Fossil Record 29 (1) 2026, 411–428 | DOI 10.3897/fr.29.183059

PENSOFT

MUSEUM FÜR NATURKUNDE BERLIN

First anguid record (Anguidae, Squamata) from the Late Miocene *Konservat-Lagerstätte* Libros (Teruel, Spain) and its palaeoenvironmental implications

Adriana Linares-Martín[1,2], Tomáš Přikryl[3], Andrea Villa[4], Massimo Delfino[4,5], Bruno Gómez De Soler[1,2], Hugues-Alexandre Blain[1,2]

1 *Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), Tarragona, 43007, Spain*

2 *Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, Avinguda de Catalunya 35, Tarragona, 43002, Spain*

3 *Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, Prague 6 - Lysolaje, 165 00, Czech Republic*

4 *Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Edifici ICTA-ICP, c/Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Valles, Barcelona, Spain*

5 *Dipartimento di Scienze della Terra, Universita degli Studi di Torino, Via T. Valperga Caluso 35, 10125 Torino, Italy*

https://zoobank.org/B8741D5D-FDCE-4C60-BBA5-7C9ABC6D1A5D

Corresponding authors: Adriana Linares-Martín (alinares@iphes.cat); Hugues-Alexandre Blain (hablain@iphes.cat)

Academic editor: Johannes Müller ♦ **Received** 20 December 2025 ♦ **Accepted** 1 June 2026 ♦ **Published** 19 June 2026

Abstract

For the first time, fossil evidence of anguine material is reported from the middle–late Tortonian *Konservat-Lagerstätte* locality of Libros (Teruel, Spain). So far, only mammals, birds, snakes, amphibians, insects and flora in excellent conditions of preservation were described from the lacustrine sediments of this site. The size and fragility of the new fossil, partially embedded in the sediment, required the application of non-invasive techniques for their study. Micro-CT scans were conducted, resulting in satisfactory three-dimensional models. The skeleton is partially articulated and preserves the nasal bone, dozens of vertebrae, eleven ribs and hundreds of osteoderms. Amongst them, the two best-preserved trunk vertebrae and one caudal vertebra, along with osteoderm dermal sculpturing, suggest attribution to the genus *Pseudopus* (Family Anguidae). This new fossil record not only provides information from a global palaeobiogeographical perspective, but also constitutes a valuable contribution to the understanding of the ecosystems surrounding the Libros palaeolake.

Key Words

Computed tomography, Europe, limbless lizard, *Pseudopus*

Introduction

The palaeontological site of Libros is regarded as one of the most prominent Lagerstätten of the Miocene (McNamara et al. 2012; Blain et al. 2023). The exceptional preservation of its fossil remains has promoted taphonomic, taxonomic and environmental studies, which contribute to a more accurate reconstruction of the landscape of the site.

Minas de Libros, also known as "La azufrera" or "La zofrera" was a mining village exploited from the late 18th to the mid-19th century. The exploitation focused mainly on gypsum-rich materials with sulphur occurrences from the Minas de Libros Unit, which forms part of the sedimentary infill of the Teruel Basin (Early Miocene–Late Pliocene), deposited over Triassic materials and Cretaceous carbonates. The fossils discovered during mining activities were not properly documented; instead, they were ultimately purchased from the workers and the local population (Castro 2002; Luque and Alcalá 2002), except for a fossil frog recovered in

2022 on the ceiling in one of the abandoned galleries of the mine (Blain et al. 2023).

It was not until 1920 that the first scientific investigations began with the studies conducted by Navás (1920, 1922). These studies revealed a substantial number of well-preserved specimens of ranids, salamandrids and snakes, as well as wading birds. Although a snake attributed to the natricid *Natrix* has been reported from the Libros site (Teruel), there is no published evidence confirming this yet (Navás 1922; Szyndlar and Alférez 2005; McNamara et al. 2016). Additionally, the presence of insects and arachnids was noted by Navás (1920, 1922), a subject that would later be addressed by Peñalver (1996). After that, the compilation of the recovered specimens extended to a list of numerous taxa. Olson (1995) described the finding of the bird *Thiornis sociata*. Fernández-Marrón (1972) published a preliminary ecological study with the identification of different specimens of insects (*Hipporrhinus heeri*, *Cleonus försteri* and aff. *Rhymosia försteri*), arachnids (suborder Araneomorphae) and leaves (*Salix denticulata*). Larval remains of dragonflies (suborder Anisoptera) have also been identified (Peñalver 1996). Several authors have documented the presence of frogs in lacustrine deposits through various research contexts, ranging from taphonomic studies (McNamara et al. 2010) to discussions regarding their phylogeny (Sanchíz Gil de Avalle 1977), as well as the identification of the only in situ *Pelophylax pueyoi* specimen (Blain et al. 2023). Finally, although a single mammal — a fossil beaver (Cuenca-Bescós 2020) — has been securely identified from the Libros site, historical references to additional mammalian remains from the area are reported by Román (1926, 1927) and summarised in Geological and Mining Institute of Spain (IGME 1983).

Likewise, the exceptional preservation of fossil remains has enabled the conservation of bird tracheae, gastropods ingested by frogs, the eyes of amphibian larvae and, in some cases, feathers in birds (Castro 2002).

The present paper focuses on the morphology and taxonomy of fossil in the slab MNCN 63766, which hosts a legless lizard of the genus *Pseudopus* (Anguidae, Anguinae) broadening the former diversity of taxa identified at the site, providing significant palaeoenvironmental information and, therefore, contributes to the reconstruction of the ancient landscape.

This new evidence enhances the fossil record of anguine lizards in the European Miocene, which is notable for the presence of *Anguis*, *Fontisaurus*, *Ophisaurus* s.l., *Pseudopus* and *Smithosaurus* (Alba et al. 2006; Klembara et al. 2010, 2019; Klembara 2012; Marquina-Blasco et al. 2016, 2025; Vasilyan et al. 2016, 2022; Čerňanský et al. 2017b; Klembara and Rummel 2018; Roček 2019; Villa and Delfino 2019; Villa et al. 2021a, 2021b, 2025; Casanovas-Vilar et al. 2022; Loréal et al. 2023, 2025). Despite the abundance of the anguine fossil record, these findings are often based on disarticulated material, which makes understanding the evolutionary history of this subfamily difficult (Klembara et al. 2014). Furthermore, taxonomic identification, based on single skeletal elements, along with the lack of identification at the genus and/or species level, has led to a long list of synonyms as explained by Klembara et al. (2010).

To date, there are few articulated skeletons including postcranial elements preserved from the Miocene in Europe (Klembara et al. 2010; Čerňanský and Klembara 2017; Loréal et al. 2025), apart from the anguine from Libros site.

The discovery of MNCN 63766 enriches the Late Miocene fossil record of anguines from the Iberian Peninsula, thereby extending the known distribution of this subfamily within the region. Moreover, as one of the westernmost records of *Pseudopus* in Eurasia, it may provide valuable insights into the palaeobiogeographic setting in relation to climatic changes. Similarly, the discovery of an anguine at the Libros site provides palaeoenvironmental information that contributes to the reconstruction of the landscape of this *Konservat-Lagerstätte*.

Geological context

The fossil site of Libros is located in the Teruel basin, northeast of the Iberian Peninsula (Fig. 1A, B). This Neogene half graben-like basin was controlled by tectonic extension and subsidence along its multiple faults located in the eastern part of the basin (Garcés et al. 1997; Alonso-Zarza et al. 2002). The Early Miocene-Late Pliocene infill of the basin is deposited over the Upper Triassic gypsum and Cretaceous carbonates. The Libros lacustrine facies consist of different units (in stratigraphic order) (Fig. 1C, D): 1) 150 m of detritic deposits (conglomerates, sandstones and reddish lutites); 2) 25 m of El Morrón gypsums; 3) 50 m of El Bolage limestones (wackestones and packstones) intercalated with marls and lignites with fossil remains and 4) 80–100 m of Libros gypsums (Garcés et al. 1997; Castro 2002). The Libros gypsum unit is well-preserved in Libros Village. This unit represents a marginal to deep sequence of lacustrine sediments of 120 m that begins with subunits of lutites and gypsums with limestones intercalations (Fig. 1D). While the lake deepens, the presence of gypsum is reduced to thin layers initiating a subunit of bituminous-calcareous mudstones. This sequence of laminated bituminous mudstones (including oil shales) and charophytic wackestones - packestones represents the deepest part of the lake (Anadón et al. 2004). This alternation suggests fluctuations between oxic conditions and anoxic conditions due to the presence of fossiliferous carbonates (wackestones) and organic-rich mudstones, which also indicates a low sedimentation rate and energy deposited in non-saline or slightly saline waters (Anadón et al. 1992; Castro 2002). In the upper part of the stratigraphic section, as depth decreases, carbonates begin to be replaced by thin-bedded clotted gypsums. For the occurrences of sulphurs along the Libros gypsum unit, isotopic studies carried out show an early sulphate-reducing bacterial activity in the lake bottom. In view of that, Ortí et al. (2003) suggested that the sulphate was derived from the chemical recycling

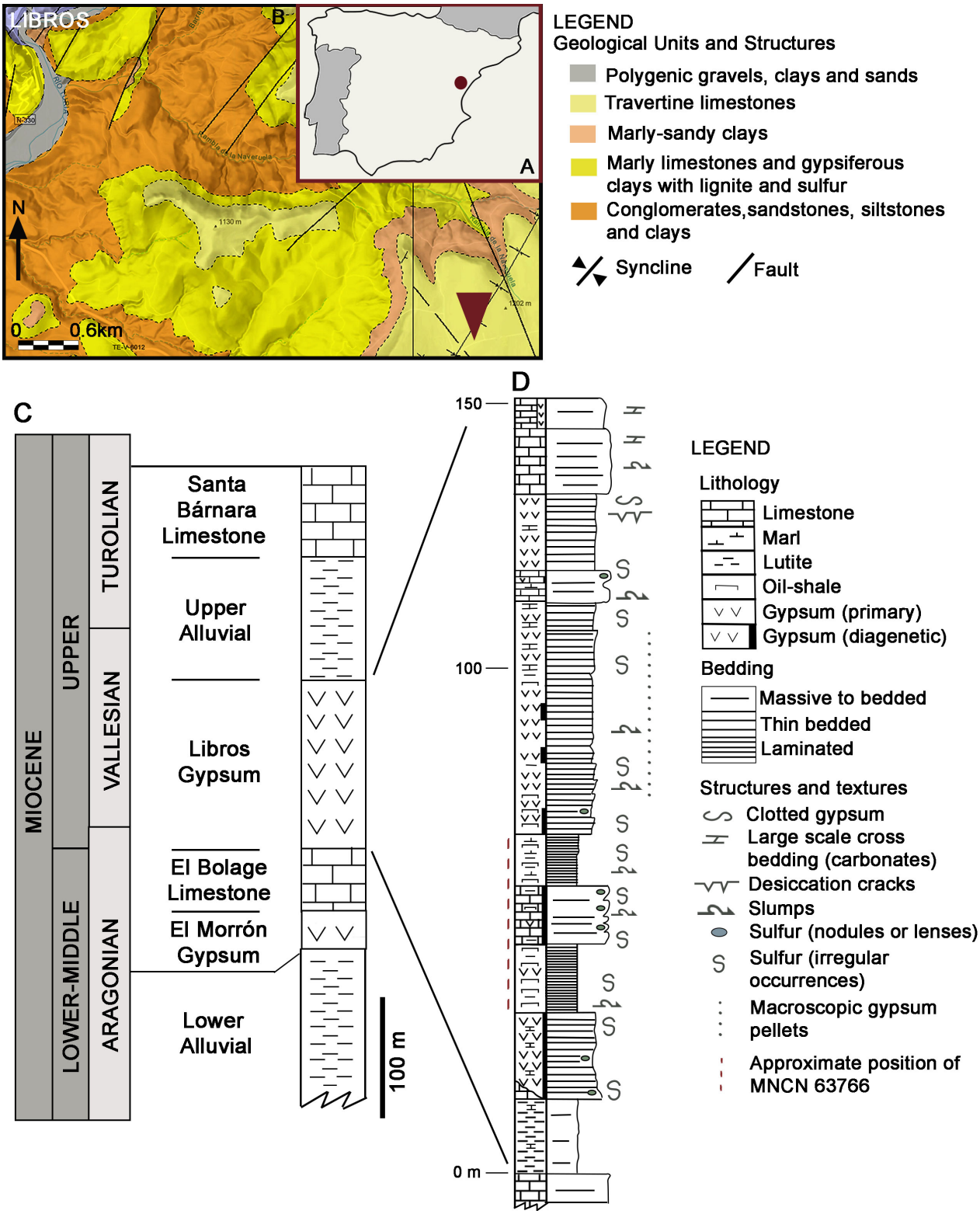

Figure 1. Geographic and geological context of the fossil site of Libros (modified from IGME (1983); Ortí et al. (2010); Blain et al. (2023)). **A** Geographic map of the Iberian Peninsula; **B** Topographic and geological map of the Libros area; **C** General stratigraphic section of Las Minas area; **D** Detailed stratigraphic section of the Libros Gypsum unit with the approximate stratigraphic position of the fossil.

of Triassic evaporites. The unit, referred to as the Libros Gypsum unit, corresponds to the Vindobonian–Pontian sequence (middle–late Tortonian), described in detail in geological studies by the Geological and Mining Institute of Spain (IGME 1983), within which sedimentary structures, such as cross-bedding and synsedimentary palaeochannels, have been documented.

