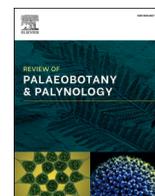


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Review papers

The biostratigraphy and biogeography of Middle Jurassic (late Bajocian to Bathonian) dinoflagellate cysts from the Barents Sea

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ABSTRACT

The Barents Sea region was an important pathway for Jurassic-Cretaceous marine microplankton and faunal migration and is a key area for high-resolution bio- and sequence-stratigraphic correlations within the Panboreal Superrealm. New records of Late Bajocian-Bathonian dinoflagellate cyst assemblages in ammonite zone correlated strata in the Central Barents Sea are compared with contemporaneous assemblages from Central Europe and diachronic first and last appearances are noted. Species diversities areas are generally low, and calculated diversities and similarity-indexes between the Barents Sea dinoflagellate cyst assemblages and contemporaneous assemblages in Canadian Arctic, East Greenland, NW and Central Europe, Iran, Morocco and Australia indicate limited biogeographic connections in Late Bajocian-Early Bathonian times compared to in Late Bathonian to Early Oxfordian times. The Late Bajocian- mid Bathonian biogeographic differences, and the following Late Bathonian-Early Oxfordian increase in similarities among world-wide dinoflagellate cyst assemblages, coincide with breakdowns of land-barriers, major transgressions, radiation of cyst-producing dinoflagellates and migration of marine biotas between Boreal, Sub-Boreal and Tethyan seas.

1. Introduction

The Barents Sea region, including Svalbard, is a key region for reconstructing Middle Jurassic – Early Cretaceous geological history of the Arctic. It was an important pathway for Jurassic-Cretaceous marine microplankton and faunal migration and is a key area for high-resolution bio- and sequence-stratigraphic correlations within the Panboreal Superrealm (Smelror, 1993; Smelror et al., 2018; Rogov, 2014, 2018; Rogov et al., 2023; Wierzbowski and Smelror, 1993, 2020). Through the years several correlations between Jurassic litho- and sequence-stratigraphic units in Boreal, Sub-Boreal and Tethyan basins have been published (Gradstein et al., 2020), but for parts of the Stages well-calibrated inter-regional correlations between biostratigraphic zones are still missing. This concerns the Bajocian and Early Bathonian, where biostratigraphic records with good chronostratigraphic calibrations are limited, incompletely or missing in large parts of the world (Khaffou et al., 2023).

In NW Europe, there has provided series of correlations between palynostratigraphic events and established Jurassic ammonite zones (Woollam and Riding, 1983; Riding and Thomas, 1992; Feist-Burkhardt and Monteil, 1997; Poulsen and Riding, 2003). The Bajocian stratotype

in northern France and the Bathonian type section in southern England are key reference points, but correlations with other places in the world is often problematic since in many regions the palynological records often lack independent age-controls from other groups of fossils and/or from mineral isotope dating (Riding et al., 2010). In addition to uncertainties with respect to ages and stratigraphic positions, biogeographic provinciality and variations in environmental impacts cause challenges. As an example, the comparative range chart of selected dinoflagellate cysts for the Middle and Upper Jurassic of Europe and Australia presented in Riding et al. (2010; figs. 9–10) shows numbers of discrepancies regarding first (FAD) and last appearances (LAD) and total stratigraphic ranges of several species.

The present study documents how FAD's, LAD's and biostratigraphic ranges of stratigraphic important Boreal upper Bajocian and lower Bathonian dinoflagellate cysts recovered in Barents Sea, correlate to the established NW European zonation (Riding and Thomas, 1992; Poulsen, 1998; Poulsen and Riding, 2003). Herein, the ammonite zonation presented in the revised Geological Time Scale of Gradstein et al. (2020) serves as a stratigraphic standard to which the present data are calibrated. Further, the present study presents quantitative measurements of the similarity between Late Bajocian and Bathonian dinoflagellate

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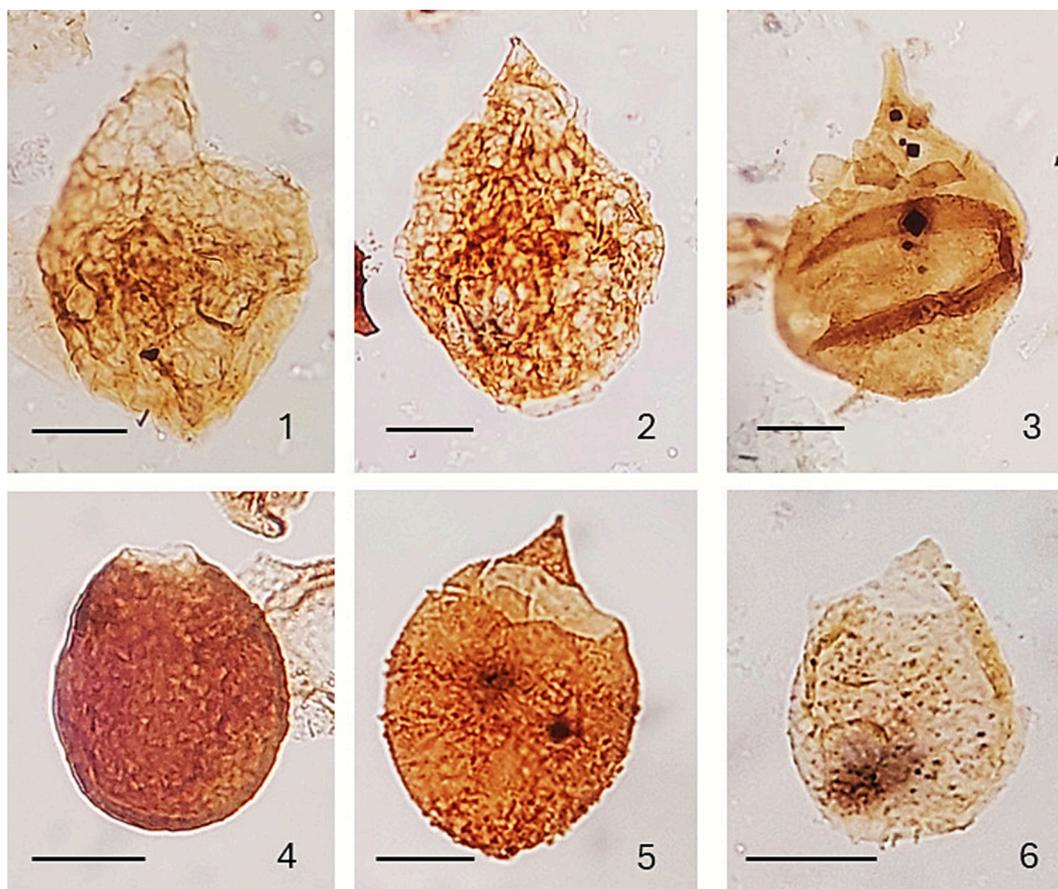


