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Author-formatted, not peer-reviewed document posted on 25/02/2026

DOI: <https://doi.org/10.3897/arphapreprints.e189735>

Early Miocene herpetofauna from the Ribesalbes-Alcora basin (Castelló, eastern Spain): a first step toward modern herpetofaunas in the Iberian Peninsula

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EARLY MIOCENE HERPETOFAUNA FROM THE RIBESALBES-ALCORA BASIN (CASTELLÓ, EASTERN SPAIN): A FIRST STEP TOWARD MODERN HERPETOFAUNAS IN THE IBERIAN PENINSULA

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ABSTRACT

The Early Miocene is a key period in the evolution of modern reptile and amphibian faunas, particularly for snakes. However, there are very few studies focused on herpetofauna in Iberian sites of this chronology. In the present work, we studied the palaeoherpetofauna from 32 sites in the Ribesalbes-Alcora Basin, which has been dated to the Early Aragonian age (MN4, Early Miocene) based on its small mammal faunas. The studied remains from these sites have been attributed to 26 taxa, with a relatively consistent faunal composition throughout the sequence. Although the assemblages are composed of taxa typical of the Early Miocene, two taxa may indicate some peculiarities in the faunal composition. The described remains of *Chalcides* sp. lack expanded crown teeth, which may be related to a probable morphotype distinct from those recovered from localities in Central and Eastern Europe and Asia. The possible presence of *Pyrenasaurus* in CBR1 is striking. This genus was previously known only from the Late Eocene, so its identification here suggests it survived the *Grande Coupure* and points to ecological stability in the region.

Using the Habitat-Environment Gradient (HEG) method on the best-sampled localities, the estimated mean annual precipitation (MAP) values exceed current regional levels in all sites, except just one case. Our results point to fluctuations in humidity throughout the sequence, with alternating “humid” and “dry” phases. This cyclical pattern has been previously documented in palaeoenvironmental data derived from small mammal assemblages.

Keywords: Amphibia; Reptilia; Palaeobiogeography; Burdigalian; MN4.

INTRODUCTION

Following the relatively cold and dry late Oligocene, the Miocene climate experienced a warming trend that culminated in the Mid-Miocene Climatic Optimum (MMCO) at ~17-15 Ma, interrupted only by punctuated glaciation periods known as Mi events (Prista et al. 2015). Moreover, a significant palaeobiogeographic event occurred at this time. The Eurasian and Afro-Arabian Plates at the Oligocene–Miocene transition (~20-18 Ma) established a continuous terrestrial corridor between Eurasia and Africa in the Middle East (Rögl 1999). Associated with the rise of this connection, known as the *Gomphotherium* Landbridge, extensive terrestrial faunal exchanges occurred between Eurasia and Africa (Harzhauser et al. 2007). Both events, the Afro-Eurasian land connection and the establishment of milder climatic conditions, had a significant impact on the palaeoherpetofaunal assemblages of the Early Miocene (Rage and Roček 2003; Rage 2013; Villa and Delfino 2019a; Ivanov 2022; Macaluso et al. 2022). Thus, during the Oligocene, the European squamate faunas were impoverished, characterized by small forms and low diversity; this interval is known as the Dark Period (Rage 2013). However, with improvements in climatic conditions during the Miocene, the diversity of amphibians and reptiles increased, mainly due to the arrival of several thermophilous taxa that reached northern areas, such as crocodylians and chamaeleonids in Central Europe (Böhme 2003; Rage and Roček 2003; Rage 2013). Although among that fauna persist some Paleogene taxa (i.e., Anilioiids snakes and the booid *Falseryx*) and newcomers included some “exotic” taxa (i.e., agamids and elapids; Ivanov 2022), in some cases, it is recorded the first members of extant genera, such as *Lacerta* (Čerňanský 2010a) and *Chalcides* (Čerňanský et al. 2020). In this sense, during the Miocene, the basis of the modern fauna was established. However, there are a few publications on the herpetological fossils of this chronology, in contrast to other faunas, i.e., mammals. In the case of the Iberian Peninsula, the number of works focused on these fossils is scarce, which include those centred on the herpetofauna (i.e., Alférez and Brea 1981; Murelaga et al. 2002) or on a specific taxon (i.e., Sanchiz 1977a; Szyndlar 2000; Delfino et al. 2013; Villa et al. 2017). Thus, the limited number of studies results in a lack of key information needed to understand the evolution of an essential component of modern ecosystems, such as herpetofauna, during the early Neogene.

The study of Early Miocene herpetofauna assemblages is not only relevant from a biogeographical perspective, but also for palaeoclimatic research. Due to their ectothermic physiology, reptiles and amphibians are highly dependent on different climatic parameters, such as evapotranspiration, solar radiation, and mean annual temperature (Vitt and Cladwell 2009). For this reason, they are handy for reconstructing the palaeoclimatic and palaeoecological context that prevailed during the formation of the palaeontological sites.

The study of the amphibian and reptile fossils in the Ribesalbes-Alcora Basin adds another crucial piece to the puzzle of the ecosystems that developed in the region at the end of the Early Miocene. Previous works focused in remain from this basin includes the description of talpids (Crespo et al. 2019a), diverse soricids (Crespo et al. 2019b), erinaceids (Crespo et al. 2020a), bats (Crespo et al. 2020b), squirrels (Crespo et al. 2021a), eomyids (Crespo et al. 2021b), dormice (Crespo et al. 2023), muroids (Crespo et al., 2025), lagomorphs and *Cainotherium* Bravard, 1828 (Crespo et al. 2022), snails (Albesa et al. 2022), reworked Cretaceous batoids (Manzanares and Crespo 2023), and even a Konservat-Lagerstätte (Álvarez-Parra et al. 2021). Among these works, it is

notable the description of new species, such as *Plesiodimylus ilercavonicus* Crespo et al. 2018 (Crespo et al. 2018), the bat *Cuvierimops penalveri* Crespo et al. 2020 (Crespo et al. 2020b), and the snail *Pseudamnicola roblesi* Albesa et al. 2022 (Albesa et al. 2022), and the southernmost documented record of the herpetotheriid *Amphiperatherium frequens erkertshofense* (von Meyer 1846) (Furió et al. 2012, Crespo et al. 2020a). Until now, the unique herpetofaunal fossils described from the Ribesalbes-Alcora Basin are those recovered from the classical site of La Rinconada (Ribesalbes, Castelló, Spain), which is slightly older than the studied localities in this work (Sanchiz 1977a; Peñalver et al. 2016).

GEOLOGICAL SETTINGS

The Ribesalbes-Alcora Basin is an intramontane basin located in the eastern Iberian Peninsula (Figure 1A), covering an area of 150 km², and is bounded by ENE-WSW to NNE-SSW normal faults (Anadón et al. 1989). The sedimentary infill of the basin can be divided into two main sequences (Agustí et al. 1988). The lower one, named the Ribesalbes sequence, is composed of alluvial and lacustrine deposits. It has a thickness of up to 600 m, which originated in the Early to Middle Miocene. The Alcora sequence is constituted by alluvial deposits up to 200 m thick. Most probably this was formed during the Middle and Late? Miocene (Anadón et al. 1989). Anadón (1983) defined five depositional units (A to E) in the Ribesalbes sequences, in which only Units B and C have yielded paleontological localities. Thus, Unit B is characterised by oil-shales and laminated bituminous dolomicrite where the konservat-lagertätten sites of La Rinconada (Ribesalbes) and San Chils (L'Alcora) are located (Peñalver et al. 2016; Álvarez-Parra and Peñalver 2019). The Araia/Mas de Antolino outcrop (Araia d'Alcora, Castelló, Spain), which includes the studied sites, belongs to Unit C in the Ribesalbes sequence (Agustí et al. 1988; Crespo et al. 2019c). This side of the ravine is formed by grey and yellow mudstones, limestones, and sandstones, ~100 m thick. It comprises seven sections, from oldest to youngest (Figure 1B): Mas dels Coixos (MCX), Mas de Torner (MTR), Araia Cantera Sud (ACS), Barranc de Campisano (BC), Foieta la Sarra (FS), Mas d'Antolino B (MAB), and Corral de Brisca (CBR) (Crespo et al. 2019c). Recently, Álvarez-Parra et al. (2021) described a new konservat-lagerstätten site in the section of FS, Foieta la Sarra A (FSA).

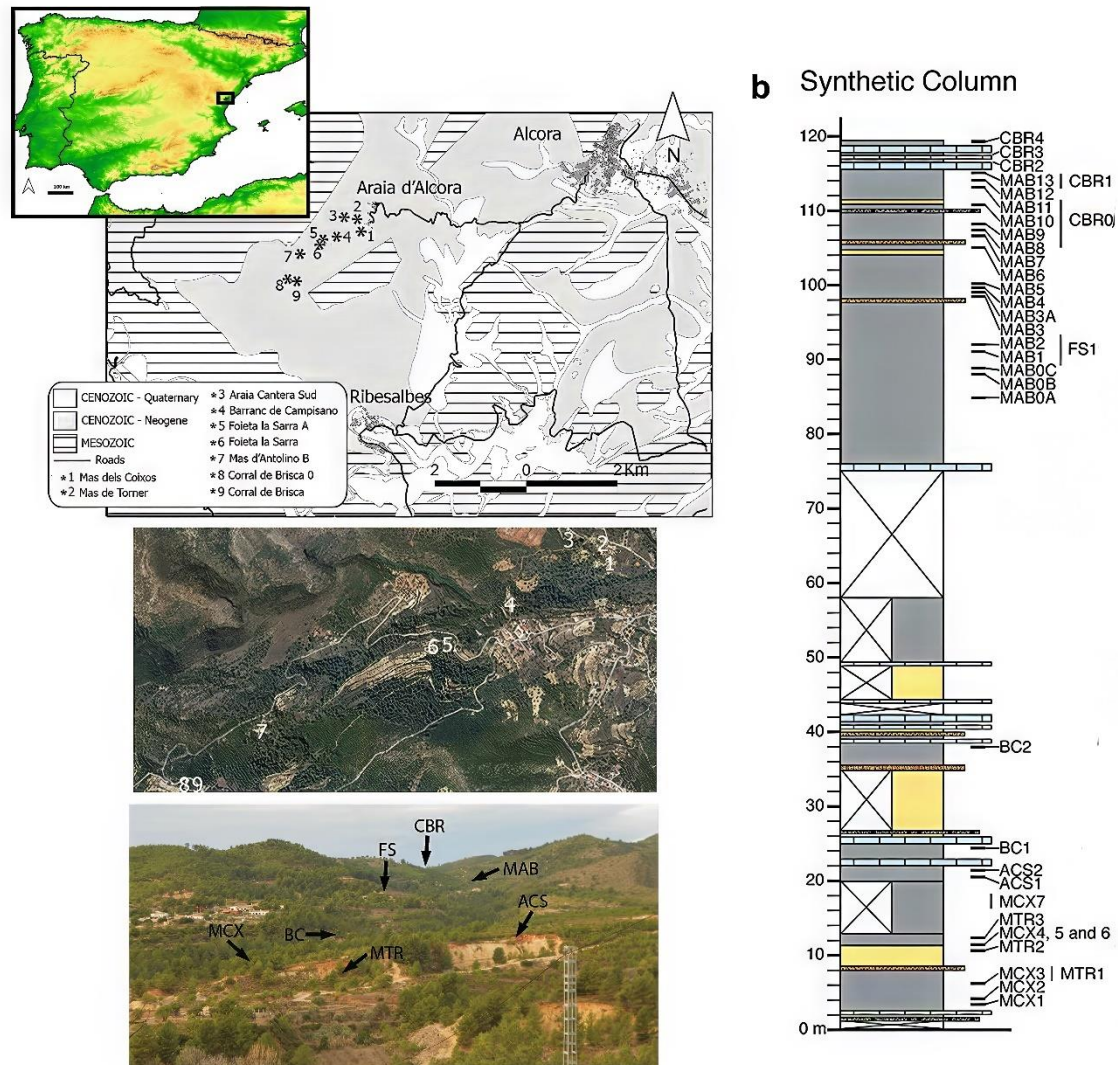


Figure 1. a) Geographic location of the Ribesalbes-Alcora Basin, showing the location of the outcrops of the Campisano Ravine. B) Synthetic stratigraphic column of the Campisano ravine. All modified from Crespo (2017) and Crespo et al. (2019c).

Crespo et al. (2019c) studied 45 new sites with mammal remains, which had been correlated with the local biozone C (MN4, early Miocene) from the Calatayud-Montalbán Basin (Spain), the type area of the Aragonian stage, with an estimated age between 16.49 and 15.98 My ago as established by Van der Meulen et al. (2012). An alternative interpretation has been proposed by Casanovas-Vilar et al. (2022), who discuss that the extinction boundary of *Ligerimys florancei* Stehlin and Schaub, 1951 falls within the MN4–MN5 transition. Under this framework, the sites of the Ribesalbes-Alcora Basin associated with the local biozone *L. florancei* would correspond to MN4. In contrast, those linked to the local biozone *L. ellipticus* would be assigned to MN5.

MATERIAL AND METHODS

The material studied here consists of disarticulated elements collected from the prospection and excavation campaigns carried out in the Alcora-Ribesalbes Basin from 2008 to 2012 by a team from the Departament de Botànica i Geologia of the Universitat de València (UV; Valencia, Spain). The sediment was water-screen-washed using

superimposed 5, 1.5, and 0.5 mm-mesh screens. The microfossils were processed, sorted, and classified using a Leica MS5 binocular microscope. Measurements were taken using a Leica MZ75 binocular microscope, with a mechanical stage displaced using Sony Magnescale measuring equipment. Photographs were taken with the digital microscopes Leica MZ75 and a Scanning Electron Microscope HITACHI 4800 at the Servei Central de Suport a la Investigació Experimental of the University of València Estudi General.

Herpetological bones remains were assigned to different taxa mainly following the criteria given by Bailon (1999) for anurans, Brochu (1999) for crocodylians, de Lapparent et Broin (2000) for turtles, and Szyndlar (1984), Bailon (1991), Blain (2009), Klembara et al. (2014), and Villa and Delfino (2019b) for Squamata. Comparisons were drawn using the collections of dry skeletons housed in the MNCN-CSIC, the Muséum national d'Histoire naturelle (Paris, France), the Gabinet de Fauna Quaternària of the Museu de Prehistòria de València (Valencia, Spain), and the Departament de Botànica i Geologia of the UV (Burjassot, Spain). The morphological nomenclature terminology mainly follows Bailon (1999) for anurans, Brochu (1999) for crocodylians, Pérez-García and Vlachos (2014) for chelonians, Villa and Delfino (2019b) for lizards, and Szyndlar (1984) for snakes. Regarding dentition, the terminology about the different cusps and striae is based on Richter (1994).

To reconstruct palaeoprecipitation in the region, we applied the Herpetological Ecophysiological Groups (HEG) method, as defined by Böhme et al. (2006). It is based on the definition of six Ecophysiological Groups, corresponding to the main strategies and adaptations for thermoregulation, water balance, and gas exchange, for every herpetological species in a given assemblage (excluding non-fossorial snakes). This clustering is based on extant species, and the information is subsequently transferred to their fossil relatives. The defined groups are: 1) heliophilic heliophile species; 2) subterranean and arboreal group; 3) periaquatic taxa; 4) semiaquatic and woodland group; 5) heliophobe group, and 6) aquatic species group. After that, each taxon was assigned a numeric index corresponding to its group. Finally, we applied Equation 6 from Böhme et al. (2006) to reconstruct palaeoprecipitation. To compare with current data, we obtained the mean annual precipitation (MAP) for the Ribesalbes-Alcora Basin from the global climatic data layer of the bioclimatic parameter BIO12 (mean annual rainfall) provided by WorldClim 2 (Fick and Hijmans 2017).

All the studied material is housed at the Museu de la Universitat de València d'Història Natural (MGUV).

LIST OF ABBREVIATIONS

ACS, Araia Cantera Sud; BC, Barranc de Campisano; CBR, Corral de Brisca; FS, Foieta la Sarra; HEG, Herpetological Ecophysiological Groups method; LAD, last appearance datum; MAB, Mas d'Antolino B; MAP, mean annual precipitation; MCX, Mas dels Coixos; MGUV, Museu de la Universitat de València d'Història Natural; MN, Mammal Neogene Stages; MNCN-CSIC, Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain); MSC, Messinian Salinity Crisis; MTR, Mas de Torner; PLA, preacetabular lateral angle; UV, Universitat de València (Valencia, Spain).

SYSTEMATIC PALAEOLOGY

Lissamphibia Haeckel, 1866

Caudata Scopoli, 1777

Urodela Duméril, 1806

Salamandridae Goldfuss, 1820

***Lissotriton* Bell, 1839**

cf. *Lissotriton* sp.

Localities: MCV7, MTR1, MTR2, ACS2, BC1, BC2, MAB0A, MAB2, MAB4, MAB8, CBR0B and CBR0D.

Figure 2A-I.

Material: 1 right dentary (MGUV-40685), 1 left dentary (MGUV-40445); 2 dentaries (MGUV-40347 and 40358), 43 tooth-bearing bones (MGUV-40342, MGUV-40350, 40384, 40394, 40606, 40609, 40655, and 40686), 2 trunk vertebrae (MGUV-40349), 1 caudal vertebra (MGUV-40688), 48 vertebral centra (MGUV-40343, 40348, 40389, 40410, 40440, 40497, 40573, 40605, 40634, 40684, 40645, and 40652), 1 ilium (MGUV-40352), and 5 phalanges (MGUV-40344, 40345, 40687, and 40646).

Description:

The preserved dentaries are elongated and curved bones in medial view. Although no teeth are present, they were densely packed pleurodont teeth positioned in the labial view (Figure 2A). The *crista dentalis* is wide. The Meckelian groove is open, but not in the most anterior portion. A wide *incisura dentalis* is present, and it seems to be located in the posterior half (Figure 2B). The symphysis is wide and kidney-shaped. Although it is broken, a slight medial expansion in the posterior direction develops, forming the medial surface that acts as a contact area with the paired dentary. No *sulcus dentalis* is present in the dorsal view. The dentary is slightly curved in a medial direction. In lingual view, two small lingual foramina are present.

The two most complete vertebrae are opisthocoelous and small-sized. In dorsal view, the prezygapophysis are rounded in shape and project anteriorly. Its medial edges are parallel (Figure 2C). In lateral view, the neural arch upwards caudally. The zygapophyseal and ventral crests are well developed. Thus, the posterior zygapophyseal crest contacts the dorsal border of the diapophysis. On its behalf, the anterior ventral crest contacts the ventral transverse process (Figure 2D and E). The condyle has a flat anterior surface, and it is slightly anteroventrally inclined. In ventral view, the centrum is elongated. The centrum shows a relatively thick and short condyle clearly separated from the vertebral centrum by a well-developed pericondylar constriction. The subcentral foramina are large, and some vertebral centra show supplementary, more or less smaller ones (Figure 2F). The ventral lamina is more or less trapezoidal (Figure 2G). In frontal view, the neural arch is laterally compressed and slightly vaulted. The condyle has a circular or elliptical shape, with the major axis oriented horizontally. The foramen at the basis of the parapophyses is small.