Geological, stratigraphic and palaeontological factors indicate a lacustrine setting that supported the presence of life; however, the exceptional preservation of fossil remains

is primarily related to specific taphonomic conditions, likely involving low-oxygen environments and reduced biological activity. These types of *Konservat-Lagerstätten* lakes are well documented in the fossil record, such as the Eocene German sites of Messel Pit (Smith et al. 2018) and Geiseltal (Falk et al. 2022) or the Pliocene lake of Camp dels Ninots in Spain (Gómez de Soler et al. 2012).

Both stratigraphic sequences are modified from those of Ortí et al. (2010). The red triangle marks the location of the village of Minas de Libros in the map.

Material and methods

The specimen herein described is preserved in a slab of bituminous mudstone, a fragile lithology whose laminations facilitate fracture along these layers (Fig. 2), measuring 41 × 22 cm. The fossil remains are mostly embedded and partially articulated. Although preliminary observations indicate the presence of cranial elements, vertebrae, ribs and osteoderms, their millimetric size and accumulation in a dense mass of poorly distinguishable remains hinder detailed identification through direct examination. This limitation justifies the application of computed tomography techniques.

The fossil slab is housed at the MNCN in Madrid (collection number MNCN 63766). Although the exact origin of this slab is uncertain, it was most likely recovered after mining activities and subsequently circulated amongst mine workers.

The precise stratigraphic position of this specimen, as in the case for most fossils from Libros, remains uncertain due to insufficient documentation and lack of precise georeferencing of the remains. Nevertheless, the palaeontological material has always been considered to belong to the same age range within the fossil site of Libros, based on geological and stratigraphical inferences (McNamara et al. 2010; Cuenca-Bescós 2020; Blain et al. 2023).

It is estimated that it originally came from the deep evaporitic-lacustrine facies of the Libros Unit (Fig. 1), as proposed for the majority of fossil remains from the Libros site (Ortí et al. 2010). The skeletal remains are preserved parallel to the lamination of the bituminous mudstones, as defined by McNamara et al. (2010).

X-ray microtomography

µ-CT scans were carried out in the computed tomography laboratory of the MNCN in Madrid. Due to the extreme fragility of the slab, resulting from its thinness relative to its length, special care was required during handling and scanning. To ensure its integrity and safety throughout the process, the restoration and computed tomography team designed and prepared a suitable support to protect it.

Given the dimensions of the slab, the small size of the fossil remains and the dimensions of the scanning device, three µ-CT scans were performed (Fig. 2A) with the CT-SCAN- XT H-160 NIKON. The maximum energy of these X-ray scanners is about 160 kV offering a maximum resolution of 3 µm.

The three scans were taken from three sections of the fossil slab, each with a maximum length of 12 cm, thus obtaining high resolution (Fig. 2). The three sections are referred to as upper, middle and lower, based on the orientation of the slab as illustrated in Fig. 2.

Digital reconstructions were made with 3D Slicer (Fedorov et al. 2012) (Figs 2, 3). This free and open access software allows the segmentation of the 2D images and the visualisation of the 3D models obtained. The measurements of the different skeletal remains were also obtained with this software. The identified skeletal remains are designated as MNCN 63766-1, MNCN 63766-2 and so forth, in accordance with the nomenclature employed by the collections service of the MNCN. As mentioned earlier, the lack of stratigraphic information for many of the fossils recovered from the Libros site made it impossible to determine their accurate positioning in the lake deposits and they can only be broadly assigned to the bituminous shale facies, based on their lithological context (Fig. 1).

Specimens examined

For the description, taxonomic identification and comparisons, various extinct and extant taxa were examined, all of which were compared with MNCN 63766. The complete list of specimens and their references is provided in the supplementary material (see Suppl. material 1). This list also includes the extant specimens of *Pseudopus apodus*, *Anguis fragilis* and *Ophisaurus ventralis* from the modern herpetological collections of the MNCN in Madrid (Spain) and the Massimo Delfino Herpetological Collection (MDHC) in Torino (Italy) which were consulted for this study. Fejérváry-Lángh (1923), Hoffstetter (1942) and Rauscher (1992) have been reviewed for the identification and comparison of osteoderms.

Finally, due to the partial preservation of the vertebral remains, only a few measurements could be obtained. These measurements were selected, based on their potential utility for the identification of the specimen from Libros site. Specifically, these measurements include the minimum centrum width, the vertebral length and the length-to-width ratio of the trunk vertebrae; full data are available in the supplementary material (see Suppl. material 2).

Data resources

Supplementary data for this manuscript can be found online in the CORA repository: https://doi.

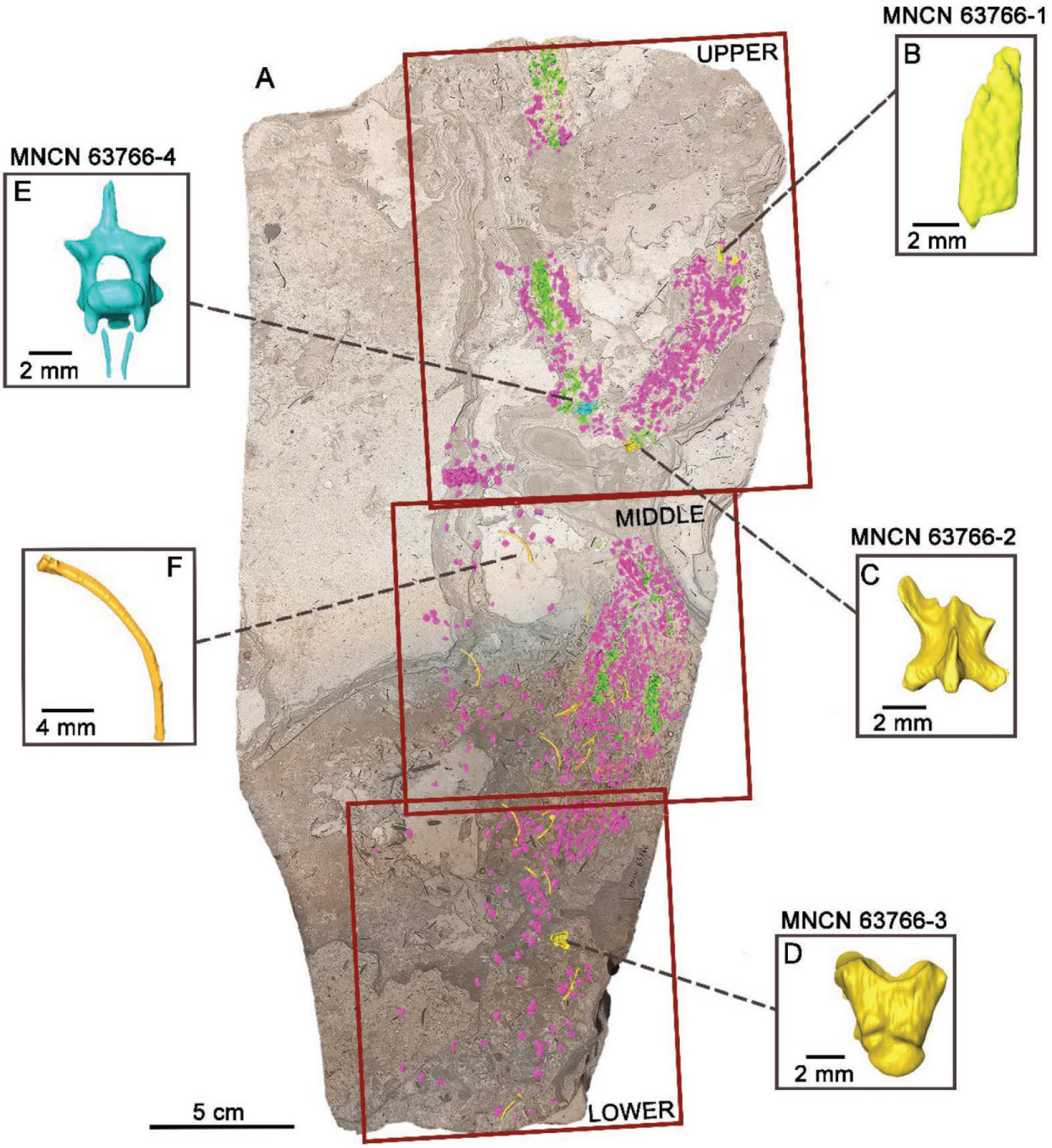

Figure 2. A. Fossil slab MNCN 63766 divided into scanning sections and 3D reconstructions of the specimen. In the fossil slab, skeletal elements are shown in yellow for the nasal bone, in green for the vertebrae, in orange for the ribs and in pink for the osteoderms. The vertebrae that have been described are highlighted in warm yellow for the dorsal vertebrae and in blue for the caudal vertebra. Specifically, the described remains are: **B.** The nasal bone (MNCN 63766-1) in dorsal view; **C.** The dorsal vertebra (MNCN 63766-2) in dorsal view; **D.** The dorsal vertebra (MNCN 63766-3) in ventral view; **E.** The caudal vertebra (MNCN 63766-4) in posterior view; **F.** The rib in posterior view.

org/10.34810/data2830, while all 3D models used in this study are deposited in the Morphosource repository: https://doi.org/10.17602/M2/M797951;https://doi.org/10.17602/M2/M798095; https://doi.org/10.17602/M2/M798101;https://doi.org/10.17602/M2/M798131; https://doi.org/10.17602/M2/M798137;https://doi.org/10.17602/M2/M797973; https://doi.org/10.17602/M2/M795563;https://doi.org/10.17602/M2/M798089; https://doi.org/10.17602/M2/M795578;https://doi.org/10.17602/M2/M795584.

Institutional abbreviations — **IPHES-CERCA**, Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, Spain; **MNCN**, Museo Nacional de Ciencias Naturales, Madrid, Spain.

