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Palaeoenvironmental reconstruction and biostratigraphy with marine palynomorphs of the Plio–Pleistocene in Tjörnes, Northern Iceland

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ABSTRACT

Deposits from the Tjörnes Peninsula in northern Iceland enable the assessment of past ocean currents and the influence of the nearby island. Most palaeoecological studies with dinoflagellate cysts from the northern and central Atlantic focus on oceanic or shelf settings and deal with outer neritic and oceanic species. Dinoflagellate cyst studies of marginal marine settings are scarce and represent only short time intervals. The Tjörnes section however accommodates 1200 m of sediments that are mainly shallow marine. The sediments are attributed to the Lower Pliocene Tjörnes beds and the overlying Upper Pliocene to Pleistocene Breidavík Group. The dinoflagellate cysts and other marine palynomorphs from 68 samples from the Tjörnes beds and 20 samples from the Breidavík Group are studied. The deposits are divided into five dinoflagellate cyst assemblage zones (DAZ) and one barren interzone (BIZ). The changes in the assemblages proved to be independent of the changes in bathymetry of the sedimentary environment. Heterotrophic dinoflagellate cysts dominate in DAZ1. An abrupt impoverishment in species diversity is observed in DAZ2 when autotrophic species dominate the assemblage. Slightly preceding the entrance of Pacific molluscs in the area in unit 14 of the *Serripes* Zone, heterotrophic species (unit 12/13) re-enter the area in DAZ3. The marked decrease and return of the heterotrophic species does not relate to conditions of preservation, but may result from the loss of nutrients. The upper part of DAZ1 and the base of DAZ3 reflect major changes in the palaeoceanography and span a period during which the polar front may have moved temporarily from the area. The first event situated at the top of DAZ1 occurred in litholog unit 4 halfway the *Tapes* Zone between circa 5 and 4.8 Ma. The second event at the top of litholog unit 12 around 4.5 Ma has been linked to the shoaling of the Central American Seaway. Heterotrophic dinoflagellates disappear almost completely from the area during the deposition of the Pleistocene Breidavík Group (DAZ4-5). A transition from a heterotrophic dominated assemblage to an autotrophic dominated assemblage is observed in the Hörgi Formation (DAZ4a). An assemblage dominated by autotrophic cold water species, comparable to the present-day assemblage of the area north of Iceland, occurs from unit 10 in the Pleistocene Svarthamar Member on (DAZ5). This study underscores that the distribution of temperature sensitive dinoflagellate cysts is influenced by the availability of nutrients and changes in ocean currents.

1. Introduction

A shallow sedimentary basin formed during the Pliocene and Pleistocene near the Tjörnes Fracture Zone, a fault zone related to the Mid Atlantic Ridge passing through Iceland (Fig. 1A). The basin was interpreted as a fjord open to the north with sediment supply from the land in the south (Strauch, 1963). Shallow marine sediments as well as terrestrial sediments and lava flows accumulated and resulted in a 1200 m thick sequence. During the Pleistocene the Tjörnes basin was uplifted as a horst structure and the beds are now exposed in the coastal cliffs. The oldest part of the sequence is the Lower Pliocene Tjörnes beds consisting mainly of marine sandstones alternating with terrestrial lignites. Lava flows are of minor importance. The Höskuldsvík lavas separate the Tjörnes beds from the overlying Upper Pliocene to Pleistocene Breidavík Group (Figs. 1B and 2). This group encompasses fourteen glacial–interglacial cycles consisting of glacial till sediments, late-glacial outwash gravels and interglacial marine sediments (Fig. 2; Eiríksson, 1981). Recent lava flows cover the Quaternary glacial–interglacial deposits.

The central position of the Tjörnes cliffs in the northern Atlantic and their easy accessibility make them a unique location for palaeontological, palaeoclimatical and palaeoceanographical studies. Bárdarson (1925) described in the Tjörnes beds 25 shell bearing marine units (1–25) and 10 lignites (A–J), and divided the sequence into three mollusc taxon-range biozones: the *Tapes* Zone, the *Mactra* Zone and the *Serripes* Zone (Figs. 1 and 2). Other palaeontological studies focussed on marine molluscs (Strauch, 1972; Norton, 1975, 1977; Gladenkov et al., 1980; McCoy, 2007; Símonarson and Eiríksson, 2008; Símonarson and Leifsdóttir, 2008), ostracods (Cronin, 1991) and dinoflagellate cysts (dinocysts)

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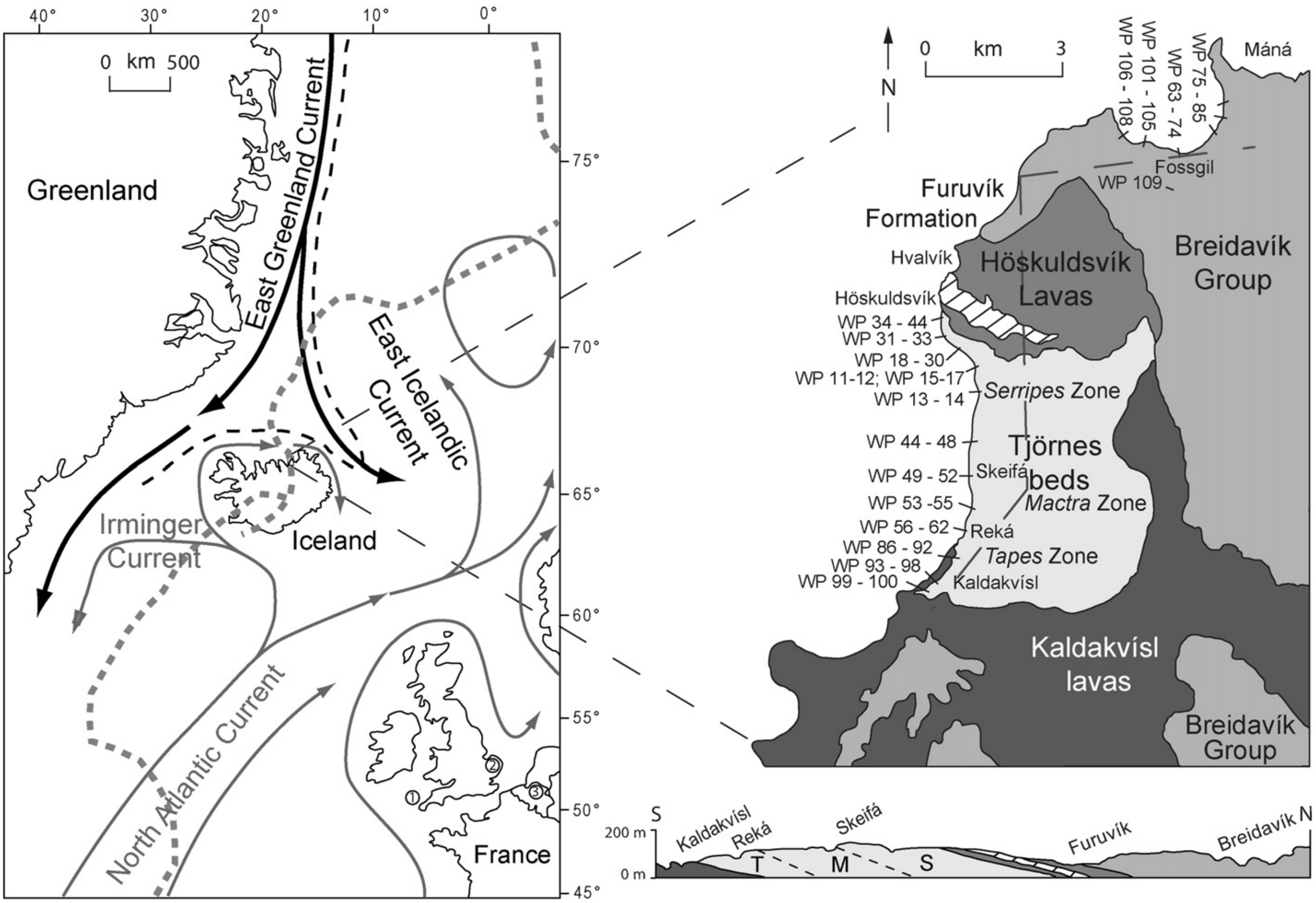


Fig. 1. A: Overview of the present-day surface currents of the North Atlantic Ocean with indication of the study area in northern Iceland. Warm water currents are indicated with thin grey arrows, cold water currents with broader black arrows (adapted from Marret et al., 2004). The Mid-Atlantic Ridge is indicated with a thick, grey dotted line. The position of the Polar Front around Iceland (black dashed line) is after Knudsen and Eiríksson (2002). The location of the cross section is indicated by a dashed, dark grey line. The encircled numbers 1–3 indicate shallow marine Pliocene deposits: (1) the St. Erth Beds, (2) the England Crags and (3) the Belgian Pliocene sands. B: Geological map of the study area, located on the western part of the Tjörnes Peninsula. An approximately north–south cross section of the area is given (dashed line on map), modified and simplified after Einarsson et al. (1967) and Eiríksson (1981), together with the sample locations and numbers.

(Verhoeven et al., 2011; Verhoeven and Louwye, 2012). Cronin (1991) recorded foraminifers but these proved difficult to extract from the consolidated siliciclastic matrix. Akhmetiev et al. (1978) made a preliminary study on the diatoms from lignites C and F, respectively in the *Tapes* Zone and the *Mactra* Zone. The diatoms however are poorly preserved, of mixed age and ecological preference and therefore the analysis was not pursued. Past sea water temperatures of the Tjörnes beds were estimated with oxygen isotopes (Buchardt and Símonarson, 2003). Eiríksson (1981, 1985) studied in detail the sedimentology of the Breidavík Group.

The organic-walled dinocysts from the Tjörnes beds and the overlying Breidavík Group were studied by Verhoeven et al. (2011) and allowed a more refined age attribution than the earlier studies (Einarsson et al., 1967; Albertsson, 1978; Buchardt and Símonarson, 2003; Símonarson and Eiríksson, 2008) and the reconstruction of the depositional history. It was established that the base of the Tjörnes beds was deposited during post-Miocene times and the top of the *Serripes* Zone around 4.0 Ma (Fig. 2). The Pacific molluscan invasion around the *Mactra*/*Serripes* Zone boundary is dated c. 4.5 Ma. Two major hiatuses of c. 700 ka occur, one between the top of the *Serripes* Zone and the Höskuldsvík lavas and one between the Furuvík Formation and the Hörgi Formation, the last formation being dated around 2.2 Ma (Fig. 2). The rest of the Breidavík Group extends from then on to recent times. The Tjörnes beds and Breidavík Group also contain pollen and spores, the study of which contributed to our knowledge of the water depth and the coastal landscape (Verhoeven et al., 2013). Only a few other shallow marine deposits of comparable age and holding well-preserved dinocyst assemblages are known from the northern and central Atlantic (Figs. 1A and 2). The Tjörnes assemblages have been compared with those of the St. Erth Beds in southwest England (±2.1–1.95 Ma), several crag deposits in southeast England (4.4–1.8 Ma) and the Belgian Pliocene sands (5–2.76 Ma).

The present study details the marine palynomorph record from the Tjörnes Peninsula and presents a new biozonation for the most complete Neogene and Pleistocene sedimentary sequence onshore Iceland. The marine palynomorph record was furthermore interpreted in terms of palaeoecological preference of dinocysts to gain further insight in the palaeoceanographical and palaeoclimatological changes in the northern Atlantic realm.

2. Previous palaeoenvironmental studies

A combined sedimentological/malacological study of the Tjörnes beds by Buchardt and Símonarson (2003) indicated a slightly fluctuating sea level during deposition of the *Tapes* Zone and the lower part of the *Mactra* Zone. Sediment supply was more or less in sync with the subsidence rate and intertidal sandstones and beach gravels alternating with lignites, remnants of coastal marshes, were deposited. Strong bottom currents transported molluscan shells of deeper water to the coastal area as revealed by the allochthonous taphocoenoses of epi- and infaunal molluscs present in the entire Tjörnes beds (Norton, 1975).

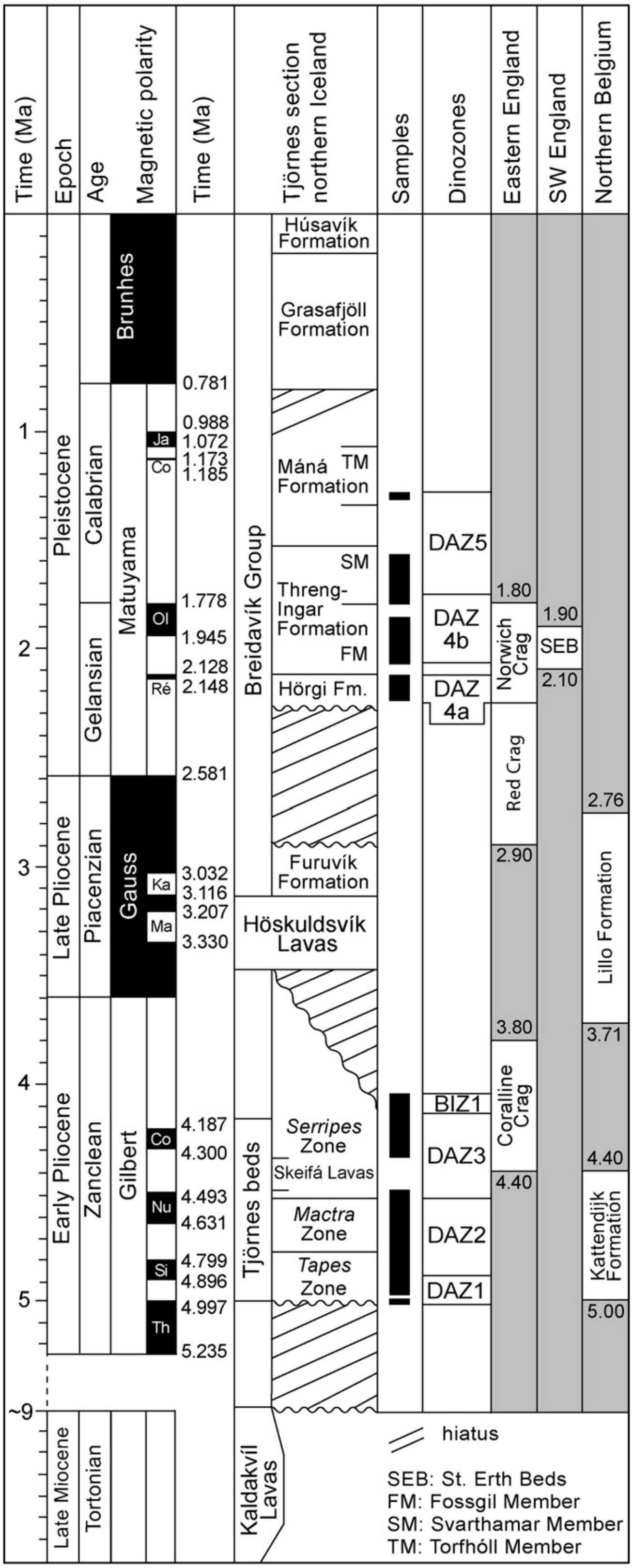


Fig. 2. Stratigraphic model of the Tjörnes section with indication of the sampled intervals (modified after Verhoeven et al., 2011). The stratigraphical position of shallow marine sediments from eastern England (Head, 1996, 1998a,b; De Schepper et al., 2009), southwest England (Head, 1993) and northern Belgium (De Schepper et al., 2009) are given.

The low-diversity and monotonous molluscan assemblages in the *Tapes* and *Mactra* Zones are indicative of a coast entirely open to the sea and a deep sub-littoral depositional environment. Small numbers of Pacific molluscs such as *Mytilus edulis*, *Modiolus modiolus* and *Zirfaea crispata* invade the depositional area during deposition of the *Tapes* and *Mactra* Zones (Fig. 5; Gladenkov et al., 1980; Buchardt and Símonarson, 2003). These early migrations were possible as the Bering Strait began to open around 5.5–5.4 Ma (Símonarson et al., 1998; Marincovich and Gladenkov, 1999; Marincovich, 2000; Gladenkov et al., 2002; Símonarson and Eiríksson, 2008).

