Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 131(1): 85-115. **March 2025**
DOI: https://doi.org/10.54103/2039-4942/22382

HERPETOFAUNAL REMAINS (ANURA, CROCODYLIA, TESTUDINES, SQUAMATA) FROM THE LATE MIOCENE OF THE CREVILLENTE AREA (SE SPAIN): PALAEOBIOGEOGRAPHICAL AND PALAEOECOLOGICAL IMPLICATIONS

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Associate Editor: David M. Alba.

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

Keywords: Palaeoherpetology; Vallesian; Turolian; Iberian Peninsula; Palaeoecology; Palaeoclimatology.

Abstract. In the present work we describe the palaeoherpetofaunal remains from the Crevillente 2 (MN11) and Crevillente 15 (MN12) sites (Crevillente, Alicante, Spain), which is a key area for understanding the faunal turnovers during the Late Miocene. Crevillente 2 has yielded a diverse assemblage composed of anurans (*Pelophylax* sp.), crocodylians (Crocodylia indet.), lizards (cf. Scinciformata indet. 1 and 2, cf. *Timon* sp., Lacertidae indet. 1 and 2, *Ophisaurus* s.l. sp., and *Pseudopus* sp.) and ophidians (Colubridae indet. 1 and 2, *Neonatrix* sp., and Viperidae indet. Oriental morphotype). The probable presence of *Timon* is discussed; if confirmed, it would be the oldest occurrence of the genus. The faunal composition is consistent with that from other coeval Iberian sites. The assemblage includes European autochthonous taxa (Lacertidae and *Ophisaurus* s.l. sp.) and taxa that likely arrived from Asia or North America during the Oligocene-Miocene transition or the Early Miocene, such as *Pseudopus*, Oriental vipers and, probably, *Neonatrix*. The studied assemblage in Crevillente 15 is limited to turtles (*Paleotestudo* sp. and Testudines indet.) and crocodylians (Crocodylia indet.). At both localities, the surrounding landscape must have been dominated by open habitats with patches of forest/shrubland formations close to water bodies. The application of the Herpetological Ecophysiological Groups method to Crevillente 2 indicates that the mean annual rainfall must have been higher than currently recorded in the area.

INTRODUCTION

Amphibians and reptiles are an important component of extant continental biotas. However, these groups have received less attention than mammals in Neogene fossil sites. This situation is particularly significant in the case of squamates, whereas the faunas of chelonians and crocodilians are better known. Although in Quaternary deposits the situation has relatively improved in the last decades in Europe, this is not the case in older deposits. This bias is mainly explained by three aspects. First, mainland vertebrate samples are generally dominated by small

Received: February 1st, 2024; accepted: November 08, 2024

mammal remains, with those attributable to reptiles and amphibians being relatively scarcer. Second, some herpetofaunal remains are often fragile and, therefore, commonly found in a poor state of preservation. This is especially relevant given that, while small mammal taxonomy is usually based solely on dental morphology, herpetofaunal taxonomy is commonly based on various bones, either cranial, axial, or appendicular elements (Bailon 1991; Blain 2009). Third, in contrast to older chronologies (i.e. Mesozoic) the number of palaeoherpetologists focused on Cenozoic remains is lower than that of experts in other vertebrates (especially palaeomammalogists). Moreover, this results in a clear difference in the number of palaeoherpetological studies between different countries (Delfino et al. 2003). As a consequence, the evolution of palaeoherpetofaunal communities is not well known (Barbadillo et al. 1997; Delfino et al. 2003).

The European herpetofauna has intensely changed over geological time due to climate changes and the appearance and disappearance of biogeographical barriers related to the movement of continental masses (Augé 2005). The beginning of the Neogene was a crucial stage for the evolution of European herpetofauna (Rage & Roček 2003; Rage 2013). During the Oligocene-Miocene boundary, a severe glacial event took place (~23.24–22.95 Ma), considered as the first major Cenozoic glaciation step (Mudelsee et al. 2014). It was the first of seven punctuated periods of glaciations (Mi) in the Early to Middle Miocene. These have been linked to the growth of continental ice sheets in both hemispheres, and its associated eustatic changes, and/or to a 1–2 °C cooling of the bottom seawater (Miller et al. 1991; Westerhold et al. 2005). The squamate fauna between the end of the Oligocene and the beginning of the Miocene included only small forms and was characterized by its low diversity; this interval is known as the Dark Period (Rage 2013). On a longer timescale, the Miocene climate experienced a warming trend that culminated in the Mid-Miocene Climatic Optimum (MMCO) at ~17–15 Ma (Mudelsee et al. 2014). Coinciding with this trend, the diversity of amphibians and reptiles increased, mainly by the entrance of several thermophilus taxa that reached northern areas, such as Central Europe (Böhme 2003; Rage & Roček 2003; Rage 2013). The end of MN4 (~16.5 Ma) marked a dramatic turnover in the snake faunas, called the MN4-Event. It showed a rapid and drastic substitution of the archaic Booidea-dominated ophidiofauna by eastern immigrants, principally representatives of Colubridae, Elapidae, and Viperidae (Szyndlar 2012). Afterwards, the Middle Miocene Climatic Transition implied a climatic cooling attributed to a large-scale reorganization of ocean circulation and the atmospheric CO_2 drawdown through organic carbon sequestration (Shevenell et al. 2004). This cooling event resulted in the extinction of some reptile clades in Europe or their restriction to southern regions, such as the Iberian Peninsula (Rage 2013). For example, alligators, chamaeleons and giant tortoises were extirpated from Central Europe at this time (Böhme 2003). The Tortonian (early Late Miocene, ~11.63–7.24 Ma) was a time of important changes in the terrestrial ecosystems (Herbert et al. 2016), the most important of which was probably the expansion of C_4 grasslands at the expense of C_3-plants dominated woodland ecosystems in tropical and subtropical latitudes (Strömberg 2011).

In Europe, two major events appear to have taken place in the Late Miocene. The first of them was the Vallesian Crisis (VC, ~9.75 Ma), which has been tentatively related with the Mi7 glacial pulse (Agustí et al. 2013). This event is defined by the disappearance and replacement of most of the forest-adapted elements characterizing the Middle Miocene by open woodland, ruminant-dominated faunas of the Late Miocene (Agustí et al. 1999). Koufos (2006), based on the study of the Eastern Europe mammal palaeocommunities, proposed a scenario of an Eastern-to-Western progressive aridification of the Mediterranean area. Following this hypothesis, the faunas of the Black Sea region were first affected by the VC during the early Vallesian (~10.0 Ma), whereas in Central and Western Europe the effect occurred slightly later during the mid-Vallesian (~9.7 Ma; Koufos 2006). Nevertheless, as Casanovas-Vilar et al. (2005) pointed out, certain problems arise when focusing on specific areas, or time spans, due to the fragmentary nature of the fossil record and/or the lack of studies dealing with this time interval. For example, in contrast to other areas, where it is still a matter of debate, the effect of the VC is well known in the Iberian Peninsula, Central Europe and the Black Sea region. In this sense, some authors suggested that, rather than an abrupt event, the VC involved a series of extinctions during a longer time span (Casanovas-

Vilar et al. 2014) or limited its impact to a local level phenomenon (Casanovas-Vilar et al. 2005; Madern et al. 2018).

The second major event, the Messinian Salinity Crisis (MSC), took place at the end of the Late Miocene. It consisted of the isolation of the Mediterranean Sea from the Atlantic Ocean by the closure of the Betic and Rifian Strait at ~7.6 and ~6.7–6.2 My, respectively (Booth-Rea et al. 2018). As a result, the Mediterranean practically dried out and large evaporite deposits accumulated in its basin (Hsü 1974). The fossil record demonstrates the intense faunal exchange between Europe, Africa, and Asia at this moment (Agustí et al. 2006; Gibert et al. 2013; García-Alix et al. 2016). Agustí et al. (2006) identified three major dispersal waves in the Western Mediterranean: (i) the Murid Event (~7.2 Ma), which implied an intense turnover in the muroid rodent association; (ii) the *Paraethomys* Event (~6.2 Ma), with the dispersal of that genus and a number of large mammals into Europe; and (iii) the Gerbil Event (~5.9–5.3 Ma), when gerbils spread into Europe from northern Africa.

The study of the evolution of the continental palaeocommunities during the Late Miocene has been centered mainly on mammal taxa, without considering the possible impacts over other faunal groups. As a result, so far, the literature on the Late Miocene or older herpetofauna assemblages is scarce. This is particularly evident in the case of the Iberian Peninsula, for which there are some works that include figures and descriptions of paleoherpetological fossils and/or assemblages, particularly in recent years (i.e., Sanchiz 1981; García-Porta & Casanovas-Vilar 2001; Villa et al. 2017, 2018, 2024; Georgalis & Szyndlar 2022); however, for many localities, only faunal lists are available (e.g. Böhme & Ilg 2003). The Iberian Peninsula, as a southernmost and westernmost region of Europe, played a crucial role in the faunal changes during the Miocene, due to its position as a biogeographic cul-de-sac. In this sense, the study of the herpetofaunal remains is fundamental to improve our knowledge about dispersal and extinction patterns during this interval. With more than thirty localities recognized that stratigraphically cover the entire Turolian (Montoya 1994; Martín-Suárez & Freudenthal 1998), the Crevillente area is suitable for shedding light in faunal dynamics during the Late Miocene. Although the mammal fossils from these sites have been the subject of numerous studies, this has not been the case with the herpetofauna. So far, the works centered in the herpetofauna are limited to the study of the chelonians from Crevillente 2 (CR2), determining the presence of three taxa (Jiménez & Montoya 2002)—"*Testudo*" aff. *catalaunica* Bataller, 1926, *Titanochelon bolivari* (Hernández-Pacheco, 1917), and Testudines indet.—, along with a few remains of anurans from the Crevillente 4, 5 and 6 sites (Sanchiz 1998; Böhme & Ilg 2003). The rest of herpetofaunal fossils have been included in general faunal lists (i.e., Böhme & Ilg 2003; Mazo & Montoya 2003). In fact, this is common to many Neogene localities of the Iberian Peninsula.

We describe here the palaeoherpetofaunal assemblages (i.e., lissamphibians, crocodylians, turtles, and squamates) from the Late Miocene localities of CR2 (MN11) and CR15 (MN12). Also, we discuss the palaeobiogeographical and palaeoecological implications of both assemblages in the Iberian and European context.

Geological setting

The area of Crevillente (Alicante, Spain) has yielded various continental fossil sites (Fig. 1). The section, named Los Orones-Cerro de Castro (Montenat 1973), comprises beds deposited in the northern margin of the Bajo Segura Basin during the Late Miocene. It consists of a sequence of littoral, fan-delta, deltaic and reef deposits described by Montenat (1973) and Santisteban et al. (1997). This sequence is about 260 m-thick and overlies, through an angular unconformity, the pre-Tortonian substratum formed by Keuper red clays and Middle Miocene calcarenites and sandstones. These deposits have been subdivided into six units, based on the depositional systems represented in them (Santisteban et al. 1997).

The Crevillente 2 site (CR2) is located in Depositional Unit V (Fig. 2A), which was formed in a distal alluvial plain transitional to a fluvial environment and contains characteristic floodplain sediments (Santisteban et al. 1997). CR2 constitutes one of the few early Turolian localities with an abundant fauna of both micro- and macromammal species. It was therefore designated as the reference locality for MN11 (early Turolian, Late Miocene; Mein 1990; Bruijn et al. 1992). The CR2 site consists of

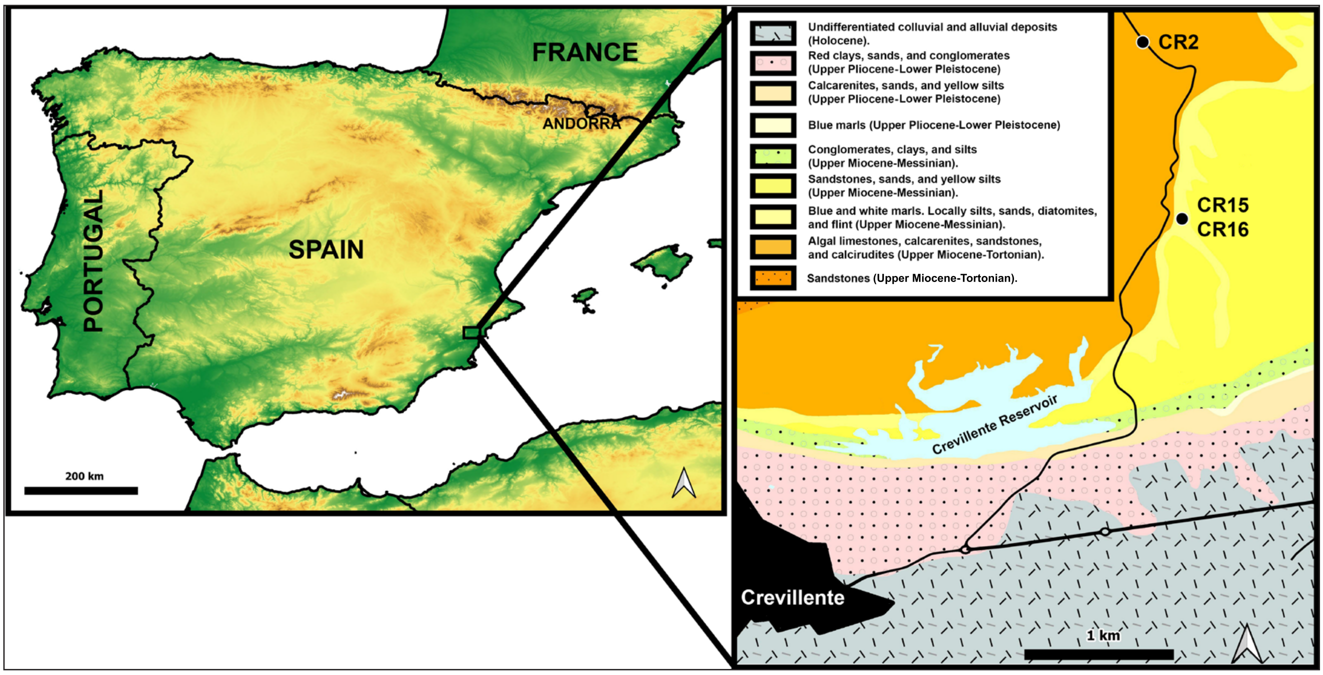

Fig. 1 - Geographical location of Crevillente 2, 15 and 16 palaeontological sites. The geological map is based in Roldán et al. (2009).

a stratigraphic sequence of six horizons of alternating marls and dark coloured carbonaceous clays, displaying a dip of approximately 15° and a dip direction of 120°N (Montoya 1994).

The Crevillente 15 (CR15) site is located in Depositional Unit VI (Fig. 2B), which was formed in a delta-like transitional environment and consists of a series of units organised in transgressive-regressive sequences. CR15 is located in a 1.5 m-thick level bed of white to grey calcareous marls, particularly rich in micromammal fossils and other vertebrate remains, with continental gastropods. Macromammal remains have also been found at the site (Montoya & Alberdi 1995).

Martin-Suárez & Freudenthal (1998) proposed a biostratigraphic local biozonation based on small mammal assemblages (Fig. 2C). As mentioned above, all these sites are attributed to the Late Miocene. In total, these authors defined five biozones. The *Occitanomys sondaari* zone, defined by the simultaneous occurrence of *Occitanomys sondaari* Van der Weerd, 1976 and *Apodemus lugdunensis* (Schaub, 1938), was correlated with MN11, and includes the CR2, CR23, and CR4B localities. CR2 is considered as the oldest site in the area. The *Huerzelerimys turoliensis* Zone is restricted to the deposits where *Huerzelerimys turoliensis* (Michaux, 1969) and *Apodemus barbarae* Van der Weerd, 1976 are found associated. This zone is correlated with MN12, and includes the CR5A, CR15, and CR18 sites. Also correlated with MN12, the local *Apodemus meini* Zone is defined as the interval between the first appearance datum (FAD) of *Apodemus meini* (Martín-Suárez & Freudenthal, 1993) and the FAD of *Stephanomys ramblensis* Van der Weerd, 1976. In this zone, only one species of *Occitanomys* Michaux, 1969 occurs—in this case, *Occitanomys adroveri* (Thaler, 1966)—without any *Huerzelerimys* species. The sites included in this zone are: CR8, CR7, and CR17. The *Castromys inflatus* Zone, or *Castromys* Zone for Martín-Suárez et al. (2001), is defined as the interval between the FAD of *S. ramblensis*, and the FAD of *Paraethomys meini* (Michaux, 1969). The CR31, CR14, and CR22 sites are included in this zone. Finally, the base of the *Paraethomys* Zone coincides with the last appearance datum (LAD) of *Occitanomys adroveri* and *Castromys inflatus* (Mein et al., 1990). The *Paraethomys* Zone includes the localities CR6, CR28, and CR19. Both, the *Castromys* and the *Paraethomys* Petter, 1968 zones are correlated with MN13.

MATERIAL AND METHODS

The studied material consists of disarticulated elements collected during the prospections

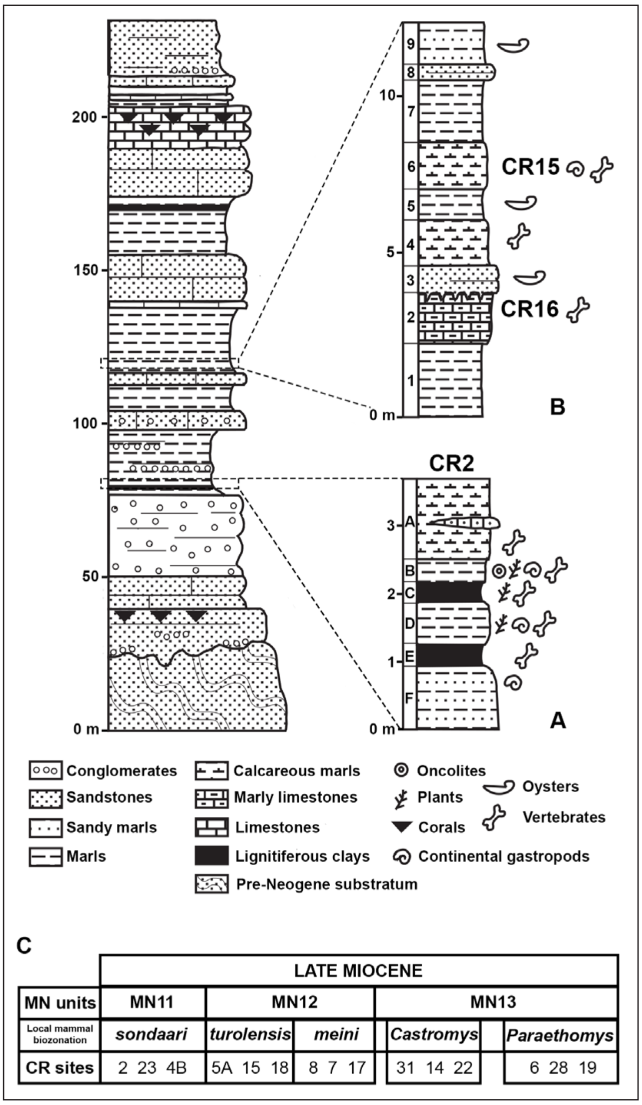

Fig. 2 - A-B) Stratigraphic position of the studied sites, Crevillente (CR) 2, A, and 15, B. Modified from Mazo & Montoya (2003). C) Correlation of the main vertebrate fossil localities of Crevillente area. It is indicated the local biozonation and Mammal Neogene (MN) units. Modified from Martín-Suárez & Freudenthal (1998) and Martín-Suárez et al. (2001).

and excavations carried out from 1985 to 1988 by the Universitat de València (UV; Valencia, Spain) and the Museo Nacional de Ciencias Naturales-Consejo Superior de Investigaciones Científicas (MNCN-CSIC; Madrid, Spain). The sediment was screen-washed using superimposed 1.5 and 0.5 mm-mesh screens. The microfossils were sorted using a Leica MS5 binocular microscope. Measurements were taken on a Leica MZ75 stereomicroscope, by means of displacement of a mechanical stage, connected to Sony Magnescale measuring equipment. Photographs were taken with a digital microscope Leica MZ75. All the studied material is housed at the Museu de la Universitat de València d'Història Natural (MGUV).

