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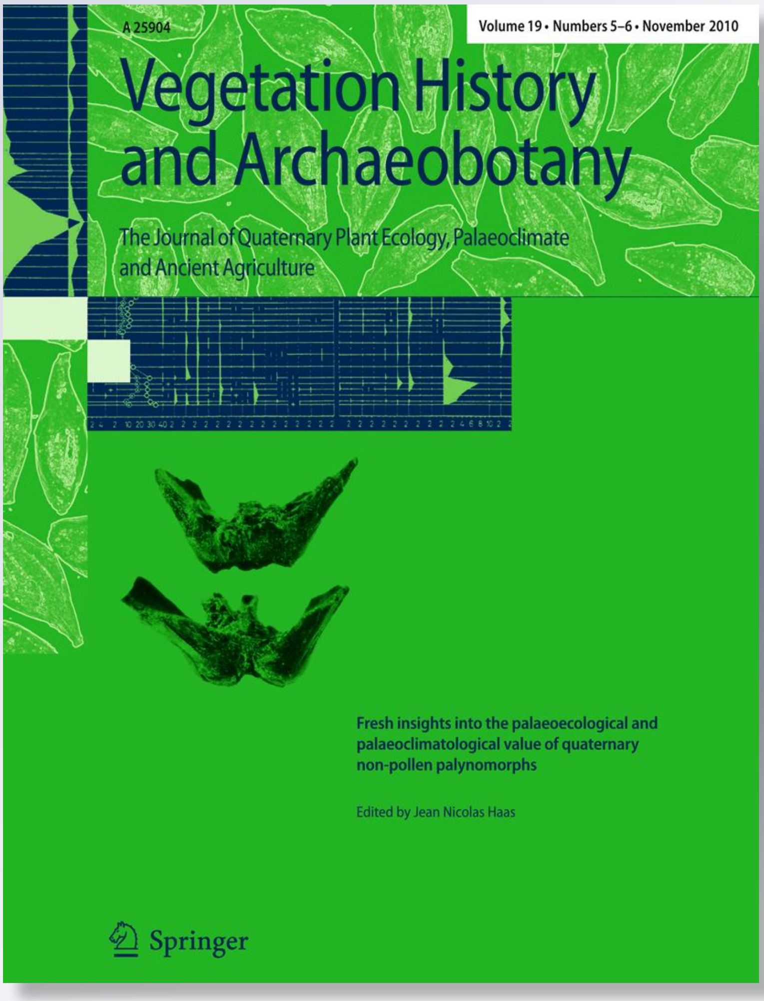

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ORIGINAL ARTICLE

Non-pollen palynomorphs in the Black Sea corridor

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Abstract There have been few studies of non-pollen palynomorphs (NPP) in Holocene brackish water environments. The Black Sea is one of the world's largest and deepest bodies of stable brackish water and a natural laboratory for study of marine carbon cycling to anoxic sediments. The main NPP in the modern sediments of this brackish water sea are dinoflagellate cysts (dinocysts), acritarchs (mainly the prasinophytes *Cymatiosphaera*, *Micrhystridium*, *Sigmopollis* and *Pseudoschizaea*) and diverse fungal remains. Other NPP include colonial algae, tintinnids, copepod and cladoceran egg covers, testate amoebae and microforaminiferal linings. These NPP assemblages are similar to those in the marginal marine environment of the Pliocene St. Erth Beds (England), but have more abundant NPP, and virtually lack scolecodonts. In the Black Sea corridor, modern assemblages from areas with salinity >22‰ have higher percentages of microforaminiferal linings and fewer prasinophytes, colonial algae and fungal spores. Prasinophytes dominate only in mid-Holocene sediments, during a 2000 years interval of sea level transgression and sapropel deposition. Early Holocene sediments have lower dinocyst diversity, increased fresh–brackish water colonial algae (*Pediastrum* spp. and *Botryococcus braunii*), zygnemataceous spores and desmids (including *Zygnema*, *Cosmarium*), ostracod linings and fewer foraminiferal linings. These assemblages are similar to those in the Baltic Sea where the annual salinity is about 6–8‰.

Keywords Non-pollen palynomorphs · Shales · Black Sea · Pleistocene · Holocene

Introduction

The Black Sea is the world's largest anoxic marine basin and is an important natural laboratory for the study of marine carbon cycling, and a prototype for some of Earth's ancient oceans (Murray et al. 2007). This large, semi-enclosed marginal sea provides a model for the environmental conditions associated with North Atlantic Mesozoic bituminous black shales which are important potential petroleum source rocks (Tissot and Welte 1978; Hay 1995). Some black shales have high contents of non-pollen palynomorphs (NPP), particularly the prasinophyte *Tasmanites* and the colonial green alga, *Botryococcus* (Tissot and Welte 1978). Hence, there is great interest in examining the microplankton that contributes to the high organic content (~100 g OC m^{-1} yr^{-1}) of the postglacial and modern sediments of the Black Sea. Also, there is much interest in using dinoflagellate cysts (dinocysts), and other

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NPP as markers of sea-surface salinity changes during the postglacial flooding of the brackish-water Black Sea by Mediterranean waters during the Holocene (Mudie et al. 2002; Hiscott et al. 2007; Marret et al. 2009).

Circulation of water and development of anoxia in the Black Sea is controlled by its connection through the Marmara Sea and its straits, the Bosphorus and Dardanelles to the Mediterranean seas and the world oceans (Fig. 1). Together, these inland seas and straits are known as the Black Sea Corridor. The stagnant bottom waters of the Black Sea are sustained by a stratified estuarine-type circulation coupled with high nutrient inputs and bioproduction (Fig. 2). In the Black Sea Corridor, evaporation exceeds precipitation, but the freshwater balance is positive because of large volumes of river runoff (Murray et al. 2007; Mudie et al. 2002; Aksu et al. 2002). The Black Sea is one of the world's largest bodies of stable brackish water. Average surface water salinity is 18‰ (but lower, 10–18‰, in the north). The deep water salinity is 22‰ compared to 35‰ for normal sea water and 36–39‰ for the eastern Mediterranean seas (Fig. 1). Average surface temperatures range from 19–23°C in summer to 6–8.4°C in winter, with a thin sea-ice cover forming in the north. Average background NO_3 and PO_4 levels are about 5 and 6 µmol, respectively (Mee et al. 2005), but inputs from agriculture and human waste in the Danube River Basin doubled the N and P values from A.D. 1960 to 1990.

Despite the importance of NPP and other kerogen sources for understanding the composition and taphonomy of particulate organic matter in oceanic carbon cycles (Zonneveld et al. 2007) and in black shale formations (e.g. Batten 1996; de la Rue et al. 2007), there have been few studies of NPP in the Black Sea Corridor. Wall et al. (1973) first recognized the importance of dinocysts and the prasinophyte *Cymatiosphaera globulosa* as environmental markers in the Holocene sediments. Traverse (1974) illustrated two dinocyst species and three acritarchs, and interpreted acritarch abundance peaks as indicating increased salinity and/or lower sedimentation rate. Traverse (1978) illustrated and documented stratigraphic distributions of other NPP, including fungal spores, *Botryococcus*, *Pediastrum*, *Pseudoschizaea* (as "Circuli"), *Cymatiosphaera*, *Tasmanites* and a few spherical acritarch

