Universidade de Lisboa
Faculdade de Ciências

Université Claude Bernard Lyon 1
Ecole Doctorale E2M2:
Evolution, Ecosystemes,
Microbiologie, Modelisation

Palaeoenvironmental and palaeoceanographic changes during the Lower to Middle Jurassic (Toarcian-Aalenian, ~183-171 Ma). New evidences from calcareous nannofossils of the Lusitanian Basin.

Jorge Humberto Gomes Ferreira

Thesis directed by
Emanuela Mattioli & Mário Cachão

2015

Document prepared to obtain the degree of Doctor in Geology
with specialty in Palaeontology and Stratigraphy

Abstract

At ~183 Ma when large amounts of organic matter was dumped onto the ocean beds (known as the Toarcian Oceanic Anoxic Event, T-OAE), the Early Toarcian marine biota experienced one of the most important biological crises in Earth history. Calcareous nannoplankton was deeply affected and started only to recover from the end of the Early Toarcian. After the T-OAE, as phytoplankton communities dwelling the oceans photic layer recover from the previous disturbing conditions, the ecological niches once occupied by calcareous nannoplankton are again replenished. Located in the westernmost part of the Tethyan ocean, the Lusitanian Basin acted as a seaway between the NW Tethys and the Mediterranean Tethys provinces, therefore been actively influenced by these two different water masses. Hence such a region stands as the perfect spot to study the calcareous nannoplankton community, as its fossil remains bears species typical of both provinces.

In order to appraise the nannoplankton demise and subsequent recovery, absolute and relative abundances of nannofossils were determined from pelagic marl-limestone couplets from three sections of the Lusitanian Basin. Also brachiopods shells were investigated for stable carbon and oxygen isotopes analysis. In order to independently assess the morphologic evolution of *Lotharingius* coccoliths, a Toarcian section from south France was studied. Different statistic methodologies were used throughout this work, in order to screen for robust and significant information from the numerous datasets that were built.

New data from Portugal and France allowed for a new biostratigraphic scheme to be herein suggested for the western Tethys. Robust and distinct major bioevents are acknowledged at three major periods. The uppermost part of the lower Toarcian is acknowledged through the First Occurrence (FO) of *Watznaueria colacicchii*. The middle-upper Toarcian boundary is consistently recognized through the FO of *Discorhabdus criotus* whereas the Toarcian-Aalenian limit is clearly identified by the FO of *Watznaueria contracta* and *Hexalithus magharensis*. Sedimentological interpretation and carbon and oxygen isotopic data, together with the nannofossil record, allowed to characterized both the biotic and abiotic changes that occurred in the water column of the Lusitanian Basin over a period of ~10 myr. Three distinctive palaeoenvironmental and palaeoceanographic settings are inferred. (1) The basal Toarcian was characterized by very unstable environmental conditions. Across this period both Boreal and Mediterranean water masses freely mixed as supported by the high abundance of nannofossils with geographic affinities from both Tethyan realms. The nannofossil record together with isotopic data upholds the trophic character of the water column across this warm and transgressive period as mainly meso-eutrophic. (2) During the long-term regressive period that started from the middle Toarcian, as the water masses gradually cooled down, the dominant water mass in the basin has its origin in the

Boreal province and the deepening of the nutricline provides the ecological niches for deep dwelling coccolithophores. This period is interpreted as being mainly stable and oligotrophic. (3) Starting from the upper Toarcian and although not as stressful as before, the water column again acquires a predominant meso-eutrophic character as inferred from the carbon isotopic data and nannofossil record. This was a period where the connection between the two Tethyan water masses were at a minimum if not lost at all, and mainly Mediterranean waters filled the basin.

These environmental changes are mirrored by the size variation in the coccoliths of the *Lotharingius* genus. Biometry results show a double influence of environmental factors (acting on the short-term) and evolution (mainly noticeable on the long-term) in two discrete western Tethys sections. Small coccoliths of *Lotharingius* are more abundant in strata here interpreted as likely deposited during stressed and meso-eutrophic environmental conditions where nutrients would be more abundant, whereas larger coccoliths dominate the assemblages in stable and stratified waters masses. However, a major size change is observed during the middle Toarcian, when the average size of *Lotharingius* coccoliths goes from smaller to larger than 4 μm. This size change likely illustrates both the Cope's rule and the Left Wall model.

Calcareous nannofossils proved to be a privileged proxy in documenting long-term environmental changes occurring in the T-OAE aftermath, either through the analysis of their assemblage composition either through their size changes. They are a particularly useful palaeoceanographic tool, which allowed infer on the water mass exchanges that occurred across the Lusitanian Basin seaway. Calcareous nannofossil biostratigraphy acknowledged in this work renders a clear and unequivocal recognition of main Toarcian substages boundaries, susceptible to be integrated in the future Geological Time Scale.

Résumé étendu

Le biome marin du Toarcien inférieur a subi une des crises les plus significatives de l'histoire de la Terre, qui a affecté les mers épicontinentales du globe. Ces bassins épicontinentaux sont également caractérisés par l'accumulation de grandes quantités de matière organique dans les sédiments de l'époque, ce qui a été interprété comme le résultat d'un Evénement Anoxique au Toarcien inférieur (T-OAE, ~183 Ma). Le nannoplancton calcaire, qui fait partie des organismes le plus sensibles aux conditions environnementales des eaux océaniques de surface, a été profondément affecté par cette crise et sa récupération se mit en place seulement à la fin du Toarcien inférieur. Si le T-OAE a été étudié en grand détail ces dernières années, la période de récupération est beaucoup moins bien connue. A ce stade, nous ne savons pas, notamment, si la récupération de la production carbonatée primaire est représentée par un épisode rapide ou par une suite d'événements (qui feraient partie d'un plus long processus) intervenus sur quelques millions d'années après le T-OAE. Pendant les perturbations environnementales qui ont eu lieu au Toarcien inférieur, des fluctuations importantes du niveau marin ont été interprétées ainsi que des variations de la température des eaux océaniques. Après le T-OAE, le niveau marin et les températures montrent des changements plus graduels pendant une grande partie du Toarcien supérieur-Aalénien inférieur et les niches écologiques occupées par le nannoplancton calcaire sont ré-établies. Ces conditions de relative stabilité sur le long terme (~10 Ma) sont idéales pour étudier les dynamiques de la communauté des nannofossiles calcaires et, notamment, comment les différents taxons réorganisent leurs relations synécologiques. Le Toarcien-Aalénien est une période clé dans l'évolution du nannoplancton calcaire, avec des nouveaux genres qui apparaissent. Les nannofossiles de cet intervalle restent relativement peu étudié dans le Bassin Lusitanien, malgré l'importance de cette région d'un point de vue paléocéanographique. En effet ce bassin, qui était à l'origine un rift avorté lié à l'ouverture de l'Atlantique, a permis les connections entre des masses d'eaux de provenance NW européenne et sud-téthysienne. C'est dans cette région que nous retrouvons donc des mélanges de taxons liés à des différentes provinces géographiques.

En parallèle de l'analyse des changements des assemblages de nannofossiles calcaires observés sur le long-terme, le Bassin Lusitanien qui présente des coupes continues et bien datées par ammonites, est un site idéale pour étudier l'évolution des tailles du genre le plus représentatif au Toarcien, le *Lotharingius*. Il est en effet crucial de pouvoir appréhender les rôles respectifs du contrôle environnementale et de l'évolution sur les changements de taille au cours du temps. En comparant les mesures de taille du genre *Lotharingius* aux autres données environnementales, telles que les tendances mesurées sur le $\delta^{13}C$ et le $\delta^{18}O$, il sera possible d'évaluer l'influence du

paléoenvironnement (et notamment la température et la productivité des eaux de surface) sur les changements de tailles observés.

Dans le but de mieux comprendre les dynamiques des assemblages lors de la crise et de la subséquente récupération post-T-OAE, les abondances relatives et absolues des nannofossiles ont été mesurées dans les alternances marno-calcaires de trois coupes hémi-pélagiques du Bassin Lusitanien. En parallèle, la calcite des brachiopodes a été utilisée pour des mesures isotopiques ($\delta^{13}C$ et $\delta^{18}O$). Une coupe a été également sélectionnée dans le centre-sud de la France (Bassin des Causses) afin de comparer les variations de taille des coccolithes et de mieux contraindre l'influence de facteur locaux *vs.* globaux. De nombreux tests statistiques ont été appliqués avec l'objectif de traiter le plus correctement possible l'ensemble des données acquises.

Sur la base des observations des assemblages de nannofossiles calcaires du Portugal et du Sud de la France, il a été possible de reconnaître plusieurs événements (premières et dernières apparitions) qui ont aidé à la définition de différentes zones à nannofossiles et à conforter ou, vice-versa, à émender les schémas de biozonation existants pour le NW européen et le Sud de la Téthys. L'analyse des assemblages de nannofossiles a permis de mettre en évidence les changements environnementaux sur le long terme, les dominances successives des différents taxons et de préciser les préférences écologiques de ces taxons. La biométrie du genre *Lotharingius* montre des fluctuations à court terme qui s'emboîtent dans des variations à plus long terme. Cet étude met en évidence la grande plasticité morphologique du genre.

Les nouvelles données biostratigraphique obtenues dans le cadre de cette thèse permettent de mieux caractériser trois intervalles en particulier : la limite Toarcien inférieur/moyen est reconnaissable grâce à la première apparition (FO) de *Watznaueria colacicchii*. La limite Toarcien moyen/supérieur est bien caractérisée par la FO de *Discorhabdus criotus*. La limite Toarcien/Aalénien est identifiée par la FO de *Watznaueria contracta* et *Hexalithus magharensis*.

Les interprétations sédimentologiques, couplées aux données isotopiques ($\delta^{13}C$ et le $\delta^{18}O$) et aux données issues des assemblages de nannofossiles calcaires ont permis la caractérisation des changements biotiques et abiotiques majeurs qui ont eu lieu dans les eaux de surface du Bassin Lusitanien. Trois types d'environnements ont été détectés : (1) le Toarcien basale était caractérisé par des conditions environnementales très instables et par un mélange des masses d'eau boréales et méditerranéennes, comme le montrent les assemblages de nannofossiles. Les eaux de surface étaient chaudes et méso-eutrophes. L'équivalent du T-OAE à Rabaçal est très pauvre en nannofossiles calcaires et montre de nombreux spécimens remaniés. Ces données sont cohérentes avec la nature des sédiments qui sont des tempestites. (2) Pendant la période régressive à partir du Toarcien moyen, les masses d'eau refroidissent progressivement. Une forte présence des formes de nannofossiles calcaires d'affinité boréale est observée avec des évidences de stratification des eaux et une nutricline profonde, où dominent des taxons avec un mode de vie de type deep-dwelling. Cette période est caractérisée par des conditions environnementales stables et plutôt oligotrophes. (3) A partir du Toarcien supérieur et jusqu'à l'Aalénien inférieur, les eaux de surface montrent de nouveau un caractère instable et méso-eutrophe, d'après les nannofossiles calcaires et les isotopes stables du carbone, même si dans l'absolu des conditions aussi extrêmes qu'au Toarcien inférieur ne sont plus atteintes. Les connections entre les différentes masses d'eau étaient minimes, et le Bassin Lusitanien montre une claire affinité Méditerranéenne.

La taille du genre *Lotharingius* semble varier en concert avec les changements environnementaux enregistrés sur le long terme. Les résultats biométriques montrent une double influence des changements paléoenvironnementaux (surtout visible sur le court terme) et de l'évolution (long terme). De petits coccolithes sont retrouvés pendant des conditions de stress environnementale et méso-eutrophiques, en revanche des gros coccolithes sont typiques de conditions globalement plus stables et d'eaux stratifiées. Un changement de taille significative est observé au Toarcien moyen avec des coccolithes en moyenne plus petits de 4 µm dans des sédiments plus anciens et des coccolithes > 4 µm dans des sédiments plus récents. Cette variation de la taille des *Lotharingius* illustre la loi de Cope.

En synthèse, les nannofossiles calcaires représentent un très bon outil pour interpréter les changements paléoenvironnementaux sur le long terme, que ce soit au travers de l'analyse de ses assemblages ou de leur taille. Ce microfossiles sont particulièrement utiles en paléocéanographie pour reconstituer l'histoire des connections entre masses d'eau différentes (provinces NO européenne et Téthys méditerranéenne) au cours du Toarcien. Les nouvelles données biostratigraphiques présentées dans ce travail permettent de manière claire et non équivoque d'identifier les limites entre différents sous-étages. Ces nouvelles données sont susceptibles d'être intégrées à la future édition de la Geological Time Scale.

Resumo alargado

Há cerca de 183 milhões de anos atrás, a biota marinha sofreu uma das mais importantes crises biológicas na história do planeta, quando grandes quantidades de matéria orgânica foram depositadas nos fundos oceânicos. Este episódio que teve lugar durante o Toarciano, resultou de um Evento Anóxico Oceânico (T-OAE), e afectou os mares epicontinentais à escala global. O nanoplâncton calcário, um grupo de organismos extremamente sensível às variações nas condições ambientais que têm lugar na camada superficial das massas de água, foi profundamente afectado. Foi somente no final do Toarciano Inferior que a sua recuperação se iniciou. Apesar de já muito se ter escrito sobre o T-OAE, a previsível recuperação deste grupo nunca foi sistemática nem detalhadamente estudada. Até hoje, não se sabia ainda se esta recuperação teria sido relativamente rápida, ou resultado de um processo lento e gradual que teria durado milhões de anos. Durante o Toarciano Inferior, quando as condições ambientais eram extremamente instáveis, ocorreram importantes e drásticas oscilações na temperatura e no nível médio dos oceanos. Após o T-OAE e durante todo o Toarciano e Aaleniano Inferior, as oscilações do nível médio dos oceanos e de temperatura são bastante mais suaves. À medida que a comunidade fitoplanctónica instalada na zona fótica recupera das condições extremas anteriores, os nichos ecológicos antes ocupados por nanoplâncton calcário, começam novamente a ser preenchidos. Apesar das prolongadas e suaves variações abióticas, é num ambiente então mais estável, que melhor se pode observar a evolução deste grupo, e de que forma as suas relações sinecológicas se alteraram ao longo de aproximadamente 10 milhões de anos. Apesar de ser considerado como um período onde a comunidade nanoplanctónica sofreu importantes alterações, nada se sabe em concreto que alterações foram essas que tiveram lugar após o T-OAE num local tão estratégico como a Bacia Lusitânica. Situada na extremidade Oeste do Tétis e fazendo parte de um rift originado pela abertura do Atlântico, a Bacia Lusitânica actuou como um corredor que ligava livremente as massas de água das províncias mediterrânica e NW do Tétis, sendo por estas, activamente influenciada. Por essa razão, tal situação geográfica constitui um local excepcional para se estudar a comunidade de nanoplâncton calcário, uma vez que o seu registo fóssil compreende espécies típicas destas duas províncias do Tétis.

Para além das alterações a longo prazo na comunidade de nanoplâncton, as secções contínuas e bem calibradas da Bacia Lusitânica são ideais para se estudar em pormenor a contribuição do controlo ambiental *versus* tendência evolutiva, do táxon dominante durante o Toarciano, o género *Lotharingius*. Através da medição do comprimento dos seus cocólitos, deverá ser possível avaliar alterações na evolução filogenética deste táxon, e após comparação com outros indicadores ambientais como o valor de isótopos estáveis de carbono e oxigénio, inferir se alguma das alterações detectadas derivam ou não de factores ambientais. De facto, tal como é

amplamente referido na literatura, os isótopos estáveis de carbono e oxigénio fornecem a informação mais precisa e fiável sobre respectivamente o carácter trófico e temperatura da coluna de água.

Para avaliar o declínio e subsequente recuperação do nanoplâncton durante o Toarciano e Aaleniano Inferior, foram determinadas as abundâncas absolutas e relativas de nanofósseis a partir de amostras recolhidas de margas e calcários hemipelágicos de três afloramentos, bem como o teor em isótopos estáveis de carbono e oxigénio de conchas de braquiópodes. Para aferir discretamente a evolução morfológica dos cocólitos de *Lotharingius*, foi estudado um outro afloramento do Sul de França. No decurso deste trabalho foram utilizados diversos métodos estatísticos, com o objectivo de discriminar informação robusta e significativa de entre as numerosas bases de dados construídas.

Do estudo das associações de nanofósseis do Oeste português e Sul de França, foi possível identificar bioeventos síncronos (primeiras ocorrências de diferentes taxónes) que para além de serem úteis na definição das diferentes Zonas de Nanofósseis nas duas sequências sedimentares estudadas, contribuiram para melhorar e actualizar os esquemas biostratigráficas já publicados para as províncias boreal e mediterrânica do Tétis. Foi possível obter para a Bacia Lusitânica uma descrição detalhada e a longo prazo da evolução da comunidade de nanoplâncton e a sua resposta às alterações ambientais e paleoceanográficas, para além de corroborar o que é possível encontrar na literatura sobre as preferencias ecológicas dos taxónes mais importantes do Jurássico Inferior, adicionando em alguns casos importantes detalhes. A biometria de cocólitos de *Lotharingius* forneceu valiosa informação sobre a sua evolução a longo prazo e sobre a sua resposta no curto prazo a alterações ambientais, revelando assim a plasticidade ecológica deste grupo, mesmo estando geneticamente constrangida.

Este trabalho permitiu construir e sugerir um novo esquema biostratigráfico para o Oeste do Tétis através da identificação de bioeventos robustos e singulares observados durante três importantes períodos. O Toarciano Inferior terminal é identificado pela Primeira Ocorrência (FO) de *Watznaueria colacicchii*, a fronteira entre o Toarciano Inferior e Médio é consistentemente reconhecida pela FO de *Discorhabdus criotus* enquanto que o limite Toarciano-Aaleniano é claramente identificado pela FO de *Watznaueria contracta* e *Hexalithus magharensis*.

A integração de informação sedimentológica, isotópica e micropaleontológica, permitiu caracterizar as alterações bióticas e abióticas sofridas na coluna de água da Bacia Lusitânica durante um período de ~10 milhões de anos, onde três cenários paleoambientes e paleoceanográficos são inferidas. (1) Apesar das camadas correspondentes ao equivalente temporal do T-OAE serem pobres em nanofósseis, e sendo grande parte constituída por espécimes remobilizados uma vez que estas rochas se formaram a partir de episódios de tempestade, o Tarciano Inferior foi um período caracterizado por condições ambientais muito instáveis. A elevada abundância de nanofósseis com afinidade geográfica de ambas as províncias

tetianas corrobora que estas massas de água se misturavam livremente, para além de que a composição fossilífera conjuntamente com os dados isotópicos permitem atribuir a este período transgressivo e quente, um carácter predominantemente meso-eutrófico. (2) Durante o longo período regressivo que se inicia no Toarciano Médio, e enquanto as massas de água arrefecem progressivamente, a bacia é predominantemente preenchida por águas boreais. O afundamento da nutriclina permite o aparecimento de nichos ecológicos para cocolitóforos com preferência pela zona fótica inferior. Este intervalo de tempo é predominantemente estável e oligotrófico. (3) Apesar de não ser tão instável como antes, os dados isotópicos e fossilíferos sugerem que a partir do Toarciano Superior a coluna de água adquire novamente um carácter meso-eutrófico. Durante este período a ligação entre as duas massas de água tetianas seria residual ou estaria interrompida, e eram as águas mediterrânicas que dominavam a bacia.

Estas alterações ambientais são espelhadas pela variação no tamanho dos cocólitos de *Lotharingius*. Os resultados biométricos revelam uma dupla influência de factores ambientais (que actuam no curto prazo) e evolutivos (detectáveis principalmente a longo prazo) em duas sucessões sedimentares distintas do Oeste do Tétis. Os cocólitos pequenos de *Lotharingius* são mais abundantes nos estratos aqui interpretados como tendo sido depositados em condições ambientais instáveis e meso-eutróficas, onde os nutrientes seriam mais abundantes, enquanto que os cocólitos maiores dominam as associações de águas estáveis e estratificadas. Contudo, uma importante mudança é registada durante o Toarciano Médio, quando o tamanho médio dos cocólitos de *Lotharingius* passa de <4 µm a >4 µm. Esta alteração segue muito provavelmente quer a regra de Cope quer o modelo de Left Wall.

Em síntese, quer através da análise da composição das suas associações, quer através do estudo da sua variação morfológica, os nanofósseis calcários provam ser um privilegiado indicador na documentação das alterações ambientais que tiveram lugar após o T-OAE. São igualmente uma ferramenta paleoceanográfica particularmente valiosa, que permitu inferir sobre as trocas entre as massas de água das províncias do NW europeu e do Sul do Tétis no corredor da Bacia Lusitânica. Por último, a biostratigrafia de nanofósseis calcários reconhecida neste trabalho produziu uma clara e inequívoca identificação dos principais sub-andares toarcianos, susceptíveis de serem integrados na futura Geological Time Scale.

Acknowledgments

I wish to thank the corner stone of this work without whom none of this would have been possible. She warmly welcomed me in the LGL and always tried her best to put me at easy in this new environment. Besides being a world-class scientist, Emanuela Mattioli is also a world-class human being and teacher. I cannot thank her enough for all that she tirelessly and with a supernatural patience and kindness, taught me over the past almost four years. Apart from introducing me to Jurassic nannofossils, it was from her that I learned how to better test scientific hypothesis and above all, how to elaborate "les modèles".

Very special thanks go to Mário Cachão for the ongoing support that goes back aeons ago. My teacher during the undergraduated years and a good friend today, always there to help, inspire, and push me to go further in the nannofossil study.

Bernard Pittet and Luis Vitor Duarte are thanked for their valuable help during the fieldwork in Portugal, fruitful discussions and their sedimentological inputs on this manuscript.

Guillaume Suan for introducing me to the wonderful world of stable isotopes, for his encouragement services, valuable advises and discussions.

Baptiste Suchéras-Marx, who proved to be a good friend in times of need. Showing up at my office door always in the exact moment I had a problem to solve, to which he would then help me find the best solution. Also for having the time to teach me how to work with various software that proved to be vital for this study.

Fabienne Giraud for telling me once "Leave the biostratigraphy alone. It is now time for you to know all there is to know about the Toarcian". These words led me to read for weeks on end all that I could find about the subject, setting a turning point in the path of my work. One of the best advices I had, which rendered valuable results. Thank you also for your encouraging words and inestimable suggestions.

Samer Kenjo, hopefully in good health, for the zillions of coffee breaks we had during our time together in the LGL, until he had to rush to his torn by war home country, Syria. Also Abel Barral, Peggy Vincent, Anne Sabinne, Julien Plancq, Samuel Mailliot and Barbara Gollain for the support, parleys, endless small talk and beer sessions after a day of work, making my time in the LGL much more enjoyable.

Last, but by no means the least, and though he refused to pick up where he left the study of Toarcian ammonites, I whish to thank Carlos Marques da Silva, for being a long time friend. His keen analytical sense and ongoing words of encouragement and support, kept me going on the right track for the past four years.

PALAVRAS-CHAVE:
Nanofósseis calcários; Biostratigrafia; Paleoecologia; Biometria, Bacia Lusitânica

MOTS-CLÉS:
Nannofossiles calcaires; Biostratigraphie; Paléoécologie; Biométrie, Bassin Lusitanien

DISCIPLINA: Geologia; paleontologia e estratigrafia.

DISCIPLINE: Sciences de la Terre; paléontologie, stratigraphie.

Departamento de Geologia
Faculdade de Ciências da Universidade de Lisboa
Campo Grande
1749-016 Lisboa; Portugal

Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement
UMR CNRS 5276 (CNRS, ENS, Université Lyon 1)
Université Claude Bernard Lyon 1
Campus de la Doua, bâtiment GEODE
2, rue Raphaël Dubois
69622 Villeurbanne Cedex; France

CONTENTS

4. Biostratigraphy:

5. Palaeoecology:

6. Biometry:

1. Introduction

The transformations that occurred during the transition from neritic oceans *sensu* Ridgwell (2005) to modern oceans, as well their time frame throughout the Mesozoic are today poorly known. According to this author, the period where this transition seems to have taken place is sited at the base of the Hettangian (Lower Jurassic), which according to the Geologic Time Scale 2012 (Gradstein et al., 2012) corresponds to ~201 Ma. From the Lower Jurassic, the global carbon cycle was stabilized with the proliferation of planktic calcifiers thus representing a profound change in the biogeochemical cycling of calcium carbonate. The Mid Mesozoic Revolution heralded the development of a responsive deep-sea carbonate sink that introduced a new and powerful negative feedback to the Earth system rendering a relatively low degree of over-saturated oceans.

Planktic calcifiers (mainly calcareous nannoplankton), however, were rare and low diversified during the Lower Jurassic (Bown, 1987b; Bown et al., 2004; Mattioli et al., 2009). It was only during the late Early Toarcian (~183 Ma) that the new coccolith genus *Watznaueria,* which will later on dominate the oceans throughout the Mesozoic, first appeared (Cobianchi et al., 1992; Mattioli, 1996; Mattioli and Erba 1999). This event occurred at the end of a major palaeoceanographic and palaeoclimatic event, the Early Toarcian Oceanic Anoxic Event (T-OAE), which represented a major biotic crisis probably linked to a global warming period and to a likely ocean acidification (Kemp et al., 2005; Beerling and Brentnall, 2007). The *Watznaueria* genus represents a major success in biological evolution, probably like no other ever recorded in Earth history. Besides dominating all oceanic coccolith assemblages from the Middle Jurassic to the end of the Cretaceous, some species from the Watznaueriaceae family were even able to survive the major biological crisis that took place at the K/T boundary and endure until today. Actually, recent molecular phylogenetic studies carried out by Hagino et al. (2015) support that the extant coccolithophore *Tergestiella adriatica* recently re-discovered in Japanese and Croatian coastal-nearshore waters, besides being morphologically identical to the Mesozoic genus *Cyclagelosphaera* (Watznaueriaceae), is its direct descendent. It is therefore crucial to follow the evolutionary steps of the Watznaueriaceae family from the moment the *Watznaueria* genus first occurs, until the ecological takeover that occurred during the Bajocian, when this genus replaces other Mesozoic taxa such as its phylogenetic predecessor *Lotharingius*, and is eventually established as the dominant coccolithophore during the Middle Jurassic (Mattioli, 1997; Mattioli and Erba, 1999; Aguado et al., 2008; Suchéras-Marx, et al., 2015).

The world at the Lower to Middle Jurassic transition deeply differs from the world today in several major aspects, being the Toarcian and Aalenian time periods of particular interest in the geological history of the planet. Important global palaeoenvironmental changes took place across this time interval, where major and drastic temperature shifts and eustatic oscillations occurred (e.g., Hallam, 1981; Duarte et al., 2007; Gómez et al., 2008; Dera et al., 2009, 2011), as well as major basalt production in the Karoo and Ferrar large igneous provinces (Pálfy and Smith, 2000; McElwain et al., 2005; Svensen et al., 2007). The most significant global change was probably the most important thermal maximum recorded during the Mesozoic at the base of the Toarcian, also corresponding to the T-OAE, an interval of almost global widespread burial of organic matter (e.g., Jenkyns, 1988; McArthur et al., 2008; Suan et al., 2008). Such an important time period in the history of our planet is well represented in the Lusitanian Basin by continuous Lower and Middle Jurassic outcrops possessing a close biostratigraphic ammonite control. The geological evolution of this aborted marine basin is considered to be a sedimentological and stratigraphic model besides a case study for researchers in the oil industry. The Toarcian-Aalenian time interval, particularly well represented in west Central Portugal, is a crucial period on the history of the planet. As Pangaea was breaking-up, ongoing major palaeoceanographic changes towards a modern ocean system took place. The present work aims to unravel the early biotic and abiotic developments, leading to a global ocean dominated by *Watznaueria* placoliths, after murolihts and *Lotharingius* placoliths shared and ruled the ocean photic zone during the Lower Jurassic. This objective will be pursuit through a high-resolution palaeoecological study focused on the examination and comparison of calcareous nannofossil assemblages from the Lusitanian Basin to other western Tethys regions, together with carbon and oxygen isotopic analysis from collected brachiopods in the Figueira da Foz region.

Additionally, also a comprehensive Toarcian-Early Aalenian calcareous nannofossil biostratigraphic revision will be undertaken. While calcareous nannofossil biostratigraphy has received much attention in the Lusitanian Basin (e.g., Hamilton, 1977, 1979; de Kænel and Bergen, 1993; Mattioli et al., 2008; Reggiani et al., 2010a, 2010b) none of these papers have ever addressed in detail the Toarcian-Aalenian interval. Although Perilli and Duarte (2006) have studied the Toarcian interval in the Rabaçal section, they have merely performed a qualitative approach of calcareous nannofossil abundance. By using relative and absolute nannofossil quantification, new data of biostratigraphic and statistic significance was added in the present study, besides filling the gap concerning the middle-to-upper Toarcian and lower Aalenian biostratigraphic interval, which is what this work mainly intends to do.

This dissertation is divided in seven sections, being Introduction and Conclusions and perspectives its end-member chapters. The 2nd chapter is dedicated to the geological settings of the studied areas whereas the 3rd chapter is dedicated to the material and different methodology used throughout this study. Three core chapters follow Material and methods, and they represent the different main subjects addressed in detail in this manuscript. The 4th chapter contains the biostratigraphic results from the Lusitanian and Causses basins, and their application to Mediterranean Tethys sections. The 5th chapter is dedicated to the environmental changes that occurred in the Lusitanian Basin across the Toarcian and Early Aalenian and how it directly affected the nannoplankton community, and is represented by a peer-review article in Palaeo3.

The 6th chapter addresses the size changes of the *Lotharingius* genus across the Toarcian and Early Aalenian in the Lusitanian and Causses basins, and tries to clarify its variations both through evolution and environmental forcing mechanisms.

1.1. Purpose of investigation

Although the Toarcian-Aalenian interval is such a crucial period in Earth history, there are still important questions to be answered regarding the phytoplanktonic community dwelling in the oceans photic zone at that time. Sitting at the bottom of the global food chain, calcareous nannoplankton plays a major role in the Earth carbon cycle due to its ability to synthesize a calcite exoskeleton. This work mainly addresses in detail the recovery process of the coccolithophore community after the T-OAE in a specific western Tethys epicontinental sea: the Lusitanian Basin. Also the background evolution occurring from the middle Toarcian and the synecological relationships in the nannoplankton community are to be investigated and ultimately related to palaeoceanographic and environmental shifts. Through the study of coccolith assemblages, stable carbon and oxygen isotopes record from brachiopod shells, and coccolith biometry, this work focuses and reviews the evolution and ecological relationships of the Toarcian calcareous nannoplankton community. Moreover, it addresses and discusses the palaeoceanographic settings in this west Tethyan basin, before the dominance of the *Watznaueria* genus from the Aalenian age. The following objectives will be addressed:

- Improve the Toarcian-Early Aalenian calcareous nannofossil biostratigraphy for the western Tethys, and fully revise the biostratigraphic charts used today (Bown and Cooper, 1998; Mattioli and Erba, 1999), as some taxonomic revisions (Mattioli et al, 2004; Suchéras-Marx et al., 2010; López-Otálvaro et al., 2012) and new and updated relative position of some nannofossil bioevents have been acknowledged. This represents a major interest for the oil industry as large-scale calcareous nannofossil biostratigraphic studies are often used to date and correlate oceanic cores.
- Assessment of calcareous nannoplankton community development after the T-OAE, through the reconstruction of synecological and oceanographic evolution that occurred in the Lusitanian Basin, from the first record of the first *Watznaueria* species until this taxon starts to dominate the nannofloral community.
- Assessment of environmental conditions such as water masses temperature, oceanic primary productivity and nutricline shifts in the Lusitanian Basin seaway, through nannofossil assemblage composition, carbon and oxygen stable isotope data record, and ponder on their possible triggers.

- Assessment of the *Lotharingius* genus size evolution, and investigate the respective role of evolution and environmental shifts on its phenotypic changes.
- Assessment of calcareous nannoplankton palaeobiogeographic provinces across the Toarcian-Early Aalenian in the western Tethys by combining the data acquired in the present work with recently published and unpublished available data.

1.2. State of the art

1.2.1. Modern coccolithophores

Coccolithophores are mainly marine, unicellular phytoplanktonic algae, belonging to the Haptophyte phylum, and represent the main component of extant calcareous nannoplankton (Jordan et al., 2004). Their calcified scales, the coccoliths, are well represented in deep-sea sediments above the calcite compensation depth (Bown and Young, 1998). After burial they are named calcareous nannofossils. These algae are at the base of the ocean food chain and are the sole extant organisms closely linked with the carbon cycle whether through photosynthesis whether through carbon calcium crystallization (Westbroek et al., 1993). Despite their minute size they are responsible for approximately half of the total pelagic carbonate produced today. It is estimated that ~20-60% in weight of marine pelagic carbonate is due to coccolithophores (Brand, 1994; Winter et al., 1994). Actually, those micrometric calcite plates synthesized by coccolithophores are today accountable for 50 to 80% of all oceanic carbonates produced during one year worldwide (Milliman, 1993). This microfossil group, which is abundant from polar to equatorial regions, is thought to be responsible for more then half of the $CaCO_3$ in marine sediments from the Late Triassic onwards (Berger and Roth, 1975; Winter et al., 1979).

The coccoliths are produced through biomineralization of minuscule calcite crystals arranged according to specific arrays, displaying morphological and optical patterns with taxonomic and phylogenetic significance (Pienaar, 1994; Young, 1994). Coccoliths preserved in the geological record bear valuable information of palaeoenvironmental conditions from the oceans photic zone (e.g., Baumann et al., 2000; Bœckel and Baumann, 2008) and can thus be used as proxies of palaeoceanographic processes, sea surface primary productivity and climate change (Beaufort et al., 2001, 2011; Flores et al., 2000; Ziveri et al., 2004; Silva et al., 2008). Actually, coccoliths reflect persistent or strong enough ecological and oceanographic conditions that can be preserved in the fossil record. Although exposed to a variety of biostratonomic processes, coccolith thanatocoenosis in surface sediments can be closely related to the coccolithophore communities dwelling in the upper photic layer (e.g., Baumann et al., 2000, 2005; Kinkel et al., 2000; Sprengel et al., 2002; Boeckel and Baumann, 2008). Their swift transfer from the photic zone to the seabed through their incorporation in fast-sinking faecal pellets produced by grazing zooplankton and within marine snow aggregates, explains the presence of pristine coccoliths below the calcite compensation depth (Roth, 1994; Steinmetz, 1994; Balch, 2004) (see Fig. 1). Although during fossildiagenesis coccoliths and *incertae sedis* undergo chemical and physical changes including pressure-dissolution etching that mainly affect the most delicate species, and recrystallization, they show a fairly good resistance to burial processes (Adelseck et al., 1973; Roth, 1984). Besides calcareous nannofossils being extremely useful biostratigraphic markers due to their morphological diversity, fast evolution and global distribution, their extracellular calcareous scales play a major role both in the carbonate cycle and in the organic carbon cycle. Moreover, through the emission of dimethyl-sulfide by these phytoplanktonic algae, which may affect cloud albedo, calcareous nannoplankton also produces an additional feedback to climate change (Westbroeck et al., 1993).

In the past, calcareous nannofossils were responsible for creating and maintain a vertical alkalinity gradient in the world oceans (Riebesell et al., 2000). Since the first occurrence of coccolithophores ~240 millions years ago, these organisms play a key role in the gradual displacement of oceanic carbonate production from epicontinental seas into deep oceanic basins, forming this way the sedimentological and palaeontological features we find today on modern oceanic sediments (Ridgwell, 2005). The oldest calcareous nannofossil record dates back to the Lower Carnian (Triassic). Nannoliths and calcispheres produced by calcareous dinoflagellates, were found in Southern Alps sediments with ~230 Ma (Janofske, 1990; 1992). Only later in the Triassic during the Norian age (~220 Ma; Gradstein et al, 2012) the first record of muroliths coccoliths is reported (Bown, 1998). It was later during the Pliensbachian (~190 Ma) that the most common coccoliths found in the oceans today - the placoliths - first occur. From the Late Toarcian, the cosmopolitan *Watznaueria* genus gradually starts to replace its phylogenetic predecessor, *Lotharingius*, as the dominant coccolith taxon. This phenomenon represents a major ecological event as this genus will dominate the photic zone of global oceans for approximately ~100 myr until the K/T extinction event.

The distribution of calcareous nannofossils is influenced by climatic and hydrological conditions. Though seawater temperature has been considered to be the most important factor controlling the distribution of calcareous nannoplankton, trophic resources also play an important role in their distribution and abundance in past and modern oceans. The major limiting nutrients are nitrate and phosphate though the presence of trace elements and vitamins are also thought to be significant (Brand, 1994). In general, extant calcareous nannoplankton exhibit a vertical zonation within the water column. Most of the species dwell in the upper photic zone (0-60 m) whereas in the deeper photic zone (60-200 m) robust and thick nannoliths like *Florisphaera profunda* and *Gladiolithus flabellatus* occur (Molfino and McIntyre, 1990). According to Molfino and McIntyre (1990) high abundances of lower photic zone species are linked with a deep nutri- and thermocline, whilst low abundances are associated of shallow nutri- and thermocline. When comparing Lower Jurassic nannofossil assemblages with modern nannoplankton communities one can make similar assumptions for those robust and thick taxa such as *Crepidolithus crassus* and *Mitrolithus jansae* as species inhabiting the deep photic zone (Bucefalo Palliani and Mattioli, 1995; Mattioli and Pittet, 2004; Bour et al., 2007; Mattioli et al., 2008; Reggiani et al., 2010b; Suchéras-Marx et al., 2010), whereas thin and delicate placoliths coccoliths mainly belonging to *Lotharingius* and *Biscutum/Similiscutum* genera are interpreted as shallow-dwellers (e.g., Bucefalo Palliani and Mattioli, 1995; Pittet and Mattioli, 2002; Mattioli and Pittet, 2004; Reggiani et al., 2010b).

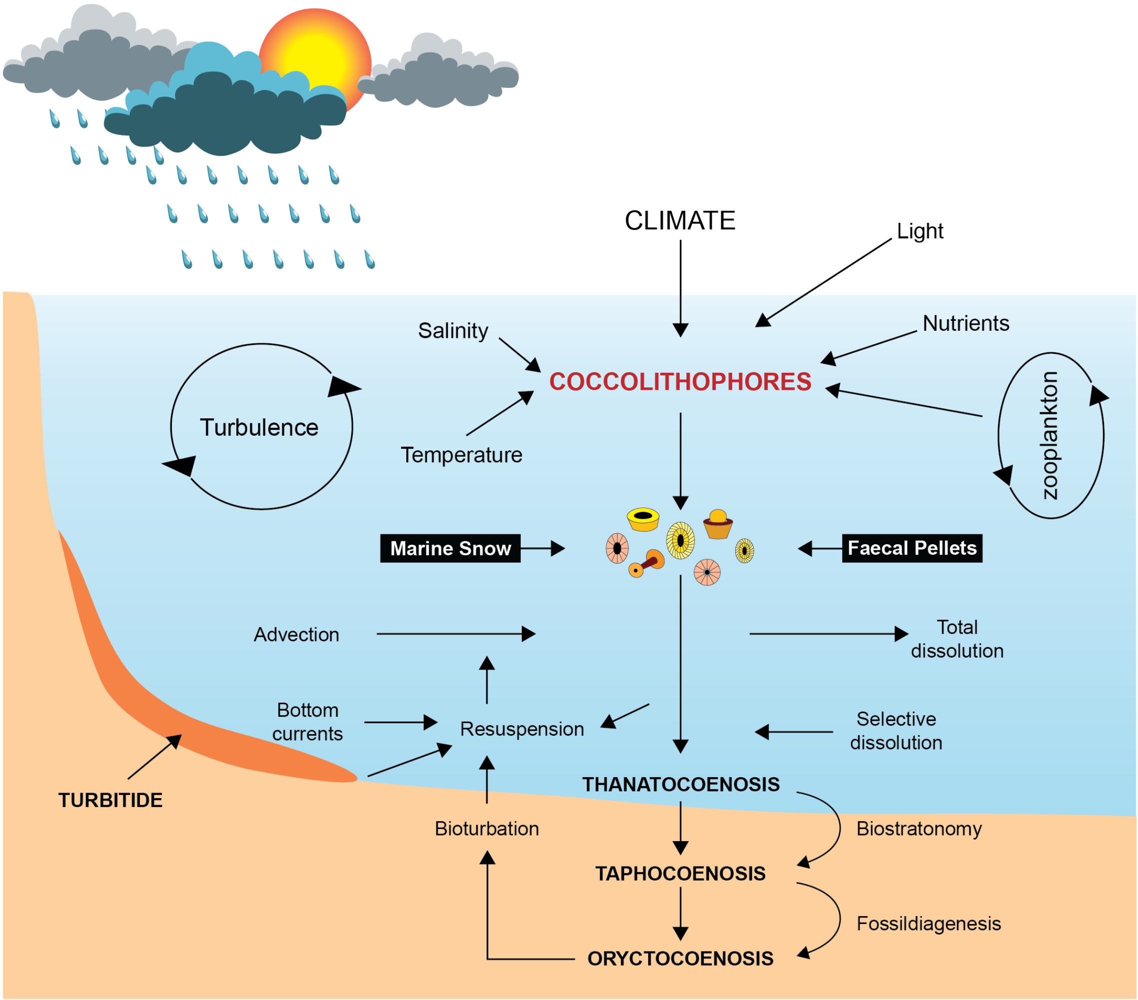


Figure 1 - Schematic sketch of major chemical and physical processes controlling the taphonomy of coccoliths in marine sediments.

1.2.2. Jurassic nannofossils

Coccolithophores, the *incertae sedis Orthogonoides hamiltoniae* and the probable dinoflagellate cyst *Schizosphaerella punctulata* mainly represent the Jurassic nannofossil assemblages. Notwithstanding their potential as palaeobiogeographic, palaeoceanographic and palaeoecological proxies, much is still yet to be done regarding ecological and biogeographic preferences of Jurassic calcareous nannoplankton. Recent works however, have improved what is known today about their marine palaeobioprovinces and auto- and synecological relationships within the water column (e.g., Mattioli and Pittet, 2004; Tremolada et al., 2005, 2006a, 2006b; Giraud et al., 2006, 2009; Lees et al., 2006; Bour et al., 2007; Mattioli et al., 2008; Reggiani et al, 2010b; Suchéras-Marx et al., 2015).

Ubiquitous in the southern Tethyan margin, the Jurassic *Schizosphaerella* is regarded as an opportunistic taxon that either thrived under intense vertical mixing (Mattioli, 1997; Walsworth-Bell, 2001) or as an oligotrophic taxon which profited from sporadic pulses of nutrients during storms in generally oligotrophic environments (Mattioli and Pittet, 2004). Though still debatable, for Mattioli et al. (2008), Reggiani et al. (2010b) and Ferreira et al. (2015) this taxon is interpreted as a shallow-dweller, abundant in warm and neritic southern Mediterranean Tethys waters that progressively decreases its abundance towards higher latitudes. Additionally, Bartolini et al. (2003) recorded in SW Germany a progressive increase in the relative abundance of *Schizosphaerella* that correlates to a shift from humid conditions in the earliest Late Oxfordian to a drier and warmer climate in the earliest Kimmeridgian. Adapted to shallow waters and generally oligotrophic environmental conditions (Pittet and Mattioli, 2002; Mattioli and Pittet, 2004), which is a consistent interpretation with modern oceans calcareous dinoflagellates which are generally found in oligotrophic water masses (Höll et al, 1999), this taxon is more abundant in shallow and near-shore environments (Mattioli and Pittet, 2004) where nutrients are regularly recycled in surface waters by intensified storms and during favourable periods of carbonate sedimentation (Mattioli, 1997). Actually, Ferreira et al. (2015) shows that *Schizosphaerella* is a southern Tethys taxon thriving preferentially in more neritic and shallow environments, increasing its abundance as it profits from water nutrification within unstable and meso-eutrophic environments (see Fig. 2).

Also an almost exclusive southern western Tethys species that has rarely been recorded at higher latitudes is the murolith *Mitrolithus jansae* (Bown, 1987a; Mattioli et al., 2008). Like *Crepidolithus*, its robust morphology has enabled it to be interpreted as a deep-dweller and showing no clear ecological preference either for proximal or distal settings (Bucefalo Palliani and Mattioli, 1995; Mattioli and Pittet, 2004). Other authors though, consider this species as an intermediate dweller (Erba, 2004; Tremolada et al., 2005). The genus *Calyculus* was first considered a deep-dweller in stratified and oligotrophic waters (Bucefalo Palliani and Mattioli, 1995). Later, it was interpreted as a meso-eutrophic taxon (Mattioli and Pittet, 2004) and ultimately as a surface dweller inhabiting preferentially the Mediterranean Tethys in oligotrophic conditions, as it coccoliths closely resemble the extant genus *Umbellosphaera* (Mattioli et al., 2008).

Being far more abundant in the NW European Tethys, the *Crepidolithus* genus is made up of robust and thick murolith coccoliths, and interpreted as deep-dweller taxa thriving in deep nutrient-rich waters when surface water masses are stratified and oligotrophic (Bour et al., 2007; Mattioli et al., 2008). Besides acting as sunlight refraction enhancers in the deep photic zone, their beefy coccoliths would have increased the coccosphere mass therefore contributing to retain them deep down in the water column, as interpreted from modern coccoliths by Young (1994). Also preferentially inhabiting NW Tethys waters, *Sollasites* and *Bussonius* genera are interpreted as being mesotrophic (Bucefalo Palliani et al., 2002). Similarly displaying higher abundances at higher latitudes and ecological affinity for lower temperature waters are species like *Parhabdolithus liasicus* and *Tubirhabdus patulus* (Mattioli et al., 2008).

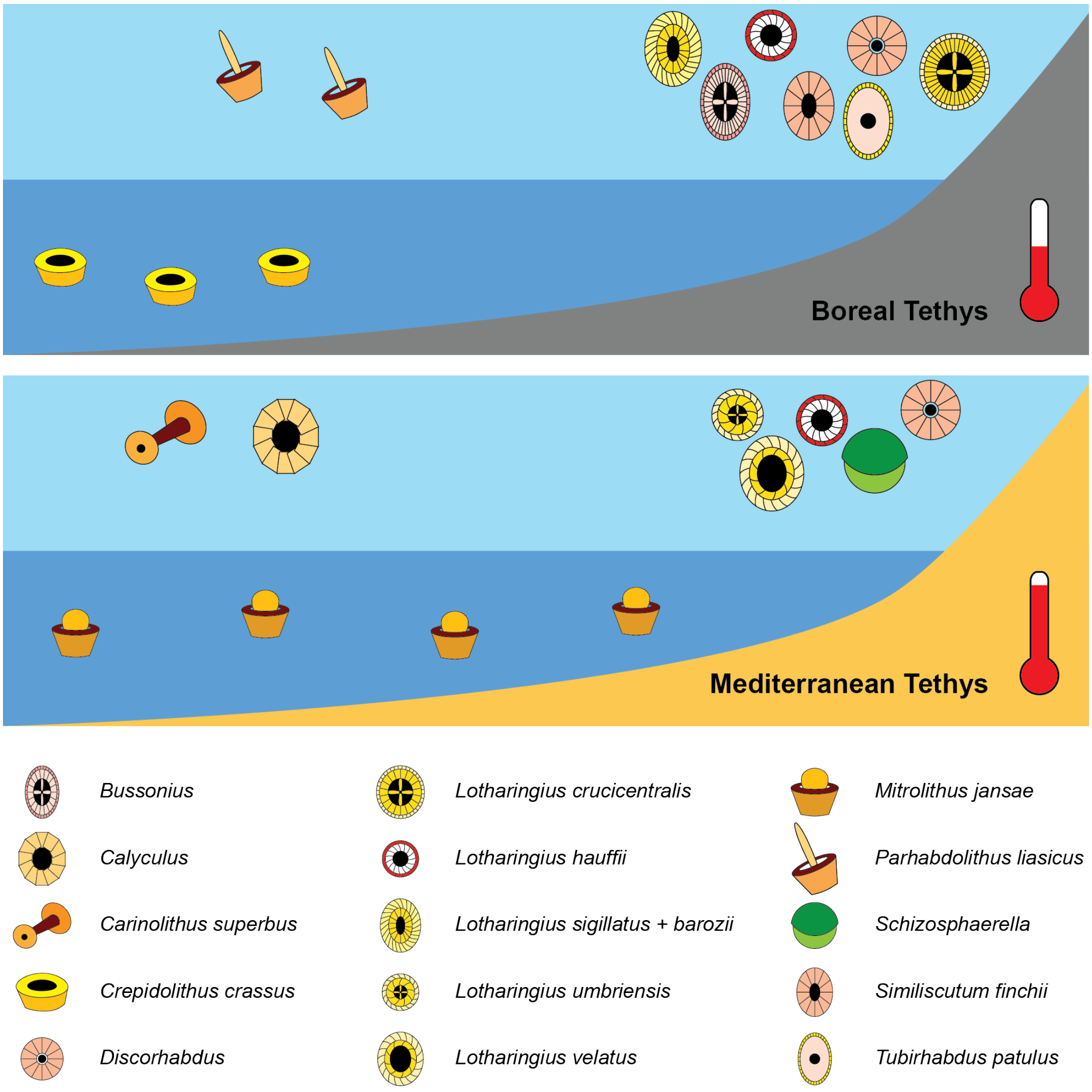


Figure 2 - Schematic sketch of ecological and geographic preferences of Toarcian coccoliths in warmer and colder western Tethys waters, in accordingly predominant carbonate and clay sedimentation settings.

The genera *Similiscutum* and *Lotharingius* are regarded as meso-eutrophic taxa occupying the upper photic layer (Bucefalo Palliani and Mattioli, 1995; Bucefalo Palliani et al., 2002; Pittet and

Mattioli, 2002; Mattioli and Pittet, 2004; Olivier et al., 2004; Tremolada et al., 2005; Mattioli et al., 2008; Reggiani et al., 2010b). If *Similiscutum cruciulus* grouped together with *Lotharingius umbriensis* and *L. velatus* exhibits its highest abundances in southern Tethys, conversely other species like *S. finchii* and *S. novum* together with some *Lotharingius* species like *L. barozii, L. crucicentralis* and *L. sigillatus* display a latitudinal positive gradient towards north (Mattioli et al., 2008). Additionally, *Lotharingius hauffii* is interpreted as a meso-eutrophic species dominating the coccolith assemblages (Pittet and Mattioli, 2002; Mattioli and Pittet, 2004; Olivier et al., 2004; Tremolada et al., 2005) during high trophic conditions within the water column. As also shown by Mattioli et al. (2004), the *Lotharingius* genus does not display a strong ecological preference for either proximal or distal environments. *Zeugrhabdotus erectus* and *Biscutum constans* are in turn interpreted as indices of higher fertility of surface waters because of their high abundances in C_{org}-rich sediments and palaeo-upwelling areas (e.g., Roth and Krumbach, 1986; Watkins, 1989; Erba, 1992; Erba et al., 1992). The *Discorhabdus* genus is considered a meso-eutrophic taxon (e.g., Premoli Silva et al., 1989; Giraud et al., 2003; Mattioli et al., 2008; Giraud, 2009), so far without a preferential latitudinal province.