Herpetological bone remains were assigned to different taxa mainly following the criteria given by Bailon (1999) for anurans, Brochu (1999) for crocodylians, Lapparent de Broin (2000) for turtles, and Szyndlar (1984), Bailon (1991), Blain (2009), Klembara et al. (2014), and Villa & Delfino (2019a) for squamates. 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 anatomical terminology mainly follows Bailon (1999) for anurans, Brochu (1999) for crocodylians, Pérez-García & Vlachos (2014) for chelonians, Villa & Delfino (2019a) for lizards, and Szyndlar (1984) for snakes.

To estimate the palaeoprecipitation in the region we applied the Herpetological Ecophysiologic Groups (HEG) method defined by Böhme et al. (2006). It is based on the definition of six ecophysiologic groups corresponding to the main strategies and adaptations for thermoregulation, water balance, and gas exchange for every herpetological species of a determined assemblage (excluding non-fossorial snakes). This clustering is based on extant species, posteriorly transferred to fossil relatives. The defined groups are: 1) heliophile species; 2) subterranean and arboreal group; 3) periaquatic taxa; 4) semiaquatic and woodland group; 5) heliophobe group, and 6) aquatic group. Each taxon was assigned a numeric index based on its assigned group. Finally, we applied the Equation 6 in Böhme et al. (2006) for the palaeoprecipitation reconstruction. To compare with current data, we obtained the present mean annual precipitation (MAP) value for the municipality area of Crevillente using the global climatic data layer of the bioclimatic parameter BIO12 (mean annual precipitation) provided by World Clim 2 (Fick & Hijmans 2017).

Abbreviations: CR, Crevillente palaeontological site; FAD, first appearance datum; HEG, Herpetological Ecohysiological Groups method; LAD, last appearance datum; MAP, mean annual precipitation; 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; PLA, preacetabular lateral angle; UV, Universitat de València (Valencia, Spain); VC, Vallesian Crisis.

Systematic Palaeontology

Class **LISSAMPHIBIA** Haeckel, 1866
Order **Anura** Duméril, 1805
Family Ranidae Batsch, 1796
Genus *Pelophylax* Fitzinger, 1843

Pelophylax sp.

Fig. 3A, B

Material: *Crevillente 2*. MGUV-15439a, 1 left ilium; MGUV-15439b, 1 tibiofibula; MGUV-15439c, 2 tarsals; MGUV-15439d, 2 right maxillae; MGUV-15439e, 2 left maxillae; MGUV-15439f, 1 1 indeterminate maxilla; MGUV-15439g, two centra of a dorsal vertebra.

Description. Five maxilla fragments have been recovered from CR2. These remains have a smooth labial surface. In lingual view, the maxillae have pedicellate pleurodont teeth, which are closely packed. The palatine process is not well developed. Although broken, the frontal process does not appear to be individualised with respect to the rest of the bone.

Two centra of a dorsal vertebra have been recovered. They are procoelous and dorsoventrally flattened (Fig. 3A). In lateral view, the centrum is flat.

The ilium only preserves its distal area. In lateral view, the fossil has a well-developed *crista dorsalis* (Fig. 3B). The distal end of the latter structure has a well-differentiated *tuber superior*, but it is broken, so its morphology is not visible. At its base, a large preacetabular fossa is present. Both the ischial and pubic processes are broken. The acetabulum is large and subcircular in shape. This specimen shows a nearly 90° preacetabular lateral angle (PLA).

MGUV-15439b is a poorly preserved long and gracile tibiofibula with both ends broken.

Remarks. The overall morphology of the maxilla (poorly developed palatin process, and a probable not individualized frontal process) and the ilium (high *crista dorsalis* topped by a distinct *tuber superior*, and the presence of a well-developed supracetabular fossa) is consistent with a taxonomic attribution to the genus *Pelophylax* (Sanchiz et al. 1993).

Previous works reported ranid taxa in five localities in the Crevillente area (Böhme & Ilg 2003). *Pelophylax* gr. *ridibundus* (Pallas, 1771) has been cited in CR2, in CR4 (MN12) together with *Pelophylax pueyoi* (Navás, 1922) and Böhme & Ilg (2003) also cited this taxon in CR5. Finally, *Rana* sp. is included in the faunal list of CR6 (MN13) localities (Sanchiz 1998).

Class **REPTILIA** Laurenti, 1768
Order **Crocodylia** Owen, 1842
Crocodylia indet.

Fig. 3C, D

Material: *Crevillente 2*. MGUV-8136, 8137, 8139 and 15434, 23 teeth; MGUV-8140 and 8193, 2 indeterminae bones. *Crevillente 15*. MGUV-9501 and 99523, 2 teeth; MGUV-9522 and 9560, 2 osteoderms; MGUV-9500, one vertebral centrum.

Description. Several teeth have been recovered from CR2 and CR15. Only the crown is preserved, which is subconical and variably pointed apically (Fig. 3C, D). Lingually, the teeth are slightly concave, whereas they show a convex surface in labial view. In both lingual and labial views, the surface shows vertical striations. The mesiodistal carinae are non-serrated (Fig. 3C'). Two morphotypes can be identified: either slender, long and more pointed teeth or more massive with a bulbous aspect and apically blunt.

MGUV-9500 is an isolated centrum of a procoelous vertebra, ventrally convex in lateral view. In ventral view, the surface is smooth. The condyle and the cotyle are both rounded but slightly dorsoventrally depressed.

The recovered fragments of osteoderms are large and subtriangular in dorsal view. The surface presents a dense ornamentation consisting of pits than can be either deep and enlarged or small, rounded, and shallow. MGUV-9522 has an apparent longitudinal keel.

Remarks. Brochu (2000) pointed out that isolated teeth and osteoderms have low taxonomic value, thus the recovered remains can only be assigned to an indeterminate crocodylian. During the Late Miocene, three crocodylian genera have been reported from European sites (Böhme & Ilg 2003): the alligatoroid *Diplocynodon* Pomel, 1847; the gavialid *Tomistoma* Müller, 1838, and the crocodyloid *Crocodylus* Laurenti, 1768. In this sense, *Diplocynodon* is cited in the faunal list provided by Böhme & Ilg (2003) for CR4. However, these materials have been neither figured nor described. An additional indeterminate crocodylian was cited from CR3 by the same authors.

Order **Testudines** Linnaeus, 1758
Suborder **Cryptodira** Cope, 1868
Family Testudinidae Batsch, 1788
Genus *Paleotestudo* de Lapparent de Broin, 2000

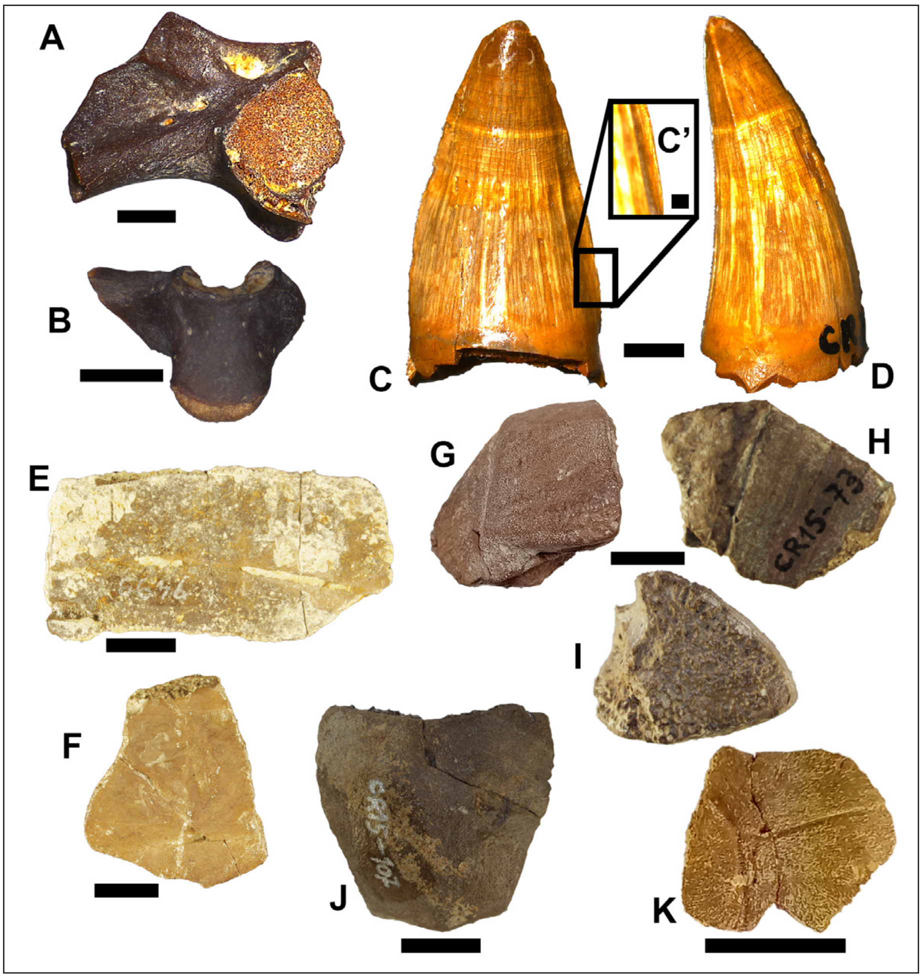

Fig. 3 - Lissamphibians and crocodiles from Crevillente 2 site and turtles from Crevillente 15. A-B, *Pelophylax* sp., left ilium, MGUV-15439a, in lateral view (A); vertebral centrum, MGUV-15439g, in ventral view (B). C-D, Crocodylia indet., teeth crown, MGUV-8136, in labial (C) and mesial (D) views. C', detailed of the mesiodistal carinae. E-J, *Paleotestudo* sp., costal plate, MGUV-9499, in dorsal view (E); peripheral plate, MGUV-9493, in dorsal view (F); left epiplastral (G-I), MGUV-9492, in dorsal (G), ventral (H), and medial (I) views; pygal (J), MGUV-11109, in posterior view. K, Testudines indet., indeterminate plate, MGUV-9497, in dorsal (K) view. Scale bar: 10 mm, except for A, B and C' (1 mm).

Paleotestudo sp.

Fig. 3E–J

Material: *Crevillente 15*. MGUV-9495 and MGUV-9499, 3 costal plates; MGUV-9492, 1 left epiplastron; MGUV-9493, MGUV-9494 and MGUV-9532, 3 peripheral plates; MGUV-11109, one pygal; MGUV-9498, and MGUV-9524, 4 indeterminate plate fragments.

Description. All the plates attributed to this taxon are relatively thick and have pronounced growth rings. Also, the sulci corresponding with the contact areas between the scutes are, in general, well developed.

The recovered left epiplastron (MGUV-9492) is subpentagonal in shape (Fig. 3G–I). This element is wider than long. Both on its dorsal and ventral surfaces the epiplastron is crossed by the gulo-humeral sulcus (Figs. 3G-H). The anterior margin of the epiplastron undergoes a curvature change in its contact with the mentioned sulcus. In lateral view, MGUV-9492 has a well-developed convex epiplastral lip. The latter structure does not overlap the entoplastron. A very shallow gular pocket is present (Fig. 3I).

The only preserved pygal (MGUV-11109) is trapezoidal (Fig. 3J). This plate is longer than wide, and it is wider anteriorly than posteriorly. Its anterior border is more or less straight in dorsal view. No lateral-anterior edges are present. The lateral margins are curved, and its posterior border is convex in posterior view. There is no sulcus on the dorsal surface of the pygal (Fig. 3J). In lateral view, the pygal shows a slight convexity.

Remarks. The presence of an epiplastral lip that does not reach the entoplastron, forming a shallow gular pocket, and the trapezoidal shape of the pygal, without any sulcus on its dorsal surface, and showing a small convexity in lateral view, are traits compatible with the genus *Paleotestudo* (Lapparent de Broin 2000; Pérez-García 2016).

However, our material is really scarce, thus precluding a specific attribution of the taxon presents in the CR15 site. *Paleotestudo* has been reported from many Iberian sites (Pérez-García & Murelaga 2013). Jiménez & Montoya (2002) described the turtle fossil remains from CR2, among which

"*Testudo*" aff. *catalaunica* is included. The taxonomy of the taxon is still unresolved. In this sense, Luján et al. (2016) related it with the genus *Chersine*, although these authors considered the latter as subgenus. In turn, Pérez-García (2016) recognized "*T.*" *catalaunica* as junior synonym of *Paleotestudo antiqua*, and proposed that *P. antiqua* the only species of the genus present in the Iberian Early Miocene.

Testudines indet.

Fig. 3K

Material: *Crevillente 2.* MGUV-9496, 1 costal. *Crevillente 15.* MGUV-9497, 1 indeterminate plastral plate.

Description. The studied plate fragments are thinner than those attributed to *Paleotestudo* sp. Their dorsal surface does not show marked growth rings, but a faint ornamentation formed by small elongated pits. MGUV-9496, a possible costal plate fragment, shows the contact sulcus between the neural and pleural scutes, as well as between two pleural scutes. These sulci are relatively well marked, but less so than in the other chelonian taxa studied (Fig. 3K). This fragment is flat in both anterior and posterior views.

Remarks. Although the fossils are very fragmentary, their ascription to tortoises (Testudinidae) can be ruled out, given the absence of growth ring marks and the fact that the neuro-costal and intercostal sulci are less marked than in testudinids (Bailon 2010). Furthermore, given that the studied costal fragment is flat, it is likely that both remains belonged to a freshwater turtle.

During the Early Miocene, the European record of freshwater turtles included the clades Chelydridae Gray, 1831; Trionychidae Fitzinger, 1826; Emydidae Rafinesque, 1815; and Geoemydidae Theobald, 1868 (Pérez-García 2017). Only the two latter inhabit Europe at present (Spreybroeck et al. 2016). The presence of sulci between scutes and the little marked dorsal ornamentation discount the presence of Trionychidae in the CR15 fossil assemblage.

Order **Squamata** Oppel, 1811
Infraorder **Scinciformata** Vidal & Hedges, 2005
cf. **Scinciformata** indet. 1

Fig. 4A, B

Material: *Crevillente 2.* MGUV-15437b, 1 left maxilla; MGUV-15437c, 1 right dentary.

Description. Only the posterior region of the recovered maxilla (MGUV-15437b) has been preserved, showing the basis of the posterior process (Fig. 4A–B). This specimen possesses seven tooth positions, with four teeth still in place. They are pleurodont and cylindrical with a triangular blunt apex. The tooth necks are medially expanded in lingual view. In labial view, the teeth appear as monocuspid (a blunt labial cusp), but in lingual view, underneath the labial cuspid, a smaller lingual cusp may be present. The crowns of the teeth, labially convex, do not appear to be striated; however, some of them do appear to show a horizontal groove at the base of the tooth apex. In occlusal view, the tooth necks are slightly enlarged lingually. The supradental shelf, partially broken, is wide and slightly arched. In labial view, only the tooth crown exceed the dental crest. The bone labial surface is smooth. The dentary shows an open Meckelian groove. This specimen has seven tooth positions, with only three teeth preserved. The teeth are morphologically similar but slightly narrower than those preserved in the maxilla. Rounded medium-sized resorption pits are present at their base.

Remarks. See below.

cf. **Scinciformata** indet. 2

Fig. 4C

Material: *Crevillente 2.* MGUV-15437a, 1 indeterminate tooth-bearing bone.

Description. MGUV-15437a is a highly fragmentary indeterminate tooth-bearing bone. A single tooth is present, morphologically different from those described above (Fig. 4C). In this regard, the tooth is pleurodont, cylindrical, and unicuspid, with a blunt apex. In contrast to the previously described teeth, the crown is convex. Its lingual surface is concave. Both, lingually and labially, the crown is smooth; however, this could be due to the erosion of the crown.

Remarks. The fully open Meckelian groove, the transversally bicuspid teeth, and the apparent apicobasal striation present in some tooth crowns (in our case only a basal horizontal stria has been observed) indicate their affinity with the clade Scinciformata. Among the described material, there are

Fig. 4 - Squamates from Crevillente 2. A-B), cf. Scinciformata indet. 1, left maxilla, MGUV-15437b, in labial (A) and lingual (B) views. C) cf. Scinciformata indet. 2, indeterminate tooth bearing bone, MGUV-15437a, in lingual (C) view. D-G) cf. *Timon* sp., right maxilla, MGUV-15436d, in lingual (D) and labial (E) views; parietal, MGUV-39632, in dorsal (F) and ventral (G) views. H-I) Lacertidae indet. 1, right dentary, MGUV-15436a, in lingual (H) and labial (I) views. J-K), Lacertidae indet. 2, MGUV-15436a, dentary in lingual (J) and labial (K) views. L-M) *Ophisaurus* s.l. sp., right dentary in lingual (L) and labial (M) views. N-T) *Pseudopus* sp., left dentary, MGUV-15438b, in lingual (N) view; right dentary (O-P), MGUV-15438c, in lingual (O) and labial (P) views; dorsal vertebra (Q-S), MGUV-8132, in dorsal (Q), ventral (R), and anterior (S) views; caudal vertebra (T), MGUV-8131, in anterior view. U) Anguidae indet., osteoderm, MGUV-8130, in dorsal view. Scale bar: 1 mm, except for Q, R, S, and T (2 mm).

apparently two morphotypes which probably belong to two different taxa. However, poor preservation state of the material precludes a more precise taxonomical attribution.

Family Lacertidae Oppel, 1811
Genus *Timon* Tschudi, 1836

cf. ***Timon*** **sp.**

Figs. 4D-G and 5A

Material. *Crevillente 2.* MGUV-39637, 1 right maxilla; MGUV-15436d, 2 indeterminate tooth-bearing bones; MGUV-39632, 1 parietal.

