# Calcareous nannoplankton changes across the early Toarcian oceanic anoxic event in the western Tethys

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[1]   Calcareous nannoplankton were profoundly affected by environmental perturbations coincident with the early Toarcian oceanic anoxic event (T-OAE). We quantify the abundance of nannofossils across the T-OAE at three locations in Western Europe, where the event is marked by a prominent negative carbon isotope excursion (CIE). Data were treated by statistical analysis, and the Shannon diversity index was applied in order to describe nannofossil assemblage changes related to paleoenvironmental evolution. In the basal Toarcian, before the T-OAE, high proportions of taxa with an affinity for low temperature (e.g., *P. liasicus*, *T. patulus*, *Bussonius*) occurred. This observation is consistent with interpretations of published oxygen isotope records. During the T-OAE, the lowest abundance of nannofossils is observed, but there is a peak of a coccolith (*Calyculus*) from an organism that probably thrived in low-saline surface waters depleted of nitrate. At the end of the perturbation, the lowest diversities of nannofossils occurred, and assemblages are dominated by *Crepidolithus crassus*, a deep dweller. This interval corresponded to progressive reoxygenation of deep water and the reoccupation of the deep photic zone by nannoplankton. The highest abundance of nannofossils is recorded above the CIE and testifies to the recovery of the entire nannoplankton community. The T-OAE was widespread (perhaps global) and probably linked to major changes in the atmosphere and hydrosphere. However, the record of this event varies in the basins surrounding the western Tethys, suggesting regional imprints on the global signal. The regional variability may attest to establishment of effective connections between the Arctic and Tethys oceans, which allowed cool, low-saline water formed at high latitudes to stream toward the western Tethys.

## 1.   Introduction

[2]   The early Toarcian oceanic anoxic event (T-OAE) [*Jenkyns*, 1988] of the Early Jurassic (∼183 Ma ago) was characterized by widespread black shale deposition, and major biological changes in marine ecosystems [*Little and Benton*, 1995; *Harries and Little*, 1999; *Wignall et al.*, 2006], including nannofossils [*Bucefalo Palliani et al.*, 2002; *Erba*, 2004; *Mattioli and Pittet*, 2004; *Tremolada et al.*, 2005]. It was also marked by a perturbation of the global carbon cycle, as evidenced by a prominent negative carbon isotope excursion (CIE) recorded in marine carbonate, organic matter, biomarkers and fossil wood [*Jenkyns and Clayton*, 1997; *Hesselbo et al.*, 2000, 2007; *Schouten et al.*, 2000; *Röhl et al.*, 2001; *Jenkyns et al.*, 2002; *Schmid-Röhl et al.*, 2002; *van Breugel et al.*, 2006]. However, *van de Schootbrugge et al.* [2005] did not find the CIE in low-Mg calcite belemnite rostra spanning the T-OAE. This may be an artifact of sampling resolution [*Hesselbo et al.*, 2007]. Alternatively, different expressions of the carbon perturbation may have occurred in various settings of the western Tethys.

[3]   Certainly, the organic carbon content varies significantly between studied sections in this region [*van de Schootbrugge et al.*, 2005]. Organic-rich deposits formed during the T-OAE may have resulted from enhanced primary productivity, either from intensified upwelling [*Jenkyns*, 1988] or from increased continental weathering and runoff [*Cohen et al.*, 2004]. Both mechanisms might have promoted nutrification of surface waters and ultimately primary production. However, a significant turnover is observed among the primary producers across the T-OAE. A quantification of the abundance of dinoflagellates and coccolithophorids indicates a significant decrease, until a temporary disappearance during the crisis acme [*Bucefalo Palliani et al.*, 2002; *Mattioli et al.*, 2004b]. Primary productivity was thus solely sustained by phototrophic bacteria (Chlorobiaceae) [*van de Schootbrugge et al.*, 2005] or by green algae (*Tasmanites*) [*Bucefalo Palliani et al.*, 2002; *Mattioli et al.*, 2004b; *van de Schootbrugge et al.*, 2005].

[4]   The western Tethys represents a key area for paleoceanographic studies because it was located between the open, oceanic Tethys to the west, and the Laurasian Seaway leading to the Arctic Ocean to the north (Figure 1). Although southward circulation of water from the Arctic Ocean to the Tethys has been inferred for the early Toarcian [*Bjerrum et al.*, 2001], the impact of this flow has not been considered in most discussions of the T-OAE. Southward flow of cool, low-density waters should have impacted nannoplankton assemblages, and be responsible for the differences observed in geochemical and nannofossil record of the western Tethys.

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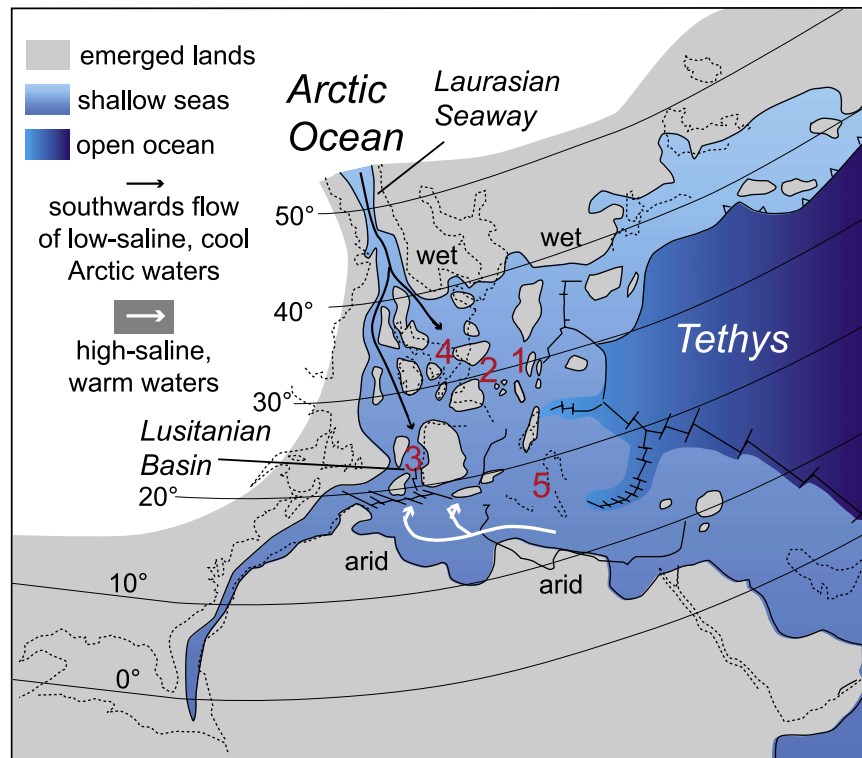
**MAIN LOCATIONS:**
1. SW Germany (Dotternhausen)
2. NE France (ANDRA HTM-102 Borehole)
3. Portugal (Peniche)

**COMPARATIVE LOCATIONS:**
4. Northern England (Brown Moor BGS Borehole)
5. Central Italy (Colle d'Orlando and Pozzale)

**Figure 1.** Paleogeography of the western Tethys at about 183 Ma (redrawn after *Bassoulet et al.* [1993]) showing locations of the three sections studied in this account (Dotternhausen and ANDRA HTM 102 Borehole along the northern Tethyan margin, Peniche in the Lusitanian basin) and two additional locations previously examined (Brown Moor BGS Borehole in northern England and Colle d'Orlando and Pozzale in central Italy). The five locations span a paleolatitudinal gradient of about 20°.

[5] The nature of primary producers and the evolution of temperature in surface ocean waters during the T-OAE need to be elucidated in order to better understand environmental conditions of this and other times of widespread anoxia. Calcareous nannoplankton are an ideal group of micro-organisms to address these questions because modern coccolithophorids are an important group of primary producers and because their distributions, species richness and abundances are largely controlled by temperature, nutrients, and salinity of surface waters [*Winter et al.*, 1994].

[6] We present detailed nannofossil assemblage records across the T-OAE from three locations in the western Tethys (Figure 1) in order to unravel global *versus* local environmental influences upon primary production during the T-OAE. These records are compared to published geochemical data. Although high organic carbon content has often been used to mark an oceanic anoxic event at a site, we use the negative CIE (start to finish) to signify the

acme of the T-OAE. All three studied sections display this isotope anomaly [*Röhl et al.*, 2001; *van Breugel et al.*, 2006; *Hesselbo et al.*, 2007; *Suan et al.*, 2008a], whereas sediments enriched in organic matter are recorded at Dotternhausen and in the HTM-102 Borehole through the Middle Toarcian [*Röhl et al.*, 2001; *van Breugel et al.*, 2006], and those at Peniche have low TOC over the considered stratigraphic interval [*Hesselbo et al.*, 2007].