The most successful coccolithophorid during the Mesozoic was the *Watznaueria* genus (Lees et al., 2005; Erba, 2006). It was across the Aalenian-Bajocian boundary that both relative and absolute abundance of this genus integrated and overcame by numbers other nannoplanktonic taxa. This switchover was likely linked to a climatic driven eutrophication event, but also due to its opportunistic mode of life (Lees et al., 2006; Giraud 2009; Suchéras-Marx et al., 2015). Despite not all the species of the Watznaueriaceae family are found in Toarcian sediments, the first occurrence of this genus happens at the end of the Early Toarcian and lingers on throughout the Mesozoic and even survives the K/T extinction. Hence a brief summary of what is today known about this taxon ecological preferences is presented. The species *Watznaueria manivitae* is considered as being typical of Late Jurassic-Early Cretaceous low latitude assemblages (Cooper, 1989). This species displays in the Late Jurassic of SW Germany the same trend of *Schizosphaerella*, probably indicating similar ecological preferences, i.e., low nutrient concentrations and warmer surface water (Bartolini et al., 2003). Though still unclear, palaeoecological affinities of *Watznaueria britannica*, a plexus of different-sized morphotypes and the dominant coccolithophore across de Middle-Upper Jurassic, have according to Giraud et al. (2006) and Giraud (2009) two different meanings. If on one-hand high abundances of small *W. britannica* placoliths indicates mesotrophic conditions, *W. britannica* placoliths with increasing size corresponds to more stable environmental conditions whether in meso- or oligotrophic and warm surface-waters. As for the cosmopolitan *Watznaueria barnesiae*, high quantities of this species recorded in moderate to well-preserved nannofossil assemblages are generally interpreted as indicative of oligotrophic surface waters (e.g., Roth and Krumbach, 1986; Premoli Silva et al., 1989; Williams and Bralower, 1995; Burns and Bralower, 1998). Furthermore, abundances of *W.*

barnesiae are generally in "phase opposition" with those of eutrophic taxa such as *Z. erectus* and *B. constans* (Erba et al., 1992; Herrle, 2003; Tremolada et al., 2006a). Conversely, blooms of *W. barnesiae* in the Kimmeridge Clay Formation are interpreted as indicative of enhanced primary productivity (Lees et al., 2006). Supported by sediments carbonate differentiated content, these authors tentatively postulate that *W. britannica* or *Cyclagelosphaera margerelii* occupied a higher trophic position than *W. barnesiae* and *W. fossacincta* (believed to represent end-members of a morphological continuum) being *C. margerelii* the most opportunistic species and responding to possibly more extreme nutrification intervals and/or lowered sea level. Actually, as *C. margerelii* survived the K/T boundary extinction event, it has been argued that it was likely a neritic taxon (Street and Bown, 2000; Bown et al., 2004). Similar high trophic conditions supporting the eurytopic watznaueriaceans array was already suggested by Pittet and Mattioli (2002) for the Late Oxfordian in southern Germany. Corroborated by the different species relative abundance and sediments $CaCO_3$ content, these authors suggest that *L. hauffii, W. britannica, C. margerelii, W. barnesiae, W. manivitae* and *Schizosphaerella* would thus represent a trophic preference continuum from more eutrophic to oligotrophic conditions, i.e., from carbonate-rich to clay-rich sediments.

1.2.3. Jurassic nannofossil biostratigraphy

Over the past decades much attention has been given to the European Jurassic calcareous nannofossil biostratigraphy (e.g., Crux 1984, 1987; Young et al. 1986; Bown 1987a, b, 1996; Bown and Cooper 1989, Cobianchi 1990, 1992; Baldanza et al. 1990; Erba 1990; Lozar 1992; Reale et al. 1992; de Kænel and Bergen 1993; Bucefalo Palliani and Mattioli 1994; de Kænel et al. 1996). But for the past 16 years, the European Jurassic calcareous nannofossil biostratigraphy has been on halt, although some biometry works and taxonomic revisions occurred (Mattioli et al., 2004; Fraguas and Erba, 2010; Fraguas and Young, 2011; López-Otálvaro et al., 2012) that changed to some extent the species conceptions. Since Mattioli and Erba (1999) no big attention has been given to this subject notwithstanding different biozonations have been recommended for various regions. Bown (1996) and de Kænel et al. (1996) summarized the nannofossil biozonations available for different areas, but with limited data available for the Tethyan realm. The most recent syntheses and those commonly used in the literature are those from de Kænel et al. (1996) for western Portugal, Bown and Cooper (1998) for NW Europe and Mattioli and Erba (1999) for central Italy.

The first studies of Lower Jurassic calcareous nannofossils from the Lusitanian Basin are from Hamilton (1977; 1979). Later Bown (1987a) and de Kænel and Bergen (1993) studied the nannofossil content from the Brenha section. The Portuguese succession of nannofossil events ranging from Late Sinemurian to Callovian were acknowledged by Bergen (unpublished data) and reported by the synthesis work of de Kænel (1996) and Bown and Cooper (1998). Recent works however, were made in the Iberian Peninsula addressing the Pliensbachian and Toarcian nannofossil biostratigraphy (Perilli, 2000; Perilli et al., 2004; Perilli and Duarte, 2006), though the taxonomy adopted by the previous authors is not in complete accordance with the one followed here.

References

Adelseck, C.G., Jr., Geehan, G.W., Roth, P.H., 1973. Experimental evidence for the selective dissolution and overgrowth of calcareous nannofossils during diagenesis. Geological Society of America Bulletin 84, 2755-2762.

Aguado, R., O´Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the Western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Marine Micropaleontology 68, 268-285.

Balch, W.M., 2004. Re-evaluation of the physiological ecology of coccolithophores. In: Thierstein, H.R. and Young, J.R. (Eds.) Coccolithophores From Molecular Process to Global Impact. Springer-Verlag, Berlin, pp. 165-190.

Baldanza A., Cresta S., Mattioli, E., 1990. Bajocian Calcareous Nannofossils from Monte Nerone Area (Urnbro-Marchean Apennine, Italy). Mem. Descr. Carta Geol. d'Italia 40, 225-236.

Bartolini, A., Pittet, B., Mattioli, E., Hunzicker, J., 2003. Regional control on stable isotope signature in deep-shelf sediments: an example of the Late Jurassic of southern Germany (Oxfordian-Kimmeridgian). Sedimentary Geology 160, 107-130.

Baumann, K.-H., Andruleit, H.A., Samtleben, C., 2000. Coccolithophores in the Nordic Seas: comparison of living communities with surface sediment assemblages. Deep-Sea Research II 47, 1743-1772.

Baumann, K.-H., Andruleit, H.A., Bockel, B., Geisen, M., Kinkel, H., 2005. The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and paleoproductivity: a review. Paläontologische Zeitschrift 79, 93-112.

Beaufort, L., de Garidel-Thoron, T., Mix, A.C., 2001. ENSO-like forcing on Oceanic Primary Production During the Late Pleistocene. Science 293, 2440-2444.

Beaufort, L., Probert, I., de Garidel-Thoron, T., Bendif, E.M., Ruiz-Pino, D., Metzl, N., Goyet, C., Buchet, N., Coupel, P., Grelaud, M., Rost, B., Rickaby, R.E.M., de Vargas, C., 2011. Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. Nature 476, 80-83.

Beerling, D.J., Brentnall, S.J. 2007. Numerical evaluation of mechanisms driving Early Jurassic changes in global carbon cycling, Geology, 35, 247-250.

Berger, W.H., Roth, P.H., 1975. Oceanic Micropaleontology: Progress and Prospect. Reviews of Geophysical Space Research 13, 561-585.

Bœckel, B., Baumann, K.-H., 2008. Vertical and lateral variations in coccolithophore community structure across the subtropical frontal zone in the South Atlantic Ocean. Marine Micropaleontology 76, 255-273.

Bour, I., Mattioli, E., Pittet, B., 2007. Nannofacies analysis as a tool to reconstruct palaeoenvironmental changes during the Early Toarcian anoxic event. Palaeogeography, Palaeoclimatology, Palaeoecology 249, 58-79.

Bown, P.R., 1987a. Taxonomy, evolution and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. Special Papers in Palaeontology 38, 1-118.

Bown P.R., 1987b. The structural development of early Mesozoic coccoliths and its evolutionary and taxonomic significance. Abh. Geol. Bunds 39, 33-49.

Bown, P.R. with contributions from the International Nannoplankton Association, Jurassic Working Group, 1996. Recent advances in Jurassic calcareous nannofossil research. GeoResearch Forurn, v. 1-2, 55-66.

Bown, P.R., 1998. Calcareous nannofossil biostratigraphy. British Micropaleontological Society Publication Series. Chapman and Hall. 315 pp.

Bown P.R. and Cooper M.K.E., 1989. New Calcareous Nannofossil taxa from the Jurassic. Journal of Micropaleontology 8, 91-96.

Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.) Calcareous Nannofossils Biostratigraphy. British Micropalaeontological Society Publication Series. Kluver Academic Publishers, Cambridge, pp. 34-85.

Bown, P.R., Lees, J.A., Young, J.R., 2004. Calcareous nannoplankton evolution and diversity through time. In: Thierstein, H.R. and Young, J.R. (Eds.) Coccolithophores From Molecular Process to Global Impact. Springer-Verlag, Berlin, pp. 481-508.

Bown, P.R., Young, J.R., 1998. Introduction. In: Bown, P.R. (Ed.) Calcareous Nannofossil Biostratigraphy. British Micropalaeontological Society Publication Series. Kluver Academic Publishers, Cambridge, pp. 1-15.

Brand, L.E., 1994. Physiological ecology of marine coccolithophores. In: Winter, A., Siesser, W. (Eds.) Coccolithophores, Cambridge University Press, pp. 39-49.

Bucefalo Palliani, R., Mattioli, E., 1994. Enrichment in organic matter within the Early Toarcian Marne di Monte Serrone Formation: a synchronous event in the Umbria-Marche Basin (Central Italy). Palaeopelagos 4, 175-188.

Bucefalo Palliani, R., Mattioli, E., 1995. Ecology of dinoflagellate cysts and calcareous nannofossils from bituminous facies of the Early Toarcian, central Italy. Proc. III EPA Workshop: Black Shales Models, Dotternhausen, pp. 60-62.

Bucefalo Palliani, R., Mattioli, E., Riding, J.B., 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.

Burns, C.E., Bralower, T.J., 1998. Upper Cretaceous nannofossil assemblages across the Western Interior Seaway: implications for the origins of lithologic cycles in the Greenhorn and Niobrara Formations. SEPM Special Publication, Concepts Sedimentology Paleontology 6, 35-58.

Cobianchi M.A., 1990. Biostratigrafia a nannofossili celcarei del passaggio Domeriano-Toarciano in Val Navezze (Brescia). Atti Ticinensi di Scienze della Terra 33, 19-25.

Cobianchi M.A., 1992. Sinemurian-Early Bajocian Calcareous Nannofossil Biostratigraphy of the Lombardy Basin (Southern Calcareous Alps; Northern Italy). Atti Ticinensi di Scienze della Terra 35, 61-106.

Cooper, M.K.E., 1989. Nannofossil provincialism in the Late Jurassic-Early Cretaceous (Kimmeridgian to Valanginian) period. In: Crux, J.A., van Heck, S. (Eds.), Nannofossils and their Applications. British Micropalaeontology Society Series, Ellis Horwood, Chichester, pp. 223-246.

Crux J. A., 1984. Biostratigraphy of Early Jurassic Calcareous Nannofossils from southwest Germany. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 169, 160-186

Crux J. A., 1987. Early Jurassic calcareous nannofossil biostratigraphic events. Newsletters on Stratigraphy 17, 79-100.

de Kænel, E., Bergen, J.A., 1993. New early and middle Jurassic coccolith taxa and biostratigraphy from the eastern proto-Atlantic (Morocco, Portugal and DSDP Site 547 B). Eclogae geologicae Helvetiae 86, 861-908.

de Kænel, E., Bergen, J.A., von Salis Perch-Nielsen, K. 1996. Jurassic calcareous nannofossil biostratigraphy of western Europe. Compilation of recent studies and calibration of bioevents. Bulletin de la Societe Géologique de France 167, 15-28.

Dera, G., Pellenard, P., Neige, P., Deconinck, J.F., Puceat, E., Dommergues, J.L., 2009. Distribution of clay minerals in Early Jurassic Peritethyan seas: Palaeoclimatic significance inferred from multiproxy comparisons. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 39-51.

Dera, G., Neige, P., Dommergues, J.-L., Brayard, A., 2011. Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Global and Planetary Change 78, 92-105.

Duarte, L.V., Oliveira, L.C., Rodrigues, R., 2007. Carbon isotopes as a sequence stratigraphic tool: examples from the Lower and Middle Toarcian marly limestones of Portugal. Boletín Geológico y Minero 118, 3-18.

Erba, E., 1990. Calcareous nannofossil biostratigraphy of some Bajocian sections from the Digne area (SE France). Mem. Descr. Carta Geol. d'Italia 40, 237-256.

Erba, E., 1992. Middle Cretaceous calcareous nannofossils from the Western Pacific (ODP Leg 129): evidence for paleoequatorial crossings. Sci. Res. ODP 129, 189-201.

Erba, E., 2004. Calcareous nannofossils and Mesozoic oceanic anoxic events. Marine Micropaleontology 52, 85-106.

Erba, E., 2006. The first 150 million years history of calcareous nannoplankton: biosphere-geosphere interactions. Palaeogeography, Palaeoclimatology, Palaeoecology 232, 237-250.

Erba, E., Castradori, D., Guasti, G., Ripepe, M., 1992. Calcareous nannofossils and Milankovitch cycles: the example of the Albian Gault Clay Formation (Southern England). Palaeogeography Palaeoclimatology Palaeoecology 93, 47-69.

Ferreira, J., Mattioli, E., Pittet, B., Cachão, M., Spangenberg, J.E., 2015. Palaeoecological insights on Toarcian and lower Aalenian calcareous nannofossils from the Lusitanian Basin (Portugal). Palaeogeography, Palaeoclimatology, Palaeoecology 436, 245-262.

Flores, J.-A., Bárcena, M.A., Sierro, F.J., 2000. Ocean-surface and wind dynamics in the Atlantic Ocean off Northwest Africa during the last 140,000 years. Palaeogeography, Palaeoclimatology, Palaeoecology 161, 459-478.

Fraguas, A., Erba, E., 2010. Biometric analyses as a tool for the differentiation of two coccolith species of the genus Crepidolithus (Pliensbachian, Lower Jurassic) in the Basque-Cantabrian Basin (Northern Spain). Marine Micropaleontology 77, 125-136.

Fraguas, A., Young, J., 2011. Evolution of the coccolith genus Lotharingius during the Late Pliensbachian-Early Toarcian interval in Asturias (N Spain). Consequences of the Early Toarcian environmental perturbations. Geobios 44, 361-375.

Giraud, 2009. Calcareous nannofossil productivity and carbonate production across the Middle-Late Jurassic transition in the French Subalpine Basin. Geobios 42, 699-714.

Giraud, F., Olivero, D., Baudin, F., Reboulet, S., Pittet, B., Proux, O., 2003. Minor changes in surface water fertility across the Oceanic Anoxic Event 1d (latest Albian, SE France) evidenced by calcareous nannofossils. International Journal of Earth Sciences 92, 267-284.

Giraud, F., Pittet, B., Mattioli, E., Audoin, V., 2006. Paleoenvironmental controls on the morphology and abundance of the coccolith *Watznaueria britannica* (Late Jurassic, southern Germany). Marine Micropaleontology 60, 205-225.

Gómez, J.J., Goy, A., Canales, M.L., 2008. Seawater temperature and carbon isotope variations in belemnites linked to mass extinction during the Toarcian (Early Jurassic) in Central and Northern Spain. Comparison with other European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 258, 28-58.

Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G., 2012. The Geological Time Scale 2012. pp. 1144. Elsevier.

Hagino, K., Young, J.R., Bown, P.R., Godrijan, J., Kulhanek, D.K., Kogame, K., Horiguchi, T., 2015. Re-discovery of a “living fossil” coccolithophore from the coastal waters of Japan and Croatia. Marine Micropaleontology 116, 28-37.

Hallam, A., 1981. A revised sea-level curve for the Early Jurassic. Journal of the Geological Society 138, 735-743.

Hamilton, G.B., 1977. Early Jurassic calcareous nannofossils from Portugal and their biostratigraphic use. Eclogae geologicae Helvetiae 70, 575-597.

Hamilton, G.B., 1979. Lower and Middle Jurassic calcareous nannofossils from Portugal. Eclogae geologicae Helvetiae 72, 1-17.

Herrle, J.O., 2003. Reconstructing nutricline dynamics of mid-Cretaceous oceans: evidence from calcareous nannofossils from the Niveau Paquier black shale (SE France). Marine Micropaleontology 47, 307-321.

Höll, C., Karwath, B., Rühlemann, C., Zonneveld, K.A.F., Willems, H., 1999. Palaeoenvironmental information gained from calcareous dinoflagellates: the Late Quaternary eastern and western tropical Atlantic Ocean in comparison. Palaeogeography Palaeoclimatology Palaeoecology 146, 147-164.

Jenkyns, H.C., 1988. The Early Toarcian (Jurassic) anoxic event: stratigraphic, sedimentary and geochemical evidence. American Journal of Science 288, 101-151.

Janofske, D., 1990. Eine neue "Calcisphaere", Carnicalyxia tabellata n.g. n.sp. aus den Cassianer Schichten (Cordevol, unteres Karn) der Dolomiten. Berliner Geowissenschaftlichen Abhandlungen 124, 259-269.

Janofske. D., 1992. Calcareous nannofossils of the Alpine Upper Triassic. In Hamrsmîd, B., Young, J.R. (Eds.) Nannoplankton Research, Vol. 1, Knihovnicka ZPZ 14a, 1, 87-109.

Jordan, R., Cros, L., Young, J., 2004. A revised classification scheme for living haptophytes. Micropaleontology 50, 55-79.

Kemp, D.B., Coe, A.L., Cohen, A.S., Schwark, L. 2005. Astronomical pacing of methane release in the Early Jurassic period, Nature, 437, 396-399.

Kinkel, H., Baumann, K.-H., Cepek, M., 2000. Coccolithophores in the equatorial Atlantic Ocean: response to seasonal and Late Quaternary surface water variability. Marine Micropaleontology 39, 87-112.

Lees, J.A., Bown, P.R., Mattioli, E. 2005. Problems with proxies? Cautionary tales of calcareous nannofossil paleoenvironmental indicators. Micropaleontology 51, 333-343.

Lees, J.A., Bown, P.R., Young, J.R., 2006. Photic zone palaeoenvironments of the Kimmeridge Clay Formation (Upper Jurassic, UK) suggested by calcareous nannoplankton palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 235, 110-134.

López-Otálvaro, G.-E., Baptiste Suchéras-Marx, B., Giraud, F., Mattioli, E., Lécuyer, C., 2012. Discorhabdus as a key coccolith genus for paleoenvironmental reconstructions (Middle Jurassic, Lusitanian Basin): Biometry and taxonomic status. Marine Micropaleontology 94-95, 45-57.

Lozar, F., 1992. Biostratigrafia a Nannofossili calcarei nel Lias: risultati di alcune sezioni nel Bacino Lombardo e nel Bacino Delfinese. Palaeopelagos 2, 89-98.

Mattioli, E., 1996. New Calcareous Nannofossil species from the Early Jurassic of Tethys. Rivista Italiana di Paliontologia e Stratigrafia 102, 397-412.

Mattioli, E., 1997. Nannoplankton productivity and diagenesis in the rhythmically bedded Toarcian-Aalenian Fiuminata sequence (Umbria-Marche Apennine, Central Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 130, 113-134.

Mattioli, E., Erba, E., 1999. Synthesis of calcareous nannofossil events in Tethyan Lower and Middle Jurassic successions. Rivista Italiana di Paleontologia e Stratigrafia 105, 343-376.

Mattioli, E., Pittet, B., 2004. Spatial and temporal distribution of calcareous nannofossils along a proximal-distal transect in the Lower Jurassic of the Umbria-Marche Basin (central Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 205, 295-316.

Mattioli, E., Pittet, B., Petitpierre, L., Mailliot, S., 2009. Dramatic decrease of pelagic carbonate production by nannoplankton across the Early Toarcian anoxic event (T-OAE). Global and Planetary Change 65, 134-145.

Mattioli E., Pittet B., Suan, G., Mailliot S., 2008. Calcareous nannoplankton across the Early Toarcian Anoxic Event: implications for paleoceanography within the western Tethys. Paleoceanography 23, PA3208.

Mattioli, E.; Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian-Toarcian (Lower Jurassic) coccoliths of the family *Biscutaceae*: intra- and interspecific variability versus palaeoenvironmental influence. Marine Micropaleontology 52, 5-27.

McElwain, J.C., Wade-Murphy, J., Hesselbo, S.P., 2005. Changes in the carbon dioxide during an anoxic event linked to intrusion into Gondwana coals. Nature 435, 479-482.

Milliman, J.D., 1993. Global Biogeochemical Cycles 7, 927-957.

Molfino, B, McIntyre, A., 1990. Precessional Forcing of Nutricline Dynamics in the Equatorial Atlantic. Science 249, 766-769.

Olivier, N., Pittet, B., Mattioli, E., 2004. Palaeoenvironmental control on sponge-reefs and contemporaneous deep-shelf marl-limestone deposition (Late Oxfordian, southern Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 212, 233-263.

Pálfy, J., Smith, P.L., 2000. Synchrony between Early Jurassic extinction, oceanic anoxic event, and the Karoo-Ferrar flood basalt volcanism. Geology 28, 747-750.

Perilli, N., 2000. Calibration of early-middle Toarcian nannofossil events based on high-resolution ammonite biostratigraphy in two expanded sections from the Iberian Range (East Spain). Marine Micropaleontology 39, 293-308.

Perilli, N., Duarte, L.V., 2006. Toarcian nannobiohorizons from Lusitanian Basin (Portugal) and their calibration against ammonite zones. Rivista Italiana di Paleontologia e Stratigrafia 112, 417-434.

Perilli, N., Goy, A., Comas-Rengifo, M.J., 2004. Calibration of the Pliensbachian-Toarcian calcareous nannofossil zone boundaries based on ammonite (Basque-Cantabrian area, Spain). Rivista Italiana di Paleontologia e Stratigrafia 110, 97-107.

Pienaar, R.N., 1994. Ultrastructure and calcification of coccolithophores. In: Winter, A., Siesser, W.G. (Eds.) Coccolithophores. Cambridge University Press, pp. 13-37.

Pittet, B., Mattioli, E., 2002. The carbonate signal and calcareous nannofossil distribution in an Upper Jurassic section (Balingen-Tieringen, Late Oxfordian, southern Germany). Palaeogeography, Palaeoclimatology, Palaeoecology 179, 71-96.

Premoli Silva, I., Erba, E., Tornaghi, M., 1989. Paleoenvironmental signals and changes in surface fertility in mid Cretaceous C_{org}-rich pelagic facies of the Fucoid Marls (Central Italy). Geobios 11, 225-236.

Reale, V, Baldanza, A., Monechi, S., Mattioli, E., 1992. Calcareous Nannofossil biostratigraphic events from the Early-Middle Jurassic sequences of the Umbria-Marche area (Central Italy). Mem. Sc. Geol. Padova. 43, 41-75.

Reggiani, L., Mattioli, E., Pittet, B., 2010a. Spatial distribution of Late Pliensbachian (Early Jurassic) calcareous nannofossils within the Lusitanian basin (Portugal). Geobios 43, 87-97.

Reggiani, L., Mattioli, E., Pittet, b., Duarte, L.V., Veiga de Oliveira, L.C., Comas-Rengifo, M.J. 2010b. Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian Basin, Portugal): A clue for palaeoenvironmental reconstructions. Marine Micropaleontology 75, 1-16.

Ridgwell, A., 2005. A Mid Mesozoic Revolution in the regulation of ocean chemistry. Marine Geology 217 339-357.

Riebesell, U., Zondervan, I., Rost, B., et al., 2000. Reduced calcification of marine plankton in response to increased atmospheric CO_2. Nature 407, 364-367.

Roth, P.H., 1984. Preservation of calcareous nannofossils and fine-grained carbonate particles in mid-Cretaceous sediments from the southern Angola Basin. In: Hay, W.W., Sibuet, J.C., et al. (Eds.), Init. Rep. DSDP 75, 651-655.

Roth, P.H., 1994. Distribution of coccoliths in oceanic sediments. In: Winter, A., Siesser, W. (Eds.) Coccolithophores, Cambridge University Press, pp. 199-218.

Roth, P.H., Krumbach, K.R., 1986. Middle Cretaceous calcareous nannofossil biogeography and preservation in the Atlantic and Indian Oceans: implications for paleoceanography. Marine Micropaleontology 10, 235-266.

Silva, A., Palma, S., Moita, M.T., 2008. Coccolithophores in the upwelling waters of Portugal: Four years of weekly distribution in Lisboa bay. Continental Shelf Research 28, 2601-2613.

Sprengel, C., Baumann, K.-H., Henderiks, J., Henrich, R., Neuer, S., 2002. Modern coccolithophore and carbonate sedimentation along a productivity gradient in the Canary Islands region: seasonal export production and surface accumulation rates. Deep-Sea Research II 49, 3577-3598.

Steinmetz, J.C., 1994. Sedimentation of coccolithophores. In: Winter, A., Siesser, W. (Eds.) Coccolithophores, Cambridge University Press, pp. 13-37.

Suan, G., Mattioli, E., Pittet, B., Mailliot, S., Lécuyer, C., 2008. Evidence for major environmental perturbation prior to and during the Toarcian (Early Jurassic) oceanic anoxic event from the Lusitanian Basin, Portugal. Paleoceanography 23, PA1202.

Suchéras-Marx, B., Mattioli, E., Giraud, F., Escarguel, G., 2015. Paleoenvironmental and paleobiological origins of coccolithophorid genus Watznaueria emergence during the late Aalenian-early Bajocian. Paleobiology DOI: 10.1017/pab.2015.8.

Suchéras-Marx, B., Mattioli, E., Pittet, B., Escarguel, G., Suan, G., 2010. Astronomically-paced coccolith size variations during the early Pliensbachian (Early Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 295, 281-292.

Svensen, H., Planke, S., Chevallier, L., Malthe-Sorenssen, A., Corfu, F., Jamtveit, B., 2007. Hydrothermal venting of greenhouse gases triggering Early Jurassic global warming. Earth and Planetary Science Letters 256, 554-566.

Tremolada, F., Erba, E., Bralower, T.J., 2006a. Late Barremian to early Aptian calcareous nannofossil paleoceanography and paleoecology from the Ocean Drilling Program Hole 641C (Galicia Margin). Cretaceous Research 27, 887-897.

Tremolada, F., Erba, E., van de Schootbrugge, B., Mattioli, E., 2006b. Calcareous nannofossil changes during the late Callovian-early Oxfordian cooling phase. Marine Micropaleontology 59, 197-209.

Tremolada, F., van de Schootbrugge, B., Erba, E., 2005. Early Jurassic schizosphaerellid crisis in Cantabria, Spain: Implications for calcification rates and phytoplankton evolution across the Toarcian oceanic anoxic event. Paleoceanography 20, doi:10.1029/2004PA001120.

Walsworth-Bell, E.B., 2001. Jurassic calcareous nannofossils and environmental cycles. Unpublished PhD thesis, 140 pp. University College London, London, UK.

Watkins, D.K., 1989. Nannoplankton productivity fluctuations and rhythmically bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous). Palaeogeography Palaeoclimatology Palaeoecology 74, 75-86.

Westbroek, P., Brown, C.W., Bleijswijk, J.V., Brownlee, C., Brummer, G.J., Conte, M., Egge, J., Fernández, E., Jordan, R., Knappertsbusch, M., Stefels, J., Veldhuis, M., van der Wal, P., Young, J., 1993. A model system approach to biological climate forcing. The example of *Emiliania huxleyi*. Global and Planetary Change 8 27-46.

Williams, J.R., Bralower, T.J., 1995. Nannofossil assemblages, fine fraction stable isotopes, and the paleoceanography of the Valanginian-Barremian (Early Cretaceous) North Sea Basin. Paleoceanography 10, 815-864.

Winter, A., Jordan, R., Roth, P., 1994. Biogeography of living coccolithophores in ocean waters. In: Winter, A., Siesser, W. (Eds.) Coccolithophores, Cambridge University Press, pp. 161-177.

Winter, A., Reiss, Z., Lutz, B., 1979. Distribution of living coccolithophore assemblages in the gulf of Elat (Aqaba). Marine Micropaleontology 4, 197-223.

Young J.R., Teale T., Bown P.R., 1986. Revision of the Stratigraphy of the Longobucco group (Liassic, southern Italy), based on new data from nannofossils and ammonites. Eclogae geologicae Helvetiae 79, 117-135.

Young, J.R., 1994. The functions of coccoliths. In: Winter, A., Siesser, W. (Eds.) Coccolithophores, Cambridge University Press, pp. 63-82.

Ziveri, P., Baumann, K.-H., Boeckel, B., Bollmann, J., Young, J.R., 2004. Biogeography of selected Holocene coccoliths in the Atlantic Ocean. In: Thierstein, H.R. and Young, J.R. (Eds.) Coccolithophores From Molecular Process to Global Impact. Springer-Verlag, Berlin, pp. 403-428.

2. Study area

2.1. The Lusitanian Basin

The Lusitanian Basin is located on the western margin of the Iberian Plate (Portugal), and is a marginal basin formed during the Triassic period. Its orientation is NE-SW and it is approximately 300 km in length and 150 km wide, with a maximum sediment thickness of 5 km (Veiga de Oliveira et al, 2007). The sedimentary rocks range from Upper Triassic to Upper Cretaceous, and are mainly of Jurassic age overlain by Tertiary. The Lower Jurassic is particularly well represented in the Lusitanian Basin, especially in the Peniche region (Duarte and Soares, 2002). During the Early Jurassic, the western Tethys Ocean mainly consisted of a shallow sea lying between the African and the European landmasses (Fig. 3). It was in this region that the Lusitanian Basin started to open during an aborted rift phase in the Late Triassic (Pinheiro et al., 1996). It was then a relatively narrow and elongated epicontinental (<200 m in depth according to Bjerrum et al., 2001) seaway connecting the Hispanic Seaway southern waters to the NW European waters.

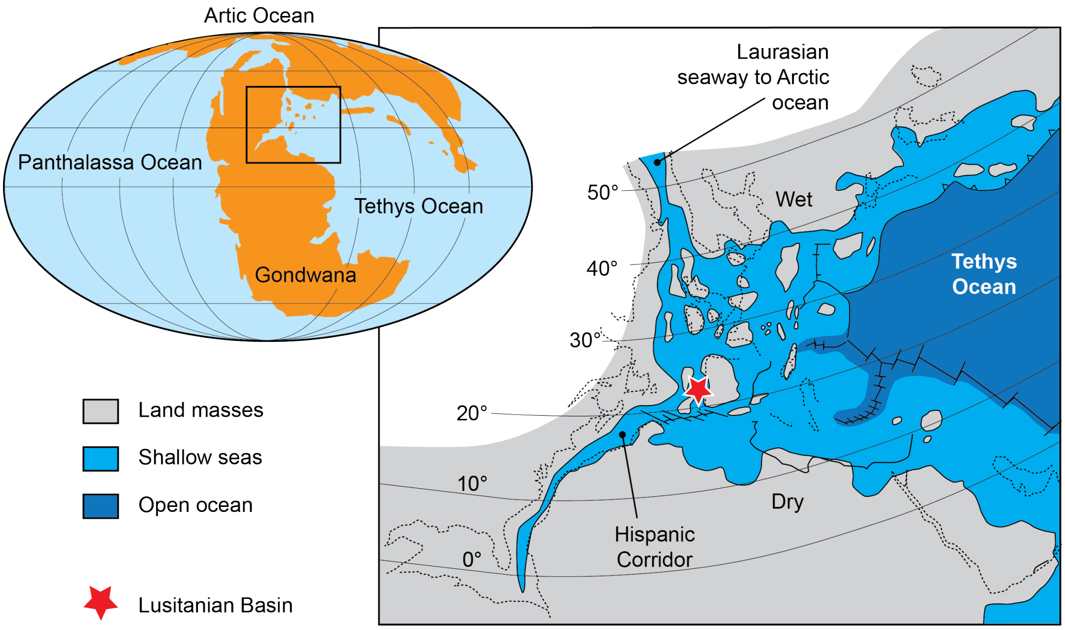


Figure 3 - Location of the Lusitanian Basin during the Early Jurassic in the western Tethys epicontinental sea (modified after Bassoulet et al., 1993).

Roughly N-S orientated, this basin was bounded in the east by the Iberian Meseta and in the west by the Berlengas-Farilhões igneous and metamorphic horst at a palaeolatitude between 25 and 30ºN (Dercourt et al., 2000) (see Fig. 4). In modern oceans this palaeolatitude range corresponds to the transition between the Subtropical to Temperate waters. The mixing between higher NW European and lower latitude Mediterranean waters in this passageway has been described by various authors and supported by a mix of ammonite faunas and calcareous nannofossil assemblages during the Early Jurassic (Mouterde and Ruget, 1975; Dommergues and Mouterde, 1980; Reggiani et al. 2010; Dera et al., 2011a). The three sections studied in this work are located in the Coimbra and Figueira da Foz region and represent 286 m of a complete and continuous succession of marine hemipelagic marl and limestone couplets deposited on a homoclinal, low-angle ramp with a NW dipping (Duarte, 2004). The Rabaçal section corresponds to the most proximal part of the studied area and Cabo Mondego to the most distal, with the Brenha section positioned between these two. In all of the three sections macrofossils such as ammonites, brachiopods, belemnites, bivalves and some fossilized wood are commonly found. Though the Rabaçal section spans from the uppermost Pliensbachian to the uppermost Toarcian, only the first 42 m comprising the Polymorphum, Levisoni (Early Toarcian) and the lowermost Bifrons (middle Toarcian) ammonite zones were sampled for nannofossil study. The 157 m of sediments from the Brenha section correspond to the uppermost part of the lower Toarcian to the lower Aalenian. The 87 m of the Cabo Mondego section include the Speciosum, Meneghinii, Aalensis (Late Toarcian) and the Opalinum (Early Aalenian) ammonite zones. The three sections are tightly correlated by means of ammonite and nannofossil biostratigraphies, and by means of lithostratigraphy.

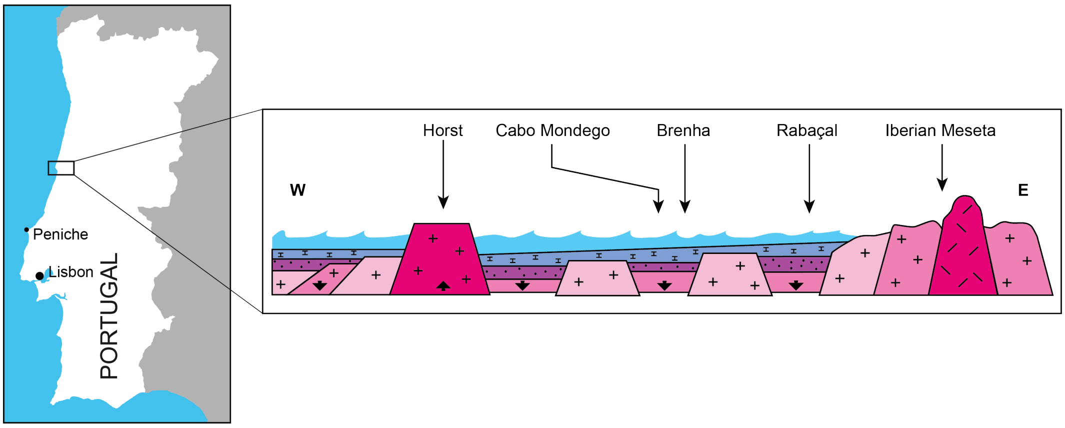


Figure 4 - Cross section of the Lusitanian Basin during the Toarcian, and sampled sections in the Coimbra and Figueira da Foz region.

2.2. The Causses Basin

In southern France, Jurassic sedimentation occurred in numerous interconnected shallow marine basins that were bordered by the Massif Central to the north and were open to the south in various degrees towards the Tethys Ocean (Harazim et al., 2012). Hemipelagic marly sedimentation started In the Causses Basin during the lower Pliensbachian, which is informally known in France as the Carixian. The lithological boundary between the Carixian and the Late Pliensbachian (Domerian) units is acknowledged by marls with some intercalated limestone beds. An abrupt facies transition occurred during the Earliest Toarcian with the onset of deposition of organic matter-rich shales belonging to the Schistes Cartons Formation. Such equivalent sedimentary rocks, as the Posidona Shales in Germany and the Jet Rock in the UK, can be traced throughout Europe (Howarth, 1962; Reitner and Urlichs, 1983). This interval contains organic-rich mudstones that are interbedded with two prominent limestone beds. On the top of the Schistes Cartons follows the Fontaneilles Formation, a monotonous marl succession of middle and Late Toarcian age in the Truc-de-Balduc (TBC) area. The upper part of the Toarcian is marked by a gradual transition into the Aalenian *Cancellophycus* facies, massive, sandy limestones with abundant bioturbation (Trümpy, 1983; Harazim et al., 2012).

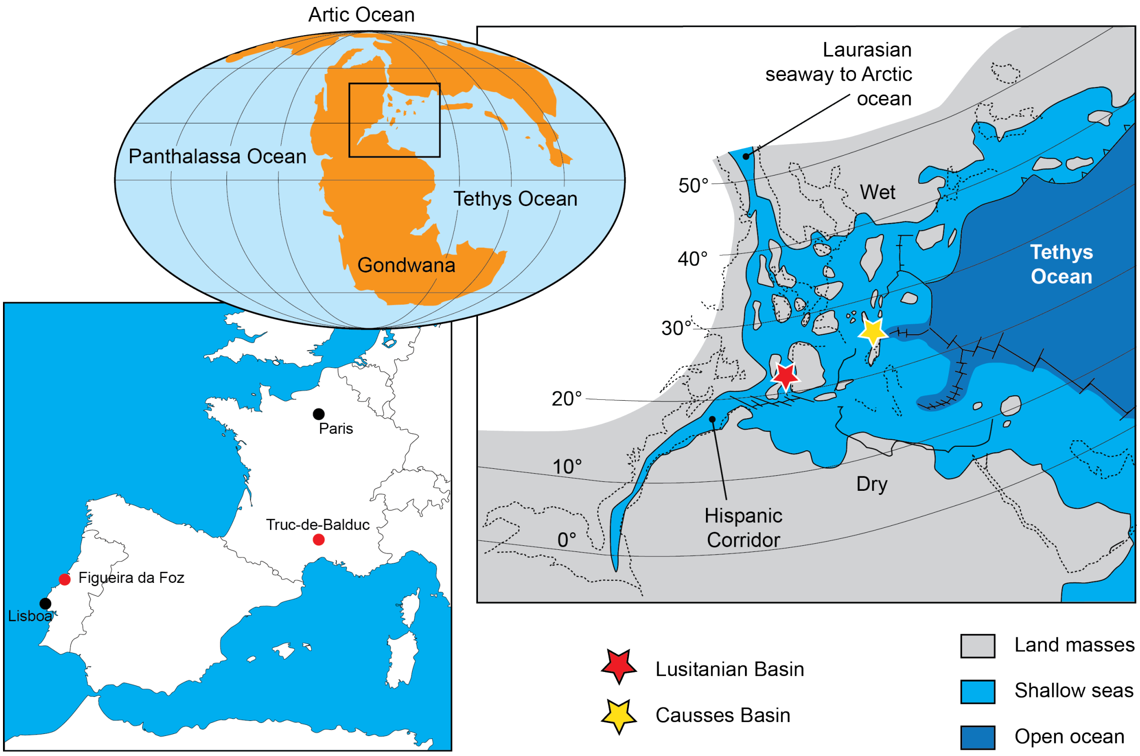


Figure 5 - Location of both studied basins during the Early Jurassic in western Tethys epicontinental sea (modified after Bassoulet et al., 1993).

The TBC section exposes Late Pliensbachian to Aalenian sedimentary rocks, and includes a complete succession of Toarcian beds. It is located on a small mountain 5 km southeast of the city of Mende, and belongs to the Causses Basin in south France (Fig. 5). During the Early Toarcian this was a small, partly enclosed, intracratonic basin in the western Tethys epicontinental sea, and was positioned at a palaeolatitude comprised between 25 and 30ºN. Bounded by Hercynian crystalline rocks, its morphology was largely controlled by the late Hercynian structural evolution (Trümpy, 1983). Subsidence was more pronounced in the central part of the basin and the Lower Jurassic succession thickness varies from its margins to its depocentre (Morard, 2004) (see Fig. 6).

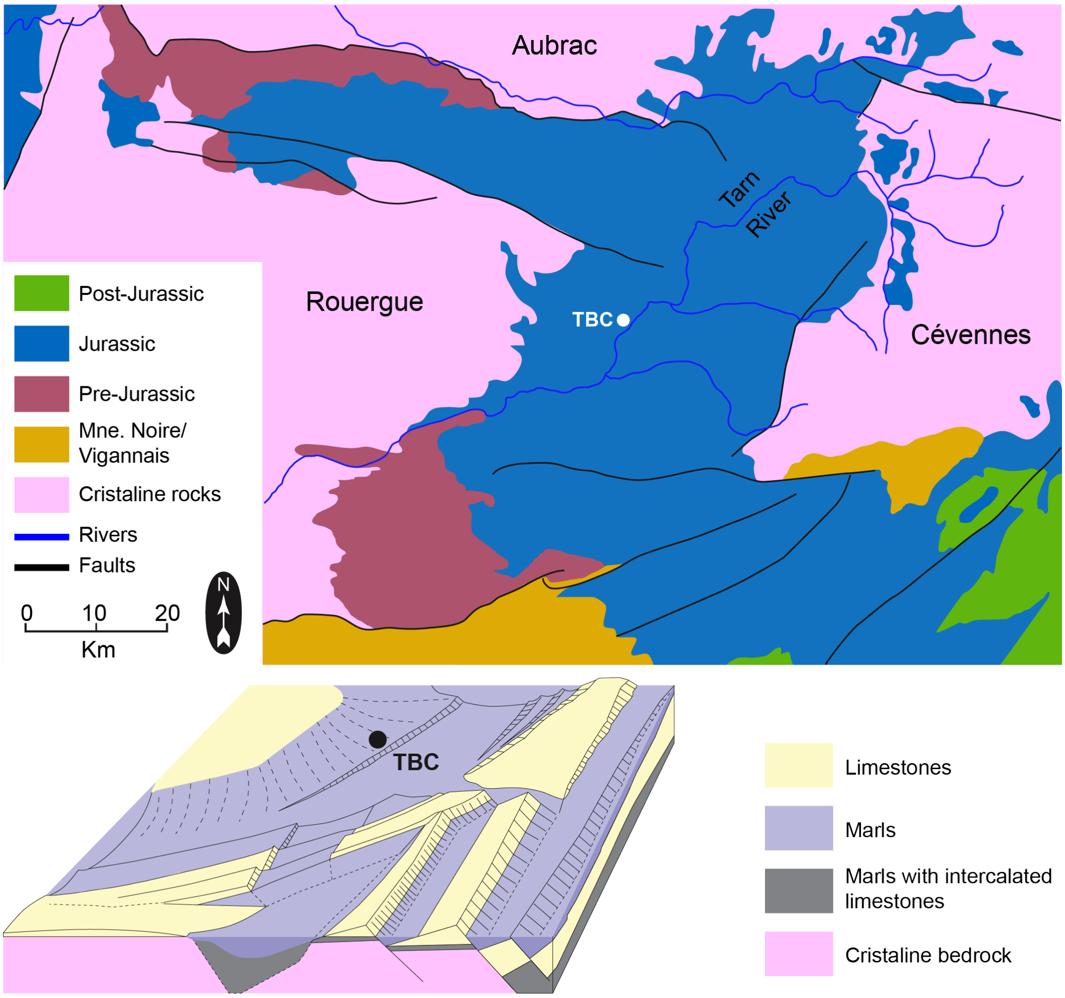


Figure 6 - Simplified geological map and 3-D diagram of the Causses Basin (modified after Trümpy, 1983) showing the location of Truc-de-Balduc.

In the TBC area, the Late Pliensbachian (*Pleuroceras spinatum* zone) is represented by a 12 m thick marly succession, followed by 12 m of black shales spanning from the *Dactylioceras tenuicostatum* to the *Harpoceras serpentinum* zone (Early Toarcian, Harazim et al., 2012). The Tenuicostatum zone is extremely reduced at this site, with approximately 0.3 m thick, whereas the Serpentinum zone appears to be fully represented. Alternating shales and marls mark the transition to the middle Toarcian and the Fontaneilles Formation (*Hildoceras bifrons* and *Haugia variabilis* zones). Due to vegetation cover, sampling at TBC was interrupted for approximately 30 m in upper Toarcian beds. The Bifrons zone is 17 m thick and ammonite zones above Bifrons are based on rather scarce ammonite finds. From this point up, marls dominate the Late Toarcian at TBC. The first occurrence of the ammonite *Pleydellia mactra* at ~57 m marks the boundary between middle and upper Toarcian beds (Elmi et al., 1994; Macchioni and Cecca, 2002) allowing the placing of the Late Toarcian *Pleydellia aalensis* zone. Compared with the underlying succession, fossil abundances decline in the Late Toarcian, possibly due to an enhanced sedimentation rate and hence dilution, whereas diversity remains high (Fürsich et al., 2001).

References

Bassoulet, J.P., Elmi, S., Poisson, A., Cecca, F., Bellion, Y., Guiraud, R., Baudin, F., 1993. Mid Toarcian. In: Dercourt, J., Ricou, L.E., Vrielynck, B. (Eds.) Atlas of Tethys Paleoenvironmental Maps. Becip-Franlab, Rueil-Malmaison, France, pp. 63-80.

Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical Paleoceanographic study of the Early Jurassic transcontinental Laurasian Seaway, Paleoceanography 16, 390-404.

Dera, G., Neige, P., Dommergues, J.-L., Brayard, A., 2011a. Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Global and Planetary Change 78, 92-105.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, 2000. Atlas Peri-Tethys, Palaeogeographical maps. CCGM/CGMW, Paris.

Dommergues, J.L., Mouterde, R., 1980. Modalités d'installation et d'évolution des harpocératinès (Ammonitina) au Domérien inférieur dans le Sud-Ouest de l'Europe. Geobios 13, 289-325.

Duarte, L.V., 2004. The geological heritage of the Lower Jurassic of Central Portugal: selected sites, inventory and main scientific arguments. Rivista Italiana di Paleontologia e Stratigrafia 110, 381-387.

Duarte, L.V., Soares, A.F., 2002. Litostratigrafia das séries margo-calcárias do Jurássico inferior da Bacia Lusitânica (Portugal). Comunicações do Instituto Geológico e Mineiro 89, 115-134.

Elmi, S., Gabilly, J., Mouterde, R., Rulleau, L. and Rocha, R.B., 1994. The European stage in Europe and in the Tethyan realm: divisions and correlations. Geobios, 27, 149-159.

Fürsich, F.T., Berndt, R., Scheuer, T., Gahr, M., 2001. Comparative ecological analysis of Toarcian (Lower Jurassic) benthic faunas from southern France and east-central Spain. Lethaia, 34, 169-199.

Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2012. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian-Toarcian). Sedimentology 60, 359-390.

Howarth, M.K., 1962. The Jet Rock Series and the Alum Shale Series of the Yorkshire coast. Proceedings of the Yorkshire Geological Society 33, 381-422.

Macchioni, F., Cecca, F., 2002. Biodiversity and biogeography of middle-late Liassic ammonoids: implications for the Early Toarcian mass-extinction. Geobios, 35, 165-175.

Morard, A., 2004. Les événements du passage Domérien-Toarcien entre Téthys occidentale et Europe du Nord-Ouest. Thèse, Université Lausanne, Géologie - Paléontologie, pp. 1-158.

Mouterde, R., Ruget, C., 1975. Esquisse de la paleogeographie du jurassique inférieur et moyen en Portugal. Bulletin de la Societe Geologique de France 14, 779-786.

Pinheiro, L.M., Wilson, R.C.L., Pena dos Reis, R., Whitmarsh, R.B., Ribeiro, A., 1996. In: Whitmarsh, R.B., Sawyer, D.S., Klus, A., Masson, D.G. (Eds.). The western Iberia margin: a geophysical and geological overview: Proceeding of the Ocean drilling Program, Scientific Results 149, pp. 3-23.

Reggiani, L., Mattioli, E., Pittet, B., Duarte, L.V., Veiga de Oliveira, L.C., Comas-Rengifo, M.J., 2010. Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian Basin, Portugal): a clue for palaeoenvironmental reconstructions. Marine Micropaleontology 75, 1-16.

Reitner, J., Urlichs, M., 1983. Echte Weichteilbelemniten aus dem Untertoarcium (Posidonienschiefer) Südwestdeutschlands. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 165, 450-465.

Trümpy, D.M., 1983. Le Lias Moyen et Supérieur des Grands Causses et de la région de Rodez: contributions stratigraphiques, sédimentologiques et géochimiques à la connaissance d'un bassin à sédimentation marneuse. Cahiers de l'Université, Université de Pau et des Pays de l'Adour 19, 1-363.

3. Material and methods

The studied material for the present work was attained by means of diverse origins. Already 139 rock samples from Rabaçal were available at the Laboratoire de Géologie de Lyon, whereas 130 samples from Brenha and 72 belonging to Cabo Mondego sections were collected during field work in the summer of 2012. As for the Truc-de-Balduc section, the 65 rock samples were kindly tendered by Bas Van de Schootbrugge from the Institute of Geosciences, Goethe University Frankfurt.

3.1. Sample preparation

In order to study the nannofossil assemblages, relatively high-resolution sampling was performed. Across the studied sections, a total of 406 samples were prepared, and besides the association composition also the absolute and relative abundance of calcareous nannofossils were investigated. The morphospecies taxonomic concept of Bown (1987, 1998), Mattioli (1996) and Mattioli et al. (2004) has been followed.

For palaeoecological purposes, the nannofossil quantification was performed using the random settling method determined after Geisen et al. (1999). The basic principle of this technique is the homogenous distribution onto a cover slide of calcareous nannofossils. The samples preparation started with the weighing of a small amount of powdered rock (~30 mg) that was dried and mixed with water that was oversaturated with respect to carbonates and with a basic pH, in a magnetic stirrer in order to obtain a homogeneous suspension. This suspension was then let settle on a cover slide in a settling box for 24 h after which the water was very slowly drained and the cover slide recovered, dried and permanently mounted on a microscope slide. Smear slides were studied with a Leica polarizing optical microscope at 1000x magnification. The absolute abundance of coccoliths was determined after the following equation:

$$X=\frac{N \cdot V}{m \cdot F \cdot S \cdot h}$$

where X is the number of nannofossils per gram of rock; N is the number of nannofossils counted in each sample; V is the water volume used to make the water-powder solution; m is the sample weighted and used to mix with water; F is number of fields of view counted; S is the area of each field of view; h is the height of the water column above the cover slides in the settling boxes.

At least 300 coccoliths were counted in every sample. All coccoliths with at least more than half of the specimen preserved have been included in the counting. The dinoflagellate cyst *Schizosphaerella* was tallied in the same number of fields of view as the 300 coccoliths were being recorded. According to Fatela and Taborda (2002) the counting of 300 specimens per sample is statistically robust to record all the species making up more than 1.7% of the total assemblage with a confidence level of 99.5%. Some Rabaçal samples where coccoliths were scarce and a 300 count was not achievable, at least 400 fields of view were scanned. The relative abundance of coccolith species was calculated after the overall coccolith assemblage. Conversely, the relative abundance of the nannolith *Schizosphaerella* was obtained after the total nannofossil assemblage so that it would be easier to compare the changes of these two discrete planktonic groups.

3.2. Stable isotopes

Besides determining seawater temperature changes from Jurassic marine sediments, long and short-term carbon and oxygen isotopes records for the Lower and Middle Jurassic have also been used to established global organic carbon budgets during OAE's and primary productivity reconstruction. However, one should bear in mind that carbon and oxygen isotope signals depend on several factors such as the global carbon and oxygen reservoirs, vital effects, age and source of water masses, thermodynamic fractionation at the sea-atmosphere boundary, and diagenesis (Saltzman and Thomas, 2012). Oxygen isotopic ratios are reported in delta (δ) notation relative to an internationally accepted standard such as SMOW (Standard Mean Ocean Water) and PDB (Peedee Belemnite) whereas carbon isotope ratios are solely relative to PDB. SMOW is a composite of seawater samples meant to approximate the average oxygen and hydrogen isotopic composition of seawater (Craig, 1961). Because the supply of SMOW has long been exhausted, VSMOW (Vienna SMOW) a new water standard analytically indistinguishable in $\delta^{18}O$ from SMOW was prepared and distributed.

