LÓPEZ-MARTÍNEZ N., FERNÁNDEZ-MARRÓN M.T. & VALLE M.F. 1999. The succession of Vertebrates and Plants across the Cretaceous-Tertiary boundary in the Tremp Formation, Ager valley (South-central Pyrenees, Spain). [La succession de vertébrés et de plantes à travers la limite Crétacé-Tertiaire dans la Formation Tremp, vallée d'Ager (Pyrénées sud-centrales, Espagne)]. (

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ABSTRACT - The Tremp Formation red beds in the Ager valley (Fontllonga section, Lleida, Spain) have yielded plants (macrorests, palynomorphs) and vertebrates (teeth, bones, eggshells and footprints) at different levels from Early Maastrichtian to Early Palaeocene. A decrease in diversity affected both, plants and vertebrates, but not synchronously. Plant diversity decreases early in the Maastrichtian, while the change in vertebrate assemblages (sudden extinction of the dinosaurs) occurs later on, at the Cretaceous-Tertiary (K/T) boundary. This pattern agrees with the record of France and China, but contrasts with that of North American Western Interior, where both changes coincide with the K/T boundary.

KEYWORDS: CRETACEOUS-TERTIARY BOUNDARY, PALAEOBOTANY, VERTEBRATES, TREMP FM., PYRENEES.

RÉSUMÉ - Les dépôts continentaux de la Formation Tremp dans la vallée d'Ager (coupe de Fontllonga, Lleida, Spain) ont fourni des fossiles de plantes (palynomorphes et macrorestes) et de vertébrés (ossements, dents, oeufs et traces) datés du Maastrichtien inférieur-Paléocène inférieur. Les deux groupes montrent une réduction de la diversité mais celle-ci n'est pas synchrone: la crise florale a eu lieu pendant le Maastrichtien, et celle des vertébrés terrestres s'est passée plus tard, à la limite K/T. Ceci est en accord avec les données de la France et de la Chine, mais contraste avec celles du Western Interior de l'Amérique du Nord où les deux changements coïncident avec la limite Crétacé-Tertiaire.

MOTS-CLÉS: LIMITE CRÉTACÉ-TERTIAIRE, PALÉOBOTANIQUE, VERTÉBRÉS, FORMATION TREMP, PYRÉNÉES.

INTRODUCTION

The Tremp Formation in the south-central Pyrenees (Lleida, Spain), dated from Early Maastrichtian to Late Palaeocene, is one of the rare areas in the world preserving the geological record across the Cretaceous/Tertiary (K/T) boundary in continental environments. Its study is relevant in order to assess the conditions, extent and intensity of the K/T boundary crisis far from the area of the extraterrestrial impact.

The lack of sedimentary continuity in continental palaeoenvironments often produces ambiguous results when studying palaeoenvironmental changes. This is the case in US Western Interior, the only continental area in the world were the K/T boundary crisis has been intensively documented (Tschudy et al. 1984; Lerbekmo et al. 1986; Smit et al. 1987; Sheenan et al. 1991; Archibald 1996). The abundant erosive episodes and the fossil content from presumably reworked channel-fill sediments, seriously flaw the interpretations of the palaeoenvironmental crisis. Also in other areas of the world (Southern France, China), the K/T boundary in continental formations cannot yet be unambiguosly situated (Jaeger & Westphal 1989; Zao et al. 1991; Stets et al. 1996). The study of new sections in continental formations is thus necessary for collecting high resolution geological data.

The Tremp Fm. has the suitable conditions in thickness, facies and continuity for enabling the study of the palaeoenvironmental changes during this critical period. Its red beds are rich in fossil remains from shallow marine, coastal and non- marine environments: algae, benthic foraminifera, rudists, plants, fish, dinosaurs and mammals. On the basis of palaeomagnetic and biostratigraphic data, the K/T boundary can be accurately placed in the Ager valley (Lleida, Spain), where the

Fontllonga section contains an almost complete sequence from the Early Maastrichtian to the Early Danian. (Llompart & Krauss 1982; Feist & Colombo 1983; Médus et al. 1988, 1992; Galbrun et al. 1993; Alvarez- Sierra et al. 1994; López Martínez et al. 1998 a; Vianey-Liaud & López-Martínez 1997).

In our present study, we compare the vertebrate and the new plant fossil records around the K/T boundary in the Fontllonga section and in the surrounding Ager valley, which allow us to interpret the pattern of changes of the terrestrial biota in the area during the K/T transition.

GEOLOGICAL SETTING

The Pyrenean foredeep basin was formed subsequently to the opening of the Bay of Biscay during the Early Cretaceous. It constitutes the first stage of the history of the Pyrenean orogeny, caused by the oblique collision between the Iberian and European plates. The compressive tectonics responsible for the Pyrenean orogeny has divided the basin into several tectonic units by a progressive series of thrusts.

The Tremp Formation represents the last filling episode of the Pyrenean foredeep basin. It is underlain and intercalated with the near-shore marine Arén Sandstone (Late Campanian-Early Maastrichtian), and overlain by the Ilerdian transgressive *Alveolina* limestones and marls (Late Palaeocene-Early Eocene, Fig. 1) (Mey et al. 1968; Díaz Molina 1987; Krauss 1990).

The Tremp Formation crops out in the central and western part of the Southern Pyrenees, reaching about 900 m at the depocenter near the type locality (Tremp, Lleida province, Spain). Fossil vertebrates and plants from this area have been studied

