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Keywords	Normampolles; Fagales; France; Late Cretaceous; Chera
Taxonomy	Earth History, Geology, Biogeoscience
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Palynological counts of the Chera vertebrate site

Vegetation of the Late Cretaceous vertebrate site of Chera (Valencia, Spain) and its significance in mosaic vegetation from southwestern Europe.

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Abstract

A palynological analysis of the Late Cretaceous vertebrate sites of Chera (Valencia, Spain) has been carried out. The occurrence of diversified Normapolles including various species of *Vancampopollenites*, *Papillopollis* and *Pseudoromeinipollenites* suggest a late Campanian/early Maachtrichtian age. The inferred assemblages indicate an azonal vegetation involving peat-mosses, sedges and palms colonizing wetlands with ephemeral or semi-permanent pools and lakes. The abundant and diverse Normapolles reflect the regional presence of woodlands or other open vegetation types with prominent Fagales. The integration of Chera pollen assemblages with contemporaneous palynological and paleobotanical data from SW Europe indicates the co-existence of numerous, structurally different and taxonomically individualized plant communities. The inferred paleofloral heterogeneity is compatible with the current paleogeographical reconstructions of SW Europe and probably enhance the appearance of the highly diverse fauna with insular characteristics of the latter part of the Late Cretaceous.

1. Introduction

The Cretaceous Period is characterized by a drastic change in vegetation and the advent of plant communities including prominent flowering plants. The transition from conifer- to angiosperm-dominated ecosystems has been gradual and varied dramatically across geographical areas (Crane and Lidgard, 1989; Peyrot et al., 2008; Friis et al., 2011; Korasidis et al., 2016; Heimhofer et al., 2018). During the Late Cretaceous, a significant part of Northern Hemisphere was covered by vegetation involving wind-pollinated angiosperms related to Fagales and producing pollen grains with complex apertures called Normapolles (Vakhrameev, 1991). During the latter part of this period,

Normapolles-producers reached high diversity and often formed the dominant component of open vegetation types covering vast expanses of Western Europe (Batten, 1986a; Peyrot et al., 2013). The distinctiveness of Campanian–Maastrichtian pollen assemblages recovered from Portugal and Spain prompted various authors to recognize Iberia as a separate paleobiogeographic province (Batten and Li, 1987; Herngreen et al., 1996) and suggests high levels of endemism probably related with the fragmented nature of emerged lands (Smith et al., 1994; Seton et al., 2009; Handy et al., 2010). In spite of constituting the main framework of terrestrial ecosystems where prodigiously diverse fauna evolved and thrived (Csiki-Sava et al., 2015; Ortega et al., 2015; Pereda-Suberbiola et al., 2015), the structure and composition of Late Cretaceous European and Iberian plant communities remain poorly characterized (Diéguez et al., 2010). The present study presents a palynological analysis, new biostratigraphic data, vegetation reconstruction and vertebrate inventory of the Late Cretaceous site of Chera (Valencia, Spain) and compare them with floral data from other coetaneous locations of Western Europe.

2. Geological settings

The Chera Basin is well-known to host one of the richest Late Cretaceous vertebrate outcrops of Iberia (Company et al. 2005, 2009a; Company, 2004, 2011; Company and Szentesi, 2012). It is located in the southwestern Iberian Range (Valencia province, Eastern Spain) and includes numerous fossiliferous localities which yield diverse vertebrate assemblages (see e.g., Company, 2004; Company and Szentesi, 2012). The studied outcrops are characterized by a rich vertebrate assemblage including dinosaurs (*Rhabdodon*, *Struthiosaurus*, *Lirainosaurus*, maniraptoran and abelisauroid theropods), pterosaurs and microvertebrate remains of aquatic and semi-aquatic organisms such as bony fishes, amphibians and squamates (Company, 2004; Company et al., 2009b). Chelonians (*Solemys*, *Polysternon* and *Dortoka*) and crocodilians (*Acynodon*, *Musturzabalsuchus*, *Doratodon*) represented the most diverse recorded faunal groups. Preliminary palynological studies suggested a high diversity of Normapolles-types and a great abundance of sphagnaceous spores and freshwater algae (Peyrot et al., 2009).

