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# Differential accumulation of miospores in Upper Miocene sediments of the La Cerdaña basin (eastern Pyrenees, Spain)

Eduardo Barrón [a,*], María José Comas-Rengifo [b]

[a] *Museo Geominero, Instituto Geológico y Minero de España (IGME), Ríos Rosas 23, 28003 Madrid, Spain*
[b] *Departamento de Paleontología, Facultad de Ciencias Geológicas (UCM), José Antonio Novais 2, 28040 Madrid, Spain*

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**Abstract**

The Upper Miocene basin of La Cerdaña (eastern Pyrenees, Spain) is characterised by siliciclastic sedimentation in alluvial, fluvial, deltaic, and lacustrine depositional settings. The lacustrine deposits in the southwestern part of the basin show intercalations of levels rich in organic matter linked to plant accumulations. The differential accumulation of miospores in this part of the basin is due to the intrinsic features of the miospores themselves and of their producers, and extrinsic factors such as the palaeoecology of the miospore producers and the characteristics of the depositional setting. The features of the miospore assemblages and the factors that produced their accumulation are analysed. The proportions of the different miospores in the studied assemblages showed that their accumulation occurred differently in the various lake sediments; this agrees well with a NE–SW running Neves effect. This latter effect is mainly a result of the type of transport the miospores underwent, which was influenced by the vegetation and climate, the structure of the lake, and other phenomena such as fires. The sediments from swampy areas were characterised by high percentages of local and extra-local miospores of parautochthonous and allochthonous nature, whereas those from deepwater areas showed mainly extra-local and regional miospores. The means by which the miospores were preserved in the different lithologies of the La Cerdaña basin are analysed. ***To cite this article: E. Barrón, M.J. Comas-Rengifo, C. R. Palevol 6 (2007).***


**Résumé**

**Accumulation différentielle des miospores dans les sédiments du Miocène supérieur du bassin de Cerdagne (Est des Pyrénées, Espagne).** Le bassin de Cerdagne (Est des Pyrénées, Espagne), daté du Miocène supérieur, est caractérisé par une sédimentation silicoclastique où dominent les dépôts alluviaux, fluviatiles et deltaïques. Les dépôts lacustres, riches en matière organique et incluant des restes végétaux, se sont déposés au sud-ouest du bassin. Une accumulation différentielle des miospores est essentiellement due à la coexistence de facteurs intrinsèques (caractéristiques de la miospore et de son producteur) et extrinsèques (paramètres environnementaux). Les différents assemblages de miospores fossiles ainsi que les facteurs qui ont déterminé leur accumulation dans les sédiments lacustres du Miocène supérieur de Cerdagne sont analysés dans ce travail. La concentration pollinique des différents niveaux étudiés révèle une accumulation différentielle dans les sédiments lacustres, en accord avec l'effet Neves, orienté NE–SW. Cet effet est lié au type de transport des miospores, à la végétation et au climat, à la structure du lac et à la fréquence d'événements tels que les incendies. Ainsi, les sédiments

* Corresponding author.
*E-mail address:* e.barron@igme.es (E. Barrón).

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provenant de zones marécageuses sont caractérisés par des pourcentages élevés en miospores locales et extra-locales à caractère para-autochtone et allochtone, alors que les sédiments provenant d'eaux profondes révèlent principalement des miospores extra-locales et régionales à caractère allochtone. La préservation des miospores provenant des différentes lithologies rencontrées dans le bassin de Cerdagne a également été analysée. ***Pour citer cet article : E. Barrón, M.J. Comas-Rengifo, C. R. Palevol 6 (2007).***


*Keywords:* Palynology; Taphonomy; Thanatocoenosis; Neves Effect; Upper Miocene; La Cerdaña basin; Spain

*Mots clés :* Palynologie ; Taphonomie ; Thanatocénose ; Effet Neves ; Miocène supérieur ; Bassin de Cerdagne ; Espagne

## 1. Introduction

A fossil plant assemblage is an accumulation of plant parts derived from one or more individuals entombed within a volume of sediments laid down under essentially common conditions [64]. The composition and structure of plant fossil assemblages are the result of a combination of biological features (the type, size, shape, number, and composition of their remains), taphonomic factors (transport, degradation, and diagenesis), and ecological patterns (community composition and structure). Thus, a plant assemblage may differ significantly from the plant community from which it was derived [30].

The pollen and spore walls of plants are composed of sporopollenin, a complex polymer of carotenoids and carotenoid esters [21]. This compound is remarkably resistant to degradation (although it eventually decays in aerobic conditions via oxidative processes) [28,36,37]. Miospores (*sensu* Guennel [35]) can therefore accumulate in abundance and are preserved in an essentially unaltered state (duripartic preservation *sensu* Schopf [63]) in a variety of materials, from which they can be recovered and identified.

Lake bottoms with anoxic waterlogged sediments are one of the best environments for miospore preservation [40]. In such places, large numbers accumulate and fossilize, and they are easy to extract for study. Their accumulations also provide information about the organization and distribution of the sediments in lacustrine basins, and therefore of the environmental conditions that existed at the time of their formation.

Owing to its richness in preserved phytocoenoses, the palaeobotany of the lacustrine rocks of the La Cerdaña basin has been known since the 19$^{th}$ Century [9,44,47,58]. These rocks contain huge quantities of well-preserved miospores that represent mixed mesophytic mountainous and subtropical forests [9,18]. The first palynological studies were carried out in the 1950s [41] and have continued until the present day [7,9,18,46].

The main aim of the present work was to describe the different miospore accumulations (thanatocoenoses; *sensu* Ochev [50]) in the Upper Miocene lacustrine rocks of the La Cerdaña basin. The results complement existing knowledge of the basin's plant taphonomy [8–10,44,46].

