

3. POLLEN AND DINOFLAGELLATE CYSTS OF THE UPPER 50 M OF SITE 958¹

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ABSTRACT

Palynological investigation (pollen, spores, and dinoflagellate cysts) of 39 samples from the upper 50 m of Ocean Drilling Program (ODP) Site 958 provides some complementary information about the history of the northeast trade winds and the African Easterly Jet. Unfortunately, with the exception of upper Pliocene sediments from Hole 958A between 31 and 41 mbsf and one other sample at 22.25 mbsf, most of the investigated sediments being of late Pliocene and Pleistocene age showed a poor pollen preservation. Samples with good pollen preservation showed a flora dominated by pine pollen. Pollen from the Sahara was infrequently found indicating that the African Easterly Jet was very weak. The dinoflagellate cyst assemblage is typical for the oceanic environment of the North Atlantic. A hiatus between 44 and 42.50 mbsf is confirmed by the last occurrence of cysts of *Invertocysta*.

INTRODUCTION

Ocean Drilling Program (ODP) Site 958 (24°00'N; 20°00'W) is situated on the northwestern fringe of the present-day dust plume brought over the East Atlantic by the northern branch of the African Easterly Jet (AEJ; Fig. 1; Sarnthein et al., 1981). The AEJ dust plume can be distinguished by its pollen content, which predominantly contains Chenopodiaceae-Amaranthaceae (Cheno-Ams) pollen from the Sahara (Hooghiemstra et al., 1986). The site is also situated at a latitude where trade winds still bring considerable amounts of pine pollen from the Canary Islands, but where the relative abundance of trade-blown pollen from the Mediterranean area diminishes rapidly southward (Hooghiemstra et al., 1986). Influences of the two wind systems are well recorded at sites located somewhat nearer to the continent between 23°N and 25°N. Sediments of those sites show abundant pine pollen as well as a dominance of Cheno-Ams pollen. In sediments farther south, the relative abundance of pine declines to low values, and farther north, the domination of Cheno-Ams pollen ceases (Agwu and Beug, 1982; Hooghiemstra, 1988a; Dupont et al., 1989; Hooghiemstra et al., 1992). The pollen record of Site 958 has the potential to record the balance between the strength of the trade winds and the range of the AEJ. Analysis of dinoflagellate cysts can provide information about stratigraphy and surface water properties.

MATERIAL AND METHODS

For this pilot study, one sample per section (1.5 m) was obtained. Samples of ~20 mL were split over a 250- μ m sieve, after the actual sample volume was measured by water displacement (Tables 1, 2). The larger fraction (mainly foraminifer shells) was dried and stored. The smaller fraction was decalcified in diluted HCl and two *Lycopodium* tablets were added, each containing $12,542 \pm 512$ marker spores. Afterward, concentrated HF (~70%) was added up to twice the sample volume. Samples were kept in the HF solution for several days. After washing with water, the clay and organic debris fraction smaller than 10 μ m was removed by ultrasonic sieving. The final residue was stored in glycerine, in which the slides were mounted and analyzed as well.

Samples were counted until either 300 dinoflagellate cysts and/or 300 pollen grains were found or all material was analyzed. Especially in very poor samples, losses caused by the preparation are considerable. By the ratio of added to found markers, I determined the proportion of the original sample that was actually analyzed. This value is given—in percentages—in Tables 1 and 2. By dividing the given counts with the volume (column 2) and the percentage of the sample counted (column 3) and multiplying the result by 100, concentration

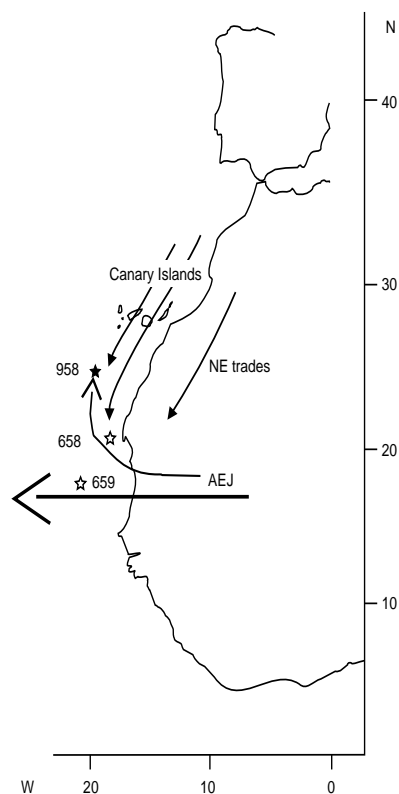


Figure 1. Outline of West Africa and Spain. Locations of ODP Site 958 (solid star) and ODP Sites 658 and 659 (open stars); trajectory of the northeast trade winds (solid arrows) and the mid-tropospheric African Easterly Jet (AEJ; open arrows).