A significant deepening of the depositional area is observed in the upper part of the *Mactra* Zone until the upper part of the *Serripes* Zone as indicated by the progressively more diverse and new molluscan fauna characteristic for the *Serripes* Zone (Norton, 1975). At the base of the *Serripes* Zone a major influx (25% of the assemblage) of sublittoral Pacific molluscs such as *Serripes groenlandicus* and *Macoma calcarea* occurs (Bárdarson, 1925; Norton, 1975, 1977; Gladenkov et al., 1980; Símonarson and Eiríksson, 2008). The invasion is linked to the shoaling of the Central American Seaway around 4.5 Ma and led to the introduction of Pacific water through the Bering Strait into the Atlantic realm (Verhoeven et al., 2011). The introduction of many Arctic bivalves in the Tjörnes area is however not indicative of a sudden cooling, for the O^{16}/O^{18} record does not show such an event (Buchardt and Símonarson, 2003). It has been suggested that the Arctic Ocean acted as a filter, allowing only cold water molluscs to migrate to the Atlantic (Einarsson et al., 1967; Símonarson and Eiríksson, 2008). Furthermore, new entrances of Atlantic Boreal and Lusitanian species, probably brought in by the Gulf Stream, are noted in the *Serripes* Zone (Bárdarson, 1925). The open coast setting during deposition of the *Tapes* and *Mactra* Zones was replaced in the *Serripes* Zone by a more sheltered and deeper water basin in which a wide range of molluscan communities thrived (Norton, 1975). The sedimentary environment became estuarine and intertidal in the upper part of the *Serripes* Zone.

3. Material and method

3.1. Palynological preparation

A total of 68 samples from the Tjörnes beds and 20 samples from the Breidavík Group were analysed for dinocysts, pollen and spores (Figs. 1B and 2). Deposits from four interglacial periods from the Breidavík Group were studied: the Hörgi Formation, the Fossgil Member, the Svarthamar Member and the Torfhóll Member (Fig. 2). Every bed of the Tjörnes beds as defined by Bárdarson (1925) was sampled at least once, except units J and 25 (Table 1a). The average sampling interval was 6.5 m. Samples are taken in vertical transects out of the cliffs. When the exact allocation to a certain Bárdarson unit was ambiguous, an interpolated position was taken. For example, the notation 15/16 comprehends a sample situated in between two distinct mollusc accumulation layers attributed respectively to unit 15 and to unit 16 (Table 1a). Quite large samples of minimal 40 to 50 g were mechanically crushed with a mortar into pieces of c. 0.5 cm and oven dried for 24 h at 58 °C. One *Lycopodium clavatum* tablet (batch 483216; $n = 18583 \pm 1708$) was added before the chemical treatment for the calculation of absolute concentration of palynomorphs. The marine sediments were treated according to the standard maceration procedure involving demineralisation with 2 M cold HCl (6.1%) followed by 40% cold HF for the removal of carbonates and silicates respectively (Louwye et al., 2007). Repeated cycles of the acid treatment proved necessary for the dissolution of the silicates and the newly formed fluorosilicates. The residues were sieved on a 10 μm nylon mesh, stained with Safranine O and mounted with glycerol gelatine on slides. Lignites were processed following the standard Erdtmann maceration protocol for pollen analysis (Fægri and Iversen, 1989). Only small samples of c. 2 g were oven dried, treated with 10% KOH and an acetolysis mixture (9/10 H_2SO_4 and 1/10 $C_4H_6O_3$). The lignite residues were mounted on fixed slides without sieving and staining. Microscope work was carried out on a Zeiss®

Table 1

a: Relative abundances of dinocysts, acritarchs and other palynomorphs from the Tjörnes section. Lithology: L: lignite, S: sandstone, CS: coarse grained sandstone, M: mudstone, W: wood, P: plant remains, SH: shell bed, C: conglomerate.

						Laboratory						Dinoflagellate cysts																															
Stratigraphy and mollusc biozones		G.P.S. Way Point; sample number	Bårdarsons Beds	Thickness, m	Sediment	Standard treatment (HCl, HF, HCl)	KOH, Acetolysis	Heavy liquid separation. ZnCl2	# *Lycopodium clavatum* tablets (batch 483216, x=18583 +/- 1708)	Dry weight sediment	*Lycopodium clavatum* (spike)	Dinocyst sp. indet.	*Achomosphaera* sp.	*Amiculosphaera umbraculum*	*Barssidinium pliocenicum*	*Batiacasphaera hirsuta*	*Batiacasphaera minuta*	*Bitectatodinium tepikiense*	*Bitectatodinium? serratum*	*Brigantedinium cariacoense*	*Brigantedinium simplex*	*Brigantedinium* sp.	*Capisocysta lyellii*	*Cristadinium* sp.	*Echinidinium euaxum*	*Echinidinium karaense*	*Echinidinium* sp.	*Filisphaera filifera* subsp. *filifera*	*Habibacysta tectata*	*Impagidinium aculeatum*	*Impagidinium patulum*	*Impagidinium plicatum*	*Impagidinium* sp.	*Islandinium minutum*	*Lejeunecysta catomus*	*Lejeunecysta mariae*	*Lejeunecysta oliva*	*Lejeunecysta sabrina*	*Lejeunecysta* sp.	*Lingulodinium machaerophorum*	*Melitasphaeridium choanophorum*	*Nematosphaeropsis labyrinthus*	*O. centrocarpum* sensu W. & D. (1966)	*O. centro.* sensu W. & D. short processes
Breidavík Group	Torfhóll Member	WP 82	14	889.8	S	x			1	55.6	587	14						7.1																													5	7
			WP 83	14	888.5	M	x			1	54.4	1185							5																											
		WP 84	14	883.5	M	x			1	50.7	1360	2.8						7.4				2.8					1.5													1			25	
		WP 85	14	878.9	M	x			1	63.1	307	1.2	0.3					3.6			0.3	1.6									0.3			0									2	
	Svarthamar Member	WP 77	12	835.0	C	x			1	63.8	565	1.1	0.6					23																	8						0			0	
		WP 69	10	823.4	M	x			1	44.3	190	1.2						0.8																	1									1	0
		WP 70	10	819.8	M	x			1	54.2	281	2.9	1.4					10				0.8																				0			6	
		WP 71	10	817.2	M	x			1	46.6	2643	13						23											3.2													6		3	3	
		WP 73	8	816.3	M	x			1	66.7	4227	5																																	5
		WP 68	8	813.0	S	x			1	53.1	3848	23	14	4.5																										10				
	Fossgil	WP 67		782.0	M	x			1	58.1	1347																																	
		WP 109		778.0	M	x			1	62.3	2242	76																																
	Hörgi Formation	WP 101		769.0	M	x			1	48.0	2697	15	2.4																											7				
		WP 108		765.0	S	x			1	56.9	1506	32	8.5		5.7							1.1							1.1							1.1				1			
		WP 102		762.1	M	x			1	48.5	2471	25	25																														
		WP 107		758.0	S	x			1	58.6	833	22			3.2	3.2																										2		
		WP 103		753.0	M	x			1	41.9	1072	19															4.8												4.8	19				
		WP 104		752.5	M	x			1	54.6	1161	22	3.7		7.5																									4				
		WP 106		750.0	S	x			1	52.1	450	2.9	5.9		8.8	12									2.9																	6	3			
		WP 105		744.0	M	x			1	40.7	1529	9.7																											10				
Tjörnes beds	*Serripes* Zone	WP 43	24	478.0	CS,W	x			1	39.1	1716																																	
		WP 40	I	477.6	M	x			1	60.0	3864																																	
		WP 42	H	476.7	M	x			1	48.6	1005																																	
		WP 38	H	462.8	CS,W	x			1	72.3	2003																																	
		WP 37	G	452.6	M	x			1	41.8	895																																	
		WP 36	23	449.8	SH	x			1	43.6	1411																																	
		WP 31	22/23	447.0	CS	x			1	63.6	1187																																	
		WP 27	22	442.6	S	x			1	37.8	2361	6.3			13						6.3	19			31												6.3								
		WP 28	21/22	439.4	S	x			1	59.4	2137	1.2	12		18		1.2					1.6	4.8					19									1.2								
		WP 32	?	439.3	S	x			1	51.6	204																																	
		WP 24	21/22	427.2	S	x		x	1	62.2	1474	4.8			63		1			1.9					4.8			8.6								1								
		WP 33	?	426.5	SH	x			1	62.1	2489	2.9			2.9					1.5	4.4	29			7.4			7.4												1.5					
		WP 25	21	424.8	SH	x		x	1	66.5	3992	22	6.9		1.7						1.7	3.4			13			1.3								1.7						2	
		WP 26	20/21	424.4	S	x			1	52.1	2375	1.5	1.5		23		1.5			1.5	1.5	20			3.3			3.3												1.5					
		WP 23	20	423.7	SH	x		x	1	50.0	1269	13	1.7		15		3.4		0.9		1.7	9.5			16												5.2								
		WP 22	19/20	422.9	S	x		x	1	39.2	764	0.3		0.3	2.4	0.7	1.5		0.3	2.4		20		0.3	12			0.7								2.1			1.2				0	
		WP 21	19	422.2	SH	x		x	1	82.8	929	8			27	0.4			1.9	0.7	1.4	1.6		0.7	0.7			2.5											0.4					
		WP 20	18/19	420.0	S	x			1	49.0	2253	4			18	2	1.3					24		3.3	25	0.7		2								0.7								
		WP 19	18	417.6	SH	x		x	1	40.3	1262	24			14			3.4				3.4						3.4					3.4				3							
		WP 18	17/18	415.8	S	x			1	52.6	1261	5.3	0.3	0.3	7.3		13	0.3	0.3	2.2	2.2	21		1.4	2.7			5.3									1	0.8	0.8					
		WP 17	17/18	406.5	S	x		x	1	47.1	1176	12	3.8		24							12			19			12																	
		WP 16	17	402.2	S	x		x	1	53.5	2397	7.1	1.8		8.9					1.8	3.6	21		1.8	17			3.6								1.8		1.8	1.8					
		WP 3	16	379.3	SH	x			1	44.1	1383																																	
		WP 4	15/16	375.8	S	x			1	48.7	617	2.7	0.9	16	0.7	0.3	6.4				1.5	8.2			7.9			5.2							2	1.2	1	0.3						
		WP 5	15	368.8	SH	x			1	50.5	1808	2.7		12	0.9		11				5.2	31		0.9	1.4			0.9					0.9			0.9			0.9					
		WP 6	14/15	367.9	S	x		x	1	67.8	488	3.5	7.3	1.8	3.5		30		3.5	0.7	1.2	1.8						1.2	1.2												2	1			
		WP 7	14	363.9	SH	x			1	53.9	591		1.5				5.3					32			16			5.3																	
		WP 8	13/14	360.1	S	x			1	45.2	191	3.4	36		5.4						0.5	0.5			0.5										0	1			0.5					
		WP 9	13	359.2	S	x			1	70.5	151	5.6	8.1		1.2	0.2	1.2			0.5	0.5	9.3			16									0	3.7	0	0.2	1.2		0	0		
		WP10	12/13	357.2	S	x			1	72.1	361	6.3	3.2		1.6	1.6						4.8						27	3.2						3.2			4.8	3				
	Mactra Zone	WP 11	12	356.0	S	x			1	56.0	1393				2																	2													6	
		WP 12	11	350.0	SH	x		x	1	51.7	3139			1	1												3																	
		WP 13	11	340.0	CS	x			1	41.7	3572	2.8	0.9		0.9	0.9													0.9											4			67	6
		WP 14	11	330.0	S	x			1	69.0	3676	3.8					15																											
		WP 44	10	295.0	SH	x			1	34.4	253					13	13													13	13													13		
		WP 45	10	291.2	S	x			1	52.3	288	6.7	6.7		6.7	2																												
		WP 48	9	286.1	SH	x			1	41.6	1029	17				33													33	17														
		WP 46	9	277.8	SH	x			1	57.2	1282					18																											
		WP 47	?	272.0	SH	x			1	46.8	184					6																											
		WP 49	F	260.5	L		x		1	2.4	17																																	
		WP 50	F	252.0	M,P	x			1	33.8	5																																	
		WP 51	E	244.0	CS	x		x	1	50.0	478																																	
		WP 52	8	230.0	SH	x		x	1	74.3	656	3.8				38													7.7															
		WP 53	D	211.1	M,W	x			1	3.2	128	2.5	5		2.5														58															
		WP 56	D	207.9	L	x			1	3.5	35																																	
		WP 54	D	203.7	L	x			1	34.2	77	5																																
		WP 57	7	195.3	S	x		x	1	46.8	566																																	
		Wp 58	7	188.0	M,W	x			1	3.4	1080																																	
		WP 55	7	185.0	S	x		x	1	38.2	25	5.4	6.4		2.1							0.7			2.1				2.7			0.7			1									1
		WP 59	6	183.0	S	x		x	1	42.8	428	2.6	3.8		1.7							3.2			5.2				6.9		0.3		0.3		0						0			
	Tapes Zone	WP 60	C	145.0	L		x		1	2.4	51																																	
		WP 61	C	144.0	S	x		x	1	31.7	1248	38			7.7									3.8																				
		WP 62	5	129.0	S	x		x	1	43.9	1620						1																											
		WP 86	4	83.2	S	x		x	1	47.7	1306	5			7.5		68	5											2.5												3				
		WP 87	4	78.0	S	x		x	1	49.7	846				3.8														4															
		WP 88	4	69.0	S	x		x	1	49.5	697				27		13					6.7														6.7								
		WP 89	B	68.0	L		x		1	2.4	2																																	
		WP 90	3	66.2	S	x		x	1	49.9	149	5.7			0.9		5.7			0.9	1.9	14			22												2.8	1			1				
		WP 91	3	65.1	S	x		x	1	38.0	531	1					3.3			3.3		2			6.7				6.7																
		WP 92	c	45.0	L		x		1	2.5	6																																	
		WP 93	2, b	36.2	L		x		1	2.6	6																																	
		WP 94	2	35.3	S	x		x	1	48.7	343	5.7			42		3.7	0.6		1.2		5.9						1.2	0.3					1	2.8	1		0.3					
		WP 95	2	29.4	S	x		x	1	38.4	1850							4				1							2																
		WP 96	2, a	22.4	L		x		1	2.4	8																																	
		WP 97	2	20.4	S	x		x	1	32.5	222	5.4			23					3.6		13			17			3.6	1.8						4	1.8								
		WP 98	2	13.7	S	x			1	60.2	516	11				5.6									17				11						6		5.6				6				
		WP 100	1	5.0	S	x			1	42.7	38	14			46													2.9																	
		WP 99	A	3.0	L		x		1	4.0	10																																	

(*continued on next page*)

Table 1 (*continued*)

