THE EFFECTS OF GLOBAL OCEANOGRAPHIC CHANGES ON EARLY DINOFLAGELLATE EVOLUTION

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Abstract

Calculation of evolutionary rates reveals the patterns of, and possible processes responsible for, early dinoflagellate evolution. Speciations, extinctions, turnover rates and diversities of dinoflagellate cysts are synchronous to the main Early Jurassic (Toarcian) palaeoceanographic events, which include eustatic changes, anoxic intervals and isotopic events. The synchronicity is strongly indicative of abiotic control on dinoflagellate evolution. Different distribution patterns, stratigraphical ranges and evolutionary rates for dinoflagellate cysts in the Boreal and Tethyan Realms are related to different reactions of these two provincial communities to the palaeogeographical changes.

Key words: Dinoflagellate cysts, evolutionary rates, palaeoceanography, Early Jurassic

1 INTRODUCTION

Global biological events in the geological past have been discussed since the beginnings of the earth sciences. The events have affected organic evolution, because they are selective with respect to biota, ecosystems and palaeogeography. The events have mainly been associated with major facies changes and have given rise to regular evolutionary patterns of extinction events followed by radiations and diversifications. Most global bioevents are caused primarily by palaeoenvironmental changes in, for example, oceanic conditions, sea level and climate.

Dinoflagellates are algae classified in the Division (or Phylum) Dinoflagellata [1]. Some forms include an encysted stage in their life cycle. The cysts can fossilise and are therefore of primary interest to palaeontologists. Dinoflagellate cysts are important Triassic to Quaternary biostratigraphical markers due to their relatively rapid evolution, ease of recognition and high abundance. Furthermore, dinoflagellates are largely planktonic and geographically extensive, hence dinoflagellate cysts permit reliable stratal correlations over wide areas [2,3]. Ultrastructural and molecular phylogenetic data suggest that the dinoflagellates diverged as a separate protistan lineage during the Precambrian [4-7]. However, fossil dinoflagellates are rare, absent or unrecognised in pre-Mesozoic strata. They first emerged unequivocally during the Triassic, increasing in species diversity until the Mid Cretaceous, from when species numbers have declined [8,9]. Fensome *et al.* [5] considered this Triassic-Early Jurassic emergence to be a unequivocal radiation, characterised by major innovations and significant variety in morphologies, principally reflected in tabulation ('plating') patterns. The Pliensbachian-Toarcian (Early Jurassic) is important in dinoflagellate evolutionary history as, at that time, a major diversification/radiation event occurred. The main elements of the Mesozoic-Cenozoic dinoflagellate floras emerged during this interval and these became established during the later Jurassic and Cretaceous [1,9]. In addition, a significant extinction event affecting many fossil groups, including the dinoflagellate cysts, occurred in the early Toarcian [10-12].

Speciation and extinction events have different manifestations in northern and southern Europe (the Boreal and Tethyan Realms, respectively), due to differing palaeoenvironmental and palaeoecological settings. [11,12]. These differences also affected the stratigraphical ranges of dinoflagellate cysts and their geographical distributions.

The patterns, processes, and possible causes of Pliensbachian-Toarcian dinoflagellate cyst evolution are analysed in this study. Specifically, the driving mechanisms, timing and intensity of evolutionary change in dinoflagellate cysts and the temporal and causal relationships between evolutionary and palaeogeographical events are investigated.