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Table 1. Pollen counts from Hole 958A.

Core, section, interval (cm)	Volume (mL)	Percent of sample counted	Total pollen counted	Total spores	Counts of selected pollen taxa															
					Asteraceae Liguliflorae	Asteraceae Tubuliflorae	Artemisia	Caryophyllaceae	<i>Gypsophila</i>	Chenopodiaceae- Amaranthaceae	Cyperaceae	<i>Ephedra</i>	<i>Indigofera</i>	<i>Cassia</i>	<i>Olea</i>	<i>Pinus</i>	cf. <i>Cathaya</i>	Poaceae	cf. <i>Podocarpus</i>	
159T-958A-																				
3H-3, 25-30	25	1.62	271	5	5	19	3	1	2	43	4	4					158		16	5
4H-2, 25-30	20	6.95	301	5	2	7	19	20	5	64	34	22	1			1	99		17	
4H-3, 25-30	24	12.48	297	7	1	3	23	4	1	31	14	10	1			1	181		20	
4H-4, 25-30	24	3.32	296	2		2				1		2					288		2	
4H-5, 25-30	23	6.21	292	5	1	2		1		2						1	272		4	
4H-6, 25-30	23	9.99	275	8	5	6	2		1		1					1	239		5	3
4H-7, 25-30	21	1.98	319	5	5	10	2			1	2	6					278	1	4	1
5H-1, 25-30	21	9.82	312	5	7	6	17	20		43	14	13	1			3	136		18	1
5H-2, 25-30	18	18.54	250	4	2	6	7	23	1	50	11	6				1	124		9	
5H-3, 25-30	20	11.56	304	3	1	4			1	1	1						291		4	
5H-4, 25-30	21	3.83	305	2	3	6				1	2	2				1	267		4	11

Table 2. Dinoflagellate cyst counts from Holes 958A and 958B.

