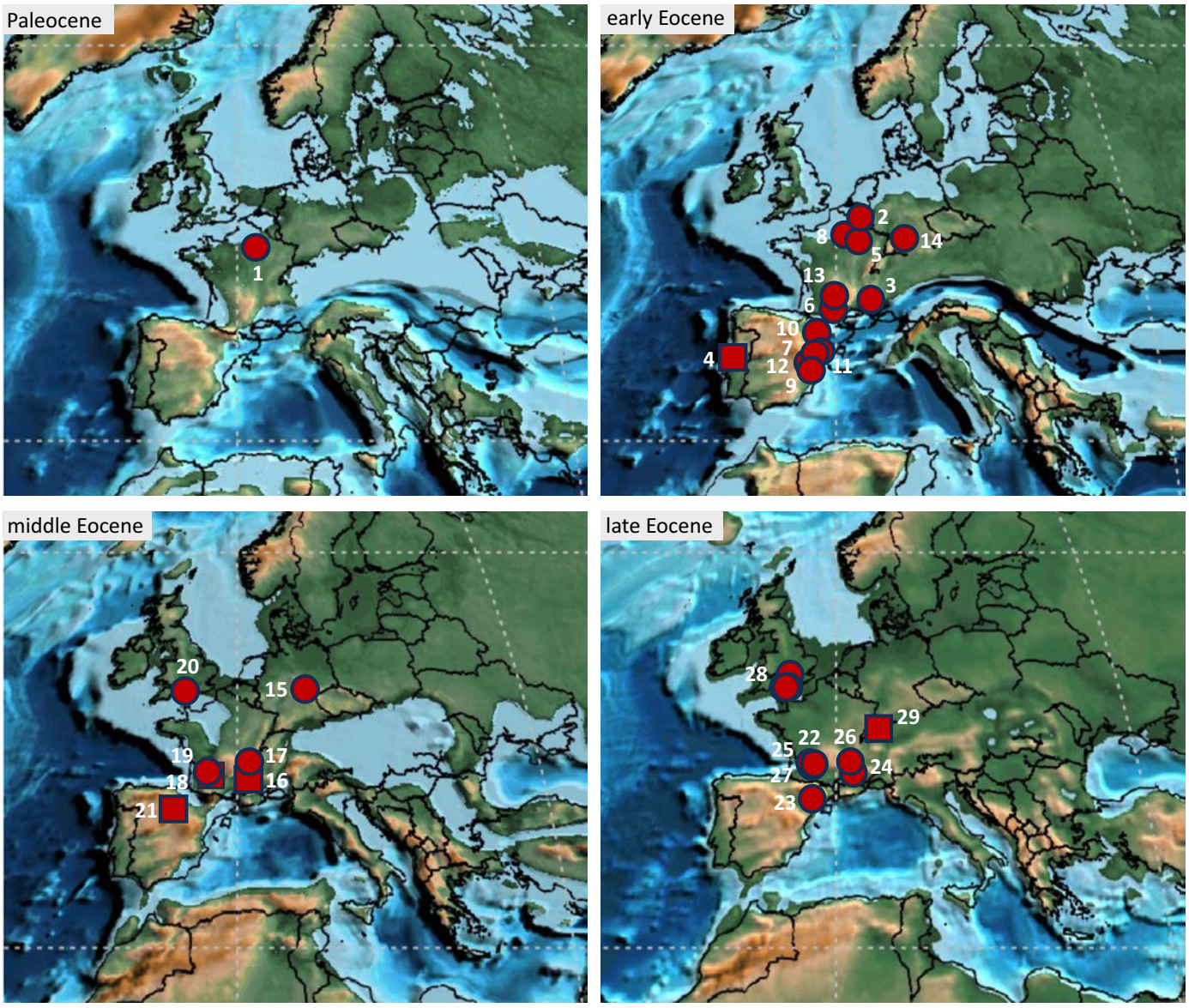

Fig. 3. Palaeogeographic maps of Europe during the Paleocene and Eocene (modified from Scotese 2021), showing all formally described glyptosaurid occurrences. Data on occurrences are based on Table 1. Circles and squares indicate a minimum number of 1 and 2 glyptosaurid taxa, respectively, from each locality. Occurrences from the "old collections" of the Phosphorites du Quercy with no precise locality and age data are not indicated here. 1, Cernay (= Cernay-lès-Reims), Paris Basin; 2, Dormaal (= Orsmael), Flemish Brabant; 3, Rians C; 4, Silveirinha, Coimbra; 5, Condé-en-Brie, Aisne, Paris Basin; 6, La Borie, Saint-Papoul, Aude, Occitanie; 7, Masia de l'Hereuet, Catalonia; 8, Prémontré, Aisne, Hauts-de-France; 9, Barranc del Fusteró, Catalonia; 10, Escarlà, Catalonia; 11, La Morera (= La Coma), Catalonia; 12, Font del Torricó, Catalonia; 13, Cos, near Caylus, Quercy, Tarn-et-Garonne, Occitanie; 14, Messel, Hesse; 15, Geiseltal, Saxony-Anhalt; 16, Saint-Maximin, Gard; 17, Lissieu, Auvergne-Rhône-Alpes; 18, Lavergne, Quercy, Occitanie; 19, Le Bretou, Quercy, Tarn-et-Garonne; 20, Creechbarrow, Dorset; 21, Mazaterón, Soria, Castile and León; 22, La Bouffie (= Bouffie), Quercy, Lot; 23, Sossís, Catalonia; 24, Euzet (= Euzet-les-Bains), Gard; 25, Perrière, Quercy, Lot; 26, La Débruge (Sainte-Radegonde d'Apt = Sainte-Redegonde = Sainte Aldegarde), Vaucluse, Provence-Alpes-Côte d'Azur; 27, Sainte Néboule (Ste.-Néboule), Quercy, Lot; 28, Headon Hill, Isle of Wight; Hatherwood Limestone, Hampshire; Osborne, Isle of Wight; Bembridge, Isle of Wight; 29, Mount Mormont (= Mormont = Mauremont), near Éclépens, Vaud.

from North America to Europe during the PETM, facilitated by the very warm temperatures and the terrestrial corridors between the two landmasses, likely via Greenland (see discussion in Georgalis and Mennecart 2025 and references therein). The identification of early Eocene glyptosaurid lizards as far north as Ellesmere island (Estes and Hutchison 1980) supported the claim that these lizards could have indeed used such north dispersal routes in order to reach Europe. Recently, it was suggested that another, brief, global warming event (Pre-Onset Excursion [POE]) occurred during the latest Paleocene, slightly before the PETM (Tabuce et al. 2025). During this brief event, there is now evidence that some terrestrial mammals managed to disperse from North America to Europe ("precursor" dispersers), taking advantage of large terrestrial corridors of evergreen forests that emerged in high latitudes (Tabuce et al. 2025). With an age pertaining to the latest Paleocene, the Cernay specimen shows that among these "precursor" dis-

