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Contrasting origins of Early Cretaceous black shales in the Vocontian basin: Evidence from palynological and calcareous nannofossil records

Ulrich Heimhofer [a,*], Peter A. Hochuli [b,1], Jens O. Herrle [a,2], Helmut Weissert [a,3]

[a] Geological Institute, ETH Zürich, Sonneggstr. 5, 8092 Zürich, Switzerland
[b] Palaeontological Institute, University of Zürich, Karl Schmid-Strasse 4, 8006 Zürich, Switzerland

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Abstract

Detailed records of spore–pollen assemblages, particulate organic matter (OM), dinoflagellate cysts and calcareous nannofossils provide new insights into the palaeoclimatic and palaeoceanographic conditions during formation of Early Cretaceous black shales in the Vocontian basin (southeastern France). The early Aptian Niveau Goguel, which corresponds to the OAE1a, and the regionally distributed late Aptian Niveau Jacob have been studied with regard to changes in terrestrial vegetation patterns, terrigenous inputs and palaeofertility conditions. Palynological results from both black shale intervals exhibit a rich and stable floral pattern, dominated by various ferns, different types of cycads, bennettites as well as by several conifer families. Dinoflagellate cyst assemblages and the calcareous nannofossil-based nutrient index show no prominent changes in surface water productivity across the two studied intervals in the Vocontian basin. Significant variations are observed in terrestrial detrital input indicated by changes in absolute abundances of marine and terrestrial palynomorphs. According to our results, the laminated, OM-rich horizons of the Niveau Goguel interval reflect deposition during times of reduced siliciclastic input. Episodes of pronounced condensation were accompanied by anoxic conditions preventing degradation of the predominantly marine-derived OM. In contrast, the Niveau Jacob is characterised by a strong increase in terrestrial palynomorphs, most probably reflecting an abrupt increase in riverine runoff. The enhanced terrestrial OM input may have triggered oxygen-depletion in bottom waters, resulting in turn in increased OM preservation. Our results highlight the variety of processes that controlled the accumulation of OM in the Vocontian basin and they illustrate that enhanced surface water productivity is not an indispensable prerequisite for the formation of mid-Cretaceous black shales.

Keywords: OAE; Black shale; Cretaceous; Palynomorphs; Dinoflagellate cysts; Calcareous nannofossils

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[*] Corresponding author. Present address: Department of Earth Sciences, University of Oxford, Oxford OX1 3RPR, United Kingdom. Tel.: +44 1865 282113.

E-mail addresses: uli.heimhofer@earth.ox.ac.uk (U. Heimhofer), peter.hochuli@erdw.ethz.ch (P.A. Hochuli), Jens.Herrle@soc.soton.ac.uk (J.O. Herrle), helmi@erdw.ethz.ch (H. Weissert).

[1] Tel.: +41 1 6342338.

[2] Present address: Southampton Oceanography Centre, School of Ocean and Earth Science, European Way, Southampton SO14 3ZH, United Kingdom. Tel.: +44 23 80596449.

[3] Tel.: +41 1 6323715.

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1. Introduction

The Aptian to Turonian interval (~120–90 Ma, Gradstein et al., 1995) has been described as a time of exceptionally warm climates (Hallam, 1985; Wilson and Norris, 2001), low equator-to-pole thermal gradients (Barron, 1983; Huber et al., 1995; Jenkyns et al., 2004) and high levels of atmospheric carbon dioxide (Freeman and Hayes, 1992; Berner, 1994; Beerling and Royer, 2002). This period of greenhouse conditions was accompanied by the episodic formation of organic carbon-rich sediments ("black shales") in the world oceans, which have been interpreted to reflect major perturbations of the ocean-atmosphere system (Arthur et al., 1988; Bralower et al., 1994; Jenkyns, 1999; Herrle et al., 2003b; Erba and Tremolada, 2004; Wagner et al., 2004; Weissert and Erba, 2004). The relatively short-lived intervals (~50 to 500 ka) of organic carbon (OC) accumulation were confined to marine pelagic and hemipelagic environments and have been termed oceanic anoxic events (OAEs) by Schlanger and Jenkyns (1976). Besides the occurrence of globally distributed OC-rich deposits generated during OAEs, additional black shale intervals of only regional distribution are observed in Aptian to Albian sediments from the Atlantic and western Tethyan Oceans (Erba, 1991; Bréhéret, 1994; Erbacher et al., 1996; Friedrich et al., 2003; Herrle et al., 2004).

The processes that controlled the formation of the OC-rich deposits during the mid-Cretaceous are still a matter of debate. During the last decades, a variety of different palaeoceanographic models have been proposed, most of which can be assigned to one of two contrasting hypotheses. (1) The productivity model is based on the observation that enhanced fertility in ocean surface waters results in an increased flux of OM to the seafloor. This in turn causes increasing oxygen deficiency within the water column and hence, increased OM preservation under dysoxic to anoxic bottom waters. The important role of enhanced oceanic palaeoproductivity for the increase in OM burial during the mid-Cretaceous OAEs has been emphasised in various studies (e.g. Arthur et al., 1987; Pedersen and Calvert, 1990; Erba, 1994; Weissert et al., 1998; Jenkyns, 1999; Premoli Silva et al., 1999; Erba and Tremolada, 2004). (2) In contrast to this, the stagnant ocean model argues for a reduction of deep-water renewal and/or enhanced water column stratification. The decline in oxygen-rich deep water production prevents the aerobic degradation of OM within the water column and at the sediment–water interface, resulting in its accumulation at the seafloor

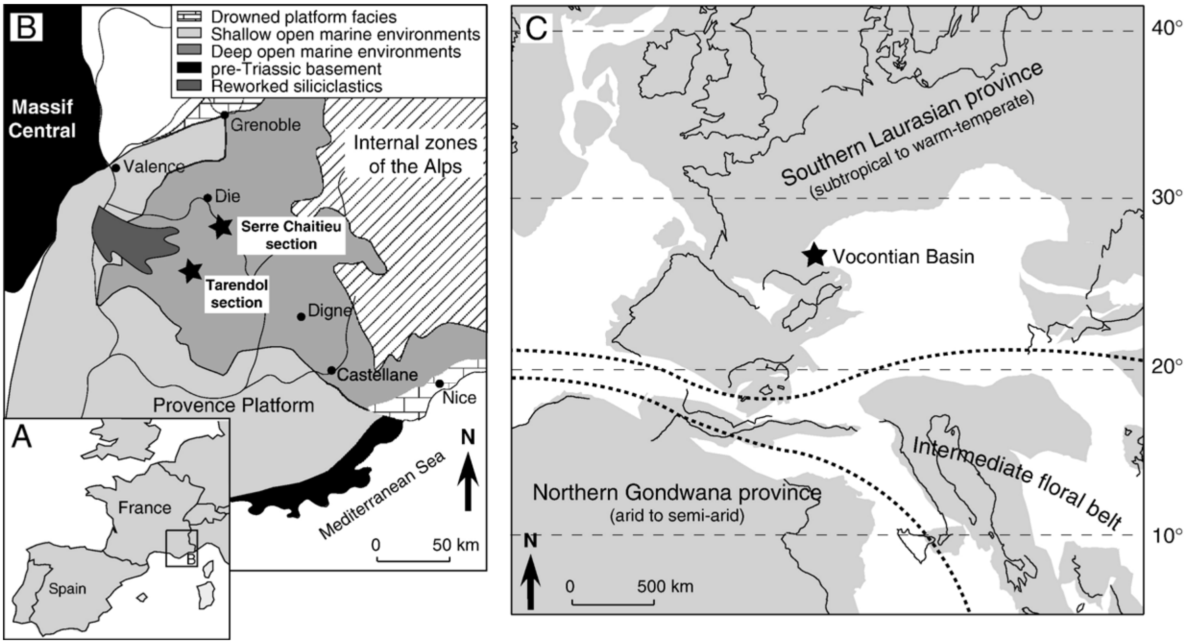


Fig. 1. (A) Location of the Vocontian basin in southeastern France. (B) Spatial distribution of different depositional settings within the Vocontian basin during the Early Cretaceous. Locations of the studied sections are marked with an asterisk. Map modified after Arnaud and Lemoine (1993). (C) Plate tectonic reconstruction of the western Tethys realm during the Early Cretaceous (~115 Ma). Position of the Vocontian basin is marked with an asterisk. Floral provinces and inferred climates after Brenner (1976) and Hochuli (1981). Map modified after Geomar map generator (www.odsn.de).

and in sediments (e.g. Schlanger and Jenkyns, 1976; Bralower and Thierstein, 1984; Arthur et al., 1990; Tyson, 1995; Erbacher et al., 2001). In addition, sea-level fluctuations have been suggested by various authors to play a key role in the formation of black shales in hemipelagic and pelagic settings (e.g. Bréhéret, 1994; Erbacher et al., 1996; Strasser et al., 2001). A number of studies have emphasised the important role of climatic fluctuations and the complex interplay between various factors (e.g. palaeoceanographic setting, basin configuration) in controlling the formation of OC-rich deposits (Kuypers et al., 2002; Herrle et al., 2003a; Wagner et al., 2004).