Core, section, interval (cm)	Volume (mL)	Percent of sample counted	Total cysts counted	<i>S. hyperacanthus</i>	<i>S. membranaceus</i>	<i>S. mirabilis</i>	<i>S. pachydermis</i>	<i>S. ramosus</i>	<i>S. bulloides</i>	<i>S. belerius</i>	<i>S. delicatus</i>	<i>N. labyrinthus</i>	<i>I. aculeatum</i>	<i>I. pattulum</i>	<i>I. striolatum</i>	<i>I. paradoxum</i>	<i>I. sphaericum</i>	<i>O. israelianum</i>	<i>O. centrocarpum</i>	<i>O. janducheni</i>	<i>B. tepikiense</i>	<i>P. zoharyi</i>	<i>L. machaerophorum</i>	<i>Brigantedinium</i> sp.	<i>P. faroense</i>	<i>S. nephroides</i>	<i>P. reticulata</i>	<i>A. choanum</i> , <i>A. confisum</i> *	<i>Invertocysta</i> sp.		
159T-958B-																															
1H-1, 25-30	23	11.71	303	2	7	12						2	137	98	12	20	3			3		1	1								
1H-2, 25-30	22.5		Sterile																												
1H-3, 25-30	21	6.66	302	3	5			1			2	5	173	60	17	10	4		5	3				6							
1H-4, 25-30	24	12.16	186										108	74		1				2											
1H-5, 25-30	21	7.29	313	3	2	9	1		1	3		99	116	23	21	1	1		1	1		1	1								
1H-6, 25-30	19	16.06	300	1	1	2						4	265	10	2	5	2		3	1		1									
159T-958A-																															
1H-1, 23-28	17	8.56	228	8	9	22		2	3		3	7	86	30	4	10	2	1	12	3		1	10	1	1			2			
1H-2, 25-30	19.5	3.12	109		1	10						2	75	6		1		2	4	2		6									
1H-3, 23-28	27	3.94	299	4	6	6				1		18	209	16	2	12	2		6	1		2	2								
1H-4, 26-31	23		Sterile																												
1H-5, 25-30	23	6.38	303	2	2	3		2		2	4	10	147	90	2	6	1		3	3		13	1	1	1		1				
1H-6, 25-30	21	8.14	226	1	1	1		1	1			5	126	12	3	36	2	4	24	3			1	1	1						
1H-7, 25-30	23	4.58	300		1	2					1	8	259	12	2	12	1		1												
2H-1, 25-30	23	5.44	265	4	4	5		1	3	1	6	22	153	22	1	18			9	1		1	1					1			
2H-2, 25-30	22	1.42	303	1	4	11		1	1	1	1	4	203	54	2	7			9			1						1			
2H-3, 25-30	26		Sterile																												
2H-4, 25-30	23		Sterile																												
2H-5, 25-30	20	1.48	307	16	20	42				1	2	3	57	136	1	7	1		4	2			1								
2H-6, 25-30	19	2.49	312	3	3	18			2		3	3	130	28	7	38	1	2	9	4		1	44			1	1				
2H-7, 15-20	18	7.92	306	3	4	6		1			4	7	185	48	2	25			2	4			4						7		
3H-1, 25-30	21	7.06	268	7	15	12			2		13	2	134	43	2	11	1		4	1		1	1		1	1					
3H-2, 25-30	24	5.00	274	34	26	33					2	4	96	20	11	10			16	1											
3H-3, 25-30	25	0.24	317	28	15	37	2	2	8	4	38	4	54	18	2	7		7	23		8	8		3	2						
3H-4, 25-30	22	7.07	315	13	7	24	1				1	141	30	7	25	2	1	22		1		1									
3H-5, 25-30	22	2.52	331	46	26	71	1		1			3	79	45	4	7		1		1											
3H-6, 25-30	21	4.39	325	22	10	63	6				1	2	4	121	7	3	14	1	9	25		1	2								
4H-1, 25-30	19	2.66	316	4	8	20		1	1	4	5	179	15	1	14	1	2	19		1		3	3						17		
4H-2, 25-30	20	6.95	306	16	8	35		2		1	2	143	18	4	18	1	4	8	1		1	2	12		1	1	1	1	4		
4H-3, 25-30	24	3.15	346	1		2		1			5	2	66	10	1	15		1			228				1		1	1			
4H-4, 25-30	24	3.32	323	2	6	9		1	2		2		143	58	9	30		10	30	1	1	1	7						7		
4H-5, 25-30	23	6.21	316	2	4	7			2	2	7		156	15	7	43	1	16	13			22							1	1	
4H-6, 25-30	23	2.98	306	1	2		1		1		7	2	147	52	2	37	1	4	14				5	4	2		3	7			
4H-7, 25-30	21	0.67	410	10	2	9		3	15	13	11	11	191	12	6	45	1	14	9		1	2	3	8		15	9		1		
5H-1, 25-30	21	3.42	336	2	1	6		2	2	3	7	151	13	8	77	1	20	7			2	1	12	1		3	5		5		
5H-2, 25-30	18	7.43	302	1	3	5		29	4	1	20	10	81	40	6	57	1	5											3	1	
5H-3, 25-30	20	4.04	308			2	1				1	3	144	71	10	21		38				1	4	1				4	2		
5H-4, 25-30	21	3.83	340	2		3	2	1	19	4	2	3	124	6	7	101	3	3	11		1	2	1	3	2	13	5		8		
5H-5, 25-30	20	6.01	318	4	1	2				1	2		91	16	2	34		15	21	5						2	2		97		
5H-6, 25-30	19	1.98	304		3	11					9	8	62	11	6	41		8	11	2		1				5	1*		105		

values per milliliter may be obtained. In Table 1, those samples that did not provide statistically reliable pollen counts have been omitted.

Pollen grains were identified using the reference collection of the Institute of Palynology and Quaternary Sciences in Göttingen (Federal Republic of Germany) and literature concerning African pollen morphology. Dinoflagellate cysts have been determined mainly after Turon (1984), Marret (1994), De Vernal et al. (1992), and in personal communication with Fabienne Marret (1991), Gerard Versteegh (1996), and Lucy Edwards (1996).

RESULTS AND DISCUSSION

Preservation of Palynomorphs

From the upper 50 m of sediments of Hole 958A and from the upper 10 m of Hole 958B, one sample per section was analyzed. The samples turned out to be poor in palynomorphs. Samples 159-958B-1H-2, 25–30 cm, 159-958A-1H-4, 26–31 cm, 159-958A-2H-3, 25–30 cm, and 159-958A-2H-4, 25–30 cm, were sterile. The other samples contained dinoflagellate cysts ranging in concentration from 100 to 1000 cysts per milliliter with two exceptions: 159-958A-3H-3, 25–30 cm, and 159-958A-4H-7, 25–30 cm, which contained about 5400 and 3000 cysts per milliliter, respectively. Those two samples also contained numerous pollen (~700 and 800 grains per milliliter). Other samples that contained pollen were found in Hole 958A between 31 and 41 mbsf (159-958A-4H-2, 25–30 cm, through 5H-4, 25–30 cm). Pollen concentrations in that part ran between 70 and 400 grains per milliliter. Other samples were sterile or semisterile in pollen. Table 1 gives the pollen counts of those samples that were not sterile or semisterile; Table 2 gives the dinoflagellate cyst counts.