The material described herein was collected from several exposures of the Sierra Perenchiza Formation in the Chera Basin (southwestern Iberian Range, Valencia

Province, Spain), approximately 2 km south of the village of Chera (Fig. 1). The formation is a continental, shallow-water carbonate unit dated as late Campanian/early Maastrichtian (Vilas et al., 1982; Garcia et al., 2004; Pueyo et al., 2014) and outcrops in the southeastern margin of the Iberian Range, where it reaches a maximum thickness of about 50 m. It consists of lagoonal micritic and brecciated limestones, grading upwards to palustrine carbonates with evidence of pedogenic modifications including rooting, mottling and pseudomicrokarst (Platt, 1989; Alonso et al., 1991). The lower part of the Sierra Perenchiza Formation consists mainly in medium to thick-bedded brecciated limestones and yield a biota including gastropods (*Pyrgulifera armata*, Potamididae, Ellobiidae) and ostracods (Cyprididae) suggesting depositional settings in shallow and low-salinity waterbodies (Platt and Wright, 1992). Oligohaline conditions are also supported by the presence of the charophytes *Amblyochara*, *Peckichara* and *Platychara* (Company, 2004). The upper part of the unit is mainly represented by interbedded marls and limestones interpreted to represent small, coastal, ephemeral, carbonate lakes and ponds. The pedogenic structures occurring in this interval indicate subaerial exposures suggesting fluctuations of water table which have been linked to episodic or seasonal aridity (Company, 2004).

3. Material and methods

Two detailed stratigraphic sections of the upper part of the Sierra Perenchiza Formation were logged in the study area. The sections were measured in the Barranco del Agua Creek and in La Castellana Creek. Samples labelled as CH- were collected from the Barranco del Agua exposures, whereas the samples labelled LC come from the La Castellana site (Fig. 1). The first section corresponds to one of the parastratotypes of the Sierra Perenchiza Fm. (Vilas et al., 1982) and presents a thickness of about 50 m. The exposures are characterized by a succession of dark grey, green, white, and pink marls intercalated with limestone lenses. Up to 7 samples have been collected from the marls (Fig. 1). Four of them were barren, and only two of the sampled levels produced palynomorphs (CH-I-4 and CH-III-1b).

- Sample CH-I-4 has been collected from a thick, massive, dark grey, mudstone containing abundant vertebrate remains. This bed provided the richest vertebrate

assemblage of the formation and is the type locality of the ziphodont crocodyliform *Doratodon ibericus* (Company et al., 2005). The faunal assemblage also includes gastropods and bivalves and is accompanied by abundant carbonized plant remains and charophytes.

- Sample CH-III-1b comes from a narrow dark clay lens interbedded between palustrine limestones with abundant root traces and strong pedogenic modifications. This level has produced gastropods, ostracods, abundant micro-remains of bony fish, amphibians and charophytes.

In La Castellana Creek, ravine incision has produced extremely good exposures of the upper part Sierra Perenchiza Formation. All soft horizons in a 30 meters-thick section were systematically sampled, but only one of them produced palynomorphs: LC-I-5 was collected for a narrow grey level intercalated between couplets of palustrine limestones.

The samples were prepared following standard palynological processing techniques, involving HCl and HF treatments and excluding any oxidative maceration in order not to degrade delicate palynomorphs (Batten, 1999). Photographs of the more representative taxa (Figs. 2, 4–5) were taken using a Color View Illu camera coupled to an Olympus BX51 microscope. Confocal laser scanning microscopy was employed to characterize several specimens using the methodology explained in Peyrot et al. (2007). A palynofloral list of the taxa recovered and organized according to known, inferred or supposed botanical affinities is presented in Table 1.

4. Results

4.1. Assemblage description

The palynomorphs presented a fairly good preservation and a light colour suggesting low thermal maturation (Batten, 1996a). The assemblages yielded more than 83 types of palynomorphs (Table 1), mainly consisting of angiosperm pollen grains (42 taxa), bryophyte and pteridophyte spores (24 taxa) and gymnosperm pollen grains (7 taxa). Palynomorphs with a presumed marine origin include dinoflagellate specimens attributed to *Spinidinium* (Figs. 2A–C) and have been recorded in only one sample (CH-I-4). Freshwater palynomorphs are relatively diverse (8 taxa) and observed in all the

productive samples. These include coenobia of *Botryococcus* spp. (Fig. 2D) and resting cysts attributed to *Ovoidites spriggii* (Fig. 2E), *Ovoidites* cf. *ligneolus* (Fig. 2F), *Ovoidites* spp. (Fig. 2G), *Tetranguladinium conspicum* (Fig. 2H), *Protoellipsodinium fibratum* (Figs. 2L–M) and *Spicadinium* cf. *akidoton* (Fig. 2N–O). Freshwater algae reach numerical significance (8% of the total assemblage, Fig. 3) in one sample (CH-III-1b) and are only sporadically observed elsewhere.