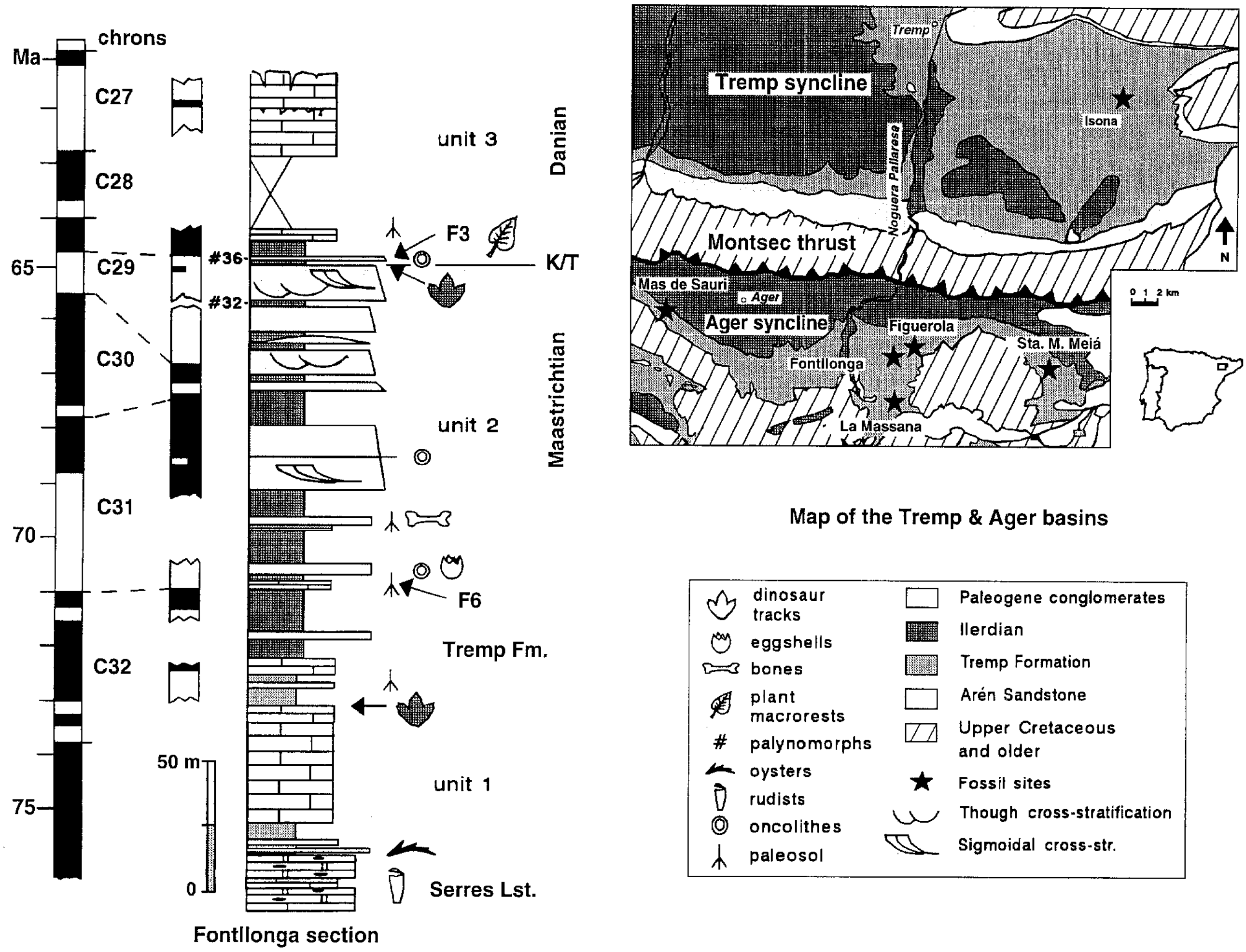


FIGURE 1 - Geological map of the Tremp-Ager area, and stratigraphic column of the Fontllonga section with the situation of the main fossil localities. Palaeomagnetic data from Galbrun et al., 1993; stratigraphic data from L. Ardévol, in López-Martínez et al. (1998a).
Carte géologique de la région de Tremp-Ager, et colonne stratigraphique de la coupe de Fontllonga avec la situation des principales localités fossilifères. Données paléomagnétiques d'après Galbrun et al, 1993; données stratigraphiques d'après L. Ardévol, in López-Martínez et al. (1998a).

by Casanovas et al. (1987), De Porta et al. (1985), Ashraf & Erben (1986), Médus et al. (1988, 1992) and Barrón & Diéguez (1992). South of this area, the Montsec thrust separates two large, asymmetric synclines oriented W-E, the Tremp syncline in the North from the Ager valley in the South (Fig. 1).

The Tremp Formation in the Ager valley, where the Fontllonga section is located, reaches about 700 m in thickness and has been divided into four units: Unit 1 consists of limestones and marls up to 70 m thick with minor intercalations of sandstones. It has a diverse fossil content with remains of oysters, *Girvanella,* charophytes, plants, benthic foraminifers, ostracods and dinosaurs footprints near the top of the unit. Unit 2 consists of up to 150 m thick reddish mudstones and sandstones with minor intercalations of limestones and gypsum. It contains plant, ostracod, gastropod and vertebrate remains. Unit 3 and 4 consist of up to 400 m thick limestones, mudstones and sandstones with minor intercalations of gypsum. Its main fossil content is *Microcodium* in the lower part, gastropods and large benthic foraminifera in the upper part.

Detailed studies of the stratigraphy, sedimentology, paleontology and isotopic content of the Tremp Formation in the Ager syncline can be found in López-Martínez et al. (1998 a) and references therein.

The Chron C29r containing the K/T boundary is located in a 24 m thick succession of sandstone and mudstone deposits from estuarine environments in the upper part of this unit (Galbrun et al. 1993). The K/T boundary interval can be situated in a 3 m thick silt level near the top of the section correlated to the upper part of chron C29r. This interval separates the last record of dinosaurs from a strong excursion in ^{13}C isotopic content of carbonates (López-Martínez et al. 1996b, 1998a). The thickness and uniformity of the deposits in this section during the K/T boundary interval suggest a relative continuity of the sedimentary conditions. The main change occurs after the K/T boundary, upward in the section where limestones, evaporites and paleosols dominate.

VERTEBRATES

Unit 2 of the Tremp Fm. at Fontllonga section contains two rich vertebrate assemblages, Fontllonga- 6 (F6) in the Early Maastrichtian and Fontllonga- 3 (F3) in the Early Danian (Fig. 1). Some scattered samples have been collected from other levels. Additionally, five other sites from the Ager syncline correlated with the Fontllonga section have a rich record of dinosaur tracks. They allow us to document a vertebrate fossil sequence across the K/T boundary with eleven sites from the Early Maastrichtian to the Danian in stratigraphical superposition correlated with the geomagnetic time scale (López-Martínez et al. 1996a, 1998a).

Two Early Maastrichtian sites contain large sauropod footprints, situated about 150 m below the K/T boundary interval at the top of Unit 1. La Massana site, in the Fontllonga section is an extend dinoturbated surface with hundreds of round- shaped dinosaur footprints bimodal in size (40 and 60 cm in diameter; López- Martínez et al. 1998b). Peralba site, 10 km east from Fontllonga, shows several large footprints similar to those from La Massana.

The Fontllonga-6 site is situated about 100 m below the K/T boundary interval, near the base of the chron C31r (Early Maastrichtian). It has yielded remains of fish (scales from bony fishes, teeth from the rays *Igdabatis indicus* and *Rhombodus* sp.), amphibians, turtles, lizards, crocodiles and dinosaurs (dromeosaurs, titanosaurian sauropods, ankylosaurs and seven types of eggshells) (Alvarez- Sierra et al. 1994; Soler- Gijón & De la Peña 1995; Vianey-Liaud & López-Martínez 1997; Soler Gijón & López-Martínez 1998). Scattered bones and eggshell remains of dinosaurs are documented as well along this section, reaching up to about 70 m below the K/T boundary interval (Galbrun et al. 1993). Additionally, a mandible of a large hadrosaur has been reported from the Fontllonga section, about 60 m below the K/T boundary interval (Le Loeuff, verbal com. 1996).

This record has been interpreted by Galbrun (1997) as evidence of a diachronous extinction of the dinosaurs, which would disappear in Europe before than in North America. On the contrary, the record of dinosaur footprints near the end of the Cretaceous in the Ager valley provides new evidence supporting a synchronous extinction of dinosaurs in both continents.

