

The palynological record across the Cretaceous–Tertiary boundary in differing palaeogeographical settings from the southern Pyrenees, Spain

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Abstract: North American and Pacific spore-pollen records show a major extinction event at the Cretaceous–Tertiary (K–T) boundary, and abrupt changes are similarly found in many marine organisms world-wide. In contrast, records from the Old World reveal little evidence of terrestrial vegetational change across the boundary. In order to improve the characterization of changes across the K–T boundary, palynological assemblages from two sections in the southern Pyrenees have been evaluated. The abundance and diversity of trilete fern spores are high in Maastrichtian samples and show a statistically significant decrease during the Danian. The ‘fern spike’ of low-diversity spores found elsewhere is not recorded in the Pyrenean region. Minor replacements of taxa across the K–T boundary are also noted, as well as an increase in inaperturate gymnosperm pollen in the Danian. Comparing our two examined sections with one another reveals important differences in angiosperm pollen composition.

Dramatic floral changes have been documented across the Cretaceous–Tertiary (K–T) boundary in the North American and Pacific records. Here, a major extinction event in the plant record, and a sudden, brief increase in fern abundance (the ‘fern spike’), have been correlated with an iridium anomaly related to an extraterrestrial impact at the boundary (Johnson *et al.* 2000; Vajda *et al.* 2001, and references therein). However, the palynological record in the Old World has not yet shown any appreciable changes during this critical period, which hinders the detection of the K–T boundary. Until now, some of the best-documented continuous sections dated by biostratigraphy and magnetostratigraphy across the K–T boundary in Europe and Africa have failed to show any significant palynological changes (Méon 1990, 1991; Médus *et al.* 1988, 1992; López-Martínez *et al.* 1999; Mayr *et al.* 1999). This lack of a clear palynological K–T boundary in the Old World contrasts with the abrupt change observed in the fossil record of many protists (coccoliths, planktonic foraminifera) and metazoans (molluscs, sharks and reptiles).

In the Pyrenean Basin, a thick succession of red beds characterizes the Tremp Formation, which dates from Late Cretaceous to Early Tertiary. Within this succession Ashraf & Erben

(1986) recorded an impoverishment of plant species, which they interpreted as representing the palynological K–T boundary. However, biostratigraphic and magnetostratigraphic dating subsequently demonstrated an older age for this interval – at around the Campanian–Maastrichtian transition (*sensu* Gradstein *et al.* 1995; López-Martínez *et al.* 1999; Ardèvol *et al.* 2000; López-Martínez *et al.* 2001). A decrease in plant diversity is recorded in other Old World regions (Stets *et al.* 1996; Markevitch *et al.* 2000), but this event can be correlated better with the Campanian–Maastrichtian transition than with the K–T boundary. Therefore, no regional events in the Old World Late Cretaceous palynological succession have yet been demonstrably correlated with this boundary.

The apparently smooth transition across the K–T boundary in the palynological record of the Old World may be due to incomplete sampling or to palaeoenvironmental factors. We have therefore studied the palynological record across the boundary in the south central Pyrenees (Spain) by comparing two sections about 50 km apart in differing palaeogeographical settings:

- (1) The Fontllonga section (Lleida, Catalonia) representing upper estuarine deposits with a

sedimentation rate between 10 and 100 m Ma⁻¹ near the K–T boundary (Alvarez-Sierra *et al.* 1994; López-Martínez *et al.* 1998a; Mayr *et al.* 1999).

- (2) The Campo section (Huesca, Aragón), a highly expanded stratigraphic section of marine platform deposits with a sedimentation rate up to 200 m Ma⁻¹ (López-Martínez *et al.* 1998b; Ardévol *et al.* 2000; Fernández-Marrón *et al.* 2000).

Correlating two palynological successions across the K–T boundary from the same region but representing different palaeogeographical settings should help to detect the palaeoenvironmental, climatic and evolutionary factors that affected the plant fossil record during this critical interval.

Geological setting

The south central Pyrenees (Spain) contain a rich geological record across the Cretaceous–Tertiary transition, represented by marine and non-marine deposits from the Aren and Tremp Formations (Fig. 1). Middle Campanian to Palaeocene deposits exceeding 2000 m in thickness are preserved in excellent outcrops. The Aren Formation consists of biocalcarenic and hybrid sandstones from nearshore environments, intercalated with offshore marls and turbidite deposits basinwards (i.e. westwards); its age ranges from Mid-Campanian to Late Maastrichtian. The Tremp Formation consists of red beds and peritidal limestones deposited in coastal and continental settings. The middle part of the formation contains the K–T boundary; its lower part intercalates with the Aren Formation (Ardévol *et al.* 2000; López-Martínez *et al.* 2001).

The Fontllonga and Campo sections are situated in the South Pyrenean Central Unit, which is a complex allochthonous tectonic slab formed by a detached Mesozoic cover thrust over the foreland Ebro Basin. The South Pyrenean Central Unit is made up of several thrust sheets, which have noticeably shortened the original distance between sections. The Fontllonga and the Campo sections are separated by the Montsec thrust anticline (Fig. 1), whose shortening effect has been estimated at least about 17 km (Ardévol *et al.* 2000).