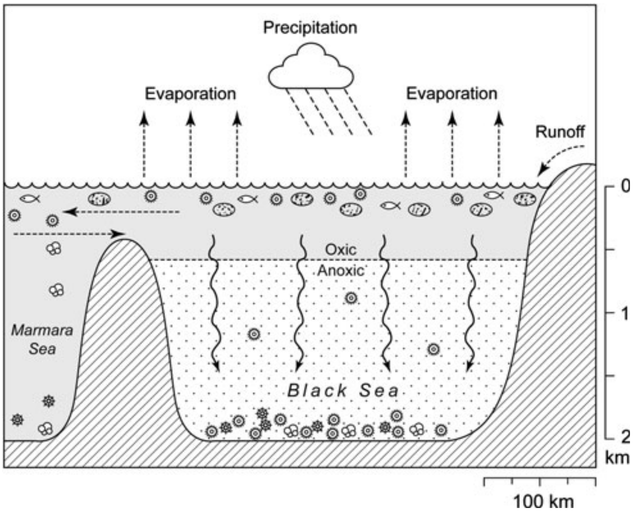


Fig. 2 The stagnant basin model for deposition of organic carbon-rich sediments in the anoxic Black Sea environment (after Hay 1995). *Horizontal arrows* indicate surface water inflow and outflow; the *dotted area* denotes dysaerobic-anoxic conditions below the strongly stratified water column. *Wavy vertical arrows* represent sinking organic particulates

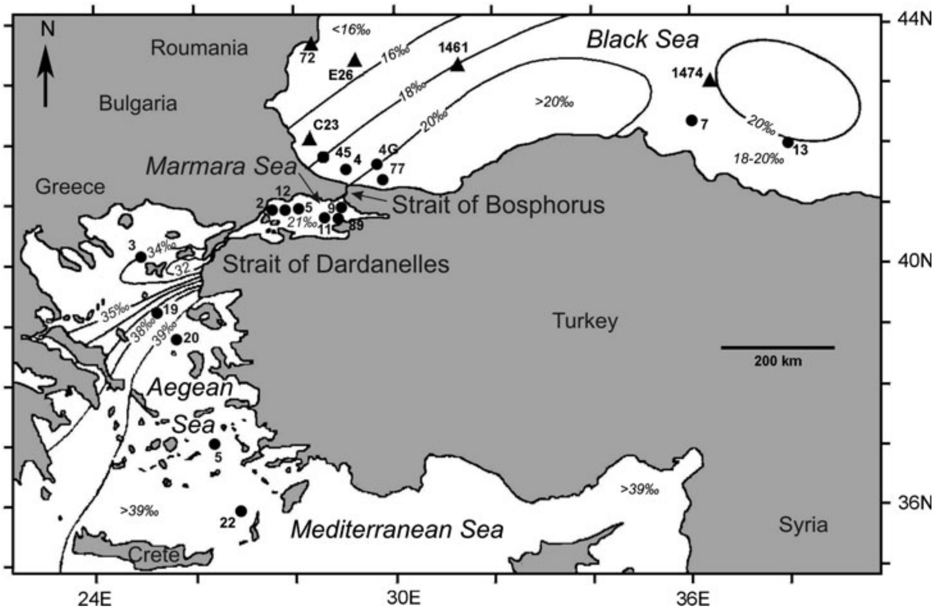


Fig. 1 Map of the Black Sea corridor showing present day surface water salinity and locations of core top surface samples and cores used in this study (*black dots*) and other published data (Roman 1974; Wall and Dale 1974) on NPP (*black triangles*)

morphotypes. He also introduced a Marine Influence (MI) index, using the ratio of dinocysts + acritarchs to total palynoflora, which he believed was a tracer of transgressive-regressive cycles. Most recently, Mudie et al. (2002) and Marret et al. (2009) documented quantitative variations in abundances of dinocysts, acritarchs (including prasinophytes), colonial algae and fungi in the late Pleistocene–Holocene sediments of the Marmara and Black Seas.

In this paper, we summarise the importance of dinocysts as indicators of salinity and eutrophication in the Black Sea and marginal marine basins of the Near East, and we document other NPP associated with the late Pleistocene–early Holocene brackish water (~5 to 13‰) interval and the mid-late Holocene brackish–marine (16–22‰) environments. The non-dinocyst NPP include prasinophytes, acritarchs, chlorococcalean colonial algae, zygnematalean spores, cyanophyte filaments, fungal spores, microforaminiferal linings, tintinnids, cladoceran and copepod egg covers. We also re-evaluate the Marine Influence index (MI) in light of new data on the ecological affinities of NPP.

Materials and methods

Samples for this study (Table 1) are from sediment cores taken at 17 sites in the Aegean, Marmara and Black Seas (Mudie et al. 2007). Multiple AMS radiocarbon shell dates showed maximum ages of ca. 37.6–23 cal. kyr B.P. (Aksu et al. 2002). Core sedimentation rates vary from 360 cm/kyr (Black Sea) to 6–9 cm/kyr Aegean Sea (Aksu et al. 2002; Hiscott et al. 2007).

The laboratory methods used to extract the NPP were selected to minimize damage to thin walled microfossils which are harmed by processing with acetolysis (Table 1) or strong alkalis (Marret 1993; Mudie and McCarthy 2006). For example, acetolysed samples from the western Black Sea shelf (Roman 1974) yielded much lower dinocyst concentrations than samples processed with cold hydrochloric (HCl) and hydrofluoric acid (HF). Nitric acid (37%) and prolonged exposure (>48 h) to 52% HF may damage NPP (Reid and John 1981), but heavy liquid separation methods are satisfactory (Traverse 1978).

Our samples (4–8 g dry weight) were prepared by first disaggregating the sediment in 5% Calgon detergent, then sieving at 125 μm and/or 10 μm to remove coarse particles and clay-sized sediment. Thereafter, carbonates were removed by treatment with cold 10% HCl, and silicates were removed using cold 48% hydrofluoric acid for up to 24 h (Marret et al. 2009). An exotic spore marker was added to estimate palynomorph concentrations and residues were mounted in glycerin jelly. When possible, 300 dinocysts were counted, but many samples had lower contents and counts of 100 cysts. Relative abundances of dinocysts are based on total dinocysts.

In parallel with the dinocyst counts, coenobia of *Pediastrum* and *Botryococcus*, cyanobacterial spores, microforaminiferal and ostracod linings, and fungal parts were also routinely counted. Relative abundances (percentages) of these NPP were mostly determined from the base number Sum of dinocysts + freshwater alga + animal remains (see Mudie et al. 2004 for results). Prasinophyte phycomata such as *Cymatiosphaera*, *Concentricystes* Rossignol 1962, acritarchs such as *Micrhystridium*, *Sigmopollis*, and *Halodinium*, and tintinnid loricas were counted in the same way as the dinocysts, but large numbers of small prasinophytes and acritarchs were scored qualitatively using a scale of abundant (≥30 per scanned line) to rare (<5 per scanned line). Copepod/cladoceran egg coverings were noted but not counted systematically because of uncertainty regarding identification. Other rare NPP, such as ostracod mandibles or crustacean remains were just noted if present.

The taxonomy of organic-walled dinocysts follows studies by Wall et al. (1973), Fensome and Williams (2004) and Marret et al. (2004). Details on identification of *Brigantedinium* spp., *Spiniferites* spp. and *Echinidinium* species-group are given by Marret and Zonneveld (2003). Microreticulate *Gymnodinium* cysts were systematically measured and identified by size and surface reticulation (Ellegaard and Moestrup 1999; Bolch and Reynolds 2002). Separation of non-toxic *Gymnodinium nolleri* from toxic *Gyymnodinium catenatum* is based on paracingulum reticulation; our cysts are probably *G. catenatum* (Ellegaard, pers. commun.). *Alexandrium*-type cysts were identified from reference slides of recent cysts of *Alexandrium tamarense* that have smooth, hyaline walls in contrast to the wrinkled-walled cysts of *Scrippsiella* (Head et al. 2006). Specimens of *Lingulodinium machaerophorum* have variable spine morphology (Fig. 3-11 to 15) and four eco-morphological groups (vars. A–D) were distinguished (Marret et al. 2004). Taxonomy of the acritarchs and prasinophytes follows that of Fensome et al. (1990) and Matthiessen and Brenner (1996), unless noted. Taxonomy of the fossil fungi follows that of Kalgutkar and Jansonius (2000) and van Geel and Aptroot (2006).