MGUV-40688 is an amphicoelous vertebra. Although it is broken, the presence of the basis of a pair of haemapophysis denotes that it is a caudal vertebra. It starts posteriorly in the centrum, which indicates that this bone may be the first or second caudal vertebra (Figure 2H). In dorsal view, MGUV-50688 has a not pronounced interzygapophyseal constriction. The neural arch is short and rectangular. The transverse process starts posteriorly and projects posterolaterally. The prezygapophyseal process is subovoid-shaped and projects laterally. In lateral view, the neural crest, although it is broken, is higher in its posterior region than in the anterior one. The anterior zygapophyseal crest

is horizontal, prominent, and contacts the prezygapophysis with the dorsal edge of the diapophysis. The anterior ventral crest contacts the ventral edge of the parapophysis. The *incisura ventralis caudalis* is well marked. The posterior ventral crest is prominent. In ventral view, the centrum is triangular. No pericondilar constriction is present. The ventral lamina is straight. The haemapophysis is bifurcated, and its base runs along the entire length of the centrum. The latter presents a pair of large subcentral foramina. In the anterior view, the neural arch is dorsoventrally compressed. Its roof is vaulted and overpasses the edge of the prezygapophysis. The latter, which projects laterally, forms an angle of approximately 30° with respect to the horizontal axis. The condyle is rounded in this view. In the posterior view, the neural arch is laterally compressed and vaulted. The cotyle is broken.

The ilial shaft is rod-like. Its surface is smooth. The acetabular region is large and well-defined. It has a well-developed ventrolateral tuberosity, which projects laterodorsally. No *tuber superior* is present. The pars ascendens and pars descendens are short. The pars ascendens runs straight at the same height as the *pars cilindrifomis*. The acetabulum is large, flat, and wide. The preacetabular fossa is large and well-defined. The pubic process is straight and projects ventrally. The articulation area with both the pubic and the ischium is damaged. Preacetabular Lateral Angle (PLA) is approximately 135° (Figure 2I).

Remarks

The described traits of the vertebra are consistent with a taxonomical attribution to the genus *Lissotriton*: a small opisthocoelous vertebra with a well-defined pericondylar constriction, well-developed crests, and the trapezoidal shape of the ventral lamina (Macaluso et al. 2023). The latter trait is coincident with the extant species *Lissotriton boscai* (Lataste, 1879) (Sanchiz 1988a; Macaluso et al. 2023). Despite all the above, the poor state of preservation of the remains studied does not allow for a precise attribution.

Palaeoecology: Smooth Newts inhabit Europe, from the Iberian Peninsula to the Caucasus, and some areas of the Middle East (Dufresnes 2019). *Lissotriton* currently comprises 10 species that inhabit lentic environments without strict habitat preferences.

Nowadays, two species inhabit the Iberian Peninsula (Speybroeck et al. 2016): the Palmate Newt, *Lissotriton helveticus* (Razoumovsky, 1789), in the northern realm of Spain and the northern half of Portugal, and the Bosca's Newt, *Lissotriton boscai* (Lataste, 1879), in Western Iberia. However, a possible third species, Maltzan's Newt *Lissotriton maltzani* (Boettger, 1879), inhabits southwestern Portugal (Dufresnes 2019). Both species are highly adaptable, using a wide range of different water bodies (Speybroeck et al. 2016).

Anura Duméril, 1866

Bufonidae Gray, 1825

Bufonidae indet.

Locality: BC1.

Figure 2J-K.

Material: 1 centrum of a sacral vertebra (MGUV-40353).

Description:

In ventral view, the procoelus centra is wider than long and trapezoidal in shape. It has two condyles, which articulate with the urostyle (Figure 2J). In anterior and posterior views, the cotyle and the condyles are dorso-ventrally compressed. Although they are eroded, they seem to contact in their medial region. In the posterior view, the walls of the neural arch are short and wide (Figure 2K).

Remarks

Among the European anuran families, only Pelodytidae, Hylidae, and Bufonidae have bicondylar procoelous vertebrae. However, Pelodytidae has elongated centra, and the condyles are small and clearly separated (Sanchiz 1978; Bailon 1991). Regarding Hylidae, the centrum is more gracile and longer than the studied remains.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

Anura indet.

Localities: MAB2.

Figure 2L-M.

Material: 1 vertebral centrum (MGUV-40574).

Description:

MGUV-40574 is an isolated procoelous vertebral centrum. In ventral view, the centrum is slightly longer than wide. A large foramen is present. The lateral walls of the neural arch are wide (Figure 2L). In posterior view, the condyle is dorsoventrally compressed (Figure 2M).

Remarks: The poor conservation state of the studied material precludes any attempt to propose a taxonomical attribution at the order level.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

Lissamphibia indet.

Localities: MCX3, BC1, MAB2, and MAB3.

Figure 2N.

Material: 1 tooth-bearing bone (premaxilla?) (MGUV-40674), and 7 phalanges (MGUV-40351, 40575, and 40576).

Description:

The scarce taxonomical value and/or the poor state of conservation of the included material preclude any tentative taxonomical attribution.

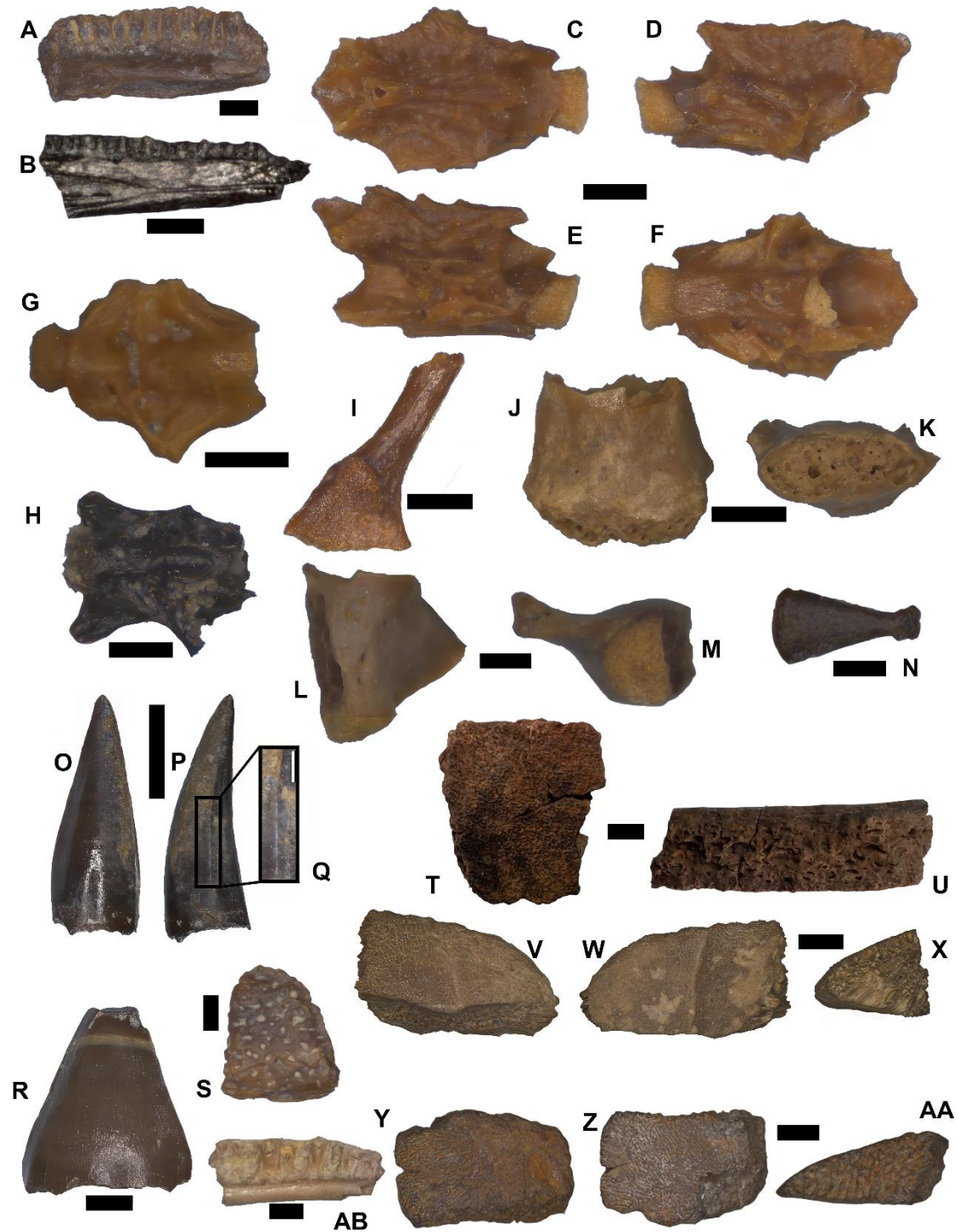


Figure 2. Amphibian, crocodilian, chelonian, and gekkotan remains from the Ribesalbes-Alcora Basin. A-I) cf. *Lissotriton* sp.: A, right dentary (MGUV-40685) in labial view; B) left dentary (MGUV-40445) in labial view; C-F) trunk vertebra (MGUV-40349) in dorsal (C), left lateral (D), right lateral (E), and ventral (F) views; G) trunk vertebral centrum (MGUV-40348) in ventral view; H) caudal vertebra (MGUV-40688) in ventral view; I) left ilium (MGUV-40352) in lateral view. J-K) Bufonidae indet., sacral vertebral centrum (MGUV-40353) in ventral (J) and posterior (K) views. L-M) Anura indet., trunk vertebral centrum (MGUV-40574) in ventral (L) and posterior (M) views. N) Lissamphibia indet., phalanx (MGUV-

40575). O-S) Crocodilia indet., isolated teeth (MGUV-38788) in labial (O) and medial (P) views, and detail of the mesiodental carinae (Q); isolated teeth (MGUV-26258) in labial (R) view; and osteoderm (MGUV-40432) in dorsal (S) view. T-U) cf. Testudinidae indet., undetermined plate (MGUV-40567) in external view (T) and lateral (U) views. V-AA) Testudines indet., peripheral plate (MGUV-40414) in dorsal (V), ventral (W), and lateral (X) views; peripheral plate (MGUV-40620) in dorsal (Y), ventral (Z), and lateral (AA) views. AB) Gekkota indet., left dentary (MGUV-40479) in lingual view. Scale bar equal to 0.5 mm, except for J and K (1mm), T and U (4 mm), and V to AA (2mm).

Reptilia Laurenti, 1768

Crocodilia Owen, 1842

Crocodilia indet.

Localities: MEX3, MTR2, BC1, BC2, MAB0A, MAB0B, MAB-3, MAB3A, FS1, MAB9, MAB10, MAB11, MAB11A, MAB11B, CBR0A, CBR0B, CBR0D, MAB13, CBR1, CBR3, and CBR4.

Figure 2O-S.

Material: 298 teeth (MGUV-25293, 25294, 25295, 25340, 25341, 25342, 26256, 26257, 26258, 36658, 36669, 36738, 36739, 36740, 36807, 36811, 36905, 36908, 38379, 38404, 38540, 38557, 38558, 38568, 38788, 38789, 38792, 40390, 40457, 40477, 40528, and 40542) and 17 osteoderms (MGUV-40381, 40432, 40478, 40504, 40541, 40543, 40635, and 40670).

Description:

Several teeth have been recovered from the different studied sites. All of them only preserve the crown, which is subconical and variably pointed apically (Figure 2O and P). Lingually, the teeth are slightly concave, whereas they show a convex surface in labial view (Figure 2O and P). In both views, their surfaces are generally smooth, but some specimens exhibit wrinkles and slight vertical striations. The mesiodistal carina is unserrated (Figure 2Q). Among the teeth, two morphotypes can be identified: the first consists of slender, long, and more pointed teeth (Figure 2O and P), whereas the second features more massive teeth with a bulbous aspect and apically blunt (Figure 2R).

The recovered osteoderms are fragmentary. On its external surface, large, rounded pits ornament these remains (Figure 2S). MGUV-40543 is a small osteoderm with poorly developed ornamentation, which could be interpreted as belonging to a juvenile individual (Pereda Suberbiola et al. 2001).

Remarks: As Brochu (2000) notes, isolated teeth and osteoderms have little taxonomic value. Thus, the recovered remains can only be assigned to an indeterminate Crocodylian. However, some observations can be made. The two tooth morphotypes correspond to different positions along the tooth row. The slender, elongated, and pointed teeth likely belonged to the anterior region, whereas the second morphotype—characterised by massive, blunt, and bulbous teeth—was located in the posterior region of the tooth-bearing bones (Martin et al. 2014). The presence of bulbous posterior teeth is a trait observed in the alligatoroid *Diplocynodon* Pomel, 1847, but is absent in the gavialid *Gavialosuchus* Toulou & Kail, 1885 (Górka et al. 2025). Unfortunately, the recovered crocodylian osteoderms are too fragmentary to determine whether a longitudinal keel is present, a typical feature of *Diplocynodon* but generally absent in

gavialids (Martin et al. 2014). In summary, the poor preservation of the material precludes a precise taxonomic identification of the crocodylian remains from the Ribesalbes–Alcora Basin.

Palaeoecology: Traditionally, crocodylians have been considered indicators of warm climatic conditions. In this context, extant crocodylian genera are primarily distributed in low latitudes, generally within 30° of the Equator (Marwick 1998). However, during the Eocene–Oligocene boundary, *Diplocynodon* appeared at higher—and therefore cooler—latitudes, coinciding with the development of a continental ice sheet in Europe. Its presence may serve as indirect evidence of a possible ability to withstand low temperatures, perhaps through thermoregulatory strategies (Martin 2010). For example, *Alligator sinensis* (Fauvel, 1879) ceases feeding and enters hibernation during the winter when temperatures drop, a process involving complex molecular mechanisms (Lin et al. 2020).

Testudines Linnaeus, 1758

Testudinidae Linnaeus, 1758

cf. Testudinidae indet.

Localities: MAB11.

Figure 2T-U.

Material: 2 fragments of plates (MGUV-40567 and 40568).

Description:

The remains are a relatively large, thick fragment of an undetermined plate (Figure 2T). Undoubtedly, these remains belong to a large/medium turtle. The surface of the remains presents a delicate ornamentation consisting of small circular hollows and vermicular pits. This fragment of plaque is relatively thick in lateral view (Figure 2U).

Remarks: The relative thickness of the plates is one of the criteria to differentiate Testudinidae from the rest of the European chelonian families during the Neogene (Hervet 2000). Probably this remains belonged to an undetermined Testudinidae. However, this attribution is highly tentative.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

Testudines indet. (Geomydidae or Emydidae)

Localities: MAB5 and CBR0B.

Figure 2V-AA.

Material: 1 peripheral (MGUV-40620 and 40643) and 3 fragments of plate (MGUV-40414, and 40644).

Description:

MGUV- 40414 is a trapezoidal-shaped fragment of a relatively thick plate. Both the dorsal and ventral surfaces exhibit a well-marked straight sulcus (Figure 2V and W). Its anterior border is convex, forming a small curvature of approximately 120°. The ornamentation of the plates is composed of small circular hollows and vermicular pits (Figure 2V). In lateral view, the external surface is narrower than the innermost region (Figure 2W).

MGUV-40643 is a peripheral plate, probably of the right side of the carapace. This plate is rectangular, clearly longer than wide. The sulcus between the marginal scutes is present, both in dorsal and ventral views (Figure 2V and W). The ornamentation of the plate is similar to those observed in MGUV-40414. This plate is strongly flat (Figure 2AA).

Remarks: The presence of a pleuromarginal sulcus that does not coincide with the costal-peripheral suture allows us to rule out some chelonian taxa present in Europe during the Miocene. This feature is absent in both Testudinidae and pan-Chelydridae, in which the sulcus typically overlaps the suture between the costal and peripheral plates (Hervet 2000; Joyce 2016). Moreover, the presence of a sulcus between the scutes suggests that these remains did not belong to Tryonichidae, as these marks are absent in this group (Georgalis and Joyce 2017). Taking into account the fossil record of the group during the Miocene (Pérez-García 2017), and after discarding the aforementioned clades, only two taxa could potentially be attributed to the described remains: Geomydidae and Emydidae. The distinction between the two groups is highly problematic (de Lapparent de Broin 2001). Traditionally, the location of the pleuromarginal sulcus with respect to the costo-peripheral suture has been used as a criterion for the discrimination between both groups, at least in Quaternary deposits (i.e., Bailon 2010). Thus, under that premise, MAB5-941 could belong to the family Emydidae; however, the studied remains are in very poor condition, precluding any close taxonomic attribution. Moreover, emydids appear in the European fossil record only during the Late Miocene of Eastern Europe (Fritz 1995). Despite this, Böhme and Ilg (2003) include undetermined emydids from some Spanish Early Miocene localities. If future work could confirm the presence of that taxon in that chronology, it would imply a remarkable change in the palaeobiogeography of the group, which is supposed that reached Eurasia during the Late Miocene (Fritz 1995).

Palaeoecology: These remains could belong to an undetermined terrapin species. These kinds of turtles inhabit different types of water bodies.

Squamata Opperl, 1811

Gekkota Cuvier, 1817

Gekkota indet.

Localities: BC1, MAB3, MAB5, and FS1.

Figure 2AB.

Material: 1 probable maxilla (MGUV-40386), 4 left dentaries (MGUV-40479, 40480, 40597, and 40624).

Description:

A probable maxilla has been recovered from BC1. This fossil is very fragmentary. In a lingual view, MGUV-40386 has eight packaged pleurodontal tooth positions, but only one tooth is preserved. It is slender and conical, lacking its apex. Its base presents a small, rounded resorption pit. The palatal shelf is straight and highly damaged. In labial view, the surface of the fossil has one large labial foramen and another small one in a more dorsal position relative to the former.

The fragmentary dentary exhibits a slightly convex ventral edge (Figure 2AB). In lingual view, the bone has a tall alveolar shelf that contains a large number, probably ten, of closely packed pleurodont dental positions. The Meckelian canal is closed. In a labial view, the dentary has two large, elliptical labial foramina.

Remarks. The morphology of the teeth and the dentary, with a convex ventral border and a closed Meckelian canal, are characteristics of Gekkota (Bailon 1991). This clade is represented in the European Miocene by three genera: a gekkonoid, *Palaeogekko* Schleich, 1987, and two sphaerodactylids, *Gerandogekko* Hoffstetter, 1946, and *Euleptes* Fitzinger, 1843 (Daza et al. 2014). Of which, the latter is the only one with current representatives (Speybroeck et al. 2016). Unfortunately, the studied material is too fragmentary for a generic assignment.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation. However, Gekkotans are considered indicators of warm conditions in palaeontological sites.