## 2. Sites

[7] The western Tethys Ocean in the Early Jurassic predominantly consisted of shallow sea extending between the European and African landmasses (Figure 1). The northern subtropical margin (~27–35°N) corresponded to the wide north European epicontinental shelf and was dominated by siliciclastic sedimentation. By contrast, the southern tropical margin (~17–23°N) comprised relatively shallow basins separated by large carbonate platforms. The
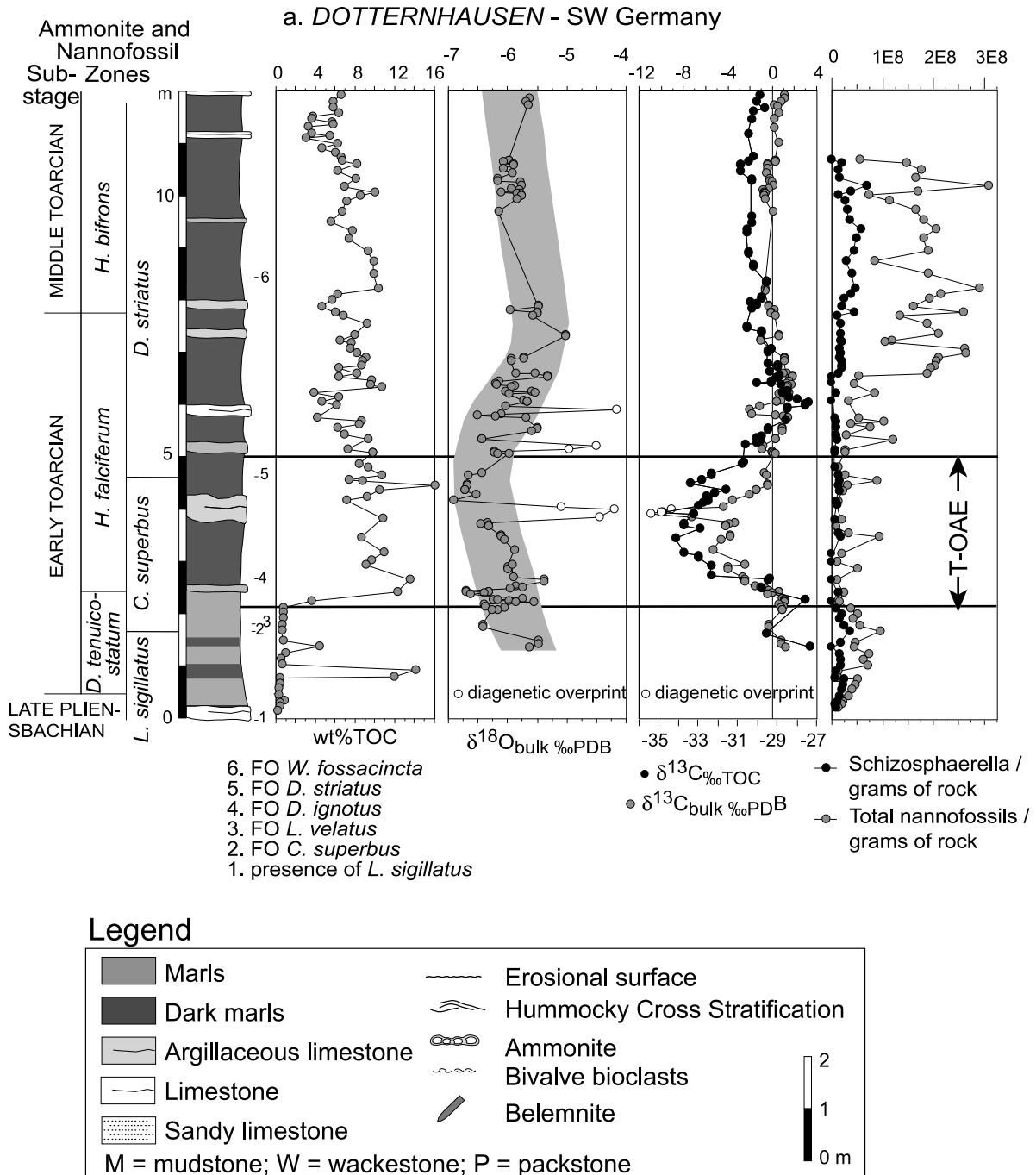
**Figure 2a.** Lithology and biostratigraphy of the three studied sections. Absolute nannofossil abundance is also reported. For the Dotternhausen section (SW Germany), ammonite zones are after *Riegraf* [1984]. Geochemical data (wt % total organic carbon (TOC), $\delta^{18}O$, $\delta^{13}C_{bulk}$, and $\delta^{13}C_{TOC}$) are from *Röhl et al.* [2001] and *Schmid-Röhl et al.* [2002]. These authors interpreted some isotopic values (empty dots) as diagenetic in origin. Nannofossil abundance is after *Mattioli et al.* [2004b].

Lusitanian Basin, part of an aborted rift system (Figure 1), was a narrow, elongated basin in the westernmost Tethys that allowed exchange of water masses between the northern and southern margins [*Bassoulet et al.*, 1993].

[8] Two sites examined in this study (Dotternhausen, SW Germany; ANDRA Borehole HTM-102, NE France) were located on the northern margin of the Tethys. The third section (Peniche, W Portugal) is from the Lusitanian Basin, and has affinities with the southern margin.

[9] Biostratigraphy and lithostratigraphy of the studied sections and borehole are illustrated in Figure 2, along with available geochemical data. The CIE that corresponds to the
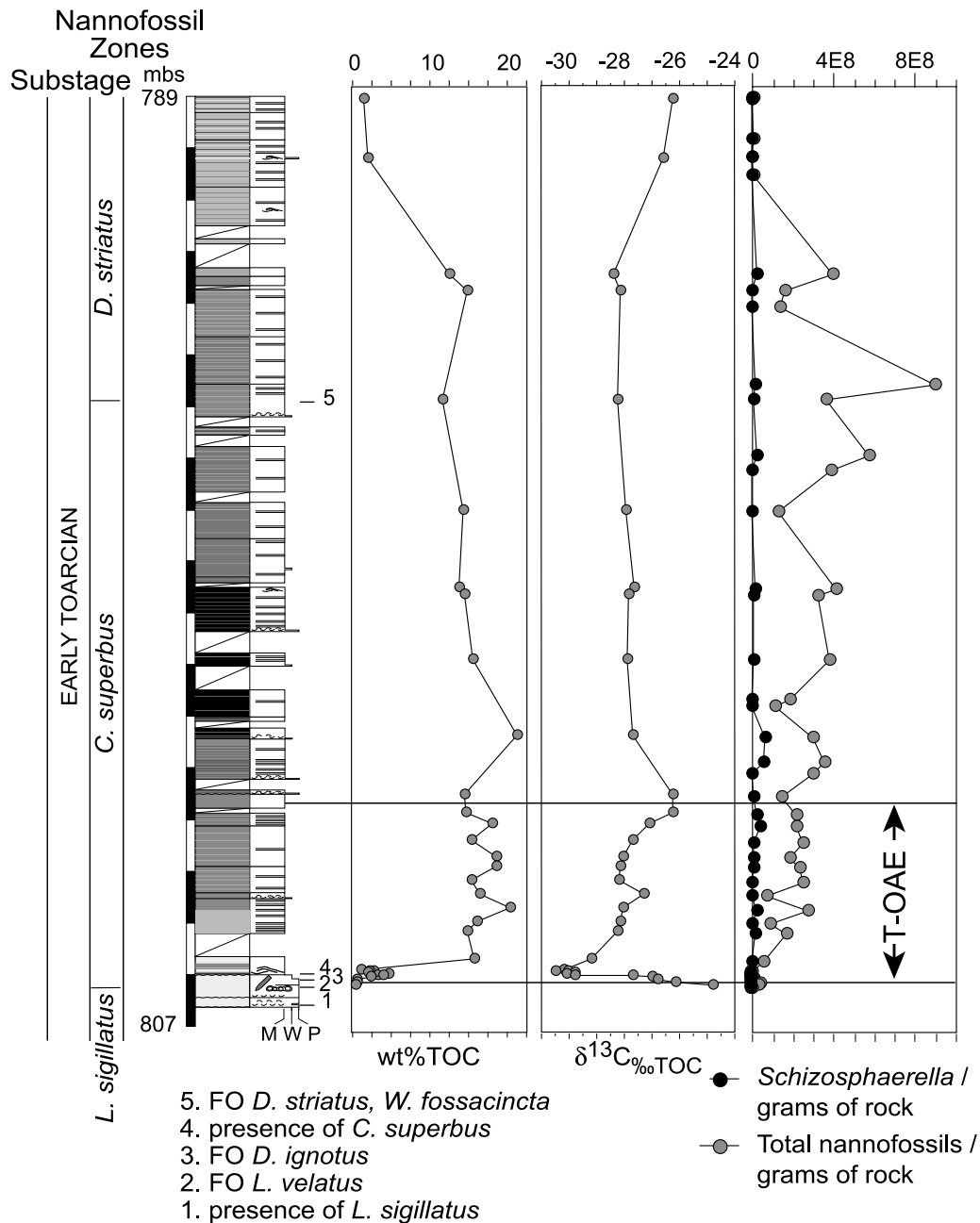
## b. *ANDRA BOREHOLE HTM-102* - NE France



**Figure 2b.**   Geochemical data (wt % TOC and $\delta^{13}C_{TOC}$) of the ANDRA Borehole HTM-102, located in NE France, are from *van Breugel et al.* [2006]. Note that the ANDRA HTM-102 Borehole section is very condensed in its basal part; hiatuses are probably present at its base where sediments are packstones, and erosion surfaces are observed. Accumulation rate greatly increases in the second half of the negative isotope excursion, likely because of an important increase in siliciclastic input. Note that the stratigraphic position of the first occurrence (FO) of *W. fossacincta* is more effective than the FO of *D. striatus* for establishing correlation between Dotternhausen and the HTM-102 Borehole.

T-OAE has been dated as *Harpoceras falciferum* Ammonite Zone (*H. exaratum* Subzone) of NW Europe and its time equivalent in other settings of western Tethys [*Bucefalo Palliani et al.*, 2002; *Jenkyns et al.*, 2002], or to the nannofossil Zone *Carinolithus superbus* [*Mattioli et al.*, 2004b].