The Fontllonga section (41° 58' N, 0° 51' E), situated on the Ager syncline at Lleida, is located within the Sierras Marginales thrust sheet, which consists of Jurassic, Upper Cretaceous and Palaeogene limestones and sandstones overlying Upper Triassic gypsum. The Tremp

Formation here consists of about 700 m of Campanian to Palaeocene red beds, interpreted as transitional marine/non-marine sediments (paralic deposits) formed in peritidal and upper estuarine palaeoenvironments. Mixed marine and freshwater influence within this red bed succession is attested by tidal sedimentary structures (sigmoidal cross-stratification, mud drapes), remains of marine organisms (the cyanobacterium *Girvanella*, marine dinoflagellates, and the rays *Igdabatis* and *Rhombodus*) and marine bioclastic components within the sandstones (red algae, marine molluscs), remains of terrestrial and lacustrine organisms (dinosaur eggshells, continental ostracodes and molluscs) and isotopic composition (Álvarez-Sierra *et al.* 1994; López-Martínez *et al.* 1998a; Mayr *et al.* 1999).

The Campo section (42° 23' N and 0° 24' E) is located in the Cotiella thrust sheet, formed by Upper Cretaceous and Palaeogene platform limestones, slope breccias, marls and turbidites. Campanian and Maastrichtian deposits here reach more than 2000 m in thickness, formed by turbidites and marls in the lower part, and deltaic sandstones and shelfal calcarenites in the upper part. The overlying red beds equivalent to the lower Tremp Formation consist of a 60-m thick interval comprising red mudstones and sandstones with minor intercalations of black shales and dolostones (Eichenseer 1988; Robador *et al.* 1990). This section is situated in a basinward position relative to Fontllonga. The marine origin of the Campo red beds is attested by the presence of non-reworked dinoflagellates, micro- and macroforaminifera (*Laffiteina bibensis*), autochthonous rudists and a drifted ammonite shell (*Pachydiscus gollevillensis*).

The Cretaceous–Tertiary boundary

The Cretaceous–Tertiary boundary has been located within the middle of the Tremp Formation in the south central Pyrenees, using biostratigraphy (foraminifera, charophytes, rudists, ammonites, vertebrates), magnetostratigraphy and chemostratigraphy. In the Fontllonga section, the K–T boundary occurs within a 1- to 3-m thick lutite interval near the top of a thick sandstone unit correlated with Chron C29r (Galbrun *et al.* 1993). Dinosaur remains are common below this interval but disappear just above it, where a $\delta^{13}\text{C}$ isotopic anomaly indicates a marked change in organic productivity. Vertebrate remains allow this geochemical anomaly to be placed in the earliest Palaeocene (López-Martínez *et al.* 1998a, 1999).

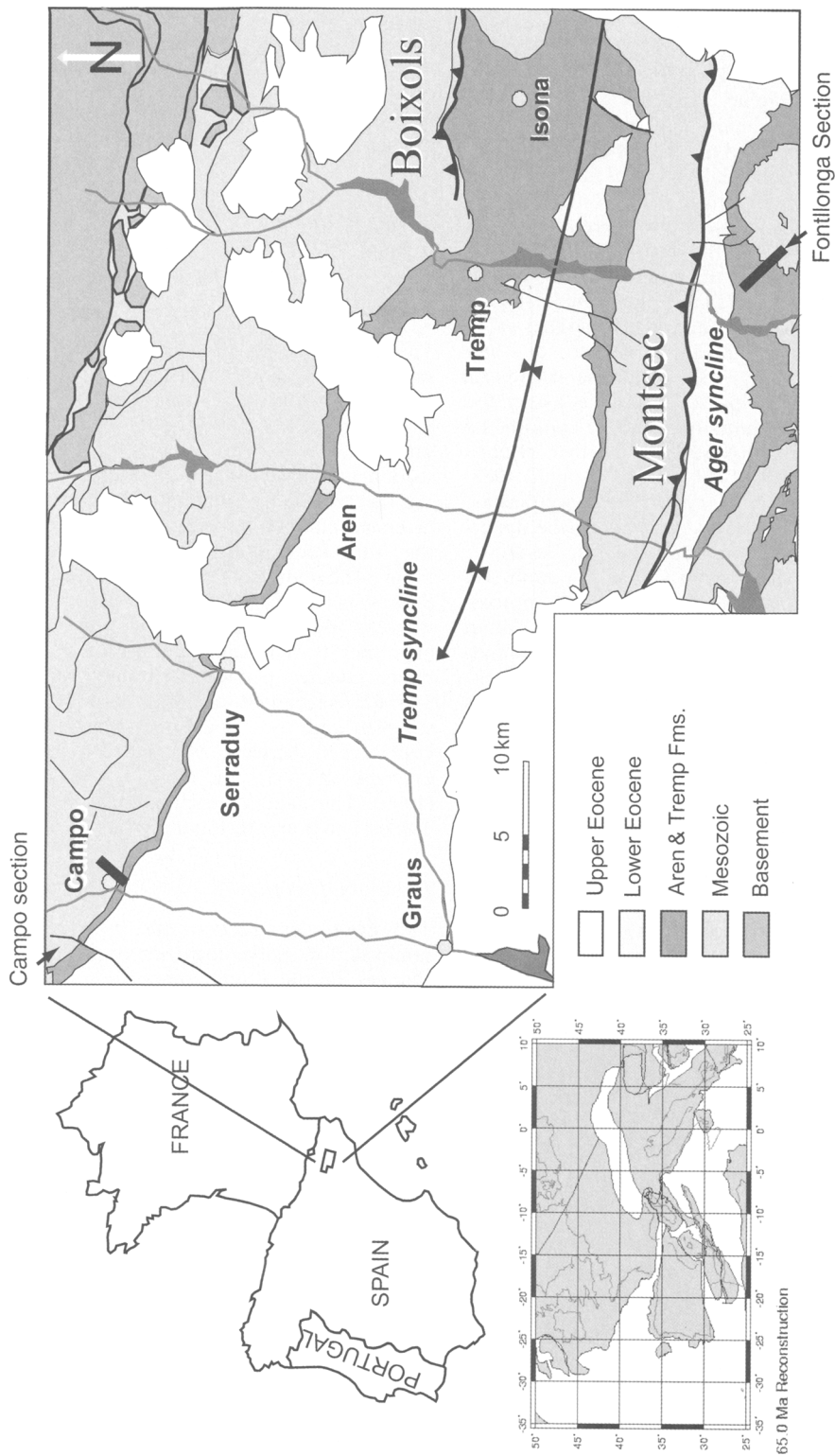


Fig. 1. Geological map of the studied area showing Fontllonga and Campo sections and a palaeogeographical map for the uppermost Maastrichtian-lowermost Palaeocene interval. Plate reconstruction according to http://www.odsn.de/odsn/services/paleomap/adv_map.html.