There are three possible explanations for the low pollen concentrations of sediments of ODP Site 958: first, no pollen may have been produced in the vicinity, neither in the Mediterranean area nor in the Sahara or on the Canary Islands; second, pollen may have been produced, but was never transported to the site; third, pollen may have reached the site, but was destroyed afterwards in the sediment. The first option is ruled out because the numerous Pleistocene and Pliocene pollen diagrams from the western Mediterranean area, Northwest Africa, and the East Atlantic Ocean give evidence of Mediterranean Pine and Oak forests, *Artemisia* steppes, increase of *Ephedra* during glacial periods, abundant Chenopodiaceae-Amaranthaceae pollen from the Sahara, and Poaceae pollen from the Sahel, etc. (for instance Cour and Duzer, 1980; Agwu and Beug, 1982; Suc, 1986; Suc et al., 1995a, 1995b; Hooghiemstra, 1988a, 1989; Hooghiemstra et al., 1992; Lezine et al., 1990; Leroy and Dupont, 1994). The second option is also unlikely because the semisterile or sterile samples would imply a complete cessation of the different wind systems (trades, AEJ) as pollen carriers, which is in strong contrast with findings from other sites in this part of the eastern Atlantic (Caratini et al., 1979; Caratini and Cour, 1980; Agwu and Beug, 1992; Hooghiemstra et al., 1986; Dupont et al., 1989; Leroy and Dupont, 1994). This leaves us with the last option, the possibility of destruction of pollen in the sediment.

Lithology of the pollen-bearing sediments indicates nannofossil oozes without many foraminifers that are mottled light green to white or greenish in color. The color of the sediments lacking pollen is mostly white to light gray with pink or brown (Firth et al., 1996). The color may indicate oxidation processes that may have destroyed pollen in the sediments after deposition. Keil et al. (1994) showed that pollen is more oxygen sensitive than dinoflagellate cysts are, which explains why in pollen-bare sediments dinoflagellate cysts still have been found. With one exception, the pollen-bearing sediments are restricted to the physical properties Unit P2 (from 159-958A-4H-1, 33–38 cm, through 5H-5, 33–38 cm) characterized by low grain densities and lower porosities (Fig. 2; Firth et al., 1996). The different structure

of the sediments of Unit P2 may have prevented the penetration of enough oxygen to destroy its pollen content, or—the other way round—reduced oxidation of the sediments preserved organic matter explaining the lower grain densities. The one pollen-rich sample outside Unit P2 is a quartz-bearing light- to olive-gray nannofossil ooze (159-958A-3H-3, 25–30 cm). The palynological content, so far investigated, is thus rather disappointing. The lower parts of the section also have high grain densities; therefore, further palynological investigation is not particularly promising.

Pollen

The samples that do contain pollen are dated by nannofossil stratigraphy between 1.60 and 2.76 Ma (Firth et al., 1996). They show a flora strongly dominated by pine pollen (Fig. 3). The flora is comparable to the one found in samples of DSDP Site 397 (at 27°N, south of Gran Canaria) of about the same age (Leroy, unpubl. data), but differs strongly from the flora found at ODP Site 658 (20°45'N, 18°35'W; Leroy and Dupont, 1994) and farther south (ODP Site 659: 18°04'N, 21°02'W). The dominance of pine pollen may be an effect of differential decomposition (Havinga, 1984; Rossignol-Strick and Planchais, 1989). However, the samples with the lower pollen concentrations do not have the higher *Pinus* percentages. More probably, they are recording the existence of pines growing on the Canary Islands. Although pine pollen coming from the western Mediterranean area is not excluded, the nearest possible source area is on the Canary Islands, and therefore the more important one. Pine trees never grew in the Sahara; thus, that area can be excluded as a source.

The transport of pine pollen southward by the northeast trade winds combined with a reload from the Canary Islands is well demonstrated in sediments of Holocene age (Hooghiemstra et al., 1987). During the late Quaternary interglacial–glacial cycles, fluctuations in the atmospheric circulation, and the growth of pine trees on the Canary Islands alter the proportion of pine and Chenopods pollen (Du-