Fig. 3. Selected dinoflagellate cysts from borehole 7533/03-U-01. A: *Evansia perireticulata* (Arhus et al.) Leintin & Williams 1993, sample 120.07 m; B: *Evansia perireticulata* (Arhus et al.) Leintin & Williams 1993, sample 120.07 m; C: *Evansia alaskensis* (Wiggins) Below, 1990, sample 109.86 m; D: *Fromea tornatilis* (Drugg) Lentin & Williams 1981, sample 109.86 m; E: *Evansia evittii* (Pocock) Jansonius 1986, sample 100.03 m; F: *Evansia barentsensis* (Smelror) Below, 1990, sample 120.07 m. Scale bars equal 20 μ m.

An ammonite found at 99.42 m assigned to *Keplerites* indicates a Bathonian age (Wierzbowski and Smelror, 2020), but more precise ages of these two uppermost analyzed samples are not determined. The presence of the dinocyst *Carphatodinium predae* at 100.03 m indicates a general Bajocian to Middle Bathonian age. In the British Jurassic, this species has its last occurrence datum in the Middle Bathonian Progracilis ammonite zone (Riding and Thomas, 1992). In East Greenland, Lund and Pedersen (1985) only found this species in Bajocian strata.

4. Palynostratigraphic correlations

During the Bajocian dinoflagellates underwent major radiation and over 100 species appeared (Fensome et al., 1996; Wiggan et al., 2017, 2018). However, records of Boreal Late Bajocian and Bathonian ammonites (Wierzbowski and Smelror, 2020) and the dinoflagellate cysts recoveries presented in the present paper document distinct biogeographic variations which influence the possibilities for regional correlations based on the fossils (Figs. 6, 7). The presence of key stratigraphic species and their first and last appearance may vary between the oceans and seaways.

Synthesis of stratigraphic ranges and events, and zonations of dinoflagellate cysts for the British Jurassic and the Sub-Boreal NW Europe have been published by Riding and Thomas (1992) and Poulsen and Riding (2003). In both zonations the dinoflagellate cyst zones were calibrated to ammonite chronozones. Dinoflagellate cyst zonations calibrated to ammonite stratigraphy have been published for the Middle to early Late Jurassic of East Greenland (Smelror, 1988), the Barents Sea region (Smelror and Below, 1992) and Arctic Russia (Nikitenko et al.,

2013), but records covering the Bajocian and Early to Middle Bathonian were missing. Based on the more recent ammonite stratigraphy and chronostratigraphic subdivision of Middle Jurassic strata in East Greenland presented by Kelly et al. (2015), the events, zones and previous proposed regional correlations for the Bajocian and Bathonian time intervals need reconsiderations and re-calibrations to a more recent Geological Time Scales (Gradstein et al., 2020). In the recent extensive survey of palynostratigraphic Jurassic events in the Circum-Arctic regions presented by Bujak et al. (2022), there are only few records from Bajocian and lower-middle Bathonian strata. The present records from the upper Bajocian and Bathonian deposits of core 7533/03-U-01 on the Sentralbanken High provide new information on the first and last occurrences of some key dinoflagellate cysts used for regional correlations (Figs. 2–6).

The thick and relatively complete Jurassic succession of eastern Greenland has provided a rich record of ammonites and the substantial work of Callomon and colleagues resulted in a stratigraphic subdivision of 93 Boreal ammonite horizons and the Boreal cardioceratids provide an almost continuous zonal lineage from the Bajocian to the Kimmeridgian (Callomon, 1985, 1993, 1994, 2003; Callomon et al., 2015). Most of the Greenland ammonite fauna are Boreal, but there are also some Tethyan or oceanic derived elements present, for example in the *Arctioceras ishmae* Zone in Jameson Land (Kelly et al., 2015).

Ammonites of the *Ishmae* zone are known from Alaska, Canadian Arctic, East Greenland, Northern Siberia and Svalbard and the ammonite zone was originally dated as Late Bathonian (Poulton, 1987). In the most recent East Greenland ammonite zonation and in the updated Geological Time Scale (GTS 2021), this ammonite zone is