[10]   The lithostratigraphy of the Dotternhausen section has been described by *Röhl et al.* [2001], and accompanying ammonite and nannofossil biostratigraphies have been established by *Riegraf* [1984] and *Mattioli et al.* [2004b], respectively. The 12 m thick succession is made of marls
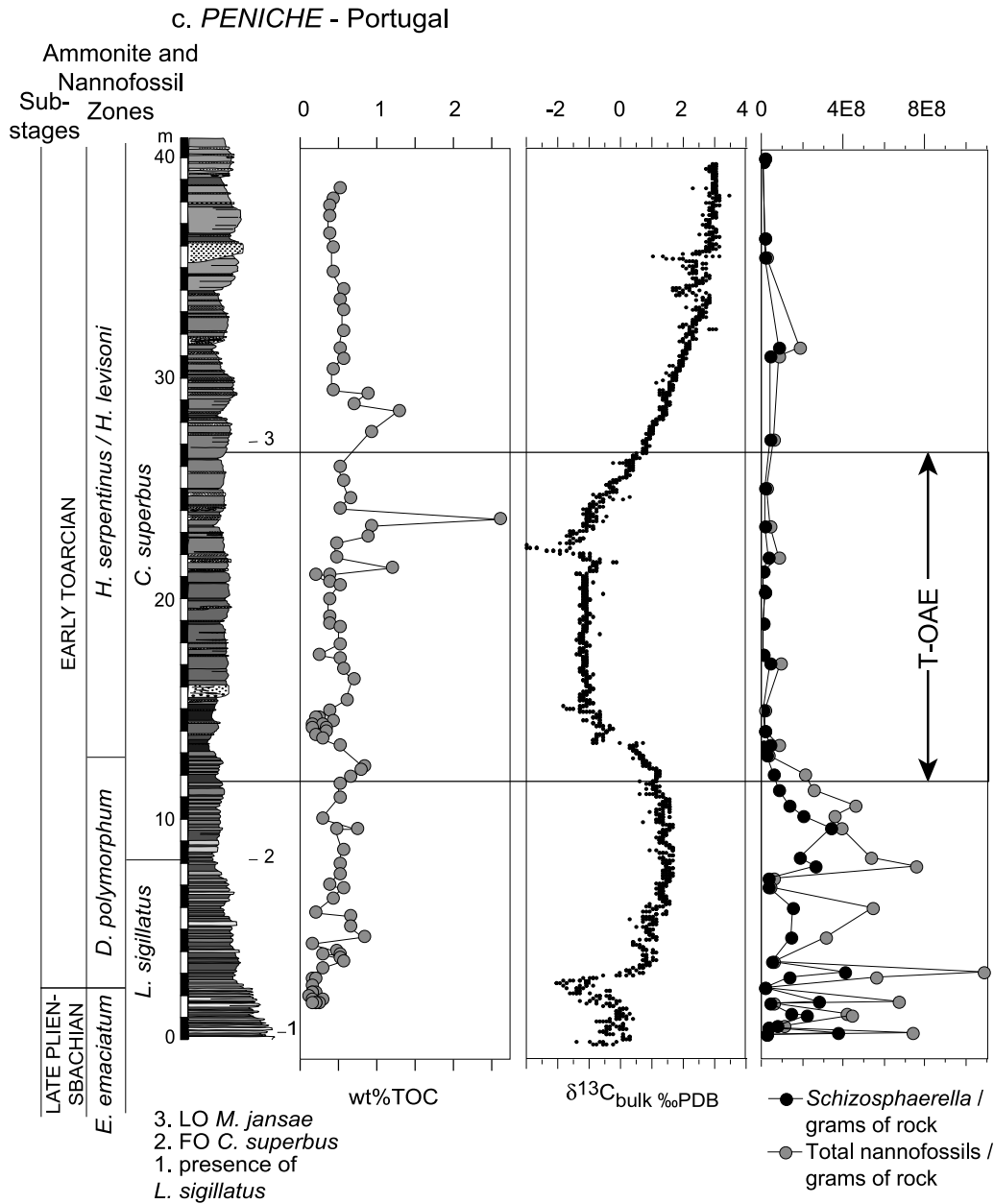
**Figure 2c.** For the Peniche section, wt % TOC and $\delta^{13}C_{bulk}$ data are from *Hesselbo et al.* [2007]. Ammonite zones are from *Mouterde* [1955]. Note that the vertical scale (meters) is different for the three sections. Nannofossil biostratigraphy has been established using the framework provided by *Mattioli and Erba* [1999].

and limestones, bearing rich and diverse benthic fauna at the base (0–2.10 m; uppermost Pliensbachian-earliest Toarcian; Figure 2a). Dark marls and argillaceous limestones occur in the uppermost *D. tenuicostatum* to *H. falciferum* Ammonite Zones. In these, TOC increases to 10–16 wt %, and $\delta^{13}C$ records of TOC and carbonate display pronounced negative shifts. The upper part of the section (6.20–12 m; upper *H. falciferum* to *H. bifrons* Ammonite Zones) is composed of dark marls where TOC remains moderately high (1–10 wt %), but where $\delta^{13}C$ records come back to more positive values.

[11] The basal part of the HTM-102 Borehole consists of bioclastic packstones separated by erosion surfaces (Figure 2b). These horizons are interpreted as storm deposits. Moreover, overall accumulation rate varied significantly. Specifically, the basal part of the HTM-102 Borehole is condensed (or contains a hiatus), while accumulation rate increases above. A sedimentary hiatus across the Pliensbachian/Toarcian boundary and the first ammonite zone of the Toarcian (*D. tenuicostatum*) [*Guex et al.*, 2001; *Jenkyns et al.*, 2002] has been recorded in most sedimentary basins of the northern margin of the Tethys. Ammonites, which are
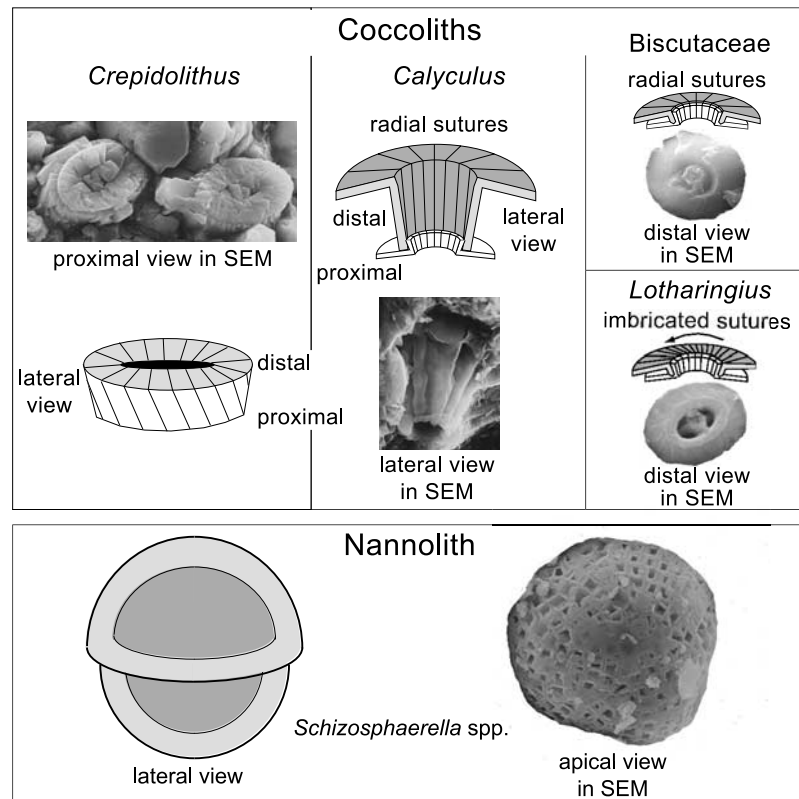
**Figure 3.** Drawings and scanning electron microscope micrographs illustrating the morphology of the coccoliths and nannoliths most commonly recorded in the Toarcian. Terminology is after *Bown* [1987]. *Crepidolithus* coccoliths are formed by calcite elements that grow distally and form a basket-like shape coccolith. *Biscutaceae*, *Calyculus*, and *Lotharingius* coccoliths are composed of radial elements, and their general shape is a concavo-convex, double-layered shield. The distal and proximal views refer to the position of the coccolith with respect to the coccolithophorid cell. The coccoliths of the genus *Calyculus* are characterized by an inner wall that extends distally with respect to the cell surface. *Schizosphaerella*, a probable calcareous dinoflagellate [*Kälin and Bernoulli*, 1984], is formed by two slightly elliptical hemivalves, which are made of the assemblage of tiny calcite crystals.

present as fragments, are difficult to identify at the species level so correlations with the two other studied sections are based upon calcareous nannofossil biostratigraphy.

[12] The Peniche section (Figure 2c) is the GSSP candidate for the Pliensbachian/Toarcian boundary [*Elmi*, 2006]. Upper Pliensbachian sedimentry rocks of this section are dominated by carbonates, similar to those of other sections of the southern Tethys margin [*Bucefalo Palliani et al.*, 1998; *Mattioli and Pittet*, 2004]. An important decrease in carbonate accumulation happened during the lower Toarcian and across the T-OAE, resulting in a clay-dominated interval. A recovery to mixed carbonate-siliciclastic sedimentation occurred at the end of the lower Toarcian. Several turbidite layers enriched in siliciclastic material are found in the interval corresponding to the entire $\delta^{13}C$ perturbation [*Hesselbo et al.*, 2007, Figure 2c].

