Geology and paleontology of Tresjuncos (Cuenca, Spain), a new diatomaceous deposit with Konservat-Lagerstätte characteristics from the European late Miocene

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ABSTRACT

We describe a new Iberian Konservat-Lagerstätte discovered in Tresjuncos (Cuenca, Spain). Based upon geological context, stratigraphy, lithology, sedimentology and genesis of the rocks, we describe and interpret the new fossil site as originated in a lacustrine environment. The micromammalian remains found in the Tresjuncos 1 outcrop suggest that the main site is Turolian in age (uppermost Miocene), continental chronological unit MN13. The fossils are preserved in laminates comprising rhythmic, millimeter-scale alternations of diatomites and calcareous diatomites. A preliminary analysis of the lake paleobiota includes amphibians, crustaceans, insects, plants, and diatoms. The diatoms are dominated by Cyclotella iris, indicating the occurrence of seasonal blooms; the whole assemblage is indicative of a planktonic community developed in somewhat alkaline waters. An extremely well preserved premetamorphic Pelobates (Pelobatidae) tadpole was discovered; it is remarkable because of its gigantic size, greater than the largest living representatives. Its digestive tract predominantly contains the rare diatom Navicula halionata var directa, likely associated with the shore vegetation in which it presumably lived and fed. The arthropods found form a typical lacustrine aquatic assemblage, lacking fish. This assemblage is made up of small filtering crustaceans and of both predator and non-predator insects of diverse sizes. The plant remains, not very diverse, are typical of shore environments. The available evidence on Tresjuncos shows the extraordinary potential for paleontological information that can be expected from this new Konservat-Lagerstätte, which constitutes a significant finding that improves our understanding of continental late Miocene Mediterranean environments.

1. Introduction

Geological sites containing fossils in which delicate structures and soft parts have been preserved are infrequent, and were called Konservat-Lagerstätten by Dolf Seilacher and collaborators in 1985 (Seilacher et al. 1985). These relatively rare deposits are scientifically relevant because they provide significant geological and paleontological information that cannot usually be obtained by other means. In some cases, peculiar conditions of fossilization have even enabled preservation of the labile tissues of animals and plants in incredible detail (Seilacher et al. 1985; Seilacher 1990; Allison and Briggs 1991). Furthermore, the great abundance of specimens frequently found in Konservat-Lagerstätten also allows more accurate analysis of the original composition of the paleoecosystem; this is especially useful in the reconstruction of the paleoenvironments. One of these deposits was discovered in the village of Tresjuncos (Cuenca Province, Spain), during works to modify road access to the town. Preliminary paleontological surveys were conducted, confirming the exceptional potential for conservation shown by these deposits. This led to further studies on the geology, fossil contents, taphonomy, and genesis of the diatomaceous deposits.

In the present study we provide the geological and paleogeographical context of this locality, we perform a detailed analysis of the diatomaceous deposits and their genesis, and we identify the fossil samples obtained in the limited excavations conducted. However, a multidisciplinary approach combining divergent disciplines was required in order to infer the processes that have permitted the formation of this peculiar deposit, as well as the paleoecological and paleoenvironmental conditions locally prevalent at that time.

2. Geological setting

The paleontological site of Tresjuncos is located in the southeast of the Altomira Range close to its limit with the Loranca Basin (Fig. 1A, B). The Loranca Basin is a non-sequenced foreland basin of the Iberian Range (Gómez et al. 1996) and the Altomira Range is a fold and thrust belt (Gómez et al. 1996), interpreted as a westward extrusion of the Mesozoic-Paleogene cover in favor of the plastic facies of the Keuper (Muñoz Martín and De Vicente 1998). The Altomira Range separates the Madrid Basin from the Loranca Basin in Central Spain (Fig. 1A).

In the Altomira Range the oldest Cenozoic stratigraphic unit was named Unit I (Gómez et al. 1996). This unit was affected by the generation of the early folds; nonetheless, tectonic deformation continued until the Vallesian-Turolian (Unit V; see Fig. 2). It is 270 m thick and its deposition took place during Rhenanian-Suevian time (see Unit I; Fig. 2). Tectonic deformation continued over time, however, even affecting Unit V (Fig. 2). The stratigraphic succession of Unit I comprises conglomerates, sandstones, lutites, limestones, marls and gypsum, which are interpreted as deposits of fluvial, alluvial and lacustrine environments. In the Altomira Range this stratigraphic unit lies unconformable and a large erosional hiatus presumably exists between the Cenozoic deposits and the underlying rocks. The subsequent uplift of the Altomira Range led to erosion from the Oligocene, while deposition continued in the Loranca Basin up to the Aragonian (Fig. 2).

Three other younger stratigraphic units (Units II-IV) are distinguished in the Loranca Basin (Fig. 2). Units II and III are mainly composed of conglomerates, sandstones and lutites, interpreted as deposits of a fluvial fan (Díaz-Molina and Tortosa 1996), which laterally pass to marls, limestones and gypsum of lacustrine environments (Gómez et al. 1996; Arribas and Díaz-Molina 1996). During the Aragonian and the lower Vallesian there was a drop in the regional base level and the Loranca Basin was subsequently eroded. The paleorelief originated was partially filled up during the Vallesian-Turolian (Upper Miocene) by limestones, lutites, sandstones and conglomerates from Unit V (Fig. 2), deposited by alluvial fans and in lacustrine environments (Hernáiz Huerta and Cabra Gil 1998). In the Loranca Basin the top of Unit V has been dated as Turolian, based on a micromammalian fauna containing Occitanomys cf. adroveri and Prolagus sp. (Daams et al. 1986). However, Vallesian foss ils have not vet been found. Reactivation of the Altomira Range folds caused the development of the alluvial fans, which were deposited at the edge of the Madrid and Loranca basins, as well as in the elongated depressions located between the growing anticlines of the Altomira belt (Gómez et al. 1996). The source area of these deposits was the Altomira Range itself, and they extended laterally towards the Loranca and the Madrid basins. In the Loranca Basin, Unit V changes laterally to more distal deposits consisting of lutites, marls and limestones.

The Tresjuncos paleontological site is included in diatomaceous deposits within the Vallesian-Turolian Unit, or Unit V, and fossilizes the paleorelief cut out in the folded Altomira Range since the Eocene (Fig. 2). As a result, the Vallesian-Turolian Unit lies unconformable, and onlaps older Cenozoic and Mesozoic deposits.

3. Materials and methods

Fossils were found in slabs obtained from layers of centimetric thickness in the rubble from public works dumped to the south of the town of Tresjuncos. The original site, from

where the sedimentary rocks were removed during the road works, is accurately established (coordinates Lat. 39° 42' 11" N and Long. 2° 45' 20" W); (Fig. 3). The rocks from this location, as well as the *in situ* beds they came from, are mainly diatomaceous deposits rich in fossils preserving soft tissues (Fig. 3C).

Samples for the geological study were obtained from the original site the sedimentary rocks were removed from (Fig. 4, section 3), as well as from different points nearby in Cerro Molino, where the town of Tresjuncos is located (Fig. 4, sections 1, 2 and 4).

We studied samples of diatomaceous deposits, limestones, dolostones and clayed beds using conventional mineralogical, petrographic and geochemical techniques. The basic mineralogical and petrographic study involved transmitted light microscopy inspection of thin sections under polarized light. Petrographic differentiation between calcite and dolomite phases in thin section was achieved following the staining method of Dickson (1966).

We obtained powder X-ray diffraction (XRD) patterns from pressed powder mounts using a Philips semiautomatic PW 1710 diffractometer with monochromatized CuK α radiation. Clay mineralogy was determined in oriented, glycol-solvated aggregates heated to 550°C.

Scanning electron microscopy (SEM) observations were made with a FEI INSPECT microscope, working at 30 kv and a distance of 10 mm, operating in high-vacuum mode and using secondary electrons and backscatter detectors. This instrument was equipped with an Oxford Analytical-Inca X-ray energy-dispersive system (EDX).