In order to obtain an understanding of the mechanisms controlling the formation of black shales during the mid-Cretaceous, both marine and terrestrial inputs need to be considered. In this study, the supraregionally distributed Niveau Goguel (OAE1a) and the regionally distributed Niveau Jacob, both deposited in the Vocontian basin (southeastern France) during the Aptian are chosen for comparison (Fig. 1). Spore–pollen records are combined with data based on calcareous nannofossils, organic-walled plankton, particulate organic matter and with geochemical results. The main objectives are: (i) to trace changes in terrestrial vegetation patterns across black shale episodes; (ii) to reconstruct variations in terrigenous input and sedimentation rates, and; (iii) to obtain information on changes in palaeoproductivity during periods of OM accumulation.

2. Material and methods

2.1. Palynology

Sixteen samples from the Serre Chaitieu section (Niveau Goguel) and thirteen samples from the Tarendol section (Niveau Jacob) were prepared for palynological analysis. Cleaned and weighed (10 to 12 g) samples were treated with hydrochloric and hydrofluoric acid following standard palynological preparation techniques (Traverse, 1988). The residue was sieved with an 11-μm mesh sieve and a first set of strew mounts was prepared for palynofacies analysis. A short oxidation with HNO_3 was performed on all residues before the preparation of a second set of strew mounts for palynological purposes. *Lycopodium* marker spores were added prior to preparation to obtain absolute counts per gram sediment. For palynofacies analysis the following major categories of particulate OM were distinguished: amorphous organic matter (AOM), opaque and translucent phytoclasts, cuticles, dinoflagellate cysts, other algae, foraminifera test linings and sporomorphs (incl. spores and pollen). Quantitative analysis involved three steps: (i) for palynofacies analysis, a minimum of 350 particles were counted per sample (excl. AOM), (ii) a minimum of 200 palynomorphs were counted for the determination of the absolute abundances of terrestrial and marine palynomorphs, (iii) a minimum of 200 sporomorphs were determined and counted for the pollen and spores assemblage and at least one slide per sample was screened for additional sporomorph taxa.

2.2. Calcareous nannofossils

Quantitative analyses of calcareous nannofossils were performed on 29 samples using the random settling technique of Geisen et al. (1999). At least 300 individuals were counted per sample in random traverses at ×1250 magnification. In addition to total abundance of calcareous nannoplankton, *Discorhabdus rotatorius*, *Zeugrhabdotus erectus*, *Watznaueria barnesae*, *Assipetra infracretacea*, *Rucinolithus terebrodentarius* and *Nannoconus* spp. have been counted separately because of their special palaeoecological and palaeoceanographic significance. In order to assess surface water productivity the nutrient index (NI) of calcareous nannofossils was calculated following Herrle et al. (2003b), where the high-productivity assemblage comprises *Z. erectus*, *D. rotatorius,* and the low-fertility assemblage consists of *W. barnesae*. To assess nannofossil preservation, light microscope identification of etching and overgrowth effects was used (e.g. Bown and Young, 1999).

2.3. Carbon isotope analysis, total organic carbon and carbonate carbon contents

To analyse the $\delta^{13}C$ composition of bulk carbonate carbon, powdered samples were treated with phosphoric acid at 90 °C. Subsequently, the liberated CO_2 gas was analysed with a VG PRISM mass spectrometer. All carbon isotope ratios are expressed in the standard (‰) notation in per mil (‰) relative to the international VPDB isotope standard. The $\delta^{13}C$ values of the carbonate carbon were calibrated against a laboratory internal standard (Carrara marble; $\delta^{13}C = 2.14‰$); analytical reproducibility was ±0.05‰. Carbonate carbon ($CaCO_3$) contents were determined using an UIC CM 5012 coulometer system. Powdered samples were treated with 2N $HClO_4$ to release the CO_2 from any carbonate minerals, which was subsequently measured by coulometric titration. Total carbon (TC) contents were measured on a CNS Elemental Analyser (Carlo

Erba Instruments). Total organic carbon (TOC) contents were calculated from the difference between TC and $CaCO_3$ contents.

3. Geological setting and studied sections

3.1. Geological setting

During the mid-Cretaceous, the Vocontian basin was situated at a palaeolatitude of 25° to 30°N (Hay et al., 1999), forming part of the northern continental margin of the Alpine Tethyan Ocean (Fig. 1). The *Marnes Bleues* formation, a thick monotonous succession of grey to dark-grey marls intercalated with calcareous marls, limestones and numerous black shale horizons was deposited in the basin between early Aptian and early Cenomanian times (Flandrin, 1963). Accumulation of fine-grained sediments in the Vocontian basin was largely confined to pelagic and hemipelagic environments. The basin was surrounded by slope and platform settings, resulting in the intercalation of hemipelagic facies with shallow-water sediments in marginal settings (Arnaud and Lemoine, 1993). To the east, the basin was open towards the Tethys Ocean facilitating exchange with Tethyan water masses. The studied sections were situated in the northern, deep marine part of the Vocontian basin, tens of kilometers south of the northern palaeo-margin (Arnaud and Lemoine, 1993).

3.2. Serre Chaitieu section (Niveau Goguel)

The Niveau Goguel has been sampled at the Serre Chaitieu section, which is located 20 km southeast of Die, about 1 km south of the village Lesches-en-Diois, Département Drôme, southeastern France (Figs. 1 and 2). The studied interval comprises 12 m, predominantly of dark-grey marls that are highly bioturbated with *Chondrites* and *Planolites* as the most common trace fossils (Bréhéret, 1997). Intercalated within the marls are six finely laminated, dark-grey to black paper shales ranging in thickness from 20 to 35 cm. The individual paper shales are labelled PS-1 to PS-6 in Fig. 4.

Based on biostratigraphic results (Moullade, 1966; Bréhéret, 1994, 1997; Herrle and Mutterlose, 2003) the studied interval is assigned to the early Aptian *Deshayesites deshayesi*/*Tropaeum bowerbanki* ammonite Zones and the middle part of the *Leupoldina cabri* planktic foraminiferal Zone (Fig. 2). The first occurrence of *Eprolithus floralis* can be recognized between the paper shales PS-3 and PS-4, a fossil that marks the lower part of the NC7A (*Rhagodiscus angustus*) and the top of the NC6 (*Chiastozygus litterarius*) calcareous nannofossil Zones.

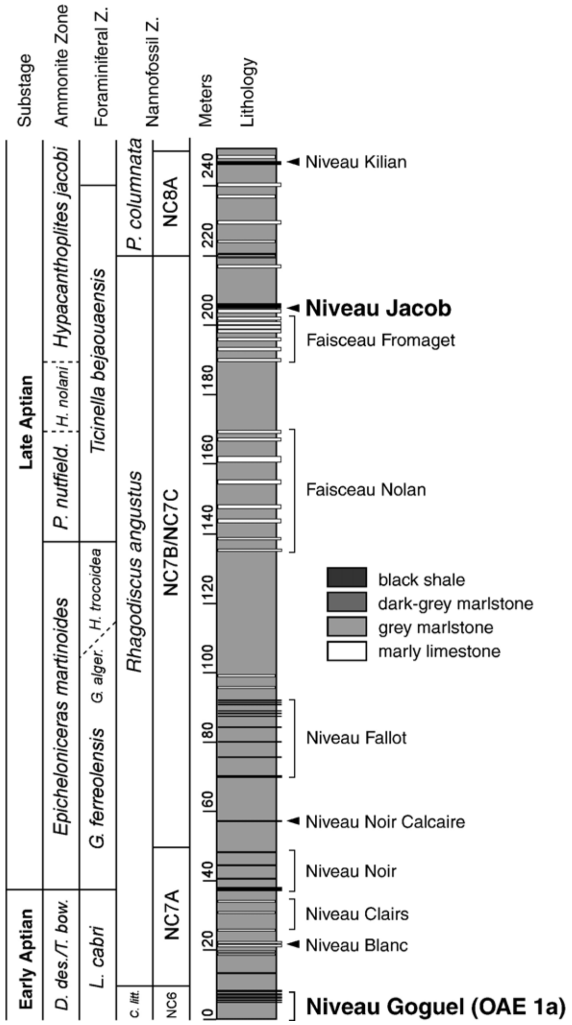


Fig. 2. Compiled lithological column and key beds of the Aptian *Marnes Bleues* succession in the Vocontian basin (southeastern France) plotted against biostratigraphy. Planktic foraminiferal and ammonite biostratigraphy after Bréhéret (1997 and references therein), calcareous nannofossil zonation after Herrle and Mutterlose (2003). *D. des*., *Deshayesites deshayesi*; *T. bow*., *Tropaeum bowerbanki*; *P. nutfield*., *Parahoplites nutfieldiensis*; *H. nolani*, *Hypacanthoplites nolani*; *L. cabri*, *Leupoldina cabri*; *G. ferreolensis*, *Globigerinelloides ferreolensis*; *G. alger*., *Globigerinelloides algerianus*; *H. trocoidea*, *Hedbergella trocoidea*; *C. litt*., *Chiastozygus litterarius*; *P. columnata*, *Prediscosphaera columnata*.