Results

Modern distribution of NPP

Core-top data from 17 sites along a salinity gradient from 39.5‰ in the Aegean Sea to 17.1‰ in the Black Sea (Table 1) show that dinocysts are the most abundant NPP throughout, with the ratio of pollen + spores to dinocysts (P:D) being mostly 2.1 or less, except in the deep Black

Table 1 NPP data from surface samples of 17 cores in this study (black dots in Fig. 1) and from three other cores with data published in 1974, with corresponding sea-surface salinities for the core sites

Subregion:	S	Aegean Sea			N	SW	Marmara Sea				NE
Core sample number:	22	G5	20	19	3	2	12	5	11	89	9
Surface salinity (‰):	39.5	39.3	39.1	38.4	34.0	24.0	23.0	22.0	22.0	20.8	20.1
Pollen-spores/g × 1,000	0.11	0.06	0.21	1.23	0.37	5.8	3.2	2.73	5.78	8.03	3.89
Dinocysts/g × 1,000	0.12	0.13	0.37	0.16	0.37	2.7	2.53	6.09	7.87	4.76	2.33
P:D ratio	0.92	0.46	0.57	7.7	1	2.1	1.26	0.45	0.73	1.69	1.67
Total acritarchs + prasinophytes/g	0	0	0	0	0	1,000	60	426	400	1,487	500
Pediastrum coenobia/g	0	0	24	0	0	0	50	0	0	0	0
Fungal spores/g	0	0	12	0	100	20	272	500	172	1,189	278
Microforaminifera/g	50	10	32	5	46	8	376	0	515	595	500
Acritarch types											
Leiosphere (Acritarch-8 of Traverse)	0	0	0	0	0	0	0	0	0	149	0
Pseudoschizaea rubina	0	0	0	0	0	8	0	0	57	0	5
Cymatiosphaera spp.	0	0	0	0	0	0	30	0	0	0	0
Sigmopollis spp.	0	0	0	0	0	0	0	40	57	0	24
Cf. copepod eggs	X	0	0	0	0	500	0	0	0	446	0

Subregion:	W			Black Sea					E
Core sample number:	4	4G	77	72*	1,461*	45	13	7	1,474[a]
Surface salinity (‰):	17.6	17.3	17.1	15.0	17.0	18.0	22.0	22.0	22.0
Pollen-spores/g × 1,000	3.11	11.9	7,41	0.15	6	5.96	55.94	42	160
Dinocysts/g × 1,000	2.97	5.27	4.64	0.5	0.12	3.99	2.07	12	2–62.0
P:D ratio	1.05	2.3	1.8	0.3	50	1.49	27	3.5	2.6
Total acritarchs + prasinophytes/g	1,124	1,094	748	15	20	1,800	1,094	12,000	22,000
Pediastrum coenobia/g	0	0	15	5 to 20	10	2	2,232	7,240	C
Fungal spores/g	591	1,231	640	X	X	C	2,399	8,447	C
Microforaminifera/g	59	205	91	nd	nd	870	0	0	nd
Acritarch types									
Leiosphere (Acritarch-8 of Traverse)	160	102	45	X	nd	R	558	4,425	X
Pseudoschizaea rubina	148	68	X	X	nd	282	148	1,199	X
Cymatiosphaera spp.	0	274	30	X	20	R	50	200	900
Sigmopollis spp.	148	205	X	nd	nd	C	2232	7,240	nd
Cf. copepod eggs	0	680	229	nd	nd	O	0	0	0

All samples were processed using methods for marine palynomorphs except those marked *asterisk* which are data from Roman (1974) after acetolysis treatment

[a] Crosses indicate data published by Wall and Dale (1974)

X Taxon present outside the count, *C* common occurrence, *O* occasional occurrence, *R* rare, *nd* no data

Sea basins where some ratios are 3.0 or more. There is a general decrease in concentrations of most NPP with distance away from the relatively low salinity, nutrient-rich surface water of the Marmara and Black Seas; the low values of dinocysts near the Danube River (sites 72 and 1461) probably reflect processing with acetolysis that destroys thin-wall NPP. The main exception is the occurrence of microforaminiferal linings; these primarily marine palynomorphs are most abundant in the Marmara Sea where 58 species have been reported (Aksu et al. 2002). The main acritarchs and prasinophytes are *Sigmopollis psilatum*, *Micrhystridium* spp., *Cymatiosphaera globulosa*, *Pseudoschizaea rubinus* (*Concentricystes* cf. *C. rubinus* Rossignol 1962) and cf. Acritarch-8 of Traverse (1978), all of which are absent from the Aegean Sea and decrease in abundance with increasing salinity. Coenobia of the algae *Pediastrum* and *Botryococcus* are almost totally confined to the Black Sea but have rare occurrences in the low salinity (22–24‰) in the Marmara Sea and saline (>35‰) North Aegean, indicating long-distance transport in surface currents. Fungal remains show a similar distribution pattern to the freshwater acritarchs, indicating their origin from terrestrial environments; there are no fossilisable marine aquatic fungi (Mudie et al. 2002).

Dinocysts

In both the Black and Marmara Seas, mid-late Holocene assemblages (<6.5 to 7.5 cal. kyr B.P.) are dominated by *Lingulodinium machaerophorum*, *Operculodinium centrocarpum* and halophilic Mediterranean *Spiniferites* spp., including *Spiniferites mirabilis* (Fig. 3-25), *S. ramosus/hyperacanthus* (Fig. 3-23, 24) and *S. bentorii* (Fig. 3-20) as reported by Mudie et al. (2004) and Marret et al. (2009). A few common North Atlantic dinocysts e.g. *Pyxidinopsis reticulata* (Fig. 3-1), *Ataxiodinium choanum* (Fig. 3-19), and the subtropical species *Tectatodinium pellitum* (Fig. 3-22) are also present. A diversity of acetolysis-sensitive heterotrophic protoperidinioids, such as *Brigantedinium* (Fig. 3-3, 4 to 21), *Echinidinium* (Fig. 3-17, 18), *Protoperidinium stellatum* (Fig. 3-7), *Protoperidinium americanum* (Fig. 3-4), *Quinquecuspis* (Fig. 3-30), *Selenopemphix* (Fig. 3-29), *Votadinium calvum* (Fig. 3-21) and the endemic *Peridinium ponticum* (Fig. 3-2, 9) and *Polykrikos* species (Fig. 3-26, 27) are also characteristic in both sapropels and brown lutites. In contrast, the early Holocene interval has fewer halophilic *Spiniferites* species, and other Mediterranean taxa (e.g. *Operculodinium israelianum*, *Polysphaeridium zoharyi*) are absent. These assemblages are dominated by the low salinity indicators *Pyxidinopsis psilata* (Figs. 3-6, 4-15, 16), *S. cruciformis* forms 1–5 of Mudie et al. (2002) (Fig. 4-13, 14, 18) and the freshwater species *Gonyaulax apiculata* (Fig. 4-17) is present. Occasional Caspian Sea taxa such as *Spiniferites cruciformis* type C of Marret et al. (2004) (Fig. 4-22), *Caspidinium rugosum* (Fig. 4-19) and *Impagidinium caspienense* (Fig. 4-20) may indicate periodic flooding from the Caspian-Aral Sea basins.