Description. The maxilla only preserves its most anterior part (Fig. 4D–E). Thus, a short premaxillary process is observable. In dorsal view, the anterior premaxillary process has a deep anterior concavity bordered by the anteromedial process (which is broken) and the anterolateral process. The latter is straight but its end is not preserved. A large

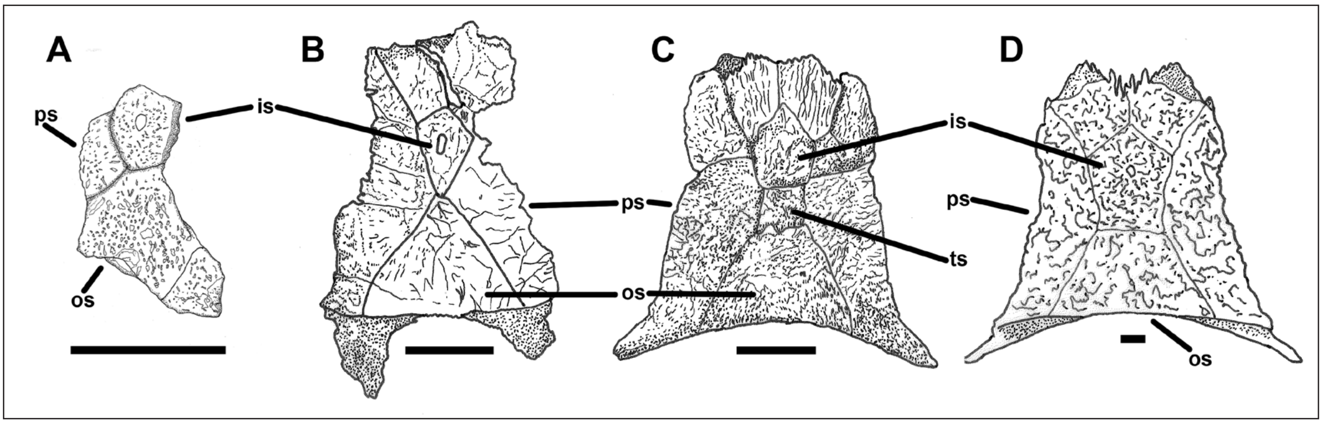

Fig. 5 - Parietal of some Paleogene and Neogene lacertid taxa with wide occipital scute. A) cf. *Timon* sp., MGUV-39632, Crevillente 2 site (MN11, Late Miocene; Spain). B) *Dracaenosaurus croizeti*, Cournon (late Oligocene; France). Redrawn from Čerňanský et al. (2017). C) *Plesiolacerta lydekkeri*, MNHN QU 17 168, Phosphorites du Quercy (Oligocene; France). Redrawn from Čerňanský & Augé (2013). D) *Timon lepidus*, current. Redrawn from Barahona (1996). is, interparietal shield; os, occipital shield; ps, parietal shield; ts, transitional shield. Scale bar: 5 mm.

vomeronasal foramen is located at the base of both the anteromedial and the posterolateral processes. In lingual view, the preserved teeth are pleurodont, long, cylindrical, and bicuspid. Large and subcircular resorption pits are present at the base of some teeth. Lingually, the teeth are convex (Fig. 4D). In labial view, the bone preserves an osteoderm. Its surface is ornamented with small circular or vermicular grooves. Four large ventrolateral foramina are present (Fig. 4E).

MGUV-39632 is a strongly fragmentary parietal. Only the middle region of the parietal table is preserved. In dorsal view, it is covered by several osteodermal shields, which are separated by well-defined grooves. The interparietal shield is large, slightly longer than wide and subhexagonal in shape. This shield is pierced by a large and oval-shaped parietal foramen in its medial region. The occipital shield is wide, occupying a large area of the posterior portion of the parietal table. It is, at least, three times wider than the interparietal shield. Part of the left lateral shield is preserved. The dorsal surface of the fossil shows a well-marked vermicular sculpturing sensu Glynne et al. (2020; Fig. 4F). In ventral view, only part of the medial ventral crest is preserved. Although it is clearly well developed, it is highly eroded thus precluding further description. A deep parietal fossa is located in the posterior midline of the medial ventral crest. This fossa is narrow and triangular. A contact between the medial and the posterolateral ventral crest is absent (Fig. 4G).

Remarks. The presence of a wide occipital shield is typical of the genus *Timon* among the extant lacertid genera in Europe (Fig. 5A, D; Barahona 1996; Barahona & Barbadillo 1997; Arnold et al. 2007; Villa & Delfino 2019a). Moreover, a triangular parietal fossa and the fact that the medial and the posterolateral ventral crests are not in contact are both characters compatible with *Timon* (Villa & Delfino 2019a). The morphology of the parietal is known in few of the extinct lacertid taxa present in Eurasia. In most of them, the occipital shield is narrow, such as *Pseudeumeces cadurcensis* (Filholi, 1877) (Augé & Hervet 2009), *Succinilacerta succinea* (Boulenger, 1917) (Borsuk-Białynicka et al. 1999), *Janosikia ulmensis* (Gerhardt, 1903) (Čerňanský et al. 2016), and *Lacerta* cf. *trilineata* Bedriaga, 1886 (Čerňanský & Syromyatnikova 2019). Thus, *Dracaenosaurus croizeti* Gervais, 1848 and *Plesiolacerta lydekkeri* (Hoffstetter, 1942) are the only extinct lacertid taxa with a wide occipital shield. However, in *D. croizeti* this shield is equilateral triangular in shape, and it is in contact with a rhomboidal interparietal shield (Fig. 5B). In ventral view, the posterolateral and the medial crests are not in contact, but arranged in parallel, whereas in *Timon* both crests are perpendicular to each other (Čerňanský et al. 2017). As mentioned above, *P. lydekkeri* also has a wide occipital shield, but it is trapezoidal in shape (Fig. 5C). However, in the congeneric taxon *Plesiolacerta eratosthenesi* Čerňanský & Augé, 2013, the occipital scute is narrow and rectangular (Čerňanský & Augé 2013). Moreover, in this genus, a transverse groove divides the lateral shield into two asymmetrical portions (an anterior and a posterior one). This groove also divides the interparietal shield, forming a short so-called transitional shield (Čerňanský & Augé 2013). In summary, while the general morphology of the studied remains is close to that of *Timon*, given their poor preservation state and the limited understanding of parietal morphology in several extinct lacertid taxa, we prefer to use open nomenclature until new material can provide further clarification on this matter. The tooth morphology differs from the other two taxa of Lacertidae described from CR2. These teeth are longer than those of Lacertidae indet. 1 and 2., and present a more robust aspect. Therefore both fossils are potentially attributed to *Timon*.

Lacertidae indet. 1

Fig. 4H, I

Material: *Crevillente 2*. MGUV-15436a, 1 right dentary.

Description. MGUV-15436a is a small-sized right dentary, whit only part of its posterior edge preserved. Despite its poor preservation state, it clearly shows an arched ventral edge. The dentary presents a fully open Meckelian groove, the width of which decreases towards the anterior part of the bone. It shows seven/eight tooth positions, with four teeth pleurodont, cylindrical, bi- or tricuspid still in place. The tooth morphology is characterized by a main central cuspid, with smaller mesial and distal cusps. At the base of the rearmost teeth, a large elliptical resorption pit is present. The supradental shelf is wide, and increases in width towards the anterior region of the bone (Fig. 4H). In labial view, only the crown of the teeth exceeds the dental crest. Two large labial foramina are present (Fig. 4I).

Remarks. The remains have some traits clearly attributable to Lacertidae, such as the open Meckelian groove, the arched ventral edge and the cylindrical pleurodont teeth, with two or three cuspids, whit the central one as the most developed (Bailon 1991; Blain 2009). However, the current osteology of this group is still poorly understood. Moreover, the cranial osteology seems to be strongly conservative in the group (Villa & Delfino 2019a). Therefore, it is not possible to propose a more specific attribution.

Lacertidae indet. 2

Fig. 4J, K

Material: *Crevillente 2*. MGUV-15436b, 1 dentary.

Description. The highly damaged dentary shows three tooth positions with only two teeth present, whose morphology strongly differs those described above. The teeth are pleurodont, cylindrical, and tricuspid. In this case, however, the three cusps are well developed, whit the central one more developed than the other two. The mesial and distal cusps are well developed with well-marked interdental grooves directed ventrally in both labial and lingual views. The resorption tips are small-sized and elliptical (Fig. 4J). In labial view, two labial foramina are present (Fig. 4K).

Remarks. Tricuspidity is a common trait reported in some groups of lizards, such as Iguanidae Oppel, 1811, Teiidae Gray,1827, and Lacertidae (Evans 2008). However, the Iguanidae disappeared from Europe in the late Oligocene (Augé & Pouit 2012) and the presence of Teiidae in this continent was brief (limited to MP17, late Eocene; Augé & Brizuela 2020). Different species of lacertids are known to have tricuspid teeth, either extant, like *Gallotia* Boulenger, 1916 (Barahona et al. 2000), or extinct, like for example *Miolacerta* Roček, 1984 (Roček 1984) *a*nd *Lacerta* s.l. *filholi* Augé, 1988 (Augé 2005). The poor preservation state of the studied remains prevents a more precise taxonomic ascription.

Family Anguidae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus s.l. **sp.**

Fig. 4L, M

Material: *Crevillente 2*. MGUV-15435, 1 right dentary; MGUV-39638, 1 left dentary.

Description. MGUV-15435 is a fragmentary right dentary, whit only its posterior end preserved. In lingual view, it shows a fully open Meckelian groove. It is divided by an intramandibular septum at the level of the foremost preserved teeth. This structure constitutes a subhorizontal wall forming the floor of the alveolar canal. The bone has three tooth positions, with only two teeth preserved, which are subpleurodont, relatively robust, and caniniform with an acute apex slightly curved backwards. Their base is medially expanded. The resorption pit is rounded and medium-sized. The interdental gap is relatively wide (about one fifth of the width of the tooth base; Fig. 4L). In labial view, the surface is smooth except at the level of the foremost teeth, where a large labial foramen is present (Fig. 4M).

Remarks. The dentary shows some traits, such as subpleurodont, robust, caniniform teeth, compatible with an attribution to the genus *Ophisaurus* s.l. (Bailon 1991; Klembara et al. 2014). Molecular studies have shown that this clade actually represents three highly divergent lineages: *Ophisaurus* s.s. from North America, *Dopasia* Gray, 1853 from southeast Asia, and *Hyalosaurus* Günther, 1873 from northern Africa (Macey et al. 1999; Lavin & Girman 2019). Unfortunately, the osteological differences between them are still unknown. The small size of the studied remain and its lack of striation in the lingual surface of the dentary suggests that it may belong to a juvenile individual (Klembara et al. 2014). During the adult phase all extant species of *Ophisaurus* s.l. show a striation on the lingual side of the teeth apex (Klembara et al. 2014); however, taxa lacking this feature have been reported from the Early Miocene. This is the case of, for example, *Ophisaurus acuminatus* Jörg, 1965 (Klembara & Čerňanský 2020).

Genus *Pseudopus* Merrem, 1820

***Pseudopus* sp.**

Fig. 4N–T

Material: *Crevillente 2*. MGUV-15438a, 1 right maxilla; MGUV-15438b, 1 right dentary; MGUV-15438c, 1 left dentary; MGUV-15438d, 1 isolated tooth; MGUV-8131 and 16801, 2 caudal vertebrae; MGUV-8132, 1 dorsal vertebra.

Description. MGUV-15438a is the rearmost portion of a right maxilla. The posterior process is long and slender in labial view, but its tip is missing. In lingual view, the preserved teeth are large, cylindrical, robust, and subpleurodont. Their crowns are blunt and rounded, provided with striae in both lingual and labial sides. The teeth are closely spaced. In labial view, a large and rounded foramen is present.

The recovered tooth-bearing bones correspond to the foremost end of a right dentary (MGUV-15438b; Fig. 4N) and the posterior region of a left one (MGUV-15438c; Figs. 4O-P). MGUV-15438b shows four teeth positions, but only three teeth are preserved. They are pleurodont, monocuspid, cylindrical and slightly robust. Their apices are pointed but not curved. The teeth are well-spaced and non-striated. The Meckelian groove is fully open and wide. The symphysis is large, kidney-shaped and postero-medially projected (Fig. 4N). In dorsal view, the symphysis forms a short medially developed expansion of its posterior end. In labial view, two large foramina are present. On the other hand, the left dentary MGUV-15438c has a teeth morphology similar to that described for the maxilla. In lingual view, the dental crest shows a wide lamella for the articulation with the splenial. A short and wide splenial spine is posteriorly present to the lamella. Over the splenial spine is located a shallow notch. Both structures, the notch and the splenial spine, form the anterior margin of the antero-posteriorly elongated anterior inferior alveolar foramen. A facet for the articulation of the splenial is posteriorly located to the anterior inferior alveolar foramen. The coronoid is thus excluded from the latter. The alveolar foramen, which supposes the opening of the alveolar canal, is located at the level of the posterior portion of the anterior inferior alveolar foramen. The broken intermandibular septum forms the anteroventral shelf of the foramen (Fig. 4O). In labial view, MGUV-15438c shows three oval-shaped labial foramina (Fig. 4P).

The vertebra is large sized and procoelous (Figs. 4Q–S). In dorsal view, the interzigapophyseal constriction is strong. The prezygapophyses are well differentiated and oval-shaped, and the postzygapophyses are short, wide and rounded. The neural spine is broken (Fig. 4Q). In ventral view, the triangular centrum has a flat surface with an elevated posterior part. The centrum shows a straight *margo ventralis* (= subcentral ridge, *margo inferior*; Fig. 4R). The centrum is shallowly convex in lateral view. The condyle is broken. In anterior view, the *pars tectiformis* is dome-shaped, giving the neural canal a subtriangular appearance. The prezygapophysis projects dorsolaterally. The cotyle, strongly dorsoventrally flattened, is lower than the height of the neural arch (Fig. 4S). MGUV-8131 (Fig. 4T) and MGUV-16801 present a pair of haemapophysis, for this reason they are considered as caudal vertebrae (Čerňanský et al. 2019).

Remarks. The studied material shares the following characters with the genus *Pseudopus* (Čerňanský et al. 2019; Klembara et al. 2014): presence of anterior pleurodont, cylindrical and straight teeth, posterior teeth subpleurodont, large and with blunt and rounded tips, and vertebral centrum with a straight *margo ventralis* in ventral view. Nowadays, the genus is limited to only a single species, *Pseudopus apodus* (Pallas, 1775). Its distribution includes the Balkans, Crimean Peninsula, and Ciscaucasia region in Europe, and Asia Minor and the Middle East (Speybroeck et al. 2016). So far four extinct species have been recognized: *Pseudopus confertus* Klembara & Rummel, 2018 (Early Miocene, MN3, Ahníkov I, Merkur North opencast mine, Czech Republic), *Pseudopus ahnikoviensis* Klembara, 2012 (Early Miocene, MN3, Central Europe), *Pseudopus laurillardi* (Lartet, 1851) (Early–Middle Miocene of Europe), and *Pseudopus pannonicus* (Kormos, 1911) (Late Miocene–Middle Pleistocene of central and eastern Europe; Klembara & Rummel 2018). Although the studied remains are highly damaged, some taxonomic conclusions can be drawn. Thus, the presence of a facet for the splenial posteriorly to the anterior inferior alveolar foramen allows us to discount their ascription to *P. apodus* (it should be noted that the dentary of *P. confertus* is unknown; Loréal et al. 2023). In fact, the absence of *P. apodus* in CR2 locality is consistent with the oldest known record of the species in MN15 (latest Early Pliocene) at Ivanovce in Slovakia (Klembara 1986). The Iberian fossil record of *Pseudopus* is scarce and mainly limited to the Early–Middle Pleistocene of eastern Spain (Blain et al. 2016). The oldest Iberian record corresponds to the locality of els Casots (earliest MN5, Middle Miocene; Vallès-Penedès Basin, Catalonia, Spain), where a trunk vertebra morphologically similar to those of *Pseudopus* has been recovered (Casanovas-Vilar et al. 2022).

Anguidae indet.

Fig. 4U

Material: *Crevillente 2.* MGUV-39639 and 39640, 2 dorsal vertebrae; MGUV-8078a, 39641, and 39640, 3 centra of dorsal vertebra; MGUV-8075, 8076, 8132, 65 osteoderms.

Description. The most complete osteoderms are rectangular. In dorsal view, the surface of the remains present two distinct areas. The larger one has a vermicular ornamentation with a longitudinal keel. The smaller area is smooth, the gliding surface sensu Hoffstetter (1962). This part is originally covered by the preceding osteoderm in skeleton of the animal (Fig. 4U).

The vertebrae are procoelous and craniocaudally elongated. The neural crest is very low and starts over the *pars tectiformis* in a small protuberance. The neural arch is low in its first half of its length, projecting dorsally posteriorly. The prezygapophyses are not preserved; however, it can be inferred that they were anterolaterally projected. In its middle region, the neural spine is almost imperceptible, but in its last stretch the structure is fully visible and ends in a mucro. Since the postzygapophyses are broken it is not possible to know whether they would be overlapped by the neural spine. The centrum is triangular and slightly concave in lateral view. Its ventral surface lacks any haemal keel or hypapophysis. A large pair of subcentral foramina is present. The *margo ventralis* is convex. Whereas the neural canal is ventrodorsally compressed in anterior view, the neural canal is laterally compressed in posterior view. The roof of the neural canal is domed. Both the cotyle and the condyle are dorsoventrally compressed in anterior and posterior views, respectively.

Remarks. The subrectangular shape of the osteodems and the presence of a keel are traits found in non-*Anguis* anguine taxa (i.e., *Pseudopus* or *Ophisaurus* s.l.; Hoffstetter 1962). Regarding the studied vertebrae, the presence of convex *margo ventralis* in ventral view supports their attribution to *Ophisaurus* s.l. according to Čerňanský et al. (2019). However, these same authors pointed out that this trait might also be found in juvenile *Pseudopus*. In summary, due to the relatively low taxonomical value of the remains it is not possible to assign them to any of the anguid genera recovered from CR2. Thus, we attribute them to Anguidae indet. An indeterminate anguid was reported by Böhme & Ilg (2003) from CR3. Nevertheless, these remains have not been formally described or figured, making it impossible to compare them with the taxa described here.

Suborder **Serpentes** Linnaeus, 1758
Family Colubridae s.l. Oppel, 1811
Colubridae s.l. indet. 1

Figs. 6A–E

Material: *Crevillente 2.* MGUV-16805, 1 precaudal vertebra; MGUV-39645, 1 vertebral centrum.