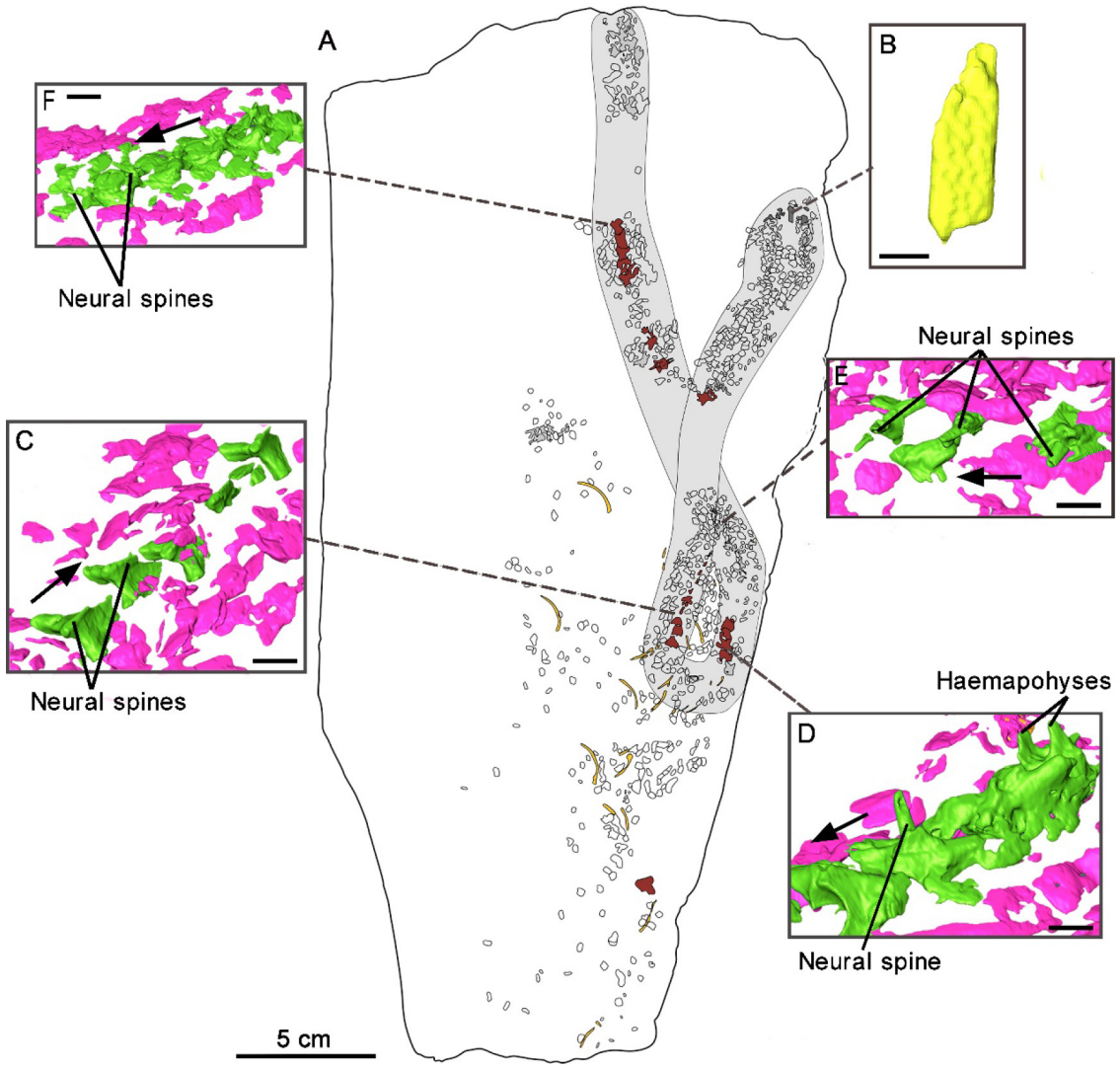

Figure 3. A Reconstruction of the possible death position of the specimen MNCN 63766. In red, the identified vertebral remains, in grey, the remains of unidentified vertebrae, in orange, the ribs, in dark grey, the cranial remains and in white, the osteoderms. 3D reconstructions of the nasal bone (**B**) and dorsal surface of the vertebrae (**C–F**). The arrow points to the anterior part of the specimen. Scale bars: 2 mm.

Results

Systematic Palaeontology

SQUAMATA Oppel, 1811.
ANGUIMORPHA Furbringer, 1900.
ANGUIDAE Gray, 1825.
ANGUINAE Gray, 1825.
Pseudopus Merrem, 1820.
cf. *Pseudopus* sp.

Referred specimen— MNCN 63766, a partial skeleton from the Late Miocene of Libros (Teruel, Spain).

Anatomical description using scanner technologies

The 3D models show a partially articulated skeleton in which only vertebrae and some osteoderms are articulated (Figs 2, 3). Most of the remains are damaged and their distribution results in a mass of bones that, upon naked-eye examination, are difficult to describe and, in most cases, to identify. The abundance of skeletal elements decreases towards the peripheries of the carcass. Micro-CT scans display cranial and postcranial remains embedded in their dorsal or ventral side.

The cranial elements are severely fragmented and impossible to identify, with the exception of an anterior fragment of a nasal bone (Figs 2B, 3C, 4).

The same is true for the postcranial remains. Vertebrae, ribs and osteoderms are identified, but most of them are heavily damaged. Micro-CT scans only show three isolated vertebrae perfectly identifiable. Similarly, fragments of both dorsal and caudal portions of the vertebral column, partially connected, have been observed. The preservation of the neural spine is the only feature that allowed for their identification, but not for a proper description.

Eleven ribs and hundreds of osteoderms have also been identified in the micro-CT scans. The ribs are frequently well preserved. The sculpturing of the osteoderms is barely discernible.

According to the disposition of the bones along the slab, the living specimen would have had a minimum total length of 50 cm. The state of preservation of most of the vertebrae makes it impossible to estimate the maximum length this specimen could have reached. In fact, the difference in snout-vent length (SVL) varies considerably amongst Anguidae species. For example, in *Pseudopus apodus*, SVL ranges from 25 to 40 cm, whereas in *Anguis*, it ranges from 10 to 20 cm (Lambertz et al. 2018).

Nasal — The nasal bone is exposed on its dorsal side. Despite being fractured and not completely preserved, a lateral extension of the sculptured surface beyond the margin of the main body of the bone is observed (Fig. 4A, B).

The anteromedial smooth surface of the bone corresponds to the articular facet for the ascending nasal

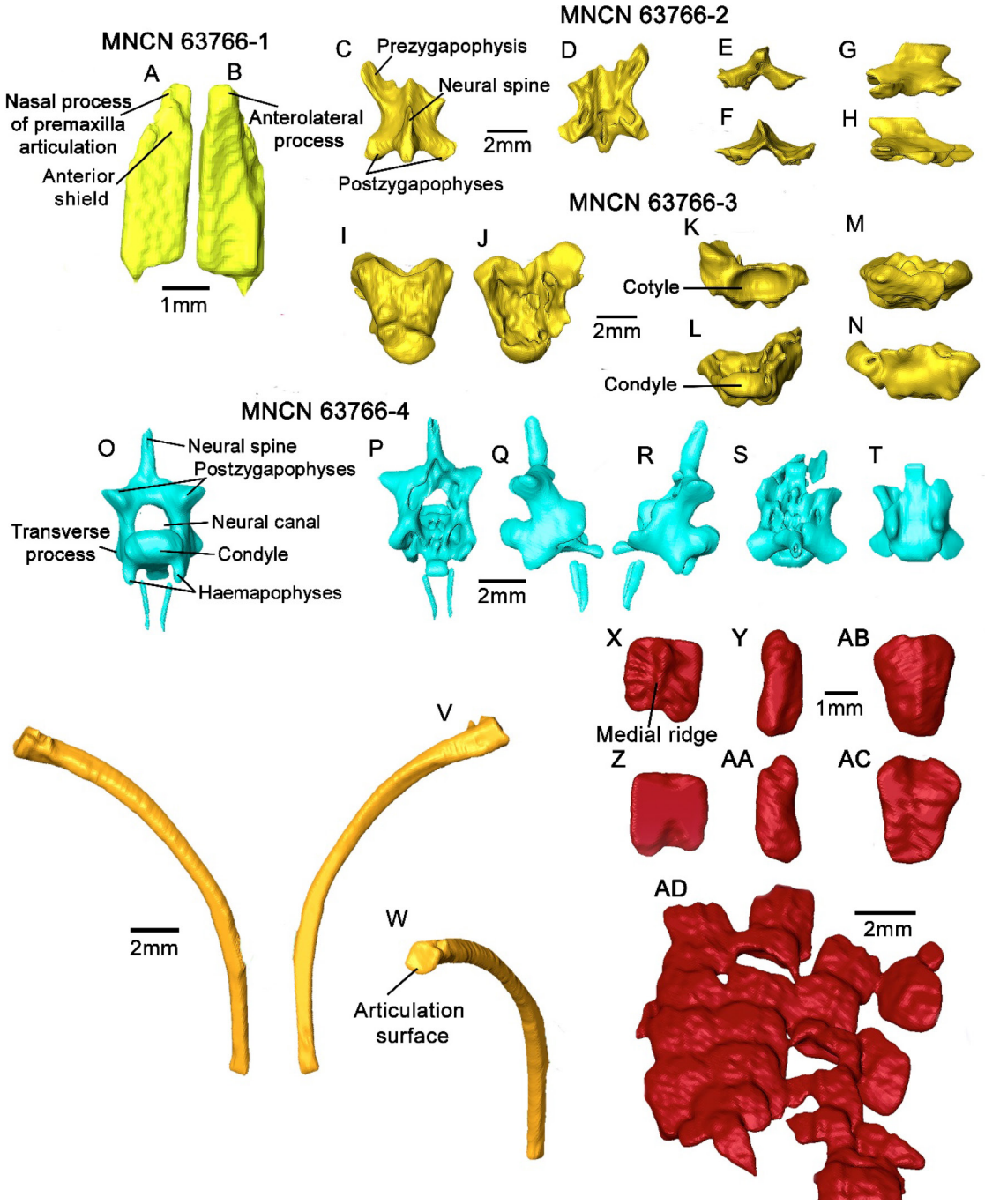

Figure 4. Fossil remains from the specimen MNCN 63766: nasal bone (MNCN 63766-1) in dorsal (**A**) and ventral (**B**) views; dorsal vertebra (MNCN 63766-2) in dorsal (**C**), ventral (**D**), posterior (**E**), anterior (**F**) and lateral (**G, H**) views; dorsal vertebra (MNCN 63766-3) in ventral (**I**), dorsal (**J**), anterior (**K**), posterior (**L**), lateral (**M-N**) views; caudal vertebra (MNCN 63766-4) in posterior (**O**), anterior (**P**), lateral (**Q, R**), dorsal (**S**) and ventral (**T**) views; ribs in posterior (**U**), anterior (**V**) and medial (**W**) views; caudal osteoderms in external (**X, Y**) and internal views (**Z, AA**); medial dorsal osteoderms in external (**AB**) and internal views (**AC**) and articulated osteoderms (**AD**). The osteoderms were coloured red to better highlight the dermal sculpture.

process of the premaxilla and the ventral surface is smooth. In lateral view, it is slightly convex.

Dorsal vertebrae — Fragments of the dorsal vertebrae were found scattered on the slab. The high degree of fragmentation of these remains results in only the dorsal and/or the ventral surfaces of the vertebrae being preserved (Figs 2C, D, 4C–N). Some of them are partially articulated preserving the neural spine (Fig. 3C).

In the upper section of the slab, an isolated vertebra (MNCN 63766-2) is preserved, including the neural spine, the prezygapophyses and the postzygapophyses (Figs 2C, 4C–H). The neural spine is laterally and antero-posteriorly elongated. The pre- and postzygapophyses extend laterally. Another isolated vertebra (MNCN 63766-3) is found in the lower section of the plate preserving the ventral, posterior and anterior surfaces (Figs 2D, 4I–N). In ventral view, the subcentral ridges are straight and broaden towards the anterior part, outlining a triangular morphology. The ventral surface is flat. The cotyle is elliptical in shape and not pronouncedly depressed. The synapophyses expand anterolaterally. Almost the entirety of the condyle is preserved, which makes it possible to identify its dorsoventrally depressed, elliptical shape.

Caudal vertebrae — Fragments of caudal vertebrae are preserved, sometimes articulated (Fig. 3D–F). The vertebrae are highly fragmented, preserving only part of the dorsal surface, which is embedded in hard sediment. In some cases, the neural spine is also preserved (Fig. 3D–F). The neural spine exhibits a widening in its proximal portion, which narrows abruptly towards its end, culminating in a rounded tip.

Only one isolated caudal vertebra (MNCN 63766-4) is better preserved (Figs 2E, 4O–T). The posterior surface is embedded in hard sediments. Fragments located near the ventral surface of the vertebra could hypothetically belong to fragmented pleurapophyses, which are not preserved in connection with the vertebra. In lateral view, the postzygapophyses are expanded more dorsally than posteriorly, almost reaching the posterior margin of the condyle. In dorsal view, they expand more anteroposteriorly than laterally with an angle of almost 40° (from the horizontal plane). The inner margins of the postzygapophyses are slightly curved. The neural spine gradually narrows dorsally and is slightly damaged at its pointed end. Laterally, the posterior surface of the neural spine is straight. In lateral view, there is no constriction at about the mid-length of the neural spine. The condyle is elliptical and not depressed and the neural canal is oval. The haemal arch (haemapophyses) is fractured, but its most proximal part is fused to the vertebra. The haemal spine is not preserved. In ventral view, the subcentral ridges are straight as in the dorsal vertebra (Fig. 4I–N).

According to these traits and based on comparisons with fossils and extant specimens, we identify MNCN 63766-3 as a caudal vertebra.

Ribs — Eleven ribs are preserved (Figs 2F, 4U–W). At the holocephalous head of the rib, the anteroventral and posterodorsal processes are not developed in the well-preserved ribs. There is no evidence of taphonomic phenomena that could have fragmented these processes. The ribs are curved slightly ventrally and narrow distally. The distal end of the rib is preserved in almost all of them.