We determined diatoms using optical and SEM microscopies. Diatom slide preparation involved treating 1 cm³ of samples with hydrochloric acid and hydrogen peroxide. An aliquot of the resulting slurry was evaporated onto coverslips and subsequently mounted onto glass slides with Naprax (n= 1.74). Frustules were identified along random transects, under oil immersion using light microscopy at 1000X magnification. SEM observations were carried out directly on the diatomites to study the main species.

We studied several small samples from laminated diatomaceous deposits presenting fossil arthropods (28 specimens in total, except ostracod shells), as well as the plant remains. The arthropods were studied using an Olympus SZ X9 stereomicroscope, and some specimens were moistened with alcohol during observation to enhance their contrast in relation to the rock matrix. The fossil tadpole was studied by means of binocular and scanning electron microscopy.

Fossil mammal species were sought in order to determine the age of the deposits. The material was obtained with the use of washing and screening techniques in a 30 cm layer of grey brownish marls (paleomammalian locality herein named Tresjuncos 1). This site is one of the several spots that were sampled in layers present in the margins of the main lacustrine deposits.

All fossils from this locality belong to the collection of the Museo Paleontológico de Castilla-La Mancha (MPCM) in Cuenca (Spain).

4. Results

4.1. Stratigraphy

Two subunits can be distinguished in the stratigraphic succession of the Vallesian-Turolian Unit (Unit V). A lower subunit (SU-1) contains alluvial fan deposits, red lutites and conglomerates, which pass upwards to the upper subunit (SU-2) containing limestones, calcareous and non-calcareous diatomites, marls and lutites (Figs. 2 and 4). In Tresjuncos, the lower and upper subunits are 37 m and 11 m thick, respectively, although the Vallessian-Turolian Unit (Unit V) is up to 300 m thick in this area (Hernáiz Huerta and Cabra Gil 1998). The fossils described in the present paper come from subunit SU-2 (member M-1, see below).

In the hill located to the north of Tresjuncos ("Cerro Molino" in Fig. 4) a syncline is outlined by the beds of the SU-2; therein two members are distinguished, which we will refer to in the text as M-1 and M-2, which are 6.5 m and 5 m thick, respectively (Fig. 4).

Observations and sampling of member M-1 were performed in four places (sections 1, 2, 3 and 4 in Fig. 4), and this member exhibits remarkable facies changes. Towards the east, M-1 contains gray lutites, limestones and two paleosols of different thicknesses, the thinner one located at the base and the thicker one between limestone layers (Fig. 4, section 1). These paleosols show marmorization and columnar structures characteristic of soil profiles, in addition to calcitizied gypsum crystals.

By contrast, carbonates predominate towards the west in member M-1 (Fig. 4, section 2), either compact or soft massive to laminated centimetric beds, interstratified with gray marls up to 4 cm thick. Towards the south (Fig. 4, section 3), M-1 shows facies similar to those of section 2, although centimetric calcareous diatomites with thin intercalations of diatomites up to 3 cm thick predominate (Fig. 5 A, B). Both are fine laminated. The thickness of the diatomaceous layers increases towards the southeast (Fig. 4, section 4).

The upper member, M-2, is only preserved in section 1 (Fig. 4) and mainly comprises limestones containing gastropod and bivalve shell fragments. The micromammal fauna was obtained from the gray marls at the base of member M-2.

4.2. Petrology

After the analytical studies, four rock types were defined in member M-1 as follows:

4.2.1. Diatomites and calcareous diatomites

The diatomites are white or yellowish in color and are easily split into very thin sheets. They present a parallel inframillimetric lamination (Fig. 3B and Fig. 5A), which shows folds and minifractures, likely produced by landslides resulting from compaction. Fragments of leaves, stems and seeds are common on the stratification planes and between the laminations. The diatomites and calcareous diatomites alternate at the millimetric and centimeter scale, with gray lutites or marls forming rhythmic sequences. They also alternate with millimetric to centimetric beds of limestones or dolostones (Fig. 5B). According to XRD and thin-section analyses, they are made up of opal A, and minor amounts of palygorskite (\leq 15%), gypsum (\leq 10%), calcite (\leq 50%) or dolomite (\leq 50%), and detrital quartz and feldspar (\leq 5).

Under SEM, the white diatomite beds show loose diatoms in a detrital matrix formed by fragments of the same type of diatoms (Fig. 5C). Occasionally, siliceous sponge spicules appear (Fig. 5D). Locally, palygorskite covers the diatoms (Fig. 5E). The darker diatomaceous beds include carbonates in varying proportions, which in some cases are calcite cements and in others, dolomite forming a matrix of small crystals, from 2 to 4 μ m (Fig. 5F).

4.2.2. Limestones

In thin section, the limestones of member M-1 are generally ostracod-rich wackestones/packestones also containing gastropods, charophytes, pellets and minor amounts of detrital quartz. They comprise calcite (90%), palygorskite ($\leq 10\%$) and detrital quartz ($\leq 5\%$). Minor amounts of gypsum sometimes appear.

The outcrop of section 3 (Fig. 4) shows other types of limestones. They are compact centimetric beds of up to 15 cm thick, which have white, gray, cream or brown millimetric laminations, sometimes rhythmic. Occasionally, the laminations present folds, as occurs in the diatomites. Fragments of plants, articulated insects, etc., and even an extraordinarily well-preserved tadpole, appear in these laminations.

In thin section, these limestones consist of mosaics of calcite crystals (crystal sizes up to 25 μ m) cementing and replacing diatoms, only some of which are conserved. Exceptionally, the original diatomites are preserved, constituting the most favorable laminae for the conservation of the fossils. Sometimes calcification is total, but the original laminated structure has been preserved with or without micro-folds. Locally, calcitized gypsum lenticular crystals, made up of calcite crystals (\leq 100 μ m in size), are observed. Some detrital quartz also can appear. Under SEM, the remaining diatoms are well preserved. The calcite crystals (euhedral, subhedral and anhedral) and the diatoms are usually coated by silica microspheres and palygorskite fibers.

4.2.3. Dolostones

They exhibit similar characteristics to those of the limestones in relation to the color and laminated structure. They are composed mainly of dolomite with minor amounts (\leq 5%) of gypsum, palygorskite, and quartz (traces). In thin section, they are dolomicrites whose genesis appears to be diverse because some diatoms were occasionally preserved, but on other occasions they present ostracods and can exhibit stromatolitic structures. Under SEM, dolomite crystals are seen to have different habits (from euhedral to anhedral), and are usually very small (crystal size \leq 5 µm). The diatom relics are well conserved, and both dolomite and diatoms are coated with palygorskite fibers.

4.2.4. Grey lutites and marls

They appear towards the base of member M-1 interlayered between the noncalcareous and calcareous diatomites, limestones and dolomites. Their thicknesses vary from several millimeters to 4 cm, and they have a parallel lamination. XRD analyses mainly show palygorskite, with small proportions of detrital quartz (15%) and feldspars (\leq 5%). Some of the beds are marls, because of their high proportion of calcite (\leq 50%). Occasionally, they can incorporate gypsum (\leq 5%).

Under SEM, the palygorskite shows the fibers forming tapestries and skeins. Among the fibers, calcite crystals and dispersed diatoms can be observed. The EDX analyses reveal that the fibers contain Si, AI, Mg and also a high proportion of Fe and K. In some zones, the palygorskites show a poorly defined shape, and there is a high proportion of C that is attributed to the presence of dispersed organic matter.

4.3. Paleontology

As previously indicated, with the exception of the mammal remains, all the fossils studied were found in slabs from the diatomaceous layers obtained from the public works debris removed from the modified road access to the town.

4.3.1. Diatoms

We studied the fossil diatom assemblages from section 3 (Fig. 4). Identification of the diatom taxa and their paleoecological inferences were performed based on the standard general literature (Pantocsek 1886; Krammer and Lange-Bertalot 1991), and with available references to the Neogene sedimentary rocks of different geographical areas (Schauderma 1983; Serieyssol 1984; Servant-Vildary 1986; Ognjanova-Rumenova 1996; Calvo et al. 1988; Temniskova-Topalova et al. 1996).