						Laboratory						Dinoflagellate cysts																													Other palynom.					
Stratigraphy and mollusc biozones		G.P.S. Way Point; sample number	Bårdarsons Beds	Thickness, m	Sediment	Standard treatment (HCl, HF, HCl)	KOH, Acetolysis	Heavy liquid separation. ZnCl2	# *Lycopodium clavatum* tablets (batch 483216, x=18583 +/- 1708)	Dry weight sediment	*Lycopodium clavatum* (spike)	*Operculodinium centrocarpum* s.s.	*Operculodinium? eirikianum*	*Operculodinium* sp.	*Operculodinium tegillatum*	cyst of *Pentapharsodinium dalei*	*Quinquecuspis concreta*	*Reticulatosphaera actinocoronata*	*Scrippsiella trifida*	*Selenopemphix brevispinosa*	*Selenopemphix conspicua*	*Selenopemphix islandensis*	*Selenopemphix dionaeacysta*	*Selenopemphix nephroides*	*Selenopemphix quanta*	*Selenopemphix* sp.	*Spiniferites bulloideus*	*Spiniferites delicatus*	*Spiniferites elongatus*	*Spiniferites membranaceus*	*Spiniferites mirabilis*	*Spiniferites ramosus*	*Spiniferites* sp. indet.	*Tectatodinium pellitum*	*Trinovantedinium applanatum*	*Trinovantedinium ferugnomatum*	*Trinovantedinium glorianum*	*Trinovantedinium harpagonium*	*Trinovantedinium* sp.	*Tuberculodinium vancampoae*	*Crustacean* egg	Foram lingings: planispiral	Foram lingings: trochospiral	Invertibrate mandibles	*Tasmanites* sp.	Total non acritarch marine
Breidavík Group	Torfhöll Member	WP 82	14	889.8	S	x			1	55.6	587					21																														
		WP 83	14	888.5	M	x			1	54.4	1185					5																														
		WP 84	14	883.5	M	x			1	50.7	1360	3				48													3			1	4													
		WP 85	14	878.9	M	x			1	63.1	307	2				83									0				3			0	2													
	Svarthamar Member	WP 77	12	835.0	C	x			1	63.8	565					65													0			0	1									1				1
		WP 69	10	823.4	M	x			1	44.3	190					83											0		5			3	6													
		WP 70	10	819.8	M	x			1	54.2	281	0				64			6										0			1	9									0				0
		WP 71	10	817.2	M	x			1	46.6	2643	35				10																	3													
		WP 73	8	816.3	M	x			1	66.7	4227	8																					1													
		WP 68	8	813.0	S	x			1	53.1	3848	36																					14									5				5
	Fossgil	WP 67		782.0	M	x			1	58.1	1347																																			
		WP 109		778.0	M	x			1	62.3	2242	12																					12													
	Hörgi Formation	WP 101		769.0	M	x			1	48.0	2697	68															1						7									1		1		2
		WP 108		765.0	S	x			1	56.9	1506	32		2		1		1					1				1		1				7					2								
		WP 102		762.1	M	x			1	48.5	2471	25						25																								25				25
		WP 107		758.0	S	x			1	58.6	833	6				5												2					10				3					8				8
		WP 103		753.0	M	x			1	41.9	1072	39	5		5																		5													
		WP 104		752.5	M	x			1	54.6	1161	5																					22													
		WP 106		750.0	S	x			1	52.1	450	15				15		6		3											3		12		3	3										
		WP 105		744.0	M	x			1	40.7	1529	77																				3														
Tjörnes beds	*Serripes* Zone	WP 43	24	478.0	CS,W	x			1	39.1	1716																																			
		WP 40	I	477.6	M	x			1	60.0	3864																																			
		WP 42	H	476.7	M	x			1	48.6	1005																																			
		WP 38	H	462.8	CS,W	x			1	72.3	2003																																			
		WP 37	G	452.6	M	x			1	41.8	895																																			
		WP 36	23	449.8	SH	x			1	43.6	1411																																			
		WP 31	22/23	447.0	CS	x			1	63.6	1187																																			
		WP 27	22	442.6	S	x			1	37.8	2361											13										6									6	##				##
		WP 28	21/22	439.4	S	x			1	59.4	2137	1			6	1						2										5	18									1				1
		WP 32	?	439.3	S	x			1	51.6	204																																			
		WP 24	21/22	427.2	S	x		x	1	62.2	1474											3		1								4	2		1		3		2			5				5
		WP 33	?	426.5	SH	x			1	62.1	2489	16				6				1		3		3								1	1		4	1	4					9	1			1
		WP 25	21	424.8	SH	x		x	1	66.5	3992	3				7				2		2											2				3		2			14				14
		WP 26	20/21	424.4	S	x			1	52.1	2375	10			3	10				5		8		3												2	5				3	71				74
		WP 23	20	423.7	SH	x		x	1	50.0	1269	4				9				2		8		1								3	3		2	2	1	1				20				20
		WP 22	19/20	422.9	S	x		x	1	39.2	764				3	23						5		1								2			1	2	1	0				10				10
		WP 21	19	422.2	SH	x		x	1	82.8	929	2			1	29						8		3								1	0		0	0	2					8				8
		WP 20	18/19	420.0	S	x			1	49.0	2253				1	5						2		1								7	1				1	2				##				##
		WP 19	18	417.6	SH	x		x	1	40.3	1262	7			7	14								1									7									24				24
		WP 18	17/18	415.8	S	x			1	52.6	1261	1			1	4	0				1	1		4	4							1	1		0	1	2					7			0.3	8
		WP 17	17/18	406.5	S	x		x	1	47.1	1176													15	4																	24				24
		WP 16	17	402.2	S	x		x	1	53.5	2397	2			2	5		2			4				2							5	4			2	2					##				##
		WP 3	16	379.3	SH	x			1	44.1	1383																																			
		WP 4	15/16	375.8	S	x			1	48.7	617	4			14	0						2	0	2								1	2		5	2	16		0			5				5
		WP 5	15	368.8	SH	x			1	50.5	1808	3			1	3	1					3		2								1			2		8					2				2
		WP 6	14/15	367.9	S	x		x	1	67.8	488	23			7	1		1		2		4										2	1		1	1		1				1			0.7	1
		WP 7	14	363.9	SH	x			1	53.9	591	26																									5					79				79
		WP 8	13/14	360.1	S	x			1	45.2	191					2		0		1	2	2	8	2	3	2						1	7		0	11										
		WP 9	13	359.2	S	x			1	70.5	151	6			0	3		2		6		1	1	1	12	1						0	4		3	0	4	1				4		0		4
		WP10	12/13	357.2	S	x			1	72.1	361	5				6				5			6							2		6	2		8	2						2			1.6	3
	Mactra Zone	WP 11	12	356.0	S	x			1	56.0	1393																															62				62
		WP 12	11	350.0	SH	x		x	1	51.7	3139				4																	1														
		WP 13	11	340.0	CS	x			1	41.7	3572	8		1		2		1														3	4											1		1
		WP 14	11	330.0	S	x			1	69.0	3676	24			27	15																4	12													
		WP 44	10	295.0	SH	x			1	34.4	253	13				25																														
		WP 45	10	291.2	S	x			1	52.3	288	2				13		7															2													
		WP 48	9	286.1	SH	x			1	41.6	1029																															33				33
		WP 46	9	277.8	SH	x			1	57.2	1282	64						18																												
		WP 47	?	272.0	SH	x			1	46.8	184	4																																		
		WP 49	F	260.5	L		x		1	2.4	17																																			
		WP 50	F	252.0	M,P	x			1	33.8	5																																			
		WP 51	E	244.0	CS	x		x	1	50.0	478																																			
		WP 52	8	230.0	SH	x		x	1	74.3	656	15																					8													
		WP 53	D	211.1	M,W	x			1	3.2	128					15		3												8		3	5													
		WP 56	D	207.9	L	x			1	3.5	35																																			
		WP 54	D	203.7	L	x			1	34.2	77									5																										
		WP 57	7	195.3	S	x		x	1	46.8	566																																			
		Wp 58	7	188.0	M,W	x			1	3.4	1080																								1											
		WP 55	7	185.0	S	x		x	1	38.2	25	18		1				5		9	1		1									3	36			3	2					7				7
		WP 59	6	183.0	S	x		x	1	42.8	428	65				2											0					1	4		0		3					15				15
	Tapes Zone	WP 60	C	145.0	L		x		1	2.4	51																																			
		WP 61	C	144.0	S	x		x	1	31.7	1248																										24					##			7.7	##
		WP 62	5	129.0	S	x		x	1	43.9	1620																																			
		WP 86	4	83.2	S	x		x	1	47.7	1306					8																	3													
		WP 87	4	78.0	S	x		x	1	49.7	846	46						5									1													4						
		WP 88	4	69.0	S	x		x	1	49.5	697	7											7													33						13				13
		WP 89	B	68.0	L		x		1	2.4	2																																			
		WP 90	3	66.2	S	x		x	1	49.9	149	8				2	11			5			6							1	1	1	2		2	5	2					2				2
		WP 91	3	65.1	S	x		x	1	38.0	531					3	7			13			7														2					63				63
		WP 92	c	45.0	L		x		1	2.5	6																																			
		WP 93	2, b	36.2	L		x		1	2.6	6																																			
		WP 94	2	35.3	S	x		x	1	48.7	343	2				8	0			4			2				0		0			2	6		1	3	6		1							
		WP 95	2	29.4	S	x		x	1	38.4	1850					3																										1				1
		WP 96	2, a	22.4	L		x		1	2.4	8																																			
		WP 97	2	20.4	S	x		x	1	32.5	222					5	4						4											4		2	2					4				4
		WP 98	2	13.7	S	x			1	60.2	516	6											11									6	6				11					44				44
		WP 100	1	5.0	S	x			1	42.7	38	9				3	6			6													6			3	6									
		WP 99	A	3.0	L		x		1	4.0	10					5																	5													

Table 1 (*continued*)

						Laboratory						Acritarchs												Indices															
Stratigraphy and mollusc biozones		G.P.S. Way Point; sample number	Bárdarsons Beds	Thickness, m	Sediment	Standard treatment (HCl, HF, HCl)	KOH, Acetolysis	Heavy liquid separation. ZnCl2	# *Lycopodium clavatum* tablets (batch 483216, x=18583 +/- 1708)	Dry weight sediment	*Lycopodium clavatum* (spike)	Acritarch sp. indet.	*Cyclopsiella? trematophora*	*Cyclopsiella* sp.	*Cymathiosphaera invaginata*	*Halodinium minor*	*Halodinium major*	*Halodinium scopaeum*	Acritarch type 1 (this study)	*Paralecaniella indentata*	Algae type A De Schepper (2006)	Algae cyst type 1 Head (1996)	Total acritarch	Shannon-Wiener Index (dinocysts)	Evenness (dinocysts)	Dinocyst conc. (# cysts/g sediment)	Terrestrial palynomorph concentration	# warm dinocyst species (n)	# cold dinocyst species (n)	W/C index (n warm / (n warm + n cold))	Heterotrophic species (n)	Autotrophic species (n)	n H / (n H + n A)	IN/ON=nIN/(nIN+nON)	N/O=nN/(nN+nO)	P (total recent pollen)	S (total recent spores)	nP/(nP + nD)	(nP+nS)/(nP+nS+nD)
Breidavík Group	Torfhóll Member	WP 82	14	889.8	S	x			1	55.6	587													0.73	0.53	7.97	0.93	0	4	0	0	2	0	1	1	1	0	0.07	0.07
		WP 83	14	888.5	M	x			1	54.4	1185													0.48	0.69	0.58	3.29	0	2	0	0	1	0	1	1	39	5	0.95	0.96
		WP 84	14	883.5	M	x			1	50.7	1360													1.04	0.45	19.1	1.01	1	41	0.02	3	14	0.18	0.87	1	37	8	0.34	0.39
		WP 85	14	878.9	M	x			1	63.1	307				0.3								0.3	0.53	0.21	319	1.82	1	300	0	8	39	0.17	0.94	1	88	27	0.21	0.26
	Svarthamar Member	WP 77	12	835.0	C	x			1	63.8	565													0.66	0.3	180	0.19	1	338	0	27	90	0.23	0.98	1	3	8	0.01	0.03
		WP 69	10	823.4	M	x			1	44.3	190				0.3								0.3	0.49	0.22	865	1.56	0	350	0	3	58	0.05	0.86	1	63	6	0.14	0.15
		WP 70	10	819.8	M	x			1	54.2	281													0.85	0.35	469	0.83	1	283	0	3	78	0.04	0.88	1	21	23	0.05	0.1
		WP 71	10	817.2	M	x			1	46.6	2643											9.7	9.7	1.07	0.52	4.68	2.92	2	11	0.15	0	23	0	0.93	0.93	101	28	0.77	0.81
		WP 73	8	816.3	M	x			1	66.7	4227													0.39	0.35	1.32	4.01	0	0	0	0	19	0	0	1	169	91	0.89	0.93
		WP 68	8	813.0	S	x			1	53.1	3848				4.5							10	14	0.88	0.55	2	6.18	2	0	1	0	17	0	0.33	1	169	154	0.88	0.94
	Fossgil	WP 67		782.0	M	x			1	58.1	1347													0	0	0	5.75	0	0	0	0	0	0	0	0	261	60	1	1
		WP 109		778.0	M	x			1	62.3	2242													0.35	0.5	2.26	5.04	0	0	0	0	4	0	0	1	220	75	0.93	0.95
	Hörgi Formation	WP 101		769.0	M	x			1	48.0	2697													0.55	0.34	11.8	7.06	6	0	1	0	70	0	0.46	1	207	120	0.72	0.8
		WP 108		765.0	S	x			1	56.9	1506											1.1	1.1	1.08	0.4	18.9	6.1	6	3	0.67	10	47	0.18	0.47	1	239	107	0.73	0.8
		WP 102		762.1	M	x			1	48.5	2471													0.72	0.66	0.62	2.08	0	0	0	0	2	0	0	0	60	40	0.94	0.96
		WP 107		758.0	S	x			1	58.6	833													0.81	0.39	24	6.14	2	4	0.33	4	42	0.09	0.42	0.92	240	117	0.79	0.85
		WP 103		753.0	M	x			1	41.9	1072											14	14	0.98	0.5	8.69	7.95	5	1	0.83	1	16	0.06	0.71	1	257	69	0.92	0.94
		WP 104		752.5	M	x			1	54.6	1161													0.79	0.49	7.92	1.39	3	0	1	2	19	0.1	0.33	1	45	31	0.63	0.74
		WP 106		750.0	S	x			1	52.1	450													1.67	0.62	26.9	8.52	8	5	0.62	7	18	0.28	0.69	1	258	183	0.88	0.93
		WP 105		744.0	M	x			1	40.7	1529													0.37	0.34	9.26	10.3	3	0	1	0	28	0	0.75	1	290	123	0.9	0.93
Tjörnes beds	*Serripes* Zone	WP 43	24	478.0	CS,W	x			1	39.1	1716													0	0	0	0.33	0	0	0	0	0	0	0	0	4	1	1	1
		WP 40	I	477.6	M	x			1	60.0	3864													0	0	0	0.03	0	0	0	0	0	0	0	0	2	0	1	1
		WP 42	H	476.7	M	x			1	48.6	1005													0	0	0	2.68	0	0	0	0	0	0	0	0	2	0	1	1
		WP 38	H	462.8	CS,W	x			1	72.3	2003													0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		WP 37	G	452.6	M	x			1	41.8	895													0	0	0	0.38	0	0	0	0	0	0	0	0	15	1	1	1
		WP 36	23	449.8	SH	x			1	43.6	1411													0	0	0	0.07	0	0	0	0	0	0	0	0	2	1	1	1
		WP 31	22/23	447.0	CS	x			1	63.6	1187													0	0	0	1.71	0	0	0	0	0	0	0	0	9	0	1	1
		WP 27	22	442.6	S	x			1	37.8	2361					6.3		69	13				88	1.19	0.61	3.33	6.35	7	0	1	14	1	0.93	0.67	1	61	178	0.79	0.94
		WP 28	21/22	439.4	S	x			1	59.4	2137				4.8								4.8	1.5	0.59	12.5	39.7	15	17	0.47	27	56	0.33	0.63	1	281	2071	0.77	0.97
		WP 32	?	439.3	S	x			1	51.6	204													0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0
		WP 24	21/22	427.2	S	x		x	1	62.2	1474		1					3.9					4.8	0.96	0.37	21.3	8.44	72	9	0.89	84	16	0.84	0.93	1	22	503	0.17	0.83
		WP 33	?	426.5	SH	x			1	62.1	2489		5.9		1.5			51				1.5	6.3	1.6	0.56	8.17	14.3	9	9	0.5	44	18	0.71	0.85	1	48	821	0.41	0.93
		WP 25	21	424.8	SH	x		x	1	66.5	3992				5.2			40					45	1.37	0.51	4.06	25.8	8	10	0.44	17	23	0.43	0.92	1	69	1645	0.54	0.97
		WP 26	20/21	424.4	S	x			1	52.1	2375				10			10	4.5				15	1.65	0.58	9.92	30.1	19	8	0.7	47	11	0.81	1	1	126	1440	0.66	0.96
		WP 23	20	423.7	SH	x		x	1	50.0	1269	0.9			2.6			14					17	1.61	0.55	34	18.1	36	11	0.77	72	18	0.8	0.82	1	79	828	0.41	0.89
		WP 22	19/20	422.9	S	x		x	1	39.2	764		0.3		1.8				2.7				4.9	1.54	0.5	204	3.01	110	76	0.59	222	30	0.88	0.94	1	22	94	0.06	0.26
		WP 21	19	422.2	SH	x		x	1	82.8	929	0.7			2.5			1.9					4.3	1.33	0.44	66.6	2.62	84	86	0.49	152	23	0.87	0.97	1	30	183	0.1	0.44
		WP 20	18/19	420.0	S	x			1	49.0	2253		3.3		3.3			31	7.3	1.3			46	1.43	0.5	25.4	15.6	66	10	0.87	116	22	0.84	0.76	1	132	628	0.47	0.83
		WP 19	18	417.6	SH	x		x	1	40.3	1262				6.9								6.9	1.33	0.55	10.6	6.92	7	6	0.54	9	9	0.5	0.83	0.92	20	258	0.41	0.91
		WP 18	17/18	415.8	S	x			1	52.6	1261		8.7		1.7			2.5	0.6	0.6		4.2	18	1.66	0.5	100	13.9	111	30	0.79	248	81	0.75	0.92	1	93	635	0.21	0.67
		WP 17	17/18	406.5	S	x		x	1	47.1	1176		12		15			8.8		3.8			112	1.17	0.6	8.72	10.7	15	3	0.83	19	4	0.83	1	1	65	437	0.71	0.95
		WP 16	17	402.2	S	x		x	1	53.5	2397		170		7.1			38					214	1.73	0.57	8.12	14.6	14	5	0.74	38	10	0.79	0.67	1	124	655	0.69	0.93
		WP 3	16	379.3	SH	x			1	44.1	1383													0	0	0	3.06	0	0	0	0	0	0	0	0	67	68	1	1
		WP 4	15/16	375.8	S	x			1	48.7	617	0.9	14		0.3							1.2	16	1.77	0.55	203	10.2	33	18	0.65	158	160	0.5	0.25	1	341	150	0.51	0.6
		WP 5	15	368.8	SH	x			1	50.5	1808		50		1.7			3.5					55	1.56	0.52	23.4	10.8	15	4	0.79	75	34	0.69	0.25	0.95	342	197	0.75	0.82
		WP 6	14/15	367.9	S	x		x	1	67.8	488		21		1.8			0.7		1.2		3.7	29	1.57	0.5	92.1	10.9	9	6	0.6	24	131	0.15	0.62	1	357	382	0.69	0.82
		WP 7	14	363.9	SH	x			1	53.9	591		32					16					47	1.18	0.61	11.1	6.21	3	1	0.75	10	9	0.53	1	1	156	177	0.89	0.95
		WP 8	13/14	360.1	S	x			1	45.2	191		2.9		4.4							12	19	1.5	0.49	441	89.9	17	4	0.81	104	89	0.54	0.48	1	1300	2765	0.86	0.95
		WP 9	13	359.2	S	x			1	70.5	151		1.9	0.2	2.3			0.7				13	18	1.86	0.54	754	8.41	118	9	0.93	302	89	0.77	0.73	0.99	289	295	0.4	0.57
		WP10	12/13	357.2	S	x			1	72.1	361											7.9	7.9	1.68	0.58	45	8.33	4	23	0.15	22	33	0.4	0.8	1	331	270	0.84	0.91
	Mactra Zone	WP 11	12	356.0	S	x			1	56.0	1393				6			6				6	18	0.66	0.6	1.19	18.3	2	0	1	1	1	0.5	1	0.5	547	473	0.99	1
		WP 12	11	350.0	SH	x		x	1	51.7	3139													0.98	0.61	1.15	19.6	1	3	0.25	1	9	0.1	0.67	1	509	498	0.98	0.99
		WP 13	11	340.0	CS	x			1	41.7	3572											1.9	1.9	0.91	0.35	13.6	29.2	5	3	0.63	1	30	0.03	0.5	1	615	601	0.85	0.92
		WP 14	11	330.0	S	x			1	69.0	3676											12	12	1.14	0.58	1.9	19.8	0	4	0	0	20	0	0.5	1	497	870	0.95	0.98
		WP 44	10	295.0	SH	x			1	34.4	253											13	13	1.32	0.68	17.1	1.66	0	3	0	0	6	0	1	0.5	14	43	0.64	0.88
		WP 45	10	291.2	S	x			1	52.3	288													1.23	0.63	18.5	7.04	1	2	0.33	1	10	0.09	0.5	1	70	298	0.82	0.96
		WP 48	9	286.1	SH	x			1	41.6	1029													0.71	0.65	2.6	0.96	0	2	0	0	5	0	0	0	10	30	0.63	0.87
		WP 46	9	277.8	SH	x			1	57.2	1282										10		10	0.63	0.57	2.79	2.59	0	0	0	0	9	0	0	0	41	107	0.79	0.93
		WP 47	?	272.0	SH	x			1	46.8	184													0.47	0.67	21.6	7.12	0	0	0	0	10	0	0	0	27	305	0.73	0.97
		WP 49	F	260.5	L		x		1	2.4	17													0	0	0	145	0	0	0	0	0	0	0	0	332	0	1	1
		WP 50	F	252.0	M,P	x			1	33.8	5													0	0	0	13.5	0	0	0	0	0	0	0	0	439	16	1	1
		WP 51	E	244.0	CS	x		x	1	50.0	478													0	0	0	0.14	0	0	0	0	0	0	0	0	5	2	1	1
		WP 52	8	230.0	SH	x		x	1	74.3	656											7.7	7.7	0.73	0.53	4.96	2.29	0	1	0	0	9	0	0	1	49	120	0.79	0.93
		WP 53	D	211.1	M,W	x			1	3.2	128													0.95	0.46	1809	115	4	29	0.12	1	31	0.03	0.54	1	313	53	0.89	0.9
		WP 56	D	207.9	L	x			1	3.5	35													0	0	0	108	0	0	0	0	0	0	0	0	379	0	1	1
		WP 54	D	203.7	L	x			1	34.2	77													0.24	0	14.1	19.4	0	0	0	1	0	1	0	0	101	563	0.98	1
		WP 57	7	195.3	S	x		x	1	46.8	566													0	0	0	0.58	0	0	0	0	0	0	0	0	9	18	1	1
		Wp 58	7	188.0	M,W	x			1	3.4	1080													0	0	5.11	6.23	0	0	0	1	0	1	0	0	21	0	0.95	0.95
		WP 55	7	185.0	S	x		x	1	38.2	25				2.1							0.7	2.7	1.41	0.49	2899	8.85	6	4	0.6	32	101	0.24	0.05	0.98	200	131	0.57	0.69
		WP 59	6	183.0	S	x		x	1	42.8	428				3.8						0.3	3.5	7.5	0.96	0.35	351	2.2	26	30	0.46	49	282	0.15	0.42	0.94	58	36	0.14	0.21
	Tapes Zone	WP 60	C	145.0	L		x		1	2.4	51													0	0	0	121	0	0	0	0	0	0	0	0	256	26	1	1
		WP 61	C	144.0	S	x		x	1	31.7	1248													0.62	0.57	6.11	11.2	5	0	1	8	0	1	1	1	58	298	0.82	0.96
		WP 62	5	129.0	S	x		x	1	43.9	1620													0	0	0.26	9.76	0	0	0	0	1	0	0	0	61	367	0.98	1
		WP 86	4	83.2	S	x		x	1	47.7	1306				5							3	35	0.75	0.38	11.9	7.44	4	6	0.4	3	32	0.09	0.9	1	152	201	0.79	0.9
		WP 87	4	78.0	S	x		x	1	49.7	846													0.81	0.45	35.4	7.65	6	32	0.16	3	73	0.04	0.86	1	71	307	0.47	0.83
		WP 88	4	69.0	S	x		x	1	49.5	697													1.18	0.61	8.08	6.69	4	0	1	12	3	0.8	1	1	291	40	0.95	0.96
		WP 89	B	68.0	L		x		1	2.4	2													0	0	0	6.81	0	0	0	0	0	0	0	0	14	0	1	1
		WP 90	3	66.2	S	x		x	1	49.9	149													1.7	0.56	265	7.79	27	2	0.93	78	20	0.8	0.44	1	78	310	0.42	0.79
		WP 91	3	65.1	S	x		x	1	38.0	531				13								13	1.37	0.59	27.6	9.52	2	3	0.4	23	3	0.88	1	1	58	303	0.66	0.92
		WP 92	c	45.0	L		x		1	2.5	6													0	0	0	170	0	0	0	0	0	0	0	0	174	218	1	1
		WP 93	2, b	36.2	L		x		1	2.6	6													0	0	0	134	0	0	0	0	0	0	0	0	329	20	1	1
		WP 94	2	35.3	S	x		x	1	48.7	343				1.6								1.6	1.48	0.47	357	8.23	134	33	0.8	227	51	0.82	0.86	1	114	286	0.26	0.55
		WP 95	2	29.4	S	x		x	1	38.4	1850													0.89	0.64	2.62	8.63	0	9	0	1	6	0.14	1	1	40	291	0.8	0.97
		WP 96	2, a	22.4	L		x		1	2.4	8													0	0	0	150	0	0	0	0	0	0	0	0	364	3	1	1
		WP 97	2	20.4	S	x		x	1	32.5	222													1.54	0.58	144	11.6	24	6	0.8	45	5	0.9	1	1	87	287	0.61	0.87
		WP 98	2	13.7	S	x			1	60.2	516			5.6								11	17	1.49	0.62	10.8	8.37	4	3	0.57	9	7	0.56	0.33	1	82	418	0.82	0.97
		WP 100	1	5.0	S	x			1	42.7	38											5.7	5.7	1.06	0.48	400	10.7	16	2	0.89	23	6	0.79	0.9	1	234	220	0.87	0.93
		WP 99	A	3.0	L		x		1	4.0	10											5	5	0.48	0.69	941	3.54	0	1	0	0	1	0	0.5	1	10	3	0.83	0.87