Osteoderms — Hundreds of osteoderms are preserved in various states of exposure, showing either their external or internal surfaces (Figs 2, 4X–AD). They can be found articulated, associated, but disarticulated or isolated. In the upper section, the osteoderms are exposed in external view and are in anatomical connection. In the intermediate section, they are exposed in either external or internal views and are partially articulated and dispersed towards the most distal part of the specimen. Finally, in the lower section, the osteoderms are entirely dispersed. Osteoderms are flat structures, with a thickness slightly less than 0.5 mm and exhibit a variety of sizes, generally ranging from 2 to 3 mm. The smaller osteoderms are located in the lower section and have a more elongated morphology. In contrast, in the upper section, the osteoderms are larger and display more square and rectangular shapes. The internal surface of the osteoderms is smooth and slightly concave. The external surface has a weakly developed ridge running along its middle part. The exposed surface of the osteoderms, which is usually the external one, does not preserve totally the sculpturing. Due to this, the latter is difficult to reconstruct virtually, but it is possible to identify it in some of the osteoderms. However, amongst those that are preserved articulated, the central ridge is perfectly visible (Fig. 4AD). Following the works of Fejérváry-Lángh (1923), Hoffstetter (1942) and Rauscher (1992), medial dorsal and caudal medial osteoderms could be identified in the upper and middle sections (Figs 2, 3). Ventral osteoderms are present at the periphery of the carcass. Similar to the other osteoderms, the sculpturing cannot be digitised, as it is either not fully preserved or not fully developed (Figs 2, 3).

Taphonomic inferences

Based on the disposition of the articulated vertebrae and the hypothetical location of the skull, we infer the death posture of the specimen (Fig. 3). In the upper scanned section (see Material and Methods and Fig. 2), the presence of articulated dorsal and caudal vertebrae suggests that the dorsal part of the vertebral column could extend downwards and curve upwards to connect with the articulated caudal part. This disposition has previously been documented in sites such as Messel Pit, specifically in specimens of snakes (Smith and Wuttke 2012; McNamara et al. 2016).

The distribution of skeletal elements along the slab provides insight into the post-mortem processes. The preservation is partial and the remains show varying degrees of wear. Only some elements are preserved in good condition, typically on the surfaces that remain embedded in the sediment, whereas exposed surfaces are more affected by degradation. A similar pattern of preservation is documented in other anguid specimens (Čerňanský and Klembara 2017).

The remains are unevenly distributed, showing distinct patterns of articulation and dispersal across the slab. In the upper and middle sections, the specimen preserves partially articulated regions. In these areas, vertebrae remain in anatomical connection and are associated with numerous osteoderms. Despite this, many elements exhibit fractures, particularly affecting the neural spines and haemal arches.

In contrast, the central portion of the slab, corresponding to a coiled region of the body where the vertebral column bends and the caudal portion curves upwards towards the anterior region, shows a markedly different pattern. In this coiled portion, no articulated vertebrae are preserved. Instead, the remains are disarticulated and redistributed.

The lower section of the slab contains a concentration of displaced elements, including ribs, osteoderms and occasional dorsal vertebrae. This pattern suggests post-mortem disruption and limited redistribution within the boundaries of the carcass. This distribution is consistent with the rupture of the abdominal region due to the accumulation of gases, which may have caused an explosion of the visceral cavity. These processes have been simulated in reptiles (Richter and Wuttke 2012) and mammals (Schwermann et al. 2012). This could support the hypothesis that the rupture of the abdominal region due to gas accumulation contributed to the scattering of these elements.

According to the taphonomic experiments of Lev et al. (2020), none of the modifications of the bone surface of squamate vertebrae exposed in aerial conditions (i.e. trampling) can be observed on MNCN 63766. In addition, no modifications due to abrasion or digestion are visible. This type of surface alteration may reflect post-depositional modification, potentially caused by sediment abrasion in an aquatic environment (e.g. fluvial transport), although the precise mechanism remains uncertain.

Discussion

Taxonomic identification of the libros material

Comparative studies with extinct and extant genera have been carried out to identify distinctive traits in vertebrae and osteoderms that facilitate genus identification.

Vertebrae represent the most abundant and readily identifiable elements in the fossil record of lizards. Diagnostic traits, including variations in the morphology and size of the vertebral apophyses and the neural spine, as well as the shape of the centrum and the proportions between the neural canal and the cotyle, are useful for taxonomic classification (see Klembara et al. (2010); Čerňanský et al. (2019)). However, in most cases, they have not been identified at the genus level (Čerňanský et al. 2017b; Vasilyan et al. 2022), as fossil vertebrae are often fragmented (e.g. Čerňanský et al. (2017b); Čerňanský and Klembara (2017)), which complicates taxonomic identification. This is also the case in the specimen from the Libros site, where the remains are fragmented and/or incompletely preserved. Moreover, taxonomic identification, based solely on isolated elements, complicates our understanding of vertebral morphology and the association between cranial and postcranial bones.

In the case of osteoderms, they are not in optimal condition for taxonomic identification, based on morphological aspects. Using 2D images from micro-CT scanners and some 3D models, it is possible to observe their sculpturing for comparison purposes.

CT-scans also show the alignment of the vertebrae in an elongated vertebral column, with a pattern that may resemble the appearance of a snake or an elongated lizard.

Regarding the dorsal vertebrae, in MNCN 63766, the ventral surface of the centrum is flat, a characteristic trait in amphisbaenians, Varanidae, Helodermatidae and Anguidae (Augé 2005). The absence or strong reduction of the neural spine in amphisbaenians permits us to rule out an attribution of this fossil from Libros site to these squamates. The absence of limbs and girdles may suggest that MNCN 63766 belonged to a limbless squamate, although their absence may be due to taphonomic loss. In addition to this trait, the families Helodermatidae and Varanidae can be excluded, based on differences with MNCN 63766, specifically in osteoderm morphology and sculpturing in the case of Helodermatidae and vertebral morphology in the case of Varanidae. The osteoderms of Helodermatidae exhibit shapes ranging from hexagonal to circular and even dome-like, with tuberculated sculpturing (Bhullar and Smith 2008). On the other hand, in *Varanus*, the vertebrae are usually larger and more robust than observed in MNCN 63766, the condyle is more flattened than in our fossil and there is a precondylar constriction in ventral view (e.g. Smith et al. (2008)), which is absent in the Libros squamate. Likewise, the neural spine of the caudal vertebrae is not only longer in *Varanus* than that observed in MNCN 63766, but also in monitor lizards, it becomes narrow towards its dorsal side (Woolley et al. 2025). Although the non-preservation of the limbs could be due to a taphonomic bias, the elongation of the body and the large number of vertebrae are associated with limb loss or reduction, as explained in Wiens and Slingluff (2001); see also Čerňanský and Klembara (2017). On the other hand, the vertebrae of MNCN 63766 are not as robust as those of limbed lizards. Conrad et al. (2012) indicated that regions of the vertebral column supporting the limbs are proportionally more robust. These characters, together with the disposition of osteoderms along the body, suggest a close affinity of the fossil described from Libros site with the family Anguidae.

Comparisons between MNCN 63766 and the American lineages Gerrhonotinae (Scarpetta 2018) and Anniellinae (Bell and Whistler 1996) as well as Diploglossidae (Syromyatnikova and Aranda 2023) show that the cranial and postcranial remains of our specimen are large, in

the context of anguioids. Likewise, the osteoderms of our specimen differ from those of Glyptosaurinae (Augé 2005; Glyptosauridae in an alternative taxonomic scheme; see Čerňanský et al. (2023)), which are irregular and/or hexagonal with a tuberculate sculpturing pattern, as observed in the Eocene anguid, *Placosaurus rugosus*, whose osteoderms are also thick.

Within the subfamily Anguinae, the undetermined material from the Eocene and Miocene (Suppl. material 2) differs from MNCN 63766 in the subcentral ridges of the vertebra, which are less straight, and in having greater length-to-width ratio compared to our specimen.

MNCN 63766 differs from *Anguis* in the following features: 1) the inner margins of the postzygapophyses, in dorsal view, are slightly more curved in the vertebrae of *Anguis* than in those observed in MNCN 63766; 2) in dorsal view, the postzygapophyses expand slightly more posteriorly in the vertebrae of *Anguis* than laterally as in the vertebrae of MNCN 63766; 3) the subcentral ridges of the dorsal vertebra are straight and oblique in MNCN 63766 and parallel in *Anguis* with their anteriormost regions expanded laterally; 4) in dorsal and ventral views, the length-to-width ratio of the dorsal vertebra is higher in *Anguis* than in MNCN 63766, emulating a somewhat elongated shape; and 5) the neural spine of the caudal and sacral vertebrae is wide and short in *Anguis*, in contrast to the narrow and long neural spine observed in MNCN 63766.

MNCN 63766 differs from *Ophisaurus* in the following features: 1) in ventral view, the subcentral ridges of the dorsal vertebra are concave in *Ophisaurus*; 2) the condyle in posterior view and the cotyle in anterior view are small and slightly flatter in the vertebrae of *Ophisaurus*; 3) the neural spine of the caudal and sacral vertebra in *Ophisaurus* is wide and short and/or not as expanded posteriorly in lateral view; 4) in dorsal view, the postzygapophyses of the caudal vertebrae are expanded more posteriorly than laterally in *Ophisaurus*. Similarly, in lateral view, the postzygapophyses are either not expanded dorsally or are slightly expanded; 5) in dorsal view, the length-to-width ratio of the vertebrae is higher in *Ophisaurus* than in MNCN 63766, emulating an elongated shape; 6) in the sacral and caudal vertebrae, the postzygapophyses have different orientations, expanding from laterally (*O. ventralis*) to posteriorly (*O. mimicus*), the latter being similar to MNCN 63766; and 7) the osteoderms of *Ophisaurus* morphotype 1 (Klembara et al. 2019) and that of *Ophisaurus spinari* are larger than our specimen.

Morphological characters of the caudal vertebrae of *O. mimicus* are closer to our specimen, including: 1) the morphology of the condyle and 2) the anteroposterior extension of the postzygapophyses. Nevertheless, the postzygapophyses of the caudal vertebra of *O. mimicus* are not as dorsally expanded in lateral view as in MNCN 63766-4.

Likewise, the North African specimens of *Ophisaurus* (= *Hyalosaurus*) and South Asian specimens (= *Dopasia*) (Gray 1853; Günther 1873) are discarded due to their morphological similarity to *Ophisaurus* and their small size compared with MNCN 63766.

The differences between MNCN 63766 and *Ragesaurus* and *Smithosaurus* are based on the size of the scarce preserved cranial remains, which are larger in MNCN 63766. Comparisons with *Fontisaurus* are largely prevented by the available material of the latter genus, which is currently limited to an articulated cranium with a few associated postcranial bones from north-eastern Iberia and an isolated parietal from Germany (Villa et al. 2025). Ongoing study by some of the authors may suggest that the vertebral morphology of *Fontisaurus* is indeed different from that of *Pseudopus* (and, by extension, that of the Libros anguine; A.V., pers. obs.), but this should be confirmed by additional work. In any case, for the time being, we preliminarily disregard *Fontisaurus* affinities for the Libros specimen, based on the *Pseudopus* features of the dorsal vertebrae (i.e. triangular vertebral centrum in ventral view, with straight lateral margins converging posteriorly).

After discarding all previously mentioned anguid specimens, we propose a list of characters observed in the species of the genus *Pseudopus* (*P. apodus*, *P. pannonicus*, *P. laurillardi*, *P. ahnikoviensis* and *P. confertus*), which are shared with MNCN 63766: 1) in ventral and dorsal views, the length-to-width ratio of the vertebrae is low, emulating a quadrangular shape; 2) in dorsal view, the inner margins of the postzygapophyses are straight in the dorsal, sacral and caudal vertebrae; 3) in dorsal view, the postzygapophyses of the dorsal and caudal vertebrae are expanded more laterally than posteriorly; 4) in lateral view, the neural spine of the dorsal vertebrae is short and wide. In the caudal vertebrae, the spine is narrow and posteriorly extended; 5) the subcentral ridges of the dorsal vertebra are straight; and 6) in posterior view, the morphology of the condyle is elliptical.

However, MNCN 63766 possesses characteristics that distinguish it from *Pseudopus*: 1) the vertebrae of MNCN 63766 are smaller than usual in *Pseudopus*; 2) the neural spine of the dorsal vertebra in MNCN 63766 is slightly more extended posteriorly than dorsally and 3) the neural canal of the caudal vertebra has a pronounced arch shape in MNCN 63766.

