

## Early Jurassic climate change and the radiation of organic-walled phytoplankton in the Tethys Ocean

Bas van de Schootbrugge, Trevor R. Bailey, Yair Rosenthal, Miriam E. Katz, James D. Wright, Kenneth G. Miller, Susanne Feist-Burkhardt, and Paul G. Falkowski

**Abstract.**—During the Early Jurassic, cyst-forming dinoflagellates began a long-term radiation that would portend ecological importance of these taxa in the pelagic plankton community throughout the rest of the Mesozoic era. The factors that contributed to the evolutionary success of dinoflagellates are poorly understood. Here we examine the relationship between oceanographic and climatic conditions during the Hettangian–Toarcian interval in relation to the radiation of dinoflagellates and other organic-walled phytoplankton taxa in the Tethys Ocean. Our analysis is based on two data sets. The first includes  $\delta^{13}\text{C}_{\text{carb}}$ ,  $\delta^{13}\text{C}_{\text{org}}$ , total organic carbon (TOC), and quantitative palynological observations derived from the Mochras Core (Wales, U.K.), which spans the complete Early Jurassic. The second is a coupled Mg/Ca and  $\delta^{18}\text{O}$  record derived from analyses of belemnite calcite obtained from three sections in northern Spain, covering the upper Sinemurian to Toarcian. From these two data sets we reconstructed the influence of sea level, trophism, temperature, and salinity on dinoflagellate cyst abundance and diversity in northwest Europe. Our results suggest that organic-walled phytoplankton (acritarchs, prasinophytes, and dinoflagellates) diversity increased through the Early Jurassic. The radiation coincides with a long-term eustatic rise and overall increase in the areal extent of continental shelves, a factor critical to cyst germination. On shorter timescales, we observed short bursts of dinoflagellate diversification during the late Sinemurian and late Pliensbachian. The former diversification is consistent with the opening of the Hispanic Corridor during the late Sinemurian, which apparently allowed the pioneer dinoflagellate, *Liasidium variable*, to invade the Tethys from the Paleo-Pacific. A true radiation pulse during the late Pliensbachian, with predominantly cold-water taxa, occurred during sea level fall, suggesting that climate change was critical to setting the evolutionary tempo. Our belemnite  $\delta^{18}\text{O}$  and Mg/Ca data indicate that late Pliensbachian water masses cooled ( $\Delta T \approx -6^\circ\text{C}$ ) and became more saline ( $\Delta S \approx +2$  psu). Cooling episodes during generally warm and humid Early Jurassic climate conditions would have produced stronger winter monsoon northeast trade winds, resulting in hydrographic instability, increased vertical mixing, and ventilation of bottom waters. During the late Pliensbachian, dinoflagellates replaced green algae, including prasinophytes and acritarchs, as primary producers. By producing benthic resting cysts, dinoflagellates may have been better adapted to oxidized ocean regimes. This hypothesis is supported by palynological data from the early Toarcian ocean anoxic event, which was marked by highly stratified anoxic bottom water overlain by low-salinity, warm surface waters. These conditions were advantageous to green algae, while cyst-producing dinoflagellates temporarily disappeared. Our results suggest that the rise in dinoflagellate diversity later in the Jurassic appears to correspond to deep water ventilation as a result of the opening of the Atlantic seaway, conditions that appear to have simultaneously led to a loss of prasinophyte dominance in the global oceans.

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### Introduction

The Early Jurassic (Hettangian–Toarcian) witnessed major marine faunal and floral turnovers in the aftermath of the Triassic/Jurassic boundary mass extinction (Little and Benton 1995). All levels of the marine food

web underwent extensive reorganization; predators such as ammonites, and especially belemnites, flourished in open waters, providing useful biostratigraphic markers and “fast food” for a highly diverse community of marine reptiles, such as the ichthyosaurs (Gus-

tomesov 1978). Contemporaneously, new groups of photosynthetic eukaryotic phytoplankton taxa, including cyst-forming dinoflagellates and calcareous nannoplankton, which first appeared in the Middle–Late Triassic, radiated rapidly during the Early Jurassic (Bown et al. 1992; Stover et al. 1996; Fensome et al. 1999). Modern members of these algal groups contain “red” plastids (characterized by the presence of chlorophyll *a* and *c* in their photosynthetic organelles). These “red” phytoplankton appear to have displaced “green” plastid eukaryotic algae (characterized by the presence of chlorophyll *a* + *b*) as dominant primary producers from the Mesozoic to the present (Falkowski et al. in press). Here we examine the early evolution of one of these groups, the dinoflagellates.

The evolution of dinoflagellates is reconstructed from the taxonomy of cysts, which are dominantly nonmotile (hypnozygotic) resting stages of motile pelagic cells. The cysts are made of extremely durable biopolymers (dinosporin), sometimes coated with silica or carbonate. Whereas motile (free-swimming) dinoflagellates appear to prefer well-stratified waters, cyst formation (although still poorly understood) has been related to changes in water column stability, such as increased turbulence during late spring and autumn (Dale 1983). In the contemporary ocean, cysts tend to be most abundant in seas of temperate latitudes (Wall et al. 1977). Encystment has also been shown by many neontologists (e.g., Pfister and Anderson 1987) to be strongly related to nutrient depletion (N and P). Other triggers for encystment include decreasing temperatures, high population density and low light (Wall et al. 1977; Dale 1976, see overview in Tyson 1995).

Although there is no body fossil evidence to suggest that dinoflagellates originated before the Middle Triassic (except for a handful of acritarchs with dinoflagellate affinities), organic geochemical (dinosteranes) and molecular phylogenetic evidence indicates that dinoflagellates were present since at least the Cambrian (Moldovan and Talyzina 1998). However, Fensome et al. (1999) showed that the radiation of cyst-forming dinoflagellates from the Late Triassic to the Early Jurassic was a

true evolutionary event. On the basis of this finding, one might hypothesize that the “invention” of benthic resting cysts was a major contribution to the evolutionary success of dinoflagellates during the Mesozoic. Hence, understanding environmental changes controlling cyst-forming dinoflagellates can be used to further our understanding of the group as a whole.

In this paper, we present a multi-proxy data set that includes long-term  $\delta^{13}\text{C}_{\text{carb}}$  and  $\delta^{13}\text{C}_{\text{org}}$  isotope and total organic carbon (TOC) records obtained from the Llanbedr Mochras Farm Borehole core in Wales (U.K.). These data permit analysis of changes in carbon cycling in surface waters, trophism, and water stability (ventilation of bottom waters) from the northern reaches of the Tethys Ocean during the Early Jurassic. Our palynological analyses from the same core include dinoflagellates, acritarchs, and prasinophytes (representatives of the green line). To assess the influence of temperature and salinity on dinoflagellate abundance and diversity, we generated detailed  $\delta^{18}\text{O}$  and Mg/Ca records from Early Jurassic belemnites sampled in nearby Cantabria, northern Spain. Our data set is used to address the following questions:

1. *When did the founder species of cyst-forming dinoflagellates first appear in the Tethys Ocean and what were their origins?*

In the early late Sinemurian, almost exclusively cysts of the dinoflagellate *Liasidium variable* Drugg 1978 are found in the fossil record. This species shares some morphological similarities with Late Triassic Rhaetogonyaulacaceae and appears to have been the progenitor of Early and Middle Jurassic dinoflagellates. We examine what tectonic and paleoenvironmental conditions may have contributed to the rise of *L. variable* in the Tethys in the Early Jurassic.

2. *What paleoenvironmental factors contributed to the radiation of dinoflagellates in the late Pliensbachian?*

The late Pliensbachian was a crucial time for dinoflagellates, because it shows the appearance of another missing link from the extinct order Nannoceratopsiales. Nannoceratopsiales combine characters of dinophysoid tab-

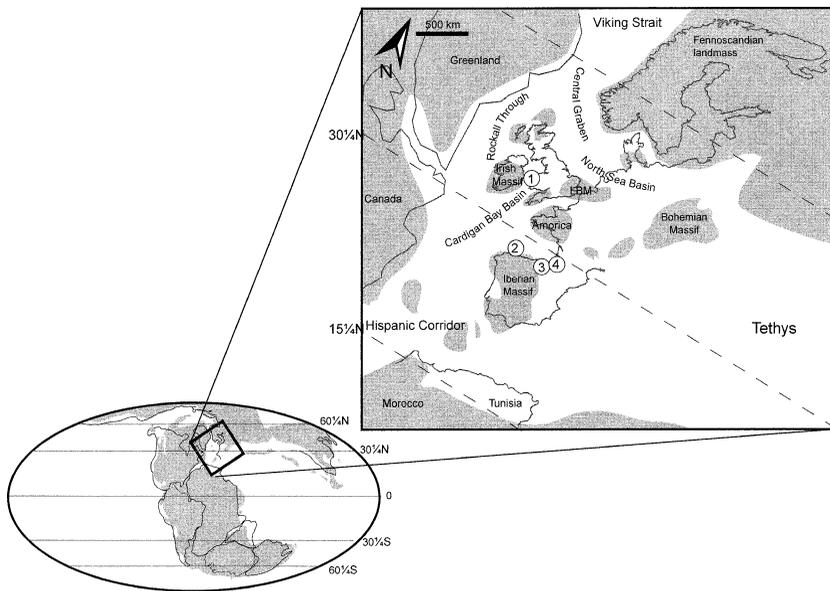


FIGURE 1. Palaeogeography for the Early Jurassic (Pliensbachian; 195 Ma). Studied sections are indicated: 1, Mochras Borehole. 2, Playa de la Griega. The Playa de la Griega (PLG) section is located toward the northeast of Oviedo along the Cantabrian shoreline and was previously studied by Suarez Vega (1974). 3, Castillo de Pedroso. The Castillo de Pedroso (CDP) section was studied previously by Comas-Rengifo et al. (1988). 4, Camino. The Camino (CAM) section close to Reinosa covers the upper Sinemurian to upper Pliensbachian and has been studied for its ammonite biostratigraphy by Braga et al. (1988).

ulation, which is found almost exclusively in extant dinoflagellates and some putative Devonian forms, and features of peridinioid-gonyaulacoid tabulation, which is characteristic for many of the groups that became abundant later in the Mesozoic (Fensome et al. 1999). Using trace element (Mg/Ca) and oxygen isotope analyses derived from belemnite calcite (Bailey et al. 2003), we examine how changes in water mass conditions set the stage for the expansion of cyst-forming dinoflagellates. The late Pliensbachian radiation is also of special interest because it directly precedes the Toarcian Oceanic Anoxic Event (T-OAE).

### 3. What role did the Toarcian OAE play in selecting phytoplankton taxa?

The lower Toarcian black shales mark a dramatic paleoceanographic perturbation that has been recognized in marine successions worldwide (Jenkyns and Clayton 1986; Jenkyns 1988; Jenkyns et al. 2001). Cyst-forming dinoflagellates temporarily disappeared from successions across northwest Europe, leading to a “dinoflagellate cyst blackout” in the earliest Toarcian. They were being replaced by the “old” lineage of green algae (Prauss and

Riegel 1989; Prauss et al. 1991; Feist-Burkhardt 1992; Bucefalo Palliani and Riding 1999; Bucefalo Palliani et al. 2002). What paleo-environmental conditions temporarily changed the oceans from “red” back to “green”?

## Geological Background

The Llanbedr Mochras Farm Borehole (Fig. 1), drilled by the British Geological Survey in 1969 (Woodland 1971) has been studied for benthic foraminifera (Müller 1990), ostracods (Boomer 1991; Boomer and Whatley 1992), TOC,  $\delta^{13}\text{C}_{\text{carb}}$ ,  $\delta^{13}\text{C}_{\text{org}}$ , sulphur contents (Jenkyns and Clayton 1997; Hesselbo et al. 2000), as well as  $\delta^{15}\text{N}$  (Jenkyns et al. 2001). No geochemical study has been undertaken that spans the whole Jurassic section of the core. The extreme thickness (1305 m) of the Liassic in Mochras can be ascribed to the paleogeographic position close to the depositional center of the Cardigan Bay Basin, and also points to continuous subsidence. Ammonite biostratigraphy reveals no significant hiatuses. Plant debris is dispersed throughout the whole Lower Jurassic of Mochras, indicating the presence of nearby landmasses, such as Cor-

nubia to the south, the Irish Massif toward the west, and the London-Brabant Massif toward the east (Fig. 1). Proximity to the North American continent may also have influenced deposition in the Cardigan Bay Basin.

The Liassic in Mochras consists predominantly of alternating shaly limestones, marly siltstones, and micaceous mudstones. In contrast to other areas, no extensive sandy facies is developed at Mochras (Woodland 1971). From 1560 to 1370 m, ferruginous nodules occur and pyrite, which is present throughout, is particularly abundant. Much of the carbonate accumulating in Tethyan pelagic settings during the Early Jurassic was delivered from shallow marine carbonate platforms (Cobianchi and Picotti 2001). There is arguably evidence for the occurrence of calcareous nannoplankton in the Mochras core. However, due to the poor preservation of the nannoplankton fossils, a quantitative assessment of its contribution to carbonate deposition in Mochras is not available (F. Tremolada personal communication 2004). It is therefore likely that the bulk carbonate includes components of both shallow marine platform-derived and pelagic carbonates.

Belemnites were sampled from three sections in Cantabria (northern Spain; Fig. 1). The Camino section presents a classic example of a gradually deepening carbonate ramp with a thick Hettangian-Sinemurian succession consisting of inner-neritic platform carbonates and dolomites overlain by a very expanded upper Sinemurian to Toarcian succession of hemipelagic marls, limestones, and occasional black shales (Comas-Rengifo et al. 1988). In Camino, belemnites are abundant throughout the Pliensbachian. The Castillo de Pedroso section shows a similar facies development as the Camino section (Braga et al. 1988). Belemnites are abundant in the upper Pliensbachian *Pleuroceras spinatum* Zone, but unfortunately are rare across the black shales in the lowermost Toarcian *Dactyloceras tenuicostatum* Zone. The Playa de la Griega section represents a more offshore facies than the other two sections and covers the upper Sinemurian to upper Pliensbachian. Belemnites become abundant above a ferruginous upper Sinemurian hardground with abundant brachio-

pods that is tentatively placed in the *Oxynotoceras oxynotum* Zone (Suarez Vega 1974). This section shows a pronounced black shale interval in the upper Pliensbachian *Amaltheus margaritatus* Zone.