## 2. Geological setting

The La Cerdaña basin is one of the small basins that formed during the Neogene in connection with a series of NE–SW- and east–west-running fractures [23,62] in the Axial Zone of the eastern Pyrenees. At its southeastern edge, it is bound by the La Têt Fault, and by another large, normal east–west-running fault that separates Tertiary from Palaeozoic materials (Fig. 1). The northeastern margin is more irregular, and corresponds basically to an unconformity [59,62]. This imparts a very asymmetric shape to the basin. Towards the southeast, the Neogene materials attain a thickness of up to 1000 m [23,42,56]. Two depositional units have traditionally been distinguished within these predominantly siliciclastic materials, each presenting a very different spatial distribution. These correspond to two stages in the evolution of the Neogene basin, in which tectonics and sedimentation played significant roles [6,23,60,62]. The Lower Unit, which comprises the oldest (Vallesian; Upper Miocene) sediments is responsible for the majority of the present outcrops in the basin, while the Upper Unit, which at its base is Turolian in age [1], is represented only at the southern end of the basin. A clear change in lithology occurs between these two units [61], and the detritic components of their rocks are quite different in character. This is a consequence of an important alteration in the origin of the sediments that continue to fill the basin.

This paper concentrates on the analysis of the miospore associations identified in the Lower Unit materials (400–800 m), a thick succession of alluvial, fluvial, deltaic, and lacustrine sediments [2,42,59].

The Puigcerda sub-basin, situated to the north (Fig. 1), is dominated by alluvial fans and fluvial plains that change distally to deltaic-palustrine facies and finally to lacustrine facies [23]. The southern part of this sub-basin is dominated by the sedimentation of sandstones, lutites rich in organic material, and lignite beds. This part of the sub-basin is home to the localities of Sanavas-

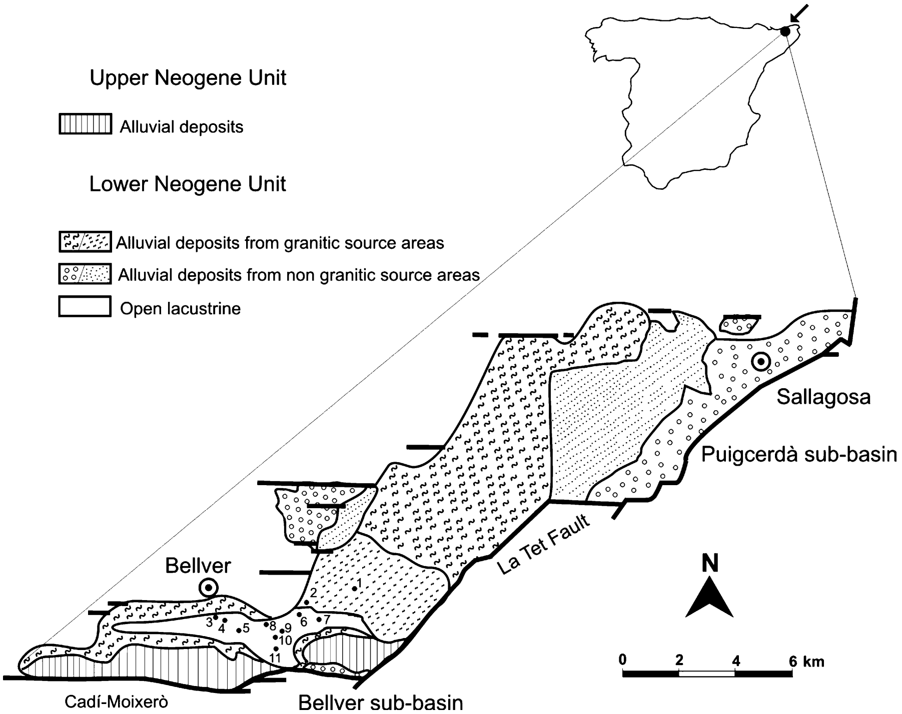


Fig. 1. Geological context of La Cerdaña basin modified from Roca [61]. The location of the studied outcrops is shown. (1) Opencast Sanavastre lignite mine. (2) Opencast Sampsor lignite mine. (3) Bellver de Cerdanya outcrop. (4) Barranc de Salanca outcrop. (5) Torrent de Vilella outcrop. (6) Coll de Saig outcrop. (7) Prats outcrop. (8) Riu de Santa María outcrop. (9) Baltarga outcrop. (10) Beders outcrop. (11) Torrent de la Bavosa outcrop.
Fig. 1. Contexte géologique du bassin de Cerdagne, modifié d'après Roca [61]. La localisation des affleurements est signalée. (1) Mine de lignite à ciel ouvert de Sanavastre. (2) Mine de lignite à ciel ouvert de Sampsor. (3) Gisement de Bellver de Cerdanya. (4) Gisement de Barranc de Salanca. (5) Gisement de Torrent de Vilella. (6) Gisement de Coll de Saig. (7) Gisement de Prats. (8) Gisement de Riu de Santa María. (9) Gisement de Baltarga. (10) Gisement de Beders. (11) Gisement de Torrent de la Bavosa.

tre (SAN) and Sampsor (SAM), which were studied by Barrón [9,11,12] (Figs. 1 and 2). The palustrine-deltaic character of the materials in this area provides an interesting succession of miospore associations, which can be readily studied.

The sub-basin of Bellver, situated to the south, is dominated by a very uniform lacustrine sedimentation of highly laminated diatomites and lutites rich in organic materials. At certain points, there is a well-preserved palaeofauna, including insects [14]. The remaining localities studied (Figs. 1 and 3) lie in this sub-basin, in which all the possible productive levels (from a palynological point of view) were sampled. It is difficult to establish precisely the stratigraphic position of the levels studied, due to the difficulty in finding continuous outcrops; the stratigraphic successions of Roca [61,62] and Martín-Closas et al. [46] were therefore taken into account. To facilitate the analysis of the palynological successions, the localities were grouped into two sectors according to the distribution of the facies in the sub-basin. The eastern sector included the outcrops of Coll de Saig (COL), Prats (PRAT), Riu de Santa María (RIU), Baltarga (BAL), Beders (BED), and Torrent de la Bavosa (TOB), while the western sector included Bellver de Cerdanya (BEL), Barranc de Salanca (BAR), and Torrent de Vilella (TOV). The eastern outcrops were related to the fan delta facies, while those of the west corresponded to the more distal sediments of the lake.