In view of all these considerations, we carefully identified MNCN 63766 as cf. *Pseudopus*. In fact, its identification as *Pseudopus*, together with the known body size of the genus (25–40 cm from the snout to the vent; Lambertz et al. (2018)), supports the interpretation that at least the entire trunk and a portion of the tail are preserved. This would be consistent with the finding of only ribs and a greater dispersion of remains in the lower section of the fossil slab, likely resulting from an explosion caused by gas accumulation in the viscera. On the other hand, given that the tail of a glass lizard is longer than its body (even extending to twice its length; Spinner et al. (2015); Kukushkin and Dovgal (2018)), this specimen could be expected to reach approximately one metre in total length.

The overall body proportions, excluding the skull, are consistent with those of an adult or subadult specimen. Moreover, according to Čerňanský et al. (2019), there is an important vertebral feature for identifying a juvenile

Pseudopus; the subcentral ridges of the dorsal vertebrae are slightly concave. This character is not observed in MNCN 63766, supporting its status as an adult.

Lastly, the incomplete development or partial preservation of the osteoderm sculpturing cannot be conclusively associated with the subadult stage of this individual, nor solely attributed to taphonomic processes.

Palaeobiogeography of genus *Pseudopus* during the Miocene and Pliocene

The Miocene–Pliocene fossil record of the genus *Pseudopus* shows a wide distribution across Eurasia. The spatial distribution of occurrences suggests a broad geographic range during the Miocene, particularly in Central Europe and western Asia, where several species (e.g. *P. laurillardi*, *P. pannonicus*, *P. ahnikoviensis*, *P. confertus*) have been documented (Klembara 2015; Čerňanský et al. 2017b; Klembara and Rummel 2018; Đurić 2019; Loréal et al. 2023; see Suppl. material 1 for additional references). This pattern is consistent with previously proposed links between the expansion of *Pseudopus* and warm climatic intervals, such as the Miocene Climatic Optimum (Klembara et al. 2010).

The temporal and geographical distribution of *Pseudopus* occurrences (see Loréal et al. (2025)) further supports this pattern, with a higher number of records during intervals interpreted as relatively warm and climatically stable (Klembara et al. 2010). Although this correlation should be interpreted cautiously, it is consistent with the general sensitivity of ectothermic vertebrates to temperature (Böhme 2003; Böhme and Vasilyan 2014). Following this interval, a reduction in the number of records and a more restricted geographic distribution can be observed, particularly towards the Late Miocene.

Within this framework, the Iberian Peninsula represents the westernmost extent of the genus in Eurasia. Several localities in eastern Spain document the presence of *Pseudopus* during the Miocene (Alba et al. 2006; Marquina et al. 2016, 2025; Casanovas-Vilar et al. 2022) and the specimen from Libros (Teruel) adds to this record. Its position, both geographically and chronologically, is consistent with the persistence of the genus in south-western Europe during the Late Miocene.

The distribution of Iberian occurrences through time suggests that *Pseudopus* remained present in the region even during intervals of increasing aridity towards the end of the Miocene (Jiménez-Moreno et al. 2010, 2013). This may indicate a certain degree of ecological flexibility within the genus, as also suggested by the ecology of the extant *Pseudopus apodus* (Valakos et al. 2008).

During the Pliocene, *Pseudopus pannonicus* is mainly recorded in Central and Eastern Europe (Čerňanský et al. 2017a; Loréal et al. 2025), indicating a more restricted distribution compared to the Miocene. The temporal trend could suggest a decline in the number of occurrences towards the end of this interval, possibly related to long-term climatic changes (Salzmann et al. 2011; Jiménez-Moreno et al. 2013), although this interpretation remains tentative.

Overall, the patterns observed in both the spatial and temporal distribution of *Pseudopus* suggest that its evolutionary history during the Miocene and Pliocene was influenced by large-scale climatic trends. In this context, the Libros specimen provides additional evidence for the presence of the genus in the westernmost part of its Eurasian range during the Late Miocene.

Contribution to the palaeoenvironment of Libros site

To date, the faunistic list and the excellent preservation of the fossil remains offer valuable insights into the palaeoenvironment of the fossil site of Libros. Although detailed palaeoenvironmental reconstruction has not been suggested, several authors have considered different ecological aspects. McNamara et al. (2012) mentioned some environmental factors (e.g. geological, hydrological and sedimentological) that are conducive to the optimal preservation of fossil remains.

Anoxic waters, which inhibit bioturbation, facilitated the exceptional preservation of fossil remains at the lake bottom following death.

The lithological factors and associated geochemical processes are consistent with previous palaeoenvironmental observations (Ortí et al. 2003; Anadón et al. 2004; McNamara et al. 2012; Falk et al. 2022; Martínez-Monzón et al. 2023). The presence of sulphur compounds is consistent with bacterial sulphate reduction processes, typical of anoxic environments (Deng et al. 2018). In addition, the occurrence of lignite indicates the accumulation and preservation of organic matter under oxygen-depleted conditions (Rodríguez Pire 1951; Falk et al. 2022). Collectively, these features are characteristic of lacustrine and wetland systems (Smieja-Król et al. 2015; Lu et al. 2017; Deng et al. 2018). According to IGME (1983), the Vindobonian–Pontian units contain sedimentary structures, such as cross-bedding and synsedimentary palaeochannels, which, in this context, may reflect a local swamp or marsh episode rather than a purely lacustrine environment.

This interpretation is reinforced by the presence of riparian vegetation (e.g. Salicaceae) and taxa associated with lentic or slow-flowing waters, including aquatic birds (*Thiornis sociata*), amphibians (*Pelophylax pueyoi* and *Pelophylax quellembergi*) and semi-aquatic mammals. Beavers, in particular, may have acted as ecosystem engineers, promoting the formation of shallow waterbodies through dam-building activities (Brazier et al. 2021). Such processes increase habitat heterogeneity, enhance organic matter accumulation and support the development of riparian vegetation (Campbell-Palmer et al. 2016; Dalbeck et al. 2020). These conditions are generally favourable for amphibian reproduction and larval development (Bylak et al. 2014; Dalbeck et al. 2014), although they may locally restrict fish populations by altering

hydrological connectivity and oxygen dynamics. In this sense, fish migrations could be impeded during periods of low water flow, as suggested by Lokteff et al. (2013).

Within this framework, the presence of Anguidae not only provides valuable palaeoenvironmental information, but also contributes to refining the previously held preliminary view of the Libros site landscape. Based on the current knowledge of the palaeoecology of Libros, almost all taxa found (i.e. amphibians, semi-aquatic mammals and wading birds) are tied to aquatic environments and, therefore, indicate the presence of a body of water. As for reptiles, this could be also supported by the presence of *Natrix*, if finally confirmed and *Pseudopus*. This anguine lizard is typically associated with open or semi-open habitats, often linked to riparian shrublands rather than densely forested environments (see Valakos et al. (2008); Telenchev et al. (2017); Nasrabadi et al. (2018); Ertem and Çiçek (2025)). Its presence at Libros is, therefore, consistent with the existence of exposed, vegetated margins surrounding the waterbody.

In general terms, the Miocene climate of the Iberian Peninsula was highly dynamic, characterised by long-term cooling and increasing aridification, as well as marked seasonality (Jiménez-Moreno et al. 2010; Steinthorsdottir et al. 2021). These conditions promoted a mosaic of environments ranging from open Mediterranean woodlands to more closed forested areas in humid regions. Within this regional climatic framework, the Libros site fits within a landscape dominated by seasonal climates and heterogeneous vegetation, consistent with the co-existence of riparian habitats, open areas and more wooded zones inferred from the fossil assemblage.

In the case of Libros, the co-occurrence of *Salix* and *Pseudopus* may suggest a more open environment or riparian shrubland rather than a closed forest. Modern beavers are known to preferentially exploit trees with smaller diameters and soft, flexible wood, such as *Salix* (Urban et al. 2008), although the extent to which this preference can be directly extrapolated to fossil taxa remains uncertain. Nevertheless, the proximity of such vegetation to the waterbody would have provided suitable material for dam construction. Comparable environmental settings have been documented in other Lagerstätten, such as Geiseltal or Pula (Kovács et al. 2020; Falk et al. 2022), although the Libros assemblage is notable for the apparent absence of fish.

The higher proportion of semi-aquatic taxa compared to strictly terrestrial ones could reflect either an ecological signal or a taphonomic bias favouring organisms inhabiting areas close to the water. In this context, the presence of *Pseudopus* is particularly relevant, although its ecological interpretation must be treated with caution. Unlike related taxa such as *Ophisaurus*, which are known to enter aquatic environments and use water as a refuge (McConkey 1954; Gans and Gasc 1990), there is no documented data on the swimming abilities of *Pseudopus*. More generally, aquatic locomotion in squamates is highly variable and influenced by factors, such as body size, preventing direct extrapolation of this behaviour (Shine et al. 2003; Fosseries et al. 2024). Consequently, its presence at Libros does not necessarily indicate a strong aquatic affinity and may alternatively reflect post-mortem transport by predators or fluvial processes as has been suggested for mammals in other fossil sites, such as Enspel or Camp dels Ninots (Mähler et al. 2015; Linares-Martín et al. 2025).

On the other hand, it is true that the record of semi-aquatic specimens is higher than that of terrestrial ones, which could be related to a greater preference for the semi-aquatic ecosystem. However, the presence of *Pseudopus* reinforces the idea that there could be a bias in preservation; there would probably be a greater preference for preserving taxa living in the vicinity of the water. This is also considered in the biodiversity studies conducted in Messel (Smith et al. 2025), where there is a substantial difference in the abundance of preserved aquatic and semi-aquatic taxa compared with terrestrial specimens. This can also be extrapolated, given the abundance of aquatic and semi-aquatic specimens found, to the Camp dels Ninots site (Gómez de Soler et al. 2012; Claude et al. 2014; Blain et al. 2024; Přikryl et al. 2025).

Furthermore, the presence of beavers, riparian birds, dragonfly larvae and riparian vegetation, such as *Salix*, indicates a setting that differs from classical deep lacustrine systems, such as Messel and is more consistent with shallow wetland environments or marginal zones within a larger lacustrine system. The occurrence of anguid lizards in other swampy and floodplain environments, such as the fossil localities of Geiseltal and Hambach (Čerňanský and Klembara 2017; Čerňanský et al. 2017a; Falk et al. 2022; Villa et al. 2024), further supports this interpretation. In this framework, the formation and abandonment of beaver-influenced wetlands may have promoted habitat succession towards more open and riparian landscapes (Brazier et al. 2021), potentially creating suitable ecological conditions for taxa, such as *Pseudopus* in shallow or marginal areas of the lake system rather than in its deeper, central zones.

Conclusions

A partial skeleton of an anguine lizard has been described at the Libros fossil site in Teruel. The documentation of this specimen enriches the Miocene fossil record of anguids on the Eurasian continent, which is often represented by isolated remains. The skeletal elements are partially embedded in the sediment. Consequently and for an optimal description and overall visualisation of all these remains, three micro-CT scans have been carried out, focused on different portions of the fossil. Tridimensional reconstructions reveal fragments of cranial and postcranial remains. A nasal bone, dorsal and caudal vertebrae, osteoderms and ribs have been identified. The remains are mostly preserved in a disarticulated and fragmented state resulting in a mass of bones. Some of these remains are also isolated, particularly on the

periphery of the carcass. However, the 2D images show fragmentary articulated portions of the vertebral column, which partially preserve the neural spines. The disposition and orientation of the disarticulated and articulated skeletal elements configure the possible position of death of the specimen from the Libros site.

The partial preservation of the vertebrae, nasal bone and osteoderms has made possible the identification of diagnostic traits for the taxonomic classification of this specimen. Morphological characteristics, such as the orientation of the processes, as well as the projection of the condyle or neural spine observed in the dorsal and caudal vertebrae, have been fundamental to the identification of MNCN 63766 as cf. *Pseudopus*.

The discovery of a specimen of *Pseudopus* in Libros site adds another occurrence of this genus to the list, further becoming one of the westernmost finds recorded across the Eurasian continent.

The fossil record of *Pseudopus* highlights its ecological adaptability and close link to Miocene climatic fluctuations. Its diversification across Eurasia, including the Iberian Peninsula, was favoured by warm periods, while climatic changes influenced its geographic distribution. Eastern Iberian occurrences, including Libros site, indicate adaptation to dry, open habitats, underscoring the role of temperature and ecological preferences in shaping the evolutionary history of the genus.