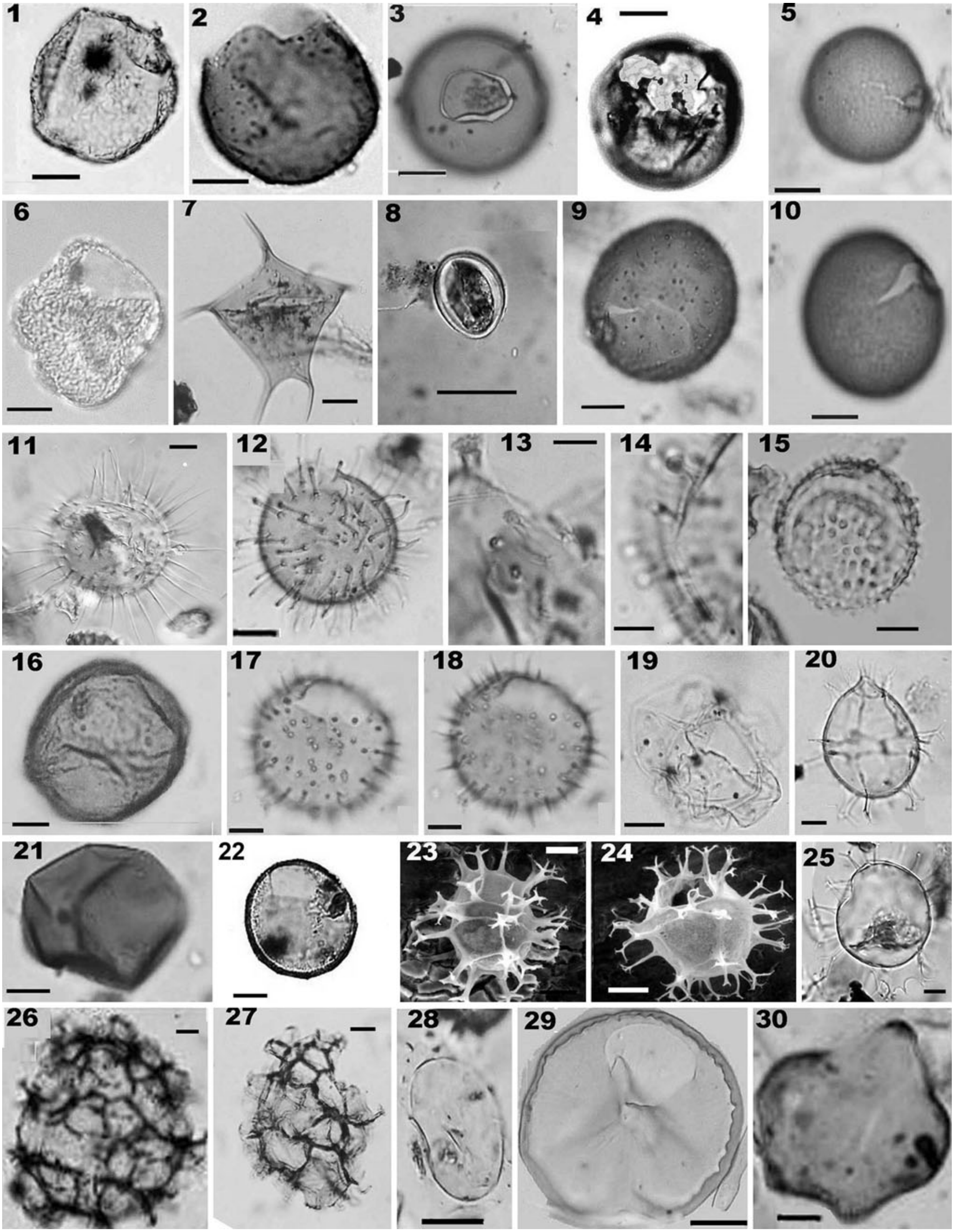
This succession of dinocyst associations shows that a major pulse of marine waters entered the Black Sea around 9.5 cal. kyr B.P. Recent information about ecological affinities of *S. cruciformis*, *P. psilata* and *L. machaerophorum* (Marret et al. 2009; Mertens et al. 2009) allows qualitative reconstruction of the salinity before full connection with the Mediterranean. It establishes that the early Holocene Neoeuxinian "Lake" was brackish, with a salinity range of 5–12‰. The transition from brackish to fully euryhaline/stenohaline dinocyst associations is gradual over about 1,500 years and marked by large variations in the morphology of *Spiniferites belerius* (see illustrations in Marret et al. 2009), *S. bentorii* (Fig. 3-20), *S. cruciformis* and *L. machaerophorum*. It is also characterized by major oscillations in dinocysts relative to colonial algae and prasinophytes (Marret et al. 2009). There is a succession of NPP from early dominance of *Pediastrum* and common zygnematalean spores to abundant brackish water dinocysts, followed by a *Botryococcus* peak just prior to the invasion of the "weedy" (opportunistic, fast growing) dinocyst species *L. machaerophorum* that causes harmful algal blooms (HABs) from ca. 6500–5000 cal. B.P. This invasion is succeeded by a peak of the prasinophyte *Cymatiosphaera globulosa* (Fig. 5-3, 4) in the deep southeastern basin (Wall and Dale 1974). Subsequently, the late Holocene is characterized by increased diversity of dinocysts, occurrence of tintinnids, and decreases in zygnematalean and colonial chlorophytes. The youngest sediments show increased diversity and frequency of dinocyst HABs, e.g. *Alexandrium* (Fig. 3-8), *Scrippsiella* (Fig. 3-28), *Gymnodinium catenatum* (Fig. 3-5, 10) and other *Gymnodinium* species (Fig. 3-16), apparently correlated with Global Warming and eutrophication over the past 30 yrs (Mee et al. 2005).

Colonial algae

The well known chlorophyte genera *Pediastrum* and *Botryococcus* (Class Chlorophyceae; Order Chlorococcales/Tetrasporales) are occasional to common in the surface sediments of the Black Sea but are almost absent elsewhere in the Black Sea corridor (Table 1). The *Pediastrum* species include *Pediastrum simplex* Mayen 1829 (Fig. 4-2, 3), *Pediastrum boryanum* (Turpin 1828) Meneghini 1840 (Fig. 4-7) and *Pediastrum kawraiskyi* Schmidle 1897 (not shown). *Botryococcus braunii* Kützing (Fig. 4-1) is rare in the late Holocene sediments of the SW Black Sea (Core M02-45) and occasionally present from ca. 10200–7560 cal. B.P., with a small peak from 8380–7560 B.P. during the main Holocene marine transgression (Marret et al. 2009). *Pediastrum simplex* is rare during the late Holocene and common in the earlier Holocene, with a peak during the main transgression. The other *Pediastrum* species are common to rare in the early Holocene when the salinity was about 5‰ (Hiscott et al. 2007).