In the Campo section, stable isotopic analyses have not yet revealed a $\delta^{13}\text{C}$ isotopic anomaly related to the K–T boundary. Preliminary magnetostratigraphic analyses have shown reversed polarity in the uppermost 30 m of the Aren Sandstone and in the 60-m thick lower Tremp Formation (Galbrun *et al.* in press) that is compatible with Chron C29r containing this boundary. Biostratigraphic interpretation relies on the presence of the benthic foraminiferid *Laffiteina bibensis* in the middle part of the red beds. This species has been interpreted as being earliest Palaeocene in age, by Serra-Kiel *et al.* (1998), who used it as a marker for their lowermost Tertiary SBZ-1 biozone. However, in the Campo section this species is associated with rudists and ammonites, which confirms its Cretaceous age as deduced in other regions (Eichenseer 1988; Loeblich & Tappan 1988; López-Martínez *et al.* 1998b). Palaeocene charophyte taxa are reported just above the uppermost rudist- and ammonite-bearing level (Y. Tambareau, pers. comm.). The foraminiferid *Laffiteina bibensis* is observed until approximately 55 m above the base of the Tremp Formation (Fig. 2). Therefore, the K–T boundary in the Campo section can be placed above the highest occurrence of rudists, ammonites and dinosaurs and below the massive carbonate Unit 3 of Danian age, correlated to the middle part of the Tremp Formation and to the Salarons Formation (Eichenseer 1988; Robador *et al.* 1990; Fig. 2). Lithostratigraphic correlation indicates that the K–T boundary can probably be placed within the lower 10 m of this 16-m thick interval, which corresponds with a reversed magnetic polarity interval (Galbrun *et al.* in press; O. Oms, pers. comm.).

In continental sections from the Old World, no iridium anomaly has yet been associated with a K–T boundary level as determined by biostratigraphic methods. The Fontllonga and Campo sections are among the best-calibrated Old World continental sections for this critical period. Although hiatuses across the K–T boundary interval cannot be excluded, they are not likely in either section: the critical interval in both sections lies within a thick reversed magnetic interval correlated with Chron C29r. In the Fontllonga section, the stratigraphic interval correlated with Chron C29r is 35.8 m thick, whereas in the Campo section it exceeds 38 m. The K–T boundary interval in the Fontllonga section is situated within a detrital unit whose sedimentation rate is estimated at about 50 m/Ma^{-1} . The uppermost part of the Chron C29r interval, which is of Tertiary age, corresponds to a limestone unit with palaeosols,

indicating a strong drop in sedimentation rate. For this reason, the K–T boundary lies near the top of the Chron C29r interval in this section (Fig. 2).

The Campo section does not yet have a clearly delimited Chron C29r interval. A hiatus is expected to be present in the Danian part of the section (above CP-13 sample, Fig. 2) because the normal polarity chrons C29n and C28n are lacking.

Palynology

This study analyses data statistically from nine samples of the Fontllonga section (two samples from López-Martínez *et al.*, 1999; six samples from Mayr *et al.*, 1999; and the newly analysed sample #31) and six samples of the Campo section (all newly analysed). Indices employed are the abundance (number of specimens) and diversity (number of species) of spores relative to the total spore–pollen assemblage, excluding fungi. The indices are treated as percentages. Spores include bryophytes, lycopods and ferns; whereas pollen includes gymnosperms and angiosperms. The total number of spores and pollen counted per sample ranges between 29 and 632 specimens (average of 185) for our samples and those of López-Martínez *et al.* (1999), and between 90 and 270 specimens (average of 162) for those of Mayr *et al.* (1999). The data for each sample are given in Tables 1 to 3 and in Figure 3.

Fontllonga section

The Fontllonga section has been repeatedly sampled for palynology in order to detect changes in the floral composition across the K–T boundary (Médus *et al.* 1988, 1992; López-Martínez *et al.* 1999; Mayr *et al.* 1999). The Fontllonga palynological record includes samples from the boundary interval studied by Médus *et al.* (1988), two samples embracing the boundary studied by López-Martínez *et al.* (1999, samples F#32 and F#36) and six samples studied by Mayr *et al.* (1999), three of them from the Maastrichtian (CH-21, CH-25 and CH-26) and three from the Lower Danian (CH-16, CH-27 and CH-20). Mayr *et al.* (1999) included another Danian sample from the neighbouring Figuerola section. These previous studies show only small, fluctuating changes in the palynological succession across the K–T boundary.