3.2.1. Stable carbon isotopes

The variation in the $^{13}C/^{12}C$ ratio of total dissolved inorganic carbon (DIC, i.e., aqueous CO_2 + bicarbonate ion + carbonate ion) has long been well documented mainly through the study of marine carbonate bulk rocks. The distribution of carbon isotopes in the ocean ($\delta^{13}C$) is related to nutrient cycling within the water column and the biological productivity in the photic zone. In general, plants preferentially incorporate through photosynthesis light ^{12}C in their organic compounds (Maslin and Thomas, 2003), therefore leaving the surface waters enriched in heavier ^{13}C. Though less well known when compared to land plants, the photosynthetic reaction of marine phytoplankton renders $\delta^{13}C$ values from -10 to -32‰ (most lying between -17 and -22‰) depending upon seawater temperature (Sarmiento and Gruber, 2006). Hence, increasing bioproductivity in the photic zone leads to an increase of $\delta^{13}C$ in carbonates ions produced in surface waters. The contrast between surface and bottom waters $\delta^{13}C$ values is described as "internal fractionation" or biological pumping (Berger and Vincent, 1986; Marshall, 1992; Grossman, 1994). Oceans surface waters are thus characterized by more positive $\delta^{13}C$ values (~2.5 ‰) when compared to deep waters at approximately 3000 m (~0.5 ‰) (Kump, 1991; Holster et al., 1995). Ratios of stable carbon isotopes have therefore been used in many studies as proxies for sea surface primary productivity and water masses ventilation (e.g., Jenkyns and Clayton, 1986; Kump and Arthur, 1999; Jenkyns et al., 2002; Brand et al., 2003; Porter et al., 2014). This proxy has also been used in Jurassic sedimentary basins around the Iberian Peninsula (Tremolada et al., 2005; Hesselbo et al., 2007; Aguado et al., 2008; Suan et al., 2008, 2010; Ferreira et al., 2015).

Variations in oceanic $\delta^{13}C$ values are also influenced by atmospheric carbon circulation, as fractionation occurs through the exchange of CO_2 between the ocean-atmosphere interface. In fact, the fractionation depends on several factors such as sea-surface temperature, CO_2 exchange rate, and surface water residence time. The equilibrium fractionation between dissolved CO_2 and bicarbonate (DIC) is not achieved anywhere as surface waters are replaced too quickly. Actually, colder waters generally bear higher $\delta^{13}C$ values in DIC than warmer waters (Saltzman and Thomas, 2012). However, as colder surface waters invariably sink and ventilate the deep ocean, this effect called "the solubility pump" would thus result in a surface-to-bottom gradient where the DIC in surface waters would be isotopically lighter than deeper waters (Raven and Falkowski, 1999). But what we observe in present day oceans is the reverse, i.e., surface waters bear heavier $\delta^{13}C$ values by +2 to +3‰ than bottom waters, with the average whole ocean $\delta^{13}C$ value of total DIC of approximately 1‰ (Gruber et al., 1999; Sarmiento and Gruber, 2006). This vertical gradient is due to the biological activity in the upper photic layers, depleting it in ^{13}C from DIC. Below the photic zone though, $\delta^{13}C$ values are lower as organic matter sinks and isotopically light carbon dioxide from its remineralization is added to these waters (Raven and Falkowski, 1999; Sarmiento and Gruber, 2006). The concentration of nutrients (nitrate and phosphate) and isotopically light carbon derived from remineralization of organic matter increases accordingly with water-masses residence times in the deep ocean (Lynch-Stieglitz, 2003; Sarmiento and Gruber, 2006). In fact, when the net deposition of organic matter occurs globally, $\delta^{13}C$ values of dissolved inorganic carbon in the whole ocean increases, whereas contrariwise when there is net oxidation of organic matter globally, the $\delta^{13}C$ value of DIC in the whole ocean decreases (Saltzman and Thomas, 2012). Meaning that remineralization of organic matter in deeper waters causes the lowering in $\delta^{13}C$ of the total dissolved CO_2.

Another source of variations in marine $\delta^{13}C$ is the continental freshwater runoff. The CO_2 dissolved in ground water derives from organic matter degradation leading to very low $\delta^{13}C$ values in river and coastal waters especially close to major river inflows. The $\delta^{13}C$ fluvial runoff values based on dissolution of carbonates and oxidation of organic matter, exhibits values of up to -5 ‰ (Kump, 1991; Holster et al., 1995). Also the thermal dissociation of methane hydrates as been highlighted by several authors for short periods of the Jurassic, Cretaceous and Paleogene. The release of high amounts of isotopically light methane into the oceanic water column and therefore into the atmosphere, may have therefore led to a global shift of marine carbon isotope signatures to vigorously negative $\delta^{13}C$ values. Such negative carbon isotope excursions include the one during the Paleocene-Eocene Thermal Maximum at ~56 Ma (Kennet and Stott, 1991; Sluijs et al, 2007), and earlier events in the Cretaceous and during the late-Early Jurassic ~183 Ma Oceanic Anoxic Events (e.g., Jenkyns, 1985, 2010; Cohen et al., 2007; Hesselbo et al., 2000, 2007; Suan et al., 2008), besides the Permo-Triassic extinction event (e.g., Berner 2002; Retallack and Jahren, 2008). Though still under debate, the origin of these rapid and global negative excursions require a fast input of large amounts of isotopically light carbon into the ocean-atmosphere from a lithospheric source such as methane from dissociation of clathrates, as proposed for the Permo-Triassic by Erwin (1993) and for the Paleocene-Eocene by Dickens et al. (1995) and Matsumoto (1995), or even organic matter heated by volcanic intrusions (Svensen et al., 2004), or assorted combinations of oxidation of organic matter and hydrates (Zeebe et al., 2009; Dickens, 2011).

3.2.2. Stable oxygen isotopes

Seawater temperature and the water mass isotopic signature mainly determine the oxygen isotope composition recorded in biogenic carbonates and phosphates, i.e., fossils and microfossils, enabling the reconstruction of oceanic palaeothermometry. The $\delta^{18}O$ of authigenic sedimentary minerals depends on the precipitation temperature of surrounding waters and $\delta^{18}O$ of the oxygen source, whether it is coming from DIC, phosphate ions or dissolved silica. Whether carbonate tests from planktonic organisms like foraminifera, or benthic organisms like brachiopods shells are used, either surface or bottom water temperatures can de determined. Palaeotemperatures have been ascertained after the empirically derived equation of Epstein (1975) mostly based on mollusk shells, modified by Anderson and Arthur (1983):

$$T\ (^{o}C) = 16.0 - 4.14\ (\delta^{18}O_{shell} - \delta^{18}O_{sw}) + 0.13\ (\delta^{18}O_{shell} - \delta^{18}O_{seawater})^2$$

where $\delta^{18}O_{shell}$ is the isotopic composition of the calcite shell in ‰ relative to PDB standard, and $\delta^{18}O_{seawater}$ is the mean isotopic composition in ‰ of the global ocean. The modern mean value of surface seawater $\delta^{18}O_{seawater}$ is around 0‰ (VSMOW). This value can vary strongly with latitude in response to different evaporation/precipitation rates and is unknown for the Early Jurassic. Since the total melting of present polar icecaps would lower the $\delta^{18}O_{seawater}$ value to -1‰ (VSMOW), this is hence the value that is generally used for Jurassic palaeotemperature calculations, considering that no ice caps were present at that time (e.g., Gómez et al., 2008; Suan et al., 2008; Dera et al., 2009; Krencker et al., 2014).

The application of oxygen isotopes requires rapid changes in the fossil $\delta^{18}O$ as a response to rapid changes in temperature and/or global seawater $\delta^{18}O$ composition, the latter resulting from shifts in the glacial ice volume. During glacial periods, the storage of ^{16}O-enriched water as glacial ice results in ^{18}O enrichment in seawater and consequently in marine authigenic minerals. Hence, lower temperatures during glacial intervals bolster $\delta^{18}O$ values triggered by glacial ice accumulation. Deglaciation on the other hand, flushes ^{16}O-enriched water into the oceans, therefore lowering global seawater $\delta^{18}O$ (Grossman, 2012). Marine authi- and biogenic carbonates with lower $\delta^{18}O$ values are thus interpreted as had been produced during interglacial periods.

In general, the oxygen isotope ratio in seawater is linked to the hydrological cycle driven by evaporation, transport of atmospheric water vapor, and the return of fresh water to the ocean via precipitation and continental runoff. Furthermore, the distribution of $\delta^{18}O$ in the oceans also depends on advection and mixing of water masses from different regions (Rohling and Cooke, 1999). Besides $\delta^{18}O$ values can vary locally in marginal marine environments and epicontinental seas, thus complicating palaeotemperature reconstructions, also non-equilibrium isotope fractionation in biogenic carbonates, a.k.a. "vital effect", can be a problem. The vital effect phenomena is closely linked with taxonomy and physiology, and adjustment factors have sometimes to be used on $\delta^{18}O$ results from corals (Leder et al., 1996) and benthic foraminifera (Shackleton, 1974; Zachos et al., 2001). Conversely, mollusks, brachiopods, sclerosponges and many small foraminifera typically segregate their skeletons out of oxygen isotopic equilibrium with seawater (González and Lohmann, 1985; Grossman, 1987; Wefer and Berger, 1991; Swart et al., 1998; Brand et al., 2003). As for coccolithophores, Hermoso et al. (2009) showed that Toarcian coccoliths displayed the same $\delta^{13}C$ magnitude of bulk carbonate, being the observed biogenic offset probably related to the vital effect phenomena. Actually, Dudley and Nelson (1994) have shown that when a vital effect adjustment based on in-vitro cultures of coccolithophorids, which segregate their coccoliths out of equilibrium with seawater, is applied to the $\delta^{18}O$ of nannofossils, the resulting values are similar to those of planktic foraminifera.

Oxygen isotopic composition of fossils is particularly susceptible to diagenesis. As diagenetic water bears abundant oxygen derived from H_2O available for isotopic exchange, diagenesis resistant fossils should thus be favoured in palaeotemperature studies. Low-magnesium calcite fossils such as brachiopods shells are more resilient to diagenetic processes than those made of magnesium rich, or aragonite shells, therefore persisting longer in the geological record without significant recrystallization. Actually, articulate brachiopod shells are favoured in oxygen palaeothermometric works since they are abundant, diagenetically resilient and possess a wide chronostratigraphic distribution, ranging from the Cambrian to Recent (Compston, 1960; Lowenstam, 1961; Veizer et al., 1986; Popp et al., 1986; Grossman, 1994). Moreover, being benthic and having a sessile life mode, ensures *in situ* bottom water palaeotemperatures. In fact, when making isotopic studies of fossils, complications can arise with nektonic taxa such as belemnites, conodonts and fishes, since they can live whether in surface or deep waters, besides accrete skeletal elements far from their site of deposition. The resistance of brachiopods to diagenesis derives from their calcitic mineralogy, low magnesium content, relative large size and thickness, and particularly their dense microstructure, rendering typically 2-3‰ higher $\delta^{18}O$ values, i.e., a colder signal, then the diagenetically modified bulk carbonate (Veizer et al., 1999; Mii et al., 1999).

Since seawater temperatures vary with season, depth and latitude, it is important to understand the depositional environment and palaeoecology of fossils one is working with, as $\delta^{18}O$ values will depend upon their palaeogeographic distribution, their habitat depth and their growth season. Though fossils retrieved from epicontinental seas usually display lower $\delta^{18}O$ values as they may reflect oxygen exchange with ^{18}O-depleted meteoric water (Grossman, 2012), Early Jurassic studies are restricted to sediments from continental margins and epicontinental seas such as the Lusitanian and Causses Basins as no deep-sea floor older than ~180 Ma is available in today's oceans.

3.2.3. Stable isotopes analyzed in this work

A total of 50 brachiopods shells taken from Cabo Mondego and Rabaçal sections were analyzed for stable carbon and oxygen isotopes. Analyses were performed by Dr. Jorge Spangenberg at the Institute of Earth Surface Dynamics of the University of Lausanne, using a Thermo Fisher Scientific (Bremen, Germany) Gas Bench II carbonate preparation device connected to a Delta Plus XL isotope ratio mass spectrometer. The CO_2 extraction was done by reaction of 100-200 µg of powdered rock with anhydrous phosphoric acid at 70°C. The stable carbon and oxygen isotope ratios are reported in the delta (δ) notation as the per mil (‰) deviation relative to the Vienna Pee Dee belemnite standard (VPDB). The standardization of the $\delta^{13}C$ and $\delta^{18}O$ values relative to the international VPDB scale was done by calibration of the reference gases and working standards with IAEA standards. Analytical uncertainty (1σ), monitored by replicate analyses of the international calcite standard NBS-19 and the laboratory standards Carrara Marble was not greater than ±0.05‰ for $\delta^{13}C$ and ±0.1‰ for $\delta^{18}O$. The isotopic composition of the measured samples is expressed as $\delta^{18}O$ or $\delta^{13}C$ according the following equation:

$$\delta_{sample}\,(‰) = \left[\frac{R_{sample} - R_{standard}}{R_{standard}}\right] \times 1000$$

where R represents the ratio between $^{18}O/^{16}O$ or $^{13}C/^{12}C$, and δ_{sample} represents the parts per thousand difference (per mil) between the sample R ratio and that of the international VPDB standard carbonate. See Krauskopf and Bird (1995) for further information and detailed description on mass spectrometry and sample preparation.

3.3. Data analysis and statistics

Multivariate analysis is used here to compare global coccolith assemblages where variables (i.e., assemblages) with correlative linear behaviour can be pointed out and their importance hierarchized. All statistics and data analysis of calcareous nannofossil assemblages performed in this work, were carried out using the software package PAST 3.01. The principal components analysis (r-mode) was used to illustrate the relationship between samples and variables, i.e., the different species. This analytical method allow to reduce a great number of variables to a smaller number of independent eigenvectors (factors) that in turn, would explain a large part of the total variance of the dataset. In turn, the factor-loading matrix that is also computed with this method, shows the importance of a species within each of the factors, or assemblages. Whether the loadings are >0 or <0 indicates a positive or negative relationship within each species or group of species, for each of the factors. The factors scores display the stratigraphic evolution for each factor through the studied sections, thus showing the importance of each variable through time.

In the same way that the diameter of a sphere is an index of its volume but is not itself the volume, diversity indices like the Shannon entropy index (H) are not themselves diversities, but rather indices of diversity. For example, the true diversity associated with a Shannon index of 4.5 is exp(4.5) = 90 effective species, in the way that 90 is the number of equally common species required to give a particular value of an index. This is the true diversity of the community in question. Nonetheless, the Shannon diversity index is herein used as a species diversity measure based on the proportional abundance of each species. The index, which is the negative sum of each taxon proportional abundance multiplied by the log of its proportional abundance, is a measure of the amount of information (entropy) in the system and is positively correlated with species richness and evenness (distribution of individuals over species), giving more weight per individual to rare than common species (Shannon and Weaver, 1949; Hill et al., 2003). The Shannon index was determined for each of the sections separately according to the following equation:

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

where *i* is the a given species, *s* the total number of species, i.e., species richness, and P_i is the relative abundance of a given species. Irrespective of its faults, when compared to other diversity indexes like the Species Richness, the Shannon index seems a useful general diversity index that is influenced by both richness and evenness and is more sensitive to changes in abundance of the rare groups. The meaning of the number is more understandable when expressed as the exponential. The conversion of H' to a more useful and comprehensible number (of species) by expressing this index as the exponential $e^{H'}$ ($10^{H'}$ with $\log_{10}$ and $2^{H'}$ with $\log_2$) since it represents the number of equally common taxa required to reach the same value of H', is the key to a unified and intuitive interpretation of diversity (Hill et al., 2003; Jost et al., 2006). Actually, the Species Richness is the least informative and most imprecise diversity index, in the sense that it is more subject to random variation than any other index as it does not distinguish between one or a million individuals of a given species.

Other simple statistic parameters such as the mean, geometric mean, standard deviation, median, 25th and 75th percentile were estimated during the biometry work of *Lotharingius* coccoliths. In order to infer and measure the strength of any relationship between the coccoliths dimensional variables, the coefficient of correlation (r) and coefficient of determination (r^2) between these coccolith parameters were calculated. Other inferential statistics tests were used in order to test the equality of means of coccoliths lengths. Such tests include the parametric univariate analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) post-hoc test.

The basic idea of ANOVA is to calculate the observations mean value within each group and then compare the variance among these means to the average variance within each group. Under the null hypothesis that the observations in the different groups all have the same mean, the weighted among-group variance will be the same as the within-group variance. As the means get further apart, the variance among the means increases. The test statistic is thus the ratio of the variance among means divided by the average variance within groups, or Fs. This statistic has a known distribution under the null hypothesis, so the probability of obtaining the observed Fs under the null hypothesis can be calculated (McDonald, 2008).

When the analysis of variance renders a significant result, this indicates that at least one group differs from the other groups. As so, in order to analyze the pattern of differences between means, the ANOVA was followed by specific comparisons. The most commonly used involves comparing two means, the so-called "pairwise comparisons". An easy and frequently used pairwise comparison technique is the HSD developed by Tukey. The main idea of this test is to compute the honestly significant difference between two means using a statistical distribution defined by Student (*t*) and called the *q* distribution. This distribution gives the exact sampling distribution of the largest difference between a set of means originating from the same population. All pairwise differences are then evaluated using the same sampling distribution used for the largest difference. (Abdi and Williams, 2010). With this test, all pairs of samples which are significantly different, considering a significance level of 0.05, were identified, as this method applies simultaneously to the all set of pairwise comparisons.

Also the maximum-likelihood method Mixture Analysis was used. This method aims to identify the existence of two or more distinct distributions in an initially pooled sample and estimate their descriptive parameters. One or more group model comparison can be obtained by comparing their Akaike Information Criterion (AIC), which is a way to select a model from a set of models. A minimum value for AIC indicates that we have chosen the number of groups that produces the best fit without overfitting (Akaike, 1974).

References

Adbi, H., Williams, L.J., 2010. Tukey's Honestly Significant Difference (HSD) Test. In: Salkind, N. (Ed.) Encyclopedia of Research Design, Thousanf Oaks.

Aguado, R., O´Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the Western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Marine Micropaleontology 68, 268-285.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19, 716-723.

Anderson, T.F., Arthur, M.A., 1983. Stable isotopes of oxygen and carbon and their applications to sedimentologic and palaeontological problems. Econ. Palaeontol. Mineral. Short Course 10, 151.

Berger, W.H., Vincent, E., 1986. Deep-sea carbonates: Reading the carbon isotope signal. Geologische Rundschau 75, 249-269.

Berner, R.A., 2002. Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modeling. Proceedings of the National Academy of Sciences USA. 99, 4172-4177.

Bown, P.R., 1987. Taxonomy, evolution and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. Special Papers in Palaeontology 38, 1-118.

Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.) Calcareous Nannofossils Biostratigraphy. British Micropalaeontological Society Publication Series. Kluver Academic Publishers, Cambridge, pp. 34-85.

Brand, U., Logan, A., Hiller, N., Richardson, J., 2003. Geochemistry of modern brachiopods: applications and implications for oceanography and paleoceanography. Chemical Geology 198, 305-334.

Cohen, A.S., Coe, A.L., Kemp, D.B., 2007. The Late Palaeocene-Early Eocene and Toarcian (Early Jurassic) carbon isotope excursions: A comparison of their time scales, associated environmental changes, causes and consequences. Journal of the Geological Society 164, 1093-1108.

Compston, W., 1960. The carbon isotopic composition of certain marine invertebrates and coals from the Australian Permian. Geochimica et Cosmochimica Acta 18, 1-22.

Craig, H., 1961. Standard for reporting concentrations of deuterium and oxygen-18 in natural waters. Science 133, 1833-1834.

Dera, G., Pellenard, P., Neige, P., Deconinck, J.F., Puceat, E., Dommergues, J.L., 2009. Distribution of clay minerals in Early Jurassic Peritethyan seas: Palaeoclimatic significance inferred from multiproxy comparisons. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 39-51.

Dickens, G.R., 2011. Down the Rabbit Hole: Toward appropriate discussion of methane release from gas hydrate systems during the Paleocene- Eocene thermal maximum and other past hyperthermal events. Climates of the Past 7, 831-846.

Dickens, G.R., O'Neil, J.R., Rea, D.K., Owen, R.M., 1995. Dissociation of oceanic methane hydrate as a cause of the carbon isotope excursion at the end of the Paleocene. Paleoceanography 10, 965-971.

Dudley, W.C., Nelson, C.S., 1994. The influence of non-equilibrium isotope fractionation on the Quaternary calcareous nannofossil stable isotope signal in the southwest Pacific Ocean DSDP site 594. Marine Micropaleontology 24, 3-27.

Geisen, M., Bollman, J., Herrle, J.O., Mutterlose, J., Young, J.R., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437-442.

Epstein, S., Buchsbaum, R., Lowenstam, H.A., Urey, H.C., 1975. Revided carbonate-water isotopic temperature scale. Geological Society of America Bulletin 64, 1315-1326.

Erwin, D.H., 1993. The Great Paleozoic Crisis: Life and Death in the Permian. Columbia University Press, p. 327.

Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil assemblages. Marine Micropaleontology 45, 169-174.

Ferreira, J., Mattioli, E., Pittet, B., Cachão, M., Spangenberg, J.E., 2015. Palaeoecological insights on Toarcian and lower Aalenian calcareous nannofossils from the Lusitanian Basin (Portugal). Palaeogeography, Palaeoclimatology, Palaeoecology 436, 245-262.

Gómez, J.J., Goy, A., Canales, M.L., 2008. Seawater temperature and carbon isotope variations in belemnites linked to mass extinction during the Toarcian (Early Jurassic) in Central and Northern Spain. Comparison with other European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 258, 28-58.

González, L.A., Lohmann, K.C., 1985. Carbon and oxygen isotopic composition of Holocene reefal carbonates. Geology 13, 811-814.

Grossman, E.L., 1987. Stable isotopes in modern benthic foraminifera study of vital effect. Journal of Foraminiferal Research 17, 48-61.

Grossman, E.L., 1994. The carbon and oxygen isotope record during the evolution of Pangea: Carboniferous to Triassic. In: Klein, G.D. (Ed.) Pangea: Paleoclimate, Tectonics, and Sedimentation During Accretion, Zenith, and Breakup of a Supercontinent, Vol. 288, pp. 207-228. Geological Society of America Special Paper, Boulder, Colorado.

Grossmann, E.L., 2012. Oxygen Isotope Stratigraphy. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.) The Geologic Time Scale 2012, Vol. 1, Elsevier, pp. 181-206.

Gruber, N., Keeling, C.D., Bacastow, R.B., Guenther, P.R., Lueker, T.J., Wahlen, M., Meijer, H.A.J., Mook, W.G., Stocker, T.F., 1999. Spatio-temporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. Global Biogeochemical Cycles 13, 307-335.

Hermoso, M., Le Callonec, L., Minoletti, F., Renard, M., Hesselbo, S.P., 2009. Expression of the Early Toarcian negative carbon-isotope excursion in separated carbonate microfractions (Jurassic, Paris Basin). EPSL 277, 194-203.

Hesselbo, S.P., Gröcke, D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Morgans-Bell, H.S., Green, O.R., 2000. Massive dissociation of gas hydrate during a Jurassic oceanic event, Nature 406, 392-395.

Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V., Oliveira, L.C.V., 2007. Carbon-isotope record of the Early Jurassic (Toarcian) Oceanic Anoxic Event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). EPSL 253, 455-470.

Hill, T.C.J., Walsh, K.A., Harris, J.A., Moffett, B.F., 2003. Using ecological diversity measures with bacterial communities. FEMS Microbiology Ecology 43, 1-11.

Holster, W.T., Magaritz, M., Ripperdan, R.L., 1995. Global isotopic events. In: Walliser, O.H. (Eds.) Global events and eventstratigraphy in the Phanerozoic, pp. 63-88. Springer-Verlag, Berlin/Heidelberg.

Jenkyns, H.C., 1985. The Early Toarcian and Cenomanian-Turonian anoxic events in Europe: Comparisons and contrasts. International Journal of Earth Sciences 74, 505-518.

Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. Geochemistry, Geophysics, Geosystems 11, Q03004.

Jenkyns, H.C., Clayton, C.J., 1986. Black shales and carbon isotopes in pelagic sediments from the Tethyan Lower Jurassic. Sedimentology 33, 87-106.

Jenkyns, H.C., Jones, C.E., Gröcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. Journal of the Geological Society 159, 351-372.

Jost, L., 2006. Entropy and diversity. Oikos, 113, 363-375.

Kennett, J.P., Stott, L.D., 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. Nature 353, 225-229.

Krauskopf, K.B., Bird, D.K., 1995. Introduction to geochemistry. McGraw-Hill International Editions, pp. 241-272.

Krencker, F.N., Bodin, S., Hoffmann, R., Suan, G., Mattioli, E., Kabiri, L., Föllmi, K.B., Immenhauser, A., 2014. The middle Toarcian cold snap: Trigger of mass extinction and carbonate factory demise. Global and Planetary Change 117, 64-78.

Kump, L.R., 1991. Interpreting carbon-isotope excursions: Strangelove oceans. Geology 19, 299-302.

Kump, L.R., Arthur M.A., 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. Chemical Geology 161, 181-198.

Leder, J.J., Swart, P.K., Szmant, A.M., Dodge, R.E., 1996. The origin of variations in the isotopic record of scleractinian corals: 1. Oxygen. Geochimica et Cosmochimica Acta 60, 2857-2870.

Lowenstam, H.A., 1961. Mineralogy, O^{18}/O^{16} ratios, and strontium and magnesium contents of recent and fossil brachiopods and their bearing on the history of the oceans. Journal of Geology 69, 241-260.

Lynch-Stieglitz, J., 2003. Tracers of Past Ocean Circulation. Treatise on Geochemistry 6, 433-451.

Marshall, J.D., 1992. Climatic and oceanographic isotopic signals from the carbonate rock records and their preservation. Geological Magazine 129, 143-160.

Maslin, M.A., Thomas, E., 2003. Balancing the deglacial global carbon budget: The hydrate factor. Quaternary Science Reviews 22, 1729-1736.

Mattioli, E., 1996. New Calcareous Nannofossil species from the Early Jurassic of Tethys. Rivista Italiana di Paliontoligia e Stratigrafia 102, 397-412.

Mattioli, E., Pittet, B., Young, J., Bown, P.R., 2004. Biometric analysis of Pliensbachian-Toarcian (Lower Jurassic) coccoliths of the family *Biscutaceae*: intra- and interspecific variability versus palaeoenvironmental influence. Marine Micropaleontology 52, 5-27.

Matsumoto, R., 1995. Causes of the $\delta^{13}C$ anomalies of carbonates and a new paradigm “gas hydrate hypothesis”. Journal of the Geological Society of Japan 101, 902-924.

McDonald, J.H., 2008. Handbook of Biological Statistics. University of Delaware. Sparky House Publishing.

Mii, H.S., Grossman, E.L., Yancey, T.E., 1999. Carboniferous isotope stratigraphies of North America: Implications for Carboniferous paleoceanography and Mississippian glaciation. Geological Society of America Bulletin 111, 960-973.

Popp, B.N., Anderson, T.F., Sandberg, P.A., 1986. Brachiopods as indicators of original isotopic compositions in some Paleozoic limestones. Geological Society of America Bulletin 97, 1262-1269.

Porter, S.J., Smith, P.L., Caruthers, A.H., Hou, P., Gröcke, D.R., Selby, D., 2014. New high resolution geochemistry of Lower Jurassic marine sections in western North America: A global positive carbon isotope excursion in the Sinemurian? EPSL 397, 19-31.

Raven, J.A., Falkowski, P.G., 1999. Oceanic sinks for atmospheric CO2. Plant, Cell and Environment 22 6, 741-755.

Retallack, G.J., Jahren, A.H., 2008. Methane release from igneous intrusion. The Journal of Geology of coal during Late Permian extinction events 116, 1-20.

Rohling, E.J., Cook, S., 1999. Stable Oxygen and Carbon Isotopes in Foraminiferal Carbonate Shells. In: Gupta, B.K.S. (Eds.) Modern Foraminifera, Kluwer Academic Press, pp. 239-258.

Saltzman, M.R., Thomas, E., 2012. Carbon Isotope Stratigraphy. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.) The Geologic Time Scale 2012, Vol. 1, Elsevier, pp. 207-232.

Sarmiento, J.L., Gruber, N., 2006. Ocean Biogeochemical Dynamics. Princeton University Press, Princeton NJ (USA), pp. 503.

Shackleton, N.J., 1974. Attainment of isotopic equilibrium between ocean water and the benthonic foraminifera genus Uvigerina: Isotopic changes in the ocean during the last glacial. Centre National de la Recherche Scientifique Colloques Internationaux 219, 203-209.

Shannon, C.E., and Weaver, W., 1949, The Mathematical Theory of Communication, University of Illinois Press, Urbana, Illinois.

Sluijs, A., Bowen, G.J., Brinkhuis, H., Lourens, L.J., Thomas, E., 2007. The Palaeocene-Eocene Thermal maximum super greenhouse: Biotic and geochemical signatures, age models and mechanisms of global change. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), Deep Time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies. The Micropalaeontological Society, Special Publications, The Geological Society, London, pp. 323-351.

Suan, G., Mattioli, E., Pittet, B., Mailliot, S., Lécuyer, C., 2008. Evidence for major environmental perturbation prior to and during the Toarcian (Early Jurassic) oceanic anoxic event from the Lusitanian Basin, Portugal. Paleoceanography 23, PA1202.

Suan, G., Mattioli, E., Pittet, B., Lécuyer C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. EPSL 290, 448-458.

Svensen, H., Planke, S., Malthe-Sorenssen, A., Jamtveit, B., Myklebust, R., Rasmussen-Eidem, T., Rey, S.S., 2004. Release of methane from a volcanic basin as mechanism for initial Eocene global warming. Nature 429, 542-545.

Swart, P.K., Moore, M., Charles, C., Bohm, F., 1998. Sclerosponges may hold new keys to marine paleoclimate. Eos 79, 633-636.

Tremolada, F., van de Schootbrugge, B., Erba, E., 2005. Early Jurassic schizosphaerellid crisis in Cantabria, Spain: Implications for calcification rates and phytoplankton evolution across the Toarcian oceanic anoxic event. Paleoceanography 20, 1-11.

Veiga de Oliveira, L.C., Dino, R., Duarte, L.V., Perilli, N., 2007. Calcareous Nannofossils and Palynomorphs From Pliensbachian-Toarcian Boundary in Lusitanian Basin, Portugal. Revista Brasileira de Paleontologia 10, 5-16.

Veizer, J., Ala, D., Azmy, K., Bruckschen, P., Buhl, D., Bruhn, F., Carden, G.A.F., Diener, A., Ebneth, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O.G., Strauss, H., 1999. $^{87}Sr/^{86}Sr$, $\delta^{13}C$ and $\delta^{18}O$ evolution of Phanerozoic seawater. Chemical Geology 161, 59-88.

Veizer, J., Fritz, P., Jones, B., 1986. Geochemistry of brachiopods e oxygen and carbon isotopic records of Paleozoic oceans. Geochimica et Cosmochimica Acta 50, 1679-1696.

Wefer, G., Berger, W.H., 1991. Isotope paleontology e growth and composition of extant calcareous species. Marine Geology 100, 207-248.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686-693.

Zeebe, R.E., Zachos, J.C., Dickens, G.R., 2009. Carbon dioxide forcing alone insufficient to explain Palaeocene-Eocene Thermal Maximum warming. Nature Geoscience 2, 576-580.

4. Biostratigraphy

"Reviewing Toarcian calcareous nannofossil biostratigraphy in western Tethys"

[*To be submitted to Journal of Micropalaeontology*]

Keywords: Biostratigraphy, Causses Basin, Lusitanian Basin, Nannofossil, Toarcian

ABSTRACT

This work reviews and updates the calcareous nannofossil biostratigraphy for the Toarcian in western Tethys based on two sections from west Portugal and south France. Nannofossil bioevents were calibrated with ammonite biostratigraphy in both sections whenever they existed. In Portugal though, also lithostratigraphic correlation was used to link the three studied sections building up the complete Toarcian sequence. The high-resolution sampling gathered from both sections allowed estimations and reproducibility of single events. As result, 18 main bioevents based on diagenesis resistant and common taxa, are recognized. A revised and updated biostratigraphic scheme for the western Tethys Toarcian age is henceforth proposed. The proposed biostratigraphic scheme is then compared to previous schemes built for Portugal, NW Europe and central Italy. Though several events are reproducible in various regions and Tethyan provinces, apparent diachroneity of some events seems to derive from different ammonite biostratigraphies applied in different regions. Boundaries between lower-middle, middle-upper Toarcian are acknowledged through synchronous nannofossil events in both basins. Moreover, Lower-Middle Jurassic boundary has been acknowledged by means of two robust bioevents.

Introduction

Two major palaeogeographic provinces are recognized in the European Jurassic. Gradual faunal and floral differences in biological groups such as ammonites (Dommergues et al., 2009; Dera et al., 2011), brachiopods (Vörös, 2005, 2014), bivalves (Liu et al., 1998), foraminifera (Ruban and Tyszka, 2005), ostracods (Arias, 2007; Arias and Whatley, 2005, 2009; Arias, 2013), dinoflagellate cysts (Bucefalo Palliani and Riding, 2003) and calcareous nannoplankton (Bown, 1987; Mattioli et al., 2008; Reggiani et al, 2010) characterized two western Tethyan regions, namely the Boreal and south Tethyan realms. In fact, ammonite assemblages vary both qualitatively and quantitatively between Mediterranean and Boreal provinces (Dera et al., 2011). Though ammonite recovery can be scarce in some lithotypes and particular areas due to differential preservation and provincialism, the Jurassic chronostratigraphy is based on ammonite biostratigraphy. This results in partial correlations between different palaeogeographic realms and hampers the calibration of other fossil groups. Moreover, cephalopods are sometimes rare and discontinuously distributed hence ammonite biostratigraphic dating is often related to discrete horizons rather than continuous intervals (Cope, 1994; Ruban, 2013). Also, Baudin (1989) and Wignall et al. (2005), using ammonite biostratigraphy, observed that organic matter-rich levels and the associated isotopic event are not fully synchronous between the northern and southern parts of the Tethys Ocean.

Unlike nannofossil zones, which bear a continuous and contiguous nannofossiliferous record in marine sediments, ammonite zones are established based on the vertical range of index species, even if this record is sometimes absent throughout the sedimentary succession. Indeed Local Range Zones, (e.g., Polymorphum, Semicelatum and Tenuicostatum) either Total or Partial, are the most common practice in Jurassic ammonite stratigraphy, and the index species appears at the base of the nominal zone (Cope, 1994). In fact, due to the discontinuous and non-adjacent nature of ammonite Range Zones, Lower Jurassic ammonite zonation is often established through Concurrent or Interval Zones, therefore rendering diachronic FO and LO for a given index ammonite species. In order to overcome the ammonite biostratigraphic incompleteness issues and limitations when using ammonite Interval Zones, Mailliot et al. (2006) used the ubiquitous nannofossil record to ascribe Unitary Associations, which are similar to Oppel Zones, and precisely correlate and date the T-OAE in western Tethys. The biostratigraphic potential of calcareous nannofossils is indeed quite high in the Lower and Middle Jurassic, due to their rapid evolutionary rates and to their common and continuous occurrence in marine sediments. Although diagenesis modifies calcareous nannoflora and strong dissolution and/or overgrowth can partially or totally destroy the most delicate taxa the common occurrence of diagenesis-resistant forms provides a good stratigraphic resolution (Mattioli and Erba, 1999).

Since Mattioli and Erba (1999) no new biozonation schemes have been proposed for the Jurassic, although in the past decade some works have addressed the biostratigraphy in various Tethyan regions (e.g., Aguado et al., 2008; Boomer et al., 2009; Fraguas et al., 2012, 2014; Sandoval et al., 2012; Mattioli et al., 2013). Bown (1996) and de Kænel et al. (1996) summarized the nannofossil biozonations available for different areas, but with limited data available for the Tethyan realm. The more recent syntheses and those commonly used in the literature are those from de Kænel et al. (1996) for western Portugal, Bown and Cooper (1998) for NW Europe and Mattioli and Erba (1999) for central Italy. The first studies of Lower Jurassic calcareous nannofossils from the Lusitanian Basin are from Hamilton (1977; 1979). Later Bown (1987) and de Kænel and Bergen (1993) studied the nannofossil content from the Brenha section. The Portuguese succession of nannofossil events ranging from Late Sinemurian to Callovian were acknowledged by Bergen (unpublished data) and reported by the synthesis work of de Kænel

(1996) and Bown and Cooper (1998). Recent works however, were made in the Iberian Peninsula addressing the Pliensbachian and Toarcian nannofossil biostratigraphy (Perilli, 2000; Perilli et al., 2004; Perilli and Duarte, 2006; Perilli et al., 2009), though the taxonomy adopted by the previous authors is somehow different with respect to the one followed here. Actually, over the past years some taxonomic works based on biometric studies of Jurassic coccoliths have been published. As a result, the taxonomy of the genera *Similiscutum/Biscutum* (de Kænel and Bergen, 1996; Mattioli et al., 2004), *Lotharingius* (Mattioli, 1996; Fraguas and Young, 2011), *Crepidolithus* (Suchéras-Marx et al., 2010; Fraguas and Erba, 2010), *Discorhabdus* (López-Otálvaro et al., 2012), and *Watznaueria* (Giraud et al., 2006) have been partly revised. Such a revision has profound implication on biostratigraphy, as the range of newly defined taxa should thus be precisely ascertained.

Most of nannofossil biostratigraphic studies were carried out in NW European sections, namely England, Germany and Northern France (e.g., Bown et al., 1988; Bown, 1996), or Tethyan sections (e.g., Cobianchi, 1992; Lozar, 1992, 1995; Mattioli and Erba, 1999). The present work focuses on the Lusitanian Basin, which was a connecting seaway between NW Europe and south Tethyan water masses. This work therefore aims to refine and update the Toarcian nannofossil biostratigraphy for the Lusitanian Basin and to contribute with a biozonation scheme for the southern France Toarcian section in the Causses Basin.

Geological settings

The Lusitanian Basin was a small, narrow North-South elongated basin, located on the occidental side of the Iberian Massif and bounded to the west by several basement horsts (Fig. 7). This basin is one of the several rift-related peri-Tethyan Mesozoic basins whose origin is related to the opening of the Atlantic Ocean (e.g., Pinheiro et al., 1996; Alves et al., 2002). During this time interval, deposition in the Lusitanian Basin took place on a northwesterly dipping, low-energy marine carbonate ramp (Duarte, 2007), where the maximum depth of the water column should not have exceeded 200 m (Bjerrum et al., 2001). This elongated and shallow epicontinental seaway connected the western Tethys to the NW European basins. Mixing between higher NW European and lower latitude Mediterranean waters has been described by various authors and supported by the mixing of ammonite fauna, ostracods and calcareous nannofossils during the Early Jurassic (Mouterde and Ruget, 1975; Dommergues and Mouterde, 1980; Arias, 2007; Reggiani et al., 2010; Dera et al., 2011). The Lusitanian Basin was located at a palaeolatitude comprised between 25 and 30ºN (Dercourt et al., 2000), which corresponds in modern oceans to the transition between the subtropical and temperate climatic belts. The three sections studied in Portugal represent 286 m of a complete and continuous succession of marine hemipelagic marlstone and limestone couplets deposited on a homoclinal, low-angle ramp with a NW dipping (Duarte, 2004). The

Rabaçal section is located in the proximal part of the basin whereas Cabo Mondego in the distal part, and the Brenha section in an intermediate position. In all the three sections macrofossils such as ammonites, brachiopods, belemnites, bivalves and some fossilized wood fragments are commonly found. Though the Rabaçal section spans from the uppermost Pliensbachian to the uppermost upper Toarcian, only the first 42 m comprising the Polymorphum, Levisoni (lower Toarcian) and the lowermost Bifrons (middle Toarcian) ammonite zones were sampled for nannofossil study. The 157 m of the Brenha section correspond to the uppermost part of the lower Toarcian up to the lower Aalenian sediments. The 87 m of the Cabo Mondego section include the Speciosum, Meneghinii, Aalensis (upper Toarcian) and the Opalinum (lower Aalenian) ammonite zones. The three sections are correlated by means of ammonite and nannofossil biostratigraphies, and by means of lithostratigraphy.

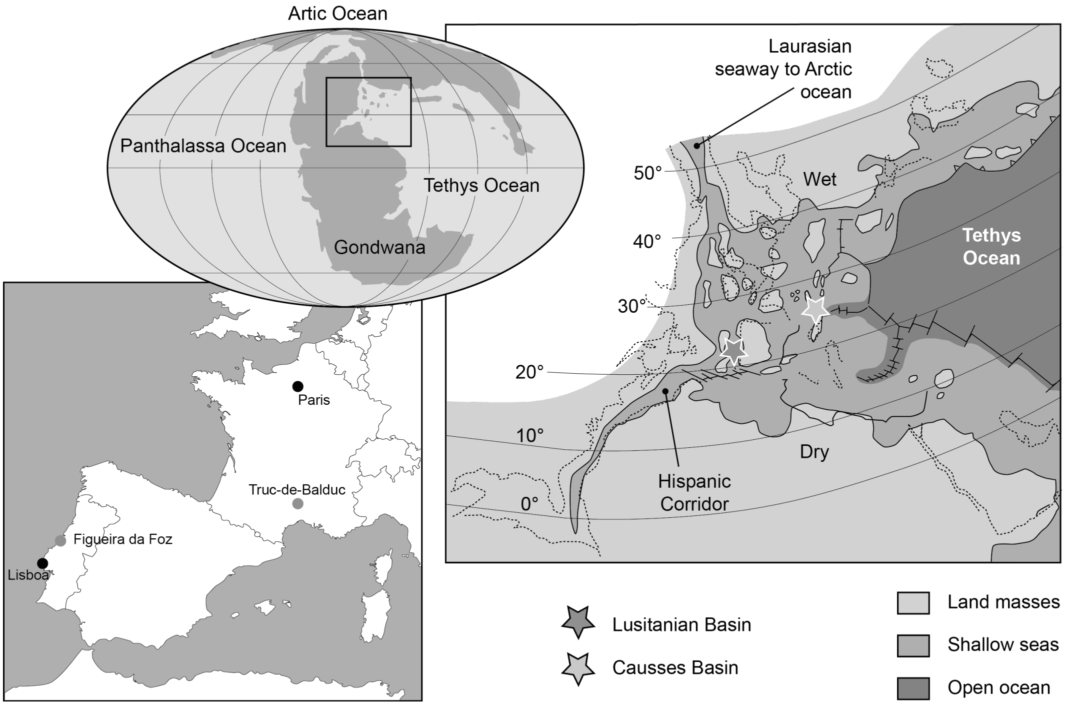


Figure 7 - Location of both studied basins during the Early Jurassic in western Tethys epicontinental sea (modified after Bassoulet et al., 1993).

The Truc-de-Balduc section is located on a small mountain 5 km southeast of the city of Mende, and belongs to the Causses Basin in south France (Fig. 7). During the Early Toarcian this basin was a small, partly enclosed, intracratonic basin in the western Tethys epicontinental sea, and was positioned at a palaeolatitude comprised between 25 and 30ºN. Bounded by Hercynian crystalline rocks (Trümpy, 1983), its morphology was largely controlled by the late Hercynian structural evolution. Subsidence was more pronounced in the central part of the basin and the

Lower Jurassic succession thickness varies from its margins to its depocentre (Morard, 2004; Mailliot et al., 2009). In this region an abrupt facies transition occurred in the lowermost Toarcian with the onset of deposition of organic matter-rich shales belonging to the Schistes Cartons Formation. On top of this formation stands the Fontaneilles Formation, a monotonous marl succession of the middle and upper Toarcian. The gradual transition to the Aalenian stage is characterized by sandy limestones with abundant bioturbation (Harazim et al., 2012). Representing ~145 m of almost continuous Toarcian and Early Aalenian beds, the fossiliferous nature of the Truc-de-Balduc section allowed an ammonite biostratigraphic framework to be established by Trümpy (1983). However, the Causses Basin was located directly on the border between the Boreal and the Tethyan realms, complicating the use of a standard ammonite zonation. Due to the dominant northwest European ammonite faunas in this basin during Toarcian to Aalenian times, the northwest European standard biozonation was chosen (Elmi et al., 1994; Macchioni and Cecca, 2002).

Material and methods

In total, 406 dense and closely spaced sampling was performed in both Portuguese and French sections. For nannofossil quantification and biostratigraphy, 65 samples from Truc-de-Balduc were studied, and a total of 341 samples were collected in the marl-limestone couplets in the three sections from the Figueira da Foz region: 139 samples from Rabaçal, 130 from Brenha and 72 from Cabo Mondego. Absolute abundances per gram of powdered rock were obtained following the Geisen et al. (1999) method. Briefly, about 30 mg of dried rock powder were mixed with water that was oversaturated with respect to $CaCO_3$ and with a basic pH, and allowed to settle for 24h on a cover slide in a settling box. The cover slide was then recovered after drying and permanently mounted on a microscope slide. At least 300 coccoliths were counted in every sample and studied under an optical polarized microscope with x1000 magnification. According to Fatela and Taborda (2002) the counting of 300 specimens per sample is statistically robust to record all the species making up more than 1% of the total assemblage with a confidence level of 95%. In order to check for rare or very rare taxa, at least one transect of each smear slide was scanned after counting was over.

Nannofossil bioevents

The synthesis of nannofossil events recorded in this work is summarized in Figure 8 where calcareous nannofossil biomarkers First and Last Occurrences (FO and LO) and First Common Occurrences (FCO) are calibrated with already established ammonite zones whenever they existed. By studying the Truc-de-Balduc section, it allowed to compare bioevents in the Lusitanian

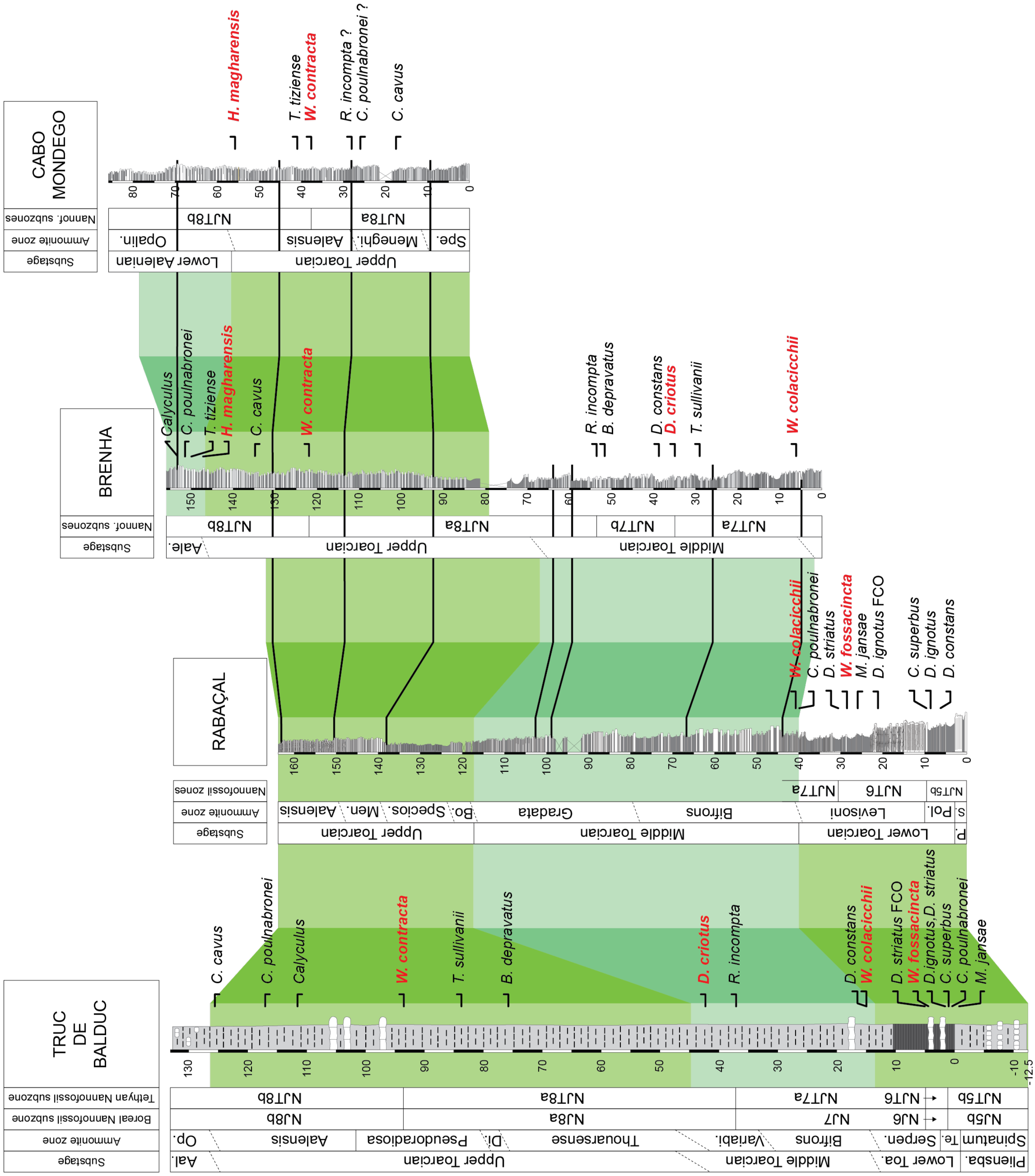


Figure 8 - Lithostratigraphic and biostratigraphic correlation between the studied sections in the Lusitanian and Causses Basins.

Basin with those occurring in a different palaeogeographic domain and therefore infer on their reproducibility and consistency. Eighteen major bioevents are acknowledged along the Toarcian and Early Aalenian in both basins (14 FOs and 4 LOs). These events are based on diagenesis-resistant taxa that are frequent to common in the studied sections and are thus easily recognized even in diagenetically altered material. Every bioevent is discussed in stratigraphic order from bottom to top. Whenever needed, taxonomy is herein discussed and findings are compared to stratigraphic ranges already reported in the literature for the Mediterranean and Boreal palaeogeographic provinces (see Fig. 9).

Lower Toarcian

FO of *Diductius constans* Goy, 1979

Though not a common species, the FO of *D. constans* varies in the three analyzed sections. In Rabaçal it is first observed during the lower Toarcian in the Polymorphum zone and NJT5b. Also de Kænel et al. (1996) recorded in Switzerland its FO during the lower Toarcian though in the Serpentinum zone. Both in Truc-de-Balduc and Brenha, this taxon first occurs during the middle Toarcian in the nannofossil zone NJT7a and NJT7b accordingly.

FO of *Discorhabdus ignotus* (Górka, 1957) Perch-Nielsen, 1968

This species first occurs in the Polymorphum zone in Rabaçal and displays its first common occurrence (FCO) during the Levisoni zone, as already acknowledged in Peniche by Mattioli et al. (2013). In the Causses basin, a hiatus occurs at the base of the Toarcian and the Tenuicostatum zone is very condensed (Mailliot et al., 2009). This is the reason why only the FCO of *D. ignotus* could be recognized in Truc-de-Balduc in the uppermost Tenuicostatum zone. This event was already acknowledged in central Italy at the top of the Tenuicostatum zone and hence proposed as a marker for the Tenuicostatum-Serpentinum (Polymorphum-Levisoni) boundary (Mattioli and Erba, 1999). Later however, Mattioli et al. (2013) recorded that *D. ignotus* was very rare from the base of Toarcian (base of Tenuicostatum zone) in the central Italy Valdorbia section, after which it temporarily disappears during the T-OAE and consistently shows up again as its FCO eventually in the Serpentinum zone. The apparent discrepancy between Mattioli and Erba (1999) and Mattioli et al. (2013) is due to ammonite zone definition. In fact, since ammonites are almost absent in central Italy lower Toarcian sediments corresponding to the T-OAE, ammonite zones are established as interval zones, namely based after the FO of a zonal marker (see for example Macchioni, 2002). As the FO of *Harpoceras serpentinum* was recorded above the T-OAE, this oceanographic event was assigned to the Tenuicostatum zone. Later, Bilotta et al. (2010) revised the ammonite zonation in central Italy and placed the T-OAE in an interval not dated by ammonites, before the Serpentinum zone.