Zygnematales and cyanophyta

Zygnematales are charaphycean green algae that reproduce by conjugation to produce resting spores or zygotes with a sporopollenin-like wall. This order includes unbranched filamentous green algae (family Zygnemataceae) and single-celled algae (family Desmidiaceae or sometimes a separate order, Desmidiales). In the Black Sea corridor, zygnematacean zygospores similar to those reported by van Geel (2001 and references therein) have only been reported for early Holocene shelf sediments. On the southwestern Black Sea shelf, occasional spores of the *Spirogyra*- (Fig. 4-12) and *Zygnema*-type (Fig. 4-11) are found together with *Pediastrum.* Occasional hemi-cells of *Cosmarium*-type desmids (Fig. 4-4) occur in the overlying sapropelic silty mud unit,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◀ **Fig. 3** Black Sea late Holocene and modern dinocysts. Reference numbers are in parentheses. Scale = 10 µm. **1** *Pyxidinopsis reticulata* (B7); **2**, **9** *Peridinium ponticum* (M45P); **3** *Brigantedinium simplex* (A3); **4** *Protoperidinium americanum* (M45P); **5**, **10** *Gymnodinium catenatum* cysts (M45T; M45P); **6** *Pyxidinopsis psilata* (B7); **7** *Protoperidinium stellatum* (M45T); **8** *Alexandrium* cyst, topotype, Woods Hole USA; **11–15** *Lingulodinium machaerophorum*: **11** long-spined morphotype (M5-04), **12** long flexuous spines (M97-2), **13** short blunt spines, **14** short club-tipped spines, **15** Form D with short conical spines (M5-04); **16** *Gymnodinium* sp. (M4-5G); **17**, **18** *Echinidinium transparantum* (M45P); **19** *Ataxiodinium choanum* (B7); **20** *Spiniferites bentorii* (M45P); **21** *Votadinium calvum* (M5-4G); **22** *Tectatodinium pellitum* (M2-89); **23**, **24** *Spiniferites ramosus/hyperacanthus* (M94-5); **25** *Spiniferites mirabilis* (M45P); **26**, **27** *Polykrikos kofoidii* cyst (M45); **28** *Scrippsiella* cyst (M5-4G); **29** *Selenopemphix nephroides* (A3); **30** *Quinquecuspis concreta* (M45)

together with rare *Mougeotia*-type spores (not shown here); however, few *Cosmarium-type* zygotes were observed (Fig. 4-4b), suggesting that most of the empty hemi-cells were transported from onshore habitats. Zygnemataceae live typically in shallow, stagnant fresh water lakes, ponds or wet soil (van Geel 2001), producing spores in the spring when conditions are warm. As noted for the St. Erth NPP assemblages in England (Head 1992), it is likely that most of the sporadically occurring zygnematalean spores in the Black Sea are transported by rivers.

Fossil cyanophytes (blue green algae) seem rare in the Black Sea although the marine form *Gloeocapsomorpha* dominates in Palaeozoic kukersite oil shale (Batten 1996), and *Anabaena* is common in Holocene sediments of the Caspian Sea (S.A.G. Leroy, pers. commun. 2007). A few trichomes of *Phormidium* cf. *P. ambiguum* Gomont (Fig. 4-6) were found in the late Holocene sediments on the southwestern Black Sea shelf. This salt-tolerant filamentous blue green alga is listed with marine algae for several coastal regions of the Black Sea, e.g. Samsun (Aysel et al. 2008 and references therein).

Prasinophytes and acritarchs

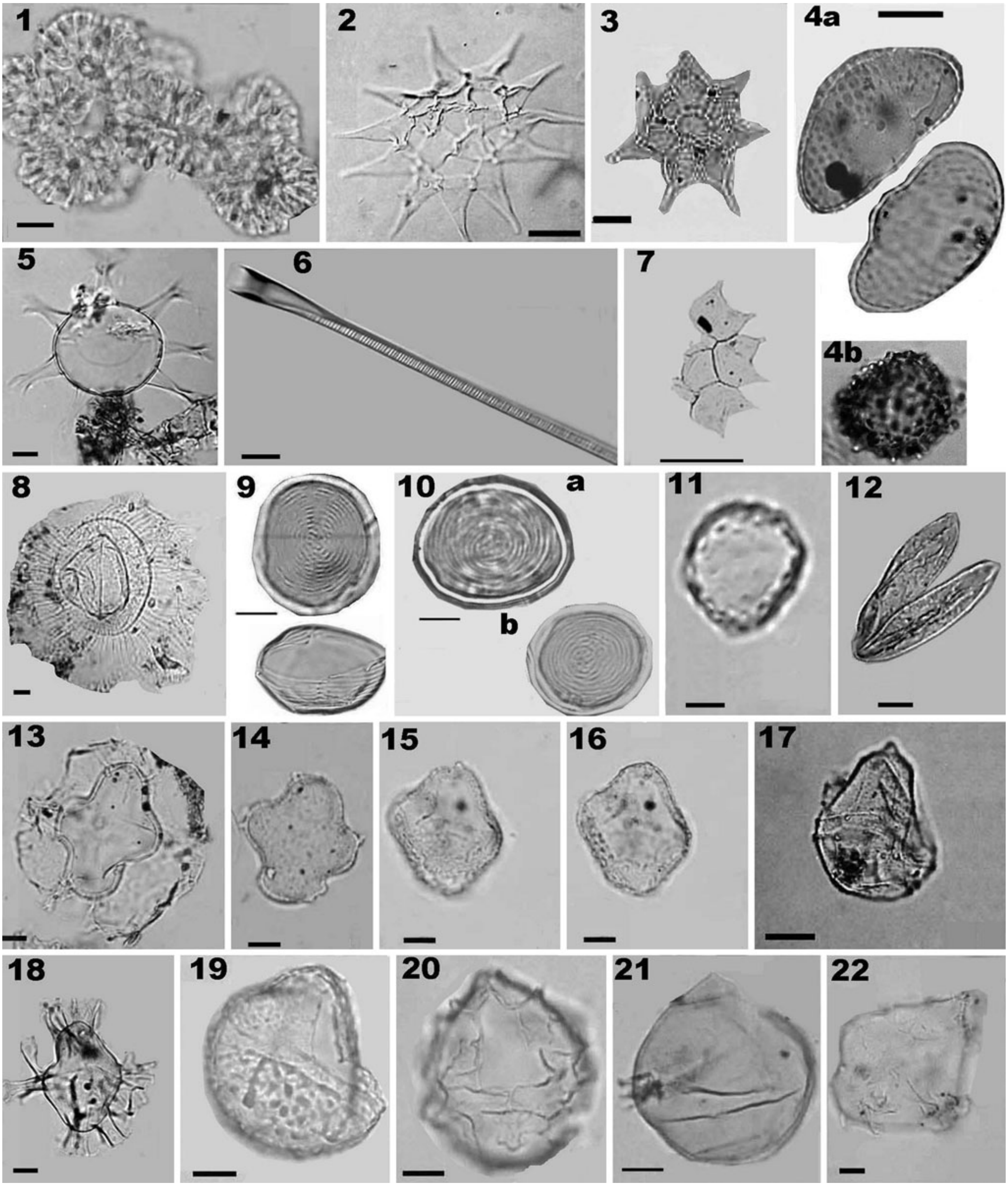
Prasinophytes and acritarchs, together with dinocysts, are sometimes referred to as organic-walled microphytoplankton (Playford 2003). However, prasinophyte phycomata are the fossilized cyst-like, non-motile stage of the earliest green algae, the Prasinophyceae (=Micromonadophyceae), whereas acritarchs are "small microfossils of unknown and probably varied biological affinities", consisting of a single or multiple-layered wall surrounding a vesicle with variable ornamentation, and opening by a slit-like or irregular rupture or by a circular pylome. Classifications of the phylum Prasinophyta are given by Tomas (1993) and Guy-Olsen (1996), who lists four orders and eight Holocene families of mainly oceanic planktonic and benthic microalgae.