In our study we included another palynological assemblage dated as Late Maastrichtian (sample F#31); additional intermediate samples were prepared but did not contain palyno-

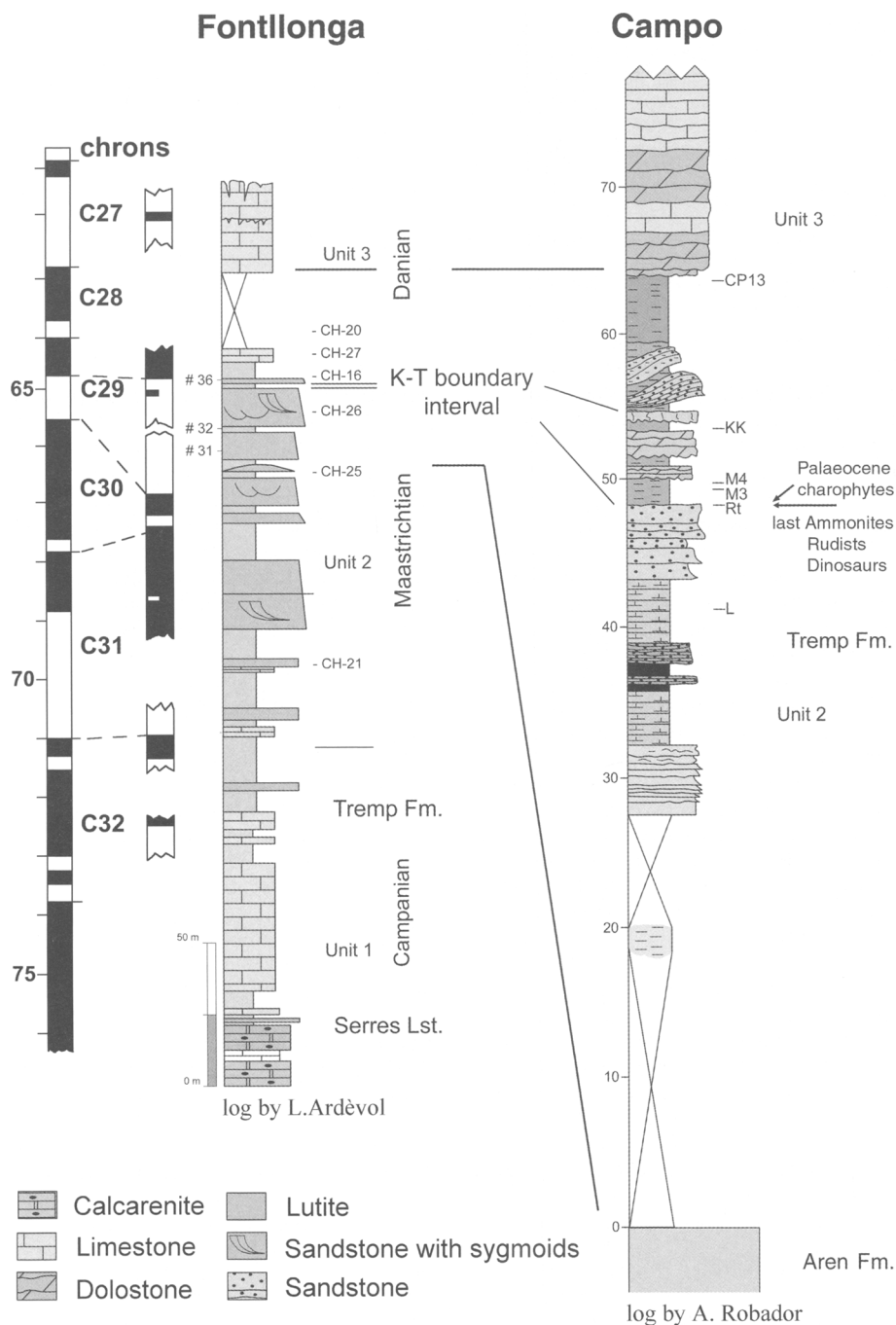


Fig. 2. The position of palynological samples evaluated in the present study. Left, Fontllonga stratigraphic section showing palaeomagnetic polarity and proposed correlation (Galbrun *et al.* 1993; López-Martínez *et al.* 1998a; and Mayr *et al.* 1999). Sample #31 is from the present study, samples #32 and #36 are from López-Martínez *et al.* (1999), and samples CH-16 to CH-27 are from Mayr *et al.* (1999). Right, Campo stratigraphic section corresponding mostly with a reversed polarity chron assumed to be C29r. Lines of correlation to the Fontllonga section are based on sequence stratigraphy and biostratigraphy (Robador *et al.* 1990; Ardevol *et al.* 2000).

Table 1. Comparison of spore frequency (species diversity and relative abundance) in palynomorph assemblages below and above the K–T boundary in the Fontllonga section.

Fontllonga section	Diversity (%)			Abundance (%)			No. of sample
	Max.	Mean	Min.	Max.	Mean	Min.	
Uppermost Maastrichtian	66.7	50.5	40.0	78.7	54.8	30.1	6
Lowermost Danian	50.0	43.1	36.4	48.0	37.0	28.5	4
<i>t</i> -test probability	16.4% (–)			7.3% (–)			

Data from López-Martínez *et al.* (1999), Mayr *et al.* (1999) and new data from this work (see Table 3). (–) not statistically significant.

morphs. The positions of all samples statistically analysed in this paper for the Fontllonga section are shown in Figure 2.

Spores are the main component of the three palynomorph assemblages, and are generally large trilete types: psilate *Leiotriletes* spp. and *Cyathidites* spp., ornamented and thick-walled *Lycopodiumsporites* sp., *Matthesia* spp., *Polypodiaceo* spp. and *Echinatisporites* spp., as well as cingulate *Patellasporites* sp. and taeniate *Cicatricosisporites* sp. spores. The flora was thus dominated by lycopods and ferns, mainly from the Schizaceae, Gleicheniaceae, Cyatheaceae and Polypodiaceae families. Thick-walled spores reach 90–94% of the spore assemblage, indicating the strong influence of locally developed fern forests.