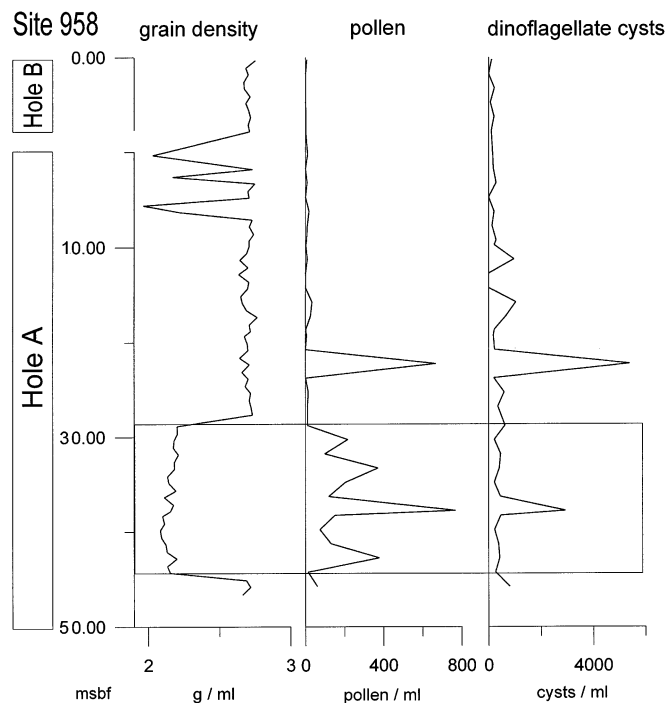


Figure 2. Grain density (g dry weight per mL, after Firth et al., 1996), pollen concentrations per milliliter, and dinoflagellate cyst concentrations per milliliter. Rectangle indicates physical properties unit P2 (Firth et al., 1996).

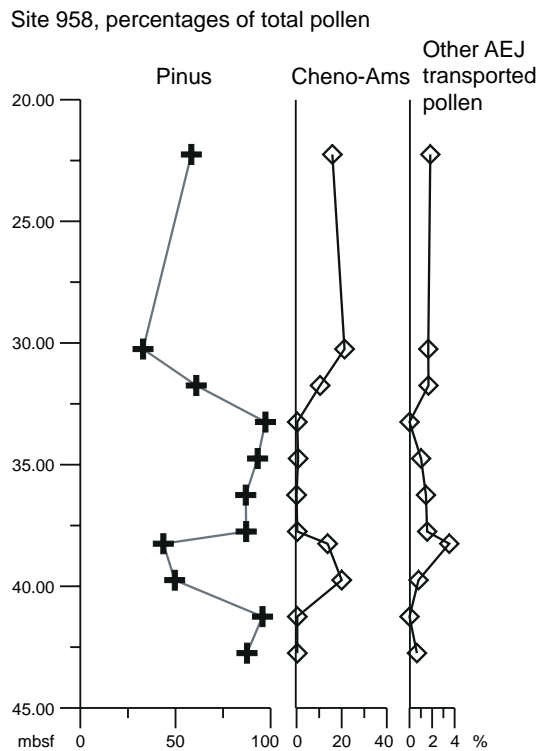


Figure 3. Percentages of *Pinus*, Chenopodiaceae-Amaranthaceae (Cheno-Ams), and other AEJ-transported pollen types calculated on the total of pollen counted. Only samples of Hole 958A containing sufficient amounts of pollen were plotted.

pont, 1989). Although at full interglacial conditions trade wind strength decreases, pine pollen percentages increased to 35% at 23°30'N and to 60% at 25°N because of the increased source area of pine pollen on the Canary Islands (Agwu and Beug, 1982). A strong reload of the trade winds with pine pollen thus compensates their reduced transport capacity (Hooghiemstra et al., 1987; Hooghiemstra, 1988b, 1989). At full glacial conditions, the AEJ stays at about the same latitude as during an interglacial, whereas the range of the AEJ dust plume with, among others, Cheno-Ams pollen reaches farther oceanward, thus increasing the relative abundance of Cheno-Ams pollen (Sarnthein et al., 1981; Sarnthein and Koopmann, 1980; Hooghiemstra et al., 1987). Palynological investigation of marine surface sediments and comparison with terrestrial surface samples show that Cheno-Ams pollen is indicative of the outflow of both the Saharan Air Layer and of the AEJ (Hooghiemstra et al., 1987; Lezine and Hooghiemstra, 1990).

The extremely high pollen percentages of *Pinus* and the very low ones of Cheno-Ams can theoretically indicate strong trade winds, many pine trees, a weak AEJ, or a combination of these things. During the Pliocene, several steps toward a more arid climate occurred in Northwest Africa. The dust record of ODP Site 659 showed an early start of the aridification of the southern Sahara and Sahel 4.6 Ma followed by further aridification steps at 4.3, 4.0, 3.6, 2.1, and 0.8 Ma. It is likely that rivers existed in the central Sahara, drying up during the Pliocene. However, the position of ODP Site 958 is too far from the coast to expect large amounts of river-borne pollen grains. Sediments of ODP Site 658 record a stepwise increase of the trade winds. However, the atmospheric circulation was weaker than today and trade winds are estimated to have been much weaker compared to their vigor during the Brunhes Chron (Chamley and Diester-Haass,

1979; Tiedemann et al., 1989; Stein et al., 1989; Leroy and Dupont, 1994). The possibility of strong trade winds is, therefore, unlikely.