## 3. Material and methods

Twenty-two samples from the Sanavastre open cast lignite mine were examined, along with 31 samples from the Sampsor open cast lignite mine (Fig. 2), and 30 from different outcrops containing diatomites (Fig. 3).

Samples were prepared following the standard palynological technique [16] based on acid treatment (HCl, HF, $HNO_3$) at high temperature. Residues were sieved through 500-, 250-, 75-, 50- and 10-μm sieves. Slides were mounted in glycerine jelly. Some 500–1000 palynomorphs (on up to four slides) were identified per sample to determine the species ratios. The miospore concentration was calculated using the formula proposed by Cour [26].

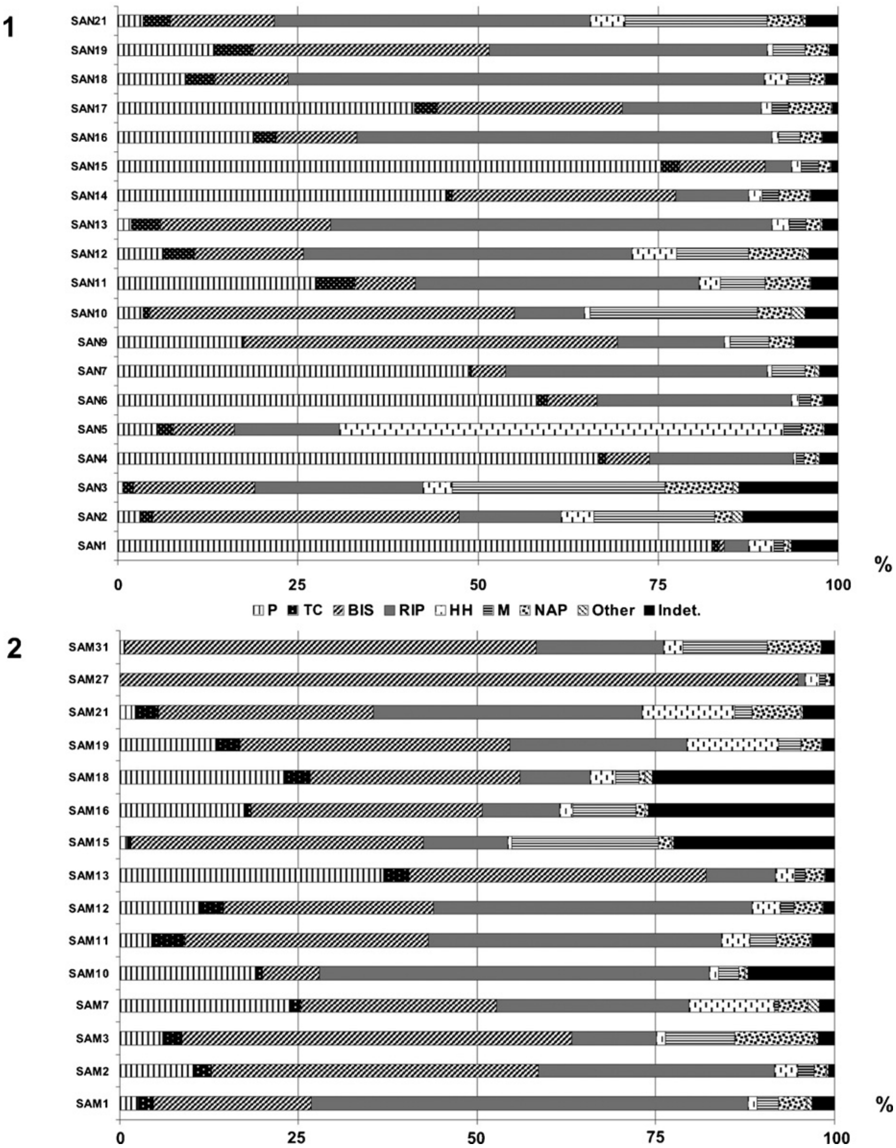


Fig. 2. Proportions of the different palynological groups in the La Cerdaña basin at (1) the Sanavastre mine (SAN), (2) the Sampsor mine (SAM).
Fig. 2. Pourcentages des différents groupes palynologiques définis pour le bassin de Cerdagne : (1) mine à ciel ouvert de lignite de Sanavastre (SAN), (2) mine à ciel ouvert de lignite de Sampsor (SAM).

To study the different accumulations of spores and pollen in the Vallesian rocks of the La Cerdaña basin, nine palynological groups of miospores were taken into account according to their bio- and ecological characteristics: (*i*) pteridophytes (P): trilete and monolete spores; (*ii*) Taxodiaceae-Cupressaceae (TC); (*iii*) bisaccate pollen grains (BIS): pollen of conifers such as *Abies*, *Cathaya*, *Picea*, *Pinus* (Fig. 4.5); (*iv*) riparian trees (RIP), numerically dominated by *Alnus* pollen (Fig. 4.7); (*v*) hydro-hygrophilous (HH): pollen of herbaceous plants from aquatic and shoreline areas such as *Potamogeton*, *Trapa* (Fig. 4.13), *Sparganium* (Fig. 4.11), and Nymphaeaceae; (*vi*) non-riparian mesophytic trees (M), pollen of deciduous trees such as *Fagus*, *Carpinus*, *Carya*, *Quercus* (Fig. 4.14), and *Tilia* (Fig. 4.9), which were not directly associated with the lake shore; (*vii*) herbs (NAP): pollen of non-riparian and non-aquatic herbs such as *Saxifraga* (Fig. 4.8), Apiaceae (Fig. 4.6), Caryophyllaceae, Asteraceae; (viii) 'other miospores'; all those remaining that were identifiable, including pollen grains of taxa such as *Engelhardia* (Fig. 4.12), Arecaceae and Sapotaceae, which could not be included in other groups because of their ecological preferences); and finally (*ix*) unidentified pollen grains. Figs. 2 and 3