Correlation of the two regions (Wales and Spain) is achieved by ammonite biostratigraphy; however, the correlation is complicated by diachrony in the ammonite zones, especially around the Pliensbachian/Toarcian boundary. The black shales that mark the early Toarcian OAE occur at the base of the *Harpoceras falciferum* Zone in the more Boreal influenced Mochras core, whereas they are assigned to the top of the *D. tenuicostatum* Zone in Spain (Comas-Rengifo et al. 1988). Sections in northern Spain have a mixed Boreal/Tethyan ammonite assemblage. The discrepancy in the correlation of the lower Toarcian Boreal *Harpoceras falciferum* Zone and Tethyan *Hildaites serpentinus* Zone was clearly illustrated by using C-isotope stratigraphy (Jenkyns and Clayton 1997) and also by applying nanofossil biostratigraphy to the Brown Moor Borehole (U.K.) and central Italy (Bucefalo Palliani et al. 2002).

## Methods

Carbon stable isotope data were obtained by using a multi-prep peripheral device connected with an Optima mass spectrometer at Rutgers University. Replicate analyses of NBS19 yielded precision better than  $\pm 0.06$  per mil for  $\delta^{13}\text{C}$  and better than  $\pm 0.08$  per mil for  $\delta^{18}\text{O}$ . Values are reported in ‰ PDB.

Belemnite samples were prepared following procedures discussed at length by Bailey et al. (2003). Belemnites were crushed to millimeter size chips and approximately ten fragments, judged pristine, were handpicked with the help of a dissecting microscope and crushed to powder. This homogenization helps to exclude ontogenetic effects on isotope and trace element measurements. We took special care to avoid the outside laminae and apical line as these parts of the belemnite rostrum have been shown to be often diagenetically altered. Powdered samples were analyzed for Mg/Ca with a Finnigan MAT Element Sector Field Inductively Coupled Plasma Mass Spectrometer (ICP-MS) operated in low resolution ( $m/\Delta m =$

300) following the method outlined in Rosenthal et al. (1999) as modified by Lear et al. (2002). Analytical precision, determined by replicate analysis of standards, was <2% rsd ( $1\sigma$ ) for Mg/Ca (6.1 mmol/mol). To assess the diagenetic alteration of belemnite rostra geochemically, Mn/Ca ratios were measured simultaneously.

$\delta^{13}\text{C}_{\text{org}}$  isotopes were measured directly on the organic matter residues obtained from the palynological processing (see below). Paleo-Science Inc. in Miami made the measurements with a Costech elemental combustion system coupled to a ThermoFinnigan Delta Plus mass spectrometer. Calibration was done with NIST 8541 and precision was better than 0.25‰ VPDB.

Palynological processing of selected crushed, air-dried, marly samples was accomplished by dissolving 15 g of rock in concentrated HCl and HF in alternating steps. After washing with distilled  $\text{H}_2\text{O}$ , the acid-resistant fraction was sieved with a 15- $\mu\text{m}$  mesh sieve. We had to refrain from the use of spiked samples, as the addition of *Lycopodium* would have compromised our organic carbon isotope analyses. The residues were split and one-half was analyzed for organic carbon isotopes (see above). Because most samples contain varying amounts of amorphous organic matter and pyrite, which hamper visual determination of palynomorphs, oxidative maceration was done with Schulze's solution ( $\text{KClO}_3$  and 65%  $\text{HNO}_3$ ). Bismarck Brown stained fractions were mounted on microscope slides with Loc-tite or glycerin jelly and studied in transmitted light at 400–1000 $\times$  magnifications. Up to 200 structured palynomorphs were counted per slide. Initially only dinoflagellate cysts were determined to the species level. Other marine palynomorphs (acritarchs, prasinophytes, and foraminifera linings) were counted as part of widely used groups such as *Microhystridium*- and *Verhachium*-complex, leiospherids, prasinophyte phycmata, and foraminifera organic inner-wall linings. When counting was completed, slides were scanned entirely for acritarchs, which were classified according to Wall (1965), in order to get an estimate of acritarch diversity. This scanning also increased the likelihood of finding rare

dinoflagellate cysts. The reported number of acritarch species must be taken as a minimum value, as the use of a 15- $\mu\text{m}$  mesh sieve potentially leads to a loss of very small acritarchs. *Classopollis* spp. (*Circulina* spp.) pollen were counted separately from the remaining pollen assemblage, because this genus is believed to be a good marker for warm and especially arid conditions (Vakhrameev 1981) and may therefore lend insight into paleo-environmental changes on land that correlate to phytoplankton events in the ocean.

Total organic carbon (TOC) of selected bulk rock samples was determined by using a Rock-Eval 6 at the Geological Institute of the University of Neuchâtel, Switzerland (courtesy of Philipp Steinmann).

## Results

*Bulk Carbonate and Organic Carbon Isotopes.*—The bulk  $\delta^{13}\text{C}_{\text{carb}}$  isotope record (Fig. 2A) (tabulated in Katz et al. <http://mychrons.chronos.org>; NGDC web archive) is the first complete long-term record available for the Early Jurassic that is calibrated with ammonite zones. Bulk  $\delta^{13}\text{C}_{\text{carb}}$  isotope values fluctuate between about 0 and +2‰ PDB from the base of the Hettangian up to the middle Sinemurian. These relatively stable values are interrupted by several smaller-scale negative excursions. An upper Sinemurian (*Oxynoticerias oxynotum* Zone) shift of -4‰ is the most prominent of these short-term negative shifts. From the lower-upper Sinemurian boundary values gradually increase from around -1.0‰ to +3.90‰ in the lower upper Pliensbachian. The upper Pliensbachian (*Amaltheus margaritatus*-*Pleuroceras spinatum* Zones) to lower Toarcian (*Dactylioceras tenuicostatum* Zone) shows a relatively rapid decrease from +3.90‰ back to values of around 0‰. Toward the top of the *D. tenuicostatum* Zone,  $\delta^{13}\text{C}_{\text{carb}}$  values start to increase again (+1‰), but this positive shift is followed by a sharp negative excursion (-7‰) in the lowermost *Harpoceras falciferum* Zone. This transient excursion was first reported from Mochras and other European locations and discussed by Hesselbo et al. (2000). Values rebound to background values of around +2‰ in the upper Toarcian *Hildoceras bifrons* to *Dumortieria levesquei* ammo-



TABLE 1. Mochras Borehole organic matter data.

Sample no.	Depth (m)	Zone	TOC [%]	HI [mg HC/g TOC]	OI [mg CO <sub>2</sub> /g TOC]	Tmax [°C]	S1 [mg HC/g]	S2 [mg HC/g]	δ <sup>13</sup> C <sub>org</sub> per mil
2500.83	762.25	<i>H. bifrons</i>	0.75	125	49	430	0.01	0.94	-26.00
2548.17	776.68	<i>H. falciferum</i>	0.29	112	72	430	0.06	0.33	-25.40
2608.25	794.99	<i>H. falciferum</i>	0.76	122	60	430	0.03	0.93	-24.20
2692.33	820.62	<i>H. falciferum</i>	2.02	242	60	423	0.11	4.88	-31.20
2746.75	837.21	<i>D. tenuicostatum</i>	0.64	70	66	428	0.03	0.45	-23.80
2849.33	868.48	<i>P. spinatum</i>	0.74	140	59	431	0.08	1.04	-26.30
2896.50	882.85	<i>P. spinatum</i>	0.63	113	62	431	0.04	0.71	-26.00
2956.67	901.19	<i>P. spinatum</i>	0.59	144	81	428	0.12	0.85	
3045.67	928.32	<i>A. margaritatus</i>	0.54	76	84	428	0.20	0.41	-24.00
3138.33	956.56	<i>A. margaritatus</i>	0.99	248	48	426	0.29	2.44	-25.20
3174.00	967.44	<i>A. margaritatus</i>	0.57	123	78	430	0.07	0.70	-24.80
3273.17	997.66	<i>A. margaritatus</i>	0.56	123	88	429	0.06	0.69	
3358.25	1023.59	<i>P. dawoei</i>	1.24	255	51	426	0.10	3.15	-26.30
3430.75	1045.69	<i>T. ibex</i>	0.90	199	46	432	0.11	1.79	-25.10
3489.67	1063.65	<i>T. ibex</i>	0.50	178	44	430	0.02	0.89	-26.10
3516.50	1071.83	<i>T. ibex</i>	1.45	198	85	427	0.17	2.88	
3548.33	1081.53	<i>T. ibex</i>	2.23	298	55	425	0.14	6.63	
3576.17	1090.02	<i>T. ibex</i>	1.31	313	41	424	0.11	4.11	
3607.50	1099.57	<i>T. ibex</i>	0.93	223	77	427	0.06	2.08	
3649.00	1112.22	<i>T. ibex</i>	1.72	268	48	427	0.08	4.61	
3670.58	1118.79	<i>T. ibex</i>	1.32	234	46	424	0.08	3.10	-27.40
3697.08	1126.87	<i>U. jamesoni</i>	0.57	76	86	434	0.00	0.44	
3740.08	1139.98	<i>U. jamesoni</i>	1.10	245	79	434	0.05	2.70	-27.30
3766.33	1147.98	<i>U. jamesoni</i>	1.01	178	166	433	0.10	1.80	
3797.75	1157.55	<i>U. jamesoni</i>	0.45	112	69	432	0.02	0.50	-25.90
3859.92	1176.50	<i>U. jamesoni</i>	0.89	249	65	421	0.21	2.23	
3920.33	1194.92	<i>U. jamesoni</i>	0.56	53	120	432	0.00	0.30	
3948.17	1203.40	<i>U. jamesoni</i>	2.15	313	51	425	0.11	6.71	-28.00
3976.67	1212.09	<i>U. jamesoni</i>	0.83	186	44	427	0.02	1.54	
4005.25	1220.80	<i>U. jamesoni</i>	1.73	276	69	431	0.13	4.78	-27.40
4038.50	1230.93	<i>U. jamesoni</i>	1.25	199	36	429	0.05	2.49	
4067.33	1239.72	<i>U. jamesoni</i>	0.99	150	32	429	0.02	1.48	-26.90
4095.00	1248.16	<i>U. jamesoni</i>	1.37	85	81	432	0.02	1.16	
4127.50	1258.06	<i>E. raricostatum</i>	1.75	182	38	426	0.05	3.19	
4187.33	1276.30	<i>E. raricostatum</i>	1.36	152	44	430	0.02	2.06	-26.00
4210.75	1283.44	<i>E. raricostatum</i>	1.32	97	42	430	0.02	1.28	
4275.50	1303.17	<i>E. raricostatum</i>	1.21	76	43	431	0.02	0.91	
4308.33	1313.18	<i>E. raricostatum</i>	1.19	161	38	432	0.03	1.92	-26.40
4454.33	1357.68	<i>O. oxynotum</i>	0.86	53	43	431	0.01	0.45	-24.40
4547.67	1386.13	<i>O. oxynotum</i>	0.34	19	43	429	0.01	0.07	-24.60
4606.67	1404.11	<i>A. obtusum</i>	0.84	29	60	426	0.00	0.24	-23.80
4668.58	1422.98	<i>A. obtusum</i>	0.87	68	37	433	0.00	0.59	-24.10
4811.50	1466.55	<i>A. obtusum</i>	0.83	29	39	427	0.00	0.24	-23.90
5011.33	1527.45	<i>A. semicostatum</i>	0.92	53	30	432	0.00	0.48	
5100.5	1554.63	<i>A. semicostatum</i>							-24.50
5162.17	1573.43	<i>A. semicostatum</i>	1.37	76	26	433	0.00	1.05	-25.10
5250.25	1600.28	<i>A. semicostatum</i>	1.36	50	24	434	0.00	0.68	-24.60
5494.17	1674.62	<i>A. bucklandi</i>	0.70	38	59	429	0.00	0.26	-25.20
5655.17	1723.69	<i>A. bucklandi</i>	0.25	35	106	429	0.00	0.09	
5865.17	1787.70	<i>S. angulata</i>	0.12	36	48	424	0.01	0.04	
6091.4	1856.66	<i>S. angulata</i>							-26.20

overlap for the lower Pliensbachian. The Pliensbachian shows gradually increasing δ<sup>18</sup>O values from -2.5‰ at the top of the *P. dawoei* Zone to 0‰ in the lower part of the *P. spinatum* Zone. Mg/Ca decreases through this interval, from 12 mmol/mol to 4 mmol/mol.

In the upper part of the *P. spinatum* Zone, up to the Pliensbachian/Toarcian boundary, there is a 1‰ δ<sup>18</sup>O increase and a positive increase of 4 mmol/mol for the Mg/Ca record. We were unable to find belemnites in the black shales that occur in the middle part of *D. ten-*

TABLE 2. Belemnite data from Spain.