Some pollen grains of plants from the dry tropical forest (for instance from *Cassia* or *Indigofera*; Table 3) were found, but are rare. Those pollen grains could have been transported from the southern Sahara to the site by means of the northern branch of the AEJ. The dust record of ODP Site 659 indicates that the AEJ already existed in the Pliocene (Tiedemann et al., 1989). However, the low Cheno-Ams pollen percentages and the scarcity of other southern elements indicate that the AEJ—at least its northern branch—was very weak.

Dinoflagellate Cysts

Dinoflagellate cyst flora (Table 4) resembles the oceanic flora of the North Atlantic upper Pliocene and Pleistocene (Harland, 1979, 1983; Mudie, 1987; McCarthy and Mudie, 1996; Versteegh, 1995). The most abundant species is *Impagidinium aculeatum* (Fig. 4). Because the pollen is mostly gone from the sediments, selective decomposition of dinoflagellate cysts at the site must be taken into account. This may explain the low counts of *Brigantedinium* and other peridinioid cysts, and the high counts for *I. aculeatum* (Zonneveld et al., 1997). Although the high relative abundance of this species is probably enhanced by its low sensibility to oxidation, *I. aculeatum* still indicates the full oceanic conditions of the surface waters over the site. The samples that also contain pollen, indicating relatively good preservation conditions, have *I. aculeatum* percentages of up to 50%.

Sample 159-958A-4H-3, 25–30 cm, shows surprisingly high values of *Polysphaeridium zoharyi* (66% of the cysts total). Cysts of *P. zoharyi* are found in estuarine tropical environments and high salinity conditions (Wall et al., 1977; Harland, 1983; Morzadec-Kerfourn, 1988a, 1988b, 1992). *P. zoharyi* cysts have rarely been found in tropical deep-sea sediments or along the continental slope in substantial amounts (Wall et al., 1977; Morzadec-Kerfourn, 1988a), although Harland (1983) described up to 10% of *P. zoharyi* cysts in deep-sea samples from the east Atlantic that are located in the relative vicinity of ODP Site 958. However, the finding of extremely large percentages (exceeding 60%) remains unexplained. The sedimentology of Hole 958A gives no evidence of strong disturbances or turbidites that could explain displacement over long distances from the coast to the site. An explanation including high salinity levels caused by an outflow event of the Mediterranean would need much more corroboration and seems also unlikely in the view of the southern position of the site.

Samples 159-958A-5H-5, 25–30 cm, and 5H-6, 25–30 cm, contain ~30% *Invertocysta* cysts (Fig. 4). Relative abundance of *Invertocysta* sharply drops to 2% at 5H-4, 25–30 cm, and occurs with single specimens up to 4H-7, 25–30 cm. Both *Invertocysta tabulata* and *Invertocysta lacrymosa* occur. However, due to uncertainties in the identification, I have lumped both taxa together. *I. lacrymosa* shows high relative abundances (up to 30% at DSDP Site 607) in the North Atlantic Ocean and the Mediterranean (Singa section) just before it disappears during nannofossil zone NN16 at 2.75 Ma (Versteegh, 1995). After that date, *Invertocysta* (*I. lacrymosa* and *I. tabulata*) are only rarely found. An exception is reported by McCarthy and Mudie (1996). They found *I. lacrymosa* from nannofossil Zone NN19 in turbiditic sediments of ODP Site 898 at the Iberian Abyssal Plain. The high percentages of *Invertocysta* suggest that Sample 159-958A-5H-5, 25–30 cm, is not later than 2.75 Ma. The hiatus observed in the nannofossil stratigraphy is thereby confirmed (Firth et al., 1996).

CONCLUSIONS

Pollen is badly preserved in sediments of ODP Site 958 except for the section between 31 and 41 mbsf (Hole 958A), where grain density

Table 3. Possible AEJ-transported pollen grains found at ODP Site 958.