Description. A procoelous small-sized vertebra has been recovered from CR2 (Fig. 6A). In dorsal view, the interzigapophyseal constriction is well marked. The left prezygapophysis, the only one preserved, is as large as wide. It is anterolaterally projected. The articular surface of the prezygapophysis is large and oval. Although broken, the zygosphene is concave sensu Auffenberg (1967). The postzigapophysis is short and wide (Fig. 6A). In lateral view, the neural crest is broken. The *margo lateralis* (=interzygapophyseal ridge, zygapophyseal ridge, lateral ridge) is not well marked. The epizigapophyseal spine is weakly prominent and wide. The lateral foramen is large, and it is located at the base of the prezigapophyseal process within a relatively deep depression. The *margo inferior* is moderately developed (Fig. 6B). In ventral view, the centrum is triangular, and longer than wide. The cotylar neck is marked but short. The paradiapophysis is large, with the diapophysis relatively differentiated from the parapophysis and the latter larger than the former. The haemal keel is spatulate and ridge-like. It ends in a more or less rounded tip. A pair of small subcentral foramina is present (Fig. 6C). In anterior view, the neural canal is large and dorsoventrally slightly flattened. Its roof is flat but slightly concave. The condyle is large and round but, as the neural canal, it is dorsoventrally slightly depressed. The paracotylar foramina are large and deep. The parapophyses extend beyond the ventral margin of the cotylar rim (Fig. 6D). In posterior view, the condyle is large and rounded (Fig. 6E).

Remarks. The specimens are attributed to a colubrids on the basis of its overall morphology (a slightly longer than wide vertebra lacking the hypapophysis). Their poor preservation state hinders a more detailed taxonomic attribution. However, several aspects can be pointed out when comparing these specimens with other chronologically related taxa of colubrids. Thus, MGUV-16805 differs from *Coluber* s.l. Linnaeus, 1758 in its smaller size, the lack of a step in the haemal keel in lateral view, and a non-displaced diapophysis in relation to the parapophysis (Bailon et al. 2005; Rage & Bailon 2005). On the other hand, *Texasophis* Holman, 1977 has a more elongated centrum and well developed subcentral grooves and *margo ventralis* (Szyndlar 1991a). It is interesting to note that certain aspects of the fossil show certain similarities, as an elongated vertebral centrum provided with a prominent narrow haemal keel, the presence of a short cotylar neck, and sinapophysis smaller than the parapophysis, but both are not well differentiated, with *Malpolon* Fitzinger 1826, a psammophiioid currently present in southern Europe (Bailon 1991).

Colubridae s.l. indet. 2

Fig. 6F

Material: *Crevillente 2*. MGUV-16804, 1 vertebral centrum.

Description. MGUV-16804 is an isolated centrum of a trunk vertebra. It is clearly longer than wide. The haemal keel is wide, spatulated, and flattened (Fig. 6F). It ends in a pointed tip, which is prominent in posterior view. A shallow precondylar constriction is present. Although broken, it can be clearly observed that the parapophysis are small-sized. Apparently, the diapophysis and the parapophysis were similar in size. The *margo lateralis* is evident in the anterior half of the centrum in lateral view, although it appears blunt in ventral view. The subcentral foramina are very small (Fig. 6F). In anterior view, the cotyle is large, rounded, and dorsoventrally slightly flattened. The paracotylar foramina are large and well defined. The paradiapophysis does not seem to overlap the ventral margin of the cotylar rim.

Remarks. The overall morphology of the centrum is compatible with colubrids, based on the fact that it is longer than it is wide and lacks a hypapophysis. The studied remain is similar to the "Colubrines" indet., type 1 from the Early Miocene (MN4) of Mokrá-Western Quarry (Czech Republic; see Ivanov et al. 2020: Fig. 10.H). However, the poor state of preservation of our material precludes any further comparison.

Subfamily Natricinae Bonaparte, 1838
Genus *Neonatrix* Holman, 1973

Neonatrix sp.

Fig. 6G–J

Material: *Crevillente 2*. MGUV-39636, 1 precaudal vertebra; MGUV-39643, 1 vertebral centrum.

Description. MGUV-39636 is a small procoelus precaudal vertebra (Fig. 6G–J). In dorsal view, the vertebra is elongated. The preservation state is poor: the neural spine, the prezygapophysis and the postzigapophysis are broken (Fig. 6G). In lateral view, the *margo lateralis* is marked. The lateral fora-

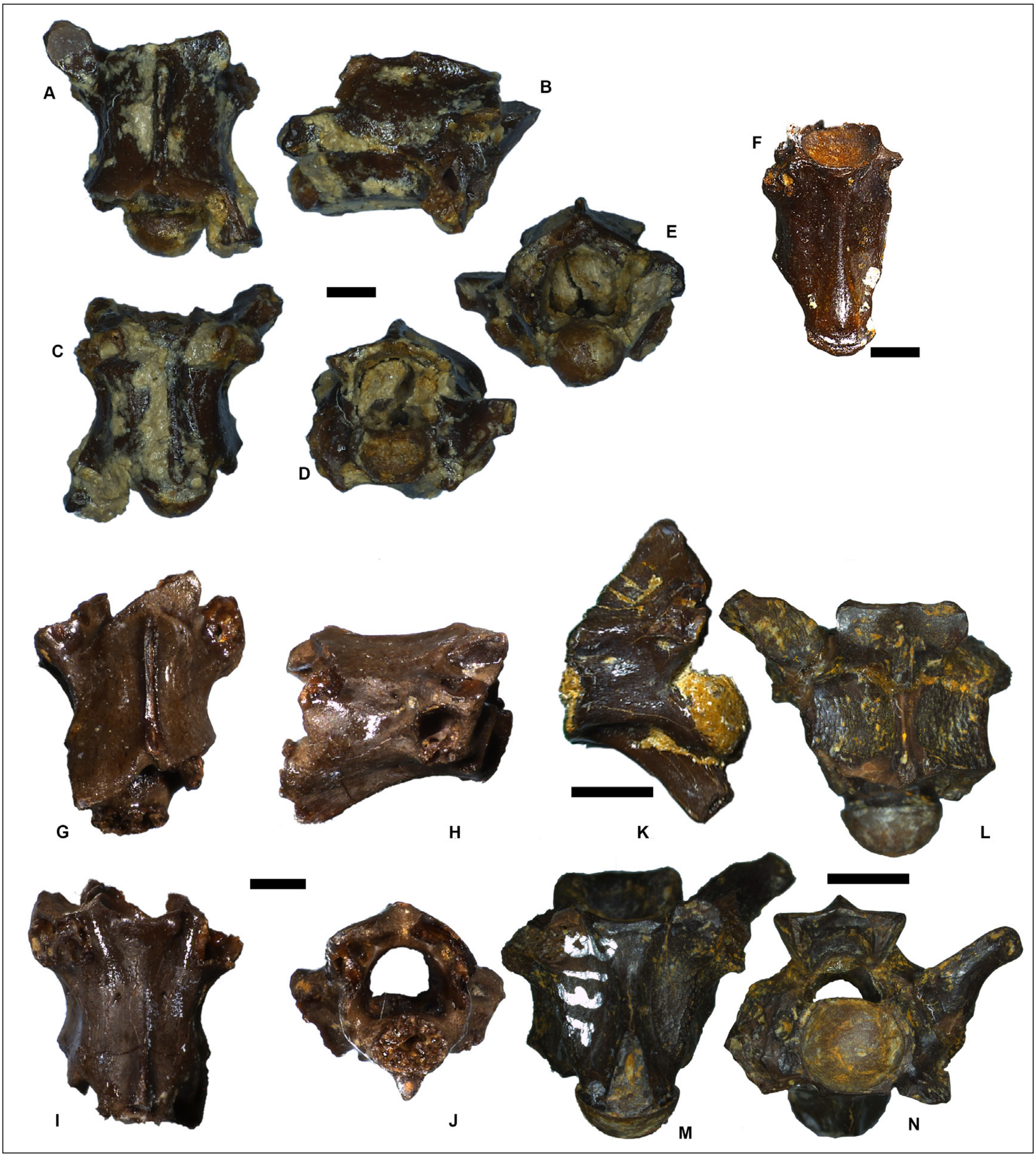

Fig. 6 - Ophidians from Crevillente 2. A-E) Colubridae indet. 1, precaudal vertebra, MGUV-16805, in dorsal (A), lateral (B), ventral (C), anterior (D), and posterior (E) views. F) Colubridae indet. 2, vertebral centrum, MGUV-16804, in ventral view. G-J), Neonatrix sp., precaudal vertebra, MGUV-39636, in dorsal (G), lateral (H), ventral (I), and posterior (J) views. K-N) Viperidae indet. Oriental Morphotype, precaudal vertebra, MGUV-16799, in lateral (K). MGUV-8135d in dorsal (L), ventral (M), and anterior (N) views. Scale bar: 1 mm, except for K-N (5 mm).

men is located within a deep depression and is surrounded by two extra foramina. The *margo ventralis* is weak. The hypapophysis is very short and sigmoid (Fig. 6H). In ventral view, the centrum is much longer than wide (Fig. 6I). The hypapophysis is modified anteriorly into a widened anterior keel, but its lateral borders are diffuse. MGUV-39643 is an isolated centrum of a precloacal vertebra, with a prominent haemal keel. The subcentral grooves are absent and the subcentral foramina are small. A very weak precondylar constriction is present. In anterior view, the cotyle is rounded, with a straight bottom border. The paracotylar foramen is large. The condyle is small, dorsoventrally flattened, and subcircular but more rounded than in MGUV-39636. The neural arch is vaulted in posterior view (Fig. 6J).

Remarks. MGUV-39636 is attributed to a natricine colubrid because it is a lightly built elongated vertebra with a short and sigmoid hypapophysis, and a domed neural arch in posterior view (Szyndlar 1984, 1991b). The hypapophysis is strongly reduced, which is a diagnostic feature of the genus *Neonatrix* (Augé & Rage 2000). Szyndlar & Schleich (1993) proposed to restrict the generic name *Neonatrix* exclusively to its North American members, i.e., *Neonatrix elongata* Holman, 1973, and *Neonatrix magna* Holman, 1982. Following Szyndlar & Schleich (1993), the European forms have a generic assignment uncertain because the osteology of the most Afro-Asiatic natricines is unknow. However, we prefer here to maintain the generic status until further research resolves this issue.

Family Viperidae Oppel, 1811
Viperidae indet. "Oriental viper morphotype"

Fig. 6K–N

Material: *Crevillente 2.* MGUV-8133 to 8135, 16799, 16800, 16802, and 16803, 10 precaudal vertebrae; MGUV-16806, 4 centra of precaudal vertebra.

Description. The studied vertebrae are procoelous, large-sized and robust (Fig. 6K-N). In lateral view, the vertebrae are relatively short and high. In all specimens the neural crest is broken. MGUV-16799 is the only fossil with a partially complete neural crest, which does not appear to be higher than long. The *margo lateralis* is well defined. The lateral foramina are large. At the basis of the postzigapophysis, a distinct foramen is present. The paradiapophysis are large, but there is no clear distinction between the parapophysis and the diapophysis. The parapophyseal process is wide and short; it is antero-ventrally projected. The *margo ventralis* is well defined. It extends backward from the posterior margin of the parapophysis, but does not reach the condyle. Although distally broken, it can be observed that the hypapophysis is long, straight and postero-ventrally projected (Fig. 6K). In dorsal view, the prezygapophyses are well differentiated with regard to the neural arch, which is dorso and anterolaterally projected. The articular surface of the prezygapophysis is large and oval (Fig. 6L). The zygosphene is large, and shows a variable morphology (from completely concave to slightly trilobulated, with a very weakly marked central lobe). The neural spine runs along the entire length of the neural arch, except for the foremost tip of the zygosphene. The postzygapophysis is wide and postero-laterally projected. In ventral view, the centrum is triangular and longer than wide, the cotylar lip is well defined and the parapophyseal process is subquadrate in shape and exceeds the cotylar lip (Fig. 6M). The subcentral foramina are small. The hypapophysis is relatively wide at the base, and it is connected to a prominent haemal keel. Moreover, the base of the hypapophysis is in contact with the cotyle (Fig. 6M). In anterior view, the neural canal is dorsoventrally compressed, with its roof slightly doomed. The zygosphene is straight. The prezygapophyses are strongly tilted upward (approximately 45° respect to the horizontal axis; Fig. 6N). The cotyle is large and rounded, except for its ventral border which is flat. The paracotylar foramina are distinct. The parapophyseal processes exceed the ventral edge of the cotyle. In posterior view, the neural arch is clearly dorsoventrally depressed. The zygantra are large. The condyle is large and rounded (Fig. 6N).

Remarks. The overall morphology of the studied vertebra is compatible with Viperidae, based mainly on the presence of a dorsal vertebra with hypapophysis, neural arch dorsoventrally depressed, vertebral centrum longer than wide, well-developed condyle and cotyle, presence of parapophyseal processes, and the articular surface of the pre- and postzygapophyses dorsally inclined. Following Szyndlar & Rage (1999), palaeontologists differentiate four morphotypes of European vipers based on trunk vertebrae: the *Vipera aspis* complex, *Vipera berus* complex, Oriental vipers, and *Daboia* Shaw & Nodder, 1797. Whereas the two first morphotypes have small-sized vertebrae, Oriental vipers and *Daboia* are characterized by their large size. The Oriental vipers vertebrae are relatively short and with high spines and hypapophysis. Trunk vertebrae of the *Daboia* morphotype differ from the Oriental vipers in their much higher neural spines. MGUV-16799 is the only fossil with part of its neural spine still preserve which is clearly as tall as it is long. This trait relates our material to the Oriental vipers. An osteological differentiation between the members of this group has been tentatively proposed based on the shape of the articulation surface of the prezygapophysis, the presence/absence of the epizygapophyseal spine, the degree of dorsal tilt of the prezygapophyses and the shape and protrusion of the anterior border of the neural spine (Bailon 1991; Szyndlar 1987; Szyndlar & Schleich 1993). Our material shows an oval articular surface of the prezygapophysis, which is strongly tilted upward. Both traits are compatible with the *Vipera xanthina* complex proposed by Szyndlar & Schleich (1993), in contrast to the *Vipera lebetinus* complex in which the articular surface is subrectangular and the prezygapophysis is less upward inclined. However, these characters are very variable. In this sense, Szyndlar & Rage (1999) pointed out that the vertebrae of both complexes are actually almost indistinguishable. These authors stated that the only trait potentially discriminating between *Macrovipera lebetinus* (Linnaeus, 1758) and the other taxa is the presence of a triangle-shaped hypapophysis in the three/one last trunk vertebrae. Recently, Codrea et al. (2017) provided some characters for the recognition of *Macrovipera* Reuss, 1927 species basing on vertebrae. However, these authors did not provide any character for *Montivipera* Nilson et al., 1999, the other genus included in the Oriental vipers group, or *Daboia*. Moreover, the features provided for *Macrovipera* by Codrea et al. (2017) constitute in fact generalized characters for viperids (Georgalis et al. 2019).

Serpentes indet.

Material: *Crevillente 2*. MGUV-8077, 2 isolated teeth; MGUV-8078c, 39630, 39634, 39635, and 39647: 8 caudal vertebrae; MGUV-8078b, 4 centra of caudal vertebra. *Crevillente 16*. MGUV-9562, 1 centrum of a precaudal vertebra.

Description. The preserved teeth show the general ophidian morphology (long, pointed, and recurved tubular teeth). They do not show any groove nor venom discharge orifice in anterior view.

The centrum is large and triangular. In ventral view, it has a broad flattened haemal keel, which probably finishes in a broken hypapophysis. The poor preservation state of this fossil prevents a more precise taxonomical attribution.

Remarks. The remains included in this taxon have low taxonomical value. For this reason, it is not possible to ascribe them to any of the ophidian taxa described in the present work. However, the absence of a venom discharge orifice or a suture in the anterior surface of the teeth discounts their attribution to Elapidae or Viperidae (Bailon et al. 2002). An indeterminate ophidian was reported by Böhme & Ilg (2003) from CR3. Nevertheless, these remains have been neither formally described nor figured, thus precluding their comparison with the taxa described here.

Discussion

Diversity, affinities, and palaeobiogeography

A total of 181 remains of reptiles and amphibians have been studied from the Upper Miocene localities of CR2 (MN11, local biozone of *Occitanomys sondaari* sensu Martín-Suárez & Freudenthal, 1988) and CR15 (MN12, *Huerzelerimys turoliensis* local biozone sensu Martín-Suárez & Freudenthal, 1988). We have also included in the study material from CR16; however, the fossils from the latter site are limited to a single taxon (Serpentes indet.). This locality has therefore not been included in the Discussion.

The faunal list of CR2 includes one anuran (*Pelophylax* sp.), one crocodylian (Crocodylia indet.), seven lizards (cf. Scinciformata indet. 1, cf. Scinciformata indet. 2, cf. *Timon* sp., Lacertidae indet. 1, Lacertidae indet. 2, *Ophisaurus* sp. s.l., and *Pseudopus* sp.), and four snakes (Colubridae s.l. indet. 1, Colubridae s.l. indet. 2, *Neonatrix* sp., and Viperidae indet., Oriental Morphotype; Tab. 1). Our finding increases the knowledge about the herpetofauna of this classic site, which is considered as the reference locality for MN11 (Mein 1990; Bruijn et al. 1992); so far, the assemblage was limited to testudines ("*Testudo*" aff. *catalaunica*, *Titanochelon bolivari*, and Testudines indet., in updated nomenclature) and one anuran (*Pelophylax* gr. *ridibundus*; Jiménez & Montoya 2002; Böhme & Ilg 2003). The reptile and amphibian fossils studied in this work were included in previous faunal lists (i.e., Mazo & Montoya 2003), but had not been formally described until now.

The studied assemblage from CR15 consists of Crocodilya indet., *Palaeotestudo* sp., and Testudines indet., the latter presumably a freshwater turtle (Tab. 1).

Compared to mammals, the amphibian and reptile faunas of the Late Miocene of the Iberian Peninsula are poorly known, with few examples of

	CR2	CR3	CR4	CR5	**CR15**	**CR16**
Pelophylax pueyoi						
Pelophylax gr. *ridibundus*				+		
Pelophylax sp.	**X**					
Rana sp.						
Diplocynodon sp.			+			
Crocodylia indet.	**X**	+			**X**	
Palaeotestudo aff. *antiqua**	X					
Palaeotestudo sp.					**X**	
*Titanochelon bolivari**	X					
Testudines indet.*	X				**X**	
Amphisbaenia indet.		+				
Scincidae indet. 1		+				
Scincidae indet. 2		+				
Scincidae indet. 3		+				
cf. Scinciformata indet. 1	**X**					
cf. Scinciformata indet. 2	**X**					
Lacertidae indet. 1	**X**					
Lacertidae indet. 2	**X**					
Lacertidae indet. 3	**X**					
Ophisaurus s.l. sp.	**X**					
Pseudopus sp.	**X**					
Anguidae indet.		+				
Colubridae indet. 1	**X**					
Colubridae indet. 2	**X**					
Neonatrix sp.	**X**					
Viperidae indet., oriental morphotype	**X**					
Serpentes indet.	**X**	+				**X**

Tab. 1 - Faunal list from the studied sites (Crevillente 2, 15, and 16). X, presence; *, additional information provided by Jiménez & Montoya (2002) for Crevillente 2.

illustrated and accurately described assemblages or taxon that would allow for proper comparison (i.e., Sanchiz 1981; García-Porta & Casanovas-Vilar 2001; Villa et al. 2017, 2018, 2024; Georgalis & Szyndlar 2022). However, some broad remarks can be discussed at a family/genus rank.