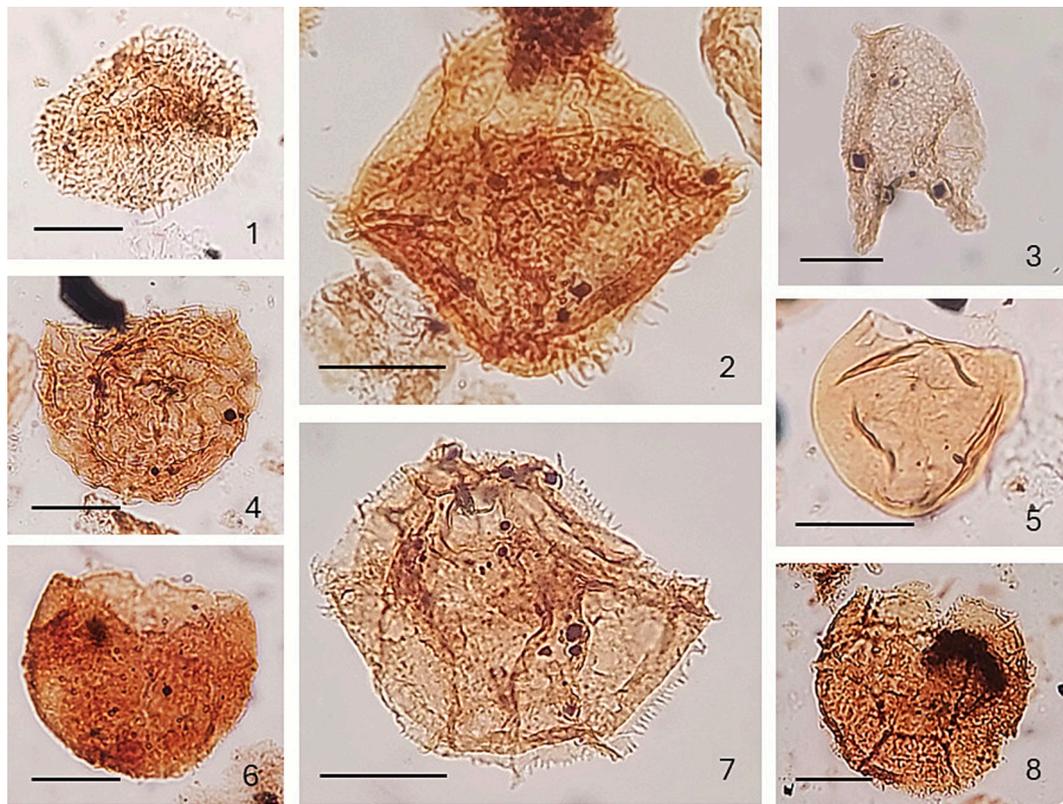


Fig. 4. Selected dinoflagellate cysts from borehole 7533/03-U-01. A: *Chlamyphorella ectotabulata* Smelror 1989, sample 109.86 m; B: *Ctenidodinium ornatum* (Eisenack) Deflandre 1939, sample 100.03 m; C: *Nannoceratopsis gracilis* Alberti 1961, sample 100.03 m; D: *Valensiella ovulum* (Eisenack) Deflandre 1963, sample 100.03 m; E: *Chytroisphaeridia chytroides* (Sarjeant) Downie & Sarjeant 1965, sample 120.07 m; F: *Meiourogonyaux* sp., sample 100.03 m; G: *Ctenidodinium continuum* Gocht 1970, sample 109.8 m; H: *Meiourogonyaux caytonensis* Sarjeant 1959, sample 100.03 m. Scale bars equal 20 μ m.

placed in the latest Early to earliest Middle Bathonian (Kelly et al., 2015; Gradstein et al., 2020). The lower boundary of the *Sirmiodinium grossii* range-zone of Smelror and Below (1992) is concurrent with the Ishmae ammonite zone, and the older part of this dinoflagellate cyst zone was revised to cover the entire Bathonian, not only the Late Bathonian as originally proposed.

In Poland, Poulsen (1998) placed the first appearance datum of *Sirmiodinium grossii* together with the LAD of *Carpathodinium predae* in the Early Bathonian Aurigerus ammonite zone. In East Greenland, the oldest record of *Sirmiodinium grossii* is in the earliest Bathonian *Arctoccephalites arcticus* Zone (Larsen et al., 2003; Kelly et al., 2015). Based on the record from the Sentralbanken High the earliest appearance of this species can be moved down to the Late Bajocian *Cranocephalites indistinctus* Zone (Figs. 2, 7) and correlated with the Sub-Boreal and Tethyan *Garantiana garantiana* Zone (Bujak et al., 2022).

Other diachronic Bathonian first appearances in the Barents Sea compared the dinoflagellate cyst ranges presented by Riding and Thomas (1992) are the earliest appearances of *Ctenidodinium ornatum* and *Mendicodinium groenlandicum* which in the British Jurassic first appear in the Late Bathonian (Fig. 7). In borehole 7533/03-U-01 on the Sentralbanken High these species are present in strata that most likely are Early Bathonian in age (Fig. 2). In Northwest Germany Prauss (1989) found that *C. ornatum* first appear in the Late Bajocian *Garantiana* ammonite zone. In Alsace and in Ardèche, France, *C. ornatum* has been recorded in middle and upper Bajocian deposits (Rauscher and Schmitt, 1990; Fauconnier et al., 1996), *Ctenidodinium ornatum* has also been found in Early Bathonian strata in the Middle Atlas, Morocco (Khaffou et al., 2023).

Mendicodinium groenlandicum has been found in the Lower Bathonian in the northern Lusitanian Basin, Portugal (Correia et al., 2019) and the uppermost Bajocian in Iran (Mafi et al., 2013). Riding et al. (2010) also

recovered rare/inconsistent occurrences of *M. groenlandicum* in the Bajocian of the North-West Shelf of Australia.

Key stratigraphic Bajocian species in the Sub-Boreal and northern Tethyan areas of Central and Southern Europe (Riding and Thomas, 1992; Feist-Burkhardt and Monteil, 1997; Wiggan et al., 2017) like *Acanthaulax crista* and *Cenidodinium combazii* were not recovered in the present Barents Sea material. These species are not reported from the Bajocian-Early Bathonian in Arctic Canada and East Greenland. In contrast, characteristic species like *Evansia alaskensis*, *Evansia barentsensis*, *Evansia perireticulata* and *Pluriarvalium osmingtonense* found in the Arctic areas are not reported from the Sub-boreal and Tethyan areas included in the present records (Tables 1–3).

Although it is not a dinoflagellate cyst, but an Acritarcha, the stratigraphic range of *Limbycysta bjaerkei* should also be given some consideration (Fig. 5A). Bailey and Hogg (1995) who recorded this species consistently in the Late Pliensbachian to Early Bathonian in northwest Europe, suggested that the younger records from the Late Bathonian and Callovian on Svalbard and Franz Josef Land (cg. Bjarke, 1977; Smelror, 1987, 1988) were due to reworking. Both the recoveries on Svalbard and Franz Josef Land were linked to ammonite faunas which originally have been dated as Late Bathonian and Callovian (Dihner and Shulgina, 1960), but which subsequently were placed in the Middle Bathonian (Poulton, 1987) and presently the Early Bathonian (e.g., the Arctic ammonite zone). Records from borehole DH2 in Central Spitsbergen places the last occurrence datum of *Limbycysta bjaerkei* in the Late Bathonian Calyx ammonite zone (Fig. 6).