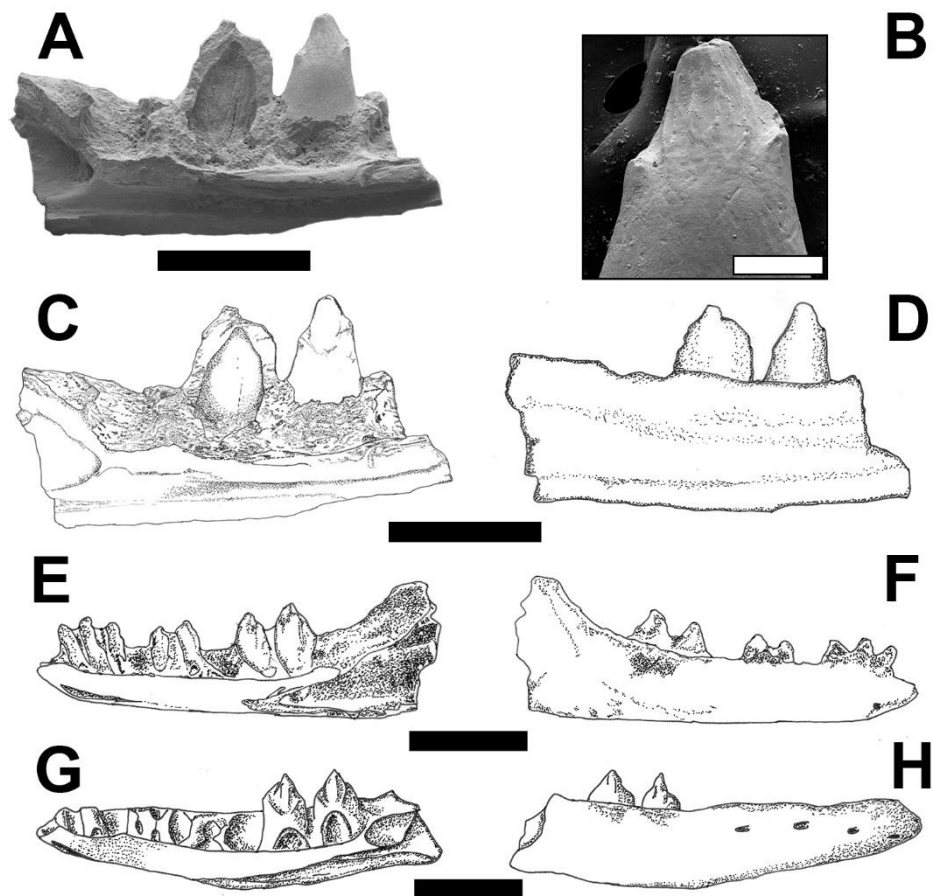


Figure 3. Scincoidean from the Ribesalbes-Alcora Basin and other taxa morphologically similar to those from the Eocene and Miocene of Western Europe. A-D) cf. *Pyrenasaurus* sp., left dentary (MGUV-40463) in lingual view (A), detail of the tooth crown in lingual view (B), and interpretative drawing in lingual (C) and labial (D) views. E-F) *Pyrenasaurus evansae*, right dentary (UM-ECB 1703) in lingual (E) and labial (F) views, from Escamps B (Phosphorites du Quercy, France). G-H) *Scincomorpha* indet. B, right dentary (USTL, MAL 605) in

lingual (G) and labial (H) views, from Malpérié (France; MP17, middle Eocene). F and G redrawn from Bolet & Augé (2014) and H and I from Augé (2005). Scale bar equal to 0.5 mm, except for B (0.1 mm).

Scincoidea Opper, 1811

Pyrenasaurus Bolet & Augé, 2014

cf. *Pyrenasaurus* sp.

Locality: CBR1.

Figure 3A-E.

Material: 1 left dentary (MGUV-40463)

Description:

The material studied is fragmentary and only involves the posterior region of a left dentary, in which the processes are absent (Figure 3A-E). This remains shows three dental positions, with only two of them being present. The teeth are triangular in shape, taller than wide, and labio-lingually compressed in occlusal view. The only two preserved teeth have a robust appearance and a marked triangular shape in labial view (Figure 3A). These are pleurodonts, with the *crista dentalis* exceeding half the height of the tooth. The interdental gap is narrow. The crown is tricuspid, with a medial one more developed than the lateral ones. Thus, the mesial cusp is slightly more developed than the distal one. The crown presents a deflection in its convexity. Lingually, five or six faint striae run parallel to the tooth's axis (Figure 3B). A hypothetical rounded resorption pit is located in the central region at the base of the tooth (Figure 3A). Labially, the central part of the tooth is bulging, and lingually to it, it is somewhat flattened. The *lamina horizontalis* is narrow and has a uniform thickness along its entire preserved length. A well-developed intermandibular septum is present, lying ventromedially from the oval-shaped alveolar canal, and located in a posterior position at the level of the last teeth of the dental shelf. The *lamina horizontalis* finishes posteriorly close to the base of the most posterior dental position. The ventral region of the dentary is broken; thus, it is not possible to discern if the Meckelian groove was open or closed. No foramen is present on the labial surface of the dentary (Figure 3D).

Remarks. MGUV-40463 shows a particular morphology (Figure 3A-D). Among the different squamate taxa described in the Paleogene and Neogene in Eurasia, the general tooth morphology of the remain is similar to *Pyrenasaurus evansae* Bolet & Augé, 2014, from the sites of Escamps B (MP 19, Late Eocene, Phosphorites du Quercy, France) and Sossís (MP17a, Late Eocene, Central Southern Pyrenean Basin, Spain) (Figure 3F-G). Thus, in this taxon, the posterior teeth are large, labiolingually compressed, with a characteristic deflection in the convexity of the crown, so resembling a short obelisk (less developed) shafts close to the tip, and striation is only present on the lingual side of the crown (Bolet and Augé 2014). These authors have tentatively assigned *P. evansae* to Scincomorpha (a probably paraphyletic clade, e. g. Simões and Pyron 2021). Another taxon that shares some characteristics with MGUV-40463 is "Scincomorpha indéterminé Forme B" (USTL, MAL 605) from the French site of Malpérié (MP17; middle Eocene) (Augé 2005) (Figure 3H-I). In contrast to *P. evansae*, MGUV-40463, and USTL, MAL 605 has a more pronounced tricuspid condition (Augé 2005; Bolet and Augé 2014). As Bolet and Augé (2014) pointed out, it is possible that the differences between *P. evansae* and USTL, MAL 605, and, by extension, MGUV-40463, may represent different but related genera.

Palaeoecology: *Pyrenasaurus evansae* has been interpreted as a burrowing or surface-dwelling lizard based on the short dentary, low number of teeth, high coronoid process, and dentary miniaturization (Bolet and Augé 2014).

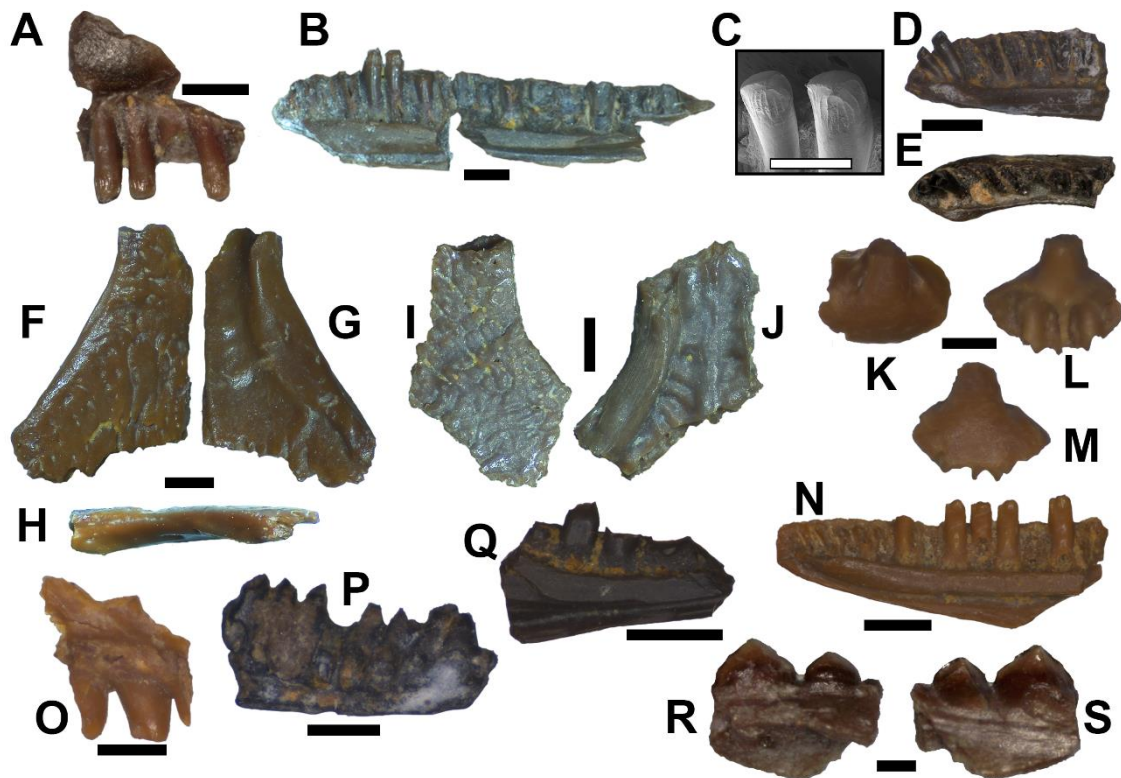


Figure 4. Some lizards from the Ribesalbes-Alcora Basin. A-E) *Chalcides* sp., A, left maxilla (MGUV-40577) in lingual view; B, right dentary (MGUV-40579) in lingual view; C-E, right dentary (MGUV-40578), detail of the tooth crown in dorsolingually view (C), and dentary in lingual (D) and occlusal (E) views. F-N) Lacertidae indet., unfused frontal (MGUV-40355) in dorsal (F), ventral (G), and lateral (H) views; I-J) fused frontal (MGUV-40357) in dorsal (I) and ventral (J) views; K-M) premaxilla (MGUV-26252) in dorsal (K), posterior (M), and anterior (N) views; N) right dentary (MGUV-26259) in lingual view. O-Q) Blanidae indet., left maxilla (MGUV-40361) in lingual view (O), and right dentaries (P, MGUV-40616; Q, MGUV-40552) both in lingual (P and Q) views. R-S) ?Chamaeleonidae indet., tooth-bearing bone (MGUV-40413) in lingual (R) and labial (S) views. Scale bar equal to 0.5 mm, except for C (0.3 mm).

Scincidae Opperl, 1811

***Chalcides* (Laurenti, 1768)**

***Chalcides* sp.**

Localities: MCX3, BC1, and MAB3.

Figure 4A-E.

Material: 1 left maxilla (MGUV-40577), 1 left dentary (MGUV-40679), 3 right dentaries (MGUV-40578 and 40579), 2 dentaries (MGUV-40360), and 3 tooth-bearing bones (MGUV-40580).

Description:

The preserved maxilla (MGUV-40577) only presents its most anterior region (Figure 4A). In dorsal view, it presents a deep U-shaped concavity. Neither the anterolateral process nor the anteromedial process is preserved. In the lingual view, a well-defined foramen is present. In labial view, only three teeth are present. These are pleurodont, closely spaced, cylindrical, and bicuspid (one labially, and a second lingually, smaller than the former). No expansion of the crown of the teeth is observed (Figure 4A). In the lingual view, the tooth crown bears striations.

The most complete dentary (MGUV-40579) shows 16 tooth positions (Figure 4B). The morphology of the teeth is similar to that described in the maxilla, but they show its striation more marked than the maxilla. Although the teeth appear monocuspid, in lingual view, underneath the labial cuspid, a smaller lingual cuspid may be present. The *antrum intercristatum* is a well-marked groove located on one side and on the other, between the lingual and labial cuspids. They are prominent and pointed, and are connected by a short *crista intercuspidalis* in occlusal view. The *crista distalis* and *mesialis* have the same length and are bow-shaped, being it narrower in the anterior teeth. The *culmines lateres* are prominent. Seven-eight pronounced, straight, and parallel *striae* run in the flattened lingual surface of the teeth (Figure 4C). The Meckelian canal opens along the entire length of the dentaries. The location and width of this structure vary; in the posterior region (MGUV-40579), it is laterally expanded (Figure 4B), whereas in a more anterior position, it is narrow and located ventrally (MGUV-40578) (Figure 4D). The symphysis is large, oval-shaped, almost horizontal, and located in a ventral position, and the ventral end of the maxilla is straight. In labial view, the most complete dentary (MGUV-40578) has four dental foramina. The studied remains do not show any impression of the coronoid. In the occlusal view, a *sulcus dentalis* is present. It is narrow and not well developed (Figure 4E).

Remarks. The overall morphology of the dentary (ventral end straight, the Meckelian canal is fully open, narrowing anteriorly, and its anterior-half opens in ventral direction, both the *sulcus dentalis* and the subdental ridge are patent, absence of an impression of the coronoid, and the lack of bi- or tricuspid teeth) are characters shared by Scincidae and Cordilydae (Augé and Smith 2009), which are highly related clades. Both were present in Europe during the Miocene (Böhme and Ilg 2003). And, as Gao and Fox (1996) pointed out, both groups are often difficult to distinguish. However, in cordylids, the symphysis is more horizontal than in scincids (Čerňanský 2012), and, although the teeth are very similar, cordylids often have their base slightly expanded related to their crown (Roček, 1984). The presence of an open Meckelian canal is only present in some scincid genera. In the case of current European taxa, this condition is present in *Chalcides*, *Ophiomorus* Duméril and Bibron, 1839, and *Eumeces* Wiegmann, 1834. Thus, *Heremites* Gray, 1845, and *Ablepharus* Fitzinger in Eversmann, 1823 are the unique scincids of the continent with a closed Meckelian canal (Bailon 1991; Camaiti et al. 2019; Čerňanský and Syromyatnikova 2021). The studied remains have gracile teeth more similar to *Chalcides* than to *Ophiomorus* and especially to *Eumeces*, in which these teeth are inflated with rounded tips (Čerňanský and Syromyatnikova 2021). However, the incompleteness of the studied remains precludes the specific attribution of the taxon.

Palaeoecology: *Chalcides* is a genus of scincid lizards found in Macaronesia, the Mediterranean Basin, Western and Eastern Africa, and the Middle East through to Pakistan. In general, the species included in that genus show a generalist ecology, and perhaps occur in a broad range of habitats (Caputo et al. 1995).

Lacertoidea Opper, 1811

Lacertidae Opper, 1811

Lacertidae indet.

Localities: MCX1, MCX2, MCX3, MTR1, MTR2, BC1, MAB0A, MAB0B, MAB2, MAB3, MAB3A, MAB4, MAB5, FS1, MAB11, MAB0A, CBR0B, CBR0G, CBR1 and CBR4.

Figure 4F-N.

Material: 10 premaxillae (MGUV-26252, 40599, 40615, 40625, and 40663); 4 left maxillae (MGUV-26264 and 40601), 1 right maxilla (MGUV-36906), 5 left dentaries (MGUV-40492 and 40582), 6 maxillae (MGUV-26263, 40435, and 40454), 29 frontals (MGUV-26265, 40355, 40356, 40357, 40408, 40411, 40462, 40472, 40489, 40503, 40532, 40545, 40603, 40647, and 40677), 6 right dentaries (MGUV-40581 and 40692), 1 left dentary (MGUV-40614), 8 right dentaries (MGUV-23382, 26259, and 26262), 8 dentaries (MGUV-26261 and 40433), 143 tooth-bearing bones (MGUV-25296, 25299, 25300, 26253, 26260, MGUV-36907, 40412, 40434, 40460, 40461, 40476, 40529, 40572, 40585, 40613, 40623, 40666, 40667, 40656 and 40657), 1 vertebra (MGUV-40368), 2 caudal vertebrae (MGUV-40371), 21 vertebral centra (MGUV-40365, 40425, 40499, 40553, 40610, 40620, and 40668), and 1 left coxal (MGUV-40354).

Description:

Frontals are anteroposteriorly elongated bones. Within the studied material, there are the unfused (MGUV-26265, 40355, 40356, 40408, 40462, 40472, 40489, 40503, 40532, 40545, 40603, 40635, 40647, and 40677) and fused frontals (MGUV-40357 and 40411) (Figure 4F-J). In the latter cases, a not well-marked suture line is present in the middle region of its ventral surface (Figure 4J). Although that, all the elements have a very similar morphology; for this reason, they probably belong to different ontogenetic stages of the taxon. Frontals have a subtriangular shape with a relatively well-marked constriction. The dorsal surface is totally covered by fused osteodermal shield that show a vermicular ornamentation. The sulcus interfacialis, which separates frontal and frontoparietal scutes, is slightly convex anteriorly and is located approximately at the point of maximum constriction (Figure 4A and I). Unfortunately, neither the medial nor the lateral process nor the posterolateral is preserved. The posterior margin of these frontals is slightly interdigitated. In lateral view, the prefrontal facet is broad and wedge-shaped. Posteriorly, the facet for the postfrontal is thin and few-marked. Neither facet is in contact; thus, the frontal may have been exposed on the orbital when the animal was alive (Figure 4H). In ventral view, the *crista cranii* is broad and dorsoventrally flattened (Figure 4G and J). At least three well-defined foramina pierce this structure. The subolfactory process is broken.

Premaxillae are small and preserve only their alveolar region. Thus, any nasal processes are preserved. However, a pair of foramina is present at the base of this broken process (Figure 4K). In labial view, the premaxillae have a broad and short incisive process. 7-8 tooth positions are present, teeth are pleurodonts, isodonts, and cylindrical (Figure 4L). The lingual surface of the premaxillae is smooth (Figure 4M).

In lingual view, the dentaries show an open meckelian groove along their whole length. The most complete dentary (MGUV-26259) bears 14 tooth positions, with only four teeth in their life positions. These teeth are pleurodont, isodont, cylindrical, mono and bicuspid, and have a blunt apex. The ventral end of the dentary is concave. In labial view, the

dentaries show seven labial foramina. The posterior end of the dentary is not preserved (Figure 4N).

Remarks. Although the middle constriction is well-marked, it is less pronounced than the genera included in the tribe Eremiadini. Moreover, this clade has a typically fused frontal lacking a longitudinal suture line in the ventral view (Arnold 1989; Villa and Delfino 2019b). Some specimens of our sample (MGUV-40357 and 40411) show that line. This character has been interpreted as resulting from the fusion of the two halves during the late stages of ontogeny. As a result, few examples of current Lacertini genera show their frontals fused. Among Iberian genera, Barahona (1996) has reported that in large specimens of *Psammodromus algirus* (Linnaeus, 1758) and *Podarcis hispanicus* s.l. Steindachner, 1870, the frontal can be fused, and even if the suture is not visible. Regarding extinct lacertid taxa present in Eurasia, frontals are known in a few cases, and in those, they are from large species. Some of them seem to have unfused frontals, such as *Janosikia ulmensis* (Gerhardt, 1903) (Čerňanský et al. 2016) and *Plesiolacerta erasthenesi* Čerňanský and Augé, 2013 (Čerňanský and Augé 2013). On its behalf, taxa with fused frontals with ventral sutures are *Dracaenosaurus croizeti* Gervais, 1848 (Čerňanský et al. 2017); *Dormaalisaurus* sp. (Augé and Smith 2002); and *Pseudeumeces cadurcensis* Filhol, 1877 (Augé and Hervet 2009). All these taxa not only differ from our material by their larger size, but also by some morphological traits. Thus, *Dormaalisaurus* sp. has more pronounced interdigitations than the studied frontals (Augé and Smith 2002). The prefrontal facet is clearly wider in *Dr. croizeti* than in our material (Čerňanský et al. 2017). And, finally, the parietal tab is wider and more marked in *Ps. Cadurcensis* than the studied frontals (Augé and Hervet 2009).

The rest of the material included within this taxon has characters attributable to Lacertidae (i. e., fused premaxilla with an undivided palatal process distinct and developed; dentaries and maxillae with pleurodont teeth, with mono, bi, or tricuspid; dentaries with the Meckelian groove totally open and the ventral border of the bone concave). However, due to the osteology of the lacertid still being poorly understood, it is not possible to propose a more confident taxonomic attribution.