2 MATERIALS AND METHODS

The information used in this study comprises Boreal and Tethyan composite range charts of Lower Jurassic dinoflagellate cysts (Figs. 1, 2). The stratigraphical data pertaining to Tethyan dinoflagellate cysts (Fig. 1) were compiled from recent literature [13-21]. The principal sources for the compilation of the Boreal range chart (Fig. 2) include [22-33]. The stratigraphical distribution of the dinoflagellate cysts is made at the substage level for the Pliensbachian and at the ammonite zonal level for the Toarcian. The timescale used is that of Gradstein *et al.* [34]. The relationship between Early Jurassic dinoflagellate cyst evolution and global palaeoceanographic changes was investigated via the calculation of evolutionary rates. The indices used have been described in [35-37]. The rates of speciation (rs) and extinction (re) are:

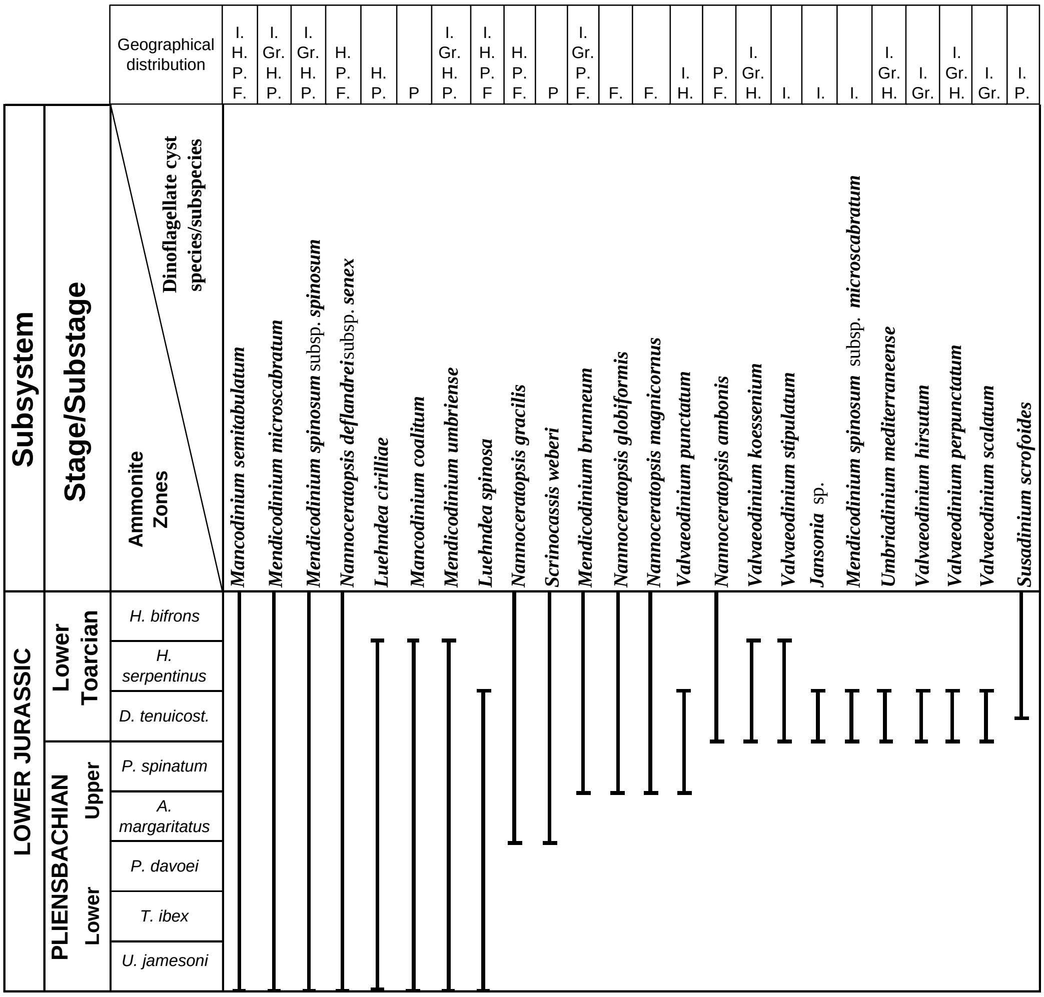

Fig. 1. Composite range chart of Lower Jurassic (Pliensbachian-Lower Toarcian) dinoflagellate cysts in the Tethyan Realm. F = France; Gr = Greece; H = Hungary; I = Italy; P = Portugal.

$$rs = (1/D)\,(S/t)\,100 \qquad (1)$$

$$re = (1/D)\,(E/t)\,100 \qquad (2)$$

where S is the number of inceptions occurring during time interval t, E is the number of extinctions, and D is the diversity. The rate of diversification (rd) is the difference between rs and re (rd = rs - re), and the total change of assemblages, rs + re, denotes the rate of turnover, rt.