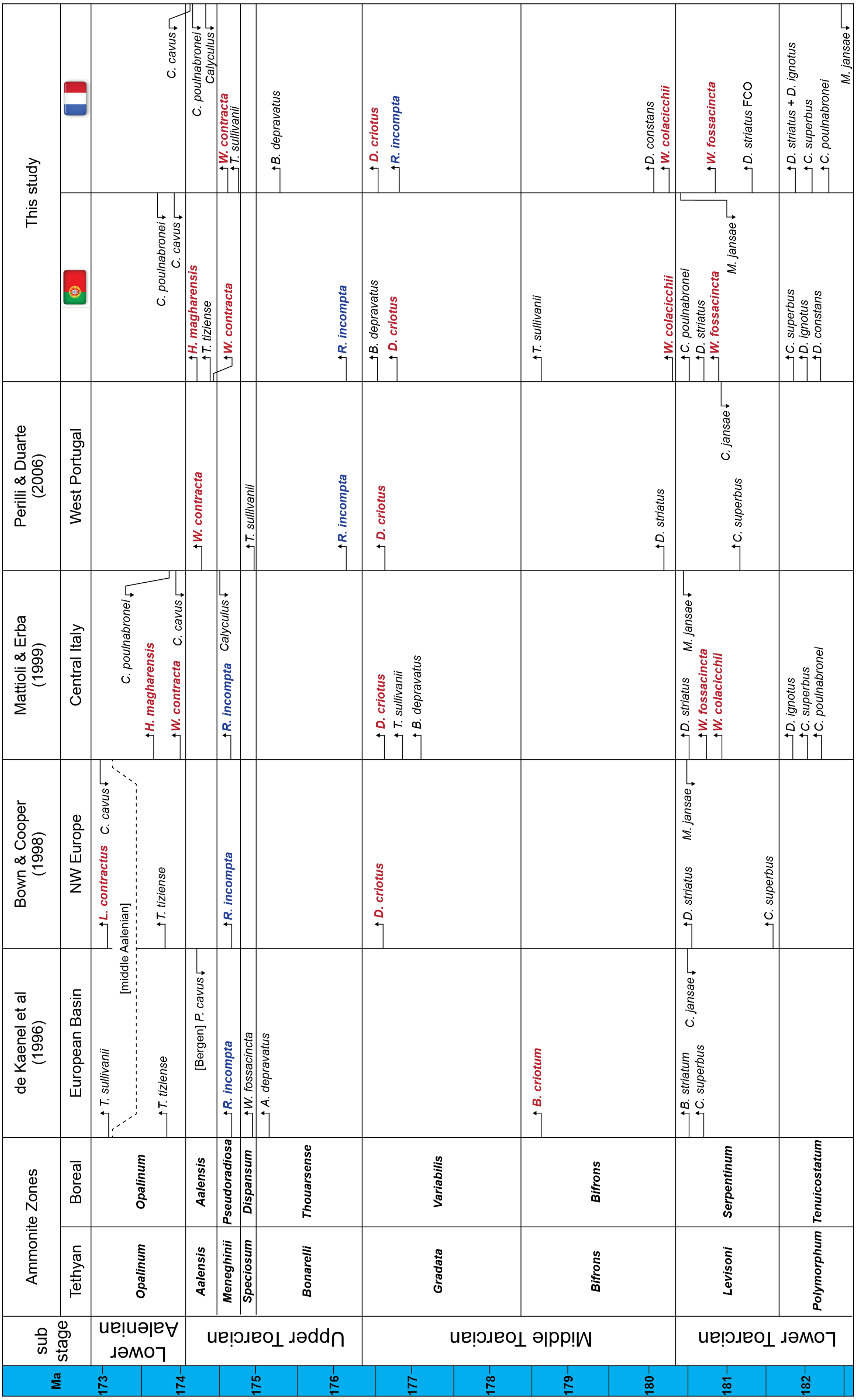

Ma
173
174
175
176
177
178
179
180
181
182
sub stage
Lower Aalenian
Upper Toarcian
Middle Toarcian
Lower Toarcian
Ammonite Zones
Tethyan
Boreal
Opalinum
Aalensis
Meneghinii
Pseudoradiosa
Speciosum
Dispansum
Bonarelli
Thouarsense
Gradata
Variabilis
Bifrons
Levisoni
Serpentinum
Polymorphum
Tenuicostatum
de Kaenel et al (1996)
European Basin
T. sullivanii
T. tiziense
[middle Aalenian]
[Bergen] P. cavus
R. incompta
W. fossacincta
A. depravatus
B. criotum
B. striatum
C. superbus
C. jansae
Bown & Cooper (1998)
NW Europe
L. contractus
C. cavus
T. tiziense
R. incompta
D. criotus
D. striatus
M. jansae
C. superbus
Mattioli & Erba (1999)
Central Italy
C. poulnabronei
H. magharensis
W. contracta
C. cavus
R. incompta
Calyculus
D. criotus
T. sullivanii
B. depravatus
D. striatus
W. fossacincta
W. colacicchii
M. jansae
D. ignotus
C. superbus
C. poulnabronei
Perilli & Duarte (2006)
West Portugal
W. contracta
T. sullivanii
R. incompta
D. criotus
D. striatus
C. superbus
C. jansae
This study
C. poulnabronei
C. cavus
H. magharensis
T. tiziense
W. contracta
R. incompta
B. depravatus
D. criotus
T. sullivanii
W. colacicchii
C. poulnabronei
D. striatus
W. fossacincta
M. jansae
C. superbus
D. ignotus
D. constans
C. cavus
C. poulnabronei
Calyculus
W. contracta
T. sullivanii
B. depravatus
D. criotus
R. incompta
D. constans
W. colacicchii
W. fossacincta
D. striatus FCO
D. striatus + D. ignotus
C. superbus
C. poulnabronei
M. jansae

Figure 9 - Comparison between major bioevents considered in this study and those reported in the main literature. In bold are the nannofossil events reproducible in various areas that allow inter-regional correlations.

LO of *Mitrolithus jansae* (Wiegand, 1984) Bown and Young in Young et al., 1986

The LO of the murolith *M. jansae* is recorded in Rabaçal in the uppermost lower Toarcian in the Levisoni ammonite zone and nannofossil zone NJT7a. Though sporadic occurrences are reported in middle and upper Toarcian Italian sections (Cobianchi, 1992; Reale et al., 1992; Baldanza and Mattioli, 1992) these are very likely due to reworking. The preference of this species for the southern Tethys water masses (Bown, 1987; Bucefalo Palliani et al., 2002; Mattioli et al., 2008) make it almost absent in Truc-de-Balduc where its local LO is recorded at the Pliensbachian-Toarcian boundary NJT5b. The LO of *M. jansae* can be regarded as a synchronous event across the Early Toarcian. Actually its LO has been observed in the Levisoni zone, NJT6, in several sections throughout the Lusitanian Basin by Perilli and Duarte (2006) and Mattioli et al. (2013) and in East Spain by Perilli (2000). Moreover, de Kænel et al. (1996) and Bown and Cooper (1998) also place this species LO at the uppermost Early Toarcian. Such consistency makes this event a remarkable proxy for the upper part of lower Toarcian, for at least the southern Tethys region.

FO of *Carinolithus poulnabronei* Mattioli, 1996

This species is interpreted as a transitional form between the genus *Calyculus* and *Carinolithus*, and is characterized by a vertically extended distal shield slightly thicker than in *C. superbus* and with a wider axial canal (Mattioli and Erba, 1999). It first occurs in Truc-de-Balduc during the lower Toarcian in the Tenuicostatum ammonite zone, NJT5b, slightly earlier than *C. superbus*, as also recorded in Central and Northern Italy by Mattioli and Erba (1999). Although Bown (1987) reported the transitional phase between the two genera as restricted to the Tenuicostatum zone, in the Rabaçal section *C. poulnabronei* occurs later in the lower Toarcian, at the uppermost Levisoni ammonite zone, NJT7, whereas in Peniche, Mattioli et al. (2013) records this event during the NJT6, at the Polymorphum-Levisoni boundary.

FO of *Carinolithus superbus* (Deflandre in Deflandre and Fert, 1954) Prins in Grün et al., 1974

In both studied successions this species first occurs at the base of the Toarcian in the Tenuicostatum or Polymorphum zone, thus defining the start of the nannofossil zone NJT6. Also in central Italy and Peniche, *C. superbus* first occurs in the Tenuicostatum or Polymorphum zone (Mattioli and Erba, 1999; Mattioli et al., 2013). De Kænel et al. (1996), Perilli (2000) and Perilli and Duarte (2006) observe this event in this Tenuicostatum or Polymorphum ammonite zone though in its uppermost part. Conversely, Bown and Cooper (1998) place this species FO at the base of the Serpentinum (Levisoni) zone in the northern margin of Tethys (England), where *C. superbus* is also generally scarcer. This species is resilient to dissolution and bears a continuous record throughout this age, being more abundant during the middle Toarcian in the Bifrons zone.

FO of *Discorhabdus striatus* Moshkovitz and Ehrlich, 1976

This species first occurs in the Lusitanian Basin during the lower Toarcian in the Levisoni (Serpentinum) ammonite zone whereas in Truc-de-Balduc it is recorded in the uppermost Tenuicostatum (Polymorphum) zone. This diachroneity is probably due to high accumulation rates and hence extremely low nannofossil abundances that are observed in Rabaçal after the T-OAE equivalent, as was also recorded in Peniche by Mattioli et al. (2008). In Truc-de-Balduc the First Common Occurrence (FCO) of *D. striatus* happens in the Serpentinum (Levisoni) zone and is hence used to define the nannofossil zone NJ7 and nannofossil subzone NJT7a. According to López-Otálvaro et al. (2012) this species can be distinguished from *D. ignotus* because of its larger size (>5 μm) and brighter birefringence colours in polarizing light. The FO of *D. striatus* is a consistent and synchronous event in different south Tethyan domains and therefore represents a good biostratigraphic marker for the Early Toarcian. Although Perilli and Duarte (2006) sets this event in west Portugal at the base of the Bifrons zone in the middle Toarcian, this is not what is actually observed in the Lusitanian and Causses basins. Actually, de Kænel et al. (1996), Bown and Cooper (1998), Mattioli and Erba (1999) and Perilli (2000) acknowledged this species FO at the topmost of the Serpentinum zone, close to the lower-middle Toarcian limit.

FO of *Watznaueria fossacincta* (Black, 1971) Bown in Bown and Cooper, 1989

The entry of the watznaueriaceans into the world oceans was made with the appearance of the species *W. fossacincta*. This specimen was observed both in Truc-de-Balduc and Rabaçal in the Lower Toarcian in the uppermost Serpentinum (Levisoni) ammonite zone in the top of NJT6 and base of NJT7a accordingly. Also in central Italy this species FO is coeval with the observations from this work (Mattioli and Erba, 1999).

Middle Toarcian

FO of *Watznaueria colacicchii* Mattioli and Reale in Mattioli, 1996

This species is consistently first observed in Truc-de-Balduc, Rabaçal and Brenha sections at the lower-middle Toarcian limit, i.e., Serpentinum (Levisoni)/Bifrons ammonite zones in NJT7a. Mattioli and Erba (1999) also found this species in the uppermost lower Toarcian in central Italy though they recorded its occurrence before the FO of *W. fossacincta*. This taxon is quite similar in shape to *W. contracta* but is smaller than the type species and has a slightly different width and shape of the central area (Mattioli, 1996). This bioevent is therefore a strategic marker for the lower-middle Toarcian limit.

FO of *Retecapsa incompta* Bown and Cooper, 1989

The FO of this species defines the nannofossil subzone NJT8a and it first occurs both in Truc-de-Balduc and Brenha in the uppermost middle Toarcian, in the Variabilis (Gradata) ammonite zone. In Cabo Mondego, *R. incompta* is first recorded solely in the upper Toarcian probably due to its scarcity in the Lusitanian Basin. Despite being consistently dated by several authors as a Late Toarcian biomarker in the Pseudoradiosa (Meneghinii) ammonite zone, whether in NW European and Portuguese sedimentary sequences (Baldanza and Mattioli, 1992; Mattioli, 1994; de Kænel et al. 1996; Bown and Cooper, 1998; Mattioli and Erba, 1999) this is not consistent with the records from both the Lusitanian and Causses basins. Noteworthy though, Perilli and Duarte (2006) place this taxon FO in the lowermost upper Toarcian in the Bonarelli ammonite zone in two sections from the Lusitanian Basin: Rabaçal and Cantanhede.

FO of *Discorhabdus criotus* Bown, 1987

This is a very consistent and easily identifiable biomarker for the uppermost middle Toarcian, which defines for Mediterranean sections the nannofossil zone NJT7b in the Variabilis (Gradata) ammonite zone. This nannofossil zone however, was not possible to be identified in Truc-de-Balduc as *D. criotus* is first recorded after the FO of *R. incompta*, the NJT8a biomarker. The *D. criotus* FO bioevent has already been acknowledged in Morocco, Portugal, NW Europe and central Italy by several authors (de Kænel et al., 1996; Bown and Cooper, 1998; Mattioli and Erba, 1999; Perilii and Duarte, 2006) thus representing an important biomarker in for the middle-upper Toarcian transition when used together with the FO of *R. incompta*.

FO of *Biscutum depravatus* (Grün and Zweili, 1980) Bown, 1987

Though never abundant in the assemblages, *B. depravatus* is easily distinguishable from other *Biscutum* species due to its very open central area and its axial thick cross. Its FO in Brenha occurs during the middle Toarcian in the probably uppermost Variabilis (Gradata) ammonite zone and NJT7b, which was also reported by Mattioli and Erba (1999) in central Italy. Conversely, in Truc-de-Balduc the FO of *B. depravatus* happens in the Thouarsense (Bonarelli) zone, NJT8a, which is in accordance with de Kænel et al. (1996) and Bown (1987).

FO of *Triscutum sullivanii* de Kænel and Bergen, 1993

Though this species is never abundant in the Toarcian assemblages, its FO can be considered as an important event in the middle Toarcian. It has been acknowledged in central Italy at the boundary between middle and upper Toarcian (Mattioli and Erba, 1999) and in the middle

Toarcian in the Brenha section where it first occurs in NJT7a. The lack of ammonite constrains in Brenha make it impossible to place this event in an ammonite zone. In Truc-de-Balduc though, *T. sullivanii* occurs later in the sequence during the upper Toarcian NJT8a in the Pseudoradiosa (Meneghinii) zone. Also Perilli and Duarte (2006) recorded this species FO in the upper Toarcian though in the Dispansum (Speciosum) zone in west Portugal. Contrariwise, de Kænel et al. (1996) place the FO of *T. sullivanii* during the middle Aalenian in the Brenha section. The distribution of this species seems to be restricted to the Tethyan and Pacific realms (Mattioli and Erba, 1999).

Upper Toarcian

FO of *Watznaueria contracta* (Bown and Cooper, 1989) Cobianchi et al., 1992

In Brenha, Cabo Mondego and Truc-de-Balduc this taxon consistently first occurs during the upper Toarcian in the Aalensis and Pseudoradiosa zones (see Fig. 8). The FO of this species defines the nannofossil subzone NJT8b. Despite our records, different authors place the FO of *W. contracta* in the basal Early Aalenian in west Portugal (de Kænel et al., 1996) and central Italy (Mattioli and Erba, 1999) or even in the middle Aalenian for Boreal sections (Bown and Cooper, 1998). Additionally, Perilli and Duarte (2006) also observed the FO of *W. contracta* in the Aalensis zone in west Portugal. The FO of *W. contracta* therefore represents a paramount biomarker for the Lower-Middle Jurassic transition.

LO of *Crepidolithus cavus* Prins ex Rood et al., 1973

The LO of this species consistently happens around the Lower-Middle Jurassic limit making this event a helpful proxy to identify this stratigraphic boundary. Though the LO of *C. cavus* in Cabo Mondego is observed in the Meneghinii zone in NJT8a, both in Brenha and Truc-de-Balduc this event occurs at the topmost of the Aalensis zone, NJT8b, as already recorded by de Kænel et al. (1996) in west Portugal and by Mattioli and Erba (1999) in central Italy. This event however, is acknowledged in NW Europe by Bown and Cooper (1998) in the middle Aalenian.

LO of *Carinolithus poulnabronei* Mattioli, 1996

This species last occurrence is consistently placed at the Toarcian-Aalenian limit in Truc-de-Balduc, Brenha and Cabo Mondego in the nannofossil zone NJT8b, making this bioevent another helpful proxy for the Lower-Middle Jurassic transition. As also reported by Mattioli and Erba (1999) for central Italy, in the Lusitanian Basin this event occurs at the lowermost Aalenian whereas in the Causses Basin it happens at the uppermost upper Toarcian in the Aalensis ammonite zone.

LO of *Calyculus* spp. Noël, 1973

According to Mattioli and Erba (1999) the smaller forms of *Calyculus* (<6 µm) disappear in the Late Toarcian during the Meneghinii (Pseudoradiosa) ammonite zone. However, despite this taxon LO is placed in Truc-de-Balduc also in the uppermost Toarcian in the Aalensis zone, NJT8b, in the Lusitanian Basin its permanent record in the Cabo Mondego section throughout the Early Aalenian prevents the determination of this taxon LO event. The continuous record in the Lusitanian Basin supports the lower latitude preferences of this taxon as inferred already by Mattioli et al. (2008).

FO of *Triscutum tiziense* de Kænel and Bergen, 1993

Though this species was never recorded in Truc-de-Balduc, therefore suggesting lower latitude preferences, its FO in the Lusitanian Basin happens in Brenha at the Toarcian-Aalenian boundary at NJT8b in the Opalinum zone. In Cabo Mondego however, *T. tiziense* FO happens during the uppermost Late Toarcian in the Aalensis zone also at NJT8b. This event is well correlated with the works of de Kænel et al. (1996) in Portugal and Morocco, and also with NW Europe data from Bown and Cooper (1998). This event is hence deemed a good proxy for the Lower-Middle Jurassic stratigraphic limit.

FO of *Hexalithus magharensis* Moshkovitz and Ehrlich, 1976

In the studied sections of the Lusitanian Basin the FO of *H. magharensis* was consistently found at the Toarcian-Aalenian limit in NJT8b and used to indicate the transition from the Lower to the Middle Jurassic. Already in central Italy, Mattioli and Erba (1999) recorded this taxon FO at the lowermost Early Aalenian. This species was never recorded in the Causses Basin therefore suggesting its Mediterranean Tethys preferences, as previously inferred by Bown and Cooper (1998). This event is a reliable proxy for the Toarcian-Aalenian boundary in Mediterranean Tethys.

Discussion

Comparing the studied sections with previous studies in the Lusitanian Basin

Although Bown (1987) and Bergen (in de Kænel et al., 1996) had briefly addressed the biostratigraphy in the Brenha section for the Lusitanian Basin, revised nannofossil taxonomy (e.g., de Kænel and Bergen, 1996; Mattioli, 1996; Mattioli et al., 2004; Giraud et al., 2006; Fraguas and Erba, 2010; Suchéras-Marx et al., 2010; Fraguas and Young, 2011; López-Otálvaro et al., 2012) and updated bioevents had been propose for Mediterranean Tethys sections (Mattioli and Erba, 1999). Since then, only Perilli and Duarte (2006) had addressed the Toarcian biostratigraphy in the Lusitanian Basin, although Mattioli et al. (2013) also refers to the lower Toarcian biostratigraphy for the Peniche section. Some differences emerged from the results of the present work and those previously obtained by other authors in the Lusitanian basin. The FO of *C. poulnabronei* is recorded in this work in the Levisoni zone whereas Mattioli et al. (2013) observed this event earlier in Peniche, at the limit of the Polymorphum-Levisoni zones. This difference can be linked to a discontinuous record of this species in the Lusitanian Basin. In this work the FO of *C. superbus* is observed at the Polymorphum zone in Rabaçal, whereas Perilli and Duarte (2006) acknowledged this event later in the Levisoni zone. Again the discontinuous record of this species can explain this discrepancy as Mattioli et al. (2013) also acknowledged this event in Peniche in the Polymorphum zone, whereas Bergen (in de Kænel et al., 1996) observed this event in Brenha during the middle Toarcian in the Bifrons zone. Although the FO of *D. striatus* is here recorded in the Levisoni zone, Perilli and Duarte (2006) place its FO at the basal middle Toarcian in the Bifrons zone whereas Bown (1987) place it at the Bifrons-Gradata boundary. However, the taxonomic conception of *D. striatus* slightly changed after the biometric work of López-Otálvaro et al. (2012). Furthermore, such divergences could be also justified by poor preservation in Rabaçal, or due to the scarcity of this species during the Early Toarcian coupled with different methodologies adopted. If the counting of at least 300 coccoliths per sample ensures the record of all the species making up more than 1.7% of the assemblage within a confidence interval of 99.5% (Fatela and Taborda, 2002), a qualitative analysis or a lesser counting in coccoliths would thus reduce the confidence interval, i.e., the size of the sample, or conversely increase the significance level, i.e., the error or part of the sample that is deliberately ignored. Hence this taxon might have been missed in previous works. Another significant difference between this work and that of Perilli and Duarte (2006) is the FO of *T. sullivanii*. The latter authors place this bioevent in the upper Toarcian Speciosum zone, whereas in this study this event is observed at the top of the Bifrons zone, in the middle Toarcian. The scarcity of this species and the different methodology adopted can be appointed for the difference observed in both works. As for the FO of *R. incompta* and *W. fossacincta*, it is observed by Bergen (in de Kænel et al., 1996) during the upper Toarcian in the Meneghinii zone and Bonarelli-Speciosum limit accordingly. Conversely, Perilli and Duarte (2006) place the FO of *R. incompta* in the Bonarelli zone, as is also acknowledged in this study. If the rarity of *R. incompta* and the methodology adopted can be the reason for this difference, the FO of *W. fossacincta* attributed by Bergen can be only interpreted as the use of different taxonomic criteria, since the transition between the genus *Lotharingius* and *Watznaueria* displayed intermediate morphologies across the Toarcian hindering sometimes a correct identification.

Provincialism impact on the observed records

Palaeogeographic barriers, paleoenvironmental differences, and strong climatic gradients accounted for a strong and marked ammonite palaeobiogeographic partitioning across the Pliensbachian and Toarcian between the Boreal and Mediterranean realms in the western Tethys (Elmi et al., 1994; Macchioni, 2002; Dera et al., 2011). During the Early Toarcian, the palaeobiogeographic pattern was first disrupted with a northward expansion of Mediterranean ammonite (Dera et al., 2011) and the mixing of Mediterranean and Boreal nannoplankton (Reggiani et al., 2010; Ferreira et al., 2015) species into the Lusitanian Basin throughout the

Polymorphum zone. Across the Levisoni zone, faunal and floral homogenization was established and was related to a major marine transgression and temperature rise, allowing better connections between Mediterranean and Boreal provinces. Ammonite and nannofossil provincialism closely related to sea level fall and temperature decrease after the Bifrons zone, was progressively reestablished during the Middle Toarcian, and maintained until the beginning of the Late Toarcian. Palaeoclimatic changes, sea-level fluctuations, and extinction events explain most of the palaeobiogeographic patterns displayed by ammonites and nannofossils. Palaeoclimatic changes physically drive the displacements, expansion, or reductions of palaeoecological niches inhabited by ammonite and nannoplankton communities, whereas sea-level oscillations regulate the basinal connections that modulate the dispersion or the segregation of faunas. Moreover, extinction events remove endemic species and facilitate the invasion and the proliferation of cosmopolitan taxa in vacated domains (Dera et al., 2011). The nannoplankton palaeoprovincialism established in west Tethyan water masses, also observed for such a variety of faunal and floral groups such as molluscs, dinoflagellates, ostracods or foraminifera, hinders the establishment of a global nannofossil biozonation scheme. Hence, Boreal and Mediterranean nannofossil bioevents must be severed and specific zonation schemes adopted. Actually, events like the LO of *M. jansae* or the FO of *H. magharensis*, *T. sullivanii* and *R. incompta* are best acknowledged in sections from the Mediterranean realm and consequently these events should not be chosen as biomarkers for sections from the Boreal province.

Resolution of calcareous nannofossil biostratigraphy

Following the Triassic/Jurassic extinction, the Early Jurassic nannoplankton evolutionary radiation was initiated and by the Early Toarcian, most major innovations had already been introduced. Subsequently, speciation and diversification rates fell to levels which were broadly maintained through the remainder of the Mesozoic (background levels) (Bown et al., 2004). Nevertheless, when compared to the Triassic/Jurassic radiation, even within a period of general evolutionary stasis like the Toarcian, it is possible to acknowledge three different periods of increased radiation and diversification (see Fig. 9). Early and Late Toarcian periods display an extremely high nannofossil resolution, whereas during the middle Toarcian, a period of more stable environmental conditions seems to be coeval with an evolutionary stasis. In fact, during the latter time intervals, several nannofossil zones or subzones have a time span shorter than one ammonite zone. Conversely, nannofossil zones and subzones are much longer during low evolutionary rates displayed across the middle Toarcian, and their duration can reach almost three million years. Despite the low stratigraphic resolution provided by nannofossils for the aforementioned interval, nannofossil biostratigraphy is still very important as ammonites can be scarce or absent and nannofossils virtually constitute the only biostratigraphic tool available. Early-middle Toarcian boundary approximately coincides with the base of the NJT7a, whereas the Late

Toarcian limit roughly corresponds to the base of the NJT8a subzone, and not NJT7b as indicated by Mattioli and Erba (1999). As also reported by the previous authors, this work shows that the Toarcian-Aalenian boundary lies within the very short NJT8b thus supporting and validating their observation. When comparing the Mediterranean and Boreal Tethyan nannofossil bioevents one can observe a relatively high correlation for the most important events. Moreover, the stratigraphic resolution of the proposed bioevents is fairly high and comparable to other proposed nannofossil biozonations schemes.

Actually, inconstant nannofloral evolutionary rates seem to be responsible for a non-uniform biostratigraphic resolution of calcareous nannofossils during the Toarcian. As highlighted by Geisen et al. (2004), coccolithophores appear to show evidence for both classic models of evolution, i.e., phyletic gradualism and punctuated equilibria (allopatric speciation) (Eldredge, 1971; Eldredge and Gould, 1972; Gould and Eldredge, 1977; Young and Bown, 1994). If morphological evolution is not slow and gradual but rather occurs in association with speciation, then the envelopment of speciation, geographical isolation and new ecological opportunities means that a correlation between episodes of rapid speciation and morphological evolution and diversification is to be expected (Charlesworth, 1990). Actually, that is what is observed in the Lusitanian Basin during the Early and Late Toarcian, where the number of bioevents are far higher then across the middle Toarcian, and are coeval with important environmental perturbations (Ferreira et al., 2015). In fact, environmental changes such as regional sea level oscillations in northwestern Caucasus have been regarded as an important factor influencing the evolutionary rates of Triassic marine macrofauna such as ammonoids, brachiopods, bivalves, sponges and corals (Ruban, 2008). Moreover, also Cooper et al. (2014) suggests that the evolutionary rates of graptolites during the Ordovician-Silurian global climate change are fine-tuned with sea surface temperature oscillations.

Results from both studied basins were compared with those from the literature and allowed to acknowledge for the southern Tethys margin consistent bioevents: 1) Though the Lazarous behaviour of *D. ignotus*, hiatuses or very condensed sedimentary beds often found in west Tethyan sections (Mattioli et al., 2013) can be pointed out for some discrepancies, the FO of *D. ignotus* combined with the FO of *C. superbus* stands out as a robust event defining the Polymorphum-Levisoni biohorizon, as acknowledged in the Peniche GSSP succession; 2) The LO of *M. jansae* is a consistent biomarker in the Early Toarcian occurring at the topmost Levisoni zone in NJT7a; 3) The consistent FO of *W. colacicchii* is herein proposed as the most accurate biomarker for the Levisoni-Bifrons biohorizon and should therefore define its own nannofossil subzone; 4) The FO of *D. criotus* is consistent and synchronous throughout the literature thus defining the nannofossil zone NJT7b; 5) The FO of *W. contracta* is consistent in all sections and thus defines NJT8b and represents a good proxy for the Aalensis-Opalinum transition; 6) The LO of *C. cavus* is a consistent auxiliary event occurring at the Aalensis-Opalinum boundary; 7) Like *C.*

cavus, also the LO of *C. poulnabronei* represents a consistent auxiliary event occurring at the Aalensis-Opalinum boundary; 8) The FO of *T. tiziense* in both provinces makes this event a useful marker for the Aalensis-Opalinum limit; 9) The FO of *H. magharensis* represents the best bioevent in the Mediterranean province for the Lower-Middle Jurassic limit, and was therefore used in the definition of the GSSP for the base of the Aalenian stage at Fuentelsaz section (Cresta et al., 2001).

Conclusions

The biostratigraphic synthesis here presented for the west Mediterranean Tethyan Province is compared to previous biostratigraphic schemes compiled for west Portugal, Morocco and Switzerland (de Kænel et al., 1996), central Italy (Mattioli and Erba, 1999) and with those from the Boreal Realm such as Great Britain, Germany and north of France (Bown et al., 1988; Bown, 1996). Comparing different biostratigraphic schemes however, is not a simple task. Due to the ammonite discontinuous sedimentary record and to their distinct palaeoprovincialism in the Jurassic period, an unequivocal and independent check on the synchronicity of nannofossil events in different palaeogeographic domains is therefore vulnerable. Moreover, the establishment of most ammonite zones boundaries is sometimes too ambiguous, hindering a straightforward correlation between different nannofossil zones.

Although several bioevents are undoubtedly correlated between high and low latitude provinces (Fig. 9), others appear to be diachronous. As previously mentioned, most divergences are deemed biased whether due to different ammonite biostratigraphies applied in different areas, whether to the scarcity and discontinuity of the ammonite record. The LOs are in general more diachronous than the FOs. This is probably due to reworking phenomena and therefore to apparent diachronism, or to the survival of certain species in a particular micro-environment (Mattioli and Erba, 1999). The LO of *C. cavus* in the Lusitanian Basin, is a fine example of probable reworking as it is continuously recorded in Brenha whereas in Cabo Mondego its LO happens during the upper Toarcian. As for *M. jansae* it is a clear matter of provincialism. The present study underlines the importance of calcareous nannofossil biostratigraphy in the Early, middle and Late Toarcian and demonstrates the high resolution that is possible to accomplish in intra- and inter-regional correlations. When compared to previous works addressing Toarcian biostratigraphy, this study provides an increasing number of bioevents that can be correlated in west Mediterranean Tethyan successions. Moreover, being the nannofossil zonation supported by a continuous and contiguous record of index species, its boundaries have demonstrated to be more precise then many of those provided by Jurassic ammonites.

References

Aguado, R., O'Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Marine Micropaleontology 68, 268-285.

Alves, T.M., Gawthorpe, R.L., Hunt, D.W., Monteiro, J.H., 2002. Jurassic tectono-sedimentary evolution of the Northern Lusitanian Basin (offshore Portugal). Marine and Petroleum Geology 19, 727-754.

Arias, C., 2007. Pliensbachian-Toarcian ostracod biogeography in NW Europe: Evidence for water mass structure evolution. Palaeogeography, Palaeoclimatology, Palaeoecology 251, 398-421.

Arias, C., 2013. The early Toarcian (early Jurassic) ostracod extinction events in the Iberian Range: The effect of temperature changes and prolonged exposure to low dissolved oxygen concentrations. Palaeogeography, Palaeoclimatology, Palaeoecology 387, 40-55.

Arias, C., Whatley, R.C., 2005. Palaeozoogeography of Western European Lower Jurassic (Pliensbachian and Toarcian) Ostracoda. Geobios 38, 697-724.

Arias, C., Whatley, R.C., 2009. Multivariate hierarchical analyses of Early Jurassic Ostracoda assemblages. Lethaia 42, 495-510.

Arkell, W.S., 1946. Standard of the European Jurassic. Geological Society of America Bulletin 57, 1-34.

Baldanza, A., Mattioli, E., 1992. Biozonazione a Nannofossili Calcarei del Giurassico Inferiore-Medio della Provincia Mediterranea (Dominio Tetideo): revisione ed ampliamento. Paleopelagos. 2, 69-78.

Bassoulet, J.P., Elmi, S., Poisson, A., Cecca, F., Bellion, Y., Guiraud, R., Baudin, F., 1993. Mid Toarcian. In: Dercourt, J., Ricou, L.E., Vrielynck, B. (Eds.) Atlas of Tethys Paleoenvironmental Maps. Becip-Franlab, Rueil-Malmaison, France, pp. 63-80.

Baudin, F. 1989. Caractérisation géochimique et sédimentologique de la matière organique du Toarcien téthysien (Méditerranée, Moyen-Orient), significations paléogeographiques. PhD Thesis, Université Pierre et Marie Curie (Paris VI). 246pp.

Bilotta, M., Venturi, F., Sassaroli, S., 2010. Ammonite faunas, OAE and the Pliensbachian-Toarcian boundary (Early Jurassic) in the Apennines. Lethaia 43, 357-380.

Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical Paleoceanographic study of the Early Jurassic transcontinental Laurasian Seaway, Paleoceanography 16, 390-404.

Boomer, I., Lord, A.R., Page, K.N., Bown, P.R., Lowry, F.M.D., Riding, J.B., 2009. The biostratigraphy of the Upper Pliensbachian-Toarcian (Lower Jurassic) sequence at Ilminster, Somerset. Journal of Micropaleontology 28, 67-85.

Bown, P.R., 1987. Taxonomy, evolution and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. Special Papers in Palaeontology 38, 1-118.

Bown, P.R. with contributions from the International Nannoplankton Association, Jurassic Working Group, 1996. Recent advances in Jurassic calcareous nannofossil research. GeoResearch Forurn, v. 1-2, 55-66.

Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.) Calcareous Nannofossils Biostratigraphy. British Micropalaeontological Society Publication Series. Kluver Academic Publishers, Cambridge, pp. 34-85.

Bown, P.R., Cooper, M.K.E., Lord, A.R., 1988. A calcareous nannofossil Biozonation scheme for the early to mid Mesozoic. Newsletter Stratigraphy 20, 91-111.

Bown, P.R., Lees, J.A., Young, J.R., 2004. Calcareous nannoplankton evolution and diversity through time. In: Thierstein, H.R. and Young, J.R. (Eds.) Coccolithophores From Molecular Process to Global Impact. Springer-Verlag, Berlin, pp. 481-508.

Bucefalo Palliani, R., Mattioli, E., Riding, J.B., 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.

Bucefalo Palliani, R., Riding, J.B., 2003. Biostratigraphy, provincialism and evolution of European Early Jurassic (Pliensbachian to Early Toarcian) dinoflagellate cysts. Palynology 27, 179-214.

Charlesworth, B., 1990. Speciation. In Briggs, D.E.G, Crowther, P.R. (Eds.) Paleobiology a synthesis, Blackwell Science, pp. 100-106.

Cobianchi M.A., 1992. Sinemurian-Early Bajocian Calcareous Nannofossil Biostratigraphy of the Lombardy Basin (Southern Calcareous Alps; Northern Italy). Atti Ticinensi Sc. Terra 35, 61-106.

Cooper, R.A., Sadler, P.R., Munnecke, A., Crampton, J.S., 2014. Graptoloid evolutionary rates track Ordovician-Silurian global climate change. Geological Magazine 151, 349-364.

Cope, J.C.W., 1994. The nature and resolution of Jurassic ammonites biozones. Geobios 17, 127-132.

Cresta, S., Goy, A., Ureta, S., Arias, C., Barrón, E., Bernard, J., Canales, M.L., García-Joral, F., García-Romero, E., Gialanella, P.R., Gómez, J.J., González, J.A., Herrero, C., Martínez, G., Osete, M.L., Perilli, N., Villalaín, J.J., 2001. The global stratotype section and point (GSSP) of the Toarcian-Aalenian boundary (Lower-Middle Jurassic). Episodes 24, 166-175.

de Kænel, E., Bergen, J.A., 1993. New early and middle Jurassic coccolith taxa and biostratigraphy from the eastern proto-Atlantic (Morocco, Portugal and DSDP Site 547 B). Eclogae geologicae Helvetiae 86, 861-908.

de Kænel, E., Bergen, J.A., von Salis Perch-Nielsen, K. 1996. Jurassic calcareous nannofossil biostratigraphy of western Europe. Compilation of recent studies and calibration of bioevents. Bulletin de la Societe Géologique de France 167, 15-28.

Dera, G., Neige, P., Dommergues, J.-L., Brayard, A., 2011. Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Global and Planetary Change 78, 92-105.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, 2000. Atlas Peri-Tethys, Palaeogeographical maps. CCGM/CGMW, Paris.

Dommergues, J.L., Fara, E., Meister, C., 2009. Ammonite diversity and its palaeobiogeographical structure during the early Pliensbachian (Jurassic) in the western Tethys and adjacent areas. Palaeogeography, Palaeoclimatology, Palaeoecology 280, 64-77.

Dommergues, J.L., Mouterde, R., 1980. Modalités d'installation et d'évolution des harpocératinès (Ammonitina) au Domérien inférieur dans le Sud-Ouest de l'Europe. Geobios 13, 289-325.

Duarte, L.V., 2004. The geological heritage of the Lower Jurassic of Central Portugal: selected sites, inventory and main scientific arguments. Rivista Italiana di Paleontologia e Stratigrafia 110, 381-387.

Duarte, L.V., 2007. Lithostratigraphy, sequence stratigraphy and depositional setting of the Pliensbachian and Toarcian series in the Lusitanian Basin (Portugal). In: Rocha, R.B. (Ed.), The Peniche Section (Portugal). Contributions to the Definition of the Toarcian GSSP. International Subcommission on Jurassic Stratigraphy, 17-23.

Eldredge, N., 1971. The allopatric model and phylogeny in Paleozoic invertebrates. Evolution 25, 156-167.

Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf, T.J.M. (Ed.) Models in Paleobiology. Freeman, Cooper, and Co., San Francisco, pp 82-115.

Elmi, S., Gabilly, J., Mouterde, R., Rulleau, L. and Rocha, R.B., 1994. The European stage in Europe and in the Tethyan realm: divisions and correlations. Geobios, 27, 149-159.

Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil assemblages. Marine Micropaleontology 45, 169-174.

Ferreira, J., Mattioli, E., Pittet, B., Cachão, M., Spangenberg, J.E., 2015. Palaeoecological insights on Toarcian and lower Aalenian calcareous nannofossils from the Lusitanian Basin (Portugal). Palaeogeography, Palaeoclimatology, Palaeoecology 436, 245-262.

Fraguas, A., 2014. *Crepidolithus cantabriensis* nov. sp., a new calcareous nannofossil (Prymnesiophyceae) from the Lower Jurassic of northern Spain. Geobios 47, 31-38.

Fraguas, A., Comas-Rengifo, M.J., Gómez, J.J., Goy, A., 2012. The calcareous nannofossil crisis in Northern Spain (Asturias province) linked to the Early Toarcian warming-driven mass extinction. Marine Micropaleontology 94-95, 58-71.

Fraguas, A., Erba, E., 2010. Biometric analyses as a tool for the differentiation of two coccolith species of the genus Crepidolithus (Pliensbachian, Lower Jurassic) in the Basque-Cantabrian Basin (Northern Spain). Marine Micropaleontology 77, 125-136.

Fraguas, A., Young, J., 2011. Evolution of the coccolith genus Lotharingius during the Late Pliensbachian-Early Toarcian interval in Asturias (N Spain). Consequences of the Early Toarcian environmental perturbations. Geobios 44, 361-375.

Geisen, M., Bollman, J., Herrle, J.O., Mutterlose, J., Young, J.R., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437-442.

Geisen, M., Young, J.R., Probert, I., Sáez, A.G., Baumann, K.-H., Sprengel, C., Bollmann, Y., Cros, L., de Vargas, C., Medlin, L.K., 2004. Species level variation in coccolithophores. In: Thierstein, H.R. and Young, J.R. (Eds.) Coccolithophores From Molecular Process to Global Impact. Springer-Verlag, Berlin, pp. 327-366.

Giraud, F., Pittet, B., Mattioli, E., Audouin, V., 2006. Paleoenvironmental controls on the morphology and abundance of the coccolith *Watznaueria britannica* (Late Jurassic, southern Germany). Marine Micropaleontology 60, 205-225.

Gould, S.J., Eldredge, N., 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3, 115-151.

Hamilton, G., 1977. Early Jurassic calcareous nannofossils from Portugal and their biostratigraphic use. Eclogae geologicae Helvetiae 72, 575-598.

Hamilton, G., 1979. Lower and Middle Jurassic calcareous nannofossils from Portugal. Eclogae geologicae Helvetiae 72, 1-17.

Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2012. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian-Toarcian). Sedimentology 60, 359-390.

Liu, Ch., Heinze, M., Fürsich, F.T., 1998. Bivalve provinces in the Proto Atlantic and along the southern margin of the Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology 137, 127-151.

López-Otálvaro, G.-E., Baptiste Suchéras-Marx, B., Giraud, F., Mattioli, E., Lécuyer, C., 2012. Discorhabdus as a key coccolith genus for paleoenvironmental reconstructions (Middle Jurassic, Lusitanian Basin): Biometry and taxonomic status. Marine Micropaleontology 94-95, 45-57.

Lozar, F., 1992. Biostratigrafia a Nannofossili calcarei nel Lias: risultati di alcune sezioni nel Bacino Lombardo e nel Bacino Delfinese. Paleopelagos 2, 89-98.

Lozar, F., 1995. Calcareous nannofossil biostratigraphy of Lower Liassic from Western Tethys. Palaeontographia Italica 82, 91-121.

Macchioni, F., 2002. Myths and legends in the correlation between the Boreal and Tethyan Realms. Implications on the dating of the Early Toarcian mass extinctions and the oceanic anoxic event. Geobios, Mémoire Spécial 24, 150-164.

Macchioni, F., Cecca, F., 2002. Biodiversity and biogeography of middle-late Liassic ammonoids: implications for the Early Toarcian mass-extinction. Geobios, 35, 165-175.

Mailliot, S., Mattioli, E., Bartolini, A., Baudin, F., Pittet, B., Guex, J., 2009. Late Pliensbachian Early Toarcian (Early Jurassic) environmental changes in an epicontinental basin of NW Europe (Causses area, central France): A micropaleontological and geochemical approach. Palaeoceanography, Palaeoclimatology, Palaeoecology 273, 346-364.

Mailliot, S., Mattioli, E., Guex, J., Pittet, B., 2006. The Early Toarcian anoxia, a synchronous event in the Western Tethys? An approach by quantitative biochronology (Unitary Associations), applied on calcareous nannofossils. Palaeogeography Palaeoclimatology Palaeoecology 240, 562-586.

Mattioli E., 1994. Calcareous nannofossil content of the Toarcian-Aalenian Fiuminata section (Central Apennines, Italy). Palaeopelagos 4, 175-188,

Mattioli E., 1996. New calcareous nannofossil species from the Early Jurassic of Tethys. Rivista Italiana di Paleontologia e Stratigrafia 102, 397-412.

Mattioli, E., Erba, E., 1999. Biostratigraphic synthesis of calcareous nannofossil events in the Tethyan Jurassic. Rivista Italiana di Paleontologia e Stratigrafia 105, 343-376.

Mattioli E., Pittet B., Suan, G., Mailliot S., 2008. Calcareous nannoplankton across the Early Toarcian Anoxic Event: implications for paleoceanography within the western Tethys. Paleoceanography 23, PA3208.

Mattioli, E., Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian-Toarcian (Lower Jurassic) coccoliths of the family Biscutaceae: intra- and interspecific variability versus palaeoenvironmental influence. Marine Micropalaeontology 52, 5-27.

Mattioli, E., Plancq, J., Boussaha, M., Duarte, L.V., Pittet, B., 2013. Calcareous nannofossil biostratigraphy: new data from the Lower Jurassic of the Lusitanian Basin. Comunicações Geológicas 100, 69-76.

Morard, A., 2004. Les événements du passage Domérien-Toarcien entre Téthys occidentale et Europe du Nord-Ouest. Thèse, Université Lausanne, Géologie - Paléontologie, pp. 1-158.

Mouterde, R., Ruget, C., 1975. Esquisse de la paleogeographie du jurassique inférieur et moyen en Portugal. Bulletin de la Societe Geologique de France 14, 779-786.

Perilli, N., 2000. Calibration of early-middle Toarcian nannofossil events based on high-resolution ammonite biostratigraphy in two expanded sections from the Iberian Range (East Spain). Marine Micropaleontology 39, 293-308.

Perilli, N., Duarte, L.V., 2006. Toarcian nannobiohorizons from Lusitanian Basin (Portugal) and their calibration against ammonite zones. Rivista Italiana di Paleontologia e Stratigrafia 112, 417-434.

Perilli, N., Fraguas, A., Comas-Rengifo, M.J., 2009. Reproducibility and reliability of the Pliensbachian calcareous nannofossil biohorizons from the Basque-Cantabrian Basin (Northern Spain). Geobios 43, 77-85.

Perilli, N., Goy, A., Comas-Rengifo, M.J., 2004. Calibration of the Pliensbachian-Toarcian calcareous nannofossil zone boundaries based on ammonite (Basque-Cantabrian area, Spain). Rivista Italiana di Paleontologia e Stratigrafia 110, 97-107.

Pinheiro, L.M., Wilson, R.C.L., Pena dos Reis, R., Whitmarsh, R.B., Ribeiro, A., 1996. The western Iberia margin: a geophysical and geological overview. In: Whitmarsh, R.B., Sawyer, D.S., Klaus, A., Masson, D.G. (Eds.), Proceedings of the Ocean drilling Program. Scientific Results 149, 3-23.

Reale, V, Baldanza, A., Monechi, S., Mattioli, E., 1992. Calcareous Nannofossil biostratigraphic events from the Early-Middle Jurassic sequences of the Urnbria-Marche area (Central Italy). Mem. Sc. Geol. Padova. 43, 41-75.

Reggiani, L., Mattioli, E., Pittet, b., Duarte, L.V., Veiga de Oliveira, L.C., Comas-Rengifo, M.J. 2010. Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian Basin, Portugal): A clue for palaeoenvironmental reconstructions. Marine Micropaleontology 75, 1-16.

Ruban, D.A., 2008. Evolutionary rates of the Triassic marine macrofauna and sea-level changes: Evidences from the Northwestern Caucasus, Northern Neotethys (Russia). Palaeoworld 17, 115-125.

Ruban, D.A., 2013. Spatial heterogeneity of the Early-Middle Toarcian (Jurassic) ammonite diversity and basin geometry in the Northwestern Caucasus (southwestern Russia; northern Neo-Tethys). Palaeogeography, Palaeoclimatology, Palaeoecology 386, 225-232.

Ruban, D.A., Tyszka, J., 2005. Diversity dynamics and mass extinctions of the Early-Middle Jurassic foraminifers: a record from the Northwestern Caucasus. Palaeogeography, Palaeoclimatology, Palaeoecology 222, 329-343.

Suchéras-Marx, B., Mattioli, E., Pittet, B., Escarguel, G., Suan, G., 2010. Astronomically-paced coccolith size variations during the early Pliensbachian (Early Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 295, 281-292.

Trümpy, D.M., 1983. Le Lias Moyen et Supérieur des Grands Causses et de la région de Rodez: contributions stratigraphiques, sédimentologiques et géochimiques à la connaissance d'un bassin à sédimentation marneuse. Cahiers de l'Université, Université de Pau et des Pays de l'Adour 19, 1-363.

Vörös, A., 2005. The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders? Palaeogeography Palaeoclimatology Palaeoecology 223, 222-242.

Vörös, A., 2014. Latitudinal variation of brachiopod ornamentation in the Jurassic faunas from the western Tethys and its possible relation to a predation gradient. Palaeogeography Palaeoclimatology Palaeoecology 403, 57-65.

Young, J.R., Bown, P.R., 1994. Palaeontological perspectives. In: Green J.C., Leadbeater B.S.C. (Eds.) The Haptophyte Algae. Clarendon Press, Oxford.

Wignall, P.B., Newton, R.J., Little, C.T.S., 2005. The timing of paleoenvironmental change and cause-and-effect relationships during the Early Jurassic mass extinction in Europe. American Journal of Science 305, 1014-1032.

5. Palaeoecology

Palaeogeography, Palaeoclimatology, Palaeoecology 436 (2015) 245–262

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeoecological insights on Toarcian and lower Aalenian calcareous nannofossils from the Lusitanian Basin (Portugal)

Jorge Ferreira [a,b,*], Emanuela Mattioli [a], Bernard Pittet [a], Mário Cachão [b], Jorge E. Spangenberg [c]

[a] UMR CNRS 5276 LGL-TPE, Université Claude Bernard Lyon1, ENS Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne Cedex, France
[b] Instituto Dom Luiz (IDL), University of Lisbon, 1749-016 Lisbon, Portugal
[c] Institute of Earth Surface Dynamics, University of Lausanne, Building Géopolis,1015 Lausanne, Switzerland

ARTICLE INFO

Article history:
Received 3 January 2015
Received in revised form 6 July 2015
Accepted 10 July 2015
Available online 18 July 2015

Keywords:
Calcareous nannofossils
Carbon and oxygen stable isotopes
Torcian-Aalenian
Lusitanian Basin

ABSTRACT

A comprehensive and detailed account is presented of the calcareous nannofossil evolution across the Toarcian and Early Aalenian from the strategically located Lusitanian Basin in Portugal. The basin connected NW Tethys and Mediterranean water masses during the Toarcian and thus the in situ nannoplankton community responded to this double influence. Biostratigraphic control by ammonites from two well calibrated and continuous sections was compared to an intermediate section, which rendered a complete 286 m of Toarcian and lower Aalenian succession. Quantification of calcareous nannofossils, Factor Analysis, stable carbon and oxygen isotope analysis from brachiopods shells was performed. Temperature, water masses exchanges and primary productivity were highlighted by three extracted factors. Three major ecological events were identified in this work. Throughout the Early Toarcian during the onset of a warming transgressive period with an intensified hydrological cycle where calcareous nannoplankton thrived, NW Tethys waters started flooding the Lusitanian Basin which became dominated by Mediterranean taxa such as *M. jansae* and *Schizosphaerella*. Water mixing between NW European and Mediterranean water masses occurred, as recorded by nannofossil assemblages typical of the two provinces. Across the middle and part of the Late Toarcian, as climatic conditions stabilized during the long-term regressive period that had just begun, NW European connections were still effective, waters became more stratified and primary productivity decreased as indicated by the $\delta^{13}C$ data, the coeval decrease in total nannofossil abundances and increase in diversity. From part of the Late Toarcian, the connection between north and south water masses was diminutive and Mediterranean waters filled and dominated the basin, as inferred from the steady increase in *Schizosphaerella* and the near disappearance of *Crepidolithus crassus*. The calcareous nannoplankton increase in abundance and decrease in diversity show that under a humid climate, environmental conditions in such a shallow basin would tend to be more meso-eutrophic.

1. Introduction

Lower Toarcian calcareous nannofossils have been extensively studied for palaeoenvironmental purposes (e.g., Mattioli & Pittet, 2004; Mattioli et al., 2004, 2008, 2009; Tremolada et al., 2005; Suan et al., 2008a, 2010; Mailliot et al., 2009; Fraguas et al., 2012; Reolid et al., 2014), but with few exceptions (e.g. Mattioli, 1997; Mattioli & Erba, 1999; Sandoval et al., 2012) little attention has been given to middle and upper Toarcian substages. The Toarcian and Aalenian ages are of particular interest in the geological history of the planet. Palaeoenvironmental changes took place across this time interval, where important and drastic temperature shifts and eustatic oscillations occurred (Hallam, 1981; Duarte et al., 2007; Gómez et al., 2008; Dera et al., 2009a, 2011a; Pittet et al., 2014), including one of the most important thermal maximum recorded during the Mesozoic at the base of the Toarcian, also corresponding to the Toarcian Oceanic Anoxic Event (T-OAE), an interval of widespread organic matter burial (Jenkyns, 1988; Duarte, 1998; Jenkyns et al., 2001; Bailey et al., 2003; Hesselbo et al., 2007; McArthur et al., 2008; Suan et al., 2008b). Being a major component of the extant marine phytoplankton, coccolithophores are one of the main open-ocean primary producers, and their calcified scales (coccoliths) are well represented in deep-sea sediments above the calcite compensation depth (Bown & Young, 1998). Their importance in palaeoceanographic, palaeoecological and biostratigraphic studies is highly significant due to their rapid evolution and radiation, and above all, for their distribution, abundance and diversity. Though the influence of temperature and pCO_2 on unicellular algae is still a complex and ongoing debated subject, the whole plankton structure is influenced by a multitude of external

---

[*] Corresponding author at: Université Claude Bernard Lyon1, ENS Lyon, Campus de la DOUA, Bâtiment Géode, 69622 Villeurbanne Cedex, France.
E-mail address: jorge.hgf@gmail.com (J. Ferreira).

http://dx.doi.org/10.1016/j.palaeo.2015.07.012
0031-0182/

factors that affect their metabolism and diversity (Lewandowska et al., 2012; Spielmeyer & Pohnert, 2012) such as water temperature, nutrients concentration and salinity (Winter et al., 1994). A synecological approach is thus important to better understand the long-term behaviour of calcareous nannoplankton associations during the Toarcian and Early Aalenian and to infer any relationships with chemo-physical parameters such as nutrient concentration and shifts in water temperature that can be extracted from their fossil record. For this purpose three sections representing the stratigraphic continuum of the totality of the Toarcian and lower Aalenian stages outcropping in the Lusitanian Basin, Portugal, spanning across approximately 10 Myrs (Gradstein et al., 2012), were studied. A quantitative and qualitative study of coccoliths is herein presented, as well as the absolute and relative abundances of the calcareous dinoflagellate cyst *Schizosphaerella*. During the time interval to which this work refers to, the Lusitanian Basin was a narrow corridor connecting epicontinental water masses in the north (Euro-Boreal realm) and south (Mediterranean Tethys realm) making it a perfect place to study changes occurring in the western Tethys between these two domains and their influence on calcareous nannoplankton assemblages. Age calibration was defined according to the ammonite content described in the literature and to nannofossil bioevents. In order to assess bottom water temperatures and their carbon isotope signature in this sector during the time interval of interest, geochemical data was collected, and afterwards brachiopod shells were analyzed for their carbon and oxygen isotope composition. This work aims to address the long-term evolution of calcareous nannofossil assemblages in the Lusitanian Basin. In particular, the assemblage composition was studied in order to understand its response to long-term environmental changes during the Toarcian and Early Aalenian, following sharp and extreme palaeoceanographical conditions that occurred during the T-OAE.