The paper shales and OM-rich marls of the Niveau Goguel correspond to the supraregionally distributed OAE1a (Weissert and Bréhéret, 1991; Bréhéret, 1997; Herrle et al., 2004). This event represents the first demonstrably global identified black shale event of the Cretaceous and was marked by several discrete episodes of OM deposition. The OAE1a was accompanied by dramatic turnovers in calcareous nannofossils (nannoconid-crisis of Erba, 1994; Erba and Tremolada, 2004) as well as in planktic foraminifera (Premoli Silva et al., 1999; Leckie et al., 2002) and radiolarians (Erbacher et al., 1996). Prominent changes in the global carbon budget before, during and after formation of the OAE1a are reflected in the $^{13}C/^{12}C$ ratio of organic and carbonate carbon. The resulting $\delta^{13}C$ pattern is characteristic for the early Aptian and has been documented worldwide from various depositional settings (Jenkyns, 1995; Menegatti et al., 1998; Bralower et al., 1999; Price, 2003; Herrle et al., 2004). Detailed chemostratigraphic correlation with the Cismon section of northern Italy (Menegatti et al., 1998) shows that the entire lower part (0 to 6.5 m) of the studied succession corresponds to the OAE1a interval (Heimhofer et al., 2004). Based on this observation, the entire lower part of the Serre Chaitieu section is referred to as Niveau Goguel in this study (Fig. 7A).

3.3. Tarendol section (Niveau Jacob)

The Niveau Jacob has been sampled at the Tarendol section, which is located about 2 km southwest of the village Tarendol (Département Drôme, southeastern France) on the eastern hillside of St. Etienne (Bréhéret, 1983) (Fig. 1). The 2 m of studied section encompasses the Niveau Jacob interval, which is composed of two, 35 and 25 cm thick, dark-grey indistinctly laminated horizons. The two black shale layers are characterised by mass-occurrences of ammonite compression fossils (*Hypacanthoplites jacobi*). Apart from the two black shale horizons, the section is composed of dark-grey, bioturbated marls with a marly limestone bed at the base (Délits Calcaire 1).

Biostratigraphically, the late Aptian Niveau Jacob is situated within the *H. jacobi* ammonite Zone, between the lowest occurrences of *Prediscosphaera spinosa* and *P. columnata* in the upper part of the *R. angustus* calcareous nannofossil Zone (NC7), and within the *Ticinella bejaouaensis* foraminiferal Zone (Bréhéret, 1983; Herrle and Mutterlose, 2003) (Fig. 2).

In contrast to the Niveau Goguel, the late Aptian Niveau Jacob interval is of only regional extent. A tentative correlation with the Livello 113 in the Umbria–Marche basin, Italy as well as with an OM-rich horizon in the Atlantic Ocean (DSDP Site 545) has been proposed by Erba et al. (1989) and Herrle et al. (2004), respectively. For the Niveau Jacob, neither a prominent carbon isotope anomaly nor a prominent faunal turnover in the benthic foraminiferal assemblage has been reported (Erbacher et al., 1998; Herrle et al., 2004).

4. Results and discussion

4.1. Preservation of the particulate OM

Although the sporopollenin of pollen and spore walls is relatively resistant to degradation, chemical and biological processes during transport and deposition as well as post-depositional alteration can corrode or even destroy palynomorphs. Generally, palynomorphs are more affected by degradation processes than refractory organic material (e.g. phytoclasts), which can result in an enrichment of the latter in the sediment (Tyson, 1995). Furthermore, thin-walled pollen grains are less resistant to biological/chemical alteration and more easily decomposed than thick-walled spores and pollen, leading to preferential preservation of particular thick-walled sporomorph groups. In order to exclude a strong preservational bias of the studied fossil palynofloral assemblages, the preservation of the OM has been carefully examined.

Visually, the preservation of the palynomorphs is good to excellent. The occurrence of well-preserved, fine-sculptured and thin-walled angiosperm pollen (e.g. *Retimonocolpites* spp; *Clavatipollenites* spp.) throughout the Serre Chaitieu section indicates the absence of a strong preservational bias towards more robust, thick-walled sporomorphs. In addition, the chemically less stable palynomorphs and the more degradation-resistant phytoclast fraction show similar variations in absolute abundances (particles/g sediment) in both studied sections, which is expressed in the good correlation between the two particle groups (Fig. 3). This indicates that selective preservation of palynomorphs in OM-rich horizons does not control the observed distribution patterns of the spore–pollen assemblage. However, distinct differences in sporomorph preservation can be observed between the two studied black shale intervals. The absence of thin-walled angiosperm pollen and the occurrence of biodegradation marks on individual spores in samples from the Tarendol section point to a moderate decomposition of the sporomorph fraction. The absence of similar signs of degradation in the marine-derived dinoflagellate cyst association in this interval indicates that alteration of the sporomorphs took place prior to deposition, most probably during transport.

Thermally unaltered conditions for the sedimentary OM in both section is inferred from $T_{\max}$ values of 420 to 435 °C (Bréhéret, 1994), unchanged colouring of the palynomorphs (thermal alteration index <2) and moderate to strong UV fluorescence of the amorphous fraction and the palynomorphs. In addition, several biomarker maturity indices including the 22S/(22R+22S)-hopane

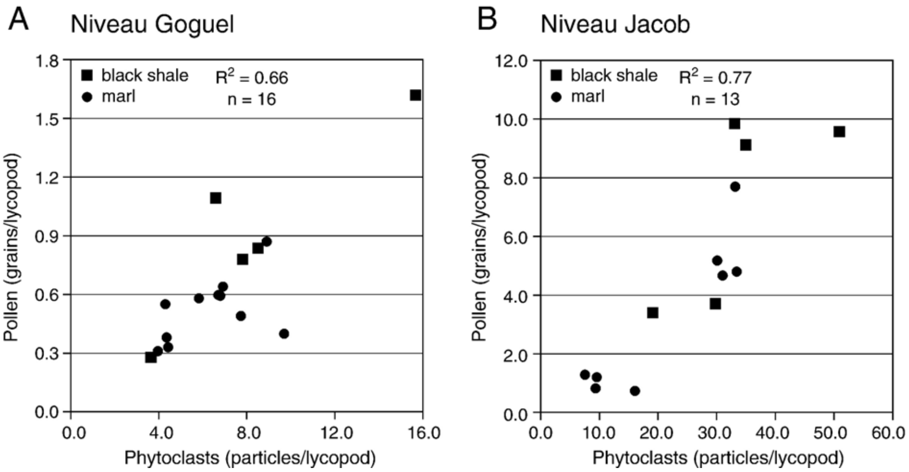


Fig. 3. Cross-plots of absolute abundances of pollen grains versus phytoclasts of the Niveau Goguel (A) and Niveau Jacob (B) from the Vocontian basin, southeastern France. Counted pollen grains exclude spores, bisaccate pollen and *Classopollis* spp. Squares correspond to samples from black shales, dots represent samples from bioturbated, marly lithology. Note the good correlation between the chemically less stable pollen grains and the more refractory phytoclast fraction.

(C_{31}) index, the Mor/(Mor+Hop) index and the Ts/(Ts+Tm) confirm the immature state of the organic matter with respect to hydrocarbon generation in both sections (Heimhofer et al., 2004).

4.2. Spore–pollen assemblages

4.2.1. Serre Chaitieu section (Niveau Goguel)

We distinguished 18 groups of spores and 19 groups of pollen grains in the microflora of the Serre Chaitieu section (Fig. 4A). *Classopollis* spp. is dominant and accounts for 16.7% to 42.3% (mean 29.2%) of the entire assemblage. Other common gymnosperm pollen includes *Araucariacites* spp. (5.9% to 12.9%; mean 7.2%), *Inaperturopollenites* spp. (2.5% to 11.3%; mean 5.7%) and *Sciadopityspollenites* spp. (1.0% to 5.5%; mean 2.8%). *Exesipollenites* spp. displays low abundance in the lower part (mean 3.7%) but is relatively common in the upper part (mean 9.7%). Bisaccate pollen (e.g. *Podocarpidites* spp., *Alisporites* spp.) accounts for less than 12.9% in most samples. Slightly increased abundance of bisaccates (up to 20.0%) occurs in paper shales (PS-1, 2 and 5). Representatives of angiosperm pollen include *Clavatipollenites* spp. and *Retimonocolpites* spp., which form a rare element of the observed floral assemblage (<2.0%; mean 0.5%). Pteridophyte spores represent another important constituent of the palynoflora. *Deltoidospora* spp. (11.4 to 20.6%; mean 15.1%) and *Gleicheniidites* spp. (2.5 to 10.9%; mean 6.1%) dominate the spore spectrum, whereas other spores like *Cicatricosisporites* spp., *Leptolepidites* spp. and *Retitriletes* spp. are of minor importance.