4.3.1.1. Taxonomic inventory

The diatomaceous beds are mainly composed of *Cyclotella iris* Brun and Heribaud, 1893 (over 95%). (Fig. 6A, B). In addition, the following species have occasionally been recognized: *Navicula halionata* var. *directa* Pantocsek, 1886 (Fig. 6C, D), *Rhopalodiagibba* (Ehr.) Mülle, 1895, *Rhopalodiagibba* var. *paralella* (Grunow) Holmboe, 1899, *Diploneisovalis* (Hilse) Cleve, 1891, *Amphiprora paludosa* Smith, 1853, *Gomphonema dichotomum* Kützing, 1834, *Cymbella affinis* Kützing, 1844, *Cymbella cymbiformis* Agardh, 1830, *Hantzschia amphioxus* (Ehr.) Grunow, 1880, *Nitzschia recta* Hantzsch in Cleve and Grunow, 1880, *Navicula radiosa* Kützing, 1844, *Navicula oblonga* Kützing, 1844, and *Cocconeis placentula* Ehrenberg, 1838. The diatom assemblage found in the diatomites is very different from the one present in the digestive tract of the tadpole (see below), in which *Navicula halionata* var. *directa* Pantocsek, 1886 is predominant, the abundance of other species being very low.

4.3.1.2. Features of Cyclotella iris Brun and Heribaud, 1893

The specimens observed are circular and slightly convex, varying in diameter between 7 and 75 μ m. The central circular area is wider in some specimens than in others, with numerous bumps (Fig. 6A, B). The number of striae is 16 in 10 μ m. They are of unequal length, and some of them are bipolar out towards the margin (Fig. 6B). Numerous small pores occur along the interstrial strips. The frustule interior presents a complex alveolar structure with marginal fultoportula marked externally by a small pore near the margin.

Cyclotella iris is a variable centric diatom that has been extensively studied by means of optical microscopy and SEM (Serieyssol 1984). It has been cited in the Upper Miocene of France (Serieyssol 1984; Ognjanova-Rumenova 1996) and Spain (Hellín Basin; Servant-Vildary 1986); In Bulgaria has been cited in Miocene and younger strata (Ognjanova-Rumenova 1996). The species has been found in the Pliocene of Turkey (Gürel and Yildiz 2007), Greece (Owen et al. 2010) and East Africa (Gasse 1986).

4.3.1.3. Features of Navicula halionata var. directa Pantocsek, 1886

In the samples studied herein, the frustules are highly fragmented rather than dissolved, and have long axis lengths of between 80 and 190 μ m, and minor axis lengths from 16 to 40 μ m, showing 9-10 striae in 10 μ m. The number of striae, the length of the central axial area, and the large size of the frustules, coincide with these characteristic features of *N. halionata* var. *directa*. The axial area (Fig. 6C, D) is longitudinally fissured. The fissures are formed by dissolution, when the pore alignment observed in the hyaline

axial area deteriorates (Fig. 6D). In the apical area, the end of the raphe has the shape of a hook (Fig. 6E), and in some specimens the interatrial structure can be seen (Fig. 6F).

Being quite scarce, *N. haliolata* var. *directa* has rarely been described in the bibliography. However, mention has been made of this species from the Miocene of Hungary (Pantocsek 1886), Romania (Saint Martin and Saint Martin 2005) and Bulgaria (Temniskova-Topalova et al. 1988).

4.3.2. Plants

Many plant remains, small fruits and seeds, some of them very well preserved, have been found on several diatomaceous laminae (Fig. 7). The studied plant assemblage is quite uniform because it corresponds to hydrophytes and shore plants that constitute a characteristic flora of lacustrine environments. The major part of the fossil plants belongs to Monocots (Liliopsida), with frequent Equisetaceae stems also appearing. Remains of dicotiledons have not been found (Fernández Marrón et al. 2006), most likely due to the small sample obtained.

Remains of Equisetales are very characteristic. They are represented (Fig. 7C) by fragments of stems with the nodes and internodes well differentiated, and by the distinct longitudinal internodal ridges of the horsetails (*Equisetum*).

We found a very interesting remain that is difficult to determine (Fig. 7A). It might be a freshwater algal talli, or more likely the stem of a Monocot with dichotomous ramifications. Some water plants show leaf dimorphism depending on their position on the stem (plunged or emerged). Likewise, leaves of different systematic groups, even phylogenetically distant ones, present adaptive convergences towards certain ecological conditions (Álvarez Ramis and Fernández Marrón 1981).

In cases in which the specimens do not preserve cuticular remains, taxonomic assignments should be based exclusively on macroscopical morphological features. Concerning the Najadaceae remain, and without completely rejecting the possibility that it is an algal remain, this specimen (Fig. 7E) might be better interpreted as a branch with opposite ribbon leaves, and as a leaf sheath showing a close morphological resemblance to the extant genus *Najas* Linnaeus, in the same family and currently living submerged in freshwater environments. Very small fragments of Taxodiaceae are one of the most common plant remains recovered in our sample (Fig. 8)

Abundant seeds and small well-preserved fruits of Cyperaceae were found in the Tresjuncos deposits (Fig. 7D). They consist of trigonous achenes without the modified structure that surrounds them (peryginium). The fruit has a protective layer of suberin which helps dispersal through the water. This type of achenes are called *Cyperocarpus* sp. We also found some fossils with a parallel venation attributed to *Cyperites* sp. leaves. The abundance of seeds and fruits (Fig. 7F) in relation to leaves can be explained by their longer permanence and greater buoyancy, regardless of the dimensions of the diaspora or the species (Martín-Closas and Gomez 2004).

Many of the leaf remains are difficult to assign to a precise morphogenus. There are parallel-veined leaves with central careens more or less marked (Fig. 7A, B). These morphological features are characteristic of diverse genera of Monocotots of the intrazonal lacustrine vegetation. They are cited herein as Monocotyledoneae gen. sp. varia since they could correspond to the genera *Cyperus*, *Typha*, *Sparganium*, etc.

There are two elliptical-oval shaped coriaceous leaves with apical sharp entire margin and a parallel venation pattern (Fig. 7H), similar to the floating leaves of *Potamogeton* sp. It is a typical perennial aquatic plant, present in quiet waters with a slow-moving current. An achene with a careen was found that might also belong to *Potamogeton* sp.

Some fragments taken from the samples with fossil plants were prepared with palynological treatments without success. Pollen grains, spores and biostructured phytoclasts have not been found either.

All the plants belonged to a band of herbaceous marsh vegetation that included species of *Equisetum*, *Potamogeton* and a *Typha*-like Monocotyldoneae. This assemblage constitutes a monotypic and specific flora indicative of lacustrine environments. Apart from the immediate local environment, which included taxodiaceans (Fig. 8), we can make no general inferences regarding vegetation and climate based on this flora. The intrazonal lacustrine vegetation mainly depends on edaphic factors and not on aspects relating to the broad climatic zone.

4.3.3. Arthropods

The crustacean record is constituted by ephippia of cladocerans (family Daphniidae) and ostracod shells. Five ephippia are well preserved and are very similar to the abundant ephippia recorded in Rubielos de Mora paleolake (Teruel Province), commonly as mass records (Peñalver et al. 1996). They are broad (approx. 2.0 mm long and 0.8 mm wide), sub-rectangular in shape, with two eggs oriented parallel to the main axis (Fig. 9A). The fossils from Tresjuncos also can be considered as belonging to the subgenus *Daphnia* (*Ctenodaphnia*). Additional Spanish lacustrine localities with Miocene ephippia are Bellver de Cerdanya in Lleida (Martín-Closas and Delclòs 2007) and Benimarfull in Alicante. Ostracod shells without apparent ornamentation, 1.1-2 mm in length, have been recorded in the laminated slabs with plants and insects (Fig. 9B), sometimes as blooms, and some are present in a caddisfly case partially constructed with ostracod shells, ca. 1.8 mm long.