In conclusion, although the studied frontal bones exhibit certain similarities with the extant genera *Psammodromus* and *Podarcis*, it is not possible to propose an attribution below the family level. This is due to the significant osteological homogeneity of lacertids and the fact that the osteological differences between their various taxa are not yet fully understood. Furthermore, the possibility that the studied material corresponds to more than one taxon cannot be ruled out, given the high diversity of lacertids in modern ecosystems and their status as a dominant element of the European herpetofauna since the spectacular radiation of the group during the Neogene (Arnold et al. 2007).

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

Amphisbaenia Gray, 1844

Blanidae Kearney, 2003

Blanidae indet.

Localities: BC1, MAB5, and MAB11.

Figure 4O-Q.

Material: 1 left maxilla (MGUV-40361) and 3 left dentaries (MGUV-40552 and 40616).

Description:

MGUV-40361 is a left maxilla with a poor state of conservation (Figure 4O). Only preserves three fragmentary teeth. The largest of them is the central one. In labial view, two large foramina are present.

MGUV-40616 is a robust, short left dentary with eight dental positions, probably 9, and 7 teeth present (Figure 4P). They are pleurodont, conical, laterally compressed, unicuspid, and closely spaced. Moreover, the teeth are slightly inclined anteriorly. The first one is markedly expanded, with a broad base, being the most robust tooth of the dentary. The distal edge of the bone is broken. Thus, the mandibular symphysis is lost. The Meckelian groove is fully open along the entire length of the dentary. Although its proximal end has some mineral concretions, the surface of the bone seems smooth, without any foramina present, in labial view. On its behalf, MGUV-40552 includes two left dentaries that only preserve their proximal ends (Figure 4Q). The subdental shelf shows a constant depth, and at the last tooth position, it is narrow and turns dorsally. The intramandibular septum is well-preserved. Its ventral margin is fused with the medial wall of the dentary. Its posterior edge has a wide, subtriangular notch. At the base of the septum, a narrow and elongated incision is present. It might correspond to the impression of the splenial.

Remarks. The presence of a short, robust dentary indicates an Amphisbaenid among the material recovered from MAB5. Despite the poor state of preservation of the piece, some considerations about its taxonomy may be noted. Among the European fossil record of this order, the remains differ from the family Polyodontobaenidae in having, in contrast to the latter, the anterior teeth more developed than the posterior ones (Folie et al. 2016). Regarding Blanidae, the general morphology resembles the genus *Palaeoblanus*, in which the most anterior tooth is clearly more robust than the rest. Nevertheless, in MGUV-40616, this tooth is not the tallest; it is probably the second one, but it is eroded. Moreover, neither the number of teeth (seven in *Palaeoblanus*, eight, or nine in MGUV-40616) nor the tiny interdental gap has been reported in that blanid genus (Schleich 1988; Böhme 1999). The presence of enlarged anterior teeth has been reported in other Paleogene blanid genera, for example, *Cuvieribaena carlgansi* Čerňanský et al., 2015 from the locality of Le Bretou (Phosphorites du Quercy, late middle Eocene) (Čerňanský et al. 2015). Our material differs from the latter by a large number of teeth, and, apparently, in MGUV-40616, the teeth do not reach a uniform height. Regarding *Blanus*, our material does not fully match the general morphology of this genus. The different species of the genus *Blanus* have seven or eight teeth, with the ninth position only recorded in very exceptional cases (Bolet et al. 2014; Villa et al. 2019). The enlargement of the third tooth is a typical trait of the genus (Bailon 1991), but in our material, that tooth is not present. Thus, the generic attribution is unclear for that material.

Palaeoecology: Amphisbaenians are fossorial reptiles that currently inhabit tropical and subtropical regions (Augé 2012). However, the broad taxonomical attribution precludes any palaeoecological interpretation.

Iguania Coppe, 1864

Chamaeleonidae Rafinesque, 1815

?Chamaeleonidae indet.

Locality: CBR0B.

Figure 4R-S.

Material: 1 undetermined dental bone (MGUV-40413).

Description:

MGUV-40413 is a very fragmentary, undetermined dentary bone. The only two preserved teeth have an acrodont implantation, being fused to the upper margin of the bone. The teeth are mediolaterally compressed, large, and triangular in shape, with pointed apices. Both teeth are clearly well-spaced, with gaps measuring between 10% and 15% of the tooth length. An accessory cusp is apparently present on the anterior edge of the larger tooth (Figure 4R). In lingual view, the interdental grooves are ventrally directed, and the lateral surface of the teeth appears concave (Figure 4S). In the occlusal view, the interdental gap is well-developed. The cut edge of the teeth projects anterolaterally with respect to the central axis of the bone.

Remarks. Some features observed in the specimen, such as the acrodont dentition fused to the dorsal surface of the bone and the labiolingual compression of the teeth with a flattened lingual surface, are characteristic of Chamaeleonidae (Moody and Roček 1980). However, as Georgalis et al. (2023) pointed out, these traits are shared with some agamid taxa. Thus, under this premise and due to the poor preservation of the specimen, the attribution of this remain as chamaeleon needs to be met with some caution.

Chamaeleonids are a group of highly specialized and charismatic squamates, with 228 described species distributed across Africa, the Middle East, southern India, and Sri Lanka, as well as some Mediterranean islands and parts of southern Europe (Speybroek et al. 2016). Molecular data suggest a Cretaceous origin of chamaeleonids in Africa (Tolley et al. 2013); however, their fossil record remains sparse (Bolet and Evans 2014). The earliest fossils have been reported from the Early Miocene of Europe and Kenya (Bolet and Evans 2014). Chamaeleonids are thought to have reached Europe during MN3 (Čerňanský et al. 2015). Traditionally, the European fossil record of the group has been considered limited primarily to the Early and Middle Miocene of Central Europe. However, in recent years, new discoveries have expanded their known distribution within Europe for this time period. For instance, Georgalis et al. (2016) described the presence of chamaeleonids in Greece.

In the Iberian Peninsula, Böhme and Ilg (2003) noted the presence of *Chamaeleo* aff. *caroliquarti* at the Agramón site (MN3 or MN3/4, see Szyndlar and Alférez, 2005). Unfortunately, those fossils are now lost (Georgalis et al. 2016). More recently, Bolet et al. (2022) reported Chamaeleonidae indet. from the site of Turó de les Forques 1 (Vallès-Penedès Basin, Catalonia, northeastern Spain; MN3). Together with the material described in this study, these findings confirm the presence of chameleons in the Early Miocene of the Iberian Peninsula. In addition, Talavera and Sanchiz (1983) described remains of *Chamaeleo chamaeleon* from the Bronze Age site of Rincón de la Victoria (Málaga, southern Spain). Currently, this taxon occurs discontinuously along coastal regions in the south and east of the Iberian Peninsula, from the Algarve (Portugal) to Valencia (Spain). The origin of these Iberian populations was likely anthropogenic, resulting from recent introductions (Salvador 2014).

Palaeoecology. To date, all Eurasian chamaeleonid fossils have been tentatively assigned to the genus *Chamaeleo* (Čerňanský 2010b, 2011; Sankhyan and Čerňanský 2016). Although, as Georgalis et al. (2016) noted, the absence of a particular group in the fossil record does not preclude its existence at a given time, there is currently no evidence for the presence of other chamaeleonid genera in Eurasia during the Miocene.

Most species within *Chamaeleo* are typically arboreal. However, some exhibit less arboreal behaviour, such as *Chamaeleo arabicus* Matschie, 1893 (van der Kooij 2000) and *Chamaeleo namaquensis* Smith, 1831 (Tolley and Burger 2007). Čerňanský (2010b) hypothesized that chameleons with non-contacting tooth bases inhabited closed habitats. Following this hypothesis, the studied specimen may belong to a chameleon that lived in forested or densely vegetated shrubland environments.

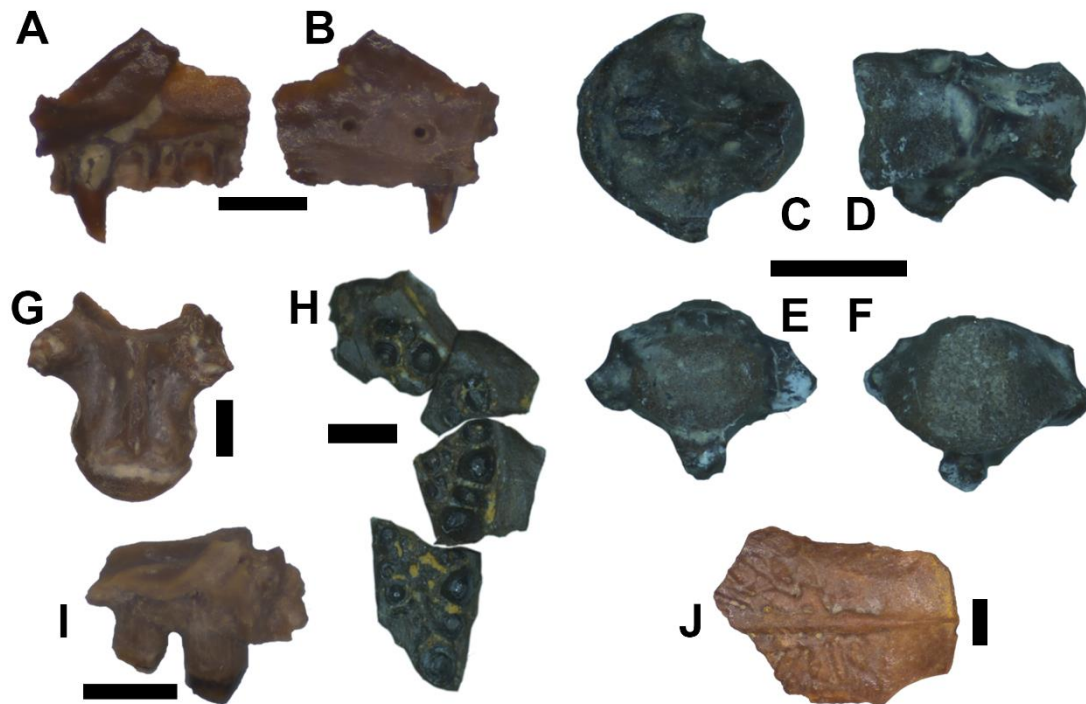


Figure 5. Anguids from Ribesalbes-Alcora Basin. A-G) *Ophisaurus* sp., A-B, right maxilla (MGUV-40681) in lingual (A) and labial (B) views; C-F, axis (MGUV-40450) in ventral (C), lateral (D), anterior (E), and posterior (F) views; G, dorsal vertebra (MGUV-40422) in ventral view. H-I) cf. *Pseudopus* sp., possible pterigoides (MGUV-40550) in ventral view (H) and tooth-bearing bone (MGUV-40496) in lingual view (I). J) Anguidae indet., osteoderm (MGUV-40653) in dorsal view (J). Scale bar equal to 0.5 mm.

Anguimorpha Fürbringer, 1900

Anguidae Gray, 1825

Ophisaurus Linnaeus, 1766

Ophisaurus sp. sensu lato

Localities: MCX4, BC1, MAB0B, MAB3, MAB6, MAB11, MAB0A, MAB0B, MAB0G, and CBR3.

Figure 5A-G.

Material: 1555 osteoderms (MGUV-40403, 40417, 40418, 40419, 40427, 40431, 40455, 40466, 40601, 40629, and 40680), 2 right maxillae (MGUV-40537 and 40681), 1 maxilla (MGUV-40451), 1 left dentary (MGUV-40565), 7 tooth-bearing bones (MGUV-38352, 40388, 40436, and 40596), 3 isolated teeth (MGUV-40494), 1 axis (MGUV-40450), and

58 vertebral centra (MGUV-40420, 40421, 40422, 40452, 40453, 40456, 40554, 40556, 40586, and 40630).

Description:

A large number of osteoderms have been recovered from numerous sites within the studied basin. The most complete specimens are rectangular in shape and longer than wide. These osteoderms display two clearly distinct regions. The anterior region has a smooth surface (gliding surface *sensu* Hoffstetter 1962), initially covered by the preceding osteoderm in the living animal. The remaining surface exhibits vermiculate ornamentation and a low longitudinal keel running centrally across it.

Four fragments of potential maxillae were recovered. All are small in size. The highest number of tooth positions is six in specimen MGUV-40681. The preserved teeth are pleurodont, conical, and slightly recurved both distally and lingually. The apices possess well-developed and sharp mesial and distal cutting edges. No striations are visible on the tooth apices. The interdental gaps measure approximately one-third of the total tooth width. The *sulcus dentalis* is poorly developed (Figure 5A). In lingual view, only one third of the preserved tooth in MGUV-40596, which, based on its size, likely belonged to the middle region of the tooth row, extends above the *crista dentalis* (Figure 5B).

As with maxillae, the dentaries are also fragmentary. The teeth are similar to those described above. In lingual view, the Meckelian groove is open. MGUV-40405 presents the Meckelian groove in lateral position.

The centrum of the axis is large and robust. The odontoid process is fused to the centrum without any suture. This process is short and wide, with a blunt border. In ventral view, the odontoid process slightly projects beyond the anterior edge of the centrum. In this view, the *margo lateralis* is straight, giving the centrum a rhomboid shape. The centre is of similar width and length. The anterior region of the centrum is clearly convex. The synapophysis, which is wide and short, projects posterolaterally, forming an angle of about 45° with respect to the axis of the centrum. This inclination gives the front part of the centrum a rounded appearance. The axis shows the bases of two robust intercentra, which are not fused. A protruding keel connects both intercentra, formed by the robust intercentrum 3. A well-defined pair of subcentral foramina is present (Figure 5C). In a lateral view, the odontoid process projects anterodorsally and is inclined at approximately 130° relative to the horizontal plane (Figure 5D). In anterior view, this structure is ovoid in shape. The anterior articular surface is wider than tall. Due to the anterior projection of the odontoid process on the dorsal part of the facet, the entire surface is dorsoventrally concave (Figure 5E). In the posterior view, the condyle is dorsoventrally flattened and broader than it is tall, having an elliptical shape. In this view, the dorsal margin of the condyle is slightly convex (Figure 5F).

58 vertebral centra have been recovered in five sites of the Ribesalbes-Alcora Basin (CBR0B, CBR0G, MAB3, MAB6, and MAB11). All are procoelous and longer than wide (Figure 5G). In ventral view, the *margo lateralis* of the centrum is slightly concave. In its anterior region, the centra show a pair of well-defined subcentral foramina. Some centra have a faintly defined haemal keel occupying two-thirds of their total length. However, the studied material presents a high degree of variability. Thus, there are centra with clearly concave *margo lateralis*, whereas other fossils show parallel borders (MGUV-40451). Moreover, defining this character is difficult because of damage to the anterior region in some specimens. In the anterior and posterior views, the cotyle and condyle are dorsoventrally depressed, respectively.

Remarks. Some traits are consistent with an attribution to the genus *Ophisaurus* sensu lato, i.e., presence of recurved, sharply pointed, and broadly based teeth; elliptical condyle of the axis with a convex dorsal edge in posterior view, and dorsal vertebra with convex *margo lateralis* (Klembara et al. 2014; Čerňanský et al. 2019). *Ophisaurus* traditionally includes three highly divergent lineages: *Ophisaurus* s.s. from North America, *Dopasia* from Southeast Asia, and *Hyalosaurus* from North Africa (Macey et al. 1999). However, osteological differentiation among these taxa is still poorly understood. Among the various axis vertebrae identified by Čerňanský et al. (2019) for the extant species of *Ophisaurus* s.l., the studied material resembles that of *Dopasia* (= *Ophisaurus*) *gracilis* (Gray, 1845). Nevertheless, the tooth morphology is not consistent with any extant species of the genus, as they typically exhibit lingual striations (Klembara et al. 2014). Although most tooth-bearing bones studied are small and may belong to juveniles (where such striation is apparently absent or weakly developed, as noted by Klembara et al. 2014), the presence of a large isolated tooth (MAB3-890) demonstrates that adult specimens also lacked striations.

Numerous fossil remains of *Ophisaurus*-like taxa with unstriated teeth have been described from localities of similar age, including *Ophisaurus* sp. from Béon 1 (France) (Rage and Bailon 2005), *Ophisaurus* cf. *spinari*, *Ophisaurus* sp. 1 and 2 from Dolnice (Czech Republic) (Roček 1984), *Ophisaurus* from Oberdorf 4 (Germany) (Čerňanský et al. 2015), *Ophisaurus* morphotype 2 from Ulm-Westtangente (Germany) (Klembara et al. 2019), Anguine morphotype I from Merkur-Nord (Czech Republic) (Klembara 2015), and cf. *Ophisaurus* sp. from Karydia-3 (Greece) (Georgalis et al. 2019). Some differences between our material and these taxa concern the width of the tooth base relative to the apex, the degree of curvature, and the extent to which the tooth height exceeds the crista dentalis. However, Roček (1984) noted that such traits can exhibit intraspecific variability.

Nowadays, *Ophisaurus* s.l. is represented in Asia by six species distributed from northern India through the Indochinese Peninsula southwards to Indonesia: *Ophisaurus buettikoferi* Lidth de Jeude, 1905; *Ophisaurus gracilis* (Gray, 1845); *Ophisaurus hainanensis* Yang, 1983; *Ophisaurus harti* Boulenger, 1899; *Ophisaurus sokolovi* Darevsky and Nguyen, 1983; and *Ophisaurus wegneri* Mertens, 1959 (Nguyen et al. 2011). As discussed above, many neontologists consider these taxa to belong to the genus *Dopasia*. Regarding North Africa, only *Ophisaurus koellikeri* (Günther, 1873) is recorded in northern Morocco, which has been transferred to the monotypic genus *Hyalosaurus* Günther, 1873 (Macey et al. 1999).

Palaeoecology: The Eurasian taxa of *Ophisaurus* s.l. include *Dopasia* and *Hyalosaurus*. The former forest-dwelling species, although little is known about their ecology (Nguyen et al. 2011). *Hyalosaurus koellikeri*, the sole species in its genus, is better understood and considered a forest-dwelling lizard (Escoriza and Comas 2015). According to the latter authors, the occurrence of the species is mainly explained by the presence of forest land, but *H. koellikeri* does not have a strong preference for a specific habitat composition and was found occupying both dry forests of junipers and evergreen oaks and humid deciduous forests.

Members of *Ophisaurus* inhabited Europe until the latest Middle Pleistocene, coinciding with the disappearance of the subtropical humid forest biome around 1.2 Ma. The extirpation of the genus in this area occurred during the Early-Middle Pleistocene transition, an episode of major climatic change associated with the intensification of Northern Hemisphere glaciation between 1.4 and 0.7 Ma (Blain and Bailon 2019). In this sense, the *Ophisaurus* taxa with unstriated teeth recovered in European localities have

been interpreted as forest species (i.e., *Ophisaurus acuminatus* (Klembara and Čerňanský 2020).

***Pseudopus* Merrem, 1820**

cf. *Pseudopus* sp.

Locality: MAB0A and MAB11.

Figure 5H-I.

Material: 197 osteoderms (MGUV-40490, 40502, 40506, and 40516), 1 pterygoides (MGUV-40550), 2 tooth-bearing bones (MGUV-40496 and 40549), 6 vertebral centra (MGUV-40501 and 40517).