[13] Besides these lithological differences, the magnitude of the CIE in marine carbonates and amount of TOC are different between the northern Tethyan margin sites (Dotternhausen, HTM-102) and Peniche (Figure 2). The magnitude of the CIE recorded in bulk carbonate is −5 to −6‰, and TOC reaches up to ∼16−18 wt % in sections representing the northern shelf (Figure 2). Conversely, the CIE is −2 to −3‰, and the TOC much lower (<3 wt %) in the Peniche section.

## 3. Samples and Methods

[14] Nannofossils (both coccoliths and the nannolith *Schizosphaerella*, a probable calcareous dinoflagellate; Figure 3) have been quantified in 81 samples from the Dotternhausen section, 47 samples from the HTM-102 Borehole, and 44 samples from the Peniche section. Absolute abundances per gram of rock were evaluated according to the method described by *Geisen et al.* [1999]. Briefly, this method involves the following steps. A suspension of 30 mg of dried rock powder and water (oversaturated with respect to $CaCO_3$ and with a basic pH) is homogenized and let settled for 24 h on a cover slide in a settling device. The cover slide is recovered, dried and attached to a microscope slide. Between 250 and 350 nannofossils are counted using a Zeiss polarizing microscope (1000X). Preservation of

nannofossils is carefully checked using an optical microscope and a scanning electron microscope. In order to obtain a consistent data set, only samples showing good preservation and high absolute abundances ($>2*10^6$ nannofossils per gram of rock) are retained for statistical analyses. (After this procedure, three, four, and one samples from the three studied sections, respectively, were removed from the data set.)

[15] Principal component analysis (PCA) was applied to the nannofossil assemblages. This multivariate statistical method allows analysis of the entire nannofossil community, instead of changes in single taxa abundance. This method also permits better interpretations of complex data sets, and reduces a large data matrix composed of several variables to a small number of factors representing the main modes of variations [*Beaufort and Heussner*, 2001]. PCA was computed with the StatView 5.0 software. The extraction method for eigenvalues was Orthotran/Varimax. Only relative abundances of coccoliths (calculated from the total coccolith population) were introduced in the PCA analysis because coccoliths and *Schizosphaerella* are fossil remains of organisms presumably having had different modes of life and biological affinities. Because it is impossible to unambiguously assess if rare and discontinuous species were actually absent in the biocenosis, or if their absence in the fossil assemblage is due to sampling, counting biases, and/ or taphonomic problems, coccolith species with a mean relative abundance <2% were not incorporated into PCA. Some species (such as *Lotharingius crucicentralis* and *L. sigillatus*; *Bussonius prinsii* and *B. leufuensis*) were grouped because they display abundance peaks in the same samples. The *Similiscutum cruciulus* group comprises three morphotypes, namely *S. cruciulus*, *S. orbiculus*, and *S. avitum* [*de Kaenel and Bergen*, 1993; *Mattioli et al.*, 2004a]. The matrix in our study consists of 15 to 17 taxa according to the different analyzed sections.

[16] We also calculated the Shannon Index (H), a mathematical measure of species diversity in a community [*Shannon and Weaver*, 1949]. This is calculated as:

$$H = -\sum_{i=1}^{s}(Pi * \ln[Pi])$$

where *i* is a species, *s* is the number of species (i.e., species richness), *Pi* is the relative abundance of each species.

# 4. Results

## 4.1. Absolute Abundances of Nannofossils

[17] At Dotternhausen, both coccolith and *Schizosphaerella* abundances increase in rocks deposited from the uppermost Pliensbachian to the base of Toarcian. However, across the negative CIE, nannofossil quantities are the lowest, with the exception of a few samples. A first increase of absolute abundance (mainly coccoliths) is observed in the interval above the excursion until the highest abundance (both groups) below the boundary between the *H. falciferum* and *H. bifrons* ammonite Zones.

[18] The interval corresponding to the base of the Dotternhausen section is lacking at the HTM-102 Borehole because of condensation and possible hiatuses. Absolute abundance of nannofossils is the lowest during the CIE, and increases significantly in the following interval, becoming notably higher than in Dotternhausen. *Schizosphaerella* is much rarer compared to Dotternhausen (Figure 2b).

[19] At the base of the Peniche section, below the interval characterized by the carbon isotope perturbation, absolute abundances of both coccoliths and *Schizosphaerella* are the highest. A drastic decline of nannofossil quantities occurs when $\delta^{13}$C values begin to decrease. Abundances stay low during the entire CIE and in the samples analyzed just above it. The highest proportions of *Schizosphaerella* are recorded at Peniche (Figure 2c).

## 4.2. Principal Component Analysis

[20] Only species with a high sampling adequacy and having a loading higher than ±0.5 on one of the extracted factors are considered in the following paragraphs. Factors are here regarded as significant only when they have a contribution to the variance higher than 15% and a weak (<0.2) correlation between each other.

[21] Principal component analysis (PCA) gives five main factors for samples from Dotternhausen, the first three accounting for the 70.5% of the total variance (Figure 4a). The first factor (26.1% of the variance) has an important loading of *Lotharingius* species (*L. frodoi*, *L. umbriensis*, *L. sigillatus/crucicentralis*, *L. hauffii*, and to a minor extent *L. velatus*); these are opposite to *Crepidolithus crassus*. The *Lotharingius* are relatively small coccoliths (Figure 3); *Crepidolithus*, conversely, are thick and robust coccoliths (Figure 3). The second factor (25.7%) displays a strong loading of *Crepidolithus* sp. aff. *ocellatus*, *Bussonius*, *Similiscutum novum*, *S. finchii*, and *P. liasicus*. The third factor (18.7%) exhibits strong positive loading of *Calyculus* and *Crepidolithus cavus*.

[22] For samples from the HTM-102 Borehole, three factors were extracted by PCA (Figure 4b). The first, like that for Dotternhausen, displays a strong loading (∼0.75) of *Lotharingius* species (*L. hauffii*, *L. crucicentralis/sigillatus*, *L. umbriensis*, *L. frodoi*). These species, with respect to Dotternhausen, are opposed to *Tubirhabdus patulus* and *Parhabdolithus liasicus*. The second factor has a loading of *L. barozii*, *Bussonius* (analogously to the second factor at Dotternhausen), and *L. velatus* with *C. granulatus* in weak opposition. The third PCA factor displays important contribution of *S. finchii* and *Calyculus* (similarly to the third factor at Dotternhausen) on positive values, and a weak contribution of *C. crassus* on the negative ones.

[23] At Peniche (Figure 4c), PCA renders six factors, with three representing 60.5% of the total variance. The first has a very strong (∼0.9) loading of *Calyculus*, *Carinolithus superbus* and *Carinolithus poulnabronei*. These placoliths have a peculiar morphology: they are formed by two shields, tied together by a trumpet-shaped structure (Figure 3). The second factor displays the opposition of *L. hauffii*, *L. frodoi*, *C. crassus* on the positive values with *M. jansae* and *P. liasicus* on the negative axis. On the third factor, load *C. cavus*, *L. velatus*, *Bussonius*, and *L. barozii*. This factor

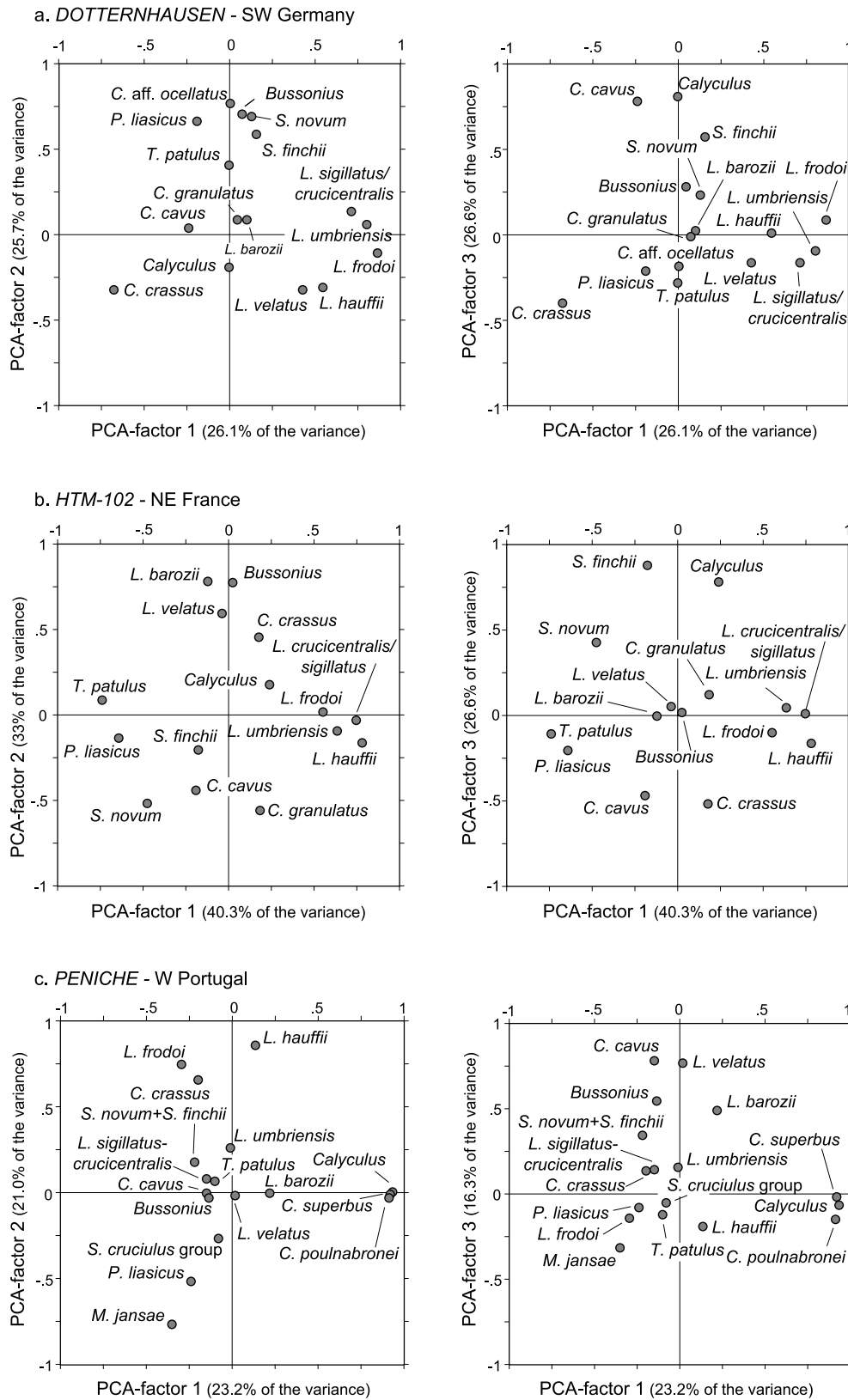**Figure 4.** Results of the principal component analysis (PCA) applied to the relative abundance of coccoliths in the three studied sections. PCA has been applied using the software StatView version 5.0; the extraction rule is eigenvalues, and the transformation method is Orthotran/Varimax. The contribution to the variance of each factor extracted by PCA is also reported. See text for further explanations.