Spores represent between 20% (CH-III-1b) and 45% (CH-I-1) of the counted palynomorphs (Fig. 3). The most frequently occurring taxa include the fern spores with uncertain affinities *Gabonisoris vigourouxii* (Fig. 4G) and *G. cristatus* (Fig. 4H) as well as representatives of Cyatheaceae/Dicksoniaceae (*Deltoidospora* spp., *Biretisporites* cf. *potonieii*, Fig. 4A), presumed Anemiaceae (*Ischyosporites* spp., Fig. 4E) and Polypodiaceae. Other spore-producers are poorly represented. Lycopsids include three taxa, and liverworts are only represented by the species *Zlivisporis reticulatus* (Fig. 4C). The level CH-III-1b, however, includes a substantial amount of presumed sphagnacean taxa including specimens herein referred to *Acanthotriletes? trigonus* (Figs. 4J–K), *Cingulatisporites levispeciosus* (Fig. 4D) and *Cingulatisporites* spp.

Gymnosperms are not diverse and only represent a subordinate component of the assemblages (c. 5%, Fig. 3). Bisaccate pollen are uncommon and the bulk of gymnosperms is constituted by polyplicate grains of the species *Equisetosporites multicostatus* (Fig. 5A) and *E. patapscoensis* (Fig. 5B), presumably related to Gnetales.

Conversely, angiosperms are diverse and quantitatively predominant (Fig. 3). In CH-III-1b, flowering plants account for 65% of the total palynomorphs, the most frequently occurring taxa being *Penetetrapites inconspicuus* (Fig. 5C) and two taxa assigned to the genus *Monocolpopollenites* (Figs. 5G–I). Fagales are diverse and represent between 6% (CH-III-1b) and 26% (LC-I-5) of the assemblages (Fig. 3). The most common taxa include *Papillopollis* spp. (Figs. 5M–N), *Trudopollis* spp. (Figs. 5K–L, 5Q), *Vacuopollis* spp. (Figs. 5AA–5AB), *Vancampopollenites* spp. (Figs. 5AD–5AE) and grains related to the Betulaceae (*Interporopollenites* spp., Figs. 6B–C). These pollen, commonly recorded in Late Cretaceous palynofloral assemblages from Western Europe but uncommon or absent in eastern North America, are also accompanied by rarer

forms, such as *Pseudoromeinipollenites laevigatus* new comb. (Appendix 1; Fig. 5O),
Tricolpites synstriatus (Fig. 6J) and specimens described herein and referred to as
Vancampopollenites? sp. 1 (Appendix 1; Figs. 6D–I).

While the three assemblages from Chera are taxonomically similar (Fig. 3), they can be
ordered according to their content in freshwater palynomorphs plus presumed
hygrophytes: (i) CH-III-1b presents a typical lacustrine signal with a high content in
freshwater algae and spores produced by plants presumably related moist and humid
environments; (ii) CH-I-4 shows a much lower content in freshwater palynomorphs and
still includes a conspicuous proportion of spores; (iii) LC-I-5, conversely, does not yield
any significant input from freshwater palynomorphs. The palynofloral association of
this level includes, however, dinoflagellate cysts and a higher number of Normapolles
(Fig. 3).

4.2. Selected taxonomy

Pseudoromeinipollenites Kedves in Kedves & Russell, 1982 emend. Legoux, 1986

type species: *Pseudoromeinipollenites paleocenicus* Kedves in Kedves & Russell, 1982,
p. 98, Pl. 7, Figs. 21–22, Text-fig. 1

Pseudoromeinipollenites laevigatus new comb. (Fig. 5O)

syn. *Romeinipollenites laevigatus* Kedves & Herngreen, 1980, p. 517–518; Pl. 9,
Figs. 1–2

syn. *Polaroporis* sp. 2 Médus, 1981, p. 22; Pl. 9, Figs. 1–3, 6

syn. *Pseudoromeinipollenites aquitanensis* Legoux, 1986, p. 415; Pl. 1, Figs. 1–3

Description: Small-size, brevixial, planaperturate pollen grains with a circular to
rounded-triangular equatorial outline. Mostly strutureless and unornamented exine.
Nexine of equal thickness, sexine thicker in apertural regions defining inconspicuous
(i.e., not protruding) ektannuli. Exoapertures are vertical slits widening towards polar
areas, endoapertures circular with ragged margins and located in subequatorial position,
atria not developed.