The most abundant insect specimens, 8 specimens of 23 fossil insects, are aquatic dragonfly naiads (Odonata, Anisoptera) of diverse sizes. One abundant morphotype, approx. 1 cm to 3 cm of body lengths, presents a broad abdomen (Fig. 9C). A second morphotype, based only upon one specimen found, has a body length of 4.8 cm and a narrow, elongated abdomen (Fig. 9D). They all correspond to late instars due to the presence of well-developed wing-sheaths. Fossil dragonfly naiads have also been recorded in several Miocene outcrops in Spain, such as Rubielos de Mora and Libros (Teruel), Ribesalbes (Castellón), Bellver de Cerdanya (Lleida) and Cuenca de Sorbas (Almería) (Peñalver et al. 1996, 1999; Martín-Closas and Delclòs 2007).

We found two cases of larval caddisflies (order Trichoptera). The complete specimen measures 36 x 8 mm and is entirely constructed of small fragments (approx. 4 mm long) of taxodioid needles, which are an abundant plant macroremain in the outcrop (Fig. 8); they are oriented along the longitudinal axis and form transverse rows (Fig. 9E). The type of fabrication indicates that the larvae customized the material by trimming fragments of leaves to an appropriate size before adding them to the case. Another caddisfly case, 2.1 mm long and 9 mm at its widest point, is partially constructed of ostracod shells.

Two chironomid pupal exuviae (Diptera, Chironomidae), also called non-biting midges, have been found (Fig. 9F). They are complete, but it is difficult to visualize some anatomical parts such as the thoracic horns or the caudal lobes. Exuviae are 10 mm long, and the visible anatomical features, such as the morphology of the head shield region, the wing sheaths and the abdominal segments, are coincident with those described in pupal exuviae recorded in other Spanish Miocene paleolakes (Rubielos de Mora, Ribesalbes and Bicorb) and classified as cf. *Chironomus* sp. of the tribe Tanytarsini (Peñalver 2002).

A specimen of giant water bug (Hemiptera, Belostomatidae) has been found (Fig. 9G). Its estimated body length, excluding the airstrap, is 6 cm, and 2.6 cm at the widest point. It is preserved in the ventral view, close to a dragonfly naiad and a taxodioid macroremain. Other hemipterans found have not preserved important anatomical characters in order to permit their taxonomic classification at the family level.

The terrestrial insects are represented by specimens of ants and beetles. The two ants found (Hymenoptera, Formicidae) are sexual, winged individuals (Fig. 9H). Classification of ants preserved as compression fossils is very difficult, and only ants well preserved in amber can be described in detail and classified at the genus level. Similarly, the 5 specimens of terrestrial beetles found, two of these as isolated elytra, are difficult to classify. Despite the apparent good preservation of some of them (Fig. 9A), identification at family level is unclear because some important anatomical characters are missing, as is the tarsal morphology.

The current paleoentomofaunal list comprises very common insect groups in Cenozoic lacustrine deposits, such as dragonflies, chironomids, beetles, ants and caddisflies, and common crustacean remains, e.g. ephippia and ostracod shells. The only specimen belonging to a group that is scarce in the Miocene fossil record is the giant water bug.

4.3.4. Amphibians

A single extremely well preserved fossil tadpole has been found, indicating the extraordinary potential in paleontological information that this site can be expected to provide. The tadpole is a very large specimen, preserved in two main slabs and several small fragments (Figs. 10 and 11). The specimen is almost complete, lacking only the final portion of the tail. Tadpoles are rare in the anuran fossil record, particularly for premetamorphic developmental stages, and a world general inventory has recently been published (Gardner 2016).

All the observable features, both in skeletal and soft parts, are very similar to those present in the living *Pelobates* Wagler, 1830 (Pelobatidae) tadpoles. The shape of the frontoparietals, for example, which are clearly displayed in the fossil (Fig. 11), is distinctive even in adults with respect to other European anurans (Bailon 1999).

The complete pelobatid fossil record has been reviewed by Roček et al. (2014). A taxonomic identification at the species level is currently not possible for the Tresjuncos tadpole, because the taxonomy of the group is based upon adult morphology. The genus *Pelobates* is known in several Iberian sites from the early Miocene (Rage and Roček 2003; Böhme and Ilg 2003), but no specific identification has been possible with the available material. However, molecular evidence indicates that the living *Pelobates cultripes*, nearly an Iberian endemism, is the sister species of the Moroccan *Pelobates*

varaldii (Busack et al. 1985; Lobo et al. 2016), with a terminal Miocene estimate for its specific differentiation. Therefore, the Tresjuncos *Pelobates* likely represents an unnamed species ancestral to the two western Palearctic living ones.

The Tresjuncos tadpole has a snout-vent length of 76.3 mm, and a total length estimation of 163 mm, considering that in *P. cultripes* the snout-vent is approximately 0.88 times the tail length (Díaz-Paniagua et al. 2005). This length indicates a gigantic size in comparison with the living representatives of the genus, which also includes the largest tadpoles in Europe (Roček et al. 2006), and the specimen is larger than the maximum recorded (65.2 mm) in the extremely favorable ecological conditions of the Doñana Biological Reserve (Díaz-Paniagua et al. 2005). Using the Normal Table of Gosner (1960) for general anuran larval development, stage 41 is the most probable for this specimen based on the ontogenetic sequence of ossification in living *Pelobates cultripes* tadpoles (Talavera 1990).The forelimbs are not yet out of the body chamber, although their exit and unfolding would have occurred in a very short time, as indicated by the ossification of the three shoulder girdle bones. The Tresjuncos tadpole is a herpetological fossil that provides much specialized paleobiological information, and which requires detailed description elsewhere.

Pelobates tadpoles mainly feed underwater on shoreline aquatic phanerogams, gnawing plants and scraping the periphyton, which could include diatoms, if present, as important nutrients (Gordon et al. 2006). Pumping and filtering water, as well as detritus consumption, are also secondarily but frequently practiced (Díaz-Paniagua et al. 2005).

The two western Palearctic *Pelobates* species, and presumably their Miocene direct ancestor, are good environmental indicators, being restricted to the warm Mediterranean realm. Their Quaternary changes and climatic favorability have recently been analyzed, particularly for *Pelobates cultripes* (Lobo et al. 2016; Gutiérrez-Rodríguez et al. 2017).

4.3.5. Mammals

The fossil mammal association from the locality of Tresjuncos 1 (Fig. 4, section 1), comprising two small mammal dental remains, is poor. It is, however, sufficient to accurately date it as being from the uppermost Miocene.

One of the fossil remains is an upper second premolar of a lagomorph of the family Ochotonidae (Fig. 12B). The size and morphology of this tooth, which exhibits a protoflexus broader and shorter than the mesoflexus and a mesial hiperloph that does not anteriorly cover the lagicone, enable us to assign it to *Prolagus* cf. *crusafonti* López Martínez, 1975. This taxon is the most frequent lagomorph in Spain from the MN9 to the MN12 continental biochronological units (Vallesian to middle Turolian), although it has also been recorded in MN13 localities (López-Martínez 1989; Dam 1997), where the most common species is *P. michauxi* López Martínez, 1975.

The second remain is a relatively damaged fragment of an upper first molar of a murid (Fig. 12A). This M1 shows an advanced degree of stephanodonty with a strong connection of the t3 with the t5 and a less-developed t1-t5 connection. The imbrication of the cusps is poorly developed and thus the bottoms of the valleys are still visible in the occlusal view. This morphology is present in early representatives of the genus *Stephanomys*, such as *S. ramblensis* van de Weerd, 1976, from the upper Turolian (MN13), and therefore the material from Tresjuncos 1 is assigned to this species. The taxon *Occitanomys adroveri* (Thaler, 1966), frequently recorded in Spanish localities of

the MN12 age, shows more primitive dental characters with less developed stephanodonty. Nevertheless, based on the available material from Tresjuncos 1, assignation to the latter species cannot be excluded.

Based on the scarce available material, the most likely age for this locality is established as late Turolian (MN 13) due to the assignation of the Tresjuncos 1 material to the genus *Stephanomys*. This genus establishes the lower limit of this continental biochronological unit, which can be dated at between 6 and 7 Ma (Dam et al. 2006; Morales et al. 2013).