Sample no.	Depth m	Zone	Mg/Ca (mmol/mol)	$\delta^{18}\text{O}$ ‰	$\delta^{13}\text{C}$ ‰	Mn ppm
CDP 11.50	131.98	<i>H. bifrons</i>	14.51	-2.72	1.07	35.37
CDP 11.14	121.02	<i>H. serpentinus</i>	13.33	-2.76	2.18	22.10
CDP 4.0	108.50	<i>D. tenuicostatum</i>	9.47	-0.69	1.70	4.92
CDP 2.7	105.84	<i>D. tenuicostatum</i>	8.54	-0.75	1.87	2.24
CDP 2.4	104.44	<i>D. tenuicostatum</i>	8.11	-0.92	2.11	2.91
CDP 2.0	102.90	<i>D. tenuicostatum</i>	9.63	-0.55	0.92	5.09
CDP 1.9	102.52	<i>D. tenuicostatum</i>	7.82	-0.80	1.58	13.72
CDP 1.8	102.30	<i>D. tenuicostatum</i>	11.23	-0.73	0.78	3.95
CDP 1.6	101.90	<i>D. tenuicostatum</i>	8.76	-0.67	1.86	5.71
CAM 4.210	99.70	<i>P. spinatum</i>	7.24	-0.26	1.46	2.96
CAM 4.194	95.15	<i>P. spinatum</i>	7.40	0.11	-0.60	4.45
CAM 4.192	94.42	<i>P. spinatum</i>	7.46	0.00	1.35	3.42
CAM 4.186	92.83	<i>P. spinatum</i>	6.43	0.34	0.48	1.33
CAM 4.181	91.53	<i>P. spinatum</i>	6.72	0.22	0.57	2.03
CAM 4.177II	89.24	<i>P. spinatum</i>	6.72	-0.05	0.95	2.96
CAM 4.177 <sub>1</sub>	89.24	<i>P. spinatum</i>	6.18	0.32	0.64	3.12
CAM 4.176B	88.64	<i>P. spinatum</i>	7.79	0.05	1.76	3.69
CAM 4.176	88.64	<i>P. spinatum</i>	6.19	0.07	1.50	3.98
CAM 4.175	88.01	<i>P. spinatum</i>	7.45	0.17	1.22	2.36
CAM 4.171	86.65	<i>P. spinatum</i>	6.31	0.43	0.92	1.05
CAM 4.166	81.87	<i>P. spinatum</i>	7.25	0.29	0.62	2.27
CAM 4.165	81.11	<i>P. spinatum</i>	7.53	-0.04	1.32	3.28
CAM 4.154	78.05	<i>P. spinatum</i>	7.91	0.07	0.79	1.59
CAM 4.152	77.29	<i>P. spinatum</i>	8.10	-0.10	0.74	1.91
CAM 4.151	76.92	<i>P. spinatum</i>	7.07	-0.33	0.38	4.55
CAM 4.150m	76.56	<i>P. spinatum</i>	7.34	-0.91	0.15	16.51
CAM 4.149	75.93	<i>A. margaritatus</i>	8.30	-0.63	0.82	41.97
CAM 4.147x	74.83	<i>A. margaritatus</i>	5.82	-0.83	0.61	2.27
CAM 4.147	74.83	<i>A. margaritatus</i>	6.00	-0.80	0.68	24.60
CAM 4.146	74.00	<i>A. margaritatus</i>	8.11	-0.27	1.02	2.32
CAM 4.143m	72.31	<i>A. margaritatus</i>	8.77	-0.74	0.66	1.97
CAM 4.142B	72.15	<i>A. margaritatus</i>	10.19	-0.66	1.75	2.53
CAM 4.142A	72.15	<i>A. margaritatus</i>	9.36	0.32	1.09	0.97
CAM4.140t	71.84	<i>A. margaritatus</i>	8.14	-1.24	1.73	3.29
CAM4.140	71.84	<i>A. margaritatus</i>	8.46	-0.96	1.02	1.79
CAM 4.137	70.12	<i>A. margaritatus</i>	5.82	-0.74	1.78	2.27
CAM 4.133t	68.06	<i>A. margaritatus</i>	6.00	-0.47	1.22	24.60
CAM 4.133b	68.06	<i>A. margaritatus</i>	8.11	-0.38	1.23	2.32
CAM 4.126	64.91	<i>A. margaritatus</i>	5.66	0.25	1.37	0.82
CAM 4.116	62.68	<i>A. margaritatus</i>	4.67	-0.16	0.91	1.28
CAM 4.115	62.52	<i>A. margaritatus</i>	10.77	-0.45	1.15	3.40
CAM 4.115xt	62.52	<i>A. margaritatus</i>	12.24	-0.61	0.69	5.99
CAM 4.108	60.00	<i>A. margaritatus</i>	12.01	-1.22	1.68	8.86
CAM 4.107xt	59.53	<i>A. margaritatus</i>	5.82	-0.73	0.81	2.58
CAM 4.107	59.53	<i>A. margaritatus</i>	5.41	-1.00	1.25	2.18
CAM 4.104	57.77	<i>A. margaritatus</i>	6.58	0.11	1.62	1.12
CAM 4.102x	56.00	<i>A. margaritatus</i>	6.75	-0.05	1.85	2.80
CAM 4.102	56.00	<i>A. margaritatus</i>	6.51	-0.37	1.00	1.46
CAM 4.99	55.61	<i>A. margaritatus</i>	8.46	-0.53	1.87	5.12
CAM 4.94	54.22	<i>A. margaritatus</i>	8.18	-0.05	2.51	2.56
CAM 4.93A	53.58	<i>A. margaritatus</i>	8.02	-0.33	1.33	1.79
CAM 4.93B	53.58	<i>A. margaritatus</i>	7.08	-0.06	1.93	2.03
CAM 4.86	50.20	<i>A. margaritatus</i>	9.33	-0.98	0.88	3.36
CAM 4.83	48.60	<i>A. margaritatus</i>	7.48	-0.81	0.91	2.97
CAM 4.76	46.48	<i>A. margaritatus</i>	9.34	-0.90	0.56	2.53
CAM 4.73	44.79	<i>A. margaritatus</i>	7.98	—	—	5.61
CAM 4.70	42.86	<i>A. margaritatus</i>	9.62	-0.88	1.73	2.46
CAM 4.63	39.64	<i>A. stokesi</i>	11.37	-0.69	0.59	7.21
CAM 4.60b	35.32	<i>A. stokesi</i>	11.45	—	—	3.11
CAM 4.60a	35.32	<i>A. stokesi</i>	10.96	-0.84	0.90	5.12
CAM 4.52	30.84	<i>A. stokesi</i>	10.71	-1.68	0.66	5.24
CAM 4.9	22.61	<i>P. davoei</i>	11.87	-2.00	0.97	15.45

TABLE 2. Continued.

Sample no.	Depth m	Zone	Mg/Ca (mmol/mol)	$\delta^{18}\text{O}$ ‰	$\delta^{13}\text{C}$ ‰	Mn ppm
CAM 4.6b	20.02	<i>P. dawoei</i>	12.76	—	—	11.76
CAM 4.6a	20.02	<i>P. dawoei</i>	14.42	—	—	34.02
CAM 4.2	17.86	<i>P. dawoei</i>	10.17	-1.58	2.92	2.77
PLG 2.35	4.24	<i>E. varicostatum</i>	12.26	-1.17	0.12	4.33
PLG 2.37t	4.88	<i>E. varicostatum</i>	10	-0.69	1.12	3.86
PLG 2.50t	7.38	<i>E. varicostatum</i>	9.95	-1.16	-0.4	11.23
PLG 2.60t	8.22	<i>E. varicostatum</i>	9.76	-0.65	0.11	5.98
PLG 2.70	10.32	<i>E. varicostatum</i>	10.43	-0.6	0.67	3.26
PLG 2.70pick	10.32	<i>E. varicostatum</i>	10	-0.47	0.76	2.93
PLG 2.75tA	11.32	<i>E. varicostatum</i>	8.85	-0.67	1.04	50.64
PLG 2.75tA	11.32	<i>E. varicostatum</i>	8.76	-1.52	-0.46	12.44
PLG 2.75tBx	11.32	<i>E. varicostatum</i>	9.05	-0.95	-0.04	11.53
PLG 2.75tC	11.32	<i>E. varicostatum</i>	10.64	—	—	4.18
PLG 2.79	12.38	<i>E. varicostatum</i>	10.07	-1.5	0.15	27.08
PLG 2.99m	17.1	<i>E. varicostatum</i>	10.22	-1.16	-0.32	5.24
PLG 2.102t	17.26	<i>U. jam.-T. ibex</i>	8.81	-0.98	0.35	8.35
PLG 2.106m	17.86	<i>U. jam.-T. ibex</i>	9.53	-0.92	-0.49	2.89
PLG 2.106t	17.86	<i>U. jam.-T. ibex</i>	9.08	-1.18	-0.27	7.71
PLG 2.107m	18.36	<i>U. jam.-T. ibex</i>	10.22	-1.41	0.04	5.57
PLG 2.109b	19	<i>U. jam.-T. ibex</i>	9.66	-0.98	0.97	5.88
PLG 2.111t	19.38	<i>U. jam.-T. ibex</i>	13.17	-1.08	1.13	9.28
PLG 2.113t	20.4	<i>U. jam.-T. ibex</i>	9.39	-1.08	1.81	15.25
PLG 2.130b	25.54	<i>U. jam.-T. ibex</i>	12.81	-2.27	1.42	12.10
PLG 2.135	26.48	<i>U. jam.-T. ibex</i>	9.28	-0.57	1.15	21.64
PLG 2.137	27.22	<i>U. jam.-T. ibex</i>	15.76	-1.84	1.02	55.86
PLG 2.144b	29.32	<i>U. jam.-T. ibex</i>	11.45	-1.65	0.86	17.04
PLG 1.16b	44.32	<i>A. margaritatus</i>	8.05	-0.39	2.09	4.72
PLG 1.15	44.66	<i>A. margaritatus</i>	9.53	-0.61	0.64	2.31
PLG 1.13tx	46.97	<i>A. margaritatus</i>	6.24	-0.68	0.81	12.06
PLG 1.10tx	48.37	<i>A. margaritatus</i>	6.81	-0.38	0.91	6.10
PLG 1.3	51.87	<i>A. margaritatus</i>	5.52	0.11	1.43	8.48
PLG 1.2	52.68	<i>A. margaritatus</i>	5.24	0.09	1.29	3.82

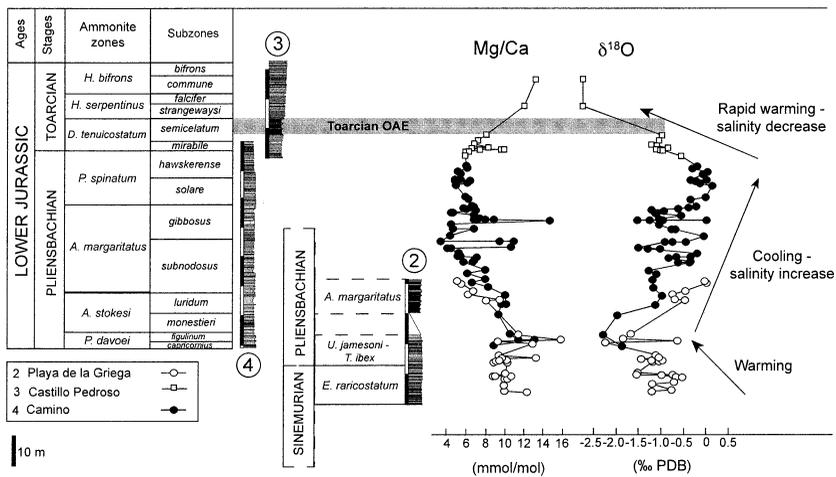


FIGURE 3. Mg/Ca and oxygen isotope data from belemnite calcite from Camino, Playa de la Griega, and Castillo de Pedroso. Ammonite biostratigraphy of the Playa de la Griega section is less well defined (Suarez Vega 1974). Belemnites become abundant above a prominent upper Sinemurian hardground. Numbers refer to Figure 1. The inverse correlation between Mg/Ca and oxygen isotopes shows temperature and salinity changes through the Pliensbachian and lower Toarcian.

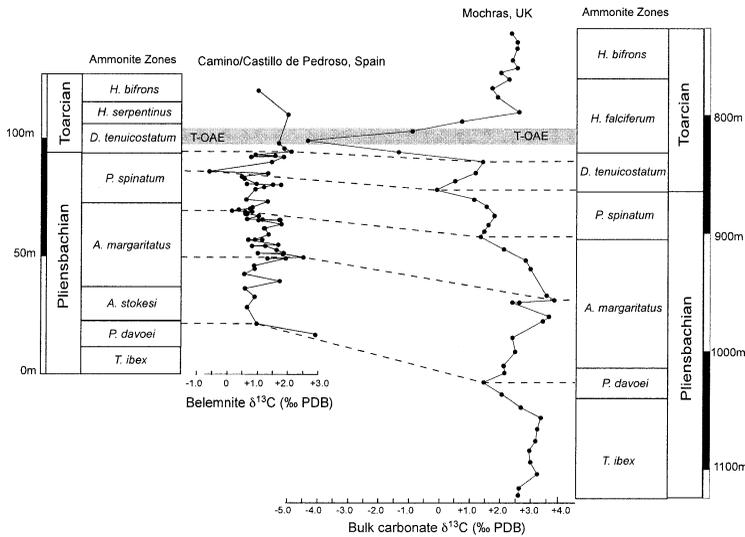


FIGURE 4. Correlation of belemnite C-isotopes from Spain and bulk carbonate C-isotopes from Mochras. This figure shows the good correlation in isotopic signature between the two regions and the diachrony between the Tethyan and Boreal ammonite zonations. The belemnites show lower-magnitude changes compared with the bulk rock values, a finding that may be related to different loci of carbonate production and precipitation (shallow marine (bulk) versus pelagic (belemnites)).

*uicostatum* Zone, but two belemnite samples from the *Harpoceras serpentinus* and *H. bifrons* Zones show negative oxygen isotope values ( $-2.7\text{‰}$ ) correlated with high Mg/Ca (14 mmol/mol).

The reliability of the belemnite (oxygen and trace element) records is further illustrated by the good correlation between the bulk rock and belemnite  $\delta^{13}\text{C}$  signal (Fig. 4). Although C-isotope stratigraphy is beyond the scope of this paper, this correlation clearly shows the diachrony in ammonite zones between the more Boreal influenced Mochras Core and more Tethyan influenced Spanish sites, which appears to become more apparent around the Pliensbachian/Toarcian boundary. The lower carbon isotope values recorded in the belemnites (but the generally higher oxygen isotope values) compared with the bulk rock signal are possibly evidence for the more offshore habitat of belemnites.

*Palynological Analyses.*—The first evidence of unequivocal dinoflagellate cysts is found within the upper Sinemurian *Asteroceras obtusum* zone (Table 3, Figs. 2G, 5A), where we identify *Liasidium variable* in sample MO-4757'1" at low abundance. A flood of *L. variable* occurs in sample MO-4696'6" with a wider range of morphotypes than described by Buc-

efalo Palliani and Riding (2000), confirming Morbey's (1978) observations of at least ten varieties of this "species." Further work is currently under way to establish the significance of all of the morphotypes of this species. We distinguish specimens with long and short apical horns as described by Bucéfalo Palliani and Riding (2000); however, other intermediary types with no antapical horns, distinct protuberances on the epicyst, and bulbous hypocysts are also present. Abundance and morphological variability decrease up core, in samples MO-4668'6" and MO-4606'8". No *L. variable* were observed above sample MO-4547'8" from the *O. oxynotum* Zone.