Table 1. List of all described occurrences of Glyptosauridae from Europe. Note that the list includes only material that has been formally described and/or figured or at least collection numbers have been provided. List appears in chronological order of the localities. Locality numbers indicate the respective entry on the maps of Fig. 3. Alternative / older names of the localities can also appear in parentheses. The locality name is further followed by the name of the broader administrative region, in order to provide a more concise geographic context. 1, Cernay (=Cernay-lès-Reims), Paris Basin; 2, Dormaal (= Orsmael), Flemish Brabant; 3, Rians C; 4, Silveirinha, Coimbra; 5, Condé-en-Brie, Aisne, Paris Basin; 6, La Borie, Saint-Papoul, Aude, Occitanie; 7, Masia de l'Hereuet, Catalonia; 8, Prémontré, Aisne, Hauts-de-France; 9, Barranc del Fusteró, Catalonia; 10, Escarlà, Catalonia; 11, La Morera (= La Coma), Catalonia; 12, Font del Torricó, Catalonia; 13, Cos, near Caylus, Quercy, Tarn-et-Garonne, Occitanie; 14, Messel, Hesse; 15, Geiseltal, Saxony-Anhalt; 16, Saint-Maximin, Gard; 17, Lissieu, Auvergne-Rhône-Alpes; 18, Lavergne, Quercy, Occitanie; 19, Le Bretou, Quercy, Tarn-et-Garonne; 20, Creechbarrow, Dorset; 21, Mazaterón, Soria, Castile and León; 22, La Bouffie (= Bouffie), Quercy, Lot; 23, Sossís, Catalonia; 24, Euzet (= Euzet-les-Bains), Gard; 25, Perrière, Quercy, Lot; 26, La Débruge (Sainte-Radegonde d'Apt = Sainte-Redegonde = Sainte Aldegarde), Vaucluse, Provence-Alpes-Côte d'Azur; 27, Sainte Néboule (Ste.-Néboule), Quercy, Lot; 28a, Headon Hill, Isle of Wight; 28b, Hatherwood Limestone, Hampshire; 28c, Osborne, Isle of Wight; 29, Mount Mormont (= Mormont = Mauremont), near Éclépens, Vaud; 28d, Bembridge, Isle of Wight.

Country	Locality	Epoch	Mammal age	Taxon	Reference	Remarks
France	1	late Paleocene	MP 6	Glyptosauridae indet.	this paper	