Based on the microvertebrate fossil record, the climatic conditions in central Spain at the time of Tresjuncos 1 site formation were probably mild with relatively high humidity (Dam 2006). The interval between 7-6 Ma has been recognized as a global cooling interval within the general cooling trend starting at the Middle Miocene (Zachos et al. 2001).

5. Discussion

5.1. Sedimentology and diagenesis of member M-1 (within the subunit SU-2)

The facies and facies associations found in the outcrops seem to represent the lateral transition from a supralittoral lacustrine fringe, section 1 (Fig. 3), to littoral, section 2, to even a relative profundal zone, sections 3 and 4 (Fig. 3) (terminology from Gierlowski-Kordesch 2010).

The different petrological data indicate that significant diagenetic processes and sedimentary processes took place in the formation of the carbonate rocks of member M-1. The less transformed limestones appear in the NW of Cerro Molino (section 2, Fig. 3.) The massive and laminated beds, the absence of exposure features and the presence of ostracods, gastropods and charophytes, indicate a lacustrine sedimentation in a littoral zone (Gierlowski-Kordesch 2010). The occasional existence of gypsum indicates that there were more saline periods associated with shallower water due to evaporation. The evaporitic conditions are also evident in the paleosols of section 1 (Fig. 4), where the gypsum originated was later calcitized.

The mineralogical and petrological characteristics of section 3 reveal that most of the limestones are diagenetic facies, formed by the replacement and cementation of the original sediments that consisted of diatomites and probably a certain micritic mud portion. Calcitization of diatoms occurs in alternating laminae, highlighting the primary lamination. The replacement is pseudomorphic, as revealed by the conservation of the typical folding of the diatomites in the diagenetic limestones. During early diagenesis, diatomites can transform to opal CT beds, as is commonly commented in the bibliography (Bustillo 2010), but the calcitization process of diatoms is rare. In the Miocene of the Madrid Basin, diatomaceous deposits formed in shallow lacustrine environments with variable alkalinity show calcitization of diatoms, but these are minor local processes (Calvo et al. 1988; Pozo Rodríguez and López 2004).

Some diatomites include dolomite instead of calcite. The dolomite crystals are very small and grow freely within the high porosity of the diatomite, cementing the diatom frustules and forming a mosaic of small crystals. The small size of dolomite crystals

suggests that dolomicrite may have been formed in primary diagenesis (Armenteros 2010).

The lutites and marls that contain mainly palygorskite were probably formed by the transformation of previous smectites during diagenesis, from solutions rich in Mg and silica, with a pH range between 8 and 9 (Chamley 2013). In the calcareous diatomites, the palygorskite is the cement covering the crystals of calcite and dolomite, and the source of silica for its formation appear to come from the dissolution of some diatoms.

5.2. The diatomaceous sedimentation

The diatomites are clearly dominated by *Cyclotella iris*, a planktonic species which, together with the lack of detrital sediments, could indicate a relatively open lacustrine environment. *Cyclotella iris* occurred in alkaline and carbonate-rich oligotrophic waters (Serieyssol 1984; Gasse 1986; Owen et al. 2010), which is indicative of an early stage in the eutrophication sequence (i.e. oligotrophic, mineral rich, and poor in organic matter).

Diatom laminae in lacustrine rocks mainly record a seasonal productivity cycle, generally the spring bloom (Kemp 1996). The diatomites, mainly comprising one species, with a few specimens of other species, result from mono-specific blooms. Mono- or duo-specific diatom laminae are most common during the spring and summer (Dean et al. 1999). Zahrer et al. (2013) described laminae formed by intense blooms composed predominantly of centric diatoms. When the mono-specific blooms are of the *Cyclotella* species, these authors found that they were formed in spring and summer layers.

The studied diatom laminae, which are generally parallel-sided, and contain unfragmented frustules of *Cyclotella iris*, are interpreted as being mainly formed by rapid deposition, as flocculated aggregates. Harding and Chant (2000) suggested that a macrobiota, in the lacustrine Oligocene of Florissant, became entrapped in mucoussecreting mats of surface water blooms of planktonic diatoms; as the mats and the incorporated macrobiota were sedimented out of the water column, the mucosal mats and their associated bacterial communities arrested decay and promoted preservation of macrobiota tissues.

Silica is a necessary nutrient for diatoms. Diatom blooms are likely a consequence of nutrients suddenly rising and reaching the most superficial part of the water, as a result of a rapid rupture of the stratification or stagnation of the water layer, usually due to sudden changes in the hydrological regime. Hurley et al. (1985) investigated the effect of a relatively small groundwater influent in the regulation of silica supply and diatom growth in Crystal Lake, a small, oligotrophic lake that does not receive stream flow or surface runoff. They found that groundwater is a major silica source for the spring diatom bloom. Studying modern African lakes, Gasse (1987) considered that sporadic influxes of freshwater (through local rainfall or through the aquifer) formed superficial lenses of dilute water where planktonic species developed. According to this author, the bloom of *Cyclotella* implies a marked change in the water budget, and coincides with high silica inputs attributed to groundwater.

The less represented diatom species, found mixed with the majoritarian *Cyclotella iris* in the diatomites of Tresjuncos, are epiphytic (on plants) or epipelic (on rock grains) according to Pantocsek (1886) and Krammer et al. (1991), and they can be interpreted as coming from the littoral zone of the lake. The near absence of benthic diatom species

in the studied section is usually attributed to a high density of phytoplankton that can overshadow the bottom and prevent its development.

Navicula halionata var. *directa*, although a minority species in the diatomites of Tresjuncos, constitutes by far the most common diatom in the digestive tract of the tadpole. *N. halionata* occurs in a diatom association of freshwater species in the Miocene of the Madrid Basin (Calvo et al. 1988). They formed sediments in small shallow lakes with marginal palustrine areas, and with variations in the water layer. They were diatoms adapted to somewhat alkaline waters, which in turn favored the palygorkite formation levels (Calvo et al. 1988).

The different diatom type in the digestive tract of the tadpole, in relation to those present in the diatomites in which the tadpole is included, is indicative of two different environments, which are littoral and open water, respectively. This striking fact could be explained by assuming the movement of the animal, or transport of its carcass, from the shore to a less peripheral lake zone.

5.3. Taphonomy and paleoecology based on the arthropods

The laminated diatomaceous deposits containing the studied fossil arthropods originated far from the lake shore, under low energy conditions. Except for the isolated beetle elytra, the insect specimens are articulated, but the carcasses of these arthropods generally suffered transport from the shorelines. The fossils combine a carbonaceous film with a slight relief (Fig. 9), as is common in the Miocene paleolake of Ribesalbes in different bituminous laminated rocks, namely shales and dolomicrites (Peñalver et al. 2016). The preservation of a slight relief from the original body tridimensionality, due to carbonate mineralization, suggests rapid burial, and most likely early mineralization, of the carcasses. The absence of bioturbation and the type of preservation of the Tresjuncos arthropods is indicative of the development of microbial mats on the lake bottom covering the arthropod carcasses, a circumstance that favored the exceptional degree of preservation observed, and which partially explains the origin of this Konservat-Lagerstätte (see Peñalver 2002; Peñalver et al. 2002).

Caddisfly cases and ephippia, including the chironomid pupal exuviae and the main ostracod shells, are ichnofossils in the broadest sense of the term, if we consider that they are remains of organic material produced by the organisms. The other specimens from Tresjuncos correspond to body fossils. Typically, the fossils of *Daphnia* in the fossil assemblages are only constituted by ephippia due to their high degree of sclerotization with respect to the rest of the body, which never remains preserved.

Most of the arthropods recorded correspond to aquatic forms. The percentage of terrestrial forms is low in comparison to other Miocene paleolakes such as Rubielos de Mora, Ribesalbes, Bicorb (Peñalver 2002) or Bellver de Cerdanya (Martín-Closas and Delclòs 2007), which are geographically close examples for comparison. The aquatic insects recorded in Tresjuncos most likely lived on the shorelines of the paleolake where meadows possibly occurred. The aquatic forms are represented by insects that obtained the dissolved oxygen from the water (dragonfly naiads, larval caddisflies, chironomids) and others that had breathing tubes to obtain air straight from the water surface (giant water bugs). This indicates that the water contained sufficient dissolved oxygen, at least in the shorelines. The larval chironomids have hemoglobin molecules in the blood; thus, this group of aquatic insects tolerated fluctuations of oxygen concentrations. This kind of

mixture has been observed in the Ribesalbes outcrop, and differs from Rubielos de Mora, where only insects that could obtain air directly from the water surface lived in the paleolake (Peñalver 2002; Peñalver et al. 2016).