Several dinoflagellate cyst species first appear in the upper Pliensbachian (*A. margaritatus* to *P. spinatum* ammonite Zones) to lowermost Toarcian (*D. tenuicostatum* Zone). These include *Nannoceratopsis gracilis* Alberti 1961, *N. senex* Van Helden 1977, *N. tricerat* Drugg 1978, *N. symmetrica* Bucéfalo Palliani and Riding 1998, *N. cf. magnicornus* Bucéfalo Palliani and Riding 2000, *Mancodinium semitabulatum* Morgenroth 1970, and *Luehndea spinosa* Morgenroth 1970. The most abundant species is *Luehndea spinosa*, with peaks in sample MO-3138'4" (*A. margaritatus* Zone) and MO-2746'9" (*D. tenuicostatum* Zone). Highest

overall dinoflagellate cyst diversity occurs in sample MO-2896'6" in the lowermost *D. tenuicostatum* Zone (Fig. 5A). In the neighboring South Germany Basin, this interval is also characterized by an abundant and diverse suite of species of the genus *Comparodinium* (Wille 1982a; Wille and Gocht 1979). These are, however, generally absent from the United Kingdom (Riding 1987). In Mochras, we note the sparse occurrence of *Comparodinium koesenium* Morbey 1975.

The acritarch assemblage is dominated by the *Micrhystridium*-complex with *M. lymense* and *M. fragile* constituting the most abundant forms (Fig. 5B). *Veryhachium* spp. and *Baltisphaeridium* spp. occur irregularly throughout the Lower Jurassic and are generally sparse. *Micrhystridium* spp. is especially abundant in samples from the Hettangian and lowermost Sinemurian, in which they constitute 70% of the total palynomorph fraction. Values drop quickly through the Sinemurian and abundance remains low with acritarchs constituting only 10% of the total fraction on average. In contrast to abundance, acritarch species diversity fluctuates considerably, with a general increase up to the Pliensbachian/Toarcian boundary. Diverse assemblages were recorded in the *A. obtusum* Zone just prior to the highest abundance of *L. variabile*, and in the *A. margaritatus* Zone prior to the highest diversity in upper Pliensbachian dinoflagellate cysts.

Foraminiferal organic inner-wall linings occur in low numbers in the Hettangian and gradually become more abundant through the Sinemurian and lowermost Pliensbachian (Fig. 2F). They reach maximum abundance (27%) in the upper part of the lower Pliensbachian *Uptonia jamesoni* Zone, where they are the most abundant marine palynomorph. Foraminiferal linings are especially scarce in the upper Pliensbachian and lowermost Toarcian, before their abundances slightly increase again in the upper part of the *H. falciferum* Zone. A diverse assemblage with many different morphotypes (trochospiral, planispiral, biserial, and uniserial) occurs in the lowermost Pliensbachian.

Prasinophytes are consistently present throughout the Lower Jurassic in the Mochras

Borehole. However, significant numbers (80% of the total palynomorph assemblage) occur only in the lower Toarcian *H. falciferum* Zone (Fig. 2H). This overwhelming prasinophyte abundance entirely consists of small spherical bodies that occur either as individuals or as clusters of variable numbers. In Mochras, *Tasmanites punctatus* occurs only sporadically, but a slightly higher abundance marks the lower Toarcian. Other prasinophyte phycmata that were encountered are various forms of *Cymatiosphaera*, most notably *C. pachythea* (Wall 1965).

The terrestrial fraction is dominated by abundant phytoclasts and pollen. *Classopollis* spp. (Fig. 2E) dominates the pollen assemblages in the upper Sinemurian and upper lower Pliensbachian. Intermittent assemblages are dominated by alete bisaccates. Distinct minima of *Classopollis* spp. were recorded in the lower Pliensbachian and uppermost Pliensbachian to lower Toarcian (Fig. 2E). These results compare well with previous work by Wall (1965). The lower Toarcian shows a very abundant influx of translucent phytoclast debris, which appears to be of monospecific origin. Spore abundances are low throughout the Mochras record, constituting only 5–15% of the total fraction. They are dominated by triangular smooth and ornamented trilete forms.

*Total Organic Carbon.*—Rock-Eval 6 analysis allows for rapid determination of type and amount of organic matter (terrestrial versus marine) as well as maturation and preservation state (Table 1). The results show low TOC (<0.5%) contents for much of the Hettangian and lower part of the Sinemurian (Fig. 2D). A relative maximum of approximately 1.5% occurs in the Sinemurian *A. semicostatum* Zone. Starting in the *O. oxynotum* Zone, the upper Sinemurian marks a gradual increase in TOC extending into the (*U. jamesoni* and *T. ibex* Zones), where TOC values reach 2.2%. The uppermost Pliensbachian shows very low TOC values before TOC increases again in the lowermost Toarcian (2%).

Moderately high HI values (up to 300 mg HC/TOC) and OI values ranging from 30 to 100 (mgCO<sub>2</sub>/TOC) indicate that the organic matter has a predominantly terrestrial source

TABLE 3. Mochras palynological data.

Sample no.	Depth (m)	Ammonite zone	Trilete spores	Mono-lete spores	Pollen indet	Classo-pollis spp.	Classo-pollis tetrads	Very-hachium complex	Micrhystridium complex	Leiofusa spp.	Balti-sphaeridium spp.	Sphericals	Tas-manites spp.
2500.83	762.25	<i>H. bifrons</i>	2	0	14	0	0	0	6	1	0	160	2
2548.17	776.68	<i>H. falciferum</i>	2	0	14	0	0	0	6	0	0	156	2
2608.25	794.99	<i>H. falciferum</i>	4	0	4	2	0	2	4	0	0	140	22
2692.33	820.62	<i>H. falciferum</i>	20	0	0	1	0	0	15	0	0	165	4
2746.75	837.21	<i>tenuicostatum</i>	24	0	74	18	0	0	28	2	0	0	0
2849.33	868.48	<i>P. spinatum</i>	12	0	120	94	0	0	16	0	0	0	6
2896.50	882.85	<i>P. spinatum</i>	11	1	120	50	0	1	17	0	0	0	0
3045.67	928.32	<i>A. margaritatus</i>	8	0	100	38	0	2	38	4	0	0	0
3138.33	956.56	<i>A. margaritatus</i>	5	4	59	79	2	1	15	0	3	0	0
3174.00	967.44	<i>A. margaritatus</i>	2	0	50	82	0	0	38	0	10	0	2
3273.17	997.66	<i>A. margaritatus</i>	4	0	10	160	0	0	8	0	1	0	0
3358.25	1023.59	<i>P. davoei</i>	28	0	96	22	0	0	18	0	0	0	14
3458.00	1054.00	<i>T. ibex</i>	6	0	87	106	0	1	6	0	7	0	4
3489.67	1063.65	<i>T. ibex</i>	6	2	106	64	0	4	8	0	0	0	2
3670.58	1118.79	<i>T. ibex</i>	6	0	76	100	0	4	16	0	0	0	0
3740.08	1139.98	<i>U. jamesoni</i>	2	0	126	54	0	0	6	0	0	0	0
3797.75	1157.55	<i>U. jamesoni</i>	8	0	110	22	0	0	6	0	0	0	0
4005.25	1220.80	<i>U. jamesoni</i>	8	0	132	6	0	0	30	0	2	0	8
4038.50	1230.93	<i>U. jamesoni</i>	6	0	152	34	0	0	2	0	0	0	2
4067.33	1239.72	<i>U. jamesoni</i>	8	0	120	30	0	0	12	0	0	0	0
4187.33	1276.30	<i>E. raricostatum</i>	6	2	126	22	0	0	6	0	0	0	0
4210.75	1283.44	<i>E. raricostatum</i>	12	0	140	14	0	0	24	4	0	0	2
4308.33	1313.18	<i>E. raricostatum</i>	8	0	86	54	0	0	12	#	0	0	2
4547.67	1386.13	<i>O. oxynotum</i>	11	2	56	115	0	0	2	0	0	0	0
4606.67	1404.11	<i>A. obtusum</i>	10	0	105	51	11	0	2	0	1	0	4
4635.33	1412.85	<i>A. obtusum</i>	8	0	89	69	9	0	6	0	1	0	2
4668.58	1422.98	<i>A. obtusum</i>	2	0	130	32	9	0	16	0	0	0	1
4696.50	1431.49	<i>A. obtusum</i>	3	0	45	68	20	0	2	0	2	0	1
4729.33	1441.50	<i>A. obtusum</i>	0	0	130	45	5	0	14	0	2	0	2
4757.08	1449.96	<i>A. obtusum</i>	5	0	125	42	8	0	7	0	1	0	1
4907.50	1495.81	<i>A. obtusum</i>	4	0	72	72	0	0	30	0	0	0	4
5100.50	1554.63	<i>A. semicostatum</i>	4	0	52	140	0	0	2	0	0	0	0
5162.17	1573.43	<i>A. semicostatum</i>	3	0	100	85	0	0	2	0	0	0	1
5250.25	1600.28	<i>A. semicostatum</i>	10	2	140	16	0	2	22	2	0	0	0
5494.17	1674.62	<i>A. bucklandi</i>	12	4	90	51	3	1	51	0	0	0	0
5655.17	1723.69	<i>A. bucklandi</i>	4	0	24	52	0	0	104	1	0	0	2
5865.17	1787.70	<i>S. angulata</i>	6	0	15	35	0	0	139	0	0	0	1
6091.42	1856.66	<i>A. liasicus</i>	10	0	20	40	0	0	130	0	0	0	0

with minor admixtures of type II marine OM (Fig. 6A). This is confirmed by the visual characterization of the palynological assemblages (see above). Elevated HI values in the lower Pliensbachian can be ascribed to increased amounts of amorphous organic matter observed under the microscope. We note a strong correlation between HI and TOC contents (Fig. 6C), which may be an indication for increased preservation under low oxygen conditions in bottom water. However, in the case of low TOC values, the mineral matrix may partly compromise the HI values owing to adsorption on clay minerals, whereas CO<sub>2</sub> generated from carbonate may lead to elevated OI values (Espitalié et al. 1985a,b). According to

Langford and Blanc-Valleron (1990) the S2 (which is the amount of hydrocarbons generated) versus TOC plot (Fig. 6D) shows this effect of matrix retention clearly by the y-intercept of the linear correlation (-1.2), and it is therefore suggested that some of the very low HI values and elevated OI values may be artifacts. The thermal maturation (T<sub>max</sub>; Fig. 6B) shows temperatures around 430°C for all samples, indicating the organic matter is only slightly metamorphosed.

## Discussion

Our results provide a context for addressing the three basic questions related to the factors controlling the origin and radiation of

TABLE 3. Extended.

<i>Botryococcus</i> spp.	Leios- phacids	<i>Liasidium</i> <i>variabile</i>	<i>Luehmdea</i> <i>spinosa</i>	Comparo- dinium <i>koessenium</i>	Nannocera- topsis <i>gracilis</i>	<i>N. triceras</i>	<i>N. senex</i>	<i>N. cf.</i> <i>magni-</i> <i>cornus</i>	<i>N. sym-</i> <i>metrica</i>	<i>M. semi-</i> <i>tabulatum</i>	<i>H. cami-</i> <i>nuspinum</i>	Forami- nifera linings
0	0	0	0	0	0	0	0	0	0	0	0	12
0	0	0	0	0	0	0	0	0	0	0	0	22
0	0	0	0	0	0	0	0	0	0	0	0	14
0	0	0	10	0	1	0	0	0	0	0	0	3
0	0	0	30	0	0	0	0	0	0	0	0	2
0	0	0	4	4	8	4	4	2	2	0	0	2
0	2	0	8	0	2	0	0	0	0	1	0	0
0	0	0	0	0	0	4	2	0	0	2	1	0
0	0	0	34	0	4	0	2	0	1	0	0	3
0	0	0	8	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	28
10	0	0	0	0	0	0	0	0	0	0	0	20
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	6
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	26
0	0	0	0	0	0	0	0	0	0	0	0	54
0	0	0	0	0	0	0	0	0	0	0	0	26
0	0	0	0	0	0	0	0	0	0	0	0	14
0	0	0	0	0	0	0	0	0	0	0	0	30
0	0	0	0	0	0	0	0	0	0	0	0	22
0	0	0	0	0	0	0	0	0	0	0	0	10
0	0	0	0	0	0	0	0	0	0	0	0	20
5	0	0	0	0	0	0	0	0	0	0	0	7
0	0	4	0	0	0	0	0	0	0	0	0	15
0	0	1	0	0	0	0	0	0	0	0	0	23
0	0	4	0	0	0	0	0	0	0	0	0	3
0	0	48	0	0	0	0	0	0	0	0	0	17
0	0	2	0	0	0	0	0	0	0	0	0	8
0	0	0	0	0	0	0	0	0	0	0	0	10
0	0	0	0	0	0	0	0	0	0	0	0	14
0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	6
0	4	0	0	0	0	0	0	0	0	0	0	13
0	0	0	0	0	0	0	0	0	0	0	0	8
0	0	0	0	0	0	0	0	0	0	0	0	4
0	0	0	0	0	0	0	0	0	0	0	0	0

cyst-forming dinoflagellates and other organic-walled phytoplankton during the Early Jurassic in the northern Tethys. We discuss these factors in chronological intervals delineated primarily by changes in the organic-walled phytoplankton assemblages: (1) the middle Sinemurian appearance of the "missing link" or pioneer species *Liasidium variabile*; (2) the late Sinemurian to early Pliensbachian nadir in dinoflagellate cyst abundance; (3) the late Pliensbachian radiation; and (4) the early Toarcian OAE and temporary dinoflagellate cyst blackout.

*Middle Sinemurian–Liasidium Variabile Pulse.* *L. variabile* is a well-recognized stratigraphic marker for the middle Sinemurian. It has been

found in this stratigraphic interval in France (Rauscher and Schmitt 1990; Fauconnier 1995), Switzerland (Feist-Burkhardt unpublished data), the United Kingdom (Riding 1987; Bucfalò Palliani and Riding 2000), the North Sea (Morbey 1978), the Celtic Sea (Ainsworth et al. 1987), Denmark (Dybkaer 1988), Germany (Weiß 1986; Feist-Burkhardt 1998; Lund 2003), and the Scotian shelf, offshore eastern Canada (Williams et al. 1990).