The evolutionary rates are compared to the main Early Jurassic eustatic, anoxic and isotopic events. Early Jurassic sea level curves [38-40] indicate a gradual rise through the Early Jurassic, reaching a highstand during the early-mid Toarcian, after which eustatic levels fall. There is also broad agreement on eustatic falls during the late Hettangian, mid Sinemurian, latest Sinemurian, mid Pliensbachian, latest Pliensbachian, mid Toarcian and latest Toarcian (Fig. 3). Extensive spread of anoxic or near anoxic marine bottom waters in western and central Europe has been recorded during the Early Jurassic (Fig. 3). The first of these episodes was in the earliest Hettangian, followed by less extensive events in the early Sinemurian and late Pliensbachian [12]. The most extensive anoxic event occurred in the early Toarcian [41]. The early Toarcian global anoxic event affected the Tethyan Realm to a lesser extent than the Boreal Realm. This was principally because Tethyan depocentres had more complex palaeotopography than those on the northern European continental shelf. Tethyan Lower Toarcian black shales are thinner than coeval strata in northern Europe and their Hydrogen Index (HI) and Total Organic Carbon (TOC) values are significantly lower [42]. Furthermore, the duration of the event was longer in the Boreal Realm, where oxygenated marine conditions were restored either in the *Harpoceras falciferum* or *Hildoceras bifrons* Ammonite Zone [43,44]. By contrast, the anoxic event in the Tethyan Realm is confined frequently to the *Dactylioceras tenuicostatum* Ammonite Zone and occasionally extends into the lower part of the *Hildaites serpentinus* Ammonite Zone [15,45]. Jenkyns and Clayton [46] discovered a regional trend in $\delta^{13}C$ composition in the early Toarcian of Europe. A pronounced negative excursion in $\delta^{13}C_{organic}$ was recorded in the mid *Harpoceras exaratum* Ammonite Subzone (*H. falciferum* Zone). This interval was characterised by high TOC values and was followed by a significant positive excursion in $\delta^{13}C_{organic}$.