5. Biogeographic connections

In the present study, the Simpson Coefficient of biotal similarity and the Koch Index of dispersity have been used to obtain quantitative

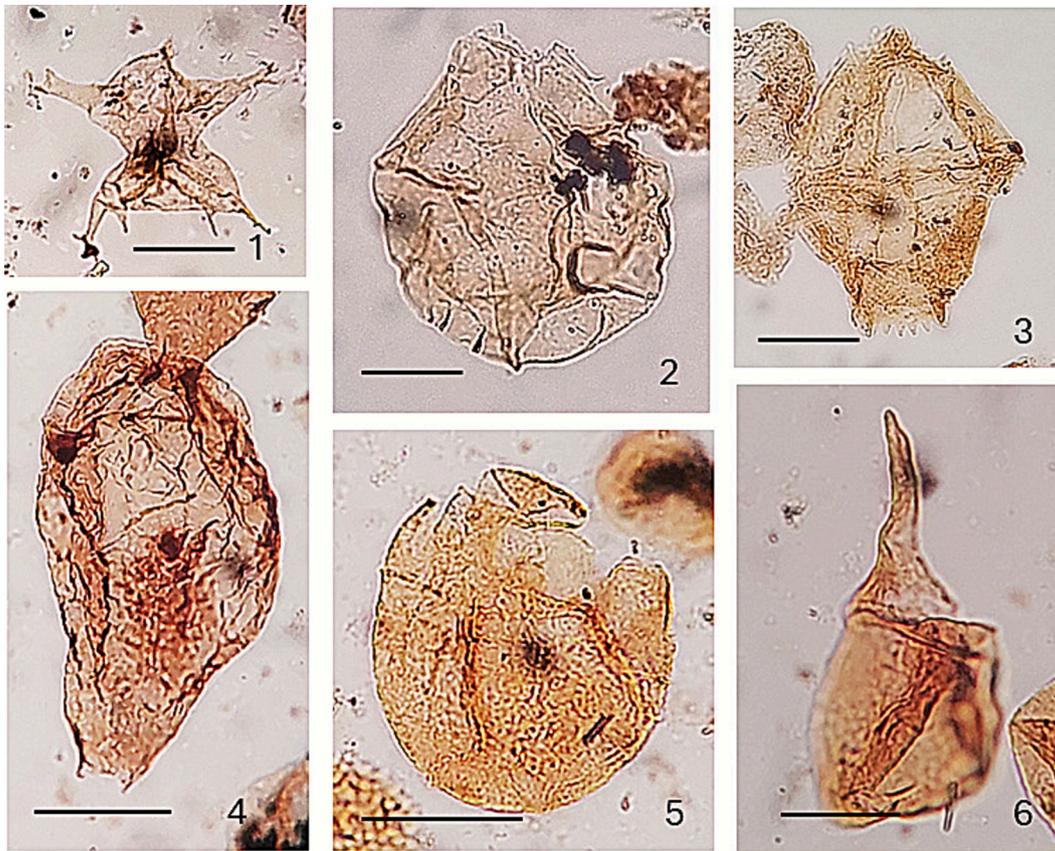


Fig. 5. Selected dinoflagellate cysts from borehole 7533/03-U-01. 1 A: *Limbicysta bjaerkei* (Smelror) MacRae et al. 1996, sample 120.07 m; B: *Sirmiodinium grossii* Alberti 1961, sample 100.03 m; C: *Gonyaulacysta pectinifera* (Gocht) Fensome, 1979; sample 100.03 m; D: *Tubotuberella* sp., sample 109.86 m; E: *Kallosphaeridium* sp., 109.86 m; F: *Pareodinia halosa* (Filatoff) Prauss, 1989, sample 109.86 m. Scale bars equal 20 µm.

Middle Jurassic	Stage	NW European ammonite zones	Barents Regon ammonite zones		
	Bathonian	apertum	apertum		FO <i>Dichadogonyaulax sellwoodi</i>
calyx		calyx			
variabile				LO <i>Limbicysta bjaerkei</i>	
cranocephaloide		cranocephaloide			
ishmae		ishmae		FO <i>Evansia evittii</i>	
greenlandicus					
arcticus					
Bajocian		pompeckji	pompeckji		FO <i>Evansia perireticulata</i>
		indistinctus	indistinctus		FO <i>Chlamyphorella ectotabulata</i>
		borealis			
	humpherisiarum			FO <i>Sirmiodinium grossi</i>	
	sauzei				
	laeviuscula			LO <i>Durotrigia daveyi</i>	
	ovale				
	discites				

Fig. 6. First (FO) and last (LO) occurrences of some biostratigraphic significant Late Bajocian- Bathonian dinoflagellate cysts in the central Barents Sea and their correlations to boreal ammonite zonation.

Middle Jurassic	Stage	NW European ammonite zones						Tethyan ammonite zones
			FO <i>Sirmiodinium grossii</i>	LO <i>Carpathodinium predae</i>	FO <i>Ctenidodinium ornatum</i>	LO <i>Limbiocysta bjaerkei</i>	FO <i>Mendicodina groenlandicum</i>	
Bathonian	apertum	E		E?			discus	
	calyx					Sv	retrocost./bremeri	
	variabile					E		
	cranocephaloide						morri./subcontra.	
	ishmae	Sv	E		E	Sv		
	greenlandicus	P?	P	B?		B?	progr./auri./zigzag	
	arcticus	G1				I?		
	pompeckji			G2			parkinson/garant.	
	indistinctus	B					niorfense	
	borealis							
Bajocian	humpherisiarum						humphriesianum	
	sauzei						propinquans	
	laeviuscula						laeviuscula	
	ovale							
	discites						discites	

Fig. 7. Records of different first (FO) and last occurrences (LO) of some selected dinoflagellate cysts and acritarch species in England (E), Poland (P), Iran (I), Greenland (G₁) and the Barents Sea (B) and Svalbard (Sv), correlated to NW European and Tethyan ammonite zones.

estimates of the similarity and connections between the Late Bajocian and Early Bathonian dinoflagellate cyst assemblages recovered on the Sentralbanken High and assemblages of same age in Arctic Canada, East Greenland, England, Poland, France, Germany, Iran, Morocco and Australia (Fig. 8). A list of species recovered in upper Bajocian-lower Bathonian strata in each of these geographic areas is shown in Tables 1–3. Quantitative estimates of biotal variations for the Barents Sea, England, France and Australia towards the other different study areas are shown in Table 4 and Fig. 9.