compares with the second one at Dotternhausen and HTM 102 Borehole.

### 4.3. Stratigraphic Changes in PCA Scores and Shannon Diversity

[24] PCA scores and Shannon diversity show some common stratigraphical patterns in the three studied sections, although the variance contribution of correlative factors (i.e., those on which the same taxa load) and absolute Shannon values are different in each section (Figure 5). The most striking similarity occurs between the third factor of Dotternhausen and of the HTM-102 Borehole, and the first factor of Peniche: these factors display high values exclusively in the interval represented by the CIE. The most important taxon loading on these factors is *Calyculus*.

[25] PCA factor 1 at Dotternhausen and HTM-102 Borehole and the correlative PCA factor 2 at Peniche show significant fluctuations, and maximum values at the end of the CIE. This is followed by an interval characterized by negative values at Dotternhausen and at the HTM-102 Borehole, which corresponds to a rise in $\delta^{13}C$ and the end of the CIE.

[26] A decreasing trend is observed for PCA factors 2 and 3 at Dotternhausen and Peniche, respectively, passing from the first to the second ammonite zone of the Toarcian (Figure 5). A similar trend is not recorded for the PCA factor 2 at HTM-102 Borehole, probably because the interval corresponding to the base of the Toarcian is not present.

[27] The highest diversity is recorded at Dotternhausen (H up to 4.3), while at HTM-102 Borehole and Peniche this parameter is slightly lower (2.6 and 3.5, respectively). These values are in the range of diversity indexes commonly recorded, independent of the organisms considered (between 0.5, very weak, and ~4.5, high) [*Frontier and Pichod-Viale*, 1998]. At Dotternhausen and at the HTM-102 Borehole, the Shannon Index shows the same stratigraphic evolution, namely fluctuating from low to relatively high values coincident with the CIE, and the lowest values when $\delta^{13}C$ records come back to more positive values. At Peniche, diversity fluctuates greatly at the base of the section but less so and with slightly lower values during the CIE. Thus, the diversity records are different at the three sites.

## 5. Discussion

### 5.1. Latitudinal Changes in Relative Abundance of Nannofossil Taxa

[28] In order to assess changes in the assemblage occurring at different paleolatitudes during the early Toarcian, the relative abundances of the most common taxa in the three localities studied here were compared to the record of the northern England (Brown Moor Borehole) [*Bucefalo Palliani et al.*, 2002], and of central Italy (Pozzale and

Colle d'Orlando sections) [*Mattioli and Pittet*, 2004] (Figure 1). The various sections and boreholes analyzed here provide us a nannofossil record from different paleolatitudes and sedimentary context, namely from the northern, epicontinental European shelf (subtropical belt; approximately 27–35°N) to the southern, Tethyan margin (tropical belt; ~17–23°N) of relatively shallow basins separated by large carbonate platforms.

[29] *Schizosphaerella* abundance progressively increases from the north toward the south (Figure 6f). Some taxa, such as *M. jansae*, have a distribution almost uniquely restricted to the southern margin of Tethys (Figure 6d). Conversely, the majority of the other taxa show a gradual decrease (or increase) along a latitudinal gradient. Some species (i.e., *P. liasicus*, *C. crassus*, *L. crucicentralis/sigillatus*; Figures 6i, 6j, and 6q) are relatively more abundant in the southernmost part of the northern margin of Tethys (Dotternhausen) analyzed in this work. Other taxa, such as the *Similiscutum cruciulus* group, display the highest relative abundances in Portugal (Figure 6a).

[30] The overall data (Figure 6) suggest a paleolatitudinal control on the relative abundance of the different taxa, even though the difference in latitude was small (~20°). In the modern ocean, a few broad coccolithophorid biogeographic zones are recognized [*McIntire and Bé*, 1967; *Okada and Honjo*, 1973; *Winter et al.*, 1994]. These biogeographic zones, roughly corresponding to latitudinal belts, are the Subarctic, Temperate, Subtropical, Tropical and Subantarctic. The boundaries of these zones are not static or sharp, as their frontal systems continuously move. Changes in taxa abundance observed within the Jurassic western Tethys occur in a paleolatitudinal range (~17–35°) that corresponds to the transition from the Subtropical to Temperate water masses as recognized in modern oceans.

[31] A transition across marine bioprovinces could explain the observed distribution of fossil coccolithophores. Contrasting water masses between the southern and northern margins of the western Tethys have been inferred on the basis of lower Toarcian ammonite assemblages [*Macchioni*, 2002, and references therein]. Besides a latitudinal control on nannoplankton species distribution and assemblage composition, there may have been an influence of different nutrient concentrations. *Van de Schootbrugge et al.* [2005] indicate a wetter climate along the northern margin of Tethys, where the sedimentary record is dominated by siliciclastic material. Such conditions may have favored higher nutrient inputs to areas situated along the northern margin of Tethys. According to *van de Schootbrugge et al.* [2005], the southern margin was arid. Such a climate regime might imply low river inputs and more oligotrophic conditions, as supported by the presence of carbonate platforms.

[32] It is worth noting that all sites discussed were located south of the Laurasian Seaway, which connected the Arctic