Axio Imager A1 transmitted light microscope under 400× and 1000× magnification. Photomicrographs were taken with a Zeiss® Axiocam MRc5 digital camera. The taxonomy of the dinocysts follows DINOFLAJ2 (Fensome et al., 2008), except for *Barssidinium pliocenicum* for which De Schepper et al. (2004) is followed.

3.2. Palaeoecological methods and indices

Versteegh (1995) and De Schepper (2006) characterised palaeoenvironmental changes by means of various palaeoecological indices based on the composition of dinocyst assemblages.

Concentration (number of dinocysts/g) and richness (number of different species/sample) are calculated, together with the Evenness (E_H) and Shannon Wiener diversity index (H′, Table 1, Fig. 4). The latter two indices indicate the distribution of the various species within a sample.

The inner neritic/outer neritic index ($IN/ON = nIN/[nIN + nON]$) gives an indication of the depositional area on the shelf, and the proximity to the coast. Typical inner neritic species are *Lingulodinium machaerophorum*, *Melitasphaeridium choanophorum*, *Barssidinium pliocenicum*, *Bitectatodinium tepikiense*, cyst of *Pentapharsodinium dalei*, *Filisphaera filifera*, *Tectatodinium pellitum* and *Tuberculodinium vancampoae*. Typical outer neritic species are *Amiculosphaera umbraculum* and *Operculodinium*? *eirikianum* var. *eirikianum*. An indication of the transport of dinocysts from an open marine environment into the shallow shelf area is given by the oceanic/neritic index ($O/N = (nO/[nO + nN])$, with N representing the inner and outer neritic species (see above) and O the oceanic species *Nematosphaeropsis labyrinthus* and *Impagidinium* spp. The P/D index ($= nP/[nP + nD]$) in which P = pollen and D = dinocysts gives an indication of the proximity to the coast or the cooling effects on the land.

Heterotrophic dinoflagellates are dependent on nutrients derived from upwelling or are transported from the land. The H/A index ($nH/[nH + nA]$) with H representing heterotrophic species (mainly protoperidinioid species) and A representing autotrophic species (gonyaulacoids and goniodomacoids) is used as a measure for upwelling. It should be noted that heterotrophic species are more susceptible to oxidation (Marret, 1993) and this may influence the ratios.

The ecological preferences of recent dinoflagellates can be deduced from their present day distribution. Marret and Zonneveld (2003) distinguish recent species by their preference for warm (W) or cold (C) surface water. A qualitative analysis relying on the warm/cold index ($W/C = nW/[nW + nC]$) is a first indication of past Sea Surface Temperatures (SST), assuming for species with a distinct present-day distribution related to surface water temperature, a comparable distribution during the Pliocene and the Pleistocene. Thus, *Impagidinium aculeatum*, *Impagidinium patulum*, *Lingulodinium machaerophorum*, *Selenopemphix nephroides*, *Spiniferites belerius*, *Spiniferites membranaceus*, *Spiniferites mirabilis*, *Tectatodinium pellitum* and *Tuberculodinium vancampoae* are considered to indicate warm surface water. *Bitectatodinium tepikiense*, *Islandinium minutum*, cyst of *Pentapharsodinium dalei*, *Spiniferites delicatus* and *Spiniferites elongatus* would indicate cold surface water. For extinct species however, we can assume temperature sensitivity only when independent proxies show that this is the case. De Schepper et al. (2011) quantified the spring/summer temperature ranges of extant and extinct dinoflagellate species through a calibration of Mg/Ca measurements of *Globigerina bulloides* from the same samples. Temperature distributions of extant species are broadly comparable for the Pliocene and modern oceans, with the Pliocene species clustering in the warmest part of the present-day distribution range. Head (1993) found large numbers of *Barssidinium pliocenicum* and *Echinidinium euaxum* in the interglacial St. Erth Beds of southwest England and could link these occurrences to a warm winter SST of 15 °C and the presence of the Gulf Stream at the time. *Melitasphaeridium choanophorum* and *Operculodinium*? *eirikianum* var. *eirikianum* are also linked to warm Pliocene SST (Head, 1997; De Schepper et al., 2011). Many authors (Head, 1994; Versteegh, 1995; Head, 1996; De Schepper et al., 2011) also found evidence for cold water affinity of the Pliocene *Filisphaera filifera* and *Habibacysta tectata*.

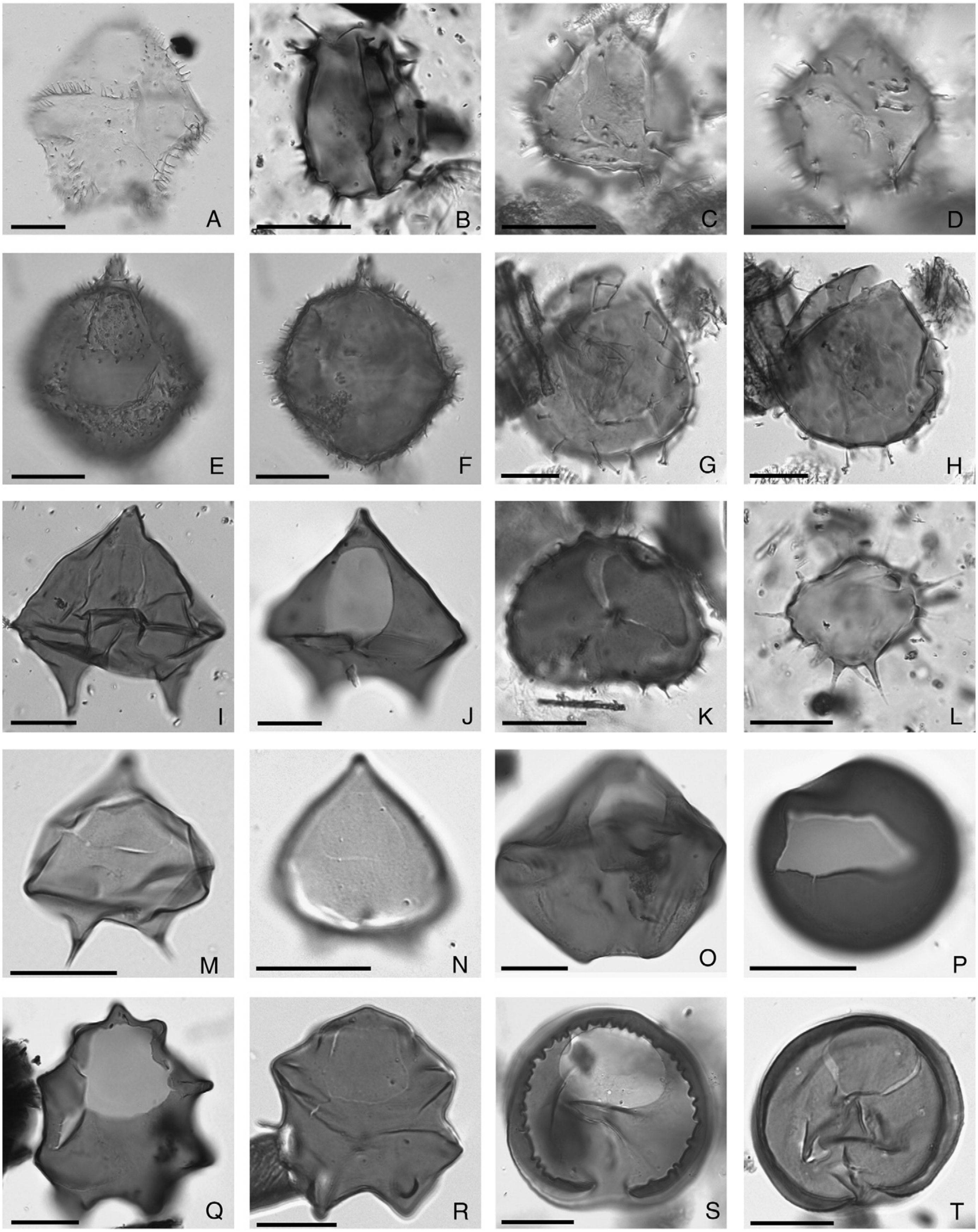
4. Results

4.1. Palynological analysis

A total of 54 dinocyst species belonging to 27 genera were counted in 88 samples from the Tjörnes and Breidavík sections (Plates 1, 2, 3, 4; Figs. 3 and 4; Table 1a, b, c and Supplementary data Table 2 for raw data). Acritarchs and freshwater green algae are present in moderate numbers, especially in the *Serripes* Zone (Plate 4). Less than 25 dinocysts were counted in 44 samples. The poorest samples come from the lignite layers, the interval between unit 8 and 10 in the *Mactra* Zone, the interval between unit 22/23 and 24 in the upper part of the *Serripes* Zone and the Fossgil Member. Twenty-four samples contained between 25 and 100 cysts and only 20 samples yielded counts of significantly more than 100 cysts. Consequently the relative abundances have to be treated with caution and a semi-quantitative and qualitative analysis was performed instead of a biostatistical analysis. Reworking of Cretaceous and Paleogene/Neogene species is limited in the entire section (Verhoeven et al., 2011).