In the Black Sea, the most abundant prasinophyte is *Cymatiosphaera globulosa* (Fig. 5-3, 4) which is regarded as co-generic with the extant genus *Pterosperma* (Parke et al. 1978), and a SEM image (Wall et al. 1973) is almost identical to the asexual cyst of the extant prasinophyte *Pterosperma cristatum* (Inouye et al. 1990). The asexual cysts (phycomata) have a sporopollenin-like wall and high oil content that makes them buoyant for a few weeks to 4 months before they germinate to release small, naked flagellated motile cells (Graham and Wilcox 2000). *Tasmanites*, the fossil phycoma stage of the extant pyramimonadalean genus *Halosphaera* is occasional in late Holocene sediments on the southwestern Black Sea shelf. Golden-brown vesicles with irregular slit-like openings have been referred to the pyramimonadalean genus *Leiosphaeridia* by Wall et al. (1973), Traverse (1978) and Mudie et al. (2002). *Leiosphaeridia*-type vesicular cells with a high oil and starch content were found in the Black Sea cores (Fig. 5-7).

Modern prasinophycean algae are mainly marine organisms and monospecific blooms may coat the sea surface with oily organic films. However, some species occur in brackish and fresh water environments, and fossil genera appear primarily associated with inshore shallow lagoonal and deltaic environments (Guy-Olsen 1996). Very light δ^{13}C values of fossil phycomata deposits suggest that algal blooms associated with black shales were favored by low temperatures and reduced salinity (de la Rue et al. 2007). Extant *Pterosperma* and *Halosphaera* are planktonic algae (Graham and Wilcox 2000). Prasinophytes are more common in cold waters, but high nutrients leading to euxinic conditions are more important than temperature or salinity (Batten 1996).

The most common acritarchs in the Black Sea are *Sigmopollis*, *Micrhystridium* and *Pseudoschizaea* (Fig. 4-9, 10). *Sigmopollis* and *Micrhystridium* are small (<15–20 µm) spherical NPP with a globally widespread distribution and believed to be planktonic algal spores (Batten 1996). Some *Sigmopollis* species with spiny ornament ("HdV Type 128" of van Geel) are found in slowly-moving shallow eutrophic to mesotrophic fresh water Holocene deposits of the Netherlands (van Geel et al. 1989; Pals et al. 1980), suggesting that it is a freshwater organism (e.g. Head 1993). However, the most common Black Sea species *Sigmopollis psilatus* (Fig. 4-1) and another *Sigmopollis* with a straight, not sigmoid suture (Fig. 4-2) are always smooth-walled and they are common in sediment beneath the cold low salinity plume (~5 to 15‰) off the Mackenzie Delta, Beaufort Sea (Matthiessen et al. 2000) and in postglacial brackish–marine sediments of outer Hudson Bay, Canada (de Vernal et al. 1989).

The most common Black Sea *Micrhystridium* (Fig. 5-5) has short (<3 µm), fine, blunt-pointed spines and resembles



M. cf. *asagaiense* and *M. minus* of Takahashi (1964), *Micrhystridium* sp. 1 of Head (1993) and NPP Type 115 of Pals et al. (1980). *M. asagaiense* is occasional to abundant in Oligocene marine muddy sandstones, while NPP Type 115 occurred in marine clays. Abundant small, round acritarchs with short processes tend to characterize nearshore, fine-grained marine deposits of variable salinity, while anoxic or low nutrient conditions rich in amorphous organic matter often have abundant acanthomorphic acritarchs and leiospheres (Batten 1996).

◀ **Fig. 4** Chlorophytes, cyanophytes and dinocyst indicators of brackish–fresh water facies in the Black and Caspian Seas. Reference numbers in parentheses. Scale bar = 10 µm. **1** *Botryococcus braunii* (M45P); **2** *Pediastrum simplex* (M45P); **3** *P. simplex* var. *sturmii* (M45P); **4** *Cosmarium* spp. (45P): (*a*) semi-cells, (*b*) zygote; **5** *Polyasterias problematica* (M4G); **6** *Phormidium* trichome and open calyptrate apical cell (M4G); **7** *Pediastrum boryanum* (M4G); **8** *Radiosperma* cf. *R. corbiferum* (M4G); **9** *Pseudoschizaea circula* (M4G): (*a*) intact cell, polar view, (*b*) hemi-cell; **10** *Pseudoschizaea* (M89P): (*a*) *P. circula*, (*b*) *P. rubina*; **11** *Zygnema*-type spore (M4G); **12** *Spirogyra* zygospore (M89P); **13** *Spiniferites cruciformis* form 1 (M45P); **14** *Spiniferites cruciformis* form 5 (M89P); **15**, **16** *Pyxidinopsis psilata* (M45P): **15** high focus, **16** mid focus; **17** *Gonyaulax apiculata* (M45P); **18** *Spiniferites cruciformis* form 3 (M89P); Southern Caspian Sea dinocysts; **19** *Caspidinium rugosum* (holotype); **20** *Impagidinium caspienense* holotype; **21** *Brigantedinium* sp. (US02-1); **22** *Spiniferites cruciformis* type C (GS05)

Only one acanthomorphic acritarch (cf. *Multiplicisphaeridium* sp. of Strother 1996; Fig. 5-18, 24) has been observed in the Black and Marmara Seas, occasionally occurring in low abundances of the upper Holocene, and more commonly, in the Late Glacial-early Holocene sediments. Mudie et al. (2002) referred this NPP to the fungal genus *Tetraploa*, but Andrea Aptroot (pers. commun., July 2007), commented that thin walls do not characterise fossil fungi, and we now refer this palynomorph to the Acritarcha. The large (>100 µm) Black Sea acritarch differs from other species of *Multiplicisphaeridium* in being distinctively yellow-brown in color and having a small triangular vesicle.

Other common acritarchs in the upper Holocene Black Sea sediments include egg cases of *Cobrisphaeridum*, a marine–brackish water copepod (Head et al. 2003) and other nearshore marine or lacustrine zooplankton. *Pseudoschizaea rubina* Rossignol ex Christopher 1976 (Fig. 4-10b) is occasionally present in upper Holocene samples of the Black and Marmara Seas. This sphaeromorphitic acritarch, with distinctive concentric markings on both hemispheres of its dorso-ventrally flattened vesicle, was first described as *Sporites* in Pliocene brown coals (Wolff 1934), and then as *Concentricystes rubinus* in marine sediments off Israel (Rossignol 1964). *P. rubina* is distinguished from the similar species *P. circula* (Fig. 4-10a) by its irregular, maze-like polar complex whereas *P. circula* has linear polar ornament (Christopher 1976). *Concentricystes s.l.* is usually considered to be a fresh-water alga because of its association with wadi or riparian deposits, and previously, *P. circula* was only been recorded for terrestrial or fluvial environments. However, *P. rubina* is absent from the early Holocene brackish water sediment facies in the Black Sea, and it seems to mark organic-rich marine silts in warm regions; it forms marine bituminous shales in the Malaysia and the Middle East, along with *Botryococcus braunii*, *Pediastrum*, marine dinocysts and foraminerifera (Konzalova 2002).

Also present in the upper Holocene sediments of the Black Sea are species of the genus *Halodinium* that was originally described as an acritarch of marine microphytoplankton origin (Bujak 1984). Subsequently, however this acritarch was linked with the testate amoebae (de Vernal et al. 1989). In the Black Sea, *Halodinium* (Fig. 5-6, 12) is occasionally present throughout the late Holocene. This NPP resembles spherical testate amoebae such as *Arcella* (e.g. Warner 1990; Beyens and Meisterfeld 2001). *Arcella* and other arcellaceans are mainly restricted to terrestrial and freshwater habitats, and high percentages of *Halodinium* are associated with estuarine or fiord-like environments (e.g. Matthiessen et al. 2000) and with the transition from marine to terrestrial conditions (de Vernal et al. 1989). Recently, however, Beyens and Meisterfeld (2001) summarized data showing the common intertidal occurrence of testate amoebae, and some species have a high salinity tolerance. It is notable, however, that *Halodinium*-type acritrachs do not occur in the brackish sediments of the Neoeuxinian Black Sea but are confined to the youngest sediments (less than 3000 yrs B.P.) and a salinity of about 16‰.