Description:

MGUV-40550 is probably a fragmentary pterygoid. This bone shows three to four tooth rows on the ventral surface of the bone. The teeth are low, stout, and blunt, but some of them bear a small cusp. The most prominent teeth are located in the lateral row, while the remaining ones are smaller (Figure 5H).

The recovered tooth-bearing bones have pleurodont, monocuspid, cylindrical, bulbous, and robust teeth. Their crowns are blunt without distinguishable cusps. The teeth are well-spaced and non-striated (Figure 5I).

Remarks: Nowadays, the genus is limited to a single species, *Pseudopus apodus* (Pallas, 1775). Its distribution includes the Balkans, the Crimean Peninsula, and the Ciscaucasia region in Europe, as well as Asia Minor and the Middle East (Speybroeck et al. 2016). So far, four extinct species have been recognized: *Pseudopus confertus* Klembara and Rummel, 2018 (Early Miocene, MN3, Ahníkov I, Merkur North opencast mine, Czech Republic), *Pseudopus ahnikoviensis* Klembara, 2012 (Early Miocene, MN3, Central Europe), *Pseudopus laurillardii* (Lartet, 1851) (Early–Middle Miocene of Europe), and *Pseudopus pannonicus* (Kormos, 1911) (Late Miocene–Middle Pleistocene of central and eastern Europe; Klembara and Rummel 2018). The Iberian fossil record of *Pseudopus* is scarce and mainly limited to the Early–Middle Pleistocene of eastern Spain (Blain et al. 2016). During the Miocene, the genus is only reported in the Iberian Peninsula from the localities of els Casots (cf. *Pseudopus*; earliest MN5, Middle Miocene; Vallès-Penedès Basin, Catalonia, Spain), and Crevillente 2 (MN11, Late Miocene; Bajo Segura Basin, Comunitat Valenciana, Spain) (Casanovas-Vilar et al. 2022; Marquina-Blasco et al. 2025).

Palaeoecology: Although the only extant species of the genus *Pseudopus*, *Pseudopus apodus*, inhabits dry and well-vegetated rocky slopes, extinct species have been interpreted as subhumid to humid forest dwellers (Klembara et al. 2010).

Anguidae indet.

Localities: MCX1, MCX2, MCX3, MTR2, MCX5, MCX6, MTR3, MCX7, BC1, BC2, MAB0A, MAB0B, MAB1, MAB3A, MAB4, MAB5, FS1, MAB7, MAB8, MAB9, MAB10, MAB11A, MAB11B, and MAB13.

Figure 5J.

Material: 1574 osteoderms (MGUV-38555, 38556, 40363, 40379, 40380, 40391, 40395, 40409, 40437, 40446, 40447, 40448, 40470, 40471, 40473, 40474, 40475, 40488, 40530, 40542, 40543, 40570, 40571, 40602, 40607, 40621, 40622, 40632, 40636,

40638, 40639, 40648, 40653, 40658, 40659, 40660, 40662, 40665, 40669, 40678, 40682, 40683, and 40689), 1 pterigoide (MGUV-40675), 2 tooth-bearing bones (MGUV-38370), and 55 vertebral centra (MGUV-40366, 40367, 40387, 40392, 40407, 40438, 40443, 40449, 40464, 40468, 40483, 40536, 40541, 40617, 40619, 40635, 40640, 40641, 40664, 40671, and 40673).

Description:

This taxon includes all the material exhibiting characters attributable to Anguinae but which cannot be confidently assigned to either of the two genera described in the present study, due to the poor state of preservation of the material or its limited taxonomic value beyond the family level.

Remarks: Despite the above, the presence of subrectangular osteoderms bearing a longitudinal keel is a trait found in non-*Anguis* anguine taxa (i.e., *Pseudopus* or *Ophisaurus* s.l.; Hoffstetter 1962).

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

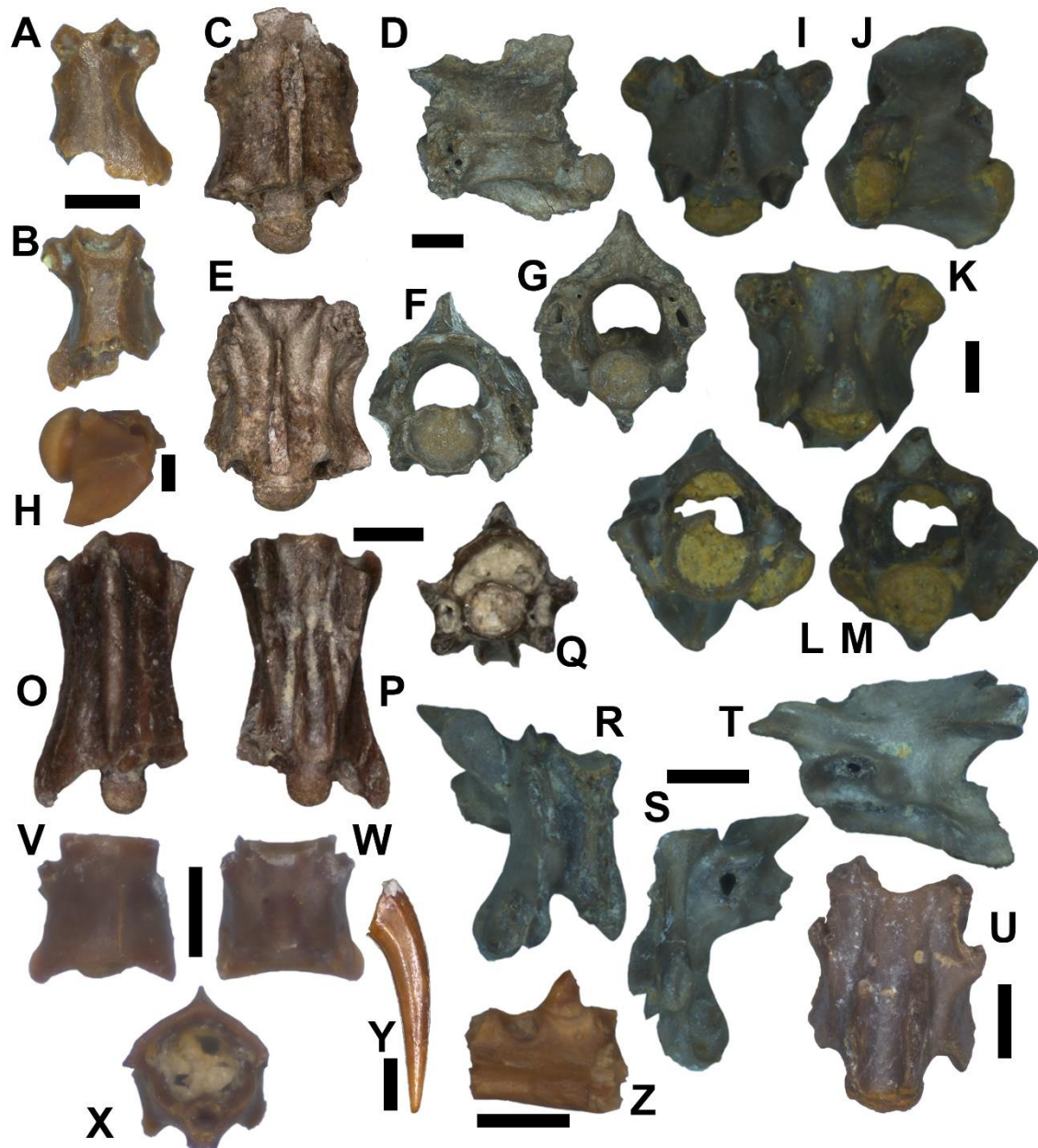


Figure 6. Snakes from Ribesalbes-Alcora Basin. A-B) *Scolecophidia* indet., precaudal vertebra (MGUV-40416) in dorsal (A) and ventral views (B). C-G) *Palaeonatrix* sp., precaudal vertebra (MGUV-40544) in dorsal (C), lateral (D), ventral (E), anterior (F), and posterior (G) views; vertebral centrum (MGUV-40382) in lateral view (H). I-M) ?*Viperidae* indet., precaudal vertebra (MGUV-40592) in dorsal (I), lateral (J), ventral (K), anterior (L), and posterior (M) views. O-Q) *Aletinophidia* indet. Morphotype 1, caudal vertebra (MGUV-40424) in dorsal (O), ventral (P), and anterior (Q) views. R-U) *Aletinophidia* indet. Morphotype 2, caudal vertebra (MGUV-40527) in dorsal (R), ventral (S), and lateral (T); U) caudal vertebral centrum (MGUV-40519) in ventral view. V-X) *Aletinophidia* indet. Morphotype 3, caudal vertebra (MGUV-40362) in dorsal (V), ventral (W), and posterior (X) views. Y-Z) *Serpentes* indet., isolated tooth (MGUV-25343) in lateral view (Y); tooth-bearing bone (MGUV-40359) in lateral view (Z). Scale bar equal to 0.5 mm, except for R-U (1 mm).

Serpentes Linneaus, 1758

Scolecophidia Coppe, 1864

Scolecophidia indet.

Locality: CBR0B.

Figure 6A-B.

Material: 1 trunk vertebra (MGUV-40416).

Description:

The vertebra has a short centrum. In dorsal view, the anterior edge of the neural arch is missing. Although it is partially broken, it is appreciable that the prezigapophysis projects anterolaterally. No neural crest is present. The postzigapophysis is broad and short (Figure 6A). In ventral view, the centrum is elongated. Its surface is relatively concave and has a pair of subcentral foramina. The centrum is devoid of any structure, as a haemal keel or hypapophysis. The posterior edge of the centrum is broken (Figure 6B). In the anterior view, the neural arch is dorsoventrally flattened. Likewise, the cotyle is dorsoventrally flattened and elliptical. In the posterior view, the neural arch is again flattened dorsoventrally, although to a lesser extent in the anterior view.

Remarks: The described characters are typical of Scolecophidia. However, vertebrae lack taxonomically valuable information below the subordinal level (Bailon 1991).

Palaeoecology: Scolecophidians are a group of fossorials, primitive snakes that inhabit tropical and subtropical regions, with greater diversity on the Gondwanan continents (Vidal et al. 2010). Currently, the unique autochthonous scolecophidian in Europe is the blind snake (*Xerotyphlops vermicularis*). This species occupies open, dry habitats, characterized by both heavily degraded vegetation and dense stands of grasses and herbs (Akman and Göçmen 2019). The main factors affecting the distribution of the species are the annual mean temperature, the driest-month precipitation, and annual precipitation (Afsar et al. 2016).

Colubridae Opperl, 1811

Natricinae Bonaparte, 1838

***Palaeonatrix* Szyndlar, 1982**

***Palaeonatrix* sp.**

Localities: BC1, MAB0B, MAB3, MAB5, and MAB11.

Figure 6C-H.

Material: 8 vertebrae (MGUV-40377, 40533, 40544, 40557, and 40583) and 40 vertebral centra (MGUV-40376, 40378, 40382, 40383, 40404, 40558, 40590, and 40618).

Description:

The studied vertebrae are procoelous and small-sized. In dorsal view, the neural crest runs along the entire length of the neural arch except for its anterior third. The interzigapophysarian constriction is poorly marked. The prezigapophysis and postzigapophysis are broken (Figure 6C). In lateral view, the neural crest is low and does not overhang posteriorly. The *margo lateralis* is well defined and reaches the condyle.

Behind the prezygapophyses, there is a large, well-defined foramen. The parapophyseal process is wide and short, projecting anteriorly. The centrum has a prominent haemal keel that terminates in a wide hypapophysis. However, the end of the haemal keel is broken. It does not contact the condyle (Figure 6D and H). In ventral view, the centrum is elongated (approximately twice as long as it is wide) and narrow. Prominent and blunt subcentral ridges are presents. The subcentral grooves are well-defined and relatively narrow. They extend almost parallel to the long axis of the vertebra (Figure 6E). Both the cotyle and the condyle are relatively small and rounded (Figure 6F and G), although in some specimens they appear slightly dorsoventrally flattened. It is not possible to discern whether this is due to deformation by sediment pressure. In anterior view, the neural arch is high, flattened laterally, and shows its upper limit slightly domed (Figure 6F).

Remarks: The presence of a prominent anterior keel accompanying the hypapophysis, a strongly developed *margo lateralis* reaching the condyle, and a vestigial neural spine are diagnostic characters of the genus *Palaeonatrix* (Szyndlar 1987; Rage and Bailon 2005). Two species are recognized within this genus, *Palaeonatrix silesiaca* Szyndlar, 1982, and *Palaeonatrix lehmani* (Rage and Roček 1983), which are distinguishable based on minor features, such as the degree of lateral expansion of the postzygapophysis and the different size of the condyle (Szyndlar 1991). The fossil record of *Palaeonatrix* is primarily known from the Miocene of Eastern Europe, whereas its record in the Western region is scarcer. Thus, a probably new taxon, morphologically very close to *P. lehmani*, has been reported from the French localities of Béon 1 (MN4) (not figured) and Sansan (MN6) (Augé and Rage 2000; Rage and Bailon 2005). In our material the size of the cotyle and the neural arch are similar. In contrast, in *P. lehmani* from Petersbusch 2, the second is slightly larger than the first, as is the case in *P. aff. lehmani* from Sansan (Augé and Rage 2000). However, the poor state of conservation of the material studied here precludes any specific attribution.

This genus is known mainly from the Early and Middle Miocene of Eastern Europe (Szyndlar 1991), but only two previous reports from Western Europe, the above-mentioned French localities of Béon 1 and Sansan (Augé and Rage 2000; Rage and Bailon 2005). Thus, the material from the Ribesalbes-Alcora Basin represents the first mention of *Palaeonatrix* from the Iberian Peninsula.

Palaeoecology: *Palaeonatrix* is presumed to have inhabited diverse aquatic environments based on taxonomic inference.

Viperidae Opperl, 1811

cf. Viperidae indet.

Localities: MAB3, MAB11 and CBR0D.

Figure 6I-M

Material: 1 vertebra (MGUV-40592) and 3 vertebral centra (MGUV-40441, 40442, and 40560).

Description:

MAB3-886 is a small-sized procoelous vertebra. It is as long as it is wide (however, MAB11-168 is a centrum slightly longer than wide). The prezygapophysis is distinct from the neural arch, but the postzygapophyses are broken. The interzygapophyseal constriction was well developed (Figure 6I). In lateral view, the diapophysis is rounded, and the parapophysis projects antero-ventrally. The centrum is transversally convex. The

hypapophysis preserves only its base, which is in contact with the condyle (Figure 6J). In ventral view, the centrum is triangular in shape, wider anteriorly than posteriorly, with a poorly defined *margo ventralis*. A pair of small subcentral foramina is located in the anterior part of the centrum (Figure 6K). The condyle and the cotyle are large and rounded, respectively, in anterior and posterior views (Figure 6L and M). In this latter view, the neural arch is slightly dorsoventrally flattened (Figure 6M).

Remarks: The studied remains share some characteristics typical of Viperidae, such as a dorsoventrally flattened neural arch, a transversely convex centrum with a vague *margo ventralis*, a well-developed cotyle and condyle, and a condyle ventrally connected to the base of the hypapophysis (Bailon 1991). However, the poor state of conservation of these remains allows us to propose only a very tentative taxonomic attribution for them.

Palaeoecology: The taxonomic attribution of this taxon precludes any palaeoecological interpretation.

Aletinophidia indet.

This taxonomic attribution includes material which, either because of its poor state of preservation or its low value for taxonomic determination, could not be included in any of the taxa described above. However, it is possible to distinguish three morphotypes of caudal vertebrae, which are described and commented.

Aletinophidia indet. Morphotype 1

Localities: MTR2, MCX7, BC1, MAB0A, MAB0B, MAB1, MAB7, MAB8, and CBR0B.

Figure 6O-Q.

Material: 22 caudal vertebrae (MGUV-40370, 40424, 40493, 40520, 40521, 40522, 40535, 40590, 40633, 40637, 40690, 40692, 40651, and 40654).

Description:

The vertebrae are procoelous, small, and elongated. In dorsal view, the interzygapophyseal constriction is poorly marked. The neural spine extends over the entire length of the neural arch, except for the region of the zygosphene. It is broad and trilobate. The prezygapophysis projects anteriorly and presents a large, elliptical articular surface. The prezygapophyseal process is broken (Figure 6O). In lateral view, the neural spine is low. The *margo lateralis* is not well defined. The pleurapophyses are well-developed, triangular in shape, and extend through the anterior three-quarters of the total centrum length. They project anteroventrally. The haemal processes are low and rounded. The lateral foramen is small and poorly defined. In ventral view, the centrum is triangular and elongated (Figure 6P). In anterior view, the neural canal is dorsoventrally compressed, with a convex roof (Figure 6Q). Cotyle and condyle are small and rounded in the anterior and posterior views, respectively.

Remarks: Among fossil colubrid taxa, those preserving caudal vertebrae are rare (Szyndlar 2012). Recently, Ivanov et al. (2025) tentatively attributed a caudal vertebra to *Palaeonatrix* aff. *lehmanni* from the Early Miocene locality of Wintershof-West, Germany, on the basis of the low neural spine and large diameter of the cotyle. Our material differs from this remain by its lower neural spine and the convex shape of the roof of the neural canal in anterior view.

Also, this type of remains is known from two taxa of the genus *Texasophis*: *Texasophis bohemiacus* Szyndlar, 1987, and *Texasophis* sp. from the Turkish site Kilçak 3B (MN1, early Miocene) (Szyndlar 1994; Syromyatnikova et al. 2019). The present material differs from *Texasophis* sp. mainly in the shape of the pleurapophyses in ventral view. In our specimens, the pleurapophyses are longer (exceeding half the centrum length) and have straight, inclined edges. In contrast, in *Texasophis* sp., the edges are obtuse, giving the pleurapophysis a trapezoidal appearance. Furthermore, in *Texasophis* sp., both cotyle and condyle are dorsoventrally flattened (Fig. 10 in Syromyatnikova et al. 2019), whereas in our specimens, both are rounded. However, these differences may be due to the vertebral position within the tail, as the Kilçak material likely corresponds to the anterior caudal region. Regarding *T. bohemiacus*, the described vertebrae are indistinguishable from those of this species from the Ehrenstein 12 site (Middle Oligocene, Germany; Szyndlar 1994). Nevertheless, two reasons prevent a genus-level assignment: (1) the absence of additional remains corroborating the presence of *Texasophis* in the studied assemblage, and (2) the limited comparative data on caudal vertebrae in fossil colubrids.

Aletinophidia indet. Morphotype 2

Locality: MAB0A.

Material: 1 caudal vertebra (MGUV-40527) and 1 caudal vertebral centrum (MGUV-40519).

Figure 6R-U

Description:

MGUV-40527 preserves only its left side. In dorsal view, the interzygapophyseal constriction is well marked (Figure 6R). The prezygapophysis is distinguishable from the rest of the vertebra MGUV-40527. The prezygapophyseal process is short and acuminate. The centrum appears slightly longer than wide in ventral view (Figure 6S). The articular surface of the postzygapophysis is rounded. The lymphapophyses are broken; however, the dorsal ramus retains its base, which is broad and dorsoventrally flattened. The presence of lymphapophyses suggests that the ventral structure corresponds to the left branch of the haemal process, which is wide, prominent, and has parallel margins; it also appears tall in lateral view (Figure 6T). The vertebra has a cotylar neck distinct from the centrum (Figure 6U).

Remarks. Unfortunately, the poor state of preservation does not allow for a more precise taxonomic attribution.