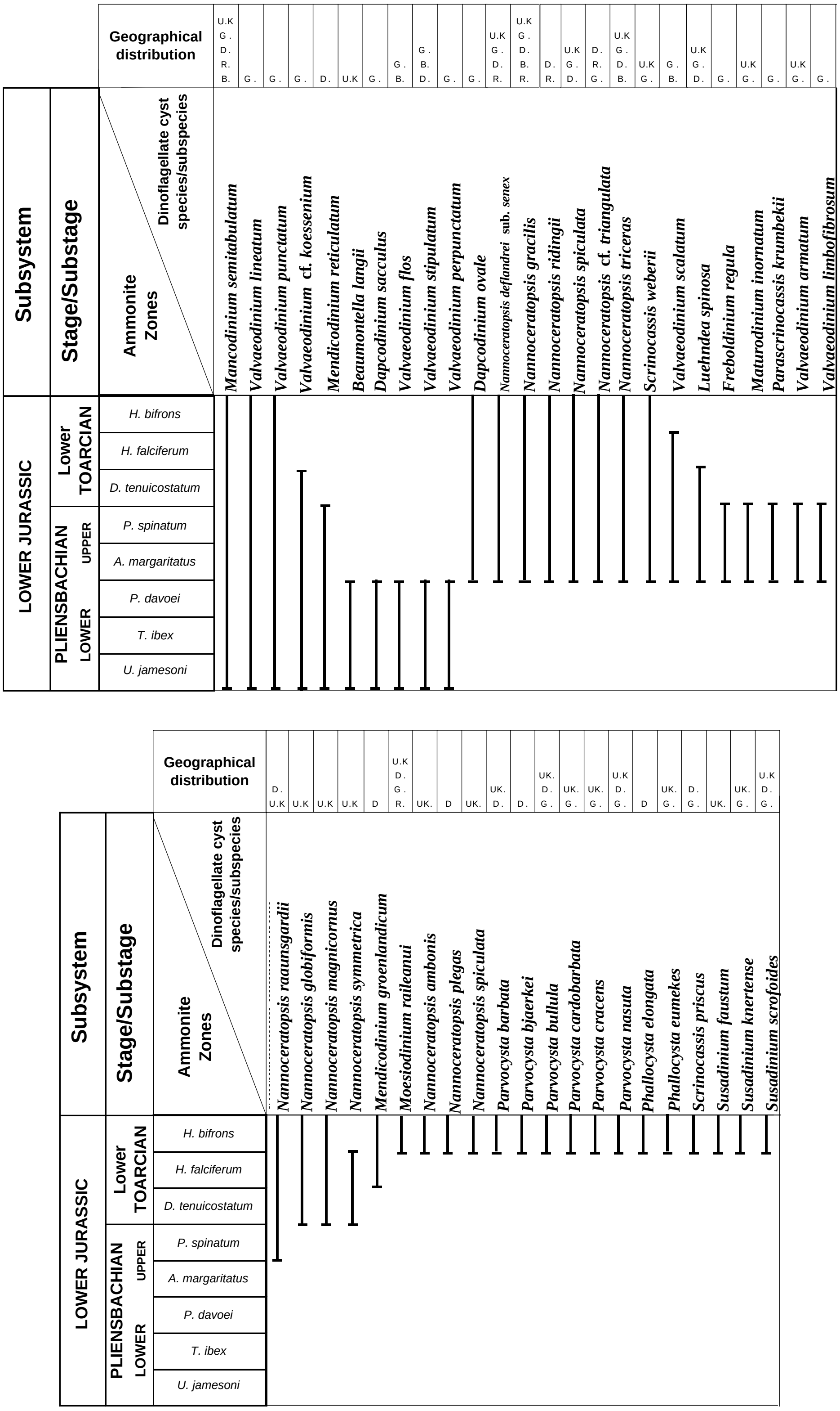

Fig. 2. Composite range chart of Lower Jurassic (Pliensbachian-Lower Toarcian) dinoflagellate cysts in the Boreal Realm. B = Bulgaria ; D = Denmark; G = Germany; R = Russia; U.K. = United Kingdom.

3 RESULTS

Boreal and Tethyan evolutionary rates of dinoflagellate cysts during the Pliensbachian and Toarcian are illustrated in Figs. 4 and 5. The Boreal speciation rates exhibit two distinct peaks in the late Pliensbachian and the *H. bifrons* Ammonite Zone. In the Tethyan Realm, speciation rates are significantly lower. A single peak occurred during the late Pliensbachian - early Toarcian (*D. tenuicostatum* Ammonite Zone) and this corresponds with high species

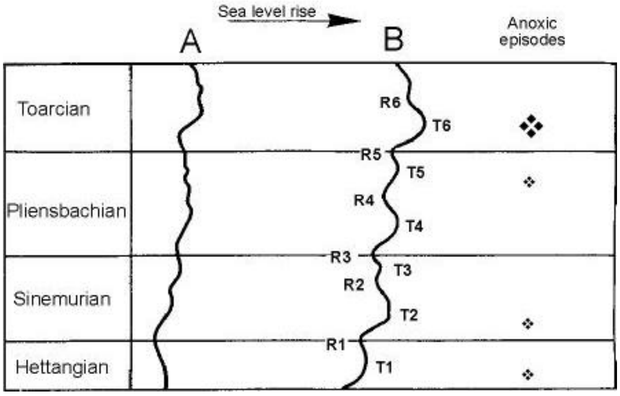

Fig. 3. Jurassic sea level curves ((a): after [39], (b): after [47]) and anoxic episodes. T and R refer to transgressive and regressive episodes, respectively. Modified from [12].

