

Early Jurassic (Pliensbachian-Toarcian) dinoflagellate migrations and cyst paleoecology in the Boreal and Tethyan realms

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ABSTRACT: The discrepancies in the stratigraphical ranges of selected dinoflagellate cysts recorded in the Boreal and Tethyan realms have revealed two migrational events during the Early Jurassic. The first event occurred at the early-late Pliensbachian boundary and consists of mutual biotic exchanges between the two realms. This is linked to a major Early Jurassic transgression which improved marine communications between the Boreal and Tethyan areas. The second dinoflagellate migrational event occurred during the mid Toarcian and was driven by paleoenvironmental factors. The numerous available Lower Jurassic dinoflagellate cyst data from the Boreal and Tethyan realms indicates that phytoplankton distribution was profoundly affected by paleoecological factors. Information pertaining to the life strategies and the paleoecological requirements of the genera *Luehndea*, *Nannoceratopsis* and *Valvaeodinium* has also been determined.

INTRODUCTION

The distributions of dinoflagellate cysts are primarily related to paleoenvironmental regimes. Certain dinoflagellate cyst taxa exhibit heterochrony over wide areas because of differences in paleoecological preferences and overall paleoenvironments (Goodman 1987). This situation has implications for the application of dinoflagellate cysts to intercontinental biostratigraphy (Bucefalo Palliani and Riding 1997a). During the Jurassic two faunal provinces, the Boreal and Tethyan realms, have been distinguished partly on the basis of different ammonite, foraminiferal, brachiopod and calcareous nannofossil assemblages (Arkell 1956; Gordon 1970; Vörös 1977; Bown 1987). Biotic differences between these realms may be characterized by relative abundances rather than by the presence or absence of specific taxa (Hallam 1969). The Boreal Realm occupied the northern part of the Northern Hemisphere; the Tethyan Realm lay to the south (Hallam 1969). During the Early Jurassic a broad transitional area with both Boreal and Tethyan biotic characteristics was developed. This intermediate belt comprises southern France, Hungary and Portugal, and was also delineated on the basis of ammonites, calcareous nannofossils and dinoflagellate cysts (Zeigler 1980; Geczy 1984; Cariou et al. 1985; Gardin and Manivit 1994; Baldanza et al. 1995). Within the Tethyan Realm, the macrofaunas allow the Mediterranean and sub-Mediterranean bioprovinces to be distinguished. The former comprises the northern margin of the Tethys Ocean, thus is of European affinity; the sub-Mediterranean is of African affinity, being on the southern margin of Tethys (Pavia and Sarti 1987). Recently these two Tethyan provinces have been differentiated using calcareous nannofossils (Baldanza and Mattioli 1992; Baldanza et al. 1995; Mattioli 1995).

The majority of publications on Lower Jurassic dinoflagellate cysts are from the Boreal domain; there are significantly fewer published data from north-west Tethys. The biogeographical distributions of Lower Jurassic dinoflagellate cysts have not been investigated in detail. On the basis of data by Davies

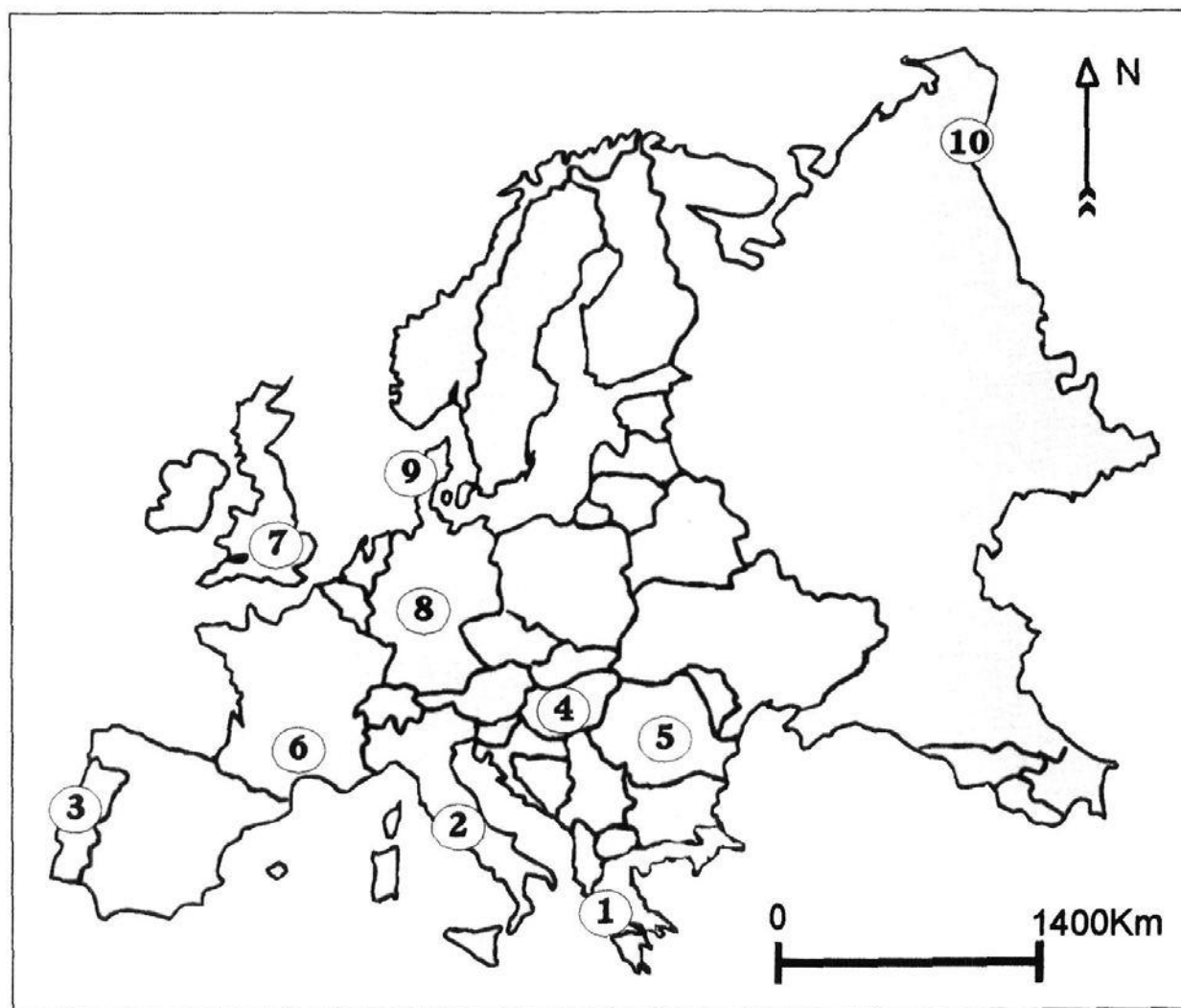
(1985) from central Portugal, Tethyan Lower Jurassic microplankton assemblages are broadly similar in generic/species content to more northerly floras. However, there are several taxa whose stratigraphical ranges differ profoundly from those in the Boreal Realm (Poulsen 1996; Riding and Ioannides 1996).

Recently, palynological studies have been carried out on ammonite- and calcareous nannofossil-dated Lower Jurassic Tethyan sections in order to define the stratigraphical ranges of dinoflagellate cysts and to compare them with their ranges in the Boreal Realm (Bucefalo Palliani 1996). The aims of this study are to distinguish and interpret the stratigraphical discrepancies between the two paleogeographical realms, to utilize the stratigraphical data to identify the areas where the main Pliensbachian-Toarcian speciation events occurred, to recognize the most important migrational events and consequently the biogeographical factors which drove the dinoflagellate cyst distributions.

MATERIAL

Samples were collected from several European Pliensbachian-early Toarcian successions (text-fig. 1). The correlations are based on the ammonite, calcareous nannofossil and dinoflagellate cyst content.

The Portuguese sections, Peniche, Rabacal and Brehna, are outcrop localities in central Portugal, north of Lisbon (text-fig. 2). The Peniche section ranges in age from the early Pliensbachian (Carixian) to the early Toarcian. It consists of intercalations of marls and more calcareous marls with interbedded black shales and detrital crinoidal limestone. The samples studied are from the Lower Pliensbachian (text-fig. 3). The late Sinemurian (Lotharingian) to early Bajocian Brenha road cutting section was dated by Mouterde et al. (1972). The Lower Pliensbachian portion of the section, made up by grey marls with marly limestone beds, has been investigated during this study (text-fig. 3).



TEXT-FIGURE 1

Map of Europe illustrating the localities considered in this work (1-Greece; 2-Italy; 3-Portugal; 4-Hungary) and those of previous major studies on Lower Jurassic (Pliensbachian-Toarcian) dinoflagellate cysts (5-Bulgaria: Dodekova and Tchoumatchenko 1989; 6-France: De Vains 1988; 7-U.K.:Riding and Thomas 1992; 8-Germany: Feist-Burkhardt and Wille 1992; 9-Denmark: Poulsen 1996).

The Rabacal section outcrops along the road from Rabacal to Condeixa and is referable to the Middle and Upper Lias (Carixian-Toarcian). The portion studied (Upper Pliensbachian-Toarcian) is made up by alternating marls and marly limestones; the samples investigated are illustrated in text-fig. 3.

The Upper Pliensbachian-Lower Toarcian Reka Valley section is located in the Mecsek Mountains area (southwest Hungary) and lithotypes represented are marly limestone and black clay (Galacz and Vörös 1989; Baldanza and Mattioli 1992; Bucefalo Palliani *et al.* 1997a).

In central Italy three Lower Toarcian successions have been investigated, Colle d'Orlando, Pozzale and Fonte Cerro, belonging to the Umbria-Marche domain (Bucefalo Palliani *et al.* 1997b).

The Lower Toarcian Greek outcrops in the Lefkas island in Kalamitzi, northwestern Greece have also been investigated

(Pettinelli *et al.* in press; Bucefalo Palliani *et al.* 1996; Bucefalo Palliani and Riding, 1997b).

The data from these Tethyan sections have been integrated with published data from the Boreal domain (Woollam and Riding 1983; De Vains 1988; Feist-Burkhardt and Wille 1992; Riding 1987; Riding *et al.* 1991; Riding and Thomas 1992; Poulsen 1996).