*L. variabile* resembles in its general ambitus large Late Triassic forms, such as *Heibergella* spp. (Carnian–Norian) and *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich and Loeblich 1968 (Rhaetian). *Heibergella asymmetrica* Bujak and Fisher 1976, the type species of the genus,

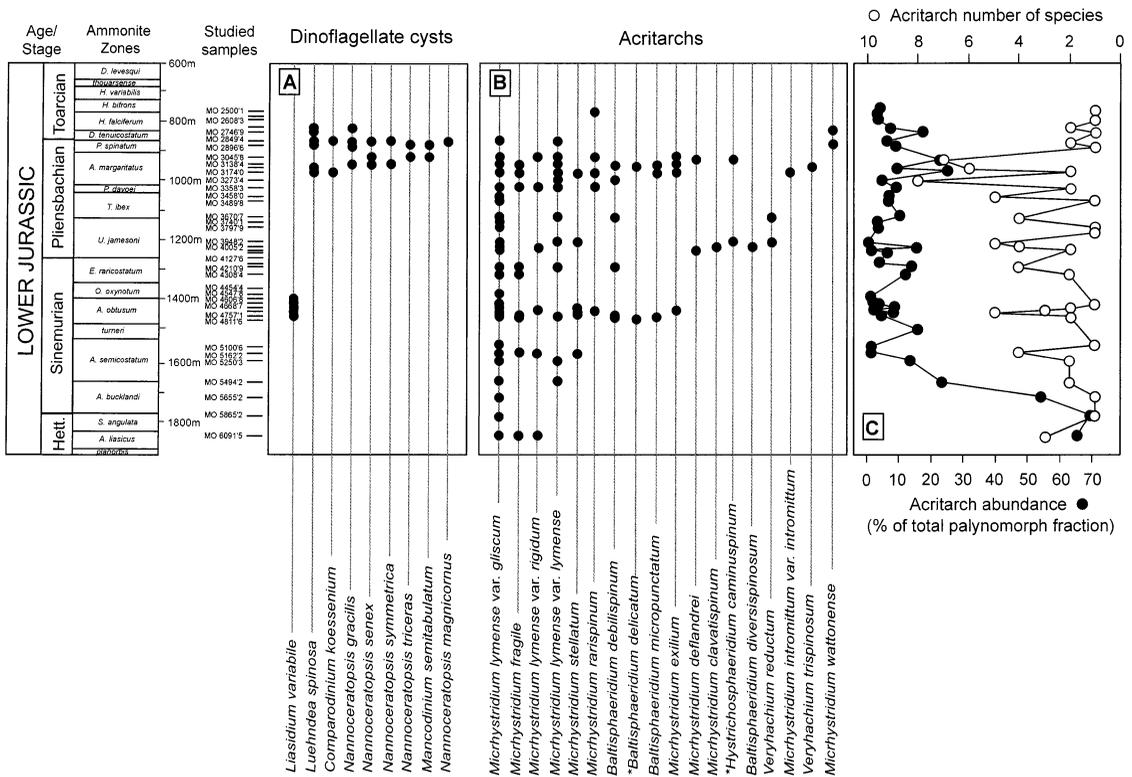


FIGURE 5. A, Range of identified dinoflagellate cyst species. B, Range of acritarch species (according to Wall 1965). C, Acritarch abundance and species numbers. Black circles, acritarch abundance. White circles, acritarch number of species. Note gradual increase in acritarch diversity through Early Jurassic, punctuated in the upper Pliensbachian by the increase in dinoflagellate cyst diversity.

is similar to *Liasidium* in its general ambitus, size, thin, smooth cyst wall that tends to fold, and the expression of paratabulation only by the cingulum and the anterior intercalary archaeopyle. Our lack of knowledge of its paratabulation makes an attribution on family level impossible. Similarities between the Triassic genus *Rhaetogomyaulax* and *Liasidium* are especially the presence of prominent horns, one apical and one right antapical horn. An antapical horn on the right-hand side of the hypocyst is an unusual feature in dinoflagellate cyst morphology and might be an important feature in describing relationships between these genera.

*Liasidium* does not show a clear paratabulation, which would be needed for a confident assignment on suprageneric taxonomic level. Its paratabulation has been only partly deduced for the epicystal part of the cyst (Below 1987), but the important hypocystal paratabulation pattern remains unresolved. On the

basis of the inferred epicystal paratabulation pattern, Fensome et al. (1993) grouped *Liasidium* with the peridinialean family *Heterocapsaceae* and thus interpreted *Liasidium* as the first representative of the Peridiniales in the geological record. The family *Heterocapsaceae* mainly includes genera that evolved and flourished after the Toarcian OAE, such as *Reutlingia* and *Dodekovia* (sensu Below 1987; Feist-Burkhardt 1995a,b). This group of well-circumscribed, generally small cysts, which have also been named "Susadinium group" (Wille 1982a) or "Parvocysta-suite" (Riding 1984), differs however considerably from *Liasidium* in the overall cyst morphology and size. Consequently, *L. variable* appears to be an enigmatic element, or "missing link," between Late Triassic and late Early Jurassic species.

The *Heterocapsaceae* are extant in the contemporary ocean (e.g., *Heterocapsa triquetra* (Ehrenberg 1840; Stein 1883)), but curiously none

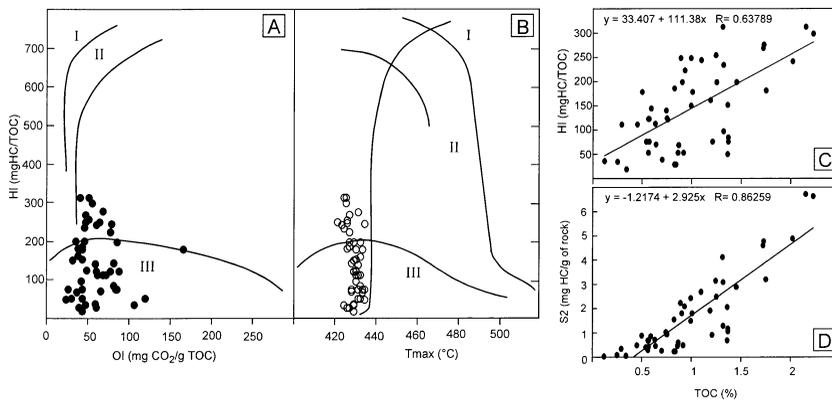


FIGURE 6. Total organic carbon data. A, B, The data show a mixed terrestrial-marine organic matter source (Type II and III). The organic matter is immature. C, D, Matrix retention effects by linear correlation of HI versus TOC and S2 versus TOC.

of the extant species are known to produce dinosporin cysts (Fensome et al. 1993). *Heibergella* is particularly diverse in the Carnian and Norian of high northern latitudes (Sverdrup Basin, Arctic Canada), prompting questions about whether cyst-producing dinoflagellates originated in cold Arctic waters (Stover et al. 1996). However, *Heibergella salebrosacea* Bujak and Fisher 1976 and *Heibergella aculeata* Bujak and Fisher 1976 were recently discovered in Late Triassic (Norian) sediments on East Timor (Martini et al., 2000), suggesting that this genus had a more global distribution and also occurred in low-southern-latitude warm waters. Hochuli and Frank (2000) described possible *Heibergella* and *Rhaetogonyaulax* spp. from the lower Carnian Raibl group of the Southern Alps, situated at northern low latitudes. How can we use *Liasidium* to learn more about origination and migration of early cyst-forming dinoflagellates?

The *L. variabile* acme in northwestern Europe occurs before the first onset of sea level rise in the *O. oxynotum* Zone (Partington et al. 1993) and possibly after a maximum flooding that is manifested by a highly diverse acritarch assemblage in the lower part of the *A. obtusum* Zone (see Fig. 5B). Therefore, we link this acme to a phase of late sea level highstand marked by regression. Indications for regression in the *A. obtusum* Zone can be observed along the Cantabrian margin in the form of coarse siliclastic beds capping shallow marine carbonates (Braga et al. 1988) and in

northern Italy, where upper Sinemurian fresh-water deposits with oligohaline ostracods lie on top of oolites (Boomer et al. 2001). Extremely low TOC values for this interval in Mochras and other regions (e.g., Swiss Jura Mountains [Gorin and Feist-Burkhardt 1990]) indicate well-oxygenated and well-mixed bottom waters during the *Liasidium* bloom period.

In general, acritarchs are thought to indicate stable, stratified, low-nutrient surface waters, whereas dinoflagellates are associated with mesotrophic conditions (Martin 1996). Relatively oligotrophic conditions during the Hettangian to early Sinemurian are inferred from the relatively stable  $\delta^{13}\text{C}_{\text{carb}}$  values that probably reflect the existence of shallow marine carbonate platforms in many areas around northwestern Europe, with high rates of carbonate deposition and low rates of organic carbon burial.

*L. variabile* is restricted to the northwest Europe Basin and its western margin (Fig. 7A); however, it appeared around a time of profound paleoceanographic changes, namely the opening of the Hispanic Corridor, which established a direct connection between the Tethyan and Paleo-Pacific (Panthalassa) domains. Aberhan (2001, 2002) made a strong case for the opening of this corridor during the latest Sinemurian to the earliest Pliensbachian. From the distribution of brachiopods, Sandy and Stanley (1993) hypothesized that the corridor opened in the Late Triassic. Cir-

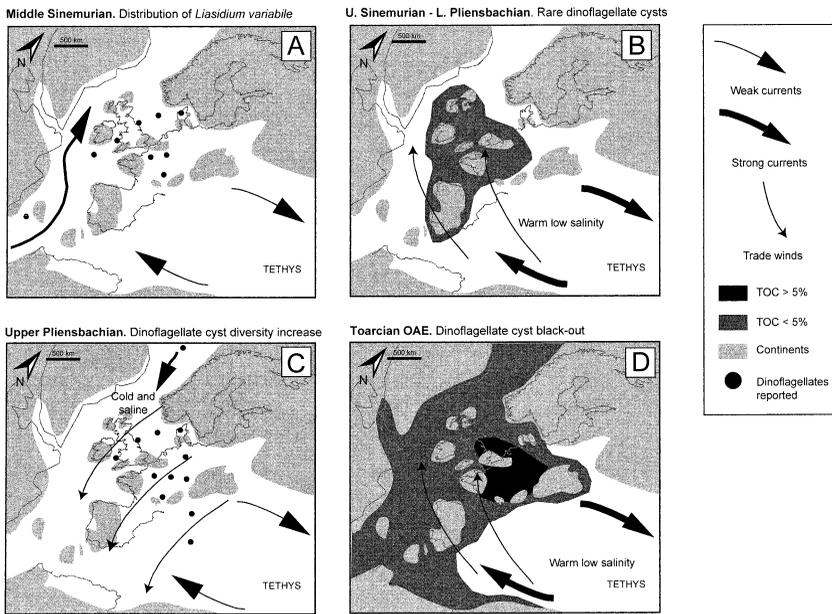


FIGURE 7. Different scenarios for the four time intervals discussed in the text, showing dinoflagellate cyst occurrences across northwestern Europe (references in text) and generalized paleogeographic and paleoclimatic conditions. A, Middle Sinemurian. B, Upper Sinemurian to lower Pliensbachian. C, Upper Pliensbachian. D, Toarcian Oceanic Anoxic Event (OAE).

culcation through the Hispanic Corridor probably was eastward, from the Pacific into the Tethys, owing to more humid conditions in the eastern part of the seaway and extremely arid conditions at the Tethyan side (Aberhan 2001; 2002). The arid conditions in the eastern region are inferred from thick Hettangian–Sinemurian successions of evaporites and dolomites in Morocco, Tunisia, Portugal, and northern Spain, leading to off-shelf flow into the Tethys. This circulation was possibly intensified during winter as saline waters in the Tethys cooled, much like present-day circulation in the Mediterranean (Aberhan 2001).

We suggest that the sudden appearance of *Liasidium* in northwestern Europe was the result of its migration from the Paleo-Pacific into the Tethys, driven by a change in oceanic circulation in the corridor or on the northwest European shelf. Unfortunately, our belemnite proxies for temperature and salinity do not extend back to the *A. obtusum* Zone; however, cooler conditions may be inferred from low  $\Delta\delta^{13}\text{C}_{\text{carb-org}}$  and a low abundance of *Clasopollis* pollen. Hence, *L. variable* was effectively a pioneer species that invaded the Te-

thys from the Paleo-Pacific but bloomed extensively (albeit, briefly) in the former basin.

The abundance and morphological variation expressed by *L. variable* in such a narrow confined zone as in northwestern Europe suggest that this species may have profited from new niches without many competitors or predators. Another possibility could be that it became genetically isolated as sea level fall in the *A. obtusum* Zone led to restriction of circulation through the Hispanic Corridor. These scenarios can be tested by looking for *L. variable* in lower and upper Sinemurian successions from the Paleo-Pacific (e.g., Chile, Peru, and/or Argentina) and by determining if it developed such a wide variety of forms in those areas as well.

*Upper Sinemurian to Lower Pliensbachian.*—A negative shift in the Mochras  $\delta^{13}\text{C}_{\text{carb}}$  signal (Fig. 2) coincides with ironstone deposition in the middle part of the *O. oxynotum* Zone, which forms the basal lag of a second-order transgressive phase that continued up to the upper Pliensbachian (Haq et al. 1987). This sea level rise is particularly well documented by Partington et al. (1993) in the adjacent North

Sea Basin. Despite sea level rise, the uppermost Sinemurian to lower Pliensbachian is generally barren of dinoflagellate cysts in northwestern Europe.

It may be argued that sea level rise did not lead to suitable shallow marine habitats for cyst-forming dinoflagellates in Mochras. One reason for this would have been a decrease in bottom water oxygen levels related to more sluggish circulation on the northwest European shelves. TOC gradually rose from background values to more than 2% in the *E. raricostatum* to *P. davoei* Zones (Fig. 2D). This trend is closely matched by an increase in the abundance of foraminiferal linings and amorphous organic matter (AOM). Benthic foraminifera organic inner wall linings can be interpreted to reflect both an increase in organic flux to bottom waters and/or dysoxic conditions (0.2–1 mlO<sub>2</sub>/l), whereas AOM is also generally associated with anoxic conditions (Tyson 1995). Low oxygen bottom waters in Mochras during this time may also be inferred from a temporary absence of metacopid ostracods (Boomer and Whatley 1992).

Low oxygen bottom waters appear to be associated with a  $\delta^{13}\text{C}_{\text{carb}}$  increase of approximately 5‰ from the middle Sinemurian to upper Pliensbachian in our Mochras record. A contemporaneous crisis in carbonate production in other areas, such as observed in Italy by Morettini et al. (2002), may have reinforced partitioning of isotopically heavy carbon in surface waters (Weissert et al. 1998; Kump and Arthur 1999). Diminished carbonate production as well as increased TOC values were also discussed by Borrego et al. (1996) and Quesada et al. (1997) for the Cantabrian and Asturian Basins (Spain). Elevated organic carbon burial in the upper Sinemurian to upper lower Pliensbachian has also been reported from France (Espitalié et al. 1986).