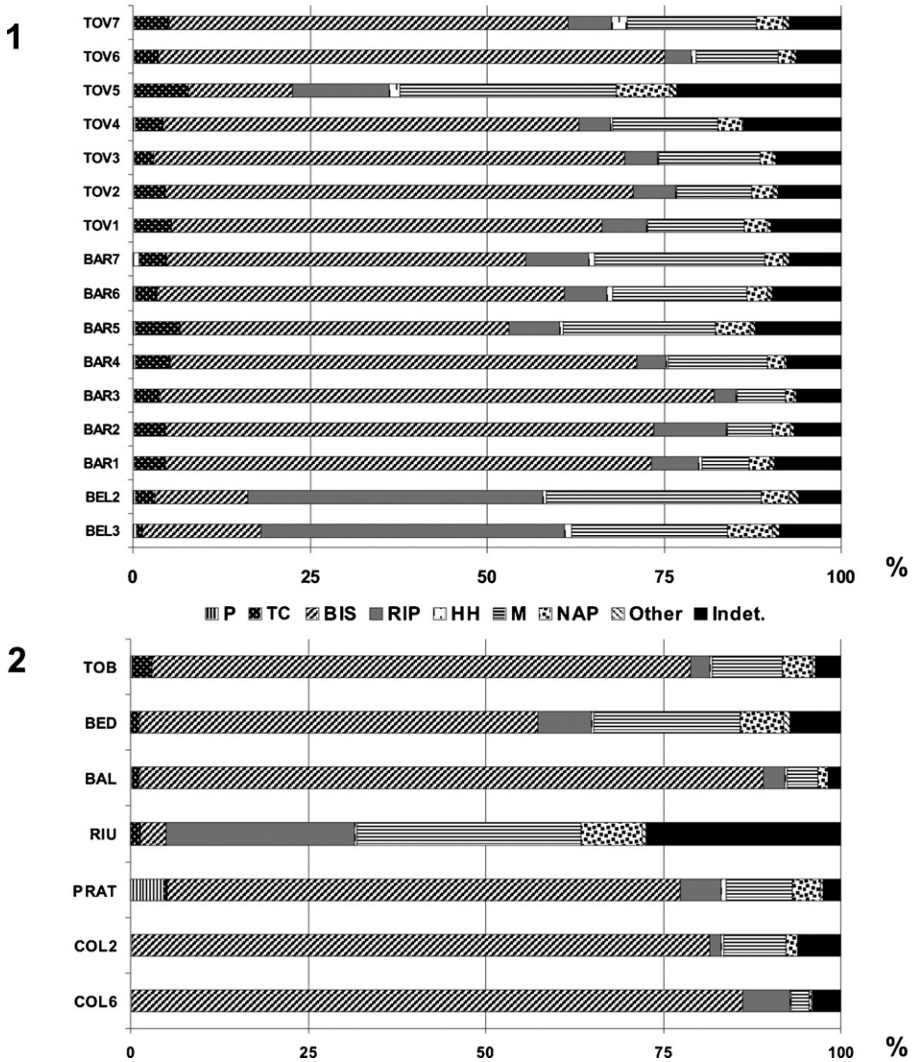


Fig. 3. Proportions of the different palynological groups in the La Cerdaña basin. (1) Western lacustrine sector. BEL: Bellver de Cerdanya outcrop, BAR: Barranc de Salanca outcrop, TOV: Torrent de Vilella outcrop. (2) Eastern lacustrine sector. COL: Coll de Saig outcrop, PRAT: Prats outcrop, RIU: Riu de Santa María outcrop, BAL: Baltarga outcrop, BED: Beders outcrop, TOB: Torrent de la Bavosa outcrop.

Fig. 3. Pourcentages des différents groupes palynologiques définis pour le bassin de Cerdagne. (1) Secteur lacustre ouest. BEL : Affleurement de Bellver de Cerdanya ; BAR : affleurement de Barranc de Salanca ; TOV : Affleurement de Torrent de Vilella. (2) Secteur lacustre est. COL : affleurement de Coll de Saig ; PRAT : affleurement de Prats ; RIU : affleurement de Riu de Santa María ; BAL : affleurement de Baltarga ; BED : affleurement de Beders ; TOB : affleurement de Torrent de la Bavosa.

show the proportions of these palynological groups for each sedimentary level.

## 4. Results

### *4.1. Palynology of the deltaic outcrops*

The palynological study of 22 levels of the Sanavastre mine led to the identification of 19 assemblages with more than 300 specimens per sample [9,12]. P, BIS, RIP, and HH were the best represented groups (Fig. 2.1). The mean miospore concentration was $579 \times 10^3$ grains/g of rock.