The spores *Biretisporites potoniaei* Delcourt & Sprumont, *Matthesia plurituberosus* Döring and *Triletes tuberculiformis* (Cookson) Dettman, proposed as Cretaceous markers by Asraf & Erben (1986), appear in our Cretaceous assemblage F#31 from Fontllonga. However, Mayr *et al.* (1999) also reported these species from Danian samples in the Fontllonga area.

The predominance of spore diversity and abundance over pollen is particularly high in

the Cretaceous samples, although the difference is not large (Fig. 3). Mayr *et al.* (1999) also reported an increase in trilete spore abundance and diversity within the uppermost Maastrichtian in the Fontllonga section, and interpreted this dominance as indicative of environmental change across the K–T boundary. When all samples are considered, the palynomorph assemblages below this boundary actually show an overall dominance in spores samples above the boundary, but the difference is not statistically significant (a 7% probability of a null hypothesis remains; see Table 1). Both spore diversity and abundance decrease across the K–T boundary, but the difference in the Fontllonga samples is too low and the overlap too high to be significant as a biostratigraphic boundary criterion.

In the Fontllonga section, those samples containing the highest spore abundance (F#32 and CH-25, 71–78%) are very close to the K–T boundary but are not the closest. Older Campanian and Maastrichtian samples from other Pyrenean areas show even higher spore ratios in the palynomorph assemblages, reaching as much as 85.3% diversity and 88.4% abundance (De Porta *et al.* 1985; Ashraf & Erben 1986;

Table 2. Comparison of spore frequency (species diversity and relative abundance) in palynomorph assemblages across the K–T boundary for the combined Fontllonga and Campo sections.

Fontllonga and Campo sections	Diversity (%)			Abundance (%)			No. of samples
	Max.	Mean	Min.	Max.	Mean	Min.	
Uppermost Maastrichtian and K–T boundary interval	74.6	58.6	40.0	80.8	61.6	30.1	11
Lowermost Danian	50.0	44.5	36.4	48.1	37.3	28.5	5
<i>t</i> -test probability	3.5%*			0.07%†			

Data from López-Martínez *et al.* (1999), Mayr *et al.* (1999), Fernández-Marrón *et al.* (2000) and new data from this work (see Table 3).

*Statistically significant.

†Highly significant.

Table 3. *Counts of palynological taxa and specimens from the Fontllonga and Campo sections.*

	Fontllonga										Campo				
	CH21*	CH25*	# 31	# 32	CH26*	# 36	CH16*	CH27*	CH20*	L	Rt	M3	M4	14kk	CP13
Diversity (taxa)	14	21	58	40	18	44	22	23	17	56	19	51	59	26	22
Spores	7	14	27	20	9	16	11	9	8	35	11	29	44	18	11
(trilete)	(6)	(13)	(23)	(18)	(9)	(14)	(9)	(9)	(6)	(33)	(11)	(24)	(43)	(18)	(10)
Gymnosperms	2	2	6	4	2	6	2	1	1	6	3	7	5	4	7
(inaperturate pollen)	(0)	(1)	(1)	(2)	(1)	(3)	(1)	(1)	(1)	(4)	(2)	(5)	(2)	(1)	(4)
Angiosperms	5	5	25	16	9	22	9	13	8	15	5	15	10	4	4
(Normapollens)	(1)	(1)	(8)	(5)	(2)	(6)	(2)	(4)	(3)	(2)	(1)	(1)	(1)	(0)	(0)
Abundance	93	239	91	552	128	632	142	270	96	80	29	82	90	64	39
Spores	28	188	40	396	68	304	41	80	38	55	17	51	71	50	15
(trilete)	(28)	(177)	(34)	(378)	(61)	(287)	(36)	(78)	(34)	(53)	(17)	(45)	(70)	(50)	(14)
Gymnosperms	20	17	15	46	4	76	18	21	25	9	6	11	8	7	18
(inaperturate pollen)	(0)	(12)	(2)	(8)	(1)	(19)	(17)	(18)	(25)	(7)	(3)	(9)	(4)	(1)	(11)
Angiosperms	45	34	36	110	56	252	83	165	33	16	6	20	11	7	6
(Normapollens)	(2)	(12)	(18)	(95)	(15)	(114)	(12)	(18)	(8)	(2)	(1)	(1)	(1)	(0)	(0)

Counts for those samples indicated by an asterisk (*) are calculated from Mayr *et al.* (1999, tables 1 and 2) excluding fungal and algal remains and dinoflagellate cysts.