Closer to the K/T boundary, three localities from the Ager basin have yielded abundant and diversified dinosaur footprints. The Mas de Sauri site shows eight footprints from a track attributed to a large ornithischian (Llompart, 1979; López-Martínez et al. 1998 a). It is situated about 25 m below the K/T boundary interval, correlated to the base of chron C29r (López- Martínez et al. 1998a). The Mas Morull and Sta. Maria de Meià sites have the youngest dinosaur footprints, situated about 8 m below the end of chron C29r. This stratigraphic interval may represent 200- 350 thousand years according to the estimated sedimentary rate (López-Martínez et al. 1998a), thus the site corresponds approximately to the chronological position of the K/T boundary assuming no major breaks in the sedimentary process. The Mas Morull site (near Figuerola, Fig. 1) shows

FIGURE 2 - Dinosaur megatracksite south of Sta Mª de Meià. The picture shows a part of the dinoturbated surface close to the Cretaceous-Tertiary boundary, containing rounded footprints attributed to a herd of probably quadrupedal, small sauropod dinosaurs. *Gisement de grandes traces de dinosaures au sud de Sta Mª de Meià. L'image montre une partie d'une surface dinoturbée proche de la limite Crétacé-Tertiaire, qui contient des traces arrondies attribuées à un troupeau de dinosaures, probablement des petits sauropodes quadrupèdes.*

thirty footprints from at least two types of dinosaurs, a large sauropod and a small type. The Sta. Maria de Meià megatracksite holds a large dinoturbated surface, about one thousand square meters in area, showing hundreds of evenly spaced rounded footprints, attributed to a herd of small sauropods (Fig. 2).

The localities Fontllonga 3 and Figuerola are correlated to the top of chron C29r (Earliest Danian). They are situated approximately 3 m above the surface containing dinosaur footprints at Mas Morull and Sta. Maria de Meià. An exhaustive sampling of these marly levels has yielded a large number of bones and teeth from fish (aff. Lepisosteiformes, Pycnodontiformes, *Coelodus* cf. *laurenti, Stephanodus* sp., Siluriformes), fragments of turtle carapaces, crocodile remains and tiny bird eggshells, as well as some teeth from mammals, but no dinosaur remains. The fish species *Coelodus* cf. *laurenti* is Paleocene in age (De la Peña & Soler Gijón 1996). The best represented mammal corresponds to the multituberculate genus *Hainina,* also known from the Lower Paleocene site Hainin (Belgium).

Other scattered vertebrate remains from Unit 2 upper sandstones, correlated to chron C29n and C28r (Danian), correspond to remains of turtles. Up to now, neither dinosaur eggshells nor bone remains have been reported in the Palaeocene part of the Tremp Formation, not even as reworked fossils. This contrasts with the situation in the Western Interior basin, were putative reworked fossils from dinosaurs have been recorded in sandstone levels above the K/T boundary (Smit el al. 1987; Argast et al. 1987).

FLORAL ASSEMBLAGES

Two rich palynological samples have been studied in the Fontllonga section: sample #32 is located 14 m below the K/T boundary interval, and sample #36, 2.5 m above it, at the vertebrate site Fontllonga-3 (Fig. 1). The age of both samples can be accurately dated, respectively at the middle part and near the top of chron C29r. In addition, a macrofossil plant assemblage has been recovered one m above the level of palynological sample #36, close to the top of chron C29r. This assemblage yielded fragmentary leaf and scarce fruit remains. Among these remains, about 50 specimens show better preservation, allowing us to identify 13 taxa. This is the first reference to a Danian plant macrofossil assemblage in Europe.

In our palynological samples the spores predominate over the gymnosperm or the angiosperm pollen, both below and above the K/T boundary (Fig. 3). They reach 72 % in the Late Cretaceous sample, and 48 % in the Danian one. They are composed of Anthocerotaceae (*Phaeocerosporites* fsp.) Lycopodiaceae (*Hamulatisporites* fsp.) Selaginellaceae (*Echinatisporis* fsp., *Gabonisporis* fsp., *Ceratosporites* fsp), ferns including Schizaeaceae (*Schizaeoisporites* fsp., *Cicatricosisporites* fsp., *Trilobosporites* fsp. and several forms of *Leiotriletes*), Polypodiaceae (*Laevigatosporites* fsp., *Converru-*

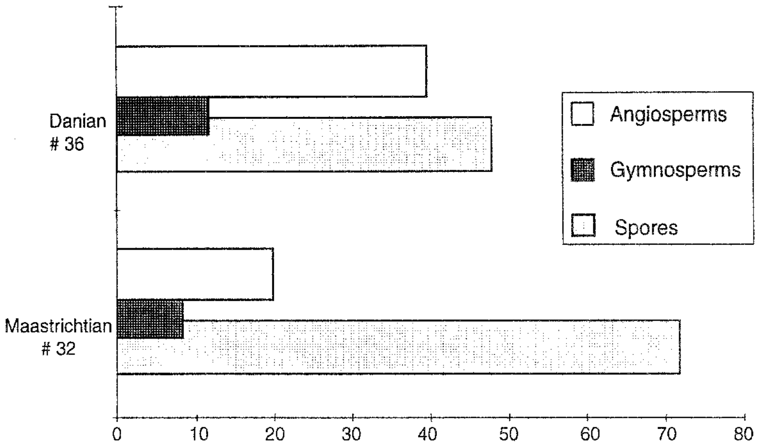


FIGURE 3 - Relative abundance of the three main plant groups represented in palynological samples from the Fontllonga section situated just below and above the K/T boundary (see fig. 1). *Fréquence relative des trois groupes principaux de plantes représentés dans la coupe de Fontllonga dans les deux échantillons palynologiques situés juste au-dessous et au-dessus de la limite Crétacé-Tertiaire (voir fig. 1).*

cosisporites fsp.), Gleichenidaceae (*Gleicheniidites* fsp., *Toroisporis* fsp.), *Granulatisporis* fsp., *Triporoletes* fsp., etc. The spores dominate in some other Maastrichtian Pyrenean assemblages, but a fern- spike at the K/T boundary has not yet been found in the Pyrenees (De Porta et al. 1985; Médus et al. 1988). However, the K/T boundary palynological event has been reported near the Maastrichtian type section, marked by an unusual abundance of bryophyte spores (Brinkhuis & Visscher 1994).

The gymnosperms are slightly more abundant relative to angiosperms in the Cretaceous sample than in the Palaeocene one (29% against 23% from the total of flowering plants, fig. 3). They are mainly represented by *Inaperturopollenites* fsp. (Cupressaceae-Taxodiaceae, *Glyptostrobus* being also present in the plant macrofossil assemblage); Cycadaceae pollen and very rare Pinaceae (*Pityosporites*) are also present. We do not observe an increase in the Pinaceae frequency from Late Cretaceous to Early Tertiary in this section, contrary to that assessed by Médus et al. (1992).

Monocots are very scarce in all Fontllonga samples of both palynological and macroremain assemblages. Only a few monocolpate pollens can be attributed to Palmaceae. This contrasts with the neighbouring palaeobotanical assemblages from Isona (Early Maastrichtian of the Tremp basin), where Palmae are very frequent or dominant, both in palynological and macroremain assemblages (De Porta et al. 1985; Barrón & Diéguez 1992).