Overall, the fossil record of *Pseudopus* shows a broad expansion during the Miocene, particularly during warm and stable climatic periods, followed by a progressive geographic contraction towards the Pliocene, probably linked to long-term climatic changes. The findings from the Iberian Peninsula, including the specimen from Libros (Teruel), confirm the persistence of the genus in the westernmost part of Eurasia during the Late Miocene and suggest a certain degree of ecological flexibility in response to increasing aridity.

The presence of *Pseudopus* at Libros site provides important insights into the palaeoenvironment. Its ecological preferences are congruent with the temperature and aridity conditions that characterised the Iberian Peninsula during the Middle to Late Miocene. Taken together with the associated faunal and floral assemblages, these observations suggest that the Libros site was dominated by an open riparian woodland surrounding a temporary waterbody.

The greater abundance of semi-aquatic specimens and species at the Libros site, relative to terrestrial ones, could suggest a preference for this lifestyle in the Late Miocene fauna in the locality and a wide diversity of habitats within the semi-aquatic ecosystem.

Sedimentological features, diverse fauna found at Libros site, riparian vegetation and the semi-aquatic lifestyle preferences of the specimens collectively support a revised interpretation of the landscape as a wetland environment. Furthermore, the presence of *Pseudopus* may serve as evidence of the terrestrial transition from this type of environment to an open, forested landscape.

Acknowledgements

We would like to thank Marta Calvo for allowing us to study comparative material of extant species from the herpetological collection at the MNCN. We are also grateful to Susana Fraile and Cristina Paradela for lending the material, preparing it and performing the CT scans. This research was funded by project GAČR 21-33751S of the Czech Science Foundation and projects PID2021-122533NB-I00 and PID2024-157622NB-I00 from the Spanish Ministry of Science and Innovation (MICINN/AEI/10.13039/501100011033/FEDER ‘Una manera de hacer Europa’). The research of ALM, AV, BGS, HAB and MD is funded by the CERCA Program/Generalitat de Catalunya. TP is supported by the Institute of Geology of the Czech Academy of Sciences (RVO67985831). AV is also funded by the Secretaria d’Universitats i Recerca of the Departament de Recerca i Universitats, Generalitat de Catalunya, through a Beatriu de Pinós postdoctoral grant (2021 BP 00038). ALM, BGS, HAB and TP belong to or are associated with the Consolidated Research Group ‘Palaeoecology of Pliocene and Pleistocene and Human Dispersals (PalHum)’, funded by projects 2021SGR-1238 (AGAUR-Generalitat de Catalunya) and 2023PFR-URV-01238 (URV). AV and MD belong to the Consolidated Research Group “Neogene and Quaternary Vertebrate Paleobiodiversity (NQVP)” (2021 SGR 00620) funded by AGAUR-Generalitat de Catalunya. The IPHES-CERCA has received financial support through the “María de Maeztu” programme for Units of Excellence (CEX2024-01485-M/funded by MICIU/AEI/10.13039/501100011033).

This work is part of the Ph.D. Dissertation of the first author, in the framework of the Ph.D. Programme ‘Quaternari i Prehistòria’ of the Universitat Rovira i Virgili (Tarragona, Spain).

References

Alba DM, Moyà-Solà S, Casanovas-Vilar I, Galindo J, Robles JM, Rotgers C, Furió M, Angelone C, Köhler M, Garcés M, Cabrera L, Almécija S, Obradó P (2006) Vertebrate fossils of the Can Mata dump (Els Hostalets de Pierola, Anoia, Catalonia), a succession of localities of the late Aragonian (MN6 and MN7+8) of the Valles-Penedes river basin. Campaigns 2002–2003, 2004 and 2005. Estudios Geológicos 62(1): 295–312.

Alonso-Zarza AM, Sancho Gómez R, Calvo JP (2002) El terciario continental del sector Alfambra-Villalba Alta, fosa de Teruel. Geogaceta 32: 255–258.

Anadón P, Rosell L, Talbot MR (1992) Carbonate replacement of lacustrine gypsum deposits in two Neogene continental basins, eastern Spain. Sedimentary Geology 78(3–4): 201–216. https://doi.org/10.1016/0037-0738(92)90020-R

Anadón P, Alcalá L, Alonso-Zarza AM, Calvo JP, Ortí F, Rosell L, Sanz-Rubio E (2004) Cuencas de la Cordillera Ibérica. In: Geología de España. Sociedad Geológica de España-IGME, 562–569.

Augé ML (2005) Évolution des lézards du Paléogène en Europe. Mémoires du Muséum National d'Histoire Naturelle 192: 1–365.

Bell CJ, Whistler DP (1996) Fossil remains of the legless lizard, *Anniella* Gray, 1852 from late Pleistocene deposits at Rancho La Brea, California. Bulletin of the Southern California Academy of Sciences 95(2): 99–102.

Bhullar BAS, Smith KT (2008) Helodermatid lizard from the Miocene of Florida, the evolution of the dentary in Helodermatidae, and comments on dentary morphology in Varanoidea. Journal of Herpetoly 42(2): 286–302. https://doi.org/10.1670/07-185.1

Blain HA, Přikryl T, Moreno-Ribas E, Canudo JI (2023) The first discovery of in situ *Pelophylax pueyoi* (Amphibia: Anura) from the Late Miocene of Libros Konservat-Lagerstätte (Teruel, Spain). Journal of Vertebrate Paleontology 42(2): 1–8. https://doi.org/10.1080/02724634.2022.2162410

Blain HA, Přikryl T, Cáceres I, Rodríguez-Salgado P, Martínez-Monzón A, Linares-Martín A, Lozano-Fernández I, Moreno-Ribas E, Grandi F, Oms O, Agustí J, Campeny Vall-Llosera G, Gómez de Soler B (2024) Skeletal taphonomy of the water frogs (Amphibia: Anura) from the Pit 7/8 of the Pliocene Camp dels Ninots site (Caldes de Malavella, NE Spain). Historical Biology 36(9): 1951–1978. https://doi.org/10.1080/08912963.2023.2237998

Böhme M (2003) The Miocene climatic optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeography, Palaeoclimatology Palaeoecology 195(3–4): 389–401. https://doi.org/10.1016/s0031-0182(03)00367-5

Böhme M, Vasilyan D (2014) Ectothermic vertebrates from the late Middle Miocene of Gratkorn (Austria, Styria). Palaeobiodiversity and Palaeoenvironments 94(1): 21–40. https://doi.org/10.1007/s12549-013-0143-7

Brazier RE, Puttock A, Graham HA, Auster RE, Davies KH, Brown CML (2021) Beaver: Nature's ecosystem engineers. Wiley Interdisciplinary Reviews 8(1): 1–29. https://doi.org/10.1002/wat2.1494

Bylak A, Kukuła K, Mitka J (2014) Beaver impact on stream fish life histories: The role of landscape and local attributes. Canadian Journal of Hisheries and Aquatic Sciencies 71(11): 1603–1615. https://doi.org/10.1139/cjfas-2014-0105

Campbell-Palmer R, Gow D, Schwab G, Halley DJ, Gurnell J, Girling S, Lisle S, Campbell R, Dickinson H, Jones S, Parker H, Rosell F (2016) The Eurasian beaver handbook: Ecology and Management of *Castor fiber*. Pelagic Publishing, United Kingdom, 288 pp. https://doi.org/10.2307/jj.28833745

Casanovas-Vilar I, Garcés M, Marcuello Á, Abella J, Madurell-Malapeira J, Jovells-Vaqué S, Cabrera L, Galindo J, Beamud E, Ledo JJ, Queralt P, Martí A, Sanjuan J, Martín-Closas C, Jiménez-Moreno G, Luján A, Villa A, DeMiguel D, Sánchez IM, Robles JM, Furió M, Van de Hoek Ostende LW, Sánchez-Marco A, Sanisidro O, Valenciano A, García-Paredes I, Angelone C, Pons-Monjo G, Azanza B, Delfino M, Bolet A, Grau-Camats M, Vizcaíno-Varo V, Mormeneo D, Kimura Y, Moyà-Solà S, Alba DM (2022) Els Casots (Subirats, Catalonia), a key site for the Miocene vertebrate record of Southwestern Europe. Historical Biology 34(8): 1494–1508. https://doi.org/10.1080/08912963.2022.2043296

Castro E (2002) Las colecciones paleontológicas de la provincia de Teruel en los colegios de La Salle: la aportación del Dr. Rafael Adrover a la paleontología turolense. In G. Meléndez Hevia, E. Peñalver Mollá (Coord.). In: El patrimonio paleontológico de Teruel. Jornadas sobre el Patrimonio de la provincia de Teruel, Paleontología, Rubielos de Mora (Spain), September 1998. Instituto de Estudios Turoliense, 413–428.

Čerňanský A, Klembara J (2017) A skeleton of *Ophisaurus* (Squamata: Anguidae) from the middle Miocene of Germany, with a revision of the partly articulated postcranial material from Slovakia using micro-computed tomography. Journal of Vertebrate Paleontology 37(4): e1333515. https://doi.org/10.1080/02724634.2017.1333515

Čerňanský A, Szyndlar Z, Mörs T (2017a) Fossil squamate faunas from the Neogene of Hambach (northwestern Germany). Palaeobiodiversity and Palaeoenvironments 97(2): 329–354. https://doi.org/10.1007/s12549-016-0252-1

Čerňanský A, Vasilyan D, Georgalis GL, Joniak P, Mayda S, Klembara J (2017b) First record of fossil anguines (Squamata; Anguidae) from the Oligocene and Miocene of Turkey. Swiss Journal of Geosciences 110(3): 741–751. https://doi.org/10.1007/s00015-017-0272-5

Čerňanský A, Yaryhin O, Ciceková J, Werneburg I, Hain M, Klembara J (2019) Vertebral comparative anatomy and morphological differences in anguine lizards with a special reference to *Pseudopus apodus*. Anatomical Record 302(2): 232–257. https://doi.org/10.1002/ar.23944

Claude J, Gómez De Soler B, Campeny G, Agusti J, Oms O (2014) Presence of a chelydrid turtle in the late Pliocene Camp dels Ninots locality (Spain). Bulletin de la Société Géologique de France 185(4): 253–256. https://doi.org/10.2113/gssgfbull.185.4.253

Conrad JL, Balcarcel AM, Mehling CM (2012) Earliest example of a giant monitor lizard (*Varanus*, Varanidae, Squamata). PLoS ONE 7 (8). https://doi.org/10.1371/journal.pone.0041767

Cuenca-Bescós G (2020) El castor europeo. Un fósil viviente. Naturaleza Aragonesa: revista de la Sociedad de Amigos del Museo Paleontológico de la Universidad de Zaragoza (36): 3–6.

Dalbeck L, Janssen J, Luise Völsgen S (2014) Beavers (*Castor fiber*) increase habitat availability, heterogeneity and connectivity for common frogs (*Rana temporaria*). Amphibia-Reptilia 35(3): 321–329. https://doi.org/10.1163/15685381-00002956

Dalbeck L, Hachtel M, Campbell-Palmer R (2020) A review of the influence of beaver *Castor fiber* on amphibian assemblages in the floodplains of European temperate streams and rivers. Journal of Herpetology 30: 135–136. https://doi.org/10.33256/hj30.3.135146

Deng Q, Wu X, Wang Y, Liu M (2018) Activity characteristics of sulfate reducing bacteria and formation mechanism of hydrogen sulfide. Applied Ecology & Environmental Research 16(5): 6369–6383. https://doi.org/10.15666/aeer/1605_63696383

Đurić DD (2019) Neogena i kvartarna herpetofauna (Anura i Squamata) Srbije PhD Thesis, University of Belgrade, Serbia.

Ertem M, Çiçek K (2025) Habitat preferences and population estimates of the European glass lizard *Pseudopus apodus* (Pallas, 1775) in the Gediz Delta, Western Anatolia. Biodiversity, 1–9. https://doi.org/10.1080/14888386.2025.2569897

Falk D, Wings O, McNamara ME (2022) The skeletal taphonomy of anurans from the Eocene Geiseltal Konservat-Lagerstätte, Germany: insights into the controls on fossil anuran preservation. Papers in Palaeontology 8(4): 1–34. https://doi.org/10.1002/spp2.1453

Fedorov A, Beichel R, Kalpathy-Cramer J, Finet J, Fillion-Robin J-C, Pujol S, Bauer C, Jennings D, Fennessy FM, Sonka M, Buatti J, Aylward SR, Miller JV, Pieper S, Kikinis R (2012) 3D Slicer as an Image Computing Platform for the Quantitative Imaging Network. Magnetic Resonance Imaging 30(9): 1323–1341. https://doi.org/10.1016/j.mri.2012.05.001

Fejérváry-Lángh AM (1923) Beiträge zu einer Monographie der fossilen Ophisaurier. Palaeontologia Hungarica 1: 123–20.