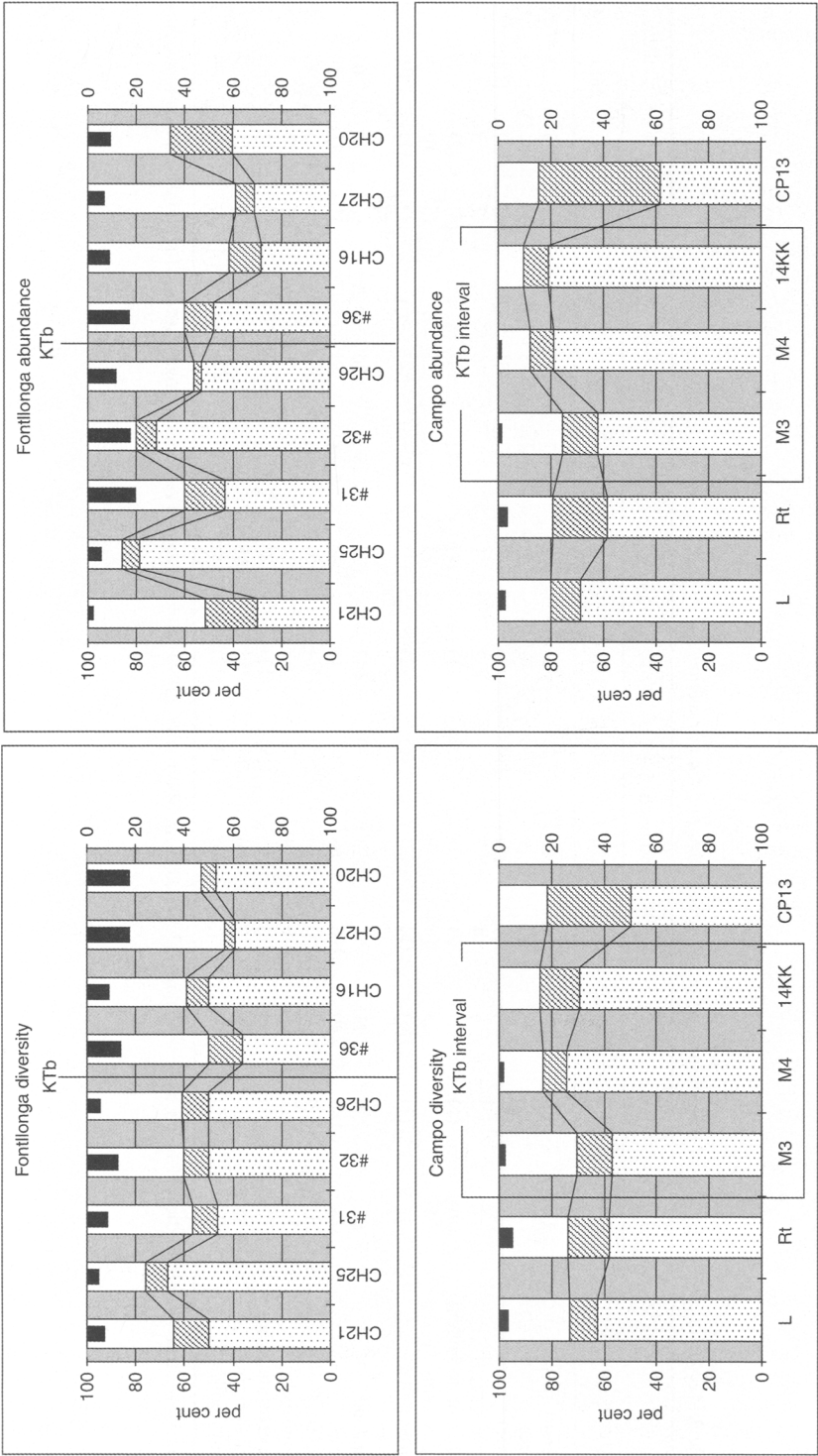


Fig. 3. Diagrams showing spore and pollen abundance and diversity. Spores, dotted; gymnosperm pollen, hatched; angiosperm pollen, white; Normapolles, black, inversely coded.

Médus *et al.* 1988). Therefore, during latest Cretaceous times, the Pyrenean region was already dominated by ferns, which increases the difficulty in detecting a fern spike similar to those reported for North America and New Zealand just above the K–T boundary (Fleming & Nichols 1990; Vajda *et al.* 2001).

Gymnosperms are a minor component of the palynomorph assemblages in the Fontllonga section, reaching about 10% of the total diversity and abundance. Cupressaceae–Taxodiaceae and Cycadaceae are the main components, the Pinaceae being extremely rare both in uppermost Cretaceous and Palaeocene samples. Samples studied by Mayr *et al.* (1999) around the K–T boundary in the Fontllonga section also show a very similar gymnosperm ratio and composition. A proposed increase in Pinaceae abundance after the boundary as a biostratigraphic criterion in the Fontllonga section (Médus *et al.* 1992) can therefore be excluded. The frequency of bisaccate pollen is often related to taphonomic factors, and in marine samples is extremely sensitive to the distance of the sample location from shore.

The pollen composition in the Fontllonga section shows a major angiosperm component, reaching more than 40% of the total spore–pollen assemblage. A diverse angiosperm flora includes: *Tricolpopollenites* sp., *Polycolpites* sp., *Rugulitriporites* sp., *Subtriporopollenites* sp., *Triporopollenites* spp., *Polyporopollenites* sp., *Triatriopollenites* sp., etc. The Normapolles group (*Trudopollis* sp., *Vacuopollis* sp., *Semioculopollis* sp., *Nudopollis* sp.) is an important component, comprising about 12% of the total assemblage diversity and 18% of the abundance, although Mayr *et al.* (1999) reported a lower Normapolles abundance and diversity (lower than 10%). The Normapolles *Pseudoromeinipollenites* cf. *paleocenicus* occurs only in Tertiary samples from Fontllonga, according to our results and those of Mayr *et al.* (1999). This species may be characteristic of the European Tertiary and different from Cretaceous forms attributed to the same genus by Médus (1986) and Médus *et al.* (1988).

Campo section

In order to obtain the highest resolution record possible across the K–T boundary, the more expanded Campo section has been chosen to explore the palynological pattern of plant change. Chron C29r containing the boundary may here span more than 90 m in thickness, compared with around 50 m in the Fontllonga section. Moreover, the grey–black shale and

clay-dominated deposits of the K–T transition in the Campo section are more favourable to continuous deposition and palynomorph preservation than in the Fontllonga section, where an amalgamation of channel sandstones correlated to Chron C29r presumably contain stratigraphic hiatuses.