4.2.2. Tarendol section (Niveau Jacob)

The Tarendol section shows a microfloral composition similar to the Serre Chaitieu section, represented by 17 spore and 12 pollen taxa (Fig. 4B). The assemblage is dominated by pteridophyte spores, which account for up to 65.8% (mean of 48.5%). Again, the most abundant spore types are *Deltoidospora* spp. (mean of 17.5%) and *Gleicheniidites* spp. (mean of 6.3%). In addition, various indeterminate spores grouped under "other spores" are quantitatively of importance (mean of 23.7%). This group results from the fact that preservation hindered precise determination of all spores to generic level. Bisaccates display an increase from roughly ~20% in the lower and uppermost part of the section towards up to 36.4% within the Niveau Jacob. The remaining gymnosperm taxa are dominated by *Classopollis* spp., which shows strong variation in relative abundance ranging from absence to up to 22.8%. Other gymnosperm pollen such as *Exesipollenites* spp., *Inaperturopollenites* spp., *Sciadopytispollenites* spp. and *Araucariacites* spp. accounts for less than 6%, respectively. The complete absence of angiosperm pollen in the Tarendol section is interpreted to represent the consequences of selective degradation which preferentially affects small and thin-walled grains.

4.2.3. Terrestrial vegetation patterns

The palynofloral assemblages of both studied sections indicate a rich and diverse flora. Besides various fern families (e.g. Gleicheniaceae, Schizaeaceae, Osmundaceae, Dicksoniaceae), different types of ginkgo-

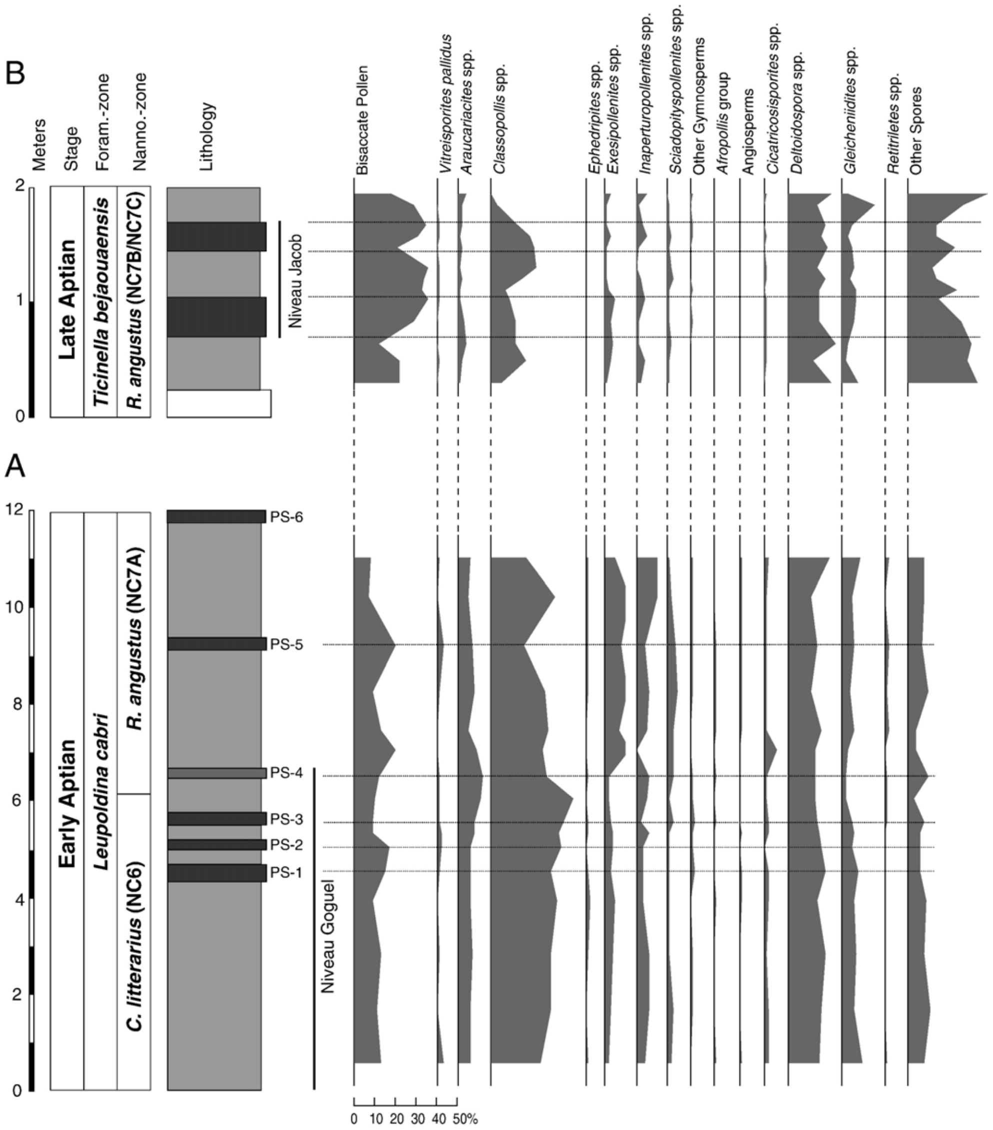


Fig. 4. Quantitative distribution patterns of selected spore and pollen types across the Niveau Goguel (A) and Niveau Jacob (B) from the Vocontian basin, southeastern France. Relative abundances of spores and pollen grains are expressed as percentages of the total sporomorph assemblage. Biostratigraphy of both sections after Herrle and Mutterlose (2003). Dotted lines mark position of individual black shale horizons. For lithological explanations see Fig. 2.

phytes, cycads, bennettites and several conifer families (incl. Araucariaceae, Cheirolepidaceae, Taxodiaceae and Podocarpaceae) can be identified. The rare but consistent occurrence of angiosperm pollen in the early Aptian deposits marks the incipient radiation of this plant group. The observed palynoflora of both studied sections is typical for the late Early Cretaceous Southern Laurasian floral province of Brenner (1976), which was characterised by a warm-temperate to subtropical humid climate (Fig. 1C). In contrast to this, the climate of the Northern Gondwana floral province further south is regarded as arid to semi-arid (Vakhrameyev, 1991; Chumakov et al., 1995). Some minor influence of the Northern Gondwana province is reflected in the rare occurrence of *Afropollis* spp. and *Ephedripites* spp. in the studied Serre Chaitieu section.

Based on the observed palynofloral association, a tentative interpretation of the corresponding habitats can be given. In Mesozoic assemblages, ferns are considered to be common elements of lush and moist vegetation along riversides and/or coastal lowlands (Mohr, 1989; Van Konijnenburg-Van Cittert and Van der Burgh, 1989). Therefore, the common occurrence of pteridophyte ferns in both sections probably indicates humid and warm habitats in the corresponding hinterland. Evidence for predominantly lowland and/or coastal vegetation can be inferred from the abundant occurrence of various pollen of bennettitalean and araucariacean affinity (Vakhrameyev, 1991; Abbink, 1998). The large quantities of *Classopollis* spp. are produced by the xerophythic and thermophilic Cheirolepidaceae, which are considered to reflect well-drained slope and upland environments (Vakhrameyev, 1982; Vakhrameyev, 1991) or mangrove-type, coastal vegetation (Watson, 1988). Bisaccate pollen, produced by Podocarpaceae and Pinaceae, is indicative of relatively dry upland vegetation; it generally dominates in boreal associations (Vakhrameyev, 1991; Abbink, 1998).

During and after the early Aptian Niveau Goguel (OAE1a), the vegetation patterns remain essentially stable and the dominant sporomorph forms persist throughout the studied record. Distinct variations can be observed only in the abundance of the thermophilic Cheirolepidaceae (*Classopollis* spp.) as well as in plants of questionable bennettitalean or taxodiacean affinity (*Exesipollenites* spp.). The increase in cheirolepidacean pollen in the upper part of the Niveau Goguel might reflect a shift to more arid conditions. Due to the ambiguous habitat preferences of the *Exesipollenites*-producing plants, a climatic interpretation cannot be given. Besides these fluctuations, we observe no indication for major disturbances in the vegetation patterns during and in the aftermath of the early Aptian Niveau Goguel (Heimhofer et al., 2004).

In contrast, the stratigraphic pattern of the Niveau Jacob spore–pollen assemblage displays some prominent variations. The most distinct feature is a strong increase in bisaccate pollen grains (from ~20% up to 35%) during deposition of the black shale that is paralleled by a significant decrease in pteridophyte spores in the same order of magnitude. Considering the fact that bisaccate pollen grains as well as thick-walled pteridophyte spores are particularly prone to selective sorting processes during transport and deposition (Heusser and Balsam, 1977; Traverse, 1988; Tyson, 1995), the observed shifts in the pollen spectra are interpreted to reflect variations in continent-derived OM supply rather than climatically driven changes of the vegetation pattern.