<i>Acacia</i> (Mimosaceae)
<i>Alchornea</i> (Euphorbiaceae)
<i>Balanites</i> (Balanitaceae)
<i>Cadaba</i> (Capparidaceae)
<i>Caesalpinziaceae</i> pp.
<i>Calligonum</i> (Polygonaceae)
<i>Canthium</i> (Rubiaceae)
<i>Cassia</i> (Caesalpinziaceae)
Chenopodiaceae-Amaranthaceae
Combretaceae
<i>Commiphora</i> (Burseraceae)
<i>Cordia</i> (Boraginaceae)
<i>Dodonaea</i> (Sapindaceae)
<i>Indigofera</i> (Fabaceae)
<i>Lansea</i> (Anacardiaceae)
<i>Nitraria</i> (Zygophyllaceae)
<i>Phyllanthus</i> (Euphorbiaceae)
<i>Premna</i> (Verbenaceae)
Sapotaceae
<i>Schreberia</i> (Oleaceae)
<i>Tamarix</i> (Tamaridaceae)
<i>Zygophyllum</i> (Zygophyllaceae)
<i>Zyziphus</i> (Rhamnaceae)

and porosity are low. Those samples show a pine-pollen-dominated microflora probably derived from the Canary Islands. Pollen grains from the desert are rarely found. The African Easterly Jet was probably very weak.

Dinoflagellate cyst assemblages show a full oceanic flora comparable to other records from the North Atlantic. A sedimentary hiatus in Core 5H of Hole 958A is confirmed and probably lies in the uppermost part of Section 4 of that core.

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Table 4. Cyst taxon, family, and thecal equivalence after Head (1996) found at Site 958.

	Cyst taxon	Family	Thecal equivalence	
	<i>A. choanum</i>	Ataxiodinium choanum	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>A. confusum</i>	Ataxiodinium confusum	Gonyaulacaceae	
	<i>B. tepikiense</i>	Bitectodinium tepikiense	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>Bragantedinium</i> sp.	<i>Bragantedinium</i> cf. <i>Hystrichokolpema</i>	Congrentidiaceae	? <i>Protoperidinium</i>
	<i>I. aculeatum</i>	<i>Impagidinium aculeatum</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp.ind.
	<i>I. paradoxum</i>	<i>Impagidinium paradoxum</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp.ind.
	<i>I. patulum</i>	<i>Impagidinium patulum</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp.ind.
	<i>I. sphaericum</i>	<i>Impagidinium sphaericum</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp.ind.
	<i>I. striolatum</i>	<i>Impagidinium striolatum</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp.ind.
	<i>Invertocysta</i> sp.	<i>Invertocysta</i> sp. <i>Lejeuncysta sabrina</i>	Congrentidiaceae	<i>Protoperidinium leonis</i>
	<i>L. machaerophorum</i>	<i>Lingulodinium machaerophorum</i> <i>Melitosphaeridium</i>	Gonyaulacaceae	<i>Ligulodinium polyedrum</i>
	<i>N. labyrinthus</i>	<i>Nematosphaeropsis labyrinthus</i>	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>O. centrocarpum</i>	<i>Operculodinium centrocarpum</i>	Gonyaulacaceae	<i>Protoceratium reticulatum</i>
	<i>O. israelianum</i>	<i>Operculodinium israelianum</i>	Gonyaulacaceae	? <i>Protoceratium reticulatum</i>
	<i>O. janduchenei</i>	<i>Operculodinium janduchenei</i>	Gonyaulacaceae	
	<i>P. zoharyi</i>	<i>Polysphaeridium zoharyi</i>	Gonyaulacaceae	<i>Pyrodinium bahamense</i>
	<i>P. faroense</i>	<i>Peridinium faroense</i>	Congrentidiaceae	<i>Peridinium faroense</i>
	<i>P. reticulata</i>	<i>Pyxidinosopsis reticulata</i>	Gonyaulacaceae	Gonyauloid lineage
	<i>S. belerius</i>	<i>Spiniferites belerius</i>	Gonyaulacaceae	<i>Gonyaulax scrippsae</i>
	<i>S. bulloides</i>	<i>Spiniferites bulloides</i>	Gonyaulacaceae	<i>Gonyaulax scrippsae</i>
	<i>S. delicatus</i>	<i>Spiniferites delicatus</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp. indet.
		<i>Spiniferites elongatus</i>	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>S. hyperacanthus</i>	<i>Spiniferites hyperacanthus</i>	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>S. membranaceus</i>	<i>Spiniferites membranaceus</i>	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>S. mirabilis</i>	<i>Spiniferites mirabilis</i>	Gonyaulacaceae	<i>Gonyaulax spinifera</i>
	<i>S. pachydermis</i>	<i>Spiniferites pachydermis</i>	Gonyaulacaceae	? <i>Gonyaulax spinifera</i>
		<i>Spiniferites pseudofurcatus</i>	Gonyaulacaceae	<i>Gonyaulax</i> sp. indet.
	<i>S. ramosus</i>	<i>Spiniferites ramosus</i>	Gonyaulacaceae	<i>Gonyaulax scrippsae</i>
	<i>S. nephroides</i>	<i>Selenopemphis nephroides</i>	Congrentidiaceae	<i>Protoperidinium subinermis</i>
		<i>Selenopemphis quanta</i>	Congrentidiaceae	<i>Protoperidinium conicum</i>
		<i>Spiniferites</i> sp.	Gonyaulacaceae	<i>Gonyaulax</i> sp. indet.
		<i>Stelladinium</i>	Congrentidiaceae	<i>Protoperidinium ?compressum</i>
		<i>Tuberculodinium vancampoeae</i>	Goniodomaceae	<i>Pyrophacus steinii</i> subsp. <i>steinii</i>
		<i>Trinovantedinium capitatum</i>	Congrentidiaceae	<i>Protoperidinium pentagonum</i>
		<i>Xandarodinium</i>	Congrentidiaceae	<i>Protoperidinium divaricatum</i>