What caused sluggish circulation in northwestern Europe during this time? A sharp decrease in *Classopollis* pollen (a marker for warm, arid conditions) and a strong increase in *Calamospora* spores (a marker for hygrophytic plant assemblages and swamps [Wall 1965]) suggests that the upper Sinemurian to lower upper Pliensbachian transgression witnessed warm, humid conditions. The Sine-

murian/Pliensbachian boundary interval also shows pronounced sharply increased values in  $\Delta\delta^{13}\text{C}_{\text{carb-org}}$  indicating elevated  $p\text{CO}_2$  levels. Indeed, belemnite Mg/Ca and oxygen isotope data from Playa de la Griega indicate warm and low-salinity water conditions across this interval in Spain (Fig. 3; see below for more discussion on the application of these records).

Several studies have reported a Sinemurian onset of fault activity and extension along the northwestern Tethyan margin (e.g., Ardeche Basin [Bonijoly et al. 1996]). The tectonic evolution of various basins, such as the Lusitanian Basin in Portugal (Rasmussen et al. 1998), shows a consistent pattern of rifting starting in the Sinemurian and continuing during the Pliensbachian. A recent compilation of absolute ages for vein mineralizations in Swiss basement rocks by Wetzel et al. (2003) shows an important phase of hydrothermal activity and reactivation of faults centered on the Sinemurian/Pliensbachian boundary.

The flooding of shallow marine margins, contemporaneous greenhouse warming and the establishment of a mega-monsoonal system above northwestern Europe with intensified summer monsoons (southeast trade winds; Röhl et al. 2001) caused a stronger influence of Tethyan low-salinity surface waters (Fig. 7B) relative to Hispanic Corridor or Boreal water masses. Draining of freshwater, resulting from intense summer monsoons with high runoff, into the Tethys, led to increased stratification. These conditions appear to have been conducive to acritarchs, which underwent a long-term increase in diversity during this interval (Fig. 5C).

*Upper Pliensbachian: Cyst-forming Dinoflagellate Radiation.*—Long-term flooding ended in the early late Pliensbachian *A. margaritatus* Zone. Black shale deposition in Spain marks the maximum flooding of this transgression coinciding with the most positive Early Jurassic  $\delta^{13}\text{C}_{\text{carb}}$  isotope signature before values decrease again up to the Pliensbachian/Toarcian boundary. A small positive  $\delta^{13}\text{C}_{\text{carb}}$  excursion in the *A. margaritatus* Zone was also reported by Jenkyns and Clayton (1986), Jenkyns (1988) and Jimenez et al. (1996), but these data sets lacked the longer-term perspective.

In the Mochras succession,  $\delta^{13}\text{C}_{\text{carb}}$  decreases by approximately 4‰ during the late Pliensbachian. This decrease correlates with data reported from the Tethyan domain (e.g., Breggia Gorge section in Switzerland [Jenkyns and Clayton 1986, 1997]). The upper Pliensbachian is well known for its poor organic carbon contents in sections around the southern margin of the Tethys (Beaudoin et al. 1990). Low TOC values and the disappearance of foraminifera organic inner-wall linings indicate that the late Pliensbachian was marked by increased bottom-water oxygenation and a decrease in Corg/Ccarb burial.

The upper Pliensbachian at Mochras stands out because of its abundant and diverse contents of dinoflagellate cysts, many of which have their first occurrences in this interval. What is striking though is that the late Pliensbachian is considered to be a period of widespread regression, which contrasts with the correlation between sea level rise and increased dinoflagellate diversity during the Mesozoic (Fensome et al. 1996). Regression in the uppermost Pliensbachian to lowermost Toarcian (*P. spinatum* Zone–lower part of *D. tenuicostatum* Zone) has been documented throughout the Tethyan seaway (e.g., Cobianchi and Picotti 2001) and is in accordance with sea level curves proposed by Haq et al. (1987). Regression is probably best shown in the adjacent North Sea Basin, where the upper Pliensbachian shows incised valleys with siliciclastic infills (Partington et al. 1993). On-shore English (Yorkshire) sections contain siliciclastics (Staites Sandstone) and ironstones (Cleveland Ironstone Formation) deposited during the *A. margaritatus*–*P. spinatum* Zones. upper Pliensbachian manganeseiferous limestones and ironstones are widespread around the western Tethys and northwest European seaway and have also been interpreted to indicate regression (Taylor 1998). Carbonate factories in Morocco, Sicily, and northern Italy were shut down during the uppermost Pliensbachian to earliest Toarcian. Although the exact causes for this crisis in carbonate production remain elusive (Blomeier and Reijmer 1999; Mallarino et al. 2002), Crevello (1990) observed extensive vadose diagenesis in up-

per Pliensbachian limestones in Morocco, indicating carbonate platforms became exposed.

Riding and Hubbard (1999) argued that the late Pliensbachian dinoflagellate cyst radiation was controlled predominantly by ocean currents and temperature. These authors determined that *Nannoceratopsis* and *Luehndea spinosa* were related to the influx of cool water onto the northwest European shelf, because they are generally more abundant in (Boreal) high northern latitudes and rare in Tethyan assemblages (Bucefalo Palliani and Riding 2003). It is generally accepted that sea level rise, and not regression, favors the exchange of fauna and flora between ocean basins. Therefore, changes in surface-water temperature and salinity may have been important controls on the radiation of cyst-forming dinoflagellates during the late Pliensbachian.

Our belemnite Mg/Ca and oxygen isotope data suggest inverse trends with decreasing Mg/Ca and increasing oxygen isotope values during the late Pliensbachian. Applying the equation of Anderson and Arthur (1983) to the change in oxygen isotopes (which increased from  $-2.5\text{‰}$  to  $0\text{‰}$ ) and assuming  $\delta_w = -1.2\text{‰}$ , the calculated decrease in temperature would amount to approximately  $10^\circ\text{C}$ , which is enormous. The incorporation of Mg into biogenic calcite is also temperature dependent, a feature well known from bivalves, ostracods, and planktonic foraminifera, and responds to an exponential increase of  $1^\circ\text{C}$  per 10% increase in Mg/Ca (Rosenthal et al. 1997). According to this relationship the change in Mg/Ca (from 12 to 4 mmol/mol = 8 mmol/mol) during the late Pliensbachian would give a  $\Delta T$  of  $6\text{--}7^\circ\text{C}$ . The Mg/Ca paleothermometer is relatively insensitive to salinity. Hence, the apparent discrepancy between the two proxies suggests that salinity increased by about 2 psu ( $\Delta\delta^{18}\text{O}/\Delta S$  ratio of  $0.5\text{‰}$  per 1 psu). These calculations suggest that water masses on the northwest European shelf became more saline and cooled substantially during the late Pliensbachian. These results are consistent with similar studies by McArthur et al. (2000) and Bailey et al. (2003) in sections from England and Germany, as well as studies in Spain (Rosales et al. 2001). This cooling period comports with the sug-

gestions of Riding and Hubbard (1999) of a temperature control on Early Jurassic dinoflagellate diversity and a dominant role for the Viking Strait, connecting the Boreal and Tethyan domains, in controlling late Pliensbachian paleoceanography (Bjerrum et al. 2001).

A late Pliensbachian influx of cool high-latitude waters on the northwest European shelf can also be inferred from the migration of other Boreal faunal elements. Important ammonite families of Boreal descent, such as the Amaltheids (Smith and Tipper 1986), penetrated as far south as Morocco. Cooler and more saline surface water, a regressive trend, and the southward push of typical Boreal faunal elements all suggest glacio-eustatic control on sea level fall during the late Pliensbachian. Price (1999), summarizing the evidence for Mesozoic glaciations, reports late Pliensbachian dropstones and glendonites, indications for a "cold snap." Interestingly, our  $\Delta\delta^{13}\text{Ccarb-org}$  record indicates a minimum in the *D. tenuicostatum* Zone on a long-term Pliensbachian decrease. If taken as a proxy for  $p\text{CO}_2$ , this would indicate gradually decreasing carbon dioxide levels through the Pliensbachian after relatively high levels in the earliest Pliensbachian.

We propose that the radiation and southward spread of late Pliensbachian cyst-forming dinoflagellate species was the result of a cooling phase that may have triggered invigorated circulation across the northwest European shelf and increased bottom-water oxygenation (Fig. 7C). A stronger seasonal contrast with cooler Northern Hemisphere winters likely intensified northeast trade winds (Röhl et al. 2001). These northeast trade winds would have led to more arid conditions during the late Pliensbachian, giving rise to a negative water budget for northwest European basins and causing intensified overturn and a density gradient that drew in high-latitude waters. These trade winds also would have weakened Tethyan inflow onto the northwest European shelves. Dinoflagellates may have been especially well suited to dealing with strong seasonal contrasts as part of their (newly developed) strategy of producing benthic-resting cysts. At the same time, they may indicate a hydrographic front of mixing Boreal

and Tethyan waters. On the basis of a high-resolution study across the lowermost Toarcian *D. tenuicostatum* Zone in Italy, Bucefalo Palliani and Riding (1999) further ascribed high dinoflagellate diversity to periods of water column instability.

*The Toarcian OAE: Dinoflagellate Cyst Black-out.*—A large negative simultaneous shift in  $\delta^{13}\text{Ccarb}$  and  $\delta^{13}\text{Corg}$  coincides with a complete absence of dinoflagellate cysts and a high abundance of fossil prasinophyte phycomata. These isotope excursions have previously been documented in more detail in other regions, as well as in Mochras (Jenkyns et al. 1997; Hesselbo et al. 2000; Röhl et al. 2001), and appear to be a distinctive feature of the Toarcian OAE. The isotopic shifts have been interpreted to be of primary or diagenetic origin (see McArthur et al. 2000). Because of the magnitude and rapidity of the isotope shift, dissociation of methane gas hydrates has recently been proposed by Hesselbo et al. (2000). An alternative explanation, such as the recycling and reutilization of light  $\text{CO}_2$  diffused into the photic zone from strongly stratified anoxic bottom waters has been favored by other authors (Küspert 1982; Hollander et al. 1991; Schouten et al. 2000; Röhl et al. 2001).

Whether the sudden outgassing of methane hydrates was the cause of the anoxic event or not, our belemnite data from Spain and those from England and Germany (McArthur et al. 2000; Bailey et al. 2003) indicate that the Toarcian OAE was accompanied by rapid warming and by a strong decrease in surface water salinity. In Spain, belemnite oxygen isotopes decrease by 2.7‰ (approximately 11°C), whereas Mg/Ca increases by 8 mmol/mol. Bailey et al. (2003) have argued for a preconditioning of shelf waters during the late Pliensbachian and a switch to strongly stratified bottom water with low salinity surface waters during the early Toarcian.

These dramatic oceanographic changes, together with the rise in sea level and culminating in the Toarcian OAE (Haq et al. 1987; Hallam 2001), did not promote dinoflagellate diversity in shallow marine epicontinental basins around Europe. In Mochras, the *H. falciferum* Zone, coinciding with the Toarcian OAE, shows the disappearance of all dinofla-

gellate cysts. A temporary dinoflagellate blackout has also been described from other areas (Prauss and Riegel 1989; Feist-Burkhardt 1992; Bucefalo Palliani et al. 2002). The results from these studies have documented the extinction of some species, such as *Luehndea spinosa*, *Nannoceratopsis tricerata*, and *Nannoceratopsis* cf. *magnicornus*, whereas other species behave as Lazarus taxa. The cause for this crisis in dinoflagellate cyst diversity is generally ascribed to bottom-water anoxia that prevented cyst-forming dinoflagellates from successfully excysting (Wille and Gocht 1979; Bucefalo Palliani et al. 2002).

In the *H. falciferum* Zone, cyst-forming dinoflagellates and acritarchs were replaced by abundant, small, spherical cysts and prasinophyte phycomata. These "sphericals" have been the focus of much debate and have previously been described as *Halosphaeropsis liasica* Mädlér 1963, inaperturate pollen (Wille and Gocht 1979), sphaeromorph acritarchs (Riding 1987), and recently as methanotrophic bacteria (Bucefalo Palliani et al. 2002). The latter assignment seems untenable as their size exceeds that of bacteria by at least ten times. The formation of clusters (or mats) is also more reminiscent of algae. As several authors have pointed out, the common co-occurrence of these "sphericals" with prasinophyte phycomata of *Tasmanites* spp. argues for a green algal origin (Prauss and Riegel 1989).

The role of prasinophytes in the Toarcian OAE is poorly understood. However, the close coincidence between the most negative carbon isotope values and the highest abundance of prasinophytes indicates that these algae can be used to understand paleoenvironmental changes during the Toarcian OAE. In contrast to many coeval sections, Mochras does not contain high amounts of amorphous organic matter, but it does preserve an overwhelming abundance of sphericals, which, like the negative carbon isotope excursion, appears to be one of the most characteristic features of Toarcian black shales in Europe. Although Schouten et al. (2000) have dismissed the possibility that a change in phytoplankton composition was responsible for the isotope shift, the extraordinary abundance of green algae pre-

served at this time may be part of the explanation.

### Summary and Conclusions

The Early Jurassic was a time of important marine faunal and floral innovation that gave rise to taxonomic prominence of several groups of photosynthetic eukaryotic phytoplankton (i.e., dinoflagellates and coccolithophorids) that play a major role as primary producers in the contemporary oceans. During the Mesozoic these groups replaced members of the green algal line (such as prasinophytes) that had dominated marine primary production since at least the Neoproterozoic. The Early Jurassic is of particular interest in the evolutionary history of organic-walled phytoplankton taxa for the following reasons:

1. It can be considered a transitional phase during which both green and red algae competed for resources and ecospace. We have shown that in the Mochras Borehole, acritarch diversity gradually increased from the Hettangian to late Pliensbachian and that dinoflagellates may have replaced acritarchs during the late Pliensbachian. Our carbon isotope and TOC data indicate that long-term sea level rise from the Hettangian to Pliensbachian was accompanied by increased greenhouse warming, leading to sluggish circulation, low-oxygen bottom waters, and possibly low salinity surface waters with a predominant Tethyan source. These conditions appear to have been conducive to prasinophytes and acritarchs.
2. Bursts of radiation in cyst-forming dinoflagellates during the late Sinemurian and late Pliensbachian coincided with significant changes in paleoceanography and paleoclimate. The sudden middle Sinemurian appearance of *Liasidium variabile*, linking Late Triassic and late Early Jurassic groups of cyst-forming dinoflagellates, was possibly related to the opening and flooding of the Hispanic Corridor. A late Pliensbachian phase of true radiation with the appearance of both opportunistic species (*Luehndea spinosa*) and long-ranging genera (*Nannoceratopsis*, *Mancodinium*) correlates with cooler climate and/or cold saline water in-

flux in northwestern Europe. These climatological changes permitted Boreal species to migrate southward, while at the same time inflow of colder high-latitude water onto the northwest European shelf led to intensified mixing. Hydrographic instabilities and well-aerated bottom waters appear to have facilitated cyst-forming dinoflagellate diversity during this interval. Our study further highlights the role of migration of dinoflagellates across oceanic regimes as a function of changes in climate and ocean circulation (Poulsen and Riding 2003). Riding and Ioannides (1996) and more recently Bucefalo Palliani and Riding (2003) discussed the existence of two principal biogeographic provinces, with a Boreal and a Tethyan rootstock. We postulate the existence of a third rootstock in the Paleo-Pacific. Clearly more attention should be paid to the Paleo-Pacific during this period.