The Shannon Wiener index has a rather constant value of c. 1.5 in the Tjörnes beds, with the exception of the central part in which a clear decrease has been noted (Fig. 4). In the successive interglacial deposits of the Breidavík Group, the index gradually decreases towards values around 0.7 in the Tórfholl Member. The evenness and the richness show the same trend. Concentrations are always low and have a highest value in the Upper Pleistocene of 924 dinocysts/g. The IN/ON index throughout the section is moderate to high and indicates a constant near coast position of the depositional area (Fig. 4). The P/D index remains very high during the entire section, except in the uppermost Breidavík Group and in some minor relapses in the upper part of the *Mactra* Zone and the base of the *Serripes* Zone. When spores are added to the index, the minor relapses disappear (Fig. 4; $(P + S)/[(P + S) + D]$). These minor changes in the P/D index thus do not indicate a slightly diminished influence of the land, but a changed vegetational composition (Verhoeven et al., 2013). The number of oceanic species is low throughout the studied section. The O/N index suggests limited transport from the ocean into the depositional area, except for the upper part of the *Mactra* Zone and the base of the *Serripes* Zone (Fig. 4). Heterotrophic species are distinctly present in the Tjörnes beds, but their numbers decrease in the second half of the *Tapes* Zone and the *Mactra* Zone (Figs. 3 and 4). Heterotrophic species are of minor importance in the Breidavík Group, where autotrophic species predominate. In the first half of the *Serripes* Zone, autotrophic species had already become quite

Plate 1. Photomicrographs of selected heterotrophic dinocyst species. Scale bars indicate 20 μm. E.F. = England Finder coordinate. A: *Trinovantedinium applanatum*, sample WP10, *Serripes* Zone, E.F.: T33/4; B: *Trinovantedinium ferugnomatum*, sample WP8, *Serripes* Zone, E.F.: X47/2; C–D: Trinovantedinium *ferugnomatum*, sample WP18, *Serripes* Zone, E.F.: X38; E–F: *Trinovantedinium glorianum*, sample WP21, *Serripes* Zone, E.F.: T50/3; G–H: *Trinovantedinium variabile*, sample WP9, *Serripes* Zone, E.F.: X56/3; I, J: *Lejeunecysta* sp., sample WP21, *Serripes* Zone, E.F.: L33/1 (I), sample WP5 (slide 2), *Serripes* Zone, E.F.: T31/1–2 (J); K: *Selenopemphix brevispinosa*, sample WP9, *Serripes* Zone, E.F.: Z54/3; L: *Selenopemphix quanta*, sample WP8, *Serripes* Zone, E.F.: T44; M, N: *Lejeunecysta marieae*, sample WP98, *Tapes* Zone, E.F.: U51/4 (M), sample WP22, *Serripes* Zone, E.F.: H56/2 (N); O: *Quinquecuspis concreta*, sample WP97, *Tapes* Zone, E.F.: M52/4; P: *Brigantedinium cariacoense*, sample WP21, *Serripes* Zone, E.F.: K38/3; Q, R: *Lejeunecysta catomus*, sample WP97, *Tapes* Zone, E.F.: M39 (Q), sample WP59, *Mactra* Zone, E.F.: X39/3 (R); S: *Selenopemphix nephroides* (undulate morphotype), sample WP18, *Serripes* Zone, E.F.: Z47/3; T: *Selenopemphix nephroides* (normal morphotype), sample WP18, *Serripes* Zone, E.F.: L52/0. Both morphotypes are grouped as *Selenopemphix nephroides*.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important. The W/C index in the Tjörnes beds is rather high, except in the second half of the *Tapes* Zone and in the *Mactra* Zone. In the first half of the *Serripes* Zone, a dip is observed that runs more or less parallel with a dip in the H/A index. A clear cooling is observed in the second half of the Svarthamar Member and in the Tórfholl Member, both at the top of the Breidavík Group.

4.2. Dinocyst assemblage zones

4.2.1. Dinocyst assemblage zone 1 (DAZ1)

DAZ1 comprises the interval from the base of the *Tapes* Zone to halfway unit 4 of the same molluscan zone (0–75 m; Fig. 5) and is defined by the dominance of the heterotrophic dinocyst species *Barssidinium pliocenicum* (average of 10.6%; Plate 3C, D), *Trinovantedinium ferugnomatum* (average 3.5%; Plate 1B; C,D), *Trinovantedinium glorianum* (average 2.2%; Plate 1E, F), *Selenopemphix dionaeacysta* (average 2.8%), *Quinquecuspis concreta* (average 2.1%, Plate 3O) and *Lejeunecysta marieae* (average 1.5%; Plate 1M, N) (Fig. 3). Autotrophic species are of minor importance. *Filisphaera filifera* subsp. *filifera* (average 0.6%; Plate 3S,T) occurs together with *Habibacysta tectata* (average 1.7%; Plate 3I, J, K), although the first species is much less well represented. The tropical species *Tectatodinium pellitum* (3.6%; Plate 3B) is recorded in unit 2 in the middle part of DAZ1. The average richness amounts to 15.6 species/sample, while the average dinocyst concentration is 118 dinocysts/g (Fig. 4). The average pollen concentration (72.290 pollen/g) and spore concentration (22.910 spores/g) are noticeably higher. Heterotrophic dinocyst species clearly dominate the assemblage as can be seen in the average H/A index of 0.82. The average W/C index amounts to 0.77 and indicates a rather warm SST. The age of DAZ1 is Early Pliocene (Fig. 2).

4.2.2. Dinocyst assemblage zone 2 (DAZ2)

Zone DAZ2 holds the sediments from the middle part of unit 4 in the upper part of the *Tapes* Zone to unit 12 in the upper part of the *Mactra* Zone (75–356.5 m; Fig. 5). The base of the zone is defined by the sudden decrease of heterotrophic species (Fig. 3). Heterotrophic species such as *Barssidinium pliocenicum* (average 1.4%), *Trinovantedinium* sp. (average 1.3%), *Echinidinium euaxum* (average 0.4%; Plate 3E, F) and *Lejeunecysta* sp. (average 0.1%) are much less represented during DAZ2 and are replaced by the autotrophic species *Operculodinium centrocarpum* s.s. (average 10.3%, Plate 2S, T), *Habibacysta tectata* (average 5.1%), *Impagidinium* sp. (average 1.3%) and *Spiniferites* spp. (average 0.9%). *Filisphaera filifera* subsp. *filifera* is notably absent (average 0.1%). The warm water species *Tuberculodinium vancampoae* (3.8%, Plate 3A) is recorded in unit 4 at the base of DAZ2. The average H/A index (0.08) and the W/C index (0.34) are much lower than in DAZ1 (Fig. 4). The average dinocyst concentration (109.4 dinocysts/g) is only slightly lower than in DAZ1 and DAZ3. Parallel with the regression of the heterotrophic species, the average richness decreases to 10.4 species/sample. The same decline is also visible in the Shannon Wiener diversity index (H') and the Evenness (E_H). The average concentration of pollen and spores amounts respectively to 13.632 pollen/g and 717 spores/g. In units 11 and 12, just under the transition from DAZ2 to DAZ3, the appearance of the cosmopolitan species *Operculodinium centrocarpum* sensu Wall and Dale (1966) is recorded. DAZ2 has an Early Pliocene age (Fig. 2).

4.2.3. Dinocyst assemblage zone 3 (DAZ3)

DAZ3 comprises the interval from the base of the *Serripes* Zone to the top of unit 22 (356.5–445 m; Fig. 5). The lower boundary is defined by the re-entrance of heterotrophic dinocysts in the assemblage, while the upper boundary is characterised by the transition to an overlying barren interval (Fig. 3). Heterotrophic species such as *Barssidinium pliocenicum* (average 10.8%), *Echinidinium euaxum* (average 8.3%), *Brigantedinium* spp. (average of 4.6%), *Trinovantedinium glorianum* (average 2.5%) and *Lejeunecysta marieae* (average 1.02%) re-appear in DAZ3 and dominate the dinocyst assemblage. *Selenopemphix islandensis* appears at the base of DAZ3 and is in the Tjörnes section restricted to this zone with an average of 2.8%. *Trinovantedinium variabile* (average 0.2%; Plate 1G, H) appears in unit 13 and maintains its limited presence in DAZ3. *Filisphaera filifera* subsp. *filifera* re-appears and *Operculodinium tegillatum* (Plate 2Q, R) appears already in unit 11 in the top of DAZ2; both are now prominently present (average 4.5% and 2%). Notable is the dominant occurrence (up to 16%) of *Amiculosphaera umbraculum* (Plate 2O, P) in the lower part of the zone (units 15 and 15/16). DAZ3 has the highest average richness (18.8 species/sample) of the entire section but still a quite low average dinocyst concentration of 118.6 dinocysts/g (Fig. 4). The heterotrophic species are again dominant with an average H/A index of 0.62. The average W/C index in DAZ3 is also high (0.65). The terrestrial input during DAZ3 is very low with an average pollen concentration of 171 pollen/g and an average spore concentration of 365 spores/g. The acritarchs *Cyclopsiella*? *trematophora* (average 14%), *Halodinium scopaeum* (average 12.6%), *Cymatiosphaera invaginata* (average 3.2%; Plate 4E, F) and *Paralecaniella indentata* (average 0.3%) occur for the first time and are relatively abundant (Fig. 3). An acritarch provisionally labelled Acritarch type 1 (average 1.2%; Plate 4M–P) appears for the first time in unit 17/18 of the *Serripes* Zone. Linings of Foraminifera are very abundant (average of 30.3%, Plate 4B). DAZ3 has an Early Pliocene age (Fig. 2).

4.2.4. Barren interzone (BIZ1)

The estuarine sediments from unit 22/23 to unit 24 (445–480 m) did not yield organic-walled phytoplankton (Figs. 3 and 5). Only a few pollen and spores were recorded. The intertidal sediments of unit 25 together with the underlying lignite J in the uppermost part of the *Serripes* Zone were not sampled.

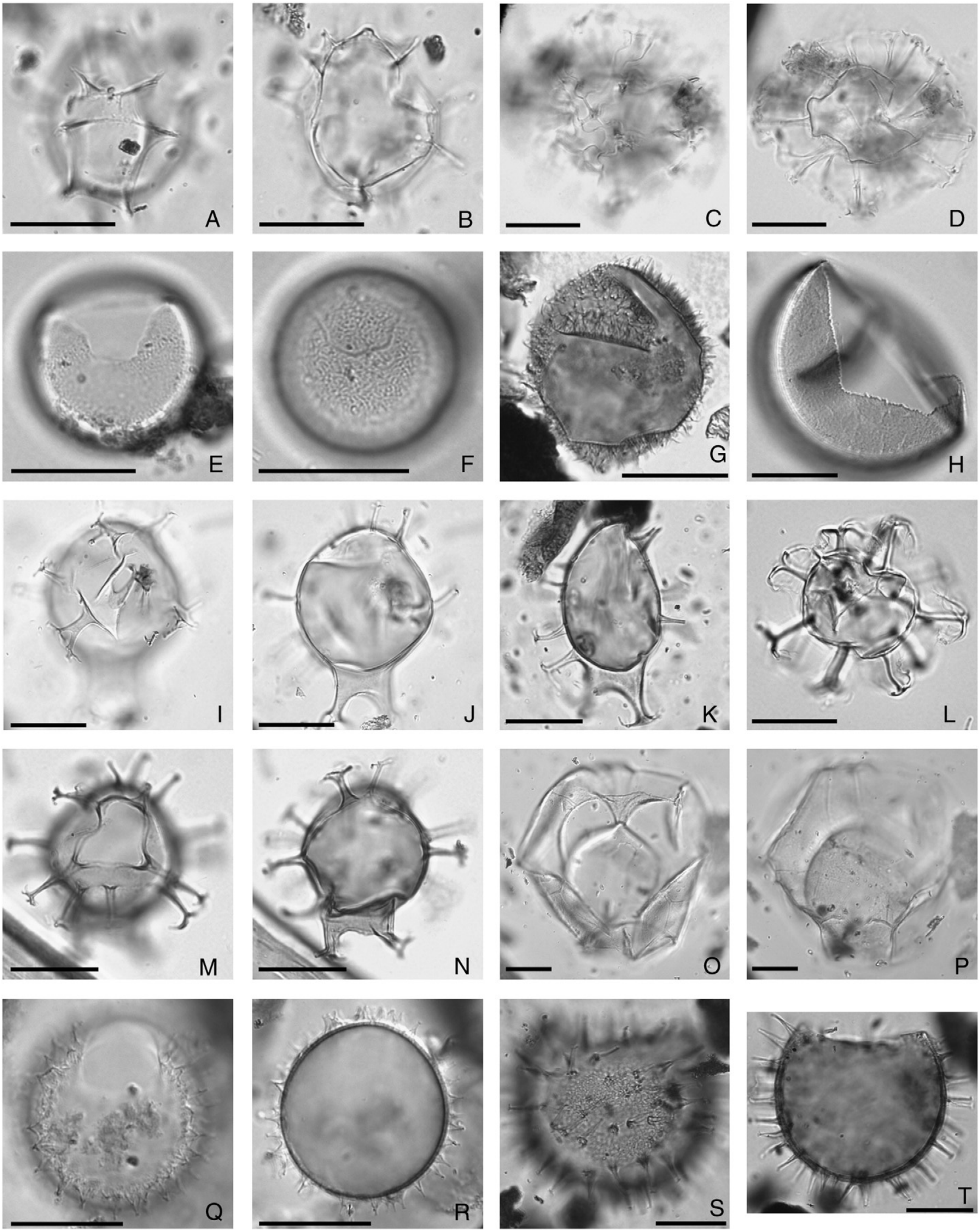
4.2.5. Dinocyst assemblage zone 4 (DAZ4)

The lower boundary of DAZ5 is defined by low numbers of heterotrophic dinocysts and the onset of the nearly continuous presence of *Lingulodinium machaerophorum* and *Operculodinium centrocarpum* s.s. The diversity of the other dinocysts and the differences in richness enable us to divide DAZ in two subzones.

4.2.6. Dinocyst assemblage subzone 4a (DAZ4a)

DAZ4a corresponds to the Hörgi Formation (744–773 m) (Fig. 3, Table 1). *Operculodinium centrocarpum* s.s. dominates the assemblage (average 33.3%), together with *Lingulodinium machaerophorum* (average 5.9%), *Batiacasphaera hirsuta* (average 1.9%, Plate 2G) and *Achomosphaera* sp. (average 5.7%; Plate 2I, J). The presence of *B. hirsuta* so high in the Gelasian (2.581–1.778 Ma) has to be treated with caution (Head, personal communication 2012). Reworking of the species is plausible as in the same sediments reworked specimens of *Reticulatosphaera actinocoronata* and *Operculodinium tegillatum*

Plate 2. Photomicrographs of selected autotrophic dinocyst species. Scale bars indicate 20 μm. E.F. = England Finder coordinate. A–B: *Impagidinium aculeatum*, sample WP48, *Mactra* Zone, E.F.: X52; C–D: *Nematosphaeropsis labyrinthus*, sample WP44, *Mactra* Zone, E.F.: E37/2.; E, F: *Batiacasphaera micropapilata*, sample WP14 (slide 1), *Mactra* Zone, E.F.: X37/2 (E), sample WP26, *Serripes* Zone, E.F.: V58/3 (F); G: *Batiacasphaera hirsuta*, sample WP9, *Serripes* Zone, E.F.: K61; H: *Bitectatodinium*? *serratum*, sample WP21, *Serripes* Zone, E.F.: T48/1; I–J: *Achomosphaera* sp., sample WP28, *Serripes* Zone, E.F.: M45; K: *Spiniferites mirabilis*, sample WP8, *Serripes* Zone, U42/3; L: *Reticulatosphaera actinocoronata*, sample WP13, *Mactra* Zone, E.F.: E55/1; M–N: *Spiniferites bulloideus*, sample WP 101, Hörgi Formation, E.F.: M61; O–P: *Amiculosphaera umbraculum*, sample WP5, *Serripes* Zone, E.F.: R47/4; Q–R: *Operculodinium tegillatum*, sample WP18, *Serripes* Zone, E.F.: Z47/4; S–T: *Operculodinium centrocarpum* s.s., sample WP4, E.F.: E55/1.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have been recorded (Verhoeven et al., 2011). Heterotrophic species such as *Barssidinium pliocenicum* (average 3.2%), *Trinovantedinium glorianum* (average 0.4%), *Lejeunecysta marieae* (average 0.14%) and *Selenopemphix brevispinosa* (average 0.4%) are recorded, albeit in lower numbers compared to the assemblage in DAZ3 (average H/A index 0.10). Remarkable is the excellent preservation of the heterotrophic cysts. The presence of *L. machaerophorum* (Plate 3G) and *B. pliocenicum* are responsible for the high average W/C index of 0.77. The cold water species cyst of *Pentapharsodinium dalei* (average 2.6%, Plate 3Q) shows low abundances comparable with those in the preceding dinocyst zones. A low average richness of 8.3 dinocyst species/sample and an average dinocyst concentration of 15.4 dinocysts/g characterises this zone (Fig. 4). Terrestrial influx is very low with an average pollen concentration of 74 pollen/g and an average spore concentration of 39 spores/g. This subzone has an Early Pleistocene age and is dated to around 2.2 Ma (Fig. 2).