Remarks: The transfer of *Romeinipollenites laevigatus* to the genus *Hungaropollis*
proposed by Polette and Batten (2017) is not followed. The circular endoaperture
mentioned in the diagnosis and apparent in illustration of the holotype (Kedves &

Herngreen, 1980, p. 517–518, Pl. 9, Fig. 2) suggests an attribution to the genus *Pseudoromeinipollenites* Kedves, 1982 emend Legoux, 1986.

Vancampopollenites Kedves & Pittau, 1979

type species: *Vancampopollenites lusitanus* Kedves & Pittau, 1979, p. 202, Pl. 7, Figs. 1–3

Vancampopollenites? sp. 1 (Fig. 6D–I)

Description: Pollen oblate with a square rounded outline in polar view. Exine 8–12 μm -thick except in polar areas. Nexine much thinner than sexine. Four complex apertures consisting in 15–20 μm -long colpi and, protruding, c. 5 μm -wide pori with ragged margins. Endogerminal characteristics not apparent.

Remarks: The polar exinal thinning relates the specimens to the genus *Vancampopollenites* Kedves & Pittau, 1969. The protruding nature of pori prevents an unquestionable generic attribution.

5. Discussion

5.1. Palynology-based biostratigraphy

The faunal assemblage of Chera includes abundant dinosaur remains attributed to *Rhabdodon*, *Struthiosaurus* and *Lirainosaurus*, as well as chelonian like solemydids and dortokids and crocodilian taxa such as *Acynodon*, *Musturzabalsuchus* and *Doratodon* (Company, 2004). This indicates that the vertebrate macrofauna of Chera is very similar to that of Laño (Condado de Treviño), which is considered as representative of the late Campanian of the Iberian Peninsula (Pereda-Suberbiola et al., 2015; Corral et al., 2016). Late Cretaceous terrestrial palynological assemblages from Western Europe are notoriously difficult to correlate due to the paucity of successions with independent calibration (Herngreen et al., 1986; Méon et al., 2001) and the great number of pollen taxa inadequately described or with a stratigraphic range poorly understood (Batten and Morrison, 1987; Batten et al., 1988). The presence of numerous ‘complex’ types of Normapolles including *Vancampopollenites* spp. (Fig. 5AD–AE) and *Papillopollis* spp. are suggesting an age not older than Campanian (Batten, 1986a; Batten and Morrison, 1987). A slightly younger age is suggested by the single specimen of *Tricolpites synstriatus* recorded in CH-III-1b as this species appears with relative frequency in

Maastrichtian assemblages of Bolivia (Vajda-Santivanez, 1999), Brazil (Regali et al., 1974a, 1974b), Senegal (Jardiné and Magloire, 1965) and Western USA (Farabee and Canright, 1986). The presence of *Pseudoromeinipollenites laevigatus* new comb. (Fig. 5N–O) suggests an early – early late Maastrichtian age as this species has been recorded in Lixhe 3 of the the Gulpen Formation, Netherlands (Kedves and Herngreen, 1980) and in strata dated as Maastrichtian from W and SW France (Médus, 1981; Legoux, 1986) and Spain (Médus, 1987). This interpretation should be considered with caution given the inconsistent (i.e., rare) distribution of the mentioned species. Conversely, the presence of abundant *Gabonisorites vigourouxii* (Fig. 4G) and *Penetetrapites inconspicuus* (Fig. 5C) may relate the palynofloras of Chera with the assemblages from the Maastrichtian *Aquilapollenites–Penetetrapites* Assemblage Zone described in Korea (Yi and Batten, 2002; Yi et al. 2003). *G. vigourouxii* did not reach numerical significance until the Maastrichtian in North Africa (Méon, 1991; Shrank, 1994) and Bolivia (Vajda-Santivanez, 1999). It seems, however, likely that *Penetetrapites* and *G. vigourouxii* reflect more local hygrophytic vegetation and present a biased stratigraphic distribution (see Paleovegetation section). Altogether, the palynological assemblages does not allow to reach a conclusive age and a conservative late Campanian/?early Maastrichtian in line with macrofaunal data is adopted.