DINOFLAGELLATE CYST DISTRIBUTIONS

Dinoflagellate cyst assemblages from the Pliensbachian and Toarcian of the Tethyan Realm are characterized by taxa which are also widespread in the Boreal Realm. These comprise *Luehndea* spp., *Mancodinium semitabulatum*, *Mendicodinium* spp., *Nannoceratopsis* spp., *Scrinocassis weberi*, *Susadinium scrofoides* and *Valvaeodinium* spp. (Woollam and Riding 1983; De Vains 1988; Dodekova and Tchoumatchenko 1989; Feist-Burkhardt and Wille 1992; Riding and Thomas 1992; Poulsen 1996). Some of these taxa exhibit the same stratigraphi-

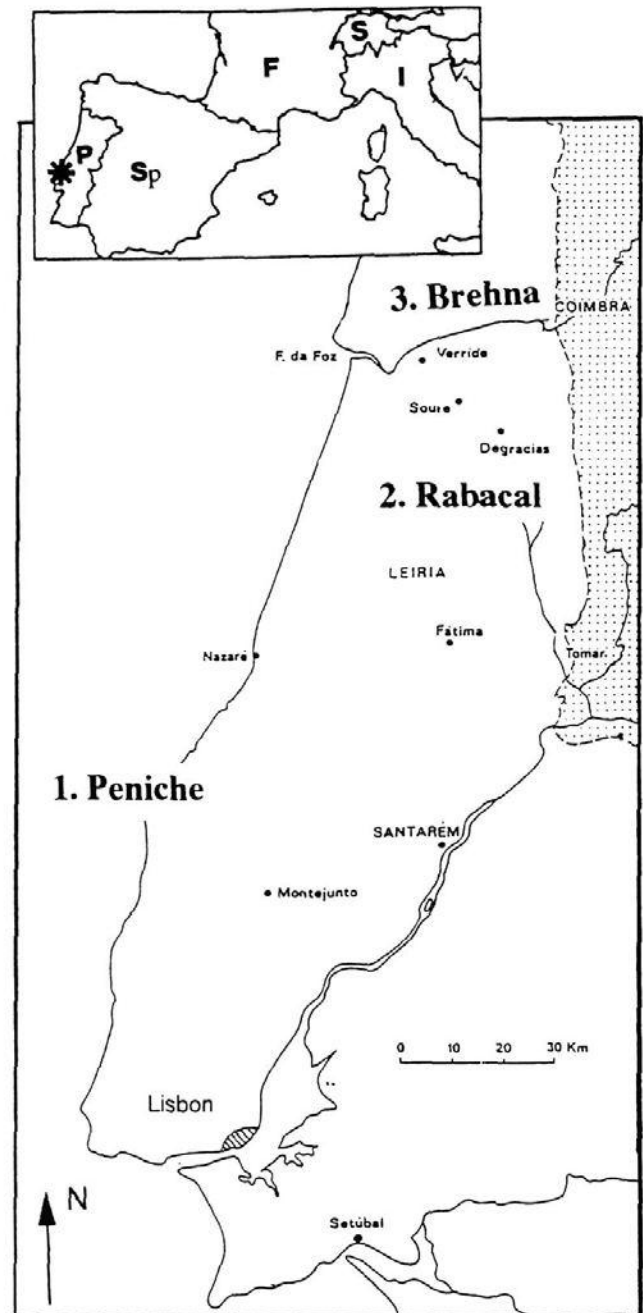
cal ranges in the two paleogeographical domains (i.e. *M. semitabulatum*, *Mendicodinium* spp. and *S. weberi*), whereas significant stratigraphical differences were observed for other dinoflagellate cysts (text-fig. 4).

The genus *Luehndea* was recorded from the Lower Pliensbachian (Carixian) of Portugal (Tethyan Realm), where it is represented by the species *Luehndea spinosa* and *Luehndea cirilliae* (text-fig. 5). At the Lower-Upper Pliensbachian (Carixian-Domerian) transition the genus is widespread throughout central and northern Europe (Denmark, England, France, Germany, Hungary and Italy). In Hungary, *L. spinosa*, *L. microreticulata* and *L. cirilliae* have been reported (Baldanza et al. 1995; Bucefalo Palliani et al. 1997a) whereas throughout the remainder of the Boreal Realm, only *L. spinosa* is present (Woollam and Riding 1983; De Vains 1988; Feist-Burkhardt and Wille 1992; Riding and Thomas 1992; Poulsen 1996).

A similar distributional trend is observed for the genus *Nannoceratopsis* (text-fig. 6). *Nannoceratopsis gracilis* and *Nannoceratopsis senex* first appeared in the Carixian of Portugal in the Tethyan domain (text-figs 4, 6). In the Domerian, *Nannoceratopsis* became widespread in the Boreal Realm and the more southerly transitional belt (Bulgaria, Denmark, England, France, Germany, Hungary and Siberia). This genus exhibited a marked increase in abundance and species diversity during the late Pliensbachian (Woollam and Riding 1983; De Vains 1988; Dodekova and Tchoumatchenko 1989; Riding and Thomas 1992; Feist-Burkhardt and Wille 1992; Ilyina et al. 1994; Poulsen 1996). During the Carixian, *Nannoceratopsis* typically represents 15% of the Portuguese dinoflagellate cyst assemblages. In the late Pliensbachian of northern Europe, *Nannoceratopsis* is normally the dominant dinoflagellate cyst genus (e.g. Woollam and Riding 1983). In the Tethyan Realm, *Nannoceratopsis* is a subordinate constituent of the dinoflagellate cyst assemblages from the sub-Mediterranean province (for example 30% in Portugal) and it is absent or very rare in the assemblages from Italy and Greece (Mediterranean province). Baudin and Lachkar (1990) recorded extremely rare *N. gracilis* from the Lower Jurassic of northwest Greece.

The first report of *Valvaedinium* was from the Upper Triassic of the Kendelbachgraben, Austria by Morbey (1975), who recorded the species *Valvaedinium koessenium*. During the early Pliensbachian, *Valvaedinium* is present in the Boreal Realm (Bulgaria, Denmark and Germany) with the species *Valvaedinium koessenium*, *V. lineatum*, *V. perpunctatum*, *V. punctatum* and *V. stipulatum* (Wille and Gocht 1979; Dodekova and Tchoumatchenko 1989; Feist-Burkhardt and Wille 1992; Poulsen 1996). In the Tethyan area, the genus *Valvaedinium* has been recorded from the Lower Toarcian of Greece and Italy (Text-figs 4, 7). In these localities no palynologically productive Upper Pliensbachian samples were encountered.

Susadinium scrofoides was recorded in the Lower Toarcian (at the top of the *D. tenuicostatum* Zone) in central Italy (Bucefalo Palliani and Mattioli 1994). Furthermore, rare and equivocal specimens of *Susadinium* sp. were observed in the Lower Pliensbachian of Portugal (text-fig. 4); Davies (1985) recorded *S. scrofoides* from the Upper Pliensbachian of Portugal. This species belong to the *Parvocysta* suite of Riding (1984) which is widespread throughout the Boreal Realm during the mid Toarcian (*H. bifrons* Zone) (Woollam and Riding 1983; Riding and Thomas 1992). In the Boreal domain, *S. scrofoides* is one of several other taxa of the *Parvocysta* suite (Riding 1984) such as



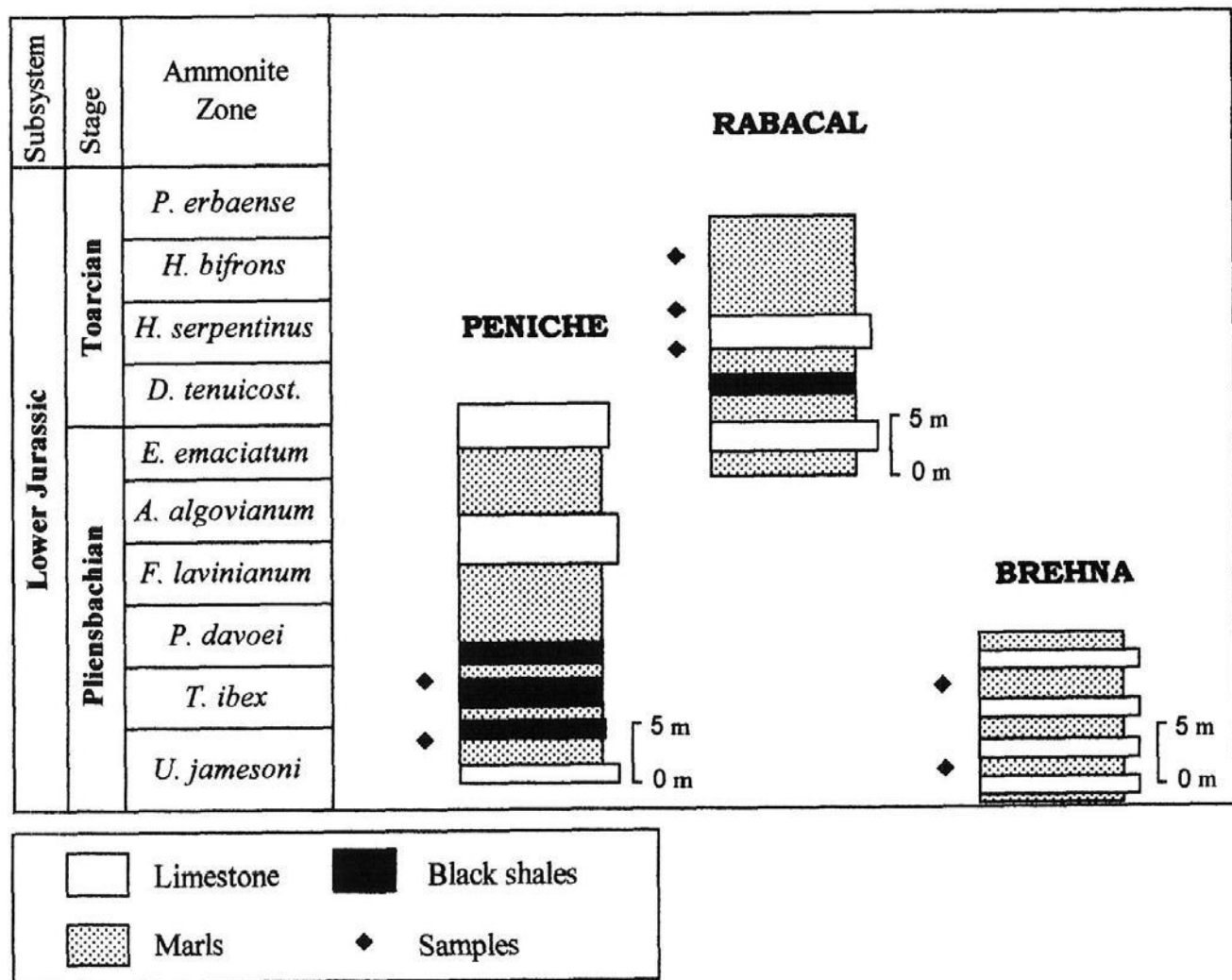
TEXT-FIGURE 2

Locality map of the three sections studied from Portugal. 1-Peniche; 2-Rabacal; 3-Brehna. The countries on the inset map are: F - France; I - Italy; P - Portugal; S - Switzerland; Sp - Spain.