Belgium	2	early Eocene	MP 7	*Gaultia ragei*	Hecht and Hoffstetter 1962; Hoffstetter 1962b; Estes 1983; Godinot et al. 1978; Augé 1990b, 2003a, 2005; Augé and Sullivan 2006; Sullivan et al. 2012; Sullivan 2019; Čerňanský et al. 2024	type locality of a valid species (originally Anguidae near *Melanosaurus* in Hecht and Hoffstetter [1962]; cf. *Melanosaurus* sp. of Hoffstetter [1962b]; *Melanosaurus*? sp. of Estes [1983]; Melanosaurini indet. of Augé [1990b]; Glyptosaurinae of Augé [2003a]; *Placosaurus* indet. of Augé [2005]; cf. *Paraplacosauriops quercyi* in Augé and Sullivan [2006]; ?*Placosaurus ragei* and cf. ?*Placosaurus ragei* of Sullivan et al. [2012]; Melanosaurini indet. of Sullivan [2019])
				Glyptosauridae indet.	Augé 1990b; Sullivan et al. 2012; Čerňanský et al. 2024	Glyptosaurinae indet. of Augé (1990b) and Sullivan et al. (2012)
France	3	early Eocene	MP 7	"Melanosaurinae" indet.	Augé 2005	Melanosaurini indet. of Augé (2005)
Portugal	4	early Eocene	MP 7	cf. *Melanosaurus* sp.	Rage and Augé 2003	
				Glyptosaurinae indet.	Rage and Augé 2003	Glyptosaurini indet. of Rage and Augé (2003)
				Glyptosauridae indet.	Rage and Augé 2003	Glyptosaurinae indet. of Rage and Augé (2003)
France	5	early Eocene	MP 8/9	cf. *Paraplacosauriops quercyi*	Augé 1990a; Augé and Sullivan 2006	*Placosaurus quercyi* of Augé (1990a, 2005)
				"Melanosaurinae" indet.	Augé 1990a	Melanosaurini indet. of Augé (1990a)
				Glyptosauridae indet.	Augé 1990a	Glyptosaurinae indet. of Augé (1990a)
France	6	early Eocene	MP 8/9	Glyptosauridae indet.	Laurent et al. 2010	Glyptosaurinae indet. of Laurent et al. (2010); not figured
Spain	7	early Eocene	MP 8/9	Glyptosaurinae indet.	Bolet 2017	Glyptosaurini indet. of Bolet (2017)
				Glyptosauridae indet.	Bolet 2017	Glyptosaurinae indet. of Bolet (2017)
France	8	early Eocene	MP 10	?*Placosauriops* sp.	Augé et al. 1997; Augé 2003b	Glyptosaurinae indet. of Augé et al. (1997)
Spain	9	early Eocene	MP 10	Glyptosauridae indet.	Bolet 2017	Glyptosaurinae indet. of Bolet (2017)
Spain	10	early Eocene	MP 10	cf. *Placosaurus* sp.	Bolet 2017	close to *Sullivanosaurus* according to Čerňanský et al. (2025)
Spain	11	early Eocene	MP 10	Glyptosaurinae indet.	Bolet 2017	Glyptosaurini indet. of Bolet (2017)
				Glyptosauridae indet.	Bolet 2017	Glyptosaurinae indet. of Bolet (2017)
Spain	12	early Eocene	MP 10 or MP 8/9	Glyptosaurinae indet.	Bolet 2017	Glyptosaurini indet. of Bolet (2017)
France	13	early Eocene	MP 10–11	*Sullivanosaurus gallicus*	Čerňanský et al. 2023a, b	type locality of a valid species
				Glyptosauridae indet.	Čerňanský et al. 2023a	