Aletinophidia indet. Morphotype 3

Localities: BC1, MAB0A, MAB3, CBR0C, and CBR1.

Figure 6V-X

Material: 11 caudal vertebrae (MGUV-40362, 40369, 40372, 40373, 40439, 40456, 40508, and 40589).

Description:

The following remains are small procoelous vertebrae. In dorsal view, the interzygapophyseal constriction is poorly marked. The zygosphene is slightly concave. Prezygapophyses are indistinct from the neural arch and project anterolaterally (Figure 6V). In the lateral view, the neural spine is low. The margo lateralis is well marked. The

lateral foramen is large, and a small accessory foramen is present behind the paradiapophysis. The margo ventralis is weakly defined. In a ventral view, the centrum is short and slightly longer than it is wide. A pair of large, well-defined subcentral foramina is present. The centrum bears paired haemal processes which, in lateral view, are short and project ventrally. The pleurapophyses are directed anteroventrally (Figure 6W). In the anterior view, the neural canal is large and dorsoventrally flattened (Figure 6X). Both cotyle and condyle are small and dorsoventrally compressed in anterior and posterior views, respectively.

Remarks. The poor preservation of the specimens prevents any precise taxonomic identification.

Serpentes indet.

Localities: MCX3, MTR2, MTR3, MCX7, BC1, BC2, MAB0A, MAB0B, MAB1, MAB3, MAB3A, MAB5, FS1, MAB6, MAB9, MAB10, MAB11, MAB11A, CBR0A, CBR0B, CBR0D, CBR0G, and CBR1.

Figure 6Y-Z.

Material: 1 left dentary (MGUV-40628), 1 right dentary (MGUV-40469), 2 dentaries (MGUV-40428 and 40589), 2 tooth-bearing bones (MGUV-40359), 32 isolated teeth (MGUV-25343, 36660, 36672, 36741, 36764, 40485, 40491, 40586, 40626, and 40627), 7 vertebrae (MGUV-40509, 40510, 40512, 40513, 40527, and 40676), 3 isolated neural arch (MGUV-40507), 262 vertebral centra (MGUV-40364, 40374, 40393, 40415, 40423, 40430, 40457, 40466, 40467, 40481, 40482, 40498, 40500, 40511, 40514, 40518, 40525, 40526, 40534, 40540, 40559, 40561, 49562, 40563, 40584, 40585, 40587, 40588, 40591, 40604, 40626, 40631, 40641, 40642, 40650, 40661, and 40691), and 27 isolated condyles (MGUV-40375).

Description:

The material included present characters attributable to Serpentes. However, the poor state of conservation precludes any more precise taxonomical attribution.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

Squamata indet.

Localities: ACS2, MAB0A, MAB0C, MAB3, MAB4, MAB8, and CBR0B.

Material: 3 osteoderms (MGUV-40505, 40538, and 40608), 2 tooth-bearing bones (MGUV-25298 and 40633), and 6 vertebral centra (MGUV-40346 and 40426).

No more precise attribution is possible for these materials due to their poor state of conservation.

Palaeoecology: The taxonomical attribution of that taxon precludes any palaeoecological interpretation.

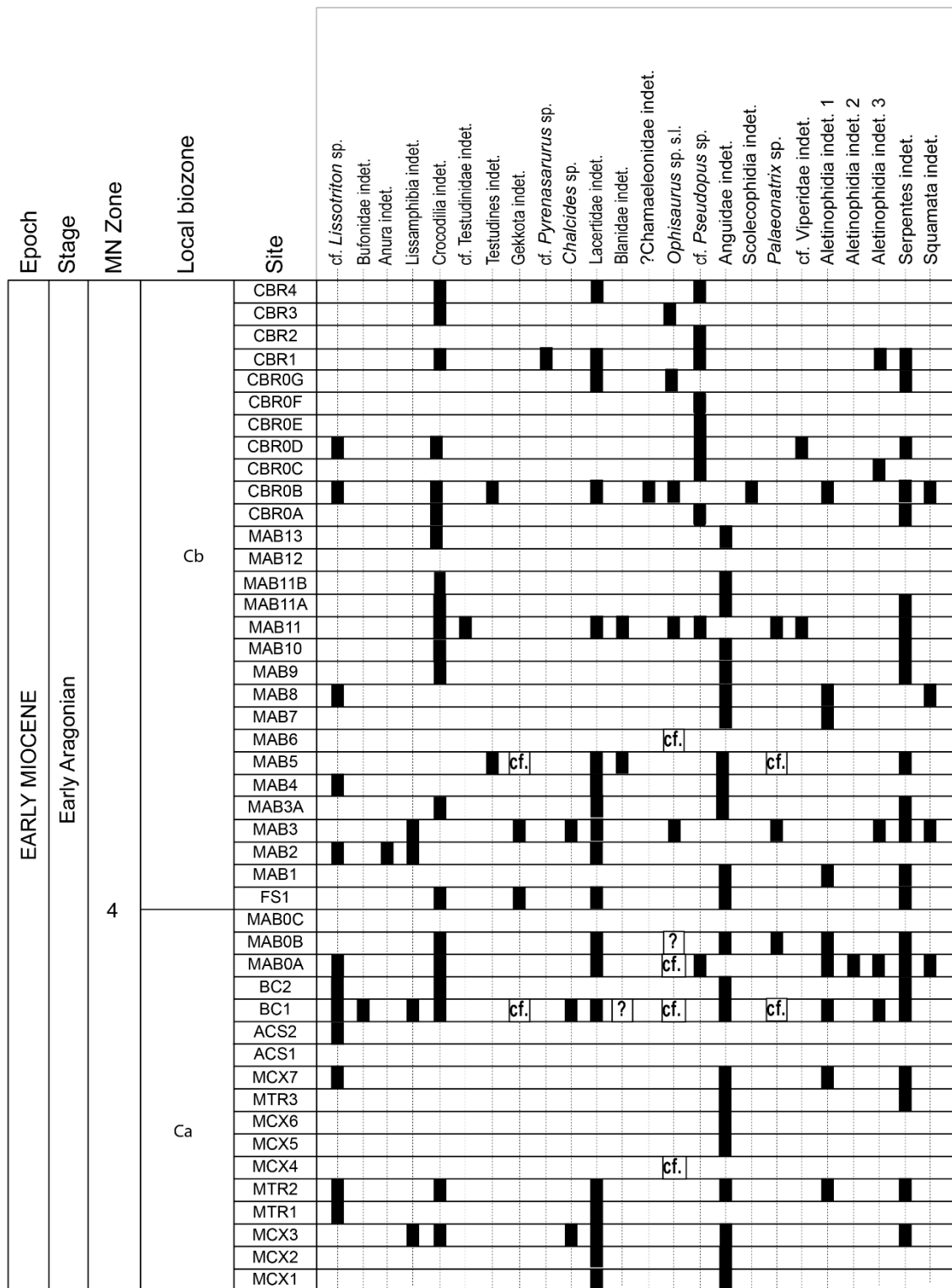


Figure 7. Biostratigraphical distribution of the palaeoherpetofaunal taxa from the different sites of the Ribesalbes-Alcora basin.

DISCUSSION

Palaeoecological implications

A total of 4,690 remains of reptiles and amphibians were recovered from various sites within the Ribesalbes-Alcora Basin (Figure 7). By far, the most common elements are

anguid osteoderms (3,317, 70.73% of the overall) (Table 1). The studied herpetofauna comprises 25 taxa. There are no significant changes in the faunal composition throughout the sequence. However, based on the appearance of specific taxa, some palaeoecological implications can be inferred. Among the localities studied, the following can be considered as intensively sampled (from the oldest to youngest): MCX3, MTR2, BC1, MAB0A, MAB0B, FS1, MAB3, MAB5, MAB11, CBR0B, and CBR1 (Crespo et al. 2019c). Therefore, the palaeoecological analysis is primarily based on these sites.

Table 1. Recovered anguid osteoderms from each studied site of the Ribesalbes-Alcora Basin. The sites are ordered from the oldest to the youngest locality.

Site	<i>Ophisaurus</i> sp.	cf. <i>Ophisaurus</i> sp.	cf. <i>Pseudopus</i> sp.	Anguidae indet.	Nº osteoderms
MCX1				4	4
MCX2				1	1
MCX3				43	43
MTR1				3	3
MTR2				203	203
MCX4		62			62
MCX5				7	7
MCX6				2	2
MTR3				2	2
MCX7				4	4
BC-1				358	358
BC-2				21	21
MAB0A			197		197
MAB0B				25	25
FS1				90	90
MAB1				1	1
MAB3	682				682
MAB3A				7	7
MAB4				10	10
MAB5				280	280
MAB6		15			15
MAB7				9	9
MAB8				65	65
MAB9				185	185
MAB10				19	19
MAB11	334				334
MAB11A				6	6
MAB11B				15	15
MAB13				4	4
CBR0A				7	7
CBR0B	428				428
CBR0C				31	31
CBR0D				25	25
CBR0E				1	1
CBR0F				2	2
CBR0G	30				30
CBR1				124	124
CBR2				4	4
CBR3				2	2
CBR4				9	9

Nº osteoderms	1474	77	197	1569	3317
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Taxa linked to aquatic habitats (i.e., lissamphibians and crocodylians) are common at most sites, although they are absent from MCX1, 2, 4, 5, and 6; MTR3; MAB0C, 1, 6, 7, and 8; and CBR0C and 2. The lithologies of the section indicate a depositional context interpreted as a distal deltaic and shallow lacustrine environment (Anadón 1983; Crespo 2017; Crespo et al. 2019c). Based on this, and following the palaeoecological inferences realized by Crespo (2017) and Albesa et al. (2022), we observe variability in “wet” and “dry” conditions throughout the Ribesalbes–Alcora Basin sequence. In this context, we have applied the HEG method to the herpetological assemblages of the MCX3, MTR2, BC1, MAB0A, MAB0B, FS1, MAB3, MAB5, MAB11, CBR0B, and CBR1 sites (Table 2). Nowadays, the Mean Annual Precipitation (MAP) of the basin is 432.19 ± 7.21 mm (MAP_{max}: 454 mm; MAP_{min}: 418 mm). Estimated MAP values indicate higher precipitation than today for all the sites, except for MAB0A.

For comparison with other proxies in the outcrop—namely, small mammals, gastropods, and isotopes (Ríos 2013; Álvarez-Parra et al. 2021; Albesa et al. 2022; Crespo 2017; Crespo et al. 2025, and references therein)—we interpret “humid (or dry) conditions” based solely on the ecological preferences of the identified taxa, as indicating high precipitation. High annual rainfall generally implies humid environments, but this is not always the case, as it depends on several factors, including the annual distribution of precipitation, actual evapotranspiration, local soil conditions, microclimate, and vegetation cover and structure (Ritchie et al. 1999; Beck et al. 2018; Wright and Francia 2024; Kim and Johnsons 2025). Nonetheless, we adopt a simplified approach to allow comparison with the aforementioned proxies.

The estimated MAP at the oldest site, MCX3, is 564.93 mm, higher than the current average for the basin and the second-lowest rainfall value in the overall sequence (Figure 8; Table 2). The oldest site, MCX3, includes both aquatic and terrestrial taxa. Among the latter, the presence of *Chalcides* sp. and Anguidae indet., taxa linked to forest or shrubland vegetation, is notable. The small mammal fauna from MCX3 seems to corroborate the presence of open forest (Crespo 2017), as indicated by the occurrence of *Galerix symeonidisi* Doukas, 1986, which is often found at lignite-rich sites (Crespo et al. 2020a). However, the rodent assemblage includes *Heteroxerus rubricati* Crusafont et al. 1955, a ground squirrel typical of warm and dry habitats (Crespo et al. 2021a), suggesting the presence of open areas around the lake.

Regarding MTR2, the site yields a high estimated MAP of 800.23 mm (Figure 8; Table 2), which contrasts with values inferred from small-mammal data (Crespo 2017). Thus, our proposed palaeoclimatic scenario indicates an increase in annual rainfall between MCX3 and MTR2. Unfortunately, the open taxonomic attribution of most taxa from MTR2 limits palaeoecological interpretations. However, the presence of Anguidae indet. implies some forest/bush cover in the area.

With an estimated rainfall of 473.76 mm, BC1 is considered the second driest site of the overall sequence. Although higher than the current MAP in the region, BC1 shows the smallest difference between the latter and the observed value (+41.57 mm) (Figure 8; Table 2). No xerophilic taxa have been recovered, but some of them have closely related species that currently inhabit this kind of habitat, such as cf. *Lissotriton* sp. and Bufonidae indet. On the other hand, particular mammal and gastropod taxa, such as the soricid *Paenelimnoecus micromorphus* (Doben-Florin, 1964) (Crespo et al. 2019b), the lagomorph *Lagopsis penai* Royo, 1928 (Crespo et al. 2022), and the helcid

Palaeotachea (Albesa et al. 2022), are indicative of open landscapes. Paradoxically, the occurrence of *L. penai* in the site is residual, ~3%, whereas in other localities, as MTR2, its presence is higher, ~24% (Crespo et al. 2022). The isotopic analysis by Ríos (2013) estimated a MAT of 20.09 °C.

Table 2. Results of the application of the HEG method (Böhme et al., 2006). It represents the ecophysiological indices for each applicable taxon from selected sites in the Ribesalbes-Alcora Basin, the mean value for each, and the obtained mean annual precipitation (MAP, in mm). Δ, Difference between values obtained from the fossil assemblages of some localities of the Ribesalbes-Alcora basin and current values there (MAP: 432.19 ± 7.21 mm).

	EFG Index	MCX-3	MTR-2	BC-1	MAB-0A	MAB-0B	FS-1	MAB-3	MAB-5	MAB-11	CBR-0B	CBR-1
<i>cf. Lissotriton sp.</i>	0.513			1	1						1	
Anura indet.	0.3918		1									
Crocodylia indet.	1	1	1	1	1	1	1	1		1	1	1
Testudines indet.	1								1	1	1	
<i>cf. Testudinidae indet.</i>	0									1		
Gekkota indet.	0.0917			1	1		1	1	1			
?Chamaeleonidae indet.	0.0917										1	
Lacertidae indet.	0	1	1	1	1	1	1	1	1	1		1
<i>Chalcides sp.</i>	0	1		1				1				
Blanidae indet.	0.0917			1					1	1		
<i>Ophisaurus sp.</i>	0			1	1	1		1		1	1	
<i>cf. Pseudopus sp.</i>	0				1					1		1
Anguidae indet.	0	1	1				1		1			
Scolecophidia indet.	0.0917										1	
	Mein Index	0.20	0.35	0.17	0.35	0.33	0.24	0.27	0.22	0.18	0.39	0.33
	MAP	564.93	800.23	473.76	401.45	765.12	620.00	488.87	532.93	682.19	889.72	765.12
	ΔMAP	132.74	368.04	41.57	-30.74	332.93	100.74	187.81	56.68	250.00	457.53	332.93

MAB0A records the lowest rainfall value of the all studied sites. In fact, it is the only locality with lower value than the recorded nowadays in the region, with a differences of -30.74 mm. However, remains attributable to *cf. Lissotriton sp.* have been found in MAB0A, supporting the higher humidity at this site than at the other ones. In line with our result, Crespo et al. (2019c) documented gypsum layers occurring at the top of the ferruginous MAB0A layer and at the bottom of MAB0B, which differ markedly from the aforementioned MAB0A layer. This aridity trend was accompanied by a increase in the

MAT for MAB0A (21.16 °C) respect to BC1 (20.09 °C), in accordance with the preliminary results of Ríos (2013).

MAB0B and FS1 yielded similar palaeoherpetological assemblages. These sites represent a new humidity peak within the sequence, with high MAP values of 765.12, and 532.93 mm, respectively. Although, it is perceptible that a progressive decrease of the MAP value from MAB0B to FS1 (Figure 8; Table 2). In this sense, the herpetofauna assemblages are composed of highly generalist taxa, as *Gekkota* indet. and *Lacertidae* indet. Compared to the previous site, MAT has recorded a significant decline (21.16 °C for MAB0A and 17.95 °C for MAB0B) (Ríos 2013).

Located at the base of section FS, the Konservat-Lagerstätte site FSA has been interpreted as a shallow, perennial, and quiet palaeolake based on its palaeofaunal assemblage, which comprises arthropods, lymnaeid and planorbid molluscs, ostracods, cladocerans, charophytes, and fishes (Álvarez-Parra et al. 2021). Nonetheless, its extension could have fluctuated probably cyclically. A key proxy for this supposition is the cladoceran crustacean *Daphnia* (*Ctenodaphnia*), which usually breeds partenogenetically. However, under unfavourable environmental conditions, they produce diploid eggs encapsulated in a protective, saddle-like structure called an ephippium, which is strongly melanized and contains two large eggs (Ebert 2005). The mass records in the rock slabs of *Daphnia* (*Ctenodaphnia*) ephippia suggest ecologically stressful conditions, such as temporary desiccation or a lack of food resources (Álvarez-Parra et al. 2021). Although La Rinconada is slightly older than the studied outcrops, Barrón et al. (2010) pointed out that the palaeoclimatology was characterised by drought seasonality. Climatic conditions during the Early Miocene in the region have been interpreted as tropical or subtropical (Peñalver et al. 2016; Crespo 2017). In this sense, shallow tropical lakes are influenced by seasonal cycles of run-off and water input. In a few cases, the loss of water by evaporation from a lake is larger than that by surface outflow. Thus, only shallow tropical lakes of the arid and semi-arid tropics are also liable to at least temporary extinction, due to long-term rainfall deficits (Talling 2001).

The downward trend in annual rainfall finishes in MAB3. The obtained value, 488.9 mm, is the second-lowest MAP among the studied sites. The presence of *Chalcides* sp. could be a proxy of some degree of dry conditions (Caputo et al. 1995). In MAB3, the small mammal assemblage shows affinities with forested environments (Crespo et al. 2019c). Among the herpetofauna, the only clearly arboreal-associated taxa are *Ophisaurus* sp. (Escoriza and Comas 2015).

MAB5, MAB11, and CBR0B represent a positive trend from the oldest (MAB5) to the youngest (CBR0B) of these sites, with MAP values of 532.93, 682.19, and 889.72 mm, respectively (Figure 8; Table 2). It is relevant to note that this phase ended with the highest MAP value of the overall sequence, at the CBR0B site. Some taxa described in this site seem to corroborate this assumption. *Ophisaurus* sp. is interpreted as a woodland inhabitant. Other potential forest-dwelling palaeoherpetofaunal assemblage from CBR0B is ?*Chamaeolinidae* indet. As mentioned previously, the presence of a tooth with its bases not in contact could be a proxy for closed-canopy forest or dense shrubland habitats (Čerňanský 2010b). At first glance, our results do not appear to contradict the palaeoecological reconstruction proposed by Crespo (2017), who identified an expansion of closed forests based on small vertebrate faunas. In this regard, the abundance of the dimyloid *Plesiodimylus ilercavonicus* in MAB5 has been interpreted as indicative of very humid conditions (Crespo et al. 2018). Moreover, the presence of the flying squirrel *Aliveria* cf. *luteyni* in CBR0B indicates wooded formations in the surrounding area of the site (Crespo et al. 2021a). Paradoxically, in CBR0B ground

squirrels, *Heteroxerus rubricati* and *Aragoxerus* sp., reached one of the highest frequencies of the overall palaeomammal assemblages (Crespo et al. 2021a). Both taxa have been linked to warm, relatively dry, and open habitats with scarce vegetation (Van Dam and Weltje 1999). The gastropod assemblage appears to support this inference (Albesa et al. 2022). This phase was accompanied by a decline in MAT in MAB5 (13.31 °C), followed by an increase in MAB11 to 19.02 °C—values comparable to those at MAB0A and MAB0B (Ríos 2013).