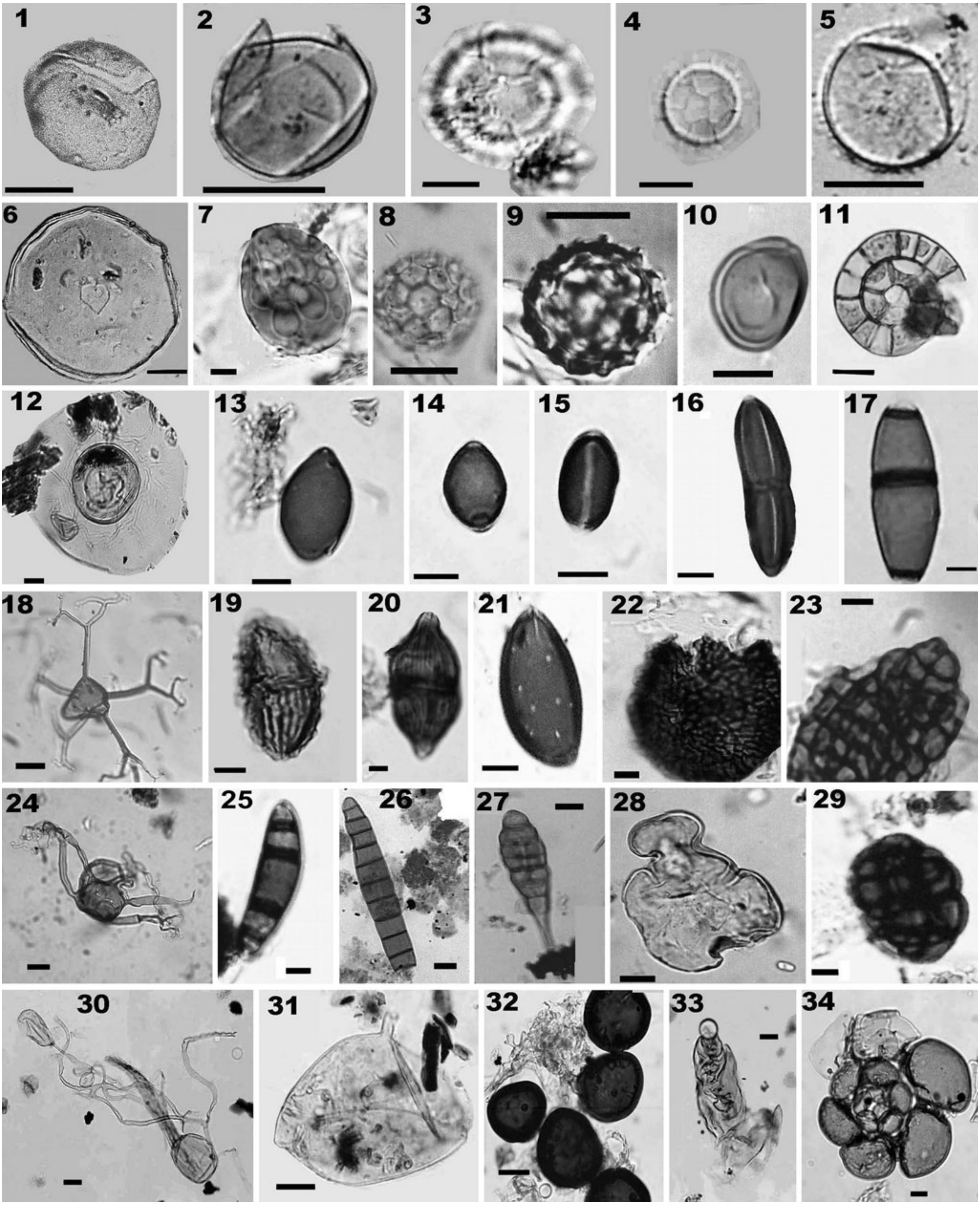
Tintinnids

Like dinoflagellates, the tintinnids are flagellated Eukaryotes (Phylum Ciliophora; Class Spirotrichea; Order Tintinnida) of primarily marine habitat (Reid and John 1978, 1981). Several NPP of tintinnid origin are occasional to common in late Holocene sediments of the southwestern Black Sea where they are most common in sediment deposited during the past 2,000 years of land clearance and agricultural development.

The most common morphotypes are *Polyasterias problematica* (Fig. 4-5) and a *Radiosperma*-type cyst (Fig. 4-8) with a flaring, fimbricated membranous wall. A similar cyst is illustrated by Kunz-Pirrung (1998) for the Laptev Sea, as *Radiosperma corbiferum* Meunier 1910, where it occurs in surface sediments with water salinities of 5–30‰, with maxima from 10 to 20‰. Other morphotypes ascribed to *R. corbiferum* and Tintinnid loricas in Eemian sediments of the Baltic Sea region were considered to be markers of highly stratified water, with a brackish surface layer above saline water of 5‰ or more.

Foraminiferal and ostracod linings

Because of the 125 µm sieve used for processing of the palynological samples, of the microforaminiferal and ostracod linings in our samples only the smaller species or juveniles of larger forms are present. In the Black Sea corridor, curvilinear (Fig. 5-33) and trochospiral (Fig. 5-34) organic linings of microforaminifera are common except in



Late Glacial and early Holocene sediments. Distributions and illustrations of the main morphotypes are reported elsewhere (Mudie et al. in press). Two types of ostracod shell linings were found in the Black Sea shelf sediments: smooth-walled oval early Holocene Leptocytheridae-types, and in the late Holocene, larger linings with reticulated or

◀ **Fig. 5** Common prasinophytes, acritarchs; fungal remains and microforaminiferal linings found in Black Sea sediments. Scale bar = 10 μm. **1** *Sigmopollis psilatus*, sigmoid suture (M45P); **2** *Sigmopollis* sp., straight suture (M45P); **3**, **4** *Cymatiosphaera globulosa* (B7, M4G); **5** *Micrhystridium* cf. *ariakense* (M45P); **6** *Halodinium minor* (M45P); **7** *Leiosphaeridia* phycoma with oil droplets and starch grains (M45T); **8**, **9** *Tilletia*-type teliospores (M45T); **10** very common small *Lycoperdon*-type ascospore (M45T); **11** *Helicoon* conidiospore (M45T); **12** *Halodinium* sp. (M4G); **13**, **14** *Sordaria* ascospores (M4G); **15**–**17** *Coniochaeta* cf. *lignaria* (M4G): **15** Monoseptate ascospores, **16** with longitudinal grooves, **17** with blunt ends; **18**, **24** *Multiplicisphaeridium*-type acritarch (M89P); **19** *Valsaria* ascospore (M45T); **20** *Caryospora callicarpa* ascospore (M45T); **21** Indet. conidium sparsely porate, common; **22** *Callimothalus*-type fruiting body (M45P); **23** *Ascoma*-type fruiting body (M45T); **25** curved 4-septate fungal spore; **26** uniseriate ascospore; **27** biseriate conidium of *Alternaria* (B7); **28** hyphopodium of *Gaeumannomyces* sp. (B7); **29** *Alternaria citri*-type conidium; **30**–**32** *Glomus* chlamydospores; **33**, **34** microforaminiferal linings (M4G): **33** uniseriate, **34** spiral

dimpled ornament. Ostracod mandibles are occasionally present, but unlike the St. Erth beds, where scolecodonts (jaws of polychaete worms) were common and diverse (Head 1993), scolecodonts were seen in only one core from the Marmara Sea, and none were found in any samples from the deep water sites in the Black and Aegean Seas.