Zone/Substage	r	Boreal	Tethyan
H. bifrons	rs	30	0
H.falciferum/H.serpentinus		5.81	0
D. tenuicostatum		0	24.16
Upper Pliensbachian		50	11.7
Lower Pliensbachian		8.25	24
H. bifrons	re	0	0
H.falciferum/H.serpentinus		59.1	25.7
D. tenuicostatum		7.5	21.25
Upper Pliensbachian		16.54	0
Lower Pliensbachian		13.75	0
H. bifrons	rd	30	0
H.falciferum/H.serpentinus		-53.29	-25.7
D. tenuicostatum		-7.5	2.66
Upper Pliensbachian		33.46	11.7
Lower Pliensbachian		-5.5	24
H. bifrons	rt	30	0
H.falciferum/H.serpentinus		64.91	25.7
D. tenuicostatum		7.5	24.16
Upper Pliensbachian		66.54	11.7
Lower Pliensbachian		22	24

Fig. 4. Lower Jurassic (Pliensbachian-Lower Toarcian) dinoflagellate cyst speciation rates (rs), extinction rates (re), diversity rates (rd) and turnover rates (tr) in the Boreal and Tethyan Realms.

turnover. The Boreal and Tethyan Realms both exhibit maximum extinction rates at the *H. falciferum-H. serpentinus* Ammonite Zone transition. The maximum is highly distinct in the Boreal Realm, but the trend is more gradual in the Tethyan Realm, where the increase in extinction rate began in the late Pliensbachian. In the Boreal Realm, the diversity trend is similar to that of the speciation rate, with maximum values in the late Pliensbachian and in the *H. bifrons* Ammonite Zone. Negative values characterise the *H. falciferum* Ammonite Zone, confirming that the extinction exceeded speciation. The Tethyan diversity decreased from the early Pliensbachian to the early Toarcian *H. serpentinus* Ammonite Zone, conform the gradual increase of extinctions with respect to speciations. The main Boreal species turnovers occurred in the late Pliensbachian, coincident with the peak in speciation rate, and in the early Toarcian *H. falciferum* Ammonite Zone, at the main extinction event. In the Tethyan Realm, high species turnover occurred mainly in the early Toarcian (*D. tenuicostatum* and *H. serpentinus* Ammonite Zones).

4 DISCUSSION

The peaks in evolutionary rates correlate with the main Pliensbachian-Toarcian palaeoceanographic changes, which strongly suggests that the environment played an important role in the evolutionary history of the dinoflagellate cysts. The speciation events and the peaks in diversity were probably linked to the Early Jurassic transgression, because it increased the number of available marine niches. In northern Europe, because of the complex palaeotopography during the Early Jurassic, the transgression increased the number of neritic habitats favourable to dinoflagellates. Consequently, higher speciation and diversity rates were recorded in the Boreal Realm. The late Pliensbachian speciation event in the Boreal Realm and the early Toarcian (*D. tenuicostatun* Ammonite Zone) speciation event in the Tethyan Realm can be related to two different transgressive episodes. These are the less intense T5 and the more intense T6 events, respectively (Fig. 3) [47]. The late Pliensbachian-early Toarcian phytoplanktonic speciation has also been linked to acceleration of the biological carbon pump produced by a significant increase of global CO_2 atmospheric-oceanic levels [48]. This acceleration, which is most distinct at low trophic levels, resulted in an increased extraction rate of biologically-fixed CO_2 into the sedimentary reservoir [49-51].