Studies of Jurassic dinoflagellate cyst biogeography and provincialism are relatively few (Fenton and Fisher, 1978; Davies and Norris, 1980; Porter, 1988; Stancliffe and Sarjeant, 1988; Smelror, 1993), and early studies of Bajocian and Early Bathonian dinoflagellate cysts were to some extent focused on classic and well-documented Jurassic outcrop localities and exploration wells in England, France and Germany (Stover, 1966; Fenton and Fisher, 1978; Davey, 1980; Fenton et al., 1980; Woollam, 1982; Gocht, 1984; Bailey, 1987, 1990; Below, 1987a, 1987b, 1990; Lund and Ecke, 1988; Prauss, 1989; Feist-Burkhardt (1990), Rauscher and Schmitt (1990), Riding et al., 1991; Fauconnier et al., 1996, Wiggan et al., 2017, 2018). The early works include studies in the Bajocian stratotype in Calvados, Normandy (Feist-Burkhardt, 1995; Feist-Burkhardt and Monteil, 1997) and the Bathonian type section in Southwest England (Riding et al., 1985). In these areas ammonite zones are established and provide independent age control of the palynostratigraphic calibrations and correlations.

Studies of Middle Jurassic marine and terrestrial palynomorphs in other European areas have been carried out in Middle Jurassic successions in Bulgaria, Denmark, Greenland, Norway, Poland, Portugal and Slovakia (Fensome, 1979; Davies, 1985; Guy-Ohlson, 1989; Lund and Pedersen, 1985; Dodekovic, 1990; Manum et al., 1991; Koppelhus and Nielsen, 1994; Poulsen, 1996, 1998; Koppelhus and Hansen, 2003; Larsen et al., 2003; Gedl, 2008, 2013; Barski et al., 2012; Gedl and Józsa, 2015; Segit et al., 2015; Correia et al., 2019). However, mostly the stratigraphic distributions presented from these works lack independent age control. There are some published (Bailey and Partington, 1991;

Butler et al., 2005) and substantial unpublished Middle Jurassic records from the North Sea and Norwegian Sea offshore areas, but also here the biostratigraphic assignments generally lack independent age-control.

Middle Jurassic dinoflagellate cysts from wells offshore Eastern Canada were included in a palynostratigraphic survey published by Bujak and Williams (1977), and the stratigraphic distribution of some Bajocian-Bathonian species were published by Van Helden (1977) and included in the Jurassic-Early Cretaceous Opperel-zonation for the Canadian Arctic published by Davies (1983). Eastwards in the Circum-Arctic, lowermost Bathonian strata (i.e., Arcticus ammonite zone) are well documented from the Anabar Region in Siberia, but records on Bajocian dinoflagellate cysts were not included in the comprehensive and detailed synthesis of uppermost Middle Jurassic to lowermost Cretaceous stratigraphy presented by Nikitenko et al. (2022).

Other works of Bajocian-Bathonian dinoflagellate cysts from outside Europa are limited but have expanded in recent years. Important records have been published from Egypt (Shahin and El-Beialy, 1989), Israel (Conway, 1990), Iran (Ghasemi-Nejad et al., 2012; Mafi et al., 2013; Al-Ameri and Al-Nagshbandi, 2015; Skupien et al., 2015), Qatar (Ibrahim et al., 2003), Morocco (Khaffou et al., 2023), Tanzania (Balduzzi et al., 1992), Argentina (Sarjeant et al., 1992; Quattrocchio and Sarjeant, 1992; Stukins et al., 2013) and Australia (Helby et al., 1987; Mantle and Riding, 2012).

In their study of the regional distribution of Bajocian and Bathonian dinoflagellate cysts of NW Europe Fenton and Fisher (1978), found an element of provinciality among the dinoflagellate cyst taxa, and they considered that some of the differences in the compositions of the microplankton assemblages ... "to reflect restricted regional distribution of certain species rather than the effects of different depositional environments". Fenton and Fisher (1978) concluded that despite the elements of provinciality, by the Late Bathonian northwest European assemblages had a relatively high number of species in common; a trend that continued into the Early Callovian. In a wider study of biogeography of Bathonian to Oxfordian dinoflagellate cysts of Arctic, NW Europe and circum-Mediterranean regions Smelror (1993) confirmed this trend. Although there are no great variations, the differences in composition of dinoflagellate cyst assemblages in the Arctic to Mediterranean regions became less prominent during Late Callovian-Early Oxfordian time compared to the Late Bathonian-Middle Callovian.

While the number of dinoflagellate cyst species recognized in the upper Bajocian-Bathonian in borehole 7533/05-U-01 in the Barents Sea (36 species) is relatively high compared to the some of the other study areas (14–20 species), the calculated Simpson Coefficients for the Barents Sea assemblages towards other regions are relatively low, ranging from 0.21 (Sverdrup Basin) to 0.50 (East Greenland) (Table 4, Fig. 9). The marked difference between the calculated similarity values of the Barents Sea and the Sverdrup Basin, and the Barents Sea and East Greenland, are noteworthy. A low number of recorded species in the Sverdrup Basin (14 species) could be an explanation but based on the record of the same low number of species in East Greenland (14 species) this explanation is not likely. The current data suggests some degree of provincialism related to the Boreal assemblages in the Sverdrup Basin.

The record showing that in Late Bajocian-Bathonian times the dinoflagellate cyst assemblages in the Barents Sea appear to have been more closely connected to the East Greenland assemblages, than the contemporaneous assemblages in the Sverdrup Basin (Table 4, Fig. 9), stands in a marked contrast to the Simpson Coefficient scores between these two areas in the Late Bathonian-earliest Callovian time and Late Callovian time, which were calculated to 1.00 (Smelror, 1993). A plausible reason for this marked difference appears to be the existence of a land barrier between the Barents Sea and the Sverdrup Basin in Late Bajocian-Early Bathonian time. The existence of a large, low lying continental landmass north of the Canadian Arctic Islands from the Carboniferous to Jurassic time was advocated by Embry (1993). This landmass, named the Crockerland, was a source area for northern Svalbard/Barents Shelf as well as the Sverdrup Basin. From mid-Jurassic

Table 1

Alphabetic list of species (A–D) recovered in upper Bajocian–lower Bathonian strata in the geographic areas included in the biogeographic similarity calculations: Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A).