Fernández-Marrón TM (1972) Nota sobre la paleoecologia del yacimiento de Libros (Teruel) en relation con los artropodas y las plantas fossiles del biotopo. Acta Geologica Hispanica 7(5): 149–153.

Fosseries G, Herrel A, Godoy-Diana R, Gaucher P, Traimond M, Joris A, Daoues K, Gouygou A, Chateau O, Gossuin H, Banzept P, Banzept C, Lefebvre D, Bonnet X (2024) Can all snakes swim? A review of the evidence and testing species across phylogeny and morphological diversity. Zoology 167: 126223. https://doi.org/10.1016/j.zool.2024.126223

Gans C, Gasc JP (1990) Tests on the locomotion of the elongate and limbless reptile *Ophisaurus apodus* (Sauna: Anguidae). Journal of Zoology 220(4): 517–536. https://doi.org/10.1111/j.1469-7998.1990.tb04731.x

Garcés M, Krijgsman W, Van Dam J, Calvo JP, Alcalá L, Alonso-Zarza AM (1997) Late Miocene alluvial sediments from the Teruel area: Magnetostratigraphy, magnetic susceptibility, and facies organization. Acta Geologica Hispanica 32(3–4): 171–184. https://doi.org/10.1016/0012-821x(95)00206-r

Günther A (1873) Description of a new saurian (*Hyalosaurus*) allied to *Pseudopus*. Journal of Natural History 11(65): 351–351. https://doi.org/10.1080/00222937308696828

Gómez de Soler B, Campeny Vall-Llosera G, van der Made J, Oms O, Agustí J, Sala R, Blain HA, Burjachs F, Claude J, García Catalán S, Riba D, Rosillo R (2012) A new key locality for the Pliocene vertebrate record of Europe: The Camp dels Ninots maar (NE Spain). Geologica Acta: an International Earth Science Journal 10(1): 1–17. https://doi.org/10.1344/105.000001702

Gray JE (1853) Descriptions of some undescribed species of reptiles collected by Dr. Joseph Hooker in the Khassia Mountains, East Bengal, and Sikkim Himalaya. Annals and Magazine of natural History 12(72): 386–392. https://doi.org/10.1080/03745485709495063

Hoffstetter R (1942) Sur les restes de Sauria du Nummulitique Européen rapportés à la famille des Iguanidae. Bulletin du Muséum National d'Histoire Naturelle 14: 233–240.

IGME [Instituto Geológico y Minero de España] (1983) Geological map of Spain, scale 1:50,000. Sheet no. 612 (Ademuz) and explanatory notes.

Jiménez-Moreno G, Suc JP, Fauquette S (2010) Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Review of Palaeobotany and Palynology 162: 403–415. https://doi.org/10.1016/j.revpalbo.2009.08.001

Jiménez-Moreno G, Burjachs F, Expósito I, Oms O, Carrancho Á, Villalaín JJ, Agustí J, Campeny G, Gómez de Soler B, van der Made J (2013) Late Pliocene vegetation and orbital-scale climate changes from the western Mediterranean area. Global and Planetary change 108: 15–28. https://doi.org/10.1016/j.gloplacha.2013.05.012

Klembara J (2012) A new species of *Pseudopus* (Squamata, Anguidae) from the early Miocene of Northwest Bohemia (Czech Republic). Journal of Vertebrate Paleontology 32(4): 854–866. https://doi.org/10.1080/02724634.2012.670177

Klembara J (2015) New finds of anguines (Squamata, Anguidae) from the Early Miocene of Northwest Bohemia (Czech Republic). Paläontologische Zeitschrift 89(2): 171–195. https://doi.org/10.1007/s12542-014-0226-4

Klembara J, Rummel M (2018) New material of *Ophisaurus*, *Anguis* and *Pseudopus* (Squamata, Anguidae, Anguinae) from the Miocene of the Czech Republic and Germany and systematic revision and palaeobiogeography of the Cenozoic Anguinae. Geological Magazine 155(1): 20–44. https://doi.org/10.1017/S0016756816000753

Klembara J, Böhme M, Rummel M (2010) Revision of the anguine lizard *Pseudopus laurillardi* (Squamata, Anguidae) from the Miocene of Europe, with comments on paleoecology. Journal of Paleontology 84(2): 159–196. https://doi.org/10.1666/09-033r1.1

Klembara J, Hain M, Dobiašová K (2014) Comparative anatomy of the lower jaw and dentition of *Pseudopus apodus* and the interrelationships of species of subfamily Anguinae (Anguimorpha, Anguidae). Anatomical Record 297(3): 516–544. https://doi.org/10.1002/ar.22854

Klembara J, Hain M, Čerňanský A (2019) The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm–Westtangente in Germany. Historical Biology 31(8): 1016–1027. https://doi.org/10.1080/08912963.2017.1416469

Kovács J, Németh K, Szabó P, Kocsis L, Kereszturi G, Újvári G, Vennemann T (2020) Volcanism and paleoenvironment of the pula maar complex: A pliocene terrestrial fossil site in Central Europe (Hungary). Palaeogeography, Palaeoclimatology, Palaeoecology 537: 109398. https://doi.org/10.1016/j.palaeo.2019.109398

Kukushkin OV, Dovgal IV (2018) Sexual dimorphism in *Pseudopus apodus* (Reptilia: Sauria: Anguidae) from the Steppe Crimea. Ecologica Montenegrina 19: 1–21. https://doi.org/10.37828/em.2018.19.1

Lambertz M, Arenz N, Grommes K (2018) Variability in pulmonary reduction and asymmetry in a serpentiform lizard: The sheltopusik, *Pseudopus apodus* (Pallas, 1775). Vertebrate Zoology 68(1): 21–26. https://doi.org/10.3897/vz.68.e32216

Lev M, Weinstein-Evron M, Yeshurun R (2020) Squamate bone taphonomy: A new experimental framework and its application to the Natufian zooarchaeological record. Scientific Reports 10(1): 9373. https://doi.org/10.1038/s41598-020-66301-5

Linares-Martín A, Furió M, Gómez de Soler B, Agustí J, Oms O, Grandi F, Blain HA, Moreno-Ribas E, Piñero P, Campeny G (2025) An unexpected Scalopini mole (Talpidae, Mammalia) from the Pliocene of Europe sheds light on the phylogeny of talpids. Scientific Reports 15(1): 1–17. https://doi.org/10.1038/s41598-025-10396-1

Lokteff RL, Roper BB, Wheaton JM (2013) Do beaver dams impede the movement of trout? Transactions of the American Fisheries Society 142(4): 1114–1125. https://doi.org/10.1080/00028487.2013.797497

Loréal E, Syromyatnikova EV, Danilov IG, Čerňanský A (2023) The easternmost record of the largest anguine lizard that has ever lived – *Pseudopus pannonicus* (Squamata, Anguidae): new fossils from the late Neogene of Eastern Europe. Fossil Record 26(1): 51–84. https://doi.org/10.3897/fr.26.100059

Loréal E, Georgalis GL, Čerňanský A (2025) *Pseudopus pannonicus* (Squamata), the largest known anguid lizard—Redescription of the type material and new specimens from the Neogene and Quaternary of Hungary and Poland. The Anatomical Reccord 308(1): 45–113. https://doi.org/10.1002/ar.25525

Lu J, Shao L, Yang M, Zhou K, Wheeley JR, Wang H, Hilton J (2017) Depositional model for peat swamp and coal facies evolution using sedimentology, coal macerals, geochemistry and sequence stratigraphy. Journal of Earth Science 28(6): 1163–1177. https://doi.org/10.1007/s12583-016-0942-7

Luque L, Alcalá L (2002) Valoración patrimonial del yacimiento paleontológico de Libros (Teruel, Spain). El patrimonio paleontológico de Teruel 243.

Mähler B, Schwermann AH, Wuttke M, Schultz JA, Martin T (2015) Four-dimensional virtopsy and the taphonomy of a mole from the Oligocene of Lake Enspel (Germany). Palaeobiodiversity and Palaeoenvironments 95(1): 115–131. https://doi.org/10.1007/s12549-014-0180-x

Marquina-Blasco R, Crespo VD, Mansino S, Fagoaga A, Ruiz-Sánchez F, Bailon S, Montoya P (2016) Amphibians and squamates from Late Miocene (MN 13) of Venta del Moro, Spain. In: 1st IMERP/XIV EJIP, Marin-Monfort & Manzanares Ubeda (coord), 107.

Marquina-Blasco R, Morales-Flores D, Bartolomé-Bombín ÁD, Montoya P (2025) Herpetofaunal remains (Anura, Crocodylia, Testudines, Squamata) from the Late Miocene of the Crevillente Area (SE Spain): Palaeobiogeographical and palaeoecological implications. Rivista Italiana di Paleontologia e Stratigrafia 131(1): 85–115.

Martínez-Monzón A, Přikryl T, Sánchez-Bandera C, Bisbal-Chinesta JF, Agustí J, Vall-Llosera GC, Gómez de Soler B, Blain HA (2023) Inferring eco-climate parameters for the Pliocene Climate Optimum using frog body size as a new proxy. Lethaia 56(2): 1–12. https://doi.org/10.18261/let.56.2.8

McConkey EH (1954) A systematic study of the North American lizards of the genus *Ophisaurus*. American Midland Naturalist 51(1): 133–171. https://doi.org/10.2307/2422217

McNamara ME, Orr PJ, Kearns SL, Alcalá L, Anadón P, Peñalver-Mollá E (2010) Exceptionally preserved tadpoles from the Miocene of Libros, Spain: Ecomorphological reconstruction and the impact of ontogeny upon taphonomy. Lethaia 43(3): 290–306. https://doi.org/10.1111/j.1502-3931.2009.00192.x

McNamara ME, Orr PJ, Alcalá L, Anadón P, Peñalver E (2012) What controls the taphonomy of exceptionally preserved taxa–environment or biology? A case study using frogs from the Miocene Libros Konservat- Lagerstätte (Teruel, Spain). Palaios 27(2): 63–77. https://doi.org/10.2110/palo.2010.p10-126r

McNamara ME, Orr PJ, Kearns SL, Alcala L, Anadon P, Penalver E (2016) Reconstructing carotenoid-based and structural coloration in fossil skin. Current Biology 26(8): 1075–1082. https://doi.org/10.1016/j.cub.2016.02.038

Nasrabadi R, Rastegar-Pouyani N, Rastegar-Pouyani E, Kami HG, Gharzi A, Yousefkhani SS (2018) Distribution and environmental suitability of the european glass lizard *Pseudopus apodus* (pallas, 1775) in the iranian plateau. Russian Journal of Herpetology 25(1): 6–10. https://doi.org/10.30906/1026-2296-2019-25-1-6-10

Navás L (1920) Fósiles del Oligoceno de Libros (Teruel). Ibérica 326: 282–283.

Navás L (1922) Algunos fósiles de Libros (Teruel). Boletin del Sociedad Ibérica de Ciencias Naturales 21: 52–61.

Olson SL (1995) *Thiornis sociata* Navás, a nearly complete Miocene Grebe (Aves: Podicipedidae). Courier Forschungsinstitut Senckenberg 181: 131–140.

Ortí F, Rosell L, Anadón P (2003) Deep to shallow lacustrine evaporites in the Libros Gypsum (southern Teruel Basin, Miocene, NE Spain): an occurrence of pelletal gypsum rhythmites. Sedimentology 50: 361–386. https://doi.org/10.1046/j.1365-3091.2003.00558.x

Ortí F, Rosell L, Anadón P (2010) Diagenetic gypsum related to sulfur deposits in evaporites (Libros Gypsum, Miocene, NE Spain). Sedimentary Geology 228: 304–318. https://doi.org/10.1016/j.sedgeo.2010.05.005

Peñalver E (1996) Los Yacimientos Con Insectos Fosiles de Aragón (España). PaleoEntomología 16: 139–146. https://doi.org/10.7203/sjp.23796

Přikryl T, Blain HA, Oms O, Rodríguez-Salgado P, Moreno-Ribas E, Agustí J, Campeny G, Gómez de Soler B (2025) Early Pliocene barb (Teleostei, Cyprinidae, Barbinae) from the Camp dels Ninots site (Spain). Rivista Italiana di Palaeontologia e Stratigrafia 131(2): 261–280. https://doi.org/10.54103/2039-4942/26982

Rauscher KL (1992) Die Echsen (Lacertilia, Reptilia) aus dem Plio-Pleistozan von Bad Deutsch-Altenburg Niederosterreich. Beiträge zur paläontologie von Österreich 17: 81–177.