4.2.7. Dinocyst assemblage subzone 4b (DAZ4b)

DAZ4b encompasses the sediments of the Fossgil Member and the lower part of the Svarthamar Member (unit 8 and the beginning of unit 10; 773–818 m) (Table 1), and is characterised by a very low palynomorph content (Fig. 4). As in DAZ4a, the dominant species are *Operculodinium centrocarpum* s.s. (average 18.3%) and *Lingulodinium machaerophorum* (average 1.6%). The upper part of the subzone holds the first appearance of *Bitectatodinium tepikiense* with a value of 22.6% (Plate 3O, P). Heterotrophic species are absent. The average richness (8.0 species/sample) and the average dinocyst concentration (2 dinocysts/g) are at their lowest values. The cold water species gain importance compared to the previous zone (average W/C index 0.15). The average pollen and spore concentration is extremely low: 26 pollen/g and 10 spores/g. This subzone has an Early Pleistocene age and is dated to around 2.1–1.8 Ma (Fig. 2).

4.2.8. Dinocyst assemblage zone 5 (DAZ5)

DAZ5 corresponds to the sediments of the middle part of unit 10 at 818 m in the Svarthamar Member to the top of the Torfhóll Member at 885 m (Fig. 3, Table 1). The zone is characterised by high numbers of cysts of *Pentapharsodinium dalei* (average 53%), *Bitectatodinium tepikiense* (average 8.2%) and *Operculodinium centrocarpum* sensu Wall and Dale (1966) (average 5.5%) and to a lesser extent *Spiniferites elongatus* (average 1.6%, Plate 3R) and *Islandinium minutum* (average 1.3%; Plate 3M, N). The species diversity is rather low with an average richness of 10.4 species/sample (Fig. 4). Cysts of thermophilic dinocysts are scarce, only a few specimens of *Lingulodinium machaerophorum* and *Impagidinium patulum* (Plate 3H, L) occur. Cold water taxa such as cysts of *P. dalei*, *B. tepikiense*, *Spiniferites elongatus* and *I. minutum* occur in high numbers and dominate the zone (W/C index 0.01). DAZ5 has the highest average dinocyst concentration (383 dinocysts/g) with a maximum of 924. The zone is dominated by autotrophic species (H/A index 0.05). The concentrations of spores (11 spores/g) and pollen (39 pollen/g) are low and testify to fully marine conditions with low terrestrial input. DAZ5 has a Middle Pleistocene age and is dated between 1.8 and 1.4 Ma (Fig. 2).

5. Discussion

5.1. Evolution to the present-day dinocyst assemblage

The dinocyst assemblages recorded in the Tjörnes beds (DAZ1-3) show much similarity to those of the Pliocene deposits from northern Belgium and England (Head, 1998a,b; Louwye et al., 2004; De Schepper et al., 2009). Stratigraphically, they correspond to the Kattendijk Formation and the lower part of the Coralline Crag (Verhoeven et al., 2011; Fig. 2). In the deposits of the southern North Sea, comparable large numbers of species of the heterotrophic genera such as *Barssidinium*, *Lejeunecysta*, *Trinovantedinium* and *Selenopemphix* occur. Encrusting acritarch species such as *Cyclopsiella*? *trematophora* and *Halodinium scopaeum* are also a significant part of the spectrum. These acritarchs in combination with the important abundance of heterotrophic dinoflagellate species might be indicative of comparable shallow sedimentary environments during the Early Pliocene in northern Iceland and in the southern North Sea basin.

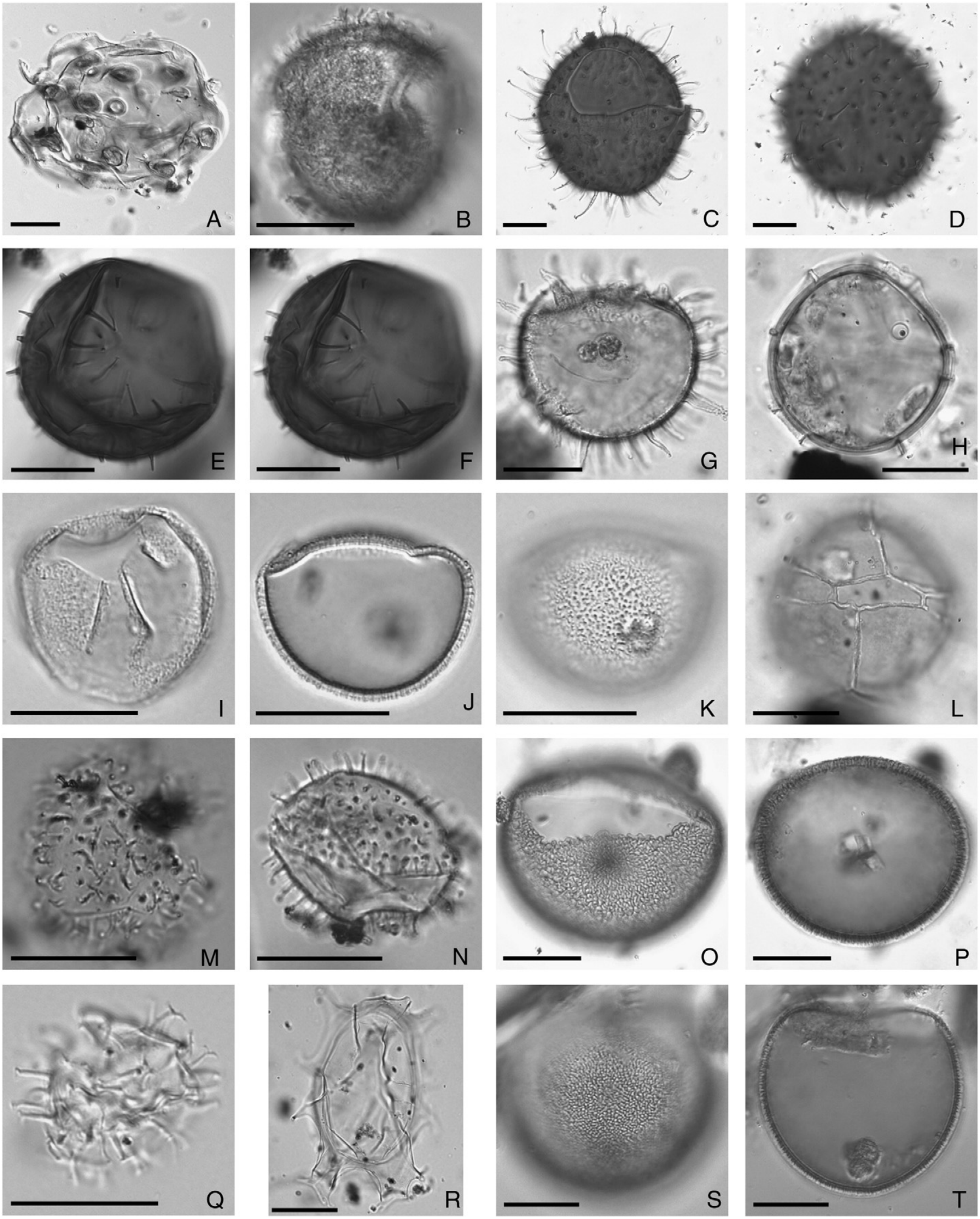
BIZ1 does not contain dinocysts. The sedimentological and malacological studies infer that these sediments were deposited in an estuarine environment (Buchardt and Símonarson, 2003). An energetic environment of this kind will prevent settling of small particles such as resting cysts of dinoflagellates. The pollen study of the sediments gave a comparably very poor signal (Verhoeven et al., 2013).

DAZ4 is a transitional assemblage with few heterotrophic species in subzone DAZ4a. Subzone DAZ4b already much resembles the Upper Pleistocene assemblage DAZ5, from which it differs by the minor importance of cold water species such as cysts of *Pentapharsodinium dalei* and *Bitectatodinium tepikiense.* DAZ5 is dominated by cysts of *P. dalei* accompanied by *Operculodinium centrocarpum* sensu Wall and Dale (1966), *B. tepikiense*, *Islandinium minutum* and *Spiniferites elongatus*. Marret et al. (2004) examined recent sea bottom sediments from the western and northern margin of Iceland. DAZ5 strongly resembles the latter authors' group II or IIIa assemblages dominated by cysts of *P. dalei* accompanied by *O. centrocarpum* sensu Wall and Dale (1966). These recent assemblages straddle the Polar Front (Fig. 1), which runs parallel to the Atlantic shelf to the west and northeast of Iceland (Marret et al., 2004). The Polar Front represents a sharp oceanographic boundary between the cold East Greenland Current (EGC) and its branch the East Icelandic Current (EIC) to the north and the warm Irminger Current (IC) to the south. In the zone of mixing along the Polar Front, the sea is very productive today and very high dinoflagellate cyst concentrations (up to 256.920 cysts/g) have been recorded by Marret et al. (2004). Our study recorded much lower concentrations but those of DAZ5 are particularly high compared with the older zones. The assemblage identified in DAZ5 and the relatively high dinocyst concentrations indicate that the Polar Front was located close to the Tjörnes area during the onset of the deposition of DAZ5, halfway unit 10 of the Svarthamar Member (Table 1). According to the age model of Verhoeven et al. (2011) this situation suggests a post-Olduvai age of around 1.7 Ma for the positioning of the recent Polar Front. Marret et al. (2004) explained the dominance of cysts of *P. dalei* on the northern Icelandic shelf to the preference of the species for a seasonally varying SST caused by the presence of the Polar Front and the enriching influence of cold and warm currents.

5.2. Dinocyst concentration variability

As already stated, the dinocyst concentrations recorded in the Tjörnes section are clearly lower than in the present-day sea bottom sediments studied by Marret et al. (2004). The difference can be explained by the location on the shelf and the continental slope of the samples analysed by the latter authors. Compared with the coastal and intertidal depositional environments of the Tjörnes area, these settings are much less energetic and permit excellent accumulation, as small particles will settle easily. Moreover, these environments

Plate 3. Photomicrographs of temperature sensitive dinocyst species. Scale bars indicate 20 μm. E.F. = England Finder coordinate. A: *Tuberculodinium vancampoae*, sample WP87, *Tapes* Zone, E.F.: J59/2; B: *Tectatodinium pellitum*, sample WP97, *Tapes* Zone, E.F.: P48/1, C–D: *Barssidinium pliocenicum*, sample WP21, *Serripes* Zone, E.F.: S44/3–4; E–F: *Echinidinium euaxum*, sample WP18, *Serripes* Zone, E.F.: R50/3; G: *Lingulodinium machaerophorum*, sample WP13, *Mactra* Zone, E.F.: B37; H, L: *Impagidinium patulum*, sample WP11, *Mactra* Zone, S35/4; I: *Habibacysta tectata*, sample WP87, *Tapes* Zone, E.F.: B58; J–K: *Habibacysta tectata*, sample WP87, *Tapes* Zone, E.F.: M39/3–4; M–N: *Islandinium minutum*, sample WP77, Svarthamar Member, E.F.: Z50/1; O–P: *Bitectatodinium tepikiense*, sample WP26, *Serripes* Zone, E.F.: O61/3; Q: cyst of *Pentapharsodinium dalei*, sample WP21, *Serripes* Zone, E.F.: K34/1; R: *Spiniferites elongatus*, sample WP84, Torfhóll Member, E.F.: D49; S–T: *Filisphaera filifera* subsp. *filifera*, sample WP18, *Serripes* Zone, E.F.: Y51/2.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are usually nutrient-enriched and associated with phytoplankton blooms (Le Fèvre, 1986; Walsh, 1988). The concentrations are low and vary around 110 cysts/g in the first three dinocyst assemblage zones of the Tjörnes beds. Although the richness shows a clear decline during DAZ2 (Fig. 4), this is not reflected in changes of the concentration. The change from a heterotrophic dominated assemblage (Plate 4T) to one dominated by autotrophic species (Plate 4S) suggests changing water characteristics that influenced only the heterotrophic species and not the dinoflagellates in general. The average dinocyst concentrations in the Pleistocene DAZ4a and DAZ4b are very low, 15.4 and 2 cysts/g respectively, but increase in DAZ5 to 383 cysts/g (Fig. 4). The first decline in the base of the Breidavík Group (DAZ4) can be explained by the general cooling caused by the onset of the glaciations, while the maximum values in DAZ5 most probably indicate the arrival of the Polar Front to the area.

5.3. Changes in nutrient supply: two major oceanographic events

The biozonations of the Tjörnes beds based on molluscs and ostracods correlate zone by zone; this is not the case for the dinocyst zonation (Fig. 5). A clear decline in diversity of heterotrophic species occurs in the base of DAZ2. Such a regression is not observed in the abundance of the freshwater green algae *Botryococcus* and *Pediastrum* (Fig. 3) or in the pollen and spore concentration (Fig. 4). The presence of freshwater green algae, brought in from the land in the depositional area can be used as a measure of the terrestrial input. Freshwater green algae are well represented in DAZ1 and DAZ3, but these differences do not militate for distinct changes in the nutrient supply from the land. Also, the P/D index does not show a changing input of pollen and spores. Moreover as the heterotrophic species are well preserved, selective degradation of such dinocysts in the DAZ2 sediments can be ruled out; the pollen are also well preserved (Verhoeven et al., 2013). The transition from a heterotrophic dominated DAZ1 to an autotrophic dominated DAZ2 marks an important oceanographic event, apparently not registered by the molluscs or ostracods. The ostracod analysis however has to be considered with caution, as the resolution in this part of the section was certainly too low to register this event. Cronin (1991) had but two samples of the *Tapes* Zone with ostracods and only the unit 5 sample yielded a significant number of specimens. Most of the molluscan studies (a.o. Bárdarson, 1925; Norton, 1975) considered the units of the *Tapes* Zone in their entirety and no differentiations within the units were made. This could explain why the transition recorded within unit 4 by the dinocysts was not recognised in the mollusc fauna. The *Tapes*/*Mactra* transition, where an assemblage dominated by *Tapes* is replaced by an assemblage dominated by *Mactra*, occurs in the top of the lignite C (Fig. 5). This lignite separates the marine units 5 and 6. Unit 5 appears to be a transitional zone, for Bárdarson (1925: p. 26) already found frequent *Mactra* shells in the *Cyprina* horizon of the unit at the Reká locality. He excluded however unit 5 from the *Mactra* Zone as this first occurrence of *Mactra* coincides with the highest occurrence of *Tapes*, the key species of the *Tapes* Zone. In our view, the onset of DAZ2 halfway unit 4 and the first occurrence of *Mactra* in unit 5 may be penecontemporaneous, signalling the same palaeoceanographic change. Most probably the decrease in nutrients during deposition of DAZ2 caused the change in the molluscan assemblage at the transition from the *Tapes* Zone to the *Mactra* Zone.