Moesiodinium raileanui, *Parvocysta nasuta*, *Phallocysta eumekes* and *Reutlingia cardobarbata*, which have never been recorded from the Tethyan domain (text-fig. 8).

MIGRATIONAL TRENDS

The discrepancies in the stratigraphical ranges of *Luehndea*, *Nannoceratopsis*, *Susadinium* and *Valvaedinium* in the Boreal and Tethyan realms reveal two distinct migrational events. The first migrational event is at the Early-Late Pliensbachian (Carixian-Domerian) boundary; mutual exchange occurred be-

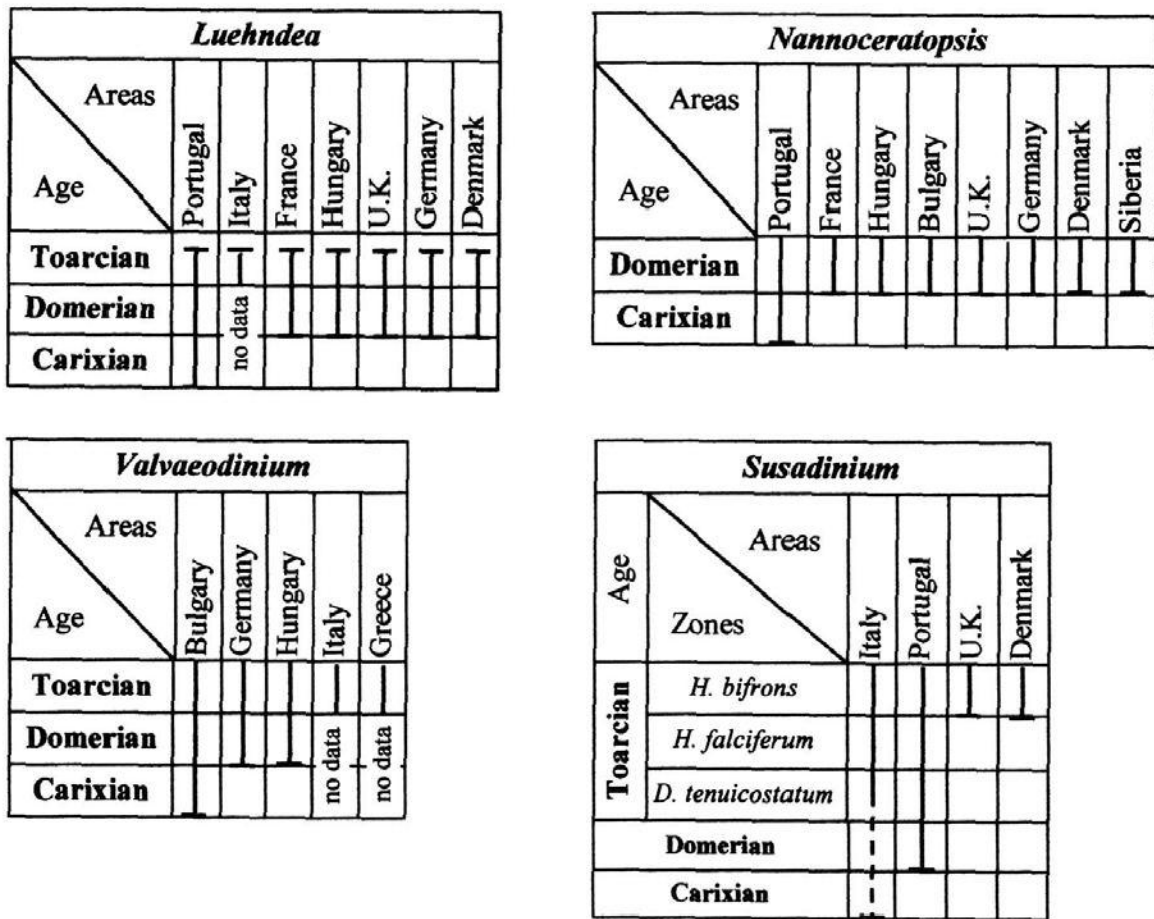


TEXT-FIGURE 3
Lithological logs, illustrating sample points, for the three sections studied from Portugal.

tween the Boreal and Tethyan realms. *Luehndea* and *Nannoceratopsis*, taxa of Tethyan origin, migrated northwards into the Boreal domain while the northern European genus *Valvaedinium* migrated southwards into the Mediterranean area (text-fig. 4). The Carixian-Domerian transition was a time of significant faunistic and floristic exchange between the two paleogeographic domains (Mouterde and Elmi 1991). At this boundary, belemnites also migrated toward the Tethyan domain (Cariou et al. 1985) and at the base of the middle Domerian, the ammonite Family Hildoceratidae (*Protogrammoceras* and *Fuciniceras*) spread northwards from the Tethyan area into Boreal Europe (Mouterde and Elmi 1991; Faraoni et al. in press). Ammonites belonging to the Boreal Family Amaltheidae, have been found in the northern and central Apennines (central Italy). They are rare during the Domerian and became more abundant during the early Toarcian (*D. tenuicostatum* Zone) (Venturi, personal communication). These migrations suggest a marine connection between the Boreal and the Tethyan realms at the end of the early Pliensbachian. Mouterde and Elmi (1991) suggested the utilization of the so-called 'Portugese corridor', used from north to south by Boreal organisms and from south to north by Tethyan taxa. However, according to Hallam (1983),

since the Pliensbachian, the migrating Boreal species used an epicontinental corridor between Greenland and Norway. As evidenced by ammonites (Ziegler 1980; Faraoni et al. in press), the dinoflagellate cysts confirm that the migration of north European elements into the Tethyan sea occurred infrequently. However, Tethyan forms are found as minor but consistent elements throughout large areas of the Boreal province. The end Carixian migrational event can be linked to the incipient Early Jurassic transgression that improved marine communications and caused a progressively larger area of the Boreal continent to be flooded, thereby increasing the number of niches available for colonization.

The second dinoflagellate cyst migration event occurred during the mid Toarcian (*H. bifrons* Zone) and is revealed by the stratigraphical ranges of *Susadinium scrofoides* in the Boreal and Tethyan domains. *Susadinium scrofoides* originated in the Tethyan Realm during the late Pliensbachian (*P. spinatum* Zone) (Davies 1985) and spread northwards into the Boreal Realm during the mid Toarcian (text-figs. 4, 8). The mid Toarcian lies within a regressive phase (Haq et al. 1987), thus this migrational event can be linked to the gradual oxygenation



TEXT-FIGURE 4
Stratigraphical ranges of selected dinoflagellate cyst genera in the Northern Hemisphere excluding North America.

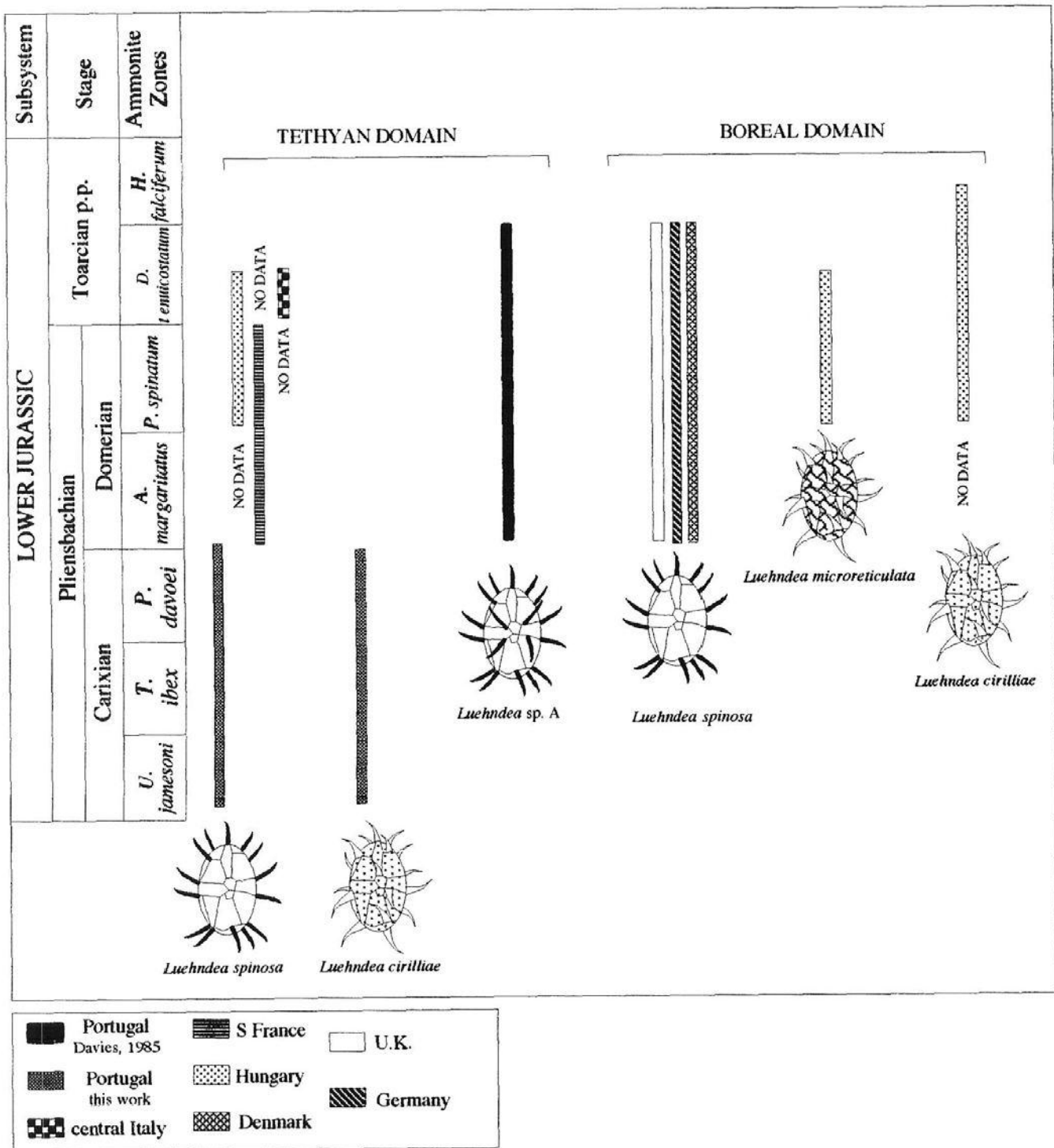
of the Boreal seas and to chemical and/or physical changes of the water column following the Lower Toarcian global anoxic event (Jenkyns 1985). In Italy, the oldest occurrence of *S. scrofoides* is in the Early Toarcian (text-figs. 4, 8) and, more precisely, at the top of the *D. tenuicostatum* Zone where the well oxygenated conditions of the sea bottom and an unstable water column were re-established after the Lower Toarcian anoxic event (Bucefalo Palliani and Mattioli 1994; Bucefalo Palliani and Riding 1997a). In the Boreal Realm the restoration of oxygenated conditions in marine paleoenvironments occurred later in the mid Toarcian with respect to the Tethyan Realm (Hallam 1987; Prauss and Riegel 1989; Jenkyns et al. 1991). Cyst-producing dinoflagellates have a benthonic stage in their life cycle (the cyst) and their distribution is affected by the ecological conditions of the paleoenvironment. It seems probable that *S. scrofoides* could not live in a stratified water column with euxinic sea bottoms, therefore its distribution was intimately controlled by the geographical and temporal extension of the Lower Toarcian anoxic event. *Susadinium scrofoides* occurred in central Italy at the top of the *D. tenuicostatum* Zone and it migrated northwards into the Boreal Realm during the mid Toarcian (*H. bifrons* Zone) when the stressed conditions, linked to the anoxic event, were overcome. This species filled the niches left vacant by the organisms which became extinct during this major event. The connection between the first occurrence of the *Parvocysta* suite and the end of the Lower