Dicots, mainly Hamamelidae, are dominant among angiosperms as both pollen and foliar remains. The pollen assemblage contains Juglandaceae (*Subtriporopollenites* and *Platycaryapollenites*), Fagaceae (*Tricolporopollenites*), Myricaceae (*Triatriopollenites* and *Labraferoidaepollenites*), Betulaceae (*Triporopollenites*), Ulmaceae (*Rugulitriporites*), Clethraceae-Cyrillaceae (*Cyrillaceaepollenites*), Tiliaceae (*Intratriporopollenites*, very scarce in #36, doubtfully in #32) and Normapolles form-genus incertae sedis (*Plicapollis, Semioculipollis, Nudopollis, Longanulipollis*).

The Danian pollen sample #36 yielded the Normapolles taxon *Pseudoromeinipollenites paleocenicus* KEDVES, 1982, similar to that described from Menat (Late Palaeocene, France). This taxon is absent in the Late Cretaceous sample #32. The morphogenus *Pseudoromeinipollenites* sensu Legoux is however reported by Médus (1986) and Médus et al. (1992) as a typical Cretaceous taxa along the complete Fontllonga section and other European localities.

The Danian macrorest assemblage from Fontllonga contains Juglandaceae (*Juglandophyllum* sp. and *Carya* sp.), Fagaceae (*Eotrigonobalanus furcinervis* [ROSSM.] Walter & Kvacek) and Myricaceae (*Myrica* sp.). Also Salicaceae (*Populus* aff. *leuce* [ROSSM.] Ung. and *P.* cf. *zaddachii* HEER) and Proteaceae (*Dryandroides quercinea* VEL.) are identified. Less frequent are Magnoliaceae (cf. *Magnolia dianae* UNG.), Lauraceae (*Daphnogene* sp.), Myrtaceae (*Rhodomyrtophyllum reticulosum* [ROSSM.] Knobloch & Kvacek and cf. *Myrtospermun cooperi* CHANDLER) and Ebenaceae (*Diospyros brachysepala* AL.BR.).

Microphyll leaves dominate this foliar assemblage, which can indicate either a subtropical seasonally dry climate or a warm- temperate moist climate. The abundance of mesotherm taxa and the presence of evergreen angiosperms (Magnoliaceae and Lauraceae) indicate a subtropical climate. Entire- margined leaves constitute approximately half of the sample, typical for subtropical forests (Wolfe 1971). Therefore we infer a subtropical seasonally dry climate for the Earliest Palaeocene in the Tremp Formation.

DISCUSSION

The record of vertebrates shows an abrupt pattern of change across the Cretaceous-Tertiary boundary in the Tremp Formation, dinosaur and ray remains disappearing at the top of unit 2. Vertebrate diversity decreases from Late Cretaceous to Earliest Tertiary mainly due to the dramatic change from associations rich in dinosaurs to associations with no dinosaurs. The absence of rays in Tertiary levels may be attributed to more freshwater palaeoenvironmental conditions, since the estuarine sandstones organized in thickening and coarsening sequence indicate a regressive trend of the unit 2 of the Tremp Formation. Sedimentary conditions are similar in both Cretaceous and Tertiary parts of the unit 2, thus the absence of dinosaur remains in the top of the unit does not seem to be linked to taphonomy. The Ager tracksites prove the presence of abundant and diverse dinosaurs living in the area just before the K/T boundary, while no dinosaur remains have yet been recorded above it. The modest increase in the mammalian abundance in the Early Tertiary does not balance the diversity loss due to dinosaur extinction.

The abrupt disappearance of dinosaurs in the Tremp Formation at the upper part of the chron C29r close to a ^{13}C isotopic excursion coincides with the K/T boundary position, located in marine sections about 250 000 years before the end of chron C29r around a ^{13}C isotopic excursion. This coincidence suggests that global palaeoenvironmental catastrophic processes were responsible for mass extinction in both marine and non-marine realms.

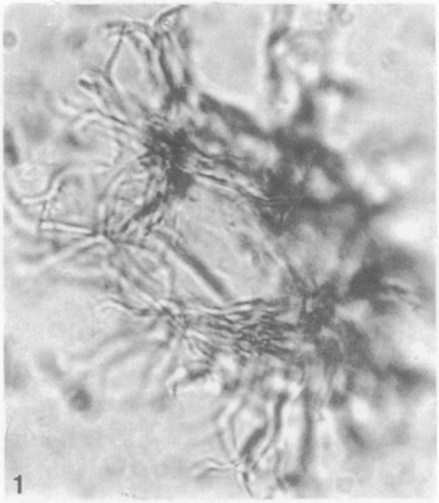
In spite of the catastrophe which could affect the terrestrial environments, a smooth transition from Late Cretaceous to Palaeocene palynological assemblages has been described in the Old World (Médus et al., 1988; Méon 1990, 1991). In the case of the European plant macrofossil assemblages, a gradual transition across the K/T boundary seems also to be the case (see Knobloch et al., 1993). In our Danian macroremain assemblage, six out of thirteen taxa (*Dryandroides quercinea, Rhodomyrtophyllum reticulosum, Populus leuce, Myrica* sp., *Diospyros brachysepala* and *Glyptostrobus* sp.) are shared with Late Cretaceous assemblages from other regions. However the extinct Cheirolepidaceae, common in the Late Cretaceous from Central Spain and Pyrenees (Isona) are absent in the Latest Maastrichtian and Danian assemblages from the Tremp Formation. A turnover in plant composition thus occurs during the Maastrichtian, before the K/T boundary.

The diversity of Danian foliar remains from Fontllonga decreases in relation to Late Cretaceous Central Spain assemblages (Gómez Porter 1983). We pass from 52 taxa (2,6 remains per species) in the Late Campanian- Early Maastrichtian assemblages from Central Spain to 13 taxa (4 remains per species) in the Danian assemblage from Fontllonga. These figures coincide with those of the foliar assemblages from the Western Interior, showing also a strong decrease in plant diversity from Cretaceous to Tertiary: the average number of taxa passes from 42 taxa in nine Cretaceous sites to 8 taxa in seven Early Palaeocene sites (Wolfe & Upchurch 1986).

A decrease in plant diversity in the Western Interior is detected in palynological taxa at the K/T boundary, passing from 200 taxa in Late Maastrichtian to 135 taxa in the Palaeocene (Nichols et al. 1990). In contrast, the diversity loss in palynological assemblages in the Pyrenees occurs during the Maastrichtian, before the K/T boundary. We go from 103 taxa in the Late Campanian- Early Maastrichtian from Central Spain, and 83 taxa in the Early Maastrichtian from Isona (Alvarez Ramis et al. 1994, 1996; De Porta et al. 1985), to 40 taxa in the Late Maastrichtian and 44 taxa in the Early Danian from Fontllonga. The same case occurs in the Nanxiong basin (China), where Stets et al. (1996) document a strong decrease in palynological diversity, from 34 to 11 taxa, located 90 m below the last dinosaur record. They propose to consider this floral event as the K/T boundary, and the youngest dinosaurs as Tertiary in age, but Zhao et al. (1990) dated the floral crisis as Late Maastrichtian, near the base of chron C29r. Therefore in Spain and China the plant diversity crisis would occur during the Maastrichtian, while in North America it apparently occurs later on, at the K/T boundary.