Dinocyst registrations – Late Bajocian - 1:										
Taxa	B	C	G ₁	E	P	F	G ₂	I	M	A
<i>Acanthaulax crispera</i>				X	X	X	X	X	X	
<i>Aldorfia aldorfensis</i>			X	X		X	X		X	
<i>Ambonisphaera hemicavata</i>	X						X			
<i>Atopodinium polygonale</i>				X	X	X	X			
<i>Batiacasphaera laevigata</i>						X				
<i>Bradleyella adela</i>				X			X			X
<i>Burtonia polygonais</i>							X			
<i>Caligodinium aceras</i>		X								
<i>Carpathodinium predae</i>	X		X	X		X	X	X		
<i>Chladymphorella ectotabulata</i>	X						X			
<i>Chytroisphaeridia chyrooides</i>	X	X	X	X	X	X	X	X		
<i>Cleistosphaeridium polytrichum</i>	X			X						
<i>Comparodinium aquilonium</i>		X								
<i>Ctenidodinium combazii</i>				X	X	X	X		X	
<i>Ctenidodinium cornigerum</i>						X	X		X	
<i>Ctenidodinium continuum</i>	X		X	X	X	X	X		X	X
<i>Ctenidodinium ornatum</i>	X		X				X			
<i>Ctenidodinium sellwoodii</i>	X			X	X	X	X		X	
<i>Ctenidodinium stauromatos</i>						X				
<i>Ctenidodinium tenellum</i>							X			
<i>Diacanthum? filapicatum</i>				X			X			
<i>Dapcodinium holotabulatum</i>		X								
<i>Dichadogonyaulax stauromata</i>							X			
<i>Dinaurelia pyrgos</i>						X				
<i>Dissiliodinium caddaense</i>										X
<i>Dissiliodinium erymnoteichos</i>				X	X		X			
<i>Dissiliodinium giganteum</i>					X		X		X	
<i>Dissiliodinium? hocneratum</i>	X			X	X	X	X			
<i>Dissiliodinium minimum</i>									X	
<i>Dissiliodinium omentum</i>									X	
<i>Dissiliodinium primum</i>									X	
<i>Dissiliodinium williei</i>					X					
<i>Durotrigia daveyi</i>	X			X		X			X	
N=	10	4	5	14	10	14	20	3	11	3
Geographic locations:	B	C	G ₁	E	P	F	G ₂	I	M	A

onwards the land area was progressively broken and transgressed as the Amerasia and Eurasia oceanic basins opened (Embry, 1993). However, as discussed in Smelror (1993), some paleogeographic barriers have been questioned and the hypothesis of a Crockerland is debated (Gilmullina et al., 2022; Pointon et al., 2023).

For the other regions considered in the present study the calculations of dinoflagellate cyst similarity to the Barents Sea assemblages are rather uniform and vary from 0.31 (Poland) to 0.44 (France, Morocco). As shown in Table 4 the Simpson coefficient scores for England and France towards the other geographic areas show a larger variation. A relatively high similarity is recorded between the dinoflagellate cyst assemblages in England and France, with a score of 0.71. The highest score of 0.89 is, however, recorded for the similarity between England and Germany (Fig. 9).

In their study of Late Bajocian-Late Callovian dinoflagellate cysts from the Central Alborz Mountains in northern Iran, Ghasemi-Nejad et al. (2012) concluded that the recovered assemblages, as the ammonite fauna, show close biogeographic relations to Northwest Europe and northwestern Tethys. Calculations of the Simpson Coefficient from the Late Bajocian-Early Bathonian dinoflagellate cysts of 0.56 for the biotal similarities between Iran and Germany and 0.50 between Iran and France, partly support this conclusion. The coefficient for dinoflagellate cyst biotal similarity between Iran and the Barents Sea is 0.39. In comparison, the coefficient for the similarity of known Late Bajocian-Early Bathonian species in Iran and Australia is 0.11 (Table 4, Fig. 9).

The recorded Simpson coefficient values for the comparisons of similarities between the published Late Bajocian-Bathonian records from Australia and the other areas included in the present study are generally lower than the records for England, France and the Barents Sea (Table 4, Fig. 9). To which degree the low similarity scores attributes to

limited data from Australia remains to be tested.

We also note that the calculated Koch Index of biotal dispersity of the Barents Sea Late Bajocian-Early Bathonian dinoflagellate cyst assemblages is also rather low, and the score of 15.4 contrast the comparable calculations published for the Late Bathonian-earliest Callovian of 46.6, Early to Middle Callovian 47.6, Late Callovian 51.4 and Early Oxfordian 52.1 (Smelror, 1993). The present calculations follow the trend of increasing values of increasing overall likeness of assemblages (species lists) through the Middle and towards the onset of Late Jurassic times.

Factors controlling the production and preservation of modern organic-walled dinoflagellate cysts are surface water temperatures, salinity, access to nutrients (nitrate, phosphate), chlorophyll- α -concentrations and bottom water oxygen concentrations (Zonneveld et al., 2013). In their study based on 2405 datapoints worldwide, Zonneveld et al. (2013) found that sea-surface temperature is the parameter corresponding to the largest variance (40%) within the dataset, followed by nitrate (34%), salinity (33%), phosphate (25%) and bottom-water oxygen concentration (24%). Temperature-salinity control has been used to explain composition and diversity differences in marine faunas between the Jurassic Boreal and Tethyan Realms (Hallam, 1969). Paleoclimate records in the Mesozoic strata of Svalbard reveals periodic cooling-warming episodes during the Middle Jurassic to Early Cretaceous, and periods with climatic cycles generated (glacio-?) eustatic sea-level variations probably lead to changes in global oceanic circulation (Smyrak-Sikora et al., 2025). Variations of temperature, salinity and inflow of nutrients into the basins and gateways influenced the production of marine algae resting spores, but paleoclimatic affinities of Jurassic dinoflagellate taxa have barely been touched upon. While a warming event in the Early Bajocian was noted by Riding and Hubbard (1999), they concluded that paleoclimatic signals in the Bathonian

Table 2

Alphabetic list of species (E–M) recovered in upper Bajocian–lower Bathonian strata in the geographic areas included in the biogeographic similarity calculations: Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A).