2. Geological settings

The western Tethys Ocean in the Early Jurassic mainly consisted of a shallow sea lying between the African and the European landmasses. It was in this region that the Lusitanian Basin started to open during an aborted rift phase in the Late Triassic (Pinheiro et al., 1996). It was a relatively narrow and elongated epicontinental (<200 m in depth according to Bjerrum et al., 2001) seaway connecting the Hispanic Seaway southern waters to the NW European waters. Roughly N-S orientated, this basin was bounded in the east by the Iberian Meseta and in the west by the Berlengas-Farilhões igneous and metamorphic horst at a palaeolatitude between 25 and 30°N (Dercourt et al., 2000) (Fig. 1). In modern oceans this palaeolatitude range corresponds to the transition between the Subtropical to Temperate waters. The mixing between higher NW European and lower latitude Mediterranean waters in this passageway has been described by various authors and supported by a mix of ammonite faunas and calcareous nannofossil assemblages during the Early Jurassic (Mouterde & Ruget, 1975; Dommergues & Mouterde, 1980; Reggiani et al., 2010; Dera et al., 2011a). The three sections studied in this work represent 286 m of a complete and continuous succession of marine hemipelagic marl and limestone couplets deposited on a homoclinal, low-angle ramp with a NW dipping (Duarte, 2004). The Rabaçal section corresponds to the most proximal part of the studied area and Cabo Mondego to the most distal, with the Brenha section positioned between these two. In all of the three sections macrofossils

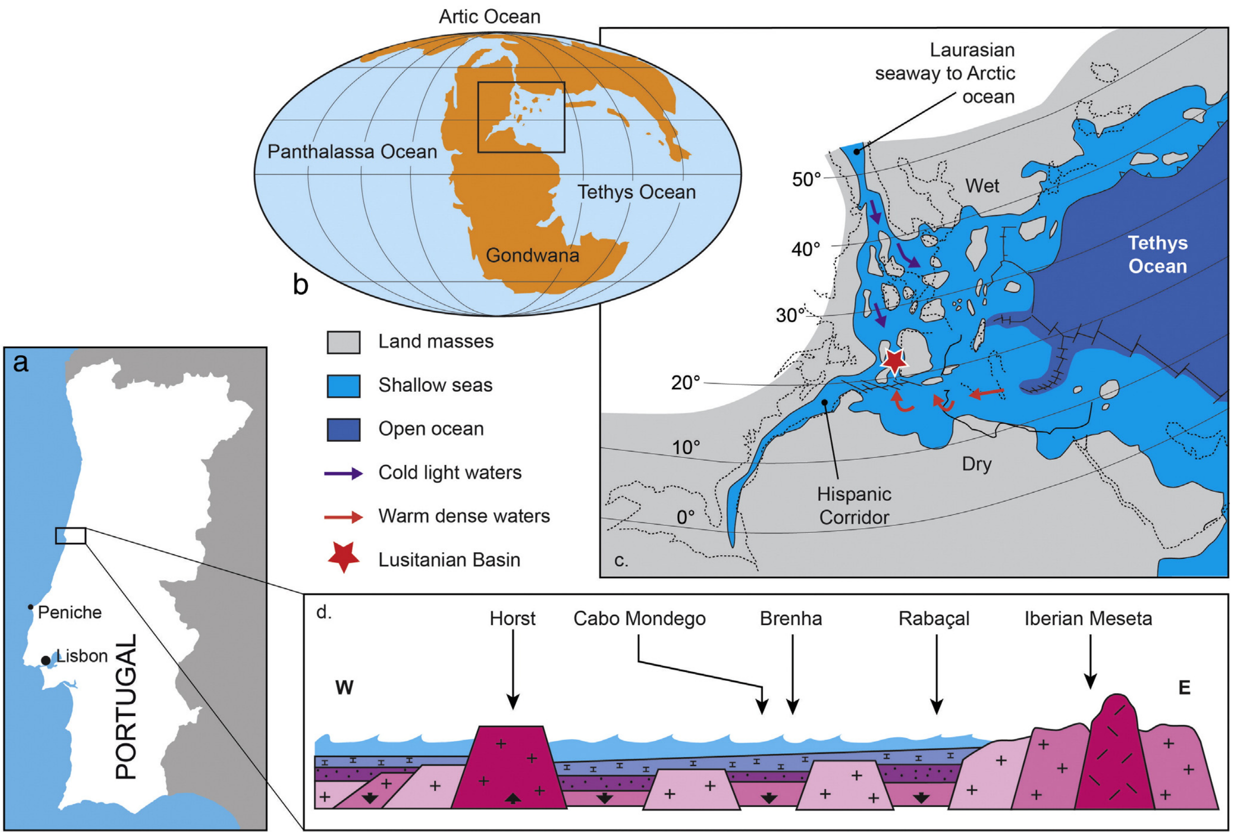


Fig. 1. a. Location of the three studied sections in the western part of Portugal. b. Palaeogeography of western Tethys and c. position of the Lusitanian Basin within the proto-Atlantic rift during the Lower Toarcian (modified after Bassoulet et al., 1993). d. Approximate location of the three sections studied in this work within the Lusitanian Basin.

such as ammonites, brachiopods, belemnites, bivalves and some fossilized wood are commonly found. Though the Rabaçal section spans from the uppermost Pliensbachian to the uppermost upper Toarcian, only the first 42 m comprising the Polymorphum, Levisoni (Early Toarcian) and the lowermost Bifrons (middle Toarcian) ammonite zones were sampled for nannofossil study. The 157 m of sediments from the Brenha section correspond to the uppermost part of the lower Toarcian to the lower Aalenian. The 87 m of the Cabo Mondego section include the Speciosum, Meneghinii, Aalensis (Late Toarcian) and the Opalinum (Early Aalenian) ammonite zones (Fig. 2). The three sections are tightly correlated by means of ammonite and nannofossil biostratigraphies, and by means of lithostratigraphy.

3. Materials and methods

3.1. Calcareous nannofossils

For nannofossil quantification, a total of 341 samples were collected in the marl-limestone couplets in the three studied sections; 139 samples from Rabaçal, 130 from Brenha and 72 from Cabo Mondego. Absolute abundances per gram of powdered rock were obtained following the Geisen et al. (1999) method. Briefly, about 30 mg of dried rock powder were mixed with water that was oversaturated with respect to $CaCO_3$ and with a basic pH, and allowed to settle for 24 h on a cover slide in a settling box. The cover slide was then recovered after drying

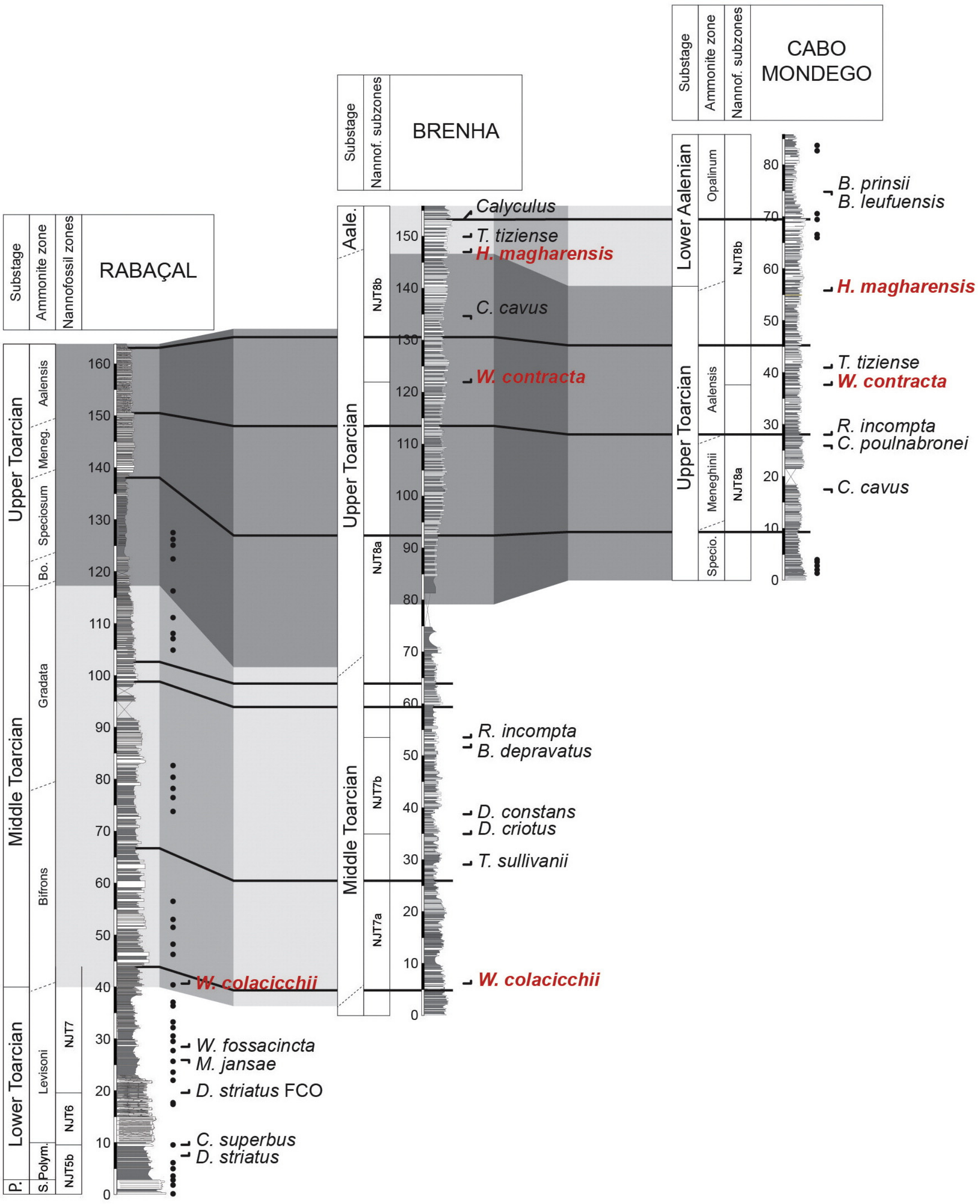


Fig. 2. Stratigraphic correlation between the three studied sections. Major bioevents and nannofossil zones/subzones are plotted. Lithostratigraphic correlation and calcareous nannofossil biostratigraphy were used to correlate Brenha with the two other sections due to the absence of ammonite calibration across this section. Black dots represent sampled brachiopods.

and permanently mounted on a microscope slide. At least 300 coccoliths were counted in every sample and studied under an optical polarized microscope with x1000 magnification. *Schizosphaerella* was tallied in the same number of fields of view as the 300 coccoliths were being recorded. According to Fatela and Taborda (2002) the counting of 300 specimens per sample is statistically robust to record all the species making up more than 1.7% of the total assemblage with a confidence level of 99.5%. Some Rabaçal samples where coccoliths were scarce and a 300 count was not feasible, at least 400 fields of view were scanned. The relative abundance of coccolith species was calculated after the overall coccolith assemblage. Conversely, the relative abundance of the nannolith *Schizosphaerella* was obtained after the total nannofossil assemblage so that it would be easier to compare the changes of these two discrete planktonic groups. Absolute nannofossil abundance was determined after Geisen et al. (1999) according to the following formula:

$$X = \frac{N \cdot V}{m \cdot F \cdot S \cdot h}$$

where X is the number of nannofossils per gram of rock; N is the number of nannofossils counted in each sample; V is the water volume used to make the water-powder solution; m is the sample weighted and used to mix with water; F is number of fields of view counted; S is the area of each field of view; h is the height of the water column above the cover slides in the settling boxes.

3.2. Factor analysis and diversity

Factor Analysis (FA) (r-mode) was performed on all the samples after their relative abundance was calculated, since the variation measured in most naturally occurring phenomena can be described by the normal distribution, hence mirroring the central limit theorem (i.e., observations which are the sums of many independently operating processes tend to be normally distributed as the number of effects becomes large; Davis, 2002). This multivariate statistical approach allows global coccolith assemblages to be compared, where variables with correlative linear behaviours can be selected and their importance recognized. It is then possible to obtain an immediate association of correlated variables. Moreover this method also provides the hierarchy of components as data discriminators. Other main advantage of FA is that once patterns are found in the data, we can then compress the data by reducing the number of dimensions without much loss of information. FA was computed with PAST 3.01, where only factors with a significant contribution to the variance were taken into account. Only taxa with an average abundance >2% were used in the data matrix since it is impossible to determine if the absence of rare taxa is due to observation bias, sampling casualness, diagenesis or simply absence in the original association. In this work the matrix algebra consists of 15 taxa and factors were extracted using a variance-covariance matrix first and then a correlation matrix where variables were normalized after being divided by their standard deviation, therefore smoothing the signal given by the most abundant taxa and enhancing the less abundant ones.

The Shannon index is herein used as a species diversity measure based on the proportional abundance of each species. The index, which is the negative sum of each taxon's proportional abundance multiplied by the log of its proportional abundance, is a measure of the amount of information (entropy) in the system and is positively correlated with species richness and evenness (distribution of individuals over species), giving more weight per individual to rare than common species (Hill et al., 2003). The Shannon index was determined for each of the sections separately using the PAST 3.01 software.

3.3. Stable carbon and oxygen isotopes

A total of 50 brachiopod shells were analyzed for their carbon and oxygen isotope composition. In Rabaçal, 39 samples spanning from the base of the Toarcian (Polymorphum ammonite zone) to the Late Toarcian (Speciosum ammonite zone) were analyzed, whereas in Cabo Mondego 11 samples spanning from Speciosum ammonite zone to Early Aalenian (Opalinum ammonite zone) were studied. The stable-isotope profiles correspond to a composite of different taxa of rhynchonellids, spiriferinids and terebratulids. As articulate brachiopods are assumed to be strictly benthic and generally sessile organisms, it is thought that their oxygen isotope composition reflects the temperature or salinity of their environment (Brand et al., 2003, 2014; Suan et al., 2008b). Considered to be secreted out from isotopic equilibrium with oceanic water in modern species (e.g., Carpenter & Lohmann, 1995; Auclair et al., 2003; Parkinson et al., 2005), the primary layer was carefully removed and it was only the second fibrous calcite layer to be sampled with a dental drill under a binocular microscope. Stable carbon and oxygen isotope analyses of brachiopod shells were performed using a Thermo Fisher Scientific (Bremen, Germany) Gas Bench II carbonate preparation device connected to a Delta Plus XL isotope ratio mass spectrometer at the Institute of Earth Surface Dynamics of the University of Lausanne. The CO_2 extraction was done by reaction of 100-200 μg of powdered rock with anhydrous phosphoric acid at 70 °C. The stable carbon and oxygen isotope ratios are reported in the delta (δ) notation as the per mil (‰) deviation relative to the Vienna Pee Dee belemnite standard (VPDB). The standardization of the $\delta^{13}C$ and $\delta^{18}O$ values relative to the international VPDB scale was done by calibration of the reference gases and working standards with IAEA standards. Analytical uncertainty (1σ), monitored by replicate analyses of the international calcite standard NBS-19 and the laboratory standards Carrara Marble was not greater than ±0.05‰ for $\delta^{13}C$ and ±0.1‰ for $\delta^{18}O$.

4. Results

4.1. Biostratigraphy

Age calibration in the Rabaçal section was based on well-established ammonite biochronology (Comas-Rengifo et al., 2013; Pittet et al., 2014), whereas ammonite zonation in Cabo Mondego was established by Canales and Henriques (2008). In the Brenha section, stages and substages were solely defined using calcareous nannofossil bioevents. The nannofossil zones and subzones used herein refer to the biostratigraphic schemes presented by Bown and Cooper (1998) for NW Europe and Mattioli and Erba (1999) for the Mediterranean Tethys. Four nannofossil zones from NJT5b to NJT8 were recognized. Though sporadic occurrences of *Discorhabdus striatus* were observed in the basal Toarcian at the top of the Polymorphum zone, its consistent occurrence was only recorded in the Levisoni zone. Therefore the First Common Occurrence (FCO) of *D. striatus* rather than its First Occurrence was used to define the nannofossil zone NJ7 (Boreal) or NJT7 (Tethyan) in Rabaçal. In Peniche, located in the southern part of the Lusitanian Basin, Mattioli et al. (2013) also observed a similar record for *D. ignotus* as its sporadic occurrence precedes its consistent occurrence. All subsequent nannofossil zonation follows accordingly both zonation schemes (Fig. 2).

4.2. Geochemical data

Long-term excursion of $\delta^{13}C_{brachiopod}$ values varied from 0.9‰ (VPDB) in the uppermost Pliensbachian to 5.4‰ in the lower Toarcian sediments. Following the same trend recorded in Peniche (Suan et al., 2008b) across the lower Toarcian, the long-term C-isotope excursion shows an increase from 1.1 to 3.9‰ during the Polymorphum zone followed by a negative excursion at the base of the Levisoni zone coeval with the T-OAE equivalent period, after which it sharply picks up again throughout the Early Toarcian displaying an average value of 4.4‰. From the middle Toarcian the δ^{13}C values gradually start declining to 2.0‰, again increasing somewhere above the Speciosum zone, reaching 3.0‰ in the Early Aalenian.

The long-term curve from $\delta^{18}O_{brachiopod}$ varies between -2.4‰ immediately above the T-OAE and 0.2‰ in the lower Aalenian sediments. The steep negative excursion in δ^{18}O that defines the boundary between the Pliensbachian and Toarcian is followed by a positive shift that lingers throughout the Polymorphum zone. Above the T-OAE, δ^{18}O values remain extremely negative throughout the Early Toarcian and part of the middle Toarcian. The onset of a long-lasting positive excursion of δ^{18}O values starting from the Bifrons zone will continue up to the Early Aalenian, notwithstanding some perturbations recorded along the way.

Since the benthic fauna was absent, no data was retrieved from the T-OAE interval, so both δ^{18}O and δ^{13}C values recorded in the two sections follow the regional and global trends as reported by Duarte et al. (2007), Suan et al. (2008b, 2010) and Dera et al. (2009a,b; 2011a,b). Isotopic temperatures were calculated after the equation of Anderson and Arthur (1983), assuming a constant isotopic δ^{18}O composition of -1‰ (VSMOW) in an ice free world:

$$\begin{aligned} T\,(^{\circ}C) \;=\; & 16.0 - 4.14\left(\delta^{18}O_{brach} - \delta^{18}O_{sw}\right) \\ & + 0.13\left(\delta^{18}O_{brach} - \delta^{18}O_{sw}\right)^{2} \end{aligned}$$

Isotopic bottom water temperatures varied in this region from 22 °C shortly after the thermal maximum in the Levisoni zone to 11 °C in the Early Aalenian. The maximum temperature recorded in this work differs by -3 °C from that obtained by Suan et al. (2008b) in Peniche using the same methodology, for the period immediately after the T-OAE. As expected, the long-term data of δ^{18}O from brachiopod shells reveal and confirm that the warming period during the T-OAE at the beginning of the Levisoni zone. The warm episode is followed by gradual cooling throughout the Toarcian and Early Aalenian. Moreover, in the middle Toarcian Gradata zone a perturbation in the long-term global cooling trend is recorded as a steep increase of 3 °C followed by a 3 °C decrease in water temperature. Another oscillation is also observed in the two last samples collected from the lower Aalenian section, displaying another warming up of bottom water masses as isotopic temperatures rose from 11 to 16.5 °C.

4.3. Nannofossil absolute abundance

Although preservation was not always good, especially between 10 and 20 m where reworked and overgrown coccoliths were common, lower Toarcian samples from the Rabaçal section rendered moderate to good preservation, therefore species identification was not hampered. In Rabaçal there is a significant shift in coccolith absolute abundance between the Polymorphum ammonite zone where total calcareous nannofossil abundances reached up to 532 millions/g and the Levisoni zone where they did not exceed 277 millions/g. The genus *Lotharingius* (Plate 1) and the species *Crepidolithus crassus* and *Similiscutum finchii* (Plate 2) have their highest absolute values in the Polymorphum ammonite zone whereas the species *Mitrolithus jansae* dominates all samples in the lower Levisoni ammonite zone until its extinction event (Fig. 3).

In Brenha the coccolith preservation was fairly good. Throughout the middle Toarcian until the Early Aalenian the overall coccolith abundance is fairly constant. Nevertheless, despite the recorded increases/decreases in absolute abundance being lithologically correlated with the marl-limestones alternations (i.e., nannofossils being more abundant in marls than in limestones), there is a slight increase in the total nannofossil abundances starting in the latest Toarcian reaching 312 millions/g. If *Lotharingius frodoi, L. hauffii, C. crassus* and *S. finchii* display their highest abundances during the middle Toarcian, in the Late Toarcian *Discorhabdus* species, *L. sigillatus, L. crucicentralis* and *L. velatus* are the most abundant taxa (Fig. 4).

Cabo Mondego rendered the best coccolith preservation from all the studied sections. Despite varying drastically according to the rhythmically hemipelagic sedimentation displayed by the most distal section of this work, the average calcareous nannofossil abundance throughout the succession was of 125 millions/g, with the highest value of 316 millions/g recorded in the Opalinum zone. Noteworthy was the steady increase in the absolute abundance of *Watznaueria colacicchii* in the lower Aalenian top three samples (Fig. 5).

Schizosphaerella absolute abundance is rather high throughout the entire studied period, with the exception for the tempestite interval in Rabaçal, where although our samples came from marly interbeds, resedimentation mainly occurred. Actually, though synchronous with the T-OAE there is no sedimentological evidence for anoxia in Rabaçal, probably due to storm events being responsible for water column re-oxygenation. During the middle Toarcian *Schizosphaerella* abundance gradually recovers reaching high values by the end of the Late Toarcian and Early Aalenian.

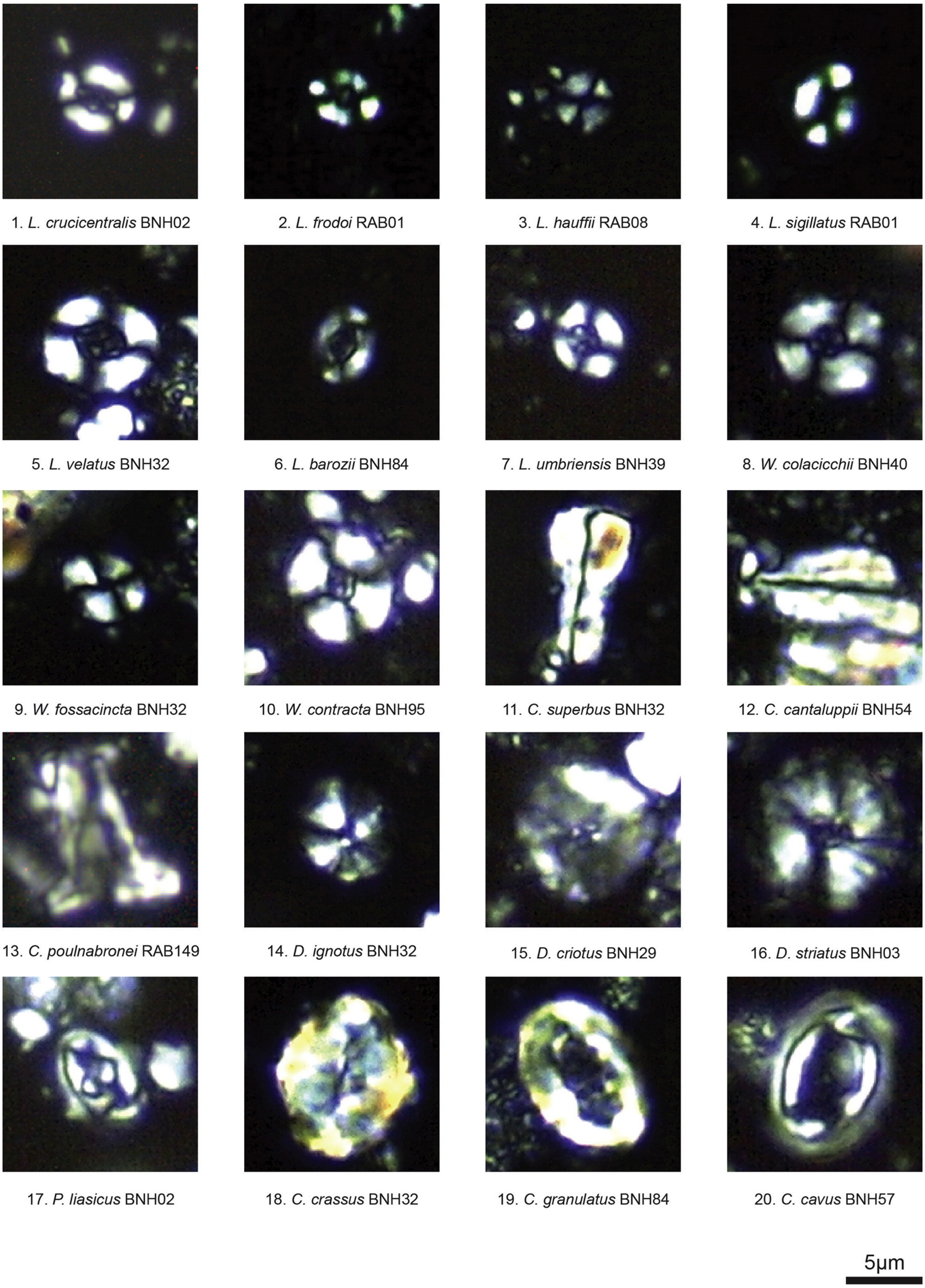
4.4. Nannofossil relative abundance

Along the three studied sections, *Schizosphaerella* tends to dominate over coccolithophores, except for the interval between 10 and 22 m in Rabaçal, where the calcarenites–calcisiltites that make up the beds at the base of the Levisoni zone dominantly exhibit storm-induced sedimentary structures, such as plane-parallel laminations and hummocky cross-stratifications (Pittet et al., 2014). It is only in the levels sampled between the tempestite beds, that in some cases this group makes up less than 10% of the nannofossil assemblage. After this extreme event, *Schizosphaerella* recovered and again dominated reaching on some occasions nearly 80% of the total assemblage. Its relative abundance is fairly constant around 50% throughout the middle and Late Toarcian though it tends to increase towards and throughout the Early Aalenian (Fig. 6).

In Rabaçal the *Lotharingius* genus is the best represented taxon in all samples with the exception for the tempestite interval in the lower Levisoni ammonite zone, where *M. jansae* dominates, reaching 100% in four of the poorest samples. In the late Levisoni ammonite zone small *Lotharingius* such as *L. hauffii, L. frodoi* and *L. sigillatus* clearly dominate all of the assemblages though their absolute abundances are low. In Brenha the *Lotharingius* genus dominates all the assemblages despite the observed increase in *C. crassus* and *S. finchii* relative abundances during the middle Toarcian. These two latter species relative abundances sharply decreased close to the boundary between the middle and Late Toarcian. It is in the Late Toarcian, somewhere in the Speciosum ammonite zone, that the *Discorhabdus* genus, and large *Lotharingius* spp. such as *L. sigillatus, L. crucicentralis* and *L. velatus* display their highest relative abundances. In Cabo Mondego the assemblages are dominated by *L. sigillatus* and *L. velatus*, closely followed by *L. crucicentralis*. A steady increase in *W. colacicchii* relative abundance is recorded in the latest Opalinum ammonite zone, reaching almost 17% of the total assemblage in the uppermost sample in this work.

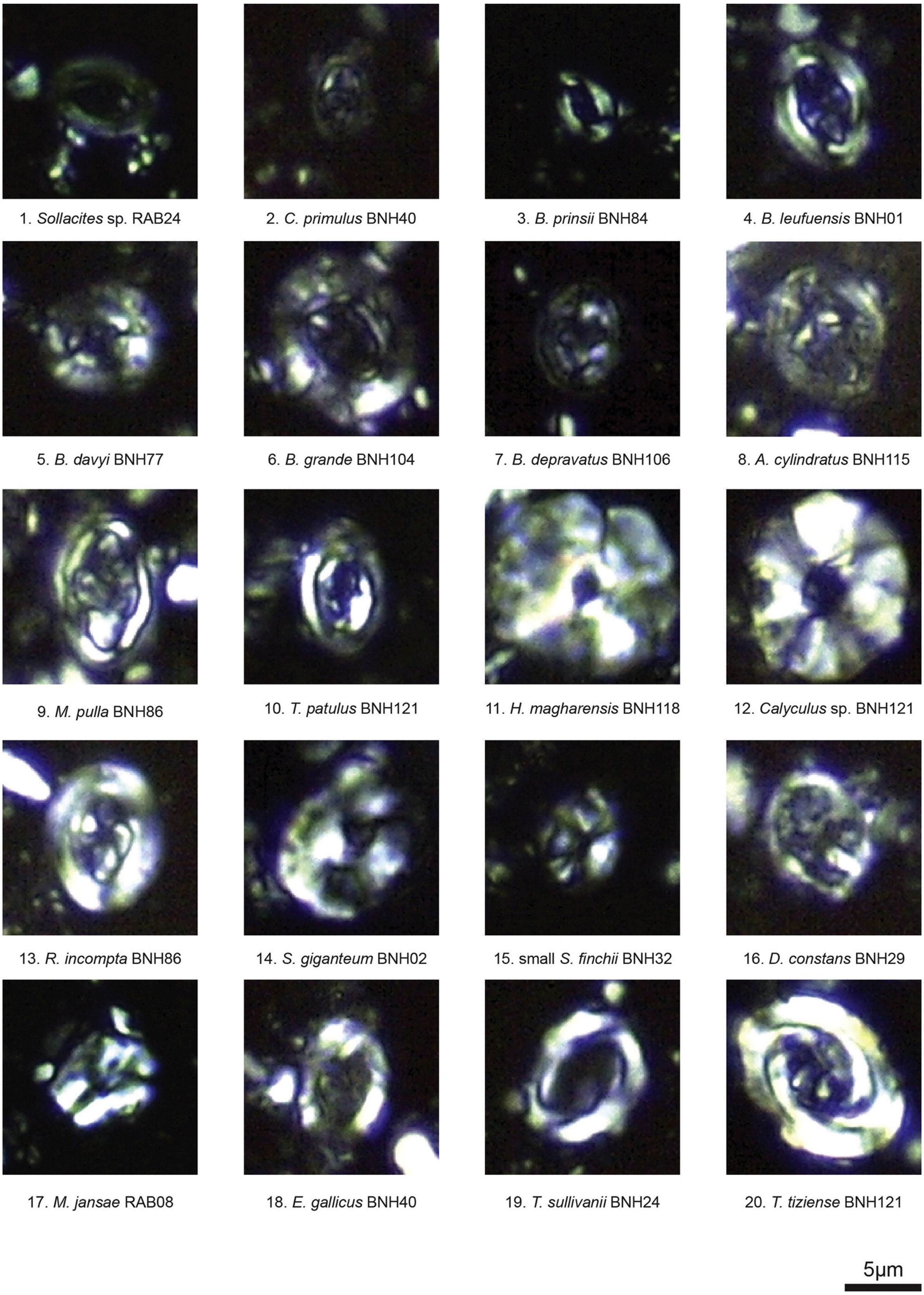
4.5. Factor analysis and diversity

Fifteen out of 52 species of coccoliths, each representing on average more than 2% of the total assemblages from the three sections were analyzed simultaneously through FA. A correlation data matrix was executed in order to better discriminate the behaviour of the less abundant species and to diminish the influence of the strong signal of *M. jansae* during the tempestite interval. The correlation data matrix rendered three main factors accountable for 53% of the total variance (Fig. 7). The first factor accounts for 27.3% of the total variance with a major contribution from *Carinolithus superbus, Discorhabdus* spp. and *L. velatus* in opposition to *L. hauffii, L. frodoi* and *M. jansae*. The second factor is accountable for 13.3% of the total variance and displays a



1. *L. crucicentralis* BNH02
2. *L. frodoi* RAB01
3. *L. hauffii* RAB08
4. *L. sigillatus* RAB01
5. *L. velatus* BNH32
6. *L. barozii* BNH84
7. *L. umbriensis* BNH39
8. *W. colacicchii* BNH40
9. *W. fossacincta* BNH32
10. *W. contracta* BNH95
11. *C. superbus* BNH32
12. *C. cantaluppii* BNH54
13. *C. poulnabronei* RAB149
14. *D. ignotus* BNH32
15. *D. criotus* BNH29
16. *D. striatus* BNH03
17. *P. liasicus* BNH02
18. *C. crassus* BNH32
19. *C. granulatus* BNH84
20. *C. cavus* BNH57

Plate 1. Micrographs taken from selected samples from Rabaçal (RAB) and Brenha (BNH) sections under cross-polarized light.



1. *Sollacites* sp. RAB24
2. *C. primulus* BNH40
3. *B. prinsii* BNH84
4. *B. leufuensis* BNH01
5. *B. davyi* BNH77
6. *B. grande* BNH104
7. *B. depravatus* BNH106
8. *A. cylindratus* BNH115
9. *M. pulla* BNH86
10. *T. patulus* BNH121
11. *H. magharensis* BNH118
12. *Calyculus* sp. BNH121
13. *R. incompta* BNH86
14. *S. giganteum* BNH02
15. small *S. finchii* BNH32
16. *D. constans* BNH29
17. *M. jansae* RAB08
18. *E. gallicus* BNH40
19. *T. sullivanii* BNH24
20. *T. tiziense* BNH121

Plate 2. Micrographs taken from selected samples from Rabaçal (RAB) and Brenha (BNH) sections under cross-polarized light.

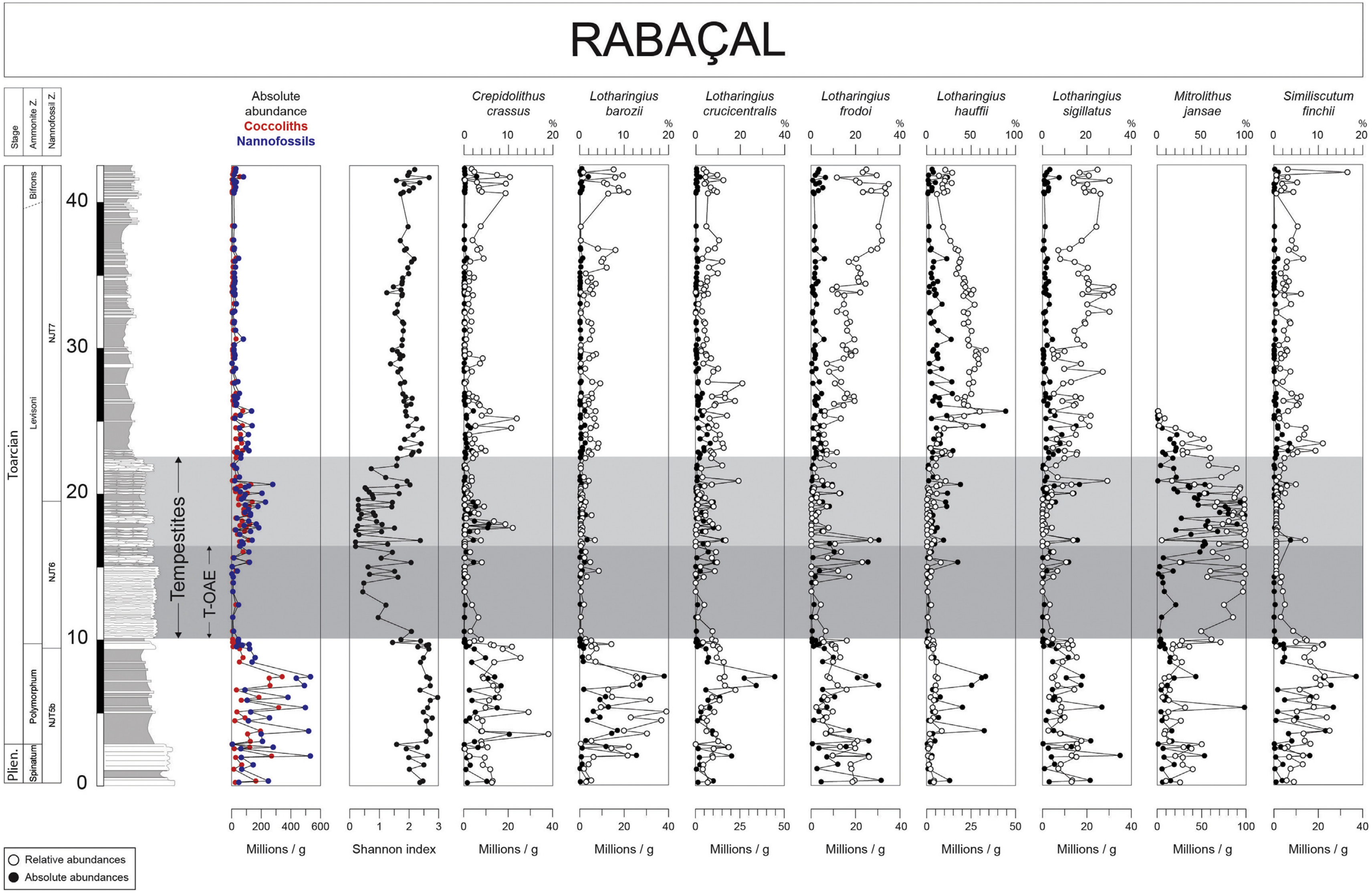


Fig. 3. Diversity, absolute and relative abundances of coccoliths making up more than 2% of the assemblage in Rabaçal.

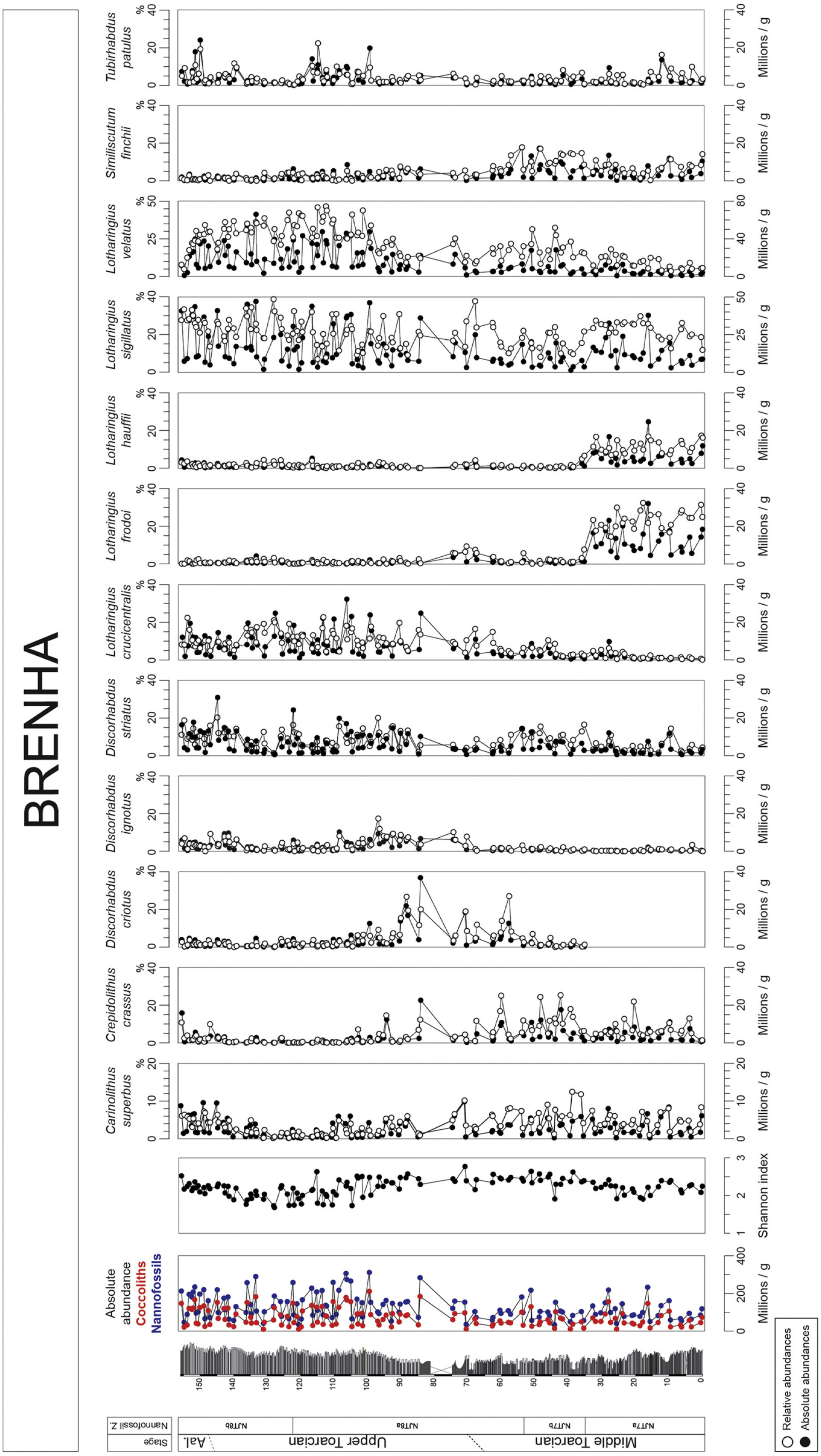


Fig. 4. Diversity, absolute and relative abundances of coccoliths making up more than 2% of the assemblage in Brenha.

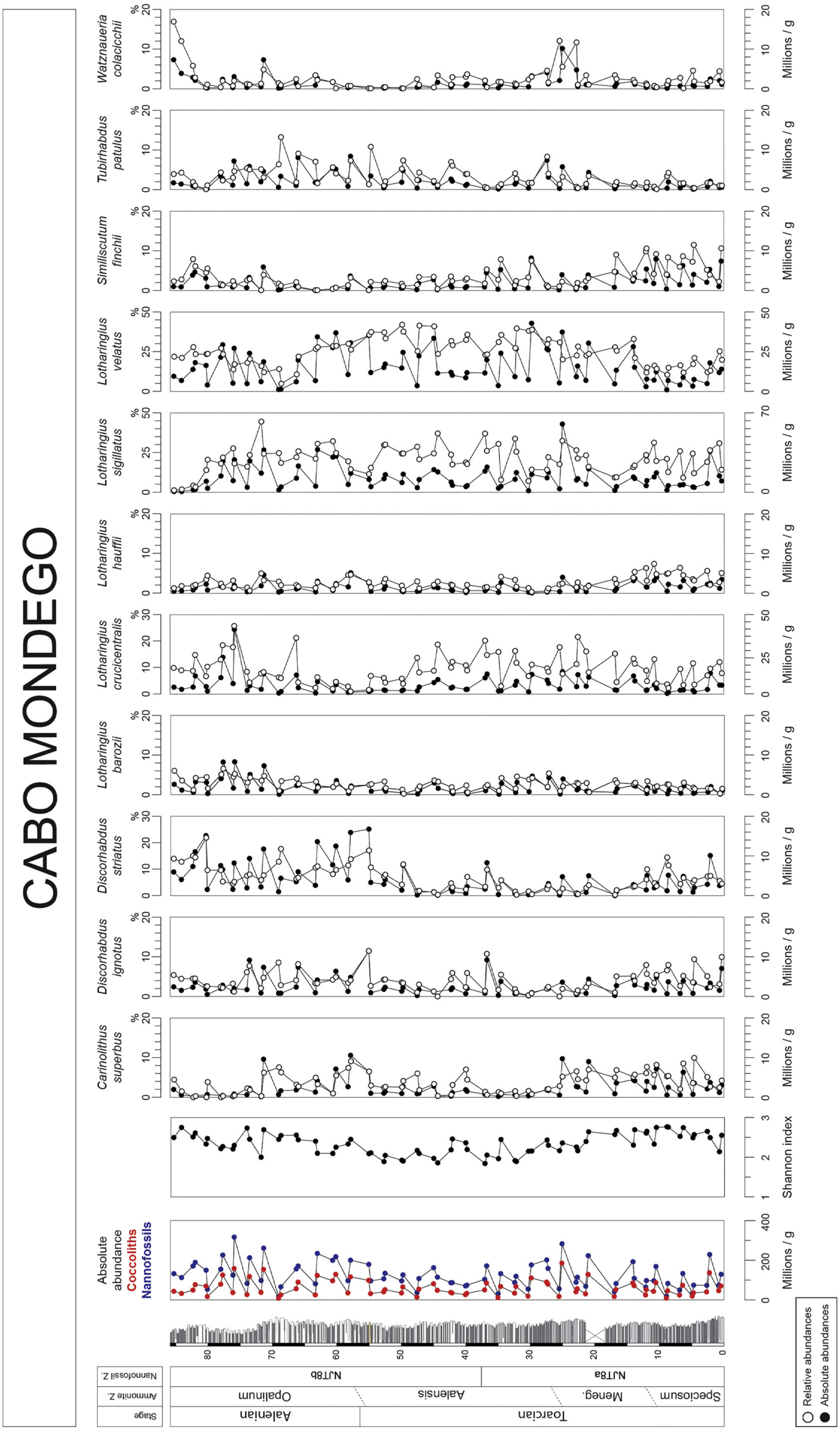


Fig. 5. Diversity, absolute and relative abundances of coccoliths making up more than 2% of the assemblage in Cabo Mondego.

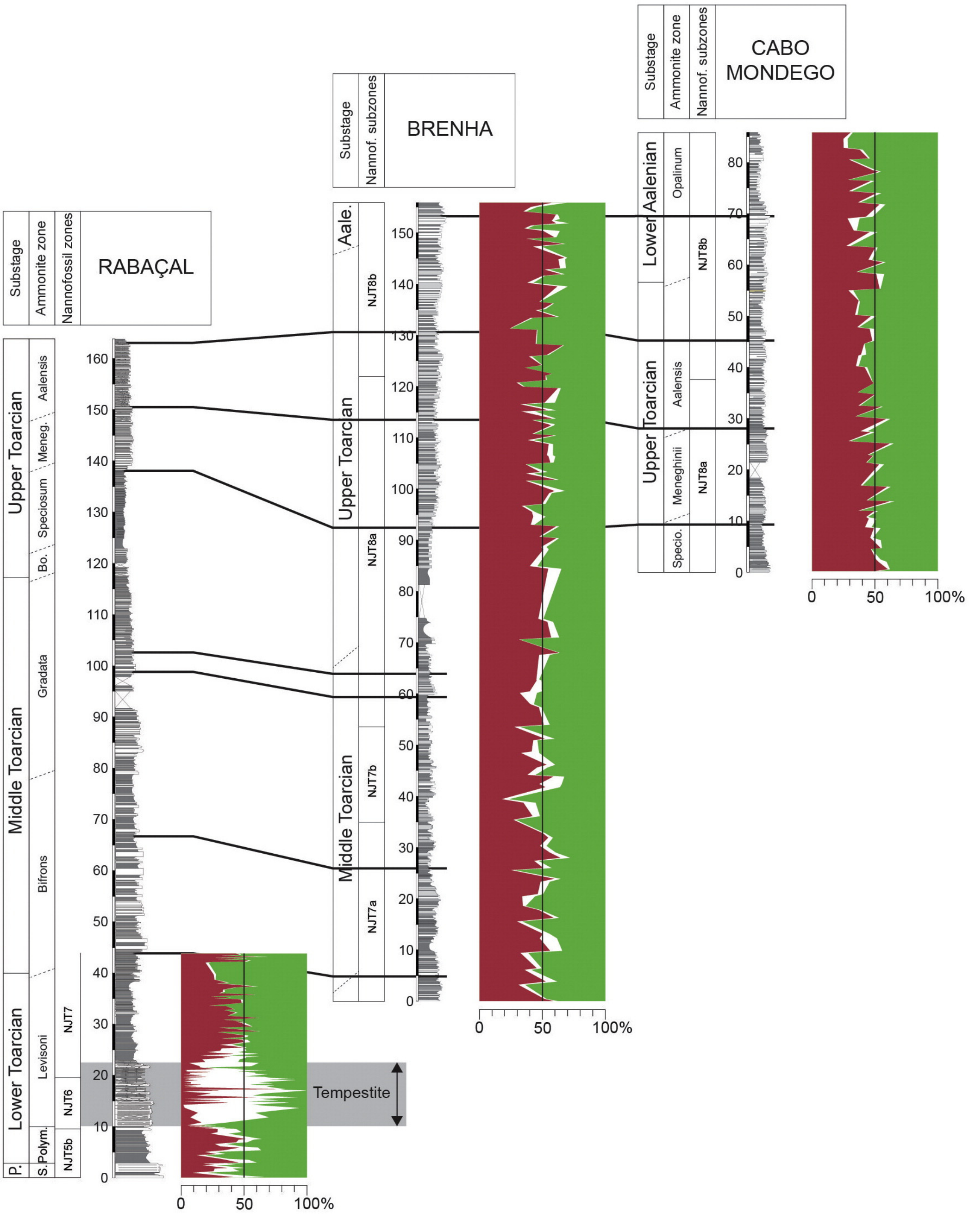


Fig. 6. Relative abundance between *Schizosphaerella* (green) and placoliths (red) and muroliths (white) in the three studied sections.

remarkable opposition between *C. crassus*, *S. finchii* and *C. superbus* against *L. crucicentralis*, *M. jansae* and *L. velatus*. The third factor (12.7% of the variance) displays the opposition between the six species of the *Lotharingius* genus against *M. jansae*. The stability of the factors has been tested by repeated treatments after excluding for instance, the interval corresponding to the tempestites or the dominant species (*M. jansae*) within this interval. It turns out that the 1st and 2nd factors are very stable whilst the third factor is not.

The record of highest coccolith diversity was attained in the Polymorphum ammonite zone in the Early Toarcian where values of the Shannon diversity index reach 3.0. In the tempestite interval at the base of the Levisoni ammonite zone, diversity drastically dropped, with a mean value of 0.74 and in some samples close to zero. Upsection, and despite never reaching the high diversity values below the tempestite interval, diversity picked up again to a mean value of 1.9 in the Levisoni zone. Above the Early Toarcian diversity stays fairly constant, displaying an average value of 2.3 throughout the middle Toarcian and 2.2 across the upper Toarcian. Across the Meneghinii-Aalensis ammonite zone though, a slight decrease in diversity is observed both in Brenha and Cabo Mondego where values closely revolve around 2.0. In the lower Aalenian sediments, diversity once more slightly rose in both the latter sections to an average value of 2.3.