4.3. Particulate OM

4.3.1. Serre Chaitieu section (Niveau Goguel)

The studied section is characterised by low to moderate $CaCO_3$ (9.0% to 36.0%) and fluctuating TOC (0.4% to 2.3%) contents (Fig. 5A). The most enriched TOC values of up to 2.3% are restricted to the laminated paper shales. Biomarker analysis and Rock Eval data (hydrogen index of up to 500 mg HC/g TOC) indicate a marine phytoplankton and/or bacterial origin for most of the sedimentary OM in the studied section (Bréhéret, 1994; Heimhofer et al., 2004). The major constituent of the particulate OM is amorphous organic matter (AOM), which accounts for ~95% of the particulate OM in the Niveau Goguel interval and for 70% to 90% in the bioturbated marls above. The dominance of glossy, inclusion-rich and strongly fluorescent AOM in the lower part of the section and particularly within paper shales is interpreted to reflect dysoxic to anoxic bottom water conditions (Tribovillard and Gorin, 1991; Tyson, 1995). The phytoclast fraction is dominated by equidimensional particles, predominantly <20 μm in size. Together, opaque and translucent phytoclasts account for 32.2% to 52.0% (mean 37.3%) of the particulate OM (excl. AOM). The observed phytoclast assemblage is typical for deep-water sediments, which are generally characterised by the dominance of small, equidimensional, oxidized woody debris and some windblown charcoal (Habib, 1982; Tyson, 1995). The palynomorph fraction is clearly dominated by dinoflagellate cysts that range from 51.2% up to 81.3% (mean 67.4%) in relative abundance, emphasizing the open marine conditions of the depositional setting. In contrast, sporomorphs account for only 23.6% on average. Foraminifera test linings display strong fluctuations, ranging from 18.4% to complete absence in particular paper shales.

4.3.2. Tarendol section (Niveau Jacob)

The Tarendol section is characterised by relatively constant $CaCO_3$ contents of 21.2% to 36.1% but distinct fluctuations in the TOC record (Fig. 5B). The Niveau Jacob displays increased TOC values up to 2.2% compared to the intervals below and above (mean of 0.8%). The sedimentary OM of the Niveau Jacob has been characterised as type III kerogen (hydrogen index of ~200 mg HC/g TOC; oxygen index of ~30 mg CO_2/g TOC), indicating a major terrestrial contribution (Bréhéret, 1997). AOM accounts for up to 60% in the Niveau Jacob but is of only subordinate importance in the lower and uppermost parts of the section (<20%). The dominance of dark-brownish, non-fluorescent to poorly fluorescent AOM, and the occurrence of indistinct lamination in the OM-rich shales, point to deposition under oxygen-depleted, but not entirely anoxic conditions (Tyson, 1995). Similar dysoxic conditions have been proposed by Erbacher et

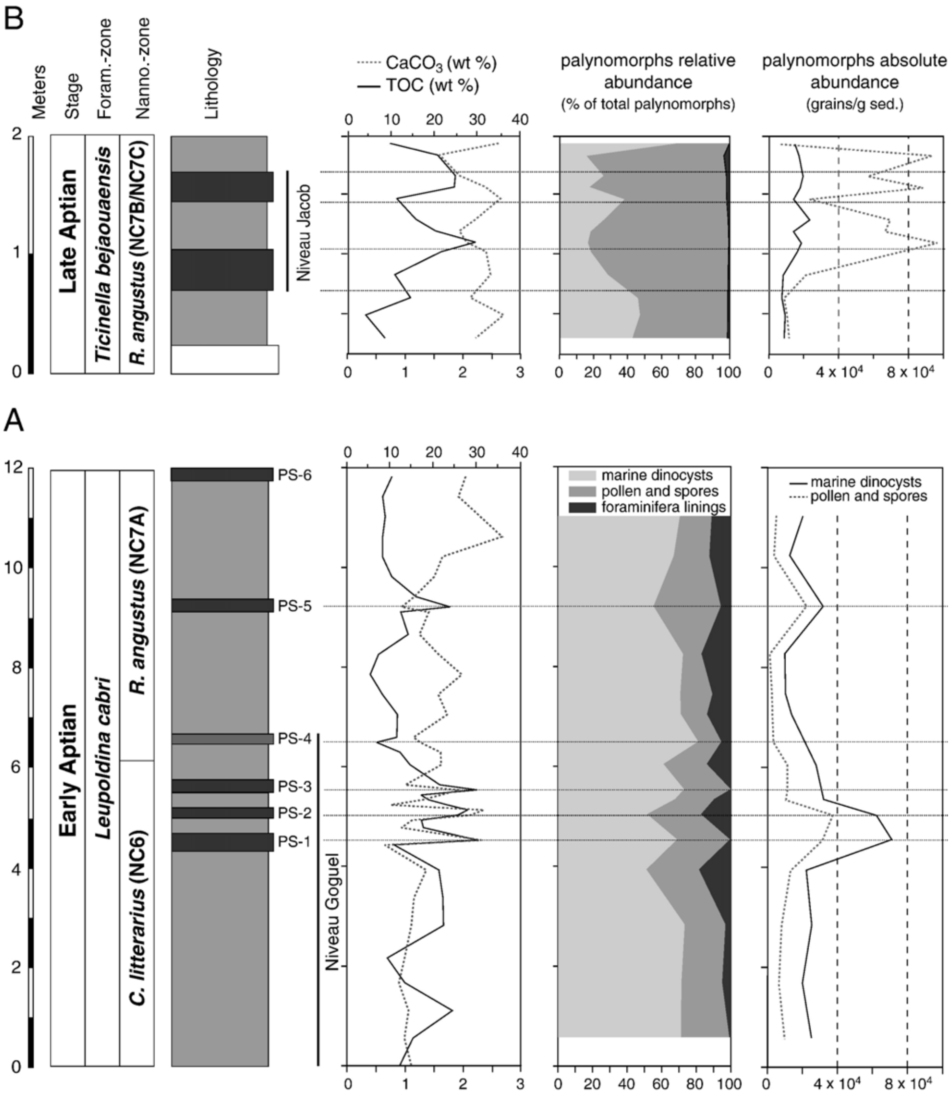


Fig. 5. Geochemical and palynofacies results across the Niveau Goguel (A) and Niveau Jacob (B) from the Vocontian basin, southeastern France. Relative abundances of dinoflagellate cysts, sporomorphs and foraminifera test linings expressed as percentages of the total palynomorph fraction. Absolute abundances of sporomorphs and dinoflagellate cysts expressed as grains per gram sediment.

al. (1998) for the deposition of the Niveau Jacob black shale based on benthic foraminiferal assemblages.

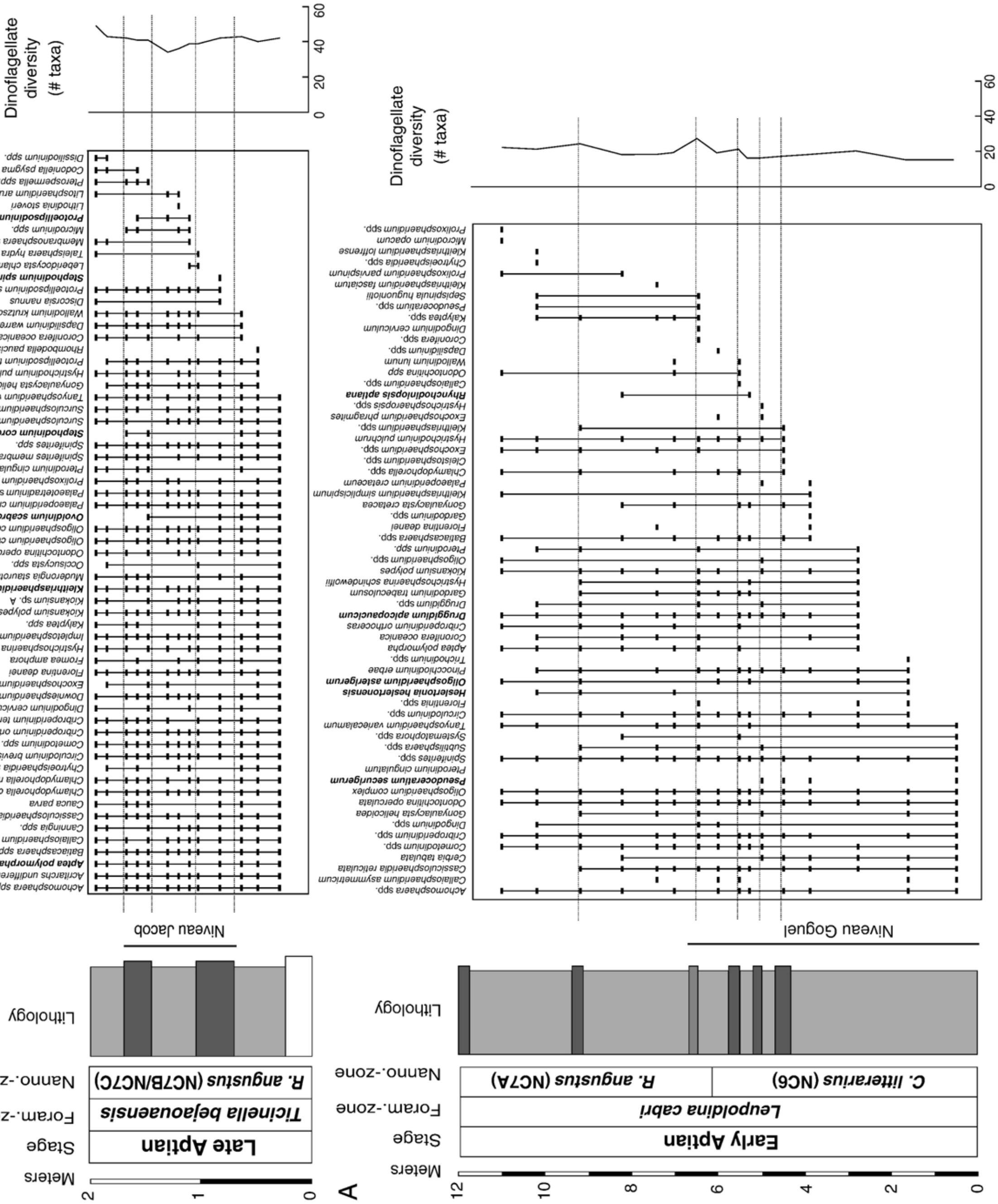
In comparison to the Serre Chaitieu section, the particulate OM composition of the Tarendol section displays a much stronger continental influence. The sediments are characterised by a considerable amount of blade-shaped phytoclasts, frequently >50 μm in size. Translucent and opaque phytoclasts are equally distributed and account for up to 70.8% (mean of 53.0%) of the total particulate OM (excl. AOM). The relative abundance of spores and pollen is considerably higher compared to the Serre Chaitieu section. Sporomorphs account for 31.3% to 83.7% (mean of ~68.0%) of the palynomorph assemblage and show a significant increase within the Niveau Jacob. Accordingly, the relative abundance of the dinoflagellate cysts shows the opposite pattern with mean values of ~31.0%. Foraminifera test linings are rare (<3.0%) or absent through most parts of the section.