Dinocyst registrations – Late Bajocian - 2:											
Taxa	B	C	G ₁	E	P	F	G ₂	I	M	A	
<i>Ellipsoidictyum cinctum</i>					X	X			X		
<i>Ellipsoidictyum reticulatum</i>											
<i>Endoscrinium asymmetricum</i>				X		X	X			X	
<i>Endoscrinium luridum</i>							X			X	
<i>Epiplosphaera gochti</i>									X		
<i>Escharisphaeridia pocockii</i>	X				X			X			
<i>Escharisphaeridia psilata</i>	X				X		X				
<i>Escharisphaeridia rudis</i>	X					X					
<i>Evansia alaskensis</i>	X										
<i>Evansia barentsensis</i>	X										
<i>Evansia evitti</i>	X	X				X					
<i>Evansia perireiculata</i>	X		X								
<i>Fentonia bjarkei</i>	X										
<i>Fromea tornatilis</i>	X						X				
<i>Glomodinium tripartitum</i>		X									
<i>Gonyaulacysta jurassica</i>	X			X		X		X	X	X	
<i>Gonyaulacysta pectinifera</i>						X	X		X		
<i>Heslertonia</i> spp.	X										
<i>Jansonia psilata</i>							X				
<i>Kallosphaeridium capulatum</i>					X						
<i>Kallosphaeridium hypornatum</i>					X	X	X			X	
<i>Kallosphaeridium prausii</i>					X						
<i>Kalyptea stegasta</i>				X	X	X	X	X	X		
<i>Korystocysta gochti</i>					X		X		X		
<i>Korystocysta aldridgei</i>											
<i>Korystocysta pachyderma</i>					X		X		X		
<i>Leptodinium subtile</i>				X	X						
<i>Lithodinia caytonensis</i>					X			X			
<i>Lithodinia deflandrei</i>		X					X				
<i>Lithodinia jurassica</i>					X		X				
<i>Mancodinium semitabulatum</i>							X			X	
<i>Meiourugonyaulax borealis</i>							X				
<i>Meiourugonyaulax callomoni</i>							X				
<i>Meiourugonyaulax caytonensis</i>	X			X			X		X	X	
<i>Meiourugonyaulax deflandrei</i>										X	
<i>Meiourugonyaulax straussi</i>										X	
<i>Meiourugonyaulax valensii</i>				X	X	X	X	X	X		
<i>Mendicodinium groenlandicum</i>	X				X	X		X		X	
<i>Mendicodinium reticulatum</i>			X			X				X	
<i>Microdinium opacum</i>		X									
N=	13	4	2	6	14	11	17	6	9	10	
Geographic locations:	B	C	G ₁	E	P	F	G ₂	I	M	A	

appear to be difficult to interpret consistently.

In a study of Middle to Late Jurassic paleoclimate and paleo-oceanographic trends in the Euro-Boreal region Vickers et al. (2022) used carbon-isotope and oxygen-isotope signals from analyses of Middle and Late Jurassic ammonites from East Greenland as primary geochemical signal of paleo-seawater. They argued that since Europe was a series of restricted basins during the Jurassic, the basins were likely gone through strong changes in salinity, connected to changes in paleocurrent directions and climatic induced changes in the hydrological cycle. These changes make it difficult to recognize clear climatic and paleo-oceanographic signals (Vickers et al., 2022). No specific conclusions were made for the Late Bajocian-Bathonian time interval, but Vickers et al. (2022) concluded that the $\delta^{18}O_{\text{bel}}$ values from Subboreal Province at Middle to Late Jurassic transition is characterized by more positive values consistent with cooling, and that this trend, together with ammonite faunal distribution patterns, indicate a strengthening of southward-flowing cold currents from the Boreal Realm into the Subboreal Province. This paleo-oceanographic pattern is in line with conclusions derived from the dinoflagellate cyst similarity calculations presented by Smelror (1993) and the overall trend seen when the previous records are combined with the results from the present study.

6. Conclusions

Upper Bajocian-Lower Bathonian deposits of the Fuglen Formation in borehole 7533/03-U-01 contain moderate diverse assemblages of dinoflagellate cysts. Ammonite control of the strata in the borehole allows calibrations of first and last occurrence of biostratigraphic significant dinoflagellate cyst species, including the first occurrences (FOs) of *Chlamydophorella ectotabulata*, *Evansia perireiculata* and *Sirmiodinium grossi* and the last occurrence (LO) *Durotrigia daveyi* in the Upper Bajocian Indistinctus ammonite zone. Other events based on the present record, combined with published records from the Barent Sea region, are FO of *Dichadogonyaulax sellwoodii* and the LO of *Limbicysta bjaerkei* in the Late Bathonian Calyx ammonite zone.

Calculations of biotal similarities between Late Bajocian-Bathonian dinoflagellate cyst assemblages from Barents Sea and contemporaneous assemblages in the Canadian Arctic, East Greenland, NW and Central Europe, Iran, Morocco and Australia indicate limited biogeographic connections compared to in the subsequent Late Bathonian to Early Oxfordian times. Species diversities in the areas included in the present study are generally low compared to diversities known from the same regions in Late Bathonian-early Callovian times. The Late Bajocian-Early Bathonian assemblages from the Barents Sea show closest connections with assemblages from East Greenland. Higher degrees of similarities have been calculated among dinoflagellate cyst

Table 3

Alphabetic list of species (N–W) recovered in upper Bajocian–lower Bathonian strata in the geographic areas geographic areas included in the biogeographic similarity calculations: Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A).

Dinocyst registrations – Late Bajocian - Early Bathonian - 3:										
Taxa	B	C	G ₁	E	P	F	G ₂	I	M	A
<i>Nannoceratopsis ambonis</i>					X	X	X			
<i>Nannoceratopsis deflandrei</i>										
<i>Nannoceratopsis evae</i>					X		X			
<i>Nannoceratopsis gracilis</i>	X	X	X	X	X	X	X			
<i>Nannoceratopsis pellucida</i>	X	X	X	X		X	X	X		
<i>Nannoceratopsis plegas</i>							X	X		
<i>Nannoceratopsis raunsgaardi</i>					X			X		
<i>Nannoceratopsis senex</i>		X	X		X	X		X		
<i>Nannoceratopsis spiculata</i>				X	X	X	X	X		
<i>Nannoceratopsis triceras</i>					X		X			
<i>Orobodinium automobile</i>						X	X			
<i>Pareodinia ceratophora</i>	X			X	X	X	X	X	X	
<i>Pareodinia halosa</i>	X				X	X	X			X
<i>Pareodinia prolongata</i>							X	X		
<i>Parvocysta</i> spp.			X					X		
<i>Phallocysta eumekes</i>		X								
<i>Phallocysta granosa</i>										X
<i>Phallocysta elongata</i>					X		X			
<i>Plurivarvium osmingtonense</i>	X									
<i>Protobatioladinium mercieri</i>							X			
<i>Reutlingia gochti</i>						X				
<i>Rhynchodiniopsis cladophora</i>					X				X	
<i>Rhynchodiniopsis regalis</i>				X		X	X		X	
<i>Rosswangia simplex</i>						X				
<i>Scriniocassis weberi</i>		X								
<i>Sentusidinium baculatum</i>							X			
<i>Sentusidinium asymmetrum</i>						X	X			
<i>Sentusidinium pelionense</i>	X		X							
<i>Sentusidinium rioulti</i>									X	
<i>Sentusidinium sparsibarbatum</i>								X		
<i>Sentusidinium verrucosum</i>						X				
<i>Sirmiodinium grossii</i>	X		X							
<i>Sirmiodiniopsis orbis</i>	X			X		X	X			X
<i>Susadinium scrofooides</i>		X								
<i>Tubotuberella</i> spp.	X								X	
<i>Valensiella ampulla</i>							X			
<i>Valensiella dictydia</i>	X		X							
<i>Valensiella ovulum</i>	X				X	X	X		X	
<i>Valensiella vermiculata</i>									X	
<i>Valvaeodinium cocki</i>										X
<i>Valvaeodinium spinosum</i>	X			X		X	X			X
<i>Valvaeodinium spongiosum</i>						X				
<i>Valvaeodinium vermipellitum</i>						X	X			
<i>Wanaea acollaris</i>	X			X	X		X		X	
<i>Wanaea enoda /verrucosa</i>										X
<i>Wanaea lacuna</i>										X
<i>Wanaea indotata</i>						X				
<i>Willeidinium baiocassinum</i>						X				
N =	13	6	7	8	13	20	22	9	8	7
N1 + N2 + N3	36	14	14	28	37	45	59	18	18	20
Geographic areas:	B	C	G ₁	E	P	F	G ₂	I	M	A