The extinction event observed at the *H. falciferum-H. serpentinus* Ammonite Zone transition in northern and southern Europe is one of the 10 principal mass extinction events of the last 250 Ma [52-53]. This extinction event is significantly smaller than preceding events, but it has proved to be coherent in a series of reinvestigations of the original dataset [54]. The early Toarcian dinoflagellate cyst extinction is related to anoxic black shale facies. This strongly suggests that the primary causal factor was a severe habitat restriction or deterioration due to either regression or the development of widespread anoxia of bottom waters. Dinoflagellate cysts are proving to be as useful for indicating paleoecological change at the sea bottom as most benthic organisms. This reflects the fact that cyst-producing dinoflagellates are not merely planktonic. The benthic resting cyst is apparently a vital stage in sexual reproduction [55]. In the Mediterranean region, the black shale facies is not widespread. At many localities, the Toarcian bituminous facies are succeeded by non-carbonaceous, reddish or grey pelagic limestones

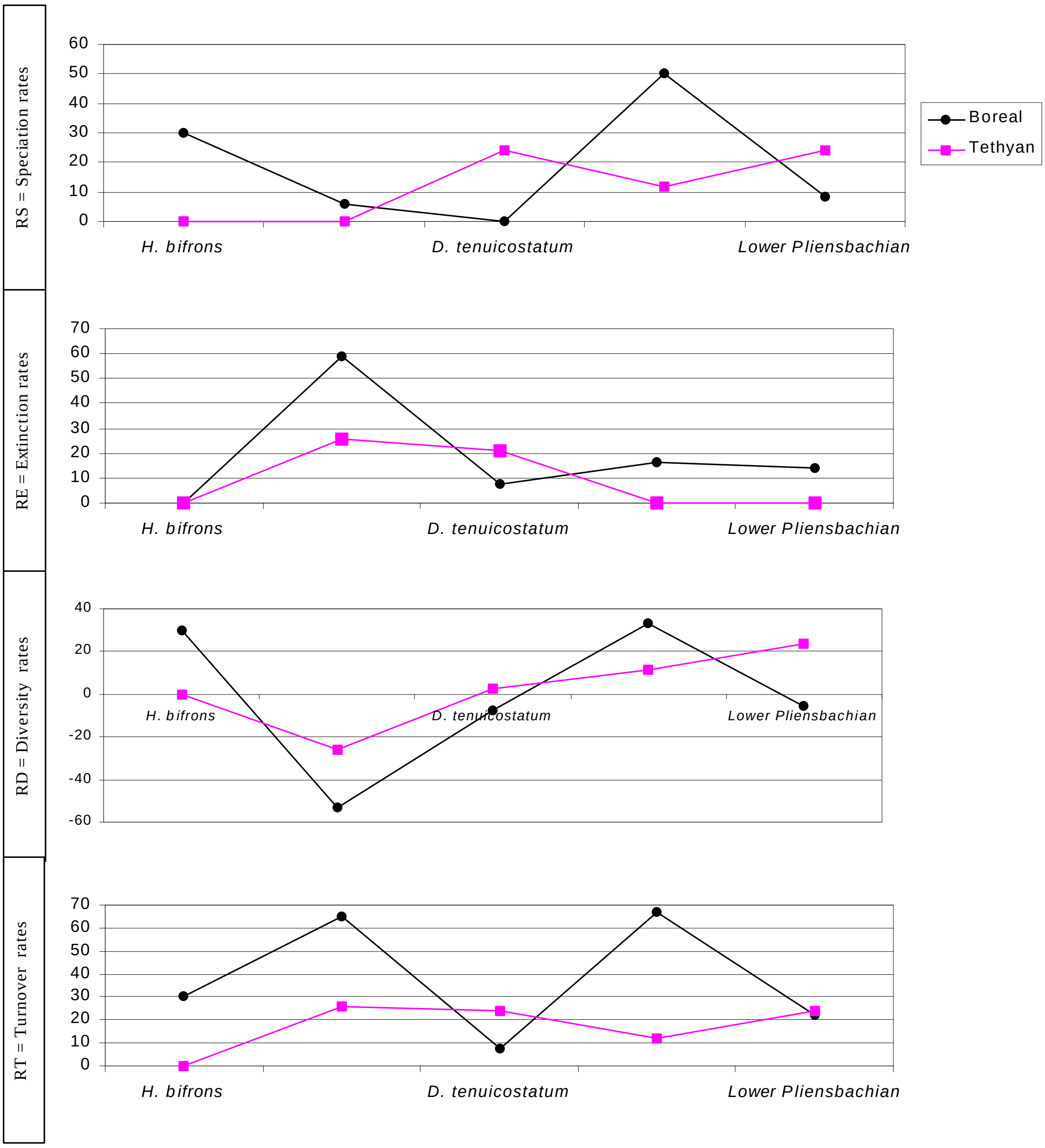

Fig. 5. Variations in evolutionary rates of Boreal and Tethyan dinoflagellate cysts during the Lower Jurassic (Pliensbachian-Lower Toarcian).

[43]. In central Italy, the sea-bottom conditions ranged from oxic to dysoxic, but pervasive anoxic conditions, such as in the Boreal Realm, were absent [56]. Furthermore, the duration of the event was longer in the Boreal Realm, where oxygenated conditions were restored either in the *H. falciferum* or the *H. bifrons* Ammonite Zones [43-44]. These palaeoecological and stratigraphical differences explain the lower extinction rate in the Tethyan region. The restoration of oxygenated conditions in the Boreal Realm during the *H. bifrons* Ammonite Zone is characterised by a speciation event and high species diversity. This indicates an increase in the available habitats despite this being a regressive phase, according to the eustatic curve [39,40,47]. This pattern is not recorded in the Tethyan Realm.