Richter A, Wuttke M (2012) Analysing the taphonomy of Mesozoic lizard aggregates from Uña (eastern Spain) by X-ray controlled decay experiments. Palaeobiodiversity and Palaeoenvironments 92(1): 5–28. https://doi.org/10.1007/s12549-011-0065-1

Roček Z (2019) A contribution to the herpetofauna from the late Miocene of Gritsev (Ukraine). Comptes Rendus Palevol 18: 817–847. https://doi.org/10.1016/j.crpv.2019.07.003

Rodríguez Pire L (1951) Origen y formación del carbón. Revista de Ciencias de la Universidad de Oviedo 12(1): 45–68.

Román F (1926) Sur la découverte d'une faune de Mammifères de l'étage Pontien à Libros (Province de Teruel). Comptes Rendus de l'Académie des Sciences 182: 1234–1235.

Román F (1927) Sur quelques restes de Mammifères découverts par le R.P. Longinos Navás dans les argiles pontiques de Libros (Teruel). Bulletin de la Société Géologique de France 27: 379–385.

Salzmann U, Williams M, Haywood AM, Johnson ALA, Kender S, Zalasiewicz J (2011) Climate and environment of a Pliocene warm world. Palaeogeography, Palaeoclimatology, Palaeoecology 309(1–2): 1–8. https://doi.org/10.1016/j.palaeo.2011.05.044

Sanchíz Gil de Avalle F (1977) Nuevos anfibios del Neógeno y Cuaternario de Europa. Origen, desarrollo y relaciones de la batrachofauna española PhD Thesis, Universidad Complutense de Madrid, Madrid, Spain.

Scarpetta S (2018) The earliest known occurrence of *Elgaria* (Squamata: Anguidae) and a minimum age for crown Gerrhonotinae: Fossils from the Split Rock Formation, Wyoming, USA. Palaeontologia Electronica, 1–8. https://doi.org/10.26879/837

Schwermann AH, Wuttke M, Schultz JA (2012) Virtopsy of the controlled decomposition of a dormouse *Eliomys quercinus* as a tool to analyse the taphonomy of *Heterohyus nanus* from Messel (Eocene, Germany). Palaeobiology and Palaeoenvironment 92(1): 29–43. https://doi.org/10.1007/s12549-011-0063-3

Shine R, Cogger HG, Reed RR, Shetty S, Bonnet X (2003) Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae). Journal of Zoology 259(3): 261–268. https://doi.org/10.1017/S0952836902003242

Smieja-Król B, Janeczek J, Bauerek A, Thorseth IH (2015) The role of authigenic sulfides in immobilization of potentially toxic metals in the Bagno Bory wetland, southern Poland. Environmental Science and Pollution Research 22(20): 15495–15505. https://doi.org/10.1007/s11356-015-4728-8

Smith KT, Bhullar BAS, Holroyd PA (2008) Earliest African record of the *Varanus* stem-clade (Squamata: Varanidae) from the early Oligocene of Egypt. Journal of Vertebrate Paleontology 28(3): 909–913. https://doi.org/10.1671/0272-4634(2008)28[909:earotv]2.0.co;2

Smith KT, Wuttke M (2012) From tree to shining sea: taphonomy of the arboreal lizard *Geiseltaliellus maarius* from Messel, Germany. Palaeobiology and Palaeoenvironment 92: 45–65. https://doi.org/10.1007/s12549-011-0064-2

Smith KT, Schaal SFK, Haberstzer J (2018) Messel: An ancient greenhouse ecosystem. Senckenberg, Frankfurt am Main, Germany, 355 pp.

Smith KT, Collinson M, Folie A, Habersetzer J, Hennicke F, Kothe E, Lehmann T, Lenz OK, Mayr G, Micklich N, Rabenstein R, Racicot R, Schaal SFK, Smith T, Tosal A, Uhl D, Wappler T, Wedmann S, Wuttke M (2025) The biodiversity of the Eocene Messel Pit. Palaeobioology and Palaeoenvironment 104(4): 859–940. https://doi.org/10.1007/s12549-024-00633-2

Spinner M, Bleckmann H, Westhoff G (2015) Morphology and frictional properties of scales of *Pseudopus apodus* (Anguidae, Reptilia). Zoology 118(3): 171–175. https://doi.org/10.1016/j.zool.2014.11.002

Steinthorsdottir M, Coxall HK, De Boer AM, Huber M, Barbolini N, Bradshaw CD, Burls NJ, Feakings E, Gasson E, Henderiks J, Holbourn AE, Kiel S, Kohn MJ, Knorr G, Kürschner WM, Lear CH, Liebrand D, Lunt DJ, Mörs T, Pearson PN, Pound MJ, Stoll H, Strömberg CAE (2021) The Miocene: The future of the past. Paleoceanography and Paleoclimatology 36(4): e2020PA004037. https://doi.org/10.1029/2020pa004037

Syromyatnikova E, Aranda E (2023) A record of galliwasp (Diploglossidae: *Diploglossus*) from the Pleistocene of Cuba. Historical Biology 35(7): 1069–1073. https://doi.org/10.1080/08912963.2022.2077108

Szyndlar Z, Alférez F (2005) Iberian snake fauna of the early/middle Miocene transition. Revista Española de Herpetología 19: 57–70.

Telenchev I, Simeonovska-Nikolova D, Tzonev R (2017) Habitat use and activity of european glass lizard, *Pseudopus apodus* (Pallas, 1775), in southeastern Bulgaria. Turkish Journal of Zoology 41(2): 286–293. https://doi.org/10.3906/zoo-1601-3

Urban J, Suchomel J, Dvořák J (2008) Contribution to the knowledge of woods preferences of European beaver (*Castor fiber* L. 1758) in bank vegetation on non-forest land in the forest district Soutok (Czech Republic). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 56(4): 289–294.

Valakos ED, Pafilis P, Sotiropulos K, Lymberakis P, Maragou P, Foufopulos J (2008) The amphibians and reptiles of Greece. Frankfurt Contribution to Natural History Vol. 32. Edition Chimaira, Frankfurt am Main, 463 pp.

Vasilyan D, Böhme M, Klembara J (2016) First record of fossil *Ophisaurus* (Anguimorpha, Anguidae) from Asia. Journal of Vertebrate Paleontology 36(6): 52–54. https://doi.org/10.1080/02724634.2016.1219739

Vasilyan D, Čerňanský A, Szyndlar Z, Mörs T (2022) Amphibian and reptilian fauna from the early Miocene of Echzell, Germany. Fossil Record 25(1): 99–145. https://doi.org/10.3897/fr.25.83781

Villa A, Delfino M (2019) Fossil lizards and worm lizards (Reptilia, Squamata) from the Neogene and Quaternary of Europe: an overview. Swiss Journal of Palaeontology 138(2): 177–211. https://doi.org/10.1007/s13358-018-0172-y

Villa A, Carnevale G, Pavia M, Rook L, Sami M, Szyndlar Z, Delfino M (2021a) An overview of the late Miocene vertebrates from the fissure fillings of Monticino Quarry (Brisighella, Italy), with new data on non-mammalian taxa. Rivista Italiana di Paleontologia e Stratigrafia 2: 297–354.

Villa A, Minnelli E, Bona F, Bellucci L, Sardella R, Delfino M (2021b) The amphibians and reptiles from the Early Pleistocene of Coste San Giacomo (Anagni Basin, Italy). Historical Biology 33(11): 3075–3083. https://doi.org/10.1080/08912963.2020.1849177

Villa A, Quadros AB, Delfino M, Luján ÀH, Bolet A, Casanovas-Vilar I, Robles JM, Alba DM (2024) The rise and fall of the Iberian cobras (Elapidae, *Naja*) in the context of their European and global fossil record. Papers in Palaeontology 10(4): e1575. https://doi.org/10.1002/spp2.1575

Villa A, Bolet A, Klembara J, Serrano-Martínez A, Luján ÀH, Fortuny J, Massimo D, Burkhard S, Alba DM (2025) A new anguine lizard (Squamata, Anguidae, Anguinae) from the Late Miocene (Vallesian) of the Vallès-Penedès Basin (NE Iberian Peninsula). Swiss Journal of Palaeontology 144(1): 1–29. https://doi.org/10.1186/s13358-025-00411-3

Wiens JJ, Slingluff JL (2001) How lizards turn into snakes: A phylogenetic analysis of body-form evolution in anguid lizards. Evolution 55(11): 2303–2318. https://doi.org/10.1111/j.0014-3820.2001.tb00744.x

Woolley CH, Sertich JJ, Melstrom KM, Irmis RB, Smith ND (2025) New monstersaur specimens from the Kaiparowits Formation of Utah reveal unexpected richness of large-bodied lizards in Late Cretaceous North America. Royal Society Open Science 12(6): 250435. https://doi.org/10.1098/rsos.250435

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

This work was supported by GAČR 21-33751S / Czech Science Foundation RVO67985831 / Geology of the Czech Academy of Sciences PID2021-122533NB-I00 / Spanish Ministry of Science and Innovation (MICINN/AEI/10.13039/501100011033/FEDER 'Una manera de hacer Europa') PID2024-157622NB-I00 / Spanish Ministry of Science and Innovation (MICINN/AEI/10.13039/501100011033/FEDER 'Una manera de hacer Europa') CERCA Program/Generalitat de Catalunya. Beatriu de Pinós postdoctoral grant (2021 BP 00038)/ Secretaria d'Universitats i Recerca of the Departament de Recerca i Universitats, Generalitat de Catalunya Paleoecology of Pliocene and Pleistocene and Human Dispersals (PalHum) research group funded by projects 2021SGR-1238 (AGAUR-Generalitat de Catalunya) and 2023PFR-URV-01238 (URV). Consolidated Research Group "Neogene and Quaternary Vertebrate Paleobiodiversity (NQVP)" (2021 SGR 00620) funded by AGAUR-Generalitat de Catalunya. "María de Maeztu" program for Units of Excellence (CEX2024-01485-M/funded by MICIU/AEI/10.13039/501100011033).

Author contributions

Adriana Linares-Martín: Conceptualization, Data Curation, Formal Analyses, Investigation, Methodology, Software, Writing - original draft. Tomáš Přikryl: Validation, Writing - review and editing. Andrea Villa: Investigation, Validation, Writing - review and editing. Massimo Delfino: Investigation, Validation, Writing - review and editing. Bruno Gómez de Soler: Funding acquisition, Resources, Supervision, Validation, Writing - review and editing. Hugues-Alexandre Blain: Conceptualization, Funding acquisition, Investigation, Resources, Supervision, Validation, Writing - review and editing.

Author ORCIDs

A. Linares-Martín https://orcid.org/0000-0002-1907-7521
A. Villa https://orcid.org/0000-0001-6544-5201
M. Delfino https://orcid.org/0000-0001-7836-7265
B. Gómez De Soler https://orcid.org/0000-0002-2539-3811
H.-A. Blain https://orcid.org/0000-0002-9920-2707

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Supplementary taxa

Authors: Adriana Linares-Martín, Tomáš Přikryl, Andrea Villa, Massimo Delfino, Bruno Gómez De Soler, Hugues-Alexandre Blain
Data type: docx
Explanation note: List of taxa used for comparison with specimen MNCN 63766 from the Libros fossil site to determine its taxonomic identification as cf. *Pseudopus* sp.

Link: https://doi.org/10.3897/fr.29.183059.suppl1

Supplementary material 2

Supplementary measurements

Authors: Adriana Linares-Martín, Tomáš Přikryl, Andrea Villa, Massimo Delfino, Bruno Gómez De Soler, Hugues-Alexandre Blain
Data type: docx
Explanation note: Measurements of the minimum width, length, and length-to-width ratio of trunk vertebrae in extinct and extant Anguidae specimens. Minimum width was defined as the minimum width of the centrum, and length was measured from the posterior margin of the condyle to the anterior margin of the cotyle in ventral view. The length-to-width ratio was calculated by dividing the vertebral length by the minimum centrum width.

Link: https://doi.org/10.3897/fr.29.183059.suppl2