The CR2 amphibian assemblage is really poor, and limited to a single taxon: *Pelophylax* sp. The current Palaearctic green frogs are distributed across Eurasia and North Africa. The genus *Pelophylax* appeared and diversified during the early Oligocene (Chan & Brown 2017) and quickly dispersed throughout Europe (Lemierre et al. 2022). As a result, the genus was present in most of western Europe during the Miocene (Roček 2013). The beginning of the Late Miocene marked the divergence of the westernmost taxa (clade B1 of Lymberakis et al. 2007) from the rest of the *Pelophylax* species (clades B2 to B6). Currently, clade B1 is constituted by *Pelophylax saharica* (Boulenger, 1913) and *Pelophylax perezi* (López Seoane, 1885), which is the only green frog species inhabiting Iberia. To date, during the Late Miocene, those fossil remains attributed to *Pelophylax* are morphologically very close to the present *Pelophylax ridibundus* (Pallas, 1771), i.e., *Pelophylax pueyoi*, or directly have been related to the latter taxon (i.e., *P.* gr. *ridibundus*). The specimens described here are younger than the estimated chronological interval for the proposed divergence between the clade B1 and the rest of green frogs (Lymberakis et al. 2007); however, their poor preservation state does not allow further conclusions.

Although currently absent from Europe, crocodylians were a common element during the Paleogene and Miocene. Several Miocene crocodylian fossils are very fragmentary or represented by isolated teeth, so that a generic or specific attribution is not possible. However, three genera can be distinguished during the European Late Miocene: *Tomistoma*, *Diplocynodon*, and *Crocodylus*. *Tomistoma* was present in Europe since the Eocene, and its last local representatives have been found in Late Miocene marginal marine deposits (Antunes & Cahuzac 1999). *Diplocynodon* also disappeared during the Late Miocene. In this sense, the Masia de la Roma 4B site seems to be one of the latest records of the genus (Böhme & Ilg 2003). Nevertheless, these remains have not been described, thus making it impossible to corroborate their ascription to *Diplocynodon*. On the other hand, *Crocodylus* has been cited in localities of the latest Late Miocene, such as Venta del Moro (MN13; Delfino et al. 2020). During the Early Pliocene, indeterminate crocodylians, probably the last European members of the clade, have been reported from several sites of southern Spain (i.e., Puerto de la Cadena site, Murcia, south-eastern Spain; Piñero et al. 2017). From a palaeobiogeographical point of view, it is probable that the fossils recovered from CR2 belong to *Diplocynodon* or one of the earliest representatives of *Crocodylus* in Europe.

Turtles are represented by, at least, two taxa from CR15: *Palaeotestudo* sp. and Testudines indet., the latter probably corresponding to an indeterminate freshwater turtle. The studied specimes complement the material from the CR2 locality previously described by Jiménez & Montoya (2002), i.e. "*Testudo*" aff. *catalaunica*, *Titanochelon bolivari*, and Testudines indet. Testudinidae are a common element in many Iberian Miocene sites (Pérez-García 2016). This assemblage is similar to that recovered from Iberian sites of similar chronology.

Lacertidae are the current dominant family of lizards in the European herpetofauna. The group radiated spectacularly in the Neogene (Čerňanský &

Smith 2018). In this sense, lacertids have a broad ecological spectrum, with forms adapted to practically all the European habitats. Three morphotypes have been recognized in the CR2 assemblage. Two of them are small-sized lizards, whereas the third one may belong to a medium-large species. Basing on the occipital shield of the parietal, the latter has been related to the genus *Timon*. If confirmed it would constitute the oldest known record for this taxon, which was until now limited to the Quaternary (Böhme & Ilg 2003; Villa & Delfino 2019b). At present, *Timon* includes six species divided in an Eastern and a Western clade, which diverged at approximately 14.5 Ma (11.2–17.8 Ma; Ahmadzadeh et al. 2016). The Eastern clade comprises two species, *Timon princeps* (Blanford, 1874) and *Timon kurdistanicus* (Suchow, 1936), both distributed in Turkey, northern Iraq, and Iran. No fossil record is known for them, most probably due to the lack of archaeological and palaeontological studies in the region (Tschopp et al. 2018). Molecular analysis dated the divergence between both species at around 7.9 Ma (5.0-11.0 Ma), perhaps associated with the uplifting of the Zagros mountains (Ahmadzadeh et al. 2016). The Western clade is formed by four species, divided in two subclades, separated by the Gibraltar Strait. The split between the European and the African subclades has been estimated at 7.4 Ma (5.9-9.0 Ma). *Timon tangitanus* (Boulenger, 1881), from the north of Morocco and northwestern Algeria, and *Timon pater* (Lataste, 1880), found in northern Algeria and northern Tunisia, are both included in the African subclade. The European subclade includes two species: *Timon lepidus* (Daudin, 1802) and *Timon nevadensis* (Bucholz. 1963). *T. lepidus* inhabits the major part of the Iberian Peninsula and south-eastern France, whereas *T. nevadensis* is limited to the eastern and south-eastern Spain (Speybroeck et al. 2016). The separation between both species, which took place around 5.7 Ma (5.3–6.3 Ma), is related with the MSC (Ahmadzadeh et al. 2016). In accordance with the chronology proposed for the CR2 site (MN11, 8.7–7.5 Ma *sensu* Agustí et al. 2001), cf. *Timon* sp. precedes the split between *T. lepidus* and *T. nevadensis*, and likely corresponds to the time interval when the European subclade separated from the African one. The current *Timon* distribution coincides with most of the sites where related taxa have been recorded; however, certain citations suggest a larger area of past distribution for the genus. This is the case of the Italian Peninsula and adjacent islands. *Timon* sp. has been cited in the Late Pleistocene sites of Cava Pirro and Cava dell'Erba (Apulia, southern Italy) by Delfino & Bailon (2000). In Sardinia, Tschopp et al. (2018) described several specimens assigned to an indeterminate species of *Timon*. Interestingly, according to these authors, this taxon became extinct due to a synergy of Pleistocene climatic fluctuations and an increase in predatory pressure due to the appearance of predators specialized in small preys. "*Lacerta*" *siculimelitensis* Böhme & Zammit-Maempel, 1982, from the Upper Pleistocene of Malta and Sicily (Böhme & Zammit-Maempel 1982; Estes 1983; Holman 1998), might actually belong to the genus *Timon* (Ahmadzadeh et al. 2016; Mateo, 2017). In this sense, Tschopp et al. (2022) indicated that "*L.*" *siculimelitensis* may belong to a genus distinct from *Lacerta* Linnaeus, 1758, thus corroborating previous works. In other Iberian localities from the same time interval, only indeterminate lacertid taxa together with the genus *Lacerta*, with three probable different forms, have been reported (Böhme & Ilg 2003). A revision of these materials is required to shed light on the early evolution of the genus *Timon*. Remains morphologically compatible with *Lacerta* are known from the Early Miocene (MN4, Dolnice, Czech Republic; Čerňanský 2010).

Anguids constitute a relatively common component of European Neogene localities; however, in many cases they are represented by fossils with poor diagnostic value, like osteoderms. In the case of CR2, anguids are represented by two taxa: *Ophisaurus* s.l. sp. and *Pseudopus* sp. Both genera are currently absent from the Iberian Peninsula, with *Anguis fragilis* Linnaeus, 1758 being the only anguid present in the region (Speybroeck et al. 2016). *Ophisaurus* s.l. includes actually three genera, *Hyalosaurus*, currently confined to North Africa, *Dopasia*, from south-eastern Asia, and *Ophisaurus* s.s., restricted to North America, which diverged during the late Oligocene (Lavin & Girman 2019). During the Miocene, the genus reached its maximum extension in Europe (Blain & Bailon 2019). At the beginning of this epoch, *Ophisaurus* is recorded in Iberia. Undescribed material of the genus has been reported from at least 15 Late Miocene Spanish localities (Böhme & Ilg 2003; Blain & Bailon 2019). Coinciding with the worsening of the climatic conditions during the Pliocene, *Ophisaurus* became restricted to the Mediterranean area. Its extirpation from Europe has been related with the climatic turnover recorded during the Early–Middle Pleistocene transition, which led to the disappearance of the subtropical humid forest biome at around 1.2 Ma (Blain & Bailon 2019). *Pseudopus*, the other anguid genus described from CR2, is currently distributed from the coastal Balkans to Central Asia (Speybroeck et al. 2016). However, *Pseudopus* was more widespread during the Neogene. In Iberia, it was present from Early Miocene until the earliest Pleistocene (Blain et al. 2016; Böhme & Ilg 2003). To date, the known Iberian fossil record of *Pseudopus* is limited to northeastern Iberia (Catalonia; Böhme & Ilg 2003). The studied remains represent the southernmost unquestionable record of the taxon in Western Europe, thus evidencing a process of expansion during the Miocene. It is interesting to note that Bailon (1991) tentatively assigned a single dorsal vertebra from the Zújar site (Guadix-Baza Basin) to the genus *Pseudopus*. This specimen is in a very poor state of preservation; thus, this attribution is highly questionable (see Bailon, 1991, Fig. 50). This expansion during the Miocene was apparently followed by a northward reduction of its distribution area, with a pattern opposite to that observed in other taxa, such as *Ophisaurus*. In this sense, *Pseudopus* is still an element recorded in Early Pliocene sites from Eastern Europe, the Balkans, and Italy (Böhme & Ilg 2003). In Western Europe, no fossils of *Pseudopus* are recorded again until the Late Pliocene in France (cf. *Pseudopus* from Sète, MN15, and Balaruc 2, MN15–MN16; Bailon & Blain 2007). Given that *Pseudopus* is easily distinguishable from other squamates, the presumed gap its fossil record in western Europe during the Late Miocene–Early Pliocene is supported by its absence from the faunal lists available in the database managed by Böhme & Ilg (2003). Further prospecting and herpetofaunal studies in Western Europe will certainly lead to the completion and/or confirmation of this probably gap in the regional fossil record of *Pseudopus*.

Snakes constitute the most diverse of the represented squamate clades from CR2, with four distinct taxa: Colubridae s.l. indet. 1 and 2, *Neonatrix* sp., and Viperidae indet. Oriental Morphotype. Among the studied material, two morphotypes/taxa of non-natricines colubrids have been described. However, considering their poor preservation state, their exact affinities cannot be precise and no biogeographic insights can be inferred. Following Szyndlar (2012), the Early to Middle Miocene in Europe can be considered as the "Age of the Natricinae". During this interval, at least three different genera have been recovered from several European localities (*Natrix* Laurenti, 1758; *Palaeonatrix* Szyndlar, 1982, and *Neonatrix*). Their dominance lasted until MN6, at least in Western Europe (Rage & Bailon 2005). With the exception of *Natrix*, the only genus in the subfamily currently present in Europe, *Neonatrix*, is the only one that persists after the Middle Miocene. Our finding fills a chronological gap, since it represents an intermediate record between those reported from several localities in central and western Europe, i.e., Dolnice, (Czech Republic) and Béon 1 (France) from the Early Miocene (MN4), and Devínska Nová Ves (Slovakia) from the Middle Miocene (Szyndlar 1982, 1991b; Rage and Bailon 2000), and the latest record of *Neonatrix* from the Hungarian locality of Osztramos 1 (MN14, Early Pliocene; cf. *Neonatrix* sp.; Venczel 2001). Also, the material from CR2 increases the distribution area of *Neonatrix* this is the first time that it is cited in the Iberian Peninsula and represents its southernmost record in Europe. Traditionally, this taxon has been considered a North-American immigrant, given that different *Neonatrix* species have been described in North America and Europe; however, it is equally likely that the genus actually dispersed into Europe from Asia, and later into North America (Rage & Holman 1984). It is even likely that *Neonatrix* is polyphyletic, and the similarity between the North American and European species is due to convergent evolution. Thus, given the lack of knowledge of the osteology of many Asian species, it cannot be ruled that the studied specimens are in fact representatives of current Asian forms (Szyndlar 1994, 2012; Venczel 2001; Rage & Bailon 2005). The "Oriental Vipers" morphotype includes large, up-to-two meters long, snakes. This group includes species in the extant genera *Montivipera*, and *Macrovipera* (Szyndlar 1991b). Both genera currently present a marginal European distribution (southeasternmost Balkans and Cyclades Islands; Speybroeck et al. 2016). However, during the Miocene, this group was widely distributed across central and southern Europe, and reached its largest geographical range, as evidenced by its discovery in northern localities, such as Dolnice (*Vipera platyspondyla* Szyndlar, 1987; MN4, Czech Republic) and Gritsev (*Vi-*

pera ukrainica, Zerova, 1992; MN9, Ukraine; Szyndlar 1991b, 2012). During the Pliocene, the distribution area of the Oriental vipers was progressive retreated to southern Europe (Szyndlar 1991b; Bailon & Blain 2007; Blain et al. 2016) and, finally, disappeared from Western Europe in the earliest Pleistocene (Blain et al. 2016).

The palaeoherpetofaunal assemblage in the Iberian and European context

The herpetofaunal assemblages from CR2 and CR15 are similar to those from other lower Turolian Iberian sites. Moreover, no taxa with clear African affinities have been recorded, in contrast to the late Turolian record (MN13; Böhme & Ilg 2003). In this regard, all of the recovered taxa seem to be part of lineages fully established in Europe at least since the Early Miocene. Basing on their origin, two groups can be distinguished: i) taxa of probable European origin, such as *Paleotestudo* (Lapparent de Broin 2000), Lacertidae (Čerňanský 2010), and, most probably, the anguid genera *Ophisaurus* s.l. sp. (Lavin & Girman 2019); ii) taxa that dispersed from North America or Asia during the Oligocene-Miocene transition or at the beginning of the Miocene, such as *Pseudopus* sp. (Vasilyan et al. 2019), *Neonatrix* (Rage & Holman 1984, but see the discussion above), and the Oriental Vipers (Szyndlar & Rage 2002).

Apparently, no drastic changes in herpetofauna have been detected at the beginning of the Vallesian (MN9–MN10; Vallesian; Fig. 7). Szyndlar (2012) pointed out that all fossil colubrid genera became extinct at this time. However, *Neonatrix* is an exception, as suggested by the same author and as confirmed by both our finding and those provided by Venczel (2001). Crocodylians suffered an important reduction in its diversity during the Late Miocene, but at least the genus *Crocodylus* survived until the Early Pliocene (Delfino et al. 2020). The last occurrence of *Tomistoma* was probably recorded in the Tago area of Portugal (10.95±0.25 Ma; Antunes & Cahuzac 1999)—but see Kotsakis et al. (2004), who proposed that *Tomistoma* survived in Italy a little longer than in Portugal. *Diplocynodon* has been also reported from Upper Miocene Iberian sites, i.e. Ribatejo (MN9) and Masía de la Roma 4B (MN10; Böhme & Ilg 2003), although these reports are not supported by descriptions (Díaz Aráez et al. 2017). At the end of MN11, the hygrophilous salamandrid *Salamandrina* Fitzinger, 1826, only reported from the MN10 localities of La Gloria 10, La Roma 1 and 2, and the MN11 sites of Masada Ruea 2 and Puente Minero 3 from the Calatayud-Teruel Basin, disappears from the Iberian Peninsula (Macaluso et al. 2021a). This extirpation was probably caused by the aridification of the region. During the Pliocene, *Salamandrina* was limited to the Italian Peninsula, which is still inhabited by two extant species (Macaluso et al. 2021a, b). Models developed by Macaluso et al. (2021b) show that the climatic suitability of Spain for *Salamandrina* remains low since 3.3 Ma.

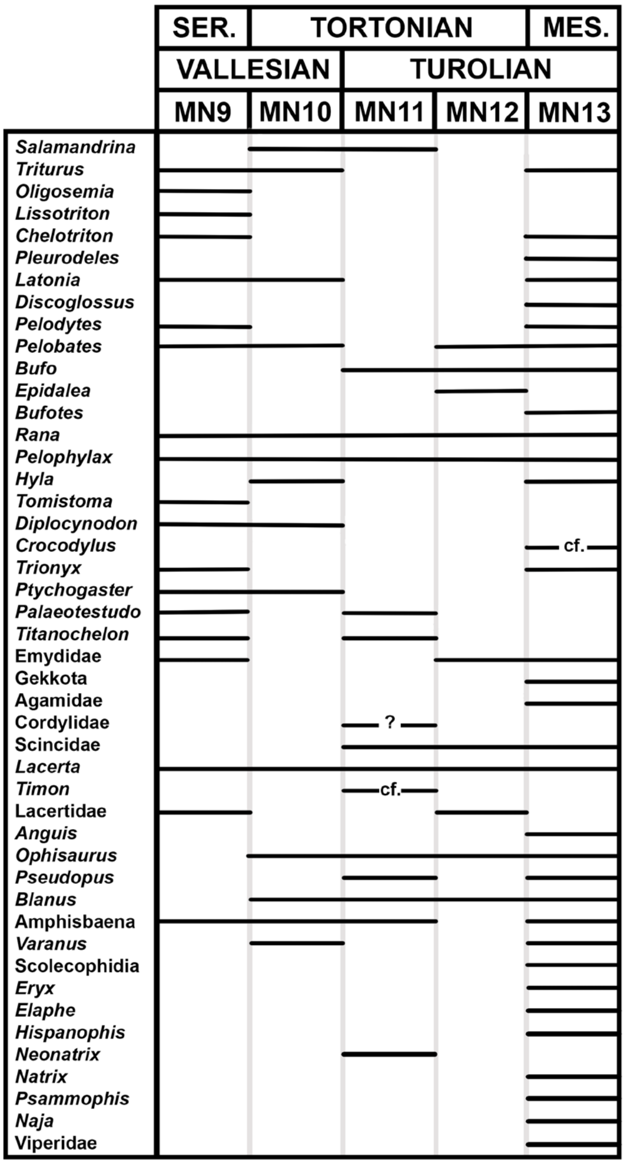

Fig. 7 - Biochronological synthesis of the amphibians and reptile Iberian fossil record during the Late Miocene based in ForFASbase database (Böhme & Ilg 2003).

The main changes in the herpetofauna palaeocommunities during the Late Miocene took place in

MN13, during or immediately prior to the MSC. It corresponded to the isolation of the Mediterranean Sea from the Atlantic Ocean by the closure of the Betic and Rifian Strait at ~7.6 and ~6.7–6.2 Ma, respectively (Booth-Rea et al. 2018). As a result, the Mediterranean practically dried out and large evaporite deposits accumulated in its basin (Hsü 1974). Associated with the MSC, diverse faunal dispersal waves occurred between Northwestern Africa and the Iberian Peninsula (Agustí et al. 2006). It was at this time when taxa with African affinities made their appareance; this is the case of ophidians, such as *Naja iberica* Szyndlar, 1985 and *Psammophis odysseus* Georgalis & Szyndlar, 2022, tortoises, like *Alatochelon myrteum* Pérez-García et al., 2020, and crocodilians, cf. *Crocodilus* sp. (Szyndlar 1985; Delfino et al., 2019; Pérez-García et al. 2020; Georgalis & Szyndlar 2022; Fig. 7). Apparently, no North African amphibian taxa spread into the Iberian Peninsula during the MSC, but the opposite occurred. This is the case of the ribbed newt *Pleurodeles* Michahelles, 1830. Molecular studies show that this salamandrid newt invaded northwest Africa through this route. Then, it diverged into two North African taxa, *Pleurodeles poireti* (Gervais, 1826) and *Pleurodeles nebulosus* (Guichenot, 1850), and one Iberian taxon, *Pleurodeles waltl* Michahelles, 1830. There seems to have been a second, very recent, human-mediated dispersal of *P. waltl* into Morocco (Carranza & Arnold 2004). It is also probable that a dispersal wave of European snakes took place during MN13. In the Algora site, Szyndlar (1985) described the oldest representative of an extant colubrid genus in the Iberian Peninsula, *Elaphe algorensis* Szyndlar, 1985. Since other *Elaphe* species have been described in pre-MN13 sites in Europe (i.e., Oggenhausen 1, MN5, Germany; Mátraszőlős 1, MN6 or MN7+8, Hungary; Böhme & Ilg 2003; Szyndlar 2012), it is likely that members of this genus dispersed into and spread throughout the Iberian Peninsula during MN13, although older dispersal event cannot be ruled out.