5.2. Paleovegetation

5.2.1. Local wetland environment of Chera

The presence of freshwater algae in association with abundant Marsileaceae (*Gabonisoris* spp.; Fig. 4G–I) allow to infer the presence of wetlands with ephemeral or semi-permanent pools and lakes colonized by aquatic or semi-aquatic spore-producers. The high number of spores presumably affiliated to Sphagnaceae recorded in CH-III-1b (*Acanthotriletes? trigonous*, *Cingulatisporites levispeciosus*, *Cingulatisporites* spp., *Stereisporites steroides*; Fig. 4D, J–K) supports this hypothesis and also suggests the presence of peat-forming environments. Modern Sphagnaceae are mosses sensitive to desiccation and are frequently observed in water-logged, nutrient-poor habitats (Alpert, 2005). These hygrophytic communities also included angiosperms producing *Penetetrapites inconspicuus* (Fig. 5C) and related to Cyperaceae (Sweet, 1986). If this interpretation is correct, the palynoflora of Chera would represent one of the oldest wetlands typified by abundant peat-mosses and sedges. The substantial

number of monocolpate grains may reflect the presence of parautochthonous palms in the azonal vegetation. These could have been quantitatively important in the driest, or episodically or seasonally aerated, habitats bordering the water-logged environments. The low number of morphotypes (e.g. only three monoaperturate grain types, Figs. 5D–E, G–I) suggest, however, that palms formed low-diversity vegetational stands.

5.2.2. *The presence of Normapolles in Chera and their significance in Late Cretaceous floras of Iberia*

The assemblages of Chera include diverse and abundant (per-)oblate pollen with complex apertures assigned to the Normapolles complex (Góczán et al., 1967; Batten and Christopher, 1981; Fig. 5K–O, Q–S, X–Z, AA–AE, AI; Fig. 6B–C). Their presence in most Upper Cretaceous assemblages has long been recognised and allowed to define the eponymous paleobiogeographic province covering eastern North America, Western Europe (excluding northern Scandinavia) and West Siberia (Batten, 1984; Herngreen et al., 1996 and reference therein). While the western and eastern boundaries of the province were delineated by epicontinental seas, the latitudinal expanse of the province (roughly 20–40°N) probably corresponded to climatic boundaries. Variations in climate have also been invoked to explain the marked differences in Normapolles composition between Iberia, Western Europe and North America (Góczán et al., 1967; Kedves, 1985; Batten and Li, 1987). The morpho-functional analysis of Normapolle grains from upper Cretaceous strata from Aveiro (Portugal) allowed Batten (1986a, 1986b) to suggest (seasonally) seasonal or semi-arid climatic conditions for Iberia.

In Chera, Normapolles outnumbers other angiosperms and represent 60% of the diversity of flowering plants (19 taxa including three informal species and seven generically attributed but binomially undesignated; Appendix 1). While Normapolles constituted still a significant proportion of Paleocene palynofloras from western USA and Western Europe, their abundance and diversity decreased subsequently and the group became extinct by the end of the Eocene (Gruas-Cavagnetto, 1968; Kedves & Russell, 1982; Ollivier-Pierre et al., 1987; Frederiksen, 1995). The replacement of Normapolles by pollen morphologically more akin to those produced by modern members of Fagales (e.g., *Momipites*, *Caryapollenites*) started during the Maastrichtian

and intensified during the Paleogene. In Iberia, Fagales represented a significant component of palynofloras during the Neogene (e.g., 38 and 18 pollen species were respectively recorded in the Oligocene of NW Spain and the late Miocene of SE Pyrenees; Barrón et al., 2016, Casas-Gallego, 2018). Modern representatives are dispatched in eight families (Angiosperm Phylogeny Group, 2016) mainly distributed in the Northern Hemisphere, where they constitute the principal elements of the temperate and cool/cold deciduous and mixed forests. With few exceptions, the majority of modern members are anemophilous and shed abundant pollen, usually well-preserved in sediments. Often, several species coexist in the same ecosystems (see e.g., Quézel et al., 1980; Assadollahi et al., 1982; Morin, 1997; Costa Tenorio et al., 2005), but usually inhabit different ecological niches (e.g., sunny or shadow places, humid or dry soils, colder or hotter microclimates, etc.) or present different physiognomies (tree- vs shrub-habit). The Normapolles-producers from the latter part of the Late Cretaceous were likely wind-pollinated shrubs or tree-size plants (Batten, 1986a; Friis et al., 2011) but probably also included few, lower stature taxa. By analogy with extant forested communities incorporating Fagales, Normapolles-producing plants were likely colonizing dry hinterland settings or moister river border and constituted or formed part of open forests (i.e. forest or woodlands) or riparian vegetation.