Toarcian bituminous facies, noted by Feist-Burkhardt and Wille (1992) and Bucefalo Palliani and Riding (1997a), is interpreted here as an opportunistic colonization and diversification of relatively unstable marine conditions. The stratigraphical data show that the *Parvocysta* suite found a more favorable paleoenvironment in the Boreal Realm as suggested by higher abundances and diversification in this region (text-fig. 8).

THE INFLUENCE OF PALEOECOLOGY ON DINOFLAGELLATE CYST DISTRIBUTIONS AND SPECIATION

Many of the dinoflagellate cysts recorded in this study are cosmopolitan taxa. They show wide geographical distributions and characterize the assemblages from both the Boreal and Tethyan domains, despite sometimes exhibiting different stratigraphical ranges. However, more detailed observations, reveal in some cases that the distributions are more or less profoundly affected by paleoecological factors.

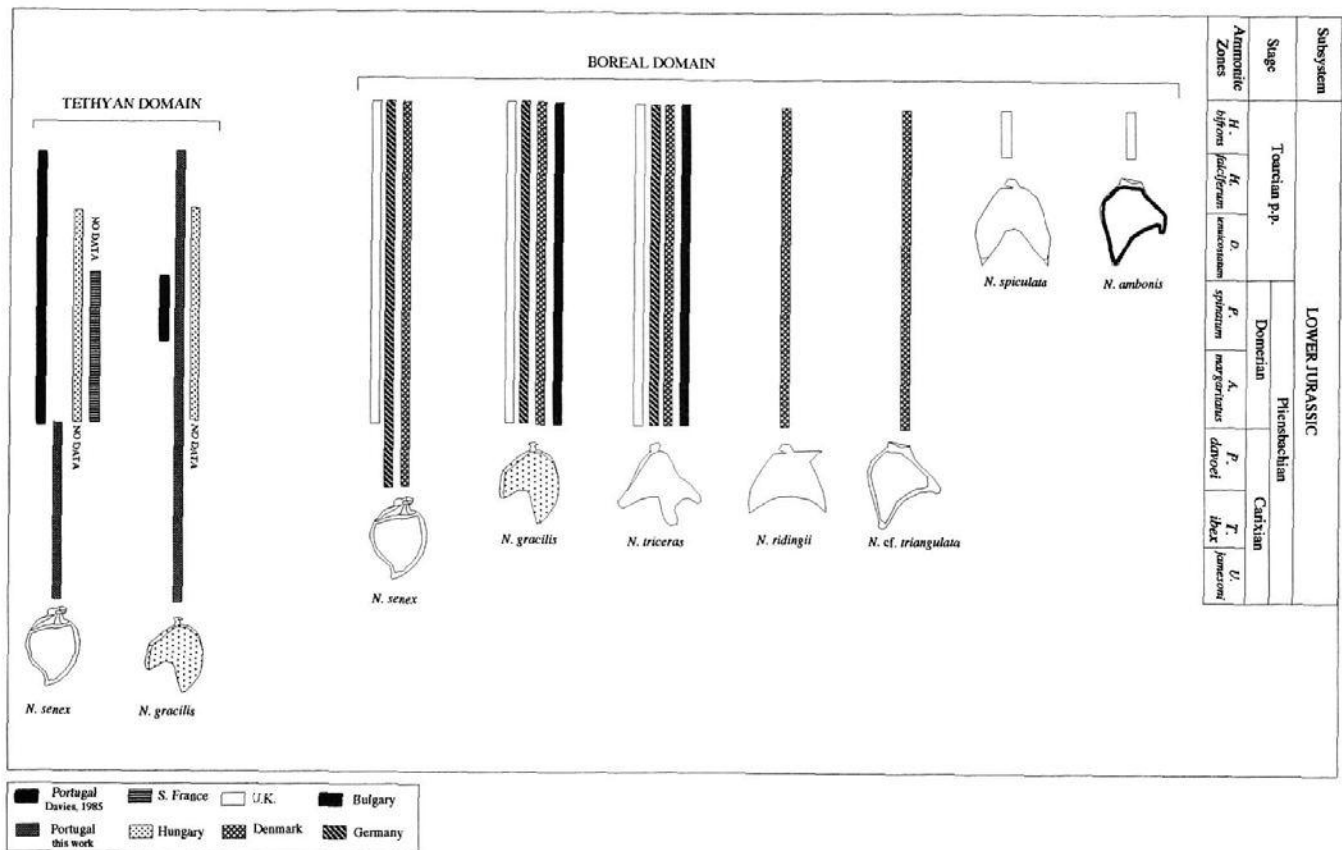
Nannoceratopsis is a Tethyan genus which colonized the Boreal seas in the early Pliensbachian, during the Early Jurassic transgression. Being present at low and high paleolatitudes and many localities (e.g. Van Helden 1977; Ilyina et al 1994), it can be considered a cosmopolitan taxa, as previously observed by Riding (1984). Moreover, due to its ubiquity in late Pliensbachian to Bajocian sediments throughout the Northern Hemi-



TEXT-FIGURE 5
The stratigraphical distributions of the species of *Luehndea* throughout the Pliensbachian and Toarcian of Europe.

sphere. *Nannoceratopsis* is also believed to be euryaline (Hancock and Fisher 1981; Riding 1983). During the Toarcian in the Boreal Realm, *Nannoceratopsis* exhibited its highest total abundance and species diversity; these values decrease gradually towards the southern Tethyan regions. Therefore, despite the cosmopolitan nature of the genus, its distribution was fa-

voured by the paleoecological conditions in the Boreal Realm. The distribution of the cosmopolitan and endemic taxa was generally controlled by the ecology of the paleoenvironment (Valentine 1973). Crucial factors included the climatic and/or environmental stability and predictability and these controlled patterns of species diversity, the width of paleoecological



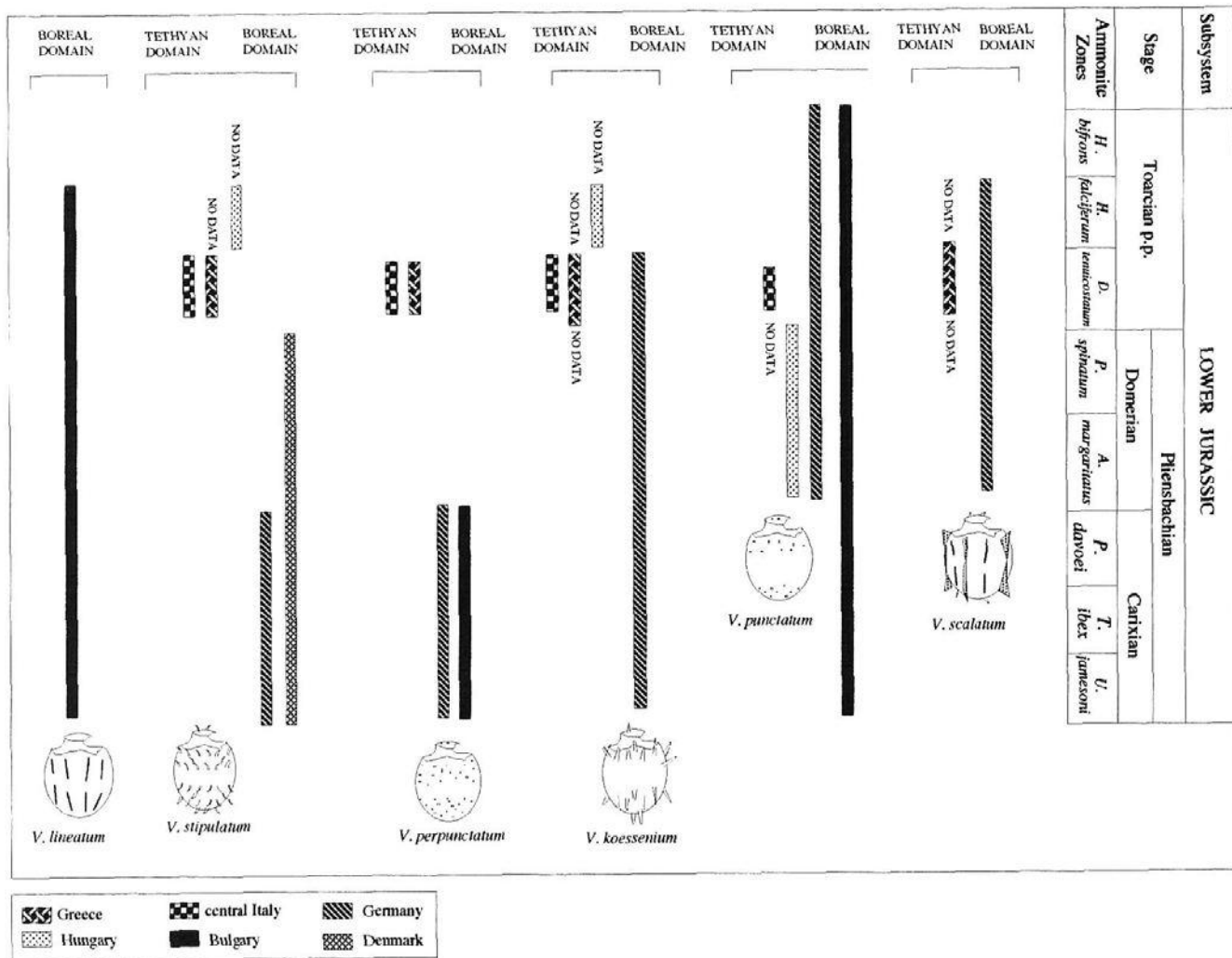
TEXT-FIGURE 6
The stratigraphical distributions of the species of *Nannoceratopsis* throughout the Pliensbachian and Toarcian of Europe.