The lissamphibians recorded in Eastern and Central Europe include taxa not yet reported in Western Europe during the Late Miocene. These assemblages included taxa highly dependent on humid environmental conditions or fully aquatic, as the cryptobranchid *Andrias scheuchzeri* Tschudi, 1837 and the genus *Mioproteus* Darevsky, 1978, for which no Iberian record is currently known (Böhme & Ilg 2003).

During the Late Miocene, the European palaeochelonofauna was composed by taxa still living in the continent, such as Emydidae, Testudinidae and Geoemydidae, together with groups that are absent from the modern fauna of Europe (Chelydridae, Trionychidae; Lapparent de Broin 2001). Nevertheless, the generic composition was more diverse in Central and Eastern than in Western Europe. Some genera currently absent from Western Europe were present at this time; this is the case of the trionychid *Rafetus* Gray, 1864, and the testudinid genera *Protestudo* Chkhikvadze, 1970 and *Testudo* Linnaeus, 1758 (Böhme & Ilg 2003). The high diversity of Geoemydidae recorded in Late Miocene deposits in Central and Eastern Europe is noteworthy. In addition to the cosmopolitan genera *Mauremys* Gray, 1869 (with current representatives in southern Europe) and *Ptychogaster* Pomel, 1847, with both subgenera *Ptychogaster* (*Ptychogaster*) Pomel, 1847 and *Ptychogaster* (*Temnoclemmys*) Bergounioux, 1958 present throughout the continent, several other genera have been recovered in deposits from Eastern and Central Europe, such as those characterized by conspicuously wide vertebral scutes, like *Clemmydopsis* Boda, 1927, *Sakya* Bogachev, 1960, *Sarmatemys* Chkhikvadze, 1983, and "*Melanochelys*" *sakyaformis* Redkozubov, 1991 (Böhme & Ilg 2003). The placement of all these taxa within Geoemydidae is still a subject of debate. Thus, for example, Danilov (2005) included all these genera in own tribe Sakyini Chkhikvadze, 1983. Recently, Vlachos et al. (2019) proposed that all these taxa form a clade nested within *Mauremys* and characterized by wide vertebral scutes. Except for *Mauremys campanii* (Ristori, 1891), from the Late Miocene of Italy, which has relatively wide vertebral scutes (Chesi et al. 2009), to date, none of these forms have been reported from the rest of Western Europe.

As for the crocodilian and squamate assemblages, they seem to be homogeneous in Europe during the Late Miocene. The regionalization of European squamate faunas started in the Pliocene, which can be related with the climate instability at this time. This process is characterized by the progressive withdrawal of the most thermophilic taxa towards southern areas (Rage 2013).

In short, the main difference between the Iberian and the rest of the European herpetofauna in the Late Miocene is the appearance of more hygrophilous amphibian taxa in Central and Eastern Europe, such as Cryptobranchidae Fitzinger, 1826 and Proteidae Gray, 1825 that dwelled in well-oxigenated environments and fully aquatic taxa like Batrachosauroididae Auffenberg, 1958. In this respect, while in the Iberian Peninsula the VC does not seem to have had a major impact on herpetofaunal palaeocommunities, this is not the case in Eastern Europe. Codrea et al. (2022) noted a shift towards more open and drier conditions during the Late Miocene in the Fălciu-Prut 1 locality (MN11–MN12; Moldova region, eastern Romania), based on its herpetofaunal assemblage, which lacks the above-mentioned hygrophile amphibian groups, and the comparison of this assemblage with older and coeval faunas from Eastern Europe (i.e., Creţeşti, MN 9, Romania; Bushor 1, MN9; Cioburciu, MN11, and Cimislia, MN12, Moldova; Gritsev, MN9, and Cherevichnoje, MN12, Ukraine; Gaverdovsky, MN11; Volchaya Balka, MN11; and Solnechnodolsk, MN13, Russia).

Palaeoecological and palaeoenvironmental implications

According to Martín-Suárez et al. (2001), the sites of CR2 and CR15 correspond with a warm phase of the Neogene sequence of Crevillente. These authors correlated the rodent association with the eustatic sea-level/temperature curve, and assigned ecological preferences to the components of the micromammal faunas at species level. It was assumed that species found in localities correlated with eustatic maxima can be considered as warm/humid proxies; in contrast, those species from sites correlated with minimum sea-level were assigned cold/dry preferences. CR2 and CR15 are located in the lower part of the Crevillente succession (Fig. 2C). The CR2 rodent fauna is dominated by the murid *Apodemus lugdunensis* (Schaub, 1938) and the cricetid *Occitanomys sondaari*, with both species constituting 40% of the available specimens (Martín-Suárez & Freudenthal 1993). In CR15, the dominant species are anagenetic descendants of the above mentioned: *Apodemus barbarae* and *Occitanomys adroveri* (Martín-Suárez & Freudenthal 1998). CR2 and CR15 are both coincident with a high-stand of the coastline. Under the previously mentioned assumption, these localities have therefore been interpreted as originated under dry climatic conditions (Martín-Suárez et al. 2001). Some components of the herpetofauna of both sites currently inhabit areas of tropical/subtropical climates. This is the case of crocodylians, terrestrial turtles, and oriental vipers. Extant crocodylians are distributed throughout in low (<30º) latitudes (Marwick 1998). At present, large-sized tortoises (with a carapace length over 30 cm) are limited to warm areas (Pérez-García et al. 2017). The presence of Oriental vipers and *Paleotestudo*, a medium-sized turtle, also indicates warm conditions but not as warm as those suggested by the previous taxa (crocodylians). As an example, *Chersine hermanni* (Merrem, 1820), a *Paleotestudo*-related taxon (Pérez-García 2017), inhabits the current Mediterranean and sub-Mediterranean regions of Europe (Bertolero et al. 2011).

The results of the application of the HEG method (Böhme et al. 2006) to the CR2 overall herpetological assemblage (this work; Jiménez & Montoya 2002) are reported in Tab. 2. The estimated MAP, 368 mm, exceeds the present average precipitation in Crevillente (323.37 ± 17.95 mm). This method is highly dependent of taphonomical bias (Böhme et al. 2006). The CR2 site has been subject to intensive sampling; the recovered assemblage of reptiles and amphibians is therefore considered as representative, with no new taxa expected to be added in future campaigns. Moreover, only a few taxa recovered in other coeval Iberian localities (i.e., Bufonidae, Salamandridae, see Fig. 7) are not recorded in CR2. Nevertheless, it still might be considered that the amphibian taxa are underrepresented, so the estimated value can be considered as biased.

Our results are in agreement with those obtained by Böhme et al. (2011), who pointed out that southwestern Europe was more humid than today at the end of the Tortonian (after 8 Ma). Curiously, at this moment (MN11) a reverse rainfall gradient is recorded, i.e., southwestern Europe was more humid than central and eastern Europe in contrast to the present situation. This rainfall decreasing trend in higher latitudes has been related with a global cooling event, which particularly affected the Northern Hemisphere, at the end of the Miocene (Böhme et al. 2011). In the Iberian Peninsula, this method has been applied to localities of the Calatayud-Teruel Basin by Böhme et al. (2008). Our results are similar to those obtained in coeval sites (Puente Minero 3, Masada Ruea 2, La Gloria 10, Los Aguanaces, Los Aguanaces 1, Los Aguanaces 3, and Vivero de Pinos). In comparison with these sites, CR2 shows

Taxon	Index
Pelophylax sp.	0.513
Crocodylia indet.	1.000
Palaeotestudo aff. *antiqua**	0.000
*Titanochelon bolivari**	0.000
Testudines indet.*	—
cf. Scinciformata indet. 1	—
cf. Scinciformata indet. 2	—
cf. *Timon* sp.	0.000
Lacertidae indet. 1	0.000
Lacertidae indet. 2	0.000
Ophisaurus s.l. sp.	0.000
Pseudopus sp.	0.000
Colubridae indet. 1	—
Colubridae indet. 2	—
Neonatrix sp.	—
Oriental viper	—
Mean Ecophysiological index	0.168
MAP	368
$\text{MAP}_{\text{Crevillente}}$	323.38
ΔMAP	44.83

Tab. 2 - Results of the application of the HEG method (Böhme et al. 2006). It is given the ecophysiological indices for each applicable taxa from Crevillente 2, the mean value for the whole assemblages and the obtained mean annual precipitation (in mm). These results are compared with the present MAP of the municipal area of Crevillente (MAPCrevillente). Current climatic data are obtained from current global climatic data layer BIO12 (MAP) from Wordclim 2 (Fick & Hijmans 2017). ΔMAP: differences between past and present MAP values. *, information provided by Jiménez & Montoya (2002) describing the chelonians for Crevillente 2.

a lower estimated rainfall, except for La Gloria 10 and Los Aguanaces. The lower CR2 estimated MAP could be attributed to its more southerly location or to the local orography. However, a bias related to the recovered herpetofauna assemblage cannot be ruled out. Van Dam (2006) used small-mammal community structure to predict late Neogene (12–3 Ma) precipitation patterns in Europe and Anatolia. His results indicated that, during the transition between MN10 and MN11 (9–8 Ma), a general aridification of southwestern Europe took place, but after this arid interval a short return to more humid conditions occurred during MN11. In the case of CR2, the MAP estimated by Van Dam (2006), based on the small mammal assemblage (504 mm), exceeds our result based on the herpetofauna (368 mm). From a palaeoecological point of view, during the Late Miocene, the area surrounding Crevillente would have been characterized by a bushland/forest landscape patched with some open areas, with permanent water bodies in the vicinity.

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). A very similar ecology has been reported for the Eurasian species of *Ophisaurus* s.l., currently included in the genera *Dopasia* and *Hyalosaurus* (Blain et al. 2016, and references therein). Unfortunately, little is known about the ecology of the eleven known *Dopasia* species. On the other hand, *Hyalosaurus koellikeri*, the only taxon included in this genus, inhabits dry forests of junipers and evergreen oaks and humid deciduous forests in central-western Morocco (Escoriza & Comas 2015). At present, members of the Western clade of *Timon* inhabit preferably bushy habitats where large rocks are frequently available (Arnold et al. 2007). The presence of forested environments at the CR2 site is supported by the occurrence of browsing herbivores, such as *Dorcatherium naui* Kaup, 1833, *Lucentia iberica* Azanza & Montoya, 1995, *Birgerbohlinia schaubi* Crusafont & Villalta, 1951, and *Deinotherium giganteum* Kaup, 1829, whose palaeoecology has been inferred through the study of the carbon and oxygen isotope variations in their tooth enamel (Domingo et al. 2013; Aiglstorfer et al. 2014).

Open habitats are inferred mainly from the presence of an indeterminate Oriental viper in CR2. Oriental vipers are found in current arid and semiarid biotopes with scarce arboreal cover, such as grasslands, savannahs, and steppes. Some species even inhabit open forests or shrubby areas. Heliophile reptile taxa are abundant within the assemblage. In this sense, lacertid lizards spend much of daily-time sunbathing for thermoregulatory purposes. Moreover, they use these exposure places for different behavioural displays (Avery 1976). Grassland is an important habitat for foraging for several tortoise species worldwide (Walton et al. 2019). As in the latter case, some mammalian taxa clearly prefer open habitats. Among small mammals, the most tangible examples are the two taxa of terrestrial ground squirrels (*Heteroxerus grivensis* Major, 1893, and aff. *Aragoxerus* sp. Cuenca, 1988) reported from CR2 (Mazo & Montoya 2003). Regarding macromammals, *Miotragocerus gaudryi* (Kretzoi, 1841), *Cre-*

mohipparion mediterraneum (Roth & Wagner, 1855), *Dihoplus schleiermacheri* (Kaup, 1834), and *Tetralophodon* cf. *longirostris* 'grandincisivoid form' (Kaup, 1832) present anatomical adaptations, dental microwear, and a δ^{13}C isotopic signal that clearly indicate that they were animals foraging in open woodlands or dry C3 grasslands (Domingo et al. 2013; Aiglstorfer et al. 2014; Bernor et al. 2021).

Hygrophile taxa are scarce among the herpetofaunal assemblage recovered from CR2. In this regard, the presence of amphibians is limited to a single taxon, *Pelophylax*. Eurasian green frogs spend much of their active time in the water. All the current species occupy all kind of sunny water bodies, but preferably in lowlands, with a high hydroperiod and with more or less developed riparian vegetation. Crocodylia indet. is another taxon linked to water habitats (Marwick 1998). As for *Neonatrix* sp., it presumably inhabited diverse aquatic environments based on taxonomical inference. In addition, Jiménez & Montoya (2002) described material attributed to an indeterminate turtle with possible affinities to Geomydidae, a group of freshwater turtles. In this regard, it is interesting to note that large testudinids, such as *Titanochelon bolivari*, are attracted to water bodies for breeding or to bathe in mud for thermoregulation purposes (Walton et al. 2019). In sum, the presence of the above-mentioned taxa indicates the presence of water bodies in the surrounding area of CR2. Other faunal taxa corroborate the existence of those habitats, such as Anatidae indet., *Dorcatherium naui*, *Deinotherium giganteum*, and *Desmanella* sp. (Mazo & Montoya 2003). The presence of the latter is noteworthy because it was probably a litter burrower that required soft soils with abundant organic matter and, therefore, a certain degree of environmental humidity (García-Alix et al. 2011).

Conclusions

The study of the fossil amphibians and reptiles assemblages from the CR2 and CR15 sites allowed us to draw the following conclusions:

The herpetofaunal assemblage from the CR2 site is composed of one anuran (*Pelophylax* sp.), one crocodylian (Crocodylia indet.), seven lizards (cf. Scinciformata indet. 1, Scinciformata indet. 2, cf.*Timon* sp., Lacertidae indet. 1, Lacertidae indet. 2, *Ophisaurus* s.l. sp., and *Pseudopus* sp.), and four snakes (Colubridae indet. 1, Colubridae indet. 2, *Neonatrix* sp., and Viperidae indet., Oriental Morphotype). To date, only the turtle taxa from the classical CR2 site has been previously described. Thus, it is substantially improved the knowledge about the palaeoherpetofauna of this locality.

A fragmentary parietal bone has been attributed to the genus *Timon*. However, given its poor preservation state and the limited understanding of parietal morphology in several extinct lacertid taxa, we prefer to use open nomenclature until new material confirms or refutes this taxonomic attribution.

In its faunal composition, CR2 is similar to other coeval Iberian sites. The assemblage is composed of European taxa (i.e., Lacertidae, *Ophisaurus* s.l.) together with Asian or North American taxa that probably reached Europe during the Oligocene-Miocene transition or at the beginning of the Miocene. Thus, unlike in central Europe, the so-called Vallesian Crisis does not seem to have had an important effect on the paleocommunities of reptiles and amphibians in the Iberian Peninsula, because no major change is recorded in the taxonomic composition (at least at the genus level) during the Late Miocene.

According to the proposed palaeoecological reconstruction, the landscape in the surrounding area of CR2 would have been dominated by a landscape composed by bushland/forest patches with some open areas, with presence of permanent waterbodies nearby.

The application of the HEG method to the CR2 palaeoherpetological assemblage suggests more humid conditions than those prevailing today in the Crevillente area. The estimated MAP (368 mm) is still lower than those obtained for different sites of the Calatayud-Teruel Basin during the MN11.

Finally, the palaeoherpetofaunal list of the CR15 site is limited to turtles (*Palaeotestudo* sp. and Testudines indet., probably a freshwater taxon) and crocodylians (Crocodylia indet.). Accordingly, the surrounding area must have been an open savannah-like habitat with nearby waterbodies.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

Acknowledements: We thank the editor David M. Alba (Institut Català de Paleontologia, Spain), the reviewer Andrea Villa (Institut Català de Paleontologia, Spain), and an anonymous reviewer for their corrections, suggestions, and constructive comments. R.M.B. is beneficiary of a Margarita Salas grant (MS21-164) for the training of young doctors, within the requalification of the Spanish university system, funded by the European Union, Next Generation EU. R.M.B. belongs to the Consolidated Research Group "Paleoecology of Pliocene and Pleistocene and Human Dispersals (PalHum)", funded by AGAUR-Generalitat de Catalunya, 2021SGR-1238 and URV 2023PFR-URV-01238. The Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) received financial support from the Spanish Ministry of Science and Innovation through the "María de Maeztu" program for Units of Excellence (CEX2019-000945-M). This research was also supported by the Spanish Ministerio de Ciencia, Innovación y Universidades PID2023-151089NB-I00.

REFERENCES

Agustí J., Cabrera L., Garcés M. & Llenas M. (1999) - Mammal turnover and global climate hange in the late Miocene terrestrial record of the Vallés–Penedès basin (NE Spain). In: Agustí J., Rook L. & Andrews P. (Eds.) - Hominoid Evolution and Climatic Change in Europe, The Evolution of the Neogene Terrestrial Ecosystems in Europe, vol. I: 82-115. Cambridge University Press, New York.

Agustí J., Cabrera L., Garcés M., Krijgsman W., Oms O. & Parés JM. (2001) - A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews*, 52: 247-260. https://doi.org/10.1016/S0012-8252(00)00025-8

Agustí J., Garcés M. & Krijgsman W. (2006) - Evidence for African–Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 5-14. https://doi.org/10.1016/j.palaeo.2006.03.013

Agustí J., Cabrera L. & Garcés M. (2013) - The Vallesian Mammal Turnover: A Late Miocene record of decoupled land–ocean evolution. *Geobios*, 46: 151-157. https://doi.org/10.1016/j.geobios.2012.10.005

Ahmadzadeh F., Flecks M., Carretero M.A., Böhme W., Ihlow F., Kapli P., Miraldo A. & Rödder D. (2016) - Separate histories in both sides of the Mediterranean Phylogeny and niche evolution of ocellated lizards. J*ournal of Biogeography,* 43: 1242-1253.