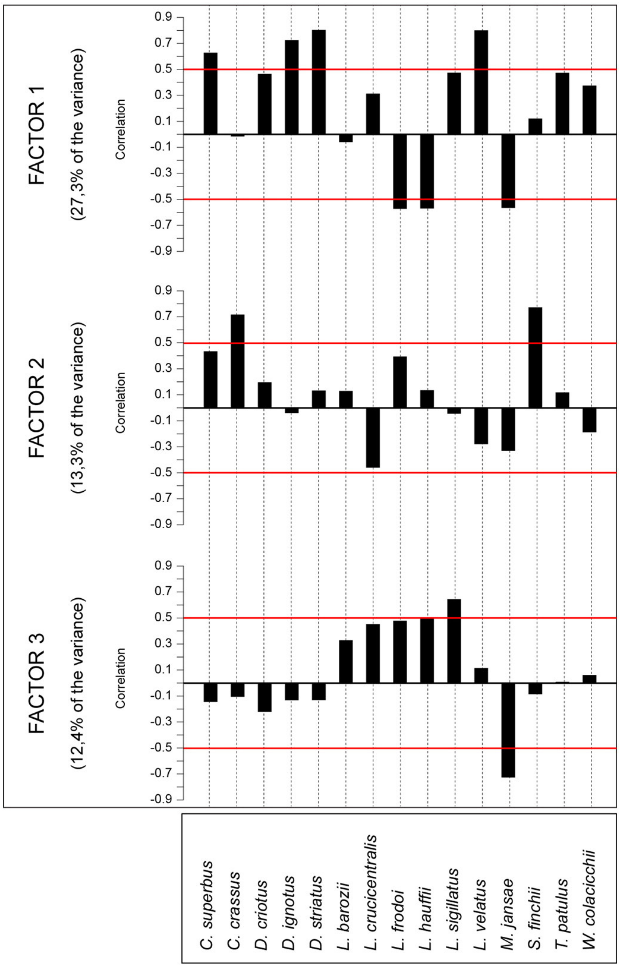


Fig. 7. Factors loadings of the 15 considered taxa. See the text for further explanations.

5. Discussion

5.1. Carbon and oxygen isotopes

A δ^{13}C positive excursion already observed in Peniche (Hesselbo et al., 2007; Suan et al., 2008b) is recorded across the Pliensbachian-Toarcian boundary (Fig. 8). In the Polymorphum zone δ^{13}C values remain fairly positive until the base of the Levisoni zone when the δ^{13}C curve undergoes a steep plunge during the tempestite interval. Though in this work no epibenthic fauna was found in the T-OAE equivalent beds, a negative excursion of whole rock δ^{13}C across this interval is well documented in Rabaçal (Pittet et al., 2014) as well as in numerous other Tethyan sites and linked with massive injection into the hydrosphere/atmosphere of isotopically light carbon related either to volcanic degassing or to methane release from continental margins (e.g., Hesselbo et al., 2000, 2007; Jenkyns et al., 2001; Suan et al., 2008a; Ruebsam et al., 2014). Above the T-OAE interval, another sharp δ^{13}C positive excursion already described in the literature (e.g., Hesselbo et al., 2007; Suan et al., 2008b; Sandoval et al., 2012; Krencker et al., 2014; Pittet et al., 2014; Reolid et al., 2014) is observed. This positive excursion lingered throughout the Early Toarcian and was associated with the maximum transgression period recorded in the Lusitanian Basin (Duarte et al., 2007). High positive values of δ^{13}C values suggest the water column returned to pre-tempestite conditions, hence enabling the rebuilding of the photic zone ecosystem, as positive δ^{13}C excursions recorded across the Early Toarcian are interpreted as reflecting oceanic primary productivity and preferential light carbon uptake in photosynthesis (e.g., Jenkyns & Clayton, 1986; Kump & Arthur, 1999; Jenkyns et al., 2002; Porter et al., 2014).

From the basal middle Toarcian, δ^{13}C values start to decline, as was already observed in other sections from Portugal (Duarte, 1998) and Spain (Sandoval et al., 2012 and references therein). From the Bifrons up to the Late Toarcian Speciosum zone, as sea level gradually receded, a gradual δ^{13}C negative excursion coupled with a decrease in nannofossil abundance is observed, suggesting a decline in primary productivity as rainfall and continental nutrient discharges would be less frequent, as inferred by the decrease in kaolinite contents in sediments of this age in the Lusitanian Basin (Duarte, 1998).

From the Speciosum to the Opalinum zone, a δ^{13}C negative trend inflects and significantly increases by 1‰ likely reflecting a small increase in oceanic productivity, probably caused by increased riverine discharges across a warm and humid Late Toarcian, as suggested by high phosphorous accumulation rates triggered by increased riverine input and enhanced weathering (Krencker et al., 2014). In fact, a significant escalation in nannofossil abundance is observed in Brenha across this

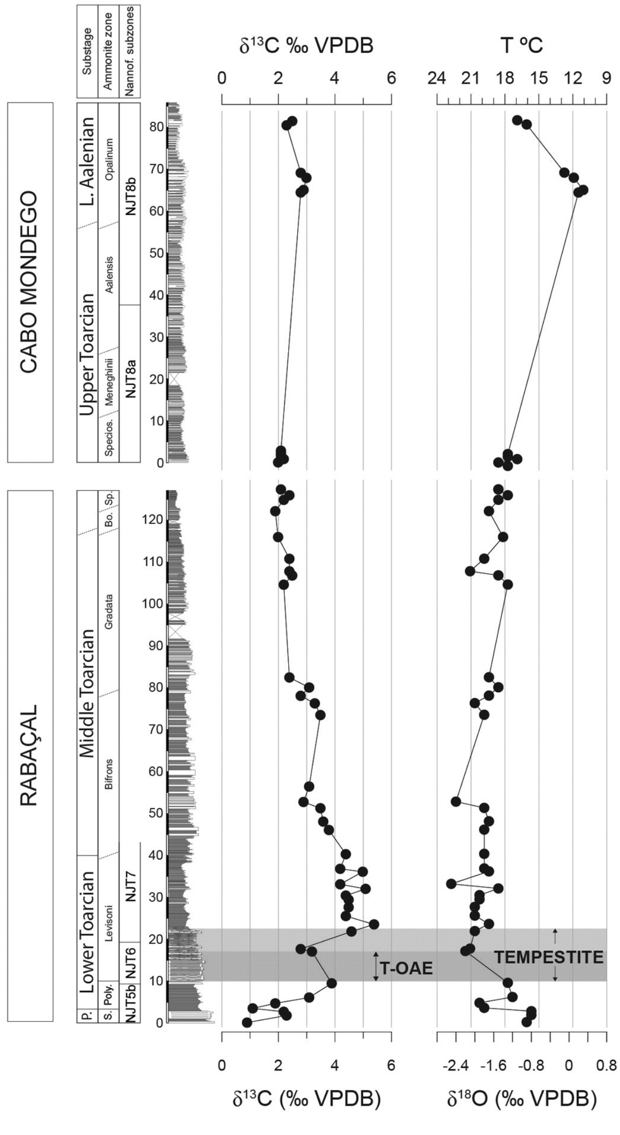


Fig. 8. Stratigraphic evolution of FA Factor scores. Eustatic levels oscillation refers to the Rabaçal section.

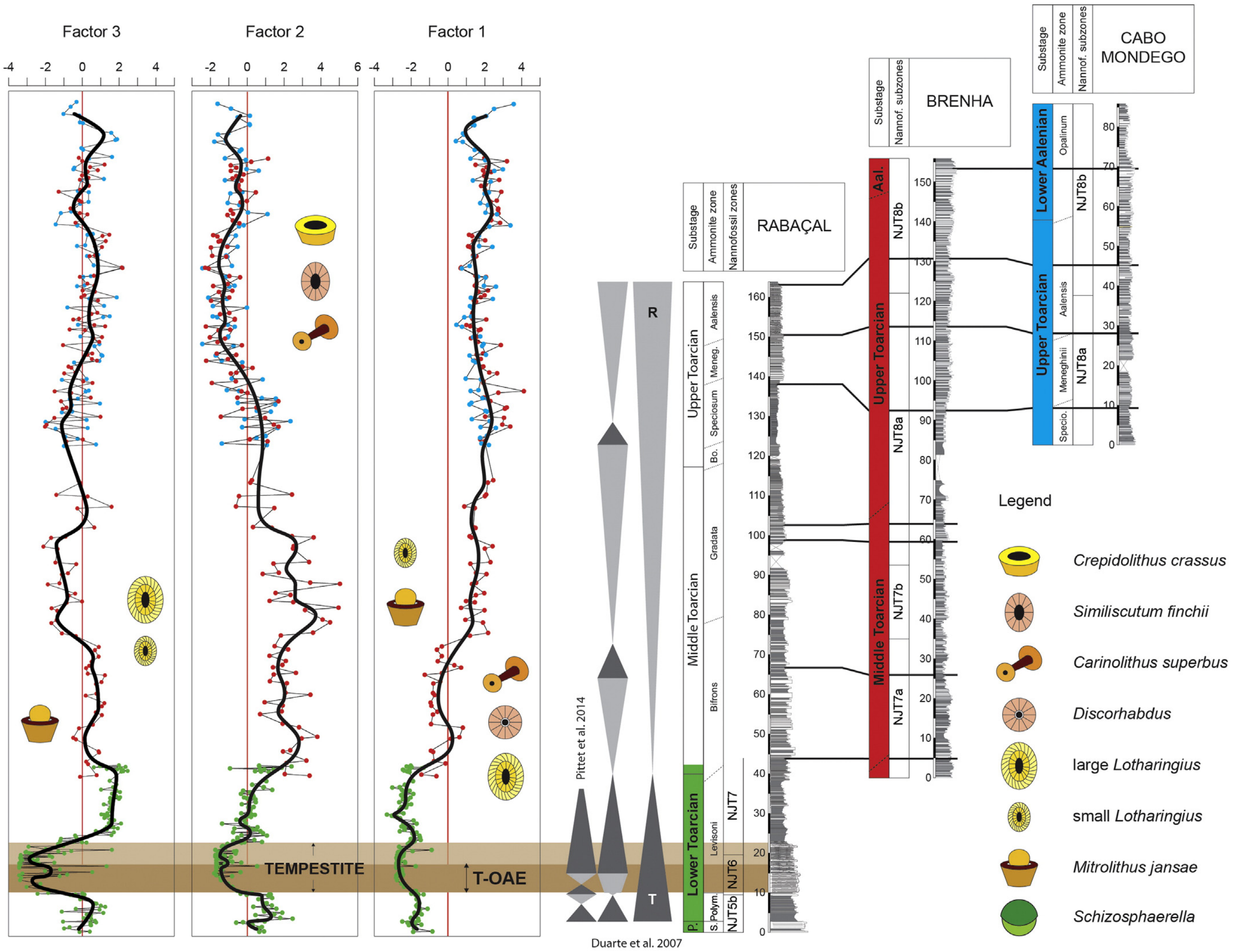


Fig. 9. Carbon and oxygen isotopic data from brachiopods shells of Rabaçal and Cabo Mondego sections.

interval. Though no isotopic data were obtained across the Speciosum-Opalinum interval in the studied sections, positive whole-rock $\delta^{13}C$ excursions are reported by Dera et al. (2011b) and Sandoval et al. (2008) for the upper Toarcian in general and starting in the Speciosum zone in detail by Krencker et al. (2014) in Morocco and by Harazin et al. (2012) in SE France. The apparent $\delta^{13}C$ negative excursion observed in the Opalinum zone is difficult to assess as only two samples were collected. Nevertheless, during a global long-term cooling trend, a short but significant perturbation in water temperature could affect the productivity in a stable, shallow and confined ecosystem such as the Lusitanian Basin.

The Pliensbachian-Toarcian boundary is also characterized by a drastic $\delta^{18}O$ negative excursion. Across this boundary water temperature shifts from approximately 15 °C in the uppermost Pliensbachian to 19.5 °C in the lowermost Toarcian, as also observed in Peniche (Suan et al., 2008b). During the Polymorphum zone a lasting $\delta^{18}O$ positive shift by ≈ 1‰ indicates bottom water temperatures of approximately 17 °C before the T-OAE equivalent. The differences in water temperature revealed by the $\delta^{18}O$ data immediately before and after this event shows a significant 4 °C increase, not much different from the 17 °C obtained in the middle Polymorphum zone and 24 °C in the middle part of the Levisoni zone obtained in Peniche by Suan et al. (2008b). After the T-OAE equivalent, $\delta^{18}O$ values remain fairly constant up to the Bifrons zone as they revolve around -2.0‰ and temperatures around 21 °C.

From the middle Toarcian and following the global cooling trend (Jenkyns et al., 2002; Dera et al., 2009a, 2011b; Krencker et al., 2014), a steady and long-lasting decrease in seawater temperature is observed in the Lusitanian Basin, supported by a gradual positive excursion in $\delta^{18}O$ values, displaying temperatures dropping progressively from approximately 21 °C to 11 °C in the Opalinum zone. The last two samples collected in the lower Aalenian show a significant absolute decrease by ≈1.4‰ in $\delta^{18}O$ values, representing a 5 °C rise in water temperature. Actually, this negative excursion cannot be fully assessed due to the reduced number of samples analyzed, though short oscillations in water temperatures have to be taken into account as it happened before in the middle Toarcian Gradata zone (Fig. 8) where temperatures fluctuated by 3 °C.

5.2. Factor analysis and fossil coccolithophore ecology

Extant coccolithophores are affected by a number of environmental factors (Brand, 1994; Winter et al., 1994; Young, 1994), so it is reasonable to infer that their Mesozoic equivalents were affected by the same factors. If they had been one of the most important primary producers in the Mesozoic oceans they would probably have been highly dependent on light penetration, nutrient supply and surface water temperature, and to a lesser extent on ocean currents and salinity (Mutterlose at al., 2005). Although the ecological affinities of Jurassic nannoplankton are yet poorly understood it is possible to infer palaeoecological,

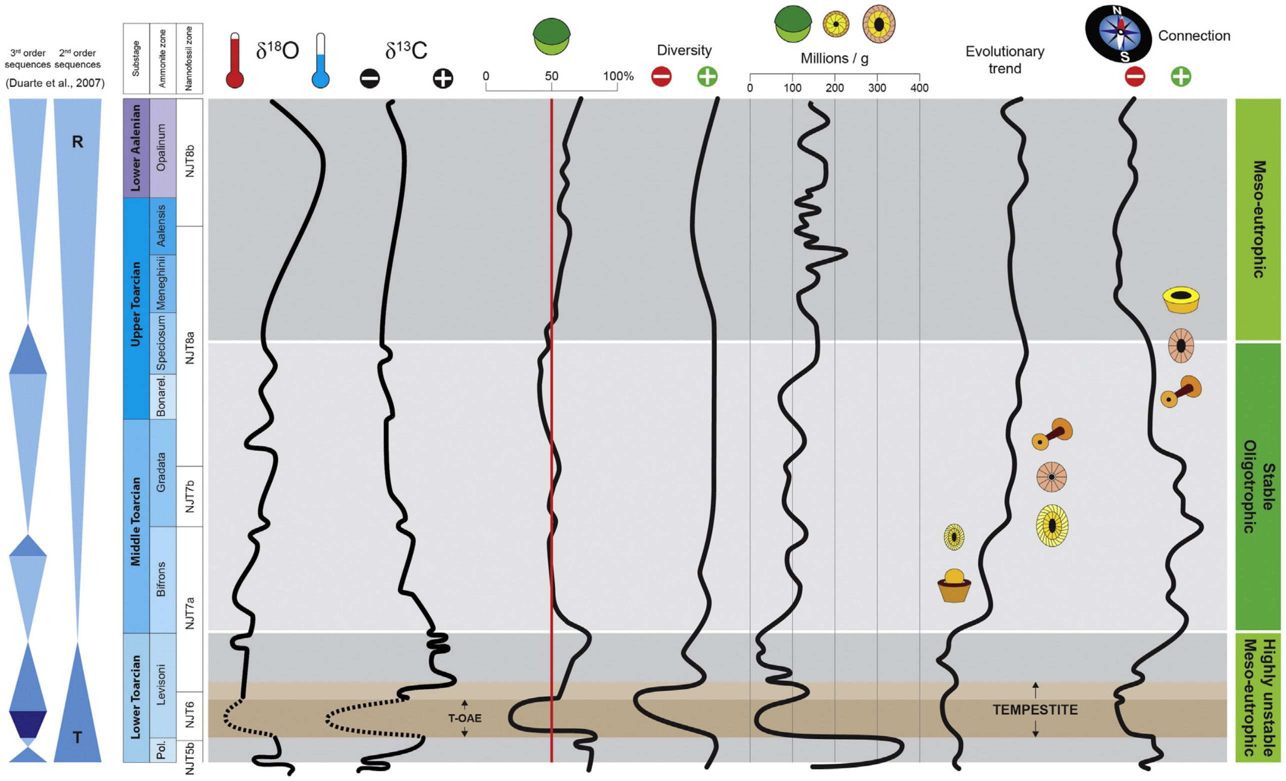


Fig. 10. Synthetic table for the three environmental changes in the Lusitanian Basin. Nannofossil absolute abundance curve was obtained after running a five points smoothing average. See legend of Fig. 9 for nannofossil explanation.

palaeoceanographic and palaeoclimatic changes through the study of their assemblages gathered from the geological record.

A correlation matrix was built for FA in order to interpret the ecological response to environmental changes of the different species. Factor 1 (Fig. 9) illustrates the strong opposition between the abundances of taxa dominating during the Early Toarcian (namely *M. jansae* and small *Lotharingius* species) and alternatively, during the middle-Late Toarcian (namely, *C. superbus*, different *Discorhabdus* spp. and large *Lotharingius* spp. such as *L. velatus*).

Factor 2 shows the coupling between *C. crassus*, *S. finchii* and to a lesser extent *C. superbus*, as opposed to *L. crucicentralis*. *Crepidolithus crassus* is interpreted as a deep-dweller within the photic zone where its large and heavy coccoliths may have allowed them to maintain a position deep within nutricline waters (Bour et al., 2007; Mattioli et al., 2008; Reggiani et al., 2010; Suchéras-Marx et al., 2010). The Biscutaceae in general and *S. finchii* in detail, together with *Lotharingius*, are interpreted as meso-eutrophic taxa dwelling mostly in the upper photic zone, as are small and thin extant coccolithophores (Bucefalo Palliani & Mattioli, 1995; Pittet & Mattioli, 2002; Mattioli & Pittet, 2004; Olivier et al., 2004; Tremolada et al., 2005; Mattioli et al., 2008; Fraguas et al., 2012). The coupling between North Tethyan affiliated species such as *C. crassus* and *S. finchii* (Mattioli et al., 2008), and *C. superbus* which is typically recorded in southern Tethys settings (Mattioli et al., 2008), can be interpreted as evidence of mixing between northern and southern water masses within the Lusitanian Basin. In stratified waters the nutrients are slowly recycled through convection between the nutricline and surface waters. *C. superbus*, a tubelike coccolith, probably thrives in the uppermost photic zone, as does the related genus *Calyculus*, which was reported to thrive in low-nutrient surface waters by Mattioli et al. (2008).

Factor 3 shows the opposition between all the species of *Lotharingius* to *M. jansae*. Even though Factor 3 should be interpreted with caution due to its small contribution to the global variance, the strong opposition between *Lotharingius* spp. and *M. jansae* may be interpreted as evidence of nutricline depth within the photic zone. In fact, *M. jansae* is interpreted as a deep dweller by some authors (Bucefalo Palliani & Mattioli, 1995; Mattioli & Pittet, 2004) and an intermediate dweller by others (Erba, 2004; Tremolada et al., 2005), besides bearing southern Tethys affinities (Bown, 1987; Mattioli et al., 2008). However, the record of *M. jansae* in the tempestite interval, when surface waters should have been efficiently mixed by storms, contrasts with water column stratification and the setting of a deep nutricline. As the specimens of *M. jansae* recorded in the tempestite interval are very poorly preserved, we can reasonably infer that these were accumulated in the tempestite interval due to reworking and winnowing of older sediments since this is a robust murolith resilient to dissolution. Actually, a major regression shortly followed by a transgression is interpreted at the base of the tempestite interval by Duarte et al. (2007) and Pittet et al. (2014). Marine erosion during this regression and ensuing transgression, as well as local subaerial exposure may have removed preexisting sediments from localized areas of the Lusitanian Basin (Pittet et al., 2014). Interestingly, *M. jansae* is a taxon resilient to taphonomic processes and is profusely recorded in upper Pliensbachian and lowermost Toarcian outcrops from the Lusitanian Basin (Mattioli et al., 2008; Reggiani et al., 2010; this study). Therefore, the negative values of Factor 3 across the tempestite interval are most likely related to reworking of *M. jansae*, hampering any further palaeoenvironmental interpretation of this factor.

5.3. Long-term palaeoecological reconstruction

In order to evaluate the long-term evolution of the nannofossil assemblages in the Lusitanian Basin and assess any relationship with abiotic parameters such as water temperature or nutrient concentration, evolution of factors from FA are interpreted together with geochemical data, diversity, nannofossil total abundances and relative abundance between placoliths, muroliths and *Schizosphaerella* (see Fig. 10).

5.3.1. Factor 1 and photic zone dynamics

The first factor extracted by FA is likely related to the Jurassic coccolithophore stratigraphic evolution (Fig. 9). The opposition between Early Toarcian dominant species (*L. hauffii*, *L. frodoi* and *M. jansae*) against those dominating the Late Toarcian (*C. superbus, Discorhabdus* spp. and *L. velatus*) stands out from the evolution of Factor 1 scores. Actually, during the Early Toarcian thermal maximum, highly unstable ecological conditions likely occurred, small *Lotharingius* dominate over larger forms, and new genera and species like *Carinolithus*, *Discorhabdus* and *Watznaueria* first occurred, whilst species dominating during the Early Toarcian like *Mitrolithus jansae* became extinct.

As shown by the δ^{18}O and δ^{13}C curves across the Early Toarcian, sea level, water temperature and oceanic primary productivity reached their highest values. At the Early-middle Toarcian boundary sea level was at its highest and the onset of an environment similar to pre-event conditions would thus promote the calcareous phytoplankton recovery, as primary productivity is likely associated to eustatic sea level rise (Donovan et al., 1979; Jenkyns & Weedon, 2013). Actually, during the onset of a transgressive period, carbonate ramp or terrestrial organic matter would be gradually recycled and as today, a warm climate would then promote primary oceanic productivity through accelerated continental weathering and ensuing runoff (De Carlo et al., 2007), in addition occasional storms would stimulate water vertical mixing and upwelling (Chen et al., 2013) hence increasing surface water nutrification and consequently nannoplankton abundance.

Despite the increase in diversity and in δ^{13}C values after the T-OAE equivalent, nannofossil abundances remain low in Rabaçal, bearing an average count of 60 millions/g. This trend was also recorded in Peniche by Mattioli et al. (2008) and is probably due to higher accumulation rates diluting nannofossil contents, and also diagenesis in Rabaçal as such low abundances are not recorded in any of the other sections where preservation is far better. Nevertheless, after the extinction event of *M. jansae* shortly after the end of the tempestite episode, the dominance of shallow-dwellers such as *Schizosphaerella* and *L. hauffii*, *L. frodoi,* and *L. sigillatus* within the calcareous nannoplankton community, suggests this was a period of gradual environment restoration of surface waters to pre-tempestite conditions.

During the middle Toarcian, temperatures and regional sea level slowly start to decrease and environmental conditions become more and more stable since rainfall and continental runoff would be less intense, as supported by the decreasing kaolinite content from five sections in the Lusitanian Basin across the Bifrons and Gradata zones (Duarte, 1998). Coeval with the decrease in δ^{13}C values and nannofossil abundances that will linger up to the Late Toarcian Speciosum zone, in the middle Toarcian we observe the replacement between the smaller *L. hauffii* and *L. frodoi*, plunging from 20-30% each to less than 5% or even absent, and the progressive dominance of the larger species *L. crucicentralis* and *L. velatus*. Conversely, *L. sigillatus* preserves its abundance around 20% throughout the middle Toarcian. It is also during this stable period that we register the first occurrence of important statigraphic markers such as *Discorhabdus criotus* and *Biscutum depravatus*, besides *Triscutum sullivanii,* and *Retecapsa incompta* (Fig. 2). These observations validate that the stable conditions inferred for the middle Toarcian favoured the ecological replacement within the *Lotharingius* genus and background evolution, as already supported by Mattioli and Erba (1999) and Aguado et al. (2008).

Both in Brenha and Cabo Mondego, the presence of *C. superbus* in all samples is noticeable, sometimes bearing abundances reaching 10% of the assemblage. Such ubiquity was never recorded in the lower Toarcian samples from Rabaçal possibly due to the proximity from maximal continental drainage and turbidity, when temperatures and sea level were at their highest. Such abundances in *C. superbus* support the interpretation that this coccolith is a good indicator of stratified and low-nutrient surface waters. Additionally, an equilibrium spanning across the Bifrons-Speciosum zones between coccolithophores and *Schizospharella* seems to have been reached as none of the phytoplanktonic groups dominate clearly over the other, as it happened before in the Early Toarcian (Fig. 6). In fact, as diversity mounts throughout the Bifrons-Speciosum zones an expanded photic zone should have boosted diversity, as more ecological slots were available for photosynthetic organisms and restraining competition for nutrients and light (Hallock, 1987). This would thus be a period characterized by persistent stratified waters, where *C. superbus* proliferated in the upper photic zone whereas *C. crassus* would have occupied the ecological niche within the deep photic zone when the nutricline was also deep.

From the warm and humid Late Toarcian Speciosum zone to the Early Aalenian, as temperatures relentlessly continue to fall, dropping from 17 to 11 °C, an increase in δ^{13}C is observed. A disruption in water stratification likely occurred during this period, as attested by the increase in the shallow-dwelling southern Tethys taxon *Schizosphaerella*, and also by the increase in nannofossil absolute abundance. An escalation in nutrient supply through runoff coupled with the ongoing and steady shoaling of the photic zone and nutricline, would thus increase water eutrophication as suggested by the progressive domination of the coccolithophore community by the meso-eutrophic genus *Discorhabdus* and large *Lotharingius* species as illustrated by Factor 1. Moreover, this period is characterized by a significant and continuous decrease in species diversity and in the abundance of the likely oligotrophic *C. superbus*, as also reflected by Factor 1. The continuous increase in *Watznaueria colacicchii* abundances at the topmost Early Aalenian suggests that it is from the Opalinum zone that the *Watznaueria* genus starts its dominance throughout the Mesozoic at the expense of its phylogenic ancestor *Lotharingius* (Mattioli, 1996). The same event was also reported and suggested by Aguado et al. (2008) for the south of Spain.

5.3.2. Factor 2, sea level and basin connections

The apparent relation between Factor 2 and the mixing of northern Tethys species such as *C. crassus* and *S. finchii*, and southern species such as *C. superbus*, seems to indicate a north and south water masses mixing within the Lusitanian seaway across the Early and middle Toarcian when sea level was at its highest (Fig. 9). This N-S connection would then be gradually cut off during the Late Toarcian. Actually, *C. crassus* and *S. finchii* are more abundant in the Early and middle Toarcian as the mixing between the Mediterranean and Euro-Boreal water masses was still easy across the onset of the lower Toarcian transgression, reaching its peak at the Early-middle Toarcian boundary (Duarte et al., 2007; Pittet et al, 2014). The apparent disconnection between Mediterranean and NW European waters during the tempestite event observed in Factor 2 is interpreted by Duarte et al. (2007) as the shallowing of the Lusitanian Basin through tectonic uplift. On the other hand, Pittet et al. (2014) interpreted this shallowing as eustatic in origin. Whatever the causes are, this shallowing and the subsequent occurrence of thresholds would explain the disconnection between Mediterranean and NW European waters and the decrease in diversity and nannofossil abundances yielded throughout this period.

Although basal middle Toarcian global seawater temperatures gradually started falling and sea level progressively receding, the Bifrons zone was still a warm period (Hallam, 1981; Dera et al., 2009a,b, 2011a) and the average water temperature in the Lusitanian Basin was approximately 21 °C. High scores from Factor 2 across this interval and the disruption between Arctic and Tethyan ammonite provincialism in the Bifrons zone support the argument that Mediterranean and Euro-Boreal waters were still homogenized (Dera et al., 2011a). Moreover, it is during the middle Toarcian that *C. crassus* reaches its highest relative abundances of almost 25% attesting the wide spread of NW Europe waters throughout the Lusitanian Basin.

From the Late Toarcian Speciosum zone upwards, as global temperature and sea level relentlessly continues to fall, the connection between NW European and Mediterranean waters was reduced to a minimum if not lost, as corroborated both by Factor 2 evolution, the decline in the relative abundance of muroliths and the gradual increase in *Schizosphaerella* relative abundance.

6. Conclusions

The calcareous nannofossil record mirrors the palaeoceanographic changes that occurred in the western Tethys. During the Toarcian and Early Aalenian three different long-term environmental conditions are acknowledged in the Lusitanian Basin. From the Polymorphum to Levisoni ammonite zones, as well during the maximum flooding period and under a warm and humid climate when NW European and Mediterranean Tethys waters masses were freely connected, the Lusitanian Basin waters bear a meso-eutrophic character. During this warm period, and as sea level rose, flooding of emerged lands and weathering of landmasses would increase the nutrient delivery to surface waters of the Lusitanian Basin. These nutrient-rich conditions would account for an overall high primary production as attested by $\delta^{13}C$ values and the proliferation of shallow-water taxa such as *Schizosphaerella* and the meso-eutrophic *Lotharingius*, and to the overall increase in nannofossil abundances. These conditions were interrupted in the T-OAE equivalent interval studied in Rabaçal, which is dominated by tempestite sedimentation related to a major sea-level fall, and numerous reworked nannofossils.

Across the middle Toarcian until part of the Speciosum zone, the highest sea level occurred promoting the mixing of NW European and Mediterranean waters, as corroborated by the mixing of typical nannoflora from both provinces. Stratified waters bearing a widened photic zone would still have supported the upper photic zone genus *Lotharingius*, but less *Schizosphaerella* and more *Carinolithus superbus* here interpreted as an oligotrophic shallow dweller, whereas in the deep photic zone *Crepidolithus crassus* would have thrived. Moreover, such stratified waters are associated with a steady increase in diversity.

During a humid period where the N-S connection was minimal as inferred by the decline in *C. crassus*, and Mediterranean waters filled the now shallower Lusitanian Basin, as accounted for the increase in *Schizosphaerella* abundance, somewhere in the Speciosum zone up to the Early Aalenian, the water column acquired a meso-eutrophic character, as the nutrification boost induced by continental discharges would have promoted the recorded increase in nannofossil abundance coeval with a decrease in diversity. These conditions occurred along with a significant rise in $\delta^{13}C$ values and a probable increase in primary production. Actually, the high fertility genera *Discorhabdus* and *Lotharingius* display high abundances during this interval whereas *C. superbus* decreases accordingly. It is in the Early Aalenian that the lowest marine temperatures are recorded.

It looks like highly unstable environmental conditions occurring in the Early Toarcian, namely nutrient concentrations and temperature fluctuations, triggered accelerated evolutionary processes within coccolithophores. Conversely, the following long-term temperature decrease in stable and stratified waters appears to be related with an assemblage replacement within the *Lotharingius* genus as recorded during the middle Toarcian Gradata zone, when small-sized *L. hauffi* and *L. frodoi* dominating in the Early Toarcian were gradually replaced by large-sized *L. velatus* and *L. crucicentralis*. Our data suggest that the *Watznaueria* inception is linked to an increase in water temperature that occurred after the temperature minimum of the Early Aalenian.

7. Species list

List of the 52 species identified in the present work, mentioned both in the text and in the plates. Taxonomy follows that of Bown (1987, 1998) and Mattioli (1996).

Anfractus harrisonii Medd, 1979
Axopodorhabdus atavus (Grün et al., 1974) Bown, 1987
Axopodorhabdus cylindratus (Noël, 1965) Wind and Wise in Wise and Wind, 1977
Biscutum davyi Perch-Nielsen, 1985
Biscutum depravatus (Grün and Zweili, 1980) Bown, 1987
Biscutum dubium (Noël, 1965) Grün in Grün et al., 1974
Biscutum grande Bown, 1987
Biscutum intermedium Bown, 1987
Bussonius leufuensis Bown and Kielbowicz, 1987 in Bown, 1987
Bussonius prinsii (Noël, 1973) Goy, 1979
Calyculus spp. Noël, 1973
Carinolithus cantaluppii Cobianchi, 1990
Carinolithus poulnabronei Mattioli, 1996
Carinolithus superbus (Deflandre in Deflandre and Fert, 1954) Prins in Grün et al., 1974
Crepidolithus cavus Prins ex Rood et al., 1973
Crepidolithus crassus (Deflandre in Deflandre and Fert, 1954) Noël, 1965
Crepidolithus granulatus Bown, 1987
Crucirhabdus minutus Jafar, 1983
Crucirhabdus primulus Prins, 1969 ex Rood et al., 1973 emend.
Diductius constans Goy, 1979
Discorhandus criotus Bown, 1987
Discorhabdus ignotus (Górka, 1957) Perch-Nielsen, 1968
Discorhabdus striatus Moshkovitz and Ehrlich, 1976
Ethmorhabdus crucifer Noël, 1965
Ethmorhabdus gallicus Noël, 1965
Hexalithus magharensis Moshkovitz and Ehrlich, 1976
Lotharingius barozii Noël, 1973
Lotharingius crucicentralis (Medd, 1971) Grün and Zweili, 1980
Lotharingius frodoi Mattioli, 1996
Lotharingius hauffii Grün and Zweili in Grün et al., 1974
Lotharingius sigillatus (Stradner, 1961) Prins in Grün et al., 1974
Lotharingius umbriensis Mattioli, 1996
Lotharingius velatus Bown and Cooper, 1989
Mazaganella pulla Bown, 1987
Mitrolithus elegans Deflandre in Deflandre and Fert, 1954
Mitrolithus jansae (Wiegand, 1984) Bown and Young in Young et al., 1986
Mitrolithus lenticularis Bown, 1987
Parhabdolithus liasicus Deflandre in Grassé, 1952
Retecapsa incompta Bown and Cooper, 1989
Silimiscutum avitum de Kaenel and Bergen, 1993
Similiscutum cruciulus de Kaenel and Bergen, 1993
Similiscutum finchii (Crux, 1984 emend. Bown, 1987) de Kaenel and Bergren, 1993
Similiscutum giganteum sp. nov. Mailliot, 2006
Similiscutum novum (Goy, 1979) Mattioli et al., 2004
Sollasites sp. Black, 1967
Triscutum sullivanii de Kaenel and Bergen, 1993
Triscutum tiziense de Kaenel and Bergen, 1993
Tubirhabdus patulus Prins ex Rood et al., 1973
Watznaueria colacicchii Mattioli and Reale in Mattioli, 1996
Watznaueria contracta (Bown and Cooper, 1989) Cobianchi et al., 1992
Watznaueria fossacincta (Black, 1971) Bown in Bown and Cooper, 1989
Zeugrhabdotus erectus (Deflandre in Deflandre and Fert, 1954) Reinhardt, 1965

Acknowledgments

The authors wish to thank Guillaume Suan for his valuable comments on the geochemical aspects of this work. We are grateful to Richard Jordan for improving and revising the English of this manuscript, and also to one anonymous reviewer for the constructive comments. This work received funding from the Portuguese FCT

(SFRH/BD/77762/2011) to JF, the Actions Intégrées Luso-Françaises 2011-2014 to EM, and the project INSU Syster 2011-2012 and Intervie 2014 to EM.

References

Aguado, R., O'Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Mar. Micropaleontol. 68, 268–285.

Anderson, T.F., Arthur, M.A., 1983. Stable isotopes of oxygen and carbon and their applications to sedimentologic and palaeontological problems. Econ. Palaeontol. Mineral. 10 (I. 1–I), 151 (Short Course).

Auclair, A.-C., Joachimski, M.M., Lécuyer, C., 2003. Deciphering kinetic, metabolic and environmental controls on stable isotope fractionations between seawater and shell of *Tetrabratalia transversa* (Brachiopoda). Chem. Geol. 202, 59–78.

Bailey, T.R., Rosenthal, Y., McArthur, J.M., van de Schootbrugge, B., Thirlwall, M.F., 2003. Paleoceanographic changes of the Late Pliensbachian–Early Toarcian interval: A possible link to the genesis of an oceanic anoxic event. Earth Planet. Sci. Lett. 212 (3–4), 307–320.

Bassoulet, J.P., Elmi, S., Poisson, A., Cecca, F., Bellion, Y., Guiraud, R., Baudin, F., 1993. Mid Toarcian. In: Dercourt, J., Ricou, L.E., Vrielynck, B. (Eds.), Atlas of Tethys Paleoenvironmental Maps. Becip-Franlab, Rueil-Malmaison, France, pp. 63–80.

Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical Paleoceanographic study of the Early Jurassic transcontinental Laurasian Seaway. Paleoceanography 16, 390–404.

Bour, I., Mattioli, E., Pittet, B., 2007. Nannofacies analysis as a tool to reconstruct palaeoenvironmental changes during the Early Toarcian anoxic event. Palaeogeogr. Palaeoclimatol. Palaeoecol. 249, 58–79.

Bown, P.R., 1987. Taxonomy, evolution and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. Spec. Pap. Palaeontol. 38, 1–118.

Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.), Calcareous nannofossilz biostratigraphy. British Micropalaeontological Society publication series. Kluver Academic Publishers, Cambridge, pp. 34–85.

Bown, P.R., Young, J.R., 1998. Introduction. In: Bown, P.R. (Ed.), Calcareous nannofossil biostratigraphy. British Micropalaeontological Society publication series. Kluver Academic Publishers, Cambridge, pp. 1–15.

Brand, L.E., 1994. Physiological ecology of marine coccolithophores. In: Winter, A., Siesser, W. (Eds.), Coccolithophores. Cambridge Univ. Press, Cambridge, pp. 39–49.

Brand, U., Logan, A., Hiller, N., Richardson, J., 2003. Geochemistry of modern brachiopods: Application and implications for oceanography and paleoceanography. Chem. Geol. 198, 305–334.

Brand, U., Azmy, K., Bitner, M.A., Logan, A., Zuschin, M., Came, R., Ruggiero, E., 2014. Oxygen isotopes and $MgCO_3$ in brachiopod calcite and a new paleotemperature equation. Chem. Geol. 359, 23–31.

Bucefalo Palliani, R., Mattioli, E., 1995. Ecology of dinoflagellate cysts and calcareous nannofossils from bituminous facies of the Early Toarcian, central Italy. Proc. III EPA Workshop: Black Shales Models, Dotternhausen, pp. 60–62.

Canales, M.L., Henriques, M.H., 2008. Foraminifera from the Aalenian and the Bajocian GSSP (Middle Jurassic) of Murtinheira section (Cabo Mondego, West Portugal): Biostratigraphy and palaeoenvironmental implications. Mar. Micropaleontol. 67, 155–179.

Carpenter, S.J., Lohmann, K.C., 1995. 18O and 13C values of modern brachiopod shells. Geochim. Cosmochim. Acta 59, 3749–3764.

Chen, X., Pan, D., Bai, Y., He, X., Chen, C.-T.A., Hao, Z., 2013. Episodic phytoplankton bloom events in the Bay of Bengal triggered by multiple forcings. Deep-Sea Res. I 73, 17–30.

Comas-Rengifo, M.J., Duarte, L.V., García joral, F., Goy, A., 2013. The brachiopod record in the Lower Toarcian (Jurassic) of the Rabaçal-Condeixa region (Portugal): stratigraphic distribution and palaeobiogeography. Comunicações GEológicas 100, 37–42.

Davis, J.C., 2002. Statistics and data analysis in geology. Wiley & Sons, New York, p. 656.

De Carlo, E.H., Hoover, D.J., Young, C.W., Hoover, R.S., Mackenzie, F.T., 2007. Impact of storm runoff from tropical watersheds on coastal water quality and productivity. Appl. Geochem. 22, 1777–1797.

Dera, G., Pellenard, P., Neige, P., Deconinck, J.F., Puceat, E., Dommergues, J.L., 2009a. Distribution of clay minerals in Early Jurassic Peritethyan seas: Palaeoclimatic significance inferred from multiproxy comparisons. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271 (1-2), 39–51.

Dera, G., Pucéat, E., Pellenard, P., Neige, P., Delsate, D., Joachimski, M.M., Reiseberg, L., Martinez, M., 2009b. Water masses exchange and variations in seawater temperature in the NW Tethys during the Early Jurassic: Evidence from neodymium and oxygen isotopes of fish teeth and belemnites. EPSL 286, 198–207.

Dera, G., Neige, P., Dommergues, J.-L., Brayard, A., 2011a. Ammonite paleobiogeogaphy during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Glob. Planet. Chang. 78, 92–105.

Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P., Joachimski, M.M., Durlet, C., 2011b. Climatic ups and downs in a disturbed Jurassic world. Geology 39, 215–218.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, 2000. Atlas Peri-Tethys, Palaeogeographical maps. CCGM/CGMW, Paris.

Dommergues, J.L., Mouterde, R., 1980. Modalités d'installation et d'évolution des harpocératinès (Ammonitina) au Domérien inférieur dans le Sud-Ouest de l'Europe. Geobios 13, 289–325.

Donovan, D.T., Horton, A., Ivimey-Cook, H.C., 1979. The transgression of the Lower Lias over the northern flank of the London Platform. J. Geol. Soc. 136, 165–173.

Duarte, L.V., 1998. Clay minerals and geochemical evolution in the Toarcian-Lower Aalenian of the Lusitanian Basin (Portugal). Cuad. Geol. Iber. 24, 69–98.

Duarte, L.V., 2004. The geological heritage of the Lower Jurassic of Central Portugal: selected sites, inventory and main scientific arguments. Riv. Ital. Paleontol. Stratigr. 110, 381–387.

Duarte, L.V., Oliveira, L.C., Rodrigues, R., 2007. Carbon isotopes as a sequence stratigraphic tool: examples from the Lower and Middle Toarcian marly limestones of Portugal. Bol. Geol. Min. 118 (1), 3–18.

Erba, E., 2004. Calcareous nannofossils and Mesozoic oceanic anoxic events. Mar. Micropaleontol. 52, 85–106.

Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil assemblages. Mar. Micropaleontol. 45, 169–174.

Fraguas, A., Comas-Rengifo, M.J., Gómez, J.J., Goy, A., 2012. The calcareous nannofossil crisis in Northern Spain (Asturias province) linked to the Early Toarcian warming-driven mass extinction. Mar. Micropaleontol. 94–95, 58–71.

Geisen, M., Bollman, J., Herrle, J.O., Mutterlose, J., Young, J.R., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437–442.

Gómez, J.J., Goy, A., Canales, M.L., 2008. Seawater temperature and carbon isotope variations in belemnites linked to mass extinction during the Toarcian (Early Jurassic) in Central and Northern Spain. Comparison with other European sections. Palaeogeogr. Palaeoclimatol. Palaeoecol. 258 (1–2), 28–58.

Gradstein, F.M., Ogg, J.G., Schmitz, M., Ogg, G., 2012. The Geological Time Scale 2012. Elsevier.

Hallam, A., 1981. A revised sea-level curve for the Early Jurassic. J. Geol. Soc. 138, 735–743.

Hallock, P., 1987. Fluctuations in the trophic resource continuum: a factor in global diversity cycles? Paleoceanography 2, 457–471.

Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2012. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian–Toarcian). Sedimentology 60, 359–390.

Hesselbo, S.P., Gröcke, D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Morgans-Bell, H.S., Green, O.R., 2000. Massive dissociation of gas hydrate during a Jurassic oceanic event. Nature 406, 392–395. http://dx.doi.org/10.1038/35019044.

Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V., Oliveira, L.C.V., 2007. Carbon-isotope record of the Early Jurassic (Toarcian) Oceanic Anoxic Event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). EPSL 253, 455–470.

Hill, T.C.J., Walsh, K.A., Harris, J.A., Moffett, B.F., 2003. Using ecological diversity measures with bacterial communities. FEMS Microbiol. Ecol. 43, 1–11.

Jenkyns, H.C., 1988. The Early Toarcian (Jurassic) anoxic event: stratigraphic, sedimentary and geochemical evidence. Am. J. Sci. 288, 101–151.

Jenkyns, H.C., Clayton, C.J., 1986. Black shales and carbon isotopes in pelagic sediments from the Tethyan Lower Jurassic. Sedimentology 33, 87–106.

Jenkyns, H.C., Weedon, G.P., 2013. Chemostratigraphy (CaCO3, TOC, δ13Corg) of Sinemurian (Lower Jurassic) black shales from the Wessex Basin, Dorset and palaeoenvironmental implications. Newsl. Stratigr. 46 (1), 1–21.

Jenkyns, H.C., Gröcke, D.R., Hesselbo, S.P., 2001. Nitrogen isotope evidence for water mass denitrification during the early Toarcian (Jurassic) oceanic anoxic event. Paleoceanography 16, 593–603.

Jenkyns, H.C., Jones, C.E., Gröcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. J. Geol. Soc. 159, 351–372.

Krencker, F.N., Bodin, S., Hoffmann, R., Suan, G., Mattioli, E., Kabiri, L., Föllmi, K.B., Immenhauser, A., 2014. The middle Toarcian cold snap: Trigger of mass extinction and carbonate factory demise. Glob. Planet. Chang. 117, 64–78.

Kump, L.R., Arthur, M.A., 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. Chem. Geol. 161, 181–198.

Lewandowska, A.M., Breithaupt, P., Hillebrand, H., Hoppe, H.-G., Klaus Jürgens, K., Sommer, U., 2012. Responses of primary productivity to increased temperature and phytoplankton diversity. J. Sea Res. 72, 87–93.

Mailliot, S., Mattioli, E., Bartolini, A., Baudin, F., Pittet, B., Guex, J., 2009. Late Pliensbachian Early Toarcian (Early Jurassic) environmental changes in an epicontinental basin of NW Europe (Causses area, central France): A micropaleontological and geochemical approach. Palaeoceanogr. Palaeoclimatol. Palaeoecol. 273, 346–364.

Mattioli, E., 1996. New Calcareous Nannofossil species from the Early Jurassic of Tethys. Riv. Ital. Paleontol. Stratigr. 102, 397–412.

Mattioli, E., 1997. Nannoplankton productivity and diagenesis in the rhytmically bedded Toarcian-Aalenian Fiuminata section (Umbria-Marche Apennine, central Italy). Palaeoceanogr. Palaeoclimatol. Palaeoecol. 130, 113–133.

Mattioli, E., Erba, E., 1999. Biostratigraphic synthesis of calcareous nannofossil events in the Tethyan Jurassic. Riv. Ital. Paleontol. Stratigr. 105, 343–376.

Mattioli, E., Pittet, B., 2004. Spatial and temporal distribution of calcareous nannofossils along a proximal-distal transect in the Lower Jurassic of the Umbria-Marche Basin (central Italy). Palaeoceanogr. Palaeoclimatol. Palaeoecol. 205, 295–316.

Mattioli, E., Pittet, B., Bucefalo Palliani, R., Rohl, H.-J., Schimidt-Rohl, A., Morettini, E., 2004. Phytoplankton evidence for the timing and correlation of palaeoceanographical changes during the early Toarcian oceanic anoxic events (Early Jurassic). J. Geol. Soc. Lond. 161, 685–693.

Mattioli, E., Pittet, B., Suan, G., Mailliot, S., 2008. Calcareous nannoplankton acros Early Toarcian anoxic event: implications for palaeoceanography within the western Tethys. Palaeoceanography 23.

Mattioli, E., Pittet, B., Petitpierre, L., Mailliot, S., 2009. Dramatic decrease of pelagic carbonate production by nannoplankton across the Early Toarcian anoxic event (T-OAE). Glob. Planet. Chang. 65, 134–145.

Mattioli, E., Plancq, J., Boussaha, M., Duarte, L.V., Pittet, B., 2013. Calcareous nannofossil biostratigraphy: new data from the Lower Jurassic of the Lusitanian Basin. Comunicações Geológicas 100 (I), 69–76 (Especial).

McArthur, J.M., Algeo, T.J., van de Schootbrugge, B., Li, Q., Howarth, R.J., 2008. Basinal restriction, black shales, Re–Os dating, and the Early Toarcian (Jurassic) oceanic anoxic event. Paleoceanography 23, PA4217.

Mouterde, R., Ruget, C., 1975. Esquisse de la paleogeographie du jurassique inférieur et moyen en Portugal. Bull. Soc. Geol. Fr. 14, 779–786.

Mutterlose, J., Bornemann, A., Herrle, J., 2005. Mesozoic calcareous nannofossils - state of the art. Paläontol. Z. 79, 113–133.

Olivier, N., Pittet, B., Mattioli, E., 2004. Palaeoenvironmental control on sponge-reefs and contemporaneous deep-shelf marl-limestone deposition (Late Oxfordian, southern Germany). Palaeoceanogr. Palaeoclimatol. Palaeoecol. 212, 233–263.

Parkinson, D., Curry, G.B., Cusack, M., Fallick, A.E., 2005. Shell structure, patterns and trends of oxygen and carbon stable isotopes in modern brachiopod shells. Chem. Geol. 219, 193–235.

Pinheiro, L.M., Wilson, R.C.L., Pena dos Reis, R., Whitmarsh, R.B., Ribeiro, A., 1996. In: Whitmarsh, R.B., Sawyer, D.S., Klus, A., Masson, D.G. (Eds.), The western Iberia margin: a geophysical and geological overview: Proceeding of the Ocean drilling Program, Scientific Results. 149, pp. 3–23.

Pittet, B., Mattioli, E., 2002. The carbonate signal and calcareous nannofossil distribution in an Upper Jurassic section (Balingen-Tieringen, Late Oxfordian, southern Germany). Palaeoceanogr. Palaeoclimatol. Palaeoecol. 179, 71–96.

Pittet, B., Suan, G., Lenoir, F., Duarte, L.V., Mattioli, E., 2014. Carbon isotope evidence for sedimentary discontinuities in the lower Toarcian of the Lusitanian Basin (Portugal): Sea level changes at the onset of the Oceanic Anoxic Event. Sediment. Geol. 303, 1–14.

Porter, S.J., Smith, P.L., Caruthers, A.H., Hou, P., Gröcke, D.R., Selby, D., 2014. New high resolution geochemistry of Lower Jurassic marine sections in western North America: A global positive carbon isotope excursion in the Sinemurian? EPSL 397, 19–31.

Reggiani, L., Mattioli, E., Pittet, B., Duarte, L.V., Veiga de Oliveira, L.C., Comas-Rengifo, M.J., 2010. Pliensbachian (Early Jurassic) calcareous nanofossils from the Peniche section (Lusitanian Basin, Portugal): a clue for pallaeoenvironmental reconstructions. Mar. Micropaleontol. 75, 1–16.

Reolid, M., Mattioli, E., Nieto, L.M., Rodríguez-Tovar, F.J., 2014. The Early Toarcian Oceanic Anoxic Event in the External Subbetic (Southiberian Palaeomargin, Westernmost Tethys): Geochemistry, nannofossils and ichnology. Palaeoceanogr. Palaeoclimatol. Palaeoecol. 411, 79–94.

Ruebsam, W., Münzberger, P., Schwark, L., 2014. Chronology of the Early Toarcian environmental crisis in the Lorraine Sub-Basin (NE Paris Basin). EPSL 404, 273–282.

Sandoval, J., O'Dogherty, L., Aguado, R., Bartolini, A., Bruchez, S., Bill, M., 2008. Aalenian carbon-isotope stratigraphy: Calibration with ammonite, radiolarian and nannofossil events in the Western Tethys. Palaeogeogr. Palaeoclimatol. Palaeoecol. 267, 115–137.

Sandoval, J., Bill, M., Aguado, R., O´Dogherty, L., Rivas, P., Morard, A., Guex, J., 2012. The Toarcian in the Subbetic basin (southern Spain): Bio-events (ammonite and calcareous nannofossils) and carbon-isotope stratigraphy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 342–343, 40–63.

Spielmeyer, A., Pohnert, G., 2012. Influence of temperature and elevated carbon dioxide on the production of dimethylsulfoniopropionate and glycine betaine by marine phytoplankton. Mar. Environ. Res. 73, 62–69.

Suan, G., Pittet, B., Bour, I., Mattioli, E., Duarte, L.V., Mailliot, S., 2008a. Duration of the Early Toarcian carbon isotope excursion deduced from spectral analysis: consequence for its possible causes. EPSL 267, 666–679.

Suan, G., Mattioli, E., Pittet, B., Mailliot, S., Lécuyer, C., 2008b. Evidence for major environmental perturbation prior to and during the Toarcian (Early Jurassic) oceanic anoxic event from the Lusitanian Basin, Portugal. Paleoceanography 23, PA1202.

Suan, G., Mattioli, E., Pittet, B., Lécuyer, C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. EPSL 290, 448–458.

Suchéras-Mar, B., Mattioli, E., Pittet, B., Escarguel, G., Suan, G., 2010. Astronomically-paced coccolith size variations during the early Pliensbachian (Early Jurassic). Palaeogeogr. Palaeoclimatol. Palaeoecol. 295, 281–292.