niches, speciation rates and the complexity of the food chain (Pianka 1960; Odum and Copeland 1974). Cosmopolitan species are generally eurytopic organisms, which tolerate a wide range of paleoenvironmental conditions and occupy wider niches. Because of their life strategies, they prefer unstable and unpredictable paleoenvironments where the flux of the trophic resources are not constant with time. At higher latitudes within the Boreal Realm, the epicontinental seas represented more unstable and unpredictable paleoenvironments than their counterparts in the Tethyan domain. In the Boreal Realm, eurytopic and cosmopolitan taxa with an 'r-selected' (*sensu* Valentine 1973) life strategy (opportunistic organisms able to rapidly increase their population densities by early maturation and reproduction), such as *Nannoceratopsis*, overwhelmingly dominated. *Nannoceratopsis* first occurs in Portugal with the species *N. gracilis* and *N. senex*, which are relatively simple in morphology with one or two antapical horns. In the Boreal Realm, the genus diversified comprising some species with more complex morphologies (Poulsen 1996). They may exhibit two or three antapical horns and, occasionally, a ventral horn (text-fig. 6). This situation may have been an effect of evolution of the genus with time which produced morphologically complex forms. Alternatively, it can be interpreted as a morphological adaptation to the different paleoecological conditions of the two biogeographical realms.

Luehndea is a cosmopolitan genus which exhibits higher abundances in the Boreal Realm. During the Pliensbachian and the

Lower Toarcian, *Luehndea* represented 40%-60% of the Boreal dinoflagellate cyst assemblages, whereas it is very rare (c.3%) in Italy (Baldanza *et al.* 1995). This abundance trend may be explained by the life strategy of *Luehndea*; it was probably an eurytopic genus such as *Nannoceratopsis*, which favored the unstable and unpredictable Boreal conditions. This genus, in northern Europe, is normally represented by the species *Luehndea spinosa* (Riding 1987; Feist-Burkhardt and Wille 1992; Poulsen 1996). In Portugal, however, *L. cirilliae* is the most abundant representative of the genus. The most diverse assemblages of *Luehndea* have been recorded in Hungary, where *L. cirilliae*, *L. microreticulata* and *L. spinosa* are present (text-fig. 5).

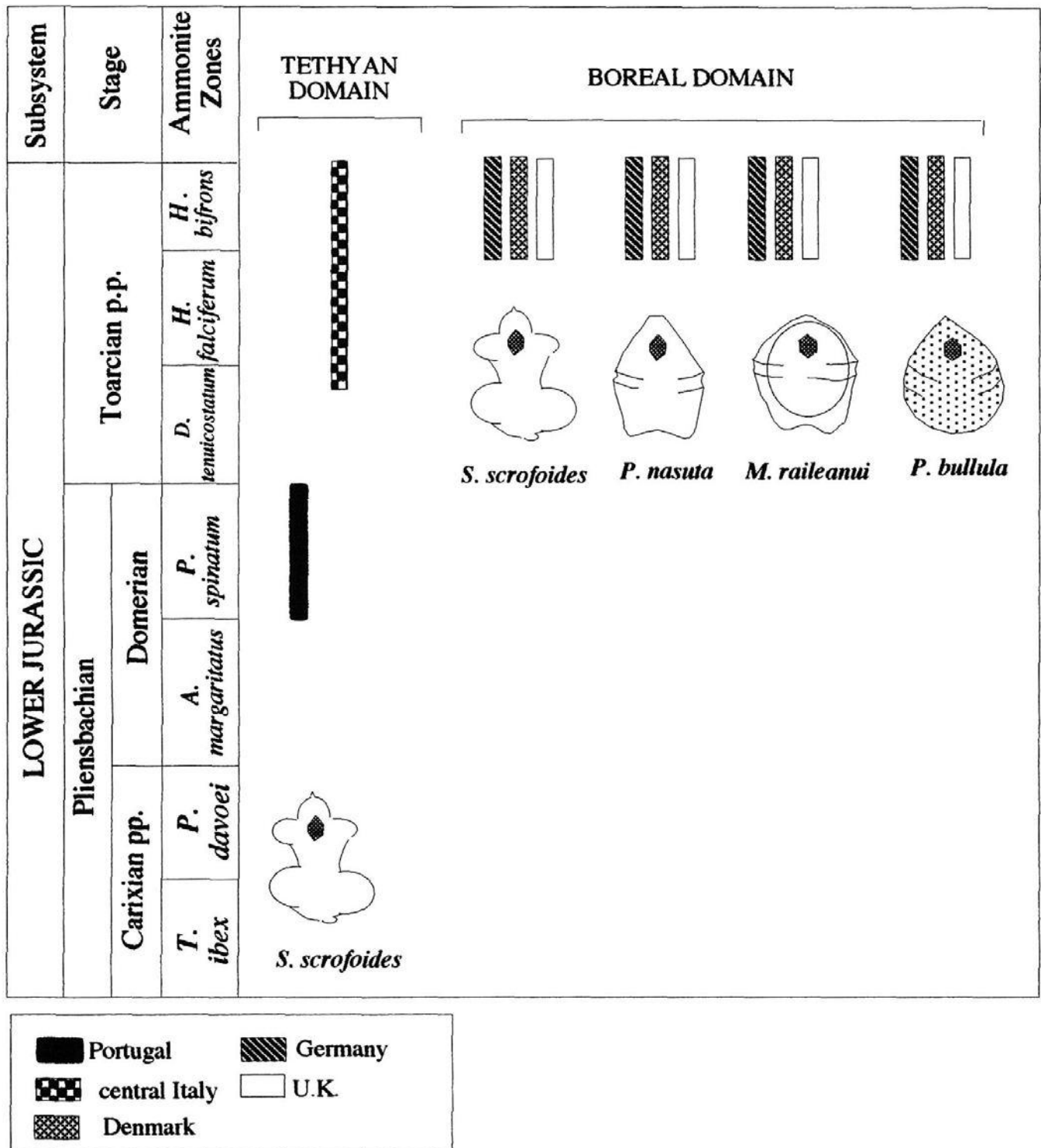
The distribution of common *Valvaeodinium* in the Pliensbachian and early Toarcian is confined to a narrow area comprising Denmark (Poulsen 1996), Germany (Wille and Gocht 1979), Hungary, Italy and Greece (text-fig. 8). This genus is absent or extremely rare and low in species diversity in England, France, Portugal and Russia (Woollam and Riding 1983; Davies 1985; De Vains 1988; Riding and Thomas 1992; Ilyina *et al.* 1994; Poulsen 1996). The distributional area of common *Valvaeodinium* is parallel to the oceanic axis of the Tethyan sea. It appears that *Valvaeodinium* was abundant close to this axial zone and was markedly rarer outside of this region (text-fig. 9). It is probable that its spreading was controlled by particular paleotemperature values, better water clarity and higher values of salinity and deepening of the marine paleoenvironment.



TEXT-FIGURE 7
The stratigraphical distributions of the species of *Valvaodinium* throughout the Pliensbachian and Toarcian of Europe.

In the Greek and Italian sections studied, numerous specimens of *Valvaodinium* cysts which are completely closed or with loosened opercula *in situ*, have been recorded together with the highest Total Organic Carbon (TOC) values (text-fig. 10). Wille and Gocht (1979) recorded many closed cysts of *Valvaodinium punctatum* (as *Comparodinium punctatum*) in the most bituminous lithotypes of the Posidonienschiefer (Lower Toarcian) in southwest Germany. According to Wille (1982), it was probable that dinoflagellate protoplasm (cell contents) which emerged via excystment into the anoxic, H₂S-poisoned bottom waters of the north European sea during the early Toarcian would have been killed. Either the algae were killed inside the closed cysts or when they tried to leave them (text-fig. 11). Wille (1982) opined that the protoplast started to open the operculum by resorption of its rim and that the cell was killed when it came into contact with the poisoned water outside. In central Italy during the early Toarcian, anaerobic conditions have been verified at the sea bottom (Bucefalo Palliani and Cirilli 1993; Bucefalo Palliani and Mattioli 1994). The Redox Potential Discontinuity (RPD) was close to the water-sediment interface, therefore a small quantity of free oxygen was available at the sea bottom,