The red-bed interval in the Campo section has yielded six significant palynological assemblages among the numerous studied samples. Two (samples L and Rt) correspond with the uppermost Maastrichtian levels containing *Laffiteina bibensis*, rudists and ammonites; three samples above them (M3, M4 and KK) correspond to a 10-m thick interval where the K–T boundary can probably be situated; and the highest analysed sample (CP-13) is considered Tertiary in age because of its close proximity to the Danian limestone unit (Fig. 2).

The total diversity in the Campo samples is similar to that in Fontllonga (an average of about 40 v. 47 taxa per sample), in spite of fewer specimens counted (66 v. 425 average specimens per sample respectively). However, the variance between samples is much more important in the Campo section (standard deviation 18.4 v. 9.4). The dominance of spores over pollen in the Campo samples, both in diversity (50% spore taxa on average) and abundance (65% spore specimens on average), is even stronger than in the Fontllonga section (44% and 54% respectively) (Fig. 3). We note the lack of cingulate and tenate spores in Campo, which are present in Fontllonga.

The trilete spore species *Biretisporites potoniei* Delcourt & Sprumont, *Cyathidites minor* Couper, *Lycopodiumsporites austroclavatidites* (Cookson) Potonié, *Matthesia sporites plurituberosus* Döring and *Polypodiaceisporites potoniei* (Potonie & Gelletich) Kedves, which are restricted to the Maastrichtian according to Asraf & Erben (1986), occur in the lowermost five spore assemblages analysed from the Campo section and are absent from the Danian sample CP-13. However, three of these taxa are reported by Mayr *et al.* (1999) in the Danian samples from Fontllonga (see above). More sampling is necessary to confirm that at least two of these forms were extinct after the K–T boundary.

The previously noted increased spore–pollen ratio below the K–T boundary at Fontllonga is also seen in assemblages from the K–T boundary interval in the Campo section, which may be chronologically closer to the boundary than those from the Fontllonga section (Fernández-Marrón *et al.* 2000). The Upper Maastrichtian L and Rt assemblages reach around 60–70% in spore diversity and abundance; the spore ratio

noticeably rises in the M4 and KK samples (around 70–75% diversity and 80% abundance), and decreases to 40–50% in the Danian CP-13 assemblage.

Gymnosperms are hardly more abundant in the Campo assemblages than in those of Fontllonga. We record three to seven taxa per sample with 9–20% average abundance. Only the Danian sample CP-13 shows a massive presence of gymnosperms, mainly *Inaperturopollenites* sp. (up to 32% diversity and 46% abundance, Fig. 3). This pollen form is present in all samples as well as *Araucariacites* sp. and pollen related to the Cycadophyta. Bisaccate pollen are rare. In all of the Campo samples, angiosperms are poor, both in diversity (average 22%) and abundance (17%), in relation to the total spore–pollen assemblage (Fig. 3). The pollen genus *Subtriporopollenites* which is represented by several species, together with *Triatriopollenites* sp. and *Polycolpites* sp., are the only significant components, whereas the Normapolles presence is insignificant (average 2% diversity and less than 1% abundance). Hence, the angiosperm pollen frequency from the Campo succession differs strongly from that of Fontllonga, this difference being statistically highly significant in both diversity and abundance (null hypothesis probability $p=0.0002$ and $p=0.002$ respectively, according to the t-test).

Both angiosperm and Normapolles frequencies decrease upwards in the Campo palynological succession, although the numbers of specimens counted in the youngest samples are not yet large enough to be conclusive. The extraordinarily low percentage of Normapolles in the Campo samples (less than 1% of about 400 counted specimens) seems related to a very low representation of angiosperms, and not to a replacement by modern-type angiosperms which is a long-term trend across the Cretaceous–Tertiary transition (López-Martínez *et al.* 1999). However, the Normapolles decline needs to be fully validated before being considered a reliable signal (see below).

Comparison between sections

When palynological samples from both the Fontllonga and Campo sections are considered together, the observed changes in spore–pollen ratio across the K–T boundary show a consistent pattern. The difference in spore–pollen ratio becomes reinforced and statistically significant or highly significant (Table 2). On average, the spore–pollen ratio across the K–T boundary falls from 59% diversity and 62% abundance, to 45% diversity and 37% abundance. Sample CP-

13 from Campo closely fits the ratio of Tertiary samples from the well-dated Fontllonga section, which supports its Danian age. The three samples from the Campo K–T boundary interval are similar to those from the Cretaceous, although the boundary itself cannot yet be confidently placed in relation to them.

The spore occurrence pattern in the Campo section shows good correlation between diversity and abundance peaks (correlation coefficient $r=0.93$), indeed a much better correlation than at Fontllonga ($r=0.58$) and also better than at other Pyrenean localities (La Posa and Coll de Nargó, $r=0.87$) (calculated from data in De Porta *et al.* 1985 and Ashraf & Erben 1986). In contrast, the North American fern spike shows a high spore abundance with low diversity (Tschudy *et al.* 1984). The two New Zealand sections which document the fern spike differ, but both show a relatively high spore diversity, that includes both ground and tree ferns, for a duration of 30 000 years (Vajda *et al.* 2001).

The unusual composition of gymnosperms from the Campo Tertiary sample shows some similarities with a Danian sample from the Figuerola section, near Fontllonga, in having an unusually high abundance of inaperturate pollen (Mayr *et al.* 1999). The New Zealand record also documents a gymnosperm-rich period during the Early Danian, lasting more than 1 Ma after the fern spike and revealed by dominance of the conifer pollen *Phyllocladidites* (Vajda *et al.* 2001).