Sources: **B (Barents Sea)**: Present study; **C (Arctic Canada)**: Davies (1983); **G₁ (East Greenland)**: Fensome (1979), Koppelhus and Hansen (2003), Larsen et al. (2003); **E (England)**: Riding (1987), Riding and Thomas (1992); **P (Poland)**: Poulsen (1996, 1998), Gedl (2013); **F (France)**: Rauscher and Schmitt (1990), Feist-Burkhardt and Monteil (1997); **G₂ (Germany)**: Prauss (1989), Wiggan et al. (2017); **I (Iran)**: Ibrahim et al. (2003), Ghasemi-Nejad et al. (2012), Mafi et al. (2013); **A (Australia)**: Riding et al. (2010), Mantle and Riding (2012)



Fig. 8. Bajocian paleogeographic map with approximate locations of the study areas included. Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A). The mollweide map of Earth 170 million years ago, overlaid by a black outline of present-day countries in their respective locations, is by [Scotese et al. \(2024\)](#), CC BY 4.0.

Table 4

Quantitative estimates of dinoflagellate cysts assemblage variations for the Barents Sea, England, France and Australia towards the other areas included in the study: Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A). The calculations are based on the list of species presented in [Tables 1–3](#).

Locations:	B	C	G ₁	E	P	F	G ₂	I	M	A
Barents Sea		0.21	0.50	0.39	0.31	0.42	0.44	0.39	0.44	0.35
England	0.50		0.43		0.54	0.71	0.89	0.44	0.72	0.35
France	0.44	0.36	0.57	0.71	0.68		0.68	0.50	0.67	0.40
Australia	0.35	0	0.14	0.30	0.20	0.40	0.50	0.11	0.17	

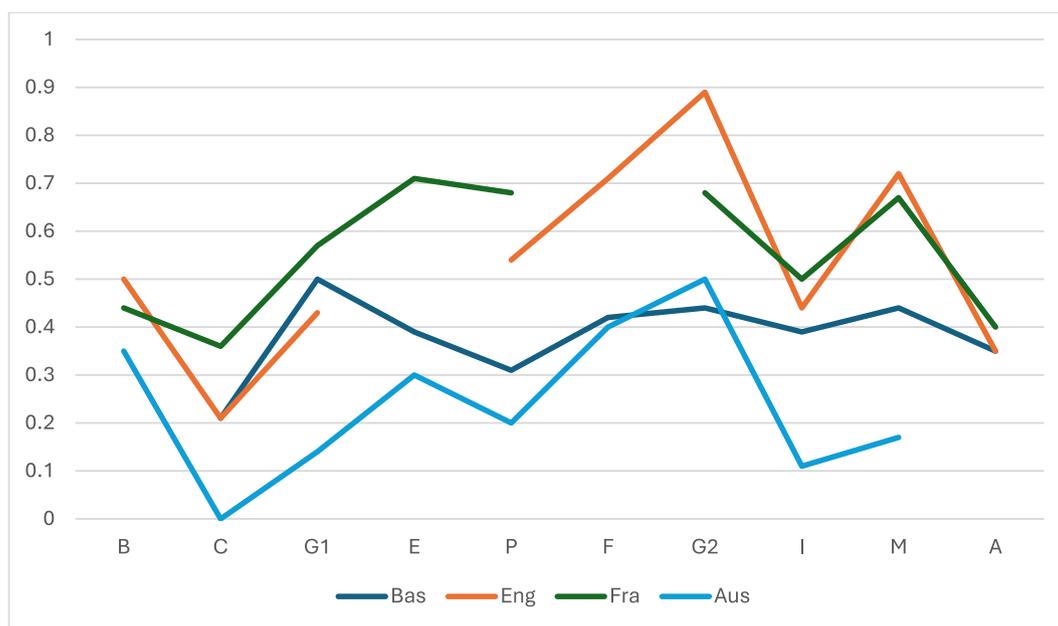


Fig. 9. Illustration of quantitative estimates of Late Bajocian-Early Bathonian dinoflagellate cysts assemblage variations for the Barents Sea (Bas, blue line), England (Eng, red line), France (Fra, dark blue line) and Australia (Aus, green line) towards the other areas included in the study: Barents Sea (B), Arctic Canada (C), East Greenland (G₁), England (E), Poland (P), France (F), Germany (G₂), Iran (I), Morocco (M) and Australia (A). The calculations are based on the list of species presented in [Tables 1–3](#). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

assemblages in England, France and Germany. The Late Bajocian-Early Bathonian biogeographic differences, and the following Late Bathonian-Early Oxfordian increase in biotal similarities, coincide the advent of breakdowns of land-barriers, major transgressions, radiation of cyst-producing dinoflagellates and migration of marine biotas between Boreal, Sub-Boreal and Tethyan seas.

Declaration of competing interest

There are no conflicts of interest linked to the submitted manuscript on Neoproterozoic carbon cenospheres.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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