4.3.3. Changes in terrigenous input and sedimentation rates

In the Serre Chaitieu section, the absolute abundances (grains/g sediment) of terrestrial sporomorphs and marine dinoflagellate cysts show a strong increase within paper shale horizons (PS-1, PS-2 and PS-5) compared to background values (Fig. 5A). Peak values of sporomorphs are as high as 3.8×10^4 sporomorphs/g sediment whereas dinoflagellate cysts account for up to 7×10^4 cysts/g sediment. Even though the two palynomorph groups are affected by completely different processes during transport and deposition, they display similar changes in absolute particle abundances. Considering the good correlation of the two records ($R^2 = 0.86$), roughly constant fluxes of both marine dinoflagellate cysts and terrestrial sporomorphs are suggested. Excluding selective preservation to account for the congruent pattern, the observed variations indicate significant changes in sedimentation rates during formation of the Niveau Goguel. Based on this interpretation, increased palynomorph abundances within paper shales correspond to lowered sedimentation rates and therefore reduced dilution by siliciclastic detrital material. In contrast, decreased abundances within bioturbated marls indicate periods of higher sediment flux and increased siliciclastic input. Our interpretation is supported by fluctuations observed in the $CaCO_3$ content. Peak values in $CaCO_3$ content correspond to OC-rich paper shale horizons, hence indicating lowered siliciclastic dilution of the hemipelagic carbonate sedimentation. Based on this interpretation, the paper shale horizons PS-1, PS-2 and PS-5 reflect episodes of pronounced condensation, most probably due to changes in sea-level and/or runoff patterns. This is in accordance to the results of Bréhéret (1994) who considered amalgamation and condensation processes to play a key role for the formation of Early Cretaceous paper shales in the Vocontian basin. The occurrence of elevated OM contents during periods of reduced sedimentation rates seems to be contradictory. To prevent the OM from degradation during its relatively long exposure at the sea floor, strongly oxygen-depleted conditions are required. Evidence for anoxic bottom water conditions during paper shale formation is provided by the finely laminated, non-bioturbated facies as well as by the dominance of glossy, fluorescent AOM. Based on organic facies analysis, similar low-oxygen bottom water conditions have been inferred for the laminated black shales of the time-equivalent Livello Selli interval (northern Italy) by Baudin et al. (1998) and Hochuli et al. (1999). Pancost et al. (2004) documented the occurrence of specific biomarkers (e.g. maleimides and high molecular weight porphyrins) from the Livello Selli horizon at Gorgo a Cerbara (Umbria–Marche basin, entral Italy). These biomarkers are diagnostic for green sulphur bacteria and indicate short-lived periods of euxinic conditions (i.e. a water column containing free H_2S) reaching the photic-zone during formation of the OAE1a.

Considering absolute palynomorph abundances, the Tarendol section exhibits a different pattern. Whereas dinoflagellate cysts show a twofold increase within the Niveau Jacob (up to 2×10^4 cysts/g sediment), pollen and spores exhibit an up to tenfold rise to peak values of 1×10^5 sporomorphs/g sediment (Fig. 5B). Pollen concentrations of similar magnitude have been reported from modern deltaic and lacustrine environments as well as from the euxinic sediments of the Black Sea (Traverse, 1988). The strong increase in continent-derived sporomorphs parallels the TOC content, indicating a predominantly terrestrial origin of the OM in the Niveau Jacob. This interpretation is in accordance with earlier results from the same section based on Rock Eval analysis of bulk rock (Bréhéret, 1994). In previous studies, the Niveau Jacob has been interpreted to reflect a sea-level lowstand and/or enhanced continental runoff, both mechanisms causing an increase in terrestrial OM flux towards the basin (Bréhéret, 1994; Erbacher et al., 1998). However, a lowered sea-level scenario is not supported by our palynological results. Bisaccate pollen has the capability to float for a relatively long time, resulting in a relative increase in abundance with increasing distance from the shoreline (Heusser and Balsam, 1977; Traverse, 1988). In contrast, thick-walled spores are in general deposited near shore, in the vicinity of river mouths (Tyson, 1995). The observed increase in bisaccate pollen grains and the concomitant decrease in pteridophyte spores in the Niveau Jacob interval are in contradiction with a proposed sea-level lowstand. Consequently, the prominent rise in terrestrial OM within the Niveau Jacob black shale is interpreted to reflect enhanced continental runoff rather than fall in sea-level. The episodic establishment of dysoxic conditions during formation of the Niveau Jacob was most probably triggered by the strongly enhanced input of land plant-derived OM towards the basin, causing increasing oxygen-deficiency in the water column and in bottom waters. Furthermore, the proposed increase in continental runoff might have caused water mass stratification in the semi-restricted Vocontian basin, resulting in diminished water mass mixing and hence, in improved OM preservation.

Fig. 6. Stratigraphic distribution of dinoflagellate cyst taxa, and dinoflagellate cyst diversity across the Niveau Goguel (A) and Niveau Jacob (B) from the Vocontian basin, southeastern France. Dinoflagellate cyst taxa ordered to first occurrences, selected dinoflagellate cyst biostratigraphic marker species are printed in bold. Dinoflagellate cyst diversity represents number of taxa per sample.