Tremolada, F., van de Schootbrugge, B., Erba, E., 2005. Early Jurassic schizosphaerellid crisis in Cantabria, Spain: Implications for calcification rates and phytoplankton evolution across the Toarcian oceanic anoxic event. Paleoceanography 20, 1–11.

Winter, A., Jordan, R.W., Roth, P.H., 1994. Biogeography of living coccolithophores in ocean waters. In: Winter, A., Siesser, W. (Eds.), Coccolithophores. Cambridge Univ. Press, Cambridge, pp. 161–177.

Young, J.R., 1994. The functions of coccoliths. In: Winter, A., Siesser, W. (Eds.), Coccolithophores. Cambridge Univ. Press, Cambridge, pp. 63–82.

6. Biometry

"Size variation of *Lotharingius* coccoliths across the Lower-Middle Jurassic: environmental forcing, evolution or both?"

[*To be submitted to Marine Micropaleontology*]

ABSTRACT

Measurements of seven morphospecies of the *Lotharingius* genus across the Toarcian and Early Aalenian, were performed in order to assess of their size evolution throughout a time span of ~10 myr. Other then plane evolutionary processes, also changes in palaeoenvironmental conditions were tested and linked to the genus pool size variation. This study was carried on using a total of 5500 specimens gathered from samples retrieved from western Mediterranean Tethys sections, specifically three sections in the Lusitanian Basin (Portugal) and one from south France Causses Basin located in a different paleoenvironmental setting. For each coccolith, its length, width and central area length and width were measured using specific measurement software. Several statistic and data analysis tools were used in order to easily evaluate statistically robust resemblances and/or differences between size groups. Two main morpho-groups are acknowledged from this study. Small *Lotharingius* are <4 µm and large *Lotharingius* are >4 µm. Although background evolution pushes the genus to larger sizes, palaeoenvironmental conditions also seem to play an important role in the genus evolution during this period. Larger coccolith size benefit from stable conditions whereas smaller forms dominate during stressed periods.

Keywords: Calcareous nannofossils; Biometry; Toarcian-Aalenian; Western Tethys; *Lotharingius*

1. **Introduction**

The respective importance of biotic, evolutionary *versus* abiotic factors (van Valen, 1973; Stenseth and Mainard Smith, 1984) in influencing the evolution of life on Earth is still a debated topic. Fossil size is a paramount parameter involved in biological processes, which is easily measurable through time. This is the reason why morphometric studies of marine microfossils have been applied in the past, in order to test either ecological responses to palaeoenvironmental changes or evolutionary patterns. Although biometric studies on Jurassic coccoliths and nannoliths have been carried out (Mattioli and Pittet, 2002; Mattioli et al., 2004; Bornemann et al., 2003; Giraud et al., 2006; Suan et al., 2008a; Suchéras-Marx et al., 2010; Tiraboschi and Erba, 2010;

Fraguas and Erba, 2010; Fraguas and Young, 2011; López-Otálvaro et al., 2012), none of them addresses the morphological evolution of the *Lotharingius* genus across the Lower-Middle Jurassic. Though a significant size increase in *Lotharingius* coccoliths across this time span has already been qualitatively acknowledged in the Lusitanian Basin (Portugal; Ferreira et al., 2015), so far no biometric evaluation has been made. In this work, the pool size from *Lotharingius* coccoliths recorded in the Coimbra and Figueira da Foz region in the Lusitanian Basin is compared to the coccolith pool size variation across the same time period in a different paleoenvironmental setting in the western Tethys, namely the Causses Basin in southern France. These two regions were selected since they represent a continuous Toarcian-lower Aalenian successions, including the rocks recording the Early Toarcian environmental perturbation, besides detailed isotopic data from $\delta^{18}O$ and $\delta^{13}C$ from brachiopods in Portugal and bulk rock in France, being available.

The Toarcian was a period of major palaeoceanographic and palaeoenvironmental changes across the western Tethys. The probably most important thermal maximum recorded in the Mesozoic during the Early Toarcian (~183 Ma) coincides with the Toarcian Oceanic Anoxic Event (T-OAE). The T-OAE was marked by widespread organic matter-rich deposits and by a prominent negative carbon isotope excursion recorded in oceanic and continental carbon reservoirs (Jenkyns, 1988; Duarte, 1998; Jenkyns et al., 2001; Bailey et al., 2003; Hesselbo et al., 2007; McArthur et al., 2008; Suan et al., 2008a). Though these shales or their equivalents can be recorded throughout Europe, there is no sedimentological evidence for anoxia in the sections from Portugal studied here, probably due to storm events being responsible for water column re-oxygenation (Mailliot et al., 2009; Ferreira et al., 2015). From the middle Toarcian, global sea level and seawater temperature initiated a long-term plunge that will linger until the Aalenian age (Hallam, 1981; Duarte et al., 2007; Gómez et al., 2008; Dera et al., 2009a, 2011a; Pittet et al., 2014).

This work addresses the coccolith size evolution of the *Lotharingius* taxon, the most abundant group of coccolithophores during a time span of ~10 myr. All the species of the genus were included in the biometric evaluation, since working on entire assemblages is a taxon-free approach, which avoids bias of subjective grouping. Investigating entire assemblages enables the analysis of long-term and global processes, since the datasets can be compiled globally and stratigraphically with the same method (Schmidt et al., 2004a,b). The genus *Lotharingius* belongs to the family Watznaueriaceae and is the oldest known imbricating placolith coccolith representing a major component of Lower Jurassic calcareous nannofossil assemblages (Bown, 1987; Mattioli and Erba, 1999). It is likely the phylogenetic predecessor of the genus *Watznaueria* (Cobianchi et al., 1992; Mattioli, 1996), a cosmopolitan coccolithophore that will dominate the global phytoplanktonic community for more than 100 myr until the K/T extinction event. The *Lotharingius* genus first occurrence happened during the Late Pliensbachian (Hamilton 1977, 1979; Bown, 1987; Mattioli, 1996), and two of its species, *L. hauffii* and *L. sigillatus*, are important biostratigraphic markers defining the calcareous nannofossil zone NJ5 (Bown and Cooper, 1998) and subzone NJT5b (Mattioli and Erba, 1999). It is thus important to better understand and quantify its morphologic evolution during the time period spanning from the first occurrence of the first *Watznaueria* coccolith at the end of the Early Toarcian, to the lowermost Middle Jurassic when a gradual increase in the *Watznaueria* genus abundance is recorded in the western Tethys (Ferreira et al., 2015).

An important shift within the *Lotharingius* assemblages is acknowledged during the middle Toarcian, when the dominance of small species like *L. hauffii* and *L. frodoi* is replaced by larger taxa such as *L. velatus* and *L. crucicentralis.* This biotic switchover coincides with a regional and global seawater cooling and sea level fall, coeval with a gradual decrease in oceanic primary productivity that started from the middle Toarcian, as recorded accordingly by $\delta^{18}O$ and $\delta^{13}C$ values gathered from brachiopods shells from the Lusitanian Basin (Ferreira et al., 2015) and bulk rock from the Causses Basin (Harazim et al., 2012). Close to the Toarcian-Aalenian boundary, a relative increase in smaller species is observed in both sections, parallel with a significant positive $\delta^{13}C$ excursion and a short-term increase in seawater temperature.

This work aims to quantify the morphologic evolution of the *Lotharingius* coccoliths across the Toarcian and lower Aalenian based on a study performed in two different palaeogeographic and palaeoceanographic settings such as the Lusitanian and the Causses Basin, and to statistically assess if the observed changes in the coccolith pool size are due to synchronous shifts in size in all of the species within the *Lotharingius* population, or conversely are due to phenotypic replacements and/or interspecific size variations. Additionally, we will attempt to expose if there is any relation between environmental changes such as those that occurred during and after the Early Toarcian perturbation, seawater temperature oscillations and oceanic primary productivity, with differences in the size of *Lotharingius* coccoliths. Or conversely, if any variability is simply due to the lineage evolution of the taxon. Statistic parameters and robust analysis tools such as Principal Components and Mixture Analysis were used, and inference tests such as ANOVA were performed in order to disclose trends and appraise the significance of the results obtained. Evolutionary theories and abiotic perturbations are discussed in order to best describe the morphological changes observed throughout the Toarcian-Early Aalenian in the *Lotharingius* pool.

2. Geological settings

In the Early Jurassic the western Tethys Ocean mainly consisted of a shallow sea comprised between the African and the European landmasses (Fig. 10). It was in this sector that during an aborted rift phase that started to develop in the Late Triassic (Pinheiro et al., 1996) the Lusitanian Basin started to open. It was a relatively narrow, elongated and shallow (<200 m in depth according to Bjerrum et al., 2001) epicontinental seaway connecting the western Tethys to the NW

European basins. Roughly N-S orientated, this basin was bounded in the east by the Iberian Meseta and in the west by the Berlengas-Farilhões igneous and metamorphic horst. In this narrow seaway, the mixing between higher NW European and lower latitude Mediterranean waters has been described by various authors and supported by the mixing of ammonite fauna and calcareous nannofossils during the Early Jurassic (Mouterde and Ruget, 1975; Dommergues and Mouterde, 1980; Dommergues and Meister, 1991; Mattioli et al, 2008; Reggiani et al., 2010; Dera et al., 2011a). Similar mixing of marine organisms has also been acknowledged for ostracods (Arias and Whatley, 2005), bivalves (Damborenea, 2002) and brachiopods (Vörös, 2002). The Lusitanian Basin was located at a palaeolatitude comprised between 25 and 30ºN (Dercourt et al., 2000), which corresponds in modern oceans to the transition between the subtropical and temperate climatic belts.

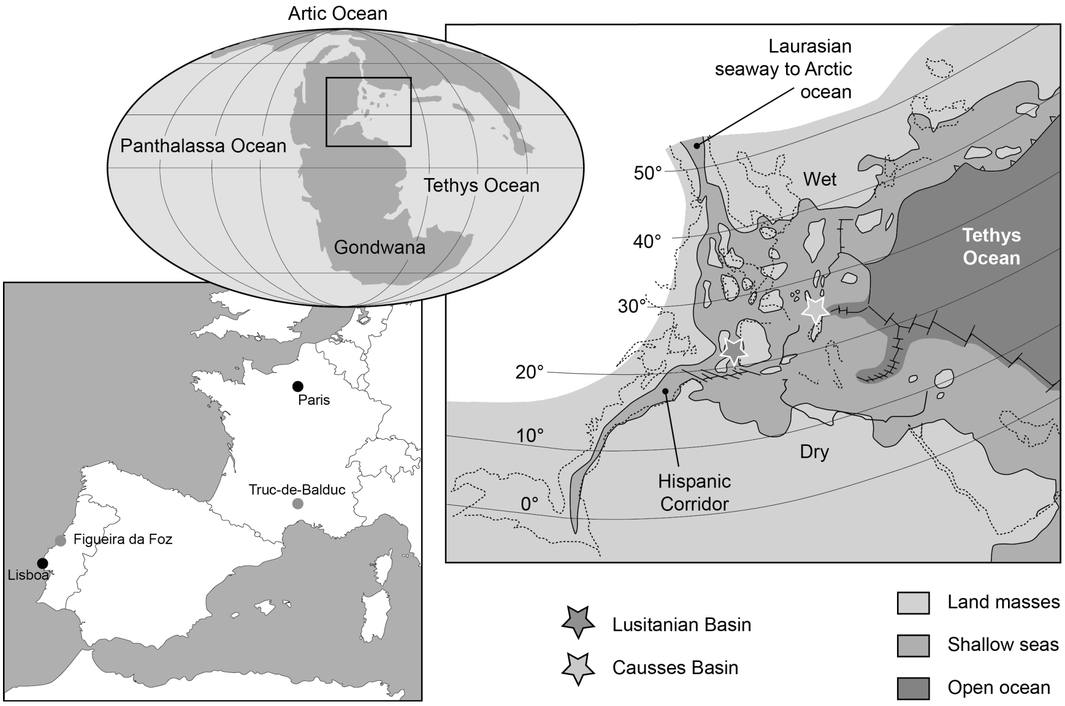


Figure 10 - Location of both studied basins during the Early Jurassic in western Tethys epicontinental sea (modified after Bassoulet et al., 1993).

The three sections studied in Portugal represent 286 m of a complete and continuous succession of marine hemipelagic marlstone and limestone couplets deposited on a homoclinal, low-angle ramp with a NW dipping (Duarte, 2004). The Rabaçal section is located in the proximal part of the basin whereas Cabo Mondego in the distal part, and the Brenha section in an intermediate position. In all the three sections macrofossils such as ammonites, brachiopods, belemnites, bivalves and some fossilized wood fragments are commonly found. Though the

Rabaçal section spans from the uppermost Pliensbachian to the uppermost upper Toarcian, only the first 42 m comprising the Polymorphum, Levisoni (lower Toarcian) and the lowermost Bifrons (middle Toarcian) ammonite zones were sampled for nannofossil study. The 157 m of the Brenha section correspond to the uppermost part of the lower Toarcian up to the lower Aalenian sediments. The 87 m of the Cabo Mondego section include the Speciosum, Meneghinii, Aalensis (upper Toarcian) and the Opalinum (lower Aalenian) ammonite zones. The three sections are correlated by means of ammonite and nannofossil biostratigraphies, and by means of lithostratigraphy.

The Truc-de-Balduc section is located on a small mountain 5 km southeast of the city of Mende, and belongs to the Causses Basin in south France (Fig. 10). During the Early Toarcian this basin was a small, partly enclosed, intracratonic basin in the western Tethys epicontinental sea, and was positioned at a palaeolatitude comprised between 25 and 30ºN. Bounded by Hercynian crystalline rocks (Trümpy, 1983), its morphology was largely controlled by the late Hercynian structural evolution. Subsidence was more pronounced in the central part of the basin and the Lower Jurassic succession thickness varies from its margins to its depocentre (Morard, 2004). In this region an abrupt facies transition occurred in the lowermost Toarcian with the onset of deposition of organic matter-rich shales belonging to the Schistes Cartons Formation. On top of this formation stands the Fontaneilles Formation, a monotonous marl succession of the middle and upper Toarcian. The gradual transition to the Aalenian stage is characterized by sandy limestones with abundant bioturbation (Harazim et al., 2012).

3. Materials and Methods

Fifty-five samples from two west Tethyan sections were used for coccolith biometry. Thirty-four samples from three sections in the Coimbra to Figueira da Foz region (5 from Rabaçal, 13 from Brenha, 16 from Cabo Mondego) and 21 from Truc-de-Balduc. Furthermore, 65 samples from Truc-de-Balduc were scanned for nannofossil absolute abundance and diversity determination. Smear slides following the random settling technique by Geisen et al. (1999) ensured a homogeneous dispersion of coccoliths on the slide. The morpho-taxonomy of the genus *Lotharingius* used in this work follows that of Mattioli et al. (1996) and Mattioli and Erba (1999), which is based upon, but slightly diverge from Bown (1987), and focus on seven morphospecies identified throughout the lower Toarcian to lower Aalenian: *L. barozii, L. crucicentralis, L. frodoi, L. hauffii, L. sigillatus, L. umbriensis* and *L. velatus*. Excellent to poorly preserved coccoliths were recorded in the analyzed samples. Partial etching of distal shield and central area elements were frequent both in small and large specimens. Well-preserved specimens or those slightly to moderately etched or overgrown were used for biometry, whereas damaged or poorly preserved coccoliths were measured only if their landmarks could be unequivocally determined. For each of the 55 samples, the image from the first 100 coccoliths observed was captured with a Leica EC3 digital camera coupled with an optical polarized light microscope with x1000 magnification. On the system used, 1 µm correspond to 17.5 pixels. For each coccolith, length (L) and width (W), and central area length (l) and width (w) were measured (Fig. 11) using the public domain image analysis software ImageJ ©.

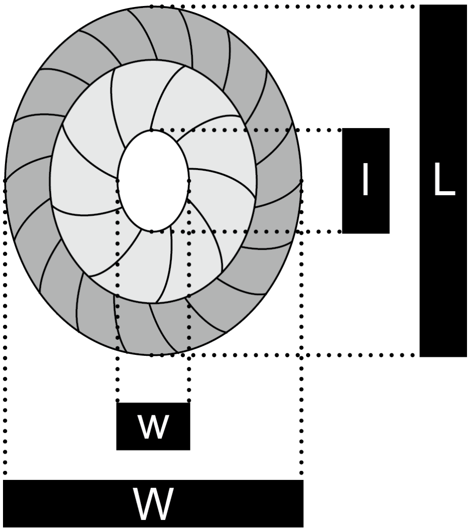


Figure 11 - Different coccoliths parameters measured in distal view: length (L), width (W), central area length (l) and central area width (w).

Statistical analysis was performed using the PAST 3.01 software package. Measurements after the coccolith length were used to calculate simple statistic parameters, such as mean, standard deviation, median, 25th and 75th percentile and total range of values. For each sample, the percentiles of the frequency of the length measurements were plotted using the box and whiskers chart. The geometric mean (L x W x l x w)^(1/4), the coccolith ellipticity (L/W), central area ellipticity (l/w), and the proportion occupied by the central area relative to the area of the coccolith were also determined. Since the goal of a correlation analysis is to test whether two measurement variables covary, and to measure the strength of any relationship between these variables, the coefficient of correlation (r) and the coefficient of determination (r^2) between the coccolith parameters were calculated. The relative abundance between six different species of *Lotharingius* was compared against the coccolith length percentiles in order to assess if changes in the pool size are someway related to shifts in the relative abundance of the different *Lotharingius* taxa, are due to a size increase in all of the species, or result from a combination of these two processes. The species *L. umbriensis* was left out, as its relative abundance is extremely low.

The L variable of the whole dataset was tested for normal distribution using the Shapiro-Wilk test. Though merely 26 out of the 55 samples show normal distribution, L mean values were compared using a parametric test since non-parametric ones often have less statistical power than parametric tests (Hammer and Harper, 2006). In order to test whether our univariate samples were taken from populations with equal means, parametric univariate analysis of variance (ANOVA) was performed on L values using a significance level of 0.05. The basic idea of this test is to calculate the mean of the observations within each group, then compare the variance among these means to the average variance within each group. Under the null hypothesis that the observations in the different groups all have the same mean, the weighted among-group variance will be the same as the within-group variance. As the means get further apart, the variance among the means increases. The statistic test is thus the ratio of the variance among means divided by the average variance within groups, or Fs. This statistic test has a known distribution under the null hypothesis, so the probability of obtaining the observed Fs under the null hypothesis can be calculated (McDonald, 2008).

After the overall samples inequality was shown, a Tukey's honestly significant difference post-hoc test was used in order to identify which particular pairs of samples are significantly different. Though ANOVA assumes for each sample normal distributions and equality of variances, these assumptions are less critical if the samples are of the same size (Hammer and Harper, 2006), which is the case in this work. As for PCA, a 0.5 µm bin was used and the frequency of the L axis size in each sample was calculated. Loadings for the totality of the samples and the stratigraphic evolution of PC1 scores for each of the sections were calculated. Also the maximum-likelihood method Mixture Analysis was used. This method aims at identifying the existence of two or more distinct distributions in an initially pooled sample and estimate their descriptive parameters. One and two group model comparison was obtained by comparing their Akaike Information Criterion (AIC), which is a way to select a model from a set of models. A minimum value for AIC indicates that we have chosen the number of groups that produces the best fit without overfitting.

4. Results

In the lower Toarcian, *Lotharingius* relative abundances in the Lusitanian Basin are quite high ranging from 40% of the total coccolith assemblage prior to the tempestite interval, to 80% and more after that (Fig. 12). Across the middle Toarcian up to the lower Aalenian its abundances vary around 60% of the total assemblage. In the Causses Basin during the upper Pliensbachian, the *Lotharingius* abundance varies between 30 and 60%. Across the lower and middle Toarcian though, its abundance stays fairly constant, revolving around 40%. In the upper Toarcian and lowermost Aalenian the abundance of *Lotharingius* slightly increases to values around 50% (Fig. 13).

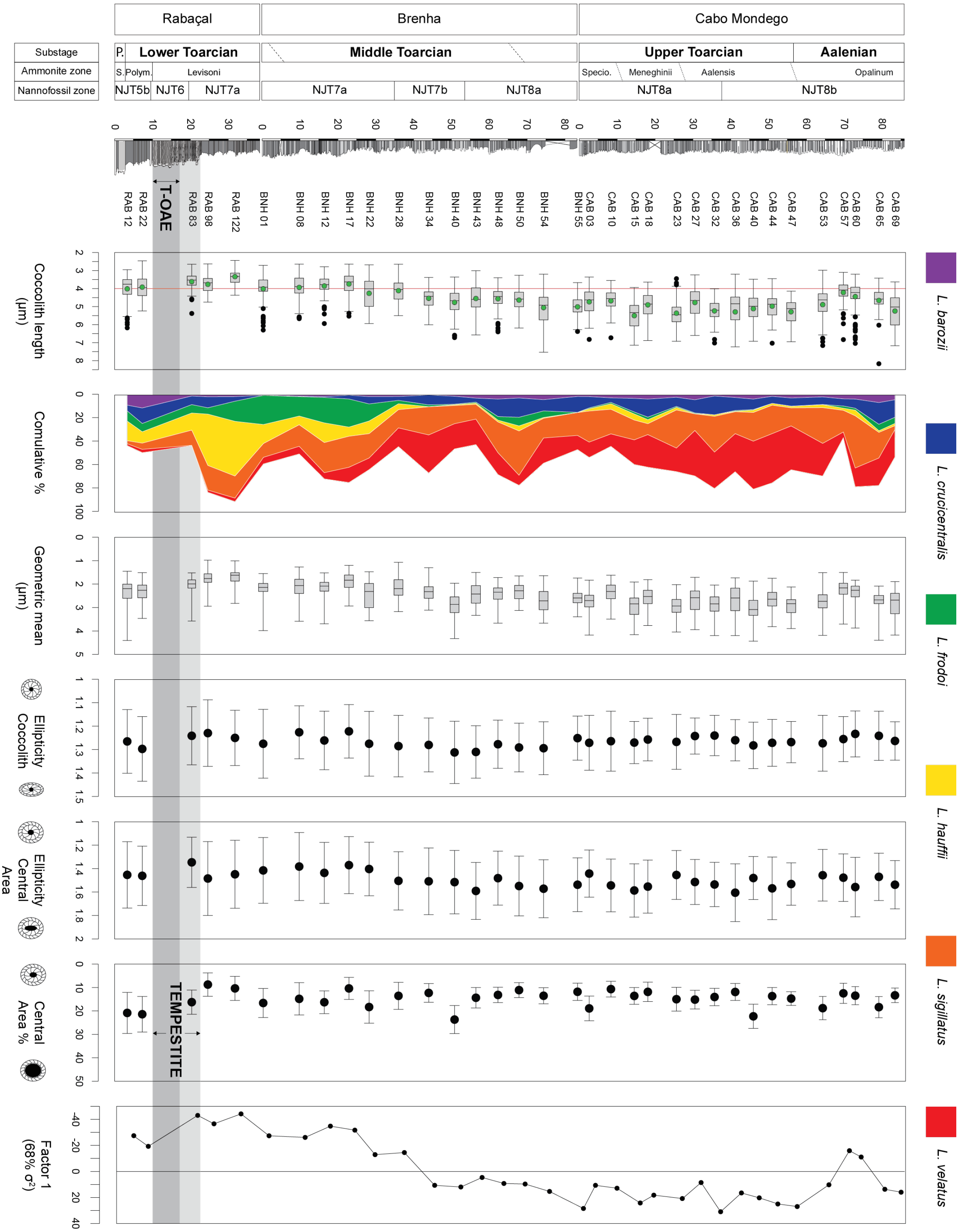


Figure 12 - Lusitanian Basin box-plotted coccoliths length and outliers, relative abundance of different species of *Lotharingius* compared to the total coccoliths abundance, plus mean and standard deviation values of coccoliths and central area ellipticity and central area proportion, and stratigraphic evolution of Factor 1 PCA scores.

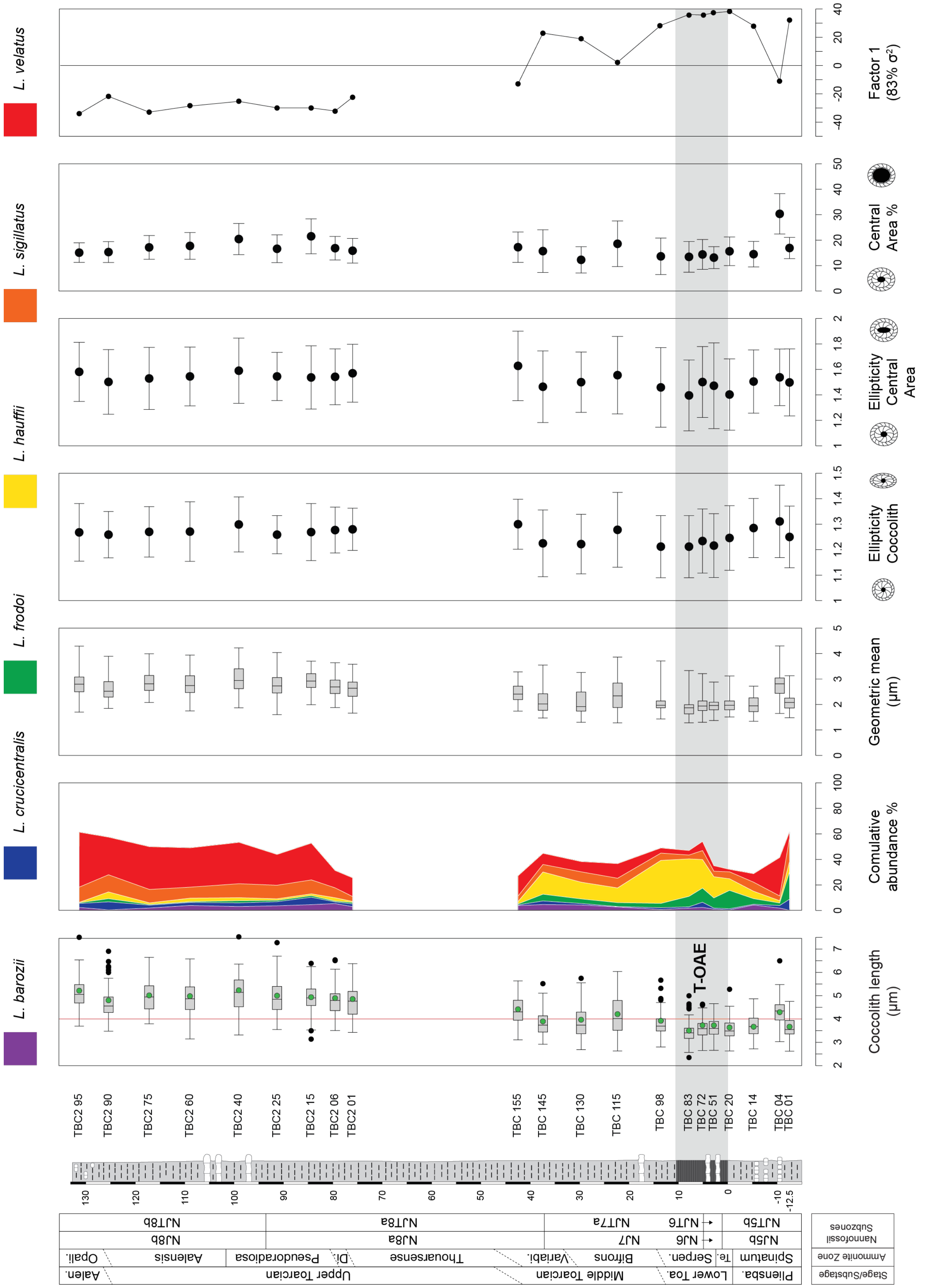


Figure 13 - Causses Basin box-plotted coccoliths length and outliers, relative abundance of different species of *Lotharingius* compared to the total coccoliths abundance, plus mean and standard deviation values of coccoliths and central area ellipticity and central area proportion, and stratigraphic evolution of Factor 1 PCA scores.

All the seven species of *Lotharingius* were considered together for biometric purposes, and statistic parameters such as mean, median, percentiles, minimum and maximum L values were calculated and displayed on a box plot chart (Fig. 12 and 13). Throughout the Toarcian and lower Aalenian a general increasing trend in the coccoliths size is acknowledged in both sections, though a slight decrease in the taxon size is observed across the Lower-Middle Jurassic boundary. Moreover, an important replacement between small and large specimens is observed during the middle Toarcian. As already reported from the Lusitanian Basin (Ferreira et al., 2015), also in the Causses Basin there is a replacement between the *Lotharingius* coccolith size pool during the middle Toarcian. In both successions there is a drastic change across the ammonite zones Bifrons-Gradata (Bifrons-Variabilis in NW Tethys) from *Lotharingius* species with less than 4 µm to species larger than 4 µm.

Complementary to the standard statistics, the geometric mean was calculated and displayed in a box plot chart in order to assess if a trend after all the measured variables could be acknowledged. As a result, the geometric mean closely follows the coccolith length stratigraphic trend throughout both successions (Lusitanian Basin r = 0.90, p = 0 and in the Causses Basin r = 0.91, p = 0), putting into evidence the importance of the major axis size as a proxy for the total dimension of the coccolith. Moreover, since r and r^2 reach the highest values between the coccolith length (L) and width (W) (Fig. 14), L is thus herein used to describe the coccolith size. In fact, when the correlation coefficient between the different variables is calculated, we observe that L is strongly correlated with W (r = 0.895) and to a lesser extent with l (r = 0.767), with zero probability (p = 0) of these two variables not being correlated. It is also possible to assess that both the coccoliths ellipticity and their central areas ellipticity is not strongly correlated (r = 0.483, p = 0), neither it is with any of the other variables. Conversely, the proportion of the central area is correlated with the coccolith l and w (r = 0.730, p = 0 and 0.735, p = 0 accordingly). Also L and W display by far the strongest determination coefficient (r^2 = 0.800, p = 0).

As for the evolution of the coccoliths ellipticity, their mean value varies in both basins between 1.2 and 1.3, and a very weak correlation between the stratigraphic evolution of coccoliths ellipticity and their size (length) is obtained (r = 0.264, p < 0.0001). Though in the long-term a gradual decrease in relative abundance of small subcircular *L. hauffii* coeval with an up-section increase in larger species such as *L. velatus* somewhere during the middle Toarcian is observed, the *Lotharingius* pool ellipticity does not change significantly. The drop in *L. hauffii* abundances can also explain the up-sequence apparent trend in both sections of more elliptical central areas within the genus. Yet, the correlation between these two variables is very weak (r = 0.175, p < 0.0001). Regarding the proportion of the coccolith central area to the total coccolith area, we observe that their mean values vary in almost all of the studied samples between 10 and 20% and that there is neither any noticeable link between this parameter with the composition of the *Lotharingius* assemblages, neither with the stratigraphic evolution of their size (r = 0.193; p < 0.0001).

r r^2	L	W	l	w	⊙	⦿	●
L		0.895	0.767	0.691	0.264	0.175	0.193
W	0.800		0.642	0.682	-0.186	-0.041	0.084
l	0.589	0.412		0.869	0.306	0.276	0.730
w	0.477	0.465	0.755		0.056	-0.210	0.735
⊙	0.070	0.035	0.094	0.003		0.483	0.257
⦿	0.037	0.007	0.533	0.540	0.066		0.005
●	0.031	0.002	0.076	0.044	0.233	0.000	

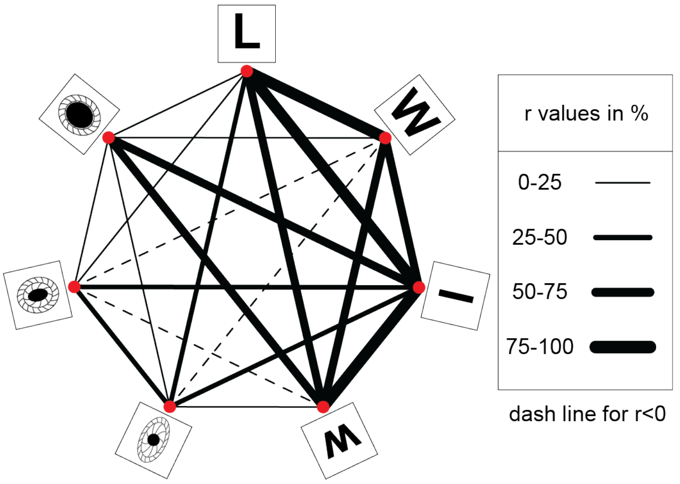


Figure 14 - Coefficient of correlation between different coccoliths parameters: length (L), width (W), central area length (l), central area width (w), coccolith ellipticity, central area ellipticity and central area proportion.

For the total of 5500 measurements of coccoliths length, PCA loadings show that for Factor 1, which represents 74% of the total variance, there is a boundary at 4 µm within the *Lotharingius* pool (Fig. 15). Although when PCA is computed separately for each section, loadings set a threshold of 4.5 µm in Portugal and 4.0 µm in France between small and large taxa. The difference in 0.5 µm for the Portuguese samples can be explained due to the dimension of the bins initially selected, as we can observe that the loadings in the Lusitanian Basin at the transition between 4 and 4.5 µm are quite feeble (Fig. 15). Moreover, the stratigraphic evolution of PC1 scores in both sections shows this same transition between small and large specimens during the middle Toarcian (Figs. 12 and 13) and a decrease in the coccolith pool size close to the Toarcian-Aalenian boundary. The same bimodal frequency and split around 4 µm for the variable L is also validated when applying Mixture Analysis to the whole dataset. This best fit method renders two distinct populations at 4 µm boundary, where the first one representing ~27% of the specimens has a mean value of 3.6 ± 0.4 µm and the second one including ~73% of the specimens has a mean value of 4.7 ± 0.8 µm (Fig. 16). This size division in the assemblages clearly represent small and large *Lotharingius* populations prior and after the middle Toarcian.

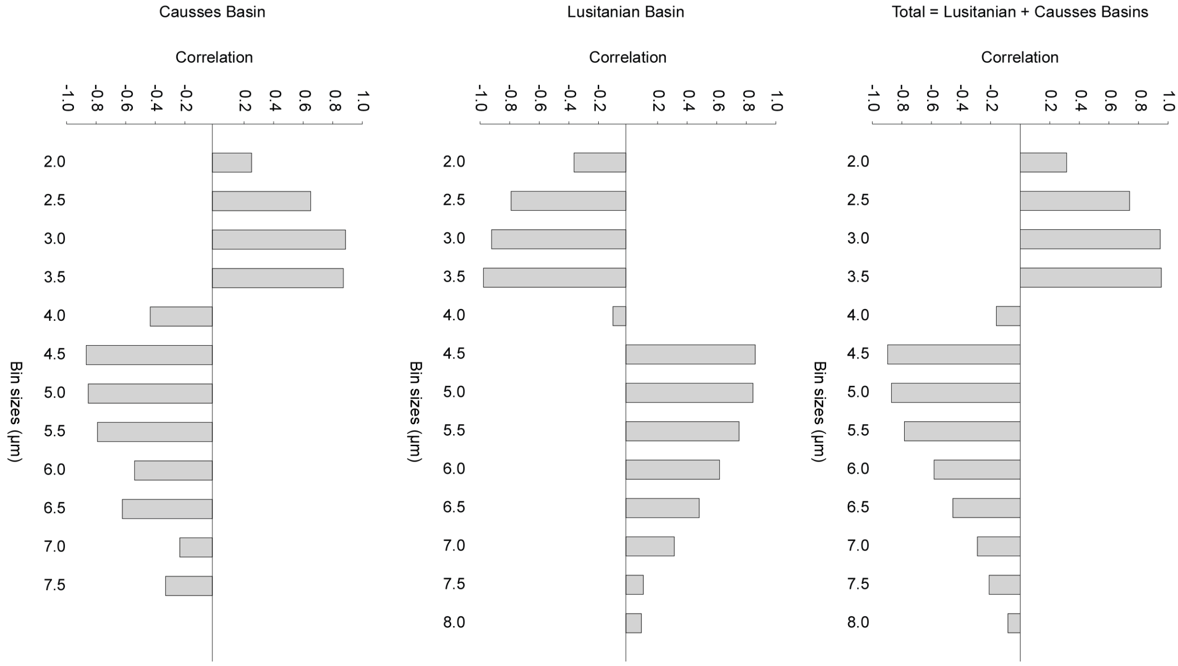


Figure 15 - PCA correlation loadings for coccoliths length in each of the studies basins and for the total *Lotharingius* coccolith pool.

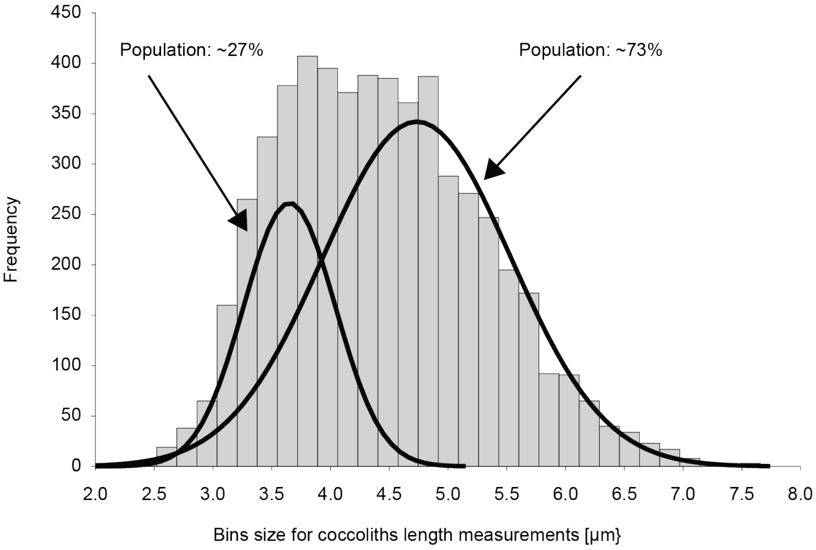


Figure 16 - Best fitted populations after running Mixture Analysis on the total measurements of coccoliths lengths from both studied basins.

In order to assess the degree of equality of means for each pair of samples, ANOVA post hoc Tukey's test was calculated for each section. In both sections two sets of samples share the same population mean: below and above the middle Toarcian (Fig. 17). Moreover, in the Lusitanian Basin we can observe that the lower Aalenian sample CAB 57 share the same mean with the lower Toarcian ones. This can also be acknowledged from looking at the box plot chart and the PCA scores (Fig. 12), where a decrease in the *Lotharingius* pool size is observed across the Toarcian-Aalenian boundary in the Lusitanian Basin.

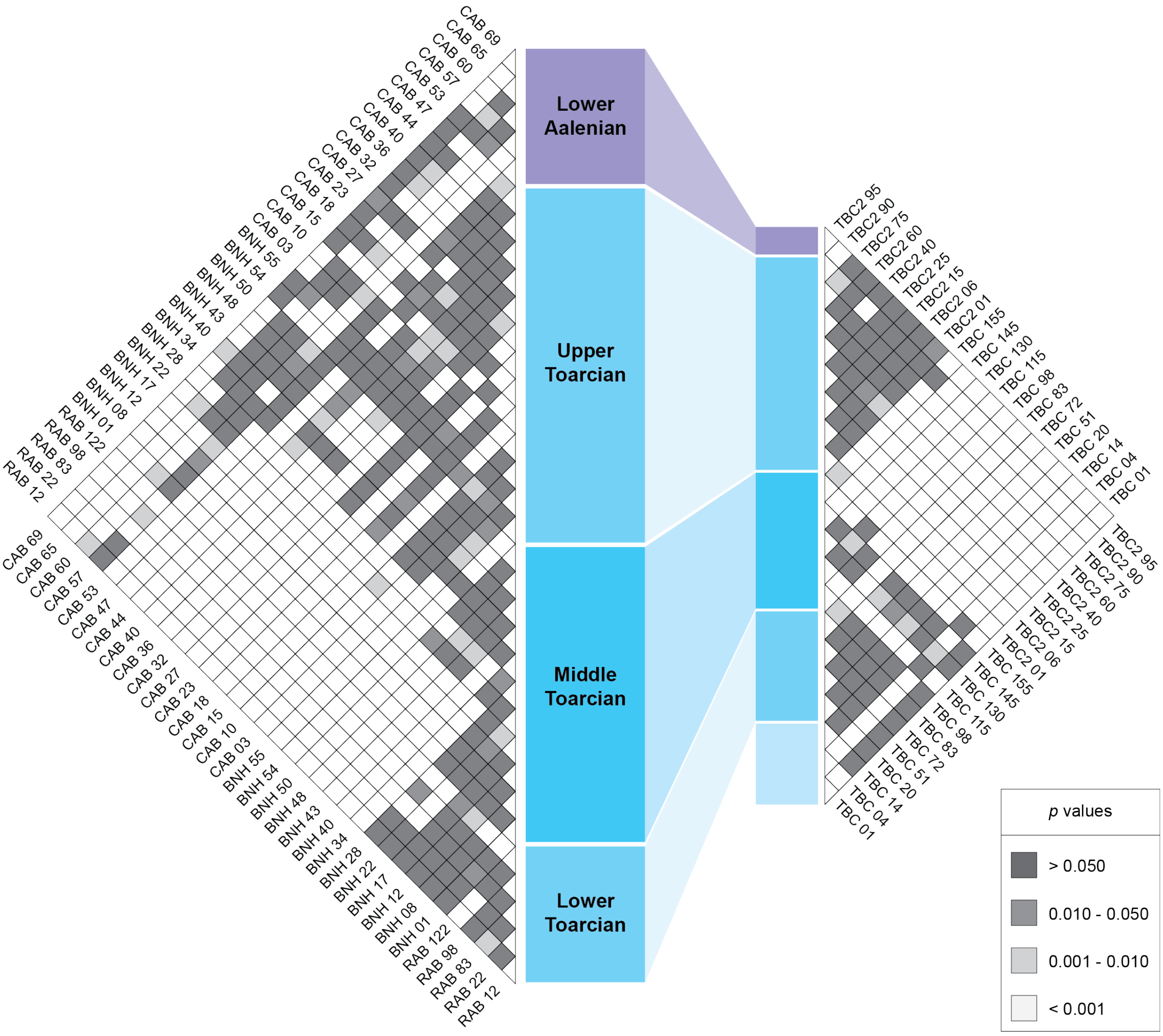


Figure 17 - Post-hoc Tukey's honesty test results between all pairs of samples from the Lusitanian (on the left hand side) and Causses basins (on the right hand side), showing the probability p of each pair of samples belonging to the same population. Dark grey colours indicate the correlation probability between each pair of samples.

After running ANOVA on the whole dataset, quantitative data rendered no significant difference between the means of the coccoliths ellipticity and central area ellipticity, whereas for the proportion of the central area significant differences between most of the samples pairs were evidenced, as also shown by the means and standard deviation box plots (Figs. 12 and 13).

5. Discussion

5.1. Palaeoenvironmental conditions deduced from geochemical data

Lithological and isotopic data show that the Early Toarcian was a disturbed and stressed period for global oceans and their ecosystems. According to the isotopic data collected from both basins (Ferreira et al., 2015; Harazim et al., 2012), with the exception of the negative $\delta^{13}C$ excursion recorded across the T-OAE, δ13C values are fairly positive and stable during the Early Toarcian therefore suggesting the water column was enabled to rebuild its photic zone ecosystem after the preceding disturbed period, as positive $\delta^{13}C$ excursions are interpreted as reflecting oceanic primary productivity (e.g. Jenkyns and Clayton, 1986; Kump and Arthur, 1999; Bartolini et al., 1999; Jenkyns et al., 2002; Sandoval et al., 2008; Brigaud et al., 2009; Gómez et al., 2009; Price, 2010; Porter et al., 2014). Although no isotopic data could be obtained from brachiopods in Rabaçal T-OAE equivalent beds as no epibenthic fauna was found across this time span, a negative excursion of bulk rock $\delta^{13}C$ across this interval is well documented in Rabaçal (Pittet et al., 2014) as well as in numerous other Tethyan sites, and linked with massive injection into the hydrosphere/atmosphere of isotopically light carbon related either to volcanic degassing or to methane release from continental margins (e.g., Hesselbo et al., 2000, 2007; Jenkyns et al., 2001; Suan et al., 2008b; Ruebsam et al., 2014). From the middle, up to the Late Toarcian, as sea level gradually recedes, $\delta^{13}C$ values start to decline, as already observed in other sections from Portugal (Duarte at el., 1998) and Spain (Sandoval et al., 2012 and references therein), suggesting a long-term decline in primary productivity coeval with the ongoing stratification build up of the water column (Ferreira et al., 2015). From the Late Toarcian to the Early Aalenian, the $\delta^{13}C$ negative trend inflects and significantly increases by 1‰ in Portugal and ~1.5‰ in France, likely reflecting an important increase in oceanic productivity in stable, shallow and confined ecosystems such as the Lusitanian and the Causses Basins would be at that time. Actually, Sandoval et al. (2008) tend to interpret this excursion, which is recorded in multiple sections from Spain, as the result of reinvigorated productivity.

The Pliensbachian-Toarcian boundary is characterized in both sites by a drastic $\delta^{18}O$ negative excursion measured on brachiopod shell calcite (Ferreira et al., 2015) and bulk rock (Harazim et al., 2012). Across this boundary, bottom water temperature increased by ~5ºC in the Lusitanian Basin and by ~6ºC in the Causses Basin. The main warming period corresponding to the Early Toarcian is followed by gradually decreasing temperatures, reaching during the middle Toarcian a local minimum of 18°C and 15ºC in the Lusitanian and Causses Basins respectively.

From the middle Toarcian and following the global cooling trend (Dera et al., 2009a, 2011b; Jenkyns et al.; 2002; Krencker et al., 2014), a steady and long-lasting decrease in seawater temperature is observed in both basins, as inferred by the persistent $\delta^{18}O$ positive excursion. Around the Toarcian-Aalenian boundary, isotopic data from both sites show an inflection in this excursion, suggesting a significant though temporary warming period of approximately 3ºC in western Tethys water masses, within a global and lasting cooling trend.

5.2. Species traits

Although there is no consistent relationship between cell and coccolith size, within most families of coccolithophores there is a good correlation between these two parameters, particularly within the heterococcoliths of dominant well-fossilised families such as the Coccolithaceae, Calcidiscaceae and Noelaerhabdaceae (Schmidt et al., 2006; Henderiks and Pagani, 2008).

The absence of significant changes in coccolith parameters such as ellipticity or central area proportion and ellipticity across the Toarcian, seems to indicate a somewhat phenotypic constrain within the *Lotharingius* genus, and eventually in each of its seven different species. Actually, the coccolith size is the main morphological character that actually varies throughout this period, hence facilitating the taxonomic identification of each of the different species under optical microscope. The original diagnosis of the *Lotharingius* by Noël (1973) described a typical watznaueriacean rim coccolith, with a slightly raised distal inner cycle and a central area spanned by a cross supported by lateral bars, giving the type species to *L. barozii*. It was only in 1979 that Goy proposed a corrected and precise description of the genus reaffirming its relationship within the Watznaueriaceae but also stating its independence as a discrete genus (Goy, 1979; Bown, 1987). The seven species of the genus are described in the taxonomic appendix.

5.3. Evolutionary push

Whether we choose to use Mixture Analysis, PCA, ANOVA or take a simple look at the box plot charts, one can clearly acknowledge a size partition in the whole dataset analyzed. The mean values of *Lotharingius* coccoliths are clearly split in both sections into two populations: smaller than 4 µm before the middle Toarcian, and larger than 4 µm after that. Genotypic variation in the taxon pool would be the plainest interpretation for this shift as the taxon evolution follows the Cope's rule that states that body size in a lineage tends to increase as it evolves, or Stanley's (1973) assumption which enunciates that size change is primarily associated with speciation events. Actually, coccolithophore evolution has been the explanation for the size increase in the *Discorhabdus* genus across the Aalenian-Bajocian in the Lusitanian Basin (López-Otálvaro et al. 2012) and for the *Lotharingius* genus across the Pliensbachian-Toarcian boundary in northern

Spain (Fraguas and Young, 2011). In the present work, however, we do not acknowledge the stratigraphic increase neither in the *Lotharingius* coccoliths ellipticity neither in the proportion of their central area as the latter authors do. Underlying different taxonomic criteria are the probable reason for this discrepancy as for these authors some pictures shown by Fraguas and Young (2011; their figures 3 and 4), although from to the same family, belong to the different and more elliptical genus *Bussonius*, and hence might have biased their final results.

Size change can also be attributed to either adaptation or to speciation. Whereas speciation is the formation of a new species (Dye, 2012), adaptation is conventionally regarded as an evolutionary process involving genetic change by which natural selection picks out organisms in a given population to fit pre-established environmental "templates" (Laland et al., 2004). Whichever the process we ponder, neither adaptation nor speciation is fully observed in any of the two basins under study. In fact, neither we observe the occurrence of new *Lotharingius* species, as all the considered *Lotharingius* species first occur during the Late Pliensbachian, neither selective environmental adaptation can be observed, as all the seven *Lotharingius* species coexist and share the same ecological niche during the ~10 myr time interval this work refers to. Since *L. hauffii* does not appreciably increase its size over time, which is in accordance with the observations made by Bown (1987) and Mattioli (1996) that acknowledged this species never exceeds 4 µm we therefore cannot strictly corroborate that the *Lotharingius* genus increasing size is an evolutionary lineage trend, though in broad terms it is clearly the product of evolutionary change, for evolution often starts near some "limiting boundary" also termed the "left wall" (Stanley, 1973), i.e., the diffusion away from an originally small-sized ancestor, as small species seem to be less prone to extinction during a catastrophic event (Norris, 1991). Actually, major shifts in coccolith size as those recorded in the fossil record of *Reticulofenestra* (Young, 1990) or *Calcidiscus* (Knappertsbusch, 2000) are interpreted as the product of evolutionary change and are likely to have occurred through selection of closely related species/sub-species rather than by anagenesis within a single lineage (Schmidt et al., 2006), i.e., the evolution of a new morphospecies by the gradual transformation of an ancestral species, without speciation or splitting event taking place (Dye, 2012).

5.4. Phenotypic replacement

The *Lotharingius* genus in general and *L. hauffii* in detail, reach in the Lusitanian Basin their highest absolute and relative abundances (reaching sometimes >80% of the total nannofossil assemblage) during the Early Toarcian, a very unstable period. Water temperature and eustatic oscillations coeval with water column nutrification fluctuations and subsequent oceanic primary productivity, are the environmental conditions that best describe this period, where primary productivity reached its peak immediately after the T-OAE time equivalent (Harazim et al, 2012;

Ferreira et al., 2015). In fact, stressed environmental settings and nutrient-rich waters masses seemed to congregate the optimum environmental conditions for opportunist taxa such as *L. hauffii* and *L. frodoi* to thrive, as these are the most abundant species in both basins during the Early Toarcian. Our data suggest that across this time span, increased oceanic productivity prompted a faster growth rate within the *Lotharingius* population just after the T-OAE recovery, which consequently led to a smaller coccolith pool size. Actually, optimum environmental conditions can lead to fast reproduction rates and smaller species, as proposed for benthic foraminifera by Bradshaw (1961). Moreover, laboratory experiments with the extant coccolithophore *E. huxleyi* cultures performed by Young and Westbroek (1991) and Shiraiwa (2003) show that the mean cell size decreases during exponential cell growth and increases during the stationary phase, which is normally nutrient limited. Also according to Shiraiwa (2003), the rapid surge in cells abundance will quickly deplete the available nutrients and therefore calcification can be rapidly enhanced by the limitation of organic matter production and suppression of growth.

By the earliest middle Toarcian when the environment has finally fully recovered from Early Toarcian unstable conditions and water stratification is restored, our data show that all species but *L. hauffii*, start to increase their coccolith size as all taxa contribute to the size pool increase (Figs. 12 and 13). If in broad terms this observation suggests a switchover between smaller and larger taxa, this should be carefully interpreted, as throughout part of the middle Toarcian while *L. hauffii* still shares the same habitat with the other taxa, its relative abundance steadily decreases without any significant increase in the abundance of the other species. This observation is more noticeable in the Cusses Basin maybe due to its structural enclosed nature and likely persistent nutrification and hence *L. hauffii* occurrence, and thus a strict replacement within the genus cannot be called for. If morphological plasticity are within their adaptive range (Mayr, 1970) changes in local environmental conditions can induce organisms to react either by producing distinct ecophenotypes, or by tracking their optimum habitat (Renaud and Schmidt, 2003). From the middle Toarcian, as seawater temperature got gradually colder and steady nutrient depletion progressed until the water column acquired an oligotrophic character, we observe in both basins that up-sections relative abundances of *L. hauffii* also get progressively lower. Since there are no indications that this species have occupied other ecological niches or displayed such an ecological plasticity that would have allowed it to maintain its previous abundances in oligotrophic waters, we interpret its low relative and absolute abundances as the lack of its optimum environmental conditions to thrive, thus corroborating its opportunist behaviour. Actually, *L. hauffii* has already been acknowledged as a taxon adapted to relatively high trophic levels (Pittet and Mattioli, 2002; Mattioli and Pittet, 2004; Giraud, 2009). Following the ecological niche division by Schmidt et al. (2006), where the environment is divided into optimum growth, reproductive range, growth limits and lethal conditions, our data suggest that throughout the first half of the middle Toarcian environmental conditions are still within *L. hauffii* reproductive range and within its growth limit after that, as it still makes its presence in all up-sections assemblages.