The Sampsor mine (Fig. 4.1) had 15 levels that yielded statistically representative assemblages [9,11]. The groups identified were the same as those in the Sanavastre mine, although HH was always in proportions below 12% (Fig. 2.2). The mean miospore concentration in this mine was $387 \times 10^3$ grains/g of rock. The proportions (and therefore the ratios) of the different palynological groups in the rocks of these mines were not related to any particular lithology: P, BIS, and RIP

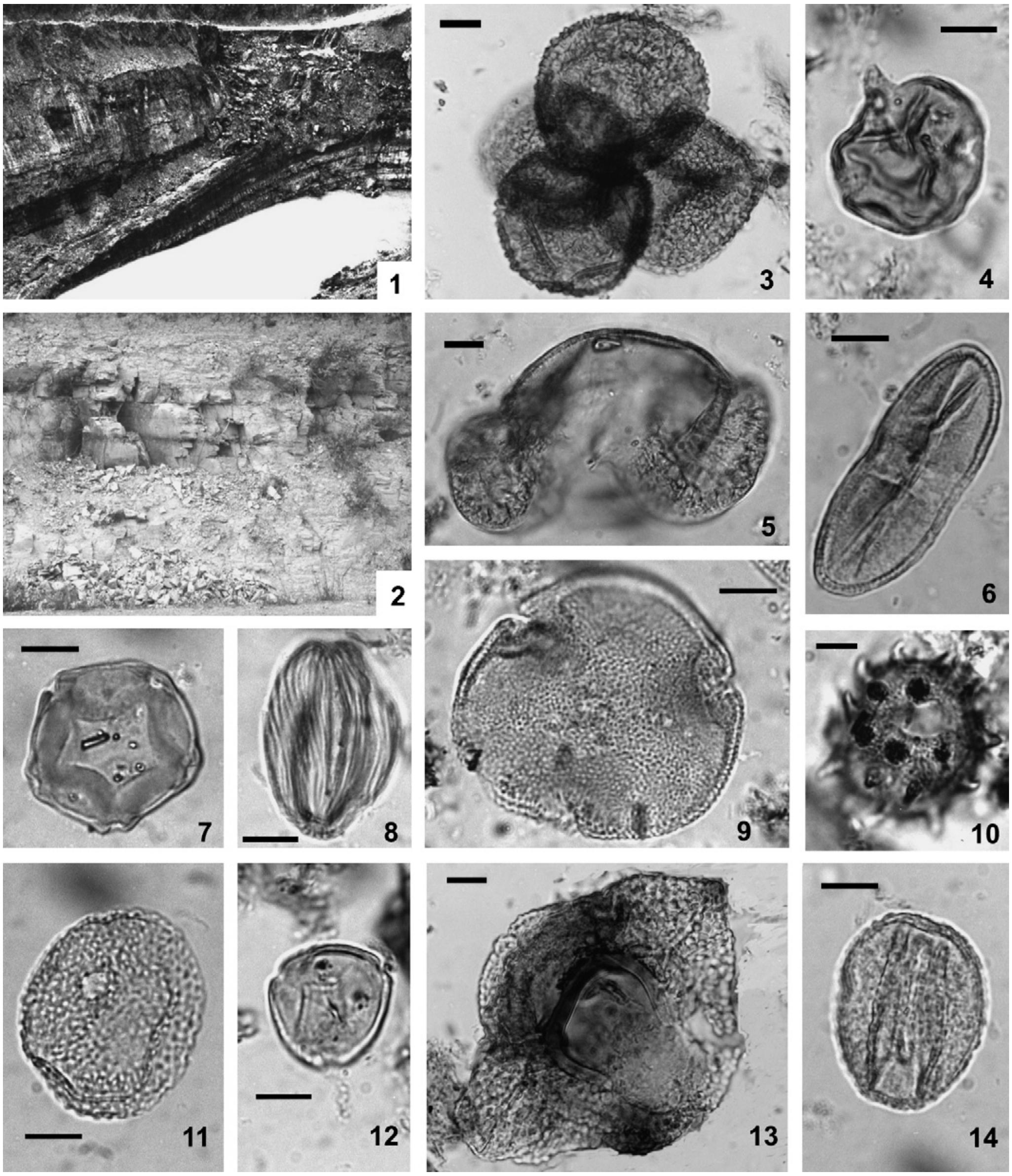

Fig. 4. (1) Photograph of the Sampsor mine taken in 1995. (2) Frontal view of the diatomiferous outcrop of Coll de Saig. (3) Tetrad of *Osmunda*, the most abundant trilete spore in the sediments of the La Cerdaña basin (included in palynological group P), Sanavastre lignite mine, level SAN7. (4) Taxodiaceae (*Sequoia* pollen type; palynological group TC), Barranc de Salanca outcrop, level BAR4. (5) *Pinus*, the most common pollen of the BIS palynological group, Torrent de Vilella outcrop, level TOV2. (6) Pollen produced by herbs of the family Apiaceae (NAP palynological group), Barranc de Salanca outcrop, level BAR1. (7) *Alnus*, the most abundant pollen of the RIP palynological group, Torrent de Vilella outcrop, level TOV6. (8) *Saxifraga*, entomophilous pollen related to the NAP palynological group, Torrent de Vilella outcrop, level TOV6. (9) *Tilia*, entomophilous pollen related to the M palynological group, Barranc de Salanca outcrop, level BAR1. (10) Extra-regional pollen of *Nypa* defined as belonging to 'other miospores', Sampsor mine, level SAM3. (11) *Sparganium* pollen produced by hygrophilous herbaceous plants (palynological group HH), Sanavastre mine, level SAN5. (12) *Engelhardia* pollen produced by subtropical/tropical trees and consequently considered to belong to 'other miospores', Sampsor mine, level SAM10. (13) *Trapa* pollen produced by aquatic (hydrophilous) plants (palynological group HH), Sanavastre mine, level SAN2. (14) *Quercus*, anemophilous pollen of the M palynological group, Beders outcrop, level BED. Bar = 10 μm.