In the Coll de Nargó area (south-central Pyrenees, Spain) and the Aix basin (Provence, France), Ashraf & Erben (1986) have reported a decrease in palynological diversity from 8 to 3 taxa (mainly Pinacea; palynozones B/C boundary) situated below several levels with dinosaur eggshells. These authors as well as Médus et al. (1988) considered this modest palynological change to be the K/T boundary, but Cojan (1989) instead situated it in the transition from Early to Late Maastrichtian, although with no positive dating. Another, older palynological change is reported by Ashraf & Erben (1986) between their palynozones A and B in the Coll de Nargó section. However the samples below and above this change contain 19 taxa, most

FIGURE 4 - **1.** *Spiniferites* fsp. Fontllonga #32. x 900. **2.** *Cicatricosisporites* fsp. Fontllonga #36. x 900. **3.** *Granulatisporites* fsp. Fontllonga #32. x 900. **4.** *Triporoletes* fsp. Fontllonga #32. x 900. **5.** *Converrucosisporites* fsp. Fontllonga #32. x 900. **6.** *Ceratosporites* fsp. Fontllonga #36. x 900. **7.** *Leiotriletes* fsp. Fontllonga #32. x 400. **8.** *Echinatisporis* fsp. Fontllonga #36. x 900.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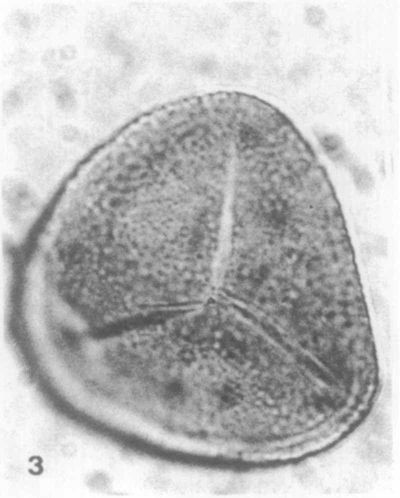
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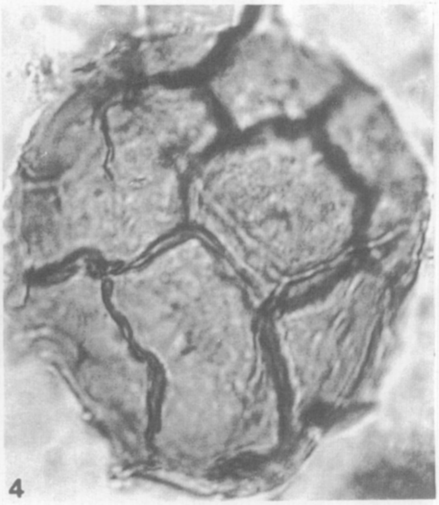
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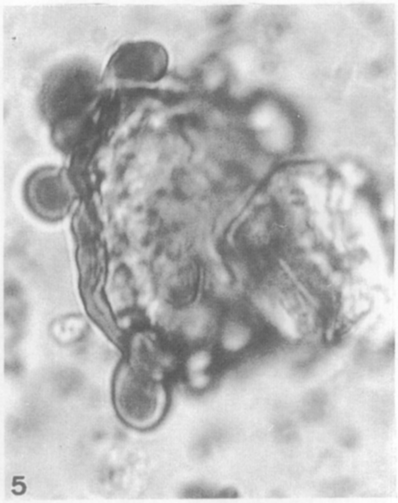
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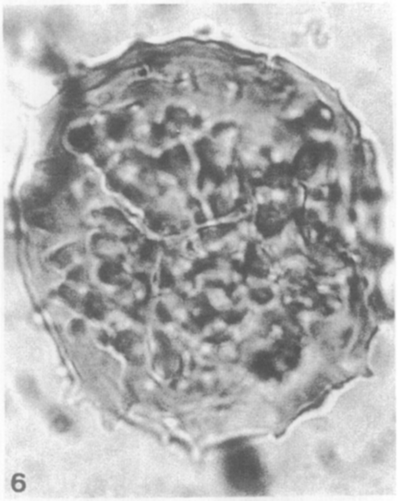
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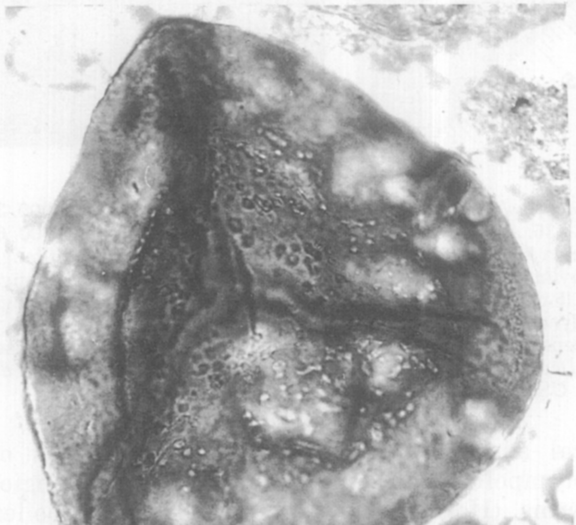
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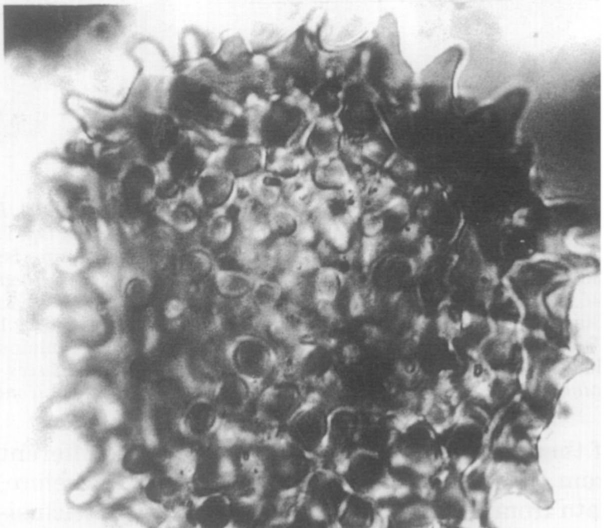
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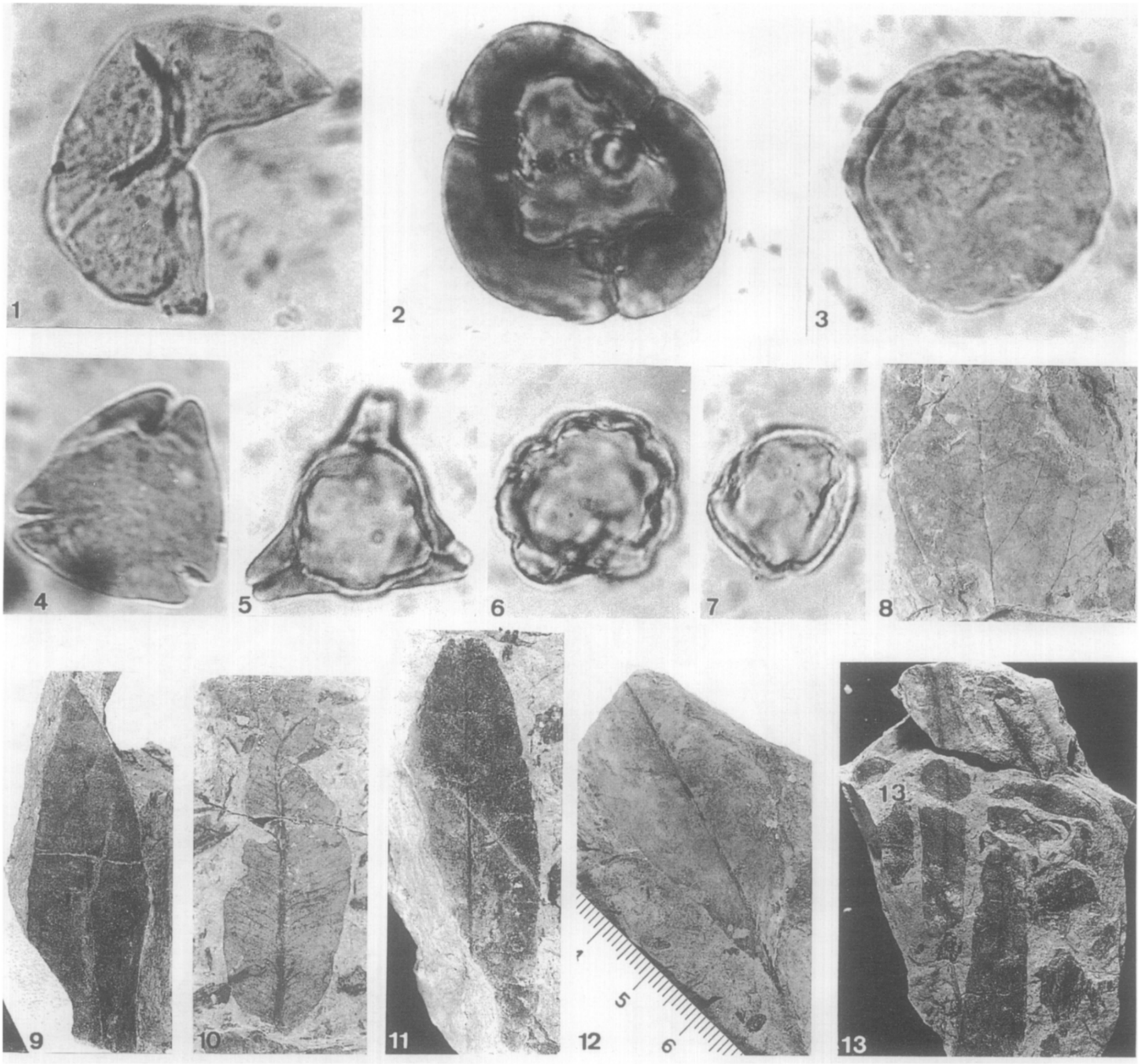