The trend line of turnover rates for the Boreal Realm also indicates that the dinoflagellate communities were sensitive to palaeoceanographic changes. The Pliensbachian shows significant turnover, which is related to the above-mentioned transgression and speciation event. A further turnover event occurred in the early Toarcian (*H. falciferum* Ammonite Zone), together with the extinction event mentioned above. In the Tethyan Realm, turnover rates were lower and only one peak was recorded in the early Toarcian (*D. tenuicostatum* and *H. serpentinus* Ammonite Zones). Different systagenetic levels of dinoflagellate cyst communities in northern and southern Europe explain the different patterns of Boreal and Tethyan evolutionary rates. Systagenesis is the evolution of a certain taxon group [57]. Generalists prevail in the assemblages at low systagenetic levels, whereas more taxa are specialised at high systagenetic levels (i.e., high diversities). Stenotopic and specialised taxa are more prone to extinction than eurytopic and unspecialised (generalist) species. Higher susceptibility, which is typical of high systagenetic levels, means that taxa may easily be wiped out, even by minor environmental changes. Boreal dinoflagellate cyst communities were probably at a higher systagenetic level than Tethyan communities. The higher species diversity in the Boreal Realm supports this. The Boreal association was highly sensitive to mild palaeoceanographic changes and therefore was liable to significant speciations, extinctions and turnovers. By contrast, Tethyan dinoflagellate cyst communities may have been at lower systagenetic levels, with lower susceptibility to environmental changes. This explains the lower magnitude of Tethyan extinction and turnover rates.

Acknowledgements. This work was undertaken as part of a Marie Curie Fellowship (1996-1998; contract number ERBFMBICT960661), awarded to Raffaella Bucefalo Palliani (Marie Curie membership number 1128), and under supervision of J.B. Riding. The reviews of Dr. M. Vecoli and Dr. S. Clemens have greatly improved the manuscript. James B. Riding publishes with the permission of the Director, British Geological Survey (NERC).

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