In Chera, the Normapolles abundance varies according to the sample considered. In CH-III-1b, their reduced abundance (Fig. 3) suggests the absence or poor representation of wind-pollinated Fagales in the vegetation close to the site of deposition. Alternatively (but not exclusively), this signal, together with the low representation of bisaccate pollen, could reflect a small-size depositional setting surrounded by closed vegetation preventing the influx of regional, air-borne, palynomorphs (Jacobson and Bradshaw, 1981). The increase in Normapolles observed in CH-I-4 and LC-I-5 (Fig. 3) is interpreted to reflect a more open vegetation.

Collectively, the pollen assemblages of Chera indicate the presence of regionally extended woodlands incorporating diversified Normapolle-producers and conifers (levels CH-I-4 and LC-I-5), hosting episodic (or seasonal) wetlands characterized by peat mosses, sedges and palm trees (level CH-III-1b). The record of several specimens of dinocyst in LC-I-5 is significant as it implies a marine incursion and brackish environment related to a coastal depositional setting.

5.3. Comparisons with other Late Cretaceous palynofloras

Upper Cretaceous assemblages from Spain may be grouped according to their content in Normapolles. The high diversity and abundance of these pollen recorded in CH-I-4 and LC-I-5 have also been described in other Campanian–Maastrichtian strata from the Iberian Peninsula: Sedano in Burgos province (Médus, 1987), Barranco de la Posa in the South-Central Pyrenees (de Porta et al., 1985; Ashraf and Erben, 1986) and the upper part of the Fontllonga succession, in the Tremp Basin (Médus et al., 1988, 1992; Mayr et al., 1999; Fernández-Marrón et al., 2004). In Sedano, Médus (1987) distinguished various plant communities and suggested the existence of lagoonal wetlands with Typhaceae/Sparganiaceae similar to the ones described at the vertebrate site of Lo Hueco (Peyrot et al., 2013). The younger Fontllonga succession spans the Cretaceous–Cenozoic transition and records higher number of Normapolles in the Danian interval (Mayr et al., 1999; Fernández-Marrón et al., 2004). In this succession, the presence of boreal elements (*Aquilapollenites*) could indicate ecological disturbance triggered by short-lived climate degradation. The lower Maastrichtian assemblages of Barranco de la Posa include diversified Normapolles in association with more evolved Fagalean pollen (e.g. presumed Juglandaceae *Platycaryapollenites*) but is numerically dominated by monocolpate and inaperturate pollen grains (de Porta et al., 1985; Ashraf and Erben, 1986). Collectively, the data from Barranco de la Posa indicates a flora incorporating Fagales and palm trees as in Chera but with a higher proportion of cypresses suggesting slightly drier environments.

The lower abundance of Normapolles in CH-III-1b relates this level with the palynoflora of Lo Hueco, central Spain (Peyrot et al. 2013) and the assemblages from Isona, Fígols-Vallcebre, Campo and the lower part of the Fontllonga succession (Mayr et al., 1999; Fernández-Marrón et al., 2004; Villalba-Breva et al., 2015). The difference between Chera and Lo Hueco is likely to reflect a biostratigraphic bias, the assemblages of the latter representing a more restricted pollen source area (Peyrot et al., 2013). The late Maastrichtian locality of Molí de Baró-1 (southeastern Pyrenees) does not include Normapolles but pollen of more evolved morphologies with Juglandacean affinities (Marmi et al., 2015). This record is interesting as it suggests local arborescent communities where Normapolles-producers have been replaced by their modern counterparts.

Taken altogether, the late Campanian–Maastrichtian palynological assemblages from northern and eastern Iberia suggest the co-existence of various types of wind-pollinated plant communities. Fagales represented a significant proportion of the local vegetation and could either incorporate exclusively Normapolles-producing plants (Chera, Lo Hueco) or plants with modern affinities (Molí de Baró-1) or a mix of the two groups (Barranco de la Posa). Conifers may have formed another component of wind-pollinated communities with regional significance as bisaccate pollen grains dominated some assemblages at Lo Hueco (Bascuña Member, Villalba de la Sierra Formation; Peyrot et al., 2013), Isona (Trempe Group, sample ISP-2 in Villalba-Breva et al., 2015 and samples V2B, V3B and V5B in Torices et al., 2012) and elsewhere in SW Europe (Médus et al., 1992). While the spatial distribution of conifer stands and their exact relationship with other arborescent communities remain uncertain, the marked signature of pollen assemblages seems to indicate plant communities with distinct composition forming a mosaic regional flora. This interpretation is coherent with and has probably been promoted by the highly fragmented paleogeographic context of Iberia and Western Europe (Csiki-Sava et al., 2015).