**Figure 5.** Stratigraphical evolution of PCA scores and Shannon diversity (H) in the three studied sections. Note that the vertical scale is different from a section to another. During the T-OAE, palynological assemblages are dominated by *Tasmanites* at Dotternhausen [*Mattioli et al.*, 2004b]. The correlative factors, i.e., those on which the same taxa load, are shown in the same order for the three sections, irrespective of their variance values. The species with important loadings on the different factorial axes are reported. Diversity is the lowest at Dotternhausen and HTM-102 Borehole in the interval above the T-OAE, while at Peniche, some of the lowest values are recorded within the interval corresponding to the T-OAE.
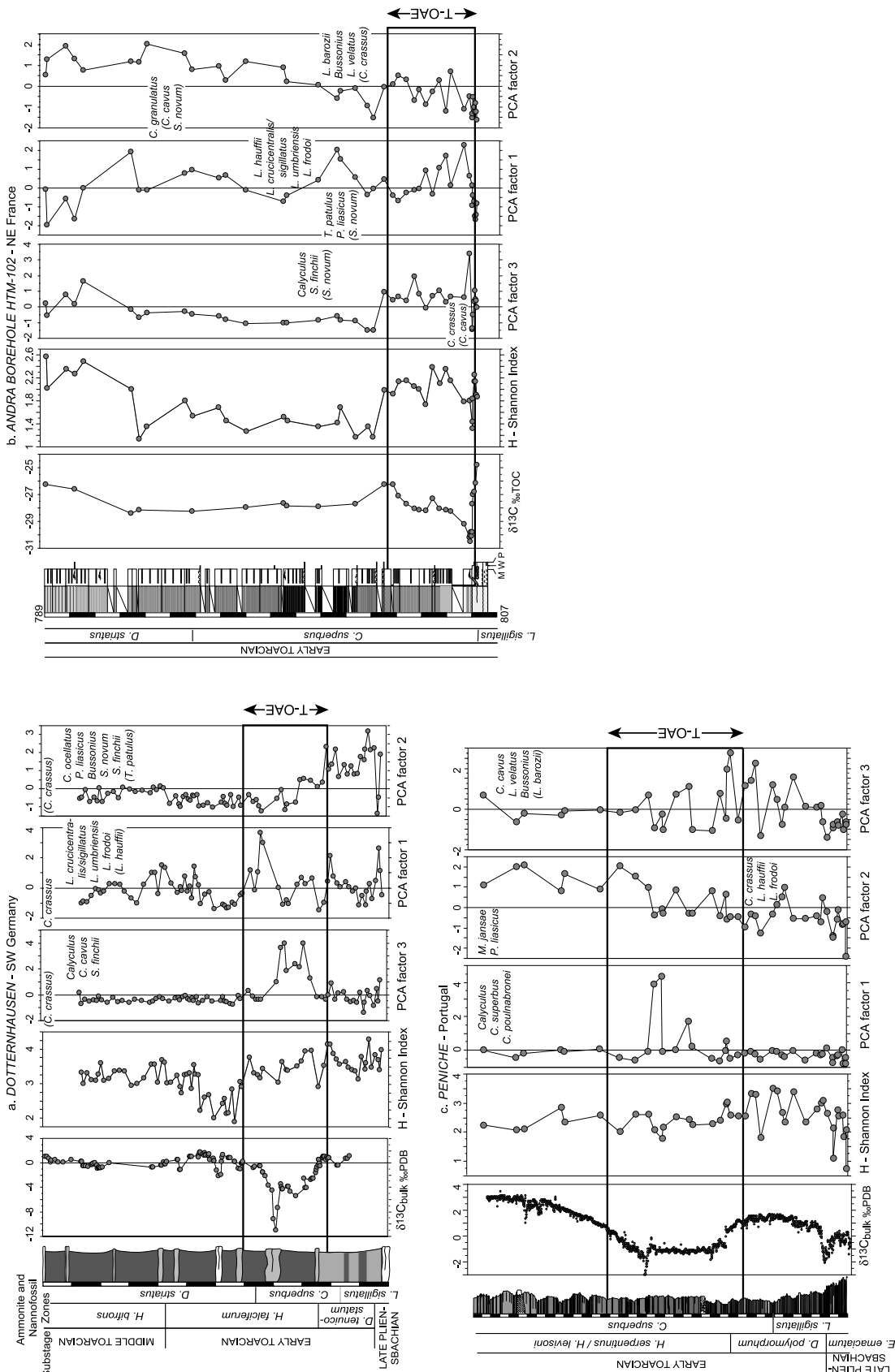
**Figure 5**
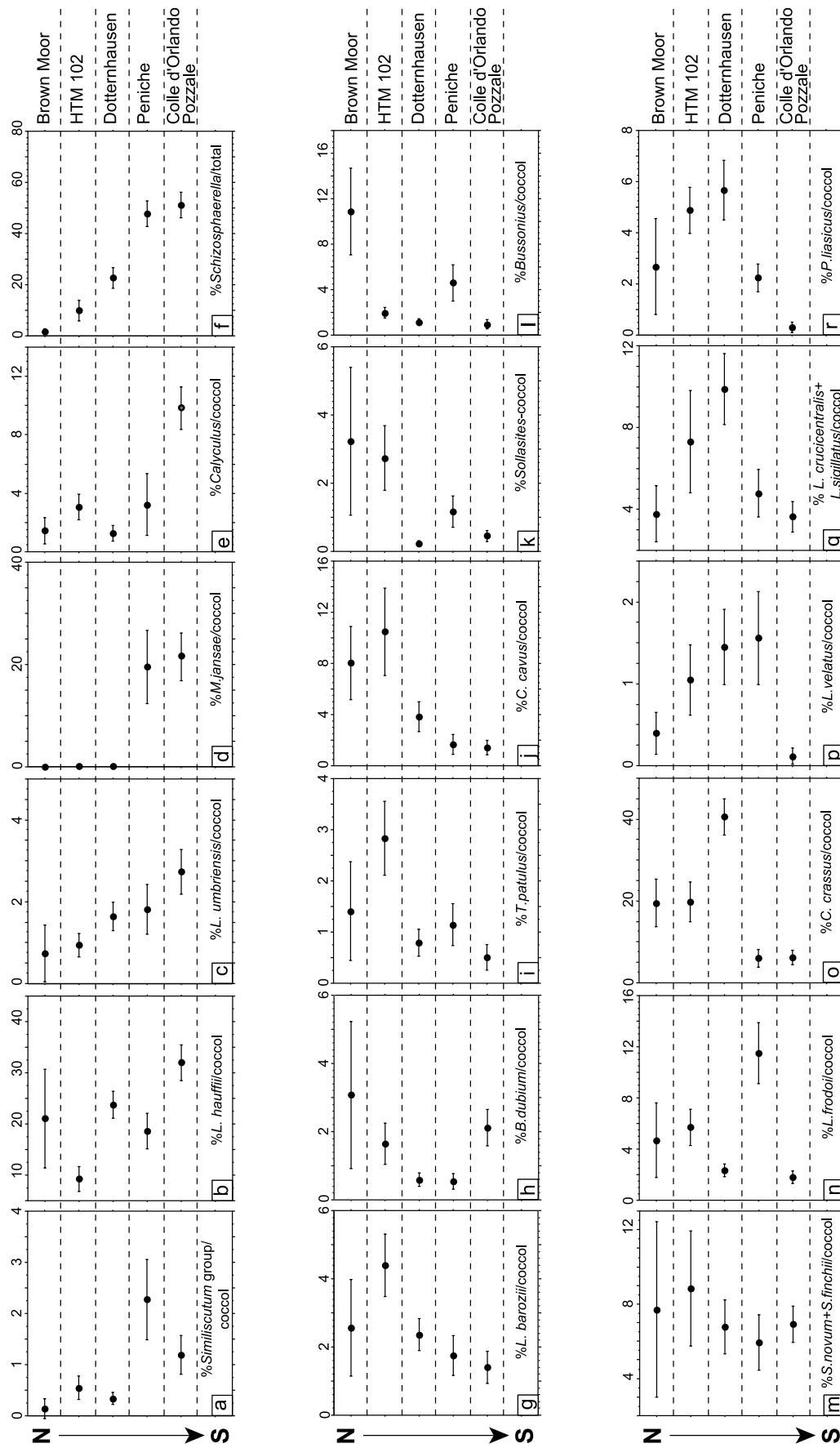
**Figure 6.** Synthesis of the paleolatitudinal distribution of some typical early Toarcian nannofossils. Dots represent mean abundance; the error bar is the 95% confidence interval. In the upper row are shown the taxa relatively more abundant in the southern margin of Tethys, while in the center and lower rows appear the coccoliths more frequent at higher or intermediate paleolatitudes. The latitudinal gradient between the five studied locations (namely, northern England, northeastern France, southwestern Germany, central Portugal, and central Italy) is less than 20°. However, this gradient might have been enhanced by the southward flow within the western Tethys of cool water masses formed in the Arctic Ocean, through the Laurasian Seaway.

**Figure 7.** Synthesis of the main geochemical and biotic events occurring across the T-OAE.

and Tethys Oceans. A current may have flowed south in this seaway during the Toarcian, and brought cool but less dense water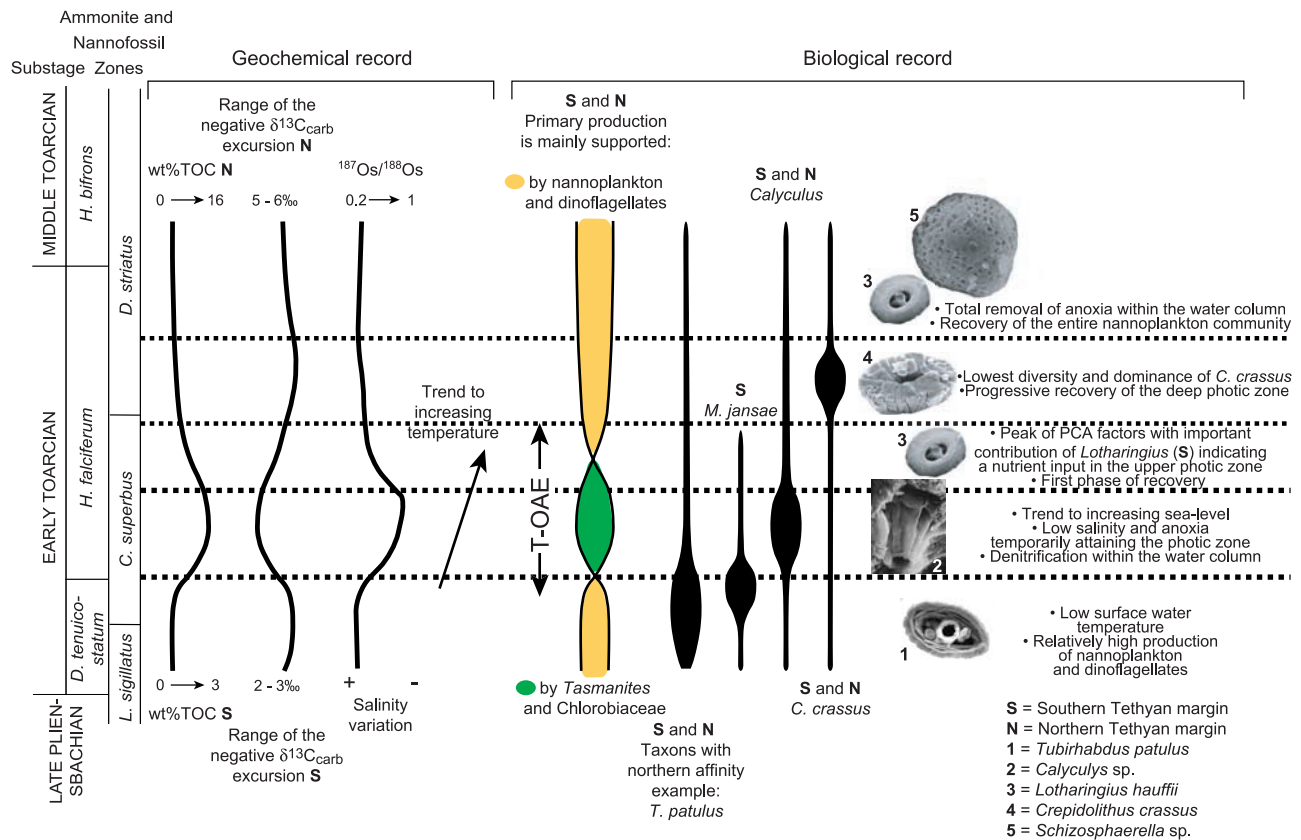s [*Bjerrum et al.*, 2001]. Such flow could have enhanced the latitudinal temperature gradient between the northern and southern margin of Tethys.