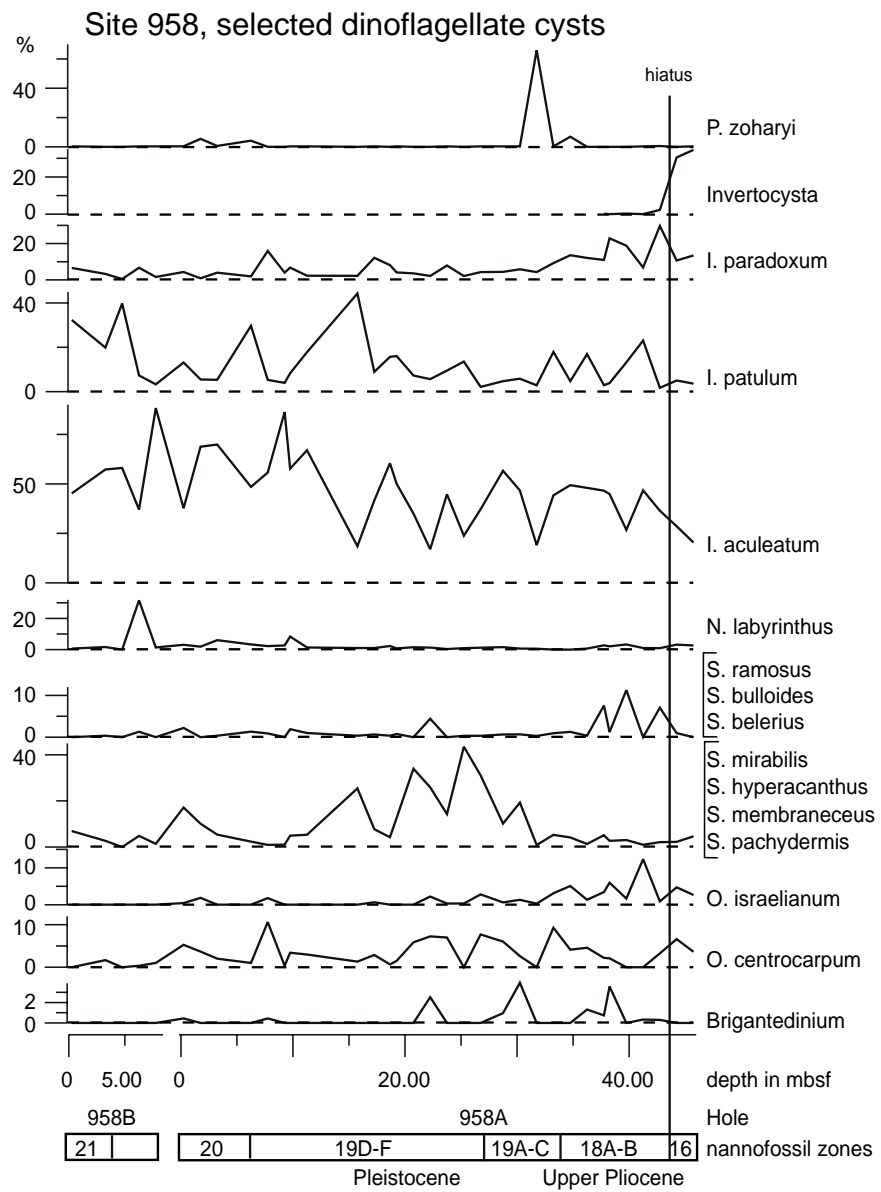


Figure 4. Percentages of a selection of dinoflagellate cyst taxa calculated on the total of cysts counted. Stratigraphy after Firth et al., 1996.