Figure 5 - **1.** *Inaperturopollenites* fsp. Fontllonga #36. x 900. **2.** *Pseudoromeinipollenites paleocenicus* Kedves. Fontllonga #36. x 900. **3.** *Rugulitriporites* fsp. Fontllonga #36. x 900. **4.** *Nudopollis* fsp. Fontllonga #36. x 900. **5.** *Longanulipollis* fsp. Fontllonga #32. x 900. **6.** *Polycolpites* fsp. Fontllonga #36. x 900. **7.** *Tricolporopollenites* fsp. Fontllonga #36. x 900. **8.** *Populus* aff. *leuce* (Rossm.) Ung. Fontllonga #36. x 1. **9.** *Juglandophyllum* sp. Fontllonga #36. x 1. **10.** *Rhodomyrtophyllum reticulosum* (Rossm.) Knobloch & Kvacek. Fontllonga #36. x 1. **11.** *Eotrigonobalanus furcinervis* (Rossm.) Walter & Kvacek. Fontllonga # 36. x 1. **12.** Diospyros brachisepala Al Br. Fontllonga #36. x 1. **13.** Dryandroides quercinea Vel. Fontllonga #36. x 1. The palynomorph slides are stored in the Department of Geology (Paleontology). University of Salamanca and the foliar remains in the Department of Paleontology, CSIC-Universidad Complutense, Madrid (Spain). *Les lames des palynomorphes sont déposées dans le Département de Géologie (Paléontologie) de l'Université de Salamanca et les restes foliaires dans le Département de Paléontologie du CSIC-Universidad Complutense, Madrid (Espagne).*

of them in common and not significantly different from those of Fontllonga #32 and #36. Therefore, data from Ashraf & Erben (1986) are not conclusive for dating the vegetation crises in the Pyrenean-Provence region. A chronological trend clearly observed in the Cretaceous-Paleocene palynological assemblages is the progressive loss of Normapolles taxa replaced by modern angiosperms (Herngreen et al. 1986). Normapolles constitute about 70-76% of pollen taxa (spores excluded) in the Gulpen Formation (Netherlands) and the Rognac Limestone at Bachasson (France);

then 57-60 % in the Maastricht Formation (Netherlands) and Central Spain; they decrease to only 25-29% at La Posa and Fontllonga #32-#36 (Spain), and to only 16% in the Rognac Limestone at Rognac, France (data from De Porta et al. 1985; Kedves et al. 1980; Herngreen et al. 1986; Médus et al. 1992; Alvarez-Ramis et al. 1994, 1996, and this paper). A decrease of Normapolles thus occurs during the Maastrichtian, although it may not be strictly synchronous in different regions.

The diversity loss in plants during the Maastrichtian in Spain is mainly due to a lower number of taxa of gymnosperms, monocots (palms) and Normapolles in the Latest Maastrichtian and Danian assemblages by comparison with the Late Campanian and Early Maastrichtian assemblages. This diversity loss does not change the overall composition of the flora, which continues being dominated by ferns, Taxodiaceae, Hamamelidae and Magnolidae. The local ecological factors thus cannot explain by themselves the observed pattern of change, towards a more modern type of flora. This change suggests indeed a decrease in temperature from megatherm (tropical) to mesotherm (subtropical- warm temperate) taxa, which coincides with many other indices of a global climatic change at the Early-Late Maastrichtian transition detected in the marine realm as well as on the continent (Barrera 1994; Le Loeuff et al. 1994).

In the Pyrenees there is not indications of an increased pluviosity across the K/T transition, such as described in the Western Interior by Wolfe & Upchurch 1986 (but see Gemmill & Johnson 1997).