## 5.2. Nannoplankton Assemblages Across the T-OAE

[33] Nannofossil assemblages at the three locations change significantly across the early Toarcian CIE. Moreover, some trends are common to all three locations (Figure 7). These trends concern the long-term (∼2 Ma) [*Suan et al.*, 2008b] evolution of environmental conditions, and do not exclude higher frequency fluctuations in environmental parameters.

[34] We exclude a control of differential preservation on the nannofossil trends observed in this account. The three sections display an overall good preservation of nannofossils, and delicate species that are susceptible to diagenetic alteration are constantly present in the assemblages. The few samples that bear signs of poor preservation were removed from the data set.

### 5.2.1. Preevent

[35] Below and at the base of the CIE, PCA displays high values of factorial scores that are controlled by taxa with an affinity for the northern margin of Tethys (i.e., *P. liasicus, C.* aff. *ocellatus, T. patulus, C. cavus, Bussonius,* see also Figure 6), or for nutrients, such as *S. novum* and *S. finchii* [*Bucefalo Palliani and Mattioli*, 1995; *Bucefalo Palliani et al.*, 2002; *Mattioli and Pittet*, 2004; *Olivier et al.*, 2004; *Tremolada et al.*, 2005]. These taxa have important con-

tributions to the PCA factor 2 of Dotternhausen, and on PCA factor 3 of Peniche (Figures 4 and 5). This record can be interpreted in terms of the occurrence of cool surface waters at low paleolatitudes before the CIE.

[36] Relatively low sea surface temperatures for the Tethys region during this time are supported by several lines of evidence. Oxygen isotopes measured on Upper Pliensbachian belemnites rostra allowed *Rosales et al.* [2004] to estimate sea temperatures at 12–13°C in northern Spain. Similarly, $\delta^{18}O$ of Upper Pliensbachian and lower Toarcian brachiopod shells suggest temperatures of 13–16°C for bottom waters of the Lusitanian basin, Portugal [*Suan et al.*, 2008a]. Water masses of the western Tethys, therefore, seem to have recorded a severe cooling event. *Philippe and Thevenard* [1996] also indicated that, during the early Toarcian, continental areas of southwest Germany and central France were dominated by *Xenoxylon* wood, a taxon adapted to cold, wet climates. Further support comes from indirect proxies for low temperatures. The stomatal index measured on mesofossil leaves from the eastern Danish basin suggests low $pCO_2$ during the first Toarcian ammonite zone (*D. tenuicostatum*) [*McElwain et al.*, 2005]. Glendonites and dropstones in Late Pliensbachian sediment deposited at high latitudes may indicate low temperatures and continental ice [*Price*, 1999].

[37] Relatively high fertility may have also occurred in surface waters at this time. Absolute abundances of both coccoliths and schizospherellids are high, as observed at Dotternhausen and Peniche (Figures 2a and 2c) and other

Tethyan settings [*Mattioli et al.*, 2004b]. We do not find an abrupt decrease in *Schizosphaerella* abundance, which has been documented across the Pliensbachian/Toarcian boundary in the Cantabria basin [*Tremolada et al.*, 2005]. However, it must be noted that these authors only presented relative abundance data (percentage), and the decrease in schizospherellids they observed may be due to a closed-sum effect. Indeed, at base of the Toarcian in our sections, coccolith abundance increased more than *Schizosphaerella* abundance. High surface water fertility in this interval is also indicated by the occurrence of mesotrophic taxa (such as *S. novum* and *S. finchii*; this work, and work by *Mattioli and Pittet* [2004] and *Tremolada et al.* [2005]). This is consistent with the trend toward higher $\delta^{13}$C values observed at Peniche passing from the Pliensbachian to the early Toarcian (Figure 2c). A similar trend, albeit with different absolute values of $\delta^{13}$C, has been reported in the Mochras Borehore from England [*Jenkyns et al.*, 2002]. One might expect that, in times of high surface water fertility, species diversity would drop [*Valentine*, 1973; *Hallock*, 1987]. However, the Shannon diversity (H) is relatively high in this interval, although it fluctuates (Figures 5a and 5c).

### 5.2.2. Event

[38] Coincident with the CIE, there is a significant peak in PCA factors with strong loadings of *Calyculus* and *Carinolithus* (factor 1 at Peniche) or *Calyculus* and *S. finchii* (factor 3 at Dotternhausen and HTM-102) (Figure 5). This period is also characterized by the lowest absolute abundances of nannofossils, and a Shannon index that fluctuates from high to low at Dotternhausen and HTM-102 but remains relatively stable and at intermediate values at Peniche.

[39] Low salinity may account for the high occurrence of *Calyculus* during the CIE, as well as the low nannofossil abundance. In modern oceans [*Brand*, 1994] and in laboratory cultures [*Paasche*, 1968], only relatively few species tolerate low salinity (S < 15–20 ppt). Palynological investigations appear to support this interpretation. The interval has a dramatic decrease in dinoflagellate abundance at Dotternhausen [*Mattioli et al.*, 2004b], as well as at other Tethyan sites [*Bucefalo Palliani et al.*, 2002; *van de Schootbrugge et al.*, 2005]. Interestingly, *Tasmanites* appear to have replaced dinoflagellates [*Bucefalo Palliani et al.*, 2002; *van de Schootbrugge et al.*, 2005]. *Tasmanites* are unicellular, flagellate green algae that can thrive under conditions of anomalously low surface water salinity. The inference of low-salinity surface waters is further supported by anomalously low $\delta^{18}$O values in bulk sediment at Dotternhausen [*Röhl et al.*, 2001; *Schmid-Röhl et al.*, 2002], and in belemnite rostra (after correction using Mg/Ca) from the northern margin of Tethys [*McArthur et al.*, 2000; *Bailey et al.*, 2003].

[40] Low surface water salinity during the CIE might reflect greater river inflow [*Röhl et al.*, 2001] or, alternatively, southward flow of low-density Arctic waters into the Tethys [*Bjerrum et al.*, 2001]. In either case, it may have triggered enhanced stratification of surface waters within the western Tethys. Stratification, in turn, favored anoxia [*Farrimond et al.*, 1989; *Prauss et al.*, 1991; *Bucefalo Palliani et al.*, 2002], which at times reached the photic

zone. This conclusion has been made for Tethyan black shales because they contain organic compounds derived from photosynthesing bacteria that use hydrogen sulfide [*Schouten et al.*, 2000; *Pancost et al.*, 2004; *Schwark and Frimmel*, 2004; *van Breugel et al.*, 2006]. Intermittent anoxia in the photic zone is possibly another factor inhibiting nannoplankton and dinoflagellate standing crops in the epicontinental Tethyan basins.

[41] Possibly, salinity fluctuated significantly during the event. When sea surface salinity approached "normal" values, a diverse coccolithophore assemblage could recolonize surface waters. This may explain the rather high values of Shannon diversity recorded in this interval at Dotternhausen and at HTM-102.

[42] If the photic zone was low saline and intermittently anoxic, *Calyculus* cannot be a deep or intermediate dweller, as previously proposed (*Bucefalo Palliani and Mattioli* [1995] and *Erba* [2004], respectively). Instead, it was more likely a shallow dweller. Intriguingly, the morphology of *Calyculus* closely resembles that of the extant genus *Umbellosphaera* that forms "two-layered" coccospheres. Species belonging to *Umbellosphaera* thrive in very shallow (<80– 100 m) surface waters under conditions of low nitrate concentrations [*Thierstein et al.*, 2004]. The "two-layered" coccospheres of *Umbellosphaera* have an extra cellular space that may functionally store nutrients or trap water [*Young*, 1994]. The coccospheres of *Calyculus* (Figure 3) may have served similar purposes. Alternatively, and as for many planktonic forms, the additional space could have reduced the overall hydrodynamic density of the organism by trapping water of relatively low density. The adaptation could allow *Calyculus* individuals to maintain their positions near the surface of stratified water columns.

[43] At sites in central Italy, high proportions of *Mitrolithus jansae* mark an interval separating sediment dominated by low-temperature taxa, and sediment where hostile conditions for nannoplankton prevailed [*Bucefalo Palliani and Mattioli*, 1995; *Bucefalo Palliani et al.*, 1998; *Mattioli and Pittet*, 2004]. The same is true at Peniche, but we show that this interval roughly corresponds to the base of the CIE (Figure 5c). *Mitrolithus jansae* likely had a deep dweller ecology [*Bucefalo Palliani and Mattioli*, 1995; *Mattioli and Pittet*, 2004; *Erba*, 2004], and dominated over other coccoliths in times of incipient stratification of the water column, when anoxia has still not attained the lower photic zone. *M. jansae* is nearly absent in the correlative interval of the settings located along the northern margin of Tethys (Figure 6d), perhaps because anoxia more frequently expanded into the photic zone compared to locations at lower paleolatitude [*Pancost et al.*, 2004]. An alternative, more likely explanation is that the intensity of sunlight irradiance was not sufficient along the northern margin of Tethys to support the development of *M. jansae*, because temperature or light penetration within the lower photic zone were not adequate. The modern species *Florisphaera profunda* (a deep dweller) also displays a sharp decrease in abundance between 30° and 40°N in the Pacific [*Okada and Honjo*, 1973].