Germany	14	early–middle Eocene	MP 11	*Placosauriops weigelti*	Keller and Schaal 1988; Keller 2009	*Xestops abderhaldeni* of Keller and Schaal (1988); *Placosauriops abderhaldeni* of Keller (2009)
Germany	15	late early or middle Eocene		*Placosauriops weigelti*	Kuhn 1940; Meszoely et al. 1978	type locality of a valid species (including type of *Placosauroides abderhaldeni* Kuhn, 1940)
				Glyptosauridae indet.	Weigelt 1929a, b; Kuhn 1940; Meszoely et al. 1978	type material of *Loricotherium waltheri* Weigelt, 1929b, and *Placosaurus waltheri* Weigelt, 1929a; material referred to *Placotherium waltheri* by Kuhn (1940b)
France	16	middle Eocene	MP 13	Glyptosaurinae indet.	Duffaud and Rage 1997	Glyptosaurini indet. of Duffaud and Rage (1997)
				"Melanosaurinae" indet.	Duffaud and Rage 1997	Melanosaurini indet. of Duffaud and Rage (1997)

France	17	middle Eocene	MP 14	Glyptosauridae indet.	Depéret 1917; Rage and Augé 2010	including type of *Placosaurus lugdunensis* Depéret, 1917; Glyptosaurinae indet. of Rage and Augé (2010)
France	18	middle Eocene	MP 16	*Paraplacosauriops quercyi*	Augé and Sullivan 2006	
				Placosaurus rugosus	Augé 2005	
				?*Placosaurus* sp.	Čerňanský et al. 2026	
				Glyptosauridae indet.	Buffrenil et al. 2010, 2011; Rage 2013; Čerňanský et al. 2026	Glyptosaurinae indet. of Buffrénil et al. (2010, 2011); Rage (2013)
France	19	middle Eocene	MP 16	*Placosaurus* sp.	Rage 1988; Augé 2005	
UK	20	middle Eocene	MP 16	Glyptosauridae indet.	Klembara and Green 2010	Glyptosaurinae indet. of Klembara and Green (2010)
Spain	21	middle Eocene	MP 16	Glyptosaurinae indet.	Bolet 2025	Glyptosaurini indet. of Bolet (2025)
				"Melanosaurinae" indet.	Bolet 2025	Glyptosaurini indet. of Bolet (2025)
France	22	late Eocene	MP 17a	*Cadurcopanoplos vaylatsensis*	Lemierre and Georgalis 2025	type locality of a valid species
				Glyptosauridae indet.	Lemierre and Georgalis 2025	
Spain	23	late Eocene	MP 17a	Glyptosaurinae indet.	Bolet and Evans 2013	Glyptosaurini indet. of Bolet and Evans (2013)
				Glyptosauridae indet.	Bolet and Evans 2013	Glyptosauridae indet. of Bolet and Evans (2013)
France	24	late Eocene	MP 17	*Placosaurus rugosus*	Depéret 1917	
France	25	late Eocene	MP 17	*Placosaurus estesi*	Sullivan and Augé 2006	type locality of a valid species (*Placosaurus quercyi* of Augé [2005])
France	26	late Eocene	MP 18	*Placosaurus rugosus*	Gervais 1848–1852; De Stefano 1903; Sullivan and Augé 2006	type locality of a valid species
France	27	late Eocene	MP 18	*Placosaurus* sp.	Rage 1978	
