The Caminonegro site (Allueva Fm., middle-upper Campanian): paleoological assemblage, sedimentary environment and genesis

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Introduction

Recent charophyte biostratigraphy and magnetostratigraphy studies in Paleocene units of the Montalbán subbasin, Teruel, (units M1-M2; Pérez *et al.,* 1983), motivated by the discovery of dinosaur remains, have allowed a chronostratigraphic reassignment of these units to the Late Cretaceous (Aurell *et al.,* 2022). This allowed the definition of a new geological unit, the Allueva Formation, with a sedimentary association characteristic of an alluvial system in mid-distal areas (Aurell *et al.,* 2022; Torromé *et al.,* 2024). Numerous and diverse paleontological sites have been found along its outcrops. One of these sites, near the villages of Allueva and Bea, is Caminonegro site (middle-late Campanian), which is notable for its content of vertebrate microfossils, especially eggshell fragments.

Methodology

A 58-meter-thick stratigraphic section was realized in the Allueva Fm, including Caminonegro site outcrop, to contextualize the site in the sedimentary environment. 25 sediment samples were taken along its length to describe the rock facies. An additional 94 kg of sediments were collected in the Caminonegro site in order to analyze its palaeontological record.

The sample was dried at room temperature for 48 hours and then bathed in a 5% hydrogen peroxide solution. The resulting mud was sieved through mesh sizes of 2, 1, and 0.5 mm. The remains retained on the sieves were dried, packaged, labeled, and sorted to separate the micropaleontological remains (bone fragments, teeth, eggshells, charophytes, gastropods, plant remains, and microbial structures). The eggshells found in the +2 mm sample were studied using Secondary Electron images acquired with a MERLIN FESEM and 30 μm thick thin sections observed in an Olympus petrographic microscope.

Sedimentary environment

In the facies analysis, seven lithofacies were identified that are consistent with an alluvial system: massive conglomerates with erosive bases, laminated sandstones, fossiliferous marls, mudstone limestones, wackestone limestones, packstone limestones with oncoids, and carbonate microconglomerates. These are laterally related in mid-distal areas of the alluvial system, where the coarse-grain detrital facies represent the paleochannels that furrowed the floodplains of the system (e.g. Nichols and Fisher, 2007).

The limestones and marls association formed in lacustrine-palustrine environments as suggested by the identified sedimentary structures (brecciation, mudcracks, bioturbation and fenestral porosity) that indicate a marsh environment with shallow water bodies and constant variations in lake level (e.g. Alonso-Zarza and Tanner, 2010). This interpretation is further supported by the identification of the association of *Lychnus sp.* and charophytes, that has been commonly associated to lacustrine environments at the end of the Cretaceous (e.g. Freytet and Plaziat, 1982; Torromé *et al.,* 2023).

The formation of the Caminonegro site is associated with both the detrital input from the alluvial streams and the carbonate fraction derived from precipitation of $CaCO_3$-rich meteoric waters (e.g. Alonso-Zarza and Tanner, 2010). The fossil content of the deposit is notable for bone fragments, fish and crocodylomorph teeth, plant remains, charophytes, gastropods and eggshells. The weathering of the fossil remains indicates transport to the lacustrine system, making it an allochthonous fossil assemblage, along with the remains of organisms that inhabited the lake areas, such as charophytes, gastropods, fish and crocodylomorphs.

Fossil and paleoological assemblage

A total of 281 eggshell fragments were identified and classified into three oofamilies: Krokolithidae, Prismatoolithidae, and Spheroolithidae.

Krokolithidae eggshells are calcite eggshells with three structural layers, with an inner layer formed by microcrystalline basal protuberances with accessory crystals forming a rosette, and a continuous layer with a tabular, book-like ultrastructure, are diagnostic characters of the oofamily, along with the block extinction in crossed nicoles. The Krokolithidae eggshells can be related to the crocodylomorph teeth present at the site, with bulbous (globidont) and conical morphologies, which, in the absence of a detailed study on the remains, are tentatively assigned to cf. *Acynodon* (Hylaeochampsidae) and Allodaposuchidae indet. respectively (Blanco *et al.,* 2020). Thus, it can be deduced that these two genera that would inhabit the lacustrine areas of the outcrop would be the animals that produce the Krokolithidae eggshells.

Prismatoolithidae eggshells show 2 structural layers, with a lower mammillary layer in a ratio with respect to the continuous prismatic layer of 1:6, together with an external surface with dispersituberculate ornamentation formed by irregular nodes with pore openings in some of them, are diagnostic characters of the oogenus *Pseudogeckoolithus*. Choi *et al.* (2020) relates the *Pseudogeckoolithus* eggshells with maniraptoran theropod dinosaurs through the EBSD study technique, focused on the crystallography of calcite prisms. In Caminonegro site there is an absence of fossil remains (teeth and bones) of these dinosaurs, as in the Allueva Fm., highlighting these eggshells as the first fossil remains of this group of animals in the Campanian of the Iberian range.

Spheroolithidae eggshells show a single calcite layer with a spherulitic structure featuring sagenotuberculate ornamentation and a protocanaliculate pore system, features diagnostic of the this oofamily. The Caminonegro site contains few centimeter-sized fossil remains, with a tooth of an indeterminate Rhabdodontidae standing out, along with isolated bone remains from the Allueva Fm. The Spheroolithidae shells, which are generally attributed to hadrosauroids (Horner and Weishampel, 1988), a group of animals belonging to the Maastrichtian that replaced the rhabdodontids (Fondevilla *et al.,* 2019), are here related to Rhabdodontidae in the absence of other preserved ornithopods.

The Caminonegro oological assemblage can be compared with other eggshell paleoassemblages from the Upper Cretaceous of Iberia. In Blasi 2 (Arén, Huesca), upper Maastrichtian age, eggshells of Spheroolithidae, Prismatoolithidae, Krokolithidae and Testudoolithidae are recognized (Pérez-Pueyo *et al.,* 2021). Similar associations have been described in several localities of the Pyrenees, including Fontllonga 6 (where the holotype of *Pseudogeckoolithus* is located) (Vianey-Liaud and López-Martínez, 1997). Other localities, such as Poyos (Guadalajara), upper Maastrichtian, most of the Localities of the Tremp Formation (late Campanian-Maastrichtian, Selles *et al.,* 2013; Sanz *et al.,* 1995), and Loarre, (late Campanian-early Maastrichtian, Moreno-Azanza *et al.,* 2022), are dominated by sauropod related ootaxa (Fusioolithidae and Megaloolithidae).

The absence of sauropod-related eggshells in Caminonegro, despite titanosaurian sauropod bones being abundant in the Allueva Fm (Aurell *et al.,* 2022) requires further examination.

In one hand, recent studies have confirmed that sauropods inhabited coastal and lowland environments, but preferred the last, in a proportion of 1 to 4 (Vázquez *et al.,* 2025). On the other hand, sauropod eggshell fragments are typically centimetric in size, several orders of magnitude larger than the largest fragment recovered in Caminonegro. Further research is needed to confirm in the total absence of these otherwise conspicuous fossils in allochthonous assemblages like Caminonegro site is a true palaeoecological signal or a taphonomic bias. In any case, the lack of sauropod-related oological remains in an alluvial environment supports the hypothesis of sauropods been selective for their nesting sites.

These results enhance the vertebrate fossil record of the Allueva Fm, previously limited to the skeletal remains of titanosaur and ornithopod dinosaurs along with crocodylomorphs (Aurell *et al.,* 2022), identifying the presence of theropod dinosaurs in the ecosystem for the first time.

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