Fig. 4. (1) Aspect général de la mine de lignite à ciel ouvert de Sampsor, en 1995. (2) Vue frontale du gisement à diatomites de Coll de Saig. (3) Tétrade d'*Osmunda*, la spore trilète la plus abondante dans les sédiments du bassin de Cerdagne, incluse dans le groupe palynologique P, mine à ciel ouvert de lignite de Sanavastre, échantillon SAN7. (4) Taxodiaceae (type *Sequoia*) du groupe palynologique TC, gisement de Barranc de Salanca, échantillon BAR4. (5) *Pinus*, grain de pollen le plus fréquent du groupe palynologique BIS, gisement de Torrent de Vilella, échantillon TOV2. (6) Grain de pollen produit par des herbes appartenant à la famille des Apiaceae (groupe palynologique NAP), gisement de Barranc de Salanca, échantillon BAR1. (7) *Alnus*, le grain de pollen le plus abondant du groupe palynologique RIP dans le bassin de Cerdagne, gisement de Torrent

were equally present in lignites and lutites (Fig. 2). Similarly, the proportion of a particular group sometimes changed between neighbouring levels of the same lithology. For instance, in the Sanavastre mine, the percentage of spores decreased from 27.6 to 1.85% in different samples (SAN11–SAN13) of lignite (Fig. 2.1). This was also seen in grey lutite samples, in which BIS ranged from 42.63% in SAN2 to just 5.97% in SAN4.

In this mine, the absolute miospore concentrations did seem to be related to the lithology. The greatest miospore concentration was found in lutites and the lowest in sands. SAN7 was the richest sample, with $1864 \times 10^3$ grains/g of rock, while the poorest sample was SAN14, with $112 \times 10^3$ grains/g of rock [9,12]. In the Sampsor mine, both the highest and lowest pollen concentrations were seen in lignites [9,11].

The Sanavastre mine and the middle section of the Sampsor mine showed similarities in terms of the proportions of palynomorph groups in each level; the mid section of the latter mine showed a stratigraphic organization similar to that seen in the Sanavastre mine [9,11,12]. Although some of the other levels of the Sampsor mine showed individual resemblance to some of those of the Sanavastre mine, their miospore proportions were modified by an increase in the quantity of sand.

### 4.2. *Palynology of lacustrine outcrops*

The rocks of the western lacustrine sector are formed from diatomites and mudstones. Sixteen samples showed a statistically representative number of palynomorphs (Fig. 3.1); all showed a scarcity of spores. The basal samples (BEL2 and BEL3) showed high percentages of RIP (42.8 and 41.5%, respectively) and M (22.1 and 30.5%, respectively). The percentage values for RIP and M underwent a marked reduction towards the top of the section, while those of BIS increased in number and became predominant in the remaining samples (except for TOV5). In all these levels, the percentages of M were higher than those of RIP. Low percentages of BIS (14.67%) and RIP (13.54%) and high percentages of M (30.48%) and undetermined pollen grains (23.17%) were seen in TOV5. The mean miospore concentration in this section was $618 \times 10^3$ grains/g of rock; the highest value was recorded for the basal sample BEL3 ($992 \times 10^3$ grains/g of rock) and the lowest for TOV5 ($302 \times 10^3$ grains/g of rock).

The comparative analysis of the assemblages from the lignite mines and of those from the lacustrine outcrops clearly reflects the Neves effect [24,25,49,66]. This is shown in the basin by the significant difference in the percentages of P, BIS, and RIP taxa in the sediments deposited in the alluvial delta zones. The three groups show noticeable percentages (Fig. 2) when compared with sediments from the deep and open lacustrine zones, which mainly contained BIS (Fig. 3.1).

Six outcrops of diatomites and mudstones were studied in the eastern sector of the palaeolake (Fig. 3.2). Generally, these samples were dominated by BIS, with percentages of 52.8–87.9%. RIU showed the smallest numbers of BIS (3.65%), but the highest of M (31.5%), RIP (26.46%), and NAP (8.62%). A large number of undetermined palynomorphs (27.43%) has also been evidenced. M was also well represented in BED (20.64%). Spores were very scarce except in PRAT (4.63%). In general, the pollen assemblages of the eastern sector (Fig. 3.2) showed a strong resemblance to those of the western sector (Fig. 3.1). BIS was the largest palynological group, except in RIU, where M and RIP predominated. The highest mean miospore concentrations were seen in the eastern section ($1560 \times 10^3$ grains/g of rock); the highest were recorded for levels BALL, BED, and TOB (more than $1800 \times 10^3$ grains/g of rock), the lowest for the Coll de Saig outcrop ($315 \times 10^3$ grains/g of rock in COL2 and $393 \times 10^3$ grains/g of rock in COL6).

## 5. Discussion and conclusions

### 5.1. *Recruitment of miospores*

The miospores incorporated into the thanatocoenoses of the La Cerdaña palaeolake clearly represent a mixture of components recruited from incoming water and

de Vilella, échantillon TOV6. (8) *Saxifraga*, grain de pollen de plante entomophile rattaché au groupe palynologique NAP, gisement de Torrent de Vilella, échantillon TOV6. (9) *Tilia*, grain de pollen de plante entomophile rattaché au groupe palynologique M, gisement de Barranc de Salanca, échantillon BAR1. (10) Grain de pollen extrarégional de *Nypa* inclus dans le groupe dénommé « autres miospores », mine de lignite à ciel ouvert de Sampsor, échantillon SAM3. (11) *Sparganium*, grain de pollen produit par des plantes herbacées hygrophiles (groupe palynologique HH), mine à ciel ouvert de lignite de Sanavastre, échantillon SAN5. (12) *Engelhardia*, grain de pollen produit par des arbres tropicaux/subtropicaux inclus dans le groupe dénommé « autres miospores », mine de lignite à ciel ouvert de Sampsor, échantillon SAM10. (13) *Trapa*, grain de pollen produit par des plantes aquatiques (hydrophiles) (groupe palynologique HH), mine de lignite à ciel ouvert de Sanavastre, échantillon SAN2. (14) *Quercus*, grain de pollen anémophile du groupe palynologique M, gisement de Beders, échantillon BED. Barre d'échelle = 10 µm.