Extant dragonfly naiads are basically warm-adapted insects, generally not present in water temperature below 10°C, and can live in brackish waters (Norling and Sahlén 1997). Extant dragonflies prefer small, nutrient rich, fish-free and non-acidic lakes and ponds (Norling and Sahlén 1997), features similar to those inferred for the Tresjuncos ancient wetland. Chironomids, the other insect group that was most likely abundant in the paleolake, can be commonly found today in brackish waters. In the Miocene of the Bicorb paleolake, abundant chironomid pupal exuviae have been found, similar to those from Tresjuncos, which have been related to the saline or brackish nature of its body waters (Peñalver and Gaudant 2010).

Giant water bugs and dragonfly naiads were part of the aquatic top predators given the lack of fish, while cladocerans, chironomids and small young tadpoles most likely constituted their prey. Chironomid larvae probably ate detrital material, while the cladocerans were filter feeders.

The presence of crustacean remains of the subgenus *Daphnia* (*Ctenodaphnia*) is very likely indicative of ephemeral waters in the paleolake, by comparison to their Recent environmental preferences.

6. Conclusions

The present paper attempts to describe a new Iberian Konservat-Lagerstätte site accidentally discovered in Tresjuncos (Cuenca, Spain). The results of the multidisciplinary analyses lead us to the following conclusions:

Study of the sedimentary facies, and their lateral variability, in member M-1 (of subunit SU-2) from Tresjuncos, indicates that they undergo a big change along a scale of hundreds of meters in the E-W direction (paleosols — lacustrine limestones — lacustrine diatomaceous deposits). This is the consequence of the previous existence of a shallow lake. The occasional presence of gypsum indicates that in the sedimentation process there were somewhat more saline periods, linked to evaporation stages in which the lake would have been smaller.

The micromammalian remains found enable this paleolake to be dated in the uppermost Miocene, continental chronological unit MN13 (Turolian).

Diatomites were formed as a consequence of monospecific blooms of *Cyclotella iris*, a planktonic diatom species. These blooms could be associated with the entry of groundwater to the lake, providing the high proportion of silica necessary for diatom proliferation. The less salty groundwater, in which the proliferation of diatoms could occur, would generate surface plumes on the more saline waters.

The types of fossil plants, arthropods, and amphibians that have been found are indicative of a shallow, littoral lacustrine environment. In this marshy border the *Pelobates* tadpole could have fed on the periphytic (non-planktonic) diatom predominant in its digestive tract, which is almost absent in the diatomites in which it has been found.

Diatom blooms produced deposits which were quickly conformed as floccular aggregates. The lamination of the deposits derives from the repeated combination of the sedimented diatom blooms, microbial mats formed on the bottom, and from the diagenetic carbonation process.

The composition of diatomaceous layers in this Konservat-Lagerstätte is peculiar. In addition to diatom-rich laminae, there are thin layers of diagenetic limestones derived from the replacement of diatoms by calcite. Most fossils are preserved in diatom laminae, but the carbonation processes have given greater durability to the layers, allowing better conservation. Some fossil insects, such as the winged ant, maintain a perceptible three-dimensional relief, also indicating carbonation. This fact could have been enabled by the microbial mats in which they were preserved.

The diatom species community present in the diatomaceous deposits is indicative of relatively deep water bodies. On the contrary, the fossils recovered are characteristic of shallow shore waters. The aquatic arthropod assemblage, still few in number, provides a coherent view of a lacustrine paleoecosystem in coastal zones, with different trophic levels ranging from large predators to small filtering crustaceans in the lower part of the trophic pyramid. Consequently, we are very likely dealing with a small lake presenting periodical oscillation of its total water content. In the general context of shallow waters, characteristic of oligotrophic water bodies, the depth of the lake would greatly increase through the entrance of groundwater. This groundwater appears to have been sufficiently significant as to allow the open-water development of spring phytoplankton blooms.

References

Allison, A. & Briggs, D.E.G. (1991). The taphonomy of soft-bodied animals. In S. K. Donovan (Ed.), *The Processes of Fossilization* (pp. 120–140). London: Belhaven Press.

Álvarez Ramis, C. & Fernández Marrón, M.T. (1981). Considérations sur le rôle des Phanérogames aquatiques du Cenozoïque dans la détermination de l'âge de leurs gisements. *Proceedings 106 Congrès National des Sociétés Savantes. Sciences*, 85– 97.

Armenteros I. 2010. Diagenesis of Carbonates in Continental Settings. In A.M. Alonso-Zarza & L.H. Tanner (Eds.), *Carbonates in Continental Settings: Processes, Facies and Applications*. Developments in Sedimentology 62, Elsevier, Amsterdam, pp. 62–151.

Arribas, J. & Díaz-Molina, M. (1996). Saline deposits associated with fluvial fan, Late Oligocene-Early Miocene, Loranca Basin, Central Spain. In P. Friend & C. Dabrio (Eds.), *Tertiary basins of Spain: the stratigraphic record of crustal kinematics* (pp. 308–312). Cambridge, UK: Cambridge University Press.

Bailon, S. (1999). Différenciation ostéologique des anoures (Amphibia, Anura) de France. *Fiches d'Ostéologie Animale pour l'Archeologie. Série C: Varia*, 1, 1–41.

Böhme, M. & Ilg, A. (2003). fosFARbase. www.wahre-staerke.com/. Accessed 10 March 2017.

Busack, S.D., Maxson, L.R., & Wilson, M.A. (1985). *Pelobates varaldii* (Anura: Pelobatidae): a morphologically conservative species. *Copeia*, 1985(1), 107–112.

Bustillo, M.A. (2010). Silicification of continental carbonates. In A.M. Alonso-Zarza & L. H. Tanner, L.H. (Eds.), *Carbonates in Continental Settings: Processes, Facies and Applications* (pp. 153–174). Developments in Sedimentology 62. Amsterdam: Elsevier.

Calvo J.P., Pozo, M., & Servant-Vildary, S. (1988). Lacustrine diatomite deposits in the Madrid Basin (Central Spain). *Geogaceta*, 4, 14–17.

Chamley H. (2013). Clay Sedimentology. Springer Science and Business Media.

Daams, R., Lacomba, J. I., & López Martínez, N. (1986). Nuevas faunas de micromamíferos del Terciario continental de la Depresión Intermedia (prov. de Cuenca, España centro oriental). *Estudios Geológicos*, 42, 181–196.

Dam, J.A. van (1997). The small mammals from the upper Miocene of the Teruel-Alfambra region (Spain): Paleobiology and paleoclimatologic reconstructions. *Geologica Ultraiectina*, 156, 1–204.

Dam, J.A. van (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.

Dam, J.A. van, Aziz, H.A., Álvarez-Sierra, M., Hilgen, F.K., Hoek Ostende, L.W. van den, Lourens, L.J., Mein, P., Meulen, A.J. van der, & Peláez-Campomanes, P. (2006). Long-period astronomical forcing of mammal turnover. *Nature*, 443, 687–691.

Dean, J.M., Kemp, A.E.S., Bull, D., Pike, J., Patterson, G., & Zolitschka, B. (1999). Taking varves to bits: Scanning electron microscopy in the study of laminated sediments and varves. *Journal of Paleolimnology*, 22, 121–136.

Díaz-Molina, M., & Tortosa, A. (1996). Wet fluvial fans of the Loranca Basin, Upper Oligocene-Lower Miocene, Central Spain. In P. Friend & C. Dabrio (Eds.), *Tertiary basins of Spain: the stratigraphic record of crustal kinematics* (pp. 300–307). Cambridge, UK: Cambridge University Press.