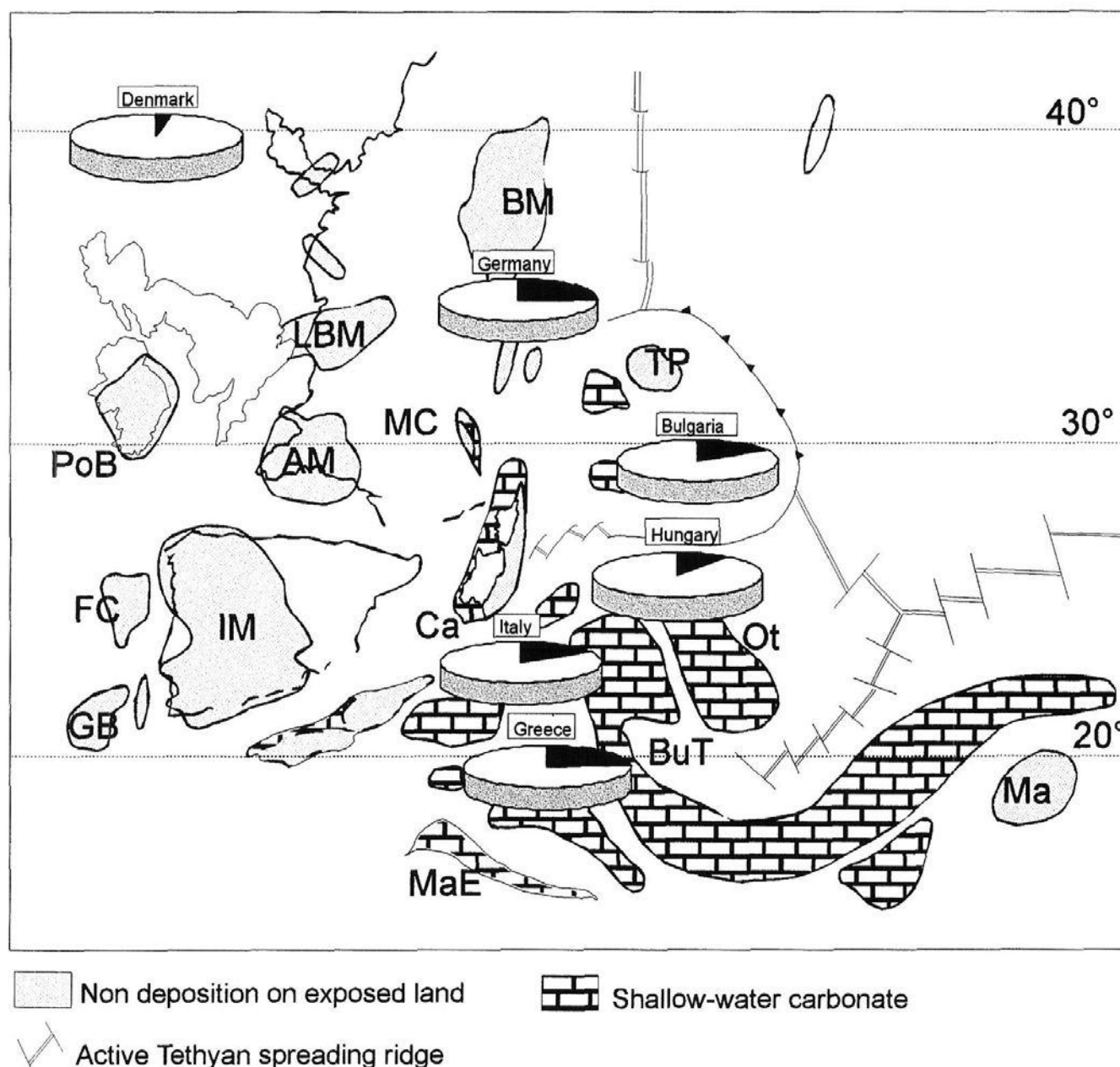
as confirmed by the paleontological data of Bartolini et al. (1992) and Nocchi (1992). Moreover, in the Greek and Italian sections, the *Valvaodinium* cysts are generally in association with *Mancodinium semitabulatum*, *Mencodinium* spp. and *Umbriadinium mediterraneense*, whose opercula are totally lacking, evidencing successful excystment. Dale (1983) observed that, for a given species of dinoflagellate, there is probably a 'temperature window' within which it may excyst, and outside of which, excystment is inhibited. The highest TOC values in central Italy have been related to the maximum paleoenvironmental stability, deepening and sedimentary starvation (Bucefalo Palliani and Cirilli 1993). The deepening and the resultant water stratification confined the heat to a surface layer bounded by the thermocline beneath and produced a lowering of the temperature at the sea bottom. This lowering of the water temperature may go below the *Valvaodinium* 'temperature window' and the *Valvaodinium* cysts, independent of other taxa, are not able to excyst (text-fig. 12). On the basis of present knowledge, temperature is a major factor inducing excystment in the natural environment (Dale 1983), but the possible roles played by other factors, such as day length, nutrient



TEXT-FIGURE 8
The stratigraphical distributions of selected representatives of the *Parvocysta* suite throughout the Pliensbachian and Toarcian of Europe.

availability and water chemistry have still not been systematically investigated. Probably both the temperature and the oxygenation level at the sea bottom affected dinoflagellate excystment in early Toarcian paleoenvironments. In Central Italy, paleotemperatures may have played a primary role.

During the early Pliensbachian, the dinoflagellate cysts recorded relatively high turnover and speciation rates (Mattioli and Bucefalo Palliani 1995). More detailed observations revealed that, during this interval, speciations were more numerous in the Tethyan domain (i.e. *Luehndea* spp., *Mendicodinium*

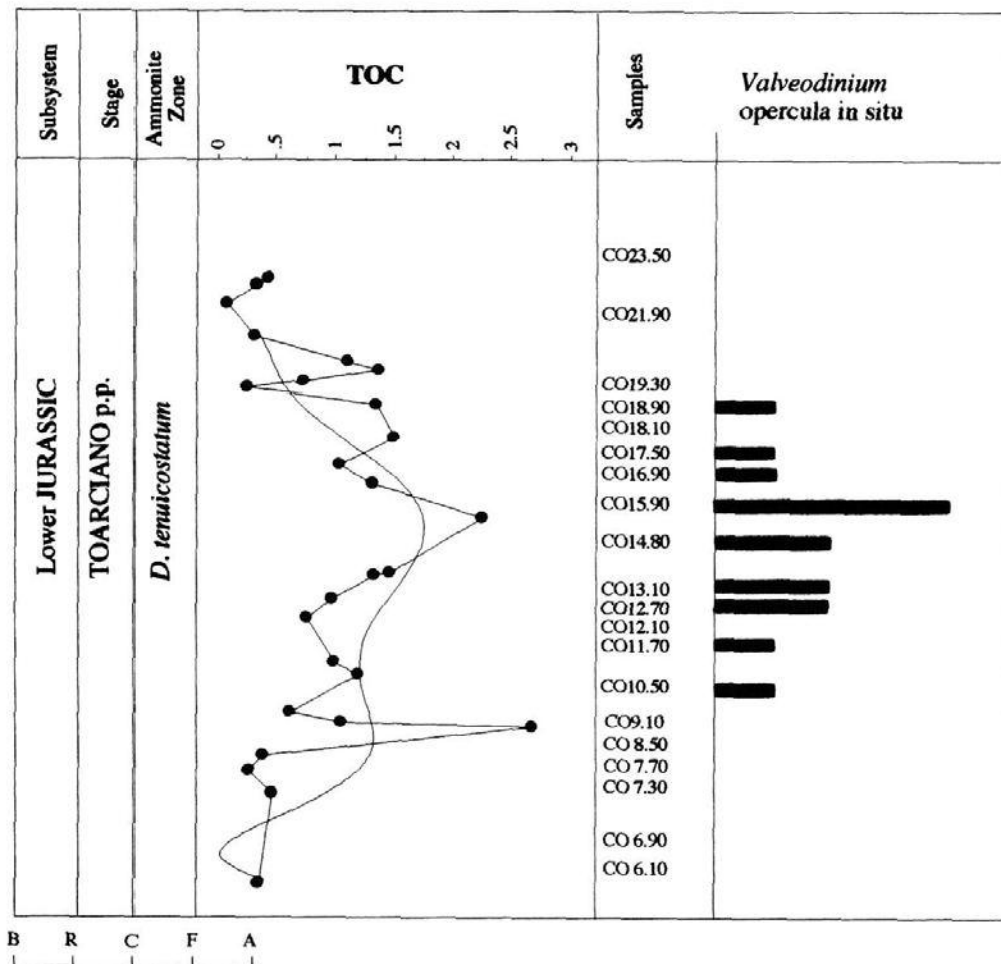


TEXT-FIGURE 9

paleogeographical map of the western and central European portion of the Boreal and Tethyan realms illustrating the common and diverse occurrences of the genus *Valvaedinium* (adapted from Dercourt et al. 1993). In the pie charts, the black areas depict the percentages of *Valvaedinium* expressed against the total dinoflagellate cyst assemblages (white areas). AM: Armorican Massif; BM: Bohemian Massif; BuT: Budva Trough; CA: Central Afghanistan; FC: Flemish Cap; GB: Galicia Bank; IM: Iberian Meseta; LBM: London Brabant Massif; MA: Moyen Atlas; MaE: Malta Escarpement; MC: Massif Central; Ot: Othrys; PoB: Porcupine Basin; TP: Tisza Plate.

spp. and *Nannoceratopsis* spp.). The reproductive isolation necessary for the origination of a new genus and/or species may be geographical or ecological separation, however, physiological or biological factors may also isolate populations. In the Boreal and Tethyan realms during the Pliensbachian, the global transgression affected several closely linked parameters, such as phytoplankton evolution, continental physiography, paleoclimate, nutrient availability, atmospheric oxygen and carbon dioxide levels. These paleoecological modifications influenced

the processes of natural selection within the dinoflagellate community. The differences in the hereditary pattern of the original population produced communities which became reproductively isolated. It is probable that natural selection was stronger and more efficient in the Tethyan Realm. This comprised stable and predictable paleoenvironments inhabited by stenotopic organisms which had a restricted range of paleoenvironmental tolerances. Casual modifications in the gene pool of partially isolated Tethyan dinoflagellate communities could have been



TEXT-FIGURE 10
 Correlation between Total Organic Carbon (TOC) values and the percentages of *Valvaedinium* cysts with *in situ* opercula in the Lower Toarcian Colle d'Orlando section, central Italy. The samples are curated in the Department of Earth Sciences, University of Perugia, Italy.

favored by the selective processes induced by paleoecological modifications, with consequent changes and the origination of new taxa.

CONCLUSIONS

The integration of the Tethyan data discussed herein with published data from the Boreal domain (Woollam and Riding 1983; De Vains 1988; Feist-Burkhardt and Wille 1992; Riding et al. 1991; Riding and Thomas 1992; Poulsen 1996) has revealed some significant stratigraphical discrepancies. The differences in the ranges of the genera *Luehndea*, *Nannoceratopsis*, *Susadinium* and *Valvaedinium* have been related to two major migrational events.

At the Lower-Upper Pliensbachian (Carixian-Domerian) boundary, the migration of *Luehndea* and *Nannoceratopsis* (which were of Tethyan origin) and *Valvaedinium* (of Boreal origin) occurred. Ammonites and dinoflagellate cysts suggest that, at this time, the migration of Tethyan elements into the north European seas occurred more frequently. The end-Carixian migration has been related to the Early Jurassic global transgression, which increased the number of niches

available for colonization in the Boreal Realm and improved marine communications.