Finally, MAP decreases again at the CBR1 site, reaching 765.12 mm (Figure 8; Table 2). However, the obtained MAP is still high, given that it has the same value as MAB0B.

CBR1 presents an assemblage composed of forest-associated taxa (cf. *Pseudopus* sp.) or generalist (Lacertidae indet.) taxa. In this sense, the small mammal assemblages from the sites indicate drier environmental conditions (Crespo 2017). CBR1 represents the second locality with the highest frequency of ground squirrels of the overall sequence. Specifically, *Aragoxerus* sp. has been recovered from CBR1, which has been interpreted as an ecology linked to warm, dry open habitats by taxonomic inference (Crespo et al. 2021a).

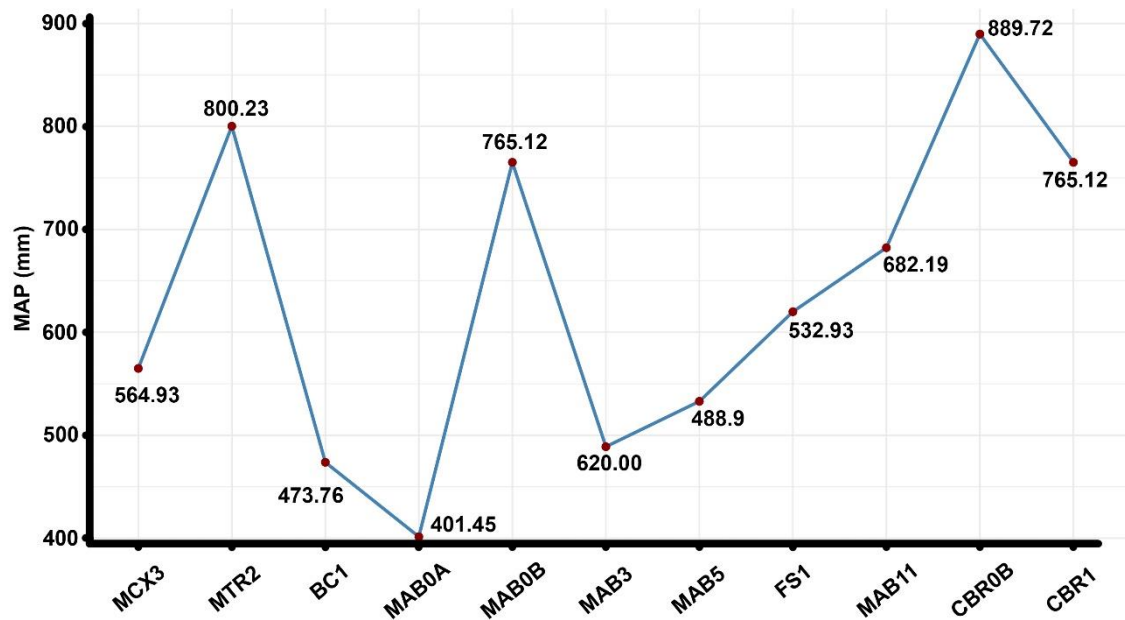


Figure 8. Evolution of the Mean Annual Precipitation (MAP, in mm) in the studied sites of the Ribesalbes-Alcora basin, based on the application of the Herpetological Ecographic Groups (HEG) method, which is based on the description of palaeoherpetofaunal assemblages in each locality. The red line represents the current MAP value in the region (432.19 mm).

The palaeoclimatic analysis based on small mammals for the same localities, as proposed by Crespo (2017), relies on the palaeoecological preferences of different taxa inferred from dental morphology. As a result, that reconstruction is qualitative, whereas our results are quantitative. Moreover, both approaches yield significantly different outcomes. Crespo (2017) suggested a continuous increase in relative humidity from MCX3 to MAB5, followed by a slight decrease in humidity at FS1 and MAB11, and then a renewed increase at CBR0B. A final decrease in moisture availability was proposed towards the end of the sequence. In contrast, our results show a more variable scenario,

with an alternation of at least three “humid” phases (MTR2; MAB0B to FS1; and MAB5 to CBR1) and three “dry” peaks (MCX3; BC1 to MAB0A; and CBR1).

These discrepancies among the three methods stem from differences in the proxies used. Both Crespo’s (2017) approach and ours are grounded in actualism—that is, reconstructing the ecology of extinct organisms through analogies with closely related extant species. This approach, however, entails certain limitations. For small mammals, the correlation between climatic ranges and dental morphology in modern taxa may not fully apply to fossil forms (Hernández-Fernández and Peláez-Campomanes 2011). Regarding reptiles and amphibians, the HEG method assumes that the physiological strategies related to thermoregulation, water balance, and gas exchange have remained largely consistent among related taxa (Böhme et al. 2006). Their distribution is primarily shaped by climatic factors (Rodríguez et al. 2005), although they exhibit a broad range of adaptations to cope with diverse environmental conditions (Vitt and Cladwell 2009). One such adaptation is the restriction of their presence to habitat patches where factors such as topography or soil type create particularly favourable microclimates (Guisan and Hofer 2003). This enables the persistence of species in regions with generally unfavourable climates (Brito et al. 2011; Peterman and Semlitsch 2013). The method we applied estimates MAP based on the climatic preferences of modern relatives of fossil taxa. However, local rainfall variability is strongly influenced by topography and other factors such as proximity to the sea (Gao et al. 2007). On the other hand, the implemented method is based solely on the presence of the identified taxa, nor on their relative abundance. MAB11 is a perfect example of that. In this site, Anguidae indet. and Crocodilia indet. supposed the 57.89 and 21.56% of the total numbers of remains, respectively; whereas cf. Testudinidae indet. is represented by just two remains, that is, 0.17 of the overall. Despite this, the three taxa have the same importance in the calculation of the palaeoclimatic parameter. Moreover, in some localities, our results differ from other proxies. In this sense, MAB11 is a thin bed of black lignituous mudstones with a ferruginous bottom (Crespo et al. 2019c). In contrast, isotopic data are subject to biases related to plant and animal physiology and behaviour, environmental chemistry, and diagenetic processes (Hayes et al. 1990; Ehleringer and Monson 1993; Koch 1998).

Vasilyan et al. (2022) applied the HEG method to the palaeoherpetofaunal assemblage from the locality of Echzell (Germany), correlated with MN4. The authors estimated a MAP value of 791 ± 254 mm, indicating more humid conditions than those currently prevailing. This rainfall value exceeds those recorded in the Ribesalbes-Alcora Basin localities, except for MTR2 (800.23 mm) and CBR0B (889.72 mm). But other sites show similar values to the estimated for Echzell, such as MAB0B (765.12 mm) and CBR0B (765.12 mm). When considered individually, these values seem to contradict previous studies that proposed a lack of pronounced latitudinal regionalization in Europe during the Burdigalian (Böhme et al. 2011; Bruch et al. 2011). These differences may reflect palaeolatitudinal or palaeoecological factors that warrant further investigation. Notably, the Ribesalbes-Alcora Basin is part of the Ibero-Levantine bioprovince, which is considered more humid than other parts of the Iberian Peninsula.

Palaeobiogeographical implications

The assemblages from the Ribesalbes-Alcora Basin do not show significant differences compared to those recovered from other coeval European and Iberian localities. This suggests a certain degree of homogeneity in the palaeoherpetological composition, at least at the family level, among European faunas during the Late Miocene. The only probable endemism is cf. *Pyrenasaurus* sp., which has also been reported from the Eocene of northern Spain and southeastern France (Bolet and Augé 2014). However,

due to the limited number of studies focused on amphibians and reptiles from this time period, particularly in the Iberian Peninsula, further research is needed to confirm or refute this observation.

In general, all sites of the Basin share common elements such as anguids and crocodylians. However, other taxa are only recovered in specific localities and/or sections, which may reflect ecological and/or taphonomic biases or sampling deficiencies. Urodeles are one such group, represented by only one form: cf. *Lissotriton* sp. The first fossils attributable to that genus were cranial and vertebral material from the extinct species *Lissotriton roehrsi* (Herre, 1955) at the German locality of Oberleichtersbach (MP30, lower Oligocene; Böhme 2008). Thus, this genus is a salamandrid taxon with a long natural history in Europe, whose fossil remains have been cited in several sites (Macaluso et al. 2022). During the MN4, remains of the genus have been cited in numerous sites of central Europe. The taxa identified at these sites are related to extant species. Thus, Böhme (2003) pointed out the presence of *Lissotriton vulgaris* (Linnaeus, 1758) in Petersbuch 38B and 36II (MN4) and Witershof Ost (MN3a), and *Lissotriton helveticus* from Petersbuch 7, 2 (MN4a), and 4 (?MN4), Stubersheim 2 and 3 (MN 3b), and finally, Weißenburg 6 (MN1). In the case of the Iberian Peninsula, the fossil record of the genus is really scarce. Until now, during the Late Miocene, taxa have been cited only in Agramón (*Lissotriton* aff. *vulgaris*) and Rubielos de Mora (*Lissotriton* sp.) (Böhme and Ilg 2003). Our finding thus represents a new record for *Lissotriton* in the region, extending its known Early Miocene distribution to the easternmost Iberian Peninsula.

The classical site of La Rinconada (Ribesalbes, Castellón), also located in the Ribesalbes-Alcora Basin, is recognized as a Konservat-Lagerstätte due to its exceptionally well-preserved fossils. Among the herpetofauna, Sanchiz (1977b) describes material assigned to three urodele taxa: *Chelotriton ogygius* (Goldfuss, 1831), cf. *Triturus* sp., and *Megalotriton filholi* Zittel, 1890. Posteriorly, in the nowadays lost online database Lisanfos KMS Martín and Sanchiz reassigned the assemblage to *Chelotriton* sp., *Salamandra* sp., and Pleudelinae indet (Peñalver et al. 2016). Also, Martín and Sanchiz reported the presence of Ranidae indet. in La Rinconada (see Peñalver et al. 2016). Although there are no direct fossils of urodeles, the other Konservat-Lagerstätte locality, San Chils, has yielded coprolites that could have been produced by adult and larval urodeles (Álvarez Parra and Peñalver 2019).

Although both sites have been considered slightly older than the outcrop studied in the present work (Peñalver et al. 2016; Álvarez Parra and Peñalver 2019), its exact chronology is not fully known. According to Scoch et al. (2015), *Chelotriton paradoxus* Pomel, 1853 has a predominantly aquatic lifestyle based on taphonomical studies, based mainly on the large number of remains and the preservation of many more or less completely preserved adult specimens recovered from the late Oligocene Enspel locality and the Miocene Randeck Maar. However, Pogoda et al. (2020) proposed a more terrestrial ecology at least for Enspel *Chelotriton* based on the similarities of the cranial morphology with the extant eastern-Asia *Echinotriton* (Pogoda et al. 2020). In this genus, the adults are fully terrestrial, and females deposit egg clutches on land. The larvae develop in lentic water bodies (Utsunomiya et al. 1978). Nowadays, *Echinotriton* inhabits perhumid, broadleaved forests at low to moderate elevations (Hernández et al. 2017). The original attribution of some articulated premetamorphic specimens by Sanchiz (1977b) to *Megalotriton filholi* was questioned by Estes (1981), who tentatively proposed its attribution to *Salamandra sansanensis* Lartet, 1851. Thus, the posterior correction by Martín and Sanchiz to *Salamandra* sp. included a new taxon, a clearly terrestrial newt

that breeds on land, which relies only on aquatic habitats during its larval stage (Dufresnes 2019). Regarding ranids, only adult remains are known from that locality (Peñalver et al. 2016). Therefore, the amphibian assemblage from La Rinconada is mainly composed of terrestrial taxa that only use waterbodies for breeding. In this sense, this assemblage is ecologically similar because we have described a clearly terrestrial anura, as *Bufo* indet., and a urodelan taxon, cf. *Lissotriton* sp., in which extant species experienced a yearly terrestrial phase (Dufresnes 2019).

Bufoids are a common element in the present-day European batrachofauna. Three genera with six species currently inhabit the continent: The Common Toads *Bufo*, Green Toads *Bufo*, and Natterjack Toads *Epidalea* (Dufresnes 2019). The earliest known bufoiid remains come from the localities of Itaboraí (middle Paleocene, Brazil) and Cernay (late Paleocene; France) (Rage 2003). Fossil remains of *Bufo* and *Bufo* are already present in the Early Miocene of Europe. For instance, *Bufo* sp. has been reported from Mokrý-Western Quarry, 2/2003 Reptile Joint (MN4; Czech Republic) (Ivanoc 2008), Erkerthofen 1, and Sandelzhausen (MN4; Germany) (Böhme 2003, 2010). In Spain, records include Buñol (MN4), Córcoles, and Valdemoros IIIb (MN4b) (Alfárez and Brea 1981; Sanchiz 1977a). The oldest record of *Bufo* comes from the Vieux-Collonges site (MN4; France) (Bailon and Hossini 1990). Regarding *Epidalea*, it has been cited in the Manchones II and Manchones localities (Sanchiz 1977a), although Böhme and Ilg (2003) reassigned those remains to *Bufo*. Therefore, the oldest unambiguous *Epidalea* comes from the late Miocene (MN12) Spanish localities of Conclud'98 (*Epidalea* aff. *calamita*) and Los Mansuetos (*Epidalea* cf. *calamita*) (Böhme and Ilg 2003; Sanchiz 1977b, 1998b). Nowadays, only two species of toads are present in the Iberian Peninsula: *Bufo spinosus* Daudin, 1803, and *Epidalea calamita* (Laurenti, 1768). However, *Bufo* was still present in eastern Spain until the late Early Pleistocene (Blain et al. 2010).

During the Early Miocene, Europe was inhabited by at most three genera of crocodylians: the alligatoroid *Diplocynodon* Pomel, 1847; and the gavialids *Tomistoma* Müller, 1846 and *Gavialosuchus* Toulou and Kail, 1885 (Böhme and Ilg 2003). The latter is mostly found in marine or estuarine deposits (Buffetaut et al. 1984). Although various European *Tomistoma* species are mainly associated with such contexts, they have also been recorded in fluvial deposits (Antunes and Pais 1993). In contrast, *Diplocynodon* is considered a freshwater crocodile (Delfino and Rossi 2013). Given the lacustrine nature of the studied sites (Anadón et al. 2004) and the abundance of similar fossil records in coeval Iberian localities (Pereda Suberbiola et al. 2001; Böhme and Ilg 2003; Casanovas-Vilar et al. 2022; Palazuelos et al. 2025), it is probable that the remains described here belong to an undetermined member of the genus *Diplocynodon*. Today, crocodiles are absent from the Mediterranean Basin, though they were present in the region until the early 20th century, from Palestine to Morocco (Trape et al. 2012; Bentley 2022). The only species currently found in the Sahel-Saharan region, the West-African crocodile (*Crocodylus suchus* Geoffroy, 1807), was extirpated due to a combination of paleogeological events, climatic shifts, and human pressure (De Smet 1998). In the Iberian Peninsula, crocodylians survived until the Early Pliocene (Castillo and Agustí 1996; Guerra-Merchán et al. 2013).

The fossil record of gekkotans is generally poor (Augé 2005), although it is relatively well represented in Europe compared to other regions (Daza et al. 2014). The oldest record dates to the earliest Eocene (MP7), with *Dollogekko dormaalensis* Čerňanský et al., 2022 of the Belgian site of Dormaal (Čerňanský et al. 2022), and Gekkota indet. from the Portuguese locality of Silveirinha (Rage and Augé 2003). Unfortunately, most European

Early Miocene consists of isolated and fragmentary elements, which prevent attribution below the order level (Čerňanský and Bauer 2010). As a result, the group's evolution remains poorly understood (Augé 2005). During MN4, undetermined gekkotans have been reported from the Iberian localities of Córcoles (Alfárez and Brea 1981), Els Casots (Casanovas-Vilar et al. 2022), Agramón (probably with two distinct forms), Artesilla, San Marcos, San Roque 3 and 5, and Vargas 1A (Böhme and Ilg 2003).

Diverse scincoids are known from various Paleogene and Neogene European sites (Böhme and Ilg 2003). In the Ribesalbes-Alcora Basin, two forms have been identified, one potentially related to the Paleogene genus *Pyrenasaurus*. If confirmed, *Pyrenasaurus* would qualify as a Lazarus taxon sensu Jablonski (1986). The only known species, *P. evansae*, is known from two Late Eocene sites in Spain and France (Bolet and Augé 2014). Its survival beyond the Grande Coupure—a major faunal turnover at the Eocene-Oligocene boundary (Stehlin 1909)—is significant, as many endemic taxa disappeared while Asian immigrants colonized Europe (Hooker et al. 2004). Although traditionally viewed as a European phenomenon, similar turnovers have been reported in North America, Asia, and Africa. The event likely correlates with the Oi-1 glaciation (~33.5 Ma), the largest Paleogene cooling pulse (Costa et al. 2011). Lizard taxa that survived mostly vanished shortly after, replaced by Asian lineages (Rage 2013). A parallel case is *Lazarussuchus*, a choristoderan thought extinct in the Eocene but later found in Miocene deposits (Evans and Klembara 2005; Kirsche et al. 2016). The youngest known choristoderan comes from Hammerschmiede 5 (MN 9, Late Miocene, Germany; Kirsche et al. 2016). The extinction of *Lazarussuchus* has been linked to the climatic deterioration throughout the Miocene, including increased seasonality and a decline in global temperatures (Evans and Klembara 2005). If *P. evansae* or a related form survived into the Miocene in the Ribesalbes-Alcora Basin, it could indicate ecological stability in the region. Supporting this, Crespo et al. (2020b) described a bat assemblage dominated by molossids—common in the early Oligocene of western Europe but rare by the Early Miocene—suggesting the persistence of tropical forests in the area.

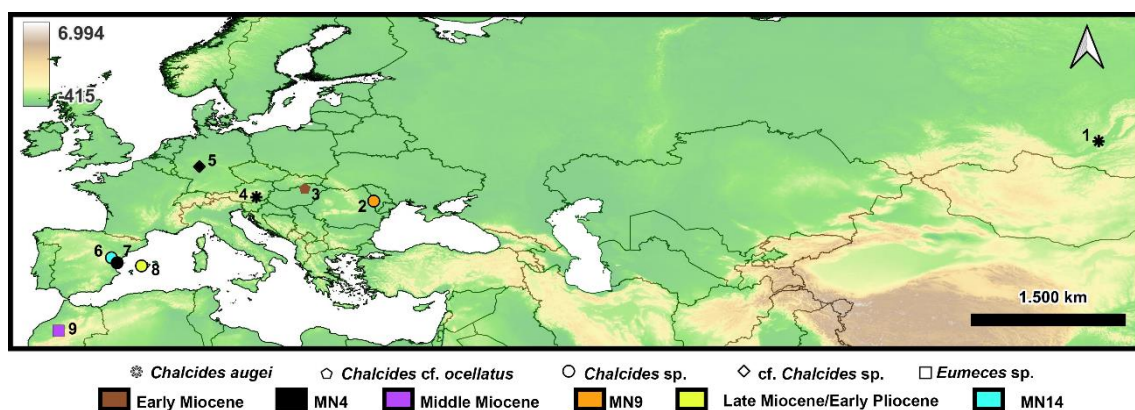


Figure 9. Location of the Eurasian and North African sites with scincid taxa uncer family level during the Miocene and Early Pliocene. The sites included in the figure are: 1, Tagay, MN4, Russia (Čerňanský et al. 2020); 2, Crețești-1, MN9, Romania (Codrea et al. 2017); 3, Felsötárkány 1, Early Miocene, Hungary (Venczel and Hír 2013); 4, Oberdorf, MN4, Austria (Čerňanský et al. 2020); 5, Echzell, MN4, Germany (Vasilyan et al. 2022); 6, La Gloria 4, MN14, Spain (Böhme and Ilg 2013); 7, Mas del Coixos 3, Barranc de Campisano 1, and Mas d’Antolino B-3, MN4, Spain (this work); 8, Na Burguesa-1, (Late Miocene/Early Pliocene, Spain (Bover et al. 2014); 9, Beni Mellal, Middle Miocene, Morocco (Rage 1976).