Aiglstorfer M., Bocherens H. & Böhme M. (2014) - Large mammal ecology in the late Middle Miocene Gratkorn locality (Austria). *Palaeobiodiversity and Palaeoenvironments*, 94: 189-213. https://doi.org/10.1007/s12549-013-0145-5

Antunes M.T. & Cahuzac B. (1999) - Crocodilian faunal renewal in the Upper Oligocene of Western Europe. *Comptes Rends de l'Academie de Sciences - Serie IIa: Sciences de la Terre et des Planetes*, 328: 67-72. https://doi.org/10.1016/S1251-8050(99)80089-5

Arnold E.N., Arribas Ó. & Carranza S. (2007) - Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squmata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, 1430: 1-86. https://doi.org/10.11646/ZOOTAXA.1430.1.1

Auffenberg W. (1967) - The fossil snakes of Florida. *Tulane Studies in Zoology*, 10: 131-216.

Augé M.L. (2005) - Évolution des lézards du Paléogène en Europe. *Mémoires du Muséum national d'Histoire naturelle* 192, Paris, 200 pp.

Augé M.L. & Brizuela S. (2020) - Transient presence of a teiid lizard in the European Eocene suggests transatlantic dispersal and rapid extinction. *Palaeobiodiversity and Palaeoenvironments*, 100: 793-817. https://doi.org/10.1007/s12549-019-00414-2

Augé M.L. & Pouit D. (2012) - Presence of iguanid lizards in the European Oligocene Lazarus taxa and fossil abundance. *Bulletin de la Societe Geologique de France*, 183: 653-660. https://doi.org/10.2113/gssgfbull.183.6.653

Augé M.L. & Hervet S. (2009) - Fossil lizards from the locality of Gannat (late Oligocene–early Miocene, France) and a revision of the genus *Pseudeumeces* (Squamata, Lacertidae). *Palaeobiodiversity and Palaeoenvironments*, 89: 191-201. https://doi.org/10.1007/s12549-009-0009-1

Augé M.L. & Rage J.-C. (2000) - Les Squamates (Reptilia) du Miocène moyen de Sansan. *Mémories du Museum nationelle d'Histoire Naturelle*, 183: 263-313.

Avery R.A. (1976) - Thermoregulation, metabolism and social behaviour in Lacertidae. In: Bellairs Ad'A. & Cox C.B. (Eds.) - Morphology and Biology of Reptiles, Linnean Society Symposium Series No. 33: 245-259. The Linnean Society, London.

Bailon S. (1991) - Amphibiens et reptiles du Pliocene et de du Quaternaire de France et d'Espagne: Mise en place et evolution des faunes. Unpublished PhD Thesis, Université Paris VII, Paris, France.

Bailon S. (1995) - Présence de *Mioproteus wezei* (Amphibia, Proteidae) dans le Pliocéne supérieur (MN 16) d'Europe de l'Ouest. *Neues Jahrbuch fur Geologie und Paläontologie, Monatshefte*: 1-8.

Bailon S. (1999) - No 1 Différenciation ostéologique des anoures (Amphibia, Anura) de France. In: Desse J. & Desse-Berset N. (Eds.) - Fiches d'óstéologie animale pour l'archéologie. Série C: varia: 3-41. Centre de Recherches Archéologiques – CNRS, Antibes.

Bailon S. (2010) - Quelonios fósiles del yacimiento de Barranco León (Pleistoceno Inferior, Orce, Granada, España). In: Toro I., Martínez-Navarro B. & Agustí J. (Eds.) - Ocupaciones humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza. Arqueología Monografías: 185-195. Consejería de Cultura (Junta de Andalucía), Sevilla.

Bailon S. & Blain H.-A. (2007) - Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pléistocène. *Quaternaire*, 18: 55-63. https://doi.org/10.4000/quaternaire.960

Bailon S., García-Porta J. & Quintana-Cardona J. (2002) - Première découverte de Viperidae (Reptilia, Serpentes) dans les Îles Baléares (Espagne): des vipères du Néogène de Minorque. Description d'une nouvelle espèce du Pliocène. *Comptes Rendus Palevol*, 1: 227-234. https://doi.org/10.1016/s1631- 0683(02)00034-9

Bailon S., Quintana J. & García Porta J. (2005) - Primer registro fósil de las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) en el Plioceno de Punta Nati (Menorca, Islas Baleares). In: Alcover J.A. & Bove P. (Eds.) - Proceedings of the International Symposium "Insular Vertebrate Evolution: The Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears: 27-32. Societat d'Història Natural de les Balears, Palma de Mallorca.

Barahona F. (1996) - Osteología craneal de lacértidos de la península ibérica e islas Canarias: Análisis sistemático filogenético. Unpublished PhD Thesis, Universidad Autónoma de Madrid, Madrid, Spain.

Barahona F. & Barbadillo L.J. (1997) - Identification of some Iberian lacertids using skull characters. *Revista Española de Herpetología*, 11: 47-62.

Barahona F., Evans S.E., Mateo J.A., García-Márquez M. & López-Jurado L.F. (2000) - Endemism, gigantism and extinction in island lizards: The genus *Gallotia* on the Canary Islands. *Journal of Zoology*, 250: 373-388. http://doi.or/10.1111/j.1469-7998.2000.tb00781.x

Barbadillo L.J., García-París M. & Sanchiz B. (1997) - Orígenes y relaciones evolutivas de la herpetofauna ibérica. In: Pleguezuelos J.M. (Ed.) - Distribución y biogeografía de los anfibios y reptiles en España y Portugal: 47-100. Universidad de Granada, Granada.

Bernor R.L., Kaya F., Kaakinen A., Saarinen J. & Fortelius M. (2021) - Old world *Hipparion* evolution, biogeography, climatology and ecology. *Earth-Science Reviews*, 221: 103784. https://doi.org/10.1016/j.earscirev.2021.103784

Bertolero A., Cheylan M., Hailey A., Livoreil B. & Willemsen R. (2011) - *Testudo hermanni* (Gmelin 1789) – Hermann's Tortoise. In: Rhodin A.G.J., Pritchard P.C.H., van Dijk P.P., Saumure R.A., Buhlmann K.A., Iverson J.B. & Mittermeier R.A. (Eds.) - Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5: 059.1-059.20.

Blain H.-A. (2009) - Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. *Treballs del Museu de Geologia de Barcelona*, 16: 39-170.

Blain H.-A. & Bailon S. (2019) - Extirpation of *Ophisaurus* (Anguimorpha, Anguidae) in Western Europe in the context of the disappearance of subtropical ecosystems at the Early-Middle Pleistocene transition. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 520: 96-113. https://doi.org/10.1016/j.palaeo.2019.01.023

Blain H.-A., Bailon S. & Agustí J. (2016) - The geographical and chronological pattern of herpetofaunal Pleistocene extinctions on the Iberian Peninsula. *Comptes Rendus Palevol*, 15: 731-744. https://doi.org/10.1016/j.crpv.2015.05.008

Böhme M. (2003) - The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 195: 389-401. https://doi.org/10.1016/S0031-0182(03)00367-5

Böhme M. & Ilg A. (2003) - fosFARbase. fosFARbase. Downloaded 13 December 2023. http://www.wahre-staerke.com/

Böhme M., Ilg A., Ossig A. & Küchenhoff H. (2006) - New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. *Geology*, 34: 425-428. https://doi.org/10.1130/G22460.1

Böhme M., Ilg A. & Winklhofer M. (2008) - Late Miocene "washhouse" climate in Europe. Earth and Planetary *Science Letters*, 275: 393-401. https://doi.org/10.1016/j.epsl.2008.09.011

Böhme M., Winklhofer M. & Ilg A. (2011) - Miocene precipitation in Europe: Temporal trends and spatial gradients. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 304: 212-218. https://doi.org/10.1016/j.palaeo.2010.09.028

Böhme M., Vasilyan D. & Winklhofer M. (2012) - Habitat tracking, range dynamics and palaeoclimatic significance of Eurasian giant salamanders (Cryptobranchidae)—Indications for elevated Central Asian humidity during Cenozoic global warm periods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 342-343: 64-72. https://doi.org/10.1016/j.palaeo.2012.04.032

Böhme W. & Zammit-Maempel G. (1982) - *Lacerta siculimelitensis* sp. n. (Sauria: Lacertidae), a giant lizard from the late Pleistocene of Malta. *Amphibia-Reptilia*, 3: 257-268.

Booth-Rea G., Ranero C. & Grevemeyer I. (2018) - The Alboran volcanic-arc modulated the Messinian faunal exchange and salinity crisis. *Scientific Reports*, 8: 13015. https://doi.org/10.1038/s41598-018-31307-7

Borsuk-Bialynicka M., Lubka M. & Böhme W. (1999) - A lizard from Baltic amber (Eocene) and the ancestry of the crown group lacertid. *Acta Palaeontologica Polonica*, 44: 349-82.

Brochu C.A. (1999) - Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. *Journal of Vertebrate Paleontology*, 19: 9-100. https://doi.org/10.1080/02724634.1999.10011201

Brochu C.A. (2000) - Phylogenetic Relationships and Divergence Timing of *Crocodylus* based on Morphology and the Fossil Record. *Copeia*, 3: 657-673.

Browne R.K., Li H., Wang Z., Hime P.M., McMillan A., Wu M., Diaz R., Hongxing Z., McGinnity D. & Briggler J.T. (2012) - The giant salamanders (Cryptobranchidae): Part A. palaeontology, phylogeny, genetics, and morphology. *Amphibian and Reptile Conservation*, 5: 17-29.

Bruijn H. de, Daams R., Daxner-Höck G., Fahlbusch V., Ginsburg L., Mein P. & Morales J. (1992) - Report of the RCMNS working group on fossil mammals, Reisensburg 1990. *Newsletters on Stratigraphy*, 26: 65-118.

Carranza S. & Arnold E.N. (2004) - History of West Mediterranean newts, *Pleurodeles* (Amphibia: Salamandridae), inferred from old and recent DNA sequences. *Systematics and Biodiversity*, 1: 327-337. https://doi.org/ 0.1017/S1477200003001221

Casanovas-Vilar I., Moyá-Solá S., Agustí J. & Köhler M. (2005) - The geography of a faunal turnover: tracking the Vallesian Crisis. In: Elewa A.M.T. (Ed.) - Migration of Organisms: Climate Geography Ecology: 247-300. Springer-Verlag Berlin Heidelberg.

Casanovas-Vilar I., van den Hoek Ostende L.W., Furió M. & Madern PA. (2014) - The range and extent of the Vallesian Crisis (Late Miocene): new prospects based on the micromammal record from the Vallès-Penedès (Catalonia, Spain). *Journal of Iberian Geology*, 40: 29-48. https://doi.org/ 10.5209/rev_JIGE.2014.v40.n1.44086

Casanovas-Vilar I., Garcés M., Marcuello Á., Abella J., Madurell-Malapeira J., Jovells-Vaqué S., Cabrera L., Galindo J., Beamud E., Ledo J.J., Queralt P., Martí A., Sanjuan J., Martín-Closas C., Jiménez-Moreno G., Luján À.H., Villa A., De Miguel D., Sánchez I.M., Robles J.M., Furió M., Van den Hoek Ostende L.W., Sánchez-Marco A., Sanisidro Ó., Valenciano A., García-Paredes I., Angelone C., Pons-Monjo G., Azanza B., Delfino M., Bolet A., Grau-Camats M., Vizcaíno-Varo V., Mormeneo D., Kimura Y., Moyà-Solà S. & Alba D.M. (2022) - Els Casots (Subirats, Catalonia), a key site for the Miocene vertebrate record of Southwestern Europe. *Historical Bi-*

ology, 34: 1494-1508. https://doi.org/10.1080/08912963.2022.2043296

Čerňanský A. (2010) - Earliest world record of green lizards (Lacertilia, Lacertidae) from the Lower Miocene of Central Europe. *Biologia*, 65: 737-741. https://doi.org/10.2478/s11756-010-0066-y

Čerňanský A. & Augé M.L. (2013). - New species of the genus *Plesiolacerta* (Squamata: Lacertidae) from the upper Oligocene (MP28) of Southern Germany and a revision of the type species *Plesiolacerta lydekkeri*. *Palaeontology*, 56: 79-94. https://doi.org/10.1111/j.1475-4983.2012.01167.x

Čerňanský A. & Smith K.T. (2018) - Eolacertidae: a new extinct clade of lizards from the Palaeogene; with comments on the origin of the dominant European reptile group–Lacertidae. *Historical Biology*, 30: 994-1014. https://doi.org/10.1080/08912963.2017.1327530

Čerňanský A. & Syromyatnikova E.V. (2019) - The first Miocene fossils of *Lacerta* cf. *trilineata* (Squamata, Lacertidae) with a comparative study of the main cranial osteological differences in green lizards and their relatives. *PLoS One*, 14: e0216191. https://doi.org/10.1371/journal.pone.0216191

Čerňanský A., Klembara J. & Smith K.T. (2016). - Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. *Zoological Journal of the Linnean Society*, 176: 861-877. https://doi.org/10.1111/zoj.12340

Čerňanský A., Bolet A., Müller J., Rage J-C., Augé M. & Herrel A. (2017) - A new exceptionally preserved specimen of *Dracaenosaurus* (Squamata, Lacertidae) from the Oligocene of France as revealed by micro-computed tomography. *Journal of Vertebrate Paleontology*, 37: e1384738. https://doi.org/10.1080/02724634.2017.1384738

Čerňanský A., Yaryhin O., Ciceková J., Werneburg I., Hain M. & Klembara J. (2019) - Vertebral Comparative Anatomy and Morphological Differences in Anguine Lizards with a Special Reference to *Pseudopus apodus*. *The Anatomical Record*, 302: 232-257. https://doi.org/10.1002/ar.23944

Chan K.O. & Brown R.M. (2017) - Did true frogs 'dispersify'? *Biology Letters*, 13: 20170299. https://doi.org/10.1098/rsbl.2017.0299

Chesi F., Delfino M. & Rook L. (2009) - Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): Evidence of terrapin persistence after a mammal turnover. *Journal of Paleontology*, 83: 379-388. https://doi.org/10.1666/08-134.1

Codrea V.A., Venczel M. & Ursachi L. (2017) - Amphibians and squamates from the early Vallesian of Crețești (Vaslui County, E-Romania). *Nymphaea*, 44: 37-56.

Codrea V.A., Bordeianu M. & Venczel M. (2022) - Amphibians and squamate reptiles from the late Miocene of Fălciu (Eastern Romania). *Palaeontologia Electronica*, 25: 1-23. https://doi.org/10.26879/1156

Danilov I.G. (2005) - Die fossilen Schildkröten Europas. In: Fritz U. (Ed.) - Handbuch der Reptilien und Amphibien Europas. Band 3/IIIB: Schildkröten (Testudines) II (Cheloniidae, Dermochelyidae, Fossile Schildkröten Europas): 329-441. AULA-Verlag GmbH, Wiebelsheim.

Delfino M. & Bailon S. (2000) - Early Pleistocene herpetofauna from Cava dell'Erba and Cava Pirro (Apulia, Southern Italy). *Herpetological Journal*, 10: 95-110.

Delfino M., Rage J.C. & Rook L. (2003) - Tertiary mammal turnover phenomena: what happened to the herpetofauna? *Deinsea*, 10: 153-161.

Delfino M., Luján À.H., Abella J., Alba D.M., Böhme M., Pérez-Ramos A., Tschopp E., Morales J. & Montoya P. (2020) - Late Miocene remains from Venta del Moro (Iberian Peninsula) provide further insights on the dispersal of crocodiles across the late Miocene Tethys. *Journal of Paleontology*, 95: 184-192. https://doi.org/10.1017/jpa.2020.62

Díaz Aráez J.L., Delfino M., Luján À.H., Fortuny J., Bernardini F. & Alba D.M. (2017) - New remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the Early Miocene of the Iberian Peninsula. *Comptes Rendus Palevol*, 16: 12-26. https://doi.org/10.1016/j.crpv.2015.11.003

Domingo L., Koch P.L., Hernández-Fernández M., Fox D.L., Domingo M.S. & Alberdi M.T. (2013) - Late Neogene and Early Quaternary Paleoenvironmental and Paleoclimatic Conditions in Southwestern Europe: Isotopic Analyses on Mammalian Taxa. *PLoS One*, 8: e63739. https://doi.org/10.1371/journal.pone.0063739.

Escoriza D. & Comas M. (2015) - Is *Hyalosaurus koellikeri* a true forest lizard?. *Herpetological Conservation and Biology*, 10: 610-620.

Escoriza D. & Amat F. (2021) - Habitat Partitioning and Overlap by Large Lacertid Lizards in Southern Europe. *Diversity*, 13: 1-11. https://doi.org/10.3390/d13040155

Estes R. (1983) - Enciclopedia of Paleoherpetology. Part 10A. Sauria terrestria, Amphisbaenia. Gustav Fischer Verlag, Stuttgart, New York.

Evans S.E. (2008) - The Skull of Lizards and Tuatara. In: Gans C., Gaunt A.S. & Adler K. (Eds.) - Biology of the Reptilia. Volume 20, Morphology H. The skull of Lepidosauria: 1-348. Society for the Study of Amphibians and Reptiles, Ithaca.

Fick S.E. & Hijmans R.J. (2017) - WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37: 4302-4315. https://doi.org/10.1002/joc.5086

García-Alix A., Minwer-Barakat R., Martín Suárez E., Freudenthal M., Aguirre J. & Kaya F. (2016) - Updating the Europe–Africa small mammal exchange during the late Messinian. *Journal of Biogeography*, 43: 1336-1348. https://doi.org/10.1111/jbi.12732

García-Alix A., Furió M., Minwer-Barakat R., Martin Suarez E. & Freudenthal M. (2011) - Environmental control on the biogeographical distribution of *Desmanella* (Soricomorpha, Mammalia) in the Miocene of the Iberian Peninsula. *Palaeontology*, 54: 753-762. https://doi.org/10.1111/j.1475-4983.2011.01062.x

García-Porta J. & Casanovas-Vilar I. (2001) - Noves localitats de Amphisbaenia fòssils i comentaris sobre el grup en el Miocè Peninsular. *Butlletí de la Societat Catalana d'Herpetologia*, 15: 91-98.

Georgalis G.L., Villa A., Ivanov M., Vasilyan D. & Delfino M. (2019) - Fossil amphibians and reptiles from the Neogene locality of Maramena (Greece), the most diverse European herpetofauna at the Miocene/Pliocene transition boundary. *Palaeontologia Electronica*, 22.3.68: 1-99. https://doi.org/doi.org/10.26879/908

Georgalis G.L. & Szyndlar Z. (2022) - First occurrence of *Psammophis* (Serpentes) from Europe witnesses another Messinian herpetofaunal dispersal from Africa–biogeographic implications and a discussion of the vertebral morphology of psammophiid snakes. *The Anatomical Record*, 305: 3263-3282. https://doi.org/10.1002/ar.24892

Gibert L., Scott G.R., Montoya P., Ruiz-Sánchez F.J., Morales

J., Luque L., Abella J. & Lería M. (2013) - Evidence for an African-Iberian mammal dispersal during the preevaporitic Messinian. *Geology*, 41: 691-694. https://doi.org/10.1130/G34164.1

Glynne E., Daza J.D. & Bauer A.M. (2020) - Surface sculpturing in the skull of gecko lizards (Squamata: Gekkota). *Biological Journal of the Linnean Society*, 131: 801-813. https://doi.org/10.1093/biolinnean/blaa144

Herbert T.D., Lawrence K.T., Tzanova A., Peterson L.C., Caballero-Gill R. & Kelly C.S. (2016) - Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience*, 9: 843-847. http://doi.org/10.1038/NGEO2813

Hoffstetter R. (1962) - Observations sur les ostéodermes et la classification des anguidés actuels et fossiles. *Bulletin du Muséum National d'Histoire Naturelle*, 34: 149-157.