3. On the basis of our belemnite Mg/Ca and oxygen isotope data, indicating low-salinity surface waters overlying anoxic bottom waters, we suggest that hypoxic conditions and intense stratification associated with the Toarcian OAE were especially advantageous to prasinophytes. Cyst-forming dinoflagellates were temporarily excluded during deposition of the most anoxic facies. We agree with Bucefalo Palliani et al. (2002) that the reason for this temporary blackout was a combination of unsuitable conditions in bottom waters (anoxic) and surface waters (low salinity, stratification). The absence of cyst-forming dinoflagellates during the most intensely stratified water conditions further illustrates the importance of turbulence and mixing.

The results presented in this study may also revive Stover et al.'s (1996) question, whether cyst-forming dinoflagellates originated in high-latitude oceans, where cyst-formation provided a strategy to survive low light and turbulent water during winter. It is widely recognized that dinoflagellate cyst diversity was considerably higher in Arctic regions during the initial radiation in the Late Triassic. This may have been the result of an evolutionary

predisposition, as Butterfield and Rainbird (1998) described numerous new species of Neoproterozoic acritarchs, some with dinoflagellate affinities, from Arctic Canada.

Recent work by Quiq et al. (2003) has shown the fundamental difference in trace metal requirements for the green and the red algal lineages. Green plastids have a consistently higher preference for Fe and Mn, elements that are more soluble under reducing conditions. The red algal photosynthetic apparatus appears to have adapted to more oxidized ocean conditions, requiring less iron and manganese. Hence, the long-term evolutionary success of dinoflagellates may have been fueled by the breaking apart of Pangea and the opening of the Atlantic Ocean, which heralded a significant increase in ocean oxygenation and an end to widespread Paleozoic anoxia.

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### Literature Cited

- Aberhan, M. 2001. Bivalve palaeobiogeography and the Hispanic Corridor: time of opening and effectiveness of a proto-Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165:375–394.
- . 2002. Opening of the Hispanic Corridor and Early Jurassic bivalve biodiversity. *In* J. A. Crame and A.W. Owen, eds. *Palaeobiogeography and biodiversity change: the Ordovician and Mesozoic-Cenozoic radiations*. Geological Society of London Special Publication 194:127–139.
- Ainsworth, N. R., M. O'Neill, M. M. Rutherford, G. Clayton, N. F. Horton, and R. A. Penney. 1987. Biostratigraphy of the Lower Cretaceous, Jurassic and uppermost Triassic of the North Celtic Sea and Fastnet Basins. Pp. 611–622 *in* J. Brooks and K. Glennie, eds. *Petroleum geology of North West Europe*. Graham and Trotman, London.
- Anderson, T. F., and M. A. Arthur. 1983. Stable isotopes of oxygen and carbon and their application to sedimentologic and paleoenvironmental problems. *SEPM Short Course* 10:1.1–1.151.

- Bailey, T. R., Y. Rosenthal, J. M. McArthur, B. van de Schootbrugge, and M. F. Thirlwall. 2003. Paleooceanographic changes of the late Pliensbachian–Early Toarcian interval: a possible link to the genesis of an Oceanic Anoxic Event. *Earth and Planetary Science Letters* 212:307–320.
- Beaudoin, F., J. P. Herbin, J. P. Bassoullet, J. Dercourt, G. Lachkar, H. Manivit, and M. Renard. 1990. Distribution of organic matter during the Toarcian in the Mediterranean Tethys and Middle East. *In* Y. Huc, ed. *Deposition of organic facies. Association of American Petroleum Geologists, Studies in Geology* 30:73–92.
- Below, R. 1987. Evolution und Systematik von Dinoflagellaten-Zysten aus der Ordnung Peridinales. I. Allgemeine Grundlagen und Subfamilie Rhaetogonyaulacoideae (Familie Peridiniaceae). *Palaeontographica, Abteilung B* 205(1–6):1–164.
- Bjerrum, C. J., F. Surlyk, J. H. Callomon, and R. L. Slingerland. 2001. Numerical paleoceanographic study of the Early Jurassic transcontinental Laurasian Seaway. *Paleoceanography* 16:390–404.
- Blomeier, D. P. G., and J. G. Reijmer. 1999. Drowning of a Lower Jurassic carbonate platform: Jbel Bou Dahar, High Atlas, Morocco. *Facies* 41:81–110.
- Bonijoly, D., J. Perrin, F. Roure, F. Bergerat, L. Courel, S. Elmi, A. Mignot, and the GPF Team. 1996. The Ardeche palaeomargin of the South-East Basin of France: Mesozoic evolution of a part of the Tethyan continental margin (Géologie Profonde de la France programme). *Marine and Petroleum Geology* 13:607–623.
- Boomer, I. D. 1991. Lower Jurassic ostracod biozonation of the Mochras Borehole. *Journal of Micropalaeontology* 9:205–218.
- Boomer, I. D., and R. Whatley. 1992. Ostracoda and dysaerobia in the Lower Jurassic of Wales: the reconstruction of past oxygen levels. *Palaeogeography, Palaeoclimatology, Palaeoecology* 99:373–379.
- Boomer, I. D., R. Whatley, D. Bassi, A. Fugagnoli, and C. Loriga. 2001. An Early Jurassic oligohaline ostracod assemblage within the carbonate platform sequence of the Venetian Prealps, NE Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166:331–344.
- Borrego, A. G., H. W. Hagemann, C. G. Blanco, M. Valenzuela, and C. Suarez de Centi. 1996. The Pliensbachian (Early Jurassic) anoxic events in Asturias, northern Spain: Santa Mera Member, Rodiles Formation. *Organic Geochemistry* 25(5–7):295–309.
- Bown, P. R., J. A. Burnett, and L. T. Gallagher. 1992. Calcareous nannoplankton evolution. *Memorie di Scienze Geologiche, Padova, XLIII*:1–17.
- Braga, J. C., M. J. Comas-Rengifo, A. Goy, P. Rivas, and A. Yebenes. 1988. El Lias inferior y medio en zona central de la cuenca Vasco-Cantabrica (Camino, Santander). *Ciencias de la Tierra Geologia* 11 (III Colloquio de estratigrafia y paleogeografia del Jurassico de España):17–43.
- Bucefalo Palliani, R., and J. B. Riding. 1999. Relationships between the Early Toarcian anoxic event and organic-walled phytoplankton in central Italy. *Marine Micropaleontology* 37:101–116.
- . 2000. A palynological investigation of the Lower and lowermost Middle Jurassic strata (Sinemurian to Aalenian) from North Yorkshire, UK. *Proceedings of the Yorkshire Geological Society* 53:1–16.
- . 2003. Biostratigraphy, provincialism and evolution of European Early Jurassic (Pliensbachian to Early Toarcian) dinoflagellate cysts. *Palynology* 27:179–214.
- Bucefalo Palliani, R., E. Mattioli, and J. B. Riding. 2002. The response of marine phytoplankton and sedimentary organic matter to the Early Toarcian (Lower Jurassic) oceanic anoxic event in northern England. *Marine Micropaleontology* 46:223–245.
- Butterfield, N. J., and R. H. Rainbird. 1998. Diverse organic-walled fossils, including possible dinoflagellates, from the Early Neoproterozoic of Arctic Canada. *Geology* 26:963–966.
- Cobianchi, M., and V. Picotti. 2001. Sedimentary and biological response to sea level and paleoceanographic changes of a Lower-Middle Jurassic Tethyan platform margin (Southern Alps, Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 169:219–244.
- Comas-Rengifo, M. J., A. Goy, P. Rivas, and A. Yebenes. 1988. El Toarciense en Castillo Pedroso (Santander). *Ciencias de la Tierra Geologia* 11 (III Colloquio de estratigrafia y paleogeografia del Jurassico de España):63–71.
- Crevello, P. D. 1990. Stratigraphic evolution of Lower Jurassic carbonate platforms: Record of rift tectonics and eustasy, central and eastern High Atlas, Morocco. Ph.D. dissertation. Colorado School of Mines, Golden.
- Dale, B. 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in Recent sediments from Trondheimsfjord, Norway. *Review of Palaeobotany and Palynology* 22:39–60.
- . 1983. Dinoflagellate resting cysts: 'benthic plankton.' Pp. 69–136 *in* G. A. Fryxell, ed. *Survival strategies of the Algae*. Cambridge University Press, Cambridge.
- Dybkaer, K. 1988. Palynological zonation and stratigraphy of the Jurassic section in the Gassum No.1-borehole, Denmark. *Geological Survey of Denmark (DGU) A* 21:5–73.
- Espitalié, J., G. Deroo, and F. Marquis. 1985a. La pyrolyse Rock-Eval et ses applications. *Partie 1. Revue de l'Institut Français du Pétrole* 40:563–579.
- . 1985b. La pyrolyse Rock-Eval et ses applications. *Partie 2. Revue de l'Institut Français du Pétrole* 40:755–784.
- . 1986. La pyrolyse Rock-Eval et ses applications. *Partie 3. Revue de l'Institut Français du Pétrole* 41:73–89.
- Falkowski, P. G., O. Schofield, M. E. Katz, B. van de Schootbrugge, and A. H. Knoll. *In press*. Why is the land green and the ocean red? *In* J. Young and H. Thierstein, eds. *Coccolithophorids: from molecular processes to global impact*. Springer.
- Fauconnier, D. 1995. Jurassic palynology from a borehole in the Champagne area, France: correlation of the Lower Callovian–middle Oxfordian using sequence stratigraphy. *Review of Palaeobotany and Palynology* 87:15–26.
- Feist-Burkhardt, S. 1992. Palynological investigations in the Lower and Middle Jurassic of Switzerland, France and Germany: palynofacies and type of organic matter, dinoflagellate cyst morphology and stratigraphy. Ph.D. thesis. Université de Genève, Geneva.
- . 1995a. Stratigraphic compilation of Below's data (1987a 1987b, and 1990) on Early and Middle Jurassic dinoflagellate cysts. *Revue de Paléobiologie* 13:313–318.
- . 1995b. *Weiachia fenestrata* gen. et sp. nov., a new Phallosystean dinoflagellate cyst from the Lower Jurassic of Switzerland. *Palynology* 19:211–219.
- . 1998. Palynostratigraphic characterization of the Sinemurian–Pliensbachian transition of the potential GSSP section at Aubach/Aselfingen, southwest Germany. Fifth international symposium on the Jurassic System, August, 12–25 1998, Vancouver, Abstracts and program, p. 29.
- Fensome, R. A., G. L. Williams, M. S. Barss, J. M. Freeman, and J. M. Hill. 1990. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. *American Association of Stratigraphic Palynologists Contributions Series* No. 25.
- Fensome, R. A., F. J. R. Taylor, G. Norris, W. A. S. Sarjeant, D. I. Wharton, and G. L. Williams. 1993. A classification of fossil and living dinoflagellates. *Micropaleontology Press Special Publication* 7.
- Fensome, R. A., R. A. MacRae, J. M. Moldowan, F. J. R. Taylor,