In contrast to the relatively rich and diverse angiosperms characterizing the Fontllonga assemblages, with Normapolles pollen comprising about half of the specimens, the low representation of Normapolles and other angiosperm pollen close to the K–T boundary in the Campo section could be considered a palaeoenvironmental signal, indicating a regressive step in the vegetation successional sequence. The frequency of angiosperms is usually a rather consistent indicator in palynological composition. However, the Normapolles frequency in other Pyrenean palynological studies seems to be highly unstable when comparing data from different authors for the same localities. For example, our Normapolles frequencies in the Fontllonga samples (17–19% of a total of 1700 spores and pollen) are significantly higher than those for the same part of the section studied by Mayr *et al.* (1999) (5–11% of up to 1455 spore and pollen), in spite of good general agreement between both palynological studies. Also in La Posa grey marl samples (latest Campanian, lower Tremp Formation, Isona, Lleida), the Normapolles reach around 20% of species.

diversity according to De Porta *et al.* (1985), but only 1.4% according to Ashraf & Erben (1986). These differences cannot be explained by random sampling effects or palaeoenvironmental factors, since the samples came from the same parts of the same section. The possibility that preparation techniques may affect the Normapolles frequency is another factor that needs to be studied. Meanwhile, we do not consider the Normapolles frequency to be a reliable signal in our analysis.

Conclusions

Palynological changes across the K–T boundary in the south central Pyrenees have been portrayed in previous studies as following a smooth transition, with minor vegetational fluctuations linked to local palaeoenvironmental factors. We have re-evaluated a previously published palynological succession from the best time-constrained section, at Fontllonga, and have analysed an additional sample. New palynological data have also been collected from the highly expanded Campo section, situated in a more paralic environment and a palaeogeographical position more distal relative to the shoreline.

Our results lead to a better characterization of the palynological K–T boundary. The most noticeable pattern in plant changes across this boundary in the Pyrenean realm is the increase in trilete spores during the latest Maastrichtian and K–T boundary interval assemblages, and its decrease in the Danian assemblages. In our study, this pattern previously observed in the Fontllonga sections and in some localities in the south of France (Médus *et al.* 1988; López-Martínez *et al.* 1999; Mayr *et al.* 1999; Fernández-Marrón *et al.* 2000) has been reinforced by showing that this difference is statistically highly significant, and by verifying the same pattern in the highly expanded Campo section. In the Pyrenees, a long interval, from uppermost Maastrichtian to the K–T boundary interval, is characterised by taxonomically diverse as well as abundant trilete spores. This contrasts with the short-duration fern-spike at the K–T boundary in North America and New Zealand, where an abrupt increase in ferns represents a low-diversity assemblage comprising the monolete form genus *Laevigatosporites* or the trilete form genus *Cyathidites*, respectively (Sweet *et al.* 1999; Vajda *et al.* 2001). It is therefore likely that the fern increase in our study is driven by different causal mechanisms from those of the fern spike in North America and New Zealand.

There are no noticeable extinctions across the K–T boundary in the studied sections. Several biostratigraphic criteria previously proposed for delimiting the boundary need to be modified or rejected. The spore species *Cyathidites minor* Couper, *Lycopodiumsporites austroclavatidites* (Cookson) Potonié, and *Polypodiaceosporites potoniei* (Potonié & Gelletich) Kedves are recorded below and above the K–T boundary, whereas *Biretisporites potoniei* Delcourt & Sprumont, *Matthesisporites plurituberosus* Döring and *Trilites tuberculiformis* (Cookson) Dettman, which are only found in our Cretaceous assemblages, have nevertheless been reported from Danian samples by Mayr *et al.* (1999). All these species were proposed as Cretaceous markers by Asraf & Erben (1986). An increase in bisaccate pollen after the K–T boundary is not observed and its fluctuations are not recommended as biostratigraphic criterion (Médus *et al.* 1992). The decrease in Normapolles abundance around the boundary (López-Martínez *et al.* 1999) is also a flawed criterion, since its fluctuations are based on unstable observations. *Pseudoromeiniipollenites* cf. *paleocenicus*, if distinguishable from its Cretaceous relatives, would be a biostratigraphically significant newcomer after the K–T boundary.

The increase in frequency of spores across the K–T boundary is better marked in the Campo section, where two fern-rich samples from the K–T boundary interval show extremely low proportions of angiosperm pollen. Following this increase in spores, two Tertiary samples from both sections show an unusual abundance in inaperturate gymnosperm pollen. This pattern in the palynological succession across the K–T boundary is similar to that from other regions where a fern spike has been documented. This correlation would imply that the youngest spore-rich samples from Campo could already correspond with the earliest Tertiary. This hypothesis can be tested by geochemical analyses across this palynologically constrained K–T boundary interval.

Funds were provided by projects PB98-0813 and BTE2002-01430 of the Spanish Ministerio de Educación and Ministerio de Ciencia & Tecnología. We acknowledge the help of project members from Barcelona (UAB), Bilbao (UPV), Madrid (UCM), Rome (La Sapienza) and Salamanca Universities, the Spanish Geological Survey (IGME), Institut d'Estudis Ilerdençs (IEI), Geoplay (Trempe, Lleida) and the villagers of Pallars Jussà (Catalonia) and Ribagorza (Aragón). We are also grateful to D. J. Nichols (US Geological Survey, Denver) and A. Sweet (Geological Survey of Canada, Calgary) for their helpful reviews of the manuscript, and especially to M. J. Head (Denart-

ment of Geography, University of Cambridge) for his very careful editorial work.

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