Díaz-Paniagua, C., Gómez Rodríguez, C., Portheault, A., & de Vries, W. (2005). *Los anfibios de Doñana*. Madrid: Parques Nacionales.

Dickson J.A.D. (1966). Carbonate identification and genesis as revealed by staining. Journal of Sedimentary Petrology, 36, 491-505.

Domingo, L., Alberdi, M.T., & Azanza, B. 2007. A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255, 361–376.

Fernández Marrón, T., Hably, L., & Díaz Molina, M. (2006). Miocene lacustrine plant remains from Tresjuncos (Iberian Range, Spain). Abstracts Book 7th European Palaeobotany-Palynology Conference, Prague. p. 88.

Gardner, J.D. (2016). The fossil record of tadpoles. Fossil Imprint, 72, 17-44.

Gasse, F. (1986). *East African diatoms. Taxonomy, ecological distribution*. Bibliotheca Diatomologica, Band 11. Berlin-Stuttgart: J. Cramer.

Gasse, F. (1987). Diatoms for reconstructing palaeoenvironments and paleohydrology in tropical semi-arid zones. *Hydrobiologia*, 154, 127–163.

Gierlowski-Kordesch, H.E. (2010). Lacustrine carbonates. In A.M. Alonso-Zarza & L.H. Tanner (Eds.), *Carbonates in Continental Settings: Processes, Facies and Applications* (pp. 2–101). Amsterdam: Developments in Sedimentology 61, Elsevier.

Gómez, J.J., Díaz-Molina, M., & Lendínez, A. (1996). Tectono-sedimentary analysis of the Loranca Basin (Upper Oligocene-Miocene, central Spain). A non-sequenced foreland basin. In P. Friend & C. Dabrio (Eds.), *Tertiary basins of Spain: The stratigraphic record of crustal kinematics* (pp. 277–286). Cambridge, UK: Cambridge University Press.

Gordon, N., Neori, A., Shpigel, M., Lee, J., & Harpaz, S. (2006). Effect of diatom diets on growth and survival of the abalone Haliotis discus hannay postlarvae. *Aquaculture*, 252, 225–233.

Gosner, K.L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.

Gürel, A. & Yildiz, A. (2007). Diatom communities, lithofacies characteristics and paleoenvironmental interpretation of Pliocene diatomite deposits in the Ihlara–Selime plain (Aksaray, Central Anatolia, Turkey). *Journal of Asian Earth Sciences*, 30, 170–180.

Gutiérrez-Rodríguez, J., Márcia Barbosa, A., & Martínez-Solano, Í. (2017). Present and past climatic effects on the current distribution and genetic diversity of the Iberian spadefoot toad (*Pelobates cultripes*): an integrative approach. *Journal of Biogeography*, 44, 245–258.

Harding, I.C. & Chant, L.C. (2000). Self-sedimented diatom mats as agents of exceptional fossil preservation in the Oligocene Florissant lake beds, Colorado, United States. *Geology*, 28, 195–198.

Hernáiz Huerta, P.P. & Cabra Gil, P. (1998). *Hoja 661 (Villarejo de Fuentes), Mapa Geológico de España a Escala 1:50.000*. Madrid: Instituto Tecnológico Geominero de España.

Hurley, J.P., Armstrong, D.E., Kenoyer, G.J., & Bowser, C.J. (1985). Ground water as a silica source for diatom production in a precipitation-dominated lake. *Science*, 227, 1576–1578.

Kemp, A.E.S. (1996). Laminated sediments as palaeo-indicators. In A.E.S. Kemp (Ed.), *Palaeoclimatology and Palaeoceanography from Laminated Sediments*. London: Geological Society Special Publication No. 116. doi:10.1144/GSL.SP.1996.116.01.01.

Krammer, K. & Lange-Bertalot, H. (1991). *Süβwasserflora von Mitteleuropa*. Stuttgart-Jena: Gustav Fischer.

Lobo, J.M., Martínez-Solano, Í., & Sanchiz, B. (2016). A review of the palaeoclimatic inference potential of Iberian Quaternary fossil batrachians. *Palaeobiodiversity and Palaeoenvironments*, 96, 125–148.

López-Martínez, N. (1989). Revisión sistemática y bioestratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. *Memorias del Museo Paleontológico de la Universidad de Zaragoza*, 3, 1–343.

Martín-Closas, C. & Delclòs, X. (2007). The Miocene Paleolake of La Cerdanya (Eastern Pyrenees). *Geo-Guías*, 3, 181–205.

Martín-Closas, C. & Gomez, B. (2004). Taphonomie des plantes et interprétations paléoécologiques. Une synthèse. *Geobios*, 37, 65–88.

Morales, J., Peláez-Campomanes, P., Abella, J., Montoya, P., Ruiz, F.J., Gibert, L., Scott, G., Cantalapiedra, J.L., & Sanisidro, O. (2013). The Ventian mammal age (latest Miocene): Present state. *Spanish Journal of Palaeontology*, 28, 149–160.

Muñoz Marín, A. & De Vicente, G. (1998). Origen y relación entre las deformaciones y esfuerzos alpinos de la zona centro-oriental de la Península Ibérica. *Revista de la Sociedad Geológica de España*, 11, 57–70.

Norling, U. & Sahlén, G. (1997). Odonata, Dragonflies and Damselflies. In A. Nilsson (Ed.), *Aquatic Insects of North Europe. A taxonomic Handbook. Vol. 2* (pp 13–65). Stenstrup, Dinamarca: Apollo Books.

Ognjanova-Rumenova, N. (1996). *Cyclotella iris* Brun & Héribaud – A group from the Upper Miocene sediments of the Sofia Basin, Bulgaria. *Geologica Carpathica*, 47, 301–310.

Owen, R.B., Renaut, R.W., & Stamatakis, M.G. (2010). Diatomaceous sedimentation in late Neogene lacustrine basins of western Macedonia, Greece. *Journal of Paleolimnology*, 44, 343–359.

Pantocsek, J. (1886). *Beiträge zur Kenntniss der Fossilen Bacillarien Ungars (Theil 1, 2*). Nagy-Tapolcsány: Buchdruckerei von Julius Platzko.

Peñalver, E. (2002). Los insectos dípteros del Mioceno del Este de la Península Ibérica; Rubielos de Mora, Ribesalbes y Bicorp. Tafonomía y sistemática. Ph.D. thesis, Universitat de València, Spain.

Peñalver, E. & Gaudant, J. (2010). Limnic food web and salinity of the Upper Miocene Bicorb palaeolake (eastern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 297, 683–696.

Peñalver, E., Barrón, E., Postigo-Mijarra, J.M., García Vives, J.A., Saura Vilar, M. (2016). *El paleolago de Ribesalbes. Un ecosistema de hace 19 millones de años.* Castellón: Diputación de Castellón e Instituto Geológico y Minero de España.

Peñalver, E., Martínez-Delclòs, X., & Arillo, A. (1999). Yacimientos con insectos fósiles en España. *Revista Española de Paleontología*, 14, 231–245.

Peñalver, E., Martínez-Delclòs, X., & De Renzi, M. (1996). Registro de pulgas de agua [Cladocera: Daphniidae: Daphnia (Ctenodaphnia)] en el Mioceno de Rubielos de Mora (Teruel, España). *Il Reunión de Tafonomía y Fosilización, Zaragoza*, 311–317.

Peñalver, E., Martínez-Delclòs, X., & De Renzi, M. (2002). Evidence of continental microbial mats based on the study of fossil insects- examples from two Spanish Konservat Fossil-Lagerstätten. In M. De Renzi, M. Pardo, M. Belinchón, E. Peñalver, P.

Montoya, A., & Márquez-Aliaga (Eds.), *Current Topics on Taphonomy and Fossilization* (pp. 281–287) Valencia: Ayuntamiento de Valencia.

Peñalver, E., Nel, A., & Martínez-Delclòs, X. (1996). Insectos del Mioceno inferior de Ribesalbes (Castellón, España). Paleoptera y Neoptera poli- y paraneoptera. *Treballs del Museu de Geologia de Barcelona*, 5, 15–95.