The assemblages from Chera lack the typical Normapolles characterizing the palynofloras of Northern and Central Europe (Goczán et al., 1967; Batten, 1984; Kedves, 1985; Batten and Li, 1987; Herngreen et al., 1996 and references therein). Conversely, the higher representation of monocolpate grains recorded at Chera and in other Iberian successions has not been observed further North in Germany (Kruttsch and Mibus, 1973), Netherlands (Kedves and Herngreen, 1980; Herngreen et al., 1986) and in Central Europe (Van Isterbeeck et al., 2015). These differences in composition may also be probably related with latitudinal climatic gradient (Batten, 1984, 1986b). This hypothesis seems likely but difficult to prove with palynological data alone given the lack of knowledge on the ecophysiological requirements of Cretaceous plants and the uncertain correspondence with dispersed pollen.

5.4. *Correspondence with plant macroremains*

The palynoflora from Chera can also be related to plant macroremains described in other Spanish Late Cretaceous outcrops (Villalba-Breva et al. 2012, 2015; Marmi et al.,

2015; Marmi, 2016). In Chera and other Iberian palynological successions, the abundance of monocolpate pollen related with Arecaceae would match well the megafloral assemblages of Isona incorporating the palm *Sabalites* and interpreted to represent a backswamp (Villalba-Breva et al., 2015). Palms have also been documented in assemblages from fluvial deposits (Marmi et al., 2015) probably representing riparian community. Altogether, this data suggest that palms were quite widespread and colonized distinct plant communities growing in wet environments.

While leaf macrorremains and floral mesofossils affiliated to Fagales have been reported in the European Late Cretaceous (see e.g, the occurrence of *Dryophyllum* in Ukraina [Vakhrameev, 1991] and flower remains in Portugal [Schönenberg et al., 2001; Friis et al., 2003, 2011]), the occurrence of macrofossils attributed to this group remains scarce in Spain. This result is surprising given the abundance of palynological data supporting their widespread occurrence in Spain (and Western Europe). This discrepancy could be related with the reduced transport capability of vegetative remains when compared with miospores. It also confirms that Normapolles producers were colonizing areas where accumulation and preservation of organic matter were not favored.

It is difficult to attribute dicotyledon leaf remains from Late Cretaceous phyllocoenosis to a determinate taxonomical order. However, the occurrence of specimens of *Alnophyllum* and *Betuliphyllum* could indicate the presence of Fagales in the lower Maastrichtian Isona outcrop (southeastern Pyrenees; Marmi, 2016).

The presence of Cheirolepidiaceae in Campanian–Maastrichtian strata from Spain (Villalba-Breva et al., 2012, 2015) remain still not supported by palynological data obtained from Chera and elsewhere in Spain.

Conclusions

1. The vertebrate-bearing site of Chera can be dated as late Campanian/?early Maastrichtian on the basis of several terrestrial markers. The lack of reliable marine marker does not allow to independently confirm this biostratigraphic inference.

2. The productive palynofloral assemblages indicate different environments of depositions and surrounding vegetations.

3. The presence of wetlands with ephemeral or semi-permanent pools and lakes colonized by a vegetation involving peat-mosses, sedges and palms can be inferred by a clear palynological signal which has not been recorded in other Cretaceous successions from Spain.

4. Normapolles-producers and more evolved Fagales colonised driest hinterlands and formed part of woodlands and/or other open vegetation types.

5. Different types of wetlands and associated lowland vegetations co-existed in Spain during the Cretaceous and included freshwater and brackish ones.

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Figure captions

Figure 1 (Geol. settings and sections)

A. Simplified map of Valencia province showing the location of the collecting sites in the vicinity of Chera village; **B.** Stratigraphic sections of the Barranco del Agua (CH) and La Castellana (LC) sections (modified from Company, 2004).

Figure 2 (plate 1)

A–C. *Spinidinium* spp. sample CH-I-4b, sample CH-III-1-4; **D.** *Botryococcus* sp., sample CH-III-1b; **E.** *Ovoidites sprigii*, sample CH-III-1b; **F.** *Ovoidites* cf. *lignaeolus*, sample CH-III-1b; **G.** *Ovoidites* sp. 1, sample CH-III-1b; **H.** *Tetranguladinium conspicuum*, sample CH-III-1b; **I–J.** *Protoellipsodinium fibratum*, sample CH-III-1b; **K–L.** *Spicadinium* cf. *akidoton*, sample CH-III-1b. Scale bar equals 10µm.