CONCLUSIONS

The K/T boundary transition on land can be documented in the Pyrenees by the study of vertebrates and plants in rather continuous sections with well-constrained dating. The record consists of eleven localities with vertebrates and five localities with plants. The succession shows that a crisis affected both plants and land vertebrates, but not synchronously. Plant diversity in the Pyrenees decreases first, during the Maastrichtian; the major vertebrate change, affecting specially dinosaurs with an apparently abrupt extinction process, occurs later on during the K/T boundary.

Compared with other areas, a similar diachronic change occurs in the Late Cretaceous of China, where plant succession changes during the Maastrichtian before the change in vertebrate succession. The plant succession change in the Pyrenees and China approximately coincides with a global climatic deterioration detected at the Early-Late Maastrichtian transition. The diachronic pattern of change in terrestrial ecosystems from the Old World contrasts with the synchronous change in plants and vertebrates at the K/T boundary described in North America.

The abrupt pattern of dinosaur extinction in the Ager basin, approximately coinciding with that of the marine realm at the Cretaceous-Tertiary boundary, is indicative of a global palaeoenvironmental catastrophe although the whole assemblages of plants were not affected by this event. The data from the Pyrenees confirm a global climatic deterioration during the Maastrichtian preceding the K/T boundary, and reinforce the catastrophic pattern of the K/T crisis demonstrating its selective effects.

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REFERENCES

Alvarez Ramis C. & Doubinger J. 1994 - Contribución al conocimiento de la palinoflora cretácica de la provincia de Madrid. Los Alcores, Guadalix de la Sierra. *Revista Española de Micropaleontología*, 26, 2: 5-22.

Alvarez Ramis C., Kedves M., Fernández Marrón T. & Clemente Belmonte P. 1996 - Nuevos datos palinológicos sobre las Angiospermas primitivas del Cretácico superior de los Alcores (Guadalix de la Sierra, Madrid). *Revista Española de Micropaleontología,* 28, 3: 101-110.

Alvarez-Sierra M.A., Arribas M.E., Ardevol L., Civis J., Daams R., Krauss S., López-Martínez N., De La Peña A., Soler R., Vianey-Liaud M., Lacasa A., Marandat B., Peláez-Campomanes P., Sevilla P. & Sigé B. 1994 - El límite Cretácico-Terciario en la seccion de Fontllonga (Cuenca de Ager, provincia de Lérida). *II Congreso G.E.T. Jaca, Comunicaciones*: 23-26.

Archibald J.D. 1996 - Testing extinction theories at the Cretaceous-Tertiary boundary using the vertebrate fossil record. *In* McLeod N. & Keller G. (eds), *Cretaceous-Tertiary mass extinctions. Biotic and environmental changes*: 373-397.

Argast S., Farlow J.O., Gabet R.M., Brinkman D.L. 1987 - Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology,* 15: 927-930.

Ashraf A.R. & Erben H.K. - 1986. Palynologische Untersuchungen an der Kreide/Tertiär-Grenze west-mediterraneaner Regionen. *Palaeontographica,* B, 200: 111-163.

Barrera E. 1994 - Global environmental changes preceding the Cretaceous-Tertiary boundary: Early-Late Maastrichtian transition. *Geology,* 22: 877-880.

Barrón E. & Dieguez M.C. 1992 - Palaeoecological aspects of a new flora from the Garumnian deposits of Isona (Lerida, Spain). *IV Conférence Organisation Internationale de Paléobotanique,* Paris: 17.

Brinkhuis H. & Visser H. 1994 - New evidence for terrestrial ecosystem collapse at the KT and Permian/Triassic boundaries. *Lunar and Planetary Institut, NASA Conference Proceedings,* 07, 825, 17 p.

Casanovas M.L., Santafé J.V., Sanz J.L. & Buscalioni A.D. 1987 - Arcosaurios (Crocodilia, Dinosauria) del Cretácico Superior de la Conca de Tremp (Lleida, España). *In* Sanz J.L. (ed.), Geología y Paleontología (Arcosaurios) de los yacimientos cretácicos de Galve (Teruel) y Tremp (Lérida). *Estudios Geológicos*: 95-110.

Cojan I. 1989 - Discontinuités majeures en milieu continental. Proposition de corrélation avec des événements globaux (Bassin de Provence, S. France, Passage Crétacé/Tertiaire). *Comptes Rendus de l'Académie des Sciences*, II, 309: 1013-1018

De La Peña A. & Soler-Gijón R. 1996 - The first siluriform from the Cretaceous-Tertiary boundary interval of Eurasia. *Lethaia,* 29: 85-86

De Porta J., Kedves M., Solé De Porta N. & Civis J. 1985 - Palinología del Maastrichtiense del Barranco de la Posa (Lérida, España). Problemática regional. *Revista d'Investigacions Geologiques*, 40: 5-28.

Diaz Molina M. 1987 - Sedimentacion sintectonica asociada a una subida relativa del nivel del mar durante el Cretacico superior. *In* Sanz J.L. (ed.), Geologia y paleontologia (Arcosaurios) de los yacimientos cretacicos de Galve (Teruel) y Tremp (Lerida). *Estudios Geológicos*, num. ext. Tremp-Galve: 69-93.

Feist M. & Colombo F. 1983 - La limite Cretacé-Tertiaire dans le nord-est de l'Espagne du point de vue des charophytes. *Géologie Méditerranéenne*, 10: 303-326

Galbrun B. 1997 - Did the European dinosaurs disappear before the K-T event? Magnetostratigraphic evidence. *Earth and Planetary Science letters*, 148: 569-579

Galbrun B., Feist M., Colombo F., Rocchia R. & Tambareau Y. 1993 - Magnetostratigraphy and biostratigraphy of Cretaceous-Tertiary continental deposits, Ager basin, province of Lerida, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 102: 41-52.

Gemmill C.E.C. & Johnson K.R. 1997 - Paleoecology of a Late Paleocene (Tiffanian) megaflora from the Northern Great Divide basin, Wyoming. *Palaios,* 12: 439-448.

Gómez Porter P. 1983 - Estudio paleobotánico de los macrorrestos de dos canteras sitas en el borde Sur del embalse del Vellón (Guadalix de la Sierra, Madrid). Memoria de Licenciatura, Universidad Complutense Madrid, 115 p. (unpublished).

Herngreen G.F.W., Felder W.M., Kedves M. & Meessen J.P.M.T. 1986 - Micropaleontology of the Maestrichtian in borehole Bunde, The Netherlands. *Review of Palaeobotany and Palynology*, 48, 70 p.

Jaeger J.J. & Westphal W. (eds) 1989 - La limite Crétacé-Tertiaire dans le bassin de L'Arc (Sud-est, France). *Cahiers Réserve géologique de Haute Provence,* Digne, 1, 60 p.

Kedves M. 1982 - Palynology of the Thanetian layers of Menat. *Palaeontographica,* B, 182: 87-150.

Kedves M. & Herngreen G.F.W. 1980 - Palynology of the stratotype of the Maastrichtian and the Gulpen Formation, Enci section, Maastricht, The Netherlands. *Pollen et Spores*, 22: 483-544.