B
Meters
2
1
0
Stage
Late Aptian
Foram.-zone
Ticinella bejaouaensis
Nanno.-zone
R. angustus (NC7B/NC7C)
Lithology
Niveau Jacob
Achomosphaera spp.
Acritarchs undifferentiated
Aptea polymorpha
Batiacasphaera spp.
Callaiosphaeridium asymmetricum
Canningia spp.
Cassiculosphaeridia reticulata
Cauca parva
Chlamydophorella discreta
Chlamydophorella nyei
Chytroeisphaeridia spp.
Circulodinium brevispinosum
Cometodinium spp.
Cribroperidinium orthoceras
Cribroperidinium tenuiceras
Dingodinium cerviculum
Downiesphaeridium aciculare
Exochosphaeridium phragmites
Florentinia deanei
Fromea amphora
Hystrichosphaerina schindewolfii
Impletosphaeridium spp.
Kalyptea spp.
Kiokansium polypes
Kiokansium sp. A
Kleithriasphaeridium simplicispinum
Mudderongia staurota
Occisucysta spp.
Odontochitina operculata
Oligosphaeridium cf. verrucosum
Oligosphaeridium complex
Ovoidinium scabrosum
Palaeoperidinium cretaceum
Palaeotetradinium sp. A
Prolixosphaeridium parvispinum
Pterodinium cingulatum
Spiniferites membranaceus
Spiniferites spp.
Stephodinium coronatum
Surculosphaeridium longifurcatum
Surculosphaeridium trunculum
Tanyosphaeridium variecalamum
Gonyaulacysta helicoidea
Hystrichodinium pulchrum
Protoellipsodinium touile
Rhombodella paucispina
Coronifera oceanica
Dapsilidinium warrenii
Wallodinium krutzschii
Discorsia nannus
Protoellipsodinium spinosum
Stephodinium spinulosum
Lebedocysta chlamydata
Taleisphaera hydra
Membranosphaera sp. A
Microdinium spp.
Protoellipsodinium spinocristatum
Lithodinia stoveri
Litosphaeridium arundum
Pterospermella spp.
Codoniella psygma
Dissiliodinium spp.
Dinoflagellate diversity (# taxa)
0
20
40
60
A
Meters
12
10
8
6
4
2
0
Stage
Early Aptian
Foram.-zone
Leupoldina cabri
Nanno.-zone
R. angustus (NC7A)
C. litterarius (NC6)
Lithology
Niveau Goguel
Achomosphaera spp.
Callaiosphaeridium asymmetricum
Cassiculosphaeridia reticulata
Cerbia tabulata
Cometodinium spp.
Cribroperidinium spp.
Dingodinium spp.
Gonyaulacysta helicoidea
Odontochitina operculata
Oligosphaeridium complex
Pseudoceratium securigerum
Pterodinium cingulatum
Spiniferites spp.
Subtilisphaera spp.
Systematophora spp.
Tanyosphaeridium variecalamum
Circulodinium spp.
Florentinia spp.
Hesletonia heslertonensis
Oligosphaeridium asterigerum
Pinocchiodinium erbae
Tichodinium spp.
Aptea polymorpha
Coronifera oceanica
Cribroperidinium orthoceras
Druggidium apicopaucicum
Druggidium spp.
Gardodinium trabeculosum
Hystrichosphaerina schindewolfii
Kiokansium polypes
Oligosphaeridium spp.
Pterodinium spp.
Batiacasphaera spp.
Florentinia deanei
Gardodinium spp.
Gonyaulacysta cretacea
Kleithriasphaeridium simplicispinum
Palaeoperidinium cretaceum
Chlamydophorella spp.
Cleistosphaeridium spp.
Exochosphaeridium spp.
Hystrichodinium pulchrum
Kleithriasphaeridium spp.
Exochosphaeridium phragmites
Hystrichosphaeropsis spp.
Rhynchodiniopsis aptiana
Callaiosphaeridium spp.
Odontochitina spp
Wallodinium lunum
Dapsilidinium spp.
Coronifera spp.
Dingodinium cerviculum
Kalyptea spp.
Pseudoceratium spp.
Sepispinula huguoniotii
Kleithriasphaeridium fasciatum
Prolixosphaeridium parvispinum
Chytroeisphaeridia spp.
Kleithriasphaeridium loffrense
Microdinium opacum
Prolixosphaeridium spp.
Dinoflagellate diversity (# taxa)
0
20
40
60

4.4. Dinoflagellate cysts and calcareous nannofossils

4.4.1. Serre Chaitieu section (Niveau Goguel)

In the Serre Chaitieu section, a total of 61 different dinoflagellate cyst taxa have been identified to genus or species level (Fig. 6A). The relatively homogenous assemblage displays a typical early Aptian composition and is dominated by long ranging forms. In the studied interval, the most important dinoflagellate cyst marker species for the early Aptian include *Pseudoceratium securigerum*, *Heslertonia heslertonensis*, *Oligosphaeridium asterigerum*, *Druggidium apicopaucicum* and *Rhynchodiniopsis aptiana*. The groups *Achomosphaera* spp. and *Spiniferites* spp. have not been differentiated on species level. The common occurrence of the dinoflagellate cyst groups *Oligosphaeridium*, *Achomosphaera* and *Spiniferites* are interpreted to indicate open marine conditions (Lister and Batten, 1988; Wilpshaar and Leereveld, 1994) which is in accordance with the hemipelagic depositional setting of the studied locality (Bréhéret, 1997). Similar early Aptian assemblages have been documented from northern Italy (Cismon APTICORE) by Torricelli (2000), central Italy (Gorgo a Cerbara section) by Coccioni et al. (1993) and southeastern France (Gare de Cassis section) by Masure et al. (1998). The diversity distribution in the Serre Chaitieu section displays a relatively stable pattern throughout the succession (mean of 20 taxa per sample) with a slight increase in diversity towards the top. An exceptionally high diversity of 28 taxa can be observed only in paper shale horizon PS-4.

The calcareous nannofossil assemblage is dominated by (in descending order) *W. barnesae*, *Z. erectus*, *D. rotatorius*, *A. infracretacea*, *R. terebrodentarius* and *Nannoconus* spp. representing on average 46.6% of the total assemblage (Fig. 7A). The proportion of the most dissolution-resistant species *W. barnesae* ranges from 17.5% to 39.2% of the total assemblage. Following Thierstein (1980) and Roth and Bowdler (1981) proportions of *W. barnesae* >40% often indicate dissolution to the extent that the original assemblages no longer yield a primary signal. Both the low percentages of *W. barnesae* and the etching and overgrowth ranking of E1 to E1-2 and O1 (slightly etched and overgrown coccolith elements) of the studied samples indicate a good preservation of the calcareous nannofossil assemblage. The calculated nutrient index (NI) following Herrle et al. (2003b) varies between 24.5% and 48.1% (mean 38.1%). Low percentages (<38%) can be recognized in the lower part of the succession (Fig. 7A).

4.4.2. Tarendol section (Niveau Jacob)

In the Tarendol section, a total of 63 different dinoflagellate cyst taxa have been identified (Fig. 6B). The assemblage is very uniform and the majority of the forms occur throughout the studied interval. The dinoflagellate cyst diversity pattern displays no significant variations, the number of taxa per sample ranges between 34 and 49 (mean of 41) with the lowest dinoflagellate cyst diversity occurring in between the two black shale horizons. Typical for the assemblages of late Aptian age is the co-occurrence of several species such as *Aptea polymorpha*, *Kleithriasphaeridium simplicispinum*, *Ovoidinium scabrosum*, *Protoellipsodinium spinocristatum*, *Stephodinium coronatum* and *St. spinulosum*. The two first mentioned species have their last occurrence in this part of the section whereas the others are first found within this range. The groups *Achomosphaera* spp. and *Spiniferites* spp. have been differentiated only to genus level. The representatives of the latter groups as well as the genera *Oligosphaeridium* and *Kleithriasphaeridium* are very common and indicative for open marine conditions whereas groups typical for near-shore and restricted marine environments such as *Muderongia* and *Circulodinium* (Lister and Batten, 1988; Wilpshaar and Leereveld, 1994) are quite rare. The *Impagidinium* group which is regarded as typical for open oceanic conditions (Stover et al., 1996) has not been observed in the present material.

The nannofossil assemblage of the Tarendol section is characterised by similar abundances compared to the Serre Chaitieu section. *W. barnesae*, *D. rotatorius*, *Z. erectus*, *A. infracretacea*, *R. terenbrodentarius* and *Nannoconus* spp. representing on average 52.5% of the total assemblage (Fig. 7B). Most of the studied samples are characterised by good preservation with etching and overgrowth rankings of E1 and O1 (slightly etched and overgrown coccolith elements). The nutrient index (NI) varies between 11.8% and 49.3% (mean of 35.3%). Higher percentages (up to 49.3%) occur in the middle part of the studied succession including both black shale beds. Before and after the Niveau Jacob the NI values are rather low (>35%).

4.4.3. Changes in surface water productivity

We observe neither a significant impoverishment nor a strong diversity increase of the organic-walled plankton within or above the Niveau Goguel interval in the Vocontian basin. The slight increase in diversity towards the top of the studied interval is considered to reflect the response of the dinoflagellate cyst assemblage to the gradual reestablishment of normal marine conditions in the aftermath of Niveau Goguel (OAE1a),