the air. Surface water appears to have been the main vector of miospore transport to the lake [20,45,51,52]. The incoming streams would have received large quantities of palynomorphs from the catchment area by runoff. In addition, this basin had high rainfall (up to 1000 mm/year), and it was probably located at a height of 1000–1300 m above sea level [9] (assuming no isostatic elevation occurred). Thus, as occurs in present-day miospore accumulations [20,29], the samples derived from runoff were biased in their miospore content due to differences in their dispersal methods, and the effects of weathering and redeposition. When miospores fall into water, their sizes and the competence of the transporting currents may allow a sorting effect to occur [38]. The most abundant spores belonged to the genus *Osmunda* (Fig. 4.3). Their primary dispersal mechanism is by wind [33,34], but they are generally heavier than pollen grains and they accumulate close to the ferns that produce them (leptokurtic distribution [31,32]). In addition, they possess no suitable structures for flotation such as cinguli or coronae. The great amount of spores in the mines (Fig. 2) may simply be the result of the proximity of fern habitats to the sampling site, as seen in Lake Tulane (Florida) [67]. The small numbers of P in the deep lake sediments (Fig. 3) indicate the low transport efficiency of this group's spores. The majority of pollen types with pores and/or colpi take up water rapidly and sink [39]. Bisaccate pollen grains, however, float for longer periods since air remains trapped in the sacci. Pine pollen can retain its buoyancy for as long as four years [39], whereas other bisaccate pollen grains such as those of *Abies* and *Picea* (which are heavier than *Pinus*) sink very quickly [57]. Large numbers of broken bisaccate pollen grains, which must have spent long periods afloat were detected in the deep lacustrine outcrops. The type-3 palynofacies described by other authors [46] contained abundant, fragmented bisaccate pollen grains. These were probably brought to the palaeolake by water.

The anemophilous pollen of trees that grew near the lakeshore (RIP taxa, e.g., *Alnus*), and of non-riparian trees with high pollen production (BIS and M taxa, e.g., *Pinus*, *Quercus*, and *Betula*) were over-represented. RIP may have fallen with a greater preponderance into the lake waters by gravity, whereas BIS, and M were transported by wind above the canopy, and also by water in the case of BIS. Both types correspond to plants that lived at a short distance from the lake; the intensity of palynological deposition decreases the further away a plant is from the deposition point, resulting in a leptokurtic distribution of miospores [19,31,32]. High production and buoyancy may account for the high levels of BIS (mainly *Pinus*; Fig. 4.5) in almost all the samples studied.

The composition of miospore assemblages was also affected by the Ferguson–Spicer effect [31,32]. According to Tauber [65] and Holmes [38], miospores deposited on soils can be later refloated by surface runoff and carried to lakes. Shore vegetation can bring a large contribution to the refloated miospore count [29]. Miospores from riparian plants in particular can occur in disproportionately large numbers in lacustrine sediments [57]. The conspicuous percentages of RIP (mainly represented by *Alnus*) in the samples from the Sanavastre and Sampsor mines may be explained by this (Fig. 2). The same process may have led to the high percentages of HH in sample SAN5 (Fig. 2.1). The low percentages of TC in the mines may indicate the low importance of this group in riparian communities (Fig. 2). Members of the Taxodiaceae and Cupressaceae may have been integrated into coniferous and mesophytic forests, as the presence of *Sequoia*-type pollen (Fig. 4.4) and the megaremains of *Cryptomeria* and Cupressaceae suggest [13].

As in extant mesophilous communities [4], the trees of the La Cerdaña forests showed different pollen productivities. Taxa such as *Tilia* (Fig. 4.9) and *Acer*, whose common presence in the basin is indicated by megaremains [9], are under-represented in pollen diagrams, since they are entomophilous. These pollen grains may have arrived in the lake by (*i*) surface runoff, (*ii*) the direct fall of inflorescences and flowers [9,55], or (*iii*) by carriage on insects such as bees and bibionids [5,48]; the pollen could have reached the lake when these insects become trapped on the surface of the water.

Other factors can affect the recruitment of miospores in a lacustrine basin, such as the morphology of the lake basin, the dominant winds of the region, the area's topography, the ecological and spatial structure of the plant communities [15,43], and phenomena such as fires. Palaeobotanical and sedimentological studies have inferred the occurrence of fires in the basin [9,44] from taphofacies containing burned plant remains [44]. Accumulations of charcoal are certainly seen in the deep lacustrine sediments. The percentages of M and undetermined miospores in samples such as TOV5 and RIU also suggest that fires occurred (Fig. 3); conifers are rapidly affected by fire, and they remain unable to produce pollen for longer periods than mesophilous plants do.

Another phenomenon that can distort the composition of thanatocoenoses is resedimentation [27,40]. Annual variations in water density produce seasonal circulation patterns that resuspend pollen from the surface sediments, even from deep areas of lakes. Studies of similar deposits in recent basins suggest that only 20% of the pollen in the lake water represents new input, while some 80% is redeposited [27]. However, in the present study, it was impossible to differentiate between newly and redeposited miospores.

### 5.2. Biostratinomy

The miospore assemblages of the alluvial sediments of both mines were mainly represented by local and extra-local elements (*sensu* Jacobson and Bradshaw [40] and Prentice [57]), and mostly transported by water or wind above the canopy. A portion of the wind-transported pollen, i.e. that produced by genera such as *Pinus* (Fig. 4.5), *Cathaya*, *Sciadopytis*, *Quercus* (Fig. 4.14), and Arecaceae, was probably of regional origin. In contrast, the assemblages from the deep lacustrine facies showed higher extra-local to regional rather than local components, indicated by the proportions of BIS and M. Thus, the presence of taxa such as *Pinus* and *Quercus* reflects a more regional input than the presence of *Fagus*, *Acer*, *Tilia* (Fig. 4.9), and many herbs [3,19,31,40], which may have come from the area that Pfefferkorn [53] refers to as the 'uplands'.