Pozo Rodríguez, M. & López, M.J. (2004). Facies biosilíceas en el neógeno de la cuenca de Madrid. Origen e implicaciones sedimentológicas. *Revista de la Sociedad Geológica de España*, 17, 229–248.

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.

Roček, Z., Böttcher, R, & Wassersug, R.J. (2006). Gigantism in tadpoles of the Neogene frog *Palaeobatrachus*. *Paleobiology*, 32(4), 666–675.

Roček, Z., Wuttke, M., Gardner, J.D., & Singh Bhullar, B.A. (2014). The Euro-American genus *Eopelobates*, and a re-definition of the family Pelobatidae (Amphibia, Anura). *Palaeobiodiversity and Palaeoenvironments*, 94, 529–567.

Saint Martin, S. & Saint Martin, J.P. (2005). Enregistrement par les diatomées des variations paléoenvironnementales durant le Sarmatien dans l'aire paratéthysienne (Roumanie). *Comptes Rendus Palevol*, 4, 191–201.

Schauderna, H. (1983). Die Diatomenflora aus den miozächen See blagerunden im Nördlinger Ries. *Palaeontographica*, 188, 83–193.

Seilacher, A. (1990). Taphonomy of *Fossil*-Lagerstätten. Overview. In E.C. Briggs & P.R. Crowther (Eds.), *Palaeobiology, a synthesis* (pp. 266–270). Cambridge, UK: Blackwell Scientific Publications.

Seilacher, A., Reif, W.E., & Westphal, F. (1985). Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society of London*, 311, 5–23.

Serieyssol, K.K. (1984). *Cyclotella iris* Brun & Héribaud. In D.G. Mann (Ed.), *Proceedings 7th International Diatom-Symposium* (pp. 197–212). Koenigstein: O. Koeltz.

Servant-Vildary, S. (1986). *Cyclotella* sp. fossiles de depots d´eau douce d´age miocène en Espagne. In M. Ricard (Ed.), *Proceedings 8th International Diatom Symposium* (pp. 495–511). Koenigstein: O. Koeltz.

Talavera, R.R. (1990). *Evolución de pelobátidos y pelodítidos (Amphibia, Anura): Morfología y desarrollo del sistema esquelético*. Madrid: Editorial Universidad Complutense de Madrid.

Temniskova-Topalova, D., Ivanov, D.A., & Popova, E. (1996). Diatom analysis on Neogene sediments from the Elhovo basin in south Bulgaria. *Geologica Carpathica*, 47, 289–300.

Zachos, J., Pagani, M. Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 686–693.

Zahrer, J., Dreibrodt, S., & Brauer, A. (2013). Evidence of the North Atlantic Oscillation in varve composition and diatom assemblages from recent, annually laminated sediments of Lake Belau, northern Germany. *Journal of Paleolimnology*, 50, 231–244.

Figure captions

Fig. 1. **A:** Location map of the study area, indicated by a red dot. 1, Madrid Basin. 2, Loranca Basin. 3, Altomira Range; **B:** Geological map (modified from Hernáiz Huerta and Cabra Gil 1998).

Fig. 2. Stratigraphy of the Loranca Basin referred to the chronological table of Domingo et al. (2007), showing the spatiotemporal relationships between Unit V, where the Tresjuncos fossil site is located, and the underlying stratigraphic units (Units I-IV), in the center of the Loranca Basin (1), and in the Altomira Range.

Fig. 3. Konservat-Lagerstätte in the village of Tresjuncos. **A**: Outcrop (lithological section 3 in Figure 4) in the access road to the village, where the deposits were removed by the road works; **B**: Detail of the laminated deposits. Rocks are limestones, calcareous diatomites, diatomites and mudstones; **C**: Remarkable fossil tadpole (MPCM-TJ-0019) found in the calcareous diatomites.

Fig. 4. Lithological sections of Tresjuncos, whose locations are indicated in the satellite image. Towards the south of the map, D indicates the place where the debris with fossils had accumulated.

Fig. 5. Petrological features. **A**: Transversal cut section of calcareous diatomites and diatomites, with interlayered brown mudstones. The clearest laminae are diatomites; **B**: Thin section of a calcareous diatomite. The dark laminae are diatomites that are isotropic under crossed nicols. The red laminae are calcitized diatomites; the calcite is stained with alizarin. Optical microscopy. Crossed nicols; **C**: Diatomite constituted by complete and fragmented *Cyclotella iris* specimens. SEM microscopy; **D**: Silica sponge spicules can occur among the diatoms. SEM microscopy; **E**: Palygorskyte fibers on a calcite crystal and diatom, SEM microscopy; **F**: Mosaics of small rhombohedral dolomite crystals between well conserved diatoms. SEM microscopy. Scale bars: 2 cm (A), 500 μ m (B), 50 μ m (C), 100 μ m (D), 2 μ m (E), 10 μ m (F).

Fig. 6. SEM micrographs showing the shape and ultrastructure of the diatom species. **A**: *Cyclotella iris* showing the valve and the girdle; **B**: Upper frustule of *Cyclotella iris* showing the bumps in the central area, bipolar striae and small pores along interstrial strips; **C**: *Naviculahalionata* var. *directa* showing the raphe, longitudinal fissures and striae; **D**: Detail of the fissured area, showing the initial lineated pores; **E**: Apical zone showing the ending of the raphe; **F**: Detail of figure **E** showing a interstrial velum of regularly arranged pores. Scale bars: 10 μm (A, D, E), 3 μm (B, F), 50 μm (C).

Fig. 7. Plant remains from Tresjuncos. **A:** Monocotyledoneae gen. et sp. varia (MPCM-TJ-0001); **B:** Monocotyledoneae gen. et sp. indet. leaf (MPCM-TJ-0002); **C:** *Equisetum* sp. (MPCM-TJ-0003); **D:** *Cyperites* sp. leaf (MPCM-TJ-0004); **E:** cf. *Najas* sp. (MPCM-TJ-0005); **F:** Fruits and seeds (MPCM-TJ-0006); **G:** Detail of some achenes of Cyperaceae or *Potamogeton* (MPCM-TJ-0007); **H:** *Potamogeton* sp. leaf (MPCM-TJ-0008). Scale bars: 3 cm (A), 3 mm (B), 5 mm (C, F, H), 5 cm (D), 1 cm (E), 2.5 mm (G).

Fig. 8. Taxodiacea indet. (MPCM-TJ-0009), one of the most common plant remains from the Tresjuncos sample. Scale bar: 1 cm.

Fig. 9. Arthropod assemblage from the Tresjuncos laminated diatomites. **A:** Cladoceran ephippium of the family Daphniidae (MPCM-TJ-0010); **B:** Ostracod shell (MPCM-TJ-0011); **C:** Dragonfly naiad of the abundant morphotype presenting a broad abdomen (MPCM-TJ-0012); **D:** Dragonfly naiad of the elongated morphotype (MPCM-TJ-0013); **E:** Caddisfly case entirely constructed with small fragments of taxodioid needles (MPCM-TJ-0014); **F:** Chironomid pupal exuvium (MPCM-TJ-0015); **G:** Giant water bug (MPCM-TJ-0016); **H:** Winged ant (MPCM-TJ-0017); **I:** Terrestrial beetle (MPCM-TJ-0018). Scale bars: 1 mm (A, B, F, I) 1 cm (C–E, G, H).

Fig. 10. Tresjuncos, tadpole of *Pelobates* sp. slab A (MPCM -TJ-0019). Scale bar: 5 cm.

Fig. 11. Tresjuncos, tadpole of *Pelobates* sp. slab B, counterpart of slab A (MPCM - TJ-0019). Note the frontoparietal shape. Scale bar: 3 cm.

Fig. 12. Tresjuncos 1 micromammals. **A:** Upper first molar of the murid *Stephanomys* cf. *ramblensis* (MPCM -TJ-0021); **B:** Upper second premolar of the ochotonid *Prolagus* cf. *crusafonti* (MPCM-TJ-0020). Scale bar: 1 mm (A, B).