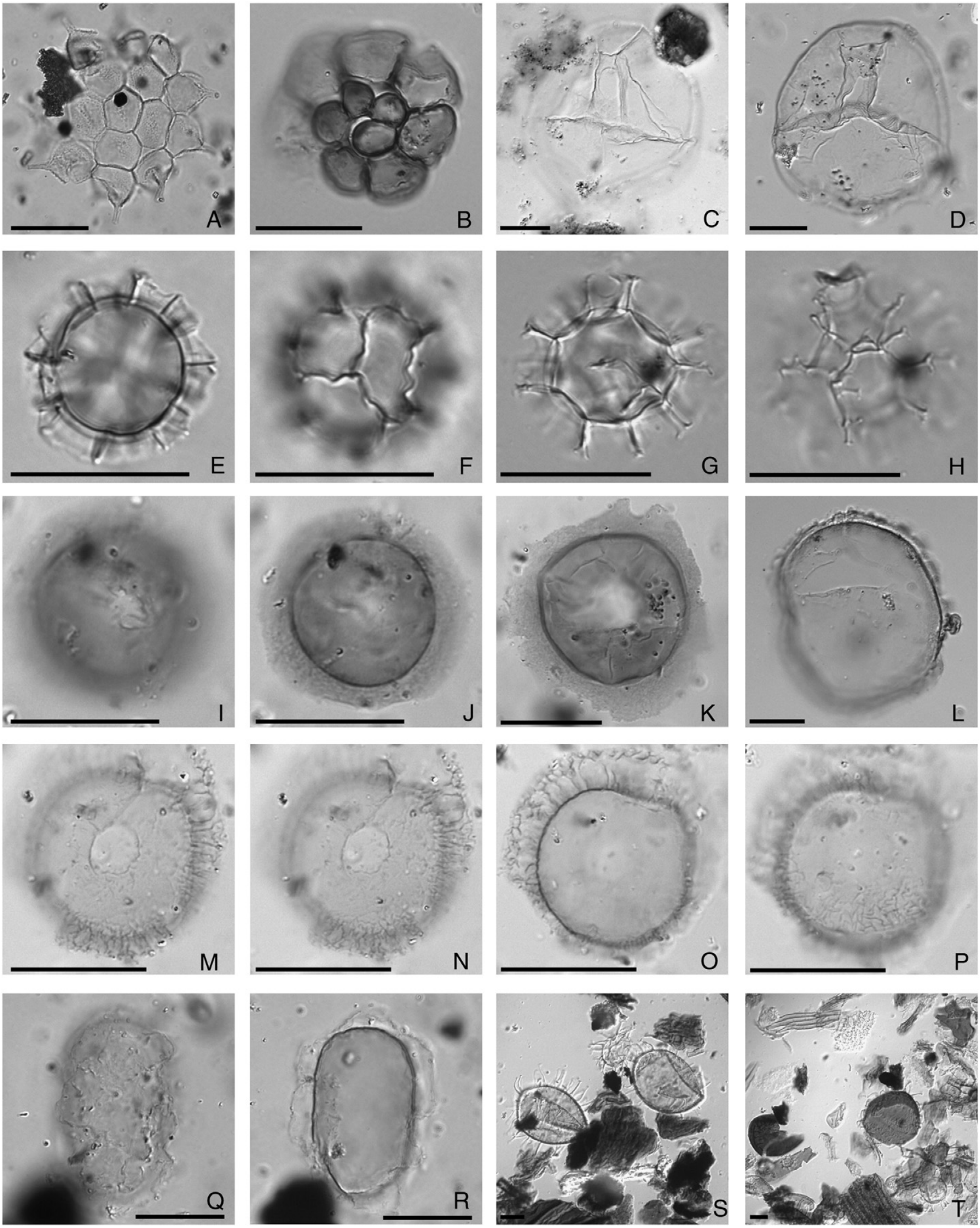
The invasion of cold water Pacific organisms around 4.5 Ma in the study area (Verhoeven et al., 2011) is a major environmental event, marked by the arrival of: (1) molluscs in unit 14 at the base of the *Serripes* Zone, (2) ostracods in unit 14 at the base of the *Cytheridae* zone and (3) dinocysts in unit 12/13 at the base of DAZ3 (Fig. 5). The dinocyst record shows at the base of DAZ3 (unit 12/13) an abrupt return of heterotrophic species. The renewed dominance of heterotrophic species may indicate an increased influx of nutrients, and a repression of the autotrophic dinoflagellates. The arrival of the Pacific species *Selenopemphix islandensis* in unit 13 marks this event (Verhoeven and Louwye, 2012). From its first arrival on, *S. islandensis* is always an important part of the assemblage (average 4.1%) and is restricted to DAZ3. *Trinovantedinium variabile* as well as the normal and undulate morphotype of *Selenopemphix nephroides* (Plate 1S, T) enter the assemblage at the beginning of DAZ3; these species were probably not present in the Tjörnes area before DAZ3. A Pacific origin can be suggested for *T. variabile* as it is a cold tolerant species, common in the Pliocene of the northern Pacific (Head, personal communication 2012). However, de Verteuil and Norris (1992) recorded both *T. variabile* and *S. nephroides* also in the Miocene of the coastal plain in Maryland and Virginia on the east coast of North America. Northward transport of these taxa by the Gulf Stream can therefore not be excluded. The shoaling of the Central American Seaway between 4.7 and 4.2 Ma forced not only Pacific water northwards through the Bering Strait but intensified at the same time the Gulf Stream (Steph et al., 2006).

The heterotrophic species *Barssidinium pliocenicum*, *Echinidinium euaxum* and *Brigantedinium* spp. flourish during the deposition of DAZ3, but were already present earlier in the Tjörnes area. The arrival of Pacific waters at the *Mactra*/*Serripes* Zone boundary at the base of DAZ3 was preceded in unit 11 by the brief appearance of *Operculodinium centrocarpum* sensu Wall and Dale (1966). This reflects changing water conditions preceding the transport of trans-Arctic water, since the species is an opportunist immediately occupying available ecological niches (Dale, 1996).

Unit 14 at the base of the *Serripes* Zone and DAZ3 is the first horizon of the zone in which Pacific invasive molluscs abound. Gladenkov et al. (1980) recognised at this level the entrance of 15 of the 22 invasive molluscs of the *Serripes* Zone (Fig. 5). The base of the *Serripes* Zone does not exactly correspond to the major invasion of Pacific molluscs, but instead to the upper limit of the presence of *Mactra* in the preceding zone. In the period between the extinction of *Mactra* in unit 12 and the entrance of Pacific molluscs in unit 14, the heterotrophic dinoflagellates already dominate in unit 12/13. Hence, the major invasion of Pacific molluscs post-dates the initial transport of Pacific water and nutrients through the Bering Strait. Although migration of Pacific molluscs was already possible during the time of unit 12/13, it was delayed for some reason.

As already mentioned, the invasive Pacific mollusc species have Arctic affinities (Bárdarson, 1925; Gladenkov et al., 1980; Símonarson and Eiríksson, 2008). As the isotope record of Buchardt and Símonarson (2003) does not show an abrupt temperature decline at the time (Fig. 6), the migration of cold water species cannot be explained by a cooling of the climate, more likely it may relate to a northward transport of water through the Bering Strait induced by the shoaling of the Central American Seaway (Verhoeven et al., 2011 and references therein). Only species adapted to cold water could cross the cold Arctic environment that acted as a filter (Einarsson et al., 1967). The opening of the Bering Strait, facilitating the Trans Arctic Invasion is dated between 5.5 and 5.4 Ma (Gladenkov et al., 2002). The age model of Verhoeven et al. (2011)

Plate 4. Photomicrographs of fresh water algae, acritarchs, linings of foraminifers and calcareous dinocyst. Scale bar indicates 20 μm. E.F. = England Finder coordinate. A: *Pediastrum* sp., sample WP4, *Serripes* Zone, E.F.: Q53; B: Foraminifera lining, planispiral, sample WP18, *Serripes* Zone, E.F.: N54/2; C, D: *Cyclopsiella*? *trematophora*, sample WP18, *Serripes* Zone, E.F.: M59/3 (C), sample WP4, *Serripes* Zone, E.F.: 33/2 (D); E–F: *Cymatiosphaera invaginata*, sample WP26, *Serripes* Zone, E.F.: O47; G–H: Algae cyst sp. 1 Head (1996), sample WP9, *Serripes* Zone, E.F.: K61/4; I–K: *Halodinium scopaeum*, sample WP26, *Serripes* Zone, E.F.: U43; L: *Paralecaniella indentata*, sample WP18, *Serripes* Zone, E.F.: N56/3; M–P: Acritarch sp.1, sample WP20, *Serripes* Zone, E.F.: Y55/4; Q–R: *Scripsciella trifida*, sample WP70, Svarthamar Member, E.F.: V48/1; S: assemblage dominated by autotrophic species such as *Operculodinium centrocarpum* s.s., sample WP59, E.F. K35; T: assemblage dominated by heterotrophic species such as *Barssidinium pliocenicum*, sample WP9, E.F.: X46/3.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dates the Trans Arctic Invasion at around 4.5 Ma; it may coincide with the shoaling of the Central American Seaway, dated between 4.7 and 4.2 Ma (Haug et al., 2001; Steph et al., 2006).

Coeval with the dominance of heterotrophic species, acritarch species such as *Cyclopsiella*? *trematophora*, *Cymatiosphaera invaginata* and *Halodinium scopaeum* appear in DAZ3. According to Matsuoka and Head (1992), the genus *Cyclopsiella* has an epilithic or encrusting form of life, and prefers shallow habitats as the organisms live in clusters on the sea floor with the pylome oriented upwards. High numbers and acmes of *Cyclopsiella* and *Paralecaniella* were recorded in the photic zone of energetic, shallow marine and nearshore deposits of the Upper Miocene Diest Formation in northern Belgium (Louwye and Laga, 2008). The restricted occurrence of these acritarchs in relatively high numbers only in DAZ3 is thus remarkable since the palaeobathymetry of the Tjörnes beds is quite low throughout the succession and theoretically suitable for these acritarchs. The sudden appearance of acritarchs in DAZ3 is most probably caused by a combination of environmental factors such as a low water depth, high energy and the trophic degree.

5.4. Temperature sensitive dinoflagellates

Dinocyst assemblages with affinity for clearly warmer sea water than today are recorded in the Early Pliocene zones DAZ1 to DAZ3, although some warm water heterotrophic species such as *Barssidinium pliocenicum* and *Echinidinium euaxum* are still present in the Lower Pleistocene DAZ4a. Thermophilic species are present in the top of DAZ1 and in the base of DAZ2. *Tectatodinium pellitum* is regarded as a thermophilic species, nowadays confined to subtropical to tropical marine environments (range 14–30 °C) (Marret and Zonneveld, 2003), and is used as an indicator of warm periods as far back as the Danian (Head and Nøhr-Hansen, 1999). *Tuberculodinium vancampoae* also has a recent tropical to subtropical distribution (range 12.7–29.5 °C) and is restricted to latitudes between 45°N and 45°S. Both species are confined to DAZ1 and the base of DAZ2 and this period can be regarded as the warmest of the studied interval at Tjörnes. No temperature maximum is however expressed in the W/C index, as only a few specimens of both species were found (Fig. 6). Nevertheless the presence of these tropical species demonstrates sufficiently that the warmest period must have been during the early deposition of the Tjörnes beds. Buchardt and Símonarson (2003) found the highest temperatures (15 to 20 °C) in the same interval of their oxygen isotope curve. The pollen study by Verhoeven et al. (2013) is in agreement with these findings and suggests summer air temperatures of at least 8 °C warmer than today during deposition of the *Tapes* Zone and 5 °C during deposition of the rest of the Tjörnes beds and the lower Pleistocene interglacial deposits.

As already mentioned, during the deposition of the Tjörnes beds and the lower part of the Pleistocene Breidavík Group, a mix of warm and cold water species occurs. Near the top of DAZ4b and DAZ5, the mixed dinocyst temperature signal changes into a distinct cold water signal indicated by the cysts of *Pentapharsodinium dalei*, *Bitectatodinium tepikiense*, *Spiniferites elongatus* and *Islandinium minutum*. *Bitectatodinium tepikiense* has the broadest thermal tolerance, but does not occur in the Arctic. The species prefers cold winter and warm summer SST. *Islandinium minutum* has a bipolar distribution, above 30°N and below 30°S. It is characteristic of subpolar and polar areas but has a broad temperature range. The species prefers large seasonal and inter-seasonal fluctuations of parameters such as temperature, salinity and insolation (Marret and Zonneveld, 2003). Cysts of *P. dalei* has a very broad temperature range, but occurs mainly in the temperate/subpolar regions of the northern hemisphere (Marret and Zonneveld, 2003). *Spiniferites elongatus* can be characterised as a cold to temperate species, accepting a broad range of temperatures (Marret and Zonneveld, 2003). The Pleistocene cooling registered in DAZ4a to DAZ6 shows a gradual trend (Fig. 3) with a continuous decrease of the warm water species *Lingulodinium machaerophorum*, a very rare species in areas with SST below 10 °C, and an increase in the cold water species cysts of *P. dalei* and *S. elongatus*. Simultaneously the cold tolerant species *B. tepikiense* shows a decrease from c. 20% to c. 6% near the top of DAZ5. The recent assemblage around Iceland (Marret et al., 2004) contains only c. 1% of this species. *Bitectatodinium tepikiense* most probably migrated southward during Middle Pleistocene times when the climate deteriorated. Based on the modern distribution of *B. tepikiense* (Marret and Zonneveld, 2003), the mean summer temperature decreased from c. 15 °C to c. 10/12 °C, and the mean winter temperatures ranged between 0 °C and 12 °C. Sea Surface Temperatures comparable with the present-day ones can thus be suggested for DAZ5. Today at the same latitude, the Irminger Current transports relatively warm water of c. 6 °C in winter to c. 11 °C in summer from the western side of Iceland to the northern part (Marret et al., 2004).

The extinct cold tolerant species *Habibacysta tectata* and *Filisphaera filifera* show a remarkable signal in the Tjörnes beds. Head (1994) suggests a broad thermal tolerance for *H. tectata*, as it is found in the Upper Miocene of the Gulf of Mexico as well as in Pleistocene sediments post-dating the northern hemisphere cooling. The species tolerates a broad range of water temperatures, from cool temperate to subtropical or tropical, but high numbers are mostly associated with cooler conditions. De Schepper et al. (2011) stated that Pliocene abundances in excess of 30% correspond to $SST_{Mg/Ca}$ values between 10 and 15 °C, confirming the cool-water affinities of the species. *Habibacysta tectata* has a highest occurrence in unit 14/15 of the *Serripes* Zone, and shows high values in the Tjörnes beds except in two samples with very few dinocyst counts. *Filisphaera filifera* has a maximum Pliocene $SST_{Mg/Ca}$ range of 10.7–25.2 °C (De Schepper et al., 2011) and is also considered to be cold tolerant (Head, 1996). *Filisphaera filifera* is present at the base of the *Tapes* Zone and then disappears from the record. The species re-appears in unit 11 (upper part of DAZ2) and has a highest occurrence in unit 21/22 (Fig. 5). *Habibacysta tectata* and *F. filifera* thus occur together in the Tjörnes beds only at the base of the *Tapes Zone* and at the base of the *Serripes* Zone (Fig. 3). In the sediments between, only *H. tectata* is present, while in the upper part of the *Serripes* Zone only *F. filifera* occurs. This may be caused by a temperature rise during deposition of the second half of the *Tapes* and the *Mactra* Zone and a temperature decline in the upper part of the *Serripes* Zone. According to this hypothesis, both species have a rather restricted latitudinal range with *F. filifera* more adapted to cold water. During the temperature rise, this species occurred north of Iceland, while during the temperature decline *H. tectata* occurred below Iceland. The isotope record by Buchardt and Símonarson (2003) however does not point to such an explicit warming (Fig. 6); their temperature curve shows rather a gradual decline with a restricted warming during deposition of the *Mactra* Zone. As no major warming is registered, the interruption of *F. filifera* during the second half of the *Tapes* Zone and the *Mactra* Zone has possibly to do with another parameter than temperature. The interruption also pre-dates the impoverishment of the dinoflagellates during DAZ2 and is hence not related to the relapse of nutrient supply.

The W/C index (Fig. 6) reflects temperature variations, but in this study it can also be influenced by changing water currents. For example, the appearance of the cold water tolerant species *Filisphaera filifera* and *Trinovantedinium variabile* at the base of DAZ3 co-occurs with high abundances of the warm water species *Barssidinium pliocenicum*, *Echinidinium euaxum* and *Brigantedinium* spp. This can be explained by the introduction of cold and nutrient rich Pacific water, favourable for heterotrophic warm water species but introducing cold tolerant species at the same time. The distribution of warm and cold water species would thus be driven not only by temperature changes of the local water masses, but also by incoming nutrients. The W/C index in the DAZ1 and DAZ2 are rather irregular and seem also to

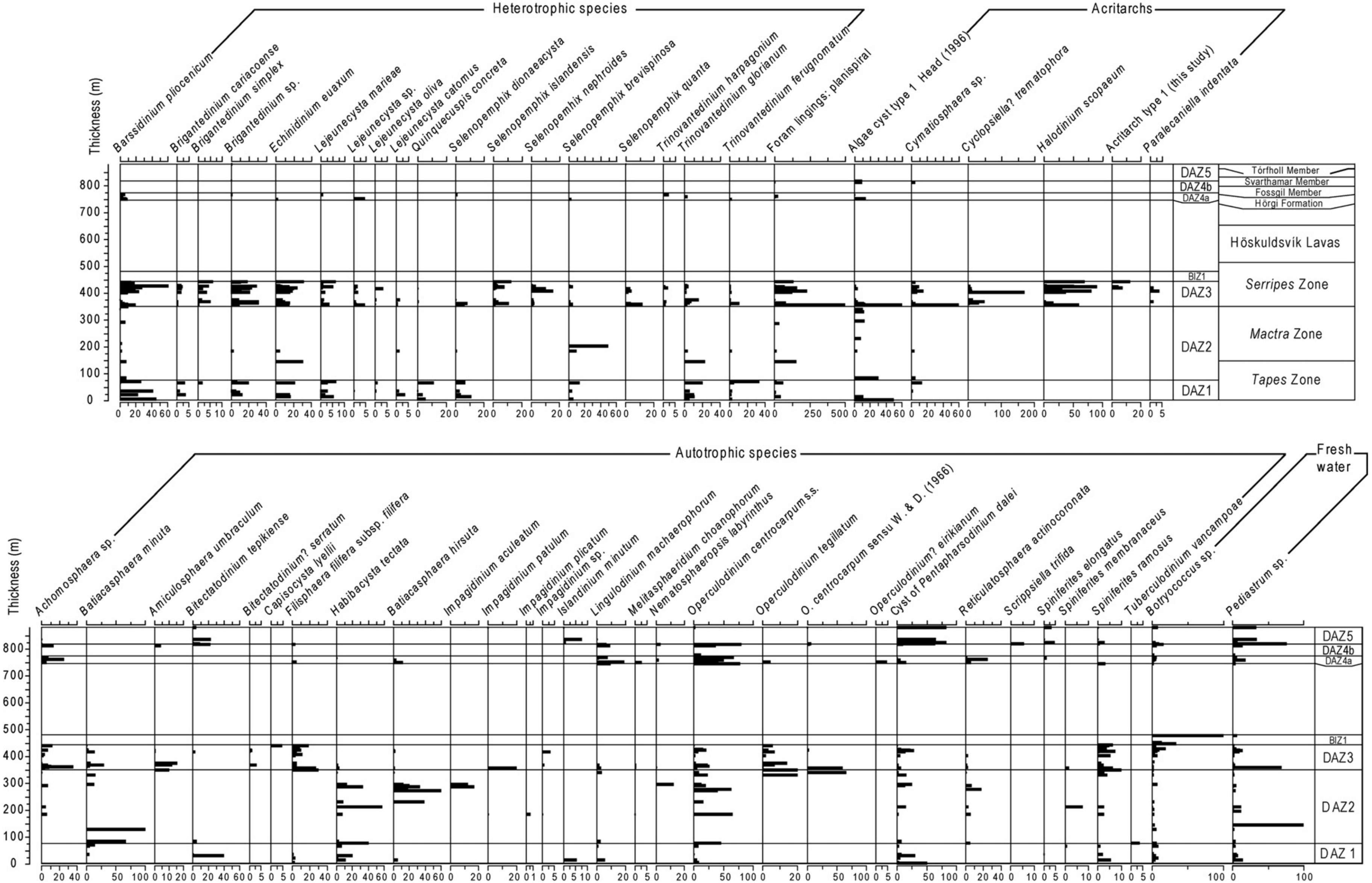

Fig. 3. Relative abundances of selected autotrophic and heterotrophic dinocyst species and acritarchs. The Dinocyst Zones (DAZ) are positioned against the stratigraphical scheme. Following Eiríksson (1981), the top of the Kaldakvísl lava's was taken as a zero-value for the thickness scale.