Moreover, in a strict stratigraphic phenotypic replacement within the *Lotharingius* pool, high determination coefficients between the different species would be expected, as they would negatively covariate. Actually, the highest correlation coefficients (r) in the Lusitanian Basin among the relative abundance of the most important *Lotharingius* species are surprisingly modest and their determination coefficient (r^2) are correspondingly even weaker. The higher *r* values were obtained between *L. hauffii* and *L. frodoi* ($r = 0.512$, $p = 0.0019$), *L. velatus* and *L. frodoi* ($r = -0.567$, $p = 0.0005$), and *L. velatus* and *L. hauffii* ($r = -0.587$, $p = 0.0003$). In the Causses Basin we can observe similar correlation coefficients. Noteworthy though, is the lack of correlation between the small species *L. hauffii* and *L. frodoi* ($r = 0.382$, $p = 0.0871$), which can be explained for the higher abundances, displayed at lower Tethyan latitudes by *L. frodoi* (Mattioli et al., 2008). Conversely, there is a significant negative correlation between the large *L. velatus* and the small *L. hauffii* ($r = -0.674$, $p = 0.0008$), and between *L. velatus* and *L. frodoi* ($r = -0.620$, $p = 0.0027$). As for *L. sigillatus*, it is solely strongly correlated with *L. crucicentralis* ($r = 0.806$, $p < 0.0001$) in the Causses Basin probably because these taxa are preferentially far more abundant at higher latitudes (Mattioli et al., 2008). If results from the correlation coefficients do not show a strong relationship between the different taxa, the determination coefficients disclose even worse associative scores. If *r* measures the strength and the direction of a linear relationship between two variables, r^2 denotes the strength of the linear association between those same variables, or the proportion (%) of the variance of one variable that is predictable from the other variable. We therefore assume that each of the variables/species is independent or weakly correlated, and hence rule out a strict phenotypic replacement within the *Lotharingius* assemblages during the middle Toarcian.

5.5. Interspecific variation and abiotic forcing

Interspecific size variation and increase in variance over time due to continuous accumulation of mutational effects (Gould, 1988; Norris, 1991; Jablonski, 1997) coupled with abiotic factors able to influence the function of organisms, seems to be a plausible interpretation and the one that better accounts for the size evolution of the *Lotharingius* pool across the Toarcian. After the fast reproduction rate period recorded at the end and just after the T-OAE, when small size specialist taxa thrived throughout stressed ecological settings, larger coccoliths and likely increased cell growth rates (Young and Westbroek, 1991; Shiraiwa, 2003) are recorded from the middle Toarcian coeval with the environment reestablishment. During the time interval spanning from the middle Toarcian up to the Late Toarcian Speciosum-Meneghinii ammonite zones in Portugal, and Pseudoradiosa zone in France, an expanded photic zone and stratified water masses in western Tethys seemed to have gathered the best environmental conditions for the genus to increase its size (see Figures 18 and 19). A close relationship between the *Lotharingius* size pool evolution and environmental change supports the stationary model (Stenseth and Maynard Smith, 1984), which suggests that evolution is largely driven by abiotic changes such as temperature, water column stratification and/or primary productivity. The stationary model also corroborates the correlation between size evolution of Cenozoic foraminifera and palaeoceanographic perturbations (Wei and Kennet, 1983; Schmidt et al., 2004a,b). Low coccolithophore abundances linked with higher diversity was already acknowledged in the Lusitanian Basin for this period of ecological stability, nutrient depleted and stratified waters (Ferreira et al., 2015), and the same liaison can also be recognized in the Causses Basin (Harazim et al., 2012). The absence of environmental stress would naturally promote the background genetic imprint of *Lotharingius* in accordance with the "left wall" model, i.e., the population drifts away from small species. Moreover, the ecological quiescence would uphold a faster coccolith growth rate and larger coccoliths, besides enhancing its interspecific variability.

But sudden and profound changes in morphological traits like those observed in the middle Toarcian demand an underlying mechanism. The causes for a morphological variation can be internal (allometry related to physical or physiological properties of an organism), or external and thus reflecting changes in interaction with abiotic and biotic environment such as predator-prey relationships or population density (McKinney, 1990b). Proposed advantages by Stanley (1973) of large size include improved ability to capture prey or avoid predators, greater reproductive success, expanded size range of acceptable food, decreased mortality, extended individual longevity and metabolic benefits such as increased heat retention per unit volume. Yet, large size also has its disadvantages like feeding efficiency must increase substantially (Schmidt et al., 2006).

Herrmann et al. (2012) showed that coccolith sizes of individual genera and the annual mean sea-surface temperature show no linear or uniform relationships for the different genera, and thus Lübke et al. (2015) do not support a simple correlation between coccolith size and sea-surface temperature for the Cretaceous. Nonetheless, the ongoing drop in seawater temperature from the middle Toarcian, might have been an additional stimulus for *Lotharingius* coccolithophores to enlarge their cell and intracellular calcification, as acknowledged by Sorrosa et al. (2005) on extant species *E. huxleyi* and *Gephyrocapsa oceanica* when these were exposed to lowered temperatures. Actually, size increase of Mesozoic nannoliths has already been linked to sea surface temperature drop. That is the case for *Schizosphaerella* during the Late Pliensbachian (Suan et al., 2008a; 2010), *Crepidolithus crassus* and *C. crucifer* across the Pliensbachian (Fraguas and Erba, 2010), or for *Nannoconus* during the Valanginian (Barbarin et al., 2012).

Both up-sections PCA scores and box-plot chart plot show that in both basins around the Toarcian-Aalenian limit there is a short-term size change in the *Lotharingius* pool towards smaller

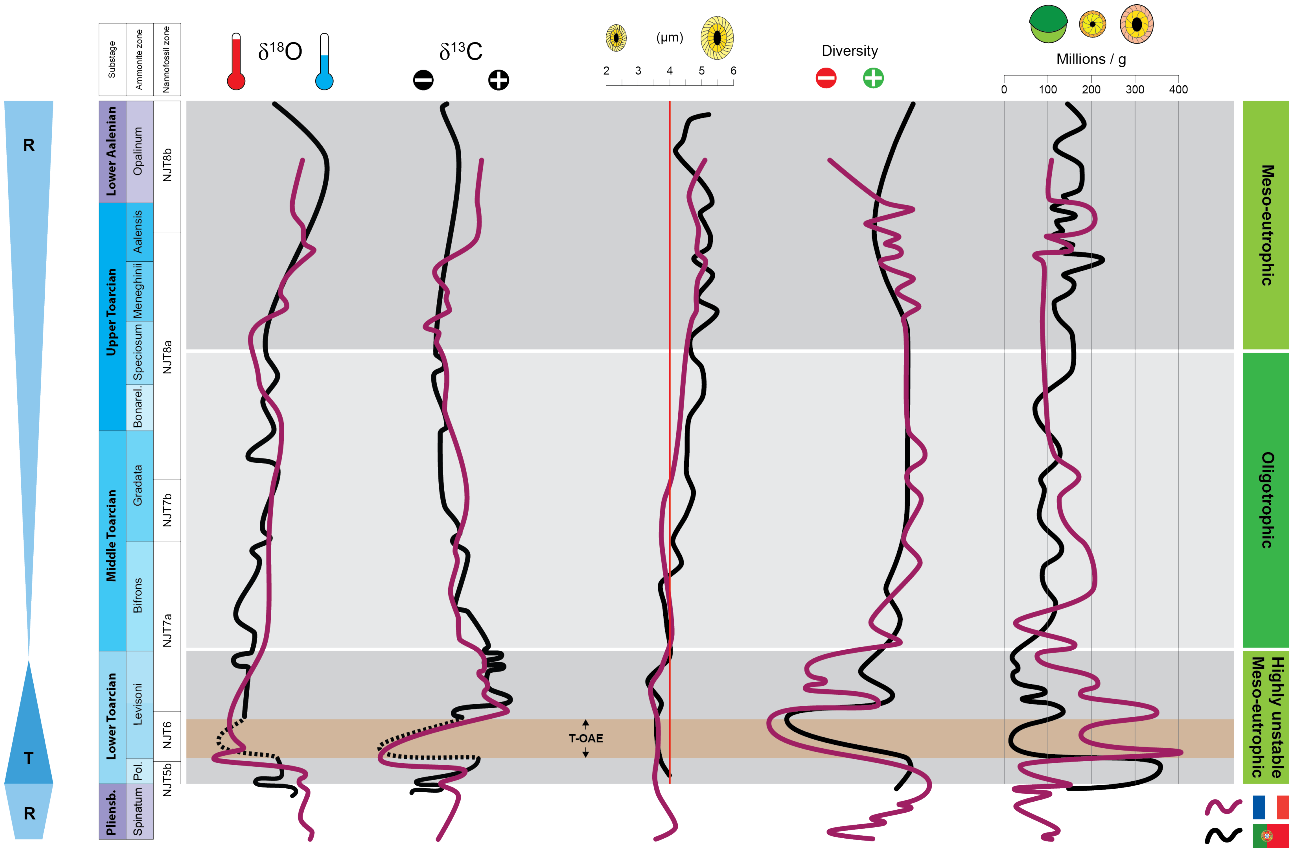


Figure 18 - Synthetic table showing the evolution from Lusitanian and Causses basins seawater temperature, water fertility, coccolith length, diversity and absolute coccolith abundance. Data from the Lusitanian Basin are from Ferreira et al. (2015) and isotopic data from the Causses Basin are from Harazim et al. (2012).

species. Also Tukey's honestly significant difference post-hoc test shows this trend for the Lusitanian Basin. If in Portugal this trend is caused by a sharp decrease in abundance of larger specimens like *L. velatus*, in France it is produced by a significant increase in small *L. hauffii*. This temporary size change seems to be linked with a major abiotic modification: the short-term increase in seawater temperature and primary productivity recorded in both regions. The *Lotharingius* size variation could thus be the by-product of a phenotypic adjustment to a short-lived, drastic environmental change, as its population growth rate increase and coccoliths size dwindle accordingly. This size decrease is observed in all *Lotharingius* species and particularly in *L. sigillatus* and *L. crucicentralis*. Moreover, with the exception for the sample CAB57, we observe an increase in the genus relative abundance, reaching proportions only recorded during the Early Toarcian (~80%). In the Causses Basin the observed increase in *L. hauffii* abundance can be interpreted as the displacement from its growth limits into its reproductive range, but never reaching its optimum environment, as environmental conditions tend to parallel those observed during the late Early Toarcian, i.e., increase in water nutrification, primary oceanic productivity and seawater temperature.

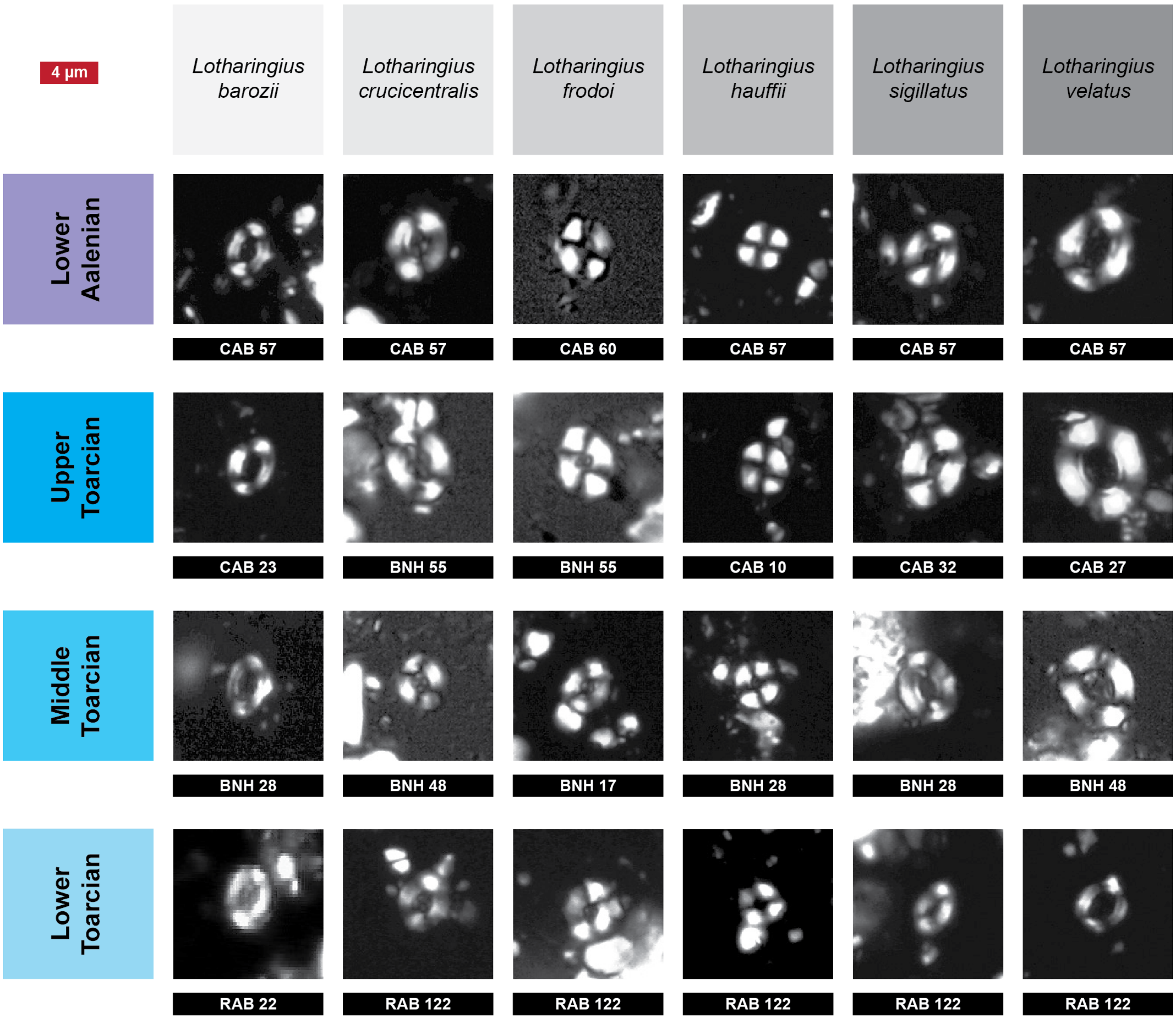


Figure 19 - Selected pictures showing the size evolution of the seven different *Lotharingius* species across the Toarcian and Early Aalenian in the Lusitanian Basin sections: Rabaçal (RAB), Brenha (BNH) and Cabo Mondego (CAB).

5.6. So where do we stand?

Though probably impossible to categorize biotic and abiotic phenomena as independent factors, a single and straightforward cause for the morphological changes observed throughout the studied Toarcian stages in the Lotharingius coccolith pool, is a complex task. Nonetheless, after the analysis of 5500 specimens, some significant indications can be drawn. An important relationship between seawater temperature, surface water nutrification and *Lotharingius* morphological evolution can be made (see Fig. 18). Two positive $\delta^{13}C$ excursions interpreted as indication of water eutrophication by primary productivity observed in both basins across the lower Toarcian and starting in the uppermost Toarcian stages, are strongly linked with humid weather and a probable increase in continental discharge. Warm and meso-eutrophic Early Toarcian waters seem to gather the optimum conditions for opportunist species to increase their relative abundance through fast reproduction when nutrients are easily available. Conversely, fierce competition for nutrients in the upper photic layer would quickly lead to nutrient depletion and suppression of growth (Shiraiwa, 2003). The *Lotharingius* pool again decreases its size during a ~3ºC rise in water temperature recorded at the Toarcian-Aalenian boundary, thus suggesting an additional increase in the nutrient input, in an already nutrient-rich environment. Interspecific variability together with the genus phenotypic plasticity is the likely driving cause involved in the gradual size increase and abrupt size shift observed between small and large morphospecies across the middle Toarcian. This change in the taxon pool size can thus reflect the *Lotharingius* adjustment to more stable conditions and to the rebuilding of the photic zone ecosystem when water column was stratified.

Despite the long-term trend in the evolution of the *Lotharingius* pool being genetically driven, leading to larger forms and thus following the Cope's rule and the "left wall" model, our data suggest that drastic changes in the environment such as temperature oscillations and water nutrification can strongly disturb this evolutionary trend by increasing the population growth and subsequently constrain the coccolith size (see Fig. 18). Nevertheless, interspecific variation and abiotic forcing are factors to be reckon with, when assessing the gradual stratigraphic increase and dominance of larger taxa within the genus. Whichever is the prevailing forcing mechanism accountable for the morphological changes in the Lotharingius genus, there seems to be no straightforward answer. As already supported by Mattioli and Erba (1999) and Aguado et al. (2008), during the middle Toarcian the coccolithophore community underwent drastic and important changes. During the long-term cooling period starting from the middle Toarcian, the taxon grows progressively bigger in a stable and oligotrophic environment, probably reflecting its natural evolutionary trend but also constrained by its interspecific variation and ecological relationships. However, during warm periods and nutrient rich waters two scenarios are deemed possible: 1) opportunist species increase their abundance and 2) fast reproduction leads to nutrient depleted environments and coccolith growth is halted (see Fig. 19).

6. Conclusions

Due to its continuous and global record in marine sediments, calcareous nannofossils stand as a valuable micropalaeontological group in palaeoenvironmental and evolutionary studies. The long-term study of a specific nannofossil taxon allows acknowledging shifts in environment conditions, as well biotic relationships in the nannofloral community. Most important of all, long-term studies allows to better recognizing the evolutionary path and trend of a given fossil morphogroup through the evolution of its phenotypic expression. In fact, as shown from two independent dataset from two geographically distant Tethyan basins, size change in *Lotharingius* coccoliths seems to closely mirror abiotic shifts in their ecological niche, being the most remarkable one, the one that occurred after the T-OAE thus representing a consistent biostratigraphic event in west Tethyan waters.

During the Toarcian and Early Aalenian, size changes of *Lotharingius* coccoliths in western Tethys are closely related with both evolutionary processes and ecological conditions. Reproduction and growth rates are the main causes affecting the size variation on the short-term whereas the genetic imprint of coccolithophores play a long-term role on their morphological evolution. On short time scales (100 thousands of years), size changes in *Lotharingius* coccoliths seem to be related to multiple independent environmental parameters such as water stratification, nutrient availability or temperature, and not to one sole variable. Our data suggest that modification in water mass nutrification is the leading reason to have influenced the morphological evolution of the genus across the Toarcian and Early Aalenian. Through its phenotypic plasticity and intraspecific size variability, this taxon was able to react and adapt to environmental changes, making these the most important biological parameters compelling its morphological evolution. In unstable meso-eutrophic environments, fast reproduction carried out predominantly by opportunist species like *L. hauffii* resulted in small coccoliths, probably due to competition and/or size inhibition caused by nutrient depletion, whereas fast growth in oligotrophic and colder waters resulted in larger coccoliths. At the Lower-Middle Jurassic transition, an oscillation in seawater temperature in fertile water masses is coeval with a slight increase in small, and a decrease in large *Lotharingius*, thus supporting this interpretation.

On the long time scale (millions of years), however, size variations driven by evolution are undoubtedly important, for across the Toarcian-Early Aalenian the genus pool size in western Tethys evolves towards bigger forms following the Cope’s rule and the Left Wall model. Dataset analysis and statistics clearly show two different populations in the *Lotharingius* genus at 4 µm boundary. Smaller population mainly consists of *L. hauffii* and *L. frodoi* whereas the larger population is essentially comprised by *L. velatus*. Even if no statistically significant differences in the *Lotharingius* coccoliths shape are observed, these two morpho-groups undoubtedly define a chronostratigraphic boundary in the middle Toarcian at the transition between the Bifrons and Gradata (Variabilis) ammonite zones.

Taxonomic appendix

L. barozii is distinguished by its broadly elliptical contour with a narrow rim and a wide and elliptical central area spanned by an axial cross; *L. crucicentralis* is a small to intermediate coccolith generally big (>5 µm) and elliptical, with a wide and elliptical central area bearing an axial prominent cross and a system of radially arranged granulations; *L. frodoi* is a small coccolith with an elliptical contour and a small central area characterized by the presence of two buttresses or bars, aligned with the minor axis of the ellipse; *L. hauffii* is characterized by its small size (≤4 µm) and subcircular to elliptical contour, with a reduced subcircular to elliptical and often empty central area that can sometimes be occupied by a knob or spine; *L. sigillatus* is distinguished by its elliptical shape and elongate central area with buttresses aligned with the major axis of the ellipse and a system of granular and radially disposed elements; *L. umbriensis* is a small coccolith with a subcircular outline with a very small central area spanned by a small cross; *L. velatus* is generally a large (>6 μm) and elliptical coccolith with a very wide central area filled with a granular plate.

Acknowledgments

The authors whish to thank Giles Escarguel for his valuable help on data analysis, and Bas van de Schootbrugge for kindly providing the Truc-de-Balduc samples.

References

Aguado, R., O’Dogherty, L., Sandoval, J., 2008. Fertility changes in surface waters during the Aalenian (mid-Jurassic) of the western Tethys as revealed by calcareous nannofossils and carbon-cycle perturbations. Marine Micropaleontology 68, 268-285.

Arias, C., Whatley, R.C., 2005. Palaeozoogeography of Western European Lower Jurassic (Pliensbachian and Toarcian) Ostracoda. Geobios 38, 697-724.

Bailey, T.R., Rosenthal, Y., McArthur, J.M., van de Schootbrugge, B., Thirlwall, M.F., 2003. Paleoceanographic 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.

Barbarin, N., Bonin, A., Mattioli, E., Pucéat, E., Cappetta, H., Gréselle, B., Pittet, B., Vennin, E., Joachimski, E., 2012. Evidence for a complex Valanginian nannoconid decline in the Vocontian basin (South East France). Marine Micropaleontology 84-85, 37-53.

Bartolini, A., Baumgartner, P.O., Guex, J., 1999. Middle and Late Jurassic radiolarian palaeoecology versus carbon-isotope stratigraphy. Palaeogeography, Palaeoclimatology, Palaeoecology 145, 43-60.

Bassoulet, J.P., Elmi, S., Poisson, A., Cecca, F., Bellion, Y., Guiraud, R., Baudin, F., 1993. Mid Toarcian. In: Dercourt, J., Ricou, L.E., Vrielynck, B. (Eds.) Atlas of Tethys Paleoenvironmental Maps. Becip-Franlab, Rueil-Malmaison, France, pp. 63-80.

Bjerrum, C.J., Surlyk, F., Callomon, J.H., Slingerland, R.L., 2001. Numerical Paleoceanographic study of the Early Jurassic transcontinental Laurasian Seaway, Paleoceanography 16, 390-404.

Bornemann, A., Aschwer, U., Mutterlose, J., 2003. The impact of calcareous nannofossils on the pelagic carbonate accumulation across the Jurassic-Cretaceous boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 199, 187-228.

Bown, P.R., 1987. Taxonomy, evolution and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. Special Papers in Palaeontology 38, 1-118.

Bown, P.R., Cooper, M.K.E., 1998. Jurassic. In: Bown, P.R. (Ed.) Calcareous Nannofossils Biostratigraphy. British Micropalaeontological Society Publication Series. Kluver Academic Publishers, Cambridge, pp. 34-85.

Bradshaw, J.S., 1961. Laboratory experiments on the ecology of foraminifera. Cushman Foundation of Foraminiferal Research 12, 87-106.

Brigaud, B., Durlet, C., Deconinck, J.-F., Vincent, B., Pucéat, E., Thierry, J., Trouiller, A., 2009. Facies and climate/environmental changes recorded on a carbonate ramp: a sedimentological and geochemical approach on Middle Jurassic carbonates (Paris Basin, France). Sedimentary Geology 222, 181-206.

Cobianchi M.A., 1992. Sinemurian-Early Bajocian Calcareous Nannofossil Biostratigraphy of the Lombardy Basin (Southern Calcareous Alps; Northern Italy). Atti Ticinensi di Scienze della Terra 35, 61-106.

Damborenea, S.E., 2002. Jurassic evolution of Southern Hemisphere marine palaeobiogeographic units based on benthonic bivalves. Geobios 35 (Supplement 1), 51-71.

Dera, G., Pellenard, P., Neige, P., Deconinck, J.F., Puceat, E., Dommergues, J.L., 2009a. Distribution of clay minerals in Early Jurassic Peritethyan seas: Palaeoclimatic significance inferred from multiproxy comparisons. Palaeogeography, Palaeoclimatology, Palaeoecology 271, 39-51.

Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J.-F., Pellenard, P., Joachimski, M.M., Durlet, C., 2011b. Climatic ups and downs in a disturbed Jurassic world. Geology 39, 215-218.

Dera, G., Neige, P., Dommergues, J.-L., Brayard, A., 2011a. Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Global and Planetary Change 78, 92-105.

Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, 2000. Atlas Peri-Tethys, Palaeogeographical maps. CCGM/CGMW, Paris.

Dommergues, J.L., Meister, C., 1991. Area of mixed marine faunas between two major palaeogeographical realms, exemplified by the Early Jurassic late Sinemurian and Pliensbachian ammonites in the Alps. Palaeogeography, Palaeoclimatology, Palaeoecology 86, 265-282.

Dommergues, J.L., Mouterde, R., 1980. Modalités d’installation et d’évolution des harpocératinès (Ammonitina) au Domérien inférieur dans le Sud-Ouest de l’Europe. Geobios 13, 289-325.

Duarte, L.V., 1998. Clay minerals and geochemical evolution in the Toarcian-Lower Aalenian of the Lusitanian Basin (Portugal). Cuadernos de Geología Ibérica 24, 69-98.

Duarte, L.V., 2004. The geological heritage of the Lower Jurassic of Central Portugal: selected sites, inventory and main scientific arguments. Rivista Italiana di Paleontologia e Stratigrafia 110, 381-387.

Duarte, L.V., Oliveira, L.C., Rodrigues, R., 2007. Carbon isotopes as a sequence stratigraphic tool: examples from the Lower and Middle Toarcian marly limestones of Portugal. Boletín Geológico y Minero 118, 3-18.

Dye, F.J., 2012. Dictionary of developmental biology and embryology. John Wiley & Sons, Inc., Hoboken, New Jersey, pp. 232.

Ferreira, J., Mattioli, E., Pittet, B., Cachão, M., Spangenberg, J.E., 2015. Palaeoecological insights on Toarcian and lower Aalenian calcareous nannofossils from the Lusitanian Basin (Portugal). Palaeogeography, Palaeoclimatology, Palaeoecology 436, 245-262.

Fraguas, A., Erba, E., 2010. Biometric analyses as a tool for the differentiation of two coccolith species of the genus Crepidolithus (Pliensbachian, Lower Jurassic) in the Basque-Cantabrian Basin (Northern Spain). Marine Micropaleontology 77, 125-136.

Fraguas, A., Young, J., 2011. Evolution of the coccolith genus Lotharingius during the Late Pliensbachian-Early Toarcian interval in Asturias (N Spain). Consequences of the Early Toarcian environmental perturbations. Geobios 44, 361-375.

Geisen, M., Bollman, J., Herrle, J.O., Mutterlose, J., Young, J.R., 1999. Calibration of the random settling technique for calculation of absolute abundances of calcareous nannoplankton. Micropaleontology 45, 437-442.

Giraud, F., 2009. Calcareous nannofossil productivity and carbonate production across the Middle-Late Jurassic transition in the French Subalpine Basin. Geobios 42, 699-714.

Giraud, F., Pittet, B., Mattioli, E., Audouin, V., 2006. Paleoenvironmental controls on the morphology and abundance of the coccolith Watznaueria britannica (Late Jurassic, southern Germany). Marine Micropaleontology 60, 205-225.

Goy, G., Noël, D., Busson, G., 1979. Les conditions de sédimentation des schistes carton (Toarcien inf.) du Basin de Paris déduites de l'étude des nannofossiles calcaires et des diagraphies. Documents des Laboratoires de Géologie de Lyon 75, 33-57.

Gómez, J.J., Canales, M.L., Ureta, S., Goy, A., 2009. Palaeoclimatic and biotic changes during the Aalenian (Middle Jurassic) at the southern Laurasian Seaway (Basque-Cantabrian Basin, northern Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 275, 14-27.

Gómez, J.J., Goy, A., Canales, M.L., 2008. Seawater temperature and carbon isotope variations in belemnites linked to mass extinction during the Toarcian (Early Jurassic) in Central and Northern Spain. Comparison with other European sections. Palaeogeography, Palaeoclimatology, Palaeoecology 258, 28-58.

Gould, S.J., 1988. Trends as changes in variance. a new slant on progress and directionality in evolution. Journal of Paleontology 62, 319-329.

Hallam, A., 1981. A revised sea-level curve for the Early Jurassic. Journal of the Geological Society 138, 735-743.

Hamilton, G.B., 1977. Early Jurassic calcareous nannofossils from Portugal and their biostratigraphic use. Eclogae geologicae Helvetiae 70, 575-597.

Hamilton, G.B., 1979. Lower and Middle Jurassic calcareous nannofossils from Portugal. Eclogae geologicae Helvetiae 72, 1-17.

Hammer, Ø. , Harper, D.A.T., 2006. Paleontological data analysis. Blackwell Publishing Ltd, pp. 35-37.

Harazim, D., van de Schootbrugge, B., Sorichter, K., Fiebig, J., Weug, A., Suan, G., Oschmann, W., 2012. Spatial variability of watermass conditions within the European Epicontinental Seaway during the Early Jurassic (Pliensbachian-Toarcian). Sedimentology 60, 359-390.

Henderiks, J., Pagani, M., 2007. Coccolithophore cell size and the Paleogene decline in atmospheric CO2. Earth and Planetary Science Letters 269, 576-584.

Herrmann, S., Thierstein, H.R., 2012. Cenozoic coccolith size changes - evolutionary and/or ecological controls? Palaeogeography, Palaeoclimatology. Palaeoecology 333-334, 92-106.

Hesselbo, S.P., Gröcke, D.R., Jenkyns, H.C., Bjerrum, C.J., Farrimond, P., Morgans-Bell, H.S., Green, O.R., 2000. Massive dissociation of gas hydrate during a Jurassic oceanic event, Nature 406, 392-395.

Hesselbo, S.P., Jenkyns, H.C., Duarte, L.V., Oliveira, L.C.V., 2007. Carbon-isotope record of the Early Jurassic (Toarcian) Oceanic Anoxic Event from fossil wood and marine carbonate (Lusitanian Basin, Portugal). EPSL 253, 455-470.

Jablonski, D., 1997. Body-size evolution in Cretaceous molluscs and the status of Cope’s rule. Nature 385, 250 - 252.

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., Clayton, C.J., 1986. Black shales and carbon isotopes in pelagic sediments from the Tethyan Lower Jurassic. Sedimentology 33, 87-106.

Jenkyns, H.C., Gröcke, D.R., Hesselbo, S.P., 2001. Nitrogen isotope evidence for water mass denitrification during the early Toarcian (Jurassic) oceanic anoxic event, Paleoceanography 16, 593-603.

Jenkyns, H.C., Jones, C.E., Gröcke, D.R., Hesselbo, S.P., Parkinson, D.N., 2002. Chemostratigraphy of the Jurassic System: applications, limitations and implications for palaeoceanography. Journal of the Geological Society 159, 351-372.

Knappertsbusch, M., 2000. Morphologic evolution of the coccolithophorid *Calcidiscus leptoporus* from the Early Miocene to Recent. Journal of Paleontology 74, 712-730.

Krencker, F.N., Bodin, S., Hoffmann, R., Suan, G., Mattioli, E., Kabiri, L., Föllmi, K.B., Immenhauser, A., 2014. The middle Toarcian cold snap: Trigger of mass extinction and carbonate factory demise. Global and Planetary Change 117, 64-78.

Kump, L.R., Arthur M.A., 1999. Interpreting carbon-isotope excursions: carbonates and organic matter. Chemical Geology 161, 181-198.

Laland, K.N., Odling-Smee, J., Feldman, M.W., 2004. Causing a commotion. Nature 429, 609.

López-Otálvaro, G.-E., Baptiste Suchéras-Marx, B., Giraud, F., Mattioli, E., Lécuyer, C., 2012. Discorhabdus as a key coccolith genus for paleoenvironmental reconstructions (Middle Jurassic, Lusitanian Basin): Biometry and taxonomic status. Marine Micropaleontology 94-95, 45-57.

Lübke, N., Mutterlose, J., Bottini, C., 2015. Size variations of coccoliths in Cretaceous oceans - A result of preservation, genetics and ecology? Marine Micropaleontology 117, 25-39.

Mailliot, S., Mattioli, E., Bartolini, A., Baudin, F., Pittet, B., Guex, J., 2009. Late Pliensbachian Early Toarcian (Early Jurassic) environmental changes in an epicontinental basin of NW Europe (Causses area, central France): A micropaleontological and geochemical approach. Palaeoceanography, Palaeoclimatology, Palaeoecology 273, 346-364.

Mattioli, E., 1996. New Calcareous Nannofossil species from the Early Jurassic of Tethys. Rivista Italiana di Paliontoligia e Stratigrafia 102, 397-412.

Mattioli, E., Erba, E., 1999. Biostratigraphic synthesis of calcareous nannofossil events in the Tethyan Jurassic. Rivista Italiana di Paleontologia e Stratigrafia 105, 343-376.

Mattioli, E., Pittet, B., 2002. The contribution of calcareous nannoplankton to the carbonate deposition: a new approach applied to the Lower Jurassic of central Italy. Marine Micropaleontology 45, 175-190.

Mattioli, E., Pittet, B., 2004. Spatial and temporal distribution of calcareous nannofossils along a proximal-distal transect in the Lower Jurassic of the Umbria-Marche Basin (central Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 205, 295-316.

Mattioli. E., Pittet, B., Suan, G., Mailliot, S., 2008. Calcareous nannoplankton across Early Toarcian anoxic event: implications for palaeoceanography within the western Tethys. Palaeoceanography 23.

Mattioli, E.; Pittet, B., Young, J.R., Bown, P.R., 2004. Biometric analysis of Pliensbachian-Toarcian (Lower Jurassic) coccoliths of the family Biscutaceae: intra- and interspecific variability versus palaeoenvironmental influence. Marine Micropaleontology 52, 5-27.

Mayr, E., 1970. Population, Species and Evolution. Harvard University Press, Boston.

McArthur, J.M., Algeo, T.J., van de Schootbrugge, B., Li, Q., Howarth, R.J., 2008. Basinal restriction, black shales, Re-Os dating, and the Early Toarcian (Jurassic) oceanic anoxic event. Paleoceanography 23, PA4217.

McDonald, J.H., 2008. Handbook of Biological Statistics. University of Delaware. Sparky House Publishing.

McKinney, M.L., 1990b. Trends in body-size evolution. In: McNamara, K.J. (Ed.), Evolutionary Trends. Belhaven Press, London, pp. 75-118.

Morard, A., 2004. Les événements du passage Domérien-Toarcien entre Téthys occidentale et Europe du Nord-Ouest. Thèse, Université Lausanne, Géologie - Paléontologie, pp. 1-158.

Mouterde, R., Ruget, C., 1975. Esquisse de la paleogeographie du jurassique inférieur et moyen en Portugal. Bulletin de la Societe Geologique de France 14, 779-786.

Noël, D., 1973. Nannofossiles calcaires de sédiments jurassiques finement laminés. Bulletin du Muséum National d'Histoire Naturelle, 3e serie, 75: 95-156.

Norris, R.D., 1991. Biased extinction and evolutionary trends. Paleobiology 17, 388-399.

Pittet, B., Suan, G., Lenoir, F., Duarte, L.V., Mattioli, E., 2014. Carbon isotope evidence for sedimentary discontinuities in the lower Toarcian of the Lusitanian Basin (Portugal): Sea level changes at the onset of the Oceanic Anoxic Event. Sedimentary Geology 303, 1-14.

Porter, S.J., Smith, P.L., Caruthers, A.H., Hou, P., Gröcke, D.R., Selby, D., 2014. New high resolution geochemistry of Lower Jurassic marine sections in western North America: A global positive carbon isotope excursion in the Sinemurian? EPSL 397, 19-31.

Price, G.D., 2010. Carbon-isotope stratigraphy and temperature change during the Early-Middle Jurassic (Toarcian-Aalenian), Raasay, Scotland, UK. Palaeogeography, Palaeoclimatology, Palaeoecology 285, 255-263.

Renaud, S., Schmidt, D.N., 2003. Habitat tracking as a response of the planktic foraminifer *Globorotalia truncatulinoide*s to environmental fluctuations during the last 140 kyr. Marine Micropaleontology 49, 97-122.

Reggiani, L., Mattioli, E., Pittet, b., Duarte, L.V., Veiga de Oliveira, L.C., Comas-Rengifo, M.J. 2010b. Pliensbachian (Early Jurassic) calcareous nannofossils from the Peniche section (Lusitanian Basin, Portugal): A clue for palaeoenvironmental reconstructions. Marine Micropaleontology 75, 1-16.

Ruebsam, W., Münzberger, P., Schwark, L., 2014. Chronology of the Early Toarcian environmental crisis in the Lorraine Sub-Basin (NE Paris Basin). EPSL 404, 273-282.

Sandoval, J., Bill, M., Aguado, R., O´Dogherty, L., Rivas, P., Morard, A., Guex, J., 2012. The Toarcian in the Subbetic basin (southern Spain): Bio-events (ammonite and calcareous nannofossils) and carbon-isotope stratigraphy. Palaeogeography, Palaeoclimatology, Palaeoecology 342-343, 40-63.

Sandoval, J., O'Dogherty, L., Aguado, R., Bartolini, A., Bruchez, S., Bill, M. 2008. Aalenian carbon-isotope stratigraphy: Calibration with ammonite, radiolarian and nannofossil events in the Western Tethys. Palaeogeography, Palaeoclimatology, Palaeoecology 267, 115-137.

Schmidt, D.N., Lazarus, D., Young, J.R., Kucera, M., 2006. Biogeography and evolution of body size in marine plankton. Earth-Science Reviews 78, 239-266.

Schmidt, D.N., Thierstein, H.R., Bollmann, J., 2004a. The evolutionary history of size variation of planktic foraminiferal assemblages in the Cenozoic. Palaeogeography, Palaeoclimatology, Palaeoecology 212, 159-180.

Schmidt, D.N., Thierstein, H.R., Bollmann, J., Schiebel, R., 2004b. Abiotic forcing of plankton evolution in the Cenozoic. Science 303, 207-210.

Shiraiwa, Y., 2003. Physiological regulation of carbon fixation in the photosynthesis and calcification of coccolithophorids. Comparative Biochemistry and Physiology Part B 136, 775-783.

Sorrosa, J.M., Satoh, M., Shiraiwa, Y., 2005. Low temperature stimulates cell enlargement and intracellular calcification of coccolithophorids. Marine Biotechnology 7, 128-133.

Stanley, S.M., 1973. An explanation for Cope's rule. Evolution 27, 1-26.

Stenseth, N.C., Maynard Smith, J., 1984. Coevolution in ecosystems: red queen evolution or stasis? Evolution 38, 870-880.

Suan, G., Mattioli, E., Pittet, B., Lécuyer C., Suchéras-Marx, B., Duarte, L.V., Philippe, M., Reggiani, L., Martineau, F., 2010. Secular environmental precursors to Early Toarcian (Jurassic) extreme climate changes. EPSL 290, 448-458.

Suan, G., Mattioli, E., Pittet, B., Mailliot, S., Lécuyer, C., 2008a. Evidence for major environmental perturbation prior to and during the Toarcian (Early Jurassic) oceanic anoxic event from the Lusitanian Basin, Portugal. Paleoceanography 23, PA1202.

Suan, G., Pittet, B., Bour, I., Mattioli, E., Duarte, L.V., Mailliot, S., 2008b. Duration of the Early Toarcian carbon isotope excursion deduced from spectral analysis: consequence for its possible causes. EPSL 267, 666-679.

Suchéras-Marx, B., Mattioli, E., Pittet, B., Escarguel, G., Suan, G., 2010. Astronomically paced coccolith size variations during the early Pliensbachian (Early Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 295, 281-292.

Tiraboschi, D., Erba, E., 2010. Calcareous nannofossil biostratigraphy (upper Bajocian-lower Bathonian) of the Ravin du Bes section (Bas Auran, Subalpine Basin, SE France); evolutionary trends of Watznaueria barnesiae and new findings of *Rucinolithus* morphotypes. Geobios 43, 59-76.

Trümpy, D.M., 1983. Le Lias Moyen et Supérieur des Grands Causses et de la région de Rodez: contributions stratigraphiques, sédimentologiques et géochimiques à la connaissance d'un bassin à sédimentation marneuse. Cahiers de l'Université, Université de Pau et des Pays de l'Adour 19, 1-363.

van Valen, L., 1973. A new evolutionary law. Evolutionary Theory 1, 1-30.

Vörös, A., 2002. Victims of the Early Toarcian anoxic event: the radiation and extinction of Jurassic Koninckinidae (Brachiopoda). Lethaia 35, 345-357.

Wei, K.-Y., Kennett, J.P., 1983. Nonconstant extinction rates of Neogene planktonic foraminifera. Nature 305, 218-220.

Young, J.R., 1990. Size variation of Neogene *Reticulofenestra* coccoliths from Indian Ocean DSDP cores. Journal of Micropalaeontology 9, 71-86.

Young, J.R., Westbroek, P., 1991. Genotypic variation in the coccolithophorid species *Emiliania huxleyi*. Marine Micropaleontology 18, 5-23.

7. Conclusions and perspectives

7.1. Conclusions

The main goal of this research was to understand how exactly the calcareous nannoplankton community evolved within the Lusitanian Basin, after the probable Mesozoic thermal maximum that occurred during the Early Toarcian. Being at the time a seaway connecting two different water masses in western Tethys, the Lusitanian Basin would therefore mirror the climatic and oceanographic changes that occurred across the Toarcian age, and therefore bear a specific micropalaeontological signature that would reflect these alterations. In order to assess the nannofloral evolution in this region, rock samples ranging from the uppermost Pliensbachian to Lower Aalenian were collected in the Lusitanian Basin, and brachiopods amassed in two of its studied sections. Calcareous nannoplankton evolution was recorded as the abundances of their fossil remains were determined, their assemblages scanned and a thorough identification work endeavored. Species bearing specific palaeogeographic affinities were identified, and their ecological preferences assessed hence enabling nutricline depth and water mass trophic levels determination. In all, changes in the nannoplankton community could be coupled with shifts in environmental conditions that occurred across the Toarcian and Early Aalenian time span. Main conclusions reached and the answer for the driving questions of this thesis go as follows:

1. Calcareous nannofossil biostratigraphy in the Lusitanian Basin was somehow biased because of (i) the existence of some contradictory seventies' works and (ii) the publication of a certain number of taxonomic revisions modifying the species concepts. This thesis work allowed to improve the biostratigraphy in west Tethyan sections by means of the recovery of consistent bioevents occurring both in the Lusitanian and Causses basins. Some events support biostratigraphic schemes found in the literature, whereas some update it. A biostratigraphic scheme for the studied sections is herein proposed from which robust and consistent events are highlighted. The FO of *Carinolithus superbus* matches the Polymorphum-Levisoni biohorizon and occurs below the T-OAE equivalent, whereas the LO of *Mitrolithus jansae* is a consistent biomarker for the topmost lower Toarcian (Levisoni zone). The FO of *Watznaueria colacicchii* is herein proposed as the most accurate biomarker for the lower-middle Toarcian limit and should therefore define its own nannofossil subzone. The FO of *Discorhabdus criotus* is a consistent and synchronous bioevent for middle Toarcian Mediterranean western Tethyan sections. The FO of *Watznaueria contracta* represents a good proxy for the Toarcian-Aalenian transition (Aalensis-Opalinum zones) whereas the LOs of *Crepidolithus cavus* and *Carinolithus poulnabronei*, and the FO of *Triscutum tiziense* are consistent auxiliary bioevents for this same limit. The FO of *Hexalithus*

magharensis stands as the best bioevent in the Mediterranean province for the Lower-Middle Jurassic limit. A new biochronological scheme can now be proposed based upon the new biostratigraphic data presented in this thesis.

2. If the Lower Toarcian interval has received much attention these last years because of the palaeoceanographic changes occurring during the T-OAE, the recovery post-anoxia conditions and the environmental conditions across the lower to middle Toarcian transition are much less known. Amongst the main results of this thesis, a published paper shows that shifts in calcareous nannofossil relative and absolute abundances recorded in the Lusitanian Basin throughout the Toarcian are closely related with palaeoceanographic changes. Three different long-term environmental settings are acknowledged in the Lusitanian Basin across the Toarcian and Early Aalenian. The lower Toarcian substage corresponds to the maximum flooding period under a warm and humid climate. Boreal and Mediterranean Tethys waters masses were freely connected in the Lusitanian Basin and its waters bore a meso-eutrophic character as shown by the proliferation of shallow-water taxa such as *Schizosphaerella*, the dominance of the meso-eutrophic genus *Lotharingius*, and also the overall increase in nannofossil absolute abundances. These nutrient-rich conditions are further supported by a general high primary production as attested by $\delta^{13}C$ values. These conditions were sharply and temporarily interrupted during the T-OAE equivalent interval in Rabaçal. Across the middle Toarcian until part of the Speciosum zone, a long-term decrease in bottom water temperature is observed whereas the highest sea level promoted the mixing of NW European and Mediterranean water masses attested by a mixing of typical nannoflora from the two provinces. During this period, low nutricline and a stratified water column is inferred by the steady increase in diversity, lower nannofossil abundance and a gradual long-term negative $\delta^{13}C$ excursion. Across this time period, nannofossil data suggest that a widened photic zone would still have bore in its upper photic layer the genus *Lotharingius*, though less *Schizosphaerella* and more *Carinolithus superbus* here interpreted as an oligotrophic shallow dweller, whereas in the deep photic zone *Crepidolithus crassus* would have thrived. From the Speciosum zone up to the Early Aalenian, Boreal and Mediterranean connection was minimal and the water column acquired a meso-eutrophic character. A boost in water nutrification supported by a significant rise in $\delta^{13}C$ values would have promoted the recorded increase in nannofossil abundance coeval with a decrease in diversity. These changes are coeval with the decline in *C. crassus* and the steady increase in *Schizosphaerella*, hence corroborating the filling of the shallower Lusitanian Basin by Mediterranean waters. Throughout this period, high fertility genera *Discorhabdus* and *Lotharingius* display high abundances whereas *C. superbus* decreases accordingly. It is noteworthy though, that after a period of sharp and rapid environmental changes T-OAE related across the lower

Toarcian, the remainder of the Toarcian age is characterized by a long-term of smooth fluctuations in environmental parameters. Such results effectively show the potential of integrating geochemical, sedimentological and micropaleontological approaches for palaeoceanographic interpretations.

3. Toarcian sediments are dominated by coccoliths of the genus *Lotharingius*. In a way similar to *Reticulofenestra* in the Cenozoic, which is represented by a plexus of morphospecies, *Lotharingius* species can be differentiated by their size and central area structures. Although the size evolution of this taxon has already been addressed either for taxonomy reasons or for very short time periods, nothing was known about long-term changes enable to shed some light on the forever-lasting dilemma between rules of evolution *vs.* paleoenvironmental constraints, on the size development of these coccoliths. The results from this research work show that size changes of *Lotharingius* coccoliths in western Tethys are closely related with both evolutionary processes and ecological parameters. Reproduction and growth rates are the main causes affecting the size variation on the short-term whereas the genetic imprint of coccolithophores play a long-term role on their morphological evolution. On the short time scale, changes in size seem to be related to environmental parameters such as water stratification, nutrient availability or temperature. Changes in water nutrification are the leading reason to have influenced the morphological evolution of the genus across the Toarcian and Early Aalenian. In unstable meso-eutrophic environments, fast reproduction resulted in small coccoliths, whereas fast growth in oligotrophic and colder waters resulted in larger coccoliths. On the long time scale, however, size variations are evolution driven as the genus pool size evolves towards bigger forms following the Cope's rule and the Left Wall model. Dataset analysis and statistics clearly show two different populations in the *Lotharingius* genus at 4 µm boundary. Even if no significant differences in the *Lotharingius* coccoliths shape are observed, these two morpho-groups undoubtedly define a chronostratigraphic boundary in the middle Toarcian at the transition between the Bifrons and Gradata (Variabilis) ammonite zones.

This work enabled to finally understand in detail the evolution of the nannoplankton community in the Lusitanian Basin waters, after the biologic crunch that the T-OAE represented. This research also adds micropalaeontological evidence supporting the eustatic oscillations inferred from sedimentological analysis described in the literature that occurred throughout the Toarcian in this region. Most important of all, the nannofossil record pinpoints the moment when the connection between Boreal and Mediterranean realms were severed, and essentially low latitude waters started to replenish this basin, making these data of potential use in future palaeoceanographic modeling works. The trend of isotopic data retrieved for the first time from benthic fossils in this basin across the Toarcian and Early Aalenian, are in accordance with bulk rock isotopic data gathered from other western Tethys regions such as Spain or Morocco thus allowing to trace supra-regional and long-term climate changes.

Since there are no extant equivalents of Jurassic calcareous nannoplankton and hence their ecological preferences are hard to determine, every lead and new data made available always represent a step forward to disclose or consolidate (or not) their ecological affinities. This work therefore validates and in some cases adds certain details, to what is known today for the most significant Lower Jurassic taxa and most important of all, adds the trophic character of the water column and bottom water temperatures to the nannoplankton habitat. Moreover, also near-shore/distal habitats and shallow/deep dwelling preferences are here supported and inferred.

The biometric work here presented spanning over ~10 myr, besides quantifying what was until now a mere hint, also places the short and long term morphological evolution of *Lotharingius* coccoliths within an abiotic and biotic frame, and for the first time, in two different and independent west Tethyan regions. This allowed to impartially validate the conclusions that were drew here. Also, the biometry work here endeavored shows that this methodology is still a powerful tool to ascertain evolutionary and phylogenetic trends, and even palaeobiogeographic provinces.

The biostratigraphic scheme presented here, acknowledges bioevents until now only reported later in the stratigraphic column, thus representing on its own a major update on Toarcian nannofossil bioevents. On the other hand, it brings to the Lusitanian Basin, i.e., further west and further south, bioevents recorded in other Tethyan regions, therefore amplifying the geographic scope of previously published biostratigraphic schemes. Moreover, it is shown here that due to their continuous record in marine sediments, the determination of nannofossil biozones and particularly their boundaries, are in most cases easier and more precise to establish then those of ammonite schemes.

7.2. Perspectives

Mapping of nannoplankton palaeobioprovinces is of extreme importance as it relays paramount palaeoceanographic information. Through the analysis of nannofossil assemblages it is possible to infer on water masses mixing or predominant ocean currents in a particular time and place. As already done in the past, establishing the geographic preferences of different calcareous nannoplankton taxa can thus render the needed pieces of information to complete or fully understand a given palaeoenvironmental setting.

Therefore I have created a database of published and unpublished data for the time interval here considered, that once treated with the adequate statistical tools, will help to better understand the palaeogeographic preferences of the dominant Lower Jurassic coccolithophore taxa. Available data from Toarcian and lower Aalenian sections from Fiuminata in central Italy, Vrines in central

France, Wittnau in southwest Germany and Djebel Chemarikh in Algeria have already started to be scanned for statistic significance. Moreover, as have been pointed out throughout this manuscript, whenever available stable carbon and oxygen isotopic signal will be interpreted in order to better characterize the distinct ecological provinces assigned to the different taxa. It will then be possible to ascribe to main Toarcian and Aalenian calcareous nannofossils observed in western Tethys successions, a specific palaeobiogeographic province.