Molecular data suggest that *Chalcides* began to diversify around 10 Ma, probably in the Moroccan region (Carranza et al. 2008). However, fossils attributable to that genus have been reported from Eurasia in chronologies older than the proposed diversification. The biogeographical scenario of the dispersal of *Chalcides* into Europe was proposed by Carranza et al. (2008). Thus, they identified at least five major colonization waves that colonized Europe. The first ones took place at about 5 Ma, coinciding with the Messinian Salinity Crisis (MSC), when the Mediterranean Sea was isolated from the Atlantic Ocean by the closure of the Betic and Rifian Strait at ~7.6 and ~6.7–6.2 My, respectively. As a result, the Mediterranean practically dried out and large evaporite deposits accumulated in its basin (Booth-Rea et al. 2018). According to the chronologies proposed by Carranza et al. (2008), the dispersal of *Chalcides* in Europe was coincident with the last of the major dispersal waves in the Western Mediterranean, the named Gerbil Event (~5.9–5.3 My), when gerbils dispersed into Europe from northern Africa (Agustí et al. 2006). From the Iberian Peninsula, the clade colonized the Balearic Islands. Fossils of *Chalcides* have been reported from Na Burguesa-1 (Late Miocene/Early Pliocene, Majorca) (Bover et al. 2014) and from a currently lost site from Menorca (Boulenger in Bate 1919). The posterior dispersal event may be transmarine from North-western Africa, and it is supposed that the invasion of Southwestern Europe by *Chalcides striatus* and *Chalcides chalcides* occurred at 2.6 and 1.4 Ma, respectively (Carranza et al. 2008).

The new material from the MCX3, BC1, and MAB3 sites draw a new possible biogeographical scenario. *Chalcides* evolved in Europe, where it is recorded in the oldest fossils of the genus, and later dispersed to Asia and Africa. In this sense, the only fossil species of the group, *Chalcides augei* Čerňanský et al., 2020 from the East Siberian Tagay locality (Baikal Lake, Russia), has been linked with the current *Chalcides ocellatus* (Forskål, 1775) on the basis of its tooth morphology (basically the tooth necks are slightly swollen lingually) and the frontal morphology and type of sculpture in its dorsal surface (Čerňanský et al. 2020). Moreover, these characters are shared with the other fossil taxa of Central and Eastern Europe from the Early Miocene, such as cf. *Chalcides* sp. from Echzell (MN4, Germany) (Vasilyan et al. 2022) and *Chalcides augei* from Oberdorf (MN4, Austria), which was originally described as an undetermined form of scincid by Čerňanský (2016), and posteriorly attributed to *C. augei* by Čerňanský et al. (2020), and from the Middle and Late Miocene from Eastern Europe, as it is denoted by the described remains attributed to *Chalcides* cf. *ocellatus* from Felsötárkány 1 and 3/10 sites (Hungary) (Venczel and Hír 2013), and *Chalcides* sp. from Crețești-1 site (MN9, Romania) (Codrea et al. 2017). On its behalf, the record from the Iberian Peninsula and the Balearic Islands presents different tooth morphology; basically, these taxa presented teeth without enlarged crowns. Böhme and Ilg (2003) include remains attributed to *Chalcides* from the La Gloria 4 site (MN14, Early Pliocene); however, they are still neither described nor figured, precluding the corroboration or refutation of this taxonomical attribution, and, therefore, it is not possible to include them in any of the two morphotypes. In this sense, in the Eurasian fossil record of *Chalcides* it is recognizable two possible morphotypes: the first one includes the “expanded crown” taxa, and it is located in Central and Eastern Europe and Central Asia, and the second one, limited to southwestern Europe, presents “not-expanded crown” (Figure 9). This contradicts the assumption that north-western Africa acted as the centre of origin for *Chalcides*, suggesting instead that it functioned as a centre of diversification from which it dispersed to Europe and the Middle East (Carranza et al. 2008; Kornilios et al. 2010). Tectonic and climatic changes recorded in the geological record significantly alter the distribution of biological communities (Erwin 2009) and are the main causes of differences between the areas of origin and diversification of taxa. An example of this is the conifer *Pinus*, whose

origin was likely in Eurasia (probably the eastern region) during the Late Cretaceous, from where it dispersed throughout the Northern Hemisphere (Millar 1993; Eckert and Hall 2006). The establishment of a tropical/subtropical climate during the early part of the Paleogene relegated the genus to three major refugial areas in the Northern Hemisphere: high latitudes, low latitudes, and upland regions of middle latitudes, especially in western North America (Millar 1993). As of this date, the African fossil record of *Chalcides* is limited to the Quaternary (Bailon et al. 2017). Thus, palaeontological studies of Northern Africa remain scarce, yet some remarks can be made. Scincids do not appear in the Moroccan palaeoherpetofaunal assemblages until the Middle Miocene. Rage (1976) studied the squamate remains from the Beni Mellal site. He described the presence of material attributable to the skink *Eumeces* Wiegmann, 1834. No scincid fossils from other areas of North Africa are known, except Scincidae indet. from the Egyptian site of Bir Tarwafi (Chibanian, middle Pleistocene) (Szyndlar 1993). Under this proposed scenario, ancestors of the current species of *Chalcides* must have dispersed onto Africa at some point during the Miocene and, probably, disappeared from Eurasia. After that, representatives of the genus recolonized Europe, dispersed from North Africa, and reached the Canary Islands at different events during the Late Miocene and Pleistocene (Carranza et al. 2008). Future molecular works combined with fossil data must shed light on the palaeogeography of the genus.

Europe is probably the centre of origin for lacertids (Arnold et al. 2007), given that the basal fossil taxa closest to this family have been found on that continent (Borsuk-Bialynicka et al. 1999; Čerňanský and Augé 2013). During the European Paleogene, the lizard fauna was dominated by a mixture of lacertids and related primitive forms (Čerňanský et al. 2016). Over time, the latter became extinct, and lacertids emerged as the dominant group in the European herpetofauna. The European fossil record of lacertids includes forms related to extant species since the beginning of the Neogene. In this context, the oldest representative of an extant genus (*Lacerta* Linnaeus, 1758) dates from the Early Miocene (MN 4b) of the Czech locality Dolnice, with the description of remains attributable to the green lizard group (*Lacerta viridis* group) (Roček 1984; Čerňanský 2010b). Recently, Marquina-Blasco et al. (2025) described remains tentatively attributable to the genus *Timon* in the locality of Crevillente 2 (MN11, Late Miocene; Crevillente, Alicante, Spain). Many extant genera are already cited in the fossil record from the early Pliocene (Villa and Delfino 2019b). Accordingly, possible remains of the genus *Podarcis* have been described from the early Pliocene of Poland and the late Pliocene of Germany (Böhme and Ilg 2013); however, the attribution of these specimens remains uncertain. Regarding *Psammodromus*, its entire fossil record is limited to the Iberian Pleistocene (Böhme and Ilg 2013). Therefore, confirmation that the studied material belongs to either of the two extant genera (*Psammodromus* or *Podarcis*) would constitute their oldest known record.

Čerňanský et al. (2015) suggested that chamaeleonids reached Europe during the MN3 biozone. Based on this and the recently described putative remains of chamaeleonids in Anatolia, chamaeleons reached Europe through Anatolia, probably via the *Gomphotherium* Land Bridge (Georgialis et al. 2016, 2022), which connected Europe with Arabia and Asia approximately between 19 and 14 Ma ago, with several interruptions before closing definitively (Harzhauser et al. 2007; Bialik et al. 2019). The oldest Anatolian record, at the Sabuncubeli site (MN3, dated at approximately 20 Ma), is chronologically similar to the oldest European record by the report of *Chamaeleo caroliquarti* at the German site of Wintershof West (Moody and Roček 1980) and Chamaeleonidae indet. in the Czech locality of Merkur-North (Čerňanský 2010b) and the Spanish Turó de les Forques 1 (Bolet et al. 2022). All these localities have been

correlated to MN3a (Daams and Freudenthal 1981; Ivanov 2002; Casanovas-Vilar et al. 2016). Thus, the colonization of Europe by chamaeleonids may have been very fast from the Anatolia Peninsula (Georgialis et al. 2022), although the apparently limited dispersal capacity of the different members of that clade (Cuadrado 2001), and it coincided with the Miocene Climatic Optimum (Georgialis et al. 2016). At the Iberian context, all the regional record is younger than Turó de les Forques 1 and located geographically further south than the first one. This indicates a probable colonisation of the Iberian Peninsula via a pass to the east of the Pyrenees. Thus, *Chamaeleo* aff. *caroliquarti* from Agramón site is dated as MN3/4 by Böhme and Ilg (2003) or MN4 by Van der Meulen in Szyndlar and Alférez (2005). Unfortunately, these remains are currently lost (Georgialis et al. 2016). The described remains in the present work, recovered from CBR0B, have been correlated with the local biozone *Ligerimys ellipticus* of the latest MN4 (or earliest MN5, after Casanovas-Vilar et al. 2021; latest Early Miocene), due to the co-occurrence of the cricetids *Democricetodon* and *Megacricetodon*, the presence, but in low numbers, of the eomyid *L. ellipticus*, and the occurrence of the insectivore *Heterosorex* (Crespo et al. 2019c, 2025).

Both anguid genera described in the Basin, *Ophisaurus* and *Pseudopus*, are cited in several Iberian localities in the Early Miocene. Thus, *Ophisaurus* is recorded in Iberia at the localities of Agramón, Barranco de Tudela 1 and 3, La Nasa 1 (Trapiazul), Rincón del Bu, Cetina de Aragón, Els Casots, Olmo Redondo 4A, San Roque 2 and 3, Vargas 4A, Villafeliche 2A, La Retama, and the Loranca Basin (Murelaga et al. 2002; Böhme and Ilg 2003; Blain and Bailon 2019). Regarding *Pseudopus*, the fossil record of the genus is mainly restricted to its northeastern region (Blain et al. 2016). Until now, only two records have been reported outside this area: *Pseudopus* sp. from the Late Miocene site of Crevillente 2 (Marquina-Blasco et al. 2025), and cf. *Pseudopus* sp. from Zújar site in the Guadix-Baza Basin (Bailon 1991), although the latter is considered questionable (Marquina-Blasco et al. 2025). Therefore, the new material presented here not only represents a novel record for southern Iberia but also constitutes the southernmost known occurrence of *Pseudopus* in the Early Miocene of Western Europe.

The fossil record of blind snakes is rather scarce. The oldest record of scolecophidian, *Boipeba tayasuensis* Fachini et al. 2020, comes from Late Cretaceous sediments in Brazil (Fachini et al. 2020); however, Head et al. (2022) considered it as a stem scolecophidian or a proximal sister taxon to the snake crown. In Europe, the group does not appear until the earliest Eocene (MP7) of Belgium. From the latest Eocene (MP19) to the earliest Early Miocene (MN1-2), blind snake remains are apparently absent, with the exception of still unpublished remains from La Colombière, France (MP30; Late Oligocene) (Rage and Bailon 2005). Scolecophidians reappear in Europe during the Early Miocene (MN4) at Dolnice, Czech Republic (Szyndlar 1987); Béon-1, France (Rage and Bailon 2005); Córcoles (Alférez and Brea 1981); and Els Casots, Spain (Casanovas-Vilar et al. 2022). Therefore, the discovery of an isolated vertebra in CBR0B is a new record at this stage. During the rest of the Miocene and the Pliocene, scolecophidians have been reported from some localities of southern Europe (Mead 2013). Regarding the Iberian Peninsula, the group seems to disappear during the Early Pleistocene (upper Villanian, MN17) (Bailon and Blain 2007; Blain et al. 2016). At present, *Xerotyphlops vermicularis* (Merrem, 1840) is the only autochthonous European species of blind snakes, which inhabits the southern regions of the Balkans. In the latter years, the Brahminy blind snake, *Indotyphlops braminus* (Daudin, 1803) has been introduced in soil imported with potted plants in two localities of Europe: Aguadulce (Almería) and Majorca (Balearic Islands) both in Spain, Malta, and Ischia Island (southern Italy); as well as in other regions of the Mediterranean basin, such as

northwestern Lybia, Egypt (around Cairo and in the Sinai), and Macaronesia, Gran Canaria (Canary Islands, Spain) and Madeira (Portugal) (Geniez 2018; Paolino et al. 2019).

During the Early to Middle Miocene, the European colubrid fauna was dominated by natricines—often referred to as the “Age of Natricinae”—which persisted in Western Europe until MN6 (Rage and Bailon 2005; Szyndlar 2012). Among the three genera described in this chronology, *Natrix*, *Neonatrix*, and *Palaeonatrix*, only the last seems to have disappeared at the Middle Miocene (Marquina-Blasco et al. 2025). Regarding the Iberian Peninsula, the fossil record of this clade from the Miocene is scarce and has been described only sporadically in the literature. Thus, during the Early Miocene, an undetermined form of Natricinae has been reported from the Agramón site (Szyndlar and Alférez 2005). In this sense, the finding of *Palaeonatrix* remains in MAB11 not only represents the first record of the taxon in the Iberian Peninsula but also enhances our understanding of the group's history in the region.

The attribution of 7 vertebrae to Viperidae from the sites CBR0D, MAB3, and MAB11 is putative, although they are of great interest. These snakes, together with Colubridae, are the current dominant element of the European ophidiofauna. The oldest record of the group consists of isolated fangs from the German site of Oppenheim/Nierstein (MN2, Early Miocene) (Kuch et al. 2006). Burdigalian was a key moment in the composition of the snake palaeocommunities. In this moment, the ophidian faunas of MN 2 and early MN 3 were markedly different from those of late MN 3 and MN 4 (Ivanov 2022). For most of the Paleogene, booids were the dominant element of the ophidiofauna. Gradually, this old fauna was displaced by modern snake lineages, specifically the families Colubridae, Viperidae, and Elapidae, during the early Oligocene. But this replacement finishes in a dramatic event named “MN-4-event”, when this archaic fauna was “literally flooded” by the mentioned modern ophidiofauna in Central and Western Europe (Szyndlar 2012). This event has been linked to climatic change from cool, arid conditions to warm, humid ones. Regarding the Iberian Peninsula, the composition of the snake fauna was similar to that of Europe (Szyndlar and Alférez 2005). Thus, the absence of ancient ophidian taxa indicates that the studied sites belonged to the late MN4, which is in accordance with the biochronological framework proposed by Crespo et al. (2019c) based on rodent assemblages from different localities in the basin.

CONCLUSIONS

The study of fossil amphibian and reptile assemblages from 32 Early Miocene sites in the Ribesalbes-Alcora Basin helps partially fill a gap in knowledge of the herpetofauna during the Early Miocene of the eastern Iberian Peninsula. Thus, the following conclusions have been drawn:

The remains from these sites have been attributed to 25 taxa. The faunal composition is, in general, similar throughout the sequence.

We have applied the HEG method to the palaeoherpetological assemblage from the most intensively sampled sites, from the oldest to the most recent: MCX3, MTR2, BC1, MAB0A, MAB0B, FS1, MAB3, MAB5, MAB11, CBR0B, and CBR1. The estimated MAP for all sites is higher than that recorded nowadays in the region, except in the case of MAB0A. Thus, the results of the application of that methodology confirm the variability in the “dry/humid” environments along the sequence of the Ribesalbes-Alcora basin previously predicted by other proxies (small mammals and isotopes). However, the

trends we propose do not fully align with those previously reported by other authors (Ríos 2013; Crespo 2017).

From a paleobiogeographic perspective, the assemblages are similar to those of other contemporary sites in Europe. In this sense, some remains are considered the first mention of the genus in the Iberian Peninsula, as *Palaeonatrix*. The most remarkable finds pertain to the lizard community, which includes four distinct forms.

Although the assemblages are composed of taxa typical for the Early Miocene, the putative presence of *Pyrenasaurus* in CBR1, a probable scincoid previously known from the Late Eocene of Sossís (northeastern Spain) and Descamps (southern France), is impressive. If this attribution is confirmed, it is assumed that the genus survived the Grande Coupure, implying some ecological stability in the region.

The presence of the skink *Chalcides* sp. in MAB3, BC1, and MAB3 could imply that the genus evolved in Europe, as the oldest fossil remains come from this continent, and later dispersed to Asia and Africa. This new biogeographical scenario contrasts with the previously proposed one based on the molecular study of Carranza et al. (2008), which proposed a North-western African origin for *Chalcides*. Moreover, two probable morphotypes were present in Europe during the Miocene based on the different morphology of the teeth: the first includes the “expanded crown” taxa, and it is located in Central and Eastern Europe and Central Asia, and the second one, limited to southwestern Europe, presents “not-expanded crown”.

Although the attribution is only tentative, the probable presence of chamaeleonids in CBR0B is a new record of the group in the Miocene of the Iberian Peninsula and, by extension, in Europe. This finding demonstrates rapid colonisation of the continent by chameleons and that the possible colonisation route to the Iberian Peninsula took place via a pass in the east of the Pyrenees.

ACKNOWLEDGMENTS

The survey and excavation campaigns in Araia d'Alcora were funded by the Conselleria de Cultura i Esports of the Generalitat Valenciana from 2008 to 2011, by projects 2008/0433-CS, 2010/0528-CS, 2011/0230-CS, GV06/304, and GVPRE/2008/320. This research was also supported by the Spanish Ministerio de Ciencia, Innovación y Universidades PID2023-151089NB-I00 (MCIU/AEI/10.13039/501100011033/FEDER, UE). The authors want to thank the editor XXXX (XXXX) and the reviewers XXXXX and XXXXX for their corrections, suggestions, and constructive comments. RMB is supported by an APOST postdoctoral grant (CIAPOS/2023/160) funded by Conselleria d'Innovació, Universitats, Ciència i Societat Digital (Generalitat Valenciana), cofinanced by the European Social Fund. V.D.C. thanks the Stimulus of Scientific Employment, Individual Support – 2021 Call grant by the Fundação para a Ciência e a Tecnologia (Portugal, CEECIND/03080/2021; DOI: 10.54499/2021.03080.CEECIND/CP1657/CT0007) and GeoBioTec. This work was funded by National funding, FCT – Fundação para a Ciência e a Tecnologia, within the framework of UID GeoBioTEC UID/04035/2025(DOI: 10.54499/UID/04035/2025).

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