Fungal spores

In the 17 core-top samples, most of the fungal remains are brown unicellular or dicellular spores of *Lycoperdon* (Fig. 5-10), *Tilletia* (Fig. 5-8, 9), *Sordaria* (Fig. 5-13, 14), and *Coniochaeta* (Fig. 5-15 to -17). However within the Black Sea, short, unbranched hyphal strands and fungal germlings resembling the hyphopodia of *Gaeumannomyces* (Head 1993) are common (Fig. 5-28), along with occasional *Valsaria* (Fig. 5-19), *Caryospora* (Fig. 5-20), uniseriate and biseriate spores and multicellar fruiting body parts (Fig. 5-22, 23, 25 to 27). Coiled multiseptate conidispores of a small Helicoon species (Fig. 5-11) are present in surface sediments of the shelf and sordariaceous porate conidia are common (Fig. 5-21). The fungal spore concentrations (excluding hyphal strands and fruiting bodies) show an order of magnitude decrease from the Black Sea to Marmara Sea, and are absent at most of our deepwater sites in the Aegean Sea, although they are common in Holocene sediments of the Nile Cone (Kholeif and Mudie 2009). Downcore there is a clear co-occurrence of peaks in fresh- or brackish-water indicators and multicellular *Alternaria*-type fungal remains (Fig. 5-27, 29) at about 10000–12000 cal. B.P. Previously (Mudie et al. 2002), we suggested that the fungal remains were an index of terrigenous sediment influx and transport by large rivers because most fungal sporomorphs are derived from soils in the watersheds and fringing marshlands (Batten 1996) and there are no marine aquatic fungi that produce fossilizable spores or other remains. However, *Alternaria*-type spores are common in salt marshes (Muhsin and Booth 1986) and *Glomus* (Fig. 5-30 to 32) is clearly associated with basin erosion around Lake Sapanca, Turkey (Mudie et al. in press).

Discussion and conclusions

NPP in carbon production and storage

As indicated by the data in Table 1 and documented by Mudie et al. (2002), the diverse NPP assemblages in the Black Sea (ca. 60 taxa, excluding the fungi) comprise about 30–50% of the palynomorphs preserved in the shelf and basin sediments. Previous geochemical studies of the Black and Marmara Sea sediments (Abrajano et al. 2002; Hiscott et al. 2007) showed that total organic carbon (TOC) is consistently high (>0.5 to 2%) in the late Pleistocene and Holocene sediments, with maxima in sapropelic muds deposited between 12 and 7 cal. kyr B.P. These TOC values are comparable to the relatively carbon-poor (2–4% OC) Frasnian (385–375 Ma) interval of the Upper Devonian New Albian black shale, but are less carbon-rich than the laminated calcareous shale with 5–14% OC overlying the Frasnian–Famennian boundary (ca. 373 Ma; de la Rue et al. 2007). Because of the virtual absence of dinoflagellates before the Jurassic (ca. 200–145 Ma), no precise comparison can be made between the Devonian shales and Black Sea anoxic sediments. However, it is interesting that in both these basin stagnation carbon sequestration models, the switch from relatively low to very high TOC is marked by change-over of NPP assemblages with small (<20 μm) herkomorphytic *Micrhystridium* or *Sigmopollis* species and long-spined acritarchs to prasinophyte-dominated assemblages, including *Cymatiosphaera*. De la Rue et al. (2007) attributed this change in palynofacies to the transition from shallow to deeper, more marine water. On the Black Sea shelf, however, the comparable switch at base of the sapropelic mud is associated primarily with increased sulphur accompanying the inflow of high salinity Aegean Sea water from ~9500 to 7800 cal. B.P. (Hiscott et al. 2007).

Although the Holocene Black Sea NPP abundances and high taxonomic diversity do not provide an exact model for Jurassic black shales, the intermittent massive blooms of dinocysts and prasinophytes and persistently higher occurrence of NPP distinguishes the assemblages from the lower diversity assemblages in the Late Pliocene St. Erth shallow water marine environment (Head 1992, 1993) where higher oxygen levels permitted survival of marine benthic worms (evident as scolecodonts). It appears that the low oxygen levels of the Black Sea bottom water and/or sediment restrict or prevent survival of benthic worms. The sporadic blooms of NPP algal spores and rapid-growing, invasive ("weedy") dinoflagellate species suggest that intervals of persistent dysoxia or anoxia, combined with high nutrient inputs from sediment and terrigenous organic matter are the main factors involved in long-term marine carbon storage and black shale formation.

Salinity and sea-level change

Although many of the NPP in the Black Sea are typically found in freshwater lakes and ponds, we have shown that most of the taxa also occur in brackish water and/or nearshore marine environments. *Pediastrum* and *Botryococcus* are commonly cited as freshwater indicators that are washed into the marine environment (e.g. Head 1992 and references therein; Batten 1996), but these algae are common in the outer Baltic Sea where the salinity ranges from about 5 to 9‰ (Matthiessen and Brenner 1996). *Botryococcus braunii* also grows in slightly saline lakes of Australia but only blooms after freshening of the lakes by rain (Wake and Hillen 1980). Matthiessen and Brenner (1996) also reported that *Pediastrum boryanum*, *P. kawraiskyi* and *Botryococcus* cf. *braunii* tolerate salinities up to 8‰, but *P. simplex* and *P. duplex* are meioeuryhaline oligohalobes found in salinities of less than 3–5‰. Van Geel (2001) notes that *Pediastrum* species are common in hard water eutrophic lakes; Nicholls (1997) shows that major summer blooms of invasive *Pediastrum* species in Lake Erie are correlated with high phosphorus loading.

The combined evidence from NPP, ostracod and foraminiferal data suggests that the early Holocene Euxinic Black Sea was a brackish water environment, with salinity ranging from ca. 4–9‰; this agrees with mollusk and benthic foraminiferal paleoecological data indicating salinities of 7–9‰ (Yanko-Hombach 2007). The mid to late Holocene assemblages contain fewer freshwater NPP and more Mediterranean dinoflagellates, but the consistent presence of a few freshwater NPP marks the high input of freshwater and terrigenous matter, as in the modern highly brackish to low salinity marine waters of the Black Sea (16–20‰).

Because of the complex mixture of freshwater and marine NPP, the simple Traverse "marine index" (MI) is of limited value for recording fluctuation in Holocene sea level within the Black Sea, although it may be valid for megacycles of marine transgression and regression during the Pliocene–Pleistocene. We have indicated that dinoflagellates and other NPP may be more sensitive to changes in nutrients than in salinity. Hence, caution is needed before concluding that an increase in selected taxa such as *Lingulodinium machaerophorum* and *Cymatiosphaera* reflect a simple rise in sea level because of increased inflow of Aegean Sea water to the Black Sea (e.g. Filipova-Marinova 2007). Likewise, the simple ratio of % *Spiniferites*:% *Lingulodinium* (Morzadec-Kerfourn 2005) must be used with caution as an index of the rate of sea-level rise.

The literature on living equivalents of the prasinophytes and tintinnids suggest that nutrients are probably more important than salinity for the blooms. Overall, it is likely that the main factors accounting for major fluctuations in the occurrences of NPP in the Holocene within the Black Sea basin are either nutrient enrichment from anthropogenic changes in the watershed or greater particulate carbon sequestration because of changes in bottom water chemistry within the stagnant basin.

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