Holman J.A. (1998) - Pleistocene amphibians and reptiles in Britain and Europe. Vol. 38. Oxford University Press, New York, USA.

Hsü K.J. (1974) - The Miocene desiccation of the Mediterranean and its climatical and zoogeographical implications. *Naturwissenschaften*, 61: 137-142.

Ivanov M., Čerňanský A., Bonilla-Salomón I. & Luján À.H. (2020) - Early Miocene squamate assemblage from the Mokrá-Western Quarry (Czech Republic) and its palaeobiogeographical and palaeoenvironmental implications. *Geodiversitas*, 20: 343-376. https://doi.org/10.5252/geodiversitas2020v42a20

Jiménez E. & Montoya P. (2002) - Quelonios del Mioceno Superior de Crevillente 2 (Alicante, España). *Stvdia Geologica Salmanticensia*, 30: 87-103.

Klembara J. (1986) - New finds of the genus *Ophisaurus* (Reptilia, Anguidae) from the Miocene of Western Slovakia (Czechoslovakia). *Acta Universitatis Carolinae Geologica*, 2: 187-203.

Klembara J. & Rummel M. (2018) - New material of *Ophisaurus*, *Anguis* and *Pseudopus* (Squamata, Anguidae, Anguinae) from the Miocene of the Czech Republic and Germany and systematic revision and palaeobiogeography of the Cenozoic Anguinae. *Geological Magazine*, 155: 20-44. https://doi.org/10.1002/ar.22854

Klembara J. & Čerňanský A. (2020) - Revision of the cranial anatomy of *Ophisaurus acuminatus* Jörg, 1965 (Anguimorpha, Anguidae) from the late Miocene of Germany. *Geodiversitas*, 42: 539-557. https://doi.org/10.5252/geodiversitas2020v42a28

Klembara J., Böhme M. & Rummel M. (2010) - Revision of the anguine lizard *Pseudopus laurillardi* (Squamata, Anguidae) from the Miocene of Europe, with comments on paleoecology. *Journal of Paleontology*, 84: 159-196.

Klembara J., Hain M. & Dobiasová K. (2014) - Comparative Anatomy of the Lower Jaw and Dentition of *Pseudopus apodus* and the Interrelationships of Species of Subfamily Anguinae (Anguimorpha, Anguidae). *The Anatomical Record*, 297: 516-544.

Kotsakis T., Delfino M. & Piras P. (2004) - Italian Cenozoic crocodilians: Taxa, timing and palaeobiogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 210: 67-87. https://doi.org/10.1016/j.palaeo.2004.03.013

Koufos G.D. (2006) - Paleoecology and chronology of the Vallesian (Late Miocene) in the Eastern Mediterranean region. *Palaeogeography Palaeoclimatology Palaeoecology*, 234: 127-145. https://doi.org/10.1016/j.palaeo.2005.01.014

Lavin B.R. & Girman D.J. (2019) - Phylogenetic relationships and divergence dating in the Glass Lizards (Anguinae). *Molecular Phylogenetics and Evolution*, 133: 128-140. https://doi.org/10.1016/j.ympev.2018.12.022

Lapparent de Broin F. (2000) - Les Chéloniens de Sansan. In: Ginsburg L. (Ed.) - La faune miocene de Sansan et son environnernent. *Mémoires du Muséum national d'Histoire naturelle*, 183: 219-216. Muséum national d'Histoire naturelle, Paris.

Lapparent de Broin F. (2001) - The European turtle fauna from the Triassic to the Present. *Dumerilia*, 4: 155-217.

Lemierre A., Gendry D., Poirier M.-M., Gillet V. & Vullo R. (2022) - The oldest articulated ranid from Europe: A *Pelophylax* specimen from the lowest Oligocene of Chartres-de-Bretagne (N.W. France). *Journal of Vertebrate Palaeontology*, 42: 4. https://doi.org/10.1080/02724634.2023.2191663

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

Luján, À.H., Delfino M., Robles J.M. & Alba D.M. (2016) - The Miocene tortoise *Testudo catalaunica* Bataller, 1926, and a revised phylogeny of extinct species of genus *Testudo* (Testudines: Testudinidae). *Zoological Journal of the Linnean Society*, 178: 312-314. https://doi.org/10.1111/zoj.12414

Lymberakis P., Poulakakis N., Manthalou G., Tsigenopoulos C.S., Magoulas A. & Mylonas M. (2007) - Mitochondrial phylogeography of *Rana (Pelophylax)* populations in the Eastern Mediterranean region. *Molecular Phylogenetics and Evolution*, 44: 115-125. https://doi.org/10.1016/j.ympev.2007.03.009

Macaluso L., Villa A., Pitruzzella G., Rook L., Carnevale G. & Delfino M. (2021a) - A progressive extirpation: An overview of the fossil record of *Salamandrina* (Salamandridae, Urodela). *Historical Biology*, 33: 3723-3740. https://doi.org/10.1080/08912963.2021.1888946

Macaluso L., Villa A., Carnevale G. & Delfino M. (2021b) - Past, present, and future climate space of the only endemic vertebrate genus of the Italian peninsula. *Scientific Report*, 11: 22139. https://doi.org/10.1038/s41598-021-01492-z

Macey J.R., Schulte II J.A., Larson A., Tuniyev B.S., Orlov N. & Papenfuss T.J. (1999) - Molecular Phylogenetics, tRNA Evolution, and Historical Biogeography in Anguid Lizards and Related Taxonomic Families. *Molecular Phylogenetics and Evolution*, 12: 250-272.

Madern P.A., van de Put J.M., Casanovas-Vilar I. & van den Hoek Ostende L.W. (2018) - Iberian micromammals show local extent of Vallesian Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 496: 18-31. https://doi.org/10.1016/j.palaeo.2017.12.033

Mateo J.A. (2017) - Lagarto ocelado - *Timon lepidus*. In: Salvador A. & Marco A. (Eds.) - Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/timlepid.html

Martín-Suárez E. & Freudenthal M. (1993) - Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica*, 103: 65-118.

Martín-Suárez E. & Freudenthal M. (1998) - Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, Spain). *Geobios*, 31: 839-847.

Martín-Suárez E., Freudenthal M. & Civis J. (2001) - Rodent palaeoecology of the continental upper Miocene of Crevillente (Alicante, SE Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 165: 349-356. https://doi.org/10.1016/S0031-0182(00)00170-X

Marwick P.J. (1998) - Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: Implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 137: 205-271. https://doi.org/10.1016/S0031-0182(97)00108-9

Mazo A.V. & Montoya P. (2003) - Proboscidea (Mammalia) from the Upper Miocene of Crevillente (Alicante, Spain). *Scripta Geologica*, 126: 79-109.

Mein P. (1990) - Updating of MN zones. In: Lindsay E.H., Fahlbusch V. & Mein P. (Eds.) - European Neogene Mammal Chronology: 73-90. Plenum, New York.

Miller K.G., Wright J.D. & Fairbanks R.G. (1991) - Unlocking the Ice House: Oligocene-Miocene oxygen isotopes, eustasy, and marginerosion. *Journal of Geophysical Research*, 96: 6829-6848. https://doi.org/10.1029/90JB02015

Montenat C. (1973) - Les Formations Néogenes et Quatemaires du Levant Espagnol (provinces d 'Alicante et de Murcia). Unpublished PhD Thesis, Université d'Orsay-Paris-Sud, Paris, France.

Montoya P. (1994) - Los macromamíferos del Mioceno superior del área de Crevillente (Alicante). Unpublished PhD Thesis, Universitat de València, Valencia, Spain.

Montoya P. & Alberdi M.T. (1995) - Crevillente 15 y Crevillente 16, dos nuevos yacimientos con macromamíferos en el Mioceno superior de Alicante. *Estudios Geológicos*, 51: 159-182.

Mudelsee M., Bickert T., Lear C.H. & Lohmann G. (2014) - Cenozoic climate changes: a review based on time series analysis of marine benthic δ^{18}O records. *Reviews of Geophysics*, 52: 333-374. https://doi.org/10.1002/2013RG000440

Pérez-García A. (2016) - Analysis of the Iberian Aragonian record of *Paleotestudo*, and refutation of the validity of the Spanish '*Testudo catalaunica*' and the French '*Paleotestudo canetotiana*'. *Spanish Journal of Palaeontology*, 31: 321-340. https://doi.org/10.7203/sjp.31.2.17159

Pérez-García A. (2017) - The Iberian fossil record of turtles: An update. *Journal of Iberian Geology*, 43: 155-191. https://doi.org/10.1007/s41513-017-0016-4

Pérez-García A. & Murelaga X. (2013) - Las tortugas del Valleniense superior del Cerro de los Batallones (Madrid, España): Nuevos datos sobre el escasamente conocido género *Paleotestudo*. *Ameghiniana*, 50: 335-353.

Pérez-García A. & Vlachos E. (2014) - New generic proposal for the European Neogene large testudinids (Cryptodira) and the first phylogenetic hypothesis for the medium and large representatives of the European Cenozoic record. *Zoological Journal of the Linnean Society*, 172: 653-719. https://doi.org/10.1111/zoj.12183

Pérez-García A., Vlachos E. & Arribas A. (2017) - The last giant continental tortoise of Europe: A survivor in the Spanish Pleistocene site of Fonelas P-1. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 470: 30-39. https://doi.org/10.1016/j.palaeo.2017.01.011

Pérez-García A., Vlachos E. & Murelaga X. (2020) - A large Testudinid with African affinities in post-Messinian (Lower Pliocene) record of South-Eastern Spain. *Palaeontology*, 63: 497-512. https://doi.org/10.1111/pala.12468

Piñero P., Agustí J., Oms O., Fierro I., Montoya P., Mansino S., Ruiz-Sánchez F.J., Alba D.M., Alberdi M.T., Blain H.-A., Laplana C., Van der Made J., Mazo A.V., Morales J., Murelaga X., Pérez-García A., Pérez-Valera F., Pérez-Valera J.A., Sevilla P., Soria J.M. & Romero G. (2017) - Early Pliocene continental vertebrate Fauna at Puerto de la Cadena (SE Spain) and its bearing on the marine-continental correlation of the Late Neogene of Eastern Betics. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 479: 102-114. https://doi.org/10.1016/j.palaeo.2017.04.020

Rage J.-C. (2013) - Mesozoic and Cenozoic squamates of Europe. *Palaeobiodiversity and Palaeoenvironments*, 93: 517-534. https://doi.org/10.1007/s12549-013-0124-x

Rage J.-C. & Holman J.A. (1984) - Des serpents (Reptilia, Squamata) de type nord-américain dans le Miocène français. Évolution parallèle ou dispersion? *Geobios*, 17: 89-104.

Rage J.-C. & Roček Z. (2003) - Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. *Amphibia-Reptilia*, 24: 133-167. https://doi.org/10.1163/156853803322390408

Rage J.-C. & Bailon S. (2005) - Amphibians and squamate reptiles from the late early Miocene (MN 4) of Béon 1 (Montréal-du-Gers, southwestern France). *Geodiversitas*, 27: 413-441.

Roček Z. (1984) - Lizards (Reptilia, Sauria) from the lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *Rozpravy Ceskoslovenské Akademie Ved, Rada Matematickych a prírodních Ved*, 94: 3-69.

Roček Z. (2013) - Mesozoic and Tertiary Anura of Laurasia. *Palaeobiodiversity and Palaeoenvironments*, 93: 397-439. https://doi.org/10.1007/s12549-013-0131-y

Roldán F.J., Rodríguez-Fernández J., Villalobos M., Lastra J., Díaz-Pinto G. & Pérez Rodríguez A.B. (2009) - Mapa Geológico Digital continuo E. 1:50.000, Zonas: Subbético, Cuenca del Guadalquivir y Campo de Gibraltar. In: GEODE. Mapa Geológico Digital continuo de España. Downloaded 16 November 2024. http://info.igme.es/cartografiadigital/geologica/geodezona.aspx?Id=Z2600

Sanchiz B. (1998) - Encyclopedia of Paleoherpetology. Part 4. Salientia. Verlag Dr. Friedrich Pfeil, München, Germany.

Sanchiz B. (1981) - Nota sobre la herpetofauna Miocénica de los Valles de Fuentidueña (Segovia). *Estudios Geológicos*, 37: 355-358.

Sanchiz B., Schleich H.H. & Esteban M. (1993) - Water frogs (Ranidae) from the Oligocene of Germany. *Journal of Herpetology*, 27: 486-488.

Santisteban C. de, Montoya P., Usera J. & Robles F. (1997) - El Terciario marino y continental de Alicante. In: Alcalá L. & Alonso A.M. (Eds.) - Itinerarios Geológicos en el Terciario del Centro y Este de la Península Ibérica: 73-107. Universidad Complutense de Madrid, Consejo Superior de Investigaciones Científicas, Madrid.

Shevenell A.E., Kennett J.P. & Lea D.W. (2004) - Middle Miocene Southern Ocean Cooling and Antarctic Cryosphere Expansion. *Science*, 305: 1766-1770. http://doi.org/10.1126/science.1100061

Speybroeck J., Beukema W., Bok B. & Van Der Voort J. (2016) - Field Guide to the Amphibians and Reptiles of Britain and Europe. Bloomsbury Publishing, London, United Kingdom.

Strömberg C.A.E. (2011) - Evolution of Grasses and Grassland Ecosystems. *Annual Review of Earth and Planetary Sciences*, 39: 517-544. http://doi.org/10.1146/annurev-earth-040809-152402

Szyndlar Z. (1984) - Fossil snakes from Poland. *Acta Zoologica Cracoviensia*, 28: 1-156.

Szyndlar Z. (1985) - Ophidian fauna (Reptilia, Serpentes) from the uppermost Miocene of Algora (Spain). *Estudios Geológicos*, 41: 447-465.

Szyndlar Z. (1987) - Snakes from the lower Miocene locality of Dolnice (Czechoslovakia). *Journal of Vertebrate Paleontology,* 7: 55-71. https://doi.org/10.1080/02724634.1987.10011637

Szyndlar Z. (1991a) - A review of Neogene and Quaternary snakes of central and eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios Geológicos*, 47: 103-126.

Szyndlar Z. (1991b) - A review of Neogene and Quaternary snakes of central and eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geológicos*, 47: 237-266.

Szyndlar Z. (1994) - Oligocene Snakes of Southern Germany. *Journal of Vertebrate Palaeontology*, 14: 24-37.

Szyndlar Z. (2012) - Early Oligocene to Pliocene Colubridae of Europe: A review. *Bulletin de la Société Géologique de France*, 6: 661-681. https://doi.org/10.2113/gssgfbull.183.6.661

Szyndlar Z. & Rage J.-C. (1999) - Oldest Fossil Vipers (Serpentes: Viperidae) from the Old World. *Kaupia, Darmstädter Beiträge zur Naturgeschichte*, 8: 9-20.

Szyndlar Z. & Rage J.-C. (2002) - Fossil record of the true vipers. In: Schuett G.W., Hoggren M., Douglas M.E. & Greene H.W. (Eds.) - Biology of the vipers: 419-444. Eagle Mountain Publishing, Utah.

Szyndlar Z. & Schleich H.H. (1993) - Description of Miocene Snakes from Petersbuch 2 with Comments on the Lower and Middle Miocene Ophidian Faunas of Southern Germany. *Stuttgarter Beiträge zur Naturkunde Serie B* (*Geologie und Paläontologie*), 192: 1-47.

Tschopp E., Villa A., Camaiti M., Ferro L., Tuveri C., Rook L., Arca M. & Delfino M. (2018) - The first fossils of *Timon* (Squamata: Lacertinae) from Sardinia (Italy) and potential causes for its local extinction in the Pleistocene. *Zoological Journal of the Linnean Society*, 20: 1-32.

Tschopp E., Napoli J.G., Wencker L.C., Delfino M. & Upchurch P. (2022) - How to render species comparable taxonomic units through deep time: a case study on intraspecific osteological variability in extant and extinct lacertid lizards. *Systematic biology*, 71: 875-900.

Van Dam J.A. (2006) - Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: The use of small mammals as paleoprecipitation proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 238: 190-218. http://doi.org/10.1016/j.palaeo.2006.03.025

Vasilyan D., Roček Z., Ayvazyan A. & Claessens L. (2019) - Fish, amphibian and reptilian faunas from latest Oligocene to middle Miocene localities from Central Turkey. *Palaeobiodiversity and Palaeoenvironments*, 99: 723-757. https://doi.org/10.1007/s12549-019-00405-3

Venczel M. (2001) - Anurans and squamates from the Lower Pliocene (MN 14) Osztramos 1 locality (Northern Hungary). *Fragmenta Palaeontologica Hungarica*, 19: 79-90.

Villa A., Delfino M., Luján À.H., Almécija S. & Alba D.M. (2017) - First record of *Latonia gigantea* (Anura, Alytidae) from the Iberian Peninsula. *Historical Biology*, 31: 371-382. https://doi.org/10.1080/08912963.2017.1371712

Villa A., Abella J., Alba D.M., Almécija S., Bolet A., Koufos G.D., Knoll F., Luján À.H., Morales J., Robles J.M., Sánchez I.M. & Delfino M. (2018) - Revision of *Varanus marathonensis* (Squamata, Varanidae) based on historical and new material: morphology, systematics, and paleobiogeography of the European monitor lizards. *PLoS One*, 13: e0207719. https://doi.org/10.1371/journal.pone.0207719

Villa A. & Delfino M. (2019a) - A comparative atlas of the skull osteology of European lizards (Reptilia: Squamata). *Zoological Journal of the Linnean Society*, 20: 1-100. https://doi.org/10.1093/zoolinnean/zlz035

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

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

Vlachos E., Sterli J., Vasileiadou K. & Syrides G. (2019) - A new species of *Mauremys* (Testudines, Geoemydidae) from the late Miocene – Pliocene of Central Macedonia (northern Greece) with exceptionally wide vertebral scutes. *Papers in Palaeontology*, 5: 177-195. https://doi.org/10.1002/spp2.1235

Walton R., Baxter R., Bunbury N., Hansen D., Fleischer-Dogley F., Greenwood S. & Schaepman-Strub G. (2019) - In the land of giants: habitat use and selection of the Aldabra giant tortoise on Aldabra Atoll. *Biodiversity and Conservation*, 28: 3183-3198. https://doi.org/10.1007/s10531-019-01813-9

Westerhold T., Bickert T. & Röhl U. (2005) - Middle to late Miocene oxygen isotope stratigraphy of ODP site 1085 (SE Atlantic): new constrains on Miocene climate variability and sea–level fluctuations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 217: 205-222. http://doi.org/10.1016/j.palaeo.2004.12.001