The second migrational event was in the mid Toarcian (*H. bifrons* Zone) and is revealed by the stratigraphical range of *Susadinium scrofoides*, which migrated from the Tethyan Realm to the Boreal Realm. This event has been related to the gradual oxygenation of the Boreal seas and to the chemical and/or physical changes of the water column following the Lower Toarcian global anoxic event (Jenkyns 1985). In the Boreal domain, these paleoecological modifications occurred later than in the Tethyan Realm. Because of its paleoecology, the spreading of *S. scrofoides* into northern Europe occurred when the stressed conditions, linked to the anoxic event, were overcome. This interpretation explains the connection between the first occurrence of the *Parvocysta* suite and the Lower Toarcian bituminous facies, noted by Feist-Burkhardt and Wille (1992) and Bucefalo Palliani and Riding (1997a).

The distributions of some dinoflagellate cysts recorded in this study were affected by paleoecological factors. *Nannoceratopsis* and *Luehndea* (genera of Tethyan origin) were eurytopic genera, with r-selected life strategies, which appear to have pre-

ferred the unstable and unpredictable Boreal conditions. The distribution of *Valvaedinium* was controlled by the position of the Tethyan oceanic axis and its spreading was dependent upon specific paleotemperatures, better water circulation and higher values of paleosalinity and the deepening of the paleo-environment.

Significant compositional differences have been recorded between the Early Jurassic Boreal and Tethyan dinoflagellate cyst floras (Baldanza et al. 1995; Bucefalo Palliani 1996). Moreover, within the Tethyan Realm, dinoflagellate cysts seem to delineate two bioprovinces on the basis of the qualitative and quantitative assemblage characteristics. The sub-Mediterranean province (i.e. Portugal and southern France) comprises a mixing of typically Boreal forms (e.g. *Luehndea* and *Nannoceratopsis*) and characteristic Tethyan genera (e.g. *Mendicodinium*). In assemblages from the Mediterranean province (i.e. Greece and Italy), however, *Nannoceratopsis* is rare or absent. The genus *Mendicodinium*, even if it is present in both two Tethyan bioprovinces, is more abundant in the Mediterranean area, where it frequently dominates the dinoflagellate cyst associations. *Mendicodinium* is also consistently present in the sub-Mediterranean assemblages but in relatively low numbers. The converse trend is exhibited by *Nannoceratopsis*, which dominates sub-Mediterranean assemblages, but it is absent in Hungary and Italy and is extremely rare in Greece (Baudin and Lachkar 1990).

The highest number of early Pliensbachian dinoflagellate cyst speciations recorded in the Tethyan Realm has been related to the stable and predictable paleoenvironments inhabited largely by stenotypic organisms. In this area, selective paleoecological processes favored reproductive isolation and subsequent taxonomic radiations.

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REFERENCES

ARKELL, W. J., 1956. Jurassic Geology of the World. Oliver and Boyd, 806 p.

BALDANZA, A., BUCEFALO PALLIANI, R., and MATTIOLI, E., 1995. Calcareous nannofossils and dinoflagellate cysts from the Late Liassic of Hungary and comparison with Central Italy assemblages. *Paleopelagos*, 5:161-174.

BALDANZA, A., and MATTIOLI, E., 1992. Biostratigraphical synthesis of nannofossils in the Early Middle Jurassic of Southern Tethys. *Knihovnicka zemniho plynu a nafty*, 1:111-141.

BARTOLINI A., NOCCHI, M., BALDANZA, A., and PARISI, G., 1992. Benthic life during the Early Toarcian Anoxic Event in the Southwestern Tethyan Umbria-Marche Basin, Central Italy. *Benthos* 90, Sendai, pp. 223-338.

BAUDIN, F. and LACHKAR, G., 1990. Géochimie organique et palynologie du Lias supérieur en zone ionienne (Grèce). Exemple

d'une sédimentation anoxique conservée dans une paléo-marge en distension. *Bulletin de la Société Géologique de France*, 8:123-132.

BOWN, P. R., 1987. Taxonomy, evolution, and biostratigraphy of Late Triassic-Early Jurassic Calcareous Nannofossils. *Special Papers in Palaeontology*, no. 38, 118 p.

BUCEFALO PALLIANI, R., 1996. Facies organiche nel Giurassico inferiore del dominio Tetideo: sedimentologia organica e biostratigrafia a cisti di dinoflagellati. Unpublished Ph.D. Thesis, University of Perugia, Italy, 250 p.

BUCEFALO PALLIANI, R. and CIRILLI, S., 1993. Palaeoenvironmental influences on the composition and preservation of the organic matter: preliminary results from the Pozzale section (Early Toarcian, Central Apennines, Italy). *Paleopelagos*, 3:129-144.

BUCEFALO PALLIANI, R. and 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). *Paleopelagos*, 4:129-140.

BUCEFALO PALLIANI, R. and RIDING, J. B., 1997a. Lower Toarcian palynostratigraphy of Pozzale, central Italy. *Palynology*, 21: 91-103.

———, 1997b. *Umbriadinium mediterraneense* gen. et sp. nov. and *Valvaedinium hirsutum* sp. nov.: two dinoflagellate cysts from the Lower Jurassic of the Tethyan Realm. *Palynology*, 21: 197-206.

BUCEFALO PALLIANI, R., RIDING, J. B., and TORRICELLI, S., 1996. *Polygonium jurassicum* sp. nov. a polygonomorph acritarch from Early Toarcian of Tethyan Realm. *Palynology*, 20:157-161.

———, 1997a. The dinoflagellate cyst *Luehndea* Morgenroth, 1970, emend. from the upper Pliensbachian (Lower Jurassic) of Hungary. *Review of Paleobotany and Palynology*, 96:113-120.

———, 1997b. The dinoflagellate cyst *Mendicodinium* Morgenroth, 1970, emend. from the lower Toarcian (Jurassic) of central Italy. *Review of Paleobotany and Palynology*, 96:99-111.

CARIOU, E., CONTINI, D., DOMMARGUES, J. L., ENAY, R., GEYSSANT, J. R., MANGOLD, C., and THIERRY, J., 1985. Biogéographie des Ammonites et évolution structurale de la Téthys au cours du Jurassique. *Bulletin de la Société Géologique de France*, série 8, 1(5):679-697.

DALE, B., 1983. Dinoflagellate resting cysts: benthic plankton. In: Frixell, G. A.(ed.), *Survival strategies of the Algae*, Cambridge University Press, pp. 69-136.

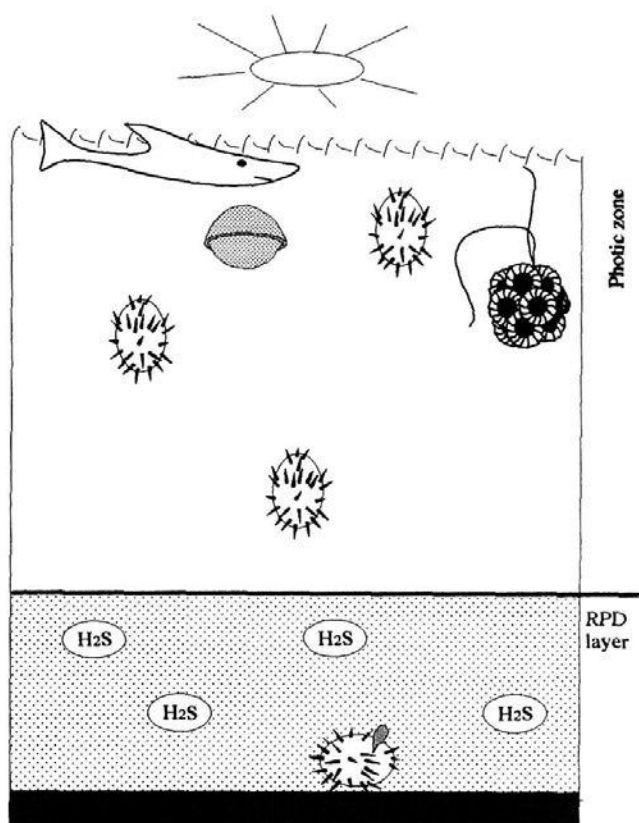
DAVIES, E. H., 1985. The miospore and dinoflagellate cyst Opper-zonation of the Lias of Portugal. *Palynology*, 9:105-132.

DERCOURT, J., RICOU, L. E. and VRIELYNCK, B. 1993. Atlas Tethys Palaeoenvironmental maps. Gauthier-Villars, 307 pp, 14 maps, 1 pl., Paris.

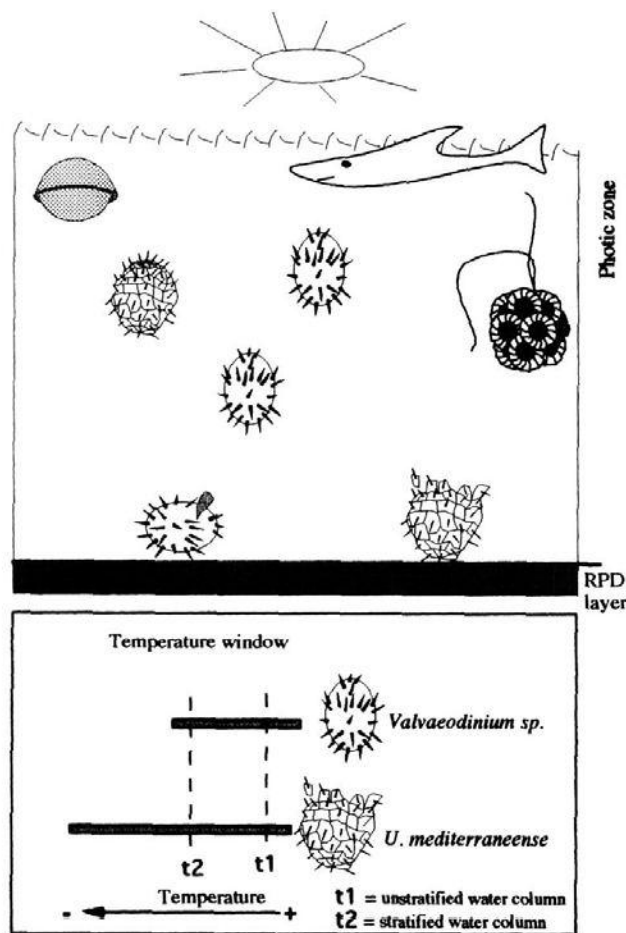
DE VAINS, G., 1988. Étude palynologique préliminaire de l'Hettangien à l'Aalénien du Quercy (France). *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine*, 12:451-469.