In the present assemblages, extra-regional pollen deposited far from the area of its production was recorded, including a very small number of pollen grains of the palm *Nypa* (Fig. 4.10). This palm typically grew in the mangrove swamps that developed along Tethysian coastlines during the Palaeogene [54]. The presence of its pollen grains in the La Cerdaña basin corroborates the existence of Indo-Pacific-type Upper Miocene mangroves in the Palaeomediterranean.

Taking into account the different miospore transport processes possible, the thanatocoenoses of both the alluvial and the deep lake environments of the La Cerdaña basin might be termed allocoenoses (*sensu* Ochev [50]), as they result from the accumulation of allochthonous remains at the sites of their production. However, they are in fact mixocoenoses, since they show high proportions of algal remains such as *Botryococcus* colonies and zygnematalean spores, which were surely buried at the site of their production. The miospore assemblages from the alluvial fan sediments would have been produced by both parautochthonous and allochthonous elements, whereas those of the deep lake sediments would have mainly come from allochthonous elements. The term 'parautochthonous' refers to remains that have been transported only over a small distance toward the deposition site [17]. This is the case of P, RIP and HH, TC, NAP, as well as that of the Sapotaceae, which may also have been produced near the lake. The presence of a large number of parautochthonous taxa in the sediments of the studied mines confirms the evidence provided by megaremains in other studies [9,44]. Remains moved from their site of production, and therefore away from their original habitat, are considered as 'allochthonous' [17]. The miospores in BIS and M and some taxa of TC, NAP and other pollen, such as that of *Arecaceae*, may be allochthonous in nature.

### 5.3. Sedimentological features

The lack of a relationship between the proportion of different palynological groups and the lithology of the levels has no satisfactory explanation, although the small size of the delta may have conditioned this. Miospores produced closest to the shore would be deposited in similar amounts in both lignites and lutites. The palaeobotanical data clearly indicate that the delta area was covered by swamp vegetation – riparian alder forests, with a fern undergrowth of Osmundaceae. There are no conclusive studies confirming the presence of *Taxodium* in the basin. The lignite seams are probably autochthonous, but mostly formed from parautochthonous plant remains [46].

Miospore preservation in the deltaic deposits of the La Cerdaña basin is however related to the type of rock. The lignites showed pollen grains with semi-destroyed exines, whereas spores were well preserved. This differential preservation is due to the high resistance of spores to diagenesis in organic matter-rich deposits (see [40]). The destruction of pollen exines is related to their lower resistance to the humification, which occurs during coalification. The same has been recorded in Oligocene lignites, where the spores of pteridophytes are dominant [22]. In the Sampsor mine, the lignite levels showed conspicuous quantities of undetermined pollen grains (Fig. 2.2) and low miospore concentrations. In contrast, the lignite levels of the Sanavastre mine had no large numbers of undetermined pollen grains (Fig. 2.1) and high miospore concentrations [9]. No satisfactory explanation can be given for this, though the lignites of the studied mines might be of different sedimentological (the siliciclastic rocks of the Sampsor mine are coarser than those of the Sanavastre mine are) and diagenetic history. The lutites showed the best-preserved palynological assemblages. The different preservation of the miospores in the lutites and lignites corresponded with their description in palynofacies 1 and 2 (respectively), as published by other authors [46].

The sands preserved the miospores less well than either the lutites or lignites (see [9,11,12]). The presence of palynomorphs in sandy levels is not common [36] and is related to the coarseness of the deposits; this was reflected in the sandy levels of the Sampsor mine (SAM4, SAM8, SAM20, SAM22, SAM24, SAM26, SAM28, SAM30), and level SAN22 of the Sanavastre mine. In contrast, palynomorphs were always present in the fine-grained sands of levels SAN3, SAN9, and SAN14 (Fig. 2.1), and SAM12, and SAM27 (Fig. 2.2).

The diatomitic sediments of the deep lacustrine facies showed the best-preserved miospore assemblages of the entire basin, a consequence of their rapid burial in an anoxic environment. All levels were characterised by the occurrence of *Botryococcus* colonies. In these rocks, plant megaremains were abundant and included *Equisetum*, *Populus*, and Lauraceae, which were not recorded via their miospores (see [9,13]). The lack of miospores of these taxa is related to their low sporopollenin content [66]. These sediments also had the highest miospore concentrations of the basin, which can be explained by an increase in the pollen influx associated with the rate of sedimentation and the action of winds in an open environment. The mean miospore concentration was significantly greater in the eastern deep lacustrine sector, which experienced a higher rate of sedimentation than the western sector.

The variation in the proportions of the palynological groups in the miospore assemblages does not allow the differentiation of palynofacies 3 and 4 described by Martín-Closas et al. [46]. These levels are characterised by high percentages of BIS (Fig. 3). The miospore associations present depend on (1) the action of fires (samples TOV5 and RIU), (2) the leaching of organic matter, and (3) changes in the vegetation due to climatic factors. The action of fires leads to reduced miospore concentrations. Therefore, levels TOV5 and RIU, though they showed remarkable values in terms of grains/g of rock [9], showed lower miospore concentrations than did other levels from the deep lacustrine facies (except for the Coll de Saig outcrop). The leaching of organic matter might also explain the low miospore concentrations of samples COL2 and COL6 from the Coll de Saig outcrop (Fig. 4.2). The sediments here showed a yellowish colour and had a lower proportion of organic matter than the rest of the outcrops studied. This might be due to a greater exposure of the outcrop to meteoric modifications [8]. Only two out of the seven samples collected from the Coll de Saig outcrop showed a palynological content, characterised by very high percentages of BIS (>80%) (Fig. 3.2).

In the western sector, the contrasting proportions of the palynological groups shown by levels BEL2 and BEL3, along with their high absolute miospore concentrations, may indicate environmental conditions that favoured M and RIP over BIS (Fig. 3.1).

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