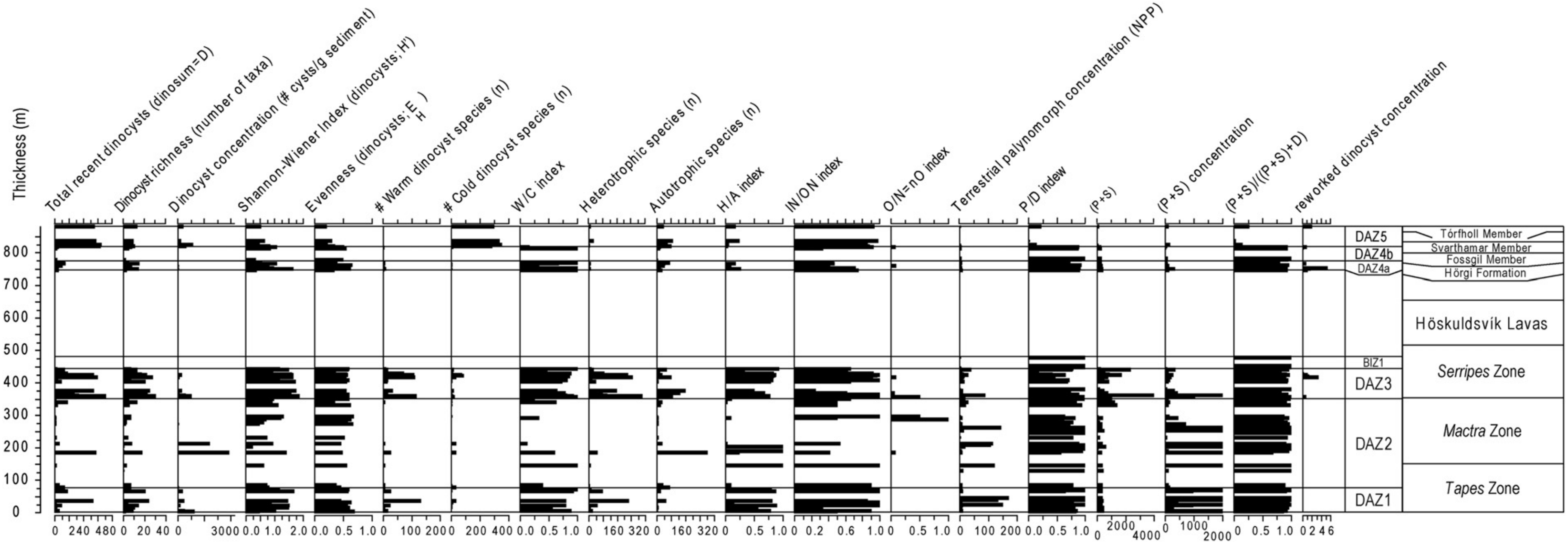

Fig. 4. Overview of palaeoecological indices with indication of the dinozones. The highest values of the pollen and spores concentration are levelled off at 2000 specimens/g for visualisation of the lower value variations. H = heterotrophic species (n); A: autotrophic species (n); IN = inner neritic species (n); ON = outer neritic species (n); P = pollen (n); S = spores (n), D = dinocysts (n).

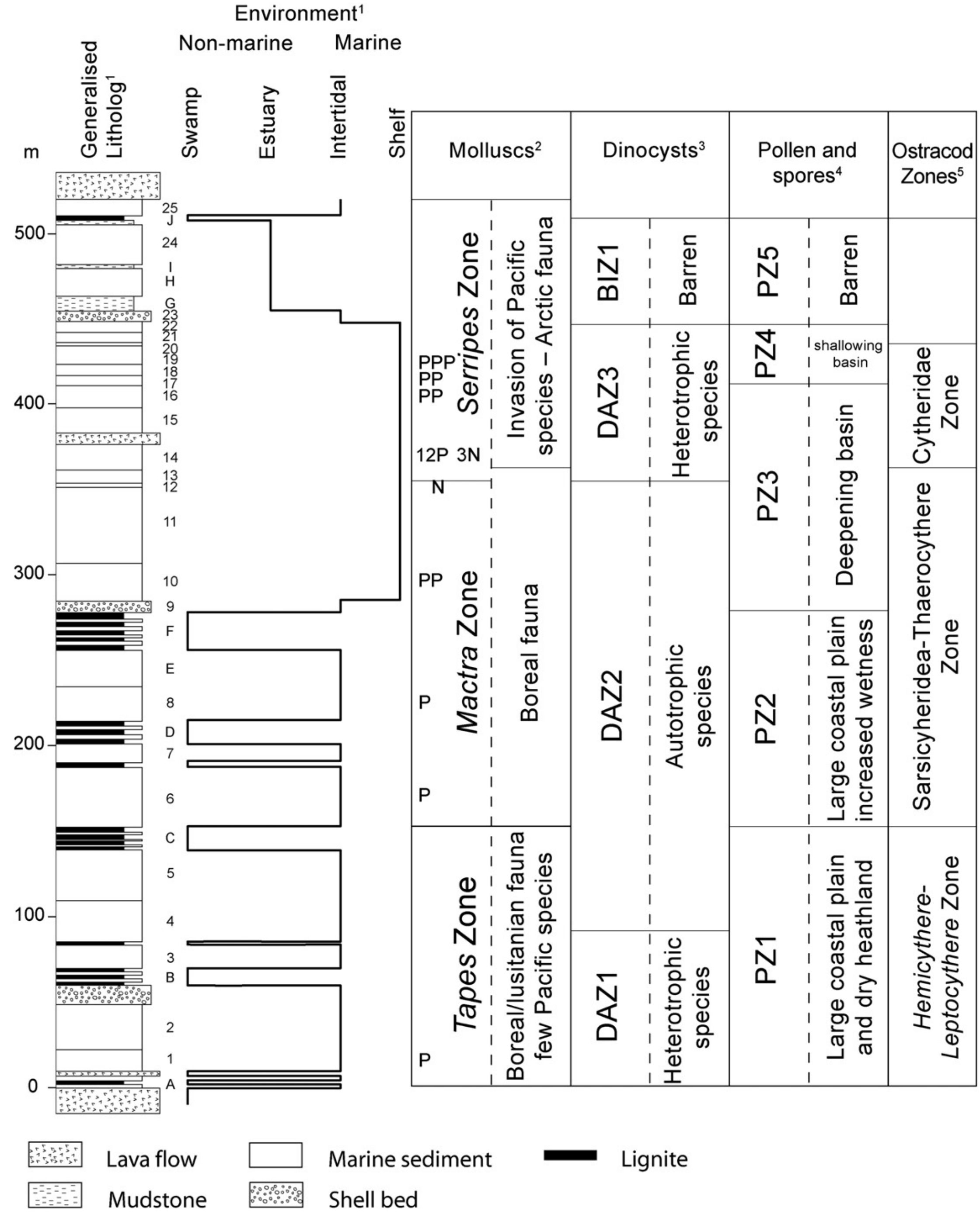

Fig. 5. The biozonations of the Tjörnes beds versus the lithology and the environmental interpretation of the depositional basin. The levels of introduction of Pacific mollusc species ("P" for general and "N" for naticids) are given (Gladenkov et al., 1980; McCoy, 2007).
1. Litholog and environmental interpretation after Buchardt and Símonarson (2003); 2. after Bárdarson (1925), Norton (1975) and Gladenkov et al. (1980); 3. this study; 4. after Verhoeven et al. (2013); 5. after Cronin (1991).

be influenced not only by temperature as registered by the O^{16}/O^{18} curve (Fig. 6). The impoverishment of the assemblage in DAZ2 resulted in the decrease of mainly warm water heterotrophic species. This resulting decline in the W/C index is not recorded by other marine or terrestrial temperature proxies (Fig. 6) and is apparently not an indication of cooling. During deposition of DAZ3 (lower *Serripes* Zone), a certain decrease in the W/C index preceding that of the oxygen isotope temperature curve occurs as recorded by the decline of *E. euaxum* and *B. pliocenicum* (Figs. 3, 6). Although cold water species appear in DAZ3, their influence is limited and the W/C index seems to follow the isotope temperature curve. However, the W/C index changes precede slightly those based on the isotopes recovered from the molluscs.

6. Conclusions

Dinocysts from 68 samples of the Tjörnes beds and 20 samples of four Lower and Middle Pleistocene interglacial units of the Breidavík Group were studied, and allowed a division of the sedimentary succession into five dinocyst assemblage zones.

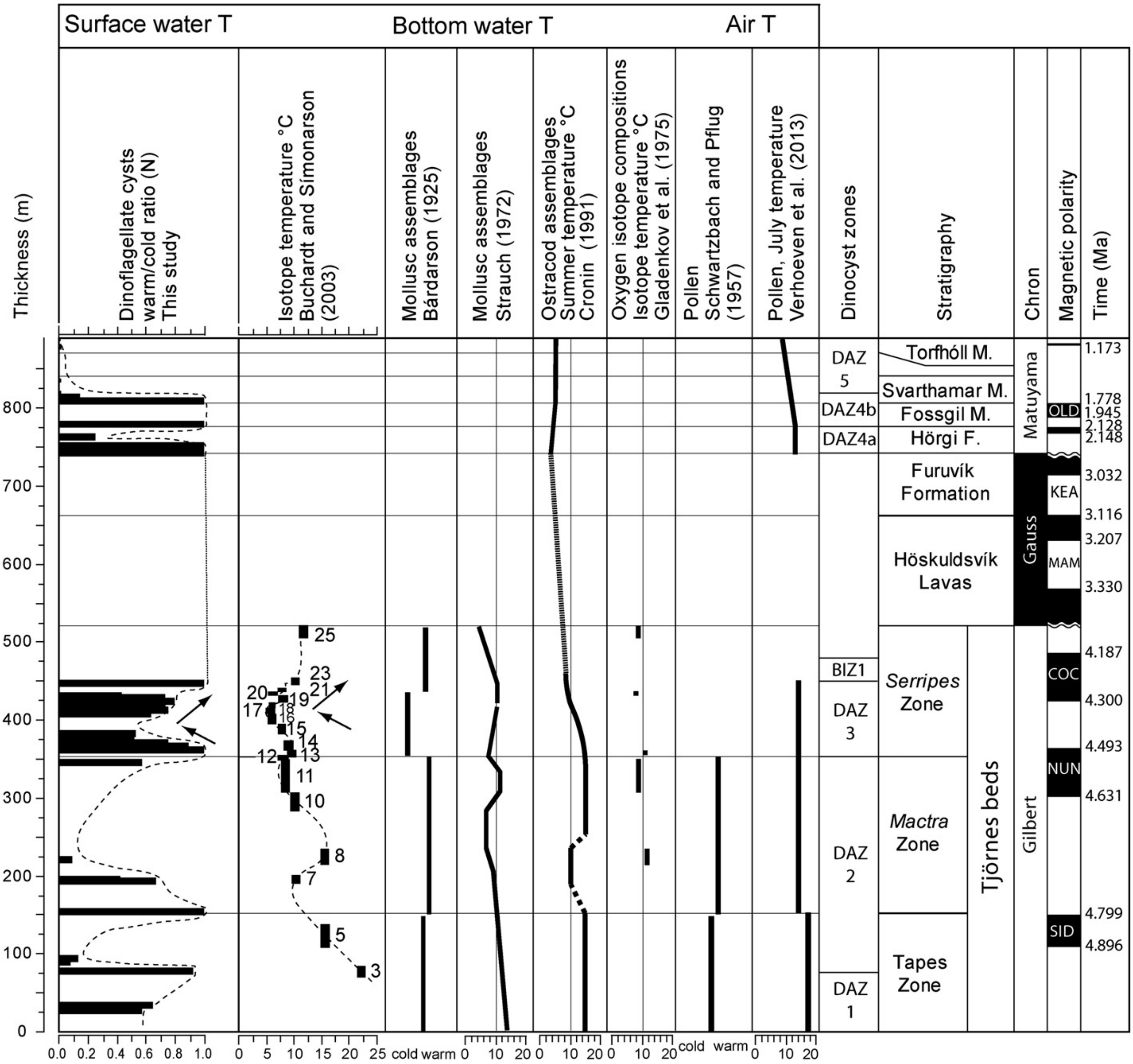

Fig. 6. The W/C index of the dinocysts compared with the temperature proxies of the Tjörnes section.
Modified after Buchardt and Símonarson (2003) and according to the age model of Verhoeven et al. (2011).

The assemblages defining DAZ1 to DAZ3, corresponding to the Tjörnes beds, are quite similar to those of the shallow marine Lower Pliocene of the southern North Sea Basin. DAZ4 can be regarded as an ecologically transitional zone during the Early Pleistocene, in which the heterotrophic species disappeared and extant cold water species are introduced. The uppermost DAZ5 starts in the middle of unit 10 of the Svarthamar Member around 1.7 Ma and much resembles the present-day assemblage north of Iceland. The assemblage of DAZ5, dominated by cysts of *Pentapharsodinium dalei* and accompanied by *Operculodinium centrocarpum* sensu Wall and Dale (1966) can be linked to a position near the Polar Front and suggests that this present-day palaeoceanography came into being at that time.

The dinocyst assemblages signal two important ecological events in the Tjörnes beds, separated by impoverished dinocyst assemblages. DAZ1 is dominated by heterotrophic dinocysts and is abruptly followed by DAZ2, dominated by autotrophic species. This event can be explained by a sudden decrease of nutrient supply, probably caused by a shift of the Polar Front. Although not entirely coincident, this event can be correlated to the change from a *Tapes* dominated molluscan assemblage to a *Mactra* dominated molluscan assemblage. The drastic decline in nutrients can be the cause of the disappearance of *Tapes* and the transition to the *Mactra* assemblage.

The second event coincides with the *Mactra*/*Serripes* transition (base DAZ3) and can be explained by the introduction of Pacific water in the northern Atlantic via the Bering Strait. This event has been linked to the shoaling of the Central American Seaway around 4.5 Ma, which pushed water northwards through the Bering Strait. The cold, nutrient rich water caused the heterotrophic species to thrive and introduced cold water tolerant species in the Tjörnes area. *Selenopemphix islandensis*, *Trinovantedinium variabile* and *Filisphaera filifera* subsp. *filifera* are now clearly present in the assemblage. A major migration wave of Pacific molluscs, observed in unit

14, apparently post-dates the opening of the northern passage through the Bering Strait by some ten thousand years.

The changes in the curves of temperature sensitive dinoflagellates show a clear relation with the presence of nutrients and changed ocean currents. W/C indices have thus to be evaluated with caution.

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