Figure 3 (quantitative data)

Circular abundance diagrams of freshwater algae, spores, angiosperms and gymnosperms constituting the fertile palynomorph assemblages of Chera.

Figure 4 (plate 2)

A. *Biretisporites* cf. *potonieii*, sample CH-III-1b; **B.** *Undulatisporites* cf. *velamentis*, sample CH-III-1b; **C.** *Zlivisporis reticulatus*, sample CH-III-1b; **D.** *Cingulatisporites levispeciosus*, sample CH-I-4; **E.** *Ischyosporites* spp., sample CH-III-1b; **F.** *Patellasporites tavaresensis*, sample LC-I-5; **G.** *Gabonisporis vigourouxii*, sample CH-III-1b; **H.** *Gabonisporis cristatus*, sample CH-III-1b; **I.** *Gabonisporis?* sp. 1, sample CH-III-1b; **J–K.** *Ancanthotriletes?* *trigonus*, sample CH-III-1b; **L.** *Polypodiaceosporites verruspeciosus*, sample CH-III-1b. Scale bar equals 10µm.

Figure 5 (Plate 3)

A. *Equisetosporites multicostatus*, sample CH-III-1b; **B.** *E. patapscoensis*, sample CH-III-1b; **C.** *Penetetrapites inconspicuus*, sample CH-III-1b; **D–E.** *Dichastopollenites dunveganensis*, sample CH-III-1b; **F.** *Caprifoliipites* cf. *paleocenicus*, sample CH-III-1b; **G–H.** *Monocolpopollenites* sp. 1, sample CH-III-1b; **I.** *Monocolpopollenites* cf. *reticulatus*, sample CH-III-1b; **J.** *Albertipollenites rosalindiae*, sample CH-III-1b; **K–L.** *Trudopollis parvotrudens*, sample CH-III-1b; **M.** *Papillopollis* cf. *aradensis*, sample CH-III-1b; **N–O.** *Pseudoromeinipollenites laevigatus* new comb., sample CH-III-1b; **P.** *Rugulitriporites* sp., sample CH-I-4; **Q.** *Trudopollis* sp., sample CH-I-4; **R.** *Oculopollis minutus*, sample LC-I-5; **S.** *Oculopollis verrucosus*, sample CH-III-1b; **T.**

781 *Triatriopollenites* sp., sample LC-I-5; **U.** *Rhoipites* sp., sample CH-III-1b; **V.**
 782 *Gallaportapollenites?* sp., sample CH-III-1b; **W.** *Tetracolporites* sp., sample CH-III-1b;
 783 **X–Y.** *Subtriporopollenites anulatus*: **X.** Sample CH-III-1b; **Y.** Sample, LC-I-5; **Z.**
 784 *Plicapollis sertae*, sample CH-III-1b; **AA.** *Vacuopollis orthopyramis*, sample CH-I-4;
 785 **AB.** *Vacuopollis microconcavus*, sample LC-I-5; **AC.** *Subtriporopollenites* cf. *nanus*,
 786 sample CH-III-1b; **AD–AE.** *Vancampopollenites* spp.: **AD.** sample CH-I-4; **AE.** sample
 787 CH-III-1b; **AF–AG.** *Tetracolporopollenites* cf. *halimbaense*: **AF.** Small specimen,
 788 sample CH-III-1b; **AG.** Large specimen, sample CH-1b; **AH.** *Tricolpites* sp. 1, sample
 789 CH-I-4; **AI.** *Nudopollis terminalis*, sample CH-3-1b. Scale bar equals 10µm.

790
791 **Figure 6 (Plate 4)**

792 **A.** *Simpsonipollis mullensis*, sample CH-I-4; **B.** *Interporopollenites proporus*, sample
 793 CH-I-4; **C.** *Interporopollenites microporus*, sample CH-III-1b; **D–I.**
 794 *Vancampopollenites?* sp. 1, sample LC-5: **D.** Specimen in equatorial view; **E.** Specimen
 795 polar view; **F.** specimens in tetrad; **G–I.** Specimen observed under light microscopy
 796 (G) and 3-D rendering (H–I) based on Confocal Laser Scanning Microscopy; **J.**
 797 *Tricolpites synstriatus*, sample CH-III-1b. Scale bar equals 10µm.