Knobloch E., Kvacek Z., Buzek C., Mai D.H. & Batten D.J. 1993 - Evolutionary significance of floristic changes in the Northern Hemisphere during the Late Cretaceous and Paleogene, with particular reference to Central Europe. *Review of Palaeobotany and Palynology,* 78: 41-54.

Krauss S. 1990 - Stratigraphy and facies of the "Garumnian" - Late Cretaceous to Early Paleogene - in the Tremp region, Central Southern Pyrenees. *Tübinger Geowissenschaft Arbeiten*, 11, 152 p.

Lerbekmo J.F. & St.Louis R.M. 1986 - The terminal Cretaceous iridium anomaly in the Red Deer Valley, Alberta, Canada. *Canadian Journal of Earth Sciences,* 23: 120-124.

Le Loeuff J., Buffetaut E. & Martin M. 1994 - The last stages of dinosaur faunal history in Europe: a succession of Maastrichtian dinosaur assemblages from the Corbières (southern France). *Geological Magazine*, 131: 625-630.

Llompart C. 1979 - Yacimiento de huellas de pisadas de reptil en el Cretácico superior prepirenaico. *Acta Geológica Hispánica*, 14: 333-336.

Llompart C. & Krauss S. 1982 - Restos de moluscos y dinosaurios en formaciones estromatolíticas garumnienses al S. del Montsec (Prov. de Lérida). *Boletín Geológico y Minero,* 93: 371-378.

López-Martínez N., Alvarez-Sierra M.A., Daams R., Peláez-Campomanes P. & Sevilla P. 1996a - Vertebrate succesion from Late Cretaceous to Early Tertiary, South Central Pyrenees (Lleida, Spain). *In* Repetski J.E. (ed.), VI N.A.P.C. Washington, Abstracts of papers. *Paleontological Society, Special Publication*, 8: 246.

López-Martínez N., Ardevol L., Arribas-Mocoroa M.E., Civis J. & González-Delgado J.A. 1996b - Transicion Cretácico-Terciario en depositos continentales de la cuenca de Tremp-Graus: datos preliminares de isotopos estables de C y O. *Geogaceta,* 20 (1): 62-65.

López-Martínez N., Ardevol L., Arribas M.E., Civis J. & Gonzalez-Delgado A. 1998 a - The geological record in non-marine environments around the K/T boundary (Tremp Formation, Spain). *Bulletin de la Société géologique de France*, 169 (1): 11-20.

López-Martínez N., Lacasa Ruiz A. & Martinez-Delclos X. 1998b - Icnites de dinosaures sauròpodes en el Cretaci superior de Camarasa (la Noguera, Lleida). *Ilerda "Ciències"*, 52: 35-46.

Médus J. 1986 - Paléogéographie et systématique du genre *Pseudoromeinipollenites* au Crétacé supérieur. *Actas de Palinología*: 321-325.

Médus J., Colombo F. & Durand J.P. 1992 - Pollen and spores assemblages of uppermost Cretaceous continental formations of South-Eastern France and North-Eastern Spain. *Cretaceous Research*, 13: 119-132.

Médus J., Feist M., Rocchia R., Batten D.J., Boclet D., Colombo F., Tambareau Y. & Villatte J. 1988 - Prospects for recognition of the palynological Cretaceous/Tertiary boundary and an iridium anormaly in nonmarine facies of the eastern Spanish Pyrenees: a preliminary report. *Newsletters on Stratigraphy*, 18 (3): 123-138.

Méon H. 1990 - Palynologic studies of the Cretaceous- Tertiary boundary interval at El Kef outcrop, northwestern Tunisia: paleogeographic implications. *Review of Palaeobotany and Palynology*, 65: 85-94.

Méon H. 1991 - Études sporopolliniques à la limite Crétacé-Tertiaire: la coupe du Kef (Tunisie Nord-Occidentale); étude systématique, stratigraphie, paléogéographie et évolution climatique. *Palaeontographica,* B, 223: 107-168.

Mey P., Nagtegaal P., Roberti K. & Hartevelt J. 1968 - Lithostratigraphic subdivision of posthercynian deposits in the South-Central Pyrenees, Spain. *Leidse Geologische Mededelingen*, 41: 221-228

Nichols D.J., Fleming R.F. & Frederiksen N.O. 1990 - Palynological evidence of effects of the terminal Cretaceous event on terrestrial floras in Western North America. *In* Kauffman E.J. & Walliser O.H. (eds), *Extinction Events in Earth History*: 351- 364 Springer-Verlag.

Sheenan P., Fastowsky D., Hoffman G., Berghaus C. & Gabriel D. 1991 - Sudden extinction of the dinosaurs: Latest Cretaceous, Upper Great Plains, U.S.A. *Science,* 254: 835-839.

Smit J., Van Der Kaars W.A. & Rigby J.K. Jr. 1987 - Stratigraphic aspects of the Cretaceous-Tertiary boundary in the Bug Creek area of Eastern Montana, USA. *Mémoires de la Société géologique de France*, N.S. 150: 53-73.

Soler-Gijón R. & De La Peña A. 1995. Fishes from the Cretaceous-Tertiary boundary interval of the Ager basin, Lerida province (Spain). *Terra Nostra*, 65 Jah. Pal.Ges. Tag., Hisdesheim: 73-74.

Soler-Gijón R. & López-Martínez N. 1998 - Sharks and rays (Chondrichthyes) from the upper Cretaceous red beds of the Central Pyrenees (Lleida, Spain): indices of a India-Eurasia connection. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 141: 1-12.

Stets J., Ashraf A.-R., Erben H.K., Hahn G., Hambach U., Krumsiek K., Thein J. & Wurster P. 1996 - The Cretaceous-Tertiary boundary in the Nanxiong basin (continental facies, Southern China). *In* McLeod N. & Keller G. (eds), *Cretaceous-Tertiary mass extinctions. Biotic and environmental changes.* Norton: 349-371.

Tschudy R.H., Pillmore C.L., Orth C.J., Gilmore J.S., Knight J.D. 1984 - Disruption of the terrestrial plant ecosystem at the Cretaceous-Tertiary boundary, Western North America. *Science,* 225: 1030-1032.

Vianey-Liaud M. & López-Martínez N. 1997 - Late Cretaceous dinosaur eggshells from the Tremp basin (Southern Pyrenees, Lleida, Spain). *Journal of Paleontology,* 71 (6): 1157-1171.

Wolfe J.A. 1971 - Tertiary climates fluctuations and methods of analysis of Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 9: 27-57.

Wolfe J.A. & Upchurch G.R.Jr. 1986 - Vegetation, climatic and floral changes at the Cretaceous-Tertiary boundary. *Nature,* 324: 148-152.

Zhao Z.K., Li H.M., Zhao Z. & Yan Z. 1991 - Extinction of the dinosaurs across the Cretaceous-Tertiary boundary in Nanxiong basin, Guandong province. *Vertebrata PalAsiatica,* 29, 2 p.

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