				Glyptosauridae indet.	Buffrénil et al. 2010, 2011	Glyptosaurinae indet. of Buffrénil et al. (2010, 2011)
UK	28a	late Eocene	MP 18	Glyptosauridae indet.	Rage and Ford 1980	Glyptosaurinae indet. of Rage and Ford (1980)
UK	28b	late Eocene	MP 18	Glyptosauridae indet.	Klembara and Green 2010	Glyptosaurinae indet. of Klembara and Green (2010)
UK	28c	late Eocene	MP 19	Glyptosauridae indet.	Klembara and Green 2010	Glyptosaurinae indet. of Klembara and Green (2010)
Switzerland	29	late Eocene	MP 19	*Paraxestops stehlini*	Hoffstetter 1962a	type locality of a valid species
				Placosaurus rugosus	Pictet et al. 1855–1857	
UK	28d	late Eocene	MP 20	Glyptosauridae indet.	Klembara and Green 2010	Glyptosaurinae indet. of Klembara and Green (2010)
France, Quercy (imprecise locality)		probably middle or late Eocene		*Paraplacosauriops quercyi*	Filhol 1882; Zittel 1887–1890; De Stefano 1903; Augé 2005; Augé and Sullivan 2006; Georgalis et al. 2021	type locality of a valid species (*Diploglossus* sp. of Zittel [1887–1890]; including type of *Diploglossus cadurcensis* De Stefano, 1903)
France, Quercy (imprecise locality, but near near Caylus, Tarn-et-Garonne)		probably middle or late Eocene		*Paraplacosauriops quercyi*	Augé and Sullivan 2006	
France Quercy (imprecise locality		probably middle or late Eocene		*Paraplacosauriops* sp.	Lydekker 1888a, b; Leenhardt 1926	Anguidae indet. of Lydekker (1888a, b); type of *Placosaurus leenhardti* Leenhardt, 1926
				"Melanosaurinae" indet.	Augé 2005; Georgalis et al. 2021	Melanosaurini indet. of Augé (2005) and Georgalis et al. (2021)
				Placosaurus rugosus	Augé 2005	
				Placosaurus sp.	Filhol 1894; De Stefano 1903; Georgalis et al. 2021	holotype of *Necrodasypus galliae* Filhol, 1894; syntypes of *Protrachysaurus gaudryi* De Stefano, 1903; lectotype of *Propseudopus cayluxi* De Stefano, 1903
				"*Placosaurus*" *europaeus*	Filhol 1876; De Stefano 1903; Sullivan and Augé 2006	type locality of a valid species
				Glyptosauridae indet.	Gervais 1876; Lydekker 1888a; Sullivan and Augé 2006	including type of *Varanus margariticeps* Gervais, 1876; *Varanus margariticeps* of Lydekker 1888a; Glyptosaurinae indet. of Sullivan and Augé (2006)

persers that reached Europe were also glyptosaurid lizards, a group that would later be iconic and widespread throughout Eocene European herpetofaunas.

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