### 5.2.3. Postevent

[44] At the end of the CIE, a peak in PCA factor 1 (with strong loadings for most *Lotharingius* species) happens at

Dotternhausen and in the HTM-102 Borehole (Figures 5b and 5c). This peak is overlain, at both localities, by samples with the lowest Shannon diversity, which coincides with still low but increasing absolute nannofossil abundance, and the dominance in the assemblages of *Crepidolithus crassus*. This trend is not observed at Peniche, probably because only a few samples were studied in the interval above the CIE. These findings may indicate a progressive return to "normal" oceanic conditions after the widespread anoxia and the isotopic perturbation, probably linked to the establishment of better connections between basins in times of high sea level.

[45] The successive pulses of *Lotharingius* and *Crepidolithus crassus* are here interpreted in terms of progressive restoration of environmental conditions at different depths within the photic zone. *Lotharingius* species probably dwelled in shallow waters and were adapted to moderate-to-high nutrient concentrations [*Pittet and Mattioli*, 2002; *Mattioli and Pittet*, 2004; *Olivier et al.*, 2004; *Tremolada et al.*, 2005]. The first pulse of these species after the T-OAE may therefore signify renewed input of nutrients to surface waters. The following dominance of *Crepidolithus crassus* (a deep dweller) [*Bour et al.*, 2007] in times of reduced species diversity suggests a progressive deepening of anoxia, and a restoration of the deep photic zone communities also corresponding to the recovery interval of marine invertebrates of *Harries and Little* [1999].

[46] Once the different habitats within the photic zone (i.e., shallow, intermediate, and deep photic zone) completely recovered, a diverse and abundant nannoplankton community became established again. Anoxia may have persisted at depth in some locations, as perhaps indicated by high TOC values in Middle Toarcian sediments at Dotternhausen and HTM-102 (Figure 2). The highest abundance of nannofossils recorded at Dotternhausen and HTM-102 corresponds to the well-known positive $\delta^{13}C$ excursion of the late early Toarcian [*Jenkyns*, 1988], and may accordingly be interpreted as the expression of high productivity in the surface waters of the western Tethys. It is worth noting that the interval of highest relative abundance of *C. crassus* occurs close to, or just after the disappearance of *M. jansae*. The same pattern was observed by *Tremolada et al.* [2005] for sections in the Basque-Cantabrian basin (northern Spain). This further supports the idea that these two taxa were deep dwellers. Because light intensity is a limiting factor in the lower photic zone, *C. crassus* and *M. jansae* probably competed.

## 5.3.   Comparison Between the T-OAE and the Paleocene-Eocene Thermal Maximum

[47] Like the T-OAE, the Paleocene-Eocene thermal maximum (PETM) about ∼55 Ma was characterized by unusual biotic turnovers in marine organisms, including nannofossils, and a major negative CIE in both marine and continental carbon reservoirs [e.g., *Koch et al.*, 1992; *Schouten et al.*, 2007]. Recent papers have recognized similarities in the events, including that both had global warming and an enhanced hydrological cycle [*Cohen et al.*, 2007; *Hesselbo et al.*, 2007]. Although not as clear as for the T-OAE, widespread intermediate water oxygen deficiency may have

also marked the PETM [*Sluijs et al.*, 2006, 2008]; it may have been an incipient oceanic anoxic event [*Cohen et al.*, 2007]. The two events may be causally related, both being associated with massive input of $^{13}C$-depleted carbon [*Dickens et al.*, 1995, 1997; *Hesselbo et al.*, 2000; *Svensen et al.*, 2007].

[48] Nannofossil records across the T-OAE and the PETM show some similarities and differences. Similar to the T-OAE, peaks in taxa indicative of cool and high-fertility surface waters (i.e., *Biscutum* and *Chiasmolithus*) are observed in pelagic sediment deposited prior to the PETM [*Bralower*, 2002]. These taxa are replaced by warmer water species, indicative of more oligotrophic conditions in surface waters during the PETM. Conversely, taxa adapted to less saline surface waters occurred at the acme of the T-OAE. In both cases, nannofossil assemblages indicate an enhanced stratification of water masses. *Gibbs et al.* [2006] documented significantly different nannoplankton assemblages in proximal and oceanic locations during the PETM. On the basis of nannofossil assemblages, as well as benthic foraminiferal and dinoflagellate data, recent papers suggest that trophic conditions were profoundly different in shelf environments with respect to the open ocean [*Bralower*, 2002; *Tremolada and Bralower*, 2004; *Gibbs et al.*, 2006]. Indeed, a decrease in open ocean productivity is observed that is coeval with increased nutrient availability in shelf areas. The difference in productivity between proximal and open ocean settings during the PETM somewhat resembles the observed variations between the northern and southern Tethyan margin across the T-OAE. However, these variations, in the context of the Toarcian paleogeography, probably translate a contrast between a wet climate along the northern margin and more arid conditions at tropical paleolatitudes (Figure 1), rather than to the distance with respect to continents and sources for nutrients.

[49] A large and rapid input of $CO_2$ into the ocean should lower seawater pH and shoal the carbonate compensation depth (CCD). This is certainly the case for the PETM, as evidenced by widespread dissolution of seafloor carbonates [*Zachos et al.*, 2005; *Zeebe and Zachos*, 2007]. A decrease in seawater pH during the T-OAE has been evoked by *Tremolada et al.* [2005] to explain sediment records in the Cantabria Basin (northern Spain). Here, the event is barren of calcareous nannofossils. However, it must be noted that this and other epicontinental basins of the western Tethys were very shallow (less than 200 m according to *Bjerrum et al.* [2001]), and such a shoaling of the CCD seems unlikely. Alternatively, we postulate that northwestern Tethyan settings closer to the Laurasian Seaway record extreme environmental conditions unfavorable to calcareous nannoplankton. Indeed, similar to observations by *Tremolada et al.* [2005], nannoplankton are absent from sediment deposited during the T-OAE in the Brown Moor Borehole (northern England) [*Bucefalo Palliani et al.*, 2002].

## 6.   Summary and Conclusions

[50] The T-OAE was marked by widespread black shale deposition, and by a prominent negative carbon isotope excursion recorded in oceanic and continental carbon res-

ervoirs. We use the negative $\delta^{13}C$ excursion (start to finish) to signify the acme of the T-OAE in this account. Calcareous nannoplankton generally responded to T-OAE environmental change similarly at the three sites from the western Tethys Ocean that we studied. Most notably, there is a decrease in nannofossil abundance, both for coccoliths and calcareous dinoflagellates. In part, this probably relates to a decrease in biocalcification due to excess $pCO_2$ and acidification of surface waters [*Mattioli et al.*, 2004b; *Erba*, 2004; *Tremolada et al.*, 2005]. However, other unfavorable conditions for nannoplankton appear to have prevailed. Contemporaneous with the lowest nannofossil abundances, there are a peak in *Calyculus* coccoliths (typical of stressed environments) and fluctuations in nannofossil species diversity. During the T-OAE in the western Tethys, anoxia may have sporadically spread into the photic zone, and salinity may have dropped in surface waters. These conditions precluded deep-dwelling coccolithophorids, and shallow-dwelling coccolithophorids intolerant to salinity fluctuations. The only coccolithophorid that seems adapted to such conditions was *Calyculus*. Low salinity in surface waters and denitrification within the water column [*Jenkyns et al.*, 2001] also accounts for an abundance of green algae remains (i.e., *Tasmanites*) [*Bucefalo Palliani et al.*, 2002; *van de Schootbrugge et al.*, 2005]. *Calyculus* taxa may have been similar to modern *Umbellosphaera*, coccolithophorids adapted to low nitrate concentrations.

[51] Sea surface temperatures warmed across the T-OAE, as indicated by oxygen isotope analyses of the calcite of belemnite rostra and brachiopod shells [*McArthur et al.*, 2000; *Bailey et al.*, 2003; *Rosales et al.*, 2004; *Suan et al.*, 2008a] and nannoplankton assemblages (this work). However, a concomitant sea level rise [*Hallam*, 2001] also expanded water connections between the Arctic Ocean and the western Tethys (Figure 1). This favored southward flow of cool, low-saline waters into the Tethys [*Bjerrum et al.*, 2001]. Although such water masses progressively warmed with decreasing latitude, especially in the context of a globally warm climate, the input of low-salinity water into the Tethys may have induced stratification and severe anoxia, particularly within the epicontinental basins of the north-western Tethys, which were closer to the Laurasian Seaway. At Peniche, which was located relatively far from the Laurasian Seaway, salinity reduction and water masses stratification were less intense. This is the reason why the *Calyculus* peaks were restricted to discrete intervals, and organic matter accumulation was low (0.5 %TOC in average) [*Hesselbo et al.* [2007] with respect to the sections belonging to the northern Tethyan margin. Southward flow of water appears to have also accentuated the north-south temperature gradient across the Tethys, as observed by differences in the relative abundance of various fossil coccolithophorid species at the studied sites. Transient connections between the Arctic and Tethys oceans, and of southward flow of water between them [*Bjerrum et al.*, 2001], should be accounted for in models pertaining to environmental changes across the T-OAE.

[52] Like the PETM, the T-OAE was characterized by global warming and an enhanced hydrological cycle. Nannofossil assemblages indicate a shift from cool, nutrient-rich surface waters to warm, oligotrophic surface waters for each event, at least in some locations. During each event, the distribution of nannoplankton production varied significantly between sites, probably depending on the hydrography and proximity to continents. The widespread dissolution of seafloor carbonates observed for the PETM is not known for the T-OAE, possibly because of the scarcity of lower Toarcian sections deposited in deep water. Future investigations might assess this expectation in the few known Toarcian sections with deep-sea sediments, such as those in southwestern Japan [*Hori*, 1997].

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