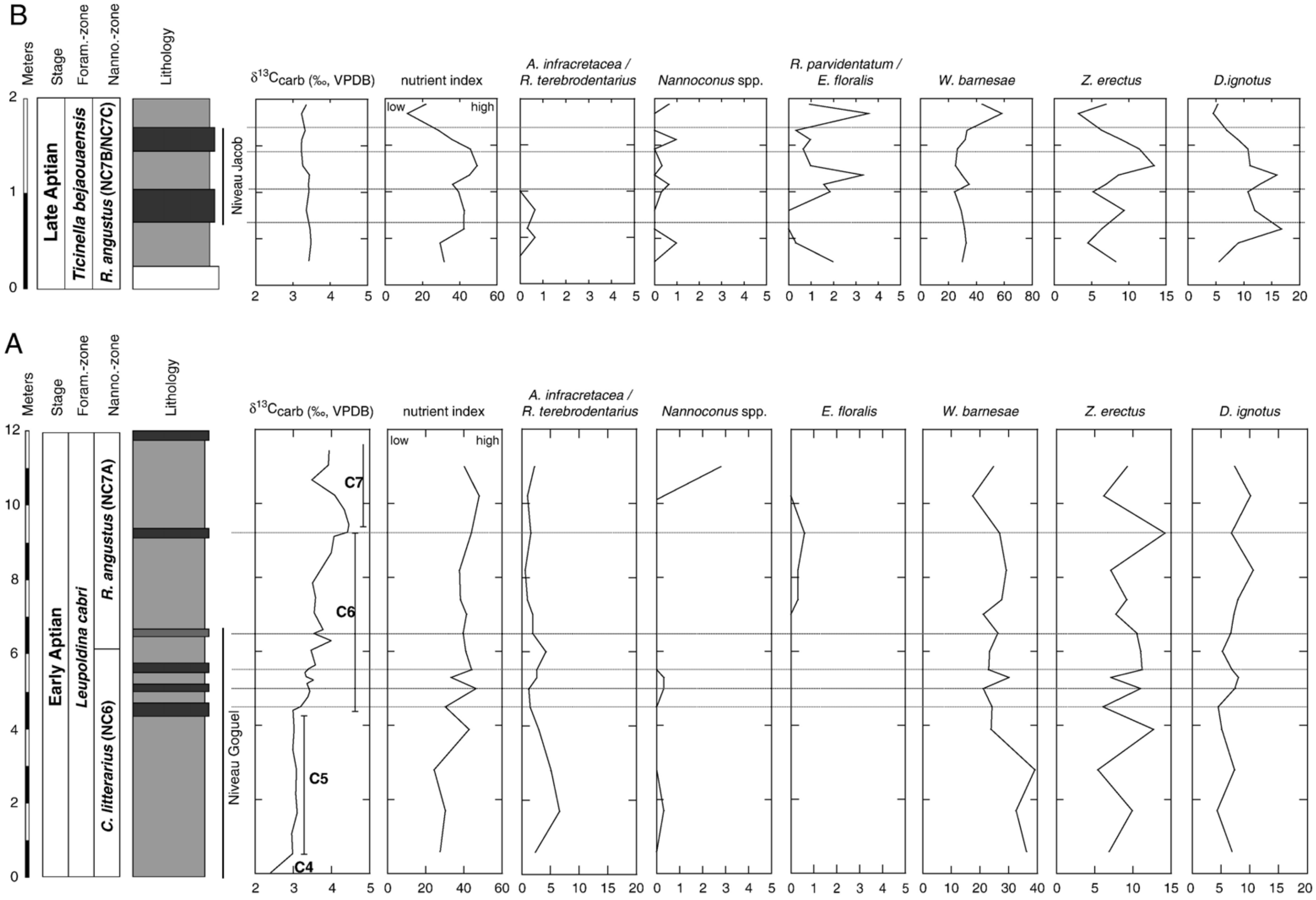


Fig. 7. Stratigraphic distribution of calcareous nannofossil taxa, calcareous nannofossil nutrient index (NI) and $\delta^{13}C_{carb}$ results across the Niveau Goguel (A) and Niveau Jacob (B) from the Vocontian basin, southeastern France. $\delta^{13}C$ of bulk carbonate carbon reported in per mil versus VPDB. Segments C4 to C7 based on chemostratigraphic correlation with isotope data from the Cismon section, northern Italy (Menegatti et al. 1998; Heimhofer et al., 2004). Calculation of calcareous nannofossil nutrient index (NI) according to Herrle et al. (2003b).

most probably accompanied by a rise in sea-level (Bréhéret, 1994; Wilpshaar and Leereveld, 1994; Strasser et al., 2001). According to Coccioni et al. (1993), the genus *Pterodinium* is characteristic of oligotrophic to mesotrophic conditions whereas *Odontochitina* is regarded to be indicative of eutrophic environments in mid-Cretaceous assemblages. In the studied Serre Chaitieu section, we observe no major change in abundance of the above mentioned dinoflagellate cyst groups.

Similarly, the calcareous nannofossil NI displays no strong evidence for a major change in surface water productivity during the Niveau Goguel. We observe no consistent pattern in NI corresponding to the occurrence of individual paper shale horizons. In comparison to earlier studies on the late Aptian Niveau Kilian (peak NI values > 65) and the early Albian Niveau Paquier (peak NI values > 75) from the Vocontian basin by Herrle et al. (2003b), the variations in surface water productivity across the Niveau Goguel interval are rather indistinct. The calculated NI values indicate low to moderate surface water productivity conditions during the Niveau Goguel and a subsequent increase above this interval. Furthermore, we observe no increase in radiolarian-derived silica or radiolarian sands across this interval in the Vocontian basin. However, due to the lack of data from the interval below the Niveau Goguel possible productivity changes preceding the black shale episode can not be evaluated.

These findings are in contrast to previous results from different Tethyan localities that highlighted the role of enhanced surface water productivity accompanied by increased OM flux to the sediments during the formation of the OAE1a. A shift towards mesotrophic/eutrophic conditions in ocean surface waters is suggested by significant changes in planktonic communities (Erba, 1994; Erbacher et al., 1996; Leckie et al., 2002; Erba and Tremolada, 2004), whereas highly eutrophic conditions were not achieved (Menegatti et al., 1998; Premoli Silva et al., 1999). A major change in the OC-fixing community during the OAE1a episode might be indicated by the high abundance of pelagic cyanobacteria remains in the corresponding sediments (Kuypers et al., 2004). Evidence for enhanced productivity is furthermore provided by peaks in geochemical proxies (e.g. Ba and P_2O_5) in OAE1a black shales (Bellanca et al., 2002). Higher nutrient availability in surface waters has been interpreted to reflect the complex interplay of accelerated hydrological cycling, increased continental weathering and enhanced runoff during greenhouse conditions (e.g. Weissert et al., 1998; Jenkyns, 1999; Larson and Erba, 1999; Premoli Silva et al., 1999; Bellanca et al., 2002).

A high-productivity scenario for the OAE1a is not supported by data from all Tethyan localities. In the Vocontian basin, neither the palynological results nor the dinoflagellate cyst and calcareous nannofossil assemblages suggest stronger hydrological cycling accompanied by an increase in phytoplankton productivity as a trigger for the formation of the Niveau Goguel and associated paper shales. Additional evidence for only moderate palaeofertility conditions during the OAE1a episode has been reported from the Gargano Promontary (southern Italy) by Luciani et al. (2001) based on planktic foraminifera and calcareous nannofossils. According to the data available, the role of enhanced productivity seems to be of variable importance for the formation of the OAE1a black shales in different areas of the western Tethys Ocean. Depending on various factors like basin configuration and prevailing circulation patterns (e.g. upwelling of nutrient-rich waters) the establishment of eutrophic environments during OAE1a was favoured in particular areas. The concurrent formation of black shales under mesotrophic conditions indicates that enhanced productivity did not represent an indispensable prerequisite for the accumulation of OM during OAE1a.

In the Tarendol section, diversity of the organic-walled plankton and NI shows a relatively stable pattern and indicate only minor changes with regard to surface water productivity during deposition of the Niveau Jacob. An increase in the NI, roughly corresponding to the two individual black shale horizons, is interpreted to reflect higher nutrient availability in surface waters, most probably due to enhanced continental runoff. This is in accordance to the results of Erbacher et al. (1998), who proposed the predominance of mesotrophic conditions throughout the Niveau Jacob based on the study of benthic foraminiferal assemblages and plankton/benthos ratios from the same outcrop.

5. Conclusions

Except for several similarities, our results highlight the different nature of the globally distributed Niveau Goguel (OAE1a) and the regionally occurring Niveau Jacob, both deposited in hemipelagic environments of the Vocontian basin during the Aptian. Both black shale intervals are characterised by enriched TOC-contents compared to the overlying and underlying strata and exhibit laminated sedimentary textures. The absence of intense bioturbation and the abundant occurrence of AOM indicates low-oxygen environments for both black shale episodes, although the degree of oxygen depletion was more pronounced in the Niveau Goguel.

The most significant differences between the two studied intervals appear in the composition and distribution of the OM, which is best illustrated in the absolute palynomorph abundances. Whereas the Niveau Jacob is clearly dominated by terrestrial OM, the Niveau Goguel exhibits a marine OM predominance. The strong increase in terrestrial OM in the Niveau Jacob most probably reflects an episode of enhanced continental runoff. The relatively abrupt increase in continent-derived OM flux towards the basin is interpreted to have triggered oxygen-depletion in the lower water column, which in turn resulted in enhanced OM preservation. In contrast, the formation of the Niveau Goguel and associated paper shales occurred during times of decreased siliciclastic input to the Vocontian basin, most probably due to changes in sea level and/or runoff. Episodes of pronounced condensation were accompanied by anoxic bottom water conditions, which protected the marine-derived OM from degradation.

The comparison of the two black shales emphasises the diversity of processes that influence the formation of OM-rich strata in the Vocontian basin. Our results illustrate that enhanced surface water productivity is not an indispensable prerequisite for the formation of black shales during the mid-Cretaceous. Discrepancies between the results from the Vocontian basin and data from other Tethyan localities might be explained by differing regional palaeoceanographic settings, resulting in different responses to global palaeoenvironmental change during the Aptian. An important precondition for the formation of OM-rich black shales was most probably given by the rather low deep-water oxygen concentrations of the mid-Cretaceous ocean basins, which resulted in a strong propensity towards dysoxic to anoxic water column conditions (Bralower and Thierstein, 1984; Bréhéret, 1994).

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