- and G. L. Williams. 1996. The Early Mesozoic radiation of dinoflagellates. *Paleobiology* 22:329–338.
- Fensome, R. A., J. F. Saldarriaga, F. J. R. Taylor. 1999. Dinoflagellate phylogeny revisited: reconciling morphological and molecular based phylogenies. *Grana* 38:66–80.
- Gorin, G. E., and S. Feist-Burkhardt. 1990. Organic facies of Lower to Middle Jurassic sediments in the Jura Mountains, Switzerland. *Review of Palaeobotany and Palynology* 65:349–355.
- Gustomesov, V. A. 1978. The pre-Jurassic ancestry of Belemnitida and the evolutionary changes in the Belemnitoidea at the boundary between the Triassic and the Jurassic. *Palaeontological Journal* 3:283–292.
- Hallam, A. 2001. A review of the broad pattern of Jurassic sea-level changes and their possible causes in the light of current knowledge. *Palaeogeography, Palaeoclimatology, Palaeoecology* 167:23–37.
- Haq, B. U., J. Hardenbol, and P. R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 255:1156–1167.
- Hesselbo, S. P., D. R. Gröcke, H. C. Jenkyns, C. J. Bjerrum, P. Farinon, H. S. Morgans Bell, and O. R. Green. 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. *Nature* 406:392–395.
- Hochüli, P., and S. M. Frank. 2000. Palynology (dinoflagellate cysts, spore-pollen) and stratigraphy of the Lower Carnian Raibl Group in the Eastern Swiss Alps. *Eclogae Geologicae Helvetiae* 93:429–443.
- Hollander, D. J., G. Bessereau, S. Belin, J. P. Houzay, and A. Y. Huc. 1991. Organic matter in the Early Toarcian shales, Paris Basin: a response to environmental change. *Review de l'Institut Français du Pétrole* 46:543–562.
- Jenkyns, H. C. 1988. The Early Toarcian (Jurassic) anoxic event: stratigraphic, sedimentary, and geochemical evidence. *American Journal of Science* 288:101–151.
- Jenkyns, H. C., and C. J. Clayton. 1986. Black shales and carbon isotopes in pelagic sediments from the Tethyan Lower Jurassic. *Sedimentology* 33:87–106.
- . 1997. Lower Jurassic epicontinental carbonates and mudstones from England and Wales: chemostratigraphic signals and the Early Toarcian anoxic event. *Sedimentology* 44:687–706.
- Jenkyns, H. C., D. R. Gröcke, and S. P. Hesselbo. 2001. Nitrogen isotope evidence for water mass denitrification during the Early Toarcian (Jurassic) oceanic anoxic event. *Palaeoceanography* 16:1–11.
- Jimenez, A. P., C. Jimenez de Cisneros, P. Rivas, and J. A. Vera. 1996. The Early Toarcian anoxic event in the westernmost Tethys (Subbetic): paleogeographic and paleobiogeographic significance. *Journal of Geology* 104:399–416.
- Katz, M. E., J. D. Wright, K. G. Miller, B. S. Cramer, K. Fennel, and P. G. Falkowski. In press. Biological overprint of the geological carbon cycle. *Marine Geology*.
- Kump, L. R., and M. A. Arthur. 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. *Chemical Geology* 161:181–198.
- Kump, L. R., M. A. Arthur, M. E. Patzkowsky, M. T. Gibbs, D. S. Pinkus, and P. M. Sheehan. 1999. A weathering hypothesis for glaciation at high atmospheric  $p\text{CO}_2$  during the Late Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology* 152:173–187.
- Küspert, W. 1982. Environmental changes during oil shale deposition as deduced from stable isotope ratios. Pp. 482–501 in G. Einsele and A. Seilacher, eds. *Cyclic and event stratification*. Springer, Berlin.
- Langford, F. F., and M. M. Blanc-Valleron. 1990. Interpreting Rock-Eval pyrolysis data using graphs of pyrolyzable hydrocarbons vs. total organic carbon. *American Association Petroleum Geologists Bulletin* 74:709–806.
- Lear, C. H., Y. Rosenthal, N. Slowey. 2002. Benthic foraminiferal Mg/Ca paleothermometry: a revised core-top calibration. *Geochimica et Cosmochimica Acta* 66:3375–3387.
- Little, C. T. S., and M. J. Benton. 1995. Early Jurassic mass extinction: a global long-term event. *Geology* 23:495–498.
- Lund, J. J. 2003. Rhaetian to Pliensbachian palynostratigraphy of the central part of the NW German Basin exemplified by the Eitzendorf 8 well. *Courier Forschungsinstitut Senckenberg* 241:69–83.
- Mallarino, G., R. H. Goldstein, and P. Di Stefano. 2002. New approach for qualifying water depth applied to the enigma of drowning carbonate platforms. *Geological Society of America Bulletin* 30:783–786.
- Martin, R. E. 1996. Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, diversity of the marine biosphere. *Palaios* 11:209–219.
- Martini, R., L. Zaninetti, M. Villeneuve, J. J. Cornee, L. Krystyn, S. Cirilli, P. De Wever, P. Dumitrica, and A. Harsolumakso. 2000. Triassic pelagic deposits of Timor: palaeogeographic and sea-level implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 160:123–151.
- McArthur, J. M., D. T. Donovan, M. F. Thirlwall, B. W. Fouke, and D. Matthey. 2000. Strontium isotope profile of the Early Toarcian (Jurassic) oceanic anoxic event, duration of ammonite biozones, and belemnite palaeotemperatures. *Earth and Planetary Science Letters* 179:269–285.
- Moldowan, J. M., and N. M. Talyzina. 1998. Biogeochemical evidence for dinoflagellate ancestors in the Early Cambrian. *Science* 281:1168–1170.
- Morbey, S. J. 1978. Late Triassic and Early Jurassic subsurface palynostratigraphy in Northwestern Europe. *Palinologia* 1:355–365.
- Morettini, E., M. Santantonio, A. Bartolini, F. Cecca, P. O. Baumgartner, and J. C. Hunziker. 2002. Carbon isotope stratigraphy and carbonate production during the Early-Middle Jurassic: examples from the Umbria-Marche-Sabina Apennines (central Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 184:251–273.
- Müller, F. L. 1990. The paleoecology of the Liassic benthic foraminifera of Great Britain. Ph.D. dissertation. Rutgers University, New Brunswick, NJ.
- Partington, M. A., P. Copestake, B. C. Mitchener, and J. R. Underhill. 1993. Biostratigraphic calibration of genetic stratigraphic sequences in the Jurassic-lowermost Cretaceous (Hettangian to Ryazanian) of the North Sea and adjacent areas. Pp. 371–386 in J. R. Parker ed. *Petroleum geology of north-west Europe: proceedings of the 4<sup>th</sup> conference*. Geological Society of London.
- Pfiester, L. A., and D. M. Anderson. 1987. Dinoflagellate reproduction. Pp. 611–648 in F. J. R. Taylor, ed. *The biology of dinoflagellates*. Botanical Monographs 21:611–648.
- Poulsen, N. E., and J. B. Riding. 2003. The Jurassic dinoflagellate cyst zonation of Subboreal north-west Europe. With a supplement by B. Buchardt: oxygen isotope palaeotemperatures from the Jurassic in Northwest Europe. In J. Ineson and F. Surlyk, eds. *The Jurassic of Denmark and Greenland*. Geological Survey of Denmark and Greenland Bulletin 1:115–144.
- Prauss, M., and W. Riegel. 1989. Evidence of phytoplankton associations for causes of black shale formation in epicontinental seas. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 11:671–682.
- Prauss, M., B. Ligouis and H. Luterbacher. 1991. Organic matter and palynomorphs in the 'Posidonienschiefer' (Toarcian, Lower Jurassic) of southern Germany. Pp. 335–352 in R. V. Tyson and T. H. Pearson, eds. *Modern and ancient continental shelf anoxia*. Geological Society, London.
- Price, G. D. 1999. The evidence and implications of polar ice during the Mesozoic. *Earth-Science Reviews* 48:183–210.

- Quesada, S., C. Dorronsoro, S. Robles, R. Chalor, and J. O. Grimalt. 1997. Geochemical correlation of oil from the Ayoluengo field to Liassic shale units in the southwestern Basque-Cantabrian Basin (northern Spain). *Organic Geochemistry*, 27(1-2):25-40.
- Quigg, A., Z. V. Finkel, A. Irwin, Y. Rosenthal, T. Y. Ho, J. R. Reinfelder, O. Schofield, F. M. M. Morel, and P. G. Falkowski. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425:291-294.
- Rasmussen, E. S., S. Lomholt, C. Andersen, and O. V. Vejbæk. 1998. Effects of structural evolution of the Lusitanian Basin in Portugal and the shelf and slope area offshore Portugal. *Tectonophysics* 300:199-225.
- Rauscher, R., and J.-P. Schmitt. 1990. Recherches palynologiques dans le Jurassique d'Alsace (France). Review of Palaeobotany and Palynology 62:107-156.
- Riding, J. B. 1984. A palynological investigation of Toarcian and Early Aalenian strata from the Blea Wyke area, Ravenscar, North Yorkshire. *Proceeding of the Yorkshire Geological Society* 45:109-122.
- . 1987. Dinoflagellate cyst stratigraphy of the Nettleton Bottom Borehole (Jurassic: Hettangian to Kimmeridgian), Lincolnshire, England. *Proceeding of the Yorkshire Geological Society* 46:231-266.
- Riding, J. B., and R. N. L. B. Hubbard. 1999. Jurassic (Toarcian-Kimmeridgian) dinoflagellate cysts and paleoclimates. *Palynology* 23:15-30.
- Riding, J. B., and N. S. Ioannides. 1996. A review of Jurassic dinoflagellate cyst biostratigraphy and global provincialism. *Bulletin de la Société Géologique de France* 167:3-14.
- Röhl, H., A. Schmid-Röhl, W. Oschmann, A. Frimmel, and L. Schwark. 2001. The Posidonia Shale (lower Toarcian) of SW-Germany: an oxygen-depleted ecosystem controlled by sea level and palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 165(1-2):27-52.
- Rosales, I., S. Quesada, and S. Robles. 2001. Primary and diagenetic isotopic signals in fossils and hemipelagic carbonates: the Lower Jurassic of northern Spain. *Sedimentology* 48:1149-1169.
- Rosenthal, Y., E. A. Boyle, and N. Slowey. 1997. Temperature control on the incorporation of magnesium, strontium, fluorine, and cadmium into benthic foraminiferal shells from Little Bahama Bank: prospects for thermocline paleoceanography. *Geochimica et Cosmochimica Acta* 61:3633-3643.
- Rosenthal, Y., M. P. Field, and R. M. Sherrell. 1999. Precise determination of element/calcium ratios in calcareous samples using sector field inductively coupled plasma mass spectrometry. *Analytical Chemistry* 71:3248-3253.
- Sandy, M. R., and G. D. Stanley Jr. 1993. Late Triassic brachiopods from the Luning Formation, Nevada, and their palaeobiogeographical significance. *Palaeontology* 36:439-480.
- Schouten, S., M. E. van Kaam-Peters, I. Rijpstra, M. Schoell, and J. S. Sinnighe Damste. 2000. Effects of an oceanic anoxic event on the stable carbon isotopic composition of Early Toarcian carbon. *American Journal of Science* 300:1-22.
- Smith, P. L., and H. W. Tipper. 1986. Plate tectonics and paleobiogeography: Early Jurassic (Pliensbachian) endemism and diversity. *Palaios* 1:399-412.
- Stover, L. E., H. Brinkhuis, S. P. Damassa, L. De Verteuil, R. J. Helby, E. Monteil, A. D. Patridge, A. J. Powell, J. B. Riding, M. Smelror, and G. L. Williams. 1996. Mesozoic-Tertiary dinoflagellates, acritarchs and prasinophytes. Pp. 641-750 in J. Jansonius and D. C. McGregor, eds. *Palynology: principles and applications*, Vol. 2. American Association of Stratigraphic Palynologists Foundation, College Station, Tex.
- Suarez Vega, L. C. 1974. Estratigrafía del Jurásico en Asturias. *Cuadernos Geológicos Iberica* 3:1-368.
- Taylor, K. G. 1998. Spatial and temporal variations in early diagenetic organic matter oxidation pathways in Lower Jurassic mudstones of eastern England. *Chemical Geology* 145:47-60.
- Tyson, R. V. 1995. *Sedimentary organic matter*. Chapman and Hall, London.
- Vakhrameev, V. A. 1981. Pollen *Classopollis*: indicator of Jurassic and Cretaceous climate. *Palaeobotanist* 28-29:301-307.
- Van de Schootbrugge, B., K. B. Föllmi, L. G. Bulot, and S. J. Burns. 2000. Paleocyanographic changes during the Early Cretaceous (Valanginian-Hauterivian): evidence from oxygen and carbon stable isotopes. *Earth and Planetary Science Letters* 181:15-31.
- Wall, D. 1965. Microplankton, pollen and spores from the Lower Jurassic in Britain. *Micropalaeontology* 11:151-90.
- Wall, D., B. Dale, G. P. Lohmann, and W. K. Smith. 1977. The environment and climatic distribution of dinoflagellate cysts in modern marine sediments from regions in the North and South Atlantic Oceans and adjacent seas. *Marine Micropalaeontology* 2:121-200.
- Weissert, H., A. Lini, K. B. Föllmi, and O. Kuhn. 1998. Correlation of Early Cretaceous carbon isotope stratigraphy and platform drowning events: a possible link? *Palaeogeography, Palaeoclimatology, Palaeoecology* 137:189-203.
- Weiß, M. 1986. *Liasidium variable*, eine Dinoflagellate mit stratigraphischem Wert an der Grenze Unter-/Ober-Sinemurium. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 5:317-320.
- Wetzel, A., R. Allenbach, and V. Allia. 2003. Reactivated basement structures affecting the sedimentary facies in a tectonically "quiescent" epicontinental basin: an example from NW Switzerland. *Sedimentary Geology* 157:153-172.
- Wille, W. 1982a. Evolution and ecology of upper Liassic dinoflagellates from SW-Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 164(1/2):74-82.
- . 1982b. Palynology of upper Liassic bituminous shales. Pp. 505 in G. Einsele and A. Seilacher, eds. *Cyclic and event stratification*. Springer, Berlin.
- Wille, W., and H. Gocht. 1979. Dinoflagellaten aus dem Lias Südwestdeutschlands, *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221-258.
- Williams, G. L., P. Ascoli, M. S. Barss, J. P. Bujak, E. H. Davies, R. A. Fensome, and M. A. Williamson. 1990. Chapter 3: Biostratigraphy and related studies. In M. J. Keen and G. L. Williams, eds. *Geology of the continental margin of eastern Canada*. *Geology of Canada* 2:86-137. Geological Survey of Canada, Ottawa.
- Williams, G. L., J. K. Lentin, and R. A. Fensome. 1998. The Lentin and Williams index of fossil dinoflagellates 1998 edition. *American Association of Stratigraphic Palynologists, Contributions Series* 34:817.
- Woodland, A. W. 1971. The Llanbedr (Mochras Farm) Borehole. Report No. 71/18. Institute of Geological Sciences, London.

#### Appendix

#### Annotated Species List

List of species identified in this study. Full references can be found in Williams et al. 1998 for dinoflagellate cysts, and in Fensome et al. 1990 for acritarchs and prasinophytes.

#### Dinoflagellate cysts

*Comparodinium koessenium* Morbey 1975

*Liasidium variable* Drugg 1978

*Luehndea spinosa* Morgenroth 1970

*Mancodinium semitabulatum* Morgenroth 1970

*Nannoceratopsis gracilis* Alberti 1961

*Nannoceratopsis* cf. *magnicornus* Bucefalo Palliani and Riding 1998

*Nannoceratopsis senex* Van Helden 1977

*Nannoceratopsis symmetrica* Bucefalo Palliani and Riding 2000  
*Nannoceratopsis tricerata* Drugg 1978

#### Acritarchs

*Baltisphaeridium debilispinum* Wall & Downie 1963  
*Baltisphaeridium delicatum* Wall 1965  
*Baltisphaeridium diversispinosum* Wall 1965  
*Baltisphaeridium micropunctatum* Wall 1965  
*Hystriosphæridium? caminuspinum* Wall 1965  
*Micrhystridium clavatispinum* Wall 1965  
*Micrhystridium deflandrei* Valensi 1949  
*Micrhystridium exilium* Wall 1965  
*Micrhystridium fragile* Deflandre 1947

*Micrhystridium intromittum* var. *intromittum* Wall 1965  
*Micrhystridium lymense* var. *gliscum* Wall 1965  
*Micrhystridium lymense* var. *lymense* Wall 1965  
*Micrhystridium lymense* var. *rigidum* Wall 1965  
*Micrhystridium rarispinum* Sarjeant 1960  
*Micrhystridium stellatum* Deflandre 1945  
*Micrhystridium wattonense* Wall 1965  
*Veryhachium reductum* (Deunff 1959) Downie & Sarjeant 1965  
*Veryhachium trispinosum* (Eisenack 1938) Stockmans & Willière 1962

#### Prasinophytes

*Cymatiosphaera pachythea* Eisenack 1957  
*Tasmanites punctatus* Eisenack 1958