DODEKOVA, L. and TCHOUMATCHENKO, P., 1989. Jurassic dinocysts from the Eastern Stara Planina Mountain. *Geologica Balcanica*, 19:88.

FARAONI, P., MARINI, A., PALLINI, G., and VENTURI, F., in press. New Carixian ammonite assemblage of the central Apennines (Italy), and their implication on the Mediterranean biozonation. *Paleopelagos*, 6.



TEXT-FIGURE 11
Schematic diagram illustrating the hypothesis of Wille (1982) on the origin of closed *Valvaodinium* cysts in the Lower Toarcian Posidonienschiefer, of southwest Germany. RPD = redox potential discontinuity.



TEXT-FIGURE 12
Schematic diagram of the origin of closed *Valvaodinium* cysts in the Lower Toarcian of the Tethyan Realm proposed herein. RPD = redox potential discontinuity.

FEIST-BURKHARDT, S. and WILLE, W., 1992. Jurassic palynology in southwest Germany - state of the art. *Cahiers de Micropaléontologie*, 7:141-156.

GALACZ, A. and VÖRÖS, A., 1989. Jurassic sedimentary formations in Transdanubia. *International Association of Sedimentologists (IAS) Excursion guidebook*.

GARDIN, S. and MANIÉ, H., 1994. Biostratigraphie des Nannofossiles calcaires du Toarcien du Quercy (Sud-Ouest de la France). *Geobios*, 17:229-244.

GECZY, B., 1984. Provincialism of Jurassic ammonites, an examples from Hungarian faunas. *Acta Geologica Hungarica*, 27:379-389.

GOODMAN, D. K., 1987. Dinoflagellate cysts in ancient and modern sediments. In: Taylor, F. J. R. (ed.), *The biology of dinoflagellates*, Blackwell, pp. 649-722.

GORDON, W. A., 1970. Biogeography of the Jurassic foraminifera. *Geological Society of America Bulletin*, 81:1689-1704.

HALLAM, A., 1969. Faunal realms and facies in the Jurassic. *Palaeontology*, 12:1-18.

———, 1983. Early and Mid-Jurassic molluscan biogeography and the establishment of the central Atlantic seaway. *Palaeogeography Palaeoclimatology Palaeoecology*, 43:181-193.

———, 1987. Mesozoic marine organic-rich shales. *Marine Petroleum Source Rocks*. Geological Society of London, Special Publication, 26:251-261.

HANCOCK, N.J. and FISHER, M.J., 1981. Middle Jurassic North Sea Deltas with Particular Reference to Yorkshire. *Petroleum Geology of the Continental Shelf of North-West Europe*: 186-195.

HAQ, B.U., HARDENBOL, J., and VAIL, P. R., 1987. Chronology of fluctuating sea levels since the Triassic. *Science*, 235:1156-1167.

ILYINA, V. I., KUL'KOVA, I. A., and LEBEDEVVA, N. K., 1994. Microphytofossils and detail (sic.) stratigraphy of marine Mesozoic and Cenozoic of Siberia. *United Institute of Geology, Geophysics and Mineralogy Transaction*, 818, 192 p. (in Russian).

JENKYN, H. C., 1985. The Early Toarcian and Cenomanian-Turonian anoxic events in Europe: comparisons and contrasts. *Geologisches Rundschau*, 74:505-518.

JENKYN, H. C., GÉCZY, B. and MARSHALL, J. D., 1991. Jurassic manganese carbonates of Central Europe and early Toarcian anoxic event. *Journal of Geology*, 99: 137-149.

MATTIOLI, E., 1995. Stratigrafia a nannofossili calcarei nel Giurassico del bacino Umbro-Marchigiano: produttività primaria,

- preservazione ed effetti della diagenesi. Unpublished PhD Thesis, Perugia University, Italy. 168 p.
- MATTIOLI, E. and BUCEFALO PALLIANI, R., 1995. Phytoplankton evolution and extinction related to Liassic global event. Proceedings volume: Black Shales model, European Paleontologists Association (EUROPAL), pp. 69-70.
- MORBAY, S. J., 1975. The palynostratigraphy of the Rhaetian stage, Upper Triassic in the Kendelbachgraben, Austria. *Palaeontographica*, Abteilung B.152:1-75.
- MOUSTERDE, R., RAMALHO, M., ROCHA, R. B., RUGET, C., and TINTINANT, H., 1972. Le Jurassique du Portugal. Esquisse stratigraphique et zonale. *Bollettino Società Geologica Portoghese*, 8(1):73-104.
- MOUSTERDE, R. and ELMI, S., 1991. Caractères différentiels des faunes d'ammonites du Toarcien des bordures de la Téthys. Signification Paléogéographique. *Bulletin de la Société Géologique de France*, 162:1185-1195.
- NOCCHI, M., 1992. Associazioni a foraminiferi bentonici del bacino umbro-marchigiano durante il Lias. *Paleopelagos*, 2:37-53.
- ODUM, E. P. and COPELAND, F., 1974. *Fundamentals of Ecology*. Sanders Philadelphia, 120 p.
- PAVIA, G. and SARTI, C., 1987. Biostratigrafia ad ammoniti del Giurassico italiano. *Bollettino della Società Paleontologica d'Italia*, 26(3):289-293.
- PETTINELLI, R., NOCCHI, M., and PARISI, G., in press. Domesian-Toarcian biostratigraphy and environmental interpretations: the Ionian basin (Lefkas Island, western Greece) as compared to the Umbria-Marchean basin. *Bollettino della Società Geologica Italiana*.
- PIANKA, E. R., 1960. Latitudinal gradients in species diversity: a review of concepts. *American Naturalists*, 100:33-46.
- POULSEN, N. E., 1996. Dinoflagellate cysts from marine Jurassic deposits of Denmark and Poland. *American Association of Stratigraphic Palynologists Foundation, Contribution Series No. 31*, 227 p.
- PRAUSS, M. and RIEGEL, W., 1989. Evidence from phytoplankton associations for causes of black shales formation in epicontinental seas. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, No.11:671-682.
- RIDING, J. B., 1983. The palynology of the Aalenian (Middle Jurassic) sediments of Jackdaw Quarry, Gloucestershire, England. *Mercian Geologist*, 9:111-120.
- , 1984. A palynological investigation of Toarcian to early Aalenian strata from the Blea Wyke area, Ravenscar, North Yorkshire. *Proceedings of the Yorkshire Geological Society*, 45:109-122.
- , 1987. Dinoflagellate cyst stratigraphy of the Nettleton Bottom Borehole (Jurassic: Hettangian to Kimmeridgian), Lincolnshire, England. *Proceedings of the Yorkshire Geological Society*, 46:231-266.
- RIDING, J. B., WALTON, W. and SHAW, D., 1991. Toarcian to Bathonian (Jurassic) palynology of the Inner Hebrides, northwest Scotland. *Palynology* 15:115-179.
- RIDING, J. B. and IOANNIDES, N. S., 1996. A review of Jurassic dinoflagellate cyst biostratigraphy and global provincialism. *Bulletin de la Société Géologique de France*, 167:3-14.
- RIDING, J. B. and THOMAS, J. E., 1992. Dinoflagellate cysts of the Jurassic System. In: Powell A. J., (ed.), *A stratigraphic index of dinoflagellate cysts*. British Micropalaeontological Society Publications Series, Chapman and Hall, London, pp. 7-97.
- VALENTINE, J. W., 1973. *Evolutionary ecology of the marine biosphere*. Prentice-Hall, Englewood Cliffs, pp. 511.
- VAN HELDEN, B. G. T., 1977. Correlation of microplankton assemblages with ammonite faunas from the Jurassic Wilkie Point Formation, Prince Patrick Island, District of Franklin. *Geological Survey of Canada Paper*, 77(1B):163-171.
- VÖRÖS, A., 1977. Provinciality of the Mediterranean Lower Jurassic brachiopod fauna: causes and plate-tectonic implications. *Palaeogeography Palaeoclimatology Palaeoecology*, 21:1-16.
- WILLE, W., 1982. Evolution and ecology of Upper Liassic dinoflagellates from SW Germany. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 164:74-82.
- WILLE, W. and GOCHT, H., 1979. Dinoflagellaten aus dem Lias Südwestdeutschlands. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 158:221-258.
- WOOLLAM, R. and RIDING, J. B., 1983. Dinoflagellate cyst zonation of the English Jurassic. *Institute of Geological Sciences Report*, No. 83/2, 42 p.
- ZEIGLER, B., 1980. Ammonoid biostratigraphy and provincialism: Jurassic-old world. *Systematics Association Special Volume, "The Ammonoidea"*, 18:433-457.

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APPENDIX 1

Alphabetical listing of the dinoflagellate cyst species mentioned in the text.

- Luehndea cirilliae* Bucefalo Palliani et al. 1997a
Luehndea microreticulata Bucefalo Palliani et al. 1997a
Luehndea sp. A of Davies 1985
Luehndea spinosa Morgenroth 1970
Mancodinium semitabulatum Morgenroth 1970 emend. Below 1987
Moesiodinium raileanui Antonescu 1971
Nannoceratopsis ambonis Drugg 1978 emend. Riding 1984
Nannoceratopsis gracilis Alberti 1961 emend. Evitt 1962 emend. Prauss 1989
Nannoceratopsis ridingii Poulsen 1992
Nannoceratopsis senex van Helden 1977
Nannoceratopsis spiculata Stover 1966
Nannoceratopsis tricerat Drugg 1978
Phallocysta eumekes Dörhöfer and Davies 1980 emend. Riding 1984
Parvocysta bullula Bjaerke 1980
Parvocysta nasuta Bjaerke 1980
Reutlingia cardobarbata Below 1987
Scrinocassis priscus Gocht 1979 emend. Prauss 1989
Susadinium scrofoides Dörhöfer and Davies 1980 emend. Below 1987
Umbriadinium mediteraneense Bucefalo Palliani and Riding 1997b
Valvaeodinium koessenium Morbey 1975 emend. Below 1987
Valvaeodinium lineatum Wille and Gocht 1979 emend. Below 1987
Valvaeodinium perpunctatum Wille and Gocht 1979 emend. Below 1987
Valvaeodinium punctatum Wille and Gocht 1979 emend. Below 1987
Valvaeodinium scalatum Wille and Gocht 1979 emend. Below 1987
Valvaeodinium stipulatum Wille and Gocht 1979 emend. Below 1987